Identification of *Heterodera* cysts by terminal and cone top structures

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Detailed examination of the cysts of 39 of the 53 described species of *Heterodera*, a cyst-forming nematode, was undertaken to provide an adequate basis for identification of these species. Taxonomic keys, based on information gained from studies of cone top and terminal areas of the cyst, are presented. Five morphologically distinct groups are recognized based on difference in vulval slit length, fenestral length, underbridge structures, and bullae. Photographs of the structures used to identify each species supplement the keys.

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L'examen détaillé des kystes de 39 des 53 espèces décrites d'*Heterodera*, nématode formant des kystes, examen entrepris dans le but de trouver une base propre a l'identification des espèces, a permis d'établir des clés d'identification fondées sur l'étude de l'extrémité conique et les régions terminales du kyste. On reconnaît cinq groupes morphologiques distincts, différant par la longueur de la fente vulvaire, la longueur de la fenêtre, les structures situées sous le pont et les bullae. Des photographies représentant les structures propres a chaque espèce illustrent les clés d'identification. [Traduit par le journal]

Oostenbrink and den Ouden (1954) were the first to use cone top structures, including fenestra, bullae, and underbridge, in the separation of cyst-forming nematodes. Cooper (1955) provided more detailed information and later Mulvey (1957, 1960), Fenwick (1959), Hesling (1965), and Green (1971) added to this information. Ancillary methods using morphological differences between larvae and males of each species and host plant preference are also used to recognize species. However, the cyst (white female which has been transformed into resistant stage), in many instances containing a few or no larvae, is available to field and laboratory workers for identification. Therefore the following work was undertaken to provide a key based on cyst shape and cone top and terminal structures.

Materials and Methods

There are presently 53 described species of *Heterodera*. Cysts for study were obtained from many countries including Canada, the United States, India, Estonian SSR, England, Ireland, Scotland, Italy, Germany, Austria, Yugoslavia, and Greece. Cysts of the 39 species examined were identified as belonging to these by the author. In all but a few instances designated type material was not available. Eight species from the USSR and three, described by Cooper (1955) were also not available.

Most cysts were fixed in 5% formol. For study the cyst was carefully cut in half, using an eye scalpel, and the contents of the posterior part (cone top) removed as much as possible without damaging the cyst wall. The cone top was then placed in absolute alcohol for about 60 s and subsequently cleared in oil of cloves. Further trimming was done until the cone top was sufficiently small to allow examination under high magnification. Care was taken to maintain the cone top structures intact. The cone top was then transferred to a drop of Canada balsam on a Cobb slide (Cobb slides were used so that both the underside and top side of the cone top could be examined) and gently pushed to the bottom of the drop and a cover slip (circular 10 mm) applied.

Cyst Structures Used for Identification

Fenestra—Thin-walled areas located at the genital end of the cyst (Figs. 1–3). All species have vulval fenestra; *Heterodera punctata* Thorne, 1928 has both vulval and anal fenestra. Fenestration is grouped into three categories, circumfenestrate (Figs. 1, 5, 7), ambifenestrate (Fig. 3), and bifenestrate (Fig. 2). Differences in fenestral length (Fig. 2) are used to separate some species. Generally the circumfenestrate type deteriorates into a hole (Figs. 1, 5) after the cyst has fully matured.

Underbridge—Generally found (Figs. 4, 6) 10–70 μ below the level of fenestra and parallel with the vulval bridge. The underbridge is composed of muscle bands which support the vagina. These bands harden as the female becomes transformed into a cyst. The underbridge, when present, varies in size and shape between the various species. Most of those belonging to group 4 have a very strongly developed underbridge, especially the *H. trifolii* and *H. sacchari*

complexes. Several species, including most of those in group 1, lose their underbridge during transformation of the female to the cyst. The presence or absence of an underbridge and its structure is a reliable character in the identification of species. During the early stages of cyst formation some species have a second underbridge (Fig. 100).

Bullae—These are knob-like, dark brown bodies (Fig. 6) inside the vulval cone, situated either immediately below the fenestral level (as in *H. avenae*) or at the level of and below the underbridge. Bullae vary considerably in size and shape. Some appear as thickenings of the cuticle and are possibly of a different origin to the true bullae. Presence or absence of bullae is also a reliable criterion for separation of certain species.

Basin—The area surrounding the fenestra (Fig. 3) distinctly set off in several species, especially in group 4. It may be used to limited extent in the separation of closely related species.

Vulval bridge and vulval slit—The width of the vulval bridge (Fig. 3) differs significantly in the bifenestrate cone and may be used to identify species of this type. The vulval slit (Figs. 3, 7) length varies from 10 μ to 65 μ and is of significant value in identifying groups.

Cyst size and shape—Cyst size varies considerably and should be used with caution in identification of species. Cyst shape (lemon-shaped, spherical, and pear-shaped) is a fairly reliable criterion of separation. However, one should consider this criterion on the basis of populations rather than on a few or a single cyst.

Posterior protuberance—Essentially the cone top (Fig. 4) and its structures form the posterior protuberance. The species without a cone top are classified as having a terminal area.

B/A ratio—Granek (1955) proposed a fairly sound method of separating cysts of *Heterodera rostochiensis* from those of *H. tabacum*. He used the ratio of anus to vulvar opening distance over the diameter as follows:

$$\frac{\text{distance from anus to nearest edge of vulvar opening}}{\text{diameter of vulvar opening}} \quad \frac{B}{A}.$$

Taxonomy

Heterodera species may be conveniently assigned to one of five groups, as follows.

KEY TO GROUPS OF *Heterodera* SCHMIDT, 1871

1. Cysts without posterior protuberance, mostly rounded or pear-shaped.....Group 1
   Cysts with posterior protuberance, mostly lemon-shaped..... 2
2. Vulval opening very short (6–19 μ)..... 3
   Vulval opening longer (> 30 μ)..... 4
3. Vulval cone circumfenestrate.....Group 2
   Vulval cone bifenestrate.....Group 3
4. Bullae present in all species, small to large, underbridge generally well developed.....Group 4
   Bullae rarely present, underbridge either absent or slender.....Group 5

GROUP 1

Cyst without posterior protuberance, rounded or pear-shaped, vulval slit very short (< 15 μ in length), underbridge rarely present, bullae present or absent, circumfenestrate (Table 1).

Heterodera leptonepia G. S. Cobb and Taylor, 1953

Described by Cobb and Taylor (1953) on the basis of three cysts, of which two contained larvae averaging 567 μ in length. Golden and Ellington (1972) examined these cysts and, in their opinion, *H. leptonepia* is a valid species since it differs to *H. rostochiensis* on cyst wall pattern and B/A ratio (0.4 vs. 2.7–8.9 for *H. rostochiensis*). Because of paucity of material available for study and lack of information on host plant and type locality, identification of this species on cyst characters is very difficult and, therefore, I have not included it in my key.

Type host—Unknown.

Distribution—Possibly Peru or Chile.

Mexican Cyst Nematode
(Figs. 8, 9, 38)

Campos Vela (1967) described and named a new species, *Heterodera mexicana*. However, there has not been a regular publication describing this proposed species and therefore I am in agreement with Golden and Ellington (1972), who consider that this name is unavailable (not properly published) as a specific name. These authors, after examination of the Mexican cyst material, consider it conspecific with *H. virginiae* Miller and Gray, 1968.

Heterodera millefolii Kirjanova and Krall, 1965
(Figs. 23–25, 40)

Described on the basis of one female by Kirjanova and Krall (1965). I have examined a collection (12 cysts, several filled with eggs and larvae) of this species from Estonian SSR, which varies only in size of eggs (85–108 μ × 38–40 μ vs. 122–140 μ × 45–52 μ for Kirjanova and Krall).

Cysts are pear-shaped without posterior protuberance. Bullae-like structures, 4–5 in number, slightly below level of fenestra (10–12 μ depth), anus very close to fenestra, and encircled with cuticular rings (Fig. 25).

Type host—*Achillea millefolium* L. (milfoil or common yarrow).

Distribution—Tallinn, Estonian SSR.

Heterodera punctata Thorne, 1928
(Figs. 1, 26–35, 41–44)

Described by Thorne (1928) on the basis of many cysts. Examination of cysts from many countries reveals considerable variation in this species. Populations from Newfoundland and Saskatchewan, Canada, contained cysts with very large bullae which are seldom found in populations from other parts of the world. Significant variations in the anal–vulval distance and size of these areas were found in exotic populations. This complex may contain at least three very closely related species. Although this species was originally described from wheat roots, it appears that grasses are the most common hosts.

Type host—*Triticum aestivum* L. (wheat and grasses).

Distribution—Many areas in Canada; Europe; United States; and Mexico.

TABLE 1

Heterodera species: measurements, in microns, of cone tops and cysts, group 1

Species	No. tops examined	Fenestra L.	Fenestra W.	B/A ratio	Vulval slit	Cyst size
Mexican cyst nematode	10	16–25	15–20	1.8–3.5 (2.5)	10–11	450–590 × 400–590
millefolii	5	20–28	15–28	1.8–2.2 (2.1)	14	400–500 × 320–420
punctata	100	18–30	18–40	0.9–3.3 (1.9)	—	310–750 × 260–500
rostochiensis England	27	12–35	13–20	1.3–4.3 (2.5)	10–11	—
Canada	100	10–30	12–20	1.2–9.5 (3.7)	10–11	360–650 × 310–550
Belgium	9	12–19	12–20	2.0–4.7 (3.3)	10–11	—
Scotland	11	11–20	12–20	1.7–3.6 (3.5)	10–11	—
solanacearum	11	22–30	18–30	1.3–2.8 (1.7)	10–11	550–630 × 490–600
tabacum	21	22–30	20–25	1.0–2.2 (1.7)	10–11	340–740 × 260–645
virginiae	17	20–30	18–25	2.4–8.9 (3.7)	9–10	560–670 × 460–580

Heterodera rostochiensis Wollenweber, 1923
(Figs. 10–13, 36)

First recorded by Kühn (1881), Wollenweber (1923) was first to recognize this was a distinct species. Green (1971) states that the morphological differences between *H. rostochiensis* pathotypes A, B, E (British notation) are as great as those between described species.

Type host—*Solanum tuberosum* L. (potato).

Distribution—Algeria; Australia; Austria; Argentina; Belgium; Bolivia; Canada; Canary Islands; Chile; Czechoslovakia; Denmark; Egypt; England; Estonia; Finland; France; Faeroe Island; Germany; Guernsey Island; Greece; Holland; Iceland; Italy; Northern Ireland; India; Israel; Japan; Jersey Island; Lebanon; Latvia; Lithuanian Republic; Luxembourg; Mexico; Norway; Peru; Portugal; Panama; Scotland; Spain; Sweden; Switzerland; U.S.A.; USSR; Venezuela; Yugoslavia; Wales.

Heterodera solanacearum Miller and Gray 1972
(Figs. 20–22, 37)

Described by Miller and Gray (1972) on the basis of many cysts. This species differs from others in the group in having a very deeply etched cuticle, especially between the anal and vulval areas.

Type host—*Solanum carolinense* L. (horse nettle).

Distribution—Blacksburg, Va., U.S.A.

Heterodera tabacum Lownsbery and Lownsbery, 1954
Syn. *H. pseudorostochiensis* Kirjanova, 1963
(Figs. 7, 17–19)

Described by Lownsbery and Lownsbery (1954) on basis of a large number of cysts. Separated from *H. rostochiensis* by ratio of anus to fenestral edge over the fenestral length (Mulvey 1960).

Type host—*Nicotiana tabacum* L. (tobacco).

Distribution—Hazardville, Connecticut, U.S.A.; and USSR.

Heterodera virginiae Miller and Gray, 1968
(Figs. 14–16, 39)

Described by Miller and Gray (1968) on population of many cysts, the characteristic fenestra and maze-like pattern between anus and fenestra separate it from other species in this group. The shingle-like effect (Fig. 14) was observed in a few of the younger cysts which I examined but not in any of the mature cysts and, therefore, is not a reliable taxonomic character.

Type host—*Solanum carolinense* L. (horse nettle).

Distribution—Suffolk, Virginia, U.S.A.

KEY TO SPECIES OF GROUP 1

1. Vulval and anal fenestra of nearly equal size ..... *punctata*
   Vulval fenestra much larger than anal area 2
2. Anal area surrounded by cuticular rings ..... *millefolii*
   Anal area not surrounded by cuticular rings but generally of typical "V" formation 3
3. Fenestral length/anal–fenestral edge distance average 1.7 (1.0–2.8) 4
   Fenestral length/anal–fenestral edge distance average 2.5–3.7 (range 1.3–9.5) 5
4. Cuticle between anus and vulval fenestra very heavily etched ..... *solanacearum*
   Cuticle between anus and vulval fenestra moderately etched ..... *tabacum*
5. Pattern of lines between anus and vulva maze-like ..... *virginiae*
   Pattern of lines between anus and vulva not maze-like ..... *rostochiensis*

Discussion—Separation of closely related species in this group, viz. *H. solanacearum*, *H. tabacum*, *H. rostochiensis*, and *H. virginiae* on terminal area differences is sometimes difficult. The cuticular pattern between the vulval fenestra and anus is a fairly reliable criterion but should be used with some caution and only when comparing populations. Green (1971), using a stereoscan electron microscope, provided valuable information for the separation of these closely related species.

GROUP 2

Cyst with posterior protuberance, spherical to lemon-shaped, vulval slit short (<20 μ long), generally circumfenestrate, bullae present or absent, underbridge absent (Table 2).

Heterodera betulae Hirschmann and Riggs, 1969

(Figs. 45–47, 56)

Described by Hirschmann and Riggs (1969) on the basis of many cysts. The characteristic pattern (Fig. 45) of the vulval area in the white female during early stages of fenestration is a good distinguishing feature.

Like other species of this group, the fenestra deteriorate as the cyst matures.

Type host—*Betula nigra* L. (river birch).

Distribution—East of Fayetteville, Arkansas, U.S.A.

Heterodera cacti Filipjev and Schuurmans Stekhoven, 1941

(Figs. 5, 48, 49, 52)

First described by Adam (1932) on the basis of large population of cysts.

Type hosts—Cacti.

Distribution—Algeria; Austria; Australia; Argentina; Czechoslovakia; England; France; Germany; Holland; Italy; Israel; Japan; Malta; Mexico; U.S.A.; USSR.

Heterodera estonica Kirjanova and Krall, 1963

(Figs. 50, 51, 55)

Described on the basis of 12 cysts by Kirjanova and Krall (1963), who placed it near *H. methwoldensis* Cooper, 1955. My studies indicate that *H. estonica* is close to *H. weissi* Steiner, 1949 but differs to this species in cyst shape and presence of small scattered bullae in mature cysts.

Type host—Unknown, possibly *Polygonum aviculare* L. (pigweed).

Distribution—Estonia (by Kirjanova and Krall); Poland; Yugoslavia; Turkey (new records from these countries).

Heterodera weissi Steiner, 1949

(Figs. 53, 54)

Described by Steiner (1949) on the basis of many cysts and by Tarjan and Sasser (1953), who provided more detailed information.

Type host—*Polygonum pennsylvanicum* L. (knotweed).

Distribution—Beltsville, Maryland, U.S.A.; Ontario and Quebec, Canada.

TABLE 2

Heterodera species: measurements, in microns, of cone tops and cysts, group 2

Species	No. tops examined	Fenestra L.	Fenestra W.	Vulval slit	Cyst size
betulae	15	25–35	25–35	7–8	600–780 × 550–670
cacti	15	20–40	18–30	15–19	430–450 × 400–420
estonica	20	18–30	20–28	—	600–1000 × 400–600
weissi	15	20–28	15–20	15–19	320–576 × 220–540

KEY TO SPECIES OF GROUP 2

1. Cysts lemon-shaped, generally twice as long as wide. Mature cysts with small scattered bullae.....*estonica*
   Cysts lemon-shaped to nearly spherical, slightly longer than wide, bullae absent..... 2
2. Circumfenestral area without cuticular punctations.....*betulae*
   Circumfenestral area with cuticular punctations..... 3
3. Cysts spherical, cuticular punctations small.....*cacti*
   Cysts mostly lemon-shaped, cuticular punctations large.....*weissi*

Discussion—Species of this group are closely related and difficult to separate on the basis of cone top structures since these are generally absent. Small scattered bullae are found in mature cysts of *H. estonica*, which differs significantly from others in the group on the basis of cyst shape. The fenestral area of *H. betulae* during late female stage is significantly different from other species. Variation in host plant and larval characters should be considered if these are available.

GROUP 3

Cyst with posterior protuberance, lemon-shaped, vulval slit short (<16 μ long), bifenestrate, bullae and underbridge present or absent (Table 3).

Heterodera avenae Wollenweber, 1924
(Figs. 57–59)

First recorded by Kühn (1874) in Germany and later described in detail by several workers, including Schmidt (1930) and Franklin (1945, 1951).

Type host—*Avena sativa* L. (oats).

Distribution—Australia; Belgium; Ontario, Canada; England; Denmark; Holland; India; Israel; Japan; Morocco; Norway; Germany; Sweden; USSR.

Heterodera major var. *arenaria* Cooper, 1955

Described by Cooper (1955) on cysts obtained from twitch marrow and other grasses, and distinguished from *H. avenae* in having thinner cyst wall and more slender and diffuse bullae. Probably a race of *H. avenae* and, since varieties have no nomenclatural status, this taxon is hereby placed in *species inquirendae*.

Heterodera bifenestra Cooper, 1955
(Fig. 60)

Cooper (1955) described and illustrated this species. I have identified specimens from Holland, Belgium, and Germany as belonging to this species.

Type host—Unknown, probably grasses.

Distribution—England (Cooper); Holland; Belgium; Germany (new records for Holland, Belgium, and Germany).

Heterodera iri Matthews, 1971
(Figs. 129, 130)

Described by Matthews (1971*b*) on the basis of many cysts characterized by heavy bullae and short underbridge, which was present in most of the cone tops I examined. Cysts are lemon-shaped and much lighter in color than either *H. avenae* or *H. mani*.

Type host—*Agrostis tenuis* Sibth. (brown top grass).

Distribution—Draperstown, Northern Ireland.

Heterodera latipons Franklin, 1969
(Figs. 61–64, 68)

Described by Franklin (1969) on the basis of many cysts. Differs significantly from other species in this group in having a very large

TABLE 3

Heterodera species: measurements, in microns, of cone top structures, group 3

Species	No. tops examined	Fenestra		Vulval bridge width	Underbridge			Vulval slit	Bullae
		L.	W.		Depth	L.	W.		
avenae	200	43–44	21–23	6–8	—	—	—	10–13	Heavy
bifenestra	55	37–45	20–25	5–7	—	—	—	10–12	None–few
iri	15	32–40	15–23	6–8	13–16	35–50	10–16	12	Heavy
latipons	25	52–72	15–20	18–39	24–25	70–120	20–28	6–16	None–few
mani	15	43–55	22–28	5–8	—	—	—	12–13	Heavy
turcomanica (after Kirjanova and Shagalina 1965)	—	71	18–24	35	—	—	14	9–14	Many
ustinovi	8	30–48	20–28	6–12	—	—	—	10–13	Heavy

underbridge and apparent lack of bullae. *H. turcomanica* is similar in fenestral structures and vulval bridge width but lacks large underbridge.

Type host—*Triticum aestivum* L. (wheat).

Distribution—Gilat (Israel), Azzahra (Tripoli), and Bulgaria (reported by Franklin 1969); Scotland; Prince Edward Island, Canada; Poland; Greece (new records from Canada, Poland, and Greece).

Heterodera mani Matthews, 1971
(Figs. 127, 128)

Matthews (1971*b*) described this species on basis of many cysts. He placed this species close to *H. avenae* although it differs in cyst shape and in having a distinct bifurcated underbridge. I have examined cone tops of *H. mani* and found no underbridge, although this structure may be present in newly formed cysts and lost during preparation.

Type host—*Lolium perenne* L. (perennial rye grass).

Distribution—Magilligan, Northern Ireland.

Heterodera turcomanica Kirjanova and Shagalina, 1965

Described by Kirjanova and Shagalina (1965) on the basis of about 10 cysts. No larvae measurements were reported and very little information was given about the underbridge except that it was distinct in one specimen.

Type host—Possibly *Chenopodium album* L. (white goosefoot).

Distribution—Ashkhabad area, Turkmenian SSR.

Heterodera ustinovi Kirjanova, 1969
(Figs. 65–67, 69)

Described by Kirjanova (1969) on the basis of 10 females. Most of description was based on white females and very little information given on cyst structures. Kirjanova considered this species to be close to *H. weissi* but subsequent examination of cysts by the author revealed closer affinity to *H. avenae*.

Type host—*Agrostis vulgaris* With. (bent grass).

Distribution—The Beskids, eastern part of Eastern Carpathians, USSR.

KEY TO SPECIES OF GROUP 3

1. Semifenestra widely separated, vulval bridge 18–39 μ wide 2
   Semifenestra not widely separated, vulval bridge < 18 μ wide 3
2. Bullae strongly developed ..... *turcomanica*
   Bullae few or absent ..... *latipons*
3. Bullae few or absent ..... *bifenestra*
   Bullae strongly developed 4
4. Underbridge present ..... *iri*
   Underbridge absent ..... *avenae*
   ..... *mani*
   ..... *ustinovi*

Discussion—Separation of *H. mani* and *H. ustinovi* from *H. avenae* on the basis of cone top structures is unreliable. These species are probably physiological races of *H. avenae*.

GROUP 4

Cysts with posterior protuberance, lemon-shaped to spherical, vulva slit long (> 35 μ), underbridge and bullae generally strongly developed, ambifenestrate (Table 4).

Heterodera cajani Koshy, 1967
(Figs. 70, 71, 102)

Described by Koshy (1967; Koshy *et al.* 1971) on the basis of a large number of cysts. Characterized by rather small cysts and very large egg sac, sometimes three times cyst volume.

Type host—*Cajanus cajani* (L.) Millsp. (pigeon pea).

Distribution—New Delhi area, India.

Heterodera fici Kirjanova, 1954
(Figs. 72–76, 105)

Described by Kirjanova (1954) on the basis of many cysts. Several authors indicate that *H. fici* is closely related morphologically to *H. humuli*. I have examined populations of both from various countries and, on the basis of fenestration, *H. fici* is ambifenestrate while *H. humuli* is generally bifenestrate, and since

bullae are present in many cysts of *H. fici* but seldom in *H. humuli*, I regard these as distinct species.

Type host—*Ficus elastica* Roxb. (rubber plant).

Distribution—Australia; South Africa; Germany; California, U.S.A.; USSR.

Heterodera galeopsidis Goffart, 1936
(Figs. 77, 78)

Described by Goffart (1936) on the basis of many cysts. Characterized by heavy bullae and underbridge.

Type host—*Galeopsis tetrahit* L. (common hemp nettle).

Distribution—England and Germany.

Heterodera glycines Ichinohe, 1952
(Figs. 79, 80, 100)

Described by Ichinohe (1952) on basis of large population. Hirschmann (1956) did a detailed study of this species and compared it with *H. trifolii*. She concluded there was very little difference in cyst structures between these two species. Characterized by heavy bullae and strongly developed underbridge. My examinations of young cysts have revealed a second underbridge in several young cysts.

Type host—*Glycine max* Merr. (soybean).

Distribution—Hokkaido, Honshu, Skikoku, and Kyushu Islands, Japan; North Carolina, Mississippi, Arkansas, Kentucky, Missouri, Tennessee, and Virginia, U.S.A.; possibly Korea and Manchuria, China.

Heterodera lespedezae Golden and G. S. Cobb, 1963
(Figs. 81, 82)

Described by Golden and Cobb (1963) on the basis of many cysts. Characterized by heavy bullae and strong underbridge.

Type host—*Lespedezae striata* Hook. (*Kobe lespedezae*).

Distribution—Union County, North Carolina, U.S.A.

Heterodera leuceilyma Di Edwardo and Perry, 1964
(Figs. 83, 84, 107)

Di Edwardo and Perry (1964) described this species on the basis of many cysts. Characterized by heavy underbridge with projecting finger-like structures and absence of heavy peripheral bullae inside the cone top.

TABLE 4

Heterodera species: cone top measurements, in microns, group 4

Species	No. tops examined	Fenestra		Vulval slit	Underbridge		
		L.	W.		L.	W.	Depth
cajani	10	38–45	28–31	48–50	70–80	20–25	22–30
fici	50	45–68	22–40	35–60	53–75	15–20	20–25
galeopsidis	50	41–46	31–38	40–50	80–100	15–25	37–40
glycines	50	38–62	32–52	45–60	70–100	15–28	35–37
lespedezae	10	45–62	35–43	50–55	90–115	16–28	30–35
leuceilyma	40	48–50	38–40	50–65	100–140	50–80	45–54
limonii (after Cooper)	—	80	58	60	140	7	—
oryzae	10	40–55	32–45	42–50	110–150	52–70	33–38
oxiana (after Kirjanova)	—	60	48	50	100	—	—
paratrifolii (after Kirjanova)	—	50–55	48–50	50	—	—	—
rosii	10	48–56	40–46	45–53	110–130	20–30	43–62
rumicis (after Poghossian)	—	34–58	31–41	51–64	100	20	—
sacchari	25	45–55	35–45	50–52	100–150	50–70	22–28
salixophila	7	28–30	28–30	44–45	85–110	15–25	30–32
schachtii	200	24–38	18–30	35–46	70–100	18–25	30–38
scleranthi (after Kaktina)	—	40–50	30–35	50	—	—	—
tadshikistanica (after Kirjanova)	—	52	42	42	140	5	10–20
trifolii	200	40–58	30–48	39–50	80–100	20–28	33–38
vigni	10	23–35	20–26	40–42	40–50	10–12	28–30
zeae	10	42–45	22–25	38–46	40–50	10–12	25–26

Type host—*Stenotaphrum secundatum* (Walt.) Kuntze (St. Augustine grass).
Distribution—West Palm Beach, Florida, U.S.A.

Heterodera limonii Cooper, 1955

Cysts described by Cooper (1955) as being with acute cone, with long, sheaf-like vagina, strongly chitinized vulval bridge, with underbridge and bullae. Closely related to *H. trifolii*.
Type host—*Limonium* sp. (sea lavender).
Distribution—England.

Heterodera oryzae Luc and Brizuela, 1961 (Figs. 85, 86)

Described on the basis of many cysts by Luc and Brizuela (1961). Characterized by having heavy underbridge with finger-like projections and few peripheral bullae inside the cone top.
Type host—*Oryzae sativa* L. (rice).
Distribution—Village of Bokakouamékno 40 km east of Bouaké, Ivory Coast.

Heterodera oxiana Kirjanova, 1962

Described by Kirjanova (1962) on the basis of several cysts. According to Kirjanova, *H. oxiana* differs from other closely related species in having two underbridges. Mulvey (1959) and in present paper (see *H. glycines*) found two underbridges in *H. trifolii* and *H. glycines*. *H. oxiana* is probably a synonym of *H. trifolii*.
Type host—*Alhagi persarum* Boiss and Buhse.
Distribution—Kungard region of Kara-Kalpakia, USSR.

Heterodera paratrifolii Kirjanova, 1963

Described by Kirjanova (1963). Vulval bridge weakly chitinized, width of fenestra significantly greater than length. Appears to differ from *H. trifolii* in fenestral measurements. Description in key only with illustrations of cysts and fenestra. No information given on larvae or eggs.
Type host—?
Distribution—USSR.

Heterodera rosii Duggan and Brennan, 1966 (Figs. 3, 89–90, 104)

Duggan and Brennan (1966) described this species on the basis of many cysts. Cyst shape and depth of underbridge vary significantly with related species.
Type host—*Rumex crispus* L. (curled dock).
Distribution—Rush County, Dublin, Ireland.

Heterodera rumicis Poghossian, 1961

Described by Poghossian (1961) on the basis of many cysts. Very closely related to *H. trifolii*, from which separation on the basis of cone top structures and cyst shape is unreliable. Further study required to determine validity of this species.
Type hosts—*Rumex alpinus* L. and *Rumex crispus* L. (curled dock).
Distribution—Armenian SSR.

Heterodera sacchari Luc and Merny, 1963 (Figs. 87, 88, 103)

Described by Luc and Merny (1963) on the basis of many cysts. Characterized in having a strongly developed underbridge with finger-like projections and few peripheral bullae in the cone top.
Type host—*Saccharum officinale* L. (sugarcane).
Distribution—Jacob, Congo-Brazzaville.

Heterodera salixophila Kirjanova, 1969 (Figs. 91, 92, 106)

Kirjanova (1969) described this species mainly on the basis of the white female. She does not present illustrations of either the fenestral or underbridge structures of the cyst. My examination of cysts revealed a medium-sized underbridge with peripheral bullae in the cone top. The fenestra are low and rounded, about as wide as long. This species differs from others in this group in shape and length of fenestra.
Type host—*Salix purpurea* L. (willow).
Distribution—Coast of Kurisch Haff of Baltic Sea near port in area of Biological Station of Zin, USSR, in Rybachy.

Heterodera schachtii Schmidt, 1871 (Figs. 93, 94)

First discovered by Schacht (1859). Schmidt (1871) erected the genus *Heterodera* and named the species *H. schachtii* in honor of Schacht. Since then several workers have described the

structure of the cyst. Oostenbrink and den Ouden (1954) presented the first description of the cone top structures. Although Cooper (1955) disagrees, I agree with Oostenbrink that *H. schachtii* can be separated from *H. trifolii* on the basis of fenestral length. In addition, the characteristic anal bullae (see Fig. 94) found in many of the cysts examined is of significance in identifying *H. schachtii*.

Type host—*Beta vulgaris* L. (sugar beet).

Distribution—Australia; Belgium; Canada; Denmark; England; France; Finland; Germany; Holland; Israel; India; Sweden; Spain; South Africa; U.S.A.; USSR; Wales; West Pakistan.

Heterodera scleranthi Kaktina, 1957

Described by Kaktina (1957) and original illustrations of cyst and fenestra published by Kirjanova (1963). Because of inadequate description of the underbridge and cone top structure, this species is placed in *species inquirendae*. It is apparently close to the *H. trifolii* complex.

Type host—*Scleranthus annuus* L. (knawel).

Distribution—Latvia.

Heterodera tadshikistanica Kirjanova and Ivanova, 1966

Described by Kirjanova and Ivanova (1966) on the basis of several cysts. Characterized by very thin vulval bridge, dense circle of bullae close to fenestral level, and very long, thin underbridge.

Type host—Possibly *Cousinia microcarpa*.

Distribution—Near Dushanbe, Tadzhikistan SSR.

Heterodera trifolii Goffart, 1932 (Figs. 4, 6, 95, 96)

First described by Goffart (1932). Several workers have carried out intensive studies of the cone top structures and underbridge. Characterized by having very heavy underbridge, peripheral bullae, and high fenestral length.

Type host—*Trifolium pratense* (red clover).

Distribution—Australia; Canada; Europe; England; Hawaii; Israel; India; U.S.A.

Heterodera vigni Edward and Misra, 1968 (Figs. 99, 101)

Described by Edward and Misra (1968). Examination of cone tops and cysts indicates its close relationship to *Heterodera cajani*.

Type host—*Vigna sinensis* (cowpea).

Distribution—India.

Heterodera zeae Koshy, Swarup, and Sethi, 1971 (Figs. 97, 98, 108)

Described on the basis of many cysts by Koshy *et al.* (1971). Characterized by rounded cyst and short underbridge.

Type host—*Zea mays* L. (maize).

Distribution—Chapli, District Udaipur, Rajasthan, India.

KEY TO SPECIES OF GROUP 4

1. Underbridge massive, with dorsoventral finger-like projections, bullae few or none on peripheral wall of cone 2
   Underbridge weakly to strongly developed without dorsoventral finger-like projections, bullae few to many on peripheral wall of cone 3
2. Underbridge at depth of 22–28 μ below fenestral level ..... *sacchari*
   Underbridge at depth of 33–54 μ below fenestral level ..... *leucellyma* *oryzae*
3. Cysts spherical, posterior protuberance short 4
   Cysts lemon-shaped, posterior protuberance long-short 5
4. Underbridge very short 40–50 μ ..... *zeae*
   Underbridge longer 85–110 μ ..... *salixophila*
5. Anal bullae distinctly molar-shaped (see Fig. 94) ..... *schachtii*
   Anal bullae without characteristic shape 6
6. Underbridge depth 22–30 μ, length 50–80 μ 7
   Underbridge depth 30–62 μ, length 70–130 μ 9

7. Bullae small, scattered, fenestral length range 45–68 μ ..... *fici*
   Bullae large, many, fenestral length range 23–45 μ 8

8. Fenestral length 23–35 μ ..... *vigni*
   Fenestral length 38–45 μ ..... *cajani*

9. Underbridge very long and thin (140 × 5–7 μ) 10
   Underbridge shorter (80–130 μ), generally heavy (15–30 μ wide) 11

10. Vulval bridge very thin (4–5 μ), fenestra 52 × 42 μ ..... *tadshikistanica*
    Vulval bridge wider (15 μ), fenestra 80 × 58 μ ..... *limonii*

11. Bullae in form of strobiloid protrusions ..... *rumicis*
    Bullae not in form of strobiloid protrusions 12

12. Underbridge depth 43–62 μ ..... *rosii*
    Underbridge depth 33–38 μ 13

13. Body length second-stage larvae 430–547 (average 500) μ, stylet length 25–30 (av. 28) μ ..... *trifolii*
    Body length second-stage larvae 396–522 (average 445) μ, stylet length 22–24 μ ..... *galeopsidis*
    ..... *glycines*

Discussion—Several species in this group are closely related, viz. *H. galeopsidis*, *H. glycines*, *H. rosii*, *H. rumicis*, and *H. trifolii*, and are extremely difficult to separate on cyst shape and vulval cone structures. Body and stylet lengths of second-stage larvae may be used if available. Body lengths of *H. rosii*, *H. rumicis*, and *H. trifolii* are 430–662 μ with average of 500–550 μ; stylet length 25–33 μ with average 29 μ. Body lengths of *H. galeopsidis* and *H. glycines* are 396–522 μ with average of 445 μ; stylet length of 22–24 μ.

Fenestra in *H. leuceilyma*, *H. oryzae*, and *H. sacchari* were rather obscurely demarcated in all the tops examined. However, the underbridge structures were distinct in most of the tops.

GROUP 5

Cyst with posterior protuberance, lemon-shaped or spherical; vulval slit long (>30 μ), underbridge absent, or, when present, slender; bullae, when present, scattered and small, ambifenestrate or bifenestrate (Table 5).

TABLE 5

Heterodera species: measurements, in microns, of cone tops and cysts, group 5

Species	No. tops examined	Fenestra L.	Fenestra W.	Vulval slit	Underbridge L.	Underbridge W.	Cyst size	Cyst shape
cardiolata (after Kirjanova)	—	51–60	30–39	40–45	Short	Thin	345–655× 210–677	Lemon-heart shaped
carotae	20	34–40	38–40	45–50	—	—	340–520× 340–450	Nearly spherical
cruciferae	50	20–38	30–50	45–55	90–110	12–33	380–500× 300–400	Nearly spherical
cyperi	10	27–35	20–28	30–35	40–60	10–12	410–450× 270–300	Lemon-shaped
goettingiana	10	40–50	30–45	43–50	90–100	10–18	400–700× 310–540	Lemon-shaped
graminis	10	45–60	25–45	40–48	70–100	10–35	490–630× 400–590	Lemon-spherical
humuli	50	40–65	18–35	32–45	40–70	6–15	400–490× 320–410	Lemon-shaped
mothi	10	33–40	30–38	38–46	55	10	500–620× 330–440	Lemon-shaped
polygoni (after Cooper)	—	—	—	—	—	—	—	Lemon-shaped
urticae	16	32–35	38–40	44–45	—	—	430–520× 390–500	Nearly spherical

Heterodera cardiolata Kirjanova and Ivanova, 1969

Described by Kirjanova and Ivanova (1969) on the basis of many cysts. Characterized by long fenestra and heart-shaped cysts.

Type host—*Cynodon dactylon* (L.) Pers. (Bermuda grass).

Distribution—Vicinity of Dusanbe, Tadzhikistan SSR.

Heterodera carotae Jones, 1950 (Figs. 109, 125)

Jones (1950) described this species on large populations of cysts. Characterized by very thin vulval bridge which is generally broken. Fenestra deteriorate rapidly as cyst matures.

Type host—*Daucus carota* L. (carrot).

Distribution—Chatteris, England; Italy; Holland.

Heterodera cruciferae Franklin, 1945 (Figs. 110, 112, 123)

Described by Franklin (1945) on basis of many cysts. Characterized by nearly spherical cysts and very low, wide fenestra. Females generally have a very large gelatinous egg sac. I have carefully examined at least 50 cone tops and in about 75% of these an underbridge was present. However, no bulla was found.

Type host—*Brassica oleracea* L. (cabbage).

Distribution—England; Wales; Belgium; Holland; California, U.S.A.; USSR (possibly); Yugoslavia.

Heterodera cyperi Golden, Rau and G. S. Cobb, 1962 (Figs. 111, 114, 124)

Described by Golden *et al.* (1962) on population of many cysts. Differs from other species in this group on basis of low fenestral length and width.

The underbridge, although flimsy and short, was present in most of the cysts I examined.

Type host—*Cyperus esculentus* L. (yellow nut grass).

Distribution—Central Florida Experimental Station, Sanford, Florida, U.S.A.

Heterodera goettingiana Liebscher, 1892 (Figs. 113, 115)

Described and named by Liebscher (1892). Distinct from other species in this group by having a brick-like pattern around fenestra. All the specimens I examined had a long, thin underbridge in the young cysts, somewhat heavier in the older cysts. A few scattered bullae were found in the older cysts.

Type host—*Pisum sativum* L. (garden pea).

Distribution—Holland; England; France; Germany; USSR.

Heterodera graminis Stynes, 1971 (Figs. 131, 132)

Described by Stynes (1971) on the basis of many cysts. Prominent underbridge but no bullae.

Type host—*Cynodon dactylon* (L.) Pers. (pasture grass).

Distribution—Newcastle, N.S.W., Australia.

Heterodera humuli Filipjev, 1934 (Figs. 2, 116, 117)

First described by Voigt (1894), then by Percival (1895), and later named *Heterodera humuli* by Filipjev (1934). Differs from other species in this group by having widely spaced semifenestra (bifenestrate). Underbridge light, present in about 60% of cysts examined. Bullae absent.

Type host—*Humulus lupulus* L. (Hop.).

Distribution—Southern England; Australia; British Columbia, Canada; U.S.A.; South Africa; Belgium; Germany; Israel; USSR; Holland; Switzerland; Greece; New Zealand.

Heterodera mothi Khan and Husain, 1965 (Figs. 118, 119, 121)

Described by Khan and Husain (1965) on basis of many cysts. Characterized by relatively low fenestral length and vulval slit length. Khan and Husain state that the bullae are prominent, in the vulval cone. However, in the cones which I examined, only one had a few scattered bullae and the underbridge was rarely present. In my opinion this species differs significantly from the *H. schachtii* group in lack of prominent bullae and underbridge.

Type host—*Cyperus rotundus* L. (nut grass).
Distribution—University Campus, Aligarh, U.P., India.

Heterodera polygoni Cooper, 1955

Cooper (1955) described this species in his key. No new information has been provided since then and, therefore, I propose placing this species in *species inquirendae* until more material is available for assessing its true relationship with other species in this genus.

Type host—*Polygonum* sp., *Chenopodium* sp., etc. (weeds).
Distribution—England.

Heterodera urticae Cooper, 1955
(Figs. 120, 122)

Described first by Cooper (1955) and later in greater detail by Matthews (1971*a*), who bases his redescription on preserved specimens supplied by Cooper from his original collection and also collections from Northern Ireland. Characterized by nearly spherical cysts, bullae few and very small, underbridge seldom present, flimsy; fenestra in older cysts obscure.

Type host—*Urtica dioca* L. (stinging nettle).
Distribution—England; Northern Ireland; Armenian SSR.

KEY TO SPECIES OF GROUP 5

1. Semifenestra separated by wide vulval bridge (bifenestrate, see Fig. 2), fenestra generally more than twice as long as wide ..... *humuli*
   Semifenestra separated by narrow to medium-wide vulval bridge (ambifenestrate, see Fig. 3), fenestra generally slightly longer than wide 2
2. Underbridge rarely present 3
   Underbridge mostly present 4
3. Cysts lemon-shaped ..... *mothi*
   Cysts nearly spherical-shaped ..... *carotae*
   ..... *urticae*
4. Fenestral arch very low, length/width > 2 ..... *cruciferae*
   Fenestral arch high, length/width < 1.5 5
5. Circumfenestral area (basin) with brick-like pattern ..... *goettingiana*
   Circumfenestral area without brick-like pattern 6
6. Underbridge long (70–100 μ), strongly developed ..... *graminis*
   Underbridge short (40–60 μ), flimsy 7
7. Cysts heart-shaped, fenestral length 51–60 μ ..... *cardiolata*
   Cysts lemon-shaped, fenestral length 27–35 μ ..... *cyperi*

Discussion—*Heterodera carotae* and *H. mothi* are very similar in cyst shape and cone top structures. In addition, larvae length, egg size, and spear length are alike.

H. indocyperi Husain and Khan, 1964, for which sufficient information is not available to include it in the key, may belong to this group.

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EXPLANATION OF FIGURES

FIGS. 1–7. Fenestrated cone tops, terminal areas, and underbridge of *Heterodera* spp.: (1) circumfenestrate, *H. punctata*; (2) bifenestrate, *H. humuli*; (3) ambifenestrate, *H. rosii*; (4, 6) underbridge and bullae, *H. trifolii*; (5, 7) circumfenestrate, *H. cacti* and *H. tabacum*.

ABBREVIATIONS: AF, anal fenestra; B, bullae; BS, basin; F, fenestra; FL, fenestral length; SF, semi-fenestra; UB, underbridge; V, vulva; VA, vagina; VB, vulval bridge; VF, vulval fenestra; VS, vulval slit.

FIGS. 8–16. Group 1. Terminal areas showing vulval slit, fenestra, and anus: (8–9) Mexican cyst nematode; (10–13) *H. rostochiensis* from England, Newfoundland, Newfoundland, and British Columbia, respectively; (14–16) *H. virginiae*, note shingle effect in Fig. 14. (Figures same magnification except Figs. 9, 11, and 15, which are lower.)

FIGS. 17–25. Group 1. Terminal areas: (17–19) *Heterodera tabacum*; (17, 18) mature cysts; (19) young cyst; (20–22) *H. solanacearum*; (23–25) *H. millefolii*; (23) note bullae-like structures; (25) anus with cuticular rings. (Figures same magnification except 17, 20, 23, and 24, which are lower.)

FIGS. 26–35. Group 1. *Heterodera punctata*, terminal areas: (26–28) from Saskatchewan, Canada; (29) from Newfoundland, Canada; (30) from Holland; (31, 34) from Ontario, Canada; (32) from England; (33) from Belgium; (35) from Austria. (All figures same magnification.)

FIGS. 36–40. Group 1. Mature cysts: (36) *Heterodera rostochiensis*; (37) *H. solanacearum*; (38) Mexican cyst nematode; (39) *H. virginiae*; (40) *H. millefolii*. (All figures same magnification.)

FIGS. 41–44. Group 1. *Heterodera punctata* mature cysts: (41) from Lebanon; (42) from Saskatchewan, Canada; (43) from England; (44) from Ontario, Canada. (All figures same magnification.)

FIGS. 45–51. Group 2. Fenestral areas: (45–47) *Heterodera betulae*; (45) from very young cyst with intact vulval slit and circumfenestra; (46, 47) from mature cyst; (48, 49) *Heterodera cacti*, showing punctations around aperture; (50, 51) *Heterodera estonica*; (51) lower level, showing bullae-like structures. (Figures same magnification except 45, which is higher.)

FIGS. 52–56. Group 2. Mature cysts and fenestral areas: (52) *Heterodera cacti*; (53, 54) *Heterodera weissi*; (54) note heavy cuticular punctations; (55) *H. estonica*; (56) *H. betulae*. (Cysts at same magnification.)

FIGS. 57–64. Group 3. Cone top structures and underbridge: (57–59) *Heterodera avenae*; (57) fenestra, from Ontario, Canada; (58) fenestra, from Germany; (59) bullae, from Ontario, Canada; (60) *H. bifenestra* from Holland; (61–64) *H. latipons*; (61) underbridge, from Prince Edward Island, Canada; (62) fenestra, from Prince Edward Island, Canada; (63, 64) fenestra with wide vulval bridge between, from Italy. (All figures at same magnification.)

FIGS. 65–69. Group 3. Cone top structures and cysts: (65–67) *Heterodera ustinovi*; (65) fenestra, mature cyst; (66) vulval slit mature female; (67) bullae; (68) *H. latipons*, mature cyst from Italy, note heavy underbridge; (69) *H. ustinovi*, mature cyst. (Cysts same magnification, other figures same except 67, which is higher.)

FIGS. 70–76. Group 4. Fenestra, bullae, and underbridges: (70, 71) *Heterodera cajani*; (72–76) *H. fici*; (72) fenestra, California, U.S.A.; (73) fenestra, Italy; (74) fenestra, Argentine; (75) underbridge, California, U.S.A.; (76) underbridge, Argentine. (All figures same magnification.)

FIGS. 77–82. Group 4. Fenestra, bullae, and underbridges: (77, 78) *Heterodera galeopsidis*; (79, 80) *H. glycines*; (81, 82) *H. lespedezae*. (All figures same magnification.)

FIGS. 83–88. Group 4. Fenestra and underbridges; note finger-like projections: (83, 84) *Heterodera leuceilyma*; (85, 86) *H. oryzae*; (87, 88) *H. sacchari*. (All figures same magnification.)

FIGS. 89–94. Group 4. Fenestra, underbridges, and bullae. (89, 90) *Heterodera rosii*; (91, 92) *H. salixophila*; (93, 94) *H. schachtii*; (94) note large molar-like anal bulla. (All figures same magnification.)

FIGS. 95–101. Group 4. Fenestra, underbridges, and bullae: (95, 96) *Heterodera trifolii*; (97, 98) *H. zeae*; (99, 101) *H. vigni*; (100) *H. glycines*, note second underbridge. (All figures same magnification.)

FIGS. 102–105. Group 4. Mature cysts: (102) *Heterodera cajani*; (103) *H. sacchari*; (104) *H. rosii*; (105) *H. fici*.

FIGS. 106–108. Group 4. Mature cysts: (106) *Heterodera salixophila*; (107) *H. leuceilyma*; (108) *H. zeae*.

FIGS. 109–116. Group 5. Fenestra and underbridges: (109) *Heterodera carotae*; (110, 112) *H. cruciferae*; (111, 114) *H. cyperi*; (114) note very flimsy underbridge; (113, 115) *H. goettingiana*; (116) *H. humuli*, older cyst, see Fig. 2, younger cyst. (All figures same magnification.)

FIGS. 117–122. Group 5. Fenestra, underbridges, and cysts: (117) *Heterodera humuli*; (118, 119) *H. mothi*; (120) *H. urticae*; (121) *H. mothi*; (122) *H. urticae*. (Cysts same magnifications; others same magnification.)

FIGS. 123–126. Group 5. Mature cysts: (123) *Heterodera cruciferae*; (124) *H. cyperi*; (125) *H. carotae*; (126) *H. humuli*.

FIGS. 127–130. Group 3. Fenestra and bullae: (127, 128) *Heterodera mani*; (129, 130) *H. iri*. (All figures same magnification.) FIGS. 131, 132. Group 5. *Heterodera graminis*, fenestra and underbridge.

NOTE: Figs. 1–132 follow.

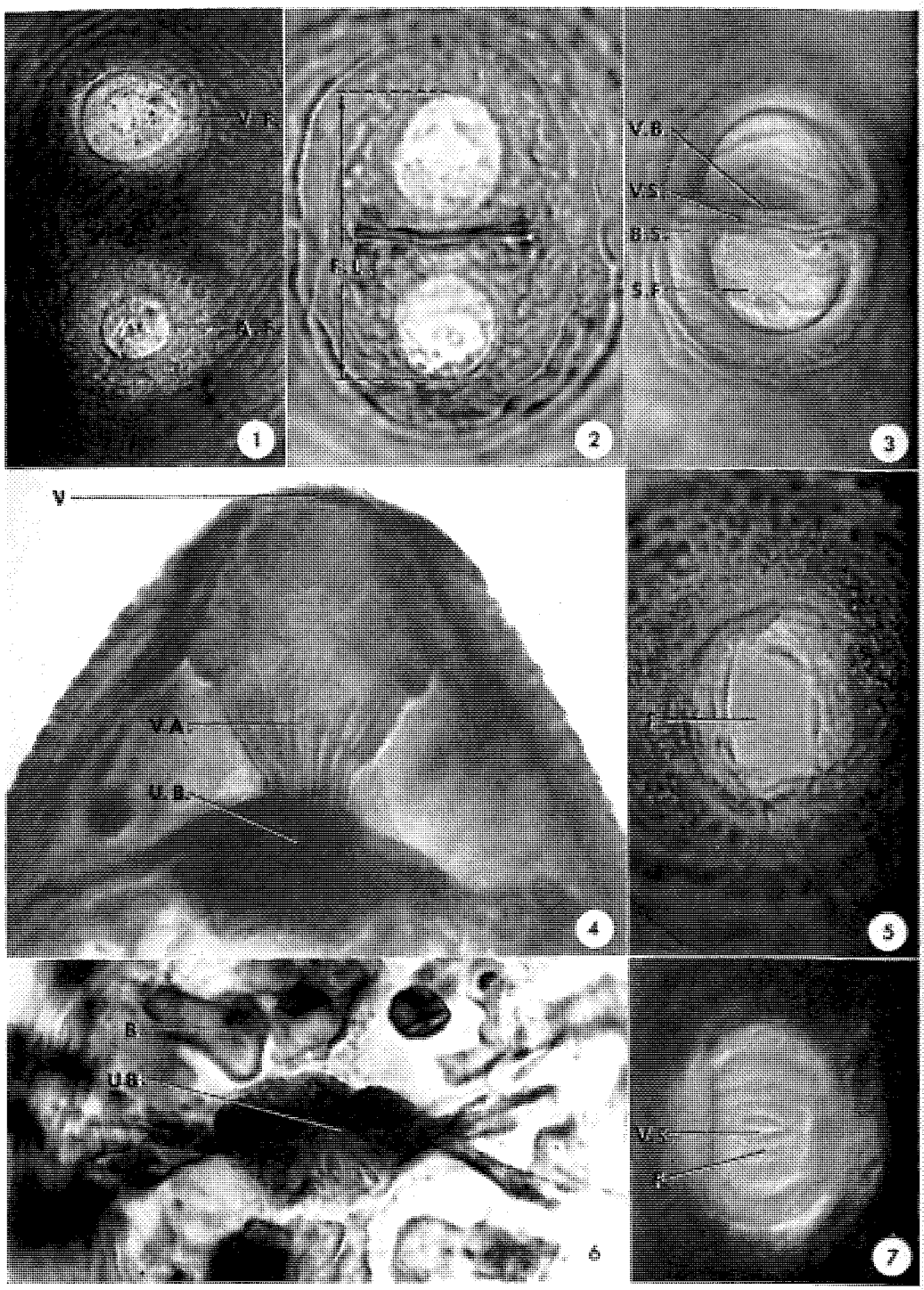
) *H. rosii*; (105)

(108) *H. zeae*,
) *H. cruciferae*;
H. humuli, older

, 119) *H. mothi*;
magnification.)
25) *H. carotae*;

All figures same

PLATE I



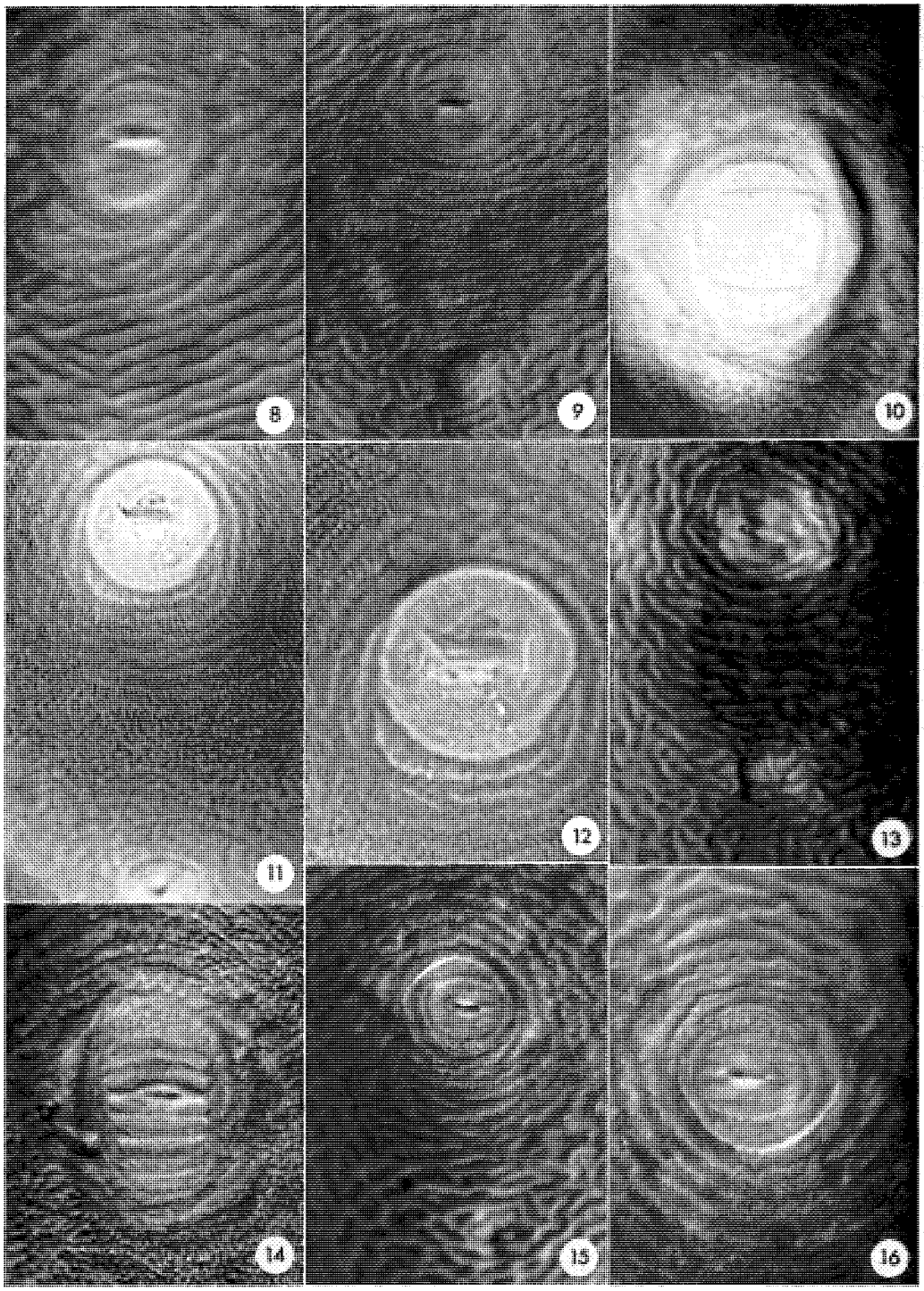

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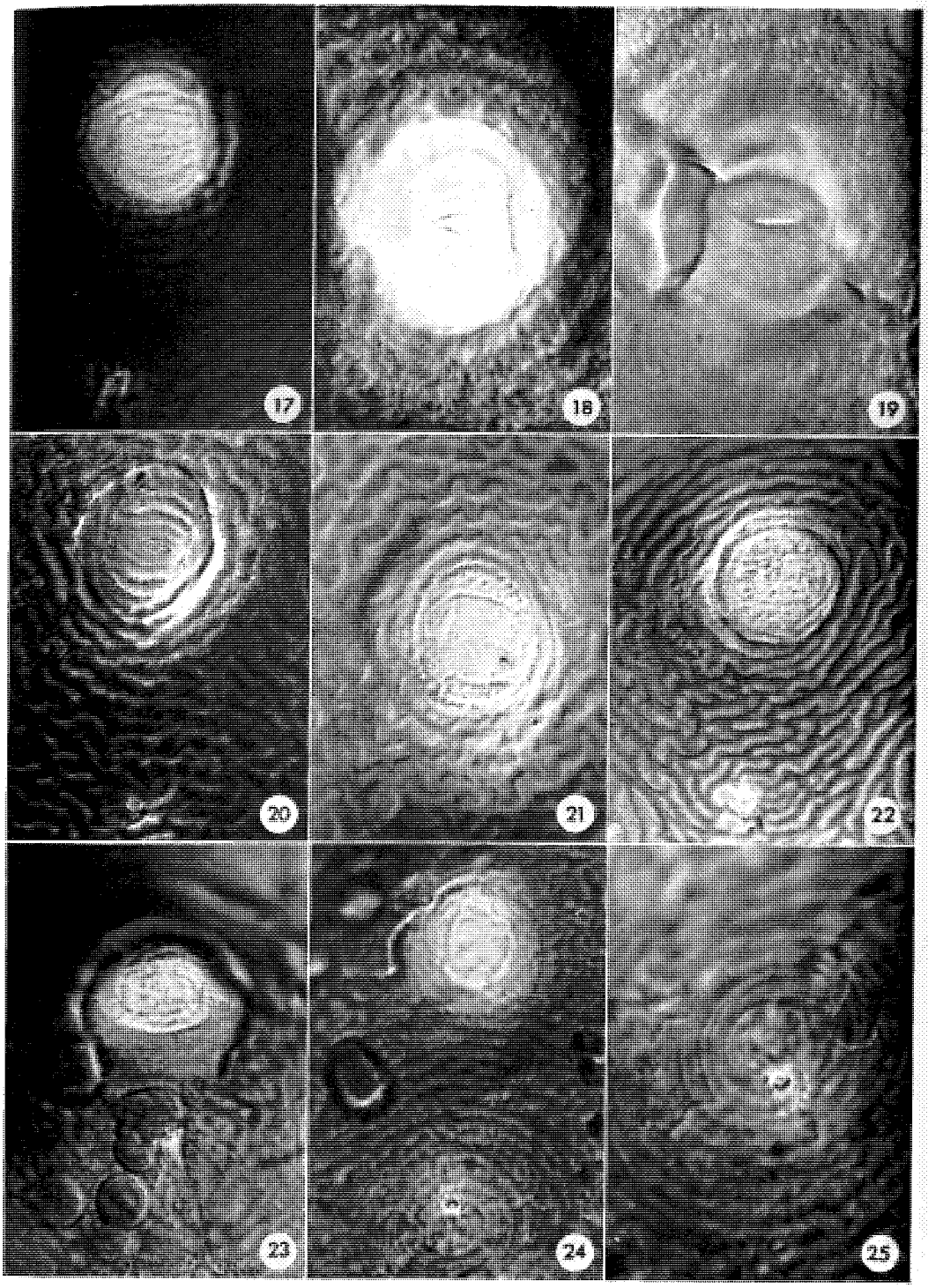
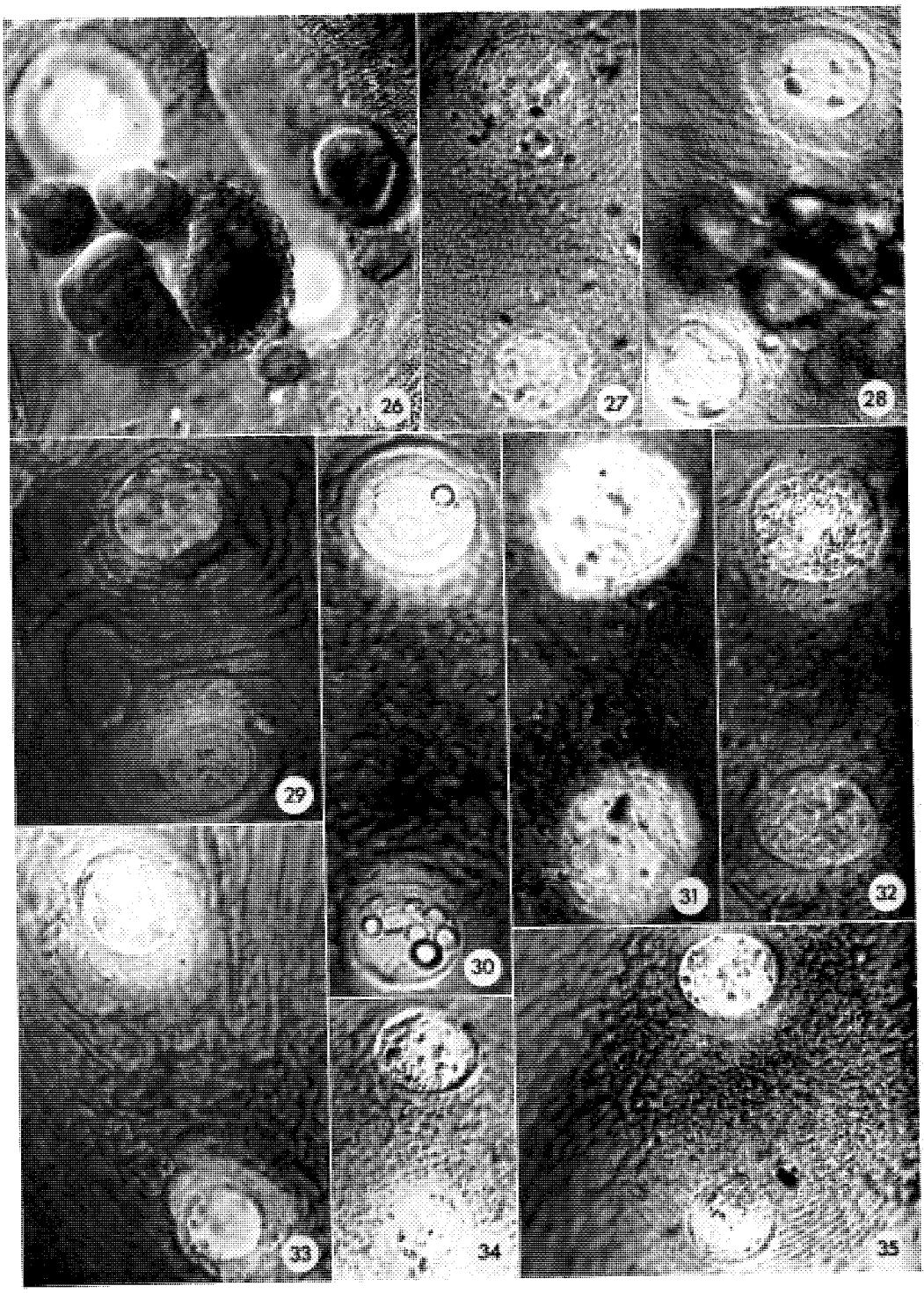
PLATE II

PLATE III

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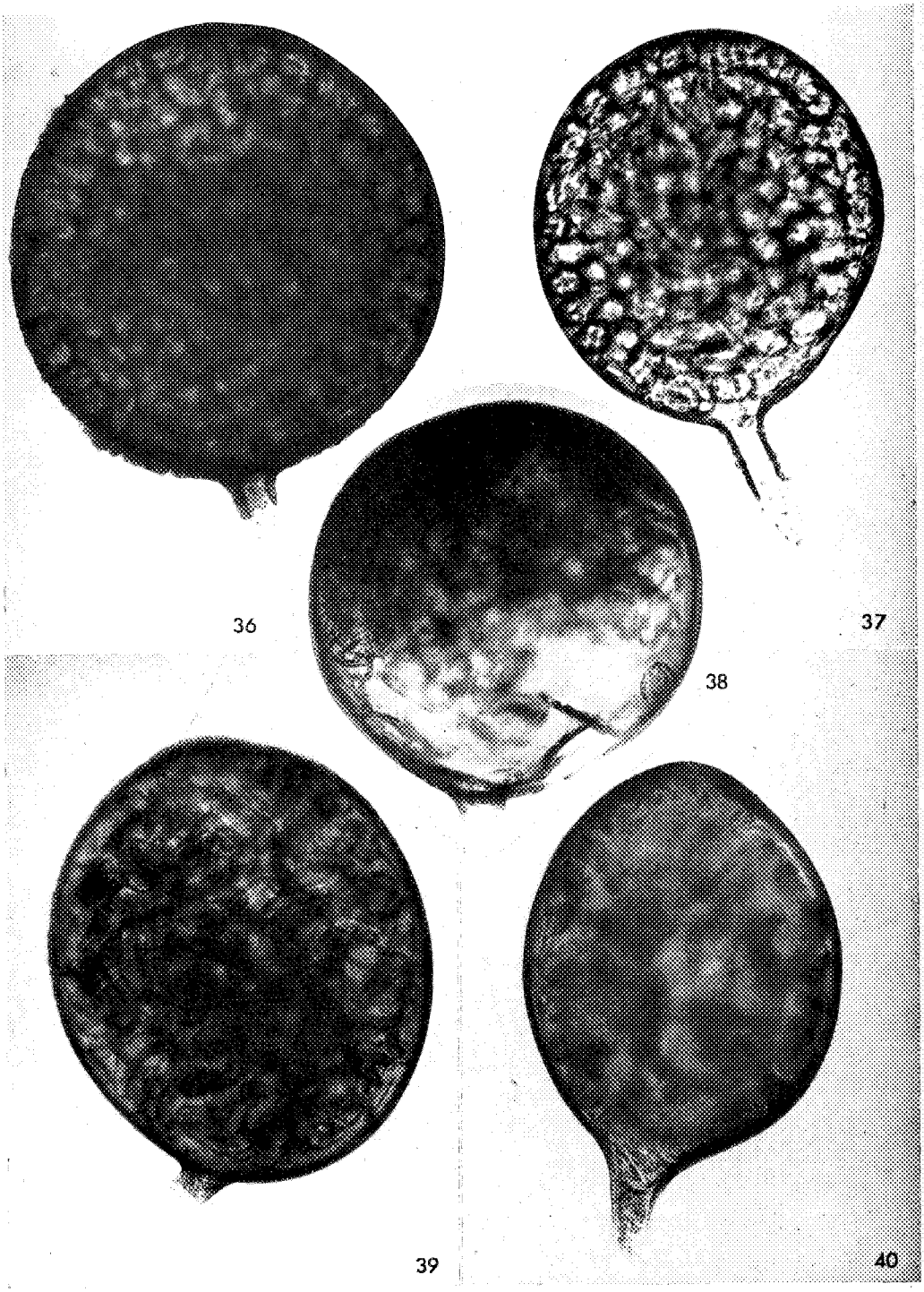

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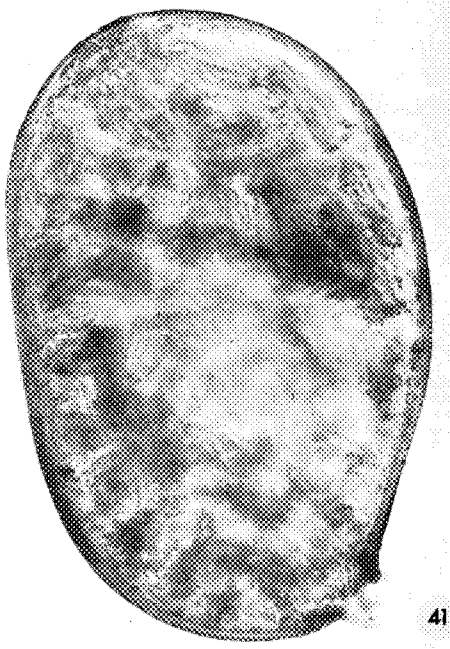

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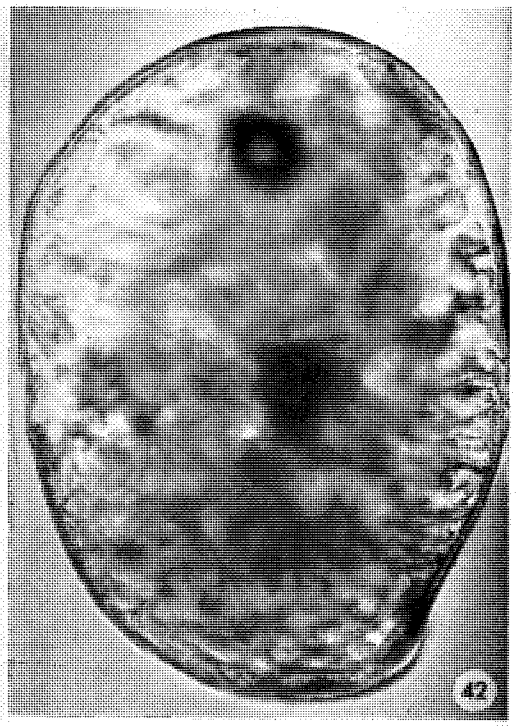

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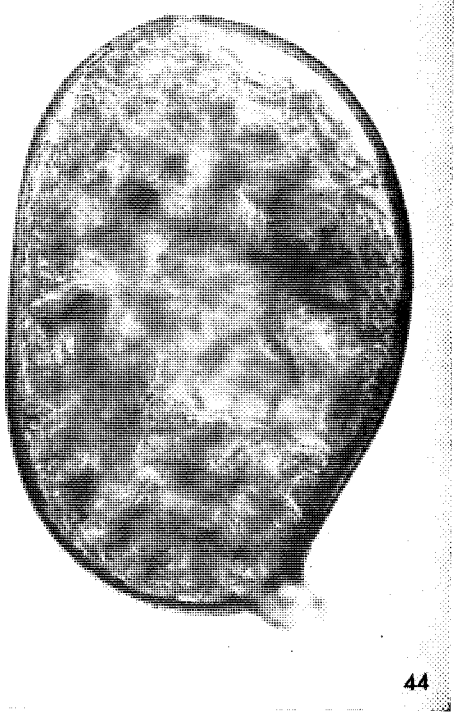

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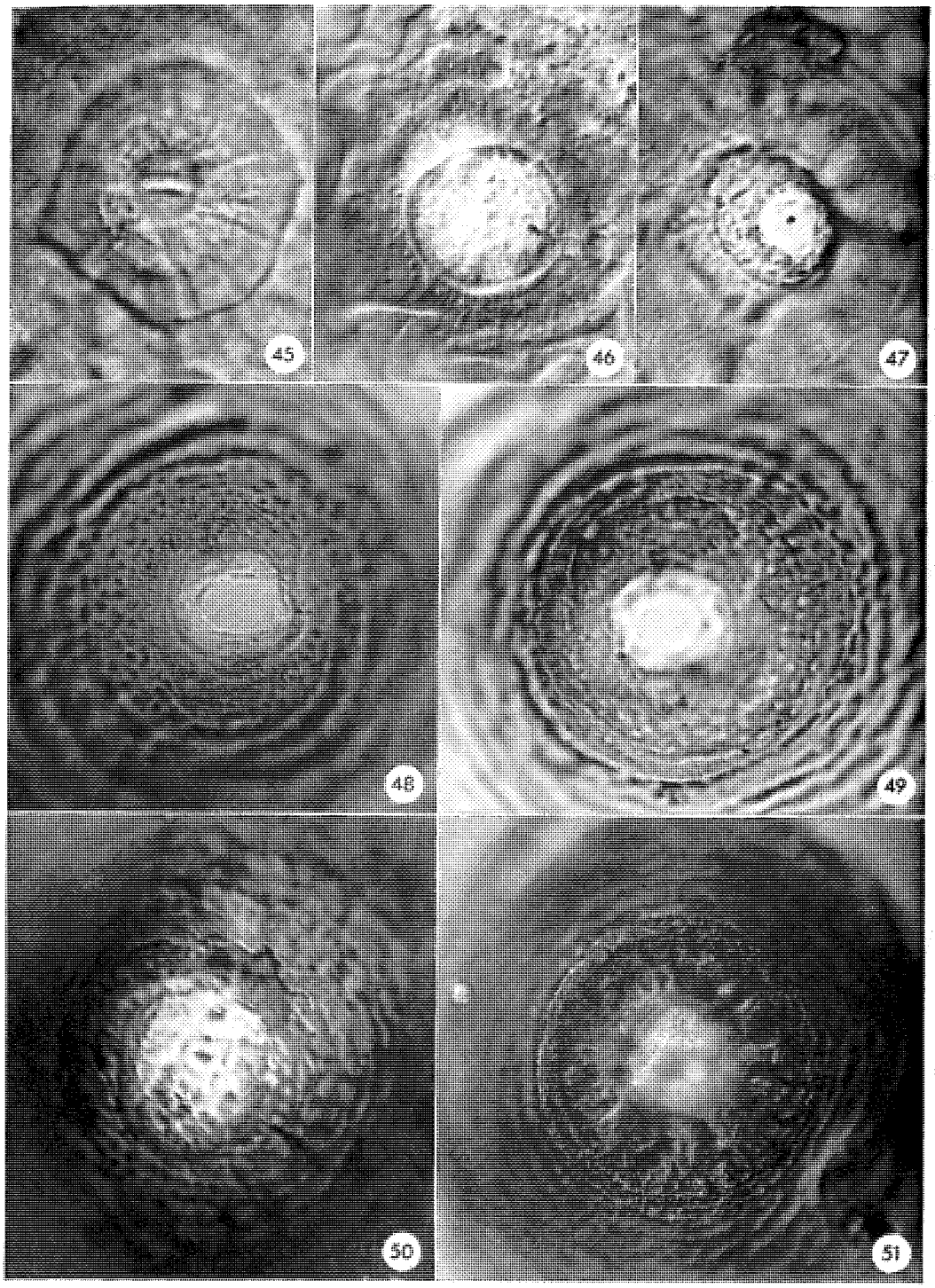
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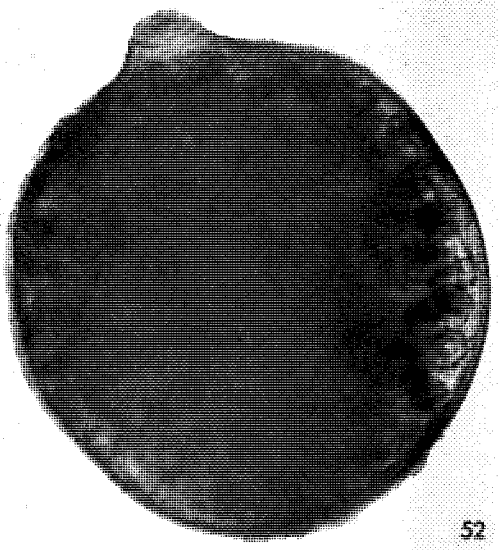

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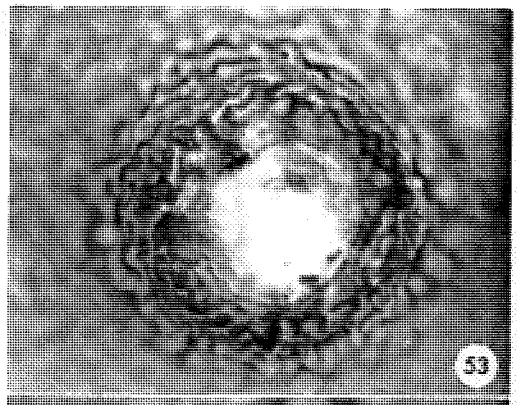

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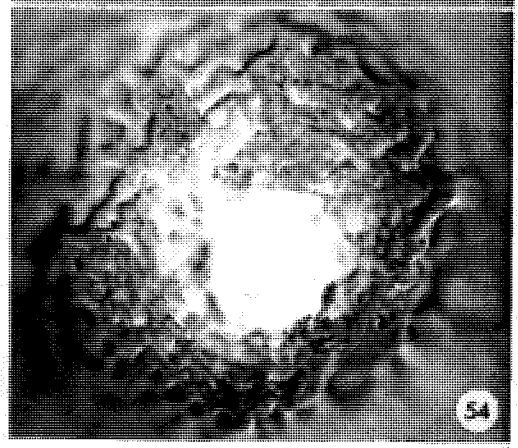

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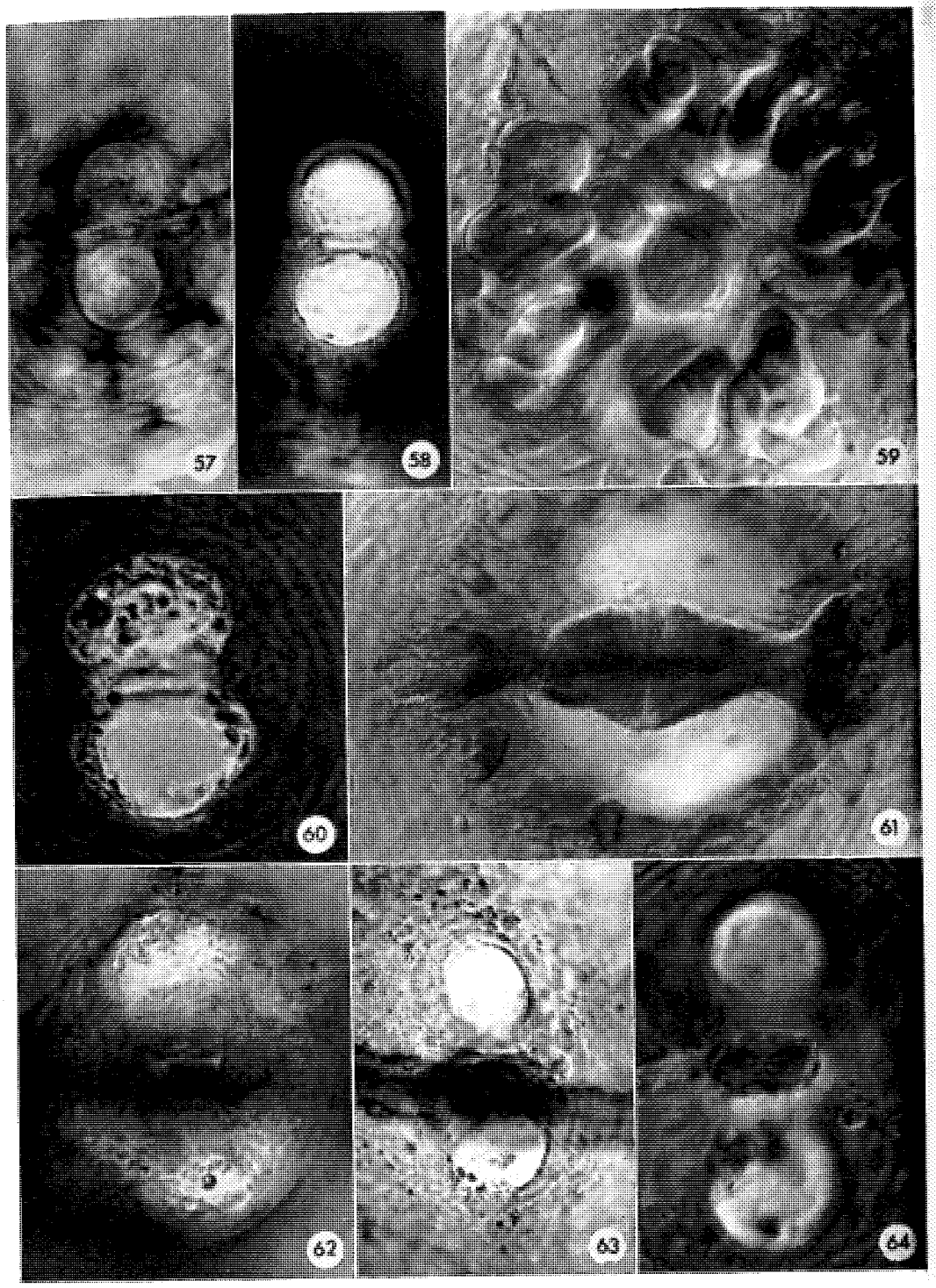
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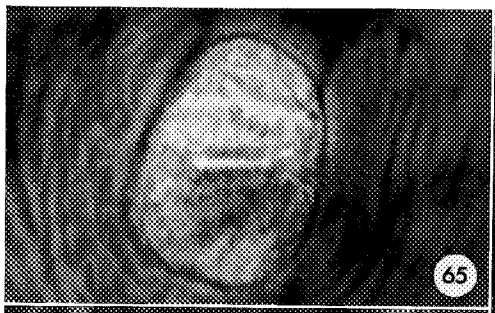
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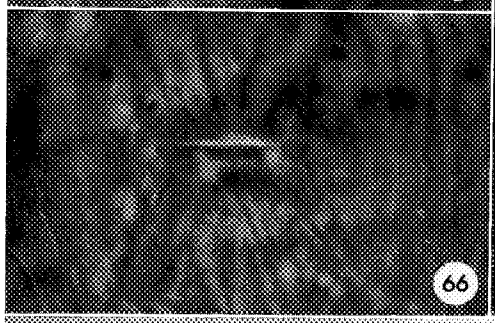
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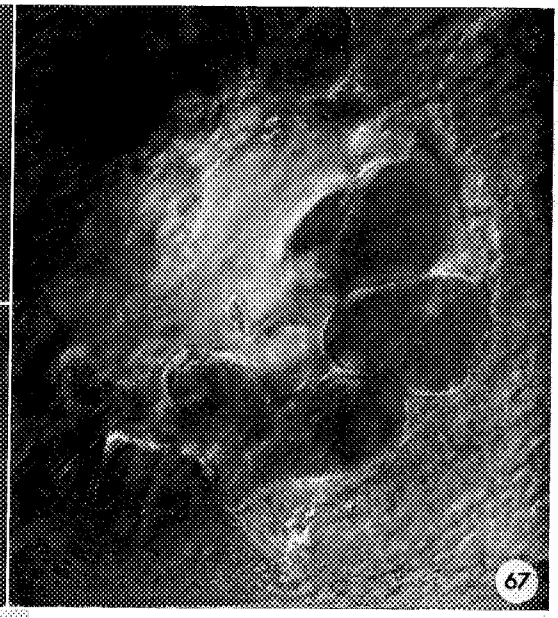
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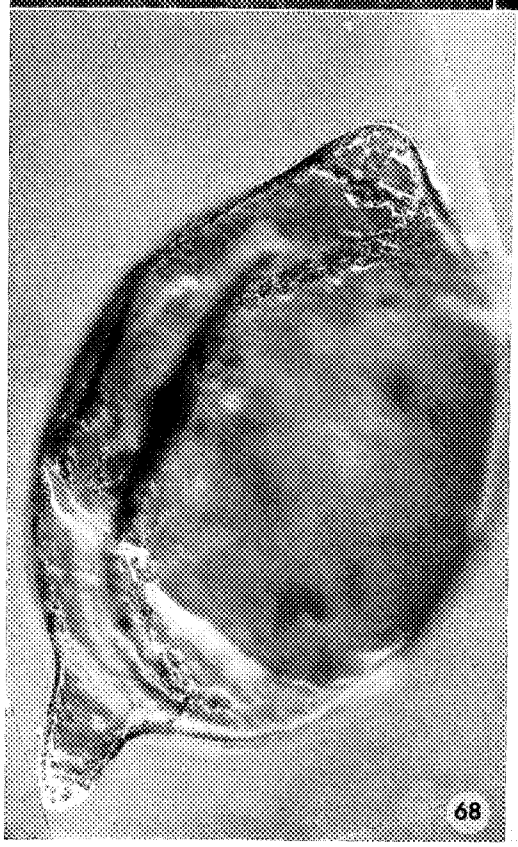
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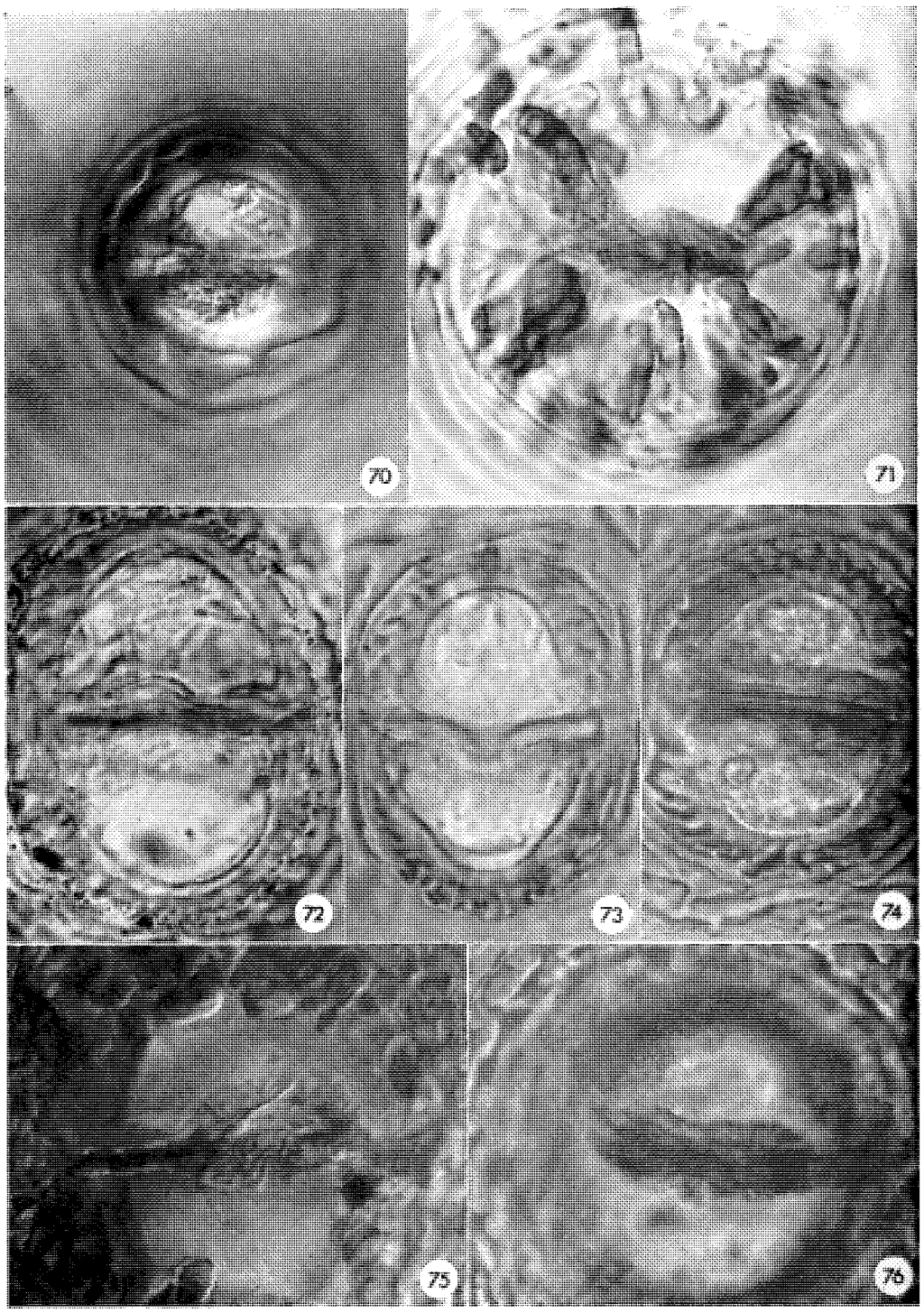
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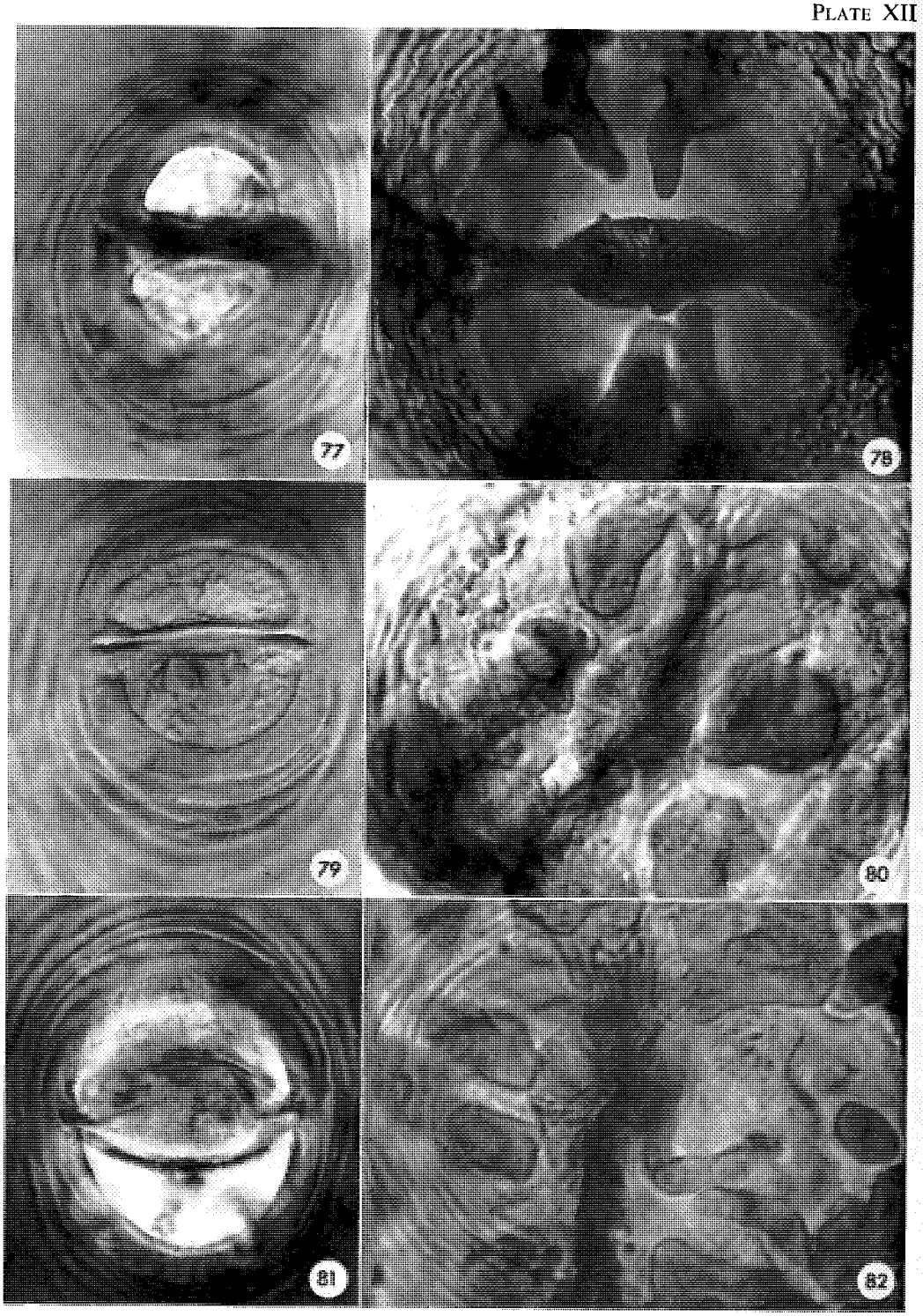
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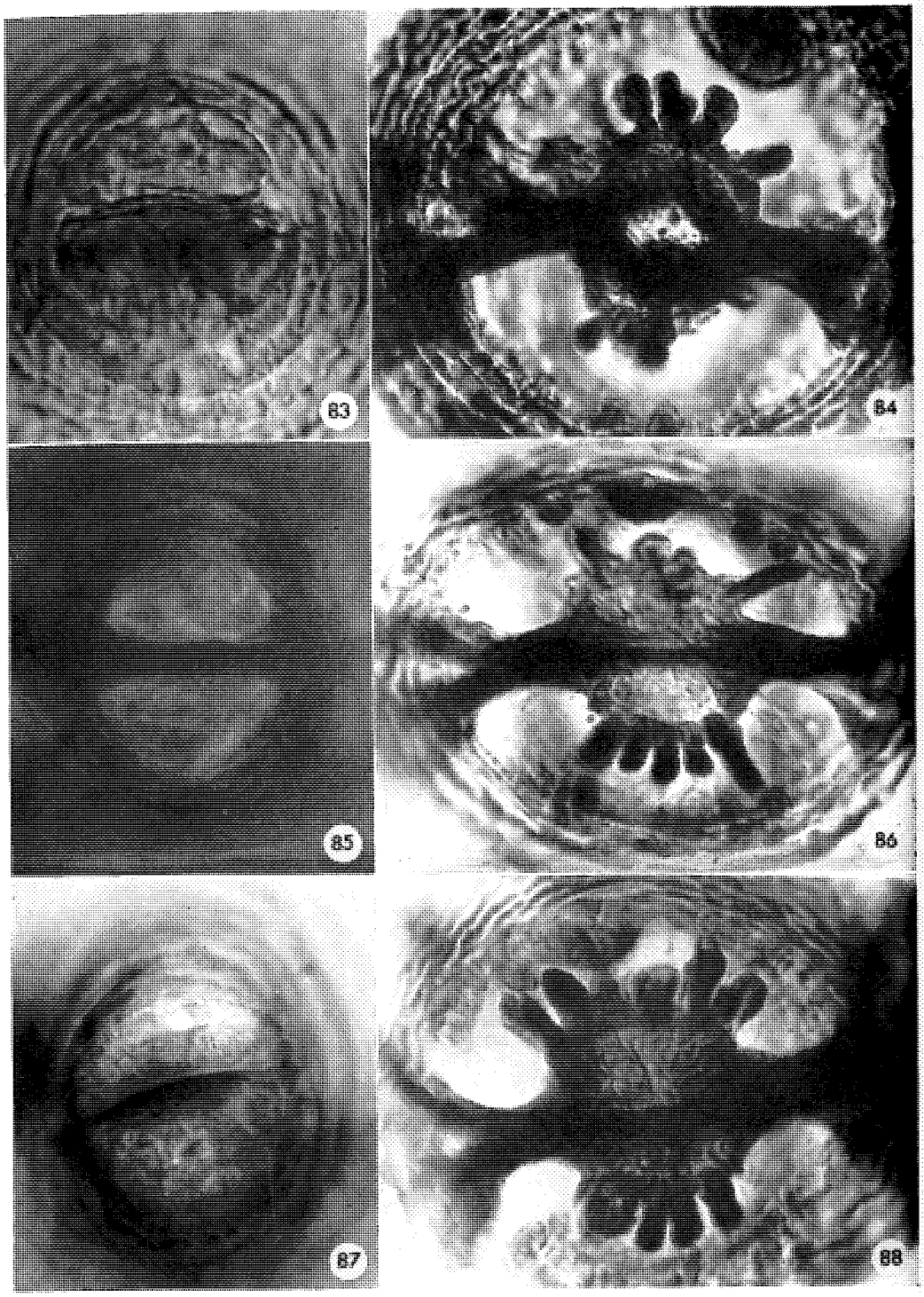
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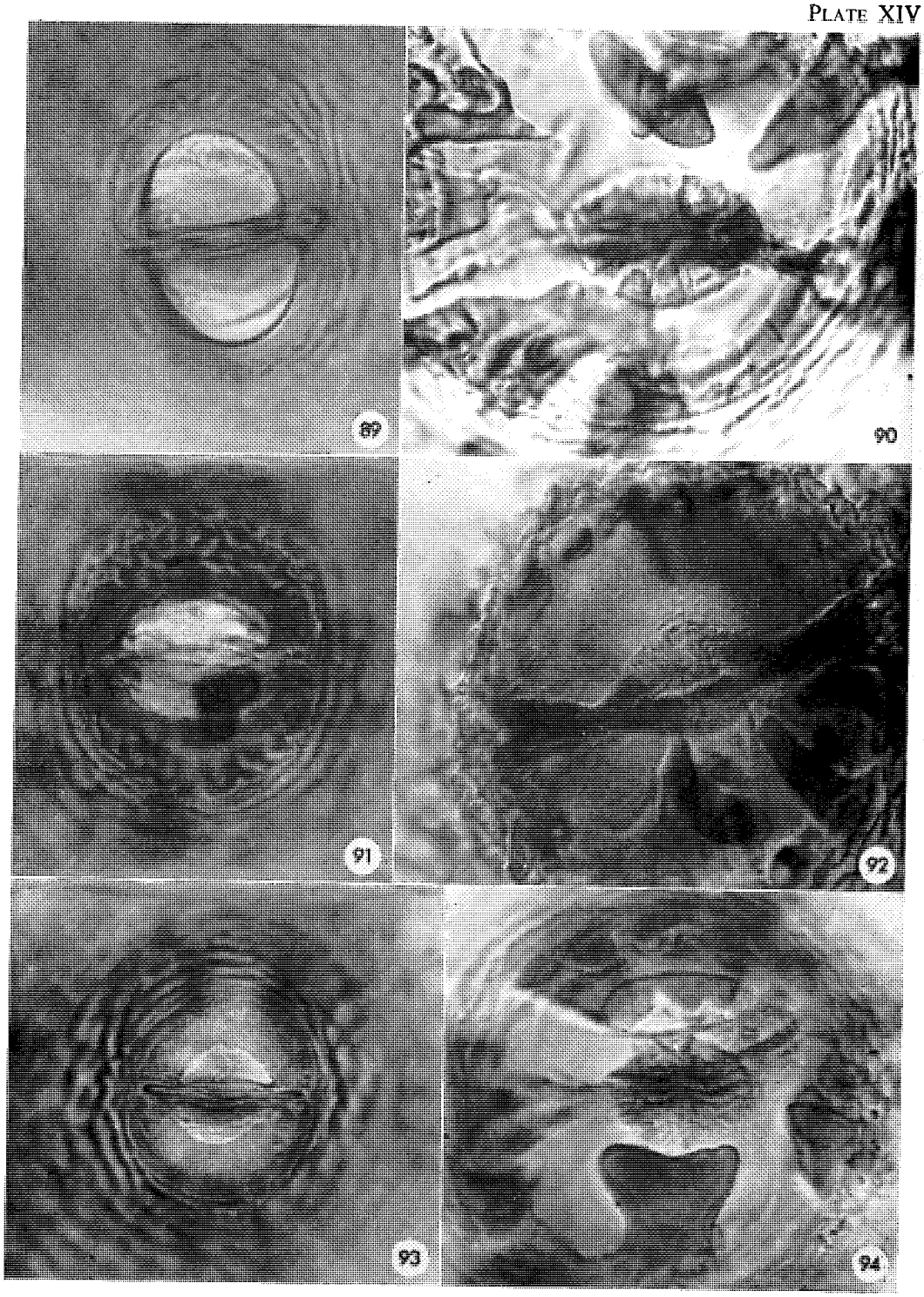
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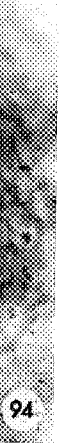

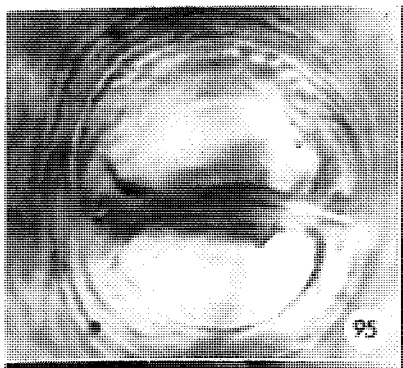

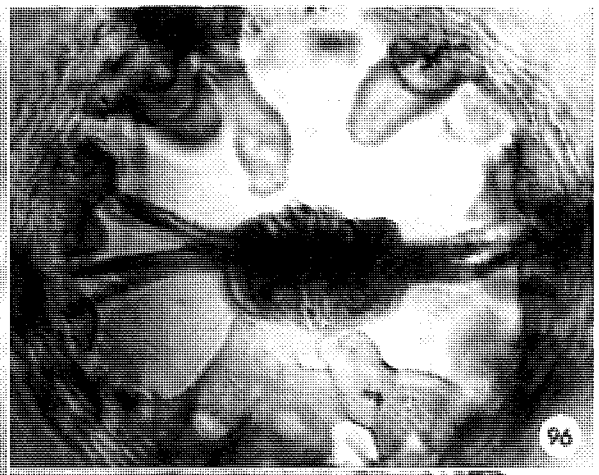

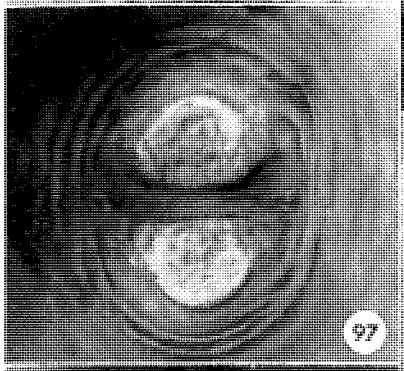

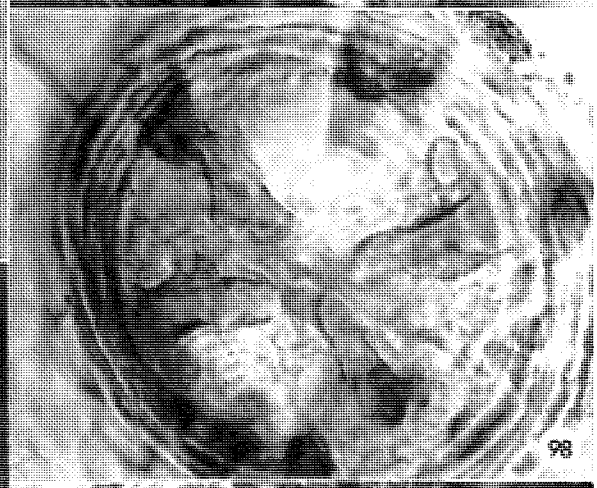

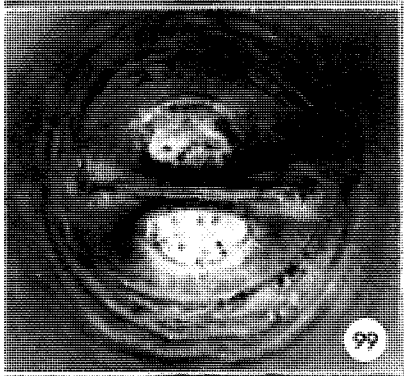

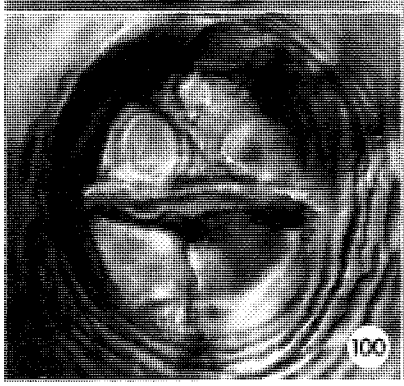

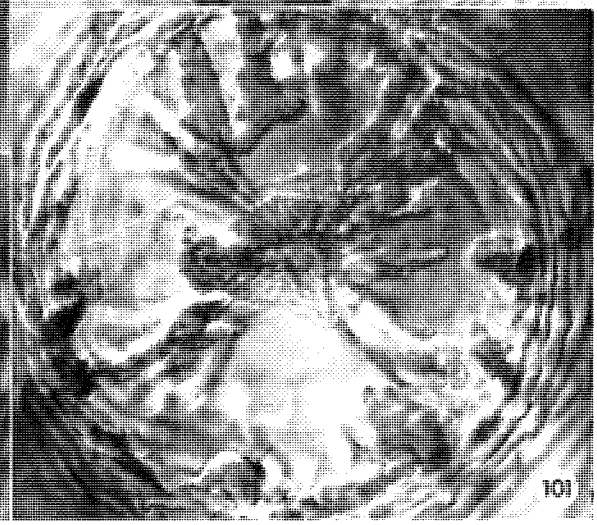

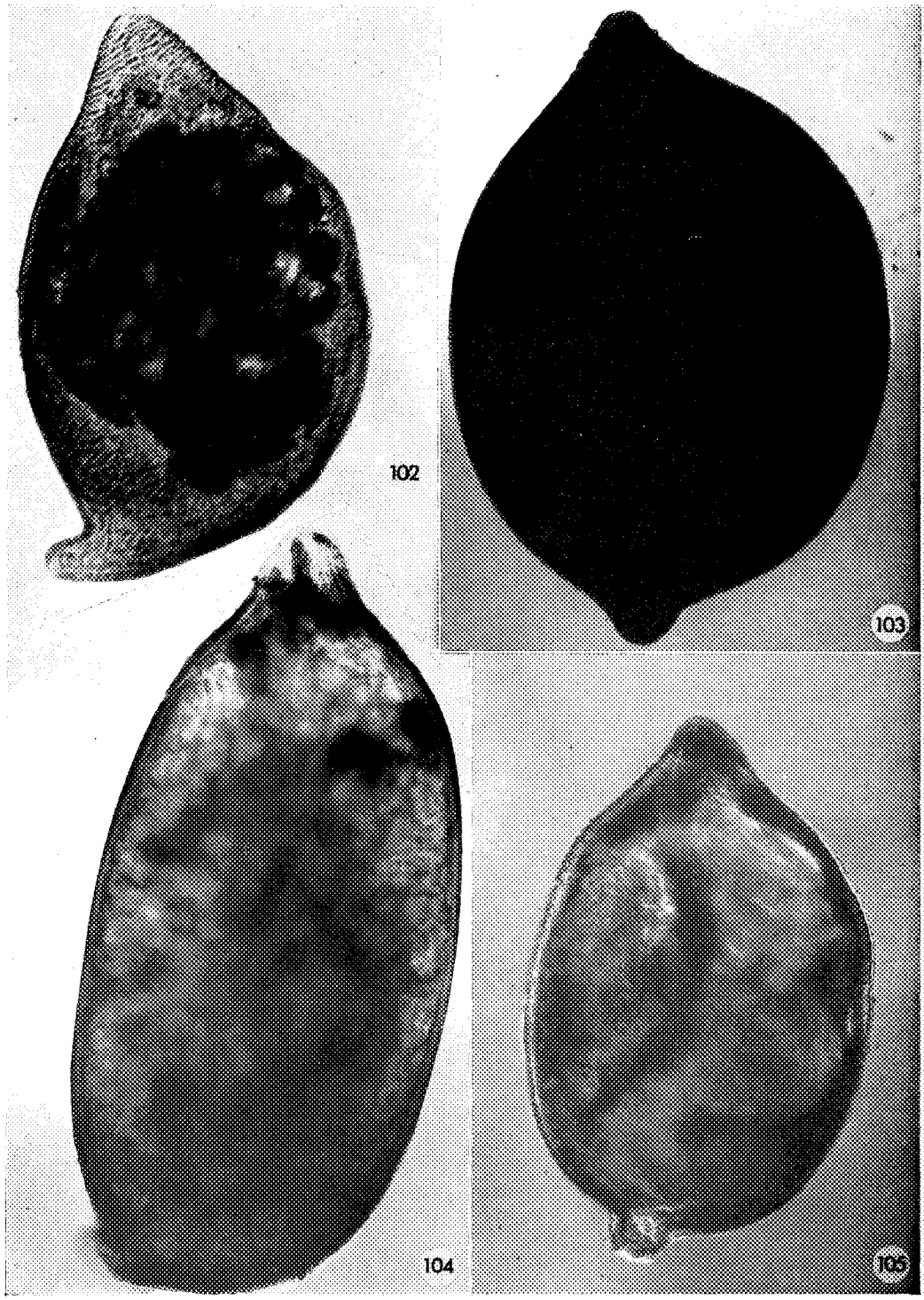
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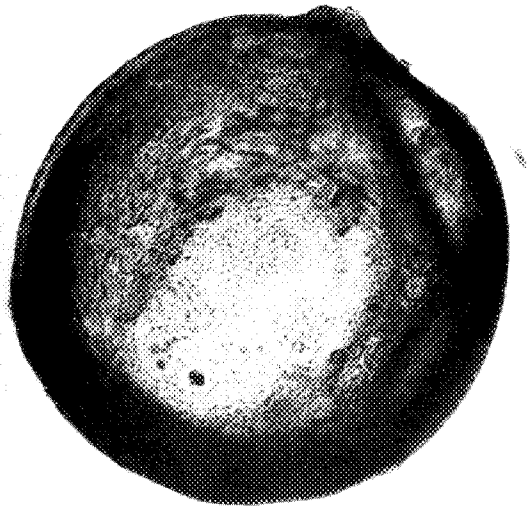

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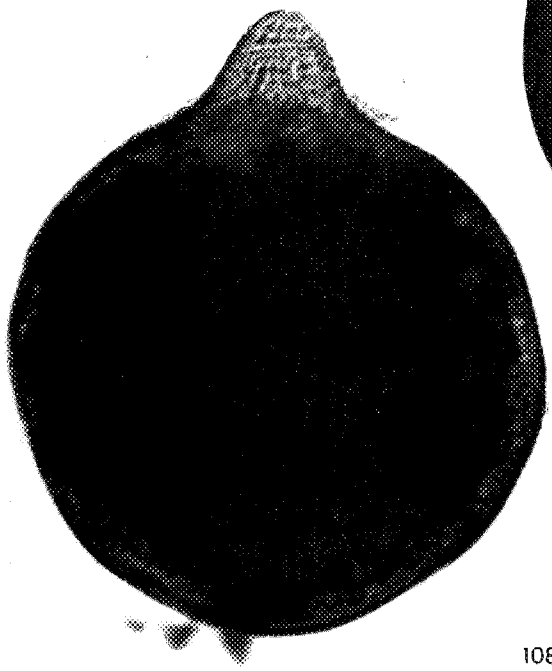

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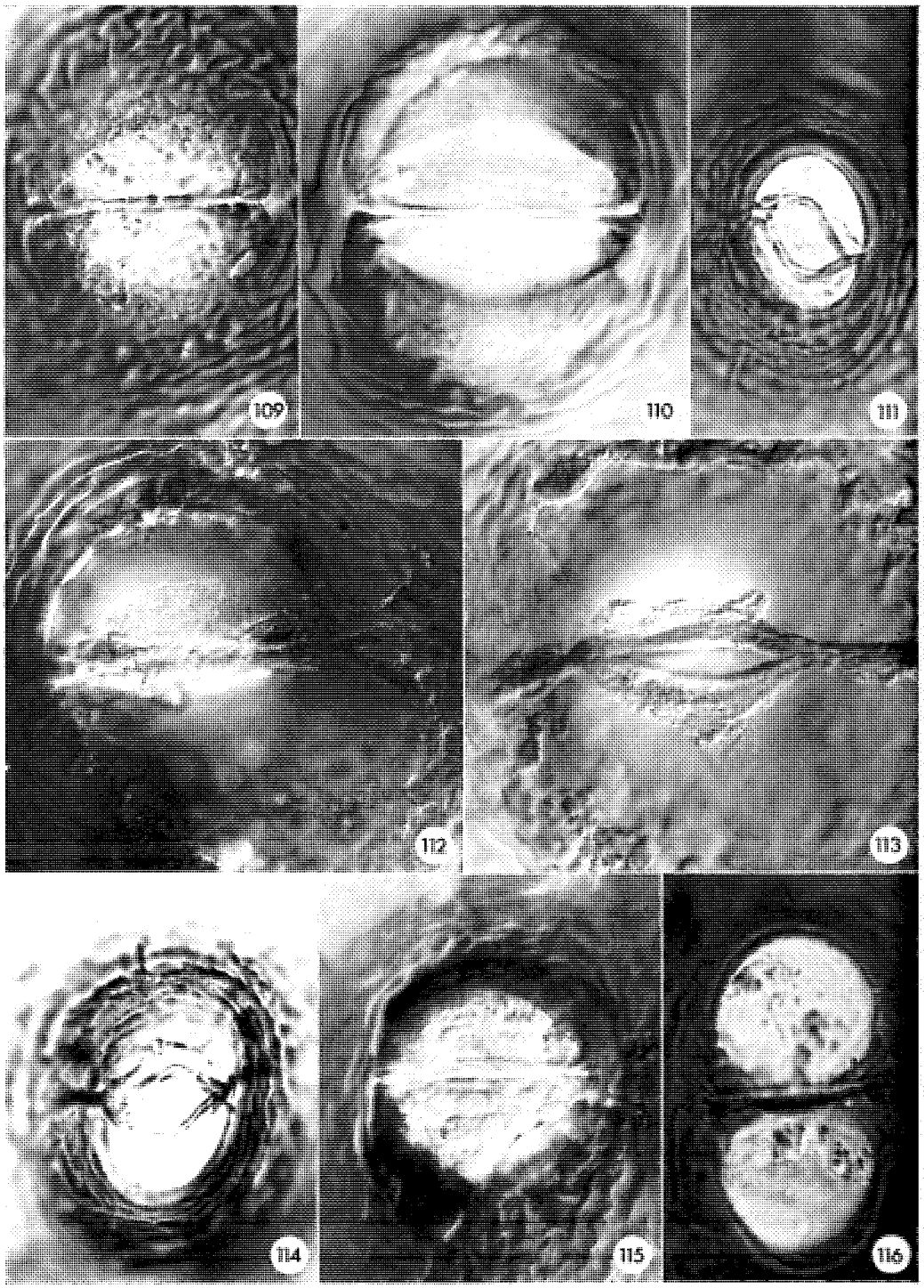
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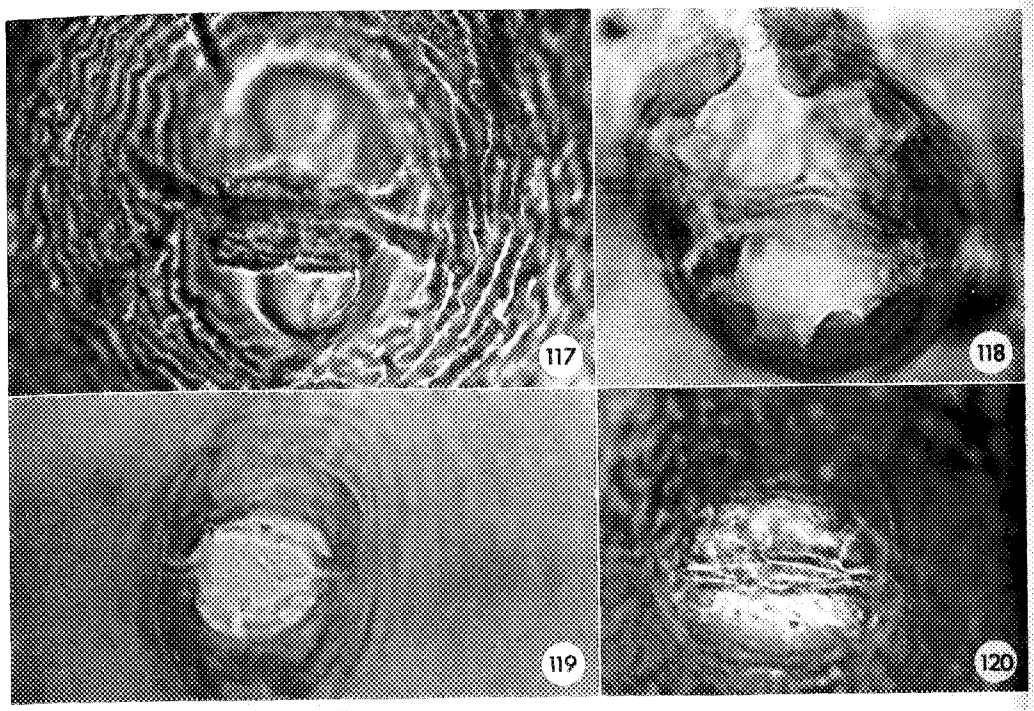
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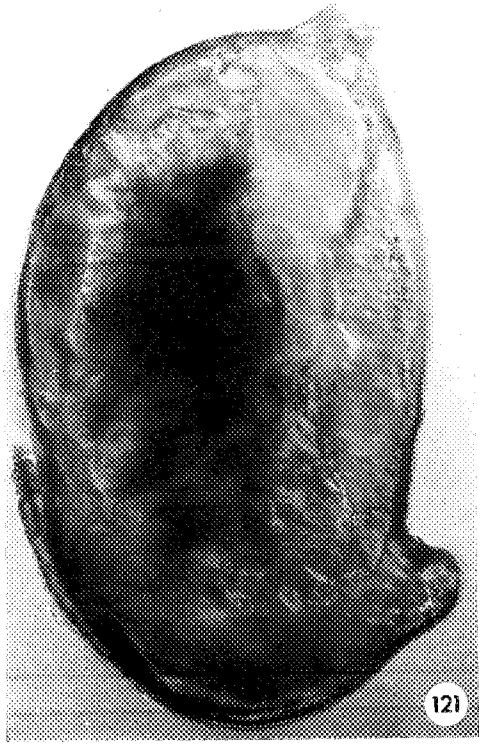
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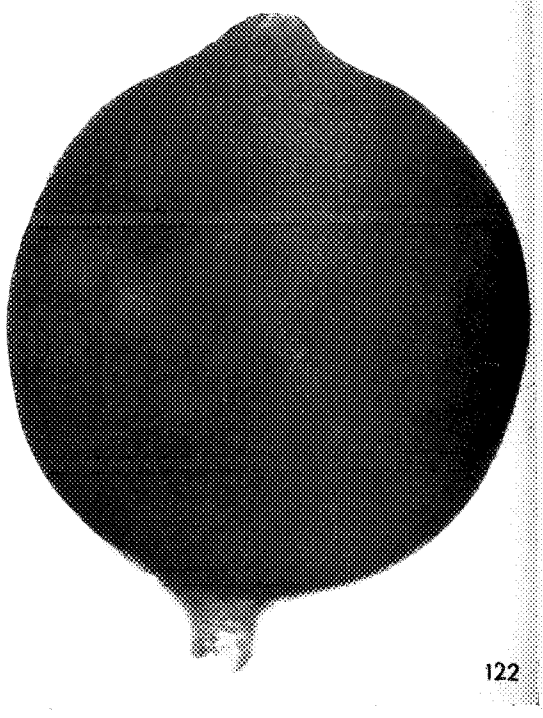
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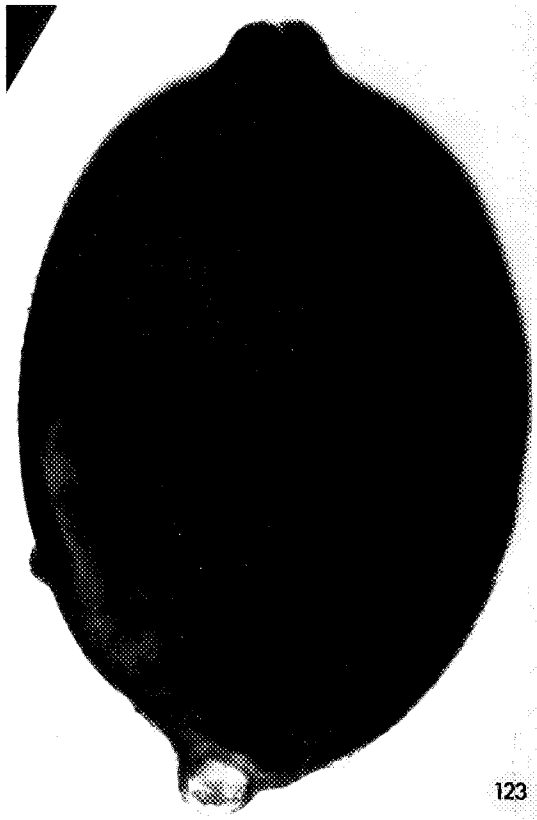

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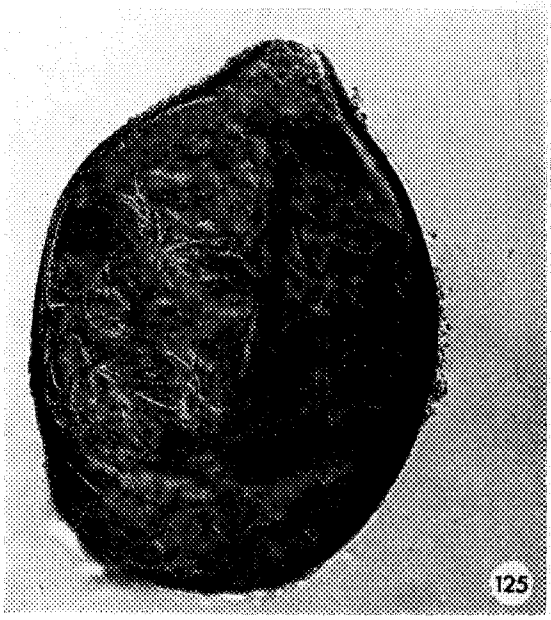

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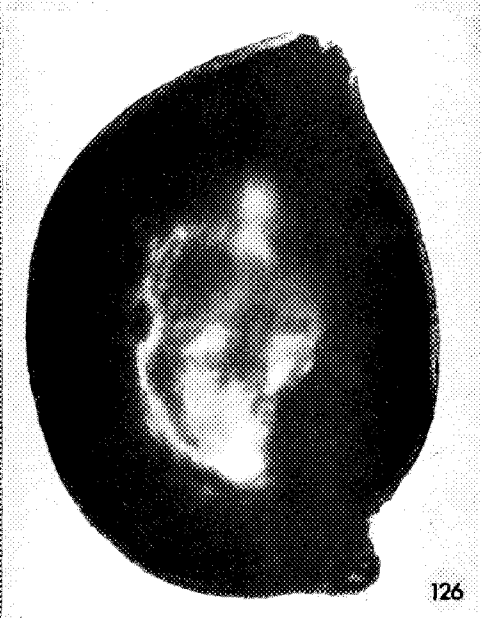

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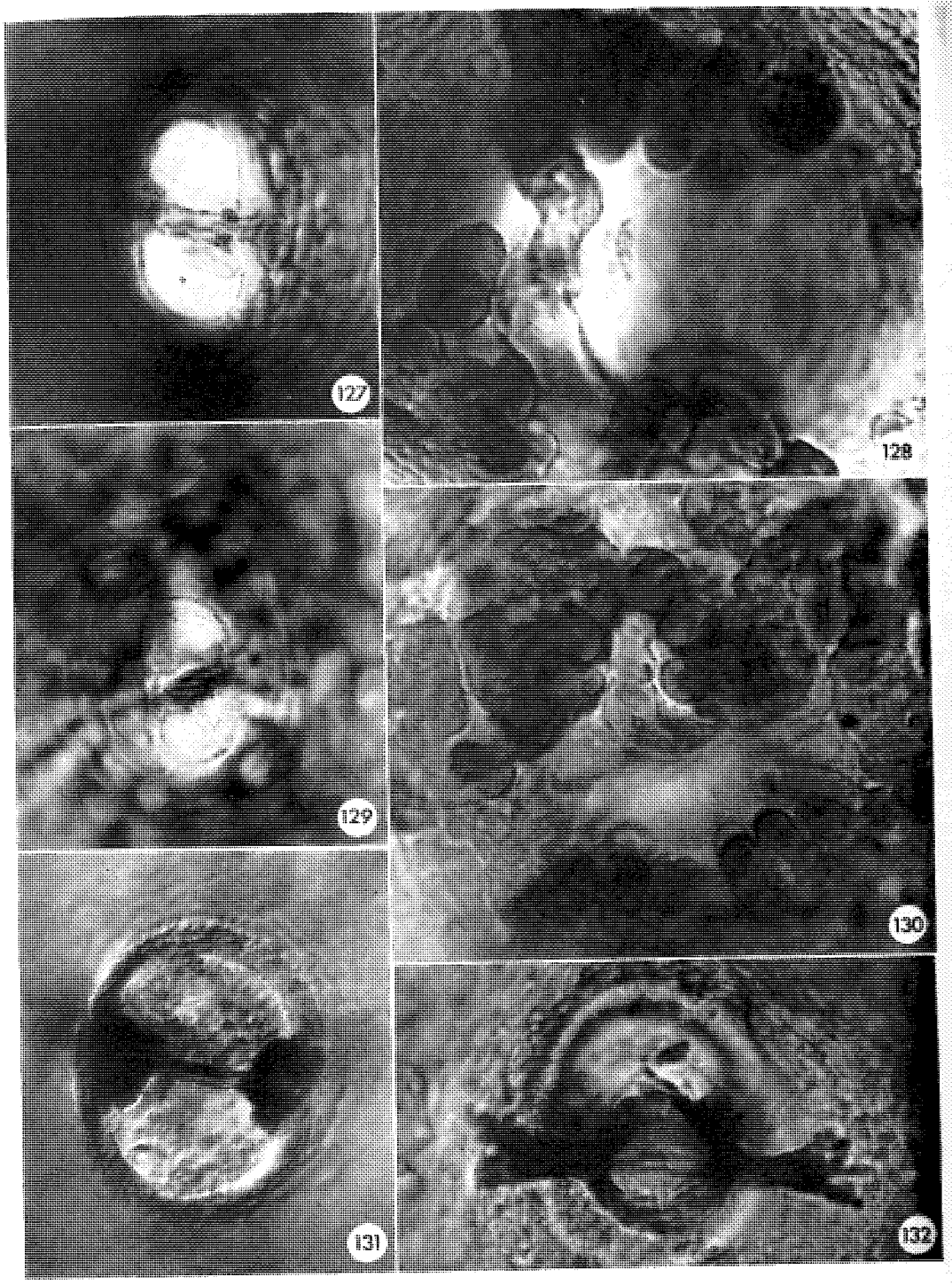
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