2 Classification and Phylogeny

North American stonefly systematics dates to 1823 with the descriptions of four species by Thomas Say, but the first major review of the Nearctic stonefly fauna was Hagen's (1861) study. Hagen considered all stoneflies as Neuroptera and placed the 61 Nearctic species and 7 genera in the family Perhna. Several genera (e.g., Pteronarcys and Leuctra) were used in the restricted sense of current stonefly systematics, but Perla contained 40 species from such disparate modern groups as Alloperla, Neoperla, Isogenoides and Pteronarcys.

Needham & Claassen's (1925) monograph provided a significant data base and stimulus for the early systematic studies of Frison and Ricker. The Needham & Claassen (1925) classification system presented a more modern appearance with the recognition of 4 families, 24 genera, and 207 species. Perhdae, however, still included elements of current Perlodidae, Chloroperlidae and Peltoperlidae, and Nemouridae also included Taeniopterygidae and Leuctridae. Several subgenera with current names such as Perlinodes, Beloneuria, Diploperla, Doddsia, and Eucapnopsis were adopted or proposed, but a hint of instability in the system was indicated by the statement that "we have not adopted all the genera that have been proposed of late. Many of the new ones . . . are based on . . . characters . . . so trivial they can hardly be considered as of more than specific value."

Frison (1942) proposed a classificatory scheme of 10 families and 35 genera, which included a definition of Perlidae restricted to those forms with branched nymphal thoracic gills, placement of *Megaleuctra* in Leuctridae, and recognition of Isoperlidae. Ricker (1943, 1952), however, strongly endorsed the "sub" category in Plecoptera systematics by giving subfamily rank to nemouroid taxa (eg. Capniinae, Leuctrinae, and Taeniopteryginae) and in recognition of subgenera (25 in 1943; 58 in 1952) rather than genera. Many subsequent authors of regional or national surveys (e.g., Gaufin et al. 1966, Jewett 1968, Hitchcock 1974) followed Ricker's generic concepts, but the vagaries of this period are aptly illustrated by the history of "Leuctra claasseni," which was described by Frison (1929) in the genus Leuctra, placed in the new genus Paraleuctra by Hanson (1941), returned to Leuctra (but in subgenus Paraleuctra) by Frison (1942), placed in the new subgenus Zealeuctra by Ricker (1952), and elevated to the genus Zealeuctra by Illies (1966). Ricker & Ross (1969) concurred with the last-named usage, although with "some regret."

Illies' (1966) world catalogue profoundly affected stonefly systematics, as subgenera were, a priori, given generic rank. This increased the number of Nearctic genera from Jewett's (1968) list of 36 to 85 for the approximately 400 species recognized at that time. More important, this opus stimulated another burst of systematic research as a new generation of workers (e.g., Baumann, Nelson, and Harper) joined Ross and Ricker in testing the phylogenetic systems and classificatory schemes proposed by Illies (1965, 1966) and Zwick (1973, 1980). Recent studies of Nearctic Plecoptera (e.g., Baumann