HERITAGE

Charles Valentine Riley: Taxonomic Contributions of an Eminent Agricultural Entomologist

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The contributions of C. V. Riley (1843-1895) (Fig. 1) were crucial to agricultural entomology's 19th-century rise to world preeminence (Sorensen 1995). As an economic entomologist, he was said to be "far and away the most eminent the world has ever seen" (Fletcher 1895). By all measures, he is among the most influential and prominent entomologists of any era. His work has been termed "epoch making" (Howard 1894), and in the words of Evans (1968), "few more remarkable figures have ever crossed the stage of entomology."[1]

As State Entomologist of Missouri (1868-1877), Riley produced annual reports "packed with facts new to science" (Packard 1895). His nine Missouri reports surpassed those of renowned state entomologists Asa Fitch in New York and B. D. Walsh[2] in Illinois, owing largely to a more attractive and readable format, detailed accounts and illustrations of insects and their life stages, and an engaging, unaffected literary style (Fletcher 1895, Howard 1930, Meiners 1943, Evans 1968). As head of the U. S. Entomological Commission (the other members were A. S. Packard and Cyrus Thomas), he gained national prominence for his work to combat ravages from the Rocky Mountain locust [*Melanoplus spretus* (Walsh)] in western states (Howard 1930, Lockwood 2004, Sorensen et al. 2008).[3] International acclaim followed the success of two major pest-suppression projects: biological control of the cottony cushion scale (*Icerya purchasi* Maskell) (Fig. 2) in California citrus orchards (Riley 1893a, Doutt 1958, Caltagirone and Doutt 1989)[4] and campaign against the grape phylloxera [*Daktulosphaira vitifoliae* (Fitch)] in France (Smith and Smith 1996, Sorensen et al. 2008). Riley also served as chief of the U.S. Department of Agriculture's Division of Entomology and advocated passage of the Hatch Act of 1888, which provided for the establishment of agricultural experiment stations in the land-grant colleges (Riley 1891, Howard 1930, Smith 1989, Smith and Smith 1996, Mitter 1999, Sorensen et al. 2008). Moreover, Riley's (and B. D. Walsh's) acceptance of Darwinian principles allowed entomologists to assume a leading role in the new field of evolutionary biology (Sorensen 1995, Sheppard 2004).[5]

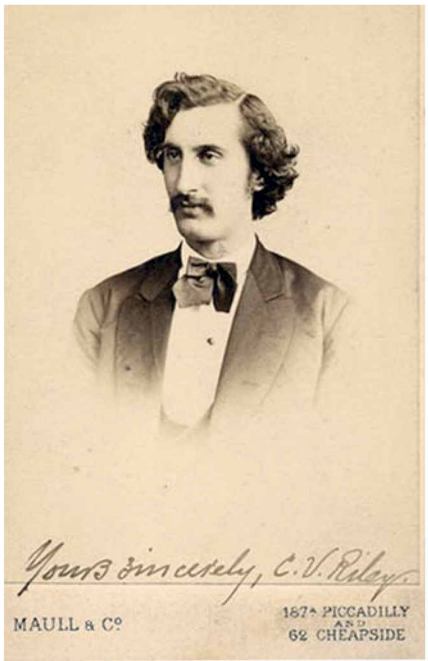

Fig. 1. Portrait of C. V. Riley, age 27 or 28 (1871), by Maull & Co., London. Courtesy of Gary L. Miller and M. Alma Solis, Systematic Entomology Laboratory, ARS, USDA, Beltsville, MD.

[1]Sorensen (1995, ch. 8) ranked Riley first among a core group of 108 entomological authors who were publishing around 1870 and explained how he ranked entomologists cited in the *Record of American Entomology* (1868-1873). Sorensen's chapter also includes a discussion of authors' geographic residence at time of birth, parents' occupation, educational background, sources of entomological training, associations with prominent teachers, fields of study, and other categories that permit the American entomological community of 1870 to be characterized. Henshaw (1889) listed 1,554 titles in a bibliography of the "more important writings" of C. V. Riley (through 1888). In *Atlantic Monthly*, a writer of a notice of Henshaw's work wondered "how much Dr. Riley's less important writings would swell the total" (Anonymous 1890).

[2]Walsh (1808-1869) served as Riley's mentor, helping shape his protégé's entomological thinking. The success of Riley's Missouri reports benefited from his association with Walsh (Howard 1930, Meiners 1943, Smith and Smith 1996, Sheppard 2004, McWilliams 2008). As State Entomologist of Illinois, Walsh had produced only one annual report before his death in 1869 as the result of a railroad accident.

[3]Lockwood's (2004) book *Locust: the Devastating Rise and Mysterious Disappearance of the Insect that Shaped the American Frontier* is an engaging account of the Rocky Mountain locust. The Entomological Commission's work later encompassed other pests, e.g. the chinch bug, Hessian fly, lepidopterans on cotton, and insects of forest and shade trees (Meiners 1943).

[4]Lintner (1890) and Howard (1930, p. 502), among other authors, stated why most of the credit for successful control of the cottony cushion scale should have gone to Riley rather than Albert Koebele, who was dispatched to Australia to look for natural enemies of the scale.

[5]In reviewing the entomological contributions of Charles Darwin, Riley (1882a) commented that of all the branches of natural science, entomology had benefited the most from Darwin's work. Riley later acknowledged that it was due to Darwin's influence that naturalists were placing less emphasis on the "dry bones" of their science and instead realized that if modern science were to solve far-reaching problems, it needed to draw more direct inspiration "from the vital manifestations of nature" (Riley 1884). Kritsky (1981) provided an index to the many references to insects in Darwin's writings.

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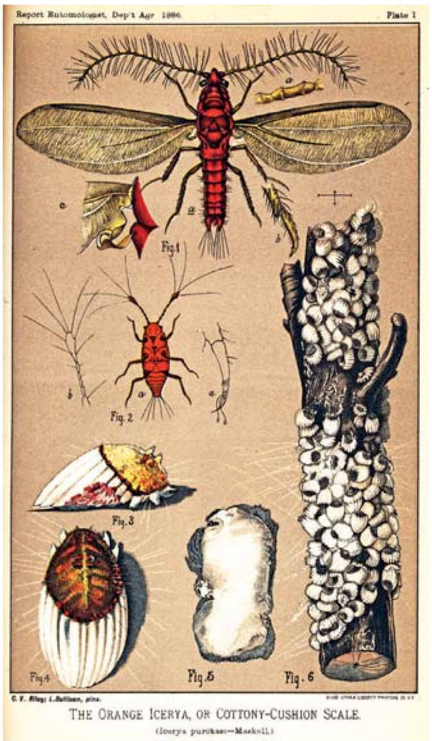

Fig. 2. Principal life stages of the cottony cushion scale, *Icerya purchasi* Maskell, illustrated by Lillie Sullivan under the supervision of C. V. Riley (or L. O. Howard). Reproduced from Report of the Commissioner of Agriculture, 1886. Government Printing Office, Washington, DC.

Biographers, understandably, have emphasized Riley's work in applied entomology and devoted scant attention to his taxonomic interests. Ever the pragmatist[6] (Riley 1891, p. 207; Smith 1989), he sometimes is said to have contributed little to systematics, having described "but few" new species (Goode 1896). We agree that Riley was not a "systematist as such" and not a "species man" (Packard 1895). He disfavored pedantry and the tendency of taxonomy to overshadow biological research (Riley 1884). His philosophy was not to see how many new species he could describe (Riley 1886):

"It is more creditable to any author to publish some full and complete account of any one insect, whose characters and habits have hitherto been unknown, or a synopsis or monograph of some genus or family, than to cast to the world a whole number of hasty descriptions of species; for while descriptive work thoroughly and faithfully done is of the highest order and most creditable, it is a fact that many entomological writers have busied themselves with descriptive work which has had little other result than to confuse and perplex all subsequent honest and serious workers in the same field."

Yet we also can side with Essig's (1931) assessment: that Riley "did a considerable amount of systematic work." His writings included comments on species concepts (e.g., Riley 1883a) and dealt with an important element of systematics—"discovery and characterization of the world's species and the range of their life stages" (Mitter 1999). Riley (1888) commented that the dearth of classificatory works and monographs hindered entomological progress in North America, realizing that taxonomic work, including accurate identifications, is crucial to biological control (e.g., Rosen 1986) and other aspects of entomology. Riley's taxonomic interests complemented his more applied work, and a proficiency with parasitic Hymenoptera might have given him a better appreciation of the potential importance of parasitoids in alleviating damage from agricultural pests. Riley (1871a, pp. 157-158) described *Trichogramma minutum* Riley, a parasitoid wasp widely used in the biological control of pest insects and the subject of numerous experimental studies (Smith 1996). It is appropriate that he be credited with establishing at the Smithsonian Institution a tradition of taxonomic research on parasitic Hymenoptera (Knutson 1991), one that has continued into the 21st century. Riley also was a principal founder and the first president of the Entomological Society of Washington, which publishes a quarterly journal (*Proc. Entomol. Soc. Wash.*) emphasizing taxonomic contributions (Riley 1886, Gurney 1976, Spilman 1984).[7]

Here, we examine the taxonomic interests and work of C. V. Riley,[8] using *taxonomy* in a broad sense to include systematics and what sometimes is termed *biosystematics*. We look at his estimate of the number of insect species on Earth; his role on a committee charged with developing a code to stabilize nomenclature for North American insects; his building of a large personal collection of insects, which eventually was donated to the Smithsonian Institution to ensure the prominence of a National Insect Collection; his investigations of insects characterized by complex life histories; and his descriptions of new taxa. We list the arthropod genera and species he described as new, indicating whether the names currently are valid, and list the taxa named in his honor (patronyms). We conclude by evaluating Riley's overall contributions to systematic entomology.

Pondering Global Insect Richness

Until the 1980s, relatively few workers had become interested in assessing the full extent of biotic diversity on our planet (Gaston 1991, Stork 1993). Erwin (1991) and Gaston (1991) remarked that naturalists at least as early as the 1830s had begun to ask how many insect species are found on Earth, referring to Westwood's (1833) article. Interest in the number of insect species actually predated the work of Linnaeus (Berenbaum 2009). Renowned British naturalist John Ray (1691) estimated insect species at 10,000 before revising his estimate to 20,000.[9] Early estimates also included 600,000 (Kirby and Spence 1815) and 400,000 species (Westwood 1833). Most early efforts at estimating the number of extant insect species were based on the number of Linnaean species, subsequent annual rates of species descriptions, and thoughts on the numbers of new species that remained to be described (Erwin 1991). Examples of the use of taxonomists' products to estimate world insect richness are papers by Metcalf (1940) and Sabrosky (1952). In the years leading up to Erwin's

[6]Riley (1891) made clear his views on the practical aspects of entomology: "Where it ["anatomic work"] is given for the purpose of describing species and synopsizing or monographing higher groups, without reference to agriculture, I am firmly of the belief that it diverts one from economic work...." Science, he felt, was best served "when the pure and the applied go hand-in-hand—when theory and practice are wedded" (Riley 1884).

[7]In its first 10 years, the *Proceedings of the Entomological Society of Washington* was characterized by a dearth of papers on systematics (Howard 1895), but soon more taxonomic contributions were published in the journal, some of substantial length (Howard 1909).

[8]Riley's work in taxonomy and other entomological endeavors, in Missouri and later in Washington, DC, benefited from that of assistants and field agents, including L. O. Howard, O. Lugger, Mary Murtfeldt, T. Pergande, E. A. Schwarz, and F. M. Webster (Howard 1930, Meiners 1943, Russell 1980, Adler et al. 2004). At the time, it was customary for scientists to assume credit for their assistants' work (Howard 1930, 1933; Evans 1968, Mallis 1980). Riley, however, was so talented and driven to excellence that he likely would be held in as high esteem today had he not received help from assistants. In all his work, Riley was the "directing mind," and in the opinion of Goode (1896), he demonstrated in his first year when he had no assistance that "he was able to have done the work unaided." Entomologists who did not work directly with Riley often held more favorable opinions of him; they were less likely to have to deal with his "many moods and whims" and his sometimes "dictatorial" and "temperamental" nature (Osborn 1937, pp. 152-156). Canadian entomologist James Fletcher, for example, found Riley to be a "kind, patient and true" friend (Fletcher 1895).

[9]Ray's revised figure of 20,000 species, at the time "reckoned a magnificent idea" (Westwood 1833, p. 118), was cited on p. 23 of Ray's (1714) edition (the sixth, corrected, published posthumously) but probably appeared in earlier revisions of his book. Gill (1897) suggested that Ray believed the number of living insects—described and undescribed—would not be much more than 20,000.

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(1982) widely cited estimate of 30 million insect species, a figure that for the first time was based on testable hypotheses, most estimates of Earth's biota ranged from 1.5 to 3–5 million species (May 1986). Aware of an earlier estimate of 10 million insect species, biologists such as Gossard (1909), Brues (1946), Sabrosky (1952), and Erwin (1982) referred to that higher figure, but without attribution. Bates (1950) credited C. T. Brues as the source of the 10-million estimate for numbers of insect species, but the "hardy soul" (Metcalf 1940) who should be credited with that estimate is C. V. Riley, nearly 60 years earlier (Berenbaum 2009).

Riley's (1892a) estimate of 10 million insect species was widely noticed at the time (e.g., Anonymous 1892, Ashmead 1893, Gill 1897, Kenyon 1897).[10] Even though Riley's (1892a) figure was merely a guess, rather than based on data from studies of insects in natural communities, it was based on several assumptions not considered by most other 19th-century estimators of insect diversity, including a correction for synonymy.

Riley (1892a) began by reviewing previous guesses of the number of insects, including John Day's of 250,000 in 1853, David Sharp's of a half million to a million in 1883, and those of Sharp and Lord Walsingham of nearly two million in 1889. For his own estimate, Riley began by estimating the number of species already described on the basis of lists and "estimates of specialists in the different orders." He then took the average number of insect species described annually since 1864 (6500 spp.), the year when the *Zoological Record* began publication, and deducted 8% to allow for synonymy. Even an estimate of 2,000,000 seemed far too low, because most species had been described from temperate regions; the "vast numbers" of species in the tropics largely remained to be characterized and described. He also noted that other areas of the planet had never been explored, and even in the best-collected regions, the majority of micro-Diptera and micro-Hymenoptera had not yet been named. Therefore, it seemed reasonable to assume that not one fifth of the insect fauna had been described. "To say that there are 10,000,000 species of insects in the world, would be…a moderate estimate" (Riley 1892a).

Similarly, more recent attempts to estimate the number of insect species in the world have relied on compiling the numbers of described species and querying taxonomic specialists regarding the number of species they suppose remain to be described in the different orders (e.g., Gaston 1991, Nielsen and Mound 1999). Earlier, L. O. Howard, at a meeting of the Entomological Society of Washington, broached the subject of how many insect species inhabit Earth and received estimates from taxonomic specialists in attendance; based on their estimates, he suggested that the total number of insect species might exceed 4,000,000 (Howard 1931). The other main approach for estimating insect richness involves extrapolations from samples (Gaston 1991, Colwell and Coddington 1994), typically from the tropics, to arrive at global estimates of insect species in other regions based on various assumptions involving host-plant specialization, vertical stratification, and other parameters (e.g., Erwin 1982, 1988; Ødegaard 2000; Stork and Grimbacher 2006; Dyer et al. 2007). Debate continues as to whether the number of extant insect species is about 5 million or less, or is 30 million or more (Adis 1990, Berenbaum 2009).[11]

Riley's involvement in estimating global insect diversity, though not based on field data that yield testable hypotheses, is important from a historical perspective and should be mentioned when early attempts to arrive at the number of insect species that exist on Earth are reviewed. He might have been the first to realize that the number of described species was inflated owing to synonymy, although his 8% correction underestimated actual rates of synonymy (e. g., Gaston and Mound 1993).

Seeking Stability in Insect Nomenclature

Systematists generally agree that stability in scientific nomenclature is desirable (Usinger 1956). Rules governing zoological nomenclature in Great Britain—the British Association (or Strickland) Code—was drawn up in 1842 and republished in 1843 in France, Italy, and the United States. Though not international in scope, it led to substantial progress toward a uniform system (Mayr et al. 1953).

North American entomologists of the 19th century, in the absence of international rules for zoological nomenclature, were not bound by the British Code. Canadian and U.S. entomologists, however, paid relatively little attention to nomenclatural matters (Edwards 1873)[12] until Scudder's (1872) publication of radical and sweeping changes he intended to use in a forthcoming treatment of North American butterflies. Scudder's resurrection of obscure generic and specific names, based on strict adherence to priority rather than prevailing usage, elicited an outcry from insect taxonomists in North America. Wholesale name changes of insects are undesirable because they can lead to confusion and discourage further study (Edwards 1873).

Entomologists at the 1872 Dubuque, Iowa, meeting of the American Association for the Advancement of Science (AAAS)[13]unanimously expressed concern over Scudder's nomenclatural changes for American butterflies. Riley moved that a committee be appointed to draft a set of nomenclatural rules pertaining to insects in the hope that Scudder might be dissuaded from introducing inappropriate names in a larger work on butterflies. Other committee members were J. G. Morris and A. S. Packard from the United States and C. J. S. Bethune and W. Saunders from Canada (Anonymous 1872). Although some taxonomists objected to establishing nomenclatural rules for insects that would deviate from those set for other animal groups, Edwards (1873) defended the right of entomologists to separate themselves from other naturalists because of the increasing popularity of entomology compared to mammalogy, ornithology, and other natural sciences. Botany, he noted, already had adopted a separate code. Before the next AAAS meeting (Portland, Maine, in 1873), Riley solicited opinions on nomenclature from the membership (Bethune 1873). At the Portland meeting, Riley requested that the committee to formulate entomological nomenclature be dismissed because certain members were absent. In the end, a new committee was appointed, with W. H. Edwards, J. L. LeConte, and Scudder joining previous members Bethune and Riley, who served as chairman (Uhler 1873). At the Buffalo, New York, meeting in 1876, the Committee on Nomenclature

[10]Howard (1931) recalled that "competent biologists said they did not believe that Professor Riley realized what a million meant." Such skepticism, however, was not expressed by the four writers we cite: Anonymous (1892), Ashmead (1893), Gill (1897), and Kenyon (1897).

[11]Erwin (2004) suggested that the total number of insect species might be as high as 80,000,000.

[12]Walsh and Riley (1869), however, were exceptions, having written an article on scientific nomenclature in which they discussed the law of priority.

[13]Before a U.S. entomological society was formed, many entomologists attended annual meetings of the AAAS. At the Dubuque meeting, entomologists discussed the formation of an entomological subsection of AAAS, which later was known as the Entomological Club (Smith 1989).

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(with A. R. Grote having joined LeConte, Riley, Saunders, and Scudder) unveiled a set of 11 rules. The committee unanimously endorsed certain rules but had divided opinion on "questions of priority raised by Scudder's revisions" (Sorensen 1995). The Entomological Club of AAAS voted unanimously to accept the rules (Anonymous 1876). Saunders (1876) was confident that the adoption of rules would help stabilize entomological nomenclature.

Riley thus played a prominent role in North American efforts to achieve greater stability of zoological names. In actuality, the debate on nomenclatural matters within AAAS probably had little effect on taxonomic practices, but it demonstrated a maturing of entomology in North America (Sorensen 1995).[14]

During the period when entomological nomenclature was being debated at AAAS meetings, Riley played the role of "abjudicator" regarding the correct name of the grape phylloxera (Sorensen et al. 2008). He first endorsed the use of Fitch's *vitifoliae* (originally described in *Pemphigus*), a name that had priority, but soon decided that *Phylloxera vastatrix* Planchon was correct, according to prevailing usage (Davidson and Nougaret 1921, pp. 26-27; Sorensen et al. 2008, pp. 142-143).[15] Other examples of Riley's familiarity with and interest in insect nomenclature include comments on the names of certain parasitic wasps (Riley 1880a) and the validity of one of Hübner's lepidopteran names (Riley 1885a), as well as the need, owing to instability of generic names, to attach names of describers (authorities) to insect species to avoid any confusion concerning the taxa intended (Riley 1876, p. 85).

In addition, Walsh and Riley (1869) explained the basics of scientific nomenclature in their journal, *American Entomologist*. Responding to an inquiry about the appropriate scientific names of certain beetles, they noted that "it should never be forgotten that scientific nomenclature is a means and not an end." They expressed their disdain for strict application of the "Law of Priority," which can result in an earlier description of a species [by author A] taking precedence over a later, often more complete, description [by author B]. "And yet, in the majority of such cases…[author] A is in his grave, and perhaps it would have been a positive benefit to science if he had never been born. So that the practical result is, that, for the sake of appeasing the indignant ghost of some obscure and long-forgotten naturalist of the last century, all the naturalists of the present day are to be inconvenienced, and a great deal of valuable time is to be expended in studying out mere scientific *phrases,* which time might be employed to much better advantage in studying out new scientific *facts.*"

Collecting Insects and Endowing a National Collection

Riley was born in London, but when he was only three years old, he and a younger brother began to live with a great-aunt in Walton-on-Thames, a "semiagricultural district" outside London (Smith and Smith 1996). The young boy, a product of the Victorian Era's naturalist tradition (Sorensen 1995, Smith and Smith 1996, Lockwood 2004), began collecting and making pencil sketches of insects[16] (Anonymous 1895, McLachlan 1895, Howard 1930). A mostly unfamiliar Nearctic insect fauna awaited when he emigrated to the United States in 1860. In the agricultural area of Kankakee County, Illinois, where he worked on a farm, and in Chicago where he moved in 1863, he continued to collect and observe insects. Even when he joined the Union army in 1864, he was able to collect insects during six months of guard duty during the Civil War (with the 134th Regiment of Illinois) (Meiners 1943, Smith and Smith 1996, Lockwood 2004). After he began to write for *The Prairie Farmer* (1863), he invited subscribers to that farm journal to send insects for identification. The specimens submitted, along with those he obtained through exchanges with local entomologists, provided a reference collection for his work in applied entomology (Smith and Smith 1996).

One of Riley's responsibilities when he became State Entomologist of Missouri in 1868 was to provide an insect collection for the State Board of Agriculture, to be used in the instructional program at the University of Missouri once an agricultural college at that institution was founded. In an agreement with Riley, the Board was to be located in the same city as the university, but the Board remained in St. Louis, whereas the College of Agriculture was established at the university in Columbia. Controversy that developed over Riley's obligation to provide a collection was resolved when a university committee ruled that he did not have to provide two collections, but merely had to give the College access to the State Board collection in St. Louis. The matter settled, Riley, in 1874, donated a type collection to the Agricultural College in Columbia (Smith and Smith 1996).

Riley's personal collection eventually provided the basis for a national collection. Work by taxonomic entomologists of the U.S. Department of Agriculture (USDA) and the Smithsonian Institution has long been so closely associated that the two units have been regarded as one: Entomology at the National Museum. Riley even served simultaneously as head of USDA entomology and curator at the Museum (Sabrosky 1964).

In 1854, Townend Glover became the first U.S. (Federal) entomologist, having joined the Bureau of Agriculture, then in the U.S. Patent Office before Congress authorized the Department of Agriculture in 1862. As an artist, Glover was not much interested in systematic entomology and described no new species (Sorensen 1995).[17] In 1858, the relatively few insect specimens that had accumulated were transferred to the Smithsonian Institution, but during the 1860s, specimens, including types, were distributed for study to specialists in various insect groups. Specimens, however, could be reclaimed by the Museum at any time (Kellogg 1946). The Department of Agriculture was designated in 1874 (or a few years earlier; Sabrosky 1964) as the repository for specimens that came to the Museum (Kel-

[14]A detailed account of the debate over entomological nomenclature in 19th-century North America, placed within the context of views toward an evolutionary classification of insects, is given by Sorensen (1995). International rules were not forthcoming until publication in 1905 of the *Règles internationales de la Nomenclature zoologique*, an outcome of the Fifth International Congress of Zoology at Berlin in 1901 (Usinger 1956, ICZN 1999). Some taxonomists, however, continued to follow their own rules when they disagreed with those prescribed in the *Règles* (Blackwelder 1967). The first edition of the *International Code of Zoological Nomenclature* was published in 1961, and the Code now is in a fourth edition (ICZN 1999).

[15]The name for the grape phylloxera approved by the Entomological Society of America is *Daktulosphaira vitifoliae* (Fitch) (http://www.entsoc.org/pubs/Common_Names/index.htm), but the correct name for this pest continues to be debated (Sorensen et al. 2008).

[16]Riley's early interest in insects apparently was inspired by the lepidopterist W. C. Hewitson, a resident of the neighboring village (Oatlands), who maintained an extensive insect collection (Meiners 1943, Mallis 1980). An example of one of his lepidopteran sketches, made at age 13, was reproduced by Smith and Smith (1996, p. 229).

[17]Townend Glover, having trained as an artist in England, had little interest in specimens and apparently left no collections (Howard 1930, Sorensen 1995). After he illustrated an insect, he apparently had little appreciation for it as a museum specimen (Wilkinson 1969). Glover was proud of having never described a new species, but he inadvertently validated the name of a psyllid (Riley 1883b, p. 69 in footnote).

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logg 1946). The National Museum came into existence in 1876, but an insect department was not organized until 1881, the year Riley returned as Chief USDA Entomologist.[18] At the time, insect holdings in the national collection were minimal; the estimate of 1,000 specimens for all orders (Dyar 1902), however, did not include unaccessioned material (Sabrosky 1964). The USDA collection was transferred to the Smithsonian in 1881, the year in which Riley also placed his personal collection on deposit at the Museum so that it might form the nucleus of an appropriate national collection. He was appointed Honorary Curator of the collection (Sabrosky 1964, Sorensen 1995). The formal donation of his collection in 1885, after he was assured of increased support for entomology in the Museum, essentially marks the beginning of the Smithsonian insect collection.[19]

Riley's collection, regarded at the time as the largest general insect collection in the country, comprised some 150,000 specimens: 766 boxes containing 115,000 mounted specimens,[20] 2,850 vials of alcoholic material, and 3,000 slides of minute insects. About 20,000 species were represented (Goode 1889, Sabrosky 1964). According to Dyar (1902), the collection was rich (about 20%) in specimens of Lepidoptera, Riley having had a preference for the group. Goode's (1889) figures showed that the number of Riley's mounted and pinned specimens actually were dominated by Coleoptera, with the numbers for Hymenoptera also exceeding Lepidoptera. Riley's own comment regarding a specialty was that for years he had been accumulating material and notes on gall insects, Homoptera, and Diptera (Riley 1886). Riley emphasized the "biological side" of the national collection by preserving material that would best suit agricultural interests. His collection thus was rich in the larval and pupal stages of insects, mainly species on which he had conducted biological studies (Goode 1889, 1896; Sabrosky 1964; Sorensen 1995). The donation of numerous immature stages of insects helped distinguish the holdings of the recently organized national collection from those of most other major insect collections. Taxonomic entomologists of the USDA continued to deposit immature stages in the National Museum (Sabrosky 1964).

Sabrosky (1964) paid tribute to the key role that Riley played in the development of a national collection of insects:

"…whatever Riley's personal faults, it may assuredly be stated that the Department of Entomology of the Museum and its collection owe a great deal to the foresight of this great USDA entomologist who insisted on *one* systematic collection, to be housed in the National Museum, who pressed constantly for salaried professional personnel and greater monetary support for the purchase of collections and the proper care of existing ones, who voluntarily and without pay acted as Curator of Insects for its first 14 years, who gave it to [*sic*; to it?] his own outstandingly valuable personal collection, and who, in the years when Museum support was scanty or non-existent, furthered the interests of the collection by detailing USDA specialists to curate, classify, and expand the collection while using it as a tool for their work for the Department of Agriculture."

That the U.S. National Collection of Insects (at the Smithsonian's National Museum of Natural History) ranks in world importance behind only the insect holdings of the Natural History Museum (London) and Muséum National d'Histoire Naturelle (Paris) (Knutson 1991) is due partly to Riley's (1890) vision of an insect collection at the National Museum:

"The ideal *cabinet* collection of a National Museum should represent, as completely as possible, the insect fauna of the country, properly classified and determined. It can, necessarily, have little interest for the public at large and should be consecrated to the use of the specialist and to the advancement of the science of entomology. …It should constitute a study collection to which workers are drawn for unpublished facts and for comparisons and determinations. It should be so well conserved and provided for as to induce describers of new species to add to it their types or authentic duplicates thereof. It will be many years ere such an ideal collection can be gotten together, and none now living may witness it, but the material now on hand forms a good foundation for it."

Unraveling Complex Life Histories

Systematics can be considered the "point at which all biology comes together" (Mound and Gaston 1993). As the scientific study of living organisms and their relationships, the discipline is so rooted in biological investigation that the word *biosystematics* is in common use as a subdiscipline of systematics. Life-history studies, encompassing bionomic aspects such as host-plant relationships and characters of immature stages, have long been regarded as integral to insect systematics (Riley 1871b, Scudder 1878, Michener 1953). Systematists who routinely go into the field realize that fieldwork is important not only for acquiring specimens that otherwise would be unavailable for current and future research, but also for obtaining distributional and ecological data on the groups in which they specialize. Data accruing from field studies of herbivore-plant interactions are important in establishing species limits; discovering cryptic (sibling) species; understanding coevolution, contemporary (rapid) evolution, and mutualisms; and interpreting phylogenetic relationships of plants and insects.

Riley's biological work essentially knew no bounds: "My own studies are confined to no one Order, but rather embrace biologic studies in all Orders" (Riley 1886). He welcomed the challenge of studying insects with complex or unusual life histories; elucidating their bionomics required "the kind of biological sleuthing he so enjoyed" (Smith 1992). Though he was well versed with major entomological works such as those by Harris, Kirby and Spence, and Westwood, Riley (1873a, p. 44) considered Nature herself the best textbook. As a naturalist, he has been compared favorably with the exceptionally talented workers with whom he corresponded: Henry Walter Bates, Thomas

[18]Riley first became Chief of the USDA Division of Entomology in 1878, succeeding Townend Glover. When Riley appealed directly to Congress for increased funding for entomological programs, he incurred the wrath of Commissioner of Agriculture William LeDuc. Riley, after only nine months in office, was forced to resign in 1879, and John Henry Comstock was brought from Cornell University to serve as head of Entomology. With a change of administration in 1881 (following the death of James A. Garfield), Riley was reappointed to his former position (Howard 1930, Marcus 1985, Sorensen 1995). Hoping one day to become Assistant Secretary of Agriculture, Riley appealed to President-elect Grover Cleveland to appoint a friend, J. Sterling Morton, as Secretary; Riley hoped his long-time friend would enable him to become Assistant Secretary. When such a position was not forthcoming, Riley expressed his displeasure, which created political tension and led to Riley's resignation in May 1894 (Howard 1930, Meiners 1943).

[19]Riley (1885c) intended to donate his personal collection "whenever such donation is justified." John B. Smith's appointment as Assistant Curator in August 1885 was crucial to assuring Riley that the Smithsonian's insect holdings would receive appropriate care (Goode 1889, Kellogg 1946, Sabrosky 1964). In the years immediately preceding that appointment, doubt as to whether the insect collection would receive proper care had been expressed in the pages of *Science* (e.g., 4 [98]: 540, 1884; 5 [100]: 25, 1885; 5[109]: 188, 1885).

[20]Riley's direct-mounting procedures included the pinning of aphids, a curious practice by modern standards but one not uncommon at the time. Pinned aphids often were remounted in balsam by Riley's assistant Theodore Pergande (Miller and Foottit 2009; G. L. Miller, personal communication).

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Belt, Charles Darwin, Asa Gray, Fritz and Hermann Müller, and Alfred Russel Wallace (Pellmyr 2003). Though the design of some of his laboratory experiments might have been flawed (Lockwood 2004), his biological observations were characterized by great accuracy and meticulousness (Osborn 1937, Davis 1967). In any problem he tackled, he displayed a "wonderfully keen appreciation of the essential factors" involved (Osborn 1937). He also was relentless in attempting to resolve unanswered questions about an insect's life cycle, such as oviposition and voltinism of the armyworm [*Pseudaletia unipuncta* (Haworth)] (Sheppard and Weinzierl 2002). Riley was able to move easily between the applied and basic aspects of his discipline, an aptitude that impressed Charles Darwin, who referred to Riley's findings in several of his books (Kritsky 1995). In a letter to Riley in May of 1877, Darwin complimented him on his Missouri reports, noting that he managed "to discuss points of general interest, besides those of practical importance" (Kritsky 1995, p. 94).

Riley's name always will be linked with the grape phylloxera. This insect's invasion of European vineyards threatened the wine industry in mid-19th-century France when that country was attempting to recover from the Franco-Prussian War and deal with a downturn in the cotton and silk industries (Smith 1992, Lockwood 2004). Resolution of the vineyard crisis featured "heroes, villains, mystery, and political intrigue" (Weber 2006). The main hero was Riley,[21] who determined that the pest plaguing France was a native North American species that had been accidentally introduced into Europe (Riley 1872, pp. 55-71). The phylloxeran's life cycle, one of the most complex in the Insecta (Sorensen et al. 2008), involves cryptic root-galling forms (gallicoles) as well as leaf-galling forms (radicoles) and multiple stages, both asexual and sexual (Riley 1872). Although leaf galls are uncommon on the European grape (*Vitis vinifera*), the roots are particularly susceptible to phylloxeran damage (Riley 1872, 1874, pp. 30-64; Smith 1992; Granett et al. 2001). After rejecting chemical control and shipping a Nearctic predatory mite[22] that became established but proved unsuccessful in suppressing phylloxeran populations, he decided that plant resistance was critical to solving the problem of an immigrant pest whose root feeding led to the decline and death of grape vines. American species of *Vitis*, having coevolved with or had long-term evolutionary contact with the phylloxeran, might show tolerance to its feeding (Riley 1872, p. 66; Wapshere and Helm 1987; Smith 2005). The eventual solution to the problem—grafting *V. vinifera* scions onto resistant rootstock of *V. labrusca* from the American Midwest[23] (Smith 2005)—is a story that has been detailed by Ordish (1972), Smith (1992), Campbell (2005), and Sorensen et al. (2008). Riley (1886) remarked that he was gratified that hundreds of square miles of once-devastated vineyards had been "reconstituted." For helping save the French wine industry, he was honored by the French government and the country's viticulturists (Smith 1992, Sorensen et al. 2008).

The insights and instincts that characterized many of Riley's entomological investigations were evident in his phylloxeran work, which demonstrated that he was one of the earliest workers to appreciate a "general understanding of the process of plant-insect coevolution" (Pellmyr 2003). Riley even predicted that the grape phylloxera would develop biotypes ("races"; Riley 1871a, p. 91; Smith 1992). About 100 years later, when isozyme analyses showed that infestations on 'Concord' and 'Niagara' grapes in the northeastern United States involved different biotypes (Williams and Shambaugh 1988, Smith 2005), Riley's prediction of a 'Concord' biotype was fulfilled (Granett et al. 2001).

Of Riley's many biological studies of insects, none had greater evolutionary significance than those involving yucca moths as the exclusive pollinators of *Yucca* species. The interrelationship between yuccas and moths of the genera *Parategeticula* and *Tegeticula* (family Prodoxidae) is considered a classic example of coevolution—one involving a tight mutualism—and one of the first and most compelling examples of evolution by natural selection (Pellmyr 2003). The moths actively pollinate the flowers, with their larvae, in turn, restricted to developing on yucca seeds. Only four other examples are known of obligate seed-feeding pollinators and their host plants (Pellmyr et al. 2006). Riley's studies of the yucca moth were important for extending investigations by entomologists beyond mimicry and polymorphism and served as additional examples of "a unique blend of theory and practice that by the 1870s characterized American entomology (Sorensen 1995)."

Reviews of yucca-yucca moth mutualisms (Baker 1986, Powell 1992, Pellmyr 2003) and an account of Riley's yucca research (Sheppard and Oliver 2004) allow us to provide only an overview of his work. Riley's observations contained "very few inaccuracies" (Pellmyr 2003), and the summary of his life-history studies of the yucca-yucca moth system (Riley 1892b) remained the definitive biological reference for about 70 years. Subsequent textbooks, however, often oversimplified yucca pollination. Biologists began to refer to *the* yucca moth as if it were the only pollinator known, even though Riley had described two yucca-pollinating species other than the principal pollinator, *T. yuccasella* (all three species originally were described in the genus *Pronuba* but now are placed in *Tegeticula*) (Baker 1986). Riley's prediction that additional prodoxid species would be found as pollinators of southwestern yuccas eventually was realized (Powell 1992, Sheppard and Oliver 2004).

Not until the 1980s did the complexity of yucca pollination become fully appreciated (Powell 1992, Sheppard and Oliver 2004). Since Davis's (1967) descriptions of new yucca moths, new pollinating species, as well as nonpollinators of yuccas, have been described (Pellmyr 1999; Pellmyr and Balcázar-Lara 2000; Pellmyr et al. 2006, 2008).[24]

Among other insects with complex or atypical life histories that Riley studied, we mention his interest in parasitism, specifically groups whose different instars exhibit different larval types. He had a particular interest in the Strepsiptera, an ectopara-

[21]A valuable collaborator was Professor J. E. Planchon of the School of Agriculture in Montpellier, France. Earlier, he had described the phylloxeran as *Phylloxera vastatrix*, now considered a synonym of *D. vitifoliae* by many taxonomists. For his role in helping save the French wine industry, Planchon was honored with a monument erected in Montpellier after his death (Smith 1992, Sorensen et al. 2008).

[22]The predatory mite (Acari: Acaridae) that Riley sent to France, "*Tyroglyphus phylloxerae*," was a species he had described as new (Riley 1874, p. 81). The identity of this acarid mite now is uncertain (Gerson et al. 2003, p. 1; B. M. OConnor, personal communication).

[23]Grafting was chosen over the planting of American vines because it allowed the use of traditional grape cultivars that French vintners preferred (Sorensen et al. 2008).

[24]Yucca-associated prodoxid moths not involved in pollination (*Prodoxus* spp.) are considered sister to the pollinating genera. Referred to as "bogus yucca moths" (e.g., Riley 1880b), species of *Prodoxus* often co-occur on yuccas with the pollinating species. Adults of nonpollinators, because they lack maxillary "tentacles" [palps], do not collect pollen; the larvae develop on flowering stalks, fruits, or leaf tissues rather than seeds (Davis 1967, Pellmyr et al. 2006).

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sitic order in which hypermetamorphosis involves active first instars or triungulins (Riley 1893b). He obtained some of the first life-history data on certain hypermetamorphic species of the beetle families Meloidae and Rhipiphoridae (Scudder 1878, Riley 1893b, Clausen 1940). Riley's meloid studies enhanced an understanding of coleopteran phylogeny (Packard 1895). Howard (1882) credited Riley with being the first to substantiate alternation of generations in cynipid wasps (Riley 1873b).[25] Other insects that attracted his attention were periodical cicadas[26] (e.g., Riley 1885d) (Fig. 3); the ectoparasitic beaver beetle (*Platypsyllus castoris* Ritsema) (e.g., Riley 1888), whose systematic position had long been problematic; the hop aphid[27][*Phorodon humuli* (Schrank)], which switches seasonally between a summer (secondary) host and a winter (primary) host (Riley 1889) (Fig. 4); and the hackberry psyllids (*Pachypsylla* spp.) (Riley 1883b, 1885b), whose life histories might be the most complicated among North American gall-inducing Psyllidae (Yang and Mitter 1994). Riley's (1883b) conclusion that psyllids inducing galls on different parts of hackberry represent distinct species has been supported by electrophoretic data (Yang and Mitter 1994).

Fig. 3. Principal life stages of the periodical cicada, *Magicicada septendecim* (L.) (*sensu* Riley 1885d), illustrated by Lillie Sullivan under the supervision of C. V. Riley. Reproduced from Report of the Commissioner of Agriculture, 1885. Government Printing Office, Washington, DC.

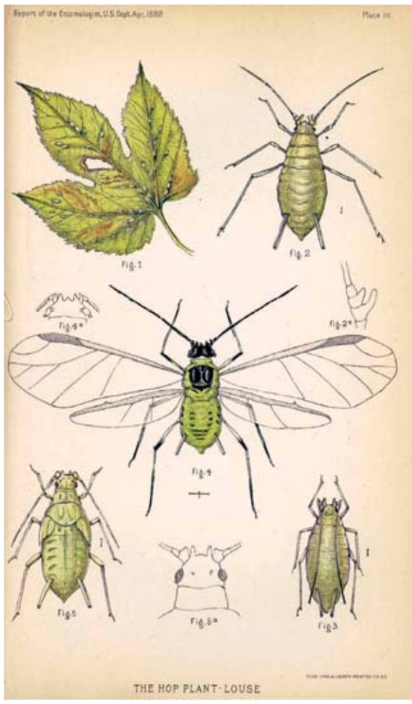

Fig. 4. Principal life stages of the hop aphid, *Phorodon humuli* (Schrank) (illustrator unknown). Reproduced from Report of the Commissioner of Agriculture, 1888. Government Printing Office, Washington, DC.

Describing New Genera and Species

Riley was aware that colleagues who pursued the purely scientific aspects of entomology tended to denigrate those who emphasized the discipline's practical applications. Walsh and Riley (1868), for example, noted that the agricultural entomologist "may perhaps occupy a lower position in the scientific world than the ingenious artists, who are every day grinding up varieties into species, and flooding science with new genera and new families, as uncalled for and unnecessary as a fifth wheel on a coach." Even though Riley chided those taxonomists whose goals seemingly were to attach their names to as many new taxa as possible, he was not averse to describing new arthropod species, mainly those of economic importance, and, occasionally, describing new insect genera. Some taxonomists resented his describing new species in the Missouri reports rather than in technical publications (Meiners 1943).

The 19 genus-group names that Riley proposed, and their current status, are listed in Table 1. Thirteen of his new genera are considered valid.

In compiling a list of species described by Riley (Table 2), we referred to Henshaw's (1890) compilation of new names he proposed, including those coauthored with L. O. Howard and B. D. Walsh, and used *Zoological Record* to find names of species Riley described after Henshaw's cut-off date for literature. To determine the status of his North American species, we relied on *Nomina Insecta Nearctica* (Poole and Gentili 1996-1997), supplemented by information in more recent taxonomic catalogs and other works on selected groups, for example, Psyllidae (Yang and Mitter 1994, Yang et al. 2001). As is the case with any major catalog or database, *Nomina Insecta Nearctica* contains omissions, misspellings, and other errors (e.g., Pollock 1996), but we did not attempt to correct any such errors in Poole and Gentili's listing of Riley's names. We also might have overlooked some of Riley's new species or incorrectly determined the current status of certain names he proposed as new.

From 1867 to 1893, Riley described 203 new insect species, mostly from the Nearctic Region, in six orders (with Hemiptera encompassing homopterans), plus 12 species of mites and ticks. Still considered valid are 133 insect species, with the original combination valid for 57 species. Of the 66 names considered invalid, 48 are synonyms (synonymy rate = 23.6%), 6 are homonyms, and 12 are *nomina nuda* (or otherwise unavailable). Of his 12 non-insectan names, 5 are valid. Twenty-one of his arthropod species (1 mite; 20 insects) bear official common names approved by the Entomological Society of America (http://www.entsoc.org/pubs/Common_Names/index.htm; Table 3).

In addition to Riley's species-group names that are available under rules of the International Commission on Zoological Nomenclature, Riley assigned manuscript names for psyllids (Hodkinson 1988) and other insects he thought were new species, but never validated the names. Workers who

[25]Riley (1873b) referred to cynipid observations by H. F. Bassett of Waterbury, Connecticut. Bassett's (1873) paper appeared a few months before the one by Riley in which cynipids were mentioned only in passing in an article on butterflies. Howard (1882) suggested that both workers should be credited with establishing that cynipids exhibit alternation of generations.

[26]In his first Missouri report, Riley (1869, pp. 18-42) was the first to refer to geographic broods of periodical cicadas. His use of Roman numerals to designate broods has continued (Meiners 1943).

[27]The hop aphid provides an example of work done by one of Riley's assistants that he published under his own name. In the case of *Phorodon humuli*, studies were done "almost totally" by T. Pergande in central New York (Russell 1980).

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Table 1. Genus-group names proposed by C.V. Riley.

Taxon	Year	Order:Family	Current status
Blastophysa	1884	Hemiptera: Psyllidae	Syn. of *Pachypsylla*
Brachylivia	1884	Hemiptera: Aphalaridae	*Nomen nudum*
Caloptenobia	1878	Hymenoptera: Scelionidae	Syn. of *Scelio*
Carphoxera	1891	Lepidoptera: Geometridae	Syn. of *Idaea*
Ceropsylla	1884	Hemiptera: Triozidae	Valid
Clydonopteron	1880	Lepidoptera: Pyralidae	Valid
Dendrotettix	1893	Orthoptera: Acrididae	Valid
Didyctium	1879	Hymenoptera: Figitidae	Valid
Hornia	1877	Coleoptera: Meloidae	Valid
Melissopus	1881	Lepidoptera: Tortricidae	Valid
Ophelosia	1890	Hymenoptera: Pteromalidae	Valid
Pachypsylla	1885	Hemiptera: Psyllidae	Valid
Paleacrita	1876	Lepidoptera: Geometridae	Valid
Pentarthron	1872	Hymenoptera: Trichogrammatidae	MS name; =*Pentartrum sensu* Dalla Torre 1898 (*pro-* thron)
Podapion	1883	Coleoptera: Brentidae	Valid
Prodoxus	1880	Lepidoptera: Prodoxidae	Valid
Pronuba	1872	Lepidoptera: Prodoxidae	Homonym; =*Tegeticula*
Proteoterus	1881	Lepidoptera: Tortricidae	Valid
Rhinopsylla	1885	Hemiptera: Triozidae	Valid

later described Riley's species sometimes used his manuscript names.

Honoring Riley with Patronymic Names

Essig (1931) recorded two genera and 23 species named in Riley's honor, implying the list was incomplete. Our list (Table 4) includes the patronyms Essig (1931) provided and 47 additional names (7 genera, 40 species), but it probably does not represent a complete listing of all taxa named for Riley.

Evaluating Riley's Taxonomic Work

Riley earns high marks for his studies in insect bionomics, many of which represented important contributions to systematics. His biological publications sometimes included comments on the systematic position of insects such as the beaver beetle, or yielded information of phylogenetic significance, such as that relating to meloid beetles. Instead of restricting his discussion of social insects to ants, bees, wasps, and termites, Riley (1894) broadened his treatment to include tent caterpillars and webworms, as well as the social butterfly *Eucheira socialis* Westwood. He was a gifted entomologist and field observer who accepted the challenge of investigating species of biological complexity. His observations were thorough, his interpretations astute, and his predictions insightful. When others challenged his research findings, especially those involving yucca moths, he relied on "powers of observation" and "clarity of reasoning" to rebut critics (Sheppard and Oliver 2004). McLachlan (1895) remarked that the "only one real *fiasco*" in Riley's career was the prediction (Riley 1876) that the Colorado potato beetle [*Leptinotarsa decemlineata* (Say)] might soon be carried to Europe. Recently, in contrast to McLachlan's remark, Riley's prediction was termed "prophetic" because the beetle was detected (but subsequently eradicated) in Germany in 1876 (Ebbels 2003).[28]

Riley's words were often prescient, as in the example of his conclusions regarding the phylogeny of yucca moths (Sheppard and Oliver 2004). Insect classification, he noted, often is based on the study of isolated groups, without an appreciation of the complex relationships that the study of a higher taxon on a worldwide basis can reveal (Riley 1882b). Moreover, his comments about how quickly native herbivores can acquire new characters and habits as they switch from wild to cultivated (presumably non-native) hosts (Riley 1886) presaged the recent interest in rapid evolution. He discouraged placing too much emphasis on

[28]Riley (1876) stated that in the summer of 1875 the Colorado potato beetle had been detected at the docks in Bremen in cargo arriving from New York. This event supported his contention that adults could be transported in commerce. McLachlan (1895) thought Riley was disappointed that the beetle did not become established in Europe as quickly as he had predicted; that is, as early as 1871 (Riley 1876, p. 76). The Colorado potato beetle became permanently established in Europe near Bordeaux in the early 1920s and reached Germany by the mid-1930s (Radcliffe 1982, Weber and Ferro 1994).

Table 2. Species-group names of arthropods proposed by C. V. Riley, including those with B. D. Walsh (W & R) and L. O. Howard (R & H).

Order: Family	Original combination	Year	Current status[a]
Prostigmata: Trombiculidae	*Leptus americanus*	1873	*Incertae sedis*
	Leptus irritans	1873	Syn. of *Eutrombicula alfreddugesi* (Oudemans)
Prostigmata: Eriophyidae	*Acarus aceriscrumena*	1870	In *Vasates*
Prostigmata: Tetranychidae	*Tetranychus 6-maculatus*	1890	Emend.; =*Tetranychus sexmaculatus* Riley
Parasitengona: Trombidiidae	*Trombidium giganteum*	1878	*Incertae sedis*
	Trombidium locustarum	1878	Valid
Trombidiformes: Microtrombidiidae	*Trombidium muscarum*	1878	In *Trichotrombium*
Trombidiformes: Hydrachnidae	*Hydrachna belostomae*	1878	*Incertae sedis*
Parasitiformes:Uropodidae	*Uropoda americana*	1877	*Incertae sedis*
Oribatida: Phthiracaridae	*Hoplophora arctata*	1874	In *Phthiracarus*
Astigmata: Acaridae	*Tyroglyphus phylloxerae*	1874	In *Acarus*
Ixodida: Ixodidae	*Ixodes bovis*	1867	Syn. of *Rhipicephalus annulatus* Say
Orthoptera: Acrididae	*Caloptenus atlanis*	1876	Syn. of *Melanoplus sanguinipes* (F.)
	Dendrotettix longipennis	1893	Syn. of *Dendrotettix quercus* Packard
Orthoptera: Gryllidae	*Oecanthus latipennis*	1881	Valid
Hemiptera: Aleyrodidae	*Aleyrodes citri* R&H	1893	Homonym; =*Dialeurodes citri* (Ashmead)
	Aleurodes citrifolii R&H	1892	Unavail.; =*Dialeurodes citri* (Ashmead)
Hemiptera: Aphididae	*Eriosoma ulmi*	1869	Homonym; =*Eriosoma rileyi* (Thomas)
	Lachnus platanicola	1883	Syn. of *Longistigma caryae* (Harris)
	Pemphigus acerifolii	1879	Syn. of *Prociphilus tessellatus* (Fitch)
	Pemphigus fraxinifolii	1879	In *Meliarhizophagus*
	Pemphigus populimonilis	1879	In *Thecabius*

Table 2. (*continued on next page*)

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Table 2. (*continued*)

Order: Family	Original combination	Year	Current status[a]
	Pemphigus populiramulorum	1879	Valid
	Pemphigus populitransversus	1879	Valid
	Pemphigus ulmifusus W&R	1869	In *Kaltenbachia*
	Schizoneura americana	1879	In *Eriosoma*
Hemiptera: Calophyidae	*Calophya nigripennis*	1884	Valid
Hemiptera: Cicadellidae	*Diedrocephala flaviceps* R&H	1880	In *Xyphon*
Hemiptera: Coccidae	*Ceroplastes utilis* R&H	1892	Unavail.; =*Ceroplastes utilis* Cockerell
	Lecanium acericola W&R	1868	In *Pulvinaria*
	Lecanium maclurae W&R	1868	*Incertae sedis*
Hemiptera: Diaspididae	*Chionaspis angustior* R&H	1893	Unavail., *incertae sedis*
	Chionaspis major R&H	1893	Unavail.; =*Rutherfordia major* (Cockerell)
	Chionaspis timidus R&H	1893	Unavail.; =*Pinnaspis dysoxyli* (Maskell)
	Mytilaspis pomicorticis	1873	Syn. of *Lepidosaphes ulmi* (L.)
	Mytilaspis ulmicorticis	1874	Syn. of *Lepidosaphes ulmi* (L.)
Hemiptera: Kermesidae	*Kermes galliformis*	1881	In *Allokermes*
Hemiptera: Lygaeidae	*Nysius destructor*	1873	Syn. of *Nysius raphanus* Howard
Hemiptera: Margarodidae	*Icerya montserratensis* R&H	1890	Valid
	Icerya palmeri R&H	1890	Valid
	Icerya rosae R&H	1890	In *Crypticerya*
Hemiptera: Phylloxeridae	*Phylloxera caryaeavellana*	1880	Valid
	Phylloxera caryaefallax	1875	Valid
	Phylloxera caryaegummosa	1875	Valid
	Phylloxera caryaescissa	1880	Valid
	Phylloxera caryaeren	1875	Valid
	Phylloxera rileyi	1875	Valid
Hemiptera: Psyllidae	*Pachypsylla celtidisasterisca*	1890	Valid
	Pachypsylla celtidiscucurbita	1890	Valid
	Pachypsylla celtidisgemma	1885	Valid
	Pachypsylla celtidisglobulus	1890	Valid
	Pachypsylla celtidispubescens	1890	Valid
	Pachypsylla celtidisumbilicus	1890	Valid
	Pachypsylla celtidisvesicula	1884	Valid
	Psylla celtidisgrandis	1876	In *Pachypsylla*
	Psylla celtidismamma	1876	In *Pachypsylla*
Hemiptera: Triozidae	*Ceropsylla sideroxyli*	1884	Valid
	Rhinopsylla schwarzii	1885	Valid
Coleoptera: Brentidae	*Podapion gallicola*	1883	Valid
Coleoptera: Chrysomelidae	*Bruchus fabae*	1871	Syn. of *Acanthoscelides obtectus* (Say)
	Physonota quinquepunctata W&R	1869	Syn. of *Physonota helianthi* (Randall)
Coleoptera: Curculionidae	*Analcis fragariae*	1871	In *Tyloderma*
	Madarus vitis	1869	Syn. of *Ampelolypter sesostris* (LeConte)
	Scolytus carya	1867	Syn. of *Scolytus quadrispinosus* Say
Coleoptera: Meloidae	*Hornia minutipennis*	1877	Valid
Diptera: Agromyzidae	*Oscinis brassicae*	1885	In *Liriomyza*
Diptera: Anisopodidae	*Mycetophila persica*	1867	Syn. of *Mycetobia divergens* Walker
Diptera: Anthomyiidae	*Anthomyia calopteni*	1877	Syn. of *Delia platura* (Meigen)
	Anthomyia zeas	1869	Syn. of *Delia platura* (Meigen)
Diptera: Asilidae	*Asilis missouriensis*	1870	Syn. of *Proctacanthus milbertii* Macquart
Diptera: Cecidomyiidae	*Cecidomyia cupressiananassa*	1870	Unavail.; =*Taxodiomyia cupressiananassa* (O. S.)
	Cecidomyia pyrivora	1886	In *Contarinia*
	Cecidomyia vitis coryloides W&R	1869	Unavail.; =*Schizomyia vitiscoryloides* (Packard)
	Cecidomyia vitis pomum W&R	1869	Unavail.; =*Schizomyia vitispomum* (Osten Sacken)
	Cecidomyia vitis lituus W&R	1870	Unavail.; =*Schizomyia viticola* (Osten Sacken)
Diptera: Sarcophagidae	*Sarcophaga sarraceniae*	1874	Valid
Diptera: Simuliidae	*Simulium meridionale*	1887	Valid
	Simulium pecuarum	1887	In *Cnephia*
	Simulium piscicidium	1870	Valid
Diptera: Tachinidae	*Exorista cecropiae*	1870	In *Winthemia*
	Exorista flavicauda	1870	Syn. of *Belvosia unifasciata* (Robineau-Desvoidy)
	Lydella doryphorae	1869	In *Myiopharus*
	Tachina aletiae	1879	In *Lespesia*
	Tachina anonyma	1872	In *Lespesia*
	Tachina archippivora	1871	In *Lespesia*
Lepidoptera: Blastobasidae	*Blastobasis iceryaeella*	1887	In *Holcocera*
	Gelechia glandulella	1871	In *Blastobasis*
Lepidoptera: Coleophoridae	*Coleophora malivorella*	1879	Syn. of *Coleophora multipulvella* Chambers
Lepidoptera: Gelechiidae	*Gelechia gallaesolidaginis*	1869	In *Gnorimoschema*
	Gelechia hallipalpis	1891	Syn. of *Trichotaphe juncidella* Clemens
Lepidoptera: Geometridae	*Aplodes flavilineata*	1870	Syn. of *Chlorochlamys chloroleucaria* (Guenee)
	Aplodes rubivora	1869	Syn. of *Synchlora aerata* (F.)

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Table 2. (*continued*)

Order: Family	Original combination	Year	Current status[a]
	Carphoxera ptelearia	1891	Syn. of *Idaea bonifata* (Hulst)
Lepidoptera: Noctuidae	*Acronycta populi*	1870	Syn. of *Acronicta lepusculiana* Guenee
	Agrotis cochranis	1867	Syn. of *Euxoa messoria* (Harris)
	Agrotis morrisoniana	1875	Syn. of *Agrotis gladiaria* Morrison
	Agrotis scandens	1869	In *Euxoa*
	Amphipyra conspersa	1871	Syn. of *Amphipyra pyramidoides* Guenee
	Anomis texana	1885	Valid
	Laphygma fulvosa	1876	Syn. of *Spodoptera frugiperda* (J.E. Smith)
	Laphygma obscura	1876	Syn. of *Spodoptera frugiperda* (J.E. Smith)
	Nola sorghiella	1882	Valid
	Plusia brassicae	1870	Syn. of *Trichoplusia ni* (Hubner)
	Prodenia autumnalis	1871	Syn. of *Spodoptera frugiperda* (J.E. Smith)
	Xanthoptera ridingsii	1874	In *Exyra*
	Xylina cinerea	1871	Syn. of *Lithophane antennata* (Walker)
Lepidoptera: Notodontidae	*Cerura multiscripta*	1875	Syn. of *Cerura scitiscripta* Walker
Lepidoptera: Prodoxidae	*Prodoxus aenescens*	1881	Valid
	Prodoxus cinereus	1881	Valid
	Prodoxus decipiens	1880	Syn. of *Prodoxus quinquepunctella* (Chambers)
	Prodoxus intermedius	1881	Syn. of *Tegeticula yuccasella* (Riley)
	Prodoxus marginatus	1881	Valid
	Prodoxus pulverulentus	1892	Valid
	Prodoxus y-inversum	1892	Valid
	Prodoxus reticulatus	1892	In *Greya*
	Prodoxus coloradensis	1892	Valid
	Prodoxus sordidus	1892	Valid
	Pronuba synthetica	1892	In *Tegeticula*
	Pronuba maculata	1881	In *Tegeticula*
	Pronuba yuccasella	1872	In *Tegeticula*
Lepidoptera: Pterophoridae	*Pterophorus carduidactylus*	1869	In *Platyptilia*
Lepidoptera: Pyralidae	*Acrobasis vaccinii*	1884	Valid
	Chilo oryzaeelus	1882	Syn. of *Chilo plejadellus* Zinck.
	Clydonopteron tecomae	1880	Syn. of *Clydonopteron sacculana* (Bosc)
	Pempelia hammondi	1872	In *Psorosin*a
	Phycita nebulella	1872	Syn. of *Acrobasis indigenella* (Zeller)
Lepidoptera: Sessidae	*Aegeria rubi*	1874	Syn. of *Pennisetia marginatum* (Harris)
Lepidoptera: Tortricidae	*Anchylopera fragariae* W&R	1869	Syn. of *Ancylis comptana* (Froelich)
	Conchylis erigeronana	1881	In *Carolella*
	Conchylis oenotherana	1881	In *Phtheochroa*
	Cydia ninana	1883	Valid
	Exartema ferrugineum	1881	in *Olethreutes*
	Exartema monetiferanum	1881	In *Olethreutes*
	Grapholitha gallae-saliciana	1881	In *Cydia*
	Grapholitha olivaceana	1881	In *Phaneta*
	Grapholitha sebastianiae	1892	Syn. of *Cydia deshaisiana* Lucas
	Mellissopus aurichalceana	1881	Syn. of *Cydia latiferreanus* (Walsingham)
	Paedisca celtisana	1881	In *Epinotia*
	Paedisca giganteana	1881	In *Eucosma*
	Penthina fullerea	1870	Syn. of *Endothenia hebesana* (Walker)
	Phoxopteris cornifoliana	1881	Syn. of *Ancylis muricana* (Walsingham)
	Phoxopteris murtfeldtiana	1881	Syn. of *Ancylis burgessiana* (Zeller)
	Proteoteras aesculana	1881	Valid
	Proteoteras claypoleana	1882	In *Zeiraphera*
	Semasia helianthana	1881	In *Suleima*
	Tortrix cinderella	1872	Syn. of *Acleris minuta* (Robinson)
Hymenoptera: Braconidae	*Apanteles acronyctae*	1881	Homonym; =*Cotesia acronyctae* (Riley)
	Apanteles aletiae	1881	In *Parapanteles*
	Apanteles argynnidis	1889	In *Cotesia*
	Apanteles cacoeciae	1881	In *Dolichogenidea*
	Apanteles cassianus	1881	In *Glyptapanteles*
	Apanteles cyaniridis	1889	In *Cotesia*
	Apanteles edwardsii	1889	Valid
	Apanteles emarginatus	1889	Homonym; =*Cotesia scitulus* (Riley)
	Apanteles flaviconchae	1881	In *Cotesia*
	Apanteles flavicornis	1889	In *Cotesia*
	Apanteles hemileucae	1881	In *Cotesia*
	Apanteles hyphantriae	1887	In *Cotesia*
	Apanteles junoniae	1889	In *Cotesia*
	Apanteles koebelei	1889	In *Cotesia*

Table 2. (*continued on next page*)

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Table 2. (*continued*)

Order: Family	Original combination	Year	Current status[a]
	Apanteles megathymi	1881	Valid
	Apanteles paleacritae	1881	In *Protapanteles*
	Apanteles pholisorae	1889	In *Cotesia*
	Apanteles politus	1881	In *Glyptapanteles*
	Apanteles rufocoxalis	1881	In *Cotesia*
	Apanteles scitulus	1881	In *Cotesia*
	Apanteles smerinthi	1881	In *Cotesia*
	Apanteles theclae	1881	In *Cotesia*
	Bracon charus	1875	In *Atanycolus*
	Exothecus prodoxi	1880	In *Heterospilus*
	Meteorus hyphantriae	1887	Valid
	Microgaster acronyctae	1870	In *Cotesia*
	Microgaster gelechiae	1869	Valid
	Microgaster limenitidis	1871	In *Cotesia*
	Microgaster pieridivora	1882	Syn. of *Cotesia glomeratus* (L.)
	Microplitis ceratomiae	1881	Valid
	Microplitis gortynae	1881	Valid
	Perilitus indagator	1872	In *Meteorus*
	Sigalphus rufus	1871	In *Nealiolus*
	Spathius trifasciatus	1873	Valid
Hymenoptera: Cephidae	*Cephus occidentalis* R&M	1891	Syn. of *Cephus cinctus* Norton
Hymenoptera: Chalcididae	*Chalcis maria*	1870	In *Conura*
Hymenoptera: Cynipidae	*Cynips quercusfloccicola*	1890	*Incertae sedis*
	Cynips quercusglandulus	1877	*Incertae sedis*
	Cynips quercusmellaria	1880	*Incertae sedis*
	Cynips quercusprunus W&R	1869	In *Amphibolips*
	Dryophanta vesiculoides	1895	Unavail.; =*Dryophanta* of authors
Hymenoptera: Eucoilidae	*Didyctium zigzag*	1879	In *Trybliographa*
Hymenoptera: Eulophidae	*Cirrospilus esurus*	1879	In *Aprostocetus*
	Cirrospilus flavicinctus	1883	Valid
	Pleurotropis phyllotretae	1885	In *Pediobius*
	Tetrastichus productus	1885	Valid
Hymenoptera: Eurytomidae	*Eurytoma bolteri*	1869	Valid
	Isosoma grandis	1884	In *Tetramesa*
	Isosoma tritici	1882	Homonym; =*Tetramesa grandis* (Riley)
Hymenoptera: Ichneumonidae	*Exochilum acronyctae*	1890	Unavail.; =*Therion fuscipennis* (Norton)
	Hemiteles alaefasciatus	1890	Unavail.; =*Chirotica confederatae* (Ashmead)
	Hemiteles cressoni	1869	In *Mastrus*
	Hemiteles thyridopteryx	1869	In *Chirotica*
	Ichneumon obsoletus	1877	Homonym; =*Cratichneumon brevipennis* (Cresson)
	Limneria lophyri	1877	In *Olesicampe*
	Porizon conotracheli	1871	In *Tersilochus*
Hymenoptera: Pteromalidae	*Merisus subapterus*	1885	In *Trichomalopsis*
	Ophelosia crawfordi	1890	Valid
Hymenoptera: Scelionidae	*Caloptenobia ovivora*	1878	In *Scelio*
	Scelio calopteni	1893	Syn. of *Scelio opaca* (Provancher)
	Scelio caloptenorum	1885	Valid
	Scelio ernstii	1885	Valid
	Scelio luggeri	1893	Syn. of *Scelio opaca* (Provancher)
	Telenomus arzamae	1893	Valid
	Telenomus bifidus	1887	Valid
	Telenomus clisiocampae	1893	Valid
Hymenoptera: Torymidae	*Stictonotus isosomatis*	1882	In *Eridontomerus*
Hymenoptera: Trichogrammatidae	*Trichogramma minuta*	1871	Valid
	Trichogramma pretiosa	1879	Valid

[a]Abbreviations: Emend.= Emendation; Syn.= synonym; Unavail.= unavailable.

biological control, noting that the success of the vedalia beetle would be difficult to repeat (Riley 1893a). He also acknowledged that the use of insecticides could destroy natural enemies of pest insects (McWilliams 2008). He was first to refute the myth that black flies (Simuliidae) are able to kill fish by "ensnaring them in silken death webs" (Adler et al. 2004). Those who criticized his findings often were rebuked in print, sometimes harshly (e.g., Sheppard and Oliver 2004). Those reprimanded by Riley might have been less upset about being the target of his barbs than in realizing that he "was usually correct in his arguments" (Davis 1967).

As expected, the availability of molecular and other modern research tools has necessitated reinterpretation of some of Riley's work or otherwise advanced our biological understanding of topics he studied, such as speciation in periodical cicadas (Cooley et al. 2001) and phylogeny of the pollinating yucca moths (Pellmyr et al. 2008). His observations sometimes were inaccurate. An example is stating that stridulation in adult passalid beetles involves the wing covers or elytra, when mainly the hind wings are used, the elytra playing only a supporting role (Costa 2006). Moreover, the bee- and

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Table 3. Species described by C. V. Riley having ESA-approved common names.

Common name	Scientific name	ORDER	Family
appleleaf skeletonizer	*Psorosina hammondi* (Riley)	Lepidoptera	Pyralidae
artichoke plume moth	*Platyptilia carduidactylua* (Riley)	Lepidoptera	Pterophoridae
cranberry fruitworm	*Acrobasis vaccini* Riley	Lepidoptera	Pyralidae
minute egg parasite	*Trichogramma minuta* Riley	Hymenoptera	Trichogrammatidae
pear midge	*Contarinia pyrivora* (Riley)	Diptera	Cecidomyiidae
pine gall weevil	*Podapion gallicola* Riley	Coleoptera	Brentidae
pistol casebearer	*Coleophora malivorella* Riley	Lepidoptera	Coleophoridae
poplar petiole gall aphid	*Pemphigus populitransversus* Riley	Hemiptera	Aphididae
poplar twig gall aphid	*Pemphigus populiramulorum* Riley	Hemiptera	Aphididae
serpentine leafminer	*Liriomyza brassicae* (Riley)	Diptera	Agromyzidae
sixspotted mite	*Eotetranychus sexmaculatus* (Riley)	Prostigmata	Tetranychidae
sorghum webworm	*Nola sorghiella* Riley	Lepidoptera	Noctuidae
southern buffalo gnat	*Cnephia pecuarum* (Riley)	Diptera	Simuliidae
strawberry crown borer	*Tyloderma fragariae* (Riley)	Coleoptera	Curculiondae
sunflower bud moth	*Suilema helianthana* (Riley)	Lepidoptera	Tortricidae
turkey gnat	*Simulium meridionale* Riley	Diptera	Simuliidae
wheat strawworm	*Tetramesa grandis* (Riley)	Hymenoptera	Eurytomidae
white cutworm	*Euxoa scandens* (Riley)	Lepidoptera	Noctuidae
woolly elm aphid	*Eriosoma americanum* (Riley)	Hemiptera	Aphididae
yellowheaded leafhopper	*Xyphon flaviceps* (Riley)	Hemiptera	Cicadellidae
yucca moth	*Tegeticula yuccasella* (Riley)	Lepidoptera	Prodoxidae

wasp-mimicking robber flies (Asilidae) he considered "aggressive mimics" are thought more likely to represent Batesian mimics (Alcock 1999).

In addition to bionomics, Riley became involved in some of the more classical aspects of taxonomy, such as nomenclature. Occasionally, he made ill-advised decisions regarding the usage of scientific names. Because he regarded strict adherence to the laws of priority as an extreme view, he stubbornly persisted in using certain names that had been synonymized. Additionally, even though he realized his generic name *Pronuba* in the lepidopteran family Prodoxidae was preoccupied, and thus a homonym, he continued to use the name (Davis 1967).

Like Fitch, Lintner, Walsh and certain other 19th-century applied entomologists, Riley had diverse interests that included the description of new species. He did not, however, produce generic revisions in a strict sense. With the North American insect fauna only beginning to be described, revisionary studies were less necessary than they are today and were not customary in Riley's time. In describing the new psyllid genus *Pachypsylla*, he did provide a key ("dichotomic table") allowing separation of the three known species: his new species, one he described previously (subsequently synonymized), and one described by Osten-Sacken (Riley 1885b). Riley and Howard (1890) gave "synoptical" keys to newly hatched larvae (crawlers) and adult females of the species of the scale insect genus *Icerya*. That he appreciated the importance of catalogs and synopses is indicated by his compilation of the principal works on European and North American insect taxonomy (the paper was motivated by inquiries about references for identifying American insects). In listing relevant taxonomic works, he criticized some of the descriptive and synoptic papers by younger authors as being "most insufficient and unsatisfactory" (Riley 1888).

Riley's descriptions of new species often were illustrated, the drawings tending to reveal an emphasis on biology and immature stages. Although it was not yet routine for North American taxonomists to illustrate the adult habitus of species being described or to provide illustrations of diagnostic characters, Riley did include such illustrations (e.g., Riley 1873a, pp. 150-151; Riley and Howard 1890). He sometimes described and illustrated male genitalia (e.g., Riley 1892c). In realizing the value of referring to host plants when labeling specimens of phytophagous insects (Riley 1873a, pp. 43),[29] he was ahead of many of his North American contemporaries (and some 20th-century workers).

As a describer of new taxa, Riley cannot be accused of nomenclatural mihilism (Dubois 2008) or the "mihi itch" (Evenhuis 2008)—that is, the unwarranted description of new species by authors seeking recognition and apparent scientific "immortality."

[29]Riley (1892a) advocated a system of indicating food plants on specimen labels, using numbers identical to those in a field notebook. This practice, however, is undesirable. Too often the notebooks are lost or else are preserved apart from the insect collections in which the specimens are housed.

His taxonomic philosophy called for evaluating morphological characters of a range of specimens—appreciating what now is termed intraspecific variation—rather than adopting a typological approach of "making species out of every little variation" (Riley 1871b, 1883a). His taxonomic work was punctuated neither by the carelessness of the British entomologist Francis Walker (e.g., Papavero and Ibáñez-Bernal 2001, Wilson and Turner 2007) nor generally considered suspect, as was that of the American coleopterist Thomas Casey (Leng, 1925, Hatch 1926). Consistent with practice typical of the time, Riley did not designate or label type material for the species he described. Types of species were not addressed in the International Rules (Règles Internationales) until they were recommended in 1913 (Mayr et al. 1953, p. 236).

Descriptions of new species can be considered equivalent to the generation of testable hypotheses in other areas of biology (Gaston and Mound 1993). One means of evaluating a taxonomist's value to his contemporaries or to later generations is to look at the percentage of species that remain valid. A taxonomic hypothesis is falsified when a proposed name is shown to apply to the same biological entity (Gaston and Mound 1993). Species still considered valid are not necessarily so—their status might never have been evaluated—and even valid descriptions often are inadequate for identification purposes. Furthermore, taxonomists producing a low rate of synonymy might not have included keys to species or

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Table 4. Insects named in recognition of C. V. Riley (patronyms), with genus-group and species-group names arranged by year of publication (descending).

Original combination	Year	Order	Family	Status[a]
GENUS-GROUP				
Rileya Ashmead	1888	Hymenoptera	Eurytomidae	Valid
Rileya Howard	1888	Hymenoptera	Encyrtidae	Homonym; =*Chrysoplatycerus*
Rileya Brauer & Bergenstamm	1893	Diptera	Tachinidae	Homonym; =*Leschenaultia*
Rileymyia Townsend	1893	Diptera	Tachinidae	New name for *Rileya* B&B; = *Lescehnaultia*
Rileyonymus Dietz	1896	Coleoptera	Curculionidae	Valid
Macrorileya Ashmead	1900	Hymenoptera	Eurytomidae	Valid
Rileyella Townsend	1909	Diptera	Tachinidae	Syn. of *Lespesia*
Rileya Melichar	1906	Hemiptera	Issidae	Homonym; =*Misodema*
Rileya Olivier	1911	Coleoptera	Lampyridae	Homonym; =*Lucidota*
SPECIES-GROUP				
Tortrix rileyana Grote	1868	Lepidoptera	Tortricidae	In *Archips*
Trogus rileyi Cresson	1868	Hymenoptera	Ichneumonidae	In *Conocalama*
Aleiodes rileyi Cresson	1869	Hymenoptera	Braconidae	In *Rogas*
Aleiodes rileyi Cresson	1869	Hymenoptera	Braconidae	In *Rogas*
Depressaria rileyella Chambers	1872	Lepidoptera	Gelechiidae	In *Gelechia*
Agrotis rileyana Morrison	1874	Lepidoptera	Noctuidae	In *Onychagrotis*
Heteropacha rileyana Harvey	1874	Lepidoptera	Lasiocampidae	Valid
Epicauta rileyi Horn	1874	Coleoptera	Meloidae	Valid
Lithocolletis rileyella Chambers	1875	Lepidoptera	Gracillariidae	In *Phyllonorycter*
Bucculatrix rileyi Frey & Boll	1876	Lepidoptera	Bucculatrigidae	Syn. of *Bucculatrix ambrosiaefoliella* Chambers
Eriosoma rileyi Thomas	1877	Hemiptera	Aphididae	Replacement name for *Eriosoma ulmi* Riley
Selandria rileyi Cresson	1880	Hymenoptera	Tenthredinidae	In *Periclista*
Lophyrus rileyi Cresson	1880	Hymenoptera	Diprionidae	Syn. of *Neodiprion abbotti* (Leach)
Lyda rileyi Cresson	1880	Hymenoptera	Pamphilidae	In *Pamphilius*
Selandria rileyi Cresson	1880	Hymenoptera	Tenthredinidae	In *Periclista*
Albuna rileyana Edwards	1881	Lepidoptera	Sesiidae	In *Synanthedon*
Batrachedra rileyi Walsingham	1882	Lepidoptera	Cosmopterygidae	In *Pyroderces*
Thyridopteryx rileyi Heylaerts	1884	Lepidoptera	Psychidae	Valid
Neuroterus rileyi Ashmead	1885	Hymenoptera	Cynipidae	Emend.; syn. of *Neuroterus quercusrileyi* (Bassett)
Doliosyrphus rileyi Williston	1887	Diptera	Syrphidae	Syn. of *Eristalis scutellaris* (F.)
Brachypalpus rileyi Williston	1887	Diptera	Syrphidae	Syn. of *Chalcosyrphus metallifera* (Bigot)
Ephestia rileyella Ragonot	1887	Lepidoptera	Pyralidae	In *Sosipatra*
Inostemma rileyi Ashmead	1887	Hymenoptera	Platygastridae	Valid
Tetrastichus rileyi Lindeman	1887	Hymenoptera	Eulophidae	Syn. of *Tetrastichus carinatus* Forbes
Fontaria rileyi Bollman	1889	Polydesmida	Xystodesmidae	In *Cleptoria*
Telenomus rileyi Howard	1889	Hymenoptera	Scelionidae	Valid
Wesmaelia rileyi Ashmead	1889	Hymenoptera	Hybrizontidae	In *Hybrizon*
Orgilus rileyi Ashmead	1889	Hymenoptera	Braconidae	Syn. of *Crassomicrodus divisus* (Cresson)
Wesmaelia rileyi Ashmead	1889	Hymenoptera	Ichneumonidae	In *Hybrizon*
Telenomus rileyi Howard	1889	Hymenoptera	Scelionidae	Valid
Masicera rileyi Williston	1889	Diptera	Tachinidae	In *Lespesia*
Leonia rileyi Dugas	1889	Coleoptera	Meloidae	Syn. of *Hornia mexicana Dugas*
Hemiteles rileyi Ashmead	1890	Hymenoptera	Ichneumonidae	Syn. of *Dichrogaster crassus* (Provancher)
Xylonomus rileyi Ashmead	1890	Hymenoptera	Ichneumonidae	In *Xorides*
Morrisonia rileyana Smith	1890	Lepidoptera	Noctuidae	Syn. of *Morrisonia mucens* (Hubner)
Metopius rileyi Marlatt	1891	Hymenoptera	Ichneumonidae	Valid
Eleodes rileyi Casey	1891	Coleoptera	Tenebrionidae	Valid
Telamona rileyi Goding	1892	Hemiptera	Membracidae	In *Telamonanthe*
Rheumatobates rileyi Bergroth	1892	Hemiptera	Gerridae	Valid
Pemphredon rileyi Fox	1892	Hymenoptera	Sphecidae	Valid
Sinea rileyi Montandon	1893	Hemiptera	Reduviidae	Valid
Mythicomyia rileyi Coquillet	1893	Diptera	Bombyliidae	Valid
Icerya rileyi Cockerell	1895	Hemiptera	Margarodidae	Valid
Andricus rileyi Ashmead	1896	Hymenoptera	Cynipidae	In *Dryocosmus*
Margarodes rileyi Giard	1897	Hemiptera	Margarodidae	Valid
Phlepsius rileyi Baker	1898	Hemiptera	Cicadellidae	In *Paraphlepsius*
Pterophorus rileyi Fernald	1898	Lepidoptera	Pterophoridae	In *Oidaematophorus*
Pterophorus rileyi Fernald	1898	Lepidoptera	Pterophoridae	In *Oidaematophorus*
Actenopoda rileyi Ashmead	1902	Hymenoptera	Pompilidae	*Nomen nudum* in *Aporus*; unavail.
Tinea rileyi Dietz	1905	Lepidoptera	Tineidae	In *Nemapogon*
Oecanthus rileyi Baker	1905	Orthoptera	Gryllidae	Valid
Apanteles rileyanus Ashmead	1906	Hymenoptera	Braconidae	*Nomen nudum* in *Apanteles*; unavail.
Rabdophaga rileyana Felt	1909	Diptera	Cecidomyiidae	Valid
Cryptapanteles rileyanus Viereck	1910	Hymenoptera	Braconidae	Syn. of *Cotesia scitula* (Riley)
Eulachnus rileyi Williams	1911	Hemiptera	Aphididae	Valid
Argyria rileyella Dyar	1914	Lepidoptera	Pyralidae	Syn. of *Argyria rufisignella* Zeller
Xyleborus rileyi Hopkins	1915	Coleoptera	Scolytidae	Syn. of *Xyleborus volvulus* (F.)

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Table 4. (continued)

Original combination	Year	Order	Family	Status[a]
Aphycus rileyi Timberlake	1916	Hymenoptera	Encyrtidae	In *Metaphycus*
Sarcophaga rileyi Aldrich	1916	Diptera	Sarcophagidae	In *Fletcherimyia*
Boophthora rileyana Enderlein	1922	Diptera	Simuliidae	Syn. of *Simulium venustum* Say
Acinopterus rileyi Lawson	1927	Hemiptera	Cicadellidae	Valid
Mammifrontia rileyi Benjamin	1936	Lepidoptera	Noctuidae	Valid
Erebia rileyi Dos Passos	1947	Lepidoptera	Satyridae	Syn. of *Erebia youngi* Holland
Lepidostoma rileyi Denning	1948	Trichoptera	Lepidostomatidae	Syn. of *Lepidostoma tibialis* (Carpenter)
Barylypa rileyi Dasch	1984	Hymenoptera	Ichneumonidae	Valid

[a]Abbreviations: Emend.= emendation; Syn.= synonym.

had substantial influence on the systematic community, such as encouraging others to pursue systematics (Hodges 1976, Gaston and Mound 1993). Comparing the rate of synonymy among taxonomic workers is complex, involving changes in species concepts (Gaston and Mound 1993, Raczkowski and Wenzel 2007), which can differ among taxonomic groups and workers, as well as other factors beyond the scope of our paper.

Just as Riley did not shy away from studying the biology of insects having complex life histories, he similarly accepted the challenge of describing new species in taxonomically difficult groups, such as acalyptrate Diptera, Aphidoidea, Chalcidoidea, Curculionoidea, microlepidoptera, and Psylloidea. Some 115 years after Riley's death, probably only a small proportion of his invalid names remains to be discovered; his synonymy rate, therefore, seems unlikely to increase substantially. Rates of synonymy vary widely among insect taxonomists (Gaston and Mound 1993). Riley's rate of 23.6% (synonyms only) or 32.5% (including other professional errors such as homonyms and *nomina nuda*) compares favorably with a current 20% (or greater) level of synonymy in Thysanoptera and certain other groups of the Insecta and is substantially better than that in certain other groups (Gaston 1991, Gaston and Mound 1993, Gaston et al. 1995, Solow et al. 1995, May 2002). Low rates of synonymy—all three of Riley's black fly species are still valid (Adler et al. 2004)—do not necessarily reflect particular expertise in a group. In the case of Simuliidae, so few North American species in this diverse family had been described at the time (Adler et al. 2004) that other workers were unlikely to have previously named those species that Riley described. Until recently, most of Riley's species of the psylloid genus *Pachypsylla* were considered synonyms (Hodkinson 1888), but allozyme studies, life-history data, and evaluation of gall morphology and host plants suggest that Riley's species are indeed distinct (Yang and Mitter 1994) and attest to his exceptional taxonomic instincts.

Concluding Thoughts

We regard C. V. Riley's contributions to taxonomic entomology as substantial. If the term *biosystematics* had been in use in the last half of the 19th century, he probably would have been considered a gifted biosystematist. He should be considered one of North America's most prominent and influential entomologists, having won national and international acclaim in agricultultural entomology. Mallis (1971), in his book *American Entomologists*, placed Riley's biographical sketch in the chapter on early federal entomologists. Mallis also could have justified placing him in the chapter on early state entomologists, or in the chapter on entomologists of diverse interests. Had Riley chosen to specialize in insect taxonomy, Mallis might have been able to place his biographical sketch in a chapter devoted to notable specialists in a particular taxonomic group. With Riley's familiarity with morphology and nomenclature, feel for characters useful in discriminating species, a taxonomic philosophy seemingly advanced for its time, knowledge of both the American and European literature in entomology, facility with French and German, and talent as an illustrator, he probably could have become a leading 19th-century taxonomist. But Riley chose to pursue his passion—conducting biological studies that would help farmers contend with their pest problems. His work in applied entomology resulted in outstanding examples of pest suppression at home and abroad and influenced the course of insect pest management, including the use of biological control, well into the 20th century.[30]

[30]Riley's successor as chief of the USDA Bureau of Entomology was his former assistant, L. O. Howard. McWilliams (2008) suggested that the later reliance on chemical insecticides to control pest insects and rise of the chemical pesticide industry was partly the result of Howard's downplaying of Riley's biological control work.

Were Riley alive today, his inherent pragmatism and love of nature might have made the conservation of biodiversity, especially insects, a good philosophical fit. Biodiversity conservation involves practical as well as moral considerations (Samways 2009). We can only wonder how he might have addressed one of the challenges of modern society: melding insect conservation, an evolving subdiscipline of entomology, with our measures for suppressing pest insects.

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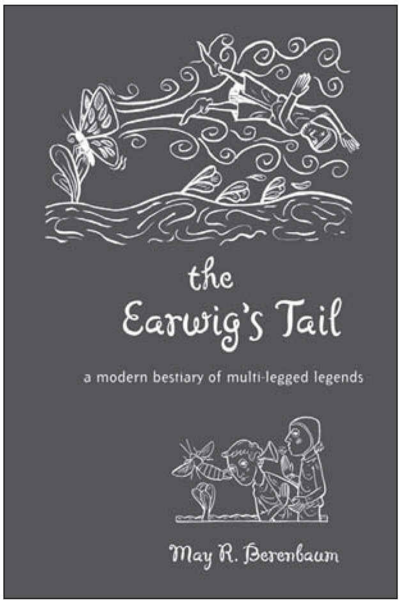

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