

ARTICLES

Mosquito Eggs II

P. F. Mattingly
 Department of Entomology
 British Museum (Natural History)
 Cromwell Road, London, S. W. 7
 ENGLAND

Dr. Marks kindly drew my attention to another species of Toxorhynchites with known egg, requiring to be added to the above list. This is T. (T.) speciosus (Skuse), described by Colledge, W. R., 1911 Proc R. Soc. Qld., 23: 121. The description is unfortunately somewhat muddled. The shell is said to split "centrally through its long axis". This, if implying a longitudinal dehiscence, would be very interesting, but as the length of the egg is given as 1/50th in. and the breadth as 1/42 in., it is somewhat equivocal. Apart from this the egg seems to differ from that of T. splendens chiefly in being much more nearly spherical (length/breadth ratio about 1.2 as compared with approximately 1.5). The chorion is said to be "finely granulated".

Mosquito Eggs III

P. F. Mattingly

II. Tribe Anophelini

The eggs of more than 200 species of Anophelini have been described. The literature includes well over 200 publications. Hinton² lists more than 50 characters of taxonomic value. The only previous attempt at an ordered classification²⁵ is long outdated. The difficulties confronting a further attempt might seem formidable. Fortunately, however, certain evolutionary trends are discernible which, once recognized, should be of some assistance.

Christophers and Barraud²⁵ considered as probably primitive the eggs of species of Subgenus Anopheles s. str. belonging to the tree hole breeding An. plumbeus group (An. barberi Coquillett^{12,26}, An. barianensis James^{25,27} and An. plumbeus Stephens^{24,28,29}). These eggs have a broad peripheral fold of chorion, the frill-float of Christophers²⁷, marked with very numerous fine striations (Fig. 1a).

Interestingly the nearest approach to these eggs is shown by An. wilsoni Evans³². This has been thought to be the most primitive member of Series Neomyzomyia, itself the most primitive series of Subgenus Cellia, by reason of its reduced or non-existent cibarial armature and other features^{30,31}. The distinctive feature of its egg is the presence of a frill-float with fine striations on which are superimposed coarser corrugations like those separating the float chambers of more typical anopheline eggs (Fig. 1b). In my view the discovery of this

egg greatly strengthens Christophers' and Barraud's hypothesis since it is clearly transitional between eggs of the plumbeus type and the more highly evolved eggs both of Anopheles s. str. and of Cellia.

If this is accepted the subsequent evolution of the anopheline egg will be seen to have consisted quite largely in a progressive shortening of the float with reduction in the number of float chambers. Various intermediate stages are still to be found, as for example in the An. hyrcanus (Pallas) complex (Fig. 1e)³³ in Anopheles s. str., or An. pharoensis Theobald (Fig. 1l)⁴⁷ in Cellia. Little more than a simple continuation of the process is required to arrive at quite highly evolved eggs such as those of the An. (An.) maculipennis Meigen complex (Fig. 1f)⁴¹ or An. (Cellia) amictus Edwards (Fig. 1i)⁴².

This is not, of course, the whole story. Other evolutionary trends have been superimposed. However, surprisingly few of these need to be invoked to account for the differences in egg structure so far encountered. A major development, already apparent in the egg of An. wilsoni, was the encroachment of chorion from the lower (morphologically dorsal) surface beyond the frill-float onto the deck. With this went the development of a delicate frill, entirely distinct from the frill-float, at the junction between dorsal chorion and deck chorion (Fig. 1b, fr.).

Formation of a frill of this kind is almost invariably observed wherever a junction is established between dorsal chorion and deck chorion. It is particularly noticeable when overgrowth of the dorsal chorion is such as to restrict the deck chorion to two or more isolated patches. This is a normal feature of many eggs. In other cases it is met with as an occasional variation (as in Fig. 1j), not infrequently in a single egg batch^{30,33}. In An. gambiae Giles it can be produced experimentally by exposure of bloodfed females to subnormal temperatures (Fig. 1c'')³⁸. In members of the An. hyrcanus complex in Japan, one of which overwinters in the egg, it is a regular seasonal phenomenon accompanying the onset of colder weather³⁷. The same is true of overwintering eggs of An. walkeri Theobald in North America³⁴⁻³⁶. Here, however, there is an inhibition of frill formation in the neighborhood of the floats in summer eggs (Fig. 1d') though encroachment of dorsal chorion in the winter eggs is accompanied by frill formation of the familiar kind (Fig. 1d'').

Another evolutionary trend has involved the migration of the floats up onto the deck. In Anopheles s. str. this has not been carried very far. The extreme condition is met with in An. algeriensis Theobald where it falls well short of fusion of the two floats (Fig. 1g)⁴¹. In african species of Series Neocellia, on the other hand, there is complete fusion of the floats (Fig. 1k)^{30,45}. Oriental species of the same series show intermediate conditions (Fig. 1j)^{25,44} suggesting that Neocellia may have had a Malaysian or Eurasian origin as proposed by Christophers⁴⁶. This is in marked contrast to Series Neomyzomyia where the african An. wilsoni and its allies have the most primitive eggs while intermediate types are found in the Oriental Region³³ and the most highly evolved eggs are those of the australasian species (Fig. 1h,i)⁴². Once again this accords well with the african origin, and subsequent eastward spread, of this group previously inferred on ecological grounds⁴³.

A still more advanced condition is attained in the purely african Series Cellia, in one member of which, An. cyddipis DeMeillon⁴⁸, fusion of the floats has been followed by extensive reduction both of these and of the frill (Fig. 1m). The climax is reached, however, in Series Paramyzomyia, all members of which have lost the float entirely. In one section, represented by An. multicolor Cambouliou^{25,30,49,74} (Fig. 2a), the frill retains its normal disposition except that the ends are rotated inwards at the points at which they would normally be attached to the floats. The resultant surfaces permit the eggs to join side by side and head to tail forming ribbons on the surface of the water. The other section of Paramyzomyia includes An. hispaniola (Theobald) (= An. italicus Raffaele)⁵⁰⁻⁵², An. cinereus Theobald^{30,45} and An. turkhudi Liston^{25,30}. In these species even the frill has been almost lost, remaining only as a small patch near the anterior end (Fig. 2b). These eggs hang vertically in the water and sink readily. Loss of the float is thought to be adaptive to oviposition among the filamentous algae on which the larvae feed by means of specialized mouthparts⁵³⁻⁵⁶.

I think there can be little doubt that the Paramyzomyia egg represents the culmination of a process involving ventral migration, and ultimately loss, of the float. The same process has taken place in parallel, with progressively increasing completeness, in Subgenus Anopheles and in Series Myzomyia, Neocellia and Cellia (see Fig. 3). At the same time, however, there exists another class of floatless anopheline eggs which I believe to have resulted from an entirely different evolutionary process.

The striking feature of these eggs is their very close resemblance to those of the culicine genus Mimomyia (usually treated, in my view incorrectly, as a subgenus of Ficalbia) (Fig. 2c-d). They have a curious, sporadic distribution, occurring in one, or at most two, species of Anopheles s. str. (An. concolor Edwards, Fig. 2e, An. sacharovi Favr', Fig. 2m) and in each of the series of Cellia, except Paramyzomyia, as follows:-

- Series Neomyzomyia. An. nili (Theobald)^{31,71} (Fig. 2h)
- Myzomyia. An. dthali Patton²⁵ (Fig. 2f)
- An. apoci Marsh⁶⁶
- Pyretophorus. An. ludlowae (Theobald)⁵⁹ (Fig. 2k)
- Neocellia. An. superpictus Grassi⁶¹ (Fig. 2g)
- An. dancalicus Corradetti⁶⁵ (Fig. 2i)
- Cellia. An. murphyi Gillies and De Meillon³⁰ (Fig. 2j).

An. concolor is interesting as being the only member of Series Anopheles occurring in tropical Africa. It is known only from the former Belgian Congo where it breeds in Sphagnum pools at the edge of gallery forest³⁰. Its relationships are obscure³⁹. It is possible that it is an ancient relict species. Coupled with the resemblance of its eggs to those of Mimomyia this might suggest that its egg is of a primitive type, more so, perhaps, even than that of the plumbeus group. However, such a hypothesis seems inconsistent with the occurrence of similar eggs in the various series of Cellia.

That each of these represents an independent reversion to a primitive condition seems intrinsically unlikely. I would think it more probable that they have arisen, in parallel, by a simple reduction of the float without the migration of the float onto the deck as in the other evolutionary trend described above. An. sacharovi would represent an intermediate stage in this process. In this species the winter eggs develop a small float which is lost with the onset of summer giving rise to eggs of the Mimomyia type⁶¹⁻⁶⁴ (Fig. 2m).

An. nili has the dorsal chorion, and to a less extent the deck chorion, ornamented with mushroom-shaped papillae said sometimes to contain air³¹. A similar claim has been made for the chorionic papillae of Toxorhynchites. This, if true, would suggest to me that in An. nili the float had been lost at an earlier evolutionary stage than in the other species which have evolved more subtle methods of securing buoyancy. (See below). I think it unlikely that the frill of the Mimomyia-type eggs represents a precursor of the frill-float. I suspect that the latter originated quite independently in a manner to be discussed in my next note in this series dealing with the New World anopheline genera and subgenera. That the frill of the Mimomyia-like egg is homologous with the frill of the other anopheline eggs is shown by its characteristic reaction to invasion of the deck by dorsal chorion in An. ludlowae (Fig. 2k)⁵⁹ and in An. hellenicus Peus (Fig. 2j)⁶⁰. The latter is evidently an atypical form of An. superpictus since the eggs on which the name was based were found in a cage full of gravid females of that species.

It has been suggested that loss of the float in An. ludlowae and An. dancalicus is in some way adaptive to the high salinity in their breeding places^{59,65}. This could also apply to An. apoci which breeds in highly saline waters and has an egg resembling that of a broad-frilled An. superpictus (Fig. 2g)⁶⁶. I do not think, however, that this is likely to have been more than a contributory factor. Even at the relatively modest level of reduction attained in the An. maculipennis complex (Fig. 1f) the float seems to make relatively little contribution to buoyancy. The eggs still float quite well when it is removed⁶⁷.

The primitive frill-float of the plumbeus group may be more important in this respect since tree hole fluid is said to have a surface tension markedly less than that of ordinary water⁶⁸. Subsequent evolution, along two different sets of parallel lines, seems in essence to have involved the progressive development of more subtle methods of achieving buoyancy and the concomitant reduction of an increasingly useless organ.

The relation of the Mimomyia egg to the Mimomyia-like eggs of Anopheles remains obscure. I do not think further work on Anopheles is likely to throw much light on this problem. What is needed is the discovery and description of the eggs of some of the many species of all three subgenera of Mimomyia for which these are still unknown, perhaps especially some of the less typical african species of Mimomyia s. str.⁷⁰.

In Fig. 3 I have illustrated the successive stages in the evolution of the Old World anopheline egg as I envisage them. For me this type of gradogenetic presentation⁷³ is more illuminating than the familiar cladogenetic tree (Fig. 4). (I also have considerable sympathy for the currently accepted classification of the malaria parasites which is purely gradogenetic⁴³).

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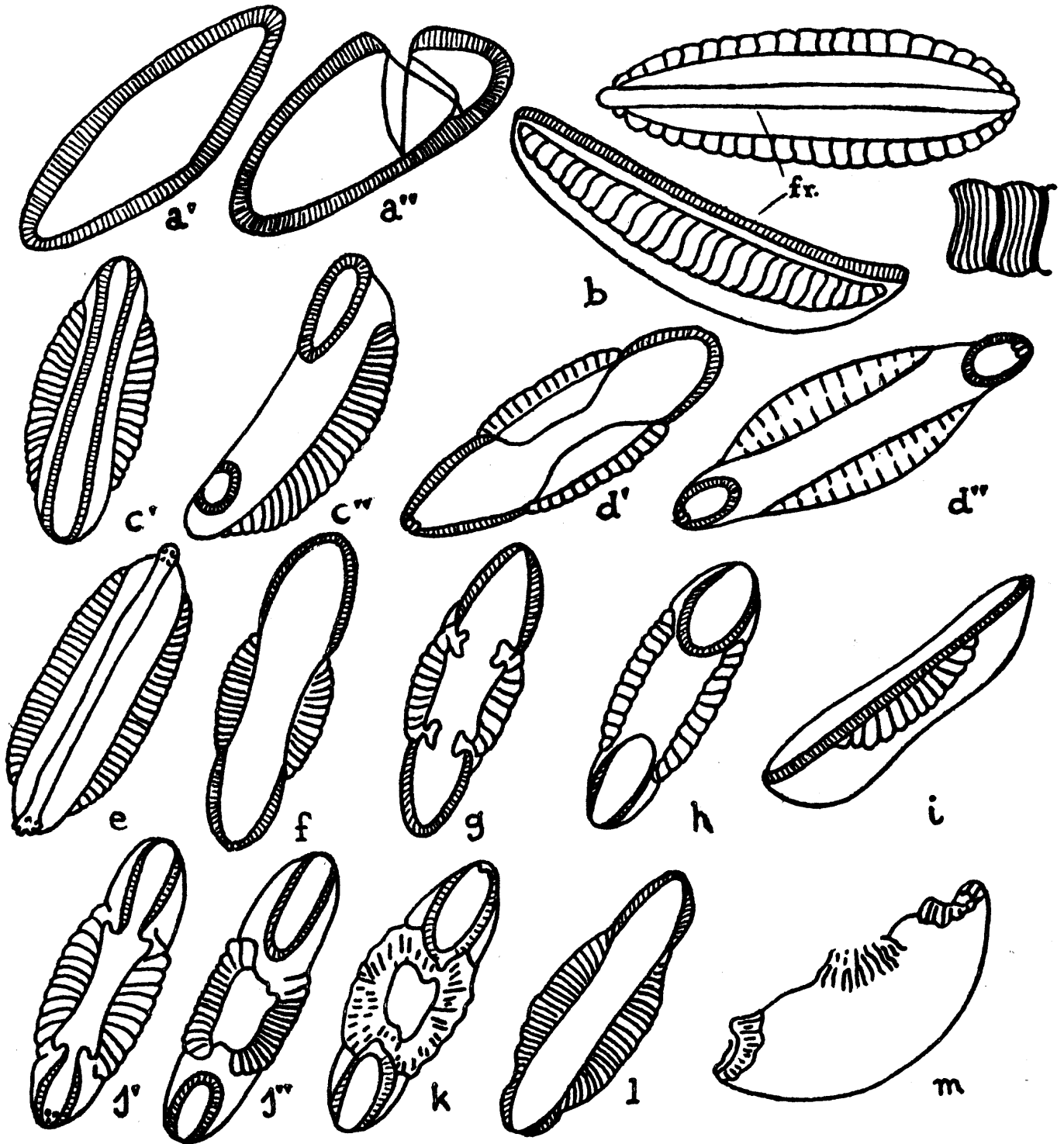


Fig. 1a'. An. plumbeus, after MacGregor, a". The same showing mode of dehiscence, after Eysell, b. An. wilsoni, after Gillies, showing details of float, c'. An. gambiae, after Gibbins, c". The same showing effect of subnormal temperatures, after Deane and Causey, d'. Summer egg of An. walkeri, d". Winter egg of the same, after Hurlbut, e. An. nigerrimus, after Reid, f. An. maculipennis, after Peus, g. An. algeriensis, after Peus, h. An. novaguinensis, after Lee and Woodhill, i. An. amictus, after Lee and Woodhill, j'. An. maculatus, after Walch and Walch-Sorgdrager, j". The same showing variation, after Christophers and Barraud, k. An. pretoriensis, after De Meillon, l. An. pharoensis, after Gibbins, m. An. cyddipis, after De Meillon.

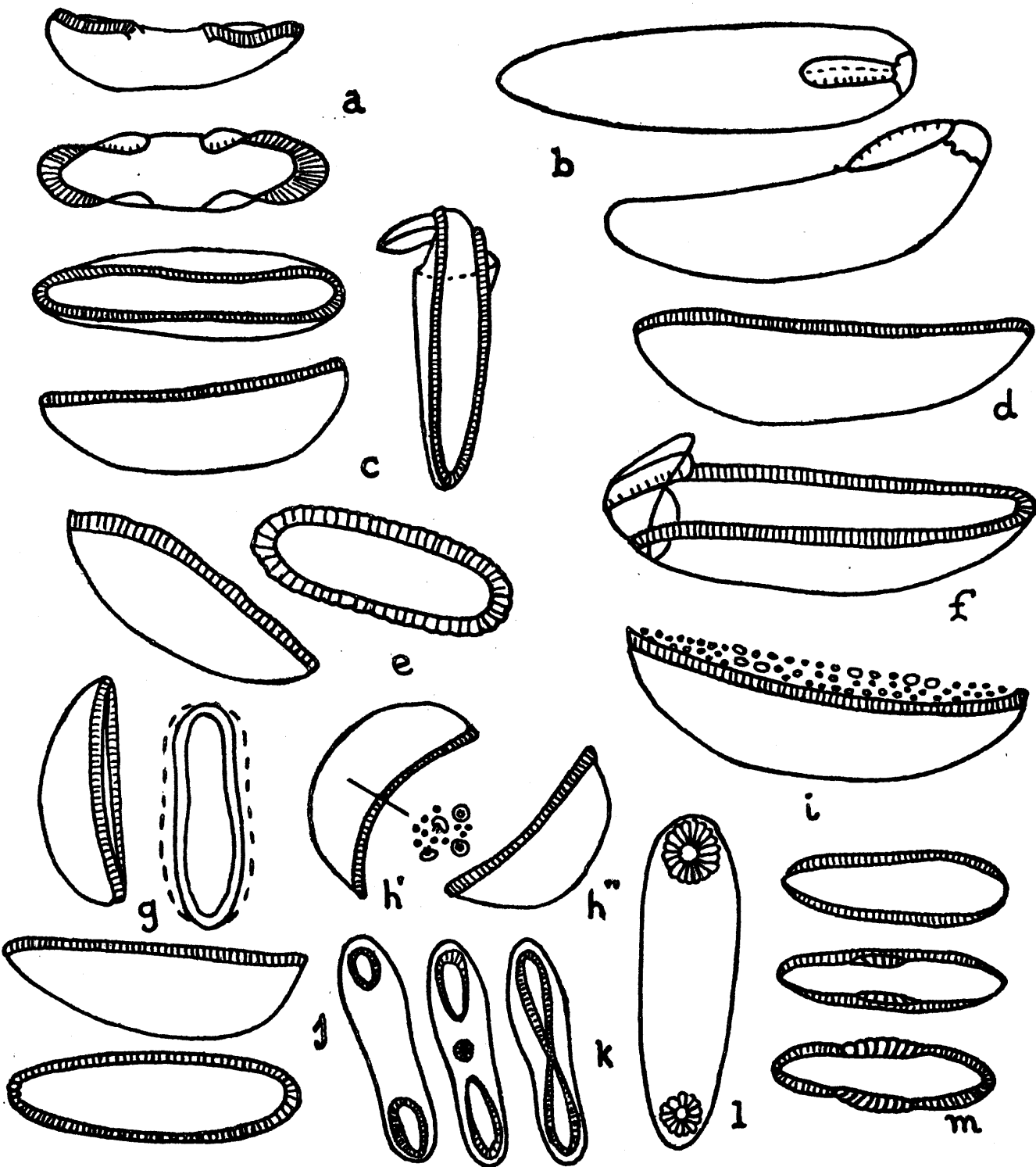


Fig. 2a. An. multicolor, after Foley, b. An. cinereus, after DeMeillon, c. Mimomyia (Mimomyia) hybrida Leicester, after Menon, d. M. (M.) chamberlaini (Ludlow), after Menon and Tampi, e. An. concolor, after Vincke and Leleup, f. An. dthali, showing mode of dehiscence, after Christophers, g. An. superpictus, showing limits of an unusually broad frill tending to turn outwards, after Theodor, h'. An. nili, after Evans, h''. The same, after Theobald, i. An. dancalicus, after Mara, j. An. murphyi Gillies and De Meillon, original, k. An. ludlowae (Theobald), showing variation, after Urbino, l. "An. hellenicus", diagrammatic, after Peus, m. An. sacharovi, showing development of float in winter eggs, after Peus and Falleroni⁷².

Anopheles s.str. Neomyzomyia Myzomyia Pyretophorus Neocellia Cellia Paramyzomyia

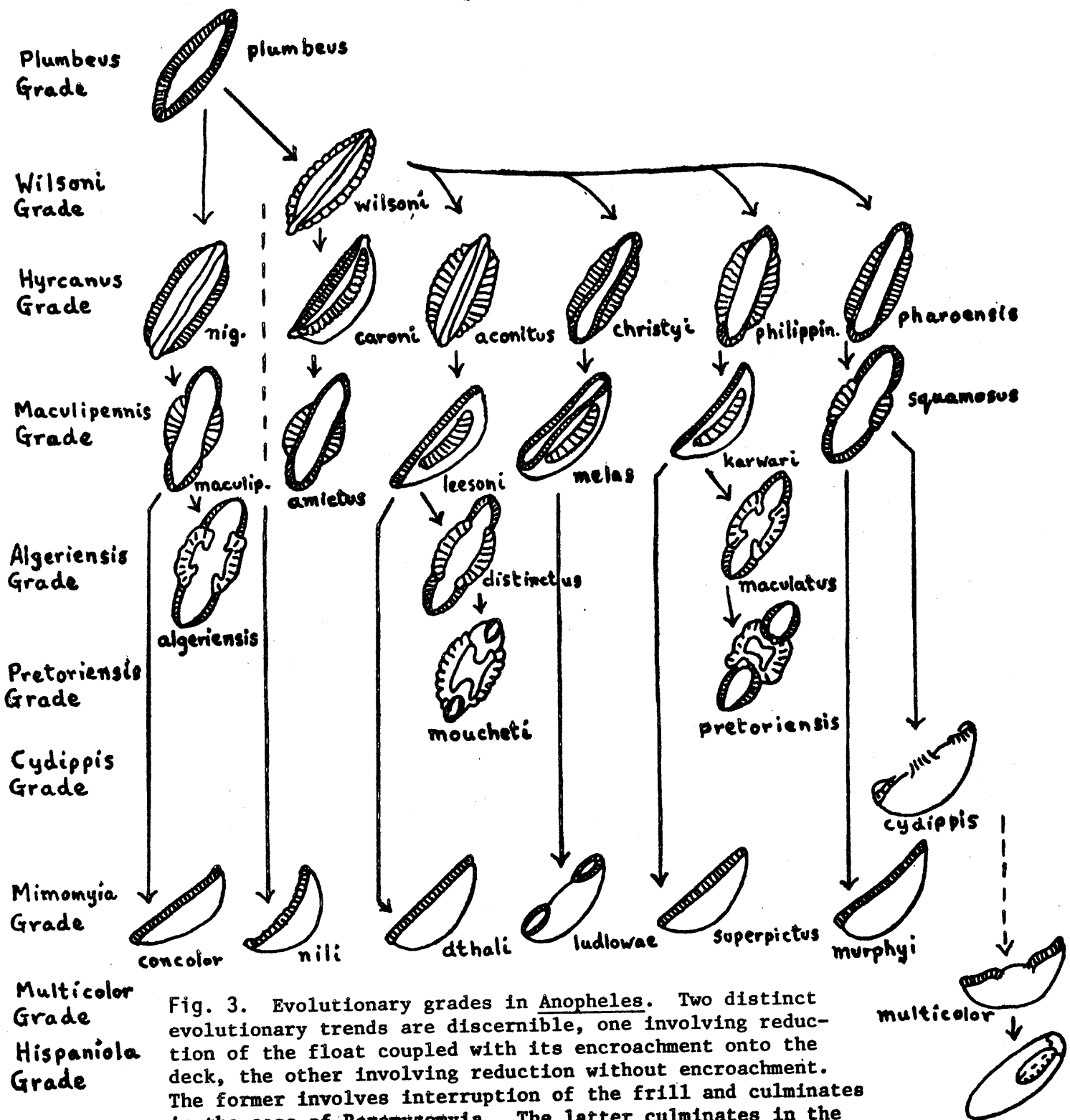


Fig. 3. Evolutionary grades in *Anopheles*. Two distinct evolutionary trends are discernible, one involving reduction of the float coupled with its encroachment onto the deck, the other involving reduction without encroachment. The former involves interruption of the frill and culminates in the eggs of *Paramyzomyia*. The latter culminates in the *Mimomyia* type of egg which may show secondary disruption of the frill by overgrowth of dorsal chorion as in *An.ludlowae*.

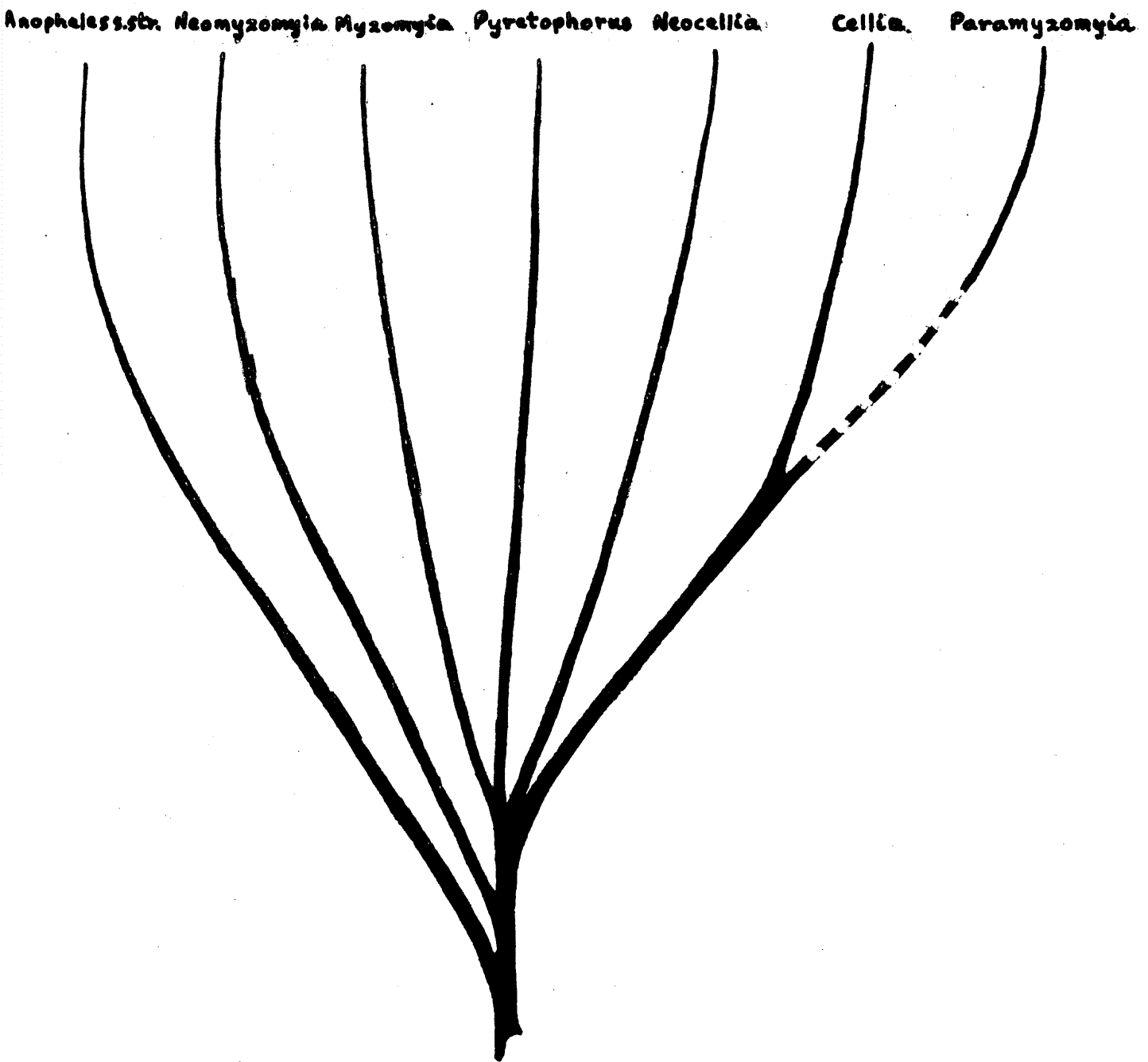


Fig. 4. For those who prefer arboriculture.