

SYSTEMATICS OF ANEPEORUS (EPHEMEROPTERA: HEPTAGENIIDAE)¹

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ABSTRACT

The enigmatic genus *Anepeorus* has a confused and complex taxonomic history that is discussed and clarified. The genus is redefined and described in the adult stage. Although larvae have been assigned to *Anepeorus*, these larvae cannot be shown at the present to be *Anepeorus*. Two North American species are known from a total of 10 adult specimens. *Anepeorus rusticus* McDunnough and *A. simplex* (Walsh) are redescribed, and a neotype is designated for the latter species. Genitalic differences are diagnostic, but the penes may be found in different states of inflation and rotation that should not be interpreted as taxonomic differences.

The genus *Anepeorus* was established by McDunnough (1925) to accommodate a new species of Heptageniidae from Saskatchewan, *Anepeorus rusticus* McDunnough (genotype by original designation). The genus was significantly characterized for adult males by fore leg and genitalic characteristics, which continue to make *Anepeorus* a clearly recognizable taxon. Systematics of the species has been obscured by a rarity of specimens, nebulous treatments, and a rather intricate nomenclatural history that requires clarification.

Walsh (1863) described *Heptagenia simplex* from Rock Island, Illinois, and in 1869 deposited the types in the Chicago Academy of Sciences. Walsh sent duplicate specimens that he identified as *H. simplex*, including some collected subsequently in 1864 from the type locality, to Hermann Hagen in Prussia. Hagen deposited these specimens in the Museum of Comparative Zoology (MCZ) at Harvard in 1870. In 1871, all of Walsh's types were destroyed in the Chicago fire. Eaton (1871 and 1885) treated *H. simplex* but added nothing to Walsh's original description, evidently not having studied the MCZ material. Nathan Banks sometime later designated a number of lectotypes at the MCZ for Walsh's species, including one for *H. simplex*. These lectotype designations were not published.

McDunnough (1929) indicated that the specimens sent by Walsh to Hagen under the name *H. simplex* did not agree with Walsh's description, and he identified them as *Heptagenia persimplex* McDunnough, a species he described from material at the Canadian National Collection (CNC) that had been collected in 1928 from Iowa near Rock Island, Illinois. (This species has recently been placed in the genus *Macdunnoa* Lehmkuhl by Flowers [1982]). At the same time, McDunnough indicated that fore leg traits described by Walsh (1863) for *H. simplex* corresponded to the generic concept of *Anepeorus* and therefore transferred *H. simplex* to *Anepeorus*. He identified one male specimen in the CNC collected near Davenport, Iowa, as *A. simplex* and figured its genitalia. McDunnough evidently believed this to be the only existent specimen verifiable as *A. simplex* at the time, and he made no mention of the type status for the species.

Burks (1953), after studying the MCZ material in 1942, indicated that Bank's designated lectotype of *A. simplex* (Walsh) should be disregarded; and a note initiated by George F. Edmunds, Jr. in 1960 and residing with the MCZ material concurs. Burks (1953) believed that there was one specimen at the MCZ that agreed with Walsh's

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simplex, but could not fully study it because the abdomen was missing. This specimen (labeled 35 / *Heptagenia simplex*), even though it does conform with Walsh's description, is not available as a lectotype because it was collected in 1864 subsequent to the original description. A neotype for *A. simplex* is formally designated below in the treatment of that species.

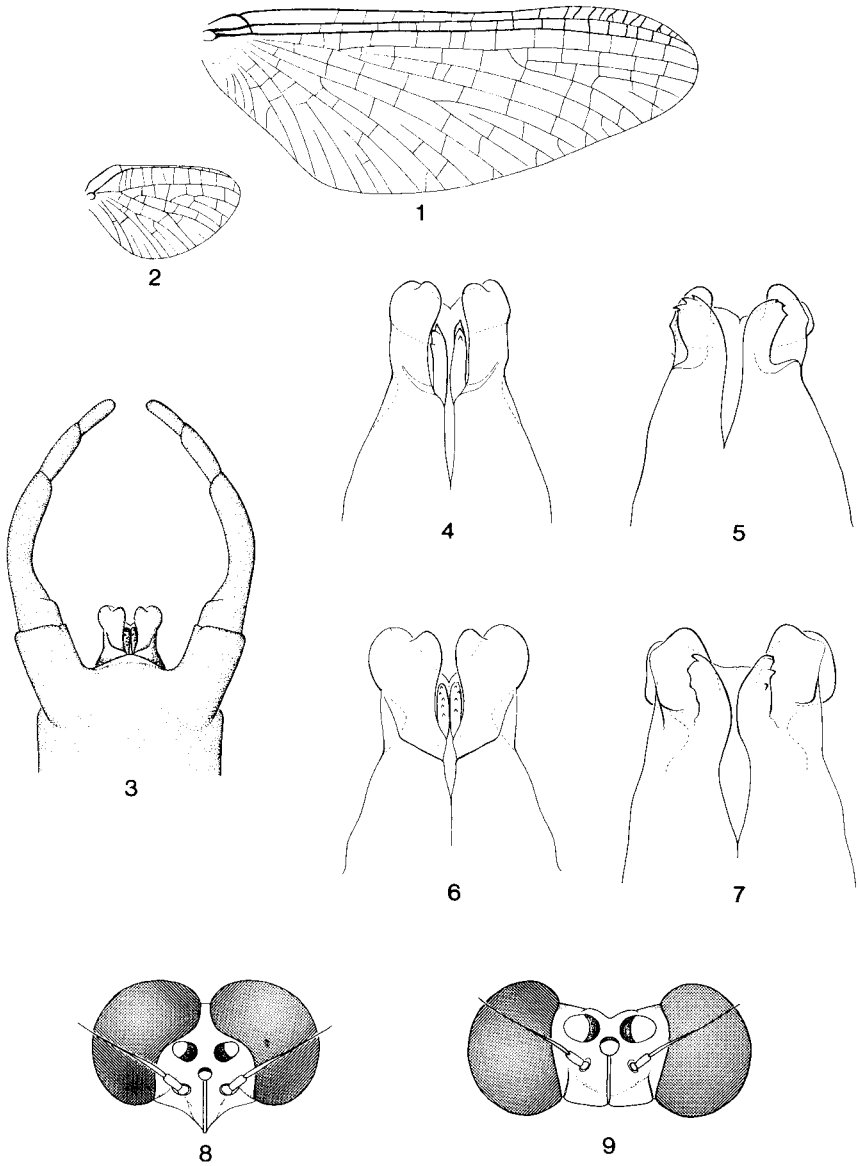
A third species of *Anepeorus* was described from China by Ulmer (1936) as *A. hummeli*. Since this description was made with stated reservation by Ulmer and was based on two adult females, and since there are presently no known female characteristics to distinguish the genus, we agree with Edmunds et al. (1976) that the generic assignment of this species is extremely questionable. The females of several species (and genera) of Heptageniidae, including those of *Macdunnhoa persimplex*, presently would conform with Walsh's brief original description of the female *A. simplex*; Walsh's females could not have been positively correlated with males in any case; and females of *A. rusticus* remain unknown. We must defer further taxonomic treatment of *A. hummeli* until female generic traits for *Anepeorus* can be established.

Larvae that have been historically assigned to *Anepeorus* have received considerable attention in the literature due to their intriguing and unusual habitus and habitat. Paradoxically, these larvae have never been definitively associated with the genus by rearing, and all references to "larvae of *Anepeorus*" are to larvae that are only provisionally assigned to the genus based on circumstantial evidence. Edmunds et al. (1976) were convinced that the adult-larval associations have been correct, and Edmunds (1962) recognized a separate subfamily Anepeorinae for the genus, probably based on the relatively aberrant nature of the supposed larvae. Accounts of these interesting, carnivorous larvae may be found in Burks (1953) and Edmunds et al. (1976). We do not treat them here because we are not convinced of an association with *Anepeorus*.

We can account for 10 male adults of *Anepeorus* in collections. The three from the type series of *A. rusticus* are at the CNC, along with one additional male from Alberta and a possible female. Traver (1935) reported seeing "specimens" of *A. rusticus* taken in Utah in 1911 and located in the Carnegie Museum. We and G. F. Edmunds, Jr. (pers. comm., 1984) have been unable to locate the Carnegie Museum *Anepeorus*. We have, however, been able to locate slide-mounted wings, legs, and genitalia of one of these Utah specimens that Traver studied and deposited in the Cornell University Collection. One specimen of *A. simplex* is located at the CNC and one broken one at the MCZ as explained above. There is also a male specimen from Georgia at Cornell that Traver (1935) identified as *A. simplex*. Burks (1953) reported studying a male adult from Rock River in Illinois, deposited in the Illinois Natural History Survey (INHS); the only material we can find from that location in the INHS are females identified as *A. simplex*, and these cannot be verified. The INHS adult male has evidently been lost; specimens bearing Burk's code numbers for *Anepeorus* are *Rhithrogena*. Burks may not have actually seen an adult male because the male genitalia he figured is an incorrect reproduction of McDunnough's (1929) figure (the ventral penes cleft was transposed dorsally). In addition to the above, we have two male adults collected from the White River, Indiana, in 1974. Our examination of all existent adult specimens from eastern and western North America has led us to the following redescription and analysis of the genus and its species.

Genus *Anepeorus* McDunnough

Adult (Male). Body 6.0–8.2 mm long. Fore legs 0.68–0.76 × body length; femur 0.71–0.89 × tibia length; tarsus 0.46–1.13 × femur length, 0.46–0.82 × tibia length; tarsal segment 2 longest or subequal to longest segment and always longer than segment 1; tarsal claws blunt and subequal. Hind legs with tibia 0.78–0.90 × femur length; tarsus 0.37–0.44 × tibia length. Fore wing (Fig. 1) 7.4–9.0 mm; 0–3 costal crossveins in basal fourth; 0–3 forked crossveins among stigmatic crossveins. Hind wing (Fig. 2) ca. one-third fore wing length; costal projection reduced and rounded, without acute or obtuse point; R_s forks attached to stem; MA forked; few free marginal intercalaries in major-vein interspaces, with one such intercalary in fork of MA and two between CuA and CuP.



Figs. 1-9. Adult *Anepeorus*: (1) Fore wing, *A. simplex*; (2) Hind wing, *A. simplex*; (3-7) Ventral male genitalia, (3) Whole genitalia, *A. simplex*, (4) Unrotated penes, *A. rusticus*, (5) Rotated penes, *A. rusticus*, (6) Unrotated penes, *A. simplex*, (7) Rotated penes, *A. simplex*; (8-9) Head, frontal view, (8) *A. rusticus*, (9) *A. simplex*.

Genitalia with four-segmented forceps (Fig. 3); basal segment very weakly demarked; posterior margin of subgenital plate roundly or sub-conically produced medially, and abruptly and more extensively produced laterally into distinct bases of forceps (Fig. 3); penes (Figs. 3-7) divided nearly to base by narrow, ventrally open cleft; transparent, medially notched septum extending between divided penes lobes dorsally (margin of septum in apical fourth of penes); each penes lobe appearing bi- or trilobular apically; toothed titillators arising medially on penes lobes at about midlength of penes; in unrotated and unseparated penes (Figs. 4 and 6) titillators remaining within ventral cleft, and titillator teeth ventrally projecting; in penes with ventral aspect subjected to ventral and outward rotation (Figs. 5 and 7) titillators appearing to originate ventrally on penes lobes, and titillator teeth laterally projecting.

Discussion. Genitalic and fore leg characteristics allow adult males of *Anepeorus* to be distinguished from other known adult male heptageniids. Comparably well-developed forceps bases together with a produced median margin of the subgenital plate are present only in *Afronurus* Lestage, *Epeorella* Ulmer, and to a lesser degree *Cinygmima* Kimmins, and *Pseudiron* McDunnough. These genera differ from *Anepeorus* in almost all other generic characters. The relative length of the fore tarsus of *Anepeorus* is the shortest among the Heptageniidae, ranging from about one-half to four-fifths the length of the fore tibia. Only in *Rhithrogeniella* Ulmer, *Afghanurus* Demoulin, and *Afronurus* do fore tarsi of some species even approach this ratio.

The recent discovery of the adult of *Spinadis* Edmunds and Jensen (McCafferty and Provonsha, 1984) indicates that *Anepeorus* and *Spinadis* may be quite similar in the adult stage even though only males of *Anepeorus* and females of *Spinadis* can presently be compared. There is even a remote possibility that *Spinadis* and *A. simplex* are one in the same. The following differences are based on a very small number of known specimens. If genitalia and fore legs are eventually found to be similar in males of both genera, they may be tentatively diagnosed by the hind wings if intercalary venation proves not to be sexually dimorphic. Short, free marginal intercalaries are present in almost every major-vein interspace in *Spinadas*, whereas in *Anepeorus* (Fig. 2) such intercalaries have been seen only in the MA fork. Both genera possess two long cubital intercalaries, but *Spinadis* possesses a short intercalary in this region also.

Anepeorus was thought to have been derived independently from "near the base of the proto-Heptageniidae," by Jensen and Edmunds (1973), but no evidence for this conclusion was given. We cannot determine the phylogenetic origin of *Anepeorus* at this time, but have data that indicate a relationship closer to *Spinadis* and *Pseudiron* than any other heptageniids, and thus would also suggest at least a strong possibility that these taxa as presently recognized were commonly derived. The adults of the three genera have several common characteristics, among which are hind wings with a costal projection that is reduced and rounded, and a head that has a straight frontal shelf (except *A. rusticus*).

Anepeorus rusticus McDunnough

Adult (Male). Body 8.0 mm long. Fore wing 9.0 mm long. Head brown; thorax dull to shiny pale brown, with mesothorax slightly darker than pro- and metathorax, sometimes mesonotum creamy white anteromedially; fore legs medium brown; middle and hind legs pale yellow-brown; abdominal terga pale brown, darker in posterior half, with pair of submedian and sublateral spots on each tergum (only sublateral marks evident on some); abdominal sterna paler than terga, with pair of submedian spots and sublateral oblique lines on each sternum. Head (Fig. 8) with eyes convergent dorsally; margin of frontal shelf distinctly produced ventromedially. Fore tarsus subequal to or slightly longer than fore femur, $0.76-0.82 \times$ fore tibia length. Lateral margins of penes (Figs. 4 and 5) not expanded apically, more-or-less parallel sided from base of titillators; titillator teeth oriented apically and restricted to apical third of titillator (Figs. 4 and 5).

Anepeorus simplex (Walsh)

Adult (Male). Body 6.0–8.0 mm long. Fore wing 7.4–9.5 mm long. Body generally devoid of maculations, and colorless except for yellowish head, thorax, and sometimes posterior abdominal segments, all of which appear gray or grayish yellow in alcohol preserved specimens. Head (Fig. 9) with eyes widely separated dorsally; margin of frontal shelf more-or-less straight, not produced ventromedially. Fore tarsus $0.48\text{--}0.59 \times$ fore femur, $0.46\text{--}0.50 \times$ fore tibia. Lateral margins of penes (Figs. 3, 6, and 7) expanded apically; titillator teeth oriented outwardly along distal one-third to two-thirds of titillators.

Neotype. Adult male: Indiana, Martin County, East Fork White River at Hindostan Falls, VI-20-1974, A. V. Provonsha and L. Dersch; in alcohol with "neotype" label in the Purdue University Entomological Research Collection, West Lafayette, Indiana. The neotype is the best undissected specimen of the species available at this time, and it is typical of Walsh's original description of the species.

Discussion. The two species of *Anepeorus* are easily differentiated from each other as male adults. *Anepeorus rusticus* is a darker species with at least some slight abdominal maculation. It has dorsally convergent eyes, a medially produced frontal shelf (Fig. 8), a longer fore tarsus relative to both the fore femur and tibia, non-bulbous penes lobes, and apical titillator teeth (Figs. 4 and 5). *Anepeorus simplex* is a pale, unmarked species that has widely separated eyes, a straight frontal shelf (Fig. 9), a shorter fore tarsus that is about half the length of both the fore femur and the fore tibia, apically bulbous penes lobes, and titillator teeth more scattered along the titillator.

The penes of *Anepeorus* (and many other heptageniids) are heavily muscled, allowing them to be variously expanded, extruded, separated, and partially rotated. For this reason, the penes of one individual may appear superficially quite different than another individual of the same species (note especially the titillator positions in Figs. 4–7). The appearance depends on such things as the state of the penes at death, the method of preservation, and the amount of pressure applied in slide mounting. Our discovery of this phenomenon in *Anepeorus* should serve as a caveat to others relying on heptageniid penes morphology for identification or descriptive purposes.

Biology. Based on all adult collections, the emergence period of *A. simplex* is early June in Georgia and southern Illinois and late June in Indiana, northern Illinois, and Iowa. The emergence period for *A. rusticus* is mid to late July in Utah and Alberta and mid September in Saskatchewan. Both species apparently develop in large rivers.

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