



## The Coleoptera of Panama. I. A first benchmark for the superfamily Dryopoidea

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### Abstract

The dryopoid beetles (Insecta: Coleoptera), which include aquatic, semiaquatic, and terrestrial species, are among a number of invertebrate taxa which have received scant recent attention in Panama. This paper brings together information from the published literature and current research to produce a first benchmark of knowledge about this coleopteran superfamily in Panama. To date, we have recorded 127 species in 54 genera distributed among 10 coleopteran families, including 50 species originally described from Panama. Of the total species and genera presented in this paper, 20 species and 6 genera are new country records for Panama. Our goals for this superfamily include expanded surficial and elevational collecting, training and development of young Panamanians in dryopoid systematics and ecology, and support for the scientific community via information dissemination. Further identifications and new descriptions are proceeding toward subsequent publications.

**Key words:** aquatic and semi-aquatic beetles, checklist, Neotropics, dryopoids

### Introduction

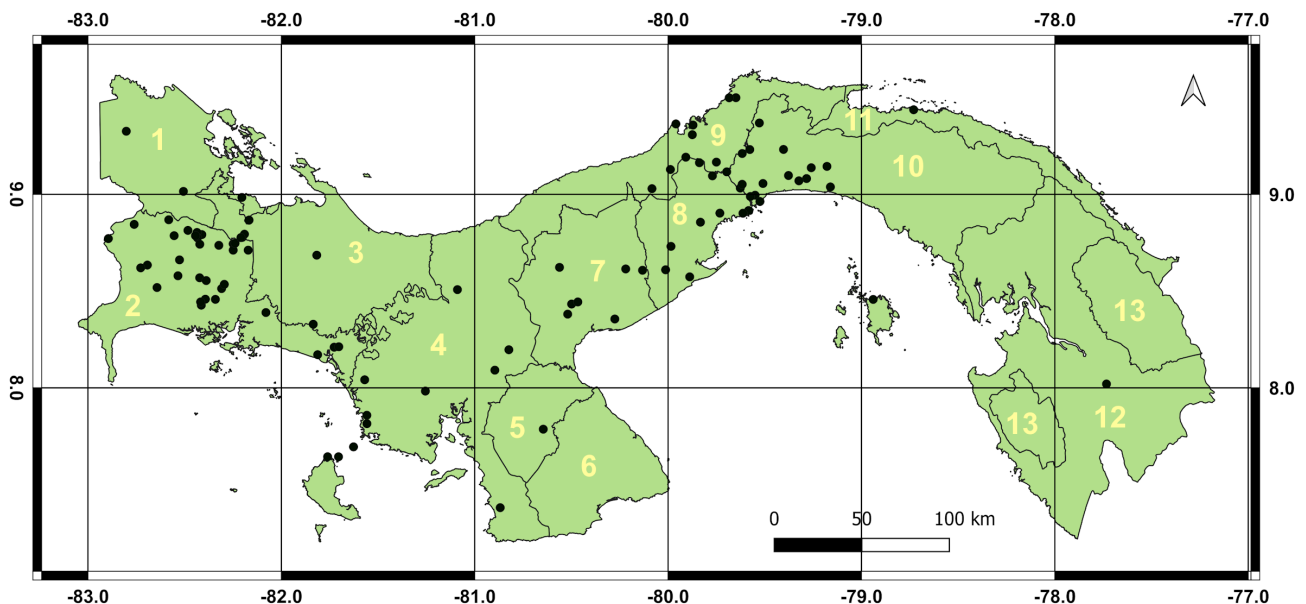
The flora and fauna of Panama are species-rich due to their tropical location and the topography of the country, resulting in a high diversity of microclimates and habitats. In terms of aquatic habitats, Panama contains over 500 rivers and countless creeks and other types of lotic and lentic waterbodies. A more thorough description of its geology, topography, climate, and habitats can be found in Armitage *et al.* (2024). An overabundance of habitats and resources exist in Panama that support diverse species and populations for the superfamily Dryopoidea (Insecta: Coleoptera), the focal group for this paper.

One of the most perplexing discoveries in biodiversity work is to find that a tropical country, with varied topography, climate, and overall high numbers of recorded taxa, hosts medium to large taxonomic groups for which no comprehensive and sustained study has occurred. Such is the case for Panama (and many other Central American countries). Even though Panama has been visited by a number of field biologists drawn to the Canal Zone and to Chiriquí Province in the western highlands, there have been few resident researchers and no trained nationals who thoroughly sampled and documented the dryopoid fauna. This provides a very incomplete picture, not only of this superfamily's diversity, but also of each species' surficial and elevational distribution within the country.

This situation is further compounded by the fact that, for the dyropoids and similar groups, no or very little type material is housed in Panamanian institutions, even though more than a few species have been described based on specimens from there. Also, most of the known fauna was recorded in the late 1800s and early 1900s. Primarily, this situation can be attributed to the relative lack of broad-based, long-term, and well-supported taxonomic training in the colleges and universities that populate Panama and many Central American countries. Costa Rica, with its positive orientation toward national biodiversity and ecotourism, is an exception, at least in part. Comparatively, Mexico, and most of the larger countries of South America (e.g., Brazil, Ecuador, Argentina, etc.) have more of a traditional taxonomic tradition copied from their Spanish and Portuguese predecessors.

The above view was supported by recent work on caddisflies (Insecta: Trichoptera) and chironomids (Insecta: Diptera) during the period 2015–2023 by the Aquatic Invertebrate Research Group (AIRG). In recent publications (Armitage *et al.* 2024; Armitage *et al.* 2025), the number of recorded species was more than doubled for both of these groups (caddisflies from 257 to 535 species; chironomids from 35 to 78 species). Furthermore, preliminary estimates indicate that each of these groups could gain 200–400 additional species with continued effort. These increases and estimates should not come as any surprise because both the order Trichoptera and the family Chironomidae are each represented by more than 15,000 species worldwide (Holzenthal & Calor 2017; Cranston 1995), with significant diversity in wet tropical and subtropical regions. Equally encouraging is the fact that two members of AIRG became the first native Panamanians to co-describe species of caddisflies. It is a fundamental goal of AIRG to encourage and support this success among Panamanians in all of the taxa that we study.

Many other groups of aquatic invertebrates have either never been studied (e.g., ostracods), or have not been seriously studied, some since the late 1800s to early to mid-1900s (e.g., aquatic and semiaquatic moths). The superfamily Dryopoidea is another example of the latter “abandoned in time” scenario. Our primary information for this group in Panama and Central America comes from the efforts of Sharp (1882) and Champion (1896, 1897) in the *Biologia Centrali-Americana* series published in the late 19<sup>th</sup> century. Additional taxonomists, including Guérin-Méneville, Hinton, Pic, Spangler, and Wooldridge, among several others (see Table 2 and References) have provided additional species and genera to the backbone of information constructed by Champion and Sharp. However, none focused primarily on Panama, but rather benefited from occasional collections by field biologists who were primarily collecting other groups of insects.



**FIGURE 1.** Map of Panama overlaid with the national administrative unit layer, showing collection locations (black dots) from which dryopoids have been identified to date. [1—Bocas del Toro Province, 2—Chiriquí Province, 3—Ngäbe-Buglé Comarca, 4—Veraguas Province, 5—Herrera Province, 6—Los Santos Province, 7—Coclé Province, 8—Panamá Oeste Province, 9—Colón Province, 10—Panamá Province, 11—Guna Yala Comarca, 12—Darién Province, 13—Emberá-Wounaan Comarca. The Naso Tjër Comarca is not shown.]

Although there has been a number of dryopoid species listed in the literature from Panama, we believe it does not reflect the true diversity of this group. The remainder of Central America requires as much, or more, attention as Panama. The purpose of this paper is to present what is known from various personal, institutional, and literature sources, to add what preliminary results we have generated to date, and to produce a first benchmark for this group against which future scientific progress can be measured and compared. Second, this paper also serves as a “first-step” to provide background information for encouraging taxonomic research in this group in Panama by students and others.

The Aquatic Invertebrate Research Group (AIRG) at the Universidad Autónoma de Chiriquí (UNACHI) and its Museo de Peces de Agua Dulce e Invertebrados (MUPADI) is currently focused on increasing our knowledge of Trichoptera (caddisflies), Plecoptera (stoneflies), chironomids (mime midges), and dryopoid beetles in Panama. Toward that goal, it has secured registered projects for these four orders of aquatic insects. The new taxonomic information presented in this paper is a direct result of executing these projects.

## Materials and Methods

**Collection methods and locality records.** Recently collected specimens made by AIRG were primarily captured in Malaise traps and UV-light traps, although a minor subset came from sweep-netting and hand-picking. Collections by WDS and CBB were made by a combination of aquatic net sampling, kick netting, hand-picking, and bulk sampling (e.g., leaf litter, leaf packs, etc.) with subsequent examination in the laboratory. Specimens were stored in 80% ethanol and later identified under dissecting and compound microscopes.

The locations of sample sites for recently collected and identified material included in this paper, as well as for those found in the literature, are provided in Figure 1. Much of the location information in the literature is non-specific. Thus, we were only able, collectively, to provide reliable insights into distribution at the major watershed (cuenca) and administrative unit (provinces, indigenous comarcas, etc.) levels. Maps in Figures 1 and 2 were produced employing QGIS 3.2—Firenze software, and the graph in Figure 3 was generated in Excel software. All of the locations in Champion (1897) which mention Bugaba and Volcán de Chiriquí are referring to the Bugaba District in Chiriquí Province and to Volcán Barú, respectively. However, Law 13, enacted in 2013, placed the upper half of the original Bugaba District in a new district, Tierras Altas. Therefore, for the Volcán Barú location the following information will be used throughout: Panama, Chiriquí Province, Tierras Altas District, Volcán Barú. In the “Material examined” sections collection sites with “WDS-A-#” refer to collection site data sheets of the second author.

**Checklist and guide to the annotated species list.** In the Annotated Species List, species records based on material we have studied are listed under “Primary collection information”. These include specimens collected by WDS and CBB (in 2006) or those resulting from projects executed by the Aquatic Invertebrate Research Group (2015 to present) and identified by the second author (WDS). Species based on records of specimens that we have not studied are listed under “Secondary collection information”. These include records listed in Sharp (1882) and Champion (1896, 1897), as well as many other publications indicated below and in Table 2. Also included in the section are records from various museums and private collections that were not examined. The use of the word “ibid.” in these two sections implies “same as the previous record, except”. This can be rather telescopic in nature, referring to only the country name to everything in the record prior except the date. The country of the type locality is indicated in square brackets “[ ]”. If there has been a name change, then the synonym (one instance) or superseded combination (many instances) are given after the type country. With two exceptions (*Callirhipis* sp. and *Chelonarium* sp.), species in the annotated species list which consist of a genus name followed by “sp.” as the epithet are based on specimens which differ morphologically from other herein listed species in the same respective genus, but which cannot be identified or associated further at this time. The two exceptions, which could include multiple species, females, new species, or duplicate species, are not included in any final totals. However, they are presented in the Annotated Species List because we do not wish to lose valuable data that might be of use to others. Countries listed in the Neotropical distribution sections are derived from locations in the included collection location information for each species or from literature sources such as Blackwelder (1944) or other sources as noted.

**Specimen depositories.** Within the “Primary collection information” and “Secondary collection information” subsections in Annotated Species List below, a number of acronyms are used to indicate depositories in which type and other specimens have been placed. The following is a list of those acronyms and their actual names.

- CAS—California Academy of Sciences (San Francisco, CA, USA)  
CSU—Stanislav Skalický Collection (Ústí nad Orlicí, Czech Republic)  
EMEC—Essig Museum of Entomology Collection (University of California, Berkeley, CA, USA)  
EASC—E. A. Schwarz Collection (Washington, DC, USA)  
FMNH—Field Museum of Natural History (Chicago, IL, USA)  
HPB—Harley P. Brown Collection, Sam Noble Oklahoma Museum of Natural History, Norman, OK USA  
IEXA—Colección Entomológica del Instituto de Ecología, A.C., (Xalapa, Mexico)  
INHS—Illinois Natural History Survey (Champaign, IL, USA)  
LSAM—Louisiana State Arthropod Museum (Baton Rouge, LA, USA)  
MCZ—Museum of Comparative Zoology (Cambridge, MA, USA)  
MIUP—University of Panamá Invertebrate Collection (Panamá City, Panamá)  
MMB—Moravian Museum—Brno (Brno, Czech Republic)  
MUPADI—Museo de Peces de Agua Dulce e Invertebrados (Universidad Autónoma de Chiriquí, David, Panamá)  
NHMUK—Natural History Museum of the United Kingdom (London, United Kingdom) (Note: the previous designation, BMNH (British Museum of Natural History) is used throughout the *Biologia Centrali-Americana* series)  
NHMW—Naturhistorisches Museum (Wien, Austria)  
OSUC—Ohio State University Collection (Columbus, OH, USA)  
STRI—Smithsonian Tropical Research Institute (Panamá City, Panamá)  
TAMU—Texas A&M University (College Station, TX, USA)  
UMC—University of Missouri (Enns Entomology Museum, Columbia, MO, USA)  
UNSM—University of Nebraska State Museum (Lincoln, NE, USA)  
USNM—United States National Museum (Washington, DC, USA)

**Comparison with adjacent faunas.** The known Panamanian dryopoid taxa is compared to known Dryopoidea from Costa Rica and Colombia (Table 3). Records from the latter two countries are from unpublished data (WDS, pers. comm.) and the literature (e.g., Hincapié-Montoya 2023; Blackwelder 1944).

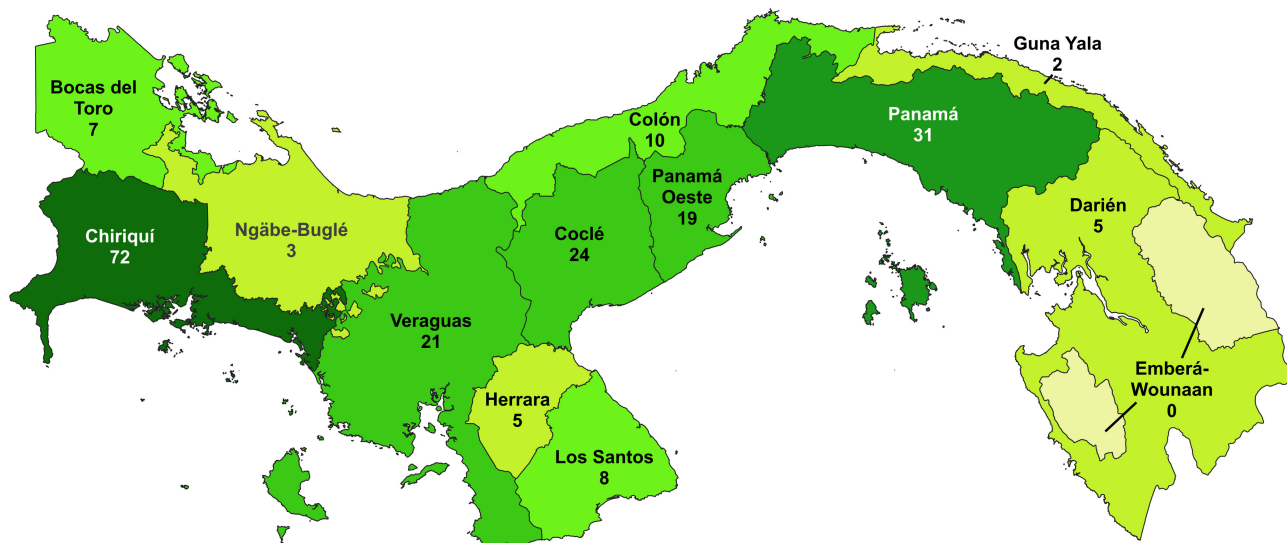
**Estimate of species richness.** The potential species richness for dryopoid beetles in Panama was estimated using Chao2 (Chao 1984, 1987; Colwell & Coddington 1994) as calculated by EstimateS software (Colwell 2013). Estimators like Chao2 use the number of rare species in a sample to estimate the likelihood of more, undiscovered species that could have been found if the sampling period or sampling area had been expanded. The theoretical origins of this non-parametric estimator of species richness can be traced back to work by Alan Turing and I.J. Good from cryptographic analysis of Wehrmacht coding machines during World War II. It was later applied by Good (1953) for use in mark-recapture models that are used in demography (Gotelli *et al.* 2024).

## Results

The extent of our knowledge of surficial and elevational distributions of dryopoid taxa is low. Several provinces and comarcas, particularly on the Caribbean side of Panama, have been poorly collected for Dryopoidea (Figure 2). Chiriqui Province is best known thanks to the early efforts of Champion and Sharp in the late 1800s. In the 1900s, Panama Province became better collected both by coleopterists (e.g., Hinton, Wooldridge, Spangler) and by other biologists. The provinces of Herrera and Darien, and the Naso Tjër Di (not shown in Fig. 1), Emberá-Wounaan, Ngäbe-Buglé and Guna Yala Comarcas require the greatest attention in the future. The distribution of families among the various province and comarcas (Table 1) also demonstrates the uneven effort of collecting throughout Panama. Chiriqui Province is the only administrative area wherein we have records of all 10 families. In general, little collecting has occurred in the indigenous comarcas areas.

To date, we have recorded 127 species in 54 genera distributed among 10 coleopteran families (Table 2). Included in these totals are 50 species first described from Panama, not one of which is deposited in Panama.

Twenty-one species and 7 genera are new country records. Further identifications and new descriptions toward a second benchmark are proceeding.



**FIGURE 2.** Map of Panama displaying the number of species of Dryopoidea collected in each province or comarca. A graduated color representation of same is also provided (from higher diversity—darkest colors to lower diversity—lightest colors); the same color is used for provinces and/or comarcas having similar diversity values.

**TABLE 1.** Distribution of families known from each province and comarca. [CAL—Callirhipidae, CHE—Chelonariidae, CNE—Cneoglossidae, DRY—Dryopidae, ELM—Elmidae, HET—Heteroceridae, LIM—Limmichidae, LUT—Lutrochidae, PSE—Psephenidae, PTY—Ptilodactylidae]

Family:	CAL	CHE	CNE	DRY	ELM	HET	LIM	LUT	PSE	PTY
<b>Province / Comarca</b>										
Bocas del Toro		X			X		X			
Chiriquí	X	X	X	X	X	X	X	X	X	X
Cocle	X	X		X	X		X		X	X
Colon		X		X	X	X	X			
Darien		X		X	X				X	
Embera										
Guna Yala					X					
Herrera					X				X	
Los Santos	X			X	X		X			
Ngabe-Bugle					X					
Panama	X	X			X	X	X	X	X	X
Panama Oeste		X		X	X	X	X	X	X	X
Veraguas		X	X	X	X	X	X		X	X

**TABLE 2.** Checklist of dryopoid beetles currently known from Panama. (\* = new country record).

Family	Genus	Species
<b>Callirhipidae Emden, 1924</b>		
	<i>Callirhipis</i> Latreille, 1829	
		<i>Callirhipis childreni</i> Gray, 1832
		<i>Callirhipis unicastata</i> Champion, 1896
		<i>Callirhipis</i> sp.

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**TABLE 2.** (Continued)

<b>Family</b>	<b>Genus</b>	<b>Species</b>
	<i>Celadonia</i>	Laporte de Castelnau, 1840
		<i>Celadonia laportei</i> (Hope, 1846)
<b>Chelonariidae Blanchard, 1845</b>		
	<i>Chelonarium</i>	Fabricius, 1801
		<i>Chelonarium chevrolati</i> var. <i>longulum</i> Sharp, 1902
		<i>Chelonarium chiriquensis</i> Sharp, 1902
		<i>Chelonarium errans</i> Sharp, 1902
		<i>Chelonarium hyphroides</i> Sharp, 1902
		<i>Chelonarium signatum</i> Dalman, 1824
		<i>Chelonarium ustulatum</i> Méquignon, 1934
		<i>Chelonarium</i> sp.
<b>Cneoglossidae Champion, 1897</b>		
	<i>Cneoglossa</i>	Guérin-Méneville, 1843
		<i>Cneoglossa brevis</i> Champion, 1897
<b>Dryopidae Billberg, 1820</b>		
	<i>Dryops</i>	Olivier, 1791
		<i>Dryops centralis</i> Sharp, 1887
		<i>Dryops detritus</i> (Sharp, 1882)
		<i>Dryops major</i> Sharp, 1887
		<i>Dryops punctipennis</i> (Sharp, 1882)
	<i>Elmoparnus</i>	Sharp, 1882
		<i>Elmoparnus brevicornis</i> Sharp, 1882
		<i>Elmoparnus pandus</i> Spangler & Perkins, 1977 *
	<i>Helichus</i>	Erichson, 1847 *
		<i>Helichus suturalis</i> LeConte, 1852 *
	<i>Momentum</i>	Perkins, 1997
		<i>Momentum hirsutum</i> Perkins, 1997
	<i>Parygrus</i>	Erichson, 1847
		<i>Paragyrrus maya</i> Barr & Shepard, 2020
	<i>Pelonomus</i>	Erichson, 1847
		<i>Pelonomus picipes</i> (Olivier, 1791)
	<i>Quadryops</i>	Perkins & Spangler, 1985
		<i>Quadryops chrysosetosus</i> Perkins & Spangler, 1985
		<i>Quadryops quasimodoi</i> Perkins & Spangler, 1985
<b>Elmidae Curtis, 1830</b>		
	<i>Austrolimnius</i>	Carter & Zeck, 1929
		<i>Austrolimnius curtulus</i> (Sharp, 1882)
		<i>Austrolimnius eris</i> Hinton, 1971
		<i>Austrolimnius formosus</i> (Sharp, 1882) *
		<i>Austrolimnius sulcicollis</i> (Sharp, 1882)
	<i>Cylloepus</i>	Erichson, 1847 *
		<i>Cylloepus barberi</i> Hinton, 1934 *
		<i>Cylloepus optatus</i> Sharp, 1882 *

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**TABLE 2.** (Continued)

Family	Genus	Species
	<i>Disersus</i> Sharp, 1882	
		<i>Disersus longipennis</i> Sharp, 1882
		<i>Disersus uncus</i> Spangler & Santiago, 1982
	<i>Heterelmis</i> Sharp, 1882 *	
		<i>Heterelmis</i> sp. *
	<i>Hexacylloepus</i> Hinton, 1940	
		<i>Hexacylloepus granulatus</i> (Sharp, 1882)
	<i>Hexanchorus</i> Sharp, 1882	
		<i>Hexanchorus browni</i> Spangler & Santiago-Fragoso, 1992
		<i>Hexanchorus crinitus</i> Spangler & Santiago-Fragoso, 1992
		<i>Hexanchorus emarginatus</i> Spangler & Santiago-Fragoso, 1992
		<i>Hexanchorus gracilipes</i> Sharp, 1882
		<i>Hexanchorus usitatus</i> Spangler & Santiago-Fragoso, 1992
	<i>Macrelmis</i> Motschulsky, 1860	
		<i>Macrelmis amazonica</i> (Hinton, 1945) *
		<i>Macrelmis sandersoni</i> (Hinton, 1936) *
		<i>Macrelmis scutellaris</i> (Hinton, 1934) *
		<i>Macrelmis striata</i> (Sharp, 1882) *
		<i>Macrelmis tarsalis</i> (Hinton, 1936)
	<i>Microcyloepus</i> Hinton, 1935 *	
		<i>Microcyloepus inaequalis</i> (Sharp, 1882) *
	<i>Neocyloepus</i> Brown, 1970	
		<i>Neocyloepus championi</i> (Sharp, 1882)
		<i>Neocyloepus sandersoni</i> Brown, 1970
		<i>Neocyloepus sculptipennis</i> (Sharp, 1882) *
	<i>Neoelmis</i> Musgrave, 1935	
		<i>Neoelmis aspera</i> Hinton, 1940
	<i>Notelmis</i> Hinton, 1941	
		<i>Notelmis nodipes</i> (Sharp, 1882)
	<i>Onychelmis</i> Hinton, 1941	
		<i>Onychelmis longicollis</i> (Sharp, 1882)
	<i>Phanocerus</i> Sharp, 1882	
		<i>Phanocerus clavicornis</i> Sharp, 1882
		<i>Phanocerus congener</i> Grouvelle, 1892 *
	<i>Pharceonus</i> Spangler & Santiago, 1992	
		<i>Pharceonus volcanus</i> Spangler & Santiago, 1992
	<i>Pseudodisersus</i> Brown, 1981	
		<i>Pseudodisersus goudotii</i> Guérin-Méneville, 1843
	<i>Stenhelmoides</i> Grouvelle, 1908	
		<i>Stenhelmoides rufulus</i> (Hinton, 1934)
	<i>Xenelmis</i> Hinton, 1936	
		<i>Xenelmis bufo</i> (Sharp, 1882)

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**TABLE 2.** (Continued)

<b>Family</b>	<b>Genus</b>	<b>Species</b>
<b>Heteroceridae MacLeay, 1825</b>		
	<i>Tropicus</i>	Pacheco, 1964
	<i>Tropicus bartolozzii</i>	Mascagni, 1994
	<i>Tropicus panamensis</i>	Skalický, 2014
	<i>Tropicus pusillus</i>	(Say, 1823)
	<i>Tropicus spangleri</i>	Skalický, 2006
<b>Limnichidae Erichson, 1846</b>		
	<i>Byrrhinus</i>	Motschulsky, 1858
	<i>Byrrhinus mimicus</i>	Wooldridge, 1987
	<i>Byrrhinus misellus</i>	(Sharp, 1902)
	<i>Byrrhinus panamensis</i>	(Sharp, 1902)
	<i>Cephalobyrrhinus</i>	Pic, 1923
	<i>Cephalobyrrhinus curticornis</i>	Pic, 1923
	<i>Cephalobyrrhinus lineatus</i>	Wooldridge, 1986
	<i>Corrinea</i>	Wooldridge, 1980
	<i>Corrinea delicata</i>	Wooldridge, 1980
	<i>Erasachus</i>	Erichson, 1847
	<i>Erasachus erichsonianus</i>	Sharp, 1902
	<i>Eulimnichus</i>	Casey, 1889
	<i>Eulimnichus acutus</i>	Wooldridge, 1979
	<i>Eulimnichus analis</i>	(LeConte, 1879)
	<i>Eulimnichus ater</i>	(LeConte, 1854)
	<i>Eulimnichus nitidulus</i>	(LeConte, 1854)
	<i>Eulimnichus sublaevis</i>	Sharp, 1902
	<i>Euthryptus</i>	Sharp, 1902
	<i>Euthryptus orbiculatus</i>	Sharp, 1902
	<i>Euthryptus trigonalis</i>	Sharp, 1902 *
	<i>Limnichoderus</i>	Casey, 1889
	<i>Limnichoderus angustus</i>	Wooldridge, 1981
	<i>Limnichoderus curtulus</i>	Sharp, 1902
	<i>Limnichoderus lutrochinus</i>	(LeConte, 1879)
	<i>Limnichoderus modicus</i>	Wooldridge, 1981
	<i>Limnichoderus moratus</i>	Wooldridge, 1981
	<i>Limnichoderus naviculatus</i>	(Casey, 1889)
	<i>Limnichoderus vicinus</i>	Pic, 1922
	<i>Martinius</i>	Spilman, 1959
	<i>Martinius tellepontis</i>	Spilman, 1959
	<i>Paralimnichus</i>	Delève, 1973
	<i>Paralimnichus panamensis</i>	Wooldridge, 1983
	<i>Phalacrichus</i>	Sharp, 1902
	<i>Phalacrichus atomarius</i>	Sharp, 1902
	<i>Phalacrichus punctatus</i>	Wooldridge, 1982
	<i>Physemus</i>	LeConte, 1854

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**TABLE 2.** (Continued)

Family	Genus	Species
		<i>Physemus latifrons</i> Wooldridge, 1976
<b>Lutrochidae Kasap &amp; Crowson, 1975</b>		
	<i>Lutrochus</i>	Erichson, 1847 *
		<i>Lutrochus</i> <b>sp. nov.</b> Maier, 2016 *
		<i>Lutrochus vestitus</i> (Sharp, 1882) *
<b>Psephenidae Lacordaire, 1854</b>		
	<i>Dicranopselaphus</i>	Guérin-Méneville, 1861 *
		<i>Dicranopselaphus</i> sp. (larva) *
	<i>Ectopria</i>	LeConte, 1853
		<i>Ectopria reticulata</i> Champion, 1897
		<i>Ectopria vermiculata</i> Champion, 1897
	<i>Eubria</i>	Latreille, 1829
		<i>Eubria mesoamericana</i> Barr & Shepard, 2017
	<i>Neoeubria</i>	Shepard & Barr, 2014
		<i>Neoeubria inbionis</i> Shepard & Barr, 2014
	<i>Psephenops</i>	Grouvelle, 1898
		<i>Psephenops bifidus</i> Arce-Pérez & Novelo-Gutiérrez, 2017
		<i>Psephenops maculicollis</i> Darlington, 1936 *
		<i>Psephenops panamensis</i> Arce-Pérez, 2015
		<i>Psephenops triangularis</i> Arce-Pérez & Novelo-Gutiérrez, 2017
	<i>Psephenus</i>	Haldeman, 1853 *
		<i>Psephenus palpalis</i> Champion, 1913 *
<b>Ptilodactylidae Laporte, 1836</b>		
	<i>Anchytarsus</i>	Guérin-Méneville, 1843
		<i>Anchytarsus folliculipalpus</i> Stribling, 1986
		<i>Anchytarsus palpalis</i> (Champion, 1897)
		<i>Anchytarsus</i> sp. A (larva) *
	<i>Apoglossa</i>	Guérin-Méneville, 1849
		<i>Apoglossa angustata</i> Champion, 1897
		<i>Apoglossa collaris</i> Guérin-Méneville, 1849
		<i>Apoglossa</i> sp. *
	<i>Cladotoma</i>	Westwood, 1897
		<i>Cladotoma cucullatus</i> (Champion, 1897) *
		<i>Cladotoma ovalis</i> Westwood, 1837
	<i>Epiptygma</i>	Stribling, 1986
		<i>Epiptygma ebenina</i> (Champion, 1897)
		<i>Epiptygma maculata</i> (Champion, 1897)
		<i>Epiptygma rufa</i> (Champion, 1897)
	<i>Octoglossa</i>	Guérin-Méneville, 1843
		<i>Octoglossa femoralis</i> Guérin-Méneville, 1843
	<i>Ptilodactyla</i>	Illiger, 1807
		<i>Ptilodactyla aequinoctialis</i> Champion, 1897
		<i>Ptilodactyla caudata</i> Champion, 1897

.....continued on the next page

**TABLE 2.** (Continued)

Family	Genus	Species
		<i>Ptilodactyla chiriquiensis</i> Champion, 1897
		<i>Ptilodactyla confinis</i> Champion, 1897
		<i>Ptilodactyla deplanata</i> Champion, 1897
		<i>Ptilodactyla dilaticollis</i> Champion, 1897
		<i>Ptilodactyla germana</i> Champion, 1897
		<i>Ptilodactyla gibbicollis</i> Champion, 1897
		<i>Ptilodactyla montana</i> Champion, 1897
		<i>Ptilodactyla opima</i> Champion, 1897
		<i>Ptilodactyla parallela</i> Champion, 1897
		<i>Ptilodactyla scapularis</i> Champion, 1897
		<i>Ptilodactyla scutata</i> Champion, 1897
		<i>Ptilodactyla serrata</i> Champion, 1897
		<i>Ptilodactyla tropicalis</i> Champion, 1897
		<i>Ptilodactyla varicornis</i> Champion, 1897
	<i>Stirophora</i> Champion, 1897	
		<i>Stirophora lyciformis</i> (Champion, 1897)
		<i>Stirophora sulcipennis</i> Champion, 1897

**Annotated Species List** (\* = new country record for Panama)**Family Callirhipidae Emden, 1924**

This small elateriform family can be distinguished by the (1) sexually dimorphic, pectinate to flabellate antennae which arise on a frontal prominence; (2) large eyes; (3) pronotum with a well-developed, basal interlocking mechanism; and, (4) the absence of an articulating prosternal process (Young 2002). There are ten genera and about 175 species (Hajek 2011; Lawrence 2016; Young 2002), primarily in low latitude zones, except Africa.

Identification of specimens is hampered by lack of identification keys. That is partially alleviated by the world catalog of Callirhipidae (Hajek 2011) which has excellent illustrations. However, little is known about callirhipid male genitalia which are necessary for species-level identifications.

**Genus *Callirhipis* Latreille, 1829*****Callirhipis childreni* Gray, 1832**

Gray, 1832: 365 [Brazil].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú.

**Neotropical distribution.** Brazil, Costa Rica, Nicaragua, Panama.

***Callirhipis unicastata* Champion, 1896**

Champion, 1896: 578 [Costa Rica—♀; Panamá—♂].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú.

**Neotropical distribution.** Colombia, Costa Rica, Panama.

***Callirhipis* sp.**

**Secondary collection information.** Panamá, Chiriquí Province, Renacimiento District, Santa Clara; 3–5 July 1976; leg D. Engleman; at light (MIUP) • *ibid.*, Reserve Forest Fortuna, Campemento del IRGHE; 1080 m a.s.l.; 8 March 1987; leg N. Salazar (MIUP) • *ibid.*, Division Continental; 1080 m a.s.l.; 8–12 April 1999; leg R. Cambra, A.

Santos; Malaise trap (MIUP) • *ibid.*, Coclé Province, Río Grande; 9 November 1978; leg M. Guerra (MIUP) • *ibid.*, Los Santos Province; Reserva Forestal La Tronosa, El Cortez; 7.4°N, 80.6333°W; 300–400 m a.s.l.; 3–6 May 2006; leg R. Cambra, A. Santos; hand picked • *ibid.*, Panamá Province, Altos de Pacora, 3.9 km S de Cerro Jefe; 30 May 2000; leg B. Ella • *ibid.*, Cerro Jefe, Chagres National Park; 1007 m a.s.l.; 20 May 1998; leg B. Eya (MIUP) • *ibid.*, Metropolitan Park, Altos de Chase; 28 March 1987; leg M. Lu • *ibid.*, Ave. Juan Pablo Segundo; 27 March 1987; leg M. Rodriguez (MIUP) • *ibid.*, Soberania National Park; 20 May 1989; leg D. Windsor (MIUP).

## Genus *Celadonia* Laporte de Castelnau, 1840

### *Celadonia laportei* (Hope, 1846)

Hope, 1846: 181 [Colombia]; *Callirhipis laportei* Hope, 1846.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú.

**Neotropical distribution.** Colombia, Costa Rica, Guatemala, Mexico, Nicaragua, Panama.

**Note.** Transferred to *Celadonia* (Emden 1926).

## Family Chelonariidae Blanchard, 1845

Commonly called “turtle beetles”, the family Chelonariidae contains over 300 species distributed in three extant and one extinct genera. The extant genera are *Chelonarium* Fabricius in both the New and Old World, *Pseudochelonarium* Méquignon in the Old World, and *Brounia* Sharp in New Zealand. Species in this family are thought to be associated with the nests of ants and termites (Kole 2022). Chelonariid adults have a seed-shaped body, with a deflexed head, legs that retract in ventral grooves, and enlarged third and fourth antennomeres (Shepard 2016). Detailed descriptions of larvae, pupae and adults are found in Beutel & Leschen (2005) and Spangler (1980, 1991).

Identification of specimens is difficult as the only available key (Méquignon 1934) is old, in French and lacks dichotomous couplets. However, using records in Blackwelder (1944) it is possible to work backward to construct a preliminary dichotomous key for specific countries, such as Panama.

## Genus *Chelonarium* Fabricius, 1801

### *Chelonarium chevrolati* var. *longulum* Sharp, 1902

Sharp, 1902: 685 [Mexico].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK) • *ibid.*, Tierras Altas District, Volcán Barú • *ibid.*, Renacimiento District, Santa Clara; 1524 m a.s.l.; 4–7 June 1986; leg B.C. Ratcliffe • *ibid.*, Colón Province, Santa Rita Ridge; 18 May 1980; leg B.C. Ratcliffe; 1 adult (UNSM).

**Neotropical distribution.** Mexico, Panama.

### *Chelonarium chiriquensis* Sharp, 1902

Sharp, 1902: 687 [Panama].

**Primary collection information.** Panamá, Bocas del Toro Province, 2 mi N of Continental Divide on Hwy 10 to Chiriquí Grande; 1 June 1986; leg B.C. Ratcliffe; 2 adults (UNSM) • *ibid.*, Chiriquí Province, Tierras Altas District, Cerro Punta; 25 May 1982; leg B.C. Ratcliffe; 1 adult (UNSM) • *ibid.*, Veraguas Province, Cuenca 116, Sona, Quebrada Monita; 7.81480°N, 81.55724°W; 26 m a.s.l.; April–July 2023; Malaise trap; leg V. Rodriguez; 1 adult (MUPADI).

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú below 1219 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

### ***Chelonarium errans* Sharp, 1902**

Sharp, 1902: 687 [Guatemala].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú below 1219 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Panama.

### ***Chelonarium hyphyroides* Sharp, 1902**

Sharp, 1902: 687 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

### ***Chelonarium signatum* Dalman, 1824**

Dalman, 1824: 32 [Brazil].

**Secondary collection information.** Panamá, Colón Province, Santa Rita Ridge; 18–21 May 1977; at light; 1 adult (UNSM) • *ibid.*, Panamá Province, altos (Isla) de Majé; 9.14036°N, 78.83463°W; 28–30 May 1982; leg B.C. Ratcliffe, C. and K. Messenger; 4 adults (UNSM) • *ibid.*, Soberania National Park, Pipeline Rd., km 2.4; 25 May 1995; leg B.C. Ratcliffe, M. Jameson; 3 adults (UNSM).

**Neotropical distribution.** Bolivia, Colombia, French Guiana, Paraguay, Panama, Peru, Venezuela.

**Note.** See Shepard & Leavengood (2021) for redescription.

### ***Chelonarium ustulatum* Méquignon, 1934**

Méquignon, 1934: 214 [Venezuela].

**Secondary collection information.** Panamá, Panamá Oeste Province, Capira District, Cerro Campana; 17 May 1982; leg B.C. Ratcliffe, K. Messenger; 1 adult (UNSM) • *ibid.*, 31 May 1986; leg B.C. Ratcliffe; 5 adults (UNSM).

**Neotropical distribution.** Panama, Venezuela.

### ***Chelonarium* sp.**

**Secondary collection information.** Panamá, Bocas del Toro Province, Corriente Grande; 9.29167°N, 82.54472°W; 100 m a.s.l.; 9 February 1980 (MIUP) • *ibid.*, Chiriquí Province, Reserva Forestal Fortuna; 12–14 September 1985; leg D. Quintero, R. Cambra (MIUP) • *ibid.*, Finca Hartmann; 18–19 May 1996; leg Wappes, Huether, Morris (MIUP) • *ibid.*, Coclé Province, El Cope; 23–24 May 1996; leg R. Gonzalez (MIUP) • *ibid.*, Chiriquí Arriba; 24 April 1994; leg D. Quintero (MIUP) • *ibid.*, Darién Province, Darién National Park, Pirre, estación Rancho Frio; 560 m a.s.l.; 21 March–4 April 2000; leg R. Cambra, A. Santos, S. Bermúdez; Malaise trap (MIUP) • *ibid.*, Panamá Province, Las Cumbres; 31 May–3 July 1984 (MIUP) • *ibid.*, Soberania National Park; 5 March 1981; leg J.C. Chang (MIUP) • *ibid.*, Cerro Campana; 25–26 May 1996; leg Wappes, Huether, Morris (MIUP) • *ibid.*, Panamá Oeste Province, Barro Colorado Island; 26 June 1984; leg H. Wolda; light trap (MIUP) • *ibid.*, Veraguas Province, Finca Martinelli, Sona; 21 February 1981; leg J.C. Chang (MIUP).

## **Family Cneoglossidae Champion, 1897**

Cneoglossidae is a small, monogeneric family of beetles (Costa *et al.* 2016). The family contains nine described species native to the Neotropical Region and which range from Mexico to Brazil. All species are very small (2–5 mm in length) and soft-bodied. The body is elongate (lampyriform), the head is deeply retracted into the prothorax, the pronotum is bicolored, and the elytra are dark. Larvae develop inside rotting submerged branches found in small fast flowing shallow streams (Costa *et al.* 2016; Shepard 2016).

There is no identification key for the nine species in this family. However, Costa *et al.* (1999) lists all species and their type localities which aids identifications.

## Genus *Cneoglossa* Guérin-Ménéville, 1843

### *Cneoglossa brevis* Champion, 1897

Champion, 1897: 595 [Panama].

**Primary collection information.** Panamá, Veraguas Province, Cuenca 116, Sona, Quebrada Monita; April to July, 2023; 7.81480°N, 81.55724°W; 26 m a.s.l.; Malaise trap; leg V. Rodriguez; 1 male (MUPADI) • *ibid.*, Isla Canales de Afuera; 5 February–6 March 2023; 7.69494°N, 81.62649°W; 29 m a.s.l.; leg V. Rodriguez; 1 male (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, Tolé District, Tolé; Champion (NHMUK).

**Neotropical distribution.** Panama.

## Family Dryopidae Billberg, 1820

Named for their large claws, long-toed water beetles of the family Dryopidae are found on all major landmasses except Australia and Antarctica. Members of this family can be aquatic, semi-aquatic, or terrestrial, and, as detritivores, feed primarily on dead plant material. There are over 300 species in 33 genera worldwide, and there are five aquatic genera in Central America (*Dryops*, *Elmoparnus*, *Helichus*, and *Onopelmus*), all of which are present in Panama. The semi-aquatic genera, *Parygyrus* and *Pelonomus* are lentic and found in roadside ditches and similar habitats. The terrestrial dryopids in Panama (*Momentum* and *Quadryops*) are found in leaf litter (Kodada *et al.* 2016; Passos *et al.* 2018).

Identifications to the generic level of aquatic and semiaquatic dryopids can be made using Shepard (2020). Species-level identifications can be made for most genera using cited literature. The main exception is the speciose genus *Dryops*. For *Dryops*, most descriptions are old, too brief, and lack illustrations of pertinent characters.

## Genus *Dryops* Olivier, 1791

### *Dryops centralis* (Sharp, 1887)

Sharp, 1887: 774 [Panama]; *Parnus centralis* Sharp, 1887.

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK) • *ibid.*, Tierras Altas District, Volcán Barú; 1219–1829 m a.s.l.; leg G.C. Champion (NHMUK) • *ibid.*, Cuenca 106, Quebrada Balsa; 8.54526°N, 82.55153°W; 326 m a.s.l.; UV light trap (MUPADI) • *ibid.*, Veraguas Province, Cuenca 132; Río Betegui; 8.36047°N, 80.99481°W; 144 m a.s.l.; 28 January 2023; leg V. Rodriguez; UV light trap (MUPADI) • *ibid.*, Cuenca 116, Las Palmas, Río Rosario; 9 m a.s.l.; 20 February 2023; UV light trap (MUPADI) • *ibid.*, 7.84691°N, 81.5672°W; 20 March 2023, UV light trap, MUPADI • *ibid.*, Río Limon; 67 m a.s.l.; 20 February 2023 (MUPADI).

**Neotropical distribution.** Panama.

**Note.** Musgrave (1935b) formally transferred all species from *Parnus* to *Dryops*.

### *Dryops detritus* (Sharp, 1882)

Sharp, 1882: 124 [Panama]; *Parnus detritus* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Atlas District, Volcán Barú; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

**Note.** Musgrave (1935b) formally transferred all species from *Parnus* to *Dryops*.

### *Dryops major* (Sharp, 1887)

Sharp, 1887: 774 [Panama]; *Parnus major* Sharp, 1887.

**Primary collection information.** Panamá, Coclé Province, Río Sofre; 8.614434°N, 80.21884°W; 291 m a.s.l.; 13 February 2023, leg C. Nieto; UV light trap (MUPADI) • *ibid.*, 13 March 2023 (MUPADI) • *ibid.*, Veraguas Province, Cuenca 116, las Palmas, Río Rosario; 7.84691°N, 81.5672°W; 9 m a.s.l.; 20 March 2023; leg V. Rodriguez; UV light trap (MUPADI) • *ibid.*, Las Palmas, Río Rosario; 7.84691°N, 81.5672°W; 8 m a.s.l.; 20 March 2023; UV

light trap • *ibid.*, Cuenca 118, La Mesa, Río San Juan, Río San Pablo; 8.19532°N, 81.25008°W; 31 April 2023 (MUPADI).

**Secondary collection information.** Panamá, Chiriquí Province, Tolé District, Tolé; leg G.C. Champion (NHMUK) • *ibid.*, Remedios District, Los Remedios; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

**Note.** Musgrave (1935b) formally transferred all species from *Parnus* to *Dryops*.

### ***Dryops punctipennis* (Sharp, 1882)**

Sharp, 1882: 124 [Guatemala]; *Parnus punctipennis* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; 244–457 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Panama.

**Note.** Musgrave (1935b) formally transferred all species from *Parnus* to *Dryops*.

## **Genus *Elmoparnus* Sharp, 1882**

### ***Elmoparnus brevicornis* Sharp, 1882**

Sharp, 1882: 125 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; 244–457 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

**Note.** See key to species in Spangler & Perkins (1986).

### ***Elmoparnus pandus* Spangler & Perkins, 1977 \***

Spangler & Perkins, 1977: 724 [Mexico].

**Secondary collection information.** Panamá, Darién Province, Darién National Park, Estación Rancho Frío, Río Perresénico; 8.01750°N, 77.72417°W; 80 m a.s.l.; 4 April 2013; leg R. Camba, 1 male (MIUP) • *ibid.*, Río Pirre cerca de Pijibasal; 8.03139°N, 77.76028°W; 68 m a.s.l.; 6 August 2013; leg R. Cambra, 1 male (MIUP).

**Neotropical distribution.** Guatemala, Honduras, Mexico, Panama.

**Note.** See key in Spangler & Perkins 1986.

## **Genus *Helichus* Erichson, 1847 \***

### ***Helichus suturalis* LeConte, 1852 \***

LeConte, 1852: 42 [U.S.A.].

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Mexico, Panama, U.S.A.

## **Genus *Momentum* Perkins, 1997**

### ***Momentum hirsutum* Perkins, 1997**

Perkins, 1997: 111 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Boquete District, Finca Lerida nr Boquete; 1722 m a.s.l.; 14 March 1959; leg H.S. Dybas; Berlese funnel (NHMUK)l.

**Neotropical distribution.** Costa Rica, Panama.

**Note.** Specimens were collected from concentrated forest floor litter and wood chips in a logging area.

## Genus *Parygrus* Erichson, 1847

### *Parygrus maya* Barr & Shepard, 2020

Barr & Shepard, 2020: 111 [Mexico].

**Primary collection information.** Panamá, Coclé Province, 5 km S of Antón nr Los Pantones; 8.35570°N, 80.27525°W; 18 m a.s.l.; 20 August 2006; leg C.B. Barr; UV black light and Mercury vapor lamp; 1 male (EMEC) • *ibid.*, 29 August 2006; leg D. Post; 3 males (EMEC); 1 male (STRI) • *ibid.*, Panamá Oeste Province, Fort Kobbe; 9 June 1976; leg E.G. Riley; UV light trap; 2 males (UMC).

**Neotropical distribution.** Belize, Costa Rica, Guatemala, Mexico, Nicaragua, Panama.

**Note.** See key to species in Barr & Shepard (2020).

## Genus *Pelonomus* Erichson, 1847

### *Pelonomus picipes* (Olivier, 1791)

Olivier, 1791: 4 [Panama]; syn. *Pelonomus palpalis* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, David District, David; leg G.C. Champion (NHMUK) • *ibid.*, Tierras Altas District, Volcán Barú; 1219–1829 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Guadeloupe, Panama.

**Note.** Darlington (1936) synonymized *P. palpalis* with *P. picipes*.

## Genus *Quadryops* Perkins & Spangler, 1985

### *Quadryops chrysosetosus* Perkins & Spangler, 1985

Perkins & Spangler, 1985: 496 [Panama].

**Secondary collection information.** Panamá, Colón Province, Colón District, Canal Zone; 5.0 mi. NW Gamboa; 9.16667°N, 79.7500°W; 100 m a.s.l.; leg Montgomery, Lubin; canopy fogging; USNM type 100893.

**Neotropical distribution.** Panama.

**Note.** Collected during a canopy pyrethrin fogging experiment (*Luehea seemanni*).

### *Quadryops quasimodoi* Perkins & Spangler, 1985

Perkins & Spangler, 1985: 506 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, “Barca” área, Finca Lerida nr Boquete; 8.81311°N, 82.48308°W; 1688 m a.s.l.; 14 March 1959; leg H.S. Dybas; Berlese funnel (FMNH).

**Neotropical distribution.** Panama.

**Note.** Collected from forest litter and wood chips in a logging area.

## Family Elmidae Curtis, 1830

Elmids are the most diverse family in Dryopoidea with species occurring on all continents except Antarctica. Elmids are nearly always intimately associated with streams and rivers. The family has two subfamilies: the larger Elminae (Neotropics: ~36 genera and >380 species) and the smaller Larinae (Neotropics: ~11 genera and >51 species) (Segura *et al.* 2013; Passos *et al.* 2018).

The Elminae life cycles are completely aquatic except for the brief pupal stage which occurs just outside streams and under moss, rocks, or other substrates. Adult elminae are usually small (<10 mm), very hard-bodied with long legs and stout claws. Panamanian Elminae include 12 genera: *Austrolimnius*, *Cylloepus*, *Heterelmis*, *Hexacylloepus*, *Macrelmis*, *Microcylloepus*, *Neocylloepus*, *Neoelmis*, *Notelmis*, *Onychelmis*, *Stenhelmoides*, and *Xenelmis*.

The Larinae life cycles have aquatic larvae but the adults are only facultatively aquatic, entering the stream only to feed. They readily fly out of the water to avoid capture and to disperse. Larinae are usually associated with waterfalls and cataracts. However, the genus *Phanocerus* is mostly found in and on leaf packs in slower flows or on overhanging riparian vegetation. Adult larvae are mostly larger (>10 mm) and soft-bodied. Panamanian Larinae include five genera: *Disersus*, *Hexanchorus*, *Phanocerus*, *Pharceonus*, and *Pseudodisersus*.

Identification of elmids to the genus-level is fairly easy using Passos *et al.* (2018) which is well illustrated. Note that not all genera are known as both adults and/or larvae. Also helpful is the world-wide catalog for Elmidae (Jäch *et al.* 2016)

## Genus *Austrolimnius* Carter & Zeck, 1929

### *Austrolimnius curtulus* (Sharp, 1882)

Sharp, 1882: 139 [Panama]; *Elmis curtula* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierra Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

**Note.** This species was transferred to *Austrolimnius* by Hinton (1940c).

### *Austrolimnius eris* Hinton, 1971

Hinton, 1971: 94 [Mexico].

**Secondary collection information.** Panamá, Coclé Province, Candelaria; June 1968; leg H.P. Brown; 6 specimens (HPB) • *ibid.*, Panamá Province, Panamá District, Pacora, nr Tocumen International Airport; June 1968; leg H.P. Brown; 6 specimens (HPB).

**Neotropical distribution.** Mexico, Panama.

### *Austrolimnius formosus* (Sharp, 1882) \*

Sharp, 1882: 140 [Guatemala]; *Elmis formosa* Sharp, 1882.

**Primary collection information.** Panamá, Chiriquí Province, Tierras Altas District, 15.6 km N of Volcán, Río Colorado; WDS-A-1711; 8.83188°N, 82.71772°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Coclé Province, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.6 km SW of El Valle, Chorro Las Mozas; WDS-A-1705; 8.59375°N, 80.14632°W; 581 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Argentina, Belize, Brazil, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, Peru, Venezuela.

**Note.** This species was transferred to *Austrolimnius* by Hinton (1940c).

### *Austrolimnius sulcicollis* (Sharp, 1882)

Sharp, 1882: 139 [Panama]; *Elmis sulcicollis* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierra Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Guatemala, Mexico, Panama.

**Note.** This species was transferred to *Austrolimnius* by Hinton (1940c).

## Genus *Cylloepus* Erichson, 1847 \*

### *Cylloepus barberi* Hinton, 1934 \*

Hinton, 1934: 193 [Guatemala].

**Secondary collection information.** Panamá, Panamá Province, Soberania National Park, Río Frijoles; 27 December 1980; leg P. Soto, M. Munoz, R. Gonzalez (MIUP).

**Neotropical distribution.** Costa Rica, Guatemala, Panama.

### *Cylloepus optatus* (Sharp, 1882) \*

Sharp, 1882: 129 [Guatemala]; *Elmis optatus* Sharp, 1882.

**Primary collection information.** Panamá, Chiriquí Province, Tierras Altas District, 15.6 km N of Volcán, Río Colorado; WDS-A-1711; 8.83188°N, 82.71772°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D.

Shepard (EMEC) • *ibid.*, Coclé Province, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, El Valle, Hotel Campestre, Río Antón; WDS-A-1707; 8.61402°N, 80.11270°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Belize, Costa Rica, Guatemala, Mexico, Nicaragua, Panama.

## Genus *Disersus* Sharp, 1882

### *Disersus longipennis* Sharp, 1882

Sharp, 1882: 127 [Panama].

**Primary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Río Colorado, at Hwy 42, 15.6 km NW of Volcán; 8.8329°N, 82.7177°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard; 2 specimens (EMEC) • *ibid.*, Coclé Province, Río Antón, El Valle, NE edge of town; 8.6140°N, 80.1127°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC) • *ibid.*, Comarca Ngäbe-Buglé, Quebrada Martinez, Bosque Protector Palo Seco, Alto de Valle, detrás de la caseta de Mi Ambiente; 8.79424°N, 82.19047°W; 480 m a.s.l., 5 June 2023; leg Y. Aguirre, T. Ríos; light trap; 1 male (MUPADI) • *ibid.*, 9 April 2023; 1 male (MUPADI) • *ibid.*, Veraguas Province, Río Mulabá, NE of Santa Fe; 8.5250°N, 81.0793°W; 319 m a.s.l.; 24 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, Tierra Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK) • *ibid.*, Renacimiento District, Santa Clara, Finca Hartmann; 23–25 May 1980; leg E. Riley, LeDoux; 1 male, 7 females • *ibid.*, Tierras Altas District, small brook, 26 km W of Volcán; 1380 m a.s.l.; 3 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 1 male (NMHN) • *ibid.*, Darién Province, Darién National Park, Estación Rancho Frío, Río Perresénico; 8.01714°N, 77.72417°W; 117 m a.s.l.; 20 November 2014; leg R. Novelo, 1 male (IEXA).

**Neotropical distribution.** Costa Rica, Guatemala, Panama.

**Note.** Spangler & Santiago (1987) list this species from Costa Rica and Panama. WDS collected it in Guatemala.

### *Disersus uncus* Spangler & Santiago, 1982

Spangler & Santiago, 1982: 69 [Costa Rica].

**Primary collection information.** Panamá, Chiriquí Province, Cuenca 108, Boquete District, Valle Escondido, Quebrada Grande; 13 July 2024; leg B. Armitage; 1 male (MUPADI) • *ibid.*, Dolega District, Río Majagua, Banquito de Palimira, Potrerillos; 8.68083°N, 82.5325°W; 840 m a.s.l., 3 July 2019; Y. Aguirre, T. Ríos; light trap; 1 male (MUPADI) • *ibid.*, 31 July 2019; 1 male (MUPADI) • *ibid.*, Río Majagua, Palma Real; 8.66138°N, 82.52639°W; 837 m a.s.l.; 31 July 2019; 1 male (MUPADI) • *ibid.*, Río Majagua; 8.66172°N, 82.53818°W; 1 male (MUPADI) • *ibid.*, Comarca Ngäbe-Buglé, Quebrada Martinez, Bosque Protector Palo Seco, Alto de Valle, detrás de la caseta de Mi Ambiente; 8.79424°N, 82.19047°W; 480 m a.s.l., 9 April 2023; leg Y. Aguirre, T. Ríos; light trap; 1 male (MUPADI) • *ibid.*, 3 July 2023; 1 male (MUPADI).

**Secondary collection information.** Panamá, Chiriquí Province, Gualaca District, Quebrada Aleman, S of Fortuna Reservoir; 1189 m a.s.l.; 11 May 1985; leg R.W. Flowers; UV light trap; 1 specimen (USNM) • *ibid.*, Quebrada Honda, N of Fortuna Reservoir; 16 May 1985; leg R.W. Flowers; UV light trap; 2 specimens (USNM) • *ibid.*, 1067 m a.s.l.; 1 June 1985; leg R.W. Flowers; 1 specimen (USNM).

**Neotropical distribution.** Costa Rica, Guatemala, Panama.

**Note.** Lectotype (female). WDS collected this species in Guatemala.

## Genus *Heterelmis* Sharp, 1882 \*

### *Heterelmis* sp. \*

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Tierras Altas District, 15.6 km N of Volcán, Río Colorado; WDS-A-1711; 8.83188°N, 82.71772°W;

1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Valle de la Mina; WDS-A-1713; 8.66572°N, 82.21661°W; 1140 m a.s.l.; 26 August 2006 (EMEC) • *ibid.*, Coclé Province, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.2 km NW of El Valle, Quebrada La Pintada; WDS-A-1706; 8.61228°N, 80.14395°W; 607 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, El Valle, Hotel Campestre, Río Antón; WDS-A-1707; 8.61402°N, 80.11270°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1 km NW of El Copé, trib. to Río Grande; WDS-A-1719; 8.62067°N, 80.58925°W; 340 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Burigón; WDS-A-1720; 8.64210°N, 80.59032°W; 358 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Herrera Province, NW of Las Minas, 9.9 km S of Ocú, Río Parita/Pacita; WDS-A-1718; 7.85730°N, 80.74537°W; 135 m a.s.l.; 28 August 2006, leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Panamá Province, 5.4 km E of Buenos Aires, unnamed river; WDS-A-2027; 9.16823°N, 79.57503°W; 99 m a.s.l.; 1 September 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Panamá Oeste Province, 4.2 km SSE of Miraflores; WDS-A-1722; 8.61550°N, 80.26860°W; 115 m a.s.l.; 30 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Veraguas Province, NE of Santa Fe, Río Mulebá; WDS-A-1710; 8.52002°N, 81.07933°W; 319 m a.s.l.; 24 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Note.** This genus has so many undescribed species that it is not currently possible to identify them conclusively.

## Genus *Hexacylloepus* Hinton, 1940

### *Hexacylloepus granulatus* (Sharp, 1882)

Sharp, 1882: 136 [Panama]; *Elmis granulatus* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Guatemala, Panama.

**Note.** This species was transferred to the genus *Hexacylloepus* by Hinton (1940c).

## Genus *Hexanchorus* Sharp, 1882

**Note.** Species can only be identified for certain from males and genitalic dissection is required. Multiple species can inhabit any stream with adults present at different times. See key to species in Spangler & Santiago-Fragoso (1992).

### *Hexanchorus browni* Spangler & Santiago-Fragoso, 1992

Spangler & Santiago-Fragoso, 1992: 40 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierra Altas District, Bambito, Río Chiriquí Viejo; 1770 m a.s.l.; 2 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 2 specimens (USNM) • *ibid.*, David District, 9 km N of David, waterfalls at Balneario San Francisco; 31 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 496 specimens (USNM) • *ibid.*, Boquete; 16–17 July 1967; leg O.S. Flint, Jr., 1 specimen (USNM) • *ibid.*, Caldera; 1770 m a.s.l.; 1 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 6 specimens (USNM) • *ibid.*, W of Concepción, Río Guigala; 18 November 1966; leg H.P. Brown; 34 specimens (HPB) • *ibid.*, Fortuna Reservoir watershed, Quebrada Honda; 16 May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Guabalá; 24 June 1968; leg H.P. Brown; 12 specimens (HPB) • *ibid.*, Dolega District, S of Dolega; 24 June 1968; leg H.P. Brown; 6 specimens (HPB) • *ibid.*, Gualaca District, S of Gualaca; 14 November 1966; leg H.P. Brown; 10 specimens (HPB) • *ibid.*, Horqueta; 24 June 1968; leg H.P. Brown; 1 specimen (HPB) • *ibid.*, Pueblo Nuevo, Río Cochea; 15–16 Nov 1966; leg H.P. Brown; 2 specimens (HPB) • *ibid.*, Coclé Province, El Valle; 26 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 11 specimens (USNM) • *ibid.*, El Valle; 27 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 2 specimens (USNM) • *ibid.*, El Valle; 10–13 June 1985; leg E. Riley, D. Rider; 4 specimens (LSAM) • *ibid.*, El Valle, Río Antón-Los Mozos; 20 May 1987; leg D. Quintero; R. Cambra; J. Tovar; R. Rodríguez; 2 specimens (MIUP) • *ibid.*, near Machuca, trib. of Río Grande; 25 June 1968; leg H.P. Brown; 8 specimens (HPB) • *ibid.*, W of

Penonome, Río Churubé; 12 November 1966; leg H.P. Brown; 4 specimens (HPB) • *ibid.*, Herrera Province, Los Pozos; 22 October 1952; leg Blanton; 1 specimen (USNM) • *ibid.*, Panamá Province, Cerro Azul, Hidroeléctrica, Río Indio; 9 June 1985; leg E. Riley, D. Rider; 62 specimens (LSAM) • *ibid.*, W of Chepo, Río Chico; 21 June 1968; leg H.P. Brown; 4 specimens (HPB) • *ibid.*, W of Chorrera, small quebrada; 12 November 1966; leg H.P. Brown; 12 specimens (HPB) • *ibid.*, N of Pacora, Río Cabra; 23 November 1971; leg H.P. Brown; 142 specimens (HPB) • *ibid.*, N of Pacora, Río Pacora; 26 June 1968; leg H.P. Brown; 16 specimens (HPB) • *ibid.*, Panamá Oeste Province, Barro Colorado Island; 30 June 1987; leg D. Quintero, R. Rodriguez, R. Cambra; 2 specimens (MIUP) • *ibid.*, Veraguas Province, near Jorones; 13 November 1966; leg H.P. Brown; 8 specimens (HPB) • *ibid.*, E of Sona; 13 November 1966; leg H.P. Brown; 7 specimens (HPB).

**Neotropical distribution.** Costa Rica, Mexico, Panama.

### ***Hexanchorus crinitus* Spangler & Santiago-Fragoso, 1992**

Spangler & Santiago-Fragoso, 1992: 31 [Costa Rica].

**Primary collection information.** Panamá, Veraguas Province, Río Mulabá, NE of Santa Fe; 8.5250°N, 81.0793°W; 319 m a.s.l.; 24 August 2006; leg C.B. Barr, W.D. Shepard; 6 specimens (EMEC) • *ibid.*, Río Guayabal, just S of Corazol; 8.0665°N, 81.44635°W; 219 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC).

**Secondary collection information.** Panamá, Bocas del Toro Province, Chiriquí Grande District, Punta Peña, Río Guarumo; 76 m a.s.l.; 28 May 1985; leg R.W. Flowers; 4 specimens (USNM) • *ibid.*, Changuinola District, Río Changuinola at Zegla; 25 April 1985; leg R.W. Flowers; at light; 1 specimen (USNM) • *ibid.*, 26 April 1985; 2 specimens (USNM) • *ibid.*, Chiriquí Province, Gualaca District, south of Gualaca; 14 November 1966; leg H.P. Brown; 8 specimens (HPB) • *ibid.*, Coclé Province, El Valle; 829 m a.s.l.; 27 May 1983; leg P.J. Spangler, R.A. Faitoute; 4 specimens (USNM) • *ibid.*, near Machuca, trib. of Río Grande; 25 June 1968; leg H.P. Brown; 506 specimens (HPB) • *ibid.*, Darién Province, Darién National Park, Estación Rancho Frío, Río Perresénico; 8.01714°N, 77.72417°W; 117 m a.s.l.; 20 November 2014; leg R. Novelo, 1 male (IEXA) • *ibid.*, Panamá Province: W of Chepo, Río Chico; 21 June 1968; leg H.P. Brown; 28 specimens (HPB) • *ibid.*, W of Chorrera, small stream; 12 November 1966; leg H.P. Brown; 11 specimens (HPB) • *ibid.*, Pacora, Río Cabra; 23 November 1971; leg H.P. Brown; 44 specimens (HPB).

**Neotropical distribution.** Costa Rica, Panama.

### ***Hexanchorus emarginatus* Spangler & Santiago-Fragoso, 1992**

Spangler & Santiago-Fragoso, 1992: 37 [Costa Rica].

**Primary collection information.** Panamá, Comarca Ngäbe-Buglé, Quebrada Martinez, Bosque Protector Palo Seco, Alto de Valle, detrás de la caseta de Mi Ambiente; 8.79424°N, 82.19047°W; 480 m a.s.l., 5 June 2023; leg Y. Aguirre, T. Ríos; light trap; 1 male (MUPADI).

**Secondary collection information.** Panamá, Chiriquí Province, south of Bodega; 24 June 1968; leg H.P. Brown; 44 specimens (HPB) • *ibid.*, west of Concepción, Río Guigala; 18 November 1966; leg H.P. Brown; 76 specimens (HPB) • *ibid.*, Gualaca District, south of Gualaca; 14 November 1966; leg H.P. Brown; 32 specimens (HPB) • *ibid.*, Pueblo Nuevo, Río Cochea; 15-16 November 1966; leg H.P. Brown; 139 specimens (HPB).

**Neotropical distribution.** Costa Rica, Panama.

### ***Hexanchorus gracilipes* Sharp, 1882**

Sharp, 1882: 43 [Mexico].

**Primary collection information.** Panamá, Coclé Province, tributary of Chorro Las Mozas, 1.6 km SW El Valle; 8.5938°N, 80.1463°W; 581 m a.s.l.; leg C.B. Barr, W.D. Shepard; 1 male (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK) • *ibid.*, Panamá Province, Panamá District, Chargres Watershed, Upper Río Pequeni; leg A.H. Jennings.

**Neotropical distribution.** Brazil, Costa Rica, Guatemala, Mexico, Panama.

### ***Hexanchorus usitatus* Spangler & Santiago-Fragoso, 1992**

Spangler & Santiago-Fragoso, 1992: 33 [Panama].

**Secondary collection information.** Panamá, Bocas del Toro Province, Pipeline Road, trib. of Río Guabo; 25

May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Punta Peña, Río Guarumo; 76 m a.s.l.; 28 May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Zegla, Río Changuinola; 26 April 1985; leg R.W. Flowers; at light; 1 specimen (USNM) • *ibid.*, Chiriquí Province, Bambito, Río Chiriquí Viejo; 16 November 1966; leg H.P. Brown; 3 specimens (HPB) • *ibid.*, Bambito, Río Chiriquí Viejo; 2 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 5 specimens (USNM) • *ibid.*, Boquete, Río Caldera; 15 November 1966; leg H.P. Brown; 24 specimens (HPB) • *ibid.*, Tierras Altas District, Cerro Punta; 23 June 1968; leg H.P. Brown; 45 specimens (HPB) • *ibid.*, Cerro Punta, Río Chiriquí Viejo; 17 November 1966; leg H.P. Brown; 8 specimens (HPB) • *ibid.*, Fortuna Reservoir watershed, Quebrada Arenal; 1067 m a.s.l.; 24 May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, 5 June 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Fortuna Reservoir watershed, Quebrada Honda; 17 May 1985; leg R.W. Flowers; 4 specimens (USNM) • *ibid.*, stream north of lake at pipeline road; 1128 m a.s.l.; 4 April 1985; leg R.W. Flowers; 2 specimens (USNM) • *ibid.*, S of Guabalá; 14 November 1966; leg H.P. Brown; 3 specimens (HPB) • *ibid.*, Horqueta; 24 June 1968; H.P. Brown; 1 specimen (HPB) • *ibid.*, Presa Fortuna, lake; 1158 m a.s.l.; 15 May 1985; leg R.W. Flowers; at light; 2 specimens (USNM) • *ibid.*, Coclé Province, El Valle; 829 m a.s.l.; 26 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 12 specimens (USNM) • *ibid.*, El Valle; 829 m a.s.l.; 26 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 9 specimens (USNM) • *ibid.*, near Machuca, trib. of Río Grande; 25 June 1968; leg H.P. Brown; 1 specimen (HPB) • *ibid.*, Guna Yala Comarca, 25 km S of Campamento Nusagandi; 1 May 1987; leg D. Quintero, H. Herrera, R. Cambra; 1 specimen (MIUP).

**Neotropical distribution.** Costa Rica, Nicaragua, Panama.

### Genus *Macrelmis* Motschulsky, 1860

#### *Macrelmis amazonica* (Hinton, 1945) \*

Hinton, 1945: 91 [Brazil]; *Elsianus amazonicus* (Hinton, 1945).

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard; (EMEC) • *ibid.*, Coclé Province, El Valle, Hotel Campestre, Río Antón; WDS-A-1707; 8.61402°N, 80.11270°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.2 km NW of El Valle, Q. La Pintada; WDS-A-1706; 8.61228°N, 80.14395°W; 607 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1 km NW of El Copé, trib. to Río Grande; WDS-A-1719; 8.62067°N, 80.58925°W; 340 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Burigon; WDS-A-1720; 8.64210°N, 80.59032°W; 358 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 4.2 km SSE of Miraflores; WDS-A-1722; 8.61550°N, 80.26860°W; 115 m a.s.l.; 30 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Herrera Province, NW of Las Minas, 9.9 km S of Ocu, Río Parita/Pacita; WDS-A-1718; 7.85730°N, 80.74537°W; 135 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Brazil, Panama, Peru.

**Note.** This species was transferred to *Macrelmis* by Brown (1984).

#### *Macrelmis sandersoni* (Hinton, 1936) \*

Hinton, 1936: 420 [Mexico]; *Elsianus sandersoni* (Hinton, 1936).

**Secondary collection information.** Panamá, Panamá Province, Soberanía National Park, Río Frijoles; 27 December 1980; leg P. Soto, M. Munoz, R. Gonzalez (MIUP).

**Neotropical distribution.** Mexico, Panama.

**Note.** This species was transferred to *Macrelmis* by Brown (1984).

#### *Macrelmis scutellaris* (Hinton, 1934) \*

Hinton, 1934: 196 [Mexico]; *Elsianus scutellaris* Hinton, 1934.

**Primary collection information.** Panamá, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Costa Rica, Mexico, Panama.

**Note.** This species was transferred to *Macrelmis* by Brown (1984).

***Macrelmis striata* (Sharp, 1882) \***

Sharp, 1882: 132 [Guatemala]; *Elsianus striatus* Sharp, 1882.

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Coclé Province, El Valle, Hotel Campestre, Río Antón; WDS-A-1707; 8.61402°N, 80.11270°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.2 km NW of El Valle, Q. La Pintada; WDS-A-1706; 8.61228°N, 80.14395°W; 607 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Veraguas Province, Corozal, Río Guayabo; WDS-A-1716; 8.06652°N, 81.44635°W; 219 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Costa Rica, Guatemala, Mexico, Panama, Peru.

**Note.** This species was transferred to *Macrelmis* by Brown (1984).

***Macrelmis tarsalis* (Hinton, 1936)**

Hinton, 1936: 419 [Costa Rica]; *Elsianus tarsalis* Hinton, 1936.

**Secondary collection information.** Panamá. Cited in Jäch *et al.* (2016).

**Neotropical distribution.** Costa Rica, Ecuador, Panama.

**Note.** This species was transferred to *Macrelmis* by Brown (1984).

**Genus *Microcylloepus* Hinton, 1935 \***

***Microcylloepus inaequalis* (Sharp, 1882) \***

Sharp, 1882: 137 [Guatemala]; *Elmis inaequalis* Sharp, 1882.

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Coclé Province, El Valle, Hotel Campestre, Río Antón; WDS-A-1707; 8.61402°N, 80.11270°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.2 km NW of El Valle, Quebrada La Pintada; WDS-A-1706; 8.61228°N, 80.14395°W; 607 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Herrera Province, NW of Las Minas, 9.9 km S of Ocú, Río Parita/Pacita; WDS-A-1718; 7.85730°N, 80.74537°W; 135 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Los Santos Province, Güerita, Río Güerita; WDS-A-1717; 7.57212°N, 80.60900°W; 181.4 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Brazil, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, Paraguay.

**Genus *Neocylloepus* Brown, 1970**

**Note:** See key to species in Brown (1970).

***Neocylloepus championi* (Sharp, 1882)**

Sharp, 1882: 134 [Panama]; *Elmis championi* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

**Note.** This species was transferred to *Neocylloepus* by Brown (1970).

***Neocylloepus sandersoni* Brown, 1970**

Brown, 1970: 18 [Costa Rica].

**Primary collection information.** Panama, Chiriquí Province, Río Majagua at Balneario Majagua, 3.9 km N of David; 8.3497°N, 82.4195°W; 364 m a.s.l.; 26 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC).

**Secondary collection information.** Panamá, Remedios District, Guabalá; November 1966 • *ibid.*, Panamá Oeste Province, small stream W of La Chorrera; November 1966 • *ibid.*, Río Pacora, N of Pacora; June 1968. All elevations < 305 m a.s.l.

**Neotropical distribution.** Colombia, Costa Rica, Panama.

***Neocyloepus sculptipennis* (Sharp, 1882) \***

Sharp, 1882: 135 [Guatemala]; *Elmis sculptipennis* Sharp, 1882.

**Primary collection information.** Panamá, Panamá Province, Soberanía National Park, Río Frijoles; 27 December 1980; leg P. Soto, M. Munoz, R. Gonzalez (MIUP).

**Neotropical distribution.** Guatemala, Mexico, Panama.

***Neocyloepus* sp.**

**Primary collection information.** Panama, Veraguas Province, Quebrada de Venado, 4 km S Las Palmas; 8.09978°N, 81.4346°W; 222 m a.s.l.; leg C.B. Barr, W.D. Shepard; 10 specimens (EMEC).

**Genus *Neoelmis* Musgrave, 1935**

***Neoelmis aspera* Hinton, 1940**

Hinton, 1940b: 330 [Mexico].

**Primary collection information.** • Panamá, Chiriquí Province, 3.9 km N of David, Río Majagua; WDS-A-1714; 8.34970°N, 82.41950°W; 364 m a.s.l.; 26 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Coclé Province, 2.5 km NW of El Valle, trib.to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, El Valle at pozos termales, Río Antón; WDS-A-1704; 8.59793°N, 80.1377°W; 584 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Herrera Province, NW of Las Minas, 9.9 km S of Ocu, Río Parita/Pacita; WDS-A-1718; 7.85730°N, 80.74537°W; 135 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1.9 km E of El Llano, 6 km W of Cañita, unnamed stream; WDS-A-1729; 9.22040°N, 78.94825°W; 40 m a.s.l.; 1 September 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Veraguas Province, Corozal, Río Guayabal; WDS-A-1716; 8.06652°N, 81.44635°W; 219 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC). • *ibid.*, NE of Santa Fe, Río Mulebá; WDS-A-1710; 8.52002°N, 81.07933°W; 319 m a.s.l.; 24 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Mexico, Nicaragua, Panama.

**Note.** The presence of this species in Panama was attributed by Jäch *et al.* (2016).

**Genus *Notelmis* Hinton, 1941**

***Notelmis nodipes* (Sharp, 1882)**

Sharp, 1882: 138 [Panama]; *Elmis nodipes* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 1219–1829 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Panama.

**Note.** This species was transferred to *Notelmis* by Hinton (1941).

**Genus *Onychelmis* Hinton, 1941**

***Onychelmis longicollis* (Sharp, 1882)**

Sharp, 1882: 138 [Panama]; *Elmis longicollis* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 1219–1829 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Colombia, Costa Rica, Guatemala, Panama.

**Note.** This species was transferred to *Onychelmis* by Hinton (1941).

## Genus *Phanocerus* Sharp, 1882

### *Phanocerus clavicornis* Sharp, 1882

Sharp, 1882: 129 [Guatemala].

**Primary collection information.** Panamá, Chiriquí Province, Renacimiento District, Río Bonita; 8.61699°N, 82.75993°W; 495 m a.s.l.; 18 May 2023; leg T. Ríos, Y. Aguirre; 1 male (MUPADI) • *ibid.*, Panamá Oeste Province, Chame District, quebrada sin nombre in the canyon; EC-06; 8.66623°N, 80.02101°W; 360 m a.s.l.; 10 May 2024; leg C. Nieto; kicknet; 1 male (MUPADI).

**Secondary collection information.** Panamá, Bocas del Toro Province, Changuinola District, Río Teribe; 23 April 1985; leg R.W. Flowers; 3 larvae (USNM) • *ibid.*, Río Teribe at Zegla; 20 April 1985; leg R.W. Flowers; 4 specimens (USNM) • *ibid.*, Chanquinola District, Ojo de Agua; 152 m a.s.l.; 4 May 1985; leg R.W. Flowers; 1 adult, 8 larvae (USNM) • *ibid.*, Miramar, Chiriquí Grande District, sea-level stream behind sawmill; 9.00°N, 82.25°W; 5 m a.s.l.; 2 May 1985; leg R.W. Flowers; 3 specimens (USNM) • *ibid.*, Chiriquí Grande District, Quebrada Canaza, Pipeline Road; 8.86685°N, 82.16688; 91 m a.s.l.; 18 May 1985; leg R.W. Flowers; 5 specimens (USNM) • *ibid.*, Chiriquí Grande District, tributary of Río Guabo, Pipeline Road; 14 May 1985; leg R.W. Flowers; UV light trap; 4 specimens (USNM) • *ibid.*, Chiriquí Province, Boquete District, 3 km NE Boquete, brook; 1250 m a.s.l.; 29 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 1 specimen (USNM) • *ibid.*, Caldera; 1 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 38 specimens (USNM) • *ibid.*, N of Boquete, Río Caldera at Bajo Lino; 1067 m a.s.l.; 17 December 1977; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, David District, 9 km N of David, waterfall at Balneario San Francisco; 31 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 18 specimens (USNM) • *ibid.*, El Velo in El Mirador, in national park; 1646 m a.s.l.; 19 December 1977; leg R.W. Flowers; 7 specimens (USNM) • *ibid.*, Renacimiento District, Santa Clara, Hartmann's Finca; 15-18 June 1985; leg E. Riley, D. Rider; 1 specimen (LSAM) • *ibid.*, Coclé Province, El Valle; 1829 m a.s.l.; 24 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 39 specimens (USNM) • *ibid.*, 26 May 1983; 112 specimens (USNM); *ibid.*, 27 May 1983; 76 specimens (USNM) • *ibid.*, Colón Province, Colón District, 4 mi NW of Gamboa, flood debris along river; 23 February 1975; leg Lawrence, Erwin; 1 specimen (MCZ) • *ibid.*, Panamá Province, Cerro Azul, Hidroeléctrica, Río Indio; 9 June 1985; leg E. Riley, D. Rider; 4 specimens (LSAM) • *ibid.*, Paraiso; 29 January 1911; leg E.A. Schwarz; 1 specimen (USNM) • *ibid.*, Panamá Oeste Province, Chorrea District, Barro Colorado Island, wet debris, small stream; 5 February 1976; leg A. Newton; 2 specimens (MCZ) • *ibid.*, Río Mendoza, 6.7 mi NW of Gamboa, flood debris along river; 19 February 1976; leg A. Newton; 1 specimen (MCZ) • *ibid.*, Río Frijoles; 24 January 1981; leg P. Soto, M. Muñoz, R. González; 4 specimens (MIUP).

**Neotropical distribution.** Belize, Brazil, Costa Rica, Cuba, Dominican Republic, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Puerto Rico.

**Note.** Redescription of the male can be found in Spangler & Santiago-Fragosa (1992), including a listing of all Panama material examined. This is the most widespread Neotropical species of elmids in the subfamily Larainae.

### *Phanocerus congener* Grouvelle, 1892 \*

Grouvelle, 1892: 46 [Grenada].

**Primary collection information.** Panamá, Coclé Province, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 1 km NW of El Copé, trib. to Río Grande; WDS-A-1719; 8.62067°N, 80.58925°W; 340 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Burigón; WDS-A-1720; 8.64210°N, 80.59032°W; 358 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, NE of La Pintada; WDS-A-172; 8.62102°N, 80.44722°W; 87 m a.s.l.; 30 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, 4.2 km SSE of Miraflores; WDS-A-1722; 8.61550°N, 80.26860°W; 115 m a.s.l.; 30 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Colón Province, Pipeline Road, 3.3 km NW of gate at Gamboa; WDS-A-1725; 9.14603°N, 79.72848°W; 68 m a.s.l.; 31 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Veraguas Province, Corozal, Río Guayabal; WDS-A-1716; 8.06652°N, 81.44635°W; 219 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Secondary collection information.** Panamá. No specific location information found. Cited in Jäch *et al.* (2016).

**Neotropical distribution.** Belize, Costa Rica, Ecuador, Grenada, Guatemala, Nicaragua, Panama, Trinidad and Tobago, Venezuela.

## Genus *Pharceonus* Spangler & Santiago, 1992

### *Pharceonus volcanus* Spangler & Santiago, 1992

Spangler & Santiago, 1992: 23 [Panama].

**Primary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Río Colorado, at Hwy 42, 15.6 km NW of Volcán; 8.8329°N, 82.7177°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard; 6 specimens (EMEC)

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, 26 km W of Volcán, small brook at culvert; 1380 m a.s.l.; 3 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 3 males (USNM).

**Neotropical distribution.** Colombia, Costa Rica, Ecuador, Panama, Venezuela.

## Genus *Pseudodisersus* Brown, 1981

### *Pseudodisersus goudotii* Guérin-Méneville, 1843

Guérin-Méneville, 1843: 53 [Colombia].

**Primary collection information.** Panamá, Boca del Toro Province, Cuenca 093, Río Changuinola, WNW of Ceiba; 9.01537°N, 82.506116°W; 438 m a.s.l.; 6 December 2017; UV light trap; leg T. Kingsley; 1 male (MUPADI) • *ibid.*, Chiriquí Province, Cuenca 108, Dolega District, Río Majagua, Banquito de Palmira, Potrerillos; 8.68083°N, 82.5325°W; 840 m a.s.l.; 3 July 2019; leg Y. Aguirre, T. Ríos; light trap; 1 male (MUPADI) • *ibid.*, 31 July 2019; 1 male (MUPADI) • *ibid.*, Tierras Altas District, Río Colorado, at Hwy 42, 15.6 km NW of Volcán; 8.8329°N, 82.7177°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC) • *ibid.*, Coclé Province, tributary of Río Grande, ca. 1 km NW El Copé, 8.6207°N, 80.5893°W; 340 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard; 2 specimens (EMEC) • *ibid.*, tributary of Río Grande at Barrigón, 3.1 km NE of El Copé; 8.6421°N, 80.5903°W; leg C.B. Barr, W.D. Shepard; 1 male (EMEC) • *ibid.*, tributary of Chorro Las Mozas, 1.6 km SW El Valle; 8.5938°N, 80.1463°W; 581 m a.s.l.; leg C.B. Barr, W.D. Shepard; 12 specimens (EMEC) • *ibid.*, Río Antón, El Valle, NE edge of town; 8.6140°N, 80.1127°W; 645 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC) • *ibid.*, 2.5 km NW of El Valle, tributary to Río Guayabo; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Secondary collection information.** Panamá, Bocas del Toro Province, Chiriquí Grande District, Miramar, Laguna de Chiriquí, stream behind sawmill, above falls; 2 May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Chiriquí Province, Gualaca District, Quebrada Honda, N of Fortuna Reservoir; 17 May 1985; leg R.W. Flowers; 1 specimen (USNM) • *ibid.*, Presa Fortuna; 8 May 1985; R.W. Flowers; light trap; 2 specimens (USNM) • *ibid.*, Renacimiento District, Santa Clara, Hartmann's Finca; 15–18 June 1985; leg E. Riley, D. Rider; 2 specimens (LSAM) • *ibid.*, Tierras Altas District, 19 km W of Volcán, small brook at culvert; 3 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 53 specimens (USNM) • *ibid.*, Guna Yala Comarca, 2.5 km S of Campamento Nusagandi; 1 May 1987; leg D. Quintero, H. Herrera, R. Cambra; 2 specimens (MIUP) • *ibid.*, Veraguas Province, Santa Fe District, Santa Fe, Quebrada Muela; 9 August 1987; leg R. Cambra; 2 specimens (MIUP) • *ibid.*, leg R. Rodriguez; 1 specimen (MIUP).

**Neotropical distribution.** Bolivia, Colombia, Costa Rica, Ecuador, Panama.

**Note.** Redescription of the male is given in Spangler & Santiago-Fragosa (1992).

## Genus *Stenhelmoides* Grouvelle, 1908

**Note.** See key to species in Spangler & Perkins (1989).

### *Stenhelmoides rufulus* (Hinton, 1934)

Hinton, 1934: 197 [Panama].

**Primary collection information.** Panama, Panama Province, Río Mamoni at Hwy. 1, 6.1 km NNE of Chepo; 9.1915°N, 79.07618°W; 33 m a.s.l.; leg. C.B. Barr, W.D. Shepard; 1 male (EMEC).

**Secondary collection information.** Panamá, Panamá Province, Paraiso; 29 January 1911; leg E.A. Schwarz (USNM).

**Neotropical distribution.** Belize, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Panama, Peru, Venezuela.

## Genus *Xenelmis* Hinton, 1936

**Note.** See key to species in Manzo (2006) and Sampaio *et al.* (2015).

### *Xenelmis bufo* (Sharp, 1882)

Sharp, 1882: 140 [Panama]; *Elmis bufo* Sharp, 1882.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK) • *ibid.*, Panamá Province, Pearl Islands, San Miguel; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Belize, Costa Rica, Guatemala, Mexico, Panama, Venezuela.

**Note.** This species was transferred to *Xenelmis* by Hinton (1936).

## Heteroceridae MacLeay, 1825

The variegated mud-loving beetles are found on every land mass except Antarctica. Most diverse in tropical and subtropical countries, they number approximately 250 species, with 87 of those from the New World and 53 from the Neotropics. Individuals are generally found in shoreline habitats, are dorso-ventrally flattened, and are brownish in color. Characterized by having large mandibles, they also have combs of well-defined spines on the dorsal margins of the fore- and mid-tibiae. Considered to be detritivores, they dig tunnels in soft soil around waterbodies, where they prey upon small vertebrates, play a role in seed dispersal, and also consume organic matter and algae (Katovich 2002).

The identification of adult Panamanian Heteroceridae is easy in that only four species, in the genus *Tropicus*, are currently known from Panama. However, more species and genera may be found with targeted collecting. Adults are distinguished by the dorsal color patterns, see Skalický (2006, 2014).

## Genus *Tropicus* Pacheco, 1964

### *Tropicus bartolozzii* Mascagni, 1994

Mascagni, 1994: 134 [Ecuador].

**Secondary collection information.** Panamá, Veraguas Province, San Francisco District, 12 km N off Santiago, near Río Santa Maria River; 18 August 2012; leg Čáp; light trap.

**Neotropical distribution.** Ecuador, Paraguay, Panama.

**Note.** First recorded from Panama by Skalický (2014).

### *Tropicus panamensis* Skalický, 2014

Skalický, 2014: 65 [Panama].

**Secondary collection information.** Panamá, Veraguas Province 12 km N of Santiago nr Río Santa Maria; 18 August 2012; light trap; 1 male (CSU), 3 females (CSU, MMB).

**Neotropical distribution.** Panama.

### *Tropicus pusillus* (Say, 1823)

Say, 1823: 200 [U.S.A.]; *Heterocerus pusillus* Say, 1823.

**Primary collection information.** Panamá, Chiriquí Province, Cuenca 108, Río Majagua, Banquito de Palmira; 8.68083°N, 82.53250°W; 840 m a.s.l.; 31 July 2019; leg T. Ríos, Y. Aguirre; Malaise trap; 1 male (MUPADI) • *ibid.*, David District, Río Papayal; 8.48419°N, 82.34822°W; 90 m a.s.l.; 15 July 2024; leg V. Ivanov, Y. Aguirre, T. Ríos; UV light trap; 1 male (MUPADI) • *ibid.*, 8.48442°N, 82.34686°W; 91 m a.s.l.; 1 male (MUPADI) • *ibid.*, San Felix District, Cuenca 112, Río San Felix, 2 km N Las Lajas; 28 May 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner (CAS) • *ibid.*, Panamá Province, Las Cumbres; 29–30 December 1975; leg H. Wolda (CAS).

**Secondary collection information.** Panamá, Panamá Province, Ancon; 4 May • *ibid.*, Panamá Oeste Province, Barro Colorado Island, Gatun Lake; 1 December.

**Neotropical distribution.** Costa Rica, Cuba, Honduras, Jamaica, Panama.

### ***Tropicus spangleri* Skalický, 2006**

Skalický, 2006: 85 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, San Felix District, 2 km N of Las Lajas, Río San Felix; 28 May 1983; blacklight; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; holotype male and 88 paratypes: 1 male (CSU); 27 males and 60 females (USNM) • *ibid.*, Río Fonseca at Pan-Am Hwy., 1 June 1972; leg T.L. and L.J. Erwin; Expedition No. 34 in notebook #1; 1 male, 1 female (USNM) • *ibid.*, Colón Province, Colón District, 5 mi NW of Gamboa; 9.16667°N, 29.75°W; 23–24 October 1975; 1 female (USNM) • *ibid.*, Panamá Province, Madden Dam; 10–13 July 1967; leg O.S. Flint, Jr.; 2 females (USNM).

**Neotropical distribution.** Costa Rica, Honduras, Panama.

### **Limnichidae Erichson, 1847**

Limnichids, often referred to as “minute marsh-loving beetles,” are very small (1–4 mm) with a compact, ovoid body, and a head that can be retracted into the thorax. There are currently 30 genera and over 350 species, with the highest diversity in the tropics. Both adults and larvae are found on submerged wood in shallow, fast-flowing streams, as well on sandy and muddy stream margins (Shepard & Chaboo 2015), however some species are terrestrial and associated with leaf litter and forest habitats.

The identification of adult Limnichidae is difficult due to their diversity, small size and old keys (Wooldridge 1975). However, a world-wide catalog exists that cites distributions (Spangler *et al.* 2001).

### **Genus *Byrrhinus* Motschulsky, 1858**

#### ***Byrrhinus mimicus* Wooldridge, 1987**

Wooldridge 1987: 308 [Panama].

**Secondary collection information.** Panamá, Coclé Province, El Valle; 671 m a.s.l.; 23 February 1950; leg H.S. Dybas; 2 specimens (FMNH) • *ibid.*, La Campana; 12 September 1954; leg Blanton; 1 specimen (USNM) • *ibid.*, Colón Province, Colón District, Canal Zone, 6.7 mi NW Gamboa; 15 June 1976; leg A. Newton; holotype male, allotype female (MCZ) • *ibid.*, same data as holotype; 3 specimens (MCZ) • *ibid.*, Canal Zone, Bohio; 8 April 1911; leg A.H. Jennings; 1 specimen (USNM) • *ibid.*, 4.1 mi NW Gamboa, Río Frijoles; 19 February 1976; leg A. Newton; 7 specimens (MCZ) • *ibid.*, 12 mi NW Gamboa, Río Agua Salud; 19 February 1976; leg A. Newton; 4 specimens (MCZ) • *ibid.*, Achiote Rd., 9 mi SW Gatun; 19 June 1976; leg A. Newton; 1 specimen (MCZ).

**Neotropical distribution.** Colombia, Panama.

#### ***Byrrhinus misellus* (Sharp, 1902)**

Sharp, 1902: 681 [Mexico]; *Cyphonichus misellus* Sharp, 1902.

**Secondary collection information.** Cited by Spangler *et al.* (2001).

**Neotropical distribution.** Colombia, Costa Rica, Mexico, Nicaragua, Panama.

**Note.** No specific record for Panama has been found in the literature.

#### ***Byrrhinus panamensis* (Sharp, 1902)**

Sharp, 1902: 679 [Panama]; *Cyphonichus panamensis* Sharp, 1902.

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg. G.C. Champion (NHMUK) • *ibid.*, Panamá Province, Pearl Islands, Isla del Rey, San Miguel; leg. G.C. Champion (NHMUK).

**Neotropical distribution.** Belize, Colombia, Costa Rica, Guatemala, Panama.

### **Genus *Cephalobyrrhinus* Pic, 1923**

**Note.** See key to species in Wooldridge (1986).

#### ***Cephalobyrrhinus curticornis* Pic, 1923**

Pic, 1923: 6 [Costa Rica].

**Secondary collection information.** Panamá, Colón Province, Camp Pina; June • *ibid.*, Panamá Province, Paraiso; January • *ibid.*, Panamá Oeste Province, Barro Colorado Island; March, July.

**Neotropical distribution.** Costa Rica, Mexico, Nicaragua, Panama, Venezuela.

***Cephalobyrrhinus lineatus* Wooldridge, 1986**

Wooldridge, 1986: 513 [Costa Rica].

**Secondary collection information.** Panamá, Bocas del Toro Province, Almirante, trail to dam on Nigua Creek; 25 March 1951; leg H.S. Dybas; 3 specimens (FMNH) • *ibid.*, 31 March 1959; 1 specimen (FMNH) • *ibid.*, Panamá Oeste Province, Barro Colorado Island; 6 February 1976; leg A. Newton; litter under rotten logs; holotype female (MCZ) • *ibid.*, same data as holotype; 5 specimens (MCZ) • *ibid.*, 13 February 1976; 9 specimens (MCZ) • *ibid.*, 17 February 1976 (MCZ) • *ibid.*, Achioté Rd., 9 mi SW Gatun; 18 June 1976; leg. A. Newton; 6 specimens (MCZ) • *ibid.*, Cerro Campana; 975 m a.s.l.; February 1976; leg A. Newton; 1 specimen (MCZ).

**Neotropical distribution.** Costa Rica, Mexico, Nicaragua, Panama, Venezuela.

**Genus *Corrinea* Wooldridge, 1980**

**Note.** See key to species in Wooldridge (1980).

***Corrinea delicata* Wooldridge, 1980**

Wooldridge, 1980: 75 [Panama].

**Secondary collection information.** Panamá, Panamá Province, Río Cabra, Pacora; 11 July 1923; leg H. Brown (USNM type #75578).

**Neotropical distribution.** Colombia, Costa Rica, Mexico, Panama.

**Genus *Ersachus* Erichson, 1847**

***Ersachus erichsonianus* Sharp, 1902**

Sharp, 1902: 683 [Mexico].

**Secondary collection information.** Panamá, Chiriquí Province, Boquete District, Caldera; leg. G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Mexico, Panama.

**Genus *Eulimnichus* Casey, 1889**

**Note.** See key to species and distributions in Wooldridge (1979).

***Eulimnichus acutus* Wooldridge, 1979**

Wooldridge, 1979: 7 [Costa Rica].

**Secondary collection information.** Cited in Spangler *et al.* (2001).

**Neotropical distribution.** Costa Rica, Colombia, El Salvador, Guatemala, Honduras, Mexico, Panama.

***Eulimnichus analis* (LeConte, 1879)**

LeConte, 1879: 515 [Texas]; *Limnichus analis* LeConte, 1879

**Material recorded:** Listed by Blackwelder (1944) as present in Panama.

**Distribution in Neotropics:** Mexico, Panama

***Eulimnichus ater* (LeConte, 1854)**

LeConte, 1854: 117 [U.S.A.]; *Limnichus ater* LeConte, 1854

**Secondary collection information.** Panamá. No specific location information found.

**Neotropical distribution.** Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Peru, Venezuela.

***Eulimnichus nitidulus* (LeConte, 1854)**

LeConte, 1854: 117 [U.S.A.]; *Limnichus nitidulus* LeConte, 1854.

**Secondary collection information.** Panamá, Canal Zone.

**Neotropical distribution.** Argentina, Brazil, Costa Rica, Ecuador, Mexico, Nicaragua, Panama.

***Eulimnichus sublaevis* Sharp, 1902**

Sharp, 1902: 674 [Guatemala].

**Secondary collection information.** Cited by Spangler *et al.* (2001).

**Neotropical distribution.** Guatemala, Panama.

**Genus *Euthryptus* Sharp, 1902**

***Euthryptus orbiculatus* Sharp, 1902**

Sharp, 1902: 682 [Guatemala].

**Secondary collection information.** Panamá. No specific location information found.

**Neotropical distribution.** Guatemala, Mexico, Panama.

***Euthryptus trigonalis* Sharp, 1902 \***

Sharp, 1902: 682 [Guatemala].

**Primary collection information.** Panamá, Coclé Province, 1 km NW of El Copé, tributary to Río Grande; WDS-A-1719; 8.62067°N, 80.58925°W; 340 m a.s.l.; 29 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Neotropical distribution.** Guatemala, Panama.

**Genus *Limnichoderus* Casey, 1889**

**Note.** See key to species and distributions in Wooldridge (1981).

***Limnichoderus angustus* Wooldridge, 1981**

Wooldridge, 1981: 180 [Venezuela].

**Secondary collection information.** Panamá, Coclé Province, Río Grande; 25 June 1968; leg H.P. Brown; 1 male, 4 females (USNM) • *ibid.*, Penonomé District, Río Churubé, W of Penonomé, 12 November 1966; leg H.P. Brown; 5 males, 4 females (HPB) • *ibid.*, Pavé, Río Pavé; 24 November 1971; leg H.P. Brown; 5 males (USNM) • *ibid.*, Panamá Oeste Province, small stream W of Chorrera; 12 November 1966; leg H.P. Brown; 2 males, 2 females (USNM).

**Neotropical distribution.** Colombia, Ecuador, Panama, Venezuela.

***Limnichoderus curtulus* Sharp, 1902**

Sharp, 1902: 678 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Boquete District, Caldera; leg G.C. Champion (NHMUK) • *ibid.*, Panamá Province, Pearl Islands, Isla del Rey, San Miguel; leg. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Panama.

**Note.** This species was redescribed in Wooldridge (1981).

***Limnichoderus lutrochinus* (LeConte, 1879)**

LeConte, 1879: 515 [U.S.A.]; *Limnichus lutrochinus* (LeConte, 1879).

**Secondary collection information.** No records of specimens from Panama were given by LeConte (1879) or Wooldridge (1981), although the latter stated he saw material from Panama.

**Neotropical distribution.** Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Panama.

**Note.** This species was placed in the genus *Limnichoderus* by Wooldridge (1981).

***Limnichoderus modicus* Wooldridge, 1981**

Wooldridge, 1981: 176 [Costa Rica].

**Secondary collection information.** Panamá, Chiriquí Province, Río Caimito, Boquerón; 23 June 1968; leg

H.P. Brown; 1 female (USNM) • *ibid.*, Río Guigala, W of Concepcion; 18 November 1966; leg H.P. Brown; 28 specimens (HPB) • *ibid.*, Panamá Province, Chepo Comaraca, Río Tapagrillo; 24 November 1971; leg H.P. Brown; 4 specimens (HPB) • *ibid.*, Veraguas Province, Soná District, small stream E of Soná; 13 November 1966; leg H.P. Brown; 20 specimens (USNM).

**Neotropical distribution.** Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Panama.

### ***Limnichoderus moratus* Wooldridge, 1981**

Wooldridge, 1981: 185 [Panama].

**Secondary collection information.** Panamá, Coclé Province, Pavé, Río Pavé; 24 November 1971; leg H.P. Brown; 8 specimens (HPB) • *ibid.*, Colón Province, Portobelo District, Porto Bello; 2 February 1911; leg E.A. Schwarz; 1 holotype male, 1 allotype female (EASC) • *ibid.*, 17 February 1930; 2 specimens (USNM) • *ibid.*, France Field, nr Colón; 9 April 1957; leg R.M. Altman; light trap; 13 specimens (INHS) • *ibid.*, Colón District, Corregimiento Ciricito; 25 February 1930; leg R.E. Blackwelder; 1 specimen (USNM) • *ibid.*, Fort Gulick; 21 December 1956; leg R.M. Altman; light trap; 4 specimens (INHS) • *ibid.*, 14 January 1957; 4 specimens (INHS) • *ibid.*, Fort Sherman; 24 January 1957; leg. R.M. Altman; light trap; 4 specimens (INHS) • *ibid.*, Porto Bello; 12 March 1911; leg A. Busck; 1 specimen (USNM) • *ibid.*, Tabernilla, Gatun Lake; 13 May 1907; leg A. Busck; 2 specimens (USNM) • *ibid.*, 6 February 1911; 1 specimen (USNM) • *ibid.*, Los Santos Province, Los Cruces; 4 February 1911; leg E.A. Schwarz; 7 specimens (USNM) • *ibid.*, 10 February 1911; 3 specimens (USNM) • *ibid.*, Panamá Province, Fort Clayton, NW of Balboa; 25 March 1945; leg K.E. Frick; 7 specimens (CAS) • *ibid.*, Gamboa; 1 May 1972; R. and E. Froeschner; 1 specimen (USNM) • *ibid.*, Panamá Oeste Province, Capira District, Río Trinidad; 7 May 1911 to 9 June 2012; leg A. Busck; 44 specimens (USNM) • *ibid.*, Panamá District, Tocumen; 6 January 1953; leg F.S. Blanton; 3 specimens (USNM) • *ibid.*, nr Bahía de Panamá; 7 February 1911; leg E.A. Schwarz; 8 specimens (USNM) • *ibid.*, Arraiján District, Corazol; 12 February 1911; leg A. Busck; 2 specimens (USNM) • *ibid.*, Chorrera; 18 April 1925; leg A. Busck; 1 specimen (USNM) • *ibid.*, Alajuela; 27 May 1912; leg A. Busck; 1 specimen (USNM) • *ibid.*, Veraguas Province, Coiba Island, Frijoles; 19 November 1925; leg E.A. Schwarz; 2 specimens (USNM) • *ibid.*, no province given, XX Plantation; 4 February 1930; leg R.E. Blackwelder; 1 specimen (USNM).

**Neotropical distribution.** Colombia, Costa Rica, Guatemala, Honduras, Panama.

### ***Limnichoderus naviculatus* (Casey, 1889)**

Casey, 1889: 156 [U.S.A.].

**Secondary collection information.** Cited in Spangler *et al.* (2001).

**Neotropical distribution.** Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Puerto Rico.

**Note.** Neither Casey (1889) nor Wooldridge (1981) provided location data for Panama, although the latter indicated it is found in Panama. Listed in Bio-Nica.org as existing in Panama.

### ***Limnichoderus vicinus* Pic, 1922**

Pic, 1922: 4 [Brazil].

**Secondary collection information.** Cited in Spangler *et al.* (2001).

**Neotropical distribution.** Brazil, Colombia, Ecuador, Panama, Venezuela.

**Note.** Panama is not indicated as a country of record by Pic (1922) or Wooldridge (1981).

### **Genus *Martinius* Spilman, 1959**

**Note.** See key to species in Spilman (1966).

### ***Martinius tellepontis* Spilman, 1959**

Spilman, 1959: 119 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Chorcha Abajo, landing, mangrove shoreline; 8.34273°N, 82.27920°W; 0.3 m a.s.l.; 17 January; leg A.R. Gillogly • *ibid.*, Panamá Province, Canal Zone; 10 February 1939; leg C.H. Richardson; holotype male (USNM No. 64214), 1 allotype female, 19 males and 20 female paratypes (USNM) • *ibid.*, February 1939; leg C.J. Drake; 2 males, 1 female (USNM).

**Neotropical distribution.** Panama.

## Genus *Paralimnichus* Delève, 1973

### *Paralimnichus panamensis* Wooldridge, 1983

Wooldridge, 1983: 232 [Panama].

**Secondary collection information.** Panamá, Panamá Oeste Province, Barro Colorado Island; May 1929; leg Darlington; 1 holotype male, 3 paratype males, 1 paratype female (MCZ) • *ibid*, 23–24 May 1940; leg J. Zetek; 1 paratype specimen (USNM).

**Neotropical distribution.** Panama.

## Genus *Phalacrichus* Sharp, 1902

**Note:** See key to species in Wooldridge (1982).

### *Phalacrichus atomarius* Sharp, 1902

Sharp, 1902: 679 [Mexico].

**Secondary collection information.** Cited in Spangler *et al.* (2001).

**Neotropical distribution.** Belize, Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Surinam, Trinidad, Venezuela.

**Note.** No Panama collection information in either Sharp (1902) or Wooldridge (1982). Listed in Bio-Nica.org as existing in Panama.

### *Phalacrichus punctatus* Wooldridge, 1982

Wooldridge, 1982: 389 [Venezuela].

**Secondary collection information.** Panamá, Panamá Province, Tocumen; 6 January 1953; leg F.S. Blanton; 1 specimen (USNM) • *ibid*, Panamá Oeste Province, Canal Zone, Ancon; 12 May 1911; leg A.H. Jennings; arc light; 1 allotype female, 2 specimens (USNM).

**Neotropical distribution.** Bolivia, Brazil, Colombia, Panama, Venezuela.

## Genus *Physemus* LeConte, 1854

**Note.** See key to species in Wooldridge (1976).

### *Physemus latifrons* Wooldridge, 1976

Wooldridge, 1976: 180 [Panama].

**Secondary collection information.** Panamá, Panamá Province, Canal Zone, Ancon; 12 May 1911; leg A.H. Jennings; arc light; 1 holotype female (USNM Type No. 73399) • *ibid*, 1 female paratype (USNM).

**Neotropical distribution.** Panama.

## Lutrochidae Kasap & Crowson, 1975

The family Lutrochidae includes aquatic beetles placed within a single genus *Lutrochus*, that are often referred to as “Travertine beetles.” Distributed from the northeastern United States to Uruguay and Argentina, approximately 21 species are known. *Lutrochus* is characterized by ovate bodies (2–6 mm in length), areas of dense gold or black setae, short antennae wherein the first two antennomeres are longer than the others and are broad with conspicuous setae, and legs with the last tarsomeres with large claws. The species are associated with submerged wood in clear, fast-flowing streams (Shepard 2002; Shepard & Chaboo 2015).

The Lutrochidae have recently been revised (Maier 2016), including numerous new species and genera. Because this work remains unpublished, those names are as yet unavailable. Lutrochid species, restricted to the New World, are listed in a world-wide catalog (Spangler *et al.* 2001).

## Genus *Lutrochus* Erichson, 1847 \*

### *Lutrochus* sp. nov. Maier, 2016 \*

Maier, 2016: 124 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Río Colorado at Volcán Rd., 5.6 rd. km NW Volcán; 8.83188°N, 82.71772°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr; 35 specimens (EMEC) • *ibid.*, trib. at Volcán Rd., ~4 km NW Volcán; 8.80675°N, 82.67567°W; 1337.5 m a.s.l.; 26 July 2006; leg C.B. Barr; 2 specimens (EMEC).

**Neotropical distribution.** Panama.

**Note.** Unpublished species described and illustrated in the Ph.D. dissertation of Crystal Maier (2016) at the University of Kansas.

### *Lutrochus vestitus* (Sharp, 1882) \*

Sharp, 1882: 126 [Guatemala]; *Byrrhomorphus vestitus* Sharp, 1882.

**Primary collection information.** Panamá, Panamá Province, 5.4 km E of Buenos Aires, unnamed river; WDS-A-2027; 9.16823°N, 79.57503°W; 99 m a.s.l.; 1 September 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Panamá Oeste Province, Chame District, quebrada sin nombre in the canyon; EC-06; 8.66623°N, 80.02101°W; 360 m a.s.l.; 10 May 2024; leg C. Nieto; kicknet; 1 male (MUPADI).

**Neotropical distribution.** Belize, Colombia, Costa Rica, Guatemala, Mexico, Panama, Venezuela.

## Psephenidae Lacordaire, 1854

Often referred to as water penny beetles, this family has aquatic larvae which are oval, flat, and brownish in color. Adults are characterized by long palps, soft elytra, and dark colors (Shepard & Chaboo 2015). Larvae occur on rocks or gravel in streams and feed on algae and detritus. Adults are found on exposed rock and other surfaces in stream riffle zones, or in overhanging vegetation. Adults do not feed as they are short-lived (Shepard & Chaboo 2015).

Adult Psephenidae are well-known in the New World. Two of the five psephenid subfamilies occur in Panama: Eubriinae and Psepheninae. Adult Eubriinae (*Dicranopselaphus*, *Eubria*, *Neoeubria*) are small, secretive, associated with stream margins and springs, and flighty when disturbed. A key to the Neotropical Eubriinae is found in Shepard & Barr (2014). Adult Psepheninae (*Psephenops* and *Psephenus* in Panama) are larger (+/- 10 mm), easily seen on emergent rocks in streams, and very quick to fly. Three species have been described from Panama by Arce-Pérez and colleagues (2015, 2017). Extraction of the male genitalia is required for species-level identifications.

## Genus *Dicranopselaphus* Guérin-Méneville, 1861 \*

### *Dicranopselaphus* sp. \*

**Primary collection information.** Panamá; Coclé Province, 2.5 km NW of El Valle, trib. to Río Guayabo; WDS-A-1703; 8.62837°N, 82.13670°W; 689 m a.s.l.; 22 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Note.** Identified by its larval stage.

## Genus *Ectopria* LeConte, 1853

**Note.** *Ectopria* is Holarctic and is not likely to occur in the Neotropics.

### *Ectopria reticulata* Champion, 1897

Champion, 1897: 598 [Panama].

**Secondary collection information.** Panama, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion; 1 holotype male, 1 paratype male, 1 paratype female (NHMUK).

**Neotropical distribution.** Panama.

**Note.** This species probably belongs in *Dicranopselaphus*.

***Ectopria vermiculata* Champion, 1897**

Champion, 1897: 599 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion;

1 holotype male, 1 paratype female (NHMUK).

**Neotropical distribution.** Panama.

**Note.** This species probably belongs in *Dicranopselaphus*.

**Genus *Eubria* Latreille, 1829**

***Eubria mesoamericana* Barr & Shepard, 2017**

Barr & Shepard, 2017: 438 [Panama].

**Primary collection information.** Panamá, Veraguas Province, Isla Canales de Afuera; 5 February–6 March 2023; 7.69494°N, 81.62649°W; 29 m a.s.l.; leg V. Rodriguez; 1 male (EMEC) • *ibid.*, Veraguas Province, Quebrada de Venado, 4 km S of Las Palmas; 8.09978°N, 81.43460°W; 222 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard; paratype male (EMEC).

**Secondary collection information.** Panamá, Coclé Province, El Valle; 829 m a.s.l.; 27 May 1983; leg P.J. Spangler; holotype male, paratype male (USNM) • *ibid.*, Colón Province, Río Guanche, 5 km S of Portobello; 9.50337°N, 79.66505°W; 100 m a.s.l.; 18 July 1999; leg J.B. Woolley; paratype male (TAMU) • *ibid.*, Portobello; March 1911; leg A. Busck; paratype male (USNM) • *ibid.*, Panamá Province, Canal Zone, Paraiso; 20 January 1911; leg A. Busck; paratype female (USNM) • *ibid.*, Panamá Oeste Province, Barro Colorado Island, Canal Zone; March–April 1949; paratype male (USNM).

**Neotropical distribution.** Costa Rica, Panama.

**Genus *Neoeubria* Shepard & Barr, 2014**

***Neoeubria inbionis* Shepard & Barr, 2014**

Shepard & Barr, 2014: [Costa Rica].

**Secondary collection information.** Panamá, Chiriquí Province, Gualaca District, Fortuna Forest Reserva; March 2004; leg Checo Colon-Gaud; 1 larva (EMEC).

**Neotropical distribution.** Costa Rica, Ecuador, Nicaragua, Panama.

**Genus *Psephenops* Grouvelle, 1898**

**Note.** See key to species in Arce-Pérez & Novelo-Gutiérrez (2017).

***Psephenops bifidus* Arce-Pérez & Novelo-Gutiérrez, 2017**

Arce-Pérez & Novelo-Gutiérrez, 2017: 110 [Panama].

**Primary collection information.** Panama, Herrera Province, Río Parita, NW of Los Minas; 7.8573°N, 80.7454°W; 132 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shephard; 1 male, 1 female (EMEC).

**Secondary collection information.** Panamá, Panamá Province, Chame District, Río Marías; 8.63367°N, 80.02517°W; 325 m a.s.l.; 26 April 2015; leg R. Novelo; holotype male, 5 paratype males (IEXA).

**Neotropical distribution.** Panama.

***Psephenops maculicollis* Darlington, 1936 \***

Darlington, 1936: 72 [Colombia].

**Primary collection information.** Panamá, Chiriquí Province, Bugaba District, nr San Andrea, Finca La Esperanza; 8.61710°N, 82.70415°W, 491 m a.s.l., 7–21 February 2022; leg Y. Aguirre, T. Ríos; Malaise Trap; 1 male (MUPADI) • *ibid.*, Panamá Oeste Province, Chame District, quebrada sin nombre in the canyon; EC-06; 8.66623°N, 80.02101°W; 360 m a.s.l.; 10 May 2024; leg C. Nieto; 1 male (MUPADI).

**Secondary collection information.** Panamá. No specific location information found.

**Neotropical distribution.** Colombia, Panama.

***Psephenops panamensis* Arce-Pérez, 2015**

Arce-Pérez in Arce-Pérez *et al.* (2015): 110 [Panama].

**Secondary collection information.** Panamá, Darién Province, Darién National Park, Estación Rancho Frío, Río Perresénico; 8.01714°N, 77.72417°W; 117 m a.s.l.; 20 November 2014; leg R. Novelo; holotype male (IEXA), 19 paratype males (IEXA 8, MIUP 8, NHMW 3).

**Neotropical distribution.** Panama.

***Psephenops triangularis* Arce-Pérez & Novelo-Gutiérrez, 2017**

Arce-Pérez & Novelo-Gutiérrez, 2017: 110 [Panama].

**Secondary collection information.** Panamá, Panamá Province, Chame District, Río Marías; 8.63367°N, 80.02517°W; 325 m a.s.l.; 26 April 2015; leg R. Novelo; holotype male, 5 paratype males (IEXA).

**Neotropical distribution.** Panama.

**Genus *Psephenus* Haldeman, 1853**

***Psephenus palpalis* Champion, 1913**

Champion, 1913: 62 [Mexico].

**Primary collection information.** Panamá, Herrera Province, Río Parita, NW of Los Minas; 7.8573°N, 80.7454°W; 132 m a.s.l.; 28 August 2006; leg C.B. Barr, W.D. Shepard; 1 male (EMEC).

**Neotropical distribution.** Mexico, Panama.

**Ptilodactylidae Laporte, 1836**

Present in most bioregions and countries (except the Palearctic and Chile), this family of semiaquatic and terrestrial beetles has its greatest diversity in the New World and Old World tropical areas. Traditionally, members of this family were recognized 1) by the pronotum, which is anteriorly narrowed and rounded and has a crenulate base, 2) by the heart-shaped mesoscutellum, 3) by the pseudotetramerous tarsi, and 4) by the pectinate antennae of the males (Shepard & Chaboo 2015; Stribling 1986b). However, exclusive use of these characters has led to some confusion in phylogenetic relationships as well as delineation of genera (Stribling 1986b). Most species are entirely terrestrial, but a few have aquatic larvae. Larvae can be found in leaf litter or in streams where they feed on dead leaves and wood (Shepard & Chaboo 2015).

Ptilodactylidae is perhaps the most difficult family in Dryopoidea in which to make adult identifications at both the genus- and species-level. Plus, very few larval descriptions are available. The family is quite diverse, especially the type genus, *Ptilodactyla*, which can be quite abundant. Many descriptions date to the late 1800s when descriptions were brief, diagnostic characters were not known, and illustrations were not common. Extraction of the male genitalia is required for most species-level identifications. Useful keys are in Stribling (1986a, 1986b) and Fernandes *et al.* (2023).

**Genus *Anchytarsus* Guérin-Méneville, 1843**

**Note.** See key to species in Fernandes *et al.* (2023).

***Anchytarsus folliculipalpus* Stribling, 1986**

Stribling, 1986b: 227 [Colombia].

**Secondary collection information.** Panamá, Chiriquí Province, Alto Lino, 4 km NE Boquete; 10 September 1975; leg H. Wolda; UV light trap (OSUC).

**Neotropical distribution.** Brazil, Colombia, Guatemala, Panama.

***Anchytarsus palpalis* (Champion, 1897)**

Champion, 1897: 594 [Mexico].

**Primary collection information.** Panamá, Veraguas Province, Isla Canales de Afuera; 5 February–6 March 2023; 7.69494°N, 81.62649°W; 29 m a.s.l.; leg V. Rodriguez; 1 male (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 1219 m a.s.l.; leg. G.C. Champion; 1 male (NHMUK) • *ibid.*, 26 km W of Volcán, small brook at culvert; 1380 m a.s.l.; 3 June 1983; leg P.J. Spangler, R.A. Faitoute, W.E. Steiner; 3 males (USNM).

**Neotropical distribution.** Belize, Mexico, Nicaragua, Panama.

**Note.** Lectotype designated by Stribling (1986b).

### *Anchytarsus* sp. A \*

Stribling, 1986b: 229.

**Primary collection information.** Panamá, Chiriquí Province, between Las Palmas and Corozal, Quebrada de Venado; WDS-A-1715; 8.09978°N, 81.43460°W; 222.2 m a.s.l.; 27 August 2006; leg C.B. Barr, W.D. Shepard (EMEC) • *ibid.*, Tierras Altas District, 15.6 km N of Volcán, Río Colorado; WDS-A-1711, 8.83188°N, 82.71772°W; 1250 m a.s.l.; 25 August 2006; leg C.B. Barr, W.D. Shepard (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, SMSH; USNM.

**Neotropical distribution.** Ecuador, Mexico, Nicaragua, Panama.

**Note.** Known only by larval stage. The larvae are collected throughout the year. Stribling (1986b) revised the genus *Anchytarsus* and provided a key to larvae, including this unassociated species.

## Genus *Apoglossa* Guérin-Méneville, 1849

### *Apoglossa angustata* Champion, 1897

Champion, 1897: 625 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion (NHMUK) • *ibid.*, Boquete District, Caldera.

**Neotropical distribution.** Panama.

**Note.** Listed in Champion (1897) as *Haploglossa angustata*.

### *Apoglossa collaris* Guérin-Méneville, 1849

Guérin-Méneville, 1849: 3 [Mexico].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Mexico, Panama.

**Note.** Listed in Champion (1987) as *Haploglossa collaris*.

### *Apoglossa* sp. \*

**Primary collection information.** Panamá, Coclé Province, Pojanol GeoSite, Río Seren; 8.58983°N, 80.21476°W; 332 m a.s.l.; 13 August 2022; UV light trap; leg C. Nieto; 1 male (MUPADI) • *ibid.*, Veraguas Province, Las Palmas District, Quebrada del Rosario; 7.87237°N, 81.51031°W; 63 m a.s.l.; 20 February 2023; leg V. Rodriguez; UV light trap; 1 male (MUPADI) • *ibid.*, 20 February–7 March 2023; 1 male (MUPADI) • *ibid.*, Sona District, Quebrada sin nombre, Isla Rancheria, Coiba National Park; 7.6396°N, 81.70475°W; 24 m a.s.l.; 20 April–6 July 2023; leg V. Rodriguez; Malaise Trap; 1 male (MUPADI).

**Neotropical distribution.** Panama.

## Genus *Cladotoma* Westwood, 1837

### *Cladotoma cucullatus* (Champion, 1897) \*

Champion, 1897: 634 [Mexico]; *Telon cucullata* Champion, 1897.

**Secondary collection information.** Panamá, Panamá Province, Canal Zone, Clayton; May 1944; leg H.E. Frick [CAS].

**Distribution in the Neotropics.** Belize, Guatemala, Honduras, Mexico, Panama.

**Note.** *Telon* synonymized under *Cladotoma* by Stribling (1986a). Blackwelder (1944) and Stribling (1986a) indicate that this species is found throughout Central America.

### *Cladotoma ovalis* Westwood, 1837

Westwood, 1837: 255.

**Secondary collection information.** Panamá, Panamá Province, Las Cumbres • *ibid.*, Panamá Oeste Province, Barro Colorado Island.

**Distribution in the Neotropics.** Brazil, Costa Rica, Mexico, Panama.

**Note.** See López-Pérez *et al.* (2020) for complete distribution.

### Genus *Epiptygma* Stribling, 1986

#### *Epiptygma ebenina* (Champion, 1897)

Champion, 1897: 631 [Mexico]; *Ptilodactyla ebenina*.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán; leg. G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Mexico, Panama.

**Note.** Comb. nov. (Stribling 1986a).

#### *Epiptygma maculata* (Champion, 1897)

Champion, 1897: 630 [Mexico]; *Ptilodactyla maculata*.

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Mexico, Guatemala, Panama.

**Note.** Comb. nov. (Stribling 1986a).

#### *Epiptygma rufa* (Champion, 1897)

Champion, 1897: 630 [Central America]; *Ptilodactyla rufa*.

**Primary collection information.** Panamá, Veraguas Province, Sona District, Cuenca 116, Quebrada Monita; 7.81480°N, 81.55724°W; 26 m a.s.l.; 9 March 2023; leg V. Rodriguez; Malaise trap; 1 male (MUPADI) • *ibid.*, Isla Canales de Afuera; 7.69494°N, 81.62649°W; 29 m a.s.l.; 5 February–6 March 2023; leg V. Rodriguez; 1 male (EMEC).

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba, Tierras Altas District, Volcán Barú; leg G.C. Champion (NHMUK) • *ibid.*, David District, David, Boquete District, Caldera; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Guatemala, Nicaragua, Panama.

**Note.** Comb. nov. (Stribling 1986a).

### Genus *Octoglossa* Guérin-Ménéville, 1843

#### *Octoglossa femoralis* Guérin-Ménéville, 1843

Guérin-Ménéville, 1843: 2 [Colombia].

**Secondary collection information.** Panamá. No specific location information found.

**Neotropical distribution.** Colombia, Panama.

### Genus *Ptilodactyla* Illiger, 1807

#### *Ptilodactyla aequinoctialis* Champion, 1897

Champion, 1897: 651 [Costa Rica].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Costa Rica, Panama.

***Ptilodactyla caudata* Champion, 1897**

Champion, 1897: 648 [Nicaragua].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Guatemala, Nicaragua, Panama.

***Ptilodactyla chiriquiensis* Champion, 1897**

Champion, 1897: 637 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 762–1219 m a.s.l.; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla confinis* Champion, 1897**

Champion, 1897: 638 [Mexico].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Belize, Guatemala, Honduras, Mexico, Nicaragua, Panama.

***Ptilodactyla deplanata* Champion, 1897**

Champion; 1897: 635 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 762–1219 m a.s.l.; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla dilaticollis* Champion, 1897**

Champion, 1897: 647 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 914 m a.s.l. ]; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla germana* Champion, 1897**

Champion, 1897: 652 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 762–1219 m a.s.l.; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla gibbicollis* Champion, 1897**

Champion, 1897: 633 [Panama].

**Primary collection information.** Panamá, Veraguas Province, Sona District, Isla Canales de Afuera; 7.69494°N, 81.62649°W; 29 m a.s.l.; 5 February–6 March 2023; leg V. Rodriguez; 1 male (MUPADI).

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla montana* Champion, 1897**

Champion, 1897: 643 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Tierras Altas District, Volcán Barú; 2438 m a.s.l.; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla opima* Champion, 1897**

Champion, 1897: 650 [Guatemala].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion; 1 male (NHMUK) • *ibid.*, Boquete District, Caldera; 1 male (MUPADI) • *ibid.*, Tierras Altas District, Volcán Barú; leg G.C. Champion; 1 male (NHMUK).

**Neotropical distribution.** Guatemala, Panama.

***Ptilodactyla parallela* Champion, 1897**

Champion, 1897: 655 [Costa Rica].

**Secondary collection information.** Panamá, Chiriquí Province; Tierras Altas District, Volcán Barú; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Panama.

***Ptilodactyla scapularis* Champion, 1897**

Champion, 1897: 643 [Panama].

**Secondary collection information.** Panamá; Chiriquí Province; Tierras Altas District; Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla scutata* Champion, 1897**

Champion, 1897: 646 [Panama].

**Secondary collection information.** Panamá; Chiriquí Province; Tierras Altas District; Volcán Barú; 610–914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Panama.

***Ptilodactyla serrata* Champion, 1897**

Champion, 1897: 652 [Costa Rica].

**Secondary collection information.** Panamá; Chiriquí Province; Tierras Altas District; Volcán Barú; 914 m a.s.l.; leg G.C. Champion (NHMUK).

**Neotropical distribution.** Costa Rica, Guatemala, Panama.

***Ptilodactyla tropicalis* Champion, 1897**

Champion, 1897: 649 [Mexico].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK) • *ibid.*, Boquete District, Caldera • *ibid.*, Tierras Altas District, Volcán Barú.

**Neotropical distribution.** Mexico, Panama.

***Ptilodactyla varicornis* Champion, 1897**

Champion, 1897: 644 [Panama].

**Secondary collection information.** Panamá, Chiriquí Province, Bugaba District, Bugaba; leg G.C. Champion (NHMUK) • *ibid.*, Boquete District, Caldera • *ibid.*, David District, David.

**Neotropical distribution.** Panama.

**Genus *Stiophora* Champion, 1897**

***Stiophora lyciformis* (Champion, 1897)**

Champion, 1897: 660 [Nicaragua]; *Chaetodactyla lyciformis* Champion, 1897.

**Secondary collection information.** Cited by Stribling (1866a).

**Neotropical distribution.** Nicaragua, Panama.

**Note.** This species was transferred to *Stiophora* by Stribling (1986a) and validated by Chatzimanolis *et al.* (2012).

***Stiophora sulcipennis* Champion, 1897**

Champion, 1897: 660 [Nicaragua].

**Secondary collection information.** Cited by Stribling (1866a).

**Neotropical distribution.** Nicaragua, Panama.

**Comparison of dryopoid faunas of Costra Rica, Panama and Colombia.** The number of dryopoid genera and species found in Colombia, Costa Rica, and Panama are presented in Table 3. This information is derived from unpublished data (WDS, pers. comm.) and the literature (e.g., Hincapié-Montoya 2023, Blackwelder 1944).

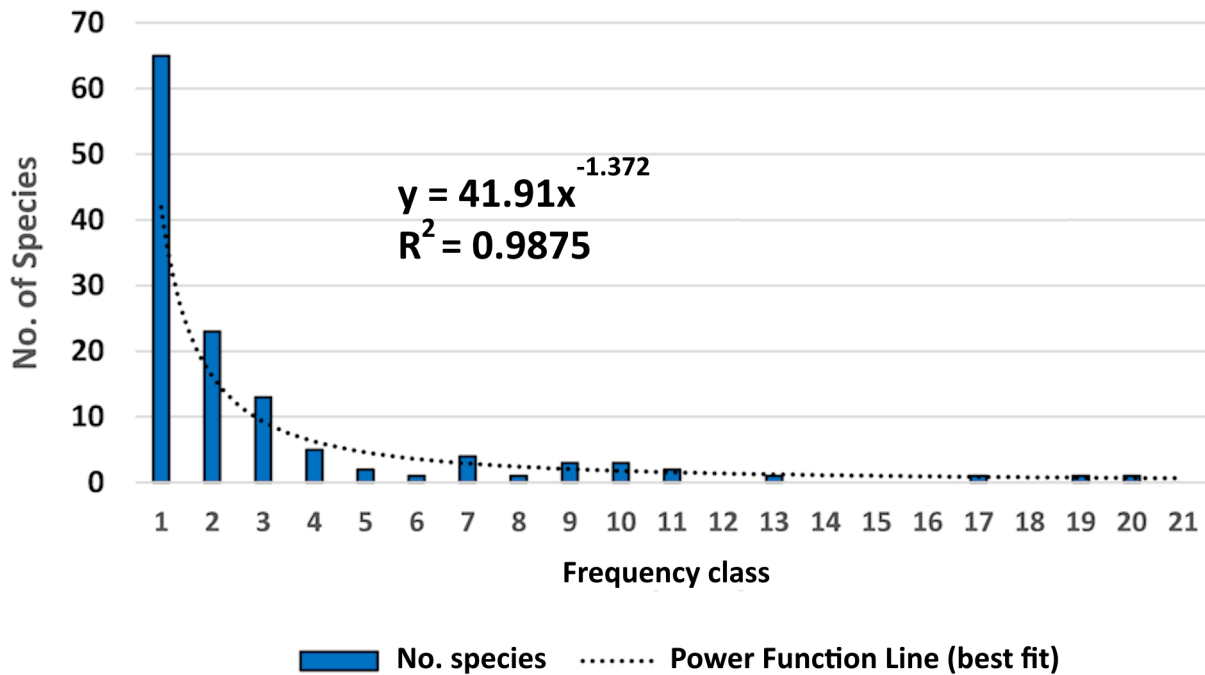
**TABLE 3.** Comparison of the number of genera and species among Costa Rica, Panama, and Colombia.

Family	Costa Rica		Panama		Colombia	
	Genera	Species	Genera	Species	Genera	Species
Callirhipidae	3	8	2	4	2	4
Chelonariidae	1	8	1	7	1	17
Cneoglossidae	0	0	1	1	1	1
Dryopidae	4	10	7	12	8	11
Elmidae	18	38	17	33	30	72
Heteroceridae	2	4	1	4	1	1
Limnichidae	12	31	11	25	8	21
Lutrochidae	1	1	1	2	1	1
Psephenidae	6	7	5	9	2	2
Ptilodactylidae	7	15	7	30	5	21
<b>Totals:</b>	<b>54</b>	<b>122</b>	<b>53</b>	<b>127</b>	<b>59</b>	<b>151</b>

**Species richness in Panama.** The Chao2 estimate for potential species richness of Dryopoidea in Panama (currently  $n = 127$  species) is 219 species.

**Frequency of Collection.** As indicated in Figure 3, ~51% ( $n = 65$  species) of the current dryopoid fauna are known from single sample locations, and an additional ~18% ( $n = 23$  species) are known from two sample locations. Thus, only ~31% ( $n = 39$  species) of Panama’s dryopoids are known from 3 to >20 locations.

### Frequency of species locations



**FIGURE 3.** Frequency of occurrence of Dryopoidea species in Panama based on number of locations.

## Discussion

**Distributions within and outside of Panama.** Costa Rica and Panama have similar numbers of dryopoid taxa and many of the same species. However, Colombia has many more dryopoid taxa than these two Central American countries. This is especially noticeable in the Elmidae where Colombia has many more genera present that are restricted to South America. To a lesser degree, the Chelonariidae of Colombia have more species and have species that are restricted to South America. In contrast the Psephenidae of Panama and Costa Rica outnumber those found in Colombia. That Costa Rica and Panama have very similar aquatic and semiaquatic dryopoids is to be expected in that they are adjacent Central American countries and have very similar geography. The richer dryopoid fauna in Colombia is likely due to the proximity of the northern end of the Andes and the filtering effect of the Darien Gap in southern Panama. This latter effect is also reflected in the comparative small affinity between Colombia and Panama for caddisflies (Armitage & Harris 2018; Armitage *et al.* 2024).

Given the country comparisons presented in Table 3, we believe that our accumulation of 129 species distributed among 54 genera represents a reasonable first approximation of the Dryopoidea of Panama. All of Central America is undercollected, so we anticipate many new additions to these countries' faunal assemblages, but that the results will mirror the current distribution of species among families and genera. The family Elmidae has the largest number of genera, and it shares representation of the largest number of species with the family Ptilodactylidae. Whether continued collecting will provide grounds for a more marked separation between Panama and Costa Rica remains to be seen. However, we believe the faunal similarities will remain strong as evidenced in other organismal groups (e.g., caddisflies; Armitage *et al.* 2024).

**Estimates of potential species richness.** Sampling limitations inherent in almost every biological survey cause species to be missed that are present, but not detected (Chao *et al.* 2017). Thus, true species richness (identified plus undetected species) is invariably underestimated. Nonparametric estimators for reduction of undersampling bias have become increasingly favored because they make no assumptions about the underlying probability distribution of the supporting species incidence or abundance data. Further, for both biological and practical reasons, incidence (presence/absence) data is preferred over abundance data in order to avoid the major problems which sometimes accompany abundance estimates (e.g., sampling errors, weather events, normal locational and year-to-year variations, etc.). Not considered here are contributions of cryptic species, if any.

In order to estimate these undetected species for incidence data, the species which are frequently encountered offer little or no insight. However, species that are detected in only a few samples contain almost all of the information about undetected species richness (Gotelli & Chao 2013). Thus, as stated in the Methods section, most of these nonparametric estimators (e.g., Chao2) are based on rare species, particularly those whose frequency is one (one time in only one sample or location) or two occurrences (one time each in two different samples or locations) for all samples in a sampling area or during a temporal period.

The Chao2 estimator, in general, provides a non-parametric lower bound of species richness (Chao 1987), if the sample size is not sufficiently large and/or the detection probability of rare, undetected species is unequal. We suspect that this describes our current situation in Panama. However, if we diversify our collecting range throughout Panama, and its many microhabitats, and sample multiple times of the year, then our sample size will become large and we will increase the probability of equal detection for rare species. Under those new conditions, the Chao2 value will become an unbiased, point estimator of true species richness. And, the combination of these efforts will force the species accumulation curve to an asymptote.

Our knowledge of the Dryopoidea of Panama is still at the rudimentary level. Judging by the first, rough estimate ( $n=219$  species) of species richness using Chao2, there remains much work to simply collect and identify the predicted 92 undetected species that are potentially present in the country. In the process, we will also gain insight into the surficial and elevational distribution of the frequently collected species. However, given the results to date, we suspect that the potential, and so far, undetected species will be infrequently collected, thus requiring more of an effort than has been expended to date. Sampling of many different and new habitats and multiple sampling events throughout the year will be necessary. Although many of the beetles in this superfamily come to lights, other collecting methods will need to be employed to capture those which do not.

**Frequency of collection.** We are confident that increased collecting and identification will increase the extent of the x-axis in Fig. 3, as the frequently collected, wide-spread species with less restrictive niche requirements will be recorded repeatedly. A lower increase will occur for those species which are currently found in 1–3 locations due

to their currently perceived, narrow niche requirements. The lowest increase will represent currently undetected, perhaps rare, species which will be discovered in 1–2 locations in the future. Some species are rare for a reason, and no amount of collecting effort at new locations will change that. Exceptions to these assumptions will come from species which are collected (1) in heretofore, uncollected habitats; (2) in the many areas of Panama which have never been collected; (3) at atypical times of the year; or, (4) by utilizing novel or labor-intensive collecting methods.

## Encouragement of future taxonomists

**Synopsis of Collection and Curation Methods.** Given that one of the purposes of this paper is to provide information to students and others who might become interested in this group of beetles, we now provide some insight into collecting and curation for the various families of dryopoid beetles, either collectively or singly, found in Panama.

As stated in Brown (1972), aside from a few exceptions (some psephenids and any flightless species), most dryopoid adults can be effectively collected with various types of lights (fluorescent, ultra-violet, mercury vapor, etc.) employing flat, reflective surfaces (sheets, windows, siding, etc.) or with diverse types of traps. Generally, light trapping is affected by moon phase. We have found that the time period between the last quarter moon through to the first quarter new moon each month yields optimum results. Some taxa are more frequently captured during humid nights. For terrestrial taxa, pitfall traps and Berlese funnel extraction of ground litter can be useful as collecting methods. For aquatic taxa, kick sampling the substrate, especially when composed of cobbles, gravel and/or sand, can be highly productive. Hand collecting from rocks and searching for beetles embedded in stream litter (e.g. leaf packs and debris dams), utilizing a downstream net to collect specimens which float away or escape underwater, can often capture species which would otherwise be undetected. Sweeping vegetation with aerial nets along streams and lentic water bodies and vigorous agitation of submerged vegetation with dipnets are usually also productive. Finally, fogging of trees with pyrethroid-based chemicals can be counted on to yield taxa not collected by other means. A general survey of collecting beetles, including these families, can be found in Iannuzzi *et al.* (2021).

Except for integrative collecting techniques like those using lights, it is useful to know a bit about the habitat where adults of each family could be found (Brown 1972; Musgrave 1935a; Stribling 1986a): Callirhipidae—attracted to lights at night or found near submerged, rotten wood; Chelonariidae—sweeping vegetation or at lights; Cneoglossidae—found on surfaces near larval habitat, which are typically inside of rotting submerged wood; Dryopidae—just above waterline, in debris dams, or at lights; Elmidae—varies by genus, but includes on exposed or submerged rocks especially in riffles and rapids, on submerged wood or in debris dams or leaf packs, and on roots or leaves of submerged aquatic plants; Heteroceridae—burrowed in mud along the margins of streams, ponds, and lakes; Limnichidae—at or above waterline on rocks or wood; Lutrochidae—at water line or on submerged rocks and wood; Psephenidae—on rocks or wood above water, sometimes submerged; and, Ptilodactylidae—often collected at lights at night and on vegetation during the day.

Specimens collected can be killed and transported in 70-80% pure ethanol. Larvae can be exposed to boiling water for a few minutes before being placed in ethanol storage; aquatic larvae (i.e., Elmidae) can be placed directly in ethanol. Adults should be pinned, or point-mounted if small, after return to the laboratory and kept in Schmitt boxes, or similar containers, with either a moth ball or paradichlorobenzene present to avoid their consumption by dermestid beetles and other pests. In most cases, it is necessary to dissect the genitalia from adult male specimens to identify them to species, and females may be unidentifiable. A suggested method for this in beetles is provided by Skelley (1993). For additional curating techniques, explore:

[https://www.depts.ttu.edu/nsrl/collections/Invertebrate\\_Zoology/curation.php](https://www.depts.ttu.edu/nsrl/collections/Invertebrate_Zoology/curation.php)

**Literature Resources.** We offer the following literature citations for consideration by students getting involved in dryopoid taxonomy and research for the first time. Whereas this is not a comprehensive list of citations, it provides additional support and pathways for the serious student of this group.

**General**—Sharp 1882, 1887, 1902; Champion 1913; Blackwelder 1944; Brown 1972; Archangelsky *et al.* 2009; Passos *et al.* 2018; Short & White, 2019.

**Callirhipidae**—cedar beetles—Hajek 2011; Lawrence 2016; Young 2002.

**Chelonariidae**—turtle beetles—Méquignon 1934; Spangler 1980, 1991; Beutel & Leschen 2005 and Shepard 2016.

**Cneoglossidae**—cneoglossid beetles—Costa *et al.* 1999, 2016; Shepard 2016.

**Dryopidae**—long-toed water beetles—Brown 1981; Sharp 1887; Perkins & Spangler 1985; Perkins 1997; Kodada *et al.* 2016; Passos *et al.* 2018; Shepard 2020.

**Elmidae**—riffle beetles—Hinton 1934, 1940a, 1940b, 1940c, 1945, 1971; Brown 1981; Spangler & Santiago 1982; Manzo 2006; Segura *et al.* 2013; Jäch *et al.* 2016; Passos *et al.* 2018.

**Heteroceridae**—variegated mud loving beetles—Masacagni 1994; Katovich 2002; Skalický 2006, 2007, 2014; Sazhnev 2024 (preprint).

**Limnichidae**—minute mud beetles—Spilman 1959, 1966; Wooldridge 1975, 1976, 1978, 1979, 1980, 1981, 1982, 1983, 1986; Spangler 1982; Spangler *et al.* 2001; Arce-Pérez & Morón 2010; Shepard & Chaboo 2015.

**Lutrochidae**—travertine beetles—Maier & Short 2014; Maier 2016; Spangler *et al.* 2001; Shepard 2002; Shepard & Chaboo 2015).

**Psephenidae**—water pennies—Brown 1981; Arce-Pérez & Shepard 2001; Shepard & Barr 2014; Shepard & Chaboo 2015; Arce-Pérez *et al.* 2015, Arce-Pérez & Novelo-Gutiérrez 2017; Barr & Shepard 2017; Passos *et al.* 2018.

**Ptilodactylidae**—ptilodactylid beetles—Stribling 1986a, 1986b; Ivie 2002; Chatzimanolis *et al.* 2012; Shepard & Chaboo 2015; Kundrata *et al.* 2021; Fernandes *et al.* (2023).

## Survey problems

We have encountered various taxonomic problems during this work that should be addressed for future workers. First, is the lack of taxonomic keys for identification. In part, some of this is circumvented by excellent catalogs of various groups, such as the Callirhipidae, Heteroceridae and Limnichidae. Also, in some families, there are good identification keys at the genus-level, but not the species-level, a situation that results in fewer taxa being known to occur in Panama. Second, many genera have such an abundance of known, but as yet undescribed, species that species-level determinations are not likely to be accurate. This is especially true in the Elmidae. Again, this reduces the number of species known to occur in Panama. Third, many taxa known from Panama have old, brief, or poor descriptions so identifications to the species-level cannot reliably be made. This is especially prevalent in the Elmidae and Ptilodactylidae. Additionally, many Panamanian species have never had illustrations of the male genitalia produced so species-level identifications cannot be verified. Fourth, it may be impossible to track all who synonymized taxa, or transferred species to different genera. Nor can specific collection localities be determined for all Panamanian species listed in the literature. Additionally, many new Panamanian records may exist in various museums that have yet to be searched. Lastly, there is the problem that much of Panama has never been collected, especially at high elevations or in odd environments such as springs, leaf litter, marine beaches, etc. None of these problems are unique to Panama, but rather are what taxonomists have to deal with all over the world.

New students of this superfamily have to develop two collections for their studies: 1) a collection of specimens from all over Panama, and 2) a collection of the pertinent literature. Even then, early identifications are likely to be incorrect until sufficient experience with the taxa and their morphologies has been accrued. Building expertise with identifications is an iterative process requiring frequent checking on previous determinations as new experience and information is gained.

## *Future steps for a research program for dryopoids in Panama*

The following are general suggested steps for our work with dryopoid beetles in Panama.

1. Continue collecting and identification to further define Panama's dryopoid fauna;
2. Expand surficial and elevational collecting to define dryopoid distributions within Panama;
3. Initiate education and development of two to three entomologists to study this group of beetles over a long period of time; and,
4. Provide support for the scientific community concerning dryopoids in Panama through various means of dissemination (e.g., online databases, publications, workshops, and other means).

**Benchmark augmentation.** The original plan for this paper was to include habitus photographs for each genus and keys to families and genera. However, time and manuscript size became limiting factors. Therefore, we plan on producing a companion publication wherein these, and perhaps other, types of useful information will be included. The primary targets of such augmentation will be, of course, students and others new to this superfamily.

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## References

- Arce-Pérez, R. & Morón, M.Á. (2010) Lista anotada y clave para los géneros de la Familia Limnichidae (Coleoptera: Byrrhoidea) de México. *Dugesiana*, 17 (1), 1–8.
- Arce-Pérez, R. & Novelo-Gutiérrez, R. (2017) Two new species of *Psephenops* Grouvelle (Coleoptera: Byrrhoidea: Psephenidae) from Panamá. *Zootaxa*, 4323 (1), 109–118.  
<https://doi.org/10.11646/zootaxa.4323.1.8>
- Arce-Pérez, R. & Shepard, W.D. (2001) Sinopsis de la familia Psephenidae (Coleoptera: Dryopoidea) de Norte y Centroamérica. *Folia Entomológica Mexicana*, 40 (3), 397–406.
- Arce-Pérez, R., Novelo-Gutiérrez, R. & Cornejo, A. (2015) *Psephenops panamaensis* sp. nov. (Coleoptera: Byrrhoidea: Psephenidae) from Panamá. *Zootaxa*, 4052 (2), 233–236.  
<https://doi.org/10.11646/zootaxa.4052.2.8>
- Arce-Pérez, R., Arriaga-Varela, E., Cifuentes-Ruiz, P. & Escobar, F. (2014) Rediscover of the genus *Ersachus* in Veracruz, Mexico, with a description of the female of *Ersachus erichsonianus* Sharp (Coleoptera: Byrrhoidea: Limnichidae). *The Coleopterous Bulletin*, 68 (4), 765–769.  
<https://doi.org/10.1649/0010-065X-68.4.765>
- Archangelsky, M., Manzo, V., Michat, M.C. & Torres, P.L.M. (2009) Capítulo 14: Coleoptera. In: Domínguez, E. & Fernández, H.R. (Eds.), *Macroinvertebrados bentónicos sudamericanos: sistemática y biología*. Fundación Miguel Lillo, Tucumán, pp. 411–468.
- Armitage, B.J. & Harris, S.C. (2018) The Trichoptera of Panama VIII. The Hydroptilidae of Panama: current status, biodiversity comparisons, projections, and needs, *Aquatic Insects*, 39 (1), 65–84.  
<https://doi.org/10.1080/01650424.2018.1438629>
- Armitage, B.J., Harris, S.C., Ríos González, T.A., Aguirre, Y.P., Blahnik, R.J., Thomson, R.E. & Arefina-Armitage, T.I. (2024) The Trichoptera of Panama XXVII. The third benchmark—a waypoint to the future. In: Lipińska, M., Lopez-Selva, M.M. & Sierra, J.M. (Eds.), Biodiversity research in Central America. *Neotropical Biology and Conservation*, 19 (2), 203–241.  
<https://doi.org/10.3897/neotropical.19.e113487>
- Armitage, B.J., Andersen, T., Gilka, W., Sánchez, K.C., Ríos González, T.A. & Aguirre E., Y.P. (2025) The Diptera of Panama. II. A first benchmark for the family Chironomidae. *Zootaxa*, 5613 (2), 201–240.  
<https://doi.org/10.11646/zootaxa.5613.2.1>
- Barr, C.B. & Shepard W.D. (2017) *Eubria mesoamericana* Barr and Shepard (Coleoptera: Psephenidae: Eubriinae), a new psephenid species from Central America with an enigmatic generic distribution. *The Coleopterists Bulletin*, 71 (33), 437–444.  
<https://doi.org/10.1649/0010-065X-71.3.437>
- Barr, C.B. & Shepard, W.D. (2020) Hiding in plain sight: rediscovery and review of *Parygrus* Erichson, 1847, with description of five new species from the Neotropics (Coleoptera: Byrrhoidea Dryopidae). *Zootaxa*, 4755 (1), 99–128.  
<https://doi.org/10.11646/zootaxa.4755.1.4>
- Beutel, R.G. & Leschen, R.A.B. (2005) 18.10 Chelonariidae Blanchard, 1845. In: Beutel, R.G. & Leschen, R.A.B. (Eds.), *Handbook of Zoology. Vol. IV. Pt. 38. Coleoptera, Beetles. Vol. 1. Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. Walter de Gruyter, Berlin, pp. 543–546.
- Blackwelder, R.E. (1944) Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America,

- Part 2. *United States National Museum Bulletin*, 185, 189–341.  
<https://doi.org/10.5479/si.03629236.185.2>
- Brown, H.P. (1970) *Neocylleopus*, a new genus from Texas and Central America. *The Coleopterists Bulletin*, 24 (1), 1–28.  
<https://doi.org/10.5962/p.372533>
- Brown, H.P. (1972) Aquatic dryopoid beetles (Coleoptera) of the United States. *Biota of Freshwater Ecosystems Identification Manual. No. 6. Water Pollution Conference Series*. United States Environmental Protection Agency, Washington, D.C., 82 pp.  
<https://doi.org/10.5962/bhl.title.4106>
- Brown, H.P. (1981) A distributional survey of the world genera of aquatic dryopoid beetles (Coleoptera: Dryopidae, Elmidae, and Psephenidae sens. lat.). *Pan-Pacific Entomologist*, 57 (1), 133–148.
- Brown, H.P. (1984) Neotropical Dryopoids, III. Major Nomenclatural Changes Affecting *Elsianus* Sharp and *Macrelmis* Motschulsky, with Checklists of Species (Coleoptera: Elmidae: Elminae). *The Coleopterist Bulletin*, 38 (2), 121–129.
- Casey, T.L. (1889) Coleopterological notices I. With an appendix on the Termitophilous Staphylinidae of Panama. *Annals of the New York Academy of Sciences*, 5, 39–198.  
<https://doi.org/10.1111/j.1749-6632.1890.tb57003.x>
- Champion, G.C. (1896) Family Rhipidoceridae, In: *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. III. Part 1. Serricornia (1882–1897)*, pp. 574–586.
- Champion, G.C. (1897) *Biologia Centrali-Americana, Insecta, Coleoptera (Dascillidae). Vol. 3. Pt. 1*. Published for the editors by R. H. Porter and Dulau & Co., London, 77 pp. [pp. 586–662]
- Champion, G.C. (1913) Notes on various Central American Coleoptera, with descriptions of new genera and species. *Transactions of the Entomological Society of London*, 1913 (1), 58–169.  
<https://doi.org/10.1111/j.1365-2311.1913.tb02781.x>
- Chao, A. (1984) Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11, 265–270.
- Chao, A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, 43, 783–791.  
<https://doi.org/10.2307/2531532>
- Chao, A., Chiu, C.-H., Colwell, R.K., Magnago, L.F.S., Chazdon, R.L. & Gotelli, N.J. (2017) Deciphering the enigma of undetected species, phylogenetic, and functional diversity based on Good–Turing theory. *Ecology*, 98 (11), 2914–2929.  
<https://doi.org/10.1002/ecy.2000>
- Chatzimanolis S., Cashion M.E., Engel M.S. & Falin Z.H. (2012) A new genus of Ptilodactylidae (Coleoptera: Byrrhoidea) in mid-Cretaceous amber from Myanmar (Burma). *Geodiversitas*, 34 (3), 569–574.  
<http://dx.doi.org/10.5252/g2012n3a6>
- Colwell, R.K. (2013) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 9*. (Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut. Available from: <https://purl.oclc.org/estimates> (accessed 7 April 2026)
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 345, 101–118.  
<https://doi.org/10.1098/rstb.1994.0091>
- Costa, C., Vanin, S.A. & Ide, S. (1999) Systematics and bionomics of Cneoglossidae with a cladistic analysis of Byrrhoidea sensu Lawrence and Newton (1995) (Coleoptera, Elateriformia). *Arquivos de Zoologia*, 35 (3), 231–300.  
<https://doi.org/10.11606/issn.2176-7793.v35i3p231-300>
- Costa, C., Vanin, S.A. & Ide, S. (2016) “Cneoglossidae Guérin-Ménéville, 1843: Coleoptera, Beetles”. In: Schmidt-Rhaesa, A. (Ed.), *Handbook of Zoology Online*. De Gruyter, Berlin and Boston, Massachusetts, pp. 629–631.
- Cranston, P.S. (1995). Introduction. In: Armitage, P.D., Cranston, P.S. & Pinder, L.C.V. (Eds.), *The Chironomidae. The biology and ecology of non-biting midges*. Chapman and Hall, London, Glasgow, Weinheim, New York, Melbourne and Madras, pp. 1–7.  
[https://doi.org/10.1007/978-94-011-0715-0\\_1](https://doi.org/10.1007/978-94-011-0715-0_1)
- Darlington, P.J. (1936) A list of the West Indian Dryopidae (Coleoptera), with a new genus and eight new species, including one from Colombia. *Psyche*, 43 (2–3), 65–83.  
<https://doi.org/10.1155/1936/73105>
- Emden, F. van (1926) Die Sandalidae (Col.) des Zoologischen Staatsinstituts und Zoologischen Museum zu Hamburg. (Zur Kenntnis der Sandalidae IV). *Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg*, 42, 30–36, pl. II.
- Fernandes, A.S., Polizei, T.T.S. & Casari, S.A. (2023) New species and immatures of the semiaquatic genus *Anchytarsus* Guérin-Ménéville, 1843 from Central Brazil (Coleoptera: Dryopoidea: Ptilodactylidae). *Biologia*, 78, 3441–3461.  
<https://doi.org/10.1007/s11756-023-01482-8>
- Good, I.J. (1953) The population frequencies of species and the estimation of population parameters. *Biometrika*, 40, 237–264.  
<https://doi.org/10.1093/biomet/40.3-4.237>
- Gotelli, N.J. & Chao, A. (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin, S.A., (Ed.), *Encyclopedia of Biodiversity. Vol. 5. 2<sup>nd</sup> Edition*. Academic Press, Waltham, Massachusetts, pp.

195–211.

<https://doi.org/10.1016/B978-0-12-384719-5.00424-X>

- Gotelli, N.J., Chao, A. & Colwell, R.K. (2024) Measuring and estimating species richness, taxonomic and phylogenetic diversity, and related biotic (dis)similarity indices from sampling data. In: Scheiner, S.M. (Ed.), *Encyclopedia of Biodiversity*. 3<sup>rd</sup> Edition. Vol. 5. Elsevier, Oxford, pp. 314–399.  
<http://dx.doi.org/10.1016/B978-0-12-822562-2.00104-3>
- Hajek, J. (2011) World catalogue of the family Callirhipidae (Coleoptera: Elateriformia), with nomenclatural notes. *Zootaxa*, 2914 (1), 1–66.  
<https://doi.org/10.11646/zootaxa.2914.1.1>
- Hincapié-Montoya, D.M., González-Rodríguez, L.M. & González-Córdoba, M. (2023) Estado actual del co-nocimiento de los coleópteros acuáticos en Colombia. *Caldasia*, 45 (3), 360–376.  
<https://doi.org/10.15446/caldasia.v45n3.104455>
- Hinton, H.E. (1934) Miscellaneous studies in the Helmidae (Dryopidae, Coleoptera). *Revista de Entomologia, Río de Janeiro*, 4 (2), 192–201.
- Hinton, H.E. (1936) Descriptions of new genera and species of Dryopidae (Coleoptera). *Transactions of the Royal Entomological Society*, 85 (18), 415–434.  
<https://doi.org/10.1111/j.1365-2311.1936.tb01018.x>
- Hinton, H.E. (1940a) A Synopsis of the Genus *Elmoparnus* Sharp (Coleoptera, Dryopidae). *The Entomologist*, 73, 183–189.
- Hinton, H.E. (1940b) A synopsis of the Brazilian species of *Neoelmis* Musgrave (Coleoptera, Elmidae). *Annals and Magazine of Natural History*, Series 11, 5, 129–153.  
<https://doi.org/10.1080/00222934008527033>
- Hinton, H.E. (1940c) A monographic revision of the Mexican water beetles of the family Elmidae. *Novitates Zoologicae*, 42, 217–396.
- Hinton, H.E. (1941) New genera and species of Elmidae (Coleoptera). *Transactions of the Royal Entomological Society of London*, 91 (3), 65–104.  
<https://doi.org/10.1111/j.1365-2311.1941.tb01044.x>
- Hinton, H.E. (1945) A synopsis of the Brazilian species of *Cylloepus* Er. (Coleoptera, Elmidae). *Annals and Magazine of Natural History*, Series 11, 12 (85), 43–67.  
<https://doi.org/10.1080/00222934508527487>
- Hinton, H.E. (1971) Some American *Austrolimnius* (Coleoptera: Elmidae). *Journal of Entomology*, Series B: Taxonomy, 40 (2), 93–99.  
<https://doi.org/10.1111/j.1365-3113.1971.tb00110.x>
- Holzenthal, R.W. & Calor, A.R. (2017), *Catalog of the Neotropical Trichoptera (Caddisflies)*, ZooKeys, 654, 1–566.  
<https://doi.org/10.3897/zookeys.654.9516>
- Iannuzzi, L., Liberal, C.N., Bezerra de Souza, T., Pellegrini, T.G., Siqueira da Cunha, J.C., Koroiva, R., Corrêa de Albuquerque, L.S., Costa, F.C., Salomão, R.P., Dália Maia, A.C. & Trevisan Leivas, F.W. (2021) Sampling Methods for Beetles (Coleoptera). In: Santos, J.C., Fernandes, G.W. (Eds.), *Measuring Arthropod Biodiversity*. Springer Nature Switzerland AG, Cham, pp. 125–185.  
[https://doi.org/10.1007/978-3-030-53226-0\\_6](https://doi.org/10.1007/978-3-030-53226-0_6)
- Ivie, M.A. (2002) Ptilodactylidae Laporte 1836. In: Arnett, R.H., Jr., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionidea*. CRC Press, New York, New York, pp. 135–136.
- Jäch, M.A., Kodada, J., Brojer, M., Shepard, W.D. & Ciampor, Jr., F. (2016) *World Catalogue of Insects. Vol. 14. Coleoptera: Elmidae and Protelmidae*. Brill, Leiden/Boston, 318 pp.  
<https://doi.org/10.1163/9789004291775>
- Katovich, K. (2002) 47. Heteroceridae MacLeay 1825. In: Arnett, R.H., Jr., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida, pp. 127–132.
- Kodada, J., Jäch, M.A. & Čiampor, F. (2016) 19.3 Dryopidae Bilberg, 1820 (1817). In: Beutel, R.G. & Leschen, R.A.B. (Eds.), *Coleoptera, Beetles. Vol. 1. Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. In: Beutel, R.G. & Kristensen, N.P. (Eds.), *Handbook of Zoology, Arthropoda: Insecta. 2<sup>nd</sup> Edition*. Walter de Gruyter, Berlin, pp. 590–602.  
<https://doi.org/10.1515/9783110373929>
- Kole, J.P. (2022) *Investigations into the West Indian Chelonarium (Coleoptera: Chelonariidae) and the Anthophagus (Coleoptera: Cryptophagidae) of Montana*. Unpublished Masters' Thesis, Montana State University, Bozeman, Montana, 107 pp.  
<https://doi.org/10.1515/9783110373929>
- Kundrata, R., Packova, G., Kairišs, K., Bukejs, A., Hoffmannova, J. & Blank, S.M. (2021) The first *Ptilodactyla* Illiger, 1807 (Coleoptera: Dryopoidea: Ptilodactylidae) described from Eocene Baltic amber. *Biology*, 10, 877.  
<https://doi.org/10.3390/biology10090877>
- Lawrence, J.F. (2016) “Callirhipidae Emden, 1924: Coleoptera, Beetles”. In: Schmidt-Rhaesa, A. (Ed.), *Handbook of Zoology Online*. De Gruyter, Berlin and Boston, Massachusetts, pp. 590–595.
- LeConte, J.L. (1879) The Coleoptera of the alpine Rocky Mountain Region. Part 11. *Bulletin of the U.S. Geological and*

*Geographical Survey of the Territories*, 5 (3), 499–520.

- López-Pérez, S., Zurita-García, M.L., Dominguez-León, D.E., González-Ramírez, M., Vega-Badillo, V., Ciruente-Ruiz, P. & Rodríguez-Mirón, G.M. (2020) First report of the genus *Clatodotoma* Westwood, 1837 (Coleoptera, Ptilodactylidae, Cladotominae) in Mexico. *Check List*, 16 (6), 1469–1473.  
<https://doi.org/10.15560/16.6.1469>
- Maier, C. (2016) *Phylogeny, Ecology, and Taxonomic Revision of the Travertine Beetles (Coleoptera: Lutrochidae)*. Unpublished Ph. D. Dissertation, University of Kansas, Lawrence, Kansas, 332 pp.
- Maier, C. & Short, A.E.Z. (2014) Review of the Lutrochidae (Coleoptera) of the Guianas and Lesser Antilles, with description of four new species. *Zootaxa*, 3895 (1), 58–72.  
<https://doi.org/10.11646/zootaxa.3895.1.3>
- Manzo, V. (2006) A review of the American species of *Xenelmis* Hinton (Coleoptera: Elmidae), with a new species from Argentina. *Zootaxa*, 1242 (1), 53–68.  
<https://doi.org/10.11646/zootaxa.1242.1.4>
- Mascagni, A. (1994) Descrizione di una nuova specie di *Tropicus* Pacheco dell Ecuador (Coleoptera: Heteroceridae). *Bollettino della Società Entomologica*, 126, 134–136. [in Italian]
- Méquignon, A. (1934) Les *Chelonarium* del'Amérique Continentale. *Annales de la Société entomologique de France*, 103, 199–256.
- Musgrave, P.N. (1935a) Notes on collecting Dryopidae (Coleoptera). *Canadian Entomologist*, LXVII (No. 3), 61–63.  
<https://doi.org/10.4039/Ent6761-3>
- Musgrave, P.N. (1935b) A synopsis of the genus *Helichus* Erichson in the United States and Canada, with description of a new species (Coleoptera: Dryopide). *Proceedings of the Entomological Society of Washington*, 27 (7), 137–145.
- Passos, M.I.S., Manzo, V. & Maier, C.A. (2018) Chapter 15.6. Families Dryopidae, Elmidae, and Psephenidae. In: Hamada, N., Thorp, J.H. & Rodgers, D.C. (Eds.), *Thorp & Covich's Freshwater Invertebrates. 4<sup>th</sup> Edition. Keys to Neotropical Hexapoda. Vol. III*. Academic Press, London, pp. 583–598.  
<https://doi.org/10.1016/B978-0-12-804223-6.00027-5>
- Perkins, P. D. (1997) *Momentum and Ghiselinius*, New Neotropical Genera of Humicolous Beetles with remarkable and divergent mouthparts (Coleoptera: Dryopidae). *Studies on Neotropical Fauna and Environment*, 32 (2), 100–117.  
<https://doi.org/10.1080/01650521.1997.9709611>
- Perkins, P. D. & Spangler, P. J. (1985) *Quadryops*, new genus, and three new species of arboreal Dryopidae (Insecta: Coleoptera) from Panama and Equador. *Proceedings of the Biological Society of Washington*, 98 (2), 490–510.
- Pic, M. (1922) Nouveautés Diverses. *Mémoires Exotico-Entomologiques*, 36, 1–32.
- Sampaio, B.H.L., Passos, M.I.S. & Ferreira, N. Jr. 2015. New species and new records of *Xenelmis* Hinton (Coleoptera: Elmidae) from Southeastern Brazil. *Zootaxa*, 3936 (1), 115–122.  
<https://doi.org/10.11646/zootaxa.3936.1.6>
- Sazhnev, A.S. (2024) Checklist of the Heteroceridae (Insecta: Coleoptera) of the world. *Preprint*. [1 January 2024]  
<https://doi.org/10.13140/RG.2.2.33704.26885>
- Segura, M. A., Dos Passos, M.I., Fonseca-Gessner, A.A. & Froehlich, C.G. (2013) Elmidae Curtis, 1830 (Coleoptera, Polyphaga, Byrrhoidea) of the Neotropical region. *Zootaxa*, 3731 (1), 1–57.  
<https://doi.org/10.11646/zootaxa.3731.1.1>
- Sharp, D. (1882) *Biologia Centrali-Americana, Insecta, Coleoptera, Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Heteroceridae, Parnidae, Georissidae, Cyathoceridae*, 1 (2), 1–114.
- Sharp, D. (1887) *Biologia Centrali-Americana, Insecta, Coleoptera, Pselaphidae, Scydmaenidae. Vol. 2. Pt. 1*. Published for the editors by R. H. Porter and Dulau & Co., London, 1–71.
- Sharp, D. (1902) *Biologia Centrali-Americana, Insecta, Coleoptera, Cryptophagidae, Lathridiidae, Mycetophagidae, Dermestidae, Byrrhidae. Vol. 2. Pt. 1*. Published for the editors by R. H. Porter and Dulau & Co., London, pp. 625–688.
- Shepard, W.D. (2002) Chapter 45. Lutrochidae Kasap and Crowson 1975. In: Arnett, R. H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2*. CRC Press, Boca Raton, Florida, pp. 123–124.
- Shepard, W.D. (2016) Beetles (Coleoptera) of Peru: A survey of families Chelonariidae Blanchard, 1845. *Journal of The Kansas Entomological Society*, 89 (3), 254–255.  
<https://doi.org/10.2317/0022-8567-89.3.254>
- Shepard, W.D. (2020) *Novopelmus* Shepard (Coleoptera: Byrrhoidea: Dryopidae), a new genus from Hispaniola, Great Antilles. *The Coleopterists Bulletin*, 74 (3), 619–625.  
<https://doi.org/10.1649/0010-065X-74.3.619>
- Shepard, W.D. & Barr, C.B. (2014) *Neoeubria inbionis* Shepard & Barr, a new genus and new species of Neotropical water penny beetle (Coleoptera: Psephenidae: Eubriinae), with a key to the adult Eubriinae of the Neotropical Zone. *Zootaxa*, 3811 (4), 553–568.  
<https://doi.org/10.11646/zootaxa.3811.4.7>
- Shepard, W.D. & Chaboo, C.S. (2015) Beetles (Coleoptera) of Peru: Beetles (Coleoptera) of Peru: A Survey of the Families Dryopidae, Limmichidae, Lutrochidae, Psephenidae, and Ptilodactylidae. *Journal of The Kansas Entomological Society*, 88 (2), 163–166.  
<https://doi.org/10.2317/kent-88-02-163-166.1>

- Shepard, W. D. & Leavengood, Jr., J.M. (2021) Redescription of *Chelonarium signatum* Dalman, 1824, with notes on its reproductive biology and occurrence in Paraguay (Coleoptera: Byrrhoidea: Chelonariidae). *The Coleopterists Bulletin*, 75 (2), 355–364.  
<https://doi.org/10.1649/0010-065X-75.2.355>
- Short, A.E.Z. & White, D.S. (2019) Chapter 21: Aquatic Coleoptera, In: Merritt, R.W., Cummins, K.W., Berg, M.B. (Eds.), *An Introduction to the Aquatic Insects of North America. 5<sup>th</sup> Edition*. Kendall Hunt Publishing Company, Dubuque, Iowa, pp. 791–908.
- Skalický, S. (2006) *Tropicus spangleri* sp. nov. from Costa Rica, Panama and Honduras. *Folia Heyrovskyana*, 14 (3), 105–108.
- Skalický, S. (2007) New species of Heteroceridae from the New World (Coleoptera: Heteroceridae). *Koleopterologische Rundschau*, 77, 171–178.
- Skalický, S. (2014) *Tropicus panamensis* sp. nov. and a new record of *Tropicus* Pacheco from Panamá (Coleoptera: Heteroceridae). *Acta Musei Moraviae, Scientiae Biologicae, Brno*, 99 (1), 65–67.
- Skelley, P.E. (1993) A method of genitalia preparation and dry preservation for Coleoptera. *Proceedings of the Entomological Society of Washington*, 95 (2), 131–138.
- Spangler, P.J. (1980) Chelonariid larvae, aquatic or not? (Coleoptera: Chelonariidae). *The Coleopterists Bulletin*, 34 (1), 105–114.
- Spangler, P.J. 1982. Coleoptera Limnichidae, In: Hurlbert, S.H. & Villalobos- Figueroa, A. (Eds.) *Aquatic Biota of Mexico, Central America and the West Indies*. San Diego State University, San Diego, California, pp. 374–376.
- Spangler, P.J. (1991) Chelonariidae (Dryopoidea). In: Stehr, F. (Ed.), *Immature Insects. Vol. 2*. Kendall/Hunt Publishing Co., Dubuque, Iowa, pp. 394–395.
- Spangler, P.J. & Perkins, P.D. (1986) A new species of aquatic beetle, *Elmoparnus jordanorum*, from Guyana (Coleoptera: Dryopidae). *The Coleopterists Bulletin*, 40 (4), 359–365.
- Spangler, P.J. & Perkins, P.D. (1989) A revision of the Neotropical aquatic beetle genus *Stenhelmoides* (Coleoptera: Elmidae). *Smithsonian Contribution to Zoology*, 479, 1–63, 262 figs.  
<https://doi.org/10.5479/si.00810282.479>
- Spangler, P.J. & Santiago, S. (1982) A New Species of Aquatic Beetle, *Disersus uncus*, from Costa Rica (Coleoptera: Elmidae: Larinae). In: Sato, M. (Ed.), *Special Issue to the Memory of Retirement of Emeritus Professor Michio Chūjō*. The Association of the Memorial Issue of Emeritus Professor M. Chūjō, Nagoya Women's University, Nagoya, pp. 17–20.
- Spangler, P.J. & Santiago, S. (1987) A revision of the Neotropical aquatic beetle genera *Disersus*, *Pseudodisersus* and *Potamophilops* (Coleoptera: Elmidae). *Smithsonian Contributions to Zoology. No. 446*. Smithsonian Institution Press, Washington, D.C., 40 pp.  
<https://doi.org/10.5479/si.00810282.446>
- Spangler, P.J. & Santiago-Fragoso, S. (1992) *The aquatic beetle subfamily Larinae (Coleoptera: Elmidae) in Mexico, Central America and the West Indies. Smithsonian Contributions to Zoology. No. 528*. Smithsonian Institution Press, Washington, C.D., 74 pp.  
<https://doi.org/10.5479/si.00810282.528>
- Spangler, P.J., Staines, C.L., Spangler, P.M. & Staines, S.L. (2001) A checklist of the Limnichidae and Lutrochidae (Coleoptera) of the world. *Insecta Mundi*, 15 (3), 151–165.
- Spilman, T.J. (1959) A study of the Thaumastodinae, with one new genus and two new species (Limnichidae). *The Coleopterists Bulletin*, 13 (4), 111–122.  
<https://doi.org/10.5962/p.372204>
- Spilman, T.J. (1966) A new species of *Martinius* from Cuba (Coleoptera: Limnichidae). *Coleopterist Bulletin*, 20 (4), 123–125.  
<https://doi.org/10.5962/p.372386>
- Stribling, J.B. (1986a) *World generic revision of Ptilodactylidae (Coleoptera: Dryopoidea) and a key to the New World genera of Ptilodactylidae*. PhD Thesis, Ohio State University, Columbus, Ohio, 200 pp.  
<https://doi.org/10.1093/aesa/79.1.219>
- Stribling, J.B. (1986b) Revision of *Anchytarsus* (Coleoptera: Dryopoidea) and a key to the New World genera of Ptilodactylidae. *Annals of the Entomological Society of America*, 79, 219–234.  
<https://doi.org/10.1093/aesa/79.1.219>
- Wooldridge, D.P. (1975) A key to the New World genera of the beetle family Limnichidae. *Entomological News*, 86 (1–2), 1–4.
- Wooldridge, D.P. (1976) New World Limnichinae I: A revision of the genus *Physemus* LeConte (Coleoptera: Limnichidae). *Coleopterists Bulletin*, 30 (2), 177–182.  
<https://doi.org/10.5962/p.371969>
- Wooldridge, D.P. (1978) New World Limnichinae IV. *Eulimnichus* Casey. A. Synonymies, lectotype designations, and redescriptions (Coleoptera: Limnichidae),” *The Great Lakes Entomologist*, 11 (3), 163–173.  
<https://doi.org/10.22543/0090-0222.1338>
- Wooldridge, D.P. (1979) New World Limnichinae IV. *Eulimnichus* Casey. B. Descriptions of new species (Coleoptera: Limnichidae). *Great Lakes Entomologist*, 12 (1), 1–11.

<https://doi.org/10.22543/0090-0222.1349>

- Wooldridge, D.P. (1980) New World Limnichinae V. *Corrinea*, a New Neotropical Genus (Limnichidae). *The Coleopterists Bulletin*, 34 (1), 69–78.
- Wooldridge, D.P. (1981) New World Limnichinae VI. A Revision of *Limnichoderus* Casey (Coleoptera: Dryopoidea: Limnichidae). *Journal of the Kansas Entomological Society*, 54 (1), 171–191.  
<http://www.jstor.org/stable/25084144>
- Wooldridge, D.P. (1982) New World Limnichinae VII: *Phalacrachus* Sharp—A recharacterization and eight new species (Coleoptera: Dryopoidea: Limnichidae). *Coleopterists Bulletin*, 36 (2), 381–389.
- Wooldridge, D.P. (1983) New World Limnichinae VIII. *Paralimnichus* Delhve (Coleoptera: Dryopoidea: Limnichidae). *Journal of the Kansas Entomological Society*, 56 (2), 232–233.
- Wooldridge, D.P. (1986) Four new Neotropical *Cephalobyrrhinus* Pic (Coleoptera: Dryopoidea: Limnichidae). *Journal of the New York Entomological Society*, 94 (4), 512–515.
- Young, D.K. (2002) “Family 52: Callirhipidae Emden, 1924”. In: Arnett, R.H. Jr., Thomas, M.C., Skelley, P.E., Frank, J.H. (Eds.), *American Beetles. Vol. II. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida, pp. 144–145. [ISBN 978-0-8493-0954-0]