

The Evolution of Integrative Insect Systematics

S. N. Okiwelu^{1*} and M. A. E. Noutcha¹

¹*Entomology and Pest Management Unit, Department of Animal and Environmental Biology, University of Port Harcourt, Nigeria.*

Authors' contributions

This work was carried out in collaboration between both authors. Author MAEN managed the literature searches and provided useful information on nucleic acid sequencing. Author SNO wrote the protocol and produce the first draft of the manuscript. All authors read and approved the final manuscript.

Review Article

Received 4th November 2013
Accepted 6th February 2014
Published 5th April 2014

ABSTRACT

Background: Traditional morphological taxonomy fails in some cases; even when it succeeds, the use of other disciplines significantly accelerates identification and enhances our understanding of the processes in speciation.

Arthropods: The arthropod tree of life is now divided into FIVE major branches: Pcnogonida, Euchelicerata, Myriapoda, Crustacea and Hexapoda. Crustacea and Hexapoda are in a clade, Tetraconata (Pancrustacea). *Blattaria* is more closely related to Isoptera; *Strepsiptera* is closely related to *Coleoptera*.

History of Entomological Classification: This history is segregated into four periods: Pre-Linnaean era, First century spanning Linnaeus' "*Systema Naturae*" to Darwin's "On the Origin of species", Darwinian Era up to the Cladistic Revolution, Hennigian Era leading to today. Classification in the pre-Linnaean era was based solely on morphological characteristics. Binomial nomenclature was developed in the first century. Phylogeny of insect orders along the lines of Darwinian evolution was evident in the third period. Hennigian Era utilized only taxa that are monophyletic. Cytogenetics, electron microscopy and DNA sequencing are widely used.

Integrative Taxonomy: In addition to morphological and molecular techniques, other disciplines (including Ecology, Behaviour, Reproductive compatibility, Life history, Zoogeography, Chemistry) are utilized. Integrated taxonomy does not replace traditional taxonomy but improves rigour.

Outcomes: Delimiting species by integrative taxonomy has yielded a better biodiversity

*Corresponding author: Email: okiwelu2003@yahoo.com;

inventory, by both increasing and decreasing species numbers. Increases have been especially due to the discovery of cryptic species. The arthropod tree of life has been re-evaluated.

Conclusion: The advances in systematics have been fuelled by: new sources of data from nucleic acid sequences, theoretical advances in the nature and analysis of systematic data, development of powerful, affordable computers and new statistical tools for data analysis, integrative taxonomy, etc. The disciplines of Insect Taxonomy and Insect Phylogenetics are complementary; thus programmes on Insect taxonomy should be inclusive.

Keywords: DNA Sequencing; evolution; integrative taxonomy; phylogenetics; systematics.

1. HISTORICAL FRAMEWORK

Systematics is the scientific study of organic diversity and the interrelationships among organisms. The word *systema* is Greek and can be defined as the classification of living organisms into hierarchical series of groups (*taxa*), emphasising their phylogenetic relationships. This inspired Carl Linnaeus (1707-1778) to produce his book *Systema Naturae* (1758) that remains the basis for systematics today. Unfortunately, some scientists have restricted systematics to emphasize hierarchical patterns [1] rather than incorporating the theory and practice of describing, naming and classifying organisms known as Taxonomy. Taxonomy is from the Greek word "*Taxis*" (=arrangement) and "*nomos*" (=law) [2]. The relationship of taxonomy to the whole of the discipline of systematics is similar to that of theoretical physics to the whole of physics [3]. The discipline of systematics therefore provides the basic tool for characterizing these organisms and the knowledge of their relationships to enable us summarize information, predict other findings and understand processes. The magnitude and cause of biological diversity are central not only to systematics but also a key problem in science. The general values of systematics are: generating major concepts in Biology and specific theories; and providing information by association, prediction, comparison and synthesis.

Systematics has been of value to other disciplines (Evolution, Ecology, Zoogeography), and led the way to the recognition of evolution and systematics developed a hierarchical classificatory system to respond to the diversity created by evolutionary forces [1]. Systematic studies in Entomology have provided key evidence for many of the inferences of zoogeography (the early separation of the southern and northern faunas of the land masses) and entomological fossil evidence documents distributional changes more directly [2]. Conclusions in ecology are limited if the taxonomic data are weak or incorrect. As Charles Elton (1900-1991), one of the founders of modern Ecology stated, "The extent to which progress in Ecology will be made depends upon accurate identification... cannot be impressed upon the beginner in Ecology. This is the essential basis of the whole thing, without it the ecologist is helpless, and the whole work may be rendered useless" [4].

Physiological and behavioural studies are assisted by comparative systematics. In some cases, Physiologists had been unable to repeat previous studies because of wrong identification of species. Consequently, voucher specimens should be preserved after studies [1].

Systematics is as old as any field in the biological sciences, but has undergone resurgence in the last four decades as a result of theoretical advances in the nature and analyses of systematic data. These advances are: the development of new sources of data from nucleic acid sequences; the development of powerful and affordable computers with which to analyse these data and the growth in the size and scope of natural history collections [5]. It is now a science driven by data, explicit hypotheses and quantitative analyses. The conceptual advances began with the work of the German Dipterologist, Hennig (1913-1976) [6], presented his work on Insect Physiology in book form, *Die Stammesgeschichte der Insekten* 1969. The posthumously published English translation was updated and annotated by a group of specialists who published in German in 1953 (translated into English in 1965). His new approach was phylogenetic systematics and currently referred to as Phylogenetics or Cladistics. Simply, the ideas are as follows: characters of a species are passed down from ancestors to descendants. Since species do not interbreed, characters from one species cannot be transferred to another; the appearance of new lineages, the process of speciation involves splitting an ancestral species into two or more descendant species. If a character changes or becomes modified from the ancestral state then the new derived character will appear only in the species in which it arose or in its descendants; therefore the sequence of appearance of lineages through time can be reconstructed by documenting the distribution of derived characters [5].

Taxonomy is broadly divided into three components. Alpha taxonomy deals with the species category, while Beta taxonomy deals with higher categories and Gamma taxonomy focuses on the analyses of intraspecific variations, ecotypes, polymorphism, etc [7]. The species category is unique in the taxonomic hierarchy, because it has claims to objective reality. Delimiting species is using empirical data to build explicit hypothesis as to which specimens belong to particular species taxa. Alpha taxonomy is central to biology. Species are the basic units of many fields and the species name provides the link to knowledge about an organism. The need for good alpha taxonomy is further increased by the biodiversity crisis, both for assisting conservation programmes and documenting diversity before it is lost [2]. Unfortunately, taxonomy's resources, including manpower, have been declining both in absolute numbers and in proportion to the rest of biology, and, this decline has strongly affected the field's vitality and accentuated the taxonomic impediment [8,9].

Taxonomy has been beset by problems; the most important is lack of funding. Funds are directed to phylogenetic, while thousands of species are threatened by imminent extinction [10]. There is a tendency among young and upwardly mobile ecologists to view museums and herbaria as "dusty" places for old people. Taxonomists often pay insufficient attention to the disciplines end users: ecologists, conservationists, pest managers and amateur naturalists who need or want to identify animals and plants [11]. There is progress. The launch of the Convention on Biological Diversity (CBD), which recognizes that taxonomists have a vital role to play in supporting biodiversity conservation, was a catalyst. In response to this declaration, the Global Taxonomy Initiative (GTI) was established to provide data for biodiversity conservation [12]. Several more initiatives (Species 2000; Integrated Taxonomic Information System) exist [13].

2. ARTHROPODS

Only 1.7 million species, approximately 10% of all biota, have been described since Linnaeus [14]. Arthropods, with nearly 85% of the described extant animal species and richest fossil record of any animal group are by far the most successful metazoan phylum [15]. Differences in opinion exist, regarding the relationships of the various arthropod groups

and the taxonomic levels at which they should be recognized. Triplehorn and Johnson [5] listed four major groups: Trilobita, Chelicerata, Crustacea and Atelocerata (Hexapoda and Myriapoda); novel approaches to studying anatomy with non-invasive, 3-dimensional reconstruction techniques to new and old fossils; and the so-called next-generation sequencing techniques were used to re-evaluate the arthropod tree. The arthropod tree of life is now divided into FIVE major branches: Pycnogonida, Euchelicerata, Myriapoda, Crustacea and Hexapoda Fig 1. The monophyly of each branch is well supported except the Crustacea, which is likely paraphyletic. The Crustacea and Hexapoda are in a clade named Tetraconata or Pancrustacea [16]. The Hexapoda consists of the Entognatha and Ectognatha (INSECTS).

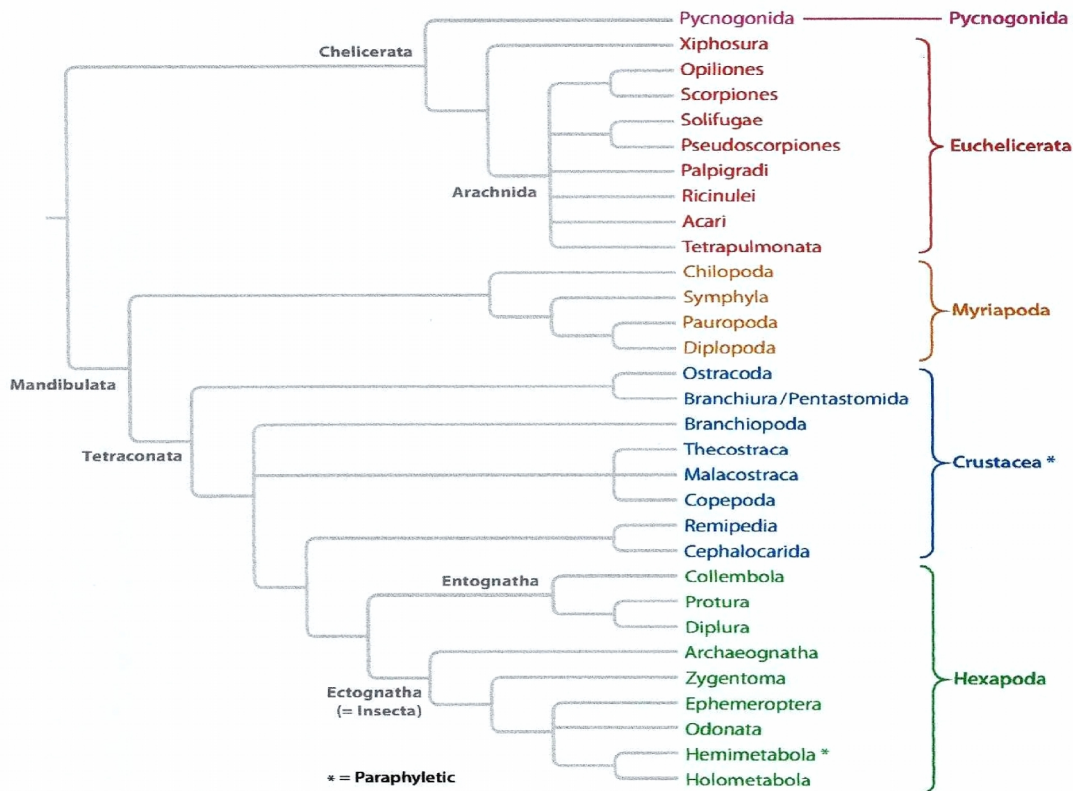


Fig. 1. Re-evaluation of the arthropod tree of life (Source: [16])

The first comprehensive attempt at establishing the phylogeny of the extant hexapod orders in the 21st century was by Wheeler et al. [17]. It was based on the marshalling of morphological and molecular data. The combination of 275 morphological variables, 1000 bases of the small subunit nuclear rDNA (18S) and 350 bases of the large subunit nuclear rDNA (28S) were subjected to a variety of analysis parameters.

The highlights of the results are: the Hexapoda is more closely related to the Crustacea than the Myriapoda; four non-Insectan Hexapodan orders (Collembola, Protura, Jopygina, Campodena) referred to as the Entognatha; two Apterygotan orders (Archaeognatha, Zygentoma) referred to as the Thysanura; the Dictyoptera that encompasses cockroaches and mantids is split into two orders, Mantodea and Blattaria; the Mallophaga (biting lice) and

Siphunculata (sucking lice) are shown to exhibit no major differences and are grouped in the order Phthiraptera; early divergence of the Hymenoptera that was considered a late divergent order among the Holometabola and the parasitic Strepsiptera (twisted-wing fly) earlier considered related to the Diptera is now described as more closely related to the Coleoptera Figs. 1 and 2. The dawn of the post-genomic era saw advances in insect phylogeny, utilising a combination of markers: morphological, rDNA, mtDNA, nuclear protein-coding DNA and phylogenomic data [18]. Some of the highlights of their results that are distinct from those of Wheeler et al. [17] are: Hexapoda and Crustacea are placed in the clade, Pancrustacea; the Blattaria more closely related to the Isoptera and the Isoptera considered “Social Cockroaches”; and the Strepsiptera (Twisted-winged, parasitic fly) more closely related to the Coleoptera Fig 3.

Despite these advances, insect identification is complicated by four factors: the vast number of different species; many insects are small and characters often difficult to see; many insects are poorly known, with little biological information and most usually only have technical names; insects have different stages in their life histories and one may only encounter a stage. Despite these drawbacks, identification had always been undertaken in five ways: availability of an expert; comparing the unidentified specimen with labelled specimens in a collection; comparing it with pictures; comparing it with descriptions; using an analytical key or by a combination of two or more of these procedures [5].

Historically, insects could be called by two types of names: scientific and common. Scientific names are used worldwide, while common names are local (specific to a language or people). Scientific names follow certain rules, outlined in the International Code of Zoological Nomenclature [19]. They are latinised but may be derived from other languages. The scientific name is a binomial, the genus and the specific epithet; that of subspecies is a trinomial. Scientific names are usually followed by the names of those who described them. If the name is in brackets, it means that the original description was in another genus. Names of categories from tribe to super family have standardized endings Table 1.

Table 1. Standardized endings of taxa

Taxon	Endings
Superfamily	oidea
Family	idae
Sub-family	inae
Tribe	ini

Recently, a new system known as the PHYLOCODE based more explicitly on evolutionary relationships instead of being grouped into ranks (genus, family, order, etc.) was suggested. Organisms are being assembled in “Clades”, defined as any set of organisms with a common ancestor [2,20]. Wagele [21] was very critical of this approach, emphasizing that it would not be accepted by the wider scientific community. Some researchers have also propagated an alternative to the time-consuming full identification of organisms in order to provide more rapid evaluation of regional biodiversity. It is referred to as parataxonomy which consists of sorting out the specimens to Recognizable Taxonomic Units (RTUs) [22]. The species are not identified but the specimens are grouped into RTUs by non-specialists on the basis of perceived differences. Although justified as a preliminary step; abuse may be dangerous. In synthesis, parataxonomy can help, but can never replace traditional taxonomy.

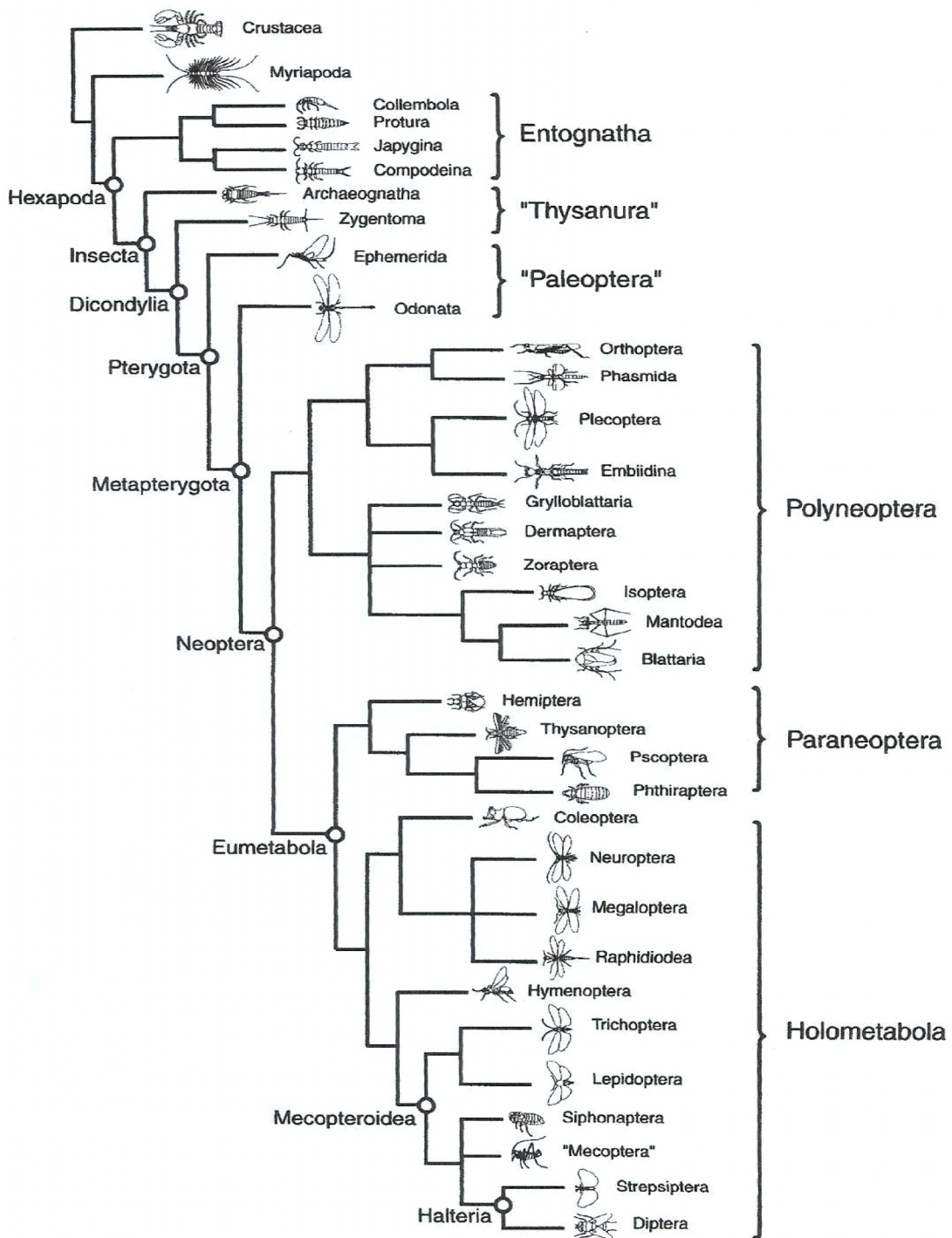


Fig. 2. Summary of hexapod relationships (source: [17])

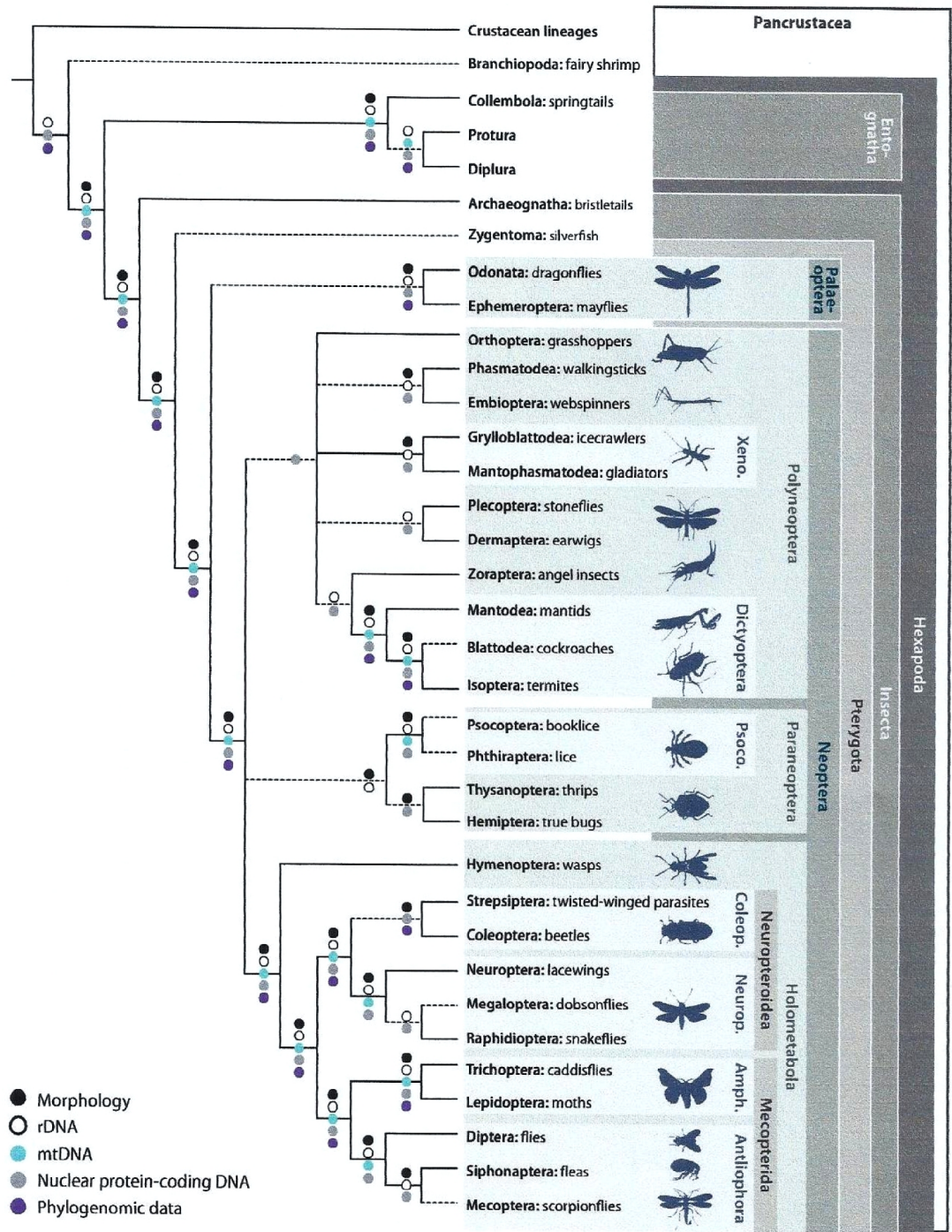


Fig. 3. Summary of Hexapod relationships at the dawn of the post-genomic era (Source: [18])

3. HISTORY OF ENTOMOLOGICAL CLASSIFICATION

The classification of insects has attempted to most effectively communicate information about this hyperdiverse lineage of life and not surprisingly has had a considerably rich historical development. The history can be coarsely segregated into four periods [23]:

- ❖ The pre-Linnaean era
- ❖ The first century spanning Linnaeus' "*Systema Naturae*" to Darwin's "On the Origin of species"
- ❖ The Darwinian Era up to the Cladistic Revolution
- ❖ The Hennigian Era leading to today

The pre-Linnaean period adopted one of the earliest surviving classifications of the natural world. Aristotle's "*Histoire Animalum*" is the earliest surviving work, based solely on morphological characters, in which a comprehensive organisation of insects is to be found [24].

The first century (1758-1859) was when Carl Linnaeus adopted uniformly his system of binomial nomenclature and in the tenth edition of his *Systema Naturae* put forth a system of classification of insects [25]. Linnaeus' foremost student, Johan Fabricius, the first systematist considered to specialize on insects, published in 1778, his *Philosophia Entomologica*, the first textbook of Entomology [26]. He considered mouthparts very important for classification. Fabricius had already set forth his system of insects in 1775 (*Systema Entomologiae*), his system of genera in 1776 (*Genera Insectorum*) and then numerous works on species, culminating in individual accounts of the species of each order. In the Darwinian Era (1859-1948), work on higher classification of insects continued largely unchanged following Darwin's publication. This was quite controversial to Haeckel who first depicted in his 1866 "*Generelle Morphologie*" an explicit phylogeny of insect orders [27]. In terms of serious entomological inquiry, it was arguably elucidated by Brauer, who made the first truly conceptual leap towards classifying insects along the lines of Darwinian evolution [28]. The second half of the 19th century saw the rise in influence of palaeontological evidence in understanding insect interrelationships [29].

The Hennigian Era (1949-present) began with Hennig's treatise [6], advocating the systematizing of organisms by synapomorphy alone, hence allowing only taxa that are monophyletic in the strict sense (having a history of their own), was referred to by Hennig as Phylogenetic Systematics. Since such systematizing is based exclusively on the branching pattern in the tree of life, it is called Cladistics (Greek, "Klados" = branch). Although some systematists use the term cladistics in a restricted sense, cladistics remains an appropriate term for all approaches to systematizing organisms according to the relative recency of common ancestry rather than some kind of similarity assessment. The core of what has been called the Hennigian or cladistic revolution in biological systematics is the restriction of the monophyly concept to taxa that include all descendants of their members' last common ancestor and the exclusion of all taxa that are non-monophyletic in this sense from the formal classification.

This era also witnessed the technical breakthrough in electron microscopy (EM) in the mid 1950s, scanning EM (SEM) a decade later added greatly to the precision of morphological observations and documentation. Chromosomal analyses in Cytogenetics with electron/fluorescent microscopy revealed the presence of puffs characteristic of certain species that took speciation a depth further. Computer aided approaches to phylogeny

reconstruction enabled analyses of sizeable character sets during the 1980s. In statistical analyses, the Bayesian inference and Markov Chain Monte Carlo techniques where the focus is on the probability of the parametric values given the data, instead of the Maximum Likelihood (ML) principle which maximizes the probability of the data, given the parameter values, enjoyed enormous popularity since they were introduced into phylogenetics in the mid-1990s [30, 31]. Biodiversity informatics, an emerging field that applies information management and analysis of species-occurrence, taxonomic character and image data is applicable in systemic Entomology. Its integration into the practice of systematics and collection curation promises to dramatically accelerate and improve the process of species discovery and description in the near future [32]. Although the term “biotechnology” had been in existence for a considerable time since it was first used in 1919 and again in 1938 [33], the term was only recognized much later. Probably the first recognition by the wider scientific community was with the publication of the Spinks report in 1980 (Biotechnology: the Report of a joint Working Party). The European Federation of Biotechnology [34] defines biotechnology, as the integrated use of biochemistry, microbiology and engineering science to achieve applications of the capabilities of microorganisms, cultured animal cells or plant cells or parts thereof in industry, agriculture, healthcare and in environmental processes. Biotechnological techniques became widely used in insect systematics, effective the 1980s. Gel electrophoresis of proteins was by far the most widely used molecular technique in insect systematics in the early 1980s [35]. Since Berlocher’s (1984) comprehensive review of molecular insect systematics, when emphasis was on Enzyme Electrophoresis, there were sweeping changes in molecular systematic [36], including the advent of polymerase chain reaction (PCR), and the development of automated sequencing [37]. Indicating temperatures and number of cycles when the DNA amplifies during Polymerase Chain Reaction (PCR). The serious use of molecular characters in classification of high-ranking insect taxa and identification of cryptic species was in the 1990s, initially drawing almost entirely on ribosomal DNA. Unfortunately, towards the end of the decade, there was an apparent lack of coordination in the breadth of insect systematics in the choice of markers [38]. This was in contrast to those of plant and vertebrate systematic communities. In these two cases a small number of generally accepted markers was singled out as standards, with the result that global phylogenies for these groups were emerging from amassed data.

The database of insect systematics grew rapidly, evidenced by bibliography. GenBank boasted of about 100,000 insect sequences; although 80,000 of those were *Drosophila* sequences, a substantial fraction had been in systematic studies [39]. Systematic studies in insects have examined around 40 protein-coding genes, all of the major ribosomal RNA genes (both mitochondrial and nuclear) as well as numerous non-coding regions. The number continues to grow as work on additional loci, most of which are nuclear protein-coding, make the jump from *Drosophila* studies to more general application. The diversity of available markers unquestionably furthered the cause of insect molecular systematics. However, the plethora of markers also brings with it the risk of pluralism, in that the use of different estimators among studies makes comparison and synthesis difficult or impossible [38]. The most commonly sequenced regions in insect taxonomy are mtDNA and nuclear rDNA. As contiguous pieces of DNA, these two classes lend themselves to easy comparison. The picture for nuclear rDNA is one of greater consistency. Sequencing much or all the 18S rRNA gene has become the standard for most high-level studies although there are exceptions. Generally, completed 18S analyses have supported relationships that are largely congruent with the previous hypothesis based on morphology [38].

DNA bar-coding is being proposed as a way to catalogue species [40]. This new technology makes use of short but specific DNA tags or barcodes to distinguish one species from

another. It uses a small part of the mitochondrial genome, 650-750 bases of cytochrome C oxidase I gene (COI) to provide a unique fingerprint of each species, but is no substitute for integrative taxonomy [41].

4. INTEGRATIVE TAXONOMY

In addition to morphological and molecular techniques, other disciplines have been utilized in systematics: Ecology (habitat, ecological niches, pathogen, symbiont, host or food plant association); Behaviour (mating-related, social or interspecific behaviour); Reproductive compatibility; Life history (spatio-temporal, physiological, reproduction-related, social traits, etc); Chemistry (Physical-cuticular hydrocarbons that form the basis for Near infrared Spectroscopy; Functional- sex pheromones, venoms); Zoogeography [42].

Crosskey first described the integrated use of cytomorphological, biochemical and zoogeography in identifying sibling species of *Simulium damnosum* complex [43]. This multisource approach that utilizes complementarity among disciplines has been called collaborative [44], combined [45], integrative [46], multidimensional [47], and multidisciplinary [48]. Three imperatives drive it: Morphological methods fail in some cases; other approaches assist significantly and speed the process; use of several methods yields results beyond just describing species [48]. Integrated taxonomy does not replace traditional taxonomy. Rather it compresses the traditional slow classical taxonomic routine of visiting a taxonomic problem repeatedly into one procedure by coordinating the findings of different disciplines under the procedure. By doing so, integrative taxonomy improves rigour [42].

Practising integrative taxonomy relies on a strong infusion of evolutionary biological thinking and many evolutionary biologists address species-level problem. Collaborations between evolutionary biologists and taxonomists are truly feasible. However, the workforce of taxonomists is small, 6,000-10,000 worldwide [42]. Thus serious taxonomic training for evolutionary biologists who delimit species is important. Such training helps alleviate the taxonomic shortage and increases research output in terms of nomenclatural consequences. Taxonomy then becomes increasingly understood in its logic and difficulties by a broader community, rather than being a term to be avoided in grant applications or when aiming at high ranking journals [49]. Yeates *et al.* criticized the use of the term integrative taxonomy because the multidisciplinary studies were exclusively qualitative [50]. They prefer the term "iterative" taxonomy for the current practice that treats species boundaries as hypotheses to be tested with new evidence. However their opinion has not received wide acceptance.

4.1 Integrative efficacy

Schlick-Steiner *et al.* used the ISI web knowledge to survey published studies from 48 journals during the period 1977-2008; 184 studies were selected that reported arthropod diversity at the species level using more than one discipline [42]. The methods were classified into 11 disciplines in order of frequency of use. The number of disciplines ranged from 2 to 8 per study Table 2. Schlick-Steiner *et al.* recommend choice of 3 disciplines because given the mean error rate of single discipline of 0.30 the combination of two disciplines should result in an average error rate of 0.09, and the combination of three disciplines in an average rate of 0.027 [42]. These average error rates represent those instances when disciplines agree but nonetheless are incorrect about the species in nature.

5. OUTCOMES

Delimiting species by integrative taxonomy has yielded a better biodiversity inventory, by both increasing and decreasing species numbers. Increases have been especially due to the discovery of cryptic species [51]. Species numbers have decreased through demonstration of conspecificity of nominal species, thus often ending longstanding taxonomic disputes [52].

Table 2. Performance of disciplines in the survey of arthropod literature

Disciplines	Species delimitation hypotheses			
	Total ^a	Delimitation Definitive ^b	Failure Rate	Performance superior to ^d
Morphology	359	302	0.23	Ecology
Mitochondrial DNA	284	235	0.33	Ecology
Nuclear DNA	142	119	0.28	Ecology
Ecology	72	65	0.60	
Enzymes	46	39	0.21	Ecology
Behaviour	27	24	0.08	Ecology
Reproductive compatibility	25	22	0.23	-
Life History	24	21	0.52	-
Cytogenetics	25	20	0.20	-
Chemistry	11	9	0.22	-
Whole Genome scans	9	8	0.38	-

Source: [42] ^aTotal number of delimitation hypotheses, ^bNumber of delimitation hypotheses for sets of specimens for which delimitation was thought definitive, ^cPortion of failure scores among delimitation hypotheses for sets of specimens for which delimitation was thought definitive eg: 68 of delimitation hypotheses by morphology for the 302 sets of specimens for which delimitation was thought definitive failed. Failure rate significantly lower than that of compared discipline (Fisher's exact test, $\alpha=0.05$, (Bonferroni-Holm adjusted)

Some of the most important outcomes of integrative taxonomy have been in Medical Entomology. The giant polytene chromosomes which are best developed in the larval silk glands provide a highly useful tool for discovering and identifying species. Giant chromosomes, particularly their banding patterns, reveal that many blackflies, *Simulium* spp. regarded as single species are actually complexes of two or more species known as cryptic or sibling species, each of which is biologically unique [43]. Dunbar and Vajime found that the *Simulium damnosum* complex in West Africa includes the migratory savanna pair of *Simulium damnosum* s.s. and *S. sirbanum*; the forest-species *Simulium squamosum* (Enderlein, 1921), *S. sanctipauli* (Vajime and Dunbar, 1975) and *S. yahense* (Vajime and Dunbar, 1975) [53]. Chromosomes of *Anopheles gambiae* complex show fixed paencentric inversion differences among the sibling species, as well as intraspecific inversion polymorphism [54,55] Plate 1. Near-Infrared Spectroscopy (NIRS), which quantitatively measures organic compound functional groups (O-H, N-H, C-H, etc) has been used in the identification of the sibling species of *Anopheles gambiae* s.l. [56]. A combination of disciplines (Cytotaxonomy, Near-Infrared Spectroscopy, PCR) has been used to identify at least 7 species (*Anopheles gambiae* s.s. (Giles, 1902), *An. arabiensis* (Patton, 1905) (inhabiting drier areas), *An. melas* (Theobald, 1903) (saltwater in West Africa), *An. merus* (Donitz, 1903) (saltwater in east Africa), *An. quadriannulatus* A and B (Theobald, 1911), *An. bwambae* (White, 1985) (restricted to Uganda) Fig. 4.

Anopheles funestus (Giles, 1900) is one of the three principal African malaria vectors; as with members of the *Anopheles gambiae* complex. *Anopheles funestus* shows marked genetic heterogeneity across the range. Currently, two unnamed species are recognized in the group with molecular and genetic markers, indicating that more may be present [58].

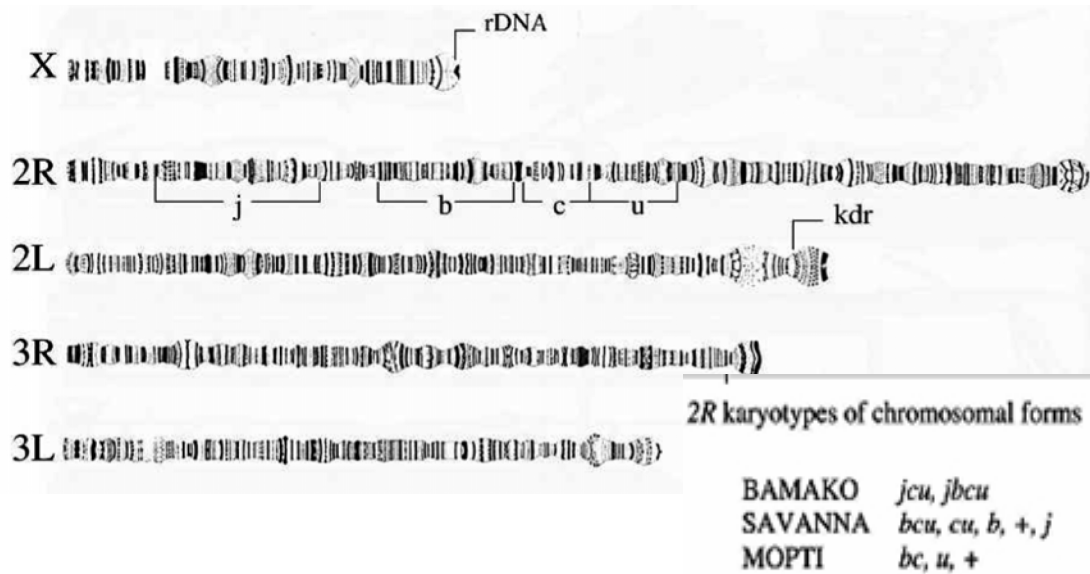


Plate 1. The inversions on anophelines polytenic chromosomes (Adapted from [55])

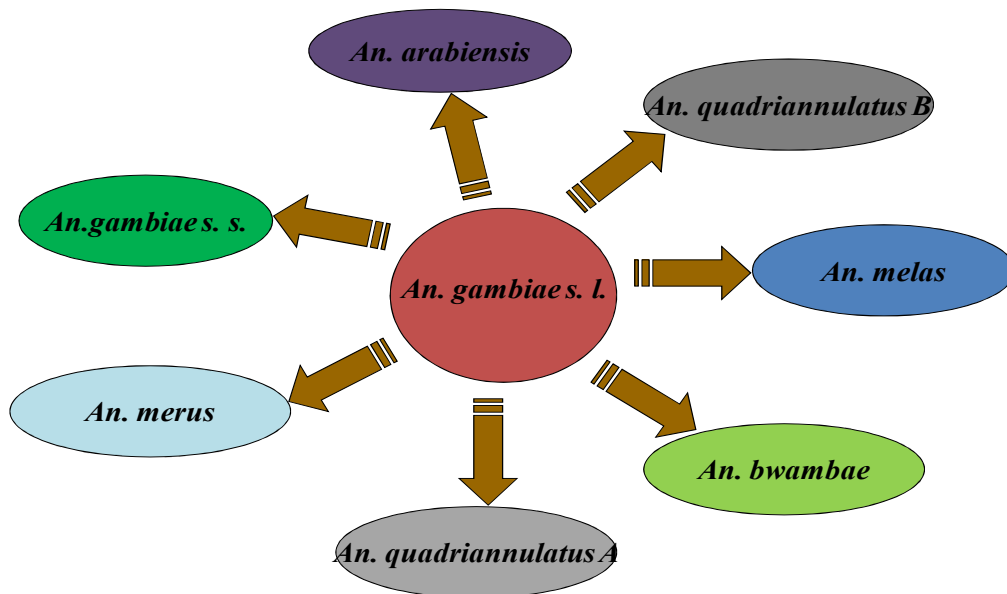


Fig. 4. The seven members of *Anopheles gambiae* complex (source: [57])

6. CONCLUSIONS

1. The advances in systematics have been fuelled by:
 - a. Theoretical advances in the nature and analysis of systematic data
 - b. The development of new sources of data from nucleic acid sequences
 - c. The availability of complementary data from a variety of disciplines
 - d. The development of powerful and affordable computers and new statistical tools to analyse these data
 - e. The growth of the size and scope of natural history collections
 - f. The integration of the emerging field of biodiversity informatics has dramatically accelerated the process of species discovery and description.
2. The re-evaluation of the arthropod tree of life: the closest relative to the Hexapoda is Crustacea, both in the clade, Pancrustacea; The Hexapod is NOT synonymous with Insecta but consists of the Ectognatha (Insecta) and Entognatha.
3. The establishment of the relationships of the extant insect orders: the closest relative to the Blattaria (Cockroaches) is the Isoptera (Termites) which have been described as "Social cockroaches"; the Strepsiptera is most closely related to the Coleoptera; the early divergence of the Hymenoptera among the Holometabola.
4. The new systematics has produced a more accurate inventory of biodiversity generally, and entomofauna specifically.
5. The disciplines of Insect Taxonomy and Insect Phylogenetics are complementary; thus programmes on taxonomy should be inclusive.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Danks HV. Systematics in support of entomology. *Ann Rev Entomol.* 1988;33:271-296.
2. Guerra-Gracia JM, Espinosa F, Garcia-Gomez JC. Trends in taxonomy today: An overview about the main topics in taxonomy. *Zool Baetica.* 2008;19:15-49.
3. Kapoor VC. Principles and practices of animal taxonomy. Science Publishers; 1998.
4. Elton C. *Animal Ecology.* Sidgwick and Jackson, London; 1927.
5. Triplehorn CA, Johnson NF. Borror & DeLong's introduction to the study of insects. Brooks/Cole, USA. 2005;864.
6. Hennig W. Kritische bemerkungen zum phylogenetischen system der insekten. *Beitr. Entomol.* 1953;3:1-85.
7. Disney H. Hands-on taxonomy. *Nature.* 2000;405:307.
8. Boert F. Light after dark: the partnership for enhancing expertise in taxonomy. *Trends Ecol Evol.* 2001;16:266.
9. Argnarsson I, Kuntner M. Taxonomy in a changing world: Seeking solutions for a science in crisis. *Syst Biol.* 2007;56:531-539.
10. Wheeler QD. Taxonomic triage and the poverty of phylogeny. *Philo Trans R Soc London B.* 2004;359:571-583.
11. Godfray HGJ. Challenges for taxonomy. *Nature.* 2002;417:17-19.

12. Taylor A. Taxonomy in support of biodiversity conservation- negotiating the acronym jungle. *Systematic and Biodiversity*. 2004;2:111-113.
13. Mallet J, Willmott K. Taxonomy: Renaissance or tower of Babel? *Trends in Ecology and Evolution*. 2003;18:57-59.
14. Wilson EO. A global diversity map. *Science*. 2000;289:2279.
15. Edgecombe GD. Palaeontological and molecular evidence linking arthropods, Onychophora and other Ecdysozoa. *Evol Educ Outreach*. 2009;2:178-190.
16. Giribet G, Edgecombe GD. Reevaluating the arthropod tree of life. *Ann Rev Entomol*. 2012;57:467-486.
17. Wheeler WC, Whitting M, Wheeler QD, Carpenter JM. The phylogeny of the extant hexapod orders. *Cladistics*. 2001;17:113-169.
18. Trautwein MD, Wiegman BM, Beutel R, Kjer KM. Advances in insect phylogeny at the dawn of the postgenomic era. *Ann Rev Entomol*. 2012;57:449-468.
19. International commission on zoological nomenclature. International code of zoological nomenclature. 4th Edition, London. 2000;306.
20. Barnes JM, Janzen DH, Hajjabaee M, Hallwachs W, Herbet PDN. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area of Conservacion Guana Caste Costa Rica. *Proc Natl Acad Sci, USA*. 2008;105:350-355.
21. Wägele JW. Foundations of phylogenetic systematic. Verlag Dr Friedrich Pfeel. Munchen, Germany; 2005.
22. Krell FT. Parataxonomy vs taxonomy in biodiversity studies- pitfalls and applicability of “monospecies” sorting. *Biodiversity and conservation*. 2004;13:795-812.
23. Engel MS, Kristensen NP. A history of entomological classification. *Ann Rev Entomol*. 2013;58:585-607.
24. Barnes J. Ed. The complete work of Aristotle. Princeton Univ. Press. Princeton NJ. 1984;1:2.
25. Linnaeus C. *Systema naturae per regna tria natura*. Laurentii Sawii. 10th Ed. Rev; 1758.
26. Fabricius JC. *Philosophia entomologica systema scientifica fundamenta*. Aedectis Definitionibus Exemplis; 1778.
27. Williams B. From Haeckel to Hennig: The early development of phylogenetics in German-speaking Europe. *Cladistics*. 2003;19:449-479.
28. Brauer P. Systematische zoologische studien. *Sitzungsber kais. Akad. Wissen Math-Naturwissen Klass. Abt I Mineral. Bot Zool Anat Geol Palaontol*. 1885;91:237-414.
29. Scudder SH. Index to the known fossil insects of the world including myriapods and arachnids. *Bull US Geol Surv*. 1891;71:1-744.
30. Yang Z, Rannala B. Bayesian phylogenetic inference using DNA sequences: A markov chain Monte Carlo method. *Mol Biol Evol*. 1997;14:717-724.
31. Renquist F, Deans AR. Bayesian phylogenetics and its influence on insect systematics. *Ann Rev Entomol*. 2010;55:189-206.
32. Johnson NF. Biodiversity informatics. *Ann Rev Entomol*. 2007;52:421-438.
33. Kennedy MJ. The evolution of the word biotechnology. *Trends in Biotechnology*. 1991;9:218-220.

34. European federation of biotechnology. Definition of biotechnology. EFB Newsletter. 1982;5:2.
35. Berlocher SH. Insect molecular systematics. Ann Rev Entomol. 1984;29:403-433.
36. Brower AW Z, DeSalle R. Practical and theoretical consideration for choice of a DNA sequence region in insect molecular systematic with a short review of published studies using nuclear gene regions. Ann Entomol Soc Am. 1994;87:702-716.
37. Mullis K, Faloons F, Scharf S, Saiki R, Horn G, Erlich H. Specific enzymatic amplification of DNA *In vitro*: The polymerase chain reaction. Cold Spring Harbor Symp Quart Biol. 1986;51:263-274.
38. Caterino MS, Soowon C, Sperling FA. The current state of insect molecular systematic: A thriving tower of Babel. Ann Rev Entomol. 2000;45:1-54.
39. Avise JC. Molecular markers, natural history and evolution. New York, Chapman & Hall. 1994;511.
40. Marshall E. Will DNA barcode breathe life into classification? Science. 2005;307:1037.
41. Ebach MC, Holdrege C. DNA barcoding is not substitute for taxonomy. Nature. 2005;434:697.
42. Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH. Integrative Taxonomy: A multisource approach to exploring biodiversity. Ann Rev Entomol. 2010;55:421-438.
43. Crosskey RW. Simuliid taxonomy- the contemporary scene. In Laird (Ed). Blackflies – the future for biological methods in integrated control. Academic Press London. 1981;339.
44. Malhotra A, Thorpe RS. Maximizing information in systematic revisions: a combined molecular and morphological analysis of a cryptic green pitvipiper complex (*Trimeresurus stejnegeri*). Biol J linn Soc. 2004;82:219-235.
45. Yader AD, Olson LF, Hanley C, Heckman KI, Rasoloarison R. A multidimensional approach for detecting species patterns in Malagasy vertebrates. Proc Natl Acad Sci USA. 2005;102:6587- 6594.
46. Dayrat B. Towards integrative taxonomy. Biol J Linn Soc. 2005;85:407-415.
47. Fisher BI, Smith MA. A revision of Malagasy species of *Anachetus* Myr and *Odontonachus* Latreille (Hymenoptera: Formicidae) Plos One. 2008;3:1787.
48. Pagel M. Phylogenetic inference methods. In Pagel M. (Ed). Oxford Encyclopaedia of evolution. Oxford University Press. Oxford. 2002;895-904.
49. Adams BJ. The species delimitation uncertainty principle. J Nematol. 2001;33:153-160.
50. Yeates DK, Seago A, Nelson L, Cameron SI, Joseph L, Trueman JH. Integrative taxonomy or Iterative Taxonomy. Systematic Entomology. 2011;36:209-217.
51. Bickford D, Lohman DJ, Sodhi NS, Ng PKI, Meier R. Cryptic species as a window on diversity and conservation. Trends Evol Ecol. 2007;22:148-155.
52. Steiner FM, Schlick-Steiner BC, Konrad HI, Moder K, Christian E. No sympatric speciation here. J Biol Evol. 2006;19:777-787.
53. Dunbar RW, Vajime CG. Cytotaxonomic analysis of the *Simulium damnosum* complex. WHO/ONCHO/71.87, WHO/VBC71.510. Monogr. Doc; 1971.

54. Coluzzi M, Sabatini A, Della Torre A. A polytene chromosome analysis of the *Anopheles gambiae* species complex. *Science*. 2002;298(5597):1415-1418.
55. Slotman MA, Della Torre A, Calzetta M, Powell JR. Differential introgression of chromosomal regions between *An. gambiae* ss and *An. arabiensis*. *Am J Trop Med Hyg*. 2005;73:326-35.
56. Sikulu M, Killeen GF, Hugo LE, Ryan RA, Dowell KM, Wirtz RA, Moore SJ, Dowell FE. Near-infrared spectroscopy as a complementary age-grading and species identification tool for African Malaria vectors. *Parasites & Vectors*. 2010;3:49.
57. Noutcha MAE. Identification, molecular and genetic characterization of *Anopheles gambiae* s. l. in selected communities in Nigeria and Cameroon. PhD thesis, Reference Section, Kenneth Dike Library, University of Ibadan, Ibadan, Oyo State, Nigeria. 2007;293.
58. Coetzee M, Koekemoer L. Molecular systematic and insecticide resistance in the major African malaria vector *Anopheles funestus*. *Ann Rev Entomol*. 2013;58:393-412.

© 2014 Okiwelu and Noutcha; This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Peer-review history:

The peer review history for this paper can be accessed here:

<http://www.sciencedomain.org/review-history.php?iid=486&id=32&aid=4247>