

A revision of the tracheal structures of the Linyphiidae (Araneae)

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A short time ago a taxonomic scheme was proposed (Millidge, 1984) for the Linyphiidae based on the tracheal structures (Blest, 1976) and the epigynal structures. The author was subsequently informed by Dr R. R. Forster (*in litt.*) that the tracheal system of the North American species *Tennesseellum formicum* (Emerton), assigned on the basis of its genitalia to the haplotracheate subfamily Micronetinae in 1984, was not simple, but complex, with the stout median tracheal trunks branching into bundles of slender tracheae which enter the prosoma, much as in the Erigoninae. In other respects, as pointed out by Forster, the tracheal system of *Tennesseellum* differs from that described for the erigonines; in particular, the spiracular fold is well anterior to the spinners, the median tracheal trunks, which are joined by a transverse duct, arise directly from two separate spiracles, and there are no lateral tracheae.

Forster's information on *Tennesseellum* prompted the author to re-examine the tracheal systems of the Linyphiidae. This investigation, reported here, has shown that in some cases the tracheal systems are at variance with the descriptions given by Blest (1976).

All the tracheal determinations reported in this paper were carried out by the cold sodium hypochlorite method (Millidge, 1984), which produces little or no disturbance or distortion of the tracheae. Where necessary, the tracheae were subsequently stained in aqueous chlorazol black.

The tracheal system of *Tennesseellum* is shown in Fig. 1; in addition to the four bundles of tracheae (two from each median trunk) which run into the prosoma, there are a number of fine tracheae arising from the trunks and radiating to most parts of the abdomen. *T. formicum* has the genitalia, both male and female, similar in form to those of the members of the Micronetinae; the only obvious difference is the presence of spurs on the male palpal femur and tibia (Kaston, 1981: fig. 310). Other members of the Micronetinae (e.g. *Microneta* Menge, *Lepthyphantes* Menge, *Meioneta* Hull) were reported by Blest (1976) to be haplotracheate. *Tennesseellum* appears to be particularly close to the group of genera *Meioneta*, *Agneta* Hull and *Syedruia* Simon, and with this in mind the tracheal forms of these genera were the first to be re-examined. Most of the British species of these genera were studied, together with a few *Meioneta* species from Africa, North America and South America. All these species proved to be desmitracheate, with the bundles of slender tracheae from the median trunks extending into the prosoma and indeed into the limbs; slender lateral tracheae are also present. Thus these genera have a tracheal form

which appears, at first sight, to be identical with that given by Blest (1976: fig. 1c) for a typical erigonine species. More detailed examination of the *Meioneta* tracheal system, however, showed that this was more complex than at first supposed. The two median trunks run directly, via a short basal section, to two spiracles (i.e. there is no atrium), and are connected by a transverse duct; the lateral tracheae, which are less than half the diameter of the median tracheae, join the latter on the short basal section, on the dorso-lateral side (Figs. 2, 3). Apart from the position of the tracheal fold and spiracles, this system is generally similar to that of *Tennesseellum*; there is a possibility, in the latter case, that the bundle of fine tracheae, which originates from near the base of each median trunk, is in fact a modified lateral trachea which has become fused at its base to the median trachea.

Re-examination of a variety of erigonine genera has shown that the tracheal structure of the Erigoninae also differs somewhat from that given by Blest (1976). The median tracheae are indeed complex, but they run directly, via a short basal section, to two spiracles; there is no atrium. There are two slender lateral tracheae, which join the median tracheae on the short basal section, on the dorso-lateral side (Fig. 4), as in the *Meioneta* group; in a few species, as noted by Blest, these lateral tracheae are branched (Fig. 5). The walls of the median trunks are joined mesally, just anterior to the basal section, but there is no connecting duct between them. This erigonine tracheal form is present in the genera *Hilaira* Simon, *Donacochara* Simon, *Leptorhoptrum* Kulcz. and *Drepanotylus* Holm, the taxonomic position of which was regarded by Blest as doubtful.

The South American genus *Laminacauda* Millidge, which has the median tracheae fairly slender and split

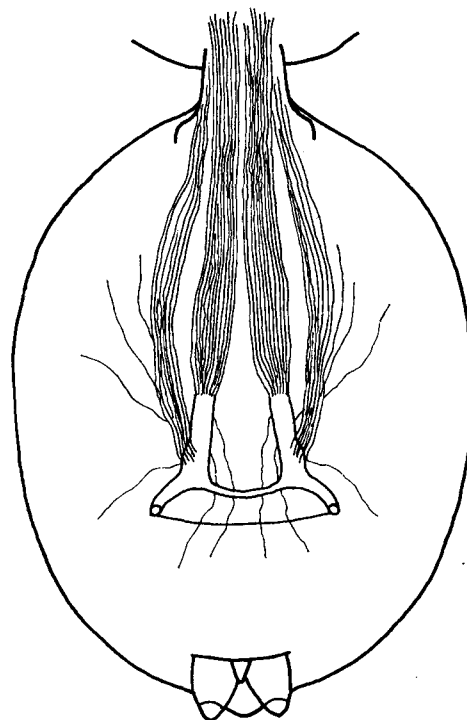


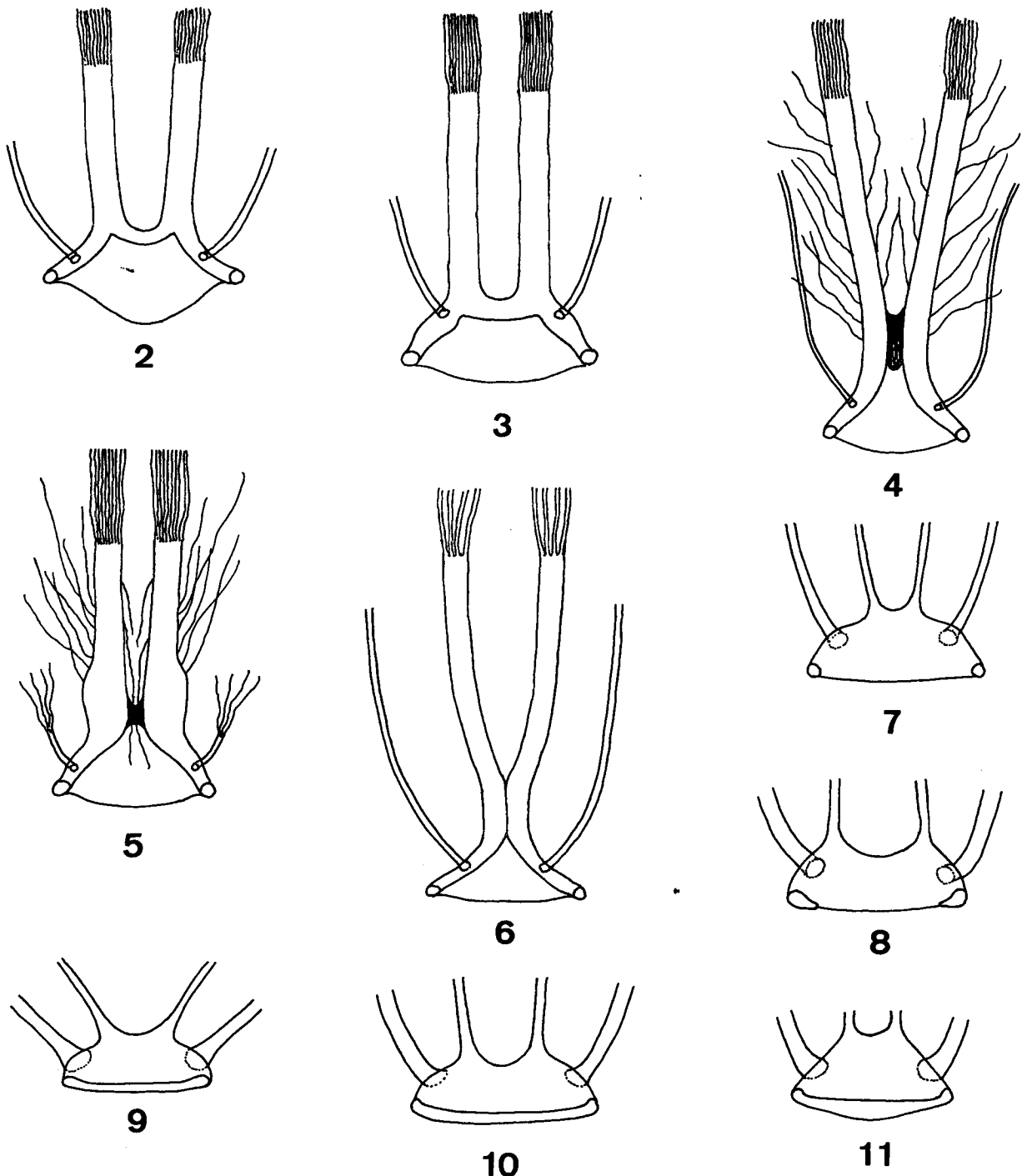
Fig. 1: *Tennesseellum formicum* (Emerton), tracheal system, ventral.

distally into 3-5 branches, only one or two of which may enter the prosoma, was assigned somewhat doubtfully to the Drapetiscinae (Millidge, 1985). Re-examination now shows that this genus has the erigonine tracheal form (Fig. 6), and consequently it should be regarded as a member (perhaps somewhat primitive) of the Erigoninae. *Laminacauda* comprises species up to 8 mm in length, which would certainly be novel for the Erigoninae.

Tennesseellum and the *Meioneta* group of genera are clearly not erigonine, and the presence in these genera of complex (desmitracheate) median tracheae immediately demolishes the hypothesis that the

Erigoninae can be defined as comprising those taxa of the Linyphiidae which have median tracheae of the complex form (Blest, 1976; Millidge, 1984). The tracheal form now known to be present in the Erigoninae, however, namely that with the median tracheae opening directly to the spiracles, but without a connecting transverse duct, is probably apomorphic within the Linyphiidae (see later), and will consequently serve to define the Erigoninae.

The haplotracheate taxa of the Linyphiidae have the four simple tracheae running into a common atrium, with the lateral tracheae entering on the dorso-lateral side. In many species (e.g. in the Micronetinae, the



Figs. 2-11: Tracheal systems, posterior part, ventral. 2 *Meioneta nigripes* (Simon); 3 *Agyneta conigera* (O. P.-C.); 4 *Diplocephalus cristatus* (Bl.); 5 *Erigone arctica* (White); 6 *Laminacauda diffusa* Millidge; 7 *Centromerus sylvaticus* (Bl.); 8 *Lepthyphantes nebulosus* (Sund.); 9 *Haplisis titan* (Blest); 10 *Linyphia clathrata* Sund.; 11 *Hormembolus aysenensis* (Tullgren).

Drapetiscinae and in most "primitive" genera of the *Stemonyphantes* group) this atrium opens to the atmosphere via two spiracles, which may be circular or slightly elongated towards the median line (Figs. 7, 8). In the Mynogleninae and the Linyphiinae, however, the atrium opens via a slit along its posterior margin (Figs. 9, 10); the ends of this slit are usually rounded and thickened, possibly representing the vestiges of the spiracles. The haplotracheate genus *Lessertinella* Denis has the atrium of this form, which supports the assignment of this genus to the Linyphiinae (Millidge, 1984). It is interesting that the South American genus *Hormembolus* Millidge, which appears to have affinities with both the Linyphiinae and the Mynogleninae, but cannot be assigned to either (Millidge, 1985), has the slit opening to the atrium (Fig. 11).

The genus *Allomengea* has a tracheal atrium which opens via two spiracles, but the fairly narrow median tracheae branch distally into several slender branches, which do not enter the prosoma (Blest, 1976).

Thus there are six different tracheal forms present in the Linyphiidae, but two of these are restricted each to a single genus. These six forms, all except one of which have retained the two individual spiracles, must have been derived from a single ancestral form, and it is interesting to speculate on the structure of this

ancestral form. Partly on the basis of the suggestions put forward by Forster (1980), it is proposed that the parent form could have had the basic characteristics of structure A (Fig. 12), and that the six forms could have been derived from it by the steps shown schematically in Fig. 12. In this hypothetical parent structure the median tracheae were derived from abdominal apodemes and the laterals from the second pair of book lungs (Purcell, 1909, 1910). The assumptions made are that the tracheae in A were all simple, that complex tracheae, once formed, do not revert to simple tracheae, and that when the tracheal atrium has evolved there is no subsequent regression to individual spiracular openings. It must also be assumed that the tracheal spiracles in A were probably located well anterior to the spinners, as in *Tennesseellum*. No present member of the Linyphiidae is known to have the tracheal structure A.

In this scheme (Fig. 12), each step in the tracheal evolution appears to involve relatively simple transformations. Apart from the movement of the spiracles posteriorly towards the spinners (not necessary in the case of *Tennesseellum*), the numbered steps involved would be as follows: 1. Closure of the transverse duct (to give intermediate B); 2. Conversion of the median tracheae to the complex form by development of fine tracheal branches (to give the

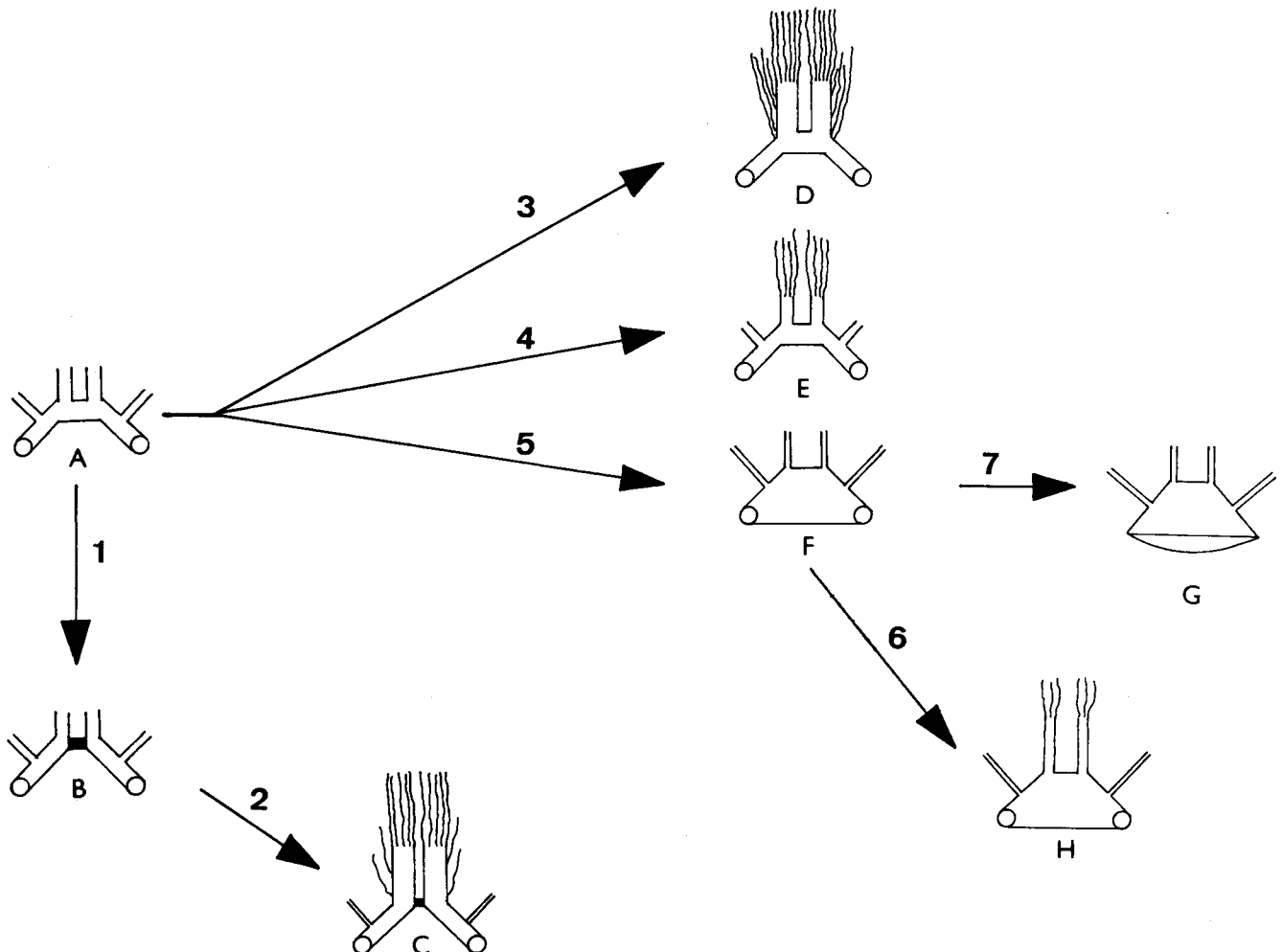


Fig. 12: Hypothetical development of linyphiid tracheal systems: for explanation, see text.

erigonine form C); 3. Conversion of the median tracheae to the complex form, and either loss of the lateral tracheae or fusion of the median and lateral tracheae at their bases (to give the *Tennesseellum* form D); 4. Conversion of the median tracheae to the complex form (to give the *Meioneta* form E); 5. Movement posteriorly of the posterior and lateral walls of the duct which links the two spiracles, to form an atrium (to give one haplotracheate form F); 6. Opening of a slit along the posterior margin of the atrium (to give the other haplotracheate form G); 7. Modification of the median tracheae by the development of a limited number of fine branches distally (to give the *Allomengea* form H). Forms G and H are represented as derivatives of the haplotracheate form F, but it is possible that there was independent development from the ancestral form A.

The evolution suggested (Fig. 12) is no doubt an over-simplification, but it is nevertheless evident that the presence of three tracheal forms in one subfamily need not be regarded as particularly surprising, if all three forms are derivable from some hypothetical precursor (A) by one or two relatively simple steps only. The differences in the tracheal forms, however, will make it desirable to place *Tennesseellum* and the *Meioneta* group into separate tribes within the Micronetinae.

If the haplotracheate form F were to be regarded as the primitive form (as was previously assumed: Millidge, 1984), that is, if the polarity of step 5 were reversed, then the tracheal character "duct from median tracheae runs direct to spiracles" which is

present in forms C, D and E would become apomorphic, and the resulting synapomorphy would suggest that the subfamily Erigoninae is related fairly closely to the genera *Meioneta* and *Tennesseellum*; such a close relationship appears, from the genitalia and other characters, to be unlikely. The preferred hypothesis, therefore, is that the polarity of step 5 is as shown, and that the basic tracheal similarity in C, D and E is based on plesiomorphy, not apomorphy. The presence of ventral spurs on the male palpal femur of *Tennesseellum* and of some erigonine species may also be an example of plesiomorphy.

The tracheal scheme (Fig. 12) would be little changed by reversing the polarity of step 1, thereby making structure B the parent form. If this were done, however, the autapomorphic character given earlier in this paper for the Erigoninae would become a plesiomorphy, and this subfamily would need to be redefined on the basis of the absence both of an atrium and of a connecting duct between the median tracheae, coupled with the presence of the complex median tracheae.

All the current tracheal forms in the Linyphiidae must be regarded as apomorphic on the basis of the tracheal hypothesis given in Fig. 12. The haplotracheate form F appears to have been evolved in more than one evolutionary line, and is consequently of little taxonomic value. The tracheal hypothesis does not conflict with (i.e. does not disprove) the taxonomic hypothesis proposed recently for the Linyphiidae (Millidge: 1985). Application of the tracheal data to the taxonomic scheme is shown in Fig. 13; it must be

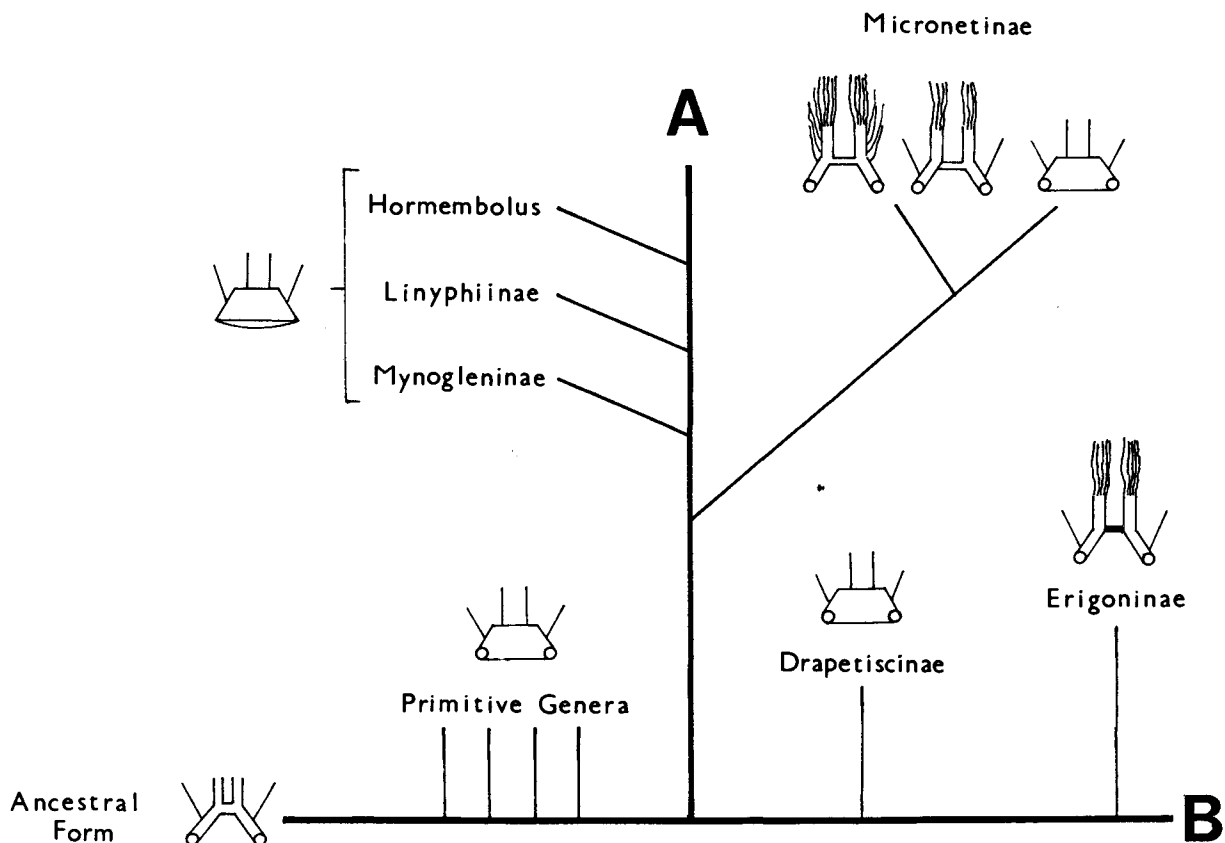


Fig. 13: Taxonomic scheme for the Linyphiidae (Millidge, 1985), to show tracheal forms. Branch A carries epigynal socket; branch B lacks epigynal socket.

emphasised that the sequence of the branchings shown here is not significant, since the chronology is not known and probably never can be known. Although hypotheses on the actual structure of the parent tracheal system in the Linyphiidae are obviously speculative, the scheme depicted in Fig. 13 does suggest strongly that the branchings to line A (which carries the epigynal socket) and to the Erigoninae must have taken place early in the evolution of the family, when the tracheal system was still of a primitive form.

If the subfamily Micronetinae comprises taxa with three tracheal forms, then it cannot be regarded as certain that other subfamilies of the Linyphiidae are restricted to one tracheal form. To date, however, no desmitracheate species are known which can legitimately be assigned to the Mynogleninae, Linyphiinae or Drapetiscinae. The tracheal progression (Fig. 12) indicates that the haplotracheate structures F and G lie on a branch of the family which is quite separate from the branch which carries the erigonine structure C; consequently it appears improbable that the evolutionary line leading to the Erigoninae will have developed the tracheal forms F or G as well as form C. This conclusion suggests that the known genitalic similarities that exist between some haplotracheate taxa of the Drapetiscinae and some taxa of the Erigoninae (e.g. the similarities between *Asthenargus* Simon and *Erigone* Aud.: Wiehle, 1960: 585) must be examples of convergence, or possibly plesiomorphy. On current knowledge, therefore, it would be unwise to transfer these haplotracheate taxa to the Erigoninae.

Why the Linyphiidae should have developed multiple tracheal systems, and particularly why a single

subfamily should have three systems, is obscure; there is no apparent correlation of the different forms with size or habitat. The tracheal system in *Tennesseellum* is the most extensive, and it seems unlikely that such tracheal exuberance can be necessary to supply the oxygen requirements of such a small spider; the tracheae of the small erigonine spiders are almost as extensive. It is possible that the evolution of such tracheal systems was the consequence, not of need, but of pleiotropic genes.

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