The Phylogeny of the Tracheae in Araneæ.

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With Plate 28, and 21 Text-figures.

INTRODUCTION.

In an excellent paper on the tracheæ of spiders E. Lamy (1902) has given an account of the tracheæ of thirty families of Araneæ, so that only four small and comparatively rare families, comprising 1—3 genera each, remain, of which the tracheæ are still unknown. It is now possible, therefore, to consider the tracheal systems of the Araneæ as a whole from a phylogenetic point of view, and as I barely touched upon this point in my paper (1909) on the development and origin of the respiratory organs in spiders, I propose to make it the subject of the present paper.

Lamy has made it perfectly clear that the degree of complication of a tracheal system, as regards the manner and extent of the branching and the structure of the internal armature (spines, spiral thread, etc.), cannot be used as a family character, since we may find the most varied degrees of complication amongst the different genera of one and the same family (e.g. in the Uloboridæ, Thomisidæ, Agelenidæ, Clubionidæ, Attidæ, etc.). Lamy concludes from this that the tracheal apparatus is evolved separately in each family and not in the Araneæ as a whole (p. 265) and this statement may, I think, be accepted as in general correct,
provided that it be not interpreted to mean the development of the tracheæ out of lung-books separately in each family but merely the development of more complicated tracheal systems from simpler ones or vice versa.

Another important point which Lamy has emphasised (p. 264) is that the number of the lung-leaves is in inverse ratio to the size of the tracheal apparatus. Thus, forms with highly-developed tracheæ have a small number of lung-leaves, as Dictyna, with 4—5 leaves (Bertkau), Segestria, with 10—12 (Bertkau), etc., while forms with a feebly-developed tracheal system have a comparatively large number of lung-leaves, as Epeira and Agelena, with 60—70 leaves (Bertkau).

Since the relative size of the tracheal apparatus in general increases proportionately with its degree of complication it further follows from the above paragraphs that the number of the lung-leaves in forms having both tracheæ and lung-books can have no greater phylogenetic value than that possessed by the degree of complication (in respect to branching and internal armature) of the tracheal apparatus and this Lamy has shown to be of subordinate phylogenetic value, without even the importance of a family character. We cannot, in fact, use either of these characters in comparing widely remote families phylogenetically, as, for instance, the Dysderidæ and Argiopidæ (Epeiridæ). Thus, assuming that the tracheæ were derived from lung-books, it would be incorrect to argue that an Argiopid, with its numerous lung-leaves and simple tracheæ is, on that account, a more primitive form than a Dysderid, with its few lung-leaves and large complicated tracheæ; or, conversely, if we admit that the Dysderidæ are more primitive than the Argiopidæ, we could not argue that because of the different relative development of these two organs in the two families, the lung-books must have been derived from tracheæ.

It does not follow, however, from any of Lamy's arguments, that the two characters just discussed are of no phylogenetic importance at all, e.g. amongst allied genera in one and the
same family, as in the Agelenidae, or between allied families, such as the Dysderidae and Oonopidae—nor that other tracheal characters, such as the acquisition of the respiratory function by the ectodermal tendons of the tracheal segment, which I have shown to have taken place in most spiders, may not have a much higher phylogenetic value.

Before entering upon this subject I wish to consider a certain remarkable conclusion drawn by Lamy, viz. that in spiders neither the lung-books nor the tracheae are the more primitive organs (p. 264), both having been produced simultaneously and replacing one another (p. 265). The sole difference Lamy sees between these two organs lies in their special mode of branching, lamellate branches producing lung-books and tubular ones tracheae (p. 267). The branchial origin of the lung-books is discarded by him as unnecessary and the formation of the tracheal organs is considered to be the consequence of the respiratory function taking place in the same conditions in all air-breathing Arthropods (pp. 266 and 267).

Lamy arrives at the above conclusion by the following arguments (p. 264):—(1) The Dysderidae and the Caponiidae come very near together, approaching one another in several characters, and ought, therefore, to be regarded as equally primitive. Nevertheless, in the latter, the first pair of lung-books is replaced by a pair of tracheae, which strongly resemble those which replace the second pair of lung-books in the Dysderidae. The fact that one sees the tracheae indifferently replacing the lung-books in these two somewhat primitive families indicates that neither organ is to be regarded as more primitive than the other. (2) The same conclusion results from the fact that we find amongst the Araneae vers1 another family, the Hypochilidae, which,

1 Simon divides the spiders as follows: Araneae theraphosae (= Mygalomorphae, Pocock + Liphistius), including all 4-lunged forms except the Hypochilidae. Araneae vers (Arachnomorphae, Pocock), including the Hypochilidae and all dipneumonous and apneumonous spiders.
although it resembles the Araneæ veræ and not the Theraphosæ in all other respects, nevertheless, has the tracheæ replaced by a second pair of lung-books.

Neither of these arguments, however, warrant the conclusion that Lamy has drawn from them, since both cases may be readily explained, even when we assume that the lung-books were in all cases the primitive organ and that the tracheæ were derived from them. Lamy's assumption that the Dysderidae and the Caponiidæ are equally primitive is certainly incorrect, since, as I shall presently show, the Caponiidæ differ from the Dysderidae, as well as from all other spiders (so far as I know), in several important anatomical characters. They are in fact, in these respects, a highly-specialised group, compared with which the Dysderidae are much more primitive. But even if these two families were equally primitive they are by no means the most primitive spiders, the vast host of mygalomorphous forms being all more primitive than they and all provided with lung-books only. Moreover, the highly-developed tracheæ of the Dysderidae, which present no obvious resemblance to lung-books, do not so strongly resemble the anterior tracheæ of the Caponiidæ as Lamy makes out, since these latter are very similar to the lung-books of a Dysderid. In fact, these anterior tracheæ may be most readily explained, as I shall presently show, as lung-books which have been transformed into tracheæ more recently than those of the second pair and which have retained the primitive shape more nearly than has been the case with the tracheæ of any other Arachnid known. They have evidently been evolved out of a few-leaved lung-book like that of a Dysderid, and their presence merely proves that tracheæ have been evolved out of lung-books within the Araneæ at least on two occasions, but it does not prove that the tracheæ and lung-books are equally primitive.

Similarly, the presence of a second pair of lung-books in the Hypochilidæ may be quite readily explained by assuming that this family is an arachnomorphous form in
which the primitive lung-books have been retained, whereas they have been replaced by tracheae or lost in all other members of the group. It is not at all necessary to assume that the Hypochilidae once possessed tracheae, nor that the lung-books and the tracheae must necessarily be equally primitive organs.

Lamy’s conception of a lung-book as developing from an ectodermal invagination with lamellate branches (p. 256) is incorrect, since, as I had already shown some years previously ('95), the two oldest saccules¹ are formed as independent invaginations on the free posterior side of an embryonic abdominal appendage, quite outside of the basal pulmonary sac (vestibule) in the anterior wall of which the remaining saccules appear,—the two oldest saccules being only later on included within the pulmonary sac, when the sinking of the appendage takes place. Lamy puts this observation aside with the remark that I am the only observer who mentions it, but it is none the less a fact.

I have already (:09) fully discussed the question of the primitiveness of the lung-books, and have shown on purely embryological grounds that the typical form of tracheae found in most spiders must have been derived in part from lung-books and in part from ectodermal tendons (entapophyses of Ray Lankester, apodemes), the lateral pair of tracheal trunks being metamorphosed lung-books and the medial pair metamorphosed entapophyses.

Starting from this as a basis, the tetrapneumonous group, Araneæ theraphosæ, appears the most primitive of living Araneæ, a view which has, in fact, long been generally recognised on account of other primitive characters of the group, such as the presence of a free nervous ganglion behind the central nervous mass in the cephalo-thorax, the

I have given the term “saccules” to the hollow air-containing leaves of a lung-book and “septa” to the partitions or lamellæ separating the cavities of adjacent air chambers (:09).
simple form of the external sexual organs, the presence of four spiracles, etc.

The remarkable genus Liphistius, which I have had no opportunity of carefully examining, appears, as Pocock ('92) has pointed out, to be much more primitive than the rest of the group, at least in some of its characters. One of the most interesting among these is the mesial position of the spinners on the under side of the abdomen, so that in this genus none of the ventral abdominal segments have been excessively elongated (text-fig. 1). Considering the apparently primitive structure of this genus, which has also its abdomen segmented dorsally like a Pedipalp, it is somewhat peculiar that both respiratory segments (judging from the figures and descriptions given by Simon and Pocock) evidently possess a deep interpulmonary or epigastric fold, like the Pedipalpi and the Araneae verae.

In the rest of the group (Pocock's Mygalomorphae) the fourth abdominal (tenth post-oral) segment has greatly

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**Text-fig. 1.**—Abdomen of Liphistius (after Pocock, '92).

**Text-fig. 2.**—Abdomen of a mygalomorphous spider.

ee. t. 8 and 9. Depressions in the integument to which the ventral longitudinal muscles are attached at the posterior margins of somites 8 and 9. g. o. External genital opening. lb', lb". First and second pair of lung-books. sp', sp". Spiracles of the first and second pair of lung-books. 7—11 denote the extent of the seventh to eleventh somites.
elongated at the expense of the following segments, being, in fact, as long as or longer than the second and third segments taken together, so as to bring the spinners to the hinder end of the abdomen (text-fig. 2). The positions of the spiracles \(s^p', s^p''\), muscular stigmata \(ec. t. 8 \text{ and } 9\), representing rudimentary entapophyses to which the longitudinal muscles are attached, and the genital opening \(g. o.\) are very primitive, at least in all the forms which I have been able to examine. All these openings are frequently perfectly exposed and separate from each other, especially in distended abdomens, as in text-fig. 2. There is at most a shallow, open, transverse depression behind the posterior edge of the segments, and the skin in this groove behind the genital segment is frequently soft and flexible, like the soft skin between the hard plates of a segmented body. When the abdomen is distended the spiracles and muscular stigmata in this soft skin are exposed, but in a contracted abdomen (such as that of a female after the deposition of the eggs) these openings may become somewhat hidden from view owing to the infolding of the flexible skin. Such a groove is, however, very different from the typical, deep, and more or less rigid infolding found behind the second and third abdominal segments in the Pedipalpi (see Tarnani, '89, p. 377, fig. 1, and Lankester, '04, fig. 5b), nearly all arachnomorphous spiders, and in Liphistius. The longitudinal muscles are attached to shallow ectodermal depressions (see my paper, '09, fig. 36), which lie either free or in the larger transverse grooves mentioned above, and there are, so far as I know, no deep invaginations or ectodermal tendons (entapophyses) like those found in Pedipalps and arachnomorphous spiders. Can this and the absence of interpulmonary folds perhaps be a secondary condition in the Mygalomorphae? Or have these folds been acquired independently in the Pedipalpi, Liphistius, and Arachnomorphae?¹

¹ Two interesting drawings by R. I. Pocock are given by Ray Lankester ('04, figs. 56 and 64) showing the genital segments of a male Thelyphonus assamensis and a female Liphistius de-
Turning now to the Aranææ veræ or Arachnomorphæ, we find that in nearly every case the second pair of respiratory organs (and in one family the first pair as well) have been replaced by tracheæ, the exceptions being the small family Hypochilidæ with two pairs of lung-books and the Pholcidae, in which there are no other respiratory organs besides the single pair of lung-books of the genital segment. Moreover, there is a deep infolding along the hind edge of each of the respiratory segments between the spiracles, so as to hide from view the genital opening and the external openings of the well-developed ectodermal tendons or entapophyses of the ventral longitudinal muscles. There are a

suitor, with the epigastric fold drawn apart so as to expose the genital opening and the edges of the septa of the lung-books. These two figures are remarkable for showing that in these two Arachnidae the pulmonary saccules of the genital segment open directly into the cleft of the epigastric fold, being, in fact, attached to the anterior wall of the fold. I examined a female of Thelyphonus caudatus, and found the conditions exactly as depicted by Pocock. The pulmonary ante-chamber opens along its entire medial side into the median part of the epigastric fold, and cannot, therefore, be said to form a separate chamber, except in its dorso-lateral prolongation or portion containing the youngest saccules. In the male (i.e. specimens with a spine on the second abdominal sternite, testa Kraepelin) of this species, however, I found the conditions different. Here there is a longitudinal fold of integument on each side between the deep median part of the epigastric fold and the anterior pulmonary chambers, so that the latter may be said to form separate chambers opening by the ventral slit only into the epigastric fold, as is usual in dipneumonous spiders. The condition depicted by Pocock in Liphistius is not known to occur in any dipneumonous spider, and may indicate that the epigastric fold of this form is directly connected with that of Thelyphonus and not of independent origin, in which case the absence of the fold in the Mygalomorphæ would be a secondary condition. Its presence in the four-lunged arachnomorphous family Hypochilidæ is also an interesting circumstance.

These two figures of Pocock's should have been included in the historical list of papers concerning the lung-books of Arachnids given at the end of my previous paper (609). They unfortunately did not come to my notice until after the paper had been sent to the press.
few rare exceptions—thus in the Dysderidæ the tracheal segment has no infolding and the genital duct sometimes opens free on the ventral surface of the pulmonary segment (male of Harpactes; see my paper :09, fig. 40).

Leaving the four-lunged Hypochilidæ, with which I am unacquainted, out of account, there appears in the first place a small group of three families (Dysderidæ, Oonopidæ, and Caponiidæ) which possess some very primitive features in connection with their respiratory segments. As these segments are of peculiar interest in connection with the phylogeny of the tracheæ, I shall give some account of their anatomy before proceeding to more general conclusions.

Material and Treatment.—The material used was the same as that given in my previous paper (:09) with the addition of specimens of a species ¹ of Oonopidæ from the neighbourhood of Cape Town.

For following the muscles, which are often very slender, suitable differential staining is very necessary, and for this purpose I found very old Delafield's hematoxylin (mine was thirteen years old) most excellent, even for old museum specimens. The sections are stained on the slide for four to five hours, placed in acidulated alcohol for three to four

¹ As this species is a new one, I append the following description:

Calculus n. g. Cephalothorax broadly ovate. Ocular area transverse, the eyes arranged as in Orchestina. Labium short and broad, as in Oonops. Coxæ of pedipalps parallel, their anterior ends widely separated and not converging.—C. bicolor n. sp. Pale yellowish, abdomen with a broad infuscate patch behind above, and narrowly blackened on each side of the spinnerets as well. Clypeus barely as wide as an anterior lateral eye. Anterior row of eyes, seen from above, almost straight, the median eyes large, a trifle longer than their distance from the anterior margin of cephalothorax; anterior lateral eyes the smallest of the six, distant about half their own width from the median eyes; posterior eyes forming a row which is only very slightly wider than the anterior row, their distance from the median eyes greater than their own width. Tibia and metatarsus of first leg with 0–2 spines near the middle below, tibia and especially the metatarsus of fourth leg more numerousy spined. Several females from the Cape Flats, near Princess and Zeekoe Vleis. Length 4 mm. Allied to Telchius, E. Sim.
minutes, washed with spirits, and then held inverted over a vessel containing a drop of ammonia in some water until the sections change colour. After this they should be mounted in balsam without delay. The nuclei become blue and the muscles reddish and easily distinguishable from other tissues.

In preparing the tracheae by the caustic potash method I obtained the best results for such highly complicated systems as those of Caponia by first allowing the object, after removal of a part of the dorsal integument, to remain in cold concentrated caustic potash for twelve hours or longer. If the solution be then gently heated and some water added the soft parts remaining will rapidly disappear without injury to the delicate tracheæ. These should be examined in water or weak alcohol, and not in glycerine or acetate of potash, since these latter cause the tubes to collapse and become distorted.

The Respiratory Segments of the Dysderidæ, Oonopidæ, and Caponiidæ.

These spiders more nearly resemble the Mygalomorphæ than they do the rest of the Arachnomorphæ in the anterior position and wide separation of the second pair of spiracles (text-fig. 3—5) and the more rudimentary condition of the ectodermal tendons (where present) of the second respiratory segment.

Further, the transverse epigastric fold, lying between the two anterior spiracles, although present, never encloses a spinous canal of communication connecting the lumens of the two anterior respiratory organs, while the Dysderidæ are unique amongst arachnomorphous spiders in having no inter-tracheal fold between the two posterior spiracles (text-fig. 3), a primitive character only met with elsewhere in the Mygalomorphæ (p. 524, text-fig. 2). Owing to the presence of tracheæ instead of lung-books in the ninth somite this segment is somewhat shortened, but in other respects the
extent of the abdominal segments in the three families much resembles that in the Mygalomorphæ.

Dysderidæ.—The lung-books in the Dysderidæ have few leaves. I counted about thirteen in Harpactes (in sections), but there are more in Dysdera and Segestria senoculata (Bertkau [72] records only ten to twelve for Segestria). The ante-chamber (pulm. a.) is strongly inclined forwards from the base at an angle of 40°—50°, and is evenly curved forwards in Harpactes (Pl. 28, fig. 5), but almost straight in Dysdera and Segestria (p. 530, text-fig. 7). It is spined on its posterior wall except quite inferiorly, where a muscle (text-fig. 7, No. 11) is attached.

TEXT-FIG. 3.—Abdomen of Dysdera sp., ad. ♂ (magn. 3).
TEXT-FIG. 4.—Abdomen of Calculus bicolor, ad. ♂ (magn. 10).
TEXT-FIG. 5.—Abdomen of Caponia spiralifera, ad. ♀ (magn. 3.)

sp′, sp″, Spiracles of the first and second respiratory segments.
7—10 denote the extent of the seventh to tenth somites.

The peculiarities of the epigastric fold have already been described (09).

The well-known tracheæ (p. 551, text-fig. 19) have been described by several authors (see Lamy [02, pp. 180—183] for some excellent figures of Dysdera and Segestria), and I have given a summary of their structure with some additional observations on the entapophyses and muscles connected with them (09).

In order to ascertain anatomically whether a trachea or a
part of one is homologous with a lung-book or with an entapophysis it is necessary first of all to identify the entapophyses of the great longitudinal muscles. These entapophyses, as I have shown for Attus and Agelena ('95 :09), arise in various abdominal segments as invaginations on the posterior side of the provisional appendages, while the invaginations which form, or correspond to, a pulmonary sac or ante-chamber always lie to the lateral side of the entapophyses. In the two segments bearing the spinners in Attus and Agelena the entapophyses are attached at the posterior, medial, basal corners of the anterior and posterior spinners. For the identification of the entapophyses anatomically a knowledge of the abdominal muscles connected with the respiratory segments is necessary, and I have given the two accompanying diagrams (text-figs. 6 and 7) to illustrate these muscles and their entochondrites in a typical Dysderid.

*List of the Entochondrites and Muscles in Text-figs. 6 and 7.*

1. Small entochondrite on the lateral side of the trachea and attached to the fold of the integument, *fd.* 2.
2. Entochondrite between the muscles 23 and 24, etc., but not attached to the integument.
3. Large entochondrite situated on the medial side of the pulmonary ante-chamber and attached to the epigastric fold.
4. Corresponding entochondrite of the tracheal segment, situated on the medial side of the trachea.

*Muscles.*

1 and 2. From the entochondrite *t.8* to upper and middle part of side of abdominal pedicel.
3. Longitudinal from the entochondrite *t.8* to the cephalothorax.
4. From the entochondrite *t.8* to ventral integument of pulmonary segment.
5. From upper part of side of abdominal pedicel to ventral integument of pulmonary segment. (1 and 5 are inserted together anteriorly.)

6. Dorso-ventral on side of abdominal pedicel. (2 and 6 are attached to the same ectodermal infolding on the medial side of 5.)

7. Oblique dorso-ventral from hinder end of the ectodermal tendon ec.t. to the ventral fold fid.1 of abdominal pedicel.

8. Oblique dorso-ventral from hinder end of the ectodermal tendon en.t. to the entochondrite t.

9. From the ectodermal tendon ec.t. to anterior integument of abdomen.

10. From the ectodermal tendon ec.t. to dorsal integument of abdomen.

11. From lateral part of posterior side of pulmonary ante-chamber in a postero-dorsal direction to the entochondrite t. (This muscle can widen the ante-chamber in Segestria.)

12. Longitudinal parietal along ventral integument of abdomen.

13. From the entochondrite t.9 to ventral integument of abdomen (some strands apparently continuous with 12.)

14. From the entochondrite t. to ventral integument of abdomen.

15. Longitudinal connecting the entochondrites t.8 and t.9.

16. From posterior side of entapophysis (ec.t.8) of pulmonary segment to anterior side of the integumental fold fid.2.

17. Subtransverse from the entochondrite t.9 in a medial direction to posterior side of base of epigastric fold.

18. Longitudinal from the entochondrite t.9 to the spinners, breaking up posteriorly into 19, 20, 21 and 22.

19. Three muscles from 18 (one large one to medial side of large posterior spinner and two smaller ones to small mesial spinner).

20. From 18 to posterior medial side of anterior spinner.

21. From 18 to medial side of same spinner.

22. From 18 to anterior side of same spinner.
23. Longitudinal connecting the entochondrites $t.$ and $t'.$
24. Longitudinal from the entochondrite $t'.$ to the spinners, dividing posteriorly into 25 and 26.
25. Two muscles from 24 to anterior lateral angle of large posterior spinner.
26. From 24 to posterior lateral angle of anterior spinner.
27. From the entochondrite $t'.$ to anterior lateral side of anterior spinner.
28. From the entochondrite $t.$ to anterior side of anterior spinner (inserted behind 22).
29. From posterior end of the cephalothoracic tracheal trunk cephal. tr. (inserted just below the origin of the short abdominal branch) to ventral integument of abdomen.
30. Subtransverse connecting the entochondrites $t.8$ and $t.$
31. Connecting the entochondrites $t.9$ and $t'.$

(Two other muscles of the female of Harpactes are given in Pl. 28, fig. 3).

The part of the epigastric fold (text-fig. 6, ec.t.8) to which the entochondrite $t.8$ is attached, plainly corresponds to the entapophysis of the pulmonary segment in other dipneumonous spiders (see my paper 09, fig. 41, ec.t.8), but the identity of the corresponding entapophysis of the tracheal segment is not at first sight so evident, since there are two entochondrites, one on each side of the trachea, and two sets of longitudinal muscles, both connected with the entochondrite $t.8$. In fact, the whole muscular system of the ninth and tenth somites is very different to that of Attus, Ageleena, Epeira, etc., which is, of course, due to the circumstance that in the latter the relative lengths of the two somites are exactly reversed. From the fact that the muscles 19—21 of the medial set in Segestria (text-fig. 6) are connected with the medial and postero-medial sides of the anterior and posterior spinners, while the muscles 25—27 of the lateral set (text-fig. 7) are connected with the lateral side of the same spinners, it is evident that the entochondrite $t.9$ is the one which in the tracheal segment corresponds to the entochondrite $t.8$ of the pulmonary segment. The
entochondrite t.9 is attached (in Segestria at least) to a small lobe of the medial side of the tracheal pedicel. This lobe (the entapophysis of the tracheal segment), which I have already described and figured (:09, figs. 32 and 33, ec.t.9), is not really a part of the trachea proper, being merely connected with the base of the pedicel and unspined internally, and I am not even sure that it is present in Dysderera or Harpactes, in which genera the entochondrite may possibly be attached directly to the integument at the medial basal angle of the tracheal pedicel. From the position of the trachea on the lateral side of the entochondrite t.9, it is evident that the whole of the trachea must be considered as homologous with a pulmonary sac or lung-book, as I have already pointed out ('95) and Lamy also agrees with this view by reason of the position and appearance of the tracheæ and the complete separation of the spiracles (:02, p. 259).

Oonopidae.—This family is very closely allied to the Dysderidæ as was pointed out by Bertkau ('78), who included Oonops in the latter. The only anatomical difference of any importance connected with the respiratory segments appears to be the presence of an intertracheal fold observed by Lamy (:02), joining the two tracheæ in the Oonopidae.

I found the muscular system connected with these segments to be practically identical in the two families, all the characteristic muscles of the Dysderidæ being present in the Oonopid, Calculus bicolor, examined by me, although sometimes in a somewhat modified form.¹ Thus the muscle 29 (text-fig. 7) is much shorter and 15 (text-fig. 6) somewhat longer in the Oonopid, as the posterior tracheæ are here placed further back. The lateral entochondrite t. is particularly conspicuous, much more so than in Segestria.

The tracheal trunks are quite similar in both families. Those of Oonops were first described by Bertkau ('78) and later in greater detail by Lamy (:02), who also examined a

¹ Three additional muscles not noticed in Segestria are given in figs. 1 and 2, but two of these (m. 38 and 40) are also found in the female of Harpactes (fig. 3).
Dysderina. Neither of these authors, however, observed the anterior ending of the cephalothoracic trunks, but quite correctly supposed them to end, as in the Dysderidae, in a bundle of tubules. In Calculus bicolor these trunks are short and very much as in text-fig. 6. They do not enter the abdominal pedicel, but break up at the anterior end into a dense cluster of fine tubules, which then pass through the pedicel into the cephalothorax. The short posterior branch, first found in this family by Lamy, is also present, and corresponds exactly to the similar branch in the Dysderidae. The anastomosing ends of the internal spines form a simple network, like that in Harpactes, but in the forms examined by Bertkau and Lamy they are said to form a spiral thread. The cavities of the two tracheal trunks are directly connected by a spinous canal of communication (fig. 1, can.), enclosed within the intertracheal fold (tr. fd.). As in the Dysderidae, the tracheal trunks and their branches are to be considered as entirely homologous with lung-books.

Another important point of resemblance to the Dysderidae is the presence in the female of a single median receptaculum seminis, pointed out by Bertkau (78), who observed that such a receptaculum is not found in any other family of spiders besides these two (p. 374). In Calculus bicolor the receptaculum forms an elongate, narrow, curved, median pouch (fig. 2, r. s.), placed horizontally with the concavity of the curvature upwards, and opening into the anterior wall of the epigastric fold (ep. fd.). From the under side of the pouch a large vertical keel (k.) hangs downwards, reaching to the body hypodermis. Each side of this keel serves for the attachment of a powerful muscle (m. 38), which runs obliquely backwards and outwards to the anterior surface of the entapophysis of the epigastric fold (fig. 1). There is also a median muscle (m. 40) running from the under side of the pouch along the posterior edge of the keel to the ventral body integument. In Harpactes Hombergi I found a very similar receptaculum, provided with a similar remark-
able keel and pair of muscles (fig. 3). Bertkau ('78) pointed out the similarity between Oonops and Harpactes as regards their female sexual organs (p. 371), but he does not describe or figure the keel and muscles ('78, pl. xii, fig. 8). In Segestria and Dysdera the receptaculum seems to be differently formed. (See Bertkau, '75, pl. vii, fig. 12, and '78, pl. xii, fig. 6.)

The lung-book in the Oonopid which I examined has nearly twenty leaves. Its ante-chamber differs from that of the Dysderidae and has the normal shape found in many other dipneumonous spiders, that is to say, it rises vertically from its pedicel but soon curves gradually forwards to form a long "horn," which is nearly horizontal in its anterior part. The ante-chamber is densely spined on its posterior wall, except along its lateral edge inferiorly, where a small muscle (corresponding to No. 11 in text-fig. 7, p. 530) is attached.

There is a distinct and deep epigastric (interpulmonary) fold, which ends laterally just behind the medial ends of the pulmonary spiracles, but is not continuous with them. There is, therefore, no canal of communication between the lung-books and no part of the fold is lined with spines (see fig. 2). As in Dysdera and Segestria, the portion of the fold between the entochondrites is much deeper than the portions which lie laterally to these. The lateral corners of this deepened part of the fold form the entapophyses to which the entochondrites (fig. 1, t. 8) of the ventral longitudinal muscles are attached. These entapophyses are somewhat unusual in form, their deeper part forming a solid, darkly staining plate (fig. 1, ec. t. 8), the anterior face of which serves for the attachment of the obliquely transverse muscle (m. 38) connected with the keel of the receptaculum seminis, while the entochondrite (t. 8) is attached to the upper lateral edge of the plate.

Caponiidae.—This small but very interesting family bears some external resemblance to the Dysderidae and Oonopidae but it differs from these and, so far as I know, from all other spiders as well, in four unique and remarkable anato-
mical characters connected with the respiratory segments. These are (1) the presence of an anterior pair of tracheae in place of the lung-books (apneumonous spiders), (2) the presence of a peculiar sense-organ within the second pair of tracheae, (3) the absence of the segments (corresponding to 15 and 18, text-fig. 6) of the great, ventral, longitudinal muscles, so conspicuous in other spiders, belonging to somites 9 and 10 and of the entochondrites connected with them, and (4) the replacement in the female of the usual receptacula seminis of the epigastric fold by a pair of great chamber-like dilations of the oviducts in the upper anterior part of the abdomen.

The tracheae of Caponia and Nops have been very well described and figured in Simon ('93, pp. 326 and 327, figs. 294 and 295) from drawings made by Bertkau (also reproduced by Lamy [:02, p. 184, figs. 24 and 25]). The following description was made from a number of sections and other preparations of Caponia spiralifera, Purc., specimens of which were collected for me at Hanover, Cape Colony, and well preserved in spirits by my friend, Mr. S. C. Cronwright Schreiner.

The anterior pair of tracheae (p. 545, text-fig. 17, and fig. 9, u.tr.) are situated in precisely the same place which is occupied by the lung-books in dipneumonous spiders, and they are evidently merely a pair of lung-books of which the saccules have been metamorphosed into branched tracheal tubules. Fig. 10 shows one of these tracheae, prepared in caustic potash and seen from the medial side. Figs. 11 and 12 are from sagittal sections.

The spineless, thick-walled pedicel (fig. 11, ped.), which is continuous with the adjacent epigastric fold and much resembles it in sagittal sections, leads from the spiracle (sp') into an ante-chamber (tr.a.). The latter is shaped much like that of the lung-book of a Dysderid, being strongly inclined forwards and slightly outwards, broadest near the base and tapering towards the higher anterior end or apex (figs. 10 and 12). It is, however, somewhat more capacious, owing to the
greater elongation of its ventral side. Internally the ante-
chamber is lined with anastomosing spines (spi.), except laterally near the base of the upper (posterior) wall, where there is a fold (fd.) to which a short muscle (No. 11 in text-
fig. 17, p. 545) is attached, exactly as in the Dysderidae. Nearly all the tracheal tubules, except a medial group of four, spring from the ascending anterior side of the ante-
chamber and run forwards. They occupy exactly the position of the saccules of a lung-book (c.f. text-figs. 7 and 17) from which they are plainly derived. In fact, if the 13 or 14 saccules of the lung-book of a Harpactes (fig. 5) were each divided longitudinally into several tubules, we should have the condition found in Caponia. To illustrate this, as well as the arrangement and origin of the tubules on the anterior wall of the ante-chamber, I have given a series of consecutive transverse sections (text-figs. 8—15), of which text-fig. 8 through the ante-chamber represents the most posterior of the eight. It will be observed that the tubes are frequently
somewhat flattened dorso-ventrally at their origin, only to divide into a couple or more cylindrical tubes in the next section, e.g. the lowest tube in text-fig. 9. The tracheal tubes are not long, being only about three or four times the length of the ante-chamber, and they do not enter the abdominal pedicel. All, or nearly all, are several times branched, the branches becoming slenderer towards the apex where they frequently end in a short fork (fig. 10). They are either cylindrical or compressed, being then mostly flattened dorso-ventrally, like the saccules of lung-books, and are lined internally, except quite at the base, with a fine, probably spiral, thickening of the cuticle, just like the tracheal tubules of the Dysderidae, etc. The bi-nucleate columns of the original saccules have, of course, disappeared. The anastomosing spines of the ante-chamber enter the bases of the tubes for a short distance and the free edges of the tubes bordering on the cavity of the ante-chamber have very much the appearance of those of pulmonary saccules in sagittal sections (cf. fig. 5 of the lung-book of Harpactes with figs. 11 and 12 of the tracheæ of Caponia). In a young specimen examined the tubules were much fewer than in any of the adult specimens, hence it is evident that they increase in number with the growth of the spider.

In addition to the above there is a small group of tubules which start from a slightly projecting portion of the ante-chamber at its base on the medial side. This group is composed of a bunch of four tubules, which may, however, subdivide into several more. They take at first a transverse medial direction and then bend and run some distance backwards on the lateral side of the second pair of tracheæ (fig. 9, med. tub.). This group of tubules has no equivalent in the lung-book of the Dysderidae and is to be looked upon as a new formation. They may, perhaps, be the posterior group of six tubules represented in one of Bertkau’s figures (Simon, fig. 294, or Lamy, fig. 25).

The second pair of tracheæ of Caponia forms perhaps the most complete and extensive tracheal system known
in any spider. It furnishes the abdomen, cephalothorax and appendages with a very great number of fine air-tubes, but only a portion of these are represented in fig. 9 in which the terminal parts of the numerous branching tubules, often measuring only $3 \mu$ in diameter, have not been drawn in.

The pedicel of the posterior trachea opens into a capacious tracheal trunk (p. 545, text-fig. 16, c.tr.) lined with spines, which runs forwards at an inclination of about $45^\circ$ for a very short distance only before dividing into two sub-cylindrical branches of equal length and thickness, which may be called the cephalothoracic trunks (fig. 9, ceph. tr.), and run horizontally forwards into the cephalothorax, becoming thinner anteriorly. They remain in contact one above the other but the upper one a little more to the lateral side, and are somewhat flattened along the place of contact. Soon after passing through the pedicel of the abdomen they each break up into a bunch of fine tubules which then spread in various directions. Those of the right upper trunk are drawn in fig. 9, from which it will be seen that most of the tubules of the right trunk cross over to the left side and, generally remaining unbranched, enter the coxae of the left appendages, whereas only the posterior appendages of the right side receive tubules from this trunk. Several of the tubules give off dendritic branches (d.br.), which ramify within the cephalothorax and supply its upper part with air. While the inferior cephalothoracic trunks remain unbranched except at apex, the two upper ones each give off a small branch (fig. 9, br.) from the upper side near the middle. This branch is arborescent in form and divides into a number of tubules which supply the region above the anterior pair of tracheae.

In addition to the two anterior trunks each of the short main trunks also gives off from its posterior side at base a cylindrical posterior trunk of half the diameter of either of the anterior ones. This trunk, which may be called the abdominal trunk, runs first in an upward and medial direction, and then curves and runs horizontally towards the
posterior part of the body. It is of a pronounced arborescent form, but only its larger branches are provided with spines.

The spines which line the various trunks within are arranged in longitudinal rows (fig. 4, *spi*'), and are connected at apex by transverse threads (*thr.*), which, however, also anastomose with adjacent threads, the whole arrangement being very much as in Dysdera (see Lamy 182, pp. 180 and 181, figs. 20 and 21). The larger tracheal branches in the abdomen have similar spines, but the finer branches or tubules in the abdomen and all the tubules in the cephalothorax have the transverse threads only, but no spines.

Each of the short main trunks (text-fig. 16, c. *tr.*) is also produced laterally, together with the pedicel and spiracle, beyond the points of origin of the three principal branch trunks to form a small but very curious, lateral pocket (fig. 9, l. *p.*), indicated by Bertkau in his two figures. This pocket is divided into a higher posterior and a lower anterior compartment, each compressed from before and behind. The posterior compartment (fig. 8, p. *c.*) is provided with anastomosing spines, directly continuous with those of the main trunk, along its upper and medial edges only (*spi.*), the rest of its surface being spineless but much crumpled. It gives off three small branches, viz. one from the upper edge in an antero-lateral direction, and one each from the upper lateral and medial angles. These soon subdivide and end in fine tubules; they are shown in fig. 9, and have also been indicated in Bertkau's figures.

The anterior compartment (figs. 6—8, a. *c.*) of the lateral pocket is lined with anastomosing spines on its anterior side (fig. 8, *spi*'), but the upper part of this side and that of the posterior side is furnished with short sharp spines, the rest of the posterior surface being spineless but much crumpled. From the upper edge of the compartment two (in the male) or three (in the female) peculiar stout rods or processes (*rd.*) of the cuticula project downwards into the lumen of the compartment, each being armed at the base with some
minute, sharp, conical spines, and with some longer ones towards the apex.

The hypodermis of the upper and posterior sides of the anterior compartment, and especially that of the anterior side of the posterior compartment, is much thicker than elsewhere, and its cuticula has a corrugated appearance in sagittal sections, and stains more deeply than the adjacent cuticula does (fig. 8). Plainly the whole of this structure has some function other than respiratory. The hypodermis bearing the three rods is connected at base by means of a strand with some cells or fibrous tissue, which may be a nerve (fig. 8, n). As, however, the specimens were not especially preserved for histological purposes, it is impossible to say anything definite about the character of these structures, except that the rods certainly strongly resemble sense organs.

There are well-developed, transverse, intertracheal folds of the integument connecting the spiracles of each pair and already indicated by Bertkau in his figures. That of the posterior pair (fig. 9, tr fd.) encloses a spinous canal of communication (p. 545, text-fig. 16, can.), which connects the lumens of the short main trunks (c.tr.) with one another. In the anterior segment there is no spinous canal of communication, although the lateral parts of the fold are directly continuous with the pedicels of the anterior pair of tracheae.

The well-developed anterior (epigastric) fold (text-figs. 16 and 18, ep fd.) is strongly inclined forwards or even horizontal, especially throughout the median half, where the genital duct opens into its anterior wall. Each lateral fourth of the fold, lying (in the female) between the opening of the genital duct and the tracheal pedicels, appears twice bent (text-fig. 18), first upwards or slightly backwards, and then more sharply forwards and downwards, the whole of the anterior deflected portion (l.) serving for the attachment of a broad and powerful muscle (No. 4 in text-figs. 16 and 18). Near to the trachea the upper part of the fold is somewhat inflated, and produced upwards to form a conspicuous enta-
pophysis (text-fig. 16 and fig. 8, ec.t. 8) for the attachment of the muscles 1—3. The hollow entapophysis of Caponia much resembles the solid one of the Oonopidæ (fig. 1), and muscle No. 4 in the former corresponds exactly as regards its place of attachment to the muscle 38 in the latter, although not homologous with it.

The muscular system of the abdomen of Caponia is in some respects very peculiar. That connected with the respiratory segments (with the exception of the muscles of the oviducts) is given in text-figs. 16—18 and explained in the following list:

**List of the Muscles in Text-figs. 16—18.**

1. From the entapophysis ec.t. 8 to upper and middle part of side of abdominal pedicel.
2. Longitudinal from the entapophysis ec.t. 8 to the cephalothorax.
3. From lower lobe of the entapophysis ec.t. 8 to ventral integument of anterior respiratory segment.
4. From upper part of side of abdominal pedicel to ventral integument of anterior respiratory segment. (1 and 5 are inserted together anteriorly.)
5. Dorso-ventral on side of pedicel. (2 and 6 are attached to the same ectodermal infolding on the medial side of 5.)
6. Oblique dorso-ventral from hinder end of the ectodermal tendon ec.t. to the ventral fold fd. 1 of abdominal pedicel.
7. Oblique dorso-ventral from hinder end of the ectodermal tendon ec.t. to the integumental fold fd. 2 on lateral side of posterior spiracles.
8. From the ectodermal tendon ec.t. to anterior integument of abdomen.
9. Two muscles from the ectodermal tendon ec.t. to dorsal integument of abdomen.
10. Short muscle from lateral part of posterior (upper) wall

1 Throughout this paper homologous muscles are indicated by the same numbers.
of anterior tracheal ante-chamber in a dorso-lateral direction to the body integument on the lateral side.

12. Longitudinal parietal along ventral integument of abdomen.

13. From posterior intertracheal fold to integument of abdomen (many or most of the strands continuous with 12).

23a. Longitudinal from x to the spinners, running along side of the abdominal tracheal trunk for the greater part of its course and dividing posteriorly into several muscles, the lowest of which is attached to the lateral or middle part of the anterior side of the mesial anterior spinner (thus apparently corresponding to 27 or 28 in Segestria).

30. From the apex of the entapophysis ec.t. 8 in a dorso lateral direction to integument of abdomen on lateral side of anterior spiracles (inserted immediately behind 11).

30a. Longitudinal from the apex of the entapophysis ec.t. 8 to x. (See also Pl. 28, fig. 8, m. 30 a.)

32. From x to posterior side of posterior intertracheal fold (inserted at extreme medial end of the spiracle).

33. From x in an antero-dorsal direction to the oviduct, meeting the latter at the point where the muscle ends in the figure. (The muscles 23a, 30a, 32, and 33 are continuous with each other at x on the lateral side of the abdominal tracheal trunk.)

34. Oblique from medial and posterior side of the common basal part (c.tr.) of tracheal trunk to anterior intertracheal fold (inserted on medial side of the entapophysis ec.t. 8).

35. From upper edge of posterior intertracheal fold to base of anterior intertracheal fold (many strands apparently continuous with 13).

36. Subtransverse from posterior medial edge of anterior tracheal pedicel (in a transverse line with the cross x in text-fig. 17) to between the upper and lower cephalothoracic trunks of the posterior trachea. (See also fig. 8, m. 36.)

37. From the spineless, basal, posterior part of the second trachea and its lateral pocket in a dorso-lateral direction to the integument on the lateral side of the second spiracle
The most remarkable features of this muscular system are the complete absence of all entochondrites, and as well as of those segments of the great, ventral, longitudinal muscles which belong to the second respiratory and the anterior spinner segments (somites 9 and 10).

The muscles 1—10 are identical in the Dysderidae and Caponiidae, 1—4, however, being attached in the latter directly to the anterior side of the entapophysis (ect. 8) without the interposition of an entochondrite. No. 4 is a very broad and powerful muscle, being attached, as already explained, to the whole anterior side of the lateral deflected lobe (l.) of the epigastric fold, and is represented in the Dysderidae by several feeble strands only. The muscles 1—3 are attached in Caponia to the prominent lateral entapophysis (ect. 8), which is, therefore, plainly homologous with the entapophysis of the pulmonary segment of the Dysderidae (p. 530, text-fig. 6, ect. 8) and other dipneu- monous spiders. It may be noticed that in Caponia this entapophysis has completely taken the place of the entochondrite (t. 8) of the Dysderidae, its anterior surface being correspondingly expanded to take the four large muscles.

The three muscles, 8, 11, and 30, which in the Dysde- ridae are attached to the enchondrite t. (p. 530, text-fig. 7), are also represented in Caponia, only here the lateral ends of these muscles are attached separately to the body integument, and are more dispersed (although still quite close together) owing to the absence of the entochondrite, and 11 runs parallel to the transverse plane, while in Segestria its fibres lie in sagittal planes.

The parietal muscle 12 is a part of the abdominal muscular sac which lies immediately within the outer hypodermis and envelops the intestines. The ventral strands of the sac are here longitudinal, and form a continuous layer from side to side, where they are again continuous with the lateral walls of the sac. Anteriorly the ventral strands of the sac ascend
(No. 13) to the upper edge of the posterior intertracheal fold along its whole extent, but the descending strands (No. 35) on the anterior side of this fold are only met with in the lateral part, being absent from the median part of the fold. A similar parietal muscle is met with in the Dysderidæ and Oonopidæ, differing only in so far that the lateral ascending strands (No. 13, p. 530, text-fig. 6) are attached to the large entochondrite (t. 9) of the tracheal segment.¹

I could find no trace of the usual medial longitudinal muscles corresponding to 15 and 18 in the Dysderidæ, and connecting the anterior entapophysis (ect. 8) with the spinners on the medial side of the tracheæ. In fact, the only muscle connecting the respiratory segments with the spinners, and lying inside of the abdominal muscular sac, is the slender muscle 23α, which, however, lies on the lateral side of the trachea, and is, I think, probably homologous with muscle 23 of the Dysderidæ. This little muscle in Caponia divides posteriorly into at least two muscles and the most ventral of these branches,² corresponding to 27 or 28 of Segestria, is attached to the lateral (3) or middle (?) part of the anterior side of the mesial anterior spinners, which I take to represent the anterior pair of the Dysderidæ. Anteriorly 23α unites with three other small muscles, 30α, 32, and 33, at a point x at the base of the lateral side of the abdominal tracheal trunk (abd.tr.). The four muscles are here in contact with the trachea, and their fibres intermingle without forming an entochondrite. One of them, 30α, passes on to the apex of the entapophysis (ect. 8), and

¹ The abdominal muscular sac in other spiders has been described by various authors, particularly by Causard (96, pp. 22–24, pl. iii, figs. 1 and 2), and more recently by Lamy (02, p. 158, pl. vii). Of the muscular nature of its fibres there can be no doubt whatever, as the typical transverse striations may be frequently observed in the Caponiidae, the Dysderidæ, and other forms.

² I could not make out where the posterior ends of the dorsal branch or branches were attached.
may possibly represent a strand which became separated from 30 when the lateral entochondrite (p. 530, text-fig. 7, t.) disappeared.

From a comparison with the Dysderidæ it is evident that the tracheae of the second respiratory segment in Caponia correspond to those of the Dysderidæ, and, like the latter, are to be considered as entirely homologous with lung-books, for there is no evidence that entapophyses took any part in their formation.

The receptacula seminis are paired, and consist of an enormous dilation of each oviduct apparently at the point where the ectodermal and mesodermal elements of the duct meet. They are placed nearer the upper part of the abdomen just above the area enclosed between the four spiracles, but extend for some distance to the front and behind this area as well. The ventral wall of each dilation has a cuticular lining, but the dorsal wall and the greater part of the side walls have none. Apparently the latter represent the mesodermal part of the oviduct and the former the ectodermal part. The ventral wall with its cuticula is continuous with the basal portions of the oviducts, which open into the lateral ends of the unpaired median portion of the duct. This latter again opens into the epigastric fold along a wide cleft occupying about one half of the distance between the two anterior tracheae. The spacious lumen of each receptaculum contains coagulated stainable matter and numerous spermatophors. This form of receptacula is apparently quite unique amongst spiders, the usual ones which open directly into the epigastric fold, and are evidently invaginations of the body integument, being quite absent in Caponia.

**General Conclusions.**

A tracheal system may be imagined to have been evolved out of a lung-book in either of the following ways:

1. The pulmonary saccules may have been converted into
more or less cylindrical tubes (say, by longitudinal division), accompanied by the disappearance of the bicellular columns of the septa. The trachea thus produced would be composed of an ante-chamber formed out of the pulmonary ante-chamber, with a bunch of tubules on its anterior surface, formed out of metamorphosed pulmonary saccules. This metamorphosis does not involve a reduction in the effectiveness of the respiratory organ, and I imagine the trachea so produced to be in no way inferior, but rather superior, to the lung-book. Accordingly it would doubtless increase in size and take over the main respiratory functions, and this would be accompanied, in the case of the second respiratory segment, by a corresponding reduction in the number of the leaves of the anterior lung-books, in accordance with Lamy's law of the inverse correlation between the size of the tracheae and the number of the lung-leaves.

(2) The saccules may have disappeared, leaving only the pulmonary sac or ante-chamber, which would then constitute a trachea, and may subsequently elongate or even acquire secondary branches. These latter, however, would not be homologous with pulmonary saccules. This method of origin really consists in a reduction in the effectiveness of the respiratory organ of the somite, and would be accompanied, in the case of the second respiratory segment, by a corresponding increase in the number of the leaves of the anterior lung-books, which would then become the principal organ of respiration. This, then, would be exactly the opposite process to that which would have taken place in the first case.

It appears to me very probable that both these methods of origin have actually occurred in the Araneæ, the first method being applicable to the Dysderidae and their allies, and the second to the rest of the tracheate spiders. It will be convenient to take these two sections of spiders in turn.

(1) The Dysderidae, Oonopidae, and Caponiidae, being those forms with the tracheal spiracles far apart and not moved backwards, i.e. still nearly in their primitive positions.—If, after the metamor-
phosis of the saccules into the tubules in the case of the first of the two methods given above, we further imagined the ventral part of the ante-chamber to lengthen slightly, we should have almost exactly the condition found in the anterior pair of tracheae of Caponia, which differs from this ideal case only in two minor points, viz. in the presence of transverse or spiral thickenings in the tubules instead of small spines, and of a medial group of tubules at the base of the ante-chamber. In fact, as I have shown above, the anterior pair of tracheae of Caponia may be taken to represent the most primitive form of metamorphosed lung-books known in which the saccules still persist as tubules.


The second pair of tracheae in Caponia, being wholly homologous with lung-books, plainly belong to the same type as the tracheae of the Dysderidae and Oonopidae, and are merely somewhat more complicated by the duplication of each of the cephalothoracic trunks and the elongation of the abdominal branch of the latter. The simplest form of this type, such as that found in Harpactes (text-fig. 19) and in Calculus (in both of which the anastomosing spines of the trunks still form a simple network and do not bear a spiral thread or inner perforated tube), may be easily derived from the anterior tracheae of Caponia by merely exaggerating the tubular elongation of the ante-chamber, already commenced.
in the anterior tracheae, and by the addition of the short posterior branch in place of the medial basal group of tubules. In such case the bunch of tubules at the anterior end of the cephalothoracic trunks (ceph.tr.) would represent metamorphosed pulmonary saccules, but those of the posterior abdominal branch (abd.tr.) would be, of course, new formations.

In a previous paper (909) I had already indicated the possibility of the anterior bunch of tubules being derived from saccules, but after studying the tracheae of Caponia more thoroughly, I am now much more strongly inclined to believe that such has actually been their origin. A study of the embryology would, however, be necessary to settle this interesting point.

If, as I have assumed, the posterior pair of tracheae in Caponia and those in the Dysderidæ had a common origin, it follows that the anterior pair of tracheae in the former must have developed later and independently of the posterior pair, and that, therefore, tracheæ must have originated from lung-books at least twice in the Araneæ. The same conclusion would follow even if we assumed that both pairs of tracheæ in Caponia originated at the same time and not as separate metamorphoses, for in that case both pairs of tracheæ must have originated independently of those of other tracheate spiders, since these latter still possess the anterior pair of lung-books.

The morphology of the respiratory segments bears out the view that the three families discussed above are intermediate in position between the mygalomorphous spiders and the rest of the arachnomorphous forms. This view was demonstrated by Bertkau (78) a good while ago for the Dysderidæ and the Oonopidæ, and this author even went so far as to include these families with the mygalomorphous forms in a common group, the Tetrasticta (i.e. with four stigmata). No doubt these two families are the most primitive of the three, but the Caponiidæ may be considered as an allied but in several respects a very aberrant type, standing apart from the other two families.
(2) Forms with the tracheal spiracles approximated and moved more or less toward the hinder end of the body.—All the remaining tracheate spiders come under this heading,¹ and may be considered in two groups, viz. group A, those in which the entapophyses of the tracheal system are non-respiratory (Filistatidæ, Sicariidæ, and Palpimanidæ), and, group B, those in which these entapophyses have been transformed into tracheæ (including all the remaining families).

A very simple and interesting type of tracheæ of the first group is that of Filistata (text-fig. 20), which is known to us from Lamy’s description.

The simplest and most usual type of the second group, a

¹ In some cases, e.g. Argyroneta, the common tracheal spiracle appears to have secondarily moved forward again.
type found, according to Lamy, in about half of the total number of genera examined, consists of four simple tracheal trunks united at base, as in text-fig. 21. It is known from the embryology that the lateral trunks of this type were derived from the pulmonary sac or ante-chamber of a lung-book, and are, therefore, homologous with the lateral trunks in Filistata,—while the medial trunks represent metamorphosed entapophyses (ectodermal tendons of muscles), and are, as Lamy (p. 172) has pointed out, homologous with
the medial trunks of Filistata, which this author has shown to be entapophyses.

In both groups more complicated types than the two simple ones just described are frequently found, and it is important to notice that this complication takes place along different lines in each group. Thus in group A some Sicariidae and Palpimanidae were found by Lamy (p. 176, fig. 15, and p. 188, fig. 30) to possess branched tracheae, the branching being confined to the lateral or tracheal trunks. In group B, on the other hand, in all cases where the lateral and medial trunks can be identified from Lamy's figures and show different degrees of development, it is invariably the medial trunks which show the greatest complexity and the highest degree of development as respiratory organs. This rule appears to me to furnish the key to the phylogeny of the trachea in these spiders. We may also fairly deduce from it that the medial tracheae must be more efficient as respiratory organs than the lateral tracheae are, and the reason for this, as I have already pointed out (69), may be their position in the large ventral sinus containing venous

1 This is self-evident from Lamy's excellent figures in many cases e.g. Cecobiidae (Lamy, p. 170, fig. 10), Argiopidae (pp. 197—199, figs. 38—42), Thomisidae (pp. 206 and 207, figs. 49 and 50), and Agelenidae (pp. 214—216, figs. 59—61). In arborescent types of tracheae (see my paper 69) it is not so self-evident, but the same conclusion may be deduced from the great similarity which this form of tracheae shows to that of the Attidae, of which the identity of the parts is known from the embryology. There remain, however, certain Dictynidae and Agelenidae, the homology of whose tracheae cannot be ascertained with any degree of certainty from Lamy's figures. In Argyroneta I found (69), from the position of the muscles and entochondrites, that the entire trachea appears to have been derived from the medial trunks, but I have had no opportunity of examining any of the other forms, viz. Dictyna (Lamy, p. 169, fig. 8), Antista (p. 213, fig. 57), Cybaeus (p. 217, fig. 62), and Chorizomma (p. 219, fig. 64). If these, too, could be proved to follow the rule given above, the arguments in the following pages would be greatly strengthened. I may add here that in the marine Agelenid, Desis tubicola, Poc., the tracheae, which have not been hitherto described, closely resemble those of Attus.
blood. This greater efficiency would account for the higher degree of development of the medial trunks in many forms.

Now out of the twenty-four families in which the medial entapophyses have been converted into tracheae, twenty-two, according to Lamy's investigations, possess tracheal systems consisting of four simple tubes (p. 554, text-fig. 21) in some of their genera at least, while eight of these families possess both this simple type and more complicated types as well. In fact, only two very small families (Ecoibiidae and Prodidomidae) have the more complicated type only. And since the type with branched medial trunks must have been derived from the type with simple trunks, as the medial ones were originally simple entapophyses, we may fairly conclude that the common type with four simple tubes is the primitive one for the entire group, and that the more complicated types must have been developed from the simpler types within each family separately and independently of similar complicated types in other families. This statement is in agreement with Lamy's view referred to in the introduction, except that this author does not consider any particular type as more primitive than another.

Again, it is evident that the type of trachea in which the entapophyses are not respiratory must be considered as more primitive than those in which they are respiratory, since the more efficient medial tracheal trunks would not be likely to revert to their original function after once being metamorphosed. Hence the tracheae of the Filistatidae, Sicariidae, and Palpimanidae must be looked upon as more primitive than those of group B with metamorphosed medial trunks, and it seems to me very probable that the tracheae of the latter group were originally derived from some such form as that found in Filistata (p. 553, text-fig. 20). In this spider the tracheae are placed, according to Lamy (p. 172, fig. 11), about midway between the spinners and the interpulmonary fold. The anterior end of each of the tracheal entapophyses is situated near this fold, and consequently the segments of the longitudinal muscles between the entocho-
drites of the pulmonary and tracheal segments are doubtless quite short. If now the tracheal spiracle moved to the hinder end of the body and the entapophyses elongated correspondingly and became converted into a trachea we should get the type represented in text-fig. 21 (p. 554), which I consider to be the primitive type of all forms with metamorphosed entapophyses. The anterior ends of the entapophyses would still be near the interpulmonary fold, and the connecting muscular segment would still be quite short, as it always is in the spiders of group B.

In Scytodes and Palpimanus the spiracle has moved to the hinder part of the body without any additional lengthening of the entapophysis. Hence in these two forms the segments of the longitudinal muscles belonging to the tracheal somite are greatly elongated, and in this respect these forms (and allied genera) are apparently unique.

The Pholcidae, which Bertkau found to have no trachea at all, were perhaps derived from some form with a type of trachea similar to that of Filistata, since according to Lamy's investigations a pair of entapophyses persists in some Pholcidae in the same position in which those of Filistata are found (502, pp. 191 and 192, figs. 32 and 33). The Pholcidae, therefore, should perhaps belong, as regards the structure of their ninth somite (the tracheal segment in other spiders), to the same group as the Filistatidae, Sicariidae, and Palpimanidae.

In a previous paragraph two possible solutions were suggested for the derivation of a tracheal system from lung-books, one of which appeared particularly applicable to the tracheal system of the Dysderidae, etc. Now the second method suggested, which consists in the reduction of the respiratory functions of the lung-books by the abortion of the saccules, appears to me to exactly meet the conditions found in the spiders with four simple tracheal trunks (or with two tracheal trunks and two entapophyses), in which the lung-books have numerous leaves, and obviously play the most important part in the respiration. The size of the
lung-books in Filistata is not known, but judging from Lamy's figure (p. 172, fig. 11) they appear here, too, to be very large to compensate for the feeble development of the tracheae. This relatively greater size of the anterior lung-books is exactly what I have explained should take place if the posterior lung-books became reduced to their ante-chambers only.

If we imagined a tetrapneumonous spider with both pairs of lung-books connected by interpulmonary folds (the arachnomorphous spider Hypochilus appears to be such a form), and the entapophyses prominently developed in the second respiratory segment, as well as in the first, it would be perfectly simple to derive from it a form with tracheae exactly resembling those of Filistata. All that would be necessary would be that the saccules of the second pair of lung-books should disappear, leaving the two ante-chambers only; and that the two spiracles should come a little nearer together so as to form practically one opening with the intertracheal fold. It appears to me very probable that the tracheae of Filistata and of all other spiders (except the Dysderidæ and their allies) had this mode of origin, which is in entire agreement with the account given by Lamy of the structure of the tracheae in Filistata. The two short lateral tracheal sacs (p. 553, text-fig. 20, t.tr.) of this form are lined with spines and triangular in shape, exactly resembling a pulmonary sac deprived of its saccules. A study of the Hypochilidæ would probably throw some further light upon this subject, since here the second pair of lung-books are placed, according to Simon's figure ('Hist. Araign.,' 2nd ed., i, p. 201, fig. 145), far back, about midway between the anterior pair and the spinners, corresponding exactly in position to the tracheal system of the Filistatidæ.

I have made no attempt to explain the origin of those tracheal tubules, which cannot by any line of argument be derived from pulmonary saccules. The numerous tubules emitted from the large tracheal trunks in the Attidæ are a case in point, since these trunks, with the exception of their
lateral basal lobes, are metamorphosed entapophyses. These tubules may have originated simply as outgrowths of the trunks, and would then, of course, be of ectodermal origin. Ray Lankester is of opinion (1904, p. 223) that the tracheal tubules in Arachnida (and in all other Tracheata) have developed "by adaptation of the vasifactive tissue of the blood-vessels," which have come to open in the case of the Arachnids into the lung-chambers (and elsewhere). Instances of mesodermal tubes attaching themselves to, and opening into ectodermal invaginations are, of course, well known, e.g. the genital ducts. No actual embryological observations, however, exist, so far as I am aware, regarding the development of the fine tracheal tubules in Arachnida. In Attus floricola no trace of these tubules was found up to the stage formed at the second moult, and I had no later stages at my disposal.1

Summary.—The theoretical suggestions in the preceding paragraphs may be summed up as follows:

In the first place I suppose the saccules of the second pair of lung-books to have been converted into tracheal tubules in the common ancestor of the Dysderidae, Oonopidae, and Caponiidae. The resultant tracheae then increased in size, and, as the number of the leaves of the anterior lung-books decreased in inverse ratio, the former became the principal organs of respiration. The second pair of spiracles retained their position, or may even have moved slightly forwards, and the conversion of the entapophyses into tracheae could not take place here, and would, moreover, be quite unnecessary. In the Caponiidae the anterior pair of lung-books were converted into tracheae in a similar manner, but at a later period, and independently of the conversion of the posterior pair; but as the latter already provided almost the

1 A paper by R. Janeck entitled "Entwicklung der Blättertracheen und der Tracheen bei den Spinnen" has recently appeared ('Jena Zeitschr. Naturw.,' xli, Hft. 2—4, 1909), but I have not hitherto had access to this publication.
entire body with tracheae, the anterior pair did not further increase in size.

In the second place, in the progenitor (or progenitors) of the remaining tracheate spiders, the posterior lung-books became reduced in size and effectiveness by the disappearance of their saccules, accompanied by an increase in the number of the leaves of the anterior lung-books. Further, the posterior spiracles became approximated and united to a single spiracle, and moved towards the hinder end of the body, thereby causing the entapophyses of the tracheal segment to elongate. In this condition the Filistatidæ, Sicariidæ, and Palpimanidæ have remained, with slight modifications, such as the division of the tracheal antechambers into branches in some forms. In the great majority of the families, however, the elongated entapophyses became transformed into a pair of medial tracheal trunks, thus producing a tracheal system consisting of four simple unbranched trunks, which is still found in some genera at least, in nearly all the families. A new factor having been introduced, viz. the presence of the respiratory entapophyses lying in the large ventral sinus containing venous blood requiring aeration, we accordingly find the second respiratory segment again taking a prominent part in the respiration in many forms, owing to the increase in size and the branching of the medial trunks, accompanied ultimately by a corresponding reduction in the size of the anterior lung-books, e.g. in the Attidæ. This method of origin of the tracheae is independent of that of the Dysderidæ and its allies, and the tracheal tubules, when present, would here not be derived from saccules, but be new formations.

List of Literature.


THE PHYLOGENY OF THE TRACHEÆ IN ARANÉÆ. 561


EXPLANATION OF PLATE 28,
Illustrating Mr. W. F. Purcell’s paper on “The Phylogeny of the Tracheæ in Araneæ.”

ABBREVIATIONS.


All the figures, except fig. 9, were drawn with the aid of a drawing apparatus. Transverse and sagittal sections are so arranged that the horizontal plane of the body is parallel to the lower edge of the paper.

Fig. 1.—(Zeiss, objective C, ocular II, spirits.) Calculus bicolor, adult 2. Sagittal section through the entapophysis of the pulmonary segment.

Fig. 2.—(Zeiss, C, II, spirits.) Median section through the receptaculum seminis and epigastric fold, from the same series as fig. 1.

Fig. 3.—(Zeiss, C, II, warm Flemming's solution + alcohol.) Harpactes Hombergi, ad. 2. Similar section to fig. 2.

Fig. 4.—(Zeiss, 1/2 oil immers., IV.) Caponia spiralifera. Internal chitinous threads of cephalothoracic tracheal trunks.

FIG. 6.—(Zeiss, A, IV, spirits.) Caponia spiralifera, ad. ♀. Transverse section through the basal part of the trachea of the second respiratory segment.

FIG. 7.—(Zeiss, C, IV, spirits.) Lateral part of fig. 6.

FIG. 8.—(Zeiss, C, IV, spirits.) Caponia spiralifera, ad. ♀. Sagittal section through the entapophysis of the first and the lateral tracheal pocket of the second respiratory segments.

FIG. 9.—(Caustic potash.) Caponia spiralifera, ad. ♀, showing tracheal system (the ends of the tubules of the trachea of the second respiratory segment are not drawn in).

FIG. 10.—(Zeiss, A, IV, caustic potash.) Caponia spiralifera, ad. ♀. Right anterior trachea from the medial side.

FIGS. 11 and 12 (Zeiss, C, IV, spirits.) Same series as fig. 8. Sagittal sections through the left and right anterior trachea respectively. In fig. 12 the cuticula of the posterior side and the hypodermis of both sides of the pedicel have not been drawn in.