A biotic survey and inventory of the dynastine scarab beetles of Mesoamerica, North America, and the West Indies: review of a long-term, multi-country project

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ABSTRACT
This biotic inventory will document the species-level diversity of dynastine scarabs, their spatial and temporal distributions, ecological preferences, and biology. The long term, multi-country research project explores a biotically megadiverse region that is seriously at risk from deforestation, environmental homogenization, invasive species, and urban sprawl. Objectives of this survey are: 1) to understand the biodiversity of dynastine scarab beetles in Mesoamerica; 2) disseminate this information in print and electronic forms; 3) train students, parataxonomists, and collection managers in the study area about dynastine taxonomy and identification, care of collections, dissemination of information, and conservation; and 4) assemble authoritatively identified voucher collections and associated databases in Mexico, Guatemala and the U.S. It fully complements our recently completed inventories of the dynastines in southern Mesoamerica. The electronic database and monograph will make information available to a broad user community of researchers, students, natural resource managers, government entities, and general public. Broader impacts of this research encompass discovery while promoting learning, solidifying partnerships to explore biodiversity, and enhancement of research infrastructure by creation/augmentation/dissemination of databases, training of students and technicians, and establishment of authoritatively identified collections. Benefits to society include a better understanding of the importance of and threats to biodiversity, enhanced ability to monitor habitats using taxonomic knowledge, educating students and the public about science, training future scientists or technicians, and instilling in the peoples of developing tropical countries a greater interest in their own rich biota so they may benefit from it and better care for it.

KEY WORDS
Insecta, Coleoptera, Scarabaeidae, Dynastinae, Mesoamerica.
Dynastinae of Mesoamerica, which I am now pursuing with my colleague, Ronald Cave. Our biodiversity inventory of this large area is the subject of this review. Accordingly, this paper is dedicated to Dr Paulian’s memory and the inspiration that he provided for me and to many other coleopterists.

INTRODUCTION

Why shouldn’t something new and wonderful lie in such a country? And why shouldn’t we be the men to find it out? (Sir Arthur Conan Doyle, *The Lost World*, 1912)

The beetle family Scarabaeidae is a large (c. 35,000 species), diverse, cosmopolitan group of beetles. The
Dynastinae (Fig. 2) is one of the most conspicuous subfamilies of Scarabaeidae (Jameson & Ratcliffe 2002), and it occurs in all the major biogeographic regions of the world. It is monophyletic (Browne & Scholtz 1999) and contains c. 1500 species, but the total world fauna may reach 2000 species (Endrödi 1985). More species are found in the Neotropics than in any other realm. In the New World, there are currently 86 genera and c. 800 species. Adult dynastines are small (4 mm) to very large (160 mm) beetles. Males in some species possess extravagant horns on the head or thorax which, together with their large size, has given rise to popular names such as rhinoceros or hercules beetles. The adults of nearly all species are nocturnal or crepuscular, and most are readily attracted to lights at night. Adults are known to feed on rotting fruit, slime flux, and plant roots. Some are now recognized as important, accidental pollinators of palms and aroids (Araceae) resulting from their feeding on floral parts (Beach 1982, 1984; Young 1986; Gottsberger 1989; Gottsberger & Silberbauer-Gottsberger 1991). Larvae are primarily saprophagous or phytophagous and live in the soil or in decaying logs where they are important in nutrient cycling. The immature stages and life cycle for most dynastine species remain unknown.

PROJECT OBJECTIVES

Our research will thoroughly document the Dynastinae in Mesoamerica, North America, and the West Indies. The first two phases of this plan are completed and resulted in two large monographs: “The Dynastine Scarab Beetles of Costa Rica and Panama” (Ratcliffe 2003) and “The Dynastine Scarab Beetles of Honduras, Nicaragua, and El Salvador” (Ratcliffe & Cave 2006). Phase 3, ongoing, will study the Dynastinae of Mexico, Guatemala, and Belize. Phase 4 will cover the West Indies, and phase 5 the USA and Canada (Fig. 3). Our objectives are:

1. To understand the biodiversity of dynastine scarab beetles in Mesoamerica, North America, and the West Indies. We will survey intensively the Dynastinae residing in systematics research collections in the study area in order to gather data on spatial and temporal distribution and life history or habitat data associated with the specimens. We also collect extensively in the study area utilizing a program designed to provide reasonably complete geographic coverage and accounting for seasonality as it affects activity of adult dynastines. Field collecting provides habitat and life history information not found on specimen labels.

2. To disseminate dynastine biodiversity data in print form and electronically to the scientific community, K-12 students, university students, and the public. Included will be keys (in English and Spanish) for identification of all species, descriptions and diagnosis of each species, and information on geographic and temporal distribution, elevational range, vegetation zone, and other life history data. A specimen-level database generated by the study is disseminated electronically.

3. To train graduate students, parataxonomists, curators, collection managers, and university students in the study area about Dynastinae, care and management of collections, databasing, taxonomy, biodiversity, and conservation.

4. To provide educational opportunities to K-12 students, the public, and groups underrepresented in science in the study area via outreach activities that address the importance of biodiversity and understanding of science.

Collection of new material and inventories of existing collections are needed in order to explore
and catalog biotic diversity and to facilitate further research. These are different, but complementary, components of biotic surveys. This inventory discovers and documents the species-level diversity of dynastine scarabs, their spatial and temporal distributions, and habitat preferences and makes this information available for studies in biodiversity, ecology, biogeography, conservation and applied agriculture. The results will have applications to conservation, education, ecotourism, pest management, and habitat monitoring. The geographic scale of the project, while geopolitical, remains a natural and compelling biological focus.

Disseminating and applying taxonomic information is critically important. Resource managers in all of the countries in the study area need baseline information about their fauna, much of which remains unknown and may be threatened due to habitat loss. Biodiversity inventories are essential to understanding and managing these natural resources. Moreover, there is urgency to conducting faunistic studies in Mesoamerica and the West Indies because burgeoning human populations and associated human activities are rapidly eliminating habitats that sustain so much tropical biodiversity (Myers 1980; Savage 1982; National Science Board 1989; McNeely et al. 1990; Blackmore 1996).

HISTORICAL BACKGROUND

The first attempt at an identification manual for the Mesoamerican Scarabaeidae was written by Bates (1888) in the Biologia Centrali-Americana series. An identification manual for the dynastine world fauna was produced by Endrödi (1985). This work was an English version condensation of his 22 papers in German on the subfamily (Endrödi 1966, 1967, 1968, 1969, 1970, 1971, 1974, 1976a, b, 1977a-c, 1978). The manual was intended as an identification guide rather than a monograph since it did not provide descriptions or synonymies, temporal distributions, life history data, habitat associations, or detailed distributions. Many new
The study area contains six of the eight tribes of world Dynastinae and 50 of the 83 world genera, or 60% of the world dynastine genera. Mesoamerica is one of 25 global Biodiversity Hotspots where exceptional concentrations of biodiversity are undergoing rapid loss of habitat (Mittermeier et al. 1999a; Myers et al. 2000). The 25 hotspots (including the Mesoamerican one) comprise only 1.4% of the land surface of the Earth, but they contain the sole remaining habitats of 44% of the Earth’s vascular plants and 35% of its vertebrate species, and, by extension, sizeable numbers of insects (Myers et al. 2000).

The subfamily Dynastinae in the study area consists of 50 genera in six tribes. The tribe Cyclocephalini contains 15 genera and about 385 species. All species have also been described since 1985, and so the keys in Endrödi’s manual are not totally accurate. For example, 90 species of Cyclocephala have been described since the manual was published, and so the keys in it should be used with great caution because there now exists 43% more species than were included in the keys published in 1985!

**TAXONOMIC COMPOSITION**

Mesoamerica, North America, and the West Indies have an incredibly diverse fauna, and understanding this biodiversity is essential for systematics, ecological studies, habitat monitoring, and conservation efforts.
Cyclocephalini occur in the New World except for *Ruteloryctes*, which is African. Seven genera occur in the study area, and the majority of species occur in Mexico, Costa Rica, and Panama. The most speciose genus is *Cyclocephala* with 107 currently known species in the study area (over one-third of all described species in the genus).

World-wide, the Pentodontini has about 75 genera and over 500 species. In the New World there are 23 genera and about 170 species. There are 14 genera of Pentodontini in the study area, and Mexico has the highest percentage of species due mostly to the high numbers of species in the genera *Orizabus* (14 species) and *Tomarus* (15 species).

The tribe Oryctini contains 31 genera and about 230 species. In the New World there are 14 genera and about 130 species, and in the study area there are 13 genera. Mexico has the highest number of species.

The tribe Phileurini has 35 genera and about 225 species. Twenty one genera with about 135 species are found in the New World. Eleven of these genera (a little over 50%) are monotypic. Such a high degree of monotypic genera suggests either a group that is so poorly collected and studied that we are left with large gaps (a likely scenario in our view), or that our ideas of what constitutes genera need adjusting, or, that we are, in fact, really observing small, isolated, relictual genera. In the study area there are currently nine genera.

The Agaocephalini has 11 genera and 40 species, all of which are found in the New World. Four genera are found in the study area.

World-wide, the tribe Dynastini contains 10 genera and 60 species. Three genera and 23 species occur in the New World, and all three genera occur in the study area. Mexico has a high percentage of species because of the greater number of species of *Golofa* (nine species) and *Megasoma* (eight species).

**PROGRESS TO DATE**

We have generated a preliminary checklist of the species known to occur in the study area.

The 157 species of dynastines that occur in Costa Rica and Panama have been comprehensively reviewed (Ratcliffe 2003). That study provided the first extensive documentation of the taxonomic, geographic, and temporal distribution of Neotropical dynastines in any mainland country of Latin America. An apprentice curator was trained at INBio, which now has the largest and the best curated collection of Dynastinae in Mesoamerica. Costa Rica’s 35 parataxonomists greatly augmented the database with numerous specimens they collected, new locality information, and new species. The project’s electronic database contains 34,728 specimen-level entries. Twelve scientific papers were published as part of this project.

The 116 species of dynastine scarabs that occur in Honduras, Nicaragua, and El Salvador have also been comprehensively reviewed (Ratcliffe & Cave 2006). Dynastine scarabs in the 10 research and teaching collections housing Coleoptera in the study area were identified, augmented, curated, and databased. We published 31 papers for this phase of the project, including 14 by the Ph.D. student that was trained. The project’s electronic database contains 21,150 entries. School presentations in Honduras and media exposure (television, magazines, newspapers) about biodiversity promoted learning, thus empowering students to be more involved with conservation and supportive of science endeavors.

The third phase of the inventory, a review of the dynastines of Mexico, Guatemala, and Belize, has just been funded by the National Science Foundation and research is ongoing.

**METHODS**

**COLLECTIONS-BASED RESEARCH**

Museums contain a vast amount of biodiversity information, and access to this information (via databases) is critical to planning future research and conservation efforts. We will database collections so that specimen information can be easily accessed by workers for future surveys. On-site visits to all the principal collections holding material from the study area will be conducted, thousands of identifications will be made, collections will be properly curated, and the data recorded.
FIELD RESEARCH
The study area is a complex region where Nearctic North American and Neotropical Central and South American taxa overlap (Ryan 1963; Sawyer & Lindsey 1971; Holdridge et al. 1971). The insect fauna of this area is exceptionally rich because of the influence of mixed topography, isolated oceanic islands in the Caribbean, and multiple microclimates due to elevation, exposure, or weather patterns. In Mexico, for example, the insect fauna of high mountains (above 2000 m) in the Mexican Transition Zone north of the Isthmus of Tehuantepec is more disparate from that of the contiguous lowlands than most other parts of the world (Hafiter 1987). The broken topography has produced the region’s own unique species resulting in some of the highest levels of diversity on Earth and creating a fauna endemic to the Mexican Transition Zone itself (Mittermeier et al. 1999b).

Field collecting is needed to supplement museum specimens, establish tissue collections, better define temporal and geographic distributions of species, and gain first-hand experience of life history, behavior, and habitat associations. Collecting efforts are specifically selected for areas that have high biodiversity, lack baseline data, are threatened with habitat destruction, or have special conservation status. There is urgency to surveying because parts of the study area are threatened with imminent habitat destruction due to human activities (Anonymous 1980; National Research Council 1982).

Most Dynastinae are attracted to lights at night, and use of mercury vapor lamps and ultraviolet lights are our primary trapping methods to determine diversity and abundance in any given area. We have seen some species of Cyclocephala, Mimeoma, and Megaceras that arrived in a single, brief “pulse” of activity during a single night but were otherwise never seen again. Rain, unless heavy, will not generally inhibit flight activity at night nor will the relatively cool temperatures at higher elevations. Efficient use of light traps necessitates that the lights be on from dusk to dawn in all kinds of weather.

The field itinerary is carefully planned so that a maximum amount of time is actually spent collecting Scarabaeidae. Protocol for field collecting typically consists of seeking out a suitable collecting site followed by photographing the site; setting up the flight intercept, bait, and light traps; recording weather, geographic coordinates, elevation, and habitat data; collecting from flowering aroids; and conducting diurnal sweeps of vegetation or excavating rotten logs for larvae or Phileurini (many species of phileurines are not readily attracted to lights because of their reclusive habits in rotting logs). Nocturnal foliage gleaning away from the lights is also conducted in order to collect and observe dynastines feeding. In this way, host plant information can be gathered and recorded, and plant samples are collected for later identification. All insect and plant samples collected are temporarily curated at the nearest processing center (camp site, park building, or hotel room) prior to being transported to the University of Nebraska or the principal collection facility in the host country for final preparation. All specimens are properly curated, labeled, authoritatively identified, and vouchered in each of the participating collections in the study area. Tissue samples are properly preserved (ultracold storage in 95% ETOH) and vouchered in the Biosynthesis Laboratory at the University of Nebraska State Museum.

The study area has 13 different Holdridge life zones (Holdridge 1967) or 30 ecoregions (Dinerstein et al. 1995). Collections are made in each zone/region supporting scarabs. Special attention is given to the many montane cloud forest areas because they are more species-diverse and rich in endemic species than lowland forests (Janzen 1973; Stout & Vandermeer 1975; Fjeldsa 1994; Churchill et al. 1995; Roy et al. 1997; Anderson & Ashe 2000; Hall 2006; Ratcliffe & Cave 2006), and because they are one of the most endangered of all forest types (Conservation International 2006).

Our training of students in field collecting techniques, preparation of collected material, and the regulations and permitting procedures of host countries is an essential component of field work. Similarly, enhanced cooperation with students and scientists in developing countries is important because, ultimately, they will help to generate the collections and databases that will arm conservationists, policy makers, and biological resource managers with the knowledge necessary to sustain and use their nation’s biological diversity.
DATA MANAGEMENT
Specimen-level data is entered into the Mantis database template, designed by P. Nasrecki, that uses FileMaker Pro, a relational, web-ready software program. The locality field will have all newly sampled sites fully geo-referenced using GPS technology to facilitate mapping and GIS applications. The specimen data is available on the world wide web.

STUDENT TRAINING
In keeping with our philosophy of student training, we believe in active, hands-on apprenticeships where students participate in all aspects of the project. Our students are taught the discipline of entomology, the science of systematics, the ethics of becoming a professional scientist, and the methods of monography, field work, and collections-based research. This training is facilitated by our experience as well as by travel, seminars, outside speakers, coursework, and interactions with collaborators. These combined elements provide students with assets necessary to contribute to the fields of insect systematics, invertebrate biology, conservation, and museum studies. Training students in museum collection protocols (curation, database management, knowledgeable use of type specimens, and authoritative identifications) is an essential component of systematics and biodiversity research. Interactions with foreign colleagues are emphasized as a means to promote professional development and international collaboration.

PUBLICATION
Publication of each monograph in the Bulletin of the University of Nebraska State Museum concludes each phase of the project. Included in each monograph is a brief introduction to the countries involved that addresses climate, land forms, vegetation, conservation, and dynastine biology and distribution. Each tribe and genus is characterized and discussed, and taxonomic keys (in English and Spanish) are given for all tribes, genera, and species. Each species account consists of complete synonymies, descriptions, diagnoses, distributional and temporal data, habitat and ecological information, and larval and life history information when known. Illustrations consist of habitat photographs, habitus and line drawings, and digital images. The parameres of the male genitalia are all illustrated because they are necessary for the identification of dynastine species. Distribution maps showing elevation are provided. The actual users of these manuals are systematists and collection managers working with dynastines; Latin American scientists and students studying their entomofauna; ecologists who encounter these insects in their studies and who need identifications and information on biology and distribution; biogeographers needing annotated distributional data; park and reserve managers needing to know the composition of faunal elements for establishing management plans, educational programs, or research opportunities; applied entomologists in each country requiring information about pest status; and a fairly large amateur community of scarab watchers and collectors.

EXPECTED SIGNIFICANCE
AND BROADER IMPACTS
Broader impacts of this research encompass discovery while promoting learning, solidifying partnerships to explore biodiversity, enhancement of research infrastructure by creation/augmentation/dissemination of databases, training of students and technicians, enhanced ability to monitor habitats using taxonomic knowledge, and establishment of authoritatively identified collections. The electronic database and published monographs make information available to a worldwide user community of researchers, students at all levels, natural resource managers, government entities, and amateur naturalists. We teach about biodiversity and conservation, through outreach activities and research-based educational materials, to K-12 students, nature centers associated with reserves, and the general public in the study area, thus promoting citizen science.

Taxonomic monographs contain descriptions, illustrations, identification keys, nomenclature, and lists, and, as such, are cornerstones of comparative biology (Anonymous 1995). Comprehensive and accurate characterizations of the Dynastinae species, their distributions (geographic, elevational, temporal), and life history information are the principal contributions to systematics. Cyclocephala, for
example, is a large genus (c. 311 species) in which new species are being described continuously. Over 90 species have been described since Endrödi’s (1985) all-inclusive key, meaning that there are no reliable means for identification for 26% of the species. Additional collecting and analysis of each species in this research will recognize new species and clarify the status of others and, concomitantly, provide new keys and an extensive database for subsequent studies dealing with phylogeny and biogeography. Except for those older works on the Lesser Antilles (Chalumeau 1983), Cuba (Chapin 1932), and the newer studies on Costa Rica and Panama (Ratcliffe 2003) and Honduras, Nicaragua, and El Salvador (Ratcliffe & Cave 2006), the capability to identify and analyze dynastines does not exist for any other country in the New World tropics. This research will extend that capability. We adhere to the Phylogenetic Species Concept (Wheeler & Platnick 2000), which is defined as the smallest aggregation of populations or lineages diagnosable by a unique combination of character states.

Ronquist & Gärdenfors (2003) noted that the geographical constraint of area-limited surveys is not ideal from a scientific perspective but is the forte of national inventories, because they can provide society with the necessary deliverables of illustrated identification keys and basic facts concerning the distribution and biology of species. This will broaden the knowledge base for identification and monitoring of biodiversity, provide a rich information source for educators, and significantly heighten public awareness of local biodiversity and its conservation. Wilson (2004) observed that descriptive taxonomy is our pioneering exploration of life on Earth, and that among its cascade of derivative functions it establishes the foundation for the phylogenetic tree of life, provides a requisite database for ecology and conservation science, and makes accessible the vast and still largely unused benefits offered by biodiversity to humanity. Systematics Agenda 2000’s first global objective is to discover, describe and classify the world’s species (Systematics Agenda 2000 1994). This is one of our contributions to that effort.

Most of the countries of Mesoamerica and the West Indies are small, but they have a great amount of physiographic diversity that contributes directly to the richness of their biota. But they are also countries of intense land development where pristine areas are succumbing to “development”. “Costa Rica, for example, has been a magnet for overseas money for conservation because it possesses tremendous biological diversity packed into an area the size of the small U.S. state of West Virginia. It is one of the biggest centers of tropical research in the world. Moreover, it stands nearly alone among developing countries in making a concerted effort to halt – perhaps even reverse – the destruction of habitats that in turn is leading to the potential loss of countless species of plants and animals throughout the tropics” (Janzen 1983). According to Mittermeier et al. (1999b), nearly half of the people in Mesoamerica live in rural areas where they depend directly on natural resources surrounding them; and yet this area has some of the highest deforestation rates in the world where 80% of the region’s original primary forest has been cleared or significantly altered.

The growing recognition of the importance to humankind of tropical forests and the mounting concern for their future is well-known (Raven 1981, 1983; Myers 1981, 1984; Ulfstrand 1992; Schaller 1997), and yet the developing countries in the study area have mixed success in genuinely protecting areas designated as parks and reserves because financial, physical, and human resources are limited. The causes of biodiversity loss include human impacts on habitats (habitat destruction, degradation, fragmentation, restructuring) and on organisms (over-exploitation and introduction of invasive species, predators and parasites) (Wilson 1992; Pimm et al. 1995; Vitousek et al. 1996; Mooney & Cleland 2001). We know that human population growth is causing the extinction of biodiversity, and that it is altering biosphere-level processes that we depend on for $3-33 trillion of environmental services annually (Constanza et al. 1997; Pimental et al. 1997). The efficient and rational use of natural resources depends on accurate ecological knowledge, but the major deterrent to ecological studies is the lack of taxonomic data that is fundamental for all subsequent studies. In order to arrive at a sound view of ecology in the tropics, we must first identify and catalog the fauna. This
is an urgent task requiring quick action (National Research Council 1980; Alberch 1993; Bisby 2000; Wilson 2000; Edwards et al. 2000; Page et al. 2004). A significant percentage of all species on Earth could be lost in the next 20 years because of human activities that are now altering or destroying entire habitats. At least half of these losses will result from tropical deforestation. The pace of basic research in the tropics must be accelerated, and failure to do so will eventually limit our capability to solve impending scientific and human problems.

We are at a crisis point in cataloging and understanding the Earth’s tropical biota and find ourselves in the unenviable position of not having enough trained systematists in the developing countries to address the problem. Training future systematists, collection managers, and parataxonomists, especially in developing countries, is critical to our understanding and stewardship of the plants and animals necessary for our own survival. Workshop and training sessions for curators and collection managers are held in the study area and cover scarab biology, collecting methods, curatorial standards and techniques, equipment and supplies, conservation, and databasing. Reaching out to teachers, K-12 students, and groups underrepresented in science is important to the success of our work and represents a valuable broader impact. The general public does not understand the importance of insects to the well-being of ecosystems or to their own lives. Public education about insect life is not adequately covered in schools, museums, or zoos. Consequently, there is entomophobia in addition to indifference. More importantly, some of these individuals become future policy makers in government, industry, and education, and they often have uninformed and negative attitudes about most of the life forms on the planet, the insects. Outreach and public education are needed to educate a new generation of informed decision makers, inquisitive students, and concerned citizens (Pfirman & AC-ERE 2003).

Systematics Agenda 2000 (1994) summarized by stating that “For scientific, economic, and ethical reasons we must resolve to describe and understand the significance of species diversity before the opportunity to do so is lost. The benefits of this mission far exceed the investment required to meet the challenge of the biodiversity crisis. No greater scientific endeavor, nor promising opportunity, exists.”

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