Mosquito Eggs XIV

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Genus Armigeres Theobald (continued) and Aedes subgenus Alanstonea Mattingly

In the previous paper in this series[198] I described the known eggs of Armigeres s. str. and those of two species of Armigeres subgenus Leicesteria. The present paper deals with four further species of Leicesteria, all with eggs previously undescribed, and with Alanstonea which, although currently treated as a subgenus of Aedes, shows striking resemblances to Armigeres in which both the known species were at one time included.

Armigeres subgenus Leicesteria

Arm. digitatus (Edwards)

The following description is based on a single egg from Ulu Langat, Selangor sent by Dr. Ramalingam. It is one of 12 eggs laid in a row on water 6 days after the mother was captured in a chicken-baited trap. As it is the only egg available I have refrained from mounting it, preferring to send it to Prof. Hinton for electronscan microscopy. The following description is based on a relatively superficial examination in a wet preparation. The whole of one surface is covered with a reticular meshwork, each mesh of which is provided with a chorionic papilla (Fig. 1). Except, apparently, at the posterior and extreme anterior end these papillae are long, narrow, digitiform. I take the surface in question to be the upper (ventral) surface by analogy with the eggs of other members of the subgenus. The papillae are apparently absent from the lower surface. On the upper surface they increase in length progressively from the posterior towards the anterior end. They are somewhat comparable to the type of chorionic papilla which is a familiar feature of the eggs of Psorophora[12, 200, 201], though much more conspicuous. In view of the apparent importance of egg parasitization in this subgenus, the evidence for which is discussed below, I suspect they may have a protective function.

Egg Parasitization in Leicesteria

As noted in my previous paper, one batch of eggs of Arm. dentatus from Ulu Langat, Selangor, sent by Dr. Ramalingam, proved to be heavily parasitized. The most conspicuous feature of these eggs is the presence of numerous circular perforations in the inner chorion. (The outer chorion is wholly or largely lost). Protruding through some of these perforations are extensions of the enclosed parasites which I presume to be respiratory in function (Fig. 2). Both features suggest to me that the parasites are hymenopterous, the perforations being made by the ovipositor. To the best of my knowledge no egg parasites of mosquitoes have previously been recorded and I know of no other group of parasites of insect eggs possessing these features. Some parasitized eggs have been sent to Prof. Briggs at the WHO reference centre in Ohio State University in the hope of securing an identification though this may not be possible unless the parasite can be reared from fresh eggs. In the

meantime there are a few pointers which may be helpful. The eggs were laid some 4 days after the mother was captured biting man. This might suggest that they were parasitized by some organism in the water provided for oviposition, i.e. by one of the more or less fully aquatic Hymenoptera belonging to the families Mymaridae (Anagrus, Caraphractus), Scelionidae (Tiphodytes, Limnodytes) or Trichogrammatidae (Prestwichia)[202, 203]. If these occur in the bamboo internodes in which Arm. dentatus seems usually to breed then it might not be too difficult to find them. As an alternative phoresy cannot, I think, be entirely ruled out. Some Scelionidae and Trichogrammatidae are phoretic though only, so far as I know, on much larger insects.

I have not tried to remove any parasites from the few eggs which I have retained and they are difficult to count through the pigmented chorion. Moderately parasitized eggs appear to contain some 12-16, possibly more, and one egg is punctured in some 90 places. In this connection it is perhaps worth noting that as many as 70 Prestwichia have been reared from a single Dytiscus egg[202]. As regards the particular host association, on the other hand, Dr. Boucek of the Commonwealth Institute of Entomology has kindly pointed out to me that this might seem suggestive of Scelionidae which are known to parasitize eggs of Diptera, notably those of Tabanidae[204].

Whatever may prove to be the identity of the parasites it seems a reasonable supposition that the previously unexplained habit of some Leicesteria of carrying their eggs on their hind legs until they are ready to hatch is protective against parasitization. If I am right in believing that the peculiar ornamentation of the egg of Arm. digitatus is similarly protective in a species lacking the behavioural adaptation then this would be further evidence of the importance of egg parasitization in Leicesteria. It would be particularly interesting to know if raft formation in Arm. dentatus normally occurs in nature. This also could conceivably have a protective function. One begins to wonder just how far parasitization has played its part in the evolution of the mosquito egg.

Arm. dolichocephalus (Leicester)

The following description is based on two batches of eggs, one from Ulu Gombak, the other from Ulu Langat, Selangor, sent by Dr. Ramalingam. The former were laid in a ribbon, part of which is illustrated in Fig. 3. The latter were laid singly (perhaps by a female in articulo mortis?). Oviposition took place 4-5 days after capture of the females concerned. The most immediately conspicuous feature of these eggs is their unusual breadth, the impression of which is heightened by the fact that the outer chorion seems to be inflated at either pole (Fig. 3a). All the eggs in the ribbon are hatched but two of them still have the apical caps attached and this makes it possible to distinguish the dorsal from the ventral surface. The remaining eggs are all either hatched, split or otherwise distorted and cannot be used for determining the shape though several of them show the ornamentation well. The upper (ventral) surface is ornamented with large outer chorionic papillae which are drawn up vertically and at the same time compressed laterally. The expanded bases give them a somewhat thorn-like appearance when viewed from above while in side view they appear scalelike and more or less transparent (Fig. 3b, d). Their bases are highly irregular with numerous filamentous processes radiating outwards from the edges. They cover all or most of the ventral surface at the poles but are well developed only towards the mid line in the intervening region, progressively less well developed towards the sides. The dorsal surface is covered with very large, flat-topped chorionic papillae well separated from one another (Fig. 3c,d). These continue well up onto the sides of the egg but except towards the poles they are interrupted by a longitudinal band of compact groups of very small papillae (Fig. 3d). It seems that it is along this band that adjacent eggs adhere to one another in the ribbon. The inflated outer

chorion at the poles is ornamented with short, sinuous, linear thickenings forming a loose, discontinuous network (Fig. 3b, c). The apical cup (Fig. 3c) is of aedine type but with more the appearance of a membranous corolla than is usual in the aedine genera. The micropylar disc is strongly sclerotized and very conspicuous. Dehiscence takes place entirely in the equatorial plane and in most cases is complete.

Arm. inchoatus Barraud

Four eggs from Ulu Langat are available for description but only one has the outer chorion at all complete. This has been sent to Prof. Hinton for electronscan microscopy. The eggs are described as laid "on water surface; single in a row". Macdonald[196] records a female of this species as laying 63 eggs in two batches, one on the hind legs, the other on the surface of the water. So far as can be seen the ornamentation is very similar to that found in Arm. dentatus (Fig. 4 of my previous paper) but there is a marked difference in shape, the present species having the ends much more bluntly rounded (Fig. 4).

Arm. traubi Macdonald

The following description is based on a single batch of eggs from Ulu Langat described as "laid in raft attached to hind legs, later dropped on water surface." Dr. Ramalingam tells me that in this case the interval between oviposition and deposition of the eggs on the water surface was only a few hours. The eggs are closely similar to those of Arm. flavus, the ornamentation being apparently almost identical (Fig. 5b and see Fig. 3 of my previous paper). They are, however, somewhat darker in colour with the ornamentation slightly more conspicuous and they have a small apical cup not seen in Arm. flavus. Their shape is rather variable. Some eggs are more or less symmetrical about the long axis but the majority are sausage-shaped (Fig. 5a). Direct comparison with Arm. flavus is impossible because all the available eggs of that species are hatched and all those of Arm. traubi unhatched. The unusual shape of the apical cap in Arm. flavus seems merely to reflect the anterior position of the line of dehiscence and might also be found in the present species if dehiscence takes place near enough to the apex.

Arm. annulitarsis (Leicester), balteatus Macdonald, magnus (Theobald), pendulus (Edwards)

I have not seen eggs of any of these species. Nor has their appearance been described. Macdonald[196] has the following notes:

"Ar. annulitarsis..... lays an egg batch on the hind legs, holding the eggs between the tibia and the first tarsal segment, before depositing them on the water. When the mosquito is retained in a tube with only damp filter paper, however, egg-laying is either delayed or the eggs are laid scattered over the filter paper. There is little doubt that the normal behaviour is for an egg-batch to be laid on the hind legs and then after a delay, which in the laboratory may last several hours, the eggs are released on the water. Ar. balteatus, inchoatus and magnus are essentially similar..... In the case of magnus..... a female laid a few eggs singly on the water surface, but later, when transferred to another jar with water, laid an egg-raft on hind tarsal segments I and II, this raft being released on the water after about 20 minutes. In general Leicesteria eggs hatch about two days after being laid.

In addition to all the species already mentioned above this was confirmed for both dentatus and pendulus..... If eggs are laid on damp filter paper, they will hatch after a few days just as they would if they had been laid on water, and the young larvae will die unless they are transferred to water. This was confirmed with the eggs of annulitarsis and dolichocephalus."

Functional significance of chorionic sculpturing

The eggs of those species available to me fall into three groups: 1. Arm. flavus and traubi with chorionic sculpturing very feebly developed, 2. Arm. dentatus and inchoatus with sculpturing more strongly developed towards the poles but feebly developed in the intervening region, 3. Arm. digitatus and dolichocephalus with sculpturing very strongly developed over most of the egg. From the evidence afforded by the egg of Arm. dolichocephalus it seems that replacement of large papillae by groups of very small ones in the area of contact is necessary for the adherence of neighbouring eggs. This is also consistent with the strongly adherent eggs of Group 1. It further appears that limitation of such groups of papillae to the sides of the egg results in ribbon, as opposed to raft, formation. The possibility that the greatly hypertrophied papillae found in Group III might be protective against parasitization seems worth bearing in mind but further speculation on this point would be premature until more is known regarding the incidence of egg parasitization in the subgenus as a whole.

Aedes subgenus Alanstonea

As noted above, both species currently included in this subgenus were formerly placed in Armigeres[21]. It therefore seems appropriate to discuss them here. They were later transferred to Aedes subgenus Stegomyia[205,206] but they do not fit this at all well and a new subgenus was accordingly created for them[199]. Edwards[21] seems to have been impressed chiefly by the curved proboscis and by the general ornamentation, particularly of Ae. brevitibia. However, both these features are to be found also in Tripteroides subgenus Rachionotomyia, an affinity which possibly deserves more consideration than it has so far received, particularly in view of certain sabethine features in the early stages (reduction of pupal paddles, form of pupal trumpet, reduction of larval ventral brush). These could all be adaptive to the breeding places (Nepenthes pitchers) and since both species key readily, in both sexes and all stages, to Aedes [198] I have no hesitation in retaining them in that genus. The description by De Meijere[123] of the egg of Ae. treubi seems equally consistent with either Aedes or Armigeres s. str. but it does not bear out the possible relation to Arm. flavus suggested by the short hind tibia[207]. A translation of De Meijere's description follows. His figure is reproduced here as Fig. 6.

"The eggs (Fig. 13) are longish (ca. 0.78 mm long and 0.2 mm broad), with the end from which the larva hatches somewhat broader than the other. They are very dark, almost black. The outer surface is devoid of sculpturing. They do not float on the water but are laid separately on the inner surface of the pitchers stuck firmly along their length. Here they lie, always in a ring, parallel to the long axis of the pitcher, arranged in more or less separate groups."

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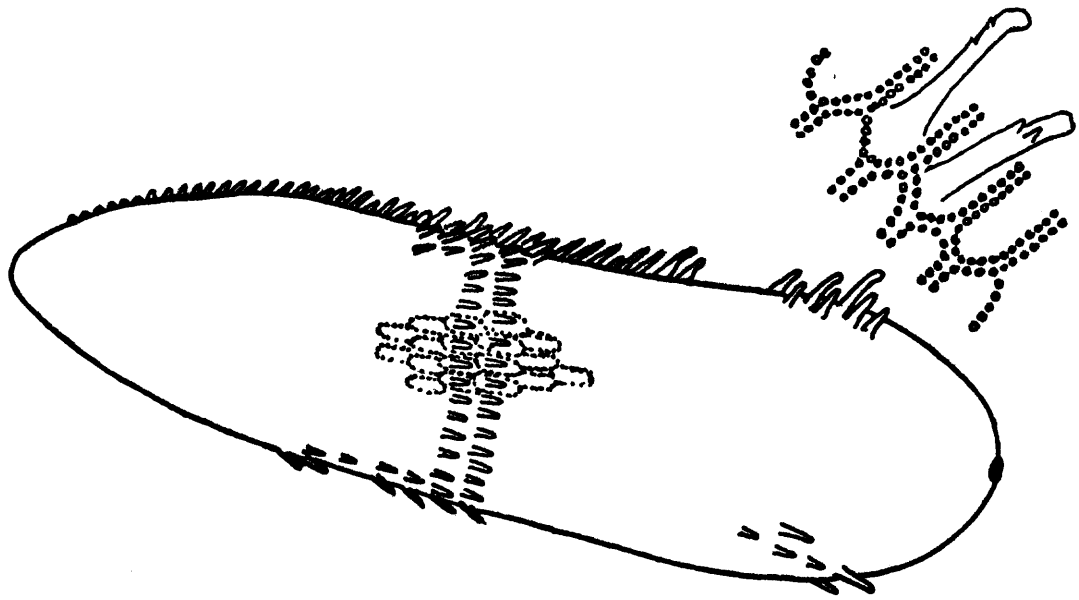

Fig. 1. Arm. (Leic.) digitatus. Whole egg showing details of ornamentation.

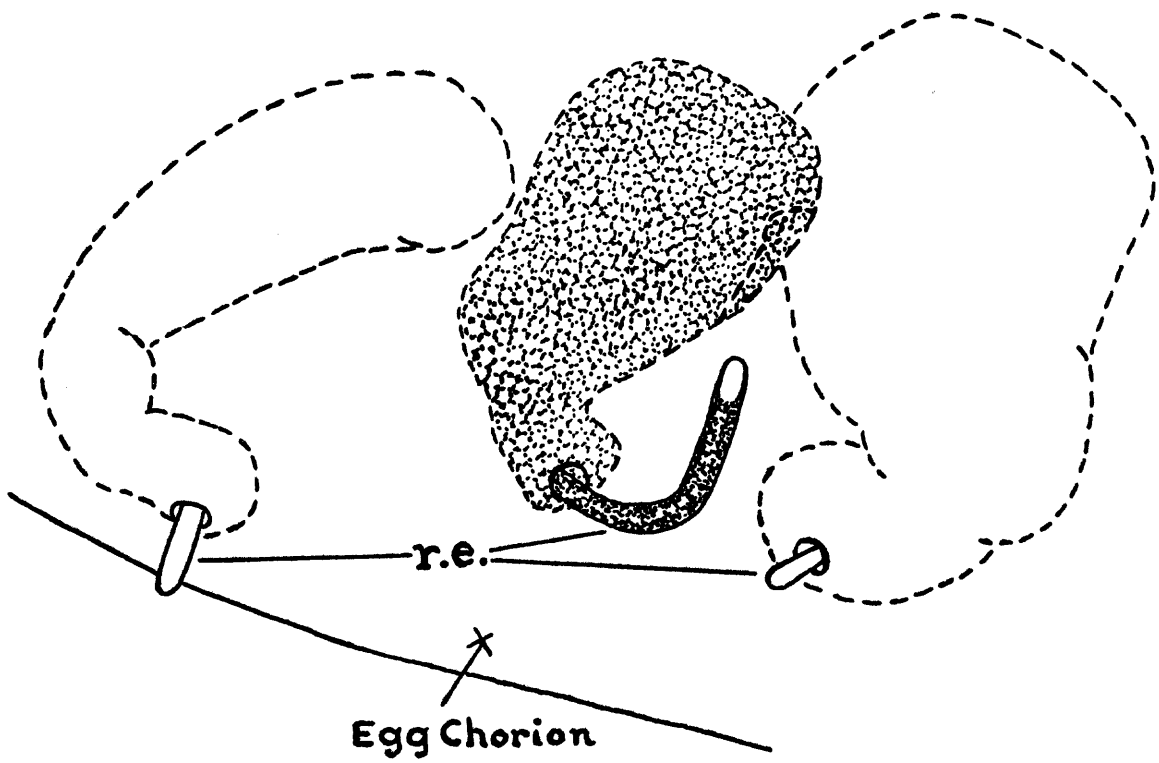

Fig. 2. Portion of parasitized egg of Arm. (Leic.) dentatus r.e. Respiratory extrusions.

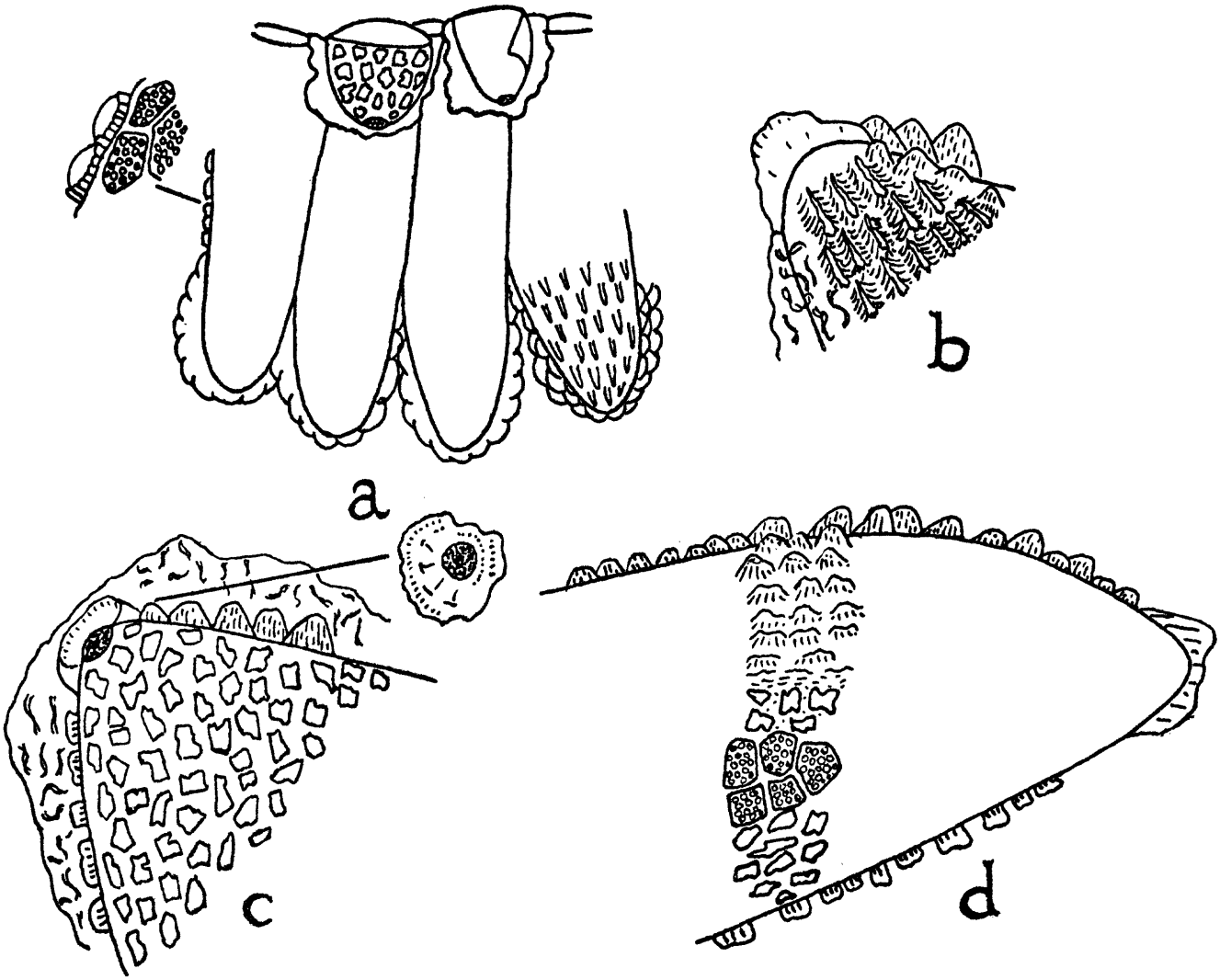

Fig. 3. Arm. (Leic.) dolichocephalus. a. Portion of hatched egg ribbon in ventral view, b. Apex of egg in ventral view, c. Apical cap in dorsal view, d. Apex of egg in left lateral view.

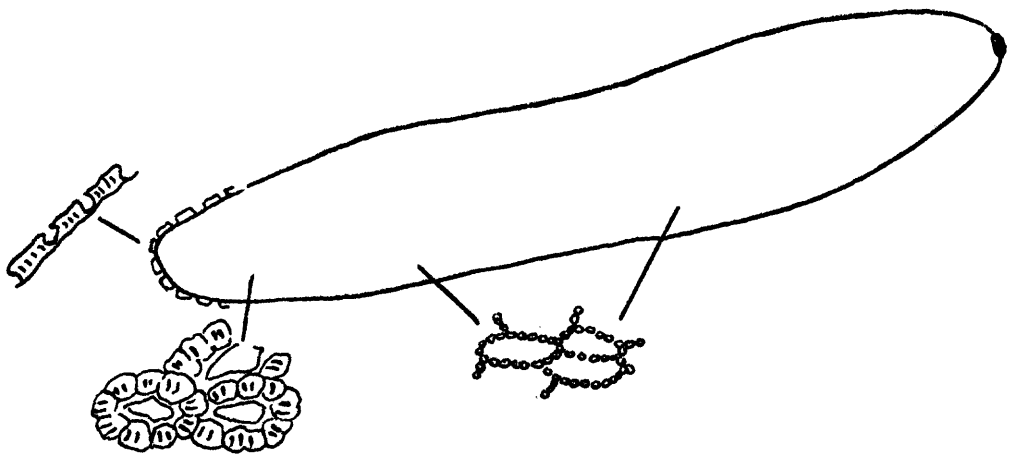

Fig. 4. Arm. (Leic.) inchoatus. Whole egg with details of ornamentation.

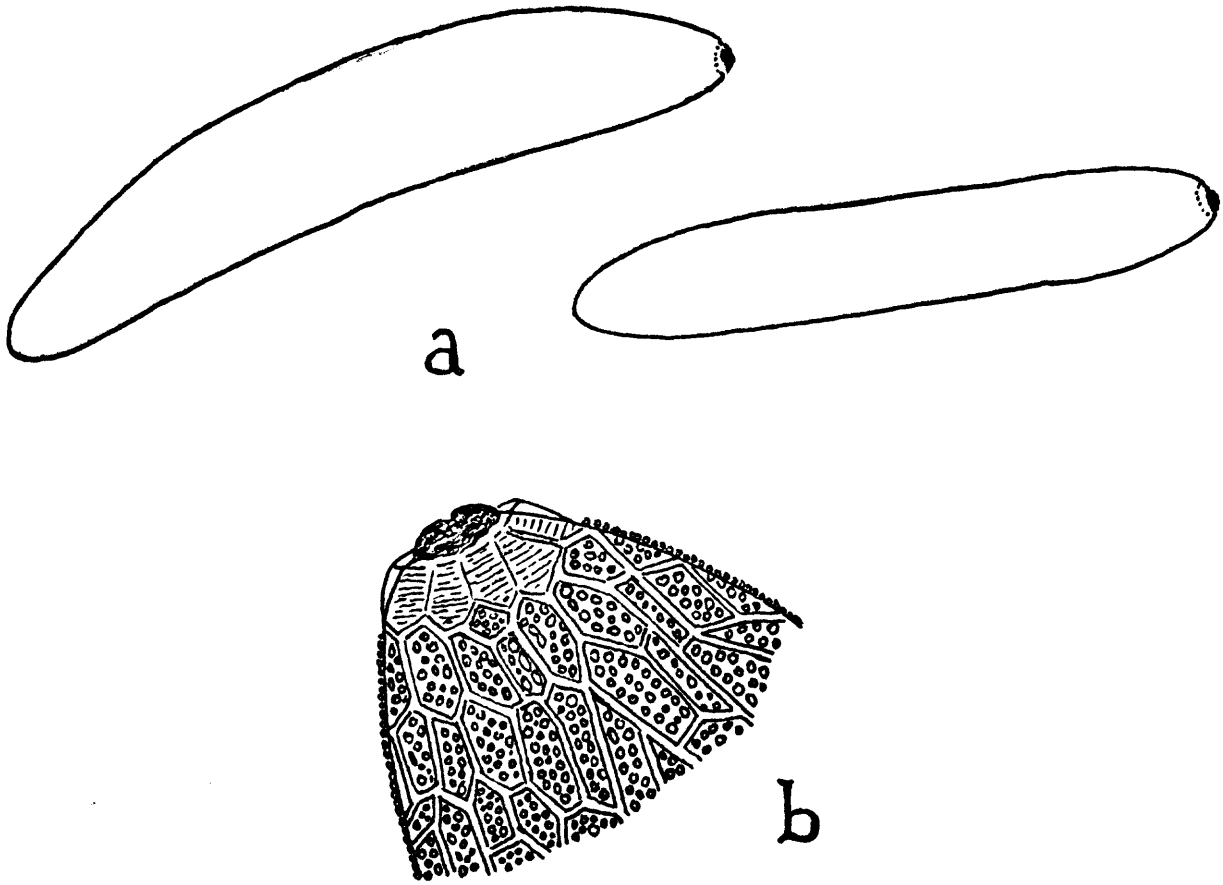

Fig. 5. Arm. (Leic.) traubi. a. Whole egg showing variation in size and shape, b. Apex of egg showing details of ornamentation.

Fig. 6. Aedes (Alanstonea) treubi. Whole egg, after De Meijere.