Transactions of the Society for British entomology
Southampton,
https://www.biodiversitylibrary.org/bibliography/150889

v.1:pt.1 (1934:June 1):
https://www.biodiversitylibrary.org/item/255703

Article/Chapter Title: CG Johnson 1934 eggs
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TRANSACTIONS OF THE SOCIETY FOR
BRITISH ENTOMOLOGY

VOL. 1. 1ST JUNE, 1934. PART 1.

ON THE EGGS OF *NOTOSTIRA ERRATICA* L. (HEMIPTERA, CAPSIDAE).

I. OBSERVATIONS ON THE STRUCTURE OF THE EGG AND THE SUB-OPERCULAR YOLK-PLUG, SWELLING OF THE EGG AND HATCHING.

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INTRODUCTION.

Throughout the extensive literature dealing with the eggs of the Hemiptera-Heteroptera scarcely any information exists concerning the presence of a plug of yolk formed beneath the operculum or micropylar cap and later extruded from the chorion at the anterior or micropylar pole.*

Haseman (1918) when describing eggs of *Lygus pratensis* L. records a short plug of yolk at the anterior pole and appears to have noticed a similar structure in eggs of related species. According to Painter (1929) this plug, which forces up the cap for a short distance, appears just before hatching. China (1925 A) has seen changes at the anterior pole of the eggs of *Notostira erratica* L. and has noticed that the black band, which develops just below the micropylar cap, seems to stretch and grow longer. These authors, however, neither figure nor describe this yolk-plug in detail nor mention the causes of its extrusion.

The present paper deals with certain features of the morphology and development of the eggs of *Notostira erratica* L. (Hemiptera) and in particular with the structure and behaviour of this sub-opercular yolk-plug. Hatching is also described.

TECHNIQUE.

Many Capsid eggs are well buried in plant tissue and this has probably accounted for the dearth of observations on the yolk-plug. The eggs of *Notostira erratica* are laid between the sheathing leaf-base and the culm of grasses (Johnson, 1932) and can easily be detached and conveniently studied.

Whole mounts of eggs were extensively used. Carnoy's and Bouin's fixatives and subsequent staining with Grenacher's Borax Carmine or Acid Fuchsin gave good results, particularly Acid Fuchsin after Bouin's. Excessive shrinkage resulted unless dehydration was gradual. Clearing agents used were Cedarwood Oil or Phenol-Xylol. Coverslips were supported on paper strips.

Sections of eggs were difficult to obtain owing to the brittleness of the chorion. Paraffin wax was preferred to celloidin and wax (double embedding), but it was found that a lengthy infiltration with very frequent changing of the wax was necessary. Fairly good sections of eggs in the oviducts were obtained by sectioning gravid females. By this method many eggs may be sectioned together without crumbling from the block. Sections were stained in Haematoxylin (Delafield's and Heiden-

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* Wherever in this paper the sub-opercular yolk-plug is mentioned it is for convenience called the 'yolk-plug,' and should not be confused with the yolk-plug remaining within the embryo after dorsal closure has taken place. (See Imms, 1925; Tillyard, 1917.)

hain's) or in Acid Fuchsin. The smaller measurements were made with a one-twelfth inch oil immersion objective and a micrometer eyepiece (× 10).

Physiological Technique.

In order to obtain eggs at a given time it was necessary to control oviposition. It was found that bugs failed to oviposit unless stems bearing leaf sheaths were offered to them. For all experiments, gravid females from the field (one locality only) were used, and they could be kept for many days out of doors on detached blades of grass (*Agropyrum caninum* Beauv. and *A. repens* Beauv. were found to be most suitable) standing in water. When eggs were required, bugs were placed on stems bearing leaf-sheaths. They usually laid readily at intervals of about three days under these conditions.

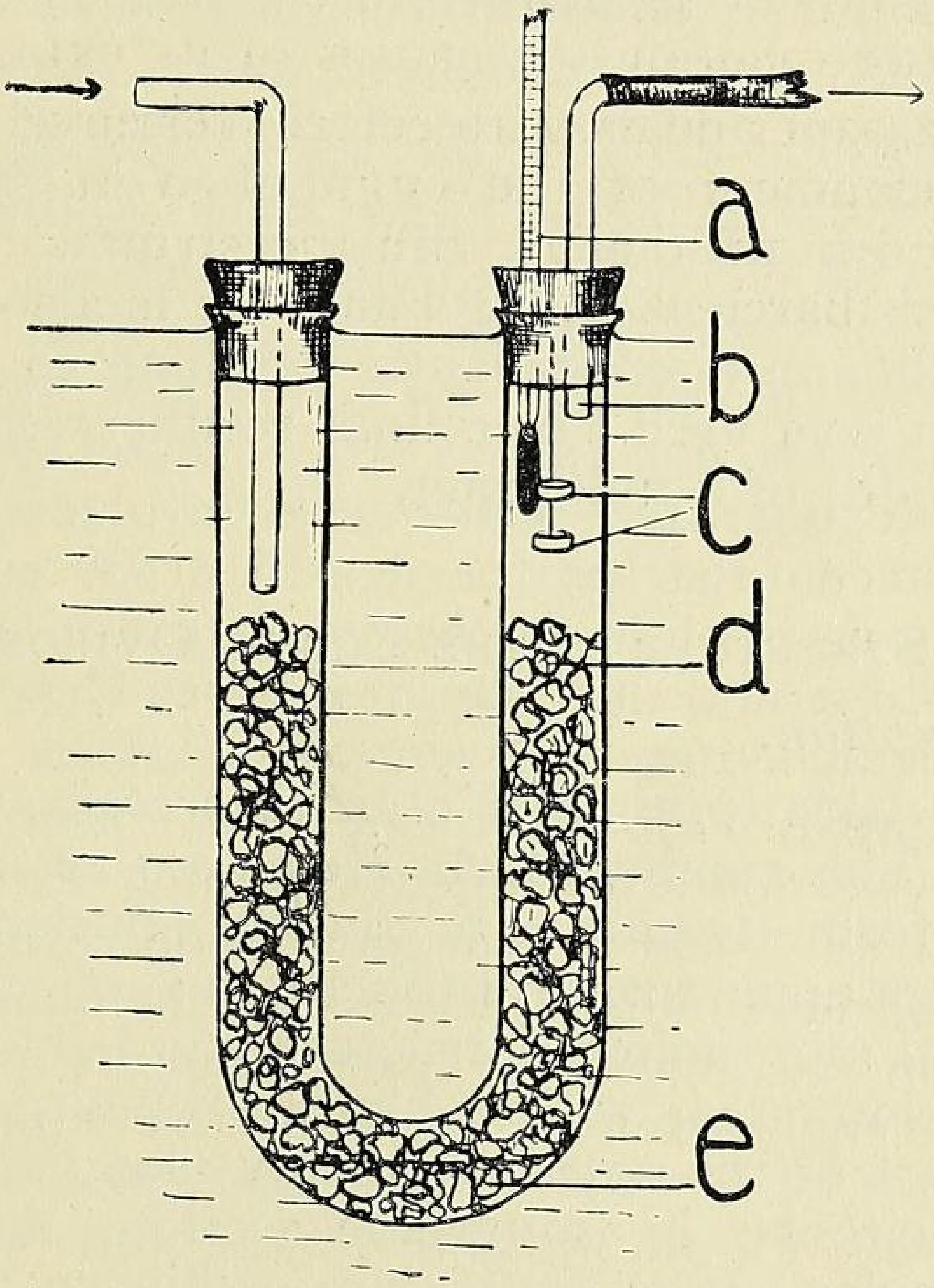

FIG. 1.—Diagram of Incubator. *a*, Thermometer. *b*, Outlet tube. *c*, Wax-coated glass shelves for eggs. *d*, Wet pumice-stone. *e*, Water.

The eggs, adhering to one another in a row, were then detached with a damp brush. It was found unnecessary to separate them except when measurements were required at the time of oviposition. In the water-saturated atmosphere of the incubators the egg cement failed to dry and eggs could easily be separated later with less likelihood of damaging them.

The incubators were kept in thermostats at 18° C. (variation 0·2°) and at 28·5° C. (variation 0·5°). Embryonic development in a saturated atmosphere is most rapid at approximately the latter temperature. Eggs were removed from day to day and quickly measured under the low power, the process taking about twenty minutes for the largest batches.

Incubators were made from glass U-tubes 2 cms. wide, 15 cms. high (Text Fig. 1). Each limb was two-thirds filled with clean wet pumice stone, and a little distilled water was kept at the bottom. Shelves for the eggs were made from the ends of small glass tubes, coated with paraffin wax and attached by a silver wire to the rubber bung, which also held a thermometer with the bulb near the shelves and an outlet tube. Air was pulled through the incubators in a slow, continuous stream. Since the eggs were removed from time to time and so subjected to a change of temperature, their surfaces were always moist, presumably due to condensed water. This factor seemed reasonably constant and was therefore neglected.

All linear measurements are expressed in the units on the eyepiece, and ten such units equal 0·09 mm. The weighings were made with batches of eggs and the mean of a single egg taken. A Kuhlmann micro-balance weighing to one-thousandth of a milligram was used. The final results were taken to the nearest hundredth of a milligram.

The Structure of the Egg at Oviposition.

General Description.

Eggs from both forms of *Notostira erratica* have been used as indicated. The summer form (female 1 of Butler) and the overwintered form (female 4 of Butler) (Butler, 1924; China, 1925 B) lay eggs apparently (in the absence of statistics) similar in their general morphology, structure and behaviour.

They are elongated, with a bluntly rounded posterior pole. The widest part of the egg is half-way along its length and is there almost circular in transverse section. Anteriorly is the whitish micropylar cap or operculum making a definite junction with the chorion at its margin (Plate I, A; Plate III, A and B). Below the cap is a laterally compressed region, the neck, merging indefinably into the bulk of the egg and making a slight angle with it. The cap is obliquely fitted to the anterior pole. The egg when seen laterally thus appears bent, with a longer convex region at which the dorsum of the embryo is finally situated and a shorter concave region. These regions are termed dorsal and ventral respectively throughout this paper. The egg is yellowish, completely filled with yolk and approximately 1·8 mm. long.

The chorion.

The whole surface of the egg, except for the micropylar cap, consists of a smooth, unsculptured, colourless chorion, composed of an exochorion and an endochorion of equal and uniform thickness (3μ to 4μ) except at the rounded base and at the neck. At about 110μ from the base, the endochorion alone gradually thickens, becoming 6μ to 9μ thick at the extreme end.

The chorion gives positive reactions with Xanthoproteic, Millon's, Biuret and Glyoxylic tests. It is insoluble in cold concentrated Nitric Acid and cold 50 per cent. Potash. The endochorion stains deeply with Heidenhain's Haematoxylin, Borax Carmine and Acid Fuchsin, while the exochorion remains colourless.

The operculum or micropylar cap (Plate I, A; Plate II, G; Plate III, B).

Seen from above the opaque, whitish micropylar cap has a sole-shaped outline, with wide dorsal and narrower ventral halves. Round the rim, running into the cap for a short distance, are about fifty faint, regularly spaced lines, some of which are micropyles. The surface of the cap has minute, faint, round markings. Seen laterally the dorsal and ventral halves of the cap are more or less bulbous, sloping gently at the margin. The inner surface of the cap next to the yolk is smooth with two concavities, one dorsal, one ventral.

The cap, which is non-cellular, has a honeycomb-like structure. Between its inner concave and outer convex surfaces are from two hundred to two hundred and fifty elongated chambers, all except the outermost occupying the shortest distance between the inner and outer cap surfaces. These chambers are from 45μ to 50μ long, those in the centre longer than those at the outside; the latter are somewhat flattened in the plane of the cap surface. Although with no visible contents, the chambers probably contain fluid at oviposition. They often contain air when mounted. Their inner ends abut on to a comparatively thick (5μ to 8μ) wall, which forms the inner surface of the cap next to the yolk. Unlike the chorion this wall is composed of a single layer which sections show to be continuous with the endochorion (Plate I, B; Plate III, B). The outer cap surface is very thin.

Thus the chambers open neither to the yolk on the inside nor to the atmosphere on the outside. The longitudinal separating walls are 1μ to 2μ thick and are twice this thickness at the extreme anterior ends. When the caps are cleared the anterior ends of the chambers are seen to be round or ovate, separated by walls 3μ to 5μ thick, and the posterior ends to be irregularly polygonal, separated by uniformly thick walls (1μ to 2μ) (Plate I, C and D). The margin of the cap where it joins the chorion has a lace-like structure. Acid Fuchsin and Heidenhain's Haematoxylin stain the cap, but the inner wall, unlike the endochorion, will not easily stain.

The micropyles (Plate I, B).

Between twenty and forty micropyles are situated at the anterior end of the egg, occurring at irregular intervals, sometimes five or six together, sometimes well spaced. Sections of the eggs show that the micropyles open to the inside of the egg by a shallow, funnel-shaped depression (round in surface view on whole mounts) 5μ to 6μ in diameter and situated in the endochorion just below its junction with the cap. This funnel leads into a tube 2μ in diameter, which passes through the endochorion. At the inner face of the exochorion it bends upwards almost at right-angles and becomes slightly wider and flatter in the plane of the cap-surface. The other openings of the micropyles have not been found, although very many sections have been cut, for as the micropyles enter the outer region of the cap, their boundaries become indistinguishable from its walls and chambers. To find if the outer pore became occluded at oviposition with the cement which attached the eggs to the leaf-sheath, longitudinal sections through gravid females were cut, but even in the unlaid eggs the anterior opening of the pore could not be seen. It is therefore unknown if there is any relation between the cavities of the cap and the micropyles.

The neck (Plate III, A and B).

The neck is that region of the egg below the cap and is slightly compressed laterally and bent ventrally at an angle with the rest of the egg. The endochorion here thickens (Plate I, B) and at the cap margin the whole chorion is 9μ to 10μ thick. Normality is gradually assumed 100μ to 120μ below this margin. The yolk-plug is moulded to the shape of this neck, within which it develops; the extra thickness of the chorion in this region probably prevents it from splitting as the yolk-plug is extruded under pressure.

The vitelline membrane (Plate III, B).

The yolk is completely surrounded by a uniformly thin (less than 1μ thick) vitelline membrane, which in live eggs is in contact with the whole internal surface of the chorion and cap, since the yolk completely fills the egg.

POST-OVIPOSITIONAL CHANGES.

Changes in size at 28·5° C. in a saturated atmosphere with uncontrolled condensation. Eggs of the summer generation, female 1.

It is convenient for purposes of description to deal with these changes in two stages. This is purely a convenience, Stage I and Stage II being continuous in reality.

Stage I.

During the first 84 (approx.) hours after oviposition and prior to the extrusion of the yolk-plug.

The eggs when laid often seem to be incompletely filled out, the chorion appearing somewhat flaccid. The eggs at this stage are very soft, easily dented and quite able to bend to the curve of the culm against which they are laid. During the first few hours of free life the chorion becomes slightly stiffer and the flaccidity disappears. Following this, there may be either a slight increase or decrease in size. This does not occur invariably, and the size may remain constant until the end of the second day, when an abrupt and rapid increase in volume takes place, so that at the end of Stage I the egg appears larger even the unaided eye.

Table I summarises the results obtained by measuring the widest part of the egg as seen from lateral view, at intervals during incubation. Text Figure 2 shows this increase in diameter plotted against time.

TABLE I.

Hours after ovipn.	No. of eggs.	Mean width per egg.	P.E. of dif. of selected means.	P.E. of dif. of adjacent means.		Significance test.
0	97	38·1				
				±0·29		Not sig.
24	29	38·1				
				±0·27		Signif.
27·7	46	39·2				
				±0·12		,,
47·6	100	38·5				
				±0·34		,,
67	24	41·6				
				±0·35		,,
75·25	38	44·0				
				±0·40		Not sig.
88	23	44·3	±0·26		Signif.	
				±0·42		Not sig.
95·9	35	45·5				
				±0·32		,,
99	20	46·2				
			±0·26	±0·29	?Signif.	Not sig.
121·1	71	45·9				
				±0·23		,,
144·2	65	46·4				
				±0·42		,,
167·5	19	45·3				
			±0·57	±0·43	Signif.	,,
172	44	45·8				
				±0·58		,,
191·3	11	43·9				
				±0·65		,,
197·3	25	44·9	±0·52		Signif.	
				±0·61		Signif.
218·25	12	41·5				

TABLE I :—Mean width of egg of *Notostira erratica* (female 1). Measurements at the widest part in lateral view at intervals between oviposition and hatching. Incubated at 28·5°C. in saturated atmosphere with uncontrolled condensation.

The probable errors of the differences of the means were calculated by the method given by Caradog Jones (1929, p. 161). Mean widths are taken to the nearest first decimal place; P.E. taken to the nearest second decimal place. Where batches of eggs (from six to twenty per batch) were measured within three hours of the same period of time after oviposition, they were grouped and the mean time taken (first column in Tables I, III and IV).

Throughout all the statistical work three times the Probable Error has been taken as significant of difference.

Means at the ends of brackets are those selected for treatment in the fourth column.

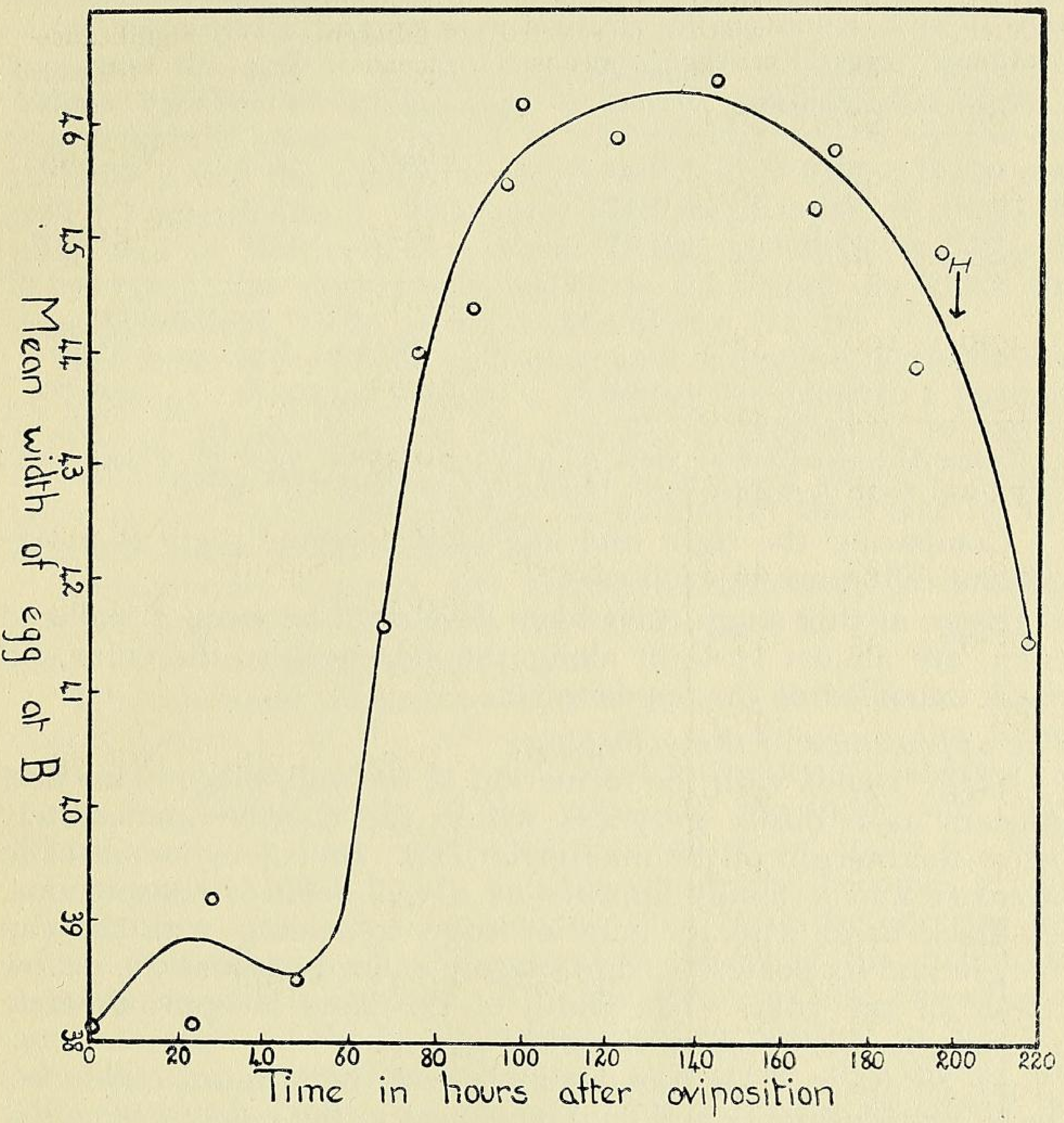

FIG. 2.—The variation in mean width at widest part of egg, with time. Eggs of *N. erratica* L. (summer generation, female 1) at 28·5°C. in a saturated atmosphere (uncontrolled condensation).
H = Mean hatching time.

The eggs do not increase in size uniformly. The greatest increase is at the middle. The neck, due to its greater thickness of chorion, increases but slightly and thus later appears as a constriction, the rest of the egg being much swollen in proportion to it. Table II expresses the mean measurements of a number of eggs (female 1) at oviposition and at the end of Stage I. At 84·1 hours the caps had just split. At 71·7 hours the black band was fully developed but the caps had not split.

TABLE II.

	At oviposition.			After 84·1 hours (Stand. Err. = ±1·39).		
	No. of eggs.	Mean measurements.	Standard error.	No. of eggs.	Mean measurements.	Standard error.
a.	97	34·9	±0·21	38	36·1	±0·22
b.	97	38·1	±0·17	38	45·2	±0·25
c.	65	37·8	±0·18	24	45·2	±0·33
				After 71·7 hours (Stand. Err. = ±0·54).		
l.	95	199·4	±0·68	52	203·6	±0·80

TABLE II :—a = Lateral view of neck; b = lateral view of widest part; c = ventral view of widest part; l = length (see Plate III, fig. A).

Comparing the right and left-hand columns there is a significant difference in each case.

Eggs at this stage, that have developed between a leaf and culm, are almost straight along the side next to the culm and much extended at the opposite side.

The appearance of the yolk-plug.

Stage I ends with the formation of the yolk-plug. This first appears as a dusky greyness within the chorion immediately below the margin of the micropylar cap. Its colour increases in intensity and it finally appears as a well-defined, conspicuous, jet black band with its anterior edge coinciding with the cap margin and its posterior edge sharply defined against the yellow colour of the yolk. The width of the band is approximately 0·3 mm., and it occupies the neck region.

At 18° C. in a saturated atmosphere, nine hours elapse between first duskiness and final blackness in the eggs of female 4. At 28·5° C. in a saturated atmosphere the period is shorter.

The structure of the yolk-plug (Plate I, F; Plate II, E, F, G; Plate III, C, D, E).

The yolk-plug consists of a mass of yolk surrounded by a non-cellular wall which is apparently secreted by the epithelium of cells lying between it and the yolk.

The wall of the yolk-plug is perfectly continuous with the outermost membrane surrounding the mass of the yolk within the chorion, and is built of an inner and an outer layer (Plate II, E, G; Plate III, E). The outer layer has pigment evenly distributed through it and has a chitinous appearance. Its pigment appears brown by transmitted light and black by reflected light, and it gives the yolk-plug its colour. This layer, which does not stain with Haematoxylin or Erythrosin, varies in thickness from 4 μ at the sides of the pigmented region to 2 μ beneath the micropylar cap. There the yolk-plug wall (except for the median region) is almost colourless, due both to the thinness of the outer layer and to the relative scarcity of pigment. The median region of the wall at the anterior end of the yolk-plug, normally hidden by the micropylar cap, is heavily pigmented and of a characteristic shape (Plate I, F; Plate III, D). It is the lid through which the embryo emerges and will be called the stenopyle (=narrow gate). The outer pigmented layer of the yolk-plug wall is relatively very thick at the stenopyle and varies from 15μ at the dorsal end, which is the hinge on which the stenopyle opens, to 6μ at the middle (Plate III, D).

The inner layer of the yolk-plug wall is hyaline, with little or no pigment. It stains heavily with either Heidenhain's Haematoxylin or Erythrosin. At the anterior unpigmented region of the yolk-plug, where the outer layer is only 2 μ thick, this inner layer is 10 μ thick and reaches its maximum thickness of 14 μ near the hinge of the stenopyle.

Immediately beneath the stenopyle, however, it is much thinner, and the thickness of the wall is there for the most part made of the outer pigmented layer.

The combined thickness of the inner and outer layers at the dorsal convexity of the yolk-plug (*i.e.* the hinge of the stenopyle) is about 20 μ, while at the ventral convexity it is about 13 μ.

In the lateral walls of the yolk-plug the inner and outer layers assume a more equal thickness (outer 4 μ, inner 5 μ, half-way along the black band), and the whole wall becomes gradually thinner until, approximately 0·5 mm. from the anterior end of the yolk-plug itself, the normal thickness of the membrane around the yolk is attained. This membrane is also non-cellular and less than 1 μ thick. It corresponds in position to Speyer's 'middle egg membrane' (Speyer, 1929; see also Sikes and Wigglesworth, 1931, for *Cimex*), and will here be called the yolk-plug membrane, since it is continuous with the walls of the yolk-plug (Plate II, E, G; Plate III, E). No pore canals have been found in either of the layers of the yolk-plug wall, but they may have been obscured by the stain (see Wigglesworth, 1933).

In yolk-plug walls of eggs from which the embryo has hatched, the inner layer had almost disappeared. Presumably it is absorbed with the remains of the yolk just before eclosion.

The cells lining the inner surface of the yolk-plug wall are very small, numerous, close together and flattened against the wall, except at the anterior end of the plug, where they are columnar. They are in contact with the yolk on the inside.

The yolk in the yolk-plug is the last to disappear (except for the gut contents of the embryo) before the embryo hatches. After eclosion the yolk-plug wall remains projecting from the chorion and it is plainly continuous with the yolk-plug membrane, which forms a sac within the empty chorion.

Stage II.

The splitting of the micropylar cap (Plate I, E).

The egg continues to swell and a condition of internal pressure is reached when the egg splits. It is convenient to regard this splitting as the commencement of Stage II.

The splitting normally occurs around the micropylar cap. The regions which split are the following :—

(1) Where the endochorion joins the inner wall of the cap. This rupture is a clean split running round the egg. It is generally obscured by the frayed edges resulting from

(2) a split at the outer face of the cap itself, just above the chorion-cap junction. This rupture is usually ragged and is more obvious than the split (1). It takes place in such a manner as to leave a narrow membranous band attached to the chorion rim. This band is joined to the exochorion but, unlike it, stains readily. Before the split occurred it was combined with the outer surface of the cap around the margin and was indistinguishable as a separate membrane. Through this membrane run portions of the cap, which appear as short white flaps, usually with micropyles running up them. In unmounted eggs it is only these flaps which are apparent (Plate III, C), and the membrane (which can be seen easily in stained preparations) is often not very obvious. The edge of the cap usually has a few white flaps similar to those on the chorion rim, but often is quite without them.

In eggs of other Hemiptera when the cap is pushed off by the embryo at eclosion, a clean rupture between cap and chorion occurs. In the eggs of *Notostira* when the yolk-plug extrudes and pushes off the cap there is, in addition to the clean break round the endochorion, a ragged split round the outer surface of the cap rim. The eggs when newly laid, however, seem from superficial examination to be similar at the junction of the cap and chorion to eggs of other species of the Order. Since no observations have been made of cases where the insect has emerged before the yolk-plug has commenced to split the cap, it cannot be said if the latter then comes off cleanly.

The actual splitting of the cap, from the time it appears to weaken until the yolk-plug can be seen plainly through the split, may take several hours at temperatures near 28° C. in a saturated atmosphere and several days in nature in cold weather. There is a certain amount of stretching of the cap, which seems to become papery, before it finally parts from the chorion. Once the rupture occurs and the resistance diminishes, the yolk-plug may move outward very slightly with a visible but slow movement. In the vast majority of cases, however, movement is too slow to be seen under low powers.

The extrusion of the yolk-plug. General description and behaviour in nature.

The internal pressure during Stage I, which results in a swelling of the egg and then in the bursting of the cap, continues into Stage II, and since the relatively inextensible cap and chorion are now no longer joined together, the yolky mass of the egg is not so limited in its longitudinal expansion. A much greater increase in length now occurs, the egg contents within the chorion extruding *beyond the chorion* at the ruptured anterior pole in the form of the yolk-plug (Plate I, E, F; Plate III, C, E).

The yolk-plug itself is inextensible and changes neither in shape nor size as it is extruded. At the same time there is a slight increase in girth of the egg (*cf.* Text Figs. 2 and 3). Yolk still completely fills the egg and the yolk-plug membrane is in close contact with the whole inner surface of the chorion. Increase in size of the egg must therefore be accommodated by a stretching of the yolk-plug membrane. Careful preparations and observations have been made to see if there is any invagination of this membrane which unfolds as the yolk-plug is extruded, but no such condition has been found.

The remains of the micropylar cap and the yolk-plug are in contact although there is no actual connection between them. The broken cap is simply pushed away from the chorion on the anterior end of the yolk-plug as the latter extrudes, and it may be easily removed without harm either to the development or the hatching of the embryo. It apparently has no further function.

The yolk-plug when extended appears black and shining and is in very close contact with the neck of the chorion, but in no way joined to it. The ovate rim of the neck is gradually stretched so that it becomes circular when the plug is well extended.

In nature the yolk-plug may extrude from less than half to the entire width of the black band before hatching occurs, and this is the amount of extension commonly seen, especially in eggs laid from March to June by the overwintered form (female 4). In the eggs of the summer form (female 1), however, the yolk-plug has been seen extruded to a distance of twice the width of the black band, exposing a thin (2μ) colourless membrane behind the posterior edge of the black band for a distance of approximately 0·3 mm. This thin membrane (about six to two times the normal thickness of the yolk-plug membrane), although well filled out, showed no signs of bursting. This difference in behaviour is probably due to environment, since yolk-plugs of eggs from both generations are capable of such a lengthy extrusion. There is often variation in behaviour of eggs of the same batch within the same leaf sheath; those which are well covered tend to extrude the yolk-plug before those more exposed.

Extrusion of the yolk-plug under controlled conditions.

Owing to the obliquity of the operculum, the dorsal side of the yolk-plug is normally slightly longer than the ventral side; all numbers expressing the length of extrusion are mean values of dorsal and ventral measurements taken from the chorion rim to distal points on the outer surface of the remains of the operculum.

Extrusion of the yolk-plug at 18° C. in a saturated atmosphere with uncontrolled condensation. Overwintered form (female 4).

The cap splits between one hundred and sixty-five and one hundred and eighty hours after oviposition. The yolk-plugs extrude similarly until about three hundred and sixty hours after oviposition, when they behave with more irregularity.

Table III shows the data on which Text Fig. 3 is based.

TABLE III.

Hours after ovipn.	No. of eggs.	Mean length.	P.E. of dif. of means.	Sig. Test.
190	14	16·2		
			±0·53	Signif.
213·75	13	18·5		
			±0·56	,,
237·5	13	23·5		
			±0·39	,,
262	13	26		
			±0·59	,,
286	13	29·7		
			±0·62	,,
304·5	14	32·4		
			±0·45	,,
330	13	34·7		
			±0·48	? Sig.
365·75	13	36·1		
			±1·06	,,
389·75	13	39·1		
			±1·67	Not sig.
410	9	40·8		

TABLE III:—Mean length of extruded yolk-plug at 18°C. in a saturated atmosphere with uncontrolled condensation. Two batches of eggs from an overwintered female (female 4) are represented. There is a significant difference between the seventh and ninth means.

Extrusion of yolk-plug at 28·5° C. in a saturated atmosphere with uncontrolled condensation. Summer form (female 1).

Observations on thirty-eight eggs showed that the cap split at eighty-four hours (standard error = ± 1·39). Table IV summarises the data and Text Fig. 3 records it graphically.

TABLE IV.

Hours after ovipn.	No. of eggs.	Mean length.	P.E. of dif. of means.	Sig. Test.
88	17	15·8		
			± 0·67	Signif.
96	33	22·3		
			± 0·84	Not sig.
99	20	22·8		
			± 0·81	Signif.
120·75	67	28·4		
			± 0·57	,,
144·2	63	34·7		
			± 0·86	,,
167·5	19	39·8		
			± 0·98	Not sig.
172	43	39·4		
			± 1·44	? Sig.
191·3	12	42·4		
			± 1·75	Not sig.
197·25	25	41·5		

TABLE IV :—Mean length of extruded yolk-plug at 28·5°C. in a saturated atmosphere with uncontrolled condensation. Summer form (female 1).

It was decided to give no equations for the curves until they could be viewed in the light of the whole continuous process of volume change.

The absorption of water.

Preliminary observations on a small scale have been made, but statistical treatment of the problem is in hand and will form the subject of a subsequent paper.

Table V summarises these preliminary results for three batches of eggs from summer generation females (female 1) kept at 28·5° C. in a saturated atmosphere with uncontrolled condensation.

TABLE V.

Hours after ovip.	No. of eggs.	Fresh wt. per egg in gms.	Increase in wet wt. per egg in gms.	Dry wt. per egg in gms.	Uncombined water per egg °/₀ wet wt.	°/₀ incr. in wet weight.
0	19	0·00011	—	0·00006	45·45	0
0	9	0·00010	—	—	—	—
193	5	0·00016	0·00006	0·00004	75	60
0	15	0·00012	—	—	—	—
233	8	0·00020	0·00008	0·00005	75	66·6

Observations also show that the egg may withstand considerable water loss. Some eggs nine days old which had been kept on damp filter paper in the laboratory had the yolk-plug completely developed but without the cap split, and with the developing embryo just visible. The filter paper was allowed to dry, and all the eggs developed deep dents along their whole length. The filter paper was re-moistened, and within twelve

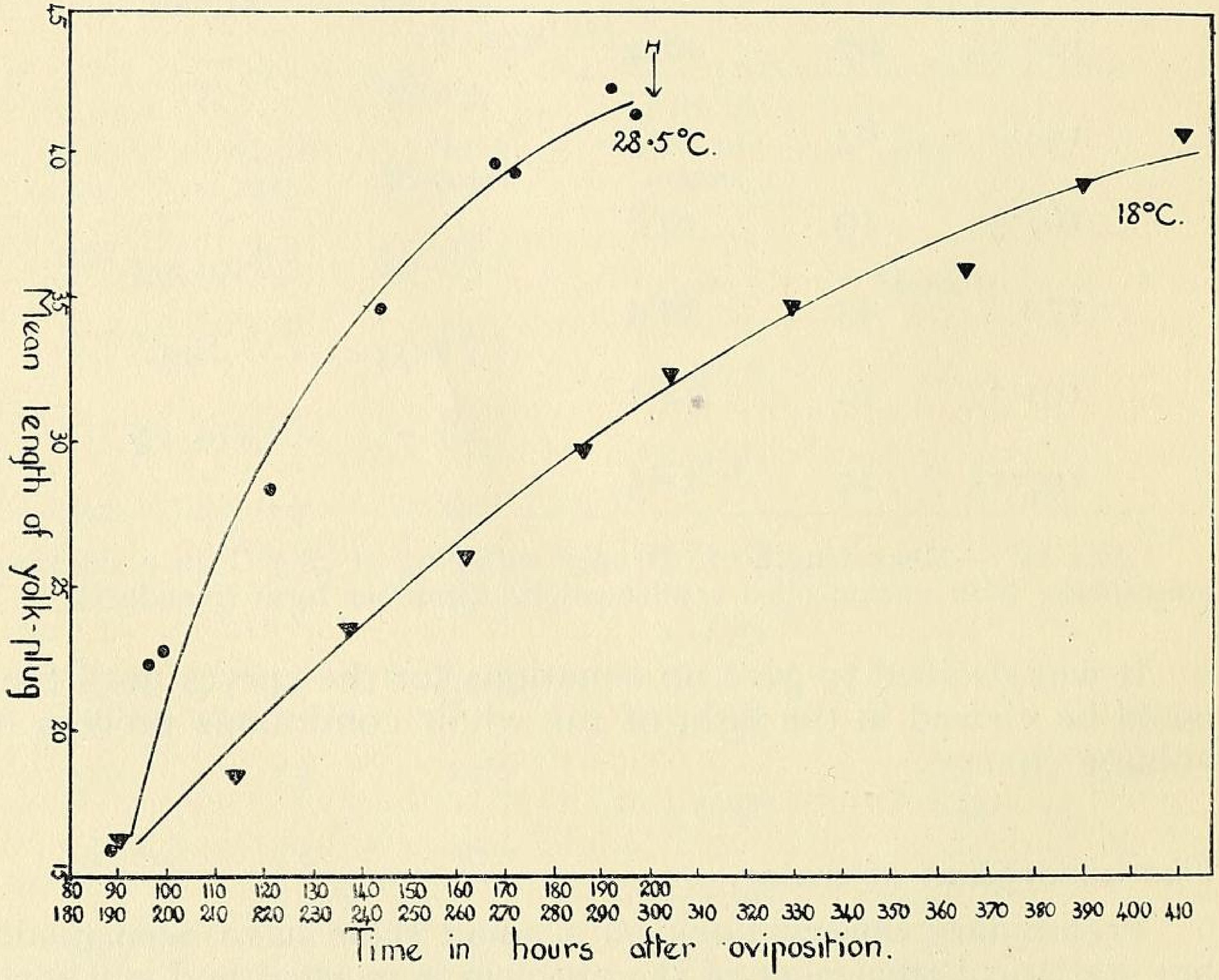

FIG. 3.—Diagram of increase in length of yolk-plug at constant temperature and saturated atmosphere (uncontrolled condensation).
Dots for eggs of summer generation (*Notostira erratica* L. female 1).
Triangles for eggs of overwintered generation (female 4).
H = Mean hatching time for eggs of summer generation.
The upper row of figures along the abscissa refers to eggs of summer generation, the lower row to eggs of overwintered generation.

hours the dents had completely disappeared, the eggs had swollen considerably and the caps were beginning to split. These eggs subsequently developed quite normally on wet filter paper and hatched. These results show that with swelling there is simultaneous absorption of water.

Discussion.

The swelling of certain insect eggs is well known and has been recorded by several observers (Torre-Bueno, 1903, 1906, 1920; Donisthorpe, 1927; Kerenski, 1930; Peacock, 1928). Steer (1929) records swelling in the eggs of *Calocoris norvegicus* Gmel. and notes a considerable difference in size of eggs of *Nabis apterus* F. Austin (1931, 1932) remarks on the difference in shape between the eggs from gravid females of *Lygus pratensis* L. and those dissected from plant tissue.

There is at present no reason to suppose that the forces which account for the extrusion of the yolk-plug in the egg of *Notostira erratica* are different from those which cause the general swelling of the egg. There is in addition, however, the force exerted by the elastic chorion as it tends to resist distension and return to its original size. This elasticity is demonstrated when the diameter of the egg decreases before hatching but when the characteristic longitudinal dent in the chorion is absent (see Text Fig. 2).

The force within the egg sometimes results in a burst before the yolk-plug is formed. A bubble of yolk is then seen usually either at the rim of the micropylar cap or at the dorsal side of the egg.

Many Capsid eggs are laid in plant tissue, even in the wood (Steer, 1929; Petherbridge and Husain, 1918; Austin, 1930; Massee and Steer, 1928, 1929), and in such situations a lateral expansion due to swelling would tend to be limited by the surrounding tissue.

Indeed, Massee and Steer (1928) with *Calocoris norvegicus* Gmel., and Petherbridge and Husain (1918) with *Plesiocoris rugicollis* Fieb., mention the pressure of the wood, which flattens the eggs slightly. In such cases it would be necessary for the egg to become accommodated in shape to the increased pressure, and the only way in which it could do so without harm would be by expanding longitudinally, thus forcing a yolk-plug out of the micropylar pole which in Capsid eggs is always directed towards the outer surface of the tissue in which it is laid. It is probable that in such cases the yolk-plug would begin to extrude before the diameter of the egg had increased appreciably. It is also probable that it is the yolk-plug which brings the cap to the surface of the plant tissue when the eggs are inserted so that the caps are well beneath the surface level, as recorded by Massee and Steer (1929).

Slingerland (1893), on *Poecilocapsus lineatus* Fabr., describes a white, finely striated portion occupying the upper third of the egg, and writes : 'With the growth of the surrounding tissue of the stem the eggs are usually forced out of the slit somewhat, so that about half or even more of the white portion of the egg projects from the slit.' This at least suggests the presence of a yolk-plug, which extrudes either under the pressure of growing plant cells or by the swelling of the egg.

In any case the yolk-plug may be regarded as a mechanism which allows the egg to swell in one direction and to survive what would otherwise be a fatal bursting due to the inherent tendency of the egg to swell.

It is at present impossible to say what significance the yolk-plug has other than that directly associated with the absorption of water and the swelling of the egg. No attempt has yet been made to study the development of the yolk-plug, and so the relation of the epithelium within its wall to other parts of the developing embryo is unknown. It seems probable that it is a portion of the serosa, since the yolk-plug is often well developed before details of structure are noticeable on the germ band when seen in whole mounts. The yolk of the yolk-plug is continuous with the yolk dorsal to the developing embryo before dorsal closure is complete (Plate II, E). As the embryo matures, the yolk of the yolk-plug leaves contact with the walls of the latter, first at the sides nearest the embryonic head, and thins down to a strand attached to the dorsal surface of the thorax (Plate II, A). This strand itself is surrounded by a cellular layer which is continuous with the epithelium of the yolk-plug (Plate II, G). These cells, together with the epithelium within the plug, eventually become absorbed with the yolk.

According to this supposition, the yolk-plug membrane is most likely to be a membrane secreted by the serosa. The membrane itself is non-cellular, as can be seen in eggs from which the embryo has hatched.

Boselli (1932), describing the eggs of *Gonocerus acuteangulatus* Goeze (Coreidae), writes of a thickened portion of the vitelline membrane above the head of the embryo. This may be a homologous structure to the yolk-plug of *Notostira*; in the latter case the vitelline membrane is probably replaced by the secreted yolk-plug wall.

HATCHING.

I. Preliminary embryonic movements.

Exact time of hatching varies considerably. At 28·5° C. the mean time for forty-five eggs was 200 hours after oviposition (standard error = ± 5·79 hours). The observations are accurate within 10 hours, but the exact time of hatching was known only in a few cases. At 18° C. for eleven eggs a similar estimate gave 423·45 hours (standard error = ±2·86).

The first visible movements occur in the posterior abdominal segments, while still a considerable amount of yolk completely fills the yolk-plug from stenopyle to embryonic head. At 28·5° C. in a saturated atmosphere this condition is reached approximately 160 hours after oviposition. Movements are of three kinds :—

(1) Muscular contractions of the abdominal wall.
(2) Intestinal peristalsis and antiperistalsis.
(3) Lateral contractions of the heart.

The succession of these movements was watched in eggs reared under laboratory conditions on damp filter paper and at 28·5° C. in a saturated atmosphere and appeared to be fairly constant.

Movements begin with spasmodic convulsions of the abdominal wall in the fifth, sixth and seventh abdominal segments, causing them to be pulled together at the intersegmental sutures. The interval between these convulsions varies at first irregularly between one and seven minutes, and becomes more regular with a quarter to three-quarter minute intervals. Other parts of the embryo show no movement whatever at this stage.

The heart then contracts sluggishly in the abdomen every two to four minutes, and feebler contractions occur in the thorax together with fairly regular intestinal peristalsis at approximately half-minute intervals. These latter seem to move the gut contents only locally, and although no longitudinal wave of contraction occurs the effect must be to squeeze them forward since contractions are only made in the terminal abdominal segments.

These movements of gut, abdominal wall and heart begin separately and irregularly, and gradually become more rhythmic and co-ordinated as eclosion is approached. An intermediate condition exists when, following a few abdominal contractions and a peristaltic wave towards the anus, more contractions of the abdominal wall precede an antiperistaltic wave towards the head. These movements are quite regular in their alternations ; contraction never takes place in the terminal abdominal segment. The anus remains closed.

Thus activity begins posteriorly and spreads forward until the heart is beating vigorously along its entire length but without perfect rhythm, and an energetic antiperistalsis entirely supersedes the peristalsis towards the anus. Antiperistalsis has then been seen to stop, while the whole body heaves dorsoventrally with increasing regularity until definite cycles of about six heaves at one second intervals alternate with a few seconds rest.

Longitudinal body twitchings now begin. The head begins to move anteriorly with invisible motion and the legs seem more widely spaced. Some yolk is still left in the plug as a strand surrounded by a membrane apparently joined to the dorsum of the thorax. The motions of the embryo cause this strand to be tugged. After hatching, but before the embryonic moult, no trace of this membrane can be seen on the embryonic cuticle. Where unoccupied by yolk, the yolk-plug contains a clear fluid which is continuous with the fluid in occupied spaces between the embryo and chorion.

Antiperistalsis is soon resumed and thoracic and abdominal segments begin to elongate, pulling the tips of the legs and antennae from the rounded base of the egg and leaving a small fluid-filled space ventral to the terminal abdominal segment. No other space between the embryo and the chorion can be seen and the abdomen completely fills the chorion at the tip.

II. Eclosion.

The remains of the operculum have now no function, and in order to hatch the insect must break through the thick yolk-plug wall.

The yolk has now almost entirely disappeared, the lengthening process of the embryo becomes more rapid, and the head enters the yolk-plug, which now contains only a clear fluid. This fluid neither escapes from the egg nor is displaced to another part. The insect either swallows or otherwise absorbs it. No pumping movements in the head have been seen, but they probably occur before the embryonic cuticle, at this stage entire, splits (see later). The embryo now elongates visibly by pumping body fluids into the head and thorax. The terminal abdominal segments, however, are still right against the base of the chorion. A small split occurs round the ventral and thinner end of the stenopyle and bubbles of air pass rapidly into the plug, displacing some fluid to the outside. Nearly all the amniotic fluid has now disappeared, and bubbles may be both pulled in and pushed out of the split as the embryo moves. Fluid has never been observed to disappear nor air to enter either the yolk-plug or the chorion before this split is made.

The main cause of the split is a lateral pressure exerted by the swelling embryonic head as it is forced by the elongating embryo into the yolk-plug, which now has thinner walls, since the inner layer has degenerated. No egg-burster is present and the split may begin before the head reaches the stenopyle. The split widens, running around the edge of the stenopyle, leaving it attached dorsally. Often the lateral walls of the yolk-plug are also split. The distance to which the yolk-plug is extruded is, therefore, a factor likely to affect hatching, for if barely extruded it will be reinforced by an elastic chorion and splitting will be more difficult to accomplish.

The head of the insect, due to the very narrow opening, emerges very slowly at first and forces apart the edges of the split, thus considerably constricting itself. At this stage eggs incubated at 28·5° C. in a saturated atmosphere, although a split is present anteriorly, show no longitudinal dent in the chorion such as occurs in normal eggs just before hatching. Lengthening of the embryo still continues until the head is completely exposed as a distended shining globule. Since the abdomen still reaches into the base of the chorion, final lengthening with the head beyond the stenopyle cannot be due to swallowing amniotic fluid, as the insect would be unable to swallow it, were it there. It must, therefore, be caused by the continued forcing of body fluids into the head and thorax, leaving the abdomen narrow, but still in contact with the sides of the chorion, which retracts slightly from its distended condition. In eggs which have a yolk-plug extended a long way the embryo elongates more than in eggs where the yolk-plug is barely extruded. This extra lengthening is made possible by the increased amount of amniotic fluid in such eggs.

The abdomen now begins to leave the base of the chorion, the head emerges further and the dents appear along the chorion.

In eggs grown under laboratory conditions on a plant, in June, these dents were observed twelve hours before hatching, before the head had started to emerge and apparently before a split had occurred in the yolk-plug. In this case the yolk-plug was not extruded so far as in the incubated eggs.

It is possible that in nature, where there is less amniotic fluid to be swallowed than in eggs grown in a saturated atmosphere which have a greatly extruded yolk-plug, the dents occur sooner.

The embryo now glides smoothly and without visible effort from the chorion, but is still enclosed within the embryonic cuticle, rhythmic antiperistalsis of the gut occurring simultaneously. In nature, the embryonic cuticle only splits after the head has emerged, and pumping in the head can then be seen while the surface of the embryo dries. The insect then frees itself from the embryonic cuticle, leaving it hanging from the mouth of the chorion.

Under conditions of constant temperature and saturated atmosphere the splitting of the embryonic cuticle is delayed until the embryo has glided completely out of the chorion and lies quite free from it, but still within the unsplit cuticle. Splitting then may occur, but usually does not if the embryo is kept in a saturated atmosphere. This suggests that a drying out of the embryonic cuticle is an important factor in successful hatching.

The embryo within the embryonic cuticle.

Behaviour of the embryo before the cuticle splits is conveniently studied in cases of delayed splitting mentioned above. It is presumably the same as when splitting comes earlier.

The embryo now is greatly elongated with the head and anterior portion of the thorax much swollen and the abdomen very narrow, tapering and cylindrical with the segments (especially the 4th, 5th and 6th) much distended longitudinally (an embryo completely free from the chorion but within the embryonic cuticle was 2·4 mm. long, while before the lengthening process commenced it was 1·3 mm. long). The dorsal region of the head is pushed forward so that it occupies a ventral position and the antennal bases lie ventrally beneath the eyes, the legs and antennae being folded together ventrally. This makes the head and thorax much shorter than in the free first instar. The stylets have their tips enclosed in small sacs of the embryonic cuticle, which lie beneath the labrum (Plate II, C). The stylets themselves lie separate within the head. The elastic embryonic cuticle, shining and hairless, covers tightly and completely the entire insect, fitting well into every groove. The abdomen contains small granules. No air is visible in any part of the embryo.

Joined to the surface of the embryonic cuticle from the antennal bases and meeting at a point in the middle line almost directly ventral to the eyes lie two thin toothless chitinous threads (Plate II, C). They are in a similar position to the toothed hatching spines on *Cimex lectularius* L. (Sikes and Wigglesworth, 1931) and are probably homologous with them. From their junction and running backwards over the head, ending blindly, dorsally, above the eyes is a wavy chitinous strip, thicker and wider than the two converging strips. The function and significance of these structures is unknown, and they serve no purpose in egg bursting, nor do they prevent the embryo from slipping back into the chorion as Sikes and Wigglesworth suggest for the structures on *Cimex*. They may, however, support the embryonic cuticle while the head is being withdrawn (Plate II, D), or prevent the cuticle from stretching ventrally and so ensure a greater amount of stretching dorsally, with more chances for a split to occur in that region.

The splitting of the embryonic cuticle.

The insect bends itself dorso-ventrally backwards and forwards, forming a bow-shape, with dorsal region alternately concave and convex. If still within the chorion, wide circling movements are made. Vigorous and persistant antiperistalsis affecting the whole body wall takes place in the direction of the head. The gut contents do not seem to go forwards although the head and thorax enlarge. The abdomen becomes narrower and loosens within the embryonic cuticle. There is much internal movement, and a peculiar motion across the dorsal surface of the first thoracic segment is seen. There, a small area is repeatedly pulled into a depression and released, so that the tapping against the embryonic cuticle possibly helps to split it (Plate II, B). Although pumping in the head about every five minutes is seen before the embryonic cuticle splits, no air gathers in the alimentary canal as in *Cimex* (Sikes and Wigglesworth, 1931), but short gleams are visible beneath the labrum, which disappear quickly, leaving no traces. At the same time, the surface of the embryo beneath the cuticle becomes shiny.

The split begins in the embryonic cuticle and runs to the free end of the wavy chitinous structure and extends dorsally backwards (Plate II, B). It it caused by local pressure of the distended thorax and head and also is probably due to the tendency for the head to take up its normal position by moving dorsally. Once the cuticle has split, air bubbles are seen to pass in beneath the labrum in quick succession at intervals of about five minutes, and there is simultaneously a vigorous pumping in the head. The bubbles collect in the thorax and run together to form large ones. They never collect in the abdomen, but swell only the thorax and widen the split in the cuticle.

Thus air bubbles help to split neither the egg shell nor the embryonic cuticle as cited for *Polyplax* and *Cimex* by Sikes and Wigglesworth (*vide supra*), and only help to widen the split caused primarily by local distension of the embryo by body fluids.

The dorsum of the thorax bulges out and hairs stand erect. Antennae and head are withdrawn and then the legs are freed, the embryo drags itself from the cuticle and immediately walks away.

Normally, the time elapsing between the splitting of the stenopyle and complete freeing of the insect varies from five to fifteen minutes. Thus the stages described above are considerably compressed when the cuticle splits normally. The length of time of endurance of embryonic activity within the egg before the stenopyle splits can be much prolonged. In one egg kept beneath a supported cover glass in a water film at room temperature the stenopyle split on May 3rd and hatching occurred on May 16th, and then only when taken from the water film.

The tracheal system has not been seen to fill, neither has it been determined where the air from the thorax goes. It disappears after about an hour, leaving the insect with a shrivelled abdomen.

The empty chorion contains the yolk-plug membrane, which can be clearly seen to be continuous with the yolk-plug walls, and of a simple sac-like shape with no segmentation corresponding to that of the embryo.

SUMMARY.

1. The structure of the egg at oviposition is described. The yolk completely fills the egg and is entirely surrounded by a very thin, uniform vitelline membrane. The whole of the yolk is within the chorion. The latter is closed by a micropylar cap fastened to it at the anterior end.

2. The swelling of the eggs before the appearance of the sub-opercular yolk-plug is described and tables of measurements and a graph are given for swelling under controlled conditions. The eggs begin to swell rapidly at the end of the second day and reach a maximum girth after the yolk-plug has commenced to extrude. There is later a decrease in girth before hatching.

3. The yolk-plug, which consists of a mass of yolk surrounded by a relatively thick wall, is apparently secreted by an epithelium of cells which lie between the wall and the yolk. The yolk-plug develops within the neck of the egg and is forced out of the anterior pole as the egg swells. In doing this it breaks the micropylar cap and carries it forward on the anterior end of the plug. This cap has no further function. Graphs and tables are given showing the extrusion of the yolk-plug under controlled conditions.

4. Swelling of the egg is accompanied by the absorption of water. A preliminary table of weights is given.

5. The possible value of the yolk-plug to the life of the egg is discussed.

6. Hatching is described in detail.

ACKNOWLEDGEMENTS.

For the many facilities received in the George Moore Botanical Laboratories and for his constant help and encouragement I wish to tender my best thanks to Professor S. Mangham; for the photographs A, B, C and D on Plate III, I am much indebted to the kindness of Mr. A. E. Clarence Smith. I also wish to thank Professor R. C. J. Howland for advice with the statistics, and Mr. F. J. Killington and Dr. B. M. Hobby for reading through the manuscript.

I also gratefully acknowledge the research grant received from University College, Southampton.

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EXPLANATION OF PLATE I.

FIG. A.—The micropylar cap or operculum at oviposition. Note well defined junction with chorion. *v*, ventral; *d*, dorsal.

FIG. B.—Longitudinal section through rim of chorion at junction of cap. *a*, Inner wall of cap continuous with the endochorion (*d*). *b*, Outer region of cap continuous with exochorion (*e*). *c*, Micropyle in longitudinal section. Arrow indicates region of clean split round endochorion.

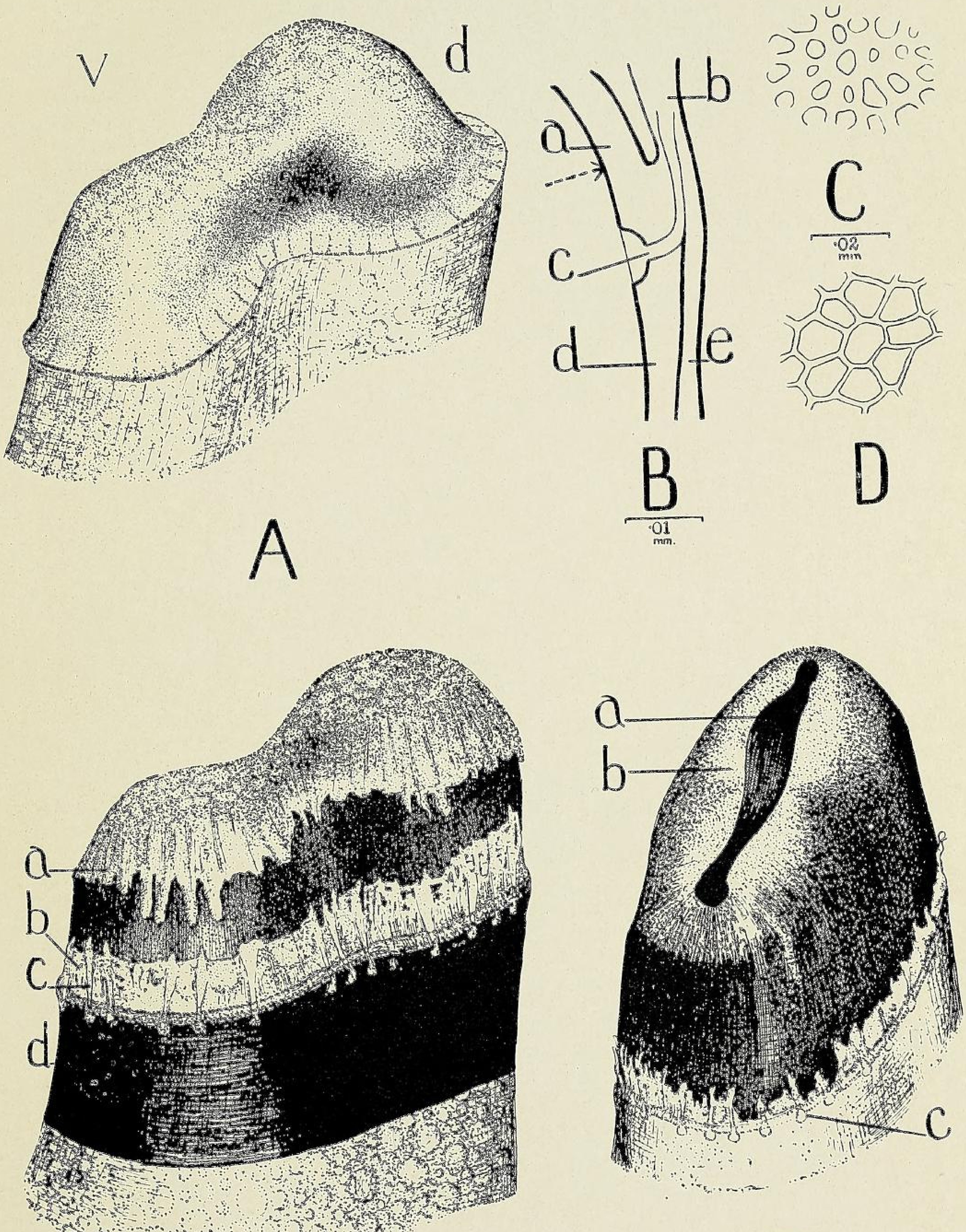
FIG. C.—View of outer surface of cleared caps, showing thickened walls of distal ends of chambers.

FIG. D.—View of inner ends of chambers of cap as seen through inner surface.

FIG. E.—Anterior region of egg with yolk-plug, fully developed, pushing off the micropylar cap. *a*, Remains of micropylar cap. *b*, Membranous outer surface of cap margin attached to the rim of the chorion. *c*, Micropylar flaps. *d*, Black band; the yolk-plug still within the neck of the egg.

FIG. F.—Yolk-plug extended from neck of egg and with micropylar cap removed. *a*, Stenopyle. *b*, Area with less pigment. *c*, Micropyle.

PLATE I.



C. G. Johnson del.

Development of Egg of *Notostira erratica* L.

EXPLANATION OF PLATE II.

FIG. A.—Anterior region of egg with well extruded yolk-plug. Most of the yolk (*yk*) has been absorbed and there only remains a strand from the dorsal surface of the thorax to the stenopyle. The yolk-plug itself is extruded for twice the width of the black band, and the thin clear yolk-plug membrane (thickened in this region) is exposed.

FIG. B.—Dorsal view of thorax of embryo just as the embryonic cuticle is splitting. Air bubbles (*b*) have been swallowed and are distending the thorax beneath the split in the cuticle. The arrows on the right hand side indicate the region of the first thoracic segment, which is pulled in and released outwards. This region extends across the thorax at this point.

FIG. C.—Ventral view of anterior region of embryo within the embryonic cuticle. *a,* The thin, toothless, chitinous strips which run from antennal bases to the wavy chitinous structure which stretches across the head. Both structures are fastened to the embryonic cuticle and are shed with it. *c,* Stylets.

FIG. D.—Lateral view of embryo emerging from embryonic cuticle. The greatly distended thorax is bulging from the split (*a*) cuticle.

FIG. E.—Semi-diagramatic representation of developing embryo within the egg, showing the yolk of the yolk-plug in direct connection with the yolk over the thorax of the embryo before dorsal closure has taken place. *a,* Yolk-plug membrane. In fixing the egg the yolk has retracted from the chorion.

FIG. F.—Surface view of epithelial cells beneath the side walls of the yolk-plug.

FIG. G.—Longitudinal section (not quite median) through the yolk-plug at a stage of development similar to that shown in Fig. A (above). The section of the micropylar cap (unlabelled) is drawn from a perfect median section. *a,* Columnar epithelium of cells lining the yolk-plug wall at the anterior end of the plug. *b,* Flattened epithelium lining the sides of the yolk-plug wall. *c,* Yolk spheres. *d,* Serosa (?). *e,* Head of embryo. *f,* Yolk-plug membrane. *g,* Chorion. Both endochorion and the inner layer of yolk-plug wall are stained, and the epithelium and yolk have retracted from the walls in fixing.

PLATE II.

C. G. Johnson del.

Development of Egg of *Notostira erratica* L.

EXPLANATION OF PLATE III.

FIG A.—Egg some time after oviposition but before the formation of the yolk-plug. Measurements in eyepiece micrometer units Region a, 35; Region b, 41; Length (l) 199. The cap shows a distinct junction with the chorion.

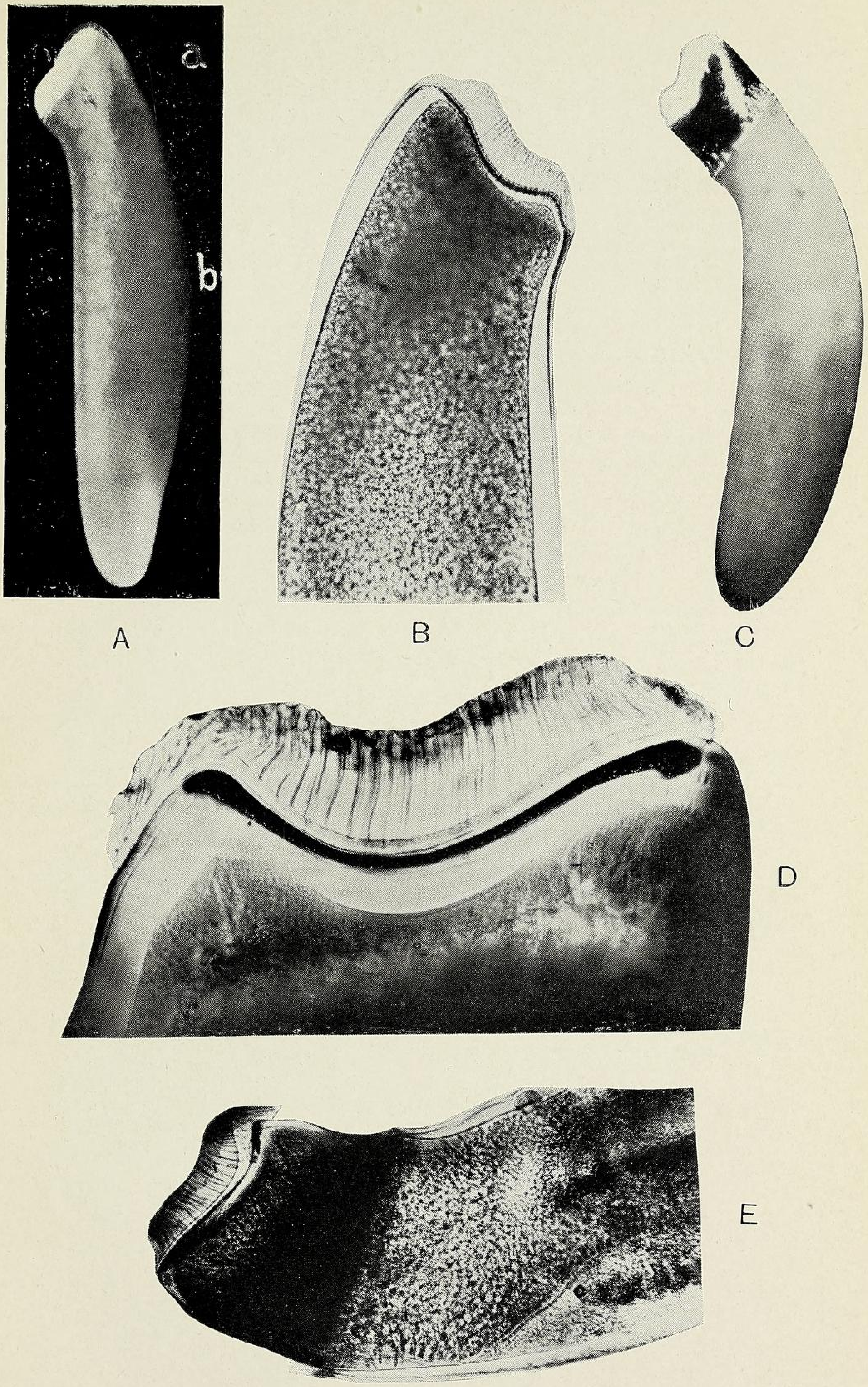
FIG. B.—Optical section of whole mount of egg immediately after oviposition. Endochorion is seen to be continuous with the inner wall of the cap. Vitelline membrane thin and of uniform thickness. The yolk has slightly shrunk from the chorion in fixing.

FIG. C.—Egg with yolk-plug extended the complete width of the black band. Remains of the micropylar cap are on the anterior end of the yolk-plug and the exochorionic fringes are visible around the cap rim. The embryo is almost ready to emerge and its eye can be seen below the neck. Note the difference in size and shape of this egg with that in Fig. A.

FIG. D.—Optical section of a whole mount, showing the anterior region of yolk-plug with the remains of the micropylar cap resting upon it. The stenopyle shows as a black streak occupying almost the complete thickness of the wall. Note the thick hinge at the dorsal convexity of the plug. The two distinct layers of the yolk-plug wall can be seen at the ventral side. The columnar epithelium across the anterior surface of the yolk can be seen, but it has shrunk from the wall in mounting.

FIG. E.—Optical section of whole mount of egg with the yolk-plug extruded the complete width of the black band. The head of the embryo still points towards the posterior pole of the egg, and abdominal segments can be seen in an early stage of development occupying the more anterior region. Note the continuity of the yolk-plug membrane with the yolk-plug wall on the dorsal surface near the chorion rim. Both are completely free from the chorion and have shrunk slightly.

PLATE III.



Photographs A—D by A. E. Clarence Smith, E by C. G. Johnson.

Development of Egg of *Notostira erratica* L.