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# EDWARD O. WILSON AND HIS CONTRIBUTIONS TO ANT SYSTEMATICS

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This Festschrift celebrates the fiftieth anniversary of the publication of the Ph.D. thesis of the world's most prominent myrmecologist. Edward O. Wilson is a towering figure in ant biology, and his influence extends well beyond myrmecology to broader aspects of science and society. Yet many of his research accomplishments, especially from the earlier years, reflect a particular concern with ant systematics and evolution. Among Wilson's many contributions to this field, his doctoral dissertation—a monographic revision of the ant genus *Lasius*—is a particularly significant milestone. Published in March 1955, it represents one of the first serious attempts to incorporate into ant systematics the principles of population biology and evolution. Wilson and his associate, William L. Brown, Jr., pioneered the introduction of these ideas into ant taxonomy, often in the face of resistance from more traditional workers.

The "new systematics", as it was called by Julian Huxley (1940), drew inspiration from the writings of Ernst Mayr, Bernard Rensch, Theodosius Dobzhansky, Sewall Wright and other architects of the neodarwinian synthesis. Mayr's (1942) *Systematics and the origin of species* had an especially influential role. Species were envisaged as groups of interbreeding populations, reproductively isolated from other such groups, and frequently containing a substantial amount of variation. This biological species concept stood in contrast to the typological view of species that was implicit in much earlier taxonomic work. Ant taxonomy itself was burdened with a peculiar and unwieldy pentanomial nomenclature (Brown, 1955), and was associated with the profligate naming of "species", "subspecies", and "varieties", often poorly diagnosed and with little thought directed to the nature of these forms or their relationships to one another.

An early assault on infraspecific names in ant taxonomy was carried out by William S. Creighton, most notably in his monumental *Ants of North America* (1950). Buhs (2000) credits Creighton with introducing the "new systematics" to myrmecology, but Wilson and Brown went further than Creighton and they had a more lasting impact. They argued compellingly against the use of subspecies names in systematics (Wilson & Brown, 1953; Brown & Wilson, 1954); they advocated a global approach to revisionary taxonomy; they were concerned with the higher classification and phylogeny of ants; and they paid greater attention than other workers to the quantification of intra- and interspecific variation. Wilson's (1955) *Lasius* monograph exemplified these ideals. It dealt with the world fauna, offered a provisional phylogeny, abandoned the use of subspecies names, and attempted to delineate species while allowing for a measure of intraspecific variation. It made extensive use of metric measurements and indices, based on large population samples, and it introduced standardized terms—still in use today—for describing the appearance of pilosity in ants.

These progressive features were not adopted by all workers. Creighton and other North American-centered ant taxonomists became quite critical of the work of the "Happy Harvard Team", as they referred to Wilson and Brown. In retrospect, most of the criticisms appear to be rather defensive and to miss their mark. One of the most persistent was that the Harvard researchers lacked sufficient field experience to make prudent judgments about species

boundaries (Buhs, 2000). This arose specifically in the context of Wilson's *Lasius* revision. The criticism is difficult to sustain since there is abundant evidence in the monograph that Wilson had direct experience in the field with most of the North American species. His taxonomic studies of Melanesian ants were similarly preceded by an intensive collecting expedition to that region of the world. And no ant systematist can—or perhaps ever will—match Bill Brown for global field experience of ants in their natural habitats.

If the taxonomic disputes are dissected more carefully one sees that they often center on the issue of how much variation one can expect to occur in single biological species. Wilson and Brown tended to be "lumpers", accepting more intraspecific variation, both ecological and phenotypic, than Creighton, Cole, Gregg, Buren, and others, who were prone to split biological diversity more finely. What is the verdict 50 years later? For many of these differences of taxonomic opinion, involving such difficult genera as *Formica* and *Lasius*, it is sobering to realize that we simply do not have adequate evidence to judge. In some instances we are dealing with closely related allopatric populations for which assessment of species status is often somewhat arbitrary. For *Lasius* it is noteworthy, however, that half a century later and after the accumulation of much more material, Wilson's treatment of the Nearctic species holds up quite well. In the Palearctic region—from which Wilson had less material and no direct field experience—the picture has undergone greater modification, with multiple species of *Lasius* now being recognized under what Wilson considered to be single polytypic species (Seifert, 1988, 1992; Schlick-Steiner *et al*., 2003). There are some genetic data to support recognition of these cryptic species (Steiner *et al*., 2004; Janda *et al*., 2004), but taxon sampling remains incomplete and information from molecular markers other than mitochondrial DNA—which can be quite misleading about species boundaries—is badly needed. If the situation in North America is comparable to that in the Old World, then it is possible that some of the Nearctic *Lasius* "species" will prove to be composed of multiple sibling species. There is ample scope here for additional research in both North America and Eurasia to determine if we are dealing with different biological species, i.e., reproductively isolated entities, or with geographical, ecological and behavioral variants.

Another notable feature of Wilson's (1955) *Lasius* revision was his exploration of the processes responsible for the genesis of taxonomic diversity. For the first time in ant taxonomy we find discussion of the patterns of species distributions and intraspecific geographical variation, and the implications of these patterns for the mode of speciation. Considerable attention was also given to biological traits. Under the accounts of individual ant species there are summaries of what is known about nesting behavior, foraging habits, and habitat preferences. The role of interspecific competition and divergent selection was of particular interest to Wilson, and led to a co-authored paper with Brown on character displacement that appeared one year later (see below).

Over a ten-year period between 1955 and 1965 Wilson published a series of additional papers on ant taxonomy that reflected the thinking of the "new systematics". This included revisionary treatments of selected groups of Melanesian ants, mostly poneromorphs (Wilson, 1957, 1958a, 1958b, 1959b, 1959c); rediscovery and description of the enigmatic Sri Lankan ant *Aneuretus simoni* (Wilson *et al*., 1956); taxonomic notes on certain *Formica* species (Wilson & Brown, 1955); a review of dacetine ant evolution (Brown & Wilson, 1959); and a revision of the Indo-Australian army ants (Wilson, 1964). The taxonomic work on Melanesian ants provided a foundation for Wilson's analysis of ecological and evolutionary trends in the ants of that region, especially a pattern of range expansion and habitat shifts that Wilson (1959a, 1961) termed the taxon cycle. Another influential idea, which arose in part from taxonomic patterns that Wilson observed in *Lasius*, was the concept of character displacement (Brown & Wilson, 1956), the notion that under some circumstances closely related species can be expected to show greater divergence in sympatry than in allopatry, as a consequence of interspecific competition, a pattern opposite to that which is predicted by occasional interspecific hybridization. Thus, not only was

Wilson's taxonomic work informed by the principles of evolutionary biology, but there was also reciprocity: taxonomic findings themselves illuminated previously undisclosed phenomena, emerging, as Wilson himself has noted, "as unplanned products of pedestrian daily research" (Wilson, 1994: 205).

After 1965 there was less taxonomic output from Wilson as his inquiries focused on other aspects of ant biology, and on broader questions about biogeography, the evolution of social behavior, and the conservation of biodiversity. Yet there continued to be periodic contributions to ant systematics, including the discovery and description of the first fossil ant from the Cretaceous period (Wilson *et al*., 1967); a monograph on the ants of Polynesia (Wilson & Taylor, 1967); a magisterial overview of social insect biology (Wilson, 1971) that included a lucid discussion of the origin of ants and the contradictions inherent in treating both *Amblyopone* and *Sphecomyrma* as models for the common ancestor of all ants; a series of taxonomic papers on fossil ants, primarily from Dominican amber (Wilson, 1985a, 1985b, 1985c, 1985d, 1986); and a useful taxonomic summary and set of keys to ant subfamilies and genera (appearing in Hölldobler & Wilson, 1990). Although their primary focus is not systematics, the much acclaimed books *The insect societies* (Wilson, 1971) and *The ants* (Hölldobler & Wilson, 1990) have had an important indirect influence on ant systematics by luring acolytes into the field with engaging and informative prose.

In 2003 Wilson published a prodigious tome on the New World *Pheidole*. Recognizing 624 species, of which more than half are new to science, this work provides the first comprehensive treatment of *Pheidole* on such a large geographic scale. The monograph is copiously illustrated, and identification of an unknown specimen is most easily accomplished by browsing the detailed line drawings within the appropriate species group, paying attention to highlighted features and lists of similar taxa. This "field guide" approach produces a more reliable result than resorting to the species identification keys, which are cumbersome and often lead the user astray.

It may be difficult for non-systematists to appreciate what an enormous improvement Wilson's (2003) revision brings to the state of *Pheidole* taxonomy. There had been no earlier synthetic work on the genus at such a scale—merely an accumulated morass of hundreds of names, often associated with ill-defined or unrecognizable taxa, and a backlog of thousands of *Pheidole* specimens in collections that could not be confidently identified to species. We now have a robust framework for the classification and identification of the New World fauna, available for further refinement and testing. Of course, this is certainly not the final word on the taxonomy of New World *Pheidole*. Numerous additional species await discovery and delineation. Longino's fine-scaled analysis of the Costa Rican fauna (Longino, 2004) yields species delimitations somewhat at variance with those of Wilson. Rather ironically—in view of earlier taxonomic controversies—Longino interprets a number of Wilson's "species" as representing intraspecific variation, thus advocating a more polytypic view of species than that adopted by Wilson.

While most of Wilson's work in ant systematics has been concerned with species-level issues, he has also contributed incisively to our understanding of the origin of ants (as noted above), especially through the discovery and analysis of key fossil taxa (Wilson, 1971, 1987; Wilson *et al*., 1967). His proposed phylogeny of *Lasius* (Wilson, 1955: 15) anticipated correctly the inclusion of *Acanthomyops* within that genus, as now confirmed by molecular data (Janda *et al*., 2004). A provisional phylogeny for Formicidae as a whole, based on internal and external anatomy, that appeared in *The ants* (Hölldobler & Wilson, 1990: 26) provides an interesting point of contrast with the picture that is emerging from molecular phylogenetic analyses. From *Lasius* to *Pheidole*, from fossil ants to extant species, what underpins all of Wilson's systematic papers is an intense interest in understanding biological diversity—its origins, causes, and consequences. His writings also convey a passion for scientific discovery and an ability to apply critical evolutionary thinking to taxonomic problems. The result is an inspiring body of work and an intellectual legacy that will continue to stimulate future generations of ant systematists.

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