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ON RESEARCH AND ENTOMOLOGICAL EDUCATION VI: FIREFLY SPECIES AND LISTS, OLD AND NOW

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ABSTRACT

Lists of insect species are useful for insect biologists and students in several fields, including taxonomy, behavioral ecology, conservation, and biological control, and they are useful to the teacher of classical entomology for the insight and drama they can provide to the history and biography of our science. Such lists can be viewed as cooperative projects that have combined the efforts and enthusiasms of naturalist/taxonomists along a time line, and as they evolve they can become ever better guides to observation and identification, and to new and interesting biotaxonomic problems. The list of NA fireflies recorded here gives the number and continental location of working species now recognized after long study of this taxon at the bench, in the library, and afield by many naturalists and taxonomists across more than two centuries, and makes status changes in a few species.

Key Words: Lampyridae, fireflies, fauna, checklist, species problems, teaching

RESUMEN

Las listas de especies de insectos son útiles para los biólogos y estudiantes de insectos en varios campos, incluyendo la taxonomía, la ecologia de comportamiento, la conservación, y el control biológico, y son útiles para los maestros de entomologia clásica para la comprensión y el drama ellas que pueden proveer a la historia y la biografía de nuestra ciencia. Tales listas pueden ser vistas como proyectos cooperativos que han combinados los esfuerzos y el entusiasmo de los naturalistas/taxónomos por toda una linea de tiempo, y mientras que ellos sean se desarrollados pueden convertirse en mejores guias para la observación e identificación y para los problemas nuevos e interesantes biotaxonómicos. La lista de luciérnagas de NA registrada aqui dá el número y la ubicación continental de especies ahora reconocidas después de un largo estudio de este taxón en el laboratorio, en la biblioteca, y en el campo por muchas naturalistas y taxónomos a travéz de más de dos siglos, y hace cambios en el estatus en algunas especies.

Ambiguous Firefly

A lightningbug flashes o'er wet meadows,
short-long,
No taxonomist 'til Barber ever noted its song;
Oh Firefly,
Did you before Barber to a species belong,
Or, is it really no matter, for
Lists can . . . not be wrong?

After forty years of pursuing firefly species via biotaxonomy using a "semiosystematic" approach (Lloyd 1969, 1990a), I ask whether it has been a fool's mission—"an unexamined life is not worth living." I knew at the outset that the chase was to be neither occupation nor career, but preoccupation and life, common among insect naturalist/taxonomists in a Camelot once upon a time. Discussions with teachers and mentors about black and sugar maples and the intermediates of these named species that range from wet bottoms to dry uplands in Michigan's hardwood forests; about virtually identical field crickets with different names in Bermuda and Florida; and about periodical cicadas across eastern U.S. with the same names but separated in time and space, all seemed to the student to reveal unfathomable taxonomic and genetic mysteries or nomenclatural anomalies. These examples with those emerging from the chase, juxtaposed and contrasted with the relative simplicity and undeniable genetic imperative, the *sine qua non* of Biological Species found in taxonomic textbooks, have encouraged uncertainty and repeated reevaluation of almost every taxonomic conclusion I have been tempted to draw about fireflies (Lloyd 2001).

While chasing in the dark I learned signals and seasonality, interactions and distributions, and watched then hand-collected (only one at a time) thousands of voucher specimens which I killed and saved, each co-referenced with verbal and sometimes electronic records of signaling behavior. This was the best of lives! And the worst of it—or was this somehow the best too?—was that the more I learned from watching fireflies flashing, the less confidence I had in my understanding of species, of what should be named and put on lists. My appreciation of *Acer*, *Gryllus*, and *Magicidada* taxonomists grew, and textbook discussions of species and speciation, driven mainly

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by vertebrate mega-models perhaps, seemed largely irrelevant for their authors mostly dwelled at grander scale.

For students who pursue the nature and origin of species while wading through literal and literature sloughs I suggest a stress-relieving addition to the Species Concept list of Mayden (1997), a perspective that I withheld last time (2001). This can help them find more appreciation for old and seemingly useless lists of species, and place their own studies in a time line of uncertain termination and perhaps infinite length. A *Transcendental Species Concept* suits my present comprehension (apprehension too) of many fireflies, and those of the genus *Photuris* in particular. It may comfort and reassure thoughtful neophyte biotaxonomists as they increasingly come to grips with: (1) the array of diversity found among "conspecific" local populations (or should I say an unexpected number of very localized "species" in the field?); (2) the seeming unreasonability and maybe even theoretical improbability of any connection and genetic cohesion among "conspecific" demes of many of them; and (3) our inadequacy to ever gain all of the information, especially the imponderables of genetics, needed to understand them and in particular, their deme histories and origins.

From handy desk and forgotten references I retrieve fragments of thoughts and phrases about things transcendent and transcendental that encourage this suggestion: . . . ideas beyond the range of experience . . . elements of experience but not from sense-perception . . . extending or lying beyond the limits of ordinary experience . . . beyond comprehension . . . we may discover many facts and learn many details but there are some things we can never truly know . . . beyond human experience but not human knowledge . . . relating to experience as determined by the mind's makeup. . . . I can also suggest this axiom, a mnemonic aphorism paraphrased from the late Mayor Richard Daley (Sr.) of Chicago, though the Mayor was speaking of politics—"All firefly biospecies are local."

In seeming contradiction, such apparent metaphysical sophistication does not cool my interest in species lists, and serves here as prelude and predicate for mentioning some old favorites, and making a new one, already looking toward next time. Entities that historically have been named and listed as species can be understood as bookmarks that taxonomists have worked up to, have reached in their reading of nature. This is because taxon recognition and the characters examined and ultimately valued up and down the hierarchy from Species (or should I start with Subspecies?) to Order have changed, intermingled, and synergized over time (Wilson & Doner 1937; Table 1), just as taxonomy's concepts, preconceptions, and preconditions for taxa have.

TABLE 1. SYSTEMS OF CLASSIFICATION THROUGH HISTORY, AFTER WILSON AND DONER (1937). THE EARLIEST MENTIONED DATES AND AUTHORS ARE SHOWN. SYSTEMS AND/OR CHARACTERS FROM THEM HAVE BEEN DISCUSSED, WINNOWED, DEVELOPED, COMBINED, AND REFINED OVER DECADES, AND CENTURIES. SOME IDEAS HAVE SEEMINGLY DISAPPEARED AS SUCH (CIRCULAR CLASSIFICATION), BUT ONE CONCEPT HAS REPLACED ALL OTHERS AS THE CENTRAL THEME AND SCAFFOLD OF BIOLOGICAL CLASSIFICATION, AND CHARACTERS FROM OTHER SYSTEMS ARE INTERPRETED ONLY THROUGH IT—PHYLOGENETICS—WHICH APPEARED SOON AFTER DARWIN'S "ORIGIN." NAMES AND DATES IN THIS TABLE ARE NOT NECESSARILY THOSE OF THE MOST IMPORTANT OR THOUGHTFUL CONTRIBUTIONS.

Insect Classification Through History

Systems and Characters	Author	Date
Alary/Wing Systems	<Aristotle	350 BC
Media Inhabited/Locomotion \Systems	Agricola	1548
Habitat/Locality Systems	Aldrovandus	1602
Metamorphic/Transformation \Systems	Swammerdam	1669
Cibarian/Maxillary Systems	Fabricius	1775
Philosophical System	Oken	1810
Use of Embryological \Characters	Home	1814
Circular Systems	Lamarck	1815
Classification From Cephali-\zation Principle	Dana	1852
Phylogenetic Systems	Haeckel	1866
Classification Via Pupal \Characters	Cooke	1882
Classification Via Thorax \Characters	Schoch	1884
Classification Via Segmentation \Characters	Prell	1912

Who cannot appreciate the fact that the species-level taxonomy of North American fireflies has evolved? It has tried and today retains and combines useful elements from external anatomy, genitalic structure, and flash pattern form and variation, accomplishing this under the guidance of lampyrid luminaries such as J. L. LeConte (>mid 1800s), F. A. McDermott and H. S. Barber (early and mid 1900s), and J. W. Green (mid 1900s). Who cannot predict that it will continue to evolve as (1) field-savvy molecular biologists translate and understand the texts, both words and syntax, and the enigmatic operations of DNA strands (K. Stanger-Hall, in prog.; M. Branham, in prog.); and (2) behavioral ecologists scrutinize the influence of signal-tracking predators (e.g., *Photuris* females) on the signal-codes cum countermeasures of their firefly prey, and sexual selection's guidance of mating behavior and repro-

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ductive morphology (Lloyd 1979ab, 1981, 1984, 1990a; Lloyd & Wing 1983; Wing 1985, 1991, et al. 1983; Lewis & Monchamp 1994)—and in particular, the variations of these in time and space?

Species on lists are beginnings and steps, but never, in our time or in any foreseeable future, the ends of biotaxonomic discernment and discrimination. Taking the remarkable *Photinus* and *Pyractomena* revisions of Green (1956, 1957) as examples, each provided an insightful and solid morphological foundation from which to pursue biospecies. Many of Green's carefully considered omnispective species (Blackwelder 1967; Mayden 1997; Lloyd 2001) are already known to be focal points of biotaxonomy's species "complexes"—isn't "fuzzy clans" more accurate and descriptive? I view species lists past and passed as mile posts, even commemorative cornerstones of taxonomic accomplishment, and a foundation for biotaxonomists and allies today as they seek and track life's more cryptic paths to diversity.

I like old species lists that include forgotten localities and other lore. I especially like old lists that tell things about comrades-in-pins who made or collected for them, who often chased insects as a way of life, and the times when they lived. The labels on two firefly specimens in the Museum of Comparative Zoology at Harvard say "Belfrage Texas" (Lloyd 1968). I couldn't find Belfrage on any Texas map or in any Gazetteer (though it should have been). Then, Prof. Irving Cantrall, himself virtually part of the collection at Ann Arbor who worked daily to put the archived orthops in good order, and a walking repository of such information, told me that Gustaf Belfrage collected and sent specimens to several museums in America and Europe, and "Irv" recommended "Naturalists On the Frontier" by Geiser (1937). Geiser's book told the tale of this Swedish nobleman who spent the last 15 years of his life collecting insects in Texas, beginning about 1867. Though his specimens were in museums from Washington to St. Petersburg, Russia, the inventory of his Texas estate was "almost indecent in its revelation of stark poverty" (Table 2). Nevertheless, on one occasion he purchased his first two glowworms (lampyrid beetle larvae) for the exorbitant price of 5 dollars (cf Table 2), out of delight in them, and later sold them for much less (Geiser 1937:304).

The hardships and hazards some travelers endured to make collections went far beyond what we encounter today—except for rare individuals such as the late Joseph Anderson, a prospective student who died not long ago of malaria while collecting fireflies in Africa—though I personally know of several scientists on one well-endowed tropical expedition who, with considerable success, "deliberately" exposed themselves to this malady by sleeping in native huts to sample fully the flavour of their exotic excursion. Who cannot be interested and smile when reading the travels of the 19th century naturalist who feigned dementia for protection from scalping abuse by residents, who even helped him to the regional trading post!; or feel the anguish when reading of the sinking of a sailing ship with the long-nurtured and carefully protected collections of an entomological or botanical adventurer's travels?; or know the grief of a father whose son died of yellow fever in the New World, mayhaps after sending

TABLE 2. THE INVENTORY AND ESTATE OF GUSTAV BELFRAGE FROM HIS RUSTIC CABIN IN CENTRAL TEXAS, CA. 1884. HE WAS A 19TH CENTURY INSECT COLLECTOR LIVING THE SIMPLE BUT NOT EASY LIFE. HIS LAST NAME APPEARS ON THE LABELS OF MANY ARCHIVED SPECIMENS AND CAN EASILY BE MISTAKEN FOR A LOCALITY—AND . . . WITH INFORMATION PROVIDED BY HIS BIOGRAPHER, INDEED IT ALMOST IS.

Estate of Gustaf W. Belfrage		
1	Gallon Can	15
2	wash basins	15
2	coffee pots and 2 frying pans	25
2	shoe brushes, 5c 1 can of Cynali of \Potassium	10
1	clock	1.00
1	looking glass	25
1	bed quilt	75
1	sheet and piece of ducking	25
1	pr of gloves	40
1	light summer coat	45
1	Jeanes coat	25
1	Linen coat	25
1	pr of pants	25
1	table cloth (oil)	25
1	Razor	40
7	shirt collars and 2 boxes blackening	40
1	Flannell Undershirt	35
2	handkerchief 2 scarfs	25
1	woolen scarf	30
1	pr old slippers 1 old straw hat	25
1	sofa	5.00
1	straw mattress and cotton pillar [pillow]	35
1	work table	15
1	stove and drum	5.00
4	cane bottomed chairs	3.00
2	cotton towels	05
1	frying pan	25
194	bound and unbound books, pamphlets: nearly all works and treatises on subjects relating to Zoology	35.00
36881	pinned insect specimens. Also coleoptera in papers, sawdust, and in alcohol, some lepidoptera in papers and pinned on the stretch board, several boxes of insects more or less damaged	368.00
1	box empty bottles	25
1	students Kerosine lamp	1.00
1	value [bale?] manuscript no value	—
1	bottle of ink 1 bottle of perfume	40
1	dozen Faber lead pencils	20
1	box and lot of empty bottles	50
1	home building (no lot or land)	50.00
TOTAL VALUE SET AT		$491.40

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him now-acclaimed specimens, three of which that became the syntypes of Fabricius' *Photuris versicolor* (Fig. 1)?

In the spirit of these FES firefly Letters (1998-2001), species lists are a passport to take students to classical insect taxonomy with the promise of personal adventure, and they can provide role models of persistence and endurance, and lifelong fulfillment—(see Osborn 1937; Peattie 1936; Geiser 1937; Mallis 1971; R. F. Smith et. al. 1973; Kastner 1977; Elman 1982; Porter 1986; Sorensen 1995)—and show that there was life before and it will and must be better after NSF, as well as encourage a spirituality and pride, and expectation that seems lacking in many academic institutions and curricula (Bennett 2001-02).

Letter 41
Regional and Other Lists Of Fireflies—More Than Passenger Lists For Arks

The hours I spent with thee, dear heart,
Are as a string of pearls to me;
I count them over, every one apart,
My Rosary.

(Robert Cameron Rogers)

Dear Fireflyers, Listing the names of insect species that occur in a region is more than an esoteric ritual of taxonomic entomologists, and such lists are more than scorecards for life-list hobbyists or doomsday records for suspicious environmentalists. In insect taxonomy species listing is as fundamental as naming species, and listing can contribute to understanding the biological, geological, and even the cultural history of a region. Species lists are as marked stepping places into a murky bayou, at first tentative and insecurely grounded, but they provide guidance and footing for further exploration, and welcome information for naturalist/taxonomists who will follow. As species lists evolve they can become annotated catalogues, with references to taxonomic histories, and eventually provide details for finding and recognizing each entered entity, with notes on their biology, and more.

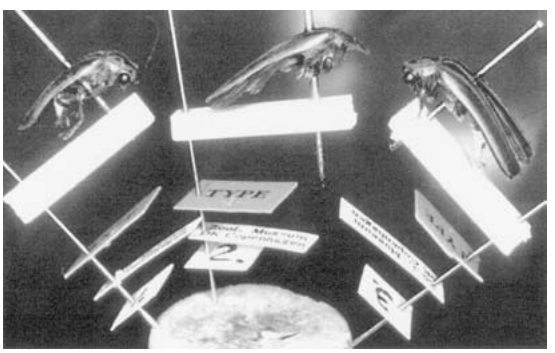


Fig. 1. The three syntypes of Fabricius' *Lampyris* (now *Photuris*) *versicolor*, perhaps sent to "Dom. Herschel" in Europe by his son, thence given to Fabricius (but see Madge 1994).

History and Overview. Over the past centuries there have been several lists with fireflies of North America. In the 1800s fireflies were included in lists of beetles found during scouting expeditions to the west by the U.S. Army, and nearly a century later the "Leng catalogue" listed all of the described species of beetles known to occur in North America north of Mexico. Leng numbered each species for easy reference (Table 3), an optimistic flourish that had been used before. In 1885 Samuel Henshaw had used different numbers in his list for the same domain—unlike scientific names, older assigned numbers for each species do not have official and compelling seniority, "priority" as it is called in taxonomy. (Leng remembered, and dedicated his list to Henshaw.)

Some lists were exclusively of fireflies and others included fireflies as but one of many families. There were lists of Lampyridae when the family included leatherwings now classified as net-winged beetles (Lycidae), giant glowworm beetles (Phengodidae), soldier beetles (Cantharidae), and Omethidae (*Matheteus*, *Ginglymocladus*) (LeConte & Horn 1883)—and some we now don't know where to classify (*Pterotus*, Branham & Wentzel 2001). One "list" was an encyclopedic 1386 page treatment of the Coleoptera of Indiana, which the author referred to as a "paper" (Blatchley 1910; Fig. 2)! This opus is a model to which any taxonomist/naturalist worthy of brass-headed, stainless-steel, German-made insect pins should aspire. It has within-state distributions, habitat notes, keys, and sketches for identification. As explanation for his monumental work Willis Blatchley wrote (:3):

> "Happiest those days in which I have wandered far and wide through field and woodland, adding here and there some specimen before unseen, noting now and again some life habit, some food plant or place of retreat, before unobserved. Ever and always, however, have I felt the need of some one work to which I could refer, some manual or descriptive list by which I could locate the name and place [i.e., relationships] of the specimens at hand. Since the beetles or Coleoptera form one of the most abundant and attractive groups of insects and are easily collected and preserved, they would furnish a favorite subject for study, especially in high schools, could they only be named and placed."

Lists sometimes had an appendix with the names and "nicknames" of habitual and favorite collecting localities in the region (Table 4). These

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TABLE 3. EXTRACTS FROM THE FIREFLY LISTING IN THE ORIGINAL LENG 1920 CATALOGUE OF NORTH AMERICAN BEETLES, A MAJOR AND EXTREMELY AMBITIOUS COMPILATION IN WHICH EACH SPECIES WAS GIVEN ITS OWN NUMBER. FORMATTING SIMULATES THAT OF LENG AND HIS (PRESUMPTIVE) ERRORS ARE KEPT. THE INDICATED HAND-CORRECTIONS WERE PRESUMABLY PENNED BY THE PREVIOUS OWNER OF MY COPY, FRANK MCDERMOTT. NOTE: SPECIES NUMBERS AT THE LEFT, HYPHENATED REFERENCE NUMBERS (DATE-PAGE), AND GEOGRAPHIC DISTRIBUTIONS; UNNUMBERED SPECIES EPITHETS ARE (A) PRESUMPTIVE SYNONYMS OF THE NUMBERED EPITHET IMMEDIATELY ABOVE, OR (B) NAMES PROPOSED BY ONE AUTHOR BUT DISPUTED BY ANOTHER. THE DOUBLE VERTICAL LINE SYMBOL UNDER 6988 INDICATES THAT "VITTIGER" WAS SYNONOMIZED BECAUSE THE NAME WAS "PREOCCUPIED," AND SINGLE RIGHT-FACING BRACKETS ([) BEFORE LOCALITIES INDICATE THAT THEY BELONG TO THE LINE ABOVE; "L. SUP." IS THE LAKE SUPERIOR REGION (PAGE VII), PROBABLY FROM A MUCH EARLIER AND WELL-KNOWN EXPEDITION THERE BY LECONTE AND OTHERS (AGASSIZ 1850).

Lampyridæ	
E. Olivier [19]10	
Photinini	
Pyractomena ~~Lec. 50-228~~ *Melsh. 45* (Lecontea E. Oliv. 99-371)	
6984. angulata (Say) 25-162)	Fla. Can. Mass.
flavocincta (Lec.) 51-336	[Ill. Ga. Ind.
85. borealis (Rand.) 38-16	Me.-Mont. Ind.
86. ecostata (Lec.) 78-406	Fla. N.J.
nitidiventris (Lec.) 78-406	
87. lucifera (Melsh.) 46-304	Mass. Pa. Tex. Ind.
linearis (Lec.) 51-336	Mich. Ga. Fla.
angustata (Lec.) 51-336	
punctiventris (Lec.) 78-407	
Photinus Lac. 57-321 (Pyrectosoma Mots. 52-38)	
6988. consanguineus Lec. 51-335	Mass. Pa. Va.
vittiger ‖ Lec. 51-336	[Ga. Fla. Ind.
zonatus Gemm. 70-120	
89. lineellus Lec. 51-335	Ga. Fla.
90. ardens Lec. 51-334	Mass. L. Sup.
obscurellus Lec. 51-335	[Kan. Ind.
taedifer Lec. 51-334	
6991. punctulatus Lec. 51-335	Ill. Kan.
92. umbratus Lec. 78-407	Fla.
93. dimissus Lec. 81-35	Tex.
94. collustrans Lec. 78-407	Fla. Tex.
Photurini	
Photuris Lec. 59-86	
7013. pennsylvanica (DeG.) 74-52	N.Y. Fla. Kan. Ind.
versicolor (Fab.) 98-123	Conn. Mich.
marginata (Panz.) 89-31	Bahamas
lineaticollis ~~(Mots.) 54-59~~ *Lec 51-337*	
vitigera (Mots.) 54-60	
7014. frontalis Lec. 51-337	Ga. Fla. Tex.
15. divisa Lec. 51-337	Kan.
congener Lec. 51-338	



Fig. 2. A portrait of Willis Blatchley at age 45, in 1904. There are several extant photographs of this naturalist/taxonomist in action, camping, panning for gold, and picking insects out of a beating umbrella, but the one most often seen, unfortunately, is from much later in his life and lacks the dynamism and strength of his personality. This photo is from his "Blatchleyana" of 1930.

are useful even today when the labels of old but especially valuable archived specimens bear obscure localities. A student might wish to determine whether a listed rare species yet survives, and if so, say, whether DNA texts or other chemicals in the dried, detached legs of museum specimens match those in legs found hopping and climbing there today. There is a dictionary of "American Place-names" (Stewart 1970), and an entomologically-focused taxonomic list with unknown places found on specimen labels (Townes & Linna 1963).

Frederich E. Melsheimer's 1853 list is one of the older for North America; in 1806 his father's had published a catalogue of Pennsylvania insects. Their personal collection is preserved at Harvard and has special value for us in our efforts to make lampyrid nomenclature as error-free as possible. Here's why: though Thomas Say's "type" (name-vouchering) specimen of *Pyractomena angulata* (Say) is lost—some say it was recycled into carpet beetles—Say corresponded with both F. E. Melsheimer and his father Frederich V., and Say may have examined and compared his *P. angulata* specimen with the Melsheimers'. Thus we have

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TABLE 4. A SELECTION OF QUAINT, PERHAPS FORGOTTEN AND OFTEN AGGRAVATING (TO A HURRY-UP WORKER) COLLECTING LOCALITIES THAT APPEAR ON ARCHIVED INSECT SPECIMENS, FROM VARIOUS SOURCES. SEVERAL "LOST" ONES LISTED IN TOWNES AND LINNA (1963) HAVE BEEN FOUND BY FIREFLYER STUDENTS FOR THEIR LAB REPORTS VIA INTERNET REFERENCES. AN ASTERISK INDICATES THOSE THAT TOWNES AND LINNA LOCATED; A ‡ INDICATES COLLECTING LOCALITIES OF FIREFLYER H. S. BARBER NEAR WASHINGTON DC.—IT MUST BE NOTED THAT EVEN MODERN LISTS AND SPECIES DESCRIPTIONS TODAY MUST SOMETIMES BE MADE VAGUE OR ENCRYPTED WITH RESPECT TO LOCALITY BECAUSE SUBSEQUENT COLLECTORS HAVE BEEN KNOWN TO TOTALLY ERADICATE LOCAL POPULATIONS OF PRIZED AND POPULAR GROUPS, FOR COMMERCE.

Beckoning Localities On Specimen Labels	
Antelope Mt. OR	Hobon Lake OR
Aqua Viva NM	Hogs Delight FL
Atila BC	Indian Ladder NY
Baiting Hollow NY*	Mill Gulch CA*
Barnum Pt. NY	Moose Riv. Cross. Ont.*
Bear Pass Creek ID*	Muscatine PA
Beaver Canyon UT*	Neuecest TX
Black Pond VA*‡	Nissequogue NY*
Blood Mt. GA*	Norway OH
Boulder Cave WA	Orestum Ont.
Bumble Bee CA*	Pelvis WA
Cameron Bay NWT*	Penn Mines WA
Camp Creek ID*	Perrytown Ont.
Camp Holsum CA	Pohono Trail CA
Canyon Creek Yuk.*	Red House Ranch NE
Carson Pass CA*	Runda NY
Chile Bar CA*	Salines Ont.
Chimney Gulch CO*	Snake Riv., Divide Cr. ID
Club Hill MD	Summerlea Que.
Cody Ranch OR	Sycamore Flat AZ
Cookshire PA	Tea Lake Ont.
Coyote Grade ID	Townesendville TX
Difficult Run VA*‡	Triangle Lake OR
Eels Lake Ont.	Webster Grvs. MO*
Fish Canyon CA	Westhome MA
Fishtrip Lake WA	Woodkill DE
Grand Bend Que.	Woodworth's Lake Ont.

Obscure Localities On Firefly Labels	
Agnedt NY	Pale Salmon, BC
Batskill NY	Perry Sound, Ont.
Brookings WY	Pokanak City NJ
Cormorant Bay, Man.	Portage du Fort, Que.
Covey Hill, Que.	Port Hope, Ont.
Cowden VA	Put In Bay, Ont.
F. Capron FL	Randolph AR
Fort Reed FL	Reidy, Sask.
J.M., NWT	Rock Bluff NE
Lane PA	S. M., Ont.
Mer Blieu, Ont.	Wales ME
Mount Elliot VA	Wingra Lake WI

circumstantial reason to believe that the Melsheimer specimens compared favorably with Say's, at least to Say's taxonomic eye—and after all, Say has been referred to as the "Father of American Descriptive Entomology" (Mallis 1971:16).

For history and flavor here are some titles and phrases from title pages of lists that include fireflies: Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean—War Department; route near the forty-seventh and forty-ninth parallels, explored by I. I. Stevens, Governor of Washington Territory, in 1853-'55—Report upon the insects collected on the survey—The coleoptera of Kansas and eastern New Mexico (accepted for publication 1859)—Coleoptera of Fort Whipple, Arizona (1866 [Wyatt Earp was about 18 and not yet in Arizona]—List of the Coleoptera of Vancouver's Island (1869)—Check list of the coleoptera of America, north of Mexico (1873)—Catalog of the Coleoptera of Mount Washington, New Hampshire (1874)—New species of Coleoptera collected by the expedition for geographical surveys west of the 100th meridian, Lt. Geo. M. Wheeler, Corps of Engineers, U.S. Army, in charge (1876)—Coleoptera of the Lake Superior Region (1878)—On the lists of Coleoptera published by the geological survey of Canada, 1842-1888 (1890);—Insect Fauna of the Mount Desert Region (1927)—Insects of North Carolina (1938)—List of Beetles of South Dakota (1975)—and finally a pragmatic, zoogeographic tally, Precinctive Insect Species In Florida (1995). Government taxonomists, both federal and state have among their responsibilities the maintenance of reference collections and lists of all the insect species that occur in their districts. For example, the late Arizona Coleopterist and Professor Floyd Werner had a computer list of all of the beetle species that occur in his State; he gave me a printout so that I could add his firefly records to my distribution maps, and a specimen of a rare species I had not previously been fortunate enough to acquire!

Arguably the most important firefly list generator before the 20th Century was John L. LeConte, a Civil War surgeon and medical inspector with the rank of lieutenant-colonel, who was connected with the Academy of Natural Sciences in Philadelphia and at one time was the Assistant Director of the U.S. Mint in Philadelphia (Mallis 1971:242). He was an energetic field-and-bench man, and journeyed to the far west in 1843, then collected around Lake Superior in 1844, working his way along the south shore and on to the source of the Mississippi River in Minnesota; in 1845 he traveled up the Platte River to Fort Laramie and then to the Rocky Mountains, and so on (Mallis: 245). I'd like to retrace his Lake Superior trip with a class of dedicated taxonomy students and find one of his now-puzzling if not gone fireflies. LeConte's name will be recognized even by beginning fireflyers as the author of many North American species (Table 5). "'LeConte was the greatest entomologist this country has yet produced' [Scudder 1886] . . . not because he named almost five thousand spe-

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cies of beetles, but because he showed their systematic relationships and pointed the way to the scientific classification of American insects." (Mallis:242). Today LeConte's beetle collection remains so important as a reference and archive for name-vouchering specimens in Coleoptera taxonomy that it is specially housed in steel cabinets in Harvard's Museum of Comparative Zoology.

In the 20th Century, after the exchange of specimens and literature was improved, two major firefly lists were published. These lists represent the most comprehensive and exhausting insect listing project that one can imagine that a taxon-focused individual might undertake, especially before the age of computers. In 1909 Ernest Olivier and again in 1966 Frank McDermott attempted to locate all of the formal species descriptions that were ever published for fireflies anywhere in the world. Each, in turn, with McDermott building on Olivier's work, tried to determine which assigned names had date seniority, had been not used previously for other species, and were based on adequate descriptions of archived, name-holding specimens of record. Note the synonymies indicated and footnotes in the excerpt from the Leng catalogue in Table 3; imagine attempting this for all firefly names in the literature. The Olivier/McDermott mission, in short, was to straighten out firefly book-keeping since the beginning of zoology's "official" species-naming system (1758). Whew! Such a mission is of course impossible, but fireflyers will keep working on it. In their respective editions of the *Coleopterorum Catalogus*, *Pars 9*, *Lampyridae*. Olivier listed 1097 species in 53 genera and McDermott 1891 species in 92 genera. Any contemporary, computer-assisted, globe-round project that attempts to list all of the organisms in the world must surely rely heavily upon McDermott's edition for the Lampyridae.

TABLE 5. FIREFLY SPECIES THAT JOHN L. LECONTE AUTHORED THAT ARE TODAY CONSIDERED VALID, WITH THE YEAR THEY WERE ORIGINALLY DESCRIBED. NAMES IN BRACKETS SHOW ORIGINAL PLACEMENT. DATA ARE FROM MCDERMOTT'S 1966 "COLEOPTERORUM CATALOGUS," PARS 9.

Some Fireflies Named by Dr. John L. LeConte

Ellychnia
- facula 1857
- flavicollis 1868 [Photinus]
- lacustris 1852
- simplex 1885 [Pyropyga]

Lucidota
- luteicollis 1878 [Pyropyga]
- punctata 1852 [Lucernuta: Lychnuris]

Microphotus
- angustus 1874
- dilatatus 1866

Phausis
- inaccensa 1878
- riversi 1884 [Lamprohiza]

Photinus
- ardens 1852
- collustrans 1878
- consanguineus 1852
- dimissus 1881
- indictus 1881 [Pyropyga]
- lineellus 1852
- marginellus 1852
- obscurellus 1852*
- punctulatus 1852
- umbratus 1878

Photuris
- congener 1852
- divisa 1852
- frontalis 1852

Pleotomus
- davisii 1881
- pallens 1866
- nigripennis 1885

Pyractomena
- angustata 1851 1852?
- ecostata 1878 [Photinus]
- linearis 1852
- punctiventris 1878

Pyropyga
- minuta 1852

. . . . . .

Matheteus theveneti 1874 [now Omethidae]

Pterotus obscuripennis 1859 [affinities uncertain; not now in Lampyridae]

Value and Problems of Species Listing. There are a number of reasons why someone might want to have a list of insects that occur in a given geographic region. Species lists with key references are useful and a necessity for students who wish to step beyond a field guide in preparing term papers or graduate theses; conservationists want to know what species occur in an area they are trying to save or restore, or to determine whether there have been species changes through local extinctions or the introduction of exotics; economic entomologists need to know what non-target species might be harmed by or could be useful for a prospective pest control measure, or when exotic species were first reported; Sunday supplement writers may compare the number of species that occur in their area, say, Central Park NYC, with the numbers found in Pelham Bay Park in the Bronx, or in the natural area on Staten Island that is connected with a museum where there was considerable taxonomic activity early in the 20th century—Charles Leng was the director of this museum when he first published his catalogue of coleoptera in 1920. In "A Natural History of the Chicago Region" Joel Greenberg (2002) included a firefly tally for his region, in connection with efforts made there for the restoration of lost ecologies.

Interestingly, through examination of early lists and other old literature that has now been collected in modern libraries and archived museum specimens, an entomology student today has at hand better information for the state of his region's taxonomy in 1875 than did taxonomists of this postwar era themselves. In fact, complete

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post facto "contemporary" lists can be made today that could never have been available to the taxonomists in their own time. Species lists from the 19th Century seem absurdly useless when compared with what we think we know today, but had these early prospectors known of this they would have carried on anyway, for fun, the solitude or companionship of the chase—still an option and choice—and perhaps the opportunity for a science presentation at their society's meeting and the personal gratification of seeing their contribution in their society's journal. They would presume that their lists would have been of some interest and value to those who followed. To save an otherwise wasted summer wouldn't you enjoy identifying and listing the insects emerging from a prostrate white pine log, one dating and rotting since the great forest mowdown of the north woods around the end of the 19th century, or living in one square meter of beach grass along the shore of a kettle (lost ice-block) lake in Minnesota, and then tell someone about it? Today you could record trophic levels with photographs and videos of interactions to illustrate your talk.

Judging from the view at the beginning of the 21st Century, early makers of comprehensive insect lists can be seen to have had the disadvantages of: (1) inadequate sampling, (2) little or no communication with each other and limited access to taxonomic literature, (3) inadequately described species, (4) few and poor keys to described species, and (5) a great underestimation of the number of insect species present, which was partly due to ignorance of the profusion of noninterbreeding, sympatric (sibling/cryptic) look-alike species. For them any "species problem" could be remedied when more "material" was available, that is, more specimens were acquired for their collections.

Today's list makers would perhaps agree that there are at least three major species problems that taxonomists need to deal with. First, we need descriptions and workable illustrated keys, with a "conservative reverence" toward maintaining a functional yet stable nomenclatural system, so that taxonomists and their client biologists and others can know with as much precision as possible, what specific organisms other workers are referring to when they present results of their studies. Second, taxonomists and biologists need to be mindful of the fact that sometimes, often, or usually there are many more independent genetic populations (biospecies), than can be estimated from contemporary, routine, omnispective methods. A third aspect of today's species problem is comparable to one listed for 19th Century taxonomists, except that we already have "the material"—millions, perhaps tens of millions of archived specimens—but much of it remains unsorted and undescribed because of the shortage of taxonomists and qualified collaborators. In the "good old days" much insect taxonomy was performed as an avocation by gentle folk with other occupations, physicians, parsons, pharmacists, and "pedagogists"; perhaps we are heading in that direction now, which would be a good thing, but professionals perhaps remain too leisurely in recruitment.

A modern and growing problem is how to deal with the quantity and complexity of information that is relevant to taxonomic practice and essential for improving the quality of lists. Once upon a time a taxonomist made species "available" to others merely by describing and naming new species, and identifying specimens for them. The latter especially was understood as their in-service function for biological research—Table 6 is a sampler of my institutional "firefly clients." Today it is necessary for taxonomists to keep track of and synthesize much more new information related to their science, and taxa, and serve more scientists representing a broader range of disciplines. Further, today identifications are often much more time-consuming and difficult because, (1) ever more of the species are "cryptic" and difficult to distinguish from close relatives, and (2) tendered specimens must be maintained and handled with more care, with sterile technique and regard for damage that can result even from room tempera-

TABLE 6. A PARTIAL LISTING OF THE INSTITUTIONS REPRESENTED AMONG JEL "CLIENTS." WHEN SUCH ARCHIVES HAVE SERIES OF SPECIMENS THAT HAVE BEEN IDENTIFIED BY A CURRENT AUTHORITY OF THE TAXON THEY CAN IN TURN PROVIDE TAXONOMIC IDENTIFICATIONS AND SERVICES FOR REGIONAL STUDENTS AND OTHER RESEARCHERS. DETERMINATION LABELS OF THE LATE JOHN WAGONER GREEN, A MASTER FIREFLY TAXONOMIST AT THE CALIFORNIA ACADEMY OF SCIENCES, ARE ATTACHED TO SPECIMENS IN MANY OF THESE INSTITUTIONS.

Sampler of Firefly "Client" IDs Since 1964

Ag. Exp. Sta., Univ. of Arkansas	Mus. Comparative Zool., Harvard
Amer. Mus. of Nat. Hist. NY	Mus. of Inverts, Univ. of Panama
Auburn Univ. Coll. AL	Mus. of Zool., Univ. of Michigan
Auburn Univ. Student Coll. AL	New York State Mus. Albany
Biosyst. Research Centre CAN	North Dakota State Univ.
Canadian Dept. Agric.	North Carolina Dept. of Agric.
Canadian National Coll.	Ohio State Univ.
Carleton College CAN	Oklahoma State Univ.
Carnegie Museum PA	Peace Corp., Ecuador
Chicago Nat. Hist. Mus. IL	Pennsylvania State Univ.
City College NYC	Purdue Univ. IN
Clemson Univ. SC	R. Marina de Carvalho, Brazil
Col. Env. Sci./For., Syracuse Univ.	Staten Island Inst. Arts & Sci. NY
Colorado State Univ.	Texas A&M Univ.
Connecticut College	Texas Tech. Univ.
Copenhagen Mus., Denmark.	Tufts Univ. MA
Cornell Univ. NY	Univ. Colorado
CTAP Secao de Entomol., Brazil	Univ. Costa Rica
Dept. of Entomol., Univ. Wisconsin	Univ. Delaware
Div. Plant Industry CA	Univ. of Georgia
Florida State Coll. of Arthropods	Univ. of Idaho
Florida A&M Univ.	Univ. of Kansas
Forest Service, Dept. of Agric. LA	Univ. of Kentucky
Guelph University CAN	Univ. of Mississippi
Illinois Nat. Hist. Survey	Univ. of Missouri
Iowa State Univ.	Univ. of Texas
Johns Hopkins Univ. MD	USDA Microbiology MD
Kansas State Univ.	Vanderbilt University TN
Michigan State Univ.	WV Pest Id. Lab.
Miss. State Univ.	Yale Univ. CT

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tures, to avoid contaminating or degrading DNA and other chemicals. Of course there is a taxonomic motivation for such "routine bench IDs", because new information can provide insight for understanding biospecies, and for further refining species lists. A taxonomist is sometimes able to provide ID guidance for prospective research—say, suggest which firefly species is the best suited to study the impact of a flash-seeking predator on species-specific signaling behavior, and which of its "sibling species" in another region would make a good comparison; or tell a DNA seeker studying the variation in the code for a particular protein, the location of suitable populations for examination. Some taxonomists will collect critical specimen samples for clients (but I always decline requests for fireflies to be released at weddings).

It comes down to this: Every insect taxon needs a *fanatical specialist* who will make a life of *passionate proprietary concern* for his "own personal" charges (explain that to a university administrator of the business model ilk). Words of Pavlov, as quoted by Blatchley, make a connection here: "Remember that Science demands from a man all his life. If you had two lives that would not be enough for you. Be passionate in your work and your searchings." The taxon that an individual taxonomist so nurtures may be a genus, family, or order, depending on its size, complexity, amount of contemporary research on the organisms, and personal interest. Indeed, such specialists, along with field books and other records of archived specimen collections, are virtually part of collections themselves, though more poorly archived (underappreciated) and obviously, because they are the caregivers themselves, shorter lived. Keep in mind that such specialists must see to the professional education and technical training of their successors. In my view, every biology department in U.S. academies should have an insect taxonomist who will take professional care of a personal taxon, teach a section and lab of introductory organismic biology to freshmen, and teach a specialized course and seminar in taxonomic/evolutionary biology. Realistically and gloomily, though it is a collective responsibility that all academic institutions have an obligation to share, I will bet that it is quite unlikely to happen.

Contemporary Firefly Lists. Some regions of North America have many species of fireflies, and local naturalists will spend many years trying to resolve the easy ones and outline and begin to unravel the problems presented by others. McDermott and Barber spent a half-century watching the fireflies around the Chesapeake Bay and lower Potomac River, but they left much for us to discover (Fig. 3). Florida and Georgia, which are the most firefly-rich States, currently have 56 listed species, including those formally named and those with informal working nicknames (Lloyd 1997). At the other extreme, Alaska apparently has only one species, a member of the *Ellychnia corrusca* clan; Hawaii briefly had three borrowed species, all of which seem to have disappeared soon (weeks?) after their introduction in the 1950s (Table 10). Some regions have only a few species, and present few if any problems in getting a fairly straight-forward general outline. North Dakota, for example, apparently has about 20 species in 6 genera, and even the species of *Photuris* present few problems. On the other hand, the list for Bay County, Florida has 34 species in 9 genera, including 5 unnamed species (Table 7, Fig. 4A).

The species list for a county in North Dakota makes an interesting contrast with the Bay County list (cf Tables 7 and 8). The species in these two as now understood and except for *Photuris*, can be identified though morphological descriptions and keys in the literature. The three *Photuris* species listed for Stutsman County (Table 8, Fig. 4B) can easily be identified in the field from Barber's monograph (1951), and the morphological, behavioral, and ecological notes he provided—given that one knows which three *Photuris* are present. However, the situation in Bay County is much more difficult because 9 or more *Photuris* species are present. The mere listing of the *Photuris* fireflies of Bay County will not allow even a persistent and dedicated user to recognize what a list maker referred to. A supplementary flash pattern chart is needed, or better yet, a key to flash patterns such as the one for east-central Alabama (Table 9; Lloyd 1990b). A student naturalist guided by an informed teacher could make such a chart and key for his region in two or three summers, but resolving the name problems would take much longer.

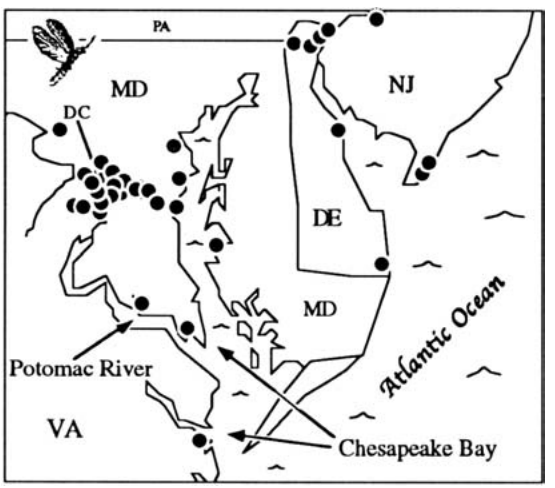


Fig. 3. The domain of fireflyer pioneers F. A. McDermott and H. S. Barber, around the Chesapeake Bay and the lower Potomac, with dots marking observation/collecting spots mentioned in their literature, and by J. W. Green in his generic revisions, from insect labels.

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TABLE 7. SPECIES LIST FOR BAY COUNTY, FLORIDA, INCLUDING ADDITIONAL DATA FOR COLLECTORS AND OBSERVERS: F-FACTORS ARE PREDICTIONS FOR THE COUNTY (AND IMMEDIATELY ADJACENT AREAS), WITH 1 BEING THE EASIEST TO FIND AND 5 BEING THE MOST DIFFICULT (SEE TEXT); IN INDICATES THE SPECIES IS KNOWN TO OCCUR OR IS SUSPECTED TO OCCUR IN BAY COUNTY; EDGE INDICATES THAT THE SPECIES IS KNOWN TO OCCUR NEAR BAY COUNTY.

Fireflies of Bay County, FL
Checklist and Expectation Guide
(Alphabetical by genus then epithet)

	Species	In	Edge	F-Factor
1.	*Ellychnia corrusca* complex		X	4
2.	*Lucidota atra* (G. Olivier)	X		2
3.	*Phausis reticulata* (Say)		X	2
4.	*Photinus australis Green*	X		2
5.	*P. collustrans* complex	X		2
6.	*P. consimilis* complex	X		1
7.	*P. floridanus* Fall		X	2
8.	*P. frosti* Green	X		3
9.	*P. ignitus* Fall		X	4
10.	*P. lineellus* LeConte	X		3
11.	*P. macdermotti* complex		X	1
12.	*P. marginellus* LeConte		X	3
13.	*P. pyralis* (Linnaeus)	X		1
14.	*P. umbratus* LeConte	X		2
15.	*Photuris* species "A"		X	1
16.	*P.* species "B"		X	3
17.	*P. cinctipennis* complex	X		3
18.	*P. congener/frontalis*	X		1
19.	*P.* species "LR"	X		1
20.	*P. salina* Barber		X	2
21.	*P.* species "SE-1"	X		3
22.	*P. versicolor* complex	X		1
23.	*P.* species "VR"		X	3
24.	*Pollaclasis bifaria* (Say)		X	3
25.	*Pyractomena angulata* (Say)	X		1
26.	*P. angustata* (LeConte)	X		1
27.	*P. barberi* Green		X	3
28.	*P. borealis* (Randall)	X		1
29.	*P. ecostata* LeConte	X		2
30.	*P. floridana* Green	X		3
31.	*P. lucifera* (Melsheimer)	X		2
32.	*P. similis* Green		X	3
33.	*Pyropyga minuta* LeConte	X		1
34.	*Tenaspis angularis* (Gorham)		X	4

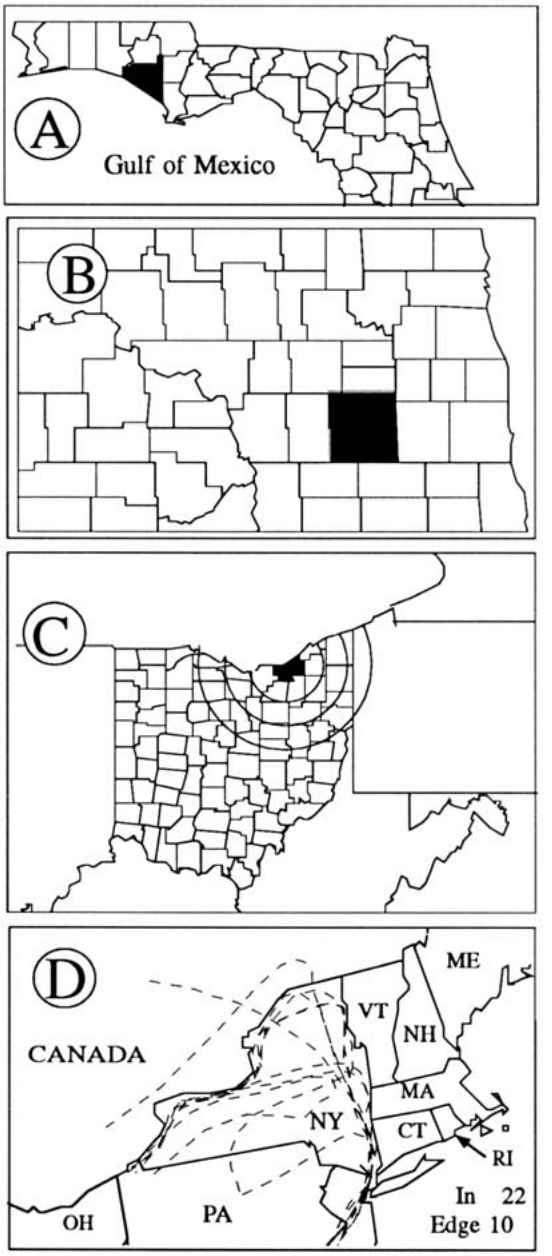


Fig. 4. Maps concerning distributions of fireflies discussed in text: (A) Location of Bay County FL, see Table 7; (B) Location of Stutsman County ND, see Table 8; (C) asymmetry of distribution rings at Cleveland OH because of Lake Erie; (D) loops of dotted lines In New York State showing the eastern or northeastern limits of known distributions of 10 EDGE fireflies "approaching" New England (i.e., VT, NH, CT, MA, RI, ME).

The difficulty a fireflyer has in actually finding populations in the field will depend upon a variety of circumstances. Some species are common, some are rare; some appear in disturbed areas, such as creek washouts, hurricane blowdowns, under power lines, and over oldfields. Some are secretive and occur only in isolated pockets in undisturbed areas, and others may be nearly extinct because their habitat is virtually gone, without our knowledge that its special circumstances even existed. Sometimes species from extinct habitats have taken up residence in special man-made situations. For example, the long-unknown, early-destroyed oak savannah that extended southwest from Chicago (Greenberg 2002), may have been the original habitat of some fireflies that are now gone too, but maybe some may still

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TABLE 8. SPECIES LIST FOR STUTSMAN COUNTY, NORTH DAKOTA. F-FACTORS, IN AND EDGE AS IN TABLE 7. IN ALL CASES THE KNOWN RANGES OF EDGE SPECIES END A FEW OR SEVERAL MILES EAST OF STUTSMAN COUNTY.

Fireflies of Stutsman, County ND
Checklist and Expectation Guide
(Alphabetical by genus then epithet)

	Species Name	In	Edge	F-Factor
1.	Ellychnia corrusca (L.)		X	1
2.	Lucidota atra (G.A. Olivier)		X	1
3.	Photinus aquilonius Lloyd		X	3
4.	P. ardens LeConte	X		2
5.	P. indictus (LeConte)		X	2
6.	P. obscurellus LeConte	X		1
7.	Photuris caerulucens Barber		X	1
8.	P. fairchildi Barber		X	2
9.	P. pennsylvanica (DeGeer)	X		1
10.	Pyractomena angulata (Say)		X	1
11.	Py. borealis (Randall)		X	1
12.	Py. dispersa Green	X		2
13.	Py. linearis (Melsheimer)	X		1
14.	Py. lucifera (Melsheimer)		X	3
15.	Py. sinuata Green	X		2
16.	Pyropyga nigricans (Say)	X		1

survive along highway and railroad swards and berms—and in old, untended graveyards, a neat bit of ecology passed along to this student by an insect curator at Ann Arbor.

The distinctiveness of flashing patterns will also influence how quickly fireflies are found or recognized as different entities, but once a local population has been found others may be more easily located near by. I once discovered an undescribed species of *Photuris* in a roadside marsh at a culvert in northwestern South Carolina, but four days later their ugly, cattail-infested puddle was bulldozed to become a pretty reflecting pool and waterfall for a golf course. I will look for fireflies flashing the same pattern, upstream and down along the valley and the montane creek that now feeds Golfers' Pool.

The lists for Stutsman and Bay Counties (Tables 7 and 8) also suggest how difficult it may be to find the initial population of each species. F-Factors abstract a subjective judgement of whether a species is rare (local), common, or abundant. It suggests the difficulty I expect a new fireflyer would have in finding a population—were one to ambitiously set out to find it, and stick with the chase. Translations are: 1, easy, find during first year; 2, relatively easy, find in two years; 3, considerable effort required, find in five years; 4, great effort required, much difficulty, find in 10 years, if at all. Fives (5's) are species presently not known. They may occur elsewhere but there is no reason to presume they are in the region. Or, they may be new species, undescribed by taxonomists,

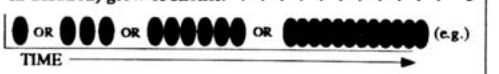
TABLE 9. SEVERAL COUPLETS OF A PICTURED KEY TO DISTINCTIVE FLASH PATTERNS OF FIREFLIES IN EAST-CENTRAL ALABAMA. ACTUALLY, TO BE USEFUL FUTURE REGIONAL KEYS TO SPECIES OF *PHOTURIS* FIREFLIES WILL REQUIRE A COMBINATION OF FLASH PATTERNS AND MORPHOLOGY.

Key To Distinctive Flash Patterns In East-Central Alabama (For Flying Males Only)

1. Nocturnal bioluminescent emission a continuous glow lasting for 6 and often many more seconds — not flickered or pulsed with an even rhythmicity/regularity. . . . 2



1'. Emission a continuing series of flash patterns, each pattern a short flash, or a group of short flashes, or a short (<5 sec in duration) glow or flicker. 3



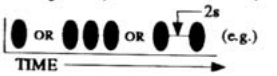
2. Glow a minute' point, moving low over the ground, as a green (blue?) spark — often low or damp forests, along creeksides; not very early spring. . . . *Phausis reticulata*

2'. Glow not so tiny; sometimes low over ground but usually @ 1–2 m, and occasionally to treetops; wet grassland, pine savannas — very early spring. . . *Pyractomena angustata*

3. Flash pattern a repeated short flicker of 3–15 modulations (pulses, flashlets) — a rhythmically lumpy glow. . . . 4



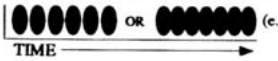
3' Flash pattern a single short flash or a group of flashes (e.g. 2, 3–6, 4–9 flashes) — the time period between flash patterns is conspicuously longer than the period between the flashes of a pattern). . . . . 7 (see Lloyd 1990b)



4. Pattern of 3–4 (rarely 5–6) rapid flashes, seen as a "jagged" flicker at warmer temperatures but seen clearly as separate flashes below 65°F; flashes often with decreasing intensity, but especially or only noticeable on last flash of a pattern; repeated at 3–7 sec. . . . . *Photuris versicolor*



4'. Pattern not as above, usually with more than 6 modulations and these of same intensity though sometimes this is scarcely apparent from some angles. 5



5. Flicker of 7–12 orange, usually not very bright modulations; season late May, one or few around boughs of trees and shrubs and occasionally in numbers over damp ground (distinguish from *Py. dispersa* which has about half the modulation rate, only 5-6 usually clearly separated yellow flashes, and not arboreal). . . . . *Pyractomena angulata*

5'. Flicker of 7–12 green or bluish, usually bright modulations; male flying rapidly (poor searching flight), sometimes emitting more than 6–12 mods, 15±. 6

6. Flicker usually over open areas, fields meadows; when answered with a flash, the male switches to a 3–5 slow-pulse flash pattern . . . . . *Photuris quadrifulgens**

6'. Flicker usually around boughs of shrubs and trees, less often over fields and then usually near hedgerows, woods; when answered with a flash male switches to short flashes at about 2 sec period. . . . . *Photuris tremulans*

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TABLE 10. A PRELIMINARY/WORKING CHECKLIST OF NORTH AMERICAN FIREFLIES. NO INFORMATION IS PROVIDED HERE TO AID IN IDENTIFICATION OR FOR DETERMINING SEASONAL OR GEOGRAPHIC DISTRIBUTIONS; THE LIST MERELY INDICATES WHICH NOMINAL SPECIES IN THE LITERATURE APPEAR TO BE LEGITIMATE, HOW MANY OTHERS HAVE BEEN DISCOVERED AFTER FOUR DECADES OF FOCUSED SEARCH, AND WITH RESPECT TO BOOKKEEPING, MAKES CHANGES IN TAXONOMIC STATUS AND INDICATES THOSE CONTEMPLATED. THE LIST ALSO REPRESENTS AN INDEX TO FILES OF DATA AND OBSERVATION SUMMARIES ON THE SPECIES, WITH ASSOCIATED FIELD BOOKS AND SPECIMEN-IDENTIFICATION RECORDS, PHOTO-MULTIPLIER CHARTS, AND SEVERAL THOUSAND VOUCHER SPECIMENS THAT WILL BE ARCHIVED FOR FUTURE REFERENCE. WORLD TOTALS ARE APPROXIMATIONS USING MCDERMOTT (1966) AS A BASE; ADDITIONAL SPECIES HAVE SINCE BEEN NAMED IN SOME GENERA BUT ARE NOT INCLUDED HERE. FOOTNOTES: (1) IF AN ESTABLISHED POPULATION IS FOUND IN NA I RECOMMEND IT BE GIVEN SPECIES RANK; (2) SPECIES HERE REMOVED FROM SYNONOMY; (3) FORMERLY VIEWED AS CONSPECIFIC WITH A CUBAN SPECIES, WILL BE DESCRIBED AS A NEW SPECIES; (4) SPECIES HERE ELEVATED FROM SUBSPECIES TO FULL SPECIES.

Lampyridae
Of the United States and Canada
and the Bahamas
(a working check list, August 2002)

Aspisoma (2 NA species?, 71 World)

costatum	Gorham	(quarantine intecept at Apopka FL— \ from Honduras)
ignitum	Gorham	TX, MX, CnA, SA, \ Caribbean
species?		Key West

Bicellonycha (1+(?) NA species,29 World)

wickershamorum	Cicero	Arizona

Brachylampis (2 NA species, 2 World)

blaisdelli	VanDyke	California
sanguinicollis	VanDyke	California

Ellychnia (12+ NA species, 25+ World)

autumnalis	Melsheimer	e USA
bivulneris	Green	Arizona
californica	Motschulski	w USA
corrusca (cplx)	(L.)	e USA, Can
facula	LeConte	nw USA
flavicollis	(LeConte)	w USA
granicollis	Fender	Oregon
greeni	Fender	nw USA
hatchi	Fender	nw USA
lacustris	LeConte	Brit. Columbia
obscurevittata	Fender	Oregon
simplex	(LeConte)	Arizona

Lamprigera (0 native US species, 16 World)

tenebrosus	(Walker)	Hawaii, Guam, biocontrol intro, 1952 from Sri Lanka; not known to be estab.

Lamprohiza (0 native US species (?), 8 World)

splendidula	(L.)	European; very old local intros: 1 specimen taken nr Chicago, 1 specimen in MD: in LeC coll. @ MCZ

Lucidota (4 NA species, 163 World)

atra	(G.A. Olivier)	e USA
GS	ms	c Georgia
luteicollis	(LeConte)	Florida
punctata	(LeConte)	e USA

Luciola (0 native US species (?), 277+ World)

cruciata	Olivier	Hawaiian Is., biocontrol intro, 1957, from Japan; not established
lateralis	Olivier	Hawaiian Is., biocontrol intro, 1957, from Japan; not established

nr Luciola (1 NA species?)

UV	(Green noted)	locality nr Uvalde, TX. (jl sought without success)

Micronaspis (1 NA species, 1 World)

floridana	Green	coastal Florida

Microphotus (7 NA species, 7 World)

angustus	LeConte	w USA
chiricahua	Green	Arizona
decarthrus	Fall	Arizona
dilatatus	LeConte	Arizona, California
fragilis	E. Olivier	Arizona
octarthrus	Fall	sw USA
pecosensis	Fall	sw USA

Paraphausis (1 NA species, 1 World)

eximia	Green	Arizona

Phausis (10+ NA species, 10+ World)

californica	Fender	California
dorothae	Fender	Oregon
inaccensa	(LeConte)	Maryland, Miss.
luminosa	Fender	Oklahoma, Ark.
marina	Fender	California
nigra	Hopping	Brit. Columbia
reticulata	(Say)	e, c USA
rhombica	Fender	nw USA
riversi	(LeConte)	w, nw USA
skelleyi	Fender	nw USA

Phosphaenus (1 NA species, 1 World)

hemipterus[1]	(Fourcroy)	Nova Scotia, from UK?, ca 1800(?)

Photinus (46+ NA species, 245+ World)

acuminatus	Green	se USA
ALD	ms	Texas
aquilonius	Lloyd	ne, nc USA/Can
ardens	LeConte	ne, nc USA/Can
australis	Green	ec USA
BL	ms	Arkansas
BRB	ms	ecUSA
brimleyi	Green	KY, NoCa, Tenn
BT	ms	Bahamas
carolinus	Green	No Ca, Tenn
collustrans	LeConte	Florida
consanguineus	LeConte	se USA
consimilis (ss)	Green	Missouri
concisus	Lloyd	Texas
cookii	Green	s USA
curtatus	Green	c to ne USA
dimissus	LeConte	Texas
FFP	ms	se USA
FLL	ms	Carolinas, Virginia
floridanus	Fall	Florida, Georgia
frigidus[2]	E. Olivier	Newfoundland
frosti	Green	Florida, Louisiana
granulatus	Fall	Oklahoma
greeni	Lloyd	e coastal USA
ignitus	Fall	e USA
immaculatus	Green	Texas
indictus	(LeConte)	sc, nc, ne USA/Can
knulli	Green	Arizona
lineellus	LeConte	Florida
LMS	ms	Mississippi
macdermotti	Lloyd	e USA
manni	Leng & Mutchler	Bahamas
marginellus	LeConte	ne, nc USA
MI	ms	sw USA
obscurellus	LeConte	ne USA/Can
punctulatus	LeConte	c USA
pyralis	(L.)	e USA
sabulosus	Green	e USA
scintillans	(Say)	NJ & vic, mw intros
SIG	ms	se US.
stellaris	Fall	Texas
tanytoxus	Lloyd	Florida
tenuicinctus	Green	Arkansas
texanus	Green	Texas
umbratus	LeConte	se USA
WS	ms	Texas

Photuris (64+ NA species, 131++ World)

A	ms	se USA
AC	ms	nc Florida
ANC	ms	se Georgia
aureolucens	Barber	nc USA
B	ms	Florida
BBB	ms	Delaware
bethaniensis	McDermott	Delaware
BH	ms	Bahamas
BR	ms	Florida
BRG	ms	ne USA
brunnipennis[3]	Jacq.-DuV.	s Florida (Cuba)
C	ms	nc Florida
caerulucens	Barber	Minnesota
CIC	ms	sc Texas
cinctipennis	Barber	e USA
congener	LeConte	Florida
D	ms	se USA
divisa	LeConte	c USA
DM	ms	Florida
E	ms	nw-pen Florida
fairchildi	Barber	e, c USA & Canada
FC	ms	e, c USA
flavicollis[4]	Fall	Texas
frontalis	LeConte	e USA
hebes	Barber	e, c USA
HB	ms	e Texas
HR	ms	se Georgia
HW	ms	e, nc. Tenn., w VA
IP	ms	Iowa
J34	ms	Florida
lineaticollis	(Motsch.)	se USA
LIV	ms	MA CT NY
lloydi	McDermott	Florida
LM	ms	sc Texas
LNR	ms	se Georgia
LR	ms	nc, nw Florida
lucicrescens	Barber	e USA
marginata	Panzer	Bahamas
MG	ms	Conn.
missouriensis	McDermott	Missouri
OR	ms	se Georgia
OZ	ms	sw Missouri
PT	ms	ne Ohio
pennsylvanica	(DeGeer)	e, nc USA
potomaca	Barber	e USA
pyralomima	Barber	ne USA
Q12	ms	seUSA
quadrifulgens[4]	Barber	e USA
RP	ms	nw Florida
salina	Barber	e, s coastal USA
SE	ms	nw-pen Florida
SFP	ms	se USA
SO	ms	ne North Dakota
SP	ms	ne, nc USA
SPP	ms	e USA
ST	ms	s Appalachians
SV	ms	e TX
TM	ms	n Michigan
TN	ms	e USA
tremulans	Barber	e USA
TW	ms	s Michigan
versicolor	(Fabricius)	e USA
VR	ms	nw pen Florida
WM	MS	FLORIDA

Pleotomodes (3 NA species, 3 World)

knulli	Green	Florida
needhami	Green	c Florida
pulsator	(Cicero)	Arizona (Mex)

Pleotomus (2 (3?) NA species, 2 (3) World)

davisii	LeConte	Tennessee
pallens	LeConte	e, c USA, Texas
nigripennis	LeConte	Arizona

Pollaclasis (1 NA species, 1 World)

bifaria	(Say)	e USA

Pyractomena (21 NA species, 29 World)

angulata	(Say)	e USA, Canada
angustata	LeConte	se USA
BAH	ms	Bahamas
barberi	Green	Florida
BML	ms	Florida
borealis	(Randall)	e USA, Canada
DD	ms	ne USA
dispersa (cmplx)	Green	e , nc USA
ecostata	(LeConte)	Florida, New Jersey
floridana	Green	Florida
gamma	(Jacq.-DuVal)	DE(?), Caribbean
HD	ms	e New York
limbicollis	Green	se USA
linearis	LeConte	ne, nc USA
lucifera	(Melsheimer)	e USA
marginalis	Green	ne USA
palustris	Green	e USA
punctiventris		LeConte Texas
similis	Green	ne USA
sinuata	Green	ne, nc USA
vexillaria	Gorham	nr sw USA

Pyropyga (4+ NA species, 12+ World)

decipiens	(Harris)	ne USA, se Canada
minuta	LeConte	se, sc USA
modesta	Green	sc USA
nigricans	(Say)	USA except se; Can

Tenaspis (1 NA species,16 World)

angularis	Gorham	Missouri, Florida, Texas

. . . . . .

Family Omethidae
(False Fireflies)
(Formerly Matheteinae of Lampyridae)

Ginglymocladus (2 NA species, 2 World)

discoidea	VanDyke	California
luteicollis	VanDyke	California

Matheteus (1 NA species, 1 World)

theveneti	LeConte	nw USA

Family ?
(species of uncertain placement [*incertae sedis*]; Formerly Pterotinae of Lampyridae)

Pterotus (2 NA species, 2 World)

curticornis	Chemsak	California
obscuripennis	LeConte	w USA



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and after one finds them it may take two or three years to be convinced that they are indeed new. Nor are 6's listed—these are species that will only be found after new ideas and methods of looking and analyzing are used for searching and understanding genetic diversity and population trajectories through evolutionary time.

Species listed as occurring at the EDGE (Tables 7 and 8) can sometimes be presumed to actually occur IN, but be too rare or too habitat-restricted to have yet been found. This is related to the question, how regional are regional lists? How far out from the specified region does the list apply? To begin to answer this one can draw a series of concentric circles around the center of a considered focus region. The further one travels from the center the less applicable the regional treatment should be. Each species will drop out at some distance from the center, but the drop-off will certainly not be gradual nor symmetrical. As an extreme condition in both respects, if Cleveland, Ohio were a used as a center, the drop off to the north, until Lake Erie someday fills and becomes marshland, would be precipitous and concentric rings highly asymmetrical (Fig. 4C). Rings around Phoenix, Arizona, for the few fireflies that occur there, would mask the patterns of distribution that actually exist because probably only gallery habitats along streams will harbor most fireflies of the region.

When listing the firefly species of New England one finds 22 species IN and 10 at the EDGE. Of the 10 near the edge, can one presume that some actually are IN but yet unfound? The 10 EDGE species approach New England from the west and southwest, and based on current distribution maps they reach their eastward limit at the Hudson River/Taconic and Green Mountains, paralleling the eastern border of New York State (Fig. 4D). In spite of highways and their bordering grasslands (swards and berms) and vehicular traffic with millions of opportunities for fast range-extending rides in sod and plant pots, and prevailing west winds blowing at this latitude, and considerable habitat modification in New England that would seem to make at least some places livable for some of these 10 species, none have yet been seen among the examined collections made there for more than a century. Note that a firefly taxonomist of no mean reputation, Henry Clinton Fall, a retired science teacher and author of *Photinus ignitus* a species of the region, lived in Massachusetts for some time—he also authored "A list of the Coleoptera of the Southern California Islands with Notes and Descriptions of New Species"! Thus, not all EDGE species are promising candidates for inclusion in a regional listing—but such species would seem excellent candidates for ecological studies to find the limiting factors responsible. Surely there is more to the apparent exclusion of these EDGE species than meets the eye.

I would like to incorporate many of the features of Willis Blatchley's Indiana list and Rev. Henry S. Gorham's "Biologia-Centrali Americana" (1880-1886) in the firefly list I am aiming for, but for the present Table 10 gives a bare bones beginning. It has codens for many unnamed species, and Find Factors would be useless at such a scale and with so many ecological unknowns. The next edition of this list promises to have distribution maps and seasonal and flash charts to aid in identification. In the meantime the centuries-long chase by firefly naturalist/taxonomists creeps resolutely onward.

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