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**THE ERIGONINE SPIDERS OF NORTH AMERICA.  
PART 1. INTRODUCTION AND TAXONOMIC BACKGROUND  
(ARANEAE: LINYPHIIDAE)**

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**ABSTRACT**

This introductory paper on North American erigonine spiders reviews the evidence for the hypothesis that the erigonines form part of the family Linyphiidae, and maintains that a strict subdivision of the family into two phylogenetically pure branches is not feasible on current data. The structure of the male palpal organ is briefly described, and its importance in the taxonomy and phylogeny of the erigonines is stressed. Other characters used in erigonine taxonomy are briefly mentioned.

**INTRODUCTION**

The author is proposing to undertake the revision of a number of North American genera of erigonine spiders, based mainly on material from the American Museum of Natural History (New York), the Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts), and the Canadian National Collection (Ottawa). It is hoped that the publication of the results will encourage others to take up the collection and study of this somewhat neglected group of spiders.

In the literature, both American and European, the erigonine spiders have often been placed in a separate family, the Erigonidae or Micryphantidae; if a family name is required, Erigonidae now seems to be preferred (Platnick and Levi 1973). The erigonine spiders are, however, regarded by many arachnologists as forming part of the family Linyphiidae; this hypothesis is not universally accepted, but in my opinion there is substantial evidence to support it (see later).

The North American erigonines have been studied and described by a number of authors, particularly by Emerton, Banks, Crosby and Bishop. Chamberlin and Ivie, and more recently by Dondale, but the majority of the descriptions are now quite old and somewhat inadequate by modern standards. The number of erigonines so far described from this geographical area, from the arctic far north to the sub-tropical south, does not much exceed 500 species, quite a few of which are known from one sex only. This number is close to the number of species known from Europe, but the European erigonines have been more thoroughly collected and investigated, and there are very few species of which both sexes are not known. There can be no doubt whatever that many new species remain to be discovered in North America.

The erigonines are not a particularly easy group for the taxonomist, and this is one of their attractions. Their small size (1-3 mm in total length) and the large number of species (particularly in northern latitudes) increase the taxonomic problems, but the difficulties should not be over-stressed. There are now keys, admittedly not completely reliable, for diagnosing most of the genera of the European erigonines, and there is no reason why similar keys should not be constructed at a later date for the North American genera. It is to be noted that many European genera are not represented in North America (except possibly in Alaska and northern Canada) and that many North American genera are not present in Europe.

The spiders of the family Linyphiidae (s. lat.) have a very generalised morphology. There appears to be no somatic character of combination of somatic characters which can be used to formulate a rigid definition of this family, which is distinguished from other families mainly by the *absence* of the somatic characters which are used to define these families. The one character which can be seen to distinguish the Linyphiidae from all other families is the structure of the male palpal organ. As a consequence of the generalised morphology, the female erigonines offer in most cases greater taxonomic and diagnostic problems than the males, which often exhibit striking secondary sexual characters. Only in rare instances can sub-adult erigonines be identified to species or even generic levels.

#### STRUCTURE OF THE MALE PALP IN THE LINYPHIIDAE

The structure of the male palpal organ has been well described by previous authors (particularly by Merrett 1963; see also Saaristo 1971), but in view of its importance in linyphiid taxonomy and phylogeny a brief account of the structure, including some new data, is given here.

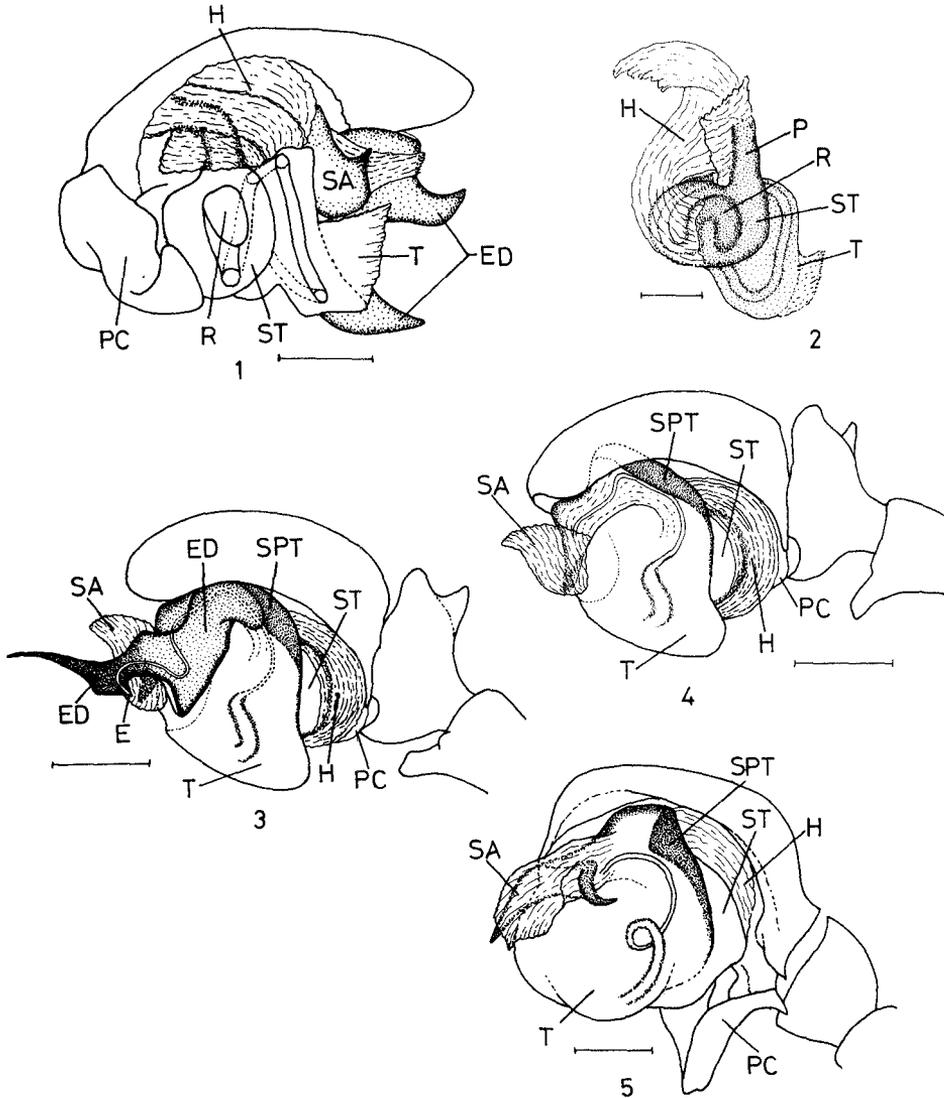
The palpal tarsus (cymbium) has a more or less flat paracymbium, which is articulated to the cymbium and lies adjacent to the ectal side of the palpal organ. This paracymbium is basically U-shaped (e.g. Fig. 9), but there is considerable variation in the detail; the paracymbium is usually, but not always, more complex in the linyphiines than in the erigonines.

The components of the palpal bulb are as follows:

(i) **The (basal) haematodocha.**—This is not a simple distensible sac as sometimes depicted, but an irregular thin-walled elastic tube coiled around the “subtegular petiole” [see (ii) and Figs. 1, 2]. This tube is attached at its basal end to the alveolus and at its distal end to the subtegulum. The haematodocha is collapsed and flattened in the unexpanded bulb, and is then practically invisible except in some cases for a small part of its distal end where it is attached to the subtegulum (Figs. 3, 4, 5). The spiral form of the haematodocha can readily be verified: after soaking the palp in 5% aqueous glycerol to soften it, the bulb can be pulled away from the cymbium with fine tweezers to reveal the coiled elastic haematodocha.

(ii) **The subtegulum.**—This sclerite is not a simple ring, but is shaped more like a shallow circular box with a short handle. The “handle”, which arises ecto-dorsally from the subtegulum (Figs. 1, 2), runs up into the alveolus and appears to be attached at its distal end to near the basal end of the haematodocha, the point of attachment being towards the ectal side of the cymbium. I propose the descriptive label “subtegular petiole” for this projection from the subtegulum. The haematodocha forms a short spiral round the petiole, and is fastened to the subtegulum on the posterior and mesal sides in the unexpanded palp (Figs. 2, 3).

(iii) **The tegulum.**—This is a sac of variable shape which is joined to the subtegulum over a relatively small area where the seminal duct passes from the subtegulum into the tegulum. There is a more or less sclerotized projection arising from the tegulum, the suprategulum (Saaristo 1971; this is referred to by Merrett 1963, as the “median apophysis”). In the unexpanded palp, the suprategulum is situated on the mesal side



Figs. 1-5.—Male palps: 1, *Eperigone tridentata* (Emerton), ectal, with part of cymbium cut away to show coiled haematodocha; 2, *Eperigone tridentata*, bulb detached from cymbium, viewed from behind: ED removed; 3, *Ceratinopsidis formosa* (Banks), mesal; 4, *Ceratinopsidis formosa*, mesal, ED removed; 5, *Leptyphantès zimmermanni* Bertkau, mesal, ED removed. Abbreviations: E, embolus; ED, embolic division; H, haematodocha; P, subtegular petiole; PC, paracymbium; R, reservoir; SA, suprategular apophysis; SPT, suprategulum; ST, subtegulum; T, tegulum (Scale lines 0.1 mm).

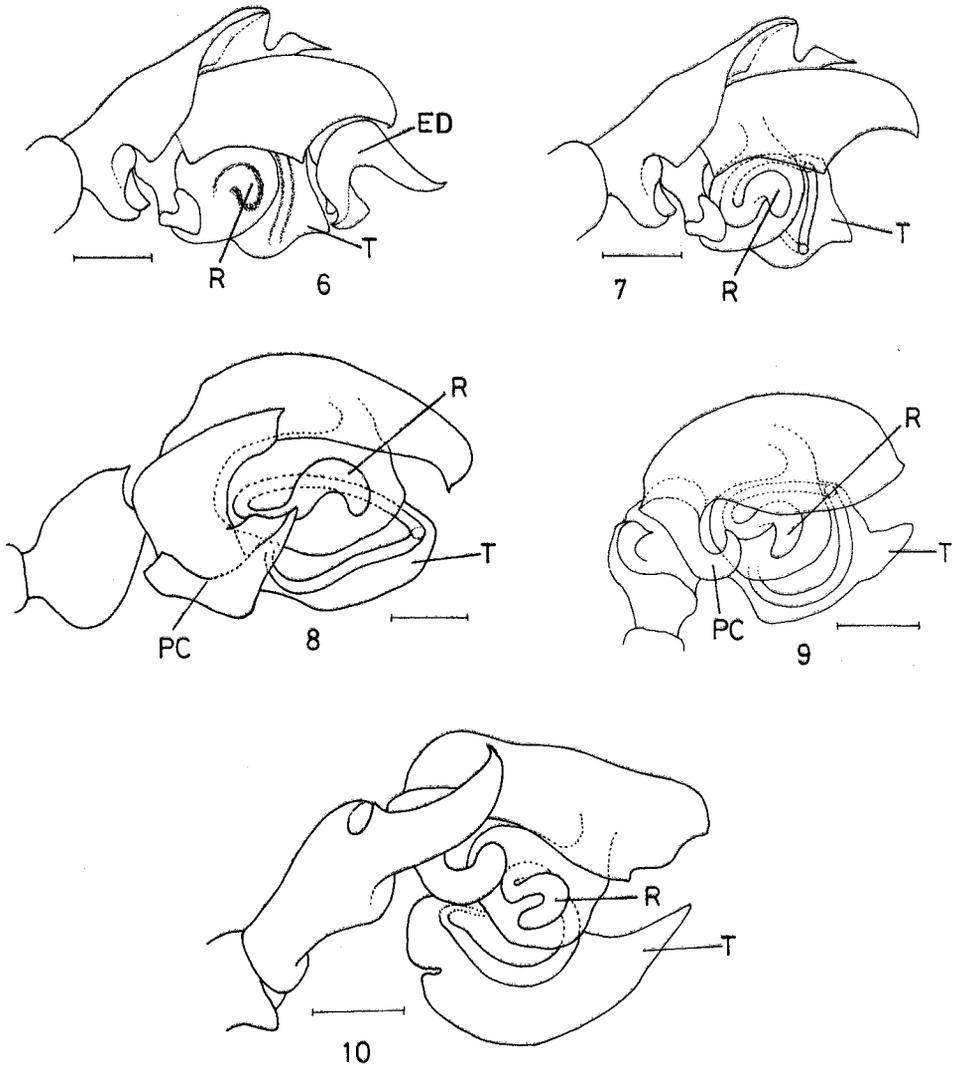
(Figs. 3, 4, 5), lying approximately along the junction between the subtegulum and the tegulum. In this position it does not have the appearance of a projection from the tegulum, but when the palp is expanded the construction becomes clearer. At its anterior (distal) end the suprattegulum carries an apophysis, the suprattegular apophysis (SA). This apophysis, which in the erigonines is often membranous, has a variety of forms ranging from the very simple to the relatively complex; in some species the apophysis may arise both from the end of the suprattegulum and from the stalk [see (iv)]. In some species there is a separate small membranous apophysis arising from the region of the stalk. The tegulum varies a good deal in shape, both in the linyphiines and in the erigonines, and may have membranous projections, particularly anteriorly.

(iv) **The embolic division (ED).**—This is a separate sclerite which carries the embolus, and is attached to the suprattegulum by a membranous stalk (Saaristo 1971, calls this the “column”). The ED is complex in form in typical linyphiine species, e.g. *Leptyphantes* Menge; it is simpler, though very variable in shape, in the typical erigonine species. The form of the ED is of prime importance for species determination, particularly in the linyphiines but often too in the erigonines; it is also valuable for the assessment of generic and suprageneric relationships. Some of the numerous forms of the ED in European species are figured by Merrett (1963).

The reservoir of the sperm duct lies in the subtegulum and is attached to its ectal wall: the marking usually visible on the subtegulum just in front of, or partially obscured by, the paracymbium (e.g. R, Fig. 6), is the area of attachment of the reservoir. This reservoir is shaped like an inverted U, with the closed end anterior (Fig. 7). From the reservoir, the duct (usually rather smaller in diameter than the reservoir) runs in an irregular spiral through the subtegulum and into the tegulum; it then runs down through the tegulum on the ectal side and finally up again on the mesal side, to enter the ED by way of the suprattegulum and the stalk (Figs. 3, 4). The reservoir seems always to be in the form of an inverted U, and the path followed by the duct is always essentially that described; this is true for all the numerous linyphiine and erigonine species I have examined, including species from Europe, North America, South America, Central Africa, Australia and New Zealand. While the form of the reservoir and the conformation of the duct appear to be essentially constant within the family, there are of course small differences in the detail. For example, in some genera, both linyphiine (e.g. *Centromerus* Dahl, Fig. 8) and erigonine (e.g. *Ceratinella* Emerton, Fig. 9), the subtegulum and tegulum are positioned more horizontally than in many erigonines, but the duct conformation is basically the same with the difference that the axis of the spiral is inclined more to the vertical than to the horizontal. Even in palpal organs which appear somewhat abnormal in construction (e.g. in *Gnathonarium* Karsch, Fig. 10) the basic duct conformation remains unchanged. In *Erigone* Audouin and some other genera the reservoir, instead of lying in the “normal” position, has been rotated through up to 90°, so that only one arm (the closed end) of the reservoir is adjacent to the ectal wall of the subtegulum (e.g. *Eperigone* Crosby and Bishop, Fig. 1); apart from this small change, the duct conformation is normal. In addition to these minor variations, the duct itself may have small twists or convolutions within the tegulum (e.g. Fig. 5).

A brief mention must be made of the expansion of the palpal organ. The supply of blood to the subtegulum, required to raise the pressure and bring about ejection of sperm from the reservoir, is probably by way of the subtegular petiole, which seems to be the only part of the subtegulum which is open (via the basal end of the haematodocha) to the blood supply in the cymbium. When the coiled haematodocha is expanded, by an increase

in the internal pressure, it tends to uncoil. The attachment of the subtegular petiole to the base of the haematodocha on the ectal side restricts the movement of the subtegulum, so that the expanding haematodocha repels the bulb from the cymbium mainly on the mesal side, and at the same time imparts some rotation to the bulb. As a result, the ED moves from the mesal side to the front of the palp or even towards the ectal side. When the embolus is fixed in the epigyne prior to expansion, a degree of rotatory movement may be imparted to the ED, possibly facilitating insertion.



Figs. 6-10.—Male palps: 6, *Diplocephalus cristatus* (Blackwall), ectal; 7, *Diplocephalus cristatus*, ectal, ED removed, cleared; 8, *Centromerus arcanus* (O.P.-Cambridge), ectal, ED removed, cleared; 9, *Ceratinella brevis* (Wider), ectal, ED removed, cleared; 10, *Gnathonarium dentatum* (Wider), ectal, ED removed, cleared. Abbreviations: ED, embolic division; PC, paracymbium; R, reservoir; T, tegulum (Scale lines 0.1 mm).

## THE LINYPHIIDAE AS A MONOPHYLETIC GROUP

The palps of typically linyphiine and typically erigonine spiders appear at first glance to be very different. Closer examination, however, shows that the differences are not in the basic construction of the palpal bulb, but only in the detail. The chief distinctions between the two forms are: (i) the embolic division is notably more complex in form in the linyphiines than in the erigonines; (ii) the suprategular apophysis is frequently more complex in the erigonines than in the linyphiines. When the embolic division is removed from the palpal organ, by breaking off at the stalk, the agreement in basic construction between linyphiine and erigonine palps becomes clear, the same structural components being present in each case (Figs. 4, 5; 8, 9).

The presence of the paracymbium as a separate articulated sclerite, the basic structure of the palpal bulb (i.e. haematodocha, subtegulum, tegulum, suprategulum with suprategular apophysis, embolic division as a separate sclerite), the form of the seminal reservoir and the route of the duct to the embolus via the suprategulum, represent a conglomerate character which is almost certainly apomorphic, having been derived either by elaboration of a more simple palpal structure (most likely) or by reduction of a more complex structure (less likely). So far as I know, this combination of characters is not present in any other branch of Araneoida. On the basis of Hennig's reasoning (Hennig 1966), the presence of this synapomorphic character, or conglomerate of synapomorphic characters, carried by all species without any currently known exceptions, offers substantial support to the hypothesis that the family Linyphiidae (s. lat.) is a monophyletic group.

## SUBDIVISIONS OF THE FAMILY

It was pointed out above that there are no somatic characters which suffice to define the family Linyphiidae. It is also true that the two groupings into which the family has usually been split, namely the subfamilies Linyphiinae and Erigoninae, cannot be defined in a scientifically acceptable manner by any combination of somatic characters. The separation of the linyphiines and erigonines (whether as separate families or as subfamilies) has in the past been carried out almost entirely on the basis of the dorsal tibial spines (of the female), the linyphiines having two spines on tibia IV while the erigonines have one (or occasionally zero). For the European fauna a more recent formula has been that those species which have *either* two dorsal spines on tibia IV *or* one dorsal spine on tibia IV plus one dorsal spine on metatarsi I and II, are linyphiine, the remainder being erigonine. This device does on the whole separate the linyphiines (with more complex palpal organs) from the erigonines (with less complex palpal organs), but it also throws up a number of anomalies: in particular, some species with the rather simple palpal organs characteristic of the erigonines are by this formula placed with the linyphiines.

It has been suggested (Blest 1976) that it may be possible to split the Linyphiidae into two groups or subfamilies on the basis of the tracheal arrangements; typical linyphiines have four simple tracheae which are confined to the abdomen, while typical erigonines have two short simple lateral tracheae and two large medial trunks which divide into numerous small branches before passing as two bundles into the cephalothorax. Division of the family on this basis does not however appear to be clear cut, and leaves a number of questions unresolved: this was emphasized by Blest and Pomeroy (1978) after their study of some aspects of the primitive genus *Mynoglenes* Simon, which possesses a mixture of linyphiine and erigonine characters, including the linyphiine type of tracheal system.

One problem which complicates the division of the Linyphiidae into two subfamilies is that although the majority of species have palpal organs which are clearly either linyphiine or erigonine in complexity, there is a sizable minority of species where the palpal organs are intermediate and do not clearly fall into either category. No taxonomist has so far been able to define the features of linyphiine and erigonine palps in such a way that all species can be placed unequivocally into one group or the other. Blest (1976) has argued that some of the intermediate palpal forms, and indeed some of the forms normally regarded as erigonine, may have been produced by reduction of the more complex (linyphiine) forms. I have suggested (Millidge 1977) that the contrary development may have taken place, and that some of the intermediate and the more complex palpal forms may have been derived by elaboration of the more simple forms. In the present state of our knowledge of the evolution of the family, it is probably sensible to accept that both processes may have taken place at different times.

Lehtinen and Saaristo (1970) and Lehtinen (1975) have also put forward the view (without however detailing the evidence on which the view was based) that the simple bifurcate splitting of the Linyphiidae is not a tenable hypothesis.

On the data available at the present time it seems clear that there is no good scientific basis (synapomorphy) for dividing the family into the two traditional groupings, the Linyphiinae and the Erigoninae. Nevertheless the terms "linyphiine" and "erigonine" are still useful descriptive labels and can continue to be used, provided that it is understood that they refer, somewhat loosely, to structural characteristics rather than to phylogenetic relationships (Millidge 1977).

The history of the many attempts to split the erigonines into suprageneric groups (often in the past designated as subfamilies of the Erigonidae) has been summarised by Merrett (1963) and will not be repeated here. It is sufficient in this paper to indicate that there is no scientific justification for splitting the erigonines into the historical suprageneric groups such as Masonini, Pelecopsini (Lophocarenini), Gonatiini, etc. The characters on which these groups were based [e.g. stout ventral spines on the anterior legs (Masonini), presence of trichobothria on metatarsus IV (Gonatiini)], are very probably not apomorphous and thus not valid for establishing phylogenetic relationships in the groups concerned. Few if any of the suprageneric categories so far proposed by various authors for the erigonines or linyphiines have been scientifically based on the presence of identified synapomorphic characters.

To sum up, there appears to be no alternative for the present but to leave unresolved the important problem of how to subdivide the Linyphiidae into phylogenetically valid subfamilies or other suprageneric groups. The wide differences which exist in the detail of the male palpal organ (particularly of the embolic division), coupled with the differences in the tracheal structures, indicate that most probably the family has evolved along several distinct lines, but there are insufficient data as yet to allow these branches of the family to be recognized and defined with any certainty. If taxonomy is to be regarded as science rather than art, then taxonomists must adhere to scientific disciplines: proposals for suprageneric categories (and indeed for new genera) should be treated as scientific hypotheses, which must be supported by fully disclosed data and reasoning. The erection of properly defined suprageneric groups in the Linyphiidae will perhaps only be possible when our knowledge of the global linyphiid fauna has been further extended, and the data have been subjected to a fresh analysis and interpretation.

## CHARACTERS USED IN THE DEFINITION AND DIAGNOSIS OF GENERA IN THE ERIGONINES

(i) **Genitalia.**—At the present time, the most reliable character for defining the erigonine genera is almost certainly the structure of the male palpal organ. In an earlier paper I discussed the possible value of this character for establishing phylogenetic relationships (Millidge 1977). The palpal organ in the Linyphiidae is geometrically fairly complex, and it is considered improbable that the structure (“conformation”) present in a given species or group of species will have been evolved on more than one occasion. In addition, the palpal organ is present in the male sex only for a limited period of the life span of the spider, and it is unlikely therefore that this organ will have been much influenced by purely environmental factors. On the basis of these premises it was put forward as a hypothesis (Millidge 1977) that the palpal conformation of erigonine spiders is an apomorphic character in the Hennig sense. Thus it should be possible, in the Linyphiidae in general, and in the erigonines in particular, to define genera as phylogenetic entities on the basis of some feature or features in the structure of the palpal organs. In this series of papers on the North American erigonines, attempts will be made to define the genera on the basis of the palpal structure together with any other character which may appear to be appropriate.

The spiders of some genera (e.g. *Erigone*) have epigyna which are fairly characteristic in appearance and which can be useful for diagnosing the genus of female specimens. The internal genitalia associated with the epigynal plate, i.e. the spermathecae and associated ducts and structures, as seen by clearing in clove oil or other suitable liquid, do not appear to be particularly complex in structure in the erigonines, and hence offer fewer characters of potential value for taxonomy than do the palpal organs. Examination by clearing in this simple way, however, cannot show up all the detail of the internal structure, and the development of more sophisticated techniques may reveal additional details and complexities. Although recognition of the genus is sometimes possible by the form of the epigynum, it is probably true that at the present time there is no instance where an erigonine genus can be satisfactorily defined on the structure of the epigynum or of the internal genitalia. It seems probable that the determination of phylogenetic relationships by means of the female genitalia, when and if this becomes possible, will be based on a combination of the form of the genital plate coupled with the structure of the internal parts, i.e. will be based on the structure of the whole genitalia.

(ii) **Chaetotaxy and other numerical characters.**—As an aid to identification, the chaetotaxy of the erigonines has proved a very useful character for the European species. There is currently insufficient information to judge whether this character will be equally useful for the North American fauna. The chaetotaxic characters most frequently used are the dorsal tibial spines and the metatarsal trichobothria.

The tibial spines (macrosetae) are usually quite distinct from the hairs (setae), being both longer and thicker; occasionally, when the spines are rather thin and short, differentiation can be more difficult. The tibiae in female erigonines normally have one or two dorsal spines, but in a few species spines may be completely absent (or indistinguishable from hairs). The number of dorsal tibial spines present is expressed by the formula  $abcd$ , where  $a$  is the number on tibia I,  $b$  the number on tibia II, etc. For the females, the formula is most frequently 1111, 2211 or 2221, but occasionally it is 0000 or 2222. The male sometimes has the same spinal formula as the female, but often the spines may be shorter and weaker or entirely absent, particularly on legs I and II.

The trichobothria are long fine hairs arising from the center of a circular pit which, under the magnifications commonly used with the light microscope, appears as a small circle. In the Linyphiidae, the metatarsi of legs I-III have one trichobothrium each, on the dorsal side, while that of leg IV has one or none; there are a few instances among the linyphiines where the metatarsi have more than one trichobothrium, particularly on leg I, but no such case among the erigonines, so far as I know. The presence or absence of the trichobothrium on metatarsus IV is sometimes of taxonomic value. The position of insertion of the trichobothrium on the metatarsus shows only small variation within a species, and often also within a genus, at least in the European genera. The method of expressing the location of the trichobothrium is shown in Fig. 11, where the position is given by the expression:  $TmI$  (i.e. position on metatarsus of leg I) =  $a/b$ , expressed as a decimal fraction. The variation in the value of  $TmI$  within a species is probably up to  $\pm 10\%$ , but even so this function can often be useful in diagnosis. The position of a leg spine can be expressed in a similar way if desired.

The leg spines are fairly readily lost if the specimens are shaken around in large vials, and unfortunately this has sometimes been the case with museum specimens. The trichobothria are lost less readily, and even when they have broken off the small pit at their base is almost always visible, even in old and faded specimens.

The chaetotaxy (tibial spines and metatarsal trichobothria) is often fairly constant within probably good genera, but by no means invariably so. Thus although useful for diagnostic purposes, this character cannot be regarded as a reliable one for deciding phylogenetic relationships.

The number of trichobothria present dorsally on the palpal tibia, of either sex, can in some instances be of diagnostic value.

It may on occasions be found useful for diagnosis to record a few other characters expressed numerically, e.g. the stoutness of the legs as given by the ratio: length/diameter ( $l/d$ ) of a leg segment (Fig. 11), the ratio of length of one leg segment to another, etc.

(iii) **Male palpal tibia and male carapace.**—In some genera the male palpal tibia has a fairly constant basic form, which differs only in detail from species to species. In other genera (which may or may not be monophyletic) the tibia shows a wider degree of variation. The form of the tibia should therefore be used with caution as a indicator of relationship.

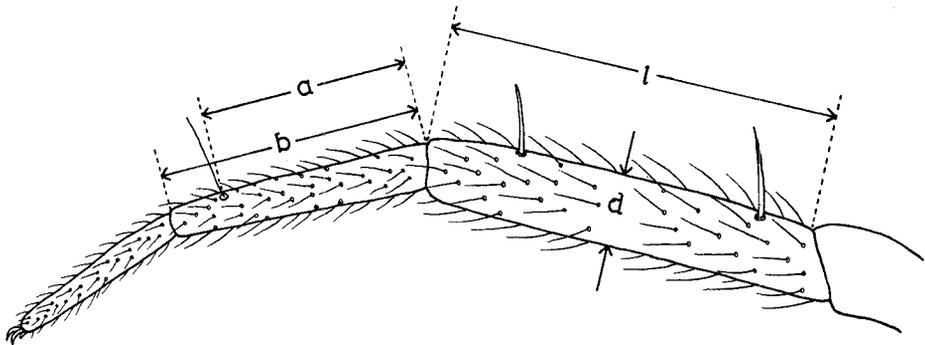


Fig. 11.—Part of leg I of erigonine spider, to illustrate the methods used for expressing (i) the position of the metatarsal trichobothrium, and (ii) the length/diameter (at mid-point) of tibia - see text. (i)  $TmI = a/b = 0.80$ ; (ii)  $Tibia I l/d = ca. 5.5$

In the past, the form of the male carapace (the type and shape of protuberances, etc.) has often been used by arachnologists to define genera. Within what now appear to be properly defined genera, however, more than one type of protuberance may frequently be encountered. As with the male palpal tibia, therefore, this secondary sexual character should likewise be regarded as of questionable value for genus definition.

(iv) **Tarsal claws.**—The form of the tarsal claws is occasionally useful in diagnosis. There are a few genera in which these claws are distinctly pectinate, that is they are furnished with a comb of long teeth: this is the case for example in the genera *Walckenaeria* Blackwall, *Gonatium* Menge and *Tapinocyba* Simon. Although sometimes a useful taxonomic character, which can be used to confirm the generic position of a species, the pectinate claws are probably of little phylogenetic value, since the pectination is probably a primitive character which has occasionally been retained.

(v) **Eyes and cheliceral teeth.**—Because of the paucity of distinguishing characters visible in the erigonines, the earlier arachnologists made frequent use of the cheliceral teeth (number and size) and of the eyes (size, spacing and curvature of the rows) for genus definition. These characters are not only difficult to measure accurately, but seem to show too much individual variation to be of any real value, at least above the species level.

## DESCRIPTIONS OF ERIGONINE SPECIES

As stated earlier, the erigonine spiders are very generalised in form, apart from some sexual characters. Long descriptions (e.g. of color, leg lengths, cheliceral teeth, eye size and spacing, etc.) are usually of little or no diagnostic value and are unnecessary for most purposes. In this series of papers I propose therefore to keep the descriptions of the species as brief and economical as possible, concentrating on the characters useful for diagnosis. The work to be reported will be based almost entirely on museum specimens, in some of which the colors have faded, and in which increasing transparency has sometimes changed the appearance of the epigyna from those of fresh specimens: these points should be borne in mind when use is made of the descriptions.

## GENERAL

In order to prevent the loss of limbs, spines and trichobothria, which are diagnostically useful, erigonine spiders should not be stored loose in large vials. They should be kept in alcohol, out of bright light (which catalyses oxidation and bleaching), in small vials, e.g. 25-40 mm long by 5-8 mm diameter, which are placed in alcohol in larger vials or bottles. In small vials the spiders suffer less damage when the storage bottles are moved or shaken, e.g. when sent through the mail. If a palp or epigynum is detached (sometimes necessary for identification), it should be stored in a separate small vial and labelled. The small vials employed for storage may be plugged with cotton wool or preferably with a polyethylene closure; the larger vials or bottles should be sealed against evaporation, and a polyethylene closure is also preferred here. The use of stoppers made of rubber (natural or synthetic) is to be discouraged, since the alcohol extracts from these rubbers some oily sulfurous material, which can produce cloudiness and an unpleasant smell in the alcohol in which the specimens are examined, and may also cause precipitation of troublesome dirt and sticky oil on to the specimens.

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