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A brief history of the generic classification of the Trochilini (Aves: Trochilidae): the chaos of the past and problems to be resolved

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Abstract

The generic classification of the Trochilidae is unusually complicated because early authors, faced with a deluge of specimens with little or no data, often based species and genus names on superficial plumage characters derived from figured plates of varying artistic quality and reproduction. Working independently and with little knowledge of species distributions and with the fixation of type species for genera inconsistent or ignored, these authors produced a bewildering array of generic synonyms. The generic nomenclature of the largest and most recently derived clade of hummingbirds, the tribe Trochilini or "emeralds", presents an unusually tangled web. Here we review the history of hummingbird generic nomenclature from Linnaeus to the present, giving detailed attention to two generic names that epitomize this confusion: Amazilia (the variety of spellings, supposed type species and circumscriptions makes for an especially complicated tangle) and Leucippus (for which nearly every successive author has advocated a different circumscription). Through application of the International Code for Zoological Nomenclature, this review lays the foundation for a revision of the generic nomenclature of the emeralds to bring it into conformity with recent genetic studies elucidating the phylogeny of this clade.

Key words: Amazilia, generic nomenclature, history, hummingbirds, Leucippus, taxonomy, Trochilini

Genetic data (Bleiweiss et al. 1997; McGuire et al. 2007, 2009, 2014) have revealed several distinctive lineages within the hummingbirds (Trochilidae), the largest of which is the tribe Trochilini. Popularly known as the "emeralds", this tribe as currently defined (Dickinson & Remsen 2013) consists of 110 species in 28 genera, and thus contains nearly 30% of all species and genera in the Trochilidae. Although classification at the genus and species level has remained reasonably stable since that of Peters (1945), McGuire et al. (2014) showed that this classification conflicts extensively with phylogenetic data and thus requires a major revision. As shown by the plates in Schuchmann (1999), most species in the group are relatively drab in color by hummingbird standards, with males of most species having two or fewer bright spectral colors, and many have none at all. Highly modified flight feathers in males are restricted to the long central rectrices in Trochilus and the thickened shafts of the outer primaries in a few genera; none of these are known to produce species-specific sounds, as they do in some other clades. The females of many species are confusingly similar, with gray to white underparts and more or less whitetipped outer rectrices, and males of most sexually monochromatic species also show this kind of plumage. The emeralds are also relatively uniform in size and shape, with most species in the 4-6g range in body mass, with straight to slightly curved bills of moderate length relative to body mass. Because the traditional classification was based largely on these rather minor variations in plumage and structural characters that also typify numerous other hummingbirds, it is no surprise that this classification would be shown to be faulty.

Before we can construct a new phylogenetic classification, we must address major problems concerning nomenclature at the genus level in this tribe. The relative homogeneity among species has exacerbated these problems, which we discuss below. The goal of this paper is to disentangle the complex nomenclature of the group so that we have a firm basis for delimiting the genera in the Trochilini (Stiles, McGuire & Remsen, in review). We

first review the causes and extent of the problems with hummingbird generic classification in general, then examine the chaotic situation of emerald genera in more detail with emphasis on two especially problematic cases, the generic names *Amazilia* and *Leucippus*.

An overview of the history and problems of the classification of hummingbird genera

The generic nomenclature of the Trochilidae is among the most complicated and confusing of any avian family. This results from the great diversity of species and their often-spectacular plumages, which in turn were responsible for the massive trade in their dried skins as articles of adornment from *ca.* 1830–1910 (Chapman 1917). The trade was triggered by the independence of the Spanish colonies in the New World and the end of Spain's monopolistic policies in 1820–1821, which opened most of the Neotropics to scientific exploration and commerce. At its height in the late 19th century, Boucard (1891) estimated that 600,000 bird skins, largely hummingbirds, were exported annually from the Neotropics to Europe and later to North America during this period.

Knowledge of the diversity of hummingbirds increased sporadically in the latter half of the 18th century. Linnaeus (1758) included only 18 species in the 10th edition of the *Systema Naturae*, and added four more in the 12th edition (1766); Brisson (1760) mentioned 36. Buffon (1779) enumerated ca. 33 species in French, but refused to follow the Linnaean classification system and Latin binomial nomenclature. In the 13th edition of the *Systema Naturae*, Gmelin (1788) increased the number of species to 67, mostly drawn from the works of Buffon and Brisson; Latham (1790) mentioned 65. Figured plates were the basis for most species then known, supported with at best meager written descriptions. The plates themselves inevitably caused confusion because they were by different artists and with varying qualities of reproduction; some were even drawn second-hand from descriptions rather than from specimens. Without information on species distributions, the same species was often described several times from different countries of origin, leading to many synonyms, as well as names unidentifiable to any known species (Gould 1861a).

Although generic nomenclature lagged behind that of species, it suffered from many of the same problems. Linnaeus (1758, 1766) and Gmelin (1788) placed all their hummingbird species in the genus *Trochilus*; Gmelin ignored two genera, *Mellisugus* and *Polytmus*, named by Brisson (1760), although these were later accepted. Lacépède (1799) listed a heterogeneous group of straight-billed species under *Orthorhynchus*, which was also later accepted despite the objections of Elliot (1879). Thus, by 1800 no more than approximately 60 species and four genera had been described with certainty. Through at least 1825, new species continued to be described only in the genera *Trochilus* or *Orthorhynchus*, and many were still being described in *Trochilus* until *ca.* 1855.

With ever-increasing numbers of specimens, mostly taken by native collectors (Graves 1993), private and museum collections quickly accumulated thousands of hummingbird specimens, usually with no locality data beyond that of the country of export (Chapman 1917). This avalanche of specimens stimulated attempts to classify them, particularly in France, England and Germany. The necessity of creating new genera was evident. First, Spix (1824) named two (non-emerald) genera from Brazil. Then, Swainson (1827a, b) named several genera with differing lists of included species under the same generic name in these two publications, causing long-standing confusion (see below). Next, Lesson (1829) named the genus Ornismya for a diverse group of often-unrelated species with more or less curved bills. This "genus" soon became a catchall for any species not in Orthorhynchus or Trochilus, especially among the French authors of many new species in Ornismya in the succeeding two decades, despite a critique by Gervais (1835). As far as we can discover, no one (including Lesson) designated a type species. In naming numerous new genera between ca. 1845–1865, Gould, Reichenbach and Bonaparte included many species of Ornismya (several of them as type species of their new genera) but otherwise did not mention it, and in naming type species for many genera Gray (1840, 1855) and later Elliot (1879) did likewise (apparently by this time nothing was left in Ornismya to typify it) and this name passed into oblivion. Vieillot (1818) and Lesson (1832a) also had difficulties applying Buffon's arbitrary (1779) division of the humming birds into the mostly larger, tropical "colibris" with more curved bills and the mostly smaller, straighter-billed "oiseauxmouches", mostly from more temperate latitudes; however, this division persisted in the French literature for many vears.

The first to make an effort towards a broader generic classification was Boie (1831), who distinguished 18

genera, describing 10 or 11 as new; most are still recognized. Towards the middle of the 19th century, the pace of new generic descriptions reached its height. Working independently (and usually with little or no knowledge of hummingbirds in the field or their distributions), museum ornithologists bestowed a plethora of generic and species names, many later revealed to be synonyms (Table 1). Reichenbach (1854, 1855) was especially prolific in this regard: in addition to the over 60 genera he described, he also named ca. 50 subgenera (designated by Greek letters), many subsequently accorded generic rank. Also swelling the number of synonyms were the German ornithologists Cabanis & Heine (1860) and Heine (1863), who in the interests of Latin and Greek linguistic purity renamed many genera. As with species, genera still were frequently named on the basis of subtle differences in colors and patterns evident from plates, many of which represented no more than intraspecific individual or geographic variation. The generic explosion reached its height in the hands of French taxonomists, particularly the four-volume work by Mulsant & E. Verreaux (1874–1877), which enumerated ca. 427 species in 164 genera and subgenera, many monotypic. This work has often been ascribed to only Mulsant, but he included (posthumously) E. Verreaux as coauthor on the title page of each volume. Through this period, the proportion of new generic names later proved to be synonyms also steadily increased (Table 1). The flood of generic names abruptly dried up after about 1880, at which time virtually all species then known had been placed in one (or more) genera; relatively few valid new genera of hummingbirds have been proposed since then, largely for species not previously described.

TABLE 1. A century of chaos: approximate numbers of new generic names described, and the numbers of those later considered as synonyms, by decades from 1820 through 1921, principally from the works of Elliot (1879), Salvin (1892), Boucard (1897) and Simon (1921). Note how the proportion of names synonymized* increased through this period.

Decades	Names proposed	Names synonymized	
Before 1820	ca. 4	0	
1821–1830	10	1	
1831–1840	26	7	
1841–1850	48	20	
1851-1860	140	94	
1861–1870	59	46	
1871-1880	55	48	
1881–1890	7	5	
1890-1900	3	3	
1901–1910	11	7	
1910–1921	29	25	

^{*=}also includes preoccupied names, or names based on hybrids.

The lack of any formal procedure for naming and circumscribing genera during the early 1800s further complicated the problems of generic nomenclature. The British Association for the Advancement of Science attempted to impose strictures with the so-called "Strickland Code" (Strickland *et al.* 1843), which established the principle of priority and the necessity of naming type species for genera. Still, well into the mid-19th century many genera continued to be named for lists of often-unrelated species, and these names were frequently applied to different groups of species by different taxonomists. The fixation of type species was idiosyncratic, and type species for many genera were finally fixed only after decades of confusion. In many cases, the first species in such a generic list was assumed to be the type; in others, the species that remained in a genus after all of the rest had been transferred to different genera was automatically considered the type species by default, both procedures since disqualified by the International Commission of Zoological Nomenclature (1999, hereafter ICZN) unless a specific statement of designation was made; in still others, the species whose epithet coincided with the generic name was designated the type by tautonymy. For monospecific genera, this species automatically became the type (type by monotypy). The chaos caused by the multitude of generic names is revealed in the synonymies compiled by later authors such as Elliot (1879), Salvin (1892) and Ridgway (1911), who showed that many species had been placed in five or more different genera!

In addition, some early authors were inconsistent in defining genera, including different groups of species

under the same generic name in succeeding publications. A case in point among the emeralds was Swainson's genus *Cynanthus*. In late November 1826, Swainson apparently sent to the *Zoological Journal* a manuscript on new genera and species. However, in 1827 Swainson also published in the *Philosophical Magazine* a paper in two parts based on collections of Mexican birds; the part including the hummingbirds appeared in June 1827. Therein, Swainson (1827a) included the genus *Cynanthus*, with *latirostris* Swainson, 1827a as the first species in the list (and therefore eligible as the type by the conventions of the time); the four others were soon placed in different genera. The article in the *Zoological Journal* (Swainson 1827b) appeared in the July–November 1827 issue (no. 11, published in December 1827) and included under *Cynanthus* a different list of species, (all now in different genera), but not *latirostris*! Hence, the first use of *Cynanthus* as a generic name was in the *Philosophical Magazine* and should be accorded priority on this basis, which was only done 80 years later by Stone (1907), who fixed the type as *latirostris*. However, many authors continued to cite the *Zoological Journal* article but not that in the *Philosophical Magazine*.

The same problem occurred with Swainson's genus *Lampornis*, for which again the first use of this name in the *Philosophical Magazine* included only *amethystina* Swainson, 1827a (and therefore its type species by monotypy), whereas that in the *Zoological Journal* included another disparate group of species in *Lampornis*. The validation and precedence of Swainson's (1827a) names *Cynanthus* and *Lampornis* was finally assured in 1911 by opinion no. 30 of the ICZN (2012).

Another recommendation of the "Strickland Code" (Strickland *et al.* 1843) was to avoid tautonymy, namely using the same name for both genus and species. This induced some authors to name (or rename) prospective type species of new genera with the epithet *typica*. However, with changes in generic composition, this also caused problems through secondary homonymy, and the recommendation against tautonymy was soon abandoned.

Elliot (1879) was the first to critically revise hummingbird generic classification, and he warned against naming genera solely on the basis of minor differences in color or pattern. He sought to circumscribe genera based on structural differences (albeit often minor differences in external morphology), and pruned the 164 genera and subgenera of Mulsant & E. Verreaux (1874–1877) down to 120, but with little change in the number of species. His sequence of genera seems peculiar now, because his overall objective was to arrange genera in a smooth morphological progression with one genus leading on to the next, while predicting that the numerous gaps would be filled by yet-to-be discovered species. In this vein, Elliot (1879) also refrained from dividing the Trochilidae into subfamilies, as Gould (1861b) had done earlier in separating the Phaethornithinae and Trochilinae. Elliot paid special attention to type species in defining genera and he provided detailed synonymies and keys to species and genera. With hindsight, we can see that he was often misled by plumage homoplasies and also described several genera based on hybrids. Nevertheless, his monograph was the first step toward a modern classification of the Trochilidae.

The next major classification of the Trochilidae was that of Salvin (1892), whose principal innovation was to divide the family into three "series" based upon the presence and degree of development of bill (tomial) serrations. He also provided keys and descriptions to genera and species, as well as extensive lists of specimens with their localities for each species. Salvin (1892) added some newly described species and genera and redefined other genera, but was not always explicit regarding type species. Boucard's (1897) subsequent review involved much splitting at higher taxonomic levels: he elevated the Trochilidae to an order (Trochiliformes) and divided it into 18 (mostly paraphyletic or polyphyletic) families! For genera and species, he retained much of the now-outdated nomenclature of earlier authors including many synonyms for species. Hartert (1900) presented a classification that was largely an amalgam of Mulsant & E. Verreaux's (1874–1877) species in Salvin's (1892) genera, although he did clarify the circumscriptions and types of some genera.

The next classification, by Ridgway (1911), was meticulous, with detailed synonymies and descriptions of genera, species and subspecies, but was limited to taxa of North and Middle America. It was followed by Cory's (1918), which was the first to include subspecies for the entire family. At that time the distributions of many species were still poorly known, and many of Cory's species were based on individual or geographic variants. He did, however, make progress in redefining the generic nomenclature, and he included species and genera described after the works of Elliot (1879) and Salvin (1892). The next classification, by Simon (1921), in many respects represented a throwback to Boucard and Mulsant in its archaic recognition of multitudinous genera and species; he divided the Trochilidae into 46 "groups", many now shown to be polyphyletic. Simon also coined several new generic names, sometimes rather arbitrarily and with some inconsistencies in spelling. Most of these have been

shown to be synonyms, although a few are still considered valid. However, the detailed synonymy by Simon is helpful for tracking down many older generic names and synonyms.

The classification used through nearly all of the 20th century was that of Peters (1945). By the extensive (if sometimes arbitrary) use of subspecies, he reduced the number of species to around 320 and redefined a number of genera, in part by disqualifying some of the older names without providing specific reasons. Schuchmann's (1999) recent classification of the family in the *Handbook of Birds of the World* (hereafter HBW) included some generic refinements, mainly through merging a number of small genera into larger ones and splitting or rearranging some larger genera, producing totals of 328 species in 102 genera. However, many of his taxonomic decisions were still based on differences in color or pattern. Dickinson & Remsen (2013) based their classification mainly on the DNA-based phylogeny of McGuire *et al.* (2007), which included refutations of several of Schuchmann's (1999) lumps and splits, but was incomplete due to the limited number of species sampled in most genera.

The general trend from the classifications of Mulsant & E. Verreaux (1877) and Elliot (1879) through those of Schuchmann (1999) and Dickinson & Remsen (2013) has been to reduce the numbers of recognized genera and species. Allowing for the description of new taxa, following Elliot (1879) the number of genera remained relatively stable at around 120–140 during this period except for a final spurt of new generic names by Simon (1921), and only fell significantly with the classifications of Peters (1945) and Schuchmann (Table 2). Only minor increases in the number of species were made following Mulsant & E. Verreaux (1877) and Elliot (1879), largely due to the description of new species, prior to the drastic reduction produced by Peters's (1945) extensive use of subspecies, excepting the striking reversions by Boucard (1897) and Simon (1921) (Table 2). The relatively minor increase in the number of species by Schuchmann (1999) reflects mainly the refutation of a number of Peters's unsubstantiated lumpings and the description of new species. Only with the results of DNA-based studies (Bleiweiss *et al.* 1997; McGuire *et al.* 2007, 2014) has the phylogeny of the hummingbirds become clearer, and only McGuire *et al.* (2014) included a sufficiently complete representation of genera and species to make the necessary generic reorganization of the Trochilidae feasible. Remsen *et al.* (2015) covered the Polytminae, and herein we provide the nomenclatural basis for such a revision of the Trochilini.

TABLE 2. Numbers of genera and species in successive classifications of the Trochilidae.

Classifications	Number of genera	Number of species
Reichenbach 1854, 1855	63 (plus 50 subgenera)	345
Mulsant 1874–1877	144 (plus 20 subgenera)	427
Elliot 1879	120	420
Salvin 1892	127	424
Boucard 1897	157	545
Hartert 1900	118	465
Cory 1918	129	454
Simon 1921	183	479
Peters 1945	135	319
Schuchmann 1999	102	328
Dickinson & Remsen 2013	105	338

Untangling the Emeralds

Even in the chaotic context of hummingbird taxonomy, the generic nomenclature among the Trochilini has produced an unusually tangled web. The generic classification of the emeralds has been complicated not only by the large number of species but also due to their overall morphological uniformity—the diversity of colors and patterns far exceeds structural diversity, thus making delimitation of genera difficult. Many genera have been defined and redefined, and many species have been shifted between genera in the successive classifications. Minor differences in spelling of some names have also occurred, making it unclear whether the authors really intended to describe new genera, emend existing names, or simply made careless spelling or typographical errors.

The overall morphological uniformity of the emeralds may in part reflect their restriction to the lowland tropics: few species extend far into the subtropics, and above elevations of ca. 2000m the emeralds are essentially replaced by members of other, older groups, especially those of the Lesbiinae (as defined by Dickinson & Remsen 2013), which also show a far greater range of morphologies (Stiles 2009). Emeralds are also limited to tropical and subtropical latitudes: no emerald species extends far into North America or into the higher latitudes of South America. Among the larger hummingbird clades, only the hermits (Phaethornithinae), which also are on the whole morphologically quite uniform (Stiles 2004, 2009), are as restricted to the lowland tropics as are the emeralds.

Some of the structural features used to define genera in the emeralds also have also been shown by gene-based studies to have limited phylogenetic value. For example, the expanded red base of the bill used by several authors to define the genus *Hylocharis* also occurs in adult males of several species placed in different sections of the gene tree. The expanded and flattened rachises of the outer primaries used by Schuchmann (1999) to lump several genera evidently evolved independently several times in distantly related genera. Certain colors or patterns (*e.g.*, white underparts, contrasting gorgets) are also clearly subject to homoplasy, as are some male sexual ornaments like colorful, long or deeply forked tails. To illustrate some of the problems bedeviling the classification of the emeralds, we have selected two especially complicated cases: the generic names *Amazilia* and *Leucippus*. We attempt to unravel the confusion by reviewing the history of these generic names and the type species involved with reference to the ICZN Code (1999), referring to the specific articles involved as "Art." with the corresponding numbers.

Case 1: Amazilia

Among the numerous generic names coined for members of the Trochilini in the 19th century, *Amazilia* has caused by far the greatest confusion due to different spellings, different type species, and different interpretations of its species composition. To help guide the reader through this confusion, we present a chronological history of *Amazilia* and related names (Table 3).

The story began with R. P. Lesson and P. Garnot's write-up of the "Zoologie" of the 1822–1825 around-theworld voyage of the French corvette "La Coquille", on which they served as the ship's physician and naturalists. This report was issued in 28 parts (livraisons), published piecemeal between 1826 and 1839; for the relevant dates we follow the detailed accounts by Zimmer (1926), Cretella (2010) and Dickinson et al. (2011). In the nominal first part (by Lesson alone, dated on the cover as 1826, although its actual publication date was April 1830), Lesson mentioned and briefly described a hummingbird collected at Callao, Peru, as the "Oiseau-mouche Amazili". However, in the fourth part (the "Atlas", which included the plates of putative new species and was issued in July 1827), Lesson and Garnot had already published a plate (plate 31, fig. 3) depicting this bird as the "OISEAU-MOUCHE AMAZILI-Orthorhynchus amazilia". This made the scientific name available (Art. 12.2.7); the original species epithet was amazilia and its authorship should therefore be credited to Lesson & Garnot, 1827. The actual formal description, by Lesson alone, appeared in April 1830, again as Orthorhynchus amazilia. For the dates and contents of Lesson's three major works on hummingbirds published between 1829 and 1833, we follow Dickinson et al. (2011). Confusion in spelling began when Lesson (1829) described the genus Ornismya, in which he included amazilia and illustrated it on plate 12 but with the epithet amazili, which must be considered an incorrect subsequent spelling (hereafter abbreviated ISS), without nomenclatural standing (Art. 33.3). In his review of the family, Lesson (1832b) included this species, again with the epithet *amazili*, and separated it along with three other species under the "Race Les Amazilis"; although used in a generic sense, this name was clearly formulated in the French vernacular and thus does not qualify as a formal generic name (Arts. 4, 11.4), although some subsequent authors including Gray (1855) referred to the "genus Amazilis Lesson".

Confusion in spelling continued when Gray (1840) described the genus *Amizilis*, as follows: "*Amizilis* Lesson: *A. latirostris* (Sw.), *n*. [= new combination], Ois.M. pl. 12, *O. amizili* Less". He evidently considered *latirostris* and *amizili* [sic] as conspecific and subsumed *amizili* under the older name *latirostris*. Although clearly an ISS, *Amizilis* was properly formed and is therefore a valid name (Art. 11.5). However, by specifically naming *latirostris* as the type, Gray (1840) made *Amizilis* a synonym of *Cynanthus* Swainson (1827a), and thus not applicable to *amazilia* (or indeed, *any* amazilian emerald). Lesson (1843) finally formally named the genus *Amazilia*, an action that most subsequent authors have considered the source of this generic name for the amazilian emeralds. However, Lesson

(1843) significantly did *not* include the species *amazilia* (in any spelling) in *Amazilia*, nor did he select a type species. That was left to Stone (1918), who chose the last of Lesson's included species, *cinnamomea* (Lesson, 1842), after the rest had been moved to different genera. Even then, *cinnamomea* had to be replaced by its junior synonym *rutila* DeLattre, 1843, after Cory (1918) found that *cinnamomea* was preoccupied in *Ornismya* by *cinnamomea* (Gervais, 1835). At this point, with *Amizilis* Gray, 1840 unavailable through synonymy, the species *amazilia* Lesson & Garnot, 1827 had been left without an applicable generic name (see below).

The next use of *Amazilia* was by Reichenbach (1850) in a general treatise on avian classification. In this work, he did not mention Lesson's prior use of this name, nor did he specifically mention *any* species in writing, but illustrated the genus with Lesson's (1829) plate 12 of *Ornismya amazili* (despite the fact that Lesson had not included this species in his *Amazilia*). In his later works (1854, 1855) Reichenbach included six species in his *Amazilia* but did not explicitly name a type species, which was finally designated as *amazili* [sic] by Elliot (1879). However, *Amazilia* Lesson, 1843 clearly has priority, and Reichenbach's name is thus a junior homonym. The next step was by Gray (1855), who formally named the genus *Amazilis* and selected *amazili* [sic] as its type. Although Gray ascribed the name to Lesson, as a correctly formed generic name it must be attributed to Gray. Therefore, we consider that the first valid and available generic name for the species *amazilia* Lesson & Garnot, 1827 is *Amazilis* Gray, 1855. However, we acknowledge that an alternative interpretation could regard Gray's *Amazilis* as an ISS or emendation of *Amizilis*, which could leave the species *amazilia* again requiring a new generic name. We do not favor this course, because a new name would only create more confusion; stability with current usage is better served by simply validating Gray's *Amazilis*.

We therefore conclude that *Amazilis* Gray, 1855 and *Amazilia* Lesson, 1843 are distinct and valid generic names with different type species: *amazilia* Lesson & Garnot, 1827 and *cinnamomea* Lesson, 1842 (= *rutila* De Lattre, 1843), respectively. Moreover, when *amazilia* and *rutila* are treated as congeneric, *Amazilia* Lesson, 1843 is senior to and takes precedence over *Amazilis* Gray, 1855, as does its type species *cinnamomea=rutila* over *amazilia* (Arts. 67.11, 69.2). Therefore, use of the binomen *Amazilia amazilia* as the type species of a narrowly construed *Amazilia* is incorrect. However, for the rest of the 19th century and as late as Simon (1921), various authors continued to combine Lesson's (1830) description of the type species with Reichenbach's (1850) *Amazilia* as its genus.

Nevertheless, Oberholser (1899) advocated reviving *Amizilis*, considering *amazili* [sic] as the "proper" type of *Amizilis* Gray 1840, but he failed to note the synonymy of *Amizilis* under *Cynanthus* while disallowing Reichenbach's *Amazilia* and Gray's (1855) *Amazilis* by priority, and this was followed by Ridgway (1911). Cory (1918) used Gray's (1855) *Amazilis* (as an emendation for *Amizilis* Gray, 1840) for the amazilian emeralds with *amazili* as its type, but he also apparently overlooked the seniority of Lesson's (1843) *Amazilia* with its type *cinnamomea=rutila*.

Through the 19th century confusion in spelling continued, with *Amizilis, Amazilis* and *Amazilia,* as well as further variants *Amazilius* Bonaparte, 1850a, *Amaziliia* Sclater & Salvin, 1859, *Amazilina* Eudes-Deslongchamps 1881, and *Amazilicus* Bangs, 1900 (all ISSs) being used more or less interchangeably by various authors, and with their type species being spelled as *amazilis, amazili* or *amizili* as well as in the correct form *amazilia*. Adding to the confusion, Gould (1857) described the species *pristina* [found to be a synonym of *amazilia* by Oberholser (1899)], and this name was also used as the type species of *Amazilia* during much of the 19th century, including by Elliot (1879) and Salvin (1892).

Peters (1945) rejected *Amizilis* as "not applicable", presumably because of its synonymy under *Cynanthus*, but (as was his custom) without stating his reason. However, he was correct in using a broad *Amazilia* Lesson, 1843 with *rutila* as its type, when he considered *amazilia* and *rutila* to be congeners (see above), and this was followed by Schuchmann (1999) (Table 3).

From the middle of the 19th century, three groups of hummingbirds came to be considered as assemblages of what could be called the "amazilian complex". The first to be formally named as a genus was *Saucerottia* Bonaparte, 1850b with its type species *saucerottei* (De Lattre & Bourcier, 1846) for a group of glittering-green species. The second was *Agyrtria* Reichenbach, 1854, described for a rather disparate group of more or less white-bellied species. However, as detailed below, the generic name *Agyrtria* is not applicable to *any* member of the Trochilini! The third group was *Polyerata* Heine, 1863, described with *amabilis* (Gould, 1851) as its only species and therefore its type by monotypy. This generic name came to be used for a number of green- to blue-breasted species that are more or less sexually dimorphic (Weller 2000).

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TABLE 3. The various spellings and definitions of the genus names related to *Amazilia* and their respective type species, as used in the more important classifications of the Remsen 2013). When an author cites a work by a date other than the actual date of publication, the cited date is in quotes and the correct publication date in parentheses the first time the work is given in this table. Trochilidae from the 19th century to the present 1. Symbols: †= first listing or formal description of a valid generic or species name; * = a currently valid name (Dickinson &

Author and date	Genus name and citation	Species name and citation	Commentaries
Lesson "1826" (=1830)	None given	"Oiseau-Mouche Amazili"	Not a Latin binomen nor an acceptable species name (French vernacular)
Lesson & Garnot, 1827	Orthorhynchus	amazilia†*	First Latin binomen, correct species name by priority
Lesson, 1830a	Orthorhynchus	amazilia	Lesson's formal species description
Lesson 1829	Ornismya†	amazili †(ISS)	This and all succeeding uses of this spelling (for <i>amazilia</i> Lesson & Garnot, 1827) are incorrect subsequent spellings, without nomenclatural standing
Lesson 1832b	"Race les Amazilis"	amazili	French vernacular; unacceptable as genus name
Gray, 1840	Amizilis "Lesson" (=Gray)†	amizili †(ISS), as latirostris	Valid genus name, correct author Gray; <i>latirostris</i> misidentified as the same species as <i>amizili</i> but by specifically naming <i>latirostris</i> as its type, made <i>Amizilis</i> a synonym of <i>Cynanthus</i> Swainson 1827a
Lesson, 1843	Amazilia†*	Not included (in Ornismya)	Valid genus name; includes cinnamomea Lesson, 1842
Reichenbach, "1849" 850)	Amazilia	amazili included	Junior homonym of <i>Amazilia</i> Lesson 1843, synonym of <i>Amizilis</i> Gray; illustrated genus with Lesson's (1832a) plate of <i>amazili</i>
Bonaparte, 1850a	Amazilius (ISS)	amazili Lesson "1826" (latirostris)	Incorrect citation of species name and date, repeated (in parentheses) Gray's misidentification of <i>latirostris</i>
Gray, 1855	Amazilis†	amazili (ISS) "Lesson 1829"	Genus name based on Lesson's unacceptable name, therefore the proper Latin name is by Gray; fixed type of <i>Amazilis</i> as <i>amazili</i> (= $amazilia$ Lesson & Garnot 1827)
Cabanis & Heine, 1860	Pyrrhophaena†	amazilia (not Lesson & Garnot 1827?)	Genus name syn. <i>Amizilis</i> , included species of both <i>Amazilia</i> and <i>Amizilis</i> ; did not cite Lesson & Garnot, 1827 for species epithet (therefore a junior homonym)
Gould 1861b	Amazilia Reichenbach, "1849"; Pyrrhphaena Cabanis & Heine, 1860	pristina †Gould, 1857	Cited Lesson, "1826", 1829 for <i>amazili</i> but used <i>pristina</i> (clearly a synonym) in <i>Amazilia</i> ; considered <i>Pyrrhophaena</i> a separate genus for <i>cinnamomea</i> Lesson 1842 and relatives; effectively a synonym of <i>Amazilia</i> Lesson, 1843
Mulsant & E. Verreaux 1874	Amazilia Reichenbach "1849"; Pyrrhophaena Cabanis & Heine 1860; Leucodora and Ariana Mulsant & Verreaux, 1866	No types mentioned	A chaotic mixture; included both <i>amazili</i> (under its synonym <i>lessoni</i> Mulsant & Verreaux) and <i>cinnamomea</i> in <i>Amazilia</i> ; <i>Pyrrhophaena</i> included species otherwise placed in <i>Saucerottia</i> or <i>Amizilis</i> ; <i>Leucodora</i> included the white-bellied <i>edward</i> and two others and <i>Ariana</i> included most species of <i>Saucerottia</i> plus <i>riefferi</i> , a relative of <i>cinnamomea</i> , now in <i>Amazilia</i> Lesson, 1843
Elliot 1879	Amazilia Reichenbach "1849"	pristina Gould 1861a	Followed Gould in use of <i>pristina</i> , despite citing Lesson's ("1826", 1829) earlier name <i>amazili</i> ; subsumed all of Mulsant & Verreaux's genera into <i>Amazilia</i> , which as used is a synonym of <i>Amizilis</i> Gray, 1840
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Author and date	Genus name and citation	Species name and citation	Commentaries
Salvin 1892	Amazilia Reichenbach "1849"	pristina Gould 1861	Followed the classification of Elliot (1879)
Boucard 1897	Amazilia Reichenbach "1849"	amazili Lesson "1826"	Restored <i>amazili</i> as the type species of <i>Amazilia</i> (= <i>Amazilis</i>) with <i>pristina</i> a synonym; subsumed <i>Saucerottia</i> into <i>Amazilia</i> as did Elliot and Salvin
Oberholser 1899	Amizilis Gray, 1840	<i>amazilia</i> Lesson, 1828(=1830)	Correctly concluded that <i>Amizilis</i> Gray, 1840 has priority over <i>Amazilia</i> Reichenbach "1849" as well as <i>Amazilia</i> Lesson, 1843 but failed to note that Gray's type species was <i>latirostris</i> , thus <i>Amizilis</i> is a synonym of <i>Cynanthus</i> Swainson, 1827; cited the type species as <i>Orthorhynchus amazilia</i> Lesson "1828", not Lesson & Garnot (1827)
Hartert 1900	Amazilia Reichenbach "1849"	amazilia Lesson, 1828(=1830)	Did not cite the earliest use of this epithet by Lesson & Garnot (1827)
Ridgway 1911	Amizilis Gray 1840	amazilia Lesson, 1828(=1830)	Followed the treatment of Oberholser (1899) using Amizilis
Cory 1918	Amazilis Gray "1840"	amazili Lesson 1829!	Considered <i>Amazilis</i> an emendation of <i>Amizilis</i> and its type as <i>amazili</i> Lesson, 1829, not Lesson & Garnot, 1827; noted that <i>cinnamomea</i> Lesson, 1842 was preoccupied and replaced it with <i>rutila</i> (De Lattre, 1843)
Stone 1918	Amazilia Lesson, 1843	rutila (De Lattre, 1843)	Fixed rutila as the type of Amazilia Lesson, 1843
Simon 1921	Amazilis Gray, 1840	"A. latirostris Sw. = O . amazili Lesson, 1829"	Dismissed <i>Amizilis</i> Gray, 1840 as a "lapso"; includes both <i>rutila</i> and <i>amazilia</i> Lesson 1828 (=1830) in text account) in <i>Amazilis</i>
Peters 1945	Amazilia Lesson, 1843	rutila (De Lattre, 1843)	Rejected <i>Amizilis</i> Gray, 1840 as "not applicable", presumably due to synonymy under <i>Cynanthus</i> ; did not mention Gray's <i>Amazilis</i> nor that Lesson's <i>Amazilia</i> did not include <i>amazilia</i> ; accepted preoccupation (in <i>Ornismya</i>) of <i>cinnamomea</i> Lesson 1842 by <i>cinnamomea</i> Gervais 1835
Schuchmann 1999	Amazilia Lesson, 1843	amazilia Lesson "1826"	Incorrect date of and authorship of <i>amazilia</i> Lesson & Garnot, 1827, and did not note that this species was not included in <i>Amazilia</i> Lesson, 1843
Dickinson & Remsen 2013 Amazilia Lesson, 1843	Amazilia Lesson, 1843	rutila (De Lattre, 1843)	Included all species in <i>Amazilia</i> including <i>amazilia</i> Lesson & Garnot, 1827 (correctly cited), correctly because this name has priority over <i>Amazilis</i> Gray, 1855, but stated that <i>Amazilia</i> almost certainly will require splitting into several genera
Not included in the table	are several short-lived subseque	ent ISSs of the genus name A	Not included in the table are several short-lived subsequent ISSs of the genus name Amazilia: e. g., Amazillia Sclater & Salvin, 1859, Amazillina Eudes-Deslongchamps,

1881, and Amizillis Bangs, 1900. See text for citations.

The Agyrtria confusion began when Bonaparte (1850a) described the genus Thaumatias [sic] and included as its type by tautonymy "Tr. thaumatias Linnaeus, 1766". However, he had misspelled both the genus and species names, and because this was demonstrably an error (a lapsus calami) for thaumantias Linnaeus, 1766, it therefore required correction (Art. 32.5.1). In fact, Bonaparte (1854) did make the correction to Thaumantias thaumantias, but by this time Reichenbach (1854) had not only corrected the misspelling but also had noted that the genus name Thaumantias Bonaparte was preoccupied by Thaumantias Eschschholz,1829 for a genus of coelenterates. Reichenbach (1854) explicitly named Agyrtria to replace Thaumantias Bonaparte, 1850a [such a name should be cited with the corrected spelling but with the original author and date (Art. 19.2)]. In such cases of name replacement, the type species of the original name is automatically the type species of the replacement name (Art. 67.8). Thus, the correct type species of both Thaumantias and Agyrtria is thaumantias Linnaeus, 1766. Cabanis & Heine (1860) placed the species thaumantias in the genus Polytmus Brisson, 1760, henceforth accepted; therefore, Thaumantias Bonaparte and Agyrtria Reichenbach are both objective junior synonyms of Polytmus Brisson, 1760 because all three share the same type species [thaumantias is now considered a subspecies of P. guainumbi (Pallas, 1764)].

Gould (1861a) revived Bonaparte's "Thaumatias" [sic] not realizing that it was only an original misspelling. Elliot (1879) compounded the confusion by correctly considering Thaumatias as unallowable but then citing Agyrtria as valid "by reason of priority", not noting that its type species also was thaumantias and thus that Agyrtria was also a synonym of Polytmus.

The synonymy of Agyrtria went unnoticed for half a century, until Chubb (1916) specifically noted it and proposed the genus Agyrtrina for the species included under Agyrtria, naming Uranomitra whitelyi Boucard, 1893, as the type species of Agyrtrina. Cory (1918) recognized Agyrtrina for whitelyi and its relatives, but most subsequent authors including Schuchmann (1999) have overlooked the synonymy of Agyrtria and used this name for varying circumscriptions of white-bellied amazilian species, sometimes including species of Leucippus as well (see below) and considering Agyrtrina as simply a synonym of Agyrtria. Bonaparte (1854) earlier had created the genus Cyanomyia for several white-bellied amazilian species but did not explicitly designate a type species, which was left to Elliot (1879), who named cyanocephala (Lesson, 1829) as its type. Nevertheless, later authors repeatedly shifted white-bellied species among Agyrtria, Amazilia, Cyanomyia, Uranomitra, Leucolia Mulsant et al., 1866 and Thaumatias.

During the 19th century, Elliot (1879) had named *Ornismya brevirostris* (Lesson, 1829) (the first species on Reichenbach's list, with the original locality stated as "Guiane") as the type species of Agyrtria Reichenbach, 1854. However, and in spite of such assumption of the type species being incorrect, the identity of brevirostris has been disputed. Gould (1861b) stated that as many as a third of Lesson's type localities had proved to be erroneous and that aside from its short bill, Lesson's plate of brevirostris was at least as applicable to the species Trochilus versicolor (Vieillot, 1818) from southeastern Brazil; he suggested that brevirostris might be best considered a synonym or subspecies of versicolor. Elliot (1879) considered brevirostris to be a valid species, but gave the type locality as Brazil. Salvin (1892), Boucard (1897), Hartert (1900), Simon & Hellmayr (1908), and Cory (1918) all considered brevirostris to be a subspecies of versicolor. Bangs & Penard (1918) disagreed and, based on a series of specimens from Paramaribo, Dutch Guiana, declared that brevirostris was identical to an immature specimen of this series and ascribed the name brevirostris to "the Guiana species", then known as chionopectus (Gould, 1859) from Trinidad. They described Agyrtrina brabournea Bangs & Penard, 1918 as the subspecies of versicolor occurring in Brazil, giving Simon & Hellmayr's suggested locality of Bahia as the type locality. Weller (2009) essentially agreed and also concluded that *chionopectus* is applicable as a subspecies of *brevirostris*, a conclusion still disputed by some Brazilian ornithologists (e.g., Grantsau 1988, 2010). Whatever the relationships of these species-group taxa, Agyrtrina is the potentially valid name for the genus that includes whitelyi and related species in the amazilian complex when these are separated from Amazilia (see above).

Over the years, *Agyrtria* (or *Agyrtrina*) had become something of a catchall for the white-bellied members of the amazilian complex as well as some species of the *Leucippus* group (see below and Table 4). In fact, Reichenbach (1854) had named several other taxa of more or less white-bellied hummingbirds (*Leucochloris*, *Lepidopyga*, *Uranomitra* and *Chalybura*) as subgenera of his *Agyrtria*; these were later ranked as separate genera by at least some authors.

Salvin (1892) recognized *Agyrtria* for several white-bellied species (but without indication of its type species) and placed others in *Cyanomyia*, Bonaparte, 1854 [type species *cyanocephala* (Lesson, 1829), fixed by Elliot

1879], including those Elliot had placed in *Uranomitra* Reichenbach, 1854 [type species *franciae* Reichenbach 1854 (Elliot, 1879)]. Salvin (1892) placed everything else in *Amazilia* [with *pristina* (Gould, 1857) cited as the type species], except for *boucardi* (Mulsant, 1877), which he placed in the monotypic genus *Arinia* Mulsant & E. Verreaux, 1877. Ridgway (1911) included all the Middle American species of "*Amazilia*" in *Amizilis* Gray, 1840, assuming that the type species was *amazilia* Lesson & Garnot (see above), but he also recognized *Saucerottia*. However, Cory (1918) recognized *Agyrtrina*, *Polyerata*, *Uranomitra*, and *Saucerottia* as genera separate from *Amazilis* Gray.

We note here that the description of *boucardi* in the genus *Arinia* is also anomalous: the date usually given is "Mulsant, 1877", based on a paper read in that year by Mulsant at a meeting of the Societé Linnéene de Lyon, but the text of this presentation apparently was never published (*fide* Salvin 1892, Simon 1921, Peters 1935). However, a complete description of *Arena boucardi*, authored by Mulsant alone, appears on p.194 of volume 4 (1877) of Mulsant & E. Verreaux, and the name *Arinia boucardi* appears on plate 18 of a set of supplementary plates (undated) although apparently to have been added to Vol. 4. Simon (1921) adverted that both of these generic names were preoccupied, and described the genus *Arenella* for *boucardi*, although both Cory (1918) and Ridgway (1911) had in the interim placed *boucardi* in *Lepidopyga* Reichenbach, 1854. Unfortunately, no genetic sample of *boucardi* was available to McGuire *et al.* (2014), so its final placement remains unresolved, along with that of "*Thaumatias*" *luciae* (Lawrence 1867), considered by Schuchmann (1999) to form a superspecies with *boucardi*.

Simon (1921) recognized the genera *Saucerottia, Agyrtria, Uranomitra, Amazilis* [as spelled by Gray (1855)], *Damophila* (but not in its current circumscription), and *Arenella*. Simon (1921) also described two new genera, *Chionomesa* with *lactea* (Lesson, 1832a) as its first species, and *Hypochionis* with *cyanocephala* (Lesson, 1829), as its first species, but did not explicitly name either of these as the respective type species. He placed these, along with six other genera (including *Leucippus* and related genera and *Polytmus*) in his "*Agyrtria* group". Peters (1945) included the entire complex in *Amazilia* Lesson, 1843 with *rutila* as the type (see above) and with *Saucerottia* as a subgenus, along with *Polyerata* Heine, 1863 (in which he subsumed most of *Agyrtria*) with the rest of the species, including *amazilia*, in the subgenus *Amazilia*. Dickinson & Remsen (2013) also subsumed all of the amazilian species in *Amazilia* but without subgenera; they remarked that this genus was almost certainly polyphyletic but declined to divide it for lack of a more complete phylogeny.

Weller (2000 and unpubl. data) was the first to seriously take issue with the Peters treatment and proceeded to dismember *Amazilia*, basically along the lines of the three major groups noted above. Weller's treatment was the basis for Schuchmann's (1999) classification. The phylogeny of McGuire *et al.* (2014) showed that Weller was on the right track in splitting up *Amazilia*, but that he was misled in a number of cases by plumage homoplasies. He also underestimated the degree of polyphyly involved: members of Peters's *Amazilia* are split among no less than eight distinct subgroups of differing degrees of relatedness in the phylogeny! Providing generic allocations for these will be a major part of our attempt to bring the classification of the emeralds into congruence with the phylogeny of McGuire *et al.* (2014).

Case 2: Leucippus

Leucippus is another generic name among the emeralds with a notably tangled history. The genus was described by Bonaparte (1850a), who included two species, fallax (Bourcier, 1843) and turneri (Bourcier 1846). In 1855 Gray fixed the type species as fallax. However, in the interim Bonaparte (1854) had described the genus Doleromya, with its only species (and thus, its type) as fallax! Gray's action therefore made Doleromya an objective junior synonym of Leucippus, because the senior genus takes precedence (Arts.67.11, 69.2). However, because Bonaparte had described Doleromya before Gray fixed fallax as the type of Leucippus, Elliot (1879), Salvin (1892), Boucard (1897) and Simon (1921) all evidently concluded that the typification of fallax should be restricted to Doleromya, and they continued to recognize it as a genus distinct from Leucippus, although Salvin (1892) emended the spelling to Doleromyia without explanation.

Because *Trochilus turneri* is a synonym of *Trochilus chionogaster* (Tschudi, 1845), Elliot (1879) named *chionogaster* the type species of *Leucippus*. Salvin (1892), Boucard (1897) and Simon (1921) followed Elliot (1879) in considering *chionogaster* as the type of *Leucippus*, in which they also included several other white-bellied taxa (see Table 4). Simon (1901) described the species *baeri* in *Leucippus*, but later (1921) included it in

Doleromyia (Salvin's spelling). Most subsequent authors have returned baeri to Leucippus. Cory (1918), Peters (1945) and Schuchmann (1999) correctly did not accept Bonaparte's Doleromya, and they treated it as a synonym of Leucippus with fallax as its type, as fixed by Gray. However, the phylogeny of McGuire et al. (2014) clearly segregates Leucippus fallax from the rest of Leucippus in a monotypic genus, and this leaves at least the species chionogaster and viridicauda Berlepsch 1883) without a generic name because none has been described specifically for them. We are unable to find the basis for Schuchmann's (1999) statement that these species had been "often included in Chionogaster in the past", nor indeed any citation of "Chionogaster" being formally described as a generic name in Zoonomen (2007) or in the synonymies of any of the works consulted.

Concurrently, Mulsant & E. Verreaux (1874) had created the genus Talaphorus for chlorocercus (Gould, 1866); Elliot (1879) and Salvin (1892) included chlorocercus in Leucippus, but Cory (1918) separated it in Talaphorus. Sclater (1879) created Thaumasius for his new species taczanowskii, but Salvin (1892) included this species in Agyrtria. Elliot (1879) did not mention taczanowskii, presumably because its publication occurred too late for inclusion. Chubb (1916) rejected *Thaumasius* on the grounds that it was preoccupied by the spider genus Thaumasia Perty, 1833, and he proposed the substitute name Brabournea, with taczanowskii as its type. However, because a one-letter difference in generic names is sufficient to avoid homonymy (Art. 56.2), Chubb's action was unnecessary. Cory (1918) used *Thaumasius* for taczanowskii, with Brabournea Chubb, 1916 cited as a synonym. Gould (1853) described the genus Aphantochroa with cirrochloris (Vieillot, 1818) as its type by monotypy, and later also placed hypostictus (Gould, 1862) in Aphantochroa, which was followed by both Elliot and Salvin. Simon (1897) described the genus *Taphrospilus* with *hypostictus* its type by monotypy, but in 1918 he emended this to Taphropsilus, citing the original spelling as a "lapsus". Simon (1921) again emended the spelling to Tephropsilus without explanation, but both of Simon's subsequent spellings are best considered ISSs. Cory (1918) included hypostictus in Taphrospilus, but Peters (1945) also included in this genus taczanowskii and chlorocercus. Both Cory (1918) and Peters (1945) retained baeri in Leucippus. Zimmer (1950) included in Leucippus the species baeri, fallax, chlorocercus and taczanowskii, but transferred chionogaster and viridicauda to Amazilia, citing plumage similarities to candida and chionopectus of that genus. Meyer de Schauensee (1966) followed this arrangement, except that he recognized Taphrospilus for hypostictus. Finally, Schuchmann (1999) rejected these arrangements and subsumed all of the preceding species in Leucippus and stated that "Polytmus shares close affinities with Leucippus and Leucochloris", an arrangement strongly refuted by the phylogeny of McGuire et al. (2007, 2014). Dickinson & Remsen (2013) followed the treatment by Meyer de Schauensee (1966), retaining chionogaster and viridicauda in Amazilia and hypostictus in Taphrospilus, with the other species in Leucippus.

To summarize, the generic name *Leucippus* has had an extraordinary variety of circumscriptions since its description, with practically no two authors including in it the same groups of species (Table 4). The inconsistencies between these various treatments of the "white-bellied" emeralds clearly indicate that this type of coloration is subject to widespread homoplasy and is therefore of highly questionable phylogenetic relevance. Thus, the fate and circumscription of *Leucippus* and other "white-bellied" taxa represents another major problem to be resolved in reconciling the classification of the emeralds with their phylogeny.

Conclusion

Clearly the current generic taxonomy of the hummingbirds, particularly of the Trochilini, is inconsistent with recent studies of their phylogeny (McGuire *et al.*2007, 2014). It is also evident that the goals of preserving diagnosability and existing nomenclature in the interests of stability while producing a phylogenetically meaningful classification are to a considerable extent incompatible. We are presenting a revision (Stiles, Remsen & McGuire, submitted) of the genera and species of emeralds, in which we attempt to bring the classification and nomenclature into accord with their phylogeny. The present paper provides the historical background and nomenclatural detail for understanding the problems in generic nomenclature awaiting resolution.

Taxa	fallax Bourcier	chionogaster Tschudi 1845	hypostictus Gould	chlorocercus Gould 1866	viridicauda Berlensch 1883	taczanowskii Sclater 1879	baeri Simon 1901
Authors, dates		(turneri syn.)					
Reichenbach 1855	Leucippus	Leucippus (as	pu	pu	pu	pu	pu
Gould 1861	Dolerisca (=	Leucippus	pu	pu	pu	pu	pu
Elliot 1879	Doleromya) Doleromya	Leucippus	Aphantochroa	Leucippus	pu	pu	pu
Salvin 1892	Doleromyia	Leucippus	Aphantochroa	Leucippus	Leucippus	Agyrtria	pu
Boucard 1897	Doleromya	Leucippus	Xanthogenyx	Leucippus	Leucippus	Uranomitra	pu
Hartert 1900	Leucippus	Leucippus (as leucogaster)	Talaphorus	Talaphorus	Leucippus	Talaphorus	pu
Cory 1918	Leucippus	Leucippus	Taphrospilus	Talaphorus	Leucippus	Thaumasius	Leucippus
Simon 1921	Doleromyia	Leucippus	Tephropsilus ISS	Tephrospilus	Leucippus	Tephropsilus	Doleromya
Peters 1945	Leucippus	Leucippus	Talaphorus	Talaphorus	Talaphorus	Leucippus	Leucippus
Meyer de Schauensee 1966	Leucippus	Amazilia	Taphrospilus	Leucippus	Amazilia	Leucippus	Leucippus
Schuchmann 1999	Leucippus	Leucippus	Leucippus	Leucippus	Leucippus	Leucippus	Leucippus
Dickinson & Remsen 2013	Leucippus	Amazilia	Taphrospilus	Leucippus	Amazilia	Leucippus	Leucippus

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