STUDIES ON ARTHROPOD CUTICLE

IV. An Electron Microscope Survey of the Intima of Arthropod Tracheae[1]

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A preliminary description of the appearance of the tracheal intima of a few arthropods was given during exploratory work on the application of electron microscopy to entomological problems (Richards and Anderson, 1942a, b; Anderson and Richards, 1942). The present paper is the result of a survey made to determine the number of tracheal types in arthropods and to locate species which are most favorable for an electron microscope analysis of tracheal wall structure. The data presented herein are given to illustrate the range of variation seen in surface views of the intima of tracheae and tracheoles in a representative series of arthropod species. Some discussion is also given on the nature of the forces that might produce tubes of these diverse types, but the extreme difficulty of obtaining critical data on such minute tubes necessarily makes the discussion largely a speculative rationalization. In a subsequent paper we plan to analyze the cross-sectional composition of the tracheal walls of a few representative species in more detail.

METHODS

The membranes of tracheae and tracheoles are readily prepared for examination in an electron microscope by the simple method used in the preliminary survey. This consists of dissecting a living or at least undried specimen and allowing the extirpated tissues to undergo cytolysis in distilled water for a few minutes or some hours. Most of the preparations were prepared in this manner with little attention being given to precise timing since soaking in distilled water at room temperatures has been shown to have no detectable effect on the tracheal intima (Richards and Korda, 1948). In a few species in which the tracheae did not readily clean on soaking in distilled water, weak alkali solutions were used at room temperatures for a short time, but alkali solutions have such destructive effects that all such preparations need to be checked against ones prepared without alkali treatment (Richards and Korda, 1948). Even 5% KOH at room temperature for 10 to 15 minutes can cause some recognizable effects. A few excellent preparations have been obtained from partially rotted dead

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specimens that had never dried (*e.g.*, fig. 52) but no method has been found for making satisfactory mounts from dried or preserved material.

Some preparations of cockroach tracheae and honey bee air-sacs were shadow-cast with gold in vacuo. No additional information was obtained from these preparations although the shadows confirmed the fact (already known from curled edges in silhoutte and from stereoscopic pictures) that the darker lines and spots thought to be thickenings are indeed elevated.

The type of mounting employed depended on the size of the tracheae being sought. Large tracheae, after cytolysis of the cells, were usually split open, laid across an electron microscope mounting screen, and allowed to air dry. Smaller tracheae and tracheoles cannot be readily split and require some supporting film since they are not sufficiently large to extend across a number of supporting wires on the screen. Smaller tracheae were prepared by allowing the cells of a selected organ or tissue to cytolyze (usually incompletely), rinsing through several changes of distilled water, then spreading the resulting mass across a collodion or formvar membrane on one of these screens, and allowing to air dry. Systematic examination of such preparations were made in the electron microscope and pictures were made of portions which by chance lay favorably exposed.

Since the cells were cytolyzed and only the intima examined, our data do not cover cell-intima relationships, and do not touch the question of whether tracheoles terminate intracellularly or extracellularly.

The chief limitation to the analysis of electron microscope pictures of the tracheal intima is the question of the precise relationship between measurements made on the pictures and dimensions of the same structures when the trachea or tracheole was in the intact living insect. Calibration of the instrument is accurate to within $\pm 5\%$, and resolution on the plates selected for illustrations lie in the range of 40–100 Angstrom units (0.004 to 0.010 microns). There appears to be no significant change in the gross dimensions of larger tracheae on removal, treatment, with distilled water, subsequent drying, and moderate electron bombardment. It does not necessarily follow that the same is true for smaller tracheae or for the minute details within larger trachea Imbibition of water during cytolysis of the cells would be expected to cause some swelling, and collapsing of tracheoles would appear to increase their diameter. Drying and electron bombardment would be expected to cause some shrinkage although for a firmly attached membrane this might only result in tension without a change in gross measurements. In some cases it is possible to determine that certain tubes are collapsed, partially collapsed or uncollapsed, but in many cases we are not certain whether a particular tube has or has not collapsed. At present it is not possible to evaluate these variables in detail. All measurements given in this paper refer to dimensions on the final prints but with the above uncertainties they are not claimed to represent more than order of magnitude.

GROSS STRUCTURE OF ARTHROPOD TRACHEAE

Ripper (1931) in his critical review of arthropod tracheae has ably pointed out that it is not possible to view the tracheae of all arthropod

groups as homologous structures. He discusses and discards the nephridial, integumental gland and gill theories of origin, and concludes by proposing that tracheae arose independently in various groups in response to the need for an internal respiratory surface. This viewpoint is also shared by Snodgrass (*in litt.*). Similarities would then represent an expression of the fact that an exoskeleton can develop internal tubular systems readily, and that the forces responsible usually lead to a similar appearing structure irrespective of the function served. Rigidity together with ready permeability can be obtained by having a thin-walled tube with supporting thickenings (text fig. 1), although similar mechanical supports in salivary ducts, the pseudotracheae of Diptera, etc., show that the need for permeability is not a determining factor.

Accepting Ripper's arrangements, we recognize ten groups in which the tracheae or other internal cuticular respiratory surfaces are not homologous. These are: (1) Onychophora, (2) Araneida, [Scorpionida] and [Pedipalpia], (3) Acarina and [Ricinulei], (4) Pseudoscorpionida, (5) Phalangida, (6) [Solpugidae], (7) Isopoda, (8) Symphyla, (9) Diplopoda, and (10) Chilopoda and Insecta. Groups within brackets were not available to us for study, but representatives of nine of these ten major divisions were. Despite the non-homology, most of these groups show the same basic structure: a tubular form, usually branched, with supporting thickenings which are almost always oriented into bands called taenidia (the "spiral thread" of many authors; Remy, 1925). The exceptions are the Isopoda and at least the most common form of tube in spiders.

In certain species of terrestrial Isopoda there are "air trees" or "white bodies" on certain abdominal pleopods. These are short lobate invaginations of rather indefinite morphology (Becker, 1936; Herold, 1913; Verhoeff, 1917, 1919; Remy, 1925). These are poorly developed organs which are respiratory but inadequate for the full respiratory needs of the animal. They have cuticular walls with reticulate thickenings which show no preferred orientations (fig. 59). Perhaps because of the non-tubular structure these respiratory "trees" usually have not been called tracheae; certainly they do not resemble the tracheae of insects, etc., in either gross- or micro-anatomy.

The Araneida have tubular structures that are commonly called tracheae although their respiratory significance has been questioned by Purcell (1909) on embryological grounds and by Kastner (1929) on crude experimental data (sealing "spiracles" with vaseline does not harm *Tegenaria*). Whatever their function, these tubular ducts of spiders have no circular or helical thickenings in any of the species we examined; they do have heavy reticulations or an elaborate set of anastamosing processes that would prevent collapse. Several authors (*e.g.*, Remy, 1925) have recorded that helical thickenings are found in the tubes of only certain species of spiders and that the type we found is the common form. Excellent figures of the more complex type are to be found in the paper by Kastner; our electron micrographs revealed no additional smaller details (figs. 61–62). Small lateral branches and terminal tufts have also been recorded for certain species of spiders (Bertkow, 1872; Purcell, 1909) but we did not locate such in the species

TABLE I

SUMMARY OF FORMS EXAMINED

Abbreviations: T = trachea; Tl = tracheole; A = air sac.

[1]Data from Dakin (1920); light microscope used.
[2]Richards & Anderson (1942b).
[3]Richards and Anderson (1942a).
[4]Richards & Korda (1948).
[5]Anderson & Richards (1942).

Group	Specific Form	Larva	Pupa	Adult	Figures
[Onychophora]..	[*Peripatus*].....	.....	.....	[Tl][1]	
Araneida.....	*Theridion tepidariorum*..	.....	.....	so-called T	61, 62
	Tetragnatha elongata....	.....	.....	so-called T	
	Neoscona arabesca.....	.....	.....	so-called T	
Acarina.....	*Dermacentor variabilis*[2]..	.....	.....	T, Tl	28
	Argas persicus.....	.....	.....	T, Tl	14, 58
Phalangida.....	Not identified.....	.....	.....	T, Tl	38
Pseudo-scorpionida...	Not Identified.....	.....	.....	T, Tl	30
Isopoda.....	*Armadillidium vulgare*..	.....	.....	"air-tree"	59
Chilopoda.....	*Scolopendra* sp. [2].....	.....	.....	T	
	Lithobius sp.....	.....	.....	T	29
Diplopoda.....	*Fontaria* sp.[2].....	.....	.....	T, Tl	23
Symphyla.....	*Scutigerella immaculata*..	.....	.....	T, Tl	17, 18, 19, 60
Thysanura.....	*Lepisma saccharina*.....	.....	.....	T, Tl	2
Orthoptera.....	*Melanoplus differentialis*	T, Tl	.....	T, Tl	15, 52
	Ceuthophilus sp.....	.....	.....	T	
Blattaria.....	*Periplaneta americana*[3 4]	T, Tl	.....	T, Tl	(In R. & K.)
	Blatta orientalis.....	T, Tl	.....	.....	12, 25
Phasmida.....	*Diapheromera femorata*..	T, Tl	.....	.....	4
Plecoptera.....	*Pteronarcys* sp.....	.....	.....	T, Tl	6
Isoptera.....	*Reticulotermes flavipes*..	.....	.....	T, Tl	53
Mallophaga.....	*Eomenacanthus stramineus*.....	.....	.....	T, Tl	1, 54, 55
Anoplura.....	*Polyplax spinulosa*.....	.....	.....	T, Tl	
Ephemerida....	*Hexagenia* sp.....	.....	.....	T	
Odonata.....	*Lestes* sp.....	.....	.....	T, Tl	16, 20, 51
Thysanoptera...	*Taeniothrips gladioli*.....	.....	.....	T, Tl	9
Hemiptera.....	*Oncopeltus fasciatus*.....	T, Tl	.....	T, Tl	7
	Rhodnius prolixus.....	.....	.....	T, Tl	8, 47
Homoptera.....	*Macrostelus divisus*.....	.....	.....	T, Tl	3, 57
	Macrosiphum pisi.....	.....	.....	T	
Megaloptera....	*Corydalus cornuta*.....	T, Tl	.....	.....	5
Neuroptera.....	A myrmeleonid.....	T, Tl	.....	.....	.....
	Chrysopa sp.....	.....	.....	T, Tl	
Mecoptera.....	*Bittacus* sp.....	.....	.....	T, Tl	11
Trichoptera....	*Hesperophylax designatus*	T, Tl	.....	.....	22
Lepidoptera....	*Galleria mellonella*.....	T	T, Tl	.....	26
	Malacosoma americana..	T, Tl	.....	.....	56
Coleoptera.....	A carabid.....	.....	.....	T, Tl	
	Photinus pyralis.....	.....	.....	T, Tl	27, 33, 43, 44, 45
	A buprestid.....	T, Tl	.....	.....	.....
	Tenebrio molitor.....	T	.....	T	48
	Macrodactylus subspinosus[5].....	.....	.....	T	49, 50
	A scarabaid (May beetle)	T, Tl	.....	.....	.....
	Calandra oryzae.....	.....	.....	T, Tl	46
Hymenoptera...	*Neodiprion lecontei*.....	T	.....	.....	.....
	Camponotus herculeanus.	.....	.....	T, Tl	21, 37
	Apis mellifica[3 4].....	T, Tl	T, Tl	T, Tl, A	31, 32 (R. & A.)

TABLE I—(*Continued*)

Group	Specific Form	Larva	Pupa	Adult	Figures
Diptera.....	*Sciara coprophila*.....	T, Tl	.....	T, Tl	34
	Tipula abdominalis.....	T, Tl			
	Culex pipiens[3 5].....	T, Tl	T, Tl	T	(R. & A.)
	Aedes aegypti.....	T	T, Tl	T, Tl	24, 35
	Drosophila melanogaster.	T, Tl	.....	T, Tl	10
	Drosophila funebris.....	T	.....	A	
	Musca domestica.....	T, Tl	.....	T, A	39, 40, 41
	Phormia regina.....	T, Tl	T, Tl	T, Tl, A	13, 36, 42
Siphonaptera...	*Xenopsylla cheopis*.....	.....	.....	T, Tl	

we examined. If we accept as our definition of a trachea, "a respiratory tube with a cuticular lining," it follows that respiratory significance has to be demonstrated rather than gratuitously assumed. Certainly the presence of helical or circular thickenings is no evidence of function since such are to be found in tracheae, salivary ducts, pseudotracheae of Diptera and Phalangida, some setae, etc. It does not seem possible to evaluate the so-called tracheae of spiders until more is known about their functioning.

As for the other groups, the Onychophora and Symphyla are usually stated to lack taenidia, but Dakin (1920) has already recorded that taenidia can be seen in *Peripatus* if fresh material is examined; and we find that thickenings, sometimes reticulate, sometimes oriented as taenidia, are to be found in the minute tubes (presumed to be respiratory) of *Scutigerella* (figs. 17–19, 60). In certain questionably atracheate mites, minute ducts which have been described as tracheae have been re-interpreted by Grandjean (1937) as gland ducts. There are a few other forms not available to us for which an absence of taenidia has been reported on the basis of observations with a light microscope (e.g., Collembola, Davies, 1927; *Polydesmus*, Effenberger, 1907), but in view of the uniformity with which we have found thickenings, usually taenidial, in minute tubes in which no thickenings can be detected with a light microscope we suggest that these cases will be shown similar when examined by electron microscopy.

From our examination of forms representing almost all the tracheate groups (Table I), we conclude that all the arthropod groups with internal ducts that are presumably respiratory possess thickenings in the walls of these tubes or sacs. These thickenings are oriented in the form called taenidia with the exception of those in the isopod crustacea, the spiders, some tubes of Symphyla, and some insectan air sacs. In truly tubular tracheae, the thickenings are always organized as taenidia irrespective of the diameter of the tube (i.e., including tracheoles) except in the questionable tracheae of spiders and some but not all portions of the tubes of Symphyla.

THE ORIGIN OF TAENIDIA

There have been frequent speculations concerning the mode of origin of taenidia but the cause of the usual structure of helical or circular bands in a thin-walled tube is still not certain. Old figures of cavities within taenidia must usually have been illusions due to focusing effects.

However, there is at least one case (*Musca*, figs. 39–40) where tubular taenidia do occur and where the structure suggests taenidial origin from a corresponding groove, as Dujardin suggested in 1849. All careful cytological observations show taenidia are not "chitinized" nuclear processes (Packard, 1886). To say taenidia are equal to cuticular ornaments is either untrue or unhelpful depending on what Keilin (1944) meant. There is good evidence that they are not formed (or at least not necessarily formed) around corresponding cytoplasmic modifications which have the function of molding taenidia because they occur on the lumen side of the continuous tubular membrane (Richards and Korda, 1948), may extend without interruption across several cells (*e.g.*, Thompson, 1929), and may appear suddenly and simultaneously along the trachea (Keister, 1948). Thompson's (1929) analogy to a liquid column breaking into droplets is made untenable by our demonstration of the existence of circular taenidial bands causing the beaded appearance he saw in tracheoles. Wigglesworth (1931) has suggested that taenidia might arise from the action of some simple physical force. We favor this last suggestion. A rigorous proof would be difficult if not impossible but recent data do permit carrying the analysis somewhat further.

By both electron microscopy and optical analysis with polarized light it has been shown for cockroach tracheae that the chains of chitin molecules or micelles run longitudinally in relation to the trachea in the basic membrane (which includes the intertaenidial membrane, text fig. 1) and at a right angle to this in the taenidia (Richards and Korda, 1948). It is difficult to conceive of a crystallization (molecular aggregation) producing this effect. Certainly the effect cannot be a product of chitin molecular properties *per se* since the same result is attained in

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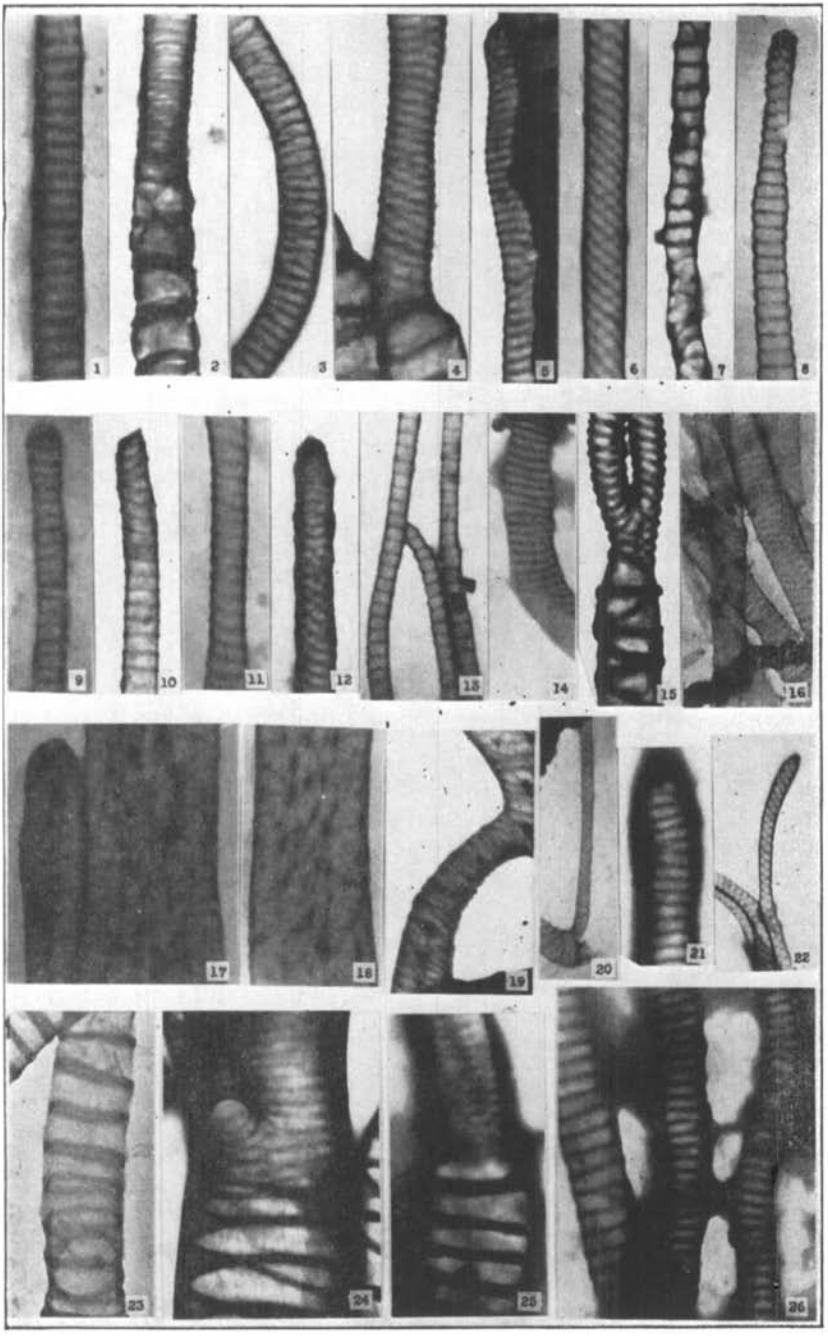
EXPLANATION OF PLATE I

Preparations of tracheae and tracheoles from general body tissues except when specific organ is named. Figs 20 and 22 at approximately 5000×; fig. 23 at 11000 ×; all others at 10000 ×.

Fig. 1. *Eomenacanthus stramineus*, adult (No. 397e). Fig. 2. *Lepisma saccharina*, adult, from around gut (No. 240e). Fig. 3. *Macrostelus divisus*, adult (No. 236a). Fig. 4. *Diapheromera femorata*, one day old nymph (No. 196a). Fig. 5. *Corydalus cornuta*, larva (No. 53d). Fig. 6. *Pteronarcys* sp., adult, from ovary (No. 399b). Fig. 7. *Oncopeltus fasciatus*, young nymph (No. 231e). Fig. 8. *Rhodnius prolixus*, adult (No. 446b). Fig. 9. *Taeniothrips gladioli*, adult (No. 236e). Fig. 10. *Drosophila melanogaster*, adult (No. 546a). Fig. 11. *Bittacus* sp., adult (No. 439a). Fig. 12. *Blatta orientalis*, adult, from around crop (No. 545a). Fig. 13. *Phormia regina*, adult, from ovary (No. 554b). Fig. 14. *Argas persicus*, adult (No. 243d). Fig. 15. *Melanoplus differentialis*, first instar nymph (No. 564e). Fig. 16. *Lestes*, sp., adult (No. 412b). Fig. 17. *Scutigerella immaculata*, adult head (No. 305a). Fig. 18. *Scutigerella immaculata*, adult head (No. 305b). Fig. 19. *Scutigerella immaculata*, adult head (No. 303e). Fig. 20. *Lestes* sp., large nymph, from gill (No. 734e). Fig. 21. *Camponotus herculeanus*, adult worker (No. 237b). Fig. 22. *Hesperophylax designatus*, larva from gill (No. 753b). Fig. 23. *Fontaria* sp., adult (Anderson No. 697a). Fig. 24. *Aedes aegypti*, adult, from ovary (No. 233c). Fig. 25. *Blatta orientalis*, adult, from around crop (No. 545b). Fig. 26. *Galleria mellonella*, young pupa, from wing (No. 26a).



tracheae with and without chitin.[2] Engineers tell us that the strongest way to make a tube of minimum weight from fibrous components is to have the fibers run longitudinally in the tube wall and then put bands of fibers at intervals around the tube. This corresponds precisely with the fibrous molecular orientations we have demonstrated in cockroach tracheal walls. Arguing backwards from this, one is led to suggest that stress forces in the tracheal wall during the viscous plastic stage orient the elongated particles (molecules or micelles) in this manner. The origin of the necessary stress tension, however, is not known, and it does not seem profitable to speculate further while we know neither the magnitude or origin of applied stresses nor the force required to orient molecules in a tracheal wall.

Some modification (not necessarily a great one) will be required to account for the tubular taenidia found in the adult housefly (figs. 39–40) and seen less clearly in certain other species of Diptera. That these are indeed tubular is shown not only by the density pattern[3] but also by the fact that the tubes or deep grooves are capable of being opened and flattened without apparent tearing in the course of making mounts (does not follow that they can open and close in the living insect). In the housefly, the tracheae are comparable to a pipe with a corrugated wall rather than a pipe with bands. Solid taenidia occur in the small tracheae and tracheoles of houseflies, and seemingly in at least some of the large tracheae of larvae.[3] There are several reasons for thinking

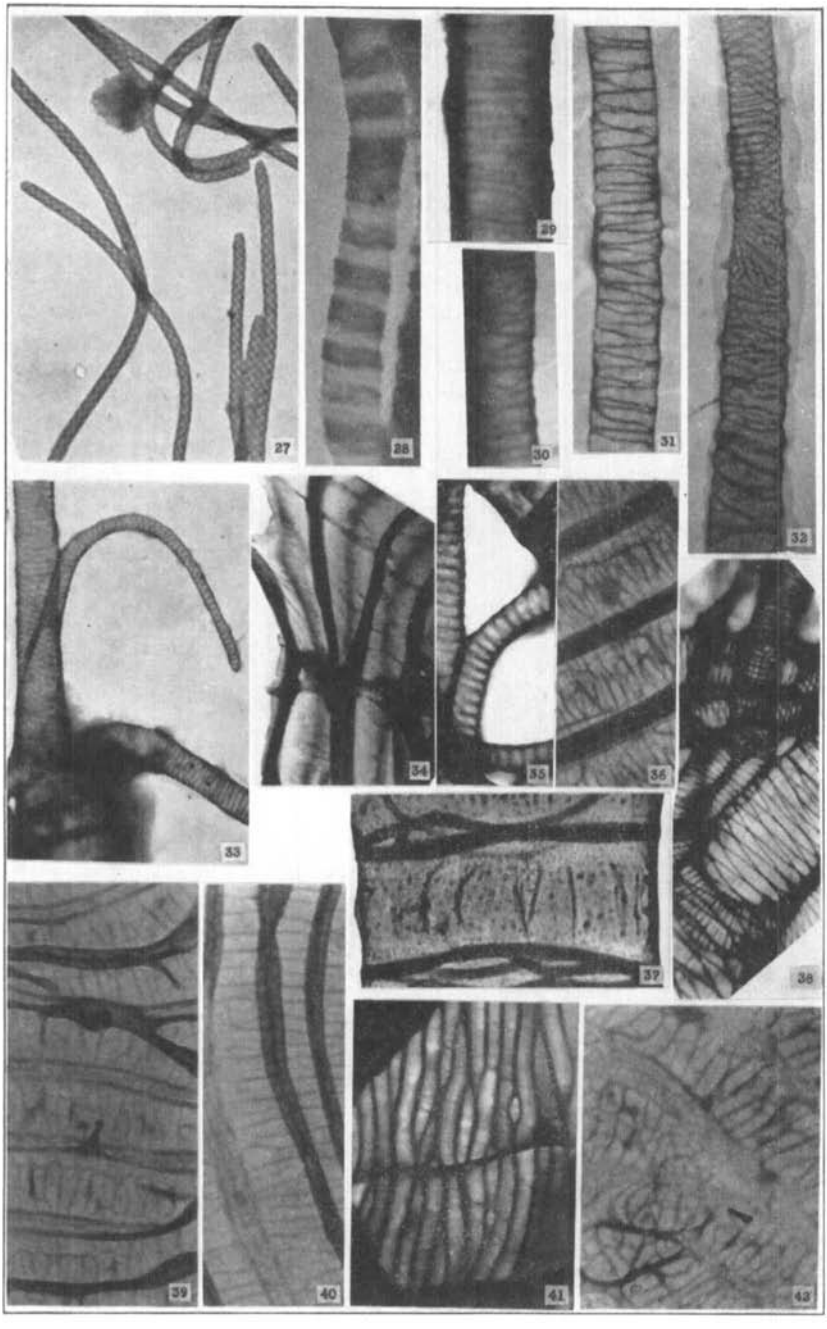
[2]We performed chitosan color tests on a few of the species. Positive tests demonstrating the presence of chitin were obtained for the larger tracheae of *Periplaneta*, *Blatta*, *Galleria*, *Calandra*, *Culex*, *Aedes*, *Neodiprion* and the larvae (not adult) of *Phormia*. Complete dissolution in the hot alkali, routinely interpreted as indicating the absence of chitin, was obtained for minute tracheae and tracheoles of all species and for the large tracheae and air sacs of *Rhodnius*, *Apis*, *Sciara*, *Drosophila*, *Musca*, adult (not larvae) *Phormia* and *Xenopsylla*.

[3]This statement is based on the fact that electron microscope pictures are density shadow pictures due to electron scattering. When a thickening shows a uniform density it must be solid. Thickenings which are corrugations should show dark edges and a lighter central line, just as lumps which are solid show homogeneity (fig. 48) whereas ones which are pimples show as dark circles (fig. 50).

EXPLANATION OF PLATE II

Preparations of tracheae and tracheoles from general body tissues except when specific organ is named. Figures 27, 32, 33 and 38 at 5000 ×; all others at 10000 × magnification.

Fig. 27. *Photinus pyralis*, adult male, from light organ (No. 450b). Fig. 28. *Dermacentor variabilis*, adult (Anderson No. 698a). Fig. 29. *Lithobius* sp., adult (No. 543b). Fig. 30. Pseudoscorpion, age unknown (No. 466e). Fig. 31. *Apis mellifica*, pupa (No. 444b). Fig. 32. *Apis mellifica*, adult, note transition of taenidia (No. 459a). Fig. 33. *Photinus pyralis*, adult, from around hindgut (No. 454e). Fig. 34. *Sciara coprophila*, fourth instar larva, dorsal longitudinal trunk (No. 529a). Fig. 35. *Aedes aegypti*, adult, from ovary (No. 232e). Fig. 36. *Phormia regina*, adult, from around ovary (No. 554e). Fig. 37. *Camponotus herculeanus*, adult (No. 238b). Fig. 38. Phalangid, adult, showing five tubes intertwined (No. 754d). Fig. 39. *Musca domestica*, adult, most taenidial tubes "opened" (No. 37c). Fig. 40. *Musca domestica*, adult, "opened" and "unopened" taenidial tubes (No. 37e). Fig. 41. *Musca domestica*, adult, showing complex taenidial fusions (No. 231b). Fig. 42. *Phormia regina*, adult air sac, note bands suggestive of rudimentary taenidia (No. 548e).



that tubular taenidia are a peculiarity of the higher Diptera rather than a developmental stage for taenidia in all groups. The strongest evidence is the fact that in other forms (*e.g.*, cockroach) the basic endocuticular membrane is continuous beneath the taenidia. More open to possible error, but nonetheless evidence, is the fact that we failed to find a tubular stage for solid taenidia. Molecular orientations in the tracheae of Diptera remain to be determined but it would seem that at least the details of taenidial origin will differ in this case even though similar stress forces may readily be conceived as producing both types.

An hypothesis of stress origin of taenidia encounters an incongruity in those species with simple or branched microtrichiae— which cannot be formed by stress forces—unless, as we think, these microtrichiae are formed around protoplasmic filaments.

Air-sac walls may show either rudimentary taenidia (flies) or no trace of taenidia (honey bee). Any hypothesis of taenidial origin could rationalize this, but it is particularly easy to postulate reduced and less oriented stresses in air-sac walls. The forces for formation of taenidia must also be poorly or only locally developed in *Scutigerella* since organized taenidia pass into regions with a relatively unorganized reticulum.

Taenidial rings as well as taenidial helices were found in almost all the species examined. Accordingly, we believe that ring-forms are quite general in occurrence, especially in tubes of small diameter. Tracheoles may have either rings or helices, and their taenidia may contrast with those of the tracheae to which they are attached. The

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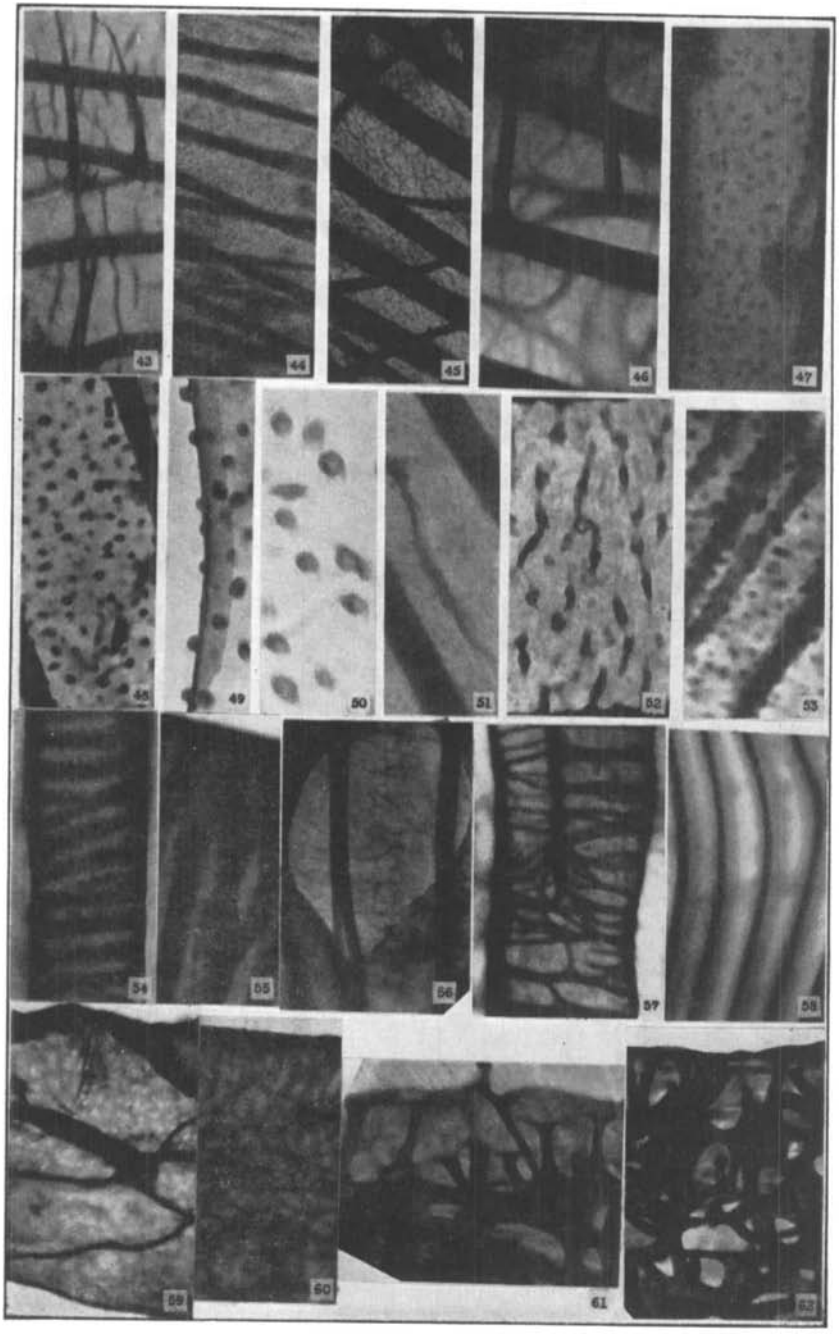
EXPLANATION OF PLATE III

Preparations of tracheae from general body tissues except when specific organ is named. Figures 43, 44 and 45 at 5000 ×; figures 49 and 50 at 18000 ×; all others at 10000 ×.

Fig. 43. *Photinus pyralis*, adult, trachea with uniform intertaenidial membrane (No. 455d). Fig. 44. *Photinus pyralis*, adult, trachea with minute lumps in intertaenidial membrane (No. 455a). Fig. 45. *Photinus pyralis*, adult, trachea with reticulated intertaenidial membrane (No. 445b). Fig. 46. *Calandra oryzae*, adult (No. 442d). Fig. 47. *Rhodnius prolixus*, adult (No. 445d). Fig. 48. *Tenebrio molitor*, adult (No. 251a). Fig. 49. *Macrodactylus subspinosus*, adult, torn area curled over showing papillae in silhouette (Anderson No. 728c). Fig. 50. *Macrodactylus subspinosus*, adult, another area of same preparation where ring-like appearance shows these lumps are really hollow papillae. Fig. 51. *Lestes* sp., adult (No. 411d). Fig. 52. *Melanoplus differentialis*, adult, prepared from partly decayed specimen (No. 561a). Fig. 53. *Reticulotermes flavipes*, adult worker (No. 263e). Fig. 54. *Eomanacanthus stramineus*, adult (No. 397b). Fig. 55. *Eomenacanthus stramineus*, adult (No. 397d). Fig. 56. *Malacosoma americana*, first instar larva (No. 377d). Fig. 57. *Macrostelus divisus*, adult (No. 236c). Fig. 58. *Argas persicus*, adult (No. 243a). Fig. 59. *Armadillidium vulgare*, adult, part of a lobe of "air tree" from abdominal pleopod (No. 733e). Fig. 60. *Scutigerella immaculata*, adult, large trachea from head (No. 303d). Fig. 61. *Theridion tepidariorum*, adult, one side of so-called trachea showing a relatively simple and therefore clearer set of pillars and cross-bars that project into lumen of this tube (No. 587e). Fig. 62. *Theridion tepidariorum*, adult, a more typical picture of one side of so-called trachea with its elaborate set of pillars and cross-bars in the lumen (No. 587a).

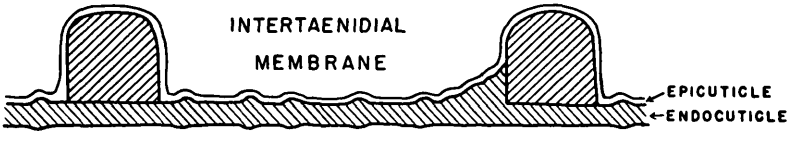


obvious postulate is that helices are developed whenever an elongational stress is added to the radial stresses we have postulated cause the observed molecular (or micellar) orientations. This would rationalize the fact that tracheoles of some species show only rings while those of others show only helices (see plates), and, coupled with Keister's (1948) demonstration of the correctness of the view that tracheoles may arise independently of tracheae, would also rationalize finding only helices in the hundreds of *Photinus* tracheoles examined while some rings occur in the small tracheae to which the tracheoles are attached.

On any hypothesis of taenidial origin one would expect to find some taenidial fusion or branching. In a few cases extensive fusion is seen at some points alone a trachea (fig. 41); at points where trachea branch the taenidia may form either simple (fig. 15) or complex configurations (fig. 57); with less well oriented forces (*e.g.*, air-sacs, Richards and Korda, 1948) even more fusion is seen; in the unique case of *Scutigerella* (figs. 17–19) it is only sometimes that the presumed stress is sufficiently oriented to produce a taenidia-like structure. More branching or fusing is found than one would expect from the literature, but whatever hypothesis one favors it seems to us surprising that taenidia are as constant as they are.

STRUCTURE OF THE INTERTAENIDIAL MEMBRANE

The tracheal membrane is a continuous tubular sheet or, at least in larger tracheae, set of sheets which is only apparently subdivided into



TEXT FIGURE 1. Diagrammatic sketch of a longitudinal section of a tracheal intima (based on cockroach). Illustrates continuity of tubular membrane with taenidia superimposed, location of swellings in intertaenidial membrane in the endocuticle, and continuous epicutile which follows the contours of the surface.

short sections by taenidia. By gentle manipulation of alkali-treated tracheae the taenidia can be removed; they uncoil from inside, giving the appearance of withdrawing a spring from a sleeve. Also the pattern of chitin micelles in the tube wall is continuous across the taenidia (Richards and Korda, 1948). These two points demonstrate that the basic tracheal membrane is a continuous sheet although intimately associated with the taenidia (text figure 1). The higher Diptera with their tubular taenidia will presumably be an exception to this but must await further study. In electron microscope pictures the taenidia are usually opaque due to their thickness; accordingly only the structure between taenidia is usually seen clearly. In this section we will consider only the structures seen in this intertaenidial area even though the same membrane usually continues under the taenidia.

The intertaenidial membrane is a continuous sheet which is not perforated by gross canals such as gland ducts or pore canals. It may possess a molecular sieve structure but, at least in dried membranes,

this is beyond the resolution of our pictures. Other data (e. g., Richards and Weygandt, 1945) suggest that the permeability of tracheal membranes is of the same order of that given by dialysis membranes which likewise show no pores in electron microscopy.

The patterns shown by intertaenidial membranes can be grouped into three general types:

(A) Membrane uniform within limits of resolution.
(B) Membrane with linear thickenings, forming
  (1) reticulum of thickenings,
  (2) more or less oriented thickenings,
    (a) parallel to taenidia,
    (b) perpendicular to taenidia.
(C) Membrane with small speckles due to
  (1) local thickenings in the endocuticle,
  (2) evaginations presumably over minute papillae.

Intermediates between these types are common, and all three types are sometimes found in different tracheae of a single individual (*e. g.*, *Photinus*, figs. 43–45) although in most cases there is reasonable constancy. The patterns may also vary from larva to pupa to adult (*e. g.*, *Culex*, see Richards and Anderson, 1942a). The patterns are independent of chitin since both reticulate and lump types are found with and without chitin.[4] If desired one could add another class for those species which have microtrichia.[5] Taking these up in order:

Intertaenidial membranes uniform within the limits of resolution are found in the tracheoles of all species examined, in the small tracheae (2–5 μ diameter) of most but not all species, and in the large tracheae of only a few species (Table II). Commonly but not always the membrane between lumps and thickenings is similarly uniform. A series of examples can be found ranging from strong to faint to vague to no discernible reticulum. This might be interpreted as meaning only that the seemingly uniform membranes have a finer reticulum beyond detection in our pictures (especially since we are uncertain how much thickening is required to produce a density differentiation visible on the plates). But this is by no means necessarily true. The thinnest tracheal membranes are considerably less than 100 A ($=0.01$ μ) thick and may well be of the magnitude of 50 A thick. Our best pictures have resolutions of this magnitude. This is the range of sizes of the lengths of smaller protein molecules. While the long axes of the molecules lie parallel to the surface of the membrane[6] there would still only be space for a few molecular thicknesses. This thickness is the same magnitude as the shortest dimension of chitin micelles found in large tracheae of cockroaches [Richards and Korda, 1948). Cuticular proteins analyzed by Fraenkel and Rudall (1947) have lattice unit spacings

[4]See footnote 2, page 56.

[5]Marcu (1931) has presented the most complete series of types to be found in previous literature. He recognized five groups: (1) simple with helical taenidia; (2) same but with intertaenidial thickenings parallel to taenidia (*Dytiscus*); (3) with a net-work or reticulate intertaenidial membrane (Hymenoptera and Coleoptera); (4) with thickenings perpendicular to taenidia (Buprestidae); and (5) species with hairs (microtrichia).

[6]This is actually known only for larger tracheae but may be presumed to be true for smaller tracheae and tracheoles also.

(determined from x-ray diffraction patterns) similar to those of chitin. Resolution in our best pictures is to within five to ten times these lattice unit dimensions which do not represent molecular sizes but only minimal molecular unit spacings. Accordingly, although our data do not prove it, uniform tracheal walls of the thickness of 100 A and less may well represent uniform monolayers of the wall units. Larger tracheae with thicker walls are known to consist of more than one layer but the nature of these separable layers and their relation to tracheae with thinner walls remains to be clarified.

Tracheal walls with reticulate thickenings are especially general in the Diptera but occur in a scattering of other species (Table II). Reticulate thickenings are also present in the walls of air-sacs we examined but it happens that those species from which we took air-sac walls were all ones whose tracheal walls are also reticulate. The reticulate thickenings commonly show no preferred orientations (figs. 45, 56) but in some cases (*Musca*, *Phormia*, etc.) the thickenings are definitely oriented perpendicular to the taenidia (figs. 39–42). If the uniform type of membrane is viewed as representing a uniform monolayer, then a reticulate membrane with uniform areas between the thickenings is most readily visualized as arising from the squeezing out of excess units from such a monolayer, the pressure presumably arising from irregularities in contraction of the membrane during hardening.[7] Carrying the reasoning one step further, the excess units squeezed out could be visualized as forming a reticulum from satisfying some of the same cohesive forces that bind the units of the uniform membrane together; if units are squeezed out more or less randomly an unoriented reticulum would result, if the units are squeezed out of a highly oriented film or are placed under stress after being squeezed out they might readily become oriented ridges perpendicular to the taenidia. This series of speculations leaves out of consideration the fact that a series of reticulations is found ranging from strong (fig. 36) to weak (fig. 57) unless one wants to assume that units squeezed out may tend to aggregate with previously expelled units or may be different sizes in different species.

Two of the examples of reticulate membranes require special mention. In *Sicara*, and less distinctly in a few other species, there is a relatively weak thickening half-way between and parallel to the taenidia (fig. 34). [Marcu (1931) has recorded thickenings paralleling taenidia in *Dytiscus*.] The origin of these is not clear. In the symphylan, *Scutigerella*, the thickenings may form only a heavy reticulum or may be oriented in some areas into somewhat imperfect taenidia, as discussed in the preceding section (figs. 17–19).

The most widespread type of intertaenidial membrane is one with localized swellings or pimples (figs. 37, 47–55). In some species these become considerably elevated and project into the lumen of the tracheal tube (fig. 49). Specimens of large tracheae of the cockroach in which the epicuticle has been manually torn or the epicuticle isolated show

[7]At least the larger reticulations cannot be produced by the drying necessary in electron microscopy because they can be seen in fresh material with a light microscope.

that these lumps are thickenings located in the endocuticle and pushing out the covering epicuticle as taenidia also do (*e. g.*, cockroach tracheae, see Richards and Korda, 1948). Presumably the same will be true for smaller tracheae which have these swellings. These lumps are usually roughly circular (fig. 48) but may be irregular (fig. 52). They may be entirely separated from one another (fig. 50), joined into ridges bracing the taenidia (cockroach, Richards and Korda, 1948), or combined with a set of reticular thickenings (honey bee, Richards and Anderson, 1942a). In a few species larger ones appear as pimples or short hollow projections which presumably represent molding around some microcytoplasmic projection; the clearest case of this is shown by the beetle *Macrodactylus* (fig. 50). The swellings may sometimes occur on taenidia (fig. 53). In the lice there is an unique situation; a row of lumps parallels each side of each taenidium (fig. 54–55).

The origin of these clearly defined swellings in intertaenidial membranes is not clear. All that we know is that in cockroach tracheae they are located in the endocuticle (text fig. 1) and disappear following treatments leading towards chitin purification (Richards and Korda, 1948), that in most species they are true swellings, (figs. 48. 53) but in some species they are papillae (fig. 50),[3] that their development is independent of the presence of chitin,[2] and that they appear fully formed in the intima of freshly molted cockroaches as well as in fully sclerotized dark specimens. One could suggest that they overlie equally small or smaller centers of production of the cuticular material but this would be virtually impossible to prove.

Three genera with microtrichia on the tracheal intima were examined: *Culex*, *Photinus* (fig. 43) and *Calandra* (fig. 46). These showed no differences from the ordinary types other than the presence of these usually simple filamentous processes. After treatment with hot alkali solutions the tracheae of *Calandra* retain their structure, including the reticulum in the intertaenidial membrane, but the bases of the microtrichia become hollow. This suggests that these, like the microtrichia of centipedes (Richards and Korda, 1947), may contain protoplasmic cores. Dujardin (1849), Marcu (1929, 1931), Keilin (1944) and others have recorded branched as well as simple hairs in other species of insects. In no case have we found any setae or other forms of sensillae in the tracheal walls; all the "hairs" and "spines" are simple cuticular projections, that is, microtrichia.

STRUCTURE OF AIR-SAC WALLS

Air-sacs have been examined in only the honey bee and three species of flies. Numerous illustrations of honey bee air-sacs have been given in previous papers (Richards and Anderson, 1942a; Richards and Korda, 1948). Honey bee air-sac walls are multilayered with irregular reticulate thickenings, most of which are true thickenings of the membrane but some (especially the larger ones) are folds or are augmented by folding. The fly air-sacs have a structure more suggestive of modified tracheae; parallel thickenings, seemingly representing rudimentary taenidia, separate strongly reticulate areas (fig. 42).

STRUCTURE OF TRACHEOLES

In all the species examined the tracheoles have been found to contain taenidia [8] Specimens of *Peripatus* were not available but Dakin (1920) has already recorded that taenidia can be seen in fresh material. The only partial exception we have found to this generality is the symphylan, *Scutigerella;* in this case most of the tubes show unoriented reticulate thickenings while some of the smaller ones show the thickenings organized like taenidia (figs. 17–19). No tracheal tubes (or air-sacs) have been found without thickenings in the walls.[9] With the representative range of forms studied it seems reasonable to conclude that all tracheoles possess supporting thickenings which, with the partial exception noted for *Scutigerella,* are organized into taenidia.

As pointed out previously (Richards and Anderson, 1942b) it is no longer possible to say tracheoles are characterized by the absence of taenidia. The taenidia are simply beyond the limits of resolution of a light microscope. No definition based on the diameter of the tubes or on the structure of the intima seems possible. A survey of the literature suggests that no rigid definition will be possible on other grounds. In specific cases, perhaps most cases, tracheoles could be defined as those minute terminal tubes which are formed *within* tracheal cells (*e. g.*, *Sciara,* see Keister, 1948) but exceptions are known. And the fact that intracellular versus extracellular origin is no fundamental distinction was pointed out as long ago as 1889 by Schäffer and has been re-emphasized by Keister's report of both tracheae and tracheoles developing intracellularly in *Sciara* larvae. Previously we suggested that since no clear distinction could be made the term tracheole be dropped. However, it is convenient to have a name for the terminal ramifications of the tracheal system, and we propose that the term tracheole be used simply to designate the minute terminal branches of the tracheal system.

For the purpose of the present paper we have called any tube less than one micron in diameter a tracheole. This is arbitrary but we have had to make some such distinction since our preparations show us only the tracheal intima. In a few species no tubes this small were found but these were ones where a single preparation was examined, and since no blind ends were found we feel that in these few cases we simply had not obtained the smallest tubes (see Table II). The tubes which seem unquestionably tracheoles (blind endings located) occupy a narrow range of diameters: 0.2 to 0.5 μ. A number of those in which the measurement is given as 0.3 μ are clearly flattened; correcting for this such tubes would have a true diameter of approximately 0.2 μ. Flattened tubes measuring 0.5 μ (*e. g.*, *Melanoplus*) would have a diameter of approximately 0.3 μ. As pointed out in the section on methods, these measurements are not to be interpreted as more than the correct order of magnitude. But accepting the measurements as indicating

[8] No tubes small enough to be classed as tracheoles and no side branches were found in any of the species of spiders examined though some authors say such occur (e.g., Bertkow, 1872). None of the lobes of the "air tree" of terrestrial isopods resemble tracheoles in size or shape.

[9] As noted in the section on *Methods*, cleaning with alkali solutions may cause some deterioration, including a decrease in definition or even apparent loss of the thickenings.

order of magnitude, we have to conclude that a tube with a diameter of approximately 0.2 μ is the lower limit of tracheal size and that this limit is attained in a large percentage of species. It is interesting to speculate as to why this is the lower limit. An obvious suggestion is that it represents the limit of curvature of the molecules composing the intima. Keister (1948) and some older authors have recorded that tracheole walls are formed around cytoplasmic canals. Accepting these reports, molecular forces within the wall itself might still place a lower limit on the possible tube diameter. However, if the diameter of the smallest tubes was controlled by molecular forces one would expect that the taenidia would be important and that tracheoles with helical taenidia would be significantly smaller than those with circular taenidia. This is not the case. The question seems insoluble but we feel inclined to place the probable control in the size of the cytoplasmic canal rather than in the molecules of the tracheole wall.

Allowing for variations in collapsing of the tubes, the tracheoles are usually of constant diameter for long distances (but note fig. 33). Then they terminate abruptly with a blunt or rounded tip. Anastamosis of tracheae into complex networks is common and well-known, but anastamosis of tracheoles is still debated (see Remy, 1925; Wigglesworth, 1931; Buck, 1948). Unfortunately, the nature of electron microscope preparations is not favorable for locating anastamosis unless there were complex multiple fusions or something characteristic about the point of fusion. Hundreds (more likely thousands) of free blind ends have been found on our preparations, but no preparation has been seen of a tracheole leaving a trachea and looping back to join it again. If such were common we would expect to have located some in the many preparations studied but not necessarily if they are rare or found only in special tissues, as is usually stated now. We have studied intensively one tissue where an anastamosing network of tracheoles has been reported, namely, the light organ of *Photinus* (fig. 27). We examined numerous preparations and observed literally hundreds of blind endings, many of which could be followed completely from their origin, but we found no evidence of anastamosis. With dense clusters of such tubes of dimensions at the limit of resolution of a light microscope one can readily imagine workers using a light microscope obtaining an illusion of anastamoses.[10] Numerous blind endings have also been

[10]Dr. Buck saw some of our pictures of *Photinus*, and added a note on them in his review (1948). His facile criticisms of electron microscopy are not well founded, but more important is the fact that he questions whether the tracheoles of which we obtained pictures are the ones with which he deals. The question is not readily answered because neither his microphotographs nor our electron micrographs cover the complete picture: the microphotographs (while most excellent microphotographs) have the limited resolution of a light microscope, and the electron micrographs while having better resolution show only a tangled mass of isolated tracheae and tracheoles removed from their normal cellular surroundings. Light microphotographs give the impression that the tracheoles do anastamose in the light organ, but we must always hold the reservation that one cannot be really sure of what is actually seen when working at the extreme lower end of resolution of any microscope. Electron micrographs of tracheae and tracheoles from isolated light organs show large numbers of tracheoles which end blindly, and that these tracheoles appear to arise in sets of two, three or four. Certainly there must be something abundant in the light organ which corresponds to the structures in our pictures. Buck records that the tracheoles always arise in sets of two, and his figures show a branched trachea with two tracheoles arising

found in gill filaments of *Lestes*, *Corydalus* and *Hesperophylax*. Considering the difficulties of flow other than diffusion through tubes a small fraction of a micron in diameter, we fail to see any material advantage that would be conferred by a tracheolar network. However, all we can report is our failure to find such a network.

It might not be superfluous to remark that nothing resembling any form of valve structure has been seen in any of the thousands of tracheae and tracheoles observed, despite the fact that we were watching for evidence of such especially at points of bifurcation of tracheae and origin of tracheoles.

The taenidia of tracheoles may be all rings (fig. 8), or rings and helices (figs. 3, 10), or only helices (fig. 27). In the two species of ticks examined the rings tend to occur in pairs (fig. 28). While only small number of tracheoles were seen for most of the species it seems that the condition is characteristic for a particular species. Whatever the nature of the origin of taenidia, it is reasonable to expect that ring forms should be more common in small tubes, as indeed they are. There is no necessary relation between the taenidia of tracheae and attached tracheoles. In Table II, tabulation of rings and helices are for both tracheae and tracheoles combined. For tracheoles alone (among species where reasonably large numbers were examined) only ring forms were found in *Taeniothrips*, *Rhodnius*, *Musca* and *Phormia*, while only helical forms were found in *Diapharomera*, *Pteronarcys*, *Lestes*, *Photinus*, *Tipula*, *Drosophila* and *Xenopsylla*.

With tubes both above and below one micron diameter (actual range 0.8 to 2.3μ) it is possible to find abrupt changes in taenidia with or without change in tube diameter (figs. 2, 24, 25, 32). With a light microscope, some of these could give the appearance of abrupt cessation of the taenidia. Such situations might originate from tracheoles growing in to connect with tracheae of the same diameter, from an extension of a trachea between moults (the part formed around a pre-existing trachea differing from the entirely new portion), perhaps from a partial shedding of the intima (Keister, 1948), or simply from an abrupt change in the forces responsible for the formation of taenidia. Locating such spots is lucky chance. Having found them in seven species in six different orders, we suspect that they are of general occurrence (located in *Lepisma*, fig. 2; *Blatta*, fig. 25; *Diapheromera; Photinus; Apis*, fig. 32; *Aedes*, fig. 24; and *Phormia*).

Buck (1948) described a "possible ultratracheolar network" as an admittedly questionable interpretation of certain metal precipitation patterns in cells of the light organs of fireflies. We did not recognize anything in our preparations that could be referred to the network Buck describes and figures.

As mentioned above, no resolvable detail has been seen in the intertaenidial membrane of tracheoles. The membrane is extremely thin ($<$100 A when dry) and uniform within the limits of resolution.

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to the end of each twig. One could argue, then, that sets of two in our electron micrographs represent one set, sets of four represent two sets of two, and sets of three represent a double set from which one has been torn or otherwise displaced. However, our electron micrographs are not conclusive on this point, and we must leave the question open. We find it difficult to believe we are not dealing with the same tracheoles Buck and other authors have described from light microscopy but we cannot prove it from our present set of pictures.

TABLE II

TABULAR PRESENTATION OF DATA OBTAINED

Arthropod	Diameter of smallest tube seen (microns)	Blind ends of tracheoles found	Ring-like taenidia seen	Helix-like taenidia seen	Intertaenidial membrane of larger tracheae
Theridion	several μ	.....	no	no	Highly reticulate with rods and elevated cross-bars, no taenidia
Tetragnatha	.....	.....	no	no	Similar to above; see figures
Neoscona	.....	.....	no	no	Reticulate heavy thickenings, without elevated rods and cross bars, no taenidia
Dermacentor	0.7	.....	yes	.....	Relatively thick, details unclear
Argas	0.5	.....	yes	yes	Taenidia not sharply demarcated, thick rings commonly double
Phalangid	0.3	.....	yes	yes	Linear thickenings normal to taenidia
Pseudoscorpion	0.7	.....	yes	yes	Relatively thick
Armadillidium	several μ	.....	no	no	Reticulate, no taenidia, lobate rather than tubular
Scolopendra	.....	.....	.....	yes	Relatively thick, details unclear
Lithobius	1.3	.....	.....	yes	Relatively thick, somewhat irregular but no definite pattern
Fontaria	1	.....	yes	yes	Granulate with minute lumps
Scutigerella	0.5	yes	.....	yes	Reticulations and incomplete taenidia; see figures
Lepisma	0.5	.....	yes	yes	Vague reticulum
Melanoplus	0.3	yes	yes	yes	Irregular lumps with faint connecting reticlum
Ceuthophilus	3–4	.....	yes	yes	Lumps (=cockroach)
Periplaneta	0.4	.....	yes	yes	Lumps, seldom connected except at taenidia, figs in earlier papers
Blatta	0.3	yes	yes	yes	Lumps, tracheae less than 2μ diameter have uniform membrane without lumps
Diapheromera	0.4	.....	.....	yes	Lumps (=cockroach)
Pteronarcys	0.5	.....	.....	yes	Mostly lumps but some areas reticulate and with heavy braces
Reticulotermes	1	.....	.....	yes	Lumps (=cockroach)
Eomenacanthus	0.6	.....	yes	yes	Row of lumps along each side of taenidia, see figure

TABLE II—(*Continued*)

Arthropod	Diameter of smallest tube seen (microns)	Blind ends of tracheoles found	Ring-like taenidia seen	Helix-like taenidia seen	Intertaenidial membrane of larger tracheae
Polyplax	0.3	.....	yes	yes	Similar to preceding but crenulated edge of taenidia less sharp
Hexagenia	.....	.....	.....	yes	Faint thickenings normal to taenidia
Lestes	0.2	yes	.....	yes	Lumps (smaller than in cockroach)
Taeniothrips	0.3	yes	yes	yes	Faint thickenings normal to taenidia
Oncopeltus	0.4	.....	yes	yes	Lumps (=cockroach)
Rhodinus	0.3	yes	yes	yes	Lumps (=cockroach)
Macrostelus	0.5	.....	yes	yes	Lumps (=cockroach)
Macrosiphum	1.5	.....	yes	yes	Faint reticulum, much taenidial branching
Corydalus	0.2	yes	yes	yes	Reticulated
Myrmelionid	0.2	yes	yes	yes	Lumps (=cockroach)
Chrysopa	0.3	.....	yes	yes	Lumps (=cockroach)
Bittacus	0.3	yes	yes	yes	Lumps plus faint reticulum
Hesperophylax	0.3	yes	.....	yes	
Galleria	0.4	yes	yes	yes	Reticulated, some with lumps also
Malacosoma	0.4	.....	yes	yes	Reticulated (=bee)
Carabid	0.4	.....	yes	yes	Lumps (=cockroach)
Photinus	0.2–0.3	yes	yes	yes	Some with lumps, some with reticulum, some intermediate, also spines and braces from taenidia
Buprestid	0.3	yes	yes	yes	Lumpy reticulum
Tenebrio	.....	.....	.....	yes	Lumps (=cockroach)
Macrodactylus	1.2	.....	yes	yes	Lumps which are distinctly pimples
Scarabaeid	0.3	.....	.....	yes	Reticulate plus some lumps
Calandra	0.4	.....	yes	yes	Reticulated, spines from taenidia
Neodiprion	.....	.....	.....	yes	Lumps, similar to ant
Camponotus	0.5	yes	yes	yes	Mostly lumps but some fusion into ridges normal to taenidia
Apis	0.2	yes	yes	yes	Reticulated, with or without lumps, air sac reticulated, see earlier papers for figures
Sciara	0.3	yes	yes	yes	Uniform or faint reticulum in larva, faint reticulum in adult
Tipula	0.5	.....	.....	yes	Too thick to be clear but not uniform
Culex	0.5	.....	yes	yes	Larva homogeneous, pupa and adult reticulate, minute spines on main longitudinal trunk taenidia

TABLE II—(*Continued*)

Arthropod	Diameter of smallest tube seen (microns)	Blind ends of tracheoles found	Ring-like taenidia seen	Helix-like taenidia seen	Intertaenidial membrane of larger tracheae
Aedes.....	0.3	.....	yes	yes	Faint lumps and reticulum in larva, reticulum in pupa, lines normal to taenidia in adult
Drosophila.....	0.2	yes	yes	yes	Reticulate with tendency for lines to be normal to taenidia
Musca.....	0.4	.....	yes	yes	Linear thickenings normal to taenidia; taenidia appear to be hollow tubes; air sacs appear to have rudimentary taenidia; see figures
Phormia.....	0.2	yes	yes	yes	Similar to preceding
Xenopsylla.....	0.4	.....	yes	yes	Lumps (=cockroach)

SUMMARY

1. Tracheae and tracheoles of species representing most of the major groups of tracheate arthropods have been examined with an electron microscope. In all cases these tubes were found to contain supporting thickenings. With the exception of the lobate "air trees" of terrestrial isopods, the so-called tracheae of spiders, some (but not all) of the tubes in the symphylan, and some insectan air-sacs, the thickenings are organized into taenidial bands.

2. Taenidial rings as well as helices were found in most of the species, especially in smaller tubes. Tracheoles commonly show exclusively one or the other as a specific characteristic. Fusion and branching of taenidia is common. Taenidia are almost always solid thickenings but in some higher Diptera they are tubular.

3. Tracheal membranes between taenidia may be uniform, with reticulate thickenings which may or may not show preferred orientations, or with local swellings. The type with minute lumps is most common; these are usually swellings in the endocuticle but in some cases are thin-walled cuticle presumably over correspondingly minute papillae. These types are independent of the presence or absence of chitin, and show no constant correlation to taxonomic relationships.

4. Microtrichia are present in relatively few cases; when present most of them arise from taenidia True setae and sensillae are absent. Gland ducts, pore canals or other gross holes were never found.

5. Nothing resembling a valve structure has been seen in the intima of any species.

6. Tracheoles contain taenidia, and cannot be identified on a basis of size or of structure of the intima. It is proposed that the term tracheole be used simply to designate the terminal branchings of the

tracheal system (irrespective of whether or not found in "tracheal end cells") without any connotation of a fundamental distinction between tracheae and tracheoles.

7. Tracheoles are of fairly constant size throughout the Arthropoda. The lower limit seems to be a tube with a diameter (when dried) of 0.2 μ, and most of those seen lie in the range of 0.2 to 0.5 μ. Blind, blunt, or rounded endings are common. No anastamoses of tracheoles were located.

8. The origin of tracheal membranes and of taenidia is considered. While the discussion is necessarily speculative, it is thought that available data are consistent with an hypothesis that a combination of monolayer phenomena and radial stress forces could bring about this type of tubular structure. Taenidia may be developed as either rings or helices, depending presumably on whether or not a longitudinal stress component is added to the postulated radial stress.

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THE LIFE OF WILLIAM T. DAVIS, by MABEL ABBOTT. Cornell University Press, Ithaca, N. Y. xv+321 pp., 26 illustrations. End paper map of Staten Island. 1949. Price $3.50.

When the writer of this review visited New York in the spring of 1922, being a coleopterist, he called on Mr. C. W. Leng at the Staten Island Institute of Arts and Sciences. In the course of the morning Mr. William T. Davis dropped in and shortly we were making our way to 146 Stuyvesent Place where on the top floor of his residence we inspected Mr. Davis' own collections, especially the cicadas. That was virtually my only contact with Mr. Davis. It was sufficient, however, so that a month or so ago, when the announcement of *The Life of William T. Davis* came to my desk, I knew at once the book was a must, and when the book arrived, I read it from cover to cover.

William T. Davis was born on Staten Island in 1862, descended on his mother's side from an old and prosperous Staten Island family. His parents were divorced when he was a boy, and he lived with his mother, grandmother, sister, and two maiden aunts! He early became absorbed in field natural history, and between the ages of 17 and 73 he kept intermittent "Natural History Notes"—seven bulky volumes of long pages written in longhand on both sides of the paper. Between 1883 and 1944 Mr. Davis published nearly 400 papers and reviews and over 150 notes, mostly on natural history topics. From 1883 to 1909 he worked in the office of the New York Produce Exchange Gratuity Fund in Manhattan. For fleeting months at the turn of the century it seemed that Davis' passion for nature might share itself with a wife, but Mrs. Davis died thirteen months after their marriage, and the beloved naturalist of Staten Island was left undisturbed with his natural history for another 43 years!

Even if it were possible, it would be superfluous to retell here the joys and sorrows, the laughter in spite of tears, of the 83 years that Mabel Abbott relates so sympathetically and so well. We see "Willie" Davis as a boy prowling the fields of Staten Island. We see him as a young man assisting in founding the Natural Science Association of Staten Island (later the Staten Island Institute of Arts and Sciences). We see him after his "retirement" in 1909 going further afield—to Florida, Virginia, and elsewhere—but always returning to the Staten Island he so loved. We see him becoming a world authority on cicadas and we experience the anticipation with which he traced the generations of Brood Two of the seventeen-year cicada on Staten Island: 1894—1911—1928. We see William T. Davis growing old in body—but never in spirit. We see him bed-ridden during his last six months—worrying about his finances even though about to leave the Staten Island Institute nearly $200,000—dying January 22, 1945, within three months of the appearance of Brood Two!

But I keep you too long from the delight of the book itself!

—MELVILLE H. HATCH.