GROWTH CHANGES OF THE RADULA IN LAND-MOLLUSKS.

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The radula, or lingual membrane of the glossophorous mollusca has been most assiduously studied, being a very attractive and interesting object in itself, and a valuable character for systematic distinctions. Its features in the land mollusca of America have been investigated by W. G. Binney ;[1] but thus far the adult animals only have been considered, and conclusions regarding the morphology of the teeth have been based chiefly upon these. Of the development of the radula and its changes with advancing age, very little is known. The writer published some years ago, a short article on the subject,[2] but the considerations then advanced prove to be quite insufficient.

During the last few months a number of species have been examined with special reference to these changes, and the results prove to be of unexpected value. The subject has been studied from a morphological standpoint only. For histological details the publications of Kœlliker, Semper, A. Ruecker and others must be consulted.

The special cases to be described in detail below may be more readily understood by attention to the following general considerations. If we carefully examine a well prepared and extended radula of a young specimen, it will be seen that in the anterior, or older part (which was formed, however, by the animal when younger), a transverse row contains fewer teeth than a row in the posterior or more lately formed part. In other words, new teeth, one or more new longitudinal rows, are added. The new teeth are at first mere traces, resembling the outermost marginals in general form, being small, roundish nodules, transverse or longitudinally elongated plates, which, by gradual changes in each succeeding transverse row, develop into true marginal teeth. At the same time it may be found that there are, in a transverse row at the anterior, one or more laterals fewer than in a row at the posterior part; and a closer

[1] Terr. Moll. U. S., Vol. V.; and Jaw and Dentition of Pulmonate Mollusks, Annals N. Y. Acad. of Sci., Vol. III.

[2] Altersverschiedenheiten der Radula bei *Hyalinia*, Nachrichtsbl. d. Deutschen Malak. Gesellschaft, 1882, p. 172-177.

attention will show that in a certain longitudinal row at the margin of the "central field," a transition tooth gradually transforms into a well shaped lateral, a marginal into a transition tooth, and finally, in turn, into a lateral.

In these few lines the development and transformation of the radula is briefly outlined. This organ is not, as has generally been supposed, always of the same formation, number of teeth, etc., in a given species, and only smaller in the young examples, but there are actually fewer transverse rows in the young, and fewer teeth in each row. Moreover, the teeth at first are of very simple form, and by gradual changes by replacement they assume their final shape. The transformation is never simple, but is accomplished through one or several intermediate stages, sometimes widely different; and moreover, the process differs widely in the various species and groups.

The general considerations above presented are based upon the examination of the few species with which the present communication deals. This paper must be regarded as the beginning of a long series of examinations, which should comprise all species. Such a research will doubtless give results not only highly interesting in themselves, but also of great taxonomic value. Certain characters of the radula which are very indistinct in the adult, or even overlooked by careful observers, become of characteristic value in the light gained by the examination of the earliest stages of growth. In the embryonal animal we find forms of teeth present then and there only, disappearing entirely in post-embryonal life; so we may properly speak of a true metamorphosis of the radula.

The species examined with reference to this metamorphosis are as follows: *Limax campestris* Say; *Zonitoides arboreus* Say; *Z. ligerus* Say; *Zonitoides* sp. undet. from Tennessee; *Z. suppressus* Say; *Patula striatella* Anth.; *alternata* Say; *solitaria* Say; *Polygyra* (*Triodopsis*) *tridentata* Say; *P.* (*Stenotrema*) *hirsuta* Say. Of most of these I had no embryos at hand for examination, but very young specimens.

Limax campestris Say. Pl. 10.

This species, and probably all of the genus, are very favorable subjects for our purpose, since oviposition is continued throughout the season, so that ova, young, adolescent and adult examples may be found and compared at almost any time. The ova are not usually deposited in clusters consisting of great numbers, as in most other land mollusca, but singly or few aggregated. They are at first not globular, but distinctly ellipsoidal, the shell being perfectly glassy and transparent, so that yolk division and the formation and development of the embryo may be observed through it.

The buccal body and radula develop rather rapidly. In an embryo taken from the ovum, about 2·5 mm. long when extended, not quite mature, with the caudal bladder still rather large, but the heart formed and regularly contracting, the shell measured about 0·35 mm. long. The radula was 0·35 mm. long and had as many as 34 transverse rows of teeth. In the first of them there were 3 teeth, the central and a lateral on either side, appearing as thin, barely visible plates, or mere traces (O[3], in fig. 1). Other specimens showed the same more distinct, as represented in fig. VI. In the following transverse rows they are larger, and rapidly develop in shape, while at the margin new teeth of the same character are added, at first with each row, then at greater and greater intervals, so that, in the radula mentioned above, the formula was 12·c·12 in the twenty-fifth transverse row. The development of the radula proceeds comparatively very fast, in this and other species, faster than the growth of the animal, so that even very young specimens have the radula far advanced and show nothing more of the earliest formed teeth. The addition of new teeth is not always regular and symmetrical on both sides; thus, the fifth longitudinal row may begin at the sixth transverse row on one side, and with the seventh on the other, so that the formula for the sixth would then be 5·c·4.

Not all of the teeth are formed and transformed in the same way, in this and other species, as may be seen by the figures. But *Limax campestris*, and other *Limaco-Zonitidæ* and *Helicidæ*, show such new and unexpected features that they must be considered more in detail.

For a better understanding and easier reference the following table gives the particulars of a series of the specimens examined, all of them, except two, being represented in figs. I-V on Pl. 10.

	Embryo 2·0 mm. long;	radula 0·3 mm. long,	with 27 transverse rows.
Fig. 1.	Embryo 2·5 mm. long;	radula 0·35 mm. long,	with 34 transverse rows.
	Animal 3·0 mm. long;	radula 0·55 mm. long,	with 56 transverse rows.
Fig. 2.	Animal 3·5 mm. long;	radula 0·72 mm. long,	with 65 transverse rows.
Fig. 3.	Animal 7 mm. long;	radula 1·15 mm. long,	with 86 transverse rows.
Fig. 4.	Animal 15 mm. long;	radula 2·24 mm. long,	with 104 transverse rows.
Fig. 5.	Animal 27 mm. long;	radula 2·72 mm. long,	with 105 transverse rows.

[3] They were first overlooked, and afterward designated as O in the original drawing, of which the present is a copy.

THE CENTRAL TEETH.

The central tooth is first formed as a simple, roundish or oval nodule, with a blunt point directed backward (fig. I and VI), rapidly increasing in length in the following rows. At the same time one or two somewhat irregular side cusps appear on either side, which on about the eighth tooth become more constant, more marked, and single on each side. There are, however, occasional exceptions as shown in the tenth of fig. VI, where on the right[4] side there are again two side cusps. Thus it attains its final shape, but is somewhat unsymmetrical, and so it remains, not only in one specimen, but as a rule in all (see figs. II-VI). This is also the case in other species. In some individuals the right side cusp is more posterior, in others the left. It early becomes noticeable that the central tooth stands more posteriorly than the laterals on either side of it, as represented in fig. VI. Comparatively early the plate of attachment extends backward, at first quite small, barely noticeable, and only on the side bearing the anterior side-cusp; but later it extends on both sides.

These facts make it evident that the central tooth is simple primarily, not formed by the coalescence of two original laterals as has been supposed.

THE LATERAL TEETH.

An adult specimen of *Limax campestris* has about 11 to 18[5] lateral teeth. And to my surprise I found that, although they are exactly alike in their final shape, they are formed in two widely different ways:

(1). The 6 or 7 *mesial laterals* on each side first appear as thin, simple, transverse, nearly rectangular plates, each as a rule preceded by a short, nodule-like "trace," (see figs. I and VI). They soon become longer at their inner ends, more triangular, and the mesodont forms, being at first short and blunt, but immediately growing longer,

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[4] Right and left are here given as they appear under the microscope.

[5] These limits are exceptionally wide and may be considerably narrowed by subsequent careful observations. The specimens with fewer laterals may very likely be immature. In the slugs there is no definite criterion of maturity, except probably in the genital organs, which should be consulted in every case. W. G. Binney found the tooth formula to be c. 18·22 in one specimen, c. 11·25 in another; I counted c. 14x1·31 in an individual 27 mm. long but still probably not fully mature.

more slender, sharp pointed and spine-like. At the same time 2 or 3, or even 4 smaller cusps are formed on the outer side, and one (an endodont) or sometimes two cusps on the inner, so that there are typically 4 or 5, sometimes 6 or even 7 cusps on a tooth (see fig. VI first lateral in the second and fifth transverse rows.) This peculiar formation of the *inner group of laterals* is found in the embryonal or larval stage of the animal only; and in order to have an appropriate name for this form of tooth, we may properly term it *echinate*.

The teeth, passing through the echinate stage, gradually again change in form; the body of the tooth becomes longer, the mesodont loses its spine-like form, becoming wider, and its free cutting point shorter; the endodont becomes more coalescent with the mesodont, with a short and less acute point; but it remains constant, being visible in all specimens in different stages of growth which were examined, from this locality.[6]

Further modifications are that one or two of the distal cusps disappear, and the one or two remaining are transformed into the single ectodont of the adult (conf. fig. VI, the first lateral in the eighth to eleventh transverse rows); moreover the plate of attachment begins to be prolonged backward, at first being very thin and small, barely visible. The outcome of this series of changes is the perfect lateral tooth of the adult *Limax*.

All of the forms above described may be seen in one transverse row, (as represented in the fifteenth row of fig. I), and the different stages of transformation are shown in every longitudinal row of the same figure and fig. VI; but it must be added that the transverse rows, especially in the anterior part of the radula, are closer together than represented in the drawing, in which they are separated for the sake of distinctness; and the cusps reach further backward over the body of each following tooth. The individual teeth are fully as wide in the front part of the radula as more posteriorly.

(2). The *distal laterals* are evolved through other intermediate stages much resembling those undergone by the later aculeate marginals, as illustrated in figs. II-V. Fig. II represents at A the thirtieth, at B the forty-fifth transverse row of teeth from a spec-

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[6] It may be noted here that in the persistence of the endodont, *Limax campestris* offers no distinctive character from *Limax agrestis* Linn.; and it may be added that in drawings made in 1882, of the radula of *Limax tenellus* Nils. and *L. cinereus* Lister, from the Swiss Alps, the endodont is distinctly shown.

imen which had been hatched a few days. This radula measured 0·72 mm. long, and was in the posterior part 0·28 mm. wide. It has 65 transverse rows of teeth numbering 7·c·7 in front, 10·8c8·10 in the posterior part; so that the new longitudinal rows formed during its growth are 11 on either side. The first transverse row of this radula corresponds approximately to the twelfth in fig. I or VI, thus the thirtieth to the forty-second, the forty-fifth to the fifty-seventh of the whole series; the teeth of about the 11 first formed transverse rows were cast off.

All teeth present in fig. II would become typical laterals in the adult animal. They are primarily transverse bars; at the inner end of each bar the mesodont is formed, at first quite small, and then two or threee ectodonts appear, which, as the mesodont grows, come to stand on the latter; (figs. II, 45: 13-11; III, 13) with the exception of one which remains upon the common reflection, and is transformed into the final ectodont. Of the endodont not a trace is present originally; and it forms only later when the tooth passes through the intermediate or "transition" stage to become a true lateral. The consequent stages may be seen in comparing the teeth with corresponding numbers in figs. II-V; thus tooth 15 is shown from its beginning almost to full maturity; and the figures give a better idea of the changes than any description. A main factor in the development of the tooth is the growth of the plate of attachment, forward and backward from the "body" of the tooth.

THE MARGINAL TEETH.

The marginals, although much resembling the outer laterals in a certain stage, are somewhat different from the first. Instead of being a transverse bar, the base of attachment is longitudinally elongated, as seen in figs. III, 28; IV, 40, 41; and V 45, 46. The aculeate mesodont is at first very small, but it grows rapidly, and is at once directed obliquely inward.

The marginals are not all alike. Those toward the inside are seen quite early to bear ectodonts (fig. III, 20-27). The ectodont becomes rather large, but subsequently disappears (fig. V, 25). There is, however, a decided irregularity in this character, for in the same longitudinal row there may be teeth with, and others without an ectodont (fig. IV, 30). The distal marginals seem always to be simple, without an ectodont (fig. IV and V). It may be noted for comparison, that in *Limax tenellus* Nils., all (32) marginals were found to have a distinct "outer cusp"; but on the marginals of *L. cinereus* Lister (about 130 on each side) no ectodonts were seen.

A similar formation of the earliest teeth will probably be found in other *Limaces*, and in such *Zonitidæ* as *Hyalinia radiatula* Gray, *petrophila* Bld., *capsella* Gld., etc., species in which the laterals bear distinct endodonts.

Zonitoides arboreus Say. Pl. 11, figs. I, II.

No embryo of this species was obtained, but a very young specimen with shell and soft parts nearly colorless, the former measuring 1·1 mm. diameter, with 1½ whorls. The radula (fig. I), was 0·39 mm. long, and had 48 transverse rows, of which, however, some of the youngest, at the posterior end, could not be clearly seen. Here there are 7·c·7 teeth, three of which are rather well formed laterals. Very few rows and teeth could have been lost from the front end of the radula, and the first present in the specimen examined were evidently of primitive shape, and a type entirely different from that of *Limax*, rather resembling those of *Patula striatella*, conf. fig. VIII.

The central teeth have a wide, short base or "body," with a distinct mesodont and at least quite early a side cusp on each side. Comparatively soon the plate of attachment is seen posteriorly, though very small. The laterals (about 5 in the adult) are wide transverse plates, somewhat irregular, longer in the mesial half, with a short, wide, blunt mesodont gradually becoming longer and more slender, and 2 or 3 small cusps in place of the later ectodont. No trace of an endodont is seen. As the teeth without much change gain their definite shape, the plates of attachment also develop.

Fig. II represents the radula of a nearly adult specimen, the shell having a diameter of 4·3 mm. The radula is 1·05 mm. long, 0·35 wide, and has 77 transverse rows of 17·5 c. 5·17 teeth. Only the first marginal bears an ectodont. Another example, of 4·5 mm. diameter, had a radula 1·33 mm. long, 0·45 wide, with 19-1x5· c. 5x1·19 teeth. Another of a peculiar form from Alabama gave the formula 20·1x4· c. ·4x1·20.

Embryonic specimens remain to be examined, and the earliest form of the central and inner lateral teeth ascertained.

Zonitoides ligerus Say. Pl. 11, figs. III, IV.

We have in Pennsylvania and Ohio, a very small form measuring 9-10 mm. diameter, which has been considered *Z. ligerus*, although with some doubt. Besides other differential characters, there are two accessory glands near the head of the dart sac, while W. G. Binney found only one in typical *ligerus*.

No embryo has been secured thus far. The smallest examples found measured about 3 mm. in diameter; and the radula of one of these is represented in fig. III, having 20· c ·20 teeth, of which 6 are perfectly formed laterals and the 7th and 8th nearly so, the latter corresponding with the 13th of an adult, and the "transition tooth" 9 to 14. At least 9-13 then, of the younger specimen, will be transformed into laterals. In either example all the teeth showing the transition from the aculeate marginals to the laterals have been represented in my figures, 14-7 in III, 17-11 in IV,[7] so that the transformation can immediately be seen by comparing the teeth bearing the same numbers. We specially notice: first, the total absence of endodonts in all teeth, just as in *Z. arboreus*; second, the absence of ectodonts in the distal, newly formed, aculeate teeth—*i. e.* in most marginals except a few mesial; and third, the longitudinally elongated plates of the youngest marginals.

Besides *Z. ligerus*, young and adult examples of a few other nearly related species were examined, one from Tennessee probably new, and *Z. suppressus* Say. They gave essentially the same results as *ligerus*.

Patula striatella Anth. Pl. 11, figs. VII, VIII, IX.

Several embryos from the eggs were examined. Fig. IX shows the buccal body of a quite young specimen with the commencement of the radual, in optical section. Diameter of the buccal body 0·12 mm. The spindle-shaped cells above are the developing retractor muscle.

Of an embryo more advanced, about 1 mm. long, and nearly mature, having a shell of 1½ whorls, and the caudal bladder small but still slowly contracting, the radula is represented in fig. VIII. It is 0·14 mm. long, with 21 transverse rows, in the last 9·c·9 teeth. But the formation of new teeth is somewhat irregular on the two sides

[7] For distinctness they are separated in the drawing; in nature they lie close together; this is indicated by the sign.

in this as well as some other species. The first transverse row is represented only by the first lateral on the right; the second by 1·c·1 and so on, as shown in the figure. The transformation is rather simple and decidedly slow. The *centrals* are wide and short, at first with a short, wide, blunt median projection which develops into the mesodont, and very slowly, like the side cusps. All other teeth are first formed as simple transverse bars or plates, the *laterals* gradually assuming their definite shapes without intermediate stages; even the ectodonts seem to be always single. Otherwise there is much similarity to *Z. arboreus*, but the forms are somewhat more plump.

The first formation and development of the *marginals* has not yet been observed with sufficient exactness. The mesodont and partly the ectodont are "double-pointed," and it appears probable that the mesial small cusp of the former is really the entodont, as it first stands near the base (fig. VII, 15) and then gradually ascends on the mesodont and becomes evanescent, as seen in fig. VII, 12-8. This figure represents the radula, 1·4 mm. long, from a specimen having a shell of 5·3 mm. diameter, apparently not quite mature. Yet in all the 94 transverse rows, no new teeth are added; the formula is c. 6x1:10. There is very little change in the shapes of the single teeth, except that the plates of the sixth and seventh laterals are noticeably longer in the posterior than in the front part of the radula.

Of *Patula alternata* Say, a number of examples were examined. One having a shell of 20 mm. diameter had a radula 4·5 mm. long, 1·5 wide, with 143 transverse rows of 34·c·34 teeth, with about 15 laterals. In a young specimen of 3 mm. diameter the radula was 0·88 mm. long, and had 72 transverse rows of 11·c·11 in the anterior, 12·c·12 in the posterior part.

The radula of *Patula solitaria* Say, extracted from a shell of 23 mm. diameter, is 5 mm. long, 1·8 wide, with 142 transverse rows of 31·c·31 teeth, 16 laterals, In a young one, the shell of 5·3 mm. diameter, I counted 68 transverse rows of 13·c·13 teeth in the anterior 15·c·15 in the posterior part.

Polygyra[8] **(Triodopsis) tridentata** Say. Pl. 11, figs. V, VI.

No embryo or quite young specimens were at my disposition. The smallest found had a shell measuring about 6 mm. in diameter,

[8] See Pilsbry, Preliminary outline of a new classification of the Helices. Proc. Acad. Nat. Sc., Phila., 1892, p. 400.

and its radula was 1·63 mm. long, 0·70 wide, with 88 transverse rows. In a mature specimen of 15 mm. diameter, the radula was 3·85 mm. long, 1·34 wide, with 112 transverse rows. The former had (in the middle part) 20·c·20 teeth, of which five were laterals and two very nearly so; in the latter part there were 30·c·30 in the anterior, 31·c·31 in the posterior part, about 10 of them laterals. They are represented in figs. V and VI, and the form of the teeth is essentially the same in both. The centrals have distinct side cusps; in the laterals there is not a trace of the endodont, while the mesial cusp, adjacent to the mesodont of the "marginals," seems to be an endodont, since it stands nearly isolated on the base in the younger teeth, as shown in 29, fig. VI, and then (as in many other species of this genus, of *Patula*, and of *Helicidæ* generally), gradually coalesces with the mesodont, ascends upon it, and finally becomes obsolete. There is, however, considerable variation as to this in the distal laterals, even in the same longitudinal row, as shown in fig. VI, 25-29,

Polygyra (*Stenotrema*) *hirsuta* Say gave essentially the same result.

As already said, the observations presented above have been made on but few species, and not complete even in most of these. They must be carried further. Yet the results obtained appear to be for the most part new and valuable; they may briefly be comprised in the following conclusions:

1. The radula in land mollusca is quite different in the various stages of life, both as to the number and the shape of the teeth.

2. As to number: there are very few teeth in the first formed transverse rows, and new ones, forming new longitudinal rows, are added at the lateral margins, at first rapidly, then at greater and greater intervals. The development of the radula goes on faster than the growth of the animal, comparatively, so that in young examples it is larger in proportion to the size of the animal than in the adult.

3. As to shape: the first formed teeth are of very simple shape and by gradual transformation give place to teeth of the final form. This transformation may go through different stages, or by different modes in cases where the form becomes ultimately the same.

4. The question whether the addition of new teeth and the transformation of teeth goes on as long as life lasts, or ceases with maturity is not yet decided.

5. In certain species and groups there are forms of teeth in the embryonal, or larval stage, entirely different from those found in post-embryonal life, so that we may properly speak of the change as a metamorphosis.

6. The new formation and transformation of teeth is, as a rule, not exactly symmetrical on the two sides of the radula, so that a formula of one side is often only approximately true.

7. The width of the individual teeth, (and of the longitudinal rows), is the same from the earliest formation to the later stages and the increase in width of the whole radula is effected exclusively by the addition of new longitudinal rows.

8. The central teeth seem to be[9] (and in some species are doubtless) simple from their first formation; not a product of the coalescence of two original laterals.

9. They are, as a rule, more or less markedly asymmetrical.

10. The terms "lateral" and "marginal" teeth are not of absolute significance: The "marginals" of a younger specimen, or a part of them, will have transformed into laterals when the animal is adult.

11. It is also quite inadmissible to speak of the marginals as modified laterals, for a transformation never takes place in this direction. We should not say, as has been usual, that the simple mesodont of the laterals becomes split, or bicuspid, in the marginals; but the contrary is true: the "double pointed mesodont" of the marginal loses its endodont and becomes simple as the tooth is gradually replaced by a lateral. It is incorrect to say: "The teeth become smaller towards the margins," as they virtually increase in size from the margin toward the middle.

12. The expression "transition teeth" between marginals and laterals (not the reverse) has become of a real, actual meaning, just as the word "relationship" among organisms has gained its proper meaning by the theory of descent,

13. The different ways in which the teeth are formed and transformed will probably furnish valuable hints for systematic malacology.

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[9] At least in the land Pulmonata (Nephropneusta v. Ih.); in some Limnaeidæ, e. g. *Limnæa palustris* Müll., there is a strong probability that the centrals are double in first formation.

14. The rate of increase in number of the teeth will furnish the means for calculating the rate of the new formation of the radula as a whole. This is more rapid than is generally supposed.[10]

15. It is evident that the morphology of a radula can be thoroughly understood only by examining and comparing the different stages of its formation.

In the text nothing has been said about the methods of preparation and manipulation of the radulæ,—not much is necessary. As far as possible, the radula has been removed from the fresh animal unchanged. Caustic alkali has been used where necessary. By careful desiccation, and also by the action of chromic acid solution, for staining, valuable results may be obtained, as the teeth and especially the plates of attachment shrink somewhat and thus are separated from each other, and seen more exactly. But it is almost unnecessary to add that this means can only be used in connection with observations on the intact radula, for without this check artificial might be mistaken for natural features.

Explanation of Plates 10 and 11.

Plate 10, Fig. I—Radula of an embryo of *Limax campestris* Say, not quite mature, showing first part of radula formed.

II—Radula of a specimen a few days old (after hatching), and measuring 3·5 mm. long.

a. 30th transverse row (about 42nd of total number).

b. 45th transverse row (about 57th of total number).

III—Radula of a specimen 7 mm. long, one-half of a transverse row, formula c. 10·18.

IV—Radula of a specimen 15 mm. long, one-half of a transverse row, formula, c. 14·27.

V—Radula of a specimen 15 mm. long, one-half of a transverse row, formula, c. 14·32.

[10] Without repeating the calculations here, it may be said that I found the radula of *Limax campestris* to form about 800 transverse rows in all—probably considerably more; this would mean that the radula is about eight times entirely changed during life. For *Polygyra* (*Mesodon*) *thyroides* about 2000 transverse rows were found, corresponding to about 16 to 18 total renewals.

VI—Left side of first part of radula of another embryo.

PLATE 11, Fig. I—*Zonitoides arboreus* Say, quite young, anterior part; x 600.

II—The same, nearly mature; x ca. 750.

III—*Zonitoides ligerus* Say, young, 3 mm. diam.; x 400.

IV—The same, adult, 9·5 mm. diam.; x 400.

V—*Polygyra tridentata* Say, young, 6 mm. diam.; x 400.

VI—The same, adult, 15 mm. diam.; x 400.

VII—*Patula striatella* Anth., adult, 5·3 mm. diam.; x 470.

VIII—The same, embryo, 1·0 mm. diam.; x 400.

IX—The same, very young embryo, buccal body, 0·12 mm. diam.