ARTICLES

CLASSICAL TAXONOMY OF MOSQUITOES—A MEMORIAL TO JOHN N. BELKIN[1,2]

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ABSTRACT. The major contributions of John N. Belkin to the field of mosquito systematics are noted. Hallmarks of his publications are presented and his hypotheses about the evolution, speciation, competition, distribution and classification of mosquitoes are summarized. The current status of the field of mosquito systematics is examined. It is argued that mosquito systematics is still largely at the alpha taxonomy level, that at best only 25-50% of mosquito species are known, and that we have not even begun to develop a natural classification for the Culicidae. It is concluded that there will be little improvement in the status of mosquito taxonomy unless there is increased support for systematics.

INTRODUCTION

The scientist we honor this year is John N. Belkin, one of the finest systematists ever to work with mosquitoes. He was a painstaking worker, a perfectionist if you wish, whose publications set the standard for accuracy and completeness that others must now strive to reach. He made major contributions to the field of mosquito systematics, contributions that will influence the field for decades to come. Among these are the development of: field and laboratory techniques for studying mosquitoes; a standard descriptive terminology for all stages of mosquitoes; an explicitly stated taxonomic methodology for mosquitoes; a classification scheme for all culicids; and hypotheses to explain the evolution, speciation and distributions of mosquitoes. Belkin amassed the finest research quality collection of mosquitoes in existence. If it is properly curated, it will be a priceless heritage for future generations. In recognition of his outstanding contributions to mosquito systematics, the American Mosquito Control Association awarded Belkin the Medal of Honor—the highest honor given by the Society—at the Annual Meeting in Salt Lake City in April 1980. Two weeks later he died.

I entered UCLA as a graduate student in systematic botany in 1961. As soon as the older graduate students in botany learned that I had an interest in entomology also, they told me about a fantastic systematist in the Zoology Department, a man who studied mosquitoes. That man was, of course, John Belkin. Since his course in "Principles of Systematic Zoology" was required of all students in systematic botany, the older graduate students were very familiar with him and his work. I met John the next year, and after discussing his research with him, I decided to pursue my doctoral studies under his direction. I finished my master's in botany and joined his research group shortly thereafter. John suggested several projects that I could undertake for my dissertation. Among these were a cytotaxonomic study of the *Anopheles* species in California, a revision of the crab hole breeding genus *Deinocerites*, and a revision of the tree hole breeding genus *Orthopodomyia*. All of these were projects in which John was interested. Because of my fascination with tree hole mosquitoes, I chose to work on *Orthopodomyia*. I completed my doctorate in 1967. Instead of leaving UCLA, I stayed and worked with John on his "Mosquitoes of Middle America" project. Because of my long association with John, it is perhaps appropriate that I present this memorial to him.

JOHN BELKIN AND HIS SCIENTIFIC CONTRIBUTIONS

On the personal side, John was a kind and generous man. He could, however, be a difficult man to work for. He demanded a lot of himself, and he accepted no less of others. On occasion, he would be brusque, irascible, obstinate. His demeanor and his encyclopedic knowledge were intimidating to many. But if a person wasn't deterred by John, and proved himself to be

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[1] Twelfth Annual AMCA Memorial Lecture delivered at the 56th Annual Meeting of the American Mosquito Control Association, Lexington, Kentucky, April 2, 1990.

[2] Acknowledgments are made to the Lowndes Engineering Company for their participation in sponsoring the 1990 Memorial Lecture.

capable and hardworking, then he would come to know the warm and caring person that John was. Everyone who worked for John for several years became, for all practical purposes, part of his family.

Belkin was born in Russia in 1913. His family came to the United States in 1928 and settled in New York. He attended Cornell University where he received his bachelor's and graduate degrees. During World War II, Belkin interrupted his doctoral studies to serve in the United States Army as Commanding Officer of the 420th Malarial Survey Detachment in the Solomon Islands. He spent 21 months on Guadalcanal Island, where he conducted a survey of the mosquito fauna of the coastal region (Figs. 1 and 2). Approximately 20,000 adult mosquitoes and an even greater number of larvae from this survey were preserved. This material formed the nucleus for his study of the mosquitoes of the South Pacific. During his stay on Guadalcanal, he developed the collecting and rearing techniques and data recording system that are widely used today. After the war, he returned to Cornell and completed his Ph.D. under Professor Robert Matheson in 1946. His dissertation was published as "Mosquitoes of the genus *Tripteroides* in the Solomon Islands" in 1950.[3]

In 1949, Belkin joined the faculty of the Department of Entomology at UCLA. His studies of the mosquitoes of the South Pacific continued through the 1950s and culminated with the publication of his classical 2-volume *Mosquitoes of the South Pacific* in 1962. As part of his research on the mosquitoes of the South Pacific, Belkin developed a standard morphological terminology for all stages of mosquitoes. He was a conservative man, and he chose to refine an existing terminology that was already in use rather than propose wholesale changes. He adopted and expanded the terminology used by Edwards for adult mosquitoes, by Matheson for male genitalia, by Martini for larvae and by Knight and Chamberlain for pupae. The system of nomenclature for the chaetotaxy of the larvae and pupae that is used by virtually all mosquito taxonomists today was developed by Belkin in a series of papers in the early 1950s.

One of Belkin's associates at UCLA in the 1950s was William A. McDonald. McDonald was an enthusiastic collector who made many valuable collections of mosquitoes in the southwestern United States and northern Mexico. McDonald and Belkin, individually or jointly, published several papers on the taxonomy and biology of mosquitoes found in Death Valley, CA, and the mountains of Arizona in the late 1950s. Belkin's attempt to identify crab hole mosquitoes collected by McDonald along the west coast of Mexico in 1956 led to the review of *Deinocerites* by John Belkin and Charles L. Hogue in 1959. The review of *Deinocerites* was Belkin's first major study of neotropical mosquitoes. Through it he learned that only fragmentary material was available for study, that characters used by others to separate the species of the genus were inadequate, that many misidentifications had been made, and that additional undescribed species existed. All in all, the study demonstrated to him our very limited knowledge of the mosquitoes found in the New World tropics, and it was instrumental in his decision to organize a project on the "Mosquitoes of Middle America." It was no accident that the geographic boundaries of the "Mosquitoes of Middle America" project nearly coincided with the distribution of *Deinocerites.*

Belkin's "Mosquitoes of Middle America" project began in 1962 and continued until his

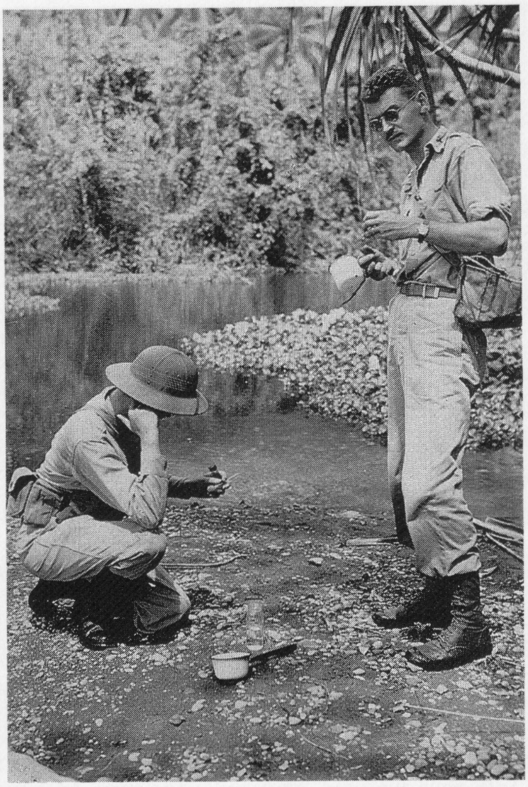

Fig. 1. John Belkin (standing) and colleague collecting mosquitoes on Guadalcanal during World War II.

[3] Complete citations to John N. Belkin's publications may be found in the bibliography of his papers prepared by Sandra J. Heinemann and George K. Bryce and published in Mosquito Systematics 12:285–289 (1980).

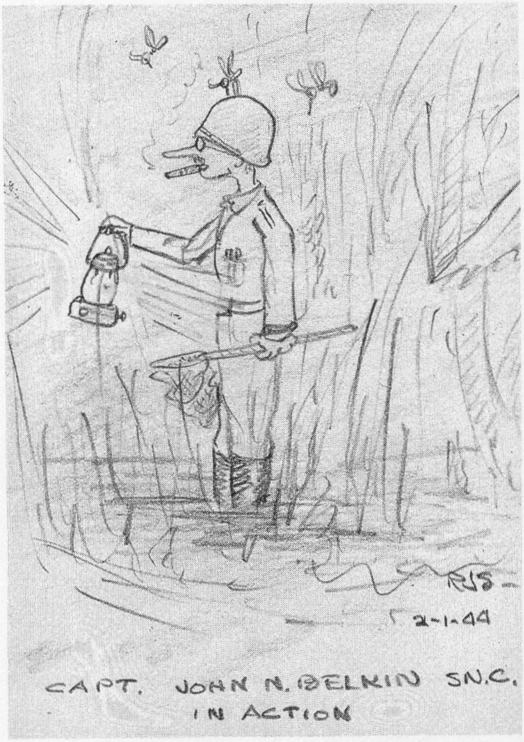

Fig. 2. Cartoon by R. J. Schlosser showing John Belkin collecting mosquitoes on Guadalcanal.

death in 1980. He did not believe it would be possible to discover and describe every species of mosquito in the American tropics in a lifetime. He did believe, though, that a lasting contribution toward the classification of the fauna could be made by careful taxonomic study of the species already known to exist in the region. Such a study would provide a framework into which species discovered in the future could be incorporated. To establish the identity of all species recorded from the region without doubt, fieldwork for the project concentrated on obtaining individual or progeny rearings of every previously described nominal taxon from its type locality.

A great many papers on Neotropical mosquitoes were published by Belkin, his students and co-investigators, and cooperators to the "Mosquitoes of Middle America" project. The papers with the most lasting value are, of course, the 15 or so revisions and regional studies. As important as these are, however, they treat only a fraction of the mosquitoes found in the Neotropics. The figures for Panama (Heinemann and Belkin 1978) can be used for illustration. By my count, there are 21 genera and at least 330 described or undescribed species of mosquitoes in Panama. Of these, only 10 genera were treated even in part, and only 70 species, or 21%, were described and illustrated in the typical Belkin fashion. Obviously, much work remains to be done.

During his career at UCLA, Belkin trained a dozen doctoral or postdoctoral students, the majority of them in mosquito systematics. Few of these have found permanent employment that has enabled them to utilize their training in mosquito systematics. It is a sad commentary on our times that several of Belkin's students hold nonacademic positions totally unrelated to their doctoral training.

Belkin's publications have several characteristics that distinguish them. One of their hallmarks is that many are major contributions to the field. Belkin was of the opinion that many scientific papers are so trivial that they are never read by anyone except the author. Rather than publish many minor reports, Belkin accumulated information until he had enough for a significant paper. Neither Belkin nor his students cluttered the zoological literature with redescriptions of holotypes, descriptions of previously unknown stages, lectotype designations or range extensions. All such matters were made part of a major taxonomic revision. Another hallmark of Belkin's publications is their thoroughness. He provided detailed descriptions of mosquitoes based on examination of many specimens, not brief diagnoses based on just a few typical specimens. He illustrated the complete larval and pupal chaetotaxy, not just the heads and tails of larvae. If a special terminology was needed, then he developed it. If background information on the geology or climate of a region was necessary to understand distributions, then he provided it. Yet another hallmark of Belkin's publications is their accuracy. Belkin was a meticulous worker. He developed various forms and ledgers to insure that data were recorded accurately and permanently. All manuscripts were proofed again and again to prevent as many errors as possible. The last hallmark of Belkin's publications that I will mention is, I believe, the most important of all. It is his attempts at interpretation. He tried to analyze the faunas he studied, and to make inferences about their origins, histories and evolution. He attempted to explain the origin of species and the basis for similarities and differences among them. For example, in the South Pacific, where others looked and only saw mosquitoes on islands, he looked and saw relicts of various ages. This begged for explanation, and he provided it in the form of multiple dispersals over continuous or nearly continuous routes that are no longer available, but whose existence could be inferred from bathymetric charts.

Several themes run through Belkin's publications. Some of these ideas or hypotheses were developed by Belkin himself; some were borrowed from other biological disciplines. Some are controversial views that have not gained widespread acceptance among culicidologists or zoologists in general. All these themes demonstrate, though, his overriding concern with analysis and explanation. One hypothesis that Belkin developed was that the intercontinental regions in both the Old World and New World tropics were "Centers of Origin" where major new adaptive types of mosquitoes originated. He saw the intercontinental regions as geologically unstable areas where land bridges were formed and fragmented repeatedly. During fragmentation, populations of mosquitoes would be reduced in size and isolated, creating the kind of situation that could lead to the rapid fixation of new adaptive types. These would become better adapted with time, and would disperse to adjacent regions when land bridges reformed. Belkin also saw evidence for other methods of speciation in mosquitoes. He proposed sympatric speciation as the explanation for the existence of flocks of closely related species in groups utilizing specialized, restricted breeding sites such as leaf axils and pitcher plants. Without doubt, the single most controversial proposition advanced by Belkin was that hybridization was a major factor in the speciation and evolution of mosquitoes. He saw evidence for hybridization in taxa of all ranks—species, subgenera, genera, tribes. At the species level, he considered hybridization as the most parsimonious explanation for the combination of blocks of characters from 2 species in the different sexes or stages of a third species. In the case of higher taxa, he believed that hybridization in the distant past was the explanation for the annectent groups that exist today. He reasoned that taxa that had formed in isolation on fragments of former land bridges may have been morphologically distinct but not reproductively isolated, and that they may have hybridized when the fragments rejoined. Belkin's familiarity with the role of hybridization in the speciation of flowering plants undoubtedly played a part in his willingness to embrace this concept for mosquitoes. More than 40% of flowering plant species are of hybrid origin. They are fertile tetraploids formed by doubling the chromosome number of partly or completely sterile hybrids between 2 diploid species. Belkin believed that he saw the same kind of morphological evidence for hybridization in mosquitoes that botanists saw in plants. He once told me that the only distinction between the situation in plants and the situation in mosquitoes was that botanists knew the mechanism by which hybrid species of plants formed, whereas we did not yet know that mechanism for mosquitoes.

Belkin was strongly influenced by ecological thought, particularly that related to competition. He did not believe that there could be 2 or more species of the same species complex breeding in the same habitat in the same area. In the section on methodology in his *Mosquitoes of the South Pacific*, he stated that he used data from morphology, bionomics and distribution. The bionomical data to which he referred were the habitats of the immatures. The first steps in his taxonomic procedure were to sort material to geographical source and habitat. His belief that 2 or more species of the same complex could not coexist in the same habitat went a long way in preventing the description of intraspecific variants, particularly hairy larval and pupal morphs, as distinct species. Belkin also saw competition as shaping entire mosquito faunas. His comments about the tribes Aedini and Sabethini are relevant in this regard. The greater number of sabethine lineages in the New World tropics relative to the Old World tropics could be interpreted as indicating that the tribe originated in the New World and radiated there in the absence of competition from aedines. Alternatively, if the sabethines originated in the Old World tropics, which was, by the way, what Belkin believed, then they had been largely replaced there by the more recently evolved plant-breeding aedine mosquitoes.

In interpreting distributional data, Belkin considered common, widespread mosquitoes to be the most recently evolved species in their group. He envisioned them as arising in a source area, which, for the faunas he was interested in, was an intercontinental area in the tropics, then spreading into adjacent areas when dispersal routes became available and eliminating previously evolved species. Species with limited distributions were considered to be relicts, or paleoendemics, particularly if they occurred in unusual habitats for their group or occurred near the limits of distribution for their group. Belkin believed most of the mosquitoes endemic to the islands of the South Pacific were older than their relatives in the source area to the west. They were relicts whose absence in the source area was due to extinction. Incidentally, Belkin considered the mosquitoes of New Zealand to be an ancient continental fauna, and the species of this fauna to be the most primitive living representatives in their phyletic lines to be found anywhere in the world. This belief profoundly influenced his ideas about the evolution of the Culicidae.

In the classification of mosquitoes, Belkin placed emphasis on characters of the immature stages rather than on the general ornamentation of adults or the secondary sexual characters of males. He believed larvae preserved phyletic characters better than adults. He went so far as to say that we needed to study all instars of larvae in order to develop a natural classification for the family. In the true mosquitoes Belkin recognized 12 tribes. This arrangement was a marked departure from recognizing only 3 coordinate groups, the anophelines, toxorhynchitines and culicines. It was Belkin's conviction, though, that the unusual features of anophelines and toxorhynchitines had been overemphasized, and that these groups were no more distinct than many of the lineages traditionally placed in the culicines. Furthermore, he did not believe that the culicines were a monophyletic group. In his *Mosquitoes of the South Pacific*, Belkin presented a list of the 12 tribes, placing the more generalized tribes centrally and the more specialized and annectent tribes at the ends of the list. This can be interpreted as a "phylogenetic bush," with the more specialized tribes radiating out in several lines from the central core of generalized forms. Groups considered to be primitive in more traditional classifications, like the anophelines and sabethines, were considered highly specialized tribes by Belkin. Although his classification is radical in its arrangement of genera, it continues the conservative tradition of recognizing only a relatively few genera for mosquitoes.

CURRENT STATUS OF MOSQUITO TAXONOMY

Where is the field of mosquito taxonomy today? The taxonomy of every group passes through 3 overlapping and intergrading levels commonly called alpha, beta and gamma taxonomy. At the alpha level of taxonomy, the main concerns are the discovery, characterization and naming of species. These species are placed into large, comprehensive genera. At the beta level of taxonomy, the primary concern is the development of a natural classification. The species are studied in greater detail and are reclassified into smaller and more numerous genera that indicate their genetic relationships more accurately. At the gamma level of taxonomy, the primary concerns are various biological aspects of organisms, such as the structure of natural populations, the genetic basis of phenotypic characteristics, the nature of isolating mechanisms, and the rates of evolution and speciation. This level of taxonomy emphasizes the interpretation of biological diversity. So, where does the field of mosquito taxonomy stand in this classification of taxonomies? Sadly, it is still by and large at the alpha taxonomy level. Emphasis is still on recognizing, characterizing and naming species. Even many who utilize nonmorphological techniques, like electrophoresis, are alpha taxonomists whose primary concern is the recognition and characterization of species. How many species of mosquitoes are there? How many more remain to be discovered? The rate at which species are discovered in any group of organisms can be depicted as a sigmoid curve (Fig. 3). The rate is slow initially, increases exponentially as interest in the group rises, starts to slow when more than half the species are known, and finally approaches asymptotically the total number of species in the group. The graph showing the total number of presently valid species of *Aedes* known at 25-year intervals from 1750 to 1975 shows the expected upturn, but gives no hint of slowing (Fig. 4). A bar graph showing the number of presently valid species of *Aedes* described in each 5-year period from 1900 to 1980 shows more variation in the rate of taxonomic work (Fig. 5). Those periods of time in which relatively few species were described generally coincide with times of warfare or economic depression. However, the period in which the fewest species were described is 1975–80. Does this slowing down indicate that we have found more than half the species of *Aedes*, or does it indicate only a decrease in taxonomic effort? I suspect it shows only the latter. If the rate of description of *Aedes* has not started to slow and if our knowledge of this genus is representative of the Culicidae in general, then we know less than half the species in the family at this time. Belkin believed that the 155 named zoological species of true mosquitoes that he treated in the *Mosquitoes of the*

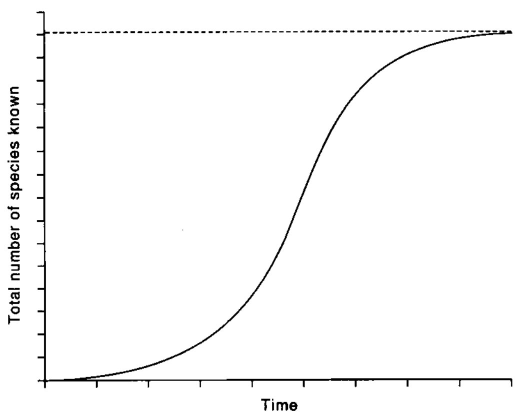

Fig. 3. Sigmoid curve showing the increase in the number of species known for any group of organisms. The broken line represents the total number of species in the group.

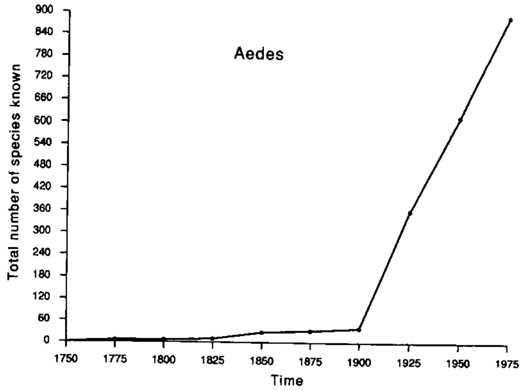

Fig. 4. Number of presently valid species of *Aedes* known at 25-year intervals from 1750 to 1975.

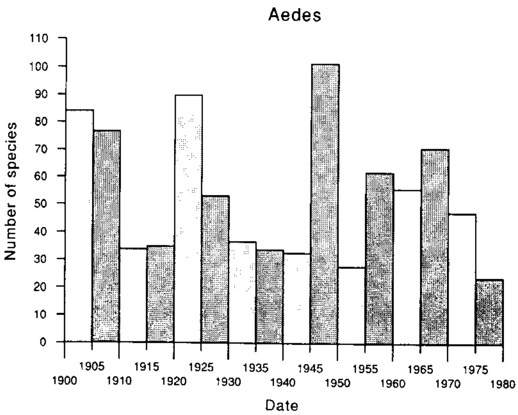

Fig. 5. Number of presently valid species of *Aedes* described in each 5-year period from 1900 to 1980.

South Pacific represented less than half the fauna, because practically no collecting had been done in the interior of any of the islands. Because Belkin described as new or resurrected from synonymy 77, or 50%, of these 155 species, the number of species known from the region before his studies may have been as little as 25% of the actual fauna. I would estimate, then, that we know at best only somewhere between 25 and 50% of mosquito species.

In those groups of organisms that have achieved the beta level of taxonomic work, it has been noted that a graph of the number of genera to the number of species per genus is a hollow curve that approaches both axes asymptotically (Fig. 6). At one extreme, there are many monotypic or ditypic genera. At the other extreme, there are only one or 2 large genera. In the middle, there are relatively few genera with just a few species. Mathematically, this curve is a hyperbola with the equation $XY = K$. For any group of organisms, K is the square root of the number of species in that group. For mosquitoes, the number of valid species presently known is about 3,146. The square root of this is 56. Theoretically, for mosquitoes there should be 56 monotypic genera and the largest genus should have 56 species. How different is the real situation! The graph for mosquitoes is almost a straight line (Fig. 7). We recognize only 3 monotypic genera and no more than 2 genera of any other particular size. At the right end of the graph, 6 genera with over 100 to nearly 1,000 species each are way off scale. The graph for mosquitoes is clear evidence that we have not even begun to develop a natural classification for the family. Incidentally, an estimate of the total number of genera that should, theoretically, be recognized in a family the size of the Culicidae can be obtained by integration of the equation $XY = 56$. The number is 225. We recognize just 37 at this time.

Not all taxa are studied at the same rate. Although study of mosquitoes is still at the alpha taxonomic level for the most part, there are some groups where study has reached the gamma level of sophistication. Included among these are sev-

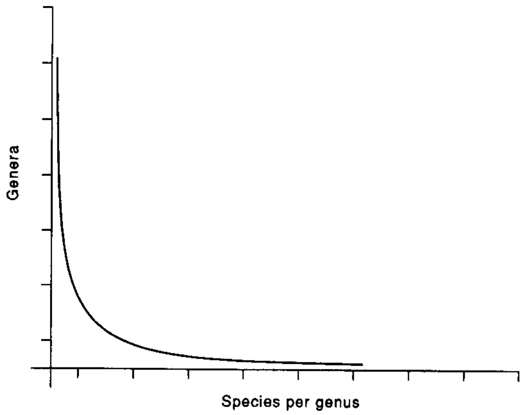

Fig. 6. Hollow curve showing the decrease in the number of genera as the number of species per genus increases for any group of organisms with a sound, natural classification.

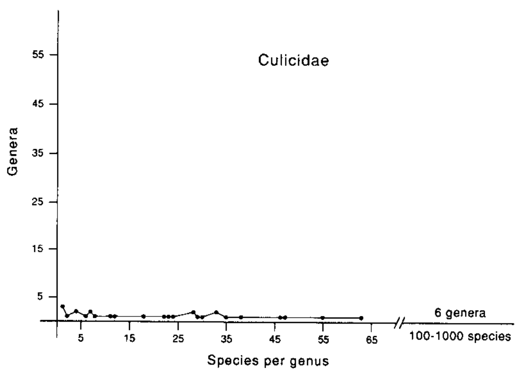

Fig. 7. Number of mosquito genera with the number of species indicated.

eral species groups in the genera *Aedes*, *Anopheles* and *Culex*. Interestingly, most gamma level taxonomic work done in the United States is done by individuals who do not consider themselves to be taxonomists. They are instead vector biologists, geneticists, evolutionists or ecologists. I used the genus *Aedes* as an example earlier, so let me use it again by saying that the various studies of groups of *Aedes* that have been done in the laboratories of George B. Craig and Karamjit S. Rai at the University of Notre Dame are among the finest gamma level taxonomic studies ever done on mosquitoes.

FUTURE OF MOSQUITO TAXONOMY

What is the future for mosquito taxonomy? Systematics is a much misunderstood and maligned science. As noted by Simpson years ago (1945), systematics is both the most elementary and most inclusive of the biological sciences. It is the most elementary because organisms must be discovered and named before we can study them and record information about them. It is the most inclusive because everything that is eventually learned about organisms is utilized in systematics to help recognize taxa and understand the relationships among them. Too many biologists have equated systematics with only the description and naming of species. They have failed to see the central role of systematics in the interpretation of biological diversity. As a result, systematics has been in long-term decline. The field is understaffed and underfunded, and relatively few students are being trained. The situation in mosquito systematics is essentially the same as that in systematics as a whole. The scientific community seems to be awakening to the fact that we know only a very small percentage of the species on earth. Some biologists estimate that the 1.5 million species of organisms we know are only 5% of the total that exist. The scientific community seems also to be awakening to the fact that the number of systematists is inadequate to perform the work that is still needed. In recent years a number of scientists have called for national or global biological surveys and have argued for greater support of systematics through the creation of positions, the funding of research and the training of students. Many biologists attach great urgency to these matters because the growing human population is accelerating the rate at which habitats are being destroyed and species are going extinct. Some estimate that 25 to 50% of the species on earth will be extinct within the next 30 years. Some even see this mass extinction of biological diversity as a threat to the survival of human civilization.

The future will be, I believe, exactly what the larger community of biologists wants it to be. If no value is given to systematic studies and the field of systematics continues to be understaffed and underfunded, then there will be little progress in mosquito taxonomy. There will be some revisionary work, but no major syntheses, no development of a natural classification and no major faunal studies. Gamma level taxonomic studies will continue, but a point will be reached where such studies will be hindered by the lack of a modern classification for mosquitoes. If, on the other hand, support for mosquito systematics increases, then the kinds of studies that will lead to the development of a natural classification of the family will be possible. Faunal studies like the "Mosquitoes of Middle America" and the "Southeast Asia Mosquito Project" should be resurrected and continued. It is only through major projects like these that the diversity of mosquitoes becomes known. Taxonomic revisions produced by projects like these provide the data that will ultimately lead to the development of a natural classification. That classification will, in turn, suggest innumerable hypotheses that can be tested by studies at the gamma level of taxonomy, and may provide some basis for understanding the interrelationships between mosquitoes and the disease-causing organisms they vector.

CONCLUSION

In conclusion, let me note that we all stand on the shoulders of our predecessors. The field of mosquito systematics is fortunate to have had a man with the intellect and motivation of John Belkin. He showed us the kind of studies that could be done and left us explicit instructions on how to do them. All that remains is to complete the work that Belkin had hoped to do himself.

ACKNOWLEDGMENTS

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REFERENCES CITED

Heinemann, S. J. and J. H. Belkin. 1978. Collection records of the project "Mosquitoes of Middle America." 10. Panama, including Canal Zone (PA,GG). Mosq. Syst. 10:119–196.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85:1–350.