Mosquito Eggs XIX

Genus Mansonia (Subgenus Mansonioides Theobald)

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Early authors (Theobald [257], Banks[7]) describe the eggs of this subgenus as laid singly on the water surface. It seems, however, that their observations were made in the laboratory without any alternative substrate. All later authors agree that, in nature, they are laid in compact, rosette-like masses on the floating leaves of water plants (Fig. 1a). In the laboratory floating pieces of cork, live or dead leaves of non-aquatic plants or paper discs may be substituted [258-60]. The first description of naturally occurring egg masses that I have been able to find is by Ingram & De Meillon[261], probably of M. uniformis (Theobald). They have since proved easy to obtain both in the field and the laboratory. In consequence there is a quite large, though scattered, body of literature relating to oviposition behaviour. This will be summarised before describing the eggs themselves.

Mass oviposition. Sporadic mass ovipositions were postulated by Zanetti[262] to account for periodic invasions of Léopoldville by Mansonioides adults. Bonne-Wepster & Brug[263] have some evidence suggestive of bursts of oviposition by M. annulifera (Theobald). I do not think these can be ruled out but it seems that their observations could be explained in other ways. Laurence[264] found that oviposition continued at a more or less uniform rate over the eight successive nights during which observations were maintained. Wharton[265] has some evidence for unusually long intervals between successive blood meals and the subject is one which might repay further study.

Oviposition cycle. Very little is known. Oviposition takes place in the laboratory both by day and by night[258,265] but it is thought that it may take place only by night in nature[265].

Oviposition sites. Iyengar[266-8] obtained egg masses of M. uniformis on Lemna polyrhiza in the laboratory but considered that, in nature, this and the other Indian species (M. annulifera and M. indiana Edwards) laid only on Pistia. Later authors have shown, however, that M. uniformis, at least, is much less conservative. Egg masses wholly or mainly of this species have been found on Eichornia and Lemna in India[269], Jussieua, Hymenachne, Isachne, Oryza, Spirodela, Azolla, Nymphaea and Salvinia in Java[263] and Mikania, Limnanthemum, Hydrolea, Alternanthera, Polygonum, Colocasia, Sphenoclea, Cyperus, Marsilea, Axonopus, Panicum, Leersia, Hygrorhiza, Brachiara, Sacciolepsis, Ischaemum and Nymphoides in Ceylon[270,271]. Alternative plants may be used even in the presence of Pistia[263,269] and may yield egg masses in large numbers. Carter[270] found 58 closely set egg masses on a single grass blade 7 inches long and Laurence & Samarawickrema [271], also working in Ceylon, found egg masses on Salvinia, Nymphaea, Nymphoides and grasses in densities of up to 30-40 per leaf.

It seems that other species, though not restricted exclusively to Pistia, may be more selective. In the Tonkin delta Galliard[272] found egg masses of "M. annulipes" (=M. annulifera) and M. indiana rarely on Pistia and never on Eichornia but abundantly on Salvinia. Further south, however, they were found increasingly on Pistia[273]. Burton[269] found egg masses of M. annulifera on both Pistia and Eichornia and the same author[274] has a photograph of egg masses on Salvinia. Jayewickreme & Niles[275] found that oviposition occurred readily on Salvinia in the laboratory but Laurence & Smith[258], also using a strain from Ceylon, found that, unlike M. uniformis, it would lay on this plant only with reluctance even when enclosed with it in the oviposition pots. Information regarding African species is limited. Records from Ludwigia and Lemna minor[261] most probably refer to M. uniformis but others from Nymphaea, Marsilea, Heterantha, Echinochloa and Oryza[264] may refer either to this species or to M. africana (Theobald) or to both. Schwetz[276] obtained egg masses of M. africana on Pistia, in the laboratory but failed with Hydrolea and Impatiens. Both species will lay on Salvinia in the laboratory but M. africana does so only with reluctance unless it is enclosed in the actual oviposition pot[258].

The eggs are invariably deposited below the water line so that a plant such as Eichornia will only be used when young enough for the lowest leaves to touch the water[269]. Aside from this little is known as to factors governing the utilization or otherwise of particular kinds of plants. Nor is much known regarding other factors affecting the oviposition site. Iyengar[266-8] considered that organic pollution was a prerequisite for oviposition in nature but Laurence [260] found that both M. uniformis and M. africana oviposited more readily with unpolluted than with polluted water in the laboratory with M. africana the more discriminating. In the laboratory M. uniformis lay more often on leaves of Salvinia floating above a dark than on those floating above a light background. No such distinction was observed in the case of M. africana[260]. Factors governing the choice of individual plants, as opposed to different kinds of plants, are a little better understood and will be discussed in the following sections.

Pre-oviposition behaviour. Laurence[260,264] found egg masses of M. uniformis and M. africana mainly on Nymphaea micrantha which was the commonest floating plant in his study area, Pistia being comparatively rare. Eggs were never found on leaves floating more than 15 cm. from standing vegetation. He concluded that gravid females were attracted first to the erect vegetation and only later to the floating leaves. I would agree strongly with this interpretation which parallels closely my own observations on oviposition behaviour in Culex pipiens fatigans Wiedemann in Rangoon[169]. In this case gravid females were regularly found resting on dry vertical surfaces at most about 4 ft, often much less, from the point at which the egg rafts were subsequently deposited. Laurence & Samarawickreme[271] studied an oviposition site in Ceylon stocked by them with Nymphaea and Nymphoides in a regular pattern. This yielded 384 egg masses of M. uniformis from approximately 1.5 m^2 in 24 nights. Aggregation occurred on certain leaves but subsequent laboratory investigations failed to provide any evidence that favoured leaves had been rendered more attractive by previous visits from ovipositing females.

Oviposition behaviour. This was described by Iyengar[266] for M. annulifera. The behaviour of M. indiana and M. uniformis is said to be the same. That of the New World M. (Mansonia) titillans also appears to be very similar[277]. Laurence[264] describes and figures a similar form of behaviour in the African species. The tip of the proboscis is employed to locate a small area of water adjacent to the edge of a leaf. The apex of the abdomen is then pushed forward between the legs, inserted into the water and pushed backwards below the leaf (Fig. 1b). During oviposition the tip of the abdomen is moved from side to side and at the same time slowly withdrawn. Although the eggs are normally laid on the under side of the leaf, Iyengar occasionally observed oviposition on the submerged basal portion of the upper surface. This involved a change of attitude with the wing tips and dorsal surface of the abdomen pressed against the upper surface of the leaf instead of being above and below the leaf respectively (Fig. 1c). It would seem from his description that the essential feature common to both types of behaviour would be 1. Location of leaf/water interface, 2. Downward and forward curvature of the abdomen towards the intersection, 3. Immersion of the tip of the abdomen, 4. Extension of the dorsal surface of the abdomen along the leaf surface (whether upper or lower). The resultant attitude will then depend less on any modification of behaviour than on the nature of the intersection. Schwetz[276] found an egg mass of M. africana in an isolated drop of water on the upper surface of a Pistia leaf. This could, perhaps, be accounted for by interruption of the normal routine while the abdomen was still thrust forward between the legs. As noted by Laurence[260,264] a necessary consequence of the normal oviposition behaviour is that eggs are always found near the edge of the leaf except where this is fenestrated (Fig. 1d). This applies, however, only to leaves floating flat on the water. Where the leaf emerges at an angle from the water the ovipositing female may stand on the lower surface and deposit them at any point along the line of intersection. Iyengar[237] has a figure suggestive of this type of behaviour (Fig. 1e) which recalls the interesting observation by Moore that egg masses of M. titillans on the under side of Pistia leaves are generally found between the ribs[277]. Laurence[264] found that, in the field, medium sized leaves of N. micrantha yielded significantly more egg masses than larger ones. He suggests that this is directly attributable to the oviposition behaviour, gravid females tending to fly away before locating the edges of leaves more than about 12 cm. in diameter. Smaller leaves also yielded fewer egg masses and it is suggested that this may have been due to the shorter time for which they had been available. In the laboratory leaves of Lemna and Salvinia were preferred to those of Azolla while leaves of Salvinia floating among those of Lemna were preferred to the latter possibly because the Lemna leaves have a keeled surface meeting the water at an angle[260].

Diapause and hatching. The interval between deposition and hatching appears usually to be 4-6 days, varying to some extent with temperature[258-260,265]. Wharton[259] records occasional hatching of M. uniformis after only 3 days. At the other extreme the same author[265] observed occasional delayed hatching in M. annulifera after 8 days and in M. bonneae Edwards and M. dives (Schiner) after 12 days. Laurence[260] records intervals of 5-6 days in M. uniformis and 6-7 days in M. africana at 27-29° C. At 24° C. the interval was prolonged by 1 day. Wharton[259] found that eggs of M. uniformis would survive drying for up to 2 days provided they were first kept moist for 1-3 days. Eggs of M. africana remained viable for 4 days after laying, sandwiched between moist cotton wool and filter paper in a sealed perspex tube during transit by air[278]. Wharton[259], using a similar technique, was able to send viable eggs from Malaya to London. Laurence[260] found that drying over calcium chloride for more than 2 hours completely inhibited hatching. Attempts at initiating diapause by drying were unsuccessful. Hatching took place mainly between sunset and sunrise. Eggs placed in darkness just before they were due to hatch, and those kept in continuous darkness, showed the same hatching rhythm as those kept in a normal light-dark regime. All authors agree that hatching is by apical dehiscence (Fig. 2a). Lincoln[279] could find no hatching line in eggs of M. africana prior to dehiscence. I have observed a tendency to longitudinal splitting in sterile eggs similar to that observed in Aedes and Armigeres.

Egg masses. Numerous photographs are available [256,258,266,268,269,272,274,276] but M. africana is the only species for which the egg mass has been described in detail[279]. Air is said to be trapped between the individual eggs, below the level of the apical processes, possibly forced out of solution by the strongly hydrophobic properties of the outer chorion covering the main body of the egg (Fig. 2b). As development proceeds this becomes increasingly wettable so that shortly before hatching the air bubble is lost. This also happens if the eggs die. The outer chorion consists only of a single layer less than 1 mu thick and oxygen diffuses into the eggs from the bubble surrounding them. If the buble is removed it is not reformed. This account differs from that given for M. titillans in which air is said to be entrapped between the apical processes of the eggs[277]. It is possible that the discrepancy is a real one in view of the different distribution of chorionic tanning in the two species. (See next section). The egg masses are said by Lincoln to be glued to the leaf by a cement matrix.

Differences in size and shape of the egg masses may be partially diagnostic as between species. Iyengar[266-8] considered the egg masses of M. annulifera, indiana and uniformis to be indistinguishable but Burton[269], also working in India, found that those of M. uniformis were often less regularly circular than those of M. annulifera while Rodenwaldt[280], working in Java, found the egg masses of M. indiana to be larger and more circular than those of M. annulifera. According to Iyengar the number of eggs in individual egg masses of Indian species varies from 75 to 120.

Eggs. These are much as described for subgenus Mansonia with a long, narrow apical process terminating in a small cup within which are several minute projections of the inner chorion (Fig. 2c,d). Most of the available descriptions are very meagre but it is clear from the figures which accompany them that the majority of species have the apical process darker than the rest of the egg. This is an interesting distinction from the eggs of Mansonia s. str. almost all of which have the apical process paler than the remainder. The only known exception is the egg of M. humeralis Dyar & Knab which is peculiar in other respects[277]. The contrast is best seen in immature or hatched eggs. The main body of eggs containing developing larvae appears much darker. This is well seen in Rodenwaldt's photographs of hatching eggs (Fig. 2a). It may account for the discrepancy between Wharton's description of the eggs of M. annulifera, bonneae, indiana and uniformis as dark brown to black and his generalized figure of the Mansonioides egg which shows very conspicuous apical darkening (Fig. 2e). Iyengar[266-8] considered the eggs of M. annulifera, indiana and uniformis to be indistinguishable. Wharton[265] agrees and adds to these the eggs of M. bonneae but Rodenwaldt[280] found that eggs of M. indiana were larger than those of M. annulifera (1.01mm. x 0.2 mm. as against 0.8 mm. x at most 0.18 mm.). Banks[7] gives the length as 0.82 mm. in Philippines M. annulifera. According to Rodenwaldt the difference in length is due to the much longer apical process in M. indiana. (Fig. 2f,g). Burton[269] found that eggs of M. annulifera containing well developed embryos could be distinguished from those of M. uniformis by characters affecting the saddle hair and the spines at the tip of the antenna but these are larval characters rather than egg characters as such. The only other diagnostic characters cited in the literature concern the eggs of M. dives and M. annulata Leicester. According to Wharton[265] these are milky white in colour which would distinguish them from the eggs of all other known Mansonia. The eggs of M. annulata are said to have a longer apical process so that the maximum breadth occurs at about midway between base and apex instead of at 2/3-3/4 of the distance from base as in M. dives. Chorionic ornamentation, though present, receives little mention, none on a comparative basis. Banks[7] describes the egg of M. annulifera as having "numerous flat, circular air chambers" at the neck end and these are shown, apparently much exaggerated in his figure (Fig. 2h). Rodenwaldt[280] describes the surface of eggs of the same species from Java as finely granulated. He does not mention larger chorionic papillae at the anterior end but these can be seen in his photographs (Fig. 2a, g). According to the same author the eggs of M. indiana have the outer surface covered with a fine mosaic-like speckling (Flaechenmuster). Traces of this can also be seen in one of his photographs (Fig. 2f). The only other character with potential diagnostic value mentioned in the literature concerns the teeth at the tip of the apical process. Their presence in M. annulifera (and by inference in M. indiana and uniformis) is mentioned by Iyengar[268] but he gives no details. Lincoln[279] notes that there are 4-7, usually 5, in M. africana. No information is available regarding other species. To check the various potential diagnostic characters mentioned in the literature I have examined eggs of M. uniformis from Malaya, Ceylon and Uganda, M. africana from Tanzania, Uganda, Congo (Kinshasa) and Ghana and M. annulifera from Ceylon. I am indebted to Dr. Ramalingam for the eggs from Malaya and to Dr. B. R. Laurence for most of the others. A brief description follows.

M. uniformis. Eggs of both the oriental and the African forms are covered with chorionic papillae except at the extreme posterior end, where this is inserted into the thick, conspicuous glue, and the tip of the anterior process which is inserted into the apical cup. In the region of the shoulders the papillae are much larger than elsewhere and are relatively prominent. Elsewhere they are very small and only slightly raised though somewhat larger towards the posterior end (Fig. 3a). Hatched eggs of the African form show the area of enlarged papillae on the shoulders to be roughly coterminous with the line of dehiscence of the apical cap (Fig. 3b). The apical cup is seen under phase contrast to have an infolded lip on one aspect and a small invagination on another (Fig.3a). The inner chorion at the extreme tip forms 3 larger and 2 smaller teeth whose appearance varies with aspect (Fig. 3c). Eggs from Ceylon and Uganda closely resemble those from Malaya in the shape of these teeth and in the chorionic ornamentation.

M. africana. Eggs of this species do not appear to differ significantly in any respect from those of M. uniformis.

M. annulifera. The two egg masses available to me are in poor condition. On the main body of the egg the chorionic papillae are distinctly larger than in M. uniformis (Fig. 3d). Those on the shoulders are mostly rubbed or obscured. I have the impression that they are considerably larger and might be of diagnostic value but this needs to be confirmed with better material. The teeth at the tip of the apical process closely resemble those of M. uniformis. The apical process itself tends to be a little shorter than in Malayan and African M. uniformis but there is some variation in individual eggs and those of M. uniformis from Ceylon tend to be intermediate (Fig. 3e). Taking the subgenus as a whole there is evidently a striking resemblance to the eggs of Mansonia s. str. and, neglecting the apical process, to those of Ficalbia277.

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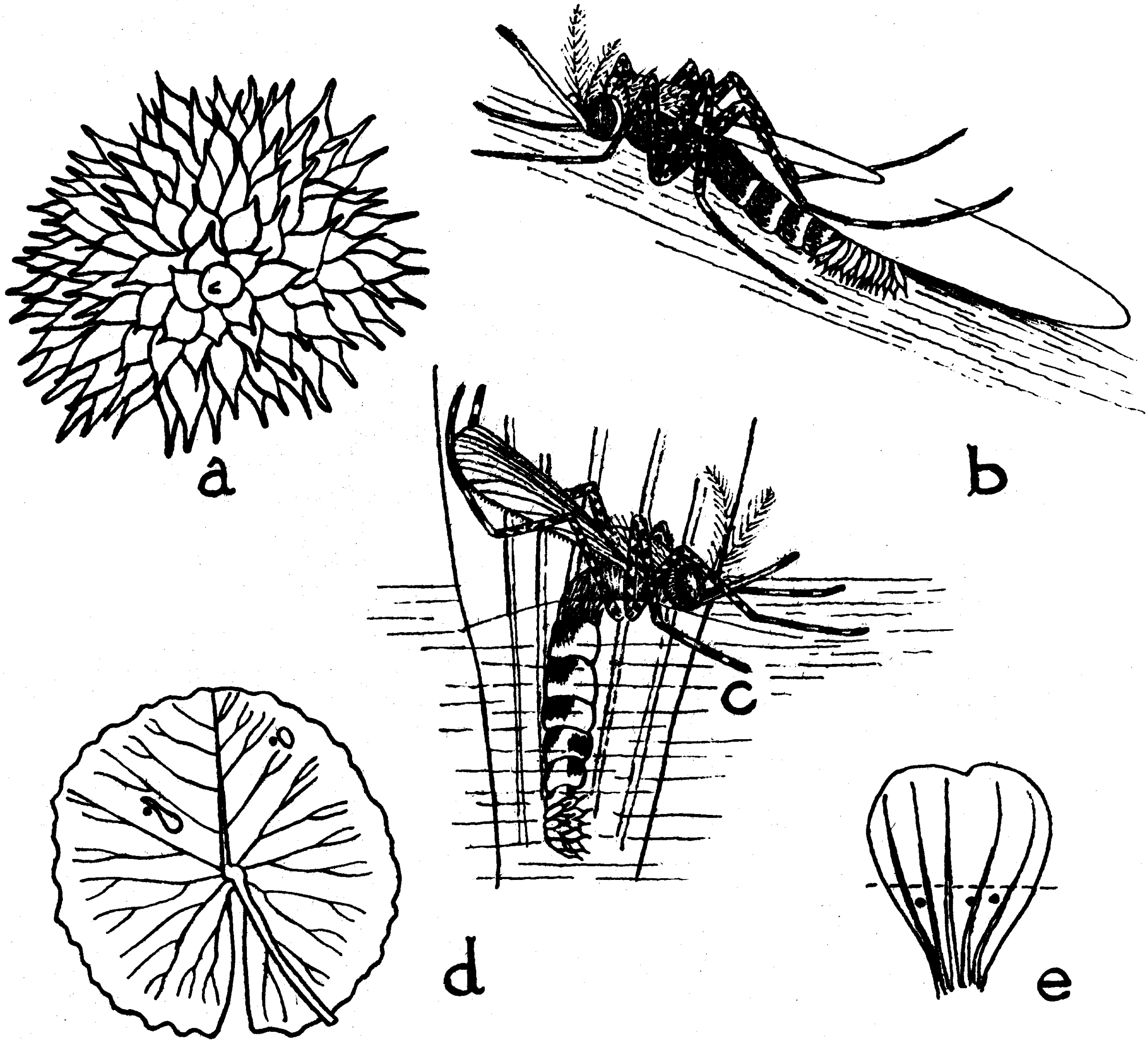

Fig. 1. a. Egg mass of M. annulifera (after Iyengar[237]), b., c. Ovipositing M. annulifera (after Iyengar[266]), d. Egg masses on fenestrated leaf of Nymphaea lotus (after Laurence[264]), e. Egg masses on under surface of Pistia leaf (after Iyengar[237]).

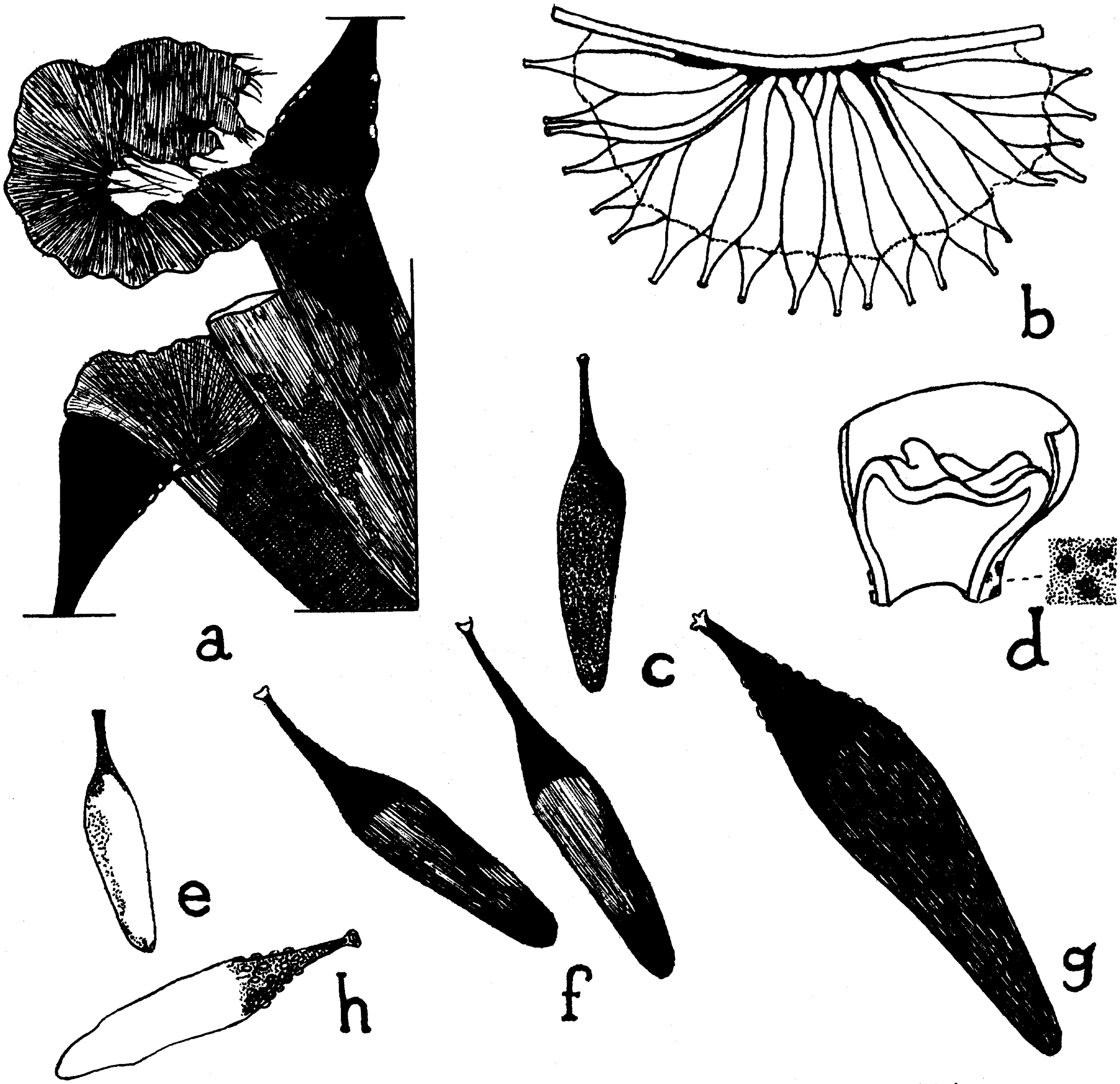

Fig. 2. a. Hatched eggs of M. annulifera (after Rodenwaldt), b. Egg mass of M. africana, in section, showing trapped air (after Lincoln), c. Egg of M. annulifera (after Iyengar[237]), d. Tip of egg of M. africana, in section (after Lincoln), e. Egg of M. (Mansonioides) sp. (after Wharton[265]), f. Eggs of M. indiana (after Rodenwaldt), g. Egg of M. annulifera (after Rodenwaldt), h. Egg of M. annulifera (after Banks).

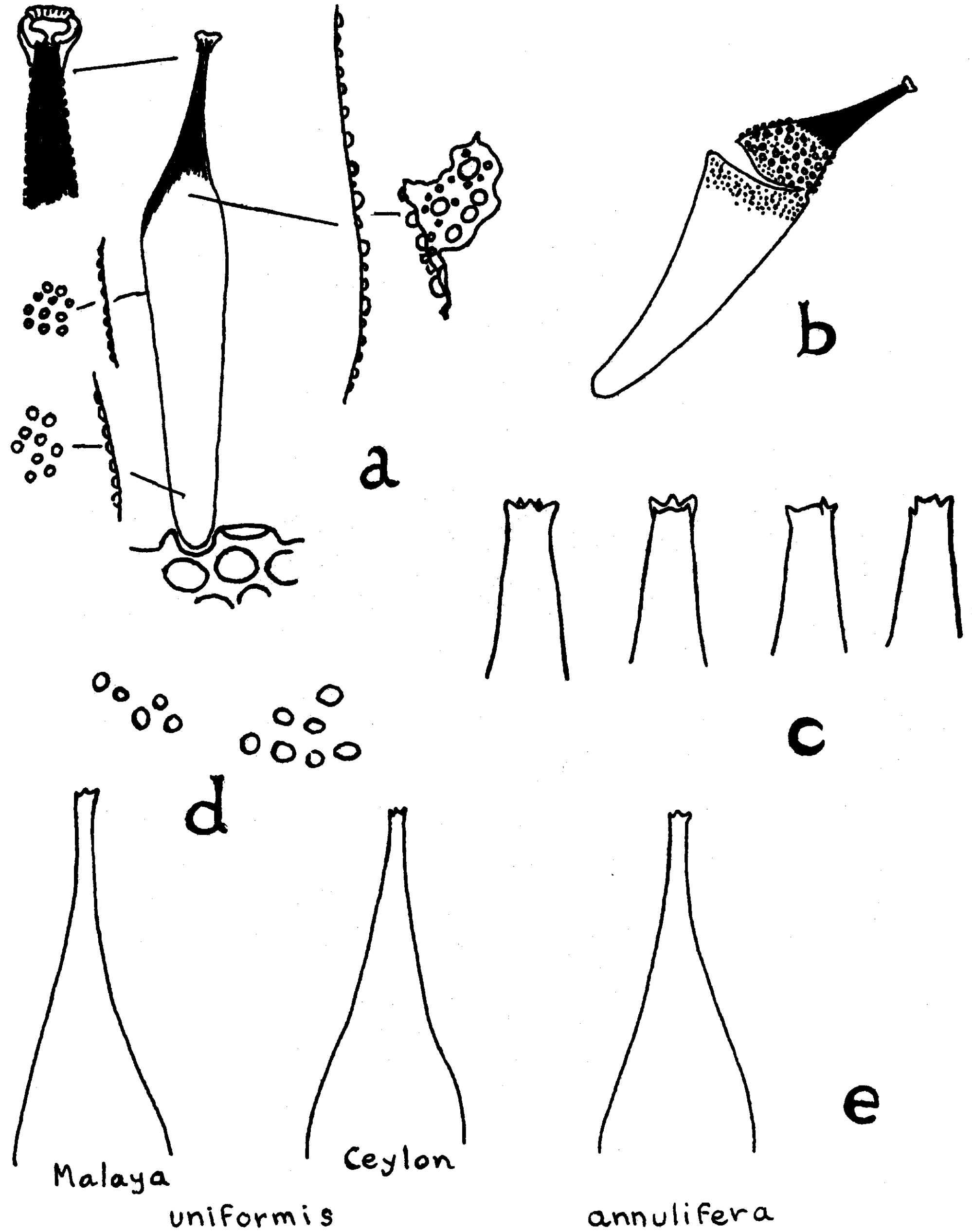

Fig. 3. Egg of M. uniformis (Malaya) with details of chorionic ornamentation and apical cup, b. Hatched egg of M. uniformis (Uganda), c. Tips of eggs of M. uniformis (Malaya) with apical cups removed, d. Chorionic papillae from posterior ends of eggs of M. uniformis and M. annulifera at same magnification for comparison, e. Apices of eggs of M. uniformis from Malaya and Ceylon and of M. annulifera. All of these original.