

SEM EXAMINATION OF THE EGGS OF FIVE BRITISH *Aedes* SPECIES

M. W. SERVICE,¹ D. DUZAK² AND J. R. LINLEY^{2,3}

ABSTRACT. Ultrastructure descriptions are given of the eggs of five British *Aedes* species, namely *Aedes (Aedes) cinereus* Meigen, *Aedes (Ochlerotatus) cantans* (Meigen), *Aedes (Ochlerotatus) punctor* (Kirby), *Aedes (Ochlerotatus) detritus* (Haliday), and *Aedes (Ochlerotatus) rusticus* (Rossi). Eggs of the first 4 species are broadly cigar/boat-shaped, with those of *Ae. cinereus* being characteristically long and narrow, in contrast to the overall shape of *Ae. rusticus*, which is quite distinct, being in profile almost subtriangular with rounded corners, and is completely species-diagnostic. In *Ae. cantans*, *Ae. punctor*, and *Ae. rusticus* there is usually a single large tubercle in each chorionic cell and there is little, if any, difference in the sculpturing of the ventral and dorsal surfaces, whereas in *Ae. detritus* each cell contains more than 20 tubercles, and in *Ae. cinereus* there are usually 6 tubercles per cell ventrally, but dorsally there are no tubercles or distinct cells but numerous cone-shaped papillae. All 5 species can be separated from each other by SEM examination of their chorionic patterns.

INTRODUCTION

All 5 *Aedes* species considered in this paper, *Aedes (Aedes) cinereus* Meigen, *Aedes (Ochlerotatus) cantans* (Meigen), *Aedes (O.) detritus* (Haliday), *Aedes (O.) punctor* (Kirby), and *Aedes (O.) rusticus* (Rossi), are northern temperate mosquitoes having a Holarctic or Palearctic distribution. Eggs of all species were obtained from females collected in England.

Females of all species bite mammals, including humans, and all can be serious pests. Although a few arboviruses have been isolated from some of these species, such as Tahyna virus from *Ae. cantans* and *Ae. cinereus* (Lundström 1994), none is considered an important disease vector. All species lay their eggs in mud and damp leaf litter of ground water collections. Their eggs can withstand desiccation and most enter winter diapause and hatch in installments in the spring.

Aedes cinereus is the only representative of the subgenus *Aedes* in Britain, although 3 other species in this subgenus occur in continental Europe. This species occurs also in North America (Canada, USA), Europe, northeast China, Korea, and Japan and is subject to morphological variation, leading Bohart and Washino (1978) to raise a subspecific form proposed by Dyar to species status, thus naming Californian populations as *Aedes hemiteus* Dyar. However, while agreeing that Nearctic populations of *Ae. cinereus* are variable and that a complex of sibling species likely exists, Wood et al. (1979) are more conservative and believe that the name *Ae. cinereus* should be retained for all populations in North America until a thorough taxonomic study is completed. Nevertheless, Darsie and

Ward (1981), in their keys to the mosquitoes of North America north of Mexico, recognized *Ae. hemiteus* as the species occurring in California, with *Ae. cinereus* as being found elsewhere in North America. It would be interesting to compare egg morphology of different geographical populations with the morphology described here for typical European *Ae. cinereus*. Larvae of *Ae. cinereus* occur in more or less open and sunlit pools, ponds, ditches, flooded meadows, marshes, and sphagnum bogs. Eggs may not hatch until they have been soaked many times (Service 1968a).

Aedes punctor occurs widely in North America, northern Europe, and eastward to Siberia. Larval habitats consist generally of acidic ponds and pools or sphagnum bogs that are in sunlight or partial shade, such as in or at the edges of coniferous forests. Larvae are often found with those of *Ae. cinereus*.

Aedes cantans is confined to Europe, occurring mostly north of the Alps but eastward to western Siberia, the northern Caucasus, and the Crimea. It is a woodland species, and the larvae occur in shaded woodland pools, ponds, and ditches. Eggs can remain viable for at least 3.5 years (Service 1977).

Aedes rusticus occurs in Europe eastward to western Russia, but also in Algeria and Spanish and French Morocco. Larvae are found in shaded or semishaded woodland pools, ponds, and ditches, and are sometimes found with those of *Ae. punctor* and *Ae. cantans*, depending on the extend of shading of the aquatic habitats. Little is known about the biology of the eggs except that they hatch in installments and undergo diapause (Marshall 1938).

Aedes detritus is normally confined to brackish waters and consequently most records are from coastal localities, although it breeds in inland areas where there is a high concentration of sodium chloride, such as near salt mines and salt factories in Cheshire, England. More unusually *Ae. detritus* has been found breeding in inland freshwater habitats in England (Service 1972). Larvae can tolerate 133% seawater (Marshall 1938). Larval habitats comprise exposed sunlit saltwater marshes, pools,

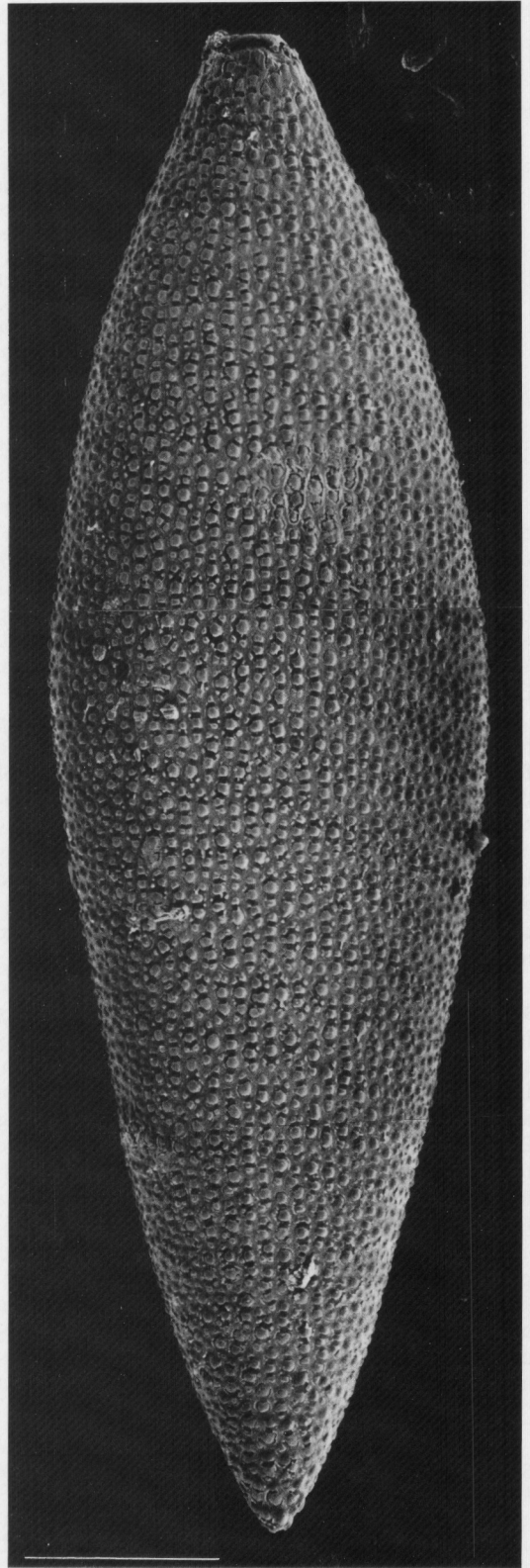
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³ Sadly, John Linley died before the results of this study were written up.

Table 1. Dimensions (μm) of the eggs of 5 British *Aedes* species.

Species (n)	Length		Width		L/W ratio	
	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range
<i>Ae. cinereus</i> (10)	1,003.8 \pm 13.6	920.4-1,047.4	258.4 \pm 7.8	225.4-295.1	3.92 \pm 0.14	3.17-4.60
<i>Ae. cantans</i> (8)	1,150.8 \pm 8.7	1,103.1-1,186.0	365.7 \pm 6.8	338.4-386.4	3.15 \pm 0.05	2.97-3.41
<i>Ae. punctator</i> (9)	959.1 \pm 8.4	932.0-1,001.5	320.5 \pm 1.6	313.5-328.9	2.93 \pm 0.05	2.86-3.01
<i>Ae. detritus</i> (10)	950.9 \pm 22.3	862.3-1,055.5	266.0 \pm 2.9	252.5-278.5	3.58 \pm 0.10	3.15-3.99
<i>Ae. rusticus</i> (11)	806.8 \pm 7.1	769.3-839.7	429.4 \pm 2.3	419.0-443.8	1.88 \pm 0.02	1.80-2.00

Fig. 1. *Aedes cinereus*. Entire egg, ventral view, anterior end at top. Scale = 100 μm .

and ponds. The species is common in European coastal districts from the Baltic to Aegean, Mediterranean, and Red seas, it also occurs in North Africa and Palestine. Although eggs can withstand desiccation for more than a year they can hatch in any month (Service 1968b). Two blood meals may be necessary for complete development of the ovaries (Service 1968c), but in southern France and Sicily autogeny is exhibited (Guilvard et al. 1979), but despite much work on British populations autogeny has never been reported. Differences between isoenzymes indicate that in the Mediterranean *Ae. detritus* consists of 2, as yet unnamed, sympatric sibling species (Pasteur et al. 1977).

The outline shape of the eggs of British populations of all the above species is given by Marshall (1938). In addition, an outline of the shape of the egg of *Ae. cinereus* is given by Craig and Horsfall (1958), while Horsfall and Voorhees (1972) present a photograph depicting the shape of the egg of *Ae. punctor*, both presumably from USA specimens. The SEM photographs of the "side of the shell" of *Ae. cantans* eggs collected from Britain are presented by Hinton and Service (1969). Hinton (1981), in his book on insect eggs, presented SEM photographs of 11 *Aedes* species that are found in Britain, including those of *Ae. cantans*, *Ae. punctor*, *Ae. detritus*, and *Ae. rusticus*, but non-British eggs of *Ae. flavescens* (Mueller), *Ae. communis* (De Geer), *Ae. leucomelas* (Meigen), and *Ae. sticticus* (Meigen) were used (personal information). These photographs are of limited use, because some are from damaged eggs, and most are just labeled as a "side" view. However, it is interesting to note that no differences were found in the surface structure of *Ae. detritus* eggs I obtained from a typical coastal saline habitat in Britain and those obtained from adults breeding in an inland nonsaline habitat (Service 1972). Apart from these studies there have been no detailed descriptions of the eggs of any of these five species.

MATERIALS AND METHODS

Eggs of all species were obtained by one of the authors (MWS) undertaking human bait catches in England, and letting the females fully engorge on him. When these females became gravid they were placed individually in small glass vials for oviposition on a substrate of wet cotton covered with white filter paper. Eggs so obtained were kept damp for 2 weeks to ensure embryonation and were then

washed with alcoholic Bouins fluid into small vials for later examination.

Procedures for preparing and examining the eggs were as described by Linley and Service (1994, 1995). Eggs were critical-point dried, then mounted on stubs with sticky tape, dried in a calcium chloride desiccator, and sputter-coated with gold/palladium. Eggs were examined with a Hitachi S-510 scanning electron microscope. Measurements were obtained from micrographs using a digitized tablet. Lengths of the chorionic cells were taken in the longitudinal axis while width was measured across the circumferential axis. The widths of the eggs were measured at the widest point of the egg; cell lengths and widths were measured from midpoints of the reticulum. Measurements of tubercles were from their bases, except when these could not be clearly seen, as in *Ae. detritus*, and so were taken from their tops. Measurements are given as means \pm SE and/or a range.

Terminology used is that of Harbach and Knight (1980), plus "micropylar dome," a term proposed by Linley et al. (1991).

DESCRIPTIONS

Aedes (Aedes) cinereus (Figs. 1–3)

Locality: Arne Peninsular, Poole (50°43'N, 02°00'W), Dorset, England, July 1994.

Size: As in Table 1.

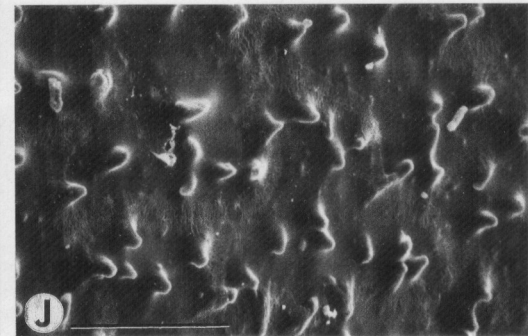
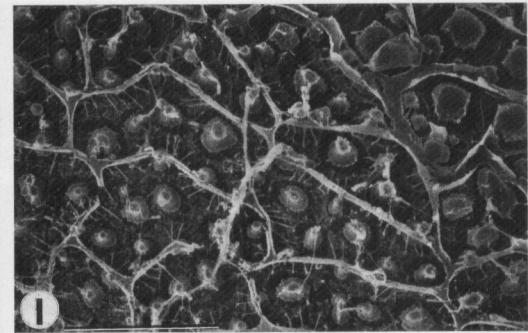
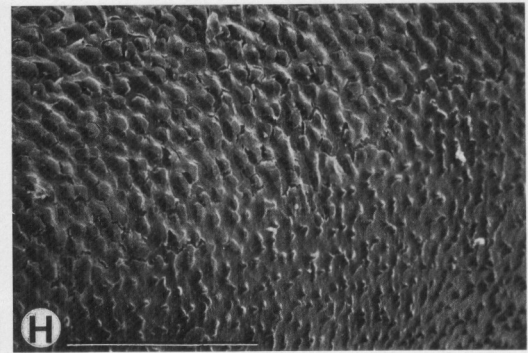
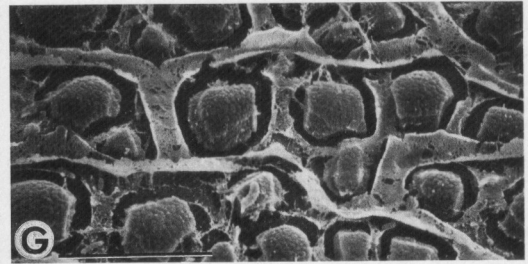
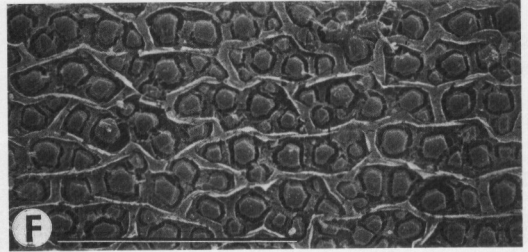
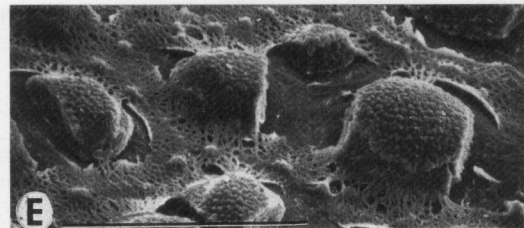
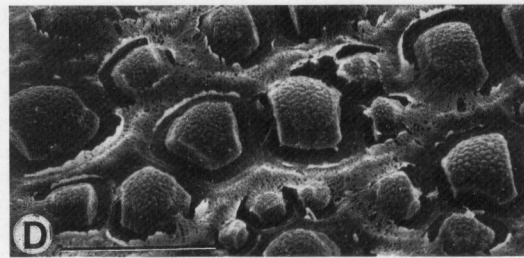
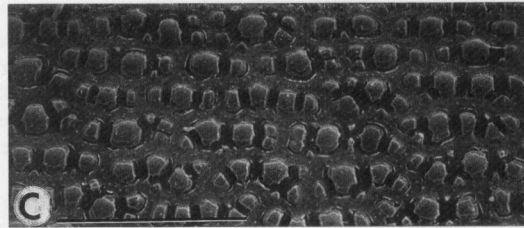
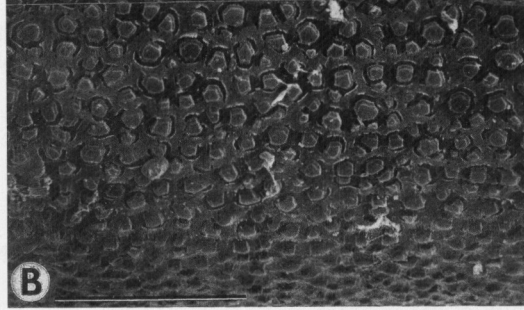
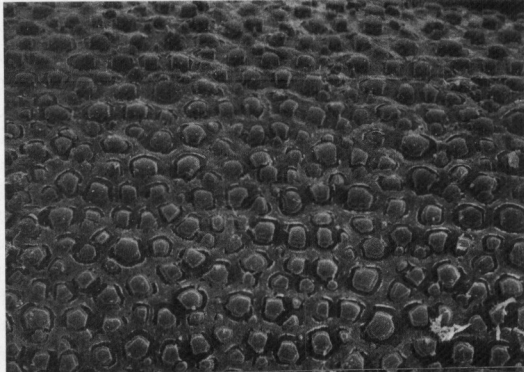
Color: Black.

Overall Shape: Boat-shaped but rather narrow, ventral view widest at about anterior 0.43, anteriorly more rounded, posteriorly tapering sharply from about middle of egg (Fig. 1), slightly more curved ventrally than dorsally (Fig. 2A). Collar and micropyle fairly conspicuous.

Chorion, ventral (upper) surface: Outer chorionic cells vary considerably in shape and size, sides of cells have rounded or angular corners, most cells are polygonal but some are roughly pentagonal, others are hexagonal (Figs. 2D–2G), length variable from 19.7–35.3 μm (mean $28.1 \pm 1.1 \mu\text{m}$, $n = 21$), width also very variable from 9.1–21.0 μm (mean $12.5 \pm 0.6 \mu\text{m}$, $n = 21$). Reticulum with many small perforations, thin with jagged edges, width 1.2–2.0 μm , cell floors smooth apart from thin and rather indistinct cellulose walls separating tubercles enclosed with reticulum (Figs. 2D, 2E, 2G). Two to 6, but usually 6, tubercles enclosed within reticulum (Fig. 2F), tubercles of usually 2 distinct sizes,

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Fig. 2. *Aedes cinereus*. A, Entire egg, lateral view, ventral surface at top, anterior end to left; B, chorionic cells, lateral surface, ventral to dorsal transition; C, chorionic cells of ventral surface; D, chorionic cells of ventral surface in detail; E, chorionic cells, ventral surface showing 2–6 tubercles enclosed by reticulum; G, chorionic cells, ventral surface; H, chorionic cells, lateral surface, ventral–dorsal transition showing conical papillae dorsally; I, chorionic cells of lateral transition surface showing tuberculate papillae; J, dorsal lateral surface showing conical papillae. Scale = 10 μm (D, E, G), 20 μm (I), 50 μm (B, C, F, H), 100 μm (J), and 500 μm (A).



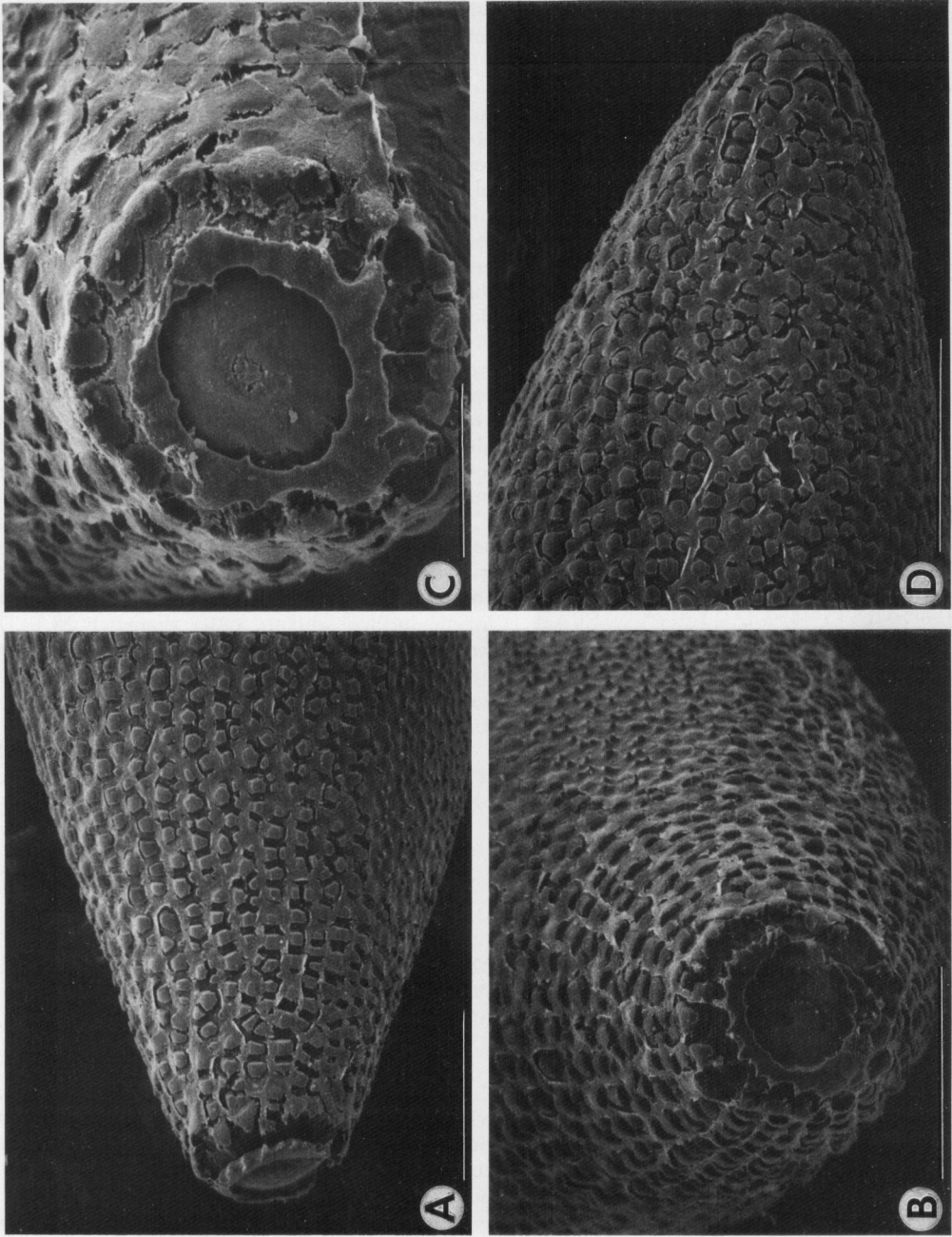


Fig. 3. *Aedes cinereus*. A, Anterior end; B, anterior end showing micropyle; C, micropyle; D, posterior end. Scale = 20 μm (C) and 50 μm (A, B, D).

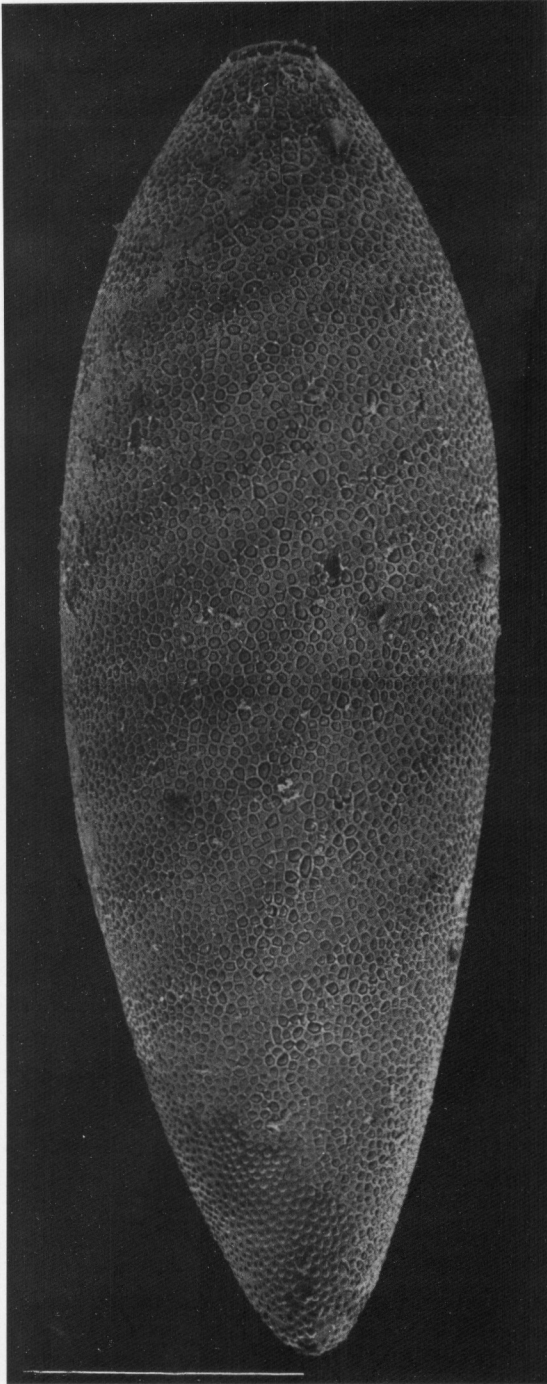


Fig. 4. *Aedes cantans*. Entire egg, ventral view, anterior end at top. Scale = 200 μm .

large and small, but with some intermediate ones, length varies from 4.1–9.0 μm (means $6.3 \pm 0.2 \mu\text{m}$, $n = 50$), width 2.7–7.6 μm (mean $5.0 \pm 0.2 \mu\text{m}$, $n = 50$) (Figs. 2C–2G). Most tubercles have vertical sides, and a slightly domed top that is finely but conspicuously nodular. Some tubercles separated from reticulum (Fig. 2G) but others fused with reticulum (Fig. 2E).

Chorion, lateral surface (ventral–dorsal transition): Most of lateral surface resembles ventral surface (Fig. 2B) but more dorsally there is a fairly abrupt change (Fig. 2H) with the tubercles being replaced by short and variously shaped conical papillae (Fig. 2H) which do not appear to be surrounded by any reticulum. However, in some areas these papillae are more tubercular-shaped (Fig. 2I) and are enclosed by reticula, and there are straight threadlike projections from the reticula onto the cell floor (Fig. 2I).

Chorion dorsal (lower) surface: Very different from ventral surface, there are no tubercles, the surface being covered with rounded conical papillae, vertical or slanting in any direction (Fig. 2J), usually spaced singly but sometimes 2 or 3 papillae joined basally, or even confluent laterally. Very faint reticular surround groups of papillae (Fig. 2J).

Anterior end, micropyle: Ventrally chorionic cells and tubercles much as found elsewhere ventrally (Fig. 3A). Collar of micropyle prominent and complete (Figs. 3A–3C), outer and inner rims scalloped, surface smooth, outer diameter 28.1–37.6 μm , wall diameter 1.3–8.5 μm . Diameter of micropylar disc 20.9–24.7 μm (Fig. 3C), micropylar dome not very prominent, orifice diameter about 7.1 μm .

Posterior end: Chorionic cells and tubercles (Fig. 3D) much as found ventrally on middle of egg.

Aedes (Ochlerotatus) cantans

(Figs. 4–6)

Locality: Arne Peninsular, Poole (50°43'N, 02°00'W), Dorset, England, July 1994, and Ness Woods (53°17'N, 3°15'W), Merseyside, England, July 1994.

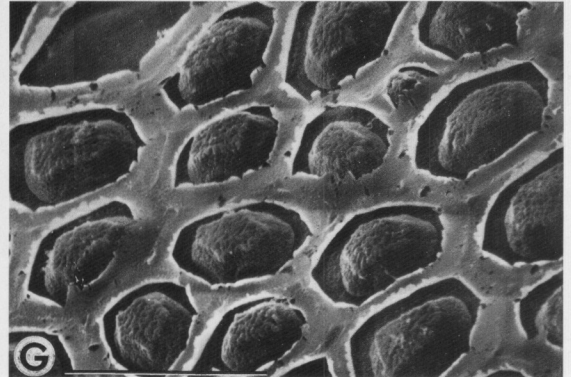
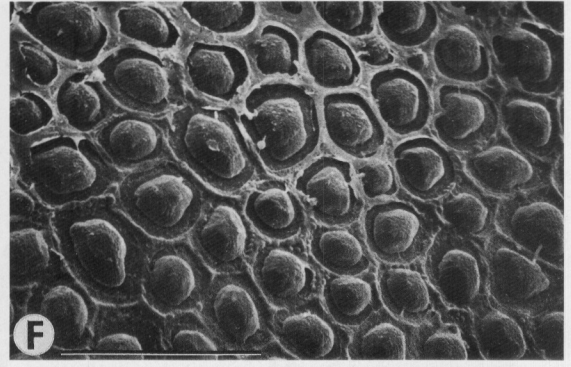
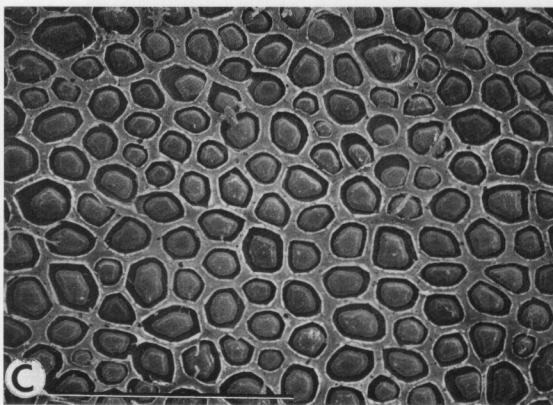
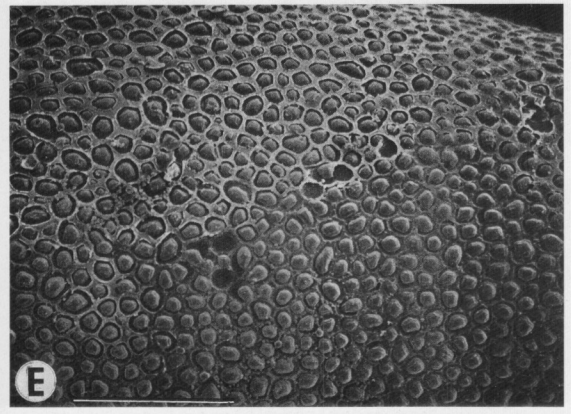
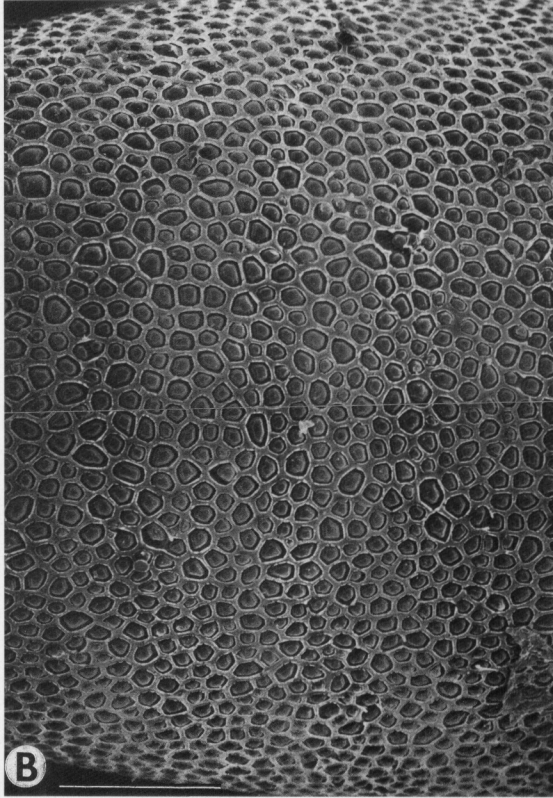
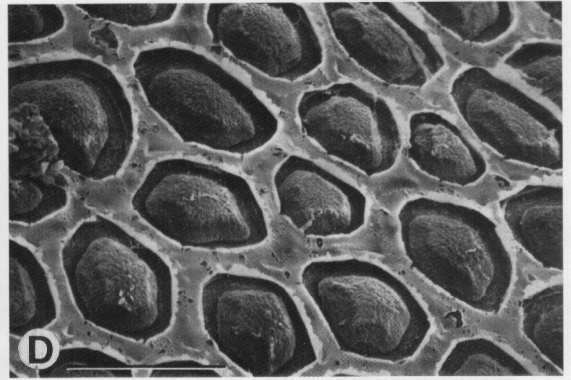
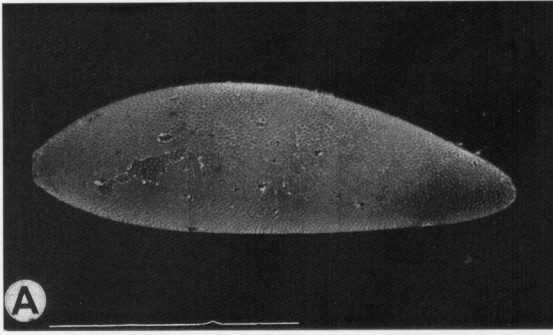
Size: As in Table 1.

Color: Black.

Overall shape: Rather boat-shaped, ventral view widest at about anterior 0.33, more rounded anteriorly and more tapered posteriorly (Fig. 4), more curved ventrally than dorsally (Fig. 5A). Collar of micropyle fairly conspicuous.

Chorion, ventral (upper) surface: Outer chori-

Fig. 5. *Aedes cantans*. A, Entire egg, lateral view, ventral surface at top, anterior end to left; B, chorionic cells, lateral surface, ventral–dorsal transition; C, chorionic cells of middle ventral surface; D, chorionic cell details, ventral surface; E, chorionic cells of lateral surface; F, chorionic cells in detail of lateral surface; G, chorionic cells, dorsal surface. Scale = 10 μm (D, G), 20 μm (F), 50 μm (B, C, E), and 500 μm (A).



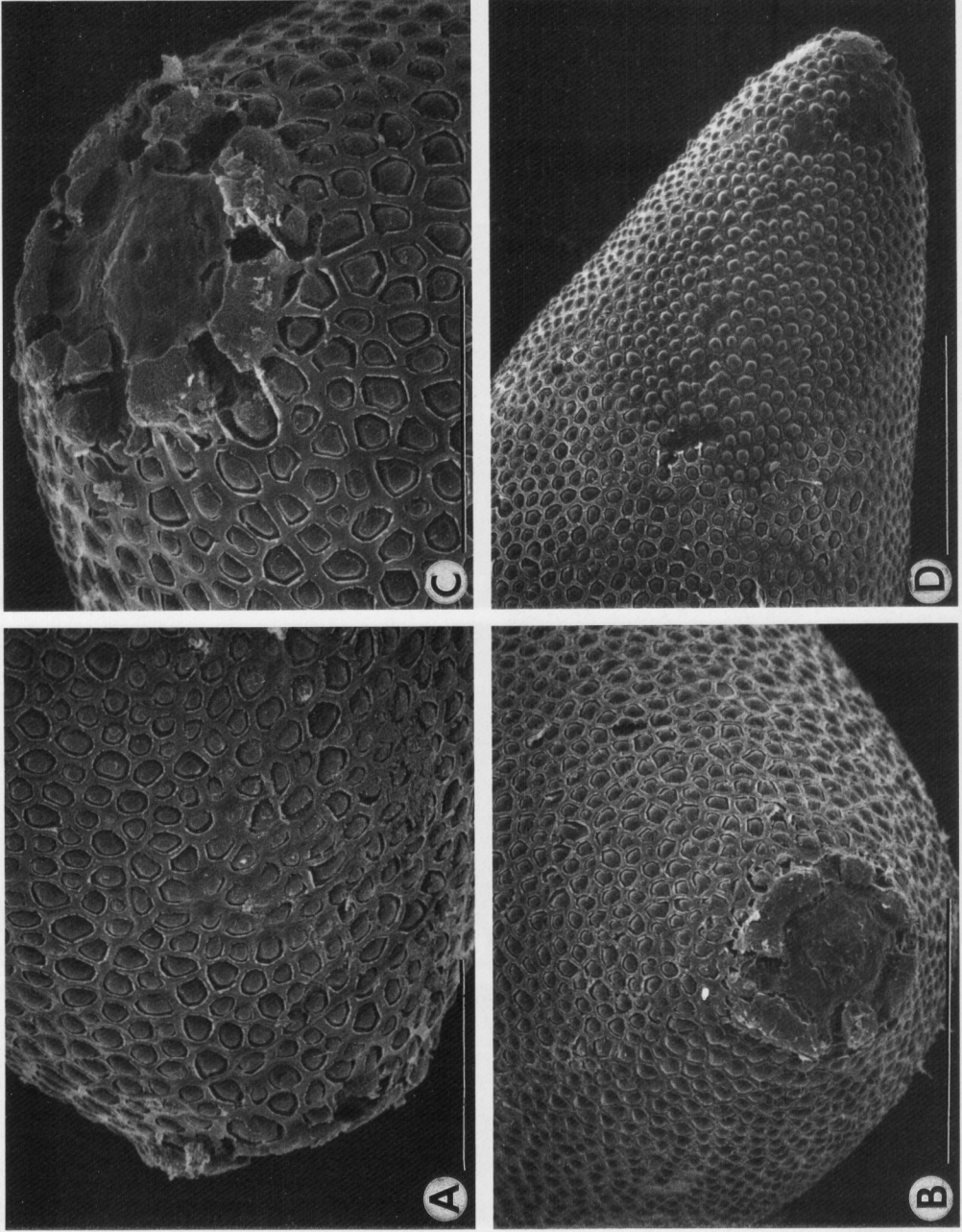


Fig. 6. *Aedes cantans*. A, Anterior end; B, anterior end showing micropyle; C, micropyle; D, posterior end. Scale = 50 μm (A, C) and 100 μm (B, D).

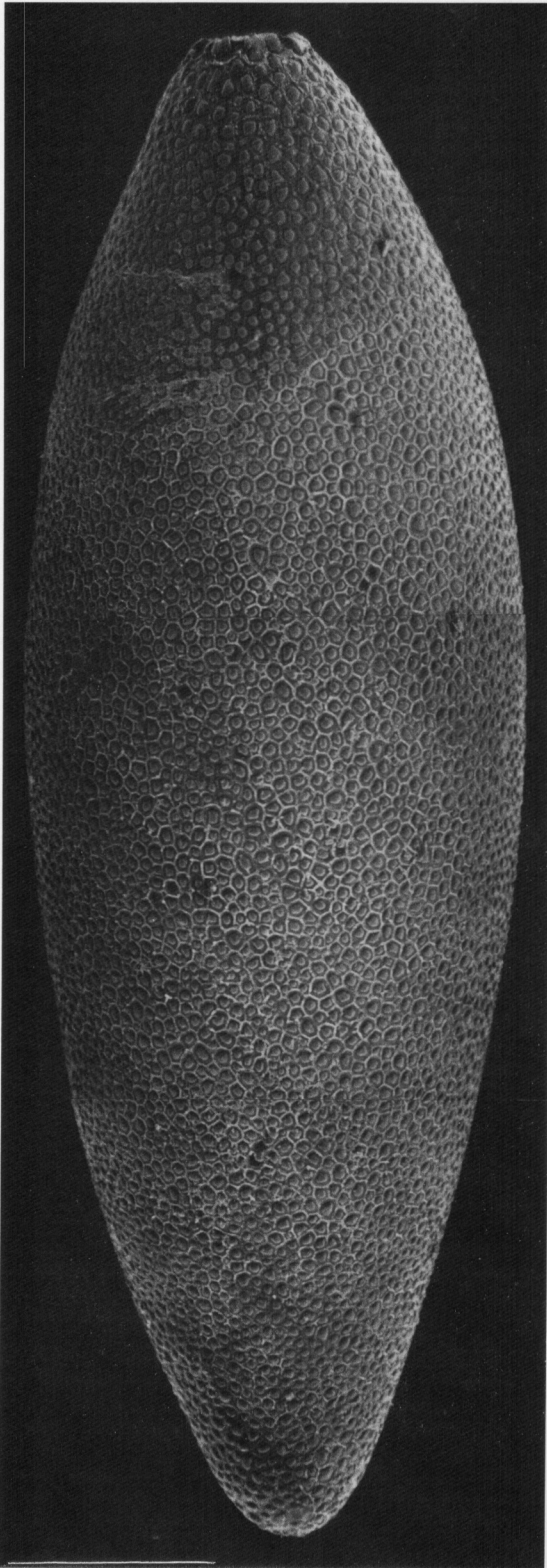


Fig. 7. *Aedes punctor*. Entire egg, ventral view, anterior end at top. Scale = 100 μm .

onic cells very distinct, of various sizes and shapes but basically pentagonal but some are almost rounded in outline (Figs. 5B–5G), length varies from 8.5–14.6 μm (mean $11.2 \pm 0.2 \mu\text{m}$, $n = 50$) and is greater than width (6.5–10.2 μm , mean $8.3 \pm 0.1 \mu\text{m}$, $n = 50$), reticulum more or less smooth, straight-sided and rather broad (width 1.6–2.6 μm), cell floor smooth (Fig. 5D). Each cell enclosing a single large, prominent, centrally located tubercle (Fig. 5D, 5G) having sloping sides and a more or less flat top, length at top of tubercle 5.0–9.3 μm (mean $6.8 \pm 0.1 \mu\text{m}$, $n = 50$), width 3.6–6.3 μm (mean $5.1 \pm 0.09 \mu\text{m}$, $n = 50$) (Fig. 5C). Tubercle with top and sides finely tuberculate.

Chorion, lateral surface (ventral–dorsal transition): No appreciable difference in shape and size of cells or tubercles (Fig. 5B). The chorion is uniform ventrally and dorsally.

Chorion, dorsal (lower) surface: Cells, reticula, and tubercles (Fig. 5G) much as those found ventrally (Fig. 5D). Figure 5F shows an alternate cell type, with smaller reticula than in Figs. 5D, 5G.

Anterior end, micropyle: Chorionic cells and tubercles similar to middle of egg, not conspicuously smaller (Fig. 6A). Collar of micropyle prominent but incomplete (Figs. 6B, 6C), outer diameter 70.2–76.7 μm , wall diameter 12.7–20.2 μm . Diameter of micropylar disc 46.1–52.0 μm , micropylar dome not very prominent, orifice diameter 1.2–2.6 μm (Figs. 6B, 6C).

Posterior end: Chorionic cells and tubercles near posterior end (Fig. 6D) differ from those on other areas (Figs. 6A–6C) of the egg, in that the reticula are considerably thinner and not nestling the tubercles so much.

Aedes (Ochlerotatus) punctor (Figs. 7–9)

Locality: Arne Peninsular, Poole (50°43'N, 02°00'W), Dorset, England, July 1994.

Size: As in Table 1.

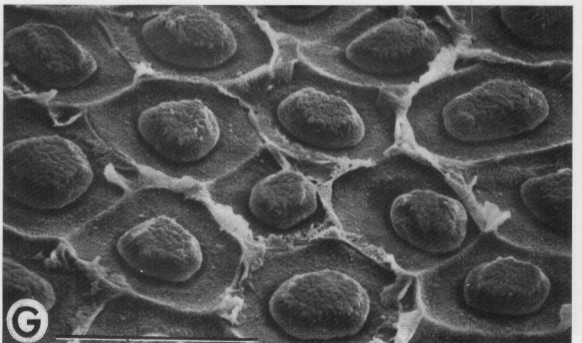
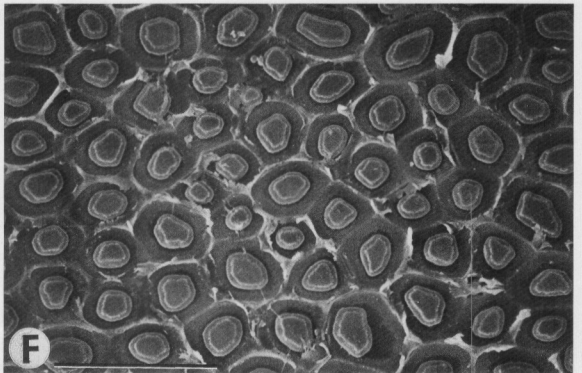
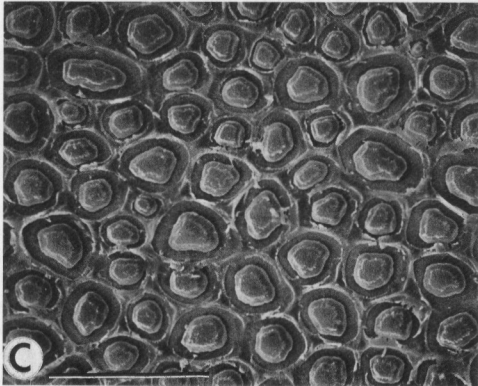
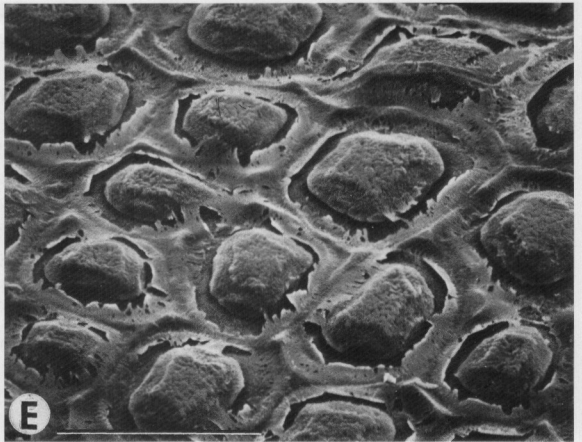
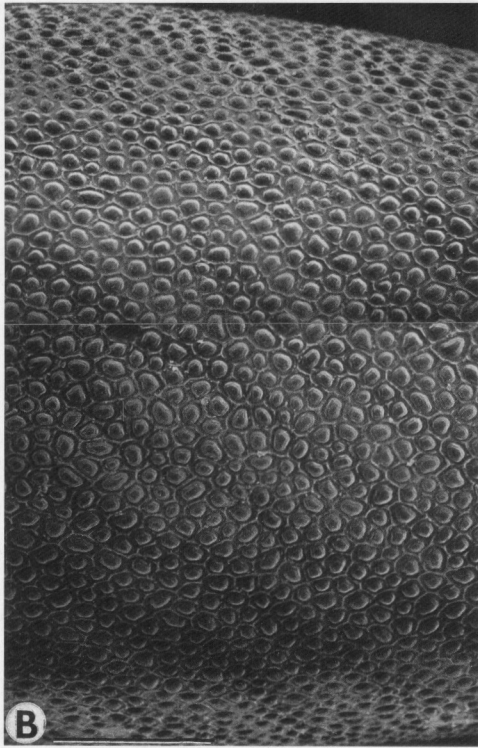
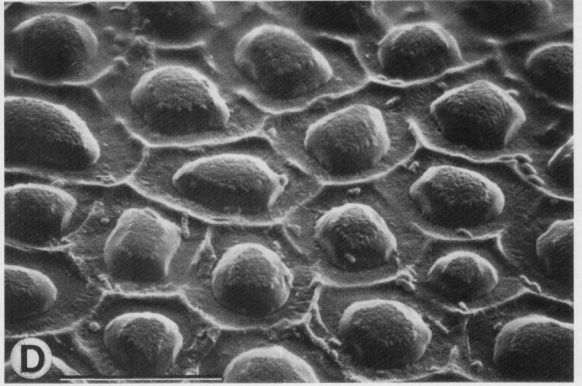
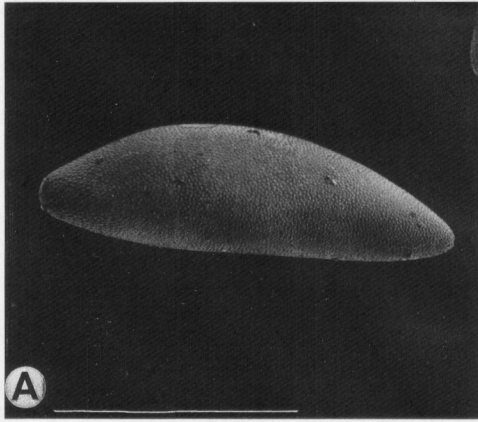
Color: Black.

Overall shape: Boat-shaped, ventral view widest at about anterior 0.43, slightly more rounded anteriorly than posteriorly (Fig. 7), distinctly more curved ventrally than dorsally (Fig. 8A). Collar of micropyle not very conspicuous.

Chorion, ventral (upper) surface: Outer chori-

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Fig. 8. *Aedes punctor*. A, Entire egg, lateral view, ventral surface at top, anterior end to left; B, chorionic cells, lateral surface, ventral–dorsal transition; C, chorionic cells of middle ventral surface; D, chorionic cell detail of middle ventral surface showing concave cell floors; E, chorionic cells of ventral surface showing tubercles occupying most of cell; F, chorionic cells of middle dorsal surface; G, chorionic cell detail of dorsal surface. Scale = 10 μm (D, E, G), 20 μm (C, F), 50 μm (B), and 500 μm (A).



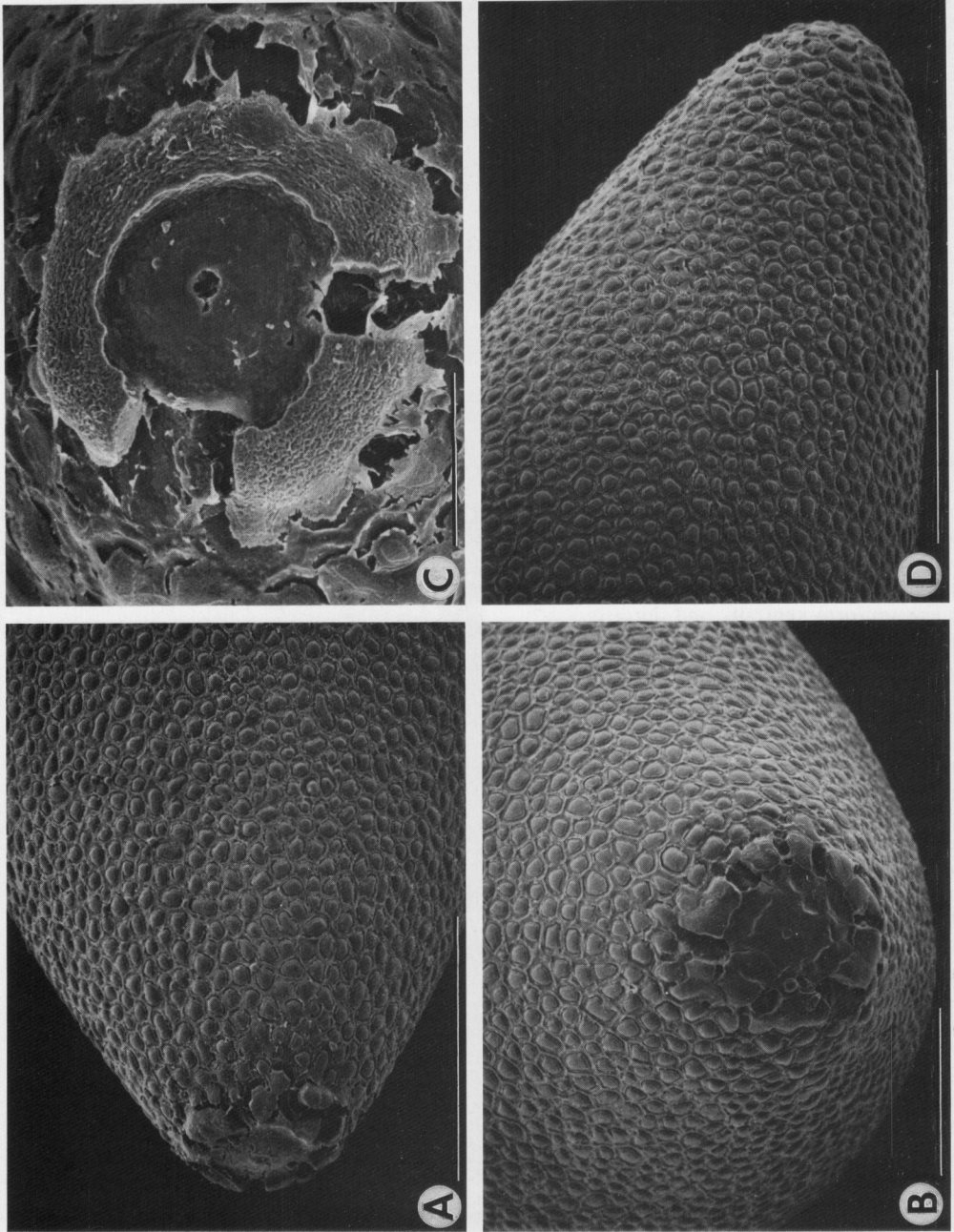


Fig. 9. *Aedes punctor*. A, Anterior end; B, anterior end with micropyle; C, micropyle; D, posterior end. Scale = 20 μm (C), 50 μm (B, D), and 100 μm (A).

onic cells very distinct, of various sizes (length 5.9–13.0 μm , width 3.3–8.6 μm) and shapes, with rounded corners, some cells elliptical or roundish, others quadrilateral or pentagonal with curved sides (Figs. 8C, 8D), length (mean $8.8 \pm 0.2 \mu\text{m}$, $n = 50$) greater than width (mean $6.5 \pm 0.2 \mu\text{m}$, $n = 50$), reticulum narrow (0.65 μm), distinctly raised and more or less smooth-sided, but occasionally overlaid by a wider irregular ribbonlike structure (Fig. 8E), but not apparent on dorsal surface (Fig. 8F). Cell floor concave and very finely tuberculate (Figs. 8C, 8D). Each cell enclosing a single large, prominent, centrally located tubercle (Figs. 8C, 8D) having curved sloping sides and a more or less flat top, size (length 2.7–8.1 μm , mean $5.1 \pm 0.1 \mu\text{m}$, $n = 50$; width 2.9–5.0 μm , mean $3.9 \pm 0.09 \mu\text{m}$, $n = 50$) and shape (Figs. 8C, 8D) of tubercle various. Tubercle surface finely tuberculate on top, walls appear smooth. An alternative pattern is exhibited by eggs laid by some females (Fig. 8E) in which the tubercle (length 4.3–6.7 μm , width 3.1–4.6 μm) appears to occupy more of the cell (length 5.9–9.3 μm , width 3.1–5.6 μm), the floor of which is not obviously concave (Fig. 8E), but the most conspicuous difference is shown by the reticulum, which is much wider (1.7–2.6 μm) and has very irregular edges and a few perforations.

Chorion, lateral (ventral–dorsal transition): No appreciable difference in shape or size of cells and tubercles (Fig. 8B). The chorionic pattern seems more or less uniform ventrally and dorsally.

Chorion, dorsal (lower) surface: Shape and size of cells (length 7.1–12.3 μm , mean $9.5 \pm 0.2 \mu\text{m}$, $n = 50$; width 4.6–8.9 μm , mean $6.7 \pm 0.1 \mu\text{m}$, $n = 50$) and tubercles (length 3.2–6.6 μm , mean $4.9 \pm 0.1 \mu\text{m}$, $n = 50$; width 2.4–4.9 μm , mean $3.8 \pm 0.08 \mu\text{m}$, $n = 50$) (Figs. 8E, 8G) similar to those on ventral surface. But more dorsally reticulum appears more ragged in some places (Fig. 8G) due to superposition of a ribbonlike structure.

Anterior end, micropyle: Chorionic cells and tubercles (Figs. 9A, 9B) similar to those in middle of egg. Collar of micropyle prominent, appears incomplete (Fig. 9C) but this may be an artifact, inner rim appears scalloped, outer rim irregular outline, surface rough, outer diameter 45.87–52.7 μm , wall diameter 7.4–15.4 μm . Diameter of micropyle disc 25.3–30.5 μm , orifice round, diameter 2.2–3.3 μm (Fig. 9C).

Posterior end: Chorionic cells and tubercles near posterior end (Fig. 9D) not appreciably different from those on other areas of egg.

Aedes (Ochlerotatus) detritus
(Figs. 10–12)

Locality: Arne Peninsular, Poole (50°43'N, 02°00'W), Dorset, England, July 1994.

Size: As in Table 1.

Color: Black.

Overall shape: Cigar-shaped, ventral view wid-

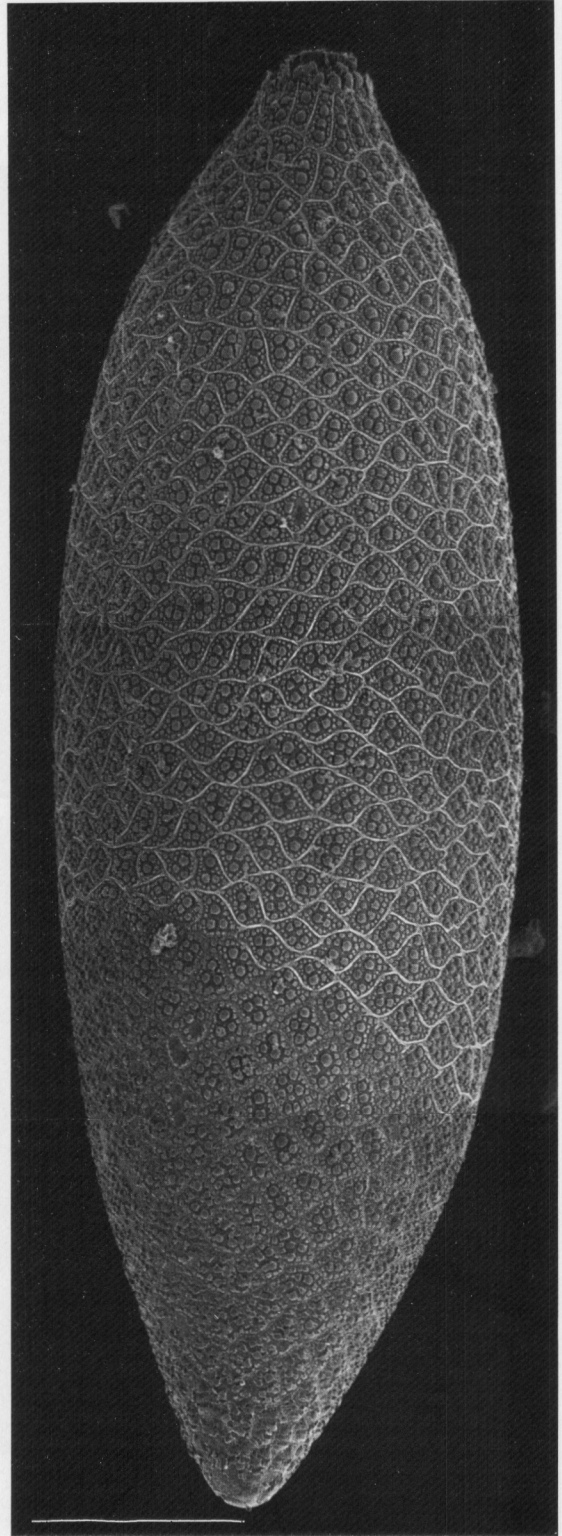


Fig. 10. *Aedes detritus*. Entire egg, ventral view, anterior end at top. Scale = 100 μm .

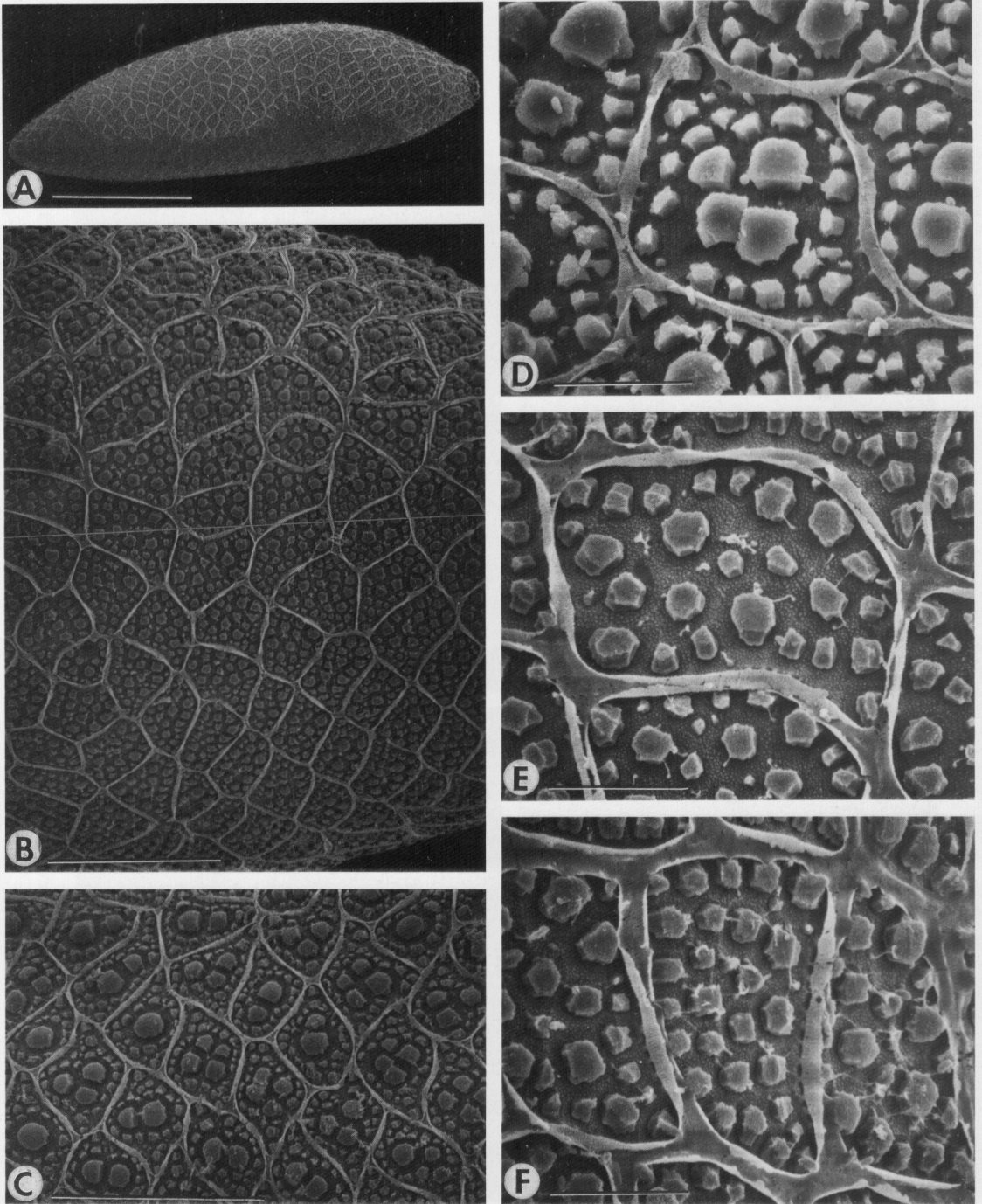


Fig. 11. *Aedes detritus*. A, Entire egg, lateral view, ventral surface at top, anterior end to right; B, chorionic cells, lateral surface, ventral-dorsal transition; C, chorionic cells of middle ventral surface; D, chorionic detail of middle ventral surface; E, chorionic detail, lateral surface; F, chorionic detail of ventral surface. Scale = 10 μm (D, E, F), 50 μm (B, C), and 200 μm (A).

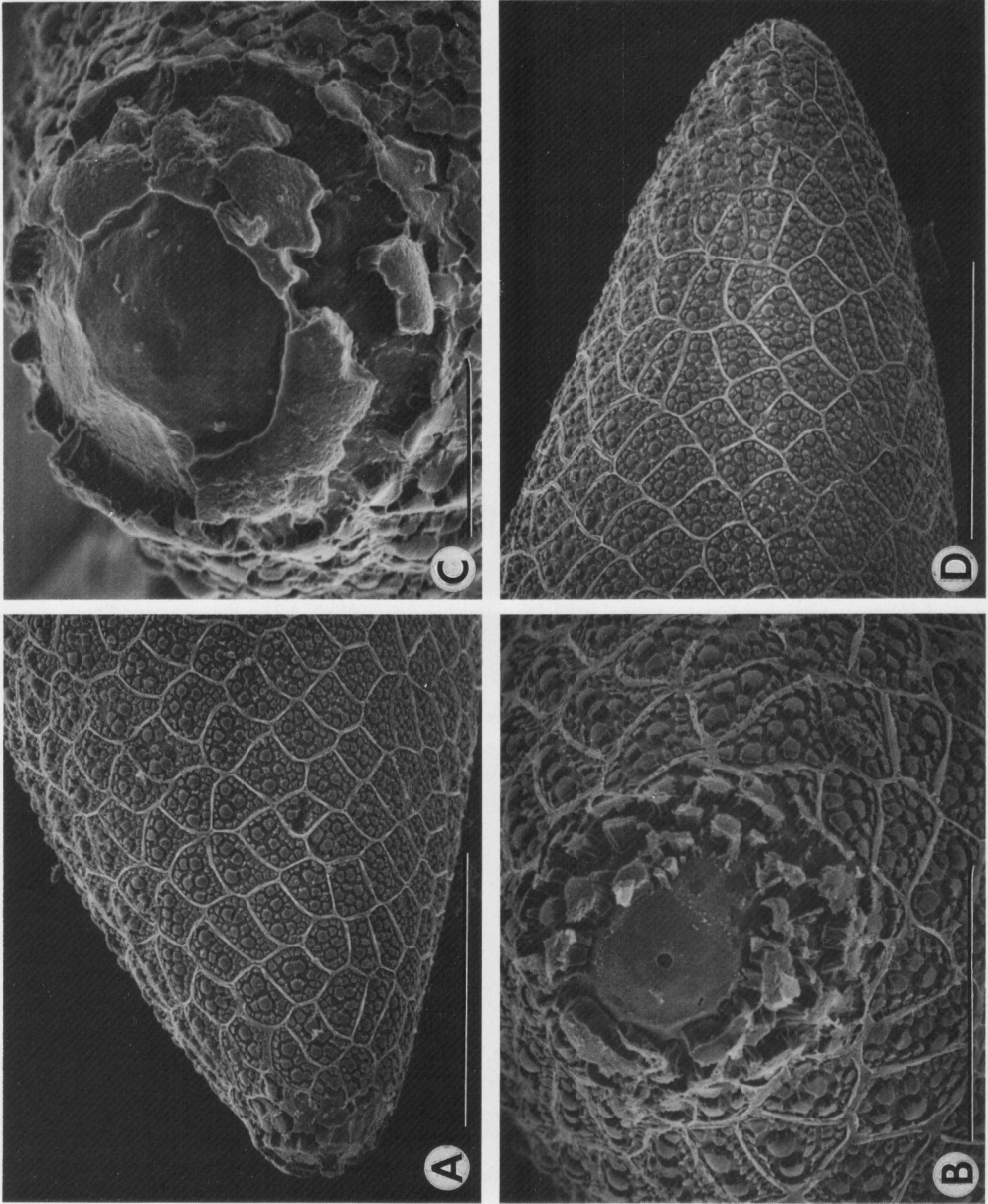


Fig. 12. *Aedes detritus*. A, Anterior end; B, anterior end showing micropyle; C, micropyle; D, posterior end. Scale = 20 μm (C), 50 μm (B), and 100 μm (A, D).

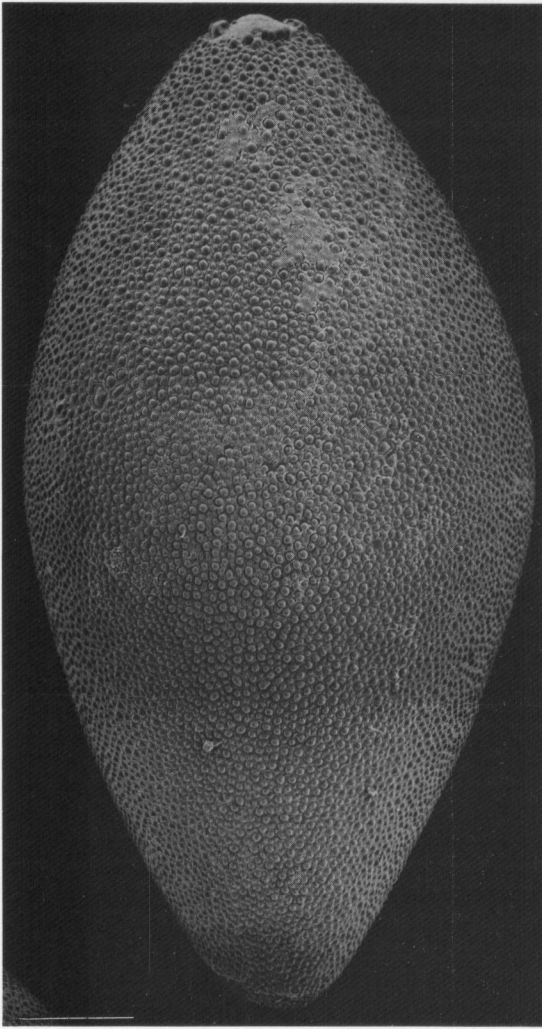


Fig. 13. *Aedes rusticus*. Entire egg, ventral view, anterior end at top. Scale = 100 μm .

est at 0.36–0.46 from anterior end (Fig. 10), slightly more tapering at posterior end, more curved on ventral surface than dorsal surface, which is flat for much of its length (Fig. 11A). Collar of micropyle visible but not very conspicuous when viewed on whole egg (Figs. 10, 11A).

Chorion, ventral (upper) surface: Outer chorionic cells very distinct forming a latticelike pattern over entire egg. Cells have angular or rounded corners, but usually with one corner drawn out and more pointed than others (Figs. 11C, 11D), most cells are quadrilateral, length (22.1–30.6 μm , mean $27.2 \pm 0.7 \mu\text{m}$, $n = 12$) greater than width (10.8–25.6 μm , mean $18.8 \pm 1.2 \mu\text{m}$, $n = 12$). Reticulum narrow (width about 0.7 μm) and appearing to twist over like a ribbon, sides of reticulum smooth, cell floor finely granular (Figs. 11D–11F). Each cell contains 1 to 4 larger tubercles surrounded by 20–

26 variously sized smaller tubercles (Figs. 11D–11F), and several of what appear to be very small fragments of tubercles (Fig. 11D). Length of tubercles, excluding “fragments,” varies from 1.2 to 4.8 μm (mean $2.2 \pm 0.2 \mu\text{m}$, $n = 20$), width 0.7–3.8 μm (mean $1.4 \pm 0.2 \mu\text{m}$, $n = 20$). Tubercles have vertical sides and flat very finely tuberculate tops.

Chorion, lateral surface (ventral–dorsal transition): Cell size and reticulum much as for ventral surface but a fairly abrupt transition laterally from typical ventral surface characterized by a few larger tubercles surrounded by smaller ones to numerous (20–26) more equally sized tubercles (Figs. 11B, 11E), length 1.2–3.3 μm (mean $2.3 \pm 0.1 \mu\text{m}$, $n = 20$), width 0.8–3.0 μm (mean $1.8 \pm 0.2 \mu\text{m}$, $n = 20$), distinction between larger and smaller tubercles less toward dorsal surface (Fig. 11B). Several tubercles have 1 or 2 threadlike radii ending in a rounded knob or connecting with another tubercle (Fig. 11E).

Chorion, dorsal (lower) surface: Shape and size of cells much the same as ventrally but ribbonlike reticula often wider (about 1.8 μm) (Fig. 11F), tubercles similar to the more dorsal of the lateral ones (length 1.5–2.9 μm , mean $2.1 \pm 0.08 \mu\text{m}$, $n = 20$); width 0.9–2.0 μm , mean $1.6 \pm 0.06 \mu\text{m}$; $n = 20$) but more have threadlike radii that, if not terminating in small rounded knobs, stretch from one tubercle to another.

Anterior end, micropyle: Chorionic cells and tubercles appear similar to those elsewhere on ventral and dorsal surfaces (Figs. 12A, 12B). Collar of micropyle prominent, probably complete although appears broken in Figs. 12B, 12C, outer diameter about 48.4 μm , wall diameter about 9.7 μm . Diameter of micropylar disc about 25.2 μm , orifice round (Fig. 12B), diameter about 1.84 μm .

Posterior end: Chorionic cells and tubercles (Fig. 12D) much as elsewhere on dorsal, ventral, and lateral surfaces of the egg.

Aedes (Ochlerotatus) rusticus (Figs. 13–15)

Locality: Arne Peninsular, Poole (50°43'N, 02°00'W), Dorset, England, July 1994; Ness Woods (53°17'N, 3°15'W), Merseyside, England, July 1994.

Size: As in Table 1.

Color: Black.

Overall shape: Completely diagnostic among British *Aedes* species (Marshall 1938), short but very wide (Fig. 13), length:width ratio about 1.9, ventral view widest at about anterior 0.45, about equally rounded at both ends, ventral surface characteristically arched in middle (Fig. 14A), dorsal surface slightly curved. Collar of micropyle not very conspicuous (Fig. 13).

Chorion, ventral (upper) surface: Outer chorionic cells mainly roundish or elliptical, a few are quadrilateral or pentagonal with straighter sides

(Fig. 14C, 14D), length 5.6–9.4 μm (mean 7.7 \pm 0.1 μm , $n = 50$) only a little greater than width 4.3–8.8 μm (mean 6.8 \pm 0.1 μm , $n = 50$), reticulum usually with smooth sides and sometimes has small perforations (Fig. 14D), width 0.5–1.4 μm , cell floor smooth. Each cell encloses a single variously sized, but usually large, tubercle with finely granular sloping sides and a domed tuberculate top (Fig. 14D), length of tubercle 3.8–7.2 μm (mean 5.7 \pm 0.1 μm , $n = 50$), width 3.2–6.1 μm (mean 4.9 \pm 0.1 μm , $n = 50$). However, eggs from a few females have much larger quadrilateral or pentagonal cells (length 20.4–30.4 μm) enclosing 12–15 smaller cells (4.5–7.8 μm) each having 1–3 tubercles (Fig. 14E) and separated from each other by ridges in cell floor (Fig. 14F). Shape and size of tubercles much as in more typical cells.

Chorion, lateral surface (ventral–dorsal transition): No appreciable difference in shape and size of cells and tubercles (Fig. 14B). The chorion is more or less uniform ventrally and dorsally.

Chorion, dorsal (lower) surface: Shape of cells and tubercles much as ventrally but cell length 6.9–11.9 μm (mean 9.1 \pm 0.2 μm , $n = 50$) and width 4.9–9.8 μm (mean 7.5 \pm 0.1 μm , $n = 50$) a little larger, and tubercle length 4.4–8.9 μm (mean 6.5 \pm 0.1 μm) and width 3.4–6.5 μm (5.2 \pm 0.1 μm , $n = 50$) also a little larger (Figs. 14G, 14H), reticulum same as ventrally. A few eggs have larger cells enclosing 3–10 smaller cells each having 1 or 2 tubercles, much as found in ventral surface of these atypical eggs.

Anterior end, micropyle: Chorionic cells and tubercles similar to middle of egg and not conspicuously smaller (Figs. 15A, 15B). Collar of micropyle not very prominent, most probably complete despite cracks and gaps shown in Figs. 15B, 15C, outer diameter 62.2–70.9 μm , wall diameter 11.2–16.1 μm . Diameter of micropyle disc 32.7–35.8 μm (Fig. 15C), orifice of micropyle not obvious in any specimens examined (Figs. 15B, 15C).

Posterior end: Chorionic cells and tubercles near posterior end (Fig. 15D) not appreciably different from those on other areas of egg.

DISCUSSION

The eggs of *Ae. cantans* and *Ae. punctor* are similar in overall shape (Figs. 4, 5A, 7, 8A) although those of *Ae. cantans* are a little larger; the chorionic sculpturing of these two species is also similar (Figs. 5, 8). Adults of both species are readily dis-

tinguished from each other, as are fourth-instar larvae, but younger instar larvae are very difficult and sometimes impossible to distinguish with certainty, and they often occur in the same habitats.

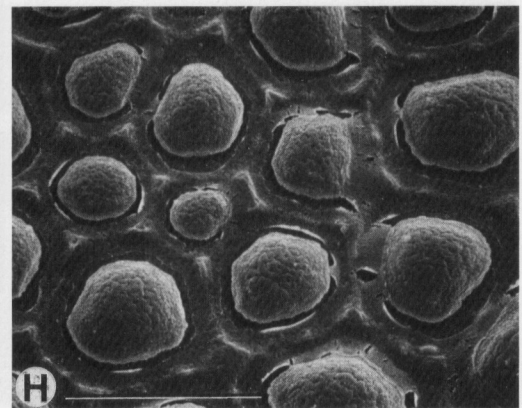
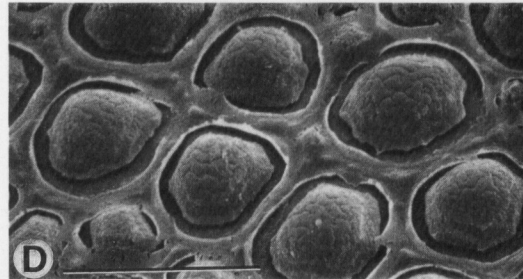
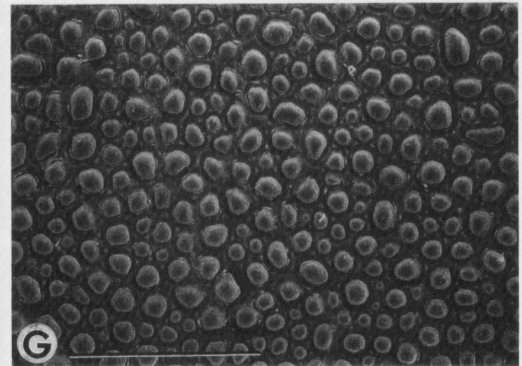
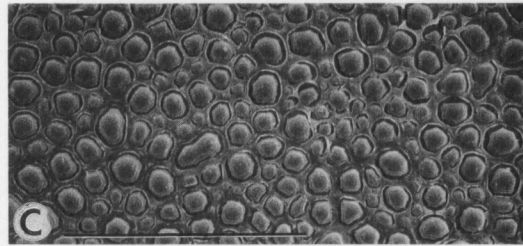
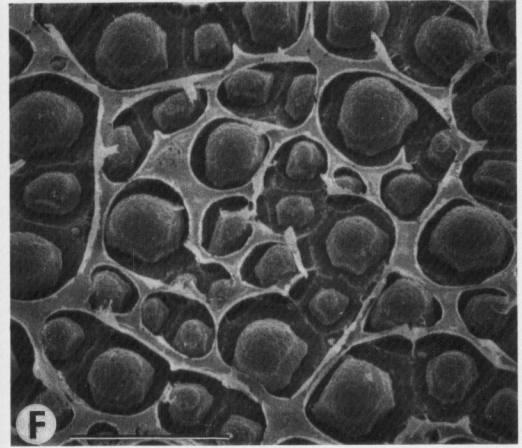
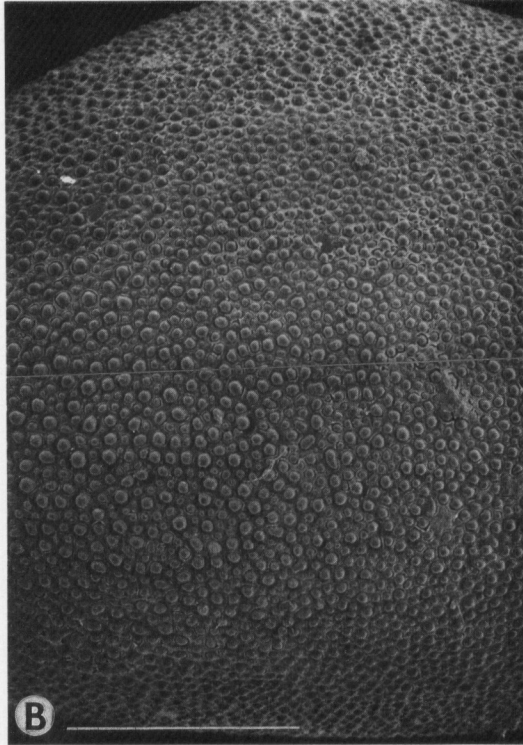
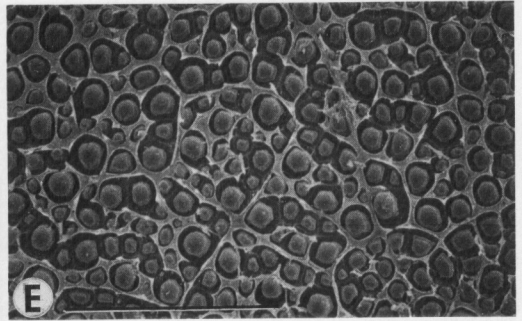
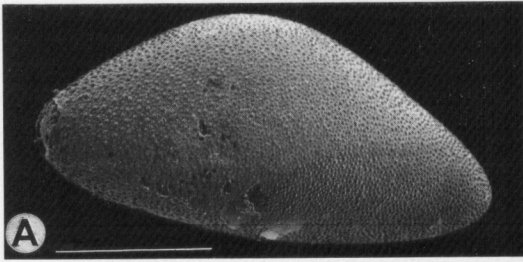
The chorionic pattern of the ventral surface of the present eggs of *Ae. cantans* from Poole in Dorset is identical to the pattern observed on eggs obtained from Monks Wood, Hutingdonshire (Hinton and Service 1969) some 200 km to the southeast. It would be interesting to compare the detailed morphology of the eggs of *Ae. cantans* with those of *Aedes annulipes* (Meigen), because female adults of the 2 species are very difficult to separate and larvae are virtually indistinguishable, although larval habitats are said to differ. Hinton (1981) in fact shows a single SEM photograph of the "side" view of the eggs of each of these 2 species and the chorionic pattern appears almost identical, but unfortunately there are no details as to whether the same lateral aspects of the eggs are being compared. Eggs of *Ae. cantans* and *Ae. punctor* differ markedly in shape and size from those of *Ae. rusticus*, which also breeds in shaded woodland pools and sometimes occupies the same larval habitats, especially of *Ae. cantans*.

Illustrations of the outlines of 10 of the 14 British *Aedes* species given by Marshall (1938) show that in both ventral and lateral views the eggs of *Ae. rusticus* are readily distinguished from those of all the other species, and this same diagnostic shape is shown in the present studies. *Aedes rusticus* is an easily recognized species in the adult and all larval instars and eggs, which facilitates detailed ecological studies when other *Aedes* species are in the same habitat. The chorionic pattern of *Ae. rusticus* eggs is not too dissimilar to that of *Ae. cantans* and *Ae. punctor*, except that eggs from a few females are rather atypical in the pattern of the reticulum (Figs. 14E, 14F). Whether the variations in the chorionic patterns exhibited by eggs laid by some female of *Ae. punctor* (e.g., Fig. 8E) and *Ae. rusticus* (e.g., Figs. 14E, 14F) represent intraspecific variations or distinct taxa is unknown, but merits further study.

Aedes detritus breeds in saline waters and the sculpturing on the egg and shape and arrangement of the tubercles are completely different (Fig. 10) from all 3 previous species. *Aedes cinereus* (Fig. 1) is the only British species in the subgenus *Aedes* and their eggs, as well as being rather long and narrow, differ from those of the other 4 species examined by having a completely different pattern

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Fig. 14. *Aedes rusticus*. A, Entire egg, lateral view, ventral surface at top, anterior end to left; B, chorionic cells, lateral surface, ventral–dorsal transition; C, chorionic cells of middle ventral surface; D, chorionic details of middle ventral surface; E, chorionic details of middle ventral surface showing variation of much larger cells enclosing numerous tubercles; F, chorionic details of middle ventral surface showing ridges in cell floor; G, chorionic cells of dorsal middle surface; H, chorionic details of middle dorsal surface. Scale = 10 μm (D, F, H), 50 μm (C, E, G), 100 μm (B), and 200 μm (A).



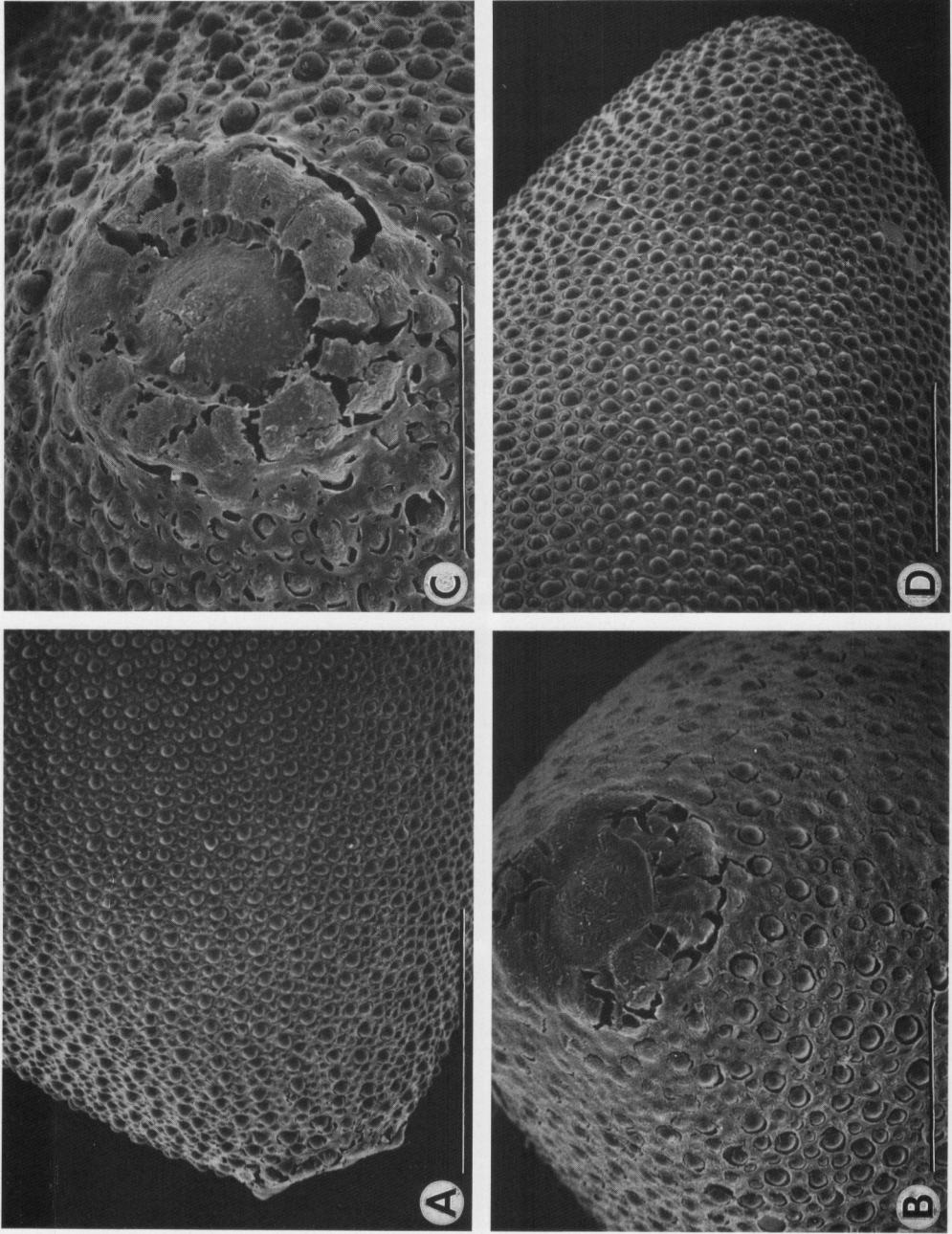


Fig. 15. *Aedes rusticus*. A, Anterior end; B, anterior end showing microphyte; C, microphyte; D, posterior end. Scale = 50 μ m (B, C, D) and 100 μ m (A).

ventrally and dorsally (Fig. 2), although ventrally the tubercles are rather similar to those of *Ae. rusticus*.

Eggs of *Aedes geniculatus* (Olivier), the only British species in the subgenus *Finlaya*, have not been described in detail, but eggs of *Aedes vexans* (Meigen), the only British representative of subgenus *Aedimorphus*, have been described from the USA, and SEM studies on specimens from Florida (Linley 1990) show that the chorionic sculpturing is quite different from that seen in any of the other British *Aedes* species so far examined.

ACKNOWLEDGMENTS

We would like to thank Drs. J. F. Day, L. P. Lounibos, and J. K. Nayar for reviewing the manuscript. This is University of Florida—IFAS Experiment Station Journal Series No. R-05302.

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