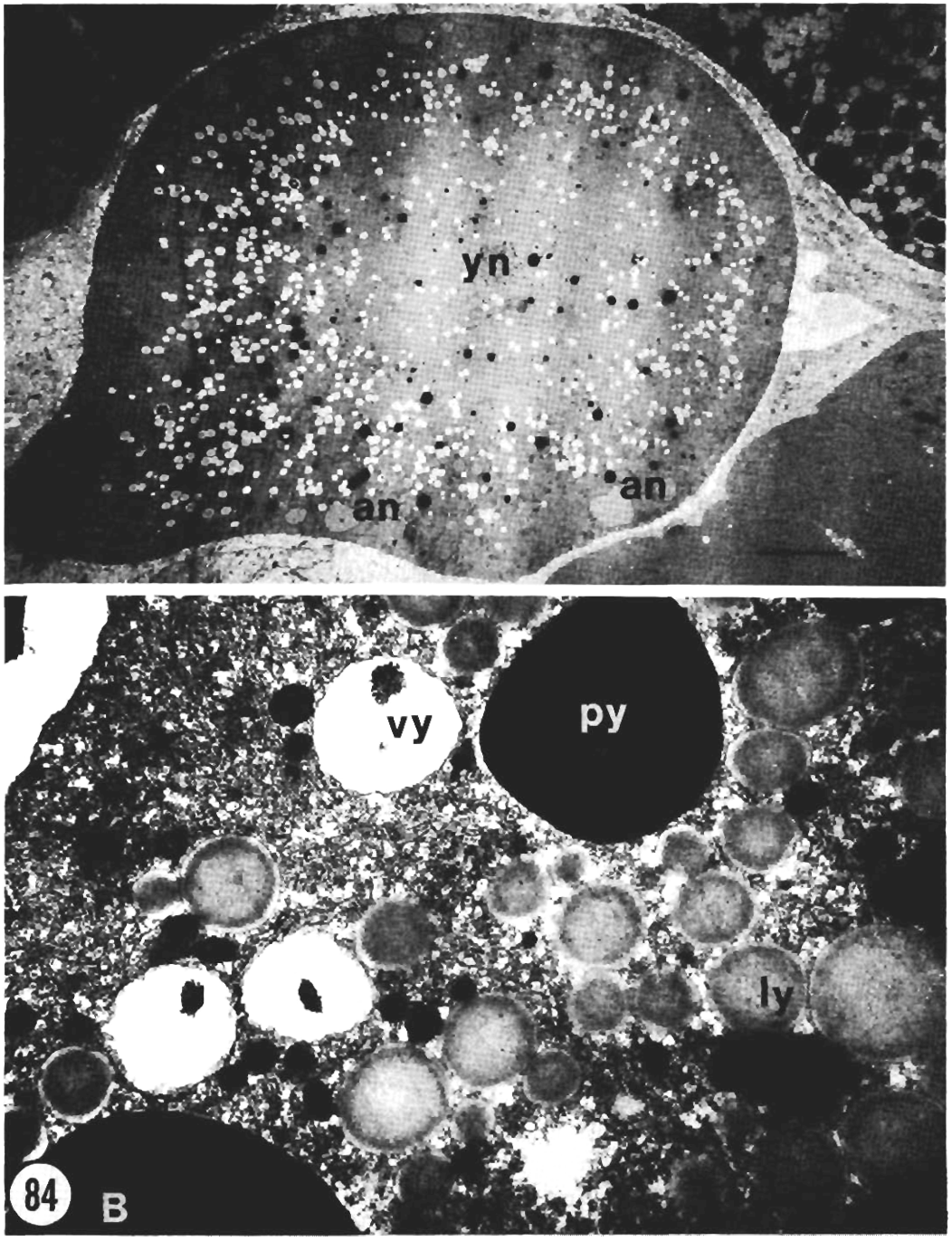

Fig. 84. The *Artemia* oocyte in early vitellogenesis. (After Criel, 1989.) **A:** Low magnification of oocyte in early vitellogenesis. Yolk nucleus (yn) is in cell center with several accessory nuclei (an) around periphery of oocyte. Scale bar = 5 μm. **B:** The four known yolk products: lipid yolk droplets (ly), proteinaceous yolk platelets (py), vesicular yolk bodies (vy), and ER cisternae with granular material (arrow).

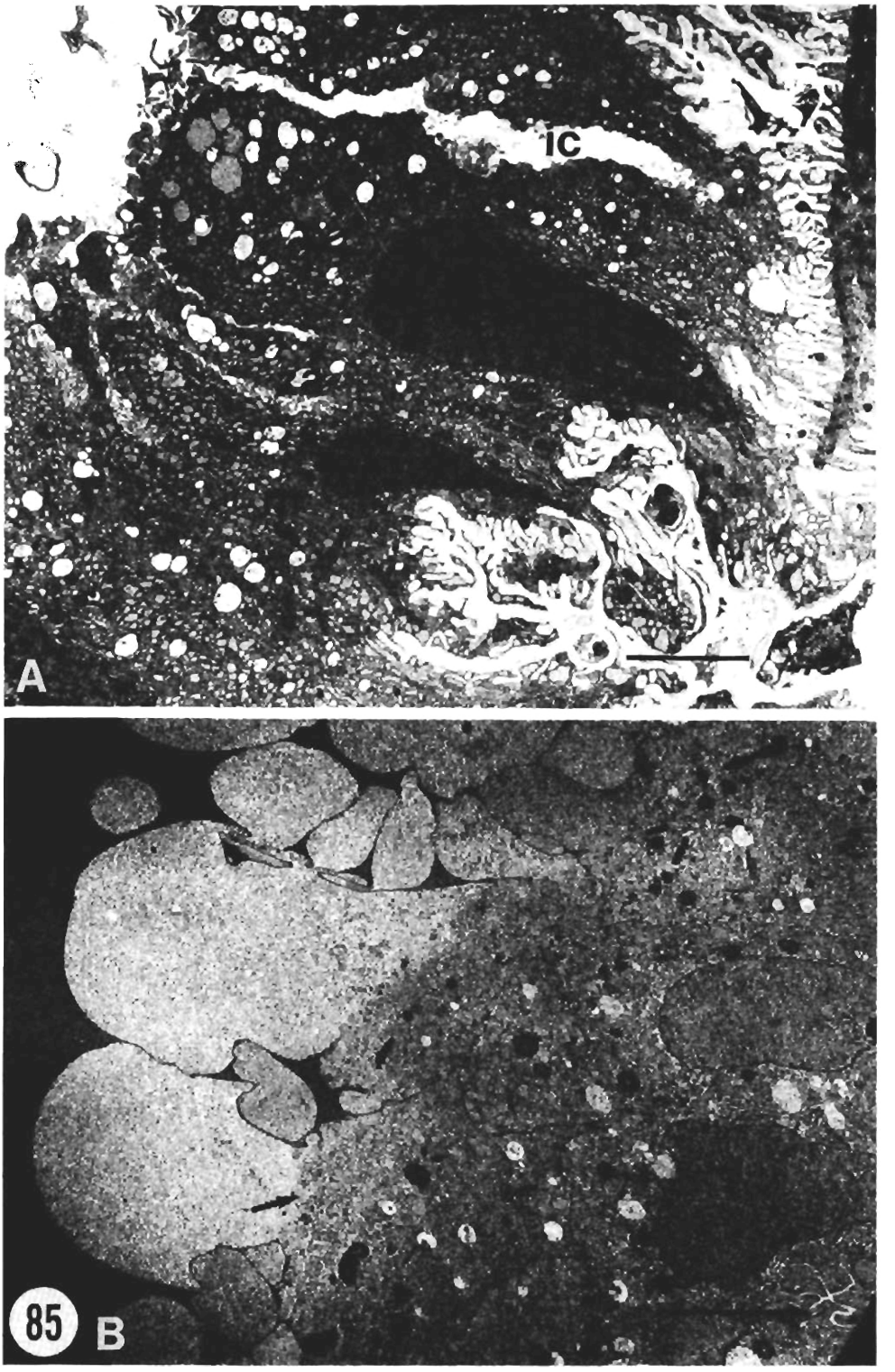

Fig. 85. The *Artemia* oviduct. (After Criel, 1980b.) **A:** Part of oviduct just after descent of eggs. Scale bar = 5 μm. **B:** Apical protrusions of oviduct cells 76 h after release of eggs into uterus. Note demarcation (arrow) between cell body and apical protrusion. Scale bar = 5 μm. ic, intercellular canaliculus; g, Golgi complexes; m, mitochondria; za, zonula adherens.

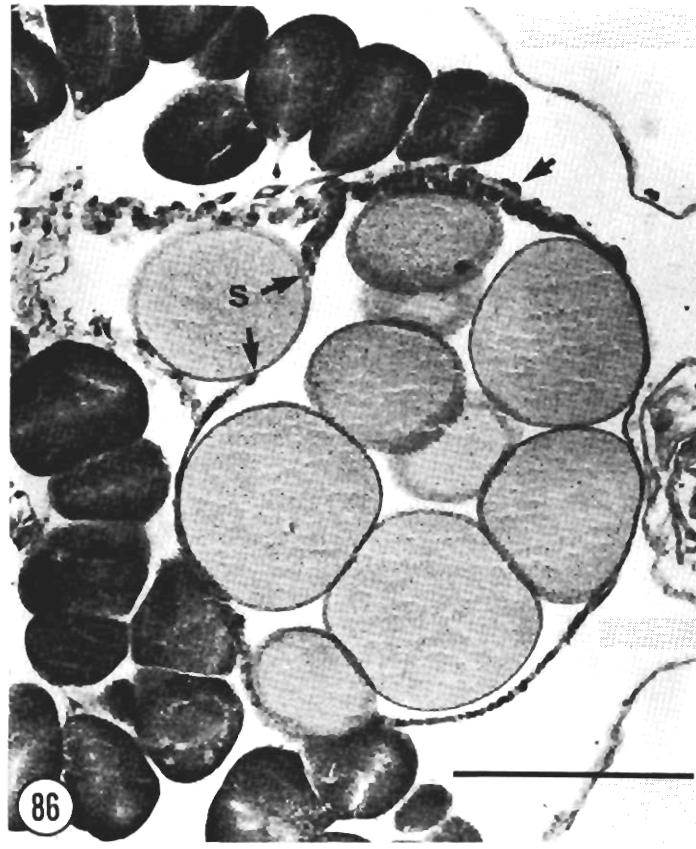

Fig. 86. Release of eggs from the lateral pouches of the *Artemia* oviduct, showing the opened "shutter" mechanism (S) and the beginning retraction of the extended oviduct (arrow). Scale bar = 200 μm. (After Criel, 1980a.)

nium, each mitosis having incomplete cytokinesis. These four cells are connected by intercellular cytoplasmic bridges (Figs. 90, 91), 0.9–1.9 μm wide, reflecting the incomplete cytokinesis. These broad regions of cell communication might infer synchronous maturation of the four sister-follicular cells, or possibly a trophic relationship where nurse cells support the oocyte (Anteunis et al., 1966; Trentini and Sabelli Scanabissi, 1978). A trophic relationship is supported by the observation of Trentini and Sabelli Scanabissi (1978) that yolk globules are present in the nurse cell cytoplasm, the first report of yolk droplets in nurse cells of any arthropod. The finding of yolk in the nurse cell cytoplasm, and the implication that it is subsequently delivered via cytoplasmic bridges to the oocyte, also supports the theory that the nurse cells are abortive oocytes, i.e., they are derived from true germ cell precursors that begin growth as oocytes but do not undergo meiosis following yolk production (Trentini and Sabelli Scanabissi, 1978). Such cytoplasmic bridges are also known from female germ cells in the Anomopoda (*Daphnia*) (Zaffagnini and Lucchi, 1965) and Anostraca (Anteunis et al., 1966). Nurse cells are differentiated from true oocytes early in development. They increase in size much more rapidly than does the oocyte (in contrast to the situation in all other branchiopods), and their nuclei con-

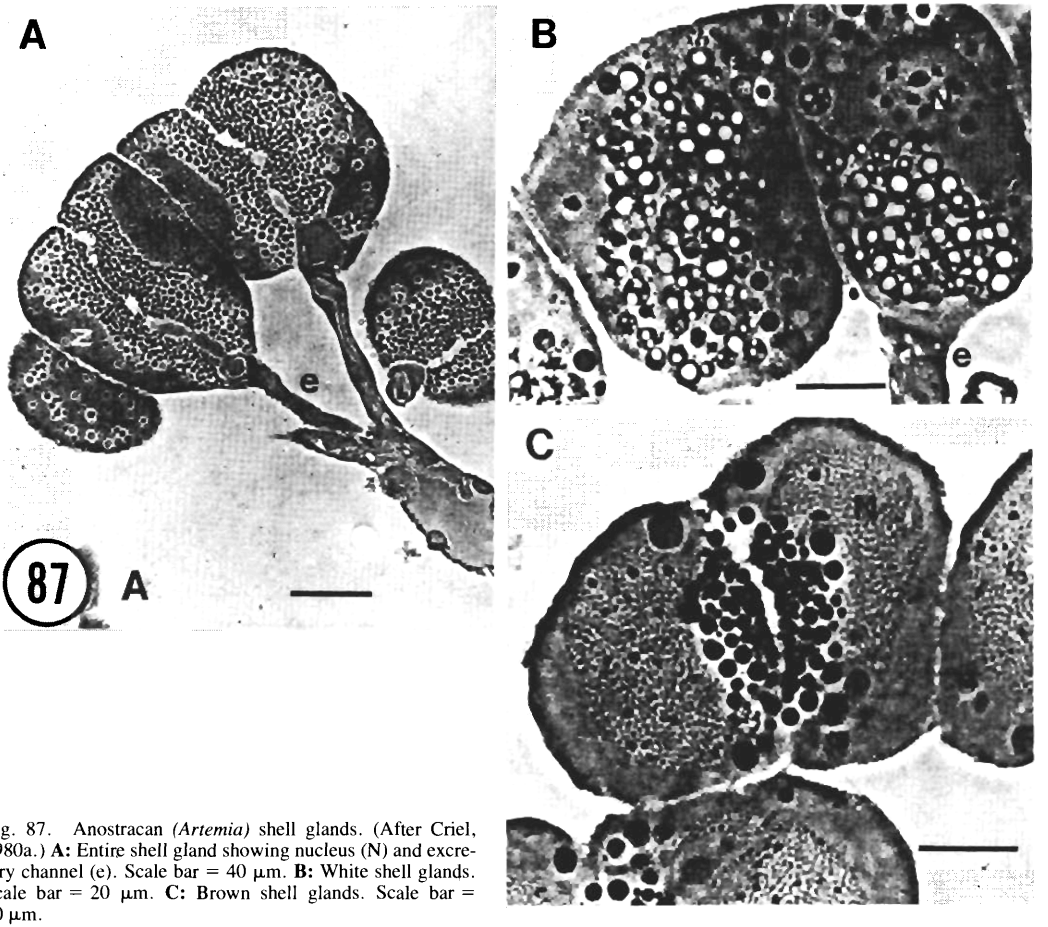

Fig. 87. Anostracan *(Artemia)* shell glands. (After Criel, 1980a.) **A:** Entire shell gland showing nucleus (N) and excretory channel (e). Scale bar = 40 μm. **B:** White shell glands. Scale bar = 20 μm. **C:** Brown shell glands. Scale bar = 20 μm.

tain many more nucleoli than does the nucleus of the oocyte. Additionally, nurse cell cytoplasm contains scattered chromatin, many free ribosomes (giving it a darker appearance than oocyte cytoplasm), few scattered long mitochondria, and concentrically arranged membranes of SER. The number and nature of these cellular components change during the stages of follicle development (see Trentini and Sabelli Scanabissi, 1978). In later stages, groups of vesicular bodies are seen near the larger yolk globules, possibly resulting from the breakup of large yolk globules at the end of the nurse cell growing stage (stage IV of Trentini and Sabelli Scanabissi, 1978).

The oocyte exhibits many similarities with the nurse cells, again inferring that the four cells had a similar precursor and that nurse cells are abortive oocytes. Shared components include concentrically arranged ER in early stages of oocyte development, yolk globules, and annulate lamellae (later stages only). Oocytes differ in having a single nucleolus in the nucleus, synaptonemal complexes visible in the nucleus (which previously had been reported only from crustacean spermatocytes), annulate lamellae, and other structures peculiar to germ cells that are not found in the nurse cells (Sabelli Scanabissi and Trentini, 1979). Although it increases in size, the oocyte is still smaller than surrounding nurse cells at the end of maturation, which is not the

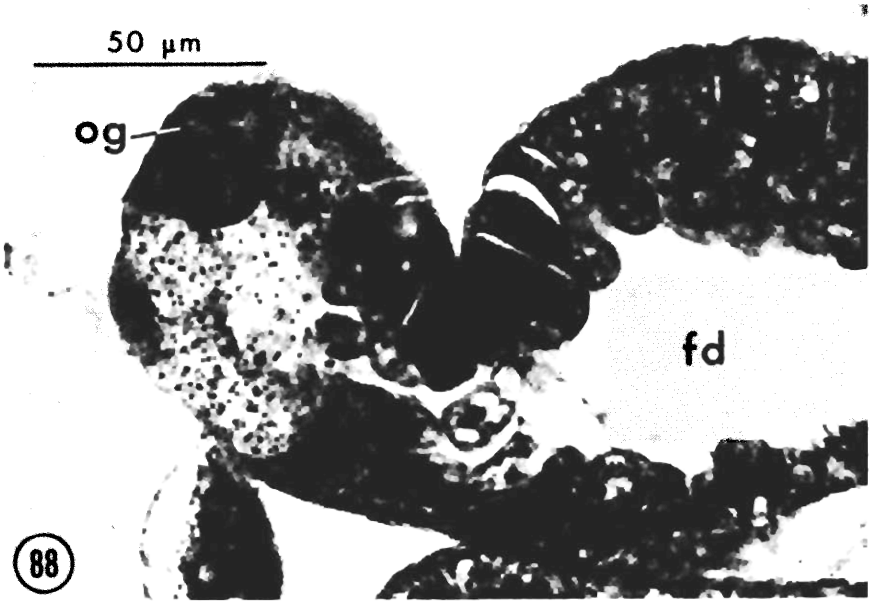

Fig. 88. Hermaphroditic *Triops cancriformis* (Notostraca) with testicular lobe containing oocyte group (og) coming off the follicular duct (fd). (From Zaffagnini and Trentini, 1980.)

case in other orders. The synaptonemal complexes (SC) are 90 nm wide centrally with lateral elements of 30 nm, and they are anchored to the nuclear envelope, which is indented at the point of insertion of the SC (Sabelli Scanabissi and Trentini, 1979). As the oocyte enlarges, several groups of concentrically arranged membranes can be seen in the cytoplasm; these appear similar to those seen in notostracan nurse cells. In later (larger) stages of development, the nuclear envelope displays many pore complexes, with pores regularly spaced and having a constant diameter of about 60 nm. Groups of evenly arranged annulate lamellae (AL), consisting of up to 20 layers of paired annulated membranes, can be seen in the cytoplasm. These AL are similar to those previously reported for brine shrimp and may indicate a high metabolic rate for these cells (see Sabelli Scanabissi and Trentini, 1979).

As the notostracan oocyte matures, it passes down the follicular duct (Fig. 89). This duct is lined with a single-layered epithelium that also produces the "eggshell" (tertiary envelope) material. These epithelial cells are closely packed, average 28 μm high × 7 μm wide, possess an elliptical nucleus with (usually) two types of nucleoli, and bear short, apical microvilli (Trentini and Sabelli Scanabissi, 1982). The nuclear envelope has few deep infoldings and is always covered with ribosomes and pierced by pores. Cytoplasm of these cells appears electron-dense, partly because of the numerous free ribosomes, but mostly because of the extensive development of RER, the presumed site of synthesis of the eggshell material, a "paracrystalline" substance that is subsequently stored in large vacuoles before being excreted into the lumen of the follicular duct in the form of discrete electron-dense spheres (Trentini and Sabelli Scanabissi, 1982). Basally, these cells contain large (about 2 μm diameter) vacuoles that arise from cytoplasmic membranes in intercellular spaces. Maturing oocytes (about 0.3 μm diameter) descend along the follicular ducts toward the oviduct, and in so doing they

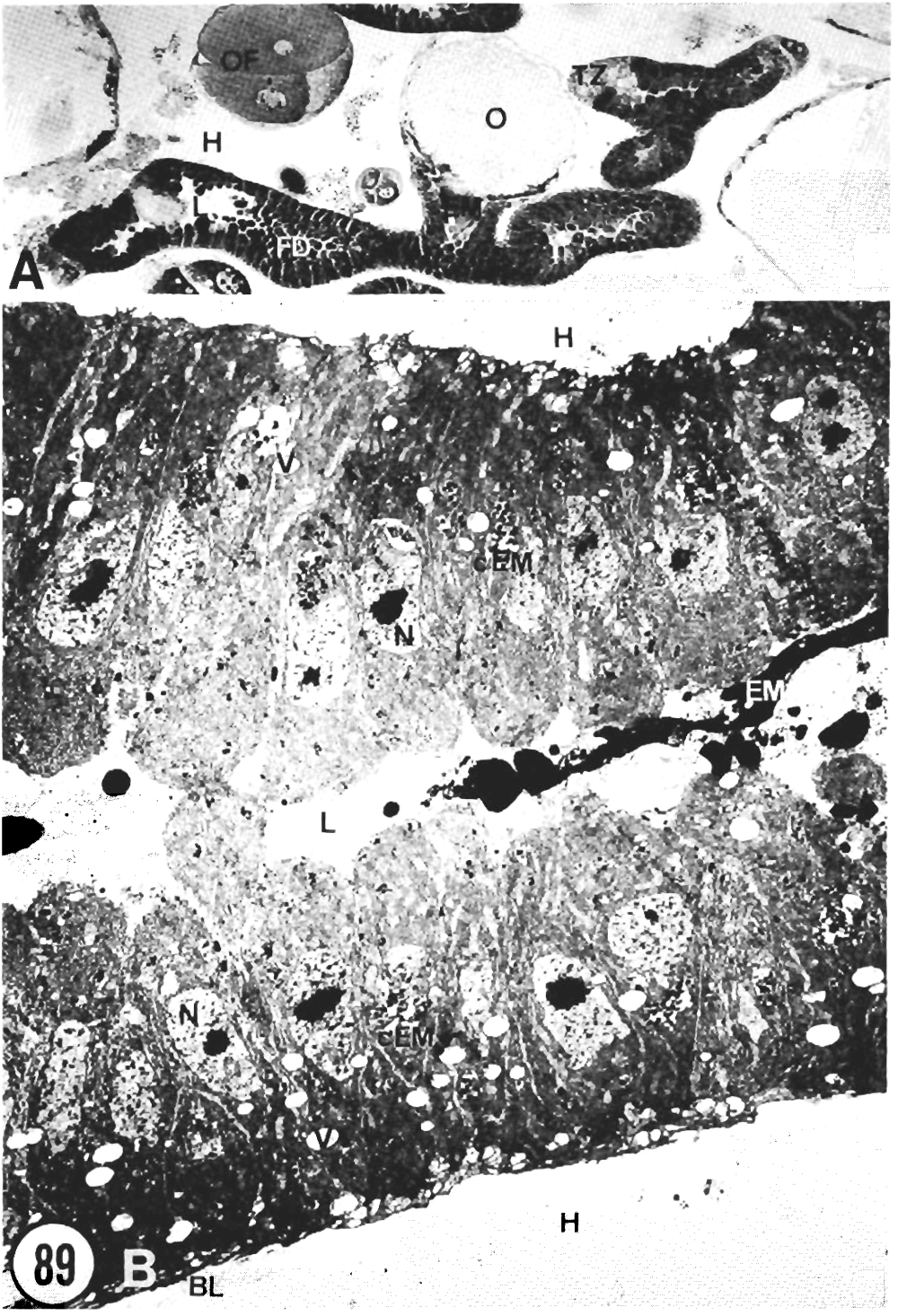

Fig. 89. Follicular duct of *Triops cancriformis* (Notostraca). (From Trentini and Sabelli Scanabissi, 1982.) **A:** Low-magnification overview showing germinal zones. ×140. **B:** Longitudinal section. ×2,100. BL, basal lamina; cEM, condensing eggshell material; EM, eggshell material in duct lumen; FD, follicular duct; H, hemocoel; L, lumen; N, nucleus; O, oocyte contacting eggshell material; OF, oocyte follicle; TZ, testicular zone; V, vacuoles.

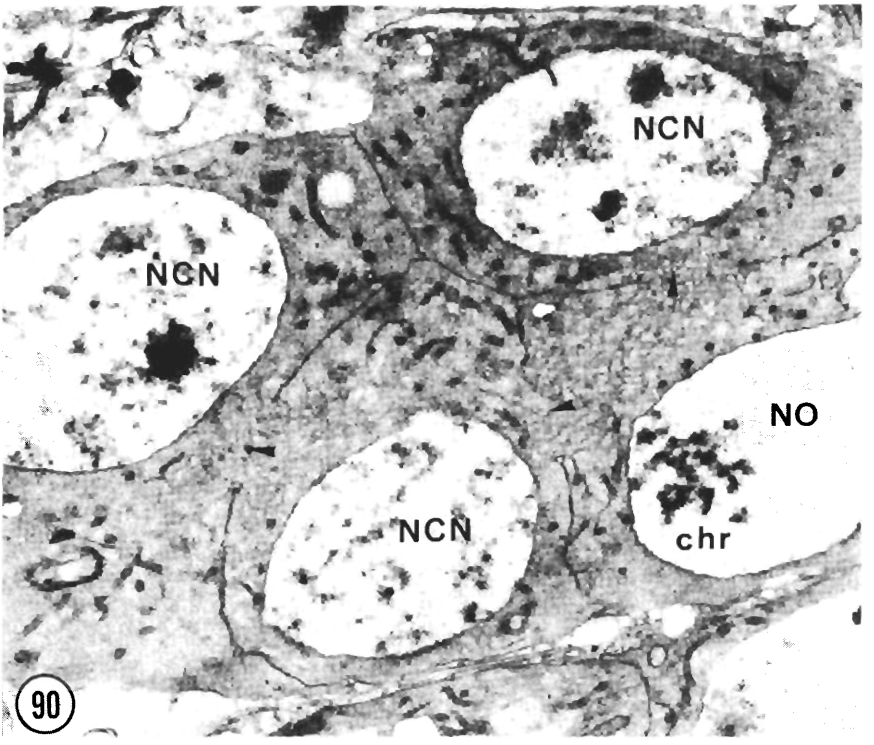

Fig. 90. Intercellular bridges (arrowheads) connecting the four follicle cells (oocyte and three nurse cells) in *Triops cancriformis* (Notostraca). (From Trentini and Sabelli Scanabissi, 1978.) ×6,400. chr, chromatin; NCN, nurse cell nucleus; NO, oocyte nucleus.

pass through the secreted eggshell material in the lumen of the duct. The passage involves great dilation of the follicular duct, with a resulting flattening of the follicular epithelial cells (from 30 down to 3 μm height). With the exception of the loss of the apical microvilli and basal vacuoles, the greatly flattened cells undergo no changes in ultrastructure. It is possible that passage of the oocyte physically causes additional secretion of the eggshell material. Oocytes are covered by this secreted material by the time they reach the oviduct, but the final form of the eggshell is not seen until this outer layer becomes "vacuolated" on its way toward the storage pouch of the modified 11th trunk limb (see below).

In the Spinicaudata, some taxa display oogenesis similar to that seen in notostracans. Specifically, the limnadiid *Limnadia lenticularis* has hernialike protrusions of the tubular gonad into the surrounding hemocoel, and oogenesis occurs in these germarium pockets (Zaffagnini, 1968). Zeni and Zaffagnini (1989) described discrete follicles in *Leptestheria dahalacensis* (Figs. 92, 93), but this may not hold true for all spinicaudatans. Oogenesis occurs not in discrete follicular enclosures but is scattered all along the length of the tubular gonad, with no clear developmental gradient, i.e., the oocytes arise via "diffuse gametogenesis" (*Eoleptestheria* and *Leptestheria,* Tommasini and Scanabissi Sabelli, 1989; Scanabissi Sabelli and Tommasini, 1990a). In these two genera, oocytes are formed via karyokinesis that is not followed by cytokinesis, resulting in an unorganized "plasmodium" (Scanabissi Sabelli and Tommasini, 1990a). Synaptonemal complexes are

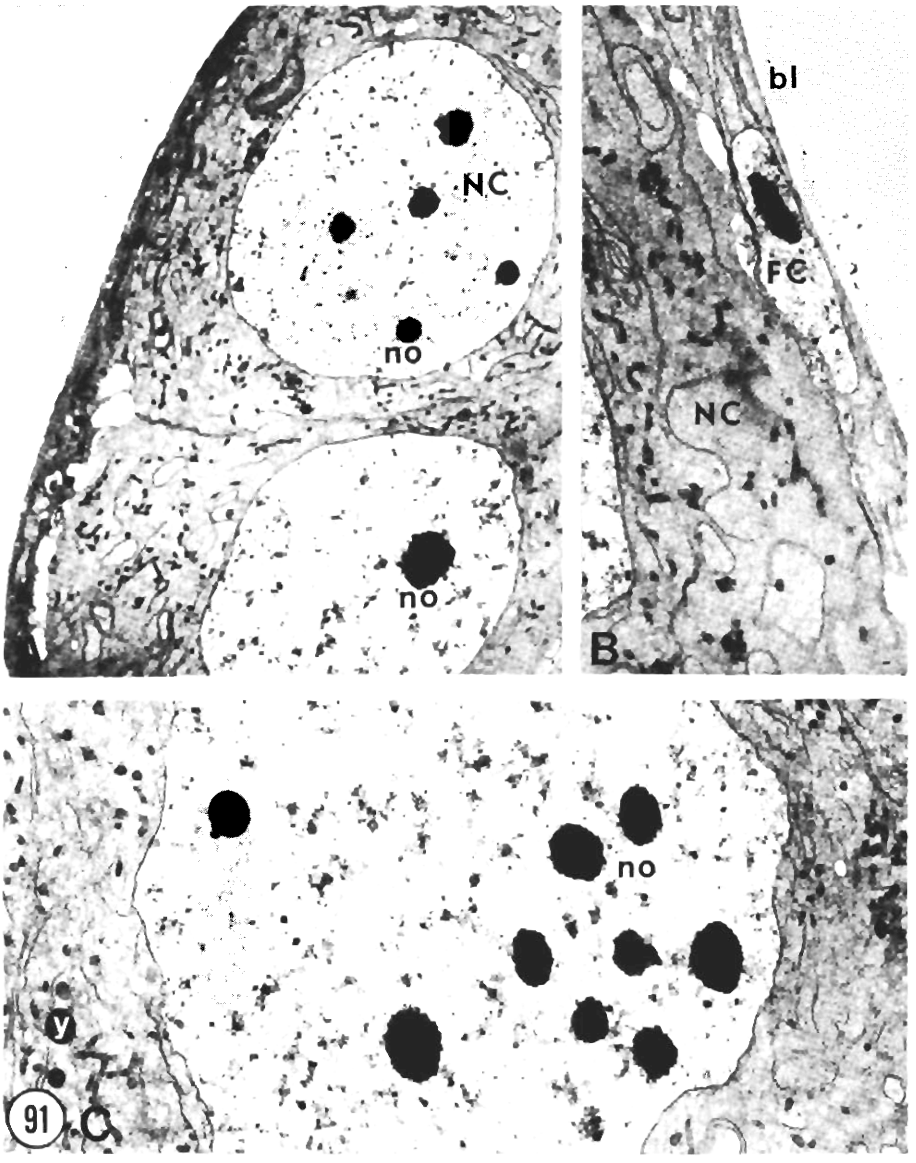

Fig. 91. Development of nurse cells in *Triops cancriformis*. (From Trentini and Sabelli Scanabissi, 1978.) **A:** Early development (stage II) of nurse cells (NC) with nucleoli (no). ×2,300. **B:** Flattened follicular cell (FC) enveloping ovarian follicle and nurse cell (NC) and separated from hemocoel by basal lamina (bl). **C:** Part of stage III nurse cell with many nucleoli (no) showing first yolk droplets (y). ×4,600.

present, as is extensive RER. The walls of the tubular gonad are composed of long follicular cells. The cytoplasm of these cells is reduced to a thin strip no more than 0.1 μm thick, but nevertheless contains many of the same components described above for the Notostraca. A basal lamina of about 0.2 μm separates this layer of cells from the hemocoel, but no nurse cells or intercellular bridges were described (Tommasini and Scanabissi Sabelli, 1989; Scanabissi Sabelli and Tommasini, 1990a), in contrast to Zeni and Zaffagnini's (1989) find-

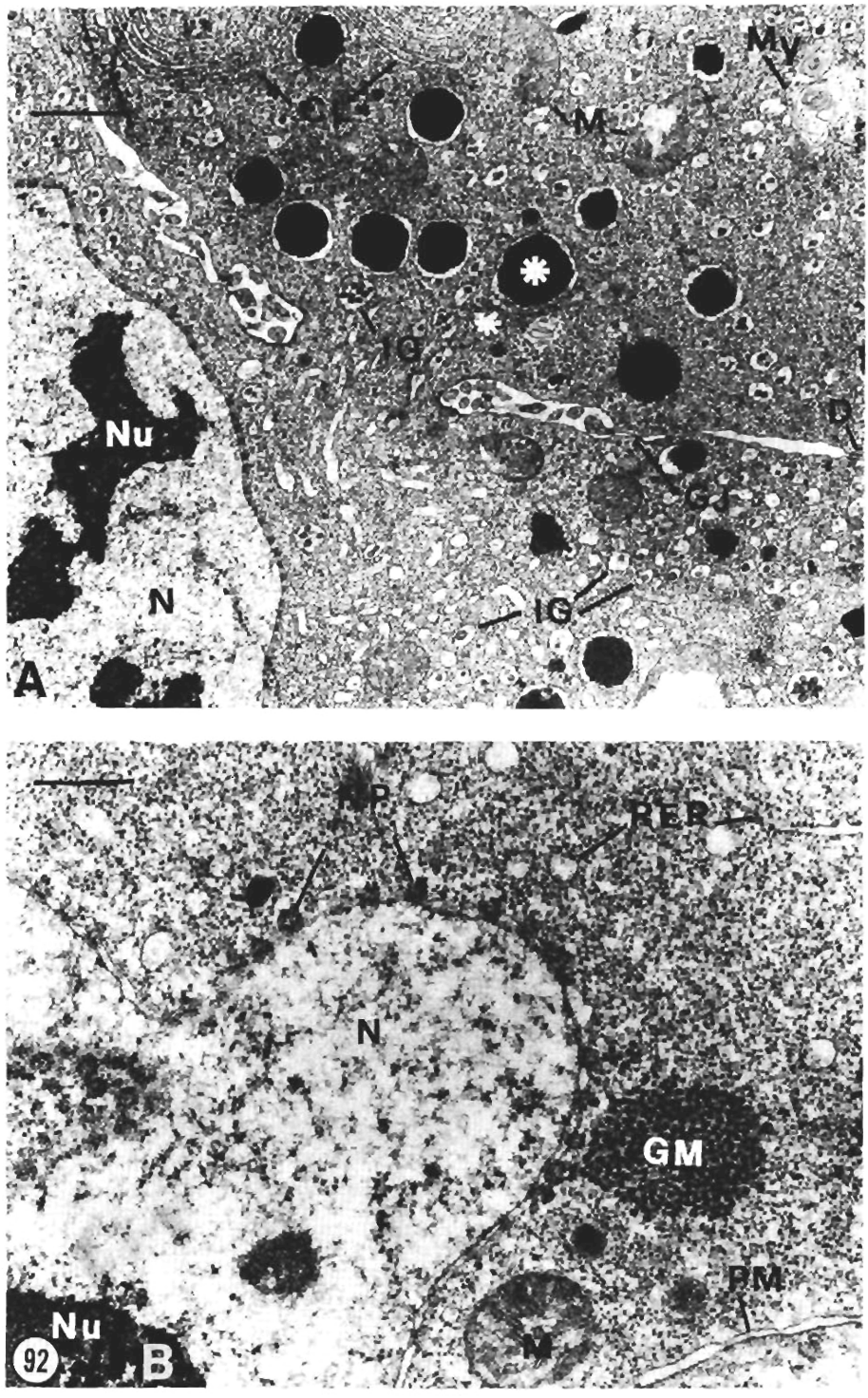

Fig. 92. Details of oocytes and nurse cells in *Leptestheria dahalacensis* (Spinicaudata). (From Zeni and Zaffagnini, 1989.) **A:** Intercellular bridge between oocyte and one nurse cell. Scale bar = 1 μm. **B:** Detail of nucleus in a previtellogenic oocyte. Scale bar = 0.5 μm. *, homogeneous material around intracisternal granule; CL, concentric lamellae of RER; D, desmosome; GJ, gap junction; GM, granular mass; IG, intracisternal granules; M, mitochondria; My, myelin figure; N, nucleus; NP, nuclear pores; Nu, nucleolus; PM, plasma membrane of oocyte contacting nurse cell; RER, rough endoplasmic reticulum.