ON RESEARCH AND ENTOMOLOGICAL EDUCATION V: A SPECIES (C)ONCEPT FOR FIREFLYERS, AT THE BENCH AND IN OLD FIELDS, AND BACK TO THE WISCONSIAN GLACIER

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Abstract

There is no lack of species concepts available for consideration, nor of discussion and speculation about what a species concept should be and do, but nothing seen in recent literature is suitable nor adequately clear and descriptive for firefly naturalist/taxonomists as they begin their studies. A reasonable ad hoc solution combines the now-classical and practical omnispective view of the phenotype for pragmatic utility, with a composite of early 20th-century elements and theoretical (notional) fragments from various nominal "Concepts," particularly the Biological Species Concept, and places natural selection and inevitable population divergence into foremost consideration, to provide a microevolutionary expectation of firefly populations in nature. A short history of about 18,000 years is introduced because of the possible existence of geologically dated, clear evidence of population changes that may be recognizable in fireflies living in regions that came under the influence of the last major NA glacier.

Key Words: Lampyridae, fireflies, taxonomy, species concepts, species problem

Resumen

Para los naturalistas/taxonomistas de luciérnagas que comienzan sus estudios, no se ha visto nada en la literatura reciente que sea apropiado o adecuadamente claro o descriptivo, ya que no se carece de conceptos de especies para la consideración o discusión y especulación sobre lo que un concepto de especie debe ser y hacer. Una solución razonable para este caso combina la perspectiva práctica y ahora clásica de fenotipo para el uso pragmático, con una composición de elementos de comienzo del siglo 20 y fragmentos teóricos (hipotéticos) de varios "Conceptos" nominales, en particular el Concepto de Especie Biológico, y coloca a la selección natural y a la inevitable divergencia de población bajo la consideración mas destacada, para proveer una esperanza microevolucionaria de las poblaciones de luciérnagas en la naturaleza. Se introduce una corta historia de alrededor de 18,000 años debido a la posible existencia de evidencia clara, con fecha geológica, de cambios de población que pueden ser reconocibles en luciérnagas que viven en regiones que estuvieron bajo la influencia del último glaciar importante de NA.

"Among the diverse aspects of the so-called species problem, there is none that has received more unsatisfactory treatment than the study of species. . . . comparative studies of species, first-hand contacts with thousands of individuals of hundreds of related species, the careful examination of these individuals with modern laboratory facilities, and the correlation of such studies with the findings of genetics . . . has only occasionally been accomplished." (Alfred Kinsey 1930)

"a variety of species concepts is necessary to adequately capture the complexity of variation patterns in nature. To subsume this variation under the rubric of any one concept leads to confusion and tends to obscure important evolutionary questions." (Mishler & Donoghue 1982)

Naturalist's Introduction

"What is a species?" Does not this question presume too much? Could there possibly be anything real in nature such as preDarwinians created and saw, and almost everyone until recently has expected? Should not Darwin's "Origin" have put an end to obsession or flirtation with any form of essentialism?—should it not have quickly led to realization that an expectation of *species* as a universal in the living world was quite unrealistic? Today among professional systematists the question can often mean, "what arbitrary, utilitarian definition for your personal research subjects do you wish to refer to, want to write about, when you use the word 'species'." But a half-century ago when Ernst Mayr, Theodosius Dobzhansky and others taught us about what has come to be known as the Biological Species Concept (BSC), a very good seed, they seemed to focus and guide us toward an intrinsically defined taxonomic unit, toward making a truly definable "natural species" a scientific reality for the first time. For a brief and golden moment, a Camelot looking back on it, the naturalist had his species and could go back and forth easily and comfortably between the morphology under the microscope and the flashing of populations of his biological species in the field. We remember this as a good time, we were modernized, and we thought it would never end.

It is important that educators remember that before the BSC there was some very good thinking too, by naturalists, taxonomists, and phylogeneticists who got the century off to an admirable start. For those who were paying attention to the species question, there were sound perspectives and ideas to help them in research and teaching. Gordon Ferris' text "The Principles of Systematic Entomology" (1928) taught a generation of insect taxonomists, and at the end of the second chapter, "The Scope of Systematic Biology," he wrote, in italics: "Systematic biology should include in proper proportion all those activities which arise from or are connected with the study of those *aggregates of organisms we call species* [jel emphasis]. It is in its broad implications essentially synonymous with the study of organic evolution." A quotation Ferris used in his consideration of species that is particularly relevant for fireflyers was from Harvey Hall and Frederick Clements' "The Phylogenetic Method in Taxonomy" (1923): "The evolutionary view of the species is that it is a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads. As they have recently come from the same stock, these variads are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, *at the same time they mark its further differentiation* [jel emphasis]." For a comprehensive statement about species and speciation, yet economy of words, it is difficult to do better than that!

When we learn about species from field work, and at the same time, consider the pragmatic responsibilities of species taxonomists and naturalists, we should not forget Alfred Kinsey—who later became famous as a pioneer sexologist—and his monograph "The gall wasp genus *Cynips*: a study in the origin of species" (1930): "If taxonomy has been in ill repute, it is because we have considered as our chief function the solution of something other than biologic problems. . . . The older definition of a species as a group of similar (implying nearly identical) individuals fails because of the amount of variation actually found in nature. . . . if [instead] species are defined as populations with common heredity, we obtain a concept which seems genetically sound and which, we will try to show, is a reality in nature. . . . after such field experience, one comes to feel there is a reality summed up in the word 'species' which is more than a few cabinet specimens or a bottle full of experimental material or a Latin binomial in a textbook." Kinsey noted, as reminder or for those who were not of the taxonomist's cloth, that there were two often confused uses of the term "species" in taxonomy: "It must be pointed out that there is a biologic concept called species and a taxonomic category called species, and that the two are not always synonymous. The concept we have developed is the biologic concept to which all except the taxonomist must refer whenever they consider the problem of species. This is the sense in which even taxonomists, including ourselves, intend the word when it is used in most biologic connections."

Returning to the mid-century developers of the BSC, they went on to discuss "reproductive isolating mechanisms" and saw them as population adaptations that prevented genetic pollution from other species. It was eventually realized that this view needed rethinking. Selectionists argued the importance of carefully identifying the actors, the so-called selected entities, and led BSC advocates to focus their attention on reproductive individuals making up their biological populations. Mate selection became apparent as a reasonable self-defining element of a biological species, at least ideally, making this BSC even more different from other Species Concepts. In this revised edition, individual members of a species themselves set the boundaries of their species, and for (soft) evidence of this a fireflyer saw individual fireflies flash communicate, antennate, then copulate.

This BSC2, envisioning a mutual gene pool of self-defining individuals as a theoretical description of reality might seem to have it all, for we would not necessarily require that a theoretical model be verifiable—we cannot usually know whether copulations produce successful fertilizations, or fertilizations produce surviving, competitive offspring. But in a good theory reach will exceed grasp: "a concept cannot be completely operational and still be useful for the growth of science" (D. Hull, seen in Mishler & Donoghue 1982). But BSC2 embodied another, long-recognized imperfection for fireflyers. Mate choice and gene flow cannot easily be presumed to maintain a mega-population's unit integrity across half a continent, or when a presumptive gene pool is fragmented into small and variably-isolated local populations. As Mayr has pointed out, when they are separated across space we cannot know the *relational* status of local "conspecific" populations—that is, know whether they are independent units, have diverged a little, significantly, or too much to be in fact the same species. Likewise, when experimentally transported individuals from distant regions of a "continuous" mega-population communicate and copulate, what can we find or should we read into the results? (But some might view this experiment as an in-vivo molecular technique and make some use of it.)

What this means is that many of our "good" operational (cabinet) firefly species with such distributions, e.g. *Photinus pyralis* (L.) and *Photinus cookii* Green (Figs. 1-3), should only be thought of as bookkeeping (formally named, operational, working) species. We can imagine that once there was a gene-pool unity about each of them, and in the simplest of models and however spaced out they occur now, that each originally derived from a single, local population, a real and true biological species. But it is obvious that when we conceptualize about such species as these two, that we have a relativity problem, a riddle in space and time. Nevertheless, it is axiomatic that knowledge of the genetics of contemporary species-designates, and the tenuous and recent-past interconnections of their local populations are necessary for understanding what we seek to know about the existence of the things we call firefly species. Whatever notional fragments he eventually adopts into a mental construct, the fireflyer can never abandon the fertile seed present in the BSC.

What fireflyers could use is a simple but explicit conceptual framework, one which would include first an operational plan, and second, a comprehensible, somewhat theoretical overview and expectation of such "biological-species-gone-apart-too-far-too-long"—something as understood by Hall and Clements in their quotation given above. Fireflies, with their lights that identify not only them but their mating seasons, their micro-locale and -spreeing hot-spots, and even their

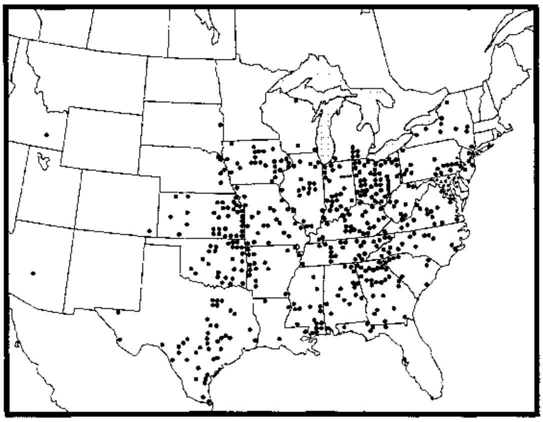

Fig. 2. Known geographic distribution of working species *Photinus pyralis* (L.), a seeming mega-population spread over a vast region. Locality records shown are from the examination of extensive museum and other archival holdings, and personal observations since 1963.

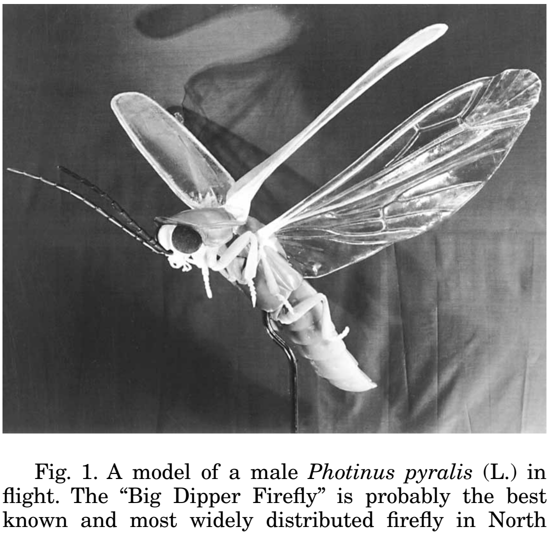

Fig. 1. A model of a male *Photinus pyralis* (L.) in flight. The "Big Dipper Firefly" is probably the best known and most widely distributed firefly in North America, and should be celebrated on a cereal box or in a book of records for having raced more children across lawns at twilight than any other species. This early-plastic sculpture was probably made in the 1950s and may be "lost" in a museum somewhere in northeastern U.S. It was made from a photograph taken by Frank McDermott which was published in a beetle journal in 1954. An article about it and the artist may have been published in the popular press, though this reference with the details has long been mislaid. This print was made from one found in McDermott's files after his death.

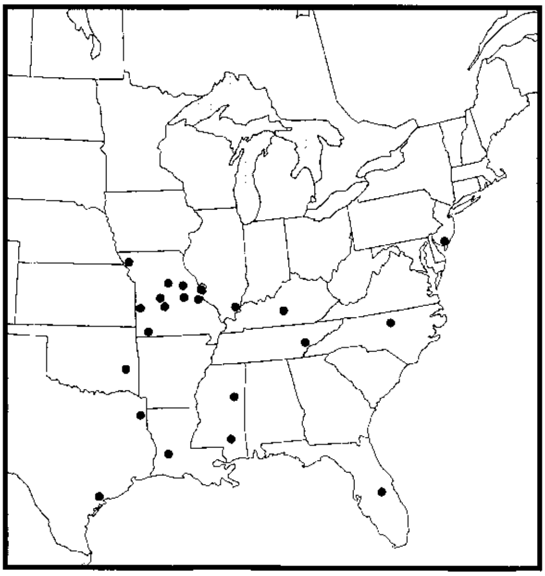

Fig. 3. Known geographic locations of (working) *Photinus cookii* Green, a seldom collected firefly with a fragmented distribution, based on examination of extensive museum and other archival holdings, and personal observations since 1963. There may be hundreds of local populations of this rarely collected species, and those represented here should be viewed in a comparative way, and understood as evidence for the occurrence of a relatively uncommon firefly.

wanderings, including travels among local active sites (demes), seem ideal for such study. And, incidentally, flashed patterns represent neurological hence soft parts of the phenotype, and maybe they sometimes evolve more rapidly than hard parts, and are more quickly tuned by selection to the exigencies of life, than characters that are usually available for such study and comparison? A useful image would also project us back in time just a little, for this reason: local populations in sites across the US and Canada may still reveal recognizable evidence of genetic population developments that occurred as a consequence of the Wisconsian glacier—North America's recent, omnipotent, geography-, climate-, and habitat-altering presence. What is more, geologists may be able to tell us how long ago these events took place!

One of the most significant intellectual moments I recall having as a graduate student was when my mentor explained that what I had discovered about the biology and distribution of a firefly—suggesting that it had started from west of the Mississippi River and moved eastward—was a pattern observed in several other organisms from orthops to snakes. I could imagine millions of flashes in the twilights of a few thousand summers, gradually moving eastward through a new prairie-like grassland across what is now Illinois, northern Indiana and Ohio, and into the corridor of the Mohawk Valley of New York. It was quite a "kick" to realize that I had found descendants of this little firefly, flourishing after generations of interbreeding with a "closest relative" in the Valley all the way to the Hudson River, and in particular, on the lawn of my boyhood home among glacial hills just south of the Valley.

SYSTEMATIST'S INTRODUCTION

In their Preface to "Species Concepts and Phylogenetic Theory: A Debate," editors Wheeler and Meier observe: "Surprisingly, and in spite of literally thousands of scientific papers relevant to the subject, there are more species concepts in popular usage today than at any point in the past century, and the consensus in zoology about the Biological Species Concept has begun to unravel. An aggressive search for a species concept that is consistent with phylogenetic theory has begun." I am truly glad for their progress . . . but a phylogenetic concept will not help fireflyers answer the questions they ask. After 38 years of chasing and trying to understand the species of flashing fireflies I see in the field—having taken up the flash-focused taxonomy begun by pioneers F. A. McDermott and H. S. Barber early in the 20th century—I would find no more comfort in phylogenetic species than in the metaphysical musings and promises of celestial guides. Fireflyers have a pretty good operational program for sorting, describing, and naming; what they need is to have this made a part of a comprehensive view that addresses the apparent, or "seemingly likely" genetic circumstances and reality of firefly populations in nature, in the here and now, and fairly recent past.

Here I must step to the front of the stage for a moment, and tell any outsider onlookers in the balcony that when working taxonomists and systematists, such as phylogeneticists, bacteriologists, virologists and fireflyers offer different points of view and come up with different so-called Species Concepts, we are wrestling the problems of how best to define or specify what we will term "species" for our own research needs and taxons' peculiarities. I suppose you might consider this a "lower case" species problem, and though there may be a connection with the species problem that philosophers of science have pondered—and led one to say, regarding "species":

> "It should be a matter of considerable embarrassment to biology that one of its central notions—indeed, one of its oldest concepts—should remain to this day the subject of heated intratheoretical controversy. No definition of the term has found universal adoption; indeed, some responsible biologists dispute its intelligibility altogether. Despite its apparently crucial role in the most imposing of biological achievements, the theory of 'On the Origin of Species,' the term is still without clear meaning." (Rosenberg 1985)

—it is the difference between a can of worms and Pandora's Box. (I think it should be a matter of considerable embarrassment to philosophy that after all of this time they still have not been able answer to some satisfaction, the most important question from their domain, "Why all of this?")

Our species problem has been with entomologists since Darwin, and a survey of the literature on the subject should convince nearly anyone except an end-timer that it is not likely to go away. There are numerous treatments of or around the subject, with titles that catch the attention and raise hopes of attentive and confused biologists: species, "the units of evolution" and "the units of biodiversity", their "concepts and phylogenetic theory", "as individuals", and the "metaphysics of"! One title in particular caught my attention—"Species: New Interdisciplinary Essays"—and am I glad I read a review first!: "More species concepts! I opened the book with a sense of foreboding. Its authors are anthropologists, philosophers and psychologists, as well as systematists. We biologists can't solve the species problem, so call in the shrinks, eh?" (Mallet 2000). The authors, the reviewer went on, and here I freely paraphrase his survey, lay out questions about whether there is more than one type of species, whether species are real or human constructs, whether species definitions are useful and to what extent are they are influenced by the history of human thought rather than biological reality, and whence our psychological need to classify organisms as species? Mallet suggests that "most authors were more interested in species concepts as a way of studying how we think." Such is not the view, review, or overview that a working virologist, botanist, phylogeneticist, or fireflyer will be looking for, at least until he permanently reaches some "higher and gray retirement of the museum and library."

Now, to address the species problem at the operational level, whence most nominal Species Concepts arise, along with the difficulties of cross-communication. When I get to it, I will use for comparison with natural history what may be the most dynamic though acerbic discipline of the bunch. But first, as prelude and predicate, consider this, from a book entitled "Why People Believe Weird Things": "'what there is depends upon what paradigm you hold. For Priestly, there literally was no such thing as oxygen. . . . In the case of Lavoisier, he not only believed in oxygen: oxygen existed' [P. Ruse]. . . . Similarly, for Georges Buffon and Charles Lyell, varieties in a population were merely degenerates from the originally created kind; nature eliminated them to preserve the essence of the species. For Charles Darwin and Alfred Russell Wallace, varieties were the key to evolutionary change. Each view depends on a different ontological paradigm: Buffon and Lyell could not see varieties as evolutionary engines because evolution did not exist for them; Darwin and Wallace did not view varieties as degenerates because degeneration is irrelevant to evolution." (Shermer 1997).

A Species Problem, 2001

cladists in our bio world
are electron quick; contention!
they will know a species is,
resolve, hot cold convention.
but chasing flashes as i do,
looking, seeking here and now,
i can't embrace mere digit bliss,
less kiss a sacred cow.
i follow little lights at night,
cross Boone's mounts and streams,
far from madding, clicking plight,
pc-peeps and ranting dreams.
alone, i hear "whose cooking?" owls,
Carr's "bean'n-bacon" frogs,
follow my own drinking gourd,
an odyssey in foggy bogs. (Fig. 4)

Now consider the unraveling of the BSC and the search for a concept that is consistent with phylogenetic theory. The long view into the past from a computer keyboard and detailed character matrix is not the same as the one fireflyers try to see. We peer across old fields through hedgerows and into the next old field, and beyond, and back to the northeastern forests and fire-maintained grasslands of the day before Europe arrived (see MacLeish 1994), to a summer after the Wisconsian Glacier. Perhaps biological species cannot exist for a phylogeneticist because in his much longer view, summers past with living populations are so compressed as to be but fragmented membranes of carbon between layers of shale. Consider what a fireflyer does within his membrane of time: he locates populations of flashed patterns in the field, makes electronic recordings of them, collects voucher specimens emitting them (to be examined under the microscope) and photographs them, and sends living vouchers to Johns Hopkins U. to have their bioluminescence spectra analyzed; he sees whether such pattern-flashers change their patterns through the evening, or in response to answering (female) flashes, or to different levels of male competition, or to variations in the vegetation they search, and whether any of their patterns match those of those of other species flashing at the same time and in the same space; and then, driving with head-lights off, the fireflyer finds other flash-conforming populations down the road, out of town, across the state, and over the mountain. If there is time, there is also consideration of cuticular hydrocarbons, mollecute and *Wolbachia* infections . . . and DNA. . . .

Fireflyers will be very interested in following developments in professional systematics' search for a phylogenetically useful definition/concept, because the data fireflyers collect may be organized, coded, ordered, and interpreted most objectively using the cladistic analysis procedures and perspectives developed in this arena, and with the kind help of phylogeneticists. We will view our tables of flash patterns with cladograms that are developed from their character matrices, for insight and interpretation, and then combine all of this with what we know about geographic and seasonal distributions. And then we will be able to look way, way back, long before the Wisconsian with the vision of the phylogeneticist. But this is not where we are now, and it is not to our point of light. We want to see each of our fireflies and flash patterns in the field and in as many populations as we can, and from this speculate and experiment with how flashed patterns and species may evolve (Lloyd 1984), and maybe even see something actually in progress among differentiating "conspecific" populations in the field, as Hall and Clements said we would. It's as simple, untechnical, unprofound, and myopic as that.

So that fireflyers will know where they might begin thinking about what we have called firefly species, and how early fireflyers thought, and how to explore the paths that fireflies have taken to be the way we find them, and to help students develop a conceptual framework that can carry them

Fig. 4. The tamarack swamp in Wisconsin where Eunice Myers, Herbert Barber's technician, and her student Bernard Boland on 8 July 1926 collected the *Photuris* specimens that Barber subsequently named *Photuris aureolucens*. Myers and Boland took me to this site in the summer of 1970 when I was learning Barber's species. Miss Myers noted that not much had changed in the years since they collected there, though when I visited the site in the 1990s the vegetation was much denser and the land was posted. This photo is from a Polaroid® print.

intelligently and heuristically from their bench to the field, and back, with a temporary shortcut through the long-accumulated literature, wisdom, confusion, dialogue, debate, frustration, and tension on the subject, here is a brief introduction.

Letter XXXX

The Firefly Species Problem, and A concept With A View For Fireflyers

"'To be is to be experienced.'
. . . That which falls beyond the possibility
of being experienced is not real.'"
(Berkeley, seen in Sahakian
& Sahakian 1993)"?" (jel 2001)

Dear Fireflyers, In our discussions of fireflies and their biology, especially their species-specific flashing, we have up till now spoken as though each named species was a real and natural entity in nature, and that the mission of firefly taxonomy was to discover and name every one of them that lives in North America—maybe even the World—to make them all available for research and conservation. Once upon a time biologists thought this was possible, but after decades of collecting, comparing, analyzing, thinking, and theorizing, it now seems fairly certain to many biologists that specialize in the fields of taxonomy and evolution that not only is such a project impossible, as incredible as it may sound, there actually is no general and real class of species-things that exists in nature. Thus, one should not ask or develop an introductory lesson on "real firefly species" around the question, "What is a species" but instead, should address such questions as "why is the reality of species questioned?" and "what, then, is the real (i.e., scientific) nature of the species-like entities that we observe—that have seduced everyman and taxonomists into believing in them with so much conviction for so long?" The uncertainty thus identified may be termed the "firefly species problem." A practical question to be answered is, "how, then, do we determine those entities that we should formally recognize with scientific names?"

Historical synopsis: For a century and a half after Linnaeus first named fireflies (1758), firefly taxonomists continued to name their species exclusively “on the pin” by their morphological distinctiveness, so judging their uniqueness, their “species-ness.” Given prevailing beliefs until Darwin’s “Origin” (1859), this seemed “theoretically logical,” though today we could simply view it as “theologically ordained.” Before Darwin it was presumed that each species of “Creation” had a unique and distinctive existence/character (≈ Essence), and representative specimens would not only fit their species’ Pattern, each Pattern, which is to say each species would remain unchanged through time, for they were as Plato’s circle and triangle, perfect and immortal. The work plan from this World View lingered for a long time after evolution was discovered, for although this Essentialist Concept of species was no longer carried in the mind, taxonomists at their bench continued with the same general methods for finding and naming new species—this is not a criticism, because when faced with millions of unidentified and unnamed pinned specimens, and the only information available about them is on their cuticle and labels, there is no alternative toward accomplishing mission impossible.

In the early and mid 1900s appeared two key contributions of significance for fireflyers: (1) Frank McDermott published a series of papers reporting that flashed mating signals were useful for species identification and reservedly used them to make a token but formal nomenclatural (name) change, and (2) Herbert Barber applied this thinking to show that the flash patterns of *Photuris* fireflies were useful taxonomic characters for the species-distinguishing problems this genus had long presented, aligning his approach with the best-informed evolutionary thinking of the time. These fireflies had given taxonomists fits for decades because their morphology seemed a hodge-podge of chaotic and relentless variation, never promising, always confusing, and beetle experts knew something fishy was going on—”some day somebody is going to split that thing up,” said Barber’s mentor E. A. Schwarz, of the catch-all *Photuris pennsylvanica*, in 1910.

Barber’s studies resolved a few specific problems, but more importantly he identified key elements of the larger puzzle of *Photuris*, and provided invaluable guides, practical examples, and intellectual encouragement for his successors. Unfortunately, publication of Barber’s work was suppressed until after his death and he never lived to see it receive the recognition it deserved. For one thing, it was deemed inappropriate for government employees to study insects that had no commercial or practical significance, and for another, museum taxonomists refused to accept the impractical notion that behavior should be used in classification (species “systematization”). They argued that one could not observe flash patterns on a pin, and as noted, virtually all of the specimens they processed were pinned or in vials of preservative. Barber’s futile response to this was written shortly before his death in a 1949 letter to McDermott: “Taxonomy from old mummies which fill collections is a misguided concept. It leads to the misidentification of rotten old samples in collections. How these poor fireflies would resent being placed in such diverse company—among specimens of enemy species—if they were alive and intelligent! What contempt they would feel for the ‘damned taxonomist.’” Long before this letter was written Barber had demonstrated that behavior could indeed be preserved on an insect pin (Fig. 5).

Barber was tuned to the old and legitimate understanding (<1700s) that members of a species could interbreed, with the emerging sophistication that members of a species formed a genetic population, and more to the point, he appreciated that his responsibility as a taxonomist was to work toward the discovery of such populations. He wrote in his notes in 1945: “. . . each species is an isolated self-perpetuating population, limitless in individuals by past and future generations, and . . . our taxonomy must correctly interpret these natural species which contrast so hopelessly with the customary ‘taxonomic’ species. . . . ” You may recognize that Barber’s view of species in 1945 was what one now learns

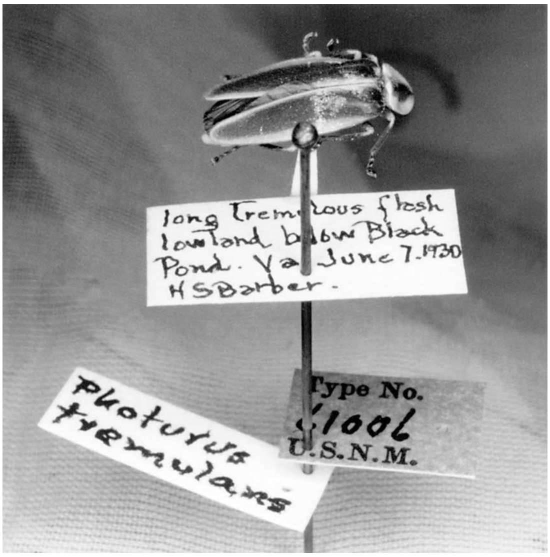

Fig. 5. One of Barber’s specimens, the taxonomic Type specimen and flash pattern voucher specimen of *Photuris tremulans*, which he observed and then captured in the lowland below Black Pond, Virginia, on 7 June 1930. This firefly emitted a long tremulous flash, according to the label, demonstrating that flash pattern data also can be put on an insect pin. Barber discovered that males of this species emit two distinctive flash patterns, one of his especially significant discoveries for fireflyers that use flash patterns for taxonomy.

in biology texts, and is referred to as the "Biological Species Concept" (BSC), though Barber included "past and future generations" providing an historical dimension, as found in the slightly more recent "Evolutionary Species Concept," a view used by some systematists today. Actually there are many so-called "Species Concepts," most intended to satisfy working requirements presented by different groups of organisms and the interests and focus of researchers (Table 1).

The BSC was mainstream thinking on species for decades (1940-1990?) in zoology, though not in botany, and not without serious and sometimes acrimonious debate and criticism, and when progressive museum entomologists looked at unit trays of elderly and faded *Photinus pyralis* and other specimens that had been identified via morphology, in their minds they saw populations and gene pools, so easily and thoroughly could the apparent logic of the BSC meld with work-a-day taxonomic thinking. When you next look at the masterful 1950s generic revisions of *Photinus* and *Pyractomena* by John Wagoner Green you will see that they are based exclusively on dead-specimen morphology, but the spirit of the BSC is present and comes through. In the jargon of Species Concept addicts and purveyors, Green used the "Morphological Species Concept" for his bench work on firefly taxonomy but he thought with the BSC, or an antecedent of it.

Firefly species brought into question. Now, with the level of understanding made possible by Green's revision of *Photinus*, it is possible to move on and ask basic questions about "nature's reality" and its presumptive "evolutionary units" using examples from this genus. Consider specimens identified in Green's key as *P. pyralis* (Fig. 1). The map in Fig. 2 is based on label data from more than 1200 specimens sequestered in more than thirty museums and individual collections, fireflies caught during twilights on the veranda, family travels, Fourth of July weekends, picnics, camping, and camp meetings, and the netting, pinning, labeling, and unbroken responsible preservation by hundreds of entomologists, beginning with a specimen in the Cornell collection from Peoria, Illinois, summer of 1875; another from Spirit Lake, Iowa, June 1896; and another caught "flying around lawn at evening" in Birmingham, Alabama, 1904. (Be reminded that on these antique dates, twilight trips at such localities could expose collectors to malaria or yellow fever!)

Is it reasonable, in view of such vast real-estate, virtually a half a continent, and the uncertainty of the efficacy of gene flow to maintain a population's genetic integrity, to consider *P. pyralis* a real and true biological (genetic) population, a species of nature, or again, a unit of evolution, as species are repeatedly being called? Toward finding an answer to this I have observed *P. pyralis* flash patterns, twilight activity, and various other "*pyralis*-typical" behavior at more than 300 localities throughout this broad distribution, unsuccessfully seeking eye-catching differences. In spite of this, and though *P. pyralis* is (now especially) ubiquitous, occurring along highway and powerline grassways, in pastures, meadows, and croplands, in lawns, parks, cemetaries, and orchards, does it make sense to perfunctorily accept *P. pyralis* as a biological species, without consideration and examination of mechanisms and circumstances that would make this possible, or impossible? How quickly must genes flow and what else must occur to hold such a population all together? Perhaps there are hidden (i.e. sibling, cryptic) species, such as Barber found in *Photuris*, and subtly different flashed mating codes that have evolved locally and trick resident *Photuris* femmes fatales in their deceptive predations, that have been overlooked?

TABLE 1. A LIST OF SO-CALLED SPECIES CONCEPTS, FROM VARIOUS SOURCES INCLUDING THREE (2+1) NAMED FOR ILLUSTRATION HERE, SEVERAL FROM R. L. MAYDEN, IN CLARIDGE, DAWAH, AND WILSON 1997, AND OTHERS FROM MAYR 1991.

Species Concepts

1. Nominalist Species Concept
2. Biological Species Concept
3. Recognition Species Concept
4. Morphological Species Concept
5. Evolutionary Species Concept
6. Essentialist Species Concept
7. Typological Species Concept
8. Phylogenetic Species Concept
9. Taxonomic Species Concept
10. Agamospecies Concept
11. Cladistic Species Concept
12. Composite Species Concept
13. Ecological Species Concept
14. Genetic Species Concept
15. Non-Dimensional Species Concept
16. Phenetic Species Concept
17. Successional Species Concept
18. Hennegian Species Concept
19. Cohesion Species Concept
20. Composite Species Concept
21. Geneological Concordance Concept
22. Internodal Species Concept
23. Polythetic Species Concept
24. Omnispective Species Concept
25. Extended-r Species Concept
26. [Ferris, Hall, Clements, and Barber's little-c Species (c)oncept]

With respect to gene flow serving as a glue to tie members of an overgrown population together as a species unit, studies on butterflies have shown that individuals do not necessarily move very far from their "birth(hatch)places" but we have no information about this for fireflies, and it could differ greatly among the various kinds of fireflies—a brachypterous female of *Photinus collustrans* LeConte is not going put her eggs far from her birth burrow. If *P. pyralis* is genetically connected across its broad span, perhaps the Mississippi River is enough of a barrier to retard flow such that differences can be detected in the DNA? Should it be that such huge and seemingly unmanageable populations are unitary, but certainly sluggish to change(?), does this result in detectable evolutionary stagnation for long periods of time? In the view I recommend, *P. pyralis* remains only a working species, one that invites us to learn more about and from it.

Another step into species/population uncertainty is illustrated by the firefly *Photinus cookii* Green. This is a daylight, dark firefly without a light, that is rarely found in museum collections, and seemingly occurs in relatively few, scattered localities (Fig. 3). Gene-flow connections are obviously tenuous, maybe stretched to the breaking point if not already broken at weakened joints in some places. (Remember, though, that there certainly are many, maybe even hundreds more local populations, and collections and map dots can only suggest relative abundance and site spacing.) When local populations are isolated what brings them to a speciation point—excessive time between contact, strongly differential selection pressures, narrow mate-selection criteria, local and idiosyncratic genetic disturbances (Table 2)? *P. cookii* too can correctly only be viewed as a working (morphological) species. At least in the case of *P. cookii* we can have some confidence that (individuals of) its local populations are reproductively isolated from all sympatric, closely related species—being lantern-less as it is—which is more than we can say about others in its species-group if they do not occur together (see below).

Florida's *Micronaspis floridana* Green (Fig. 6) illustrates the shoestring variation of this geographic isolation theme, because it is only known to occur at the edges of salt water marshes around the coast of the peninsula, between Volusia and Levy Counties (Fig. 7), and any gene flow among its populations must be linear and jumping, as on an island archipelago. Such distribution and spatial separation would be a common pattern in species whose suitable-habitat sites are isolated by inhospitable conditions, such as stream-bank (riparian) fireflies, especially those in the high and dry plains of west Texas, or species in the deep valleys of mountains in Colorado, and strand species along the shores of huge islands or bodies of water.

A more complex and instructional case of population isolation and the firefly species problem can be illustrated with two other species in Green's *Photinus* Division I—the species group to which *P. cookii* belongs. As you read the historical-fiction-based-on-fact account below, (1) note how these fireflies illustrate the occurrence of stochastic (long-shot, fortuitous) juxtaposition of re-

TABLE 2. POTENTIAL FACTORS IN THE EVOLUTIONARY COHESION AND DIVERGENCE OF LOCAL POPULATIONS. FLASHING FIREFLIES MAY LEND THEMSELVES TO GATHERING EMPIRICAL DATA AND THE QUANTIFICATION OF SOME OF THESE.

Factors In Deme Cohesion/Divergence	
Cohesion Enhancement	
1.	broad habitat utilization, generalists, little physical separation of inhabitable sites
2.	ecologically similar selection pressures
3.	extensive flight movement, local and emigration; winged females
4.	broad season of adult sexual activity
5.	synchronous mating of demes—astronomical cues?
6.	mate selection weak, tolerant
7.	female control of fertilization weak, mating system polyandrous
8.	internal (genomic) resistance to genetic variation, change
Divergence Enhancement	
1.	narrow habitat utilization, specialists, separation of inhabitable sites
2.	ecologically different and strong selection pressures
3.	little, weak flight movement; females flightless
4.	short season of adult mating activity
5.	mating among demes asynchronous—cues local conditions
6.	mate selection rigorous, narrow, progressive
7.	female control of fertilization strong, mating system monandrous
8.	weak internal genetic resistance to variation, "genetics in revolution"

Fig. 6. Habitus of *Micronaspis floridana* Green, the "Fiddler Crab Firefly." This firefly occurs around coastal marshes in Florida, and its larvae probably prey upon snails. See its known distribution in Fig. 7. Carbon-dust illustration by Laura Line.

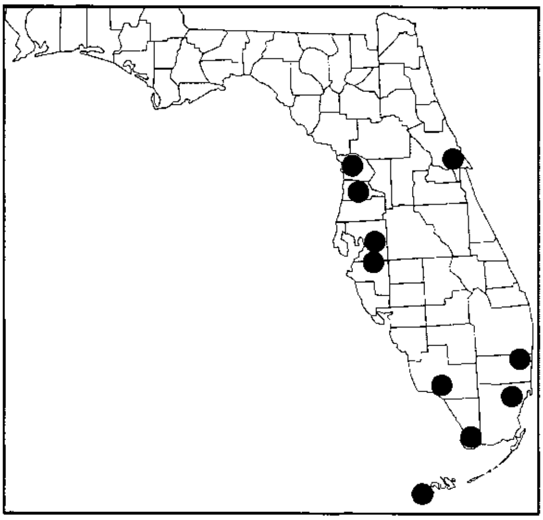

Fig. 7. Known geographic distribution of working species *Micronaspis floridana* Green, a shoestring distribution around the coast of Florida. The map is based on Green's data, my examination of museum and other archival holdings, and personal observations. Gene flow between Volusia County on the Atlantic and Levy County on the Gulf has probably been slow, even before the emergence of Ft. Lauderdale, Miami, and Tampa/St. Pete.

gional ecology and firefly population divergence in time and space, and then, (2) how they challenge us to think more about what we expect a "good and true natural species" is, or ought be, and the sometimes ephemeral nature of species, as well as of our own sound and well-reasoned conclusions in such matters!

Background: Known Division I fireflies, except for *P. cookii*, are generally twilight fireflies with yellow light and simple mating signals (male: single flash—female: "no" response delay, single-flash), each characterized and easily identified by distinctive male genitalia. These fireflies are "good species" by Morphological Concept standards, but we ask, if certain species combinations never occur together, if their geographic ranges do not overlap so that we can observe that they remain independent populations, are we justified in assuming any more about their "true" species status? This question broaches the issue of whether the "condition" of being a "natural" (real) species is something a population has unto (all by) itself, or is necessarily dependent upon its sexual/reproductive relationship to/with other such populations (correctly said: upon sexual relationships its members have with those of other such populations!).

Certainly a taxonomist would be justified in considering that a morphological species was more than mere working species if it occurred with (was sympatric with) a closely related species but there was no interbreeding. But, is this judgement for such a species only valid in respect (relationship) to this single other species? Sound silly?; think about it. Suppose distinctive morphological species never come into such contact; can morphology alone ever provide sufficient reason for considering them different natural (real) species? The species criterion in the first and simpler situation is the non-interbreeding relationship between the two sympatric populations; in the second, intrinsic features (e.g., distinctive morphology) of a population are accepted for making a nomenclatural decision. But, in this second case with no contact, real species-ness is only presumed, the decision arbitrary and untested, and unless the isolated populations are clearly, distantly related, we are only bookkeeping . . . aren't we? What would be a measure of "distantly related"? (I am not merely sandbagging here, i.e., tactically withholding "the answers" to these questions, being rhetorical for instructional purposes!)

We must return to basics for a suitable answer, like the losing football coach that on Monday holds up a ball and tells his team "this specimen is a football," we ask, to remind ourselves, what is the fireflyer's real intent, purpose, goal, and main focus in chasing "real species of nature"? It is to discover and understand the genetic descent of populations through time and space and learn the kinds of things that happen to them in their passages through time and space. To do this we need to name recognizable working units so we can share, discuss, and store/retrieve information about them. And, we must expect to intercept different genetic lineages at different points and stages in their individual evolutions, in trivial and permanent divergences, and sometimes even convergences. Our taxonomy and species identifications must, as Barber understood, promote this. Now, with this as prelude, the following is a brief and only a partly fictional account in the history of two Division I fireflies, as a simple instructive exemplar:

A Species-Problem Case History: *P. marginellus* LeConte has an extensive distribution in eastern NA and its close relative *Photinus curtatus* Green occurs from Kansas and Oklahoma eastward, in a teardrop-shaped distribution that narrows as it reaches western New York State, whence its influence is seen all along the Mohawk Valley eastward to the Hudson River as it interbreeds with *P. marginellus* in a "hybrid swarm" (Fig. 8). Hybrid populations present an array of genitalic intermediates between the two parent species (Fig. 9). In contrast, only a few questionable hybrids have been found west of New York State, though there is broad and long-time geographic overlap with potential contact and intermingling. After the Wisconsian Glacier retreated, following its maximum 18,000 years before the present (B. P.) occurred a xerothermic (warm dry) period, and a prairie-like grassland extended from the Mississippi River eastward across midwestern states and connected with an east-west (steppe-like) corridor in (what became) New York State. Several western species of organisms moved eastward along this so-called Prairie Peninsula, and *P. curtatus* apparently was one of them, pushing eastward, further into the range of *P. marginellus.*

If we had a time-machine, and at the Glacial maximum about 18,000 B. P. observed and collected specimens of this pair in the west and in the east we would have found two morphologically distinct populations, and would appropriately have named them as "good" (working) species. On a similar trip, say at 10,000 B. P. we might have found the two together in "Illinois," northern "Indiana" and "Ohio" not interbreeding,

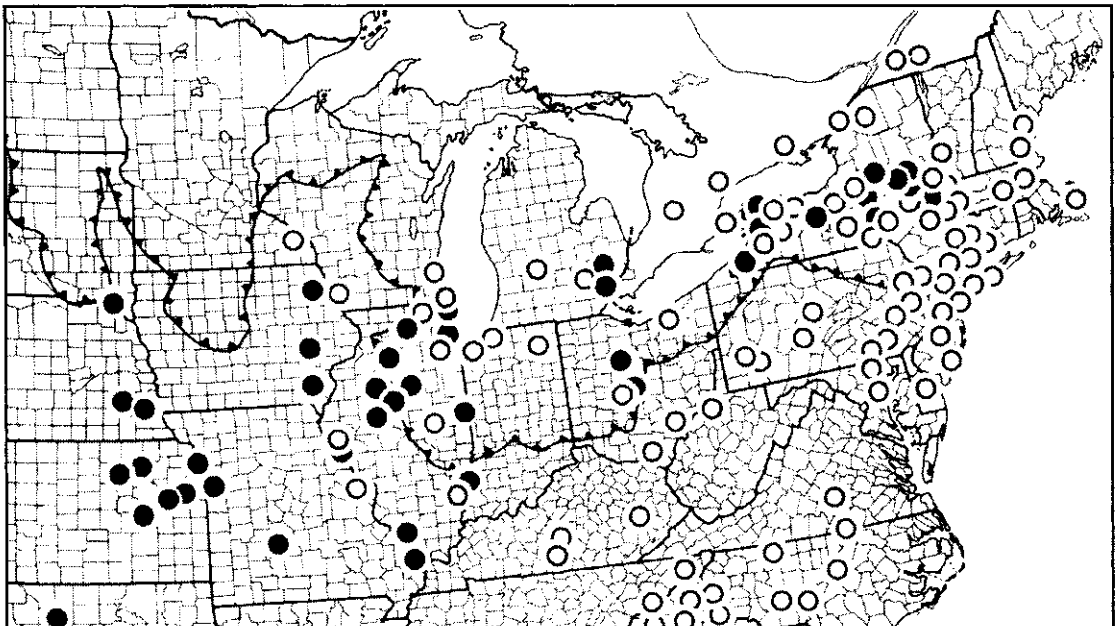

Fig. 8. Geographic distribution of *P. curtatus* Green (dots) and *P. marginellus* LeConte (circles). Where they overlap along the so-called steppe-corridor from Lake Erie east to the Hudson River occurs what could be termed a hybrid swarm, with an array of intermediates, based on the analysis of male genitalia. The toothed line shows the southernmost extent of the Wisconsian Glacier.

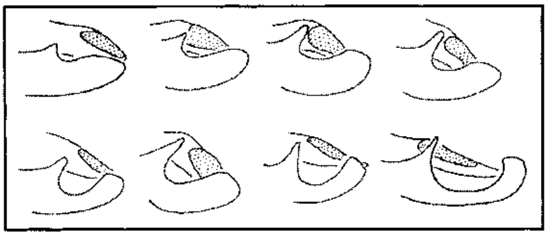

Fig. 9. Six examples of genitalic variation in the hybrid swarm of the Mohawk Valley, arranged between "pure" *P. curtatus* (upper left) and "pure" *P. marginellus* (lower right) from outside the region of sympatry. Each drawing shows a lateral lobe and the median lobe in a slightly dorso-lateral view.

and we could, with personal satisfaction, have recognized that our two working species were actually distinct evolutionary units, "real and natural" species. But, at 2,000 B. P. in apparent contradicton, we found the two hybridizing in the "Mohawk Valley." This is all reasonable, though unknowable, but at least possible. The point of this scenario for fireflyers: as we work today with living populations, we must expect to intercept firefly populations in obscure, mostly unknowable transitions, and recognize our species judiciously, with understanding and purpose, and in a manner that will disclose evolutionary questions and promote nomenclatural (bookkeeping) stability. (Can you develop another historical explanation for the data?; hint: would it help you to know where the questionable western hybrids were collected?—or how *P. marginellus* varies throughout its distribution?)

Postscript. The diurnal and lightless *P. cooki* occurs with several other Division I species, but there is no evidence that it interbreeds with any of them. Could mating interference and failed (e.g., sterile) hybridizations with close relatives with identical bioluminescent signals have been the reason for *cookii's* lantern loss and behavioral changes? Wouldn't it be neat if isolated local populations of working *P. cookii* reveal different degrees of divergence and lantern loss, and show us something of what has happened . . . is happening now? Also, note that in this Letter I have assumed that geographic isolation was the external factor responsible for the initial genetic isolation of the populations (the allopatric speciation model). This model is graphic, easily generating pictures in the mind, and is simple to grasp, but there is an alternative though too little is known about firefly biology to appreciate how it might work. This is the sympatric (same locality) speciation model as developed by Guy Bush from his studies on fruit fly host-plant preference. Perhaps a theoretical model could be invented for *Photuris* fireflies, say involving female aggressive mimicry and/or male flash pattern mimicry(?).

The bottom line of this section, in which I tried to bring the always-assumed, seemingly-obvious reality of firefly species into question and doubt, is spelled out in the next section where I will sketch a "work view with reminders" for seeking the reality of fireflies in nature.

Constructing a conceptual framework for chasing "real fireflies". According to a recent analysis there are 22 distinctively different nominal Species Concepts used in biology today (see R. L. Mayden, in Claridge et al. 1997). Table 1 lists several of these, and also some from the past that may now be extinct, and some I have invented here, but please, only for the moment! Though the term "concept" is confusing, because it should refer to a mental image or construct in the mind, it slipped into usage for non-formal, verbal definitions of species decades ago. With this usage a person may have more than one concept simultaneously—a working one for weekdays and a thinking one for Sundays perhaps! Concepts range between the operational, used for getting on with the sorting and naming bench work (e.g., the Morphological Species Concept), the philosophical, which address the learned/reflective nature of things (e.g., the Essentialist Species Concept, from Plato's supernatural world view), and the theoretical, an outline of what logically seems to be the hidden reality, the mystery of species, if we could only get to the bottom and crux of it scientifically, with observation and experimentation (the BSC in part).

A useful mental construct for fireflyers combines two elements: (A) a more inclusive alternative to the Morphological Concept, with (B) a theoretical stand-in for the BSC, made from fragments of Concepts listed in Table 1. The A part is self explanatory, and we use it when we inspect, organize, and describe our specimens, certainly with some thought to apparent genetic relationships, and make decisions about how the specimens and the populations they represent should be formally recognized or informally noted in the taxonomic literature. Part B is the theoretical and more difficult part of our mental construct, where we address the question raised at the beginning, "what, then, is the real nature of the species-like entities that we have observed?" I will develop these two notions, A and B:

(A) Working species recognition, characterization, and formal description can involve a variety of phenotypic attributes in addition to gross morphology, and were fireflyers to put a "Concept" name on it, we could call it the "Omnispective Concept," from the view that alpha taxonomy should be all-viewing in its search for species. According to the critical "Concept" analysis referred to, such a view is the equivalent of the Taxonomic Species Concept of botanists. Fireflyers in North America use a variety of characters including genitalia morphology, sclerite coloration, setal patterns, and luminescent signal patterns, but eventually other features, perhaps cuticular hydrocarbons, chromosome structure, and DNA will be used too.

(B) We must abridge the original BSC to construct a more genetically correct, heuristic, and user friendly theoretical concept. There are two parts of the BSC I want to "mend": First, the BSC directed attention to gene pools and populations, and embodied (genetically illogical) group selection, failing to recognize that it was the competitively breeding individuals of these populations that were the actual operative (selected) elements of species. There are a couple of images (models) that may be helpful guides and reminders for applying the necessary, so-called "selection thinking" scalpel (the hallmark of sociobiology and behavioral ecology). Here are two mnemonic images that can be used as crutches to remind us that a species must first and foremost be presumed to be nothing more than the aggregate of its participating free agents.—*The Firefly Tree Image*: This model finds an analogy (homology?) with the firefly trees in Thailand, New Guinea, Malaysia, and other exotic places in this part of the world, where multitudes of male fireflies gather in various broad-leaved trees, often along waterways, and some species emit their flashes in precise and splendiferous rhythmic synchrony. These pulsing treefulls were long explained solely as beacons that benefited other members of their species, with no analytical thought to how each individual firefly that burned his time and luciferin flashing for others was promoting the perpetuation of his own genes, the ones responsible for his behavior and chemistry. Truly, couldn't you just as easily make a genetic argument that the "beacon tree" phenomenon evolved for the navigation of Thai boatman? Today most students can appreciate that the logical genetic explanation is that each male is interacting, even cooperating with near-neighbors to maintain the species-identifying rhythm of his local spot on the tree (Figs. 10-12), and when an attracted female lands within his group, he will compete with his former cooperators now-become rivals until she chooses one (maybe more?) of them, or flies off to inspect males at other hot-spots on the tree. A pulsing treeful, a conspicuous reality in nature, nevertheless is the net result of interconnecting selfish cooperations over its foliage, and though it is real (i.e., not an illusion) and spectacular, no evidence has yet come to light that it is more than an *epiphenomenon* like a "cloud" of gnats shaped like a cedar tree or an airborne fish. The object lesson: view a species as the (mere) consequence of sexually selfish individuals of similar phenotypes and genotypes seeking mates and breeding with others that fall within each individual's window of acceptability; do this until empirical evidence or a reasonable genetic model suggests otherwise.

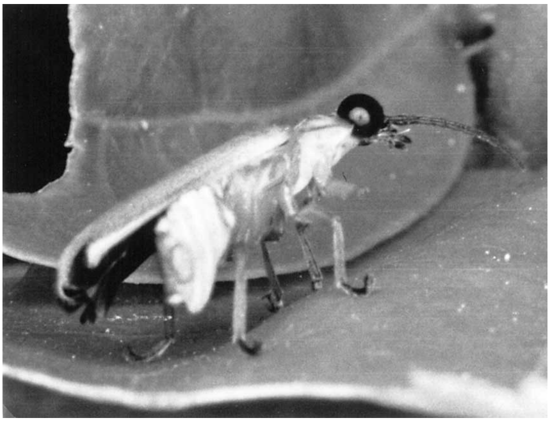

Fig. 10. An individual male *Pteroptyx valida* E. Olivier firefly in a Thailand nipa-palm swamp with his lantern aimed outward, illustrating the true essence of a firefly tree. Males are surrounded by rivals competing for fertilizations. His genes provided the instructions during development for the neural and structural mechanisms that make it possible for him to aim his lantern outward and flash attractively in the direction of approaching potential mates, as he burns luciferin that his own genes have manufactured correctly, in a reaction catalyzed by enzyme products (luciferase) of another of his time-tested genes. His flashing may also warn rivals to keep clear of his private landing space—perhaps it is the leaf in front of him—for incoming females, to which he will deliver copies of these genes.

Ecological Niche Image: This model adds a dimension to the well-known ecological niche concept. Sometimes ecologists speak of the aggregate (totality) of requirements for bodily (somatic) survival of a species as its ecological niche. In their species' niche is where individuals find food, places to nest, and so on. Likewise, a mate can be viewed as a niche necessity/dimension for genetic survival. A female has eggs, and must join with a cooperator, an injector of sperm. She needs a cooperator with DNA and accessories that are within certain restricted limits of variation, two of which we oversimplify and abbreviate (to our own confusion) as "of the opposite sex." and "of the same species." When next you see male fireflies cruising over an old-field seeking females, see lone-operators pursuing a limited necessity in their reproduction niche, surrounded by blood-rivals and the worst kind of enemies, looking for the same thing. The species to which they belong is merely the aggregate of all of the selfish individuals that seek cooperators in the same reproductive niche.

The second part of the BSC I want to "adjust" for fireflyer purposes is the view of the isolated but similar populations that the BSC includes in its sometimes omitted but nevertheless implicit phrase "potentially interbreeding populations." This is ok theory, for even if we cannot easily test it we can at least know that there often will be

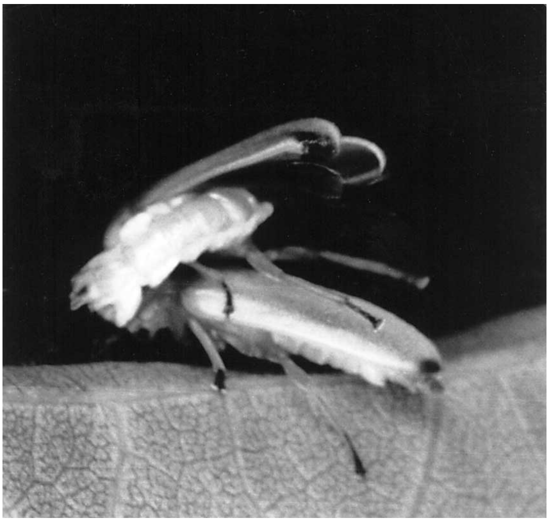

Fig. 11. A *P. valida* male atop a female, his back toward the camera and tail bent around in an "in your face" courtship, perhaps giving her a chemical message concerning his individual qualifications as a genetic cooperator in reproduction.

some isolated local populations that qualify. But, we want to emphasize our uncertainties about such populations, to promote suspicion, inspection, and analysis of them. We lump them all for bookkeeping convenience and out of ignorance, in the Omnispective (working species) part of our program, but we need to be reminded to think of such populations as an astronomer views other points of light in his expanding universe, as always moving away from his reference point where he sets up his telescope (the first local population we study), unless there is evidence to the contrary. There is a "definition" by Hall and Clements (1923) that makes this point very clearly, and I modify it only slightly here:—<A species is phylogenetic stock (breeding population), sprung from and related to similar stocks, and itself undergoing modification into a number of diverging branches. Because they have recently come from the same stock, these branches are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, *and at the same time they mark its further differentiation.*>

Fig. 12. A *P. valida* male (left) has maneuvered his elytral tips under those of the female and his abdomen tip under her abdomen, these structures forming a clamp that hold her for sperm injection and probably against separation and genital intrusions by other males. See Wing et al. (1983) for details.

As a "Concept" term for this "Part B," if there must be one, there is a useful analogy from the genetics of nuclear and extended families, the latter being relatives of decreasing genetic affinity as they have departed from each other and their ancestral common connection—an "Extended-r Species Concept"—analogizing from kin considerations of sociobiology (recall, siblings and parent-offspring generally have an r of 0.5, first cousins, 0.25, and so on). Populations tentatively included under this concept would initially be those identified in the Omnispective Concept, but they would remain under suspicion until research gave reason to view them differently. Some isolated local populations we especially want to follow, like the uncle from the down the road that moves to California to pan gold and is never heard from again, they may evolve off in a new direction; another may start to break away, remain in limbo for a while, then move back, regain connections, and remain become part of the Extended-r species network. (note that this imagery merely analogizes non-genetic social connections)

A patch-work synthesis for an Extended-r notion would incorporate fragments from the Biological, Nominalist, Recognition, and Evolutionary Species Concepts (Table 1), focusing on competitive individuals, the mate-recognizing-choosing fireflies making up the populations, and seeing back about 18,000 years to the Wisconsian Glacier, because this amazing mountain range of ice and out-flowing frigid air will have had a significant influence on North America's climate and ecology, and some firefly populations today can be expected to yet show evidence of its larger-than-life, continental presence.

Now, fuse the Omnispective and Extended-r Concepts into a single mental construct—call it the "Ferris, Hall, Clements, and Barber's little-c Species (c)oncept" if you wish (the FHCBc!; Table 1, no. 26), because together these men combine ideas and practices we want to be certain to adopt: the first one emphasized species as aggregates of individuals; the next two had a keen perception of populations (stocks) in nature in space and time; and the last was an omnispective fireflyer, careful in his field observations (and provided good voucher specimens), and theoretically aware, and he exercised farsighted yet conservative judgement in his use of zoological nomenclature—and was an intellectual and entomological inspiration to those who would next chase firefly species in field and lab, and he did it without electronic recording devices, a computer, or the approval of his politically sensitive bosses—who were never his superiors.

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