

OVARIAN DEVELOPMENT AND AGE RECOGNITION IN
THE DAMSELFLY, *ARGIA MOESTA* (HAGEN, 1961)
(ZYGOPTERA: COENAGRIONIDAE)

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This study traces ovarian development from the teneral through four post-teneral ages in *Argia moesta*. Terminal follicle size and proportions of ovarioles having specific follicle sizes distinguish these ages internally. Externally, the ages relate to color patterns and pruinescence. Asynchronous function of ovarioles, follicle resorption, and follicular relic recognition complicate use of these structures in projecting ecological parameters. No useful relations appear possible in ovariole number and follicle number per ovariole. The largely undeveloped tenerals inherit little to no fatty tissue from the larval stage drawing attention to the importance of conditions at emergence. Tandem marks and filled spermathecae identify mated females. Four post-teneral male ages exist scored by degree of pruinescence development and condition of seminal vesicles. The study recognizes geographic variability in the age-dependent changes.

INTRODUCTION

This study identifies adult ages of the damselfly, *Argia moesta*, relates the ages to ovarian development, and distinguishes mated females. Changes of the external cuticle initially used by BORROR (1934) in studying Ohio specimens serve as age criteria. Ovarian structures in some insects also provide data on their reproductive history (i.e. fecundity and parous vs nulliparous

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conditions). Observations obtained in this study evaluate the technique for damselflies. *Argia moesta* has a wide distribution and, not unexpectedly, thoracic stripe pattern and age-dependent changes vary geographically. The ages recognized by Borror do not apply fully to other regions and criteria presented here specifically permit age determinations in southeastern populations.

Specimens taken periodically from June through August of 1971 and 1972 along the Santa Fe River north of High Springs, Alachua County, Florida, provided the data. The ages became apparent early in the study. Subsequent collecting concentrated on obtaining at least 30 individuals of each age for dissection. The number examined per age appears below. Preparation of most specimens occurred while still in the field. The procedure for handling females consisted of initially inactivating in jars charged with ethyl acetate, dissecting at the basal end of abdominal segment 1 and then placing each specimen into a separate vial of 80 per cent ethyl alcohol with an identification number. Alcohol apparently penetrates throughout the abdomen readily as good preservation occurred in all specimens. Initial samples included other fixatives for comparison with alcohol but none appeared more suitable for study of whole, unsectioned organs. Male samples provided both a series of dried specimens and live individuals for examination of the seminal vesicles. Notes on color and pattern taken on individuals subsequently preserved as dried specimens formed a comparison series when scoring cuticle conditions in museum specimens. Other methods appear below where applicable.

Abbreviations

Structures discussed in the text appear with the following abbreviations. a, unidentifiable body in oviduct; AGD, accessory gland ducts; BC, bursa copulatrix; C, collar; CO, common oviduct; FPT₁ – FPT₄, post-teneral female ages; FR, follicular relic; LO, lateral oviduct; ME, mature follicle or egg; MPT₁ – MPT₄, post-teneral male ages; NFO, nonfunctioning ovariole; OE, oviducal egg; RB, resorption body; SPT, spermatheca; VV, ventral valvulae (portion of ovipositor).

FEMALES

WHEDON (1919) and ASAHINA (1954) briefly describe the reproductive systems in representatives of the Zygoptera genera, *Calopteryx*, *Megaloprepus*, and *Mnais*. Ovarian structure in Odonata is similar to the Orthoptera as indicated by CORBET (1961). The detailed studies of PHIPPS (1949, 1950, 1959) and SINGH (1958) are therefore valuable orientations to odonate conditions. Comparisons to other insects appear for processes insufficiently

described for orthopterans.

The narrow, elongate damselfly abdomen requires careful dissection. Small dissecting instruments are essential: number 3 insect pins with points filed into scapel-shaped 'blades' are helpful and smaller pins aid in teasing apart ovarioles etc. The interpleural membranes between sterna and tergites are cut on both sides from segment 1 posteriorly to about segment 8. The complex of intestine, ovary, oviducts, ventrally-attached sterna and associated systems lift out, generally intact, from the lateral and dorsal portions of the exocuticle. Most damage at this stage occurs about segment 7 where the intestine and lateral oviducts, LO's, easily tear. Measurements were by ocular micrometer.

A recently-emerged individual possesses a soft, light tan exocuticle, pale brownish thoracic stripes, and has only a weak, fluttering flight. The exceedingly soft cuticle, wings and pale stripe pattern readily identify teneral individuals. The term, teneral, applies here to this youngest immature phase of the adult. Tenerals typically remain in low vegetation while the cuticle hardens and are not usually taken by net unless specifically sought. Older female ages are post-teneral, FPT. The ovarian conditions found in a mature parous female appear directly below followed by comparisons with tenerals and other FPT ages. Fully mature, parous females are blue in the antehumeral areas lying between the black middorsal stripe (or simply carina) and the lateral humeral stripes: the blue color occurs also for a variable distance posterior to the humeral stripe. Three younger FPT ages exist, thus this terminal age is FPT₄ (Fig. 1).

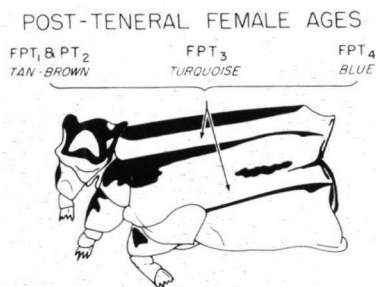


Fig. 1. External criteria for post-teneral female ages, FPT's, in *Argia moesta* using color of antehumeral stripes and lateral thoracic sides.

The left ovary of a mature, parous *Argia moesta* appears diagrammatically in Figure 2. The numerous panoistic-type ovarioles extend from the basal end of segment 2 through 6. Terminal filaments of the anterior-most ovarioles and anterior ends of the LO's extend forward into segment 1. Occasionally ovario-

les occur posteriorly into the anterior part of segment 7; however, segments 7 and 8 typically have only LO's converging ventrally to form the common oviduct, CO, entering the anterior end of the bursa copulatrix, BC, in the posterior part of segment 8. Each functioning ovariole, shown clear without shading in Figure 2, with a large mature terminal follicle or mature egg, ME, attaches by a pedicle to the medial side of the LO. Oviducts have exceedingly thin walls and tear easily in dissection. Whereas the pedicle connection of ME's to the LO's is usually verifiable, the other nonfunctioning ovarioles, NFO's, shown in black in Figure 2, do not connect to the LO's. The pedicle's origin or relation to ovulation whereby the ME enters the LO was not clear from my observations.

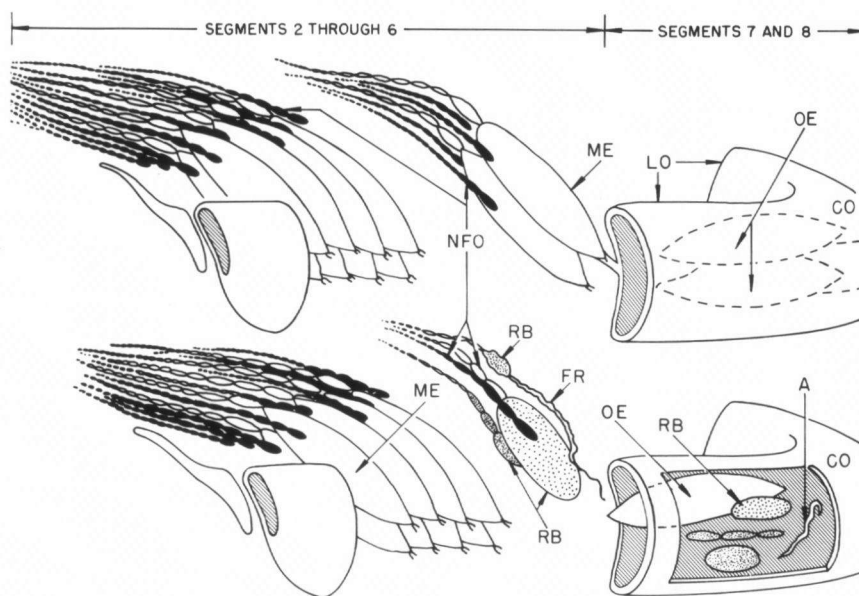


Fig. 2. Diagrammatic views of the left ovary, left lateral oviduct and common oviduct. Relative position in abdomen shown by segments above. Functional ovarioles with mature egg, ME, are clear, nonfunctional ovarioles, NFO, are black. Lower ovary shows resorption bodies, RB's, stippled. Other abbreviations in text.

The number of ovarioles is large and I could not accurately count their number on a single side or for a given segment length. Several hundred ovarioles exist and, while absolute counts are unavailable, relative estimates suggest individuals of similar age may vary by at least a factor of three. PHIPPS (1962) and LINLEY (1965) note that ovariole number in a species may vary

with body size and geographic distribution. UVAROV (1966) also found asymmetry in ovariole numbers of left and right ovaries of Orthoptera. The mean length of the ME is approximately 0.90 mm and they lie obliquely-oriented on each side of the intestine (Fig. 2). The distance along the longitudinal axis of the abdomen occupied by such an egg is approximately 0.70 mm and, over this distance, the terminal follicles of 50 or more ovarioles exist. The approximately circular cross-section of an egg has a mean diameter (width) of 0.22 mm with an area of 0.038 sq. mm. Only 31 such eggs stacked side by side require more area than available in a cross-section of the abdomen. Synchronous ovariole development would place 50 eggs in this space. The approximately circular abdominal cross-section has a diameter of 1.2 mm and an area of 1.13 sq. mm and the above figures ignore cuticle, intestinal space etc. A cross-section at any point along the ovary reveals only 4 to 9, mostly 6, ME's. These observations underline the fact that ovarioles can not produce eggs simultaneously as also noted by SINGH (1958), SCHMIDT (1972) and others. The number of follicles per ovariole varies, at least in part with age. Ovariole examination for follicle number requires care in locating the terminal follicle without breakage; however, I believe the following figures represent undamaged ovarioles. In young immature females, age FPT₁, see below, I found a maximum of 15 follicles per ovariole, most ovarioles having about 10. I counted ovarioles with follicle number ranging from 10 to 35, most over 20, in age FPT₄. SINGH (1958) and SCHMIDT (1972) also found "egg rudiments", follicles, to increase toward maturity in orthopterans and dipterans.

Oviducal eggs, OE's, in the LO's and particularly from segment 6 posteriorly overlap variably suggesting that several eggs move together to the BC similar to *Calopteryx* but unlike *Megaloprepus* (WHEDON, 1919). The LO's converge into the CO at variable distances from the anterior end of the BC. The OE's have the same dimensions given above for the ME's and the BC is only slightly longer than one OE. Each egg must pass singly through the BC to the genital pore opening just dorsal to the base of the ventral valvulae, VV. A characteristically curved, diverticula-like tube, the spermatheca, SPT, arises dorsally from the anterior end of the BC. A chitinous structure occurs in the BC, actually appears to form its dorsolateral walls, and is probably homologous to a structure named the collar, C, by TILLYARD (1917) and noted also by PRASAD & SRIVASTAVA (1961). The structure in *Zygoptera* I have examined consists of two oblong plates lying vertical and parallel to the longitudinal midline. The C has no connection to chitin of the exocuticle and its function is unknown. Only one specimen examined actually had an egg within the BC. It was held between the plates of C as in B of Figure 3. The plates are otherwise found closely pressed together. The penis of the male at copula may penetrate to C and it is conceivable that C may partially support

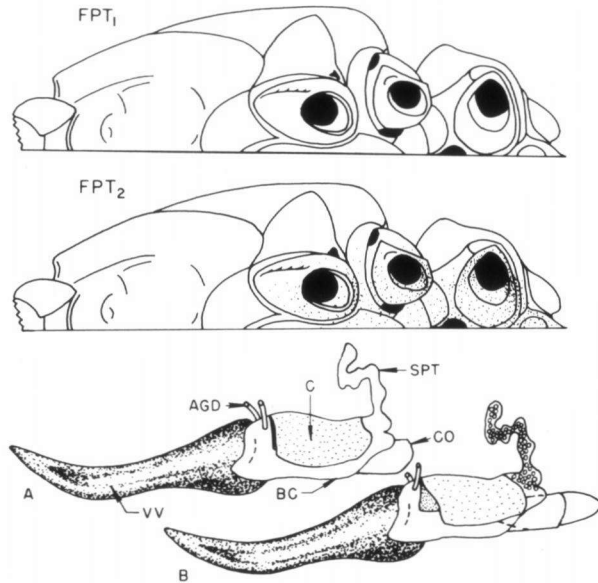


Fig. 3. Upper figures distinguish female ages, FPT₁ and FPT₂, by ventral thoracic pruinose (stippled) in latter age. Lower figures show bursa copulatrix, BC, collar, C, ventral valvulae, VV, and spermathecae, SPT's. An egg entering the BC having a filled-STP appears in B.

the linkage. Ducts of two accessory glands, ADG, connect to the posterior dorsal wall of BC. These glands, lying in segment 9, are very similar to glands illustrated for *Mnais* by ASAHINA (1954).

The remains of tissue at the terminal end of an ovariole following ovulation of its most recent ME, the follicular relic, FR, aid recognition of parous females of some insects (SINGH, 1958; ANDERSON, 1964; SCHMIDT, 1972, etc.). Complications attend the recognition of FR's in *Argia moesta* even assuming a faultless dissection. The large number of ovarioles are near-impossible to count and while FR's would be less due to asynchronous ovariole development, many could be overlooked. Within the LO's and CO, elongate bodies (a of Figure 2) exist similar to FR's. These observations suggest that FR's may break away from the ovariole and enter the LO's, perhaps during the ovulation process. Finally, follicles may cease development and enter into a resorption phase called resorption bodies, RB's. Follicle resorption is apparently not uncommon in insects. SINGH (1958), CLEMENTS (1963), HOPKINS & KING (1964), and SCHMIDT (1972) describe the process in several species. Resorption, when observed in *Argia moesta*, affects the terminal follicle, occasionally the last 3 to 4 follicles of a single ovariole, or the

follicle just behind the ME. In the latter case, the FR is then attached to the RB. These RB's appear in the lower portion of Figure 2. The RB's occur in various shades of yellow to orange and the same range in color exists in freshly dissected ovaries as those preserved for several months in ethyl alcohol. Various sizes of RB's exist. The typical ME shape (when resorption initiates at that state) changes, judging from the intermediate sizes and shapes, into a small rounded orange body. When a small follicle begins resorption, a similar comparison of sizes indicates that it approaches the FR in appearance. FR's are difficult therefore to distinguish from small RB's and considerable care should attend recognition of parous females by FR's in damselflies similar to *Argia moesta*. Resorption may also occur while females are still virgin judging by tandem marks and spermathecae, see below. SCHMIDT (1972) was able to count FR's and functional ovarioles, yet could not relate these to known number of eggs laid and the dipteran he studied has far fewer ovarioles than damselflies.

In *Argia moesta*, various sizes of RB's also occur in the LO's and occasionally a series of several small degenerating, but still connected follicles exist (Fig. 2). How the RB's reach the LO's is not clear. I have kept various-aged females contained over damp white filter paper and examined the paper twice daily. I have never seen any evidence, in this way, of RB's being voided from the body. HOPKINS & KING (1964) apparently found resorbing eggs extruded at the ovipositor in an hymenopteran.

Ovaries possess a thin layer of fatty tissue filling the interovariole spaces and supplied by a network of branching tracheal tubules. The haemocoel about segments 7 and 8 may also have large aggregations of fatty tissue. Membranes forming the dorsolateral walls of the haemocoel and just dorsal to the sterna possess aggregates of pigment deposits, green, pink and black. These colors play no apparent part in the cuticular color patterns.

Classifying ovary age rests in part on size of the terminal follicle. This follicle is not always the largest one in panoistic ovarioles (CORNWELL, 1968); however, it was consistently so in my observations. Conditions found in FPT₄ specimens have largely developed after emergence. Teneral, judging from 32 dissected specimens have only a narrow bundle of ovarioles lying dorsal to the intestine and terminating about segment 5. The largest terminal follicle occurring in tenerals was 0.66 mm in greatest diameter. This age apparently inherits little or no abdominal fat from the larval period. Abdominal muscles are poorly developed and muscles inserting on the ovipositor are highly undeveloped. Pigment deposits in the membranes are absent. FPT₁ individuals, judged from 33 dissections, have a much hardened, brown thoracic cuticle, the stripes being dark brown to black (Fig. 1). These specimens are also fully agile in flight and clearly distinct from true teneral conditions given above. The largest terminal follicles are 0.16 to 0.40 mm in greatest

diameter. Individuals having the larger follicles also have distinct deposits of fat and pigment aggregations in the membranes. RB's occurred in 5 of 21 individuals with terminal follicles greater than 0.32 mm in diameter; RB's were absent in the 12 individuals having smaller follicles. Ovipositor muscles are still undeveloped and all females were virgin, see below. Duration of this age probably exceeds ages FPT₂ and FPT₃ judging from the relative degree of ovarian development. FPT₁ individuals completely lack pruinescence (a whitish exudate) on the coxae and ventral surfaces of the thorax distinguishing them from FPT₂'s (Fig. 3). FPT₂ specimens, judged from 31 dissections, have cuticle color and pattern similar to FPT₁'s with somewhat blacker stripes. The single external criterion consists of pruinescence deposited on the ventral thoracic surface and coxae (Fig. 3). This pruinescence accumulates from this age throughout life although individual differences exist (some FPT₂'s have as much or more exudate as some FPT₄'s). The largest terminal follicles range from 0.60 to 0.72 mm in greatest diameter in 18 specimens. The remaining 13 individuals had 15 to 20 OE's, some reaching to the anterior end of the BC. Ten of the 31 specimens possessed RB's. The ovipositor muscles are much enlarged. All specimens were virgins, indicating that OE's may accumulate prior to mating.

FPT₃ specimens, judged from 30 dissections, have the brownish color between the thoracic stripes of earlier ages replaced with a turquoise color. Greater than half of the ovarian tissue consists of terminal follicles ranging between 0.65 and 0.80 mm in greatest diameter. Remaining ovarioles have smaller follicles or ME's. OE's occurred the full length of both LO's. Six specimens of the sample had RB's. As indicated, FPT₃'s closely approach FPT₄'s described above. The former probably has a shorter duration than either FPT₂'s or FPT₃'s judging from the difficulty in obtaining the sample of 30. Differences in ovarian tissue of FPT₃ and FPT₄ ages involve proportions of follicles. Less than half of the ovarioles in 36 FPT₄'s dissected had terminal follicles in the range of 0.65 to 0.80 mm in diameter, most ovarioles had smaller follicles but the LO's held larger numbers of OE's. Eight of the 36 FPT₄'s had RB's. All dissected FPT₃'s and FPT₄'s had mated, see below. Fat and pigment deposits occur in both ages but fatty tissue is more extensive in the FPT₃'s. The tracheoles and malpighian tubules are helpful in aging some insects (CLEMENTS, 1963; SCHMIDT, 1972 etc.); however, I noted no consistent changes with age. The accessory glands to the BC also undergo no noticeable change with age.

Individuals collected in the above ages, maintained in outdoor cages, and supplied with food undergo cuticle changes predicted. The turquoise character of FPT₃ specimens is not, from all available data, a phase mature individuals may temporarily adopt as exists in *Argia apicalis* (BICK & BICK, 1965). Likewise, the fully dark female, a similar temporary form of *Argia moesta*,

described in Ohio specimens by Borror, is absent. The duration of each age judging from preliminary data varies with weather factors. Data on this subject will appear in a later report.

T a n d e m m a r k s

In males, two tubercles occur between and dorsal to the superior abdominal appendages (toreolae of GLOYD, 1958; toreale of JOHNSON, 1972). A white exudate extruded by or near these structures collects on the appendages and in the torifer depression. The tandem linkage of the male places the torifer over the dorsal pterothoracic surface of the female directly posterior to the mesostigmal plates (WALKER, 1913). The contact leaves a semi-circular, whitish deposit on the female, the tandem mark. This material remains on dried museum specimens and on those preserved in alcohol. It is actually difficult to remove with a camel's hair brush and is generally distinct, if present, even in the field where a 20× hand lens resolves the few questionable individuals. The exudate develops on males prior to ages having sperm in the seminal vesicles, see below, so that mating by males sufficiently undeveloped to mark the female is unlikely. All tandem pairs I observed closely involved males clearly able to leave marks. Once in tandem, the female seems to carry the mark through life.

WILLIAMSON (1906) and RIS (1910) referred to exudate received by females as copulation marks although only tandem linkage produces them. A comparison of the SPT in marked females supports the copulation assumption. The characteristically-shaped tube of the SPT lies enveloped in glandular or fatty tissue. This tissue will separate on careful teasing leaving the SPT tube intact. A yellowish to amber material, I assume sperm and seminal fluid, filled the tubular SPT of all 66 preserved and dissected specimens of ages FPT₃ and FPT₄. These individuals all possessed tandem marks. All 99 teneral, FPT₁'s and FPT₂'s lacked marks and the SPT's were transparent without detectable contents. I assume the majority of females with marks have mated. Most mated females have probably oviposited at least once. Much oviposition in *Argia moesta* occurs while still in the tandem position (BICK & BICK, 1972). Above ages are recognizable in dried specimens and a survey of available collections gave a mating with age distribution of: teneral, 41 virgins; FPT₁, 66 virgins; FPT₂, 60 virgins, 3 mated; FPT₃, 5 virgins, 55 mated; FPT₄, 76 mated.

MALES

Males emerge as teneral having essentially the same cuticle and wing attributes as females. Intrapopulation differences in stripe patterns, when

present, do not affect age recognition given for southeastern populations. The soft cuticle and pale pattern readily identify the teneral age. A progressive deposition of whitish pruinescence on the thoracic dorsum characterizes much of the post-teneral period. This dorsal thoracic pruinescence is a sexually dimorphic attribute of *Argia moesta* and its pattern of deposition is progressive with time giving four post-teneral male, MPT, ages.

Individuals of MPT₁ age have a well-hardened thorax (distinguishing them from tenerals), the antehumeral and lateral pale areas of the thorax are brown, the stripes being black or brownish-black. MPT₂ specimens have a thin layer of pruinescence confined to the region of the middorsal thoracic stripe. In 30 dissected individuals each of ages MPT₁ and MPT₂, sperm was not found in the seminal vesicles. In MPT₃ specimens, the pruinescence has spread laterally across the thorax into both antehumeral areas; however, lateral borders of the black middorsal stripe beneath are still clearly distinct. In MPT₄ individuals, the pruinescence occurs all the way to the humeral stripe, occasionally encroaching partly upon it. The deposition of pruinescence has thickened and the outline of the middorsal thoracic stripe is no longer detectable. Seminal vesicles of 30 specimens each of MPT₃ and MPT₄ ages possessed sperm. These male thoracic patterns appear in Figure 4. Pruinescence occurs also on the prothorax, head and terminal abdominal segments; however, the sequence of development on those structures does not correlate well with the thoracic changes. The pruinescence patterns of western populations differ distinctly with the whole body becoming pruinose.

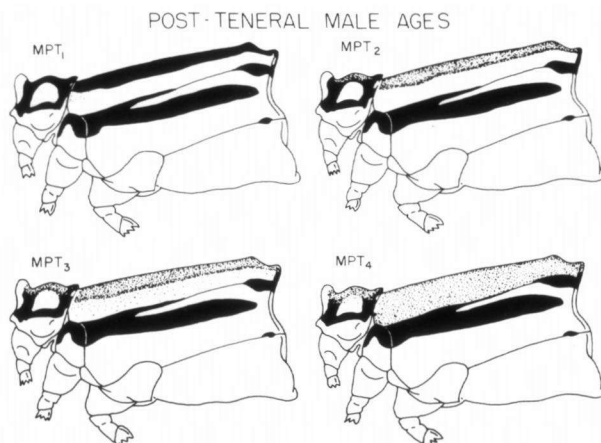


Fig. 4. External criteria for post-teneral male ages, MPT's, of *Argia moesta* using thoracic pruinescence development shown in stippling.

DISCUSSION

The absence of fat reserves, undeveloped ovaries and ovipositor muscles in teneral indicate the importance of conditions at the season of emergence. The maturation period must provide ample opportunities for the teneral to feed. Unfavorable conditions, apparently food shortage, related to ovarian resorption in one study of orthopterans (SINGH, 1958). CLEMENTS (1963) concludes that resorption occurs normally each gonotrophic cycle in mosquitoes. Large numbers of prey-sized organisms occur at the Santa Fe River habitat and it seems unlikely at first glance that *Argia moesta* was experiencing food shortage. Successive days of cloud overcast and rain produce sub-optimal feeding opportunities and further studies of resorption frequency should record these conditions. The resorption frequency was somewhat higher for FPT₂ specimens in material discussed here.

CORBET (1963) speculated on a possible relationship of adult longevity to the ratio of ovariole number/follicle number per ovariole. Variability of these parameters and the difficulty in obtaining accurate values limit this approach in damselflies similar to *Argia moesta*. UVAROV (1966) found no correlations in ovariole and oocyte or follicle numbers in Orthoptera. Ovarian dissections of parous females appear unlikely to give a reliable picture of fecundity for similar reasons. Counts of eggs laid by field-collected individuals known for a relative age will probably give better estimates of realized fecundity.

WILLIAMSON (1912), in synonymizing *Argia moesta* and *A. putrida*, studied thoracic stripe patterns. Borror's Ohio study involved the "putrida" form, a name apparently intended also for southeastern populations. The development of the sexually dimorphic pruinescence also varies geographically and the southeastern "putrida" clearly differ from the "putrida" of Ohio. Since pruinescence may operate in mate recognition (JOHNSON, 1962), further studies on the variation should include the pruinescence patterns. Studies are lacking on the chemical nature of pruinescence. One may speculate that it is a process of nitrogen elimination acted on by sexual selection producing mate recognition clues. Malpighian tubules show no gross changes with age.

The characteristically-shaped SPT's occurred in all dissected females. Dissections of other local *Argia* species, *A. fumipennis*, *A. sedula*, and *A. tibialis*, revealed distinctly shaped SPT's. These species and *A. moesta* could well be separated on SPT characters suggesting the potential taxonomic value for difficult groups. Dried specimens, some several years old, soaked for three days in Barbour's Fluid and dissected, possessed recognizable SPT's. The fatty tissue and muscles typically enclosing the SPT in fresh and alcohol-preserved material were essentially absent, yet the characteristic tubular shape of the SPT remained well-preserved.

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