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SYSTEMATIC AND ZOOGEOGRAPHIC ASPECTS OF ASIATIC EPHEMERIDAE (EPHEMEROPTERA)[1]

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ABSTRACT. The Ephemeridae of the Asiatic area are treated with particular emphasis given to those of the Oriental Region. A reevaluation and illustrated synopsis of the genus *Eatonigenia* Ulmer are presented, including the description of the nymphal stage of the genus for the first time. *E. chaperi* (Navas) is described from Thailand, and two new species, *E. trirama*, and *E. seca* are described from India and Thailand respectively. The previous *Hexagenia indica* Chopra is newly placed as *E. indica* (Chopra) comb. nov. Inferred relationships of all Asiatic ephemerid genera are discussed in terms of phyletic and zoogeographic affinities. The actual occurrence of *Hexagenia* Walsh in the area appears highly doubtful.

INTRODUCTION

The mayfly family Ephemeridae is widespread geographically, being cosmopolitan excepting its absence in Australia and the oceanic islands. Thirty-two described species have been reported from the Oriental Region including the island of Formosa and the Philippines. If one were to consider far eastern Palearctic species also, the list of recorded Asiatic ephemerids would be increased by an additional fifteen species. Of these species, all but three have been referable to the genus *Ephemera* Linn.[2]

By comparison of geographical regions, the number of Asiatic *Ephemera* species is relatively large, and is represented by several forms which are relatively unique morphologically. Highly specialized characterization is seen particularly in regards to the male genitalia, e g., *E. purpurata* Ulmer, *E. pictiventris* McLachlan, and *E. pictipennis* Ulmer, all of which have been figured by Hsu (1936-37). Nymphs from West Pakistan described by Ali (1967) as *E. soanica* Ali (later emended to *E. soanensis*) would appear extremely atypical for the genus on the basis of his description and figures of the frontal process and antennae. A good deal of adaptive radiation has evidently taken place in Tropical Asia, whereas the genus is only sparsely represented in Africa (see McCafferty, 1971a), and is not found in the New World tropics. Otherwise, the

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2. The species recently described as a member of the genus *Ichthybotus* Eaton by Dubey (1971) from Northwest Himalaya has not been studied and is not treated in the present account.

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genus is basically Holarctic. Our knowledge of the Oriental *Ephemera*, however, is very poor as indicated by an almost complete lack of information on nymphal forms, biosystematics of species, and ecology.

The first Asiatic Ephemeridae were described from India by Walker (1860) as *Potamanthus exspectans* Walker. Later, Eaton (1871) transferred this species to *Ephemera* and also described two additional Oriental forms, *Ephemera immaculata* Eaton from India and *E. serica* Eaton from southern China. Since then several workers have contributed to our knowledge of Asiatic *Ephemera*. Among the taxonomic treatments several faunistic reviews are of summarial importance, notably that of Hafiz (1937) for the Indian Ephemeroidea and that of Hsu (1936-38) for the Chinese species. In addition, Matsumura (1931) added significantly to the list of Japanese species of *Ephemera*. Undoubtedly, a complete understanding of the Asiatic forms of this genus will be an important key to interpreting the phylogeny and zoogeography of the Ephemeridae, and will require a thorough association of nymphal diversity through aquatic sampling and rearing.

The remaining, previously recorded Ephemeridae of the Oriental Region involve two other genera, one of which persists obscurely. Navas (1935) described an ephemerid from the East Indies which he assigned to the genus *Hexagenia* Walsh and named *H. chaperi* Navas. Ulmer (1939), in his monumental work on the mayfly fauna of the Soenda Islands, recognized the uniqueness of this species and therefore established for it the monospecific genus *Eatonigenia* Ulmer. The validity for generic status, based on considerable variant characterization in the imagos of *E. chaperi*, has remained unquestioned even though the nymphal stage has not been previously known.

Although no species were formally named, Eaton (1883-88) reportedly had seen what he believed to be *Hexagenia* material from Eastern Siberia. This would represent the only existent possible record of *Hexagenia* from the Palearctic Region to date. In addition, Eaton figured the wings of what he termed *Hexagenia* sp. from northwestern India. These were the only data given by Eaton. From the venational pattern of the wings, the taxa would not be assignable to *Ephemera*, although it is quite definitely an ephemerid. Moreover, the heavy crossvenation and marginal reticulation of the figured wings is suggestive of that found in *Eatonigenia*.

Hexagenia philippina Navas was described in 1933, from a single specimen. The very incomplete description and figure of part of the wing which accompanies it are unfortunately of no value in verifying Navas' generic placement. In addition to this supposed species of *Hexagenia*, there has existed one other from the Oriental Region. On the basis of eleven female imago specimens found on Chilka Lake, India, Chopra (1924) described *H. indica* Chopra. Since male imagos of this species are not known, it has been difficult to confirm generic placement again in this instance. The characters of the females discussed by Chopra would classify the species in the Ephemeridae; however, the vestigial terminal filament would obviously exclude it from consideration

as *Ephemera*. Spieth (1941) stated that it seemed probable that both *H. indica* and *H. philippina* belonged to *Eatonigenia*. He reasoned that it would be highly unlikely for *Hexagenia* to exist in North America and Tropical Asia and yet be completely absent from China and Japan. The paucity of morphological data on the two above named species evidently discouraged Spieth from making any formal nomenclatural recombinations at that time.

Our present state of knowledge regarding Asiatic Ephemeridae is obviously very incomplete. A detailed phylogenetic study by the author based on comparative exoskeletal morphology has led to a reinterpretation and revision of the superspecific classification of this family. The purpose of this particular work is to make available new taxonomic descriptions regarding *Eatonigenia*, clarify the zoogeography of the family in the Asiatic region, and lay a more complete foundation for biosystematic analysis on a world basis.

During the study a number of Asiatic specimens were made available to me for examination. Amongst the original material was a single, previously unstudied ephemerid nymph from the R. Bhavani, India. This nymph was morphologically unlike any other nymphs of known ephemerid genera. In light of the diversity of the total world fauna, it became obvious that the specimen was either representative of a new genus or perhaps the undescribed nymphal stage of *Eatonigenia*. The phylogenetic position of this uncertain taxon, based on comparative nymphal morphology and character analysis, approximated very closely that of *Eatonigenia* which had necessarily been hypothesized on the basis of adults only. In essence, the proposed family tree of the world Ephemeridae was predictive of the nymph actually being *Eatonigenia* or close to it. However, the lack of any rearing association or exact geographic correlation allowed only a speculative taxonomic placement at the time.

Recently, Dr. George F. Edmunds, Jr., generously permitted me to study additional ephemerid nymphs he had received from Thailand. Not only was the Thailand material similar in general facies to the above mentioned Indian nymph, but definite proof was found that they were actually the nymphs of *Eatonigenia*. Adults of *Eatonigenia* had been collected at the same locality, and in addition, one large male nymph possessed relatively well developed genitalic structures, the penes of which were unmistakably of the *Eatonigenia* form.

With the discovery of *Eatonigenia* nymphs, all of the presently recognized genera and subgenera of Ephemeridae are known from both the adult and nymphal stage. A treatment of *Eatonigenia* and its specific variability follows.

Systematic Account

Genus **Eatonigenia** Ulmer

Eatonigenia Ulmer, 1937, *Arch. Hydrobiol. Suppl.*, **16**: 479. Type: *Hexagenia chaperi* Navas, 1935, by original designation.

Imago (in alcohol). *Size* : Length of male body, 11.0-21.5 mm; fore wings, 10.5-17.0 mm; cerci 2.5-3.1 times body; terminal filament vestigial. Length of female body, 10.0-21.0 mm; fore wings, 12.0-19.0 mm; cerci 1.8-1.9 times body terminal filament vestigal.

Head : Compound eyes unicolorous (Figs. 1 and 2). Compound eyes of male large and nearly contiguous dorsally; median margins strongly convergent dorsally in facial view (Fig. 1). Compound eyes of female separated anteriorly by distance 1.8-2.5 times width of one eye; median margins convergent dorsally in facial view (Fig. 2). Transverse shelf of head below antennae not extended as far as nasal carina (Figs. 1 and 2).

Thorax : Pronotum with posterior width 1.4-2.0 times length; lateral margins tapered anteriorly or narrowed mostly in anterior third; anterior width approximately two thirds of posterior width; pronotum not constricted sublaterally in anterior third. Scutellum of mesothorax acute posteriorly in dorsal view as in figure 3. Length of male body 1.2-1.7 times fore legs; tibiae of fore legs 1.6-2.3 times femora, tarsi 1.2-1.5 times tibiae. Length of female body 1.9-3.1 times fore legs; tibiae of fore legs 1.0-1.4 times femora, tarsi 0.8-1.1 times femora. Fore wings (Fig. 4) with crossveins not crowded near bullae; R_{3a} two-thirds or more of length of IR_2; cubital area heavily reticulated; A_1 paralleling but arching less than CuP; 5-11 veinlets between A_1 and anal margin; A_2 indistinct, anal area with veinlets only. Hind wings (Fig. 5) usually with 1 intercalary between R_2 and IR_3, extended from margin less than one third of length of IR_3; usually 1 intercalary between IR_3 and R_{4+5}, extended from margin less than one third of length of IR_3; A_1 ending on margin well over one half of length of anal margin; anal venation with much reticulation.

Abdomen : Genitalia of male (Figs. 9-12) with posterior margin of subgenital plate somewhat indistinct mesally, folded dorsally to penal base, produced distally at posterolateral corners to form distinct forceps bases; forceps three-segmented, second segment longest, curved medially for entire length and dorsal to semi-globose basal segment at attachment, terminal segment approximately one half or less length of basal segment; penes fused for entire sagittal length, somewhat constricted basally, with lateral margins divergent distally, posterior margin slightly concave as seen in ventral view, extending dorsally and posteriorly from base, gonopores approximating each other on ventral surface and associated with a variously shaped pair of small nipple-like structures. Terminal abdominal sternum of female with no distinct posterolateral processes.

Mature nymph (in alcohol). *Head :* Frontal process appearing somewhat truncate, broader than long; lateral margins nearly parallel (Figs. 13 and 14). Supra-antennal processes of head not similar to frontal process (Figs. 13 and 14), surrounding bases of antennae, somewhat expanded laterally, emarginate anteriorly as seen in dorsal view, exposing entire scape of antennae. Antennae with pedicel at least as long as scape (Figs. 13 and 14), flagellum with sparse

minute setae only. Labrum with distal margin strongly convex, nearly conical (Figs. 15 and 16). Mandibular tusks (Figs. 13, 14, and 17) stout, approaching triangulate in cross section with distinct longitudinal median ridge and somewhat weaker dorsal ridge (Fig. 17); length of tusk approximately one and one half times length of body of mandible. Hypopharynx with median lingua very slightly emarginate to straight (Fig. 18). Maxillae slender, palpi three-segmented (Fig. 19); galea-laciniae acute apically, with slender forked apical spine as in figure 20. Labial palpi two-segmented, terminal segment spuriferous apically (Fig. 21), median margin of basal segment with distinct lobular protuberance originating near base and extending distally to near distal margin of segment.

Thorax : General shape of prothoracic legs as in figure 22; tibiae convexly broadened posteriorly, rounding posterodistally, with distinct dorsodistal process at anterodistal corner, with comb of stout apical setae at ventrodistal margin, and with small tubercle on distal margin basad of prominent dorsodistal process; tarsal claws highly reduced, inset in variously notched distal apices of tarsus (Figs. 23 and 24). Tibiae of mesothoracic legs distinctly produced posterodistally beyond posterior origin of tarsi, and with distinct comb of stout apical setae of convex posterodistal margin. Tibiae of metathoracic legs (Fig. 25) with distal margin having minute notch fitting small proximal ridge of tarsus on ventral (inner) surface, and with tibial process subequal to tarsi in length, slender and acute.

Abdomen : Gill 1 bifid in distal half only, and slender throughout (Fig. 26). Dorsal branch of gill 2 with outer margin of lamella distinctly broadened convexly in basal half.

Remarks : The descriptive style used follows that of McCafferty (1971b) wherein several characters found to be of generic consequence within the Ephemeridae were first introduced. Thusly, as pertains to the adults many new characters not considered by Ulmer (1939) in his original description of the genus are included. The broad spectrum of characterization discussed will hopefully insure that at least parts of the description will remain applicable if in the future additional species or variation are recognized for the genus.

Eatonigenia adults can be differentiated from all other ephemerid adults on the basis of several character states not found in other related genera. Generally, there is more crossvenation and marginal reticulation in the wings of *Eatonigenia* (Figs. 4 and 5) than in other Ephemeridae. The head of the male imago (Fig. 1) is quite conspicuous in possessing large dorsally convergent compound eyes and a shallow transverse shelf below the antennae. Most diagnostic is the male genitalia (Figs. 10-13). The penal structure found in *Eatonigenia*, as discussed previously, is unlike that in any other mayfly. The female imagos are somewhat more difficult to differentiate on a generic level, and a combination of character states must be recognized. Besides consideration of wing venation as mentioned above, the medioapical acuteness of the

mesoscutellum (Fig. 3) will serve to separate *Eatonigenia* from *Hexagenia* whose mesoscutellum possesses a medioapical notch. The transverse shelf of the head below the antennae (Fig. 2) is not extended ventrally and is not bilobular as is the case in *Litobrancha* McCafferty from North America. Finally, the lack of a well developed terminal filament, among other things, will differentiate *Eatonigenia* females from those of *Eatonica* Navas from Africa.

The nymphs of *Eatonigenia*, here described for the first time, demonstrate many characters not only of value in generic differentiation but also of phylogenetic utility. Diagonstically the cephalic structures and mouthparts of *Eatonigenia* are of greatest importance. Character states seen exclusively in *Eatonigenia* nymphs include the relatively enlarged anterolateral corners of the frons (Figs. 13 and 14) which have been termed the supra-antennal processes. These processes, unlike in other ephemerid genera, are expanded laterally and notched anteriorly. Additional, rather unique character states are first, the highly convex, almost conical labrum (Figs. 15 and 16) which is much more convex than in most other ephemerid genera, and second, the shape of the mandibular tusks (Figs. 13, 14, and 17). The tusked portion of the mandibles is somewhat aberrant in that it is flattened on three sides and therefore more or less triangular if viewed in cross section. In other Ephemeridae the tusks are nearly round in cross section, or at the most flattened somewhat on two sides. In addition, the highly reduced tarsal claws of the prothoracic legs (Figs. 22–24) are unique to this genus of Ephemeridae.

In consideration of the overall composition and variation of the Ephemeridae, *Eatonigenia* appears to be most similar to *Eatonica*, but also similar to *Litobrancha*, and more distantly to *Hexagenia*. If the nymphs that Demoulin (1968) has tentatively described as *Eatonica schoutedeni* (Navas) are considered, then several distinct morphological affinities are evident among the above mentioned genera. These can be seen, for instance, in the complete frontal process of the head (Figs. 13 and 14), lack of armature on the mandibular tusks (Figs. 13, 14, and 17), and structure of the labium (Fig. 21) and legs (Figs. 22-24). Several character states of the mouthparts and gills are found in common between *Eatonigenia* and *Eatonica*, hence adding credence to their deduced common ancestry. Additionally, several adult characters infer a close relationship between *Eatonigenia* and *Eatonica*.

Certain facets of biology are thought to be highly predictable on the basis of phylogenetic interpretation and a knowledge of the functional morphology of related taxa. Hence, although the biology of *Eatonigenia* spp. is presently unknown, the nymphal habit is presumably similar to that of related ephemerids, i.e., burrowers in soft substrate of lakes and streams. Moreover, the fact that a large amount of fine silt was found over the entire body and interspersed amongst the setae of some of the nymphal material when first examined would substantiate the conclusion that these are fossorial in habit. For a summary of the known biology of the related genus *Hexagenia*, and comprehensive treat-

ments of *H. limbata* (Serville) and other North American species, see Hunt (1953) and Fremling (1970).

1. Eatonigenia chaperi (Navas) (Figs. 1-7, 9, 13, 15, and 24)

Hexagenia chaperi Navas, 1935, *Broteria*, **31** : 99.

Eatonigenia chaperi : Ulmer, 1939, *Arch. Hydrobiol. Suppl.*, **16** : 479.

Male imago (in alcohol). Length : body 17.0-21.5 mm; fore wings 14.0-17.0 mm. Body generally light; head and thorax somewhat darker than abdomen (color patterns as discussed completely faded in some alcoholic specimens). Head ivory to light yellowish-brown dorsally; bases of ocelli black; compound eyes gray to black; basal segments of antennae white.

Thorax ivory to yellowish-brown dorsally; mesoscutum and mesofurcisternum usually more heavily pigmented than remainder of thorax; legs ivory with coxae and trochanters darkening; basal third of femur of mesothoracic legs light brown medially; femur of metathoracic legs medium brown dorsomedially in basal third, distal margin of pigmentation extended and distally tapering off along dorsal edge of femur, additional light brown elliptical marking laterally; wing venation cinnamon brown in costal region; bullae white.

Abdomen ivory; tergites (Fig. 6) with pair of very pale submedian stripes, tergite 10 somewhat darker; sternites (Fig. 7) 2-7 with pair of pale submedian anterior oblique stripes and pair of short pale submedian posterior dashes; genitalia as in figure 9; penes with base constricted ventrally, posterior margin straight to nearly straight in median two thirds, arching distally only at lateral extremities, distolateral angles rounded, with broad, shallow, and sometimes indistinct median longitudinal furrow along distoventral aspect; nipples of gonopores deeply emarginate and arising at approximateley mid-length of penes; cerci white with minute light brown setae; vestigial terminal filament with longer dense medium brown setae.

Female imago (in alcohol). Length : body 19.0-21.0 mm; fore wings 17.0-19.0 mm. Examined specimens from West Java with greatly faded color pattern. According to Ulmer (1939), characters generally as in male except for usual sexual differences.

Mature nymph (in alcohol). Length : body 24.5 mm, cerci 11 mm, terminal filament 7 mm.

General body color ivory, with golden setae and spurs on body. Frontal process of head (Fig. 13) ivory, much broader than long, with anterior margin very slightly convex and having short sparse setae, and with short lateral margins rounded and having long coarse setae; supra-antennal process (Fig. 13) very large, deep concavity of anterior margin nearly symmetrical, with coarse golden setae laterally; flagellum of antennae slightly longer than head; compound eyes dark brownish-black; vertex ivory, with row of setae posterior to compound eyes; median ocellus indistinct; distal margin of labrum (Fig. 15) with row of

long setae, anterior surface densely setaceous; mandibular tusks generally densely setaceous, with row of setae bordering flattened dorsomedian surface for entire length; lateral margins of paraglossae of labium with thick brush of short setae (similar to figure 21).

Thorax and legs entirely ivory excepting densely setaceous areas casting reddish-brown tinge and dark heavily sclerotized tips such as articulating spines of coxae and trochanters; apical notch of tarsus (Fig. 24) of prothoracic legs broadly V-shaped, with reduced tarsal claw rounded apically and produced slightly beyond tarsus; proximal ridge of tarsus on ventral (inner) surface of metathoracic legs nearly indistinct.

Abdomen ivory, with no color patterns dorsally or ventrally, lateral abdominal setae gold; lamellae of gills 2-7 white with gray flecks medially, fibrillae white; gill 1 very narrow; caudal filaments setaceous laterally for nearly entire length, setae progressively shorter distad, cerci nearly twice as long as terminal filament.

Remarks : The nymphal description of *E. chaperi* is based on material as follows : one mature male nymph and three immature nymphs, Thailand : Bung Borapet, bottom fauna, 3.ix.1971, W. Junk collector. Although reared series were not available the nymphs have been associated with four male imagos of *E. chaperi* taken as follows : Tailand : Bung Borapet, light trap, 16.viii.1971, W. Junk collector. Besides being taken at the same locality at approximately the same time of year, the association was further based on the similarity in size and general coloration of the mature male nymph and male imagos. Although the fallibility of mere associations was shown for instance by McCafferty (1971a), the probability of this association being positive is considered high in veiw of the present study.

The adult description is modified from Ulmer (1939) and inclusive of additional specific characterization and individual ranges of variance based on the four male imagos mentioned above. These specimens have therefore been designated *plesiotypes*, three of which are deposited at the University of Utah, Salt Lake City, Utah, and one of which is deposited at Purdue University, West Lafayette, Indiana.

In reference to the species treated herein, the relatively large size of the body along with the abdominal color pattern (Figs. 6 and 7) appear to be adequate differentiating characters for *E. chaperi* adults. In addition, more subtle but unique character states involve the male genitalia (Fig. 9), i.e., the posterior margination of the penes and lack of a distinct median suture along the disto-ventral surface of the penes.

Experience to date has shown that body coloration and topography of setae appear to be stable characters for burrowing mayfly nymphs on a specific level, and therefore, along with some exoskeletal shape characters, these have formed the basis for the above nymphal description. A lack of an extensive series of

a population limits any description. This realization has prompted a broad morphological treatment, particularly regarding the nymphal stage, which will incorporate valid taxonomic characters. However, it is nevertheless recognized that indeed the possibility exists that some character states used may eventually prove to be more widespread or of only individual consequence, and hence variable within the species.

Preliminarily, the better diagnostic character states of the nymphs of *E. chaperi* include mainly cephalic structures. The shape and setaceousness of the frontal process (Fig. 13) and supra-antennal processes (Fig. 13) appear to be distinctive, along with the setaceousness of the labrum (Fig. 15). The unique tarsi of the prothoracic legs (Fig. 24) also provide key character states as regards the apical notch and tarsal claw.

The discovery of the species in Thailand represents a considerable extension of the known range of *E. chaperi* from Java and Borneo. This geographic range does not appear unusual for burrowing mayflies, however, since Uéno (1969) reported *Ephemera javana* Navas as occurring in northern Thailand. This case is analogous in that *E. javana* was also known originally from Java.

2. Eatonigenia indica (Chopra), comb. nov.

Hexagenia indica Chopra, 1924, *Rec. Indian Mus.*, **26** : 416; Spieth, 1941, *Amer. Midland Natural.*, **26** : 244.

The new combination is based primarily on a more complete knowledge of generic characterization within the Ephemeridae, particularly that of *Hexagenia* and *Eatonigenia*, and the description and figures of *E. indica* by Chopra (1924). Although most of Chopra's description involves color pattern, his characterization of the mesothorax aligns it with that of *Eatonigenia*, i.e., acute medio-apically, and certainly unlike the notched condition of *Hexagenia*. Moreover, the wing venation figured by Chopra, especially that of the hind wing, shows more marginal reticulation than is common to *Hexagenia*. Most assuredly, the geographic distribution, as was intimated by Spieth (1941), would tend to support the present taxonomic move. A redescription of this species is not included since material was not examined at first hand; however, from Chopra's original description of the coloration of the abdomen and legs it could easily be distinguished from the other species treated herein. According to Chopra the abdomen is white infuscated with chestnut. He described the prothoracic legs as possessing a dark stripe on the upper surface of the femur, while the femur of the meso- and metathoracic legs were described as being devoid of color stripes.

3. Eatonigenia seca, sp. nov. (Figs. 8, 10, and 11)

Male imago (in alcohol). Length : body 11.0-13.0 mm; fore wings 10.5-13.0 mm. Body generally light brown. Head light brown to fuscous dorsally; bases

of ocelli black; compound eyes grayish-black; basal segments of antennae yellowish-gray.

Thorax generally light brown; pronotum sometimes darker; prothoracic legs with coxa, trochanter, and femur medium brown, otherwise basically ivory; femur of mesothoracic legs light brown medially and basally; femur of metathoracic legs medium brown dorsomedially in basal third, distal margin of pigmentation extended and distally tapering off along dorsal edge of femur, additional very light brown spot laterally; wing venation medium to dark brown in costal region; bullae white.

Abdomen light grayish-brown to light brown; no distinctive color pattern or markings submedially; segments darkened medium to dark brown along lateral extremities and at area of overlap between segments giving abdomen transversely striped appearance (Fig. 8); terminal segments somewhat darker throughout; genitalia as in figures 10 and 11; penes with base constricted ventrally; posterior margin in approximately a very shallow V-shape with diverging margins nearly straight, distolateral margin more angulate than rounded, with distinct median longitudinal suture along ventrodistal surface; nipples of gonopores deeply emarginate, resultant processes of nipples curved somewhat dorsally, arising slightly basad of mid-length of penes; cerci ivory with tinge of light brown, with minute medium brown setae; vestigial terminal filament with longer dense medium brown setae.

Female imago (in alcohol). Length : body 10-13 mm; fore wings 12-13 mm. Characters as in male except for usual sexual differences, and color pattern less intense.

Nymph : Unknown.

Holotype : Male imago in alcohol, THAILAND : Bung Borapet, light trap, 16.vi.1971, W. Junk collector. Deposited in the collection of the University of Utah, Salt Lake City, Utah, U.S.A. *Paratypes :* 4 male imagos and 4 female imagos, same data as holotype. Deposition as holotype except 1 male imago in the collection of Purdue University, West Lafayette, Indiana, U.S.A.

Etymology : Secus, L : different.

Remarks : Present data would indicate that *E. seca* is sympatric with *E. chaperi* in at least part of its range. The morphological differences between the adults of the two species are quite distinct with *E. seca* being a much shorter and darker species than *E. chaperi*. Besides common generic characters, the two species demonstrate the greatest similarity in the color pattern of the legs with particular reference to the brown markings of the femur of the meso- and metathoracic legs. Generally, the genitalia of the above two species are quite similar with the only differences being in the shape and sulcation of the penes (Fig. 9-11).

E. seca is similar to *E. indica* in size and somewhat similar again in body coloration. The specific color patterns, especially those of the legs of *E. seca*, are quite different from those reported for *E. indica*.

Additionally, *Eatonigenia* material from Thailand has been studied as follows : five male and eight female subimagos, Thailand : near Khon Kaen, 6.vi.1970, H.E. Stark collector. All morphological evidence from the examination of these specimens points to the fact that they are unquestionably *Eatonigenia*, and indeed a species other than *E. chaperi*. Although the alcoholic specimens were received in poor condition, the following observed characterization would support the generic placement. The transverse shelf of the head is shallow (similar to figures 1 and 2). The mesoscutellum is acute posteriorly in dorsal view (similar to figure 3). The crossvenation and reticulation of the wings is of a type found in *Eatonigenia* (similar to figures 4 and 5), and there are eight or nine anal veinlets in the fore wings.

Generally speaking, as regards the structure of the male genitalia, there is often a marked change occurring with the imagal molt, and hence, subimagal genitalia have historically been of restricted taxonomic use in mayflies. For this reason the subimagal pellicle which was very loose on these specimens was removed and the underlying structures were studied. The forceps are three-segmented and the fused penes are of typical *Eatonigenia* form. The shape and suturiform nature of the penes (Fig. 12) are very similar to that found in *E. seca* (Fig. 11). Moreover, the size and coloration of these subimagos are similar to *E. seca*. For these reasons this material has been tentatively identified as *E. seca*. The so-called nippled apertures of the penes, however, are located much more basad in these male subimagos than in known male imagos of *Eatonigenia*. The subgenital plate is not well developed distally. These differences may be due to prematurity rather than taxonomic differences.

4. Eatonigenia trirama, sp. nov. (Figs. 14, 16-23, 25, and 26)

Imago : Unknown.

Mature nymph (in alcohol). Length : Body 17 mm, caudal filaments 4.0-4.3 mm. General body color very pale brown, with pale yellow setae and spurs on body. Frontal process of head (Fig. 14) yellowish-brown, approaching truncate with anterolateral angles slightly rounded, with row of pale relatively long setae along entire margin, becoming dense posterolaterally; supra-antennal processes very large, produced laterally as far as compound eyes in female, concavity of anterior margin asymmetrical, with pale dense setae anterolaterally; flagellum of antennae slightly longer than head; compound eyes dark brown; vertex medium brown, with row of setae posterior to compound eyes; median ocellus indistinct; distal margin of labrum (Fig. 16) with row of long setae, anterior surface with only sparse setae; mandibular tusks (Fig. 17) with row of setae bordering flattened dorsomedian surface for nearly entire length; lateral margin of paraglossae of labium (Fig. 21) with thick brush of short setae.

Prothorax dark brown becoming lighter on tergum posteriorly; meso- and metathorax light brown; all legs (Fig. 22 and 25) yellowish-brown, dark brown

on terminal margins of segments and angulated linear margins, moderately setaceous; prothoracic legs (Fig. 22) with setae longer marginally, tarsus with apical notch narrowly V-shaped with minute claw pointed and more or less hidden (Fig. 23); proximal ridge of tarsus on ventral (inner) surface of metathoracic legs distinct.

Abdomen very pale brown, nearly cream colored, with no discernible patterns dorsally or ventrally, lateral abdominal setae white; lamellae of gills 2-7 medium brown, fibrillae light brown to white; gill 1 (Fig. 26) very narrow; caudal filaments setaceous laterally for nearly entire length, setae longest at mid-length of caudal filaments, terminal filament slightly shorter than cerci.

Holotype : Mature nymph in alcohol (some parts mounted). South India : Madras Province, Bhavani River, vii.1962, collector anonymous. Deposited in the collection of the University of Utah, Salt Lake City, Utah, U.S.A.

Etymology : Triangulus, L : three-sided; ramus, L. : tusk.

Remarks : A comparison of the nymphs of *E. trirama* and *E. chaperi* reveals that the two species are very similar morphologically. Whether all of these similarities are common throughout the genus remains to be studied. Presently the following characteristics can be used to separate these species.

E. trirama is a smaller and darker species than *E. chaperi.* Setae are generally much thicker and with a richer gold color in *E. chaperi.* Concerning cephalic structures, the frontal process of *E. trirama* (Fig. 14) is proportionately longer than it is in *E. chaperi* (Fig. 13). The frontal processes of the two species also differ in that the setae are much sparser and shorter anteriorly in *E. chaperi.* The supra-antennal processes differ in that they are shorter, proportionately more deeply notched, and with the emargination more symmetrical in *E. chaperi* (Fig. 14) than is the case in *E. trirama* (Fig. 13). The labrum of *E. chaperi* (Fig. 15) possesses much more and longer setae over the anterior surface than does the labrum of *E. trirama* (Fig. 16). Other differences in the heads, as shown in figures 13 and 14, are interpreted as sexual (the eyes being much larger in the male nymph). The tarsi and tarsal claws differ in the two species, with the apical notch and claw being much narrower in *E. trirama* (Fig. 23) than in *E. chaperi* (Fig. 24). One more conspicuous difference has been found as regards the caudal filaments. The cerci of *E. trirama* are only slightly longer than the terminal filament, whereas in *E. chaperi* the cerci are nearly twice as long as the terminal filament.

Discussion

A more formal presentation of comparative morphology and phyletic correlation regarding the genera discussed above will be given later within a comprehensive analysis treating the entire family on a world-wide basis. Nevertheless, certain conclusions, particularly as they pertain to the zoogeography of Asiatic Ephemeridae, are relevant at this time.

Two genera of Ephemeridae occur in the Oriental Region, and a third very questionably exists there. Several species of *Ephemera* are distributed throughout Tropical Asia. The most closely related species of *Ephemera* to these are apparently to be found in the Ethiopian Region, thus demonstrating biogeographic affinities common in so many groups of organisms. The African species were placed in a separate genus, *Afromera*, by Demoulin (1955), yet their relationships with Oriental forms were suggested at that time. The question as to the geographic origin of *Ephemera* cannot be answered until such time as the phylogeny of the species of *Ephemera* has been worked out. Regardless, the Oriental Region has been the center of considerable speciation, and undoubtedly a number of species remain to be described.

The discovery of the nymphal stage of the Oriental genus *Eatonigenia* has aided in the elucidation of generic relationships within the family. Edmunds (1972) expressed the belief that *Eatonica* and *Hexagenia* are sister genera and hence show a geographic relationship between South America and Africa. Although this may have been a valid conclusion on the basis of prior information, it is not necessarily acceptable on the basis of recent morphological data on the nymphs of *Eatonica* and *Eatonigenia*. As pointed out earlier, *Eatonica* and *Eatonigenia* have proven to be very closely related, and demonstrate an additional zoogeographic affinity between Africa and Tropical Asia. Present interpretation of the phylogeny of ephemerid genera does not give evidence to direct Neotropical-Ethiopian relationships. *Eatonica* appears more distantly related to *Hexagenia* than to either *Eatonigenia* or *Litobrancha*. Furthermore, the occasional taxonomic treatments by Demoulin (1958 and 1970) wherein the Neotropical subgenus *Pseudeatonica* Spieth is placed by him within *Eatonica* rather than *Hexagenia*, as was originally proposed, are believed to be inappropriate in light of available information. These conclusions are defensible on the basis of first, the phylogenetic data and inferences presented herein, and second, the discovery and description of the nymphs of *Pseudeatonica* (see McCafferty, 1970) which are practically identical with those of the subgenus *Hexagenia* s.s.

Currently, four species of *Eatonigenia* are recognized as occurring in the Oriental Region, and the known range of the genus has been expanded from Java and Borneo to include Thailand and India. Although data on the Indian and Thailand forms are somewhat fragmentary at this time, they are perhaps indicative of a widespread distribution throughout Tropical Asia.

If indeed *Eatonigenia* and *Litobrancha* are directly related, then geographic dispersal involving the Nearctic and Oriental Regions must be explained. Granting Holarctic dispersal, the apparent anomaly is that no definite records of either genus or even a similar type have been established for the Palearctic. Eaton's (1883-88) rather obscure record of "*Hexagenia*" from Eastern Siberia provides the only possible geographic link at this time.

The presence of *Hexagenia* in the Oriental Region, being based solely on Navas' *H. philippina*, must be very seriously doubted for several reasons previously given. Taxonomic analysis of this species must necessarily rely on the future availability of more complete information; however, it would appear highly probable that *H. philippina* represents a previously described or a new species of *Eatonigenia*.

As pertains to many other groups of organisms, it is believed that the Asiatic Ephemeridae will be a most important contribution in clarifying the evolution and past dispersal of this group. Foremost in developing this background of information will be the description and association of both nymphal and imagal stages, along with the analysis of the phylogeny of the species.

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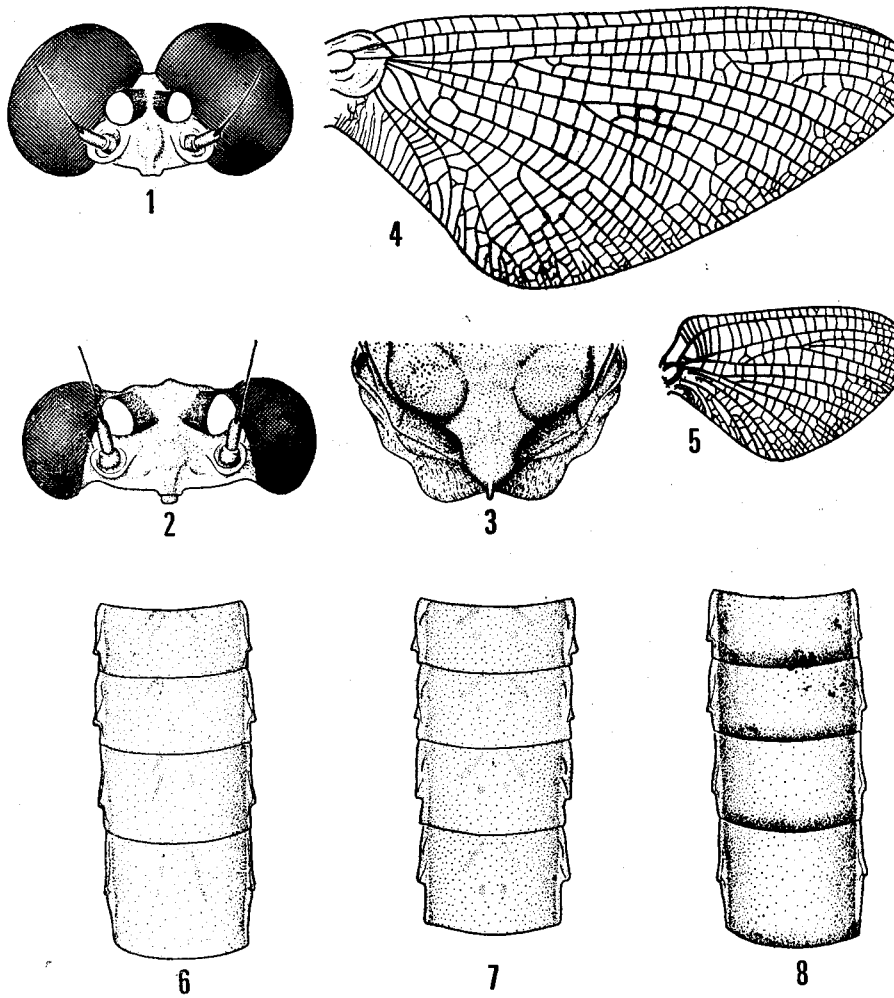


Figs. 1-7. *Eatonigenia chaperi* (Navas) : 1 and 2, Male and female head, anterior view; 3, Mesoscutellum; 4 and 5, Right fore and hind wings; 6 and 7, Male abdominal tergites and sternites 4-7; Fig. 8. *Eatonigenia seca*, sp. nov., Male abdominal tergites 4-7.

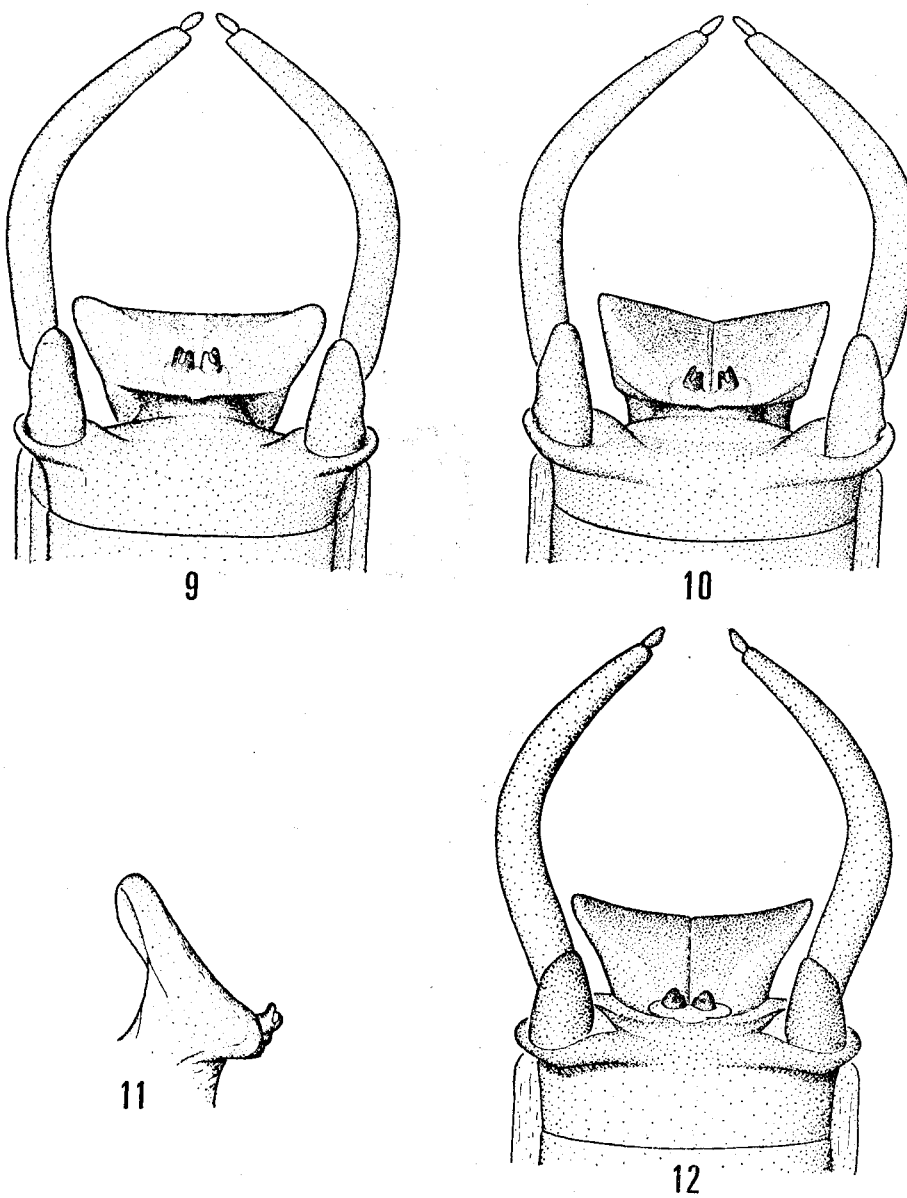
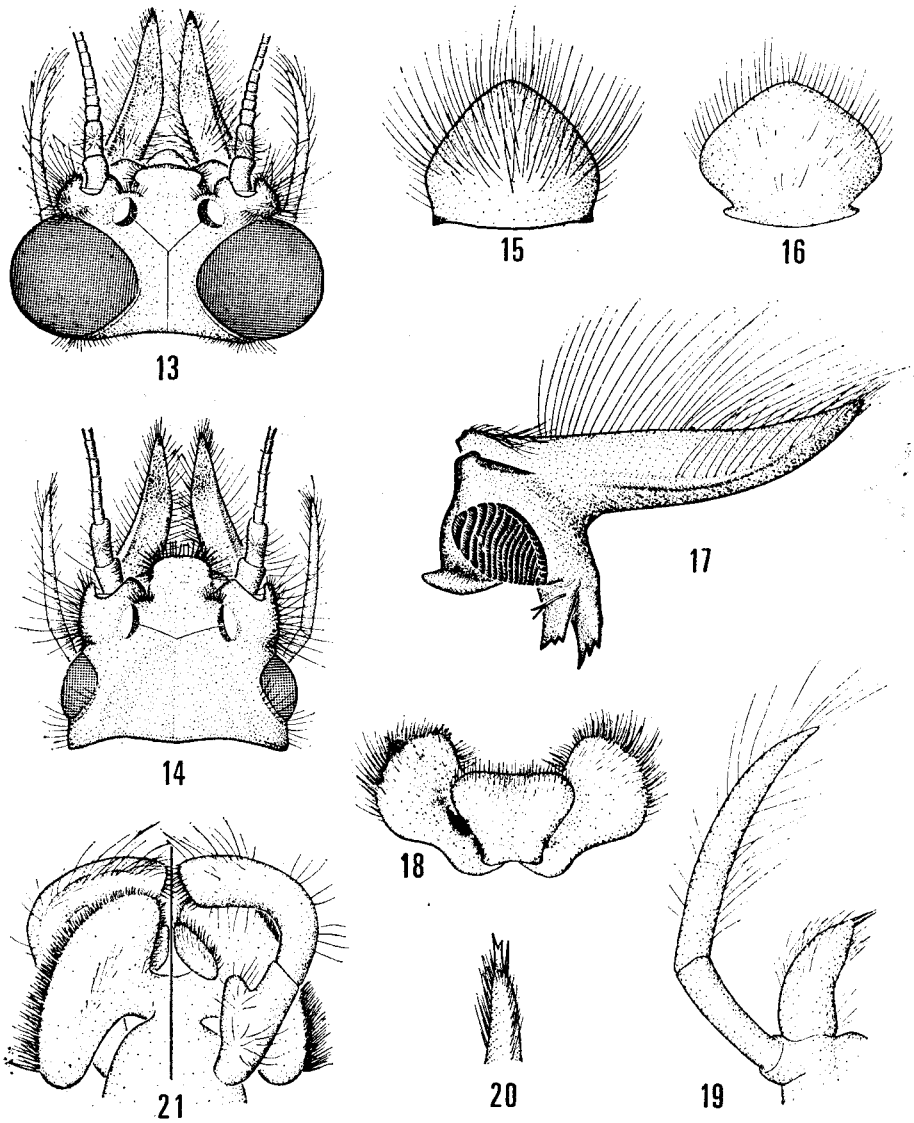
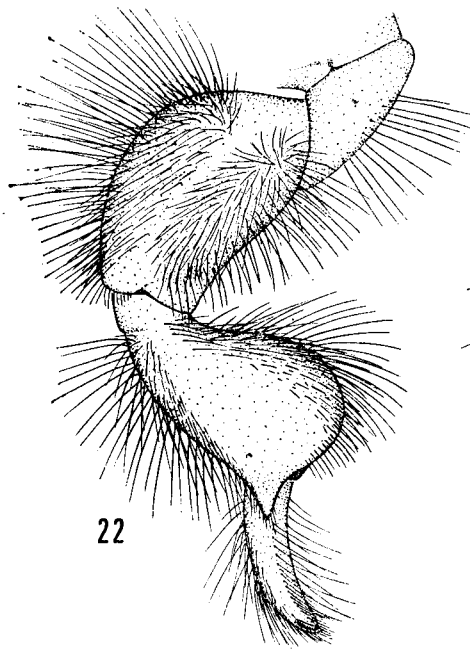
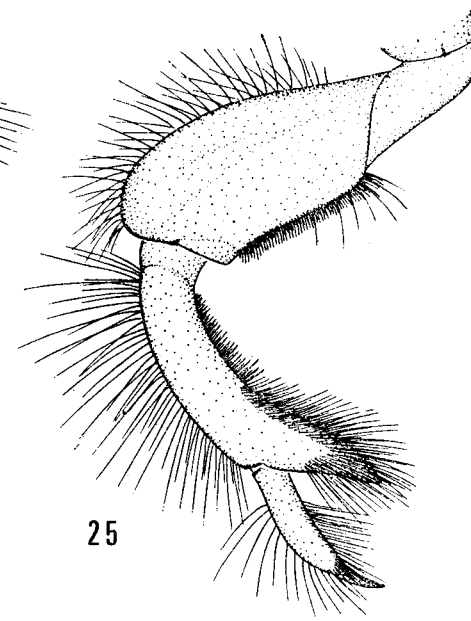


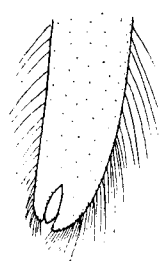
Fig. 9. *Eatonigenia chaperi* (Navas) : Male genitalia, ventral view. Figs. 10 and 11. *Eatonigenia seca*, sp. nov. : 10, Male genitalia, ventral view; 11, Penes, lateral view. Fig. 12 *Eatonigenia seca* (*?*), subimago, male genitalia, ventral view.

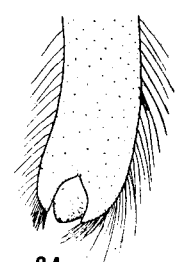


Figs. 13 and 15. *Eatonigenia chaperi* (Navas), mature nymph : 13, Male head, dorsal view; 15, Labrum, anterior view. Figs. 14 and 16-21. *Eatonigenia trirama*, sp. nov., mature nymph : 14, Female head, dorsal view; 16, Labrum, anterior view; 17, Left mandibular tusk, dorsomedian view; 18, Hypopharynx; 19, Right maxilla, posterior view; 20, Galea-lacinia, median view; 21, Labium, anterior and posterior views.









Figs. 22, 23, 25, and 26. *Eatonigenia trirama*, sp. nov., mature nymph : 22, Left prothoracic leg, dorsal (outer) view; 23, Left protarsus, posterior view; 25, Left metathoracic leg, ventral (inner) view; 26, abdominal gill 1. Fig. 24. *Eatonigenia chaperi* (Navas), Left protarsus, posterior view.