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Ovarian polymorphism in relation to reproductive diversity and associated histological and histochemical attributes in some sporophagous tubuliferan thysanoptera

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Abstract. Ovarian polymorphism involving oviparity, ovoviviparity and viviparity is discussed in relation to sporophagous species such as *Tiarothrips subramanii* (Ramk.), *Elaphrothrips denticollis* (Bagnall) and *Bacterothrips idolomorphus* Karny alongside with the comparative histology and histochemistry of polymorphic ovaries.

Keywords. Oviparity; ovoviviparity; viviparity; germarium; vitellogenic zone; pre and post vitellogenic zones.

1. Introduction

The incidence of ovoviviparity and viviparity in thrips alongside with oviparity is on record among some Phlaeothripine mycophagous species (John 1923; Bagnall 1921; Hood 1934; Viswanathan and Ananthakrishnan 1973a; Ananthakrishnan *et al* 1983b; Dhileepan and Ananthakrishnan 1984). Facultative viviparity was first reported in *Megathrips lativentris* (Heeger) by John (1923), and ovoviviparity in species of *Anactinothrips* and *Diceratothrips* species by Hood (1935). Hood (1950) showed that *Megathrips lativentris* (Heeger) and *Bactrothrips buffai* (Karny) (= *Caudothrips buffai* Karny) living in temperate regions are known to be ovoviviparous and number of other tropical species of *Diceratothrips* and *Anactinothrips* may also produce living young ones. Bournier (1951, 1956, 1957) made a detailed study on ovoviviparity common in *B. buffai* in southern France. Viswanathan and Ananthakrishnan (1973a) discussed the adaptation for survival in extreme conditions in relation to the occurrence of ovoviviparity in *Tiarothrips subramanii* (Ramk.). An analysis of reproductive strategies and behavioural aspects of some sporophagous Idolothripinae involving oviparity, ovoviviparity and viviparity in *T. subramanii*, *Elaphrothrips denticollis* (Bagnall), *Elaphrothrips procer* Schmutz were made by Ananthakrishnan *et al* (1983a). Ananthakrishnan *et al* (1983b, 1984) further described the behavioural attributes in oviposition in some of the mycophagous thrips indicated the mean fecundity rates and incubation periods of some sporophagous thrips, and showed that the oviparous forms are more fecund than the ovoviviparous and viviparous forms. Ananthakrishnan and Dhileepan (1984) also observed the functional diversity in relation to reproductive polymorphism in *Bactrothrips idolomorphus* Karny. Kiester and Strates (1984) noticed as many as 300 eggs in a colony of *Anactinothrips gustaviae* Bagnall, the eggs hatched under field conditions between 10th and 15th day after they were laid. Results herein presented relates to the histological and histochemical aspects of polymorphic ovaries and associated functional attributes.

2. Materials and methods

The sporophagous species *T. subramanii*, *B. idolomorphus*, *E. denticollis*, *E. procer* and *Adelothrips cracens* (Anan.) were collected from their respective fungus infested host plants and maintained in a BOD incubator at 27±1°C and 80% RH. Individual thrips as well as mated pairs were reared in plastic vials (4·5 × 3·0 cm) containing the specific fungal meal. Mouths of the rearing vials were covered with muslin cloth for aeration. Cotton plugs soaked in water were kept in each culturing vials for moisture, and these cotton buds were moistened periodically.

For anatomical studies, adult, pupae and larvae were dissected out in insect Ringer's solution and the testes and ovaries were fixed in Bouin's or Carnoy's fluid, dehydrated in the alcohol series, cleared in xylene, stained with Haematoxylin and Eosin and mounted in Canada Balsam. Whole-mounts of ovaries, testes and spermathecae were studied under Leitz Dialux–20 compound microscope and photographs were made using a 'wild' camera and Ilford 35 mm films (ASA 125). Numerical variations of oocytes at various stages of development both in the ovarioles as well as in the lateral oviducts were also obtained. Diagrams of the whole mounts of ovaries, testes and spermathecae were made using a camera lucida and measurements were made using a calibrated occular micrometer.

For histological studies, testes, ovaries and spermathecae were fixed in Bouin's fluid, dehydrated through the alcohol series, blocked in moulton paraffin wax and sectioned at 7 μm thickness in a rotary microtome, stained with Haematoxylin–Eosin combinations and mounted in Canada Balsam. For a study of histochemical analysis (Pearse 1968), the following tests were used: mercuric bromophenol blue test for proteins; aqueous bromophenol blue test for basic proteins; toluidine blue test for acidic proteins; Best's Carmine test for glycogen and Sudan III method for total lipids.

Mating patterns involving diverse breeding combinations between different sex-limited polymorphs were studied by freely allowing individuals to mate and the mating pairs carefully transferred to a different vial (4·0 × 3·0 cm). Without disturbing the mating process and reared separately and observations on the oviposition behaviour and fecundity were made.

3. Results

The ovaries which lie ventrolateral to the hind gut in oviparous females, extend from seventh or eighth abdominal segment to third or fourth segment, and from first or second abdominal segment and extending upto the prothorax, in view of the very long oviduct in ovoviviparous as well as viviparous forms. The lateral and common oviducts of the oviparous female is short with 4–8 fully developed oocytes laden with yolk, and never retained in the lateral oviducts, the subsequent development taking place after oviposition. Individuals with the ovoviviparous ovary have 2–4 oocytes partly laden with the yolk, developing in the long lateral oviducts only upto blastokinesis. Eggs laid in this partly developed condition hatch after a very short incubation period. All the 4 basal oocytes mature simultaneously without any yolk accumulation in the viviparous ovary. The lateral oviducts are extremely long in viviparous forms, the complete development of the pre-vitellogenic oocytes taking place in the oviducts, followed by larviposition.

The dimensions of the mature basal oocytes of the oviparous ovarioles are 3–5 and 6–10 times respectively greater than in the ovoviviparous and viviparous conditions indicating the amount of yolk deposition. The oviduct of ovoviviparous and viviparous individuals are 2–10 and 2–20 fold respectively longer than those of the oviparous individuals. Enormously long lateral oviducts facilitate the retention of the partly vitellogenic oocytes as in ovoviviparous forms till blastokinesis and the previtellogenic oocytes as in viviparous forms, till they complete their development within the lateral oviducts. The number of oocytes undergoing subsequent development in the lateral oviducts ranges from 9–11 and 5–12 in ovoviviparous and viviparous ovaries respectively.

3.1 *Histology of oviparous ovarioles*

The terminal filament, germarium, pre-vitellogenic zone with pre-vitellogenic oocytes, vitellogenic zone with vitellogenic oocytes, post-vitellogenic zone with fully mature ovum and pedicel or calyx opening into the lateral oviduct are typical of oviparous ovarioles. The post-vitellogenic zone is absent in the ovoviviparous forms with the vitellogenic zone shorter resulting in the shorter length of the ovariole. In the viviparous ovarioles only 3 regions are evident viz (i) terminal filament, (ii) germarium and (iii) pre-vitellogenic zone. Unlike oviparous ovarioles, viviparous ovarioles lack the vitellogenic and post-vitellogenic zone. As a result the pre-vitellogenic oocytes are ovulated as such, without any yolk accumulation.

The distal part of the germarium of the 4 ovarioles on each side in the oviparous individuals fuse together forming one coalescent germarium which tapers smoothly with elongated epithelial cells to form the terminal filament attached to the salivary glands. Oogonial cells of the germarium are covered by an external sheath and an internal tunica propria. Considerable differences do not occur in the number of oogonia among oviparous, ovoviviparous and viviparous ovarioles and generally the number of oogonia ranges from 8–14 in each ovariole. Each oogonium is a small spherical cell with a distinct nucleus and peripheral cytoplasm; however, the oogonia lack clear-cut demarcation from each other, these undifferentiated oogonia, mature and become fully developed by the time they reach the proximal region as they descend down the ovariole. As the oogonia descend down the pre-vitellogenic zone they have a squarish or rectangular profile with a centrally placed nucleus, occupying most of the oocyte. These pre-vitellogenic oocytes are oriented in a linear fashion and surrounded by a thin layer of follicular epithelial cells. As the pre-vitellogenic oocytes descend down, they enter the vitellogenic zone, in which continuous yolk deposition occurs and resulting in the oocytes with a solid, centrally located nucleus, increasing in dimension followed by the stretching of the follicular epithelium so as to completely cover the oocyte. It is a major zone occupying more than half the entire length of both oviparous and ovoviviparous ovarioles. The post-vitellogenic zone is characterised by the proximal, well-developed oocytes with adequate yolk reserves, each covered by an inner vitelline membrane. The interfollicular epithelial cells are very prominent in between the basal vitellogenic oocytes and the most proximal post-vitellogenic ovum. The proximal end of each ovariole opens into the distal end of the lateral oviduct through the pedicel, the lumen of which is filled by epithelial plug that is removed only during the first ovulation (figure 1).

3.2 *Histology of ovoviviparous and viviparous ovarioles*

In the ovoviviparous ovarioles, due to the absence of the post-vitellogenic zone and the relatively shorter vitellogenic zone, the ovariole length is comparatively shorter. The terminal oocytes at the proximal end of the ovarioles do not attain the full dimension as in oviparous basal oocytes indicating partial yolk accumulation. The basal oocyte is oval and externally surrounded by the follicular epithelial cells with a distinct, proximally placed nucleus.

The germarium and the pre-vitellogenic oocytes in viviparous ovarioles are almost identical to those of the oviparous and ovoviviparous ovarioles. Due to the absence of both the post-vitellogenic and vitellogenic zones, the ovarioles of viviparous ovaries are very much shorter. As the primary oogonia descend down into the pre-vitellogenic zone, they are spherical and externally covered only with ovariole sheath with a follicular epithelial covering. The pre-vitellogenic oocytes, as they descend increased moderately in their dimensions and have a large centrally placed nucleus with a very prominent compact centrally placed nucleolus (figure 2). Similarly the most proximal oocytes possess densely stained ooplasm and open into the lateral oviduct through a short pedicel. Since both vitellogenic and post-vitellogenic zones which form two-thirds of the entire length of the oviparous ovarioles are lacking, the viviparous ovarioles are 2–3 times shorter than the oviparous ones. The pre-vitellogenic oocytes without any traces of yolk ovulate into the lateral oviducts, where the subsequent embryogenesis takes place during which time they derive nutrients from maternal resource.

3.3 *Numerical variations of oocytes in polymorphic ovaries*

Considerable variations occur in the number of vitellogenic oocytes that are in the process of accumulating yolk in the ovarioles, post-vitellogenic oocytes (the most basal ovum fully laden with yolk in the ovariole), and the number of oocytes or embryos undergoing subsequent development in the lateral oviducts.

Studies on 5 species of sporophagous Tubulifera viz, *B. idolomorphus*, *T. subramanii*, *E. procer*, *E. denticollis* and *Ethirothrips agasthya* (Bagnall) indicate that the number of oogonial cells and the pre-vitellogenic oocytes does not differ among polymorphic ovaries, ranging from 46–59 and from 11–17 in each ovary. However, the number of vitellogenic oocytes in each ovary is higher (10–12/ovary) in oviparous forms, comparatively less (6–9/ovary) in ovoviviparous forms and are lacking in the viviparous ovaries. Mature ova are evident only in the oviparous forms (3–4/ovary). The number of embryos undergoing development in each lateral oviduct is higher in viviparous ovaries (10–12/each lateral oviduct) than in ovoviviparous ovaries (6–10/each lateral oviduct). A positive correlation is evident between the number of oocytes/embryos developing in the lateral oviduct and the length of the lateral oviduct, in which the latter increases proportionately with increase in the number of developing embryos.

3.4 *Histology of oviducts*

Histological studies of both lateral and common oviducts of *T. subramanii* of oviparous ovaries, revealed the presence of single layer of secretory columnar

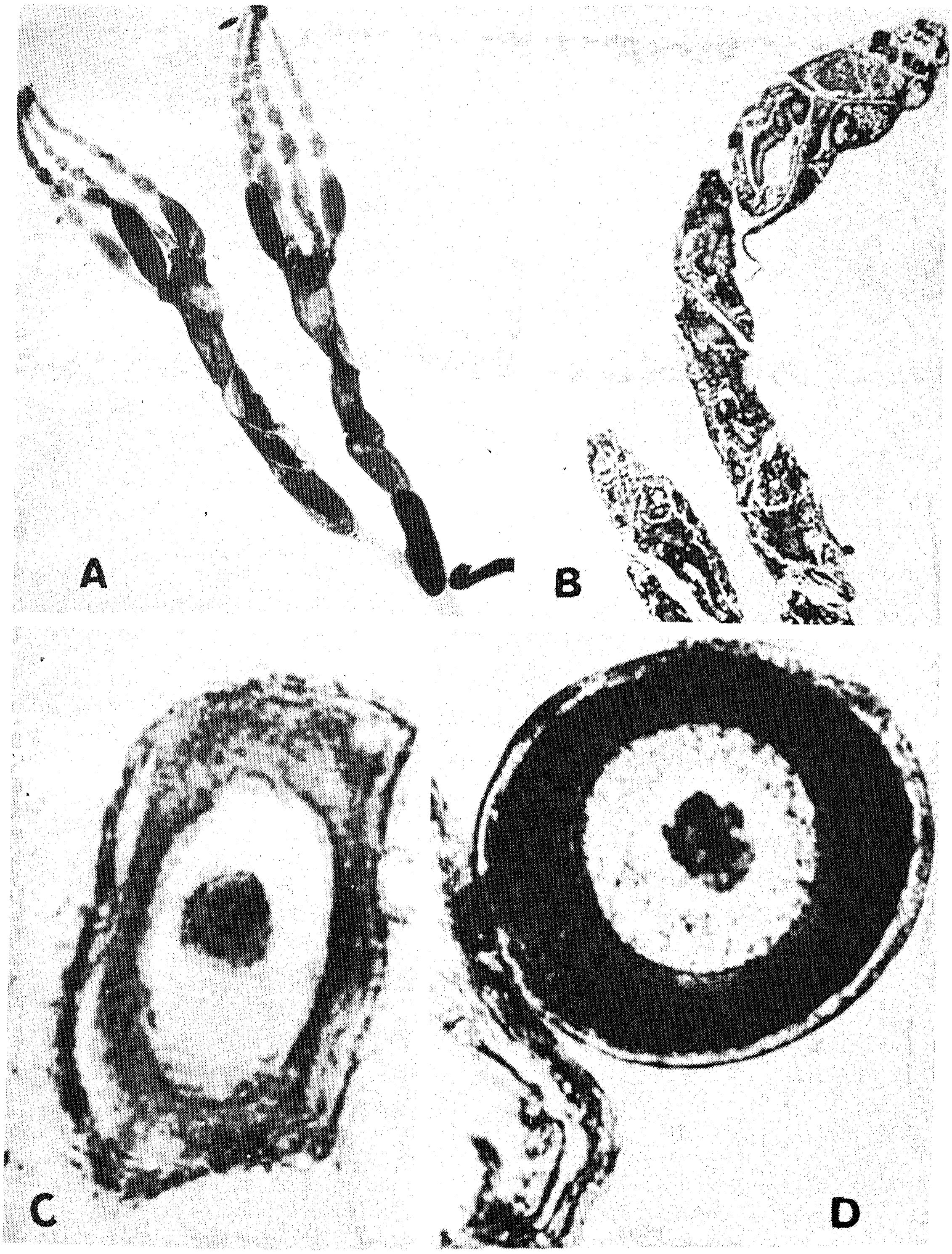

Figure 1. **A.** Oviparous ovary of Bactrothrips idolomorphus (× 35). **B.** L. S. of lateral oviduct showing developing embryos (× 125). **C.** Pre-vitellogenic oocytes (× 1000). **D.** Spherical basal pre-vitellogenic oocytes (× 780).

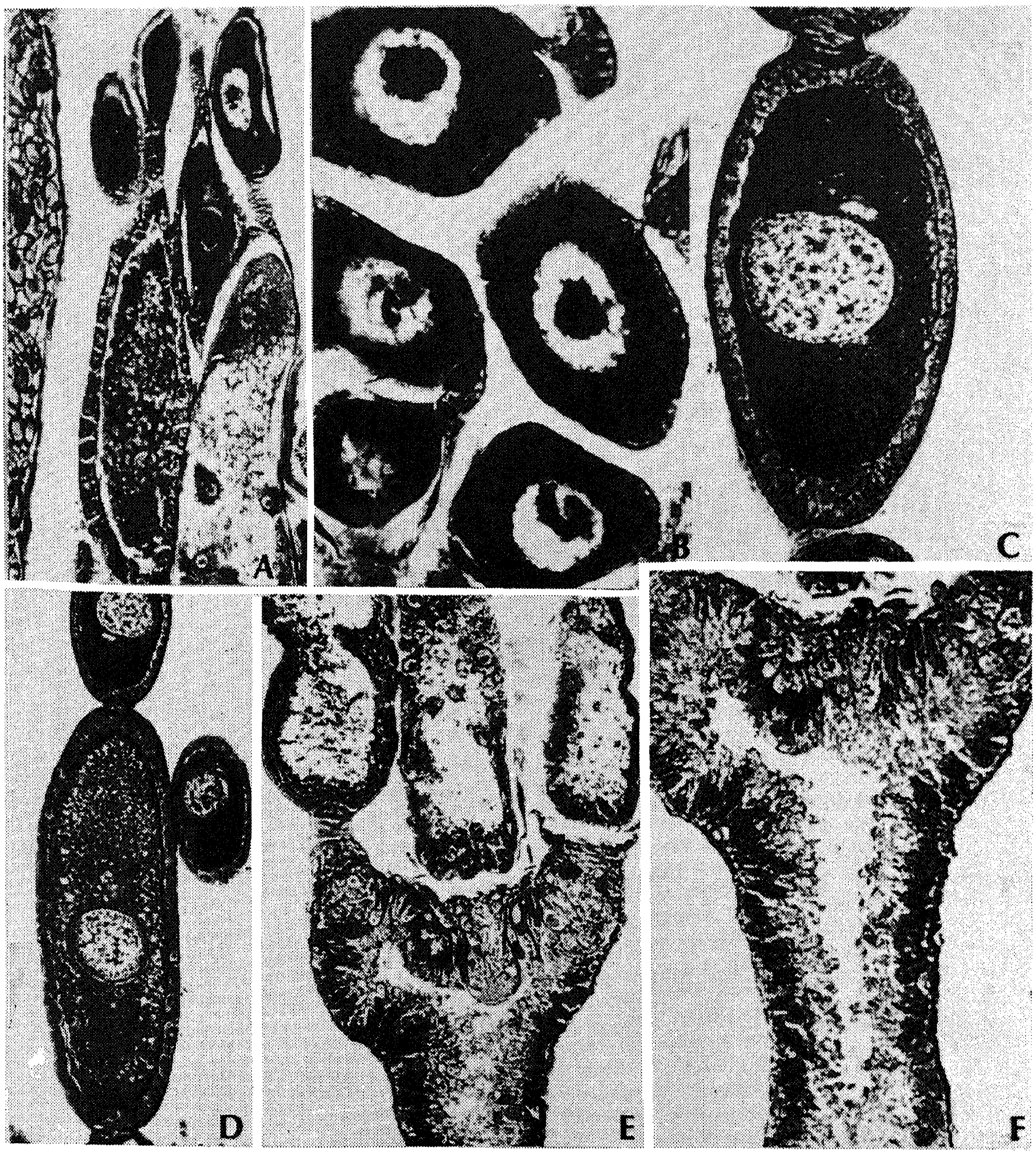

Figure 2. Histology of oviparous ovary of *T. subramanii*. **A.** L. S. of the oviparous ovary (× 300). **B.** Pre-vitellogenic oocytes (× 1250). **C.** Early vitellogenic oocytes (× 600). **D.** Vitellogenic oocytes (× 600). **E.** L. S. of lateral oviduct (× 300). **F.** L. S. of common oviduct (× 360).

epithelial cells resting on a basement membrane. These secretory epithelial cells are apocrine in nature with a very large centrally placed nucleus and a prominent, but eccentrically placed nucleus. Varying number of vacuoles are evident near the basement membrane. At the distal free margins of the secretory cells, a large number of secretory vesicles occur. The presence of secretory granules, dense cytoplasm and numerous vacuoles suggest the secretory nature of the epithelial cells.

The lateral oviducts of ovoviviparous ovaries exhibit secretory cells only at the proximal one-third of the lateral oviducts, while the rest of the distal two-thirds region lack secretory cells. In the lateral oviducts of the ovoviviparous ovaries, the secretory regions at the proximal end of the oviducts are highly variable in length, depending upon the number of oocytes/embryos undergoing development in these oviducts, as well as on the degree of the ovoviviparity, especially the gestation period of the embryos and the stage at which the embryos are laid. In ovoviviparous oviducts the secretory cells lining the proximal region of the lateral oviduct and common oviduct are tall, columnar with centrally placed nucleus and are apocrine. The secretory nature of the cells are evident only in the lateral oviducts where the embryos are in an advanced stage of development. In those lateral oviducts with embryos in the early stage of development, the cells are inactive with dense cytoplasm and without any secretory granules. With the ovulation of the mature ovum with partly deposited yolk, the subsequent development of the oocyte takes place in the distal region of the lateral oviducts which are devoid of any secretory cells. In the viviparous ovaries both the lateral and common oviducts do not have any secretory cells and consist only of the basement membrane.

3.5 *Histochemistry of polymorphic ovaries*

Histochemical studies involving total proteins, acidic proteins, basic proteins, glycogen and lipids indicated the diversity in yolk deposition in polymorphic ovaries. Pre-vitellogenic oocytes in oviparous, ovoviviparous and viviparous ovaries show a protein positive reaction, where acidic proteins are abundant in the nucleus and perinuclear cytoplasm. Pre-vitellogenic oocytes of all the 3 types of ovaries showed a negative reaction to the glycogen and a weak lipid reaction. In the vitellogenic oocytes of both oviparous and ovoviviparous forms the intensity of protein and lipids increase both in nucleus and in ooplasm (figures 3 and 4).

Histochemical observations of the yolk granules of polymorphic ovaries indicate the incidence of increased total proteins as well as both basic and acidic protein yolk granules evenly dispersed in the ooplasm of the vitellogenic and post-vitellogenic oocytes. In the oviparous ovarioles the protein yolk granules, especially the acidic ones are more dense than the basic protein granules. In addition, both glycogen and lipid yolk granules are evenly distributed. In the vitellogenic oocytes of ovoviviparous ovarioles the glycogen granules are more abundant than in the oviparous vitellogenic oocytes. Moreover the ooplasm also has protein and lipid yolk evenly distributed in the peripheral ooplasm. In viviparous ovarioles with only pre-vitellogenic oocytes no yolk granules were evident, indicating the absence of yolk deposition.

3.6 *Embryogenesis in polymorphic ovaries*

In oviparous ovaries the fully mature eggs with yolk reserves are laid with a protective chorion and the embryogenesis takes place only after they are laid. In the ovoviviparous ovaries, mature oocytes in partly yolk-accumulated condition are ovulated into the lateral oviduct, where embryogenesis continues upto blastokinesis. There is a positive correlation between the increase in the size of the embryos in the lateral oviducts and the distance traversed by the embryos in the lateral oviducts. This correlation suggests that there is a quantitative increase in the size of the embryo as it descends down the lateral oviducts, indirectly indicating the nutrient

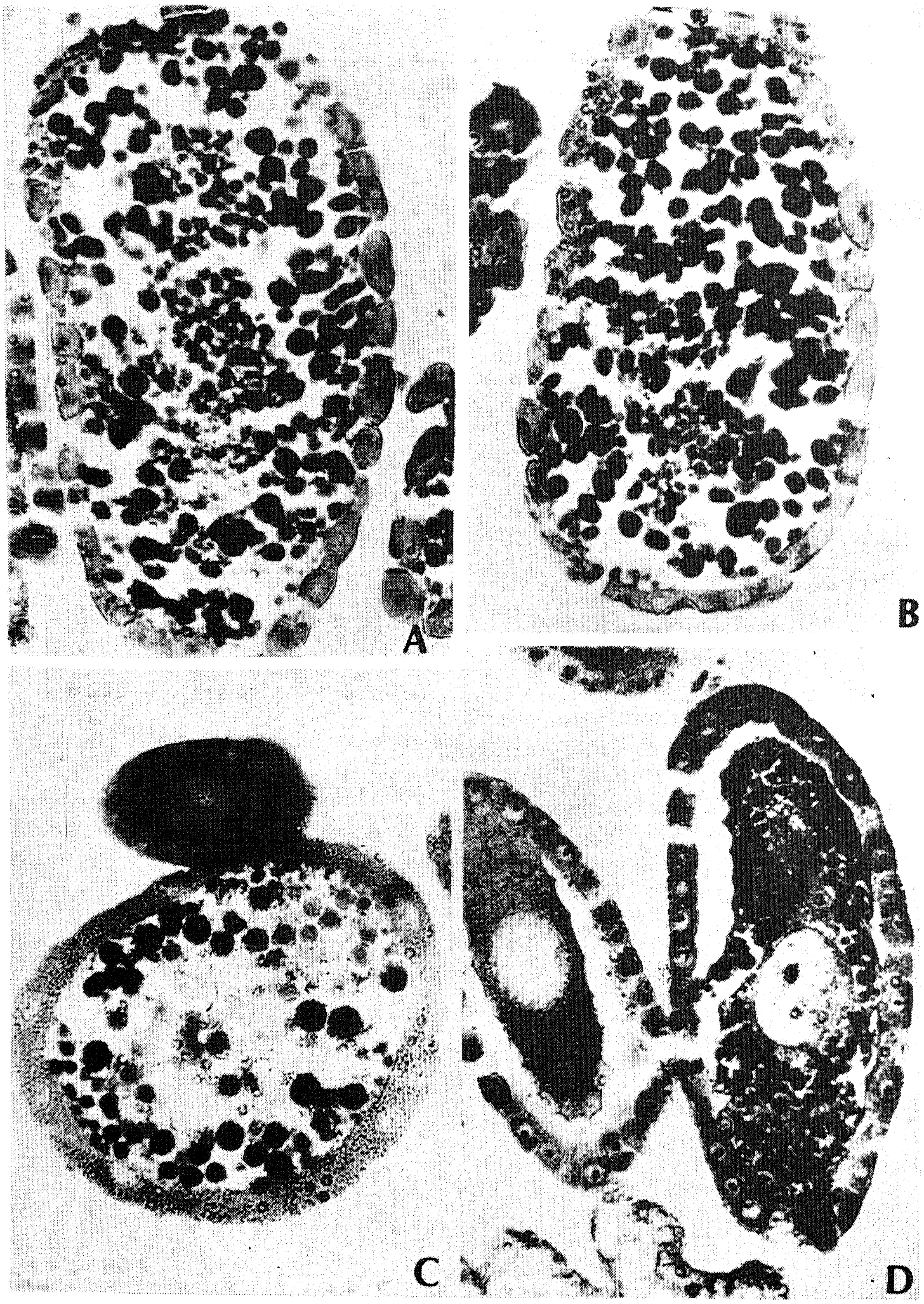

Figure 3. Histochemistry of polymorphic ovaries of *T. subramanii*. **A.** L. S. of oviparous basal oocyte showing positive reaction to total proteins (×400). **B.** Dense acidic protein evenly distributed in the ooplasm of oviparous basal oocytes (×400). **C.** Oviparous basal oocyte showing basic protein granules (×350). **D.** Ovoviviparous basal oocyte showing basic protein positive reaction (×400).

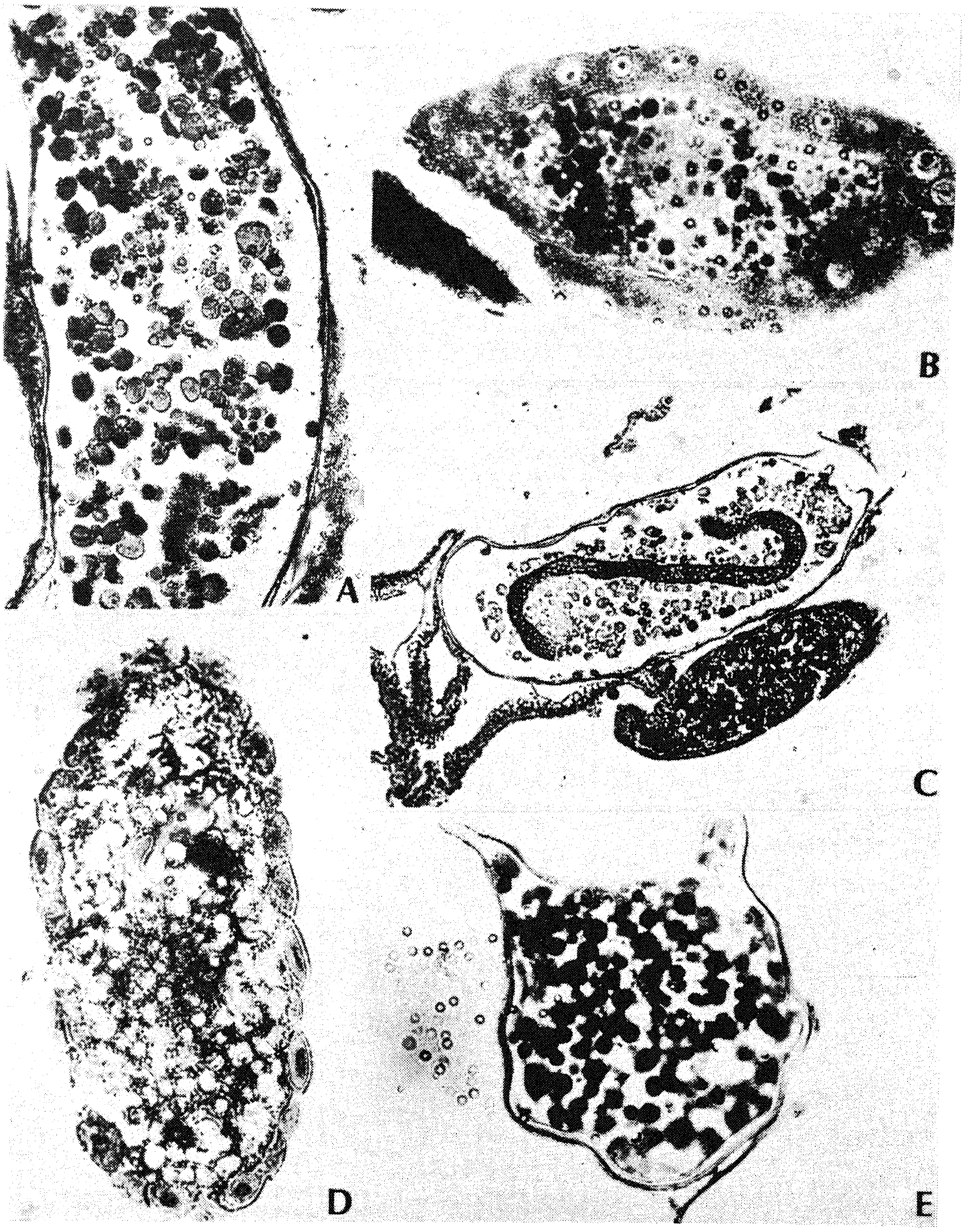

Figure 4. Histochemistry of polymorphic ovaries of *T. subramanii*. **A.** Oviparous basal oocyte showing glycogen spheres (× 650). **B.** Ovoviviparous basal oocyte showing acidic protein positive reaction (× 400). **C.** L. S. of ovoviviparous embryo in the lateral oviduct with glycogen granules (× 300). **D.** Ovoviviparous basal oocyte with lipid yolk granules (× 350). **E.** Oviparous basal oocyte showing protein yolk granules (× 350).

intake from maternal resource. The remaining embryonic development takes place after they are laid. In viviparous ovaries the pre-vitellogenic oocytes without any yolk reserves are ovulated into the lateral oviduct where the complete embryonic development takes place and fully developed larvae are laid as such. Histology of the lateral oviducts with developing embryos whose stage of development increased towards the distal most region of the lateral oviduct which opens into the common oviducts. Embryos at the proximal end of the lateral oviduct are only at initial stage of embryogenesis and smaller in size. As they move down, there are large number of embryos at various developmental stages. Those at the distal end of the lateral oviduct or in the common oviducts are in the stage of completing the embryogenesis or as fully formed larvae. Since the lateral oviducts of the viviparous ovaries contain many embryos, histological studies revealed all the stages of embryonic development in a sequence. Further there is a significant, proportionate increase in the size of the embryos as they descend down in the lateral oviduct.

4. Discussion

Both the ovoviviparous and viviparous ovaries differ from each other, as well as from oviparous ovaries in structure and function. Statistical analysis of 5 species of diversely reproducing idolothripines like *B. idolomorphus*, *T. subramanii*, *E. procer*, *E. denticollis* and *M. menoni* indicated a significant reduction in the ovarioles of both ovoviviparous and viviparous forms with corresponding elongation of the lateral oviducts. The oviparous ovarioles are longer due to long vitellogenic zone with post-vitellogenic zone containing larger basal oocytes. The viviparous ovarioles are shorter due to the absence of vitellarium. However, in ovoviviparous ovarioles the vitellarium is short with partly developed basal oocytes, resulting in shorter size. Since the vitellarium occupies 2/3 of the entire ovariole, their absence or reduction significantly alters the ovariole length. Similar reduction of vitellarium was also reported in ovoviviparous and viviparous Blattaria (Roth 1964).

The enormously long lateral oviducts facilitate the retention and nourishment of the embryos. The elongation is pronounced as early as the pupal stage when ovulation has not yet commenced. This increased length of the lateral oviducts is due to continuous ovulation and retention of oocytes/embryos. This is supported by the positive correlation between the increase in the lateral oviduct length and increase in the number of embryos in the lateral oviduct. Bournier (1957, 1962, 1966) noticed the retention of eggs in the long lateral oviducts of ovoviviparous *B. buffai*, but their structural adaptations in relation to egg retention were not revealed. Similar long lateral oviducts retaining embryos were also reported in ovoviviparous *T. subramanii* (Viswanathan and Ananthakrishnan 1973) and *B. brevitubus* (Haga 1975).

As a result of structural variations among polymorphic ovaries their relative position in the females were also considerably altered. In both ovoviviparous and viviparous forms the elongated lateral oviducts resulted in the shifting of the ovarioles towards the anterior side of the abdomen, near the metathorax. In oviparous ovaries, due to the short lateral oviducts, the long ovarioles emerged from the posterior portion of the abdomen and extended upto metathorax. Haga (1975) has also mentioned about the relative position of ovaries of the oviparous and ovoviviparous *B. brevitubus*.

Both ovoviviparous basal oocytes with partial yolk deposition and viviparous basal oocytes without any yolk are not covered with chorion, before ovulation. John (1923) also reported in *M. lativentris* the absence of chorion when larvae were laid and the presence of a distinct chorion when the insects laid eggs. A similar phenomenon is also observed in the polyctenid *Hesperoctenes fumarius* Westwood and several other viviparous species (Hagan 1951). The most important role of follicular epithelium during insect oogenesis has been considered to be synthesis and deposition of egg envelope during choriogenesis (Mahowald 1972). However, in the gall midge *Heteropeza pygmaea* Winnertz, which exhibits paedogenesis, the chorion is not formed at the end of oogenesis and the growing embryos remain enveloped by the folliculae epithelium (Junquera 1983). Hansen (1894) and Heymons (1909, 1912) noticed that the eggs of viviparous *Hemimerus taploides* Walker has no chorion and contains little yolk and the thickened follicular epithelium provides nutrients for the growing embryo.

4.1 *Numerical variation of oocytes in polymorphic ovaries*

In addition to anatomical and histological variations, numerical variation of oocytes and embryos in the polymorphic ovaries also occur. The higher number of vitellogenic and post-vitellogenic oocytes in oviparous forms and comparatively lesser number of only vitellogenic oocytes in ovoviviparous forms appear to be due to the long vitellarium as in oviparous forms and shorter in ovoviviparous species. Incidence of post-vitellogenic ovum only in oviparous forms suggests that complete maturation of the ovum occurs only in oviparous forms. Correspondingly the number of embryos in the lateral oviducts of the viviparous ovaries are higher than in ovoviviparous ovaries. This is because of the prolonged gestation period of the viviparous embryos than the ovoviviparous embryos. Haga (1974) reported as many as 24 embryos, 11 in the right and 13 in the left lateral oviducts of *B. brevitubus*. As more number of pre-vitellogenic oocytes undergo vitellogenesis to become vitellogenic oocytes, the number of pre-vitellogenic oocytes are retained as such resulting in their increased numbers. Moreover the frequency of ovulation of pre-vitellogenic oocytes is low in viviparous forms, as compared to the ovulation of mature ova and partly developed ova in oviparous and ovoviviparous ovaries respectively.

4.2 *Histochemistry of polymorphic ovaries*

Histochemical analysis revealed no yolk granules in basal oocytes of viviparous ovarioles indicating the absence of vitellogenesis. On the contrary in both ovoviviparous and oviparous ovaries, protein, lipid and glycogen yolk granules were evident substantiating the occurrence of vitellogenesis. Bonhag (1958) reported the incidence of protein, lipid and glycogen particles as the main deutoplasmic substances of oocytes, where the protein yolk are numerous while the glycogen may not be present in all insect eggs. The intensity of these yolk granules was dense in oviparous forms, and less dense in ovoviviparous basal oocytes. Though the incidence of glycogen yolk granules is not very common among insects (Bonhag 1958), present observations indicate the presence of glycogen granules in both oviparous and ovoviviparous oocytes, their intensity being higher in the latter. Instances of glycogen deposition in eggs during vitellogenesis are reported in Anoplura (Ries 1932), Bumble bees and *Anisolabis* sp. (Bonhag 1958).

Structural and functional modifications involving the histology of the lateral and common oviducts, to suit the type of reproduction, vary among polymorphic ovaries. In both complete ovoviviparous and viviparous ovaries the lateral oviduct wall is without any secretory cells and are stretched into a thin membrane. The developing embryos without chorionic covering lie close to the wall of the lateral oviducts and derive nutrients through thin membranous part. Haga (1975) also reported similar thin and transparent lateral and common oviduct walls in ovoviviparous *B. brevitubus*. Thus, the absence of secretory cells facilitates the embryonic nourishment through the lateral oviduct walls. However, in partial ovoviviparous ovaries, the secretory cells at the distal end of the lateral oviducts alone are concerned with the embryonic nourishment, whereas those at the proximal secretory region are responsible for the chorion secretion, for the eggs that are laid. Thus the length of the secretory region of the oviduct is inversely proportional to the stage of the embryonic development at the time of laying. Greater the secretory region, earlier is the stage of the embryo laid, and when the secretory cells are absent, fully developed larvae are laid. Though in general, the chorion is secreted by the follicular epithelium in the ovariole (Mahowald 1972), in both ovoviviparous and viviparous ovaries presently observed, the oocytes that are ovulated are without chorion. Since only embryonated eggs are laid in ovoviviparous forms, it is assumed that the chorion might be secreted by the cells lining the lateral and common oviducts. However, in viviparous forms showing direct larviposition secretory cells are absent.

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