

Global trends in the description of aquatic and semiaquatic Heteroptera species, 1758–2004

John T. Polhemus & Dan A. Polhemus

Species description trends for the 4782 species of aquatic and semiaquatic Heteroptera (Gerromorpha, Nepomorpha, and Leptopodomorpha) named during the 246 year interval from 1758 through 2004 are analyzed in regard to number of species descriptions per year and cumulative number of species. These data are graphed both on a world basis, and for seven major zoogeographic regions (Palearctic, Nearctic, Neotropical, Afrotropical, Oriental, Australian and Pacific). This analysis reveals that our taxonomic knowledge of aquatic and semiaquatic Heteroptera, as measured by species descriptions, has accumulated at a progressively faster rate over time when assessed on a world basis, albeit in an episodic and uneven fashion, with peaks of high activity interspersed with periods of relatively low output. When examined at the level of individual zoogeographic regions, the accumulation of taxonomic descriptions is seen to be pronouncedly episodic, and contingent upon the productivity of particular regional experts during the courses of their careers, with just ten authors accounting for over 40 percent of all currently accepted species descriptions. Species accumulation curves, based on published descriptions, indicate that description of extant aquatic and semiaquatic Heteroptera species is nearly complete for the Palearctic and Nearctic regions, and well advanced for the Neotropical region. The Oriental and Australian (including New Guinea) regions show continuing sharp upward trends, indicating that these regions are still far from completely documented. The flattening of the description accumulation curves in the Afrotropical and Pacific regions is interpreted to be an artifact produced by a relative paucity of recent taxonomic work in these regions, and thus not truly indicative of well documented biotas in these areas. Rates of species description in aquatic and semiaquatic Heteroptera were highest immediately after World War II, a level of productivity that has been approached once again in recent decades. If the current average rate of 51 species descriptions per year can be maintained, the estimated 1100 species of aquatic Heteroptera remaining undescribed on a global basis will be formally named within the next 25 years, basically completing the taxonomic documentation of this group.

Dr. John T. Polhemus*, Colorado Entomological Institute, 3115 S. York St., Englewood, CO 80113, USA. jtpolhemus@msn.com

Dr. Dan A. Polhemus, Department of Natural Sciences, Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA. bugman@bishopmuseum.org

Introduction

The accumulation of taxonomic knowledge is often assumed to have been a steady and continuous process over time, following the introduction of binomial nomenclature by Linnaeus in 1758. However,

a close examination of the process for one particular group of insects, the aquatic and semiaquatic Heteroptera (constituting the infraorders Leptopodomorpha, Gerromorpha and Nepomorpha, and referred to subsequently as “aquatic Heteroptera” or “water

bugs”), reveals that this has not been the case. Instead, taxonomic knowledge, as measured by species descriptions, has accumulated at a progressively faster rate over time, albeit in an episodic and uneven fashion, with peaks of high activity interspersed with periods of relatively low output. When examined at the level of individual regions, the accumulation of taxonomic descriptions is seen to be pronouncedly episodic, and contingent upon the productivity of particular regional experts during the courses of their careers. In this paper we provide a detailed analysis of these trends from the pre-Linnean period to present, with particular emphasis on the 246 year interval from 1758 to the close of 2004.

Material and methods

In the preparation of this manuscript, we have examined the original descriptions of all 4782 currently accepted species of aquatic Heteroptera known to have been published through the end of calendar year 2004. Our analysis also includes pre-Linnean references to aquatic Heteroptera, the majority of which are in rare or obscure works. Many of these are held in the library of the senior author, and for the pre-Linnean period we have made direct reference to them, along with excerpts from more modern works on the history of entomology and biology (Duméril 1823; Nordenskiöld 1935; Raven 1947; Smith et al. 1973).

The graphs depicting the analyses from 1758–2004 of published names by year, and cumulative published names (Figs 1–16), are based on a manuscript catalog of aquatic Heteroptera prepared over a period of fifty years by the senior author and converted into an electronic data base of currently accepted species-group names with the help of the junior author and others. This data file does not include fossils or synonyms, but does include all currently accepted species that are valid species group taxa as defined by the Code of Zoological Nomenclature through the end of 2004.

Because the emphasis of this paper is on discovery and documentation rather than distribution, the large scale zoogeographic region to which each species has been assigned is based on the type locality of the species, if one can be determined, regardless of whether the species is known to have a more widespread distribution. The only taxa for which we have failed to constrain a definite type locality within a given zoogeographic region are two pantropical species of *Halobates* collected by Johann F. Eschscholtz on the ship *Rurik*, commanded by Otto von Kotzebue on a voyage that circled the globe during the years 1815 to 1818 (Eschscholtz 1822).

The zoogeographical regions utilized (Fig. 17) are those defined by Polhemus & Polhemus (in press) in a paper analyzing global patterns of species richness in aquatic Heteroptera; these regions also closely conform to those defined in the *Catalog of Palaearctic Heteroptera* (Aukema & Rieger 1995).

History of descriptive work on aquatic Heteroptera

The pre-Linnean era

The first putative references to aquatic Heteroptera that we can positively identify are found in Guillaume Rondeletius (1555). Here he gives “De Cicada fluviatili” along with a crude woodcut that Frederick Bodenheimer (1929) lists as “= *Naucoris*? a water bug”, but Izya Kerzhner (in litt.) believes may be a corixid, because Rondelet largely followed Aristotle’s works, and the Greek considered any sound-producing insect a “cicada” (Aristotle and Pliny were the only classical authoritative sources of entomological study recognized by the church in the Renaissance period). Rondelet also makes reference to “De Musca fluviatili”, although with no accompanying figure, which Bodenheimer (1928) listed as “= *Notonecta*.” We suspect that there are probably a few other references to aquatic Heteroptera not evident to us, hidden away in more ancient works, particularly from Asia.

In 1592, Georg Hoefnagel published elaborate plates that included good figures of *Nepa*, *Notonecta*, a *Corixa* nymph, *Gerris* and *Hydrometra*. These are the earliest accurate water bug figures we have seen. Bodenheimer (1928, Band I, p. 306) also reproduced the crude figures of *Gerris* and *Nepa* from Joh. Bauhin’s 1598 *Fauna Bollandensis*.

During the second half of the 1500s, several workers were rushing to publish the first book entirely on insects. As it developed, Ulysse Aldrovandi (1522–1605) and his assistants easily won the “race” with the publication of *De Animalibus Insectis Libri VII* in 1602 (with later editions in 1618, 1623 and 1638); the section on water insects also includes starfish and marine worms. Aldrovandi was a field worker, collecting and observing many of the insects that he wrote about, and because Gessner, his contemporary, never published on insects (see below), he was essentially on his own for this work. He had his draftsman and scribe with him in the field to record observations and draw selected insects, including *Ranatra*. Much under the influence of Aristotle and other scholastics, he was nonetheless a pioneer of pure natural research and stands out among the compilers of his time. He produced the first known dichotomous key for the

higher groups, all morphologically defined.

Conrad Gesner (1516–1565), who compiled one of the finest zoological works of all time, the *Historia animalium*, comprising about 3500 pages, was preparing a section on insects when he unfortunately died of the plague in Zurich. Edward Wotton (1492–1555) also prepared manuscripts on insects at the same time. Thomas Penny (1530–c.1588) acquired some of these manuscripts, and spent 15 years preparing to write a book on insects, but finally gave the materials to his young friend Thomas Mouffet (1553–1604), who reorganized them, added his own comments plus about 150 more figures, and prepared but never published a Latin manuscript. His widow sold it to Theodore Mayerne who finally published it in England in 1634 (Mouffet 1634). This work included water bugs illustrated with rather crude woodcuts. An English translation was published later in 1658 as volume 3 of Edward Topsell's *History of Four-Footed Beasts and Serpents* (Egerton 2003).

A later compiler, John Jonstonus, published comprehensive books in 1653 and 1657 (which are essentially the same) that depended almost entirely upon Aldrovandi and Mouffet, and lacked any really new contributions. The illustrations were taken almost exclusively from the publications of these two authors, but for the first time were based on copper engravings.

The invention of the microscope opened entirely new opportunities for detailed examination of insect morphology and anatomy. The first to carefully study water bugs with this new tool was the religious fanatic Jan Swammerdam (1637–1685), a Dutchman who produced incredibly accurate and detailed drawings of the anatomy of various insects including tiny lice, and the water scorpion *Ranatra linearis* Linnaeus (which at that time was lumped with the terrestrial scorpions). He also created a system that classified insects as ametabolic, hemimetabolic and holometabolic (although he did not use these terms), a system still used today. These observations were in his principal book, the *Bybel der Natuure*, brought out in Leiden in 1737–1738 by Boerhave and Gaubius in both Dutch and Latin, long after his death; this work was subsequently translated into German, French and English (Swammerdam 1758). John Ray (1628–1705) and Swammerdam proposed classification systems of insects roughly on the same basis (Ray 1710). Ray's book has only a few water bugs on pages 57–58, without figures, as *Cimex aquaticus figurae longioris* (= *Gerris lacustris* Linnaeus, 1758), *Cimex brevis* (= *Saldula saltatoria* Linnaeus, 1758), *Notonecta primae* (= *Notonecta glauca* Linnaeus, 1758) and *Scorpio lacustris* (= *Nepa cinerea* Linnaeus, 1758).

In 1720–1738 Johann Leonhard Frisch (1666–1743) published in 13 parts the *Beschreibung von allerley Insekten in Teutschland* (Berlin 1720–1738) that has many excellent observations, including some on water bugs. Each part has a fold-out plate illustrating various insects that he discussed in the text. In part 6 he claims to have heard sound production in *Naucoris* (= *Ilyocoris cimicoides* (Linnaeus, 1758)).

Carolus de Geer (1720–1778) made many important observations on insects, including water bugs. He was Swedish but of Dutch origin, studied in Utrecht, and was so impressed by René Réaumur's work that he published his "journal of observations" with the same title in French (de Geer, 1773). One aquatic Heteroptera species carries his name because, although he gave Latin diagnoses in pre-Linnean style, Anreas J. Retzius (1742–1821) tabulated these in the correct Linnean way in his *Caroli de Geer genera et species insectorum* (Retzius 1783). Volume 3 has an entire section on water bugs, with excellent figures of some, i.e. *Salda littoralis* (Linnaeus, 1758), *Hydrometra stagnorum* (Linnaeus, 1758), *Aquarius najas* (De Geer, 1773), *Gerris lacustris* (Linnaeus, 1758), *Nepa cinerea* Linnaeus, 1758, *Notonecta glauca* Linnaeus, 1758, *Ranatra linearis* (Linnaeus, 1758), *Ilyocoris cimicoides* (Linnaeus, 1758), *Sigara striata* (Linnaeus, 1758), and *Lethocerus grandis* (Linnaeus, 1758).

Overall, in the 200 years of natural history works prior to Linnaeus, only eleven species of aquatic Heteroptera had been treated in any way. All but one of these were European taxa.

The Linnean Era

Carolus Linnaeus (1707–1778) studied in Leiden from 1735 to 1738, where he published first editions of several important works on zoology and botany. Among these was his *Systema Naturae* (Linnaeus 1735), which recognized four orders of insects; used a nested system of classes, orders, genera and species as never before; and in one stroke set up the classification system for organisms that is still in use today. Three species of aquatic Heteroptera were included in this work: *Tipula aquatica* (= *Gerris lacustris*), *Notonecta aquatica* (= *Notonecta glauca*) and *Scorpio aquatica* (= *Nepa cinerea*).

Linnaeus' 12th edition (published in 1766, with a new printing in 1767 that is page for page exactly the same as the 12th edition) was long considered to be the starting point for zoological nomenclature (the "Strickland Code"), until this was changed to the 10th edition of his *Systema Naturae* (Linnaeus 1758) by the International Commission on Zoological Nomenclature at the Fourth International Congress in Cambridge in 1898, and adopted by the Fifth

International Congress in Berlin in 1901. Our analysis therefore deals with taxa described from 1758 until 2004. The 10th edition treated just twelve species of aquatic Heteroptera: nine from the Palaearctic region, two from the Afrotropical region, and one from the Neotropical region. Eleven of these had been described or figured in various earlier works. This contrasts with the current 4782 species of aquatic Heteroptera described as of the end of 2004, plus another 1100+ morphospecies known but undescribed (Polhemus & Polhemus in press).

Johann C. Fabricius (1745–1808) was the star pupil of Linnaeus, and concentrated heavily on entomology. While Linnaeus described about 2000 species of insects, Fabricius, working first in Copenhagen, Denmark, then in Kiel, Germany, named nearly 10,000. Even so, his total included descriptions of only 25 water bugs that are currently accepted today. His first major work was the *Systema entomologiae* in 1775, followed by six more major works culminating in *Systema Rhyngotorum* in 1803, which lists eleven Gerromorpha, six Leptopodomorpha and 35 Nepomorpha. His *Philosophica Entomologica* in 1778 was the first entomology text book.

Ambroise Palisot de Beauvois (1752–1820) was a contemporary of Fabricius who described insects from Africa and America, many of which he collected himself, in *Insectes recueillis en Afrique et en Amerique* (1805–1821). As such, he was one of the few early taxonomist field workers. The above contains descriptions of four species of Nepomorpha from the New World.

This period also saw the publication of the first books devoted entirely to Heteroptera. Caspar Stoll (?–1795) published a beautifully illustrated iconography on “Cicaden en Wanzen” from 1780 to 1788 but, while useful, this work did not adhere to the Linnean system. Somewhat later, the German Johann F. Wolff (1778–1806) published his only work, *Icones Cimicum*, in 5 parts from 1800 to 1811 using the Linnean system. Neither of these workers described any new water bug species.

Post-Linnaean era

In the 100 years following the introduction of the Linnean system, only 277 species of aquatic Heteroptera were described. This situation began to change rapidly after 1850. Carl Stål (1833–1878) wrote some of the most important works on Heteroptera still in use today. Although he only published 66 new species of water bugs, he produced the *Hemiptera Fabriciana* (1868–1869) and *Enumeratio Hemipterorum* (1870–1876), a pair of works that are very useful in dealing with the early names.

Odo M. Reuter (1850–1913) also authored some

very useful works, especially his *Revisio Synonymica Hemipterorum Palaearcticorum* in 1888 that dealt with publications from Linnaeus 1758 to Latreille 1806, with a critical analysis and discussion of synonymies. He also provided a number of monographs including one on Saldidae in 1912.

Overall, the majority of the world's currently known aquatic Heteroptera were described during the twentieth century. The most significant contributors to this effort, defined as those workers who have described more than 150 currently accepted species group taxa, are listed below:

- John T. Polhemus – 457 from all zoogeographic regions.
- Raymond A. Poisson – 348 (including many subspecies) mostly African, with some Palearctic.
- Dan A. Polhemus – 330 from all zoogeographic regions.
- Herbert Zettel – 315 (including many subspecies) mainly from Southeast Asia.
- Carl J. Drake – 313 from all zoogeographic regions, but with a Neotropical concentration.
- Herbert B. Hungerford – 282 from all zoogeographic regions.
- Nico Nieser – 235 from most zoogeographic regions.
- Arnold L. Montandon – 185 from all zoogeographic regions, mostly Nepomorpha.
- Nils M. Andersen – 183 from all zoogeographic regions, mostly Gerromorpha.
- Ping-ping Chen – 156 mainly from Southeast Asia.

The list above contains some degree of overlap in numbers due to co-authorship of taxa, but even with this factor taken into account, the preceding ten workers have accounted for over 40 percent of all aquatic Heteroptera described from 1758–2004. Certain of the taxa attributed to the above authors are subspecies or varieties that may eventually prove to be no more than intraspecific variants, but are considered valid species group names for the purposes of this study. In addition, we recognize that the number of species descriptions in and of itself is not the full measure of a worker's impact in the field, but such statistics are germane to the purposes of the present study.

Description trends, 1758–2004

In this section we analyze species descriptions on a year-by-year basis from 1758–2004, as well as cumulative species descriptions across the same period. The graphs presented provide an initial analysis on a global scale, followed by individual analyses for each major zoogeographic region.

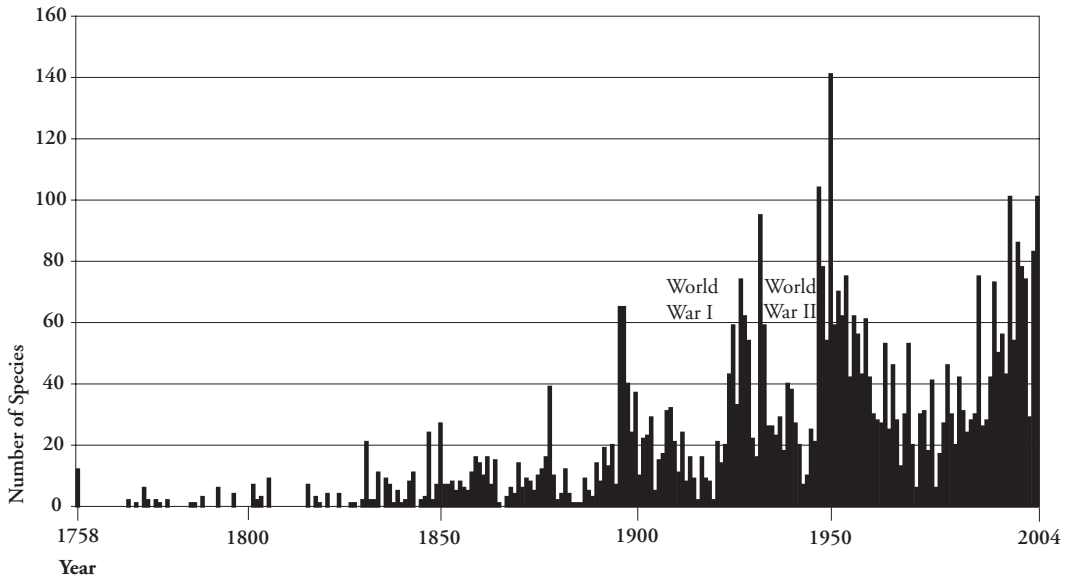


Fig. 1. Number of aquatic Heteroptera species described by year on a world basis, 1758–2004.

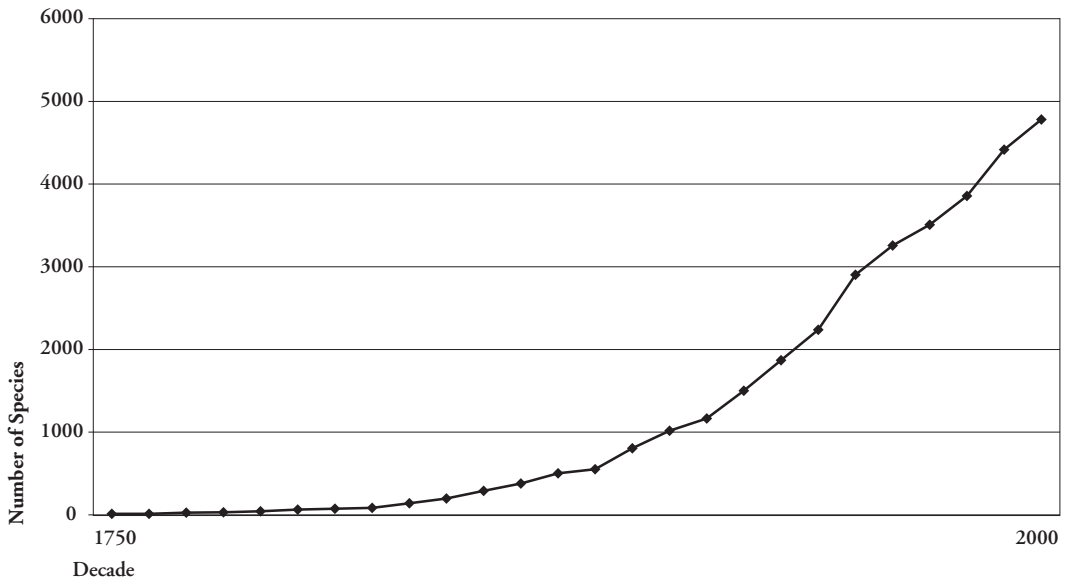


Fig. 2. Cumulative species descriptions of aquatic Heteroptera on a world basis, 1758–2004.

World

The species description analysis of aquatic Heteroptera for the world over time (Fig. 1) shows a series of sharp up and down pulses, with maximum rates of yearly productivity having been realized in the years directly following World War II. Overall, the pattern

has been one of gradually escalating productivity over time, but with significant interruptions during World War I, World War II, and in the period from 1960–1980. The taxonomic productivity of the peak years following World War II has never again been equalled.

The cumulative curve for published aquatic Heteroptera species descriptions on a world basis (Fig. 2) rises steadily and increasingly steeply over time, with no indication of levelling. This indicates that the world biota of aquatic Heteroptera is still far from completely described, even though the fauna of the temperate Northern Hemisphere regions is almost completely documented.

Palaearctic Region

The species description analysis for the Palaearctic region over time (Fig. 3) shows a rather even distribution of effort, and by far the greatest amount of publication for any region prior to 1900. The major early spike in descriptions immediately preceding 1850 is attributable to Franz Fieber's 1848 work on Corixidae. Surprisingly, a significant amount of taxonomic work was also published immediately before and after World War II, with that conflict creating only a short, 4 year hiatus from 1942–1945, despite the extensive conflict in Europe and damage to many major museums. The significant late spike of descriptions in 1985 is due to René Cobben's work on Saldidae.

The Palaearctic region also includes Japan, where interest in the taxonomic study of water bugs was slow to materialize. The groundwork was laid by Shonen Matsumura (1872–1960), who published various papers from 1905 to 1931 dealing with aquatic Heteroptera. His work was carried forward by many Japanese scientists, but perhaps foremost is Syōiti Miyamoto and his disciples, who are still producing well illustrated works; Miyamoto has described 48 species of water bugs to date.

The relatively steady pace of taxonomic work in the Palaearctic region is also reflected in the cumulative curve for published species descriptions (Fig. 4), which rises at a relatively even rate from 1830–1980. The noticeable flattening of this curve from 1990–2004 indicates that documentation of the aquatic Heteroptera biota is nearly complete for the Palaearctic region, with the remaining discoveries likely to come from eastern Asia or the arctic regions.

Nearctic Region

The species description analysis for the Nearctic region over time (Fig. 5) shows minimal taxonomic publication prior to 1830; the subsequent early spike in 1832 reflects the work of Thomas Say (1787–1834). The productivity from 1850 to 1900 is largely attributable to Phillip R. Uhler (1835–1913) (e.g. Uhler 1877), who received many specimens from government expeditions to western North America. Following 1900, work on Nearctic aquatic Heteroptera entered an extremely active phase that

lasted until 1955. Interestingly, the Great Depression and World War II created a far more pronounced hiatus in taxonomic work on aquatic Heteroptera in North America than it did in Europe, producing two periods of intense activity separated by a slow period from 1930 to 1948. The pre-war period, from 1890–1930, was driven by workers such as George W. Kirkaldy and Jose Rollin de la Torre-Bueno, while the post-war period, from 1948–1955 was dominated by Carl J. Drake and Herbert B. Hungerford, as well as the students of the latter. The significant spike in 1948 is largely due to Hungerford's huge monograph on New World Corixidae that appeared in that year. After 1955, taxonomic descriptions in this region declined markedly, largely due to the fact that most species had been collected and named.

The species accumulation curve based on published descriptions (Fig. 6), similarly indicates that documentation of the aquatic Heteroptera biota is nearly complete for the Nearctic region. The curve shows a very sharp rise from 1880 to 1950, then essentially flattens from 1960–2000. In this regard it is an exemplar pattern for a taxonomically mature region.

Neotropical Region

The species description analysis for the Neotropical region over time (Fig. 7) is similar to the Nearctic region in that it shows very little work prior to 1830. George Champion's Heteroptera volume in the *Biologia Centrali Americana* (Champion 1897–1901) was the first comprehensive treatment for the region, and formed a foundation for further work. Champion's book, coupled with Arnold Montandon's papers on Nepomorpha, account for the pronounced spike in Neotropical species descriptions seen in 1898. Following this period, there was a relative lull in taxonomic work on Neotropical water bugs until the early 1920s, when C.J. Drake and colleagues began an intensive period of faunal documentation. Drake and his colleague Halbert Harris were major contributors up to the end of 1945, when Harris abruptly ceased publishing because of an acrimonious battle over the chairmanship of the entomology department at Iowa State University, which culminated in Drake taking his extensive collections and library elsewhere, ultimately to the Smithsonian Institution, thereby depriving Harris of his water bug research materials. Drake continued to be active during the tremendously productive period following World War II (a conflict which, oddly, had a relatively minor effect on descriptive activity in the Neotropical region), and was joined by Hungerford and his students at the University of Kansas, most notably Fred Truxal, John A. Bacon and Ryuichi Matsuda. Also active during these years were

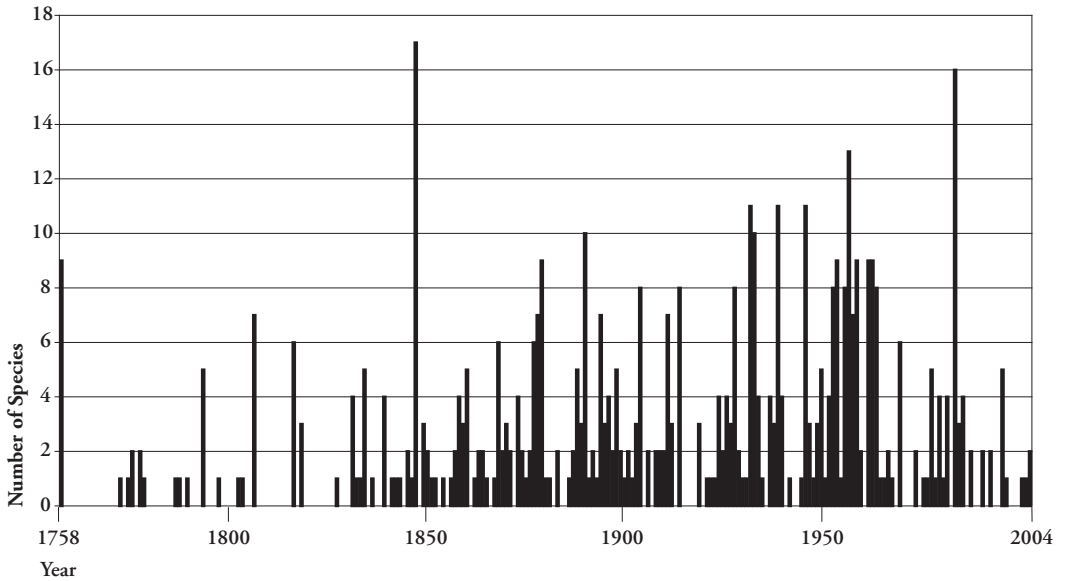


Fig. 3. Number of aquatic Heteroptera species described from the Palearctic region, 1758–2004.

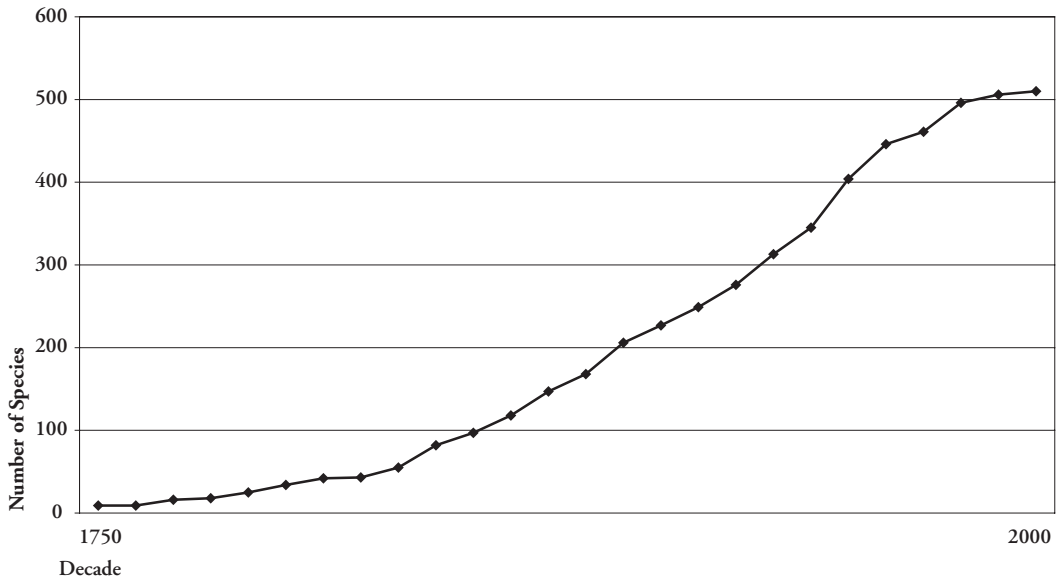


Fig. 4. Cumulative species descriptions of aquatic Heteroptera in the Palearctic region, 1758–2004.

Robert L. Usinger and his students at the University of California at Berkeley, especially Ira La Rivers; David Lauck, who monographed *Belostoma* as his doctoral dissertation at the University of Illinois (e.g. Lauck 1962); and Jose De Carlo in Buenos Aires, the only South American worker to make a significant

impact in regard to Neotropical water bug taxonomy during this period. From 1970 onward taxonomic descriptions for Neotropical aquatic Heteroptera gradually but steadily declined; most taxonomic activity during this period was due to the work of Nico Nieser, who dealt with the biota of Suriname and

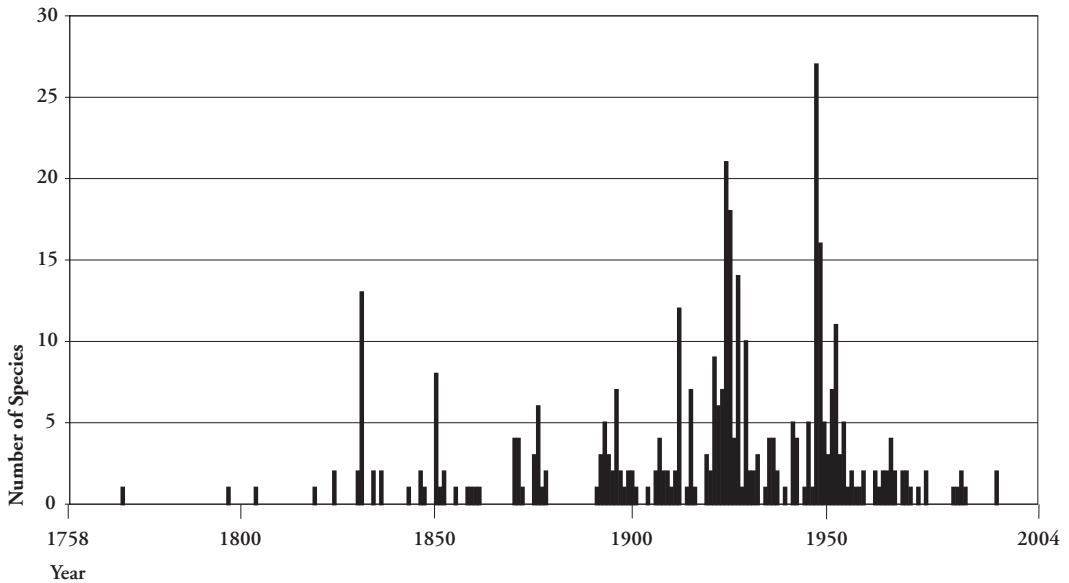


Fig. 5. Number of aquatic Heteroptera species described from the Nearctic region, 1758–2004.

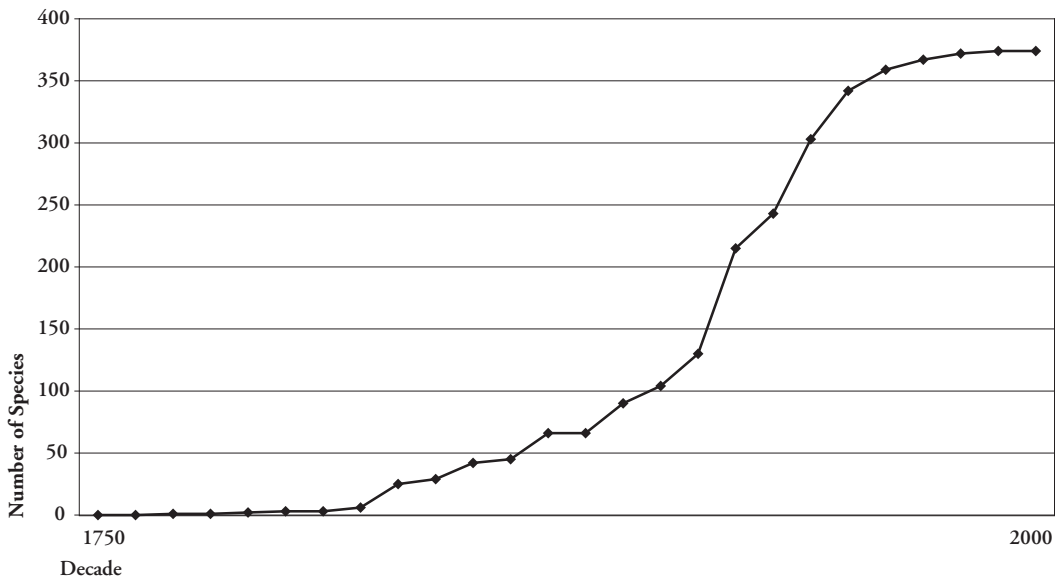


Fig. 6. Cumulative species descriptions of aquatic Heteroptera in the Nearctic region, 1758–2004.

adjacent northern South America and the Caribbean, and J.T. Polhemus, who concentrated on Mexico. The one anomalous exception to this declining trend is a major spike of descriptions in 1997, attributable to the publication of a monograph on Neotropical *Rhagovelia* by D.A. Polhemus.

The species accumulation curve for the Neotropical region, based on published descriptions (Fig. 8), rises steeply from 1910 to 1950, then gradually moderates. This indicates that documentation of the aquatic Heteroptera biota is well advanced for the neotropics, although by no means complete.

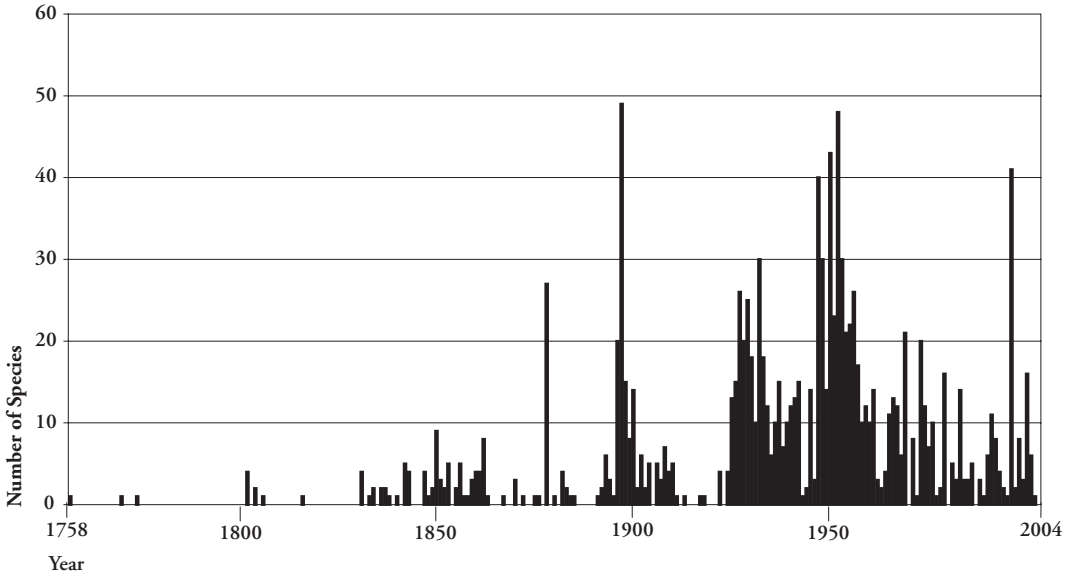


Fig. 7. Number of aquatic Heteroptera species described from the Neotropical region, 1758–2004.

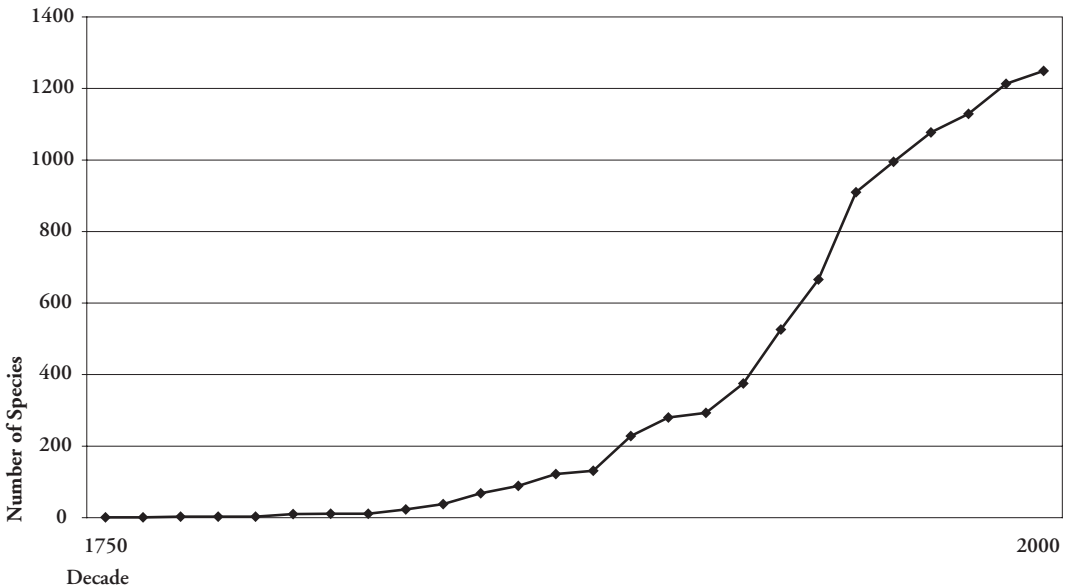


Fig. 8. Cumulative species descriptions of aquatic Heteroptera in the Neotropical region, 1758–2004.

In particular, the authors are aware of many undescribed species in the families Ochteridae, Saldidae and Veliidae (Microveliinae) that should keep the curve on an upward trend for at least another two decades at current rates of taxonomic productivity.

Afrotropical Region

The species description analysis for the Afrotropical region over time (Fig. 9) is highly skewed toward a period of intensive species descriptions centered around 1950; this is almost entirely attributable to the work of Raymond Poisson (1895–1973), who

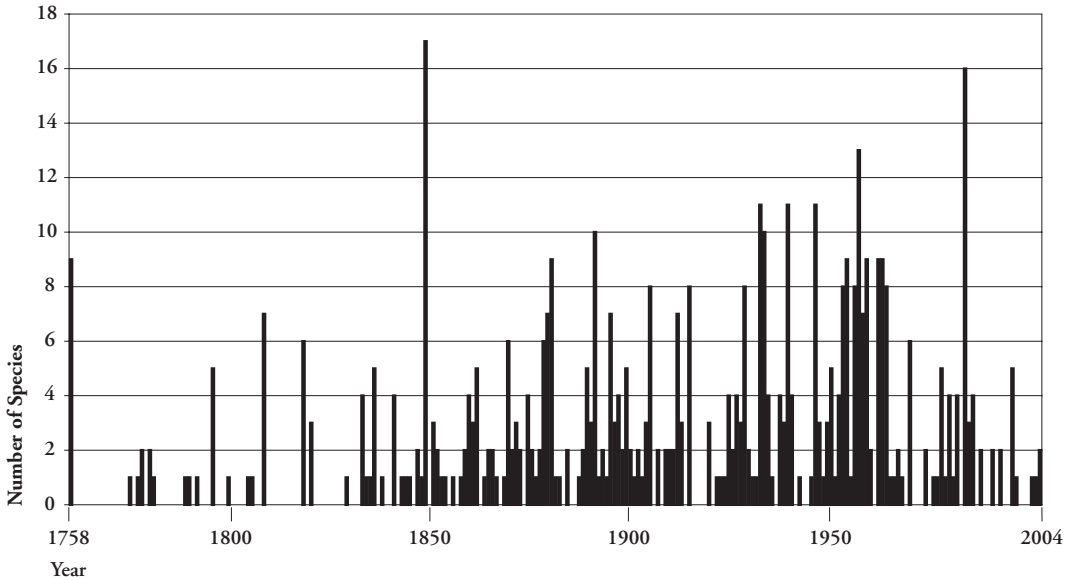


Fig. 9. Number of aquatic Heteroptera species described from the Afrotropical region, 1758–2004.

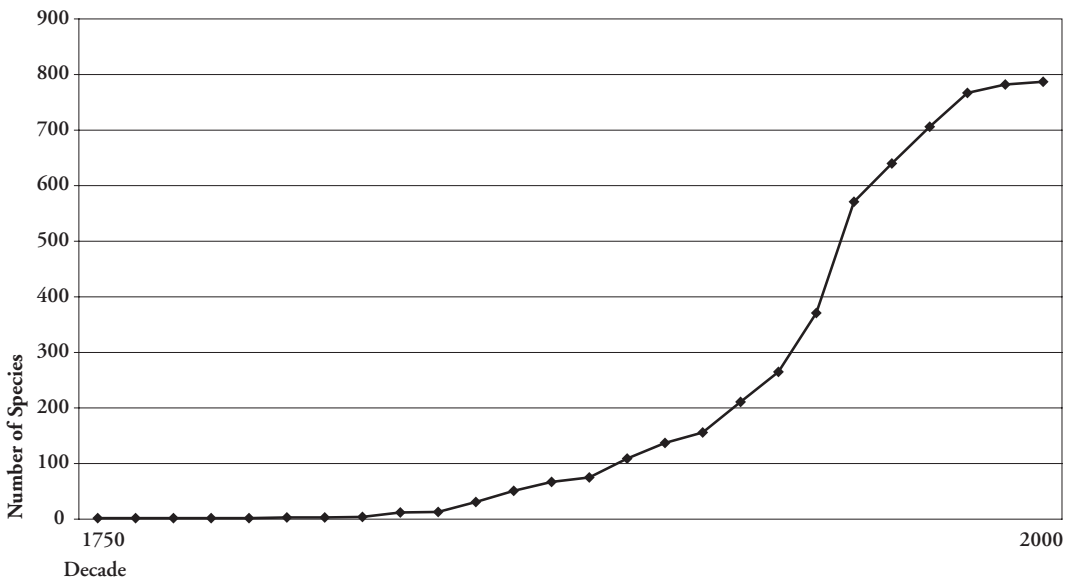


Fig. 10. Cumulative species descriptions of aquatic Heteroptera in the Afrotropical region, 1758–2004.

worked out of Rennes, France. No other major zoogeographic region has had the taxonomic documentation of its aquatic Heteroptera biota so dominated by a single worker. He published 348 new species group taxa of water bugs in publications spanning the period from 1919 to 1968, which also included

a few Palearctic species. Many of Poisson's African taxa were subspecies or varieties that may eventually prove to be local populations or color morphs. From 1960 onward, taxonomic publications on African water bugs have steadily dwindled, in spite of the work of Rauno Linnavuori, and in recent decades

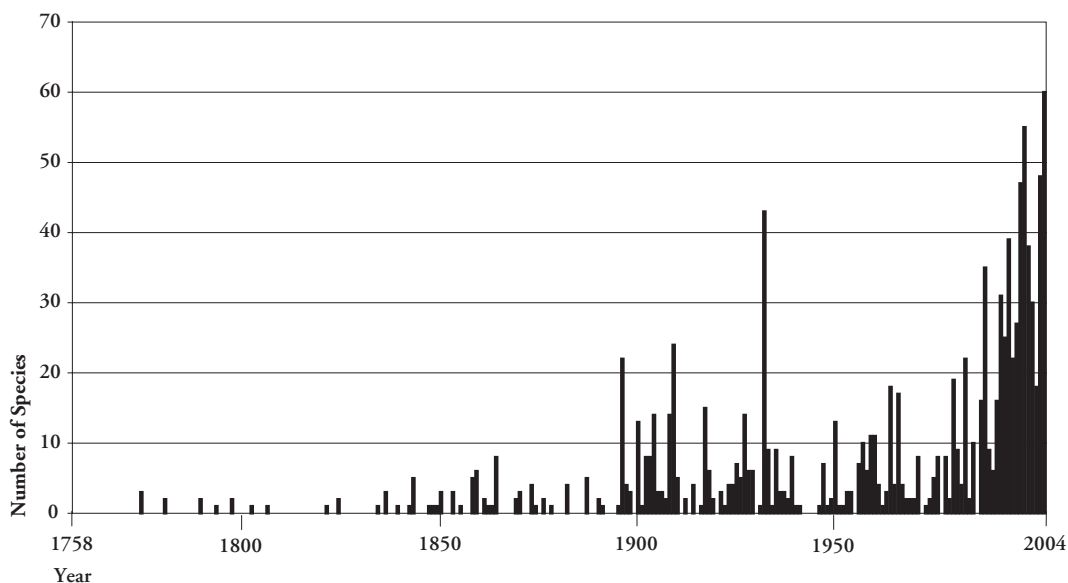


Fig. 11. Number of aquatic Heteroptera species described from the Oriental region, 1758–2004.

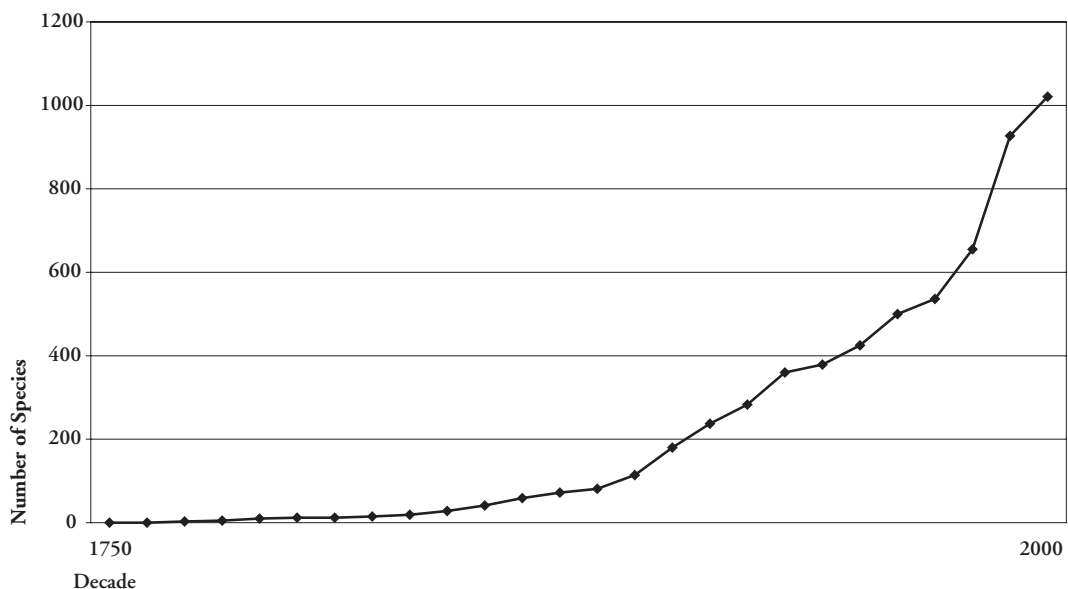


Fig. 12. Cumulative species descriptions of aquatic Heteroptera in the Oriental region, 1758–2004.

activity has been minimal. This is not due to the lack of undescribed species, but more likely to the political instability of the continent, which has hindered modern field surveys.

The species accumulation curve for the Afrotropical region (Fig. 10), based on published

descriptions, shows a flattening trend that would indicate that documentation of the African aquatic Heteroptera biota is well advanced. However, we believe that the flattening of the description accumulation curve for this region is an artifact produced by a relative paucity of recent taxonomic work, especially

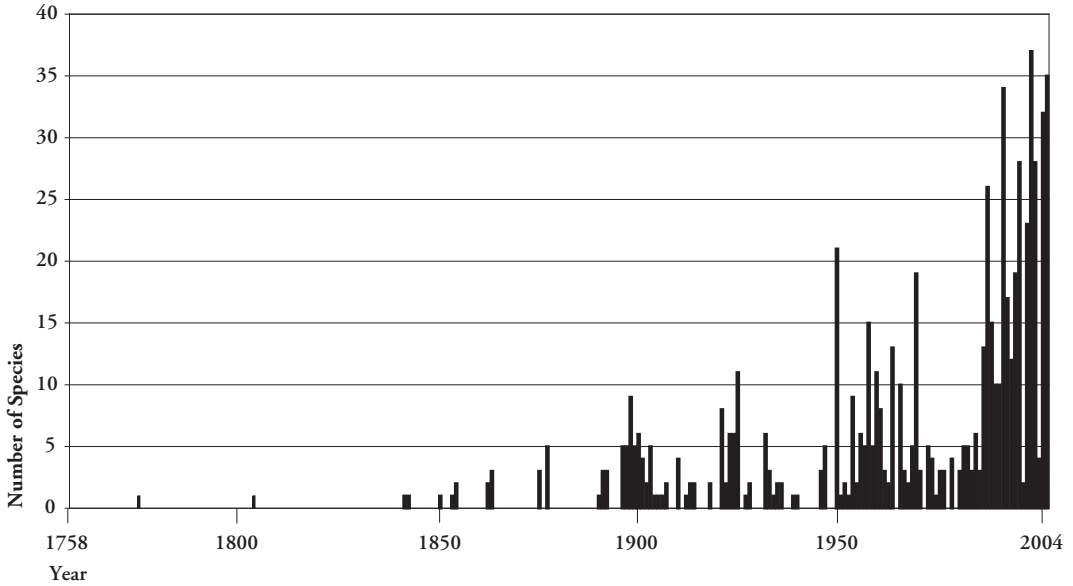


Fig. 13. Number of aquatic Heteroptera species described from the Australian region, 1758–2004.

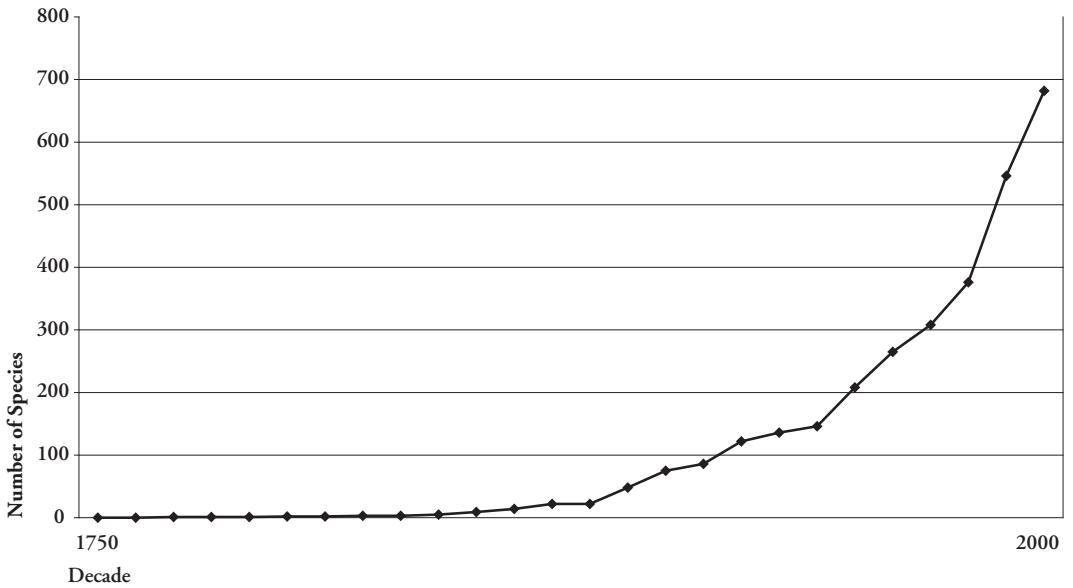


Fig. 14. Cumulative species descriptions of aquatic Heteroptera in the Australian region, 1758–2004.

considering the large number of new species still to be described from Madagascar in the families Veliidae and Aphelocheiridae. Even based on just the specimens now extant in world collections, there are sufficient new taxa in hand to send the species accumulation curve for the Afrotropical region sharply upward over

the next several decades were taxonomists available or willing to undertake such analyses. We also consider Africa to be the most undersampled tropical region in regard to aquatic Heteroptera, further increasing the likelihood of further sharp upward trends to the description accumulation curve in future years.

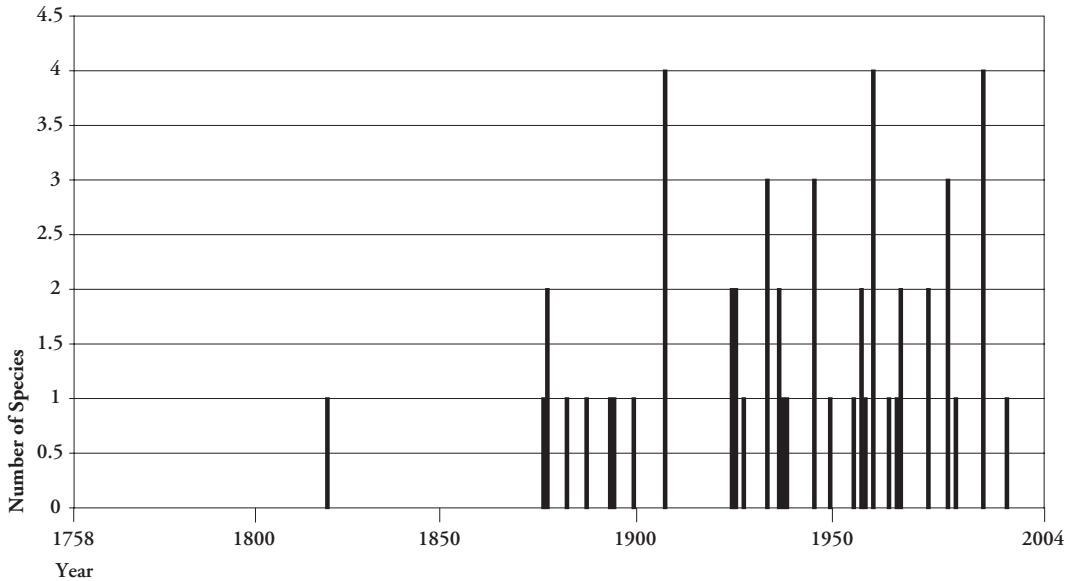


Fig. 15. Number of aquatic Heteroptera species described from the Pacific region, 1758–2004.

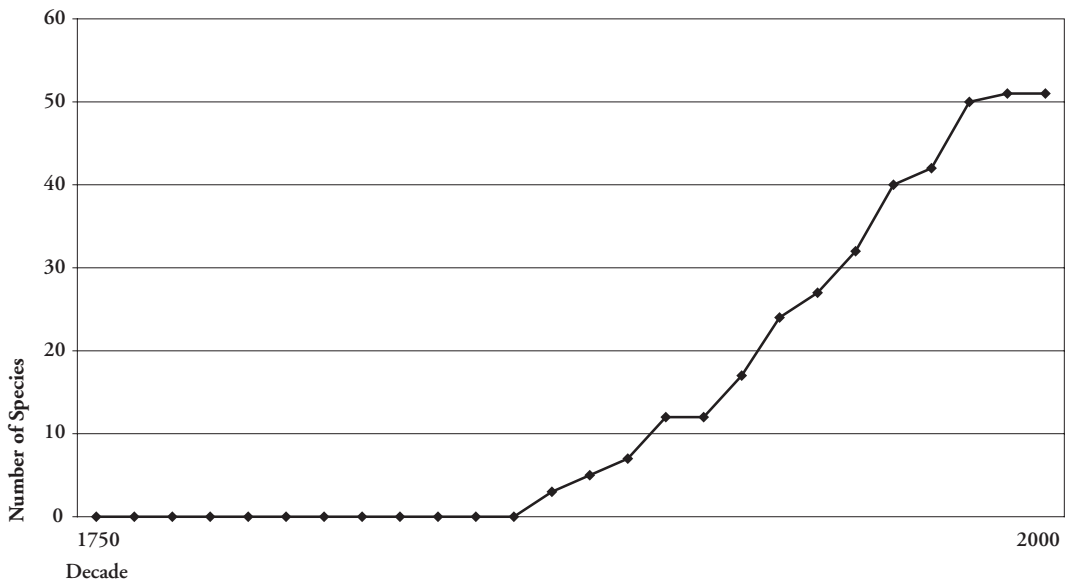


Fig. 16. Cumulative species descriptions of aquatic Heteroptera in the Pacific region, 1758–2004.

Oriental Region

The species description analysis for the Oriental region over time (Fig. 11) shows a steadily increasing pace activity from 1850 to the present. Significant early work was done by Arnold Montandon and George Kirkaldy, based on specimens obtained

by collectors such as Leonardo Fea and Lamberto Loria from the Genoa Museum under the direction of Raffaello Gestro. The major spike in descriptions in 1933 is attributable to the publication of Olov Lundblad's seminal book on the Southeast Asian fauna, which laid the foundation for modern

water bug taxonomy in the region. Taxonomic documentation of the Asian biota was strongly affected by World War II, essentially ceasing between 1941 and 1947, a period which saw the Dutch abandon the museum at Bogor, and the collections of Charles Baker destroyed in the Philippines when the Japanese occupied Los Banos. From 1950 onward there was a slow renaissance of taxonomic publication in the Oriental region, due initially to the work of Hungerford and Matsuda at the University of Kansas, and subsequently joined by Nils M. Andersen in Copenhagen. From 1985 onward there was a significant acceleration of taxonomic documentation in the Oriental region due to simultaneous work on the regional biota by P.-p. Chen, N. Nieser, D.A. Polhemus, J.T. Polhemus, and H. Zettel, a level of activity that continues to the present.

The accumulation curve for published descriptions in the Oriental region (Fig. 12) shows a continuing sharp upward trend, indicating that this area's aquatic Heteroptera biota is still far from completely documented. Although more remains to be done in terms of the rich biotas of Indochina and the Malay Archipelago, the recent spate of taxonomic activity will likely moderate in the next several decades given that many of the most speciose groups have now been dealt with, and that many formerly remote or unknown regions have now been subject to modern surveys. In addition, many of the more recent names have been subspecies, which have served to inflate the total in the context of the current analysis.

Australian Region

The species description analysis for the Australian region over time (Fig. 13) shows relatively little activity prior to 1900, a period of modest activity from 1900 to 1950, and then a period of intensified activity from 1950 to 1975, the latter based largely on the work of Hungerford and Matsuda, who benefited from a base of New Guinea specimens obtained by collectors from the Bishop Museum, notably T.C. Maa and J. Sedlacek. Following a period of very low productivity from 1975 to 1985, taxonomic descriptions in the Australian region exploded to their highest levels in history, a trend that continues to this day. This period of intense documentation was driven largely by the work of J.T. Polhemus and D.A. Polhemus on New Guinea and surrounding Melanesian islands, a region they first began visiting in 1983, and by the concurrent work of Andersen and Tom Weir in Australia, which began in 1994.

The species accumulation curve for the Australian region (Fig. 14), based on published descriptions, is similar to that for the Oriental region in showing a continuing sharp upward trend in the last

two decades. This indicates that the region's aquatic Heteroptera biota is still far from completely documented, particularly in regard to the rich species assemblages of Veliidae and Ochteridae on New Guinea. Although the water bug biota of Australia itself is now largely described, that of Melanesia is significantly underdocumented, and we believe that the current steep upward trend in accumulation of species descriptions can probably be sustained for at least another decade or two.

Pacific Region

The species description analysis for the Pacific region over time (Fig. 15) is interesting in showing no obvious peak or concentration of taxonomic productivity. Instead, it most closely resembles the graph for the Palearctic region, in that there has been a relatively steady accumulation of knowledge over time, from 1877 to the present. Although the biota of the Pacific region is relatively modest in comparison to other zoogeographical regions, it is highly endemic and insular, and the region itself spans over a third of the planet.

The early descriptions of aquatic Heteroptera from the Pacific region were published by Kirkaldy, based on collections made by members of the Hawaiian Sugar Planters Association in Hawaii and Fiji. The most productive period for species descriptions in this region, from 1900–1950, largely overlaps the Japanese colonial presence in the Pacific, and the corresponding work of Teiso Esaki (1899–1957) of Fukuoka, Japan, who described a number of species from islands of the Pacific that are now the Federated States of Micronesia, as well others from Samoa in the *Insects of Samoa* series. Further contributions were made by various authors, many in special publications that dealt with Heteroptera or Insecta in general, rather than aquatic Heteroptera in particular; these include the work of Usinger on the insects of Guam (1946), of Hungerford on the Marquesas (1939), and of Drake on Micronesia (1961). The only true monographic work on a phylogenetically defined Pacific water bug radiation was René Cobben's monograph on the Saldidae of Hawaii (1980), which accounts for the description spike in 1980.

The species accumulation curve for the Pacific region (Fig. 16), based on published descriptions, shows a flattening trend that would indicate that documentation of the aquatic Heteroptera biota is well advanced for the area. However, we believe that the flattening of the description accumulation curve in this region is an artifact produced by a relative paucity of recent taxonomic work on the Pacific islands, and is a false pattern similar to that which we interpret for

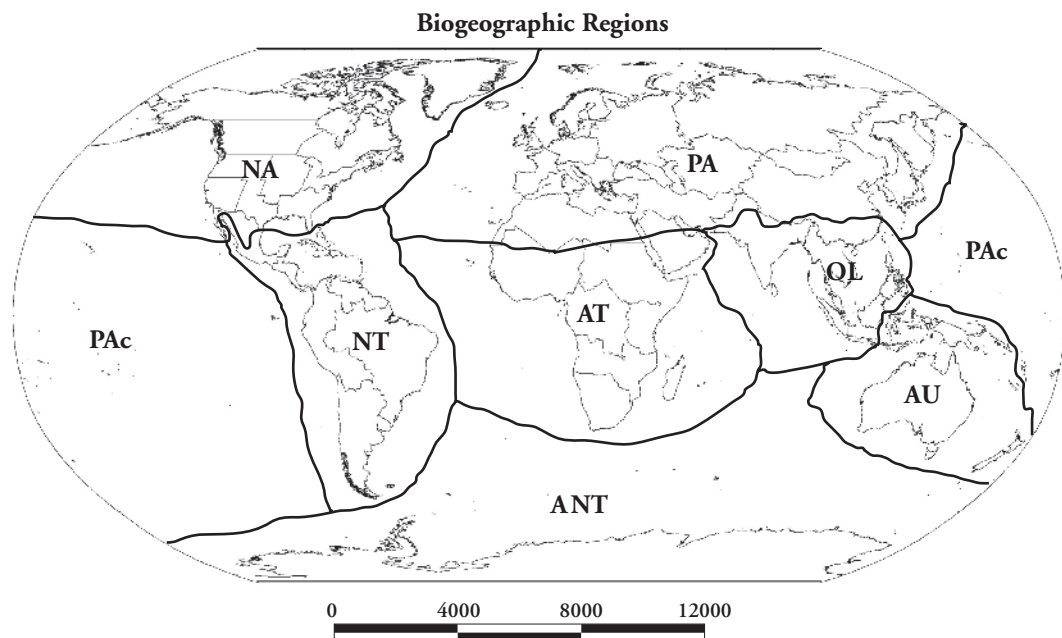


Fig. 17. Zoogeographic map of the world. Abbreviations for regions as follows: NA = Nearctic, NT = Neotropical, PA = Palearctic, AT = Afrotropical, OL = Oriental, AU = Australian, PAc = Pacific, ANT = Antarctic.

the Afrotropical region. Although the numbers of remaining undescribed species are lower for the Pacific than for other tropical regions with more favorable land to water ratios, we are aware of numerous additional species of Veliidae, Saldidae, and Hydrometridae that will lead to a marked upward adjustment of this curve once they are described. A comprehensive monograph of the aquatic Heteroptera of the Pacific region has never been prepared (even the long-awaited contribution on water bugs exclusive of Saldidae in the *Insects of Micronesia* series, originally planned by Teiso Esaki, never materialized), and production of such a work would produce a very different picture than that reflected in the present analysis.

Discussion

Although it might be assumed that accumulation of taxonomic knowledge has been a steady process following the introduction of the system of binominal nomenclature by Linnaeus in 1758, our current analysis of species description trends in aquatic Heteroptera shows that for this group at least, that has not been the case. Instead, of the 4782 species of aquatic Heteroptera described and considered valid by the end of 2004, only 277, or slightly less than

6 percent, had been described in the 100 years following the introduction of the Linnaean system, from 1758–1857. Thus, if one looks at the entire period of 246 years represented by the analysis in this paper, the average rate of species descriptions for aquatic Heteroptera is slightly over 19 species per year. However, if one looks at the period from 1858 to present, the average rate of species description is nearly 31 species per year on a world basis.

In terms of taxonomic productivity trends over time for aquatic Heteroptera, as indicated by published species descriptions per year (and counting only those species currently accepted), one can see from Figure 1 that there was a steadily rising upward trend from 1758 to approximately 1950, followed by a dramatic decline from 1950 to 1980. Despite a resurgence of productivity from 1980 to present, we have only just reattained the levels of descriptive activity reached immediately after World War II. For instance, the 25-year period from 1946–1970 saw the description of 1279 species of aquatic Heteroptera, representing 25 percent of the current total published at an average rate of 51 species per year. In comparison, the most recent 25-year period, from 1980–2004, saw the description of 1277 species, which once again represent 25 percent of the world total at an average rate of 51 species per year. The major difference

in the two periods lies in geographic distribution of effort: in the post-war era, descriptions were well balanced across all global regions, while during the last 25 years effort has been largely concentrated in the Oriental and Australian regions.

The reasons for the significant hiatus in taxonomic work on aquatic Heteroptera on a global scale from 1960 to 1980 (Fig. 1) are difficult to determine. There was no lack of new species to describe, as shown by subsequent species description trends from 1980 onward. Nor does lack of institutional support seem to have been a factor; during this period, funding for major natural history museums and associated taxonomic positions was more robust than at the present day. The Vietnam War created a distraction in the United States during this period, but this hardly seems an explanation given that the far more fundamental conflicts of World War I and World War II had far less impact on the taxonomic enterprise, despite massive social displacements and damage to major museums. Instead, the notable drop in productivity for about 20 years following 1960 correlates most closely to the deaths of Hungerford (1963), Drake (1965), Usinger (1968), and Poisson (1973), who were tireless and very productive workers in the field. Usinger, and especially Hungerford, inspired graduate students to produce impressive monographs that added a great number of new species, but the publications essentially ceased after the deaths of these mentoring professors, and the students themselves frequently chose to follow other career paths.

We also speculate that the rush of taxonomic work following World War II may have outrun the existing collection base in major museums, leading to an impression that the world aquatic Heteroptera biota had been largely documented. We further note that it was only after the Vietnam War that a resurgence of taxonomic activity in aquatic Heteroptera occurred, when access to improved global air travel, sophisticated outdoor equipment, pyrethrin fogging techniques, and helicopter-mediated access to formerly remote regions resulted in the collection of many formerly overlooked or inaccessible species, often in collaboration with increasingly influential and affluent non-governmental conservation organizations.

As noted above, this renewed taxonomic activity has not benefited all zoogeographic regions equally. In the Afrotropical and Pacific regions, work has been minimal for decades, while in the Palearctic and Nearctic regions the fauna is largely documented, leading once again to a dearth of recent descriptive work. In the Neotropical region, despite a rich and still incompletely documented biota, activity has dropped steadily for decades, punctuated by

occasional spurts of description linked to sporadic individual monographs. Instead, it is the Oriental and Australian regions that have gained the predominant benefit from the renewed pace of descriptive activity in aquatic Heteroptera over the last 20 years, and will probably continue to do so for the immediate future, despite pressing needs in both Africa and South America.

In addition, our results clearly show that taxonomic documentation in particular regions is a pulsed process driven by the focus and energy of individual workers, rather than any pre-meditated institutional research program. In this regard, it resembles an artistic more than a scientific endeavor. Despite attempts to modernize the taxonomic enterprise and adapt its management to business-based models, productivity in terms of documenting the biotas of many tropical regions lags well behind that seen in the years following World War II. Only in the Oriental and Australian regions has significant progress been made in recent decades, and this has been the result once again of individually focused researchers who have chosen to concentrate on these regions for personal reasons, often without significant institutional support, rather than the outcome of institutionally directed, large scale research programs. In terms of taxonomic productivity, we conclude that the most cost effective solution to faunal documentation is to solidly fund whichever individual specialists are currently extant in positions that allow them to devote undivided attention to such work, so as to maximize the benefit of their knowledge and energy during their lifetimes. Attempts to transfer such knowledge institutionally have proven singularly unsuccessful in the past, as witnessed by the efforts of workers like Hungerford and Usinger, and may continue to be so in the future, even if research positions can be adequately compensated and redefined in such a way as to minimize duties secondary to taxonomic productivity.

As noted previously, we have estimated that there are approximately 1100 morphospecies of aquatic Heteroptera still to be described in world collections; at least several hundred more than that are no doubt still to be collected, although modern field surveys in recent decades have closed many gaps in this regard. If these estimates are correct, and if the current rate of approximately 50 species descriptions per year can be maintained, then nearly all of the world's remaining aquatic Heteroptera will have been collected and formally named within the next 25 years. On a global scale, the age of discovery for aquatic Heteroptera is therefore drawing to a close, much as it did in North America and Europe half a century earlier. The task of naming this biota still remains,

but we believe that in terms of the historic timeline, we have come 90 percent of the distance in what will have been the 300 year effort to describe the aquatic Heteroptera of the world.

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