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THE BIOLOGY OF MARINE MYXOSPORIDIA AND AN INVESTIGATION INTO THE EFFECTS OF THESE PARASITES ON TELEOSTS

by

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VOLUME 2

Thesis submitted to the
Council for National Academic Awards
in candidature for the degree of
Doctor of Philosophy

School of Environmental Sciences
Plymouth Polytechnic
Plymouth
DEVON

MAY 1981

KEY TO PLATES

bi	Bile
bm	Basement membrane
c	Cisternae
cb	Club-shaped body
ce	Cytoplasmic extensions
cm	Cell membrane
cn	Capsulogenic nucleus
cp	Capsule
cw	Cyst wall
et	External tube
f	Fibres
fb	Fibroblast
fl	Fibrous layer
g	Glyco-calyx-like layer
gbe	Gall bladder epithelium
gc	Germinative cell
gn	Germinative nucleus
gr	Granular material
gv	Glycogenous vacuole
hc	Host cell
hcn	Host cell nucleus
iz	Internal zone
lc	Large epithelioid cell
lr	Longitudinal ridge
m	Microvilli
mt	Microtubules
mu	Muscle
n	Nucleus
nc	Nurse cell
pc	Polar capsule
pf	Polar filament

KEY continued

pl	Plaque
pm	Plasmodium
pmm	Plasmodium membrane
ps	Pseudopodium
r	Ring
re	Reflexed junction
sb	Sporoblast
sbm	Sporoblast membrane
sc	Scale
sc	Sutural crest
sm	Sporoplasmic membrane
sn	Sporoplasmic nucleus
sp	Spore
spc	Spore cavity
spm	Sporoplasm
spme	Spore membrane
sr	Sutural ridge
su	Suture
tz	Trophozoite
v	Vacuole
vc	Valvulogenic cell
ven	Vegetative nucleus
vn/vcn	Valve cell nucleus

PLATE 1

Myxosporidian species of teleosts in South-Western waters

1-A Plasmodium of Sphaerospora divergens containing spores, from a tissue-impression smear of Blennius pholis x 300 Giemsa-stained

1-B Myxidium sp. - trophozoites in the bile collecting ducts of the liver of Ciliata mustela x 500 Haematoxylin and Eosin

1-C Chloromyxum quadratum - single cyst containing numerous spores, from skeletal musculature of Callionymus lyra x 100 Heidenhain's Iron Haematoxylin

1-D Sphaerospora divergens - mature spore from the lumen of a kidney tubule of Blennius pholis x 2700 Giemsa

1-E Myxidium incurvatum - sporoblast containing two maturing spores from the bile of Crenimugil labrosus x 1610 live, phase contrast

1-F Chloromyxum sp. - sporoblast with sporogenic nuclei from the bile of Ciliata mustela x 3636 live, phase contrast

1-G Sphaeromyxa balbianii - sectioned portion of a polysporous trophozoite from the bile of Gaidropsarus mediterraneus x 85 Heidenhain's Iron Haematoxylin

1-H Sphaeromyxa balbianii - mature spore with both polar filaments extruded x 1440 Giemsa, phase contrast

1-I Sphaeromyxa balbianii - intact mature spore x 1440 Giemsa, phase contrast

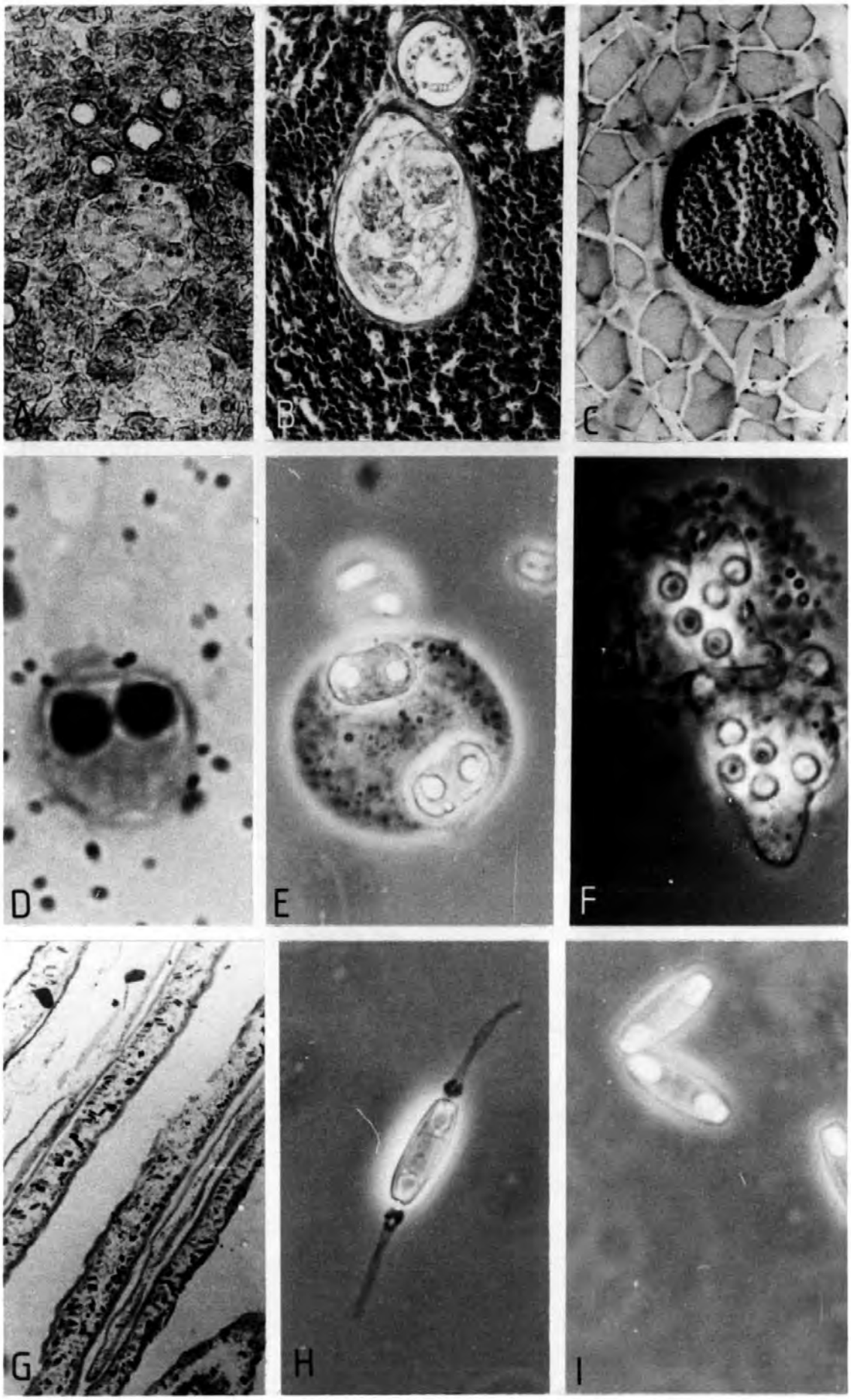
A
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PLATE 2

Species of Ceratomyxa recorded in teleosts of South-Western waters

2-A Ceratomyxa dubia - disporous sporoblast from the bile of Taurulus bubalis x 700 live, phase contrast

2-B Ceratomyxa dubia - spores and young trophozoites from the bile of Myxocephalus scorpius x 286 Giemsa

2-C Ceratomyxa dubia - pansporoblasts from Myxocephalus scorpius x 653 Giemsa

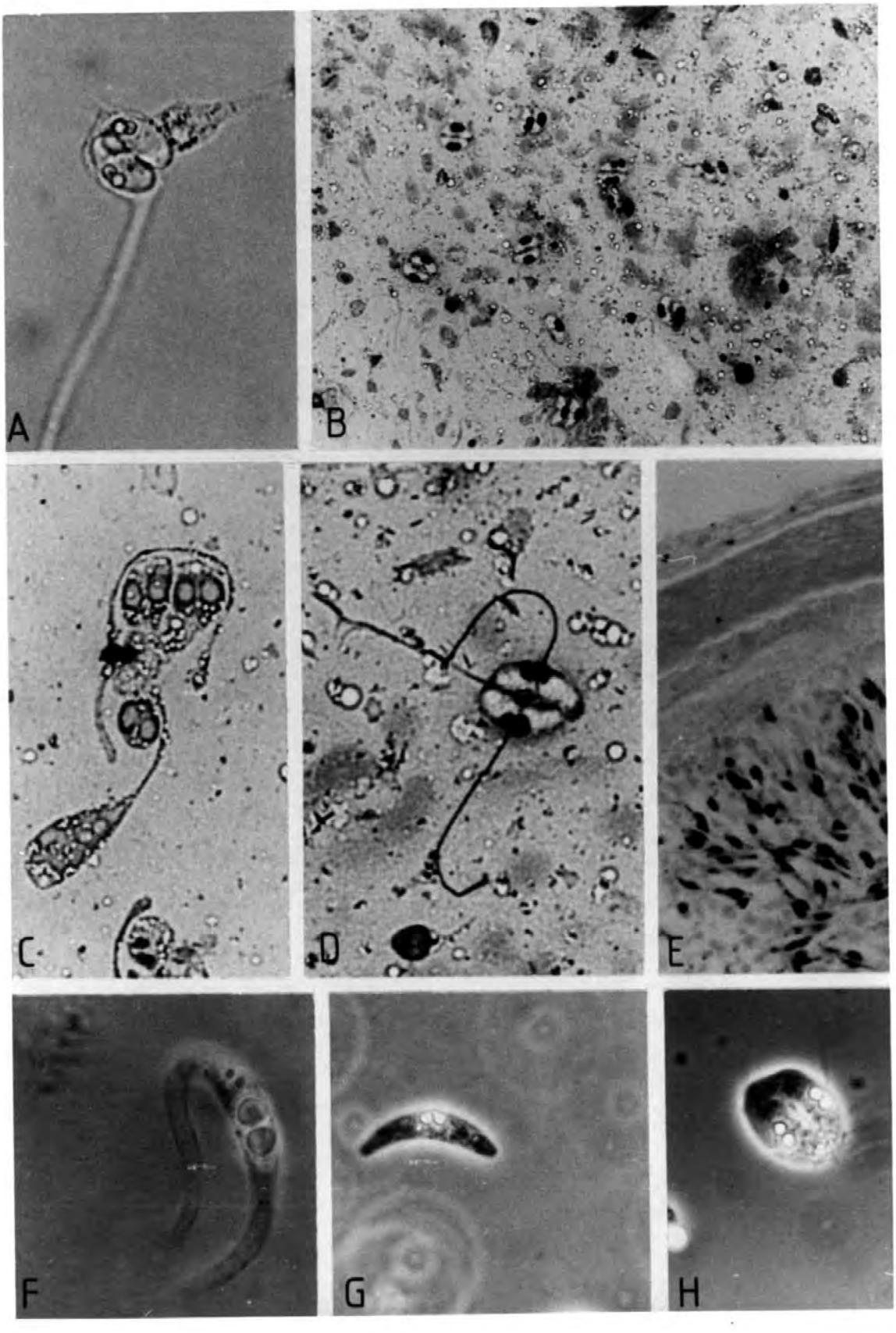
2-D Ceratomyxa dubia - sporoblast containing two spores, each with a single polar filament extruded x 1000 Giemsa

2-E Ceratomyxa arcuata - sectioned portion of the gall bladder of Crenilabrus melops, with spores and developmental stages in the lumen; polar capsules appear as dark-staining bodies x 500 Heidenhain's Iron Haematoxylin

2-F Ceratomyxa sp. - single spore from the bile of Trigla lucerna x 800 live, phase contrast

2-G Ceratomyxa arcuata - spore from the bile of Liparis liparis x 800 live, phase contrast

2-H Ceratomyxa arcuata - disporous sporoblast from Liparis liparis x 800 live, phase contrast


A
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H

PLATE 3

Scanning electron micrographs of selected spores from teleosts of South-Western waters

3-A *Chloromyxum quadratum* - from the bile of *Taurulus bubalis*, showing detail of the foramen for extrusion of filaments x 8825

3-B *Ceratomyxa arcuata* - from the bile of *Callionymus lyra* x 3800

3-C *Sphaeromyxa balbianii* - from *Ciliata mustela*, showing longitudinal striations x 6150

3-D *Chloromyxum quadratum* - from *Callionymus lyra*, showing four distinct suture lines x 7000

3-E *Zschokkella russelli* - from *Gaidropsarus mediterraneus* x 7200

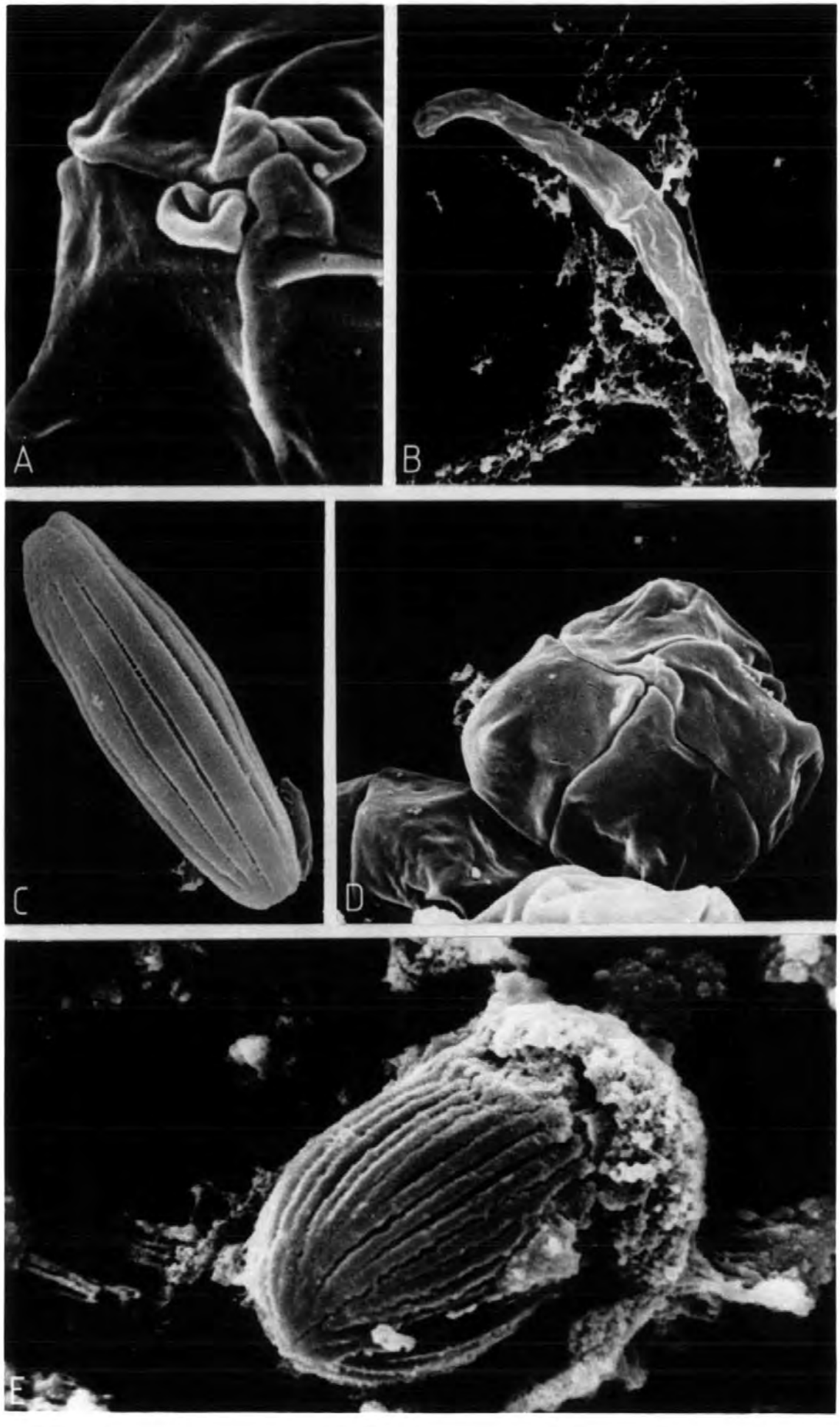
A
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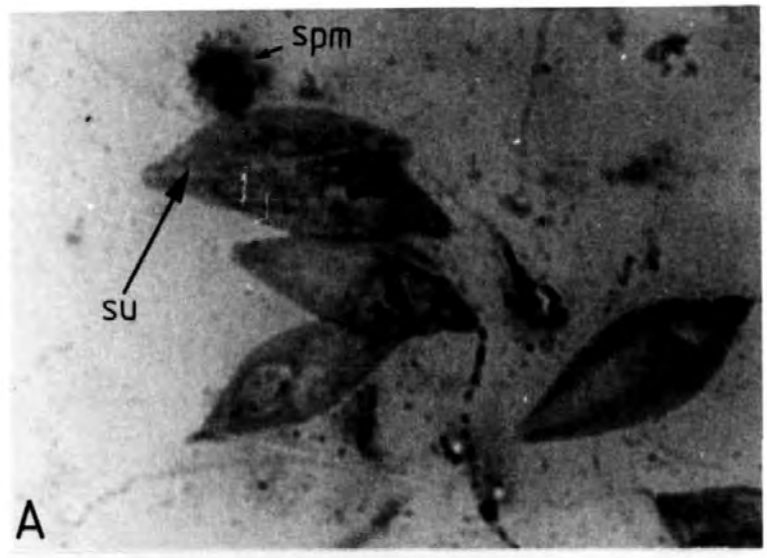
PLATE 4

Myxidium incurvatum : investigations on spore structure and function

4-A To show the effects of application of saturated urea solution, with spores cleaving to release the sporoplasm. Note the prominent sutural line on one of the spores. x 4000 Giemsa

4-B To show complete cleavage of spore valves and polar filament extrusion, with a released sporoplasm between the valves, following treatment with urea. x 2222 live, phase contrast

4-C Spores recovered from the faeces of Callionymus lyra, stained with Acridine orange to distinguish the degenerating sporogenic nuclei. x 3666 Acridine Orange Fluorescence


spm
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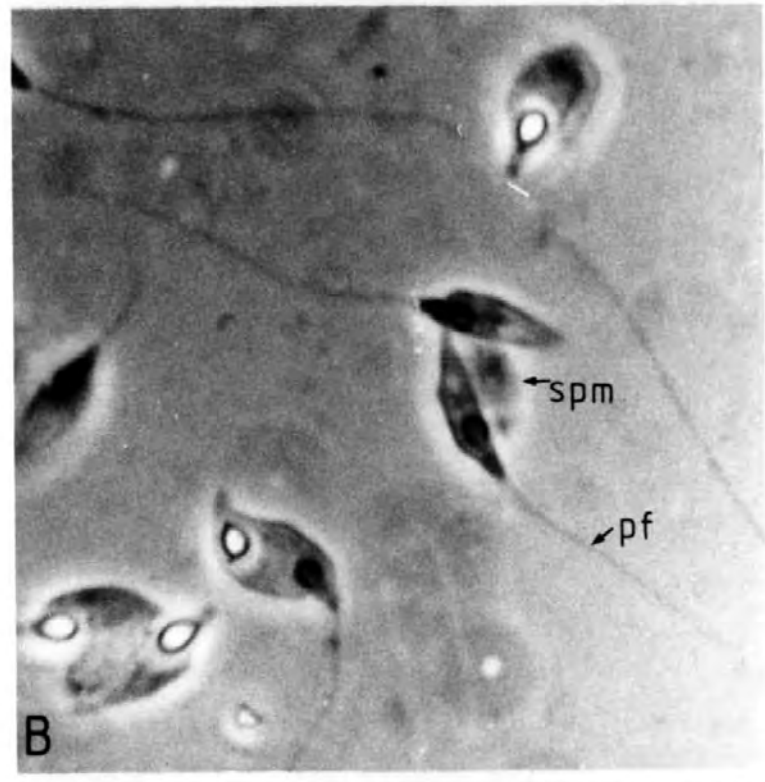
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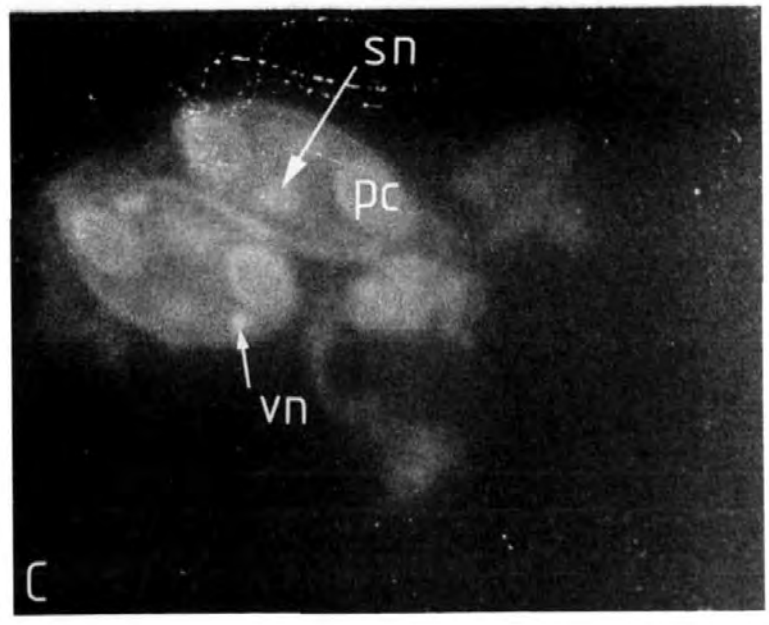
sn
pc
vn
C

PLATE 5

Myxobolus exiguus : to show the effects of various chemical treatments on spores

5-A Spores exposed to pepsin (24 hours), followed by trypsin (48 hours) at 10°C. The prominent sutural line (arrowed) indicates possible sites of enzyme activity. x 1785 Giemsa

5-B Scanning electron micrograph of a spore, following treatment with Chloros for 4 hours at 12°C, showing extensive damage to the spore valves. Note arrow indicating the position of the foramen for the polar filament. x 10500

5-C Spores exposed to pepsin (24 hours), followed by trypsin (12 hours) at 20°C, showing polar filament extrusion (arrows) and initiation of cleavage. x 1785 Giemsa

5-D Spores exposed to pepsin (24 hours) and trypsin (48 hours) at 37°C. Arrows indicate areas of splitting on the spore valves. x 1785 Giemsa

5-E Scanning electron micrograph of a spore treated as for 5-D above, showing blistering and damage to the valves. x 9950

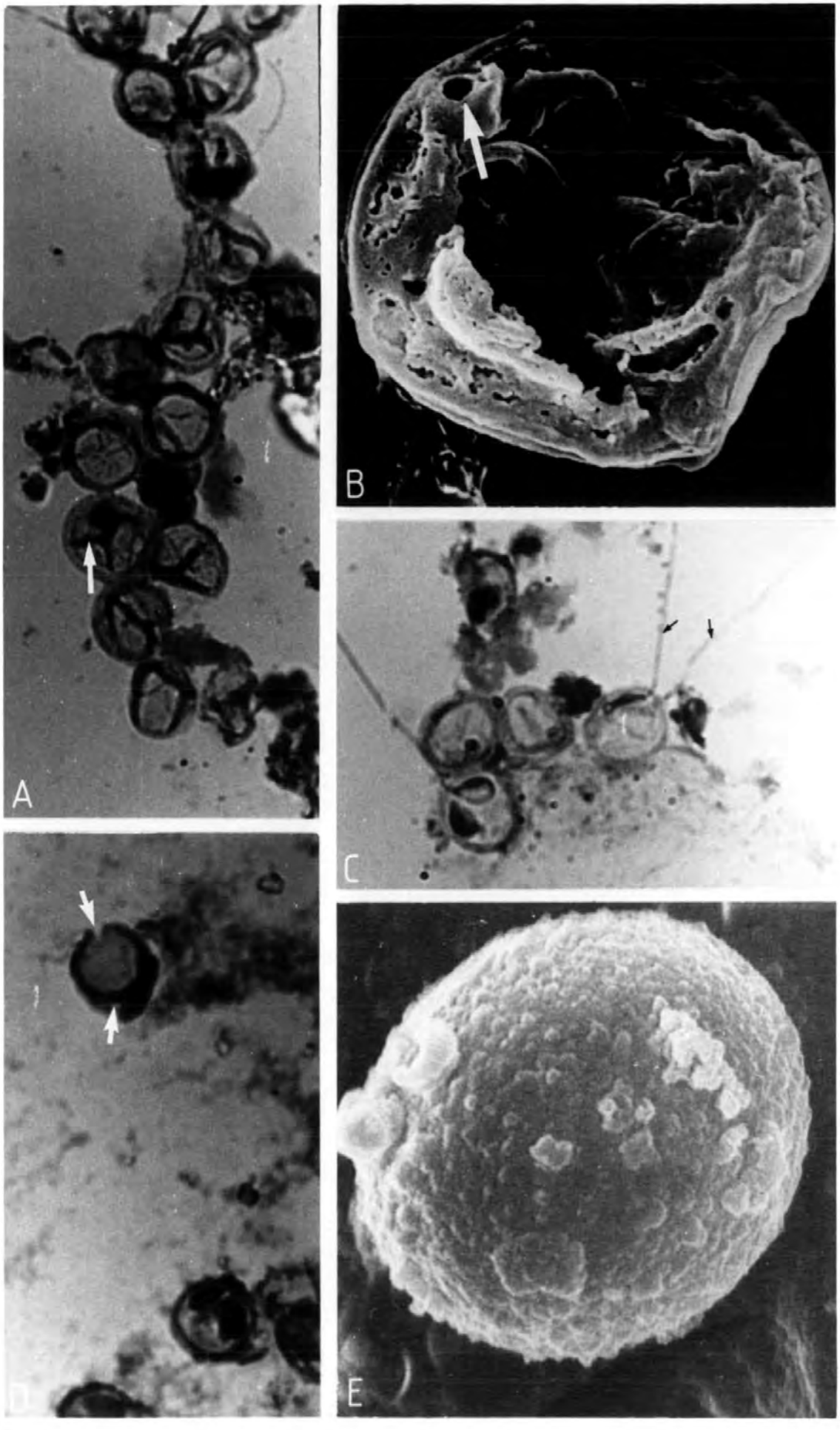
A
B
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PLATE 6

Myxobolus exiguus : cysts on the gut of *Crenimugil labrosus*

6-A Heavy infestation of the pyloric caecae with white cysts x 3

6-B Portion of the small intestine to show cysts in the peripheral region of the gut wall x 12.5

6-C Three cysts on the gut wall, as seen with scanning electron microscopy x 345

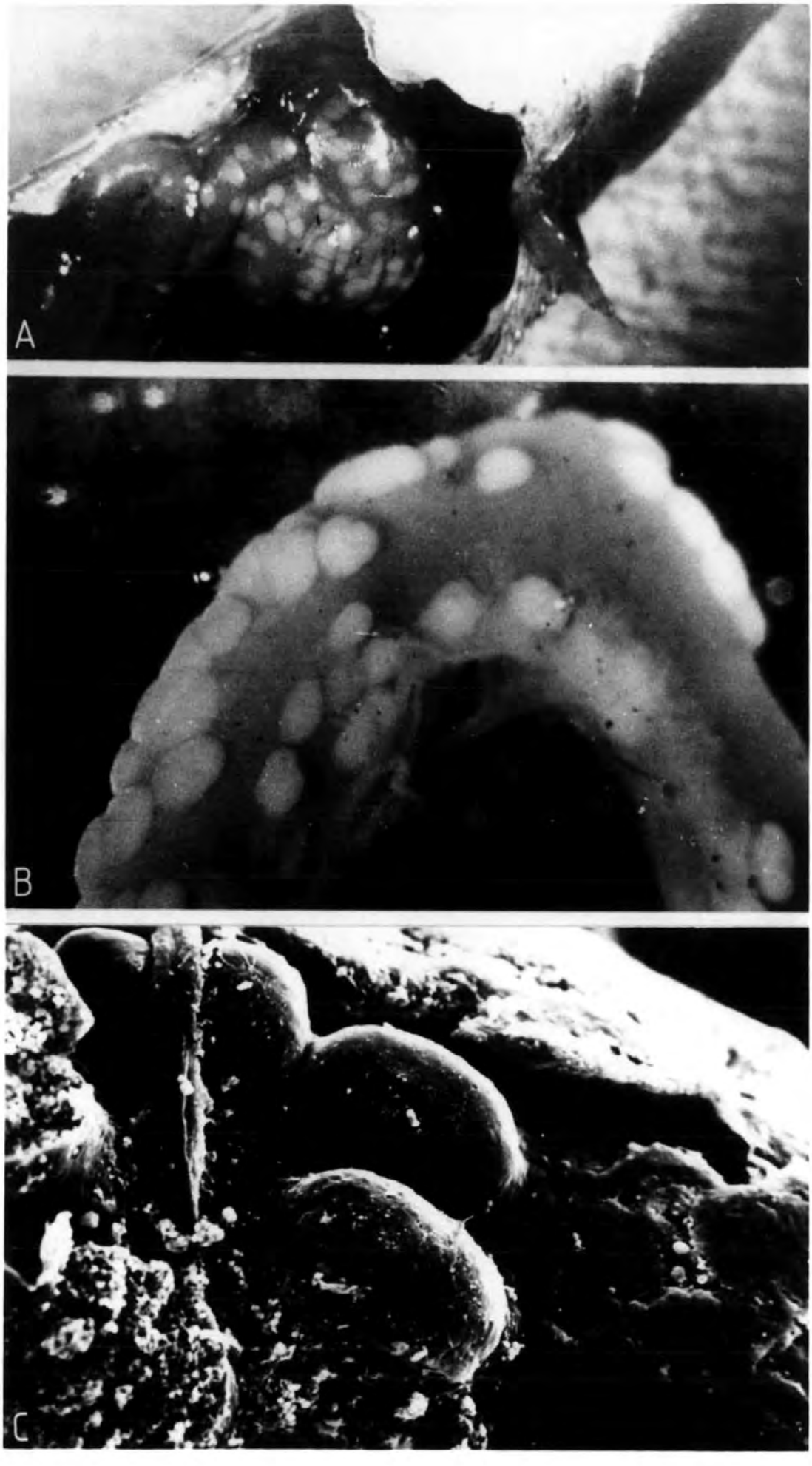

A
B
C

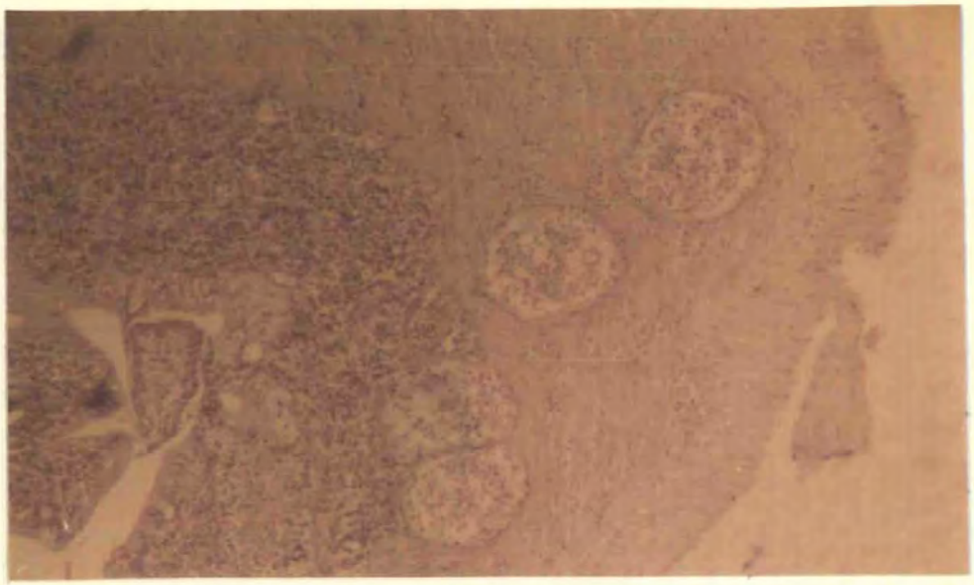
PLATE 7

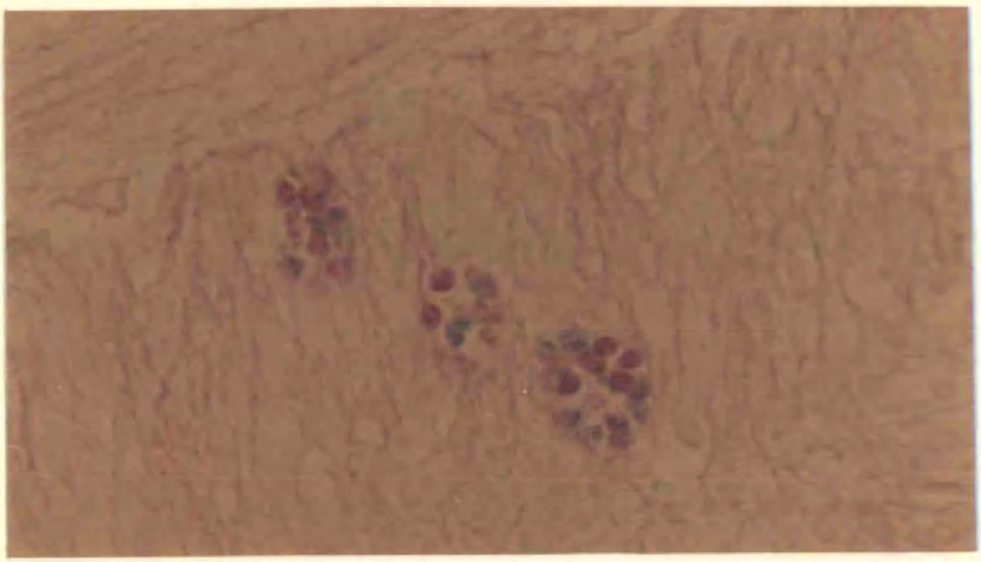
Myxobolus exiguus : experimental infection of *Crenimugil labrosus* with the gut form

7-A Section of mullet gut 8 weeks post-infection, showing a single locus of infection x 250 P.A.S./Alcian blue

7-B Section of mullet gut 8 weeks post-infection, with three loci containing sporulating masses x 384 P.A.S./Alcian blue

7-C Section of mullet gut 10 weeks post-infection, showing larger sporulating plasmodia x 150 Haematoxylin





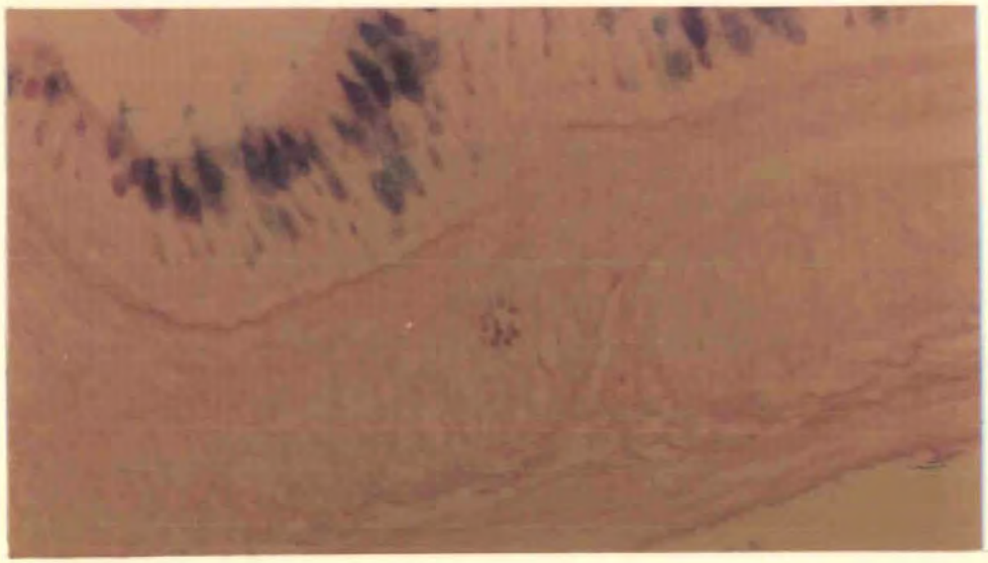


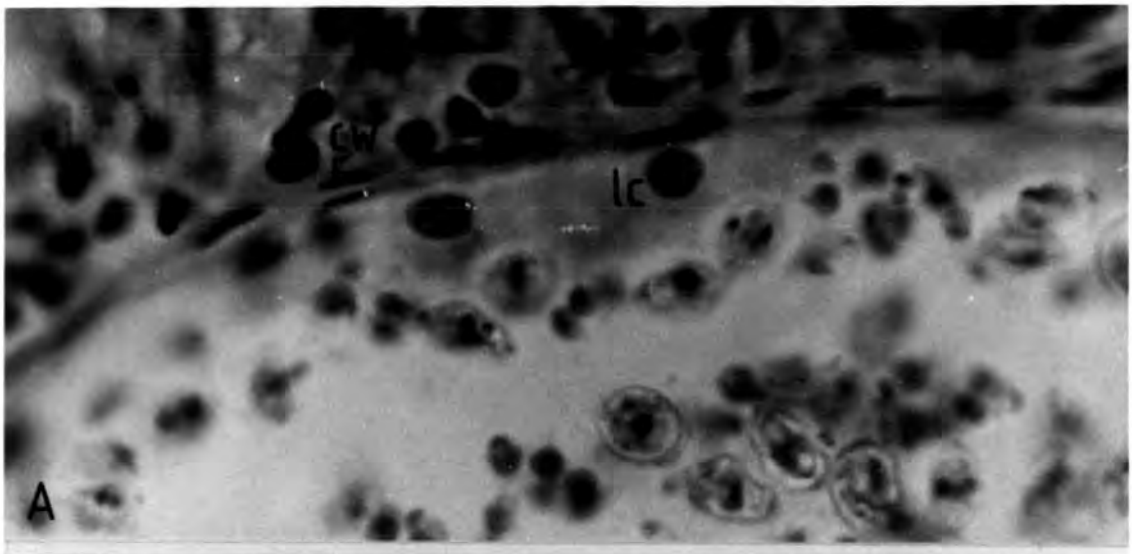
PLATE 8

Myxobolus exiguus : experimental infection of Crenimugil labrosus with the gut form, at 12 weeks post-exposure

8-A Section of plasmodium, showing the cyst wall and peripheral region of the plasmodial mass. Two large epithelioid cells are evident beneath the plasmodium membrane. x 1500 Haematoxylin and Eosin

8-B Section of the intestinal wall, at the level of the lamina propria, showing a single plasmodium enclosed by a cyst wall. Large epithelioid cells are evident at the periphery of the plasmodium, with developing spores at the centre of the mass. Host cell infiltration in the area of infection is also prominent. x 750 Haematoxylin and Eosin

8-C Section through the entire gut wall, containing a single plasmodium x 250 Haematoxylin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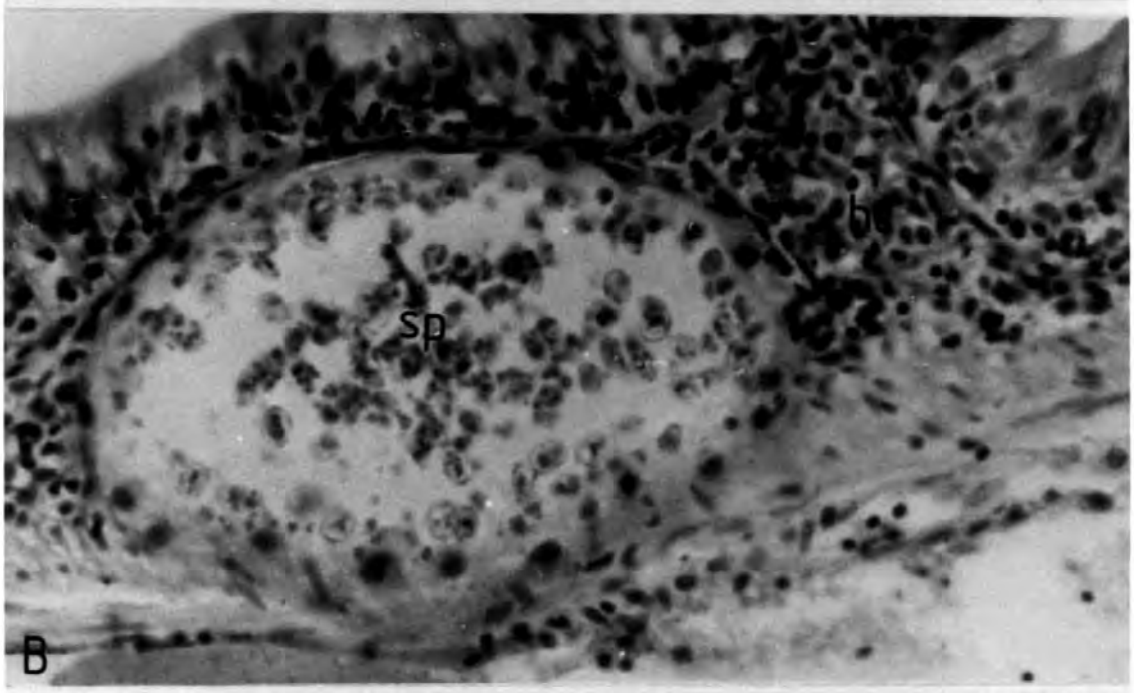
b
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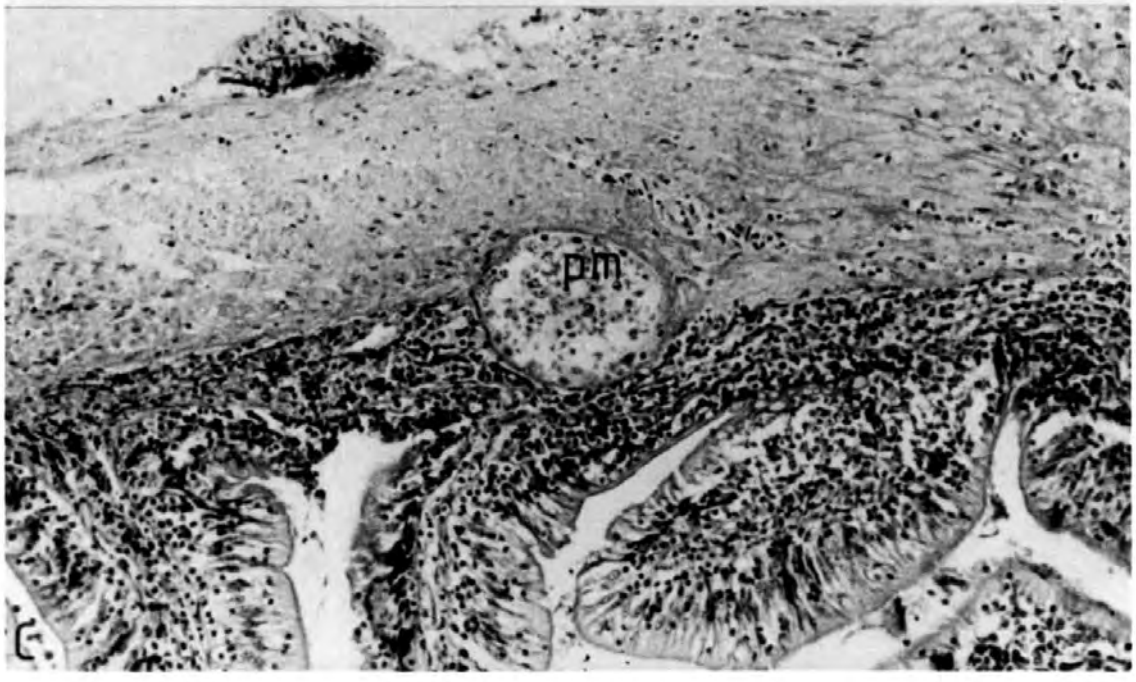

pm
C

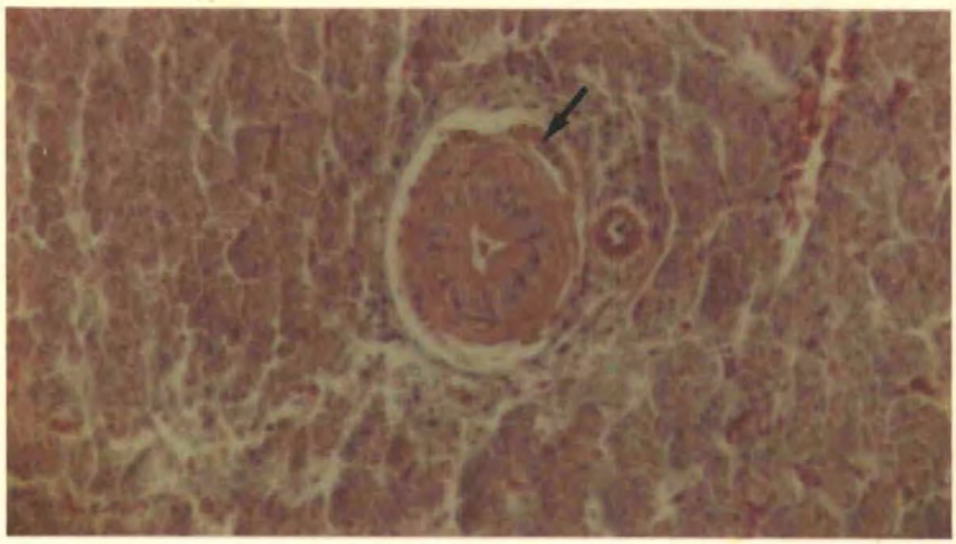
PLATE 9

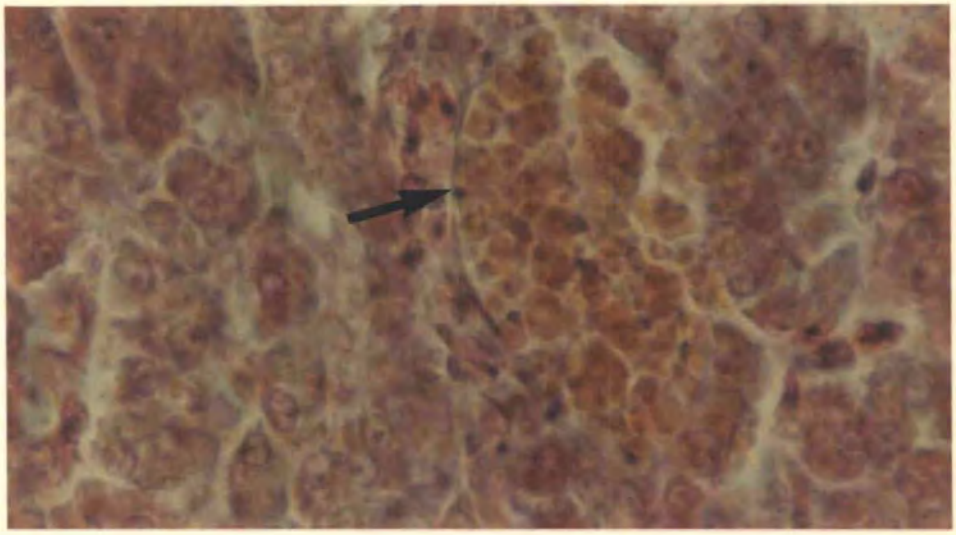
Myxobolus exiguus : hepatic sites of infection in Crenimugil labrosus

9-A Section through hepatic tissue, showing a small plasmodium on the outer surface of a bile collecting duct (arrowed) x 133 Papanicolaou

9-B Section through hepatic tissue containing a plasmodium, enclosed by a thin cyst wall composed of fibroblasts. Sporulating bodies are evident within the plasmodium. x 625 Papanicolaou

9-C Section through a portal area of the liver, showing two P.A.S.-positive loci of infection at each end of the central blood vessel x 81 P.A.S./Coles Haematoxylin





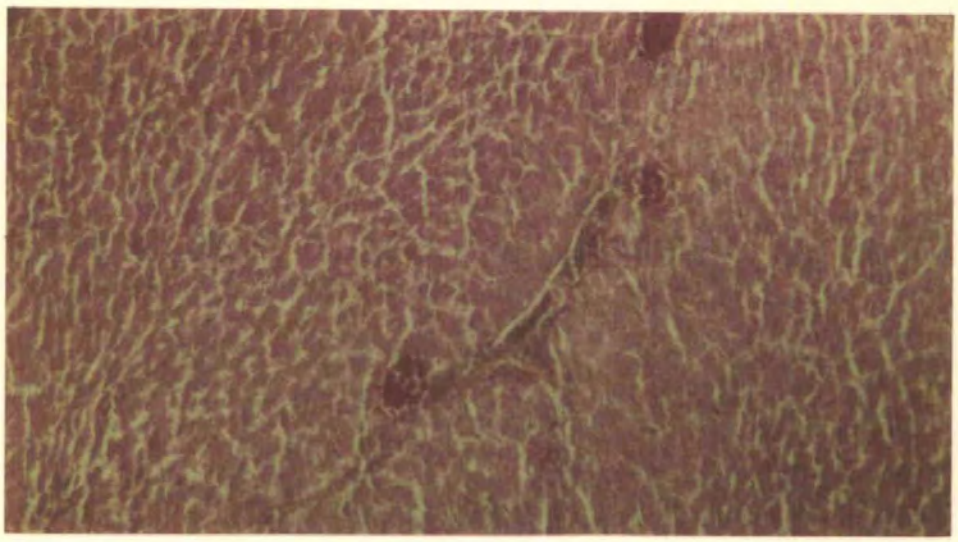
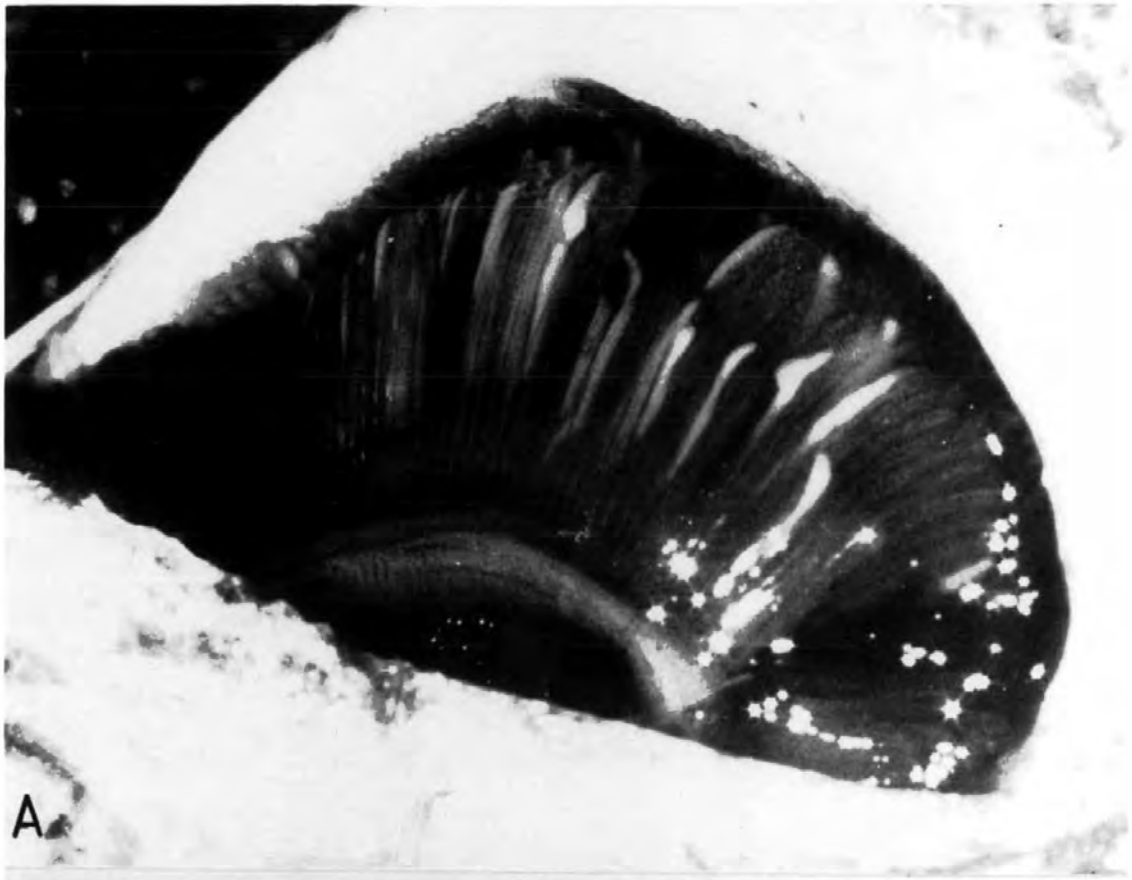


PLATE 10

Myxobolus exiguus : to show distribution of plasmodia in the gill of *Crenimugil labrosus*

10-A Micrograph of an infected gill arch *in situ*, showing elongate white cysts laying along the longitudinal axes of individual filaments x 11

10-B Excised filaments containing plasmodia with prominent white sporulating areas x 110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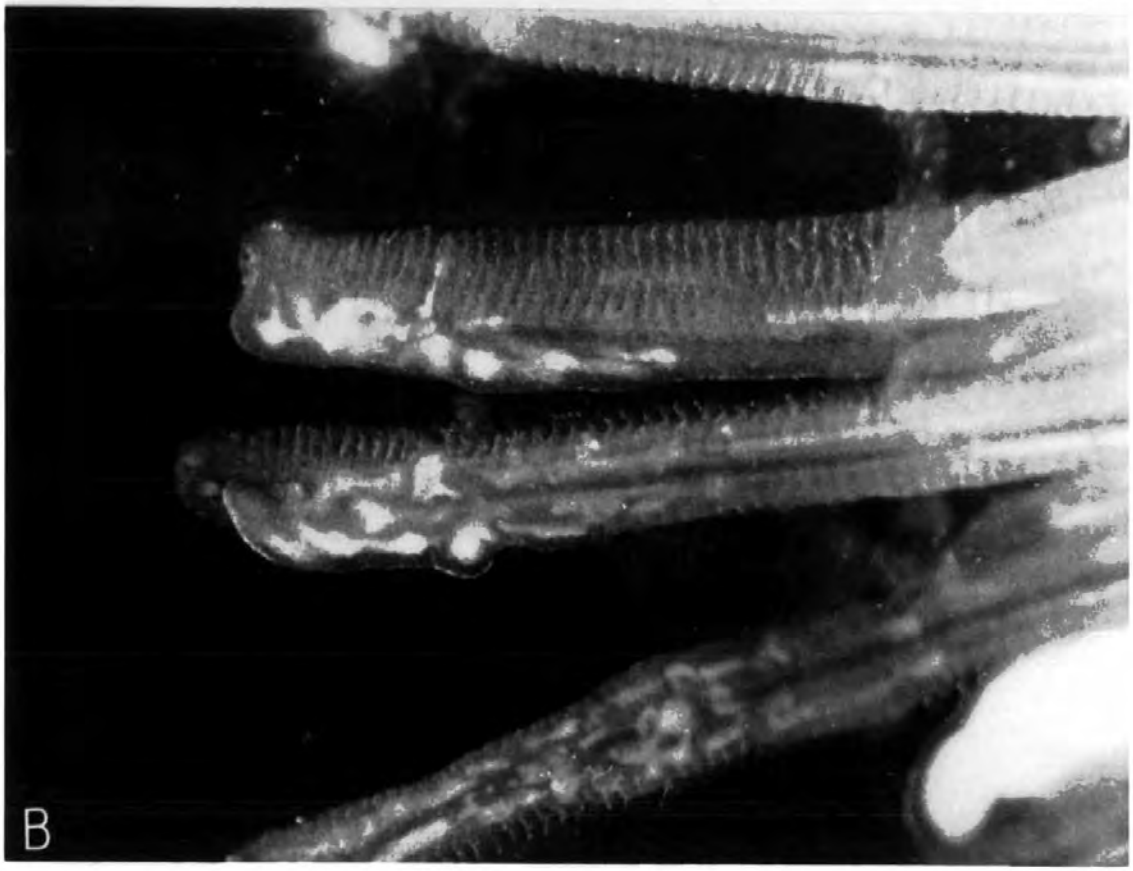
B

PLATE 11

Myxobolus exiguus : scanning electron micrographs of gill plasmodia from Crenimugil labrosus

11-A Large cyst lying on the longitudinal axis of a gill filament x 400

11-B Oblique section of a cyst, cleaved during processing, showing the 'honeycomb' appearance of spores in the plasmodial matrix x 320

11-C Transverse section through a cyst containing numerous well-developed spores. Note the epithelial cells covering the outer surface of the plasmodium x 525

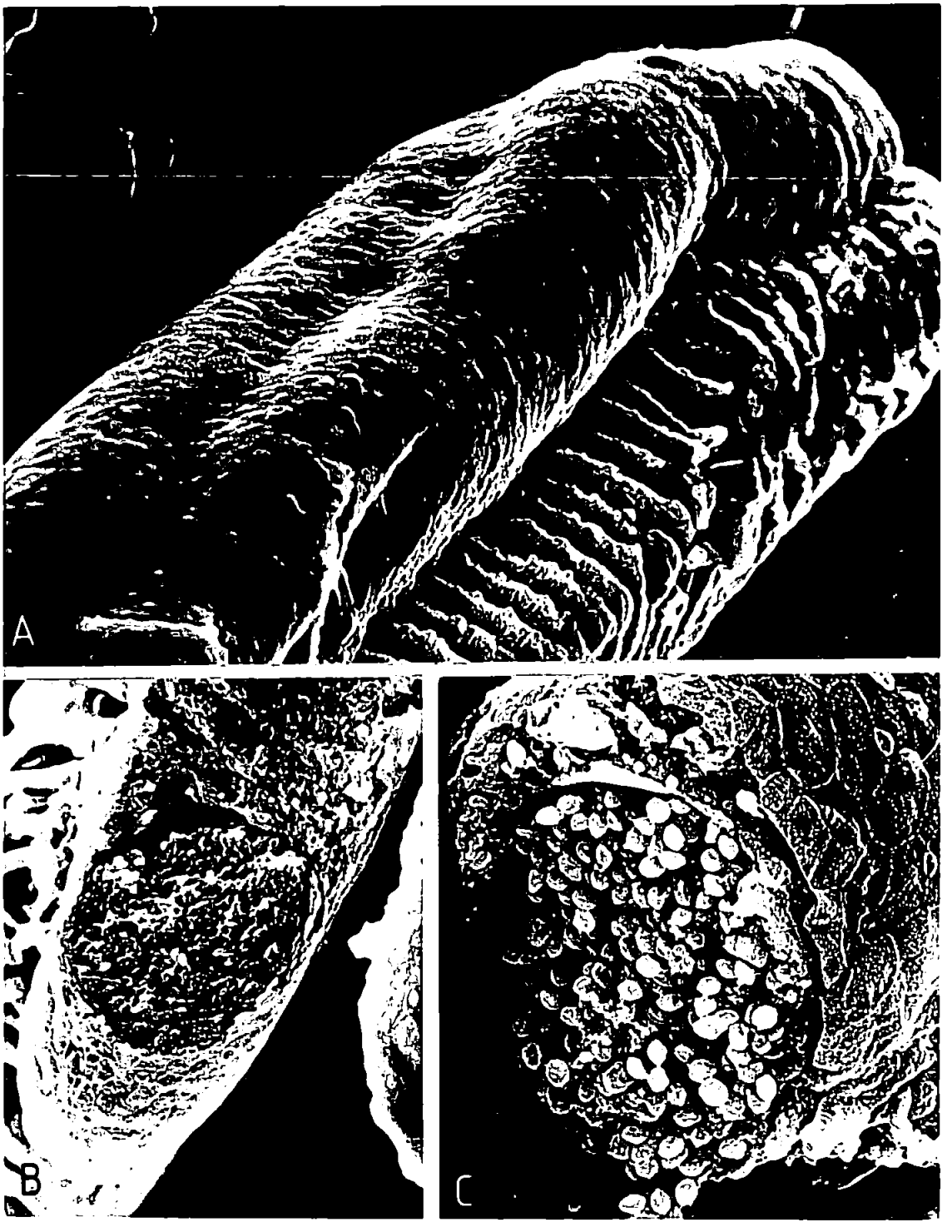
A
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PLATE 12

Myxobolus exiguus : light micrographs of sectioned gill plasmodia from Crenimugil labrosus

12-A Infected gill filaments to show the extent of plasmodia and the loss of secondary lamellae x 82 Haematoxylin and Eosin

12-B Longitudinal section through the basal cartilage of a gill arch to show two sporulating plasmodia (arrowed) x 75 Haematoxylin

12-C Transverse section of infected filaments showing one side of the filaments occupied by plasmodia, with a corresponding loss of lamellae x 230 Haematoxylin and Eosin

12-D Transverse section of a plasmodium with two large individual masses containing spores, and a third distal locus of development containing early nuclei surrounded by a prominent microtubular layer x 440 Haematoxylin and Eosin

12-E Longitudinal section of a filament completely occupied by plasmodia with spores x 440 Haematoxylin

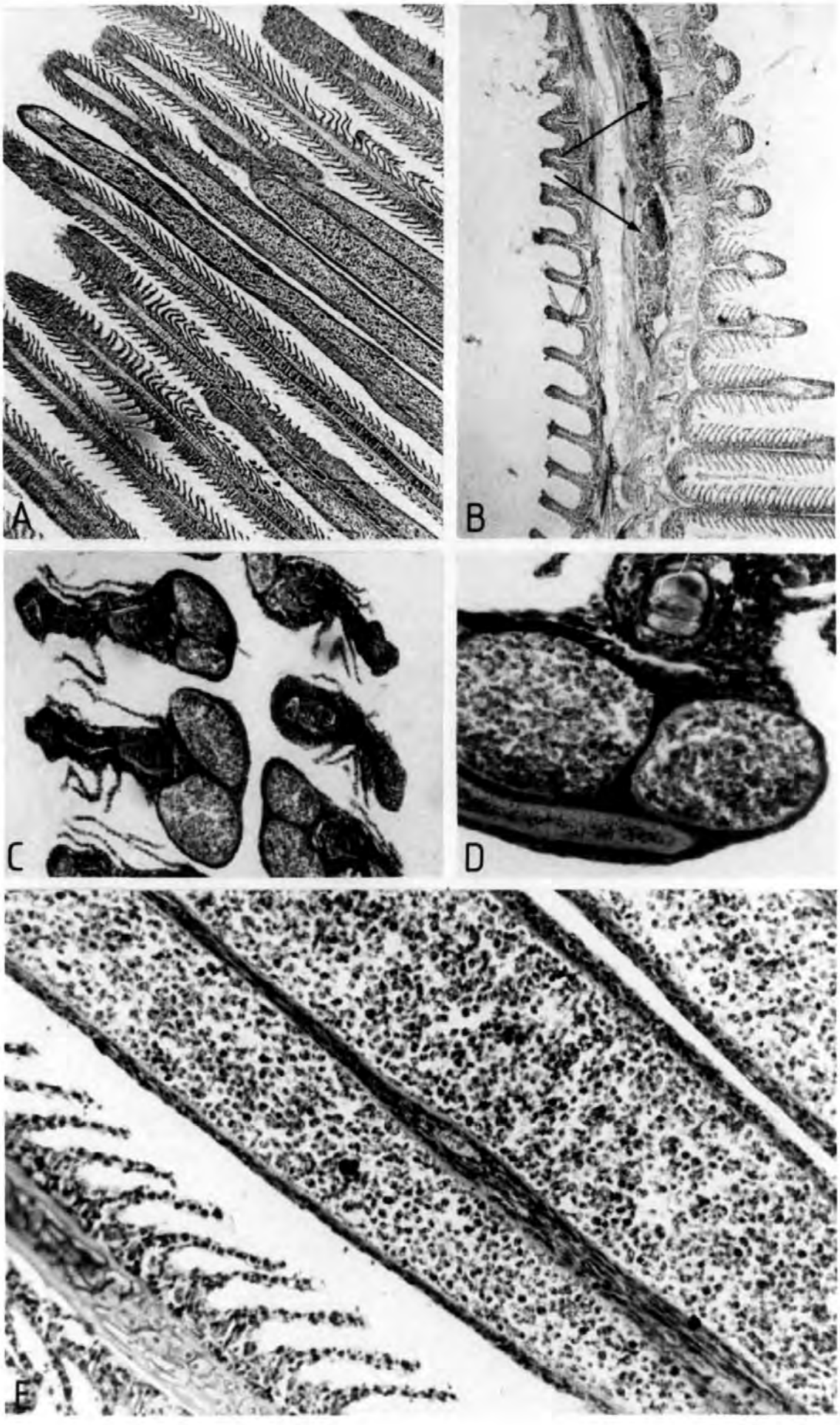
A
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PLATE 13

Myxobolus exiguus : infection of the tegument of Crenimugil labrosus I

13-A Dorsal surface of a 1-group mullet to show several pale cysts x 5

13-B Detached scales infected with segmented plasmodia. Note the expanded melanophores in the epithelial layers covering the masses x 8.5

13-C 0-group mullet infected with numerous dark plasmodia on the dorsal and lateral surfaces x 2

13-D Single detached scale infected with a plasmodium overlaid by epithelium containing melanophores x 65

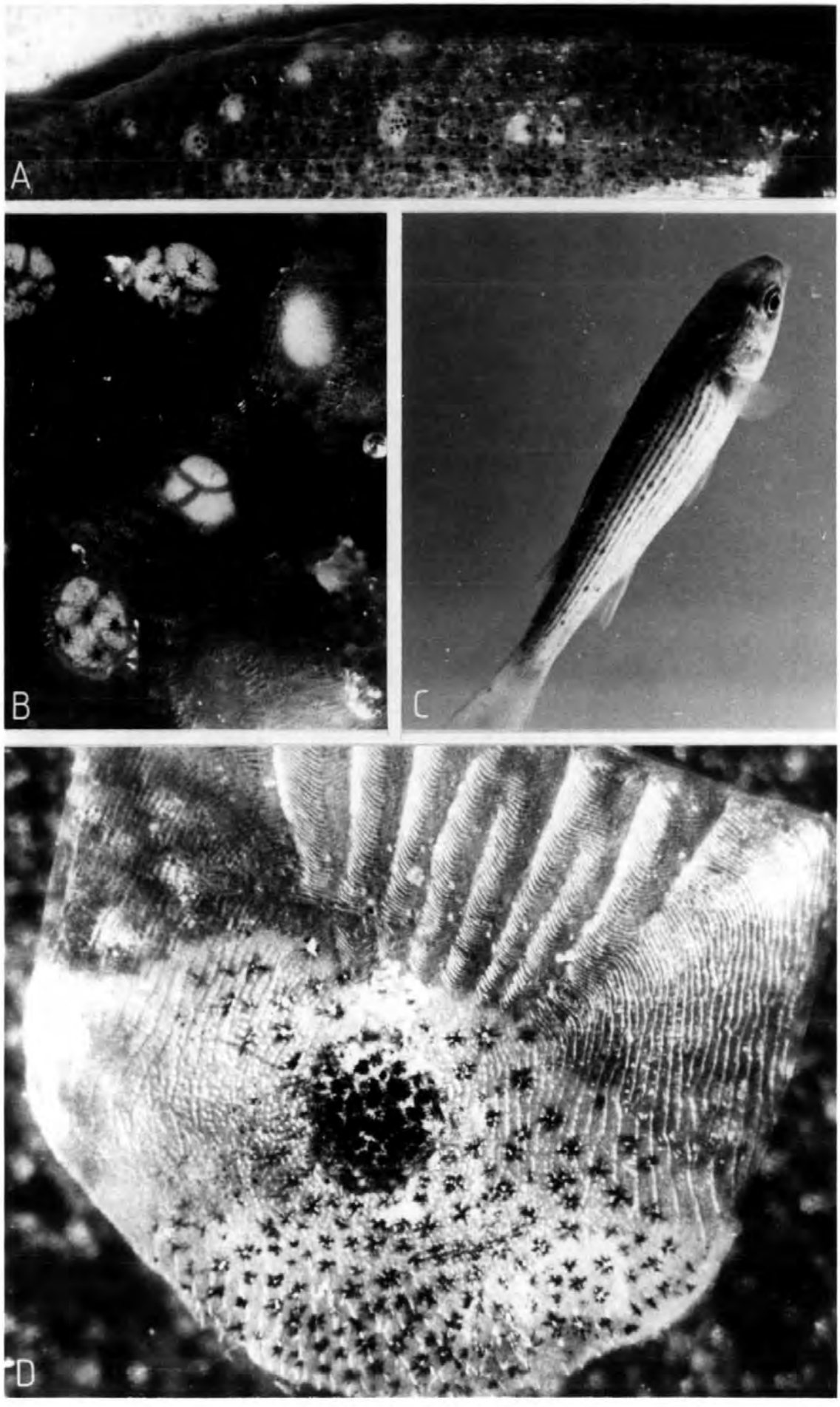
A
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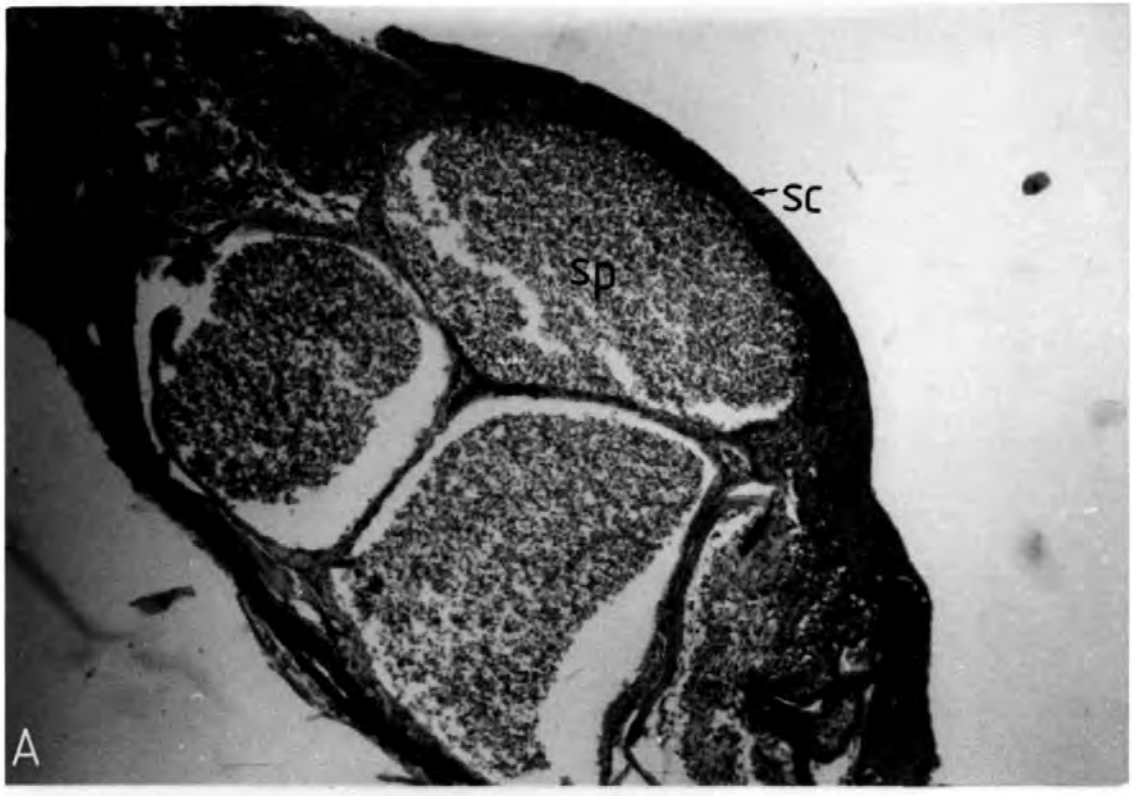
PLATE 14

Myxobolus exiguus : infection of the tegument of Creminugil labrosus II

14-A Section through the outer tegument showing a plasmodium beneath a scale. Note the compartmental appearance of the mass x 220 Haematoxylin and Eosin

14-B Transmission electron micrograph to show the host-plasmodium interface, with a fibrous layer adjacent to the plasmodium x 7292

14-C Transmission electron micrograph of a plasmodium, showing spores developing in the interior zone, and a reticulated matrix x 3000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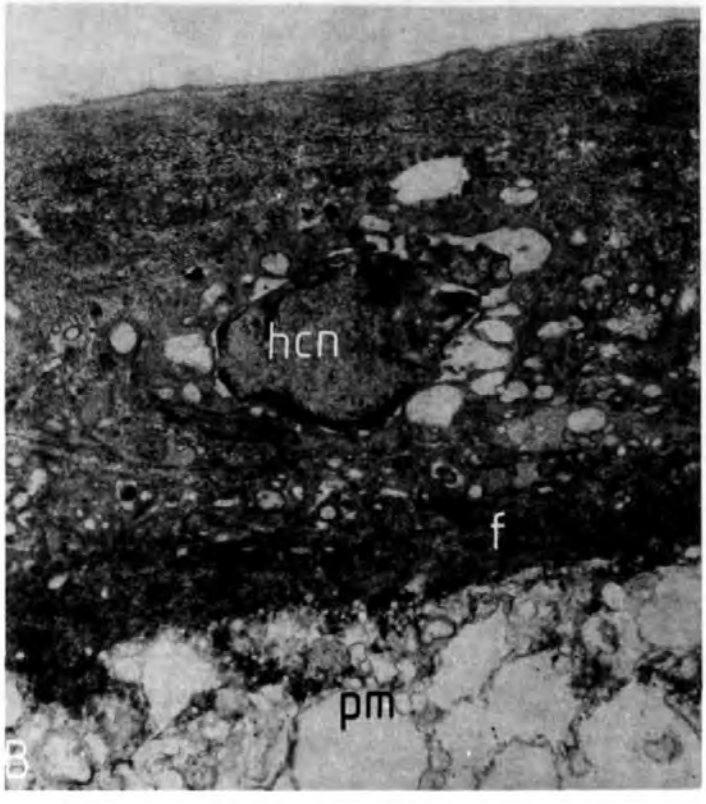
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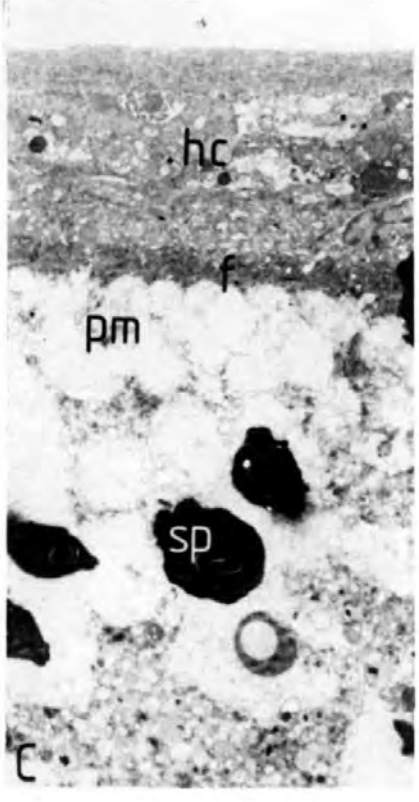
hc
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PLATE 15

Myxobolus exiguus : ultrastructure of infected gill filaments of Crenimugil labrosus

Transmission electron micrograph to show the general structure of the plasmodium and surrounding host cells. The plasmodium is at an advanced stage of development, exhibiting active sporogenesis. Note the structure of the peripheral layers of the plasmodium containing microtubular and vesicular zones.
x 2943

PM
mt
Sb
sp

PLATE 16

Myxobolus exiguus : ultrastructure of the host-parasite interface in gill infections in Crenimugil labrosus

16-A Section at the interface, showing plasmodium membrane (arrowed) with underlying microtubular and interior zones. Note the host cells surrounding the mass x 6591

16-B High power detail of tubules in the microtubular zone (arrowed) x 125,000

16-C Section through outer zone of the plasmodium to show prominent microtubules arranged perpendicular to the membrane of the plasmodium. Note the microsporidian spore at the periphery of the internal zone (arrowed). x 12000

16-D Peripheral zones of the plasmodium to show microtubules and vacuoles in their respective layers x 9050

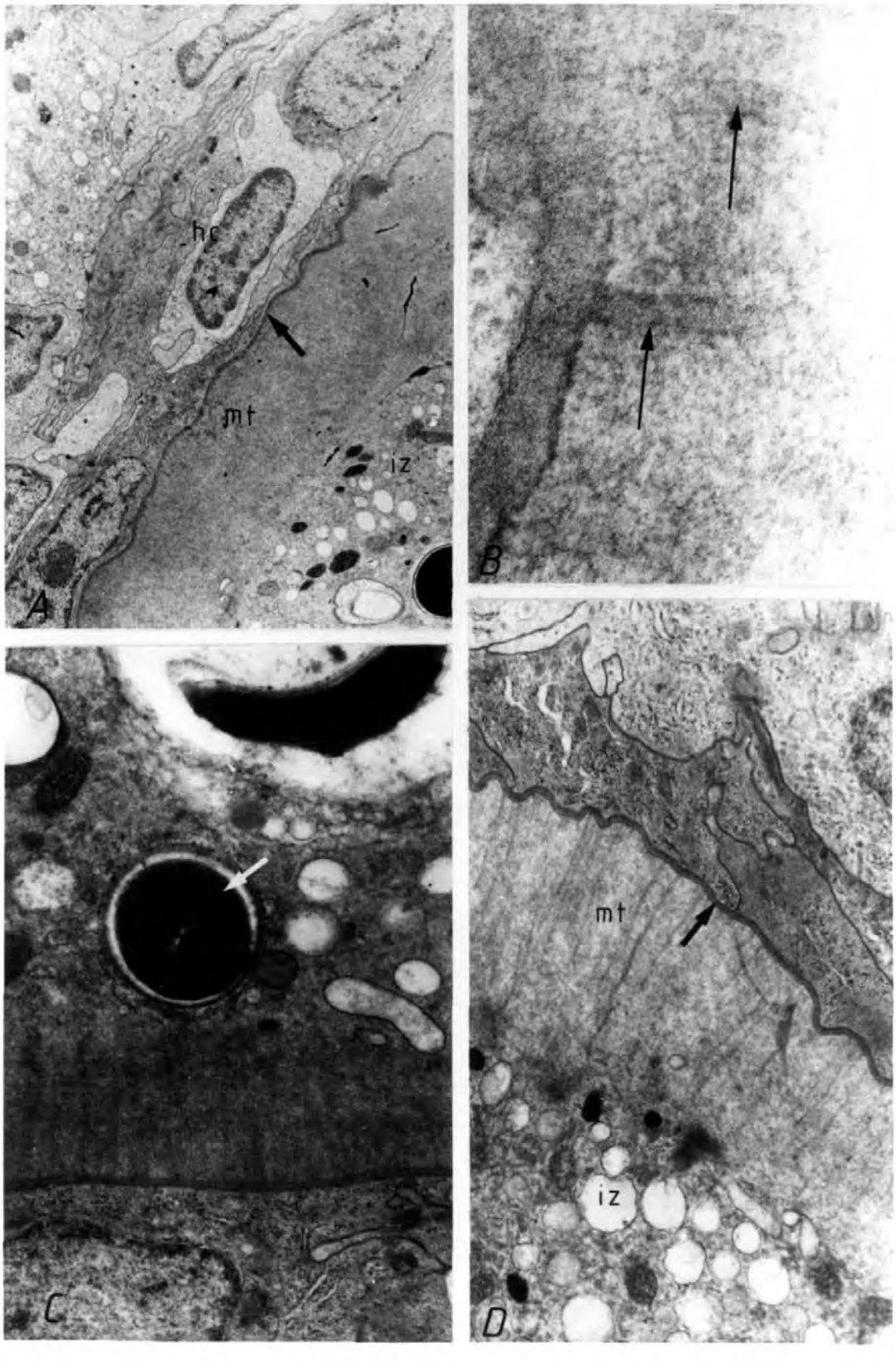
hc
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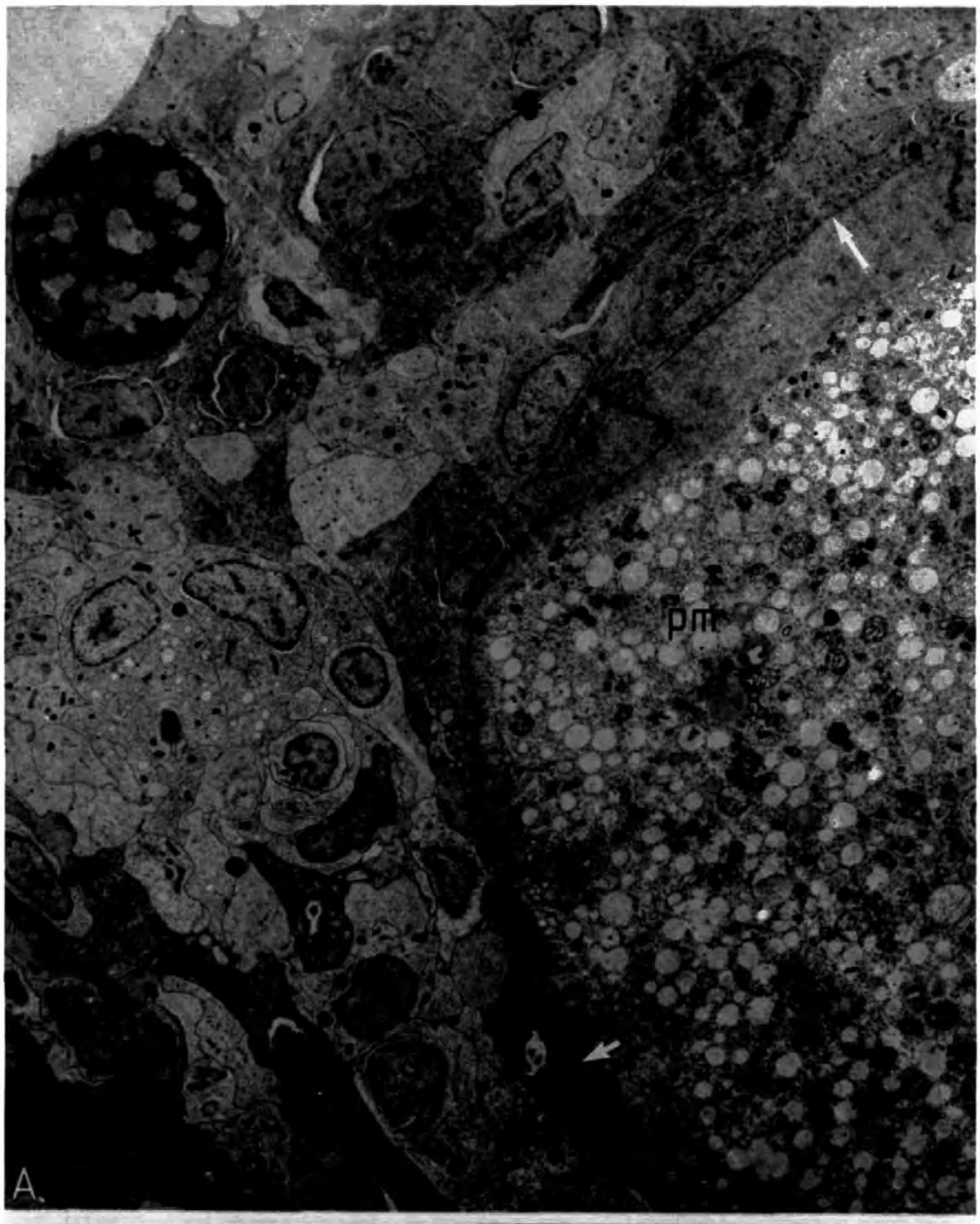
PLATE 17

Myxobolus exiguus : ultrastructure of young gill plasmodia from Crenimugil labrosus

17-A Section through an infected lamella to show the general structure of the young plasmodium. Note early generative nuclei in the interior of the mass, with the microtubular layer at the periphery. x 3575

17-B The surface of an early plasmodium in the gill, to show microvilli originating from the plasmodial membrane (arrowed). Note microtubules beneath the outer membrane. x 38250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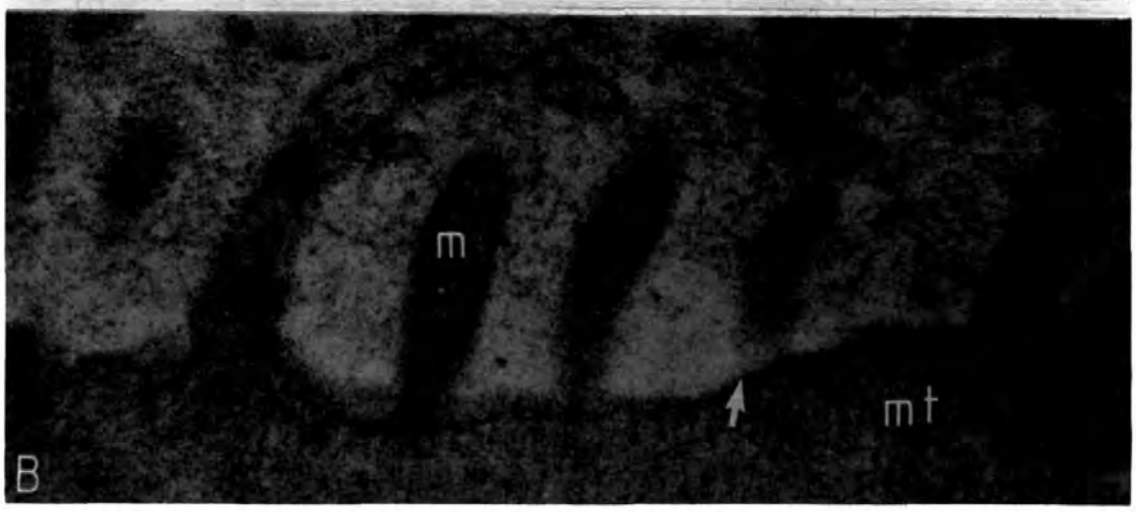
m
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B

PLATE 18

Myxobolus exiguus : ultrastructure of young plasmodia from the intestine of Crenimugil labrosus

18-A Section through an entire young plasmodium, surrounded by a cyst wall of fibroblasts. Note the large epithelioid cells at the periphery, with their cytoplasm spreading along the inner boundary of the outer membrane, and germinative cells at the centre of the plasmodium. x 3250

18-B Early plasmodium, containing centrally-located large epithelioid cells (arrowed) x 3000

18-C Peripheral region of plasmodium, to show the cytoplasmic extensions of the epithelioid cells covering the plasmodial membrane. Note the numerous membranous elements. x 3300

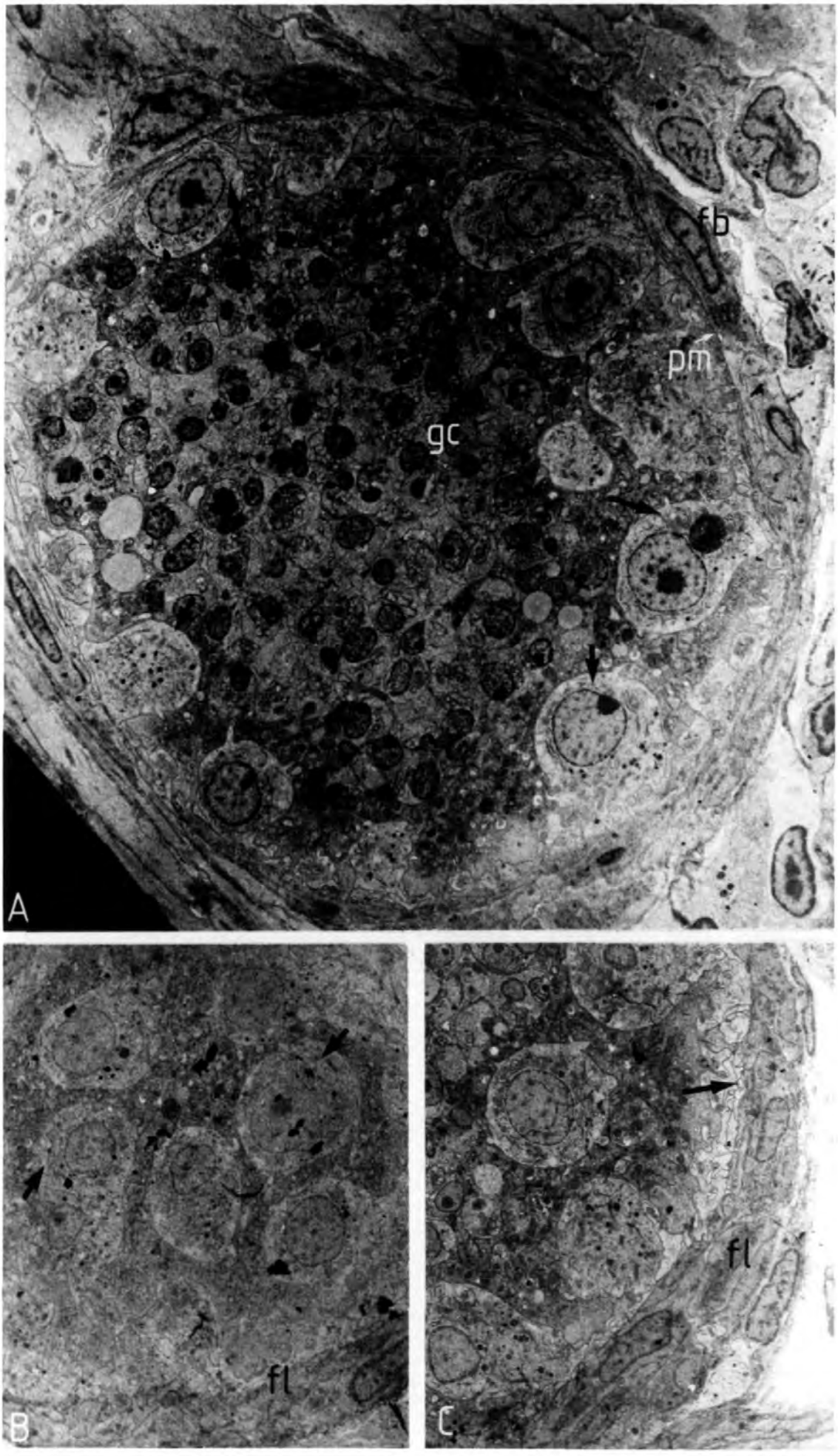
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PLATE 19

Myxobolus exiguus : ultrastructure of large epithelioid cells from gut plasmodia of Crenimugil labrosus

19-A Epithelioid cells dividing. Note the large nuclei and cytoplasmic extensions from the cell membranes. x 11,000

19-B Epithelioid cell adjacent to the plasmodium membrane. Note the arrangement of cytoplasmic and membranous elements along the boundary of the plasmodium. x 5520

19-C Section at the host-parasite interface, to show an epithelioid cell at the periphery of the plasmodium. Note the proliferation of membranous elements along the plasmodial membrane (arrowed). x 7950

19-D Further development of the epithelioid cell cytoplasm at the periphery of the plasmodium. Arrows indicate the cell membrane of the large cell. x 8820

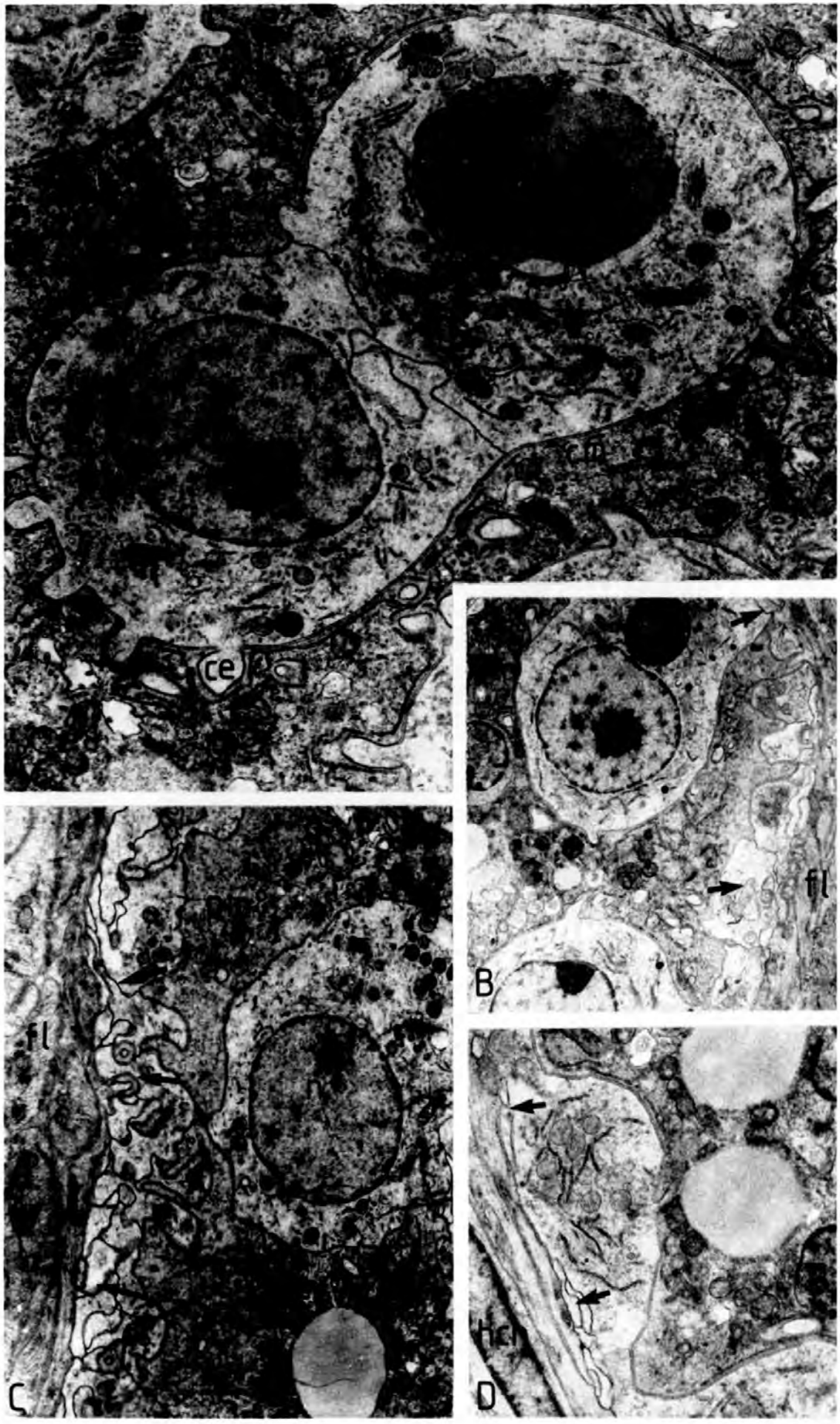
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PLATE 20

Myxobolus exiguus : histochemical studies on stages from Crenimugil labrosus

20-A Transverse section through an infected gill filament
Alcian yellow x 940

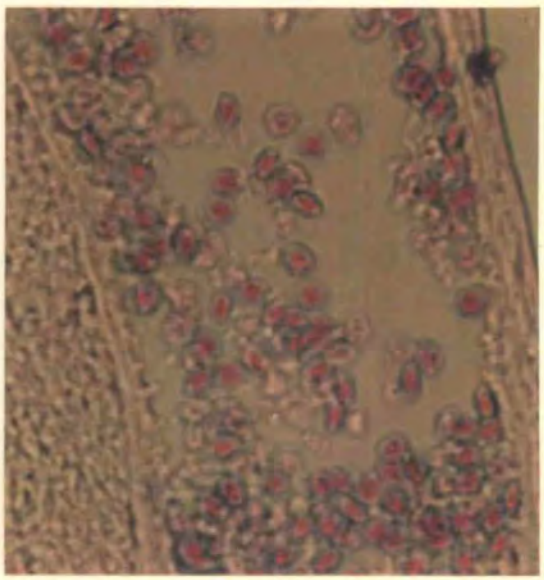
20-B Longitudinal section through an infected filament
Alcian blue pH 1.0 x 1000

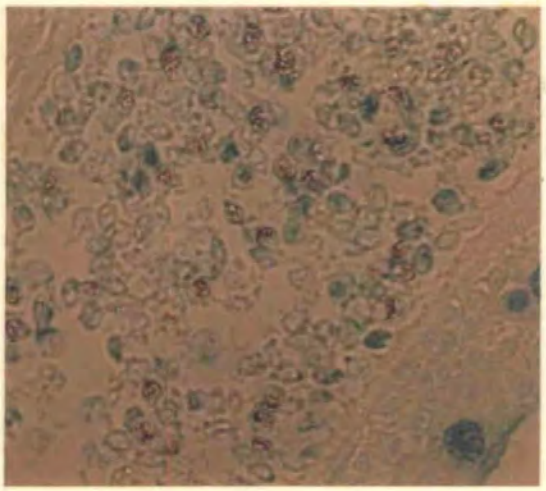
20-C Longitudinal section through an infected filament
P.A.S. x 950

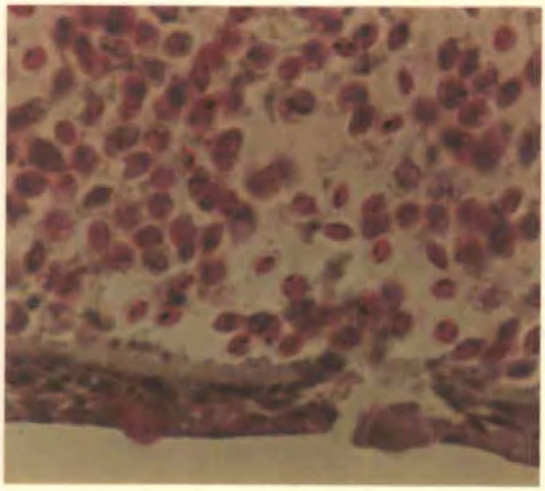
20-D Longitudinal section through an infected filament
Alcian blue pH 2.5 x 1200

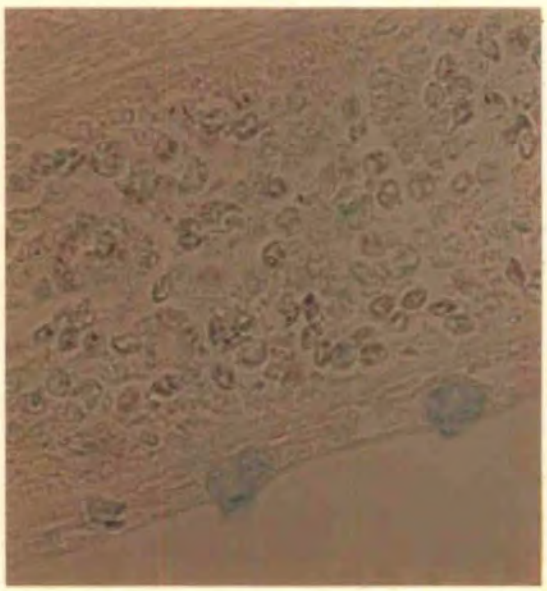
20-E Oblique section through an intestinal plasmodium
P.A.S. - Alcian blue x 960

20-F Longitudinal section through an infected filament
Toluidine blue x 470









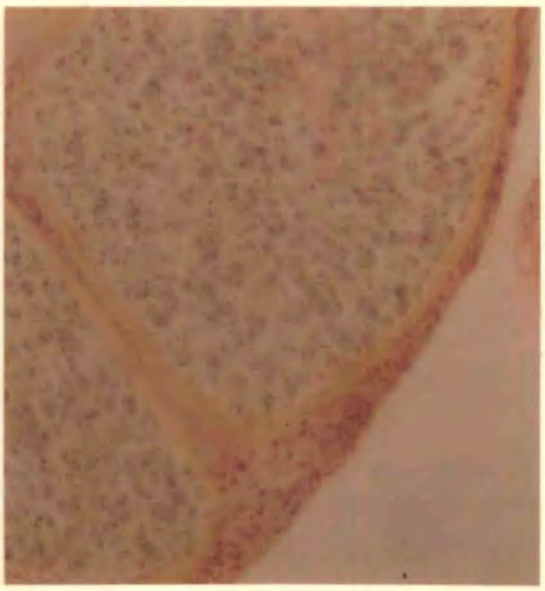


PLATE 21

Myxobolus exiguus : the development of sporogenic cells in plasmodia from Crenimugil labrosus

21-A Section through a monosporoblast to show the three types of sporogenic cell. Note the transverse section of a loop of external tube in the capsulogenic cell (arrowed). x 10873

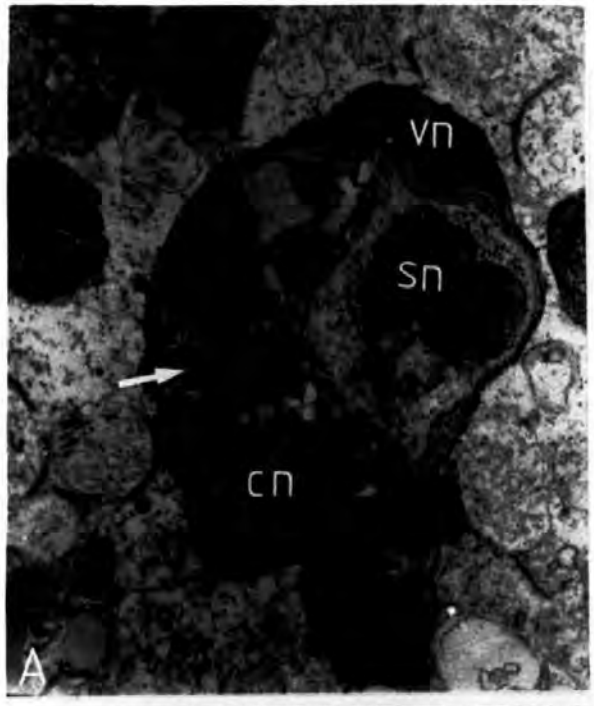
21-B Section through a sporoblast at the level of the capsulogenic cells x 15290

21-C Section of a disporous sporoblast showing differentiating sporogenic cells. The arrows indicate early capsular primordia within capsulogenic cells. x 13420

21-D Entire disporous sporoblast to show the two developing spore masses. Note the prominent capsulogenic and sporoplasmic nuclei, and the capsular primordium (arrowed). x 7850

21-E Two germinative cells to show the large nuclei and nucleoli, and the enclosing nurse cell with a degenerating nucleus. x 15900

21-F Single germinative cell, with adjacent enveloping nurse cell. x 20,020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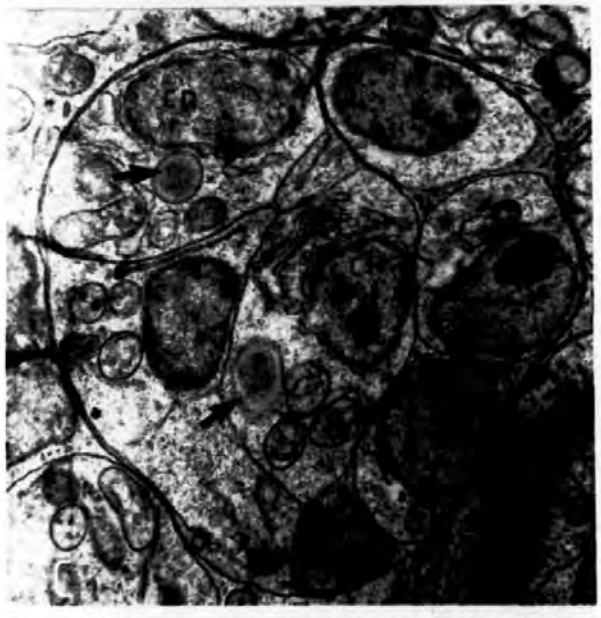
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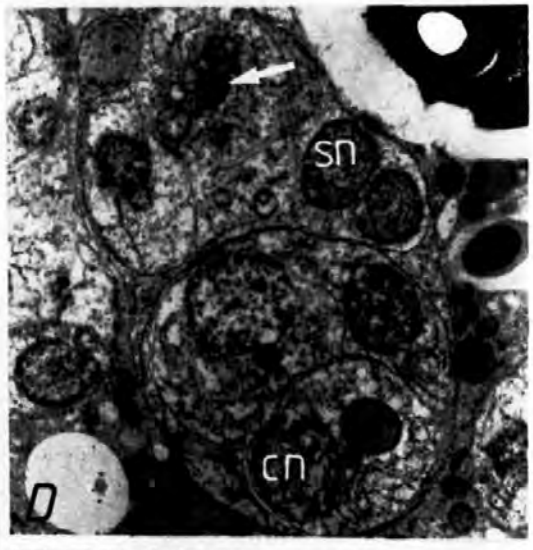
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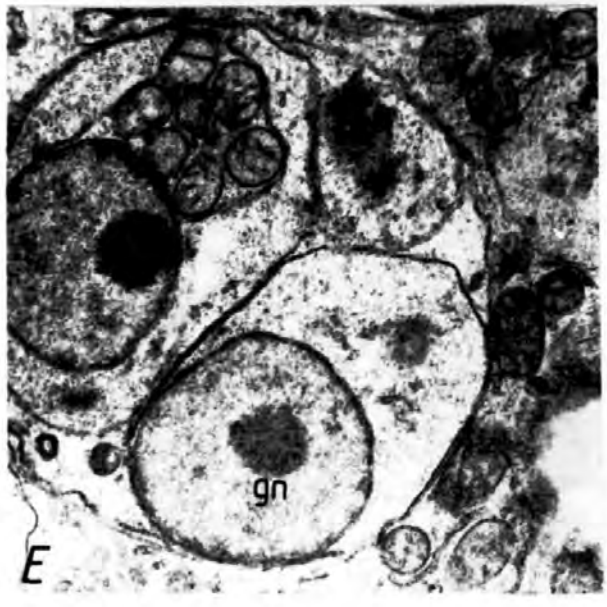
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PLATE 22

Myxobolus exiguus : development of the spore valves in plasmodia from Crenimugil labrosus

22-A Section through a sporoblast to show a developing spore at a stage where the valve cells have almost completely surrounded the other sporogenic elements. Note the area of incomplete enclosure (arrowed). x 13860

22-B More advanced section to show complete enclosure of the sporogenic mass by the valve cells. The cytoplasm of the enclosing cells contains degenerating elements as electron-dense masses. Note the initiation of a sutural junction at each end of the spore body. x 11147

22-C Section of the posterior end of a spore to show the formation of the sutural junction, with microtubules present in apposing limbs of the valve cells. x 26200

22-D The sutural junction showing microtubules in longitudinal section. Note the single large electron-dense body in the valve cell cytoplasm. x 31,440

22-E Further development of the suture in an immature spore, showing a degenerating valve cell nucleus. x 41,400

22-F The sutural joint, and expanded sutural ridge in a well-developed spore x 22,000

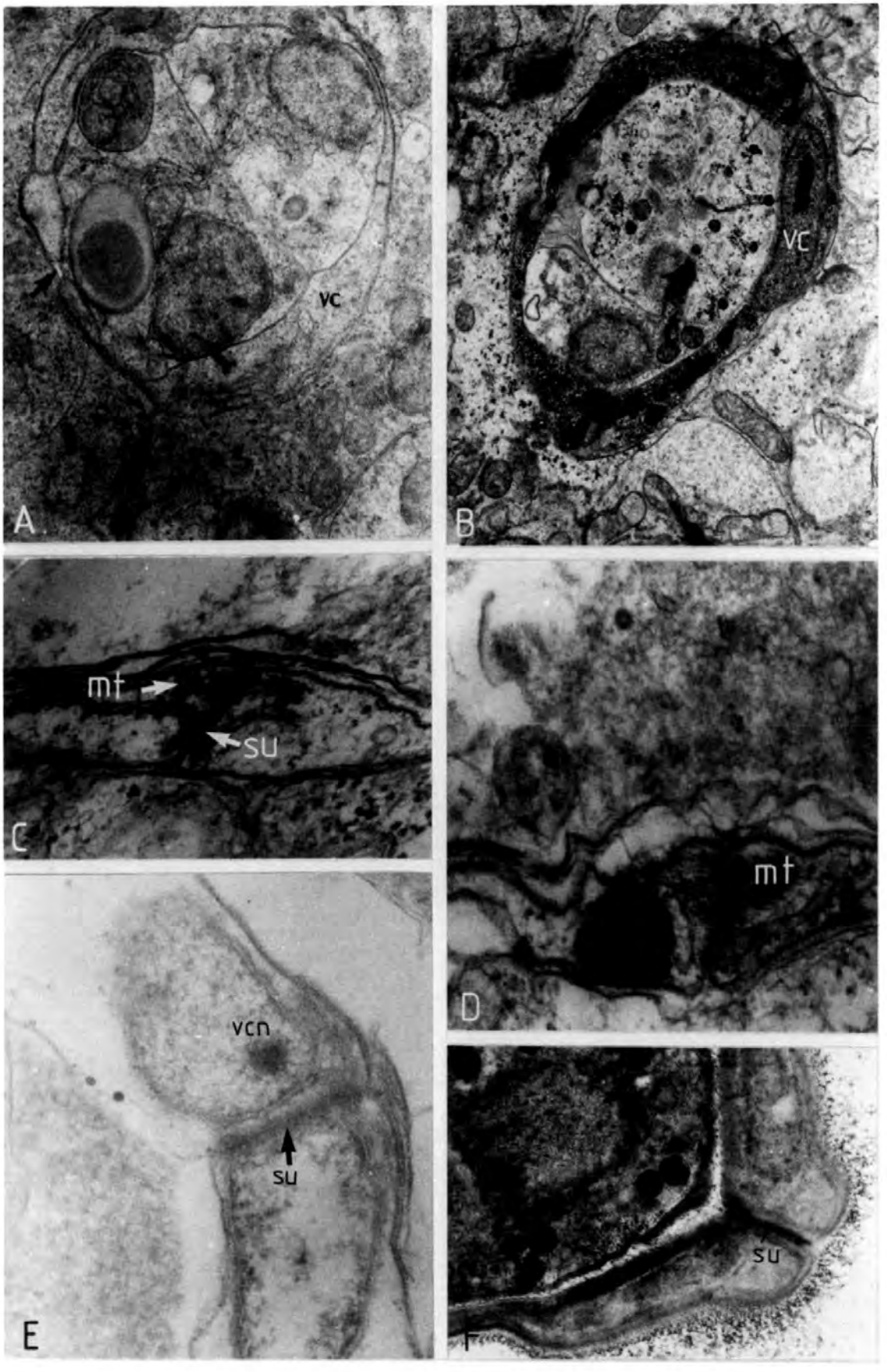
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PLATE 23

Myxobolus exiguus : development of the polar capsules I

23-A Section through a capsular cell to show the capsule primordium containing filament precursor substance. Note the reflexed junction of the capsule and the external tube. x 19,428

23-B Early capsular cell retaining the nucleus adjacent to the club-shaped body. Note the electron-dense ring at the apex of the primordium. x 36,400

23-C Section of the capsule to show continuity of the filament precursor substance with the external tube x 16,500

23-D Disporous sporoblast in which both spore members contain reflexed capsular sacs x 7800

23-E Club-shaped bodies in the cytoplasm of the capsular cells (arrowed) x 10,140

23-F Cross-section of the external tube from the cytoplasm of a capsular cell. The tube appears hollow with electron-dense walls, re-inforced with microtubular elements. x 118,518

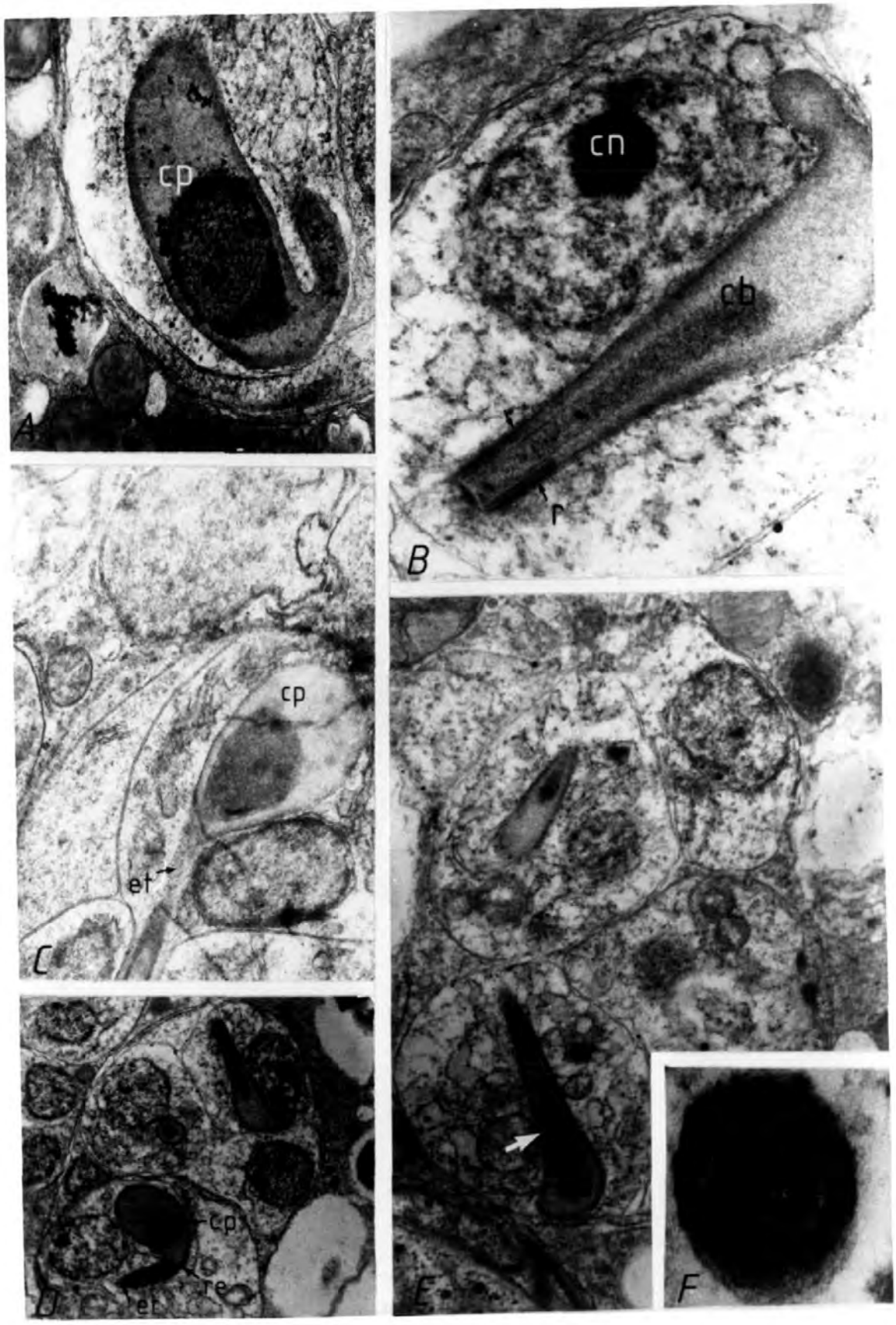
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PLATE 24

Myxobolus exiguus : development of the polar capsules II

24-A Section through the anterior portion of a sporoblast to show two well developed polar capsules with withdrawn coiled filaments x 19,500

24-B Section through a single spore member of a developing sporoblast at the level of the capsule cells. One cell contains several elements of the external tube close to the capsular sac; the other cell shows the point of reflex between the sac and tube in transverse section (arrowed). x 24,440

24-C Sporoblast containing spores with capsules in various stages of development. The upper capsule is aligned opposite to an electron-dense plaque in the valve cell membrane (arrowed). The lower capsule shows the tube in the process of withdrawal. x 10,140

24-D Developing capsules surrounded by cross-sections of the external tube in the cytoplasm, to show the degree of internal coiling and length of the tube. x 10,636

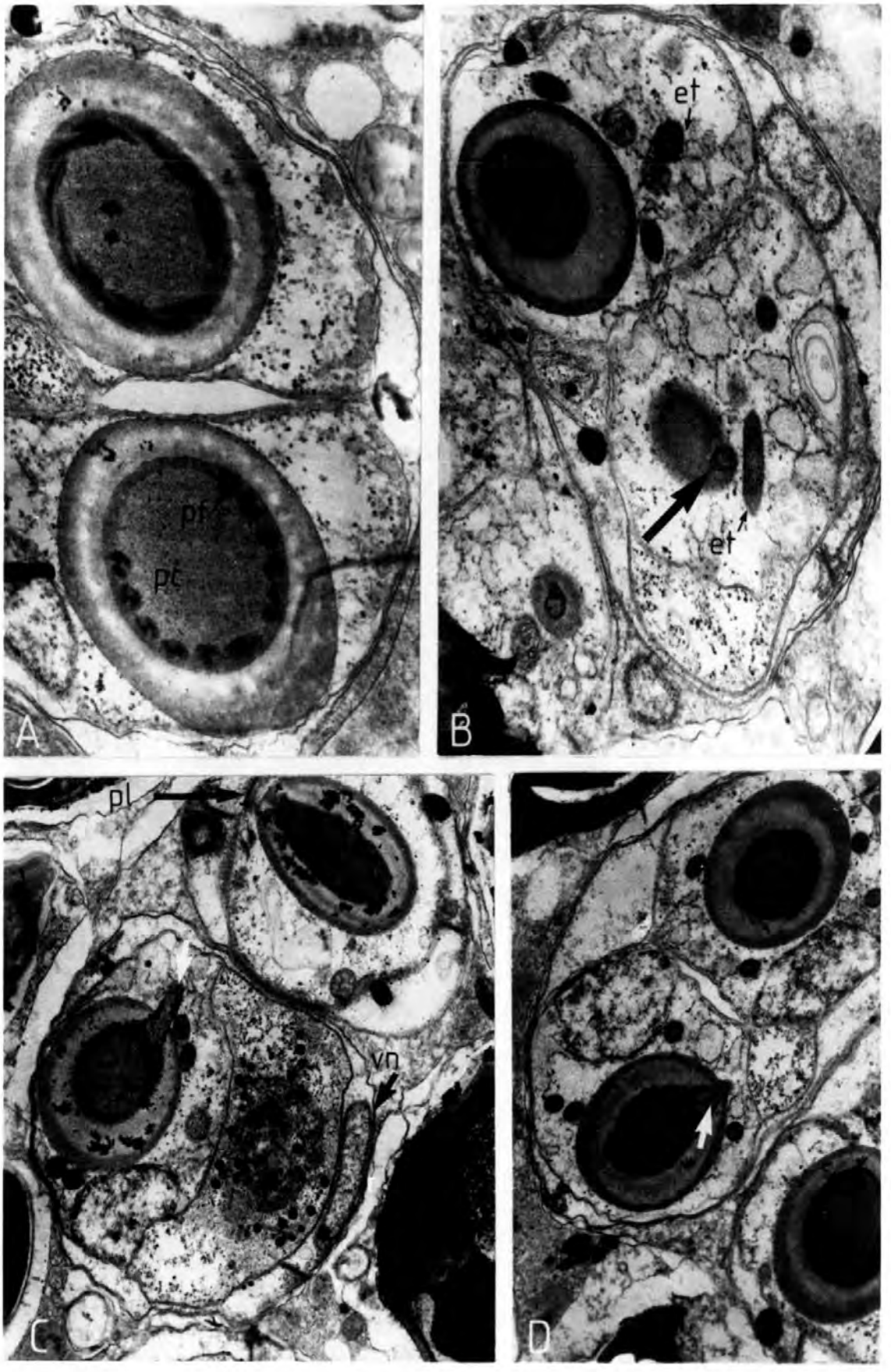
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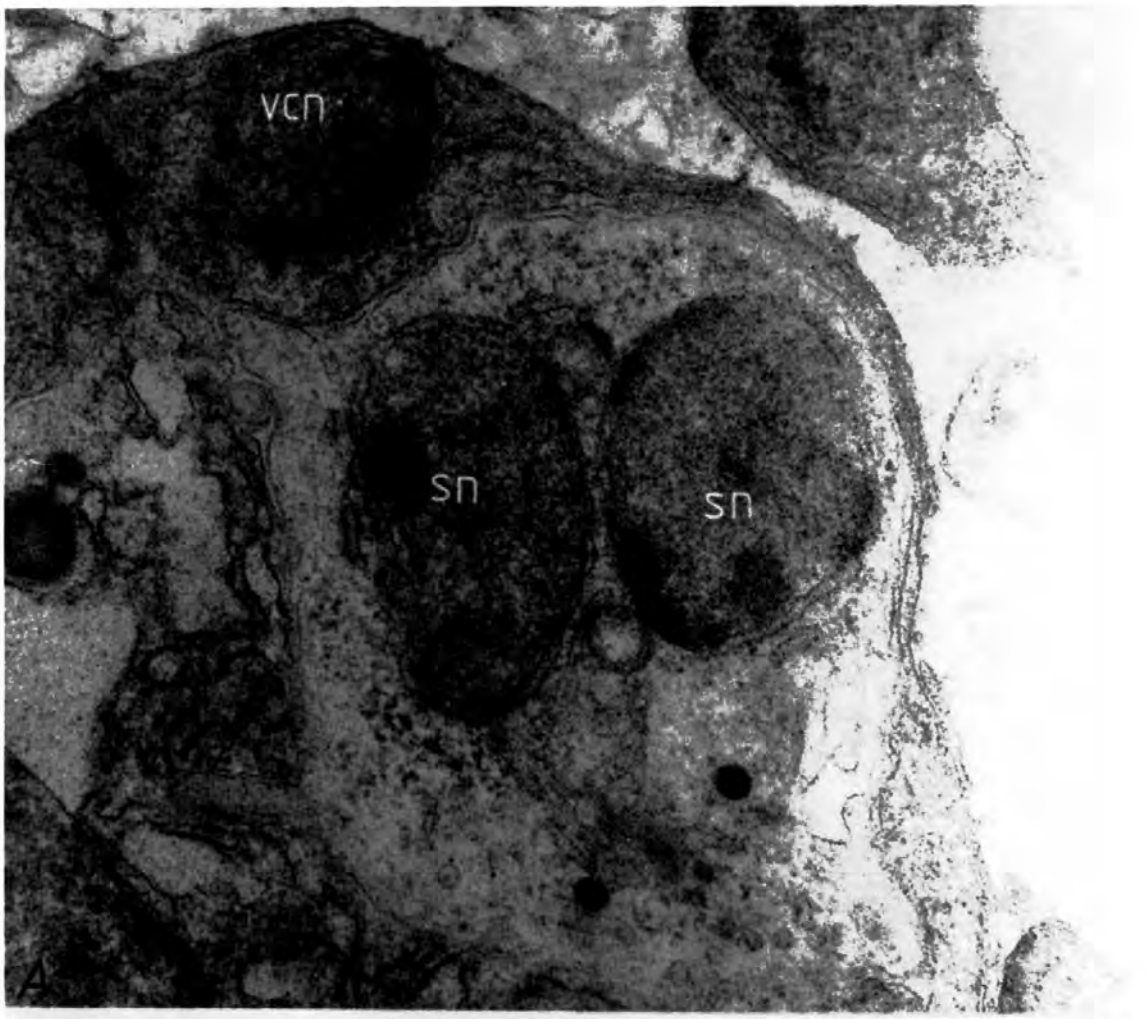
PLATE 25

Myxobolus exiguus : sporoplasm development

25-A Section through a sporoblast to show a sporoplasmic cell containing two nuclei x 36,040

25-B Section through the sporoplasm of a developing spore, showing pseudopodial-like extensions of the cell membrane. Granular material resembling glycogen is present in large amounts, and other granules of high electron-density and large size (arrowed) are also present. Note membranous cisternae in the cytoplasm, and products of valve degeneration apparent as an electron-dense body and a whorled structure. x 46,200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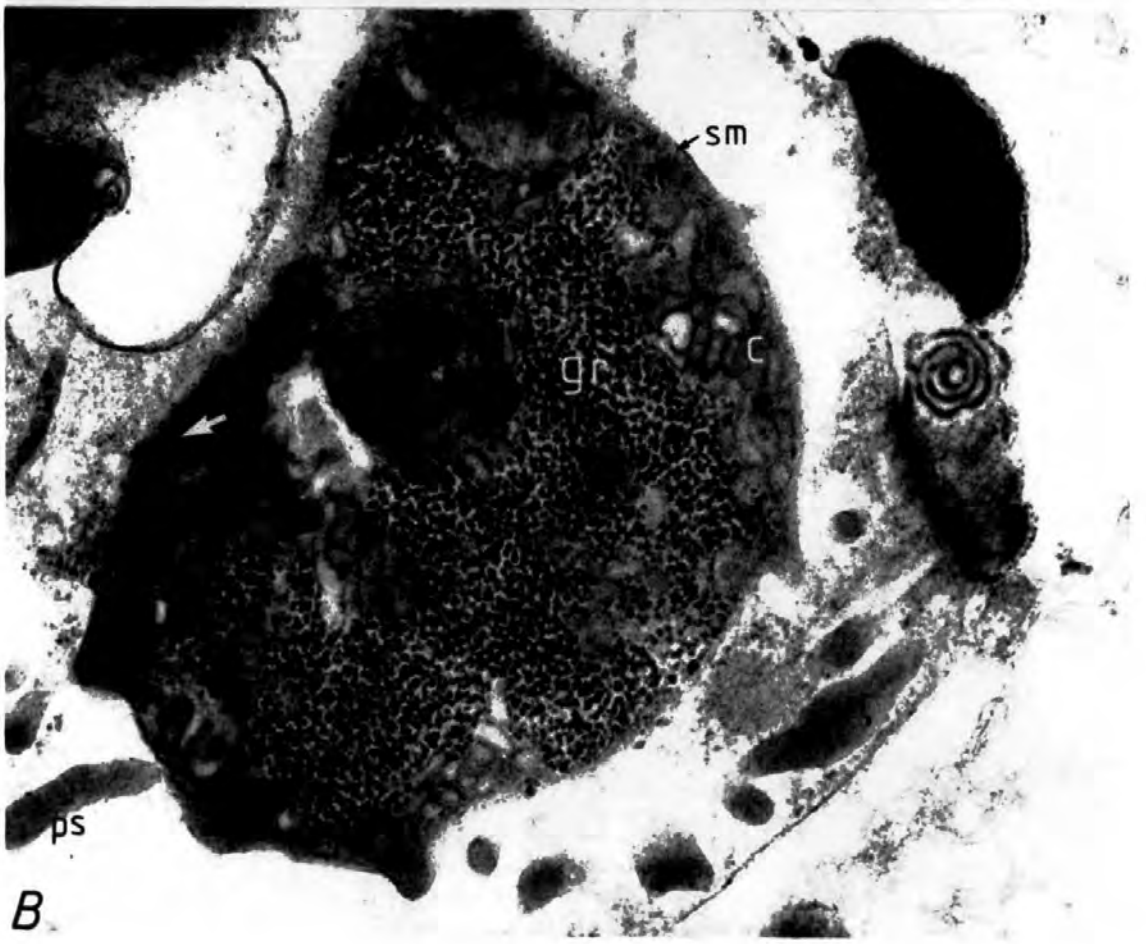
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PLATE 26

Myxobolus exiguus : ultrastructure of spores from Crenimugil labrosus

26-A Section through an almost mature spore to show the polar capsule, binucleate sporoplasm, the posterior suture and the sutural ridge x 20,250

26-B Section of spore to show the sporoplasm within the sporoplasmic cavity. Note the large 'glycogenous-like' vacuole occupying most of the sporoplasm, and poorly-developed capsular apparatus beneath the sporoplasm. The arrows indicate the sutural ridge. x 13,540

26-C Section through a sporoblast to show two maturing spores still retained within the sporoblast membrane x 11,475

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PLATE 27

Myxobolus exiguus : scanning electron microscopy of spores I

27-A Interior detail of a single spore valve, to show the polar capsule sac adjacent to the foramen through which the filament is extruded x 27,450

27-B Postero-lateral view of a spore showing the sutural line and ridge, with the marginal ribs arranged radially across the ridge x 9955

27-C Lateral aspect of a spore to show the unsculpted nature of the spore body, and the ribbed margins. Note the twisted appearance of the extruded polar filaments. x 5125

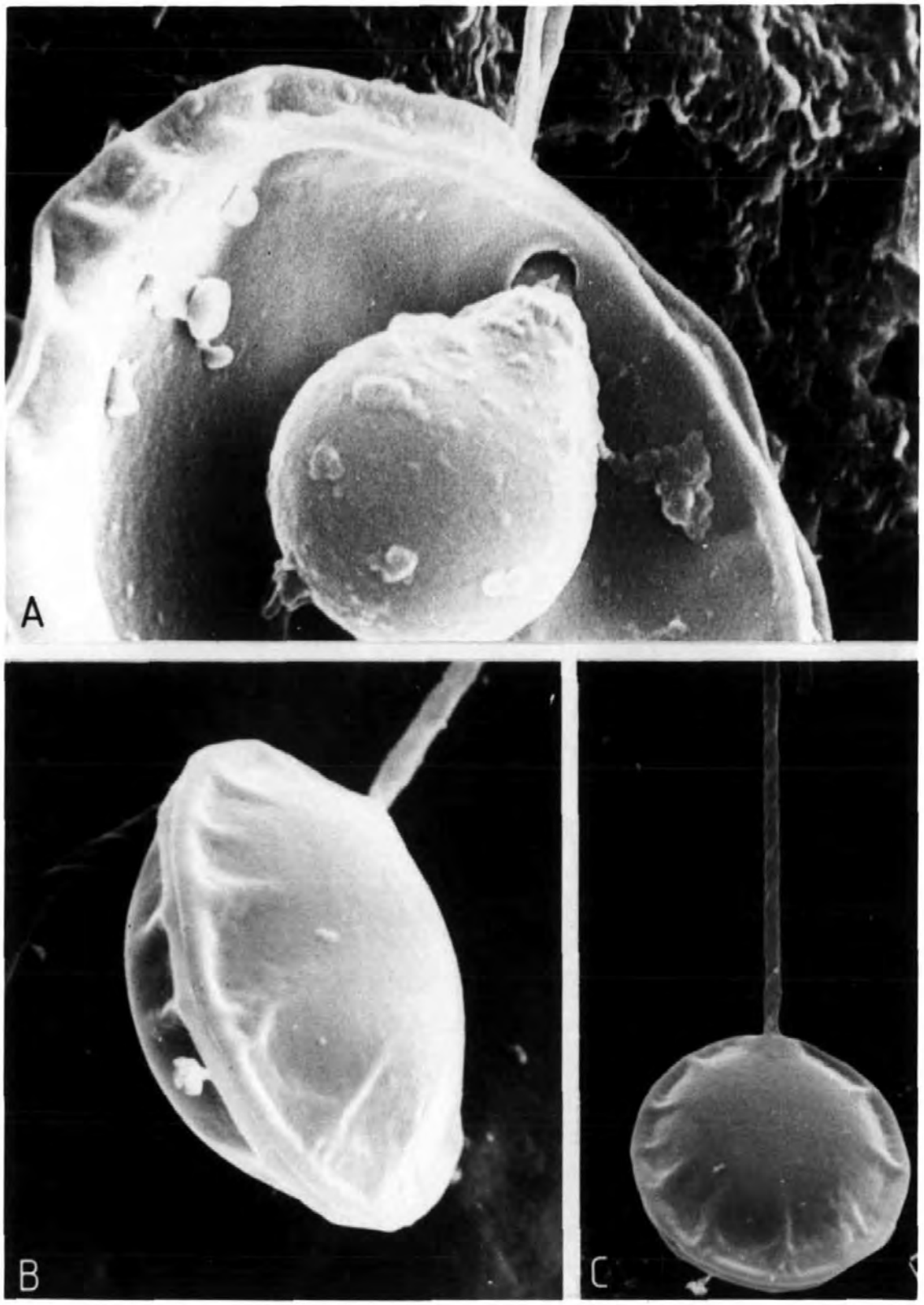
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PLATE 28

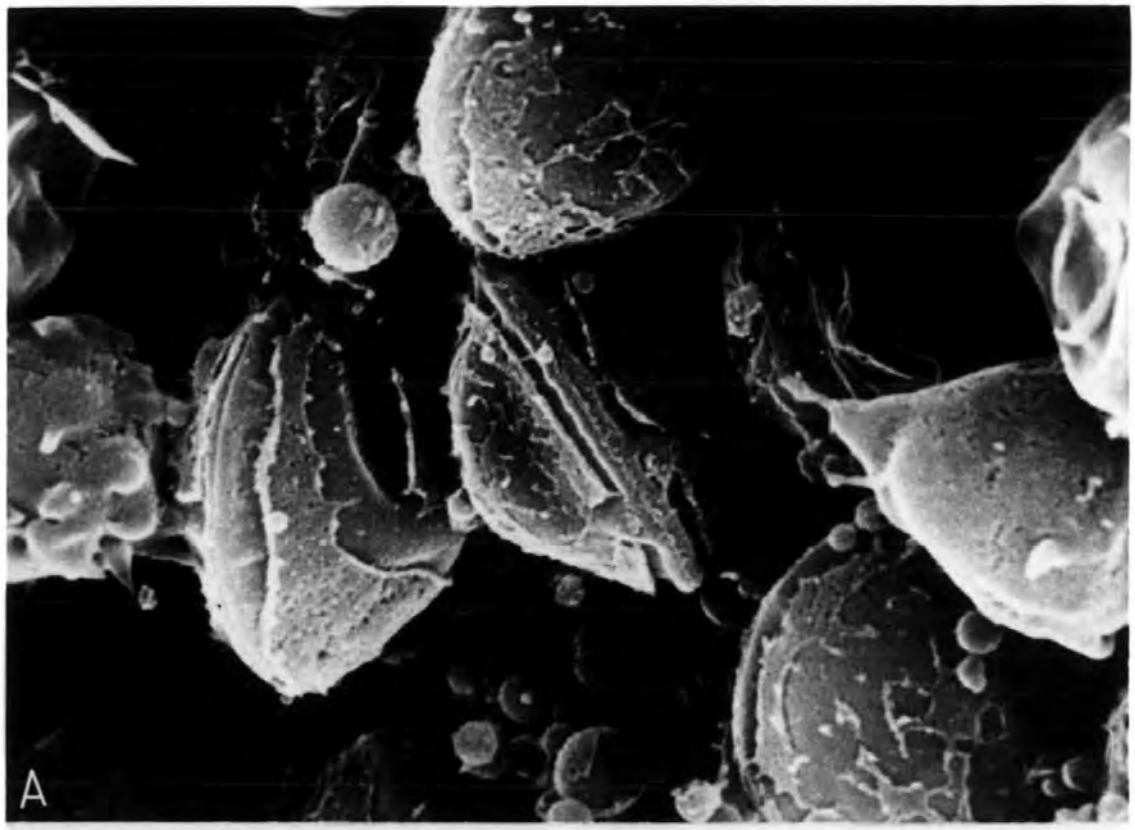
Myxobolus exiguus : scanning electron microscopy of spores II

28-A Spores retained within the plasmodium. Note the fine coat of material on the surface of the spores. x 6800

28-B Anterior aspect of a spore, to show the unplugged foramen for the exit of the polar filament x 8850

28-C Single spore showing partial separation of the valves. Note the outline of the polar capsule against the spore body. x 7550

28-D Spore set in the plasmodial matrix, exhibiting a 'honeycomb'-like arrangement x 1910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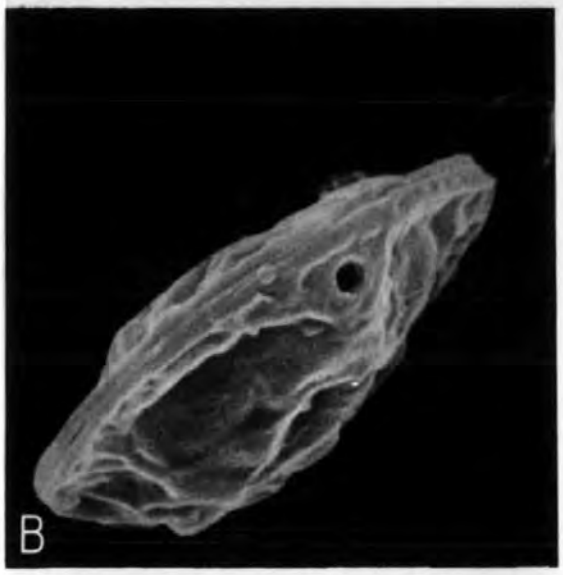
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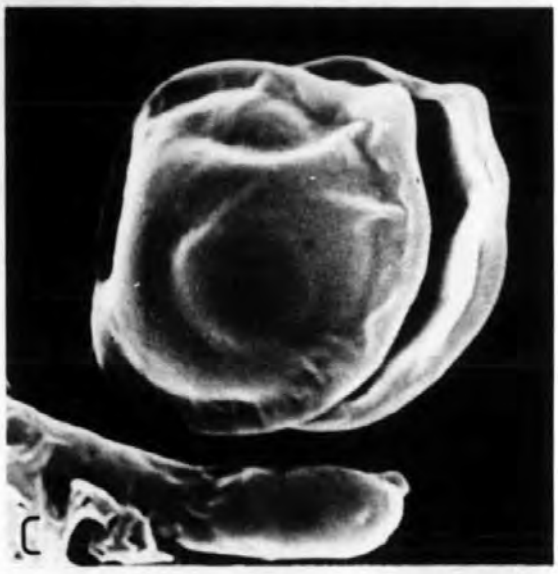
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PLATE 29

Myxidium incurvatum : trophozoites from the gallbladder of Callionymus lyra

29-A Light micrograph of trophozoites, sporoblasts, and spores in a bile smear x 840 live, phase contrast

29-B Transmission electron micrograph of an early developmental stage, to show glycogen-like granules within the fusiform body x 21,794

29-C Section through the gall bladder to show trophozoites localised in the biliary epithelium (arrowed) x 625 P.A.S.

29-D Transmission electron micrograph showing young trophozoites free in the bile, x 5953

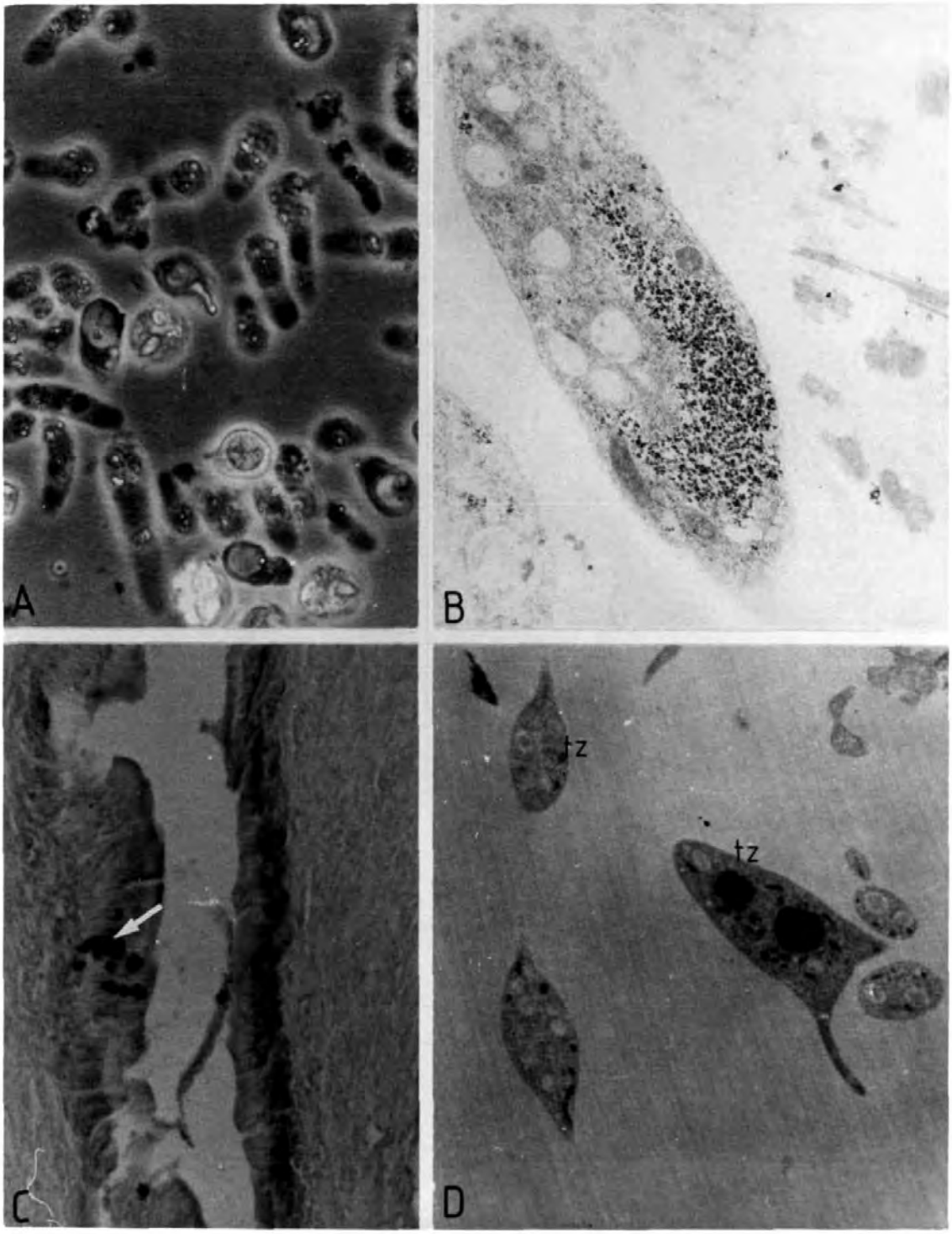
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PLATE 30

Myxidium incurvatum : transmission electron microscopy of the host-parasite interface in Callionymus lyra

30-A Single trophozoite attached to the epithelium in between biliary microvilli x 56,000

30-B Highly-branched trophozoite adjacent to the epithelial surface. Note cross sections of biliary microvilli with portions of pseudopodia between them. x 23,181

30-C Interface between pseudopodium of the trophozoite and the gall bladder epithelium to show an area of apparent erosion x 92,307

30-D Interface to show a pseudopodium in close contact with epithelium. Note indentation caused by the parasitic element, with an area of apparent erosion. x 91,800

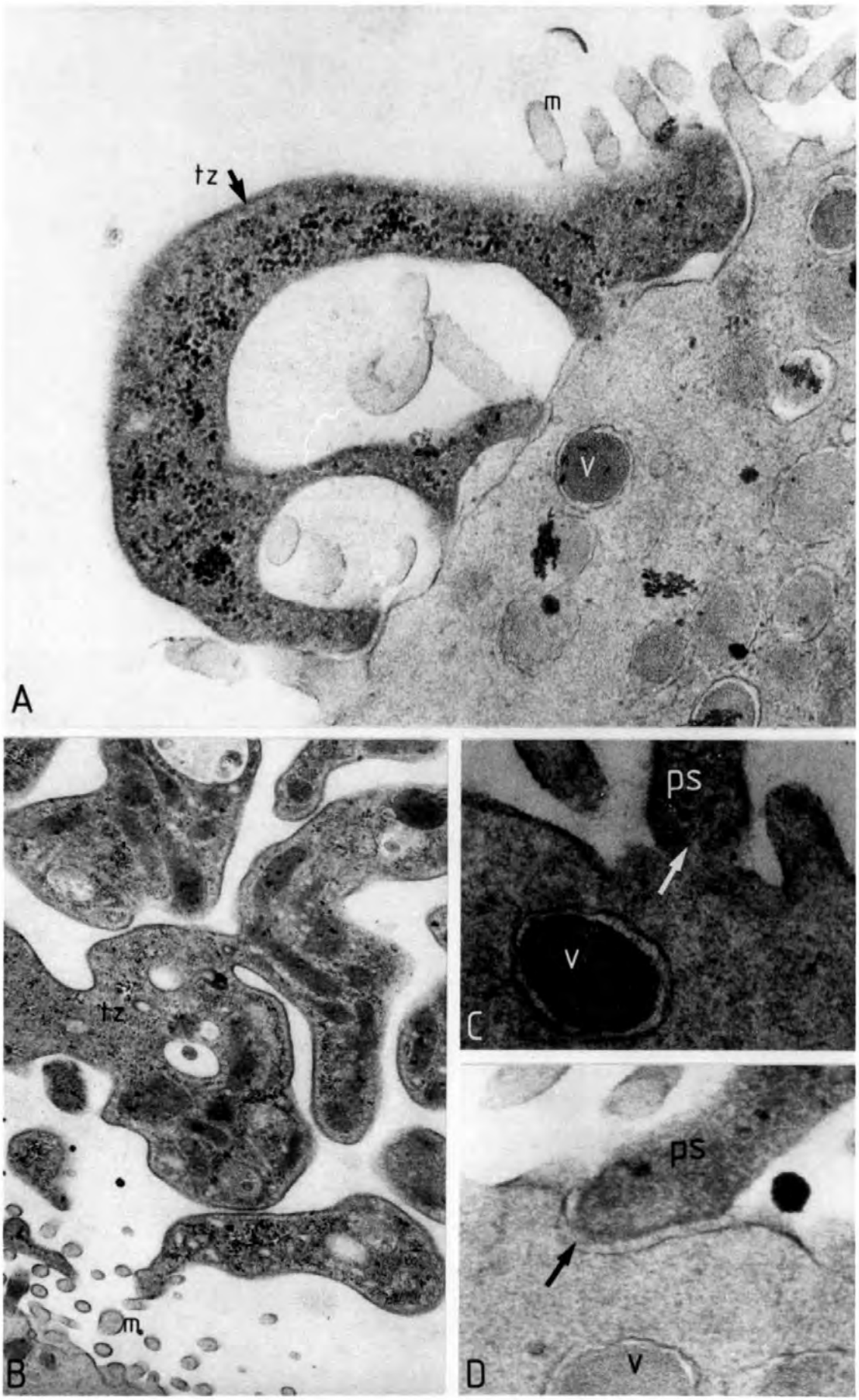
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PLATE 31

Myxidium incurvatum : biliary infection in Callionymus lyra

Transmission electron micrograph of a large trophozoite showing orientation of the pseudopodia towards the epithelial surface, from which it has become detached during processing
x 13,183

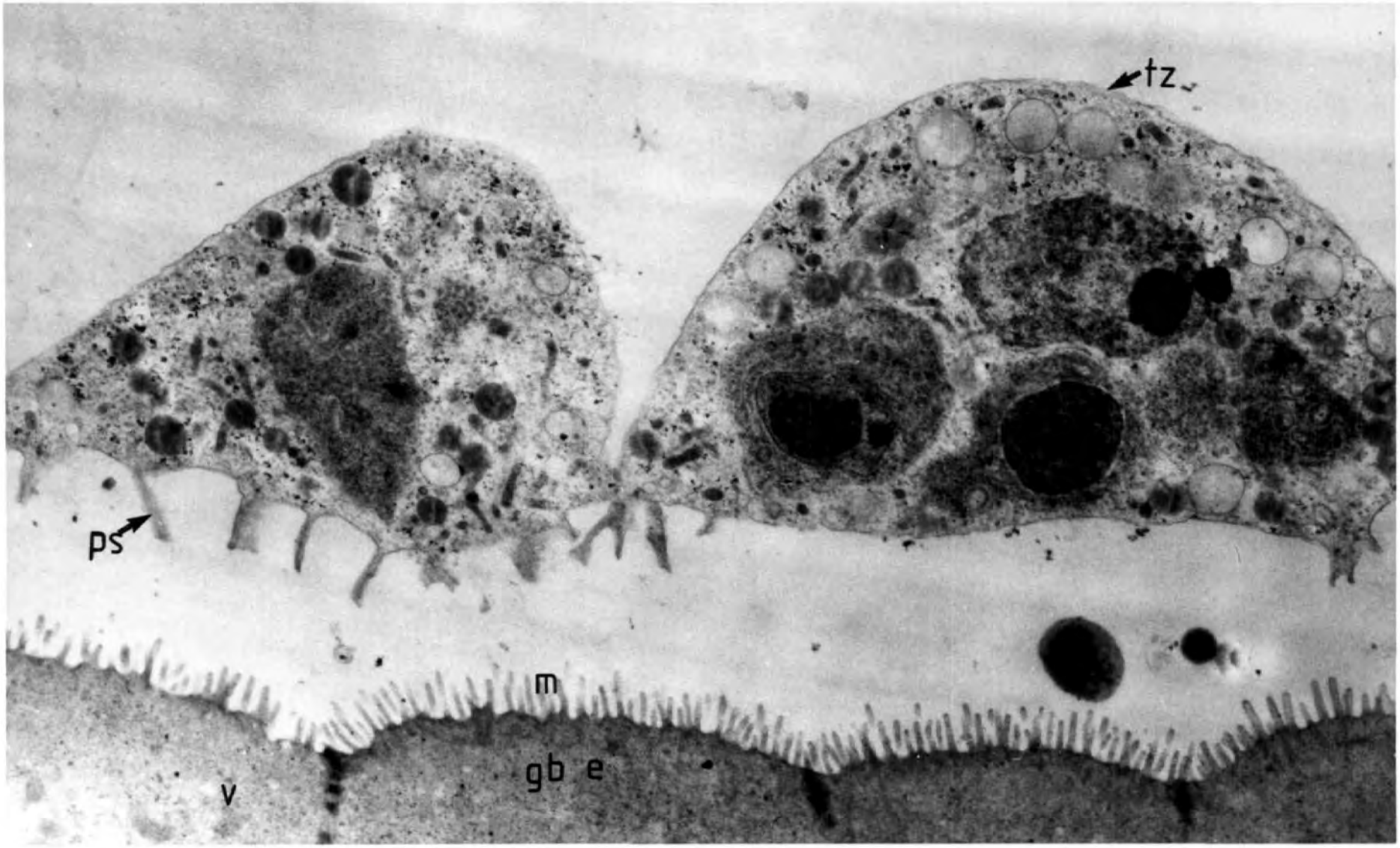
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PLATE 32

Myxidium incurvatum : biliary infection in Callionymus lyra

Transmission electron micrograph to show a general view of developmental stages distributed in the lumen of the gall bladder and adjacent to the biliary epithelium x 3785

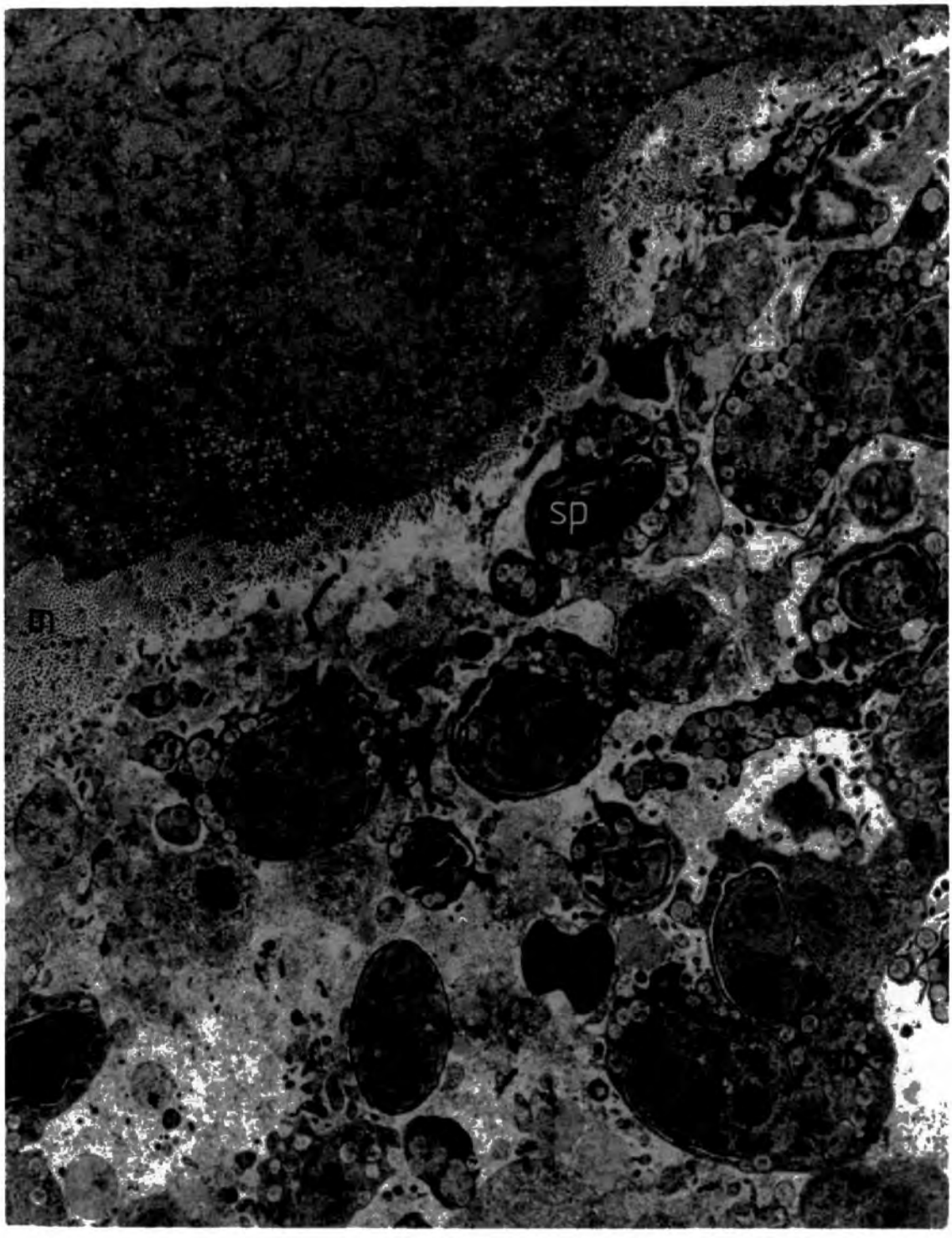
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PLATE 33

Myxidium incurvatum : structure of spores from Callionymus lyra

33-A Transmission electron micrograph of a well-developed spore, retained within the plasmodium. Note the polar capsules and capsular cells, with a sporoplasm occupying most of the intra-spore cavity. x 16,714

33-B Scanning electron micrograph of a spore to show the capsular apex at each end of the spore, with the foramen for the exit of the polar filament x 8500

33-C Transmission electron micrograph to show a transverse section through a spore at the level of the sporoplasm. Note the numerous granules and the sutural overlap (arrowed). x 12,000

33-D Light micrograph of spores free in the bile x 1555 live, phase contrast

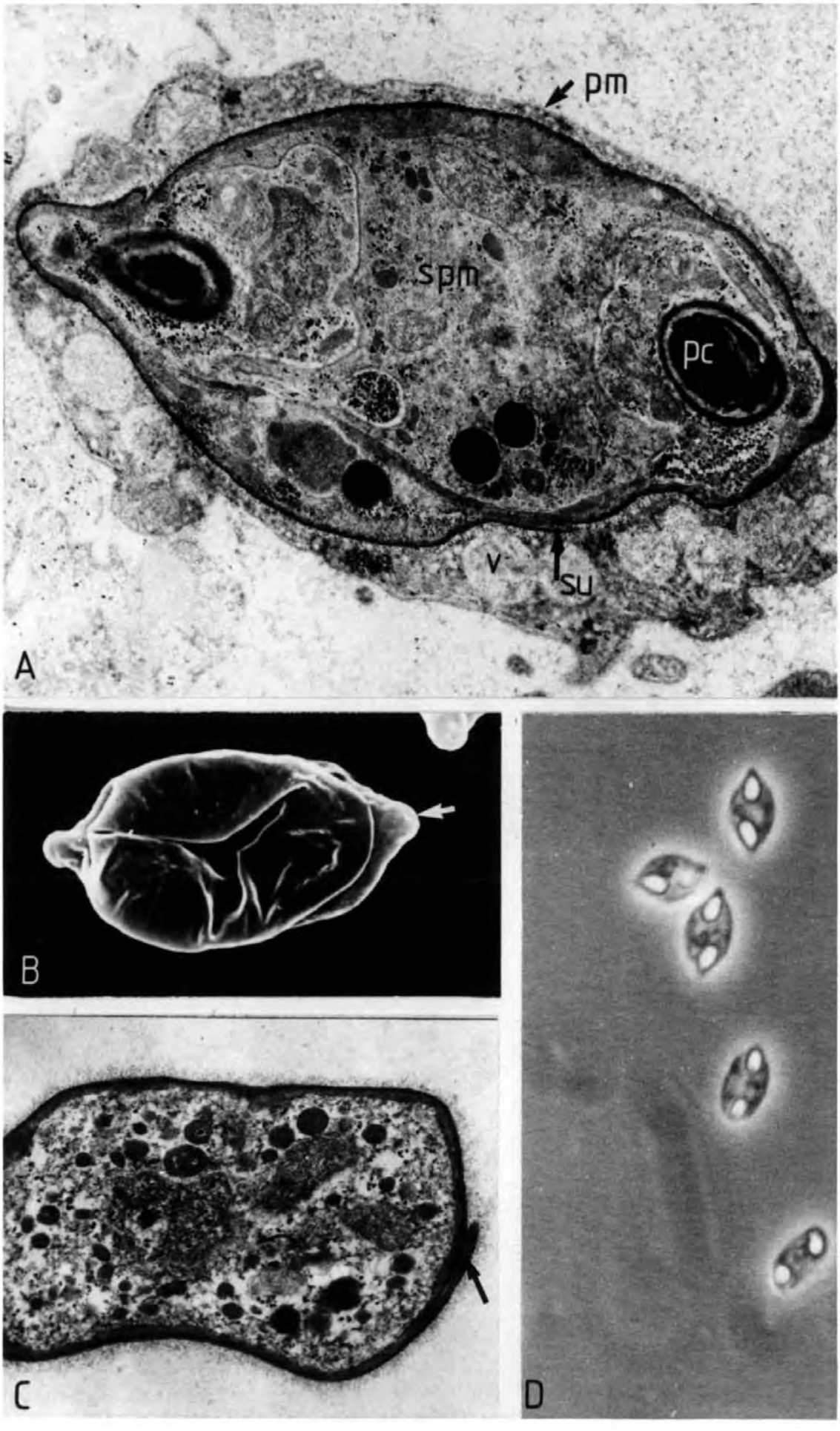
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PLATE 34

Myxidium incurvatum : sporoblasts from the gall bladder of Callionymus lyra

34-A Disporous sporoblast containing two well-developed spores x 2800 Giemsa

34-B Sporoblast containing two spores, accompanied by several nuclei in the cytoplasm of the sporoblast x 2705 Giemsa

34-C Polysporous sporoblast with six spores, accompanied by many sporogenic nuclei x 2730 Giemsa

34-D Large polysporous sporoblast containing many spores and nuclei x 777 live, phase contrast

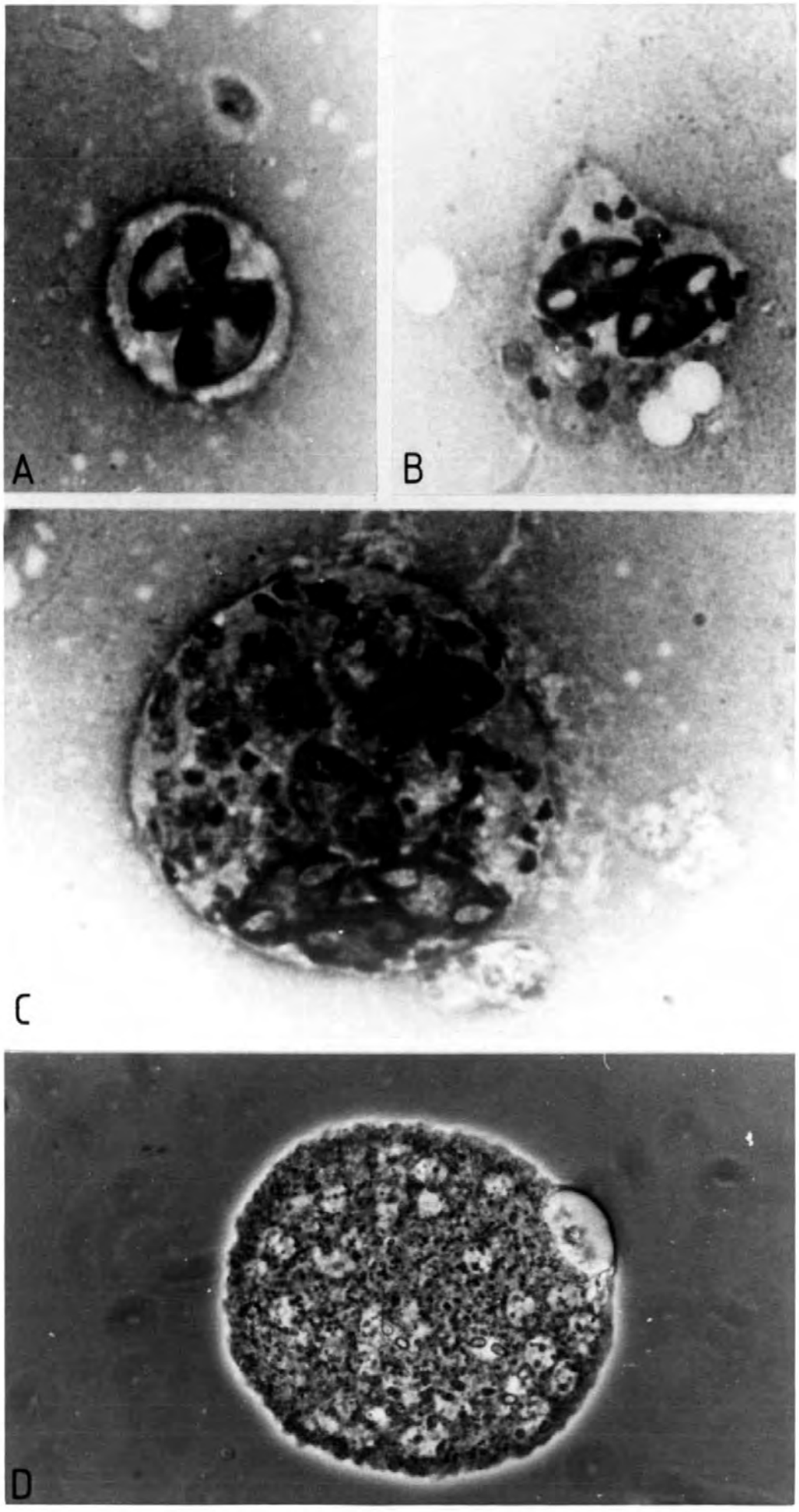
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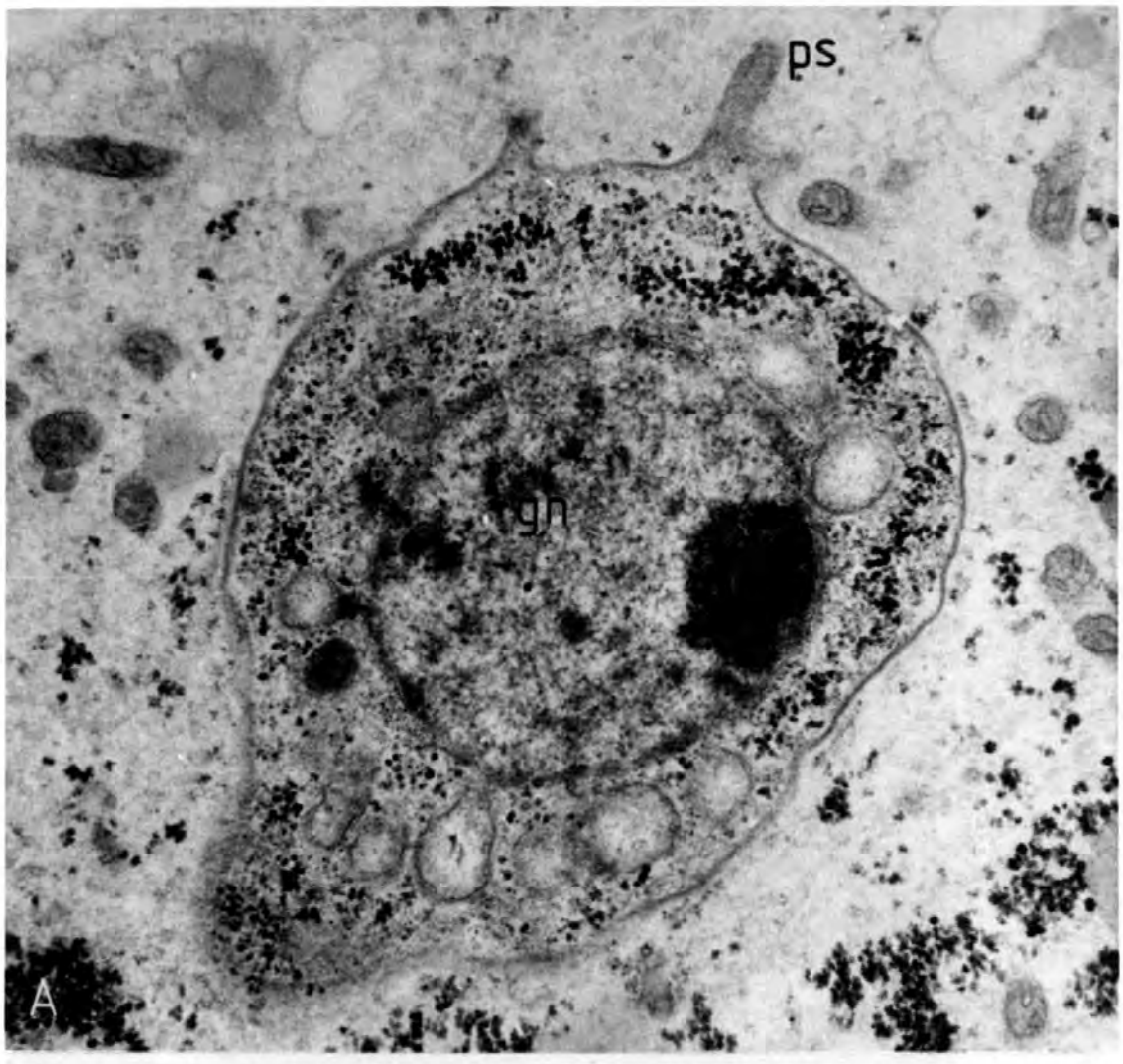
PLATE 35

Myxidium incurvatum : ultrastructure of early developmental stages from the gall bladder of Callionymus lyra

35-A Germinative cell from the cytoplasm of the trophozoite, to show the prominent germinal nucleus and nucleolus, with pseudopodial-like extensions of the cell membrane x 30,875

35-B A germinative cell adjacent to a vegetative nucleus of an early trophozoite x 16,500

35-C Trophozoite from the bile, containing vegetative nuclei and a germinative cell. Note the prominent pseudopodia at the periphery of the vegetative body. x 6600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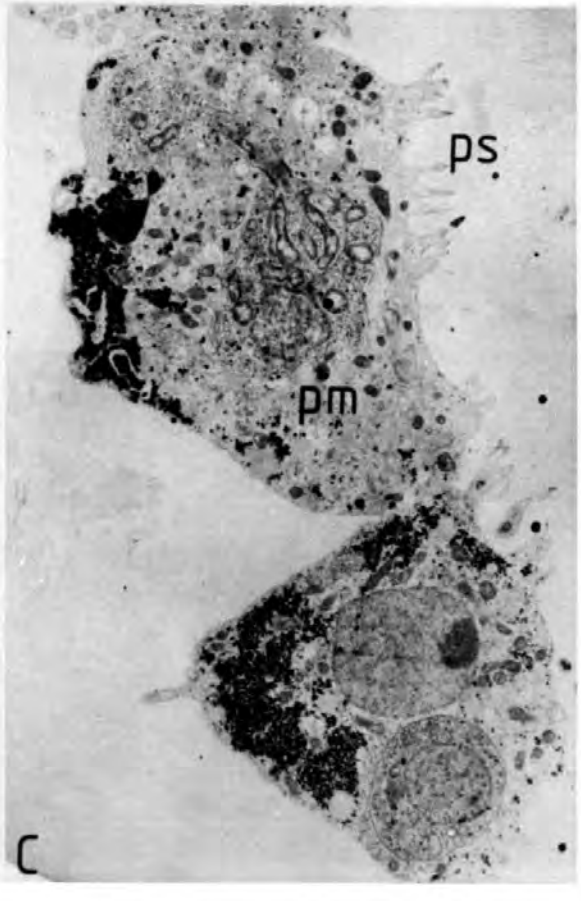
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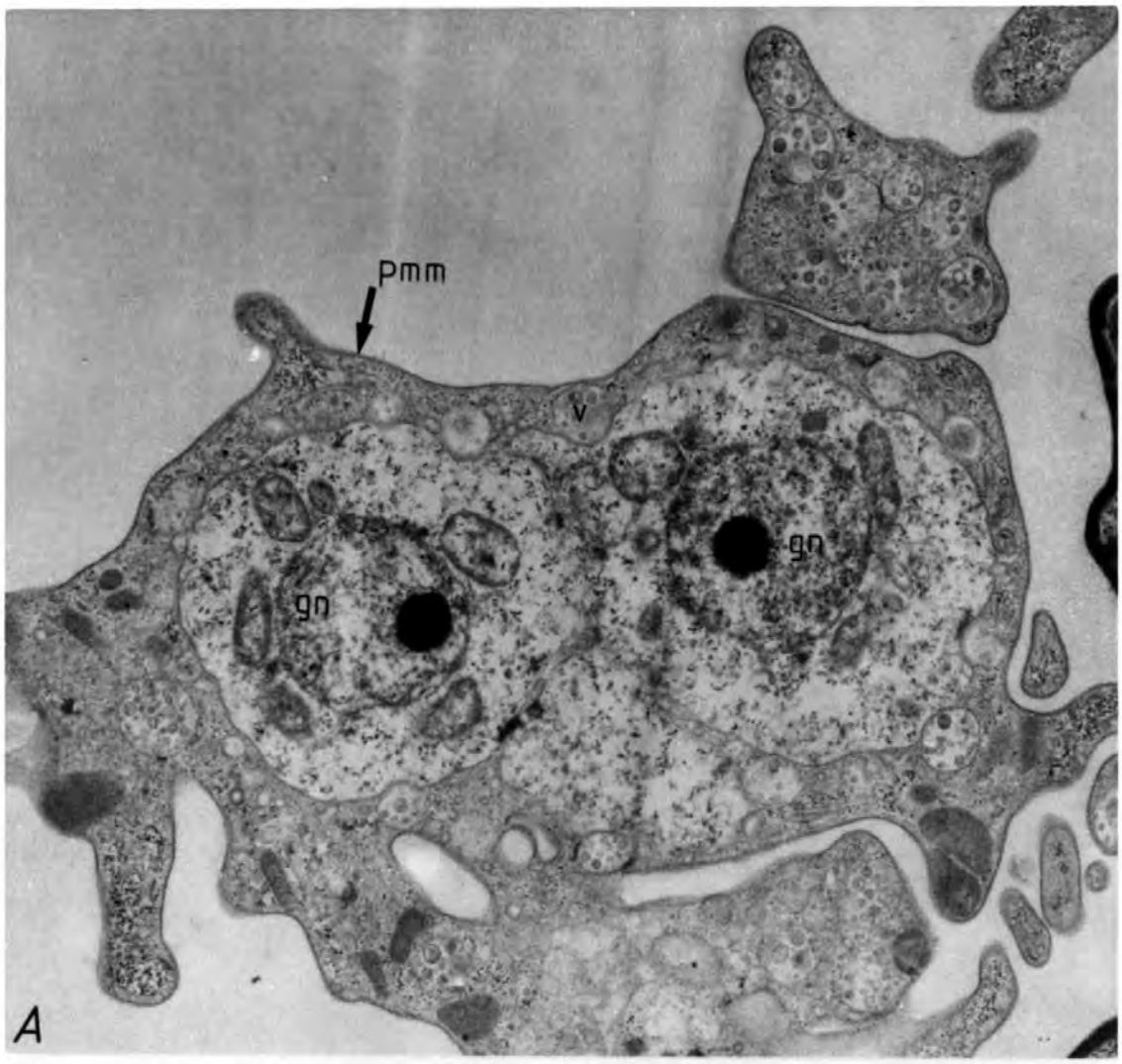
PLATE 36

Myxidium incurvatum : early stages in sporogenesis

36-A Transmission electron micrograph of a trophozoite to show two germinative cells, and the early appearance of multivesicular vacuoles in the cytoplasm external to the germ cells. The trophozoite is much-branched with many pseudopodial extensions. x 12,750

36-B Trophozoite showing the differentiation of sporogenic cells. Note the capsulogenic and sporoplasmic nuclei in the sporogenic mass. x 6545

36-C Section through a disporous sporoblast at an early stage of development. Note the two spore-forming bodies, surrounded by multivesicular vacuoles (arrowed). x 6350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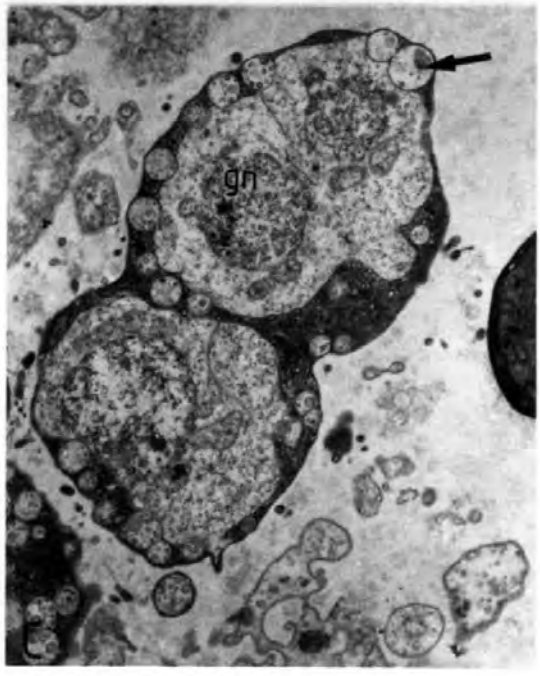
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PLATE 37

Myxidium incurvatum : differentiation of polar capsules

37-A Transmission electron micrograph of an early sporogenic mass, surrounded by vacuoles. Note the fusiform body in the centre, constituting an early capsular primordium. x 12,480

37-B Capsular cell within a sporoblast, to show cross-sections of the external tube. Note the point of contact between a multi-vesicular vacuole and the spore wall (arrowed). x 13,000

37-C Capsular cell to show longitudinal profiles of the external tube x 9937

37-D Developing spore mass with a capsular cell containing an early capsule sac x 9471

37-E Monosporous sporoblast, containing an immature spore. Note the two capsule cells. x 9779

37-F Section of the capsular sac at its junction with the external tube. Note the reflexed junction, re-inforced by an electron-dense ring (arrowed). x 26,875

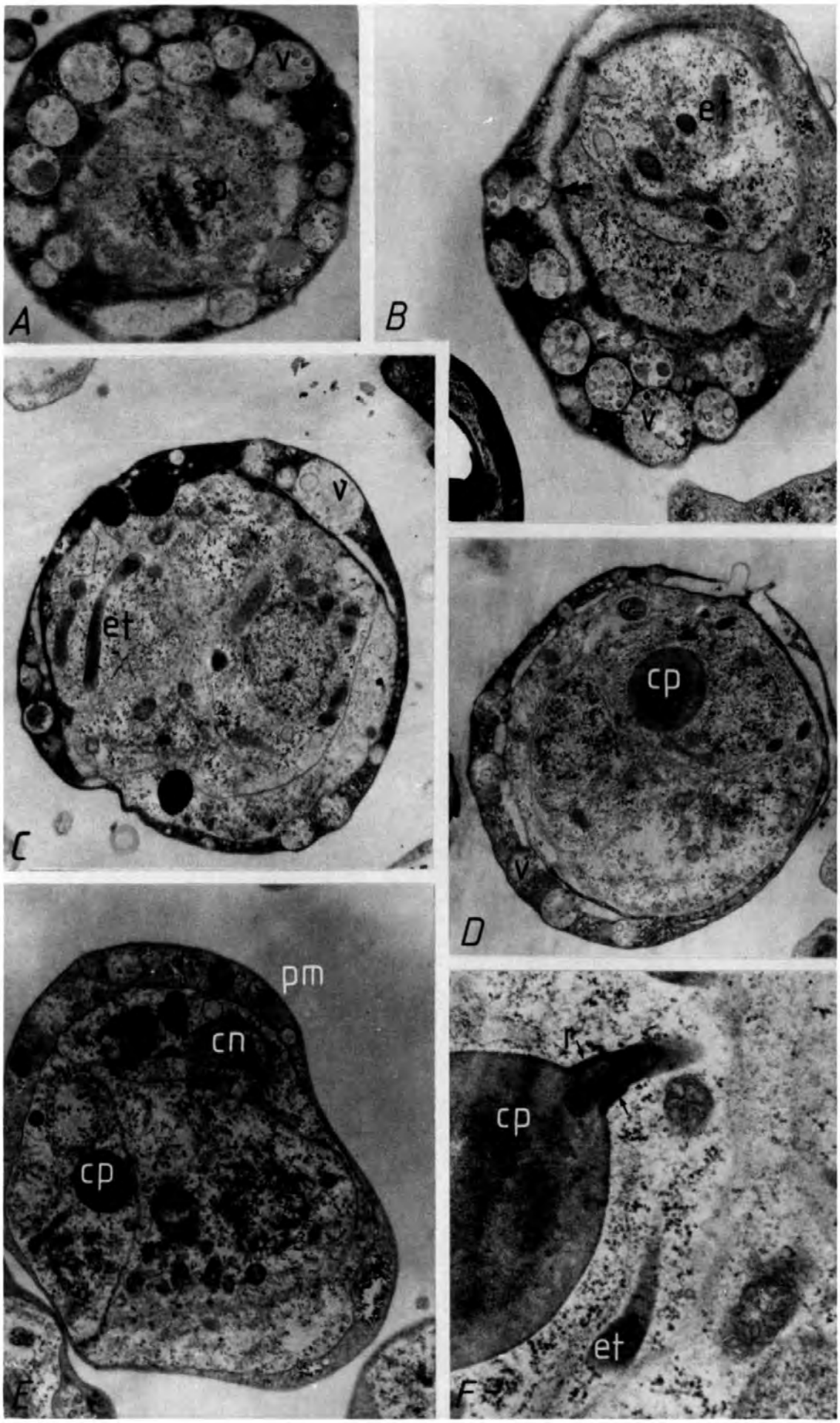
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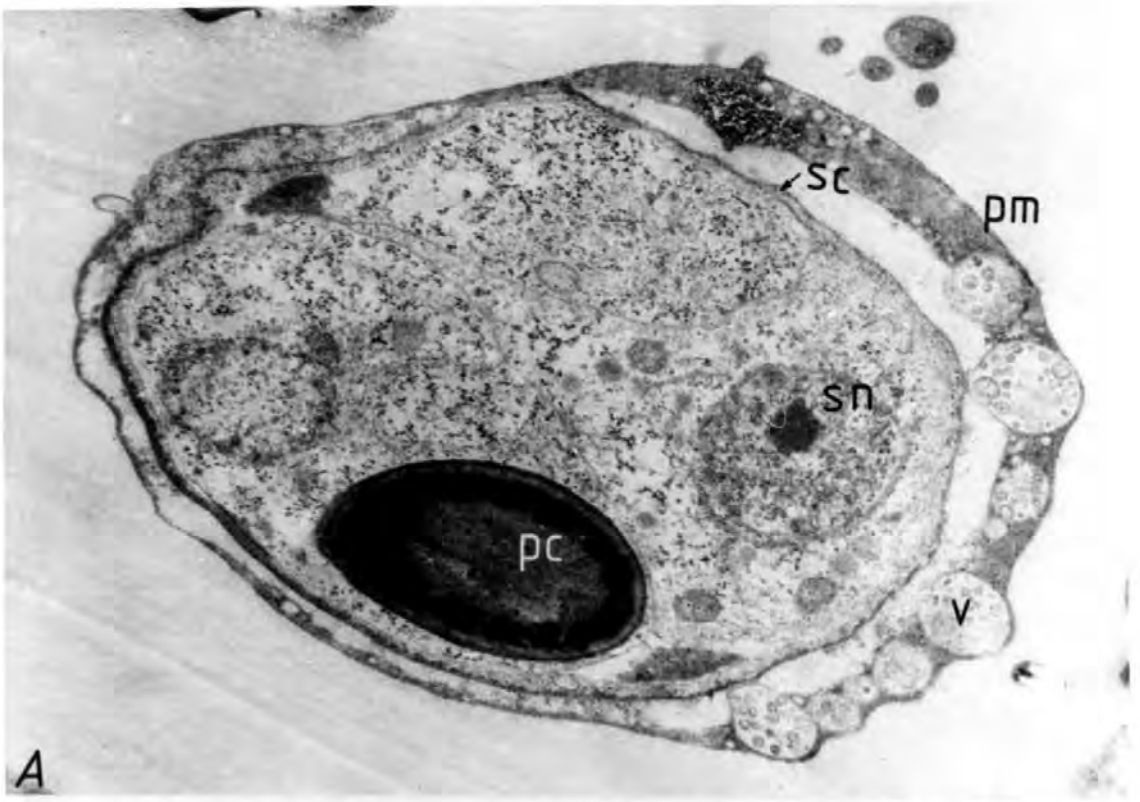
PLATE 38

Myxidium incurvatum : sporoblasts containing spores with capsules in various degrees of development

38-A Transmission electron micrograph of a maturing sporoblast. Note the spore containing a well-developed capsule into which the filament is withdrawn. The arrow indicates the sutural crest formed by the overlap of valve cells. x 17,325

38-B Capsular cell containing a nucleus, with several longitudinal profiles of the external tube in the cytoplasm x 26,565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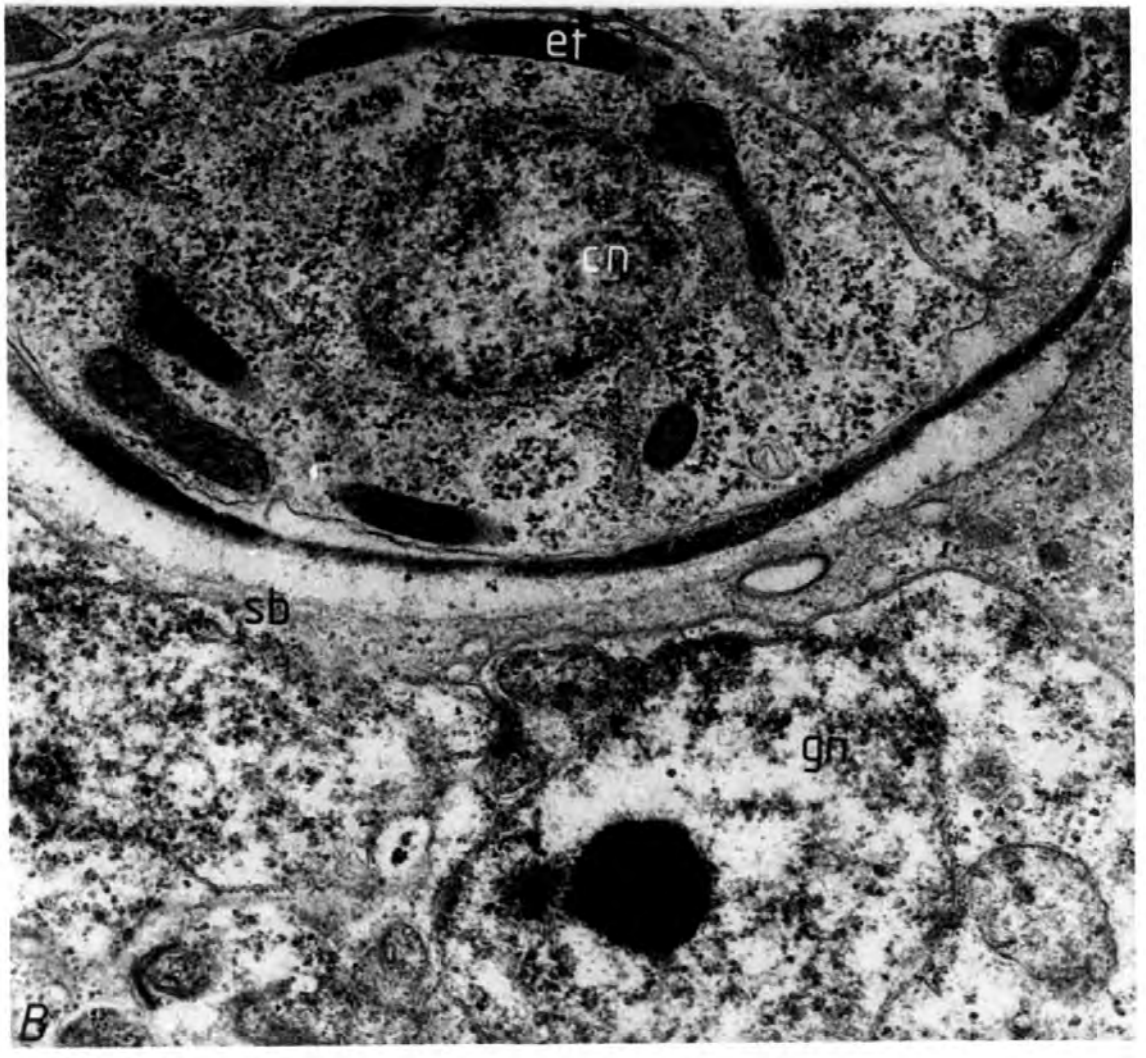
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PLATE 39

Myxidium incurvatum : maturation of the polar capsules

39-A Transmission electron micrograph of a longitudinal section of polar capsule to show the filament during the process of coiling x 35,690

39-B Capsule with sections of the filament at the periphery. Note the electron-lucent and granular areas at the centre of the capsule. x 50,400

39-C Capsule with coiled filaments. Note that light granular material has replaced the electron-lucent and heavy electron-dense material of the core. x 46,500

39-D Section through a capsule to show the coiled filament and the point of exit for the filament at the capsular apex x 35,475

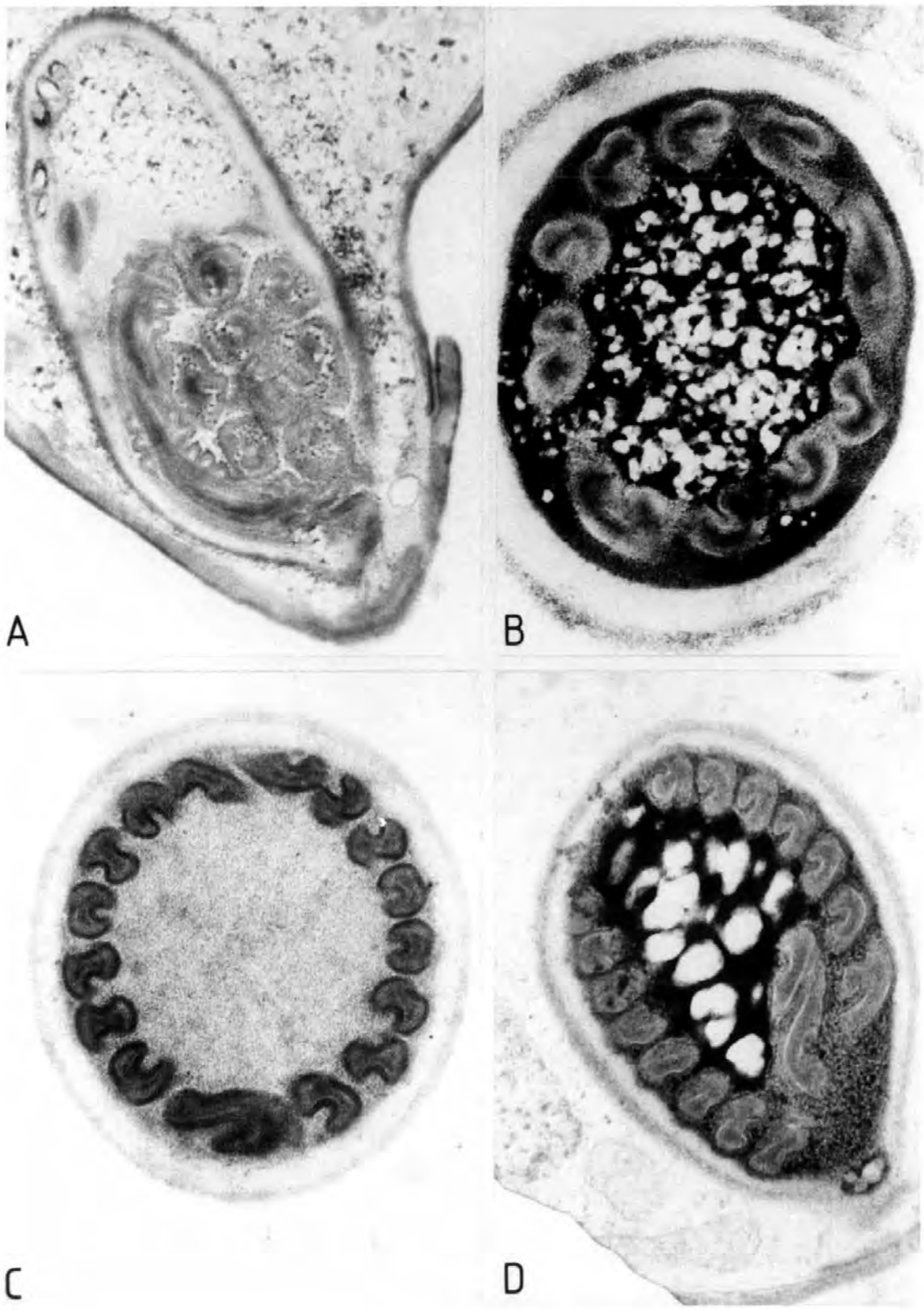
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PLATE 40

Myxidium incurvatum : sporoblasts containing spores in various stages of formation

40-A Transmission electron micrograph of a monosporous sporoblast containing a spore in which the outer valves have formed. Note the suture formed by the overlap of apposing valve cell membranes (arrowed). Large amounts of cytoplasm still remain within the valve cells, which have totally surrounded the other sporogenic cells. x 16,107

40-B Sporoblast surrounding a well-developed spore to show the function of the sporoblast membrane as a 'nurse cell' x 7143

40-C Sutural junction of a spore, formed as an overlap of valve cells x 43,000

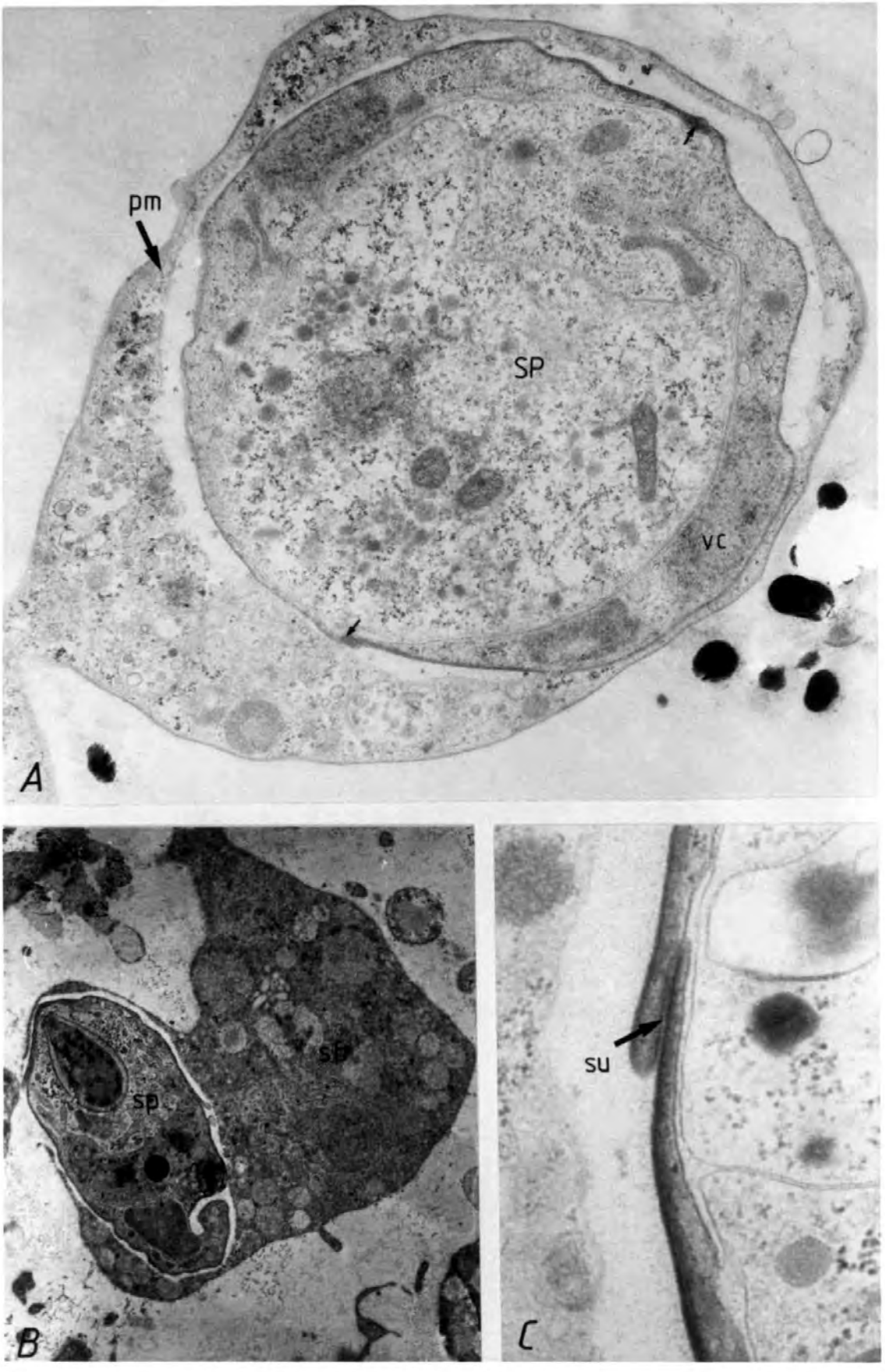
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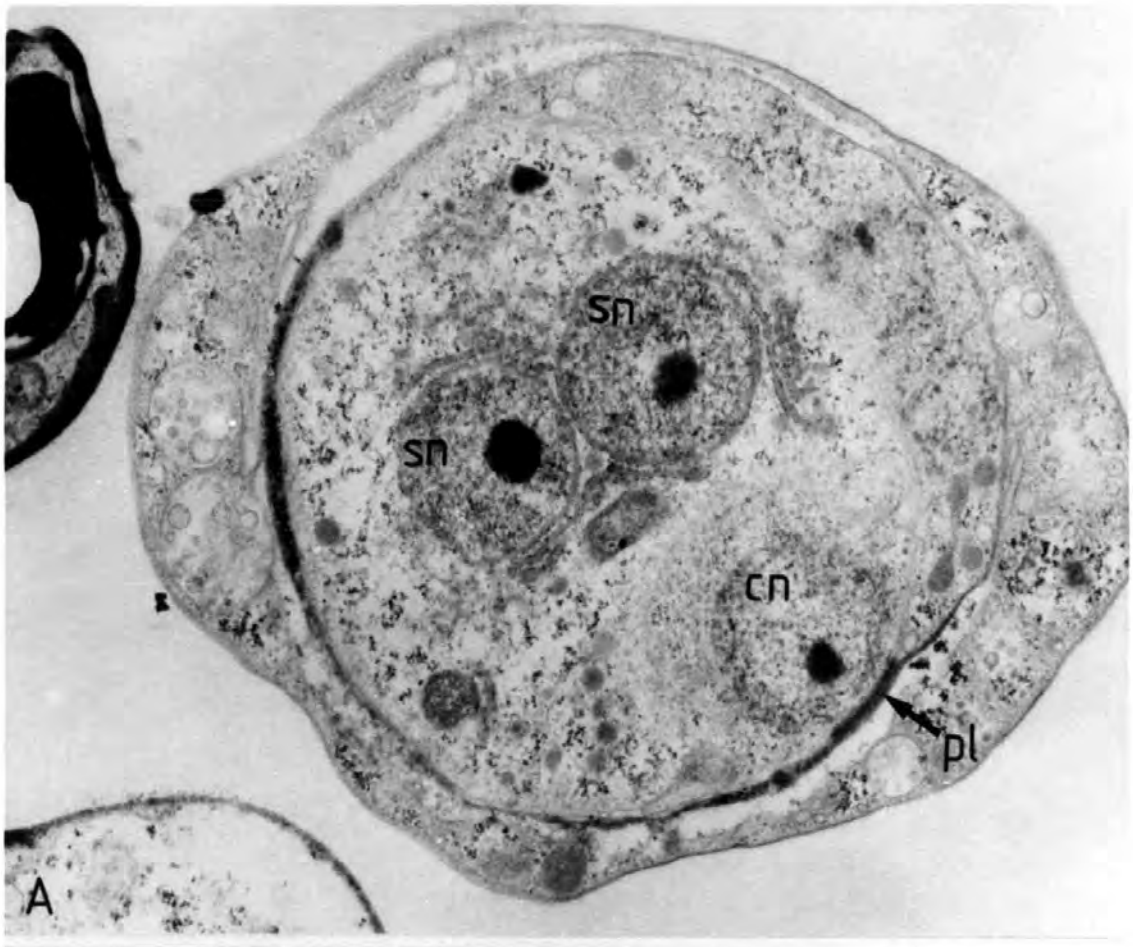
PLATE 41

Myxidium incurvatum : development of the sporoplasm

41-A Transmission electron micrograph of the sporoblast to show a binucleate sporoplasm cell within the spore body. Note the prominent nucleoli in the nuclei, and the strands of endoplasmic reticulum in the cell cytoplasm. A capsulogenic nucleus is also present, aligned opposite to an electron-dense plaque (arrowed) in the valve cell wall. x 15,400

41-B Developing spore in which the sporoplasm fills approximately half the spore cavity. One sporoplasmic nucleus is apparent, with one of the polar capsules, and both sutures are shown. Note the elongate,bilobed mitochondria. x 16,100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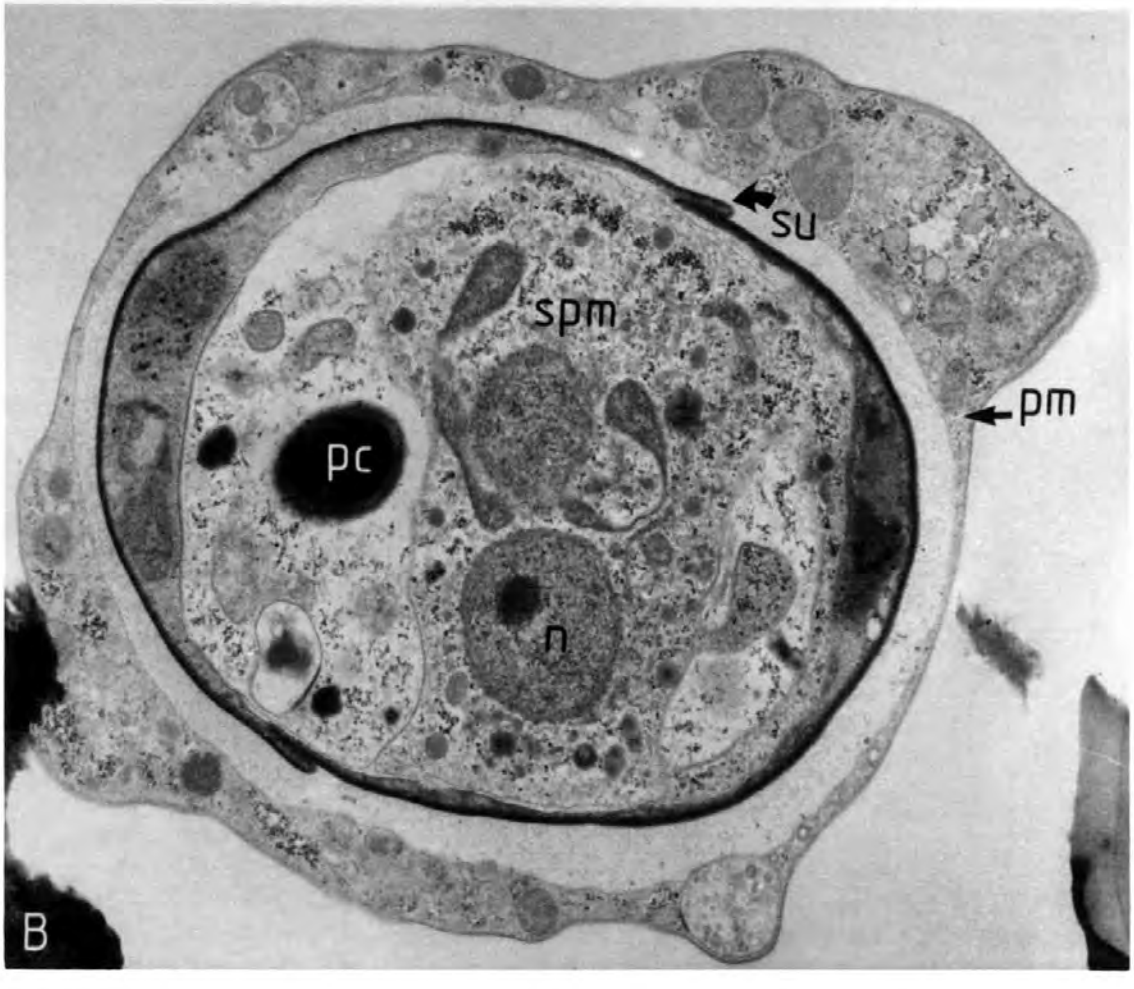
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PLATE 42

Myxidium incurvatum : mature sporoblast

Transmission electron micrograph of a sporoblast containing a well developed spore, illustrating most of the major features of a mature spore. Both polar capsules are advanced in development, with coiled filaments. Note the capsule on the left, aligned opposite a plaque in the valve coat, with a prominent capsular apex. Vacuoles containing vesicular elements (arrowed) are present in the cytoplasm of the surrounding plasmodium.
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PLATE 43

Myxidium giardi : stages from various infection sites in Anguilla anguilla

43-A Transmission electron micrograph of a mature spore to show the prominent longitudinal ridges on the valves, a binucleate sporoplasm, and one of the polar capsules x 12,012

43-B Scanning electron micrograph of a spore, showing the pattern of ridges, and the foramen for the exit of the polar filament at the apex x 11,612

43-C Light micrograph of a section through an infected gill filament to show an intralamellar cyst containing spores x 1000 Papanicolaou

43-D Light micrograph of a portion of an entire eel transverse section, showing the kidney to be infected with three large cysts (arrowed) x 60 P.A.S.

43-E Light micrograph of infected eel intestine in transverse section to show a single large cyst (arrowed) in gut tissue x 300 P.A.S.

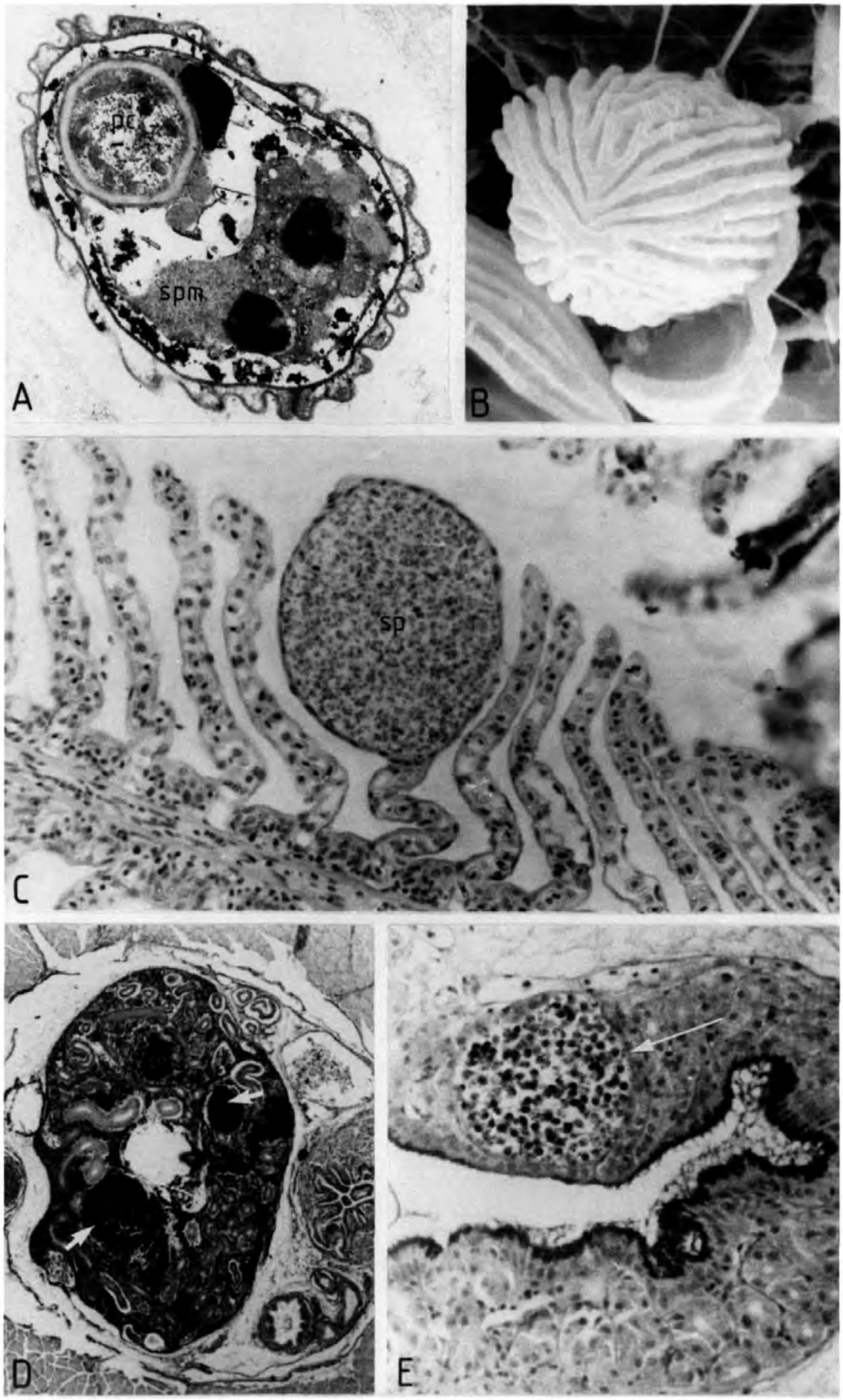
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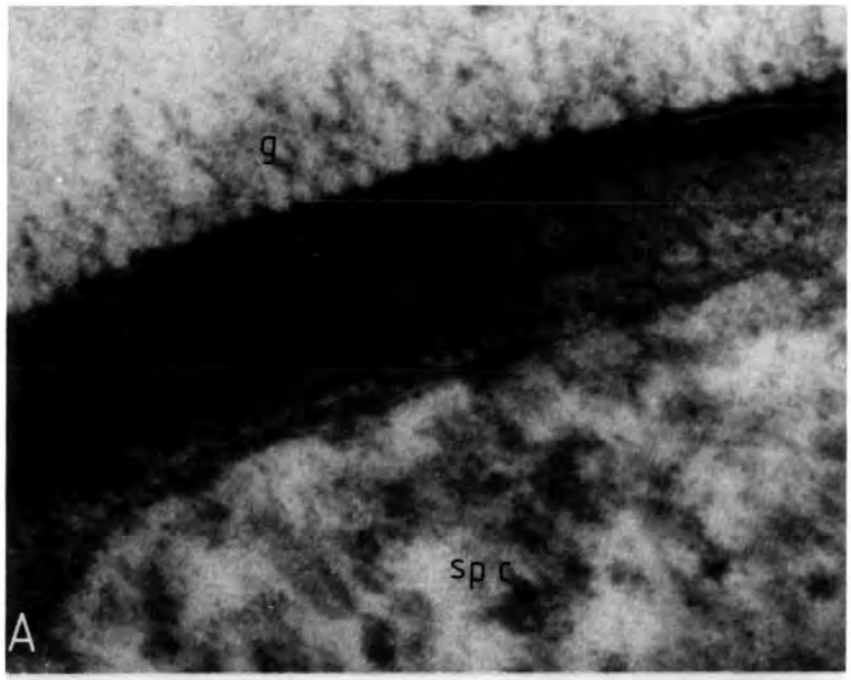
PLATE 44

Transmission electron microscopy of the spore coat in three species of Myxosporidia

44-A Coat of *Myxidium incurvatum*, showing the fuzzy 'glycocalyx'-like layer on the surface x 290,000

44-B Coat of *Myxidium giardi*, to show the laminar structure, and the longitudinal ridges x 120,000

44-C Coat of *Myxobolus exiguus*, to show the fuzzy 'glycocalyx' and laminar structure of the valves x 116,666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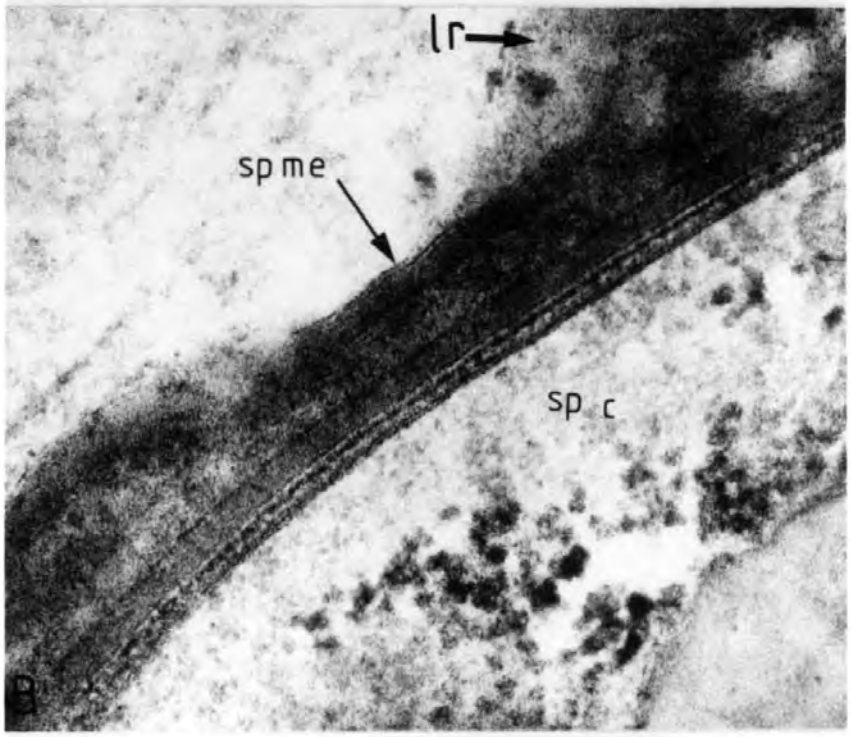
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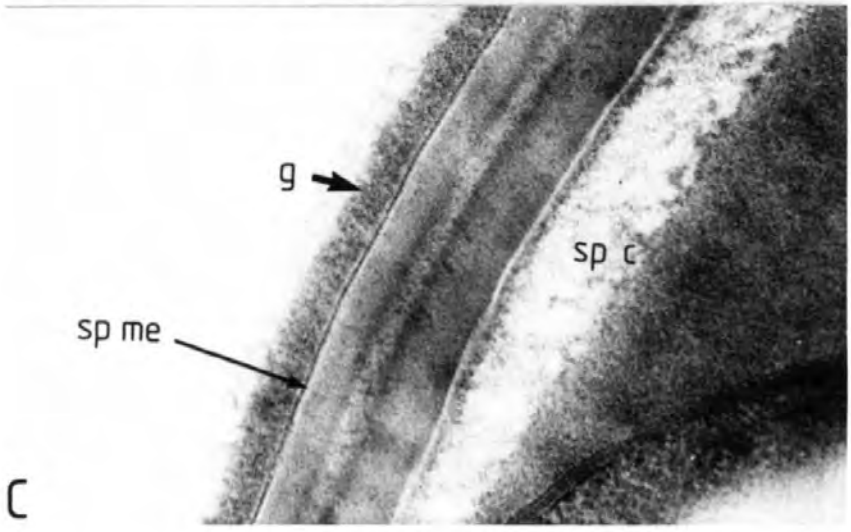
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PLATE 45

Myxidium incurvatum : the effect of infection on the gall bladder epithelium of Callionymus lyra

45-A Transmission electron micrograph of the gall bladder to show trophozoites adjacent to the surface of the biliary epithelium x 1820

45-B Epithelial cell from an uninfected gall bladder x 7200

45-C Section through the gall bladder wall of a heavily-infected Dragonet. Note the severe erosion of the epithelium, and proliferation of fibrous elements beneath the basement membrane. x 15,400

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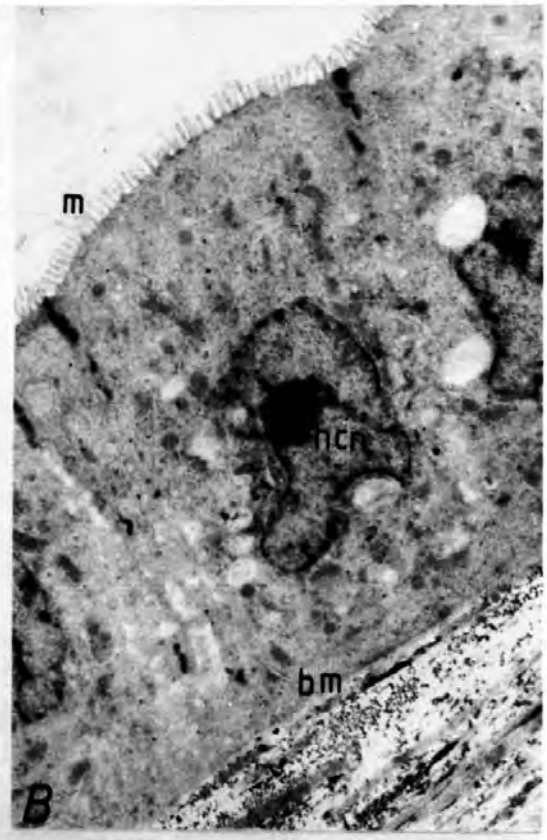
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PLATE 46

The effect of Myxosporidiosis on gill tissues I

46-A Light micrograph of a section through uninfected gill filaments of Crenimugil labrosus, to show free secondary lamellae and constant lamellar width x 225 Haematoxylin and Eosin

46-B Spores of Myxidium giardi in the filament vessel (arrowed) of eel gill x 650 P.A.S./Coles Haematoxylin

46-C Section through gill filaments of Crenimugil labrosus infected with Myxobolus exiguus to show hyperplasia and fusion of adjacent filaments (arrowed). Note also the destruction and engulfment of secondary lamellae by developing plasmodia x 140 P.A.S./ Alcian blue

46-D Scanning electron micrograph of the surface of a gill cyst, to show the host epithelial layer covering the plasmodium x 3525

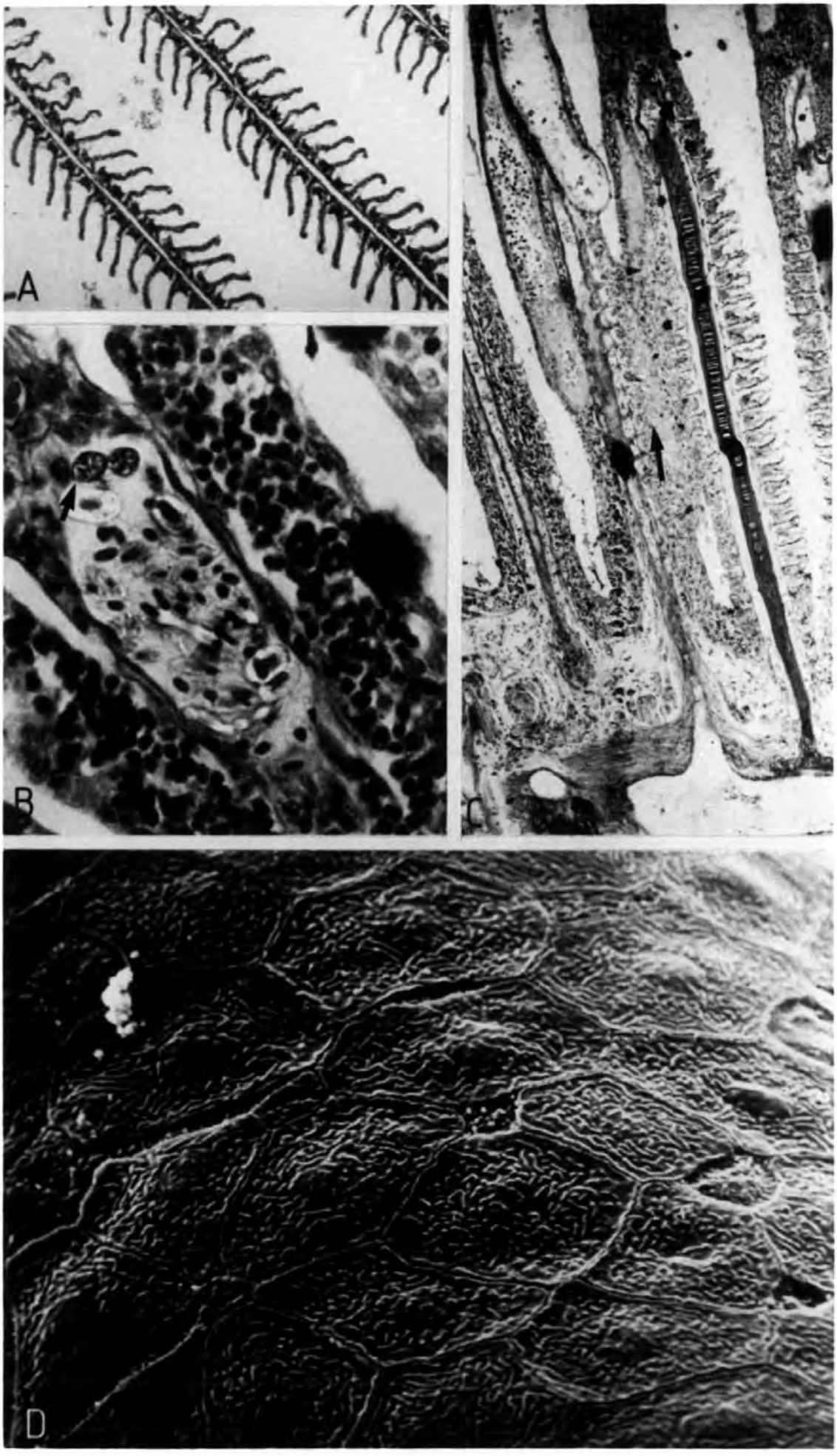
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PLATE 47

The effect of Myxosporidiosis on gill tissues II

47-A Infected gill filaments of Crenimugil labrosus in longitudinal section, containing cysts of Myxobolus exiguus at the tips of the filaments x 130 P.A.S./Alcian blue

47-B Tip of a gill filament from Crenimugil labrosus containing a small developing plasmodium of Myxobolus exiguus. Note the intense hyperplastic reaction of the epithelial tissue which has engulfed the secondary lamellae x 600 Haematoxylin and Eosin

47-C Longitudinal section of a gill filament of Crenimugil labrosus to show denudation of lamellae, which have been replaced by a compartmentalised plasmodium of Myxobolus exiguus x 150 Haematoxylin and Eosin

47-D Tip of a gill filament of Crenimugil labrosus showing a hyperplastic reaction in epithelial tissue at the distal end. Note the respiratory epithelium of the remaining lamellae which has ballooned and lifted away from the lamellar vessel. x 510 P.A.S./Coles Haematoxylin

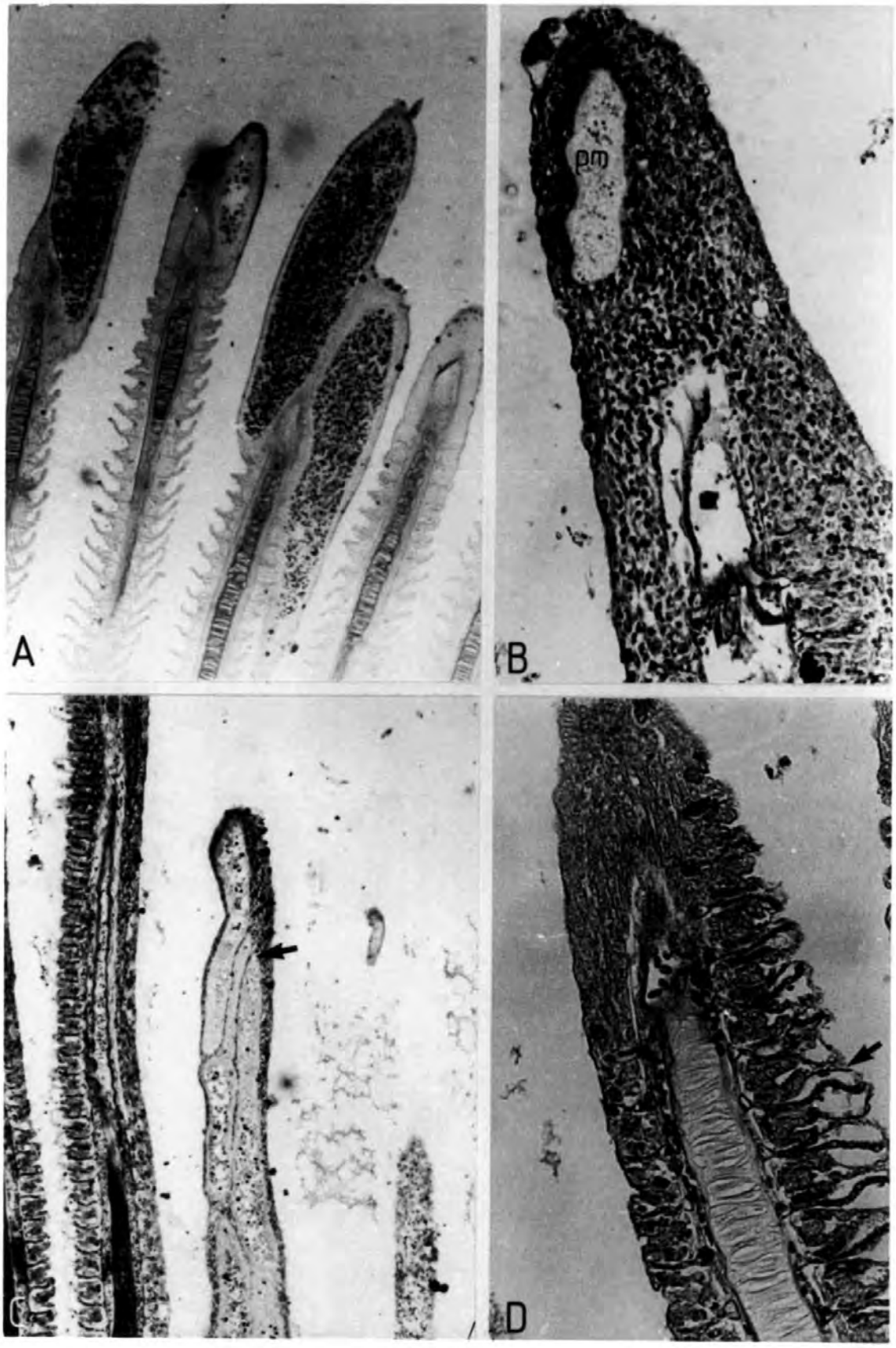
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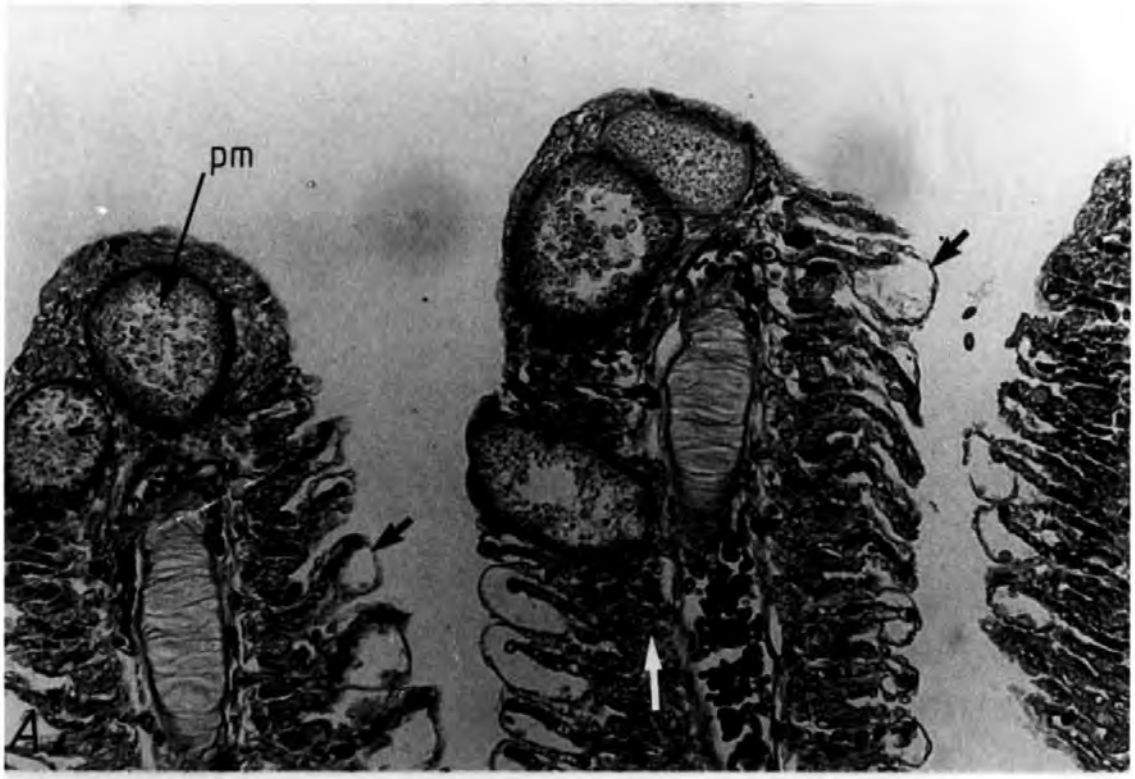
PLATE 48

The effect of Myxosporidiosis on gill tissues III

48-A Section through the tips of gill filaments of *Crenimugil labrosus* experimentally-infected with *Myxobolus exiguus* to show the developing plasmodia with accompanying effects on respiratory epithelium. Some hyperplasia is evident, but the principal effect is a ballooning and lifting of epithelium from the lamellar vessel (arrowed) x 695 Haematoxylin and Eosin

48-B A filament from the same preparation as A) above, to show the proliferation of epithelium beyond the tips of secondary lamellae on one side, and complete destruction of lamellae on the other (arrowed) x 600 Haematoxylin and Eosin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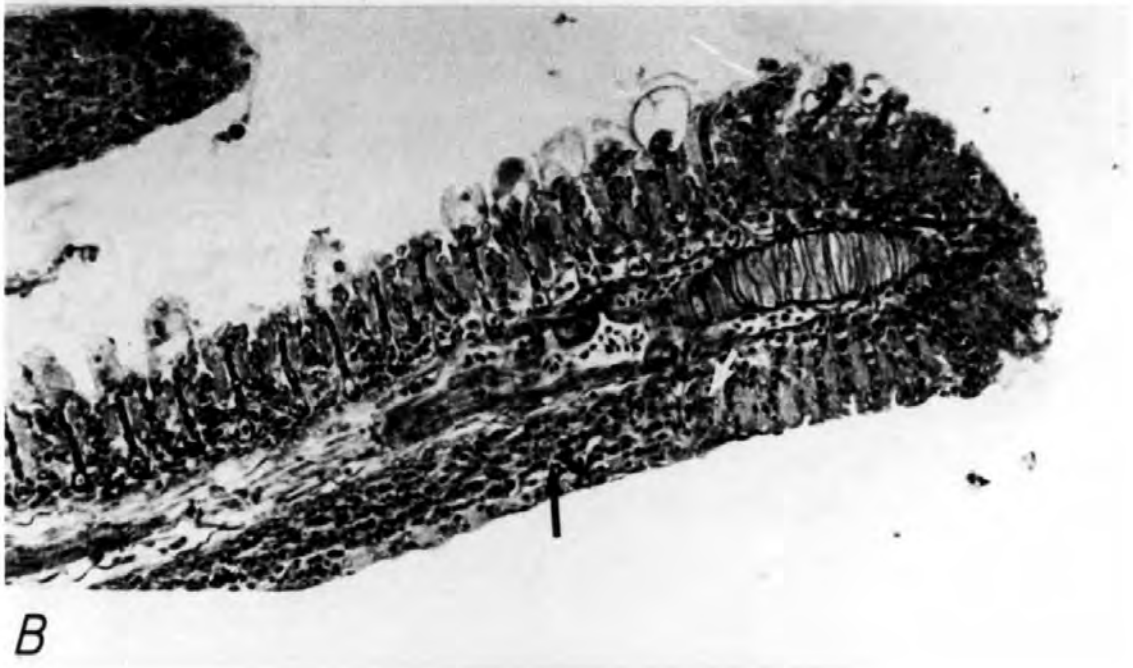
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PLATE 49

The effect of Myxosporidiosis on gill tissues IV

49-A Section of a gill filament of *Anguilla anguilla*, infected with an intralamellar cyst of *Myxidium giardi*. Note the distortion and compaction of lamellae, and proliferation of mucus cells in the basal epithelium. x 1400 P.A.S.

49-B Single infected lamella from an eel gill filament with an early plasmodium of *Myxidium giardi* at the tip x 1250 Haematoxylin and Eosin

49-C Plasmodium of *Myxobolus exiguus* covering several secondary lamellae in the gill of *Crenimugil labrosus*. Note the mucus cells in the overlying epithelium. x 930 P.A.S.

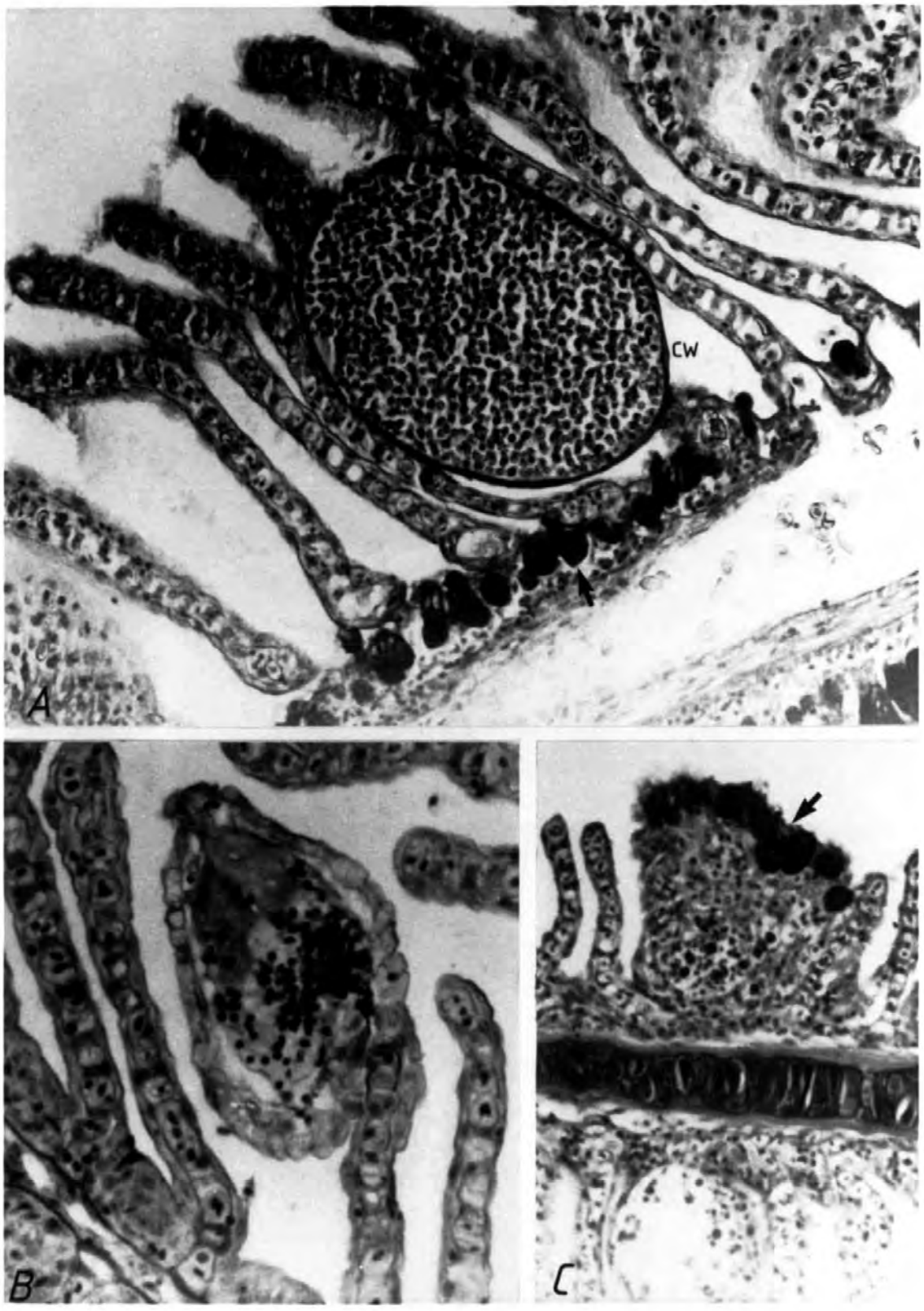
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PLATE 50

The effect of Myxosporidiosis on the alimentary tract and associated organs

50-A Section of a small plasmodium of Myxobolus exiguus in the intestine of Crenimugil labrosus. Note the hypercellular reaction, and degenerate appearance of the interior of the plasmodium. although no host cell infiltration is apparent x 760 Haematoxylin and Eosin

50-B Section through mullet liver tissue showing a plasmodium of Myxobolus exiguus (arrowed) adjacent to a bile collecting duct. Note the fibrotic layer around the duct wall. x 230 Haematoxylin and Eosin

50-C Intestinal wall of Anguilla anguilla showing a single plasmodium of Myxidium giardi. Some disorganisation and disruption of the muscle layers is apparent, and the plasmodium has caused separation of the outer layers from the lamina propria and gut epithelium. x 550 P.A.S.

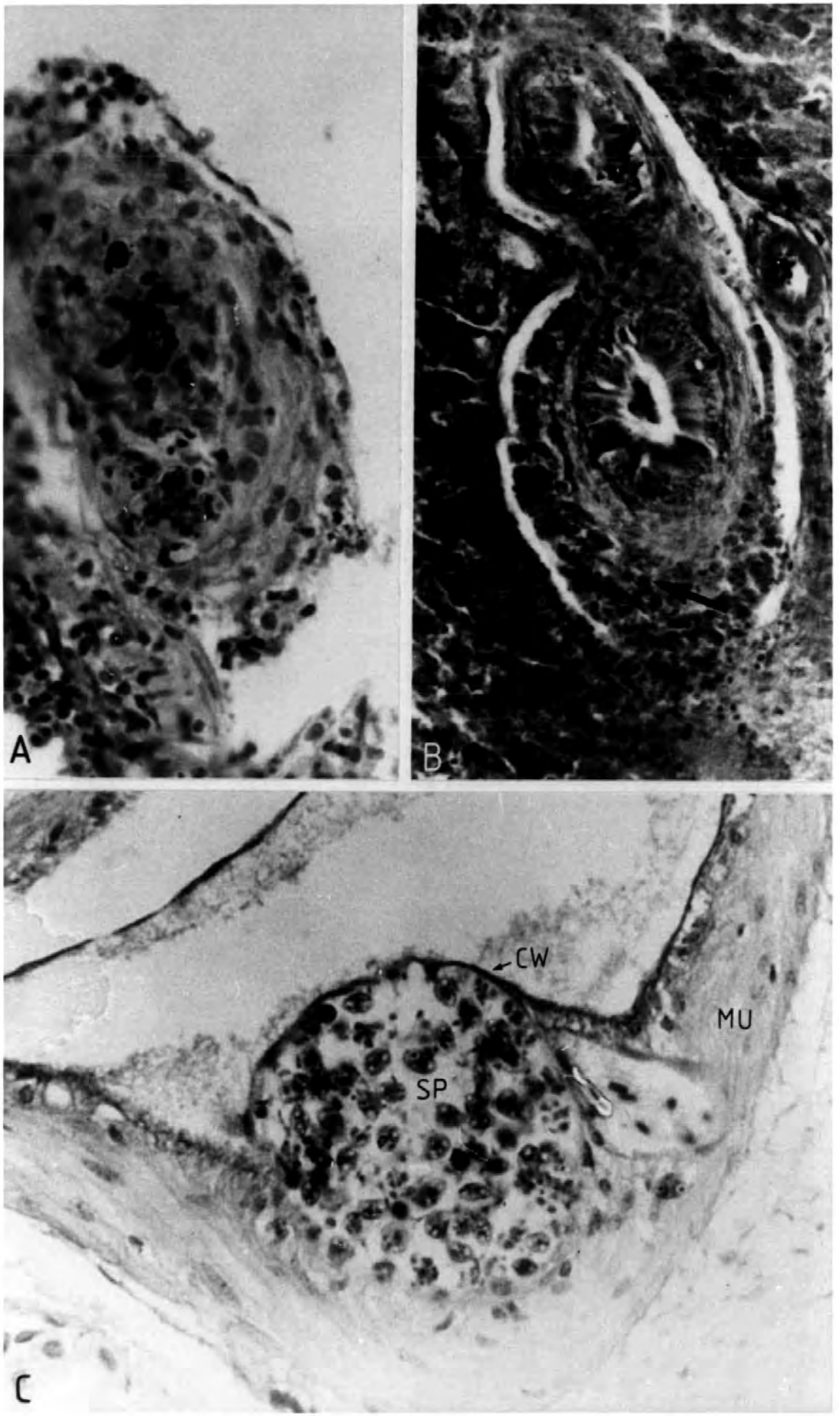
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PLATE 51

Myxobolus exiguus : effects of infection in Crenimugil labrosus at the ultrastructural level

51-A Plasmodium in mullet intestine, showing an adjacent fibroblast layer. Fibrous elements are in the process of being laid down, and the peripheral zone of the plasmodium is still developing, with membranous elements underlying the outer membrane. x 10,140

51-B Host cells in between two plasmodia in the gill. Note the compaction of cells, and the presence of granulocyte-type cells x 4554

51-C Development of a fine layer of fibres at the margin of a plasmodium (arrowed) in gut tissue x 10,920

51-D Fibroblast with an elongate nucleus in the cyst wall between two plasmodia in the gill. Note compression of host tissue. x 6750

51-E Several granulocyte-type cells (arrowed) in the vicinity of an intestinal plasmodium x 1560

51-F Interface between plasmodium and host cells in a gill infection, to show compression of adjacent host cells by the parasite x 29,700

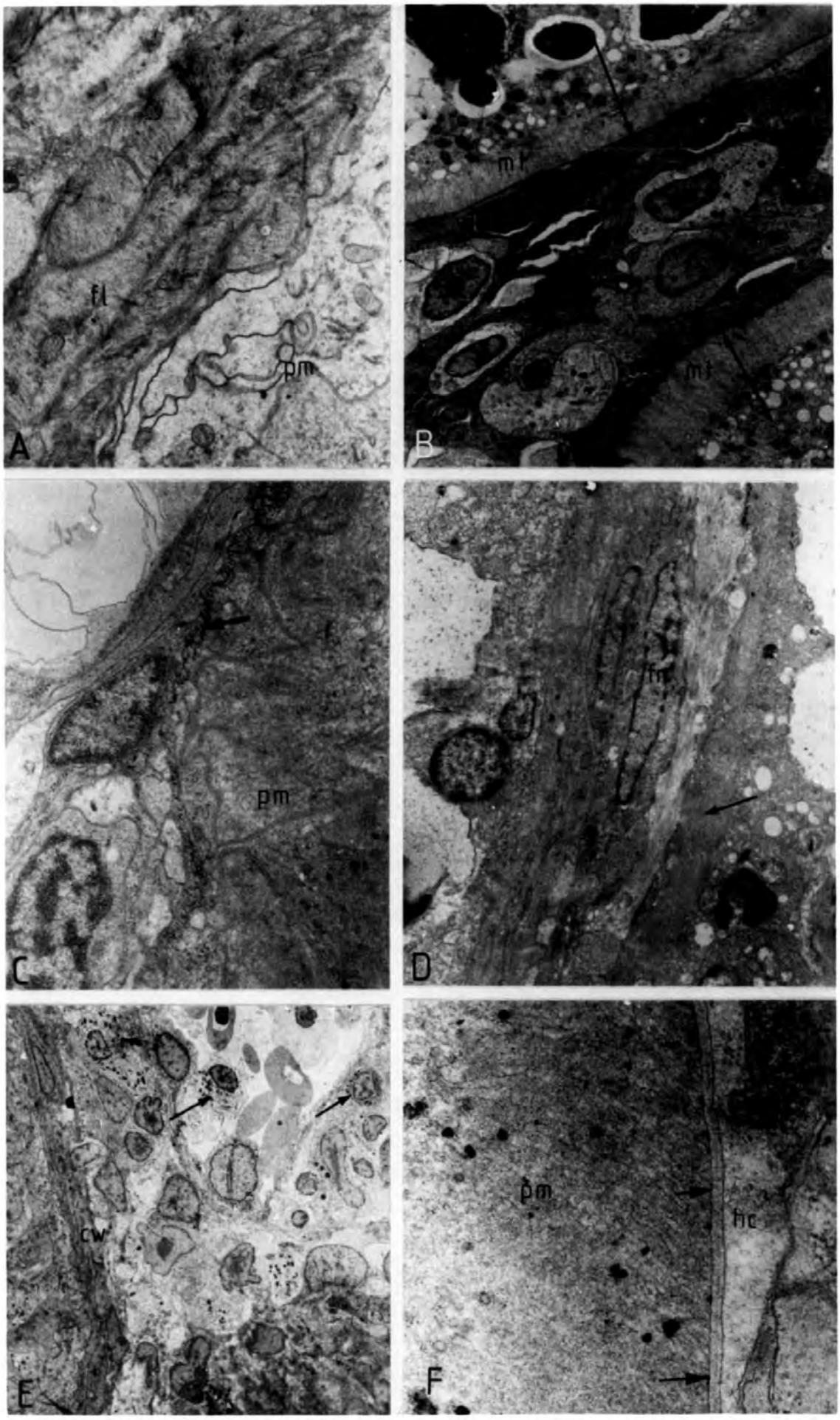
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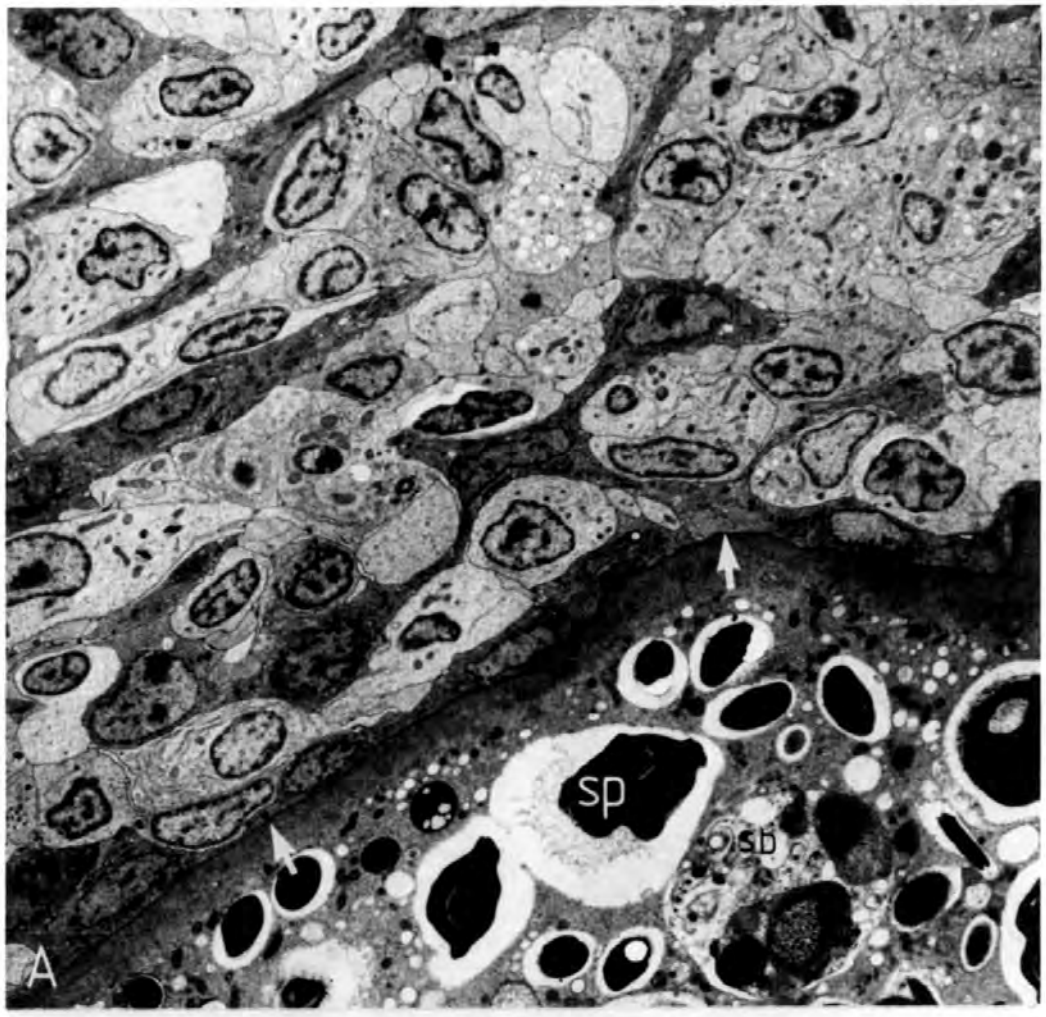
PLATE 52

Myxobolus exiguus : ultrastructural observations on host cells adjacent to plasmodia in *Crenimugil labrosus*

52-A Host cells adjacent to a plasmodium in the gill, including fibroblasts forming the cyst wall, and granulocytes. Limits of the plasmodium are indicated by arrows. x 3950

52-B Granulocytes (arrowed) in host tissues adjacent to an intestinal infection x 2510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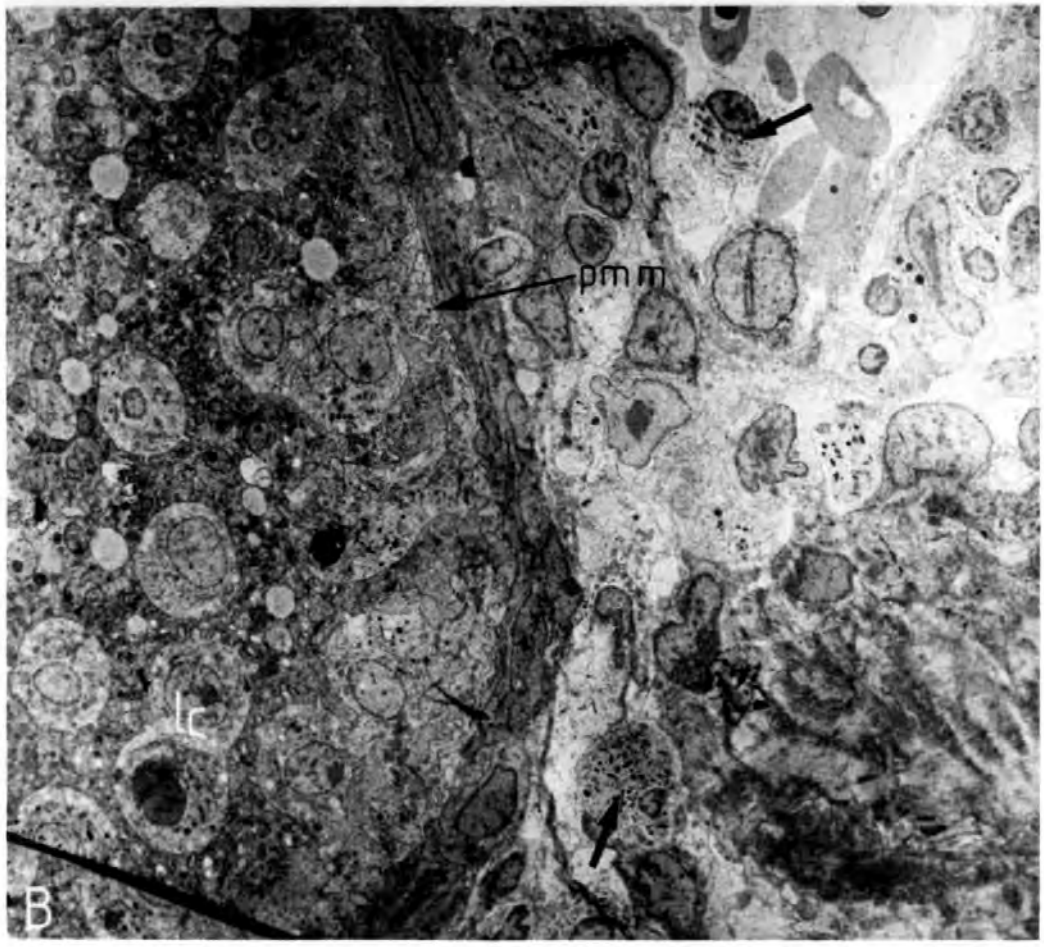
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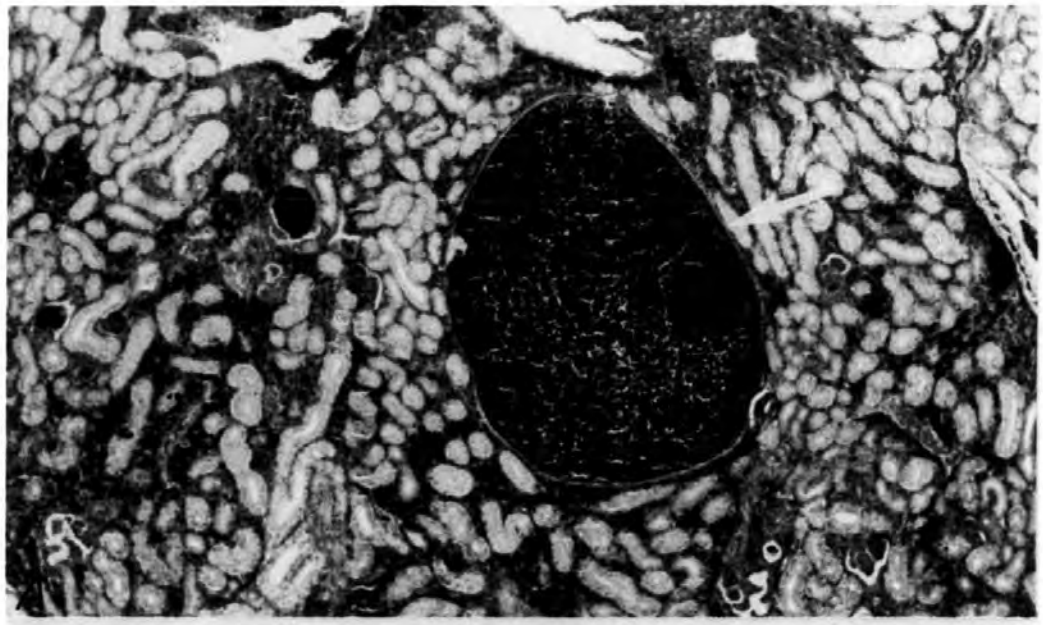
PLATE 53

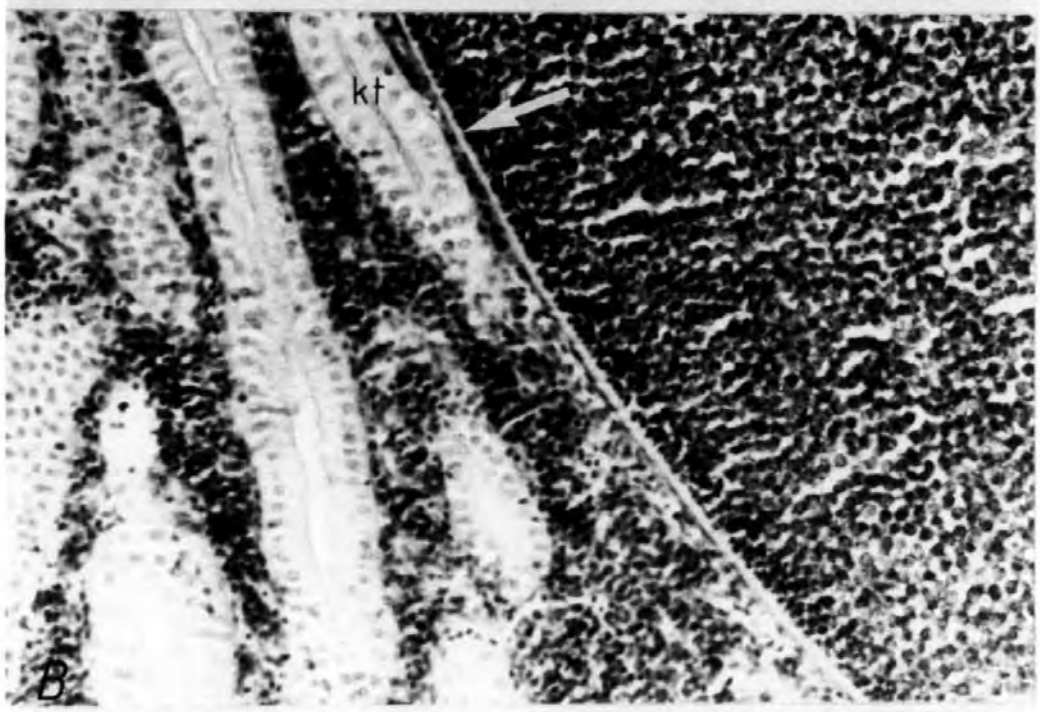
Myxidium giardi : the effects of renal infection in Anguilla anguilla

53-A Large cyst occupying approximately $^1/_6$th of the kidney in transverse section x 83 P.A.S.

53-B Host-parasite interface between plasmodium and renal tissue. The limits of the plasmodium are arrowed. Note compression of kidney tubules adjacent to the cyst. x 382 P.A.S.

53-C Spores of Myxidium giardi within the lumen of a kidney tubule. Note distorted and ruptured areas of tubular epithelium, where spores have been released into the interstitial cell regions. x 808 Haematoxylin and Eosin

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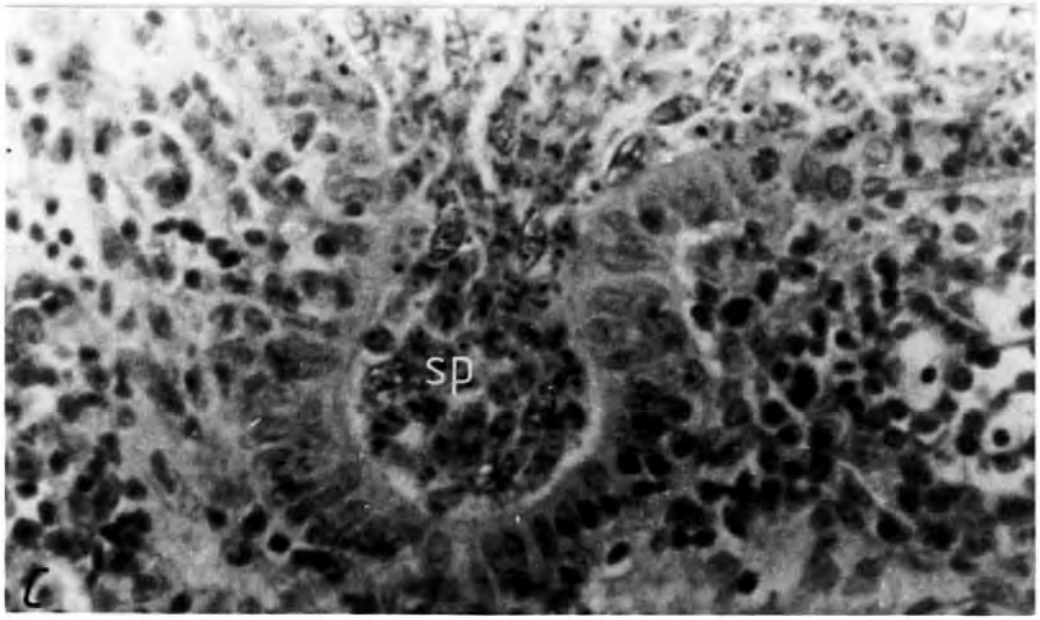
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PLATE 54

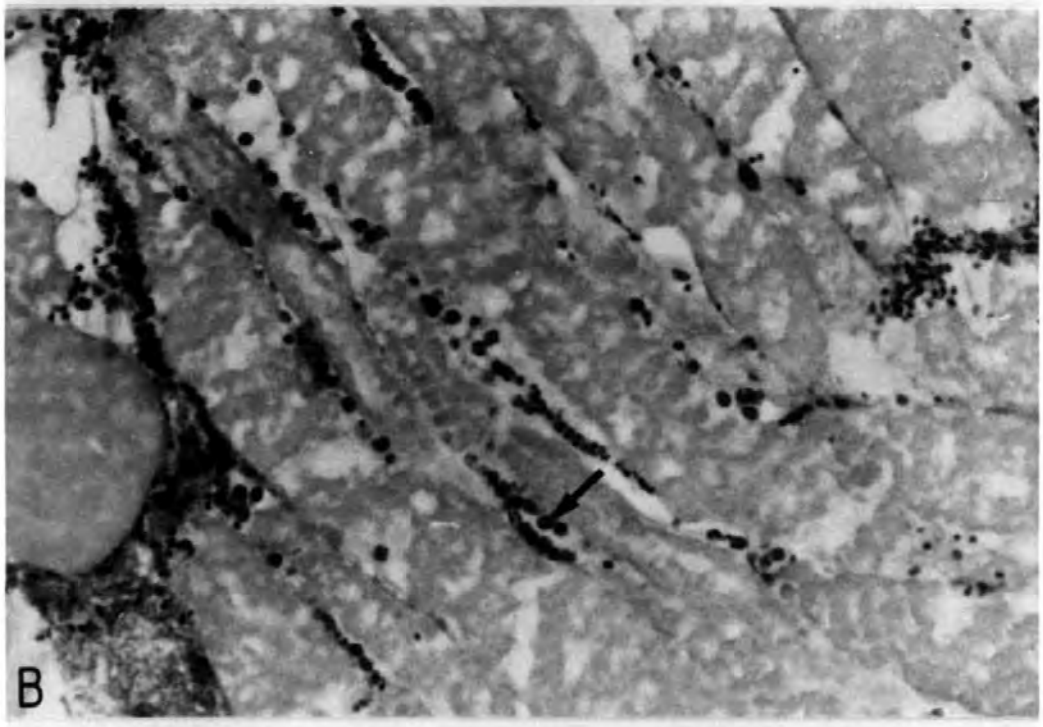
Myxobolus exiguus : the effects of infection of the musculature of Crenimugil labrosus

54-A Oblique section through the tegument to show areas of sub-cutaneous tissue infiltrated with spores (arrowed) x 65 Haematoxylin and Eosin

54-B Section of skeletal musculature four days post-injection with spores (arrowed). No plasmodium development is apparent. x 214 P.A.S.

54-C Section of skeletal musculature 12 weeks post-injection with spores. Note the developing plasmodium (arrowed) adjacent to muscle fibres. x 134 P.A.S.

A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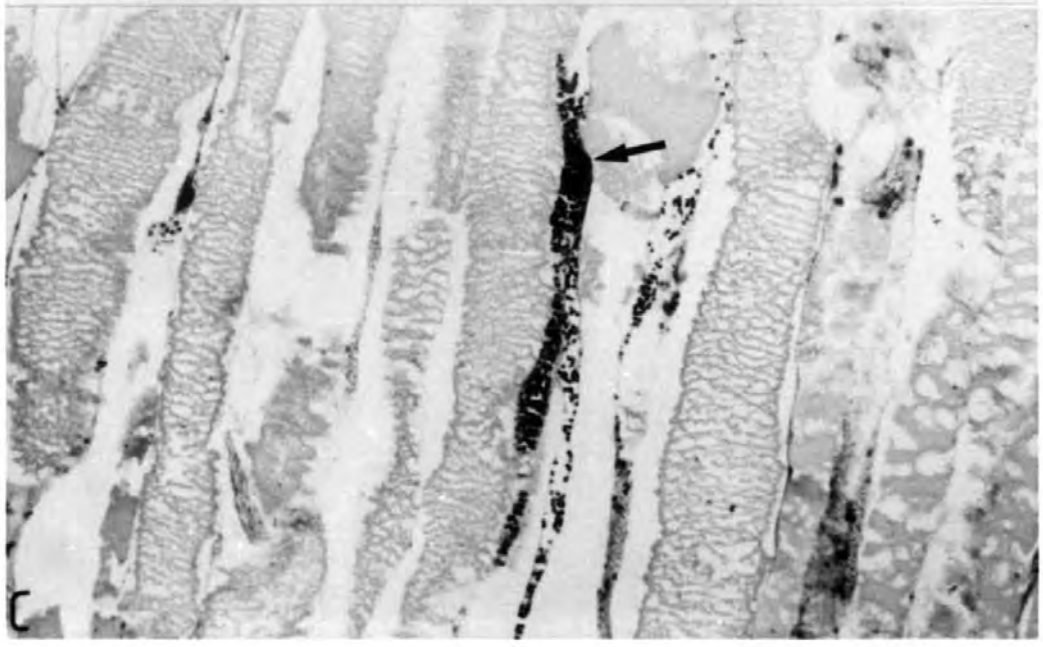
C

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Appendix 1A

Previous descriptions of *Myxidium incurvatum*

Myxidium incurvatum : Thélohan, 1892b, 1895
Parisi, 1912
Auerbach, 1913
Georgévitch, 1916a
Davis, 1917
Kudo, 1920
Dunkerly, 1920, 1925
Jameson, 1929
Naville, 1930
Petrushevsky, 1932
Noble, 1941b
Shulman and Shulman - Albova, 1953
Laird, 1953
Shulman and Shtein, 1962

Habitat : Gall bladder of *Nerophis aequoreus*, *N. annulatus*, *N. lumbriciformis*, *Blennius pholis*, *Callionymus lyra*, *Fundulus majalis*, *Gambusia affinis*, *Hippocampus brevirostris*, *Mugil cephalus*, *Scorpaena scrofa*, *Dialarchus snyderi*, *Sebastodes caurinus*, *Syngnathus acus*, *S. typhle*, *S. schlegeli*, *Cyclopterus lumpus*, *Ammodytes tobianus*, *Limanda limanda*, *Platichthys flesus*, *Myxocephalus scorpius*, *Diplocrepis puniceus*, *Notoclinus fenestratus*, *Oliverichterus melobesia* and *Acanthoclinus quadridactylus*

Localities : France, Italy, Norway, Monaco, U.S.A., U.S.S.R. and New Zealand

Appendix 1B

Previous descriptions of *Myxobolus exiguus*

Myxobolus exiguus : Thélohan, 1895
Wegener, 1910
Parisi, 1912
Kudo, 1920
Jirovec, 1942
Lom, 1961
Shulman and Shtein, 1962
Shulman, 1966a

Habitat : Gills, walls of stomach, pyloric caecae, intestine, spleen, liver, kidney and skin of *Abramis brama*, *A. ballerus*, *A. sapa*, *Mugil chelo*, *M. capito*, *M. cephalus*, *M. saliens*, *M. auratus*, *M. ramada*, *Crenimugil labrosus*, *Chondrostoma nasus*, *C. cyri*, *Pelecus cultratus*, *Alburnus alburnus*, *Blicca bjoerkna*, *Aspius aspius*, *Rutilus rutilus*, *Leuciscus idus*, *L. cephalus*, *Cyprinus carpio* and *Scardinia erythrophthalmus*

Localities : France, Germany, Switzerland, Italy, Czechoslovakia and U.S.S.R.

Appendix 2

Members of the Mugilidae recorded as hosts for Myxobolus species

Unless otherwise stated, all records below are from Shulman and Shtein (1962) :

Host	Parasite	Site of Infection
Mugil cephalus	Myxobolus mulleri	connective tissues
	M. exiguus	walls of stomach, gills, pyloric caecae, intestine and skin
	M. parvus	gills
	M. achmerovi	gills, fins, mesenteries
	M. cheni	skeletal muscle
Mugil soiuy	M. parvus	gills
	M. cheni	skeletal muscle
	M. achmerovi	gills, fins, mesenteries
Mugil saliens	M. mulleri	connective tissues
Mugil chelo	M. exiguus	walls of stomach, gills, pyloric caecae, intestine and skin
Mugil capito	M. exiguus	as above
Liza ramada	M. exiguus	as above
Liza auratus	M. exiguus	as above
Mugil sp. (Lahav, 1974)	Myxobolus sp.	gills

Appendix 3

Infection with Myxosporidia related to sex of the host
(figures in parenthesis = % of total in group)

	Total	♂	♀	immature
Total fish species				
N° examined	1216	264(21.7)	481(39.5)	471(38.7)
% infection	37.5	34.5(7.5)	38.5(15.2)	38.1(14.7)
Taurulus bubalis				
N° examined	62	19(30.6)	33(53.2)	10(16.1)
% infection	38.7	52.6(16.1)	36.4(19.3)	20(3.2)
Ciliata mustela				
N° examined	37	12(32.4)	25(67.5)	0 -
% infection	21.6	33.3(10.7)	16(10.8)	0 -
Gobius paganellus				
N° examined	39	13(33.3)	15(38.5)	11(28.2)
% infection	20.5	30.8(10.2)	26.6(10.24)	0 -
Gaidropsarus mediterraneus				
N° examined	14	7(50)	6(42.8)	1(7)
% infection	64.3	71.4(35.7)	66.6(28.5)	0 -
Blennius pholis				
N° examined	74	26(35.1)	45(60.8)	3(4)
% infection	43.2	46.2(16.2)	42.2(25.6)	33.3(1.3)
Crenilabrus melops				
N° examined	26	10(38.4)	13(50)	3(11.5)
% infection	53.8	60(23.0)	38.5(19.2)	100(11.5)
Pollachius pollachius				
N° examined	40	8(20)	17(42.5)	15(37.5)
% infection	37.5	50(10.0)	47(19.9)	20(7.5)

Appendix 3 (continued)

Combined total of 7 selected species				
N° examined	292	95(32.5)	154(52.7)	43(14.7)
% infection	37.6	47.3(15.4)	36.3(19.1)	20.9(3.1)

Appendix 4

Infection related to size of host in three teleost species recovered from South-Western waters

Host species	Size class (cm)	N° in group	N° infected	%
Taurulus bubalis (infected with Ceratomyxa dubia)	0.1-5.0	19	6	31.6
	5.1-10.0	41	16	39.0
	10.1-15.0	4	2	50.0
	15.1-20.0	1	0	0
Blennius pholis (infected with Myxidium incurvatum)	3.6-5.5	11	2	18.2
	5.6-7.5	21	6	28.6
	7.6-9.5	14	9	64.2
	9.6-11.5	15	9	60.0
	11.6-13.5	9	4	44.4
	13.6-15.5	3	2	66.6
	15.6-17.5	1	0	0
Gobius paganellus (infected with Ceratomyxa arcuata)	0-4.0	9	0	0
	5.0-8.0	18	3	16.6
	9.0-12.0	5	2	40.0
	13.0-16.0	4	2	50.0
	17.0-20.0	3	1	66.6

Appendix 5

To show % infection of grey mullet with *Myxobolus exiguus* for the total number of infections, and % infection and numbers of cysts associated with different sites of infection in different size classes of fish

Length class	Number in class	Number infected	% infection	Number infected at different sites			% infection at different sites			Mean number of cysts		
				gut	gill	skin	gut	gill	skin	gut	gill	skin
1.0- 1.9	13	0	0	0	0	0	0	0	0	0	0	0
2.0- 2.9	42	0	0	0	0	0	0	0	0	0	0	0
3.0- 3.9	99	51	51.5	51	0	13	100	0	25.5	33.5	0	58
4.0- 4.9	87	46	52.8	45	2	7	97.8	4.3	15.2	50.2	4	15
5.0- 5.9	124	44	35.5	41	3	1	93.1	6.8	2.3	38	16	50
6.0- 6.9	84	28	33.3	16	11	1	57.1	39.2	3.6	28	20	20
7.0- 7.9	39	9	23	4	5	0	44.4	55.6	0	8	35	0
8.0- 8.9	15	4	26.6	0	4	0	0	100	0	0	28	0
9.0- 9.9	12	1	8.3	1	0	1	100	0	100	2	0	12

Appendix 5 (continued)

Length class	Number in class	Number infected	% infection	Number infected at different sites			% infection at different sites			Mean number of cysts		
				gut	gill	skin	gut	gill	skin	gut	gill	skin
10.0-10.9	21	3	14.3	0	3	0	0	100	0	0	6	0
11.0-11.9	8	0	0	0	0	0	0	0	0	0	0	0
12.0-12.9	8	2	25	1	1	0	50	50	0	3	20	0
13.0-13.9	8	1	12.5	0	1	0	0	100	0	0	10	0
14.0-14.9	5	0	0	0	0	0	0	0	0	0	0	0
TOTAL	565											

Appendix 6

Mean Cyst Numbers and % infection at various sites with *Myxobolus exiguus*, for size classes of Mullet (total data)

		3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9
Mean number of cysts in group	gut	33.5	50.2	38	28	8	0	2	00	0	3	0
	gill	0	4	16	20	35	28	0	6	0	20	10
	skin	58	15	50	20	0	0	12	0	0	0	0
% of total individuals in group infected with gut, gill & skin cysts	gut	100	97.8	93.1	57.1	44.4	0	100	0	0	50	0
	gill	0	4.3	6.8	39.2	55.6	100	0	100	0	50	0
	skin	25.5	15.2	2.3	3.6	0	0	100	0	0	0	0

Appendix 7

% Infection of all species collected October 1976-September 1978

Month & Year of sample		% Infection
October	1976	50
November		47
December		71
January	1977	80
February		28
March		61
April		100
May		60
June		42
July		21
August		22
September		27
October		41
November		35
December		100
January	1978	45
February		58
March		No sampling conducted
April		32
May		37
June		28
July		50
August		22
September		43

Appendix 8

% totals and infections for different size classes of Grey Mullet from Aveton, and St. John's Hake at four times of the year

Size classes of Mullet	Aveton - July		St.Johns - July		St.Johns - Oct.		St.Johns - Feb.		St.Johns - April/May	
	% of total in group	% in-fection	% of total in group	% in-fection	% of total in group	% in-fection	% of total in group	% in-fection	% of total in group	% in-fection
1 - 1.9	-	-	13 9.8	-	-	-	-	-	-	-
2 - 2.9	-	-	42 31.8	-	-	-	-	-	-	-
3 - 3.9	-	-	23 17.4	-	51.2	74 67.6	2 3.3	50	-	-
4 - 4.9	7 3.6	57.1	1 0.8	-	33.3	48 66.6	30 50	30	1 2.9	100
5 - 5.9	87 44.6	36.8	4 3	-	8.3	12 41.6	16 26.7	25	5 14.7	60
6 - 6.9	41 21	31.7	29 21.9	34.5	1.3	0	8 13.3	37.5	4 11.8	50
7 - 7.9	11 5.7	9.1	16 12.1	25	-	-	2 3.3	50	10 29.4	30
8 - 8.9	6 3	16.6	3 2.3	0	-	-	-	-	6 17.6	50
9 - 9.9	6 3	16.6	-	-	1.3 2	0	-	-	4 11.8	0
10 - 10.9	13 6.8	7.5	-	-	3.3 5	20	2 3.3	50	1 2.9	0
11 - 11.9	7 3.6	0	1 0.8	0	-	-	-	-	-	-
12 - 12.9	6 3	16.6	-	-	1.3 2	0	-	-	1 2.9	100
13 - 13.9	6 3	0	-	-	-	-	-	-	2 5.9	50
14 - 14.9	5 2.7	0	-	-	-	-	-	-	-	-