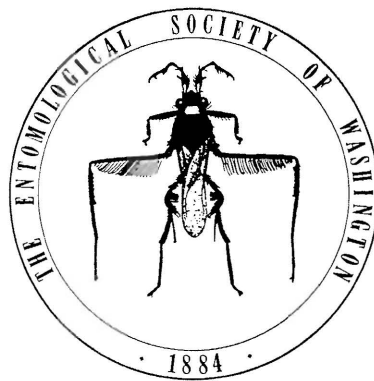


Revision of the Genus
Anoplophora
(Coleoptera: Cerambycidae)

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and
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Back cover: See back endpaper for legend.

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PREFACE

The impetus for this work is directly attributable to the first-time discovery of an invasive woodboring beetle of the cerambycid genus *Anoplophora* in New York City in 1996. Below is a chronology of the incident and its effects.

In early August 1996, Ingram Carner, a long-time resident of Greenpoint, Brooklyn, began noticing that many of his Norway maple trees along McGuinness Avenue were showing signs of distress. The trees had numerous large circular holes, 3/8–3/4 inch in diameter, in the trunks and branches. At the base of the trunks and in the crotches of the larger branches were large amounts of coarse sawdust. Mr. Carner believed that these street trees were being damaged by vandals using cordless drills. However, on August 19, while again examining these damaged trees, he noticed a large, shiny, black beetle emerging from one of the circular holes in the trunk. This time he guessed that the damage might be due to these beetles. He notified the New York City Department of Parks and Recreation and they dispatched a forestry inspector, Harry Rothar, who collected a beetle and returned it to his office. Unable to identify the beetle, it was sent to Cornell University's Department of Entomology. There, it arrived at the Insect Diagnostic Lab on August 26, and diagnostician Carolyn Klass, who did not recognize it, sent it along to E. R. Hoebeke for identification. Shortly thereafter, on September 2, Hoebeke identified the mystery woodboring beetle as *Anoplophora glabripennis*, a native of China and Korea. On September 5, he traveled to Greenpoint, Brooklyn, met with Harry Rothar, and went directly to the site where the beetle was first discovered. More street trees in the vicinity of McGuinness Avenue were discovered to be heavily infested, and additional beetles were collected. Upon his return to Cornell, Hoebeke sent specimens to the USDA Agricultural Research Service's Steven W. Lingafelter, a specialist of the Cerambycidae, and to Allan G. Samuelson of the Bernice Bishop Museum, Honolulu, Hawaii, another cerambycid expert, for their confirmation. By September 13, both systematists had confirmed Hoebeke's identification of *Anoplophora glabripennis*.

A month later, in October 1996, another infested area was found in Amityville, New York, about 40 miles east of Brooklyn, on Long Island. A tree cutting company of this community had been pruning and removing dead or dying trees from the metropolitan New York area in previous years and much of this wood was stored on their property in Amityville where it was sold as firewood. Many of the street trees bordering this property and elsewhere in the immediate vicinity were infested by this Asian

longhorned beetle. In an attempt to eradicate this destructive woodboring pest from these New York neighborhoods, federal, state, and local regulatory agencies began removing and destroying all trees with damage symptoms of this beetle—i.e., circular exit holes in trunks and branches and accumulations of coarse sawdust at the base of trees and in branch crotches. This cut-and-destroy mission began in March 1997, first with infested trees of McCarren Park, Greenpoint, Brooklyn.

In early July 1998, Garry Luka, an employee of the Skokie Park District, just north of Chicago, sawed off a dead tree branch that was overhanging his property in the 4300 block of North Winchester Avenue, Ravenswood, and offered the wood to his friend Barry Albach, to use for an upcoming camping trip. Mr. Albach placed the firewood in the back of his pickup truck, where it sat under a fiberglass cover for a week. Then on July 9, his mother and a neighbor spotted a large black beetle crawling on Albach's rear view mirror. When Mr. Albach uncovered the wood in the back of his truck, he discovered more of the beetles crawling about. Curiosity brought him to his computer, where he did a simple Internet search on "beetles" and luck would have it that the very first site he found was one on the Asian longhorned beetle in New York. What was illustrated in this pest alert by the USDA was exactly what Mr. Albach saw in the back of his truck. He decided immediately to contact the local USDA office and notify them of his find. After a site visit by USDA inspectors, it was determined that another major infestation of Asian longhorned beetle was present in the northside Chicago community of Ravenswood. In the next few weeks, local Chicago television, radio, and newspapers provided outstanding coverage of this newly discovered beetle infestation. As a result of this publicity, local citizens were responsible for the discovery of two additional, but smaller, areas of infestation—one near Addison, DuPage County, about 5 miles southeast of O'Hare International Airport, and another in Summit, a suburb about 15 miles southwest of downtown Chicago. With the detection of the Asian longhorned beetle in Chicago, the federal government was compelled to take some action. On September 11, Secretary of Agriculture Daniel Glickman held a news conference in Chicago to announce interim U.S. trade restrictions with China. The newly announced regulations—set to go into effect on December 17, 1998—would require that goods from China be packed in non-wood material or wood that had been treated with heat or chemical fumigation to kill insects. Removal of beetle-infested trees in Chicago began on February 4, 1999. Infested trees continue to be found in New York and Chicago. As of

August 4, 2001, a total of 5,324 infested trees in New York and 1,522 infested trees in Chicago have been detected and destroyed.

No one knows exactly how long the Asian longhorned beetle has been present in the United States, or when it first began infesting trees in New York City or Chicago. Fortuitously, a property owner in Bayside, Queens, came forth shortly after the discovery of infested trees in this neighborhood in February 1999 with a Polaroid print of the Asian longhorned beetle, dated from 1992. There is little doubt that this dangerous tree-infesting beetle gained entry into North America in solid wood packing material, such as crating, pallets, and dunnage, originating from China, and used extensively in the international trade industry for packaging goods and merchandise. Prior to the Asian longhorned beetle's discovery in August 1996, there were only two known interceptions of *Anoplophora glabripennis* in North America. One was from Chinese crating in Loudenville, Ohio, in 1992, and another on wood crating and dunnage, also from China, in Vancouver, British Columbia, in 1992. Since August, 1996, numerous interceptions of *A. glabripennis* have been made at major U.S. ports and in numerous warehouses countrywide. Other countries are also dealing with this as a new invasive pest. Recently, its first occurrence in Europe was indicated in July, 2001, in Braunau, Austria (Tomiczek 2001). However, *A. glabripennis* is not the only species of the genus to be intercepted in the United States. Other serious tree pests of Asia also have been found as unintentional hitchhikers in 1999. Several live specimens of *Anoplophora chinensis*, one of Asia's most serious citrus pests, were found in April in a greenhouse in Athens, Georgia, where Crepe Myrtle bonsai trees from China were infested, and another interception of a single live specimen of the white-spotted longicorn beetle, *Anoplophora chinensis* (form *malasiaca*), was made by a homeowner in June on an infested, potted dwarf Japanese maple in Delavan, Wisconsin. Very recently, in August, 2001, 4 specimens of *Anoplophora chinensis* (form *malasiaca*) were found in two nurseries in the Seattle area, Washington state (Tukwila and Lacey). These specimens were also associated with a shipment of bonsai Jap-

anese maples that were destroyed. Intensive surveys there are being coordinated by state and federal agencies. This species has also been introduced into England (Cooter 1998) and established recently in Italy (Colombo and Limonta 2001).

Because the volume of commodities imported annually from China associated with solid wood packing material is estimated to be in the millions of shipments, it is expected that other non-native woodboring beetles will continue to find their way into North American urban landscapes using this pathway. USDA port officials have been placed on higher alert, and continue to inspect high-risk cargoes from Asia for species of *Anoplophora* and other woodboring pests.

The U.S. Department of Agriculture's Agricultural Research Service (ARS) continues to support an Asian longhorned beetle research program that provides necessary research leading to environmentally and publicly acceptable technologies for mitigating beetle populations. Based on recommendations of a Science Advisory Panel, ARS was advised in October 1996 that top priorities should include beetle systematics, determination of basic biology, pheromone identification and isolation, field detection and trapping technologies, evaluation of beetle reproductive biology, and identification and testing of potential natural enemies.

In early 1998, USDA-ARS awarded Steven W. Lingafelter and E. Richard Hoebeke a grant to undertake a comprehensive taxonomic revision of the Oriental genus *Anoplophora* and to prepare an illustrated handbook for the identification of species in the genus. The identification guide is intended to be part of a national strategy to eradicate this woodboring pest and to help port-of-entry regulatory officials nationwide distinguish this Asian pest and its close relatives from the hundreds of native species of Cerambycidae. We trust that this monograph will be a positive contribution to that end.

E. R. Hoebeke
S. W. Lingafelter
November, 2001

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INTRODUCTION

Anoplophora is a moderate-sized genus of 36 species of woodboring beetles that occur throughout Asia, with the highest diversity in the tropical and subtropical regions. Most species have beautiful colors on the elytra, pronotum, antennae, tarsi, and venter. These colors superficially seem like mere patterns of the integument, but under high magnification are revealed to be due to very dense patches of short pubescence. In many species, these colored pubescent patches on the elytra are arranged in round spots, in others they are arranged in transverse bands. Most species have very long antennae (about 1.3–1.6 times the body length in males, 1.0–1.5 times the body length in females of most species) and most are large, some over 50 mm. In the larval stage, species in this genus develop in and consume wood of many species of trees.

Anoplophora is a familiar genus to many Asians, attested to through the abundance of common names in the literature, and their representation in art. Two common names are used widely by laypersons in Asia for various species: The Sky Ox Beetle and Starry Night Sky Beetle. Many Japanese netsuke carvings from ivory and wood feature *Anoplophora* (see Frontispiece). The recent introductions of *Anoplophora glabripennis* in the United States have established its notoriety in the New World (Becker 1998, Becker 2000, Cole 1999, Milius 1999, Stimmel 1999).

Despite the wide familiarity of the genus, much confusion has existed concerning the identity and definition of the various species. This study was done to provide a resource for the identification of all species in the genus *Anoplophora*. Thorough studies of external and internal features, and their variation, for adults of all species were made and are presented here. We have provided numerous illustrations, many in color, to allow even the non-specialist the ability to make identifications with confidence. We include an identification key and distribution maps for each species. A general description of larvae is presented, although this is necessarily brief since larvae of most species are unknown.

One important goal was to stabilize the taxonomy of this group by designating synonyms where we discovered multiple names being used for the same taxon. This can only be done in a project such as this which is revisionary in scope, treats all the fauna, and focuses on examination of all type specimens. Only by studying all species and numerous specimens of a taxon to assess variation and constancy of characters (on which we base our species concepts

herein), can taxonomic stability be achieved, and we have approached this project from that perspective.

SUMMARY OF TAXONOMIC CHANGES

The Asian longhorned beetles of the genus *Anoplophora* include 36 species as a result of this study. The following 20 new synonyms are made: *Melanauster granulipennis* Breuning 1938 and *Anoplophora subberyllina* Breuning 1964 are new synonyms of *Anoplophora beryllina* (Hope); *Anoplophora stanleyana* var. *grisea* Tippmann 1953, is a new synonym of *Anoplophora birmanica* Hüdepohl; *Callophora abbreviata* Thomson 1865, *Callophora malasiaca* Thomson 1865, and *Melanauster perroudi* Pic 1953 are new synonyms of *Anoplophora chinensis* (Forster); *Melanauster adonis* Pic 1925b, *Melanauster adonis* var. *vitalisi* Pic 1936, and *Anoplophora alboapicalis* Chiang 1951 are new synonyms of *Anoplophora davidis* (Fairmaire); *Cyriocrates depressinotatus* Chiang 1951 is a new synonym of *Anoplophora fruhstorferi* (Aurivillius); *Melanauster nobilis* Ganglbauer 1890 is a new synonym of *Anoplophora glabripennis* (Motschulsky); *Melanauster pirouletii* Fairmaire 1889 is a new synonym of *Anoplophora imitator* (White); *Anoplophora parelegans* Chiang 1981 is a new synonym of *Anoplophora longehirsuta* Breuning; *Anoplophora lucipor lumawigi* Hüdepohl 1989 is a new synonym of *Anoplophora lucipor* Newman; *Anoplophora malasiaca tokunoshimana* Samuelson 1965, *Melanauster oshimani* Fairmaire 1895, and *Anoplophora oshimani ryukyensis* Breuning and Ohbayashi 1964 are new synonyms of *Anoplophora macularia* (Thomson); *Anoplophora tonkinea* Breuning 1944a, *Anoplophora stanleyana* var. *gloriosa* Tippmann 1953, and *Anoplophora stanleyana* var. *melancholica* Tippmann 1953 are new synonyms of *Anoplophora stanleyana* Hope.

The following four taxa are transferred to *Anoplophora* and represent new combinations: *Anoplophora albopicta* (Matsushita 1933); *Anoplophora fruhstorferi* (Aurivillius 1902); *Anoplophora graafi* (Ritsema 1880); and *Anoplophora sollii* (Hope 1839). The following taxa are removed from *Anoplophora* and represent new or revised combinations: *Pseudonemophas versteegii* (Ritsema 1881c), new combination; *Nemophas ammiralis* (Schwarzer 1931), new combination; *Nemophas bennigseni* Aurivillius 1908, restored combination; *Monochamus itzingeri* (Breuning 1938), new combination; and *Pharsalia rondoniana* (Breuning 1964), new combination. The following taxa are designated as *incertae sedis*: *Anoplophora wusheana* Chang 1960, as *wusheana* Chang, *incertae sedis* and *Callophora tonkinea* Pic 1907, as *tonkinea* Pic, *incertae sedis*. The following new synonyms are made for these taxa excluded from *Anoplophora*: *Monocha-*

mus glabronotatus Pic 1934a, and *Monochamus albescens* v. *subuniformis* Pic 1934a are new synonyms of *Pseudonemophas versteegii* (Ritsema 1881c).

Lectotypes are designated for the following names: *Monochamus beryllinus* Hope; *Callophora luctuosa* Thomson; *Callophora malasiaca* Thomson; *Melanauster davidis* Fairmaire; *Melanauster macrospilus* Gahan; *Cerosterna glabripennis* Motschulsky; *Melanauster pirouletii* Fairmaire; *Callophora macularia* Thomson. Types for the following species were not located and neotypes are herein designated: *Anoplophora asuanga* Schultzze; *Anoplophora ma-maua* Schultzze; *Anoplophora tianaca* Schultzze.

METHODS

We present an overview of the nomenclatural history of *Anoplophora* and its tribal association. We provide a discussion of biology and distribution of *Anoplophora*. We then provide generic descriptions and diagnoses of larval and adult *Anoplophora*. A catalog for all currently recognized species of *Anoplophora*, with complete lists of synonyms and abbreviated references, is included. Detailed descriptions and diagnoses of each species, based on all material at hand and examined from museums and collections around the world, are presented. Morphological characters are thoroughly illustrated and an atlas of features for *Anoplophora* is provided as a reference (Fig. 4).

Illustrations and photographs are provided as follows: 34 full color photographic plates of all species of *Anoplophora* and available holotype, lectotype, syntype, or neotype specimens are presented. The first 18 plates are of mostly pristine examples of both sexes for most species and are arranged to facilitate identification, with similar species located together. Following these are three plates (Plates 19–21) showing examples of genera related to *Anoplophora*. Legends for Plates 1–21 also show actual sized silhouettes of the beetles photographed. These 21 plates are located prominently in the middle of the book. The last 13 plates (Plates 22–34) show most available primary type specimens, mostly arranged alphabetically by specific epithet and are located at the end of the book, immediately following the figures.

Over 60 figures are provided (each as a plate with numerous individually labelled elements) of *Anoplophora in situ*, morphological dissections, and line drawings of various features. These are all together at the end of the book, immediately before the remaining Plates and Maps, with the exception of the full color biological figures (Figs. 1–3) that are located within the chapter on biology.

A comprehensive revision of this nature depends on a thorough study of specimens. We have conducted field work in Japan, China, South Korea, Tai-

wan, and Nepal in an effort to gain fresh material and biological and distributional data. More importantly, we have carefully examined museum holdings, some of which have been accumulated for over 200 years. We have visited nearly 50 museums in Europe, Asia, and North America, and received over a thousand specimens from them and other institutions and individuals listed below and in the Acknowledgments.

A list of institutional collections follows. Acronyms are from Arnett et al. (1993), and are in alphabetical order by acronym. Curators for institutional and private collections are listed in the Acknowledgments.

- AMNH** American Museum of Natural History, New York City, New York, USA
- ANSP** Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
- ANUC** Andong National University, Andong, South Korea
- BMNH** The Natural History Museum, London, United Kingdom
- BMSC** Buffalo Museum of Science, Buffalo, New York, USA
- BPBM** Bernice P. Bishop Museum, Honolulu, Hawaii, USA
- CASC** California Academy of Sciences, San Francisco, California, USA
- CFRB** Chinese Academy of Forestry, Forest Research Institute, Beijing, China
- CHPC** Carolus Holzschuh Private Collection, Vienna, Austria
- CMNH** Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
- CNCI** Canadian National Collection of Insects, Ottawa, Ontario, Canada
- CNUC** Chungnam National University, Daejeon, South Korea
- CUIC** Cornell University Insect Collection, Ithaca, New York, USA
- DHPC** Dan Heffern Private Collection, Houston, Texas, USA
- EIHU** Entomological Institute, Hokkaido University, Sapporo, Japan
- EMEC** Essig Museum of Entomology, University of California, Berkeley, California, USA
- EUMJ** Ehime University and Ohbayashi Collection, Matsuyama, Japan
- EWUC** Ewha Women's University, Seoul, South Korea
- FCBS** Frey Collection and Natural History Museum, Basel, Switzerland
- FMNH** Field Museum of Natural History, Chicago, Illinois, USA

- FRIC** Forestry and Forest Products Research Institute, Fruit Tree Sciences, Tsukuba, Japan
- FRIS** Forestry Research Institute, Seoul, South Korea
- FSCA** Florida State Collection of Arthropods, Gainesville, Florida, USA
- HNHM** Hungarian Natural History Museum, Budapest, Hungary
- HUNM** Hannam University Natural History Museum, Daejeon, South Korea
- ICRI** Zhongshan University Collection, Guangzhou, China
- ITLJ** National Institute of Agro-Environmental Sciences, Tsukuba, Japan
- IZAS** Zoological Institute, Academia Sinica, Beijing, China
- JCPC** Jim Cope Private Collection, San Jose, California, USA
- KEIU** Korean Entomological Institute, Korea University, Seoul, South Korea
- KNUC** Center for Insect Systematics, Kangwon National University, Chuncheon, South Korea
- KUEC** Kyushu University Insect Collection, Kyushu, Japan
- LACM** Natural History Museum of Los Angeles County, Los Angeles, California, USA
- LBPC** Larry Bezark Private Collection, Sacramento, California, USA
- LSUK** Linnean Society Collection, Burlington House, Piccadilly, London, United Kingdom
- MCZC** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
- MNHN** Muséum National d'Histoire Naturelle, Paris, France
- MSUC** Moscow State University, Moscow, Russia
- NCSU** North Carolina State University, Raleigh, North Carolina, USA
- NHMW** Naturhistorisches Museum, Vienna, Austria
- NHRS** Naturhistoriska Riksmuseet, Stockholm, Sweden
- NIAS** National Institute of Agricultural Sciences, Suwon, South Korea
- NMNS** National Museum of Natural Science, Taichung, Taiwan
- NSMK** National Science Museum, Seoul, South Korea
- NSMT** National Science Museum, Tokyo, Japan
- NTUC** National Taiwan University, Taipei, Taiwan
- NYSM** New York State Museum Collection, Albany, New York, USA
- OMNH** Osaka Natural History Museum, Osaka, Japan
- OXUM** Hope Entomological Collections, Oxford, United Kingdom
- ROME** Royal Ontario Museum, Toronto, Canada
- SACA** Southwest Agricultural University, Beibei, Chongqing, China
- SEAN** Servicio Entomológico Autónomo, Museo Entomológico, León, Nicaragua
- SEMC** Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA
- TARI** Taiwan Agricultural Research Institute Collection, Taichung, Taiwan
- TFRI** Taiwan Forestry Research Institute, Taipei, Taiwan
- UGCA** University of Georgia Collection of Arthropods, Athens, Georgia, USA
- UNSM** University of Nebraska State Museum, Lincoln, Nebraska, USA
- USNM** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
- ZMAS** Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

For our descriptions, at least one specimen of most species was completely cleared and disarticulated to carefully reveal morphological characters. Too few specimens were available for several species, and therefore we could not make dissections. For others, the genitalia were carefully dissected from both sexes, when available, and the internal sac was everted and studied. Characters were illustrated, mostly on scratchboard, using a Leica dissecting microscope and camera lucida, and photographed through the same scope with a Sony DKC-5000™ digital camera. We have prepared, with much help from Kent Loeffler (Cornell University), color photographs of dorsal views of good specimens of both sexes for most species using a Nikon™ camera system (F3 body, 105 Micro Nikkor™ with bellows), scanning in slides using Nikon LS-2000™ and Umax Powerlook 3000™ scanners, and providing prints using a Codonics dye sublimation printer. The specimens are reproduced at the maximum size allowable to fit on the page so that features are easily visible. Therefore, specimens are not represented to scale, but we have included ranges of lengths for each species along with silhouettes of actual size. Further, the back cover illustration shows most species to approximate relative scale, so relative sizes can be easily discerned.

Following each species description and diagnosis section, we provide a discussion of all the types and include color photographs of most primary types (Plates 22–34). For all new synonymies and many

earlier synonymies, we provide justifications. We list all the type material and other specimens examined for each species. These data are sorted and subsorted for each species by country, state or province, and often specific locality, and latitude/longitude to facilitate examination for specific locality data. This also makes it easier for the user to relate a specific dot on a map to a record in the data (although in many cases, a dot on a map may represent several proximal localities).

We provide at the end of the book 14 maps showing the known collection localities for all species of *Anoplophora*. Some discussion is warranted regarding our map generation process. For most localities we have researched the currently accepted spelling of the place name along with latitude and longitude based on the National Imagery and Mapping Agency's (www.nima.mil) Geonet Names Server. This is a crucial step since so many transliterations exist for many localities in Asia, especially China. Also, many names have simply changed and older specimen data is not reconcilable with simple comparison to current maps. The NIMA site was crucial to help us establish localities. Still, in some cases, the locality remained indecipherable or ambiguous. In the case of ambiguous localities, we either made our best guess (often based on distributional data from other specimens), or placed the locality with a "?" in the symbol on the map, or did not plot the locality.

Once we established the locality, the NIMA site provided latitude and longitude coordinates which we copied into our specimen database. Records from this database were exported and reformatted into the decimal format recognized by the United States Geological Survey's Crusty Simple Map Generator (<http://crusty.er.usgs.gov/mapit/index.html>). By entering the coordinate data into the web program, a simple map was produced for each species. We downloaded high resolution postscript files of those maps and overlaid them on detailed topographic maps from the Mountain High Maps™ series. Through layering manipulation using Photoshop™ software, the final version of each map was produced.

Finally, we present a key to the recognized species in *Anoplophora*. Where possible, the key has relied on easily seen characters which are defined in such a way that variability is not a hindrance. For variable species, we have multiple entries in the key to facilitate identification.

BIOLOGY OF ANOPLOPHORA

Perspectives and Overview.—We provide a comprehensive review of the biology of species of the Oriental and eastern Palearctic genus *Anoplophora*, summarizing the published literature on this econom-

ically important group of woodboring beetles. Because most biological literature on these beetles is published in Chinese, especially that treating *Anoplophora glabripennis* and the other major citrus pests of the genus, it has been difficult to gain access to past and present research on these woodborers. Those papers published exclusively in Chinese, but with at least an English abstract, have been cited in the overall discussion. However, in the following review, we do not discuss or summarize the published literature that deals mostly with the management and control (chemical, cultural, or biological) of the economically important species. Of the 36 species herein recognized in *Anoplophora*, the biology, habits, and host plants are known for only one-third. The majority of the published papers concern the economically important species (that is, *A. chinensis* including form *malasiaca*, *A. macularia*, *A. glabripennis* including form *nobilis*, and *Pseudonemophas versteegii*). Although, we include coverage of the biology of *P. versteegii* here in this review, it is our opinion (and N. Ohbayashi, pers. comm.), based on external and internal morphology, that this species belongs in *Pseudonemophas*.

Because *A. glabripennis* has been a critical focus of federal, state, and local agricultural officials since its detection in New York in the summer of 1996, and since it has the potential to be a serious tree pest in urban and native forests of North America, we treat it first separately. The next section provides a summary of biology for it and the other species for which biological data are known.

Biology of Anoplophora glabripennis.—Since the late 1970s, the Asian longhorned beetle, *Anoplophora glabripennis*, has become a major forest pest in mainland China. It is endemic to mainland China (Hua et al. 1992) and Korea (Kim et al. 1994). Although, a few specimen records from Japan have been seen, there are no known populations of *A. glabripennis* occurring there. In China, it is found throughout a vast geographic range, 21°N to 43°N latitude and 100°E to 127°E longitude (Yan 1985), nearly equivalent to all of North America, from the Great Lakes region and southern Canada to southern Mexico. Indeed, Peterson and Vieglais (2001) demonstrated through ecological modelling, its potential to survive throughout most of the United States. Its prevalence and range in China has increased in the past several decades as a result of widespread planting of susceptible poplar (*Populus*) hybrids (EPPO 2001). Yan (1985) provided a map showing *A. glabripennis* to be most damaging in a zone of eastern China extending from Liaoning to Jiangsu province and inland to Shanxi, Henan, and Hubei provinces; it is also present further west to Gansu, Sichuan and

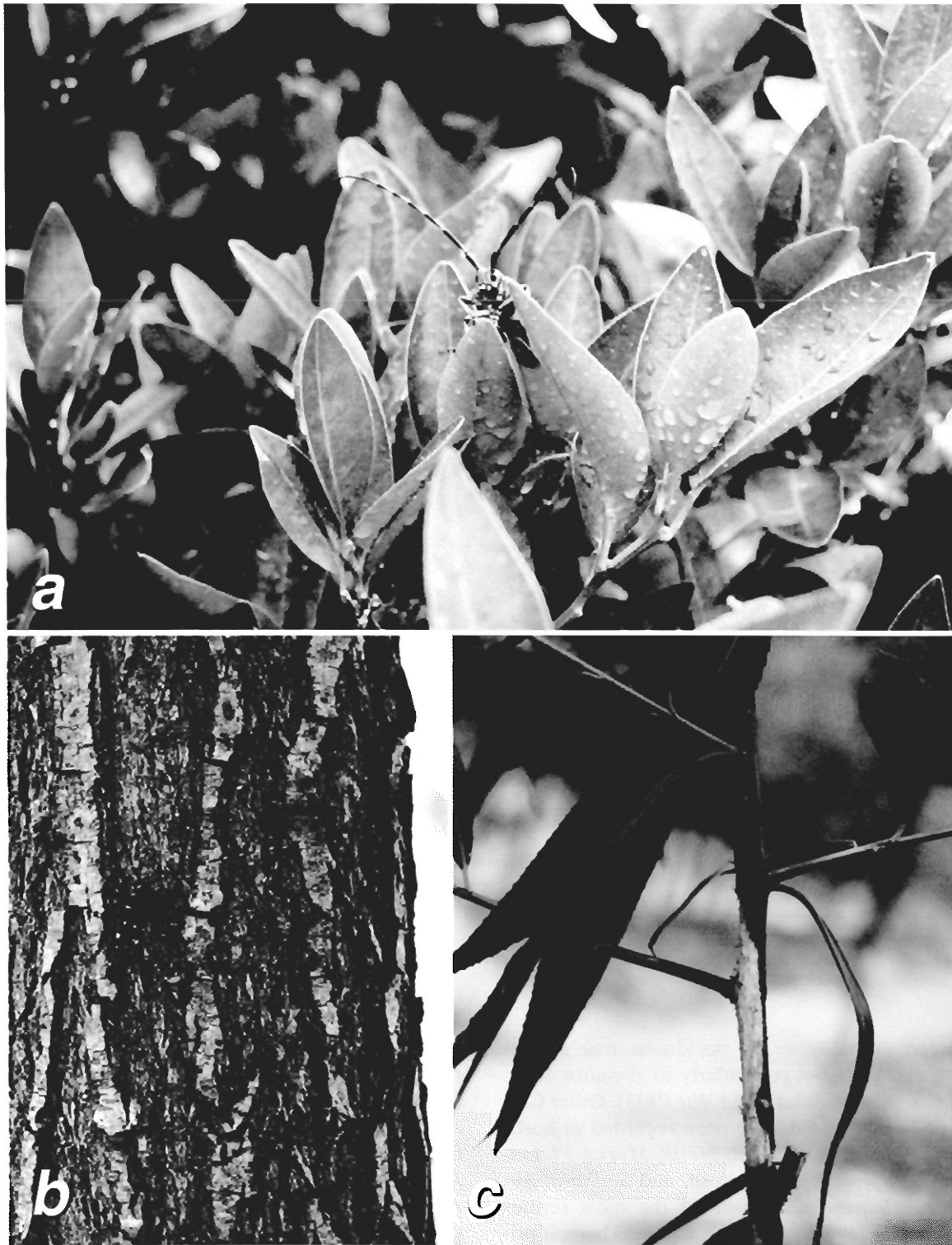


Fig. 1. a, *Anoplophora chinensis* (Forster) (form *malasiaca*) on *Citrus* near Matsuyama, Shikoku, Japan, June, 1998. b, *A. glabripennis* (Motschulsky) (form *nobilis*) on *Salix* in Langfang City, Hebei, China, June 26, 1998. c, Adult feeding damage of *A. glabripennis* on young *Salix* branchlets in Langfang City, Hebei, China, June 26, 1998.

Yunnan provinces, and farther south (but not in southeast China) (EPPO 2001). Li and Wu (1993) recorded *A. glabripennis* nearly throughout the country, but found it absent from the Chinese provinces

of Qinghai, Xinjiang, and Xizang (= Tibet) in the west. Map 6 depicts all the locality records we have gleaned from actual specimens.

In China, larval feeding by *A. glabripennis* causes



Fig. 2. a, Egg scars of *Anoplophora glabripennis* (Motschulsky) on *Salix* in Langfang City, Hebei, China, June 26, 1998 (note adult below). b, mating pair of *A. chinensis* (Forster) (form *malasiaca*) at base of *Citrus* in Fukuoka Fruit Tree Research Station, Fukuoka City, Japan, July 8, 1998. c, same as b, on trunk of *Citrus*.

widespread mortality to 24 deciduous tree species (Yang et al. 1995), but particularly to *Populus*, *Salix*, and *Ulmus* (Xiao 1980, Li and Wu 1993). Other Chinese woody plants also have been recorded as hosts, including *Acer*, *Alnus*, *Malus*, *Melia*, *Morus*, *Platanus*, *Prunus*, *Pyrus*, *Robinia*, *Rosa*, and *Sophora*. *Anoplophora glabripennis* is one of the most serious pests of poplar (*Populus* spp.) in China. There, it primarily attacks species and hybrids in the *Aegeiros* section of *Populus* (*P. nigra*, *P. deltoides*, *P. × canadensis*, and the Chinensis hybrid *P. dakhuanensis*) (Li and Wu 1993, Luo and Li 1999). Other sections of the genus (*Alba* and *Tacamahaca*) are also attacked, but are only slightly susceptible (Li and Wu 1993). In the United States (New York and Chicago), *A. glabripennis* attacks and oviposits on a number of

urban street trees, including *Populus*, *Salix*, *Ulmus*, *Fraxinus*, *Hibiscus*, *Aesculus*, *Betula*, but most important, *Acer* (Haack et al. 1997). Any species of *Acer* is highly attractive to this exotic pest, with the following species as confirmed hosts: *Acer negundo*, *A. platanoides*, *A. saccharinum*, *A. saccharum*, *A. rubrum*, and *A. pseudoplatanus*. Unlike most other Cerambycidae, *A. glabripennis* attacks not only apparently healthy and vigorous trees, but also stressed trees and recently cut logs (Hua et al. 1992, Gao et al. 1993, He and Huang 1993). Young and old trees are attacked indiscriminately.

Throughout its native range, this woodborer usually has a single generation annually (univoltine) but occasionally some individuals require up to two years (bivoltine) to complete their development (Hua et al.



Fig. 3. a, *Anoplophora macularia* (Thomson) (2 spotted form with H3 and H4 separated) on *Citrus* in Yangmingshan, Taipei County, Taiwan, June 11, 1999. b, *A. chinensis* (Forster) (form *malasiaca*) mating on *Citrus* in Fukuoka Fruit Tree Research Station, Fukuoka City, Japan, July 8, 1998 (note similarity to *A. macularia*).

1992). Summarizing from Hua et al. (1992), in the Chinese provinces of Liaoning, Shandong, Henan, and Jiangsu, *A. glabripennis* is univoltine or bivoltine. In Liaoning Province, over 80% of the population is univoltine, with first to third instar larvae overwintering, while another 11–20% of the population is bivoltine and with mature larvae overwintering. In Jiangsu Province, 98% are univoltine, with 2% bivoltine, and the overwintering stage is the mature larva. In Henan Province, 14% are univoltine and 86% bivoltine. In the spring, mature, overwintered larvae pupate, while other larvae feed until late March and make a pupal chamber in the larval galleries from late April to early May. The prepupal stage lasts 9–39 days (Mean: 21.8 days), while the pupal stage ranges from 13–24 days (mean: 19.6 days). After emergence, adults remain in the pupal chamber for 6–15 days (mode: 7 days) and then chew their way to the outside. In China, adults begin to appear in early April, with peak emergence from mid-June to early July, and they are still active in October.

Newly emerged adults feed first (maturation feeding) on the tender bark of small twigs and branches (Fig. 1c), and sometimes on tender leaves and leaf petioles, and then mate on branches and trunks. It is unclear whether long-range pheromones are utilized by the sexes to attract each other for mating purposes; recent investigations indicate that they do not exist, but that the sexes instead find each other on the host tree after being attracted there by host volatiles. Once mated, a female chews through the bark of the host tree to the cambial layer, forming the “egg scars” (Fig. 2a), then turns and inserts her ovipositor, and lays a single egg, just under the inner bark (phloem). Typically, females lay eggs in the upper trunk and along major branches where the bark is thin, smooth, and tender. Also, small branches in the upper canopy are attacked and used for oviposition sites as well. As the tree crown begins to die, the beetle will attack and oviposit along the entire trunk and even on the exposed roots of larger, older trees. Adults tend to return to the same tree to lay eggs if the tree remains viable. The literature above suggests that females lay 25–40 eggs, but some can lay as many as 100+ eggs during their life span. Females live 14–66 days while males are shorter lived, at 3–50 days. In New York and Chicago, females lay eggs from July to early November. Eggs hatch in one to two weeks, and first-instar larvae feed exclusively in rotting cambium and remain in this region for the first two molts, and enter the sapwood only after the third instar. Second-instar larvae feed on healthy phloem and xylem, passing brown feces and sawdust from the oviposition site; late third and fourth instars, feeding on the xylem

tissue, pass whitish feces and sawdust from the egg site (Xiao 1980). Maturing larvae tunnel upward into a branch or trunk for 10–30 cm. Full-grown larvae can attain a size of 50–60 mm. A final instar larva creates a chamber or cell near the outer bark and transform into a pupa. Newly emerging adults chew an exit hole through the inner bark, exiting the host tree through 6–18 mm circular exit holes.

Although adult feeding can cause twig mortality, this is minor compared to the damage caused by larvae feeding as they tunnel through branches and trunks. If larval densities are high, individual branches or entire trees can die. For heavily infested trees, strong winds or heavy snow pack can cause branches and even whole trees to break or collapse. Larval feeding can reduce the quality of hardwood lumber, veneer, and wood fiber. The Asian longhorned beetle's preference for maple species (*Acer*) is considered by most as an enormous threat to maple sugar production in the northeastern United States if the beetle becomes widely established there. In addition, property values are reduced in areas where the beetle is established, and areas where fall foliage tourism is important likely will become severely impacted if infested (Kucera 1996, Appleby 1999).

General summary of known biology for Anoplophora species.—*Host trees:* *Anoplophora* species attack and damage numerous hardwood trees, across many families of angiosperms, and also some coniferous trees. Host trees, cited in the published literature, are summarized in the species accounts, under the subheading “Hosts.” *Damage and Economic Importance:* In general, members of the family Cerambycidae are phytophagous in their feeding habits (Linsley 1959). Their larvae usually bore into tissues of woody plants ranging from moribund to dead and decomposing, while some species (in the genera *Agapanthia* and *Tetraopes*, for example) feed in the stems of living herbaceous plants (Hanks 1999). In contrast, some cerambycid species (especially in the subfamilies Cerambycinae and Lamiinae) infest living but stressed woody angiosperms, and thus are considered important pests of forest, plantation, and street trees. The Cerambycinae and Lamiinae include many species that are among the world's most important tree pests (Hanks 1999).

Longhorned beetles of the genus *Anoplophora* include species that oviposit in healthy and vigorous host trees, but also in weakened trees. Larval feeding may contribute to decline of host trees, particularly when they are repeatedly attacked by multiple generations of the borer. Other species in the genus attack host trees that are alive and growing but whose defenses have been compromised by chronically poor growing conditions such as soil compaction, low soil

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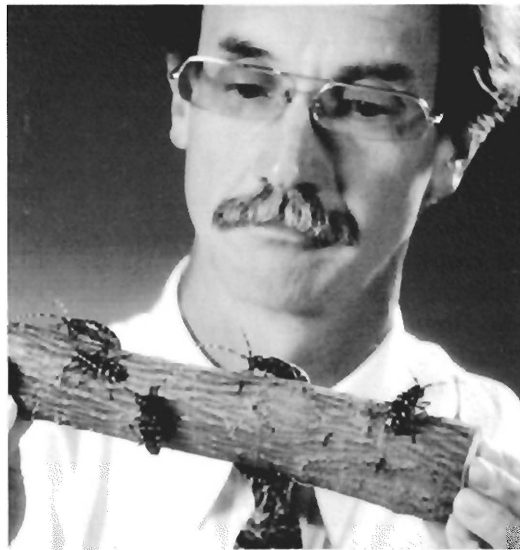
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