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CONTEMPORARY PATTERNS IN A HISTORICAL CONTEXT: PHYLOGEOGRAPHIC HISTORY OF THE PIPEVINE SWALLOWTAIL, *BATTUS PHILENOR* (PAPILIONIDAE)

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Abstract.—We examined mitochondrial DNA (mtDNA) variation in pipevine swallowtail butterflies (*Battus philenor*) from throughout its extant range to provide a historical, phylogeographical context for ecological studies of the disjunct population in California. We evaluate current hypotheses regarding host plant use, behavior, and mimetic relationships of *B. philenor* populations and generate alternative hypotheses. Compared to populations throughout the rest of the species' range, California populations are ecologically distinct in that they lack mimics, lay significantly larger clutches of eggs, and exclusively use a unique, endemic larval host plant. Analysis of molecular variance, tests of population differentiation, and nested clade analysis of mtDNA variation indicate that, despite low levels of population genetic structure across the species' range, there is evidence of recent range expansion from presumed Pleistocene refuge(s) in southeastern North America. Colonization of California appears to have been a recent event. This phylogeographic investigation also suggests that the evolution of life-history adaptations to a novel larval host has occurred rapidly in California and the lack of mimics in California may be attributable to the recency of colonization.

Key words.—*Battus philenor*, geographic variation, mimicry, phylogeography, pipevine swallowtail, plant-insect interactions, range expansion.

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Phylogeographic studies provide ecologists and evolutionary biologists with a historical context in which observed patterns in nature can be placed (Avise 2000). Understanding the temporal component of a species' distribution can be used to explain ecological and phenotypic discontinuities observed across the extant range of a species (Brown et al. 1996; Groman and Pellmyr 2000; Althoff and Thompson 2001; Althoff et al. 2001). Such studies can also reveal extensive periods of allopatry among populations that, until now, were not recognizable (Taylor et al. 1998; Omland et al. 2000). Investigations concerning ongoing ecological processes that lead to differentiation among populations benefit by placing them in such a historical context because different histories can lead to different adaptive strategies, including behavioral, physiological, and life history traits (Althoff and Thompson 1999; Després and Jaeger 1999). Additionally, the magnitude of recent range changes is essential knowledge for investigators employing methodologies that are sensitive to range changes, yet use current distributions to test evolutionary hypotheses (Barraclough and Vogler 2000).

This study attempts to broadly describe the phylogeographic history of the pipevine swallowtail, *Battus philenor* (Papilionidae), throughout its current range. *Battus philenor* is the northernmost member of this Neotropical genus, extending throughout the southeastern portion of North America, as far south as Honduras, and disjunctly in California (Fig. 1) (Scott 1986; Tyler et al. 1994). Although at least five subspecies have been described (Racheli and Pariset 1992; Tyler et al. 1994), based largely on locality, *B. philenor* shows remarkably little phenotypic variation throughout its range (Scott 1986). All members of the genus *Battus* are monophagous, feeding only on plants in the genus *Aristolochia* (Aristolochiaceae) as larvae (Racheli and Pariset 1992). This is in contrast to some other swallowtail genera, such as *Papilio*, which use a number of plant families and where host shifts have been documented (Shapiro and Masuda 1980; Thompson 1995). Consequently, the range of the pipevine swallowtail is constrained by the range of its host plants, most of which are restricted to tropical or subtropical regions (Pfeifer 1966, 1970). *Aristolochia* species contain toxic alkaloids called aristolochic acids, which *B. philenor* sequester as larvae causing the larvae and adults to be chemically protected from many predators (Rothschild et al. 1970; Fordyce 2000, 2001; Sime et al. 2000; Sime 2002). The unpalatability of *B. philenor* larvae and adults is advertised through aposematic coloration. Larvae are covered with red spines contrasting with a black or dull-red background and adults are mostly black with orange spots on the underside of the hindwing, making them exceedingly conspicuous. As a result, throughout most of its range, *B. philenor* is involved in mimicry complexes with more palatable species of butterflies, including *Papilio polyxenes*, *P. troilus*, *P. glaucus*, *Speyeria diana*, and *Limenitis arthemis* (Poulton 1909; Brower and Brower 1962; Platt et al. 1971; Jeffords et al. 1979; Racheli and Pariset 1992). Indeed, *B. philenor* was a seminal component of Brower's (1958) early investigations into the effectiveness of mimicry. Additionally, *B. philenor* has been used as a model system by numerous investigators studying, for example, female oviposition behavior (Rausher 1981, 1983; Rausher and Papaj 1983; Papaj 1986; Papaj and Rausher 1987; Rausher and Odendaal 1987; Pilson and Rausher 1988; Tatar 1991), larval ecology (Rausher 1980, 1981; Stamp 1986; Fordyce and Agrawal 2001), pupal color polymorphisms (Sims and Shapiro 1983a, b), phenology (Sims and Shapiro 1983c, d), and chemical ecology (Rothschild et al. 1970; Papaj et al. 1992; Sime et al. 2000; Sime 2002; Fordyce 2000, 2001). Although *B. philenor* is well studied, few investigations have examined geographical variation in the phenomena under study (Papaj 1986; Pilson and Rausher 1988;