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by Rosser W. Garrison

University of California Press

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(Odonata: Coenagrionidae)

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Abstract

This paper revises nine species of *Enallagma* (Charpentier) from the western United States. Synonymies, keys, and diagnoses are presented for *E. anna* Williamson, *E. basidens* Calvert, *E. boreale* Selys, *E. carunculatum* Morse, *E. civile* (Hagen), *E. clausum* Morse, *E. cyathigerum* (Charpentier), *E. ebrium* (Hagen), and *E. praevarum* (Hagen). Adults of three poorly described species are fully redescribed: *E. anna*, *E. basidens*, *E. praevarum*; and the previously unknown larva of *E. anna* is described. Lectotypes are designated for *E. calverti* Morse, *E. carunculatum, Agrion civile, E. clausum, Agrion ebrium, E. plebeium* Selys, *Agrion praevarum*, and *E. simile* Selys. *Enallagma simile* is synonymized with *E. civile*. Larvae of all species are diagnosed using new characters, the pharate caudal appendages (cerci) on abdominal segment 10. Female larvae of *E. boreale*, *E. carunculatum*, *E. civile*, *E. cyathigerum*, *E. praevarum*, and male larvae of *E. boreale* and *E. cyathigerum* are analyzed by discriminant analysis because traditional taxonomic characters are largely useless to identify them. Several characters of the cerci and a few characters of the gills were most useful in discriminant analysis. A special key using discriminant analysis enables workers with scant familiarity in the taxonomy of Odonata to identify larvae of these species. Detailed distribution maps and figures of all taxonomic characters for adults and larvae are included.

Introduction

The genus *Enallagma* contains about 75 species worldwide and about 45 in the United States. Nine species, *E. anna* Williamson, *E. basidens* Calvert, *E. boreale* Selys, *E. carunculatum* Morse, *E. civile* (Hagen), *E. clausum* Morse, *E. cyathigerum* (Charpentier), *E. ebrium* (Hagen), and *E. praevarum* (Hagen), are found in the United States west of the Rocky Mountains. Four additional species, *E. eiseni* Calvert, *E. novaehispaniae* Calvert, *E. rua* Donnelly, and *E. semicircularis* Selys, are found in Mexico, though *E. novaehispaniae* penetrates southern Texas. One additional species, *E. hageni* Walsh, occurs in British Columbia. In the western United States, the adults are conspicuous insects near water and are often abundant. They are primarily blue with black markings, about 2-4 cm long. Females are dichromatic with blue and black or olive and black markings. The larvae are common in lentic systems, where limnologists and aquatic ecologists often encounter them during routine sampling. Although the immature stages of the Odonata are better known than those of other insect groups, *Enallagma* larvae and adult females can still be difficult to identify because of similar morphology among species.

At least 16 names (Table 1) have been applied to the nine species discussed in this paper. *Enallagma* was proposed as a subgenus of *Agrion* by Charpentier (1840) to contain the widely distributed holarctic species *A. cyathigerum*. Selys (1875) described *Aenallagma boreale* from Newfoundland, but in 1876 corrected it to Charpentier's usage, *Enallagma*. Cowley (1934) credited the genus to Selys because he believed that Charpentier did not "adopt the name", whereas Selys' (1875) specific descriptions were "sufficient to characterize the genus". Other un-adopted generic names do exist (*e.g.*, *Orthetrum* Newman, 1833), but they have generally been credited to their original authors. Modern usage credits *Enallagma* to Charpentier.

Works describing and diagnosing western species of *Enallagma* are few. Hagen (1861) described *Agrion annexum* (= *E. cyathigerum*), *E. civile*, *E. ebrium*, and *E. praevarum* based on color patterns and male caudal appendages. Selys (1876) reviewed the genus worldwide, treating *E. annexum*, *E. boreale*, and *E. robustum* as doubtfully distinct races of *E. cyathigerum*. He also described *E. plebeium* and *E. simile* as races of *E. civile*. Provancher (1876) described *Agrion canadense* (previously thought to = *E. civile* but now thought to be *Ischnura ramburi* (Selys) or *I. verticalis* (Say)), while Morse (1895) described *E. calverti* (= *E.*

boreale), *E. carunculatum*, and *E. clausum* from Franktown, near Lake Tahoe, Nevada. Williamson (1900) described *E. anna* from Wyoming but did not diagnose the female. Calvert (1902) added *E. basidens* to the western fauna and provided keys to the known adult southwestern and Mexican species. Kennedy (1915, 1917) listed and, in some cases, elaborated on the behavior of the West Coast species. Byers (1927, 1929) provided keys and short descriptions of all North American species, based almost entirely on color pattern and shape of male caudal appendages. He also (1927) described *E. culicinorum* (= *E. anna*). Seemann (1927) wrote keys to the adults and larvae of southern California, and Walker (1953) offered the most complete assessment of the Canadian species. His meticulous work was probably fashioned after Garman's (1917) treatment of the Zygoptera of Illinois. Both authors used the mesostigmal plates to separate adult females. Pritchard and Smith (1956) and Cannings and Stuart (1977) also keyed the adults and larvae of *Enallagma* from California and British Columbia, respectively, but their characters were taken primarily from Walker (1953).

Compared with eastern North America, the West has received scanty coverage. For example, no specific work has appeared for Idaho, and other states and provinces are poorly known. The best treated area of the West is undoubtedly British Columbia (Currie, 1905; Osburn, 1905; Buckell, 1937; Walker and Ricker, 1938; Whitehouse, 1941; Walker, 1953; Scudder *et al.*, 1976; and Cannings and Stuart, 1977).

Many of the adult females of western *Enallagma* are difficult to identify. Even though females were collected along with Morse's type males, Morse (1895) did not describe females or include any in the type series of *E. calverti*, *E. carunculatum*, or *E. clausum*, apparently because he could not distinguish the females of sympatric species. Williamson (1900) elaborated upon the differences between male *E. annexum* (= *cyathigerum*) and *E. calverti* (= *boreale*), but in describing the female of *E. calverti* noted that the description "will serve as well for the female of *annexum*". Currie (1905) could not distinguish female *E. cyathigerum* from *E. boreale*. Williamson (1906) reported seeing 20-30 out of 500 sympatric male *E. civile* and *E. carunculatum* that were intermediate. Johnson (1972) noted that females of *E. carunculatum*, *E. civile*, and *E. praevarum* are so similar that their "separation requires care", and he included an extended paragraph on the separation of those species.

A thorough review of the species from the western United States is needed because some (*e.g.*, *E. basidens* and *E. civile*) have greatly expanded their ranges, and larvae and females of others have remained poorly known or have not been adequately diagnosed. Lectotypes and type localities have not been designated for most species, and no work adequately treats the adults and larvae from the western United States. The larvae have been especially difficult to determine, and none of the existing works can be used to identify specimens with confidence. Moreover, these larvae are common and would be good candidates for monitoring changes in aquatic ecosystems, if they could be easily identified.

This work is a review of the western U.S. species of *Enallagma*, and describes adults and ultimate larval instars, provides keys for their separation, and gives synonymies, diagnoses, and discussions of their distribution. I examined larvae and adults of all nine species and selected new characters from the larvae and females. The phenetics treatment should simplify the identification of larvae of this difficult genus for workers with little taxonomic experience. During this study, 2372 adults, 180 larvae, and 63 types and syntypes were examined. Of the 16 names treated, types had been designated for five, four are lost or are of uncertain identity, and I have designated lectotypes and type localities for the other seven.

Adult Behavior and Life History

Mature *Enallagma* are active during midday and are found primarily at still water although one species, *E. anna*, seems to prefer slowly moving streams. All species occupy habitats from below sea level to high mountainous elevations. No species is known to have a disjunct distribution (Figs. 33-41), which suggests that these insects disperse freely. There is good evidence that two species, *E. basidens* and *E. civile*, have substantially increased their ranges within the last 60 years (Montgomery, 1942, 1966; Paulson and Garrison, 1977).

Immediately upon transformation, the adults are soft and pale and remain so for about 24 hours. About 30 minutes after transformation, they fly away from the water sites, probably to avoid predators and contact with mature *Enallagma*. These juvenile adults forage away from water for one to three weeks (Corbet, 1962), the maturation period.

Juvenile specimens are pale blue (♂♂) or straw brown (♀♀). Maturation time has been measured as the period between peak emergence and highest adult density at water in *Pyrrhosoma nymphula* (Sulzer) (Corbet, 1952) and *E. boreale* and *E. carunculatum* (Logan, 1971). Exact times are difficult to measure because marking teneral individuals and recapturing them when mature has generally been unsuccessful (Garrison, 1978; Parr, 1976) although Tennessen (1975) estimated a maturation period of 7-17 days for two sympatric sibling *Enallagma*, *E. pollutum* (Hagen) and *E. signatum* (Hagen) in Florida.

When mature, the blue and black males congregate at ponds. Mature females generally remain away from water, appearing there only to mate and oviposit. Females are dichromatic: the andromorphs are blue and black, while heteromorphs are brown (or olive) and black. Some females are predominantly of one pale color but will often possess a little of the other pale coloration along the middle abdominal segments. Both sexes leave the water sites late in the afternoon and probably roost among shrubs or other vegetation during the night. Adults typically perch on upright sedges, cattails, or grass growing at or near the water's edge. Most of their time is spent resting, but they often fly over the water to investigate other damselflies or to feed. Males generally arrive earlier and leave later in the day than females.

A rudimentary transient territoriality may be exhibited by males. Problems with territoriality revolve on the definition of the concept from a simple one such as Noble's (1939) "any defended area", to more restrictive ones involving signaling, overt defense, scattering of individuals, and prolonged residency in an area. Wilson (1975:261) defines a territory as an area "occupied more or less exclusively by animals or groups of animals by means of repulsion through overt aggression or advertisement". Tennessen (1975) uses Noble's definition because "it is simple and implies no particular function", and concludes that "the main function of territoriality, clearly recognized by Johnson (1965), is to prevent other males from interfering with courtship, mating, and oviposition". Tennessen (1975) believes *E. pollutum* and *E. signatum* are territorial but remarks that "the defended area is very transitory, and...males are merely maintaining a certain distance between themselves and other males. The advantage of maintaining such a position at water is that an individual is better able to detect and secure a female". I believe male aggressive behavior to be of an investigatory nature rather than competition for territory or mates.

Enallagma copulate near oviposition sites. The process leading to mechanics of copulation is well described (Corbet, 1962; Miller and Miller, 1981; Walker, 1953). No courtship activity has been reported for enallagmas before copulation. Single males fly toward and attempt to grasp a female. The male alights on the dorsum of the female prothorax, swings his abdomen between his legs and attaches his caudal appendages to the anterior edge of the synthorax (mesostigmal plates), resulting in a tandem position. The tandem pair usually alights and the male transfers sperm from the genital aperture on the ninth sternite to the extended penis on the third sternite. Shortly afterwards, the male attempts, by curving abdominal movements, to contact the female's genitalia with his penis. Several trials lasting several minutes may pass before the copulatory position is achieved. Undisturbed copulation may last up to 44 minutes in *E. civile* (Bick and Bick, 1963). Observations by Miller and Miller (1981) indicate that the male's penis removes the sperm of a previous male before depositing his own sperm in the spermatheca. These results are consistent with the hypothesis of Waage (1979), who believes that the zygopteran penis acts in the removal as well as the deposition of sperm. Mating usually takes place during the midday hours.

Eggs are inserted into plant tissues and females may be in tandem or single during oviposition. When ovipositing, females may completely submerge themselves up to about an hour. When in tandem, males immediately release themselves from submerging females, but females are not always able to free themselves from males.

Generation time in the laboratory averages about 3-4 months for *E. civile*, but this time interval is almost certainly longer in nature. The slender, translucent, gray, brown or green larvae climb submerged vegetation along the pool fringes. The larvae probably undergo 10-12 instars. Wing pads begin to appear on the F-5 or F-4 instar (final instar-minus-n number of moults). The final instar ceases to feed 2-3 days before eclosion. Transformation time in the laboratory is about 30 minutes, the same as I have observed in nature.

Phenetics

INTRODUCTION

Enallagma larvae are often common in ponds and slow-moving streams in the West. Proper species identification is necessary in order to adequately evaluate changes in aquatic ecosystems. Since the adults of some species are very similar in appearance, one expects to experience an even higher magnitude of difficulty in discriminating the larvae. Disregarding isolated and often inadequate descriptions of the larvae themselves (Needham, 1903; Needham and Cockerell, 1903), the first attempt to adequately describe and key *Enallagma* larvae in the United States was Garman (1917), who used characters of the caudal gills and setae on the pleura of the first abdominal segment. Garman (1917) described four western species (*E. calverti* [= *boreale*], *E. cyathigerum*, *E. carunculatum*, and *E. civile*), but was not able to discriminate between larvae of the first two species. Walker (1916) discussed the differences between larvae of *E. cyathigerum* and *E. boreale* and concluded, based on differences between the gill characters of his material and previously published European larval descriptions of *E. cyathigerum*, that they could be separated only by the pharate caudal appendages (cerci).

Seemann (1927) offered a key to the southern California *Enallagma* species using gill characters and setal counts of the prementum. The best and most complete treatment of larvae was by Walker (1953) in his treatment of the Canadian species. His descriptions of *E. boreale*, *E. cyathigerum*, *E. carunculatum*, *E. civile*, *E. clausum*, and *E. ebrium* were complete and were often based on reared material. Pritchard and Smith's (1956) and Cannings and Stuart's (1977) keys are slightly modified from those of Walker (1953).

A preliminary assessment of the larvae of the nine western species indicates that five, *E. boreale*, *E. carunculatum*, *E. civile*, *E. cyathigerum*, and *E. praevarum*, present extreme taxonomic difficulties. The other four species, *E. anna*, *E. basidens*, *E. clausum*, and *E. ebrium*, are more easily recognizable and are not further considered in this section. Walker (1944), who published more concerning the taxonomy of the genus than any other worker, acknowledged the extreme difficulty in segregating the larvae of the sibling congeneric pair, *E. boreale* and *E. cyathigerum*: "Characters have been given by the writer (Walker, 1916) for separating them but further study of *boreale* in large series and of the single reared specimen we possess of *cyathigerum* indicate that characters given are not reliable" and none of the previously described characters "appear to be reliable for the separation of these two nearly related species in their nymphal stages, and it is quite possible that they are not separable". Johnson (1972) notes the difficulty in separating adult females of *E. carunculatum*, *E. civile*, and *E. praevarum*. I also find keys separating the larvae of these species to be unsatisfactory.

My purpose here is to provide an accurate and reliable method to identify the five common western species, *E. boreale*, *E. cyathigerum*, *E. carunculatum*, *E. civile*, and *E. praevarum*. The data, mostly from reared specimens, were subjected to discriminant analysis techniques because this method enables one who is inexperienced in the knowledge of larval Odonata to properly identify unknown specimens.

SAMPLES

This study required a series of positively identified larvae or exuviae so that good discriminatory characters could be found. Each species was represented by a series of reared larvae (knowns) from three or more localities comprising five or more specimens. These samples probably encompass the scope of intra- and interdemic variation of characters.

Reference samples of *Enallagma* were established either by collecting larvae in the field and rearing them to maturity or by rearing larvae from eggs in isolation in plastic Petri dishes. Before transformation, tripods constructed from pipe cleaners were placed in each dish. Cultures were checked every day for emergence. To obtain eggs, females were confined to plastic boxes with a moist paper towel on the bottom. This rough substrate was suitable for egg-laying and also provided enough humidity to prevent desiccation of the adults. Smaller instars were fed various infusoria until they could eat first instar mosquito larvae. The delicate caudal gills dry out and fold upon themselves after emergence from the water, making it difficult to record some gill measurements. Therefore, before emergence, gills were removed and placed in alcohol.

Once satisfactory characters were established for both male and female larvae of all species, field collected, preserved larvae constituted the unknown groups to be identified. Some of these were collected along with larvae from the reference samples, and provided a check in identification by discriminant analysis. A total of 82 specimens was used in the reference samples, and 69 larvae constituted the unknown samples (Table 2).

CHARACTERS

Two character sets were used in this study. The first (Table 3) consisted of 23 characters, most of which have been used by other odonatists in diagnosing the various species of larvae. Odonate systematists have traditionally used characters from the prementum (MENS-number of premental setae, MAGS-number of marginal setae, LATS-number of palpal setae, MENL-length of prementum, MEDW, and MEBW-distal and basal widths of prementum [Figs. 2 and 3]), median gill (XDSD-number of dorsal antenodal setae, XDSV-number of ventral antenodal setae, XDSL and XVSL-lengths of dorsal and ventral rows of setae, GILL-gill length, and GILW-gill width [Fig. 1]), and lateral gill (XVSD-number of dorsal antenodal setae and XVSV-number of ventral antenodal setae). I included characters from the antenna (SEG1-SEG6), wing pad length (HWPD), length of abdominal segment 10 (TENL), and caudal appendage length (APPL) to complete the first character set. All character measurements were meristic or discontinuous and were measured to the nearest 0.01 mm under a Wild stereoscopic microscope with an ocular micrometer. All the antennal and gill measurements were made under temporary slide mounts to minimize depth distortion. Male and female larvae were pooled for this analysis.

When the characters in the first set showed little success in discriminating the five species, another set of characters was used to discriminate between male *E. boreale* and *E. cyathigerum* (Table 4) and among the females of all five species (Table 5). The pharate sexual characters of male *E. carunculatum*, *E. civile*, and *E. praevarum* were sufficiently salient that numerical methods of discrimination were not required. Characters were recorded from the pharate caudal appendages (cerci) and ovipositor (females). After the gills were broken at the joints, the ninth (females) and tenth abdominal segments were removed so the structures could be easily measured. The genital characters given in Tables 4 and 5 were measured to the nearest 0.01 mm, except for ARC (Table 5), which was measured to the nearest 0.001 mm.

ANALYTICAL TECHNIQUES

Because the reference material comprised five sibling species, discriminant analyses were performed on this known material in order to maximize their differences. The subprogram DISCRIMINANT (Klecka, 1975) of the SPSS package performs a direct or stepwise analysis and was used in this study. In direct discriminant analysis all variables are entered simultaneously while the stepwise program enters a new variable with each iteration. This, in combination with previously entered variables, yields the best discrimination. Stepwise discriminant analysis enables the user to ignore those characters which add only a small contribution to the classification. A convenient system allows for the separation of closely related OTU's (Operational Taxonomic Units) or, in this case, specimens, with as few characters as possible.

Each OTU is defined by a linear combination of variables, $D_1 = d_{i1}Z_1 + d_{i2}Z_2 + \ldots d_{ip}Z_p + C$, where D_1 is the discriminant score, d_i's the unstandardized weighting coefficients, Z's the measured variables used for the analysis, and C the discriminant function constant or correction factor. For example, if measurements (Z) for a male *E. boreale* are DVHEIG = 0.20, LATHEIG = 0.27, STUBHEI = 0.16, then, using the unstandardized discriminant function coefficients and constant from

Table 10, $D_{boreale\ ♂}$ = (-11.691 x 0.20) + (8.527 x 0.27) + (69.953 x 0.16) + (-7.568) = 3.59. The average for all reference OTU's represents the average mean for that taxon (for example, 2.10 for *E. boreale* males, Fig. 29). Half the distance between two mean scores represents the critical value or midpoint between groups (0.55, Fig. 29). Unknown specimens can be identified by measuring and calculating as above and comparing the results with the appropriate table and figures. Specimen values which fall on or near critical values cannot be positively identified according to the characters used. Unstandardized coefficients and constants are shown in Tables 7, 10, 12, and 15. See Appendix for more detailed instructions. The DISCRIMINANT package also contains a classification table (Tables 8, 13, and 16) for reference specimens and provides a useful tool in identifying unknown material.

The standardized discriminant scores (Tables 6, 9, 11, and 14) indicate the relative importance of all variables; the higher positive and negative values indicate a higher discriminatory value. Each eigenvalue corresponds to the total percent of variation explained. The canonical correlations explain the degree of variation in each function and Wilks' lambda is an inverse measure of the significance of discrimination of each component not previously explained: the lower the value of Wilks' lambda, the better discriminatory power that function has.

Discriminant analysis has been used to analyze geographic variation in dragonflies (Garrison, 1976), to identify carabid beetles (Barlow *et al.*, 1969) and honeybees (Daly and Balling, 1978), and to assess hybrid intermediates of butterflies (Hafernik, 1983), birds (Rohwer, 1972), and foxes (Rohwer and Kilgore, 1973). These studies have facilitated the identification of questionable unknown specimens against positively identified reference material and are attractive in part because no previous familiarity with the organisms is required when subsequent users assess unknown samples.

RESULTS

Figures 20, 21, and 22 are comparisons of the key character differences given by Walker (1953) in his key for the separation of *Enallagma cyathigerum* from *E. boreale* and *E. carunculatum* from *E. civile*. According to Walker (1953:199), larvae of *E. boreale* have a median gill width one fourth the length of the median gill (GILW/GILL = 0.25, Fig. 20); but for *E. cyathigerum* this value is only one third (0.33). The gill length of *E. boreale* is stated to be one fourth to one half longer than the outer wing cases (HW/GILL = 0.67-0.80, Fig. 21); but the value for *E. cyathigerum* is only one fifth (0.83). The X's on the abscissas represent the values given by Walker in his key for separating both species, while histograms of 10 *E. boreale* and 17 *E. cyathigerum* represent data I measured from reared specimens. The data, which are not normally distributed, were subjected to a series of Wilcoxon two-sample tests (Sokal and Rohlf, 1969:393) and were not found to be significantly different. The key characters given by Walker for the separation of these two species are not adequate and will result in large numbers of misidentified specimens.

According to Walker (1953:197,199) the length of the dorsal setigerous margin of the median gill is three-sevenths the length of the gill in *E. carunculatum* (XDSL/GILL = 0.43) and only one third (0.33) the length in *E. civile*. Again, data from reared specimens (Fig. 22), according to the Wilcoxon two-sample test, show no significant differences between 14 *E. carunculatum* and 15 *E. civile*. Garman (1917) and Walker (1953) also separated *E. carunculatum* from *E. civile* by the presence of a few spinose setae on the first abdominal pleuron, but of 14 *E. carunculatum* I reared, none possessed any setae, and two of 15 reared *E. civile* possessed a few small setae. The final character in Walker's key is the difference in shape of the pharate caudal appendages between male larvae of *E. carunculatum* and *E. civile* and is the only character that can be used to separate males of the two species.

A multiple stepwise discriminant analysis showed five characters, XDSD, XVSD, XDSL, GILL, and SEG4 (Table 3), to be the most valuable in separating the five species. The combination was only slightly less efficient than when all 23 characters were used together. Figure 23 shows the distribution of the reference samples according to the first two components. Large circles are minimum diameter circles that will enclose the respective reference groups. Eleven of 77 (14.3%) specimens were misclassified, but results were of less value when unknowns were computed. Figures 24-28 indicate that almost 40% of the unknowns were misclassified (Table 8). The first two functions accounted for 84.7% of the total variation (Table 6, 58.8% and 25.9%), so the last two functions were ignored.

The two most similar species, *E. cyathigerum* and *E. boreale*, were hardest to separate: 50% of the unknowns were incorrectly classified into either group (Table 8). SEG4 was primarily responsible for the separation of *E. praevarum* from *E. carunculatum*, because the means are significantly different (*E. praevarum* = 0.44 mm, s = 0.03; *E. carunculatum* = 0.32 mm, s = 0.05).

Odonatists have divided the five species into two subgroups, and the results of the discriminant analysis support this division. The first group has dorsal and ventral setal patterns of about equal length on the median gill in both sexes and includes *E. cyathigerum* and *E. boreale* (Figs. 80, 81). *E. carunculatum*, *E. civile*, and *E. praevarum* define the second group by having a dorsal antenodal distance about twice the length of the ventral series on the median gill (Figs. 82-84). The characters XDSD, XVSD, and XDSL reflect these measurements and are primarily responsible for subgroup division. Misclassification according to groups was only 2.6% for knowns and 10.9% for unknowns (Table 8).

Reference males of *E. cyathigerum* and *E. boreale* were best separated by the pharate caudal appendages (Figs. 7, 8). STUBHEI proved to be the best discriminatory character (Table 9), and only one *E. boreale* reference was misclassified (Table 13, Fig. 29). The STUBHEI of *E. boreale* is significantly greater than for *E. cyathigerum* (*E. boreale*: $\bar{Y}$= 0.15, N = 7; *E. cyathigerum*: $\bar{Y}$ = 0.10, N = 15; F_s = 41.26, $P < 0.001$). Walker (1916) noted that the caudal appendages of *E. boreale* were longest near the dorsum, while in *E. cyathigerum* they were longest along the ventral edge of the appendage (Figs. 103c and 104c). I could not measure this character appropriately because the base of the cercus was obscured by the margin of the tenth abdominal tergite, and I could not define the farthest posterior point on the appendage. Therefore, I used this qualitative character to subjectively segregate unknowns for the discriminant analysis, although not all reared specimens conformed to these distinctions. Only one unknown, *E. boreale*, was incorrectly classified (Fig. 29), so this analysis can be used with a high degree of success in identifying male larvae of these two species.

The female pharate caudal appendages of all five species are similar, because they form a conical point. Unidentified female larvae are best classified into their respective groups based upon the five gill and antennal characters (Table 7) before identification proceeds to the species level. After division into the two subgroups, four characters from the ovipositor and seven from the caudal appendages were then subjected to a further stepwise discriminant analysis for each group (Table 5). As with the males, STUBHEI (Table 11) was primarily important in separating female *E. boreale* from *E. cyathigerum*. STUBHEI was greater in *E. boreale* than in *E. cyathigerum*. Three characters, BOTTOM, APPLENG, and STUBHEI (Figs. 9-14) were the most useful in distinguishing these sibling species. DISTAL, MESAL, and TOP (Fig. 9) were not very useful characters, because accurate measurements depend on the position of the appendage when viewed posteriorly. Fig. 30 shows that 100% of the knowns were classified correctly, but three of eight unknown *E. cyathigerum* were misclassifed as *E. boreale*. One of these misclassified specimens was a probable *E. cyathigerum*, because it was taken in association with several reared specimens. The other two specimens were subjectively identified as *E. cyathigerum*, but I have no proof that they are that species. Twenty-five percent of the unknown larvae were misidentified (Table 13), so the characters used here cannot be used with great confidence in separating female larvae of these two sibling species.

The same characters used for *E. boreale* and *E. cyathigerum* were used for the female larvae of *E. carunculatum*, *E. civile*, and *E. praevarum*, except one extra character ARC (Table 5) was included. A stepwise discriminant analysis showed four characters, BASALHEI, APPLENG, GONOPHY, and ARC, were best in discriminating the reference samples (Fig. 31). Standardized discriminant values show APPLENG was the primary means of separating *E. civile* from *E. carunculatum* and *E. praevarum* (Table 14). The appendages of *E. civile* ($\bar{Y}$ = 0.31 mm, s = 0.12, N = 9) are longer than those of *E. carunculatum* ($\bar{Y}$ = 0.26 mm, s = 0.01, N = 8) or *E. praevarum* ($\bar{Y}$ = 0.25 mm, s = 0.02, N = 7), and parallel the longer adult and larval appendage length of male *E. civile*. ARC played a secondary role in separating the three species and was primarily responsible for discriminating between *E. carunculatum* and *E. praevarum* (Table 14, DF 2). A very small or no concavity exists in the appendages of *E. carunculatum* ($\bar{Y}$ = 0.004 mm, s = 0.004), while a moderate concavity is present in *E. praevarum* ($\bar{Y}$ = 0.016 mm, s = 0.006). A very deep concavity exists in *E. civile* ($\bar{Y}$ = 0.027 mm, s = 0.006). APPLENG primarily accounted for the separation along the first discriminant function, while ARC explained most of the variation along the second function.

Classification of unknown *E. carunculatum*, *E. civile*, and *E. praevarum* (Fig. 32, Table 16) shows three of 22 (13.6%) females misidentified. Two *E. carunculatum* were identified as *E. praevarum* and one *E.*

praevarum was identified as *E. civile*. The sexual characters used show a high degree of success in differentiating among these three species.

DISCUSSION

Use of discriminant analysis showed a much higher success than traditional methods in identifying members of the five sibling species of western *Enallagma* larvae. The use of new characters from the pharate caudal appendages and adequate series of reared material to encompass the high degree of inter- and intrademic variation were responsible for this success. The traditional set of characters (= first character set of this study) was useful only in separating the five species into two groups: *E. boreale* and *E. cyathigerum* from *E. carunculatum*, *E. civile*, and *E. praevarum*. None of the traditional characters of the prementum (MENS, MAGS, and LATS, Table 3) proved useful in this study. A high degree of variability with considerable overlap was encountered in the setal counts of the prementum. Previous keys and diagnoses using these characters (Seemann, 1927; Pritchard and Smith, 1956) were probably based on one or two specimens.

A lack of good series from several different localities has obscured the degree of variation in most of the previously recorded characters. Lucas (1930) and MacNeill (1950) were surprised at the extreme differences in gill characters in British specimens of the Holarctic *E. cyathigerum* from Walker's (1916) description of the same species from Canada. Gloyd (1943) described *E. vernale* from the eastern United States, and Walker (1952) assigned his previous description (1916) of *E. cyathigerum* to *E. vernale*. While this might explain the extreme differences alleged for *E. cyathigerum* by European authors, I have observed as great differences in size, gill banding patterns, and antenodal setal counts from reared specimens of *E. cyathigerum* from coastal California and the Sierra Nevada. Adults of *E. vernale* are weakly differentiated from true *E. cyathigerum* and appear to be allopatric in the northeastern United States and Canada. *E. vernale* is probably an ecotype of *E. cyathigerum*.

The pharate caudal appendages have received little attention since Walker (1916) described them for *E. boreale* and *E. cyathigerum*. Because the best characters for distinguishing adult males are the superior caudal appendages, it is logical to assume some value in the same characters in the larvae. The similarity between adults and larvae can be striking. For example, the male cerci of *E. anna* and *E. praevarum* show the distinct concavity (Figs. 107b and 108b) that approximates the divided forking of the same appendages of the adults (Figs. 60a and 62a). The differentiated convex tubercle in adult *E. carunculatum* and *E. civile* (Figs. 63a and 64a) is illustrated by the convex posterior margins of the larval cerci in lateral view (Figs. 105b and 106b). The adult female cerci of all five species are similar and are not used in identification. This explains why the pharate caudal appendages of the female larvae were not as discriminatory as in the males. Nevertheless, the larval female appendages often show striking similarities to their male counterparts. Both sexes of *E. cyathigerum*, for example, have the long, narrow character STUBHEI which equals the narrow upturned appendage in the adult male (Figs. 7, 11, and 67a). The significantly longer cerci of female *E. civile* correspond to those of the male larva and adult, which are the longest appendages of the five species.

Usually, one or two characters were significant in separating species pairs. STUBHEI for male and female *E. boreale* and *E. cyathigerum*, and ARC and APPLENG for female *E. carunculatum*, *E. civile*, and *E. praevarum* could probably be used with a high degree of success in separating the five species. However, even when there is a significant difference between the means of these single characters, additional material can still be misidentified; and the inclusion of less discriminatory characters will often contribute to the classification success.

The caudal appendages are also useful because these structures, unlike the deciduous gills, are intact on preserved specimens. Series of different species preserved in liquid often lose their caudal gills, and it is impossible to associate the parts with the respective specimens.

Only one of 12 male unknown *E. boreale-E. cyathigerum* was misclassified. Six of 34 (17.7%) of all the unknown females were misclassified. Most misclassifications of the females resulted between the sibling pairs *E. boreale-E. cyathigerum* and *E. carunculatum-E. praevarum*. Female imagines of *E. carunculatum* and *E. praevarum* can be very difficult to distinguish, but characters SEG4 and ARC, from the first and second set of characters respectively, will correctly identify most of their larvae. Of the two misidentified *E. carunculatum* female larvae (Table 16), one was correctly classified as *E. carunculatum* according to the first set of characters (Table 8). SEG4 of both of the misclassified specimens was 0.36 mm, well below the larger value for *E. praevarum* ($\bar{Y}$ = 0.44 mm, s = 0.03), but within the range for known *E. carunculatum* (0.25 - 0.39 mm, N = 15). Only one known *E. praevarum* had a SEG4 length less than 0.40 mm.

Females of the other sibling pair, *E. boreale* and *E. cyathigerum*, are difficult to identify, and discriminant analysis can result in a moderately large number (*ca.* 35%) of misidentifications.

Taxonomy

CHARACTERS AND TERMINOLOGY

The best diagnostic characters for adults are found on the superior caudal appendages of males and mesostigmal plates of females. The shape of the superior caudal appendages has been illustrated by many workers, usually as simple line drawings, many of which are inadequate. Dorsolateral views of the superior appendages are often necessary to illustrate the differences. Most species have pale tubercles which are best viewed dorsomesally. Their placement and shape offer reliable and relatively easy means of identification. All views of the caudal appendages (except Fig. 60d) are shown without the sparse covering of hairs, which obscures the shape and sculpturing of the appendages if not removed.

The mesostigmal plates of females are the contact points for the mesal side of the superior caudal appendages of males during the tandem position. The plates are bilaterally symmetrical, rectangular, and more or less planar structures located at the anterior end of the synthorax, directly behind the pronotum. The pronotum may have to be removed on some specimens to reveal the plates. Figure 71 illustrates the principal parts of the mesostigmal plate of *E. ebrium*. The middorsal thoracic carina expands anteriorly to form the ramus (rm), and the ramus divides laterally, forming the posterior arms of the frame (paf). The lateral arms of the frame (laf) form the sides of the frame, which encloses the mesothoracic pit. The angle of the lateral arms relative to the posterior arms is of prime importance in identifying some species. The posterior margin of the plate is an important character in identifying other species. This structure may be linear, sinuate, well-defined, or obscure. The actual sculpturing of the plates themselves is often difficult to depict in drawings, and great variability is often expressed within a single species. I have illustrated specimens I consider typical and have described the variations under each species description.

General body patterns of both sexes are useful in field identification of the species, but they also show some variation in the extent of the black markings. While many of the older works (*e.g.*, Byers, 1927, 1929) used body markings as chief aids in identification, they are often unreliable and positive identifications should be made by the caudal appendages (males) and mesostigmal plates (females).

Most of the characters used in identifying the larvae are discussed in detail under "Phenetics". The best characters are the shape and size

SYNONYMY

Synonymies include all major works on taxonomy, biology, and all works treating these species in the western United States and Canada. The latest catalog which fully treats these species is Muttkowski (1910), but it is vastly incomplete. Notes and comments are abbreviated as follows:

behav., adult behavior
cat., catalog
diag., diagnosis
distr., geographic distribution followed by states, usually with comments. New locality records or faunal lists are listed by the state(s).
Dmsfls., damselflies
Drfls., dragonflies
fn., footnote
key, key for identification
morph., morphology
larva, description of larva
Odon., Odonata
rearing, reports rearing
syn., synonymizes taxon
taxon., taxonomic comments
♂, description of male
♀, description of female

All other notes (*e.g.*, "phylogeny" or "water quality data") are self-explanatory.

Genus *Enallagma* Charpentier

Enallagma Charpentier, 1840. Libellulinae Europaeae descriptae ac depictae. Lipsiae, Leopold Voss, 4:21. Type species: *Agrion cyathigerum* Charpentier, 1840, designated by Kirby, 1890:145 (first included species).

Aenallagma Selys, 1875, Notes on Odonata from Newfoundland, collected by Dr. John Milne. Entomol. Mon. Mag., 11:242. Lapsus or unjustified emendation of *Enallagma* Charpentier, 1840.

Diagnosis. Adult *Enallagma* in the western Nearctic region most closely resemble members of two other genera: *Coenagrion* Kirby and *Ischnura* Charpentier. Male *Enallagma* lack the long, membranous filament at the distal end of the penis found in *Coenagrion*. Female *Enallagma* possess a ventral spine on the posterior ventral end of segment 8; this structure is absent in *Coenagrion*.

All western species of *Enallagma* except *E. basidens* have R_3 originating from R_2 between the fourth and fifth postnodal crossveins in the forewing, and between the third and fourth crossveins in the hind wing. *Ischnura* have R_3 originating from between the third and fourth, and second and third crossveins in the fore wing and hind wing, respectively. The characteristic divided antehumeral stripe (Fig. 43) separates *E. basidens* from all *Ischnura* species.

All larvae of *Enallagma* possess six antennal segments, but *Coenagrion* and *Ischnura* possess seven.

KEY TO ADULTS OF *ENALLAGMA* OF THE WESTERN UNITED STATES

1. Vein R_3 arising from R_2 between 3rd and 4th postnodal cs. in FW, between 2nd and 3rd in HW; black humeral stripe finely divided by a narrow pale line one-fifth as wide as black stripe on either side (Fig. 43) . . . . *basidens*

1'. Vein R_3 arising from R_2 between 4th and 5th postnodal cs. in FW, between 3rd and 4th in HW; black humeral stripe entire, not divided by a fine pale line 2

2(1'). Accessory genitalia present on abdominal sternites 2 and 3 (males) 3

2'. Accessory genitalia absent on abdominal sternites 2 and 3 (females) .10

3(2). Superior appendages shorter than inferior appendages, in lateral view their extremities rounded and entire, attenuate, or with a small upturned protuberance 4

3'. Superior appendages as long as or longer than inferior appendages, in lateral view their extremities with an upper and lower arm which may or may not surround a pale tubercle 6

4(3). Bases of superior appendages in dorsal view with enlarged overlapping mesal flaps (Fig. 68c); no glabrous tooth on upper extremity of superior appendage. *clausum*

4'. Bases of superior appendages in dorsal view with no mesally widened flaps, their mesal edges not overlapping; a small glabrous oval tooth on upper extremity of superior appendage (Figs. 66b, 67b) 5

5(4'). Extremity of superior appendage in oblique dorsal view with distinct glabrous tooth entirely oval, about twice as long as wide, and anteriorly pointing in an oblique (45°) angle with respect to the longitudinal axis of the abdomen (Fig. 66c). No pale tubercle adjacent to posterior margin of prominence. . . . . *boreale*

5'. Extremity of superior appendage in oblique dorsal view with glabrous tooth indistinct, pointed at its mesal end, and positioned at about 90° with respect to longitudinal axis of abdomen. A pale tubercle on outer margin of prominence (Fig. 67b). . . . . *cyathigerum*

6(3'). End of superior appendage in lateral view with a pale tubercle between upper and lower arms (Figs. 63a, 64a). 7

6'. End of superior appendage in lateral view without pale tubercle between upper and lower arms. 8

7(6). In dorsolateral view, a mesally pointed black tooth on lower arm of superior appendage; upper end of tubercle as long as upper arm of superior appendage (Fig. 64b). Dorsum of abdominal segments 3-5 with posterior one-fourth black (Fig. 46) . . . . *civile*

7'. In dorsolateral view, black tooth on lower arm of superior appendage not visible, obscured by a pale tubercle; upper end of tubercle longer than upper arm of superior appendage (Fig. 63b). Dorsum of abdominal segments 3-5 with posterior 0.50 to 0.75 black (Fig. 45). . . . *carunculatum*

8(6'). In lateral view, upper and lower branches of superior appendage equal in length (Fig. 65a). . . . . . *ebrium*

8'. In lateral view, upper branch of superior appendage 2-3 times longer than ventrally-directed lower branch (Figs. 60a, 62a). 9

9(8'). In dorsolateral view, a conspicuous pale tubercle posterior to inferior branch of superior appendage (Fig. 60b); inferior branch in dorsolateral view forming a right angle (90°) to superior appendage (Fig. 60b). . . . . *anna*

9'. Inferior branch of superior appendage without tubercle (Fig. 62b); this area only pale and weakly differentiated from rest of appendage; inferior branch in dorsolateral view forming an angle of less than 90° from superior appendage (Fig. 62b) . . . . *praevarum*

10(2'). Mesostigmal plate as wide as long; the posterior margin convex posteriorly forming a semicircle (Fig. 71) . . . . *ebrium*

10'. Mesostigmal plate rectangular (Figs. 72-79), 2-3 times longer than wide; posterior margin straight, sinuate, or only slightly convex posteriorly. 11

11(10'). Dorsal thoracic carina abruptly narrows forming a contrasting ridge before ramus (Fig. 73); abdominal segment 8 entirely blue (Fig. 59) . . . . . . *clausum*

11'. Dorsal thoracic carina of uniform width along its entire length before ramus (Figs. 72, 74-79), dorsum of abdominal segment 8 usually with some black (Figs. 51-58). 12

12(11'). Lateral arms of mesostigmal plate converging anteriorly, *i.e.*, forming an acute angle with posterior arms of frame (Figs, 72, 74-76). If lateral arms of frame diverge anteriorly, then abdominal segment 8 with dorsal black spot lacking or covering primarily the posterior half to two-thirds of segment (Fig. 57), anterior pale spot on segment larger than pale area on segment 7 13

12'. Lateral arms of mesostigmal plate diverging anteriorly, *i.e.*, forming an obtuse angle with posterior arms of frame (Figs. 77-79). Dorsal black spot on segment 8 extensive, covering almost entire segment (except for some *praevarum*, but this species always has obtuse lateral arms on frame), pale areas on side small and of similar size and configuration to those on segment 7 (Figs. 54-55) 15

13(12). Posterior margin of mesostigmal plate indistinct along distal half; an indistinct circular depression occupying this area and directly posterior to raised anterior edge of plate.

Junctures of posterior and lateral arms of frame often with a pale spot (Fig. 72). . . . . *anna*

13'. Entire posterior margin of mesostigmal plate distinct, forming a furrow along distal half; anterior edge of plate may be raised, but with no broad circular depression behind it. Junctures of posterior and lateral arms of frame lacking a pale spot (Figs. 74-76) 14

14(13'). Posterior margin of mesostigmal plate distinct throughout its entire length; anterodistal margin of plate usually not raised and not forming a diagonal furrow along plate; juncture of lateral and posterior arms of frame usually not forming a distinct swollen area (Figs. 75, 76) . . . . *cyathigerum*

14'. Posterior margin of mesostigmal plate distinct only along its distal half; anterodistal margin of plate raised, forming a diagonal furrow along plate; juncture of lateral and posterior arms of frame usually forming a distinct swollen area (Fig. 74) . . . . *boreale*

15(12'). Mesostigmal plate flat, anterior distal margin often elevated slightly, giving the appearance of a broad, shallow, diagonal furrow from anterior portion of lateral arms of frame to posterodistal margin of plate. Lateral arms of ramus usually short and constricted at middle (Fig. 78) . . . . *civile*

15'. Mesostigmal plate with a prominent diagonal ridge arising from posteromesal part of plate (at juncture of lateral and posterior arms of frame) to anterodistal part of plate. A triangular to circular depression just lateral to lateral arms of frame. Lateral arms of frame not, or only very slightly, constricted (Figs. 77, 79). 16

16(15'). Posterior margin of mesostigmal plate distinct and linear. Depression at anteromesal part of plate circular or triangular (base facing anteriorly) (Fig. 79) . . . . *praevarum*

16'. Posterior margin of mesostigmal plate indistinct and sinuate. Depression at anteromesal part of plate transversely oval (Fig. 77). . . . . *carunculatum*

KEY TO FINAL INSTAR LARVAE
(See also Appendix)

1. Antennal segment 1 longer than 2, posterolateral margins of head angulate (Fig. 101) . . . . *basidens*
1'. Antennal segment 1 shorter than 2, posterolateral margins of head broadly convex (Fig. 102). 2
2(1'). Gills with intermediate areas of darkened tracheation (Fig. 92). . . . . *ebrium*
2'. Gills with tracheation of same color intensity throughout. 3
3(2'). Sternum of abdominal segment 9 without an ovipositor between lateral gonopophyses (males). 4
3'. Sternum of abdominal segment 9 with an ovipositor between lateral gonopophyses (females) (Fig. 4) 10
4(3). Cerci in posterior view with mesal margins widely divergent ventrally (Fig. 99). . . . . *clausum*
4'. Cerci in posterior view with mesal margins convergent (Figs. 93, 94), parallel, or only a little divergent ventrally (Figs. 95, 98) 5
5(4'). Cercus in dorsolateral view circular, about as long as high (Figs. 103c, 104c); dorsal surface planar or slightly concave (Figs. 103d, 104d) 6
5'. Cercus in dorsolateral view about 1.5 to 3 times longer than wide (Figs. 105c, 106c, 107c), dorsal surface strongly convex and usually with a longitudinal mesal furrow (Figs. 105d, 106d, 107d) 7
6(5). In posterior view, distal stub (=STUBHEI, Fig. 8) measured near proximal third of cercus 0.14-0.19 mm high; greatest length of cercus is along outer margin when viewed dorsally (Fig. 103c). . . . . *boreale*
6'. In posterior view, distal stub (=STUBHEI, Fig. 7) measured near proximal third of cercus 0.19-0.24 mm high; greatest length of cercus is along mesal margin when viewed dorsally (Fig. 104c) . . . . *cyathigerum*
7(5'). Ventral surface of cercus strongly concave when viewed ventrolaterally (Figs. 107b, 108b) 8
7'. Ventral surface of cercus broadly convex when viewed ventrolaterally (Figs. 105b, 106b) 9
8(7). Cercus very large and robust, 0.40-0.47 mm long dorsally (Fig. 108d) . . . . *anna*
8'. Cercus slender, 0.24-0.31 mm long dorsally (Fig. 107d) . . . . *praevarum*
9(7'). Posterior view of cercus with dorsoproximal to ventrodistal width (=DVHEIG, Fig. 7) less than ventroproximal to dorsodistal width (=LATHEIG,

Fig. 7); cercus length dorsally 0.24-0.31 mm (Figs. 95, 105d) . . . . *carunculatum*

9'. Posterior view of cercus with DVHEIG greater than LATHEIG; cercus length dorsally 0.29-0.40 mm (Figs. 97, 106d). . . . . *civile*

10(3'). Bases of cerci in dorsal view very broad, almost touching mesal margins diverging widely from base (Fig. 112d) . . . . *clausum*

10'. Bases of cerci in dorsal view separated from each other by a distance about equal to basal width of each cercus; mesal margins only slightly diverging from base (Figs. 113d, 114d). 11

11(10'). Ratio of length of ventral series of antenodal setae (XVSL, Fig. 1) to length of dorsal series of antenodal setae (XDSL, Fig. 1) of median gill 0.55 or more. 12

11'. Ratio of XVSL to XDSL of median gill 0.54 or less 13

12(11). STUBHEI (Fig. 10) of cercus in posterior view broad (0.12 mm or more); usually only a dorsal fold present . . . . *boreale*

12'. STUBHEI (Figs. 11-13) of cercus in posterior view narrow (0.06-0.12 mm), well demarcated above and below with abrupt folds . . . . *cyathigerum*

13(11'). Length of cercus dorsally 0.29 mm or longer. 14

13'. Length of cercus dorsally 0.22-0.28 mm 15

14(13). Proximal edge of cercus viewed ventrolaterally distinctly arcuate; greatest concavity measured from line drawn from proximal base of appendage to tip (=ARC, Fig. 18) 0.016 mm or more . . . . . . *civile*

14'. Cercus viewed ventrolaterally not distinctly arcuate; ARC = 0.006 mm or less . . . . *anna*

15(13'). Fourth antennal segment length 0.40 mm or less, cercus viewed ventrolaterally slightly convex, straight or only slightly arcuate; ARC = 0.008 mm or less. (Fig. 17). . . . . *carunculatum*

15'. Fourth antennal segment length 0.41 mm or more, cercus viewed ventrolaterally moderately concave; ARC = 0.006 mm or more (Fig. 19) . . . . . . *praevarum*

Enallagma anna Williamson
(Figs. 33, 42, 51, 60, 72, 90, 108, 111)

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Needham and Heywood, Handbook Drfls. N.A., p. 338 (key, ♂, ♀, Utah); Essig, 1929, Insects Western N.A., p. 145; Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:15 (Utah); Ahrens, 1938, Entomol. News, 49:16 (Utah); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1940, Pomona College J. Entomol. Zool., 32:67 (behav.); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:274 (distr. U.S.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (keys); Kormondy, 1957, J. Kans. Entomol. Soc., 30:109 (S. Dak., Wyo.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Nebr.); Donnelly, 1968, Fla. Entomol., 51:103 (diag.); Newell, 1970, Proc. Mont. Acad. Sci., 30:49 (Mont.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:4 (Wyo.); Roemhild, 1975, Dmsfls. Mont., p. 46 (key, distr. Mont); Provonsha, 1975, Great Basin Nat., 35:385 (behav., Utah); Provonsha and McCafferty, 1977, Entomol. News, 88:25 (S. Dak.); Paulson and Garrison, 1977, Pan-Pac. Entomol., 53:148 (Calif.); Bick *et al.*, 1977, Fla. Entomol., 60:159 (S. Dak., Iowa); Molnar and Lavigne, 1979, Odon. Wyo., p. 85 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Enallagma culicinorum Byers, 1927, Trans. Amer. Entomol. Soc., 53:249 (♂, diag., Utah, key); Byers, 1927, Ann. Entomol. Soc. Amer., 20: 390; Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N. Amer., p. 336 (key, ♂); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:15 (syn.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (syn.).

Male. *Head*: Dorsum black with blue triangular postocular spots between but not touching eyes and hind margin of occiput; thin mesal blue line at rear of occiput, sometimes connecting with postocular spots; rear of head pale blue; face, genae blue; postclypeus black with narrow blue margin. Anteclypeus, labrum, labium pale blue, antennae black. *Thorax*: Pronotum black with lateral blue spots; anterior lobe and hind margin of prothorax blue; prothoracic pleura and sternum light blue meeting black pronotum on sides. Pterothorax blue with black longitudinal stripes; mesal portion of mesostigmal plates and median half of mesepisterna black; antealar crests black with anterior ridge and posterior half of middorsal carina blue; black humeral stripe straight, twice as wide toward legs as near wings, and about one third width of middorsal stripe. Remainder of thorax blue except following black areas: anterior fourth of mesenfraepisternum, spot at upper end of second lateral suture, spot at posterior margin of metepimeron. Legs pale with extensor surfaces of femora black; basal black lines on exterior surfaces and basal fourth to half of flexor surfaces of tibiae; tarsi pale blue to ivory with black at joints, black spines and carinae. *Abdomen* (Fig. 42): Mostly blue above, paler at sides with following parts black: basal fourth of segment 1 dorsally and small posterolateral spots at articulation points; on 2 a dorsal transverse spot connected to apical annulus; 3 with longitudinal spot covering apical fourth, attenuate anteriorly and broadly confluent with annulus; 4 similar to 3; 5 and 6 of same configuration as 3 and 4 but spot extending to half or more segment length; entire dorsum of 7 except for basal and small distal annulus; dorsum of segment 10; segment 8-9 blue with black transverse carinae at distal annuli; superior appendage black, paler at base; inferior appendage pale, black at tip. Superior appendage (Fig. 60) in profile notched with superior arm almost as long as segment 10, tapering to blunt mesally decurved knob; lower arm small, projecting ventrally at right angle to upper arm and with pale tubercle along posterior margin seen in oblique dorsal view.

Female. Similarly but less extensively marked than male. Pale areas light brown or blue with black markings on head, thorax, and legs. *Abdomen* (Fig. 51): Segment 1 like male; following black: segment 2 with longitudinal dorsal black spot slightly constricted at middle, expanding to form lateral points at apical fourth, then narrowing again to connect with distal black annulus; segment 3 like 2 but anterior fifth of dorsal spot tapering to point, constricted near posterior fourth, expanding laterally to form points, narrowing again to connect with distal annulus; segments 4-7 similar to 3 but black wider laterally with progressive recession of pointed anterior spots so that pale brown on sides connects dorsally, annulus directly behind black transverse carinae of 7 brown; 8 pale brown with dorsal black spot widening posteriorly forming club on basal half ending there or narrowing and continuing to annulus; 9 brown with parallel dorsal black spot on anterior three-fourths; 10 with basal black annulus giving rise to longitudinal dorsal spot along entire length.

Mesostigmal plates (Fig. 72) with lateral arms of frame as long as posterior arms, forming acute 75°-80° angle. Mesostigmal plate flat with low transverse ridge from posterior corner of frame to anterodistal part of plate; anterior ridge of lamina raised toward extremity; indistinct circular depression at distal posterior area of plate behind diagonal ridge. Posterior margin of plate distinct along mesal half, becoming less so distally, curving anteriad between diagonal ridge and circular depression, then continuing in linear fashion toward side; or outer half of margin completely indistinct.

Postnodal cs.: FW ♂ 10-11, ♀ 10-13; HW ♂ 8-11, ♀ 8-10

Total length: ♂ 32-36, ♀ 33-36; Abd. ♂ 24-27, ♀ 25-28; HW ♂ 19-21, ♀ 20-22.

Larva. *Head*: Pale with slight markings on dorsum, posterolateral margin broadly convex with small patch of setae. Antennae a little longer than half the width of head, antennal segment length (mm): 0.36-0.40; 0.48-0.60; 0.80-0.84, 0.40; 0.28; 0.24-0.40; each segment darker on sides, especially on outer side of segment 2. Prementum when appressed extends to prothoracic coxae. Ratio of distal width to length of prementum 0.86-0.88; premental setae 3, marginal setae 6-11, palpal setae 5-6; apical ends of palpal lobes with 5 minute teeth with usual divided cleft followed ventrally by large, prominent tooth. *Thorax*: Pale, lateral margins of pronotum obtusely angulate, lateral and posterior margins of thoracic sclera darkened in alcoholic specimens. Legs pale with slight banding patterns at distal fourth of femora. Wing pads extend to anterior fourth of fourth abdominal segment. *Abdomen*: Pale, sprinkled with irregular setal patterns, setae larger on lateral keels but absent from segment 1. Gills short, broad, and bluntly pointed. Median gill length 4.3-5.8, greatest width 1.2-1.9. Dorsal series of antenodal setae on median gill and ventral series on lateral gill extending about two thirds gill length; respective lengths of opposite sides about 20-45% of gill length. Gills pale with darkened tracheal patterns as shown in Fig. 90. Antenodal setae: med. gill: d. 36-45 v. 9-17; lat. gill: d. 10-29, v. 52-57.

♂ superior appendage (Fig. 108) 0.40-0.47 mm long, robust, concave ventrally, approximating divided superior appendage of adult.

♀ superior appendage (Fig. 111) 0.27-0.31 mm long, pointed, with slight mesal concavity 0.003-0.006 mm in length (see ARC character in phenetics) when measured ventrolaterally. Appendage tips converge slightly when viewed dorsally.

Type data. *Enallagma anna*: holotype ♂ and allotype from Sheep Creek, Albany Co., Wyo., 23 July 1899 (*E*. B. Williamson), in University of Michigan, Ann Arbor (Examined). *E. culicinorum*: holotype ♂ from Logan River, nr. Logan City, Cache Co., Utah (J.G. Needham) in Cornell University collection, Ithaca. Examination of the type shows this specimen to be a teneral *E. anna*. No significant differences exist between the caudal appendages (Figs. 60 b, d) or maculation of the two. Byers (1927) distinguished *E. culicinorum* from *E. anna* by the presence of black on antennal segment 1. Byers described this structure as pale in *anna*, but typical *anna* from Utah also have the first antennal segment black.

Adult diagnosis. This large, robust *Enallagma* is most similar to *E. praevarum* in the form of the ♂ anal appendages. *E. anna* possesses a white tubercle on the rear margin of the lower branch of the superior appendage; no tubercle exists in *E. praevarum*. The same lower branch of *E. anna* is directed ventrad at 90° from the upper branch, while this structure is directed more caudad at less than 90° in *E. praevarum*; the superior branches of *E. praevarum* are not as long or robust as in *E. anna*. *Enallagma anna* is longer (32-36 mm) than *E. praevarum* (28-34 mm), although the mesostigmal plates are similar. The abdominal patterns are different: the black dorsal spots on segments 3, 4, and 5 cover half to more than half the length of each segment in *E. praevarum*; usually a half to only a fourth in *E. anna*.

Female *E. anna* may be distinguished with certainty only by their mesostigmal plates. They approximate those of *E. civile*, but differ in the long, acutely angled lateral arms of the frame; in *E. civile* they are shorter and generally form more of an obtuse angle (> 90°) from the posterior border of the frame. The plate is generally flat with an elevated distal anterior edge like *E. civile*; *E. anna* possesses a small (sometimes indistinct) diagonal ridge which is absent in *E. civile*. One character unique to *E. anna* is the circular depressed pits at the distal posterior margins of the plates, though in some specimens they are indistinct.

Larval diagnosis. No other sympatric male *Enallagma* (Figs. 35 - 41) has caudal appendages as long as *E. anna*. The male appendages are longer than those of male *E. civile* (*E. anna*: 0.40-0.47 mm, *E. civile*: 0.31-0.37 mm) and lack the characteristic convexity of that species (Fig. 108b). Only male *E. praevarum* (Fig. 107b) possess the distinctive concave appendages as in *E. anna*, but they are much shorter (0.24-0.27 mm).

Females also have long appendages (0.27-0.31 mm), and are matched only by specimens of *E. civile* (0.30-0.33 mm) from the Owens Valley, where the two are sympatric. Qualitatively, the cerci of *E. anna* are similar to *E. civile*; the female appendages are more concave in *E. civile* (ARC = 0.016-0.043 mm) than in *E. anna* (ARC = 0.003-0.006 mm) when viewed ventrolaterally. The measurements for *E. anna* are based on only two reared specimens, and may be more variable.

The setal pattern of the gills of *E. anna* places it in the subgroup with unequal dorsal and ventral setal lengths: *E. carunculatum*, *E. civile*, and *E. praevarum*. The gills of *E. anna* appear to be broader than any of the other three species, but are too variable to be of much diagnostic value.

Distribution (Fig. 33). *E. anna* is confined to the western United States, ranging from Montana (Newell, 1970; Roemhild, 1975) and Oregon (Paulson, pers. comm., 1983) south to Arizona and New Mexico (Williamson, 1900), west to Plumas Co., Calif. (Paulson and Garrison, 1977) and east to Colorado (Donnelly, pers. comm., 1983), and eastern South Dakota (Kormondy, 1957; Provonsha and McCafferty, 1977) and Iowa (Bick *et al.*, 1977), indicating restriction to arid, elevated desert type habitats. It occurs within the Great Basin but is absent from the lower elevations of the Sonoran and Colorado deserts and penetrates east of the Rocky Mountains only in the northern part of its range. Provonsha (1975) gives an altitudinal range in Utah from 4,200-7,000 feet.

Comments. Larval development according to Provonsha (1975) takes place only in slow running streams or rivers. My field observations support this view. The females are dichromatic and a large sample from a small stream 3 mi. S. of Wild Horse Reservoir, Elko Co., Nev., consisted of 14 blue and 25 brown morphs, suggesting a 1:2 ratio.

Material examined. 105 ♂♂, 62 ♀♀, 14 larvae (5 reared). Adults: CALIF. Inyo Co.: N. of Bishop; S. Big Pine. Lassen Co.: Eagle Lake; Hallelujah Jct., SE Doyle. Modoc Co.: Pond and ditch 1 mi. E. Likely. Plumas Co.: Bucks Lake. IDAHO. Bannock Co.: Pocatello. Elmore Co.: Snake River at Idaho Hwy. 51. Lincoln Co.: Rest area at jct. U.S. Hwy. 26 and Idaho Hwy. 75. Owyhee Co.: small stream by Idaho Hwy. 51, 1 mi. S. Riddle. Twin Falls Co.: Snake River Gorge, just W. of U.S. Hwy 93, Twin Falls. MONT. Granite Co.: Bearmouth; Nimrod Warm Springs, I-90. NEVADA. Elko Co.: Maggie Cr., E. Carlin; Wild Horse; Clover Valley, S. Wells. Lander Co.: SW Austin. Storey Co.: Reno. N. MEX. Catron Co.: Luna. Colfax Co.: Springer. S. DAK. Custer Co.: Custer St. Park. UTAH. Box Elder Co.: nr. Thiokol Corp., by Utah Hwy 83. Cache Co.: Logan River, nr. Logan City. Salt Lake Co.: N. 9600 St., between Camp Williams and Jordan R. Summit Co.: small str. 1 mi. S. Henefer. Tooele Co.: Tempe Hot Spr. at Hwy. 40. WYO. Goshen Co.: 20 mi. S. Lusk. Yellowstone Co.: Firehole R.

Larvae: CALIF. Inyo Co.: N. of Bishop. Modoc Co.: 1 mi. E. Likely. MONT. Granite Co.: Nimrod Warm Spr., I-90. UTAH. Summit Co.: small str. 1 mi. S. Henefer. Tooele Co.: Tempe Spr. at Hwy. 40.

Enallagma basidens Calvert
(Figs. 34, 43, 52, 61, 100, 101)

Enallagma basidens Calvert, 1902, Biol. Cent. Amer., p. 114 (Tex.); Needham and Cockerell, 1903, Psyche, 10:139 (N. Mex); Calvert, 1907, Biol. Cent. Amer., p. 379 (key); Tucker, 1908, Psyche, 15:98 (Tex.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:55 (cat.); Williamson, 1914, Entomol. News, 25:445 (Tex.); Kennedy, 1917, Bull. Univ. Kans., 11:135 (Kans.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:254 (key); Byers, 1928, Can. Entomol., 60:5 (larva unknown); Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N.A., p. 339 (key, ♂, ♀); Bird, 1931, Entomol. News, 42:276 (larva); Bird, 1932, Publ. Univ. Okla. Biol. Survey, 4:57 (Okla.); Ferguson, 1940, Field and Lab., 8:9 (Tex.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:277 (distr. U.S.); Ferguson, 1942, Field and Lab., 10:149 (Tex.); Ferguson, 1944, Field and Lab., 12:19 (larva); Harwell, 1951, Tex. J. Sci., 3:207 (Tex.); Bick, 1951, J. Tenn. Acad. Sci., 26:178; Bick and Bick, 1957, Southwestern Nat., 2:11 (Okla.); Westfall, 1957, Yr. Book Amer. Phil. Soc., p. 258 (rearing); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Montgomery, 1966, *in* Chandler, Natural Features of Indiana, p. 349 (distr. causes); Roback and Westfall, 1967, Trans. Amer. Entomol. Soc., 93:110 (water quality data); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Kans., Nebr.); Johnson and Westfall, 1970, Bull. Fla. St. Mus., 15:78 (keys); Johnson, 1972, Bull. Fla. St. Mus., 16:100 (key, distr. Tex.); Bick and Hornuff, 1974, Proc. Entomol. Soc. Wash., 76:91 (Colo.); Huggins *et al.*, 1976, Tech. Publ. St. Biol. Survey Kans., 1:39 (Kans.); Paulson and Garrison, 1977, Pan-Pac. Entomol., 53:149 (Calif., distr. causes); Huggins, 1978, Tech. Publ. St. Biol. Survey Kans., 6:22 (Kans.); Huggins, 1978, J. Kans. Entomol. Soc., 51:222 (redescr. larva); Donnelly, 1978, Notul. Odonatol., 1:6 (Tex.); Bick and Bick, 1978, Notul. Odonatol., 2:18 (Ariz.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Male. *Head*: Dorsum black with following areas blue: small circular postocular spots sometimes connected by transverse occipital line; small spot anteromesad of each lateral ocellus; first antennal segment; front of head and genae. Postclypeus black surrounding small blue linear spot on each side; anteclypeus blue. Rear of head, labium and mouth parts pale blue; labrum pale blue with small black spots medially at base and sides. *Thorax*: Pronotum black with usual blue lateral spots, sometimes with small blue spot on dorsum; front lobe and rim of hind lobe blue, pleura and prothoracic sternum blue to pale blue. Medial three-fourths of mesostigmal plates, medial half of mesepisternum, and antealar crests black; anterior ridge of antealar crests and middorsal carina blue, this latter line widening anteriorly toward ramus. Large black humeral stripe finely divided by blue along first thoracic suture, ending at base above mesenfraepisternum; black stripe continues basally to anterior fourth of mesenfraepisternum; remainder of pterothorax blue becoming paler ventrally. Legs pale blue or ivory with black along outer surfaces of femora, along entire surface of first and second, but confined to distal fourth of third femora. Remainder of legs pale blue to white with faint traces of black along basal flexor surfaces of tibiae; spines and joints of tarsi, tips of claws black. *Abdomen* (Fig. 43): Blue with following black parts: entire dorsum of segment 1, except apical blue annulus, small spot at lateral articulation points; entire dorsum of 2 constricted slightly in its middle, connected to apical annulus; entire dorsum of 3 and 4 with small truncate lateral projections before black apical annulus; 4 to 6 with dorsal spot tapering anteriorly so that blue meets on dorsum on anterior fifth to half of segment, confluent lateral truncate spots less conspicuous on 5 and 6; entire dorsum of 7 except basal and apical annuli; 8 and 9 entirely blue with basal small black triangular spot on 8 and lateral articulation points; dorsum of 10 black smoothly constricted near the middle; superior appendages black, inferiors white with black tips. Superior appendage (Fig. 61) in profile notched with superior arm flaring posteriorly forming truncated tip, inferior branch of superior appendage small, inconspicuous, branching ventrally at 90° angle from upper branch, forming acuminate tip directed slightly posterad. Small pale tubercle located mesoanterad of lower branch. Superior appendage about half the length of segment 10. Inferior appendage bluntly pointed with small tip directed dorsally.

Female. Pale brown or blue with head and thoracic markings similar to male. *Head*: Pale areas larger; postocular spots broadly confluent with occipital line; spots anterior to median ocelli more extensive surrounding anterior half, sometimes a pale spot anterior to median ocellus; labrum pale except for narrow black base line. *Thorax*: Similar to male but with larger prothoracic pale spots; pterothoracic black stripes smaller with divided black humeral stripes often not connecting at ends. *Abdomen* (Fig. 52): Pale with black longitudinal spots covering all to most of dorsum; usually with bluntly pointed anterior ends on segments 3-7; those same segments with spots slightly constricted near posterior fifth, then expanding laterally to pointed (segment 1-2) or rounded (segments 4-6) projections and connecting to distal black annuli; segment 7 black on dorsum, slightly tapering to rounded point anteriorly; apical annulus posterior to transverse carinae pale; segment 8 like 7 but sides of dorsal spot parallel; segment 9 with anterior triangulate spots on either side of middorsal line, their points terminating just beyond half segment length; segment 10, cerci entirely pale.

Mesostigmal plates with shallow circular depression in mesal halves; anterior margin raised to form blunt curved ridge ending about at outer fourth; a similar, more pointed projection just distad of posterior corner of frame along posterior margin of plate.

Postnodal cs.: FW ♂ 6-9, ♀ 6-8; HW ♂ 6-8, ♀ 5-7
Total length: ♂ 21-28, ♀ 21-28; Abd. ♂ 18-22, ♀ 17-22;
HW ♂ 10-15, ♀ 11-15.5.

Larva. Larva as described by Huggins (1978a), but specimens from Maricopa Co., Arizona, much paler and with usual dark contrasting body patterns pale or almost absent. Posterolateral margin of head (Fig. 101) not as sharply angulated as figured by Huggins (1978a) or as compared with specimens from eastern Texas. Gills (Fig. 100) as illustrated by Huggins (1978a) but with lighter banding patterns. Median gill length 4.6, greatest width 1.0. Antenodal setae: med. gill: d. 22-30, v. 9-11; lat. gill: d. 6-14, v. 26-31.

Type data. Holotype ♂: Corpus Christi Region?, Texas (S.F. Aaron?), Stated to be in Academy of Natural Sciences, Philadelphia (Calvert, 1908; Muttkowski, 1910), but apparently lost. I have been told that the holotype is not in the type collection nor in the general collection of that institution (D. Azuma, pers. comm., 1982).

Adult diagnosis. *E. basidens* is separated from other western Nearctic species by the pattern and venational characters stated in the key. In addition, males are the only species with a completely black dorsum on segments 1 and 2; only some males of *E. praevarum* have the dorsum of segment 2 black. The females are the only western species with the dorsum of segment 10 entirely pale; all other species possess some degree of black.

Larval diagnosis. The larva of *E. basidens* is easily separated from all other western species by two important characters: 1) antennal segment 1 is longer than segment 2 (Fig. 101); and 2) the posterolateral margins of the head are angulate (Fig. 101). The other eight western species have antennal segment 2 longer than segment 1 and the posterolateral margins of the head broadly convex (Fig. 102). Specimens from Maricopa Co., Arizona, are much paler than typical eastern specimens, and have the hind margins of the head less acutely angled, but are still easily assigned to *E. basidens*.

Distribution (Fig. 34). This species was originally described from Texas. Montgomery (1942, 1966) and Paulson and Garrison (1977) have noted that *E. basidens* has recently invaded new areas of the West, probably in response to extensive irrigation which affords suitable breeding places. From the Colorado River in Imperial Co., Calif., the species ranges east in Arizona to Maricopa and Santa Cruz Cos. and southern New Mexico (Paulson, pers. comm., 1983). East of the Rocky Mountains, it extends north to northern Colorado (Bick and Hornuff, 1974) and Nebraska (Pruess, 1967), as well as south to northern Mexico.

Material examined. 28 ♂♂, 15 ♀♀, 9 larvae. Adults: ARIZ. Cochise Co.: San Simon. Maricopa Co.: Lake Pleasant, 10 mi. W. New River; Verde River, Ft. McDowell Ind. Res. N. MEX. Eddy Co.: Black River at Rte. 396. Hildago Co.: San Simon Marshes. TEXAS. El Paso Co.: El Paso. Gonzales Co.: Plametto St. Park, S. Luling. Hildago Co.: Santa Ana Wildlife Refuge. Taylor Co.: Abilene St. Park. Williamson Co.: Taylor. MEXICO. Chihuahua: Cuidad Camargo, Rio Conchos.

Larvae: ARIZ. Maricopa Co.: Verde River, Ft. McDowell Ind. Res. TEXAS. Williamson Co.: Mustang Cr., Taylor.

Enallagma boreale Selys
(Figs. 1, 4, 8-10, 14, 35, 48, 57, 66, 74, 80, 85, 93, 103, 113)

Aenallagma boreale Selys, 1875, Entomol. Month. Mag., 11:242 (♂, ♀, White Bay, Nfld.).

Enallagma cyathigerum, race ? *boreale*; Selys, 1876, Bull. Acad. Belg., (2) 41:507 (♂, ♀, diag.).

Enallagma boreale; Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:54 (cat.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:251 (fn. syn., key); Walker, 1927, Bull. Prov. Mus. Nat. Hist., Victoria, B.C., p. 5 (B.C.); Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N.A., p. 323 (key, ♂, ♀); Bird and Rulon, 1933, Entomol. News, 44:44 (Colo.); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:14 (Utah); Buckell, 1937, Proc. Entomol. Soc. B.C., 34:57 (B.C.); Ahrens, 1938, Entomol. News, 49:15 (Idaho, Utah); Gloyd, 1938, Entomol. News, 49:199 (Admiralty Is., Alaska); Ahrens, 1938, Entomol. News, 49:227 (S. Alaska); Gloyd, 1939, Entomol. News, 50:14 (Alaska); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1940, Pomona College J. Entomol. Zool., 32:66 (Nev., behav.); La Rivers, 1941, Entomol. News, 52:41 (Nev.); Whitehouse, 1941, Amer. Midl. Nat., 26:501 (B.C.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:274 (distr. U.S.); Walker, 1943, Can. Entomol., 75:80 (distr. N. Can.); Gloyd, 1943, Occ. Pap. Mus. Zool. Univ. Mich., 479:7 (diag.); Walker, 1944, Can. Entomol., 76:234 (larva); Walker, 1947, Can. Entomol., 79:63 (N.W. Terr.); Whitehouse, 1948, Trans. Roy. Can. Inst., 27:12 (distr. Can., Alaska); Walker, 1951, Can. Entomol., 83:270 (Yuk. Terr., B.C.); Walker, 1953, Odon. Can. Alaska, p. 213 (key, descr., behav.); Gibbs, 1955, Psyche, 62:17 (♀ key, taxon.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (keys); Westfall, 1957, Yr. Book Amer. Phil. Soc., p. 258 (rearing); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:118 (phylogeny); Robert, 1963, Les Lib. du Quebec, p. 87 (keys); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Nebr., N. Dak.); Cook and Antonelli, 1969, Ann. Entomol. Soc. Amer., 62:264 (Wash.); Paulson, 1970, Pan-Pac. Entomol., 46:196 (Wash.); Newell, 1970, Proc. Mont. Acad. Sci., 30:49 (Mont.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:4 (Wyo.); Roemhild, 1975, Dmsfls. Mont., p. 41 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:386 (behav., Utah); Rivard *et al.*, 1975, Odonatologica, 4:271 (egg development); Scudder *et al.*, 1976, Syesis, 9:145 (B.C.); Bick *et al.*, 1977, Fla. Entomol., 60:159 (N.Dak., S.Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 74 (descr., key); Lebuis and Pilon, 1977, Ann. Soc. Entomol. Québec, 22:78 (biological cycle); Molnar, 1978, Cordulia, 3:141 (Wyo.); Bick and Bick, 1978, Notul. Odonatol., 1:18 (Ariz.); Bick and Bick, 1978, Odonatologica, 7:6 (wing clapping); Molnar and Lavigne, 1979, Odon. Wyo., p. 90 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Enallagma calverti Morse, 1895, Psyche, 7:208 (♂, Nev., Mass.); Williamson, 1900, Entomol. News, 11:455 (♀, Wyo.); Currie, 1901, Proc. Wash. Acad. Sci., 3:218 (♂, Alaska); Harvey, 1901, Entomol. News, 12:127 (♀); Calvert, 1902, Biol. Cent. Amer., p. 109 (N. Dak., Mont., Wash., Colo., Utah, N. Mex.); Calvert, 1903, Trans. Amer. Entomol. Soc., 29:42 (N. Mex.); Currie, 1905, Proc. Entomol. Soc. Wash., 7:18 (B.C.); Osburn, 1905, Entomol. News, 16:187 (B.C.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:55 (cat.); Williamson, 1913, Entomol. News, 24:372 (Colo.); Walker, 1913, Can. Entomol., 45:162 (larva); Kennedy, 1915, Proc. U.S. Natl. Mus., 49:325 (Ore., Wash.); Walker, 1916, Can. Entomol., 48:192 (larva, diag.); Kennedy, 1917, Proc. U.S. Natl. Mus., 52:594 (Calif., Nev.); Garman, 1917, Bull. Ill. St. Lab. Nat. Hist., 12:525 (keys, ♂, ♀, larva); Essig, 1926, Insects W. N. Amer., p. 145; Seemann, 1927, Pomona College J. Entomol. Zool., 19:14 (key, Calif.); Garman, 1927, Conn. Geol. Nat. Hist. Survey Bull., 39:65 (keys, larva, ♂, ♀); Byers, 1927, Trans. Amer. Entomol. Soc., 53:251 (fn. syn.).

Enallagma deserti boreale Jurzitza, 1975, Forma et Functio, 8:39 (syn., taxon.).

Male. Head, thorax, and legs as in *E. anna* but with black areas more extensive. Northern specimens may have thin black line along second lateral suture. Black may also cover antealar crests, thoracic carina, dorsal fourth of mesenfraepisternum, coxae, extensor and exterior surfaces of femora, and tibiae. Narrow black convex wedge on dorsum of abdominal segment 2 may form semicircle in heavily marked specimens. Abdominal patterns as described by Walker (1953) with black areas more extensive in heavily marked specimens. Segments 9 and 10 blue, occasionally with lateral small black spot just above lateral margin of terga and posteriorly at sides along transverse carinae.

Superior appendage in profile blunt, rounded, shorter than inferior appendage. Small mesal lobe present on inner ventral surface of superior appendage; upper surface of lobe pale, contrasting at juncture with appendage. Black ovaloid or kidney-shaped glabrous tooth diagonally directed above mesal lobe, anteriorly forming an acute angle from end of appendage.

Female. Pale areas blue-green, tan, or blue as in male. Abdomen (Fig. 57) as described by Walker (1953) but with following variations: black spot on segment 2 covering dorsum, broad at base, narrowing posteriorly and widening again to form diamond at posterior fourth and joining distal annulus. Heavily marked specimens with ill-defined lateral spots connecting lateral expansions of diamond. Extensive black dorsal spots of segments 4-7 often covering posterior sides of segments except for small pale spot anterior to annulus. Segment 8 variable; entirely blue to mostly black with 2 pale midlateral spots at base larger than those on segment 7. Most specimens have posterior half of segment black on dorsum, narrowing anteriorly to a middorsal point connecting to segment 7.

Mesostigmal plate (Fig. 74) with lateral arms of frames forming acute angles to posterior arms; junctures of these arms usually tumid and pronounced, expanding distally and abruptly ending at or near posterior margin of plate. Anterodistal half of plate strongly upturned, forming a prominent, well-demarcated posterior diagonal ridge or furrow, but becoming less evident mesally as anterior margin of plate narrows and becomes more planar; furrow proceeds mesoanteriorly toward anterior margin of frame.

Postnodal cs.: FW ♂ 11-14, ♀ 11-12; HW ♂ 11-14, ♀ 9-12

Total length: ♂ 29-36, ♀ 30-34; Abd. ♂ 23-28, ♀ 25-26; HW ♂ 19-21, ♀ 20-21.

Larva. Body and gills (Figs. 80 and 85) as described by Walker (1953). Median gill length 5.7-6.6, greatest width 2.1. Antenodal setae: med. gill: d. 25-34, v. 16-29; lat. gill: d. 20-33, v. 34-49.

♂ appendage (Figs. 93 and 103) flat, semicircular, longest toward their distal extremities (Fig. 103c). Dorsal surface planar or slightly concave, ventral surface often convex or nearly planar, rarely concave. In posterior view, appendage ovaloid (Fig. 93), a little wider than high. Characteristic blunt tip (= STUBHEI, see phenetics) about as thick as appendage, height at mesal third of stub 0.12-0.17 mm.

♀ appendage (Fig. 113) conical, 0.27-0.28 mm long, mesal sides straight or slightly concave. In posterior view (Figs. 9-10) cercus circular or nearly so, blunt tip (STUBHEI) higher than wide.

Type data. *Aenallagma boreale*: types presumably lost: described from 1 ♂ and 1 ♀ from White Bay, Newfoundland, 1874 (John Milne). Muttkowski (1910) states that the types are in "coll. MacLachlan, & Selys" but Kimmins (1970) does not list them in MacLachlan's collection at the British Museum (Nat. Hist.) and I did not find them in the Selys collection in Brussels. *Enallagma calverti*: lectotype ♂ by present designation: Franktown, Washoe Co., Nev., no date (S.W. Denton) in Museum of Comparative Zoology, Cambridge, Type No. 6 (of 6 ♂♂)-48. (Examined).

Adult diagnosis. Male *E. boreale* and *E. cyathigerum* are the only western Nearctic species which possess a black inverted wedge or semicircle on the posterior fourth of the dorsum of segment 2. However, some specimens of each may have this spot connected to the black distal annulus approximating the dorsal spot in other species. The superior caudal appendages of *E. boreale* are shorter than the inferiors, thus separating this species from all others except *E. cyathigerum* and *E. clausum*. *E. clausum* (Fig. 68) lacks the glabrous tooth present in the other two and they lack the mesal overlapping lobes at the base of the superiors of *E. clausum*. Males of *E. boreale* and *E. cyathigerum* can be identified with assurance only by the superior caudal appendages. I have been unable to find characters with which to separate them in the field. The mesoposterior area of the superior appendages of both species possesses a compact linear black glabrous tooth, but its shape and placement are different. In *E. boreale* (Fig. 66b), the tooth projects horizontally, forming an acute angle from the mesal margin of the appendage; in *E. cyathigerum* (Fig. 67b), it is approximately perpendicular or only slightly diagonal to the mesal margin and is at the tip of the appendage. The tooth in *E. boreale* is kidney-shaped, the sides parallel, the ends rounded. In *E. cyathigerum* the mesal end is distinctly pointed and sides divergent. A pale tubercle is present in *E.*

cyathigerum directly posterior to the glabrous tooth; no such tubercle is present in *E. boreale*. In *E. boreale*, a mesally-directed semicircular lobe lies beneath the glabrous tooth; the upper surface of the lobe usually consists of a pale area in contrast to the dark appendage. This area probably consists of specialized structures homologous to the posterior lobe in *E. cyathigerum*.

Female *E. boreale* are similar to *E. cyathigerum* and can be distinguished only by their mesostigmal plates. A distinct groove only along the distal half of the hind border of the mesostigmal plate (Fig. 74) characterizes *E. boreale*. The anterior distal half of the mesostigmal plate is strongly upturned and the juncture of the lateral and posterior arms of the frame is tumid. In *E. cyathigerum*, the posterior margin of the plate is well-defined along its entire length (Figs. 75, 76), the anterior distal half of the plate is planar, and the posterolateral junctures of the frame are not swollen.

Examination of a large number of specimens shows the shape and sculpturing of the mesostigmal plates to be highly variable. Pritchard and Smith's (1956) figures do not clearly show the diagonal furrow in *E. boreale* or the characteristic hind margin differences of the mesostigmal plates. The swollen juncture of the frame in *E. boreale* may be so great that a small anterior hollow may be present. Some *E. cyathigerum* also possess this hollow, thus the key characters given by Pritchard and Smith (1956) are not entirely satisfactory. Gibbs (1955) differentiated the females of both species by the greater acuteness of the "mesal edge of the lamina" (= lateral arm of the frame) in *E. cyathigerum*, but this character also seems too variable to be of much use.

E. boreale and *E. cyathigerum* females usually have black only on the posterior half of segment 8 (Figs. 57, 58), although an anterior middorsal stripe may separate the two anterior midlateral pale spots. *E. civile* and *E. carunculatum* usually have segment 8 with a more extensive black spot (Figs. 54, 55). *E. anna* may have the dorsum of 8 mostly black as in *E. civile* or *E. carunculatum*, or only the anterior half of the segment may be black. *E. praevarum* and *E. clausum* may have abdominal markings similar to *E. boreale* and *E. cyathigerum* and need to be differentiated by their mesostigmal plates. Neither *E. boreale* nor *E. cyathigerum* bears the distinctive pinched area of the anterior portion of the middorsal thoracic carina in *E. clausum* (Fig. 73). Some specimens of *E. boreale* and *E. cyathigerum* have obtuse lateral arms of the frame and the same type of abdominal markings as *E. praevarum*, but the diagonal furrow in *E. praevarum* (Fig. 79) extends from the posteromesal base of the frame to the anterodistal end of the plate, not from the anterior part of the frame to the distal base of the plate as in *E. boreale*.

Larval diagnosis. Larvae of *E. boreale* can be separated from all other western congeners except *E. cyathigerum* by the ventral series of antenodal setae equal to half or more the length of the dorsal series of antenodal setae on the median gill (Fig. 1). Only cerci of male *E. boreale*, *E. cyathigerum*, and *E. ebrium* are semicircular and flattened dorsally. However, the gills of *E. ebrium* (Fig. 92) have different concentrations of darkened tracheation, while the gills of the other two species are of the same intensity throughout. The appendage of male *E. boreale* is thicker than that of *E. cyathigerum*, which reflects the thicker stub height when viewed posteriorly. In the same view, the cerci of male *E. boreale* resemble boxing gloves (Fig. 93); the tip is evenly dorsoventrally convex instead of compressed to form a transverse ridge as in *E. cyathigerum* (Fig. 94).

Differentiation between female *E. boreale* and *E. cyathigerum* is difficult, even with the use of discriminant analysis, and a moderate proportion of specimens is likely to be misidentified. Cerci of ♀ *E. boreale* have a thicker stub height than do most *E. cyathigerum*, but there is an overlap in measurements. Qualitatively, the mesal margins of the cerci of *E. boreale* (Fig. 113c) when viewed dorsolaterally appear less concave than in *E. cyathigerum* (Fig. 114c). See phenetics for further discussion.

Distribution (Fig. 35). *Enallagma boreale* occurs over the entire northern United States and most of Canada and southern Alaska. In the West, it occurs in every state and has been collected in Durango, Mexico (pond 4.4 mi. NE of El Salto, 8100', 29 Aug. 1965, D. R. Paulson, FSCA). It probably occurs in other high montane areas in northern Mexico and Baja California. There are no U.S. records west of the Great Plains in the southcentral tier of states. The Great Basin affords a suitable climate for *E. boreale* but that area is apparently not preferred by *E. cyathigerum* (Fig. 39). Walker (1953:216) states that *E. boreale* and *E. cyathigerum* "for some unknown reason...do not often occur together in the same lake or pond", and I have rarely collected the two abundantly together at the same time or place. For example, at Del Puerto Canyon, Stanislaus Co., Calif., *E. boreale* is very rare, while *E. cyathigerum* is abundant; and at Zunino Reservoir north of Jiggs, Elko Co., Nevada, the reverse is true. In 1978, I encountered both species at only six of 27 localities in Nevada, Idaho, and Alberta where one or both species occurred. However, Paulson (pers. comm.) has found both species to coexist commonly at some localities in Washington. It is tempting to attribute their mostly allopatric distributions to competitive displacement. There is no quantitative evidence for interspecific copulations in the field. Indeed, it is impossible to separate males and especially females of these species in the field, so field studies will have to await refined methods of discrimination. Both species could also be sensitive to minor physical changes between habitats, resulting in their frequent mosaic distributions in montane regions.

Comments. Jurzitza (1975) considers *E. boreale* a subspecies of the Old World *E. deserti* Selys. The appendages of both forms are similar, and his scanning electron microscope photographs of the male appendages give considerable support to this view. However, *E. deserti* is poorly known and is apparently confined to the arid areas of northern Africa. Similar species have been named from Japan (*E. circulatum* Selys, *E. yezoensis* Asahina) and China (*E. strouhali* Schmidt, *E. ambiguum* Navás) and could represent a highly variable Holarctic species. Until a thorough study is conducted on the little-known Old World forms, it would be imprudent to sink *E. boreale* in favor of *E. deserti*. *E. cyathigerum* also occurs over much of Europe and Asia, and there is some confusion about its distinctness from *E. deserti*.

Material examined. 257 ♂♂, 163 ♀♀, 23 larvae (10 reared). Adults: ALASKA: Chichagof Island. CANADA: Alberta. UNITED STATES (Counties): ARIZ.: Apache, Coconino, Yavapai. CALIF.: Contra Costa, Glenn, Mendocino, Modoc, Mono, Napa, Nevada, Riverside, San Benito, San Luis Obispo, San Mateo, Shasta, Sierra, Siskiyou, Sonoma, Stanislaus, Tehama, Tuolumne. COLO.: Gunnison. IDAHO: Adams, Blaine, Bonneville, Boundary, Custer, Elmore, Latah, Lemhi, Lewis, Kootenai, Owyhee. MONT.: Flathead, Lake, Missoula, Ravalli. NEV.: Carson City, Douglas, Elko, Pershing, Washoe, White Pine. N. MEX.: Colfax, Mora. N. DAK.: Sheridan. ORE.: Deschutes, Harney, Lake. UTAH: Beaver, Servier. WYO.: Yellowstone. MEXICO (States): Durango.

Larvae. See Table 2.

Enallagma carunculatum Morse
(Figs. 16, 17, 36, 45, 54, 63, 77, 82, 87, 95, 105, 115)

Enallagma carunculatum Morse, 1895, Psyche, 7:208 (♂,Nev.); Needham, 1903, N.Y. State Mus. Bull. 68, p. 255 (larva); Currie, 1903, Proc. Entomol. Soc. Wash., 5:301 (Ariz.); Currie, 1905, Proc. Entomol. Soc. Wash., 7:18 (B.C.); Osburn, 1905, Entomol. News, 16:188 (B.C.); Muttkowski, 1910, Bull. Publ. Mus. Milwaukee, 1:56 (cat.); Williamson, 1913, Entomol. News, 24:372 (Colo.); Kennedy, 1915, Proc. U.S. Natl. Mus., 49:331 (Ore., Wash.); Kennedy, 1917, Bull. Univ. Kans., 11:136 (Kans.); Kennedy, 1917, Proc. U.S. Natl. Mus., 52:594 (Calif.); Garman, 1917, Bull. Ill. St. Lab. Nat. Hist., 12:528 (keys, ♂, ♀, larva); Needham, 1924, Pomona College J. Entomol. Zool., 16:9 (Calif.); Essig, 1926, Insects West. N.A., p. 145; Seemann, 1927, Pomona College J. Entomol. Zool., 19:14 (key, Calif.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:253 (key); Walker, 1927, Bull. Proc. Mus. Nat. Hist., Victoria, B.C., p. 6 (distr., B.C.); Garman, 1927, Conn. Geol. Nat. Hist. Survey Bull., 39:67 (keys, desc.); Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N.A., p. 335 (key, ♂, ♀, distr.); Bird, 1932, Publ. Univ. Okla. Biol. Survey, 4:56 (Okla.); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:14 (distr., Utah); Buckell, 1937, Proc. Entomol. Soc. B.C., 34:58 (distr., B.C.); Walker and Ricker, 1938, Can. Entomol., 70:148 (B.C.); Ahrens, 1938, Entomol. News, 49:16 (W. U.S., Baja Calif.); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Whitehouse, 1941, Amer. Midland Nat., 26:504 (distr. B.C.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:274 (distr. U.S.); Whitehouse, 1948, Trans. Roy. Can. Inst., 27:14 (distr. Can.); Walker, 1953, Odon. Can. Alaska, p. 200 (♂, ♀, larva, keys, distr. B.C., Sask., Man.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (key); Bick and Bick, 1957, Southwestern Nat., 2:11 (Okla.); Kormondy, 1957, J. Kans. Entomol. Soc., 30: 109 (Nebr.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:118 (phylogeny); Robert, 1963, Les Lib. du Québec, p. 84 (keys); Roback and Westfall, 1967, Trans. Amer. Entomol. Soc., 93:110 (water quality data); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Kans., Nebr.); Cook and Antonelli, 1969, Ann. Entomol. Soc. Amer., 62:264 (Wash.); Paulson, 1970, Pan-Pac. Entomol., 46:196 (Wash.); Newell, 1970, Proc. Mont. Acad. Sci. 30:49 (Mont.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo., S. Dak.); Johnson, 1972, Bull. Fla. St. Mus. Biol Sci., 16:94 (key, Tex.); Roemhild, 1975, Dmsfls. Mont., pp. 39, 42 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:386 (distr., Utah); Scudder *et al.*, 1976, Syesis, 9:146 (B.C.); Huggins *et al.*, 1976, Tech. Pub. St. Biol. Survey Kans., 1:39 (Kans.); Bick *et al.*, 1977, Fla. Entomol., 60:159 (N. Dak., S. Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 76 (keys, ♂, ♀, larva); Bick and Bick, 1978, Odonatologica, 7:6 (wing clapping); Molnar and Lavigne, 1979, Odon. Wyo., p. 92 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Walker (1953) provides an excellent description of the adults and larva of this species.

Male. Head and thoracic pattern the same as *E. anna* and *E. boreale*, but blue often with a slightly green cast. Abdominal pattern (Fig. 45) with more black than in species described above. Black on dorsum of abdominal segments 3-8 often 0.50 to 0.75 length of each segment, though one specimen from Maricopa Co., Ariz. (10 mi. W. New River, Lake Pleasant) has black on segments 3-5 occupying basal 0.25 of each segment. Superior appendage (Fig. 63) forked with dorsal and ventral arms equal in lateral view, housing pale tubercle between arms. Tubercle extends beyond dorsal arm when viewed dorsoventrally (Fig. 63b). Some specimens with ventral tooth projecting mesally beside pale tubercle as in Fig. 64b for *E. civile*.

Female. Head and body as in male, abdominal pattern (Fig. 54) as described by Walker (1953). Black areas on abdominal segments successively more extensive posteriorly, sides often parallel and bluntly accuminate at anterior extremities. Dorsal black spot covering anterior 0.50 to 0.75 of abdominal segment 1, segment 8 with black covering all or most of dorsum.

Mesostigmal plates (Fig. 77) variable but always with a transverse diagonal ridge extending from anterior distal edge of plate to juncture of lateral and posterior arms of ramus. Transverse oval depression occupying mesal half of plate, bordered anteriorly and posteriorly by anterior rim of plate and transverse diagonal ridge, respectively. Anterior distal half of plate abruptly raised often with ill-defined depression behind it. Lateral arms of ramus about 0.5 as long as posterior arms, forming obtuse angle with posterior arms. Posterior margin of plate ill-defined, often a furrow following diagonal ridge extending anteriorly to middle of plate, then veering posteriorly to distal end of plate.

Postnodal cs.: FW ♂ 10-12, ♀ 9-10; HW ♂ 9-10, ♀ 8-9

Total length: ♂ 26-35, ♀ 30-35; Abd. ♂ 19-26, ♀ 21-27; HW ♂ 14-20, ♀ 16-20.

Larva. Body and gills (Figs. 82, 87) as described by Walker (1953). Median gill length 5.4-7.0, greatest width 2.0. Antenodal setae: med. gill: d. 20-36, v. 5-16; lat. gill: d. 4-16, v. 27-45.

♂ appendage (Figs. 95 and 105) about 1.5 times longer than high, outer side evenly convex, inner side with longitudinal furrow best seen in dorsal view. Cercus tapers slightly posteriorly. In posterior view, cercus roughly circular with inner concavity.

♀ appendage (Fig. 115) conical, 0.23-0.30 mm long, mesal margins of cercus in ventrolateral view barely, if at all, arcuate (Fig. 17) and sometimes slightly convex.

Type data. *Enallagma carunculatum*: lectotype ♂ by present designation: Franktown, Washoe Co., Nev., no date (S.W. Denton), in Museum of Comparative Zoology, Cambridge, Type No. 3 (of 8 ♂♂)-49 (Examined).

Adult diagnosis. *E. carunculatum* has heavy black markings similar to *E. praevarum* (Figs. 44, 45) and appendages similar to *E. civile* (Figs. 63, 64). Male *E. carunculatum* possess a majority of black on abdominal segments 3-8 as in *E. praevarum*, but their abdominal appendages are different. *E. praevarum* does not have the pale tubercle present in *E. carunculatum*. From *E. civile*, *E. carunculatum* can be distinguished by its smaller size. (*E. carunculatum*: 26-35 mm, *E. civile*: 30-38 mm) and the amount of black on abdominal segments 3-8. *E. civile* possesses black on the posterior 0.25 of each segment compared to 0.50 to 0.75 for *E. carunculatum*. The superior appendages of *E. carunculatum* and *E. civile* are similar, but the upper branch is shorter in *E. carunculatum*, so the pale tubercle surpasses the appendage tips (Fig. 63b). In *E. civile*, the upper branch of the superior appendage is longer than the inferior branch, and the pale tubercle does not surpass the upper branch.

Female *E. carunculatum* are similar to female *E. praevarum*, and both species can be identified only by the mesostigmal plates. Johnson (1972) distinguished the two species by the shape of the mesostigmal depression: in *E. carunculatum*, it is transversely oval, while it is circular in *E. praevarum*. I have found this character to be fallible as there is overlap in the depression shapes. Most *E. praevarum* possess a distinctly inverted triangular depression (Fig. 79). The posterior margin of the mesostigmal plate in *E. praevarum* is well-defined and straight, not sinuate and indistinct as in *E. carunculatum*. This character is more reliable than the depression shapes. Johnson's (1972) outline drawings (Figs. 15L and 18F) show the straight *vs.* sinuate margins accurately.

Larval diagnosis. Male larvae have cerci similar to *E. civile*, but shorter (*E. carunculatum*: 0.28-0.31 mm; *E. civile*: 0.31-0.37 mm). Viewed posteriorly, the appendages of *E. carunculatum* (Fig. 95) are more circular than *E. civile* (Fig. 97). The appendages of *E. civile* are dorsoventrally higher than wide (DVHEIG > LATHEIG), whereas the opposite is true for *E. carunculatum*. The caudal appendages of *E. civile* extend posterodorsally while they extend only posteriorly in *E. carunculatum*.

Female appendages are similar to *E. praevarum*, but the mesal margin of the cercus is only slightly arcuate or even convex (0-0.008 mm, Fig. 17) compared to *E. praevarum* (> 0.006 mm, Fig. 19). The length of antennal segment 4 is less ($\leq$0.40) than for *E. praevarum* (0.41-0.48 mm), or for *E. civile* (0.42-0.58 mm).

The key characters given by Walker (1953) and Cannings and Stuart (1977) (Fig. 22) will not adequately distinguish these two species.

Distribution (Fig. 36). *E. carunculatum* occurs in every state west of the Rocky Mountains, but is apparently rare in southern Arizona, New Mexico, and absent in Texas. Ahrens (1938) mentions "specimens taken frequently through western United States and Baja California", but I have not seen any specimens from south of the U.S. border. The absence of specimens from Alberta is probably because collecting has not been done there.

Material examined. 275 ♂♂, 173 ♀♀, 36 larvae (14 reared). Adults: UNITED STATES (Counties): ARIZ.: Coconino, Maricopa. CALIF.: Alameda, Butte, Calaveras, Colusa, Contra Costa, El Dorado, Fresno, Glenn, Inyo, Lassen, Los Angeles, Madera, Marin, Merced, Modoc, Mono, Napa, Nevada, Riverside, Sacramento, San Bernardino, San Diego, San Joaquin, San Luis Obispo, Santa Barbara, Shasta, Sierra, Siskiyou, Solano, Stanislaus, Yolo. COLO.: Gunnison, Larimer, Mesa, Moffatt, Weld. IDAHO: Ada, Boundary, Elmore, Kootenai, Lemhi, Letah, Oneida, Owyhee, Twin Falls. MONT.: Big Horn, Carter, Lake, Missoula. NEB.: Lincoln. NEV.: Churchill, Douglas, Elko, Humboldt, Lyon, Pershing, Washoe. N. MEX,: Colfax. ORE.: Benton, Harney, Lake, Lane. S. DAK.: Pennington, Roberts, Yankton. UTAH: Boxelder, Kane, Salt Lake, Weber.

Larvae. See Table 2.

Enallagma civile (Hagen)

(Figs. 5, 15, 18, 37, 46, 55, 64, 78, 83, 88, 97, 106, 116)

Agrion civile Hagen, 1861, Syn. Neur. N.A., p. 88 (♂,♀,Wash., Tex., Mex.).

Enallagma civile; Selys, 1876, Bull. Acad. Belg., (2) 41:514 (descr., Calif.); Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Williamson, 1900, Entomol. News, 11:455 (Wyo.); Calvert, 1902, Biol. Cent. Amer., p. 110 (Colo., N. Mex., Tex.); Currie, 1903, Proc. Entomol. Soc. Wash., 7:301 (Ariz.); Needham and Cockerell, 1903, Psyche, 10:137 (larva); Calvert, 1907, Biol. Cent. Amer., p. 380; Muttkowski, 1908, Bull. Wisc. Nat. Hist. Soc., 6:74 (key); Tucker, 1908, Psyche, 15:98 (Tex.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:56 (cat.); Woodworth, 1913, Guide Insects Calif., p. 333 (Calif.); Williamson, 1913, Entomol. News, 24:372 (Colo.); Williamson, 1914, Entomol. News, 25:225 (Ariz.); Williamson, 1914, Entomol. News, 25:445 (Tex., Okla.); Garman, 1917, Bull. Ill. St. Lab. Nat. Hist., 12:518 (keys, ♂, ♀, larva); Kennedy, 1917, Bull. Univ. Kans., 11:136 (distr. Kans.); Essig, 1926, Insects West. N.A., p. 145; Byers, 1927, Trans. Amer. Entomol. Soc., 53:254 (key); Byers, 1929, *in* Needham and Heywood, Drfls. N.A., p. 318 (key, ♂, ♀, distr.); Bird, 1932, Publ. Univ. Okla. Biol. Survey, 4:57 (Okla.); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291: 15 (distr. Utah); Ahrens, 1938, Entomol. News, 49:16 (distr.); Ferguson, 1940, Field and Lab., 8:9 (Tex.); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Ferguson, 1942, Field and Lab., 10:149 (Tex.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:273 (distr. U.S.); Whitehouse, 1948, Trans. Roy. Can. Inst., 27:14 (distr. Can.); Harwell, 1951, Tex. J. Sci., 3:207 (Tex.); Walker, 1953, Odon. Can. and Alaska, p. 205 (♂, ♀, larva, keys, distr. Sask., Man.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (key); Bick and Bick, 1957, Southwestern Nat., 2:11 (Okla.); Kormondy, 1957, J. Kans. Entomol. Soc., 30:109 (Nebr.); Westfall, 1957, Yr. Book Amer. Phil. Soc., p. 258 (rearing); Gloyd, 1958, Occ. Pap. Mus. Zool. Univ. Mich., 593:21 (W. Tex.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Bick and Bick, 1963, Southwestern Nat., 8:57 (population dynamics); Bick, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:110 (reproductive behav.); Johnson, 1964, Amer. Midl. Nat., 72:408 (polymorphism); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Kans., N. Dak., Nebr.); Johnson and Westfall, 1970, Bull. Fla. St. Mus. Biol. Sci., 15:78 (key); Newell, 1970, Proc. Montana Acad. Sci., 30:49 (Montana); Johnson, 1972, Bull. Fla. St. Mus. Biol. Sci., 16:100 (key, distr. Tex.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo.); Roemhild, 1975, Dmsfls. of Mont., p. 43 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:386 (distr. Utah); Scudder *et al.*, 1976, Syesis, 9:146 (B.C.); Huggins *et al.*, 1976, Tech. Pub. St. Biol. Survey Kans., 1:39 (Kans.); Paulson and Garrison, 1977, Pan-Pac. Entomol., 53:149 (distr. Calif.); Bick *et al.*, 1977, Fla. Entomol., 60:159 (N.Dak., S.Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 78 (keys, descr.); Donnelly, 1978, Notul. Odonatol., 1:6 (Tex.); Molnar and Lavigne, 1979, p. 94 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Enallagma civile plebeium Selys 1876, Bull. Acad. Belg., (2) 41, p. 515 (Putla, Oaxaca, Mex.); Calvert, 1902, Biol Cent. Amer., p. 110 (syn.).

Enallagma civile race? *simile* Selys 1876, Bull. Acad. Belg., (2) 41, p. 515 (Merida and St. Urban (Colombia) and Bogota) NEW SYNONYMY.

Agrion canadense Provancher, 1876, Nat. Can., 8:325; Provancher, 1878, Nat. Can., 10:127 (syn.); Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:56 (cat.).

Male. Head and thoracic patterns the same as in other species. Abdominal pattern (Fig. 46) with black spots covering the posterior 0.25 of abdominal segments 2-5, black on 6 and 7 more extensive, covering basal 0.50 to 0.80 of each segment. Superior appendage (Fig. 64) forked, upper branch longer than ventral branch, enclosing pale tubercle. In dorsolateral view, tubercle not extending beyond upper branch of superior appendage. Ventral branch of superior appendage with black tooth projecting mesally through pale tubercle (Fig. 64b).

Female. Head and body as in male, abdominal pattern (Fig. 55), next to *E. ebrium*, with most extensive black markings. Black abdominal pattern similar to female *E. carunculatum*; segment 8 with black covering almost entire dorsum, except for small anterior midlateral pale spots.

Mesostigmal plate (Fig. 78) planar, about twice as long as wide. Lateral arms of frame short, usually constricted at midpoints, forming an obtuse angle with posterior arms. Mesostigmal plate rectangular with anterior distal portion slightly elevated, giving appearance of a diagonal furrow from anterior portion of ramus to posterodistal portion of plate. Hind margin of plate with well-defined border.

Postnodal cs.: FW ♂ 10-12, ♀ 10-11; HW ♂ 9-10, ♀ 8-11

Total length: ♂ 30-38, ♀ 31-34; Abd. ♂ 24-29, ♀ 24-26; HW ♂ 16-21, ♀ 18-20.

Larva. Body and gills (Figs. 83 and 88) as described by Walker (1953). Median gill length 5.7-7.4, greatest width 2.1. Antenodal setae: med. gill: d. 21-32, v. 5-14; lat. gill: d. 5-15, v. 32-49.

♂ appendage (Figs. 97, 106) about twice as long as high, ventral side strongly convex, inner side with a longitudinal furrow similar to *E. carunculatum*. Cercus extends dorsoventrally so that in posterior view, appendage is dorsoventrally higher than wide (DVHEIG > LATHEIG). Cercus in posterior view with a median concavity at base so that extremity of cercus is kidney-shaped. Mesal bases of cerci convergent ventrally, ventromedial portion of cercus in posterior view often forming a mesal lobe.

♀ appendage (Fig. 116) conical, 0.29-0.35 mm long, mesal margin of cercus in ventrolateral view strongly (0.016-0.034 mm) arcuate (Fig. 18).

Type data. *Agrion civile*: lectotype ♂ by present designation: "Pecos River, Texas [now thought to be near Roswell, Chaves Co., N. Mex. (Needham and Cockerell, 1903)], Aug. 17" no year (J. Pope), in Museum of Comparative Zoology, Cambridge, Type No. 14 (of 20 specimens from N.Y., Md., Washington, D.C., Tex., and Mexico)-1676 (examined). *E. civile plebeium*: Lectotype ♂ (of 5 males) by present designation: "Putla (Mexique du Pacifique)", in Institut Royal des Sciences Naturelles de Belgique, Brussels (examined). *E. civile* race? *simile*: lectotype ♂ by present designation: "Merida" (Colombia?), no date, in Museum of Comparative Zoology, Cambridge, Type No. 2-12277 (examined). I can see no appreciable differences between *E. simile* and typical *E. civile* and believe them to be synonyms. *Agrion canadense*: Type not in Provancher collection, Université Laval, Québec, and presumed lost (J.M. Perron, pers. comm., 1982). Even though the type of *A. canadense* is lost, Provancher's (1876) description clearly shows that he described a young specimen of *Agrion iners* Hagen [=*Ischnura ramburi* (Selys)] or *Ischnura verticalis* (Say).

Adult diagnosis. Male *E. civile* possess the least amount of black of all western Nearctic species (Fig. 46). The caudal appendages are similar only to *E. carunculatum* and are diagnosed under that species.

Female *E. civile* are easily distinguished from *E. carunculatum* by the characters stated in the key. The mesostigmal plates are similar to those of *E. anna*, and the two species are diagnosed under that species.

Larval diagnosis. See diagnoses for *E. carunculatum* males and *E. anna* females, and phenetics for further discussion.

Distribution (Fig. 37). *E. civile* is primarily a southern species. It occurs from Colombia and Venezuela north to southern Canada, but is absent from the northwestern United States. As mentioned earlier, *E. civile* has apparently extended its range into California within the past 70 years. The captures from western Montana (Roemhild, 1975) and British Columbia (Scudder *et al.*, 1976; Cannings and Stuart, 1977) are far from other localities and probably represent a recent invasion into those areas.

Material examined. 347 ♂♂, 150 ♀♀, 28 larvae (19 reared). Adults: UNITED STATES (Counties): ARIZ.: Cochise, Maricopa, Pima, Pinal, Santa Cruz, Yavapai, Yuma. CALIF.: Butte, Contra Costa, Fresno, Glenn, Imperial, Inyo, Kern, Los Angeles, Marin, Merced, Napa, Orange, Riverside, Sacramento, San Benito, San Bernardino, San Diego, San Joaquin, Santa Barbara, Solano, Stanislaus, Sutter, Tulare, Ventura, Yolo. COLO.: Huerfano, Larimer, Logan, Mesa, Morgan, Prowers, Weld. KANS.: Douglas, Scott. NEV.: Clark. N. MEX.: Bernalillo, Colfax, Eddy, Hildago, Mora, Otero, Quey. OKLA.: Cimarron. S. DAK.: Roberts. TEX.: Bexar, Brewster, Caldwell, El Paso, Hildago, Nueces, Presidio, Real, Travis. UTAH: Kane, Washington. MEXICO (States): Coahuilla, Jalisco, Sinaloa.

Larvae. See Table 2.

Enallagma clausum Morse
(Figs. 38, 50, 59, 68, 73, 91, 99, 109, 112)

Enallagma clausum Morse, 1895, Psyche, 7:209 (Nev.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:56 (cat.); Williamson, 1913, Entomol. News, 24:372 (Colo.); Kennedy, 1915, Proc. U.S. Natl. Mus., 49:341 (Wash.); Kennedy, 1915, Ann. Entomol. Soc. Amer., 8:299 (behav., Nev.); Kennedy, 1917, Bull. Univ. Kans., 11:136 (distr. Kans.); Kennedy, 1917, Proc. U.S. Natl. Mus., 52:619 (behav., Nev.); Essig, 1926, Insects West. N.A., p. 145 (Nev.); Walker, 1927, Bull. Prov. Mus. Nat. Hist., Victoria, B.C., p. 6 (distr. B.C.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:253 (key); Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N.A., p. 324 (keys, ♂, ♀, distr.); Bird and Rulon, 1933, Entomol. News, 44:44 (Colo.); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:14 (distr. Utah); Buckell, 1937, Proc. Entomol. Soc. B.C., 34:58 (distr. B.C.); Ahrens, 1938, Entomol. News, 49:15 (Utah); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Whitehouse, 1941, Amer. Midl. Nat., 26:501 (distr. B.C.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:274 (distr. U.S.); Walker, 1944, Can. Entomol., 76:234 (larva); La Rivers, 1946, Entomol. News, 57:214 (behav., Nev.); Whitehouse, 1948, Trans. Roy. Can. Inst., 27:12 (distr. Can.); Walker, 1953, Odon. Can. and Alaska, p. 209 (key, descr., behav.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (key); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Robert, 1963, Les Lib. du Québec, pp. 88, 94 (keys); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Kans., N.Dak., Nebr.); Paulson, 1970, Pan-Pac. Entomol., 46:196 (Wash.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo.); Provonsha, 1975, Great Basin Nat., 35:387 (distr. Utah); Scudder *et al.*, 1976, Syesis, 9:146 (B.C.); Huggins *et al.*, 1976, Tech. Pub. St. Biol. Survey Kans., 1:42 (questions occurrence in Kans.); Paulson and Garrison, 1977, Pan-Pac. Entomol., 53:149

(distr.); Bick *et al.*, 1977, Fla. Entomol., 60:159 (N.Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 79 (keys, descr.); Molnar and Lavigne, 1979, Odon. Wyo., p. 96 (distr. Wyo.).

Male. Head and thorax with same patterns as other western Nearctic *Enallagma*. Abdominal pattern (Fig. 50) virtually identical to *E. boreale* and *E. cyathigerum*. Black spots on abdominal segments 2-5 cover 0.25 to 0.50 of each segment. Black on segments 6-7 more extensive, covering distal 0.75 of dorsum, anterior ends of spots broadly or pointedly convex. Superior appendage (Fig. 68) shorter than inferior appendage, in profile sloping to a small, upturned point. In dorsal view, superior appendage very broad at base, with overlapping mesal plates. Remainder of appendage strongly divergent from base. Dorsal surface of superior appendage bare with no black glabrous tooth as in *E. boreale* and *E. cyathigerum*.

Female. Pale areas blue or tan. Head, thorax, and legs as in male. Abdominal pattern (Fig. 59) similar to those of *E. boreale* and *E. cyathigerum*. Black dorsal spot on segment 2 may be small and isolated, occupying distal half of segment, or narrow black stripe may proceed anteriorly from spot to posterior of segment 1. Spots on segments 3-6 with usual inflated longitudinal black spots, but not extending as far laterally as in *E. boreale* and *E. cyathigerum*. Segment 8 entirely pale or with just a touch of black. Black spots on segments 9 and 10 small and usually confined to basal 0.50 to 0.75 though occasionally occupying entire dorsum of each segment.

Mesostigmal plates (Fig. 73) planar, with defined posterior margin. Base of middorsal thoracic carina abruptly constricted and raised before ramus, thereby advancing mesal areas of plates slightly.

Postnodal cs.: FW ♂ 9-12, ♀ 10-12; HW ♂ 8-10, ♀ 8-10

Total length: ♂ 28-37, ♀ 31-36.5; Abd. ♂ 22-28, ♀ 24-28; HW ♂ 16-22, ♀ 19-22.

Larva. Body and gills (Fig. 91) as described by Walker (1944, 1953), except that gills may be entirely pale as in *E. boreale* and *E. cyathigerum*. Median gill length 5.5-5.9, greatest width 1.9. Antenodal setae: med. gill: d. 28-33, v. 10-19; lat. gill: d. 11-17, v. 37-47.

♂ appendage (Figs. 99 and 109) blunt, broad at base, about twice as wide at base as long. In posterior view, cerci almost touch at base, but mesal sides widely divergent ventrally. In posterior view, tips of cerci depressed dorsoventrally (in diagonal direction), forming stub with parallel sides.

♀ appendage (Fig. 112) conical, with broad base as in male, but in dorsal view, mesal sides concave, not straight as in males. Base of cercus at least twice as wide as long. In posterior view, cerci almost meet at dorsal mesal edges; distances between them about 0.25 or less width of cercus.

Type data. *Enallagma clausum*: lectotype ♂ by present designation: Franktown, Washoe Co., Nev., no date (S.W. Denton), in Museum of Comparative Zoology, Cambridge, Type No. 3 (of 4 ♂♂)-50 (examined).

Adult Diagnosis. Male *E. clausum* are easily distinguished by their unique caudal appendages. This is the only species in which mesal margins of the cerci overlap. In profile, the appendages are most similar to those of *E. cyathigerum*, but *E. clausum* lacks the black, glabrous tooth present in that species (Figs. 67b, 68b).

Color patterns for female *E. clausum* can only be confused with some females of *E. boreale* and *E. cyathigerum*. While all other species have some degree of black on the dorsum of segment 8, *E. clausum* almost always has segment 8 entirely pale. Some specimens of *E. boreale* and *E. cyathigerum* occasionally have segment 8 immaculate, but they may be distinguished by their mesostigmal plates. *E. clausum* is unique in possessing an elevated, constricted area at the base of the middorsal thoracic carina (Fig. 73).

Larval diagnosis. Walker (1953) differentiated larvae of *E. clausum* from those of *E. boreale* and *E. cyathigerum* by their different ratios of dorsal and ventral antenodal setal distances in the gills and by the relative lengths of the cerci. The following characters are better in discriminating between these species:

Viewed posteriorly, the cerci of male *E. clausum* are widely divergent ventrally (Fig. 99). Males of all other species have their mesal borders convergent, parallel, or only slightly divergent (Figs. 93-98). This condition reflects the broad, overlapping mesal flaps found in the adult male.

In the female, the cerci also have very broad bases, and their mesal edges almost meet. Only some female *E. cyathigerum* approach this condition, but the base of the cercus in that species is not as broad. When viewed dorsally, the mesal edges of the cerci of *E. clausum* are broadly concave (Fig. 112d), while in *E. cyathigerum*, the margin is straight and/or convex basally (Fig. 114d).

The larval diagnoses are based on two reared males and one reared female, and while the sample size is small, the characters are distinct enough to allow easy identification.

Distribution (Fig. 38). *E. clausum* occurs primarily in the Great Basin, but extends east to Ontario and Quebec (Walker, 1953). In Saskatchewan, it occurs as far north as 55°N. The species is most commonly encountered about stagnant alkali water areas in the Great Basin. The specimens reported from southwestern Kansas (Kennedy, 1917) could not be confirmed by Huggins *et al.* (1976). The species may occur in northern Arizona and New Mexico, where few collections have been made.

Material examined. 110 ♂♂, 62 ♀♀, 3 larvae (reared). Adults: CALIF. Inyo Co.: Lone Pine; Dirty Sock Mineral Spgs., 5.1 mi. NE Olancha. Lassen Co.: Spauldings. Modoc Co.: Tule Lake Refuge, 2 mi. S. of HQ, 4000 ft. Mono Co.: Topaz Lake, 5050 ft. IDAHO. Elmore Co.: Snake River at Idaho Hwy. 51. NEV. Elko Co.: Wild Horse Reservoir, lower end, by Nev. Hwy. 43. Humboldt Co.: Humboldt River at Golconda. Pershing Co.: 22 mi. NE Lovelock; Humboldt River at Lovelock, 3297 ft.; Rye Patch Dam at Rye Patch Reservoir, N. of I-80, 4000 ft. Washoe Co.: Truckee River, 4 mi. S. Nixon. N. DAK. Ramsey Co.: Devil's Lake. S. DAK. Roberts Co.: Lake Traverse, 12 mi. SE Sisseton. N. MEX. Mora Co.: 2.4 mi. S. Ft. Union. ORE. Lake Co.: Lake Abert. WASH. Grant Co.: Soap Lake. UTAH. Weber Co.: pond 5.6 mi. W. jct. I-80 and Utah Hwy. 39, W. Ogden.

Larvae. NEV. Pershing Co., *ab. ovum* from ♀, Rye Patch Dam at Rye Patch Reservoir, N. of I-80, 4000 ft.

Enallagma cyathigerum (Charpentier)
(Figs. 6, 7, 11-13, 39, 49, 58, 67, 69, 70, 75, 76, 81, 86, 94, 104, 114)

Agrion hastulatum; Stephens, 1836 (*nec* Charpentier, 1825), Ill. Brit. Entomol. Mand., 6:73.

Agrion cyathigerum Charpentier, 1840, Lib. Eur., p. 163; Selys, 1850, Rev. Odon., p. 205 (descr.).

Enallagma cyathigerum; Selys, 1876, Bull. Acad. Belg., (2) 41:503 (descr.); Kirby, 1890, Syn. Cat. Neur. Odon., p. 145 (cat.); Lucas, 1900, Brit. Drfls., p. 297 (♂, ♀, larva); Williamson, 1902, Proc. Ind. Acad. Sci., p. 121 (syn. *calverti*, Wyo.); Calvert, 1902, Biol. Cent. Amer., p. 108 (descr., N.Dak., S.Dak., Mont., B.C., Wash., Utah, N. Mex.); Currie, 1905, Proc. Entomol. Soc. Wash., 8:17 (B.C.); Osburn, 1905, Entomol. News, 16:187 (B.C.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:57 (cat.); Woodworth, 1913, Guide Insects Calif., p. 333 (Calif.); Kennedy, 1915, Proc. U.S. Natl. Mus., 49:325 (Ore., Wash.); Walker, 1916, Can. Entomol., 48:192 (larva); Kennedy, 1917, Proc. U.S. Natl. Mus., 52:594 (Calif.); Garman, 1917, Bull. Ill. St. Lab. Nat. Hist., 12:534 (keys, ♂, ♀, larva); Essig, 1926, Insects West. N.A., p. 145; Garman, 1927, Conn. Geol. Nat. Hist. Survey Bull., 39:70 (keys, ♂, ♀, larva); Seemann, 1927, Pomona College J. Entomol. Zool., 19:14 (keys, Calif.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:251 (fn., keys); Walker, 1927, Bull. Prov. Mus. Nat. Hist., Victoria, B.C., p. 6 (B.C.); Byers, 1929, *in* Needham and Heywood, Drfls. N.A., p. 324 (key, ♂, ♀); Lucas, 1930, Aquatic Stages Brit. Drfls., p. 127 (larva); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:14 (Utah); Buckell, 1937, Proc. Entomol. Soc. B.C., 34:58 (B.C.); Longfield, 1937, Drfls. British Isles, p. 203 (descr.); Walker and Ricker, 1938, Can. Entomol., 70:148 (B.C.); Gloyd, 1938, Entomol. News, 49:200 (Admiralty Is., Alaska); Ahrens, 1938, Entomol. News, 49:15 (Calif., N. Mex.); Ahrens, 1938, Entomol. News, 49:227 (S. Alaska); Gloyd, 1939, Entomol. News, 50:14 (Alaska); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Whitehouse, 1941, Amer. Midl. Nat., 26:502 (distr. B.C.); Montgomery, 1942, Proc. Ind. Acad. Sci., 51:273 (distr. U.S., Can., Old World); Valle, 1942, Ann. Entomologici Fennici, 8:165 (Wyo.); Walker, 1943, Can. Entomol., 75:80 (distr. N. Can.); Gloyd, 1943, Occ. Pap. Mus. Zool. Univ. Mich., 479:7 (diag.); Walker, 1944, Can. Entomol., 76:233 (larva); Walker, 1947, Can. Entomol., 79:63 (N.W. Terr.); Whitehouse, 1948, Trans. Roy. Canad. Inst., 27:12 (distr. Can., Alaska); MacNeill, 1950, Entomol. Mon. Mag., 86:234 (larva); Walker, 1951, Can. Entomol., 83:271 (Yuk. Terr.); Walker, 1953, Odon. Can. Alaska, p. 217 (key, descr., behav.); Gibbs, 1955, Psyche, 62:17 (♀ key, diag.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 149 (keys); Kormondy, 1959, Pan-Pac. Entomol., 35:98 (Calif.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Robert, 1963, Les Lib.

du Québec, p. 88 (keys); Roback and Westfall, 1967, Trans. Amer. Entomol. Soc., 93:110 (Calif.); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Nebr., N.Dak.); Aguesse, 1968, Les Odonates de l'Europe Occidentale, p. 102 (keys, descr.); Paulson, 1970, Pan-Pac. Entomol., 46:196 (Wash.); Newell, 1970, Proc. Montana Acad. Sci., 30:49 (Mont.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo.); Macan, 1974, Odonatologica, 3:118 (larval phenology); Jurzitza, 1975, Forma et Functio, 8:36 (morph. ♂ app., mesostig. lam. ♂ and ♀); Roemhild, 1975, Dmsfls. of Mont., p. 39 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:387 (distr. Utah); Scudder *et al.*, 1976, Syesis, 9:146 (B.C.); Parr, 1976, Odonatologica, 5:45 (population biology); Bick *et al.*, 1977, Fla. Entomol., 60:160 (N.Dak., S.Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 81 (descr., keys); Hammond, 1977, Drfls. Gr. Britain, Ireland, p. 66 (keys); Molnar, 1978, Cordulia, 3:141 (Wyo.); Garrison, 1978, Odonatologica, 7:223 (population dynamics); Bick and Bick, 1978, Notul. Odonatol., 1:18 (Ariz., Colo.); Molnar and Lavigne, 1979, p. 98 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography); Doerksen, 1980, Odonatologica, 9:293 (reproductive behavior); Miller and Miller, 1981, Odonatologica, 10:201 (morphology and structure of ♂ genitalia).

Agrion annexum Hagen, 1861, Syn. Neur. N.A., p. 87 (Sitka).

Enallagma cyathigerum race? *annexum*; Selys, 1876, Bull. Acad. Belg., (2) 41:506.

Enallagma annexum; Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Williamson, 1900, Entomol. News, 11:454 (syn., Calif., Wash., Wyo.); Williamson, 1902, Proc. Ind. Acad. Sci., p. 121 (syn.); Calvert, 1902, Biol. Cent. Amer., p. 108 (syn.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:57 (cat.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:521 (fn., syn.).

Aenallagma robustum Selys, 1875, Entomol. Mon. Mag., 11:243 (♀, Calif.).

Enallagma cyathigerum race? *robustum*; Selys, 1876, Bull. Acad. Belg., (2) 41:509.

Enallagma robustum; Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Woodworth, 1913, Calif. Insects, p. 333 (Calif.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:61 (cat.); Essig, 1926, Insects West. N.A., p. 145; Byers, 1927, Trans. Amer. Entomol. Soc., 53:251 (fn., syn.).

Male. Head, thorax, and abdominal pattern as for *E. boreale*. Black markings more extensive on specimens from Summit Co., Utah (Trident Lake, Uinta Mtns., 9300 ft.), such that upper end of black antehumeral stripe is as wide as pale antehumeral stripe on mesepisternum. Black banding on abdomen of some specimens fully extending to sides, enclosing small, pale distal spot on side. Mesostigmal plate variable, specimens from interior California and parts of Idaho with transverse diagonal ridge extending from base of frame to anterior distal half of frame as shown in Fig. 69 and as figured by Jurzitza (1975). Specimens from other localities with mesostigmal plate flat, as shown in Fig. 70. Some populations contain specimens with both types of plates and some intermediate forms not easily assigned to either type. Superior appendage in profile blunt, shorter than inferior appendage. Small, upturned lobe visible at tip of superior appendage in profile. In dorsal view, superior appendage roughly triangular with concave mesal base. Dorsal surface concave, with variable rugose sculpturing; small, black, glabrous tooth which lies anterior to pale tubercle, mesally pointed and orthogonal to slightly diagonal to longitudinal axis of abdomen (Fig. 67b).

Female. With same maculation as *E. boreale*. Females from Summit Co., Utah, heavily marked with dorsal and antehumeral stripes connecting, thus dividing pale antehumeral stripe into two spots. Majority of specimens with normal complement of black (Fig. 58).

Mesostigmal plate planar with anterior distal margin slightly upturned; posterior margin with distinct groove to base of ramus. Some specimens with small depression at anterior mesal end of plate, lateral to frame. Lateral arms of frame forming an acute angle with posterior arms, or occasionally straight or a little obtuse. Plate roughly rectangular (Fig. 75) to distally pointed (Fig. 76).

Postnodal cs.: FW ♂ 11-16, ♀ 11-14; HW ♂ 9-15, ♀ 10-12

Total length: ♂ 29-40, ♀ 31-37; Abd. ♂ 22.5-32, ♀ 24-30; HW ♂ 17-23, ♀ 20-24.

Larva. Body and gills (Fig. 81, 86) as described by Walker (1953). Colors in life transparent, tan to brown or green. Gills immaculate or pigmented with one or two transverse chevrons. Median gill length 5.9-7.8, greatest width 2.3. Antenodal setae: med. gill: d. 27-48, v. 11-38; lat. gill: d. 13-40, v. 31-55.

♂ appendage (Figs. 94, 104) similar to *E. boreale*, circular, longest toward their mesal extremities (Fig. 104c). Dorsal and ventral surfaces concave, often associated with visible folds when viewed laterally. Blunt tip (=STUBHEI, Fig. 7) narrow, height at mesal third of stub 0.09-0.12 mm.

♀ appendage (Fig. 114) conical, 0.20-0.30 mm long, mesal sides usually moderately to strongly convex (in dorsal view), then concave toward distal half. In posterior view (Figs. 11-13), cercus circular or transversely oval, blunt tip (STUBHEI) usually narrow (0.06-0.12 mm) to conical or slightly higher than wide.

Type data. *Agrion cyathigerum*: Types lost. *Agrion annexum*: lectotype not designated. ♂♀ from Sitka, Alaska, no date (Eschscholz) presumably in Berlin Museum (Hagen, 1861; Muttkowski, 1910). In the Museum of Comparative Zoology at Cambridge, there is a ♂ labeled "Sitka" and "Type 12270". The type record book lists it as the type of *A. annexum*, but since the last 4 abdominal segments are missing, I could not confirm this. A small inked label with "A. annexum* Hag." (in Hagen's handwriting) is next to this specimen. Since the ♀ is missing, I have refrained from designating this ♂ the lectotype. *A. robustum* ♀ from "California", no date (W. Edwards) in MacLachlan collection

(Muttkowski, 1910), is apparently lost. It is not in the Selys collection (G. Demoulin, pers. comm., 1979) nor is it in the British Museum (Nat. Hist.) (Kimmins, 1970).

Adult diagnosis. Males and females of this species are most similar to *E. boreale*, and diagnoses may be found under that species.

Larval diagnosis. See diagnosis for *E. boreale* and phenetics.

Distribution (Fig. 39). This Holarctic species occurs throughout Eurasia to northern India (Fraser, 1933). In the New World, it occurs from Alaska to northern Baja California (Canyon del Tajo, de Sierra Juarez, 2-3000 ft., 1 April 1953, J. Powell, CIS) and east to the New England seaboard and Newfoundland. Longfield (1960) shows it from Florida, but *E. cyathigerum* is absent from the southeastern United States (Parr, 1976). It occurs in every state west of the Rocky Mountains, but is absent from Texas, Oklahoma, and Nebraska. *E. cyathigerum* is common in the West, found from sea level to high montane areas. In the eastern United States it exhibits a spotty distribution and is evidently rarely collected in the Northeast. It has not been taken commonly in the Great Basin or in Arizona or New Mexico. While the Baja California specimen is the first from Mexico, *E. cyathigerum* may also be present in the northern highlands of mainland Mexico. See further comments under *E. boreale* for comparison of distribution patterns.

Comments. Much has been written concerning the systematics of this widely variable species. Many species similar to *E. cyathigerum* have been described from the Old World, and there has been confusion about the distinctness of this species from the poorly known *E. deserti*. As discussed under *E. boreale*, a final determination of the various forms will have to await a comprehensive study, including Old World taxa. In the United States, *E. cyathigerum* is highly variable. Gloyd (1943) described *E. vernale* from the eastern United States, and Jurzitza (1975) gave the best basis for separating males of *E. vernale* and *E. cyathigerum*: (translated from the German): "Anterior border of 'tooth' [= glabrous chitinized tooth shown in Figs. 66b, 67b] strongly bent, forming a second, shorter, stumpy tooth...*E. vernale*. Anterior border [of tooth] only slightly bent...*E. cyathigerum* and *E. hageni*". While specimens of *E. vernale* from the eastern United States show the condition illustrated by Jurzitza (1975: Fig. 5), other specimens appear intermediate between *E. vernale* and *E. cyathigerum* in possessing a variously developed supplementary tooth. For example, two males from Centre Co., Pennsylvania, have the anterior border of the tooth bent, but not forming a sharp, pointed tooth as in *E. vernale*. One of these males has the anterior portion of the tooth completely separated and forming a separate black tooth.

I have not seen any western specimens which have the stongly bent supplementary tooth as in *E. vernale*, but there is variation in the size and shape of the glabrous tooth. Fig. 67b is typical of most specimens, but other specimens have the tooth diagonally directed anteriorly (not orthogonal) to the longitudinal axis of the abdomen, and the anterior (= distal) portion of the tooth may be bent anteriorly so that the structure resembles a "Ɔ". *E. vernale* appears to be allopatric with eastern *E. cyathigerum*, and may represent a geographical race.

Jurzitza also noticed a striking difference in the male mesostigmal plates of three male *E. cyathigerum* from Santa Rosa, Sonoma Co., California. They possessed a distinct diagonal ridge as shown in Fig. 69 and as illustrated by his Fig. 12, while the other specimens from Washington, Canada, and Europe lacked an elevated diagonal ridge (Fig. 70). A further study shows most specimens from west of the Sierra Nevada and south of the Cascade Range to have plates similar to those illustrated in Fig. 69. Other males from Owyhee and Latah counties, Idaho, show a similar morphology. All other specimens (Ore., Nev., Utah, Wyo., Alta.) show the condition in Fig. 70. However, males from Latah Co., Idaho (pond just south of Moscow, by U.S. Hwy. 95, 31 July 1978) and San Francisco (Lake Merced, 6 April 1979) have intermediate plates as well as both types of plates. Both types of males from the high crest of the Sierra Nevada, Lassen and Shasta counties are present at different localities.

Jurzitza (1975:47) concludes (translated): "the fact is very interesting that *E. cyathigerum* tends toward speciation in North America. The specimens remaining in the investigation from California are assuredly different from the European subspecies. As only scant material was available to us, however, and it was destroyed for the investigation, we must refrain from naming them". Since in the present material there appear to be no structural differences between the females of these forms, and since both types of males occur at the same place, I do not believe that populations from California should be named.

E. cyathigerum is variable in size: the largest specimens (length 35-40 mm) come from the north coast of California, and some of them are the largest of any western *Enallagma*. *E. cyathigerum* and *E. civile* occur together at a coastal pond at Point Reyes (Marin Co., pond at end of Limantour Rd.), but *E. civile* is smaller (30-36 mm) than *E. cyathigerum* from the same locale (37-40 mm). About 130 km. SE of Pt. Reyes (Del Puerto Canyon, Stanislaus Co.), *E. civile* is generally larger (31-38 mm) than *E. cyathigerum* (28-36 mm).

Material examined. 247 ♂♂, 108 ♀♀, 44 larvae (31 reared). Adults: CANADA: Alberta. UNITED STATES (Counties): ARIZ.: Coconino, Gila. CALIF.: Alameda, Butte, Contra Costa, El Dorado, Fresno, Glenn, Humboldt, Kern, Lassen, Los Angeles, Madera, Marin, Mendocino, Mono, Napa, Nevada, Plumas, Riverside, San Bernardino, San Diego, San Francisco, San Joaquin, San Mateo, Santa Barbara, Shasta, Sierra, Siskiyou, Solano, Sonoma, Stanislaus, Tulare, Tuolumne, Ventura, Yolo. COLO.: Garfield, Lake. IDAHO: Latah, Lemhi, Lewis, Owyhee. NEV.: Carson City, Elko, White Pine. ORE.: Deschutes, Lake. UTAH: Carbon, Daggett, Summit. WYO.: Yellowstone. MEXICO (States): Baja Calif. Norte.

Larvae. See Table 2.

Enallagma ebrium (Hagen)
(Figs. 40, 47, 56, 65, 71, 92, 96, 110)

Agrion ebrium Hagen, 1861, Syn. Neur. N.A., p. 89 (♂, Ill., La.).

Enallagma ebrium; Selys, 1876, Bull. Acad. Belg., (2) 41:513 (descr.); Kirby, 1890, Syn. Cat. Neur. Odon., p. 146 (cat.); Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:59 (cat.); Walker, 1914, Can. Entomol., 46:351 (larva); Lyon, 1915, Entomol. News, 26:57 (larva); Kennedy, 1915, Proc. U.S. Natl. Mus., 49:331 (Wash.); Garman, 1917, Bull. Ill. St. Lab. Nat. Hist., 12:540 (keys, ♂, ♀, larva); Essig, 1926, Insects West. N.A., p. 145; Garman, 1927, Conn. Geol. Nat. Hist. Survey Bull., 39:71 (keys, descr.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:253 (keys); Walker, 1927, Bull. Prov. Mus. Nat. Hist., Victoria, B.C., p. 6 (distr. B.C.); Byers, 1929, *in* Needham and Heywood, Drfls. N.A., p. 332 (key, ♂, ♀); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:14 (distr. Utah); Buckell, 1937, Proc. Entomol. Soc. B.C., 34:58 (distr. B.C.); Whitehouse, 1941, Amer. Midland Nat., 26:503 (distr. B.C.); Montgomery, 1942, Proc. Ind. Acad. Sci., 31:274 (distr. U.S.); Whitehouse, 1948, Trans. Roy. Can. Inst., 27:13 (distr. Can.); Walker, 1953, Odon. Can. Alaska, p. 228 (key, descr., behav.); Gibbs, 1955, Psyche, 62:16 (♀ key, diag.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Robert, 1963, Les Lib. du Québec, p. 92 (keys); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. *Amer., 22:126 (Nebr., N. Dak.); Paulson, 1970, Pan-Pac. Entomol.,* 46:196 (Wash.); Newell, 1970, Proc. Mont. Acad. Sci., 30:49 (Mont.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo, S.Dak.); Roemhild, 1975, Dmsfls. Mont., p. 48 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:387 (distr. Utah); Scudder *et al.*, 1976, Syesis, 9:147 (B.C.); Bick *et al.*, 1977, Fla. Entomol., 60:160 (N.Dak., S.Dak.); Cannings and Stuart, 1977, Drfls. B.C., p. 83 (keys, descr.); Molnar and Lavigne, 1979, Odon. Wyo., p. 102 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography); Pilon and Fontaine, 1980, Odonatologica, 9:155 (larval morphology); Pilon, 1982, Odonatologica, 11:45 (oviposition and embryonic development).

Male. Body color pattern nearly identical to *E. cyathigerum* and *E. boreale*, but with dorsal spot on abdominal segment 2 rarely crescent-shaped as in those species. Superior appendage (Fig. 65a) in profile as long as inferior appendage, forked, with semicircular hollow between dorsal and ventral arms. Dorsal arm slightly thicker than ventral arm. Ventral arm in oblique lateral view (Fig. 65b) forming a square with rounded corners; dorsal surface pale and contrasting with black on dorsal arm.

Female. Head and body as in male, abdominal pattern (Fig. 56) as described by Walker (1953). Pale colors blue or brown; black on abdomen extensive, covering most of dorsum except for anterolateral areas of segments 3-7, black on sides parallel, not mesally narrowed as in other species. Square black spot on anterior half of dorsum of 1.

Mesostigmal plates (Fig. 71) broadly triangular, posterior margin convex so plate is about 0.50 to 0.75 as broad as long. Plate slightly concave, bordered posteriorly by raised arcuate ridge and mesally by lateral arm of frame.

Postnodal cs.: FW ♂ 9-11, ♀ 10-12; HW ♂ 8-10, ♀ 9-10
Total length: ♂ 28-33, ♀ 27-34; Abd. ♂ 22-26, ♀ 21-26; HW ♂ 16-19, ♀ 17.5-21.

Larva. Body and gills (Fig. 92) as described by Walker (1953). Gills with differentiated patterns of dark tracheal areas. Median gill length 5.2, greatest width 1.3. Antenodal setae: med. gill: d. 30, v. 14; lat. gill: d. 7, v. 35.

♂ appendage (Figs. 96, 110) similar to *E. boreale*, circular, distinctly concave on dorsal surface. In dorsal view, concavity forms acute angle visible as longitudinal groove (Fig. 110d). In posterior view, cercus with distinct "L"-shaped groove (Fig. 96), ventral surface evenly rounded.

♀ appendage: No specimens available for study.

Type data. *Agrion ebrium*: lectotype ♂ by present designation: Chicago, Cook Co., Illinois, no date (Osten Sacken), in Museum of Comparative Zoology, Cambridge, Type No. 12267 (examined). Hagen (1861) indicated that he examined another "very much mutilated" specimen from New Orleans that may not have been *E. ebrium*. I could not find that specimen.

Adult diagnosis. Male *E. ebrium* are easily distinguished from other western Nearctic species by the shape of the superior appendage. No other species has the symmetrical fork of *E. ebrium* when viewed laterally. In dorsolateral view, the lower arm of the superior appendage forms a square (Fig. 65b), another unique feature.

The abdominal pattern of *E. ebrium* is similar to *E. boreale* and *E. cyathigerum*, but usually does not possess the characteristic black lunule on the dorsum of segment 2. Instead, this spot usually is enlarged posteriorly and often touches the distal end of the segment. However, the patterns of all three species can overlap and they are best distinguished by their caudal appendages.

Female *E. ebrium* are easily distinguished by the shape of the mesostigmal plates (Fig. 71). The raised posterior margin is distinctly convex, making the plate basically triangular in appearance. The plates in all other western species are roughly rectangular. The black abdominal pattern easily distinguishes this species in the field. Viewed dorsally, the abdomen appears almost totally black except for the small pale anterolateral spots of segments 3-7. Segment 8 is totally black on the dorsum, while all other species usually have a pale area along the anterolateral margins. *Enallagma civile* females have black abdominal patterns almost as extensive as *E. ebrium*, but the former species usually has the black dorsal spot of segment 1 covering the entire dorsum, not the anterior half, as in *E. ebrium*. *E. civile* females (31-36.5 mm) are generally longer than *E. ebrium* (27-34 mm).

Larval diagnosis. While I examined only one male exuvia, the distinctive gill pattern stated in the key and described by Walker (1953) is sufficient to identify this species. Only *E. basidens* is similar, and that species is distinguished by the head and antennal characters in the key. In posterior view, the male caudal appendages (Fig. 96) are similar to *E. boreale* and *E. carunculatum* but differ in possessing a well-defined "L"-shaped concavity. The concavity is nearly straight in *E. boreale* (Fig. 93) or only slightly concave and more vertically oriented in *E. carunculatum* (Fig. 95).

Distribution (Fig. 40). *E. ebrium* has been most commonly collected east of the Rocky Mountains and in British Columbia, and crosses the Rockies in eastern Washington, northern Idaho, western Montana, Colorado, and northeast Utah. Bick *et al.* (1977) report it as abundant in North Dakota, but it is apparently scarce in Nebraska and Utah and has not been collected in the southwestern United States. Walker (1953) remarked that the distribution of *E. ebrium* in Canada is interrupted by the Rocky Mountains, and its presence in central British Columbia appears to be due to a northwest extension from the United States. Further collecting in Montana (Roemhild, 1975), Utah (Provonsha, 1975), Wyoming (Bick and Hornuff, 1972; Bick, pers. comm., 1977) shows that *E. ebrium* occurs across the Northwest and I have collected it in northern Idaho and Alberta. Further collecting will probably show a continuous distribution across southern Canada.

Comments. Robert (1963:90) diagnosed female *E. ebrium* from female *E. boreale*, *E. clausum*, and *E. cyathigerum* by placement of R_3 in the forewings between the fourth and fifth postnodal cs. in *E. ebrium*, between the fifth and sixth postnodal cs. in the other species. Of the 26 females I examined, 18 (69%) had R_3 originating between the fourth and fifth postnodal cs., 7 (27%) between the fifth and sixth, and one specimen (4%) between the third and fourth postnodal cs.

Material examined. 68 ♂♂, 26 ♀♀, 1 larva (exuvia). Adults: CANADA: Alberta: stagnant pond on Alta. Hwy. 2A, 1 km. N. Innisfail; ponds by Alta. Hwy. 587, 3 km. W. jct. Alta. Hwy. 2. UNITED STATES: IDAHO. Boundary Co.: small pond by U.S. Hwy. 95, 2.5 mi. S. jct. Ida. Hwy 1; lake N. of Boundary Co. line, by U.S Hwy. 95. Kootenai Co.: Lake Coeur d'Alene just S. of Coeur d'Alene, by U.S Hwy. 95. MONT. Missoula Co.: Missoula City Park by U.S. Hwy. 93, Missoula. WASH. Pend Oreille Co.: Lost Creek, 5.4 mi. S. Tiger, 2200'; Niles Lake, 5.8 mi. SW Tiger, 3400'; Sportsman Pond, 4.3 mi. NW Wash. Hwy. 31 on Tacoma Creek Rd.; slough at Usk, 2200'. Spokane Co.: Turnbull Natl. Wildlife Refuge, Kepple Lake. Stevens Co.: Lake Gillette, 3300'; Twin Lake, SW of Middleport.

Larva. IDAHO. Kootenai Co.: Lake Coeur d'Alene just S. of Coeur d'Alene.

Enallagma praevarum (Hagen)

(Figs. 2, 3, 19, 41, 44, 53, 62, 79, 84, 89, 98, 102, 107, 117)

Agrion praevarum Hagen, 1861, Syn. Neur. N.A., p. 88 (♂, ♀, Mexico).

Enallagma praevarum; Selys, 1876, Bull. Acad. Belg., (2) 41:516 (descr.); Kirby, 1890, Syn. Cat. Neur. Odon., 146 (cat.); Williamson, 1900, Entomol. News, 456 (taxon.); Calvert, 1902, Biol. Cent. Amer., p. 111 (key, N. Mex., Ariz., Calif.); Currie, 1903, Proc. Entomol. Soc. Wash., 5:301 (Ariz., N. Mex.); Calvert, 1907, Biol. Cent. Amer., p. 380; Muttkowski, 1910, Bull. Public Mus. Milwaukee, 1:61 (cat.); Williamson, 1914, Entomol. News, 25:225 (Ariz.); Kennedy, 1917, Proc. U.S. Natl. Mus., 52:594 (Calif.);

Needham, 1924, Pomona College J. Entomol. Zool., 16:9 (Calif.); Essig, 1926, Insects West. N.A., p. 145 (Calif., Nev., Ariz., N. Mex.); Seemann, 1927, Pomona College J. Entomol. Zool., 19:14 (key, Calif.); Byers, 1927, Trans. Amer. Entomol. Soc., 53:254 (keys); Byers, 1929, *in* Needham and Heywood, Handbook Drfls. N.A., p. 337 (key, ♂, ♀); Bird, 1932, Publ. Univ. Okla. Biol. Survey, 4:57 (Okla.); Brown, 1934, Occ. Pap. Mus. Zool. Univ. Mich., 291:15 (distr. Utah); Ahrens, 1938, Entomol. News, 49:16 (N. Mex.); La Rivers, 1940, Pan-Pac. Entomol., 16:120 (Nev.); La Rivers, 1941, Entomol. News, 52:156 (Nev.); Montgomery, 1942, Proc. Ind. Acad. Sci., 31:273 (distr. U.S.); Pritchard and Smith, 1956, *in* Usinger, Aquatic Insects Calif., p. 147 (keys); Bick and Bick, 1957, Southwestern Nat., 2:11 (Okla.); Bick, 1957, Tulane Stud. Zool., 5:119 (questions distr. La.); Westfall, 1957, Year Book Amer. Phil. Soc., p. 258 (rearing); Gloyd, 1958, Occ. Pap. Mus. Zool. Univ. Mich., 593:21 (W. Tex.); Donnelly, 1963, Proc. N. Centr. Br. Entomol. Soc. Amer., 18:116 (phylogeny); Johnson, 1964, Amer. Midl. Nat., 72:408 (polymorphism); Johnson, 1964, Southwestern Nat., 9:297 (mating expectancies, sex ratio); Pruess, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:112 (Nebr.); Montgomery, 1967, Proc. N. Centr. Br. Entomol. Soc. Amer., 22:126 (Nebr.); Donnelly, 1968, Fla. Entomol., 51:103 (diag.); Johnson, 1972, Bull. Fla. St. Mus., 16:100 (taxon., keys, distr. Tex.); Bick and Hornuff, 1972, Proc. Entomol. Soc. Wash., 74:5 (Wyo.); Bick and Hornuff, 1974, Proc. Entomol. Soc. Wash., 76:91 (Mont.); Roemhild, 1975, Dmsfls. Mont., p. 47 (key, Mont.); Provonsha, 1975, Great Basin Nat., 35:387 (distr. Utah); Huggins *et al.*, 1976, Tech. Pub. St. Bio. Survey Kans., 1:40 (Kans.); Provonsha and McCafferty, 1977, Entomol. News, 88:25 (S. Dak.); Bick *et al.*, 1977, Fla. Entomol., 60:160 (N. Dak., S. Dak.); Huggins, 1978, Tech. Publ. St. Biol. Survey Kans., 6:24 (Kans.); Bick and Bick, 1978, Notul. Odonatol., 1:18 (Colo.); Molnar and Lavigne, 1979, Odon. Wyo., p. 104 (distr. Wyo.); Bick and Bick, 1980, Odonatologica, 9:8 (reproductive bibliography).

Male. Color pattern of head, thorax and legs similar to *E. anna*. Pale blue triangular postocular spots sometimes touching thin mesal blue line at rear of occiput. This mesal blue line reduced or absent in some specimens. Small pair of middorsal spots present on prothorax in some specimens. *Abdomen*: blue above, paler at sides with following parts black: basal 0.25-0.50 of segment 1 dorsally and small posterolateral spots at articulation points; dorsal spot narrowed mesally before connecting to apical annulus; 3 with spot similar to 2 but anteriorly pointed covering posterior 0.50 of segment; 4 with dorsal spot covering posterior 0.50 or more, obtusely pointed anteriorly, sides parallel and expanding laterally at distal 0.25 of segment to annulus; 5 and 6 similar to 4, but with dorsal spot extending to 0.75 of segment; entire dorsum of 7 except for pale anterior annulus, sometimes divided into a pair of midlateral spots confluent with pale sides. Segments 8 and 9 entirely blue with black transverse carinae at distal annuli, and black articulation points. Dorsum of segment 10 and superior appendages black. Superior appendage (Fig. 62a) in profile notched with superior arm about 0.50 as long as segment 10, tapering to blunt mesally decurved knob; lower arm small but prominent, projecting ventroposteriorly to upper arm with pale upper surface (Fig. 62b).

Female. Pale areas light brown or blue with markings on head, thorax, and legs similar to male, but less extensive. Pale triangular postocular spots sometimes connecting with thin mesal pale line at rim of occiput. Prothorax with pair of middorsal pale spots. Abdominal pattern (Fig. 53) with black spots covering most of dorsum on segments 2-10. Segment 1 with dorsal black spot covering anterior 0.50 to all of segment; 2 with sides of dorsal black spot parallel and lateral expansion points at apical 0.25 before constricting again and connecting with black annulus; 3 like 2, but with anterior 0.20 of dorsal spot pointed; 4-7 similar to 3, but with dorsal spots wider laterally and with progressive recession of pointed anterior apices; 8 with dorsal black spot covering posterior 0.50 to entire dorsum of segment. Pale lateral areas of 7 confluent dorsally at anterior 0.20 to 0.50 of segment or divided by narrow anterior elongation of black dorsal spot. Segments 9 and 10 black dorsally, cerci pale.

Mesostigmal plates (Fig. 79) with lateral arms of frame thick, forming obtuse 100° angle. Plate with anteromesal circular or inverted triangular depression, bordered by thick diagonal ridge originating from posterior corner of frame to anterodistal margin of plate. Distal 0.50 of mesostigmal plate flat or slightly concave with anterior margin raised, forming a convex arc. Posterior margin of plate linear or slightly convex, well-defined to ramus.

Postnodal cs.: FW ♂ 10-11, ♀ 10-11; HW ♂ 9-10, ♀ 8-9

Total length: ♂ 28-34, ♀ 28-35; Abd. ♂ 22-26, ♀ 22-27.5; HW ♂ 16-21, ♀ 16.5-21.

Larva. Head (Fig. 102) pale with slight markings on dorsum, posterolateral margin evenly convex with few setae. Antennae about 1/2 width of head, antennal segment length (mm): 0.25-0.29; 0.40-0.43; 0.60-0.70; 0.41-0.48; 0.25-0.33; 0.30-0.35; each segment darkest at base, paler distally, darkest on segment 3. Prementum when appressed extends to middle of mesothoracic coxae. Ratio of distal width to length of prementum 0.77-0.86; premental setae 3-4, marginal setae 6-9, palpal setae 5-6; apical ends of lateral lobes with 5 minute teeth followed ventrally by usual cleft and prominent tooth. Thorax and abdomen pale, sides of pronotum obtusely angulate, legs pale. Wing pads extending to basal 0.25 of abdominal segment 4. Darkened setae on abdominal pleura 2-10. Gills (Figs. 84, 89) of usual form, bluntly pointed, often with transverse chevron across middle. Median gill length 5.3-6.4, greatest width 1.5-2.1. Dorsal series of antenodal setae on median gill about twice as long as ventral series, respective lengths reversed on lateral gill. Antenodal setigerous margin extending 43-60% of median gill length. Antenodal setae: med. gill: d. 23-39, v. 5-17; lat. gill: d. 7-19, v. 37-53.

♂ appendage (Figs. 98, 107) 0.25-0.28 mm long, longer than high, concave ventrally, approximating divided superior appendage of adult. In posterior view, mesal sides of cerci parallel, upper extremity of cercus forming a perfect circle.

♀ appendage (Figs. 19, 117) 0.22-0.29 mm long, pointed with a slight concavity (ARC, Fig. 19) which, when measured lateroventrally, is

0.006-0.023 mm. In dorsal view (Fig. 117d), mesal sides of cerci slightly concave, with extremities pointing slightly mesad.

Type data. *Agrion praevarum*: 2 ♂♂ from "Mexico", no date. "Type 12275", with posterior 4 abdominal segments missing. Also 1 ♀ from "Trajos Del Oro", Mexico, "Type 3-12275" with abdomen missing. Since identification by mesostigmal plates is certain, I have designated this specimen as the lectotype. In Museum of Comparative Zoology, Cambridge.

Adult diagnosis. See diagnoses for *E. anna* and *E. carunculatum*.

Larval diagnosis. The setal patterns of *E. praevarum* are most similar to those of *E. carunculatum*, *E. civile*, and *E. clausum*, because all have unequal numbers of antenodal setae. Male *E. praevarum* are distinguished from those species by the shape of the cerci; they are long and concave ventrally (Fig. 107), not short as in *E. clausum* (Fig. 109) or distinctly convex ventrally as in *E. carunculatum* (Fig. 105) or *E. civile* (Fig. 106). Viewed posteriorly, the cerci of *E. praevarum* differ from the above-mentioned species by the circular prominence at the upper end of the appendage (Fig. 98). Only *E. anna* possess similar appendages, and these two species are diagnosed under *E. anna*.

Female *E. praevarum* are most similar to *E. carunculatum* and *E. civile*, and are diagnosed under those species.

Distribution (Fig. 41). *E. praevarum* is a southwestern species which occurs in California as far north as Lassen Co. (Termo, 23 May 1940, CIS), south to Baja California Norte (San Vicente, 8 July 1963, R.L. Langston, CIS) and Oaxaca, Mexico (Donnelly, 1968), and east through Arizona and extreme southwest Utah to the Edwards Plateau of Texas. A northern group of populations occurs in Montana (Bick and Hornuff, 1974; Roemhild, 1975), North and South Dakota (Bick *et al.*, 1977) south through western Nebraska and Kansas (Huggins, 1978b), and Oklahoma (Bird, 1932; Bick and Bick, 1957), where it meets southern populations in New Mexico and Texas. A male from western Montana (Missoula Co., Missoula City Park, by U.S. Hwy. 93, Missoula, 8 Aug. 1978, J.A. Garrison) is a northwestern record. The distribution surrounds the Sierra Nevada and the Rocky Mountains.

E. praevarum is morphologically similar to *E. anna*, but the two species have been taken together only at one locality, in southwestern South Dakota (Provonsha and McCafferty, 1977). My observations show *E. anna* to prefer slowly moving streams, while *E. praevarum* is usually found at ponds.

Material examined. 114 ♂♂, 62 ♀♀, 22 larvae (12 reared). Adults: UNITED STATES (counties): ARIZ.: Cochise, Coconino, Gila, Maricopa, Pima, Pinal, Santa Cruz, Yavapai. CALIF.: Alameda, Contra Costa, Inyo, Lassen, Los Angeles, Marin, Napa, San Bernardino, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Solano, Stanislaus, Ventura. MONT.: McCone, Missoula. OKLA.: Cimarron. S. DAK.: Custer, Fall River. TEX.: Real. WYO.: Converse, Crook, Sheridan. MEXICO (States): Baja Calif. Norte, Durango, Veracruz.

Larvae. See Table 2.

Appendix

Instructions for identifying certain final instar *Enallagma* larvae from the western United States using discriminant analysis: All except the following species and sexes may be identified by the larval key (p. 64). Only males and females of *E. boreale* and *E. cyathigerum*, and females of *E. carunculatum, E. civile*, and *E. praevarum* need be identified by discriminant analysis.

1. If larva is male, go to 2. If female, go to 5.
2. Measure (mm) DVHEIG, LATHEIG, STUBHEI characters (Table 4, Figs. 7,8).
3. Multiply each character value by its unstandardized discriminant function (Table 10) and sum the products. Add constant.
4. Plot value of unknown specimen on abscissa shown in Fig. 29. ♂ *boreale* ≧ 0.55; ♂ *cyathigerum* ≦ 0.55.*
5. If XVSL ÷ XDSL ≧ 0.55, go to 6. If XVSL ÷ XDSL ≦ 0.54, go to 9.
6. Measure (mm) BOTTOM, APPLENG, STUBHEI characters (Table 5, Figs. 9-15).
7. Multiply each character value by its unstandardized discriminant function (Table 12) and sum the products. Add constant.
8. Plot value of unknown specimen on abscissa shown in Fig. 30. ♀ *boreale* ≧ 0.55; ♀ *cyathigerum* ≦ 0.55.*
9. Measure (mm) BASALHEI, APPLENG, GONOPHY, ARC characters (Table 5, Figs. 11, 14-19).
10. Multiply each character value by its unstandardized discriminant function (DF1) (Table 15) and sum the products. Add constant. Repeat for DF2.
11. Plot value of unknown specimen on ordinate (DF2) and abscissa (DF1) shown in Fig. 31. Species is determined by name within dotted lines (territorial map): ♀ *carunculatum*, ♀ *civile*, ♀ *praevarum*.

*Identity is uncertain if discriminant value is borderline.

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Tables

Table 1. Specific and subspecific names used in the genus *Enallagma* of the western United States.

Name	Original Genus	Original Reference	Type Locality	Location of Type	Present Placement
anna	*Enallagma*	Williamson, 1900	Sheep Creek, Wyo.	Mus. Zool. Univ. Mich. (♂)[1]	*E. anna*
annexum	*Agrion*	Hagen, 1861	Sitka, Alaska	MCZ (♂)[2] lost? (♀)	*E. cyathigerum*
basidens	*Enallagma*	Calvert, 1902	Corpus Christi, Tex.	lost?	*E. basidens*
boreale	*Aenallagma*	Selys, 1875	White Bay, Nfld.	lost? (♂♀)	*E. boreale*
calverti	*Enallagma*	Morse, 1895	Franktown, Nev.	MCZ (♂)	*E. boreale*
canadense	*Agrion*	Provancher, 1876	Québec, Canada?	lost?	*Ischnura ramburi* or *I. verticalis*
carunculatum	*Enallagma*	Morse, 1895	Franktown, Nev.	MCZ (♂)	*E. carunculatum*
civile	*Agrion*	Hagen, 1861	Pecos River, Tex.	MCZ (♂)	*E. civile*
clausum	*Enallagma*	Morse, 1895	Franktown, Nev.	MCZ (♂)	*E. clausum*
culicinorum	*Enallagma*	Byers, 1927	Logan River, Utah	Cornell Univ. (♂)	*E. anna*
cyathigerum	*Agrion*	Charpentier, 1840	?	lost?	*E. cyathigerum*
ebrium	*Agrion*	Hagen, 1861	Chicago, Ill.	MCZ (♂)	*E. ebrium*
plebium	*Enallagma*	Selys, 1876	Putla, Mexico	Selys Coll., Brussels (♂)	*E. civile*
praevarum	*Agrion*	Hagen, 1861	Trajos del Oro, Mexico	MCZ (♀)	*E. praevarum*
robustum	*Enallagma*	Selys, 1875	Calif.	lost? (♀)	*E. cyathigerum*
simile	*Enallagma*	Selys, 1876	"Merida", Columbia?	MCZ (♂)	*E. civile*

[1]Museum of Zoology, University of Michigan, Ann Arbor
[2]Museum of Comparative Zoology, Cambridge, Mass.

Table 2. Samples used in phenetic analysis. Asterisks indicate reared material.

		No. of specimens ♂♂	♀♀
1.a.	*boreale* reference		
	CALIF.: Contra Costa Co., pond 1 mi. E. of Pinole	3*	5*
	CALIF.: Placer Co., small pond at Donner Pass, E. of Donner Lake	1	2*
	NEV.: Elko Co., Zunino Reservoir, by Nev. Hwy 46, N. of Jiggs	3	
b.	*boreale* unknowns		
	CANADA.: Ontario: SW Ontario Experimental Lakes Area, SE of Kenors, in Lake No. Z40	1	2
	CALIF.: Contra Costa Co., Jewell Lake	2	1
	CALIF.: Lassen Co., Siad Reservoir, Hwy. 139	2	
	NEV.: Elko Co., Zunino Reservoir, by Nev. Hwy. 46, N. of Jiggs		1
	SUBTOTAL:	12	11
2.a.	*carunculatum* reference		
	CALIF.: Alameda Co., pond nr. Livermore		1*
	NEV.: Churchill Co., slough by U.S. Hwy. 95, *ca.* 3 mi. W. jct. U.S. Hwy. 50	3*	3*
	NEV.: Washoe Co., Truckee River, 4 rd. mi. S. of Nixon, nr. Nev. Hwy. 34	3*	4*
b.	*carunculatum* unknowns		
	CALIF.: Butte Co., Llano Seco Ranch, Rice Field	1	
	CALIF.: Contra Costa Co., pond 1 mi. E. of Pinole	1	
	CALIF.: Inyo Co., Lone Pine, at Stock Pond	1	
	CALIF.: Mendocino Co., Univ. Calif. Hopland Field Station	2	2
	CALIF.: San Bernardino Co., Zzyzx Sprgs., 9 air mi. S. of Baker		1
	CALIF.: San Bernardino Co., Amagosa River Wash, Saratoga Sprgs.		1
	CALIF.: Santa Clara Co., San Antonia Val.	1	2
	CALIF.: Sonoma Co., 11 mi. W. of Two Rock	3	3
	NEV.: Washoe Co., Truckee River, 4 mi. S. of Nixon, nr. Nev. Hwy 34	2	2
	SUBTOTAL:	17	19
3.a.	civile reference		
	ARIZ.: Maricopa Co., slough ponds by Verde River, Ft. McDowell Ind. Reservation, by Ariz. Hwy. 87	1*	1*
	CALIF.: Alameda Co., pond nr. Livermore	1*	2*
	CALIF.: Stanislaus Co., Del Puerto Cyn. about 5 mi. W. of Patterson	5*	6*

Table 2, Cont.

	No. of specimens ♂♂	♀♀
b. *civile* unknowns		
CALIF.: Los Angeles Co., 3 mi. S. of Palo Verde	1	
CALIF.: Inyo Co., Lone Pine	1	
CALIF.: San Bernardino Co., Cottonwood Sprg.	1	
CALIF.: San Bernardino Co., Afton Rd., 23 mi. SW of Baker	2	
CALIF:. San Bernardino Co., Zzyzx Sprgs., 9 air mi. S. Baker	2	2
CALIF.: Alameda Co., pond nr. Livermore		2*
CALIF.: Stanislaus Co., Del Puerto Cyn. about 5 mi. W. of Patterson		1*
SUBTOTAL:	14	14
4.a. *cyathigerum* reference		
ENGLAND: Pingewood, Reading		1*
CALIF.: Madera Co., Willow Creek, NE of Fresno		1*
CALIF.: Mono Co., small pond at Tioga Pass, N. of Yosemite Nat'l Park	1*	
CALIF.: Placer Co., small pond at Donner Pass, E. of Donner Lake	5*	2*
CALIF.: Stanislaus Co., Del Puerto Cyn. at N. Fork Del Puerto Cr., 22 mi. W. of Patterson	9*	8*
b. *cyathigerum* unknowns		
CALIF.: Madera Co., Sugar Pine		2
CALIF.: Mariposa Co., 7 mi. ENE of Fish Camp	1	
CALIF.: Mono Co., small pond at Tioga Pass, N. of Yosemite Nat'l Park	1*	
CALIF.: Placer Co., small pond at Donner Pass	3*	1
CALIF.: Santa Clara Co., San Antonia Val.	1	1
CALIF.: Stanislaus Co., Del Puerto Cyn. at N. Fork Del Puerto Cr., 22 mi. N. of Patterson	1	3
NEV.: Elko Co., Zunino Reservoir, by Nev. Hwy. 6, N. of Jiggs		1
SUBTOTAL:	22	20
5.a. *praevarum* reference		
ARIZ.: Cochise Co., Herb Martyr Dam, Chiricahua Mts.	1	
ARIZ.: Maricopa Co., Cave Creek at end of Ocotillo Rd., Cave Creek	2*	7*
CALIF.: Contra Costa Co., pond, 1 mi. E. of Pinole	1*	

Table 2, Cont.

	No. of specimens ♂♂	♀♀
b. *praevarum* unknowns		
MEXICO.: Chihuahua: 23 km. E. of El Vergel (La Laguna), Rio San Juan	2	2
MEXICO.: Durango: El Pino	3	1
ARIZ.: Cochise Co., Herb Martyr Dam, Chiricahua Mts.		1
ARIZ.: Maricopa Co., Cave Creek at end of Ocotillo Rd., Cave Creek		1*
CALIF.: Alameda Co., pond nr. Livermore		1*
SUBTOTAL:	9	13
TOTAL:	74	77

Table 3. Characters used in phenetic analysis of western *Enallagma* larvae.

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1. *LABIUM*

MENS - number of premental setae (Fig. 3)

MAGS - number of marginal setae (Fig. 3)

LATS - number of palpal setae (Fig. 3)

MENL - length of prementum along midline, from apex to, but not including, hinge (Fig. 2)

MEDW - distal width of prementum at bases of palpal lobes (Fig. 2)

MEBW - basal width of prementum, excluding hinge (Fig. 2)

2. *ANTENNA*

SEG1 - length of basal segment

SEG2 - length of segment 2

SEG3 - length of segment 3

SEG4 - length of segment 4

SEG5 - length of segment 5

SEG6 - length of segment 6

3. *WINGS*

HWPD - length of hindwing pad along mesal line from concavity just before insertion to tip of pad. Measurements were not made to the point of insertion because the proximal part of the wing pad was often hidden by the dorsal edge of the synthorax.

4. *ABDOMINAL SEGMENTS*

TENL - length of abdominal segment ten measured laterally (Fig. 5)

5. *GILLS*

XVSD - number of antenodal setae on dorsal side of lateral gill

XVSV - number of antenodal setae on ventral side of lateral gill

XDSD - number of antenodal setae on dorsal side of median gill

Table 3, Cont.

XDSV - number of antenodal setae on ventral side of median gill

XDSL - length of antenodal setae row on dorsal side of median gill from base to nodal joint (Fig. 1)

XVSL - length of antenodal setae row on ventral side of median gill from base to nodal joint (Fig. 1)

GILL - length of median gill from base to tip (Fig. 1)

GILW - greatest width of median gill (Fig. 1)

6. *CAUDAL APPENDAGE*

APPL - length of cercus measured from the side (Fig. 5)

Table 4. Pharate caudal appendage characters used in phenetic analysis of male *E. boreale* and *E. cyathigerum*.

DVHEIG -	greatest length of appendage measured diagonally in a dorso-proximal to ventro-distal axis (Fig. 7)
LATHEIG -	greatest length of appendage measured diagonally in a ventroproximal to dorso-distal axis (Fig. 7)
STUBHEI -	greatest height of distal stub measured near the proximal third of appendage. In *E. cyathigerum*, this structure is narrow and well-demarcated by abrupt folds (Fig. 7). In *E. boreale*, this structure is wide and usually demarcated by an abrupt fold only dorsally. Heights were measured between these folds (Fig. 8).

Table 5. Pharate caudal appendage and ovipositor characters used in phenetic analysis of female *Enallagma* species.

1. *OVIPOSITOR*

GONOPHY	- length of lateral gonopophysis from juncture of segment 9 to tip (Fig. 4)
BASALHEI	- height of lateral gonopophysis measured along the line of transverse carinae at end of segment 9 (Fig. 4)
DISTHEI	- height of lateral gonopophysis measured from concavity just posterior to spine to dorsal emargination. This corresponds to the base of the stylus in the adult female (Fig. 4)
OVIGAP	- distance between tip of lateral gonopophysis and tip of second (dorsal) valvulae (Fig. 4)

Table 5, Cont.

2. *CERCUS*		
DISTAL	-	viewed posteriorly, greatest length measured from tip of appendage to distal edge (Fig. 9)
MESAL	-	viewed posteriorly, greatest length measured from tip of appendage to mesal edge (Fig. 9)
TOP	-	viewed posteriorly, greatest length measured from tip of appendage to dorsal edge (Fig. 9)
BOTTOM	-	viewed posteriorly, greatest length measured from tip of appendage to ventral edge (Fig. 9)
STUBHEI	-	greatest height of distal stub measured through a line bisecting the appendage tip. In *E. carunculatum*, this structure is narrow and demarcated by transverse abrupt folds. Sometimes folds lie in a diagonal position (Fig. 11). When folds are vertical, distance was measured encompassing the length of the fold (Fig. 12). In *E. boreale*, usually only the dorsal fold was apparent, and the distance was then measured dorsoventrally from dorsal fold to ventral edge of appendage (Fig. 10)
APPLENG	-	distance from tip of appendage to distal base viewed dorsoposteriorly so that distal base is not obscured by margin of abdominal segment 10 (Figs. 14-15)
ARC	-	greatest degree of concavity of proximal edge of appendage viewed ventrolaterally. Distance was measured between line drawn from proximal base of appendage to tip and median concave portion of appendage (Figs. 17-19). Measurements taken on ♀♀ *E. carunculatum*, *E. civile*, and *E. praevarum* only.

Table 6. Standardized discriminant function coefficients, eigenvalues, canonical correlation, percent variation explained, and Wilks' lambda for *Enallagma* larvae using gill and antennal characters. All lambdas are significant at the 0.001 level.

Variable	DF 1	DF 2
XDSD	0.776	-0.011
XVSD	-1.217	1.196
XDSL	-1.580	-0.990
GILL	0.779	0.513
SEG4	0.218	-1.462
Eigenvalue	4.150	1.826
Percent Variation	58.8	25.9
Canonical Correlation	0.898	0.804
Wilks' Lambda	0.031	0.157

Table 7. Unstandardized discriminant function coefficients for *Enallagma* larvae using gill and antennal characters.

Variable	DF 1	DF 2
XDSD	0.131	-0.002
XVSD	-0.140	0.138
XDSL	-3.052	-1.913
GILL	1.458	0.961
SEG4	3.185	-21.364
Constant	-3.360	5.855

Table 8. Classification tables of knowns and unknowns for five *Enallagma* species using characters XDSD, XVSD, XDSL, GILL, and SEG4. Numbers in parentheses are percentages. Group 1: *E. boreale*, *E. cyathigerum*. Group 2: *E. carunculatum*, *E. civile*, and *E. praevarum*.

	GROUP 1		GROUP 2			
KNOWNS	*boreale*	*cyathigerum*	*carunculatum*	*civile*	*praevarum*	Total
boreale	9 (90)	1 (10)	0	0	0	10
cyathigerum	6 (22.2)	20 (74.1)	0	0	1 (3.7)	27
carunculatum	0	0	14 (100)	0	0	14
civile	0	0	0	14 (93.3)	1 (6.3)	15
praevarum	1 (9.1)	0	1 (9.1)	0	9 (81.8)	11
				Total misclassified (species):		11 (14.3)
				Total misclassified (Groups):		2 (2.6)
UNKNOWNS						
boreale	3 (50)	3 (50)	0	0	0	6
cyathigerum	3 (50)	3 (50)	0	0	0	6
carunculatum	2 (10.4)	1 (5.3)	14 (73.7)	1 (5.3)	1 (5.3)	19
civile	0	0	4 (57.1)	2 (28.6)	1 (14.3)	7
praevarum	1 (12.5)	1 (12.5)	0	0	6 (75.0)	8
				Total misclassified (species):		18 (39.1)
				Total misclassified (Groups):		5 (10.9)

Table 9. Standardized discriminant function coefficients, eigenvalues, canonical correlation, percent variation explained, and Wilks' lambda for male *Enallagma boreale* and *E. cyathigerum* larvae using cercus characters. All lambdas are significant at the 0.001 level.

Variable	DF 1
DVHEIG	-0.326
LATHEIG	0.220
STUBHEI	1.740
Eigenvalue	2.227
Percent variation	100.0
Canonical correlation	0.831
Wilks' Lambda	0.301

Table 10. Unstandardized discriminant function coefficients for male *Enallagma boreale* and *E. cyathigerum* larvae using cercus characters.

Variable	DF 1
DVHEIG	-11.691
LATHEIG	8.527
STUBHEI	69.953
Constant	-7.568

Table 11. Standardized discriminant function coefficients, eigenvalues, canonical correlation, percent variation explained, and Wilks' lambda for female *Enallagma boreale* and *E. cyathigerum* larvae using cercus characters. All lambdas are significant at the 0.001 level.

Variable	DF 1
BOTTOM	-0.394
APPLENG	-0.395
STUBHEI	2.299
Eigenvalue	4.556
Percent variation	100.0
Canonical correlation	0.906
Wilks' Lambda	0.180

Table 12. Unstandardized discriminant function coefficients for female *Enallagma boreale* and *E. cyathigerum* larvae using cercus characters.

Variable	DF 1
BOTTOM	-17.733
APPLENG	-19.445
STUBHEI	68.320
Constant	-0.882

Table 13. Classification tables of knowns and unknowns for two *Enallagma* species using pharate sexual characters of larvae. Numbers in parentheses are percentages.

KNOWNS	Sex	*boreale*	*cyathigerum*	Total
boreale	♂♂	6 (85.7)	1 (14.3)	7
cyathigerum	♂♂	0	15 (100)	15
			Total misclassified:	1 (4.5)
boreale	♀♀	7 (100)	0	7
cyathigerum	♀♀	0	12 (100)	12
			Total misclassified:	0
UNKNOWNS				
boreale	♂♂	4 (80)	1 (20)	5
cyathigerum	♂♂	0	7 (100)	7
			Total misclassified:	1 (8.3)
boreale	♀♀	4 (100)	0	4
cyathigerum	♀♀	3 (37.5)	5 (62.5)	8
			Total misclassified:	3 (25)

Table 14. Standardized discriminant function coefficients, eigenvalues, canonical correlation, percent variation explained, and Wilks' lambda for female *Enallagma carunculatum*, *E. civile*, and *E. praevarum* larvae using cercus and ovipositor characters. All lambdas are significant at the 0.001 level.

Variable	DF 1	DF 2
BASALHEI	-0.515	-0.028
APPLENG	2.045	1.514
GONOPHY	-0.696	-0.511
ARC	0.933	-1.831
Eigenvalue	10.613	0.764
Percent variation	93.3	6.7
Canonical correlation	0.956	0.658
Wilks' Lambda	0.049	0.657

Table 15. Unstandardized discriminant function coefficients for female *Enallagma carunculatum*, *E. civile*, and *E. praevarum* larvae using cercus and ovipositor characters.

Variable	DF 1	DF 2
BASALHEI	-37.886	-2.045
APPLENG	65.516	48.484
GONOPHY	-11.663	-8.552
ARC	83.027	-162.916
Constant	3.816	-0.281

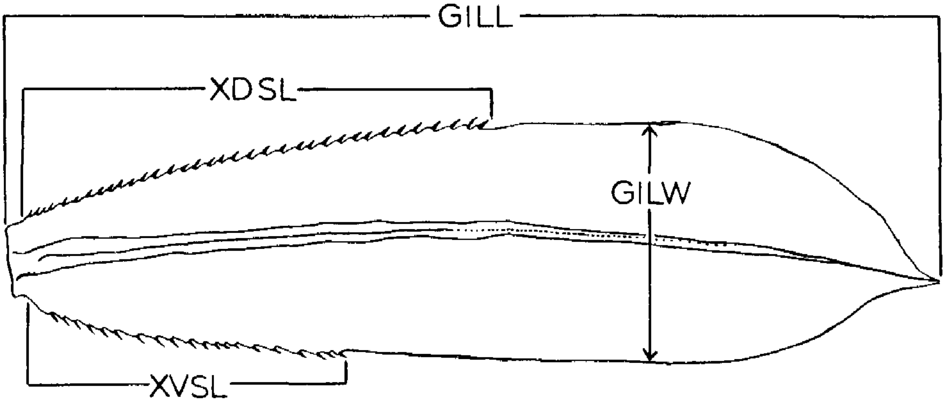
Table 16. Classification tables of knowns and unknowns for three female *Enallagma* species using pharate sexual characters of larvae. Numbers in parentheses are percentages.

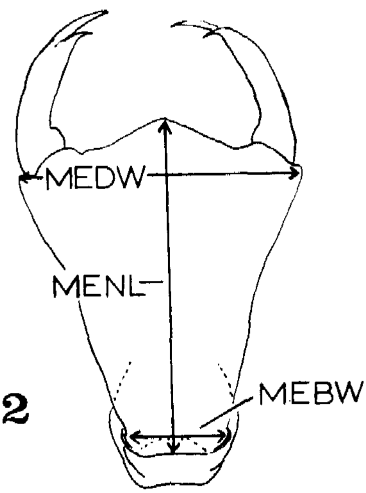
KNOWNS	*carunculatum*	*civile*	*praevarum*	Total
carunculatum	8 (100)	0	0	8
civile	0	9 (100)	0	9
praevarum	1 (14.3)	0	6 (85.7)	7
		Total misclassified:		1 (4.2)
UNKNOWNS				
carunculatum	9 (81.8)	0	2 (18.2)	11
civile	0	5 (100)	0	5
praevarum	0	1 (16.7)	5 (83.3)	6
		Total misclassified:		3 (13.6)

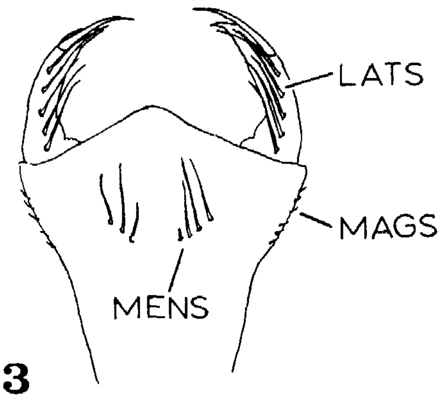
Figures

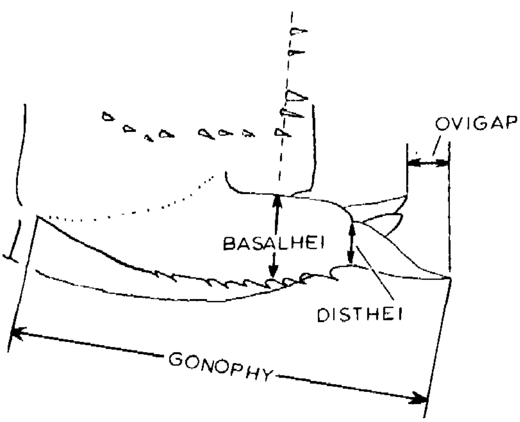
Characters of *Enallagma* larvae showing measurements used in discriminant analysis.

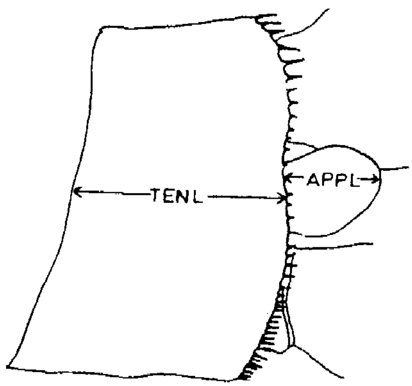
Fig. 1. Median gill of *E. boreale*.
Fig. 2. Prementum of *E. praevarum*, ventral view.
Fig. 3. Prementum of *E. praevarum*, dorsal view.
Fig. 4. Ovipositor of *E. boreale*, lateral view.
Fig. 5. Abdominal segment 10 and cercus of *E. civile* ♂, lateral view.


GILL
XDSL
GILW
XVSL
1


MEDW
MENL
MEBW
2


LATS
MAGS
MENS
3


OVIGAP
BASALHEI
DISTHEI
GONOPHY
4


TENL
APPL
5

1mm

Characters of *Enallagma* larvae showing measurements used in discriminant analysis. 0.5 mm bar for all figures except Figs. 6 and 16.

Fig. 6. *E. cyathigerum* ♂. Posterior view of abdominal segment 10 with caudal gills removed. Calif., Placer Co.

Fig. 7. *E. cyathigerum* ♂. Caudal appendages of specimen in Fig. 6, posterior view.

Fig. 8. *E. boreale* ♂. Caudal appendages, posterior view. Calif., Contra Costa Co.

Fig. 9. *E. boreale* ♀. Caudal appendages, posterior view. Calif., Placer Co.

Fig. 10. *E. boreale* ♀. Right caudal appendage of specimen in Fig. 9.

Fig. 11. *E. cyathigerum* ♀. Right caudal appendage, posterior view. Calif., Placer Co.

Fig. 12. *E. cyathigerum* ♀. Right caudal appendage, posterior view. Calif., Madera Co.

Fig. 13. *E. cyathigerum* ♀. Right caudal appendage, posterior view. England.

Fig. 14. *E. boreale* ♀. Left caudal appendage of specimen in Fig. 9, dorsal view.

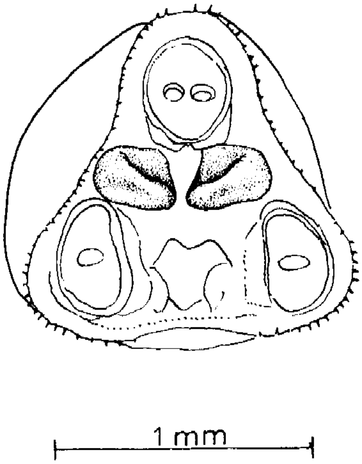
Fig. 15. *E. civile* ♀. Left caudal appendage, dorsal view. Calif., Stanislaus Co.

Fig. 16. *E. carunculatum* ♀. Abdominal segment 10 and caudal appendages with caudal gills removed, right ventrolateral view.

Fig. 17. *E. carunculatum* ♀. Right caudal appendage of specimen in Fig. 16, ventrolateral view.

Fig. 18. *E. civile* ♀. Right caudal appendage of specimen in Fig. 15, ventrolateral view.

Fig. 19. *E. praevarum* ♀. Right caudal appendage, ventrolateral view.



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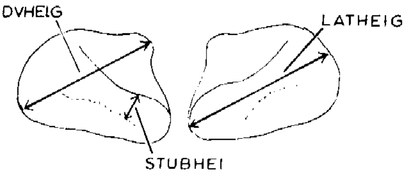

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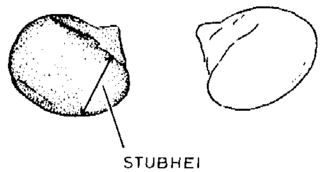

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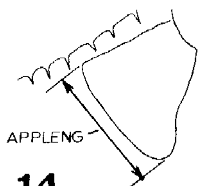

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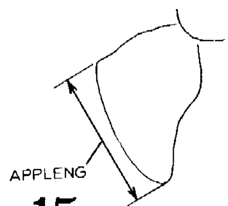

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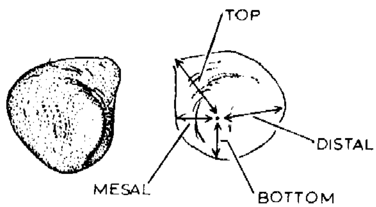

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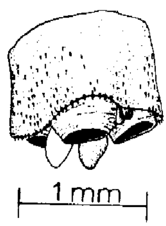

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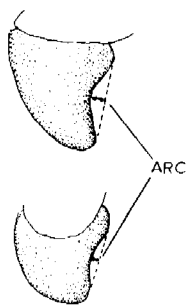
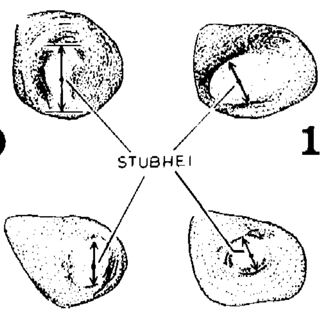


18

19

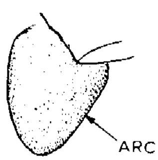


10

11

12

13



17

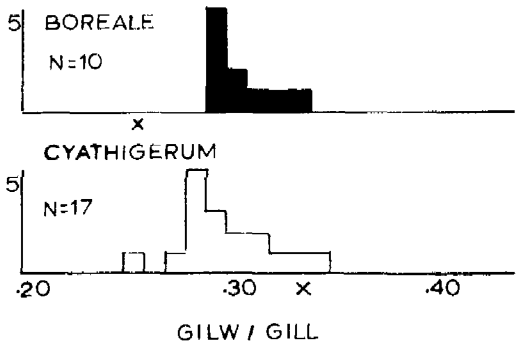
0·5mm

Fig. 20. Histograms of GILW/GILL ratios between reared *E. boreale* and *E. cyathigerum*. X's along abscissa are values from Walker's (1953) key to the larvae.

Fig. 21. Histograms of HW/GILL ratios between reared *E. boreale* and *E. cyathigerum*. X's along abscissa are values from Walker's (1953) key to the larvae.

Fig. 22. Histograms of XDSL/GILL ratios between reared *E. carunculatum* and *E. civile*. X's along abscissa are values from Walker's (1953) key to the larvae.

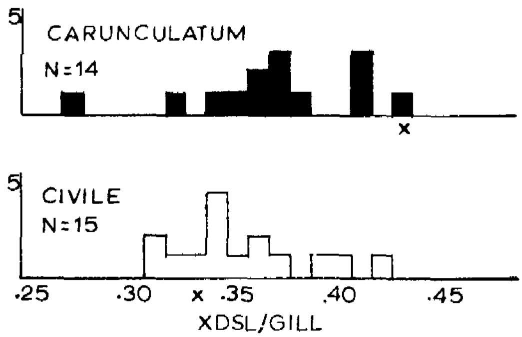
20


5
BOREALE
N=10
x
CYATHIGERUM
5
N=17
.20
.30
x
.40
GILW / GILL

21


5
BOREALE
N=10
x x x x x x x x x x x x x
5
CYATHIGERUM
N=17
.60
.70
.80
x
HW / GILL

22


5
CARUNCULATUM
N=14
x
5
CIVILE
N=15
.25
.30
x
.35
.40
.45
XDSL/GILL

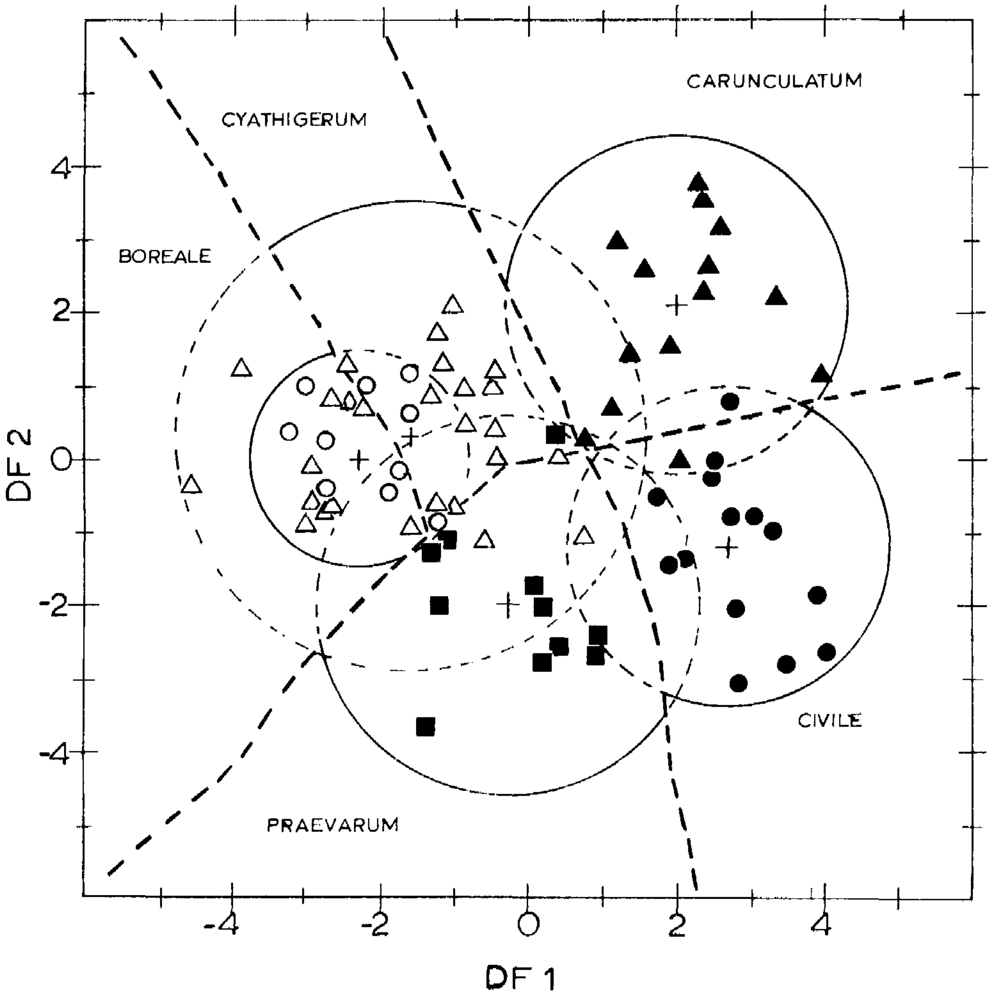


Fig. 23. Plot of discriminant scores of reference male and female *Enallagma* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. ○ = *boreale*, △ = *cyathigerum*, ▲ = *caruncula-tum*, ● = *civile*, and ■ = *praevarum*. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate critical values between adjacent taxa.

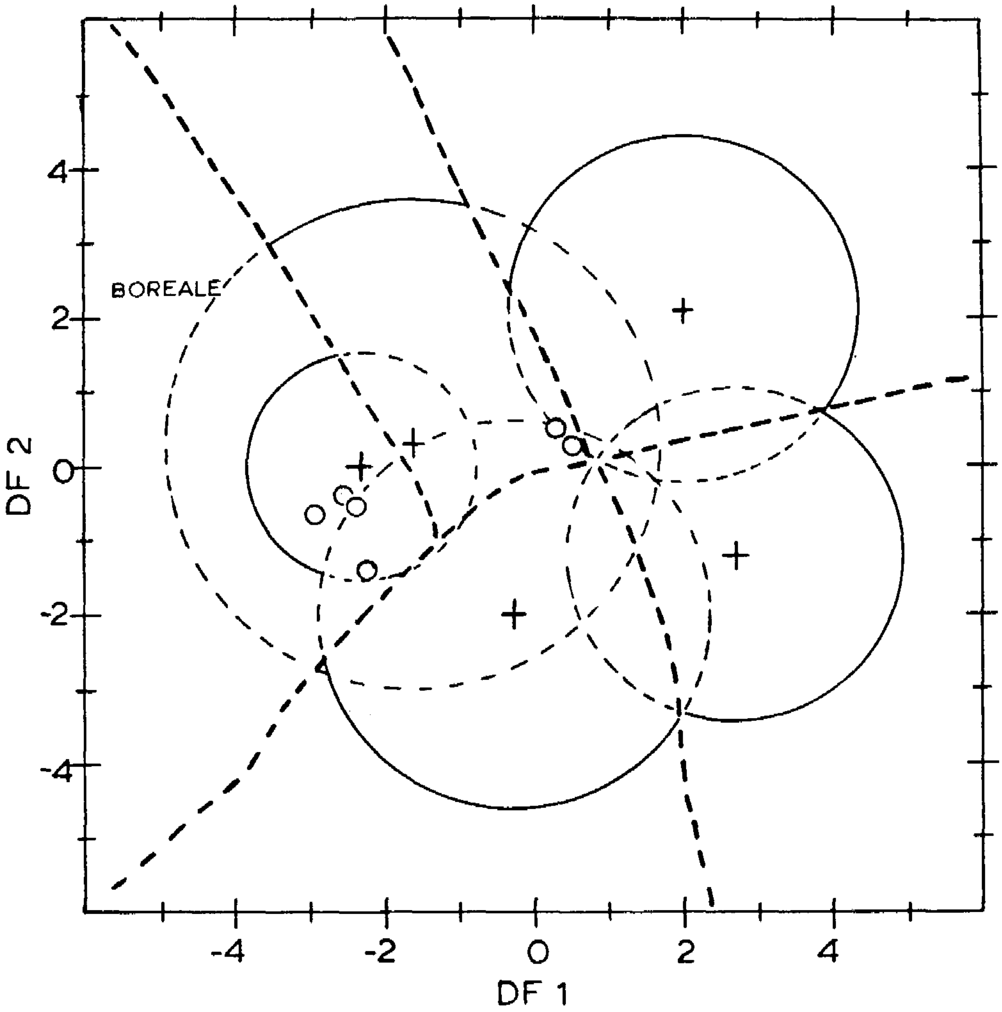


Fig. 24. Plot of discriminant scores of unknown male and female *E. boreale* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate territorial map boundaries, as indicated in Fig. 23.

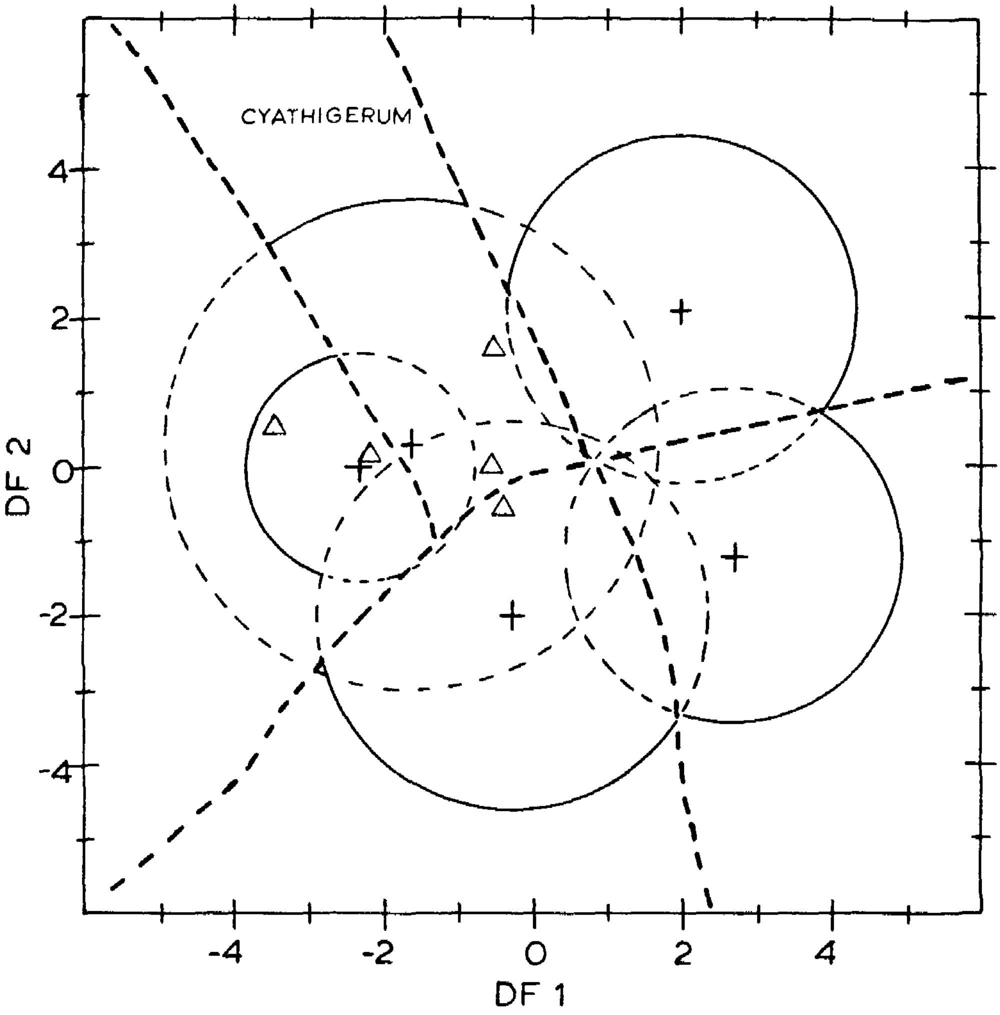


Fig. 25. Plot of discriminant scores of unknown male and female *E. cyathigerum* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate boundaries of territorial maps as indicated in Fig. 23.

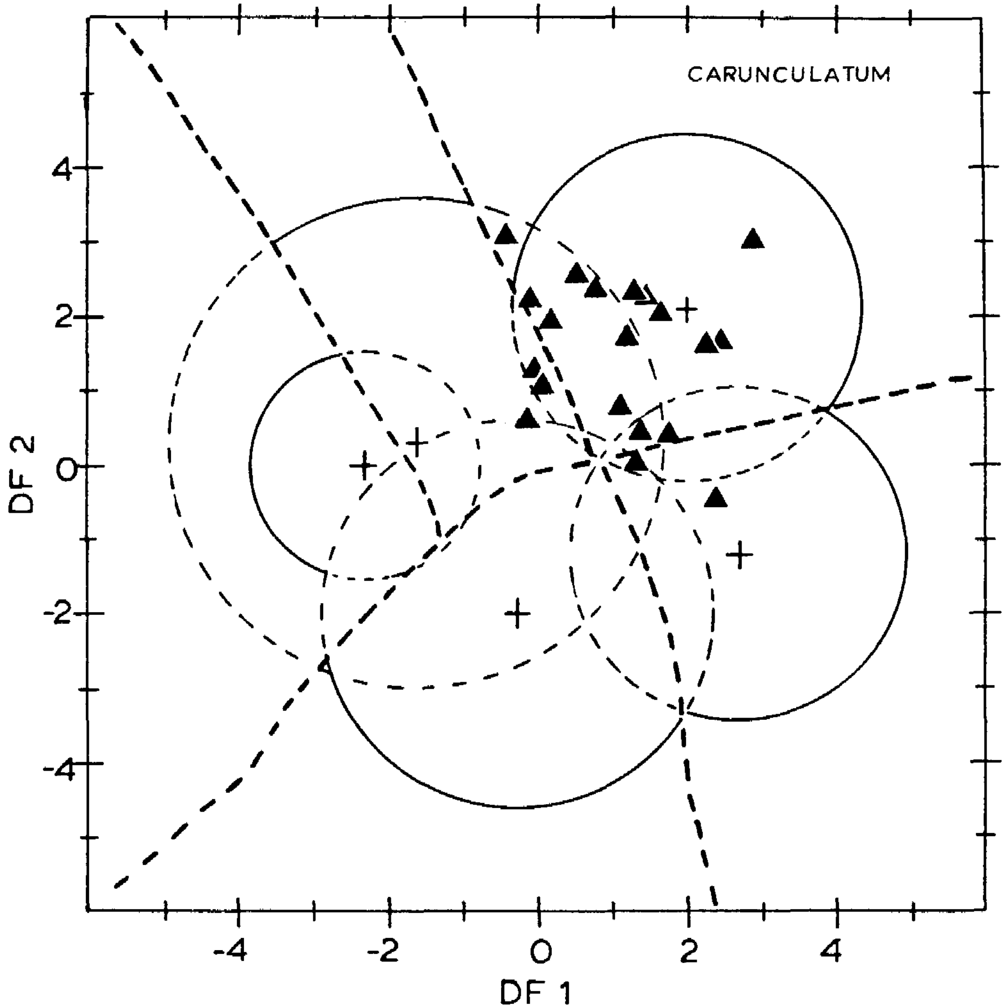


Fig. 26. Plot of discriminant scores of unknown male and female *E. carunculatum* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate boundaries of territorial maps as indicated in Fig. 23.

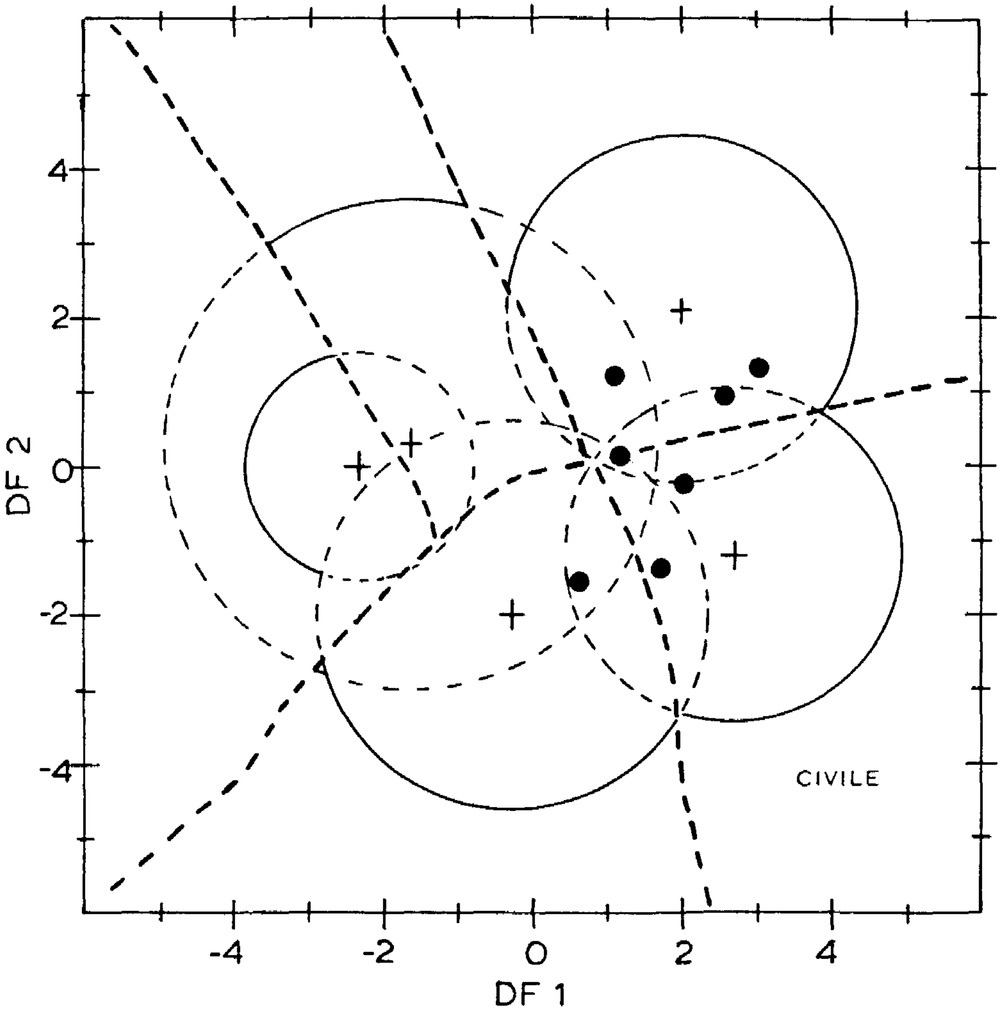


Fig. 27. Plot of discriminant scores of unknown male and female *E. civile* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate boundaries of territorial maps as indicated in Fig. 23.

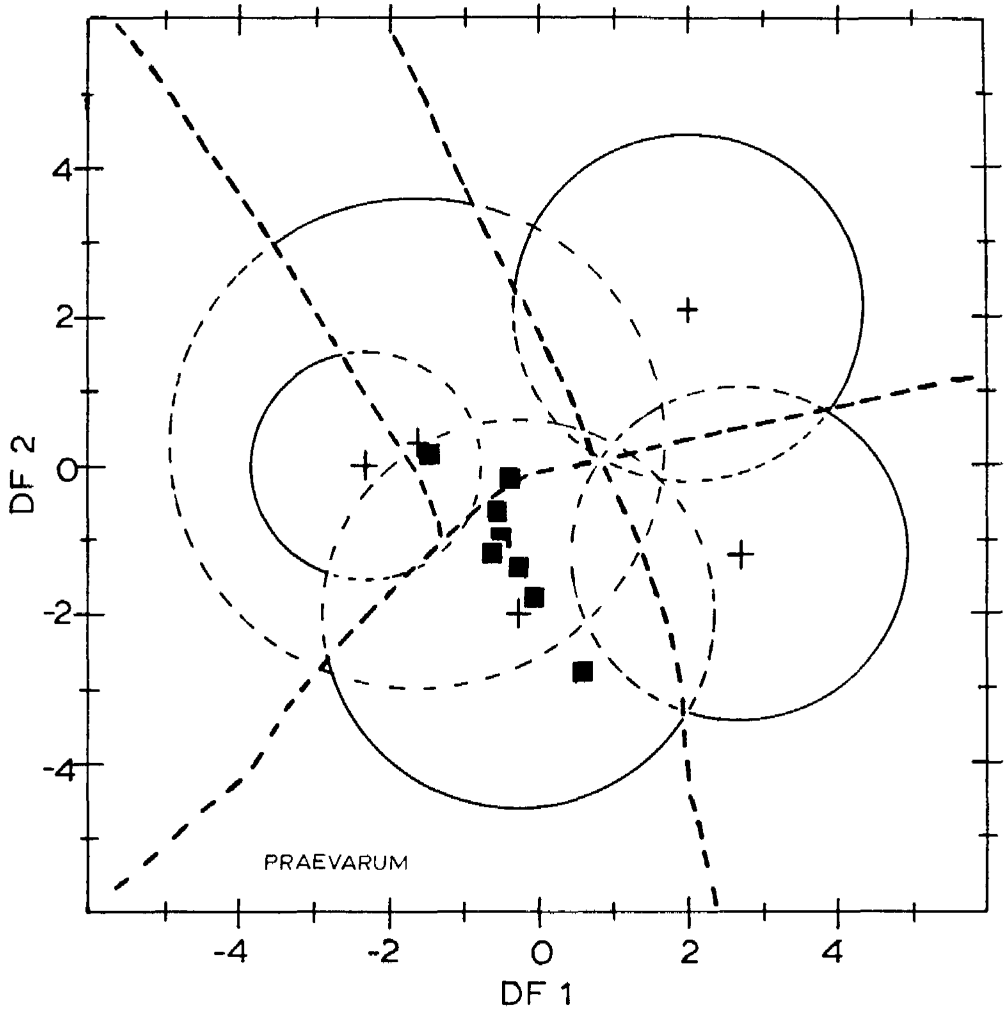
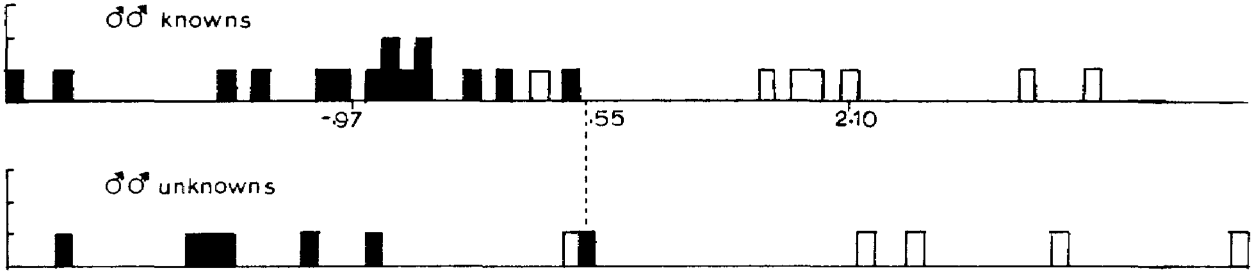


Fig. 28. Plot of discriminant scores of unknown male and female *E. praevarum* larvae based on characters XDSD, XVSD, XDSL, GILL, and SEG4. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted curvilinear lines indicate boundaries of territorial maps as indicated in Fig. 23.

Fig. 29. Linear discriminant analysis plots between known (above) and unknown (below) *E. boreale* and *E. cyathigerum* male larvae based on the characters DVHEIG, LATHEIG, and STUBHEI. Means and midpoints (dotted line) are shown for both graphs.

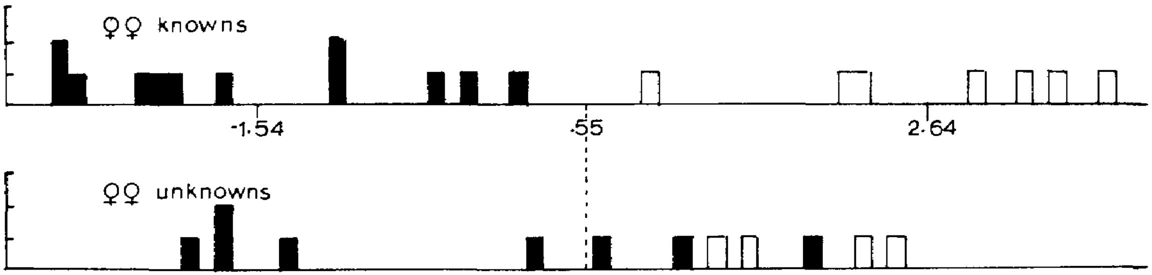
Fig. 30. Linear discriminant analysis plots between known (above) and unknown (below) *E. boreale* and *E. cyathigerum* male larvae based on the characters BOTTOM, APPLENG, and STUBHEI. Means and midpoints (dotted line) are shown for both graphs.



♂♂ knowns
-97
·55
2·10
♂♂ unknowns

29

BOREALE
CYATHIGERUM



♀♀ knowns
-1·54
·55
2·64
♀♀ unknowns

30

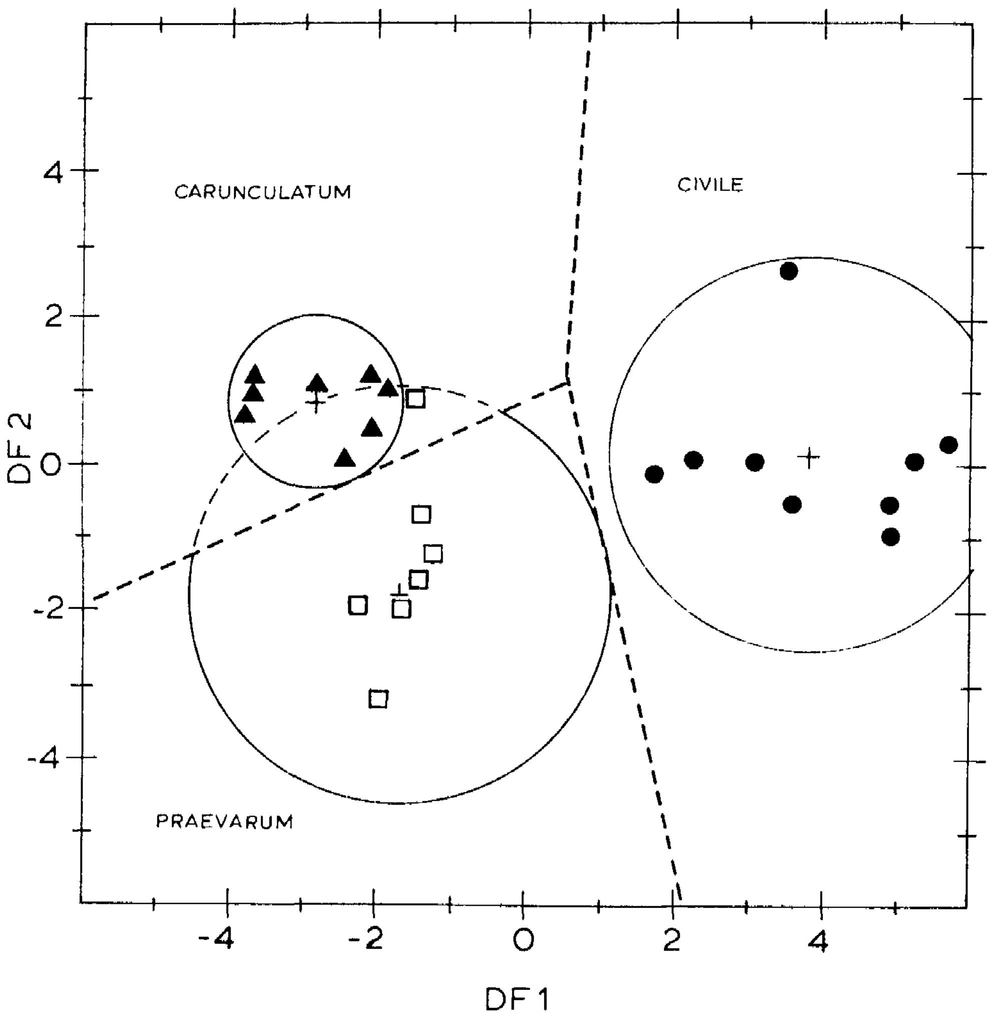


Fig. 31. Plot of discriminant scores of reference female *Enallagma* larvae using characters BASALHE, APPLENG, GONOPHY, and ARC. ▲ = *carunculatum*, ● = *civile*, □ = *praevarum*. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted lines indicate critical values between adjacent taxa.

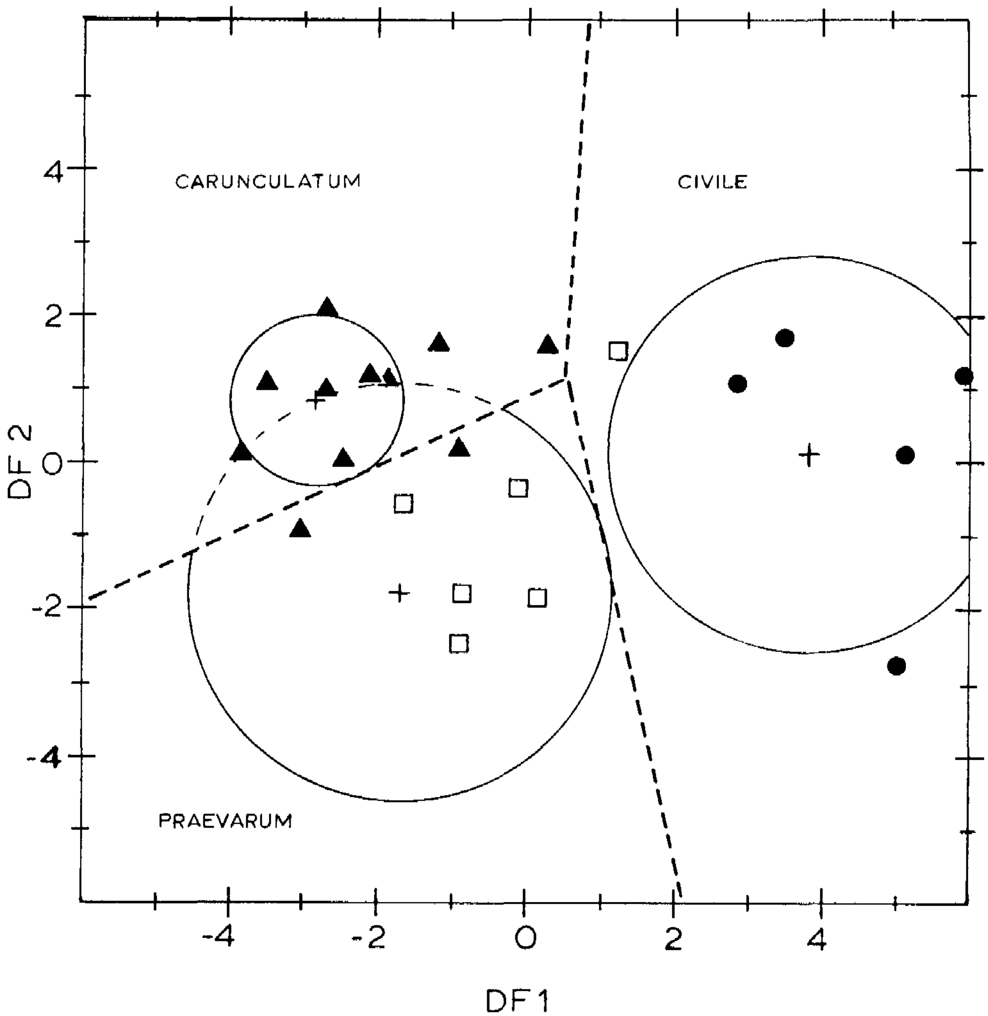


Fig. 32. Plot of discriminant scores of unknown female *Enallagma* larvae using characters BASALHE, APPLENG, GONOPHY, and ARC. ▲ = *carunculatum*, ● = *civile*, □ = *praevarum*. Large circles are minimum diameter circles that will enclose the respective reference groups. Crosses indicate group centroids. Heavy dotted lines indicate territorial map boundaries as indicated in Fig. 31.

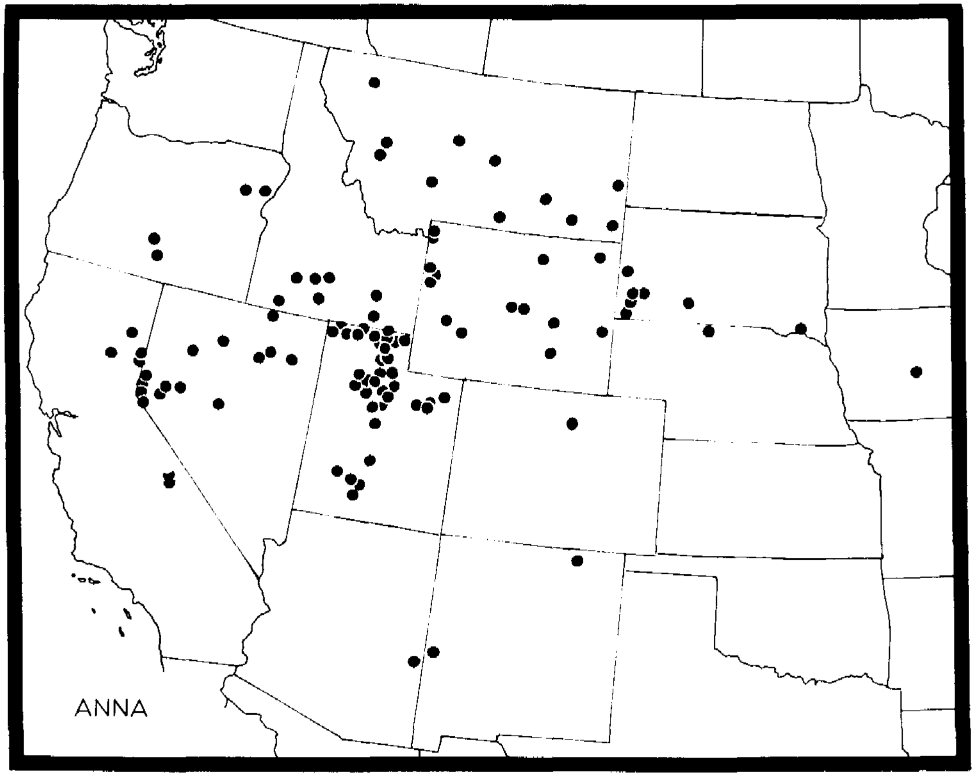


Fig. 33. Distribution of *Enallagma anna*.

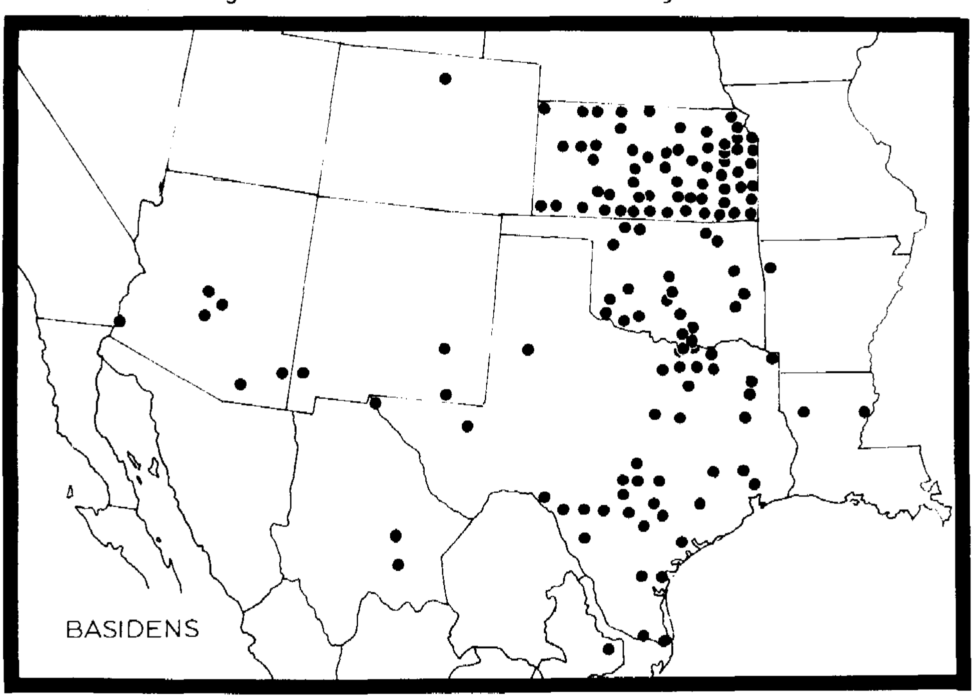


Fig. 34. Distribution of *Enallagma basidens*.

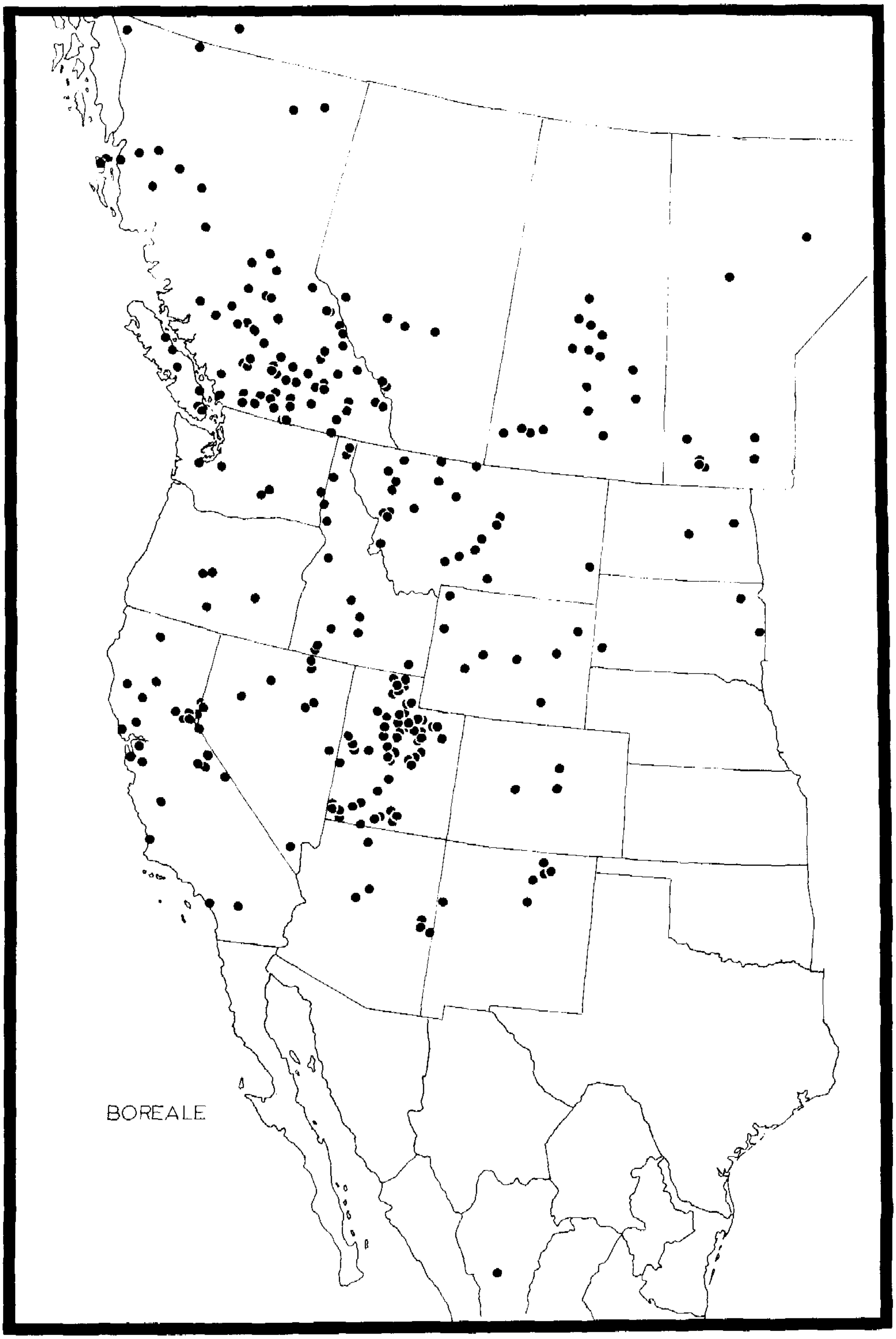


Fig. 35. Distribution of *Enallagma boreale*.

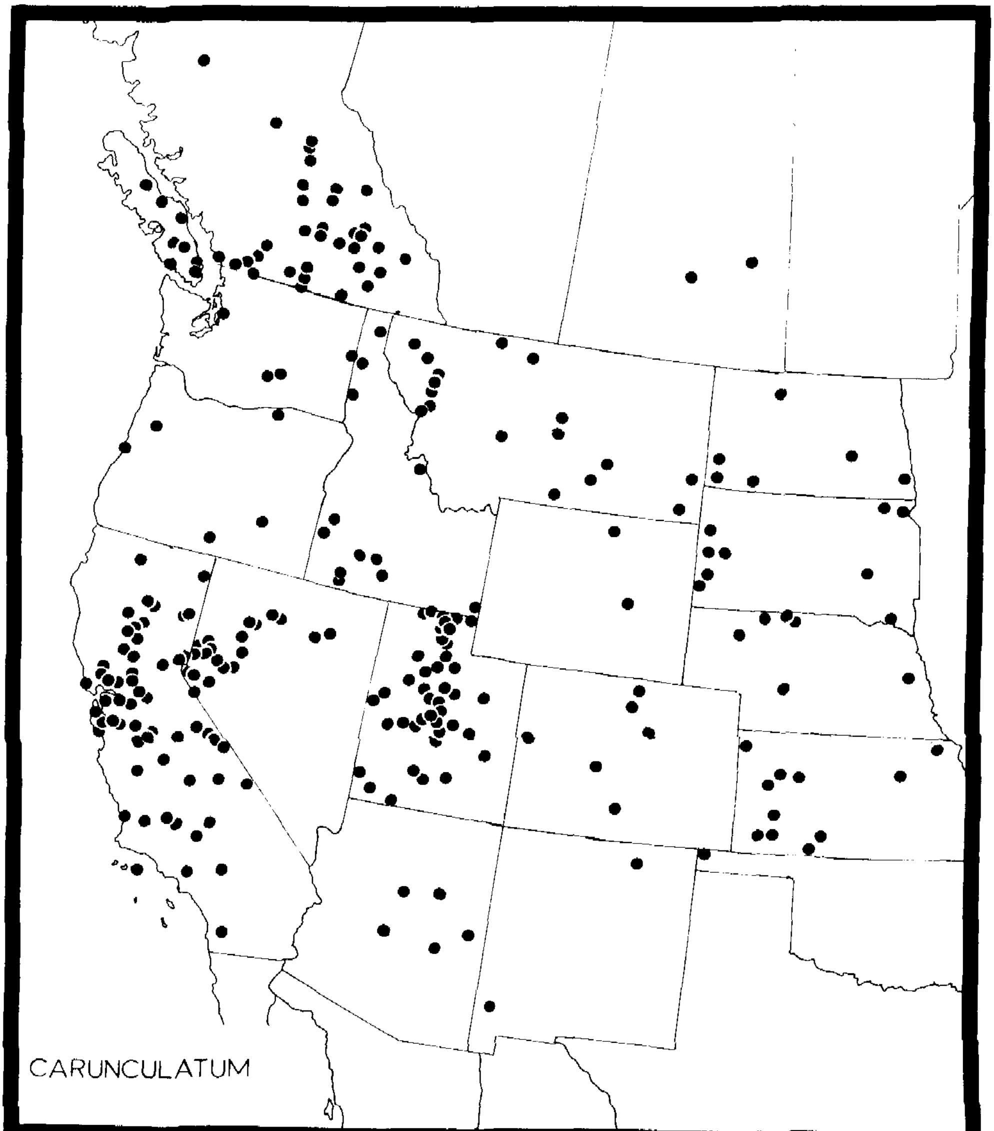


Fig. 36. Distribution of *Enallagma carunculatum*.

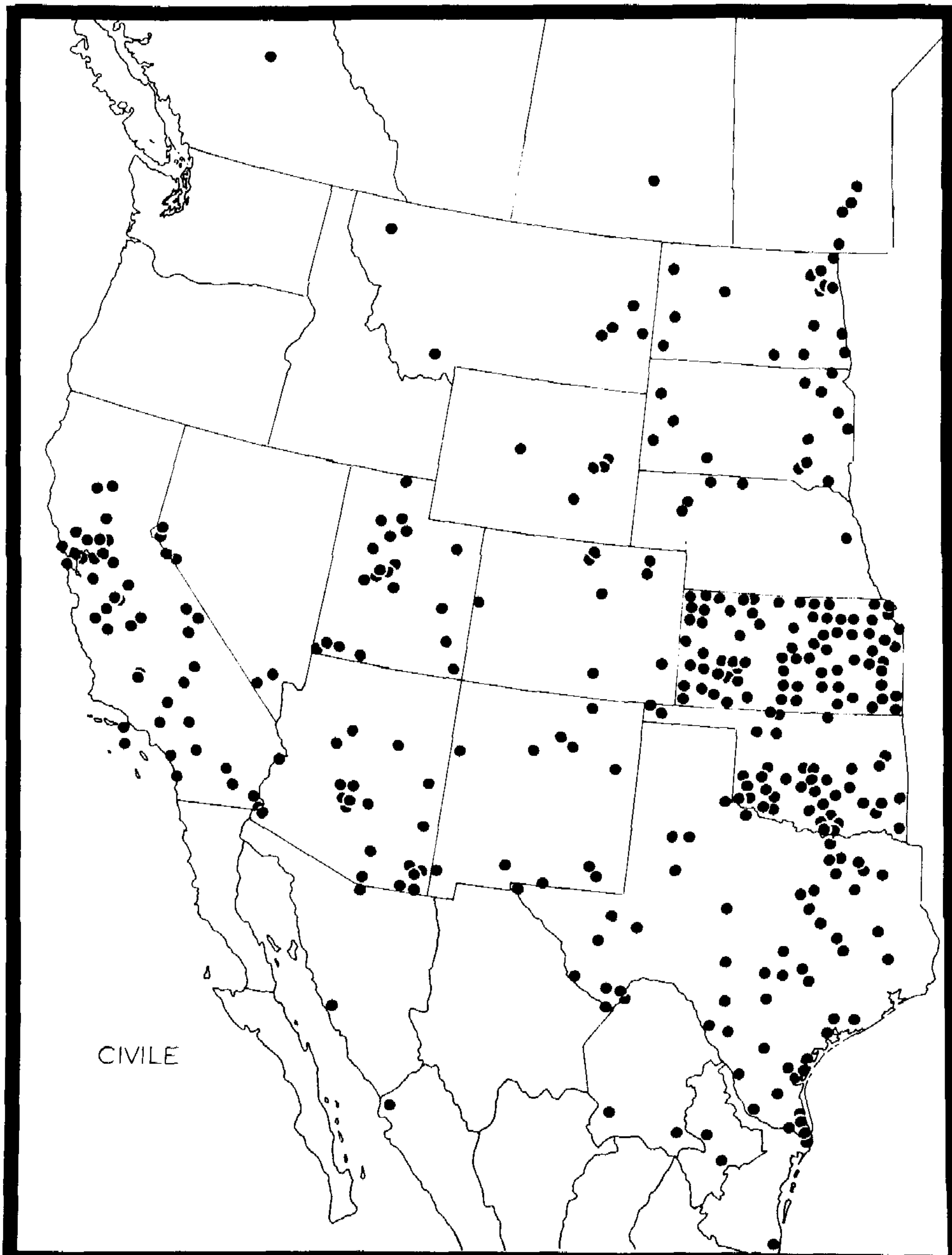


Fig. 37. Distribution of *Enallagma civile*.

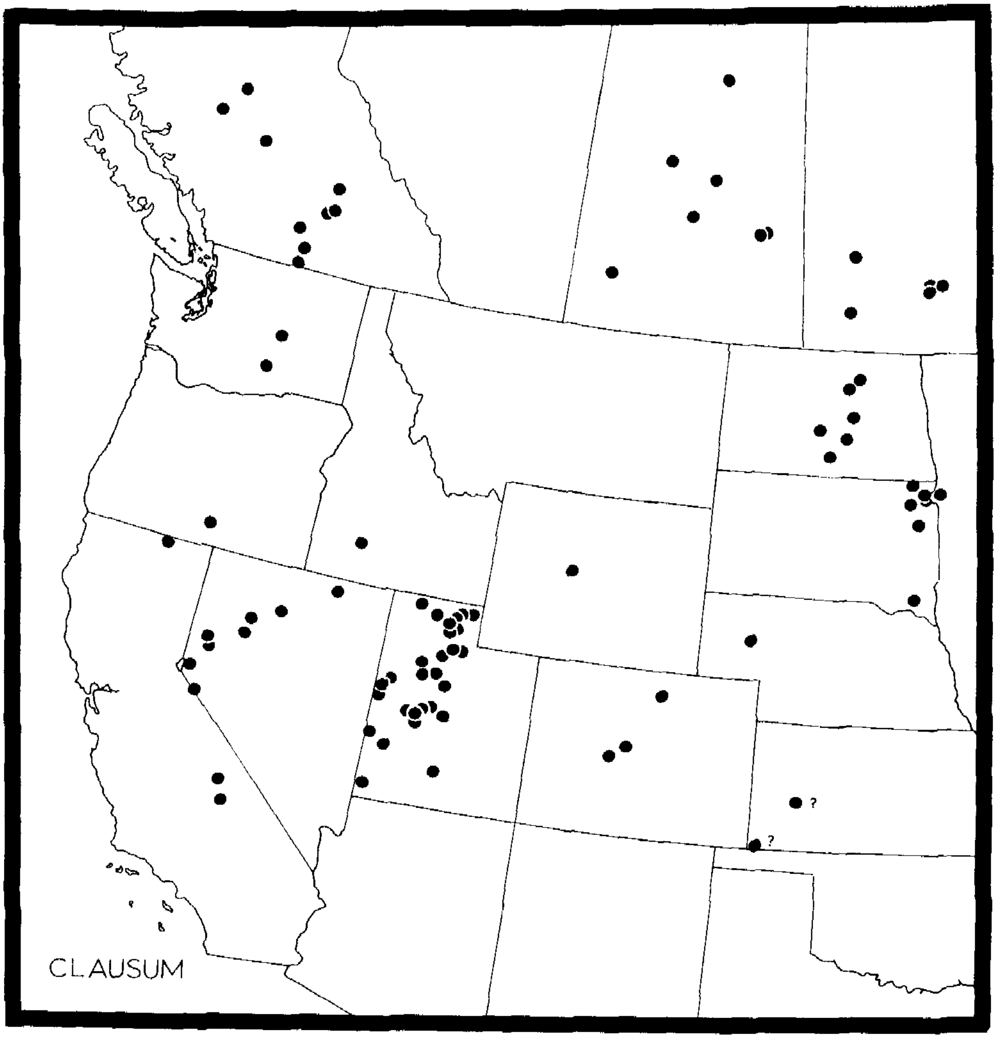


Fig. 38. Distribution of *Enallagma clausum*.

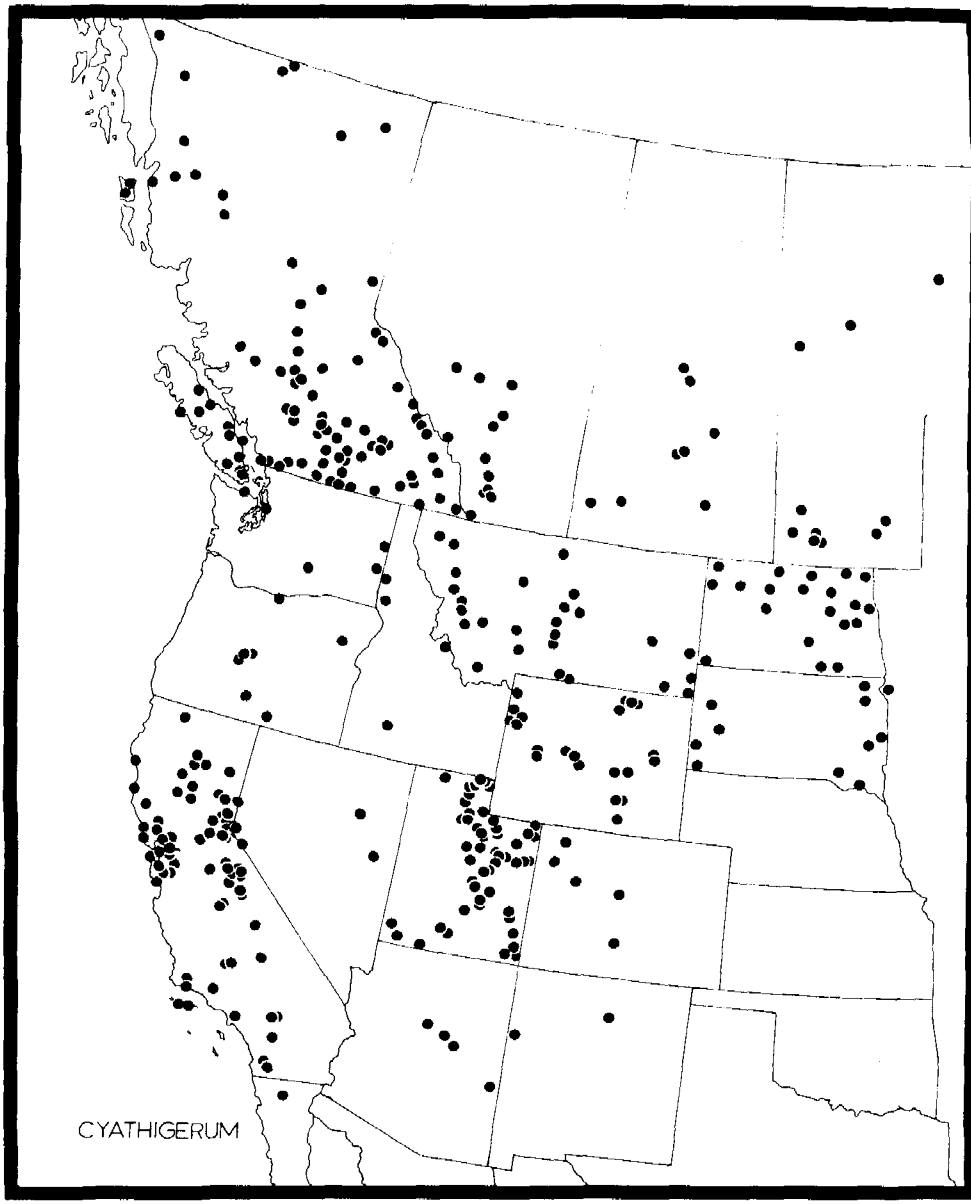


Fig. 39. Distribution of *Enallagma cyathigerum*.

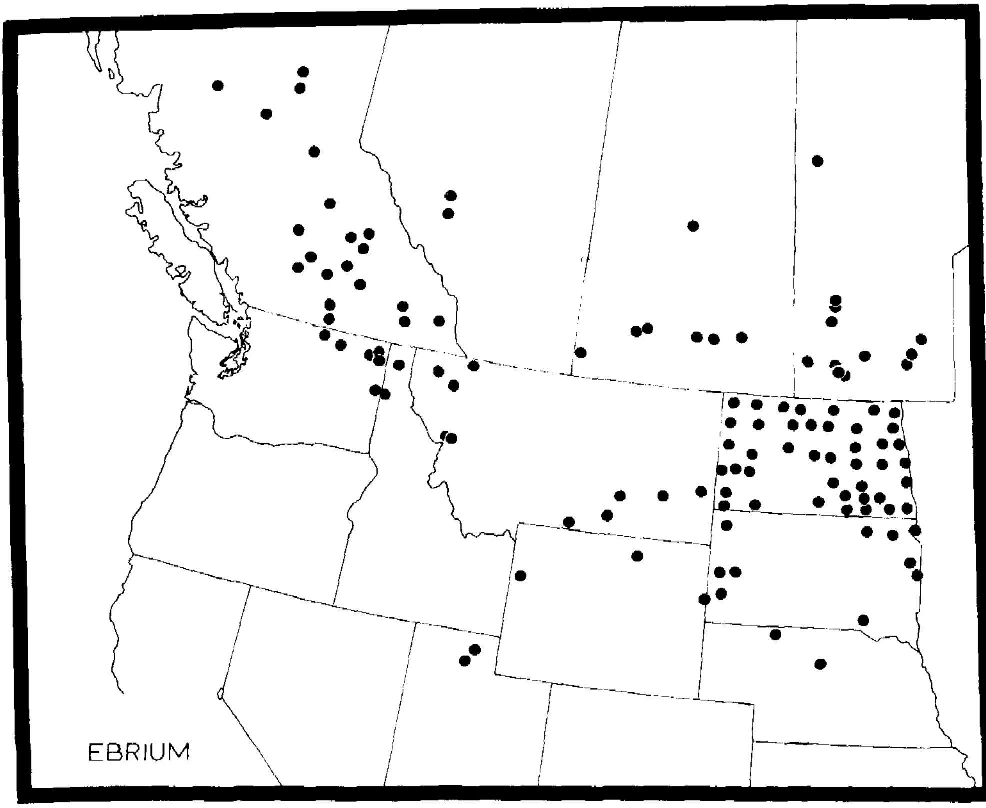


Fig. 40. Distribution of *Enallagma ebrium*.

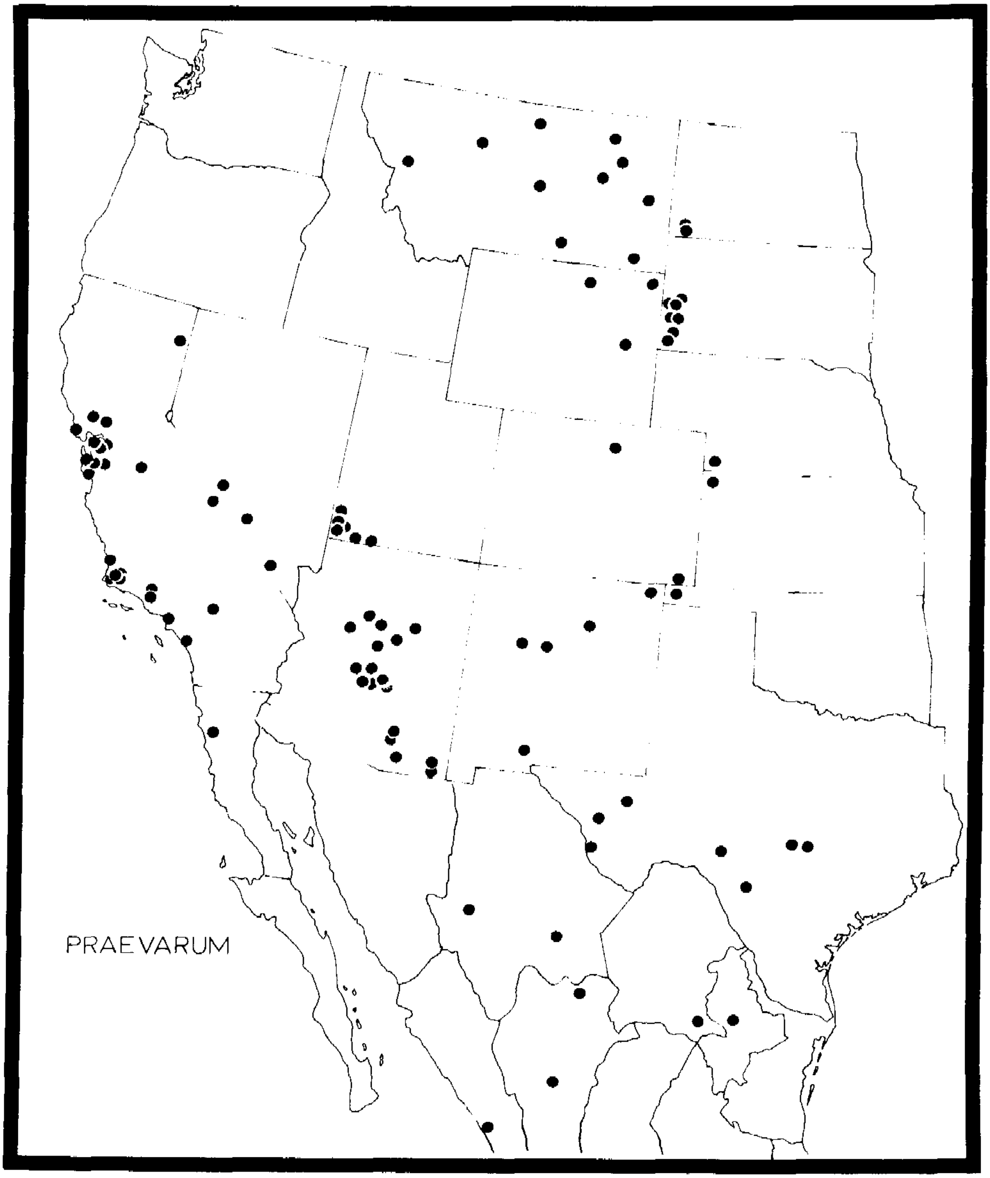
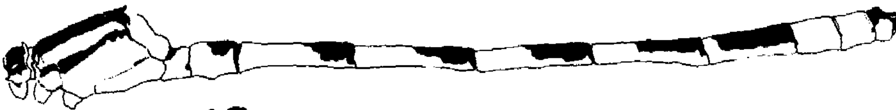


Fig. 41. Distribution of *Enallagma praevarum*.

Color pattern of *Enallagma* males, lateral view.

Fig. 42. *E. anna.* Calif., Lassen Co.
Fig. 43. *E. basidens.* Ariz., Maricopa Co.
Fig. 44. *E. praevarum.* Calif., Stanislaus Co.
Fig. 45. *E. carunculatum.* Calif., Siskiyou Co.
Fig. 46. *E. civile.* Calif., Solano Co.
Fig. 47. *E. ebrium.* Wash., Pend Oreille Co.
Fig. 48. *E. boreale.* Calif., Mono Co.
Fig. 49. *E. cyathigerum.* Calif., Solano Co.
Fig. 50. *E. clausum.* Nev., Washoe Co.



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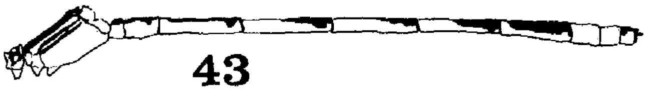

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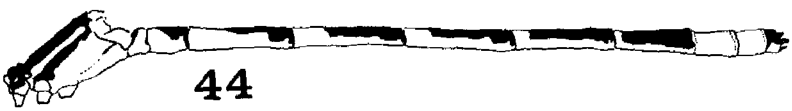

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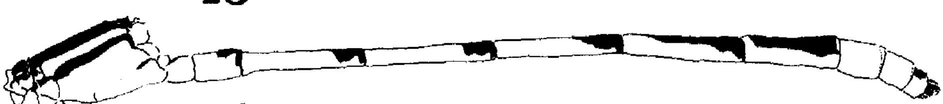
45



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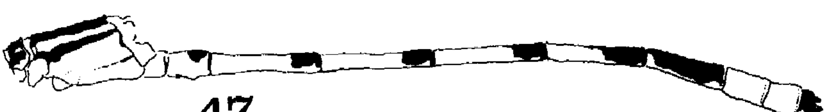

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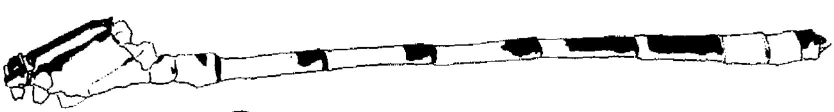
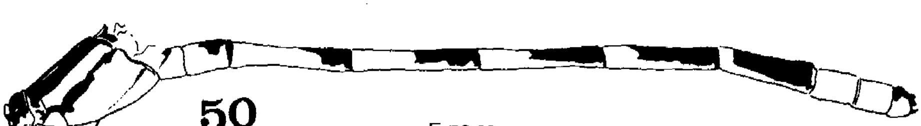


48

49

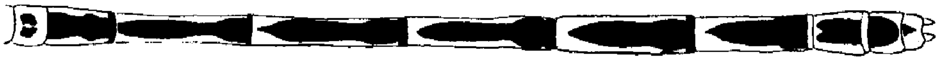


50

5mm

Color patterns of abdomens of *Enallagma* females, dorsal view.

Fig. 51. *E. anna*. Nev., Elko Co.
Fig. 52. *E. basidens*. Tex., Real Co.
Fig. 53. *E. praevarum*. Ariz., Maricopa Co.
Fig. 54. *E. carunculatum*. Calif., Butte Co.
Fig. 55. *E. civile*. Ariz., Cochise Co.
Fig. 56. *E. ebrium*. Idaho, Kootenai Co.
Fig. 57. *E. boreale*. Idaho, Boundary Co.
Fig. 58. *E. cyathigerum*. Calif., Stanislaus Co.
Fig. 59. *E. clausum*. Nev., Pershing Co.



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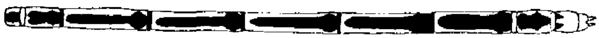

52

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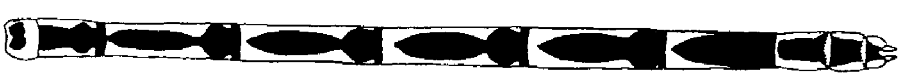
57



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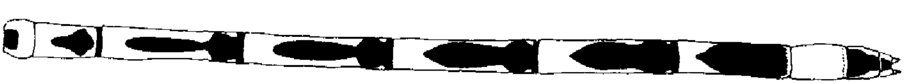

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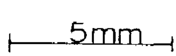
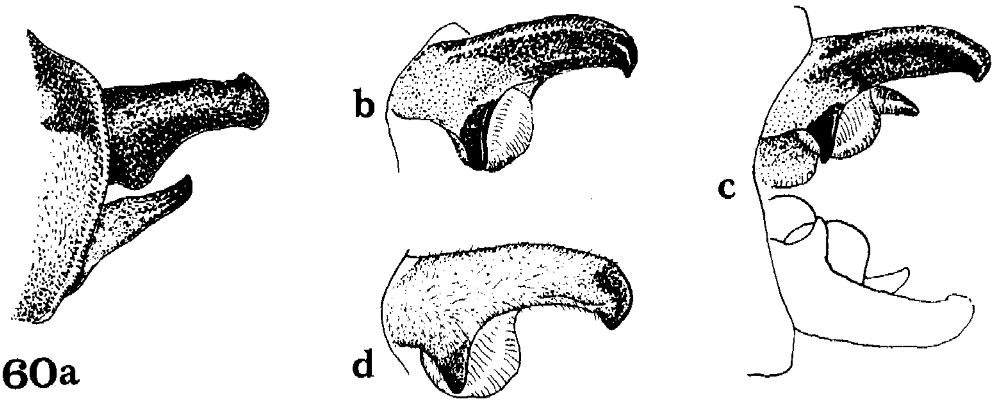
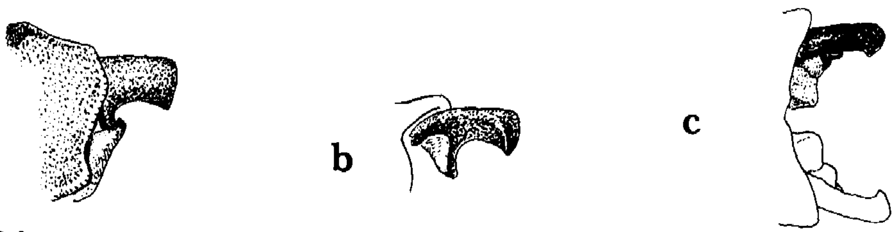


Caudal appendages of *Enallagma* males, a) lateral view, b) dorsolateral view of right superior appendage, and c) dorsal view.

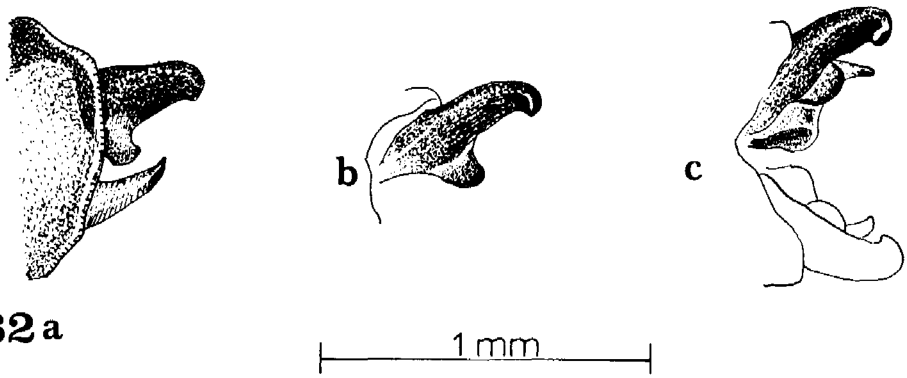
Fig. 60. *E. anna.* Calif., Inyo Co., d) *E. culicinorum*, holotype, Utah, Cache Co.
Fig. 61. *E. basidens.* Ariz., Maricopa Co.
Fig. 62. *E. praevarum.* Ariz., Cochise Co.



60a



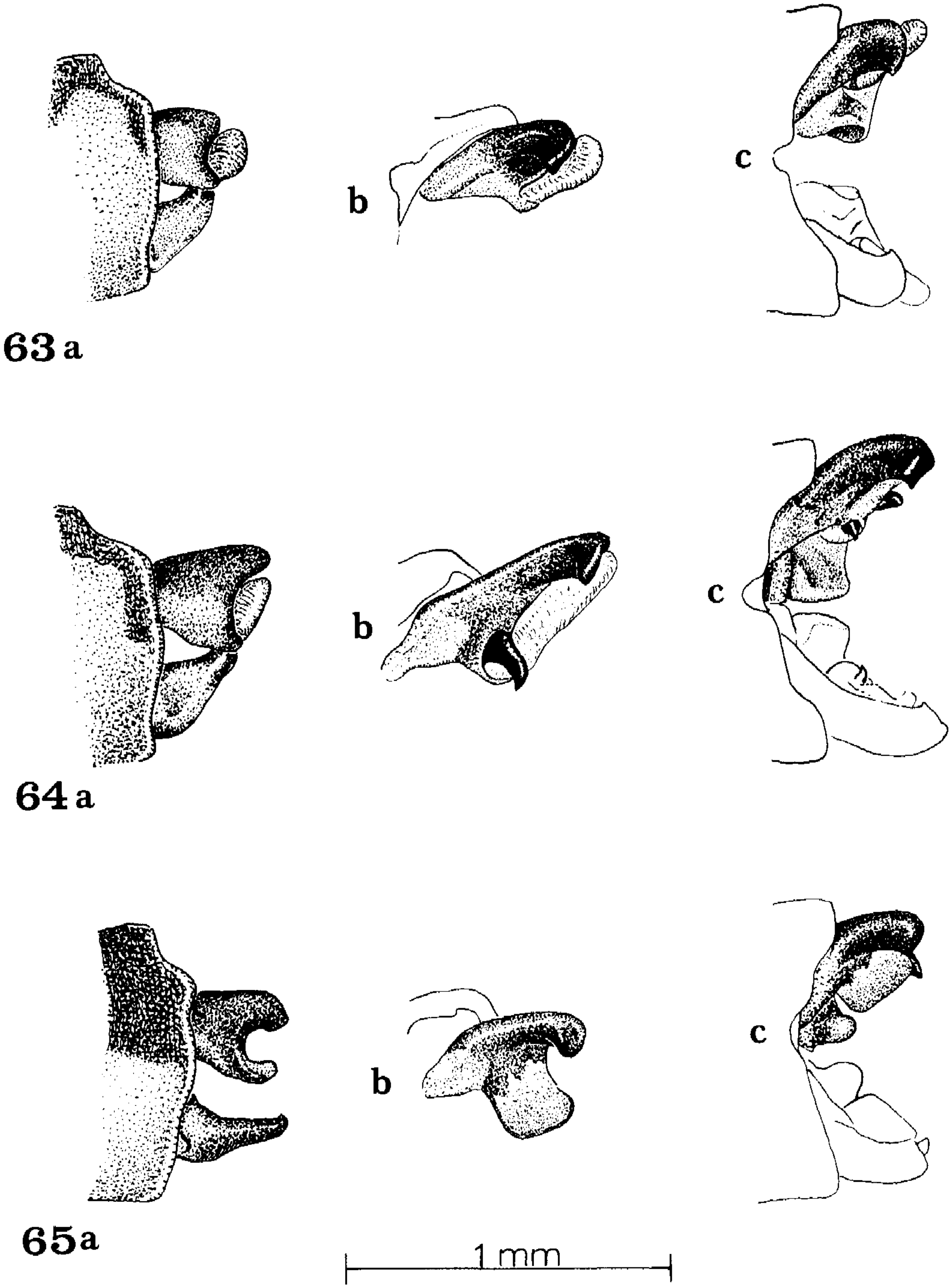
61a



62a

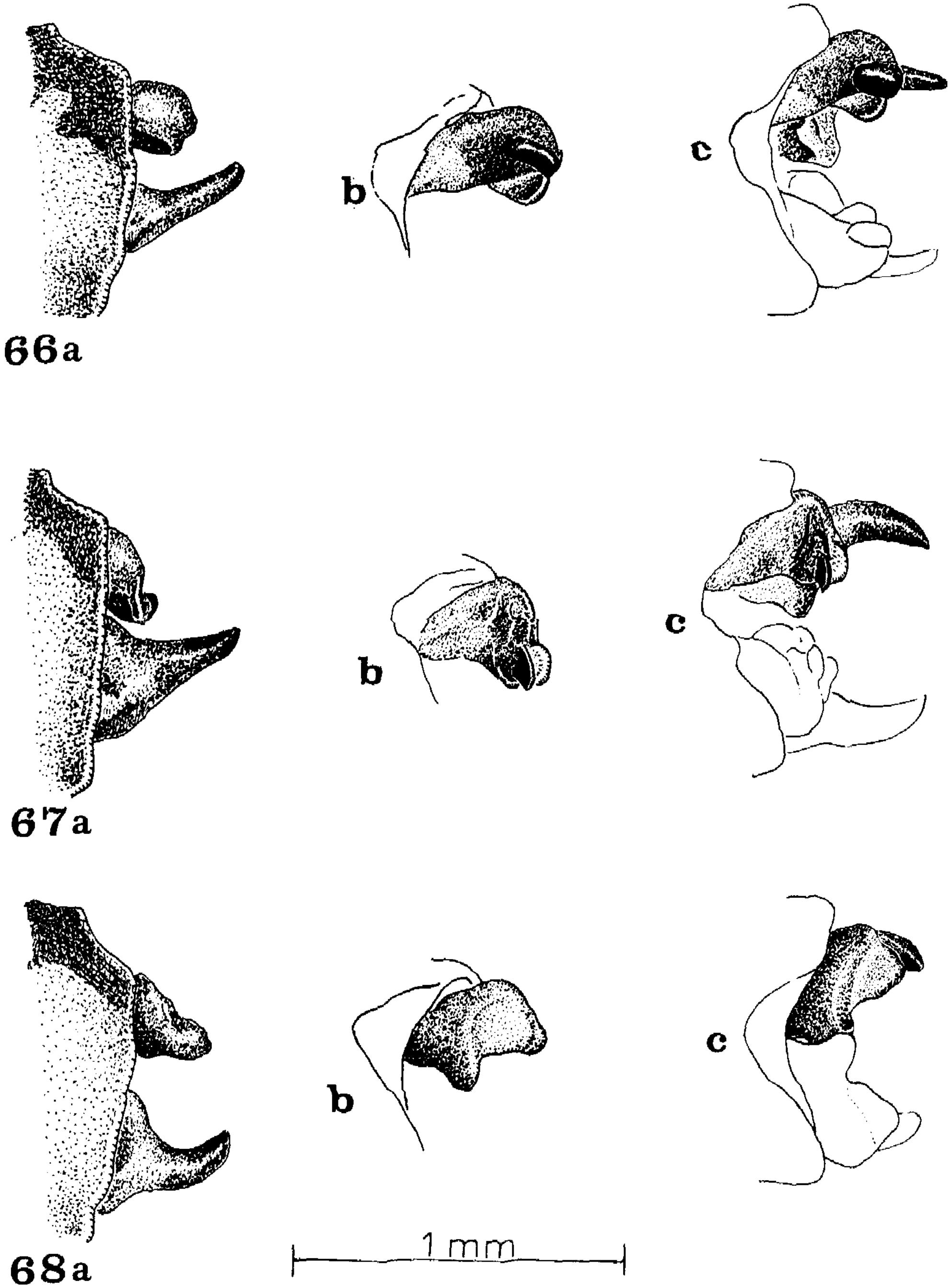
Caudal appendages of *Enallagma* males, a) lateral view, b) dorsolateral view of right superior appendage, and c) dorsal view.

Fig. 63. *E. carunculatum.* Calif., Siskiyou Co.
Fig. 64. *E. civile.* Calif., Solano Co.
Fig. 65. *E. ebrium.* Wash., Pend Oreille Co.


63 a
b
c
64 a
b
c
65 a
b
c
1 mm

Caudal appendages of *Enallagma* males, a) lateral view, b) dorsolateral view of right superior appendage, and c) dorsal view.

Fig. 66. *E. boreale.* Calif., Mono Co.
Fig. 67. *E. cyathigerum.* Calif., Butte Co.
Fig. 68. *E. clausum.* Nev., Washoe Co.


66a
b
c
67a
b
c
68a
b
c
1 mm

Enallagma mesostigmal plates, dorsal view. 1 mm scale for Figs. 69-70; 0.5 mm scale for Figs. 71-79.

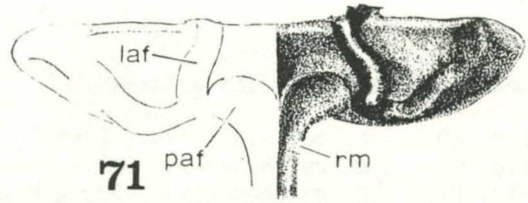
Fig. 69. *E. cyathigerum* ♂. Calif., Stanislaus Co.
Fig. 70. *E. cyathigerum* ♂. Calif., Sierra Co.
Fig. 71. *E. ebrium* ♀. Idaho, Kootenai Co. laf = lateral arms of frame; paf = posterior arms of frame; rm = ramus.
Fig. 72. *E. anna* ♀. Utah, Boxelder Co.
Fig. 73. *E. clausum* ♀. N. Mex., Mora Co.
Fig. 74. *E. boreale* ♀. Calif., Mono Co.
Fig. 75. *E. cyathigerum* ♀. Calif., Alpine Co.
Fig. 76. *E. cyathigerum* ♀. Calif., Sierra Co.
Fig. 77. *E. carunculatum* ♀. Calif., Contra Costa Co.
Fig. 78. *E. civile* ♀. Calif., San Benito Co.
Fig. 79. *E. praevarum* ♀. Calif., Santa Barbara Co.

1 mm

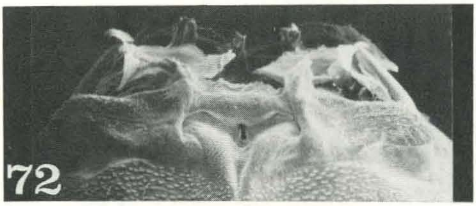
0,5mm

69

70

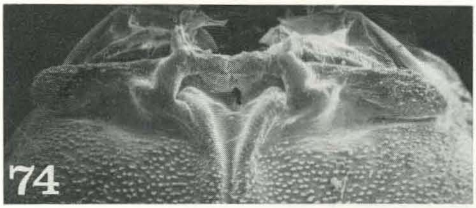


71



72

73



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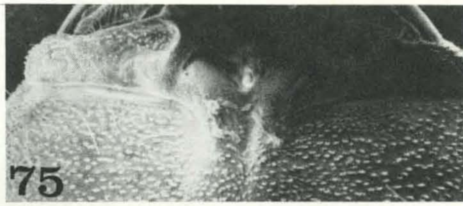

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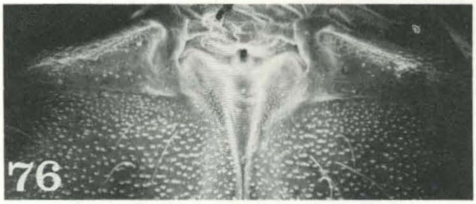

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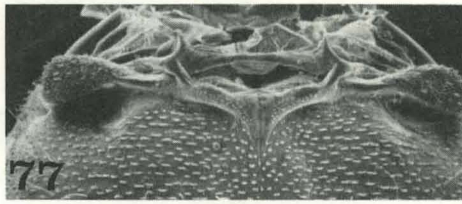

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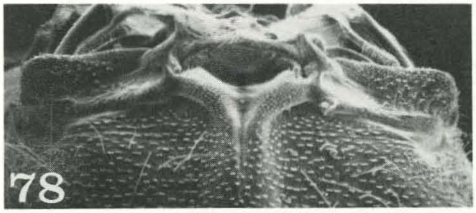

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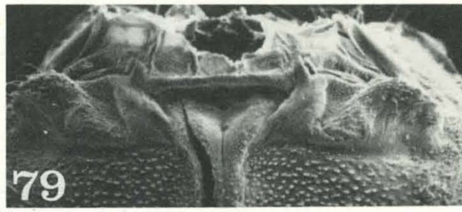
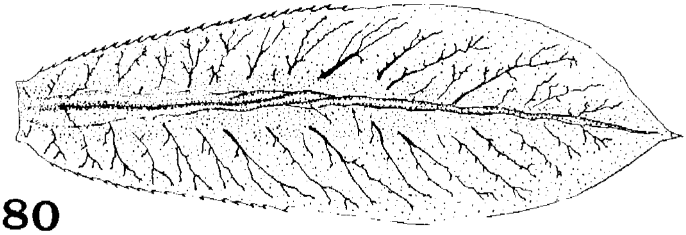


79

Median gills of *Enallagma* larvae.

Fig. 80. *E. boreale*. Nev., Elko Co.
Fig. 81. *E. cyathigerum*. Calif., Stanislaus Co.
Fig. 82. *E. carunculatum*. Nev., Washoe Co.
Fig. 83. *E. civile*. Calif., Stanislaus Co.
Fig. 84. *E. praevarum*. Ariz., Cochise Co.



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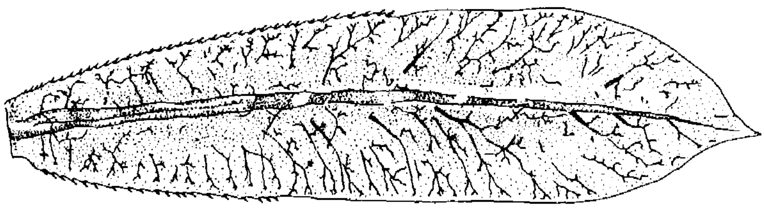

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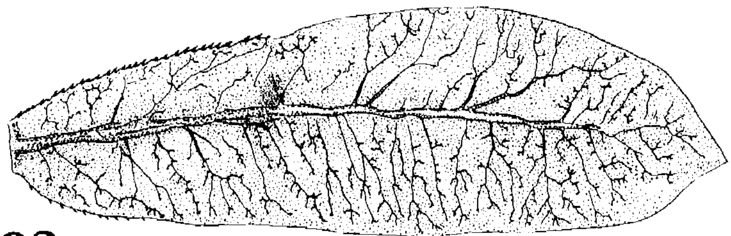

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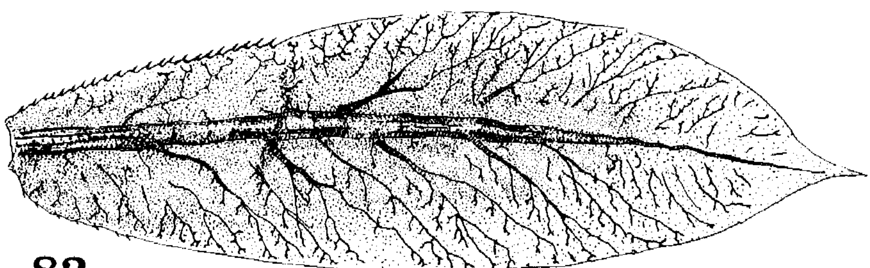

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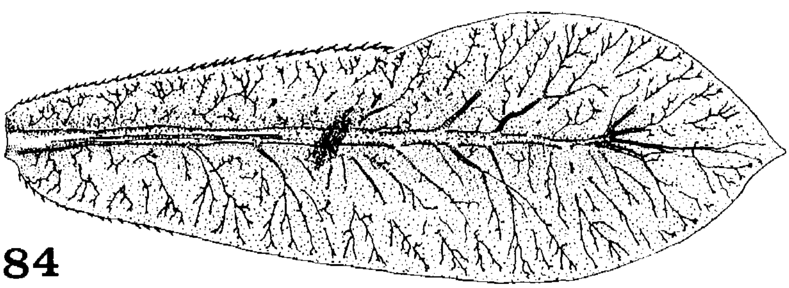

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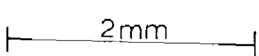
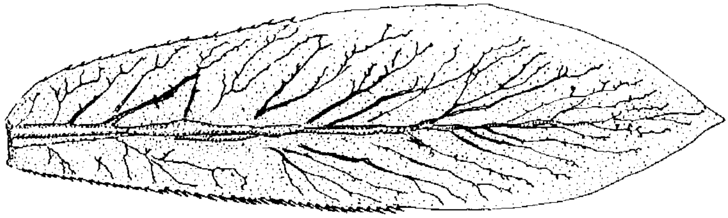


Lateral gills of *Enallagma* larvae.

Fig. 85. *E. boreale.* Nev., Elko Co.
Fig. 86. *E. cyathigerum.* Calif., Stanislaus Co.
Fig. 87. *E. carunculatum.* Nev., Washoe Co.
Fig. 88. *E. civile.* Calif., Stanislaus Co.
Fig. 89. *E. praevarum.* Ariz., Cochise Co.



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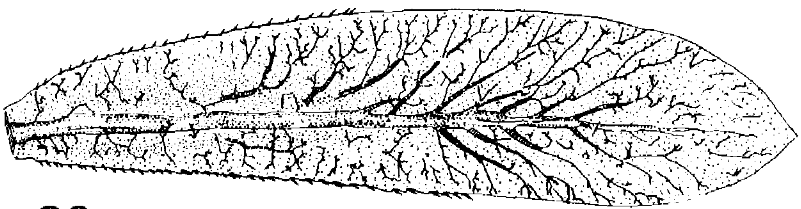
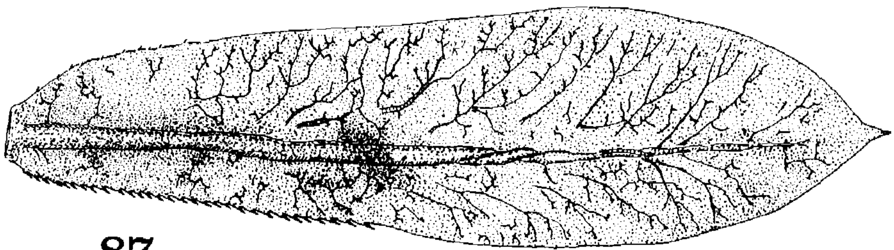


86



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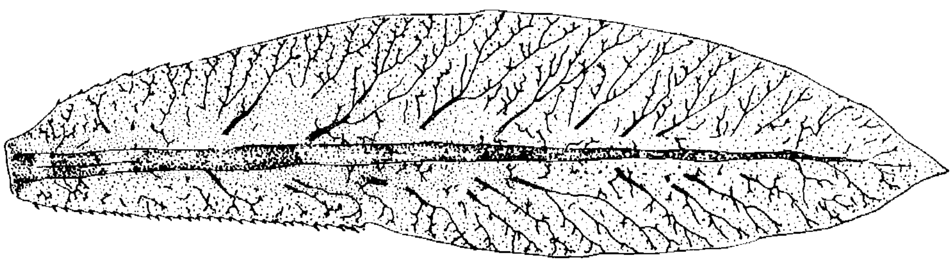

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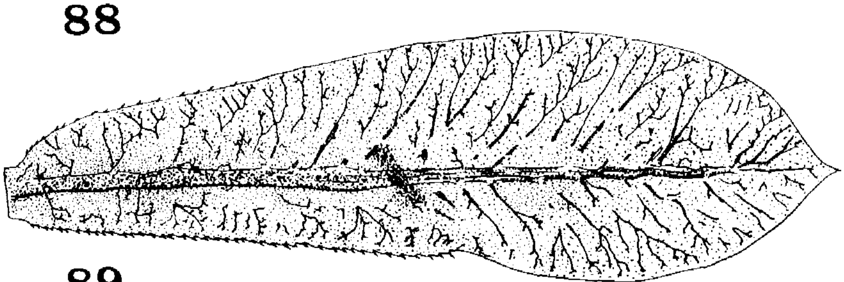
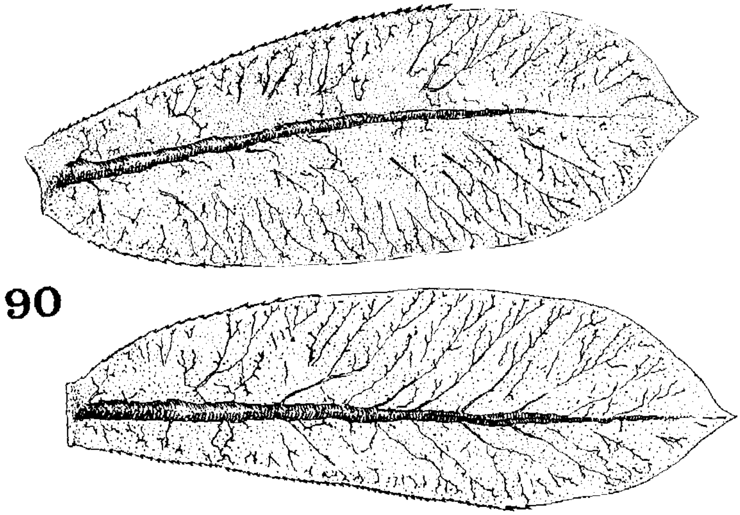


89

2mm

Caudal gills of *Enallagma* larvae.

Fig. 90. *E. anna*. Mont., Granite Co.
Fig. 91. *E. clausum*. Nev., Pershing Co.
Fig. 92. *E. ebrium*. Idaho, Kootenai Co.



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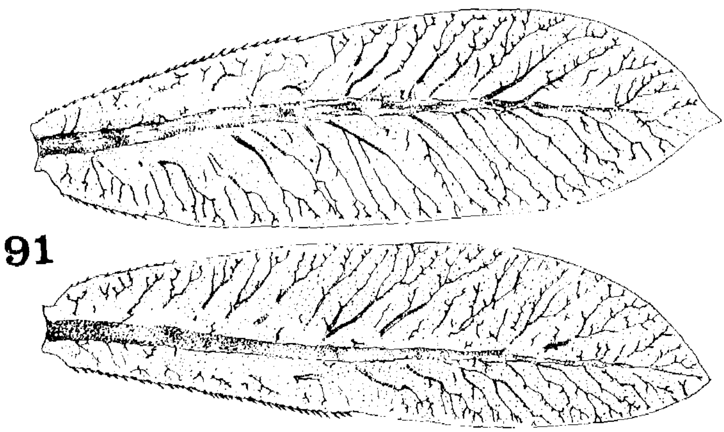

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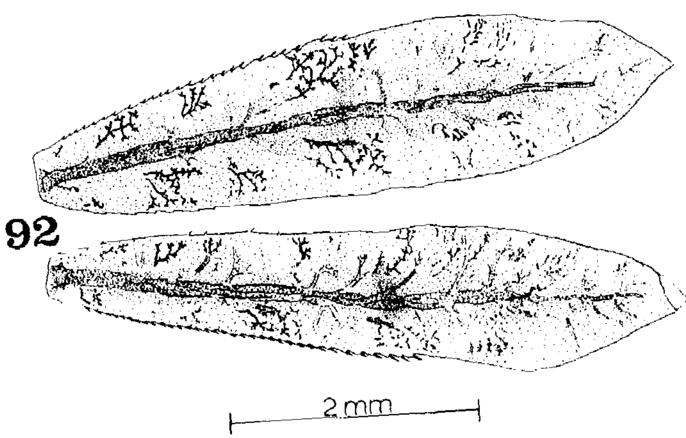
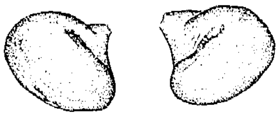


92

Caudal appendages of male *Enallagma* larvae, posterior view. 0.5 mm scale for Figs. 93-99; 2 mm scale for Figs. 100-102.

Fig. 93. *E. boreale*. Calif., Contra Costa Co.
Fig. 94. *E. cyathigerum*. Calif., Stanislaus Co.
Fig. 95. *E. carunculatum*. Nev., Washoe Co.
Fig. 96. *E. ebrium*. Idaho, Kootenai Co.
Fig. 97. *E. civile*. Ariz., Maricopa Co.
Fig. 98. *E. praevarum*. Ariz., Maricopa Co.
Fig. 99. *E. clausum*. Nev., Pershing Co.
Fig. 100. *E. basidens*, caudal gills. Ariz., Maricopa Co.
Fig. 101. *E. basidens*, larva, head, dorsal view. Ariz., Maricopa Co.
Fig. 102. *E. praevarum*, larva, head, dorsal view. Ariz., Maricopa Co.



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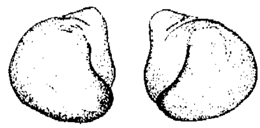

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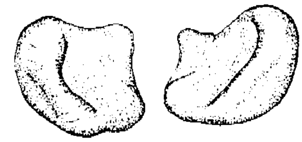

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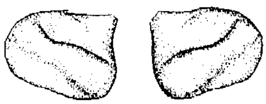

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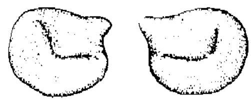

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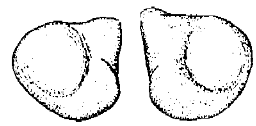
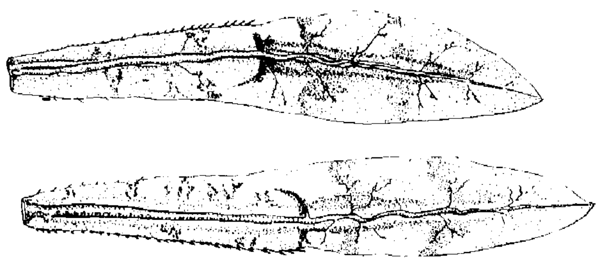


98

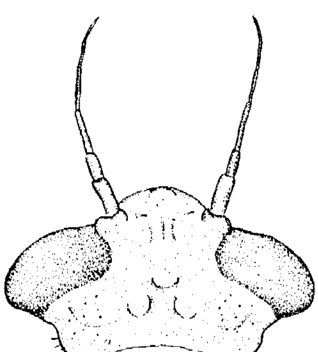
99

0.5 mm

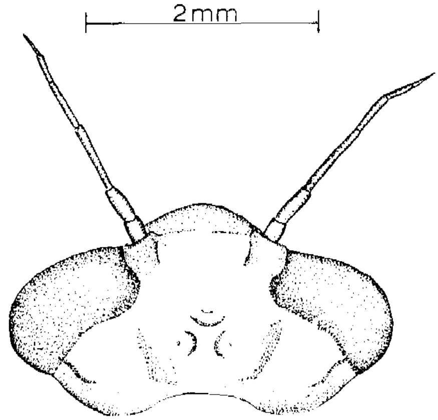


100

2 mm



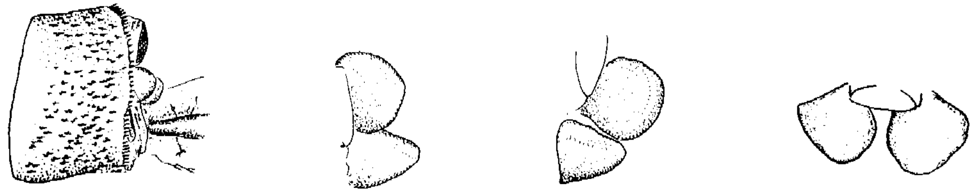
101



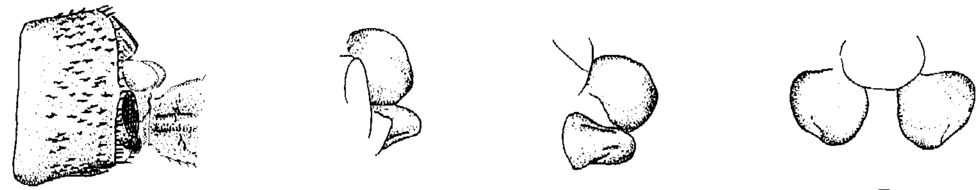
102

Caudal appendages of male *Enallagma* larvae, a) lateral view, b) ventrolateral view, c) dorsolateral view, and d) dorsal view.

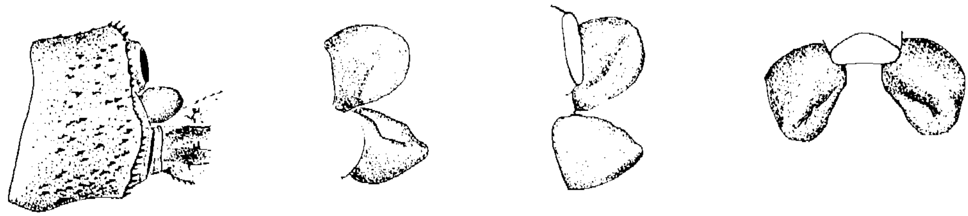
Fig. 103. *E. boreale*. Calif., Contra Costa Co.
Fig. 104. *E. cyathigerum*. Calif., Stanislaus Co.
Fig. 105. *E. carunculatum*. Nev., Washoe Co.
Fig. 106. *E. civile*. Ariz., Maricopa Co.
Fig. 107. *E. praevarum*. Ariz., Maricopa Co.



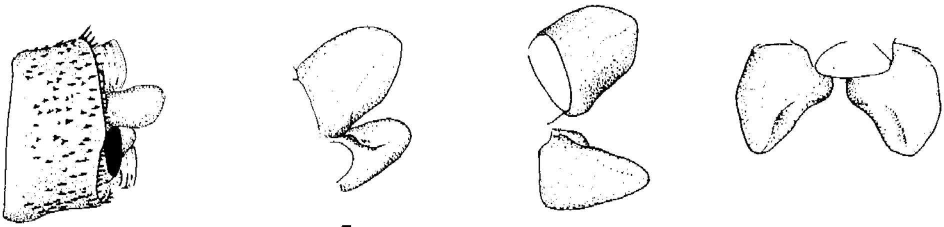
103 a b c d



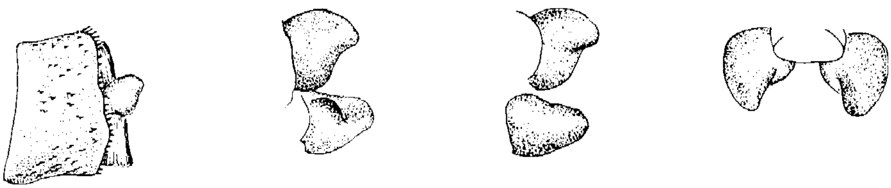
104 a b c d



105 a b c d



106 a b c d

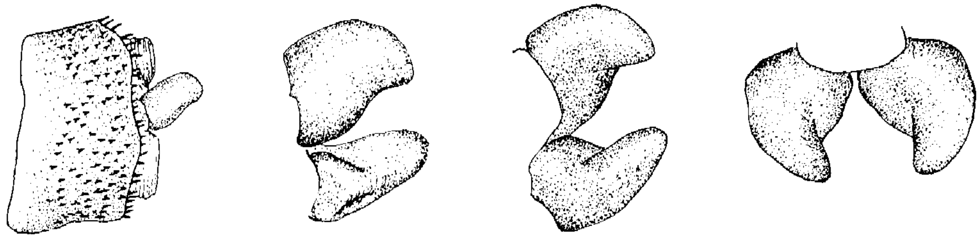


107 a b c d

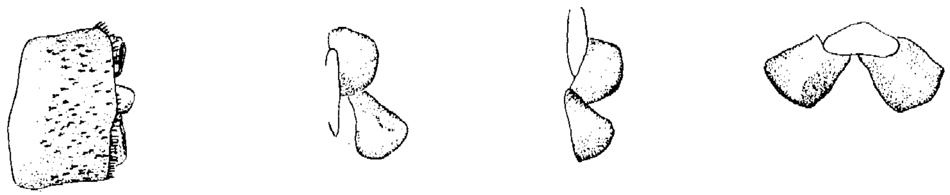
1 mm 1 mm

Caudal appendages of *Enallagma* larvae, a) lateral view, b) ventrolateral view, c) dorsolateral view, and d) dorsal view.

Fig. 108. *E. anna* ♂. Utah, Tooele Co.
Fig. 109. *E. clausum* ♂. Nev., Pershing Co.
Fig. 110. *E. ebrium* ♂. Idaho, Kootenai Co.
Fig. 111. *E. anna* ♀. Calif., Inyo Co.
Fig. 112. *E. clausum* ♀. Nev., Pershing Co.

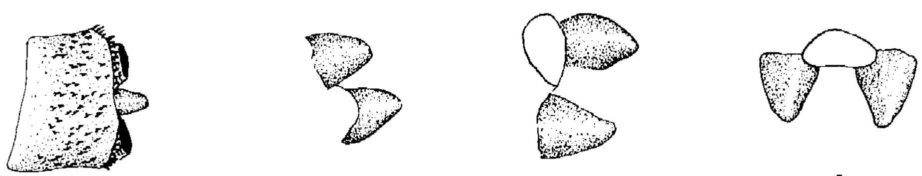


108 a b c d

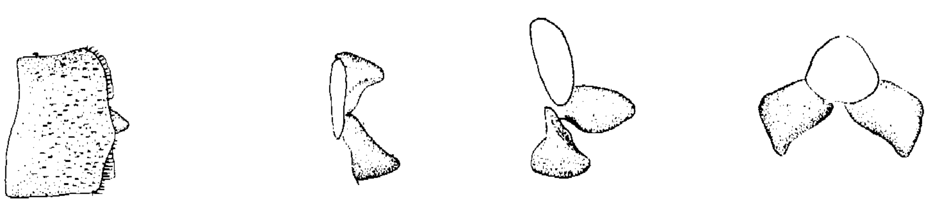


109 a b c d

110 a b c d



111 a b c d



112 a b c d

1 mm 1 mm

Caudal appendages of female *Enallagma* larvae, a) lateral view, b) ventrolateral view, c) dorsolateral view, and d) dorsal view.

Fig. 113. *E. boreale*. Calif., Contra Costa Co.
Fig. 114. *E. cyathigerum*. Calif., Stanislaus Co.
Fig. 115. *E. carunculatum*. Nev., Churchill Co.
Fig. 116. *E. civile*. Ariz., Maricopa Co.
Fig. 117. *E. praevarum*. Ariz., Maricopa Co.

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