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Cover image

Farallon Islands
See G. C. Williams & O. Breedy, New species of Whip-Like Gorgonian Coral in the Genus *Swiftia* from the Gulf of the Farallones, California
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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Species of Whip-Like Gorgonian Coral in the Genus *Swiftia* from the Gulf of the Farallones in Central California, with a Key to Eastern Pacific Species in California (Cnidaria, Octocorallia, Plexauridae)

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A new species of plexaurid gorgonian coral in the genus *Swiftia*, collected by Remotely Operated underwater Vehicle, is described from the Greater Farallones National Marine Sanctuary near the Farallon Islands off the coast of central California. The species is unlike other species of *Swiftia* in that it is whip-like and unbranched or Y-shaped with two terminal branches. The genus *Swiftia* has a wide geographic distribution – not associated with coral reefs — it is known from the eastern Pacific and the western and eastern Atlantic, as well as parts of the Indo-West Pacific, from mesophotic depths and in deeper water.

KEYWORDS: Alcyonacea, *Swiftia*, plexaurid gorgonian, central California, Farallon Islands, outer continental shelf, taxonomic key to local species.

A previously undescribed species of the gorgonian genus *Swiftia* was recently encountered during an exploratory survey by Remotely Operated underwater Vehicle (ROV) on board the National Oceanic and Atmospheric Administration (NOAA) ship R/V *Fulmar* in the then proposed expansion area of the Gulf of the Farallones National Marine Sanctuary (now known as the Greater Farallones National Marine Sanctuary) off the Sonoma County coast of northern California, USA. A single whole colony was collected by ROV, which is here designated as the holotype specimen.

The gorgoniid genus *Swiftia* Duchassaing & Michelotti, 1864 is comprised of 15 currently recognized species, widely-distributed in the eastern Pacific — the western Atlantic, the northeastern Atlantic, the northern Pacific, and the Indo-Pacific (Ofwegen 2015; Breedy et al. 2015). The new species described here makes a total of 16 species currently recognized as valid that comprise the genus.

Most species of *Swiftia* vary in depth from approximately 70–732 m with a few species recorded from as shallow as 18–30 m (Breedy et al. 2015) and as deep as at least 1829 m (Goldberg 2001; and CASIZ collections data base).

Materials and Methods

The material examined in this study is housed in the collections of the Department of Invertebrate Zoology and Geology at the California Academy of Sciences (CASIZ), San Francisco. *In situ* photographs were taken by Peter Etnoyer during the NOAA ROV cruise on board RV *Fulmar* in the Greater Farallones NMS (National Oceanic and Atmospheric Administration 2014), approximately 70 miles NW of the Farallon Islands (Fig. 1), on 6 September 2014. Photographs of preserved material were taken by the authors at the California Academy of Sciences in September of 2015. The holotype was collected by ROV at 182 m in depth. Abbreviations used in the text are: CASIZ (California Academy of Sciences, Department of Invertebrate Zoology), GFNMS (Gulf of the Farallones National Marine Sanctuary), NOAA (National Oceanic and Atmospheric Administration), and ROV (Remote Operational Vehicle).

Definitions recognized in this paper for depth zones of benthic faunal communities are as follows: shallow-water (< 40 m), mesophotic (40–150 m), and deep-water (> 150 m).

Figure 1. The Farallon Islands, approximately 40 miles west of San Francisco, California, and 70 miles southeast of the type locality of *Swiftia farallonesica* sp. nov., in the Greater Farallones National Marine Sanctuary.

Systematic Account

Subclass Octocorallia
Order Alcyonacea Lamouroux, 1812
Family Plexauridae Gray, 1859

Swiftia Duchassaing and Michelotti, 1864

Swiftia Duchassaing and Michelotti, 1864:13; Kükenthal, 1924:236; Deichmann, 1936:185–186; Bayer, 1956:F206; Bayer, 1981:945; Harden, 1979:109–110; Breedy, et al., 2015:329.
Stenogorgia Verrill, 1883:29 (see Kükenthal, 1924:347 for *Stenogorgia* synonymy).
Platycaulos Wright and Studer, 1889:61: Bayer, 1981:945.
Callistephanus Wright and Studer, 1889:62: Bayer, 1981:945.
Allogorgia Verill, 1928:7; Bayer, 1981:945.

Generic diagnosis.— Colonies unbranched, or sparsely to copiously branched. Branches mostly free or with some anastomoses. Polyp mounds conical, prominent, or slightly raised, scattered or crowded, usually biserial or present on all sides of polyp-bearing branches. Anthocodiae with points arrangements of straight to curved bar-like rods, or frequently elongate tuberculated spindles.

Type species.— *Swiftia exserta* (Ellis and Solander, 1786)

***Swiftia farallonesica* Williams and Breedy, sp. nov.**
Figures 1–9.

Leptogorgia, National Oceanic and Atmospheric Administration, 2014:1–2.

Holotype.— CASIZ 196930.

Type locality (Figs. 8–9).— Deep-sea rocky substrata at Football Shoal, Greater Farallones National Marine Sanctuary, off Bodega Bay, California, USA (38.00°26.33′N 123.00°34.19′W); 182 m depth; 06 September 2014; Gary Williams and Peter Etnoyer; one entire specimen collected by ROV.

Habitat and distribution.— Found on hard, rugose, horizontal substrata composed of relatively dense congregations of detritus-covered rounded boulders between 181 and 190 m depth, at the type locality and vicinity (Figs. 8–9). Pink and white ophiuroids (species unidentified) were observed (on the holotype and by underwater video and still imagery) attached along portions of the lengths of several colonies (Figs. 2A & D, 3A & E). Approximately 15–20 colonies were observed in total by underwater video and still photography.

Etymology.— The specific epithet is derived from the Spanish *farallón* (steep rock, cliff, headland, outcrop), and the Latin *-icus* (suffix meaning belonging to); referring to the region of the discovery of the new species — the Greater Farallones National Marine Sanctuary.

Description of the Holotype

External morphology (Figs. 2–3).— The proximal-most surface of the holdfast that adheres to the substratum is circular, approximately 10 mm in diameter and 2 mm in height. The colony is unbranched and whip-like, 378 mm in length by 3–4 mm in width. The external surface of the colony is pustular in appearance with retracted polyps forming low mounds on all sides of the branches, from the holdfast to the apex of the colony. Each protuberance is approximately 2.0

mm in diameter at their bases and 0.8–1.0 mm in height. There are approximately 25–30 polyps per every 10 mm along the length of the colony. Many of the polyps throughout the colony are entirely retracted, while others are preserved in varying states of partial retraction.

Sclerites (Figs. 4–7).— The sclerites of the polyp mounds and coenenchyme are predominantly double discs and disc spindles 0.05–0.08 mm in length (Fig. 4), eight-radiates 0.04–0.12 mm long (Fig. 5), and spindles and girdled spindles (0.08–0.20 mm in length). Some girdled spindles are wider toward one end compared to the opposite end, and thus appear somewhat club-shaped in overall appearance (Fig. 6). Sclerites of the anthocodiae are mostly elongated rods with parallel sides and are variably tuberculated, 0.09–0.21 mm long (Fig. 7). All sclerites in the colony are colorless.

Color (Figs. 2–3).— The color of the holotype is white throughout, both in life and wet-preserved.

Remarks (Figs. 2–3).— All colonies observed are whip-like and unbranched, except for one colony that was recorded by underwater still imagery and is Y-shaped with a single lateral branch (Fig. 3C). All colonies that were observed by underwater video or still imagery are also uniformly white in color (Fig 3A–E).

Discussion and Conclusion

Key to *Swiftia* species in California

1a. Colonies multiply-branched 2
1b. Colonies unbranched (flagelliform, whip-like),or Y-shaped with a single branch; with low polyp mounds distributed on all sides of branches; colonies pure white in color. . . . . ***Swiftia farallonesica* Williams and Breedy, sp. nov.**

2a.Colonies mostly dichotomously branched, somewhat fan-shaped; with low polyp mounds distributed on all sides of branches; colonies pink to bright coral red in color . . . . *Swiftia spauldingi* (Nutting, 1909)
2b.Colonies densely branched with prominent polyp mounds distributed biserially along branches; colonies red with deep red polyp mounds . . . . *Swiftia kofoidi* (Nutting, 1909)

Taxonomic Assessment

Swiftia is one of 43 currently recognized genera in the gorgonian family Plexauridae (Williams and Cairns 2015). Plexaurids are characterized by a darkly colored axis (black or brown), which is composed of a cortex of proteinaceous material (gorgonin) with spaces (loculi) that are sometimes filled with lighter calcified material. The central core of the axis is hollow and cross-chambered (Fabricius and Alderslade 2001:59; Williams 2005:54, Fig. 1).

The genus *Swiftia* is distinguished by the following combined set of characters: coenenchymal sclerites are largely capstans, many of which are modified to a lesser or greater degree as discs; polyp mounds low-rounded to cylindrical or conical, slightly raised to prominent; anthocodiae contain relatively large, conspicuously tuberculated rods (based on Bayer 1981:932).

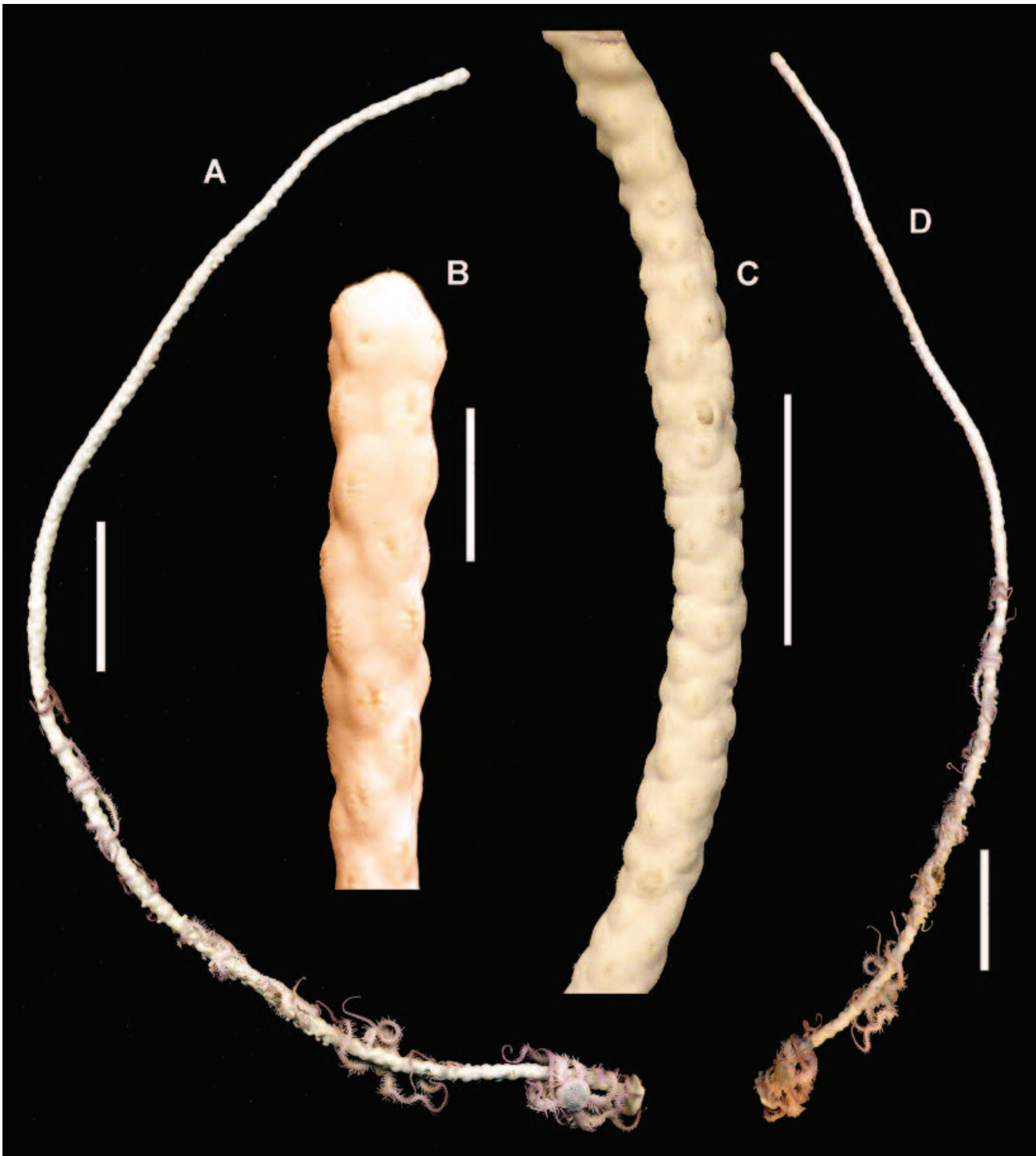

FIGURE 2. *Swiftia farallonesica* sp. nov. Wet-preserved holotype. A, D. Entire colony, scale bars = 10 mm. B. Distal apex region, scale bar = 5 mm. C. Middle portion of colony, scale bar = 10 mm.

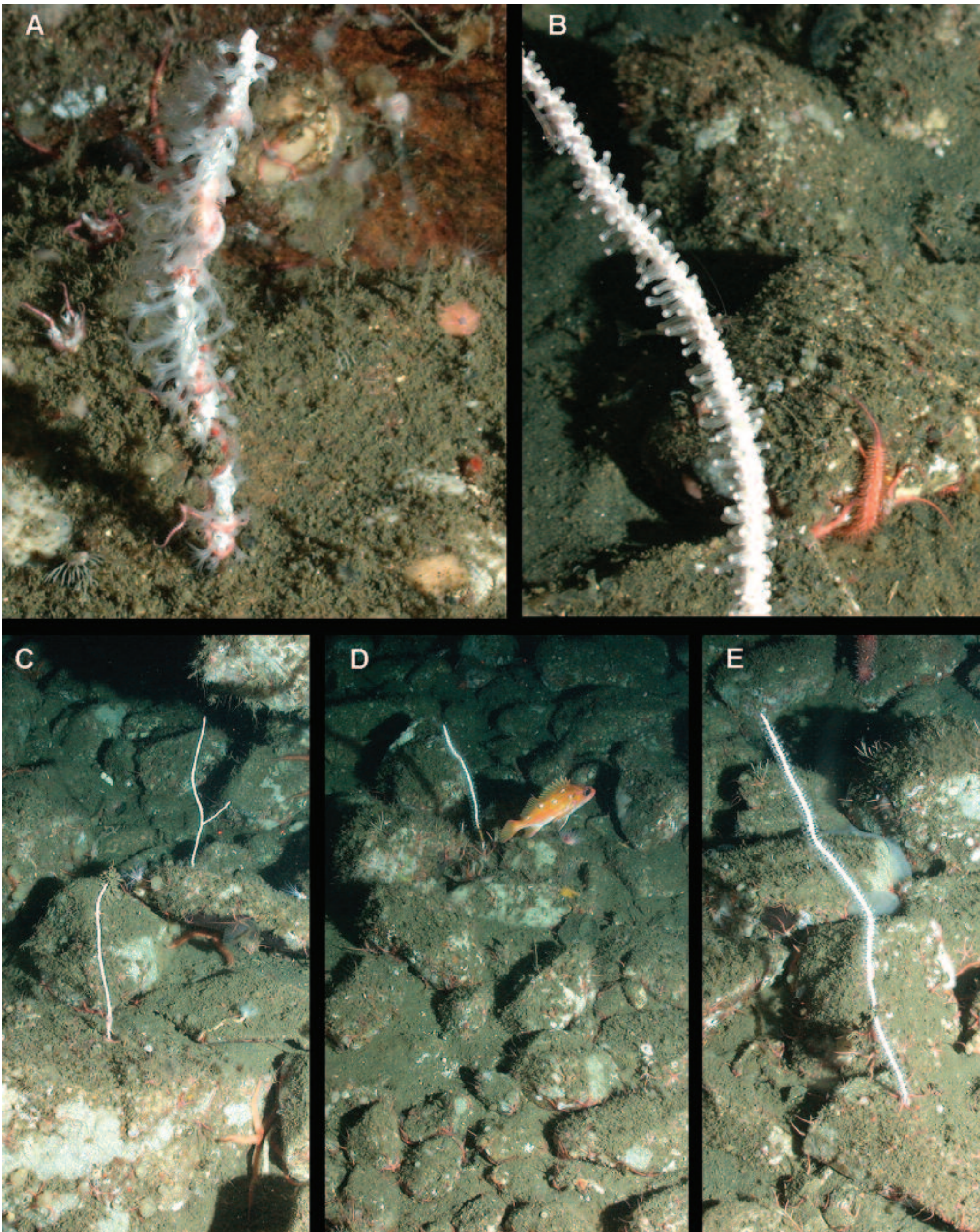

FIGURE 3. *Swiftia farallonesica* sp. nov. Underwater photographs taken *in situ* by ROV, between 181 and 190 m in depth, 6 September 2014.

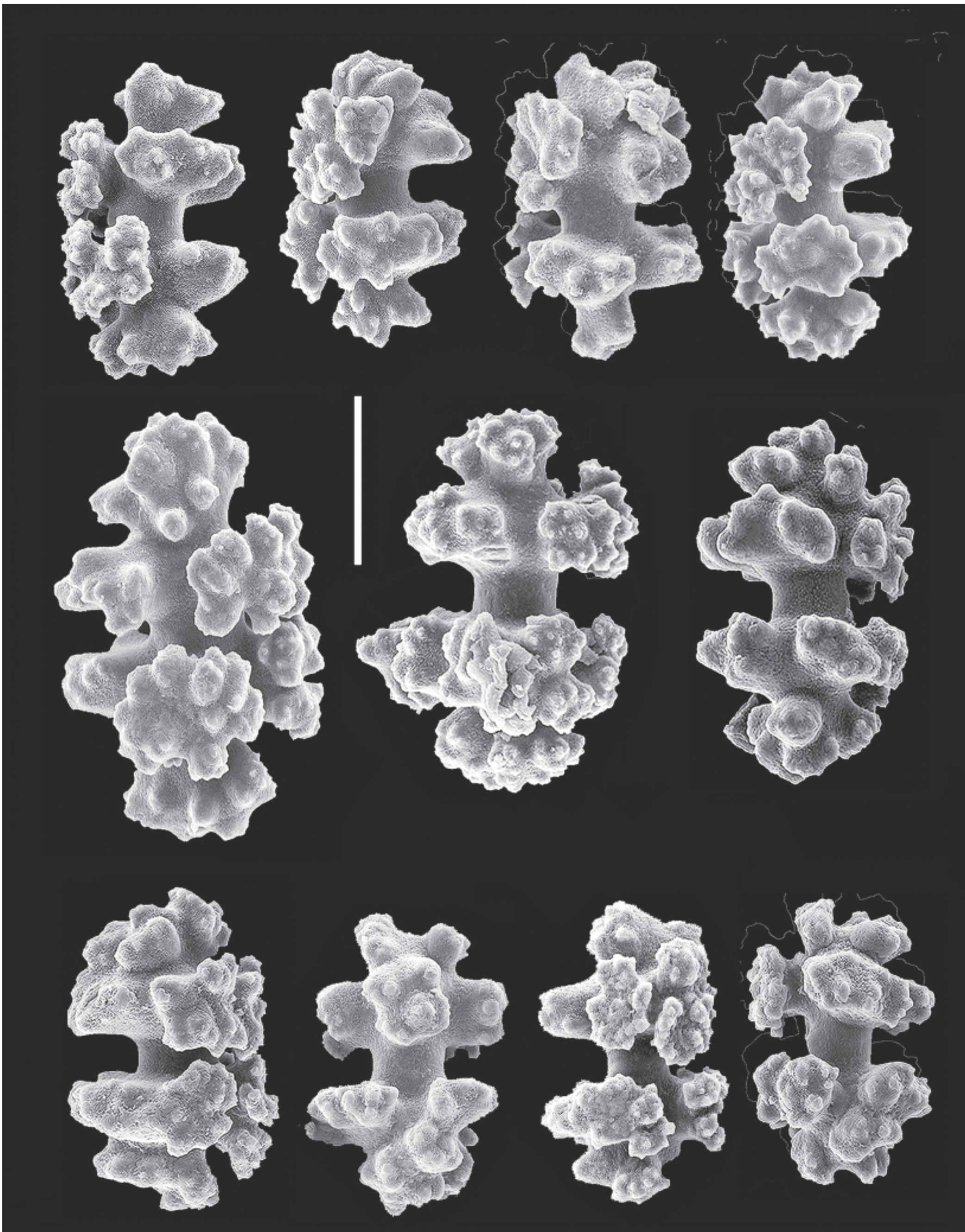

FIGURE 4. *Swiftia farallonesica* sp. nov. Scanning electron micrographs of coenenchymal sclerites — double discs and disc-spindles. Scale bar = 0.03 mm.

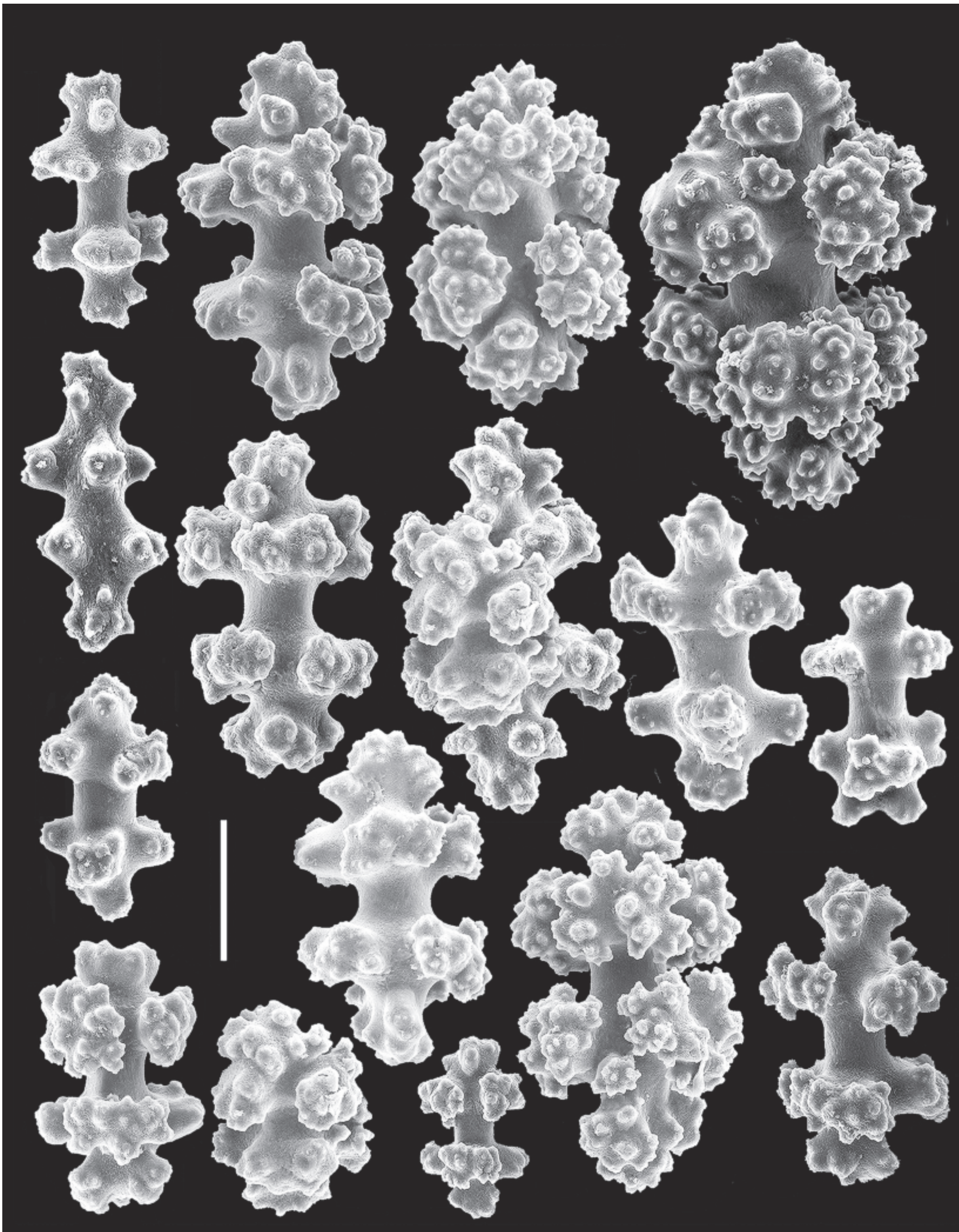

FIGURE 5. *Swiftia farallonesica* sp. nov. Scanning electron micrographs of coenenchymal sclerites — eight radiates. Scale bar = 0.03 mm.

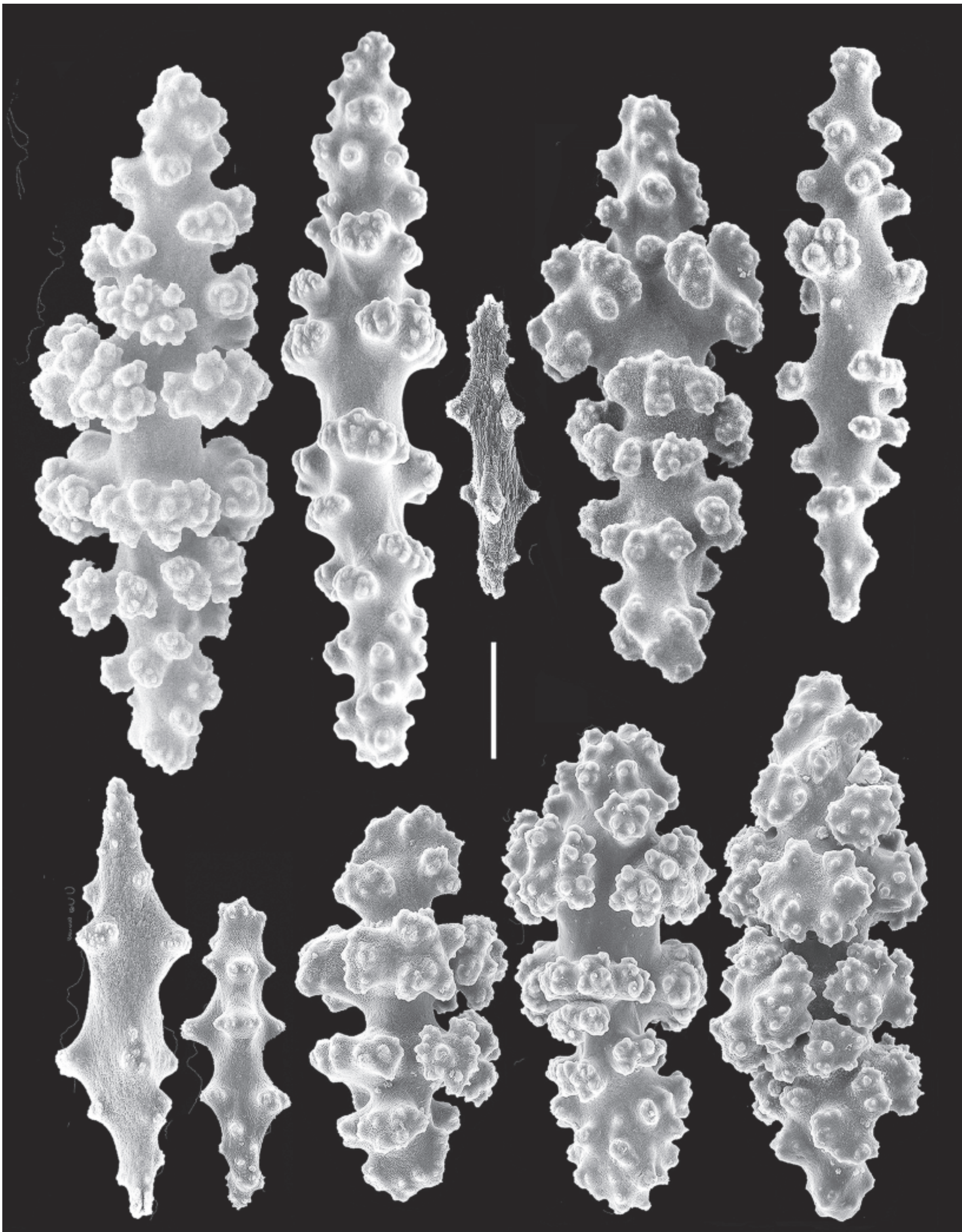

FIGURE 6. *Swiftia farallonesica* sp. nov. Scanning electron micrographs of coenenchymal sclerites — spindles. Scale bar = 0.03 mm.

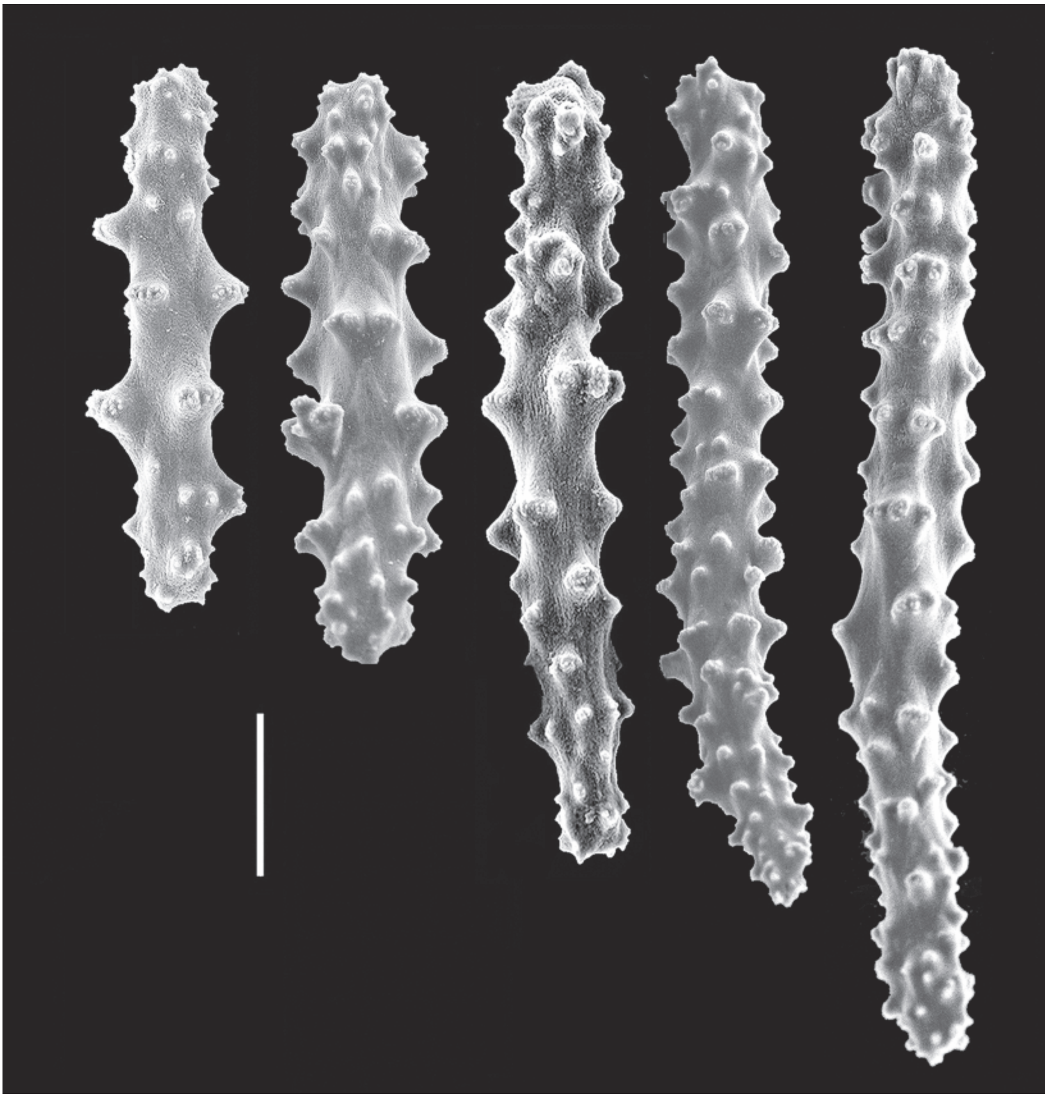

FIGURE 7. *Swiftia farallonesica* sp. nov. Scanning electron micrographs of anthocodial sclerites. Scale bar = 0.03 mm.

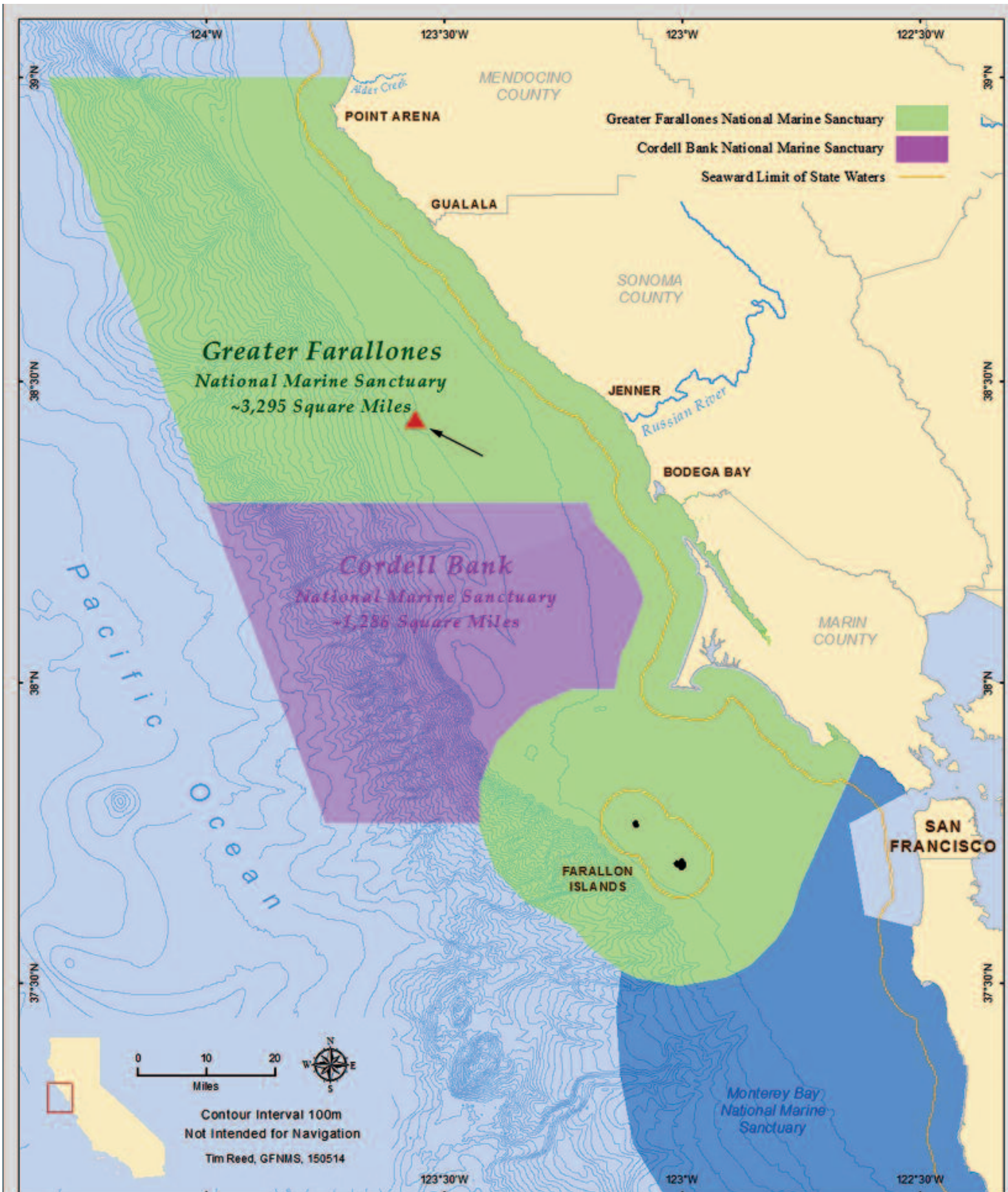

FIGURE 8. Map of the Greater Farallones National Marine Sanctuary (central California, USA), showing type locality of *Swiftia farallonesica* sp. nov. (represented by red triangle). Map modified from National Oceanic and Atmospheric Administration (2014).

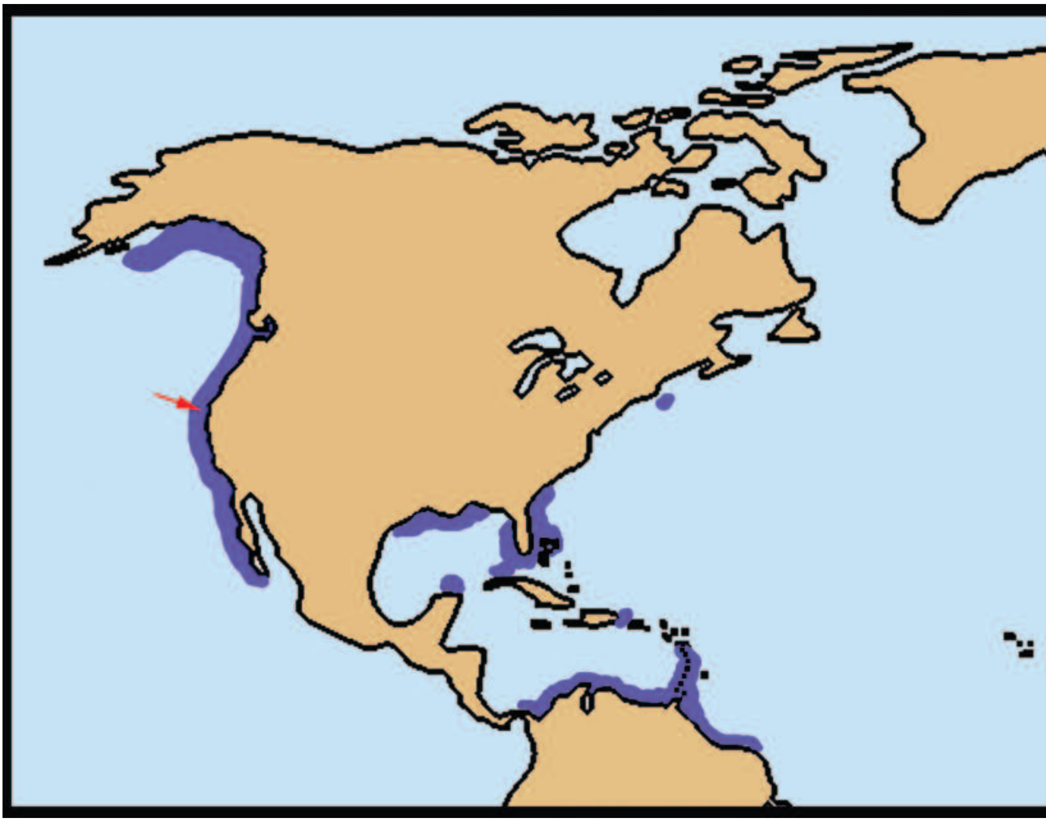

FIGURE 9. Map showing the known distribution of the genus *Swiftia* in North America and northern South America. Arrow shows type locality of *Swiftia farallonesica* sp. nov.

ACKNOWLEDGMENTS

We are indebted to the staff members of the Greater Farallones National Marine Sanctuary and the National Oceanic and Atmospheric Administration, for the opportunity to participate in ROV cruises on board R/V *Fulmar* in the GFNMS during 2012 and 2014. In particular, we thank Maria Brown, Danielle Lipski, Jan Roletto, Peter Etnoyer, and Dave Minard for their support. We are grateful to Jei-Ying Chen, California Academy of Sciences, for making many of the scanning electron micrographs, and Christina Piotrowski for curation of invertebrate material collected during the cruises.

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Herpetological Survey of Iona National Park and Namibe Regional Natural Park, with a Synoptic List of the Amphibians and Reptiles of Namibe Province, Southwestern Angola

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Namibe Province is the southernmost province of Angola and, as the result of several expeditions from the nineteenth century to the present, it is one of the most herpetofaunally well-known areas of the country. The Province harbors a high diversity of amphibians and reptiles, including roughly one-third of the reptile taxa reported for Angola as a whole. In this paper we present the results of a joint herpetological expedition to Namibe Province in 2013 by the California Academy of Sciences and the Instituto Nacionalda Biodiversidade e Áreas de Conservação, as well as a synoptic list of all the herpetological bibliographic records for the taxa known from the Province. A total of 37 herpetological taxa was collected, including at least three (then) undescribed species, two new country records, and new records for rarely cited taxa in Angola. These taxa belong to four amphibian genera and 15 reptile genera. Species accounts are provided for each of the species collected. We also highlight biogeographic patterns, conservation issues, and possible future paths for the exploration and knowledge of the herpetofauna of Namibe.

A província do Namibie situa-se no sudoeste de Angola e é uma das mais conhecidas relativamente à sua herpetofauna. Este conhecimento é resultado de várias expedições realizadas desde o século XIX até aos dias de hoje. A província alberga uma espetacular diversidade de anfíbios e répteis, que para estes ultímos representa aproximadamente a um terço dos taxa que ocorrem no país. Neste artigo apresentamos os resultados da expedição herpetológica levada a cabo pela California Academy of Sciences e o Instituto Nacional da Biodiversidade e Áreas de Conservação em 2013, bem como uma lista sinóptica de todos os registos bibliográficos para os taxa conhecidos na província. Um total de 37 taxa de anfíbios e répteis foram colectados, incluíndo pelo menos três espécies novas (uma já descrita e as outras em processo de descrição), dois novos registos de espécies para o país, bem como o registo de espé-

cies raramente citadas para o país. Estes taxa pertencem a 4 géneros de anfíbios e a 15 géneros de répteis. Todos os resultados são apresentados em fichas taxonómicas. São ainda apresentados algums comentários relativos a padrões biogeográficos e questões ligadas à conservação, e futuros caminhos para a exploração e conhecimento da herpetofauna da província do Namibe.

KEYWORDS: amphibians, Angola, biogeography, conservation, geographic distribution, Namibe Province, reptiles.

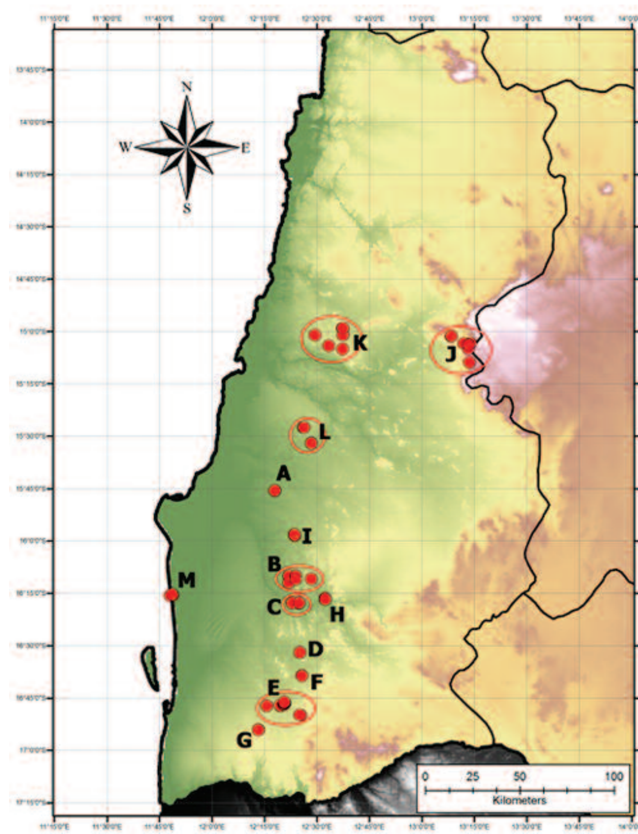

FIGURE 1. Map of the main sampled localities: A) Morro do Soba; B) Omauha Lodge; C) Rio Curoca; D) Entrada do Iona; E) Campo das espinheiras; F) Iona; G) Ford car Wreck; H) Pediva; I) Tambor; J) Serra da Leba; K) Pico do Azevedo; L) Caraculo; M) Praia do navio.

The current knowledge of Angola's herpetofauna is incomplete in contrast to neighboring countries such as Namibia (Herrmann and Branch 2013, Marques 2015). Namibe is Angola's southwesternmost province and is one of the better explored provinces in terms of herpetological diversity (Branch et al. 2014). Namibe Province occupies an area of 57,097 km^2 and is bordered by Huíla Province to the northeast, Cunene Province to the southeast, Benguela Province to the north, Namibia to the south, and the Atlantic Ocean to the west. The province is geographically separated from Huíla by the great escarpment of Serra da Leba and Chela, which separates the lower elevation areas of the Namib Desert from the Huíla Plateau. Topographically, the majority of the province has an elevation lower than 500 m, rising to 1500 m at the escarpment in the east. The highest elevation is at the Serra da Neve inselberg (2403 m) in north of the province, almost at the border with Benguela. The province has two main conservation areas – Iona National Park (INP), the largest conservation area in the country with an area 15,150 km^2, and the smaller Namibe Regional Natural Park (NNP), with an area of 4,450 km^2. Namibe lies within the African southwest arid biome, mainly comprising Kaokoveld desert, Namibian savanna, miombo woodlands, and mopane forest. The Kaokoveld desert, which extends along the coastal regions from southern Benguela Province to the Skeleton Coast in Namibia, is mostly dominated by sandy dunes and the occasional presence of *Odyssea paucinervis*, *Sporobolus spicatus*, and *Acanthosicyos horridus* dominated vegetation. The Namibian savanna woodlands in the central areas of the province are dominated by herbaceous plants of the genera *Aristida* and *Eragrostis*, dispersed shrubs of *Acacia*, *Commiphora* and *Combretum*, and, towards the southwest, extensive populations of *Welwitschia mirabilis*. The eastern portions of the province support smaller areas of Angolan mopane woodlands, which are dominated by the deciduous tree *Colophospermum mopane*, and Angolan miombo woodlands, which are dominated by *Brachystegia* trees, but also typified by *Isobertlinia angolensis*, *Julbernardia paniculata* and *Baikiaea plurijuga* (Grandvaux-Barbosa 1970). The province is bounded in the south by the Cunene (Kunene) River, and crossed by the Curoca and Giraul Rivers. Geologicaly, the south of the province is mostly dominated by schists, sometimes interspersed with granites, while the north of the province is mainly comprises granites (Anonymous 1963).

Approximately 16 species of amphibians and 95 species of reptiles are known from Namibe Province (Table 1). In separate works we are preparing a complete review of the diversity and distribution (including an annotated checklist) of the Angolan herpetofauna based published bibliographic records prior to 2014 (Marques et al., in prep.), and an annotated checklist of the herpetofauna of Namibe Province, based on bibliographic material, unpublished museum records, and recent collections (Branch et al., in prep). This paper presents the results of an expedition conducted by a team from the California Academy of Sciences (CAS), San Francisco (USA), Villanova University (VU), Villanova (USA), and the Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC), Kilamba-Kiaxi (Angola). A total of 37 herpetological taxa were collected, including at least three new species, one of which has recently been described (Stanley et al. 2016), two new country records and new records for taxa rarely cited for the country. We then provide a brief discussion of the present status and future prospects for the study of the herpetofauna of Namibe.

History of the Herpetological Exploration of the Province

Namibe Province was explored by several well documented expeditions in the nineteenth and twentieth centuries. The first herpetological surveys conducted were those of the Portuguese explorer José de Anchieta (1832–1897), who visited the region in the late nineteenth century. Anchieta's specimens were deposited in the Natural History Museum of Lisbon and largely studied by the Portuguese zoologist José Vicente Barbosa du Bocage (1823–1907), who published several papers on this material (e.g., Bocage 1867, 1873, 1896). Based on material from Anchieta, as well as others, Bocage described several herpetological taxa from Namibe Province, including Anchieta's Tree Frog, *Leptopelis anchietae* (Bocage, 1873), the Double-scaled Chameleon, *Chamaeleo anchietae* Bocage, 1872, Anchieta's Ground Agama, *Agama anchietae* Bocage, 1896, Anchieta's Shovel-snout Lizard, *Meroles anchietae* (Bocage, 1867), the Reticulate Sand Lizard, *Meroles reticulatus* (Bocage, 1867), the Speckled Sand Skink, *Trachylepis punctulata* (Bocage, 1872), the Speckled Western Burrowing Skink, *Typhlacontias punctatissimus* (Bocage, 1873), Anchieta's Worm-Lizard, *Monopeltis anchietae* (Bocage, 1873), a Skaapsteker, *Psammophylax occelatus* Bocage, 1873 (currently a synonym of the Spotted Skaapsteker, *Psammophylax rhombeatus* (Linnaeus, 1758)), a new variety of Striped Sand Snake, *Psammophis sibilans* var. *stenocephalus* (Bocage, 1877), and a new species of Giant Blind Snake, *Onychocephalus petersii* Bocage, 1873 that is currently considered a synonym of *Afrotyphlops schlegelii* (Bianconi, 1847).

At the dawn of the twentieth century, the Portuguese explorer Francisco Newton (1864–1909) collected herpetological specimens in the province for the Natural History Museum of the Polytechnic University of Porto, during a three year mission from 1903 to 1905, exploring the provinces of Kwanza-Norte, Kwanza-Sul and Namibe. The initial collections made by Newton in the two first provinces were studied and published upon by the Portuguese zoologist José Júlio Bettencourt Ferreira (1866–1948) on two different occasions (Ferreira 1906, 1906), but the Namibe Province material had remained unstudied until today (Ceríaco et al., in prep.). In 1925, the Vernay Angola Expedition explored central and southwestern Angola and collected specimens destined for the American Museum of Natural History. The herpetological results of this expedition were partly published upon by the American herpetologist Charles M. Bogert (1908–1992), in a paper dealing with the snakes (Bogert 1940). A second paper detailing the rest of the herpetological material collected on the expedition was never published. Some years later, two Swiss scientific expeditions to Angola, 1928–1929 and 1932–1933, led by the Swiss naturalist Albert Monard (1886–1952) also explored several locations in Namibe Province. The herpetological results of these expeditions were published in four different papers (Monard 1931, 1937a, b, 1938). In between the two Swiss expeditions, the Pulitzer-Carnegie Museum Expedition to Angola in 1930, led by influential American publisher Ralph Pulitzer (1879–1939) and conducted by Wilfrid Rudyerd Boulton (1901–1983) and his wife Laura Crayton Boulton (1899–1980), became one of the most important expeditions in terms of herpetological results. The material was studied and published upon by Karl Patterson Schmidt (1890–1957) in two papers — one dedicated to the reptiles (Schmidt 1933) and other to the amphibians (Schmidt 1936). These works resulted in the description of Pulitzer's Thick-toed Gecko, *Chondrodactylus pulitzerae* (Schmidt, 1933), Boulton's Namib Day Gecko, *Rhoptropus boultoni* Schmidt, 1933, and the Angolan endemic subspecies of White-Throated Monitor, *Varanus albigularis angolensis* Schmidt, 1933. More recently the Belgian herpetologist Raymond Laurent (1917–2005) published on a collection of amphibians and reptiles from Namibe (Laurent 1964) sent to him by the Portuguese entomologist and director of the former Museu do Dundo (northeast Angola), António Barros de Machado (1912–2002). This contribution was of uttmost importance for the knowledge of the southwestern Angolan herpetofauna. In addition to the several new taxa added to the list of the provincial herpetofauna, he described four new taxa endemic to the southwest of the country — Bogert's Speckled Western Burrowing Skink, *Typhlacontias bogerti* Laurent, 1964, Hellmich's Wolf Snake, *Lycophidion hellmichi* Laurent, 1964, and two Namib Day Geckos, *Rhoptropus taeniostictus* Laurent, 1964 and *R. boultoni montanus* Laurent, 1964. Wulf Haacke conducted the last systematic field surveys in the Portuguese colonial period in 1971 and 1974 and deposited his collections in the Ditsong National Museum of Natural History (TM) in Pretoria, South Africa, though this material has not been fully published upon. After independence in 1975, Angola entered a long period of civil war, which ended only in 2002. This prevented further field surveys and studies. In the past decade, several field surveys have been conducted, including in Namibe. Teams from the Porth Elizabeth Museum — Bayworld (PEM) prospected the province in three different expeditions so far, and a team from CAS, INBAC and VU conducted the survey reported in this paper. These expeditions have increased our knowledge of the southern Angolan herpetofauna, and since 2008 five new taxa from southwestern Angola (2008–2013) have been described — the Chela Mountain Reed Frog, *Hyperolius chelaensis* Conradie, Branch, Measey and Tolley, 2012, the Namib Spiny Tailed Gecko, *Afrogecko plumicaudus* Haacke, 2008, subsequently made the type species of the monotypic genus *Kolekanos* Heinicke, Daza, Greenbaum, Jackman and Bauer, 2014, Haacke's Sand Lizard, *Pedioplanis haackei* Conradie, Measey, Branch and Tolley, 2012, Huntley's Sand Lizard, *Pedioplanis huntleyi* Conradie, Measey, Branch and Tolley, 2012, and the Kaokoveld Girdled Lizard, *Cordylus namakuiyus* Stanley, Ceríaco, Bandeira, Valério, Bates and Branch, 2016 — all but the first endemic to Namibe Province.

Material and Methods

We conducted herpetological surveys in Namibe Province from 28 November to 11 December 2013, including both Iona National Park and Namibe Regional Natural Park. A total of 13 areas were surveyed (Fig. 1). In each area, we attempted to sample a combination of habitat types. Overall conditions during this fieldwork were hot and dry as this was an unusually dry year. We captured specimens using long-nooses, rubber bands, or by hand during both diurnal and nocturnal visual surveys. All specimens were euthanized following an approved IACUC protocol (#2014-2), preserved in 10% buffered formalin in the field, and then transferred to 70% ethanol for storage. Liver tissues were preserved in 95% ethanol and RNALateR. Voucher specimens and tissue samples are deposited in the herpetological collection of the California Academy of Sciences, with a subset of specimens deposited in the reference collection of INBAC. In some cases, we further confirmed species identifications by sequencing the mitochondrial 16S ribosomal RNA gene. As noted above, a complete list of all amphibians and reptile species reported from Namibe Province was assembled (Table 1). This list, including localities and associated bibliographic references was based on the ongoing project for the first atlas of the Angolan amphibians and reptiles (Marques 2015; Marques et al., in prep.). We do not include in the list unpublished museum records such as the large series in the Ditsong National Museum of Natural History collected by Wulf Haacke in the 1970s or the recent collections made by William R. Branch and Werner Conradie from the Port Elizabeth Museum (Bayworld). These specimens will be a part of a forthcoming publication (W.R. Branch, pers. comm.). However, museum material representing taxa vouchered on our expedition are noted when relevant in the species accounts.

Results

A total of 411 specimens were collected during the expedition, representing four amphibian genera and 15 reptile genera. In the following species accounts, we provide information on CAS voucher specimens, localities, and natural history. Latitude, longitude and elevation (in meters) of the collection site are provided in each species account. In addition, when appropriate, we provide brief taxonomic or geographic notes.

Species Accounts

Amphibia
Anura

Bufonidae

Hallowell's Toad
***Sclerophrys maculata* (Hallowell, 1854)**

Material.— Leba Pass, between river and highway, 5 December 2013, 15º04′13.2″S, 13º14′37.7″E, 1676 m (CAS 254877–254878).

Comments.— In Angola this species mostly occurs in the southwestern provinces of Namibe, Benguela, Bié, and Huíla (Marques 2015). The nearest records are in "Cainde" and "16 km W of Vila Nova" (Poynton and Haacke 1993; Ruas 1996, 2002). It is widespread in arreas to the south, including much of northern Namibia (du Preez and Carruthers 2009). Ohler and Dubois (2016) recently presented evidence identifying the type species of *Sclerophrys* Tschudi, 1838 as referable to *Bufo rangeri* Hewitt, 1935, thus making *Sclerophrys* the oldest available name for the clade of African toads recently referred to as *Amietophrynus* Frost et al., 2006.

Pyxicephalidae

Angola River Frog
***Amietia angolensis* (Bocage, 1866)**

Material.— Leba Pass, between river and highway, 5 December 2013, 15º4′12.2″S, 13º14′38.9″E, 1676 m (CAS 254876).

Comments.— This specimen represents the first record for the species for the province, although there are several records from the province of Huíla, in Boca de Humpata (Laurent 1964a; Ruas 1996; Channing and Baptista 2013), and Huila (Bocage 1895; Themido 1941; Perret 1976; Ruas 1996, 2002) less than 20 km east of Leba Pass. The species is widespread across the rest of the country (Marques 2015) as well as in much of the more mesic areas of southern Africa. In Namibia it occurs only where there are permanent rivers (du Preez and Carruthers 2009).

Damaraland Sand Frog
***Tomopterna damarensis* Dawood and Channing, 2002**

Material.— Pediva Hot Springs, 2 December 2013, 16º17′4.62″S, 12º33′47.86″E, 241 m (CAS 254855).

Comments.— The specimen was collected by locals on the border of the largest pond at Pediva Springs. The lower jaw is broken, but the specimen is otherwise in good condition. A dark pigmentation is visible along the jaw-line, which identifies the specimen as a male, as is common in the genus. Comparing our specimen to the recently described *Tomopterna damarensis* Dawood and Channing, 2002, from Damaraland, northwestern Namibia, it agrees with the smooth dorsum and most important morphological characters. Comparison of 16S mtDNA sequence to the type specimen confirms the identification of this specimen as *T. damarensis* (GenBank KU662310; p-distance from GenBank AY255091.1, the holotype of *T. damarensis*, is 0.7 %). Additional details on the distribution of the species in Angola and Namibia are being prepared for publication (M. Heinicke et al., in prep.). This is the first record of the species for the country, extending the range of the species considerably northwards from the type locality at Khorixas, Namibia (Dawood and Channing 2002).

Microhylidae

Marbled Rubber Frog – Fig. 2
***Phrynomantis annectens* Werner, 1910**

Material.— Omauha Lodge, 3 December 2013, 16º11′55.4″S, 12º24′0.3″E, 338 m (CAS 255056).

Comments.— Both this specimen and another now in the INBAC collections were collected inside a toilet water tank, one of few available sources of standing water in the area. These specimens represent the fourth record for the species in the country. The species reaches its northern distribution in Angola, in Novo Redondo/Gabela, Kwanza Sul Province (Poynton and Haacke 1993). *Phrynomantis annectens* has previously been recorded from the Mutiambo River and Caraculo in Namibe Province (Poynton and Haacke 1993). The current records represent the southernmost known distribution of the species in Angola, however it is common in Namibia and South Africa (Channing 2001; du Preez and Carruthers 2009) and is likely to occur throughout the province wherever water is available.

FIGURE 2. Marbled Rubber Frog, *Phrynomantis annectens* Werner, 1910, from Palmwag, Kunene Region, Namibia. Photo courtesy of Randall Babb.

Reptilia
Squamata

Agamidae

ANCHIETA'S GROUND AGAMA – Fig. 3
***Agama anchietae* Bocage, 1896**

MATERIAL.— INP, 29 November 2013, 16º39′27.12″S, 12º26′17.04″E, 459 m (CAS 254778); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254942); NNP, 28 November 2013, 15º46′27.4″S. 12º19′59.2″E, 264 m (CAS 254956).

COMMENTS.— These specimens have distinctive black-tipped spines on the palmar scales, which distinguish *A. anchietae* from the morphologically similar *A. aculeata* Merrem, 1820 that occurs sympatrically in Southern Angola and Namibia (Branch 1993). *Agama anchietae* was described from Angola by Bocage based on specimens from Catumbela, Benguela and Dombe (all in Benguela Province), and Moçamedes (currently Namibe, Namibe Province). In Angola, the species is known to occur in Namibe Province (Bocage 1896, 1897; Laurent 1964a), Benguela Province (Bocage 1863, 1896, 1897), and Bié Province (Schmidt 1933). Our specimens represent the southernmost localities of the species in Angola, although it is certainly distributed continuously across the entire province.

NAMIB ROCK AGAMA – Fig. 4
***Agama planiceps* Peters, 1862**

MATERIAL.— 'Lion Cave' at 3.4 km SW of Espinheira camp, 30 November 2013,

FIGURE 3. Anchieta's Ground Agama, *Agama anchietae* Bocage, 1866, from Sesfontein, Kunene Region, Namibia. Photo courtesy of Johan Marais.

FIGURE 4. Adult male Namib Rock Agama, *Agama planiceps* Peters, 1862, from Pico Azevedo. Photo by Luis Ceríaco.

16º48′45.0″S, 12º20′22.9″E, 463 m (CAS 254753); Omauha Lodge camp, 2 December 2013, 16º11′55.4″S, 12º24′0.3″E, 335 m (CAS 254832); INP, north of Tambor, 4 December 2013, 15º59′46.0″S, 12º24′24″E, 307 m (CAS 254839); INP, south side of Curoca River crossing, 29 November 2013, 16º18′15.6″S, 12º25′1.56″E, 209 m (CAS 254845), 1 December 2013, 16º18′14.8″S, 12º24′2159.8″E, 210 m (CAS 254848); Pediva Hot Springs, 2 December 2013, 16º7′19.7″S, 12º33′40.0″E, 244 m (CAS 254859); Namibe-Lubango road, road marker 59, 1.8 km west by road from Caraculo, north side of the road, 6 December 2013, 15º0′57.6″S, 12º38′36.8″E, 500 m (CAS 254900, CAS 254910); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254941).

Comments.— The species has been cited throughout Angola, although many previous records remain doubtful. *Agama planiceps* appears to be restricted to arid savannas and Namibe Province, or perhaps Beguela, is most probably its northernmost limit. Mertens (1938) described the subspecies *Agama planiceps shackii* from Cubal (Benguela Province), and it is likely that the central and northern Angolan records of *planiceps* are in fact *shackii*. The status of this form remains in question, but preliminary examination of topotypical material suggests that it is specifically distinct. Our specimens fit the morphological description and current known distribution of nominotypical *planiceps*. The species is cited for several localities in Namibe Province, including Biballa (Bocage 1895), Fazenda Bumbo (Laurent 1964a), and Pico Azevedo (Schmidt 1933). Some of our records represent a southern range extension of the species in the Province, although a record from the Kwito region, in Cunene Province (Angel 1923) is the southernmost Angolan record. The species likely also occurs in rocky areas extending south to the Namibian border. The majority of these specimens were seen basking on the top of rocks. Males and females present a striking sexual dimorphism, with the males being considerably larger than the females, and having an intensely red head and a dark blue body (the posterior half of the tail is usually also red). Females are typically dark-grey on the dorsum with yellow marking on the head and dorsum.

Gekkonidae

Fitzsimons' Thick-Toed Gecko – Fig. 5
***Chondrodactylus fitzsimonsi* (Loveridge, 1947)**

Material.— Espinheira, 30 November 2013, 16º47′14.3″S, 12º21′29.4″E, 457 m (CAS 254814); INP, north of Tambor, 4 December 2013, 15º59′46.9″S, 12º24′24″E, 300 m (CAS 254841).

Comments.— Only four records of this species are known for the country: Ongueria, 55 km from Sá da Bandeira (presently Lubango), in Huíla Province (Laurent 1964a), Praia das Conchas (Laurent 1964a), "around Moçâmedes in the road to Sá da Bandeira" (Laurent 1964a) and Pico Azevedo (Schmidt 1933), both in Namibe Province. Our records represent southern range extensions for the species in the country, although the species extends into west-central Namibia (Bauer et al. 1993). In both Namibia and Angola it can occur sympatrically with other, similarly sized congeners, but is generally more restricted to rocky habitats than either *C. pulitzerae* or *C. turneri.*

Pulitzer's Thick-Toed Gecko – Fig. 6
***Chondrodactylus pulitzerae* (Schmidt, 1933)**

Material.— INP, 9.65 km (by air) west-south-west of Espinheira, 30 November 2013, 16º48′43.19″S, 12º16′16.55″E, 488 m (CAS 254790–CAS 254792); Espinheira, 29 November 2013, 16º47′11.01″S, 12º21′28.77″E, 457 m (CAS 254796–254798), 16º47′8.1″S, 12º21′16.44″E, 457 m (CAS 254804, 30 November, 16º47′14.3″S, 12º21′29.4″E, 457 m (CAS 254814–254815), 16º47′15.1″S, 12º21′23.8″E, 457 m (CAS 254816), 16º47′14.0″S, 12º21′29.6″E, 457 m (CAS 254817), 16º47′17.3″S, 12º21′25.1″E, 457 m (CAS 254818), 16º47′11.1″S, 12º21′30.2″E, 457 m (CAS 254819); Omauha Lodge, 28 November 2013, 16º11′55.01″S, 12º24′3.12″E, 338 m (CAS 254830), 2 December 2013, 16º11′55.4″S, 12º24′0.3″E, 338 m (CAS 254833), 28 November 2013, 16º11′54.19″S, 12º24′2.45″E, 338 m (CAS 254843); INP, Rio Curoca in Pediva Hot Springs area, 3 December 2013, 16º17′0.93″S, 12º33′39.81″E, 247 m (CAS 254854); Namibe-Lubango road, road marker 59, 1.8 km west (by road) of Caraculo, on the north side of the road, 6 December 2013,

FIGURE 5. Adult male FitzSimons'Thick-toed Gecko, *Chondrodactylus fitzsimonsi* (Loveridge, 1947), from northern Kaokoveld, Kunene Region, Namibia. Photo courtesy of Johan Marais.

FIGURE 6. Subdult male Pulitzer'sThick-toed Gecko, *Chondrodactylus pulitzerae*. (Schmidt, 1933), from Chimalavera, Benguela Province, Angola. Photo by Luis Ceríaco.

15º0′57.3″S, 12º38′32.6″E, 497 m (CAS 254915); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254920, CAS 254943).

Comments.— This species occurs from the southern regions of Angola in Namibe (Bocage 1867, 1887, 1895; Laurent 1964a; Schmidt 1933) and Cunene (Monard 1937) provinces to Malange, where it reaches its northern distribution in Capanda (Ceríaco et al. 2014). There are records from the far northwest of Namibia as well, although these have been consistently treated as either *C. turneri* or *C. laevigatus*. This species was originally described as a subspecies of *C. bibronii* (now regarded as limited to South Africa, southern Namibia and adjacent areas; Benyr 1995; Bauer and Lamb 2005) based on material from Pico Azevedo (Schmidt 1933). Heinz (2011) provided evidence for the specific distinctness of *C. pulitzerae*; see Ceríaco et al. (2014) for brief discussion ofthe nomenclatural and taxonomic history of this taxon. One specimen (CAS 254920) represents topotypical material. The species was common and found hiding on shaded areas of rocky crevices, houses, and other structures.

Large-Scaled Thick-Toed Gecko
***Pachydactylus scutatus* Hewitt, 1927**

Material.— Espinheira, 30 November 2013, 16º47′51.8″S, 12º21′15.2″E, 457 m (CAS 254826).

Comments.— This specimen is the first published record of *Pachydactylus scutatus* for Angola. *Pachydatylus scutatus angolensis* is now recognized as a distinct species (see below; Bauer et al. 2002). Five additional specimens, all from Iona, are present in the Ditsong National Museum of Natural History (TM 40615–18 from Espinheira, TM 40751 from 16°54′S, 12°35′E).

Angolan Thick-Toed Gecko – Fig. 7
***Pachydactylus angolensis* (Loveridge, 1944)**

Material.— Namibe-Lubango road, 2 km E (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′37″S, 13º9′36″E, 625 m (CAS 254887).

Comments.— This poorly known taxon was described from Benguela Province (Loveridge

Figure 7. Juvenile Angolan Thick-toed Gecko, *Pachydactylus angolensis* (Loveridge, 1944), from Chimalavera, Benguela Province, Angola. Photo by Luis Ceríaco.

1944a). Laurent (1964a) subsequently reported additional specimens from the "environs de Moçâmedes" (now Namibe, Namibe Province). More recently, Wulf Haacke collected 16 specimens from both Bengela and Namibe Provinces. The Namibe localities include Lungo, Lucira, San Nicolau, and Saco de Giraul. There is a single record from extreme northern Namibia (J. Boone, pers. comm.), suggesting that the species actually has a fairly broad range from south of the Kunene to Hanha in Benguela (TM 46558).

Speckled Thick-Toed Gecko
***Pachydactylus punctatus* Peters, 1854**

Material.— INP, 29 November 2013, 16º39′24.1″S, 12º26′12.2″E, 460 m (CAS 254781–254784); Espinheira, 29 November 2013, 16º47′11.01″S, 12º21′28.77″E, 457 m (CAS 254799–254800), 16º47′7.02″S, 12º21′16.86″E, 457 m (CAS 254806); 16º47′4.2″S, 12º21′16.62″E, 457 m (CAS 254809–254810), 16º47′12.71″S, 12º21′28.67″E, 457 m (CAS 254812), 16º47′20.3″S, 12º21′27.6″E, 457 m (CAS 254960).

Comments.— The species is known from southwestern Angola in the provinces of Benguela (Bocage 1867, 1895; Boulenger 1885; Hellmich 1957b; Laurent 1954), Huila (Monard 1931, 1937, Laurent 1964a), Cunene (Laurent 1964a), and Namibe (Schmidt 1933, Laurent 1964a). Members of the *P. punctatus* complex have been confused with other southern African *Pachydactylus*, including *P. occellatus* and *P. geitje* (Bocage 1867, 1885, 1895; Boulenger 1905; Frade 1963). The previous report of *P. serval* in Angola (Monard 1931) likely corresponds to *P. punctatus*. A phylogeographic study of *P. punctatus* is being currently undertaken (Heinz 2011) and it appears that this taxon comprises multiple unnamed cryptic species. At least two, possibly three, taxa in this complex occur in southwestern Angola. *Pachydactylus punctatus* sensu lato is the most common terrestrial gecko in most of northern Namibia as well as southern Angola.

Kaokoland Rock Gecko
***Pachydactylus* cf. *oreophilus* McLachlan and Spence, 1967**

Material.— Omauha Lodge, 28 November 2013, 16º11′55.01″S, 12º24′3.12″E, 338 m (CAS 254829).

Comments.— *Pachydactylus oreophilus* was described from near Sesfontein in northwestern Namibia. Specimens assigned to this species extend northwards at least as far as the southern lowland portions of Benguela Province, Angola. Preliminary molecular phylogenetic data suggest that northern populations, including all of those in Angola and possibly those along the Kunene River in Namibia, are not conspecific with the nominotypic form. The specimen was collected at night, basking near a lamp 2.5 m off the ground, in Omauha Lodge.

Barnard's Namib Day Gecko – Fig. 8
***Rhoptropus barnardi* Hewitt, 1926**

Material.— Approximately 7.35 km north-west (by road) of Pico Azevedo, 7 December 2013, 15º28′30.7″S, 12º27′47.5″E, 420 m (CAS 254759, CAS 254761); Omauha Lodge, 4 December 2013, 16º12′1.2″S, 12º24′0.1″E, 343 m (CAS 254837); INP, Rio Curoca crossing, North side of the river, 1 December 2013, 16º18′6.8″S, 12º25′13.0″E, 206 m (CAS 254844); INP, Rio Curoca crossing, south side of the river, 1 December 2013, 16º18′14.7″S, 12º25′0.0″E, 210 m (CAS 254846–254847); INP, Rio Curoca in the Pediva Hot Springs area, 2 December 2013,

FIGURE 8. Adult Barnard's Namib Day Gecko, *Rhoptropus barnardi* Hewitt, 1926, from Kamanjab, Kunene Region, Namibia. Photo courtesy of Johan Marais.

16º17′0.93″S, 12º33′39.81″E, 247 m (CAS 254852), 16º17′14.3″S, 12º33′35.9″E, 238 m (CAS 254856), 16º17′24.01″S, 12º33′43.9″E, 270 m (CAS 254863), Namibe-Lubango road, 2 km east (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′40.8″S, 13º9′32.6″E, 664 m (CAS 254890); NNP, 28 November 2013, 15º46′23.4″S, 12º19′58.9″E, 264 m (CAS 254954).

COMMENTS.— Until now, this species has been known only from one published locality in Angola. Laurent (1964a) cites the specimen from a locality "60 km on the road from Moçâmedes [presently Namibe] to Sá da Bandeira [presently Lubango]", the same locality from which he described *R. taeniostictus*, which we also collected (see account below). This species is widely distributed in northwestern Namibia, occurring as far inland as the Otavi-Grootfontein region, due south of western Cuando Cubango Province. It is rupicolous and can be found on small rocky piles and ridges, as well as on larger boulders. The extent of its distribution in Angola is poorly known, in part becase many records from Namibe and Huila are assignable to a morphologically similar, but undescribed congener (see *Rhoptropus* sp. below).

TWO-PORED NAMIB DAY GECKO – Fig. 9
***Rhoptropus biporosus* Fitzsimons, 1957**

MATERIAL.— INP, 29 November 2013, 16º32′0.48″S, 12º26′44.16″E, 378 m (CAS 254779, 16º39′26.04″S, 12º26′13.5″E, 460 m (CAS 254780); INP, 20 km south-south-west (by air) of Espinheira, 30 November 2013, 16º55′54.1″S, 12º14′42.0″E, 631 m (CAS 254786–254788),

FIGURE 9. Close-up of head of adult specimen of Two-Pored Namib Day Gecko, *Rhoptropus biporosus* FitzSimons, 1957 from northwest of Palmwag, Kunene Region, Namibia. Photo courtesy of Johan Marais.

16º48′43.19″S, 12º16′16.55″E, 485 m (CAS 254959), Espinheira, 29 November 2013, 16º47′19.9″S, 12º21′27.4″E, 457 m (CAS 254794), 16º47′7.08″S, 12º21′16.02″E, 457 m (CAS 254802–254803), 16º47′7.02″S, 12º21′16.86″E, 457 m (CAS 254805), 16º47′4.26″S, 12º21′16.62″E, 457 m (CAS 254811), 16º47′12.71″S, 12º21′28.67″E, 457 m (CAS 254813), 16º47′20.2″S, 12º21′27.9″E, 457 m (CAS 254958), 30 November 2013, 16º47′14.3″S, 12º21′29.4″E (CAS 254820), 16º47′8.7″S, 12º21′30.3″E, 457 m (CAS 254821), 16º47′18.1″S, 12º21′26.2″E, 457 m (CAS 254822), 16º47′33.6′S, 12º21′19.0″E, 457 m (CAS 254823), 16º47′41.5″S, 12º21′17.3″E, 457 m (CAS 254824), 16º47′45.3″S, 12º21′15.9″E, 457 m (CAS 254825); NNP, 28 November 2013, 15º46′27.4″S, 12º19′59.2″E, 264 m (CAS 254957–254958).

COMMENTS.— The species occurs in the rocky outcrops in arid habitats inland of the northern Namib dune fields in the vicinity of Orupembe, in the Kaokoveld and across the Cunene River to Angola (Bauer and Good 1996). The only published record of this species for Angola is from the Pico Azevedo region (Bauer and Good 1996), although Wulf Haacke collected numerous specimens from localities across southern Namibe, as well as from near Otchinjau, Cunene Province (specimens in Ditsong National Museum of Natural History).

BOULTON'S NAMIB DAY GECKO – Fig. 10
***Rhoptropus boultoni boultoni* Schmidt, 1933**

MATERIAL.— INP, 3.4 km southwest (by air) of Espinheira, vicinity of "Lion Cave", 30 November 2013, 16º48′73.5″S, 12º20′23.2″E, 463 m (CAS 254752); Approximately 7.35 km north-west (by road) of Pico Azevedo, 7 December 2013, 15º28′33.2″S, 12º27′45.7″E, 421 m (CAS 254757–254758); Espinheira, 16º47′29.4″S, 12º21′6.06″E, 457 m (CAS 254795); Omauha Lodge, 28 November 2013, 16º11′52.5″S, 12º23′59.3″E, 335 m (CAS 254828, 2 December 2013,

FIGURE 10. Adult Boulton's Namibe Day Gecko, *Rhoptropus boultoni* boultoni Schmidt, 1933, from east of Kamanjab, Kunene Region, Namibia. Photo courtesy of Johan Marais.

16º12′1.2″S, 12º24′0.1″E, 343 m (CAS 254834); INP, Rio Curoca crossing, south side of river, 1 December 2013, 16º18′14.7″S, 12º25′0.0″E, 210 m (CAS 254849–254850), 2nd December 2013, 16º17′19.7″S, 12º33′40.0″E, 244 m (CAS 254857–254858, CAS 254861–254862), 29 November 2013, 16º18′15.6″S, 12º25′1.56″E, 209 m (CAS 254865); Leba Pass, between river and highway, 5 December 2013, 15º4′13.2″S, 13º14′37.7″E, 1676 m (CAS 254880); Namibe-Lubango road, 2.0 km east (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′40.8″S, 13º9′32.6″E, 664 m (CAS 254892), 15º2′40.7″S, 13º9′31″E, 640 m (CAS 254894, 15º0′55.1″S, 12º38′32.8″E, 497 m (CAS 254902); Namibe-Lubango road, road marker 59, 1.8 km west by road of Caraculo, 6 December 2013, 15º00′55.1″S, 12º38′32.8″E, 497 m (CAS 254903); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254921–254926), 15º32′5.8″S. 12º29′29.5″E, 366 m (CAS 254946–254947, CAS 254949–254950); Espinheira, 29 November 2013, 16º47′20.2″S, 12º21′27.9″E, 457 m (CAS 254958).

COMMENTS.— This taxon is widespread from northwestern Namibia north at least to northern Namibe Province.

MONTANE NAMIB DAY GECKO
***Rhoptropus boultoni montanus* Laurent, 1964**

MATERIAL.— Leba Pass overlook, 5 December 2013, 15º4′37.2″S, 13º13′58.5″E, 1682 m (CAS 254866, CAS 254867; 15º4′38.3″S, 13º13´57.0″E, 1682 m (CAS 254868); 15º4′36.0″S, 13º14′1.6″E, 1682 m (CAS 254869–254872); Leba Pass, between river and highway, 15º04′13.2″ S, 13º14′37.3″E, 1676 m (CAS 254882).

COMMENTS.— The subspecies was described from the Leba Escarpment ("60 km on the road to Moçâmedes [now Namibe, Namibe Province] from Sá da Bandeira [now Lubango, Huila

Province]", Laurent 1964a). A large series of specimens in the Ditsong National Museum of Natural History are derived from localities near Lubango, in Huila. Our specimens are topotypical and were collected on the Namibe side of the provincial boundary. Specimens were found basking on high elevation granite rocks covered with bryophytes. Molecular phylogenetic studies (A. Kuhn, unpublished) reveal that this taxon is specifically distinct from *R. boultoni*. Its formal elevation to specific status will be justified in detail elsewhere.

ANGOLAN NAMIB DAY GECKO
***Rhoptropus taeniostictus* Laurent, 1964**

MATERIAL.— Namibe-Lubango road, 2 km east (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′40.8″S, 13º9′32.6″E, 664 m (CAS 254889); Namibe-Lubango road, road marker 59, 1.8 km west (by road) of Caraculo, on the north side of the road, 6 December 2013, 15º0′58.0″S, 12º38′37.3″E, 490 m (CAS 254895);15º0′57.9″S, 12º38′42.3″E, 472 m (CAS 254897–254898), 15º0′57.6″S, 12º38′36.8″E, 500 m (CAS 254901), 15º1′0.7″S, 12º38′31.9″E, 492 m (CAS 254904–254905), 15º0′58.8″S, 12º38′33.8″E, 491 m (CAS 254908), 15º0′58.9″S, 12º38′32.4″E, 497 m (CAS 254911), 15º0′57.3″S, 12º38′32.6″E, 497 m (CAS 254916), 15º1′0.1″S, 12º38′31.9″E, 497 m (CAS 254917–254918), 15º1′0.9″S, 12º38′30.4″E, 503 m (CAS 254919).

COMMENTS.— The Angolan endemic *R. taeniostictus* was described from a single specimen from "60 km on the road from Moçâmedes [presently Namibe] to Sá da Bandeira [presently Lubango]". Laurent (1964a) also considered the populations of *R. barnardi* from Mucungo cited by Schmidt (1933) as referable to *R. taeniostictus*. The species appears restricted to Namibe Province and is represented by many specimens in our collection as well as more widespread Namibe localities in the Ditsong National Museum of Natural History.

***Rhoptropus* sp.**

MATERIAL.— Espinheira, 29 November 2013, 16º47′32.7″S, 12º21′14.4″E, 562 m (CAS 254801); Omauha Lodge, 4 December 2013, 16º12′1.2″S, 12º24′0.1″E, 343 m (CAS 254836, CAS 254955); INP, north of Tambor, 4 December 2013, 15º59′46.9″S, 12º24′24.0″E, 300 m (CAS 254842, CAS 254762, CAS 254766), 15º28′31.7″S, 12º27′43.9″E, 408 m (CAS 254765, CAS 254760); Leba Pass, between river and highway, 5 December 2013, 15º4′12.1″S, 13º14′36.5″E, 1680 m (CAS 254873), 15º4′13.2″S, 13º14′37.7″E, 1676 m (CAS 254879, CAS 254881, CAS 254883); Namibe-Lubango road, 2 m east (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′40.8″S, 13º9′32.6″E, 664 m (CAS 254890–254891), 15º2′40.7″S, 13º9′31.0″E, 640 m (CAS 254893, CAS 254894).

COMMENTS.— This undescribed species is morphologically similar to both *R. barnardi* and *R. biporosus*, but appears to be endemic to southern Angola. Populations from the Escarpment are both morphologically and genetically different from those below the Escarpment.This taxon is currently under study as part of a phylogenetic analysis and revision of the genus as a whole (A. Kuhn and A. Bauer, in prep.).

Scincidae

BOGERT'S SPECKLED WESTERN BURROWING SKINK – Fig. 11
***Typhlacontias punctatissimus bogerti* Laurent, 1964**

MATERIAL.— Espinheira, 29 November 2013, 16º47′7.02″S, 12º21′16.86″E, 457 m (CAS

254807); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254932–254938), 15º32′5.8″S, 12º29′29.5″E, 366 m (CAS 254944–254945).

COMMENTS.— Haacke (1997) reviewed the taxonomic and nomenclatural history of *Typhlacontias punctatissimus* and its subspecies and recognized two sympatric subspecies in southern Angola — *T. punctatissimus punctatissimus* Bocage, 1873, and the Angolan endemic *T. punctatissimus bogerti* Laurent, 1964. In all of our specimens, the second and third upper labials are in contact with the eye and there is a second supraocular. Both characters fit the description presented by Haacke (1997) as diagnostic for *T. punctatissimus bogerti*. The species is known to be viviparous and one female specimen (CAS 254945) contains an almost fully developed neonate.

FIGURE 11. Adult Bogert's Speckled Western Burrowing Skink *Typhlacontias punctatissimus bogerti* Laurent, 1964, from Pico Azevedo. Photo by Edward Stanley.

VARIABLE SKINK
Trachylepis varia **(Peters, 1867)**

MATERIAL.— Leba Pass, 5 December 2013, 15º4′12.1″S, 13º14′36.2″E, 1680 m (CAS 254874), 15º4′13.2″S, 13º14′37.7″E, 1676 m (CAS 254884).

COMMENTS.— The species occurs throughout Angola, with many records in the provinces of Benguela (Parker 1936; Bocage 1895, 1896; Monard 1937; Hellmich 1957a; Mertens 1938; Boulenger 1905) and Huila (Bocage 1895; Monard 1937). Although other records from Namibe are 12 km W of Humbia (TM 40128–29) and Chapeau Armado turnoff (TM 41131). This species is typically associated with relatively mesic microclimates and is, therefore, excluded from the hyperarid areas of Namibe. This skink has a broad distribution across much of sub-Saharan Africa and includes several cryptic species, two of which are present in Angola. There are records from across Angola and from all bordering countries as well. The phylogeography of the *T. varia* complex is presently under study (J. Weinell, pers. comm.).

SPECKLED SAND SKINK – Fig. 12
Trachylepis punctulata **(Bocage, 1872)**

MATERIAL.— Espinheira, 29 November 2013, 16º47′20.6″S, 12º21′27.2″E, 457 m (CAS 254793); Namibe-Lubango road, road marker 59, 1.8 km west (by road) of Caraculo, on the north side of the road, 6 December 2013, 15º0′55.1″S, 12º38′32.8″E, 497 m (CAS 254903); Praia do Navio coastal dunes, ca 124 km SSW of Namibe, 8 December 2013, 16º16′20.4″S, 11º49′53.9″E, 8 m (CAS 254769–254771), 16º16′39.3″S, 11º49′20.5″E, 8 m (CAS 254775).

COMMENTS.— The species was originally described by Bocage based on material from "Rio Coroca, sur le littoral de Mossamedes, Angola" (Bocage 1872). The type locality is presumably the region near the mouth of Curoca River, from the vicinity of Tombwa (formerly Porto Alexandre). Our specimens were collected among plants between dunes along the coast south of Tombwa, and these agree morphologically with the original description for the species. A comparison with the type material was impossible due to its destruction in the fire that destroyed the Lisbon Museum in 1978. Several uncatalogued specimens in the Museu Nacional de História Natural do Porto collected in 1905 by the Portuguese explorer Francisco Newton are congruent with the specimens collected by us. Newton's specimens are still in their original jar and are labeled "Mossamedes" (presumably refering to the province as a whole, not the city of Mossamedes = Namibe). They are part of a collection of vertebrates that the explorer made in the region. The herpetological specimens were only partly studied and published upon (Ferreira 1904, 1906; Ceríaco et al. 2014), in contrast to the bird and mammals collections (Seabra 1906a, 1906b, 1906c, 1906d, 1907). It is probable that these specimens are from Tombwa, as this was the main place where Newton collected while in the province (see bird records – Seabra 1906a). This is a common species in much of Namibia, Botswana, and central South Africa, as well as portions of Zambia, Zimbabwe, and Mozambique (Portik and Bauer 2012).

FIGURE 12. Adult Speckled Sand Skink, *Trachylepis punctulata* (Bocage, 1872), from Kamanjab, Kunene Region, Namibia. Photo courtesy of Johan Marais.

HOESCH'S SKINK – Fig. 13
***Trachylepis hoeschi* (Mertens, 1954)**

MATERIAL.— Rio Curoca in the Pediva Hot Springs area, 2 December 2013, 16º17′0.93″S, 12º33′39.81″E, 247 m (CAS 254851); NNP, 15º46′25.9″S, 12º19′59.0″E, 247 m (CAS 254952).

COMMENTS.— The only published Angolan record is from Laurent (1964a), from "Plage das Conchas," Namibe Province. Our specimens are, respectively, 75 and 135 km SE of Laurent's site. the Ditsong National Natural History Museum holds a small series of this species (TM 40733–37)

FIGURE 13. Adult Hoesch's Skink, *Trachylepis hoeschi* (Mertens, 1954), from Kamanjab, Kunene Region, Namibia. Photo courtesy of Johan Marais

from Iona National Park. The Angolan records extend the core distribution of its range in north-western Namibia (Branch 1998).

ANGOLAN BLUE-TAILED SKINK
***Trachylepis laevis* (Boulenger, 1907)**

MATERIAL.— INP, north of Tambor, 4 December 2013, 15º59′47.1″S. 12º24′25.6″E, 314 m (CAS 254838).

COMMENTS.— The species was described by Boulenger from Maconjo, in northern Namibe Province (Boulenger 1907b). Laurent (1964a) recorded this species in Namibe Province from "Munhino 50 km west of Sá da Bandeira." Hellmich (1957a) cited the species for Piri-Dembos, Kwanza Norte Province, but this record is dubious. The Ditsong National Natural History Museum houses numerous specimens from localities in Namibe and southern Benguela below the Escarpment. The species occurs also in the Kamanjab area and Damaraland in northwestern Namibia (Bauer et al. 1993). This lizard is extremely dorsoventrally depressed in association with its crevice dwelling habits and was, for a time, placed in a monotypic genus, *Oelofisa*, in recognition of its highly autapomorphic morphology (Steyn and Mitchell 1965).

WESTERN THREE-STRIPED SKINK
***Trachylepis occidentalis* (Peters, 1867)**

MATERIAL.— Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254931).

Comments.— The species has been cited from 35 km south of the city of Namibe (Laurent 1964a) and from Curoca River (Bocage 1895). Three specimens in the Ditsong Natural National History Museum originate from the Rio Curoca mouth and from Namibe. In addition to our specimen from Pico Azevedo several individuals of the species were observed near Espinheira camp (specimens not collected). In Angola this skink takes refuge in holes it digs in the sand at the base of spiny shrubs of the genus *Blepharis*. It is widely distributed in western South Africa and much of central and western Namibia (Branch 1988).

Wedged-Snouted Skink – Fig. 14
***Trachylepis acutilabris* (Peters, 1862)**

Material.— INP, 3.4 km south-west (by air) of Espinheira, vicinities of "Lion Cave", 30 November 2013, 16º48′54.4″S, 12º20′13.7″E, 450 m (CAS 254751); INP, car wreck 20 km south-south-west (by air) of Espinheira, 30 November 2013, 16º55′53.81″S, 12º14′45.42″E, 616 m (CAS 254789); Namibe-Lubango road, road marker 59, 1.8 km (by road) of Caraculo, north side of the road, 6 December 2013, 15º0′59.3″S, 12º38′33.6″E, 488 m (CAS 254899), 15º0′58.8″S, 12º38′33.8″E, 491 m (CAS 254907); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254927–254931).

Comments.— This species is similar to lacertid lizards in morphology and diet (Castanzo and Bauer 1992). Its elongate toes and countersunk lower jaw are consistent with its burrowing habits. It typically occupies burrows at the base of vegetation in sandy soils from Namibia through western Angola to the Democratic Republic of Congo and Cabinda (Branch 1998).

Western Rock Skink
***Trachylepis sulcata* (Peters, 1867)**

Material.— INP, Rio Curoca in Pediva Hot Springs area, 3 December 2013, 16º17´0.93″S, 12º33′39.81″E, 247 m (CAS 254853); Leba Pass, 5 December 2013, 15º4′12.1″S, 13º14′36.2″E, 1680 m (CAS 254875); Namibe-Lubango road, 2 km east (by road) of Mangueiras, south side of the road, 5 December 2013, 15º2′40.7″S, 13º9′31″E, 625 m (CAS 254886), 15º2′40.8″S, 13º9′32.6″E, 664 m (CAS 254888).

Comments.— *Trachylepis sulcata* is a rupicolous skink ranging from the Western Cape Province of South Africa north to southern Angola. *Trachylepis sulcata ansorgii* (Boulenger 1907b) was described from southern Angola to accommodate specimens with bright throat and infralabial coloration. Laurent (1964a) and Mertens (1971) considered it valid and the latter identified some Namibian specimens as intergrades between *T. s. ansorgii* and *T. s. sulcata*, whereas Haacke (1972) considered specimens on the Namibian side of the Kunene river to be referable to *T. s. ansorgii*. Some specimens from west of the Great Escarpment in northwestern Namibia exhibit the diagnostic coloration of *ansorgii*, but the two subspecies seem to have no fixed differences in scalation (Bauer et al. 1993). Although Portik et al. (2011) did not include typical *T. s. ansorgii* in their molecular sampling, preliminary integration of samples from our collection into their data set reveals no significant difference from putative *T. s. ansorgii* from Namibe and the nominotypical form. We therefore treat *T. sulcata* as a monotypic species.

FIGURE 14. Adult Wedged-Snouted Skink, *Trachylepis acutilabris* (Peters, 1862), from Kamanjab, Kunene Region, Namibia. Photo courtesy of Johan Marais.

Lacertidae

ANCHIETA'S SHOVEL-SNOUT LIZARD
***Meroles anchietae* (Bocage, 1867)**

MATERIAL.— Praia do Navio coastal dunes, ca 124 km SSW of Namibe, 8 December 2013, 16º16′29.1″S, 11º49′05.0″E, 8 m (CAS 254773).

COMMENTS.— Bocage (1867) described this species from "Mossamedes" (Bocage 1867). Surprisingly, this remains the only published locality for this species in Angola (Bocage, 1867, 1895), despite it being common and widely distributed in barchan dunes from the Klinghardt Mountains north through the Namib of western Namibia. In the Newton collections in Porto, there are several uncatalogued specimens corresponding to this species from "Mossamedes" and the Ditsong National Natural History Museum has material collected by Wulf Haacke from Porto Alexandre and Foz de Cunene.

RETICULATE SAND LIZARD – Fig. 15.
***Meroles reticulatus* (Bocage, 1867)**

MATERIAL.— Praia do Navio coastal dunes, ca 124 km SSW of Namibe, 8 December 2013, 16º16′39.3″S, 11º49′20.5″E, 8 m (CAS 254776).

COMMENTS.— Bocage (1867) described this species from "Mossamedes." Bocage (1895) subsequently clarified that the types had come from the littoral zone at Rio Coroca [= Rio Curoca, southern Namibe Province, Angola]. The range of this species extends towards Namibia to the area of Conception Bay on the central coast. Although it is well documented within its Namibian range, this specimen is only the third published locality for Angola. The species is, however, well represented from numerous localities in Namibe by specimens in the Ditsong National Museum of Natural History.

FIGURE 15. Adult specimen of Anchieta's Shovel-snout Lizard, *Meroles anchietae*, (Bocage, 1867) from gravel plains north of Henties Bay, Erongo Region, Namibia. Photo courtesy of Johan Marais.

Haacke's Sand Lizard
***Pedioplanis haackei* Conradie, Measey, Branch and Tolley, 2012**

Material.— 5 km NW (by road) of Pico Azevedo, 7 December 2013, 15º28′33.6″S, 12º27′41.4″E, 399 m (CAS 254767), 15º28′31.7″S, 12º27′43.9″E, 408 m (CAS 254763–253764); RNN, 28 November 2013, 15º46′22.5″S, 12º19′57.7″E, 262 m (CAS 254951), 15º46′25″S, 12º19′54.9″E, 262 m (CAS 254953); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254939); Pediva Hot Springs, south side of the river, 2 December 2013, 16º17′37.7″S, 13º33′37.2″E, 235 m (CAS 254860), 16º17′24.01″S, 12º33′43.9″E, 270 m (CAS 254864); INP, north of Tambor, 4 December 2013, 15º59′43.4″S, 12º24′23.3″E, 306 m (CAS 254840); Omauha Lodge, 4 December 2013, 16º12′1.2″S, 12º24′00.1″E, 343 m (CAS 254835).

Comments.— *Pedioplanis haackei* is one of the latest additions to the herpetofauna of Angola, and is endemic to southern Angola. Each of our specimens has 10 to 12 longitudinal rows of ventral scales, a semi-transparent lower eyelid with a brille formed of two large scales, five to six supralabials anterior to the subocular, two rows of granules separating supraoculars from supraciliaries, and the typical coloration with dots on the flanks, concordant with the diagnostic characters presented by Conradie et al. (2012) in the species description. Genetically, our specimens (GenBank accession numbers KU662311–KU662318) have an average 16S p-distance of 1% from those of Conradie et al. (2012) (GenBank accession numbers HE794000, HE793999.1; HE793998.1; HE793997.1; HE793996.1; HE793995.1; HE793994.1; HE793994.3).

Benguela Sand Lizard
***Pedioplanis benguellensis* (Bocage, 1867)**

Material.— Namibe-Lubango road, road marker 59, 1.8 km W (by road) from Caraculo, north side of the road, 6 December 2013, 15º00′57.8″S, 13º38′41.4″E, 476 m (CAS 254909), 15º00′58.8″S, 13º38′33.8″E, 491 m (CAS 254906), 15º00′57.5″S, 12º38′38.3″E, 482 m (CAS 254896).

Comments.— All of these specimens have ten to eleven longitudinal series of ventral plates and a single transparent scale in the lower eyelid. However, they also have two rows of granules separating supraoculars from supraciliaries, a character given by Conradie et al. (2012) as synapomorphic for *P. haackei*. The number of upper labials in front of the subocular is variable: CAS 254896 has three, CAS 254906 has five, and CAS 254909 has four. Molecular comparisons with specimens of *P. benguellensis* from Conradie et al. (2012) show these specimens to be conspecific (average uncorrected 16S p-distance of 1% from our specimens [GenBank accession numbers KU662319 to KU662321] from those of Conradie et al. [2012] [GenBank accession numbers HE794014.1, HE794012.1, HE794011.1, HE794010.1 and HE794013.1]).

Bushveld Lizard
***Heliobolus lugubris* (Smith, 1838)**

Material.— Namibe-Lubango road, 2 km E of Mangueiras, south side of the road, 5 December 2013, 15º02′37.0″S, 13º09′36.0″E, 625 m (CAS 254885).

Comments.— The species is widespread over much of southern Africa, particularly on sandy substrates (Bauer et al. 1993). In Angola, the majority of both bibliographic (Bocage 1867, 1895; Monard 1937; Mertens 1938; Boulenger 1921) and museum records (e.g., TM 46525) are from Benguela. However, there are also records of the species for Namibe Province from "Maconjo"

(Bocage 1895), "Capangombe" (Bocage 1895), and "Konondoto" (Boulenger 1921). The species' distribution in the country extends to the southeast in Huíla and Cunene Provinces. Our specimen is a sub-adult (55.5 mm SVL).

Cordylidae

KAOKOVELD GIRDLED LIZARD
***Cordylus namakuiyus* Stanley, Ceríaco, Bandeira, Valério, Bates and Branch, 2016**

MATERIAL.— 7.5 km NW (by road) of Pico Azevedo, 7 December 2013, 15º28′33.2″S, 12º27′45.7″E, 421 m (CAS 254754–254755, CAS 256530–256531); Namibe-Lubango road, road marker 59, 1.8 km W (by road) from Caraculo, north side of the road, 6 December 2013, 15º00′59.4″S, 12º38′31.3″E, 503 m (CAS 254912–254914); 15º00′57.3″S, 12º38′32.6″E, 509 m (CAS 256529).

COMMENTS.— Based on a combination of morphological and molercular data, Stanley et al. (2016) described this new species endemic to the arid lowlands west of the southern Angolan escarpment. The majority of the type material of *C. namakuiyus* was collected during this trip. The new species is morphologically and genetically distinct from its sister taxon *Cordylus machadoi* Laurent, 1964, which occurs in the highlands of Huila, not far from Namibe. In addition to an average 7.1% uncorrected p-distance for the mitochondrial marker ND2, the two species differ in the extent of osteodermal armament. The more complete body armor of *C. namakuiyus* may be an adaptation to the semi-arid and refuge-scarce habitat where the species occurs. Within the new species there is also a degree of internal genetic structure, with specimens from Iona (PEM R18005) and Pico Azevedo (CAS 254754, 254755, 256530, 256531) more closely related to one another than to the two specimens from Caraculo. Specimens in the American Museum of Natural Histiry identified as *Cordylus cordylus* and collected in 1925 during the Vernay Expedition in Angola are assignable to *C. namakuiyus.* Although the Vernay specimens lack specific locality information, the expedition field notes mention that significant numbers of unidentified lizards were collected at "Pico Azevedo" and "100 km east of Moçâmedes" the same areas where we collected eight specimens of *C. namakuiyus.*

DWARF PLATED LIZARD – Fig. 16
***Cordylosaurus subtessellatus* (Smith, 1844)**

MATERIAL.— INP, 20 km SSW of Espinheira, 30 November 2013, 16º55′54.1″S, 12º14′42.0″E, 631 m (CAS 254785).

COMMENTS.— The species is known from the coastal areas of Benguela Province (Bocage 1867, 1895; Boulenger 1887) and from the Curoca River in Namibe Province (Bocage 1895). This specimen represents the southernmost record for Angola. The specimen was found hiding

FIGURE 16. Adult Dwarf Plated Lizard, *Cordylosaurus subtessellatus* (Smith, 1844), from near Espinheira. Photo by Edward Stanley.

in a granite boulder crevice. Extralimitally, the species is widely distributed from the Little Karoo in the Western Cape of South Africa, north through the entire length of Namibia (Branch 1998).

Gerrhosauridae

Desert Plated Lizard – Fig. 17
***Gerrhosaurus skoogi* (Andersson, 1916)**

Material.— Praia do Navio coastal dunes, ca 124 km SSW of Namibe, 8 December 2013, 16º16′20.4″S, 11º49′53.9″E, 8 m (CAS 254772), 16º16′29.1″S, 11º49′50.0″E, 8 m (CAS 254774), 16º16′42.1″S, 11º49′21.7″E, 8 m (CAS 254777).

Comments.— This species was encountered basking at the sun in the coastal dunes SSW of Namibe, especially in dune valleys areas. When approached, these lizards dive into the sand, disappearing rapidly. The species is easily identified by its unique morphology and peculiar ecology. Sand trails resulting from the specimens walking in the dunes were noted. A total of five specimens were collected, three of which are at CAS and two at INBAC. Several additional animals were observed in the area but not collected. Males have a distinct black throat and venter, and are considerably larger than the females. The only published Angolan records are from the type locality, Porto Alexandre, between Mossamedes and the mouth of the Cunene River (Andersson 1916; Fitzsimons 1953), approximately in the same area as our material. Although the species is the most distinctive of all *Gerrhosaurus* (Nance 2007), it is unambiguously nested among more typical taxa, implying its unique features are relatively recently derived autapomorphies (Lamb et al. 2003; Lamb and Bauer 2013).

Figure 17. Adult female Desert Plated Lizard, *Gerrhosaurus skoogi* Andersson, 1916, from the coastal dunes, near Praia do Navio. Photo by Arianna Kuhn

Varanidae

Angolan Rock Monitor
***Varanus albigularis angolensis* Schmidt, 1933**

Material.— 7.5 km NW (by road) of Pico Azevedo, adult, found in a rock crevice, 7 December 2013, 15º28′33.6″S, 12º27′41.4″E, 399 m (CAS 254768).

Comments.— The subspecies was described from Gauca, Bihé (Bié) Province (Schmidt 1933). According to the original description, the subspecies differed from the nominotypic form by having larger scales everywhere on the body so that the scales around the body are about 125 instead of 150, and the transverse rows of scales from the collar to thighs are 75 instead of 100 (Schmidt 1933). Laurent (1964b) noted that the morphological differences between the nominotypic form and *angolensis* are quite subtle and that *angolensis* may, in fact, be a synonym of *albigularis*. However, Bayless (2002) considered the material from nearby localities, such as Bibala and Caraculo as *V. a. angolensis*. Given the currently accepted distribution of *angolensis* and the lower number of scales around the midbody and between the collar and the thighs, we tentatively identify our specimen as the Angolan subspecies. The subspecies appears to be the prevalent form in Angola (and possibly extending to some neighboring regions of the DRC, even if the nominotypic form occurs sympatrically, especially in the southern regions of the country (Bayless 2002).

Pythonidae

Southern African Rock Python – Fig. 18
***Python natalensis* Smith, 1840**

Material.— Beginning of the forested areas, at the start of the climb to Leba Pass (by road), near Bruco village, 5 December 2013, 15º07′15.82″S, 13º11′11.56″E. Individual observed but not collected.

Comments.— A local at a site near Bruco village was selling a single live individual of *Python natalensis*, presumably collected nearby. In the province, this species is known from Maconjo (Bocage 1895; Broadley 1984) and from Giraul River (Bocage 1896; Broadley 1984). *Python natalensis* was for many years considered as a subspecies of *Python sebae* (Gmelin, 1789) (Broadley 1984), but was elevated to specific status by Broadley (1999) based on morphological differences as well the evidence of the overlapping distributions (Broadley and Cotterill 2004). Although the current taxonomic arrangement appears appropriate, molecular analyses are needed to conclusively resolve the relationship between *P. natalensis* and *P. sebae* (Alexander 2007). Spawls and Branch (1995) and Bellosa et al. (2007) provided maps with the distribution ranges for both species, with *P. natalensis* occurring in central and southern Angola, as far north as the Kwanza River, overlaping in Luanda Province with *P. sebae*, which occurs in northern regions of Angola, including Cabinda. According to the local selling this individual, this species is sometimes collected for food or sold to tourists as pets.

Figure 18. Adult Southern Rock Python, *Python natalensis* (Gmelin, 1788), being sold by a local near Bruco village. Photo by Luis Ceríaco.

Lamprophiidae

KAROO SAND SNAKE – Fig. 19
***Psammophis notostictus* Peters, 1867**

MATERIAL.— Espinheira, 30 November 2013, 16º47′13.8″S, 12º21′27.5″E, 457 m (CAS 254827); Pico Azevedo, 7 December 2013, 15º32′2.4″S, 12º29′31.1″E, 359 m (CAS 254940).

COMMENTS.— *Psammophis notostictus* is easily recognizable from all other southern African *Psammophis* by its single cloacal shield and the presence of two preoculars (Broadley 1975b, 1977, 2002). These two specimens have both of these diagnostic characters. The species is known for Angola, but only from Namibe Province. The closest published records of the species are in Rio São Nicolau (Loveridge 1940; Broadley 1975b, 2002), Moçamedes [Namibe city] (Bocage 1887; Loveridge 1940), and Curoca River (Loveridge 1940; Broadley 2002). Our records expand the known distribution of the species further south in the country, although it is continuous southwards throughout much of western southern Africa (Branch 1998).

FIGURE 19 – Adult Karoo Sand Snake, *Psammophis notostictus* Peters, 1867, from Espinheira. Photo by Luis Ceríaco.

DISCUSSION

Namibe Province hosts a high diversity of reptile taxa, with approximately one-third of all the reptile species known for Angola (see Table 1). Not surprisingly for an arid region, the diversity of amphibians is considerably lower in this province. However, the anuran species *Tomopterna damarensis*, adapted to drier climates, is reported here for the first time. The lizard families Scincidae and Gekkonidae are the most species-rich groups for the province with 21 and 20 species/subspecies known, respectively, and for the snakes the family Lamprophiidae has the highest diversity of taxa, with 13 species known for the province. These numbers, however, are underestimates. We did not take into account unpublished voucher specimens; as noted above, a more complete synopsis of the Namibe Province taxa will be provided elsewhere (W.R. Branch, pers. comm.). There are several examples of taxa not previously recorded for Namibe, but which are found both north and south of Namibe Province and can be expected to be found here in the future.The presence of conspicuous species, such as Anchieta's Dwarf Python, *Python anchietae* Bocage, 1887, known from Benguela Province and from the northern regions of Namibia, is an excellent example of this pattern. Biogeographically, the province is interesting because it represents the northern limit of several southern African habitats and species. The entry of the coastal Namib Desert from Namibia into the southern coastal areas of the province as far north as the city of Namibe, as well as the continuation of the Kaokoveld and the Namibian savanna woodlands provides a clear dispersal path for southern African taxa. Likewise, the so-called Pro-Namib extends from northwestern Namibia, through Namibe, to the southern areas of Benguela Province. Despite these similarities, the influence of the Cunene River as a barrier should not be underestimated. There are a number of endemic Angolan species of widespread genera in southern Africa, such as *Pedioplanis haackei*, *P. huntleyi*, and the undescribed species of *Rhoptropus* collected in our expedition, as well as the endemic genus *Kolekanos*.

Given the concentration of reptile diversity in Namibe Province, conservation in this region is of special concern. Of the 95 species of reptiles that occur in the province (Table 1), several have small distributions within Namibe and ten are endemic, including the Slender Feather-tailed Gecko, *Kolekanos plumicaudus* and the recently described Kaokoveld Girdled-Lizard, *Cordylus namakuiyus*. As noted by Marques (2015), the majority of the amphibians and reptiles of Angola (1) have not been accessed by the IUCN or are listed as Data Deficient, and (2) are known from fewer than five published records for the country since the first studies published in early 1860s. Roughly one third of Namibe Province, 19,600 km^2 out of 57,091 km^2, is protected as either national park or nature reserve. In contrast to more populated provinces, human activities in Namibe that present significant threats to the herpetofauna are limited. The majority of the human population is concentrated around Namibe and Tombwa, and the main economic activities are fisheries and traditional pastoralism. While there are no studies of the impact of livestock on the herpetofauna within Namibe Province, negative impacts are known worldwide in other regions, including South Africa (Bauer and Branch 2003; Fabricius et al. 2003; Smart et al. 2005). Yet the low densities of livestock and the nomadic nature of the populations practicing pastoralism suggest that this is not a major threat to the amphibians and reptiles of Namibe. In contrast to neighboring Namibia (Herrmann and Branch 2013), there are no major mining activities in the province, even if these activites show recent signs of increase, which may in the future threathen some species. Other threats, such as climate change, are believed to have negative consequences on the distribution and abundance of southern African lizards (Erasmus et al. 2002; Bates et al. 2014). Extreme climatic events can facilitate wildfires, which unambiguously affect the availability of important habitats for reptiles (Meik et al. 2002). Lastly, for several taxa (e.g., pythons, chameleons, varanids), the impact of human harvesting for food, traditional medicine and the pet trade should not be overlooked. This is known from other African countries (Weldon et al. 2007; Alves et al. 2008; Segniagbeto et al. 2013), and we did encounter one instance of a python being sold during our brief survey.

Additional faunal surveys are clearly still needed for Namibe Province. Even if this is one of the most herpetofaunally well known provinces in Angola, the new species recently described signal that diversity likely remains underestimated, especially for groups of species that are similar in external appearance. In addition to surveying new areas, it is also important to sample type localities of previously described species. Because many of the original topotypes were lost or destroyed, especially material described by Bocage and originally housed in the Lisbon Museum (Ceríaco 2014), new topotypic material with associated genetic resources will help to address many taxonomic issues, including for groups containing undescribed cryptic diversity. Angola sits at a crossroads of southern and central Africa and is important to understanding phylogenetic and biogeographic patterns across sub-Saharan Africa. The specimens reported here were collected in the first of an ongoing series of joint American-Angolan herpetofaunal expeditions that will build local capacity within Angola and provide accessible data resources to the scientific and conservation communities through georeferenced biodiversity informatics databases (e.g., GBIF.org, Vertnet.org), molecular databases (GenBank), and digitized morphological resources (high-resolution x-ray CT-scans). Combining data from new field surveys with information from both museum specimens and literature records (Marques et al., in prep.) will provide the first detailed picture of Angola's herpetofaunal diversity.

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Appendix

Table 1

Notes

[1] Because of the morphological similarity among many *Tomopterna* species, some older records might be referable to this taxon.

[2] Records attributed in the literature to *Tomopterna cryptotis*, e.g., 25 km W of Virei (Poynton and Haacke 1993; Ruas 1996, 2001) and Miranda (Boulenger 1907a; Poynton and Haacke 1993; Ruas 1996, 2001) are likely referable to *T. tandyi*, but this requires reexamination of the relevant material.

[3] Some records may be referable to *L. bradfieldi* Hewitt, 1932.

[4] *Lygodactylus lawrencei* Hewitt, 1926 is a rocky, dry savanna species from the Kaokoveld regions in northern Namibia, extending into southern Angola (Pasteur 1964:70 [Fig. 18]; Branch 1998:247; Uetz and Hošek 2014). New surveys and aquisition of new fresh material is absolutely required to clarify the extention range of *L. lawrencei* in Angola, given the lack of literature records for this species in the country.

[5] Certainly in error, see Greer (1967).

[6] It is plausible that these records correspond to the subspecies *angolensis*. However, due to the destruction of the specimens used by Bocage in the Lisbon Museum fire and the impossibility of confirming their identity, we opt to maintain the original identification.

[7] The taxonomy of this species is in flux and a revisionary work on the *nigrolineatus* complex is underway (D.G. Broadley and M. Bates, pers. comm.).

[8] The species was described by Broadley and Schätti (1997: 172), from Namibia, near the Cunene River at Ruacana, western Ovamboland. Bauer et al. (2001:75–76, 79) suggested that this species should be expected to occur in southern Angola, due to the continuity of the mopaneveld habitat of the species on either side of the Cunene River.

[9] The species has an irregular distribution from eastern Zimbabwe and the Okavango Swampa, to Angola and Lake Malawi, through Cameroon (Hughes 1985:519 [Fig. 11]; Branch 1998:94; Chirio and LeBreton 2007:518; Wallach et al. 2014:546).

TABLE 1 – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
AMPHIBIANS	
ANURA	
Pipidae	
Genus *Xenopus* Wagler, 1827	
Xenopus petersii Bocage, 1895	Mossamedes [= Namibe] (Bocage 1867; Ruas 1996, 2002).
Bufonidae	
Genus *Sclerophrys* Tschudi, 1838	
Sclerophrys gutturalis (Power, 1927)	Mossamedes [= Namibe] (Bocage 1867); Cima [= Giraul de *Cima*] (Poynton and Haacke 1993; Ruas 1996, 2002); Saco do Giraul (Poynton and Haacke 1993; Ruas 1996, 2002); Curoca (Poynton and Haacke 1993; Ruas 1996, 2002).
Sclerophrys maculata (Hallowell, 1854)	Cainde (Poynton and Haacke 1993; Ruas 1996, 2002); 16 km W of Vila Nova (Poynton and Haacke 1993, Ruas 1996, 2002); this study.
Sclerophrys garmani (Meek, 1897)	Mossamedes [= Namibe] (Bocage 1895; Ruas 1996, 2001).
Genus *Poyntonophrynus* Frost, Grant, Falvovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Biotto, Moler, Drewes, Nussbum, Lynch, Green and Wheeler, 2006	
Poyntonophrynus dombensis (Bocage 1895)	Assunção (Poynton and Haacke 1993; Ruas 1996).
Poyntonophrynus grandisonae (Poynton and Haacke 1993)	5 km E of Assunção (Poynton and Haacke 1993; Ruas 1996); Caraculo (Poynton and Haacke 1993; Ruas 1996); Salona [= Saiona] River, 2 km N of Cainde (Poynton and Haacke 1993; Ruas 1996); 20 km W of Virei (Poynton and Haacke 1993; Ruas 1996).
Microhylidae	
Genus *Phrynomantis* Peters, 1867	
Phrynomantis annectens Werner, 1910	Mutiambo River (Poynton and Haacke 1993; Ruas 1996); Caraculo (Poynton and Haacke 1993; Ruas 1996); this study.
Brevicipitidae	
Genus *Breviceps* Merrem, 1820	
Breviceps adspersus Peters, 1882	Biballa [= Bibala] (Bocage 1895; Ruas 1996, 2002); Mossamedes [= Namibe] (Bocage 1873b).
Hemisotidae	
Genus *Hemisus* Wagler, 1827	
Hemisus guineensis Cope, 1865	Mossamedes [= Namibe] (Bocage 1887b, 1895; Ruas 1996).
Arthroleptidae	
Genus *Leptopetlis* Gunther, 1859	
Leptopelis anchietae (Bocage, 1873)	Mossamedes [= Namibe] (Bocage 1873b; Boulenger 1882; Loveridge 1957).
Phrynobatrachidae	
Genus *Phrynobatrachus* Gunther, 1862	
Phrynobatrachus natalensis (Smith 1849)	Cunene mouth (Poynton and Haacke 1993; Ruas 1996, 2002).

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Pyxicephalidae	
Genus *Amietia* Dubois, 1987	
Amietia angolensis (Bocage, 1866)	This study.
Genus *Tomopterna* Duméril and Bibron, 1841	
Tomopterna damarensis Dawood and Channing, 1999	This study[1].
Tomopterna krugerensis Passmore and Carruthers, 1975	Namibe (Channing 2001).
Tomopterna tandyi Channing and Bogart, 1996	Namibe (Channing 2001)[2].
Tomopterna tuberculosa (Boulenger, 1882)	Biballa [= Bibala] (Bocage 1895; Ruas 1996); bottom of Leba Pass (Poynton and Haacke 1993; Ruas 1996).
REPTILES	
TESTUDINES	
Pelomedusidae	
Genus *Pelomedusa* Wagler, 1830	
Pelomedusa subrufa (Bonnaterre, 1789)	Mossamedes [= Namibe] (Bocage 1887, 1895; Loveridge 1941); Mucungo (Shmidt 1933; Loveridge 1941); Maconjo (Bocage 1895; Loveridge 1941); Capangombe (Bocage 1887, 1895; Loveridge 1941).
Testudinidae	
Genus *Kinixys* Bell, 1827	
Kinixys belliana Gray, 1830	Capangombe (Bocage 1895; Loveridge and Williams 1957).
Genus *Stigmochelys* Gray, 1873	
Stigmochelys pardalis (Bell, 1828)	Mossamedes [= Namibe] (Bocage 1895); Capangombe (Loveridge and Williams, 1957).
SQUAMATA	
Gekkonidae	
Genus *Afrogecko* Bauer, Good and Branch, 1997	
Afrogecko ansorgii (Boulenger, 1907).	Maconjo (Boulenger 1907b; Bauer et al. 1997).
Genus *Chondrodactylus* Peters, 1870	
Chondrodactylus fitzsimonsi (Loveridge, 1947)	Praia das Conchas (Laurent 1964a); around Moçâmedes [= Namibe] in the road to Sá da Bandeira [= Lubango] (Laurent 1964a); this study.
Chondrodactylus pulitzerae (Schmidt, 1933)	Mossamedes [= Namibe] (Bocage 1867, 1895; Loveridge 1947; Laurent 1964a); Pico Azevedo (Schmidt 1933; Barbour and Loveridge 1946, 1947; Marx 1959); Curoca River (Bocage 1887; Loveridge 1947); this study.
Genus *Hemidactylus* Oken, 1817	
Hemidactylus longicephalus Bocage, 1873.	Capangombe (Bocage 1873b, 1895, 1897; Loveridge 1947); Curoca Rriver (Bocage 1895, 1897; Loveridge 1947).

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Genus *Kolekanos* Heinicke, Daza, Greenbaum, Jackman and Bauer, 2014	
Kolekanos plumicaudus (Haacke, 2008).	Tambor (Haacke 2008; Mashinini and Mahlangu 2013); Curoca River (Haacke 2008); 11 km NE of Iona along track towards Oncocua (Haacke 2008; Heinicke et al. 2014).
Genus *Lygodactylus* Gray, 1864	
Lygodactylus capensis (Smith, 1849)	Mucungu (Schmidt 1933; Loveridge 1947); Capangombe (Bocage 1895)[3].
Lygodactylus lawrencei Hewitt, 1926	[4]
Genus *Pachydactylus* Wiegamnn, 1834	
Pachydactylus angolensis Loveridge, 1944	Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango] at Praia das Conchas (Laurent 1964a); Lucira (Bauer 1999); San Nicolau [= São Nicolau] (Bauer 1999); Lungo (Bauer 1999); Saco de Giraul (Bauer 1999); this study.
Pachydactylus caraculicus FitzSimons, 1959	Lungo (FitzSimons 1959); Caraculo (FitzSimons 1959; Haacke 1970; Mashinini and Mahlangu 2013); Giraul de Cima, river (FitzSimons 1959); 36 mi. northwest of Mocamedes [= Namibe] (Bauer 1999).
Pachydactylus cf. *oreophilus* McLachland and Spence, 1967	Assuñcao (= Assunção) (Bauer 1999); Caraculo (Bauer 1999); 20 km W Virei (Bauer 1999); 6 km S of Coroca River towards Iona (Bauer 1999); Saiona River, 25 km NW Cainde (Bauer 1999); Mutiambo River on road to Lucira (Bauer 1999); Tambor (Bauer 1999); 7 km from Iona towards Oncocau, Iona Reserve (Bauer 1999); Furnas (Bauer 1999).
Pachydactylus punctatus Peters, 1854	60 km of the road of Moçâmedes [= Namibe] to Sá da Bandeira (Laurent 1964a); Moçâmedes [= Namibe] (Laurent 1964a); 35 km south of Moçâmedes [= Namibe] (Laurent 1964a); Pico Azevedo (Schmidt 1933; Loveridge 1947); 11 mi NE of Mocamedes [= Namibe] (Bauer and Branch 1995).
Pachydactylus rangei (Andersson, 1908)	Mossamedes [= Namibe] (Haacke 1976b); Curoca River (Haacke 1976b); Porto Alexandre (Haacke 1976b); Cunene mouth (Haacke 1976b); Lacrau (Haacke 1976b); Namib Desert (Mertens 1937).
Pachydactylus vanzyli (Steyn and Haacke, 1966)	Espinheira (Haacke 1976a); Kakolo windmill (Haacke 1976a).
Genus *Rhoptropus* Peters, 1869	
Rhoptropus afer Peters, 1869	Maconjo (Bocage 1873b); Capangombe (Bocage 1873b, 1895, 1897b); Moçâmedes [= Namibe] (Boulenger 1885); Curoca River (Bocage 1887b, 1895, 1897b).
Rhoptropus barnardi Laurent 1964a	60 km from Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango] (Laurent 1964a); this study.
Rhoptropus biporosus Fitzsimons, 1957	Pico Azevedo (Bauer and Good 1996); this study.
Rhoptropus boultoni boultoni Schmidt, 1933	60 km from Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango] (Laurent 1964a); Pico do Azevedo (Schmidt 1933; Mertens 1938; Barbour and Loveridge 1946; Marx 1959; McCoy and Richmond 1966); this study.

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & Referencess
Rhoptropus boultoni montanus Laurent, 1964	This study.
Rhoptropus taeniostictus Laurent 1964a	Mucungu (Schmidt 1933); “60 km from Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango] (Laurent 1964a); this study.
Lacertidae	
Genus *Heliobolus* Fitzinger, 1843	
Heliobolus lugubris (A. Smith, 1838)	Maconjo (Bocage 1895); Capangombe (Bocage 1895); Konondoto (Boulenger 1921); this study.
Genus *Meroles* Gray, 1838	
Meroles anchietae (Bocage, 1867)	Moçâmedes (= Namibe) (Bocage 1867, 1895, 1897; Boulenger 1887; Loveridge 1936); this study.
Meroles reticulatus (Bocage, 1867)	Moçâmedes (= Namibe) (Bocage 1867; Boulenger 1887; Loveridge 1936); Coroca River (Bocage 1895, 1897; Boulenger 1887; Bauer and Günther 1995; this study.
Genus *Nucras* Gray, 1838	
Nucras tessellata (Smith 1838)	Maconjo (Bocage 1895; Broadley 1972); 34 km from Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango] (Laurent 1964; Broadley 1972).
Genus *Pedioplanis* Fitzinger, 1843	
Pedioplanis benguellensis (Bocage, 1867)	Maconjo (Boulenger 1921; Bauer and Günther 1995; Conradie et al. 2012); Capangombe (Bocage 1895; Monard 1937); Mossamedes [= Namibe] (Bocage 1887, 1895; Monard 1937); this study.
Pedioplanis haackei Conradie, Measey, Branch and Tolley, 2012	Red Canyon at Lake Arco (Conradie et al. 2012); 10 km south of Lake Arco (Conradie et al. 2012); Road to Tambor at giant Welwitchia (Conradie et al. 2012); Road from Lake Arco to Espinheira (Conradie et al. 2012); Omauha Lodge (Conradie et al. 2012); Road to Tambor (Conradie et al. 2012); 20 km north of Omauha Lodge (Conradie et al. 2012); this study.
Pedioplanis huntleyi Conradie, Measey, Branch and Tolley, 2012	Omauha Lodge (Conradie et al. 2012). 14 km west of Moimba (Conradie et al. 2012); 23 km west of Moimba (Conradie et al. 2012); 26 km east of Iona (Conradie et al. 2012); 16 km east of Iona (Conradie et al. 2012); 8 km northeast of Iona (Conradie et al. 2012); Road to Onocua 7 km NE from Iona (Conradie et al. 2012); 26 km SE of Onocua (Conradie et al. 2012).
Scincidae	
Genus *Eumecia* Bocage, 1870	
Eumecia anchietae Bocage, 1870	Moçâmedes [= Namibe] (Boulenger 1887)[5].
Genus *Mochlus* Günther, 1864	
Mochlus sundevallii (Smith, 1849)	Campangombe (Bocage 1895); Moçâmedes (= Namibe) (Bocage 1867; 1895); Curoca River (Bocage 1895); 10mls E of Caracul [= Caraculo] (Haacke 1965; Broadley 1966).

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Genus *Panaspis* Cope, 1868	
Panaspis cabindae (Bocage, 1866)	Capangombe (Bocage 1895, 1897).
Genus *Sepsina* Bocage, 1866	
Sepsina angolensis Bocage, 1866	Capangombe (Bocage 1895; Monard 1937).
Sepsina copei Bocage, 1873	Biballa [= Bibala] (Bocage 1895, 1897).
Genus *Trachylepis* Fitzinger, 1843	
Trachylepis acutilabris (Peters, 1862)	Cahinde-Ongueira (Hellmich 1957a); Mossâmedes [= Namibe] desert, 35 km south from the city (Laurent 1964a); Curoca River (Bocage 1895); this study.
Trachylepis bayonii bayonii (Bocage, 1872)	Moçâmedes [= Namibe] (Boulenger 1887).
Trachylepis binotata (Bocage, 1867)	Capangombe (Bocage 1895); 50 km Moçâmedes [= Namibe] to Sá da Bandeira [= Lubango]" (Laurent 1964a); Maconjo (Bauer et al. 2003).
Trachylepis chimbana (Boulenger, 1887)	Chimba River (Boulenger 1887; Bocage 1872, 1895, 1897; Broadley 1975a); Assunção (Broadley 1975a); Maconjo (Bocage 1895, 1897; Broadley 1975a), Moçâmedes [= Namibe] (Boulenger 1887); Lucira (Broadley 1975a); Chapeau Armando [= Chapéu Armando] turnoff, Mossamedes [= Namibe] (Broadley 1975a); Caraculo (Broadley 1975a); 14 km NE Caraculo (Broadley 1975a); Capangombe (Bocage 1895, 1897; Broadley 1975a); Mossamedes [= Namibe] (Boulenger 1887); Saiona River, NW of Cainde (Broadley 1975a); Cainde (Broadley 1975a); Coroca River (Broadley 1975a).
Trachylepis hoeschi (Mertens, 1954)	Praia das Conchas, Moçâmedes [= Namibe] (Laurent 1964a); this study.
Trachylepis lacertiformis (Peters, 1854)	Cainde (Broadley 1975); 14 km NE of Caraculo (Broadley 1975a).
Trachylepis laevis (Boulenger, 1907)	Maconjo (Boulenger 1907b); Munhino (Laurent 1964a); this study.
Trachylepis occidentalis (Peters, 1867)	Curoca River (Bocage 1895), 35 km south of the city of Moçâmedes [= Namibe] (Laurent 1964a); this study.
Trachylepis punctulata (Bocage, 1872)	Inamango River on Lucira road (Broadley 1975a); Mucungu (Schmidt 1933; Broadley 1975a); Sao Nicolau [= São Nicolau] (Broadley 1975a); 17 km N of Sao Nicolau [= São Nicolau] (Broadley 1975a); Caraculo (Broadley 1975a); 15 km W of Caraculo (Broadley 1975a); Cima [= Giraul de Cima] (Broadley 1975a); Pico Azevedo (Broadley 1975a); 23 km W of Virei (Broadley 1975a); Coroca River (Bocage 1872, 1895, 1897; Boulenger 1887; Broadley 1975a, 2000); 6 km S of Rio Coroca on Iona road (Broadley 1975a); Porto Alexandre [= Tômbua] (Broadley 1975a); 30 km N of Tambor (Broadley 1975a); Octchinfengo River on Onocua road, Iona Reserve (Broadley 1975a); Cunene mouth (Broadley 1975a); this study.
Trachylepis sulcata (Peters, 1867)	Capangombe (Bocage 1895); Munhino (Laurent 1964a); this study.

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Trachylepis varia (Peters, 1867)	Moçâmedes [= Namibe] (Bocage 1867); Biballa [= Bibala] (Bocage 1872); this study.
Genus *Typhlacontias* Bocage, 1873	
Typhlacontias johnsonii Anderson, 1916	Curoca River (Bocage 1895; Haacke 1997); Porto Alexandre (= Tombwa) [= Tômbua] (Haacke 1997); Lacrau (Haacke 1997).
Typhlacontias punctatissimus punctatissimus Bocage, 1873	Coroca River (Bocage 1873, 1887 1895, 1897); Mossamedes [= Namibe] (Boulenger 1887); Porto Alexandre [= Tômbua] (Haacke 1997).
Typhlacontias punctatissimus bogerti Laurent, 1964	Mossamedes [= Namibe] desert, 35 km south from the city (Laurent 1964a); Curoca River (Haacke 1997); Moçâmedes [= Namibe] (Haacke 1997); 10 km S of Moçâmedes [= Namibe] (Haacke 1997); 34 km S of Moçâmedes [= Namibe] (Haacke 1997); 8 km SE of Pico Azevedo (Haacke 1970); Kakolo windmill (Haacke 1997); this study.
Typhlacontias rudebecki Haacke, 1997	São Nicolau (Haacke 1997).
Varanidae	
Genus *Varanus* Merrem, 1820	
Varanus albigularis angolensis Schmidt, 1933	This study.
Varanus albigularis albigularis (Daudin, 1802)	Chimba River (Bocage 1895); Biballa [= Bibala] (Bocage 1895)[6].
Chamaeleonidae	
Genus *Chamaeleo* Laurenti, 1768	
Chamaeleo anchietae Bocage, 1872	Namibe (Tilbury 2010: 451).
Chamaeleo dilepis Leach, 1819	Moçâmedes [= Namibe] (Bocage 1867b; 1887; 1895); Chimba (Hellmich 1957a).
Chamaeleo namaquensis Smith, 1831	Moçâmedes [= Namibe] (Günther 1865; Bocage 1867, 1872, 1895; Boulenger 1887).
Agamidae	
Genus *Agama* Daudin, 1802	
Agama aculeata Merrem, 1820	Biballa [= Bibala] (Bocage 1895); Moçâmedes [= Namibe] (Bocage 1887b, 1895); Virei-Cahinde (Hellmich 1957a); Molundo (Monard 1937); Chimporo (Monard 1937).
Agama anchietae Bocage, 1896	Moçâmedes [= Namibe] (Bocage 1896, 1897); 100 km southeast of Moçâmedes [= Namibe] (Laurent 1964); Maconjo (Boulenger and Power 1921); this study.
Agama planiceps planiceps Peters, 1862	Biballa [= Bibala] (Bocage 1895); Pico Azevedo (Schimdt 1933); this study.
Cordylidae	
Genus *Cordylus* Laurenti, 1768	
Cordylus namakuiyus Stanley, Ceríaco, Bandeira, Valério, Bates and Branch, 2015	Caraculo, on the road from Lubango and Namibe (Stanley et al. 2016); Pico Azevedo (Stanley et al. 2016); road between Namibe and Omauha Lodge (Stanley et al. 2016); this study.

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Gerrhosauridae	
Genus *Cordylosaurus* Gray, 1865 [1866]	
Cordylosaurus subtessellatus (Smith, 1844)	Curoca River (Bocage 1895); this study.
Genus *Gerrhosaurus* Wiegmann, 1828	
Gerrhosaurus nigrolineatus Hallowell, 1857	Capangombe (Bocage 1895; Loveridge 1942)[7].
Gerrhosaurus skoogi Andersson, 1916	Porto Alexandre [= Tômboa] (FitzSimons 1953); this study.
Genus *Matobosaurus* Bates and Tolley, 2013	
Matobosaurus maltzahni (De Grys, 1938)	Chimba River (Bocage 1895); Moçâmedes [= Namibe] (Bocage 1895); Tambor (Bates et al. 2013); Omauha Lodge (Bates et al. 2013).
SERPENTES	
Typhlopidae	
Genus *Afrotyphlops* Broadley and Wallach, 2009	
Afrotyphlops anomalus (Bocage, 1873)	Biballa [= Bibala] (Bocage 1895; Broadley and Wallach 2009); Moçâmedes [= Namibe] (Bocage 1873).
Afrotyphlops schlegelii (Bianconi, 1847)	Biballa [= Bibala] (Bocage 1873, 1886, 1895, 1897a; Loveridge 1933).
Leptotyphlopidae	
Genus *Leptotyphlops* Fitzinger, 1843	
Leptotyphlops scutifrons (Peters, 1854)	Biballa [= Bibala] (Bocage 1873, 1895), Capangombe (Bocage 1895).
Pythonidae	
Genus *Python* Daudin, 1803	
Python natalensis Smith, 1840	Maconjo (Bocage 1895; Broadley 1984); Giraul River (Bocage 1896; Broadley 1984); this study.
Viperidae	
Genus *Bitis* Gray, 1842	
Bitis arietans (Merrem, 1820)	Moçâmedes (= Namibe) (Günther 1865; Manaças 1981).
Bitis caudalis (Smith, 1839)	Capangombe (Bocage 1895, Manaças 1981); Moçâmedes [= Namibe] (Günther 1865; Monard 1937; Manaças 1981); Mossamedes [= Namibe] Desert, 35 km south from the city (Laurent 1964a); Curoca River (Bocage 1895; Monard 1937; Manaças 1981).
Genus *Causus* Wagler, 1830	
Causus resimus (Peters, 1862)	Chimba River (Bocage 1895; Manaças 1981); Biballa [= Bibala] (Bocage 1895; Manaças 1981); Maconjo (Bocage 1895); Macujo [= Maconjo] (Manaças 1981).
Causus rhombeatus (Lichtenstein, 1823)	Cuce River (Ferreira 1897); Mossamedes [= Namibe] (Bocage 1887a, 1895).

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Lamprophiidae	
Genus *Aparallactus* Smith, 1849	
Aparallactus capensis capensis Smith, 1849	Biballa [= Bibala] (Bocage 1895, 1897a; Loveridge 1944b; de Witte and Laurent 1947).
Genus *Boaedon* Duméril, Bibron and Duméril, 1854	
Boaedon fuliginosus complex	Biballa [= Bibala] (Bocage 1895); Capangombe (Bocage 1895).
Genus *Lycophidion* Fitzinger, 1843	
Lycophidion hellmichi Laurent, 1964	Capolopopo (Laurent 1964a; Broadley 1991, 1996).
Lycophidion multimaculatum Boettger, 1888	Moçâmedes [= Namibe] (Bocage 1895; Laurent 1968; Broadley 1996).
Genus *Hemirhagerrhis* Boettger, 1896	
Hemirhagerrhis viperina (Bocage, 1873)	Cuce River (Ferreira 1897); Munhino (Bogert 1940; Broadley 1995b; Broadley and Hughes 2000); Maconjo (Bocage 1895; Broadley 1995b; Broadley and Hughes 2000); Capangombe (Bocage 1895; Broadley 1995b; Broadley and Hughes 2000); Huxe (Broadley 1997b; Broadley and Hughes 2000); Lungo (Broadley 1997b; Broadley and Hughes 2000); Caraculo (Broadley 1997b; Broadley and Hughes 2000).
Genus *Psammophis* Boie, 1825	
Psammophis leopardinus Bocage, 1887	Capangombe (Bocage 1887; Broadley 2002); Moçâmedes [= Namibe] (Bocage 1887, 1895; Loveridge 1957); Iona (Broadley 2002; Hughes and Wade 2002).
Psammophis mossambicus Peters, 1882	Mossamedes [= Namibe] (Loveridge 1940; Broadley 2002); Coroca River (Bocage 1895); Porto Alexandre [= Tômboa] (Loveridge 1940).
Psammophis namibensis Broadley, 1975	Mossamedes [= Namibe] (Broadley 1975b, 2002b); Pico Azevedo (Broadley 2002); Coroca River (Broadley 1975b, 2002); Cunene mouth (Broadley 1975b, 2002b); Cunene Forde, 15 km NE, Iona Res. (Broadley 2002).
Psammophis notostictus Peters, 1867	São Nicolao River (Boulenger 1896; Loveridge 1940; Broadley 1975b; 2002); Coroca River (Bocage 1887, 1895; Monard 1937; Loveridge 1940; Broadley 1975b, 2002); this study.
Psammophis subtaeniatus Peters, 1882	Biballa [= Bibala] (Bocage 1895, 1897a; Loveridge 1940); Maconjo (1895, 1897a; Loveridge 1940; Broadley 2002); Chao de Chella (Broadley 2002).
Psammophis trigrammus Günther, 1865	Sao Nicolao [= São Nicolau] River (Bocage 1887; Loveridge 1940; Broadley 1977, 2002; Wallach et al. 2014); Catara River (Broadley 2002); Coroca River (Broadley 2002b); Iona Reserve, 7 km to Oncócua (Broadley 2002).
Genus *Prosymna* Gray, 1849	
Prosymna frontalis (Peters, 1867)	Moçâmedes [= Namibe] (Boulenger 1893).
Prosymna visseri Fitzsimons, 1959	near Caracul [= Caraculo], S. Angola (Fitzsimons 1959; Bauer et al. 2001); Balabaia (Broadley 1980); 5 km S of Chibemba (Broadley 1980).

TABLE 1 (continued) – Only published records are included. Additional species known from the province based on unpublished museum records are not included unless also supported by published records.

Taxon	Occurrences & References
Elapidae	
Genus *Afronaja* Wallach, Wüster and Broadley 2009	
Afronaja mossambica (Peters, 1854)	Maconjo (Manaças 1981; Broadley 1974).
Afronaja nigricincta (Bogert, 1940)	Munhino (Bogert 1940; Manaças 1981); Maconjo (Manaças 1981); Capangombe (Bocage 1895); Cunene mouth (Manaças 1981).
Afronaja nigricollis (Reinhardt, 1843)	Capangombe (Ferreira 1900b; Manaças 1981).
Genus *Aspidelaps* A. Smith, 1849	
Aspidelaps lubricus cowlesi Bogert, 1940	Munhino (Bogert 1940; Manaças 1981; Broadley and Baldwin 2003).
Genus *Boulengerina* Dollo, 1886	
Boulengerina melanoleuca Hallowell, 1857	Capangombe (Ferreira 1900b; Manaças 1981).
Genus *Elapsoidea* Bocage, 1866	
Elapsoidea semiannulata semiannulata Bocage, 1882	Maconjo (Bocage 1895, 1897c; Loveridge 1944b; Broadley 1971, 1998b; Manaças 1981).
Colubridae	
Genus *Coluber* Linnaeus, 1758	
Coluber zebrinus Broadley and Schätti, 1997	**8**
Genus *Crotaphopeltis* Fitzinger, 1843	
Crotaphopeltis hotamboeia (Laurenti, 1768)	Biballa [= Bibala] (Bocage 1895).
Genus *Philothamnus* Smith, 1840	
Philothamnus angolensis Bocage 1882	Capangombe (Bocage 1882a, 1897a; Loveridge 1951, 1957; Chirio and LeBreton 2007; Wallach et al. 2014).
Philothamnus irregularis (Leach, 1819)	Capangombe (Bocage 1882a, 1887, 1895); Mossamedes [= Namibe] (Bocage 1887, 1895).
Philothamnus ornatus Bocage, 1872	**9**
Philothamnus semivariegatus (Smith, 1840)	Maconjo (Bocage 1882a); Capangombe (Bocage 1895; Haacke 1985).
Genus *Telescopus* Wagler, 1830	
Telescopus finkeldeyi Haacke, 2013	5 km north Namibé [= Namibe] (Haacke 2013).
Genus *Thelotornis* A. Smith, 1849	
Thelotornis capensis oatesi (Günther, 1881)	Biballa [= Bibala] (Bocage 1895; Loveridge 1944b).

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Exotic Terrestrial Macro-Invertebrate Invaders in California from 1700 to 2015: An Analysis of Records

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We document that 1,686 exotic terrestrial macro-invertebrates from 278 families have developed self-sustaining populations in California, USA over the period 1700 to 2015. The majority of exotic arthropods are insects (84.4%) followed by mites (7.5%) and spiders (3.2%). The insect Order Hemiptera, Auchenorrhyncha and Sternorrhyncha combined, has the greatest insect representation at 27.6%. The Aphididae is the most successful group of invaders with 183 species established in California. Small, less mobile plant feeders (e.g., plant feeders like thrips, scales, mealybugs, whiteflies and aphids) have successfully invaded more often than large mobile invertebrates (e.g., bees and wasps, butterflies and moths, grasshoppers and katydids, or beetles). The greatest number of invaders (43.6%) most likely came to California from invasion bridgeheads established elsewhere in North America (USA and Canada). The date of first detection is known for approximately 1,116 (66%) invertebrate species and the temporal invasion rate has not remained constant over time. Fewer invaders were detected over 1970–1989 at a rate of ~ 6 species per year. This rate increased to ~ 9.7 new species detected per year from 1990 to 2010, an increase of ~ 62% since 1989. Invasion rates into California have not increased significantly post 11 September 2001 when the Department of Homeland Security assumed responsibility from United States Department of Agriculture-Animal Plant Health Inspection Service (USDA APHIS) for border protection. It is anticipated that invasion rates for invertebrates will continue to increase and more exotic organisms will establish in California because of increasing trade and tourism and a corresponding lack of increased resources for pest surveillance, detection, and post-incursion management.

KEYWORDS: invasion rates, invasive species, change point analyses, impacts of invasive species

Over the last 25 years there has been growing awareness that exotic invasive organisms can greatly modify our urban, agricultural, and native habitats (Mattson et al. 1994, Barthell et al. 1998, Pimentel et al. 2000, Jass and Klausmeier 2001, Beatty 2002, Huber et al. 2002, Hoddle et al. 2004, Sierwald et al. 2005, Footitt et al. 2006, Haack 2006, Bolger et al. 2000, Kenis et al. 2009, Aukema et al. 2010, Aukema et al. 2011, Engelkes and Mills 2011, Roy et al. 2011a,b). The literature is rich in examples, and generally includes instances of invasive species that adversely affect native flora and fauna, reduce agricultural productivity, and impact urban areas. Some invasive species affect human, animal, and plant health, while others degrade and deny citizens the use of parklands and wilderness areas (Dowell 1988; Horsfall 1983, Dowell and Gill 1989, Knight and Rust 1990, Dowell and Krass 1992, Daehler and Strong 1995, Holway 1998, Suarez and Case 2002). However, biological invasions are complex processes whose individual components are not easily understood (Kolar and Lodge 2001, Crooks 2005, Barney and Whitlow 2008).

The environmental and economic impacts that result from invasion events are the reason that regulatory agencies like the California Department of Food and Agriculture (CDFA), United States Department of Agriculture Animal Plant Health Inspection Service (USDA-APHIS), and the Department of Homeland Security (DHS) are charged to detect and prevent the establishment of non-native species within their jurisdictions. Following the passage of the 2002 Homeland Security Act, USDA-APHIS personnel were transferred into Customs and Border Protection (CBP) under the auspecies of DHS in 2003 and this resulted in the incorporation of the protection of US Agriculture into CBP's anti-terrorism mission (GAO 2006). US agriculture is a $1 trillion per year enterprise, and this significant change in focus from pest and disease exclusion to detecting terrorist activity raised concerns that US agriculture may experience increased vulnerability to invasive pests and diseases affecting crops and lifestock (GAO 2006).

For invasive species managers, researchers, and regulatory agencies, a first step in managing the invasion process is the development of lists of successful invaders and their likely area of origin (Dowell and Gill 1989). This information may help identify likely future invaders and their-probable sources, and assist with resource allocation decisions for monitoring, detection, and management programs (Crooks et al. 1983, Dowell and Gill 1989, Work et al. 2005, Koch et al. 2011). Additionally, these lists can be used to look for temporal, geographic origin, and species compostion changes in invasion rates. The suggestion that the transfer of pest detection and exclusion responsibilities from USDA-APHIS to CBP could have increased the rate of unwanted pest introductions (GAO 2006) is a hypothesis that can be examined statistically with a chronologically constructed species detection list.

Dowell and Gill (1989) published a list of exotic invaders in California and their likely origins over the period 1955–1988. Although this study (Dowell and Gill 1989) has been cited widely, it encompassed a limited timeframe and utilized one data source. Using Dowell and Gill (1989) as a reference point, the goals of this paper are: 1) to expand the timeframe of analyses to include exotic terrestrial macro-invertebrates that successfully invaded California from 1700 to 2015; 2) to utilize a wider range of information resources that document breeding populations of invasive macro-invertebrates in California; and 3) use these expanded datasets to examine the composition and origins of invading species and how they have changed over time. In particular, this dataset provided an opportunity to determine whether or not invasion rates into California increased after CBP assumed responsibility for managing unwanted pest and disease incursions. Here we refer to exotic invaders in the broadest sense, non-native species that developed reproducing populations in California. These organisms may or may not cause economic or environmental problems, but the commonality underlying this resident community is their non-native status. Additionally, some species that developed reproducing populations in California may have done so temporarily before being successfully eradicated. In the absence of eradication efforts, these species would likely still be in California, and are therefore considered species that successfully developed breeding populations before being deliberately extirpated.

Methods

Construction of an Invasive Terrestrial Invertebrate Species List for California.— To develop a list of exotic terrestrial macro-inverterbrate invaders (Appendix), we examined print and electronic sources for information on breeding populations within the state of California, USA. The following criteria were used to develop a documented evidence list (McGeoch et al. 2012): 1) One or more authorities noted that the organism was found in California, and 2) these sources noted that the organism was not native to California; 3) There was evidence of a breeding population of the organism outside of a quarantine situation initiated to contain a possible incipient infestation. For example, the discovery of a single individual, such as the male Queensland fruit fly, *Bactrocera tryoni* (Diptera: Tephritidae) found in California in 1991, was not considered evidence of a breeding population (Centre for Agriculture and Biosciences International 2016). Organisms discovered in ports, or at nurseries importing stock from outside California were considered to be contaminants and were within the State of California's quarantine system and therefore were not included in the list; 4) For analysis of electronic sources, like *BugGuide*, we included species for which we could find another source to independently confirm the presence of breeding populations or when there were one or more pictures posted on web sites documenting the invader of interest from locations outside of quarantine situations within California; 5) If an organism had invaded California several times, and reproducing populations were detected (e.g., oriental fruit fly, *Bactrocera dorsalis*) (Stephens et al. 2007), only the first successful reproducing population was considered; 6) Arthropod biological control organisms (i.e., predators and parasitoids) that were intentionally released in California were not included in the list. Neither was the deliberately introduced European honey bee, *Apis mellifera*.

The point sources of pests arriving in California may not necessarily correspond with the pest's native home range. Therefore, if a newly detected invasive species was found in California and populations of this pest existed previously elsewhere within North America (i.e., the US or Canada), the parsimonious decision was made that assumed in the absence of contrary evidence (e.g., molecular-based data if it existed) that the population of interest originated from populations already established in North America and did not represent a novel introduction directly from the native range of the invader. This decision was based partly on the volume of traffic entering California each year. In 2010 (most recent data available) some 27.3 million private vehicles entered California along with 7.14 million commercial trucks (California Department of Food and Agriculture 2011). For example, the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), almost certainly entered California from long-established populations in the eastern United States and it did not invade California directly from its native South America.

We have identified in the Appendix invertebrates that are classified not native to California and in some instances are classified as pests. For plant, home and garden, and the environment, we identify those invertebrates listed as pests in the University of California IPM online (UC IPM 2014), sheep and goat pests are from Pirelli (2013), dairy cattle pests are those identified by Geden et al. (2010), horse insect pests are from Meyer et al.(1991), swine pests are from Loftin (2013), and chicken pests are from Stafford III (2011). These sources tend to deal with animals that are established in California or are frequently detected there. We have also identified some pests not established in California (IPPC 2007) but which have been detected here and which are generally considered pests in those areas where they occur. These include the gypsy moth (*Lymantria dispar*) (Liebhold 2003), Japanese beetle (*Popillia japonica*) (Anon. 1997), Mexican bean beetle (*Epilachna varivestis*) (Sanchez-Arroyo 2015), oriental fruit fly (*Bactrocera dorsalis*), Mexican fruit fly (*Anastrepha ludens*), Caribbean fruit fly (*Anastrepha suspensa*), peach fruit fly (*Bactrocera zona-*

ta), Mediterranean fruit fly (*Ceratitis capitata*), melon fly (*Bactrocera cucurbitae*), white striped fruit fly (*Bactrocera albistrigata*), guava fruit fly (*Bactrocera correcta*) (White and Elson-Harris 1992), boll weevil (*Anthonomus grandis*) (Lange et al. 2008), varroa mite (*Varroa jacobsoni*) (Bessin 2001), red palm weevil (*Rhynchophorus vulneratus*) (Rugman-Jones et al. 2013), Diaprepes root weevil (*Diaprepes abbreviatus*) (Grafton-Cardwell et al. 2004), Asian longhorn beetle (*Anoplophora glabripennis*) (USDA APHIS 2015), and cereal leaf beetle (Walentra 2014).

The year the organism was identified from California is listed unless there is published information supporting the use of an earlier date. Organisms listed in overview works (e.g., Essig 1915, 1926) are assumed to have entered the state in the decade prior to the work's publication date. For ~34% of recorded exotic invertebrates, the date of introduction was either unknown or was uncertain and therefore not included in analyses.

Statistical Analyses.— Change point detection analyses aim to identify when a sequence of time ordered observations changes with respect to the underlying model that generates data. A common type of change point analysis is to look for a change in either the mean or the variance of the data generating model. Change point analyses were used to determine if the model for the annual number of exotic macroarthropods incurred a change point over the period 1935 to 2010. The time period 2011–2015 was not included because of the time lag in the publication of non-native animals discovered in California therein. Although the data source available for analyses extends to periods earlier than 1935, data quality was perceived to be a potential issue that could influence analyses, hence a conservative approach was taken and this 75 yr period was selected. The change point detection method used was CUSUM (cumulative sum) that detects shifts in the mean in the data series under analysis. The software package Change Analyzer, (2013), was used to identify change points using the CUSUM method. Succinctly, the CUSUM analysis was computed as follows: first, the overall average number of exotic arthropds was calculated for the time interval of interest; second, the cumulative sum for the time interval of interest was initialized at zero; and third, cumulative sums were calculated by sequentially adding deviations of current values from the average to the previous cumulative sum. A CUSUM chart, a plot of the cumulative sums versus time, was used to identify transitions or change points in the sequence. Potential change points were evaluated using bootstrap procedures to determine their statistical significance. When a significant change point was detected, its location was determined by identifying the last point before the change and the first point after the change. This sequence was divided at the change point and the CUSUM procedure was repeated on each of the new segments to determine if additional significant change points existed. Of particular interest in change point analyses performed on this data set was that of testing the hypothesis that incursions of invasive arthropods into California increased after 11 September 2001 (GAO 2006).

We used chi-square analysis (Little and Hills 1978) to compare the composition of species established in California to the worldwide composition of the taxa they represent, and to determine if the composition of the invaders by area of origin differs from global composition. All analyzes herein include the exotic organisms listed in an earlier work (Dowell and Gill 1989) and organisms are grouped by family rather than by order as done in Dowell and Gill (1989). Family-level classification provides finer taxonomic resolution and accommodates recent taxonomic nomenclatural changes. We also compared the composition by taxa of invaders from each region to their over-all composition. For this analysis, the expected values were generated by multiplying the percentage of each invading taxa over-all by the total number of invaders from each region. For example the percentage of Coleoptera in the over-all composition of invaders was multiplied by the number of invaders recorded from North America.

Results and Disussion

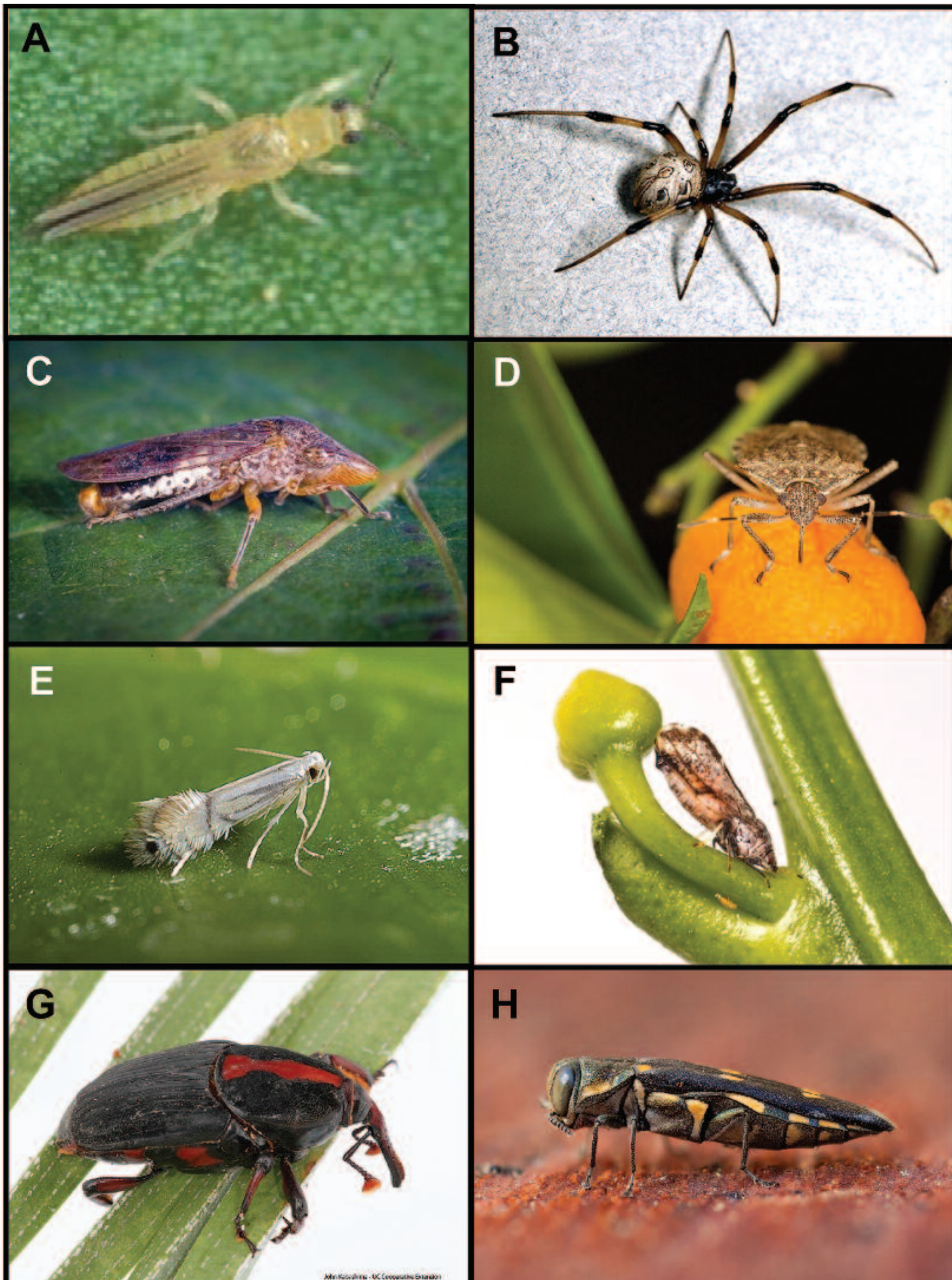
Composition of Invaders.— We identified 1,686 species of exotic terrestrial macro-invertebrates that have developed breeding infestations within California over the time period 1700 to 2015 (Appendix). These organisms include earthworms (Annelida: Oligochaeta), mites and spiders (both Arthropoda: Arachnida), centipedes (Arthropoda: Chilopoda), millipedes (Arthropoda: Diplopoda), slugs and snails (both Mollusca: Gastropoda), woodlice (Arthropoda: Isopoda), insects (Arthropoda: Insecta), and one amphipod (Arthropoda: Amphipoda) from 278 different families. The majority of these exotic organisms are insects (84.4%) followed by mites (7.4%) and spiders (3.2%) (Table 1) (Figure 1).

A number of organisms on the list (see Appendix) developed breeding populations in California that were or are being subjected to Official Action (quarantine and eradication) in accordance with internationally accepted guidelines (IPPC 2007) by the California Department of Food and Agriculture often in collaboration with the United States Department of Agriculture. Organisms subject to official action are not considered to be established in California. These include the Mediterranean fruit fly, *Ceratitis capitata*; Mexican fruit fly, *Anastrepha ludens*; peach fruit fly, *Bactrocera zonata*; guava fruit fly, *Bactrocera correcta*; gypsy moth, *Lymantria dispar*; boll weevil, *Anthonomus grandis*; Japanese beetle, *Popillia japonica*; Caribbean fruit fly, *Anastrepha suspensa*; melon fly, *Bactrocera cucurbitae*; Hall scale, *Nilotaspis halli*; red palm weevil, *Rhynchophorus vulneratus*; white striped fruit fly, *Bactrocera albistrigata*; European grapevine moth, *Lobesia botrana*; Mexican Bean Beetle, *Epilachna varivestis*; Asian gypsy moth, *Lymantria dispar asiatica*; and Asian longhorn beetle, *Anoplophora glabripennis*.

Table 1. Composition by taxon of exotic terrestrial macro-invertebrates found breeding in California 1700–2010.

Taxon[a]	Number of organisms	Percent of total organisms
Hemiptera: Auchenorrhyncha + Sternorrhyncha	467	27.6
Coleoptera	344	20.4
Lepidoptera	172	10.2
Acari	125	7.4
Diptera	122	7.2
Hymenoptera	96	5.6
Thysanoptera	63	3.7
Hemiptera- Heteroptera	50	2.9
Araneae	53	3.2
Mollusca	43	2.5
Phthiraptera	34	2.0
Dicytoptera	19	1.11
Opisthopora	16	1
Psocoptera	16	1
Isopoda	11	0.6
Orthoptera	9	0.5
Dermaptera	9	0.5
Diploda	9	0.5
Siphonaptera	9	0.5
Thysanura	5	0.3
Collembola	4	0.24
Chilopoda	2	0.12
Embiidina	2	0.12
Amphipoda	1	0.06
Isoptera	1	0.06
Phasmida	1	0.06
Symphyla	1	0.06
Total	1686	

[a] See Appendix for list of organisms.


A
B
C
D
E
F
G
H

The Hemiptera, Auchenorrhyncha, and Sternorrhyncha combined, has the greatest representation (Table 1) with 27.6% of all organisms. Next speciose are the Coleoptera (20.4%), Lepidoptera (10.2%), Acari (7.4%), Diptera (7.2%) and Hymenoptera (5.6%). Remaining taxons have no more than 3.6% of recorded organisms (Table 1). This differs somewhat from a list of non-native species for all of North America that had the Coleoptera ranked first followed by the Hymenoptera, Hemiptera, Diptera and Lepidoptera (Yamanaka et al. 2015). Yamanaka et al. (2015) included releases of biological control agents and excluded species that were eradicated, the opposite of this study.

As seen in other studies (Lawton et al. 1986, Gaston et al. 2001, Karatayev et al. 2009), the composition of invading animals deviates significantly from random ($\chi^2 = 257.497$; df = 25; $p < 0.001$) (Table 2) based on their worldwide numbers (Borror et al. 1989, Brusca 1997, Shelley 1999, Halliday et al. 2000, Triplehorn and Johnson 2005, Chapman 2009, Platnick 2011, Ramel 2011). Hemiptera (Auchenorryncha and Sternorrhyncha), Acari, Thysanoptera, Psocoptera, Siphonaptera, Dermaptera, Phthiraptera, Dictyoptera, Isopoda, and Thysanura invaded California more often than expected. Conversely, Coleoptera, Lepidoptera, Diptera, Hymenoptera, Araneae, Collembola, Chilopoda and Orthoptera invaded less often than expected. In general, small, less mobile plant feeders (e.g., whiteflies, thrips, mites, aphids and scales) invaded California more often than expected and larger more mobile insects (e.g., bees and wasps, butterflies and moths, grasshoppers, true bugs, spiders, and beetles) less often than expected. Similar invasion patterns have been seen in other studies (Lawton et al. 1986, Gaston et al. (2001).

The most successful group of invaders was the Aphididae (183 species [10.9% of the total]) (Table 3). After the aphids the most numerous invaders were, in descending order, the Curculionidae (83 species [4.9% of invasive species]), Staphylinidae (74 species [4.4%]), Eriophyidae (72 species [4.2%]), Diaspididae (71 species [4.2%]),), and Pseudococcidae (59 species [3.5%]). Other highly successful invaders were in the Cicadellidae (Hemiptera), Thripidae (Thysanoptera), Coccidae (Hemiptera), Psyllidae (Hemiptera), Aleyrodidae (Hemiptera), Formicidae (Hymenoptera), Chrysomelidae (Coleoptera), Tetranychidae (Acari), Miridae (Hemiptera: Heteroptera), Tenebrionidae (Coleoptera), and four families of moths (Lepidoptera: Gelechiidae, Noctuidae, Pyralidae and Tortricidae) (Table 3).

Successful invaders included many well known invertebrates including the codling moth (*Cydia pomonella*), silverfish (*Lepisma saccharina*), European earwig (*Forficula auricularia*), pillbug (*Armadillidium vulgare*), cabbage butterfly (*Pieris rapae*), American (*Periplaneta americana*) and German (*Blattella germanica*) cockroaches, brown garden snail (*Cornu aspersum*), house fly (*Musca domestica*), praying mantis (*Mantis religiosus*), and Argentine ant (*Linepithema humile*) (Appendix). As discussed below, many successful invaders are important pests of agricultural, horticultural and floricultural crops, wilderness areas, livestock, urban gardens, houses, pets, and people.

Origins of Invaders.— The origins of 980 of listed invaders are known or suspected (Table 4). The greatest number of invaders came to California from elsewhere in North America (i.e., USA

Figure 1 (left). Examples of non-native macro-terrestrial arthropods that have been detected in California. A. Avocado thrips, *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae). (Detected 1992). B. Brown widow spider, *Latrodectus geometricus* Koch (Araneae: Theridiidae) (detected 2003). C. Glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) (detected 1994). D. Brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae) (detected 2005). E. Citrus leafminer, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae) (detected 1999). F. Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) (detected 2008). G. Palm weevil, *Rhynchophorus vulneratus* (Panzer) (Coleoptera: Curculionidae) (detected 2010) (eradicated 2015). H. Gold spotted oak borer, *Agrilus auroguttatus* Waterhouse (Coleoptera: Buprestidae) (detected 2004).

TABLE 2. Expected versus observed number of exotic invertrbrate invaders based on their worldwide numbers.

Taxon	Expected number of invading species[h]	Observed number of invading species[i]
Hemiptera: Auchenorrhyncha plus Sternorrhyncha[a]	83	468
Coleoptera[a]	496	312
Lepidoptera[a]	248	167
Acari[b]	70	125
Diptera[a]	248	109
Hymenoptera[a]	190	94
Thysanoptera[a]	7	59
Hemiptera- Heteroptera[a]	58	55
Araneae[c]	80	52
Mollusca[d]	39	43
Phthiraptera[a]	5	34
Psocoptera[a]	5	16
Dictyoptera[a]	10	19
Isopoda[e]	8	11
Diplopoda[b]	16	9
Orthoptera[a]	33	9
Dermaptera[a]	3	9
Siphonaptera[a]	4	8
Thysanura[a]	1	5
Collembola[a]	10	4
Chilopoda[g]	5	2
Embiidina[a]	1	2
Isoptera[a]	4	1
Phasmida[a]	4	1
Symphyla[g]	1	1

[a] Based on numbers in Borrer et al. 1989 and Triplehorn and Johnson 2005.
[b] Based on numbers in Halliday et al. 2000.
[c] Based on numbers in Platnick 2011.
[d] Based on numbers in Chapman 2009.
[e] Based on numbers in rusca 1997.
[f] Based on numbers in Ramel 2011.
[g] Based on numbers in Shelley 1999.
[h] rounded to the nearest whole number or to one if less than 0.50.
[i] See Appendix for list of organisms. $\chi^2 = 2{,}688.37$; df = 25; $p < 0.001$.

TABLE 3. The twenty families with the largest number of exotic terrestrial macro-invertebrates found breeding in California.

Order	Family	Number of Species[a]
Hemiptera	Aphididae	183
Coleoptera	Curculionidae	83
Coleoptera	Staphylinidae	764
Acari	Eriophyidae	72
Hemiptera	Diaspididae	71
Hemiptera	Pseudococcidae	59
Thysanoptera	Thripidae	49
Hemiptera	Cicadellidae	47
Hemiptera	Psyllidae	37
Hemiptera	Coccidae	35
Coleoptera	Chrysomelidae	30
Lepidoptera	Pyralidae	26
Hymenoptera	Formicidae	25
Hemiptera	Miridae	24
Acari	Tetranychidae	23
Lepidoptera	Tortricidae	21
Hemiptera	Aleyrodidae	20
Lepidoptera	Gelechiidae	20
Coleoptera	Tenebrionidae	19
Lepidoptera	Noctuidae	16

[a] See Appendix for list of organisms.

TABLE 4. Number of exotic terrestrial macro-invertebrates by origin.

Origin	Number of organisms[a]	Percent of total
North America	422	43.6
Europe	243	24.8
Asia	100	10.2
Tropical America	71	7.2
Australia	48	4.9
Africa	46	4.7
Hawaii	2227	2.2
Mexico	20	2.0
Pacific Region	8	0.8
Total	980	

[a] See Appendix 1 for list of organisms. $\chi^2 =$ 1,386.31; df = 8; $p < 0.001$. Assumes an average of 108.8 invaders from each region.

and Canada) (422 species; 43.6%). These invaders were comprised of species native to the USA (e.g. the glassy-winged sharpshooter, *Homalodisca vitripennis,* which is native to the southeastern USA) (e.g., indigenous exotics (Dodds et al. [2010]) and species exotic to the USA but which likely invaded California from invasion bridgeheads within the USA (e.g., red imported fire ant and European gypsy moth). Europe was the second largest source of exotic invaders (24.8%) followed by Asia (including Japan) (10.2%), Tropical America (Central America and South America) (7.2%), Australia (4.9%), Africa (4.7%), Hawaii (2.2%), Mexico (2.0%), and the Pacific Region (areas bordering the Pacific Ocean including New Zealand but excluding Hawaii and Japan) (0.8%) (Table 4).

Mexico and Hawaii are listed separately because of their relatively close proximity to California, high reciprocal volumes of trade and tourist traffic, and the belief that numerous invaders enter California from these two areas (Dowell and Gill 1989). Organisms from the Mediterranean Region were assigned to either Africa or Europe as appropriate. The distribution of recorded invaders was not uniform ($\chi^2 = 1{,}386.31$; df = 8; $p < 0.001$) with more species than expected infiltrating California from North America and Europe and fewer invaders than expected originating from Tropical America, Australia, Africa, Hawaii, Mexico and the Pacific Region (Table 4).

Not all taxa invaded California from all regions (Table 5). Only the Acari, Diptera, Hemiptera Auchenorrhyncha and Sternorrhyncha, and Lepidoptera have representatives from every region.

No region has invaders from every taxa (Table 5). Europe has representatives from 20 of 26 taxa followed by North America (15), Africa (15), Tropical America (11), Asia and Australia (10), Hawaii (9), and Mexico (6).

Chi-square analysis found the composition of invaders from North America ($\chi^2 = 48.04$, df = 10, $p < 0.001$), Europe ($\chi^2 = 4.975$, df = 11, $P < 0.001$), Africa ($\chi^2 = 13.67$, df = 2, $p < 0.01$), Asia ($\chi^2 = 43.89$, df = 5, $p < 0.001$), Tropical America ($\chi^2 = 11.86$, df = 3, $p < 0.01$), and Australia ($\chi^2 = 20.0$, df = 3, $p < 0.001$) deviated significantly from that seen in Table 1 (Table 5). There were too few species recorded from Hawaii, Mexico and the Pacific region to analyze (Little and Hills 1978).

Invasion Frequencies into California Post September 11, 2001 — Change Point Analyses.— Count data for the number of recorded invasive species by year over the period 1935–2010 (Fig. 2) and the CUSUM plot for this 75-year data set are shown in Fig. 3. Three significant change points were identified, 1941, 1971, and 1983 (Table 6). The mean number of exot-

Table 5. Likely origins of the exotic terrestrial macro-invertebrates found breeding in California by taxon.

Taxon[a]	Mexico	North America	Europe	Africa	Asia	Hawaii	Pacific Region	Tropical America	Australia
Acari	3	24	18	2	4	2	1	4	1
Amphipoda	0	0	0	0	0	0	0	0	1
Araneae	0	4	8	1	0	0	0	4	0
Chilopoda	0	0	2	0	0	0	0	0	0
Coleoptera	1	78	50	4	10	1	0	7	6
Collembola	0	0	3	0	0	0	0	0	0
Dermaptera	0	1	1	1	0	0	0	0	0
Dictyoptera	0	4	2	4	2	0	0	0	0
Diplopoda	0	1	6	0	2	0	0	0	1
Diptera	1	32	17	2	7	4	2	7	5
Embiidina	0	0	2	0	0	0	0	0	0
Hemiptera- Heteroptera	0	17	14	1	43	1	0	3	1
Hemiptera: Auchenorrhyncha + Sternorrhyncha	9	141	58	23	58	8	3	32	21
Hymenoptera	0	33	6	5	5	3	0	3	9
Isopoda	0	0	8	1	0	0	0	0	0
Isoptera	0	0	0	0	0	1	0	0	0
Lepidoptera	5	66	19	1	5	1	1	7	1
Mollusca	0	10	22	1	0	1	0	0	0
Orthoptera	0	5	3	0	0	0	0	0	0
Phasmida	0	1	0	0	0	0	0	0	0
Phthiraptera	0	0	0	0	0	0	0	0	1
Psocoptera	0	0	4	0	0	0	0	0	0
Siphonaptera	0	0	1	0	0	0	0	1	0
Symphyla	0	0	0	0	0	0	0	0	0
Thysanoptera	1	5	9	0	3	0	1	3	1

[a] See Appendix for list of organisms.

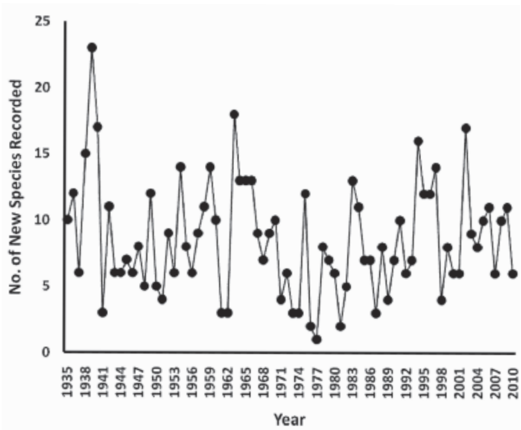


FIGURE 2. Total number of invertebrates detected in California 1935–2010.

FIGURE 3. Plot of CUSUM values for counts of exotic arthropods recorded in California over the period 1935 to 2010.

ic arthropods before and after the change was detected with 95% confidence intervals for the year of the detected change, and thus the degree of confidence was interpreted as indicating that declaring that the detected change was real. The mean estimates of the numbers of detected exotic arthropods before and after the detected changes are presented in Table 6. There is no statistical evidence to support the hypothesis that the number of invasive species recorded in California increased after 2001. A truncated data set spanning 1991–2010 (20 years) was further analyzed to assess the effect of 2001 on incursion rates in California. Again no significant change points were detected (results not shown) supporting the results of the analyses using the larger 1935–2010 data set.

TABLE 6. Significant change point results indicating year of detected change, 95% confidence interval (in years), level of confidence that the detected change point is real, and the observed change from the mean number of exotic arthopods detected before the change point to the new mean after the change occurred.

Year change was detected	95% confidence interval	Confidence level (%)	Mean number of species before change was detected	Mean number of species after change was detected
1941	1936–1949	96	13.83	8.6
1971	1949–1976	95	8.6	4.92
1983	1978–1996	94	4.92	8.89

The change point analysis detected three transitional points underlying exotic arthropod species records for California over the period 1935–2010, 1941, 1971, 1983. The causes underlying these changes are undetermined and beyond the scope of this study, which sought to determine if a significant change in arthropod numbers occurred after 2001. There are several important caveats to consider here when interpreting the significance of these results. The first concerns intensity and consistency of sampling efforts, resources invested in surveying for invasive pests, and technical capability, especially with regard to recognition and identification of new species. It is highly unlikely that these factors were consistent each year over 1935–2010. Short duration high intensity surveys focusing on invasive ants, spiders, or scale pests, as part of a research project for example, could greatly increase the number of records for new species in a particular taxon. This type of survey work, while valuable, is not uniform through time or across taxa and high intensity effects with narrow focus probably affects the quality of data sets for analysis. Additionally, data were not adjusted for other covariates that could influence invasion rates and detection and identification of new resident species. These additional factors include increasing rates of tourism, economic development, and population growth, all of which have been correlated with invasion likelihood. Political policies such as the construction and operation of additional border inspection stations, or subsequent closures and reduced hours for stations during economic recessions may also influence the rate at which exotic arthropods enter and establish in California. Although no significant change in the number of exotic arthropods in California was detected after 2001, this does not necessarily mean that the numbers of invasive pests entering and establishing has not changed. There may be a significant lag period before detection and confirmation of new species occurs, and subsequent analyses of data sets with a longer time series post-2001 may be needed to confirm or refute the result presented here.

Table 7. Number of exotic terrestrial macroinvertebrates discovered breeding in California by time period in which they were discovered.

Time Period[a]	Number Exotic Invaders	Average number per year
< 1900	112	—
1901–1929	312	108
1930–1939	99	9.9
1940–1949	76	7.6
1950–1959	84	8.4
1960–1969	95	9.5
1970–1979	53	5.9
1980–1989	68	6.8
1990–1999	99	9.96
2000–2010	118	7.9
Total	1116	

[a] See Appendix for data. The time periods <1900 and 1901–1929 were excluded from the analysis because we cannot assign the dates of arrival to specific decades. $\chi^2 = 61.37$; df = 7; $p < 0.01$ using an average number of invaders of 121.8 per decade. Data from 2011–2015 excluded due to lag in publication of invasive species information.

Temporal Patterns of Invasion.— Detection times for 1079 exotic terrestrial macroinvertebrates are presented in Table 7. The greatest number (419; 38.8%) of these organisms was detected in California prior to 1930 (Table 7).

The temporal invasion rate has not remained constant over time ($\chi^2 = 61.37$; df = 7; $p < 0.01$) with fewer than expected invaders being recorded during the period 1970–1989. The rate of invasion since 1989 has increased to levels similar to those recorded from 1950 to 1969 (Table 7). Other studies concluded that the rate of introduction of exotic pests was increasing (Aukema et al. 2010, Kirkendall and Faccoli 2010, Roy et al. 2011).

The origins of invaders have not remained constant over the time period of this study. There has been a marked increased in the number of invaders from Australia between 1980 and 2010, Asia between 2000 and 2010, Hawaii between 1980 and 1999, and Europe between 1990 and 2010 (Table 8). These trends may reflect increased trade and tourism, which are proxies for propagule pressure.

Similarly, the composition of invaders has not remained constant over time. There were marked increases in the number of Coleoptera (11 versus 45), Diptera (9 versus 33) and Hemiptera (Heteroptera) (5 versus 15) detected between 1990 and 2015 and Hymenoptera (11 versus 25) between 1990 and 1999 compared to the preceeding decades (1970–1989) (Table 9).

Examining the origin and composition data over time in the Appendix reveals interesting trends. Eighteen invasive wood boring Coleoptera (Buprestidae, Cerambycidae and Curculionidae) were discovered in California between 2000 and 2015 with five species from Asia, eight from North America, four species from Europe, and one from Africa. There were 10 Hymenoptera from Australia discovered between 1980 and 2010: eight Eulophids and two Encyritids. Australia con-

TABLE 8. Number of exotic terrestrial macro-invertebrates discovered breeding in California by time and likely origin.

Region[a]	<1901	1901–1929	1930–1939	1940–1949	1950–1959	1960–1969	1970–1979	1980–1989	1990–1999	2000–2015
Australia	5	2	1	2	3	0	2	4	4	15
Pacific Region	0	0	1	0	1	4	0	0	0	1
Africa	4	9	6	2	0	2	3	4	3	7
Asia	4	21	8	10	5	6	2	4	4	16
Tropical America	1	10	7	2	1	7	5	7	7	6
Hawaii	0	2	1	0	2	7	4	7	8	6
Mexico	2	1	1	0	1	21	0	1	5	1
Europe	26	53	17	117	9	10	2	10	12	14
North America	32	73	24	23	42	40	21	30	31	36

[a] See Appendix for list of organisms.

tributed nine Psyllidae, two Aphalaridae and one Triozidae to the California fauna between 1980 and 2010 (Appendix). These insects, especially the Hymenoptera and Psyllidae must have escaped quarantine detections and were moved to California on living plant material.

COMPARISON WITH THE EARLIER STUDY BY DOWELL AND GILL (1989).— Many of the trends reported by Dowell and Gill (1989) were repeated here. The Hemiptera, Coleoptera, Lepidoptera, Acari, Diptera, and Hymenoptera had the greatest number of invaders but the Acari were second after the Hemiptera. North America was still the origin of the greatest number of invaders entering California but the order after that was the Pacific Region (including Hawaii), Europe, Asia, Tropical America (including Mexico), Africa and Australia. Dowell and Gill (1989) reported that Hawaii contributed more invaders than any the other region except North America and Europe. In this larger analysis, Hawaii is far less important as a point of origin although this US state still contributes more exotic species to California than the rest of the Pacific Region (Table 4).

FACTORS THAT AFFECT THE LIST.— We have adopted a conservative approach to listing organisms with the requirement of evidence of a breeding population within California. This criterion differs from other groups, such as the Lepidopterists Society, that develop regional lists of organisms. In many of these other lists the occurrence of a single individual constitutes a new regional record that in some instances may over-estimate the number of species successfully established in a given area (Rickard and Grishin 2010, Bordelon and Knudson 2011, Rickard and Pasko 2011). This conservative approach has been influenced by regulatory concerns because listing the presence of an exotic organism as opposed to a breeding population may trigger official actions (IPPC 2007) by the CDFA and/or United States Department of Agriculture including the imposition of exterior/interior quarantines or eradication programs (Dowell 1988).

As noted elsewhere (Kirkendall and Faccoli 2010), the taxonomy of many arthropod organisms is fluid with changes occurring from the order level (e.g., loss of the order Homoptera and the resurrection of Hemiptera that includes Auchenrrhyncha and Sternorrchyncha), to the family and species level (e.g., Crambidae versus Pyralidae or *Solenopsis invicta* versus *Solenopsis wagneri*). We have attempted to use the most current taxonomy for species listed here realizing there may be professional disagreement about the use of particular species names and classifications.

There are often differences of opinion as to whether an organism is native or exotic to California. This is especially true for those organisms that invaded before or around 1900 (Powell et al.

TABLE 9. Taxons of exotic terrestrial macro-invertebrates found breeding in California by time period in which they were detected.

Taxon[a]	**<1900**	**1901–1929**	**1930–1939**	**1940–1949**	**1950–1959**	**1960–1969**	**1970–1979**	**1980–1989**	**1990–1999**	**2000–2015**
Acari	5	13	26	14	8	8	7	10	4	
Amphipoda		1								
Araneae			1						4	5
Chilopoda										
Coleoptera	8	59	13	15	10	15	6	5	13	32
Collembola		2	1							1
Dermaptera	2	5			1					
Dictyoptera	1	4	1	2	2	1	2	1		3
Diplopoda										
Diptera	6	32	1	5	3	11	3	6	10	23
Embiidina	1	1								
Hemiptera- Heteroptera	3	7	1	1		4	3	2	7	8
Hemiptera: Auchenor-rhyncha + Sternorrhyncha	46	112	42	20	39	26	19	30	30	25
Hymenoptera	5	11	2	4	5	7	3	8	18	7
Isopoda		2								
Isoptera									1	
Lepidoptera	16	21	7	5	12	21	78	4	5	9
Mollusca	7	2	1	4	3	5	1		1	
Orthoptera	1	6	1	1					2	
Phasmida										1
Phthiraptera	1	11	1	1	2	1	3		5	2
Psocoptera		3		1				1		
Siphonaptera										
Symphyla										
Thysanoptera										1
Thysanura										

[a] See Appendix for list of organisms.

2000). We have listed the authorities that note that each organism is not native to California recognizing that new information (molecular or phylogenetic analyzes) may change this. For example, the gopher beetle, *Ceratophyus gopherinus,* has long been considered an invasive species in California as all other known species in the genus are found in Europe (Cartwright 1966). However, *C. gopherinus* does not occur in Europe thus casting doubt on the exotic origins of this beetle. Current thinking is that *C. gopherinus* is a native species of limited distribution in California (Arnett et al. 2002).

California does not maintain a statewide survey for invasive invertebrates except for a limited number of crop pests (Gilbert et al. 2013). The discovery of exotic macro-invertebrates not targeted by CDFA depends on individuals noting and reporting damage to crops or ornamental plants, capturing unidentified organisms in local faunal surveys (e.g., light brown apple moth, *Epiphyas postvittana*) (Brown et al. 2010), or periodic CDFA surveys that target specific groups of organisms (e.g., wood boring beetles, which resulted in the detection of *Scolytus schevyrewi*). One under-appreciated avenue to the detection of new organisms that have invaded California are citizens who find species they do not recognize and then send specimens to experts for identification. One citizen scientist has discovered five exotic ant species and one exotic spider species in southern California (Martinez 1992, 1993, 1996, 1997, 2006; Martinez et al. 2011, 2014).

Pathways into California.— There are numerous pathways by which the organisms listed in the Appendix were introduced into California. Human alterations to the landscape (i.e., irrigation of desert areas and propagation of exotic plants) probably facilitated the self-introduction of the giant swallowtail butterfly, *Papilio cresphontes*. Others, especially the wood boring beetles (e.g., *Scolytus schevyrewi* and the Asian longhorn beetle) probably arrived in wooden pallets of commercial goods or in firewood transported across state lines. For example, the gold spotted oak borer (*Agrilus auroguttatus*) was likely introduced in cut oak firewood from the Dragoon Mountains in southern Arizona (Lopez et al. 2014). Large numbers of non-native species are thought to have arrived on living plants either shipped into the state commercially, arriving in vehicles (cars, trucks, and trains) moving here from other states, or via smuggling from overseas (e.g., red palm weevil [Hoddle 2015]). Several pestiferous fruit flies (Tephritidae) (e.g., Mediterranean fruit fly, *Ceratitis capitata*, and the oriental fruit fly, *Bactrocera dorsalis*) probably arrived as larvae in smuggled fruit. During the 1700's to early 1900's soil, as well as and construction debris, was used as ballast in cargo ships and the soil was dumped at the destination port (Lindroth 1957). This route was likely the avenue through which many of the Collembola, Isopoda, Staphylinidae, Dermaptera and Embiidina, among the soil inhabiting invertebrates, were introduced into California.

Some introduction pathways are unusual. Fire ants, *S. wagneri*, arrived in California in the soil of potted plants but also with beehives stacked on palletts originating in fire-ant infested areas of the US brought into California to pollinate crops, especially almonds (CDFA unpublished data). Slate, a fine grain metamorphic rock used for construction, represents another pathway for exotic organisms to enter California. Slate is stored as thin slabs on pallets with gaps between the slabs. These gaps provide dry, cool sites for many organisms, especially slugs, and lygaeid bugs, to overwinter. The pallets, with overwintering organisms included, are shipped to California in unheated boat holds making it more likely that the hitch-hiking organisms will survive and disembark in California alive (California Department of Food and Agriculture, unpublished data)

Rumors of Bioterrorism.— Speculation exists that pestiferous organisms are being deliberately introduced into California (Paine et al. 2010). For example, Paine et al. (2010) suggested that eucalyptus-specific insects have been deliberately introduced to kill *Eucalyptus* spp., non-native trees that are viewed by some as noxious weeds (Paine et al. 2010). It has been similarly suggested that Mediterranean fruit flies are punitively introduced into California to challenge the State's eradication programs. There are no data to support these suggestions. However, the large number of eucalyptus feeding insects discovered in California since 1990 is considered suspicious because there were essentially no introductions in the preceding 100+ years during which live eucalyptus were imported into the state (Paine et al. 2010).

Impacts of the exotic species.— Dowell and Gill (1989) noted that exotic pests accounted for 62% of all reported crop losses in 1978; the last year for which there are data. The economic losses to invasive pests in California were estimated at $3 billion (US) dollars in 1995 (Metcalf 1995).

TABLE 10. Percentage of exotic terrestrial macro-invertebrates pests listed in University of California on-line IPM Guides.

Situation	Percentage of listed pests that are not native to California[a]
Agricultural crops	55.2
Urban vegetables	70.3
Urban fruit trees and vines	67.7
Urban flowers	64.5
Urban homes, structures, people and pets	53.8
Urban ornamental trees and shrubs	51.4
Natural environment	42.9

[a] Available at *www.ipm.ucdavis.edu*. Accessed 15 December 2014.

Although 314 (19.2%) of the 1,686 exotic invaders are condsidered as pests in California (see Appendix), exotic invaders account for a disproportionately large number of pest species mentioned in University of California on line IPM guides and elsewhere (Table 10). Over 42% of the pest invertebrates mentioned in the University of California Integrated Pest Management Guidelines for agricultural, ornamental, and native plants are exotic in origin (Table 10; see also Appendix). This overview analysis treats all listed pests equally, which is not the case. For example, cottony cushion scale, now a minor pest of citrus, is given the same weight as California red scale, *Aonidiella aurantii*, which is a major citrus pest even though both have been subjected to classical biological control programs. These observations suggest that exotic pests caused a more disproportionate level of crop losses than would be anticipated by their percent composition in the total pest complex. Exotic invaders represent some of the most common and troublesome urban pests (cockroaches and Agrentine ants) supporting an urban pest control industry with annual revenues estimated at $1 to 2 billion (US) per year (Rust, pers. comm.) that exists to manage these pests.

Non-native species can have a devastating impact on our natural environment. The gold spotted oak borer has killed over 20,000 oaks in southern California since 2008 (Coleman and Seybold 2010). Its continued spread in infested firewood, an unregulated conduit for invasive wood pests, that poses a significant threat to ecosystems dominated by oak trees in California. The Argentine ant has displaced the native ants in many coastal areas of California, and that in turn has adversely affected native horned lizards that feed on native ants, which has contributed to the loss of the horned lizards in some cases (Suarez and Case 2002). The cause of range reduction of the native veined white, *Pieris marginalis*is*,* is thought to have occurred from competition for cruciferous host plants with the pestiferous exotic cabbage butterfly, *Pieris rapae* (Pyle 1981).

CONCLUSION

Terrestrial macro-invertebrates have been invading California since the advent of European traders and settlers. The invasion process is complex with significant changes in the composition and origins of the invaders over time. The one common thread is human activity, especially transportation networks that facilitate rapid and long distance trade and tourism and human-mediated habitat alteration (i.e., gardenification and urbanization). The impacts of increasing numbers of terrestrial macro-invertebrate species on the agriculture, wilderness, and urban areas of California will almost certainly continue to increase.

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Appendix
with
Addendum

Footnotes to Appendix table

[a] an organism that was or is the object of Official Action (quarantine and eradication) by the California Department of Food and Agriculture and is not established in California.

[b] We have identified those animals in Appendix 1 that are considered pests in or by California. For plant, home and garden and the environment we identify those animals listed as pests in the University of California IPM online (UC IPM 2013), sheep and goat pests are from Pirelli (2013), Dairy cattle pests are those identified by Geden et al. (2010), Horse insect pests are from Meyer et al.(1991), swine pests are from Loftin (2013) and chicken pests are from Stafford III (2011). These sources tend to deal with animals that are established in California or are frequently detected there. We have also identified some pests not established in California but which have been detected here and which are generally considered pests in those areas where they occur including the gypsy moth (*Lymantria dispar*) (Liebhold 2003), Japanese beetle (*Popillia japonica*) (Anon. 1997), Mexican bean beetle (*Epilachna varivestis*) (Sanchez-Arroyo 2015), oriental fruit fly (*Bactrocera dorsalis*), Mexican fruit fly (*Anastrepha ludens*), Caribbean fruit fly (*Anastrepha suspensa*), peach fruit fly (*Bactrocera zonata*), Mediterranean fruit fly (*Ceratitis capitata*), melon fly (*Bactrocera cucurbitae*), white striped fruit fly (*Bactrocera albistrigata*), and guava fruit fly (*Bactrocera correcta*) (White & Elson-Harris 1992), boll weevil (*Anthonomus grandis*) (Lange et al. 2008), varroa mite, (*Varroa jacobsoni*) (Bessen 2010), red palm weevil (*Rhynchophorus vulneratus*) (Rugman-Jones et al. 2013), Diaprepes root weevil (*Diaprepes abbreviatus*) (Grafton-Cardwell et al. 2004), Asian longhorn Beetle (*Anoplophora glabripennis*) (United States Department of Agriculture, Animal and Plant Health Inspection Service 2015).

APPENDIX. Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Acari-Acaridae				
Acarus siro (Linnaeus 1758)			Essig 1958	
Aleuroglyphus ovatus (Troupeau 1879)	1984		Dowell & Gill 1989	
Rhizoglyphus robini Claparède 1869	<1915		CDFA 1914 3:539	yes
Tyrophagus neiswanderi Johnston & Bruce 1965	1982	Europe	Dowell & Gill 1989	yes
Tyrophagus putrescentiae (Schrank 1781)			Hughes 1976	yes
Acari-Astigmata				
Sancassania berlesi (Michael 1903)			Hughes 1976	
Acari-Cheyletidae				
Chelyletiella yasguri (Smiley 1965)	1973	North America	Dowell & Gill 1989	
Acari-Dermanyssidae				
Ornithonyssus bacoti (Hirst 1913)	<1930		CDFA 1941 30:352	
Acari-Eriophyidae				
Abacarus hystrix (Nalepa 1896)	1940		CDFA 1940 29:242	
Acalitus calycophthirus (Nalepa 1891)	1984	North America	Dowell & Gill 1989	
Acaphylla steinwedeni Keifer 1943	1942	Asia	CDFA 1945 34:174	
Acarapis near *dorsalis* Morganthaler 1934	1959		Dowell & Gill 1989	
Acarapis woodi (Rennie 1921)	1986	North America	Dowell & Gill 1989	
Acaricalus hederae (Keifer 1939)	1939		CDFA 1939 28:490	
Aceria ajugae (Nalepa 1892)	1959		CDFA 1959 48:127	
Aceria aloinis Keifer 1941	1940		CDFA 1940 29:242, Keifer 1952	
Aceria cynodontis Wilson 1959			Keifer et al. 1982	
Aceria diospyri (Keifer 1944)	1943		Keifer 1952	yes
Aceria ficus (Cotte 1920)	1922	Europe	CDFA 1939 28:266	yes
Aceria fraxinivorus (Nalepa 1909)	1944		Keifer et al. 1982, Keifer 1952	
Aceria genistae (Nalepa 1892)	1994	Europe	Chan & Turner 1998	
Aceria lycopersici (Wolffenstein 1879)	1940	Tropical America	Jeppson et al. 1975	
Aceria mori (Keifer 1939)	1939		Keifer 1952	
Aceria neocynodonis Keifer 1960	1960	North America	CDFA 1960 49:200	
Aceria paradianthi Keifer 1952	1952		CDFA 1952 41:65	
Aceria parthenii Keifer 1952	1952		CDFA 1952 41:147	
Aceria peucedani (Canestrini 1891)			Jeppson et al. 1975	
Aceria sheldoni (Ewing 1937)	1937		CDFA 1937 26:433	
Aceria tulipae (Keifer 1938)	1938	Europe	CDFA 1938 27:185	
Aculops fuchsiae Keifer 1972	1982	Tropical America	Dowell & Gill 1989	yes
Aculops lycopersici (Massee 1937)	1940	Australia	Keifer et al. 1982	yes
Aculus cornutus (Banks 1905)	1914	North America	Jeppson et al. 1975	yes
Aculus ligustri (Keifer 1943)	1938		CDFA 1938 27:190	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Aculus schlectendali (Nalepa 1890)	1938		CDFA 1939 28:234	
Aculus teucrii (Nalepa 1892)	1986	North America	Dowell & Gill 1989	
Anthocoptes punctidorsa Keifer 1943	1943		Keifer 1952	
Calacarus adornatus (Keifer 1940)	1939		Keifer 1952	
Calacarus carinatus (Green 1890)			Keifer et al. 1982	
Calepitrimerus muesebecki Keifer 1940	1954	Mexico	CDFA 1940 29:113	
Calepitrimerus vitis (Nalepa 1905)		Europe	Keifer 1952	
Cecidophyes collegiatus Keifer 1961			Jeppson et al. 1975	
Cecidophyes malpighianus (Canestrini & Massalongo 1893)	1939		Keifer 1952	
Cecidophyopsis grossulariae (Collinge 1907)	1991		CPPDR 1991 10:15	
Colomerus vitis (Pagenstecher 1857)	<1915		Amrine & Stasney 1994	
Coptophylla lamimani (Keifer 1939)	1939		Keifer 1952	
Cosetacus camelliae (Keifer 1945)	1940	Asia	CDFA 1945 34:137	
Diptacus gigantorhynchus (Nalepa 1892)	1938	Europe	Keifer 1952	yrs
Epitrimerus pyri (Nalepa 1870)	1913	North America	CDFA 1915 4:12	yes
Eriophyes ajugae (Nalepa 1892)	1958		Dowell & Gill 1989	
Eriophyes canestrinii (Nalepa 1891)	1950		Keifer 1952	
Eriophyes caricis Keifer 1944	1943	Europe	Keifer 1952	
Eriophyes celtis Kendall 1929	1961	North America	Dowell & Gill 1989	
Eriophyes convolvens (Nalepa 1892)		Europe	Keifer 1952	
Eriophyes cynodoniensis Sayed 1946			Jeppson et al. 1975	yes
Eriophyes eriobotryae (Keifer 1938)	1938		CDFA 1938 27:188	
Eriophyes granati (Canestrini & Massalongo 1893)			Keifer et al. 1982	yes
Eriophyes pyri (Pagenstecher 1857)	1894	North America	CDFA 1915 4:6	yes
Eriophyes spermaphaga (Keifer 1979)	1979		Dowell & Gill 1989	
Eriophyes tiliae (Nalepa 1890)	1932		Keifer 1952	
Eriophyes vaga (Keifer 1962)	1979	Tropical America	Dowell & Gill 1989	
Eriophyes wisteriae Keifer 1939	1939		CDFA 1939 28:329	
Gammaphytoptus camphorae Keifer 1939	1938	Asia	CDFA 1939 28:148	
Mackiella phoenicis Keifer 1939	1938	Africa	Keifer 1952	
Oxypleurites maxwelli (Keifer 1939)	1939	Europe	CDFA 1914 31:175	
Phyllocoptes bougainvilleae Keifer 1959	1996	Tropical America	CPPDR 1997 16:10	
Phyllocoptes calulmi Keifer 1940	1939		CDFA 1940 29:113	
Phyllocoptes destructor Keifer 1940	1940		CDFA 1940 29:161	
Phyllocoptes gracilis (Nalepa 1890)			Jeppson et al. 1975	
Phyllocoptruta oleivora (Ashmead 1879)	1889	North America	CDFA 1934 23:201	yes
Phytoptus avellanae Nalepa 1889	1939	North America	Keifer 1952	
Phytoptus hedericola Keifer 1943	1942		Keifer 1952	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Rhynacaphytoptus ficifoliae Keifer 1939	1939	Africa	CDFA 1939 28:273	
Shevtchenkella depressus (Nalepa 1894)			Keifer 1952	
Tegolophus myersi (Keifer 1939)	1938		Keifer 1952	
Tegolophus zizyphagus (Keifer 1939)	1939		Keifer 1952	
Tegonotus carinatus (Nalepa 1891)	1964	Europe	Dowell & Gill 1989	
Tetra concava (Keifer 1944)	1939	Europe	Keifer 1952	
Trisetacus pseudotsugae Keifer 1965	1969	North America	Dowell & Gill 1989	
Vasates immigrans (Keifer 1940)	1939		Keifer 1952	
Vasates magnolivora (Keifer 1952)	1939	North America	Keifer 1952	
Acari-Glycyphagidae				
Glycyphagus destructor (Schrank 1781)			Hughes 1976	
Glycyphagus domesticus (De Geer 1778)			Hughes 1976	
Acari-Ixodidae				
Argas persicus (Oken 1881)	<1925		Furman & Loomis 1984, Essig 1926a	
Boophilus annulatus (Say 1905)	<1925		Furman & Loomis 1984, Essig 1926a	
Rhipicephalus sanguineus (Latreille 1806)			Furman & Loomis 1984	
Acari-Laelapidae				
Melittiphis alvearius (Berlese 1895)	1988	Europe	Dowell & Gill 1989	
Acari-Penthaleidae				
Penthaleus major (Duges 1834)		Europe	CDFA 1940 29:507	yes
Acari-Phytoptidae				
Phantacrus lobatus Keifer 1965	1978	North America	Dowell & Gill 1989	
Acari-Psoroptidae				
Psxoroptes equi (Raspail 1834)	<1925		Essig 1926a, 1958	
Psoroptes ovis (Hering 1838)	<1925		Essig 1926a, 1958	
Acari-Pyemotidae				
Siteroptes graminum (Reuter 1907)	1965	Hawaii	Dowell & Gill 1989	
Acari-Rhyncaphytoptidae				
Rhyncaphytoptus ulmivagrans Keifer 1939	1939	Europe	CDFA 1939 28:420	
Trimeroptes aleyrodiformis (Keifer 1951)		North America	Jeppson et al. 1975	
Acari-Tarsonemidae				
Steneotarsonemus ananas (Tryon 1898)	1980	Hawaii	Dowell & Gill 1989	
Steneotarsonemus pallidus (Banks 1899)	<1925		Jeppson et al. 1975, Essig 1926a	yes
Tarsonemus setifer Ewing 1939		Europe	Jeppson et al. 1975	
Acari-Tenuipalpidae				
Brevipalpus lewisi McGregor 1949	1942		Pritchard & Baker 1958	yes
Brevipalpus obovatus Donnadieu 1875			Jeppson et al. 1975, Pritchard & Baker 1958	
Brevipalpus phoenicis (Geijskes 1936)			Jeppson et al. 1975, Pritchard & Baker 1958	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Acari-Tetranychidae				
Bryobia praetiosa Koch 1835	1879		Jeppson et al. 1975	
Eotetranychus sexmaculatus (Riley 1890)	<1915		CDFA 1915 4:16	yes
Eotetranychus uncatus Garman 1952		North America	Jeppson et al. 1975	
Eurytetranychus buxi (Garman 1935)			Jeppson et al. 1975	
Eutetranychus banksi (McGregor 1914)	<1915		CDFA 1915 4:13	yes
Mononychellus caribbeanae (McGregor 1950)	1978		CPPDR 1996 15:79	
Mononychellus erythrinae Tuttle, Baker & Abbatiello 1976	1978		Dowell & Gill 1989	
Oligonychus aceris (Shimer 1869)	1959	North America	Dowell & Gill 1989	
Oligonychus ilicis (McGregor 1917)	1935	North America	CDFA 1939 28:240	
Oligonychus perseae Tuttle, Baker & Abbatiello 1976	1992	Mexico	CPPDR 1992 11:46	
Oligonychus pratensis (Banks 1912)			Baker & Tuttle 1994	yes
Oligonychus punicae (Hirst 1926)		Mexico	Baker & Tuttle 1994	
Panonychus citri (McGregor 1916)	1885	North America	Baker & Tuttle 1994	yes
Panonychus ulmi (Koch 1836)	<1925	North America	Essig 1926a	yes
Paraplonobia myops (Pritchard & Baker 1955)			Jeppson et al. 1975	
Petrobia cf. *apicalis* (Banks 1917)	1978	North America	Dowell & Gill 1989	
Schizonobia sp Wormsley 1940	1965		Dowell & Gill 1989	
Schizotetranychus celarius (Banks 1917)		Asia	Jeppson et al. 1975	
Tetranychus evansi Baker & Pritchard 1960	1965	Pacific Region	Jeppson et al. 1975	
Tetranychus merganser Boudreaux 1954	1963	North America	Dowell & Gill 1989	
Tetranychus tumidus Banks 1900		North America	Jeppson et al. 1975	
Tetranychus urticae (Koch 1836)	1876	Europe	Baker & Tuttle 1994	yes
Tetranycopsis horridus (Canestrini & Fanzago 1876)		Europe	Jeppson et al. 1975	
Acari-Uropodidae				
Fuscuropoda marginata (Koch 1839)	1964		Dowell & Gill 1989	
Acari-Tydeidae				
Lorryia formosa Cooreman 1958	1984	Europe	Dowell & Gill 1989	
Acari-Varroidae				
Varroa jacobsoni Oudemans 1904	1989	North America	CPPDR 1989 8:5	yes
Amphipoda-Talitridae				
Talitrus sylvaticus (Haswell 1880)	1918	Australia	Mallis 1942	
Araneae-Agelenidae				
Agriope trifasciata (Forskal 1775)			Sierwald et al. 2005, Lew 2010	
Gea heptagon (Hentz 1850)			Sierwald et al. 2005, Lew 2010	
Metazygia zilloides Banks 1989	2009	North America	Martinez et al. 2014	
Tegeneria domestica (Clerck 1757)		Europe	Herbert et al.1987	
Tegeneria pagana (Koch 1840)			Herbert et al. 1987	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Araneae-Amphinectidae				
Metaltella simoni (Keyserling 1878)	1994	Tropical America	Vetter & Visscher 1994	
Araneae-Araneidae				
Araneus diadematus Clerck 1758			BugGuide 2011, Lew 2010	
Larinoides sclopetarius (Clerek 1757)	2004	North America	Martinez 2006	
Zygiella x-notata Clerck 1757			Lindroth 1957, Lew 2010	
Neoscona crucifera Lucas 1839	1991	North America	Levi 1992	
Araneae-Desidae				
Badumna longinqua (Koch 1867)			Bryant et al. 2010, Lew 2010	
Araneae-Dictynidae				
Dictyna major Menge 1869			Lindroth 1957, Lew 2010	
Araneae -Dysderidae				
Dysdera crocata (Koch 1838)		Europe	Prentice et al. 2001, Bolger et al. 2008	
Araneae –Gnaphosidae				
Haplodrassus signifer Koch 1839			Lindroth 1957, Berrian 2005	
Scotophaeus blackwalli (Thorell 1871)			Herbert 1987, Lew 2010	
Trachyzelotes barbatus (Koch 1866)			Crespo & Mendes 2010, Prentice et al. 1998	
Trachyzelotes jaxartensis (Kroneberg 1875)			Crespo & Mendes 2010, Lew 2010	
Trachyzelotes lyonneti (Audouin 1826)			Bolger et al. 2008, Crespo & Mendes 2010	
Urozelotes rusticus (Koch 1872)			Beatty 2002, Prentice et al. 1998	
Zelotes nilicola (Cambridge 1874)			Prentice et al. 1998, Bolger et al. 2008	
Araneae-Linyphidae				
Pityohyphantes phrygianus (Koch 1836)			Jennings & Graham 2007, Lew 2010	
Araneae-Mimetidae				
Ero furcata (Villers 1789)			Lew 2010, Bolger et al. 2008	
Araneae-Miturgidae				
Cheiracanthium mildei Koch 1864			Lew 2010, BugGuide 2011, Hogg et al. 2010	
Araneae -Oecobiidae				
Oecobius annulipes Lucas 1849			Prentice et al. 1998	
Oecobius navus Blackwall 1859			Lew 2010, Bolger et al. 2008	
Oecobius putus (Cambridge 1876)			Lew 2010, Bolger et al. 2008	
Araneae-Philodromidae				
Thanatus vulgaris Simon 1870			Donale & Redner 1978, Lew 2010	
Araneae -Pholcidae				
Artema atlanta Walckenaer 1837			BugGuide 2011, Lew 2010	
Holocnemus pluchei (Scopoli 1763)		Europe	Prentice et al. 2001, Bolger et al. 2008	
Pholcus phalangioides (Fuesslin 1775)		Europe	Lew 2010, Bolger et al. 2008	
Spermophora senoculata (Duges 1836)			Beatty 2002, Lew 2010	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Araneae-Salticidae				
Menemerus bivittatus (Dufour 1831)			Prentice et al. 2001	
Menemerus semilimbatus (Hahn 1827)	1990's	Europe	Manolis & Carmichael 2010	
Phlegra fasciata (Hahn 1826)			Sierwald et al. 2005, Lew 2010	
Salticus scenicus (Clerck 1757)			Jennings & Graham 2007, Lew 2010	
Araneae-Scytodidae				
Scytodes thoracica (Latreille 1802)			Beatty 2002, Lew 2010	
Araneae-Sicariidae				
Loxosceles laeta (Nicolet, 1849)	1936	Tropical America	Robinson 2005	
Loxosceles rufescens (Dufour 1820)		Europe	Lew 2010, Yigit et al. 2008	
Araneae -Sparassidae				
Heteropoda venatoria (Linnaeus 1767)			Sherriffs 1936, Lew 2010	
Olios abnormis (Blackwall 1866)			Platnick 2010, Lew 2010	
Araneae-Theridiidae				
Achaearanea acoreensis (Berland 1932)			Lew 2010, Draney 2001	
Achaearanea ohlerti (Thorell 1870)			Lindroth 1957, Lew 2010	
Achaearanea tepediorum (Koch 1841)		Tropical America	Lew 2010, Campbell 2010	
Dipoena prona Menge 1868			Lindroth 1957, Berrian 2005	
Enoplognatha ovata (Clereck 1757)			Oxford & Reillo 1994	
Latrodectus geometricus (Koch 1841)	2003	North America	Vincent et al. 2008	yes
Steatoda albomaculata (De Geer 1778)			Sierwald 2005, Lew 2010	
Steatoda grossa (Koch 1838)		Europe	Draney 2001, Lew 2010	yes
Steatoda triangulossa (Walckenaer 1802)			Draney 2001, Prentice et al. 2001	
Theridion hemerobium Simon 1914		Europe	Lindroth 1957, Lew 2010	
Theridion melanurum (Hahn 1820)			Lindroth 1957, Lew 2010	
Theridion murarium (Emerton 1882)			Herbert et al.1987, Lindroth 1957, Lew 2010	
Araneae-Zoropsidae				
Zoropsis spinimana (Dufour 1820)	1996	Africa	Griswold & Ubick 2001	yes
Chilopoda-Scolopendromorpha-Cryptopidae				
Cryptops hortensis (Donovan 1810)		Europe	Shelley 2002	yes
Chilopoda-Scutigeromorpha-Scutigeridae				
Scutigera coleoptrata Linnaeus 1758	<1915	Europe	Lewis 1981, Essig 1915	yes
Coleoptera-Aderidae				
Aderus populneus (Creutzer in Panzer 1796)			Majka 2011	
Coleoptera-Anobiidae				
Anobium punctatum (De Geer 1774)		Europe	Philips 2002, Evans & Hogue 2006	
Ernobius mollis (Linnaeus 1758)	1990	North America	Seybold & Tupy 1993	
Gibbium psylloides (Czempinski 1778)			Philips 2002	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Lasioderma haemorrhoidale (Illiger 1807)	1981		White 1990	
Lasioderma serricorne (Fabricius 1792)	<1925		Campbell et al. 1989, Essig 1926a	yes
Mezium affine Boieldieu 1856			Philips 2002	
Mezium americanum Laporte 1840			Philips 2002	
Ptinus fur (Linneaus 1758)			Bousquet 1990, California Beetle Project 2006	
Niptus holoeucus (Faldermann 1836)			Philips 2002	
Stegobium paniceum (Linnaeus 1758)	<1925		White 1962, Essig 1926a	yes
Tricorynus herbarius (Gorham 1883)			White 1965	
Trigonogenius globulus Solier 1849			Arnett et al. 2002	
Coleoptera-Anthicidae				
Anthicus floralis (Linnaeus 1758)			Campbell et al. 1989	
Stricticomus tobias (Marseul 1879)			Peck & Thomas 1998	
Coleoptera-Anthribidae				
Araecerus fasciculatus (De Geer 1775)	1994		CPPDR 1996 15:74	
Coleoptera-Bostrichidae				
Dinoderus minutus (Fabricius 1775)			Campbell et al. 1989	
Heterobostrychus brunneus (Murray 1867)			Ivie 2002a	
Lyctus brunneus (Stephens 1830)	<1925	Europe	Campbell et al. 1989	yes
Lyctus linearis (Goeze 1777)	<1925	Europe	Campbell et al. 1989	
Micrapate sp. Casey 1898	2003		Penrose 2004	
Rhyzopertha dominica (Fabcicius 1792)	<1930		Ebling 1975	yes
Coleoptera-Brentidae				
Cylas formicarius (Fabricius 1798)	1993	North America	CPPDR 1993 12:3	yes
Trichapion simile Kirby 1811			Lindroth 1957	
Coleoptera-Buprestidae				
Agrilus anxius Gory, 1841	1992	North America	Dreistadt et al. 2004	yes
Agrilus auroguttatus Schaeffer 1905	2004	North America	Westcott 2005	yes
Agrilus cyanescans (Ratzeburg 1837)	1949	Tropical America	Chamberlin 1949	
Chrysobothris costifrons costifrons Waterhouse 1887	2005	North America	Basham et al. 2015	
Xenorhipis osborni Knull 1936	1947	North America	Thatcher 1948	
Coleoptera-Carabidae				
Amara anthobia Villa & Villa 1833		North America	Lindroth 1957	
Agonum mulleri (Herbst 1784)			Ball & Bousquet 2001	
Carabus nemoralis Müller 1764	1919	North America	Brown 1940	
Laemostenus complanatus (Dejean 1828)		North America	Lindroth 1957	
Perigona nigriceps (Dejean 1831)		North America	Bousquet 2012	
Trechus obtusus Erichson 1837		North America	Lindroth 1957, Kavanaugh & Erwin 1985	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Coleoptera-Cerambycidae				
[a]*Anoplophorus glabripennis* (Motachulsky 1853	2005	Asia	CPPDR 2006 22:4	yes
Arhopalus syriacus (Reitter 1895)	2002	Europe	Penrose 2003	
Callidellum rufipenne (Motschulsky 1860)			Aukema et al. 2010, California Beetle Project 2006	
Icosium tomentosum Lucas 1854	2006	Europe	CPPDR 2007 23:5, Bohne 2006	
Nathrius brevipennis (Mulsant 1839)	1932	Europe	Linsley 1933	
Neoclytus acuminatus (Fabricius 1775)	2002	North America	Penrose 2004	
Phoracantha recurva Newman 1840	1995	Australia	CPPDR 1997 16:10	yes
Phoracantha semipunctata Fabricius 1775	1984	Australia	Dowell & Gill 1989	yes
Phymatodes testaceus (Linnaeus 1758)		North America	Lindroth 1957	
Saperda populneus (Linnaeus 1758)		Europe	Furniss & Carolin 1977	
Coleoptera-Chrysomelidae				
Acanthoscelides obtectus (Say 1831)	<1915	North America	CDFA 1920 9:344	yes
Altica carduorum (Guerin-Memeville 1858)			Riley et al. 2003	
Amblycerus robiniae (Fabricius 1781)	1970	North America	Dowell & Gill 1989	
Bruchus brachialis Fåhraeus 1839	1949	North America	Davidson & Lyon 1987, Evans & Hogue 2006	
Bruchus pisorum (Linnaeus 1758)	<1915		CDFA 1915 4:287	
Bruchus rufimanus Boheman 1833	<1915	Europe	CDFA 1915 4:289, Essig 1926a	
Callosobruchus maculatus (Fabricius 1775)	<1915		Campbell et al. 1989	
Cassida nebulosa Linnaeus 1758	<1894	Europe	Barber 1916	
Chaetocnema sp. Stephens 1831	1948		CDFA 1948 37:211	yes
Chelymorpha cassidea (Fabricius 1775)	1909	North America	Essig 1958	
Chrysolina bankii (Fabricius 1775	2006	Europe	CPPDR 2007 23:5-6	
Chrysophthartam-fuscum Boheman 1859	2003	Australia	CPPDR 2006 22:25	yes
Crioceris asparagi (Linnaeus 1758)	1904	Europe	CDFA 1915 4:267	
Crioceris duodecimpunctata (Linnaeus 1758)	1975		Dowell & Gill 1989	
Diabrotica balteata LeConte 1865	1924	Tropical America	Metcalf 1995	
Diorhabda elongate (Brulle 1832)			Riley et al. 2003	
Epitrix fasciata Bratchley 1918	<1915		CDFA 1915 4:262	yes
Epitrix tuberis Gentner 1944	1968	North America	Dowell & Gill 1989	yes
Galerucella nymphaeae (Linnaeus 1758)	1924		Lindroth 1957	
Longitarsus jacobaeae Waterhouse 1858			LeSage 1988	
Mimosetes nubigens (Motschulsky 1874)	1991	North America	Johnson & Seeno 1993	
Phyllotreta cruciferae (Goeze 1777)			Riley et al. 2003	yes
Phyllotreta striolata (Fabricius 1803)			Campbell et al. 1989, Riley et al. 2003	yes
Specularius impressithorax (Pic 1913)	2003		Gulmahamad 2006	
Trachymela sloanei (Blackburn 1897)	1997	Australia	CPPDR 1998 17:4-6	yes
Xanthogaleruca luteola (Muller 1766)	1924	Europe	Metcalf 1995, Riley et al. 2003	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Zabrotes subfasciatus Boheman 1833	1965	Tropical America	Dowell & Gill 1989	
Zeugophora scutellaris Suffrian 1840			Riley et al. 2003, California Beetle Project 2009	
Coleoptera-Cleridae				
Necrobia ruficollis (Fabricius 1785)	<1925		Campbell et al. 1989, Essig 1926a	
Necrobia rufipes (De Geer 1775)	<1925		Campbell et al. 1989, Essig 1926a	
Necrobia violacea (Linnaeus 1758)	<1925		Campbell et al. 1989, Essig 1926a	
Paratillus carus (Newman 1840)		Europe	Grace & Wood 1985	
Tarsostenus univittatus (Rossi 1792)			Arnett 1983	
Thaneroclerus buquet (Lefebvre 1835)			California Beetle Project 2006	
Coleoptera-Coccinellidae				
[b]*Epilachna varivestis* Mulsant 1850	1946	North America	CDFA 1946 35:198	yes
Coleoptera-Colydiidae				
Microprius rufulus (Motschulsky 1863)		Europe	Ivie 2002b	
Coleoptera-Cryptophagidae				
Cryptophagus laticollis Lucas 1849			Majka & Langor 2010	
Cryptophagus pilosus Gyllenhal 1827			Campbell et al. 1989	
Coleoptera-Curculionidae				
Agasphaerops nigra Horn 1876	1876		O'Brien & Wibmer 1982	
Amalus haemorrhous (Herbst 1795)			Lindroth 1957	
Anthonomus eugenii Cano 1894	1923	Tropical America	CDFA 1923 12:360	yes
[a]*Anthonomus grandis* (Boheman 1843)	1984	North America	Dowell & Gill 1989	yes
Apion longirostre Olivier 1807	1964	North America	Dowell & Gill 1989	
Araecerus coffeae (Fabricius 1801)	2005	North America	CDFA 2005	
Araptus schwarzi (Blackman 1942)	2010	Mexico	Takahashi 2011	
Atrichonotus taeniatulus (Berg 1881)	1997	North America	CPPDR 1997 16:49	
Barypeithes pellucidus (Boheman 1843)	1947	North America	Van Dyke 1947	
Campylirhynchus castor (Fabricius 1792)			O'Brien & Wibmer 1982	
Caulophilus oryzae (Gyllenhal 1838)	<1915		CDFA 1915 4:307	
Ceutorhynchus assimilis (Paykull 1792)	1945	Europe	CDFA 1953 42:204	
Ceutorhynchus rapae Gyllenhal 1837	1920	North America	Lindroth 1957	
Coccotrypes advena Blandford 1894	2006	North America	Penrose 2007, Atkinson 2015	
Coccotrypes dactyliperda (Fabricius 1801)	1931	Africa	Wood 1982	
Coniatus splendidulus Fabricius 1781	2010	North America	Eckberg & Foster 2011	
Cosmobaris americana Casey 1920	1943	North America	O'Brien & Wibmer 1982	
Cosmobaris scolopacea Germar 1818	1939	Europe	Van Dyke 1950	
Cryptorhynchus lapathi (Linnaeus 1758)		Europe	Furniss & Carolin 1977	
Dactylotrypes longicollis (Wollaston 1864)	2009	Africa	LeBonte & Takahashi 2012	
Diaprepes abbreviatus (Linnaeus 1758)	2005	North America	Grafton-Cardwell et al. 2004	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Euwallacea fornicatus (Eichhoff 1868)	2004	Asia	Haack 2006, Atkinson 2015	yes
Gonipterus scutellatus Gyllenhal 1833	1994	Australia	CPPDR 1994 13:4	yes
Gymnetron antirrhini (Paykull 1800)		North America	Lindroth 1957	
Gymnetronpascuorum (Gyllenhal 1813)		North America	Lindroth 1957	
Gymnetron tetrum (Fabricius 1792)	1942	Europe	Lindroth 1957, CDFA 1942 31:177	
Hylastinus obscurus (Marsham 1802)	1939	North America	Davidson & Lyon 1987, Wood 1982	
Hylurgus ligniperda (Fabricius 1787)	2002	Asia	Penrose 2004, Atkinson 2015	yes
Hypera brunnipennis (Boheman 1834)	1939	North America	Metcalf 1995	yes
Hypera meles (Fabricius 1792)		North America	Davidson & Lyon 1987	
Hypera nigrirostris (Fabricius 1775)	1945	North America	CDFA 1945 34:175	
Hypera postica (Gyllenhal 1813)	1923	North America	CDFA 1923 12:359	yes
Hypera punctata (Fabricius 1775)	1908	North America	Davidson & Lyon 1987, Evans & Hogue 2006	yes
Hypothenemus californicus Hopkins 1915			Wood 1982	
Hypothenemus eruditus Westwood 1836		Tropical America	Wood 1982	
Hypurus bertrandi (Perris 1852)			Anderson 2002	
Ips calligraphus calligraphus (Germar 1824)		North America	Connor and Wilkson 1983	
Lissorhoptrus oryzophilus Kuschel 1952	1969	North America	Dowell & Gill 1989	yes
Listroderes costirostris Schonherr 1826	1926	Tropical America	CDFA 1926 15:116, Evans & Hogue 2006	
Listronotus hyperodes (Dietz 1889)	1959	North America	Dowell & Gill 1989	
Macrancylus littoralis (Broun 1880)	1949		O'Brien & Wibmer 1982	
Magdalis barbicornis (Latreille 1804)	1975	North America	Anderson & Cline 2011	
Mecinus pyraster (Herbst 1795)			Aukema et al. 2010, California Beetle Project 2006	
Naupactus leucoloma (Boheman 1840)	1988	North America	CPPDR 1988 7:8	
Orthotomicus erosus (Wollaston 1857)	2004	Europe	Haack 2004, CPPDR 2006 22:5	yes
Otiorhynchus cribricollis Gyllenhal 1834	1927	Europe	Lindroth 1957, CDFA 1929 18:567, Evans & Hogue 2006	yes
Otiorhynchus meridionalis Gyllenhal 1834	1931	Europe	CDFA 1931 20:470, Evans & Hogue 2006	
Otiorhynchus ovatus (Linnaeus 1758)	1923	Europe	Lindroth 1957, CDFA 1923 12:360, Evans & Hogue 2006	
Otiorhynchus rugostriatus (Goeze 1777)	1920	Europe	Lindroth 1957, CDFA 1930 19:17, Evans & Hogue 2006	
Otiorhynchus sulcatus (Fabricius 1775)	1925	Europe	Lindroth 1957, CDFA 1927 16:654, Evans & Hogue 2006	yes
Pagiocerus frontalis (Fabricius 1801)	2010	North America	Leathers 2015	
Pantomorus cervinus (Boheman 1840)	1879	Europe	CDFA 1930 19:17	yes
Phloeosinus armatus Reitter 1887	1989	Africa	Wood 1992	
Phloeotribus liminaris Harris 1852	2002	North America	Penrose 2004	
Pissodes strobi (Peck 1817)	1972	North America	Dowell & Gill 1989	
Proctorus decipiens (LeConte 1876)	1966	North America	Dowell & Gill 1989	
Pselactus spadix (Herbst 1795)	1966	North America	O'Brien 1970	
Rhynchaenus salicis (Linnaeus 1758)			Lindroth 1957	
[a]*Rhynchophorus vulneratus* (Panzer 1789)	2010	Asia	Rugman-Jones, et al. 2013	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Scolytus multistriatus (Marsham 1802)	1951	North America	Powell & Hogue 1979, Wood 1982	yes
Scolytus rugulosus (Ratzburg 1837)	1913	North America	Powell & Hogue 1979, Wood 1982	yes
Scolytus schevyrewi Semenov 1902	2002	Asia	Penrose 2004, Atkinson 2015	yes
Sitona crinitus (Herbst 1795)			O'Brien & Wibmer 1982	
Sitona cylindricollis Fahraeus 1840	1957	North America	Dowell & Gill 1989	
Sitona flavescens (Marsham 1802)	1907	North America	CDFA 1948 37:211, Bright 1994	
Sitona hispidula (Fabricius 1776)	1917	North America	Metcalf 1995, Bright 1994	
Sitona lepidus Gyllenhal 1834	1907	North America	Campbell et al. 1989, CDFA 1948 37:211	
Sitona lineata (Linnaeus 1758)	1966	North America	Dowell & Gill 1989	
Sitona lineellus (Bonsdorff 1785)		North America	Bright 1994	
Sitophilus granarius (Linnaeus 1758)	1769	Europe	Metcalf 1995	
Sitophilus oryzae (Linnaeus 1763)	1769	Europe	Metcalf 1995	
Sitophilus zeamais (Motschulsky 1855)			Campbell et al. 1989	
Sphenophorus venatus Chittenden 1904	1968	North America	Dowell & Gill 1989	
Tranes internatus Pascoe 1870			O'Brien & Wibmer 1982	
Trichobaris trinotata (Say 1831)	1914	North America	CDFA 1915 4:303	
Tychius picirostris (Fabricius 1787)	1950	Europe	CDFA 1950 39:183	
Xyleborinus saxeseni (Ratzeburg 1837)	< 1915		Essig 1915, Wood 1982, Ivie 2002a	
Xyleborus californicus Wood 1975	1944		Ivie 2002a	
Xyleborus dispar (Fabricius 1792)	<1926	North America	Essig 1926a	
Xyleborus pfeili (Ratzeburg 1837)	2002	Europe	Penrose 2004, Atkinson 2015	
Xyleborus xylographus (Say 1826)	1990	North America	Wood 1982, Ivie 2002a	
Xylosandrus germanus Blandford 1894	2002	Asia	Penrose 2004, Atkinson 2015	
Coleoptera-Dermestidae				
Anthrenus coloratus Reitter 1881	1969	Asia	Dowell & Gill 1989	
Anthrenus scrophulariae Linnaeus 1758			Campbell et al. 1989, CDFA 1958 47:238, 163	
Anthrenus verbasci Linnaeus 1767			California Beetle Project 2006	
Attagenus fasciatus (Thunberg 1795)	1974		Dowell & Gill 1989	
Attagenus unicolor (Brahm 1791)			California Beetle Project 2006	
Dermestes ater (De Geer 1774)			Haines 1981	
Dermestes lardarius Linnaeus 1758	<1925		Campbell et al. 1989, Essig 1926a	
Dermestes maculatus De Geer 1774			Powell & Hogue 1979	yes
Dermestes marmoratus Say 1823	<1925		Powell & Hogue 1979, Essig 1926a	
Dermestes sardous Kuster 1846	1967	Europe	Beal 1994	
Trogoderma granarium Everts 1898	1953	Asia	CDFA 1953 42:202	
Coleoptera: Dytisicidae				
Copelatus glyphicus (Say 1823)	1963		Leech 1970	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Coleoptera-Elateridae				
Conoderus bellus (Say 1824)	1924	North America	Stone 1975	
Conoderus exsul Sharp 1877	1937	Hawaii	Stone 1975	
Conoderus falli (Lane 1956)	1963	North America	Stone 1975	
Heteroderes amplicollis (Gyllenhal 1817)	1938	North America	Stone 1975	
Coleoptera-Endomychidae				
Mycetaea subterranea (Fabricus 1801)			Belov 2009	
Symbiotes gibberosus (Lucas 1849)			BugGuide 2011	
Coleoptera-Erotylidae				
Megalodacne fasciata (Fabricius 1777)	1983	North America	Kitayama 1986, Evans & Hogue 2006	
Coleoptera-Histeridae				
Margarinotus merdarius (Hoffman 1803)			Caterino 2010	
Coleoptera-Hydrophilidae				
Sphaeridium lunatum Fabricius 1792	1947	North America	Bixby 1948	
Sphaeridium scarabaeoides (Linnaeus 1758)	1920	Europe	Blackwelder 1931, Evans & Hogue 2006	
Coleoptera-Laemophloeidae				
Laemophloeus ferrugineus (Stephans 1828)	<1925		Campbell et al. 1989, Essig 1926a	
Laemophloeus pusillus (Schonherr 1817)			Campbell et al. 1989	
Coleoptera-Languriidae				
Languria mozardi Latreille 1807			Essig 1958	
Pharaxonotha kirschi Reitter 1875	1956	North America	Dowell & Gill 1989	
Coleoptera-Latridiidae				
Aridius nodifer (Westwood 1839)			Campbell et al. 1989	
Cartodere constricta (Gyllenhal 1827)			Majka et al. 2009	
Corticaria serrata (Paykull 1798)			Majka et al. 2009	
Cortinicara gibbosa (Herbst 1793)			Majka et al. 2009	
Dienerella argus (Reitter 1884)			Majka et al. 2009	
Dienerella filum (Aube 1850)			Majka et al. 2009	
Latridius minutus (Linnaeus 1767)			Majka et al. 2009	
Coleoptera-Mycteridae				
Hemipeplus marginipennis (LeConte 1854)	1958	North America	CDFA 1959 48:126	
Coleoptera-Mycetophagidae				
Mycetophagus quadriguttatus Müller 1821			Campbell et al. 1989	
Typhaea stercorea (Linnaeus 1758)			Campbell et al. 1989	
Coleoptera-Nitidulidae				
Aethina tumida Murray 1867	2005	North America	Mussen 2010	
Carpophilus dimidiatus (Fabricius 1792)	<1925		Lindroth 1957, Essig 1926a	
Carpophilus hemipterus (Linnaeus 1758)	<1925		Campbell et al. 1989, Essig 1926a	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Carpophilus lugubris Murray 1864	1974		Dowell & Gill 1989	
Nitidula carnaria (Schall 1783)			Dodge 1937	
Nitidula flavomaculata Rossi 1790	<1933		Dodge 1937, Simms & Fothergill 2014	
Stelidota geminate (Say 1825)	1957	North America	Dowell & Gill 1989	
Coleoptera-Oedemeridae				
Nacerdes melanura (Linnaeus 1758)			Furniss & Carolin 1977	
Coleoptera-Ptinidae				
Ptinus fur (Linnaeus 1758)			CDFA 1958 47:243	
Coleoptera-Scarabaeidae				
Aphodius fimetarius Linnaeus 1758	1923	Europe	Evans & Hogue 2006, Gordon & Skelley 2007	
Aphodius fossor Linnaeus 1758		Europe	Evans & Hogue 2006	
Aphodius granarius (Linnaeus 1767)		Europe	Campbell et al. 1989	
Aphodius hamatus Say 1824		Europe	Evans & Hogue 2006	
Aphodius lividus (Olivier 1789)		Europe	Evans & Hogue 2006	
Aphodius pardalis LeConte 1857		Europe	Evans & Hogue 2006	
Aphodius pseudolividus Balthasar 1941		Europe	Evans & Hogue 2006	
Aphodius vittatus Say 1825		Europe	Evans & Hogue 2006	
Australaphodius frenchi (Blackburn 1892)	2008	Africa	BugGuide 2011	
Cotinis mutabilis Gory & Percheron 1883	1925	Tropical America	CDFA 1935 24:417, Essig 1926a	yes
Onthophagus taurus (Schreber 1759)	1993	North America	Hoebeke & Beucke 1997	
Pleurophorus caesus (Creutzer 1796)		North America	Hatch 1946	
[a]*Popillia japonica* Newman 1841	1961	North America	Dowell & Gill 1989	yes
Coleoptera-Silvanidae				
Ahasverus advena (Waltl 1834)	<1925		Metcalf 1995, Campbell et al. 1989, Essig 1926a	
Oryzaephilus mercator (Fauvel 1889)			Thomas 2002	yes
Oryzaephilus surinamensis (Linnaeus 1758)	<1921		CDFA 1921 10:142	yes
Silvanus bidentatus Fabricius 1792			California Beetle Project 2006	
Coleoptera: Staphylinidae				
Aleochara bimaculata Gravenhorst 1802			Hatch 1957	
Aleochara fumata Gravenhorst 1802			Klimaszewski 1984	
Aleochara lanuginosa Gravenhorst 1802			Hatch 1957	
Aleochara lata Gravenhorst 1802			Hatch 1957	
Aleochara puberula Klug 1834			Klimaszewski 1984	
Aleochara tristis Gravenhorst 1806			California Beetle Project 2006	
Aleochara villosa Mannerheim 1830			Hatch 1957	
Aloconota cambrica (Wallaston 1855)			California Beetle Project 2006	
Amischa analis (Gravenhorst 1802)			Muona 1984	
Anotylus rugosus (Fabricius 1775)			Moore & Orth 1977	

Appendix (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Anthobium atrocephalum (Gyllenha 1827)			Moore & Legner 1975	
Atheta amicula (Stephens 1832)			Muona 1984	
Atheta coriaria Kraatz 1856			Muona 1984	
Atheta dilutipennis (Motschulsky 1858)			Muona 1984	
Atheta fungi (Gravenhorst 1806)			Muona 1984	
Atheta harwoodi Williams 1930			Muona 1984	
Atheta longicornis (Gravenhorst 1802)			Muona 1984	
Atheta nigricornis (Thomson 1852)			Muona 1984	
Atheta pallidicornis (Thomson 1856)			Muona 1984	
Autalia puncticollis Sharp 1864	1947	North America	Moore & Legner 1975	
Autalia rivularis (Gravenhorst 1802)			Moore & Orth 1977	
Bisnius sordidus (Gravenhorst 1802)			Hatch 1957, Smetana 1995	
Carpelimus pusillus (Gravenhorst 1802)			Moore & Legner 1975	
Cilea silphoides (Linnaeus 1767)			Hatch 1957	
Cordalia obscura (Gravenhorst 1802)			Muona 1984	
Dinaraea angustula (Gyllenhal 1810)			Muona 1984	
Falagria concinnus Erichson 1839			Hoebeke 1985	
Gauropterus fulgidus (Fabricius 1787)	1931		Hatch 1957	
Gyrohypnus angustatus (Stephens 1833)	1931		Klimaszewski 1984	
Gyrohypnus fracticornis (Müller 1776)			Klimaszewski 1984	
Habrocerus capillaricornis Gravenhorst 1806			California Beetle Project 2006	
Homalota plana (Gyllenhal 1810)			California Beetle Project 2006	
Leptacinus intermedius Donisthorpe 1935	1927		Klimaszewski 1984	
Leptacinus pusillus (Stephens 1833)	1894	Europe	Klimaszewski 1984	
Mannerheimia sp.			Newton et al. 2001	
Meotica apicalis Benick 1953			Muona 1984	
Ocypus ater (Gravenhorst 1802)	1936	North America	Evans & Hogue 2006	
Ocypus olens (Müller 1764)	1920	Europe	Van Dyke 1945	
Oligota parva Kraatz 1858			Moore & Legner 1975	
Olisthaerus megacephalus (Zetterstedt 1828)			Moore & Legner 1975	
Omalium caesum Gravenhorst 1806			Moore & Legner 1975	
Omalium rivulare (Paykull 1789)			Moore & Legner 1975	
Oxypoda opaca (Gravenhorst 1802)			Moore & Legner 1975	
Oxytelus sculptus Gravenhorst 1806			Hatch 1957	
Paraphloeostiba gayndahensis (MacLeay 1871)	1995	Australia	Newton et al. 2001	
Phacophallus parumpunctatus (Gyllenhal 1827)	1891	Europe	Klimaszewski 1984	
Phacophallus tricolor (Kraatz 1859)	1904	Asia	Klimaszewski 1984	
Philonthus cognatus Stephens 1832			California Beetle Project 2006	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Philonthus debilis Gravenhorst 1802			California Beetle Project 2006	
Philonthus discoideus Gravenhorst 1802	1902		Smetana 1995	
Philonthus jurgans Tottenham 1937			California Beetle Project 2006	
Philonthus longicornis Stephens 1832	1890		Smetana 1995	
Philonthus politus (Linnaeus 1758)			Smetana 1995	
Philonthus rectangulus Sharp 1874			California Beetle Project 2006	
Philonthus ventralis Gravenhorst 1802			California Beetle Project 2006	
Placusa complanata Erichson 1839			Moore & Legner 1975	
Placusa tachyporoides (Waltl 1838)			Moore & Legner 1975	
Porrhodites fenestralis (Zetterstedt 1828)			Campbell 1984	
Quedius mesomelinus (Marsham 1802)			Hatch 1957	
Stenus morio Gravenhorst 1806			Moore & Legner 1975	
Tachyporus abdominalis (Fabricius 1781)			Campbell 1979	
Tachyporus nitidulus (Fabricius 1781)			Campbell 1979	
Xantholinus linearis (Olivier 1794)			Hatch 1957	
Xantholinus longiventris Heer 1839			Newton et al. 2001	
Coleoptera-Tenebrionidae				
Alphitobius diaperinus (Panzer 1797)			Campbell et al. 1989	yes
Alphitophagus bifasciata (Say 1824)			Campbell et al. 1989	
Cynaeus angustus (LeConte 1851)			Campbell et al. 1989	
Eleodes suturalis (Say 1824)	1963	North America	Dowell & Gill 1989	
Gnathocerus cornutus (Fabricius 1798)	<1925		CDFA 1958 47:245, Essig 1926a	
Gnathocerus maxillosus (Fabricius 1801)			CDFA 1958 47:245	
Opatroides punctulatus Brulle 1832	2003	Europe	Aalbu et al. 2009	
Palorus ratzburgi (Wissmann 1848)	1954	North America	Campbell et al. 1989	
Palorus subdepressus (Wollaston 1864)	1942	North America	Campbell et al. 1989	
Sitophagus hololeptoides (Laporte 1840)			Peck & Thomas 1998	
Tenebrio molitor Linnaeus 1758	<1925		Campbell et al. 1989	
Tenebrio obscurus Fabricius 1792	<1925		Campbell et al. 1989, Essig 1926a	
Tribolium audax Triplehorn 1968			Sokoloff 1972	
Tribolium castaneum (Herbst 1797)	<1921		CDFA 1921 10:142	yes
Tribolium confusum duVal 1868	<1925		Campbell et al. 1989, Essig 1926a	yes
Tribolium destructor Uyttenboogaart 1933	<1925		Sokoloff 1972, Essig 1926a	
Tribolium ferrugineum (Fabricius 1781)	<1925		Essig 1926a	
Coleoptera-Trogidae				
Trox scabra (Linnaeus 1767)			Lindroth 1957	
Coleoptera-Trogossitidae				
Lophocateres pusillus Klug 1833	1954	North America	Arnett 1985	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Tenebroides mauritanicus (Linnaeus 1758)	<1925		Hatch 1961, Essig 1926a	
Coleoptera-Zopheridae				
Microprius rufulus (Motschulsky 1863)			Lord et al. 2011	
Collembola-Entomobryidae				
Entomobrya unostrigata Stach 1930	1938		Christiansen & Bellinger 1980	
Seira domestica (Nicolet 1841)	<1925	Europe	Essig 1926a	
Willowsia platani (Nicolet 1841)	2009	Europe	BugGuide 2011	
Collembola-Hypogastruridae				
Xenylla martima Tullberg 1869	<1925	Europe	Essig 1926a	
Dermaptera-Anisolabididae				
Anisolabis maritima (Bonelli 1832)	1921		Langston & Powell 1975	
Euborellia annulipes (Lucas 1847)	1885		Langston & Powell 1975	
Euborellia cincticollis (Gerstacker 1883)	1946	Africa	CDFA 1950 39:183	
Dermaptera-Chelisochidae				
Chelisoches morio (Fabricius 1775)	1905		Langston & Powell 1975	
Dermaptera-Forficulidae				
Doru lineare (Eschscholtz 1822)	1865		Langston & Powell 1975	
Forficula auricularia Linnaeus 1758	1923	Europe	Langston & Powell 1975	yes
Dermaptera-Labiduridae				
Labidura riparia Pallas 1773	1952	North America	CDFA 1953 42:40	yes
Dermaptera-Labiidae				
Labia minor (Linnaeus 1758)	1909		Langston & Powell 1975	
Marava arachidis (Yersin 1860)	1910		Langston & Powell 1975	
Dictyoptera-Blaberidae				
Pycnoscelus surinamensis (Linnaeus 1758)	1988	North America	Dowell & Gill 1989	
Dictyoptera-Blattellidae				
Blattella germanica (Linnaeus 1767)	<1925		Powell & Hogue 1979, Atkinson et al. 1991, Essig 1926a	yes
Blattella vaga Hebard 1935	1942	Asia	CDFA 1942 31:176	yes
Phyllodromica trivittata (Serville 1839)	2004	Europe	CPPDR 2011 25:7	
Supella longipalpa (Fabricius 1798)	1940	North America	CDFA 1952 41:50	yes
Dictyoptera-Blattidae				
Blatta lateralis Walker 1868	1978	Africa	Dowell & Gill 1989	yes
Blatta orientalis Linnaeus 1758			Powell & Hogue 1979	yes
Neostylopyga rhombifolia (Stoll 1813)	<1925	Asia	Arnett 1985, Essig 1926a	
Periplaneta americana (Linnaeus 1758)	<1925	Africa	Powell & Hogue 1979, Essig 1926a	yes
Periplaneta australasiae (Fabricius 1775)	<1925	Africa	Powell & Hogue 1979, Essig 1926a	
Periplaneta brunnea Burmeister 1838	1970	North America	Dowell & Gill 1989	yes
Periplaneta fuliginosa (Serville 1839)	1966	North America	Dowell & Gill 1989	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Dictyoptera-Ectobidae				
Luridiblatta trivattata (Servile 1839)	2009	Africa	Lee 2010,Bugguide 2015	
Dictyoptera-Mantidae				
Iris oratorius (Linnaeus 1758)	2007	Europe	Arnett 1985	
Mantis religiosus (Linnaeus 1758)	1959		Arnett 1985	
Stagmomantis carolina Johannson 1763			Arnett 1985, Essig 1926a	
Stagmomantis limbata (Hahn 1835)	1864		Buckett 1966	
Tenodera angustipennis Saussure 1869	1952		Arnett 1985	
Tenodera aridifolia Stoll 1813	1932		Arnett 1985	
Diploda-Julida-Julidae				
Brachyiulus lusitanus Verhoeff 1898		North America	Hoffman 1999, Shelley 2002, Reeves 2000	
Cylindroiulus caeruleocinctus (Wood 1864)		Europe	Shelley 2002	
Cylindroiulus truncorum (Silvestri 1896)		Europe	Shelley 2002	
Diploiulus latistriatus (Curtis, 1845)		Europe	Lindroth 1957, Verhoeff 1944	
Ophyiulus pilosus (Newport 1843)		Europe	Shelley 2002	
Opiona fisheri Gardner & Shelley 1989		Europe	Shelley 2002	
Diploda-Polydesmida-Paradoxosomatidae				
Akamptogonus novarae (Humbert & DeSaussure 1869)		Australia	Shelley 2002	
Oxidus gracilis (Koch 1847)		Asia	Shelley 2002	
Diploda-Polydesmida-Polydesmidae				
Oxidus gracilis (Koch 1847)		Asia	BugGuide 2011	
Diptera-Agromyzidae				
Chromatomyia syngenesiae Hardy 1849	1914		Spencer 1981	
Liriomyza brassicae (Riley 1885)			Spencer 1981	
Liriomyza sativae Blanchard 1938			Spencer 1981	yes
Liriomyza langei Frick 1951		Tropical America	Spencer 1981	yes
Melanagromyza splendida Frick 1953	1967	Hawaii	Dowell & Gill 1989	
Ophiomyia simplex (Loew 1869)	<1915		Spencer 1981	
Phytomyza crassiseta Zetterstedt 1860	1962	Pacific Region	Dowell & Gill 1989	
Phytomyza ilicicola Loew 1872	<1915		Davidson & Lyon 1987	
Phytomyza ranunculi (Schrank 1803)	1965	Pacific Region	Dowell & Gill 1989	
Phytomyza rufipes Meigen 1830	2006	Europe	Scheffer & Winkler 2008	
Diptera-Anthomyiidae				
Delia antiqua (Meigen 1826)	<1925	North America	Davidson & Lyon 1987, Essig 1926a	
Delia platura (Meigen 1826)	<1915	North America	Spencer 1981, CDFA 1915 4:334	
Delia radicum Linnaeus 1758		North America	Griffiths 1991	
Pegomya hyoscyami (Panzer 1809)	<1925		Essig 1926a	
Pegomya betae (Curtis 1847)	1893		CDFA 1915 4:331	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Pegomya wygodzinskyi Albuquerque 1954	1948	Australia	CDFA 1948 37:204	
Diptera-Bibionidae				
Dilophus sayi (Hardy 1966)	1950	North America	Powell & Hogue 1979	
Diptera-Braulidae				
Braula coeca Nitzsch 1818			Arnett 1985	
Diptera-Calliphoridae				
Calliphora vicina Robineau-Desvoidy 1830			Powell & Hogue 1979, James 1955	
Calliphora vomitoria (Linnaeus 1758)			James 1955	
Chrysomya megacephala (Fabricius 1794)	1988	Tropical America	Dowell & Gill 1989	
Chrysoma rufifacies (MacQuart 1843)	1987	North America	Dowell & Gill 1989	
Cochliomyia hominivorax (Coquerel 1858)			James 1955	
Lucilia illustris (Meigen 1826)	1769	Europe	Metcalf 1995	
Lucilia silvarum (Meigen 1826)			James 1955	
Lucilia sericata (Meigen 1826)	1769		Metcalf 1995, James 1955	
Phormia regina (Meigen 1826)	<1925		James 1955, Essig 1926a	
Pollenia rudis (Fabricius 1794)	<1925		Cole 1969, James 1955, Essig 1926a	
Diptera-Cecidomyiidae				
Cecidomyia balsamicola (Linter 1888)	1963	North America	Dowell & Gill 1989	
Contarinia sorghicola (Coquillett 1899)	1960	Asia	Dowell & Gill 1989	
Dasineura affinis (Kieffer 1886)	1992	Europe	CPPDR 1992 11:6	
Dasineura balsamicola (Lintner 1888)	1964		CDFA 1965 54:81	
Dasineura gleditchiae (Osten Sacken 1866)	1978	North America	Dowell & Gill 1989	yes
Dasineura leguminicola (Lintner 1879)	<1925	North America	Pritchard 1953, Essig 1926a	
Dasineura rhodophaga (Coquillett 1900)	1996	North America	CPPDR 1996 15:77	
Mayetiola destructor (Say 1817)	1879	North America	Pritchard 1953	
Mayetiola violicola (Coquillett 1900)	1967	North America	Dowell & Gill 1989	
Monarthropalpus flava (Schrank 1776)	1915	Europe	Cole 1969	yes
Rhopalomyia chrysanthemi (Ahlberg 1939)	<1925		Cole 1969, Essig 1926a	
Sitodiplosis mosellana (Géhin 1857)		North America	Davidson & Lyon 1987	
Diptera-Chaoboridae				
Mochlonyx cinctipes (Coquillett, 1903)	2003-2008	North America	Woodward et al. 2010	
Diptera: Chironomidae				
Goeldichironomus amazonicus (Fittkau 1968)	1990	Tropical America	Sublette & Mulla 1991	
Diptera-Chloropidae				
Meromyza americana Fitch 1856	<1925	North America	Davidson & Lyon 1987, Essig 1926a	yes
Oscinella frit (Linnaeus 1758)	<1925		Davidson & Lyon 1987, Essig 1926a	
Diptera-Culicidae				
Aedes aegypti (Linnaeus 1762)	1979	North America	Dowell & Gill 1989	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Culex erraticus (Dyar & Knab 1906)	1994	North America	Lothrop et al. 1995	
Culex pipiens Linnaeus 1758	< 1920	North America	Essig 1926a	
Diptera-Drosophilidae				
Dettopsomyia nigrovittata (Malloch 1924)	1949	Australia	Wheeler 1951	
Drosophila suzukii Matsumura 1931	2008	Asia	Walsh et al. 2011	yes
Drosophila virilis Sturtevant 1916			Cole 1969	
Drosophila bifurca Patterson & Wheeler,1942	2010		Castrezana 2010	
Zaprionus indianus Gupta 1970	2010		Castrezana et al. 2010	
Diptera-Ephydridae				
Hydrellia griseola (Fallén 1813)	1922	North America	Metcalf 1995	
Ochthera mantis (De Geer 1776)	<1925	Europe	Essig 1926a	
Diptera-Fannidae				
Fannia canicularis (Linnaeus 1761)	<1925		Huckett 1975, Essig 1926a	yes
Fannia incisurata (Zetterstedt 1838)			Cole 1969	
Fannia manicata (Meigen 1826)			Cole 1969	
Fannia scalaris (Fabricius 1794)	<1925		Cole 1969, Essig 1926a	
Diptera-Hippoboscidae				
Melophagus ovinus Linnaeus 1758	<1925	North America	Bequeart 1953-1954, Essig 1926a	
Pseudolynchia canariensis (Macquart 1839)	<1945	Europe	Cole 1969	
Diptera-Lonchaeidae				
Dasiops alveofrons McAlpine 1961	1945	North America	Cole 1969	
Diptera-Muscidae				
Coenosia attenuate Stein 1903	2002		Hoebeke et al. 2003	
Haematobia irritans (Linnaeus 1758)	<1900	North America	Davidson & Lyon 1987, Essig 1926a	yes
Musca autumnalis De Geer 1776	1968	North America	Dowell & Gill 1989	yes
Musca domestica Linnaeus 1758	1769	Europe	Metcalf 1995	yes
Stomoxys calcitrans (Linnaeus 1758)	<1932		Cole 1969	
Diptera-Oestridae				
Gasterophilus haemorrhoidalis (Linnaeus 1758)	<1925		Cole 1969, Essig 1926a	yes
Gasterophilus intestinalis (De Geer 1776)	<1925		Cole 1969, Essig 1926a	yes
Gasterophilus nasalis (Linnaeus 1758)	<1925		Cole 1969, Essig 1926a	yes
Hypoderma bovis (Linnaeus 1758)	<1925	North America	Cole 1969, Essig 1926a	yes
Hypoderma lineatus (De Villers 1789)	<1925	North America	Cole 1969, Essig 1926a	yes
Oestrus ovis Linnaeus 1758	<1925	Europe	Cole 1969, Essig 1926a	
Diptera-Otitidae				
Euxesta stigmatias Loew 1868	1996	Tropical America	CPPDR 1996 15:154	
Diptera-Phoridae				
Chonocephalus bentacaisei (Santos Abreu 1921)	2008	Africa	Disney & Brown 2009	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Megaselia scutellaris (Wood 1909)	2008	Europe	Disney & Brown 2009	
Megaselia seticauda (Malloch 1914)	1996	Mexico	CPPDR 1996 15:153	
Diptera-Piophilidae				
Piophila casei (Linnaeus 1758)	<1925	North America	Cole 1969, Essig 1926a	
Diptera: Platystomatidae				
Pogonortalis doclea (Walker 1849)		Australia	McAlpine 2001	
Diptera-Psilidae				
Psila rosae (Fabricius 1794)	1963	Europe	Dowell & Gill 1989	
Diptera-Sciaridae				
Pnyxia scabiei (Hopkins 1895)			Cole 1969	
Diptera-Sepsidae				
Decachaetophora aeneipes (Meijere 1913)			Cole 1969	
Diptera-Stratiomyidae				
Inopus rubriceps (Macquart 1847)	1948	Australia	Kessel 1948	yes
Neoexaireta spinigera (Weidemann 1830)	1966	Hawaii	Dowell & Gill 1989	
Diptera-Syrphidae				
Eristalinus taeniops (Wiedemann 1818)	2006	Africa	Hauser 2006	
Eristalis arbustorum (Linnaeus 1758)			Nayar 1968	
Eristalis tenax (Linnaeus 1758)	<1925	Europe	Powell & Hogue 1979, Essig 1926a	
Eumerus narcissi Smith 1928	1927		CDFA 1930 19:760, Davidson & Lyon 1987	yes
Eumerus strigatus (Fallén 1817)	<1925		CDFA 1930 19:575, Essig 1926a	yes
Eumerus tuberculatus Rondani 1857			CDFA 1933 22:142	
Merodon equestris (Fabricius 1794)	1914	Europe	Metcalf 1995	yes
Myatropha florae (Linneaus 1758)	2006	Europe	BugGuide 2011	
Syritta flaviventris Macquart 1842	2006	Europe	Hauser 2007	
Syrphus ribesi (Linnaeus 1758)	<1925	Europe	Essig 1926a	
Diptera-Tephritidae				
[a]*Anastrepha ludens* (Loew 1873)	1954	North America	CDFA 1954 43:168	yes
[a]*Anastrepha suspensa* (Loew 1862)	1984	North America	Dowell & Gill 1989	yes
[a]*Bactrocera albistrigata* (Meijere 1911)	2009	Asia	CPPDR 2011 25:9	yes
[a]*Bactrocera correcta* (Bezzi 1916)	1986	Asia	Dowell & Gill 1989	yes
[a]*Bactrocera cucurbitae* (Coquillett 1849)	1956	Hawaii	Dowell & Gill 1989	yes
[a]*Bactrocera dorsalis* (Hendel 1912)	1960	Hawaii	Dowell & Gill 1989	yes
[b]*Bactrocera zonata* (Saunders 1842)	1985	Asia	Dowell & Gill 1989	yes
Bactrocera oleae (Gmelin 1790)	1998	Europe	CPPDR 1998 17:66	yes
[a]*Bactrocera scutellata* (Hendel 1912)	2009	Asia	CPPDR 2011 25:9	
[a]*Ceratitis capitata* (Weidemann 1824)	1975	Tropical America	Dowell & Gill 1989	yes
Chaetorellia succinea (Costa 1844)	1996	North America	Pitcairn et al. 2000	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Rhagoletis completa Cresson 1929	1925	North America	CDFA 1930 19:249	yes
Rhagoletis pomonella (Walsh 1867)	1983	North America	Dowell & Gill 1989	yes
Terellia fuscicornis (Loew 1844)	1994	Europe	CPPDR 1994 13:57	
Diptera-Tipulidae				
Tipula paludosa Meigan 1830	1999	North America	Umble & Rao 2005	yes
Tipula oleracea Linnaeus 1758	2003	North America	Umble & Rao 2005, CPPDR 2006 22:7	yes
Embiidina-Oligotomidae				
Haploembia solieri (Rambur 1842)	<1900	Europe	Powell & Hogue 1979, Ross 1957	
Oligotoma nigra Hagen 1866	1890	Europe	Powell & Hogue 1979, Ross 1957	
Hemiptera-Aclerdidae				
Aclerda tokionis (Cockerell 1896)	1900	Asia	Gill 1993	
Hemiptera-Adeligidae				
Adelges abietis (Linnaeus 1758)		North America	Martineau 1984	
Adelges nordmannianae (Eckstein 1890)		North America	Furniss & Carolin 1977	
Adelges piceae (Ratzeburg 1844)	1928	North America	Blackman & Eastop 1994, Rageno-vich & Mitchell. 2006	
Hemiptera-Aleyrodidae				
Aleurodicus dugesii Cockerell 1896	1992	Mexico	CPPDR 1992 11:78	yes
Aleuroplatus berbericolus Quaintance & Baker 1917	1935	North America	Mound & Halsey 1978	
Aleurothrixus floccosus (Maskell 1896)	1966	Tropical America	Dowell & Gill 1989	yes
Aleurotuba jelinekii (Frauenfeld 1867)	1963	Europe	Dowell & Gill 1989	
Aleurotuberculatus aucubae (Kuwana 1932)	2002	Asia	CPPDR 2006 22:15	
Aleurotuberculatus jasmini (Takahashi 1932)	1997	Hawaii	CPPDR 1996 15:156	
Aleyrodes proletella (Linnaeus 1758)	2001	Europe	Penrose 2001	
Bemisia argentifolii Bellows & Perring 1994	1991	North America	Bellows et al. 1994	yes
Bemisia tabaci (Gennadius 1889)		North America	Mound & Halsey 1978	yes
Dialeurodes citri (Ashmead 1885)	1906	North America	Metcalf 1995,	yes
Dialeurodes citrifolii (Morgan 1893)	1985	North America	Dowell & Gill 1989	
Parabemisia myricae (Kuwana 1927)	1978	Asia	Dowell & Gill 1989	
Paraleyrodes minei Iaccarino 1990@	1983	Mexico	Dowell & Gill 1989	
Siphoninus phillyreae (Haliday 1835)	1988	Europe	Dowell & Gill 1989	yes
Tetraleurodes acaciae (Quaintance 1914)	1900	Mexico	Mound & Halsey 1978	
Tetraleurodes sp Cockerell 1902	1983	Tropical America	Dowell & Gill 1989	
Trialeurodes packardi (Morrill 1903)		North America	Mound & Halsey 1978	
Trialeurodes ruborum (Cockerell 1897)	1953	North America	CDFA 1953 42:203	
Trialeurodes vaporariorum (Westwood 1856)	<1915	North America	CDFA 1915 4:197	yes
Trialeurodes variabilis (Quaintance 1900)	2002	North America	CPPDR 2003 21:10	
Hemiptera-Anthocoridae				
Anthocoris nemoralis (Fabricius 1794)	1990	North America	Hagen & Dreistadt 1990; Lattin 2007	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Buchananiella continua (White 1880)	1934	Europe	Lattin 2001	
Dufouriellus ater (Dufour 1833)			Henry & Froeschner 1988; Lattin 2007	
Macrotrachelia nigronitens (Stal 1860)	2001	Tropical America	Lewis et al. 2005; Lattin 2007	
Xylocoris galactinus (Fieber 1837)			Lattin 2007	
Xylocoris sordidus (Reuter 1871)			Lattin 2007	
Hemiptera-Aphalaridae				
Ctenarytaina eucalypti (Maskell 1890)	1991	Australia	CPPDR 1991 10:5	yes
Ctenarytaina spatulata Taylor 1977	1991	Australia	CPPDR 1991 10:42	
Psyllopsis fraxinicola (Föerster 1848)	1920	Europe	Hodkinson 1988	
Hemiptera-Aphididae				
Acyrthosiphon festucae (Theobald 1917)	1970		Blackman & Eastop 1994	
Acyrthosiphon kondoi Shinji 1938	1975	Asia	Dowell & Gill 1989	
Acyrthosiphon lactucae (Passerini 1860)			Blackman & Eastop 1984, Foottit et al. 2006	
Acyrthosiphon loti (Theobald 1913)	1975		Blackman & Eastop 1984	
Acyrthosiphon malvae (Mosley 1841)			Smith & Parron 1978	
Acyrthosiphon pisum (Harris 1776)	<1915	North America	Davidson & Lyon 1987, Foottit et al. 2006	yes
Aloephagus myersi Essig 1950	1939	Africa	Blackman & Eastop 1994, Foottit et al. 2006	
Aphis arundinis (Fabricius 1775)	1881	North America	Blackman & Eastop 1994, Essig 1917	
Aphis citricola Van der Goot 1912		Mexico	Blackman & Eastop 1994	yes
Aphis craccivora Koch 1854	<1915	Tropical America	Blackman & Eastop 1994, Foottit et al. 2006	yes
Aphis cytisorum Hartig 1841			Smith & Parron 1978, Foottit et al. 2006	
Aphis fabae Scopoli 1763	<1915	North America	CDFA 1915 4:104, Foottit et al. 2006	yes
Aphis gossypii Glover 1877	<1915		CDFA 1915 4:89, Foottit et al. 2006	yes
Aphis hederae Kaltenbach 1843	1910		Blackman & Eastop 1994, Essig 1917, Foottit et al. 2006	yes
Aphis middletonii (Thomas 1879)		North America	Smith & Parron 1978	
Aphis nasturtii Kaltenbach 1843			Blackman & Eastop 1984, Foottit et al. 2006	
Aphis nerii Fonscolombe 1841	<1915		CDFA 1915 4:91, Foottit et al. 2006	
Aphis pomi De Geer 1773	<1915	North America	CDFA 1915 4:92, Foottit et al. 2006	
Asiphonella cynodonti (Das 1918)	1958	North America	CDFA 1959 48:127	
Aulacorthum circumflexum (Buckton 1876)			Blackman & Eastop 1984, Foottit et al. 2006	
Aulacorthum solani (Kaltenbach 1843)			Blackman & Eastop 1994, Foottit et al. 2006	yes
Betulaphis brevipilosa Borner 1940			Blackman & Eastop 1994, Foottit et al. 2006	
Brachycaudus cardui (Linnaeus 1758)	<1916		Blackman & Eastop 1994, Essig 1917	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Brachycaudus persicae (Passerini 1860)	1910	North America	Blackman & Eastop 1984, Foottit et al. 2006	yes
Brachycaudus rumexicolens (Patch 1917)	1984	Europe	Dowell & Gill 1989	
Brachycaudus schwartzi (Borner 1931)	1975	Europe	Blackman & Eastop 1994, Foottit et al. 2006	
Brachycaudus tragopogonis (Kaltenbach 1843)	1975	Europe	Dowell & Gill 1989	
Brachycolus asparagi Mordvilko 1928	1984	North America	Dowell & Gill 1989	
Brevicoryne brassicae (Linnaeus 1758)	1876	North America	Davidson & Lyon 1987, Foottit et al. 2006	yes
Calaphis betulicola (Kaltenbach 1843)			Blackman & Eastop 1994, Foottit et al. 2006	
Calaphis flava Mordvilko 1928			Blackman & Eastop 1994	
Calaphis juglandis Goeze 1778	1952	Asia	CDFA 1952 41:180	yes
Callipterinella calliptera (Hartig 1841)			Blackman & Eastop 1994, Foottit et al. 2006	
Callipterinella minutissima (Stroyan 1953)			Blackman & Eastop 1994, Foottit et al. 2006	
Capitophorus hippophaes (Walker 1852)			Blackman & Eastop 1994, Foottit et al. 2006	
Carolinaia howardi (Wilson 1911)	1916		Essig 1915	
Cavariella pastinacae (Linnaeus 1758)			Blackman & Eastop 1994	
Cerataphis lataniae (Boisduval 1867)	<1916		Blackman & Eastop 1984, Essig 1917, Foottit et al. 2006	yes
Cerataphis orchidearum Westwood 1879			Blackman & Eastop 1994, Foottit et al. 2006	
Chaetosiphon tetrarhodum (Walker 1849)			Blackman & Eastop 1984, Foottit et al. 2006	
Chaitophorus leucomelas Koch 1854	1966	Europe	Blackman & Eastop 1994, Foottit et al. 2006	yes
Chromaphis juglandicola (Kaltenbach 1843)	1896	Europe	CDFA 1915 4:82, Foottit et al. 2006	
Cinara atlantica (Wilson 1919)			Blackman & Eastop 1994	
Cinara cupressi (Buckton 1881)	1916	Europe	Foottit et al. 2006	yes
Cinara pilicornis (Hartig 1841)			Blackman & Eastop 1994, Foottit et al. 2006	
Cinara tujafilina (del Guercio 1909)			Furniss & Carolin 1977, Foottit et al. 2006	
Colopha ulmicola (Fitch 1859)			Blackman & Eastop 1994	
Coloradoa rufomaculata (Wilson 1908)			Blackman & Eastop 1984	
Cryptomyzus ribis (Linnaeus 1758)			Blackman & Eastop 1984, Foottit et al. 2006	
Diuraphis noxia (Mordvilko 1913)	1988	North America	Dowell & Gill 1989	yes
Drepanaphis acerifoliae Thomas 1878	<1916		CDFA 1914 3:85	yes
Drepanosiphum oregonensis Granovsky 1939			Blackman & Eastop 1994, Foottit et al. 2006	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Drepanosiphum platanoides (Schrank 1801)	1908	Europe	Foottit et al. 2006	
Dysaphis apiifolia (Theobald 1923)			Blackman & Eastop 1984, Foottit et al. 2006	yes
Dysaphis crataegi (Kaltenbach 1843)			Blackman & Eastop 1984, Foottit et al. 2006	yes
Dysaphis foeniculus (Theobald 1922)			Blackman & Eastop 1984, Foottit et al. 2006	yes
Dysaphis plantaginae (Passerini 1860)			Blackman & Eastop 1984, Foottit et al. 2006	
Dysaphis tulipae (Fonscolombe 1841)	<1925	Europe	Blackman & Eastop 1984, Essig 1926a, Foottit et al. 2006	yes
Elatobium abietina (Walker 1849)	1915	Europe	Furniss & Carolin 1977, Foottit et al. 2006	
Eriosoma americana (Riley 1879)	<1916		Blackman & Eastop 1984	yes
Eriosoma lanigera (Hausmann 1802)	1870	North America	Metcalf 1995	
Eriosoma pyricola Baker & Davidson 1916	<1925	North America	Blackman & Eastop 1994, Essig 1926a, Foottit et al. 2006	
Eriosoma rileyi Thomas 1878	1913	North America	Blackman & Eastop 1984	
Eucallipterus tiliae (Linnaeus 1758)	1909	North America	Davidson 1909, Foottit et al. 2006	
Eucarazzia elegans (Ferrari 1872)	1984	Africa	Dowell & Gill 1989	
Euceraphis betulae Koch 1855			Blackman & Eastop 1994, Foottit et al. 2006	
Euceraphis punctipennis (Zetterstedt 1828)			Furniss & Carolin 1977, Foottit et al. 2006	
Eulachnus agilis (Kaltenbach 1843)			Blackman & Eastop 1994, Foottit et al. 2006	
Eulachnus rileyi (Williams 1843)			Blackman & Eastop 1994, Foottit et al. 2006	
Euthoracaphis umbellulariae (Essig 1932)	1929	Asia	CDFA 1941 30:353, Blackman & Eastop 1994, Foottit et al. 2006	yes
Forda formicaria Heyden 1837			Blackman & Eastop 1984, Foottit et al. 2006	
Forda marginata Koch 1857			Blackman & Eastop 1984, Foottit et al. 2006	
Hayhurstia atriplicis (Linnaeus 1761)			Foottit et al. 2006	
Hyadaphis coriandri (Das 1918)	1999	Europe	CPPDR 1999 18:19, Foottit et al. 2006	
Hyadaphis foeniculi (Passerini 1860)			Blackman & Eastop 1984, Foottit et al. 2006	yes
Hyalopterus pruni (Geoffroy 1762)	1881	North America	Metcalf 1995, Foottit et al. 2006	yes
Hyperomyzus lactucae (Linnaeus 1758)	<1916		Blackman & Eastop 1984, Foottit et al. 2006	
Hysteroneura setariae (Thomas 1878)	1955	North America	CDFA 1966 55:93, Dowell & Gill 1989	
Idiopterus nephrelepidis Davis 1909	<1915		CDFA 1915 4:101, Foottit et al. 2006	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Illinoia azaleae (Mason 1925)	1954		CDFA 1954 43:76	
Illinoia liriodendri (Monell 1879)	1974	North America	Blackman & Eastop 1994	yes
Lipaphis erysimi (Kaltenbach 1843)			Blackman & Eastop 1984	yes
Macrosiphoniella sanborni (Gillette 1908)			Blackman & Eastop 1994, Foottit et al. 2006	
Macrosiphum eurphorbiae (Thomas 1878)			Blackman & Eastop 1994	yes
Macrosiphum avenae (Fabricius 1775)	1916		Essig 1915, Davidson & Lyon 1987, CDFA 1915 4:86	yes
Macrosiphum rosae (Linnaeus 1758)	<1915		CDFA 1915 4:105, Foottit et al. 2006	
Macrosiphum tiliae (Monell 1879)			Blackman & Eastop 1994	
Melanaphis sacchari (Zehntner 1895)	1997	Asia	CPPDR 1997 16:49, Foottit et al. 2006	yes
Melanocallis caryaefoliae (Davis 1910)	1958	North America	CDFA 1959 48:127	
Melaphis rhois (Fitch 1866)	<1916	North America	Essig 1915	
Metopolophium festucae (Theobald 1917)	1970		Foottit et al. 2006	
Mindarus abietinus Koch 1857			Blackman & Eastop 1994, Foottit et al. 2006	
Monellia caryella (Fitch 1855)	<1932		Blackman & Eastop 1984	yes
Monelliopsis caryae (Monell 1879)	<1925	North America	Essig 1926a	yes
Myzaphis rosarum (Kaltenbach 1843)	<1915		Blackman & Eastop 1984, Foottit et al. 2006	
Myzocallis castaneae (Fitch 1856)	1914		Essig 1915	
Myzocallis castanicola Baker 1916	1914	Europe	Blackman & Eastop 1984, Foottit et al. 2006	
Myzocallis coryli (Goeze 1778)	<1916	North America	Blackman & Eastop 1994, Foottit et al. 2006	
Myzocallis punctatus (Monell 1879)		North America	Blackman & Eastop 1994	
Myzocallis walshii (Monell 1879)		North America	Blackman & Eastop 1994	
Myzus ascalonicus Doncaster 1946		North America	Blackman & Eastop 1984, Foottit et al. 2006	
Myzus cerasi (Fabricius 1775)	<1915		Davidson & Lyon 1987, CDFA 1915 4:96, Foottit et al. 2006	yes
Myzus certus (Walker 1849)			Blackman & Eastop 1984, Foottit et al. 2006	
Myzus dianthicola Hille Ris Lambers 1966			Blackman & Eastop 1984	
Myzus formosanus Takahashi 1923	1958		Essig 1958	
Myzus hemerocallis Takahashi 1921	1959	Asia	Dowell & Gill 1989	
Myzus ligustri (Mosley 1841)			Blackman & Eastop 1984, Foottit et al. 2006	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Myzus lythri (Schrank 1801)			Blackman & Eastop 1994, Foottit et al. 2006	
Myzus ornatus Laing 1932	1926	Europe	Essig 1926b	
Myzus persicae (Sulzer 1776)	<1915	North America	Blackman & Eastop 1994, CDFA 1915 4:98	yes
Myzus varians Davidson 1912		Asia	Blackman & Eastop 1984	
Nasonovia ribisnigri (Mosley 1841)	2001	North America	CPPDR 1998 17:69, Foottit et al. 2006	yes
Nearctaphis bakeri (Cowen 1895)	<1915		Blackman & Eastop 1984	
Neophyllaphis araucariae Takahashi 1937			Blackman & Eastop 1994, Foottit et al. 2006	
Neophyllaphis podocarpi Takahashi 1920	1954	Australia	Blackman & Eastop 1994, Foottit et al. 2006	yes
Neotoxoptera formosana Takahashi 1921	1927	Asia	Blackman & Eastop 1984, Essig 1958, Foottit et al. 2006	
Neotoxoptera oliveri (Essig 1935)	1927	Asia	Blackman & Eastop 1984, Foottit et al. 2006	
Neotoxoptera violae Pergande 1900	<1915		Blackman & Eastop 1984, CDFA 1915 4:101	
Ovatus crataegarius (Walker 1850)			Smith & Parron 1978, Foottit et al. 2006	
Pachypappa pseudobyrsa (Walsh 1863)	1953	North America	Smith & Parron 1978	
Pemphigus betae Doane 1900	<1915		CDFA 1915 4:75	yes
Pemphigus bursarius (Linnaeus 1758)	1955		CDFA 1955 44:164, Foottit et al. 2006	yes
Pentalonia nigronervosa Coquerel 1859	<1916		Blackman & Eastop 1994, Foottit et al. 2006	
Periphyllus californiensis (Shinji 1917)			Furniss & Carolin 1977, Foottit et al. 2006	yes
Periphyllus lyropictus (Kessler 1886)			Furniss & Carolin 1977, Foottit et al. 2006	yes
Periphyllus testudinaceus (Fernie 1852)			Furniss & Carolin 1977, Foottit et al. 2006	yes
Phorodon humuli (Schrank 1801)	1890	North America	Blackman & Eastop 1994, Foottit et al. 2006	
Phyllaphis fagi (Linnaeus 1767)		Europe	Blackman & Eastop 1994, Foottit et al. 2006	yesS
Pleotrichophorus chrysanthemi (Theobald 1920)			Foottit et al. 2006	
Pterocallis alni (De Geer 1773)		Europe	Blackman & Eastop 1994, Foottit et al. 2006	
Pterocomma populea (Kaltenbach 1843)			Blackman & Eastop 1994, Foottit et al. 2006	
Pterocomma salicis (Linnaeus 1758)			Blackman & Eastop 1994, Foottit et al. 2006	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Rhopalomyzus poae (Gillette 1908)	1955	North America	Dowell & Gill 1989	
Rhopalosiphoninus latysiphon (Davidson 1912)			Foottit et al. 2006	
Rhopalosiphoninus staphyleae (Koch 1854)			Blackman & Eastop 1984, Foottit et al. 2006	
Rhopalosiphum insertum (Walker 1849)	1955	North America	Smith & Parron 1978	
Rhopalosiphum maidis (Fitch 1856)	<1916		Blackman & Eastop 1994, Essig 1917, Foottit et al. 2006	yes
Rhopalosiphum nymphaeae (Linnaeus 1761)	<1916		CDFA 1917 6:65, Foottit et al. 2006	
Rhopalosiphum padi (Linnaeus 1758)			Blackman & Eastop 1994	yes
Rhopalosiphum rufiabdominalis (Sasaki 1899)			Blackman & Eastop 1984, Foottit et al. 2006	
Sarucallis kahawaluokalani (Kirkaldy 1907)	1937	North America	Blackman & Eastop 1994	yes
Schizaphis graminum (Rondani 1852)	<1925	North America	Metcalf 1995, Essig 1926a, Foottit et al. 2006	yes
Schizolachnus pineti (Fabricius 1781)			Blackman & Eastop 1984, Foottit et al. 2006	
Shivaphis celti Das 1918	2002	North America	CPPDR 2006 22:8-9, Foottit et al. 2006	yes
Sinomegoura citricola (van der Goot 1917)	2009	Asia	CPPDR 2011 25:16	
Sipha flava (Forbes 1884)			Smith & Parron 1978	yes
Sipha maydis Passerini 1860	2007	Europe	CPPDR 2011 24:9-11	
Sitobion fragariae (Walker 1848)			Foottit et al. 2006	
Smynthurodes betae Westwood 1849			Blackman & Eastop 1994, Foottit et al. 2006	
Takecallis arundicolens (Clarke 1903)	1903	Asia	Blackman & Eastop 1994, CDFA 1915 4:84, Foottit et al. 2006	yes
Takecallis arundinariae (Essig 1917)	1911	Asia	Blackman & Eastop 1994, Foottit et al. 2006	
Takecallis taiwanus (Takahashi 1926)		Asia	Blackman & Eastop 1994, Foottit et al. 2006	
Tetraneura nigriabdominalis (Saski 1899)			Blackman & Eastop 1994	
Tetraneura ulmi (Linnaeus 1758)			Blackman & Eastop 1994, Foottit et al. 2006	
Thecabius affinis (Kaltenbach 1843)			Blackman & Eastop 1994	
Therioaphis riehmi (Borner 1949)	1956		Dowell & Gill 1989	
Therioaphis trifolii (Monell 1882)	1954	Europe	Metcalf 1995, Foottit et al. 2006	
Tinocallis platani (Kaltenbach 1842)	1935	Europe	Blackman & Eastop 1994, Foottit et al. 2006	
Tinocallis ulmifolii (Monell 1879)	1914	North America	Blackman & Eastop 1994	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Tinocallis ulmiparvifoliae Matsumura 1998	2001	Asia	CPPDR 1998 17:10	
Tinocallis zelkowae (Takahashi 1919)	1983	Asia	Dowell & Gill 1989	
Toxoptera aurantii (Fonscolombe 1841)	1907	Asia	CDFA 1915 4:78, Foottit et al. 2006	yes
Tuberculatus annulatus (Hartig 1841)			Blackman & Eastop 1994, Foottit et al. 2006	
Uroleucon achilleae Koch 1855	1966	Europe	Blackman & Eastop 1984, Foottit et al. 2006	
Vesiculaphis caricis (Fullaway 1910)	1962		Dowell & Gill 1989	
Hemiptera-Artheneidae				
Holcocranum saturejae (Kolenati 1845)	1997	Europe	Wheeler & Stoops 1999	
Hemiptera-Asterolecaniidae				
Asterolecanium arabidis (Signoret 1876)	1940	North America	Gill 1993	
Asterolecanium bambusae (Boisduval 1869)		Asia	Gill 1993	
Asterolecanium grandiculum Russell 1941		Tropical America	Gill 1993	
Asterolecanium minus Russell 1941		North America	Gill 1993	
Asterolecanium quercicola (Bouché 1851)		North America	Gill 1993	yes
Asterolecanium variolosum (Ratzeburg 1970)	1913	Europe	Gill 1993	
Planchonia stentae (Brain 1920)	1980	Africa	Miller et al. 2005	
Pollinia pollini (Costa 1828)	1892	Europe	Gill 1993	
Hemiptera-Cercopidae				
Philaenus spumarius (Linneaus 1758)			BugGuide 2011, Karban & Strauss 2004	
Hemiptera-Cicadelldidae				
Agalliota barretti (Ball 1900)	1972	North America	Dowell & Gill 1989	
Allygus mixtus Fabricius 1794	2007	North America	CPPDR 2011 24:6	
Anoscopus flavostriatus (Donovan 1799)		North America	Hamilton 1983	
Anoscopus serratulae (Fabricius 1775)		Europe	Hamilton 1983	
Aphrodes costatus (Panzer 1799)		Europe	Hamilton 1983	
Balclutha rosea Scott 1876	1982	Tropical America	Dowell & Gill 1989	
Circulifer tenellus (Gillette & Baker 1895)	1899	Africa	CDFA 1915 4:64, Hamilton 1983	yes
Empoasca bipunctata (Oshanin 1871)	1955	Europe	Hamilton 1983	
Empoasca fabae (Harris 1841)	<1915	North America	CDFA 1915 4:62, 21:377	yes
Empoasca cf. guevarai Gonzalez 1955	1996	Tropical America	CPPDR 1996 15:5	
Empoasca mexara Ross & Moore 1957	1964	Mexico	CDFA 1965 54:81	
Erythroneura comes (Say 1825)	1868	North America	CDFA 1929 18:766	
Eupteryx decemnotata Rey 1891	2009	Europe	CPPDR 2011 25:13	
Eupteryx melissae Curtis 1837	1903	Europe	Hamilton 1983	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Euscelis obsoleta (Kirschbaum 1858)	1956	North America	Hamilton 1983, Bugguide 2006	
Euscelis variegausa (Kirshbaum 1858)	1947	Europe	Gross 2006	
Fieberiella florii (Stål 1864)	1947	North America	Hamilton 1983	yes
Graphocephala versuta (Say 1830)	2003		CPPDR 2006 22:43	
Homalodisca vitripennis (Germar 1821)	1994	North America	CPPDR 1994 13:8	yes
Idiocerus decimaquartus (Schrank 1776)	1928	Europe	Hamilton 1983	
Idona minuenda (Moznette 1919)	1970	Tropical America	Dowell & Gill 1989	
Japananus hyalinus (Osborn 1900)	1975	North America	Dowell & Gill 1989	
Latalus misellus (Ball 1899)	1980	North America	Dowell & Gill 1989	
Macropsis mendax (Fieber 1868)	1944	Europe	Hamilton 1983	
Macropsis ulmi (Scott 1873)	1955	Europe	Dowell & Gill 1989	
Negosiana dualis (DeLong 1942)	1979	North America	Dowell & Gill 1989	
Opsius stactogalus Fieber 1866	1914	Europe	Hamilton 1983	
Psammotettix emarginatus Greene 1971	1979	North America	Dowell & Gill 1989	
Rhytidodus decimasquartus (Schrank 1776)		North America	Hamilton 1983	
Ribantiana tenerrima (Herrich-Schaeffer 1834)			BugGuide 2011	
Ribantiana ulmi (Linnaeus 1758)	1926	Europe	Hamilton 1983	
Sanctanus sonorus DeLong & Hershenberger 1946	1986	North America	Dowell & Gill 1989	
Scaphytopius nitridus (DeLong 1943)	1975	Tropical America	Dowell & Gill 1989	
Sophonia rufofascia Kuoh & Kuoh 1983	1995	Hawaii	CPPDR 1996 15:4	yes
Stirellus cf. *bicolor* Van Duzee 1892	1987	North America	Dowell & Gill 1989	
Texananus gladius DeLong 1938	1963	North America	Dowell & Gill 1989	
Thamnotettix zelleri (Kirschbaum 1868)	1995	Europe	CPPDR 1995 14:4	
Trypanalebra balli Young 1957	1983	North America	Dowell & Gill 1989	
Typhlocyba prunicola Edwards 1914	1949	Europe	Hamilton 1983	
Typhlocyba quercus (Fabricius 1777)	1955	North America	Hamilton 1983	
Typhlocyba rosae (Linnaeus 1758)			BugGuide 2011	
Hemiptera-Cimicidae				
Cimex lectularius Linnaeus 1758	<1900		Milne & Milne 1980	yes
Hemiptera-Coccidae				
Ceroplastes cistudiformis Cockerell 1893	1897	Tropical America	Gill 1988	yes
Ceroplastes sinensis Del Guercio 1900	1887	Asia	Gill 1988	yes
Coccus hesperidum Linnaeus 1758	1880	Africa	Gill 1988, Miller et al. 2005	
Coccus longulus (Douglas 1881)	1909	Africa	Gill 1988, CDFA 1915 4:140	
Coccus pseudomagnoliarum (Kuwana 1914)	1900	Asia	Gill 1988	yes
Eucalymnatus tessellatus (Signoret 1873)	1897	Tropical America	Gill 1988, CDFA 1915 4:139, Miller et al. 2005	
Eulecanium caryae (Fitch 1857)	1936	North America	Gill 1988	
Eulecanium cerasorum (Cockerell 1899)	1909	Asia	Gill 1988, Miller et al. 2005	yes

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Eulecanium excrescens (Ferris 1920)	<1925	Asia	Gill 1988, Essig 1926a	
Eulecanium kunoense (Kuwana 1907)	1896	Asia	Gill 1988	
Eulecanium tiliae (Linnaeus 1758)	1984	North America	Gill 1988	
Neopulvinaria innumerabilis (Rathvon 1854)	<1915	North America	Gill 1988, CDFA 1915 4:135	
Parasaissetia nigra (Nietner 1861)	1906	Asia	Gill 1988	
Parthenolecanium corni (Bouché 1844)	1881	North America	Gill 1988	
Parthenolecanium fletcheri (Cockerell 1893)	1889	North America	Gill 1988, Miller et al. 2005	
Parthenolecanium persicae (Fabricius 1776)	1897	Europe	Gill 1988, Miller et al. 2005	
Parthenolecanium pruinosum (Coquillett 1891)	<1915	Tropical America	Gill 1988	yes
Parthenolecanium quercifex (Fitch 1859)		North America	Gill 1988	
Physokermes hemicryphus (Dalman 1825)	1958	Europe	CDFA 1959 48:127	
Physokermes piceae (Schrank 1801)	1958	North America	Dowell & Gill 1989	
Protopulvinaria pyriformis (Cockerell 1894)	1945	North America	Gill 1988	
Pulvinaria citricola Kuwana 1914	1939	North America	Gill 1988	
Pulvinaria delottoi Gill 1979	1973	Africa	Gill 1988, Miller et al. 2005	
Pulvinaria floccifera (Westwood 1870)		North America	Gill 1988	yes
Pulvinaria hydrangeae Steinweden 1946		North America	Gill 1988	
Pulvinaria mesembryanthemi (Vallot 1829)	1971	Africa	Miller et al. 2005	
Pulvinaria phaiae Lull 1899	1906	Asia	Gill 1988, Miller et al. 2005	
Pulvinaria psidii Maskell 1893	1992	Hawaii	CPPDR 1992 11:6	yes
Pulvinaria rhois Ehrhorn 1898		North America	Gill 1988	
Pulvinaria urbicola Cockerell 1893	1993	North America	CPPDR 1992 11:8	
Pulvinaria vitis (Linnaeus 1758)	<1915	North America	Gill 1988, CDFA 1915 4:135	
Saissetia coffeae (Walker 1852)	1914	Africa	Gill 1988, Miller et al. 2005	yes
Saissetia miranda (Cockerell & Parrott 1899)		Tropical America	Gill 1988	
Saissetia oleae (Olivier 1791)	1862	Africa	Gill 1988	yes
Hemiptera-Coreidae				
Anasa tristis (De Geer 1773)	1854	Tropical America	Metcalf 1995, Essig 1926a	yes
Centrocoris variegatus Kolenati 1845	2009	Europe	CPPDR 2011 25:13	
Hemiptera-Dactylopiidae				
Dactylopius opuntiae (Cockerell 1896)		Mexico	Gill 1993	
Dactylopius tomentosus (Lamarck 1801)		Mexico	Gill 1993	
Hemiptera-Delphacidae				
Delphacodes fulvidorsum (Metcalf 1923)	1982	Tropical America	Dowell & Gill 1989	
Eurysa magnifrons (Crawford 1914)	1959		CDFA 1959 48:147	
Liburniella ornata (Stål 1862)	1939	North America	Wilson & Gill 1985	
Nilaparvata wolcotti Muir & Giffard 1924	1975	North America	Dowell & Gill 1989	
Peregrinus maidis (Ashmead 1890)	1933	Tropical America	CDFA 1934 23:414	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Sogatella kolophon (Kirkaldy 1907)	1985	Tropical America	Dowell & Gill 1989	
Hemiptera-Diaspididae				
Abgrallaspis cyanophylli (Signoret 1869)	1931	Tropical America	Gill 1997	
Abgrallaspis degeneratus (Leonardi 1896)	1928	Europe	Gill 1997	
Aonidia lauri (Bouché 1833)	1940	Asia	Gill 1997	
Aonidiella aurantii (Maskell 1879)	1872	Asia	Gill 1997	yes
Aonidiella citrina (Coquillett 1891)	1872	Asia	Gill 1997	yes
Aspidiotus nerii (Bouché 1833)	1882	Europe	Gill 1997	yes
Aspidiotus spinosus (Comstock 1883)	1932	Asia	Gill 1997	
Aulacaspis rosae (Bouché 1833)	1931	Europe	Metcalf 1995	
Carulaspis juniperi (Bouché 1851)		Europe	Gill 1997	
Carulaspis minima Targioni-Tozzetti 1868	1931	Europe	Gill 1997	yes
Chionaspis americana Johnson 1896	1933	North America	Gill 1997	
Chionaspis corni Cooley 1899	1900	North America	Gill 1997	
Chionaspis etrusca Leonardi 1908	1923	Africa	Gill 1997	
Chionaspis wistariae Cooley 1897	<1925	Asia	Gill 1997, Miller et al. 2005, Essig 1926a	
Chrysomphalus aonidium (Linnaeus 1758)	<1925		Essig 1926a	
Chrysomphalus bifasciculatus Ferris 1938	1930	Asia	Gill 1997, Miller et al. 2005	
Chrysomphalus dictyospermi (Morgan 1889)	1909	Asia	Gill 1997	
Clavaspis ulmi (Johnson 1896)	1967	North America	Gill 1997	
Comstockiella sabalis (Comstock 1883)	1917	North America	McKenzie 1956	
Diaspidiotus ancylus (Putnam 1878)	1931	North America	Gill 1997	
Diaspidiotus liquidambaris (Kotinsky 1903)	1942	North America	Gill 1997	
Diaspidiotus osborni (Newell & Cockerell 1898)	1904	North America	McKenzie 1956	
Diaspidiotus uvae (Comstock 1881)	1946	North America	Gill 1997	
Diaspis boisduvalii Signoret 1869	1930	Tropical America	Gill 1997	
Diaspis bromeliae (Kerner 1778)	1934	Tropical America	Gill 1997	
Diaspis cocois Lichtenstein 1882	1919	Tropical America	McKenzie 1956, Miller et al. 2005	
Diaspis echinocacti (Bouché 1833)	1931	Tropical America	Gill 1997	
Dynaspidiotus britannicus (Newstead 1898)	1939	Europe	Gill 1997	
Epidiaspis leperii (Signoret 1869)	1882	Europe	Gill 1997	yes
Fiorinia fioriniae (Targioni-Tozzetti 1867)	1931	North America	Gill 1997	
Fiorinia japonica Kuwana 1902	2008	Asia	CPPDR 2011 25:17-18	
Furcadaspis zamiae (Morgan 1890)	1906	Europe	Gill 1997, Miller et al. 2005	yes
Hemiberlesia candidula (Cockerell 1900)	1957	North America	Dowell & Gill 1989	
Hemiberlesia lataniae (Signoret 1869)	1931	North America	Gill 1997	yes
Hemiberlesia rapax (Comstock 1881)	1928	Hawaii	Gill 1997	yes
Kuwanaspis pseudoleucaspis (Kuwana 1902)	1938	Asia	Gill 1997	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Lepidosaphes beckii (Newman 1869)	1889	North America	Gill 1997	yes
Lepidosaphes chinensis Chamberlin 1925	1927	Asia	Gill 1997, Miller et al. 2005	
Lepidosaphes conchiformis (Gmelin 1789)	1904	Africa	Gill 1997	yes
Lepidosaphes gloverii (Packard 1869)	<1925	Asia	Gill 1997, Essig 1926a	
Lepidosaphes pinnaeformis (Bouche 1851)	1936	Asia	Gill 1997	
Lepidosaphes noxia McKenzie 1946	1944	Asia	McKenzie 1956	
Lepidosaphes pallida (Green 1896)	1935	Hawaii	Gill 1997	
Lepidosaphes sciadopitysi McKenzie 1955	1949	Asia	Gill 1997	
Lepidosaphes ulmi (Linnaeus 1758)	1870	Europe	Gill 1997	yes
Leucaspis portaeaureae Ferris 1942	1938	Pacific Region	Gill 1997	
Lindingaspis rossi (Maskell 1891)	1892	Australia	Gill 1997	yes
Melanaspis obscurus (Comstock 1881)	1897	North America	Gill 1997	yes
Mercetaspis harperi (McKenzie 1949)	1949	Asia	Gill 1997	
[a]*Nilotaspis hall*i (Green 1923)	1934	Africa	Gill 1997	
Odonaspis penicillata (Green 1905)	1936	Asia	Gill 1997	
Odonaspis ruthae Kotinsky 1907	1931	North America	Gill 1997	yes
Parlatoreopsis chinensis (Marlatt 1908)	1948	Asia	Gill 1997	
Parlatoria blanchardi (Targioni-Tozzetti 1892)	1905	Africa	Gill 1997	
Parlatoria camelliae Comstock 1883	1886	Asia	McKenzie 1956, Miller et al. 2005	
Paralatoria crotonis Douglas 1881	1935	Asia	Gill 1997	
Parlatoria oleae (Colvee 1880)	1890	Europe	CDFA 1934 23:415	yes
Parlatoria pergandei Comstock 1881	1889	North America	Gill 1997	
Parlatoria pittospori Maskell 1891	1935	Australia	Gill 1997, Miller et al. 2005	
Pinnaspis aspidistrae (Signoret 1896)	1896	North America	Gill 1997, Miller et al. 2005	
Poliaspis cycadis Comstock 1883	1993		Gill 1997	
Pseudaulacaspis pentagona Targioni-Tozzetti 1855	1888	Asia	Gill 1997	
Quadraspidiotus forbesi (Johnson 1896)	1934	North America	Gill 1997	
Quadraspidiotus juglansregiae (Comstock 1881)	1913	North America	Gill 1997	yes
Quadraspidiotus ostraeformis (Curtis 1843)	1959	North America	Dowell & Gill 1989	
Quadraspidiotus perniciosus(Comstock 1881)	1870	Asia	Gill 1997, Miller et al. 2005	yes
Selenaspidus albus McKenzie 1953	1935	Africa	Gill 1997	
Selenaspidus rubidus McKenzie 1953	1936	Africa	Miller et al. 2005	
Toumeyella liriodendri (Gmelin 1790)	1942	North America	Gill 1988	yes
Unaspis euonymi (Comstock 1881)	1945	Asia	Gill 1997	yes
Hemiptera-Eriococcidae				
Acanthococcus araucariae (Maskell 1897)	1880	Australia	Gill 1993, Miller et al. 2005	
Acanthococcus coccineus (Cockerell 1894)			Gill 1993	
Acanthococcus insignis (Newstead 1891)		Europe	Gill 1993	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Acanthococcus pittospori (Ferris 1955)	1954	Australia	Gill 1993	
Gossyparia spuria (Modeer 1778)	1893	Europe	Gill 1993	yes
Hemiptera-Flatidae				
Siphanta acuta (Walker 1851)	1983	Hawaii	Dowell & Gill 1989	
Hemiptera-Issidae				
Acanalonia conica (Say 1830)	2002	North America	CPPDR 2001 20:8	
Agalmatium bilobum (Fieber) 1877	1946	Europe	Gnezdilov & O'Brien 2006	
Asarcopus palmarum Horvath 1921	1924	Africa	Essig 1926a	
Caliscelis bonellii (Latreille 1807)	1965	Europe	O'Brien 1967	
Hemiptera-Lecanodiaspididae				
Lecanodiaspis prosopidis (Maskell 1894)		North America	Gill 1993	
Hemiptera-Leptopodidae				
Patapius spinosus (Rossi 1790)	1941	Europe	Slater & Baranowski 1978	
Hemiptera-Lygaeidae				
Blissus insularis Barber 1918	1967	North America	Dowell & Gill 1989	yes
Blissus leucopterus (Say 1832)	1885	North America	CDFA 1915 4:208	
Lachnesthus singalensis (Dohrn 1860)	1965	Asia	Slater & Lattin 1965	
Lamprodema maura (Fabricius 1803)	1979		Dowell & Gill 1989	
Megalonotus sabulicola (Thomson 1870)	1921	North America	Henry & Froeschner 1988	
Hemiptera-Margarodidae				
Icerya purchasi Maskell 1876	1868	Australia	Gill 1993	yes
Kuwania quercus (Kuwana 1902)	1966	Asia	Dowell & Gill 1989	
Margarodes meridionalis Morrison 1927	1954	North America	CDFA 1954 43:134	
Hemiptera-Membracidae				
Idioderma sp.	1988	North America	Dowell & Gill 1989	
Hemiptera-Miridae				
Calocoris norwegicus (Gmelin 1790)	1920		Henry & Froeschner 1988	yes
Campyloneura virgula (Herrick-Schaeffer 1835)	1964		Dowell & Gill 1989	
Capsus ater (Linnaeus 1758)			Wheeler & Henry 1992	
Cyrtopeltis tenuis Reuter 1895			Henry & Froeschner 1988	
Halticotoma valida Townsend 1892			CDFA 1943 32:279	
Heterotoma planicorne (Pallas 1772)	1964	North America	Dowell & Gill 1989	
Lopus decolor (Fallen 1807)			Wheeler & Henry 1992	
Melanotrichus concolor (Kirschbaum 1856)			Wheeler & Henry 1992	
Melanotrichus virescens (Douglas & Scott 1865)			Wheeler & Henry 1992	
Pilophorus clavatus (Linnaeus 1767)			Henry & Froeschner 1988	
Plagiognathus chrysanthemi (Wolff 1804)			Wheeler & Henry 1992	
Polymerus unifasciatus (Fabricius 1794)			Henry & Froeschner 1988	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Psallus ancorifer (Fieber 1858)	1914	Europe	Wheeler & Henry 1992	
Pseudatomoscelis seriatus (Reuter 1876)		North America	CPPDR 26:264	
Taylorilygus pallidulus (Blanchard 1852)	1917	North America	Wheeler & Henry 1992	
Trigonotylus tenuis Reuter 1893			Wheeler & Henry 1992	yes
Trigonotylus uhleri (Reuter 1876)	1993	North America	Daehler & Strong 1995	
Hemiptera-Nabidae				
Anaptus major (Costa 1842)			Henry & Froeschner 1988	
Hemiptera-Ortheziidae				
Orthezia insignis Brown 1887	1911		Gill 1993, CDFA 1915 4:110, Miller et al. 2005	
Hemiptera-Oxycarenidae				
Metopoplax ditomoides (Costa 1847)	2002	Europe	CPPDR 2006 22:9-10	
Hemiptera-Pentatomidae				
Agonoscelis puberula Stal 1854	1997	North America	CPPDR 2007 23: 6-7	
Aelia americana Dallas 1851	1980	North America	Dowell & Gill 1989	
Bagrada hilaris (Burmeister 1835)	2008	Africa	CPPDR 2011 25:14-15	
Elasmucha lateralis (Say 1831)	1969	North America	Dowell & Gill 1989	
Euschistus servus (Say 1832)			Henry & Froeschner 1988	yes
Halyomorpha halys (Stal 1855)	2005	North America	CPPDR 2006 22:8-9	yes
Murgantia histrionica (Hahn 1834)	<1915	North America	CPPDR 1983 2:630, Essig 1917	
Nezara viridula (Linnaeus 1758)	1986	North America	Dowell & Gill 1989	yes
Hemiptera-Phoenicococcidae				
Phoenicococcus marlatti Cockerell 1899	1890	Africa	Gill 1993	
Hemiptera--Phylloxeridae				
Daktulosphaira vitifoliae (Fitch 1855)	1852	North America	Metcalf 1995	yes
Phylloxera stellata Duncan 1922	1953	North America	CDFA 1953 42:172	
Hemiptera-Pseudococcidae				
Allococcus sp.	1980	Africa	Dowell & Gill 1989	
Antonina crawi Cockerell 1900	1900	Asia	McKenzie 1967, Miller et al. 2002	
Antonina graminis (Maskell 1897)	1957	North America	Dowell & Gill 1989	
Antonina pretiosa Ferris 1953	1915	Asia	McKenzie 1967, Miller et al. 2005	
Balanococcus diminutus (Leonardi 1918)	1906	Europe	McKenzie 1967	
Brevennia rehi (Lindinger 1943)	1967	Asia	Miller et al. 2002	
Cataenococcus olivaceus (Cockerell 1896)	1960	Tropical America	Dowell & Gill 1989	
Chorizococcus brevicruris McKenzie 1960	1965	Hawaii	Dowell & Gill 1989	
Chnaurococcus trifolii (Forbes 1885)	1916	North America	McKenzie 1967	
Chorizococcus rostellum (Lobdell 1930)	1932	North America	McKenzie 1967	
Crisicoccus azaleae (Tinsley 1898)	1898	Asia	McKenzie 1967	
Crisicoccus pini (Kuwana 1902)	1918	Asia	McKenzie 1967, Miller et al. 2002	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Delottococcus cf. *confusus* De Lotto 1977	2006	Africa	CPPDR 2007 23:10	
Dysmicoccus brevipes (Cockerell 1893)	1938	North America	McKenzie 1967	
Eriococcus pittospori (Ferris 1955)			Gill 1993	
Ferrisia gilli Gullan 2003	1968	North America	CPPDR 2006 22:16	yes
Ferrisia malvastra (McDaniel 1962)	1960's	Pacific Region	CPPDR 1997 16:8-9	
Ferreisia virgata (Cockerell 1893)	1963	Tropical America	Dowell & Gill 1989	
Heterococcus nudus (Green 1926)	1959	North America	Dowell & Gill 1989	
Hypogeococcus spinosus Ferris 1953	1951	North America	McKenzie 1967	
Maconellicoccus hirsutus (Green 1908)	1999	North America	CPPDR 1999 18:69	yes
Nipaecoccus aurilanatus (Maskell 1890)	1895	Australia	McKenzie 1967	yes
Nipaecoccus nipae (Maskell 1893)	1897	Tropical America	McKenzie 1967, Miller et al. 2002	yes
Palmicultor lumpurensis (Takahashi 1950)	2006	North America	CPPDR 2011 24: 11-12	
Phenococcus aceris (Signoret 1875)	1971	North America	Dowell & Gill 1989	
Phenacoccus celtisifoliae Hollinger 1917	1936	North America	McKenzie 1967	
Phenacoccus dearnessi King 1901	1922	North America	McKenzie 1967	
Phenacoccus gossypii Townsend & Cockerell 1898			McKenzie 1967	
Phenacoccus graminicola Leonardi 1908	1953	Europe	CDFA 1959 48:127	
Phenacoccus madeirensis Green 1923	1911	North America	McKenzie 1967	yes
Planococcus citri (Risso 1813)	1880	Europe	Metcalf 1995	yes
Planococcus ficus (Signoret 1875)	1994	Africa	CPPDR 1994 13:8	
Planococcus kraunhiae (Kuwana 1902)	1915	Asia	McKenzie 1967	
Pseudantonina arundinariae McConnell 1941	1959	North America	McKenzie 1967	
Pseudococcus affinis (Maskell 1894)	1946	North America	McKenzie 1967	
Pseudococcus calceolariae (Maskell 1897)	1915	Australia	Metcalf 1995, Miller et al. 2002	yes
Pseudococcus comstocki (Kuwana 1902)	1967	North America	Dowell & Gill 1989	yes
Pseudococcus importatus McKenzie 1960	1963	Tropical America	Dowell & Gill 1989	
Pseudococcus longispinus (Targioni-Tozzetti 1867)	1916	Asia	Metcalf 1995	yes
Pseudococcus maritimus (Ehrhorn 1900)	1909	North America	McKenzie 1967	yes
Pseudococcus microcirculus McKenzie 1960	1954	Tropical America	McKenzie 1967, Miller et al. 2002	
Pseudococcus nakaharai Gimpel & Miller 1996	1973	North America	Miller et al. 2005	
Pseudococcus sorghiellus (Forbes 1885)	1964	North America	McKenzie 1967	
Rhizoecus arabicus Hambleton 1976	1996	Tropical America	CPPDR 1996 15:5	yes
Rhizoecus associatus (Hambleton 1946)	1964	Tropical America	McKenzie 1967	yes
Rhizoecus cacticans (Hambleton 1946)	1948	Tropical America	McKenzie 1967	yes
Rhizoecus falcifer Kunckel d'Herculais 1878	1917	North America	McKenzie 1967, Miller et al. 2002	
Rhizoecus kondonis Kuwana 1923	1921	Asia	McKenzie 1967	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Rhizoecus leucosomus (Cockerell 1901)	1956	North America	McKenzie 1967	
Rhizoecus nakaharai Hambleton 1976			McKenzie 1967	
Rhizoecus dianthi Green 1926	1954	Asia	McKenzie 1967, Miller et al. 2002	
Spilococcus geraniae (Rau 1938)	1966	North America	Dowell & Gill 1989	
Spilococcus mamillariae (Bouche 1844)	1938		Miller et al. 2002	
Trionymus americanus (Cockerell 1899)	1940	North America	McKenzie 1967	
Trionymus caricis McConnell 1941	1961	North America	McKenzie 1967	
Trionymus mocus Ferris 1953	1952		McKenzie 1967	
Vryburgia amaryllidis (Bouché 1873)	1925	Africa	McKenzie 1967, Miller et al. 2005	
Vyburgia brevicruris (McKenzie 1960)	1935		McKenzie 1967	
Vrybergia trionymoides DeLotto 1961	1994	Africa	CPPDR 1994 13:84	
Hemiptera—Psyllidae				
Acizzia acaciae-baileyanae (Froggatt 1901)	1987	Australia	Dowell & Gill 1989	yes
Acizzia cf. *jucunda* (Tuthill 1952) (undescribed #22)	1992	Australia	CPPDR 1992 11:7	
Acizzia cf. *hakeae* (Tuthill 1952)	2000	Australia	CPPDR 2000 19:27-28	
Acizzia uncatoides (Ferris & Klyver 1932)	1954	Pacific Region	CDFA 1955 44:164	yes
Agonoscena pistaciae Burckhardt & Lauterer 1989			Percy 2005	
Arytaina genistae (Latreille 1804)	2010	North America	Percy et al. 2012	
Arytainilla spartiophila Forster 1848	1995	North America	Percy et al. 2012	
Bactericera cockerelli (Sulc 1909)	1930's	North America	Liu & Trumble 2007	yes
Blastopsylla occidentalis Taylor 1985	1983	Australia	Hodkinson 1988	
Boreioglycaspis melaleucae Moore 1964	2009	North America	Arakelian 2009	yes
Cacopsylla buxi (Forster 1848)	1934	Europe	CDFA 1931 20:694	
Cacopsylla fatsiae (Jensen 1957)	1937	Asia	Hodkinson 1988	
Cacopsylla pyricola (Föerster 1848)	1883	North America	CDFA 1954 43:42, Essig 1915	yes
Cacopsylla tobirae Miyatake1964	2007	Asia	Percy et al. 2012	yes
Calophya schini Tuthill 1959	1984	Tropical America	Dowell & Gill 1989	yes
Cryptoneossa triangula Taylor 1990	1995	Australia	CPPDR 1995 14:31	
Ctenarytaina eucalypti (Maskell 1895)	1991	Australia	CPPDR 1991 10: 5-7	yes
Ctenarytaina longicauda Taylor 1987	1983	Australia	Dowell & Gill 1989	
Ctenarytaina spatulata Taylor 1997	1991	Australia	Percy et al. 2012	
Diaphorina citri Kuwayama 1908	2008	North America	CPPDR 2011 25:19	yes
Eucalyptolyma maideni Froggat 1901	2000	Australia	CPPDR 2000 19:26	yes
Euphyllura olivine (Costa 1877)	2007	Europe	CPPDR 2011 24:7	yes
Freysuila dugesi Aleman 1887	1997	Mexico	Percy et al. 2012	
Glycaspis brimblecombei Moore 1964	1998	Australia	CPPDR 1998 17:4-10	yes
Freysuila dugesii Aleman 1887	1997	Mexico	CPPDR 1997 16:42	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Heteropsylla cubana Crawford 1914	1986	Hawaii	Dowell & Gill 1989	
Heteropsylla flexuosa Muddiman, Hodkinson & Hollis 1992	1996	Tropical America	CPPDR 1996 15:5	
Homotoma ficus (Linnaeus 1758)	1969	Europe	Dowell & Gill 1989	
Pachypsylla celtidismamma (Fletcher 1882)	1989	North America	CPPDR 1989 8:9	
Pachypsylla celtidisvesicula (Riley 1884)	1960	North America	Dowell & Gill 1989	
Platycorypha nigrivirga Burckhardt 1987	2008	Tropical America	CPPDR 2011 25:18	
Pseudacysta perseae (Heidemann 1908)	2004	Tropical America	CPPDR 2006 22:10-11	yes
Psylla uncatoides (Ferris & Klyver 1932)	1955	Hawaii	Dowell & Gill 1989	
Trioza alacris Flor 1861	1911	Europe	Percy et al. 2012	
Trioza eugeniae Froggatt 1901	1988	Australia	Percy et al. 2012	
Hemiptera-Pyrrhocoridae				
Scantius aegyptius Linnaeus 1758	2009	Europe	Bryant 2009	yes
Hemiptera-Rhopalidae				
Jadera haematoloma (Herrich-Schaeffer 1847)	< 1917	Tropical America	Henry and Froeschner 1988, Van Duzee 1917	
Liorhyssus hyalinus (Fabricius 1794)	<1925	Europe	Essig 1926a	
Rhopalus tigrinus (Schilling 1817)	1998	Asia	Wheeler & Hoebeke 1999	
Hemiptera-Rhyparochromidae				
Raglius alboacuminatus Goeze 1778	2002	Europe	Henry 2004, CPPDR 2006 22:12	
Xanthochilus saturnius (Rossi 1790)	1997	Europe	Henry & Adamski 1998	
Hemiptera-Tingidae				
Corythucha gossypii (Fabricius 1794)	2000	Hawaii	CPPDR 2007 23: 8	
Corythucha montivaga Drake 1919	1971		Dowell & Gill 1989	
Gargaphia arizonica Drake & Carvalho 1944	1970	North America	Dowell & Gill 1989	
Pseudacysta persea (Heidemann 1908)	2004	North America	CPPDR 2006 22:10-11	
Stephanitis pyriodes (Scott 1874)		Asia	Gyeltshen & Hodges 2006	
Teleonemia scrupulosa Stål 1873	1994	North America	CPPDR 1994 13:84	
Hemiptera-Triozidae				
Trioza alacris Flor 1861	1911	Europe	CDFA 1911-12 1:86	
Trioza chenopodii Reuter 1876	1997	Europe	CPPDR 1997 16:41	
Trioza eugeniae Froggatt 1901	1988	Australia	Dowell & Gill 1989	yes
Hymenoptera-Agaonidae				
Acophila sp. Ishii 1934	1997	Hawaii	Beardsley & Rasplus 2010	
Blastophaga psenes (Linnaeus 1758)	1891	Europe	Arnett 1985, CDFA 1915 4:366	
Eupristina verticillata Waterston 1921	1994		CPPDR 1994 13:62	
*Josephiella*Microcarpae Beardsley & Rasplus 2001	1997	Asia	Beardsley & Rasplus 2010	
Odontofroggatia galili Wiebes 1980	1994		CPPDR 1994 13:62	
Odontofroggatia ishii Wiebes 1980	1994		CPPDR 1994 13:62	
Walkerella microcarpae Boucek 1993	1994		CPPDR 1994 13:62	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Hymenoptera-Anthophoridae				
Ceratina dallatorreana (Friese 1869)	1949	Africa	Daly 1973	
Hymenoptera-Apidae				
Apis mellifer scutellata Lepeletier 1836	1985	North America	Dowell & Gill 1989	yes
Hymenoptera-Argidae				
Schizocerella pilicornis Holmgren 1868		North America	University of California 2011	
Hymenoptera-Braconidae				
Dendrosoter protuberans (Nees 1834)	1978	North America	Hajek & Dahlsten 1981	
Hymenoptera-Cephidae				
Cephus cinctus Norton 1872	1890	Asia	Ivie 2001	
Hymenoptera-Ceraphronidae				
Ceraphron abnormis Perkins 1910			Krombein & Hurd 1979	
Hymenoptera-Chrysididae				
Chrysis angolensis Radoszkowski 1881	1959	North America	CDFA 1959 48:127	
Pseudomalus auratus (Linnaeus 1758)			Bohart & Kimsey 1982	
Hymenoptera-Colletidae				
Hylaeus bisinuatus Forster 1871			Krombein & Hurd 1979	
Hylaeus punctatus (Brullé 1832)	1981	Europe	Snelling 1982	
Hymenoptera-Cynipidae				
Plagiotrochus suberi Weld 1926	1926	Europe	Zuparko 1996	
Hymenoptera-Encyritidae				
Psyllaephagus parvus Riek 1962	2007	Australia	Jones et al. 2011	
Psyllaephagus perplexus Riek 1962	2007	Australia	Jones et al. 2011	
Hymenoptera-Eulophidae				
Aprostocetus diplosidis Crawford 1907	1972	North America	Summers 1976	
Aprostocetus sp. #1 Westwood 1833	1991	Australia	CPPDR 1991 10:42	
Aprostocetus sp. #2 Westwood 1833	1994	Australia	CPPDR 1995 14:5, Headrick et al. 1995	
Cirrospilus sp. #1	1991	Australia	Headrick et al. 1995	
Epichrysocharis burwelli Schauff 2000	1999	Australia	CPPDR 1999 18:16	
Oncastichus goughi Headrick & LaSalle 1995	1980's	Australia	Headrick et al. 1995	
Quadrastichodella nova Girault 1922	1957	Australia	Timberlake 1957	
Selitrichodes globulus La Salle & Gates 2009	2008	Australia	La Salle et al. 2009	
Hymenoptera-Eupelmidae				
Macroneura versicularis (Retzius 1783)		North America	Krombein & Hurd 1979	
Hymenoptera-Eurytomidae				
Bruchophagus gibba Boheman 1836	<1915		CDFA 1915 4:368	
Bruchophagus platypterus (Walker 1834)		North America	Davidson & Lyon 1987	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Bruchophagus roddi (Gussakovsky 1933)			Davidson & Lyon 1987	
Eurytoma orchidearum (Westwood 1869)	1914	Tropical America	Krombein & Hurd 1979, Essig 1915	
Eurytoma tumoris Bugbee 1962	1964		Krombein & Hurd 1979	
Harmolita grandis (Riley 1884)	1915	North America	Metcalf 1995	
Harmolita websteri (Howard 1896)	<1925		Krombein & Hurd 1979, Essig 1926a	
Sycophila sp. Walker 1871	1994	Hawaii	CPPDR 1994 13:62	
Systole geniculata Foerster 1861		Europe	Krombein & Hurd 1979	
Tetramesa tritici (Fitch 1859)	1853		Metcalf 1995	
Hymenoptera-Figitidae				
Melanips opacus (Hartig 1840)		Europe	Krombein & Hurd 1979	
Hymenoptera-Formicidae				
Brachymyrmex patagonicus Mayr 1868	2010	North America	Martinez et al. 2011	
Camponotus sayi Emery 1893	1963	North America	Dowell & Gill 1989	
Cardiocondyla ectopia Snelling 1974	1972		Mackay 1995	
Cardiocondyla nuda (Mayr 1866)	1958	Asia	Dowell & Gill 1989	
Hypoponera gleadowi (Forel 1895)	1999		CPPDR 1999 18:19	
Hypoponera punctatissima (Roger 1859)			Krombein & Hurd 1979	
Linepithema humile (Mayr 1868)	1908	Tropical America	Knight & Rust 1990	yes
Monomorium pharaonis (Linnaeus 1758)	<1925	Africa	Knight & Rust 1990, Essig 1926a	yes
Ochetomyrmex auropunctata (Roger 1863)		Tropical America	Arnett 1985	
Paratrechina currens (Mostchoulsky 1863)	1964		CDFA 1965 54:81	
Paratrechina longicornis (Latreille 1802)	1967	North America	Dowell & Gill 1989	
Paratrechina vividula (Nylander 1846)		Mexico	Smith 1979, Ward 2005	
Pheidole fervens Smith 1858	1995	Hawaii	Martinez 1996	
Pheidole moerens Wheeler 1908	1995	North America	Martinez 1997	
Pheidole teneriffana Forel 1893	1989	Africa	Snelling 1992, Davidson & Lyon 1987, Martinez 1992	
Plagiolepis alluaudi Emery 1894		Africa	Wetterer 2013	
Solenopsis wagneri Santschi 1916	1997	North America	CPPDR 1997 16:41	yes
Strumigenys silvestri Emery 1906			Ward 2005	
Tapinoma melanocephalum (Fabricius 1793)	1991	North America	CPPDR 1991 10:68	yes
Tetramorium bicarinatum (Nylander 1846)	1990	North America	Martinez 1993	
Tetramorium caespitum (Linnaeus 1758)	<1925	North America	Knight & Rust 1990, Essig 1926a	yes
Tetramorium insolens (Smith 1861)			Bolton 1979	
Tetramorium pacificum Mayr 1870	1944		Krombein & Hurd 1979	
Tetramorium simillium (Smith 1851)			Bolton 1979	
Trichoscapa membranifera (Emery 1869)	1963	North America	Dowell & Gill 1989	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Hymenoptera-Ichneumonidae				
Stilpnus gagates Gravenhorst 1807	1985	North America	Dowell & Gill 1989	
Hymenoptera-Megachilidae				
Megachile apicalis Spinola 1808	1982	North America	Barthell et al. 1998, Cooper 1984	
Megachile argentata (Fabricius 1793)	1949	North America	Hurd 1954	
Megachile concinna Smith 1879		North America	Barthell et al. 1998	
Megachile rotundata (Fabricius 1787)	1949	North America	Powell & Hogue 1979, Barthell et al. 1998	
Hymenoptera-Pteromalidae				
Anisopteromalus calandrae (Howard 1881)			Krombein & Hurd 1979	
Cerocephala rufa (Walker 1833)			Krombein & Hurd 1979	
Cyclogastrella deplanata (Nees 1834)			Krombein & Hurd 1979	
Theocolax elegans (Westwood 1874)			Krombein & Hurd 1979	
Trichomalus perfectus (Walker 1837)			Krombein & Hurd 1979	
Hymenoptera-Spechidae				
Cemonus lethifer (Shuckard 1837)		North America	Krombein & Hurd 1979	
Rhopalum clavipes (Linnaeus 1758)			Lindroth 1957	
Hymenoptera-Tenthredinidae				
Ardis sulcata (Cameron 1882)	1937	Europe	Middlekauff 1958	
Caliroa cerasi (Linnaeus 1758)	1875	North America	Metcalf 1995	yes
Cladius difformis (Panzer 1799)	1921		Metcalf 1995	
Endelomyia aethiops (Fabricius 1781)		North America	Krombein & Hurd 1979	
Fenusa dohrnii (Tischbein 1846)	1986	North America	Dowell & Gill 1989	
Nematus ribesii (Scopoli 1763)		North America	Arnett 1985	
Pachynematus sporax Ross 1945	1951	North America	CDFA 1954 43:170	
Pristiphora abbreviata (Hartig 1837)	1881	North America	Krombein & Hurd 1979, CDFA4:360	yes
Tomostethus multicinctus (Rohwer 1909)	1950	North America	CDFA 1950 39:183	
Hymenoptera-Torymidae				
Ditropinotus aureoviridis Crawford 1907	<1915		CDFA 1915 4:370, Dowell & Gill 1989	
Megastigmus pistaciae Walker 1871	1967	Asia	Dowell & Gill 1989	yes
Megastigmus transvaalensis (Hussey 1956)	1960	Africa	Krombein & Hurd 1979, Dowell & Gill 1989	
Hymenoptera-Vespidae				
Polistes dominulus (Christ 1791)	1997	North America	CPPDR 1997 16:44	yes
Polistes apachus Saussure 1857	1921	North America	Bohart & Bechtel 1957	yes
Vespula germanica (Fabricius 1793)	1983	North America	Vetter et al. 1995	yes
Isopoda-Armadillidiidae				
Armadillidium nasatum Budde-Lund 1885		Europe	Jass & Klausmeier 2001	
Armadillidium vulgare (Latreille 1804)	<1925	Europe	Jass & Klausmeier 2000, Essig 1926a	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Isopoda-Trichoniscidae				
Haplophthalmus danicus Budde-Lund 1879		Europe	Jass & Klausmeier 2001	
Isopoda-Ligiidae				
Ligia exotica Roux 1828			Jass & Klausmeier 2001	
Ligidium elrodii (Packard 1873)		Europe	Jass & Klausmeier 2001	
Isopoda-Platyarthridae				
Niambia capensis (Dollfus 1895)		Africa	Jass & Klausmeier 2001, Brusca et al. 2001	
Isopoda-Oniscidae				
Platyarthrus aiasensis Legrand 1954		Europe	Jass & Klausmeier 2001,	
Isopoda-Porcellioniade				
Porcellio dilatatus Brandt & Ratzeburg 1831		Europe	Jass & Klausmeier 2001,	
Porcellio laevis Latreille 1804	<1915	Europe	Jass & Klausmeier 2001, Essig 1915	
Porcellio scaber Latreille 1804		Europe	Jass & Klausmeier 2001	
Porcellionides pruinosus (Brandt 1833)			Lindroth 1957, Richardson 1905	
Isoptera-Rhinotermitidae				
Coptotermes formosanus Shiraki 1909	1992	Hawaii	CPPDR 1992 11:4	yes
Lepidoptera-Argyresthiidae				
Argyresthia conjugella Zeller 1839			Zhang 1994, Carter 1984	
Argyresthia pruniella (Clerk 1759)			Carter 1984	
Lepidoptera-Arctiidae				
Hyphantria cunea (Drury 1773)	<1915	North America	Lindroth 1957, CDFA 1915 4:391, Carter 1984	yes
Lepidoptera-Bucculatrigidae				
Bucculatrix thurberiella Busck 1914		Mexico	Zhang 1994	yes
Bucculatrix tridenticola Braun 1963	1963	North America	Dowell & Gill 1989	
Lepidoptera-Choreutidae				
Choreutis pariana (Clerck 1759)	1944	North America	CDFA 1944 33:248	
Lepidoptera-Coleophoridae				
Coleophora mayrella (Hübner 1813)	1952	Europe	CDFA 1952 41:182	
Homaledra sabalella (Chambers 1880)	2000	North America	CPPDR 2000 19:29	yes
Lepidoptera-Cosmopterygidae				
Periploca nigra Hodges 1962	1962	North America	Powell & Opler 2009, Dowell & Gill 1989	
Pyroderces badia Hodges 1962	<1925	North America	Essig 1926a, Powell & Opler 2009	
Lepidoptera-Crambidae				
Asciodes gordialis Guenee 1854	2005	North America	CPPDR 2006 22: 21	
Diaphania nitidalis (Stoll 1781)	1992	North America	CPPDR 1992 11:71	
Eoreuma loftini (Dyar 1917)	1945	Asia	CDFA 1945 34:175	
Glyphodes onychinalis (Guenee 1854)	2000	Pacific Region	CPPDR 2000 19:30	
Hellula rogatalis (Hulst 1886			Powell 2005	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Lineodes elcodes Dyar 1910	2003	Tropical America	CPPDR 2006 22:20	
Loxostege sticticalis (Linnaeus, 1761)			Carter 1984	yes
Ostrinia penitalis (Grote 1796)	1952	North America	CDFA 1953 42:204	
Parapidiasia teterrella (Zincken 1821)	1954	North America	Powell 1992	
Udea ferrugalis (Hübner 1796)	1907	North America	Campbell 1927	
Uresiphita reversalis (Guenée 1854)	1929		CDFA 1933 22:410	yes
Lepidoptera-Ethmiidae				
Pyramidobela angelarum Keifer 1936	1934	Mexico	CDFA 1942 31:177	
Lepidoptera-Gelechiidae				
Anarsia lineatella Zeller 1839	1900	North America	Metcalf 1995, Carter 1984	yes
Athrips rancidella (Herrich-Schaffer 1854)	1983	Europe	Dowell & Gill 1989	
Chrysoesthia lingulacella (Clemens 1860)		North America	Powell & Opler 2009	
Dichomeris marginella (Fabricius 1781)	1922	Europe	CDFA 1928 17:17, 47	
Euscrobipalpa artemisiella (Treitschke 1833)			Powell & Hsu 2004	
Euscrobipalpa artiplicella (F. von Roslerstamm 1841)			Powell & Hsu 2004	
Euscrobipalpa instabiliella (Douglas 1846)			Powell & Hsu 2004	
Euscrobipalpa obsoletella (F. von Roslerstamm 1841)			Powell & Hsu 2004	
Keiferia lycopersicella (Walsingham 1897)	1922	Tropical America	CDFA 1934 23:301	yes
Metzneria lappella (Linnaeus 1758)	1958	North America	Powell & Opler 2009	
Mirificarma eburnella (Denis & Schiffermüller 1775)	1969		Powell & Hsu 2004, Powell & Opler 2009	
Mirificarma formosella (Hubner 1796)	1969	Europe	Dowell & Gill 1989	
Pectinophora gossypiella (Saunders 1844)	1965	Tropical America	Dowell & Gill 1989	yes
Phthorimaea operculella (Zeller 1873)	1854	Tropical America	Metcalf 1995, Carter 1984	yes
Platyedra subcinerea (Haworth 1828)	1990	Europe	Powell & Opler 2009	
Recurvaria nanella Denis and Schiffermuller 1775			Aukema et al. 2010,	
Sitotroga cerealella (Olivier 1789)	<1915		Arnett 1985	
Stenolechia bathyrodyas Meyrick 1935	1980	Asia	Dowell & Gill 1989	
Symmetrischema striatellum (Murtfeldt 1900)	1930's		Powell & Hsu 2004, Powell & Opler 2009	
Symmetrischema tangolias (Geyen 1913)	1936	Tropical America	McDunnough 1939	
Lepidoptera-Geometridae				
Alsophila pometaria (Harris 1841)	<1915	North America	CDFA 1915 4:477	yes
Disclisioprocta stellata (Guenee 1857)	2006	North America	CPPDR 2007 23:12	yes
Lepidoptera-Gracillariidae				
Caloptilia azaleella (Brants 1913)	1960's	North America	Powell & Opler 2009	
Caloptilia fraxinella (Ely 1915)			Zhang 1994	
Caloptilia negundella (Chambers 1876)			Aukema et al. 2010	
Caloptilia syringella (Fabricius 1794)			Zhang 1994	
Lithocolletis mespilella (Hübner 1805)			Zhang 1994	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Phyllocnistis citrella Stainton 1856	1999	North America	CPPDR 1999 18:79	yes
Phyllonorycter crataegella (Clemens 1859)	<1952	North America	CDFA 1952 41:181	
Phyllocnistis sp. Zeller 1848	1963	North America	Dowell & Gill 1989	
Lepidoptera-Heliodinidae				
Aetole bella Chambers 1875	1890	Europe	Powell & Opler 2009	
Lepidoptera-Limacodidae				
Sibine stimulea (Clemens 1860)	1965	North America	Dowell & Gill 1989	
Lepidoptera-Lymantriidae				
Leucoma salicis (Linnaeus 1758)	1960	North America	Dowell & Gill 1989	
[a]*Lymantria dispar* (Linnaeus 1758)	1976	North America	Dowell & Gill 1989	yes
[a]*Lymantria dispar asiatica* Vnukovskij 1926	2005	Asia	CPPDR 2006 22: 19-20	
Orgyia antiqua (Linnaeus 1758)	<1925	North America	Martineau 1984, Essig 1926a	
Lepidoptera-Lyonetiidae				
Bedellia somnulentella (Zeller 1847)			Powell & Hsu 2004, Powell 2005	
Lepidoptera-Noctuidae				
Ascalapha odorata (Linnaeus 1758)	<1925	Mexico	Powell & Hogue 1979, Essig 1926a	
Agrotis malefida Guenee 1852	1960	North America	Dowell & Gill 1989	
Amphipyra tragopoginis Clerk 1759			Aukema et al. 2010,	
Apamea indocilis Walker 1856	1970		Dowell & Gill 1989	
Athetis mindara (Barnes & McDunnough 1913)	1958		CDFA 1960 49:246	
Discestra trifolii (Hufnagel 1766)			Zhang 1994	
Euxoa ochrogaster (Guenee 1852)	1970		Dowell & Gill 1989	
Feltia jaculifera (Guenee 1852)			Powell 2005	
Macronoctua onusta Grote 1874	1963		Dowell & Gill 1989	
Noctua pronuba (Linnaeus 1758)	2001	North America	Powell 2002	
Peridroma saucia (Hubner 1808)			Aukema et al. 2010,	yes
Pseudaletia unipunctata (Haworth 1809)			CDFA 1959 48:20, Powell 2005	
Sideridis rosa Harvey 1874	1970	North America	Dowell & Gill 1989	
Spodoptera exigua (Hübner 1808)	1876	Tropical America	Davidson & Lyon 1987, Powell & Opler 2009	
Spodoptera frugiperda (J.E. Smith 1797)	1931		CDFA 1931 20:613	
Trichoplusia ni (Hubner 1803)		North America	Powell 2005	yes
Lepidoptera-Nymphalidae				
Dione vanillae (Linnaeus 1758)	1875	Mexico	Hogue 1974	
Lepidoptera-Oecophoridae				
Agonopterix alstroemeriana (Clerck 1759)	1983	North America	Powell 1991	
Agonopterix nervosa (Haworth 1811)	<1957	Europe	Hodges 1974, Powell & Opler 2009	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Batia lunaris (Haworth 1828)	1956		Powell 1964b, Powell & Opler 2009	
Borkhausenia nefrax Hodges 1974	1936		Powell 1964a	
Depressaria daucella (Denis & Schiffermüller 1775)	1957		Hodges 1974, Powell & Opler 2009	
Depressaria pastinacella (Duponchel 1838)			Zhang 1994, Carter 1984	
Endrosis sarcitrella (Linnaeus 1758)	1902		Zhang 1994, Powell & Opler 2009	
Esperia sulphurella (Fabricius 1775)	1966	Europe	Powell 1968b	
Hofmannophila pseudospretella (Stainton 1849)	1871		Hodges 1974, Powell & Opler 2009	
Lepidoptera-Papilionidae				
Papilio cresphontes Cramer 1777	1959	North America	CDFA 1959 48:127	
Lepidoptera-Pieridae				
Pieris rapae (Linnaeus 1758)	1882	North America	Metcalf 1995, Shapiro and Manolis 2007	yes
Lepidoptera-Plutellidae				
Homadaula anisocentra Meyrick 1922	1963		Dowell & Gill 1989	yes
Plutella porrectella (Linnaeus 1758)	<1871	North America	Powell 1967, Powell & Opler 2009	
Plutella xylostella (Linnaeus 1758)		North America	Powell & Hogue 1979	yes
Lepidoptera-Psychidae				
*Apterona helix (*Siebold 1850)	1940	Asia	CDFA 1944 33:250, Powell & Opler 2009	
Oiketicus townsendi (Townsend 1894)	1968	North America	Dowell & Gill 1989	
Thyridopteryx ephemeraeformis (Haworth 1803)	1953	North America	Zhang 1994	
Lepidoptera-Pterophoridae				
Emmelina monodactylus (Linnaeus 1758)			Powell & Hsu 2004	
Gillmeria pallidactyla (Haworth 1811)	1871		Powell & Hsu 2004, Powell & Opler 2009	
Hellinsia longifrons (Walsingham 1915)			Powell & Hsu 2004	
Megalorrhipida defectalis (Walker 1864)			Powell & Hsu 2004	
Platyptilia carduidactyla (Riley 1869)	1922	North America	Metcalf 1995	
Platyptilia pallidactyla (Haworth 1811)			Powell 2005	
Lepidoptera-Pyralidae				
Achroia grisella (Fabricius 1794)	1908	Europe	Zhang 1994, Carter 1984	
Acrobasis indigenella (Zeller 1848)	1924	North America	CDFA 1959 48:206	
Acrobasis nuxvorella Neunzig 1970	1924	North America	Metcalf 1995	
Aglossa caprealis (Hubner 1809)	1936		Powell & Opler 2009,	
Aglossa pinguinalis (Linnaeus 1758)	1993		Solis 2008,	
Amyelois transitella (Walker 1863)	1947	North America	CDFA 1948 37:204	
Cadra cautella (Walker 1863)	1913		Neunzig 1990, Powell & Opler 2009	
Cadra figulilella (Gregson 1871)	1930	North America	CDFA 1931 20:64	
Duponchelia fovealis Zeller 1847	2004	Europe	CPPDR 2006 22: 20-21	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Ectomyelois ceratoniae (Zeller 1839)	1983	North America	Dowell & Gill 1989	yes
Ephestia elutella (Hübner 1796)	1911	Asia	Neunzig 1990	
Ephestia kuehniella (Zeller 1879)	1889		Zhang 1994, Powell & Opler 2009	
Etiella zinckenella (Treitschke 1832)	1885	Europe	CDFA 1915 4:433, Stone 1965	
Euchromius ocelleus (Haworth 1811)	<1900	North America	Powell & Opler 2009	
Eumysia mysiella (Dyar 1905)	1975		Dowell & Gill 1989	
Galleria mellonella (Linnaeus 1758)	1875	North America	Zhang 1994	
Hymenia perspectalis (Hübner 1796)		North America	Zhang 1994	
Hypsopygia costalis (Fabricius 1775)	1968	North America	Pohl et al. 2005	
Paralipsa gularis (Zeller 1877)	<1921		CDFA 1921 10:142	
Phycitodes albatella (Ragonot 1887)			Zhang 1994	
Plodia interpunctella (Hübner 1813)	1881	Europe	Metcalf 1995	yes
Pyralis farinalis Linnaeus 1758	<1925		Zhang 1994, Essig 1926a	
Pyrausta laticlavia (Grote & Robinson 1867)	1880's	North America	Powell & Opler 2009	
Pyrausta volupialis (Grote 1877)	1991	North America	Powell & Opler 2009	
Pyla fusca (Haworth 1828)			Lafontaine & Wood 1997	
Lepidoptera-Sesiidae				
Podosesia syringae (Harris 1839)	1979	North America	Dowell & Gill 1989	yes
Synanthedon saxifragae (Edwards 1881)	1950		Smith 1950	
Synanthedon tipuliformis (Clerck 1759)	1880	North America	Zhang 1994	
Synanthedon exitiosa (Say 1823)	1914	North America	CDFA 1915 4:421	yes
Lepidoptera-Sphingidae				
Manduca sexta (Linnaeus 1763)	1871	North America	Metcalf 1995	yes
Lepidoptera-Symmocidae				
Oegoconia quadripuncta (Haworth 1828)		North America	Powell 1992	
Symmoca signatella Herrich-Schaeffer 1854		Europe	CDFA 1942 31:175	
Lepidoptera-Tineidae				
Dryadaula terpsichorella (Busck 1910)	1963	Tropical America	CPPDR 1999 18:81, Powell & Opler 2009	
Lindera tessellatella (Blanchard 1854)			Powell & Hsu 2004	
Monopis crocicapitella (Clemens 1859)			Powell & Hsu 2004	
Monopis rusticella (Hubner 1796)			Powell & Hsu 2004	
Nemapogon granellus (Linnaeus 1758)	1963		Arnett 1985	
Niditinea spretella (Denis & Schiffermüller 1775)			CDFA 1943 32:258	
Oinophila v-flava (Haworth 1828)		Europe	Powell 1964b, Powell 1992, Powell & Opler 2009	
Opogona omoscopa (Meyrick 1892)		Hawaii	Powell 1992	yes
Phereoeca praecox Gozmany & Vari 1973	1966	Africa	CPPDR 2000 19:29	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Setomorpha rutella Zeller 1852			CDFA 1958 47:248, Powell & Hsu 2004	
Tinea pallescentella Stainton 1851			Powell & Hsu 2004, Powell & Opler 2009	
Tinea pellionella (Linnaeus 1758)			Arnett 1985, Essig 1926a	yes
Tineola biselliella Hummel 1823			Arnett 1985, Essig 1926a	yes
Trichophaga tapetzella (Linnaeus 1758)	<1940		Arnett 1985, Essig 1926a	
Lepidoptera-Tortricidae				
Acleris variegana (Denis & Schiffermuller 1775)			Powell 2005, Powell & Opler 2009	
Ancylis comptana (Frolich 1828)		North America	Essig 1926a, 1958, Powell & Opler 2009	
Bactra priapeia Heinrich 1923		North America	Powell 1997	
Choristoneura conflictana (Walker 1863)		North America	Dowell & Gill 1989	
Cnephasia longana (Haworth 1811)		Europe	CDFA 1948 37:204	
Crocidosema plebejana Zeller 1847		North America	Powell 1992	
Cydia pomonella (Linnaeus 1758)		North America	Metcalf 1995, Powell & Opler 2009	
Cydia prunivora Walsh 1868		North America	Essig 1926a	
Ditula angustiorana (Haworth 1811)		Europe	CDFA 1933 22:351	
Endothenia albolineana (Kearfoot 1907)		North America	Dowell & Gill 1989	
Epinotia solandriana (Linnaeus 1758)			Aukema et al. 2010,	
Epiphyas postvittana (Walker 1863)	2007	Australia	Powell & Opler 2009	
Grapholita molesta (Busck 1916)		North America	CDFA 1942 31:175	
[b]*Lobesia botrana* (Denis & Schiffermuller 1775)		Europe	Gullian et al. 2011	yes
Lorita scarificata (Meyrick 1917)			Zhang 1994	
Platynota stultana Walsingham 1884		North America	Powell 1980	yes
Rhyacionia frustrana (Scudder, in Comstock 1880)		North America	Dowell & Gill 1989	
Spilonota ocellana (Denis & Schiffermüller 1775)		North America	CDFA 1939 28:539, Powell & Opler 2009	
Zeiraphera canadensis Mutura & Freeman 1967			Martineau 1984, Ferguson 1978	
Zeiraphera hesperiana Mutura & Freeman 1967	1968	North America	Powell 1968a	
Zeiraphera vancouverana McDunnough, 1925		North America	Dowell & Gill 1989	
Lepidoptera-Yponomeutidae				
Zelleria cf. *hepariella* Stainton 1849	1977	Europe	CPPDR 2000 19:31	
Lepidoptera-Zygaenidae	1969			
Harrisina metallica Stretch 1885	1966	Mexico	CDFA 1943 32:98	
Mollusca-Agriolimacidae	1951			
Deroceras panormitanum (Lessona & Pollonera 1882)		Europe	McDonnel et al. 2009	
Deroceras reticulatum (Müller 1774)	2002		Ebeling 1975	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Mollusca-Arionidae				
Arion ater Linnaeus 1758	1912	North America	Dowell & Gill 1989	
Arion distinctus Mabille 1868			Roth & Sadeghian 2003	
Arion hortensis Ferussac 1819		Europe	Lindroth 1957, McDonnel et al. 2009	yes
Arion intermedius Normand 1852	<1925		Lindroth 1957, McDonnel et al. 2009	
Arion rufus (Linnaeus 1758)	<1925		Roth & Sadeghian 2003	
Arion silvaticus Lohmander 1937			Roth & Sadeghian 2003	
Mollusca-Carychiidae	<1925			
Carychium minimum Muller 1774	<1925	Europe	Roth & Sadeghian 2003	
Mollusca-Daudebardiidae	<1925			
Oxychilus alliarius Miller 1822		Europe	Lindroth 1957, Hanna 1939	
Oxychilus cellarius Müller 1774		Europe	Lindroth 1957, Hanna 1939	
Oxychilus draparnaldi (Beck 1837)		Europe	Lindroth 1957, Hanna 1939	
Oxychilus helveticus (Blum 1881)			Lindroth 1957	
Mollusca-Ferrussaciidae				
Cecilioides acicula (Muller 1774)	<1925	Europe	Roth & Sadeghian 2003	
Mollusca-Helicellidae	<1925			
Cernuella virgata (Mendes de Costa 1778)	<1925	Europe	Roth & Sadeghian 2003	
Cochlicella barbara (Linnaeus 1758)		Europe	Roth & Sadeghian 2003	
Cochlicella ventrosa (Ferrussac 1821)	<1925		Dowell & Gill 1989	
Mollusca-Helicidae	<1925			
Cepaea nemoralis (Linnaeus 1758)		Europe	CDFA 1940 29:241	
Eobania vermiculata (Muller 1774)	<1900		Roth & Sadeghian 2003	
Cantareus aspertus (Born 1778)		Europe	CDFA 1941 30:352	yes
Cornu awspersum (Müller 1774)	<1925	Europe	CDFA 1939 28:302, Hanna 1939	yes
Otala lactea (Müller 1774)		Europe	CDFA 1940 29:241	
Theba pisana (Müller 1774)		Europe	CDFA 1919 8:7, Hanna 1939	yes
Mollusca-Helicodiscidae	<1925			
Lucilla singleyana (Pilsbry 1889)		North America	Roth & Sadeghian 2003	
Mollusca-Hygromiidae				
Helicella maritima (Draparnaud 1805)		Africa	Dowell & Gill 1989	
Xerotricha conspurcata (Draparnaud 1801)		Europe	CPPDR 1996 15:8	
Mollusca-Limacidae	<1925			
Lehmannia valentiana (Ferussac 1822)		Europe	Roth & Sadeghian 2003	yes
Limax flavus Linnaeus 1758		Europe	Lindroth 1957, McDonnel et al. 2009	yes
Limax maximus Linnaeus 1758		Europe	Lindroth 1957, McDonnel et al. 2009	yes
Mollusca-Milacidae				
Milax gagates (Draparnaud 1801)	<1900	Europe	Lindroth 1957, McDonnel et al. 2009	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Mollusca-Patulidae				
Discus rotundatus (Muller 1774)	<1925	Europe	Roth & Sadeghian 2003	
Mollusca-Pristilomatidae				
Hawaiia minuscula (Binney 1841)	<1925	Hawaii	Dowell & Gill 1989	
Vitrea contracta Lowe (Westerlund 1871)	<1925	Europe	Roth & Sadeghian 2003	
Mollusca-Punctidae	<1925			
Paralaoma servilis (Shuttleworth 1852)			Roth & Sadeghian 2003	
Mollusca-Pupillidae				
Pupoides albilabris (C. B. Adams 1841)		North America	Roth & Sadeghian 2003	
Mollusca-Spiraxidae				
Euglandina rosea (Ferussac 1818)		North America	Roth & Sadeghian 2003	
Mollusca-Subulinidae				
Rumina decollata (Linnaeus 1758)		North America	Dowell & Gill 1989	
Mollusca-Succineidae				
Novisuccinea ovalis (Say 1817)		North America	Roth & Sadeghian 2003	
Succinea luteola Gould 1848		North America	Roth & Sadeghian 2003	yes
Mollusca-Testacellidae				
Testacella haliotidea Draparnaud 1801		Europe	McDonnel et al. 2009	
Mollusca-Valloniidae				
Vallonia costata (Müller 1774)		North America	Roth & Sadeghian 2003	
Vallonia excentrica Sterki 1893		North America	Roth & Sadeghian 2003	
Vallonia pulchella (Müller 1774)		North America	Lindroth 1957, Hanna 1939	
Opisthopora-Lumbricidae				
Allolophora chlorotica (Savigny 1826)			Wood & James 1993	
Aporrectodea caliginosa (Savigny 1826)			Wood & James 1993	
Aporrectodea trapezoides (Duges 1828)			Wood & James 1993	
Aporrectodea tuberculata (Eisen 1874)			Wood & James 1993	
Aporrectodea sp.			Wood & James 1993	
Dendrobaena rubida (Savigny 1826)			Wood & James 1993	
Eisenia foetida Savigny 1826			Wetzel & Reynolds 2014, Bugg 2014	
Eisenia rosea (Savigny 1826)			Wood & James 1993	
Eiseniella tetraedra (Savigny 1826)	1942		Wood & James 1993	
Lumbricus rubellus Hoffmeister 1843			Wetzel and Reynolds 2014, Bugg 2014	
Lumbricus terrestris Linnaeus 1758			Wetzel & Reynolds 2014, Bugg 2014	
Octolasion cyaneum (Savigny 1826)	<1925		Wood & James 1993	
Opisthopora-Megascolecidae				
Amynthas corticis (Kinberg 1867)			Hendrix & Bohlen 2002, Bugg 2014	
Amynthas gracilis (Kinberg 1867)	<1925		Hendrix & Bohlen 2002, Bugg 2014	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Microscolex dubius (Fletcher 1887)			Wood & James 1993	
Microscolex sp Rosa 1887	<1925		Wood & James 1993	
Orthoptera-Gryllidae	<1925			
Acheta domestica (Linnaeus 1758)	<1925	North America	Arnett 1985, Weissman & Rentz 1977	
Allonemobius fasciatus (De Geer 1773)	<1925		Dowell & Gill 1989	
Gryllodes supplicans (Walker 1859)	<1900	North America	Dowell & Gill 1989	
Orthoptera-Gryllotalpidae				
Scapteriscus borellii Giglio-Tos 1894	<1931	North America	CPPDR 2011 24: 14-16	
Orthoptera-Tettigoniidae				
Anabrus simplex Haldeman 1852	1943	North America	CDFA 1943 32:201	
Neoconocephalus robustus (Scudder 1862)	1995	North America	Dowell & Gill 1989	
Phaneroptera nana Fieber 1853	<1925	Europe	Strohecker 1952	
Phaneroptera quadripunctata Brunner 1878	1949	Europe	Strohecker 1952, Cantrall 1972	
Platycleis tesselata (Charpentier 1825)	1926	Europe	CDFA 1960 49:143, Rentz 1963	
Phasmida-Phasmatidae				
Carausius morosus (Sinety 1901)		North America	CPPDR 2001 20:11	yes
Phthiraptera-Boopidae				
Heterodoxus longitarsus (Piaget 1880)	1894	Australia	Essig 1926a, 1958	
Heterodoxus spiniger (Enderlein 1909)	1945		Arnett 1985	
Phthiraptera-Gyropidae				
Gyropus ovalis Burmeister 1838	1976		Emerson 1972, Essig 1926a	
Gliricola porcelli (Schrank 1781)			Emerson 1972, Essig 1926a	
Phthiraptera-Haematopinidae	1973			
Haematopinus asini (Linnaeus 1758)	1959		Kim et al. 1986, Essig 1926a	yes
Haematopinus eurysternus Nitzsch 1818	<1925		Kim et al. 1986, Essig 1926a	yes
Haematopinus suis (Linnaeus 1758)	1959		Kim et al. 1986, Essig 1926a	yes
Phthiraptera-Hoplopleuridae				
Hoplopleura captiosa Johnson 1960	2005		Kim et al. 1986	
Hoplopleura pacifica Ewing 1924	1924		Kim et al. 1986	
Phthiraptera-Linognathidae	1940			
Linognathus africanus Kellogg & Paine 1911			Kim et al. 1986	
Linognathus setosus (Olfers 1816)			Kim et al. 1986, Essig 1926a	
Linognathus stenopsis (Burmeister 1838)			Kim et al. 1986, Essig 1926a	
Linognathus vituli (Linnaeus 1758)			Kim et al. 1986, Essig 1926a	
Phthiraptera-Menoponidae	<1925			
Menacanthus stramineus (Nitzsch 1818)			Essig 1926a	
*Menopon gallinae*Linnaeus 1758			Emerson 1972, Essig 1926a	
Phthiraptera-Pediculidae				
Pediculus humanus Linnaeus 1758			Kim et al. 1986	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Phthiraptera-Philopteridae	1996			
Campanulotes bidendatus Scopoli 1763	1968		Essig 1926a, 1958	
Goniocotes chrysocephalus Giebel 1874	1925		Emerson 1972	
Goniocotes creber Kellogg 1896	1909		Essig 1958	
Goniocotes gigas Taschenberg 1879	<1915		Essig 1926a, 1958	
Goniocotes gallinae (De Geer 1778)	1997		Emerson 1972	
Goniocotes maculatus Taschenberg 1882	<1915		Emerson 1972	
Goniocotes parviceps (Piaget 1880)	<1925		Emerson 1972	
Goniocotes rectangulatus Nitzsch 1866	1995		Emerson 1972	
Lipeurus caponis (Linnaeus 1758)	2004		Emerson 1972, Essig 1926a	
Lipeurus maculosus Clay 1938			Emerson 1972	
Lipeurus numidae (Denny 1842)	1943		Emerson 1972	
Lipeurus pavo Clay 1938			Emerson 1972	
Phthiraptera-Pthiridae	1946			
Pthirius pubis (Linnaeus 1758)			Kim et al. 1986	
Phthiraptera-Polyplacidae				
Polyplax spinulosa (Burmeister 1839)	<1925		Kim et al. 1986, Essig 1926a	
Phthiraptera-Trichodectidae	1999			
Bovicola bovis (Linnaeus 1758)	1907		Emerson 1972, Essig 1926a	yes
Trichodectes equi (Denny 1842)	1972		Emerson 1972, Essig 1926a	yes
Trichodectes canis (De Geer 1778)	1931		Essig 1926a, 1958	
Phthiraptera-Trimenoponidae	1996			
Trimenopon hispidum (Burmister 1838)	1904		Arnett 1985	
Pscoptera-Ectopsocidae				
Ctopsocus strauchi Enderlein 1906	1949		BugGuide 2011	
Pscoptera-Elipsocidae	1985			
Cuneopalpus cyanops (Rostock 1876)		Europe	Mockford 1993	
Propsocus pulchripennis Perkins 1899	<1915		Mockford 1993	
Psocoptera-Lachesillidae				
Lachesilla pedicularia (Linnaeus 1758)			Mockford 1993	
Psocoptera-Liposcelididae				
Liposcelis corrodens Heymons 1909			Mockford 1993	
Liposcelis decolor (Pearman 1925)			Mockford 1993	
Liposcelis bostrychophilus Badonnel 1931			Powell & Hogue 1979	
Liposcelis rufa Broadhead 1950		Europe	Mockford 1993	
Psocoptera-Peripscoidae				
Peripsocus reductus Badonnel 1943	<1925		Mockford 1993	
Psocoptera-Psyllipsocidae	<1925			
Psyllipsocus ramburii Selys-Longchamps 1872			Mockford 1993	

APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2010.

Taxon	Year detected	Probable origin	Reference	Listed as a pest[b]
Psocoptera-Stenopsocidae				
Graphopsocus cruciatus (Linnaeus 1768)			Mockford 1993	
Psocoptera-Trichopsocidae				
Trichopsocus clarus (Banks 1908)			BugGuide 2011	
Psocoptera-Trogiidae				
Cerobasis annulata (Hagen 1865)		Europe	Mockford 1993	
Lepinotus inquilinus Heyden 1850			Mockford 1993	
Lepinotus patruelis Pearman 1931		Europe	CDFA 1942 31:176	
Lepinotus reticulatus Enderlein 1905			Mockford 1993	
Siphonaptera-Ceratophyllidae				
Nosopsyllus fasciatus (Bosc 1800)			Hubbard 1968, Lewis et al. 1988, Essig 1926a	
Nosopsyllus londiniensis (Rothschild 1903)			Lewis et al. 1988	
Siphonaptera-Leptopsyllidae				
Leptopsylla segnis (Schonherr 1811)			Hubbard 1968, Lewis et al. 1988, Essig 1926a	
Siphonaptera-Pulicidae				
Ctenocephalides canis (Curtis 1826)			Hubbard 1968, Essig 1926a	yes
Ctenocephalides felis (Bouché 1835)			Hubbard 1968, Lewis et al. 1988, Essig 1926a	yes
Echidnophaga gallinacea (Westwood 1875)			Lewis et al. 1988, Essig 1926a	yes
Pulex irritans Linnaeus 1758		Tropical America	Lewis et al. 1988, Essig 1926a	
Xenopsylla cheopis Rothschild 1903		Europe	Hubbard 1968, Lewis et al. 1988	
Symphyla-Scolopendrellidae				
Symphylella isabellae (Grassi 1886)		Europe	Hilton 1931	
Thysanura-Lepismatidae				
Ctenolepisma ciliata (Dufour 1831)			Wygodzinsky 1972	
Ctenolepisma lineata (Fabricius 1775)			Wygodzinsky 1972	
Ctenolepisma longicaudata Escherich 1905			Wygodzinsky 1972	
Lepisma saccharina Linnaeus1758			Wygodzinsky 1972, Essig 1926a	yes
Thermobia domestica (Packard 1873)			Wygodzinsky 1972, Essig 1926a	yes

Addendum to Appendix. Exotic terrestrial macro-invertebrates found breeding in California 1700-2016

Taxon	Year detected	Probable origin	Reference	Listed as a pest
Araneae-Corinnidae				
Falconina gracilis (Keyserling 1891)	2013	Tropical America	Valle et al. 2013	
Araneae-Theridiidae				
Steatoda nobilis (Thorell 1875)	2012	Europe	Vetter and Rust 2012	
Coleoptera-Anthicidae				
Omonadus formicarius (Goeze 1777)		North America	Majka 2011, California beetle project 2016	
Coleoptera-Buprestidae				
Chrysobothris analis LeConte1860	2012	North America	Westcott et al. 2015	
Coleoptera-Carabidae				
Amara apricaria (Paykull 1790)		Europe	Sokolov and Kavanaugh 2014	
Amara familiaris (Duftschmid 1812)		North America	Bosquet 2012	
Harpalus affinis (Schrank 1781)		Europe	Sokolov and Kavanaugh 2014	
*Pterostrichus melanarius (*Illiger 1798)		North America	Bosquet 2012	
Coleoptera-Chrysomelidae				
Microtheca ochrolma Stal 1860	2011	North America	Gilbert et al. 2011	
Oulema melanopus (Linneaus 1758)	2015	North America	Dowell and Pickett (in prep)	yes
Coleoptera-Curculionidae				
Euwallacea n. sp. #2	2013		Anon. 2016	
Coleoptera-Dermestidae				
Thylodrias contractus Motshulsky 1839			California beetle project 2016	
Coleoptera-Erotylidae				
Dacne picta Crotch 1873	1990	Asia	Savary 1995	
Coleoptera-Hyborosoridae				
Hybosorus illigeri Reiche 1853			California beetle project 2016, Ocampo 2002.	
Coleoptera-Hydrophilidae				
Cercyon atricapillus (Marsham 1802)			Smetana 1988, California beetle project 2016	
Cercyon haemorrhoidales (Fabricius 1775)			Smetana 1988, California beetle project 2016	
Cercyon lateralis (Marsham 1802)			Smetana 1988, California beetle project 2016	
Cercyon pygmaeus (Illiger 1801)			Smetana 1988, California beetle project 2016	
Cercyon quisquilus (Linneaus 1761)			Smetana 1988, California beetle project 2016	
Cercyon terminalis (Marsham 1802)			Smetana 1988, California beetle project 2016	
Coloeoptera-Latridiidae				
Adistema watsoni (Wollaston 1871)			California beetle project 2016	
Cartodere notifer (Westwood 1839)			Majka et al. 2009a	
Corticaria ferruginea Marsham 1802			Majka et al. 2009a	

ADDENDUM TO APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2016

Taxon	Year detected	Probable origin	Reference	Listed as a pest
Coleoptera-Staphylinidae				
Anotylustetra carinatus (Block 1799)			California beetle project 2016, Klimaszewski et al. 2012.	
Bisnius cephalotes (Gravenhorst 1802)			California beetle project 2016, Majka et al. 2006	
Crataraea suturalis (Mannerheim 1830)			California beetle project 2016, Klimaszewski et al.2012	
Lithocharis ochracea (Gravenhorst 1802)			California beetle project 2016, Hamilton 1889	
Myrmecocephalus concinnus (Erichson 1840)			California beetle project 2016, Klimsezewski et al. 2012	
Nehemitropia lividipennis (Mannerheim 1831)			California beetle project 2016, Klimsezewski et al. 2012	
Philonthus carbonarius (Gravenhorst 1802)			California beetle project 2016. Majka et al. 2006.	
Philonthus varians (Paykull 1789)			California beetle project 2016, Staniec 2002	
Quedius fulgidus (Fabricius 1792)			Majka et al. 2009b	
Tasgius ater (Gravenhorst 1802)			California beetle project 2016, Brunke et al. 2011	
Coleoptera-Tenebrionidae				
Alphitobius laevigatus (Fabricius 1781)			California beetle project 2016, Bosquet 1990.	
Latheticus oryzae (Waterhouse 1880)			California beetle project 2016, Wittenberg et al. 2005	
Diptera-Agromyzidae				
Liriomyza huidobrensis (Blanchard 1926)		Tropical America	Steck 2006	
Napomyzae vanescens (Walker 1853)			Spencer 1981	
Phytomyza vomitoriae Kulp 1968			Lonsdale and Scheffer 2011	
Diptera-Cecidomyiidae				
Monarthropalpus buxi, (Geoffroy 1764)			Anon. 1985, 2014	
Diptera-Culicidae				
Aedes albopictus (Skuse 1849)			Anon. 2015	yes
Aedes quinquefasciatus Say 1823			Juliano and Lounibos 2005, Cornell et al. 2003	
Diptera-Dolichopodidae				
Medetera johnthomasi Bickel & Arnaud 2011	2011		Bickel and Arnaud 2011	
Diptera-Muscidae				
Athergonia orientalis (Schiner 1868)			Cole 1969, Hancock et al. 2014	
Athergonia reversura Villeneuve 1963			Bryant 2016, Hancock et al. 2014	
Diptera-Drosophilidae				
Drosophila gentica Wheeler & Takada 1962.	2014	TropicalAmerica	Grimaldi et al. 2015	
Drosophila flavohirta Malloch 1924	2014	Australia	Grimaldi et al. 2015	
Drosophila melanogaster Meigen 1830			Baudy et al. 2004, Varela et al. 2015	
Diptera-Tephritidae				
Euaresta bullans Weidemann 1830			Foote and Blanc 1963	

ADDENDUM TO APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2016

Taxon	Year detected	Probable origin	Reference	Listed as a pest
Hemiptera-Adgelidae				
Pineus boerneri Annand, 1928			Lazzari and Cardoso 2011	
Hemiptera-Aleyrodidae				
Aleurotulus nephrolepidis (Quiantance, 1900)			Anon. 2006	
Hemiptera-Aphididae				
Anoecia corni (Fabricius, 1775)			Foottit et al. 2006, Swain 1919	
Aphis eurphorbiae Kaltenbach, 1933	1933		Foottit et al. 2006	
Aphis polygonata (Nevsky, 1929)			Foottit et al. 2006, Blackman and Eastop 2007	
Aphis spiraecola Patch, 1914			Foottit et al. 2006, Reuther et al. 1978	
Aphis thalictri Koch, 1854			Foottit et al. 2006, Swain 1919	
Asiphonella dactylonii Theobald 1923			Foottit et al. 2006, Anon. 1969	
Atarsaphis agrifoliae (Ferris, 1921)	1921		Foottit et al. 2006	
Brachycaudus helichrysi (Kaltenbach, 1843)			Foottit et al. 2006. Bentley et al. 2009	
Capitophorus elaeagni (Del Guercio, 1894)			Foottit et al. 2006, Bari and Natwick 2015	
Ctenocallis zelkowae (Shinji, 1924)	1983		Foottit et al. 2006	
Greenidea psidii van der Goot, 1916	1998		Foottit et al. 2006	
Liosomaphis berberidis (Kaltenbach, 1843)			Foottit et al. 2006, Swain 1919	
Metolophium dirhodum (Walker, 1849)			Foottit et al. 2006, Glidow and Rochow 1983	
Monaphis antennata (Kaltenbach, 1843)			Foottit et al. 2006, Essig 1911	
Panaphis juglandis (Geoze, 1778)	1952		Foottit et al. 2006, Olson 1974	
Sitobion avenae (Fabricius, 1775)			Foottit et al. 2006, Summers and Godfrey 2009	
Therioaphis maculata (Buckton, 1899)			Foottit et al. 2006, Smith 1959	
Tuberolachnus salignus (Gmelin, 1790)			Stary and Schlinger 1967	
Hemiptera-Cicadellidae				
Alebra wahlbergi Boheman, 1845	1945		Hamiliton 2010, 2011	
*Aphrodes bicinctus (*Schrank, 1776)			Hamiliton 2011, Sherf and MacNab 1986	
Dalbulus maidis DeLong, 1923			Hamiliton 2011, Summers et al. 2004	
Empoascas maragdula Fallen, 1806	1916		Hamiliton 2011, van Duzee 1917	
Kyboasca bipunctata (Oshanin 1871)			Flock 1950	
Sophonia orientalis (Matsumura, 1912)			Hamiliton 2011, Bryant et al. 2016	
Hemiptera-Miridae				
Brachynotocoris puncticornis Reuter, 1880	2013	Europe	Dowell (in prep)	
Closterotomus norwegicus (Gmelin, 1790)	1966		Scudder and Foottitt 2006	
Coridromius chenopoderis Tatarnic and Cassis 2008		Australia	Tatarnic and Cassis 2008.	

ADDENDUM TO APPENDIX (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2016

Taxon	Year detected	Probable origin	Reference	Listed as a pest
Heteropsallus planicornis (Pallas 1772)			Wheeler and Henry 1992	
Lepidargyrus ancorifer (Fieber 1858)	1912		Scudder and Footitt 2006	
Megalonotus sabulicola (Thompson 1870)	1921		Scudder and Footitt 2006	
Hemiptera-Psyllidae				
Psylla buxi Linneaus, 1758			Tuthill 1943	
Psyllopsis fraxinicola Foerster 1848			Tuthill 1943	
Hymenoptera-Agaonidae				
Eupristina altissima Saunders 1882			Boucek 1997	
Hymenoptera-Apidae				
Xylocopa appendiculata Smith 1852	2012	Asia	Dahlberg et al. 2013	
Hymenoptera-Formicidae				
Phiedole megacephala (Fabricius 1793)	2014		Leathers 2014	
Lepidoptera-Crambidae				
Terastia meticulosalis Guenee & Agathodes 1854	2015	North America	Hodel et al. 2016	
Lepidoptera-Gracillaridae				
Phyllonorycter mespilella (Hubner 1805)	1936	Europe	Maier 2001	
Lepidoptera: Pyralidae				
Diaphania hyalinata Linneaus 1767			Capinera 2014, California moth database 2016	
Lepidoptera-Yponomeutidae				
Ocnerostoma piniariella Zeller 1847			California moth database 2016, Felt 1922.	
Siphonaptera-Pulicidae				
Hectopsylla psittaci Von Frauenfeld 1860		TropicalAmerica	Schwann et al. 1983	
Thysanoptera-Aeolothripidae				
Aeolothrips collaris Priesner 1919		Europe	CPPDR 16:44	
Aeolothrips ericae Bagnall 1920		Europe	CPPDR 14:6	
Aeolothrips melaleucus (Haliday 1852)			Bailey 1957	
Anaphothrips obscurus Comstock 1875			Hoddle & Mound 2012	
Aptinothrips rufus Haliday 1836			Hoddle & Mound 2012	
Rhipidothrips gratiosus Uzel 1895		Europe	Bailey 1957	
Thysanoptera-Phlaeothripidae				
Amynothrips andersoni O'Neill 1968			Hoddle & Mound 2012	
Androthrips ramachandrai Karny 1926			Hoddle & Mound 2012	
Cartomothrips browni Stannard 1962			Hoddle & Mound 2012	
Cephalothrips monilicornis O.M. Reuter 1880		Europe	Cott 1956	
Gynaikothrips ficorum (Marchal 1908)		Mexico	Clausen 1978	yes
Gyaikothrips uzeli Zimmerman 1900			Hoddle & Mound 2012	
Haplothrips leucanthemi (Schrank 1781)			Cott 1956, Essig 1926a	
Haplothrips robustus Bagnall 1918			Hoddle & Mound 2012	
Haplothrips verbasci (Osborn 1897)			Keifer et al. 1982	
Liothrips floridensis Watson 1913			Hoddle & Mound 2012	

Addendum to Appendix (continued). Exotic terrestrial macro-invertebrates found breeding in California 1700-2016

Liothrips vaneeckei Priesner 1920		Europe	CDFA 28:479	
Macrophthalmothrips argus (Karny, 1920)			Hoddle & Mound 2012	
Nesothrips propinquus (Bagnall, 1916)			Hoddle & Mound 2012	
Neurothrips magnafemoralis (Hinds 1902)			CDFA 28:538	
Thysanoptera-Thripidae				
Anaphothrips obscurus (Muller 1776)			Hoddle et al. 2004	
Aptinothrips rufus (Haliday) 1836		Europe	Essig 1926a	
Aptinothrips stylifer Trybom, 1894			Hoddle & Mound 2012	
Asprothrips seminigricornis (Girault 1926)			Hoddle et al. 2004	
Chaetanaphothrips orchidii (Moulton 1907)			Hoddle et al. 2004	
Chirothrips aculeatus Bagnell 1927			Bailey 1957	
Chirothrips manicatus (Haliday 1836)			Hoddle et al. 2004	
Danothrips trifasciatus Sakimura 1975		Pacific Region	CPPDR 15:73	
Dendrothrips howei Mound 1999	2011	North America	Hoddle & Mound 2012	
Dendrothrips ornatus (Jablonowski 1894)		North America	Dowell & Gill 1989	
Drepanothrips reuteri Uzel 1895		Europe	CDFA 17:455	
Frankliniella hemerocallis Crawford 1948		North America	CPPDR 16:44	
Frankliniella schultzei (Trybom 1910)			Hoddle & Mound 2012	
Frankliniella tenuicornis (Uzel 1895)			Hoddle & Mound 2012	
Heliothrips haemorrhoidalis (Bouché 1833)		Tropical America	CDFA 17:366	yes
Hercinothrips bicinctus (Bagnall 1919)			Hoddle & Mound 2012	
Hercinothrips femoralis (Reuter 1891)			Bailey 1957, Essig 1926a	
Limothrips angulicornis Jablonowski 1894		Europe	Bailey 1957	
Limothrips cerealium (Haliday 1836)			Bailey 1957	
Leucothrips nigripennis Reuter 1904			Hoddle & Mound 2012	
Microcephalothrips abdominalis (Crawford 1910)			Hoddle et al. 2004	
Monilothrips kempi Moulton 1929			Bailey 1957	
Neohydatothrips burungae (Hood 1935)		Tropical America	CPPDR 22:21-22	
Neohydatothrips samayunkur (Kudo 1995)		North America	CPPDR 14:28	
Odontothrips loti (Haliday 1852)			Hoddle et al. 2004	
Parthenothrips dracaenae (Heeger 1854)			Bailey 1957, Essig 1926a	
Pseudanaphothrips achaetus (Bagnall) 1916		Australia	CPPDR 19:25	
Pseudodendrothrips mori (Niwa, 1908)			Hoddle & Mound 2012	
Scirtothrips citri (Moulton 1909)		Asia	CDFA 7:465	yes
Scirtothrips inermis Priesner 1933		Europe	Dowell & Gill 1989	
Scirtothrips longipennis (Bagnall 1909)			CDFA 20:345	
Scirtothrips perseae Nakahara 1997	1996	Tropical America	CPPDR 15:4	yes
Taeniothrips inconsequens (Uzel 1895)		Asia	Davidson & Lyon 1987, Bailey 1957	yes
Tenothrips frici (Uzel 1895)			Hoddle et al. 2004	
Thrips australis (Bagnall 1915)		Australia	Bailey 1957	
Thrips hawaiiensis (Morgan 1913)		Hawaii	Dowell & Gill 1989	
Thrips nigropilosus Uzel 1895			Gentile & Bailey 1968	
Thrips tabaci Lindeman 1888		North America	CDFA 4:56,	
Thrips trehernei Priesner 1927			Hoddle et al. 2004	
Thrips simplex (Morison 1930)			Hoddle & Mound 2012	
Thrips vulgatissimus Haliday 1836			Hoddle et al. 2004	
Trichromothrips cyperaceae (Bianchi 1945)		Asia	Hoddle et al. 2004	
Trichromothrips xanthius (Williams 1917)			Hoddle et al. 2004	

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Tetramerium vargasiae (Acanthaceae), a New Species from the Basin of the Río Balsas in Guerrero, Mexico

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***Tetramerium vargasiae* is newly described and illustrated from the arid portion of the basin of the Río Balsas in Guerrero, Mexico. It is distinguished from its congeners by the combination of the following characters: shrubby habit, linear leaves, pubescent (eglandular trichomes only) and entire bracts that are 16 to 19 mm long, five-lobed calyx, pseudopapilionaceous and white (with purple markings) corollas, and glabrous capsules that are seven mm long. It is compared to the superficially similar *T. tetramerioides* from Oaxaca, Mexico.**

KEYWORDS: *Tetramerium*, Guerrero, Mexico, endemic species, Acanthaceae

Se describe e ilustra *Tetramerium vargasiae* como especie nueva de la cuenca árida del Río Balsas en Guerrero, México. Se distingue de sus congéneres por la combinación de los siguientes caracteres: hábito arbustivo, hojas lineares, brácteas pubescentes (sólo tricomas eglandulares) y enteras de 16 a 19 mm de largo, cáliz con cinco lóbulos, corolas pseudopapilionáceas y blancas (con marcas de color púrpura) y cápsulas glabras siete mm de largo. Se compara la especie nueva con *T. tetramerioides*, una especie superficialmente similar del estado de Oaxaca, México.

Tetramerium Nees consists of 29 currently recognized species (Daniel 1986, 2003) that occur from the United States to Bolivia. Most species (22) occur in Mexico, and 19 of them are endemic there. Arid and semi-arid regions in western and southern Mexico, from Jalisco to the Isthmus of Tehuantepec in Oaxaca, are especially rich in species of *Tetramerium* with at least 17 occurring there and 10 endemic to the region (Daniel 1986). Another distinctive species from this region was collected in the arid portion of the basin of the Río Balsas in Guerrero. It is described below.

Tetramerium vargasiae T.F. Daniel & Cruz Durán, sp. nov.

TYPE. MEXICO: **Guerrero**: Mpio. Huitzuco de los Figueroa, 0.7 km NE de San Francisco Ozomatlán [ca. 17°56′0.63″N, 099°19′37.41″W], 650 m, bosque tropical caducifolio, 30–III–1990 (flr, frt), *A. Vargas P. 288* (holotype: FCME!).

Tetramerium vargasiae differs from congeners by the combination of its shrubby habit, linear leaves, pubescent (eglandular trichomes only) and entire bracts that are 16–19 mm long, 5-lobed calyx, pseudopapilionaceous and white (with purple markings) corollas, and glabrous capsules that are 7 mm long.

Shrubs to 1 m tall; older stems with bark exfoliating in strips; young stems ± terete, ± evenly pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.2 mm long, nodes more densely pubescent. Leaves (immature; plants mostly leafless during anthesis) subsessile (petioles to 2 mm long), blades linear, sometimes ± conduplicate, 10–17 mm long, 0.6–0.9 mm wide, length:width = 16.7–18.9, both surfaces and margin covered with antrorsely appressed eglandular trichomes 0.05–0.2 mm long, only midvein evident. Inflorescence of terminal (sometimes terminating short axillary branches) and congested spikes to 46 mm long, 14–19 mm across (measured flat) near midspike, rachis densely and evenly pubescent with flexuous to antrorse to antrorsely appressed eglandular trichomes to 0.5 mm long, median internodes 6 mm long. Bracts ± coriaceous, lanceolate to lance-elliptic, 16–19 mm long, 1.8–3.2 mm wide, obscurely to ± prominently and palmately 3-veined, apically straight, erect, and mucronate, mucro 0.5–0.6 mm long, abaxial surface densely pubescent with antrorse to antrorsely appressed eglandular trichomes to 0.4 mm long, margin densely ciliate with spreading-flexuous, silky eglandular trichomes to 2.5 mm long (at least some trichomes > 1 mm long). Bracteoles lance-subulate, 9–14 mm long, 0.8–1.1 mm wide, only midvein evident (sometimes obscure), abaxial surface and margin pubescent like bracts. Flowers sessile. Calyx 5-lobed, 6.5–8.5 mm long, lobes lance-subulate to subulate, 6–7 mm long, 0.4–0.5 mmm wide, abaxial surface and margin pubescent like bracteoles. Corolla pseudopapilionaceous, white with purple markings on upper lip, 20 mm long, externally glabrous, tube 10.5 mm long, upper lip obovate, 9.5 mm long, 2.5 mm wide, lower lip 9 mm long, lower-central lobe conduplicate, 7 mm long, 4.6 mm wide, lateral lobes obovate, 7 mm long, 3.5 mm wide. Stamens ca. 7 mm long, thecae ca. 1.2 mm long. Capsules 7 mm long, glabrous, stipe 2.5 mm long, head 4.5 mm long. Seeds not seen.

Phenology.— Flowering and fruiting: March.

Distribution and habitat.— Endemic to Mexico where it is known only from the arid portion of the basin of the Río Balsas of north-central Guerrero in a region of tropical deciduous forest at 650 m elevation.

Conservation Assessment.— *Tetramerium vargasiae* is known from a single collection from a population that was not observed during this study. The collector of the type indicated that only a few plants were observed at that site. Given the lack of additional information, this species is assessed as Data Deficient (DD) according to IUCN guidelines (IUCN 2014).

Although *Tetramerium vargasiae* is incompletely known, it is highly distinctive. It pertains to Daniel's (1986) sect. *Tetramerium* and resembles *T. tetramerioides* (Lindau) T.F. Daniel from southeastern Oaxaca (previously known only from the type, but recently rediscovered in the vicinity of the type collection) in several characteristics, including: shape of the bracts and bracteoles, marginal pubescence of the bracts, number of calyx lobes, color and shape of the corolla, and size and surface vesture of the capsule. These two species can be distinguished by the characters noted in the following key:

1a. Young stems ± evenly pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.2 mm long; leaves (immature) subsessile (petioles to 2 mm long), blades linear, length:width = 16.7–18.9; spikes 14–19 mm wide (measured flat) near midspike, rachis pubescent with eglandular trichomes; bracts 16–19 mm long, abaxial surface densely pubescent with antrorse to antrorsely appressed eglandular trichomes to 0.4 mm long; bracteoles 9–14 mm long; calyx 6.5–8.5 mm long; corolla 20 mm long; Guerrero . . . . *T. vargasiae*

1b. Young stems ± bifariously pubescent with an understory of glandular trichomes 0.05–0.2 mm long and an overstory (absent on some internodes) of flexuose eglandular trichomes 0.2–0.7 mm long; leaves subsessile to petiolate (petioles to 15 mm long), blades lance-ovate,

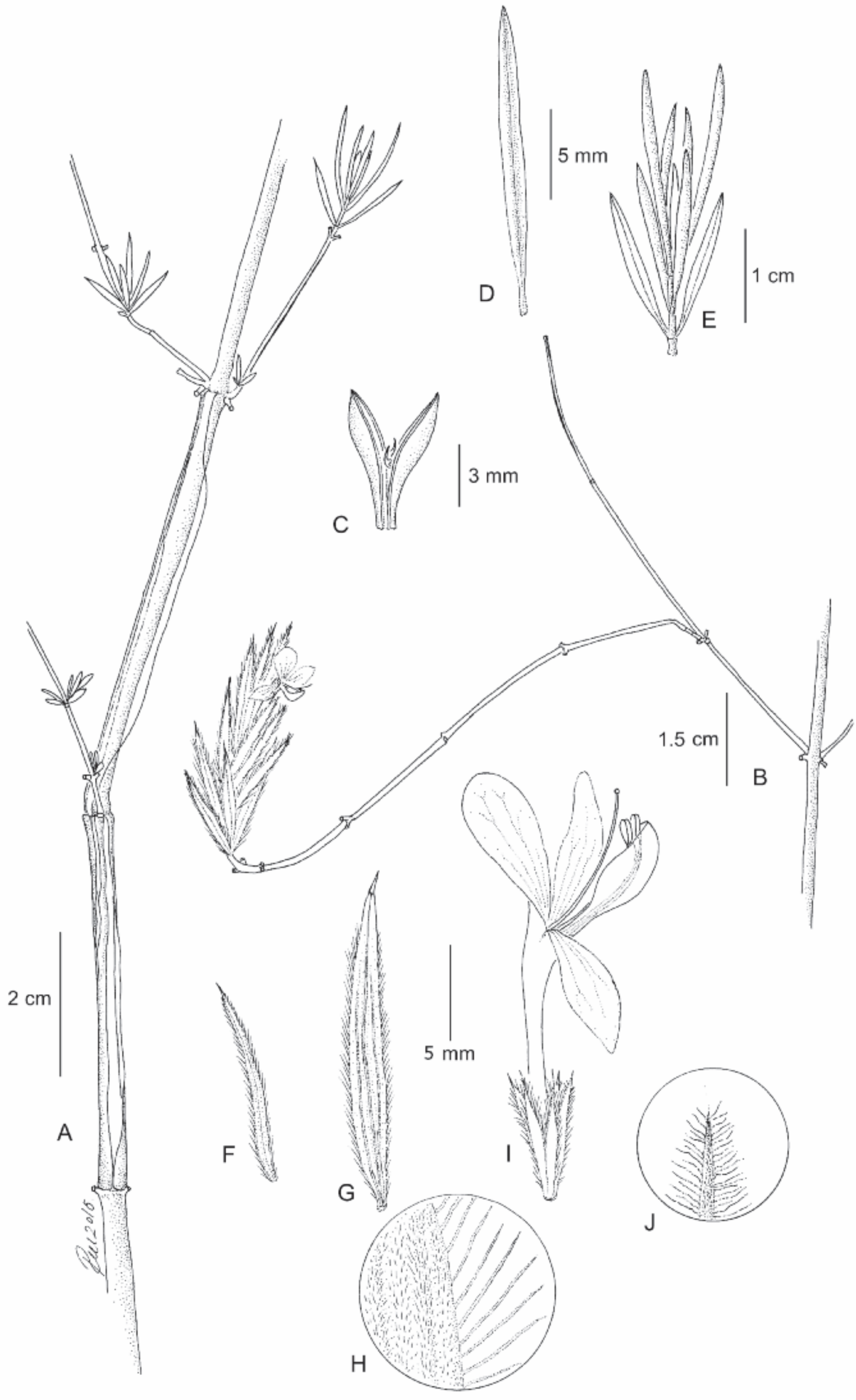

FIGURE 1. *Tetramerium vargasiae* (from the holotype). A. Stem with exfoliating epidermis and young leaves. B. Branch with terminal inflorescence. C. Capsule. D. Young leaf. E. Branch with young leaves. F. Bracteole. G. Bract. H. Detail of bract showing trichomes on margin. I. Flower. J. Detail of calyx lobe showing trichomes. Drawn by Ramiro Cruz Durán.

length:width = 2.2–3.8; spikes 3–7 mm wide (measured flat) near midspike, rachis pubescent with glandular and eglandular trichomes; bracts 7–10 mm long, abaxial surface pubescent with an inconspicuous understory of glandular trichomes 0.05–0.2 mm long and a sparse overstory (especially along the midvein) of flexuose eglandular trichomes to 1.5 mm long; bracteoles 6–8 mm long; calyx 3.2–4 mm long; corolla 14–15 mm long; Oaxaca. . . . . *T. tetramerioides*

This species is named in honor of the collector of the type, Andira Vargas Pérez, who collected plants for FCME between 1989 and 1990 during a study of the flora and vegetation in the eastern part of the basin of the Río Basas in Guerrero.

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Avicennia (Acanthaceae: Avicennioideae) in North America and Mesoamerica

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A taxonomic revision of *Avicennia*, an acanthaceous genus of mangroves, in North America and Mesoamerica recognizes three species, two native (*A. bicolor* and *A. germinans*) and one locally naturalized in southern California (*A. marina* subsp. *australasica*). Herbarium specimens from throughout the region were used to formulate descriptions of each species, obtain distributional and ecological data, and as a source for pollen in order to characterize and illustrate palynological features of each species. A distribution map, an illustration of the most common species (*A. germinans*), and photos showing diagnostic attributes of each species are provided.

Una revisión taxonómica de *Avicennia*, un género de los manglares en la familia Acanthaceae, en Norteamérica y Mesoamérica reconoce tres especies, dos nativas (*A. bicolor* y *A. germinans*) y una naturalizada localmente en el sur de California (*A. marina* subsp. *australasica*). Los ejemplares de herbario de toda la región se utilizaron para formular descripciones de cada especie, obtener datos distributivos y ecológicos, y como fuente de polen con el fin de caracterizar e ilustrar caracteres palinológicos de cada especie. Además, se ofrecen un mapa de distribución, una ilustración de la especie más comune (*A. germinans*), y fotos que muestran los atributos diagnósticos de cada especie.

Avicennia has been treated previously in several families, most prominent among them Verbenaceae and Avicenniaceae. Molecular phylogenetic analyses (Schwarzbach and McDade 2002; Borg et al. 2008; McDade et al. 2008) and studies of floral structure and development (Borg and Schönenberger 2011) reveal the genus to be monophyletic, nested among Acanthaceae *s.l.*, and sister to either subfamily Acanthoideae or more likely to subfamily Thunbergioideae. The genus is here treated as subfamily Avicennioideae. Although its taxonomic relationships have been controversial, *Avicennia* is well established as a genus of mangrove species. Indeed, they are usually treated in an ecological sense among the so-called "true" mangroves (Tomlinson 1986), which taxa generally occur exclusively in mangrove communities and exhibit both morphological and physiological specializations to the highly saline substrate. It is likely that morphological adaptations to a highly specialized environment have obscured its familial affinities. Other species of Acanthaceae in different tribes of subfamily Acanthoideae are considered to be true mangroves (e.g., *Acanthus ebracteatus* Vahl and *A. ilicifolius* L. of Acantheae *fide* Wang et al. 2011; but treated as mangrove associates by Tomlinson 1986) or mangrove associates (*Bravaisia berlandieriana* (Nees) T.F. Daniel and *B. integerrima* (Spreng.) Standl. of Ruellieae).

The economic importance of mangrove plants in general, and species of *Avicennia* in particular, was correctly pointed out by Moldenke (1960: 144) in citing and refuting another author's statement that plants of *Avicennia* are of little economic importance; Moldenke stated, "…members of this genus are of tremendous economic importance to man and his economy because of their constant battle with the sea and their great success in extending and eventually building up the surface of the land adjacent to the sea in subtropical and tropical climes." Indeed, as discussed by numerous authors (e.g., Tomlinson 1986; Odum and McIvor 1990; Costanza et al. 1997; Chivian and Bernstein 2008; Polidoro et al. 2010; and Cavanaugh et al. 2014) important ecological services provided by mangroves include: serving as home and/or nurseries for numerous marine and terrestrial organisms (e.g., fish, mammals, birds, crustaceans, worms, and insects), protecting coastlines from storm surges (e.g., buffering wave action, preventing flooding and soil erosion, and decreasing saltwater invasion), waste treatment (e.g., nutrient recycling and pollution control), carbon sequestration, and recreation (e.g., eco-tourism and sport fishing). The value of ecosystem services provided by mangrove communities worldwide has been estimated to be at least US $1.6 billion annually (Polidoro et al. 2010). The ecological and economic importance of mangroves, among which several species of *Avicennia* are noteworthy by their abundance and widespread distribution, will only increase with both growth of human populations in coastal areas and sea-level changes associated with climate alterations due to global warming.

Estimates for recent degradation and loss of mangrove vegetation worldwide is significant. Between 20 and 35 percent of mangrove habitats have been lost since about 1980, and the current rate of annual disappearance of this vegetation is estimated to be between one and eight percent (Polidoro et al. 2010). The loss of mangrove communities in Mexico has been estimated as from 15,000 sq. km. in the 1970s to ca. 5,000 sq. km. by the late 1990s (Spalding et al. 1997). Major anthropogenic threats to mangrove communities include coastal development (e.g., tourist/resident infrastructure, mariculture, agriculture, and conversion for harbor/industrial uses), pollution (e.g., sewage effluents, oil spills, and agricultural/industrial/urban runoff), fresh water diversions, and sea level changes due to global warming (e.g., Cintrón M. and Schaeffer N. 1992). For the North American and Neotropical regions, distribution models under future climate scenarios (e.g., Cerón S. et al. 2015) predict a pole-ward shift for mangroves (including *Avicennia germinans*), an overall contraction of species distributions, and a decline in species richness.

This regional taxonomic study used data from more than 650 specimens from North America and Mesoamerica (southern Mexico and Central America) in 22 herbaria to formulate descriptions of species, reproductive phenological periods, distributions, habitats, and other pertinent information. In the few instances where only an image of a specimen was studied, this is noted by "-image!" Pollen from each species was examined with scanning electron microscopy and characterized using terminology of Walker and Doyle (1975). Local names noted herein were obtained from herbarium specimens studied. Many additional local names and uses for these species can be found among references in the literature cited.

Avicennia L., Sp. Pl. 1: 110. 1753; Gen. Pl. ed. 5, 49. 1754. **Type.**— *Avicennia officinalis* L.

Bontia L., Sp. Pl. 2: 638 ("938"). 1753. **Type.**— *Bontia daphnoides* L.
Upata Adanson, Fam. 2: 201. 1763. ≡ *Avicennia* L.
Sceura Forssk., Fl. Aegypt.-Arab. 37. 1775. **Type.**— *Sceura marina* Forssk.
Halodendrum Thouars, Gen. Nov. Madagasc. 8. 1806. **Type.**— *Halodendrum thouarsii* Roem. & Schult.
Hilairanthus Tiegh., J. Bot. (Morot) 12: 358. 1898. **Type.**— Not designated (two species cited).

Shrubs or trees lacking cystoliths and with erect, aerial, and sometimes branched roots (pneumatophores) up to 4 dm tall under and beyond canopy (and infrequently also with aerial stilt roots), cystoliths absent. Leaves opposite, leathery, entire, margin flat to revolute. Inflorescence of axillary and/or terminal dense (sometimes subcapitate) pedunculate dichasiate spikes or panicles of dichasiate spikes; dichasia opposite, 1-flowered, sessile. Bracts ± leathery, concavoconvex. Bracteoles concavoconvex. Flowers sessile, protandrous. Calyx 5-lobed, lobes ± free, concavoconvex, imbricate, equal to subequal in size. Corollas white to yellow to orange, tube expanded distally, shorter than limb, limb 2-labiate or actinomorphic, 4- or 5-lobed, lobes erect to reflexed, oblong to obovate, contorted (left contort aestivation) in bud. Stamens 4, at least 2 exserted from mouth of corolla (in ours), oriented in pairs below upper lip of corolla or oriented symmetrically around corolla with each equally distant from the others; anthers 2-thecous, thecae of a pair ± equally inserted, parallel, ± equal in size, lacking basal appendages, each dehiscing toward lower lip (i.e., flower nototribic) or toward each other (i.e., flower pleurotribic) by a longitudinal slit; pollen suboblate to euprolate, 3-colporate, exine reticulate; staminodes 0. Style not evident or elongating with age of flower; stigma 2-lobed, lobes slightly unequal. Capsule podlike, leathery, ± ellipsoid to ovoid (often asymmetric), ± compressed, unilocular, retinacula absent, dehiscence not explosive, usually occurring at time of detachment or soon after being shed. Seed 1 (–2) per capsule, filling fruit and consisting mostly of ripe embryo with 2 conspicuous folded cotyledons and a pubescent radicle (cryptoviviparous).

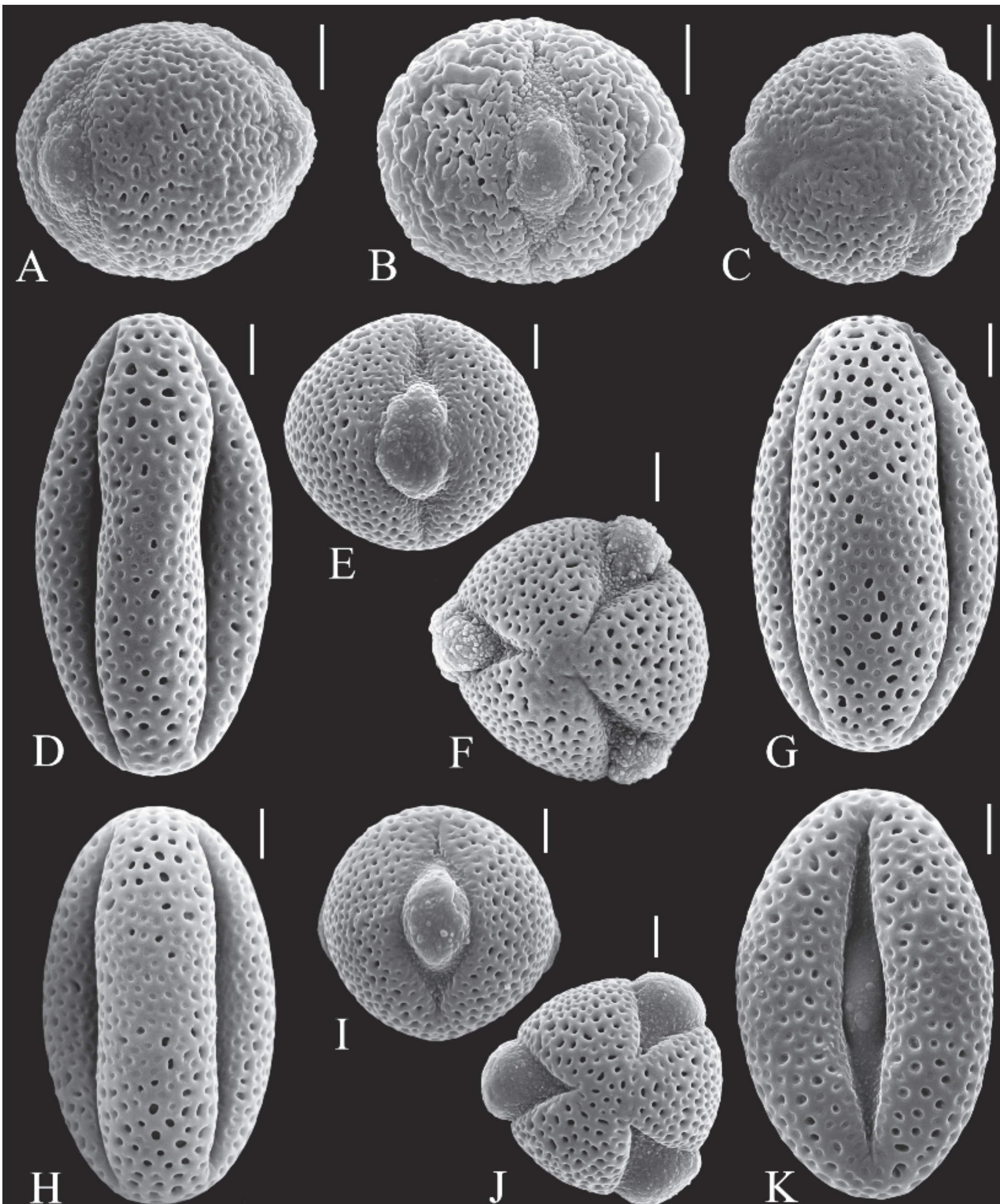
Moldenke (1960, 1973) and Duke (1991) listed additional generic synonyms.

The generic name is derived from Ibn Sina (=Avicenna), 980–1037, a Persian physician, philosopher, and naturalist.

At least eight (e.g., Duke 1991; Duke et al. 1998) species of *Avicennia* are recognized in maritime regions of the tropics and subtropics worldwide. The genus is monophyletic, and includes some of the most prominent and widely distributed “true” mangroves (cf. Tomlinson 1986). Plants occur along shorelines and in tidally influenced waterways in two mostly tropical regions: Atlantic/Caribbean/eastern Pacific (3 spp.) and Indo-western Pacific (5 spp.). Although elevations up to 150 meters have been noted on herbarium labels of American plants, occurrences at elevations much above sea level would appear to be exceptional (if accurately reported) or more likely erroneous. Leaves of *Avicennia* accumulate an external crystalline layer of excreted salt between rains. Three types of major roots are evident on plants: cable roots, anchoring roots, and pneumatophores. Cable roots extend up to several meters horizontally underground from the base of the trunk and give rise to downward growing anchoring roots and upward growing pneumatophores. At least the cable and anchoring roots also give rise to finer roots within the substrate. Pneumatophores (aerial, pencil-like roots that are evident at least at low tide and that facilitate the uptake of atmospheric oxygen) and cryptoviviparous seeds (in which the embryo swells and breaks through the seed coat, but not through the fruit wall, prior to the fruit falling from the plant) are characteristic of the genus. Macromorphological variation among several species of *Avicennia* is extensive, and often has been used in taxonomic circumscriptions. It has been shown that habitat conditions (e.g., variations in salinity and topographic position) and geography can correlate with morphology of the habit, leaves, and/or flowers (Sherrod and McMillan 1985; Duke 1991; Turner et al. 1995). Based on limited sampling (Fig. 1), pollen shape varies from suboblate to euprolate (i.e., with polar diameter:equatorial diameter [P:E] from 0.86 to 1.90). Much of this variation is evident within a single sample (i.e., *Salywon 1188* for *A. germinans*) and probably represents harmomegathic variation.

Key to the Native and Naturalized Species of *Avicennia* in North America and Mesoamerica

1a. Flower actinomorphic; corolla yellowish to orangish, upper lip entire or bifid with the division to 0.2 mm long, the four corolla lobes ovate-triangular to ovate-elliptic; stamens inserted in distal half of corolla tube near base of lobes, oriented equally distant from each other and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dehiscing toward the central gynoecium, 1.5–2 mm long, filaments 0.5–0.8 mm long; naturalized in southern California. . . . . *A. marina* subsp. *australasica*

1b. Flower ± 2-labiate; corolla white to cream (often with yellow in throat), upper lip bifid to 2-parted with the division to 3 mm long, the 4–5 lobes oblong to obovate; stamens inserted at midpoint or in proximal half of corolla tube, oriented in pairs adjacent to upper lip of corolla and dehiscing toward lower lip, 2–5 mm long, filaments 1.5–4 mm long; native in southeastern U.S.A., Mexico, and Central America 2

2a. Internodes of young stems glabrous; 1-flowered dichasia ± evenly distributed along rachis, internodes near midspike 3.5–7 (–9) mm long, rachis clearly visible; internal surface of corolla lobes glabrous; 2 stamens exserted from mouth of corolla and 2 stamens included in corolla tube (or only partly exserted from it); style not evident after corolla dehisces; capsule blackish when dry . . . . *A. bicolor*

2b. Internodes of young stems usually scurfy with shiny whitish trichome- or scale-like projections to 0.05 mm long; 1-flowered dichasia congested at or toward apex of rachis (± headlike), internodes near midspike mostly 0.8–4 mm long, rachis not or barely or only partially visible; internal surface of corolla lobes densely pubescent (at least in distal half); all 4 stamens exserted from mouth of corolla; style usually conspicuous after (and often before) corolla dehisces; capsule usually grayish when dry . . . . *A. germinans*

1. *Avicennia bicolor* Standl., J. Wash. Acad. Sci. 13: 354. 1923. **Type.**— PANAMA: **Coclé**: Aguadulce, outskirts of tidal belt, 5 XII 1911, *H. Pittier 4968* (holotype: US!; isotypes: F-image!, K-image!, BM! NY! P! US!).
Figures 1A–C, 2, 3D.

Shrubs to 3 m tall or trees to 10 (–23) m tall. Young stems of reproductive shoots glabrous (trichomes sometimes persisting around leaf scars, but internodes glabrous). Leaves petiolate, blades ovate to elliptic to broadly elliptic (to obovate), 62–175 mm long, 31–86 mm wide, length:width = 1.2–2.6, (emarginate to) rounded to subacute at apex, rounded to acute to subattenuate at base, surfaces often conspicuously discolorous (abaxial surface lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer that sometimes includes longer ± appressed eglandular trichomes. Inflorescence of axillary (from distalmost leaves) and terminal pedunculate panicles of elongate spikes, panicles ± open, to 115 mm long (including peduncle and excluding corollas) and to 120 mm wide, peduncles 25–40 mm long, glabrous or distally becoming pubescent like branches and rachises, panicle branches subtended by triangular-concave inflorescence bracts (sometimes caducous) 1–3 mm long, pubescent like rachises, fertile portion of spike 12–35 mm long, rachises clearly visible, internodes near midspike 3.5–7 (–9) mm long, densely pubescent with minute (< 0.05 mm long)

Figure 1 (left). Pollen of *Avicennia* spp. A–C. *Avicennia bicolor* (*Sediles 461*). A. Interapertural view. B. Apertural view. C. Polar view. D–G. *Avicennia germinans* (D, *Palmer 484*; E–G, *Salywon 1188*). D. Interapertural view. E. Apertural view. F. Polar view. G. Interapertural view. H–K. *Avicennia marina* subsp. *australasica* (*Moran 28024*). H. Interapertural view. I. Apertural view. J. Polar view. K. Apertural view. Scales = 5 µm.

Pollen measurements (n = number of grains measured, P = polar diameter, and E = equatorial diameter). Many additional grains from each specimen were examined, but data summarized below were made on a subset of those oriented to permit accurate measurements and photographic documentation.

Avicennia bicolor — Sediles 461 (CAS, n = 5): P = 19–22 µm, E = 19–24 µm, P:E = 0.86–0.92.

Avicennia germinans — Daniel & Araque 9478 (CAS, n = 2): P = 23 µm, E = 24–25 µm, P:E = 0.92; *de Nevers et al. 6554* (CAS, n = 2): P = 25 µm, E = 26–28 µm, P:E = 0.89; *Palmer 484* (CAS, n = 1): P = 46 µm, E = 24 µm, P:E = 1.90; *Salywon 1188* (CAS, n =4): P = 27–42 µm, E = 24–29 µm, P:E = 0.93–1.75.

Avicennia marina subsp. *australasica — Moran 28024* (CAS, n = 4): P = 28–41 µm, E = 24–27 µm, P:E = 1.04–1.70.

glandular trichomes and with antrorse (to flexuose) eglandular trichomes to 0.1 mm long. Bracts triangular-ovate to subcircular, 1–2.3 mm long, abaxially pubescent like rachis. Bracteoles similar to bracts. Flowers mostly 8–10 per spike (but up to 22 per spike). Calyx 2–4 mm long, lobes broadly ovate to subcircular, abaxially pubescent like rachis. Corollas 4.5–7 mm long, internally white to cream, externally glabrous (proximal 2/3 of tube) and densely pubescent with appressed eglandular trichomes to 0.2 mm long (distal 1/3 of tube and limb), tube 2–2.5 mm long, limb ± 2-labiate with 4–5 lobes, upper lip apically 2-parted (with division up to 2 mm long) and/or wider than lobes of lower lip, all lobes oblong to obovate, glabrous internally, 3–4.5 mm long. Stamens 4, inserted at midpoint or in proximal half of corolla tube, 2 exserted from mouth of corolla tube and 2 included in or only partially exserted from corolla tube, oriented in pairs near upper lip of corolla with thecae opening toward lower lip, 2–2.5 mm long, filaments 1.5–2 mm long, anthers presented at 2 heights, thecae 0.3–0.6 mm long; pollen suboblate to oblate spheroidal, polar diameter (P) 19–22 µm, equatorial diameter (E) 19–24 µm, P:E = 0.86–0.92. Style not evident, stigma lobes 0.2–0.4 mm long. Fruit greenish yellow, black when dry, ovoid to ellipsoid, 15–29 mm long, 7–17 mm wide, ± sparsely pubescent with antrorsely appressed eglandular trichomes to 1 mm long, these sometimes more or only evident distally on mature fruits.

Phenology.— Flowering: September–May; fruiting: February–August.

Distribution and habitats.— Pacific coast of southern Mexico (Chiapas, ca. lat. 16°02′26″N), Central America, to southern Panama (Los Santos and Darién, ca. lat. 7.98°N; Fig. 2); plants occur along and near shorelines in coastal mangrove swamps (mangals) and salt marshes at elevations at or near sea level. In addition to the provinces and departments of Central American nations from which specimens have been examined (noted below), this species potentially also occurs or occurred in the following Pacific coastal political units: Guatemala (Escuintla, Jutiapa, Retalhuleu, San Marcos, Santa Rosa, Suchitepequez), El Salvador (La Libertad, La Paz, La Unión, San Miguel, San Vicente, Sonsonate, Usulután), Nicaragua (Carazo, Managua), and Panama (Chiriquí, Veraguas). Gibson (1970) included *Avicennia bicolor* Standl. in her account of the Guatemalan taxa because of its expected occurrence in the country. Although it undoubtedly occurred or still occurs there, the species has yet to be collected in Guatemala.

The southernmost occurrence of *Avicennia bicolor* has been attributed to the Pacific coast of Colombia (e.g., Sanders 1997; Duke 2010; Aymard 2015). The sole collection cited by Aymard (2015; *Forero & Gentry 794* at COL) and another Colombian collection identified as this species (*Gentry & Juncosa 41115* at COL), both appear to pertain to *A. germinans* based on images of these collections supplied by COL. Unless other collections that conform to *A. bicolor* have been made in Colombia, the southern extent of this species appears to be in Panama at ca. 7.98°N, on both sides of the Gulf of Panama (i.e., in the provinces of Los Santos [*Dwyer 5079A*] and Darién [*Duke 5488*]).

Local names.— "Madre sal" (*DeRiemer s.n.*); "madresal prieto" (*Santamaría D. & Romero B. 1a*); "palo de sal" (*Sediles 457*); "palo de sal hoja ancha" (*Sediles 455, 460*).

Conservation status.— The extent of occurrence (EOO) of *Avicennia bicolor* is 262,479 km^2, although a major portion of that area consists of open ocean and inhospitable upland habitats. The species has been assessed as VU (vulnerable) by the IUCN (Duke 2010) based on a documented continuing decline in population under criterion A.

Discussion.— This species is readily recognized by the combination of its glabrous young stems, relatively remote dichasia in the inflorescence (Fig. 3C), bilaterally symmetric flowers with internally glabrous corolla lobes, and black fruits (when dry; Fig. 3D).

The Mexican occurrence of this species has sometimes been overlooked (e.g., Breedlove 1986; Spalding et al. 1997) or minimized (e.g., treated as a synonym of *A. germinans* for practical pur-

FIGURE 2. Map showing distribution of *Avicennia* spp. in North America and Mesoamerica. The generalized distribution of *A. germinans* is shown. The distribution of *A. germinans* in Cuba and other West Indian islands is not shown.

poses; López P. and Ezcurra 2002). Throughout its distributional range it often grows with *A. germinans* (e.g., *Pittier 4968*, the type, grows with *Pitier 4969*, a collection of *A. germinans* from the same locale). Rabinowitz (1978) noted that where these species are sympatric there is apparently no zonation between them. Like those of *A. germinans*, flowers of *A. bicolor* have been noted to be fragrant (e.g., *Knapp 1244*). Corollas are usually described by collectors as white to cream; they are sometimes noted to have a yellow throat (like *A. germinans*; e.g., Borg and Schöenenberger 2011). *Williams 78* from Panama shows exceptionally long and floriferous inflorescences with the fertile portion of spikes to 65 mm long and with up to 22 flowers (vs. usually 4–8) per spike.

Tomlinson (1986) treated *A. tonduzii* as a synonym of *A. bicolor*, and others have followed his influential taxonomic account (e.g., Aymard 2015). In his key to species of *Avicennia* and description of *A. bicolor*, Tomlinson indicated that corollas of this species were conspicuously pubescent within (as they are on the type of *A. tonduzii*, but not on the type of *A. bicolor*). Distinctions, if any, between *A. tonduzii* and *A. germinans* are not readily apparent, and others have treated these names as synonymous. Additional information about *A. tonduzii* is provided below under *A. germinans*.

ADDITIONAL SPECIMENS EXAMINED.— COSTA RICA. **Guanacaste**: Nandayura, Península de Nicoya, Playa Bejuco, 09°49′56″N, 085°20′34″W, *A. Fernández 1762* (MO); Abangares, Cuenca del Abangares, San Buenaventura, 10°10′29.8253″N, 085°09′31.4524″W, *L. González & A. Garita 3909* (MO); Tamarindo, Playa Tamarindo, 10°18′N, 085°51′W, *W. Haber & W. Zuchowski 8961* (F, MO); Port Parker, *J. Howell 10242* (CAS); Refugio Silv. Tamarindo, Estero Tamarindo, Santa

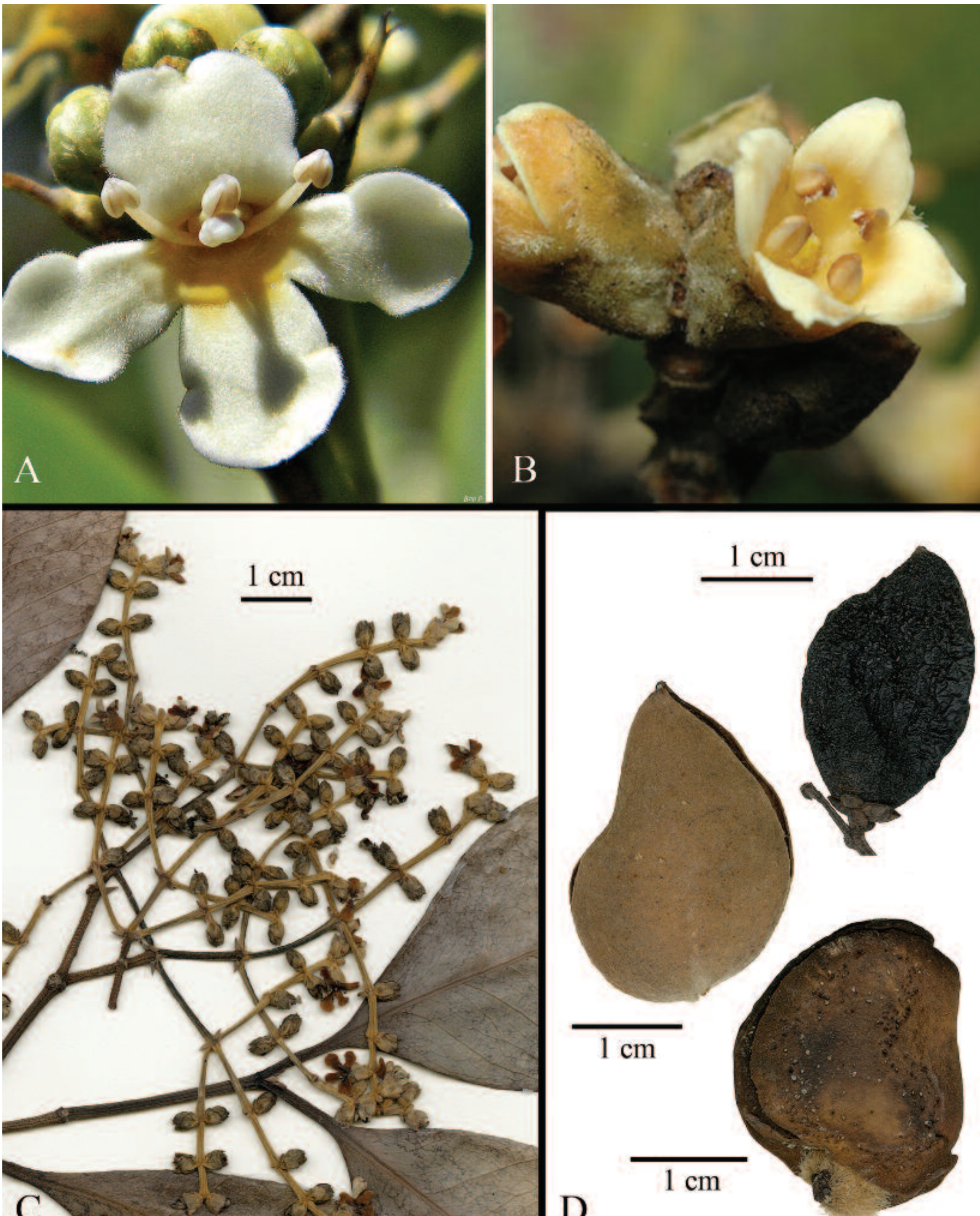

FIGURE 3. *Avicennia* spp. A. Flower of *A. germinans* in Florida (photo by Bob Peterson, cropped, creative commons license, <*https://www.flickr.com/photos/pondapple/7270558948/in/photostream*>). B Flower of *A. marina* subsp. *australasica* in Australia (photo by M. Fagg, cropped, source: Australian National Botanic Gardens at <*http://www.anbg.gov.au/photo*>). C. Inflorescence of *A. biflora* (*Sediles 461*, CAS). D. Fruits of *A. bicolor* (top; *Barrera 8*, CAS), *A. germinans* showing dehiscence (middle; *Ferris 5396*, DS), and *A. marina* subsp. *australasica* (bottom; *Nickerson 6445a* from New Zealand, CAS).

Cruz, 10°19′40″N, 85°49′20″W, *Q. Jiménez 859* (K, MO); P.N. Santa Rosa, Cantón de La Cruz, Península de Santa Elena, Estero Grande, 10°54′59″N, 085°47′03″W, *J. Morales 4142* (F, MO); P.N. Santa Rosa, Playa Naranjo, 10°47′53″N, 085°40′44″W, *J. Morales et al. 1262* (F); Puerto Jesús, *R. Pohl & G. Davidse 10588A* (F, MO, US); Cantón La Cruz, P.N. Santa Rosa, Peninsula de Santa Elena, Murciélago, 10°55′20″N, 85°44′15″W, *F. Quesada 84* (K, MO); P.N. Santa Rosa, Playa Naranjo, *N. Zamora et al. 1140* (F, MO). **Puntarenas**: Golfo de Nicoya Externo, Isla San Lucas, Punta Cañón, *J. Morales & D. Santamaria 12387* (MO); Garabito, Cuenca del Jesús María, Garabito, alrededores de Playa Punta Loros, 09°51′26.3900″N, 084°41′29.8110″W, *A. Rodríguez & V. Ramírez 6688* (MO).

El Salvador. **Ahuachapán**: without locale, *Padilla 333* (US); Las Salinas, *K. DeRiemer 1625* (US), *1626* (US); Las Chacaras, en La Barra de Santiago, *K. DeRiemer s.n.* (US).

Honduras. **Choluteca**: Playas de Cedeño, *F. Padilla 101* (BM). **Valle**: Puerto Soto, 12 km from El Tular, *A. Molina R. 21457* (BM, NY, UC, US); Puerto Soto, 15 km WSW de San Lorenzo, *C. Nelson 1323* (MO).

Mexico. **Chiapas**: Paderón, Tonala, *E. Matuda 16353* (US); Mpio. Pijijiápan, Estero San José, 15°43′39.50″N, 093°29′50.20″W, *S. Santamaría-Damián & E. Romero-Berny 1a* (MEXU), *1b* (MEXU).

Nicaragua. **Chinandega**: Mpio. El Viejo, Reserva Natural de Cosigüina, San Remigio entre El Congo y Bella Vista, 13°01′N, 097°35′W, *I. Coronado G. & R. Rueda 3626* (MEXU, MO); Mpio. Puerto Morazán, de Morazán hasta 5 km en dirección Ttonalá, 12°49′N, 087°09′W, *R. Rueda et al. 17322* (MEXU, MO). **León**: Isla del Venado, 3.3 km de Las Peñitas, *Barrera 8* (CAS); Las Peñitas, Isla Juan Venado, 12°13′N, 086°53′W, *I. Coronado G. & R. Rueda 4943* (MO); Las Peñitas, Isla Juan Venado, 12°17′N, 086°53′W, *I. Coronado G. et al. 6979* (MO); Isla del Venado, 8.2 km de Las Peñitas, 60 m del Estero Las Peñitas, *Sediles 445* (NY), *456* (NY); 3.3 km de Las Peñitas, Isla del Venado, *Sediles 454* (MO), *459* (MO), *461* (CAS); 3 km de Las Peñitas, en la Isla del Venado, *Sediles 455* (F), *460* (K); 8.1 km de Las Peñitas, en la Isla del Venado, 60 m del Estero Las Peñitas, *Sediles 457* (P); 8.3 km del Las Peñitas, en la Isla del Venado, 80 m del Estero Las Peñitas, *Sediles 458* (US). **Rivas**: “Marsella,” 11°16–17′N, 85°52–53′W, *M. Araquistain 3828* (MO, P); San Juan del Sur, entre Las Playas de Marsella y Rivas, 11°17′N, 085°54′W, *R. Rueda et al. 1435* (MO).

Panama. **Coclé**: ca. 2 km del Puerto, camino entre el puerto de Aguadulce hasta el pueblo, *M. Correa A. 4314* (MO); Isla del Pozo, salinas of Río Estero Salado, 08°11′N, 080°30′W, *S. Knapp et al. 3401* (MEXU, MO); below Aguadulce, *E. Tyson 7262* (FSU, MO). **Darién**: ca. 10 mi S of El Real on Río Pirre, *J. Duke 5488* (MO). **Herrera**: Cienega El Mangle, NE of Paris, *S. McDaniel 8020* (FSU, MO). **Los Santos**: Monagre Beach, *J. Dwyer 5079A* (MO). **Panamá**: Isla Casaya, J. Duke 10372 (MO); San José Island, ca. 55 mi SSE of Balboa, Playa Grande, *I. Johnston 1259* (DUKE, MO, P, US); Porto Posada, *R. Williams 78* (NY). **Panamá Oeste**: Punta Chame, *W. D’Arcy 10241* (MO); Punta Chame, 10–15 mi from Pan American Hwy., 08°40′N, 079°45′W, *S. Knapp 1244* (MEXU, MO).

2. *Avicennia germinans* (L.) L., Sp. Pl., ed. 3, 2: 891. 1764. *Bontia germinans* L., Syst. Nat., ed. 10, 2: 1122. 1759. **Type**.— “Habitat in Indiis” [JAMAICA], *P. Browne s.n.*, LINN Herb. No. 813.2 (lectotype, designated by Stearn [1958: 35]: LINN-image!).
Figures 1D–G, 2, 3A,D.

Avicennia nitida Jacq., Enum. Syst. Pl. 25. 1760. *Avicennia officinalis* var. *nitida* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 502. 1891. *Hilairanthus nitidus* (Jacq.) Tiegh, J. Bot. (Morot) 12: 358. 1898. **Type**.— See discussion.

Avicennia tomentosa Jacq., Enum. Syst. Pl. 25. 1760. *Hilairanthus tomentosus* (Jacq.) Tiegh, J. Bot. (Morot) 12: 358. 1898. **Type.**— See discussion.

Avicennia tomentosa Jacq. var. *campechensis* Kunth, Nov. Gen. Sp. 2: 229 (ed. folio); 284 (ed. quarto). 1818 ("1817"). **Type.**— MEXICO. **Campeche**: "Crescit prope Campeche Mexicanorum," *F. Humboldt & A. Bonpland s.n.* (holotype: P-P00670135-image!).

Avicennia floridana Raf., Atlantic J. 1: 148. 1832. **Type.**— Not designated (no specimens cited).

Avicennia floridana Gand., Bull. Soc. Bot. France 65: 64. 1918, nomen illegit. **Type.**— U.S.A. **Florida**: Lee County, Fort Meyers, *A. Hitchcock 270* (see discussion).

Avicennia oblongifolia Chapm., Fl. South. U.S. 310. 1860. **Type.**— U.S.A. **Florida**: Monroe County, Oct, Key West (fide protologue); pertinent specimens, if extant, would likely be in the Chapman herbarium at NY, but none have been located.

Avicennia tonduzii Moldenke, Phytologia 1: 273. 1938. **Type.**— COSTA RICA. **Puntarenas**: Punta Mala [ca. 09°03′54.48″N, 083°39′04.84″W], zone littorale du Pacifique, Mar 1892, *A. Tonduz 6776* (holotype: BR-image!, fragment of holotype at NY!; isotypes: BM-image!, M-image!, MICH-image!, US!).

Shrubs to 5 m tall or trees to 20 (–25) m tall. Young stems of reproductive shoots covered with dense ± antrorsely appressed or matted whitish and shiny trichomelike or scalelike projections to 0.05 mm long (scurfy) and sometimes also with longer appressed eglandular trichomes, the internodes infrequently glabrate. Leaves petiolate, blades narrowly to broadly elliptic (to obovate), 25–160 (–185) mm long, 11–50 (–63) mm wide, (1.6–) 2.7–6.9 × longer than wide, acute to rounded to emarginate at apex, acute to subattenuate at base, surfaces often conspicuously discolorous (abaxial surface lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer that includes ± appressed longer eglandular trichomes or sparsely to densely scurfy without longer trichomes. Inflorescences of axillary and terminal pedunculate densely bracteate (± headlike) spikes or panicles of these, inflorescence branches (if present) subtended by triangular- to oblate- to subovate-concave inflorescence bracts to 5 mm long (sometimes caducous), peduncles (5–) 10–50 mm long, scurfy, pairs of flowers congested at or toward apex of rachis, inflorescence internodes mostly 0.8–4 mm long near midspike, rachis not or only partially or barely visible, densely pubescent with mostly antrorse eglandular trichomes to 0.2 mm long. Bracts triangular to oblate to broadly ovate to subcircular, 1–4 mm long, abaxial surface scurfy to pubescent like rachis. Bracteoles similar to bracts. Flowers 8–14 (–26) per spike. Calyx 2–4 mm long, lobes broadly ovate to subcircular, abaxially pubescent with antrorsely appressed eglandular trichomes to 0.4 mm long. Corollas (3.5–) 4–8 mm long, internally white to cream with yellow in throat, externally glabrous (proximal portion of tube) and densely pubescent with appressed eglandular trichomes to 0.5 mm long (distal portion of tube and limb), tube (1.5–) 2–3.5 mm long, limb ± 2-labiate with 4 or 5 lobes, upper lip bifid to ± conspicuously 2-parted at apex (with division up to 3 mm long) and/or wider than lobes of lower lip, all lobes oblong to obovate, densely pubescent (at least on distal half if not throughout) internally. Stamens 4, inserted at midpoint or in proximal half of corolla tube, exserted from mouth of corolla tube, oriented in pairs near upper lip of corolla with thecae opening toward lower lip, 3–5 mm long, filaments 2.2–4 mm long, anthers presented at ± same height, thecae 0.6–1 mm long; pollen oblate spheroidal to euprolate, polar diameter (P) 23–46 µm, equatorial diameter (E) 24–29 µm, P:E = 0.92–1.90. Stigma lobes (0.2–) 0.4–0.7 mm long. Fruit ovoid to broadly elliptic to obovoid, usually grayish (rarely black) when dry, 12–32 mm long, 9–25 mm across at widest expanse, pubescent with antrorsely appressed eglandular trichomes to 0.7 mm long (especially when less mature) and scurfy (especially when more mature).

Phenology.— Flowering: throughout the year; fruiting: April–January (especially in August, and likely throughout the year).

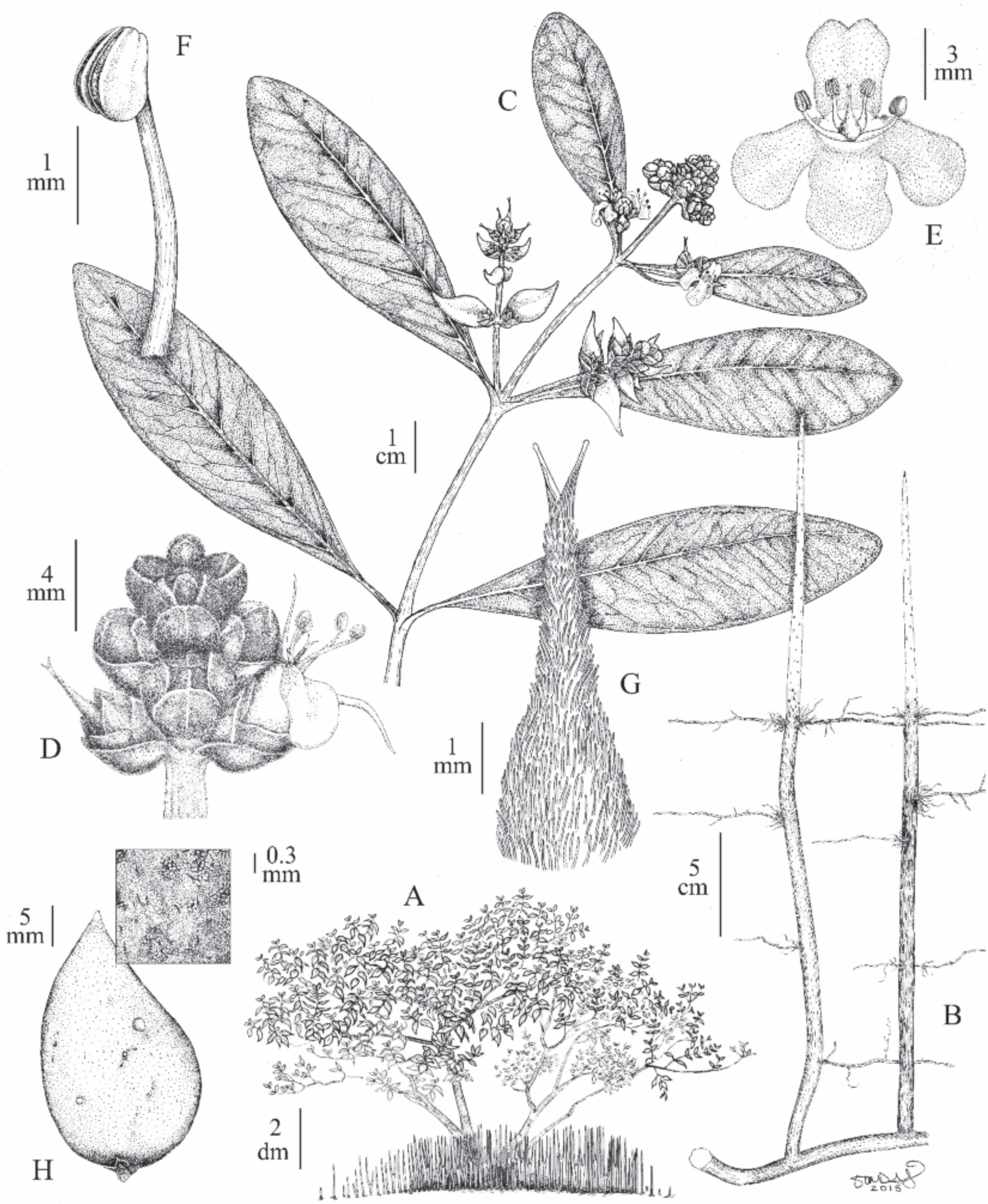

FIGURE 4. *Avicennia germinans*. A. Habit (composite from photos of living plants). B. Pneumatophore (*Schwartz & Nickerson 9119*). C. Fertile shoot (*Calzada 434*, *Pipoly 9034*, *Sousa 3112*). D. Inflorescence with flower in profile (*Lakela 29824*, *Sousa 3112*). E. Flower, front-view (*Lakela 29824*, *Sousa 3112*). F. Stamen (*Sousa 3112*). G. Gynoecium (*Lakela 29824*). H. Fruit with detail of surface (*Lundell 7009*). Drawn by Tom Davis from specimens at CAS.

Distribution and habitats.— Southern North America (southeastern USA and Mexico), Bermuda, West Indies, Central America, South America (Brazil, Colombia, Ecuador [including Galapagos Islands], French Guiana, Guyana, Peru, Surinam, and Venezuela), and tropical western Africa (see Daniel and Figuerido [2009] for distributional information on African plants, which often have been referred to as *A. africana* P. Beauv.). Figure 2 shows the generalized distribution of this species in North America and Mesoamerica. Plants occur in/on tidal flats, beaches, coastal mangrove swamps (mangals), salt marshes, sand dunes, and coastal grasslands and savannas at elevations at or near sea level. Common associates include *Allenrolfea occidentalis*, *Batis maritima*, *Bravaisia berlandieriana, Coccoloba uvifera*, *Conocarpus erectus*, *Distichlis litoralis*, *D. spicata*, *Echinochloa polystachia*, *Frankenia palmeri*, *Laguncularia racemosa*, *Maytenus phyllanthoides*, *Rhizophora mangle*, *Salicornia biguelovii*, *S. virginica*, *Scaevola plumieri*, and *Spartina alterniflora*.

Avicennia germinans is the most widely distributed species of *Avicennia* in the New World. Its northern distributional limit there is in Bermuda (ca. 32°20′N; Lacerda et al. 2002), where another true mangrove, *Rhizophora mangle* L. also attains the northern extent of its distribution; these occurrences are the northernmost of true mangroves. The northernmost occurrence of *A. germinans* on the Atlantic Coast of North America is in northern Florida (St. Johns County, 30°06.618′N, 081°22.303′W, *Williams & Eastman s.n.* at USF). On the coast of the Gulf of Mexico the northern extent of the species extends as far as the Bay St. Louis, Mississippi (Hancock or Harrison county, ca. 30°2′N, *Sanger s.n.* at NY).

Of the three true mangroves that are common on the American mainland (*A. germinans*, *Laguncularia racemosa*, and *Rizophora mangle*) *A. germinans* is the northernmost in distribution. Its northern limit in North America appears to be determined by the frequency and duration of subfreezing temperatures, which can kill the above-water parts of the plants or cause mortality (Sherrod and McMillan 1985; Cavanaugh et al. 2014). Tomlinson (1986) noted a close correlation of the limits of the distributions of mangroves with the 24° isotherm of sea surface temperatures. A decade later Rützler and Feller (1996) indicated that like corals, mangroves cannot survive where an average water temperature falls below about 23°C. In recent decades, freeze-free winters have led to an expansion of *A. germinans* into salt marshes at the northern extremes of its range in the southern United States (Guo et al. 2013). A poleward expansion of the distributional range of *A. germinans* in southern North America, likely correlated with warmer winter temperatures and less extreme freezes, was recently noted by Cavanaugh et al. (2014).

In the United States, plants have been documented from most of the coastal counties in Florida (except for most of those in the panhandle on the Gulf Coast in the northwestern portion of the state), rarely reported from at least two of the three coastal counties in Mississippi (e.g., Moldenke 1960; Scheffel et al. 2014; the locality cited for Mississippi by Lowe in 1921, Door Point, is in Louisiana), and documented from seven coastal parishes in Louisiana. In Texas the species has been collected along the Gulf Coast from Jefferson County near the Louisiana border intermittently southward to Cameron County on the Mexican border. Although it likely occurs (or occurred) in all coastal counties of Texas, based on specimens noted below and in literature reports (Turner et al. 2003 and pers. comm. in 2010 from updated but unpublished maps; Rosen and Zamirpour 2014), it has been collected in Aransas, Brazoria, Calhoun, Cameron, Galveston, Jackson, Jefferson, Kleberg, Nueces, Refugio, San Patricio, and Willacy counties. Sherrod and McMillian (1981, 1985) discussed the distributional history of mangroves, including *A. germinans*, in Texas and in the northern Gulf of Mexico. The species has not been reported from the Gulf coast of Alabama (e.g., Kral et al. 2011).

Avicennia germinans is known from all 16 coastal states of Mexico (occurring along the Gulf of Mexico, Caribbean Sea, Pacific Ocean, and Gulf of California). The species reaches its northern extent in western Mexico along the Gulf of California in Sonora (Puerto Lobos, lat. 30°15′N; Felger et al. 2001) and its northern extent on the Pacific coast in Baja California Sur (ca. lat. 26°N; Turner et al. 1995). Distribution along Pacific coast of North America does not extend as far northward as that along the coasts of the Gulf of California, Gulf of Mexico, and the Atlantic Ocean likely because of upwelling of cold waters off the western coast of the peninsula of Baja California and California that limits their northward spread. Turner et al. (1995) discuss the distributions and probable environmental factors effecting them for this species in regions around the Gulf of California.

In Central America to the south of Belize, the extent of mangrove communities and the abundance of *A. germinans* are better developed along the Pacific than the Caribbean coast. Indeed no specimens have been seen from the Caribbean coast of Costa Rica, although *A. germinans* has been reported from the mouth of the Río Moín, north of Puerto Limón (Zamora et al. 2004). In South America, as in North America, *A. germinans* has a broader distribution on the Atlantic than on the Pacific coast. Lacerda et al. (2002) indicated that the southernmost occurrences of *A. germinans* in South America are in northwestern Peru (Río Piúra, ca. 5°32′S) on the Pacific coast and in southeastern Brazil (Atafona, ca. 21°37′S) on the Atlantic coast. Like the northward limit of this species on the Pacific coast of North America, the southern distributional limit of *A. germinans* along the western coast of South America in Peru appears to have a similar cause due to the cold waters of the Humboldt Current and upwelling there (Lacerda et al. 2002).

Illustrations.— Figure 4; see also Hepper (1963: 449, fig. 309); Gibson (1970: 178, fig. 32, which is based on *Standley 87592* at F); Moldenke (1973: 151, fig. 1); Villiers (1973: 65, pl. 16); Correll and Correll (1982: 1253, fig. 540); Nash and Nee 1984: 13, fig. 2); Tomlinson (1986: 189, fig. B.8); Sanders (1997: 83, fig. 1); Proctor (2012: 586, fig. 218).

Nomenclature.— The synonymy provided above is based on types from North America and Central America or names sometimes applied to plants from these regions. Additional synonyms were listed by Moldenke (1960, 1973). Based on information provided by Stearn (1958), authorship of the combination *A. germinans* often has been attributed to "(L.) Stearn" (e.g., Tomlinson 1986; Jarvis 2007; Daniel and Figueiredo 2009). In his letter to D. Ward (17 April 1962 attached to a specimen in FLAS), Stearn indicated that the correct name for the black mangrove is *A. germinans* (L.) L., a case subsequently made by Compère (1963), and now widely accepted.

The lectotype of *Bontia germinans* at LINN also has inflorescence internodes similar to those of *A. bicolor* (i.e., ca. 4–4.5 mm long near midspike). From the image of this specimen, I have not been able to discern other diagnostic characters used here to distinguish these species. Thus, I am unable to confirm to which species it pertains.

Moldenke (1960) noted that the types of *A. nitida* and A. *tomentosa* are both *Herb. Jacquin s.n.* specimens at BM, which he annotated as such in 1936. Images of both of these very sparse specimens have been seen, and based on what is visible and available, they likely conform to *A. germinans*.

Although no specimen was designated as the type of *A. floridana* Gand., Gandoger's herbarium is at LY in France, and it is possible that the holotype is there; specimens of the type number at F, MO, Cornell, NY, and US were cited by Moldenke (1960), but he did not indicate where the holotype was located.

Local names.— "Aili sip" (Kuna; *de Nevers et al. 6554*); "arbol salado" (*Zizumbo & Colunga 500*); "black mangrove" (e.g., *Hammel 105*); "cajiel" (*Zizumbo & Colunga 500*); "istatén" (*J. González & A. Pérez 193*); "kahil" (Huave; *A. Gerardo B. 4*); "madre de sal" (*Rico-Gray & Espejel 305*); "madresal" (*Flores M. 1101*; *García B. 486*); "madre sal" (*Espejo & Hernández 2904*); "mangle de sal" (*Rico-Gray & Espejel 305*); "mangle negro" (*Chazaro B. 3299*, *Penning-*

ton & Sarukhan K. 9131); "mangle prieto" (e.g., *DIAAPROY s.n.*); "mangle pullequi" (*Moran 7151*); "mangle rojo" (*DIAAPROY s.n.*); "mangle salado" (e.g., *Arteaga et al. 130*; *Allen 5631*), "mangle senico" (*Carter 2721*); "palo de sal" (*Elorsa C. 285*); "pipi" (*Salas M. & Torres B. 825*); "puyece" (*Ferris 5396*); "puyeque" (*González O. 1131*; *Mexia 1008*); "saladillo" (*García P. & Estrada L. 1974*; *Magaña 1232*); "sahkab luk'" (*Ucán 431*); and "u najil tikin xiw" (*Tapia M. 1508*).

Uses.— Firewood (*Mexia 1008*; *García B. 486*); construction materials (*García B. 486*); and used by natives for diseases of the throat (*Choussy 1593*). Additional construction, medicinal, and food uses of the species were provided by Moldenke (1960), Burkill (1985), Cheatham et al. (2000), and Alvarez C. (2008).

Conservation.— The black mangrove is a widespread and often an abundant shrub or tree of tropical and subtropical shorelines and near coastal habitats where it is an important (often dominant) constituent of mangrove communities. Its conservation status was assessed as Least Concern (LC) by Ellison et al. (2010).

Discussion.— This species is readily distinguished by the combination of its scurfy young stems, densely spicate (headlike) inflorescences, bilaterally symmetric flowers with internally pubescent corolla lobes (Fig. 3A), styles usually conspicuously elongating near the end of anthesis or shortly thereafter as the fruits begins to form, and the grayish fruits (when dry; Fig. 3D).

Rare individuals from Mexico (e.g., *Martínez s.n.* from Baja California Sur at MEXU; *Rico-Gray 95* from Yucatán at UC) have remote nodes (to 7 mm distant, as in *A. bicolor*) near the midpoint of the spikes, but show their affiliation to *A. germinans* by their internally pubescent corolla lobes, scurfy pubescent young stems, trichomes of the rachis to 0.5 mm long, and thecae 0.8 mm long.

The fragrant flowers of *Avicennia germinans* are commonly visited by honeybees, and they are reputed to be an excellent source of honey. Corollas are often noted to be 10–20 mm long (e.g., Moldenke 1960; Tomlinson 1986). My observations concur with those of Gibson (1970), who indicated that she had seen none more than 8.5 mm in length.

Morphological variation is considerable in this species, especially with respect to habit and leaf size and shape. For example, although it is commonly a sizable tree in portions of its range, *A. germinans* becomes a dwarf shrub at the northern extent of its range in the Gulf of Mexico (Sherrod and McMillan 1985). Moldenke (1960) discussed variation in this species with respect to these and other attributes.

In a letter to Paul Standley dated 19 February 1938 (attached to *Brenes 12222* at F), Moldenke indicated that *A. tonduzii* could be "most easily" distinguished from *A. germinans* (as *A. nitida*) by the size of the flowers. Indeed some of the specimens cited and/or annotated by Moldenke as *A. tonduzii* have calyces (2–2.5 vs. 2–4) and corollas (3.5–5 vs. 4–8) that are shorter than most specimens treated as *A. germinans*. Subsequently, Moldenke (1960, 1973) distinguished *A. tonduzii* from *A. germinans* on the basis of its short (shorter than the stamens) style (vs. style exserted from the calyx when corolla is shed, surpassing the stamens) and leaf blades mostly elongate-oblong, 3–5 times as long as wide (vs. lanceolate or lance-oblong to elliptic or obovate, usually < 3 times as long as wide). Elongate styles are evident on the holotype of *A. tonduzii* at BR (and on isotypes at BR and US). The other putative distinguishing characters of *A. tonduzii* overlap those of *A. germinans* when plants from throughout the ranges of both species are considered. Tomlinson (1986) considered *A. tonduzii* as a narrow-leaved variant of *A. bicolor* and treated the name as synonymous with that species. Others have followed Tomlinson's influential account, and *A. tonduzii* has been recognized as a distinct species in some relatively recent literature (e.g., Lacerda et al. 2002).

In the southern Caribbean region and along the Atlantic coast of South America, the distribution and taxonomy of *A. germinans* become entangled with those of *A. schaueriana* Stapf & Leechman ex Moldenke. Stearn (1958) distinguished *S. schauerana* from *A. germinans* by the characters in the following couplet:

1a. Leaves mostly acute at tip; corolla lobes tomentose on both sides; style elongate . . . . *A. germinans*

1b. Leaves mostly rounded at tip, sometimes acute; corolla lobes glabrous internally, tomentose externally; style very short, the stigma nearly sessile . . . . *A. schaueriana*

Leaf tips are variable in *A. germinans*. While length of the style might be somewhat dependent on floral stage and pollination, it appears likely that styles of *A. schaueriana*, like those of *A. bicolor*, do not elongate (or at least not to the extent) as in *A. germinans*. Like *A. germinans*, *A. schaueriana* has crowded inflorescences, but pubescence of the corolla lobes would appear to be a useful character for distinguishing these species.

Representative materials examined.— **Belize**. **Belize**: St. Johns College, *J. Dwyer & R. Pippin 10030* (MO); shortcut from southern part of Belize City to Western Hwy., *A. Gentry 8560* (F); Belize, *C. Hammel 105* (K); Belize, *C. Lundell 4719* (K); W de Tropical Park, *T. Ramamoorthy et al. 3609* (MEXU); Gale’s Point, just S of Bar River mouth, ca. 17°14′N, 88°18′W, *J. Ratter et al. 6560* (K); Caye Caulker (southern island), South Point, west coast, 17°43′47″N, 088°02′15″W, *J. Rietsema & D. Beveridge 19906* (NY). **Corozal**: ca. 4 km SE of Sarteneja, ca. 18°21′N, 088°07′W, *G. Davidse & A. Brant 32658* (USF); ca. 2 km S of Sarteneja, 0.5 km NE of La Isla, 18°20′19″N, 088°07′25″W, *Z. Goodwin & G. Lopez 1583* (MO). **Stann Creek**: Northeast Cay, *F. Fosberg & D. Stoddart 53854* (US); Man-O’-War Cay, W of Tobacco Cay Range, *F. Fosberg & D. Spellman 54204* (MO, US); North Silk Cay, *F. Fosberg & D. Spellman 54272* (US); Little Water Cay, *F. Fosberg & D. Spellman 54343* (F); Buttonwood Cay, *F. Fosberg & D. Spellman 54421* (US); Scipio Cay, 16°28.135′N–16°28.295′N, 088°17.793′W–88°17.829′W, *D. Lentz et al. 2355* (NY); Long Coco Caye, off Placencia, ca. 16°29.5′N, 88°12.7′W, *D. Lentz et al. 2833* (NY); Dangriga, *G. Proctor 36197* (MO); All Pines, [16°47′00″N, 88°19′00″W], *W. Schipp 625* (UC); South Water Cay, *Spellman & Stoddart 2157* (US); Seal Cay, *Spellman & Stoddart 2481* (MO); Rendezvous Cay, *Spellman & Stoddart 2498* (MO, US); Coco Plum Cay, *Spellman & Stoddart 2567* (MO, US); 4.5 km S of Southern Highway turnoff, *D. Stevenson 1132* (K). **Toledo**: W of beach road, Punto Gorda, *J. Dwyer et al. 631* (MO).

Costa Rica. **Guanacaste**: vicinity of Playa Naranjo in P.N. Santa Rosa, *F. Almeda et al. 4205* (CAS); Playa de Coco, *R. Blaisdell 300* (FSU); P.N. Palo Verde, Valle de Tempisque, Estación Catalina, Laguna Nicaragua, 10°21′10″N, 085°13′00″W, *U. Chavarría 1243* (F); Puerto Jesús, Nicoya, *O. Cook & C. Doyle 743* (US); ca. 1 km E of Río Tempisque ferry, *G. Crow 6116* (F); between Playa Comchal and Playa Brasilito, *L. Durkee 76-386* (F); Port Parker, Salinas Bay, *F. Elmore E1* (DS); Sitio Ojochal, P.N. Santa Rosa, 10°47′35″N, 85°39′00″W, *A. Fernández 315* (K, NY); Playa de Sámara, al S de Nicoya, *A. Jiménez M. 526* (F). **Puntarenas**: Golfo Dulce, vicinity of delta of Río Esquinas, *P. Allen 5631* (DS, F, FSU, US); Quepos, *F. Almeda et al. 3398* (CAS, F, NY); Cantón Golfito, Península de Osa, P.N. Corcovado, Estación Sirena, Río Corcovado, 08°28′50″N, 83°35′30″W, *L. Angulo 136* (K); Puerto Jiménez de Osa, *A. Brenes 12222* (F); Isla de Caballo, *A. Brenes 15696* (NY); Punta Morales, *J. Gomez-Laurito 9980* (F); near mouth of Río Coto Colorado, ca. 8 km S of Golfito, 08°37′N, 083°09′W, *W. Kress & L. Cablk 94-3803* (US); between Caldera and Matalimon, E of Puntarenas, *K. Lems 5026* (NY, US); cerca de Caldera, *J. León 505* (F); near Rincon de Osa, *R. Liesner 2203* (NY); vicinity of Puntarenas, *W. Maxon & A. Harvey 7841* (US); Santo Domingo, *Pittier 7109* (K, US), *7110* (F, K, NY, US); estuaires de Santo Domingo de Golfo Dulce, *A. Tonduz 10060* (DS, NY, US); N side of Estero, Puntarenas, *I. Wiggins & D. Porter 132* (CAS).

El Salvador. **Ahuachapan**: Las Chacaras, La Barra de Santiago, *K. DeRiemer 1645* (US); San Francisco Menéndez, Garita Palmera, zanjón El Aguacate, 13°43′N, 090°04′W, *D. Rodríguez & E. Escobar 1875* (MO); Santuario de las Aves, 13°42′N, 90°00′W, *R. Villacorta y E. Montalvo 817* (K, MEXU). **La Libertad**: El Amatal, San Diego, 13°25′N, 089°14′W, *J. González 316* (MO); Estero de San Diego, *J. González & A. Pérez 193* (MEXU). **La Paz**: Estero de Jaltepeque, *P. Allen 7278* (US); near mouth of Río Jiboa, *F. Choussy 1593* (US); El Zapote, Costa del Sol, 13°21′N, 89°W, *J. González & M. Hernández 326* (MEXU, MO). **La Unión:** rocky beach, La Union, *A. Beetle 26263* (K, UC); ca. 1 km S of Barrancones, 13°26′08″N, 087°47′32″W, *G. Davidse et al. 37355* (MEXU, MO); coast near La Union, *V. Grant 716* (F); vicinity of La Unión, *P. Standley 20786* (US). **Sonsonate**: S of Acajutla, *P. Allen 6837* (F, US); Estero San Juan, *K. DeRiemer 1617* (US). **Usulután**: Jiquilisco, El Tercio, 13°15′N, 088°31′W, *R. Carballo & L. Cabrera 831* (LAGU-image!).

Guatemala. **Escuintla**: Iztapa, Canjón Morón, *M. Arrecis 106* (CAS, MEXU, MO); San José, *J. Donnell Smith 2510* (K, NY, US); San José, *W. Maxon & R. Hay 3659* (US); Had. Las Fianzas, *G. Salas 367* (US); Puerto de San José, *J. Véliz & M. Véliz 94.4076* (CAS, MEXU). **Izabal**: near Puerto Barrios, *P. Standley 72167* (F, NY). **Jutiapa**: Las Lisas, Barra el Ahumado, *M. Arrecis 74* (CAS, MEXU, MO), *121* (CAS), *122* (MEXU); Iztapa, Zanjón Morón, *M. Arrecis 105* (CAS). **Retalhuleu:** Río Ocosito en límite Tilepa, Ocós, San Marcos y Manchón, *M. Arrecis 47* (MO); Champerico, *P. Standley 66563* (F), *87592* (F, NY). **San Marcos**: Mpio Ocós, almendrales, Tilapa, *M. Arrecis 50* (MO), Ocós, *J. Steyermark 37803* (F). **Santa Rosa**: Las Lisas, *M. Lara s.n.* (MO); Las Lisas, Camaronera Mayasal, 13.80723°N, 090.21703°W, *J. López & R. Jiménez 120* (CAS); Parque de la Barra Hawaii, Aldea el Dormido, 13.84113°N, 090.34751°W, *J. López et al. 100* (CAS).

Honduras. **Atlántida**: ca. 5 km NE of Tela near Telatinza, ca. 15°48′N, 087°26′W, *T. Daniel & J. Araque 9478* (CAS, NY). **Choluteca**: Ratón Island, *A. Molina R. 22779* (US), *23287* (DS, F, NY, US); Cedeños Beach, *A. Molina R. et al. 31978* (F); Punta Ratón, 70 km NW de Cd. Choluteca, *C. Nelson et al. 3259* (MO). **Colón**: Río Guaimoreto, 4.5 km NE of Trujillo on road to Castilla, 15°57′30″N, 085°54′30″W, *J. Saunders et al. 625* (F, MO, NY). **Gracias a Dios**: Puerto Lempira, Laguna de Caratasca, *A. Díaz Z. 212* (MEXU); Puerto Lempira, Laguna de Caratasca, *M. Espinal 142* (MO). **Islas de la Bahía**: Isla de Barbareta, *C. Nelson & G. Cruz 8411* (US); Isla de Roatán, playa al E de Roatán, *C. Nelson & E. Romero 4591* (MO). **Valle**: cerca de Isla Zacate Grande, *D. Hazlett 916* (MO); San Lorenzo, *A. Molina R. 8635* (F); Golfo de Fonseca, Puerto Soto, 12 km from El Tular, *A. Molina R. 21454* (F, NY).

Mexico. **Baja California**: Bahía San Francisquito [28.40814°N, 110.57079°W], *R. Moran 12625* (SD-not seen). Observed by I. Wiggins at Bahía de los Ángeles (see Turner et al. 1995). **Baja California Sur**: Playa Santispac, carr. transpeninsular, *B. Arteaga et al. 130* (MEXU); Magdalena Bay, *T. Brandegee s.n.* (DS, UC); El Mogote, peninsula extending into La Paz Bay, 24°8–11′N, 110°19–26′W, *A. Carter 2721* (DS, K, UC); Isla Carmen, vicinity of Las Salinas, ca. 25°59′N, 111°07′W, *A. Carter 5924* (UC); Isla Carmen, Puerto Balandra, ca. 26°00.5′N, 111°10.5′W, *A. Carter & R. Ferris 3733* (CAS, UC); Bahía Concepcion, ca. 14 mi S of Mulegé, *M. Dillon et al. 1954* (F); Bahía de La Paz, Chametla, 24°09′N, 110°06′W, *R. Domínguez C. 443* (MEXU); Sierra de la Giganta, ca. 12–14 mi S of Mulegé, near Bahía Santispac, *T. Elias et al. 10812* (F, NY); 16 mi S of Mulegé at Conception Bay, *R. Ferris 8680* (DS); Mpio. La Paz, Punta Prieta cerca de Pichilingue, 14 km NE de La Paz, *F. González M. et al. 8163* (MEXU); La Paz, *I. Johnston 3045* (CAS); Coronados Island, *I. Johnston 3758* (CAS, K, UC); Carmen Island, Puerto Balandra, *I. Johnston 3821* (CAS, K, UC); San Evaristo Bay, *I. Johnston 4089* (CAS, K, UC); Puerto Escondido, *I. Johnston 4293* (CAS, K, UC); Magdalena Bay, *H. Mason 1909* (CAS, DS, K);

Ballandra Bay, Carmen Island, 26°00.5′N, 111°10.5′W, *R. Moran 3926* (DS, UC), *9168* (MEXU); El Mogote, peninsula in La Paz Bay, ca. 24°10′N, 110°20′W, *R. Moran 7151* (CAS, DS, K); Concepcion Bay, *F. Shreve 7099* (F); Isla San José, costa SW, 24°54′N, 110°38′W, *M. Sousa P. 218* (MEXU); Isla del Carmen, lado W, Puerto Balandra, 26°01′N, 111°11′W, *M. Sousa P. 242* (MEXU); Magdalena Bay near Medano Amarillo, *J. Thomas 7940* (CAS, UC); Bahía Concepción, Playa Los Cocos, 26.87763°N, 111.97499°W, *D. Valvov 2005088* (MEXU); Bahía de Concepción between Mulegé and head of bay, *I. Wiggins 5455* (CAS, DS, F, UC); Estero Salinas, arm of Almejas Bay, S of Magdalena Bay, *I. Wiggins 11487* (CAS, DS, UC); 1.8 mi E of La Paz toward Pichilinque Bay, *I. Wiggins 14563* (CAS, DS); S shore of Bahía de La Paz, *I. Wiggins 16174* (DS); Puerto Escondido, 15 mi S of Loreto, *I. Wiggins 17526* (DS); N side of Bahía Astiones, W side of Isla San José, *I. Wiggins 17672* (DS); NE part of Isla San Francisco [24°50′32.36″N, 110°33′59.94″W], *I. Wiggins 17765* (DS); Bahía de la Concepción, beach at Punta Guadalupe, *I. Wiggins & D. Wiggins 18017* (DS); N side of Santispaquis Cove, Bahía de Concepción, *I. Wiggins & D. Wiggins 18239* (CAS, DS). **Campeche**: between Sabancuy and Cd. del Carmen, *R. Burnham & R. Spicer 146* (MEXU); 30 km W de Hecelchakan, camino a Isla Jaina, *E. Cabrera & H. de Cabrera 13345* (MEXU); 6 km NE de Champotón, carretera Cd. del Carmen, *E. Cabrera et al. 8497* (MEXU); Isla de Jaina, ca. 54 km W de Hecelchacan, *E. Cabrera C. et al. 11975* (MEXU); Mpio. Calkini, Isla Punta, 20°30′N, 90°W, *C. Chan V. & J. Flores 420* (XAL); “Panga” de Zacatal, *J. Chavelas P. & C. Zamora S. ES-4752* (MEXU); Mpio. Hecelchakan, 6 km antes de la costa, en la carretera de Pomuch, Isla de Jaina, 20°14′N, 090°24′W, *E. Gongora 546* (UC, XAL); Mpio. Campeche, Palmas, Cd. de Campeche, 19°52′N, 090°30′W, *C. Gutiérrez B. 5876* (XAL); Mpio. Cd. del Carmen, 5 km NE de Sabankuy, 19°03′00″N, 091°08′00″W, *C. Gutiérrez B. 7390* (MEXU); Puerto Real, *F. Menendez L. 467* (MEXU); S de Campeche, *F. Miranda 7944* (MEXU); Mpio. Calkiní, Isla Arena, 27 km de Takuché, 20°37′25″N, 090°25′W, *M. Narváez 1365* (MEXU); Mpio. El Carmen, Punta Cochinitos, Laguna San Francisco, 18°26′N, 091°46′W, *D. Ocaña N. & A. Novelo R. 158* (MEXU); carretera Champotón–Isla del Carmen, ca. 15 km de Champotón, *T. Pennington & J. Sarukhán K. 9405* (K); carretera Champotón–Campeche, *T. Pennington & J. Sarukhán K.* 9623 (K); Mpio. Champotón, camino a El Zapote, 4 km desde el entronque con la carr. Campeche–Champotón, 19°20′N, 090°45′W, *R. Rico G. 141* (XAL); 2 km N of Cd. del Carmen, *J. Sauer 2440* (F); Champotón, *W. Steere 1751* (CAS, MICH); Mpio. Tenabo, granja camaronera de Tenabo, entre KM 27 y el mar, 20°01′30″N, 090°13′06″W, *P. Zamora C. et al. 5824* (XAL); Mpio. Cd. del Carmen, Isla del Centro de Cayo Arcas, SE parte, *S. Zamudio 103* (MEXU, XAL). **Colima**: no collections seen, but species recorded from the state (see: http://www.projects-abroad.org/_downloads/uk/conservation-management-plan/mexico-conservation-management-plan-2014.pdf). **Chiapas**: Mpio. Tonalá, W side of Mar Muerto opposite Paredón, *D. Breedlove 20771* (DS); Mpio. Tonalá, E shore of Mar Muerto, N of Paredón, *D. Breedlove & R. Thorne 20806* (DS, NY); Mpio. Arriaga, balneario La Gloria, *A. Espejo & S. Hernández 2904* (MEXU); Acapetahua, cerca al Embarcadero Las Garzas, 15°12′38.7″N, 92°48′39.1″W, *H. Gómez D. 2293* (K); Las Garzas, Acapet, *E. Matuda 2728* (K, NY); Paderon, Tonala, *E. Matuda 16279* (US); Mpio. Acapetahua, 0.5 km antes de La Palma, 15°12′16, 092°48′37″W, *S. Ochoa G. et al. 4535* (MEXU); Mpio. Tonala, Col. Miguel Hidalgo, afueras de Puerto Arista, 15°55′N, 93°50′W, *V. Rico-Gray & I. Espejel 298* (F, MEXU); Mpio. Pijijiapan, Salina atras del Chocohuital, 15°30′N, 093°15′W, *V. Rico-Gray & I. Espejel 305* (MEXU, XAL); Mpio. Tapachula, Estero de Puerto Madero, 14°45′N, 092°35′W, *V. Rico-Gray & I. Espejel 346* (F, MEXU); Mpio. Puerto Madero, Puerto Madero, *E. Ventura & E. López 91* (MEXU, XAL); Las Margaritas, Pijiiapan, *G. Zavala P. & M. Illescas 19* (MEXU). **Guerrero**: Mpio. Copala, Laguna de Chautengo, *J. Almazán 248* (FCME); Mpio. Zihuatanejo, Playa La Ropa, Bahía de Zihuatanejo, 17°40′N, 101°34′W, *G. Castil-*

lo G. 1137 (UC), *6273* (MEXU, XAL); Mpio. Jose Azueta, Barra del Potosí, 17°40′N, 101°34′W, *G. Castillo C. & P. Zamora C. 6511* (XAL); Mpio. Zihuatanejo, entre la Punta Ixtapa y el Cerro El Rialito, 17°40′N, 101°39′W, *G. Castillo C. et al. 6566* (MEXU); Mpio. Cuajinicuilapa, Punta Maldonado, *N. Diego 2213* (FCME); Mpio. Acapulco de Juárez, El Arenal, Laguna de Tres Palos, *N. Diego 4161* (FCME, MEXU); Mpio. Petatlán, Cerro Huamilule, (Morro de la Laguna Potosí), *N. Diego & R. Oviedo 6636* (FCME); Mpio. Cruz Grande, W de Las Penas, *R. Fonseca 1625* (MEXU); Mpio. Cruz Grande, Los Tamarindos, Laguna de Chautengo, *R. Gutiérrez 4* (FCME); Mpio. Tecopan de Galeana, Laguna Nuxco, extremo SE, *F. Lorea 5280* (XAL); Mpio. Atoyac de Alvárez, Arenal de Palos, Laguna de Mitla, *L. Lozada P. 418* (FCME, XAL); Laguna del Potosí, *F. Menendez L. 448* (CAS); Mpio. Petatlán, 4 km de Petatlán dirección Tecpan, *A. Nuñez 605* (MEXU, XAL); Mpio. José Azueta, Cerro Huamilule, en Barra el Potosí, 17°31′56″N, 101°27′08″W, *S. Peralta 426* (MEXU, FCME); Mpio. Tecpan de Galeana, Nuxco, laguna, 17°15′07.6″N, 101°49′18″W, *S. Peralta 444* (FCME). **Jalisco**: Puerto Vallarta, *R. Acevedo R. 1487* (NY, XAL); Mpio. La Huerta, Laguna de Corte, 19°19′00″N, 104°56′20″W, *G. Castillo C. et al. 10745* (MEXU); Mpio. La Huerta, Playa Tenacatita, 19°17′00″N, 104°51′50″W, *G. Castillo C. et al. 10848* (MEXU); Mpio. Tomatlán, Playa Chalacatepec, 19°38′50″N, 105°12′20″W, *G. Castillo C. et al. 10967* (MEXU, XAL); Mpio. Tomatlán, Laguna Xola, 19°43′10″N, 105°15′20″W, *G. Castillo C. et al. 10978* (XAL); Salina al N de Chamela, *M. González G. 152* (CAS); Mpio. La Huerta, La Manzanilla, *L. de Puga 15542* (XAL); Barra de Navidad, *J. Rzedowski 14605* (DS). **Michoacán**: Mpio. Aquila, Estero de Maquili, *B. Guerrero C. 676* (XAL); Las Salinas [vic. of delta of Río Balsas, fide McVaugh 1951], *E. Langlassé 146* (K); Mpio. Coahuayana, Boca de Apiza, *C. Soto N. et al. 7116* (MEXU). **Nayarit**: Mpio. Bahía de Banderas, Bahía de Banderas, 20°47′N, 105°15′W, *G. Castillo C. 5818* (MEXU); Mpio. Bahía de Banderas, Laguna del Quelele, 20°44′N, 105°18′W, *G. Castillo C. 6012* (MEXU); Mpio. Bahía de Banderas, Club de Golf Flamingos, cerca de Bucerías, *M. Cházaro B. & R. Romero 8472* (XAL); SE of San Blas through Matanchen, SE toward Río San Cristobal, *C. Davidson 7608* (CAS); Pochote, Santiago Ixcuintla, 21°55′20.1″N, 105°30′30.9″W, *DIAAPROY S.A. de C.V. 47383* (MEXU); Tres Marías Islands, Magdalena Island, *F. Elmore 1132* (F); vicinity of San Blas, *R. Ferris 5396* (DS); Mpio. Santiago Ixcuintla, Mezcaltitán, *J. González O. 5537* (DS); Tres Marías Islands, Isla María Magdalena, *H. Mason 1793* (CAS, F, K, NY); Mexcaltitlán, *Y. Mexia 1008* (CAS, UC); Mpio. Santiago Ixcuitla, Isla de Mexcaltitán, 21°50′36″N, 105°24′42″W, *A. Miranda & G. Villegas 2053* (MEXU); Mpio. San Blas, ca. 2 mi E of San Blas on Hwy. 54, *D. Norris & D. Taranto 13329B* (CAS); Mexcaltitán, *J. Ortega 5537* (K); Isla María Magdalena, *O. Solís 9* (MEXU). **Oaxaca**: Mpio. Santa María Huatulco, Estero Cacaluta, 15°43′20″N, 096°09′40″W, *G. Castillo C. et al. 9782* (MEXU, XAL); Chacahua Bay, *F. Elmore D21a* (DS), *D22* (UC); Distr. Juchitán, Mpio. Chahuites, camino Chahuites–Las Salinas, *A. Flores M. 1101* (CAS); Mpio. Chahuites, Rancheria Trejo, *M. García B. 486* (XAL); Mpio. Huamelula, 4 km por la carr. Pochutla–Salina Cruz, 4 km después Huamelula, *J. García P. & E. Estrada L. 1974* (MEXU); Distr. Tehuantepec, Mpio. Salina Cruz, beach at La Ventosa, ca. 16°10′N, 095°09′W, *R. Gereau & G. Martin 1921* (CAS); Laguna Superior, S of Juchitán, near Xandanl, *R. King 1549* (NY, UC); Mpio. Tututepec, Chacahua, *J. Magaña 1232* (XAL); Puerto Angel, *C. Morton & E. Makrinius 2624* (K); La Ventosa Beach, ca. 6 mi E of Salina Cruz, *A. Reznicek & D. Gregory 304* (NY); Distr. Tehuantepec, Mpio. Santiago Astata, Laguna Colorada, 4 km W de Zaachilac, 15°57′39″N, 095°34′40″W, *S. Salas M. & E. Torres B. 825* (MEXU, XAL); Distr. Tehuantepec, Mpio. Salina Cruz, 500 m W de Salinas del Marquéz, 16°10′6.9″N, 095°14′24.3″W, *S. Salas M. et al. 5596* (XAL); Distr. Tehuantepec, Mpio. San Pedro Huamelula, Rancho Paraiso, 15°51′49″N, 095°50′22″W, *N. Velázquez R. et al. 265* (MEXU); Mpio. San Mateo, Huazantlán, La Salina, *D. Zizumbo & P. Colunga 500* (MEXU). **Quintana Roo**: S de Punta Allen, Cayo Cedros, Bahía de la Ascensión, *E. Cabrera 3405* (CAS, MEXU); 10 km N de Puerto Morelos, camino a Punta Caracol, *E. Cabrera & H. de Cabrera 3134* (MEXU, NY); 4 km N de la zona hotelera de Isla de Cozumel, camino a Isla de la Pasión, *E. Cabrera & H. de Cabrera 13582* (MEXU); Isla Mujeres, camino al Puerto de Abrigo, *E. Cabrera et al. 17200* (MEXU); Mpio. Isla Mujeres, Isla Mujeres, lado W de la marina, 21°19′N, 086°46′W, *C. Chan et al. 1590* (XAL); Reserva Biósfera de Sian Ka'an, 6 km E de Ramonal, *R. Durán et al. 1120* (MEXU); Mpio. Felipe Carrillo Puerto, La Laguna Xunyanche, 20°00′N, 087°40′W, *J. Flores & E. Ucan 8352* (F); Mpio. Isla Mujeres, Isla de Contoy, 21°30′N, 086°49′W, *J. Flores & E. Ucan 8855* (MEXU); Mpio. Othón P. Blanco, Cayo Centro en el Banco Chinchorro, 18°35′N, 87°20′W, *J. Flores et al. 8959* (XAL); Cozumel Island, *G. Gaumer 146* (K); Holbox Island, *G. Gaumer s.n.* (K); Cozumel Island, *E. Goldman 653* (F, US); brecha a Punta Brava al S de Pto. Morelos, *P. Moreno 843* (MEXU); Mpio. Isla Mujeres, Isla Mujeres, lado SE, 21°14′N, 086°46′W, *A. Puch et al. 865* (XAL); Mpio. Cozumel, Isla Cozumel, 20°30′N, 086°58′W, *A. Puch et al. 1073* (XAL); Mpio. Benito Juarez, camino a Punta Nizuc desde el entronque de la carretera Cancún-Chetumal, 21°N, 086°50′W, *V. Rico-Gray 123* (MEXU); Isla Mujeres, N end, *J. Sauer & D. Gade 3265* (MICH); Mpio. Lázaro Cárdenas, Chiquilá, 21°23′N, 087°23′W, *E. Ucán 431* (XAL); Mpio. Isla Mujeres, atras del Puerto de Abrigo, zona del Sak Bajo, 21°15′N, 086°45′W, *E. Ucan E. & J. Flores 1038* (MEXU, UC); Mpio. Othón P. Blanco, camino Blanco de X-Calak, rumbo a Majahual, 18°26′N, 087°56′W, *E. Ucan E. et al. 620* (MEXU); Mpio. Felipe Carrilo Puerto, Vigía Chico, Reserva de la Biósfera Sian Ka'an, *R. Villanueva 812* (MEXU). **Sinaloa**: Mpio. Escuinapa, Palmito, 9 km E al estero "Mezcal," *J. Beltrán M. 1014* (FCME); Mpio. Rosario, E edge of Mazatlán Bay, 0.7 mi W of Mex. 15, 8.6 mi N of Río del Presidio, *D. Breedlove 1577* (DS); Estero Ballena, old channel of Río Fuerte (W of Los Mochis), *R. Felger 8437* (CAS, MEXU); Topolobampo, *A. Gibson & L. Gibson 2095* (FSU); Escuinapa, Arroyo de la Codojuiz, *J. González O. 1131* (K); Mpio. Rosario, Coacoyolitos, *J. González O. 6458* (CAS); 4 km W de El Toldo, 24°57′N, 107°57′W, *V. Lopez S. 8.1* (MEXU); vicinity of Topolobampo, *J. Rose et al. 13309* (NY); vicinity of Mazatlán, *J. Rose et al. 14046* (F); N side of Topolobampo, *D. Seigler & P. Richardson 11686* (MEXU); Mpio. Los Mochis, just W of Topolobampo, 25°35′N, 109°05′W, *T. Van Devender et al. 2000-28* (NY). **Sonora**: Bahía Kino, mouth of Río de Sonora, *F. Drouet & D. Richards 3542* (F); 18.5 mi N of Bahía Kino Nuevo, *J. Hastings & R. Turner 64-35* (DS); Estero Tastiola, NW de Guaymas, *O. Holguín s.n.* (DS); Tepoca Bay, *I. Johnston 3288* (CAS); beach S of Guaymas, *G. Lindsay 1154* (DS); ca. 1 mi W of Puerto Lobos on narrow peninsula, *C. Lowe & R. Turner 3319* (DS); Sargento, *T. Mallery & W. Turnage s.n.* (DS); Guaymas, *W. Phillips 3483* (CAS) Mpio. Hermosillo, 2.7 km N of Punta Chueca, 20°02′20″N, 112°10′W, *A. Reina G. & T. Van Devender 96-635* (MEXU); Mpio. Caborca, Puerto Lobos, 30°16′16″N, 112°51′14″W, *A. Reina et al. 97-265* (MEXU); vicinity of Guaymas, *J. Rose et al. 12578* (NY); Bahía San Carlos, W of Guaymas, *Weedons M-1091* (MEXU); bayshore at Empalme, *I. Wiggins 6341* (DS); Isla Tiburón, Estero San Miguel, 28.968611°N, 112.20194°W, *B. Wilder et al. 06-276* (CAS); Isla Tiburón, Punta Tormenta estero, 29°00′51.17″N, 112°11′54.21″W, *B. Wilder et al. 08-329* (CAS); Isla Tiburón, Cyazim It, spit in estero at Punta Perla, 29.22442°N, 112.29345°W, *B. Wilder et al. 08-377* (CAS). **Tabasco**: Mpio. Frontera, Playa Boquerón, 20 km E de Frontera, *A. Guadarrama 876* (MEXU, NY); Mpio. Centla, Ejido Nuevo Centla, antes Playa Boquerón, 18°33′10.3″N, 092°30′48″W, *M. Guadarrama O. et al. 6688* (MEXU, XAL); Mpio. Nacajuca, Laguna Bayazú, llegando por el Río Gonzalez, *A. Hanan A. et al. 981* (MEXU); Mpio. Centla, Paso San Román, *F. Ventura A. 20406* (MEXU, XAL); Mpio. Paraíso, Puerto Ceiba, Isla Dos Bocas, *F. Ventura A. 20432* (XAL); Mpio. Paraíso, 4 km N de Mecoacán, *S. Zamudio R. 117* (MEXU). **Tamaulipas**: Mpio. Altamira, Barra de Chavarria S, entrada por el Barranco, *E. de Dunas 743* (XAL); 1 km W de La Pesca, cerca de la Laguna Blanca, *L. Hernández 1567* (MEXU); Mpio. Aldama, Rancho Nuevo, 23°08′12″N, 097°46′01″W, *D. Infante et al. 445* (XAL); Mpio. Matamoros, delta del Río Bravo, 25°56′56″N, 097°09′07″W, *D. Infante & J. Vázquez 656* (XAL); Mpio. Soto la Marina, campamento totuguero La Pesca, 23°47′27″N, 97°44′12″W, *E. Martínez 39316* (MEXU); Mpio. Altamira, playa cerca del Puerto Industrial, *A. Mora O. & J. Mora L. 5450* (MEXU); Mpio. Altamira/Aldama, Barra de Chavarria, *P. Moreno C. et al. 743* (MEXU); vicinity of Tampico, *E. Palmer 484* (CAS F, K, NY). **Veracruz**: Puente de Alvarado, *J. Calzada 434* (F); Mpio. Coatzacoalcos, Laguna Ostión, camino Pajapan–San Juan Volador, 18°11′N, 94°36′W, *J. Calzada 12657* (MEXU, XAL); Mpio. Panuco, alrededores de Laguna de Tamos, 22°13′N, 098°02′W, *J. Calzada et al. 6268* (XAL); Mpio. Actopan, El Morro de La Mancha, La Laguna, 19°36′N, 096°24′W, *G. Castillo C. 182* (F, UC, XAL); Mpio. Cosoleacaque, Polvorín, carretera Polvorín–Cosoleacaque, 17°59′48′N, 094°38′12″W, *G. Castillo C. et al. 14838* (MEXU, XAL); Mpio. Agua Dulce, Río Tonala, cerca de Arroyo Blasillo, *M. Chazaro B. 3299* (XAL); Mpio. Actopan, Estación Biológica El Morro de la Mancha, 19°36′00″N, 096°22′40″W, *C.M.V.A. 2* (MEXU); Mpio. Cazones, Rancho Nuevo, Estero Boquilla, *M. Cortés 455* (XAL); Mpio. Actopan, Laguna de la Mancha, carretera Cardel–Nautla, *J. Dorantes 57* (MEXU); S de Laguna Salada, *J. Dorantes et al. 1053* (F); 16 km S de Palma Sola, Laguna del Farallon [19°39′19.58″N, 96°24′40.28″W], *J. Dorantes et al. 1171* (CAS); alrededores de Laguna Verde (SW de La Planta), Alto Lucero, *J. Dorantes et al. 5132* (NY); Mpio. Alto Lucero, Lugana de San Agustín, KM 71 carretera Cardel–Nautla, 19°55′N, 096°31′W, *C. Guttierez B. 1311* (MEXU); Mpio. Zempoala, Estación de Biología “El Morro de la Mancha,” INIREB, carretera Cardel–Nautla, *G. Ibarra M. 3b* (FCME); borde sur de la Laguna Salada, *A. Lot et al. 2055* (F); Mpio. Boca del Río, Mandinga, 19°03′05.52″N, 96°04′43.56″W, *F. Medina H. et al. 27* (MEXU, XAL); Laguna de Tampamochoco, cerca de Tuxpan, *A. Mendoza s.n.* (DS); Mpio. Tuxpan, 8 km de Barra de Tuxpan, *L. Monroy et al. 147* (CAS, XAL); Mpio. Actopan, 50 m SW de la boca de la Laguna de la Mancha, 19°35′N, 096°22′W, *A. Novelo 408* (XAL); Mpio. Alvarado, Laguna de Alvarado, 18°46′13″N, 095°45′38″W, *R. Palestina et al. 1460* (XAL); Laguna de Sontecomapan, *T. Pennington & J. Sarukhan K. 9131* (NY, K); Mpio. Coatzacoalcos, terracería La Barrillas–Laguna Ostión, 17°45′30″N, 094°42′07″W, *A. Rincón G. et al. 1731* (XAL); Barra de Tuxpan (20°58′N), N of Río de Tuxpan mouth, *J. Sauer & D. Gade 2981* (F); Río Coscoapan, *M. Sousa 3112* (F); Mpio. Cazones, Barra Cazones, *S. Vargas P. 90* (XAL); Mpio. Actopan, La Mancha, *F. Ventura A. 5226* (CAS). **Yucatán**: Mpio. Tizimín, 55 km en el camino a Las Coloradas, cerca el Puente del Río Lagartos, *J. Aguilar Z. & S. Diez M. 225* (MEXU); Mpio. Telchac, Laguna Rosa, 1 km de Puerto de Telchac, 21°20′N, 89°16′W, *J. Calzada et al. 6611* (F, XAL); Peña, *Chocarro & Jun 567* (BIGU); Mpio. Tizimín, 16 km E de Las Coloradas, 21°30′40″N, 87°50′15″W, *R. Durán et al. 2575* (MICH); Mpio. Hunucmá, 7.5 km E de Sisal hacia Celestún, *E. Estrada 283* (FCME); Mpio. Telchac Puerto, 2 km E de Telchac Puerto, *A. Feliciano K. 325* (MEXU); Mpio. Progresso, Isla Larga de los Arrecifes Alacranes, 22°26′N, 089°31′W, *J. Flores & E. Ucan 9253* (XAL); Alacran Atoll, S end of Perez Islet, *F. Fosberg 41866* (NY, US); Alacran Atoll, Pajaros Islet, *F. Fosberg 41904* (US); Las Bocas de Silam, *G. Gaumer et al. 23340* (F, NY, US); Progreso, *C. Lundell & A. Lundell 8140* (MEXU, MICH, NY); Mpio. Dzilam de Bravo, entre Santa Clara and Dzilam de Bravo, 21°25′N, 088°50′W, *J. Palma & R. Allkin 300* (MEXU); 6 km W de Dzilam de Bravo, brecha a Pto. Telchac, *H. Quero R. & R. Grether 2469* (MEXU); Mpio. Hunucmá, 2 km E de Sisal, 21°10′15″N, 090°00′45″W, *E. Reyes de los Santos 607* (MEXU); Sisal, *Schott 361* (F); Celestun, *Schott 473* (F); Mpio. Celestún, 8 km antes Celestún, viniendo de Kinchil, 20°53′N, 090°20′W, *V. Rico-Gray 60* (F, MEXU, UC, XAL); ca. 4 km de Sisal, viniendo de Hunucmá, Hunucmá, 21°13′N, 090°03′W, *V. Rico-Gray 75* (MEXU); Mpio. Progreso, 1.5 km S de Chelem, camino a Progreso, 21°15′N, 090°20′W, *V. Rico-Gray 87* (MEXU); 1.5 km E de Dzilam de Bravo, 21°25′N, 088°50′W, *V. Rico-Gray 95* (F, UC, XAL); Mpio. Telchac Puerto, 0.5 km S de Telchac Puerto, 21°20′N, 089°15′W, *V. Rico-Gray 101* (F, MEXU, UC, XAL); afueras de la cuidad de Río Lagartos, 21°35′N, 088°10′W, *V. Rico-Gray 106* (F, MEXU, XAL); between Progresso and Telchac Puerto, *J. Sauer & D. Gade 3207* (F); Progresso, *W. Steere 3092* (MICH); Mpio. Celestún, 1 km E de Celestún, 20°51′30″N, 090°24′00″W, *J. Tapia M. 1508* (MEXU); Tizimín, alrededores de El Cuyo, ca. 21°30′45″N, 087°40′46″W, *M. Ventura 158* (F); Alacran Reef, Isla Perez, S end of island, *B. Welch s.n.* (DUKE, MEXU).

Nicaragua. **León**: Poneloya, ca. 12°23′N, 087°03′W, *R. Haynes 8617* (NY); 7.1 km de Las Peñitas, orillas del Estero Las Peñitas, *Sediles 408* (K); Estero Las Peñitas, 3.1 km de Las Peñitas, 12°20′N, 086°59′W, *Sediles 413* (CAS), *443* (CAS); Estero Brasil, ca. 2 km S of Hwy. 32 on road to Velero, ca. 12°10′N, 086°45′W, *D. Stevens et al. 17293* (CAS). **Managua**: Masachapa, *J. Atwood & D. Neill AN32* (NY). **Region Autonomista Atlantico Norte** (northern Zelaya): Pozo Verde, 10 km NE de Puerto Cabezas, 14°06′N, 083°20′W, *E. Little 25401* (F, US). **Region Autonomista Atlantico Sur** (southern Zelaya): Bluefields harbor, El Bluff, *S. Marshall & D. Neill 6507* (USF). **Rivas**: Estero San Juan del Sur, 11°14–16′N, 085°51–53′W, *M. Araquistain* 3809 (CAS); San Juan del Sur, *F. Seymour 1269* (MEXU, NY, UC).

Panama. **Bocas del Toro**: Changuinola Valley, *C. Cooper & G. Slater 81* (US); Water Valley, *H. von Wedel 987* (US). **Chiriquí**: playa cerca del KM 3, *J. Him 358* (US). **Coclé:** Aguadulce, outskirts of tidal belt, *H. Pittier 4969* (US). **Colón**: vicinity of Colón, *J. Cowell 97* (NY); vicinity of Viento Frio, *H. Pittier 4116* (US). **Guna Yala**: trail from Cangandi to dock by Mandinga airport, [09°27′39.50″N, 079°05′0.70″W], *G. de Nevers et al. 6554* (CAS, US). **Herrera**: P.N. Sarigua, 08°00′41″N, 080°29′03″W, *I. Alvarez B4339* (US). **Los Santos**: Salinas de Chitre, *W. D'Arcy & T. Croat 4200* (F). **Panamá**: Perlas Archipelago, San José Island, Naval Cove, *C. Erlanson 120* (NY); Perlas Archipelago, San José Island, *I. Johnston 1129* (US); Isla San José, *H. Kennedy 2281* (F, US); Taboga Island, Gulf of Panama, *H. Pittier 3614* (NY, US); Miraflores Locks, *W. Stern et al. 50* (US).

U.S.A. **Florida**: Brevard Co.: Merritt Island, *R. Kral 4972* (FSU, UC); S end of Merritt Island, Banana River, Coquina, *R. Whetstone 9116* (MO). Broward Co.: along Dania Beach Blvd., ca. 2 mi W of beach, *S. Leonard 6924* (FSU). Charlotte Co., 4.2 km S of De Soto Co. along Peace River, 2.7 km W of US 17, 26°59′50″N, 081°59′10″W, *A. Franck & B. Upcavage 1866* (USF-image!). Citrus Co.: Shell Island, near mouth of Crystal River, *R. Long 1309* (USF). Collier Co.: near Naples, *R. Godfrey 58071* (FSU); Everglades City, *O. Lakela 29824* (NY). Flagler Co.: inland waterway in vicinity of Marineland, *R. Godfrey 61686* (FSU). Franklin Co.: between St. George Sound and small tidal marsh just NE of Culpepper home on Cannonball Acres, *L. Anderson 5580* (FSU). Hernando Co.: N of Aripeka on Fla. 595, *J. Carlton s.n.* (USF). Hillsborough Co.: Long Key, *F. Lewton s.n.* (NY). Indian River Co.: along Indian River Lagoon, Oslo Riverfront East Conservation Area, Oslo Road E of US 1, ca. 3 mi. S of Vero Beach, 27º35.193′N, 080º21.902′W, *S. Myers 1281* (USF-image!). Lee Co.: Tarpon Bay, eastern Sanibel, *W. Brumbach 7904* (NY); Little Pine Island, *H. Moldenke 929* (MO). Levy Co.: causeway to Cedar Key, *R. Godfrey & P. Redfearn 52828* (UC); near jct. A Street and 3rd Street, Cedar Key, *K. Murray 80-43-10* (NY); Cedar Keys, *I. Wiggins 19342* (DS); E side of Seahorse Key, SE of lighthouse, *I. Wiggins & D. Wiggins 19430* (DS). Manatee Co.: Palmetto, *G. Nash 2450* (MO); Palma Sola, vic. of Manatee, *J. Simpson 80* (UC). Martin Co.: Jonathan Dickinson State Park (Girl Scout Camp), *R. Woodbury & R. Roberts s.n.* (USF). Miami-Dade Co.: Coral Gables, S end of Vee Lake, 25°40.5–40.7′N, 080°16.1–16.5′W, *J. Abbott 24063* (FLAS-image!); Everglades Natl. Park, Flamingo Area, 25°08.38′N, 080°55.88′W, *W. Hess et al. 8579* (MO, NY); Kampong, 4013 Douglas Road, Coconut Grove, *W. Judd 5602* (FLAS-image!). Monroe Co.: Long Key, *D. Correll & H. Correll 40150* (MO); Rode

Harbor, Key Largo, *C. Janish & J. Janish 447* (DS, MO); Big Pine Key, *W. Muenscher & R. Thorne 18073* (UC); Lower Matecumbe Key, *J. Pruski et al. 2826* (NY); Key West, just S of airport, 24°33.162′N, 081°46.024′W, *A. Salywon 1188* (CAS); E end of Packet Key, *I. Wiggins 20081* (DS). Palm Beach Co.: Jupiter Island, *G. Cooley et al. 4864* (USF). Pasco Co.: just W of Port Richey along inlet canal from beach, *J. Ray et al. 9980* (FSU). Pinellas Co., Boca Ciega, bayside just S of Treasure Island causeway, *R. Thorne 48355* (UC). Sarasota Co.: Sarasota, Marie Selby Gardens, 27°19′33″N, 082°32′28″W, *H. Bizet 51* (MO, NY); Historic Spanish Point, in Osprey W of US 41, 27º12′15″N, 082º29′46″W, *M. Nolan 62* (USF). St. Johns Co.: between Matanzas and Marineland, *R. Godfrey 70653* (CAS, FSU, GA, UC); Anastasia State Park, Conch Island, ca. 4.75 km NNW of jct. FL A1A and FL 312, E of FL A1A; immediately S of the St. Augustine Inlet, 29º53′56″N, 081º17′21″W, *J. Kunzer et al. 2146* (USF-image!); Crescent Beach, *D. Seigler & D. Young 10211* (MEXU); Anastasia State Recreation Area, NW Conch Island, S of Vilano Point and St. Augustine Inlet, UTM-471684, 3308353, *C. Slaughter et al. 16617* (FSU); Tolomato River, 30°06.618′N, 081°22.303′W, *A. Williams & S. Eastman s.n.* (USF-image!). St. Lucie Co.: Hutchinson Island, Blind Creek access area, off Indian River, *G. Silberhorn s.n.* (USF). Taylor Co., Jug Island [29°50′31.75″N, 83°36′58.05″W], *R. Godfrey 60403* (UC). Volusia Co.: 9 mi S Daytona Beach, near Ponce de Leon Inlet, *R. Norris 541* (FSU). County undetermined: Indian River, *A. Curtiss 1972* (CAS, GA, MO), *s.n.* (NY); Tampa Bay, *P. Rolfs 248* (MO). **Louisiana**: Cameron Parish: Monkey Island near mouth of Calcasieu Ship Channel at Calcasieu Pass, adjacent to ferry landing, *W. Vermillion s.n.* (LSU-image!). Jefferson Parish: Grande Isle, *J. Carlton s.n.* (USF); Fifi Island, 29.255541°N, 089.978158°W, *D. Atha 12910* (NY). Lafourche Parish: 0.6 mi S of Fourchon Road bridge (R22E, T23S, S24), *A. Lasseigne 6146* (MEXU); S of end of La. 3090, S of Fourchon City, S of Leeville, *R. Thomas et al. 103237* (MO, NY). Orleans Parish: New Orleans, *Nuttall s.n.* (K). Plaquemines Parish: ca. 40 mi (air) SSE of New Orleans, 29.40782, -89.79907, *M. Bell s.n.* (LSU-image!). St. Bernard Parish: North Islands in North Chandeleur Sound, NE of Venice, *R. Thomas et al. 89768* (MEXU). Terrebonne Parish: E end of Isle Dernier, *F. Givens 3733* (MO); Brush Island, *F. Lloyd & S. Tracy 249* (NY). **Mississippi**: Harrison Co., Bay St. Louis [possibly Hancock Co.?], *C. Sanger s.n.* (NY); Cat Island, 30.23037°N, 89.08532°W, Scheffel et al. 2014 (living plant-image!). Jackson Co.: Ranger Lagoon, Horn Island, 30.24171°N, 88.67886°W, Scheffel et al. 2014 (living plant-image!). **Texas**: Aransas Co.: Redfish Bay, causeway to Port Aransas, Rte. 361, *S. Hill 18296* (MO, NY); Port Aransas, *B. Tharp 253* (CAS, MO, NY, UC). Cameron Co.: South Padre Island, between Old Causeway and Queen Isabella Causeway, *F. Banda 81* (USF); Padre Island, just E of Port Isabel, *D. Correll et al. 25539* (UC); 8 mi SW of Port Isabel, inlet crossed by FR 1792 (NY), *J. Crutchfield 2985* (NY); Clark Island, near Boca Chica, *C. Lundell & A. Lundell 8760* (CAS, NY, UC); Point Isabel, *H. Parks 2939* (MO); bay at Boca Chica, Brazos Santiago Island, *R. Runyon 2812* (NY); Point Isabel in Lower Rio Grande Valley, *R. Runyon 5897* (UC); boca de Río Bravo, *Schott 139* (NY); Boca Chica, *G. Webster & R. Wilbur 3035* (GA). Nueces County: Aransas Pass, causeway between Aransas Pass and Port Aransas, *P. Fryxell 5162* (MEXU). Refugio Co.: near Tivoli, *J. Williams 415* (NY).

3. *Avicennia marina* (Forsk.) Vierh., subsp. ***australasica*** (Walp.) J. Everett, Telopea 5(4): 628. 1994. *Avicennia tomentosa* Sieber var. *australasica* Walp., Repert. Bot. Syst. 4: 133. 1845. *Avicennia resinifera* G. Forst., Pl. Esc. 72. 1786. *Avicennia marina* var. *resinifera* (G. Forst.) Bakh., Bull. Jard. Bot. Buitenzorg, ser. 3, 3: 210. 1921, nom illegit. (superfl.). TYPE.— Sheet 1460 in Thunberg's herbarium (lectotype, designated by Everett [1994: 628]: UPS).
Figures 1H–K, 2, 3B,D

Shrubs to 2.3 m tall. Young stems of reproductive shoots covered with dense shiny granules or scalelike projections to 0.05 m long (scurfy), soon glabrate. Leaves petiolate, blades ovate to elliptic (to obovate), 44–100 mm long, 19–41 mm wide, 1.7–2.8 (–3.6) times longer than wide, acute (to rounded or emarginate) at apex, subattenuate to attenuate at base, surfaces discolorous (abaxial lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer. Inflorescences of axillary and terminal (sessile to) pedunculate ± headlike spikes, peduncles (0–) 1–40 mm long, scurfy or distally pubescent like rachis, rachis not or but barely visible, internodes near midspike 1–4 mm long, scurfy and pubescent with ± antrorse eglandular trichomes to 0.2 mm long. Bracts opposite, broadly ovate to triangular, concavoconvex, 3–4 mm long, abaxial surface scurfy and often pubescent like rachis. Bracteoles similar to bracts except smaller. Flowers mostly 4–16 per spike, sessile. Calyx 3.5–4 mm long, lobes elliptic to broadly elliptic, concavoconvex, imbricate, abaxially pubescent with antrorsely appressed eglandular trichomes to 0.8 mm long, margin ciliate with similar but spreading trichomes. Corollas 3.5–6.5 mm long, internally drying dark or blackish proximally and light brownish distally (those from Australasia are usually described as yellowish or orangish and the color is often darker in the corolla tube), externally glabrous (tube and base of lobes) and densely pubescent with appressed eglandular trichomes to 0.2 mm long (remainder of lobes), tube 1.5–2 mm long, limb actinomorphic, 4-lobed, lobes ovate-triangular to ovate-elliptic, 2–4.5 mm long, apically entire (or 1 lobe sometimes slightly bifid apically with division to 0.2 mm long), internally lacking eglandular trichomes (at least distally) but sometimes punctate-pitted (proximally). Stamens 4, inserted in distal half of corolla tube near base of lobes, exserted from mouth of corolla tube, oriented symmetrically (i.e., equally distant from one another) around corolla with thecae opening toward central gynoecium, 1.5–2 mm long, filaments 0.5–0.8 mm long, anthers presented at same height, thecae 1–1.2 mm long; pollen prolate spheroidal to euprolate, polar diameter (P) 28–41 µm, equatorial diameter (E) 24–27 µm, P:E = 1.04–1.75. Style not evident, stigma lobes 0.2 mm long. Fruit ovoid to subellipsoid, proximally blackish and distally light brownish when dry, 15–24 mm long, 10–19 mm across at widest expanse, pubescent with erect to flexuose to antrorse eglandular trichomes to 0.3 mm long (especially when less mature) and scurfy (especially evident when more mature). $2n = 64, 96$ (Dawson 1989).

Phenology.— Flowering: February, August–September; fruiting: February, November.

Distribution and habitat.— *Avicennia marina* has the most extensive distribution among species in the genus; it is native to eastern Africa, southern Asia, Indian Ocean and western Pacific Ocean islands, and Australia. Subspecies *australasica* occurs primarily in subtropical and temperate Australasia (i.e., southeastern Australia and northern New Zealand). It is the southernmost-occurring taxon among species of *Avicennia* in the Old World (to 38°45'S; Duke 2006), and the southernmost-occurring mangrove in the world. In southern California, where this taxon has been introduced and become naturalized (Fig. 2), plants occur in salt marshes with *Batis*, *Juamea*, *Salicornia*, *Spartina*, and *Suaeda* at or near sea level.

Illustrations.— Munir (1986: 1179, fig. 546); Duke (1991: 314, fig. 7); Clarke and Myerscough (1991: 285, fig. 1).

Nomenclature.— The name "A. marina var. australasica (Walp.) Moldenke" has been used for this taxon, but as discussed by Everett (1994), this combination was not validly published at this rank, and other infraspecific taxa of *A. marina* are currently treated as subspecies. *Avicennia marina* subsp. *australasica* and the synonyms noted above are all based on *A. resinifera*. See Moldenke (1960) and Duke (1991) for a full list of synonyms of *Avicennia marina*.

Local name.— Gray mangrove.

Conservation.— *Avicennia marina* has been assessed as a taxon of Least Concern (LC) by Duke et al. (2010). This taxon is not native in the New World, but has become naturalized locally and is potentially invasive. On his collection *28024* made in 1979, Moran noted that plants in California had been introduced from Aukland, New Zealand about 1966–69. He also noted the presence of about 100 or more flowering-size plants plus many seedlings in the wildlife reserve where his observations were made. Initial efforts to eradicate the species were unsuccessful.

Discussion.— This species is readily distinguished from those native to the western Hemisphere by its actinomorphic flowers with yellowish to orangish corollas bearing ovate-triangular to ovate-elliptic lobes and its equidistant stamens that are inserted near the base of the corolla lobes, dehisce toward the center of the flower, and vary from 1.5–2 mm in length (Fig. 3B).

Duke et al. (1998) provided genetic evidence that supported the morphological recognition of *A. marina* as a distinct species and that supported recognition of the three infraspecific taxa (treated by him as varieties, but here recognized as subspecies): subsp. *marina*, subsp. *eucalyptifolia* (Valeton) J. Everett, and subsp. *australasica*. The latter subspecies would appear to consist of or contain polyploids based on the reported chromosome numbers of $2n = 64$ and 96 (Dawson 1989, as *A. resinifera*). These numbers suggest a possible base number of $x = 8$ or $x = 16$. A chromosome number of $2n = 36$ was reported for an unspecified subspecies of *A. marina* by Subramanian (1988; without citation of voucher). These appear to be the only recent chromosome counts for both this species and for the genus. If these numbers are accurate, both polyploidy and dysploidy would appear to have played a role in the evolution of taxa in *A. marina*. The only other known chromosome counts for *Avicennia* are $2n =$ ca. 66 and $n =$ ca. 33 by Raghavan and Arora (1958; with a meiotic figure showing $n = 33$, but without citation of a voucher) for *A. alba* Bl. Sanders (1997) indicated a base chromosome number for Avicenniaceae of $x = 18$. Although no rationale was stated for this number, his conclusion was probably based largely on Subramanian's count of $2n = 36$ for *A. marina*.

Avicennia marina subsp. *australasica* was distinguished by Duke (1991) from the other two varieties of *A. marina* by the fully (or nearly so) pubescent calyces (vs. pubescent only near the base), and the gray, fissured (vs. green, chalky smooth, and often flaky in patches) bark of the mature trunk.

Specimens Examined.— **U.S.A**. **California**: San Diego Co.: Northern Wildlife Preserve, North Mission Bay, tidal area 100 m W of Rose Creek, 32.7949°N, 117.2247°W, *I. Kay 29* (UCR); E edge of Kendall/Frost Marsh, Mission Bay, San Diego, ca. 32˚47.5′N, 117˚13.8′W, sea level, 9 September 1979, *R. Moran 28024* (CAS, GH, MEXU, NY, UC, US); same locality, 12 June 1990, *R. Moran 31036* (CAS, JEPS).

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A New Species of *Serranus* from São Tomé and Príncipe, Eastern Atlantic (Pisces Teleostei, Serranidae)

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***Serranus pulcher* is described from São Tomé and Príncipe islands. It differs from all other eastern Atlantic *Serranus* species except *S. heterurus* (Cadenat, 1937) in a combination of the following characters: dorsal fin X,12, anal fin III,7; 42–50 pored lateral-line scales; interorbital area without scales; upper lobe of caudal fin pointed, lower lobe of caudal fin rounded. *Serranus pulcher* differs from *S. heterurus* in life color. *S. pulcher* probably also occurs off the coast of West Africa. It is the smallest known *Serranus* species in the eastern Atlantic.**

The percoid genus *Serranus* currently contains 14 valid species in the western Atlantic Ocean, one species (*Serranus sanctaehelenae*) endemic to the central Atlantic Islands of Ascension and St Helena, and six valid species in the eastern Atlantic (Eschmeyer and Fricke 2015). No *Serranus* species is amphi-Atlantic. Four of the six eastern Atlantic species (*S. atricauda*, *S. cabrilla*, *S. hepatus*, and *S. scriba*) reach into the Mediterranean Sea. A seventh eastern Atlantic species of *Serranus* is here described from the islands of São Tomé and Príncipe in the Gulf of Guinea.

Material and Methods

The specimens were obtained by SCUBA diving, with a hand-held aquarium net, at depths of about 2 to 30 m. They were preserved in ethanol or formol. Point-to-point measurements were taken on the left side of each specimen using a digital caliper with an accuracy of 0.01 mm and rounded to the nearest 0.1 mm. Body depth was measured at the beginning of the first dorsal fin. Body width was measured behind the insertion of the pectoral fins. Head length was measured from the tip of the snout to the end of the operculum, snout length from anterior edge of eye to tip of upper lip, pectoral fin length from ventral insertion to longest ray. Lateral-line scales were counted on the left side of the animal, where possible. Pored lateral-line scales are taken to the caudal-fin base and do not include those on the caudal fin itself. The last ray of the dorsal and anal fins is usually split to the base and is counted as one ray. Gill-raker counts are from the first arch and include all rudiments; counts of the upper arm are separated by a plus sign (+) from those of the lower arm, the raker whose roots span both the upper and lower arms of the gill arch is included in the count of the lower arm. The description of color patterns of living specimens is based on numerous underwater photographs by the first author and others (see Acknowledgments). Common abbreviations used include SL – standard length; TL – total length; HL – head length; D – dorsal; fin; A – anal fin; P – pectoral fin; V – pelvic [ventral] fin; Ll – pored lateral line scales.

Specimens mentioned in the present paper are deposited in the California Academy of Sciences (CAS); the Coleção Ictiológica Universidade Federal do Espírito Santo (CIUFES) at Vitoria, Brazil; the South African Institute for Aquatic Biodiversity (SAIAB); Stuttgart Natural History Museum (SMNS); Zoologisches Museum Hamburg (ZMH); and the Zoologische Staatssammlung at Munich (ZSM). Tissue samples of three specimens from Príncipe Island (ZSM uncatalogued) were sent to Benjamin Victor (Ocean Science Foundation) for DNA analysis. The results of his analysis will be published elsewhere.

Comparative material.— The following specimens were used for direct comparisons with the type specimens of the new species. Additional material used for general comments are listed in a synopsis of the eastern Atlantic members of the genus *Serranus* (Wirtz, Heemstra and Iwamoto, In prep.): *Chelidoperca africana*: SAIAB 26564, Cameroon. *Serranus accraensis*: ZSM 32516, Angola, ZSM 32596 Angola, ZSM 32610 Angola. *Serranus hepatus*: ZSM 25637, Croatia, ZSM 41914 France. *Serranus heterurus*: SAIAB 65552 Angola; SAIAB 65682, Angola; ZMH 11056 Senegal; ZMS 43051, Cape Verde Islands; ZMS 43730, Cape Verde Islands; ZSM uncatalogued, Cape Verde Islands; CAS 231614, São Tomé Island; CAS 231627, São Tomé Island; CAS 234709, Guinea; CAS 234711, Guinea. *Serranus scriba*: ZSM 23526, Greece.

Species Description

Serranus pulcher Wirtz and Iwamoto, sp. nov.

Figures 1–9, Tables 1–5.

Serranus sp.(“São Tomé comber“), Debelius 1998: 148. Kuiter 2004:162, figs. A-D.
Serranus n.sp., Wirtz et al. 2007:8–9, fig. 8

Material Examined.— Holotype: ZSM 43868 (59 mm SL), São Tomé Island (00º25.099′N, 006º41.718′E), near wreck “Mar Vassa“ on coral rubble in about 6 m depth, Jan. 2015, formol preserved, coll. Nuno Vasco Rodrigues. A small piece of the left pectoral fin is missing and the dorsal fin is slightly torn between the spinous and the soft-rayed part (figure 1a and b). Paratypes measured: ZSM 43869 (66 mm SL) same data as holotype. ZSM 43879 “Mar Vassa”, São Tomé Island (00º25.099′N, 006º41.718′E), Nov. 2014, coll. Nuno Vasco Rodrigues. ZSM 43880 “Mar Vassa”, São Tomé Island (00º25.099′N, 006º41.718′E), Mar. 2014, coll. Nuno Vasco Rodrigues. CAS227751 (70.5 mm SL), São Tomé Island, Kia Reef (00º25′0.01″N, 006º48′E), 25–40 ft [7.6–12.2 m], 11 Jan. 2009, coll. J.E. McCosker, D. Catania, and J.-L. Testori. CAS227753 (73 mm SL, specimen labelled DC1009), Príncipe Island (01º41′09.3″N, 007º28′07.6″E), 40 ft [12.2 m], 23 Jan. 2009; coll. J.E. McCosker and D. Catania. CAS 227754 (4 spec., 45–74 mm SL), Príncipe Island, nw side Bom Bom Is. (01º41′44.0″N, 007º24′00.3″E), 48 ft [14.6 m], 20 Jan. 2009, coll. J.E. McCosker and D. Catania. CAS227755 (1 spec.), São Tomé Island, Kia Reef (00º21′37.1″N, 006º43′08.5″E), 45–72 ft [13.7–21.9 m], 11 Jan. 2009, coll. J.E. McCosker, D. Catania, and J.-L. Testori. CAS227756 (2 spec., 75–78 mm SL), São Tomé Island, Batalleo (00º22′05.7″N, 006º45′41.6″E), 13 Jan. 2009, coll. J.E. McCosker, D. Catania, and E. Milson. CAS227757 (specimen labelled DC999), Príncipe Island, Pedro Adalia (01º42′04.0″N, 007º25′42.1″E), 21 Jan. 2009, coll. J.E. McCosker, D. Catania, and R. Van Syoc. Paratypes not measured: CAS227752 (7 juveniles), Príncipe Island, Pedro Adalia (01º42′02.3″N, 007º25′43.8″E), 52 ft [15.8 m], 19 Jan. 2009, coll. J.E. McCosker and D. Catania. CAS227757 (8 juveniles), Príncipe Island, Pedro Adalia (01º42′04.0″N, 007º25′42.1″E), 21 Jan. 2009, coll. J.E. McCosker, D. Catania, and R. Van Syoc. CAS227758 (3 spec.), Príncipe Island, Isla Santana, cave (00º14′33.1″N, 006º45′36.1″E), 62 ft [18.9 m], 28 Jan. 2009, coll. J.E. McCosker, and J.-L. Testori.CIUFES 150 (pectoral fin taken for

DNA sample), São Tomé Island; CIUFES 155 (4 spec.), São Tomé Island; ZSM uncatalogued (3 juvenile spec., tissue samples taken for DNA analysis), Príncipe Island.

Diagnosis.— Dorsal rays X,12; dorsal fin notched between spinous and soft part; anal rays III,7; pectoral rays usually 15 (rarely 14 or 16); pelvic rays I,5; gill rakers 6–9+12–14 (19–23 total); pored lateral-line scales 42–49; circumpeduncular scales 20–25, usually 22–24; interorbital without scales. Caudal fin truncate, the upper lobe slightly produced, lower lobe rounded. Dorsal, anal, and pectoral fins scaly near base. Scales ctenoid, not deciduous; 5–6 rows of scales from the beginning of the dorsal fin to the lateral line; three opercular spines, the middle one largest, the upper one often obscure, the lower one sometimes invisible to the naked eye; rear margin of anterior nostril forming a flap usually fringed with 4–6 long cirri that reach well past the rear nostril; posterior nostril a simple opening lacking a raised rim. Lips red with dark bands; a short moustache-like red streak behind end of maxillary, running across hind margin of dentary and almost meeting opposite streak at midventral line and enclosing ivory-white of mandibular rami; another red diagonal streak running from upper edge of maxillary, across lower edge of preopercle, across interopercle and branchiostegal rays, to base of pelvic fin, and enclosing white of preopercle, interopercle and chest. Size to at least 9 cm total length.

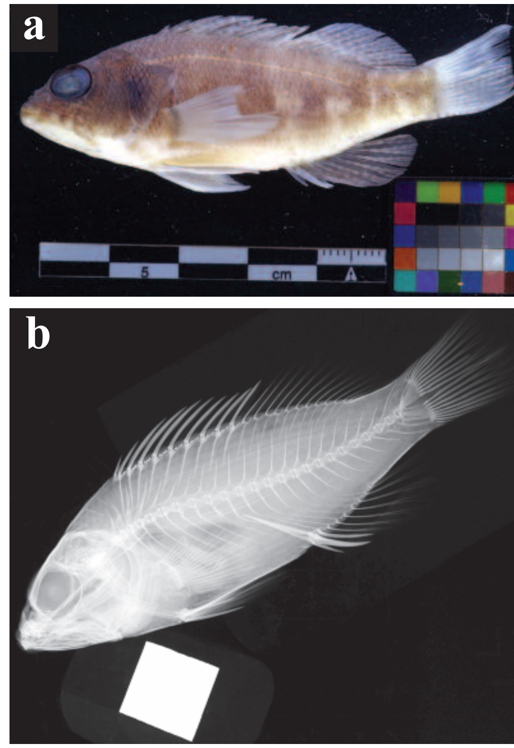

Figure 1. Holotype of *Serranus pulcher* sp. nov. ZSM 43868 (59 mm SL) left side: a) in alcohol; b) radiograph (photos Dirk Neumann).

Description.— Measurements and counts are presented in tables 1–5. Body relatively slender and compressed, width over pectoral bases about half of HL, greatest body depth about 2.7–3.2 in SL and less than HL, which is about 2.4–2.6 in SL. Dorsal and ventral profiles gently curved from tip of snout to caudal fin. Snout shorter in length than orbit diameter; both substantially more than interorbital width. Lower jaw projecting slightly beyond upper jaw; maxilla extending to below posterior half of pupil. Preopercle margin serrated with flattened spines, those at angle largest. Mouth large with upper jaw reaching to the level of the rear edge of the eye or beyond. Premaxillary teeth in a narrow band, the outer series spaced and slightly enlarged; one or more large canines at anterior end. Dentary with a band of small teeth flanked by a series of slightly enlarged outer teeth that become larger posteriorly. Vomerine tooth band broadly V-shaped, followed on each arm by narrow band of small palatine teeth.

Dorsal rays X,12; first 4–5 spines of dorsal fin graduated, the 3rd to 5th spines longest, the spines following subequal; the soft rays slightly higher than longest spines, the 3rd to 5th ray longest; a slight notch in fin profile. Anal rays III,7; anal fin relatively high, its posterior tip somewhat pointed; spines shorter than soft rays, the first spine more than half length of second and third spines, the second spine longer and stouter than the others. Pectoral 14–16, usually 15 soft rays; pectoral fin broad-based, its origin about on same vertical as those of dorsal and pelvic fins; the tip of pectoral fin extends to, or almost to, anus. Pelvic rays I,5; the distal tips of the soft rays sometimes reach the level of the anus but often they are shorter. Caudal fin with usually 15 (one specimen with 17) branched rays; caudal fin truncate; dorsal lobe slightly produced, ventral lobe rounded at tip (Fig 2). Lateral line slightly arched over pectoral fin and from there on parallel to dorsal profile. Scales on the nape from the beginning of the dorsal fin forward to the level of the serrated edge of the preoperculum, but not further forward (i.e., interorbital without scales); scales present on operculum (7 oblique rows of scales) and preoperculum (6 rows), but absent in all areas in front of eyes; six branchiostegal rays. Rear margin of anterior nostril forming a flap usually fringed with five (rarely four or six) finger-like cirri that reach well past the rear nostril; rear nostril a round hole without raised rim.

FIGURE 2. *Serranus pulcher* specimen from Príncipe Island, directly after capture (photo Dave Catania).

Counts and measurements of the holotype and paratypes in the ZSM collection are given in Table 1 and those of some specimens in the CAS collection in Table 2. Additional counts and measurements on further specimens in the CAS collection are given in Table 3. Counts and measurements taken by Phil Heemstra (SAIB) on 6 specimens from São Tomé and Príncipe, collected by P. Wirtz in 2004, are given in Table 4; these specimens apparently are lost now. Counts and measurements on 5 specimens from São Tomé Island taken by Francisco Reiner are given in Table 5; these specimens are apparently now lost.

TABLE 1: Counts and measurements (in mm) of *Serranus pulcher* holotype and ZSM paratypes.

	ZSM 43868	**ZSM 43869**	**ZSM 43879**	**ZSM 43880**
	Holotype			
SL	59.2	65.6	68.4	70.5
D	X, 12	X, 12	X, 12	X, 12
A	III, 7	III, 7	III, 7	III, 7
P	14/14	15/15	15/15	15/15
V	I, 5	I, 5	I, 5	I, 5
Ll	50	50	49	47
Circumpeduncular scales	21	22	21	24
Length V	16.4	15	15.8	15.3
Length P	17.2	16.9	18.1	18.1
Body depth	18.8	20	22.1	23.9
Head length	22	23.9	25.7	26.9
Snout length	4.9	5.6	6.8	6.9
Body width	9.3	10.3	10.8	11.7
Orbit diameter	5.7	6.1	6.3	6.2

The paratype ZSM 43879 was dissected and turned out to have the genus-typical (Erisman and Hastings 2011) hermaphroditic gonad: the ovotestis is dominated by ovarian tissue with testicular tissue restricted to the posterior and ventral part.

Color in alcohol (Fig. 1a): Alternating light and dark areas on upper and lower lip; head and upper half of body light brown; some lighter blotches on rear half of lower body; belly light; no dark spots on snout and fin membrane between the first two dorsal spines not black.

Color *in vivo*: Color extremely variable (Figs. 2–9). The following patterns appear to be most

TABLE 2: Counts and measurements (in mm) of several *Serranus pulcher* paratypes in the CAS collection.

	CAS227753	**CAS227755**	**CAS227756**	**CAS227756**	**CAS227757**
	DC1009		DC924	DC915	DC999
SL	62	57	61	59	53
D	X, 12	X, 12	X, 12	X, 12	X, 12
A	III, 7	III, 7	III, 7	III, 7	III, 7
P	15/15	16/16	16/16	16/16	18/-
Ll	44	-	47	45	47
Body depth	18	18	19.5	19	16
Head length	23	22	23.2	23.3	20
Snout length	5.4	5.8	5.3	5	4.7
Orbit diameter	5.7	6	6.2	6.4	5.2
P length	15.9	14	16.5	15	14
V length	13.7	13	16	15.4	13

TABLE 3: Counts and measurements (in mm) of additional *Serranus pulcher* paratypes in the CAS collection.

	CAS227751	**CAS227754**	**CAS227754**	**CAS227754**	**CAS227754**
	DC880	DC986	DC987	DC989	DC988
SL	56.6	60.2	47.6	37.2	39.8
D	12	12	12	12	12
A	7	7	7		7
P	15	15	15	15	14
Ll	48	46	45	45	43
Circumpeduncular scales	21	25	23		24
Head length	23.6	23.8	19	15.1	16
Snout length	5.9	5.5	4.1	3.2	3.6
Interorbital width	2.5	3.9	3.5	2.6	2.4
Orbit diameter	5.8	5.8	4.5	3.9	4.8
Suborbital width	2.2	2.4	1.7	1.6	1.5
Postorbital length	12.5	12.9	10.4	8.2	8.5
Orbit to preopercle	8.6	8.4	6.6	5.3	5.6
Upper jaw	11.3	11.1	8.6	6.9	7.5
Predorsal length	23.1	23	18.7	15.7	15.8
Preanal length	36.8	41	30.4	25.3	25.6
Body depth	21.1	18.6	17	12	12.7
Length P	15.4	14.5	12.5	9	12
Length V	13.9	13.9	12	9	10.7

common: lips red to orange with dark bands; a short moustache-like streak behind end of maxillary, running across hind margin of dentary and almost meeting opposite streak at midventral line and enclosing ivory-white of mandibular rami; another diagonal streak running from upper edge of maxillary, across lower edge of preopercle, across interopercle and branchiostegal rays, to base of pelvic fin, and enclosing white of preopercle, interopercle and chest (Fig. 8); first rays of pelvic fins white. Juveniles can have orange, white, and dark stripes (Fig. 9).

Habitat and distribution.— On hard bottoms (rock, gravel, coral rubble, or maerl) from about 1 m (juveniles) to at least 30 m depth. The new species is currently known with certainty only from the islands of São Tomé and Príncipe, where it is apparently common in suitable habitats (Luiz Rocha and John McCosker, CAS, personal communication). If the DNA analyses of an aquarium specimen taken off Ghana (Figs. 10–11) show that specimen to be the same as *S. pulcher*, the new species is also present on the mainland coast of Africa in the Gulf of Guinea.

Comparison with other eastern Atlantic species of *Serranus*.— The species most similar in morphology to *Serranus pulcher* is *S. heterurus* Cadenat, 1937. The two species share the name-giving feature of *S. heterurus*, i.e. the upper lobe of the caudal fin is pointed and the lower lobe of the caudal fin is rounded (also the case in several western Atlantic *Serranus* species). *Serranus pulcher* and *S. heterurus* are the two smallest of the eastern Atlantic *Serranus* species. *Serranus pulcher* differs from all others except *S. heterurus* in a combination of the following characters (see also Table 6): dorsal fin X, 12; anal fin III, 7; 42–50 lateral-line scales; interorbital area without scales; upper lobe of caudal fin pointed, lower lobe of caudal fin rounded.

Table 4: Counts and measurements (in mm) of *Serranus pulcher* non-type specimens, provided by Phil Heemstra.

	H1	**H2**	**H3**	**H4**	**H5**	**H6**
SL	59	60	63	63	63	60
D	X,12	X,12	X,12	X,12	X,12	X,12
A	III,7	III,7	III,7	III,7	III,7	III,7
P	16/16	16/16	-	15/15	15/15	15/15
depth at D1	18.6	19.1	20.5	-	-	19
head length	22.7	24.3	24.8	25.2	24	24
snout length	5.4	5	5.4	-	6.6	5.2
orbit diameter	6.1	6.2	6.4	7	6.6	6.4
P length	16.5	16.7	18	17	17.3	14
V length	14.5	16.3	17.1	16	17.3	16
Ll	46	47	47	42	47	44

Table 5: Counts and measurements (in mm) of *Serranus pulcher* non-type specimens, provided by Francisco Reiner.

	D	**A**	**V**	**P**	**Lateral line scales**
R1	X,12	III,7	I,5/ I,5	I6/16	47/47
R2	X,12	III, 7	I,5/I,5	16/16	47/48
R3	X,12	III, 7	I,5/I,5	16/16	47/46
R4	X, 12	III,7	I,5/I,5	16/16	47/47
R5	X,12	III,7	I,5/I,5	16/16	48/48

Table 6: Main characteristics of the eastern Atlantic *Serranus* species.

Serranus	**Dorsal fin**	**Anal fin**	**Pectoral fin**	**Lateral line scales**	**Total gill rakers**	**TL (cm)**
accraensis	X, 12–13	III, 7 (–8)	17–18	45–48	18–21	20
atricauda	X, 15–16	III, (7–) 8	15–17	77–90	20–24	35
cabrilla	X, (13-) 14–15	II, 7 (–8)	15–17	69–78	18–23	40
hepatus	X, (11-) 12 (–13)	III, (6–) 7	15	(40–) 45–50	19–23	15
heterurus	X, 12	III, (6–) 7	(15–) 16–17 (–18)	44–47	(17-) 21–26	14
pulcher	X, 12	III, 7	(14–) 15 (–16)	(42-) 45–50	17–20	9
scriba	X, (14-) 15 (–16)	III, 7 (–8)	13–16	62–75	14–19	36

FIGURE 3. The most common color pattern of *Serranus pulcher*; near Santana Islet, São Tomé (photo Peter Wirtz).

FIGURE 4. Color of paratype ZSM 43880 shortly before capture (photo Nuno Vasco Rodrigues).

FIGURE 5. Rare color pattern of *Serranus pulcher*, near Rolas Islet, São Tomé (photo Peter Wirtz).

FIGURE 6. Rare color pattern (frightened animal) of *Serranus pulcher* from near Rolas Islet, São Tomé (photo Peter Wirtz).

FIGURE 7. Rare color pattern of *Serranus pulcher* from Príncipe Island (photo Dave Catania).

FIGURE 8. Throat color of *Serranus pulcher*, near Santana Islet, São Tomé (photo Peter Wirtz).

FIGURE 9. Juvenile (about 4 cm TL) near Bom Bom Islet, Príncipe (photo Peter Wirtz).

FIGURE 10. *Serranus* sp. from Ghana (photo J.F. Hemdal).

FIGURE 11. *Serranus* sp. from Ghana (photo Joe Russo).

FIGURE 12. *Serranus heterurus* from the Cape Verde Islands (photo Rogelio Herrera).

FIGURE 13. *Serranus heterurus* from Senegal (photo Sebastien Blache).

FIGURE 14. Throat of *Serranus heterurus* from the Cape Verde Islands (photo Patrick Louisy).

FIGURE 15. *Serranus heterurus* in alcohol; specimen from the Cape Verde Islands (ZSM 430516) (photo Dirk Neumann).

The values of all morphological variables measured in nine specimens of *S. heterurus* (i.e., those mentioned in the description of *S. pulcher*, above) overlapped with those of *S. pulcher*. The two species differ in live color: *S. heterurus* has seven narrow white bars along a wine-red body, the first one on the opercle, the last one directly before the tail fin, a crescent-shaped light blue or white mark directly behind the eye and small blue spots on head and vertical fins (Figs. 12–14). In alcohol-preserved specimens of *S. heterurus* (Fig. 15) the white bars are often still visible, the area between the tip of the snout and the eyes bears dark spots, and the upper margin of the fin membrane between the first dorsal spines is often blackish; the crescent-shaped mark directly behind the eyes is often still visible but brown.

Etymology.— *pulcher,* Latin, meaning beautiful.

Proposed English common name.— São Tomé Comber.

Remarks.— In the aquarium literature, Hemdal (2009) described and figured a *Serranus* species from the coast of Ghana called "Peppermint basslet". It is similar to *S. pulcher* (compare Figs. 10 and 11) and almost certainly belongs to the same species. A tissue sample from a specimen collected for the aquarium trade at Ningo, east of Tema harbour in Ghana, at about 12 m depth (05°41.177′N, 000°17.510′E) will be analysed for its DNA sequence.

Many years ago, the first author sent specimens and photographs of the new species to Phil Heemstra (SAIB), who agreed to describe it. But after several years during which he apparently made no progress on the description, Heemstra agreed to send all the specimens back. In the ensuing years, as collecting efforts using SCUBA on the islands of São Tomé and Príncipe became more common (see Afonso et al. 1999 and Wirtz et al. 2007), many more specimens of the new species became available. The species was, in fact, discovered to be quite common in coastal waters of the islands. It also appeared to be a species taken by aquarium collectors on the mainland coast of Africa off Ghana, although the identity of fish from that country has yet to be confirmed. Because we are finalizing a manuscript reviewing all eastern Atlantic members of the genus (Wirtz, Heemstra, and Iwamoto, in prep.), and because the species is common and frequently observed on the islands, we felt it necessary for us to provide a name and description of the species.

Acknowledgements

Dirk Neumann at the Zoologische Staatssammlung München took the photographs of the preserved specimens. For the loan of specimens, we are grateful to Roger Bills (SAIAB), Dave Catania (CAS), Ronald Fricke (SMNS), and Ulrich Schliewen (ZSM). Phil Heemstra (SAIAB) and Francisco Reiner (Centro Português de Estudo dos Mamíferos Marinhos, Lisbon) kindly provided data on specimens of *S. pulcher* and *S. heterurus* in their collections (Tables 4 and 5). Nuno Vasco Rodrigues captured four fresh specimens of *S. pulcher* at São Tomé Island, including the holotype, which were essential for the description of the species. Nuno Vasco Rodrigues, Rogelio Herrera, Sebastien Blache, and Patrick Louisy provided photos of living specimens of *S. pulcher* and *S. heterurus*. Jay Hemdal kindly sent a photo of the Ghana *Serranus* which is likely to be *pulcher*. We thank John McCosker, Dave Catania, and Luiz Rocha (CAS) for collecting specimens and tissue of the new species and for use of their photographs of fresh and living specimens; McCosker also kindly reviewed the manuscript and provided sage advice. The second author (TI) gratefully acknowledges Jens-Otto Krakstad and Oddgeir Alvheim, Institute of Marine Research, Bergen, Norway, for facilitating his participation in fishery surveys of the *R/V Dr. Fridtjof Nansen*, in particular those surveys in 2010 off São Tomé and Príncipe (STeP) and in 2012 in the Canary Current Large Marine Ecosystem during which specimens of *S. heterurus* and other *Serranus* species were collected. We received necessary permits and cooperation from Arlindo Carvalho, Director-General of the Ministry of Environment, and João Pessao, Director of Fisheries, São Tomé and Príncipe (STeP). Virginia Carvalho and José Dias Sousa Lopes of STeP Fisheries were particularly helpful during the 2010 *Nansen* survey of the islands. Many thanks to Ulrich Schliewen and Dirk Neumann for providing facilities at the ZSM for the first author to examine specimens and for many helpful comments. Thanks also to Rick Feeney of the Natural History Museum of Los Angeles County for sending a copy of the unpublished Ph.D. thesis of M.R. Meisler (1987). The Centro de Ciências do Mar (CCMAR) of the University of the Algarve co-financed three trips of the first author to São Tomé and Príncipe Islands.

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Twenty-six New Species of Predaceous Ground Beetles (Coleoptera: Adephaga: Carabidae) from Ranomafana National Park, Madagascar

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As part of an inventory of the carabid beetle fauna of Ranomafana National Park, Fianarantsoa Province, Madagascar, we introduce 26 new species, for each of which the Park is designated as type locality: *Brachypelus ranomafanae* sp.nov., *Caelostomus latus* sp.nov., *C. rotundiformis* sp.nov., *Dactyleurys minimus* sp.nov., *D. ranomafanae* sp.nov., *Trichinillus* (*Mallopelmus*) *ranomafanae* sp.nov., *Chlaenius kathrynae* sp.nov., *C. robertae* sp.nov., *Omphreoides ranomafanae* sp.nov., *Perigona* (*Ripogena*) *deuvei* sp.nov., *P.* (*R.*) *ranomafanae* sp.nov., *Archicolliuris ranomafanae* sp.nov., *Thysanotus bimaculatoides* sp.nov., *Madecassina bimaculata* sp.nov., *M. quadrimaculata* sp.nov., *Pristacrus ranomafanae* sp.nov., *Eurydera ocellata* sp.nov., *E. oracle* sp.nov., *E. simplica* sp.nov., *Pseudomasoreus ranomafanae* sp.nov., *Assadecma basilewskyi* sp.nov., *Lebia laterolucida* sp.nov., *L. ranomafanae* sp.nov., *L. apicoviolacea* sp.nov., *Eunostus minimus* sp.nov., and *Erephognathus ranomafanae* sp.nov. We provide information on type material, derivation of species name, features for recognition and known geographical and habitat distributions, as well as digital images of habitus and other key features for each species, all but two of which are currently known only from the type area.

KEYWORDS: Coleoptera, Carabidae, new species, Ranomafana National Park, Madagascar

Madagascar is one of the world's most important biodiversity hotspots (Myers 1998) and conservation priorities (Mittermeier et al. 2004, Brooks et al. 2006). Most of the species living in Madagascar are precinctive (Brooks et al. 2002, Goodman and Benstead 2004). For example, almost all of Madagascar's reptile and amphibian species, and all of its lemurs can be found nowhere else on the planet. The uniqueness of the Malagasy biota can be explained at least in part by its long period of geographic isolation (for more than 65 million years (Krause 2004)), its topographical variation, its diversity of climatic zones and its great diversity of habitats, from the deserts of the hot and dry southern region to the lush rainforests of the north and east.

About 1350 carabid beetle species have been documented as occurring in Madagascar, with most of them treated by Basilewsky (1973, 1976, 1985) and Jeannel (1946, 1948, 1949). Of the known species, about 95% are precinctive. The known distributional ranges of many of the species are limited to a single or only few localities, and the fauna of much of the island remains inadequately sampled and largely unknown. It's highly probable that the Malagasy fauna, when better known, will exceed 2,000 carabid species.

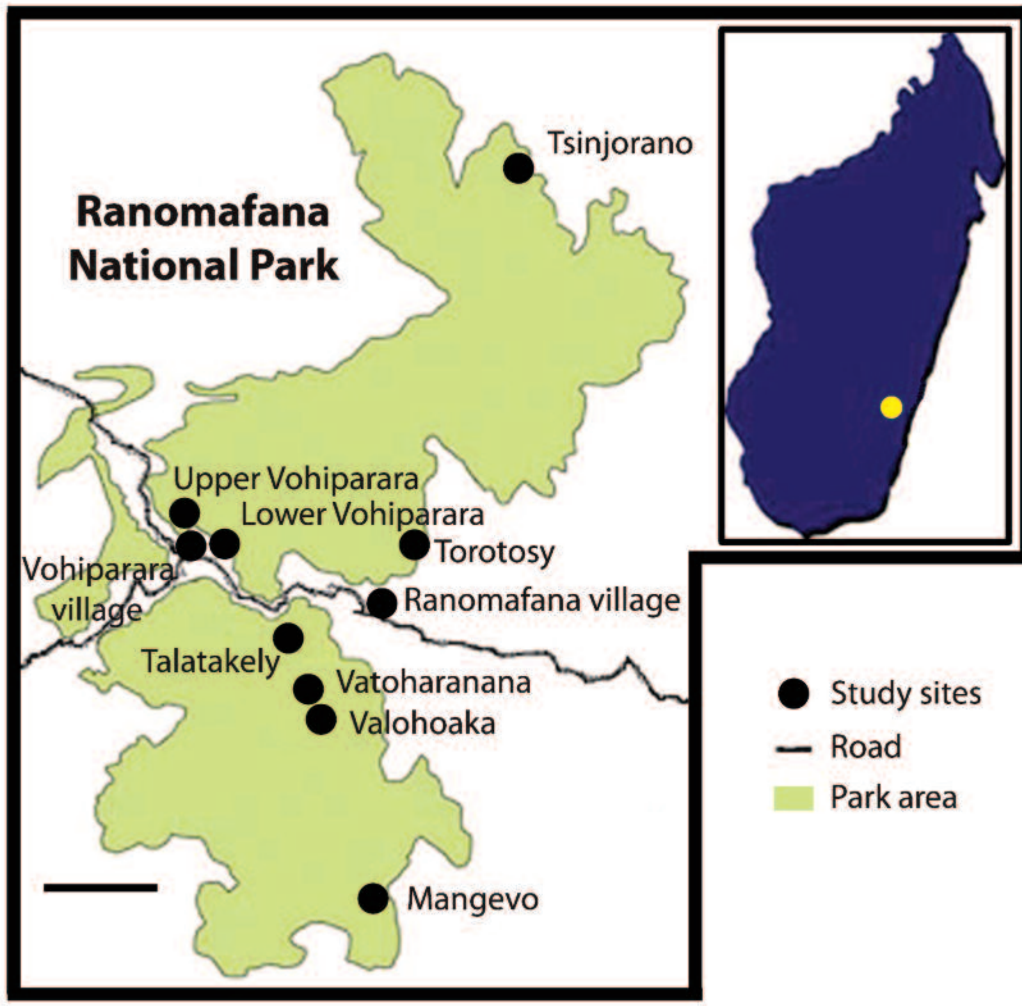

FIGURE 1. Map showing location of Ranomafana National Park in Madagscar (yellow dot in inset) and Park area, collecting sites and other places named in the text. Scale line = 5.0 km.

The geographical focus of this presentation is the carabid fauna of Ranomafana National Park (RNP), located in the southeastern part of the island, centered at about 21.25°S, 47.42°E (Fig. 1). Inaugurated in 1991 as the fourth national park in Madagascar, it is recognized both nationally and internationally as one of the world's most important conservation areas because of its exceptionally high species diversity and the immediate threat from human activity if not protected. It was included as part of the Rainforests of the Atsinanana World Heritage site in 2007. The park lies on the edge of Madagascar's High Plateau, with elevations ranging from 500 meters to 1,500 meters above sea level. The steepness of the slopes had preserved the park from exploitation before 1986. The range of altitudes allows for many different forest types, from lowland rainforest to cloud forest and high plateau forest. The park is divided into a core protected zone of 41,500 hectares surrounded by a peripheral (buffer) zone in which some exploitation of the forest is permitted. The peripheral zone contains more than 100 villages totalling more than 25,000 residents, most of them subsistence farmers.

Rainio and Niemala (2006) provided the first inventory of the carabid beetles of Ranomafana National Park. Their interest was to determine whether or not carabid beetles could be used as bioindicators of environmental change in and around the Park (Raino and Niemalä 2003). Based on fieldwork between 2000 ansd 2005, they documented 127 carabid species in the fauna of the Park, including 37 species previously undescribed. Working independently, field teams from the California Academy of Sciences sampled the carabid fauna of the Park during several expeditions between 1998 and 2002 and raised the number of species known from RNP to more than 250, including nearly 50 new species.

The purpose of this presentation is to make the names of 26 of these new species available for use by systematists, ecologists and resource managers though the presentation of economic and efficient treatments for each (see Erwin & Johnson 2000) that satisfy the requirements of the International Commission on Zoological Nomenclature (ICZN 2000) for availability and validity. The remaining undescribed species, mostly platynines, will be treated in a separate paper to follow. A full inventory of the known carabid fauna of RNP, with habitat distributions for each species included, is in preparation.

Materials and Methods

All but four of the new species described here were collected from Ranomafana National Park (RNP) or in the surrounding peripheral zone by our field teams during the period 1998–2005. Within the Park itself, collecting sites were located in both secondary (Talatakely and "Upper Vohiparara") and primary montane forests (Vatoharanana and Valohoaka). Talatakely is low secondary montane forest, which was selectively logged in 1986–1989. The range of elevations at which specimens were collected in this area is from about 925 to 1000 m. "Upper Vohiparara" is our name given to a secondary montane forest site about 2 km northwest of Vohiparara village and accessible from there by both road and trails. The range of elevations at which specimens were collected in this area is from about 1140 to 1170 m. The Vatoharanana and Valohoaka sites are in primary montane rain forest, four and eight km south of Talatakely and at elevations of about 980 and 1080 m, respectively. At Vatoharanana, there has been some logging, but Valohoaka is undisturbed. The peripheral zone consists of a varied mosaic of cultivations, abandoned tavy-fields and forest edges. Within this peripheral zone, specimens were collected from the following villages and their environs: Mangevo, Ranomafana, Torotosy, Tsinjorano and Vohiparara (see Fig. 1)

Most specimens were collected by hand using the following methods: beating vegetation and accumulations of dead leaves in vegetation up to a height up to 3 m above ground; shaking trees and scraping bark and mossy and epiphytic coatings on them onto beating sheets; breaking into decaying logs; turning logs and stones on the forest floor. Collections were made during both day (DHK and JR) and night (DHK) hours using all of these methods. Pitfall trapping and sifting of forest litter with subsequent extraction using mini-Winkler extractors (Fisher 1998) were used as additional collecting methods.

Materials.— This study is based on a total of 8,025 carabid specimens collected during the course of our respective field programs between 1998 and 2005 plus an additional 300 specimens from RNP borrowed from other collections (see below). About 265 different carabid species were represented in the material assembled, including the 26 new species described here. Except as noted in the text, holotypes were examined for all species mentioned in comparisons.

Codens used in this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

CAS California Academy of Sciences, San Francisco, U.S.A.
EMEC Essig Museum of Entomology, University of California, Berkeley, California, U.S.A.
MZF Finnish Museum of Natural History, Helsinki, Finland
MNHN Muséum National d'Histoire Naturelle, Paris, France
MTEC Montana State University, Bozeman, Montana, U.S.A.
NMNH United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Examination of specimens.— Specimens were examined using a Wild M5 and Leica MZ9.5 stereoscopic microscope with a Proline 80 LED Ring Illuminator.

Measurements.— Measurements were made using a Leitz stereoscopic dissecting microscope with a calibrated ocular grid with a scale interval of 0.1 mm. The measurements used in this report include standardized body length (SBL), which equals the sum of head length (HL), measured from the apex of the clypeus to a point on the midline at the level of the posterior margin of the ocular swelling), pronotum length (PL), measured from the apical margin to the basal margin along the midline, and elytral length (EL), measured along the midline from the apex of the scutellum to the apex of the longer elytron. Readers should be aware that SBL is typically about 15% shorter than body length measured as a single distance from apex of the mandibles or labrum to apex of the elytra, and this difference should be considered when comparing length data presented here with length data in the literature. Nonetheless, we prefer SBL as a comparative of body length because it eliminates errors due to different alignments of body regions among different specimens. In distinguishing some species, we also use certain ratios as diagnostic features. These include the ratios of: pronotal width (PW) to pronotal length (PW/PL, with PW measured cross the pronotum at its widest point); elytral length to pronotal length (EL/PL); elytral length to elytral width (EW) (EL/EW, with EW measured across both elytra at their widest point); and standardized body length to elytral width (SBL/EW).

Dissections.— Male genitalia were extracted from specimens relaxed in water immediately after it had boiled and to which a few drops of liquid detergent had been added. Genitalic preparations were then cleared in hot 10% potassium hydroxide solution for five to 10 minutes, each constantly monitored to achieve only a useful degree of clearing. They were then rinsed briefly in 10% acetic acid and then repeatedly in distilled water. After examination, preparations were stored in glycerin in polyethylene microvials and pinned beneath their specimens of origin.

Illustrations.— Digital images of whole specimens and particular structures were taken using a Leica imaging system including an M165C dissecting microscope, DFC550 video camera, and two KL1500 LCD light sources. Stacked images were captured and combined into single montage images using the Leica Application Suite V4.2.0. Plates of images were created using Adobe Photoshop CS5.

Systematics

The arrangement of species treatments and suprageneric classification used here follows Lorenz (2005), the most current world standard, rather than the arrangement and classification of Jeannel (1946, 1948, 1949). Several of Jeannel's suprageneric names are no longer in common use and the arrangement of taxa in his three-part work is different from that now recognized by most current carabid systematists.

Tribe Scaritini Bonelli 1810
Subtribe Clivinina Rafinesque 1815

Genus *Brachypelus* Putzeys 1866

Jeannel (1946) included only two species in his treatment of this precinctive Malagasy genus, and Basilewsky (1976) described three additional species. Bulirsch et al. (2005) described eight new species and provided a key to all species known at that time. Finally, Bulirsch and Moravec (2009) described one more new species, *B. janaki*, bringing the total number of known species to 14. Members of the new species described below are easily distinguish from those of all the other described species on the basis of their unique combination of features compared with excellent key characters provided by Bulirsch et al. (2005).

Brachypelus ranomafanae **Kavanaugh and Rainio, sp. nov.**
Figures 2–3

Brachypelus n. sp.1; Rainio 2009: 31 (informal designation).

Type material.— Holotype (Figs. 2A–B), a female, in CAS, labeled: "MADAGASCAR Ranomafana NP. Talatakely, X, 130 m. 15.1.2001"/ "collected in pitfall trap on forest floor, F. Ratalata & J. Rainio collectors"/ "32." [handwritten label]/ "HOLOTYPE *Brachypelus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Large for genus, SBL = 6.8 mm. Members of this species (Fig. 2A) are most similar to those of *Brachypelus obesus* Putzeys (1866), with which they share large size, only six setae on the labrum, and a single discal setiferous pore on elytral interval 3 (at apical one-fifth). They differ from *B. obesus* members in the following: transverse fronto-clypeal suture present and deeply impressed (Fig. 3A) (absent from *B. obesus* members); frons with longitudinal frontal furrows narrower and shallower than in *B. obesus*; posterior lateral margins of the eyes broadly rounded (more narrowly and angularly rounded in *B. obesus* members); elytral base (Fig. 3B) straight between intervals 3 and obliquely sloped laterally from interval 4 (elytral base straight between intervals 4 and gradually rounded laterally from interval 3 in *B. obesus* members); elytra with lateral margin distinctly toothed at humerus (smoothly rounded at humerus, without a tooth in *B. obesus* members); and elytral intervals slightly convex apically (nearly flat in *B. obesus* members). Others species with members of comparably large size include *Brachypelus rolandi* Bulirsch et al. (2005), *Brachypelus betsileo* Bulirsch et al. (2005), *Brachypelas fischeri* Bulirsch et al. (2005) and *Brachypelus janaki* Bulirsch and Moravec (2009). However, *B. ranomafanae* members differ from those of *B. rolandi* in having the labrum with only six setae (seven in *B. rolandi* members), elytra widest at middle (anterior to middle in *B. rolandi* members), and elytral intervals moderately convex throughout (flattened apical in *B. rolandi* members). Members of both *B. betsileo* and *B. fis-*

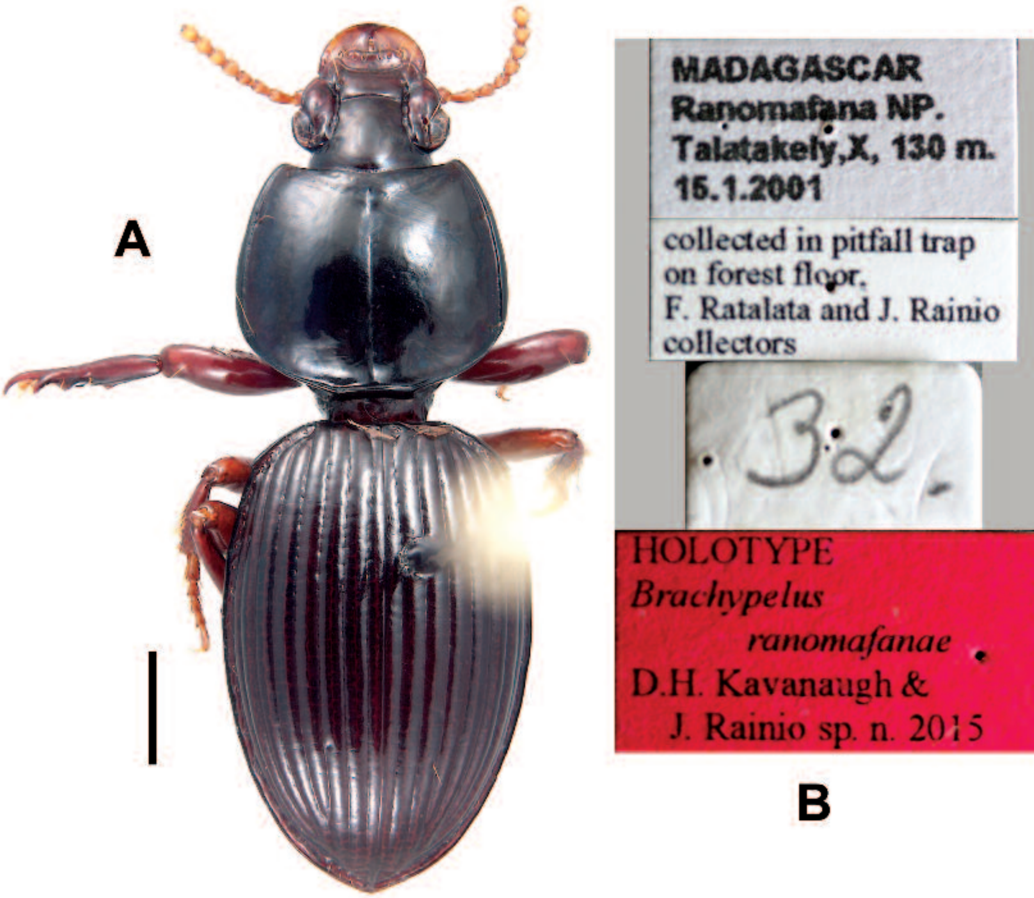

FIGURE 2. Digital images of holotype female of *Brachypelus ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

cheri have seven labral setae (whereas those of *B. ranomafanae* have only six) and lack discal setiferous pores (those of *B. ranomafanae* have a single setiferous pore in the apical one-fifth on interval 3. Finally, *B. ranomafanae* members differ from those of *B. janaki* in having only six setae on the labrum (seven labral setae in *B. janaki* members), the elytral margin with a distinct humeral tooth (tooth absent from *B. janaki* members), and only a single discal setiferous pore on elytral interval 3, with intervals 5 and 7 without such punctures (five or more such punctures on intervals 3, 5 and 7 in *B. janaki* members).

GEOGRAPHICAL DISTRIBUTION.— At present, known only from the type locality.

HABITAT DISTRIBUTION.— The unique holotype was collected in a pitfall trap placed in secondary montane rain forest in the Talatakely area, at an elevation of 900 m, at the 130 meter mark along Trail "X". Vegetation in that area consisted of bamboo, small young trees and some larger trees with diameters at breast-height (DBH) of 20–30 cm. Tree trunks and branches were mostly covered with epiphytes and lianas.

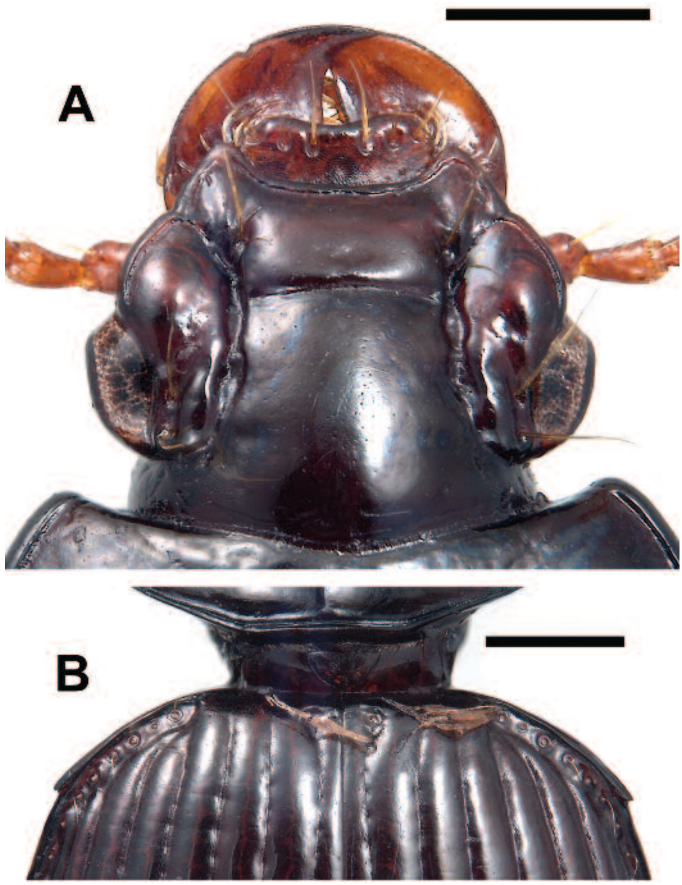

FIGURE 3. Digital images of holotype female of *Brachypelus ranomafanae* Kavanaugh & Rainio sp. nov. A. Head, dorsal aspect; B. Elytral base, dorsal aspect. Scale lines = 0.5 mm.

Cratocerinini Lacordaire 1854

Phylogenetic relationships among the "Pterostichini" in the broadest sense and the cratocerines in particular remain largely unresolved (see Grzymala and Will (2014) for an example). We follow the classification as presented in Lorenz (2005).

Substribe Drimostomatina Chaudoir 1872

Genus *Caelostomus* MacLeay 1825

Caelostomus latus **Kavanaugh and Rainio, sp. nov.**
Figure 4

TYPE MATERIAL.— Holotype (Figs. 4A–B), a female, in CAS, labeled: "MADAGASCAR Ranomafana NP. Talatakely, Trail C, 350 m. 10.5.2005"/ "HOLOTYPE *Caelostomus latus* Kavanaugh & Rainio sp. n. 2015" [red label].

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

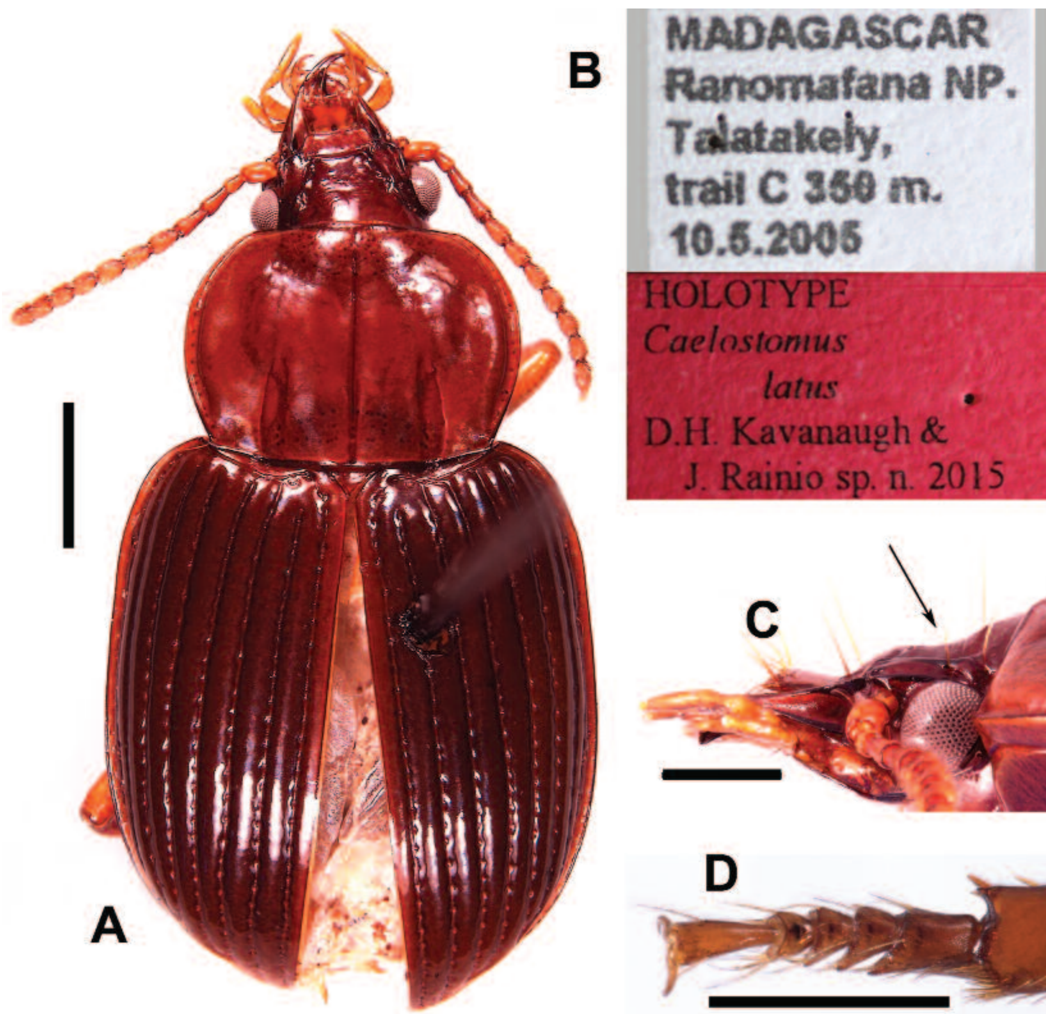

FIGURE 4. Digital images of holotype female of *Caelostomus latus* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C. Head, left lateral aspect (arrow points to tranverse depression between eyes); D. Right anterior tarsus, dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.5 mm.

DERIVATION OF SPECIES NAME.— The species epithet, *latus*, is the Latin adjective meaning broad or wide, a reference to relatively broad pronotum of the holotype specimen and, presumably, other members of this species.

RECOGNITION.— Size moderate for genus, SBL = 6.3 mm. Based on Jeannel's (1948) key, this species is a member of subgenus *Caelostomus* s. str. It's members (Fig. 4A) share with those of other members of the subgenus the following features: head with frons and frontal furrows smooth, impunctate; elytral base distinctly margined from humerus medially to base of stria 3 or 2; elytral striae 6 and 7 deeply impressed throughout, not effaced apically; lateral elytral intervals narrow, moderately convex; apical part of umbilicate series of setiferous pores not inserted in a deep groove; and female apical abdominal ventrite with (two or) three pairs of setae subapically. Within the subgenus, the following features are shared only with members of two species of Jeannel's *convexiusculus* group, namely *Caelostomus convexiusculus* Tschitschérine (1899) and *Caelosto-*

mus alluaudi Jeannel (1948): SBL greater than 6.0 mm, elytra short and broad, ratio EL/EW = 1.19, elytral disc convex; and elytral intervals distinctly punctate throughout, including in apical part. The holotype female of *C. latus* is slightly larger than members of these other two species, has a distinct and broad transverse depression between the eyes seen best in lateral view (Fig. 4C) (depression absent from members of the other two species). The pronotum in the holotype of *C. latus* is much wider than in *C. convexiusculus* members, slightly wider than in *C. alluaudi* members, and less depressed anterolaterally than in members of either of the other species; and the pronotal basal foveae are straighter and more sharply defined laterally than in members of the other two species. The elytra are less abruptly rounded laterally and apically than in *C. alluaudi* members but similar to shape in to those in *C. convexiusculus* members. Finally, anterior tarsomeres 1 to 3 of the female holotype of *C. latus* are distinctly toothed medioapically (Fig. 4D), a feature not seen in females of the other two species.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype female was collected by hand in secondary montane forest in the Talatakely area.

Caelostomus rotundiformis Kavanaugh and Rainio, sp. nov.

Figure 5

Caelostomus n. sp. 1; Rainio 2009: 31, Rainio 2012: 62 (informal designation).

Type material.— Holotype (Figs. 5A–B), a female, in CAS, labeled: “MADAGASCAR Ranomafana NP., Vatoharanana, Trail K at 50 m mark, 07.06.2000”/ “collected by hand in daytime, F. Ratalata & J. Rainio collectors”/ “13.” [handwritten label]/ “7.6.00 K 50” [handwritten label]/ “HOLOTYPE *Caelostomus rotundiformis* Kavanaugh & Rainio sp. n. 2015” [red label]. Paratypes (only 1): a female (in MNHN) labeled “MADAGASCAR Ranomafana NP. Talatakely, C1450 11.3.2004 Johanna Rainio leg.”/ “112.” [handwritten label]/ “PARATYPE *Caelostomus rotundiformis* Kavanaugh & Rainio sp. n. 2015” [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *rotundiformis*, is an adjective derived from the Latin words, *rotundus*, meaning round, and *forma*, meaning form or shape. The name refers to the very short, broad, rounded form of members of this species.

Recognition.— Size moderately small for genus, SBL = 5.4–5.5 mm (females only), body form (Fig. 5A) short and broad, ratio SBL/EW = 1.97–2.01. This species is undoubtedly a member of genus *Caelostomus* as conceived by Jeannel (1948), although we cannot confirm this based on his key because he used male features only in two couplets to distinguish *Caelostomus* members from those of several other genera and we have only female specimens. However, we examined specimens of all species in all the other Malagasy caelostomine genera while at MNHN and confirmed that this species represents none of them. Observable female features, including body form short and broad, frontal furrows simple, not doubled, parascutellar striae of elytra indistinct, basal setiferous pore situated at base of elytral stria 3, tarsomeres not densely setose ventrally, and anterior tarsomere 4 not bilobed apically (Fig. 5C), are consistent with *Caelostomus* females. Within this genus, members of *C. rotundiformis* share the following features with those of other species of the nominate subgenus: head with frons and frontal furrows smooth, impunctate; elytral base distinctly margined from humerus medially to base of stria 3 or 2; elytral striae 6 and 7 deeply impressed throughout, not effaced apically; lateral elytral intervals narrow, moderately convex; apical part of umbilicate series of setiferous pores not inserted in a deep groove; and female apical abdominal ventrite with (two or) three pairs of setae subapically. However, members of this species

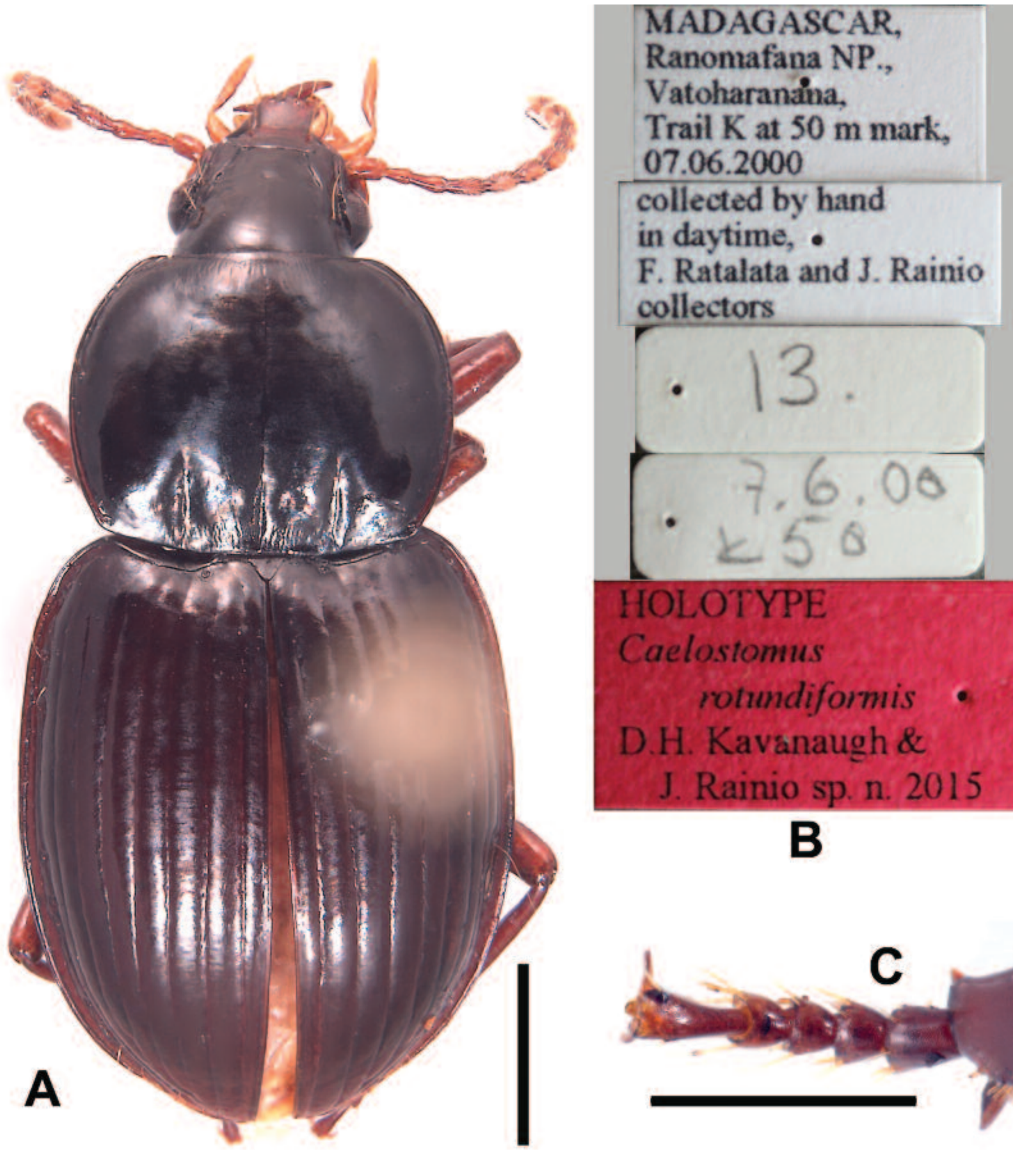

FIGURE 5. Digital images of holotype female of *Caelostomus rotundiformis* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C. Right anterior tarsus, dorsal aspect. Scale line A = 1.0 mm, C = 0.5 mm.

confound Jeannel's (1948) key to species of *Caelostomus* s. str. Their short and broad elytra (ratio EL/EW = 1.13–1.15) are shared with members of the *convexiusculus* species group, but their elytral striae are impuncate, whereas those of other species group members are markedly punctate throughout their length. Within the group, their small size (less than 6.0 mm) is shared with *Caelostomus humilis* (Tschitschérine 1903), *Caelostomus minisculus* Straneo (1940), and *Caelostomus minutissimus* Jeannel (1948); however, members of these three species are even smaller (SBL = 5.0 mm or less) and, again, have markedly punctate elytral striae. The striae in *C. rotundiformis* members are smooth, without evident punctures, and the shape of the pronotum

(Fig. 5A) is markedly different, with lateral margins evenly arcuate throughout their length and hind angles markedly obtuse. This species probably represents a distinct species group of its own within subgenus *Caelostomus* in Madagascar.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The holotype of this species was collected by hand in daytime in primary montane rain forest in the Vatoharanana area at an elevation of 1200 m, along Trail K at the 50 meter mark. The paratype specimen was collected in a pitfall trap in secondary montane rain forest in the Talatakely area at an elevation of 900 m, along Trail C at the 1450 meter mark.

Genus *Dactyleurys* Tschitschérine 1899

Jeannel (1948) recognized a single species in Madagascar, *Dactyleurys anomalus* Tschitschérine (1899) and no additional species have been described subsequently. The two new species described below bring the total for the genus to three species, all precinctive to Masdagascar.

Dactyleurys minimus Kavanaugh and Rainio, sp. nov.

Figures 6, 8A, 9A, 9D

Type material.— Holotype (Figs. 6A–B), a male, in CAS, labeled: “MADAGASCAR, Ranomafana NP, Talatakely, X at 130 m mark 12.4.2005”/ “collected by hand in daytime, F. Ratalata & Johanna Rainio collectors”/ “HOLOTYPE *Dactyleurys minimus* Kavanaugh & Rainio sp. n. 2015” [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *minimus*, is the Latin adjective meaning smallest, a reference to fact that the known adult male of this species is smaller than males of any of the other known species that we have examined.

Recognition.— Smallest adult known for the genus, SBL = 6.9 mm. The following combination of features identify members of this species as coelostomine pterostichines of the genus *Dactyleurys*: antennae with antennomere 3 attached symmetrically or nearly symmetrically to antennomere 2; mentum with deep emargination, apex of median mental tooth distinctly posterior to apices of epilobes; elytron with epipleuron interrupted by internal plica subapically; parascutellar stria not evident; basal setiferious puncture situated at base of stria 3; tarsomeres 1 to 4 of all legs with dense pads of setae ventrally; front and middle tarsomeres 1 to 3 smoothly convex dorsally; male front tarsomeres 1 to 4 wide, dilated, not latero- or medioapically toothed; aedeagus of male with right face dorsal in repose, right paramere conchoid, left paramere reduced, short, apically digitiform. Members of *D. minimus* (Fig. 6A) differ from those of *D. anomalus* in the following features: smaller size (SBL = 6.9 mm compared with 7.7–9.4 mm in *D. anomalus*); pronotum (Fig. 8A) relatively narrower, widest at middle (relatively wider (Fig. 8C) and clearly widest anterior to middle in *D. anomalus*); elytra faintly but evidently iridescence and elytral microsculpture markedly transverse with sculpticells great than 2.5 times as wide as long (elytra not iridescent and elytral microsculpture moderately transverse with sculpticells less than 2.5 times as wide as long in *D. anomalus*); and median lobe of male genitalia (Fig. 9A) with shaft abruptly bent ventrally in apical fourth with apex nearly straight in lateral aspect (shaft nearly straight ventrally (Fig. 8C) in apical fourth with apex slightly recurved dorsally in *D. anomalus*), apex narrowly rounded in dorsal aspect (Fig. 9D) (more broadly rounded (Fig. 9F) in *D. anomalus*). Members of *D. minimus* differ from those of the other new species, *Dactyleurys ranomafanae*, in the following fea-

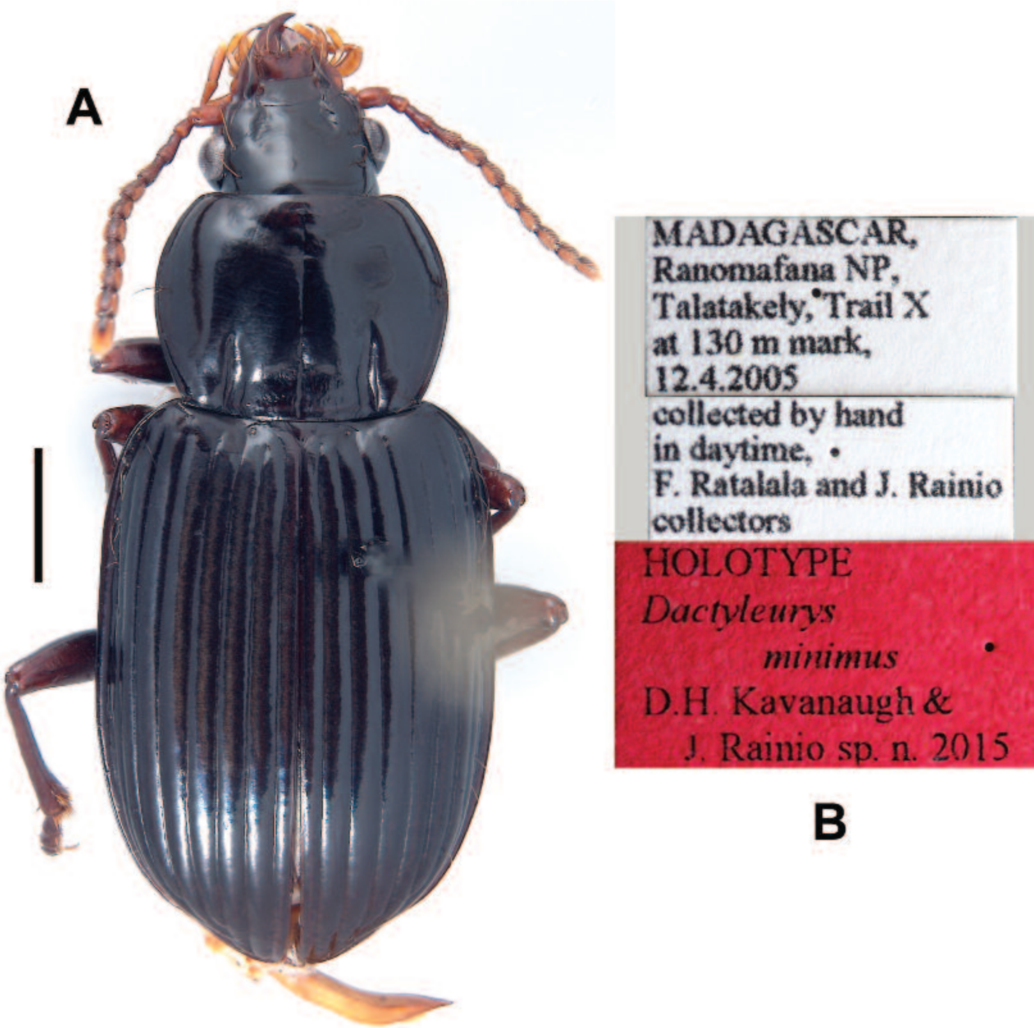

FIGURE 6. Digital images of holotype male of *Dactyleurys minimus* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

tures: smaller size (SBL = 7.7–8.3 mm in *D. ranomafanae*); pronotum (Fig. 8A) relatively narrower and with evenly rounded lateral margin (slightly wider (Fig. 8B) and with lateral margin slightly straighter in basal one-third in *D. ranomafanae*); and median lobe of male genitalia (Fig. 9A) with apex nearly straight in lateral aspect (apex slightly recurved dorsally (Fig. 9C) in *D. ranomafanae*), apical part of shaft (Fig. 9D) slightly deflected right in dorsal aspect (apical part of shaft (Fig. 9E) straight in *D. ranomafanae*).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype was collected by hand in daytime in secondary montane rain forest in the Talatakely area, at an elevation of 900 m, at the 130 meter mark along Trail "X". Vegetation in that area consisted of bamboo, small young trees and some larger trees with diameters at breast-height (DBH) of 20–30 cm. Tree trunks and branches were heavily laden with epiphytes and lianas.

Dactyleurys ranomafanae **Kavanaugh and Rainio, sp. nov.**
Figures 7, 8B, 9B, 9E

Dactyleurys n. sp. 1; Rainio 2009: 31, Rainio 2012: 62, Rainio 2013: 95 (informal designation).

Type material.— Holotype (Figs. 7A–B), a male, in CAS, labeled: “CASENT 1009744”/ “MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 26 April 1998”/ “21°15.3’S/ 47°25.9’E, Stop #98-83 D.H. Kavanaugh collector collected by beating *Pandanus* tree boluses with debris”/ “HOLOTYPE *Dactyleurys ranomafanae* Kavanaugh & Rainio sp. n. 2015” [red label]. Paratypes (a total of 35): 1 male (in MZF) labeled “MADAGASCAR Ranomafana NP. Mangevo, plot 0 m., 21.4.2005”; 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Mangevo, plot 100 m., 21.4.2005”; 2 females (in CAS) labeled same as holotype except “CASENT 1009742” and “CASENT 1009743”, respectively; 3 males and 2 females (in CAS) labeled “CASENT 1009737”, “CASENT 1009738”, “CASENT 1009739”, “CASENT 1009740” and “CASENT 1009741”, respectively/ “MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 25 April 1998”/ “21°15.3’S/ 47°25.9’E, Stop #98-78 D.H. Kavanaugh collector beaten from vegetation and suspended dead leaves”; 3 males and 2 females (in CAS and MNHN) labeled “CASENT 1009734”, “CASENT 1009735”, “CASENT 1009736”, “CASENT 1009732” and “CASENT 1009733”, respectively/ “MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,”/ “21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanaugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,”/ “E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors”/ “collected in daytime by beating live understory vegetation and/or dead leaves and other suspended debris”; 1 male and 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, 26.2.2001”; 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail B 1150 m., in *Pandanus* sp. 8.6.2000”; 1 male and 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail BF 380 m., in *Pandanus* sp. 16.6.2000”; 1 male and 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail BM 200 m., in *Pandanus* sp. 16.6.2000”; 1 male and 2 females (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail FBF 50 m., in *Pandanus* sp. 6.6.2000”; 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail FBF 380 m., in *Pandanus* sp. 6.6.2000”; 2 females (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail SP 50 m., 22.3.2001”; 1 female (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail SP 50 m., 9.2.2005”; 1 male (in MZF) labeled “MADAGASCAR Ranomafana NP. Talatakely, trail X 130 m., 12.4.2005”; 1 male (in MNHN) labeled “MADAGASCAR Ranomafana NP. Valohoaka, trail F 900 m., 28.2.2001”; 1 male (in MZF) labeled “MADAGASCAR Ranomafana NP. Valohoaka, trail F 850 m., 16.10.2002”; 1 male (in MNHN) labeled “MADAGASCAR Ranomafana NP. Valohoaka, trail F 850 m down., 18.12.2004”; 1 female (in MNHN) labeled “MADAGASCAR Ranomafana NP. Valohoaka, trail F 850 m., 25.1.2005”; 2 males and 1 female (in MNHN and MZF) labeled “MADAGASCAR Ranomafana NP. Valohoaka, trail F 850 m., 26.1.2005”. All paratypes also bear the following label: “PARATYPE *Dactyleurys ranomafanae* Kavanaugh & Rainio sp. n. 2015” [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size average for genus, SBL of males = 7.7–8.2 mm, of females = 7.8–8.4 mm . The following combination of features identify members of this species as coelostomine

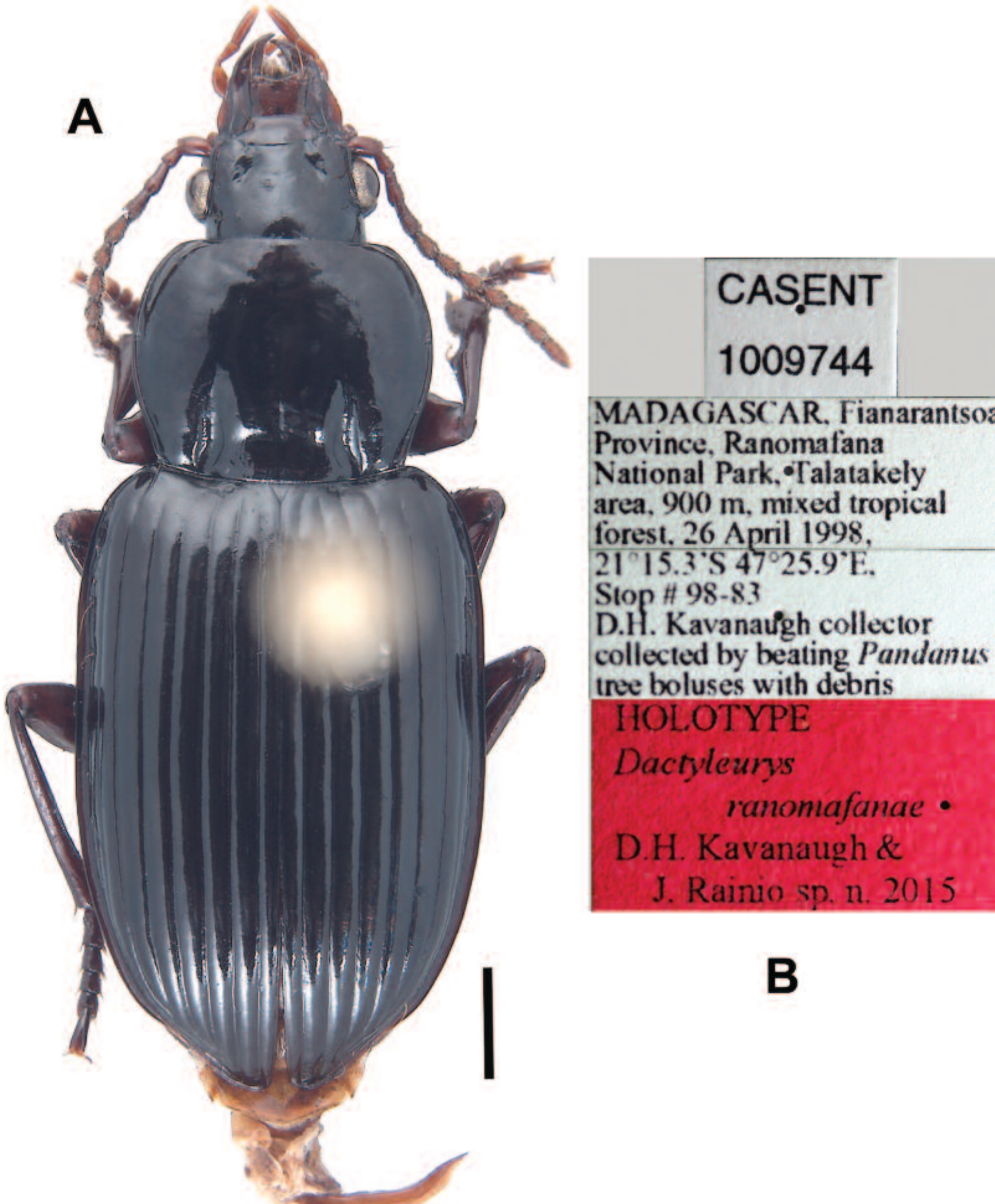

FIGURE 7. Digital images of holotype male of *Dactyleurys ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

pterostichines of the genus *Dactyleurys*: antennae with antennomere 3 attached symmetrically or nearly symmetrically to antennomere 2; mentum with deep emargination, apex of median mental tooth distinctly posterior to apices of epilobes; elytron with epipleuron interrupted by internal plica subapically; parascutellar stria not evident; basal setiferous puncture situated at base of stria 3; tarsomeres 1 to 4 of all legs with dense pads of setae ventrally; front and middle tarsomeres 1 to 3 smoothly convex dorsally; male front tarsomeres 1 to 4 wide, dilated, not latero- or medioapically toothed; aedeagus of male with right face dorsal in repose, right paramere conchoid, left paramere reduced, short, apically digitiform. Members of *D. ranomafanae* (Fig. 7A) differ from those of *D. anomalus* in the following features: pronotum (Fig. 8B) widest at middle (distinctly widest anterior to middle (Fig. 8C) in *D. anomalus*); elytra faintly but evidently iridescence and elytral microsculpture markedly transverse with sculpticells great than 2.5 times as wide as long (elytra not iridescent and elytral microsculpture moderately transverse with sculpticells less than 2.5 times as wide as long in *D. anomalus*); and median lobe of male genitalia (Fig. 9B) with shaft abruptly bent ventrally in apical fourth (shaft nearly straight ventrally (Fig. 8C) in apical fourth in *D. anomalus*), apex narrowly rounded in dorsal aspect (Fig. 9E) (more broadly rounded (Fig. 9F) in *D. anomalus*). Members of *D. ranomafanae* differ from those of the other new species, *D. minimus*, in the following features: larger size, SBL = 7.7–8.3 mm (size smaller, SBL = 6.9, in *D. minimus*); pronotum

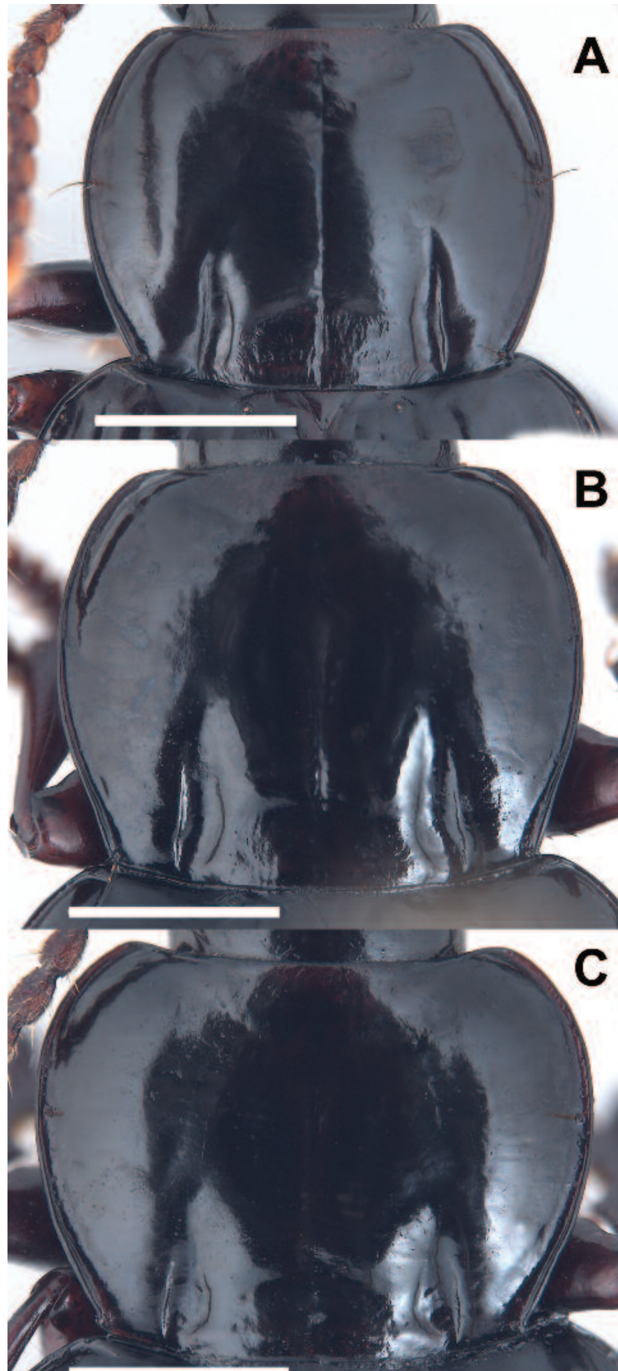

FIGURE 8. Digital images of pronota of *Dactyleurys* spp., dorsal aspect. A. Holotype of *D. minimus* Kavanaugh & Rainio sp. nov.; B. Holotype of *D. ranomafanae* Kavanaugh & Rainio sp. nov.; C. *D. anomalus* Tschitschérine. Scale lines = 1.0 mm

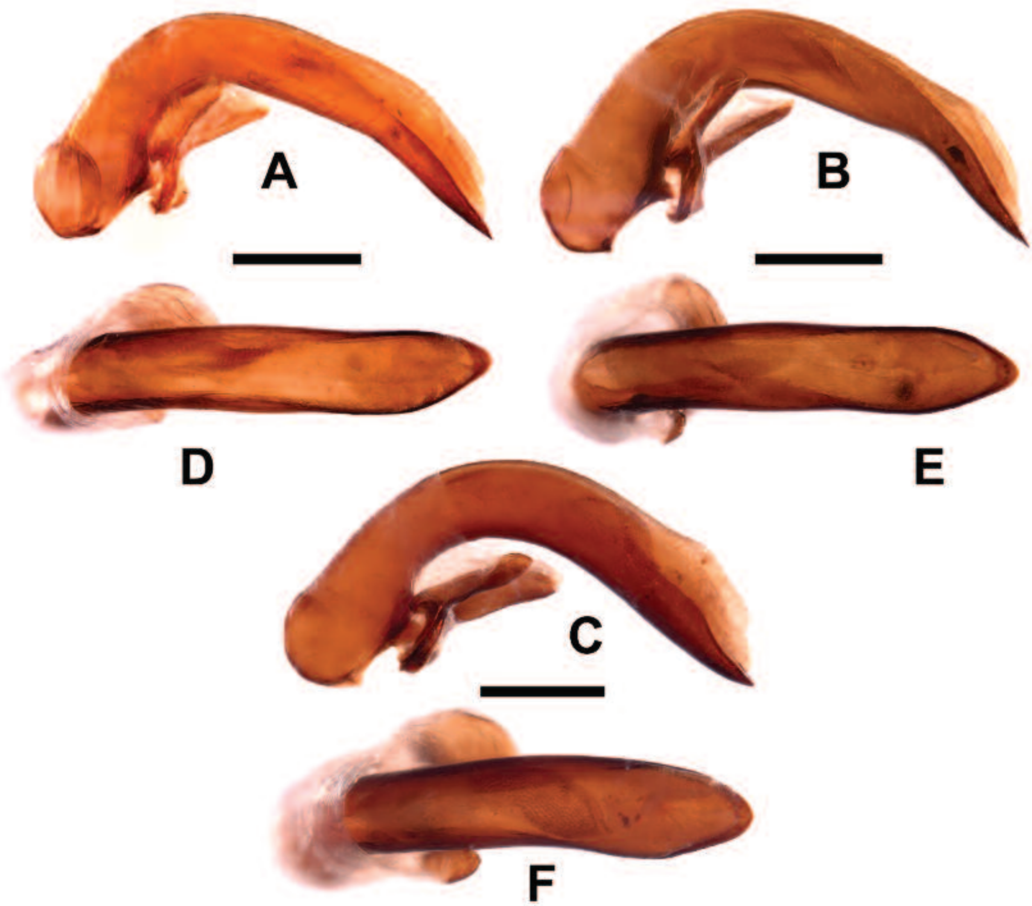

FIGURE 9. Digital images of aedeagus of male genitalia of *Dactyleurys* spp. A–C. left lateral aspect; D–F. dorsal aspect. A, D. Holotype of *D. minimus* Kavanaugh & Rainio sp. nov.; B, E. Holotype of *D. ranomafanae* Kavanaugh & Rainio sp. nov.; C, F. *D. anomalus* Tschitschérine. Scale lines = 0.5 mm.

(Fig. 8B) relatively broader and with lateral margins slightly straighter in basal one-third (slightly narrower and with lateral margins more evenly rounded (Fig. 8A) in *D. minimus*); and median lobe of male genitalia (Fig. 9B) with apex slightly recurved dorsally in lateral aspect (apex (Fig. 9A) nearly straight in *D. minimus*), apical part of shaft (Fig. 9E) straight (apical part of shaft slightly deflected right (Fig. 9D) in *D. minimus*).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Specimens of this species have been collected in both primary and secondary montane rainforest throughout RNP, at elevations ranging from of 900 to 1180 m. Most of the specimens were collected by beating vegetation, especially plants of *Pandanus* sp., and suspended accumulations of dead vegetative debris in shrubs and understory trees. One was collected in a malaise trap, another sifted from forest litter at the primary forest site, and another by hand at the secondary forest site.

Genus *Trichinillus* Straneo 1938
Subgenus *Mallopelmus* Straneo 1942

Mallopelmus Alluaud 1936, unavailable

Alluaud (1936) described this taxon as a new genus with several included species, but he failed to designate one of them as type species. This error rendered the name unavailable (ICZN 2000, Article 13.3) until Straneo (1942) designated *Mallopelmus dactyleuryoides* Alluaud (1936) (the first named species in Alluaud's (1936) paper) as the type species. Both Straneo (1938) and Jeannel (1948) treated *Mallopelmus* as a distinct genus. Straneo actually treated *Trichinillus* as a subgenus of *Mallopelmus* in his 1942 paper, apparently not realizing at the time that his designation of a type species for *Mallopelmus* changed the data of availability for that name, as well as its authorship, with the result that *Trichinillus* became the senior synonym for the genus. *Mallopelmus* is now considered a subgenus of *Trichinillus* (Lorenz 2005) and is precinctive to Madagascar.

***Trichinillus* (*Mallopelmus*) *ranomafanae* Kavanaugh and Rainio, sp. nov.**
Figure 10

Mallopelmus n. sp.1; Rainio 2009: 32, Rainio 2012: 74 (informal designation).

Type material.— Holotype (Figs. 10A–B), a male, in CAS, labeled: "MADAGASCAR Ranomafana NP. Buffer zone, degraded forest 14.10.2002"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "HOLOTYPE *Trichinillus* (*Mallopelmus*) *ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (only 1): a female (in MNHN) labelled "MADAGASCAR Ranomafana NP. Talatakely, trail B, 600 m. 05.03.2004"/ "collected by hand in daytime from dead leaves in bushes, F. Ratalata and J. Rainio collectors"/ "PARATYPE *Trichinillus* (*Mallopelmus*) *ranomafanae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Slightly smaller than average for subgenus, SBL male = 7.2 mm, female = 7.5 mm. The following combination of features identify members of this species as coelostomine pterostichines of the genus *Trichinillus*, subgenus *Mallopelmus*: antennae with antennomere 3 attached symmetrically or nearly symmetrically to antennomere 2; mentum with deep emargination, apex of median mental tooth distinctly posterior to apices of epilobes; elytron with epipleuron interrupted by internal plica subapically; parascutellar stria short but evident; striae smooth, impunctate; basal setiferious puncture situated at base of stria 2 + parascutellar stria; tarsomeres 1 to 4 of all legs with dense pads of setae ventrally; front and middle tarsomeres 1 to 3 with more or less faintly-defined longitudinal groove medially and depressed areas paralaterally on dorsal surface; male front tarsomeres 1 to 4 wide, dilated, not latero- or medioapically toothed; aedeagus of male with right face dorsal in repose, right paramere conchoid, left paramere reduced, short, apically digitiform. Of the three previously described species represented in Jeannel's (1948) key to *Mallopelmus* species, members of *T. ranomafanae* (Fig. 10A) are most similar to *Trichinillus abacetoides* (Alluaud 1936) members based on the following shared features: head with temporal area long, nearly as long as the diameter of the eye, and joined to the neck region at a very obtuse (about 165°) angle; eyes moderately convex and projected; pronotum with basal area distinctly and abruptly depressed relative to disc; and elytral base without margination medial to base of stria 6. Members of the other two species, *Trichinillus dactyleuryoides* (Alluaud 1936) and *Trichinillus perrieri* (Jeannel 1948), differ in having the head with the temporal area shorter, about one-third as

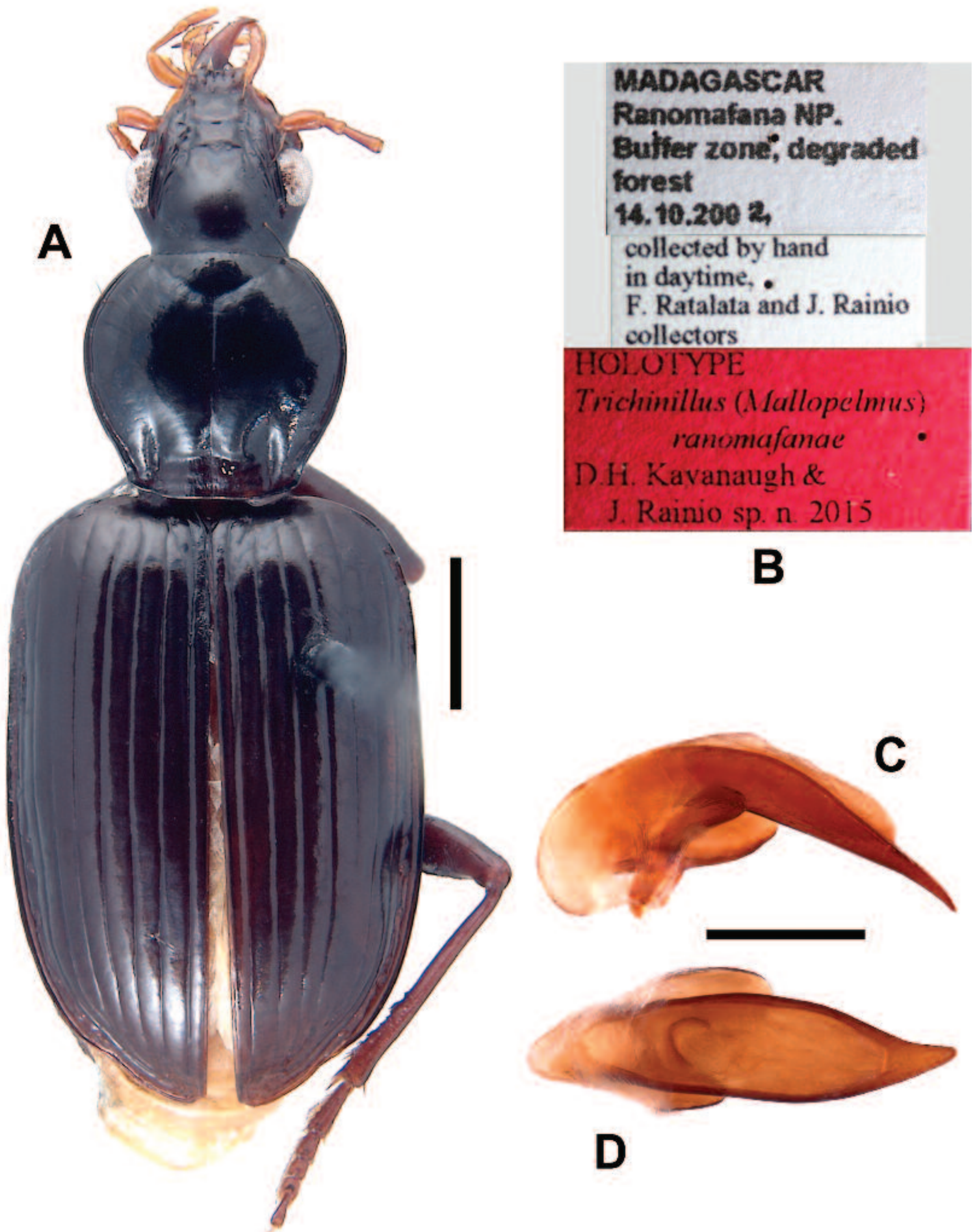

FIGURE 10. Digital images of holotype male of *Trichinillus* (*Mallopelmus*) *ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C–D. Aedeagus of genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.5 mm.

long as the diameter of the eye, and joined to the neck region at a moderately obtuse (about 135°) angle, eyes more convex and projected, pronotum not or less depressed, especially medially, and margination of the elytra base more varied, extended medially to the base of stria 3 in most individuals). The apex of the median lobe of the male genitalia is also differently shaped in each of these species (compare with Figs. 191c-d and 191f-g, respectively, in Jeannel 1948). Members of *T. ranomafanae* differ from those of *T. abacetoides* in having: slightly larger size (SBL = 6.4 mm in *T. abacetoides*); pronotum with shallow but distinct subbasal sinuation of the lateral margin (absent from *T. abacetoides* members); elytra relatively shorter and wider, especially across the base, and humeri broadly rounded and not at all sloped (humeri more slope in *T. abacetoides*, and median lobe of male genitalia with apex straighter, slightly bent ventrally toward apex in lateral aspect (Fig. 10C) and slightly deflect right in dorsal view (Fig. 10D) (not recurved dorsally and then ventrally in lateral aspect and straight in dorsal aspect as in *T. abacetoides* males; compare with Fig. 191e in Jeannel 1948)

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The male holotype of *T. ranomafanae* was collected in degraded secondary montane rainforest at an elevation of 800 m, near a village in the peripheral zone of Ranomafana National Park about1000 meters from the main gate. The female paratype was collected in secondary montane rainforest in the Talatakely area, at an elevation of 900 m, at the 600 m mark along Trail B. Vegetation in this area was dominated by young trees (DBH < 10 cm) and guava (*Psidium cattleianum*).

Tribe Chlaeniini Brullé 1834

Genus *Chlaenius* Bonelli 1810

Jeannel (1949) treated *Chlaenites* Motschulsky (1860) as a distinct genus, although it is now considered a subgenus of *Chlaenius* (Lorenz 2005) and includes only two species, both from the Palaearctic Region. Both of the new species described below key to *Chlaenites* in Jeannel's (1949) key to chlaeniine genera, but neither is a member of that subgenus as presently conceived.

Chlaenius kathrynae **Kavanaugh and Rainio, sp. nov.**
Figure 11

Type material.— Holotype (Figs.11A–B), a male, in CAS, labeled: "CASENT 1002782"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vohiparara area, 1150 m, mixed tropical forest, 2-22 January 2001,"/ "21.24032°S/ 47.39399°E, Stop# DHK-01-002, D.H. & K.M. Kavanaugh, R.L. Brett, E. Elsom, F. Vargas, Ranaivosolo,"/ "E.F. Randrianifirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime by treading marsh vegetation and shore"/ "HOLOTYPE *Chlaenius kathrynae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 8): 4 males (in CAS, MNHN and MZF) and 1 female (in CAS) labeled same as holotype except "CASENT 1002783", "CASENT 1002784", "CASENT 1002786", "CASENT 1002787", and "CASENT 1002785", respectively; 1 male (CAS) labeled "CASENT 1049008"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vohiparara area, 1050 m, mixed tropical forest, 23 April 1998,"/ "21°13.6'S/ 47°23.0'E,"/ "Stop # 98-71, D.H. Kavanaugh collector collected in soil cracks, under dirt clods, and under root clods in abandoned rice paddy area"; 2 females (in MTEC) labeled "MADAGASCAR: Fianaran. Pr. Ranomafana N.P. HQ. area 21°15'24"S 47°25'15"E 25NOV1994, at night M.A. Ivie & D.A. Pollack". All paratypes also bear the following label: "PARATYPE *Chlaenius kathrynae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

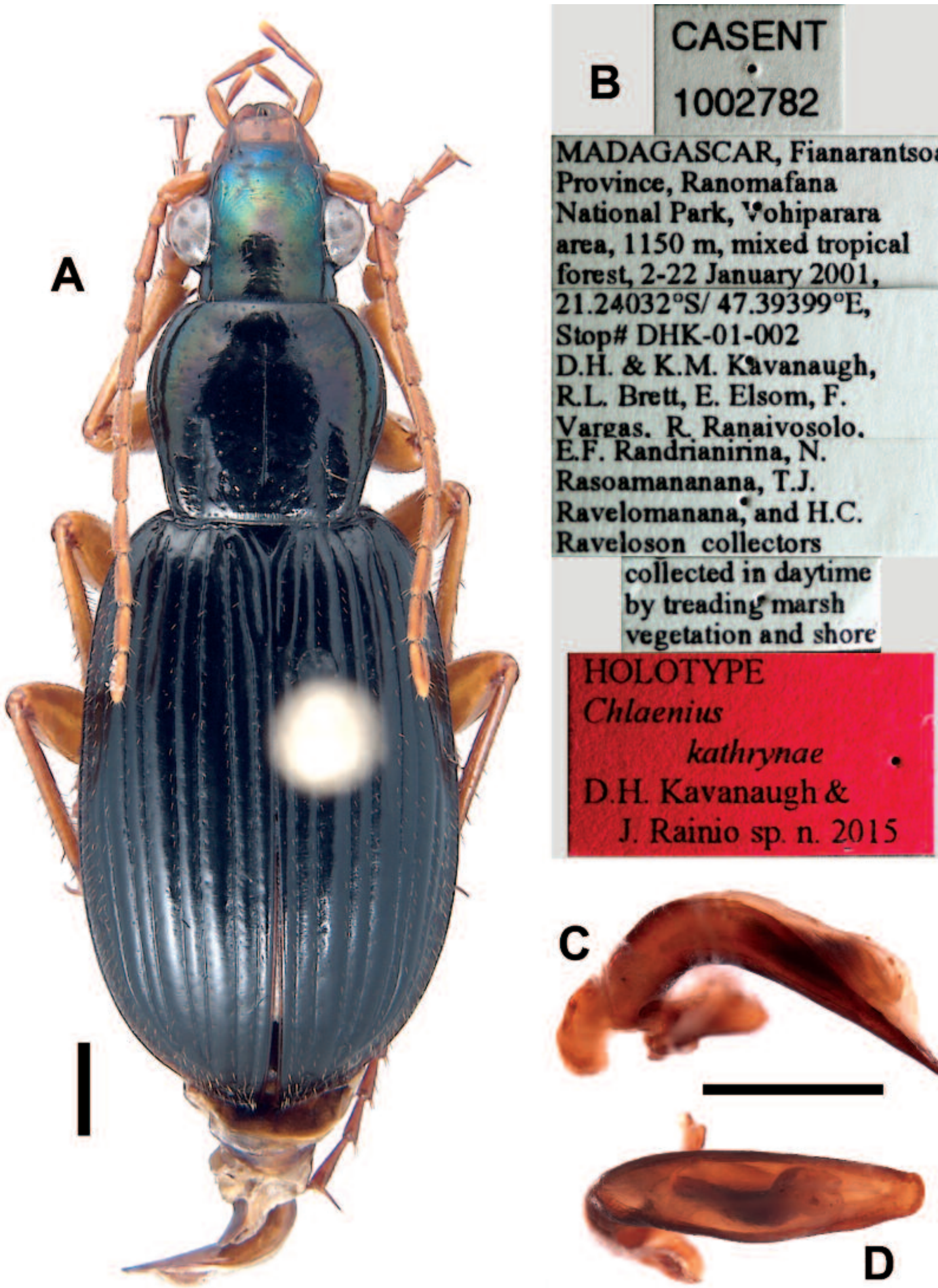

FIGURE 11. Digital images of holotype male of *Chlaenius kathrynae* Kavanaugh & Rainio sp. nov. A Habitus, dorsal aspect; B. Labels; C–D. Aedeagus of genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines = 1.0 mm.

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *kathrynae*, is a noun in the genitive case, derived from the first given name of Kathryn May Kavanaugh, daughter of DHK and one of the collectors of the type series.

Recognition.— Size slightly below average for genus, SBL of males = 10.2–10.8 mm, of females 9.8–11.1 mm. Members of this species (Fig. 11A) share the following features, which place them in genus *Chlaenites* sense Jeannel (1948): antennomere 3 longer than antennomere 4; maxillary palpi setose, penultimate labial palpomeres 4 or 5 setose; pronotum with basolateral setae inserted distinctly anterior to the hind angles; elytra with pubescence restricted to near the striae on disk (*i.e.*, not present on the centers of intervals), except more generally and densely present on lateral intervals and near apices; and tarsi asetose dorsally, tarsomeres 5 with two rows of stout setae ventrally. In Jeannel's (1949) key to subgenera of *Chlaenites*, members of this species key best, although not fully, to subgenus *Chlaeniostenus* Kuntzen (1919), which is now considered a subgenus of *Chlaenius* (Lorenz 2005). Shared with other Malagasy members of this subgenus are the following features: pronotum relatively narrow, more or less cordiform, narrowed basally, with the anterior angles not projected anterior of the basal margin and the anterolateral areas of the pronotum distinctly curved ventrally; and the setose punctures along the lateral margins of the elytral intervals not or only faintly evident, most clearly evident in the apical half only. Jeannel included three other species in this subgenus; namely, *Chlaenius attenuatus* Klug (1833), *Chlaenius subovatus* Chaudoir (1876), and *Chlaenius sellatus* Dejean (1831). Members of *C. kathrynae* differ from those of the other species in lacking any trace of the pale lateral and apical elytral border distinct in members of the other three species. They are also smaller than members of the other species (SBL in the latter ranges from 11.9 to 15.3 mm), have slightly broader and less cordiform pronota and males have genitalia (Figs. 11C–D) that are very different in form from those of any of the other species (compare with Jeannel's (1949) Figs. 388c-i)

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Most specimens of the type series were collected in open habitats at the edges of mixed tropical forest in the Vohiparara area at an elevation of 1050 m. Several were collected by treading down vegetation at the edge of a marsh, and one specimen was found under loose dirt and root clods in an abandoned rice paddy area.

Chlaenius robertae Kavanaugh and Rainio, sp. nov.

Figure 12

Type material.— Holotype (Figs.12A–B), a male, in CAS, labeled: "CASENT 1002781"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vohiparara area, 1150 m, mixed tropical forest, 2-22 January 2001,"/ "21.24032°S/ 47.39399°E, Stop# DHK-01-002, D.H. & K.M. Kavanaugh, R.L. Brett, E. Elsom, F. Vargas, Ranaivosolo,"/ "E.F. Randrianifirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime by treading marsh vegetation and shore"/ "HOLOTYPE *Chlaenius robertae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (only 1): a female (in CAS) labeled "CASENT1049009"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vohiparara area, 1050 m, mixed tropical forest, 27 April 1998,"/ "21°13.6'S/ 47°23.0'E,"/ "Stop # 98-91, D.H. Kavanaugh collector collected on bare soil at night in abandoned rice paddy area"/ "PARATYPE *Chlaenius robertae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *robertae*, is a noun in the genitive case,

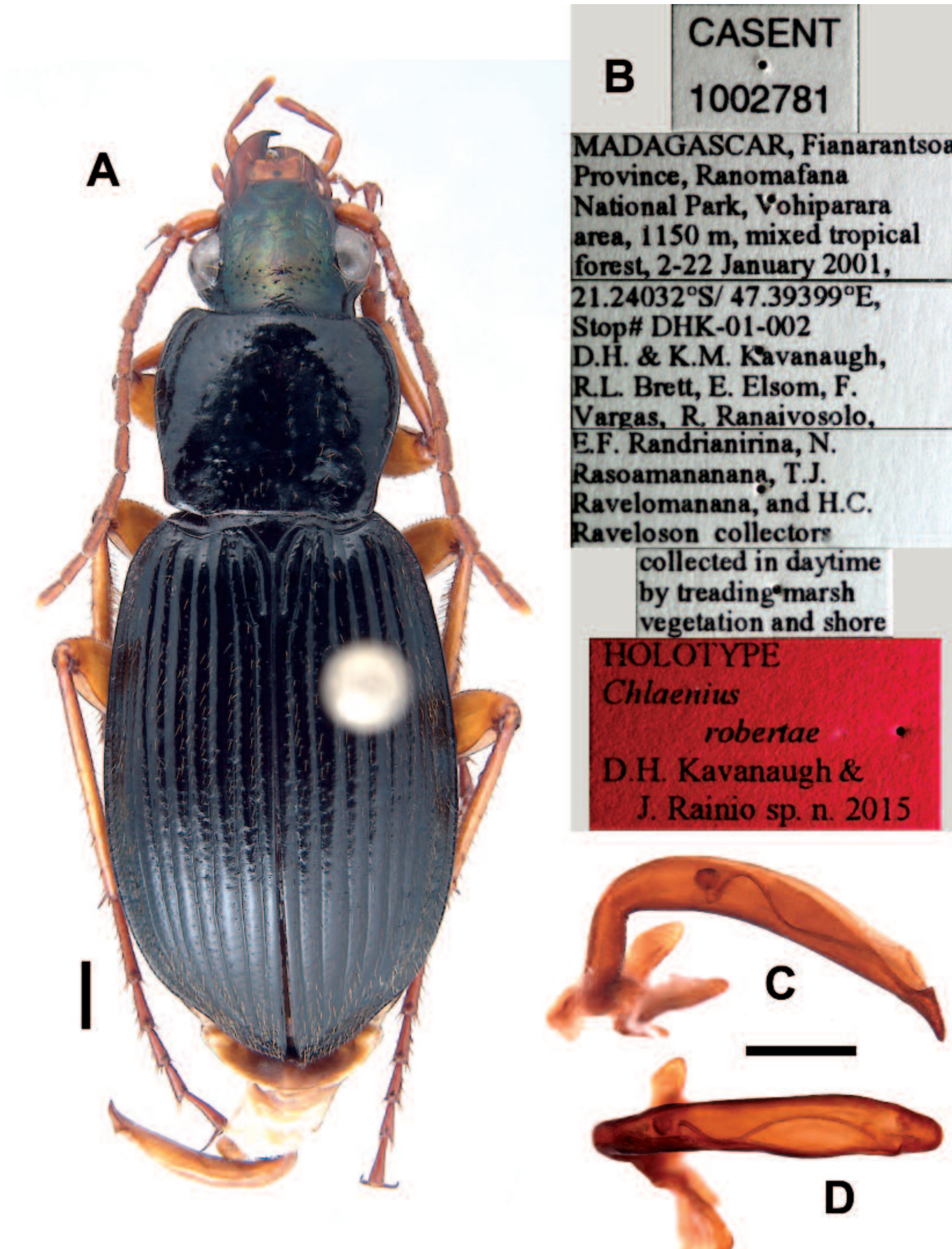

FIGURE 12. Digital images of holotype male of *Chlaenius robertae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C–D. Aedeagus of genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines = 1.0 mm.

derived from the given name of Roberta L. Brett, former graduate student and technical assistant of DHK and one of the collectors of the type series.

Recognition.— Sized moderate for genus, SBL of male = 12.9 mm, of female = 13.3 mm. Members of this species (Fig. 12A) exhibit the following features, which place them in genus *Chlaenites* sensu Jeannel (1949): antennomere 3 longer than antennomere 4; maxillary palpi setose; penultimate labial palpomeres 4 or 5 setose; pronotum with basolateral setae inserted distinctly anterior to the hind angles; elytra with pubescence restricted to near the striae on disk (i.e., not present on the centers of intervals), except more generally and densely present on lateral intervals and near apices; and tarsi asetose dorsally, tarsomeres 5 with two rows of stout setae ventrally. In Jeannel's (1949) key to subgenera of *Chlaenites*, members of this species key to his new subgenus *Chlaenitidius*, which is now considered a junior synonym of subgenus *Amblygenius* Laferté-Sénectère (1851) (Lorenz 2005), in having the pronotum relatively broad and the setose punctures along the lateral margins of the elytral intervals slightly foveate, especially in the apical half apically. Member s of *C. robertae* differ distinctly from those of the each of the four species Jeannel included in this subgenus. They differ from members of *Chlaenius cupreolus* Faimaire (1901) in having striae deeply impressed and intervals moderately convex (striae superficial only and intervals flat in *C. cupreolus* members), head with metallic green reflection but pronotum black without a trace of metallic reflection (both head and pronotum with green metallic reflection in *C. cupreolus* members), and elytra without a pale lateral and apical margin (a thin pale margin present in *C. cupreolus* members). They differ from members of *Chlaenius allacteus* Alluaud (1919), which is current classified in subgenus *Oochlaenius* Alluaud (1933) (Lorenz 2005), in having all elytral interval similarly and moderately convex (intervals 1, 3, 5 and 7 more convex and intervals 2, 4, 6 and 8 flat in *C. allacteus* members) and, again, elytra without a pale lateral and apical margin (a wide pale margin present in *C. allacteus* members). They differ from members of *Chlaenius inaequalis* Faimaire (1901) in having the pronotum black without metallic reflection (metallic green reflection present on pronotum in *C. inaequalis* members), a longer and narrower elytral form (shorter and broader elytra in *C. inaequalis* members) and elytral epipleurae black (pale in *C. inaequalis* members). Overall, members of *C. robertae* are most similar to those the fourth species, *Chlaenius lyperus* Jeannel (1949), with which they share similar elytral shape, depth of striae and convexity of intervals. However, they differ from *C. lyperus* members in having a pronotum broader basally than the latter and legs that are pale in color (dark in *C. lyperus* members). Males of *C. robertae* also have genitalia (Figs. 12C–D) that are markedly different in form those of the other four species (compare with Jeannel's (1949) Fig. 386a-d).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Both specimens of the type series were collected in open habitats at the edges of mixed tropical forest in the Vohiparara area at elevations ranging from 1050 to 1150 m. One was collected in daytime by treading down vegetation at the edge of a marsh, the other was found at night running on bare soil in an abandoned rice paddy.

Tribe Hexagoniini Horn 1881

Genus *Omphreoides* Fairmaire 1896

This genus, precinctive to Madagascar, includes five previously described species. Jeannel (1949) described a new genus, *Stenomphreoides*, for *Omphreoides quodi* Alluaud (1910), but this generic name is now considered just a junior synonym of *Omphreoides* (Lorenz 2005).

Omphreoides ranomafanae **Kavanaugh and Rainio, sp. nov.**
Figure 13

Type material.— Holotype (Figs.13A–B), a female, in NMNH, labeled: "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 900 m 17-22 February 1990 W. E. Steiner"/ "at black light in montane rainforest near river and stream"/ "HOLOTYPE *Omphreoides ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size larger than average for genus, SBL = 13.4 mm. The unique holotype female of *O. ranomafanae* (Fig. 13A) is clearly unlike members of any described species of *Omphreoides*, with several features intermediate between the four typical species and *O. quodi*. The head of the holotype (Fig. 13C) is longer and more slender than that of females of any other species except *O. quodi*, which has an even longer and narrower head (see Jeannel 1949, Fig. 364). In *O. ranomafanae*, the tempora are straight, parallel in anterior their two-thirds, slightly more than twice as long as the diameter of eye, distinctly delimited posteriorly by narrowly round angles. The dorsal longitudinal grooves typical of all members of this genus, except those of *Omphreoides bispinus* Fairmaire (1896), are extended as sharply-defined grooves only about halfway from the point of insertion of the anterior supraorbital setae to that of posterior supraorbital setae and not continued on to base of the head as they are in *Omphreoides bucculentus* Alluaud (1899a) and *Omphreoides distinctus* Alluaud (1936). Posterior to the sharply-defined segments, broad and shallow depressions extend posteriorly, arcuately convergent and nearly joined in the midline near the back of the head. The pronotum (Fig. 13C) is subquadrate, longer than wide (ratio PW/PL = 0.75), with a wavy diagonal row of sparse, coarse punctures (seen also in *O. distinctus* and *O. quodi* members but absent from those of *O. bucculentus* and *O. bispinus*) extended from near the anterior transverse impression paramedially to the basal foveae posteriorly; lateral pronotal margins with short but distinct sinuations anterior to slightly obtuse hind angles; median longitudinal impression deep, wider than in all other *Omphreoides* except *O. quodi* (in which the impression is even wider) and sparsely but coarsely punctate; lateral explanation narrow (narrower at middle than that in *O. bucculentus* members and similar to that in *O. distinctus* member. The elytra are relatively wider than in all other species; each elytron with a straight apical spine in line with interval 3.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype was collected at ultraviolet light in montane rainforest near the junction of the Namorona River and a small tributary stream.

Tribe Perigonini Horn 1881

Genus *Perigona* LaPorte 1835

Subgenus *Ripogena* Jeannel 1941a

This subgenus includes ten described species, including five from the African mainland and five from Madagascar (Basilewsky 1989). Jeannel (1948) treated this taxon as a separate genus, although he had described it originally as a subgenus of *Perigona* (Jeannel 1941a), and included the four species known to him in a key. Deuve (1998) described a fifth Malagasy species.

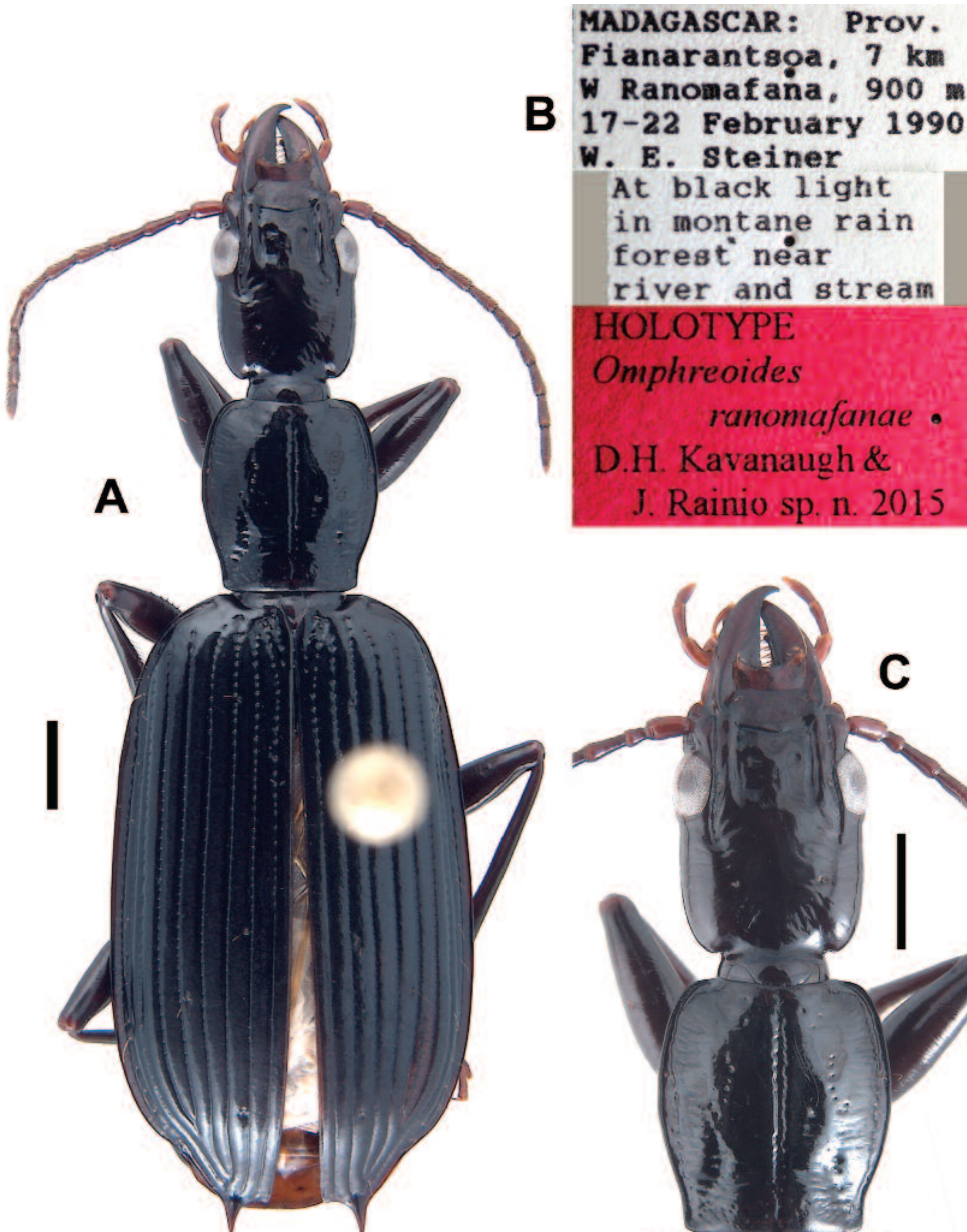

FIGURE 13. Digital images of holotype female of *Omphreoides ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C. Forebody, dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.25 mm

***Perigona* (*Ripogena*) *deuvei* Kavanaugh and Rainio, sp. nov.**
Figure 14

Ripogena n. sp. 1; Rainio 2009: 33 (informal designation).
Perigona (*Ripogena*) *n. sp. 1*; Rainio 2012: 73, Rainio 2013: 96 (informal designation).

Type material.— Holotype (Figs.14A–B), a male, in CAS, labeled: "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail K at 350 m mark, 24.07.2005"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "HOLOTYPE *Perigona* (*Ripogena*) *deuvei* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 4): 1 female (in MNHN) labeled "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail J at 50 m mark, 6.10.2005"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "239." [handwritten label]; 1 female (in CAS) labeled "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail S at 600 m mark, 9.9.2005"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "239." [handwritten label]; 1 male (in MZF) labeled "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail S at 600 m mark, 24.7.2005"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "253." [handwritten label]; 1 female (in MZF) labeled "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail S at 600 m mark, 6.10.2005"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors"/ "245." [handwritten label]. All paratypes also bear the following label: "PARATYPE *Perigona* (*Ripogena*) *deuvei* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *deuvei*, is a noun in apposition, derived from the surname of Dr. Thierry Deuve of the Laboratoire d'Entomologie at the Muséum National d'Histoire Naturelle in Paris. We are pleased to name this new species in honor of Dr. Deuve in thanks for his friendship and kind hospitality during our several visits to MNHN in the course of this study.

Recognition.— Size average for subgenus, SBL of males = 3.5–3.8 mm, of females 3.8–3.9 mm. Members of this species (Fig. 14A) share with those of *Perigona heterodera* Alluaud (1936) and *Perigona prasinus* Alluaud (1936) the following features: pronotum with lateral margins without sinuation anterior to hind angles, posterior margin slightly and smoothly convex, and hind angles either obtuse or broadly rounded. These features distinguish members of these three species from those of *Perigona bembidioides* Alluaud (1936) and *Perigona viridimicans* Jeannel (1948), which have distinct sinuation of the lateral margins anterior to rectangular hind angles and a straight basal margin. Members of *P. deuvei* differ from those of *P. prasinus* in having smaller body size (SBL = 4.7 mm in *P. prasinus*), narrower body form, and dorsum without metallic reflection (dorsum with metallic green reflection in *P. prasinus*) but elytra with moderate but distinct iridescence generated by microsculpture comprised of transverse microlines and marjkedly transverse sculpticells. They are most similar to members of *P. heterodera* in body form and size but differ from them in having the pronotum proportionately longer and male genitalia (Figs. 14C–D) with shaft markedly narrowed basally, markedly inflated in apical two-thirds, and apex longer, slender and ventrally bent in lateral view (Fig. 14C), slightly deflected left and slightly longer in dorsal view (Fig. 14D) than in *P. heterodera* (see Figs. 351b-c in Jeannel 1948). They differ from members of *Perigona descarpentriesi* (Deuve 1998) in having moderately large eyes (eyes markedly reduced eyes in size in *P. descarpentriesi*), pronotum distinctly narrower and with less rounded lateral margins, and elytra with only stria 1 deeply impressed, stria 2 and 3 shallowly impressed but evident on disk, striae 4 to 7 effaced, and stria 8 impressed only in apical one-third (striae 1–7 shallowly impressed but evident at least on disc and stria 8 deeply impressed throughout in *P. descarpentriesi* members). Also, the apex of the median lobe of the male genitalia is narrower in lateral

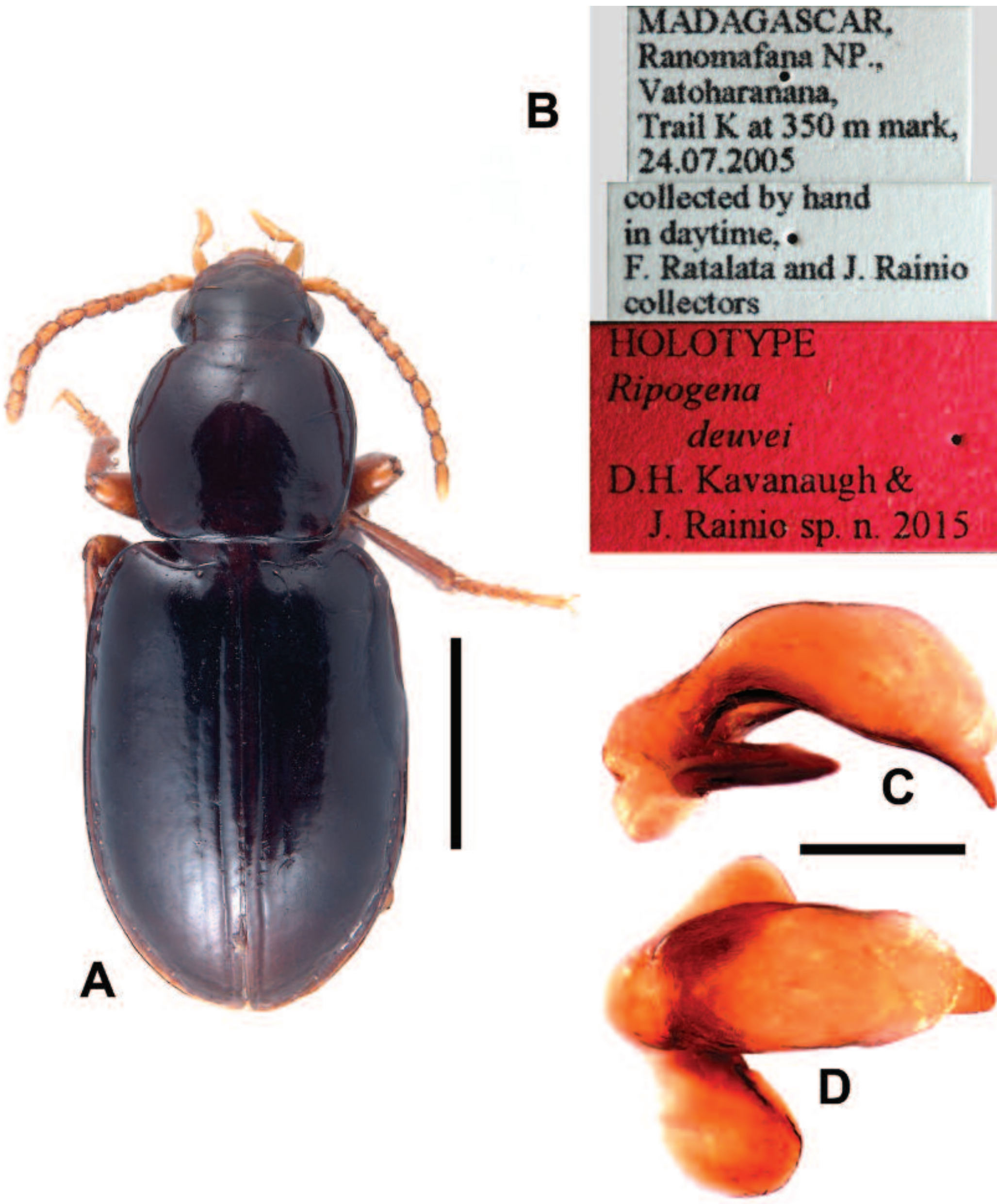

FIGURE 14. Digital images of holotype male of *Perigona* (*Ripogena*) *deuvei* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B Labels; C–D. Aedeagus of genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.25 mm.

aspect in *P. deuvei* males (Fig. 143C) than in those of *P. descarpentriesi* (see Deuve 1998, Fig. 2.). Finally, *P. deuvei* members differ from those of the new species described below in having smaller body size, pronotum with lateral margination very narrow throughout, fewer elytral striae evident, and median lobe of the male genitalia with a longer and ventrally bent apex.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— All specimens of this species were collected by hand in daytime in primary montane rainforest in the Vatoharanana area at an elevation of 1200 m.

***Perigona* (*Ripogena*) *ranomafanae* Kavanaugh and Rainio, sp. nov.**
Figure 15

Ripogena n. sp. 2; Rainio 2009: 33 (informal designation).
Perigona (*Ripogena*) *n. sp. 2*; Rainio 2012: 73, Rainio 2013: 96 (informal designation).

Type material.— Holotype (Figs.15A–B), a male, in CAS, labeled: "“CASENT 1049017”/ “MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vatoharanana area, 1050 m, Abotovory stream, 29 April 1998”/ “21°16.7’S 47° 26.1’E, Stop # 98-100, D.H. Kavanaugh collector collected in large rotting log just under loose bark with cavities”/ “HOLOTYPE *Perigona* (*Ripogena*) *ranomafanae* Kavanaugh & Rainio sp. n. 2015” [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size larger than average for subgenus, SBL = 4.4 mm. The holotype male of this species (Fig. 15A) shares with members of *Perigona heterodera* Alluaud (1936), *Perigona prasinus* Alluaud (1936) and *P. deuvei* sp. nov. the following features: pronotum with lateral margins without sinuation anterior to hind angles, posterior margin slightly and smoothly convex, and hind angles either obtuse or broadly rounded. These features distinguish members of these four species from those of *Perigona bembidioides* Alluaud (1936) and *Perigona viridimicans* Jeannel (1948), which have distinct sinuation of the lateral margins anterior to rectangular hind angles and a straight basal margin. Members of *P. ranomafanae* differ from those of *P. prasinus* in having slightly smaller body size and dorsum without metallic reflection (dorsum with metallic green reflection in *P. prasinus*). They differ from members of *P. heterodera* and *P. deuvei* in having larger body size (SBL = 3.4 mm in *P. heterodera*, 3.5 to 3.9 mm in *P. deuvei*), pronotal hind angles more sharply angulate, lateral explanation of pronotum markedly widened and flattened in region of hind angles (pronotal hind angles rounded or at least less sharply angulate and lateral explanation only slightly wider near hind angles than anteriorly in *P. heterodera* and *P. deuvei*). The unique male holotype of *P. ranomafanae* is slightly teneral and the genitalia are very soft and only lightly sclerotized. However, the apex is sclerotized sufficiently to allow comparisons with those of *P. heterodera* and *P. deuvei* males. In lateral view (Fig. 15C), the apex is slightly longer than in *P. heterodera* males (see Jeannel 1948, Fig. 351b) and distinctly shorter and straighter than in *P. deuvei* males. Finally, they differ from members of *P. descarpentriesi* in having moderately large eyes (eyes markedly reduced eyes in size in *P. descarpentriesi*), pronotum widest anterior to middle and lateral margins nearly straight in posterior half (pronotum widest at middle and lateral margins evenly arcuate throughout *P. descarpentriesi*). Also, the apex of the median lobe of the male genitalia is narrower and more pointed in lateral aspect in *P. ranomafanae* males (Fig. 15C) than in those of *P. descarpentriesi* (see Deuve 1998, Fig. 2.).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype was collected by hand in primary montane

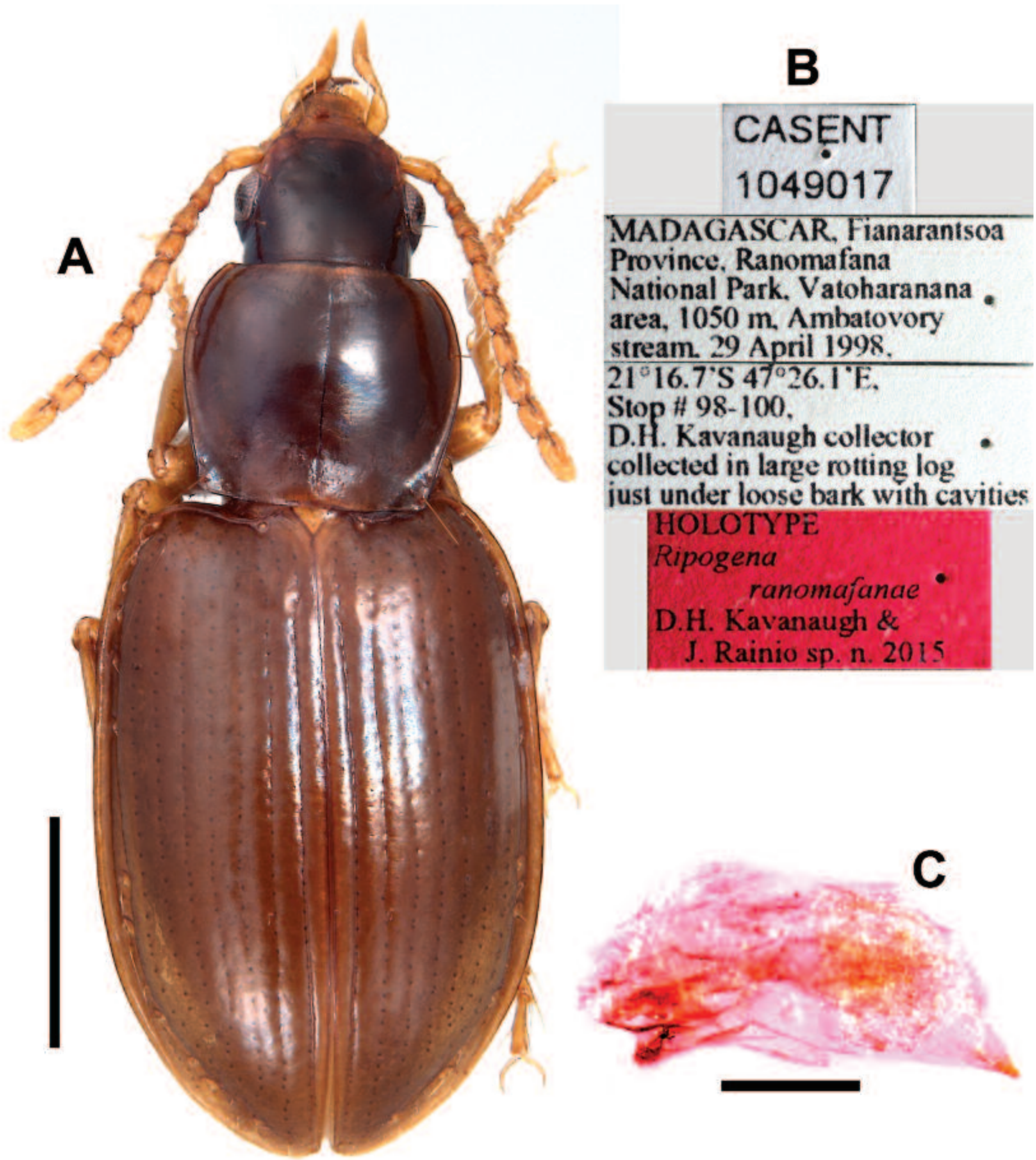

FIGURE 15. Digital images of holotype male of *Perigona* (*Ripogena*) *ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B Labels; C. Aedeagus of genitalia, left lateral aspect [dissection not fully cleaned due to teneral nature of holotype]; D. Dorsal aspect. Scale lines A = 1.0 mm, C = 0.25 mm.

rainforest in the Vatoharanana area at an elevation of 1050 m from under the loose bark of a large log on the forest floor.

Tribe Odacanthini LaPorte 1834

In his treatment of the Malagasy fauna, Jeannel (1948) assigned three species to genus "*Casnonia*" [a misspelling by Latreille and Dejean (1824) of *Cosnania* Dejean 1821], a genus that is now considered to include only Western Hemisphere species. Each of Jeannel's three "Casnonia" species is now included in a different genus (Lorenz 2005). The species with members most similar to those of the new species described below is now included in *Archicolliuris* Liebke (1931). The present supraspecific classification of odacanthines is basically that of Liebke (1931 and 1938), and no comprehensive taxonomic or phylogenic treatment of this taxon worldwide has been produced since then. Clearly, a phylogenetic analysis of relationships among and inclusiveness of odacanthine genera is needed. Pending such a study, we tentatively include our new species in genus *Archicolliuris*.

Genus *Archicolliuris* Liebke 1931

Archicolliuris ranomafanae Kavanaugh and Rainio, sp. nov.

Figure 16

Type material.— Holotype (Figs.16A–B), a female, in NMNH, labeled: "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100m 22-31 October 1988 W. E. Steiner"/ "Flight intercept-yellow pan trap, island in stream, montane rainforest"/ "HOLOTYPE *Archicolliuris ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size large for genus, SBL = 8.2 mm. The holotype female of this species (Fig. 16A) is easily distinguished from members of all other Malagasy odacanthine species based on numerous features. The following features used by Jeannel (1948) in his key to genera are shared with the three species that he included in "*Casnonia*": integument glabrous (without pubescence), pronotum long, narrow and tubular anteriorly, impunctate, with one or more setae present along each lateral margin. The holotype of *A. ranomafanae* differs from members of *Casnonia fairmairei* Gestro (1895) [currently included in genus *Erectocolliuris* Liebke (1931)] in having a pronotum black in color and with only a single pair of midlateral setae (pronotum rufotestaceous in color and with 5 or 6 pairs of lateral setae present in *E. fairmairei* members). It differs from members *Casnonia coerulans* Künckel d'Herculais (1887) [currently included in genus *Protocolliuris* Liebke (1931) in having the pronotum only about twice as long as wide (three times as long as wide in *P. coerulans*), the elytra without metallic reflection (elytra with a dark metallic blue reflection), and legs dark black to piceous, except trochanthers rufous and basal parts of all femora pale (legs pale in *P. coerulans*, except apical parts of femora dark). It is similar to members of the last of Jeannel's "*Casnonia*" species, *Colliuris olsoufieffi* Alluaud (1935) [currently included in *Archicolliuris*] in having a shiny black dorsum (with the only pale areas present as elytral pale spots), the pronotum with transverse grooves and ridges in the basal half and anterior angles projected laterally, and the elytra with a deep transverse depression at the basal one-fourth and with three or four discal setiferous pores on elytral interval 3. However, it differs with members of *A. olsoufieffi* in several features: body size larger (SBL = 6.8 mm in *A. olsoufieffi*); pronotum impunctate (coarsely punctate laterally and basally in *A. olsoufieffi*), slightly less than twice as long as wide (2.5 times as long as wide in *A. olsoufieffi*), with lateral borders vaguely present but only as very faintly impressed lines (lateral borders absent from *A. olsoufieffi* members); elytra with only one pair of small pale spots, located at apical one-third on interval 4 (both subapical and subbasal pairs of spots present in *A. olsoufieffi*) and with three or four discal setiferous pores also on interval 5 (absent from *A. olsoufieffi* members); and legs dark, except pale at base of femora and on trochanters (legs pale thoughout in *A. olsoufieffi*).

In addition, the holotype of *A. ranomafanae* is unique among members of all Malagasy

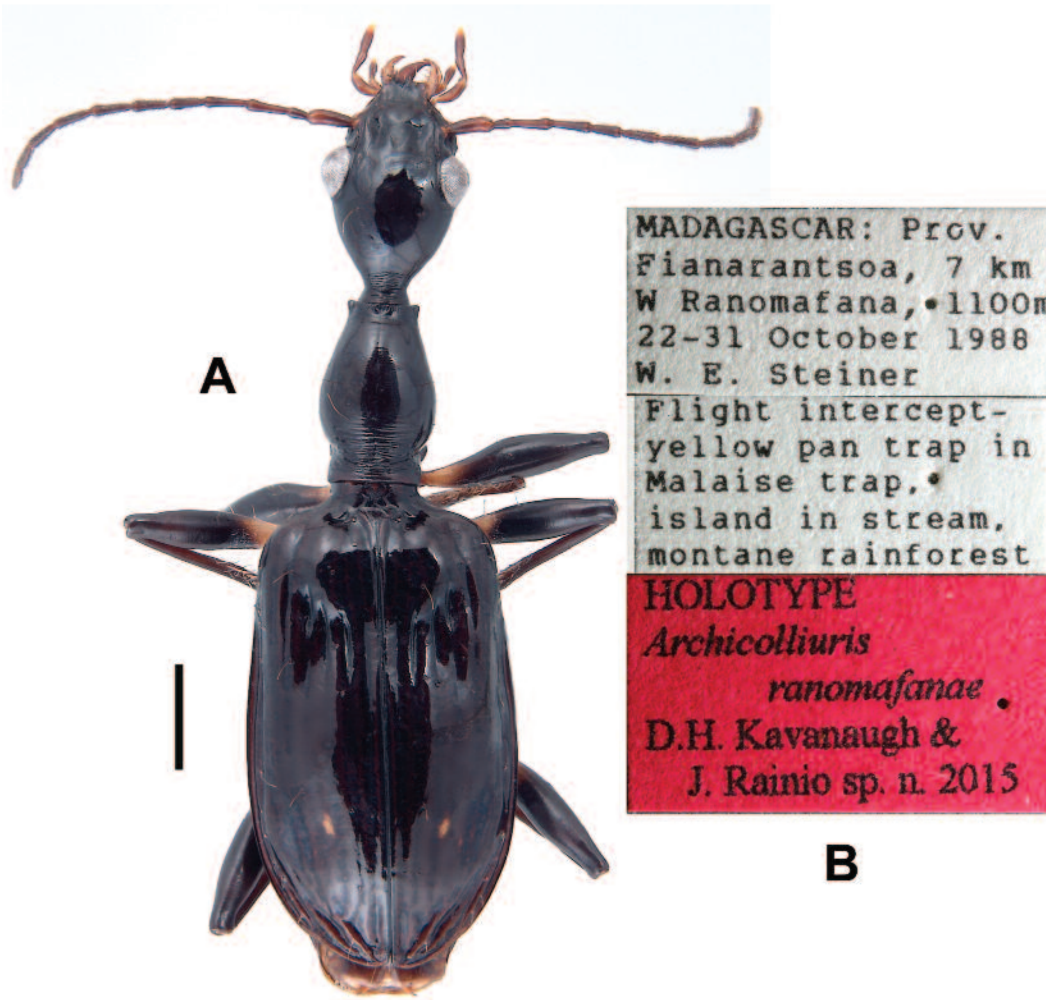

FIGURE 16. Digital images of holotype female of *Archicolliuris ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

odcanthine species in having the elytra distinctly convex throughout, except in the area of the transverse depression, elytral intervals flat, and elytral striae 3 to 7 effaced except in the transverse depression and apically, where they are evident. Striae 1 and 2 are very shallowly impressed but evident (stria 2 less so) in and posterior to the transverse depression. The form and location of the transverse depression of the elytra and the nearly effaced striae are similar to these features of members and genus *Mimocolliuris* Liebke (1933) of the eastern Palearctic and Oriental Regions.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype was collected in a flight intercept-yellow pan trap on an island in a stream in montane rainforest at an elevation of 1100 m.

Tribe Lebiini Bonelli 1810
Subtribe Pericalina Hope 1838
Genus *Thysanotus* Chaudoir 1848

Jeannel (1949) recognized 14 species in this genus precinctive Malagasy genus. Deuve (2010) described six additional new species and returned two species treated by Jeannel as junior synonyms to full species status. He also provided an excellent key to all the known species.

Thysanotus bimaculatoides **Kavanaugh and Rainio, sp. nov.**
Figures 17–18

TYPE MATERIAL.— Holotype (Figs.16A–B), a male, in CAS, labeled: "MADAGASCAR Ranomafana NP. Mangevo plot 1600m 20.4.2005"/ "240" [handwritten label]/ "HOLOTYPE

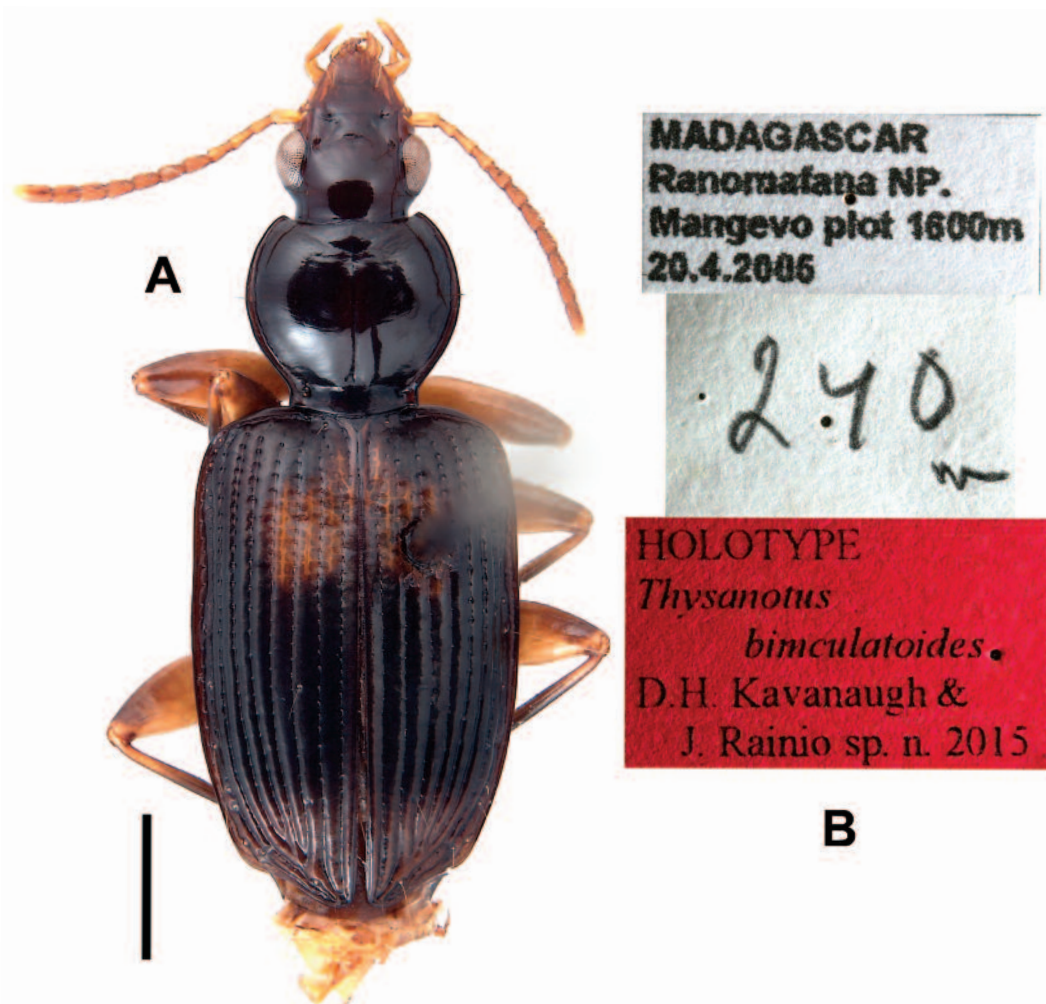

FIGURE 17. A-D. Digital images of holotype male of *Thysanotus bimaculatoides* Kavanaugh & Rainio sp. nov. A–D. A Habitus, Dorsal aspect; B. Labels. Scale line = 1.0 mm.

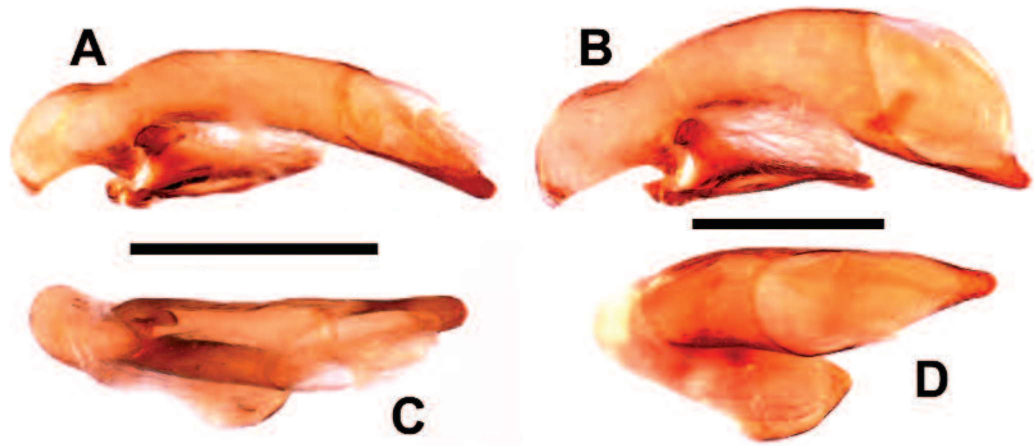

FIGURE 18. Digital images of aedeagus of male genitalia. A, C. Left lateral aspect; B, D. Dorsal aspect. A–B. Holotype male of *Thysanotus bimaculatoides* Kavanaugh & Rainio sp. nov.; B, D. *Thysanotus spinosus* Alluaud (from Ranomafana National Park). Scale lines = 0.5 mm.

Thysanotus bimaculatoides Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 2): 1 female (in MNHN) labeled "MADAGASCAR Ranomafana NP. Mangevo plot 1600m 22.4.2005"/ "240" [handwritten label]; 1 female (in CAS) labeled "CASENT 8069538"/ "MADAGASCAR: Province Fianarantsoa, Forêt d'Ambalagoavy Nord, Ikonga, Abatombe Nov-2000"/ "21°49'39"S, 47°20'20"E Calif. Acad. of Sciences colls: R. Harin'Hala & M.E. Irwin, malaise trap 625m MA-01-12-01". Both paratypes also bear the following label: "PARATYPE *Thysanotus bimaculatoides* Kavanaugh & Rainio sp. n. 2015" [yellow label].

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

DERIVATION OF SPECIES NAME.— The species epithet, *bimaculatoides*, is an adjective derived from the Latin words, *bis*, meaning two, and *macula*, meaning spot or spotted, and the Greek word *eidos*, meaning like. The name refers to the similarity between members of this species and those of *Thysanotus bimaculatus* Deuve (2010).

RECOGNITION.— Size slightly less than average for genus, SBL of male = 5.7 mm, of females = 5.3 mm. Members of this species (Fig. 17A) key to *Thysanotus bimaculatus* Deuve (2010) in Deuve's key based on the following combination of features: elytra shiny, intervals smooth, elytral microsculpture indistinct (comprised of faintly impressed microlines and markedly transverse sculpticells, each elytron with a large, pale macula near the base on intervals 2 to 4, also extended partially onto interval 1 and to scutellum at basomedial part of macula, elytral apex bluntly rounded, not toothed. Members of *T. bimaculatoides* differ from the holotype of *T. bimaculatus* in having slightly larger body size (SBL of holotype female of *T. bimaculatus* = 4.9 mm), pronotum slightly narrower, ratio of PW/PL = 1.1 (ratio of PW/PL = 1.2 in *T. bimaculatus*), narrower basally with subbasal sinuation of the lateral margin slightly longer and deeper and hind angles sharper, rectangular to distinctly acute (compare with Deuve 2010, Fig. 17). Deuve did not have a male specimen of *T. bimaculatus*, so we cannot compare male genitalia of these two species. However, for future comparative purposes, we provide digital photographs of the genitalia (Figs. 18A,C) of the holotype of *T. bimaculatoides* as well as those of a male of *Thysanotus spinosus* (Alluaud 1936c) (Figs. 18B,D) [males of this species previously unknown], to complement the illustrations of other *Thysanotus* species provided by Jeannel (1949) and Deuve (2010).

GEOGRAPHICAL DISTRIBUTION.— At present, known only from two localities, 52 km apart, in central Fianarantsoa Province. Both localities are on the eastern slope off the central plateau.

Habitat distribution.— The holotype and one paratype were collected by hand in the Mangevo area, about 1600 m distance in from the edge of montane rainforest, at an elevation of 1600 m. The other paratype was collected in a malaise trap in montane rainforest at an elevation of 650 m.

Thysanotus spinosus Alluaud 1936

This species was described on the basis of a single female specimen (holotype in MNHN). Neither Jeannel (1949) nor Deuve (2010) has a male specimen of this species available for study. We take this opportunity to provide digital photographs of the median lobe of the genitalia (Figs. 18B,D) from a male collected in RNP to complement the illustrations of other *Thysanotus* species provided by Jeannel (1949) and Deuve (2010).

Genus *Madecassina* Jeannel 1949

Jeannel (1949) recognized at total of ten species and one additional subspecies in this precinctive Malagasy genus and provided a key for identification of adults. No additional species have been described since Jeannel's study.

Madecassina bimaculata Kavanaugh and Rainio, sp. nov.

Figure 19

Type material.— Holotype (Figs.19A–B), a male, in CAS, labeled: "CASENT 1049022"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 13 April 1998, 21°14.9'S 47°25.6'E,"/ "Stop # 98-29, D. H. Kavanaugh collector collected by beating suspended clusters of dead leaves and twigs"/ "HOLOTYPE *Madecassina bimaculata* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 16): 1 female (in CAS) labeled "CASENT 1004001"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanaugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime by beating live understory vegetation and/or dead leaves and other suspended debris"; 1 female (in CAS) labeled "CASENT 1049023"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, Trail FF, 21°14.9'S 47° 25.6'E,"/ "10-16 November 1998, beaten from vines, V. F. Lee & K. J. Ribardo collector"; 1 male (in CAS) labeled "CASENT 1049024"/ "MADAGASCAR, Fianarantsoa Province, Parc National Ranomafana, Talatakely area, 900 m, mixed tropical forest, 24 April 1998,"/ "21°15.3'S 47°25.9'E,"/ "Stop # 98-76, D. H. Kavanaugh collector collected at night on standing tree trunk"; 1 male (in CAS) labeled "CASENT 8068817"/ "MADAGASCAR: Province Fianarantsoa, Ranomafana National Park, radio tower at forest edge, elev 1130 m 9-20 March 2003"/ "21°15.05'S, 47°24.43'E collector: R. Harin'Hala California Academy of Sciences malaise, mixed tropical forest MA-02-09B-55"; 1 male (in CAS) labeled "CASENT 1049026"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vohiparara area, 1150 m, mixed tropical forest, 18 April 1998, 21°12.8'S 47°23.0'E,"/ "Stop# 98-52, D. H. Kavanaugh collector collected by beating live vegetation and suspended dead leaves and twigs"; 1 female (in CAS) labeled "CASENT 1049025"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Vatoharanana area, 1050 m, Ambatovory stream, 29 April 1998, 21°16.7'S 47° 26.1'E,"/ "Stop# 98-101, D. H. Kavanaugh collector collected by beating suspended clusters of dead leaves and

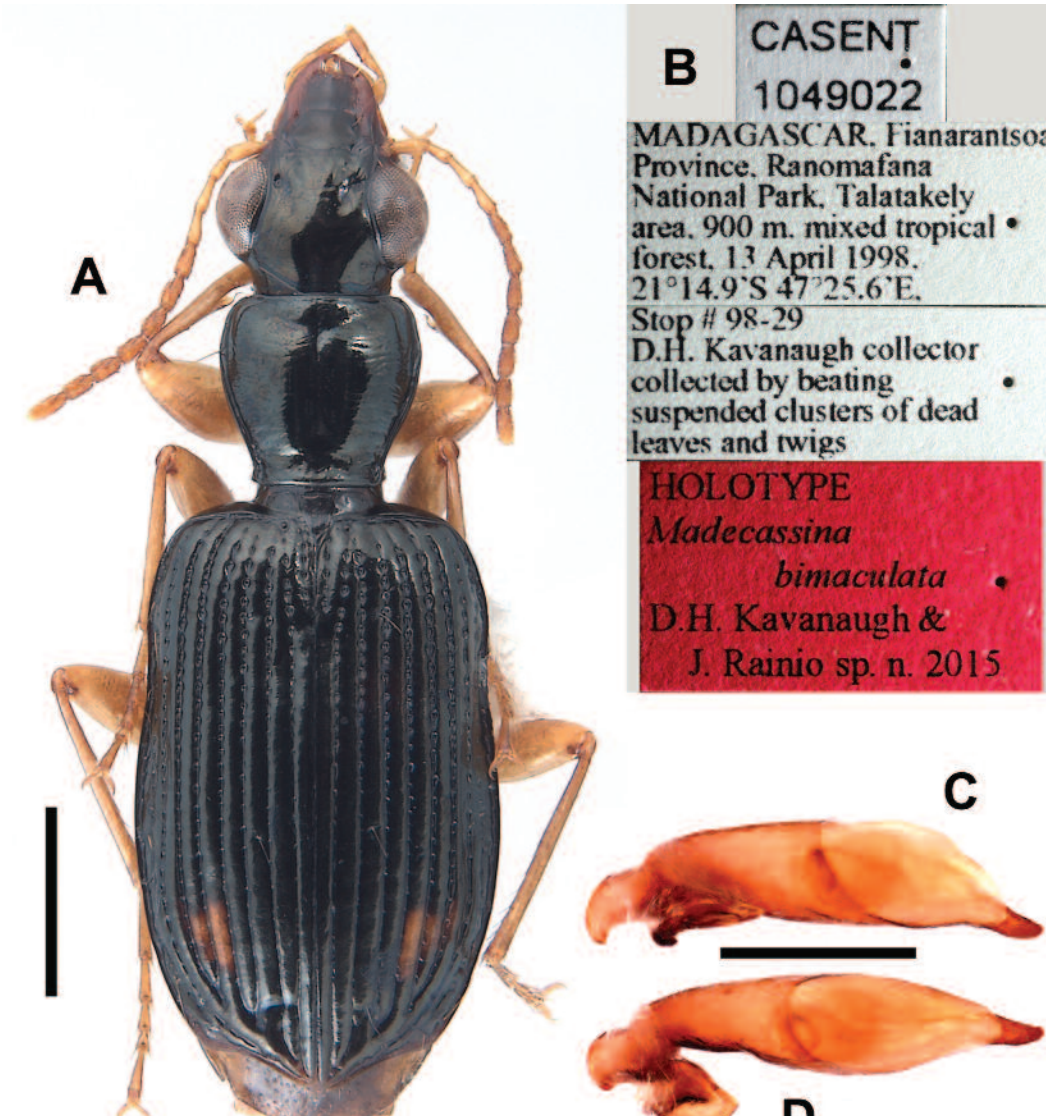

FIGURE 19. Digital images of holotype male of *Madecassina bimaculata* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels C–D. Median lobe of male genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.5 mm.

twigs"; 2 males and 1 female (in CAS and EM) labeled "CASENT 8072308" or "CASENT 8072309" or "CASENT 8072307", respectively/ "MADAGASCAR: Fianarantsoa Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana elev 1100 m 27-31 March 2003"/ "21°15'24"S, 47°26'00"E California Academy of Sciences coll. Fisher, Griswold et al. beating low veg., montane rainforest code: BLF8401"; 1 male (in MNHN) labeled "MADAGASCAR, Ranomafana NP., Vatoharanana, Trail K at 150 m mark, 25.7.2005"/ "collected by hand in daytime from dead leaves of bushes and trees, F. Ratalata & J. Rainio collectors"; 2 females (in MNHN and MZF) labeled "MADAGASCAR, Ranomafana NP., Talatakely, Trail SP at 50 m mark, 28.07.2005"/ "collected by hand in daytime from dead leaves of bushes and trees, F. Ratalata & J. Rainio collectors"; 2 females (in MNHN and MZF) labeled "MADAGASCAR, Ranomafana NP., Valohoaka, Trail B at 555 m mark, 28.01.2005"/ "collected by hand in daytime from dead leaves of bushes and trees, F. Ratalata & J. Rainio collectors"; and 2 females (in MNHN and MNHN) labeled "MADAGASCAR, Ranomafana NP.,Valohoaka, Trail B at 555 m mark, 16.11.2005"/ "collected by hand in daytime from dead leaves of bushes and trees, F. Ratalata & J. Rainio collector". All paratypes also bear the following label: "PARATYPE *Madecassina bimaculata* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *bimaculata*, is an adjective derived from the Latin words, *bis*, meaning two, and *macula*, meaning spot or spotted. The name refers to the pair of subapical elytral spots seen in members of this species.

Recognition.— Size average for genus, SBL of males = 4.7–5.5 mm, of females = 5.3–5.6 mm. Members of this species (Fig. 19A) key most closely, to *Madecassina picta* Alluaud (1897) in Jeannel's (1949) key based on the following combination of features: pronotum impunctate, elytra with two subapical pale spots and striae deeply impressed and legs testaceous in color. The only feature used in the key with which *T. bimaculata* members differ is the presence of is metallic reflection on the forebody—members of *T. picta* have evident aeneous or greenish metallic reflection on the head and pronotum, whereas *T. bimaculata* members are without metallic reflection. These two species are otherwise very similar externally; however the pronotum is proportionately slightly longer and more distinctly narrowed basally and the hind angles more sharply defined and rectangular in *T. bimaculata* members than in *T. picta* members (which have the hind angles slightly obtuse). Also, the apex of the median lobe of the male genitalia is shorter, thicker and straighter in lateral aspect (Fig. 19C) and more bluntly triangular in dorsal aspect (Fig. 19D) in *T. bimaculata* males than in those of *T. picta* males, which have the apex longer, narrower and distinctly hooked dorsally in lateral aspect and more narrowly rounded in dorsal aspect (see Jeannel 1949, Figs. 474g and 474i).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Specimens of this species have been collected in primary montane rainforest in the Vatoharanana and Valohoaka areas and in secondary montane rainforest in the Talatakely and Vohiparara areas, at elevations ranging from 900 to 1150 m. They have been collected mainly by beating live vegetation and suspended clusters of dead leaves and twigs.

Madecassina quadrimaculata Kavanaugh and Rainio, sp. nov.

Figure 20

Type material.— Holotype (Figs.20A–B), a male, in CAS, labeled: "MADAGASCAR, Ranomafana NP., montane rainforest near Tsinjorano village, 100 m in from forest edge,"/ "21.09637°S 47.52085°E, 1050 m, 19.05.2005, collected by hand in daytime, F.J. Ratelolahy collector"/ "HOLOTYPE *Madecassina quadrimaculata* Kavanaugh & Rainio sp. n. 2015" [red label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *quadrimaculata*, is an adjective derived from the Latin words, *quattuor*, meaning four, and *macula*, meaning spot or spotted. The name refers to the two (subbasal and subapical) pairs of elytral spots seen in members of this species.

Recognition.— Size average for genus, SBL = 5.2 mm. The holotype male of this species (Fig. 20A) keys to *Madecassina maculata* Alluaud (1899b) in Jeannel's (1949) key based on the following combination of features: body black, forebody without metallic reflection, pronotum

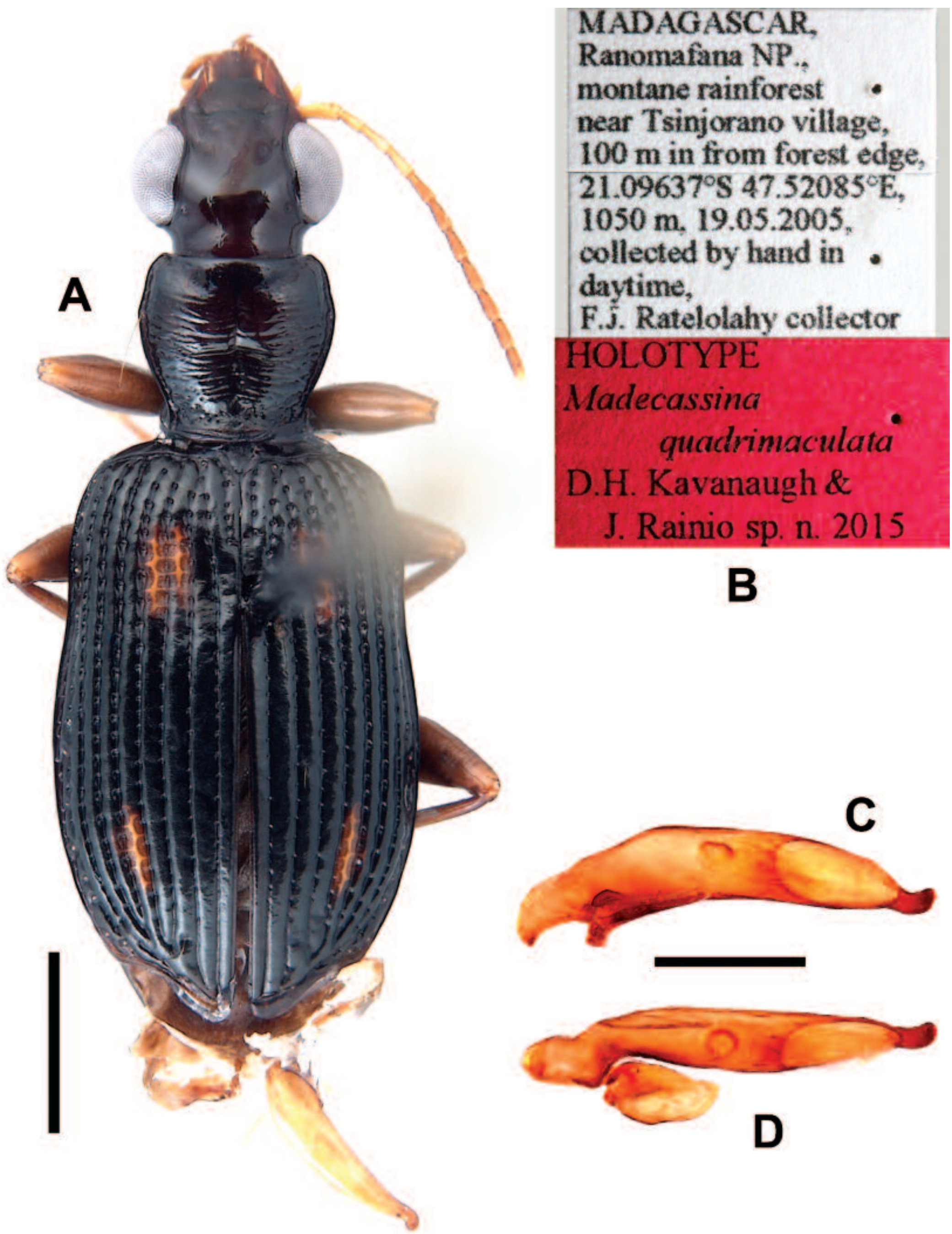

FIGURE 20. Digital images of holotype male of *Madecassina quadrimaculata* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels C–D. Aedeagus of male genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.5 mm.

punctate laterally, and elytra shiny with four pale spots. It differs from members of *M. maculata* in having a smaller body size (SBL = 5.5–6.0 mm in *M. maculata*), the pronotum punctate laterally and laterobasally only, with conspicuous transverse grooves and ridges on disc (in *M. maculata* the pronotum is punctate on the disc also, between the ridges, in contrast to what Jeannel said in his key), elytral intervals shinier due to more shallowly impressed isodiametric microsculpture (elytral intervals duller due to more deeply impressed isodiametric microsculpture in *M. maculata*), the elytral spots much more distinct (much less so in *M. maculata*) and median lobe of male genitalia with apex hooked dorsally and thicker in lateral aspect (Fig. 20C) and slightly swollen and bent right in dorsal aspect (Fig. 20D) (apex hooked but thinner in lateral aspect and more parallel-sided and straight in dorsal aspect in *M. maculata* males) (see Jeannel 1949, Fig. 474f).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The unique holotype was collected in montane rainforest near Tsinjorano village at a distance of 100 m inside the forest edge at an elevation of 1050 m.

Genus *Pristacrus* Chaudoir 1869

Jeannel (1949) recognized four species in this precinctive Malagasy genus and provided a key for distinguishing their respective members. In this key, Jeannel used two features with which we found problems. First, his statements about pronotal proportions—width in relation to pronotal length (i.e. ratio PW/PL)—appear to have been based on visual impressions only, rather than actual comparative measurements, because our measurements of these proportions in specimens (including types) of the four species have not corresponded to those stated by Jeannel. Unfortunately, this problem renders two of his three couplets (couplets 1 and 3) difficult to interpret. Second, he used shape of the sutural angle of the elytral apex (*i.e.*, whether it is broadly rounded or sharp and toothed) as the primary comparative feature in his couplet 2. In fact, based on the examination of many more specimens than were available to Jeannel, we found that members of all species except one, *Pristacrus laticollis* (Gory and Laporte 1837) have elytral apices that are sharp and toothed, including members of *Pristacrus bonotatus* (Klug 1833), which Jeannel cited as broadly rounded in his key. We point out these problems with Jeannel's key as caution to those trying to use it, as we were, for identifications. No additional species have been described since Jeannel's study.

Pristacrus ranomafanae Kavanaugh and Rainio, sp. nov.

Figures 21–22

Pristacrus n. sp. 1; Rainio 2009: 33, Rainio 2012: 73 (informal designation).

Type material.— Holotype (Figs.21A–B), a male, in CAS, labeled: "CASENT 1003833"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected at night on surface of rotting logs on forest floor or suspended just above it"/ "HOLOTYPE *Pristacrus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 19): 1 male and 1 female (in CAS) labelled "CASENT 1003832" or "CASENT 1003831", respectively, otherwise labeled same as holotype; 1 female (in CAS) labeled "CASENT 1004470"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L.

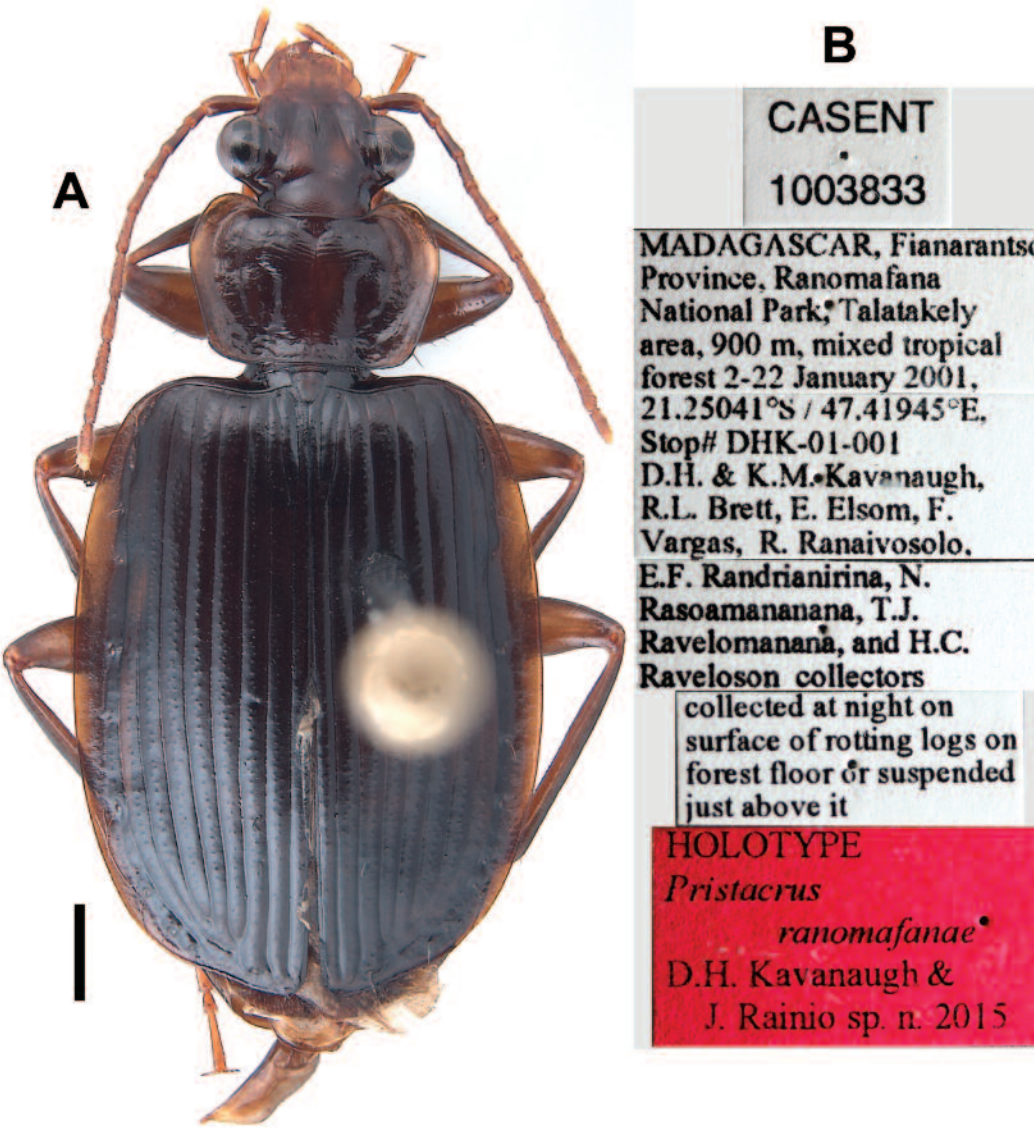

FIGURE 21. Digital images of holotype male of *Pristacrus ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B Labels. Scale line = 1.0 mm.

Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime from large accumulation of dead leaf, twig, and branch debris on and extended up to 2 m above forest floor"; 1 male (in CAS) labeled "CASENT 1002838"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime under loss bark of rotting log logs on forest floor or suspended just above it"; 1 male and two females (in CAS and MZF) labeled "CASENT 1003752", "CASENT 1003751" or "CASENT 1003753", respectively/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamanananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime on underside of rotting log logs on forest floor or suspended just above it"; 1 male (in CAS) labeled "CASENT 1004313"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamanananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime from leaf litter on forest floor"; 1 female (in CAS) labeled "CASENT 1051144"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 27 April 1998"/ "21°15.3'S 47°25.9'E, Stop # 98-85A D.H. Kavanaugh collector collected in and under rotten logs on forest floor"; 1 female (in CAS) labeled "CASENT 8068264"/ "MADAGASCAR: Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m 28 April – 5 May 2002"/ "21°15.99'S 47°25.21'E collector: R. Harin'Hala California Acad of Sciences malaise secondary tropical forest MA-02-09C-27"; 1 female (in CAS) labeled "CASENT 8068264"/ "MADAGASCAR: Province Fianarantsoa, Parc National Ranomafana, Belle Vue at Talatakely, elev 1020 m 15-22 November 2001"/ "21°15.99'S 47°25.21'E collector: R. Harin'Hala California Acad of Sciences malaise secondary tropical forest MA-02-09C-03"; 1 male (in NMNH) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 900 m 1-9 February 1990 W. E. Steiner"/ "at black light in montane rainforest near river and stream"; 1 male (in CAS) labeled "CASENT 8005762"/ "21.25041°S/ 47.41945°E MADAGASCAR, Fianarantsoa Prov Ranomafana National Park, Talatakely area, 900m, 10:1:2001 Col. K. Will headlamp search logs"; 5 males and 1 female (in EMEC and MNHN) labeled "CASENT 8005762"/ "21.25041°S/47.41945°E MADAGASCAR, Fianarantsoa Prov Ranomafana National Park, Talatakely area, 900m, 10:1:2001 Col. K. Will headlamp search logs". All paratypes also bear the following label: "PARATYPE *Pristacrus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

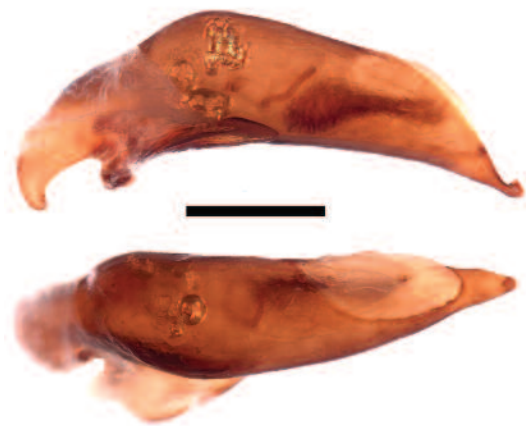

FIGURE 22. Digital images of aedeagus of genitalia of male holotype of *Pristacrus ranomafanae* Kavanaugh & Rainio sp. nov. A. Left lateral aspect; B. Dorsal aspect. Scale line = 0.5 mm.

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

DERIVATION OF SPECIES NAME.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

RECOGNITION.— Size small for genus, SBL of males = 8.3–8.5 mm, of female = 8.6 mm. Members of this species (Fig. 21A) are distinguished from those of all other species in the genus except *Pristacrus binotatus* Klug (1833) by their small body size (SBL greater than 10.0 mm in members of the three other species). They differ from members of *Pristacrus semipiceus* (Fairmaire 1887), in having much smaller body size (SBL = 13.6 to 14.5 mm in *P. semipiceus* members), a shinier dorsal surface, shorter and broadly rounded mandibles and an impunctate (but longitudinally rugulose) frons (dorsal surface duller, mandibles distinctly longer and more tapered, and frons punctate as well as rugulose in *P. semipiceus* members). They differ from members of *P. laticollis* in having slightly smaller body size (SBL = 10.2–11.1 mm), slightly shinier dorsal surface, relatively longer and narrower pronotum and elytra that are broadly ovoid with lateral margin arcuate and lateral explanation broad throughout, especially at middle, and elytral apices distinctly angulate and toothed (duller dorsal surface, relatively broader and shorter pronotum and elytra that are nearly parallel-sided at middle with lateral explanation narrower throughout and elytral apices broadly rounded in *P. laticollis* members). They differ from the unique type of *Pristacrus rotundatus* (Fairmaire 1892) in having smaller body size (SBL = 11.9 mm in *P. rotundatus* type), shinier dorsal surface, elytra less broadly rounded and humeri less anteriorly projected (dorsal surface dull and elytra markedly broad and rounded and humeri more projected anteriorly in *P. rotundatus* type). Members of *P. ranomafanae* are very similar to those of *P. binotatus* in size and overall form. Specimens of the former have the dorsal surface slightly shinier, the pronotum relatively broader basally, with subbasal sinuation of the lateral margins absent or only very faint and hind angles less sharply defined, and elytra with striae slightly more deeply impressed and intervals more convex and more roughened at the raised center than in most members of *P. binotatus*. However, at least a few specimens of *P. binotatus* share one or more of these features with *P. ranomofanae* members. They only features that most reliably distinguish members of *P. ranomafanae* from those of *P. binotatus*, as well as from members of the other species, are the male genitalia. In *P. ranomafanae* males (Fig. 22A–B), the shaft of the median lobe is inflated subbasally but lacks the large, well-defined dorsal bulge seen in males of *P. binotatus* (see Jeannel 1949, Fig. 486) and, in lateral aspect (Fig. 21A), the apex is distinctly hooked dorsally (apex not hooked in *P. binotatus* males. Males of the each of the other species also have the shaft of the median lobe uniquely shaped.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Specimens of the type series were all collected in secondary montane rainforest in the Talatakely area at elevations of 900 to 1020 m. The area is replete with invasive guava (*Psidium cattleianum*). Specimens were found in daytime in masses of dead leaves, twigs and branch debris accumulated on the forest floor, in leaf litter, and under loose bark or on the underside of rotting logs on the forest floor. Several were found at night running on the surfaces of rotting logs on the forest floor; two were collected in malaise traps and one was attracted to and collected at an ultraviolet light.

Genus *Eurydera* Laporte 1831

Jeannel (1949) recognized 24 species plus three additional subspecies in this precinctive Malagasy genus and a provided a key for identification of their members. Mateu (1973) described seven additional species. Type specimens for all of Mateu's species are deposited in MNHN, so we were able to compare our material with reliably determined specimens of all described *Eurydera* species, including the seven not included in Jeannel's key.

Eurydera ocellata Kavanaugh and Rainio, sp. nov.

Figures 23–24

Type material.— Holotype (Figs. 23A–B), a male, in CAS, labeled: "CASENT 8068800"/ "MADAGASCAR: Province Fianarantsoa, Parc National Ranomafana, Bellevue at Telatakely, elev 1020 m 12-19 February 2002"/ "21°15.99'S, 47°25.21'E collector: R. Harin'Hala California

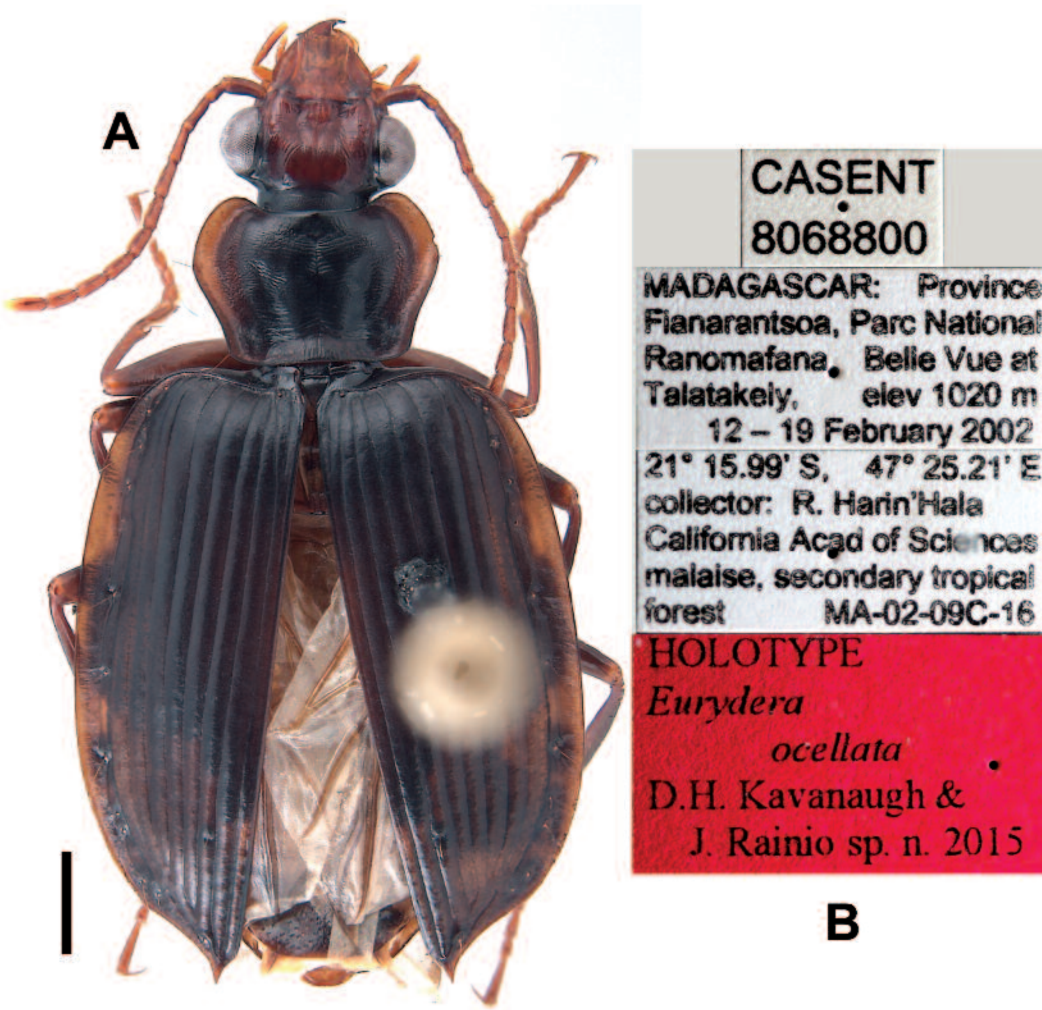

FIGURE 23. Digital images of holotype male of *Eurydera ocellata* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Label. Scale line = 1.0 mm.

Academy of Sciences malaise, secondary tropical forest MA-02-09C-16"/ "HOLOTYPE *Eurydera ocellata* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (only 1): a female (in NMNH) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 900 m 1-9 February 1990 W. E. Steiner"/ "at black light in montane rainforest near river and stream"/ "PARATYPE *Eurydera ocellata* Kavanaugh & Rainio sp. n. 2015" [yellow label].

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

DERIVATION OF SPECIES NAME.— The species epithet, *ocellata*, is the Latin adjective meaning having little eyes or marked with spots. The name refers to the small, faint dark spot on interval 3 within the subapical pale area of each elytron at the insertion point of the subapical discal setiferous pore.

RECOGNITION.— Size small for genus, SBL of male and female = 9.2 mm. Members of this species (Fig. 23A) key to *Eurydera mormolycoides* Coquerel (1851) in Jeannel's (1949) key on the

FIGURE 24. Digital images of holotype male of *Eurydera ocellata* Kavanaugh & Rainio sp. nov. A. Head, dorsal aspect; B–C. Aedeagus of male genitalia; B. Left lateral aspect; C. Dorsal aspect. Scale lines = 0.5 mm.

basis of the following combination of features: size small; head (Fig. 24A) with frontal furrows deeply impressed, smooth, divergent posteriorly and without a transverse impression uniting them, posterior part of frons smooth, narrow and triangular, without lateral grooves prolonged posteriorly beyond the posterior border of the eyes; mandibles short and broad, lateral border not broadly explanate, lateral margin only slightly convex; pronotum cordate, distinctly narrowed basally, lateral margins angulate at insertions of midlateral setae; elytra short, round and black, each with a reddish subapical spot tangential to the medial suture as well as subhumeral and subapicolateral reddish areas and reddish apical spines, elytral intervals moderately convex; median lobe of male genitalia without a large, angulate projection on the ventral margin of the shaft near the base. They differ from *E. mormolycoides* members in having: dorsal surface slightly shiny (dull in *E. mormolycoides* members); pronotum with lateral explanations pale testaceous (darker in *E. mormolycoides* members), anterior angles broadly rounded (more narrowly rounded in *E. mormolycoides* members) and lateral margins with shallow but distinct sinuation anterior to hind angles (sinuation absent from or less distinct in *E. mormolycoides* members); elytra with larger but less distinct (less contrasting with rest of elytra) pale subapical macula with black eye spot on interval three (macula extended further laterally and lateroanteriorly than in *E. mormolycoides* members) and apical spine about half as long as spine in *E. mormolycoides* members. Finally, the median lobe of the male genitalia (Figs. 24B–C) has a thicker shaft throughout and an apex shorter and thicker in lateral view (Fig. 24B) and broader and straighter in dorsal view (Fig. 24C) than in *E. mormolycoides* males (see Jeannel 1949, Fig. 492b).

GEOGRAPHICAL DISTRIBUTION.— At present, known only from the type locality.

HABITAT DISTRIBUTION.— The holotype specimen was collected in a malaise trap in secondary montane rainforest in the Talatakely area at an elevation of 1030 m. The paratype specimen was collected at ultraviolet light in secondary montane rainforest near the junction of the Namorona River and a small tributary stream.

Eurydera oracle **Kavanaugh and Rainio, sp. nov.**
Figures 25–26

Type material.— Holotype (Figs.25A–B), a male, in CAS, labeled: "CASENT 8005762"/ "21.25041°S/ 47.41945°E MADAGASCAR, Fianarantsoa Prov Ranomafana National Park, Talatakely area, 900m, 10:1:2001 Col. K. Will headlamp search logs"/ "HOLOTYPE *Eurydera oracle* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 7): 1 male (in NMNH) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100 m 1-7 November 1988 W. E. Steiner"; 1 female (in NMNH) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100 m 27-31 October 1988 W. E. Steiner"/ "Malaise trap on island in stream, montane rain forest"; 1 female (in EMEC) labeled "CASENT 1003844"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Rav-

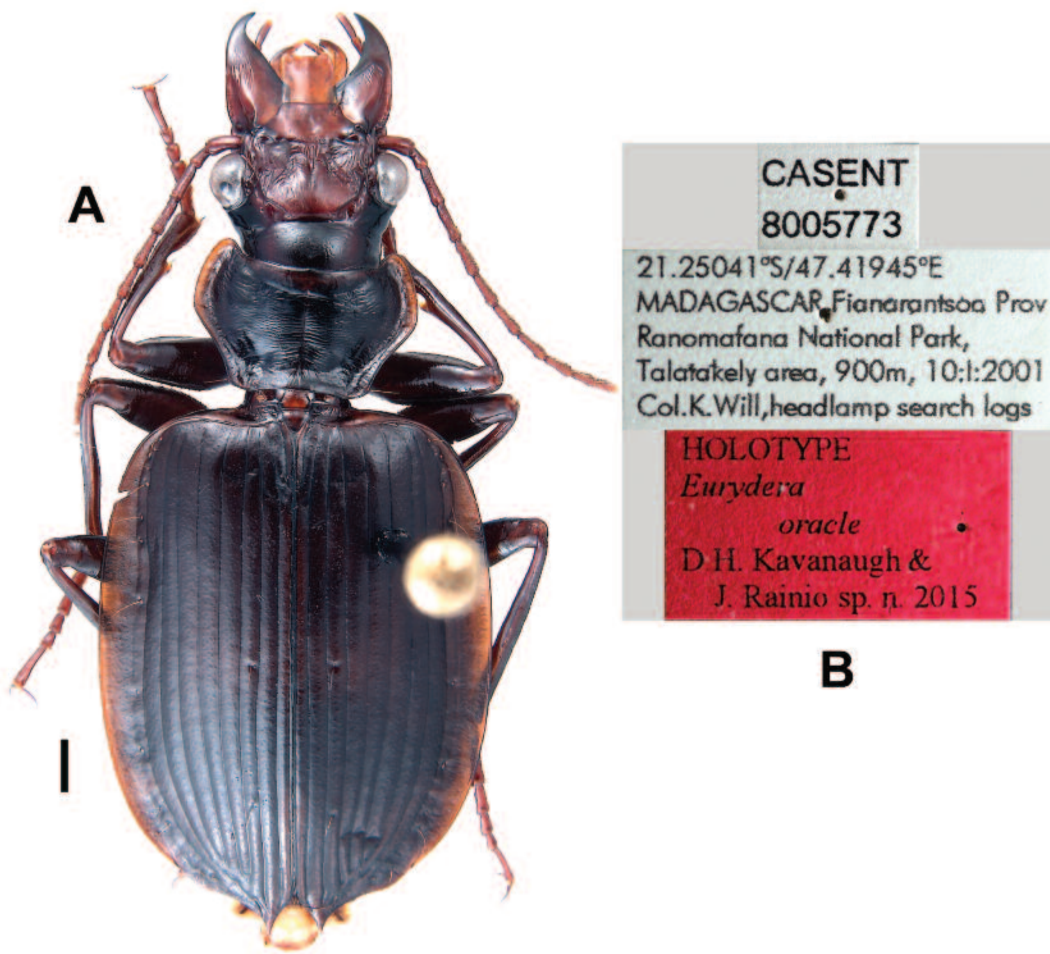

Figure 25. Digital images of holotype male of *Eurydera oracle* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Label. Scale line = 1.0 mm.

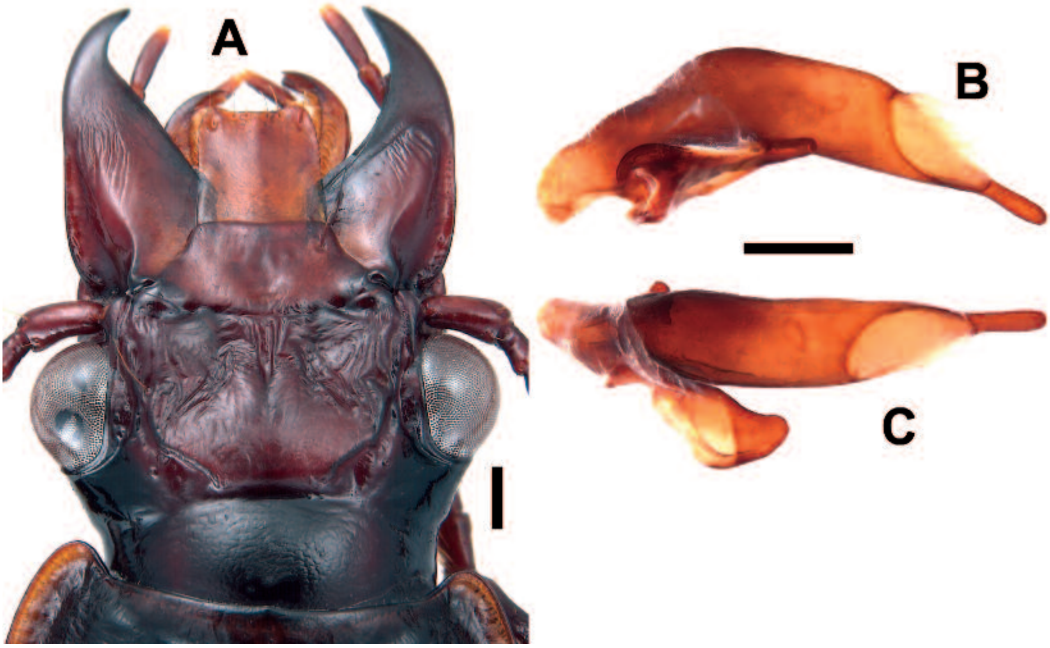

FIGURE 26. Digital images of holotype male of *Eurydera oracle* Kavanaugh & Rainio sp. nov. A. Head, dorsal aspect; B–C. Aedeagus of male genitalia; B. Left lateral aspect; C. Dorsal aspect. Scale lines = 0.5 mm.

elomanana, and H.C. Raveloson collectors"/ "collected at night on underside of shelf fungus on rotting log on forest floor or suspended just above it"; 1 female (in CAS) labeled "CASENT 1003739"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime on underside of rotting logs on forest floor or suspended just above it"; 1 female (in MNHN) labeled "CASENT 8068234"/ "MADAGASCAR: Province Fianarantsoa, Parc National Ranomafana, Bellevue at Telatakely, elev 1020 m 10-14 January 2002"/ "21°15.99'S, 47°25.21'E collector: R. Harin'Hala California Academy of Sciences malaise, secondary tropical forest MA-02-09C-11"; 1 female (in MTEC) labeled "MADAGASCAR: Fianaran. Pr. Ranomafana N.P. HQ. area 21°15'24"S 47°25'15E 25NOV1994, at night M.A. Ivie & D.A. Pollack"; and 1 female (in CAS) labeled "CASENT 8068052"/ "MADAGASCAR: Province d'Antsiranana, Montaigne Francais, elev 150 m 6-20 March 2001"/ "12°19.5'S, 49°20'E California Acad. of Sciences R. Harin'Hala coll. Malaise along forested limestone ridge MA-01-06-0. All paratypes also bear the following label: "PARATYPE *Eurydera oracle* Kavanaugh & Rainio sp. n. 2015" [yellow label].

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

DERIVATION OF SPECIES NAME.— The species epithet, *oracle*, is a noun in apposition and refers to Oracle Corporation, headquartered in Redwood City, California. We are pleased to name this new species for Oracle Corporation in recognition of and thanks for its generous support of the California Academy of Science 1998 Madagascar expedition, which produced many of the specimens on which this study has been based.

RECOGNITION.— Size above average for genus, SBL of males = 13.9–15.3 mm, of females = 12.4–14.1 mm. Members of this species (Fig. 25A) key to the *armata* group in Jeannel's (1949) key based on the following combination of features: size medium; head (Fig. 26A) with posterior part of frons formed as a broad, flat, smooth, elevated plateau, reddish in color, laterally delimited by deep furrows extended posteriorly beyond the level of the posterior margin of the eye then medially at a 45° angle and joined posteriorly (but distant from the midline) with a deep transverse furrow across the middle of the head; mandibles moderately short and broad; median lobe of male genitalia without a large, angulate projection on the ventral margin of the shaft near the base. However, within the *armata* group, they cannot be identified to species using Jeannel's key. They differ from members of *Eurydera crispatifrons* (Fairmaire 1896) in having a deep, sharply defined transverse furrow across the back of the head behind the raised frontal plateau (this furrow absent or very shallow and poorly defined in *E. crispatifrons* members). They differ from members of *Eurydera rufotincta* (Fairmaire 1868) in having the head large, nearly as wide as the pronotum (narrower in *E. rufotincta* members), black or piceous legs (rufous in *E. rufotincta* members) and in lacking transverse pale bands on the elytra (present in *E. rufotincta* members) and the deep oblong fossae present on the back of the frons in *E. rufotincta* members.

They differ from *Eurydera armata* Laporte (1831) and *Eurydera latipennis* (Klug 1835) members in having the lateral furrows on the back of the head angularly convergent toward the posterior transverse furrow whereas these furrows are virtually parallel posteriorly in *E. armata* members or very slightly convergent posteriorly in *E. latipennis* members and joined with the transverse furrow more laterally in members of both species. Also, the posterior part of the frontal plateau is much more elevated in *E. oracle* males than in those of these other two species as well as males of *Eurydera cuspidata* (Klug 1835), *Eurydera ornatipennis* (Fairmaire 1897), *Eurydera sulcicollis* Mateu (1973) and *Eurydera ambreana* Mateu (1973). Most members of *E. armata* and *E. ornatipennis* have pale bands or spots on the elytra, although some specimens lack all pale markings. None of the specimens of *E. oracle* that we have examined have similar pale markings, although several of our specimens have the apical one-fifth of elytral interval 1 narrowly pale, and two specimens also have interval 2 more dimly pale in the same area. Overall, members of *E. oracle* are most similar to those of *E. sulcicollis*, but they differ from the latter in having greater sexual dimorphism, with *E. oracle* males having relatively larger heads, more prominent eyes, frons more wrinkled and with the posterior portion of the medial area more elevated, the transverse groove deeper, and the pronotum shorter and distinctly wider than in *E. sulcicollis* male. Females of these two species are very similar. Finally, the median lobe of the genitalia of *E. oracle* males (Fig. 26B–C) is distinct from that of males all other species in the genus (compare with Jeannel 1949, Figs. 489, 491–498, 500, and Mateu 1973, Figs. 1–8) in the combined forms of the shaft and apex.

Geographical distribution.— We have examined specimens from only two areas. Seven specimens were collected in Ranomafana National Park, the type locality, on the eastern slope off the central plateau in the northeastern part of the southern half of the island of Madagascar. The eighth specimen, a female, was collected at Montagne des Français, in Antsiranana Province, at the northern end of the island and just over 1000 km distant from Ranomafana. No specimens have been recorded from intervening areas

Habitat distribution.— The specimen from Montagne des Français was collected in a malaise trap set on a forest limestone ridge at an elevation of only 150 m. All of the specimens from Ranomafana National Park were collected in secondary montane rainforest in the Talatakely area at elevations ranging from 900 to 1100 m. They have been collecting using malaise traps or by hand. In daytime, they have been found hiding on the underside of logs on the forest floor; and at night they have been found on the underside of shelf fungi on rotting logs and stumps.

Eurydera simplica **Kavanaugh and Rainio, sp. nov.**
Figures 27–28

Eurydera sp.; Rainio and Niemelä 2006: 227 (informal designation).
Eurydera n. sp. 3; Rainio 2009: 31, Rainio 2012: 72 (informal designation).

TYPE MATERIAL.— Holotype (Figs.27A–B), a male, in CAS, labeled: “MADAGASCAR, Ranomafana NP.,Talatakely, 900 m, Trail SP at 50 m mark, 08.03.2004”/ “collected by hand in daytime in secondary montane rainforest, F. Ratalata & J. Rainio collectors”/ “106” [handwritten label]/ “HOLOTYPE *Eurydera simplica* Kavanaugh & Rainio sp. n. 2015” [red label]. Paratypes

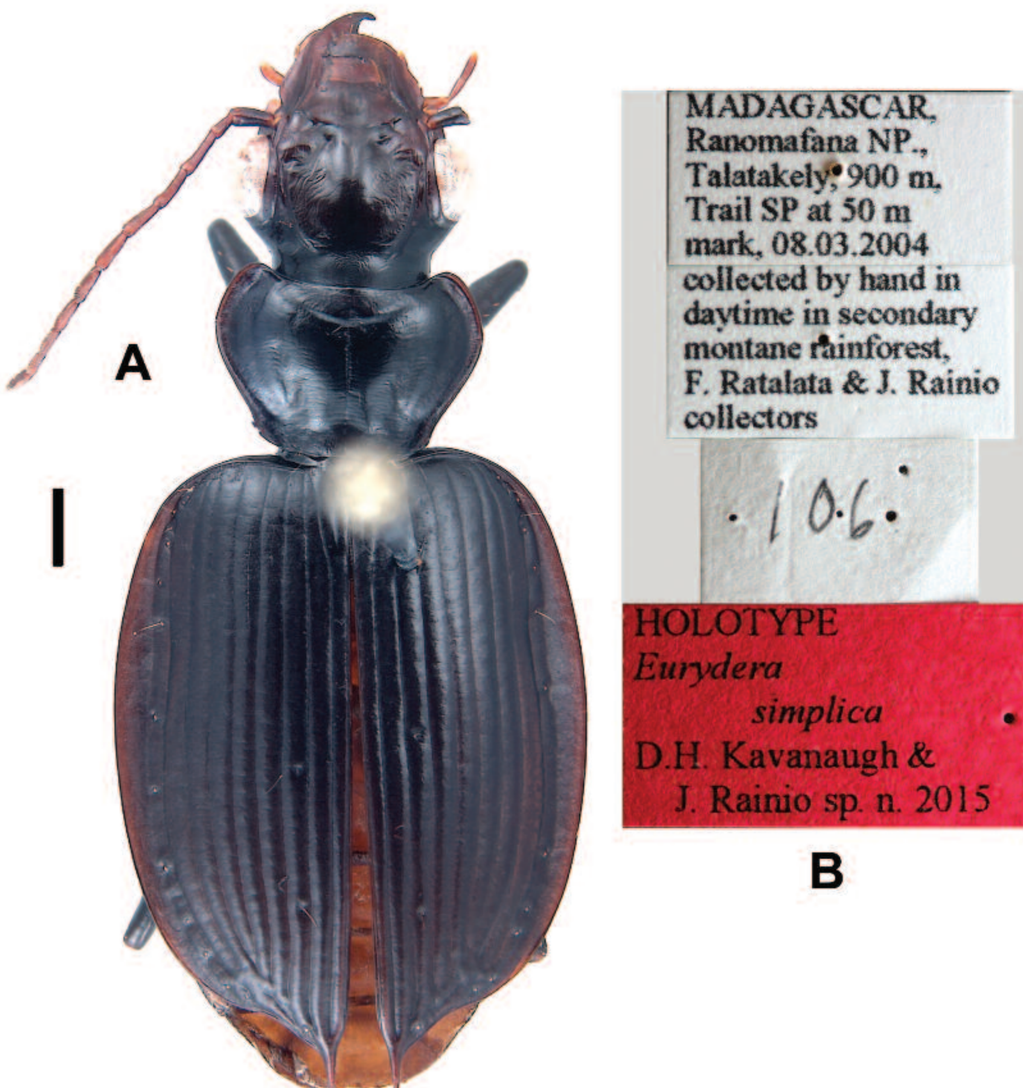

FIGURE 27. Digital images of holotype male of *Eurydera simplica* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

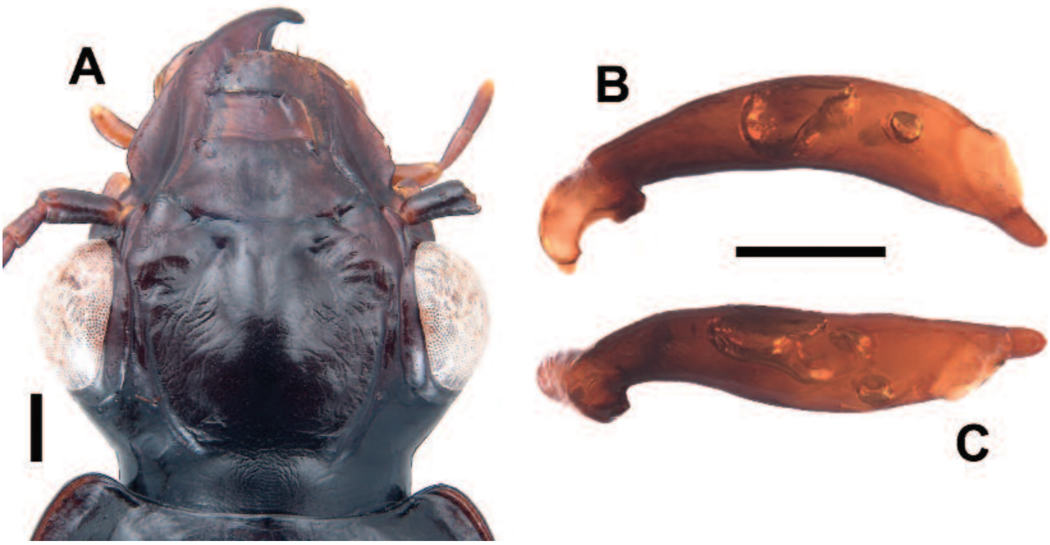

FIGURE 28. Digital images of holotype male of *Eurydera simplica* Kavanaugh & Rainio sp. nov. A. Head, dorsal aspect; B–C. Median lobe of aedeagus of genitalia; B. Left lateral aspect; C. Dorsal aspect. Scale lines = 0.5 mm.

(only 1): a female (in MNHN) labeled "“MADAGASCAR, Ranomafana NP., Talatakely, 900 m, Trail B at 1000 m mark, 15.06.2000"/ "collected by hand in daytime in secondary montane rainforest, F. Ratalata & J. Rainio collectors"/ "7/13" [handwritten label]/ "PARATYPE *Eurydera simplica* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *simplica*, is an adjective derived from the Latin word, *simplex*, meaning simple. The name refers to the relative simplicity of form and surface macrosculpture of member of this species compared with those of other species of *Eurydera*.

Recognition.— Size average for genus, SBL of male = 13.1 mm, of female = 12.4. Members of this species (Figs. 27A) are unlike those of any other species in the genus. In Jeannel's (1949) key species of *Eurydera*, they key to his *unicolor* species group, based on the following features: size medium; head (Fig. 28A) with posterior part of frons formed as a broad, flat, smooth, elevated plateau, laterally delimited by deep furrows extended posteriorly beyond the level of the posterior margin of the eye then slightly and arcuately convergent posteriorly and terminated abruptly at the level of the posterior margin of the ocular swelling and just less than halfway from the midline to the lateral margin of the head, area between the furrow smooth and only slightly elevated; mandibles moderately short and broad; median lobe of male genitalia without a large, angulate projection on the ventral margin of the shaft near the base. Jeannel included only *Eurydera unicolor* (Klug 1833) in this species group, but Mateu (1973)added another species, *Eurydera fossulata* Mateu to the group, in part based on the shared lack of sexual dimorphism in the front tarsi in members of these two species. Unlike males of most *Eurydera* species, those of *E. unicolor* and *E. fossulata* have tarsomeres 1 to 3 no wider than in females and without ventral adhesive setae. Members of *E. simplica* are easily distinguished from those of these two species, as well as from all other described *Eurydera* species, by the uniquely shaped pronotum (Fig. 27A), which is relatively small and short for the genus, with the disc smooth, lateral explanation very narrow, lateral margins with very short and shallow sinuation anterior to markedly obtuse hind angles, and basal margin obliquely angulate laterally. Unlike males of *E. unicolor* and *E. fossulata*, those of *E. simplica* have front tarsi with tarsomeres 1 to 3 wider than in females and with at least a few adhesive setae ventrally, which may call into question a close relationship with these two these species. Members of *E. simplica* also differ from those of *E. unicolor* in having the pronotum with anterior angles much less projected anteriorly. They differ from members of *E. fossulata* in having the posterior part of the head, between the lateral furrows, smooth and slightly convex, whereas *E. fossulata* members have a deep, transverse medial depression, the bottom of which is flat and covered with deep transverse creases, on that part of the head. They also have the elytral intervals without the roughened surfaces typical of members of several species in genus, including *E. fossulata* (at least subapically), and the sutural spines are very long and straight (similar to those in *E. unicolor* and *E. fossulata* members). Finally, the median lobe of male genitalia of the holotype of *E. simplica* (Fig. 28B–C) has the shaft much narrower basally and the apical orifice shorter than in *E. unicolor* males (see Jeannel 1949, Fig. 495). No male of *E. fossulata* has been available for comparison.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The two known specimens of this species both were collected by hand in daytime in secondary montane rainforest in the Talatakely area at elevations ranging from 900 to 1000 m.

Subtribe Cymindidina Laporte 1834

Ball and Hilchie (1983) considered the following two genera as subgenera of a single genus, *Hystrichopus* Boheman (1848); however we follow Casale (1998) and Lorenz (2005) in treating them as separate genera, pending a more comprehensive phylogenetic analysis of the Cymindidina.

Genus *Pseudomasoreus* Desbrochers des Loges 1904

Jeannel (1949) included only three species in his treatment of this genus for Madagascar. Mateu (1980) added six new species and provided a key to the nine Malagasy species known at that time. Casale (1998) added one additional Malagasy species, *Pseudomasoreus deuvei* Casale. This genus presently includes a total of 20 species (Lorenz 2005) with a cumulative disjunct distribution ranging from the Pyrenees of France and Spain south to southern Africa and Madagascar (Ball and Hilchie 1983).

***Pseudomasoreus ranomafanae* Kavanaugh and Rainio, sp. nov.**
Figures 29, 30A, 30C

Deuveilla n. sp. 1; Rainio 2009: 31(informal designation).
Lebiinae (n. sp. 1); Rainio 2012: 72 (informal designation).

Type material.— Holotype (Figs.29A–B), a male, in CAS, labeled: “CASENT 1004471”/ “MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,”/ “21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,”/ “E.F. Randrianirina, N. Rasoamanananana, T.J. Ravelomanana, and H.C. Raveloson collectors”/ “collected in daytime from large accumulation of dead leaf, twig, and branch debris on and extended up to 2 m above forest floor”/ “HOLOTYPE *Pseudomasoreus ranomafanae* Kavanaugh & Rainio sp. n. 2015” [red label]. Paratypes (total of 8): 1 male (in CAS) labeled same as holotype except “CASENT 1004472”; 2 males (in CAS) labeled “CASENT 1004003” and “CASENT 1004004”, respectively/

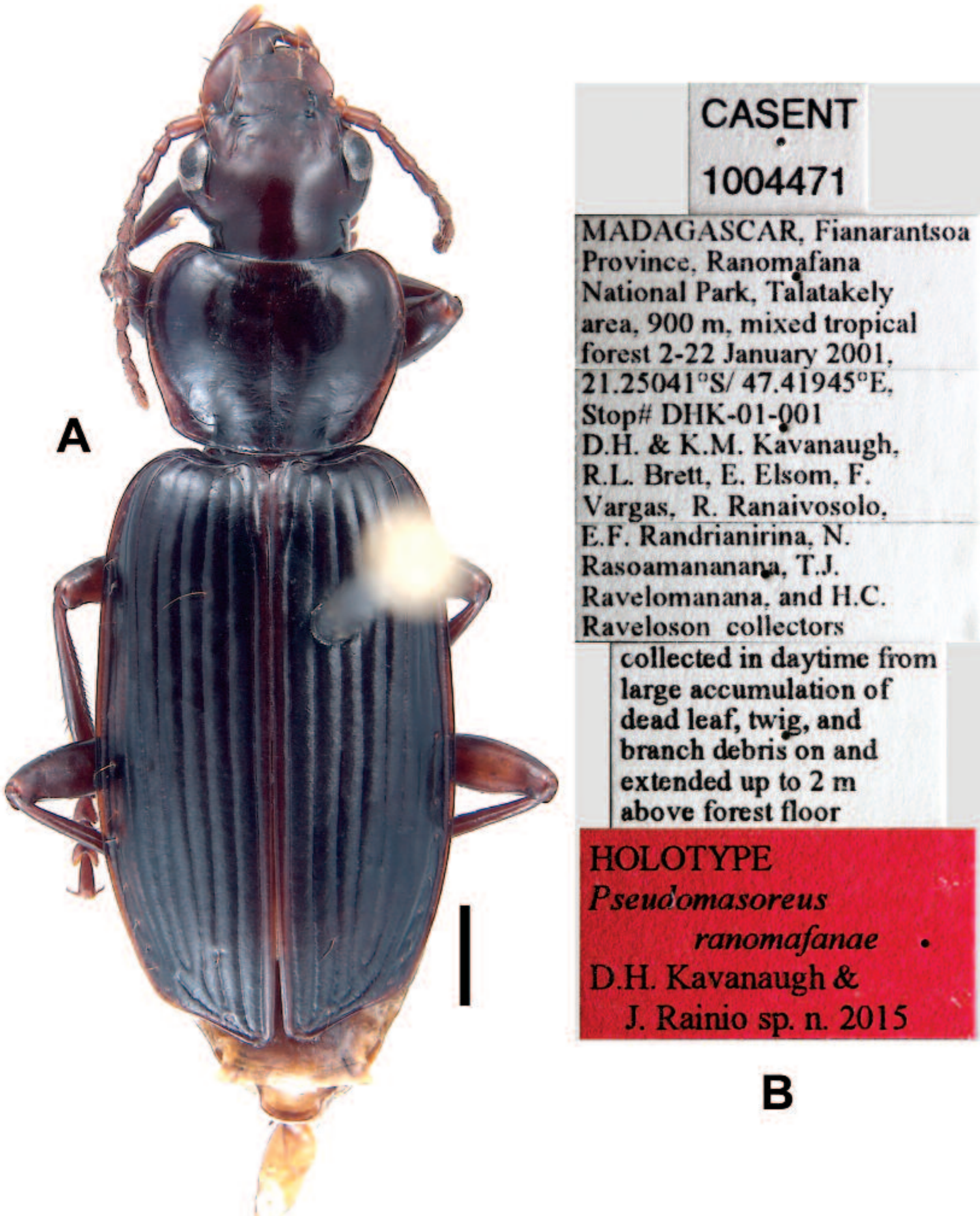

FIGURE 29. Digital images of holotype male of *Pseudomasoreus ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line A = 1.0 mm.

"MADAGASCAR, Fianarantsoa Prov-ince, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 2-22 January 2001,"/ "21.25041°S/ 47.41945°E, Stop# DHK-01-001, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime by beating live understory vegetation and/or dead leaves and other suspended debris"; 1 male (in CAS) labeled "CASENT 1002681"/ "MADAGASCAR, Fianarantsoa Prov-ince, Ranomafana National Park, Vohiparara area, 1170 m, mixed tropical forest, 2-22 January 2001,"/ "21.22644°/ 47.36979°S, Stop# DHK-01-004, D.H. & K.M Kavanugh, R.L. Brett, E. Elsom, F. Vargas, R. Ranaivosolo,"/ "E.F. Randrianirina, N. Rasoamananana, T.J. Ravelomanana, and H.C. Raveloson collectors"/ "collected in daytime by beating debris suspended in leaf whirls of *Pandanus* sp."; 1 male and 2 females (in CAS and MNHN) labeled "CASENT 1049027", "CASENT 1049028" and "CASENT 1049029", respectively/ "MADAGASCAR, Fianarantsoa Province, Ranoma-fana National Park, Vohiparara area, 1150 m, mixed tropical forest, 24 April 1998, 21°12.8'S 47° 23.0'E,"/ "Stop# 98-74, D. H. Kavanaugh collector beaten from vegetation at forest edge"; 1 male (in MZF) labeled "MADAGASCAR, Ranomafana NP.,Talatakely, 900 m, Trail BFA 75 m, 16.03.2001"/ "collected by hand in daytime, F. Ratalata & J. Rainio collectors". All paratypes also bear the following label: "PARATYPE *Pseudomasoreus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

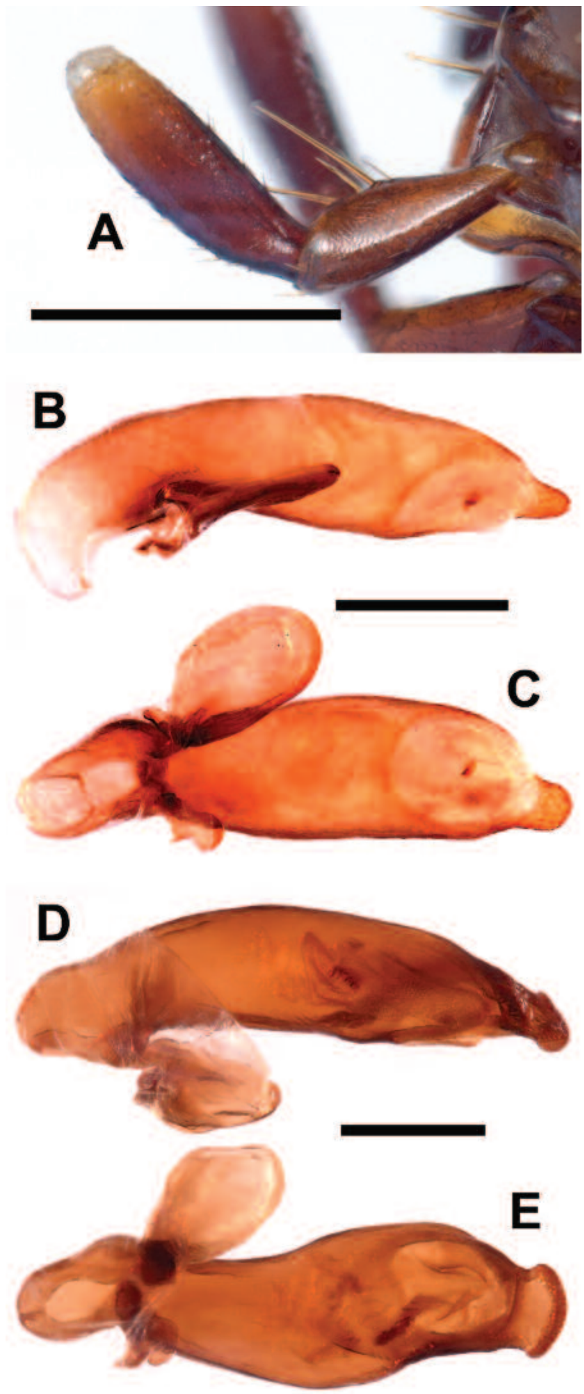

Figure 30. Digital images of *Pseudomasoreus* spp. A–C. Holotype male of *P. ranomafanae* Kavanaugh & Rainio sp. nov.; D, E. *P. catalai* Jeannel (from Ranomafana National Park). A. Right labial palpus, ventral aspect; B–E. Aedeagus of male genitalia; B, D. Left lateral aspect; C, E. Ventral aspect. Scale lines = 0.5 mm.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size large for genus, SBL of males = 9.7–10.6 mm, of females = 10.3 mm. In Mateu's (1980) key to the Malagasy species of this genus, members of *P. ranomafanae* (Fig. 29A) key to *Pseudomasoreus decorsei* Jeannel (1941b) based on the following combination of features: size large, SBL = 8.5 mm or more; elytra concolorous brown or piceous, without pale areas. However, they differ from the unique holotype of *P. decorsei* in having even larger body size (SBL = 8.5 mm in *P. decorsei* type), pronotum narrower overall and especially basally and with less rounded, more evident hind angles (pronotum broad, rounded, with hind angles effaced by smoothly rounded transition from lateral to basal margin in *P. decorsei* type), and elytral lateral margins nearly parallel (more evenly rounded in *P. decorsei* type). Members of *P. ranomafanae* are actually more similar to those of *P. deuvei*, which was not included in Mateu's key. They share large size, general body form with long, parallel-sided elytra, and antennomere 3 glabrous except for the apical whorl of fixed setae (additional pubescence seen in apical part of antennomere 3 in most other species of genus). However, their body size is slightly smaller on average (SBL = 10.2–11.5 in *P. deuvei* members), the pronotum is narrower overall and more narrowed basally, with the hind angles more distinct than in *P. deuvei* members and the lateral margins either straight or with slight sinuation anterior to the hind angles (lateral margins not at all sinuate in the latter). Also, the penultimate labial palpomeres in all specimens of the type series have three or four setae (Fig. 29C), whereas members of *P. deuvei* have only two such setae, a feature particularly noted by Casale in his original description. Finally, the median lobe of male genitalia (Figs. 30A,C) has the shaft slightly less arcuate and the apex slightly longer on more rounded apically than in *P. deuvei* males (see Casale 1998, Figs.4–5). For future comparative purposes, we also provide digital photographs of the median lobe of the genitalia of a male *Pseudomasoreus catalai* Jeannel (1949) (Figs. 30B,D) [male previously unknown] to complement the illustrations of other *Pseudomasoreus* species provided by Jeannel (1949), Mateu (1980) and Casale (1998).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Specimens of this species were are collected in secondary montane rainforest in the Talatakely and Vohiparara areas at elevations ranging from 900–1170 m. Adults were collected by hand, by beating live vegetation and suspended dead leaves and twigs, particularly dead leaves suspended is leaf whirls of *Pandanus* sp. Two specimens were found in daytime in masses of dead leaves, twigs and branch debris accumulated on the forest floor.

Genus *Assadecma* Basilewsky 1982

This genus is precinctive to Madagascar and previously represented only by the type species, *Assadecma madagascariensis* Basilewsky (1982).

Assadecma basilewskyi Kavanaugh and Rainio, sp. nov.

Figure 31A–B, 32

Type material.— Holotype (Figs. 31A–B), a male, in NMNH, labeled: "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 940m 21°16'S, 47°25'E 18 April 1994"/ "pitfall traps in montane rainforest, E. Rajeriarison & R. Malenky"/ "HOLOTYPE *Assadecma basilewskyi* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 2): 1 male (in NMNH) labeled same as holotype; 1 male (in CAS) labeled "CASENT 1051147"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 900 m, mixed tropical forest, 26 April

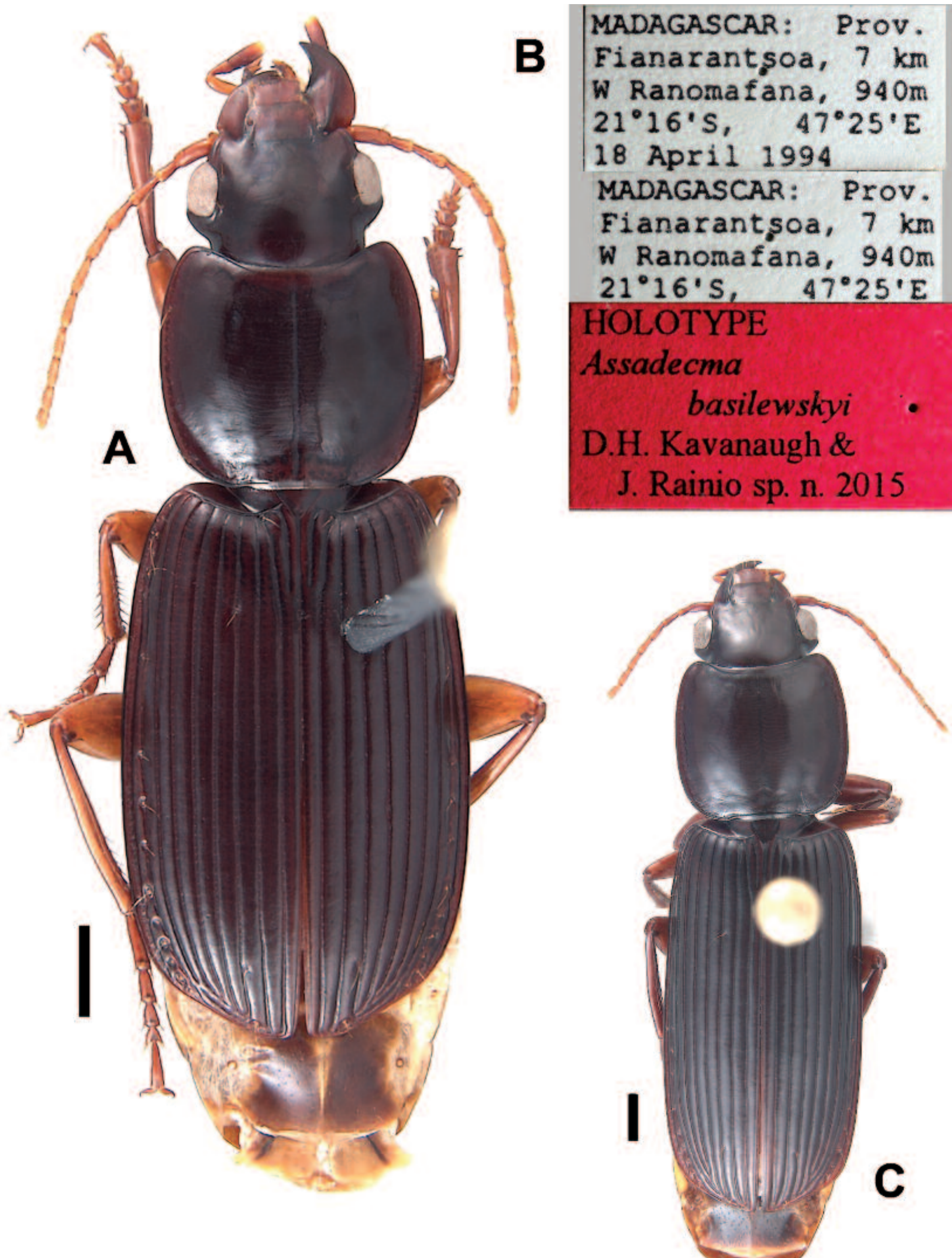

FIGURE 31. Digital images of *Assadecema* spp. A–B. Holotype male of *Assadecma basilewskyi* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C. *A. madagascariensis* Basilewsky female, dorsal habitus. Scale lines = 1.0 mm.

1998."/ "21°15.3'S 47°25.9'E, Stop # 98-84 D.H. Kavanaugh collector collected at night on ground beside trail in forest". Both paratypes also bear the following label: "PARATYPE *Assadecma basilewskyi* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *basilewskyi*, is a noun in apposition, based from the surname of Dr. Pierre Basilewsky, now deceased, who was for many years a lead entomologist at the Koninklijk Museum voor Midden Africa (Musée Royal de l'Afrique Centrale) in Tervuren. We are pleased to name this new species in honor of Dr. Basilewsky's many contributions to knowledge of the carabid beetle faunas of the Afrotropical Region in general and Madagascar in particular.

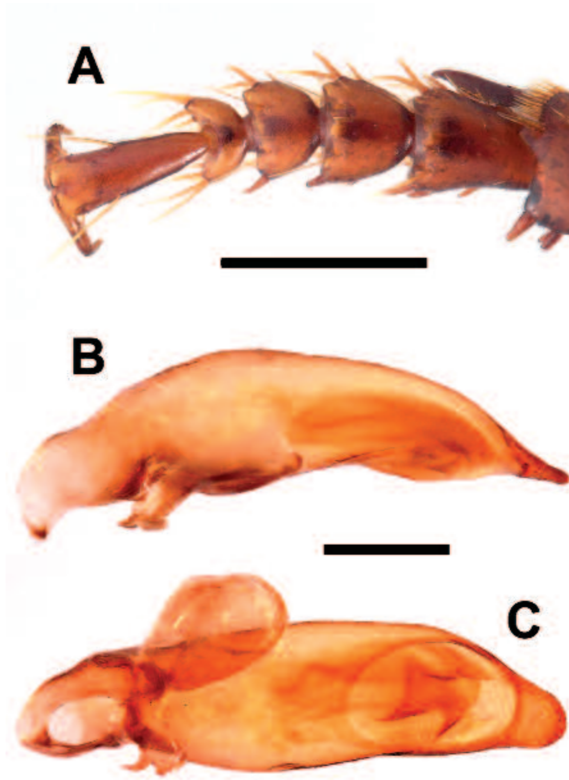

Figure 32. Digital images of holotype male of *Assadecma basilewskyi* Kavanaugh & Rainio sp. nov. A. Left front tarsus, dorsal aspect; B–C. Aedeagus of male genitalia; B. Left lateral aspect; C. Ventral aspect. Scale lines = 0.5 mm.

Recognition.— Small for genus, SBL of males = 9.5–10.8 mm, female unknown. Basilewsky (1982) included a single species, *A. madagascariensis* in this genus. We have examined the holotype male of that species and found several features that differ with those found in specimens of *A. basilewskyi* (Fig. 31A). The former is much larger (SBL = 12.9 mm), (about the same size as the *A. madagascariensis* female illustrated in Fig. 31C) than males of *A. basilewskyi*. Its elytral microsculpture is comprised of markedly transverse sculpticells, producing distinct iridescence, whereas in *A. basilewskyi* the sculpticells are only slightly transverse, producing no evident iridescence. Also the relative body shapes and proportions of males of the two species are distinctly different. In *A. madagascariensis*, the elytra are long (ratio EL/PL = about 2.5) and the elytral lateral margins are nearly parallel for most of their length (same as in the female, Fig. 31C). In *A. basilewskyi*, the elytra are relatively shorter (ratio EL/PL = about 2.3) and the elytral lateral margins are slightly rounded throughout (Fig. 31A). Front tarsomere 4 in males of *A. basilewskyi* (Fig. 32A) is not as short and broad as that in *A. madagascariensis* (see Basilewsky, 1982:23, Fig. 3a). Finally, the median lobes of the genitalia of *A. basilewskyi* males (Fig. 32B–C) and *A. madagascariensis* males (see Basilewsky 1982:22, Fig. 2d) are markedly different in form.

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— The holotype and one paratype of this species were collected in a pitfall trap in montane rainforest at an elevation of 940 m. The second paratype was found at night walking on the ground beside a trail in the same general area.

Subtribe Lebiina Bonelli 1810

Genus *Lebia* Latreille 1802

As currently conceived, this genus is a megadiverse taxon with hundreds of species arrayed in 16 subgenera (Lorenz 2005) and with a worldwide distribution in tropical to temperate regions. Jeannel (1949) considered *Lebia* and *Nematopeza* Chaudoir (1870) as distinct genera, but the latter is now generally treated as a subgenus of the former (Lorenz 2005).

Subgenus *Metalebia* Jeannel 1949

Jeannel (1949) considered this subgenus to include most of the *Lebia* species of tropical Africa, Madagascar, and India. He reported 18 species in his treatment of the Malagasy fauna. Lorenz (2005) lists a total of 36 species for this subgenus.

Lebia (*Metalebia*) *laterolucida* Kavanaugh and Rainio, sp. nov.

Figure 33

Type material.— Holotype (Figs. 33A–B), a female, in CAS, labeled: "CASENT 1006164"/ MADAGASCAR Fianarantsoa Prov. Parc Nacional Ranomafana Bell Vue Trail, tropical forest 21°15.5'S 47°25.6'E 1000 m M.E.Irwin and E.I. Schlinger MEI 99-MA-7 21-XII-1999"/ "HOLOTYPE *Lebia* (*Metalebia*) *laterolucida* Kavanaugh & Rainio sp. n. 2015" [red label].

Paratypes (only 1): a female (in CAS) labelled "CASENT 1049030"/ "MADAGASCAR, Fianarantsoa Province, Ranomafana National Park, Talatakely area, 850 m, 13 April 1998,"/ "21°14'S 47°22'E Malaise trap in mixed tropical forest, M.E.Irwin and E.I. Schlinger collectors, Stop 98-MAD-1"/ "PARATYPE *Lebia* (*Metalebia*) *laterolucida* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *laterolucida*, is an adjective derived from the Latin words, *lateris*, meaning side, and *lucidus*, meaning bright or full of light. The name refers to the pale, translucent lateral pronotal margins, which contrast markedly with the dark pronotal disc in members of this species.

Recognition.— Size moderate for genus, SBL of females = 4.5–5.0 mm. Members of this species (Fig. 33A) key to subgenus *Metalebia* Jeannel (1949) and the *madagascariensis* group in Jeannel's (1949) key: the basal elytral border is absent medially between the base of stria 3 and the scutellum; the elytral striae are deep and the elytral intervals convex and impunctate; the forebody (head plus pronotum) has no metallic reflection and the elytra are uniform in color; and the frons is slightly convex and without distinct frontal furrows between the eyes. Within the *madagascariensis* group, *L. laterolucida* members are distinguished from those of *L. alluaudana* Jeannel (1949), *L. apicoviolacea* sp. nov., *L. mirana* Alluaud (1936a), *L. ranomafanae* sp. nov., and *L. tanala* Jeannel (1949) by the absence of metallic reflection on the elytra and punctation of the anterior dorsum of the head (both features present in members of the other five species). They differ from members of *L. sulcipennis* (Fairmaire) (1889), *L. nana* Jeannel (1949), and *L. perrieri* Jeannel (1949) in having the pronotum broad, ratio PW/PL = at least 1.5, and with lateral margins distinctly rounded at least in the anterior half pronotum (narrower and less rounded anteriorly in members of the three other species). From adults of *L. rufa* Jeannel (1949), they differ in having the pronotal basal lobe distinctly margined (absent from the former). *Lebia laterolucida* adults are most similar to those of the two remaining species in Jeannel's key, *L. brunneipennis* Jeannel

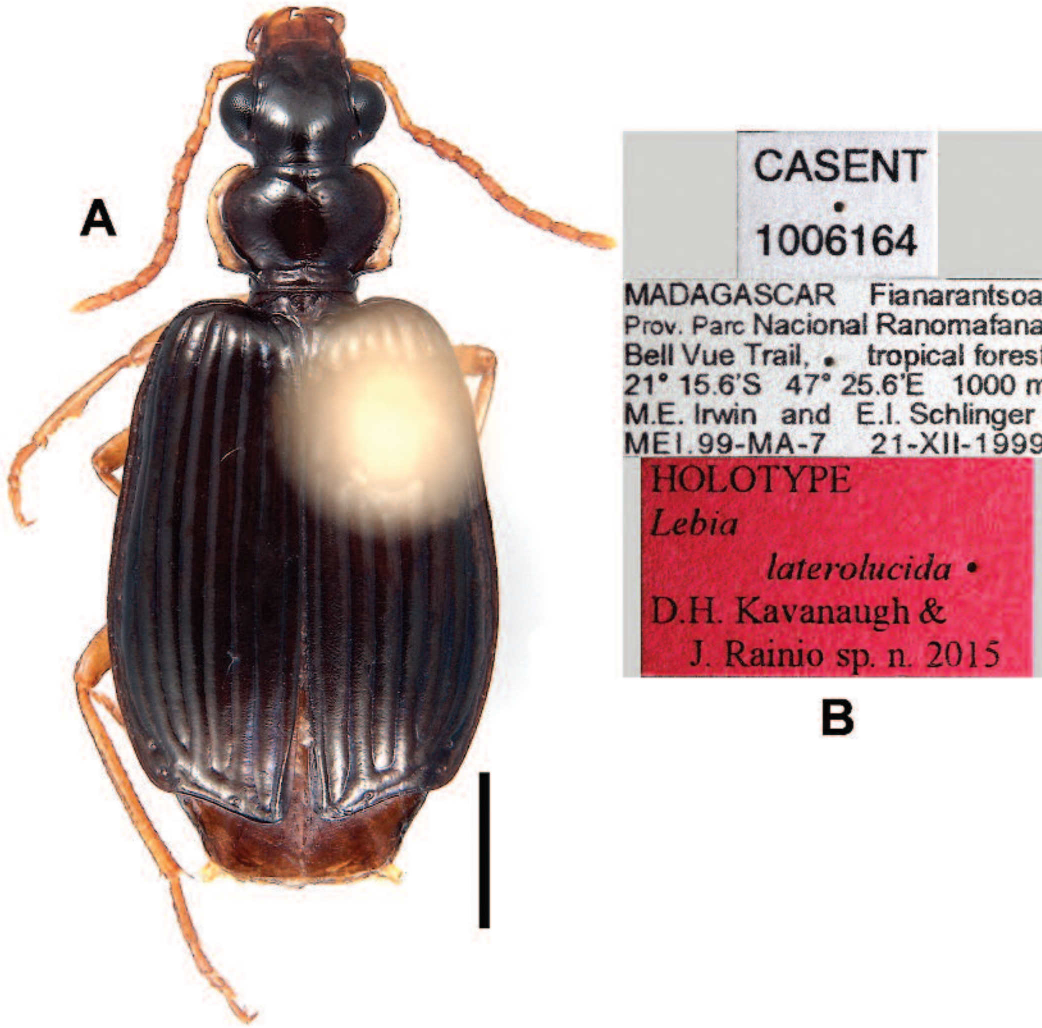

FIGURE 33. Digital images of holotype female of *Lebia* (*Metalebia*) *laterolucida* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

(1949) and *L. madagascariensis* Chaudoir (1850), but differ from them in having the dorsum of the head, pronotum and elytra dark piceous, with markedly contrasting pale yellow lateral pronotal margins (dorsum uniformly reddish brown and the lateral pronotal margins not or less markedly contrasting in color in the together two species). In addition, they are distinctly smaller than *L. madagascariensis* adults and have distinct elytral microsculpture (absent or at least very faint in *L. brunneipennis* adults).

GEOGRAPHICAL DISTRIBUTION.— At present, known only from the type locality.

HABITAT DISTRIBUTION.— Both specimens of the type series were collected in mixed secondary tropical forest in the Talatakely area in malaise traps.

Lebia* (*Metalebia*) *ranomafanae **Kavanaugh and Rainio, sp. nov.**
Figure 34

Type material.— Holotype (Figs.34A–B), a male, in NMNH, labeled: "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100m 22-31 October 1988 W. E. Steiner"/ "Malaise trap in small clearing, montane rain forest"/ "HOLOTYPE *Lebia* (*Metalebia*) *ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (only 1): a female (in CAS) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 900m 23-28 February 1990 W. E. Steiner"/ "Malaise trap in small clearing, montane rain forest"/ "PARATYPE *Lebia* (*Metalebia*) *ranomafanae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size slightly small for genus, SBL of male = 4.3 mm, of female = 4.2 mm. Members of this species (Fig. 34A) key to subgenus *Metalebia* Jeannel (1949) and the *madagascariensis* group in Jeannel's (1949) key: the basal elytral border is absent medially between the base of stria 3 and the scutellum; the elytral striae are deep and the elytral intervals convex and impunctate; the forebody (head plus pronotum) has no metallic reflection and the elytra are uniform in color (but not necessarily in reflection); and the frons is slightly convex and without distinct frontal furrows between the eyes. Within the *madagascariensis* group, *L. ranomafanae* members can be distinguished from those of all species except *L. alluaudana*, *L. apicoviolacea* sp. nov., *L. mirana* and *L. tanala* by the presence of elytral metallic reflection (metallic reflection absent from the elytra of members of the remaining seven species). They are distinguished from members of *L. mirana* by their reddish labrum (black in *L. mirana* members) and from those of *L. alluaudana* by their small size and relatively short and broad elytra, with ratio of elytra length to width = 1.3 (size larger, SBL of males = 4.6–5.0 mm, of females 4.6–5.3 mm, and elytra relatively longer, with ratio EL/EW = 1.4, in *L. alluaudana* members). They are distinguished from members of *L. tanala* in having very dark and relatively faint elytral metallic reflection, pronotum with anterior angles indistinct, smoothly rounded from apical to lateral margin and not at all projected anteriorly beyond apical margin, lateral margins nearly parallel in posterior two-thirds and not or only very slightly sinuate anterior to obtusely angulate hind angles (elytral metallic reflection more distinct, pronotum with anterior angles broadly round but slightly projected anteriorly beyond apical margin, lateral margins distinctly sinuate anterior to sharp, rectangular hind angles slightly projected laterally in members of *L. tanala*). Finally, they can be distinguished from members of *L. apicoviolacea* by slightly larger size and the faint, concolorous dark blue-green elytral metallic reflection and (size slightly smaller, SBL of male = 3.8 mm, of female = 4.0 mm, and elytra with distinct tricolored metallic reflection, green basally and on medial two-thirds, brassy on lateral one-third and violet in apical one-fifth, in *L. apicoviolacea* members. Shape of the median lobe of the male aedeagus (Fig. 34C–D) is also diagnostic, with the shaft broadest at basal one-third, slightly and evenly arcuate on ventral margin in lateral view (Fig. 34C) and apex parallel-side basally and broadly rounded apically in dorsal view (Fig. 34D).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Both specimens of the type series were collected in malaise traps in secondary montane rainforest in the Talatakely area at elevations ranging from 900 to 1100 m.

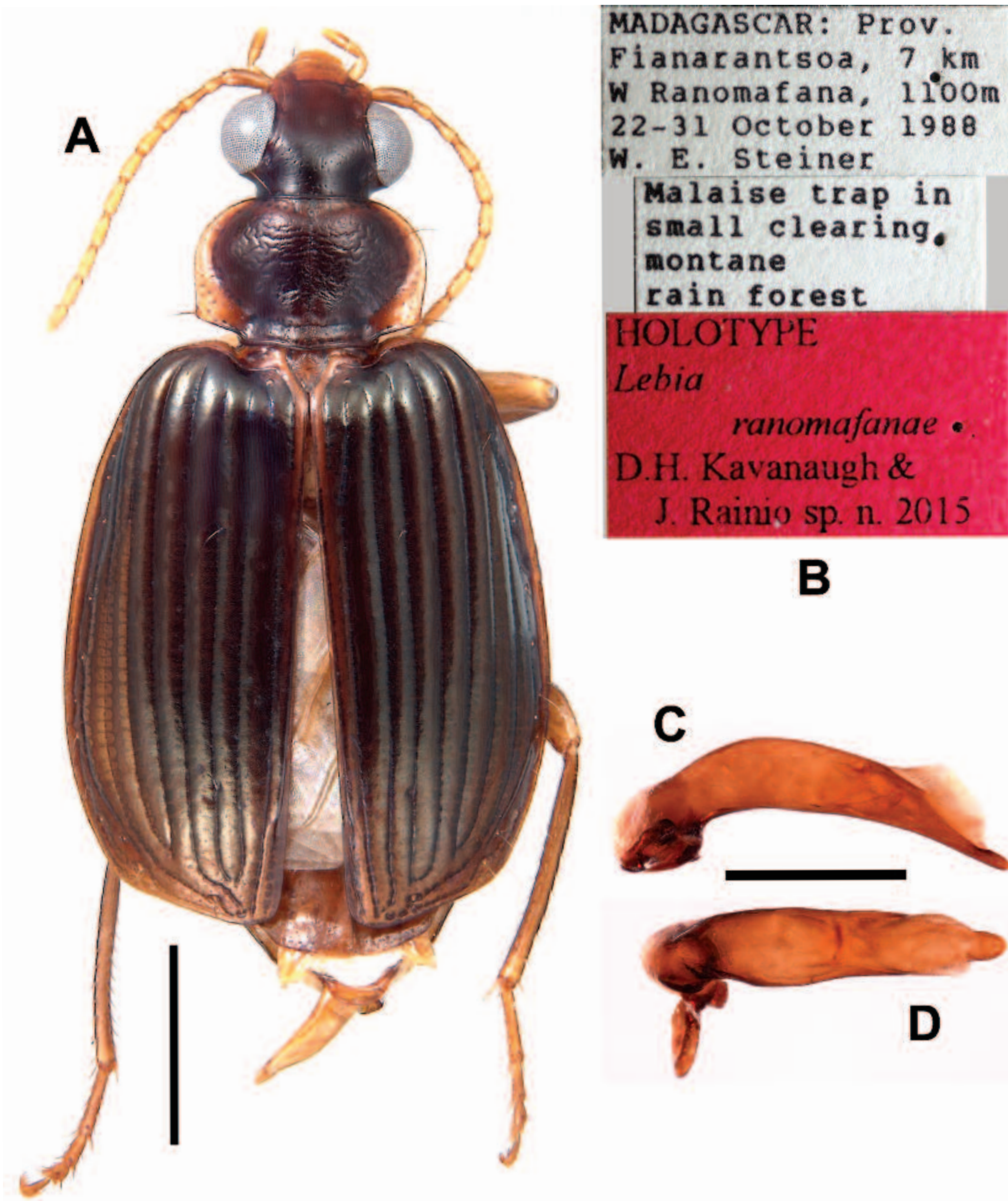

FIGURE 34. Digital images of holotype male of *Lebia* (*Metalebia*) *ranomafanae* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C–D. Aedeagus of male genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines = 0.5 mm.

***Lebia* (*Metalebia*) *apicoviolacea* Kavanaugh and Rainio, sp. nov.**
Figure 35

Type material.— Holotype (Figs. 35A–B), a male, in CAS, labeled: "MADAGASCAR: Fianaran. Pr. Ranomafana N.P. HQ. area 21°15'24"S 47°25'15E 25NOV1994, at night M.A. Ivie & D.A. Pollack"/ "HOLOTYPE *Lebia* (*Metalebia*) *apicoviolacea* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (only 1): a female (in NMHN) labeled "MADAGASCAR: Prov. Fianarantsoa, 7 km W Ranomafana, 1100 m 6-21 October 1988 W. E. Steiner"/ "At black light in montane rain forest"/ "PARATYPE *Lebia* (*Metalebia*) *apicoviolacea* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *apicoviolacea,* is an adjective derived from the Latin words, *apex*, meaning tip, and *violaceus*, meaning violet-colored. The name refers

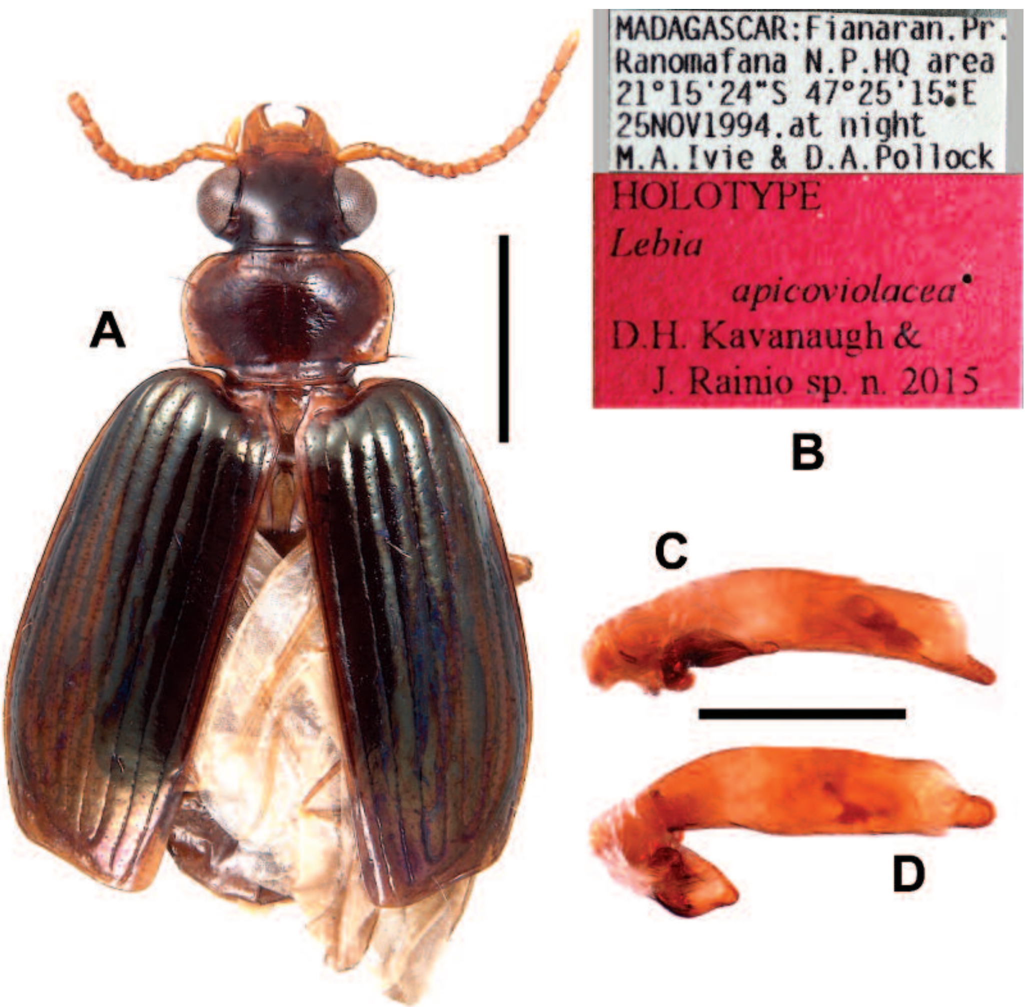

Figure 35. Digital images of holotype male of *Lebia* (*Metalebia*) *apicoviolacea* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels; C–D. Aedeagus of male genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines A = 1.0 mm, C–D = 0.5 mm.

to the violet or purple metallic reflection of elytral apices, which contrasts distinctly with the green or bronze metallic reflection of the remainder of the elytra in members of this species.

Recognition.— Size moderately small for genus, SBL of male = 3.8 mm, of female = 4.0 mm. Members of this species (Fig. 35A) key to subgenus *Metalebia* Jeannel (1949) and the *madagascariensis* group in Jeannel's (1949) key: the basal elytral border is absent medially between the base of stria 3 and the scutellum; the elytral striae are deep and the elytral intervals convex and impunctate; the forebody has no metallic reflection and the elytra are uniform in color (but not necessarily in reflection); and the frons is slightly convex and without distinct frontal furrows between the eyes. Within the *madagascariensis* group, *L. apicoviolacea* members can be distinguished from those of all species except *L. alluaudana*, *L. mirana* Alluaud, *L. ranomafanae* and *L. tanala* by the presence of elytral metallic reflection (metallic reflection absent from the elytra of members of the remaining seven species). They are distinguished from members of *L. mirana* by their reddish labrum (black in *L. mirana* members) and from those of *L. alluaudana* by their small size and relatively short and broad elytra, with ratio of elytra length to width = 1.2–1.3 (size larger, SBL of males = 4.6–5.0 mm, of females 4.6–5.3 mm, and elytra relatively longer, with ratio of elytra length to width = 1.4, in *L. alluaudana* members). They are distinguished from members of *L. tanala* in having the pronotum with lateral margins slightly sinuate anterior to slightly obtuse hind angles (lateral margins distinctly sinuate anterior to sharp, rectangular hind angles slightly projected laterally in members of *L. tanala*) and from members of both *L. ranomafanae* and *L. tanala* in having elytra with distinct tricolored metallic reflection, green basally and on medial two-thirds, brassy on lateral one-third and violet in apical one-fifth (elytral metallic reflection uniformly faint or distinct metallic green or blue in members of *L. ranomafanae* and *L. tanala*). Shape of the median lobe of the male aedeagus (Fig. 35C–D) is also diagnostic, with the shaft very slightly arcuate, dorsal and ventral margins more or less parallel in basal two-thirds in lateral view (Fig. 35C) and apex moderate in length and relatively broader in both lateral and dorsal (Fig. 35D) views than in males of other species of this species group (compare with Jeannel 1949, Fig. 440a-l).

Geographical distribution.— At present, known only from the type locality.

Habitat distribution.— Both specimens of the type series were collected in secondary montane rainforest in the Talatakely area at elevations ranging from 900 to 1100 m. Both were collected at night, one by hand from vegetation, and the other attracted to ultraviolet light.

Tribe Galeritini LeConte 1853

Genus *Eunostus* LaPorte 1835

This genus occurs only in Africa and Madagascar (Jeannel 1949) and includes 14 previously described species (Lorenz 2005), six of which are endemic to Madagascar. Jeannel (1949) provided a key to the six Malagasy species known to him.

Eunostus minimus Kavanaugh and Rainio, sp. nov.

Figures 36–37

Eunostus n. sp. 1; Rainio 2009: 31, Rainio 2012: 72 (informal designation).

Type material.— Holotype (Figs. 36A–B), a male, in CAS, labeled: "CASENT 8069195"/ "MADAGASCAR: Fianarantsoa Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana elev 1100m 27-31 Mar 2003"/ "21°17'24"S 047°26'00"E California Acad. of Sciences coll. Fisher, Griswold et al. sifted litter, montane rainforest collection code: BLF8400"/ "HOLOTYPE *Eunostus minimus* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of

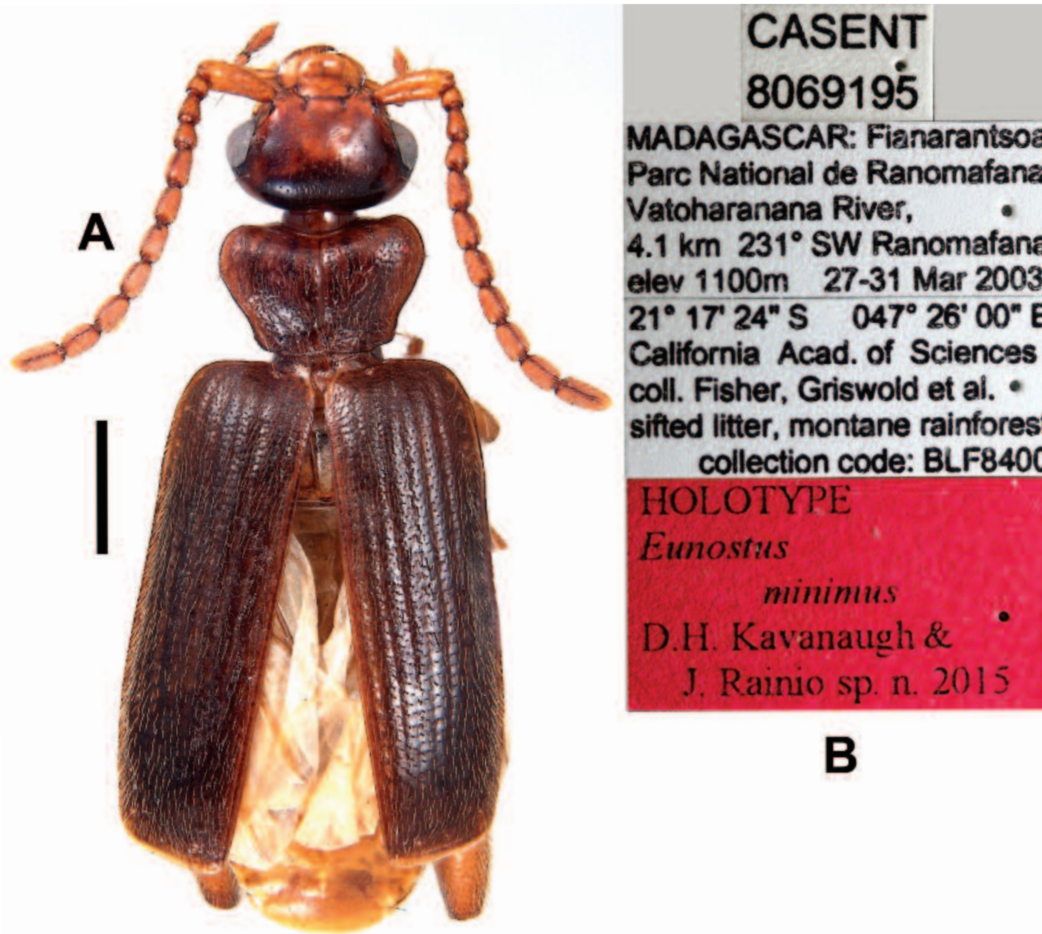

FIGURE 36. Digital images of holotype male of *Eunostus minimus* Kavanaugh & Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line A = 1.0 mm.

2): 1 male (in MNHN) labeled “CASENT 8069129”/ “MADAGASCAR: Fianarantsoa, Ranomafana JIRAMA water works, 21°14.91’S, 047°27.13’E”/ “21-24 December 2001 collector: R. Harin’Hala California Acad of Sciences malaise trap near river elev. 690 m, MA-02-09D-08”; 1 female (in CAS) labeled “CASENT 1051146”/ “MADAGASCAR Ranomafana NP, Vatoharana trail S 600 24.8.2004”/ “collected by hand in daytime, F. Ratalata & J. Rainio collectors”. Both paratypes also bear the following label: “PARATYPE *Eunostus minimus* Kavanaugh & Rainio sp. n. 2015” [yellow label].

TYPE LOCALITY.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

DERIVATION OF SPECIES NAME.— The species epithet, *minimus*, is the Latin adjective meaning smallest, a reference to fact that the known specimens of this species are smaller than those of any of the other known species that we have examined.

RECOGNITION.— Small for genus, SBL of male = 5.5 mm, of female 5.0–5.1 mm. Members of this species (Fig. 36A) do not key out in Jeannel’s (1949) key for *Eunostus* species. They are much smaller and shinier than members of any other described species. Their heads are slightly narrower, with the tempora more evenly rounded to the back of the head, their antennal scapes

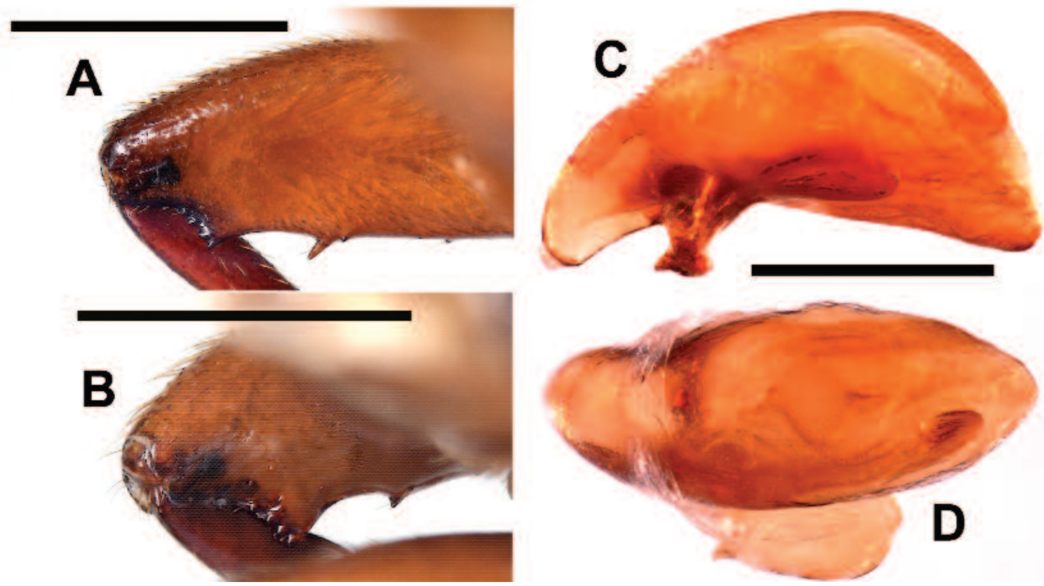

FIGURE 37. Digital images of *Eunostus minimus* Kavanaugh & Rainio sp. nov. A–B. Apical part of left hind femur, oblique medial aspect; A. Holotype male; B. Female; C–D. Aedeagus of holotype male genitalia; C. Left lateral aspect; D. Dorsal aspect. Scale lines = 0.5 mm.

shorter and thicker than in other species, thickest slightly distal to mid-length. Lateral margins of the pronotum are smoothly rounded in anterior half with a moderately short and deep subbasal sinuation anterior to slightly obtuse to rectangular hind angles. The elytral setae are generally sparser than in other species and arranged in 2 more or less distinct longitudinal rows on each interval. Male (Fig. 37A) and female (Fig. 37B) hind femora are sexual dimorphic, each unique among Malagasy species for each sex. Median lobe of male genitalia Figs. 37C–D markedly different in shape from those of the other species for which males are known (see Jeannel 1949, Fig. 513d–e).

GEOGRAPHICAL DISTRIBUTION.— At present, known only from the type locality.

HABITAT DISTRIBUTION.— Specimens of the type series were collected in both primary montane rainforest in the Vatoharanana area (at elevations ranging from of 1100 to 1200 m) and in secondary montane rainforest 1 km north of Ranomafana village at an elevation of 690 m. The specimens were collected in a malaise trap and sifted from forest litter, respectively, at the primary forest site and by hand at the secondary forest site.

Tribe Helluonini Hope 1838

Genus *Erephognathus* Alluaud 1932

This genus is endemic to Madagascar and includes only two previously described species (Lorenz 2005). Jeannel (1949) provided a key to those species.

***Erephognathus ranomafanae* Kavanaugh and Rainio, sp. nov.**
Figure 38

TYPE MATERIAL.— Holotype (Figs.38A–B), a female, in CAS, labeled: "CASENT 8068531"/ "MADAGASCAR: Province Fianarantsoa, Parc National Ranomafana, Vohiparara, at broken

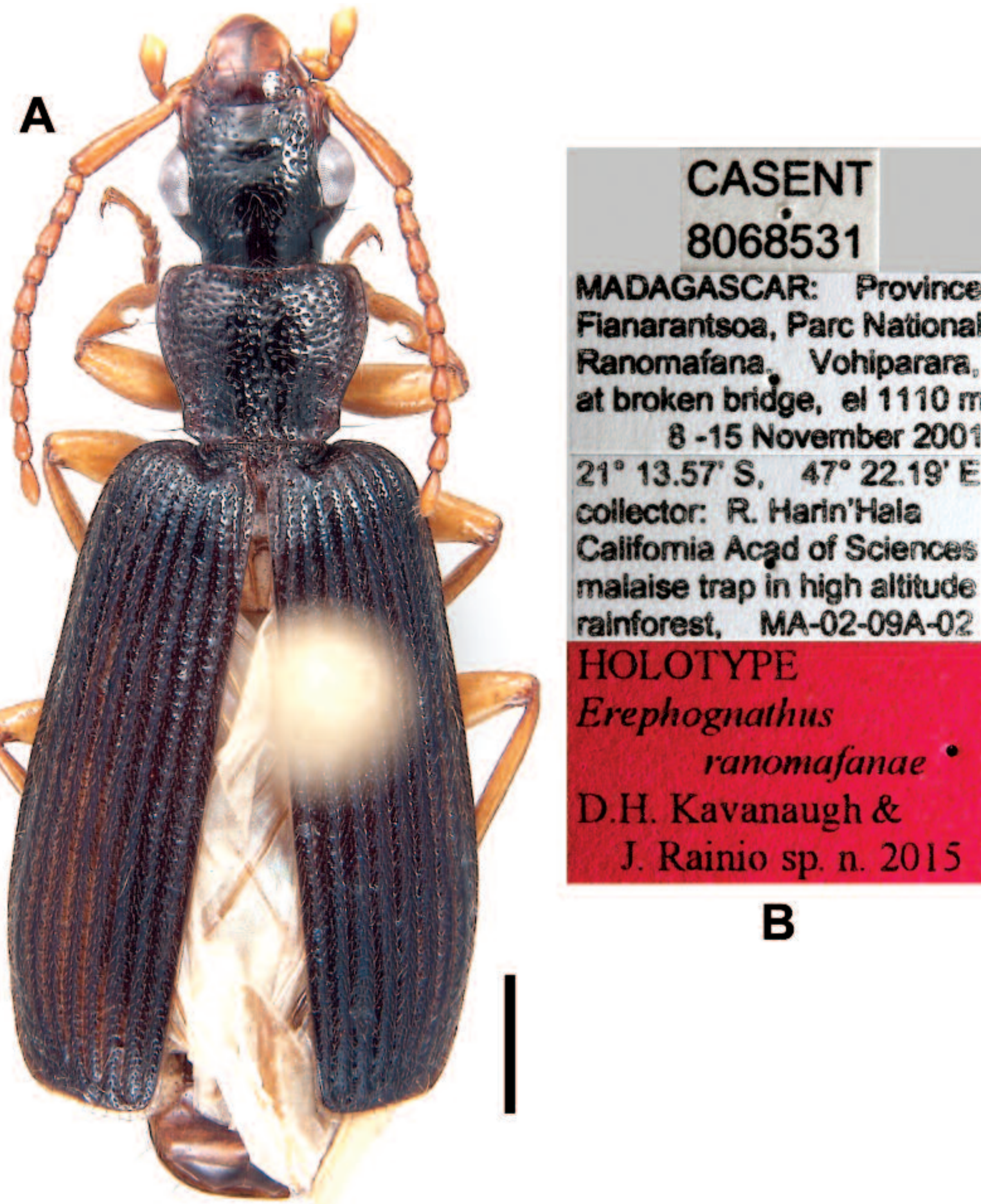

FIGURE 38. Digital images of holotype female of *Erephognathus ranomafanae* Kavanaugh and Rainio sp. nov. A. Habitus, dorsal aspect; B. Labels. Scale line = 1.0 mm.

bridge, el 1110 m 8-15 November 2001"/ "21°13.57'S, 047°22.19'E collector: R. Harin'Hala California Acad of Sciences malaise trap in high altitude rainforest, MA-02-09A-02"/ "HOLOTYPE *Erephognathus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [red label]. Paratypes (total of 2): 1 female (in CAS) labeled same as holotype, except "CASENT 8068532"; 1 female (in CAS) labeled "CASENT 8068672"/; "MADAGASCAR: Province d'Antananarivo 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe elev 1300 m 5-13 December 2000"/ "18°28'24"S

47°57'38"E coll. Fisher, Griswold et al. California Acad. of Sciences montane rainforest, malaise trap, coll. code: BLF2375". Both paratypes also bear the following label: "PARATYPE *Erephognathus ranomafanae* Kavanaugh & Rainio sp. n. 2015" [yellow label].

Type locality.— Madagascar, Fianarantsoa Province, Ranomafana National Park.

Derivation of species name.— The species epithet, *ranomafanae*, is a noun in apposition, derived from the name of the national park in which the type was collected.

Recognition.— Size moderate for genus, SBL of females = 7.5 **-** 8.9 mm. In Jeannel's (1949) key to species of *Erephognathus*, members of *E. ranomafanae* key to *E. coerulescens* (Fairmaire 1903) based on their short antennae (extended posteriorly only to the basal one-fourth of the elytra or less) and the absence of the tuft of setae from the apex of antennomere 11 (terminal antennomere) found in *E. margarithrix* Alluaud (1936a) members. The pronotum (Fig. 38A) is distinctly longer, narrower and less convex and with anterior angles more projected, narrowed and angulate than in members of *E. coerulescens*.

Geographical distribution.— We have examined specimens from only two areas. Two female specimens were collected in Ranomafana National Park, the type locality, on the eastern slope off the central plateau in the northeastern part of the southern half of the island of Madagascar. A third specimen, also a female, was collected near Anjozorobe, in Antananarivo Province, slightly north of the center of the island and just over 300 km north of Ranomafana along the eastern slope off the central plateau. No specimens have been recorded from intervening areas.

Habitat distribution.— Specimens of the type series were all collected in malaise traps in montane rainforest at elevations ranging from 1110 to 1300 m.

Acknowledgements

Fieldwork conducted by DHK and other staff from the California Academy of Sciences and their Malagasy colleagues was generously supported by a grant from Oracle Corporation, Redwood City, California. The Academy of Finland provided similar support for JR and her team during their work in Ranomafana and the Finnish Cultural Foundation provided a grant for the descriptions of new species. We also gratefully acknowledge the Institute for the Conservation of Tropical Environments (ICTE) at Stony Brook University and Madagascar Institute pour la Conservation des environments Tropicaux (MICET) in Madagascar for providing superb logistical support and facilitating permits for our work in Ranomafana National Park. Finally, we must thank Roberta Brett, Emily Elsom Cunningham, Charles Griswold, Kathryn Kavanaugh, Norman Penny, M.J. Raherilalao, E. Rajeriarison, R. Ranaivosolo, J.S. Randrianarisoa, E.F. Randrianirina, N. Rasoamanananana, François Ratalata, Félix Jean Ratelolahy, T.J. Ravelomanana, H.C. Raveloson, Jere Schweikert, Darrel Ubick, Flor Vargas, Heidi Viljanen, Helena Wirta and Kipling Will for their help with collecting specimens.

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