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BUNTONIA OLOKUNDUDUI SP. NOV. (OSTRACODA, CRUSTACEA)

A study of meristic variation in Paleocene and Recent ostracods

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Abstract. A new species of the genus *Buntonia* shows meristic variation in the number of anterior, posterior and posterolateral spines. This variation is here interpreted in terms of variation genetics. Similar meristic variation in Paleocene ostracods is analysed. The new species *Buntonia olokundudui* is described and its meristic lateral ornamental variation identified but not analysed.

I. DESCRIPTION OF *BUNTONIA OLOKUNDUDUI* SP. NOV.

In connexion with a survey of aspects of the interstitial ecology of the Niger Delta a species of *Buntonia* was discovered which was found to show a very interesting pattern of variation in the spinal ornament. Further related examples of this kind of variation have subsequently been identified in other Recent cytherids from the Delta. Owing to the importance of the principle involved for research on fossil ostracods it was considered of value to give the variation of this species a detailed description.

Holotype. The carapace figured in Pl. 2, Fig. 2, Number Af 12.

Repository. Paleontologiska Institutet, Uppsala Universitet. Paratypes in same collection.

Provenance. Off the coast of Nigeria, near the mouth of the Escravos River.

Nature of the material. The sample was collected by means of a modified orange-peel grab. The study material was obtained from the top 2 cm of sample. Only entire carapaces that stained pink with Rose Bengal were selected for study.

Derivatio nominis. From *Olokúndùdù* (Itsekiri), the deity resident in nearshore seawater; the patron saint of nearshore fishermen.

Description of appendages of female

First antenna. The stoutly built first antenna is made up of six segments. The second segment has a ventrodistal seta, which is longer on the left appendage than on the right; the third segment has a dorsodistal seta. The fourth has two dorsodistal setae and a laterodistal seta; the more distal of the dorsal setae is much stouter than the other two. The fifth segment has the same number of identically located setae as the fourth segment. The distal segment has three setae. Three of the setae of the three last segments have a claw-like construction. Pl. 7, Figs. 1, 2. (Af 14, Af 15.)

Second antenna. The stoutly built second antenna consists of four segments. The first endopod segment with a ventrodistal septum, the second with two (three?) dorsal, three ventral and two ventrodistal setae, one of which is stouter than the other. The distal segment bears three claw-like setae, of which the most dorsal is the stoutest. The exopod is long and thin. Pl. 5, Figs. 6, 9, 10; Pl. 7, Fig. 3. (Af 16, Af 17.)

Mandible. The base of the mandible is moderately stoutly built. The biting edge consists of six teeth of unequal size; the first two take up half the available space. There are two bristles posterior to the smallest and most posterior tooth. The distal segment of the palp is elongated; the first segment of the endopod bears long ventrodistal setae two of which have paired, well-spaced hairs and a very short ventrodistal seta. The second segment of the endopod has two long tapering setae with flexible hairs and a third short one. The distal segment bears two strong setae, and a third small one. The right mandible is larger than the left mandible. Pl. 6, Figs. 1, 2. (Af 18, Af 19.)

Maxilla. The vibratory plate is large. The palp consists of two segments, the second being about one third the size of the first. The distal edge of the first segment bears two long claw-like setae and two short setae. The second segment has two distinct carrot-shaped setae, and a third short one. There are three endites, each of which appears to have four distal setae. Pl. 5, Fig. 8; Pl. 6, Fig. 4. (Af 20.)

The thoracic limbs. The legs consist each of four segments; they are long with the left limbs smaller than the right ones. The setae of the first segment are notched.

First legs. There are two dorsolateral setae, the second curved, and a dorsodistal seta which curves over the "knee-joint". The second segment has a dorsodistal seta. The terminal claw is long and curved, longer than the distal segment. Pl. 5, Fig. 11; Pl. 7, Fig. 4. (Af 21, Af 22.)

Second legs. The first segment has two mid-dorsal setae and two dorsodistal setae that curve over the knee. There is a dorsodistal spine on the second segment. The terminal claw is longer than the third and fourth segments and is relatively longer on the left leg than on the right. Pl. 5, Fig. 12; Pl. 6, Figs. 5, 6. (Af 23, Af 24).

Third legs. The first segment bears a mid-dorsal curved seta and a curved dorsodistal seta. There is a long dorsodistal seta on the second segment. The third segment has a short ventrodistal spine and the fourth segment short dorsodistal and ventrodistal spines on the right leg. The terminal claw is long, exceeding all of the segments in length. Pl. 6, Fig. 7; Pl. 7, Figs. 5, 6, 7. (Af 25, Af 26).

The right mandible and three right thorax legs are larger than the counterparts of the left side.

Description of shell features

Ornament and carapace. The lateral ornament of larval shells may consist of reticulations arranged in regular lines (Pl. 5, Fig. 5) or an indefinitely reticulated pattern (Pl. 5, Fig. 2). The ornament of adult shells (Pl. 1, Fig. 7) is a development of either of these ornamental categories. Regularly ornamented individuals display a typical reticulate pattern, while the irregularly ornamented forms bear non-aligned pits, which are rounder and shallower than those of the regularly ornamented variety. The general shape of adults deviates from that of the type species, *B. shubutaensis* Howe, in that the posterior region is less truncated; otherwise the habitus is typical of the genus. A development arising from the irregular reticulations is found in some larvae, where an anastomizing pattern of riblets may develop at the expense of the pits (Pl. 5, Fig. 2). Surface pits are shown in Pl. 1, Fig. 7; Pl. 5, Fig. 1. The surface texture is shown in Pl. 1, Fig. 6; Pl. 3, Figs. 6, 7, where plates of calcite, oriented normally to the lateral surface, are visible. See also Pl. 8.

Muscle field. Four vertically aligned scars with the second one from the top the longest and the most ventral scar consisting of a coalesced pair. A coalesced pair is located anterior of the second scar from the bottom. Two scars, almost in contact, lie anterodorsally of the most dorsal scar of the central field. The muscle field here described is shown in Pl. 1, Fig. 1. This picture also shows a so-called "fulcral point".

The structure of the anterior and posterior margins. The anterior pore canals of adults (Pl. 4, Fig. 8) are typical of *Buntonia* s.str., being single, slightly flexed, and provided each with a dilation. The anterior pore canals of larvae are straight and lack median dilations (Pl. 4, Fig. 3). The posterior canals are single, 8–9 in number in adults; they dilate over about half the total length. Individuals with posterior spines tend to be slightly more pointed posteriorly among late larval stages in particular (Pl. 4, Fig. 5). See also Pl. 8.

Normal pore canals. There is more than one type of normal pore canals in this species. Internal canal openings have a rounded rim (Pl. 1, Figs. 4, 5). Types of normal pore canal openings are shown in Pl. 1, Figs. 2, 3; Pl. 3, Figs. 1–5, 8, 9.

The spines. The marginal and lateral spines of this species display an interesting pattern of variation which is analysed in the next section. Where the posterolateral spine is developed, it may occur as the posterior termination of a rib (Pl. 1, Fig. 6, a larval individual.) A ventrolateral spine is shown in Pl. 4, Fig. 7. The anteromarginal spines may be connected with an excessive amount of calcium carbonate (Pl. 4, Fig. 7); otherwise the spines sprout directly from the margin (Pl. 4, Figs. 1, 2). An unspined posterior margin is shown in Pl. 4, Fig. 9. The spines are hollow cones (Pl. 2, Figs. 1, 4, 5; Pl. 4, Figs. 2, 3, 4–6). Instead of the normal conical spine shape, broadest at the base, trianguloid spines may occur with the proximal portion

Table I. *Eigenvalues and eigenvectors of the total correlation matrix*

Eigenvalues	Eigenvectors I	II	III	IV
1.6917 < 1.9036 < 2.1760	0.6208	−0.3017	−0.2119	0.6919
1.0071 < 1.1332 < 1.2955	0.6396	0.0366	−0.3718	−0.6718
0.6102 < 0.6866 < 0.7849	0.4533	0.3767	0.8078	0.0050
0.2458 < 0.2766 < 0.3162	−0.0079	0.8750	−0.4053	0.2645

narrower than the distal part (Pl. 4, Fig. 6). A point worth noticing is that adults which lack any posterior spines may show "buds" at high magnifications. These may represent an expression of incipient spine-making potential (Pl. 4, Figs. 8, 9).

Hinge. The left hinge (Pl. 2, Figs. 6, 7) consists of a shallow anterior socket and a complex anterior tooth of a general curved form with a jutting anterior section, a postjacent incut zone and, posterior thereof, a broadening of the tooth with a trianguloid, shallow pit. The posterior element is a simple socket which opens into the valve and the dorsal edge of which is feebly notched. The central element consists of a notched bar which gradually widens posteriorly. A furrow runs dorsally along the length of this bar and

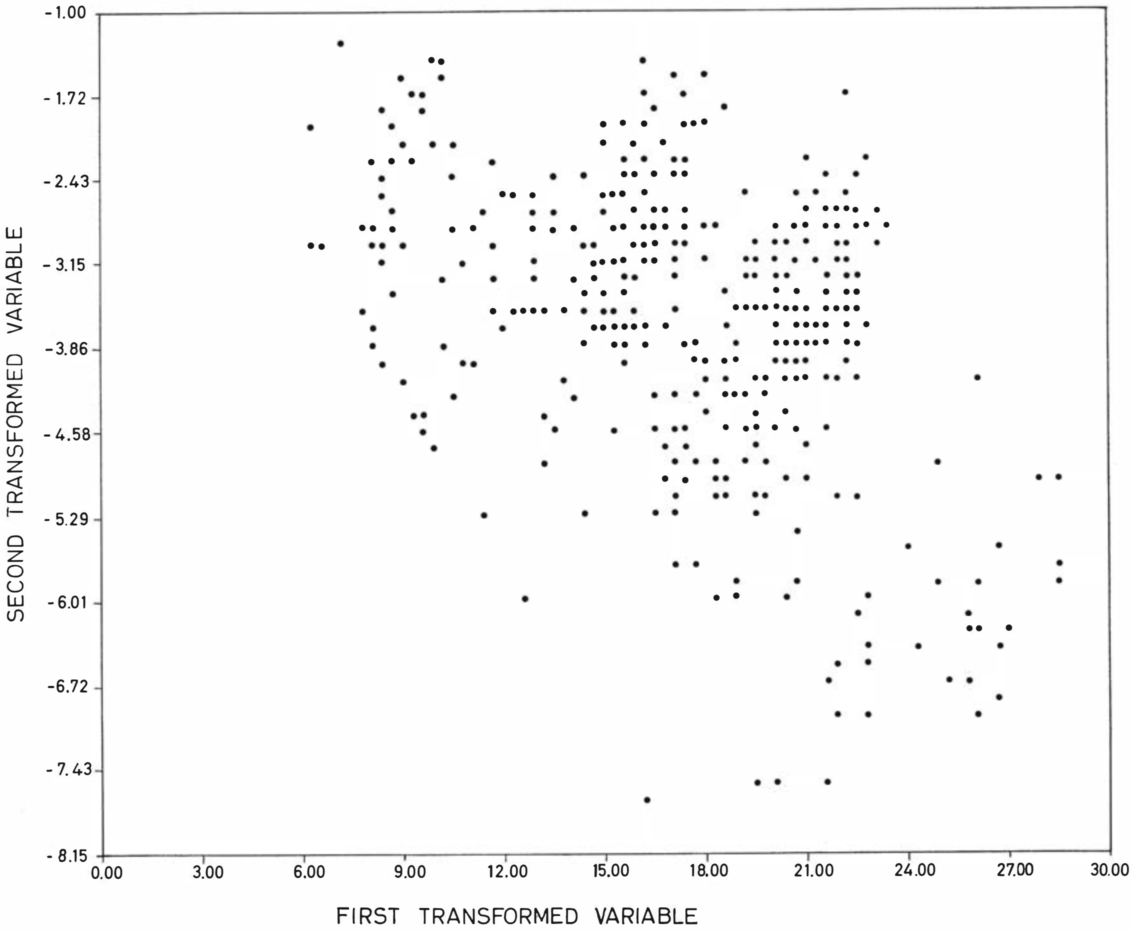

Fig. 1. Plot of the first two transformed variables of the principal component analysis.

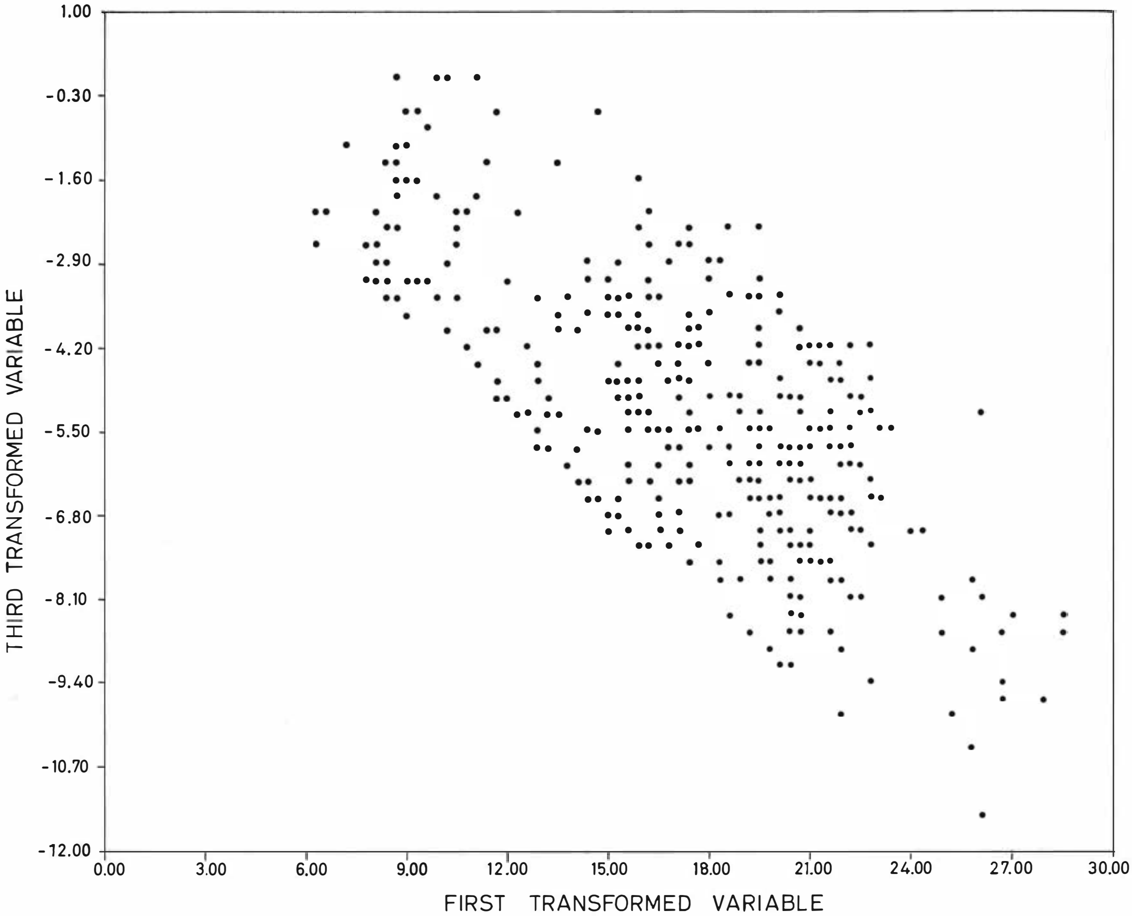

Fig. 2. Plot of the first and third transformed variables of the principal component analysis.

another one along most of the ventral side of the bar; this is barely perceptible at its posterior beginning but widens rapidly anteriorly at the expense of the median bar. The right hinge complements the left.

Eye socket. The eye socket of the left valve is ellipsoidal in shape (Pl. 2, Fig. 6) and is located a short distance below the anterior tooth with half its length anterior thereof. The right anterior tooth contains a tripartite canal system, one branch of which opens below the socket (Pl. 2, Fig. 3).

REMARKS

The species here described is typical of the genus *Buntonia* (cf. Reyment and Elofson (1959) and Lerner (1964)) with one exception, notably, the more sharply rounded posterior.

The present study has disclosed the occurrence of a fairly complicated pattern of meristic variation in the spinosities of the shell, analogous to meristic shell variation found in fossil representatives of *Buntonia.* Further work on Recent ostracods from the Niger Delta by M. E. Omatsola, Uppsala, has shown this type of variation to be fairly common among *Buntonia* and its relatives.

In the next section we examine what appears to us to be the most likely cause of the shell polymorphism in the case histories here reported. A somewhat similar polymorphism occurs, however, among marine invertebrates of the coastal region. Battaglia (1963) has discussed polychromatism in the copepod *Tisbe reticulata,* which is considered to retain its polymorphic condition by virtue of differential adjustment in relation to a great number of ecologic niches. The possibility of this situation having pertained in *B. olokundudui* seems unlikely, as the entire study sample was obtained from a small volume of homogeneous sediment.

PRINCIPAL COMPONENT ANALYSIS

The eigenvalues and eigenvectors of the correlation matrix of the entire sample are shown in Table I. The variables are: length of carapace, number of anterior spines, number of posterior spines, presence or absence of a lateral spine.

The first principal component, which accounts for roughly 48% of the variation, indicates covariation in length of the carapace and the number of anterior and posterior spines. Hence, there is a tendency for the more advanced growth stages to have a greater number of spines but the lateral spines are not included in this relationship. The second principal component is connected with approximately 28% of the variability in the material and indicates a negative correlation between size and the anterior and lateral spines. The anterior spines do not participate in this component. These first two components are of the same order of magnitude and suggest the existence of two important constituents in the biological population from which the sample was taken.

The first two principal components represent almost 76% of the variation in the sample. In a morphometric analysis one would probably be content to say that the first two components successfully explain the main part of the variation and thus largely condense the four-dimensional representation to two dimensions. In the present case, however, our aim is different from that normally pertaining in a principal components analysis, for we are here concerned with breaking up the meristic variation in the material into a spectrum of component patterns. Therefore, each of the principal components is of equal importance in the interpretation of the variational pattern of the species.

The third component, which accounts for the variation in about 17% of the material, represents the posterior spines in a negative relationship with the other variables. The remaining approximately 7% of the variation is connected with a component in which the posterior spine is absent and the anterior spine covaries positively with length, these two variables being in a negative relationship with the anterior spines. The sizes of the elements of the eigenvectors indicate the importance of each variable in the principal component.

In terms of correlations of the original variables with the principal components, carapace length and number of anterior spines are very highly correlated with the first component with $r = 0.86$, respectively 0.88. The lateral spines are very highly correlated with the second component ($r = 0.93$) and the number of posterior spines moderately strongly correlated with the first and third components. None of the variables is strongly correlated with the fourth component. Although the four variables studied in this paper are not homogeneous as to their nature, one may still plot the transformed variables of the principal components to facilitate an examination of their distributions. The plot of the first two transformed variables is given in Fig. 1. This shows a clear pattern of several distributions and would appear to reflect the spectral nature of the variation (cf. p. 92). Fig. 2, which shows the plot of the first and third transformed variables, appears at first sight to represent a homogeneous distribution, but on closer examination it is seen to be a composite of several distributions.

II. VARIATION GENETICS OF FOSSIL OSTRACODS, AND *BUNTONIA OLOKUNDUDI* SP. NOV.

Introductory remarks

The genetics of variation (cf. Van Valen, 1968) has received relatively little attention in paleontology. Aside from the many problems that can be investigated from samples of both fossil and recent forms (although not always by the same methods), the use of fossils offers two advantages not available for recent material. The more important of these advantages is that of direct extension in time. This extension can be as small as that of the often yearly varves in some consolidated or unconsolidated lake deposits, the frequently abundant cladoceran remains of which would repay careful study from this viewpoint (cf. Goulden (1966) for an excellent longer-period study of their diversity). Well-established and detailed phylogenies are still relatively rare in paleontology, and samples are often isolated and therefore of only a single time plane, but these and other difficulties

Table II. *Information on fossil samples*

	Sample Size (Adults)	Proportion (Males)	Age	Homogeneity*
Buntonia livida	648	0.18**	Late Paleocene	Various levels of two boreholes
B. keiji	74	0.12	Early Paleocene	One level of one borehole
B. apatayeriyerii	346	0.22	Early-late Paleocene	Various levels of one borehole
B. pulvinata	271	0.28	Late Paleocene	One level each of two boreholes 20 m apart
Brachycythere armata	60	0.19	Latest Cretaceous	One borehole (24 m)
Ruggieria tattami	343	0.35	Paleocene—early Eocene	Various levels of several boreholes
Leguminocythereis bopaensis	126	0.12	Late Paleocene	One level of two neighboring boreholes (1.5 m)
L. lagaghiroboensis	411	0.32**	Early—late Paleocene	Various levels of two boreholes
Cytherella sylvesterbradleyi	1728	(heterogeneous, 0.5–0.8)	Latest Cretaceous—late Paleocene	Various levels of two boreholes

* Vertical thickness of core given for continuously sampled cores.
** Variable over time in at least these species.

(notably depositional bias and small sample size) may be overcome if the material be chosen because of the problem rather than, as is usually the case, the problem being dictated by the material.

The second advantage of fossil samples is their averaging effect. This effect is particularly noticeable with respect to yearly fluctuations, which in most deposits are undetectable. The effect is also present with respect to the species occurring: for mammals, the only approximately reliable indication of the relative abundance of species with sizes and habits as different as mice and elephants is provided by a circumspect analysis of their frequency in sediments (cf. Van Valen, 1964) (the first indication of the relative scarcity of mosquitoes, except in the immediate vicinity of homotherms, was provided by their comparative scarcity in amber).

Polymorphism in Cretaceous and Paleocene ostracods

The samples to be discussed were derived from borehole cores drilled in coastal Nigeria. Two of these boreholes, referred to by Reyment (1963) as the Araromi and Gbekebo Boreholes, are near the town of Okitipupa in Western Nigeria. Two less important ones, the Ilaro Boreholes, are 20 m apart in the coastal plain northwest of Lagos. Other aspects of these samples have been presented in detail elsewhere (Reyment, 1960 *a,* 1963, 1966). The ostracods lived from the late Maestrichtian, about 65 million years ago, to the early Eocene, about 50 million years ago. (The Danian is here treated as early Paleocene.) The classification of the ostracods is as follows:

Family Cythereidae
- *Buntonia (Quasibuntonia) livida* Apostolescu
- *Buntonia (Protobuntonia) keiji* Reyment
- *Buntonia (Protobuntonia) apatayeriyerii* Reyment
- *Buntonia (Buntonia) fortunata* Apostolescu
- *Buntonia (Buntonia) pulvinata* Apostolescu
- *Brachycythere armata* Reyment
- *Ruggieria tattami* Reyment
- *Leguminocythereis bopaensis* (Apostolescu)
- *Leguminocythereis lagaghiroboensis* (Apostolescu)

Family Cytherellidae
- *Cytherella (Cytherella) sylvesterbradleyi* Reyment

Unless otherwise noted, all specimens used are adults. Relevant information on the samples is given in Table II. All the characters are discrete in the sense that no individuals of doubtful classification are present. All polymorphisms occur in both sexes: frequencies for the sexes separately are not usually available, nor are frequencies for individual levels of composite samples.

Leguminocythereis lagaghiroboensis (Reyment, 1963, p. 139) shows, like *Brachycythere armata* (Reyment, 1966, p. 70) but more strikingly, a polymorphism for a pleiotropic character. Individuals with irregular surface ornament have the posterior end of the carapace rounded or bluntly pointed, while those with a regularly reticulated surface have a mucronate posterior end. The regular morph may have attained a maximum frequency in the middle Paleocene in one borehole; it is apparently absent in the Ivory Coast. The sexes appear to have the same frequencies of the morphs. A sample of 37 larvae of the last three instars showed no heterogeneity among instars but had a significantly lower frequency (0.68) of the irregular morph.

Several species have a polymorphism of the surface ornament (Table III). In *Buntonia pulvinata* (Reyment, 1963, p. 202) the alternative states are reticulations and irregular pits. In *Ruggieria tattami* (Reyment, 1963, p. 252) a smooth surface contrasts with a reticulate one. In *Cytherella sylvesterbradleyi* (Reyment, 1963, p. 35) a few individuals have a punctate surface rather than the usual smooth one; a similar polymorphism occurs in other Paleocene and living species of this genus. In a largely immature sample of *Buntonia fortunata* (Reyment, 1963, p. 197) 80 of 271 specimens show a pitted rather than a reticulate surface. In this case, as in the others, it is not certain that one polymorphic species is present rather than two monomorphic species. We prefer the former alternative because the two forms are morphologically very similar to each other, with respect to both the external development of the shell as to habitus and internal shell structure; they are found together; they have similar sex ratios, and size dimensions as well as other characters give unimodal distributions for specific instars.

One of the features considered to be diagnostic of *Leguminocythereis* is the presence of an anterior vestibule. The ostracod carapace consists of an outer, mainly calcitic shell and an inner, roughly parallel, principally chitinous layer, which, however, may be calcified at the contact with the outer shell to produce a vestibule. A large sample of free valves of *L. bopaensis* (Reyment, 1963, p. 121) shows that a switch-mechanism can operate in the control of vestibule development, for this species is polymorphic with respect to the presence of a vestibular structure.

Table III. *Frequencies of morphs in fossil samples*

	Morph	Frequency
Buntonia livida	posterior spine	$\frac{116}{648} = 0.18$
B. keiji	posterior spine	$\frac{19}{74} = 0.25$
B. apatayeriyerii	posterior spine	$\frac{13}{171} = 0.08$
B. pulvinata	reticulate surface	$\frac{191}{271} = 0.70$
Brachycythere armata	spined	$\frac{36}{60} = 0.60$
Ruggieria tattami	reticulate surface	$\frac{89}{342} = 0.26$
Leguminocythereis bopaensis	vestibule	$\frac{105}{126} = 0.83$
L. lagaghiroboensis	irregular surface and blunt posterior	$\frac{370}{411} = 0.90$
Cytherella sylvesterbradleyi	punctate surface	$\frac{47}{1728} = 0.03$

In four species there is a polymorphism as to the presence or absence of a posterior spine on both valves of the carapace. The frequencies of spined individuals are given in Table III. In *Buntonia livida* (Reyment, 1963, p. 227), at least, the polymorphism is also present in late immature instars, and in *B. fortunata* (Reyment, 1963, p. 197) the sample, mainly of immature individuals, has 13 spined forms out of a total of 366 specimens. In *B. apatayeriyerii* (Reyment, 1963, p. 239), spined individuals occur only in the lower part (early Paleocene) of one borehole, the morph having become at least locally extinct thereafter.

Table IV. *Frequencies of spined Buntonia livida*

	Adults		Last Larval Instar	
	Spined	Un-spined	Spined	Un-spined
Araromi Borehole (combined)	49	180	0	4
Gbekebo Borehole				
703 m (latest)	0	2	2	2
710 m	1	10	2	1
711 m	5	27	3	0
712 m	1	14	0	0
720 m	11	30	0	0
721 m	8	34	4	7
725 m	5	4	0	0
733–738 m (earliest)	6	20	2	0

Table V. *Frequencies of spined individuals in growth stages of Buntonia livida*

Araromi Borehole

Instar	Spined	Unspined
Adult	49	180
A–1	0	4
A–2	2	8
A–3	7	8

The frequency given in Table III is for the polymorphic interval alone. In *Brachycythere armata,* the spined individuals have three or four posterior spines and also a spined elongation of ventrolateral winglike process, all of which the unspined individuals lack.

The frequencies of the morphs in *Buntonia livida* are the same in the two sexes, and in the Araromi Borehole there is no detectable change in the frequency (0.21) of the spined morph over the range sampled (342 to 311 m, middle Paleocene). However, in the Gbekebo Borehole there is a change in frequency in about the early Paleocene (738 to 711 m), as shown in Table IV. Furthermore, it can be seen from Tables IV and V that the frequency of spined individuals decreases with growth. This decrease could be due to a balanced natural selection against the spined forms, but by analogy with the recent species of *Buntonia* discussed below, it seems more likely that some individuals that were spined as larvae, were unspined as adults (the reverse of the change in the recent species). Thus at some times the relation between spinemaking potential and its threshold was probably similar in adults to the relation in immature instars at other times.

Variation in Buntonia olokundudui

The morphologic variation shown by a recent species of *Buntonia* from the Niger Delta is more complicated than that of any of the above fossil species. Four features are involved, in addition to sex and instar, notably, carapace length, presence or absence of a ventrolateral spine, number of spines along the anterior margin, and number of spines along the posteroventral margin. Other variates, such as spine lengths and discrete variation in lateral ornament, would also be useful in interpretations, but they are beyond the scope of the present study.

The 503 carapaces fall into five almost discrete size groups on the basis of the length variable. The group containing the largest individuals is that of the 36 males (M) and the next largest is that of the 240 females (F). Two individuals intermediate in size between these groups are called males on the basis of pronouncedly male-like states of the other characters. The next smaller group, here called instar A-1, comprises 161 specimens, while A-2 has 58 and A-3 has 5. Two specimens are intermediate between A-2 and A-1, and one is intermediate between A-1 and F; these specimens have been ignored in the sequel but would

Table VI. *Some statistics for recent Buntonia*

	A-3	A-2	A-1	F	M
Sample size	5	58	161	240	36
Anterior spines					
Mean	0	0.16	6.45	9.71	10.92
Mean_0	0	0	4.79	8.19	10.94
Mean_1	0	0.20	6.82	9.99	10.70
Coefficient of variation	(0)	330	44	28	42
Posterior spines					
Mean	0.40	1.38	1.78	2.89	2.47
Mean_0	0	0.83	1.69	2.16	2.45
Mean_1	1.00	1.52	1.80	3.02	2.70
Coefficient of variation	200	90	85	54	65
Length					
Mean (mm)	0.104	0.129	0.159	0.204	0.257
Coefficient of variation	1.1	3.3	3.7	3.7	4.4
Proportion of individuals without a lateral spine	(0.6)	0.21	0.18	0.16	0.92

Statistics for the subclasses with 0 and 1 lateral spine are distinguished by the respective subscript.

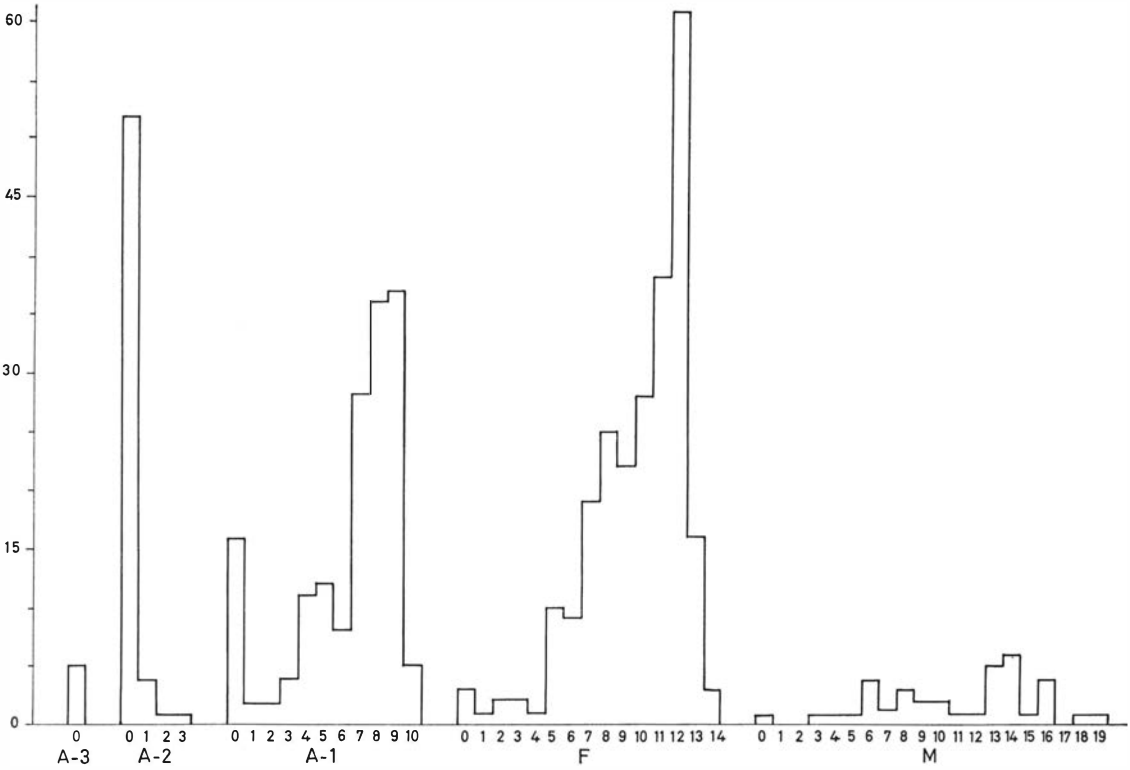

Fig. 3. Observed distributions of numbers of anterior spines for the *Buntonia* for the several size-sex classes.

not qualitatively affect the results if they had been included.

Statistics for each group are given in Table VI. Both anterior and posterior spines tend to increase in number with successive instars. The anterior spines are also more numerous in males than in females, concordant with the greater size of males, but the posterior spines average fewer in males than in females, although still more than in A-1. The proportion of individuals lacking the lateral spine is not detectably different in the immature instars, but is much greater in adult males. Combining the observed frequencies for adult males and females, with account taken of the sex ratio, leads to a frequency of 0.25. This value is not significantly different from the frequency in the immature stages, as shown by a chi-square test on the observed frequencies. It is therefore a plausible suggestion that both the sex ratio and the frequency of individuals of each sex without a lateral spine are constant, at least from instar A-2.

The numbers of anterior and posterior spines are nearly independent of each other, their correlation being 0.135, which is significantly different from 0 ($P < 0.003$) but accounts for only 0.018 of the variance of each. This correlation was derived as follows. The correlations were calculated within each group (excluding A-3) and transformed to Fisher's z. No heterogeneity was detectable among groups or among 0.005-mm length classes within groups. The weighted $\bar{z}$ was calculated and transformed back to r. By a similar method, the correlation of carapace length with number of anterior spines is -0.00, and that of carapace length with number of posterior spines is -0.10. The latter is significant at the 0.03 level. Again, no heterogeneity was detectable among age-sex groups.

The ventrolateral spine behaves differently from the number of anterior or posterior spines, although its presence or absence is more highly associated with both of these than they are with each other. There is no significant difference ($P >$

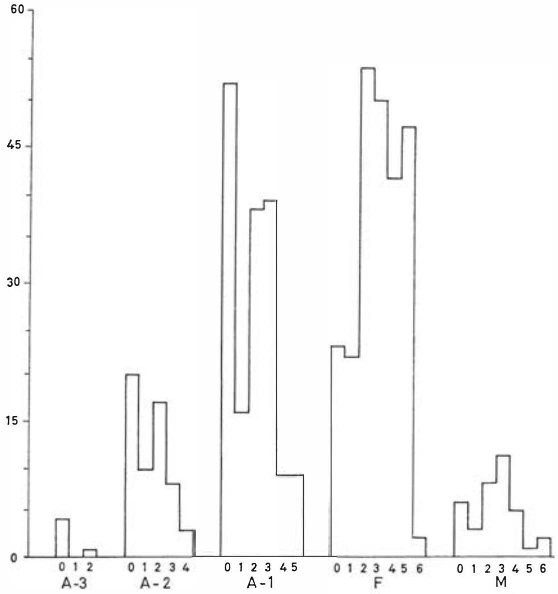

Fig. 4. Observed distributions of numbers of posterior spines for the recent *Buntonia* for the several size-sex classes.

0.5, within-group tests combined) between the lengths of carapaces with and those without a spine. On the other hand, it can be seen from Table VI that individuals with a lateral spine have more anterior and posterior spines on the average than do those lacking a lateral spine (there are only three adult males with a lateral spine).

Although the coefficients of variation for carapace length are normal for ostracods and show no detectable relation with age-sex group (if anything, the variation increases), this is not true for the variation in number of anterior and posterior spines. In both these characters the variation is very large throughout but decreases significantly in later instars. The coefficient of variation for males is significantly ($P = 0.001$) greater than that of females for the anterior spines, but although that for the posterior spines does not differ significantly between the sexes, the ratio between the sexes is not significantly different from that of the anterior spines.

These changes in the variation may be examined with the help of the frequency distributions themselves (Figs. 3 and 4). The distribution for the anterior spines are clearest because they are more subdivided. The first point to notice is that all the distributions extend into the 0-spine class, and that this class decreases in frequency as the mean number of spines increases in later age-sex groups. It is obvious that unexpressed variation, at the level of spine-making potential, is present in the 0-spine class, at least in the immature instars. The threshold at which spine production occurs would appear to shift down with each increase in age-sex group.

A less evident point, one that may be true for all the distributions but is demonstrable only for the anterior spines of the A-1 instar, is that the 0-class is disproportionately frequent relative to the adjacent part of the distribution. A precise test is possible in no case because the expected distribution is unknown. However, from inspection of Fig. 3 it would seem that the maximum expected number in the 0-class, excluding sampling error, should be considerably less than 10. The observed frequency differs at the 0.05 level even from an expected value of 10. We may therefore suggest the conclusion that the 0-class is probably in excess relative to the 1-, 2-, and 3-classes.

Two related interpretations for this situation offer themselves. One (Fig. 5) assumes that there is in fact a unimodal, smooth distribution of precursor, spine-potentiality, or the like (Rendel's (1962) "Make"), but that the thresholds at which different spine numbers occur are unevenly spaced relative to the scale of the distribution. This is the threshold-spacing model. A normal distribution with class widths increasing exponentially above the threshold of the 0-class would approximate the observed distribution (and the distributions in other instars), as would various other possibilities. The distribution of Make would then simply shift to the right with successive instars. The observed distribution for adult males, however, does not seem to fit the same underlying distribution. The thresholds should not be construed as absolute, but as themselves possibly having some nondegenerate probability distribution (due to influences other than quantity of Make) that could vary among thresholds and instars. Thresholds with such nondegenerate probability distributions may be common; they may be known as *spectral thresholds,* by an incomplete analogy with the continuous transition between the visually uniform but physically diverse regions of the infrared and ultraviolet. The concepts of Make and threshold are discussed in detail in Rendel (1967). The former concept was introduced to account

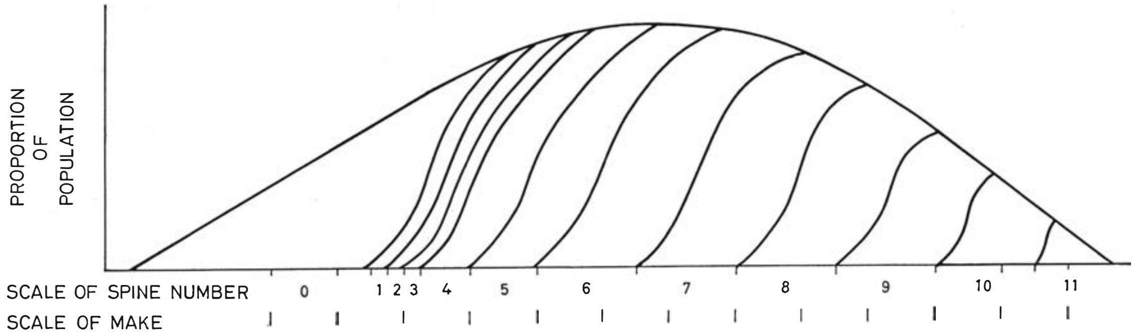

Fig. 5. Diagram to illustrate the threshold-spacing model for the A-1 anterior spine distribution. The distribution of Make has some smooth distribution, and the spectral thresholds for production of different numbers of spines are unevenly spaced.

for differences between populations with respect to phenotypes in which underlying genetic differences are largely obliterated. Although a property of an individual, it is studied by reference to a population (cf. Rendel, 1967, p. 79).

The second interpretation (Fig. 6) is modified from Grüneberg's (1951) analysis of quasicontinuous variation. Under this model the class widths can be equal, but a spectral threshold is essential as the delimiter of the 0-class. This threshold is such that it overlaps some higher thresholds, and some individuals, which would otherwise be in nearby classes, fall into the 0-class. This phenomenon would be, if it is shown to exist, analogous to incomplete penetrance. As for the threshold-spacing model, a simple shift in the distribution of Make could account for the differences among instars except for the adult males.

The quasicontinuous model is not as sharply distinct from the threshold-spacing model as the diagrams indicate, because in the latter the crowding of the 1-, 2-, and 3-class thresholds could be regarded as a result of pressure from the 0-class. However, unlike the threshold-spacing model, the quasicontinuous model includes in the 0-class some individuals with sufficient Make for them to be in nonadjacent classes. The threshold for the 0-class here extends beyond the upper threshold for the 1-class.

Summarizing remarks

Some homologous and nonhomologous polymorphisms in Paleocene ostracods show changes between instars, evolutionary changes in frequency, and other features. A recent species shows a complex pattern of variation and growth in some quasicontinuously varying characters of the carapace. One of these characters suggests the presence of spectral thresholds, defined as thresholds with nondegenerate probability distributions. The im-

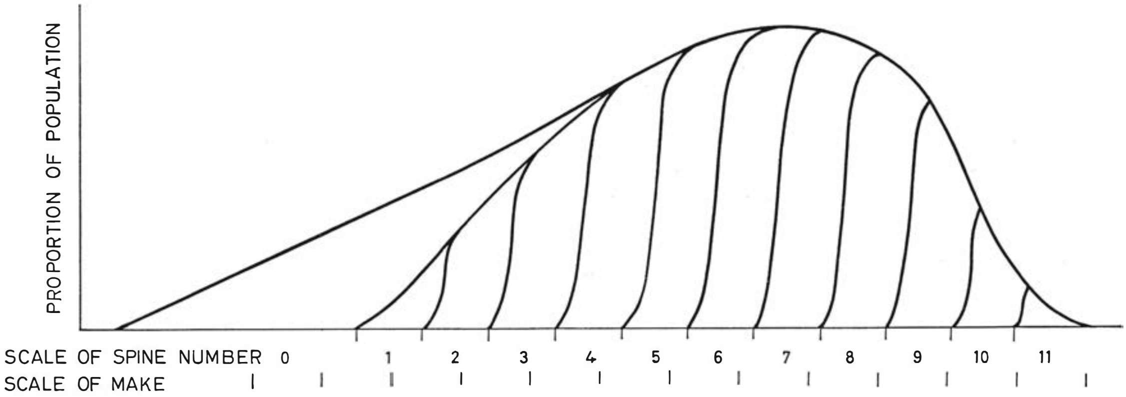

Fig. 6. Diagram to illustrate the quasicontinuous model for the A-1 anterior spine distribution. The spectral threshold above the 0-class cuts off the thresholds for nearby classes, and is superimposed on the distribution of Make.

portance of being on the lookout for this type of variation, particularly in paleontologic studies, should be kept well in mind.

ACKNOWLEDGEMENTS

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REFERENCES

Battaglia, B. 1963. Advances and problems of ecological genetics in marine animals. Section 13. Ecological Genetics. *Proc. int. Congr. Genet.* 2, 451–462.

Goulden, C. E. 1966. La Aguada de Santa Ana Vieja: an interpretive study of the cladoceran microfossils. *Arch. Hydrob.* 62, 373–404.

Grüneberg, H. 1951. The genetics of a tooth defect in the mouse. *Proc. roy. Soc.* (B) 138, 437–451.

Lerner, R. 1964. Preliminary notes on the Ostracoda of the Mediterranean coast of Israel. *Israel J. Zool.* 13, 145–176.

Rendel, J. M. 1962. The relationship between genotype and phenotype. *J. theor. Biol.* 2, 296–308.

— 1967. *Canalisation and gene control.* Academic Press, New York, London.

Reyment, R. A. 1960 *a*. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 1: Senonian and Maestrichtian Ostracoda. *Stock. Contr. Geol.* 7, 1–238.

— 1960 *b*. Notes on the study of evolutionary changes in ostracods. *Rep. int. geol. Congr.* (*21st Session*) 6, 7–17.

— 1963. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 2: Danian, Paleocene, and Eocene Ostracoda. *Stockh. Contr. Geol.* 10, 1–286.

— 1966. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 3: Stratigraphical, paleoecological and biometrical conclusions. *Stockh. Contr. Geol.* 14, 1–151.

Reyment, R. A. & Elofson, O. 1959. Zur Kenntnis der Ostrakodengattung *Buntonia. Stockh. Contr. Geol.* 3, 157–164, 3 pls.

Van Valen, L. 1964. Relative abundance of species in some fossil mammal faunas. *Amer. Nat.* 98, 109–116.

— 1967. Selection in natural populations. 6. Variation genetics, and more graphs for estimation. *Evolution* 21, 402–405.

— 1969. Variation genetics of extinct animals. *Amer. Nat.* (in press).

PLATES

Plate 1

Fig. 1. Muscle scar of adult specimen (× 400). Note the fulcral point (white). Stereoscan.
Fig. 2. Normal pore canal in posterior area of adult right valve (× 4000). Stereoscan.
Fig. 3. Same area as in Fig. 2 but at lesser magnification (× 800). Stereoscan.
Fig. 4. Normal pore canal from inside of left valve (× 4000). Stereoscan.
Fig. 5. Normal pore canals observed inside a left valve in the dorsal region (× 800). Stereoscan.
Fig. 6. Larval individual showing ventrolateral spine on well developed rib (× 145). Af 36. Stereoscan.
Fig. 7. Stereoscan photograph of left valve of adult individual (× 95). Af 35.
Fig. 8. Larval individual. Stereoscan photograph. (× 130). Af 13.

Plate 2

Fig. 1. Anterior marginal spines of adult shell (× 500). Light microscope.
Fig. 2. Holotype. Stereoscan photograph of left valve of adult individual (× 95). Af 12.
Fig. 3. Anterior left hinge element showing canals (× 350). Af 28. Light microscope.
Fig. 4. Posterior spine (× 500). Af 27. Light microscope.
Fig. 5. Same area as in Fig. 4 at a lesser magnification (× 80).
Fig. 6. Anterior part of the hinge of a left valve (× 400). Af 28. Stereoscan.
Fig. 7. Posterior part of hinge of a left valve (× 400). Same specimen as in Fig. 6. Stereoscan.
Fig. 8. Holotype. Same individual as shown in Fig. 2 of this plate (× 180). Af 12. Stereoscan photograph.
Fig. 9. Holotype. Same individual as shown in Fig. 2 of this plate (× 420). Af 12. Stereoscan photograph.

Plate 3

Figs. 1, 4. Normal pore canal in posterior part of a carapace. Fig. 1 (× 880); Fig. 4 (× 4400). Stereoscan.
Figs. 2, 5. Normal pore canal in the central part of a left valve. Fig. 5 (× 880), Fig. 2 (× 4400). Stereoscan.
Fig. 3. Normal pore canal in anterior part of valve containing bristle (× 4400). Stereoscan.
Fig. 6. Surface pits of midlateral part of shell (see also Pl. 1, Fig. 6) (× 3700). Stereoscan.
Fig. 7. Surface sculpture of another part of the test of the same individual is shown in Fig. 6 and in Pl. 1, Fig. 6 (× 3700). Note the vertically (normal to plane of surface) aligned plates of calcite. Stereoscan.
Fig. 8. Normal pore canal (× 4000). Same individual as in Pl. 5, Fig. 1. Stereoscan.
Fig. 9. Normal pore canal (× 4800). Stereoscan.

Plate 4

Fig. 1. Anterior marginal zone showing radiating canal system (× 500).
Fig. 2. Posterior margin of an adult left valve (× 450). Observe the undeveloped spinal "buds".
Fig. 3. Anterior margin of a juvenile right valve (× 360).
Fig. 4. Anterior margin of an adult left valve (× 420). Observe the undeveloped spinal "buds".
Fig. 5. Anterior marginal spines of advanced instar (× 360).
Fig. 6. Posterior margin of an adult right valve (× 350).
Fig. 7. Posterior margin of an adult left valve (× 420).
Fig. 8. Anterior marginal spines of advanced instar (× 360).
Fig. 9. Anterior margin of an adult right valve (× 260).
Fig. 10. Anterior margin of an adult right valve (× 250).

Plate 5

Fig. 1. Reticulation and pore (× 1900). Same individual as shown in Fig. 5. Af 30.
Fig. 2. Larval specimen showing ventrolateral and posterior spines and vaguely reticulated ornament (× 90). Af 30.
Fig. 3. Larval specimen showing lateral ornament and ventrolateral spine (× 160). Af 31.
Fig. 4. Larval specimen showing ventrolateral spine (× 140). Af 32.
Fig. 5. Regularly reticulated larval carapace (× 95). Af 33.
Fig. 6. Left second antenna (× 190). Af 16.
Fig. 7. Left mandible (× 85). Af 18.
Fig. 8. Portion of maxilla (× 220). Af 20.
Fig. 9. Claw of extremity shown in Pl. 7, Fig. 3 (× 220). Af 17.
Fig. 10. Part of same extremity as shown in Fig. 6 of this plate (× 220). Af 16.
Fig. 11. First left leg (× 210). Af 21.
Fig. 12. Knee of right second leg (× 370). Af 24.

Plate 6

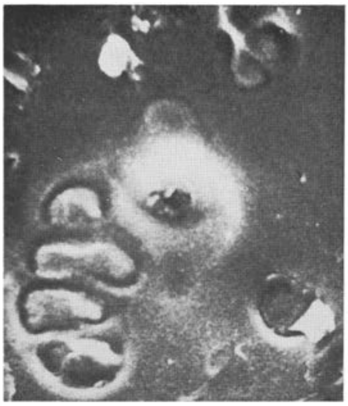
Fig. 1. Right mandible (× 250). Af 19.
Fig. 2. Right mandible (× 195). Af 19.
Fig. 3. Enlarged view of part of right first antenna (fluorescent lighting).
Fig. 4. Maxilla (× 195). Af 20.
Fig. 5. Right second leg (× 220). Af 24.
Fig. 6. Left second leg (× 220). Af 23.
Fig. 7. Third left leg (× 180). Af 26.

Plate 7

Fig. 1. Right first antenna (× 190). Af 15.
Fig. 2. Left first antenna (× 190). Af 14.
Fig. 3. Right second antenna (× 190). Af 17.
Fig. 4. Right first leg (× 210). Af 22.
Figs. 5–7. Right third leg; 5) (× 180); 6) tip of extremity (× 230); 7) photographed in fluorescent light to show brushes (× 180). Af 25.

Plate 8

Fig. 1. Right third leg (× 120).
Fig. 2. Left first antenna (× 120).
Fig. 3. Right mandible (× 120). Fluorescent light.
Fig. 4. Portion of right second antenna (× 120). The fluorescent lighting brings out the muscular arrangement.
Fig. 5. Left anterior margin of adult (× 250). Crossed nicols and gypsum plate. Observe the incipient tuberculation of the anterior margin and the developed spines.
Fig. 6. Left posterior margin of adult individual (× 420). Partial extinction and gypsum plate.



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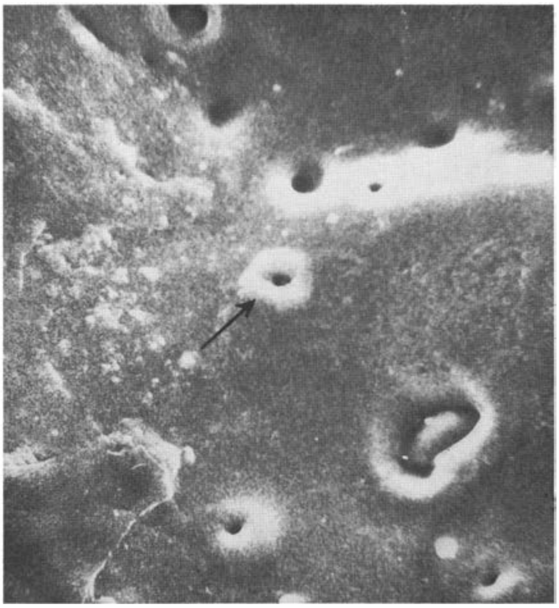

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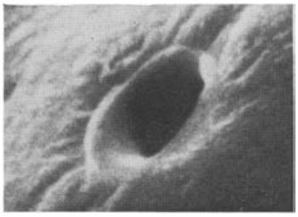

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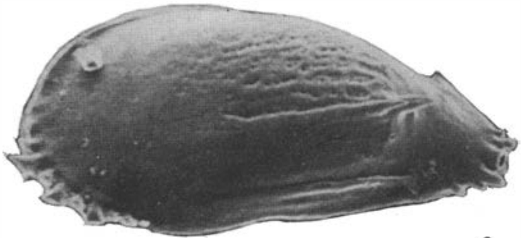

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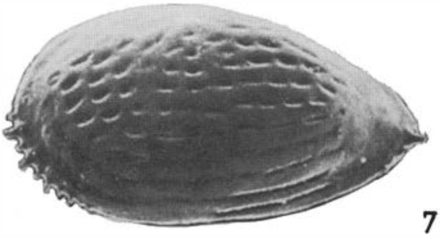

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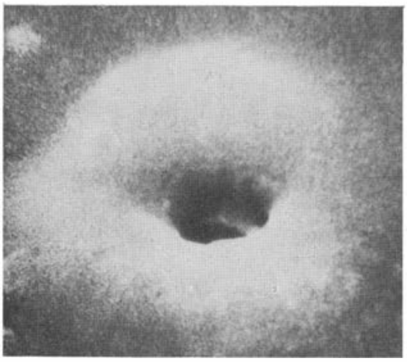

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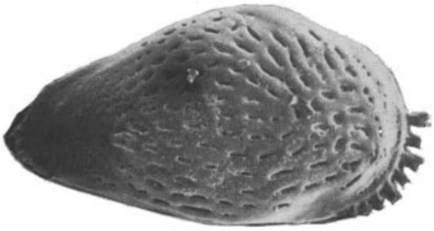

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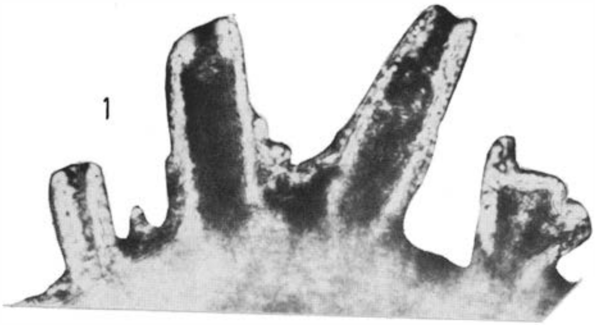
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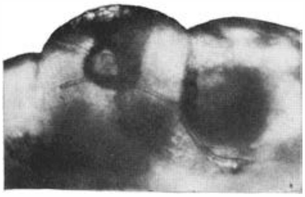
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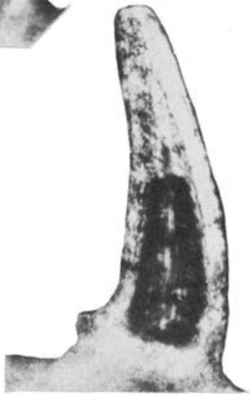
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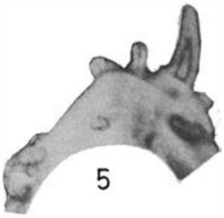
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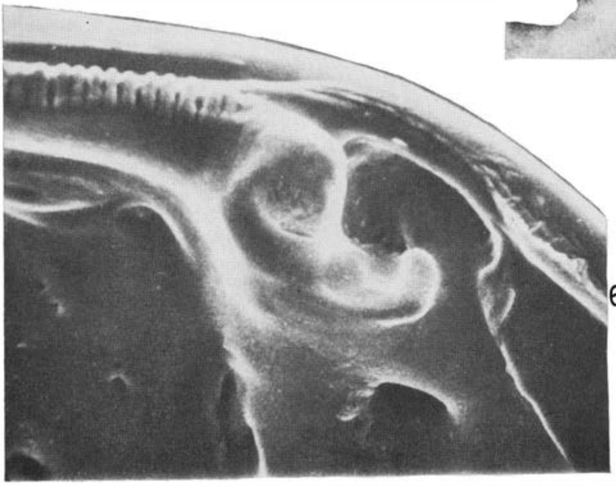
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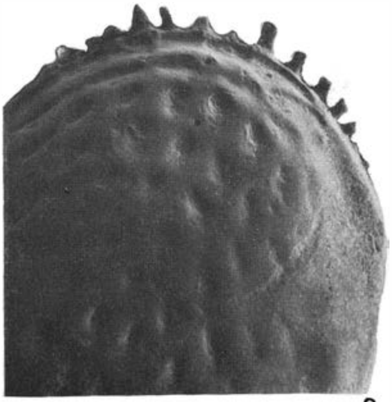
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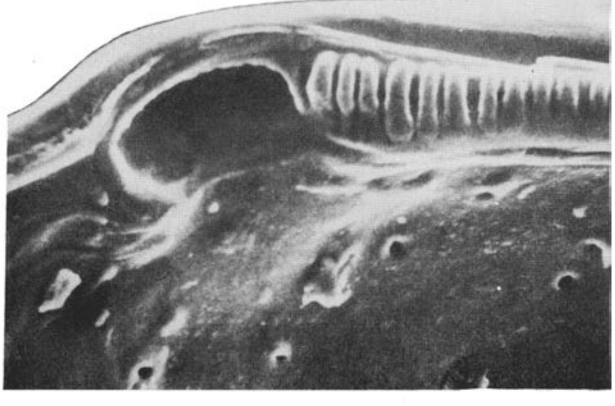
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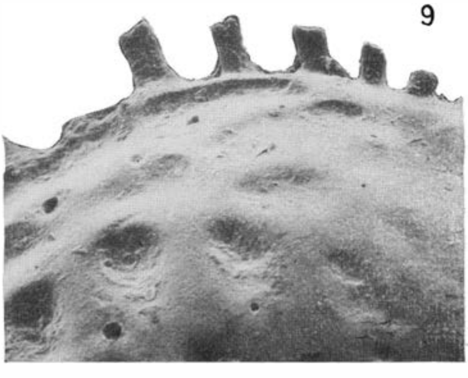
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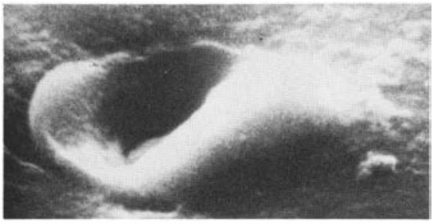
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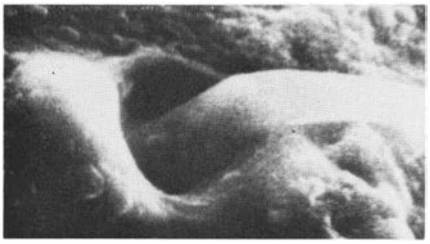
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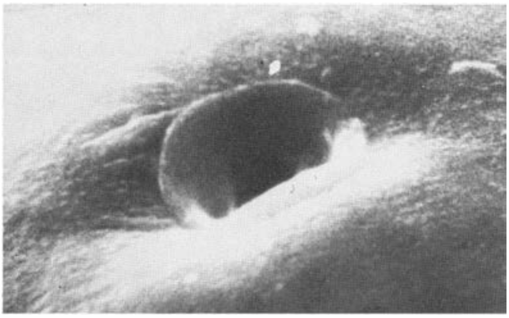
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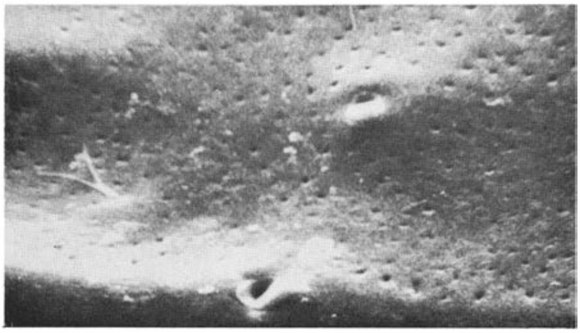
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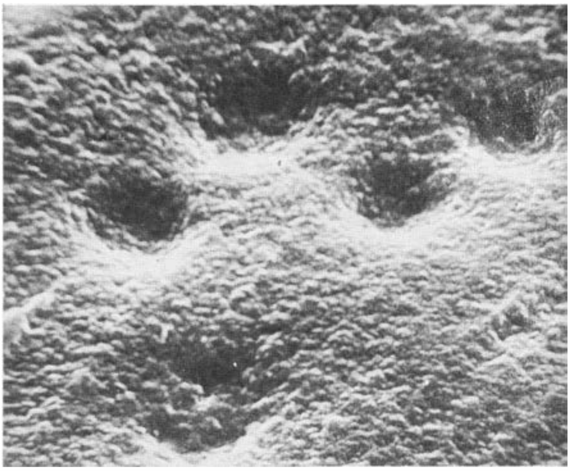
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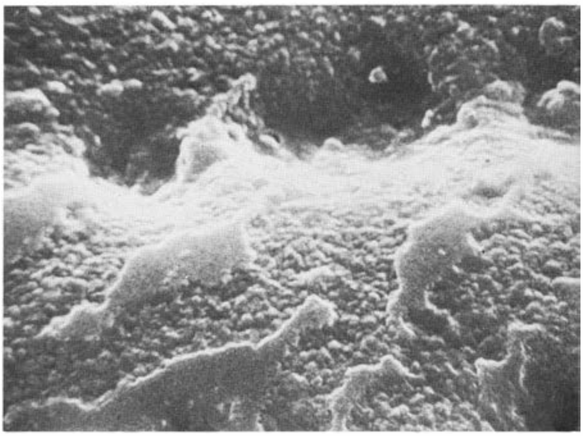
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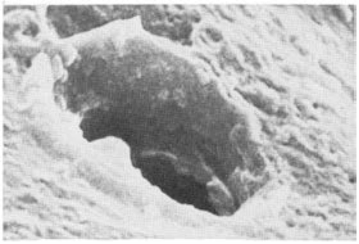
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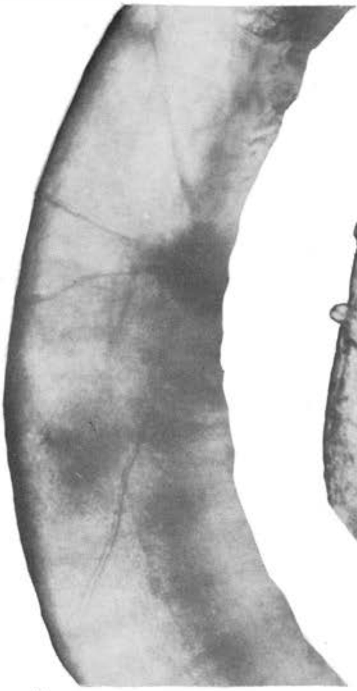
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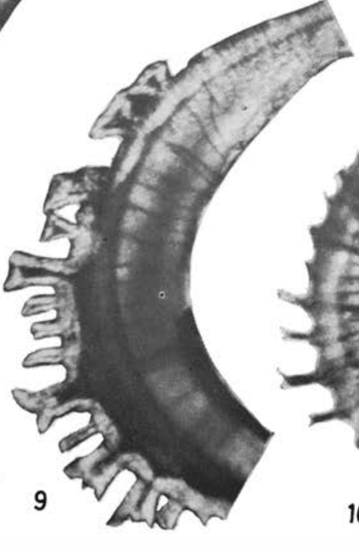
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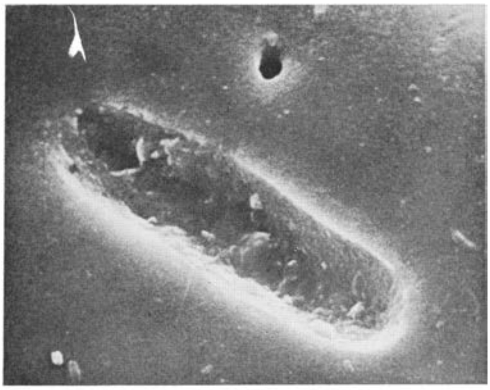
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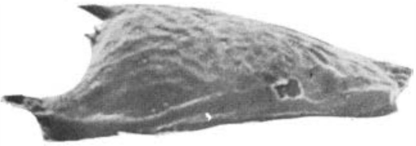
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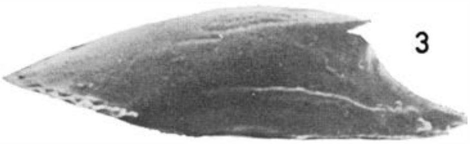
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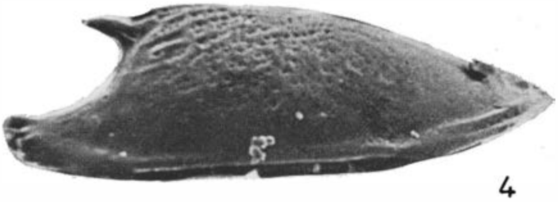
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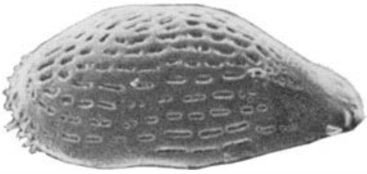
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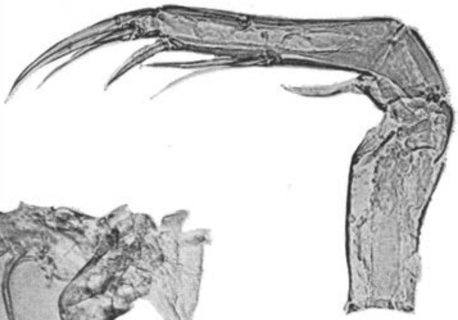
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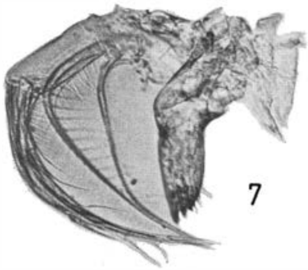
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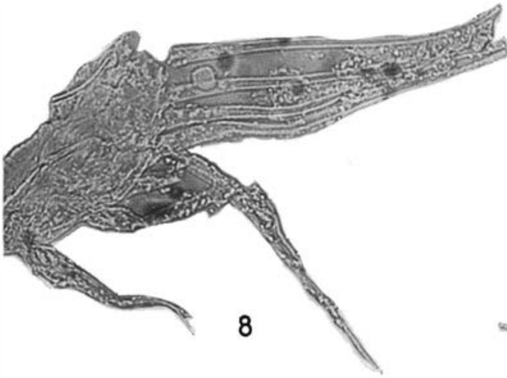
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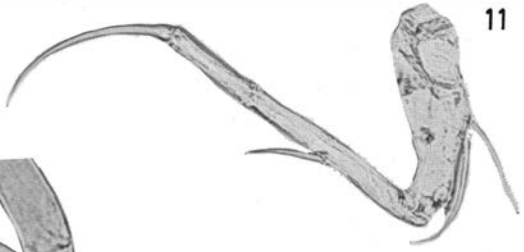
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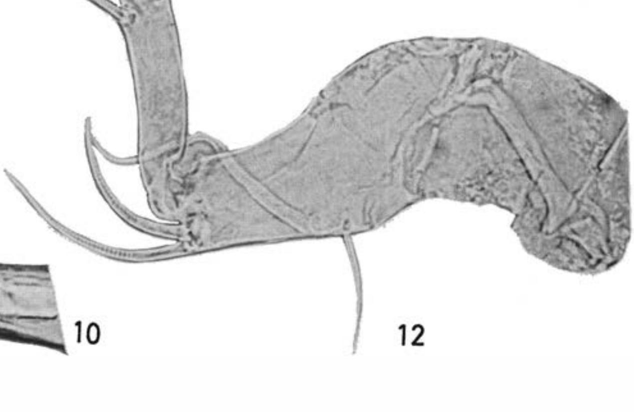
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Plate VI


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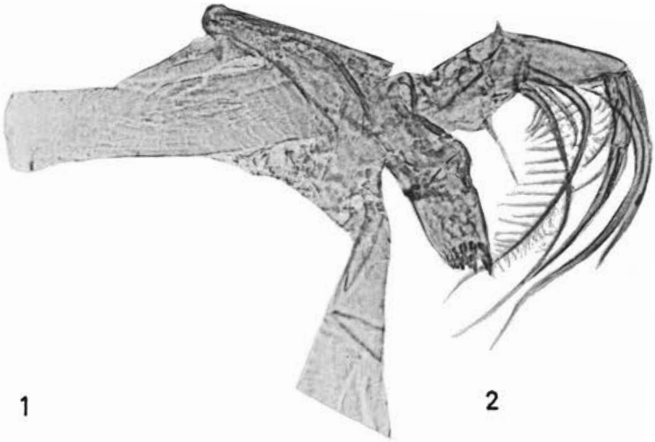
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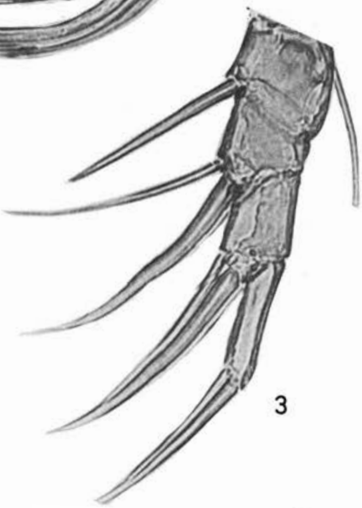
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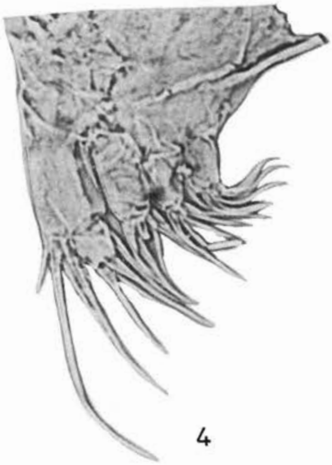
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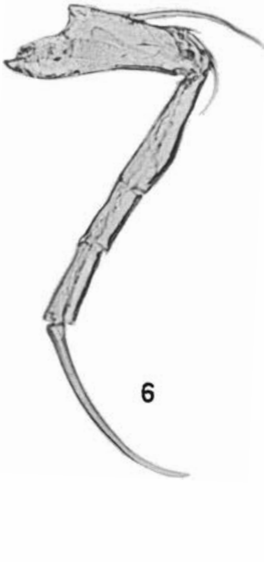
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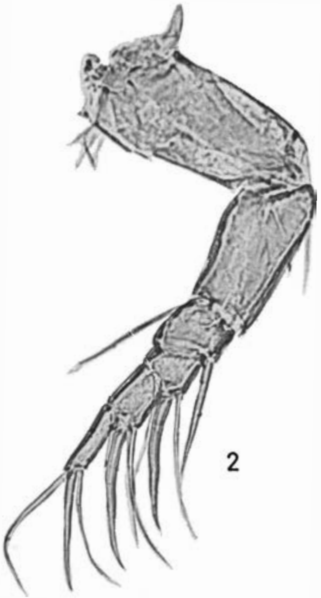
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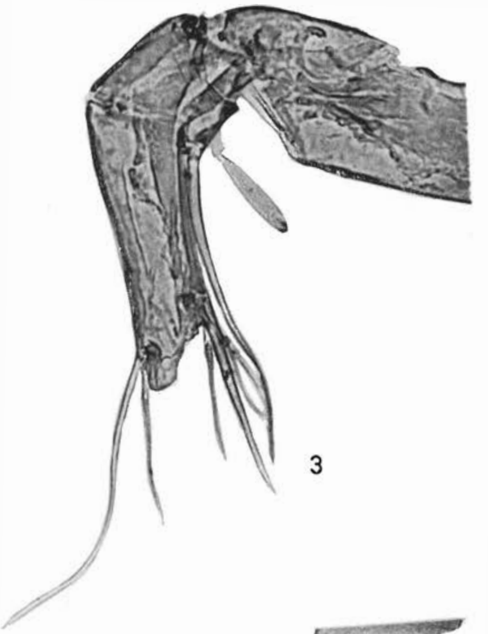
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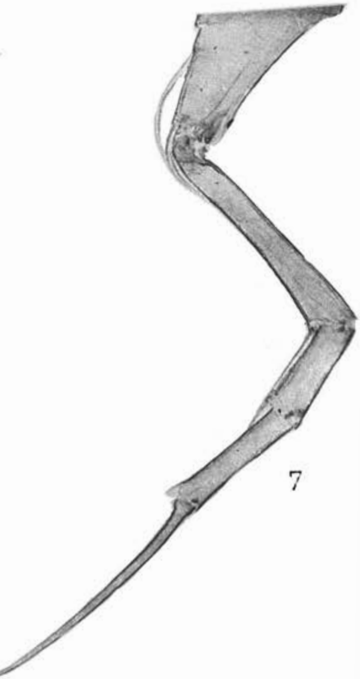
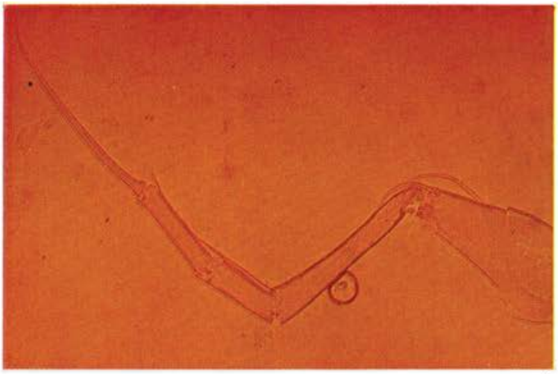

7

Plate VIII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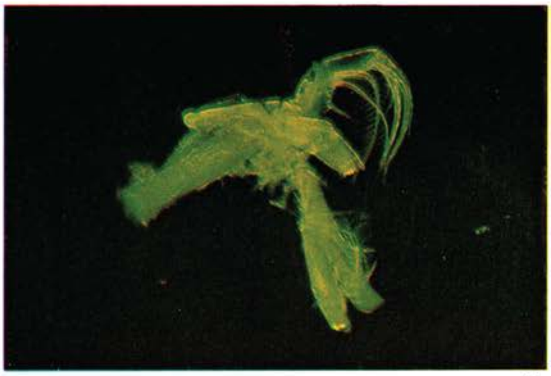
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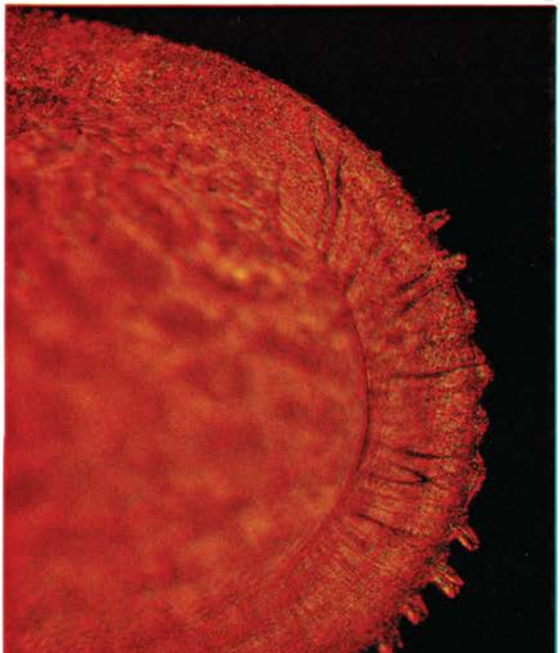
2


4


5


6