Zootaxa 3482: 1–32 (2012)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Article

urn:lsid:zoobank.org:pub:3C56DA61-02AD-4FB5-88E5-F98249A7EB45

Checklist and distribution atlas of the Scarabaeinae (Coleoptera: Scarabaeidae) of Costa Rica

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Abstract

The 182 species of Scarabaeinae known to occur in Costa Rica are listed with synonymies included. We place *Uroxys macrocularis* Howden & Young as a synonym of *U. boneti* Pereira & Halffter (**new synonym**); we also place *Uroxys depressifrons* Howden & Young as a synonym of *U. pauliani* Balthasar (**new synonym**). We conducted a mitochondrial DNA cytochrome oxidase I barcoding analysis in order to clarify some taxonomic uncertainties with *Phanaeus pyrois* Bates and *Sulcophanaeus noctis* (Bates). We elevate *Phanaeus pyrois malyi* Arnaud to *Phanaeus malyi* and revalidate *Phanaeus excelsus* Bates as valid species. We consider the species *Dichotomius nevermanni* Luederwaldt as *incertae sedis*. A Costa Rican distribution map is provided for all species except *Dichotomius costaricensis*, which is only known from a country record. We report, map, and estimate the spread of the invasive species *Euoniticellus intermedius* (Reiche) for Central America, from Chiapas to Costa Rica.

Key words: checklist, species revalidation, new synonym, new combination, invasive species, mitochondrial DNA, barcoding analysis

Introduction

During the last 22 years, the National Biodiversity Institute (INBio) in Costa Rica has conducted an extensive nationwide insect survey. Material from this survey has yielded many new species. To illustrate this, Table 1 records the increase of known species in Costa Rica from 1990, when INBio was founded, to the present day. Since INBio started operating there has been a 45% increase in the number of recorded species of Scarabaeinae in Costa Rica.

The present checklist has been compiled by verification of specimens mainly from the insect collection at INBio. However, several errors from other publications are corrected at the end of this paper. Still, our checklist might require some changes in the future because some groups, like the *Deltochilum*, have not been comprehensively reviewed so there are undoubtedly new species awaiting description and names that should be placed in synonymy. Currently, Scarabaeinae are represented in Costa Rica by seven tribes, 28 genera, and 182 species. These numbers will certainly increase in the future as new species and new country records are discovered. Additionally, preliminary results using the mitochondrial cytochrome c oxidase I (COI) gene (Hebert *et al*. 2003) suggest that new additions to this list will need to be published in a future paper. We consider Costa Rica to be perhaps one of the best-known tropical countries in relation to the taxonomy and distribution of the Scarabaeinae.

Perhaps the second best studied country in Central America in relation to the Scarabaeinae is Panama. A comparison between both countries (Table 2) would certainly put the Costa Rican fauna into context, besides making this comparison meaningful as both countries share many similar ecological, historical, and biogeographic characteristics, as well as having comparable surface areas (Costa Rica 51,100 km^2, Panama 78,200 km^2).

TABLE 1. Increase of known species of Scarabaeinae from Costa Rica starting in 1990.

1990	1993	1996	1997	2001	2002	2003	2004	2006	2008	2009	2012
125	127	136	142	153	160	163	169	171	175	179	182

Accepted by A.B. Smith: 18 Jul. 2012; published: 13 Sept. 2012

TABLE 2. Comparison of known Scarabaeinae taxa from Costa Rica and Panama.

	COSTA RICA	PANAMA
Genus	Number of Taxa	Number of Taxa
Anomiopus	1	1
Canthon	21	21
Cryptocanthon	4	4
Deltochilum	8	7
Malagoniella	1	0
Megathoposoma	1	1
Pseudocanthon	1	1
Sisyphus	1	0
Agamopus	1	1
Ateuchus	11	5
Bdelyrus	1	2
Bradypodidium	1	0
Eutrichillum	1	0
Onoreidium	1	1
Scatimus	2	2
Trichillidium	1	2
Uroxys	12	12
Canthidium	25	19
Copris	6	4
Dichotomius	11	9
Ontherus	4	3
Euoniticellus	1	0
Eurysternus	9	8
Coprophanaeus	7	6
Oxysternon	1	2
Phanaeus	8	4
Sulcophanaeus	2	2
Onthophagus	39	24
Total	182	141

CHECKLIST

DELTOCHILINI

ANOMIOPUS Westwood, 1842
Onthocharis Westwood, 1847
Hypocanthidium Balthasar, 1938
A. panamensis Paulian, 1939

CANTHON Hoffmannsegg, 1817
Coprobius Latreille, 1829
Coeloscelis Reiche, 1841

Paedohyboma Kolbe, 1893
Glaphyrocanthon Martínez, 1948
Scybalocanthon Martínez, 1948
Coprocanthon Martínez, 1950
Peltecanthon Pereira, 1953
Pseudepilissus Martínez, 1954
Anisocanthon Martínez & Pereira, 1956
Nesocanthon Pereira & Martínez, 1956
Goniocanthon Pereira & Martínez, 1956
Geocanthon Pereira & Martínez, 1956
Boreocanthon Halffter, 1958
Canthomoechus Pereira & Martínez, 1959
Trichocanthon Pereira & Martínez, 1959
Francmonrosia Pereira & Martínez, 1959
Sylvicanthon Halffter & Martínez, 1977
C. aberrans (Harold, 1868)
C. bifurcatus Robinson, 1948
C. juanae Martínez, 1949
C. plicatipennis Pereira, 1953
C. aequinoctialis Harold, 1868
C. angustatus Harold, 1867
C. caelius Bates, 1887
C. cyanellus LeConte, 1859
C. sallei Harold, 1863
C. speciosus Harold, 1868
C. guticollis Schmidt, 1920
C. triangulatus Schmidt, 1920
C. violetae Halffter, 1961
C. havranekae Martínez, 1988
C. deyrollei Harold, 1868
C. euryscelis Bates, 1887
C. hartmanni Howden & Gill, 1987
C. humboldti Solís & Kohlmann, 2002
C. indigaceus chevrolati Harold, 1868
C. inusitatus Kohlmann & Solís, 2006
C. juvencus Harold, 1868
C. raripilis Bates, 1887
C. lituratus (Germar, 1813)
Ateuchus chlorophanus Mannerheim, 1819
C. quadripustulatus Guérin-Méneville, 1855
C. meridionalis Martínez, Halffter, & Halffter, 1964
C. moniliatus Bates, 1887
C. morsei Howden, 1966
C. mutabilis Lucas, 1857
C. variomaculatum Blackwelder, 1944
C. septemmaculatus (Latreille, 1813)
Ateuchus fasciatus Mannerheim, 1829
C. coronatus Perty, 1830
Coprobius badius Burmeister, 1873
C. silvaticus Solís & Kohlmann, 2002
C. subhyalinus subhyalinus Harold, 1867
C. vazquezae Martínez, Halffter, & Halffter, 1964

CRYPTOCANTHON Balthasar, 1942
C. denticulum Cook, 2002
C. lindemanae Howden & Gill, 1987
C. osaensis Cook, 2002
C. solisi Cook, 2002

DELTOCHILUM Eschscholtz, 1822
Anamnesis Vigors, 1826
Hyboma LePeletier & Serville, 1828
Annamesis Harold, 1869
Meghyboma Kolbe, 1893
Telhyboma Kolbe, 1893
Eudactylides Paulian, 1939
D. acanthus Kohlmann & Solís, 2012
D. gibbosum panamensis Howden, 1966
D. lobipes Bates, 1887
D. mexicanum Burmeister, 1848
D. parile Bates, 1887
D. pseudoparile Paulian, 1938
D. scabriusculum Bates, 1887
D. valgum acropyge Bates, 1887

MALAGONIELLA Martínez, 1961
M. astyanax yucateca (Harold, 1863)

MEGATHOPOSOMA Balthasar, 1939
Glauconia Olsoufieff, 1935
M. candezei (Harold, 1873)
M. deltochiloides Balthasar, 1939

PSEUDOCANTHON Bates, 1887
Opiocanthon Paulian, 1947
P. perplexus (LeConte, 1847)

SISYPHINI

SISYPHUS Latreille, 1807
S. mexicanus Harold, 1863

ATEUCHINI

AGAMOPUS Bates, 1887
A. lampros Bates, 1887

ATEUCHUS Weber, 1801
Choeridium LePeletier & Serville, 1828
A. aeneomicans (Harold, 1868)
A. alutacius Kohlmann & Solís, 2012
A. candezei (Harold, 1868)
Choeridium poropyge Bates, 1887
A. earthorum Kohlmann & Solís, 2009
A. fetteri Kohlmann, 1997
A. ginae Kohlmann, 1997
A. hendrichsi Kohlmann, 1997
A. howdeni Kohlmann, 1997
A. rodriguezi (Preudhomme de Borre, 1886)
Choeridium ampliatum Bates, 1887
A. solisi Kohlmann, 1997
A. zoebischi Kohlmann, 1997

BDELYRUS Harold, 1869
B. seminudus Bates, 1887

BRADYPODIDIUM Vaz-de-Mello, 2008
B. bradyporum (Boucomont, 1928)

EUTRICHILLUM Martínez, 1969
E. arcus (Solís & Kohlmann, 2003)

ONOREIDIUM Vaz-de-Mello, 2008
O. bottimeri (Howden & Young, 1981)

SCATIMUS Erichson, 1847
S. erinnyos Kohlmann & Solís, 1996
S. ovatus Harold, 1862
    S. patruelis Preudhomme de Borre, 1886
    S. quadridentatus Balthasar, 1939

TRICHILLIDIUM Vaz-de-Mello, 2008
T. pilosum (Robinson, 1948)

UROXYS Westwood, 1842
    Pseuduroxys Balthasar, 1938
U. boneti Pereira & Halffter, 1961
    U. bidentis Howden & Young, 1981
    U. macrocularis Howden & Young, 1981 **new synonym**
U. deavilai Delgado & Kohlmann, 2006
U. dybasi Howden & Young, 1981
U. gatunensis Howden & Young, 1981
U. gorgon Arrow, 1933
U. metagorgon Howden & Young, 1981
U. microcularis Howden & Young, 1981
U. micros Bates, 1887
U. nebulinus Howden & Gill, 1987
U. pauliani Balthasar, 1940
    U. depressifrons Howden & Young, 1981 **new synonym**
U. platypyga Howden & Young, 1981
U. transversifrons Howden & Gill, 1987

COPRINI

CANTHIDIUM Erichson, 1847
    Pleronyx Lansberge, 1874
    Neocanthidium Martínez, Halffter, & Pereira, 1964
C. angusticeps Bates, 1887
C. annagabrielae Solís & Kohlmann, 2004
C. ardens Bates, 1887
    C. rhodopus Bates, 1887
C. aurifex Bates, 1887
C. centrale Boucomont, 1928
    C. martinezi Edmonds & Halffter, 1978
C. darwini Kohlmann & Solís, 2009
C. discopygidiale Howden & Young, 1981
C. emoryi Solís & Kohlmann, 2004
C. guanacaste Howden & Gill, 1987
C. haroldi Preudhomme de Borre, 1886
C. hespenheidei Howden & Young, 1981
C. laetum Harold, 1867
    C. granivorum Halffter & Halffter, 1978
C. leucopterum Howden & Young, 1981

C. macroculare Howden & Gill, 1987
C. marianelae Solís & Kohlmann, 2004
C. marielae Solís & Kohlmann, 2004
C. pallidoalatum Howden & Young, 1981
C. perceptibile Howden & Young, 1981
C. planovultum Howden & Young, 1981
C. priscillae Solís & Kohlmann, 2004
C. pseudopuncticolle Solís & Kohlmann, 2004
C. tenebrosum Howden & Young, 1981
C. tuberifrons Howden & Young, 1981
C. variolosum Howden & Young, 1981
C. vespertinum Howden & Young, 1981

COPRIS Geoffroy, 1762
Litocopris Waterhouse, 1891
Pseudopedaria Felsche, 1904
Paracopris Balthasar, 1939
C. costaricensis costaricensis Gahan, 1894
C. furcillatus Felsche, 1910
C. incertus Say, 1835
C. procidua Say, 1835
C. laeviceps Harold, 1869
C. lugubris Boheman, 1858
C. subpunctatus Gillet, 1910
C. tridentatus Solís & Kohlmann, 2003

DICHOTOMIUS Hope, 1838
Pinotus Erichson, 1847
Brachycopris Haldeman, 1848
Cephagonus Luederwaldt, 1929
D. agenor (Harold, 1869)
D. amicitiae Kohlmann & Solís, 1997
D. annae Kohlmann & Solís, 1997
D. centralis (Harold, 1869)
D. costaricensis (Luederwaldt, 1935)
D. danieli Kohlmann & Solís, 1997
D. favi Kohlmann & Solís, 1997
D. femoratus Howden & Young, 1981
D. rodrigoi Kohlmann & Solís, 1997
D. satanas (Harold, 1867)
D. yucatanus (Bates, 1887)

ONTHERUS Erichson, 1847
O. azteca Harold, 1869
O. villosus Luederwaldt, 1930
O. strius Howden & Young, 1981
O. brevipennis Harold, 1867
O. pseudodidymus Génier, 1996
O. sextuberculatus Génier, 1996

ONITICELLINI

EUONITICELLUS Janssens, 1953
E. intermedius (Reiche, 1849) (was introduced into the USA, in 1978 in California and in 1979 in Texas (Wood & Kaufman 2008) and is an invasive species in Costa Rica).

EURYSTERNUS Dalman, 1824
Aeschrotes LePeletier & Serville, 1828
Eurysternodes Martínez, 1988
Pareurysternus Martínez, 1988
Amartinezuz Özdikmen, 2009
E. caribaeus (Herbst, 1789)
E. planus Dalman, 1824
E. nebulosus Kirsch, 1871
E. peruanus Harold, 1875
E. foedus (Guérin-Méneville, 1844)
E. claudicans Kirsch, 1870
E. hamaticollis Balthasar, 1939
E. magnus Laporte, 1840
E. mexicanus Harold, 1869
E. olivaceus Génier, 2009
E. plebejus Harold, 1880
E. joffrei Martínez, 1988
E. streblus Génier, 2009
E. velutinus Bates, 1887

PHANAEINI

COPROPHANAEUS Olsoufieff, 1924
C. boucardi (Nevinson, 1891)
C. chiriquensis Olsoufieff, 1924
C. corythus (Harold, 1863)
C. kohlmanni Arnaud, 2002
C. pecki Howden & Young, 1981
C. solisi Arnaud, 1997
C. uhleri Malý & Pokorný, 2008

OXYSTERNON Laporte, 1840
Sternaspis Hope, 1837
Strombodes Gistel, 1857
O. silenus Laporte, 1840
O. smaragdinum Olsoufieff, 1924
O. sericeum Olsoufieff, 1924
O. aeneum Olsoufieff, 1924
O. zikani Pereira, 1943
O. peruanum Pereira 1943
O. dufouri Arnaud, 2001
O. jossi Arnaud, 2001
O. zagurii Arnaud, 2001
O. chicheryi Arnaud, 2001

PHANAEUS MacLeay, 1819
Lonchophorus Germar, 1824
Onthurgus Gistel, 1857
Palaeocopris Pierce, 1946
P. beltianus Bates, 1887
P. changdiazi Kohlmann & Solís, 2001
P. excelsus Bates, 1889
P. eximius Bates, 1887
P. hermes Harold, 1868
P. bogotensis, Kirsch 1871
P. malyi Arnaud, 2002

P. pyrois Bates, 1887
    P. blanchardi Olsoufieff, 1924
    P. funereus Balthasar, 1939
    P. olsoufieffi Balthasar, 1939
    P. bothrus Blackwelder, 1944
P. wagneri wagneri Harold, 1863

SULCOPHANAEUS Olsoufieff, 1924
    Eucopricus Gistel, 1857
S. noctis (Bates, 1887)
    S. cupricollis (Nevinson, 1891)
S. velutinus (Murray, 1856)

ONTHOPHAGINI

ONTHOPHAGUS Latreille, 1802
    Chalcoderus Erichson, 1848
    Monapus Erichson, 1848
    Psilax Erichson, 1848
    Gonocyphus Lansberge, 1885
    Tauronthophagus Shipp, 1895
    Macropocopris Arrow, 1920
O. acuminatus Harold, 1880
O. andersoni Howden & Gill, 1987
O. anthracinus Harold, 1873
O. atriglabrus Howden & Gill, 1987
O. atrosericeus Boucomont, 1932
O. batesi Howden & Cartwright, 1963
O. championi Bates, 1887
O. chryses Bates, 1887
O. coriaceoumbrosus Kohlmann & Solís, 2001
O. coscineus Bates, 1887
    O. digitifer Boucomont, 1932
O. crinitus Bates, 1887
    O. panamensis Bates, 1887
O. cryptodicranius Kohlmann & Solís, 2001
O. cyanellus Bates, 1887
    O. mesoamericanus Zunino & Halffter, 1988
O. dicranius Bates, 1887
O. dorsipilulus Howden & Gill, 1987
O. gazellinus Bates, 1887
O. genuinus Kohlmann & Solís, 2001
O. grataehelenae Kohlmann & Solís, 2001
O. hoepfneri Harold, 1869
O. incensus Say, 1835
O. inediapterus Kohlmann & Solís, 2001
O. landolti Harold, 1880
O. limonensis Kohlmann & Solís, 2001
O. marginicollis Harold, 1880
O. micropterus Zunino & Halffter, 1981
O. nemorivagus Kohlmann & Solís, 2001
O. notiodes Solís & Kohlmann, 2003
O. nubilus Kohlmann & Solís, 2001
O. nyctopus Bates, 1887
O. orphnoides Bates, 1887
O. praecellens Bates, 1887

O. propraecellens Howden & Gill, 1987
O. quetzalis Howden & Gill, 1993
O. sharpi Harold, 1875
O. singulariformis Kohlmann & Solís, 2001
O. solisi Howden & Gill, 1993
O. stockwelli Howden & Young, 1981
O. tapirus Sharp, 1887
O. viridivinosus Kohlmann & Solís, 2001

Taxonomic considerations

The genus *Canthon* Hoffmannsegg and its close relatives are currently under great taxonomic disarray, even after an attempt by Halffter & Martínez (1977) to organize the group. The group has been divided into a number of genera and subgenera, which in many cases have not withstood close taxonomic scrutiny using phylogenetic analyses (Kohlmann 1984, Solís & Kohlmann 2002, Medina *et al*. 2003). We have decided to adopt a conservative approach and to recognize only the genera used in this checklist, until future better classifies this complicated group of genera.

Kohlmann & Solís (2001a) cited the presence of *Onthophagus genuinus* Kohlmann & Solís and *Onthophagus inediapterus* Kohlmann & Solís from Panama. This is an error as the species have so far only been collected in Costa Rica.

Edmonds (1994) placed *Phanaeus excelsus* Bates as a synonym of *Phanaeus demon* Laporte. We disagree with this decision. Edmonds (1994) considered *P. demon* to be a highly variable species, with *P. excelsus* representing one extreme of the polymorphic variation. *Phanaeus demon* is known from inland Chiapas and *P. excelsus* from inland Guatemala, no specimens are known from the intermediate coastal areas between Oaxaca and Guatemala where Edmonds (1994) considers that intermediate forms might be present. However, no morphological intermediate forms have been recorded. *Phanaeus excelsus* has narrow, erect, and parallel-sided pronotal projections (massive and widened apically in *P. demon*), as well as a pair of long acute denticles near the anterior pronotal margin, which are lacking in *P. demon*. Both species can therefore be clearly recognized. Moreover, the distribution of these two species conforms with the observed fact that many species in Central America have a sister taxon in Mexico forming taxon pairs, like *Canthidium guanacaste* Howden & Gill—*Canthidium macclevei* Kohlmann & Solís, *Dichotomius annae* Kohlmann & Solís—*Dichotomius colonicus* (Say), *Dichotomius centralis* (Harold)—*Dichotomius amplicollis* (Harold), and *Coprophanaeus boucardi* (Nevinson)—*Coprophanaeus pluto* (Harold). The distributional border lies generally in the Oaxaca—Chiapas area. Until an actual morphological species gradient is discovered and not just proposed, we consider these to be two separate species and therefore reestablish *Phanaeus excelsus* Bates as a valid species.

In Edmonds' (1994) *Phanaeus* study, the description, photographs, line drawing, distribution map, and key of *Phanaeus beltianus* Bates, actually correspond to *Phanaeus changdiazi* Kohlmann & Solís. The specimens studied by Edmonds (1994) are from the Pacific coast of Costa Rica, where *P. changdiazi* is distributed; *P. beltianus* is native to the Caribbean coast.

A typical phenomenon observed in Costa Rica is that many closely related species pairs occur on the Caribbean and the Pacific sides (Kohlmann & Wilkinson 2007). This vicariant speciation pattern seems to be mediated by the slow emergence of the Talamanca range (Alvarado *et al*. 2007, Hoernle *et al*. 2008), which has divided the original continuous tropical forest into two separate areas; one on the Caribbean slope, the other on the Pacific slope (Kohlmann & Wilkinson 2007). This phenomenon has not been detected just in dung beetles (Kohlmann & Solís 1997, 2001a, 2001b; Kohlmann & Wilkinson 2007); many cases have also been reported for fishes, amphibians, reptiles, and birds (Fogden & Fogden 1997, Kohlmann & Wilkinson 2007). Species formation has been clear in many cases, but in others it would seem to still be going on. We can cite the case of two phanaeines. One is *Phanaeus pyrois* Bates, which has populations with the head and pronotum with a metallic red, green, or blue color on the Caribbean slope; whereas the Pacific populations have a completely black head and pronotum. This prompted Arnaud (2002) to establish two different subspecies, *P. pyrois pyrois* on the Caribbean slope and *P. pyrois malyi* Arnaud on the Pacific slope. Besides the difference in color, we have been unable to find any other morphological difference between both populations. In a second example, Edmonds (2000) discusses the case of *Sulcophanaeus noctis* (Bates) and *S. cupricollis* (Nevison), where *S. cupricollis* has a significant portion of the pronotum colored metallic red or golden and is distributed on the Caribbean slope; whereas *S. noctis* has a

almost entirely dull black pronotum, sometimes with metallic coloration confined to the very margins of the pronotum, and is distributed on the Pacific slope. The absence of clear morphological characteristics, except the color difference, prompted Edmonds (2000) to synonymize *S. cupricollis* under *S. noctis.*

In order to try to understand these complex species problems, a mitochondrial DNA barcoding analysis of a 648-base pair region of the cytochrome *c* oxidase I (COI) gene is underway for all Costa Rican Scarabaeinae species. Price (2009) has already confirmed that COI data are a good data source to resolve phylogenetic questions in the genus *Phanaeus*. This process analyzes sequence diversity in short, standardized gene regions to aid species identification. This specific gene forms the primary barcode sequence for members of the animal kingdom (Ratnasingham & Hebert 2007); more than 95% of species in test assemblages of varied animal groups have been shown to possess distinctive COI sequences (Hebert *et al*. 2003, 2004; Ward *et al*. 2005; Hajibabaei *et al*. 2006). Cases of incomplete resolution involve species that are closely allied (Ratnasingham & Hebert 2007). Although barcoding analyses are not phylogenetic analyses, mitochondrial DNA (mtDNA) has been widely employed in phylogenetic studies because it evolves much more rapidly than nuclear DNA, thus accumulating differences between closely related species (Mindell *et al*. 1997).

The analysis of Costa Rican dung beetles shows different results. The cytochrome *c* oxidase I (COI) results for *P. pyrois pyrois* and *P. pyrois malyi* show basically the same amount of mitochondrial DNA difference (average Kimura-2-parameter [K2P] = 3.8%), as found for another *Phanaeus* Caribbean-Pacific sister-species pair (Fig. 1), like *P. beltianus* and *P. changdiazi* (average Kimura-2-parameter [K2P] = 3.0%). These average values are similar to the ones that Johns & Avise (1998) found (K2P difference) of 3.5% in 47 pairs of bird sister species and divergences greater than 2% in 98% of vertebrate sister species. The COI analysis seems to support our decision to elevate *Phanaeus pyrois malyi* to the species level. Rapid paces of sequence change in mtDNA have been reported between populations that have been separated for brief periods (like the emergence of the Talamanca range, here proposed) (Hebert *et al*. 2004).

Regarding *Sulcophanaeus*, no differences in the DNA mitochondrial analysis were found that could separate Pacific populations (*Sulcophanaeus noctis*) from Caribbean populations (*S. cupricollis*) (Fig. 1). Based on these results, we therefore agree with the decision of Edmonds (2000) to synonymize *S. cupricollis* under *S. noctis.* Other similar cases have been reported where a lack of COI divergence has indicated that populations with different color morphs are part of a single species; *e.g.*, blue and white morphs of *Chen caerulescens* (Linnaeus) (Snow Goose) were thought to be different species until recently; or the color morphs of American and Black Oystercatchers (Jehl 1985). We will present a complete mitochondrial analysis of all Costa Rican dung-beetle species and shall return and treat in more detail the Caribbean-Pacific vicariance speciation process in a future publication.

Malý & Pokorný (2008) described *Coprophanaeus uhleri* Malý & Pokorný from Costa Rica, which is a close relative of *C. gilli* Arnaud. However, they did not clarify that *C. gilli* is not found in Costa Rica; this species is distributed from Mexico to Honduras. Kohlmann & Solís (2012) recently revalidated *Coprophanaeus kohlmanni* Arnaud and *C. uhleri* as valid species. *Coprophanaeus kohlmanni* is known from Nicaragua to western Panama; *C. morenoi* Arnaud, its putative synonym (Edmonds & Zidek 2010), is distributed from eastern Panama to Ecuador. The populations found in central Panama and regarded to be *C. morenoi* (Edmonds & Zidek 2010) were described as a new species, *C. gephyra* Kohlmann & Solís. *Coprophanaeus uhleri* is known to occur along the Guanacaste Cordillera to the Central Cordillera; *C. chiriquensis*, its supposed synonym (Edmonds & Zidek 2010) is distributed in the Talamanca-Chiriquí Cordillera.

Considering the nomenclature of *Oxysternon*, Arnaud (2002) and Edmonds & Zídek (2004) disagree with each other regarding the existence of subspecies within the species *Oxysternon silenus* Laporte. Arnaud (2002) has recognized the existence of several subspecies of *O. silenus* with characteristic distributions. These patterns have defined distributional areas that remind us of speciation patterns seen in many South American tropical groups that have formed the base for the postulation of the "refuge theories" on the Amazonian Basin (Haffer 1969, Vanzolini & Williams 1970). Until a detailed distributional and taxonomic analysis of *O. silenus* is done, we prefer to follow a conservative approach and not recognize any subspecies.

Regarding the taxonomic positioning and status of the different genera of the tribe Ateuchini and the transfer of the genera *Anomiopus* to Deltochilini and *Canthidium* to Coprini, we are following the recent results published by Vaz-de-Mello (2008). We are also following Bouchard *et al*. (2011) with regards to the latest family group names, especially the name change of Canthonini to Deltochilini. Regarding many generic and subgeneric placements, we have followed Vaz-de-Mello *et al*. (2011), with the exception of the treatment of the genus *Canthon* and their subgenera and closely allied genera, due to the fact that we consider that they have to be completely reworked. Regarding the taxonomic delimitation of *Copris*, we are following Marchisio & Zunino (2012).

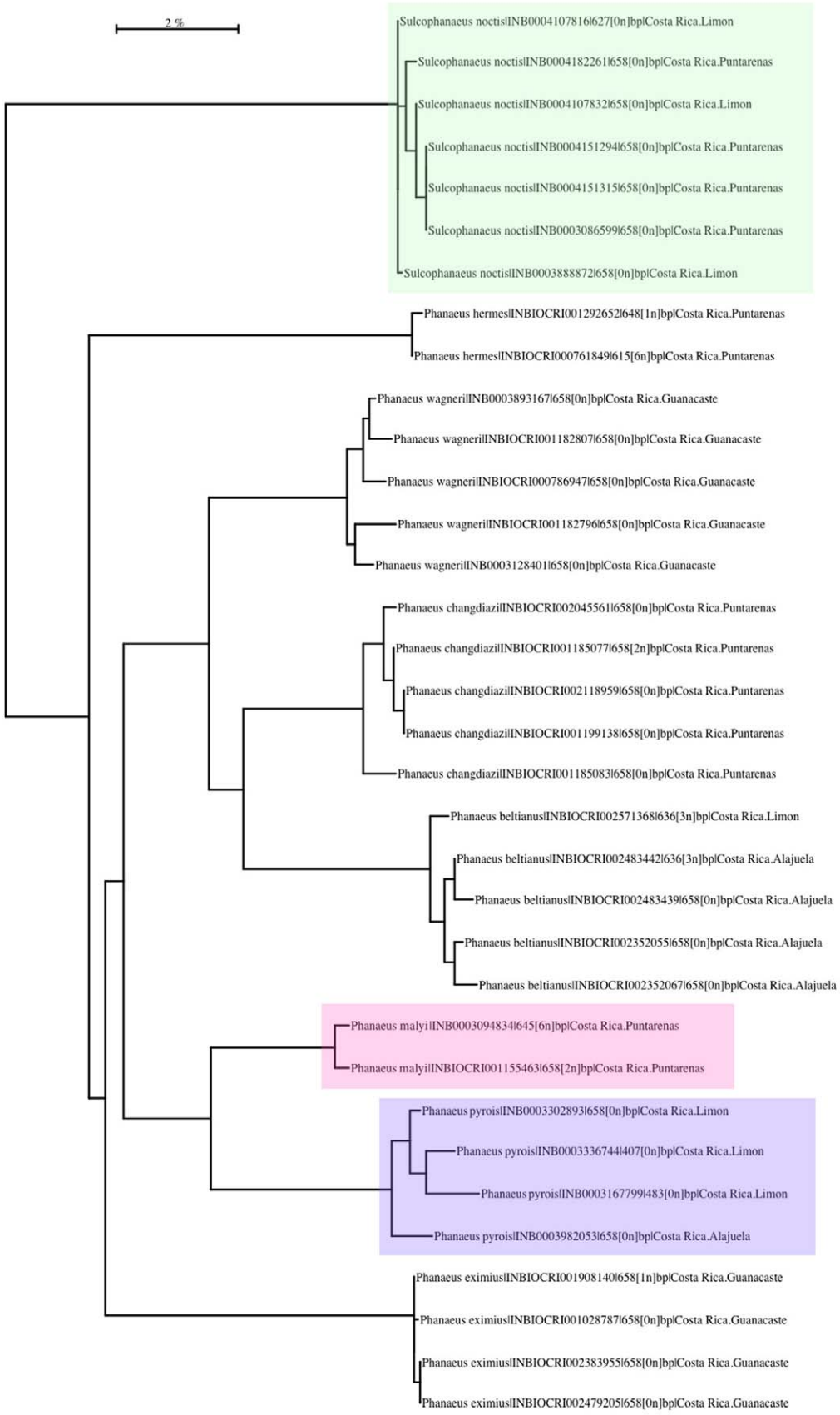

FIGURE 1. Taxon ID tree of *Sulcophanaeus noctis* and *Phanaeus* species from Costa Rica based on a mitochondrial DNA (COI) barcoding analysis. Data taken from the Barcode of Life Data Systems (http://www.boldsystems.org/). Accession numbers, nucleotide sequence lengths, and specimen localities are indicated.

The species *Onthophagus mesoamericanus* Zunino & Halffter was synonymized with *O. cyanellus* Bates by Kohlmann & Solís (2001a). Pulido & Zunino (2007) later listed both as valid species in their catalogue. However, after reanalyzing all the material from the Cedros region where *O. mesoamericanus* was originally described from, we corroborate our decision of establishing a synonym. The populations in this area tend to be greener in color (one of the main distinguishing characteristics according to Zunino & Halffter 1988), instead of the usual bluish-black color of *O. cyanellus* found from Mexico to Panama. In all other aspects, these populations are typical *O. cyanellus*.

The subspecies *Onthophagus crinitus panamensis* Bates was synonymized with *Onthophagus crinitus* Harold by Kohlmann and Solís (2001a). Pulido and Zunino (2007) continued to treat it as a subspecies. We reaffirm our decision to treat it as part of the natural variation of the species and do not confer it the subspecies status.

Solís & Kohlmann (2002) conducted a detailed body color analysis of *Canthon cyanellus* LeConte. The analysis showed the coexistence of different color morphs in all studied Costa Rican localities. The analysis concluded that *C. cyanellus* has polytopic populations and, as such, it is preferable not to recognize polytopic subspecies (Mayr & Ashlock 1991). Solís & Kohlmann (2002) therefore did not validate the existence of subspecies of *C. cyanellus* based on color as the only diagnostic characteristic. We continue with this decision in this checklist, although some authors still insist in combining morphologically identical populations into subspecies.

In their revision of the genus *Uroxys* from Mexico and Guatemala, Delgado & Kohlmann (2007) placed *U. bidentis* Howden & Young as a synonym of *U. boneti* Pereira & Halffter. Howden & Young's (1991) commented in the description of *U. macrocularis* Howden & Young that the females of this species are most similar to *U. bidentis*. This comment motivated us to check the type material of *U. macrocularis*. Howden & Young (1981: 63) indicate that the males of *U. macrocularis* "can be distinguished from males of other members of the *micros* complex in Panama by the three indentations of the anterior clypeal margin." They also indicate that (p. 63) in the case of the male protibia the "basal tooth *(is)* somewhat reduced." These characteristics had already been noted by Delgado & Kohlmann (2007: 7), who had indicated that *U. boneti* shows variation with the clypeal teeth going from bidentate to quadridentate in males, while females are almost always quadridentate; whereas the male protibial basal tooth can also vary in size, from present to greatly reduced. We also compared the aedeagi of both species and no differences were found. Taking the variation in morphology into account and after having compared the type material of *U. macrocularis* with *U. boneti*, we place *U. macrocularis* as a synonym of *U. boneti* Pereira & Halffter.

Howden & Young (1981) described *Uroxys depressifrons*, a very distinctive taxon. This species is characterized by having a quadridentate clypeal margin, clypeal elevation, a deep and straight pronotal longitudinal sulcus, posterior margin with a row of longitudinal punctures, posterior one-fifth of first and second elytral striae deeply furrowed, pygidial sulcus basally deep and straight either side of midline, and an elongate parallel-sided body shape. We checked the types of *U. depressifrons* and *U. pauliani* Balthasar, and arrived at the conclusion that *U. depressifrons* is a synonym of *U. pauliani*.

Dubious species cited from Costa Rica

Several species have been cited for Costa Rica, but have not been verified with credible collecting data or have been misidentified. These species are:

Dichotomius costaricensis (Luederwaldt) was recorded for Costa Rica (Luederwaldt 1935). However, to our knowledge it has not been collected in this country. We have seen specimens from Panama and Venezuela collected with light traps and near caves. This presents the possibility that the species is cave dwelling. It also presents the possibility that the species is not present in Costa Rica; the type specimen has a label that states Costa Rica as the collection locality with no further details.

Dichotomius nevermanni (Luederwaldt) was recorded from Costa Rica with no precise locality. According to Horn & Kahle (1935–37), Luederwaldt's type material was deposited at the Smithsonian Institution. However, several searches by different people have not produced any type material of this mysterious species, which according to Luederwaldt is similar to the female of *D. carolinus* (Linnaeus). Other collections like the museums of São Paulo, London, Paris, Hamburg, Dresden, and Berlin were checked but did not have any type material of this species. It is known that some of Luederwaldt's material was sent to the museum in Stettin, Pomerania. During the late stage of

the Second World War, this museum was looted by Polish troops and its contents sent to Warsaw, where it vanished (R. Krause, personal communication, retired curator of the Coleoptera section at the Museum für Tierkunde, Dresden, Germany). We presume that the type material is lost and consider this species as *incertae sedis*.

Another possibility concerning *D. nevermanni* is that Luederwaldt actually had a mislabeled specimen from Panama and not from Costa Rica. Through the agency of Mr. Roberto Cambra from the Invertebrate Museum of the University of Panama (MIUP), photos of *D. coenosus* have been received. This is the first time that this species is recorded from Panama. The specimens were collected at La Mesa de San Martín, Pacora, province of Panama. It is possible that Luederwaldt based his description on an underdeveloped specimen, because the holotype measured only 19 mm.

Canthon femoralis (Chevrolat) has been cited by Harold (1868) and by Rivera-Cervantes & Halffter (1999) as occurring in Costa Rica. However, we have never been able to confirm this through collecting or finding specimens in any collection. The closest known locality to Costa Rica where this species has been collected is the region around Managua, at Chocoyero, Ticuantepe, Nicaragua, collected by Blas Hernández in March 2005.

Rivera-Cervantes & Halffter (1999) cited a single specimen of *Canthon leechi* Martínez, Halffter, & Halffter from Guanacaste, Costa Rica. We have never been able to find this species in the country and believe that the specimen was a misidentified *C. meridionalis*, which is a species present in this area.

Canthon championi Bates does not occur in Costa Rica. The records by Howden & Gill (1987) and Rivera-Cervantes & Halffter (1999) were based on misidentified *C. vazquezae* Martínez, Halffter, and Halffter specimens.

Martínez & Halffter (1986) published a catalogue of *Canthidium*, in which they indicated that *Canthidium subdopuncticolle* Howden & Young was present in Costa Rica. The species does not occur in Costa Rica as Martínez & Halffter (1986) confused the correct locality of Alhajuela in Panama with the homophonous Alajuela in Costa Rica.

Species likely to be found in Costa Rica

The following species have been found close to the Costa Rican borders and probably occur in this country: *Onthophagus xiphias* Solís & Kohlmann is known so far from the Pacific slope of the Chiriquí Volcano (Panama) in cloud forest at altitudes varying from 1,220 m to 1,500 m and probably occurs in the Talamanca Range in Costa Rica (Solís & Kohlmann 2003). *Onthophagus turgidus* Kohlmann & Solís is known so far from the Caribbean slope in the Bocas del Toro area in tropical rain forest at an altitude of 800 m (Kohlmann & Solís 2012), only 6 km away from the Costa Rican border. *Cryptocanthon chiriquensis* was collected at La Fortuna Dam at 1,200 m (Cook 2002), close to the Costa Rican border; and it probably occurs in the Talamanca Range in Costa Rica.

Invasive species

We have a new record for our list of dung beetles of Costa Rica (Fig. 2): One male specimen of *Euoniticellus intermedius* was collected by our colleague Wendy Porras at Playa Flamingo (10º 25´ N, 85º 45´ W), Guanacaste Province, 13 July 2008. It was a hand collection, without traps. A second female specimen of this species was found at Hacienda Ahogados, Guanacaste Province, under cow dung, 13 April 2009. A third record was of a male found at San Pedro de Poás, province of Alajuela. This specimen was found at noon drowning in a swimming pool on 6 September 2009. A fourth series of specimens (males and females) were found 1.5 km east of Naranjito de Quepos, hand collection by another colleague, Carlos Víquez (arachnologist), 4 May 2010.

Euoniticellus intermedius was released in 1978 in California, in 1979 in Texas, and in 1984 in Georgia (Wood & Kaufman 2008). In 1992, it was recorded in north-central Mexico and in 1994 in northwestern Mexico (Montes de Oca & Halffter 1998). This same species was then reported for the first time in 1999 in the southern Mexican state of Chiapas (Fig. 2) (Morales *et al*. 2004). *Euoniticellus intermedius* continued its southward invasion and it was collected in 2002 for the first time in Guatemala (E. Cano, personal communication, Guatemala-City, Laboratorio de Entomología Sistemática, Universidad del Valle de Guatemala) and in 2003 in El Salvador from July to August in pastures near Tonacatepeque (Fuentes 2007). Carlos Víquez collected this species at San Juan del Sur in Nicaragua, in November 2007 (Fig. 2).

FIGURE 2. Dispersal map of *Euoniticellus intermedius* showing its spread from Chiapas, Mexico, to Costa Rica.

Another invasive dung beetle species, *Digitonthophagus gazella*, has not yet been collected in Costa Rica. This species was introduced in Texas, California, and Brazil and is spreading in both directions.

If we measure the distance spanned between the Chiapanecan locality of Ocozocoautla in 1999 to the Costa Rican locality of Naranjitos de Quepos in 2010 (Fig. 2), *E. intermedius* has an expansion of approximately 1,333 km over 11 years; in other words, this would mean an average dispersal rate of approximately 121 km/year. The advancing front of this species in Central America would thus seem to be slower than the mean value calculated for *Digitonthophaus gazella* along the United States-Mexican Pacific coast from 1976–1989, which was on the order of 220 km/year (Kohlmann 1994). *Euoniticellus intermedius* seems to have been spreading only along the dry tropical forest of the Pacific slope and it has been only collected in open (pastures) or disturbed areas so far. Currently, it is the first invasive non-native Scarabaeinae species detected in Costa Rica.

Acknowledgements

We are grateful to the Research Coordination of EARTH University for the help received towards the publication of this paper. We acknowledge the National Biodiversity Institute (INBio), Costa Rica, for their support. We are also thankful to Roberto Cambra, from the Invertebrate Museum of the University of Panama, for photographs of different specimens from their collection. We thank Carlos Víquez for the important information he sent to us and for his sound observations that benefitted this paper. We are indebted to Enio Cano from the Universidad del Valle de Guatemala and René Fuentes from the Universidad del Salvador, for contributing collecting localities of *Euoniticellus intermedius* from their countries. We are also grateful to Andrés Felipe Escobar, student from the Universidad del Valle in Colombia, for suggesting to us the possibility of *Uroxys depressifrons* being a synonym of *U. pauliani*. We also thank Alex Smith (University of Guelph) and the International Development and Research Centre (Government of Canada) for their support of the barcoding analysis. We are very thankful to two anonymous reviewers and especially to Andrew Smith, who undertook a very careful reading and correction of the text. Last but not least, we would like to thank the United States National Aeronautics and Space Administration for the synthetic aperture radar (SAR) image of Costa Rica, which is the basis for the maps used in this analysis.

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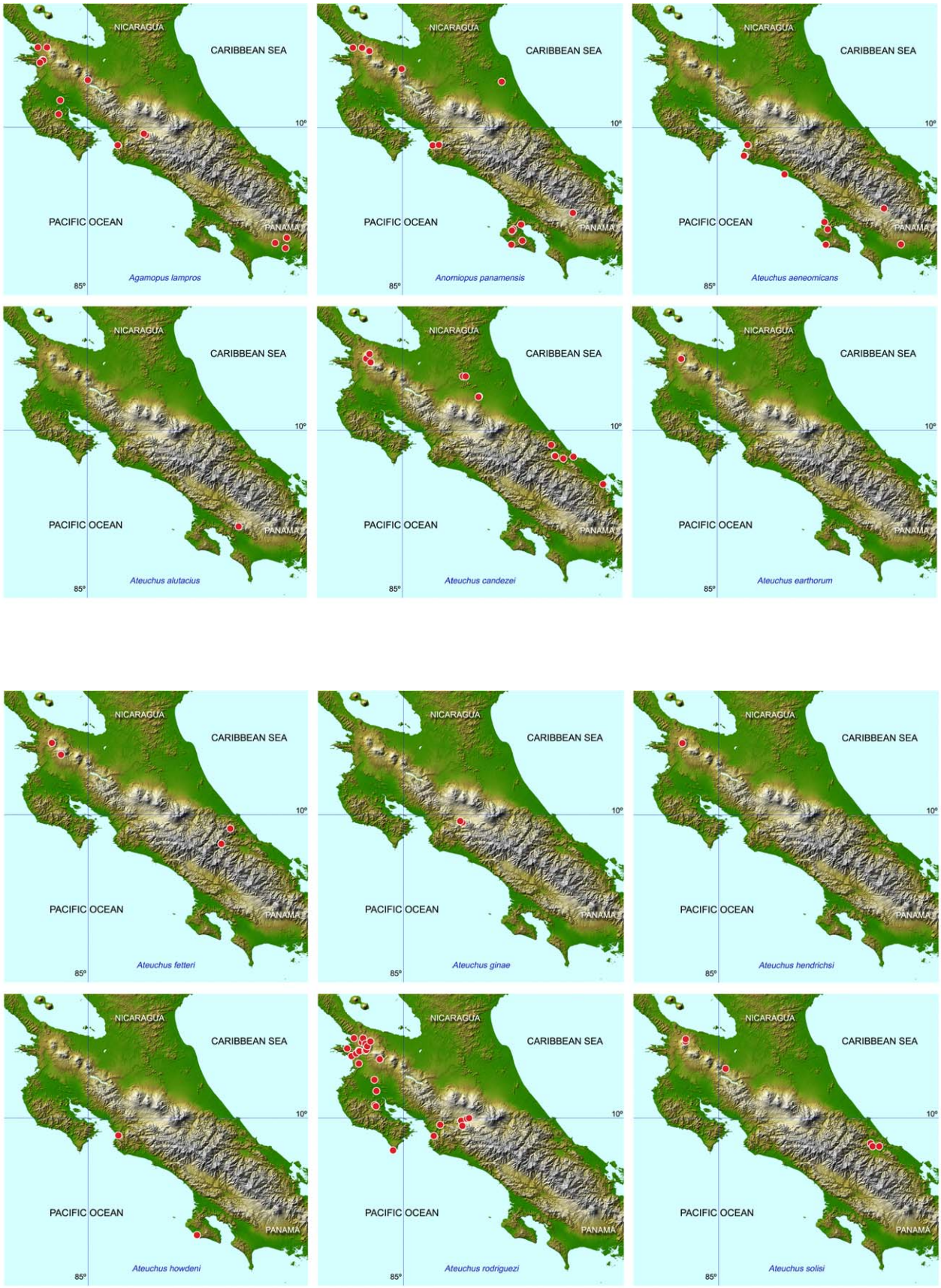
Distribution atlas of the Scarabaeinae of Costa Rica

The base map (Plate 1) used in this study derives from a synthetic aperture radar (SAR) image of Costa Rica by the United States National Aeronautics and Space Administration (NASA). All of the following distribution maps derive from this base map. Maps are arranged in alphabetical order by genus then species. The distributional data come from the Instituto Nacional de Biodiversidad (INBio), Costa Rica specimen database.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PANAMA
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Anomiopus panamensis
Ateuchus aeneomicans
Ateuchus alutacius
Ateuchus candezei
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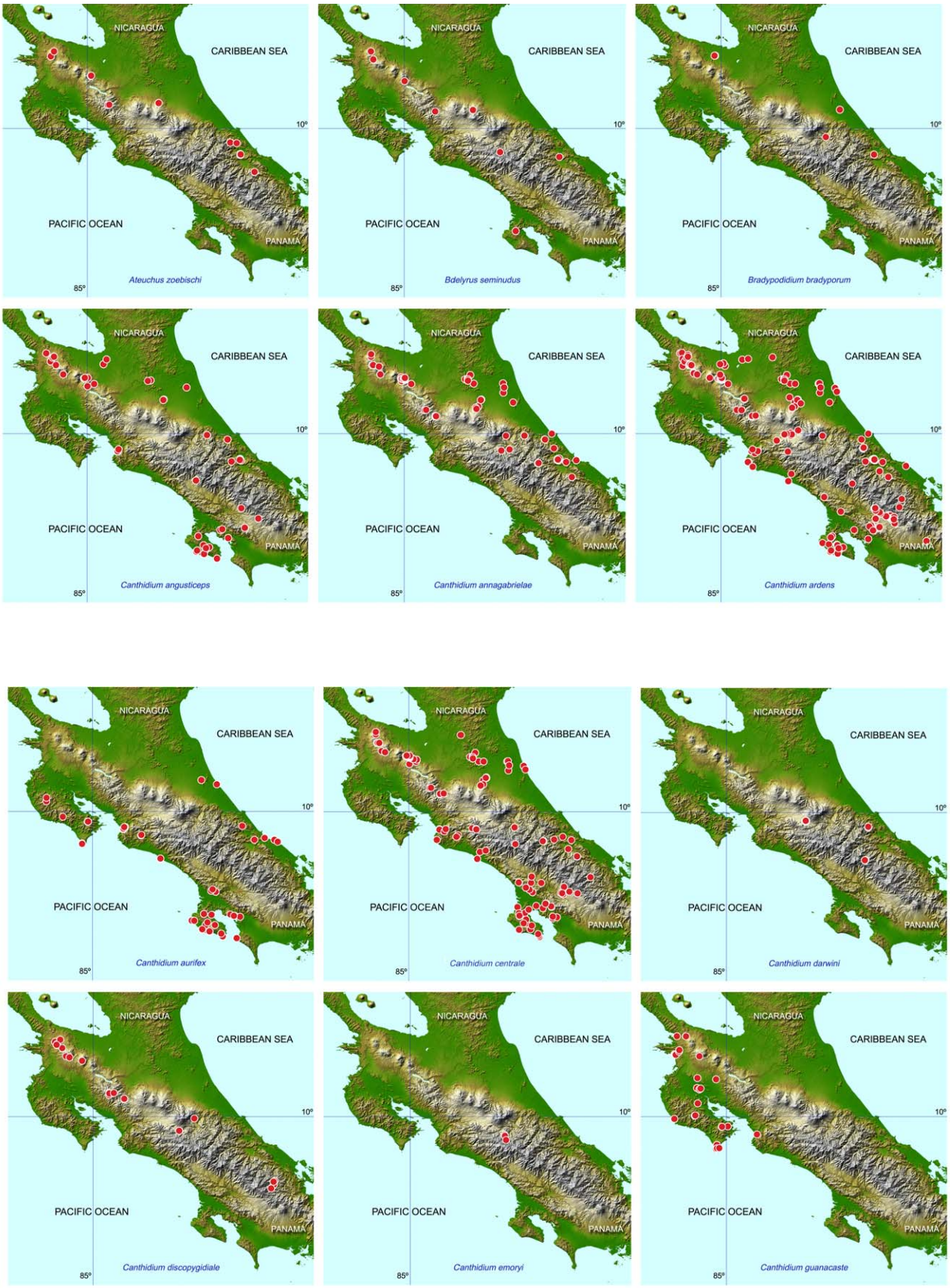
Ateuchus solisi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PACIFIC OCEAN
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Bdelyrus seminudus
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Canthidium angusticeps
Canthidium annagabrielae
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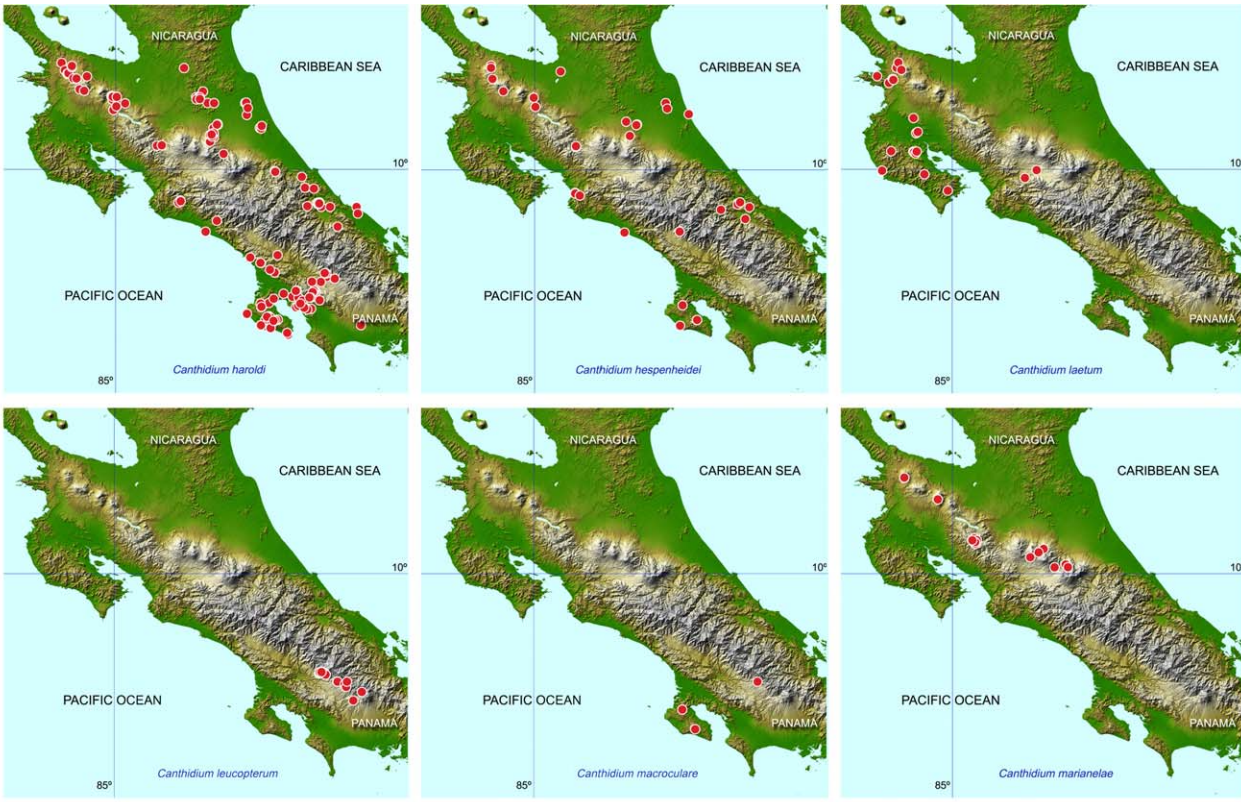
Canthidium discopygidiale
Canthidium emoryi
Canthidium guanacaste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CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10°
85°
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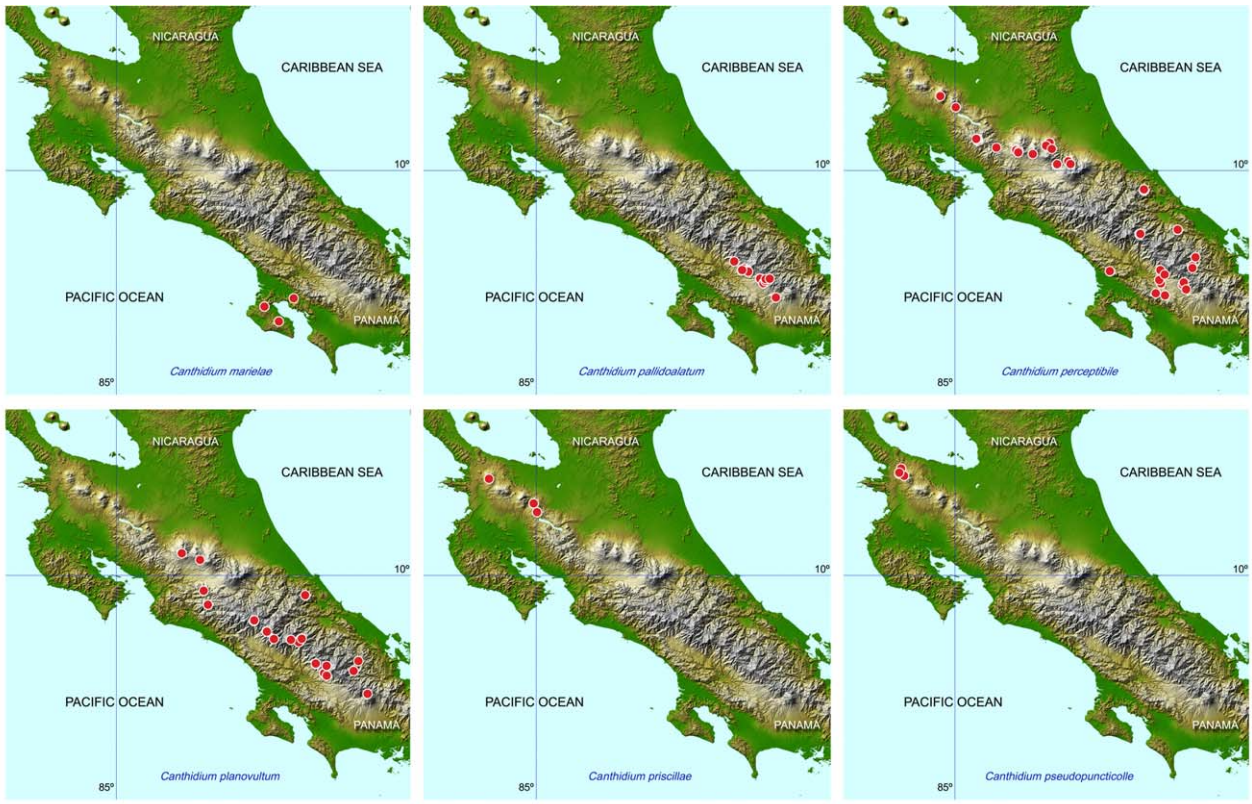
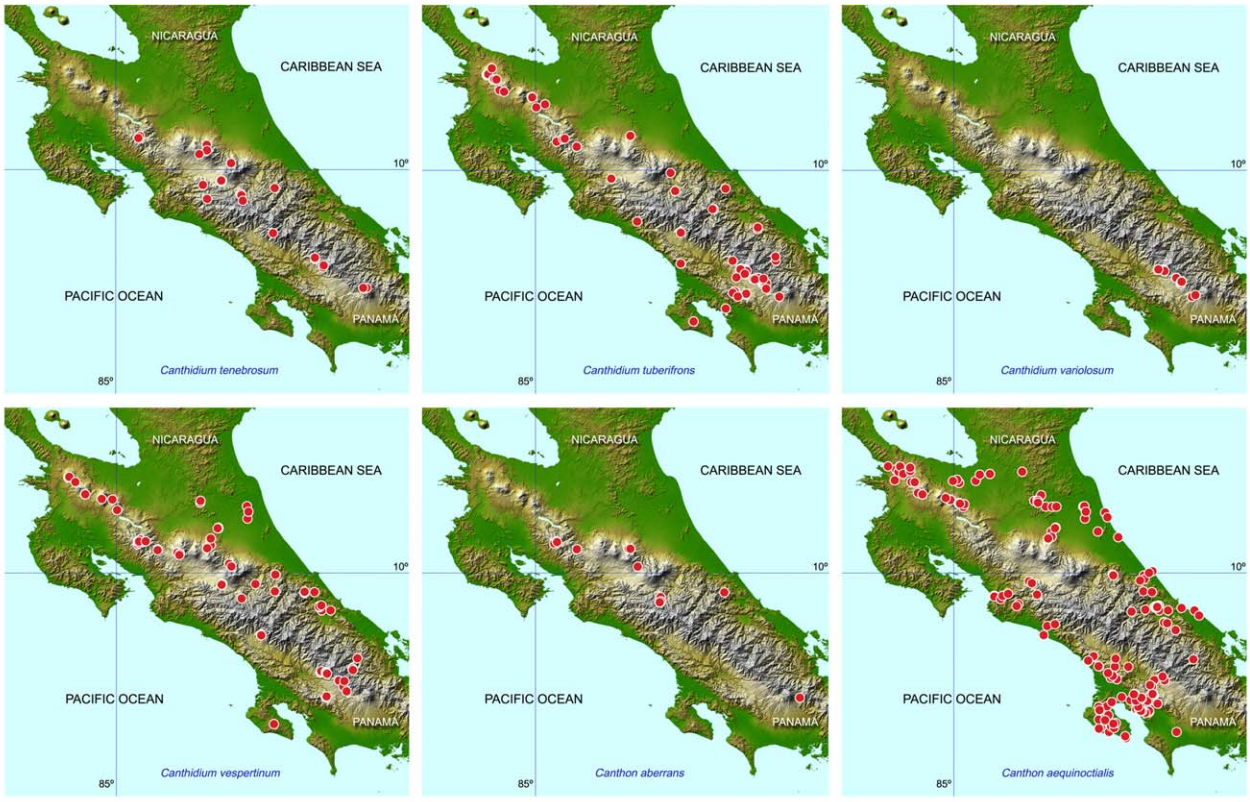
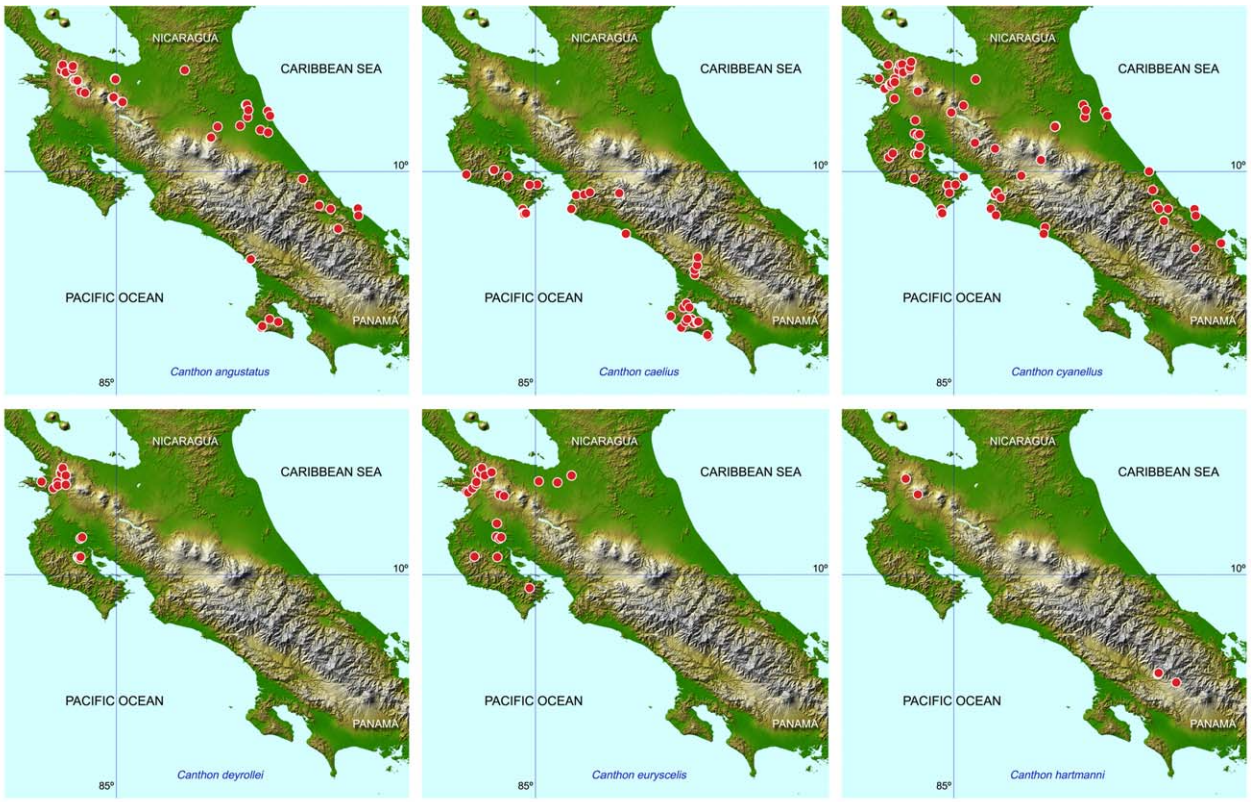
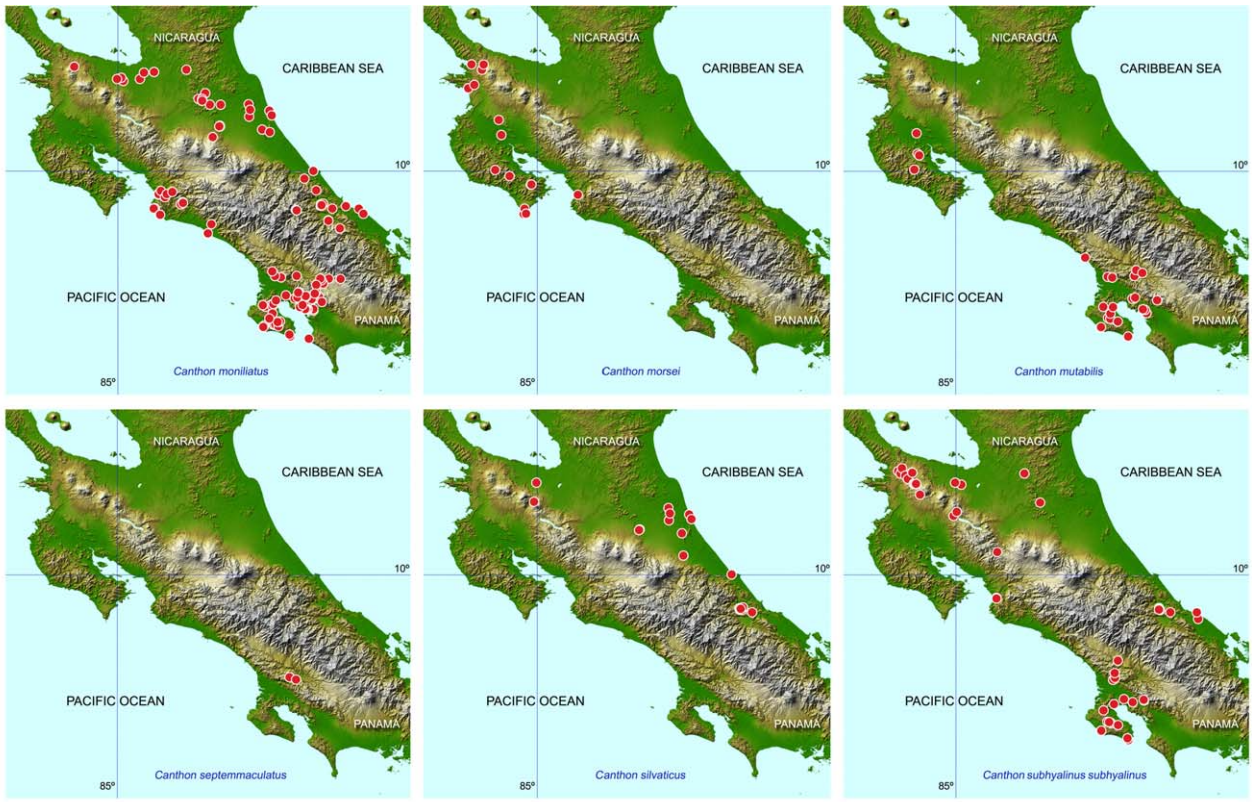
Canthidium hespenheidei
Canthidium laetum
Canthidium leucopterum
Canthidium macroculare
Canthidium marianelae


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10°
85°
Canthidium marielae
Canthidium pallidoalatum
Canthidium perceptibile
Canthidium planovultum
Canthidium priscillae
Canthidium pseudopuncticolle


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10°
85°
Canthidium tenebrosum
Canthidium tuberifrons
Canthidium variolosum
Canthidium vespertinum
Canthon aberrans
Canthon aequinoctialis


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10°
85°
Canthon angustatus
Canthon caelius
Canthon cyanellus
Canthon deyrollei
Canthon euryscelis
Canthon hartmanni


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Canthon humboldti
Canthon indigaceus chevrolati
Canthon inusitatus
Canthon juvencus
Canthon lituratus
Canthon meridionalis


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Canthon moniliatus
Canthon morsei
Canthon mutabilis
Canthon septemmaculatus
Canthon silvaticus
Canthon subhyalinus subhyalinus


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Canthon vazquezae


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris costaricensis costaricensis


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris incertus


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris laeviceps


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris lugubris


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris subpunctatus


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Copris tridentatus

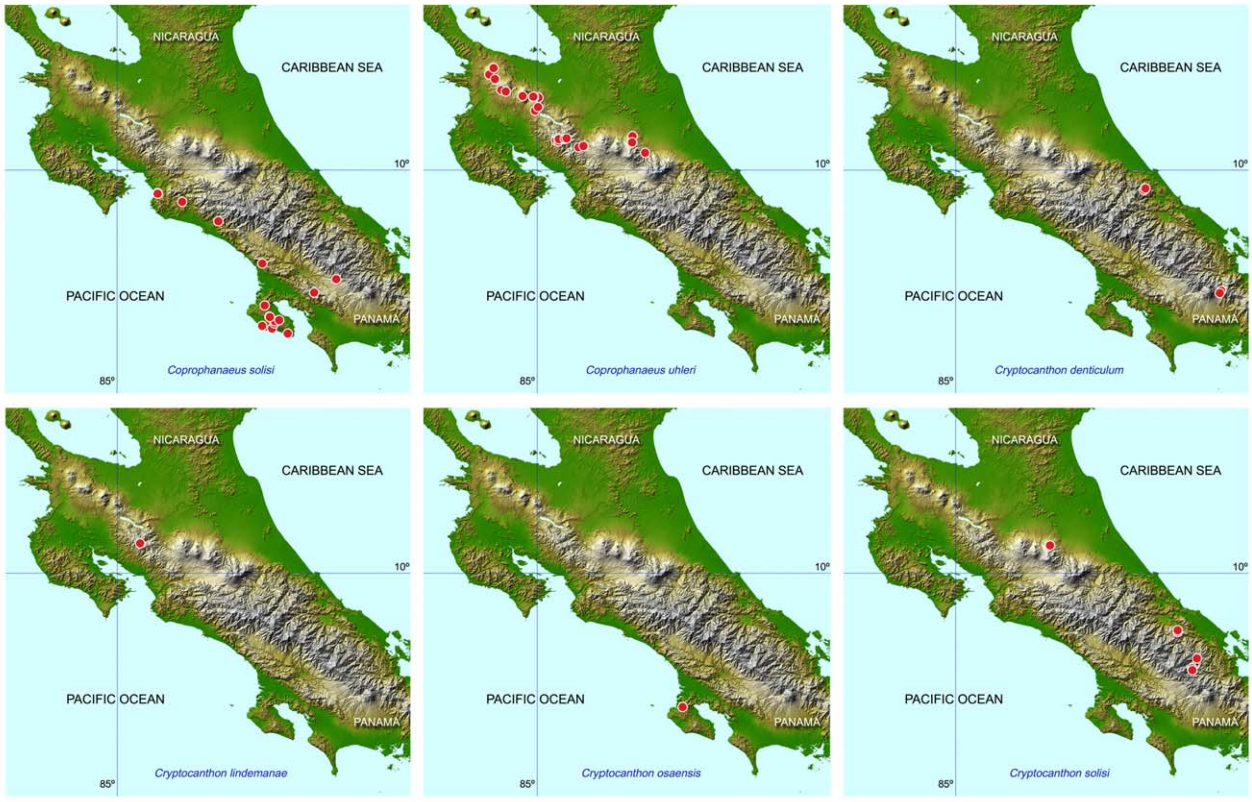

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus boucardi

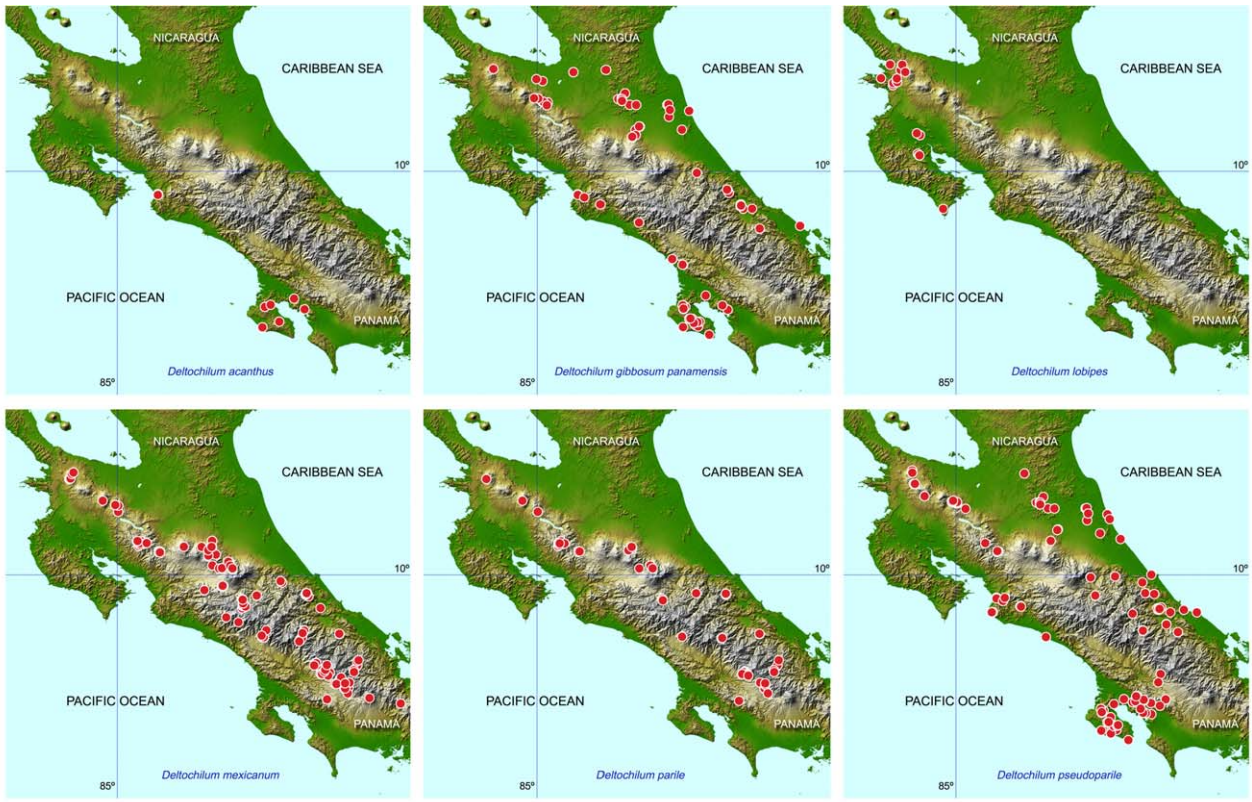

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus chiriquensis

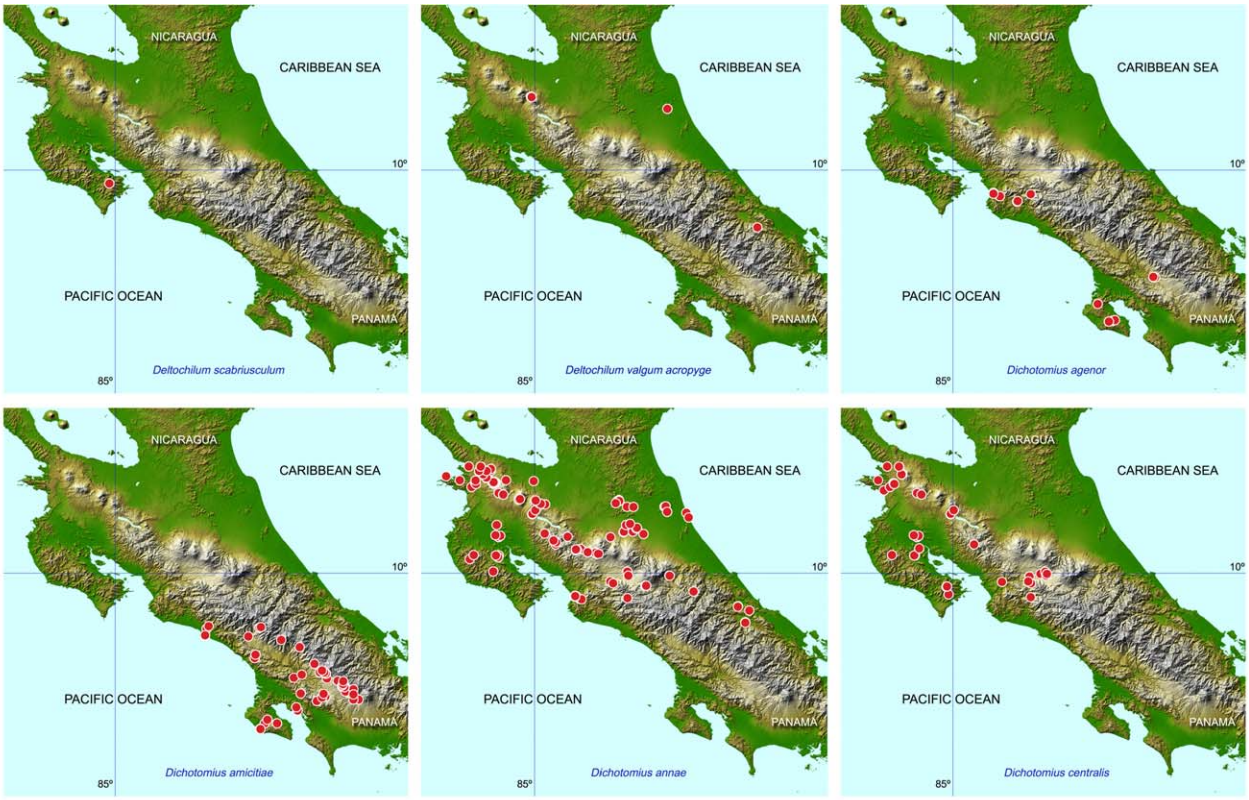

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus corythus

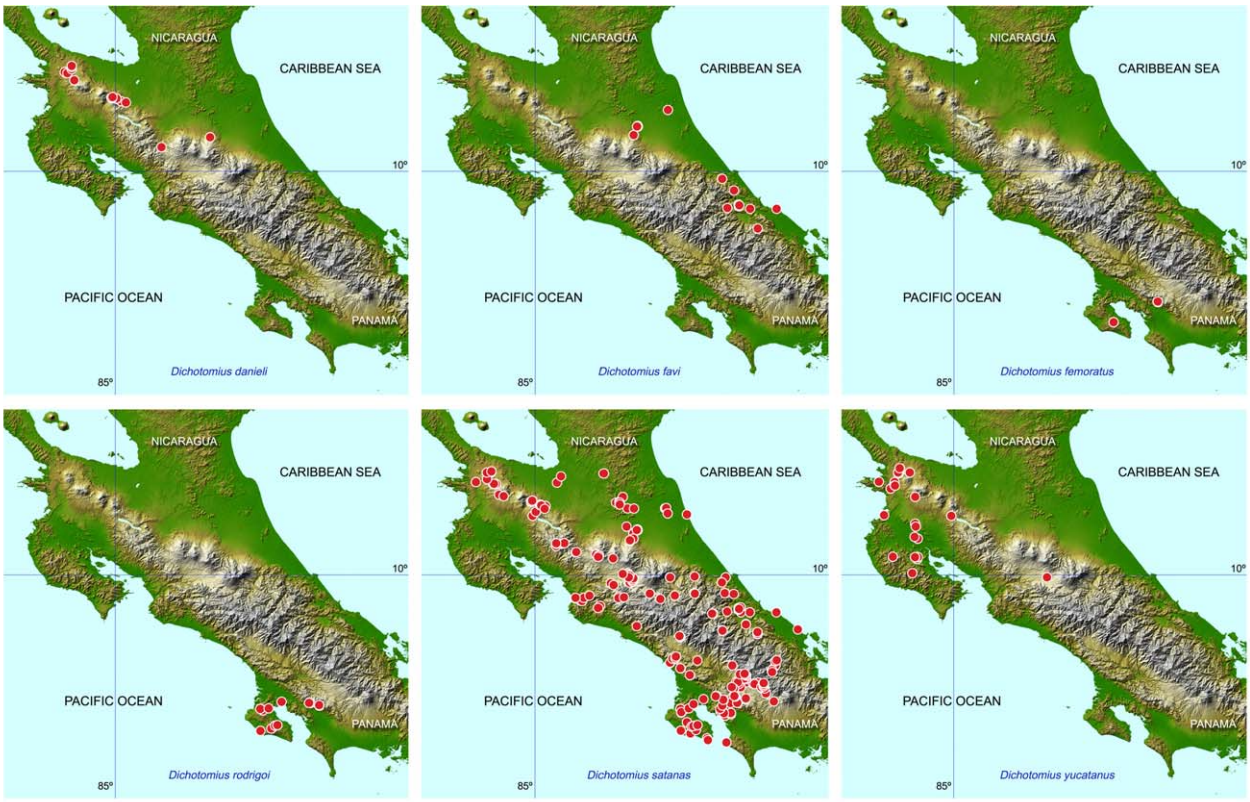

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus kohlmanni

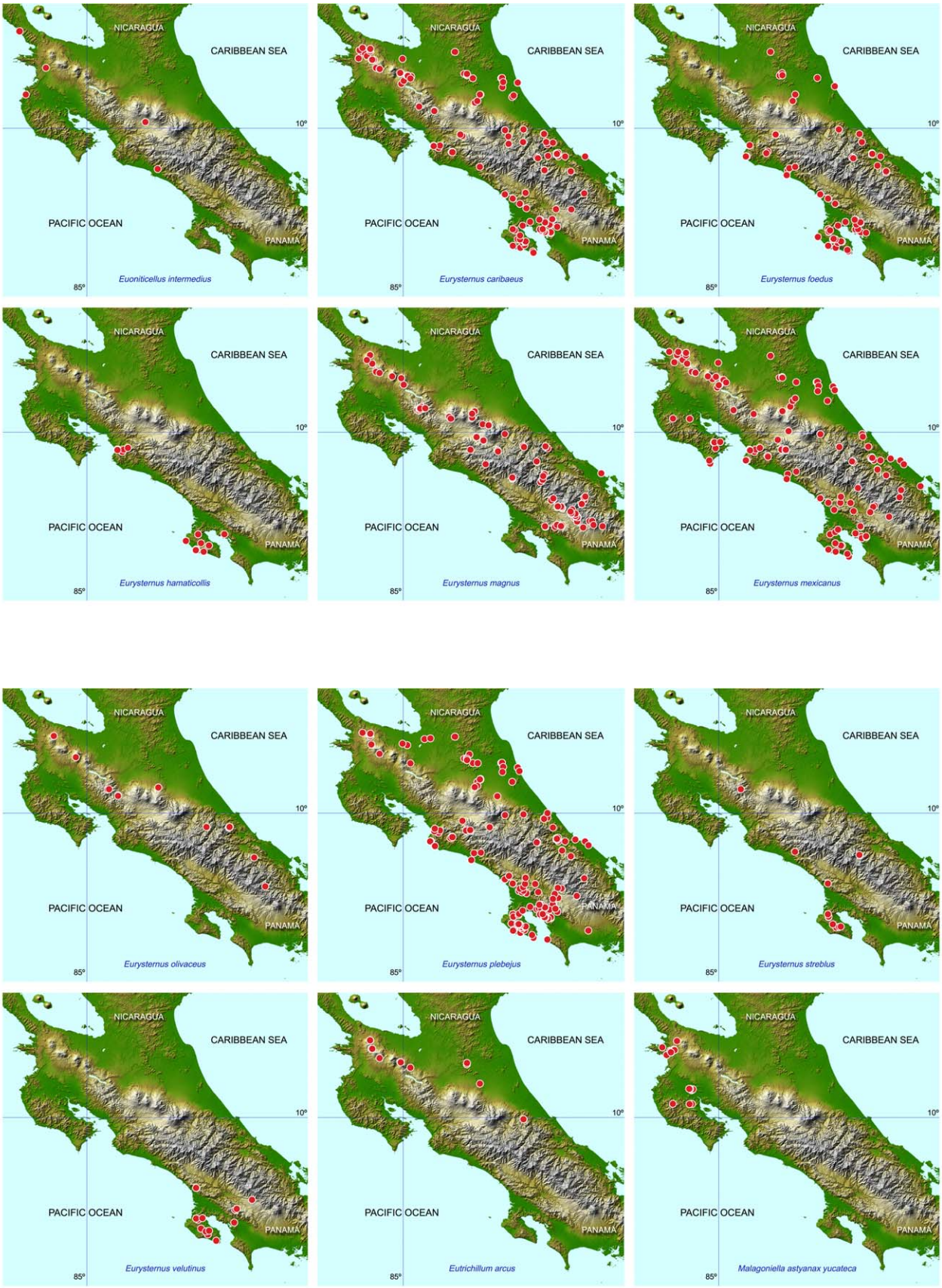

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus pecki

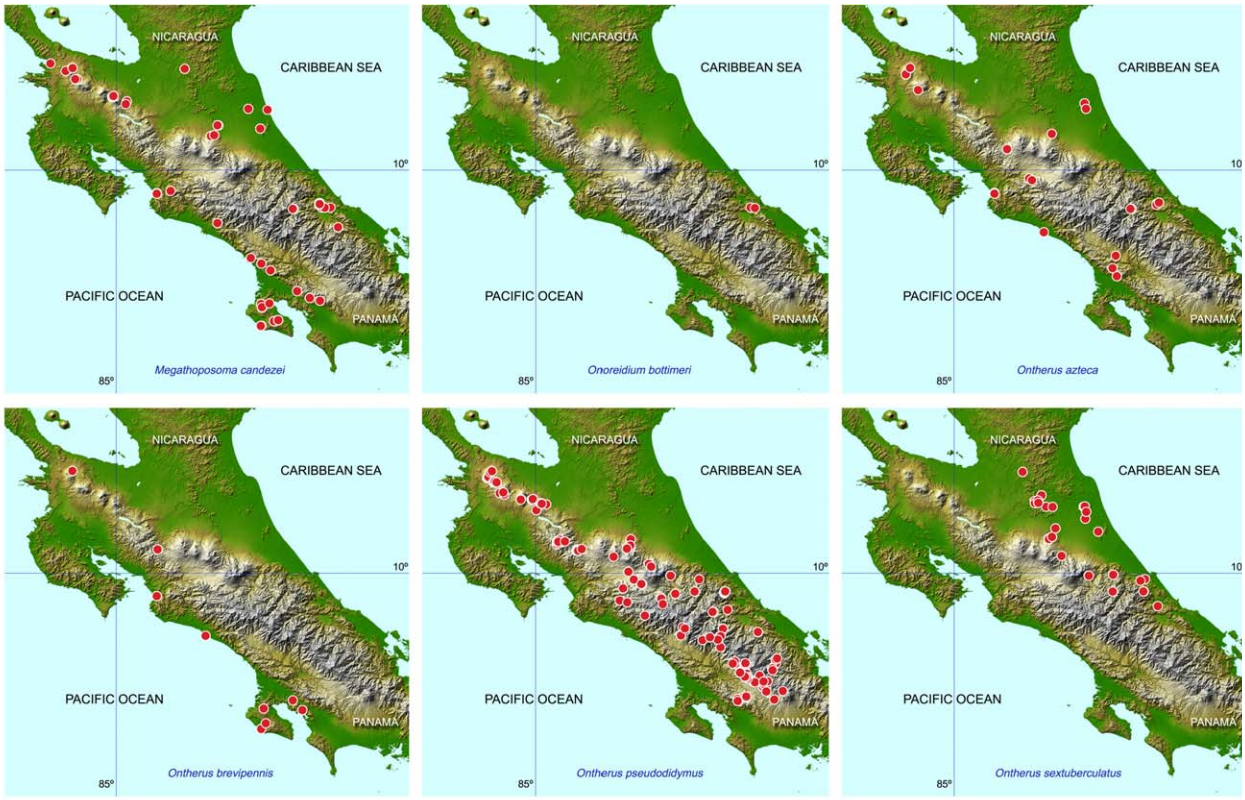

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Coprophanaeus solisi
Coprophanaeus uhleri
Cryptocanthon denticulum
Cryptocanthon lindemanae
Cryptocanthon osaensis
Cryptocanthon solisi

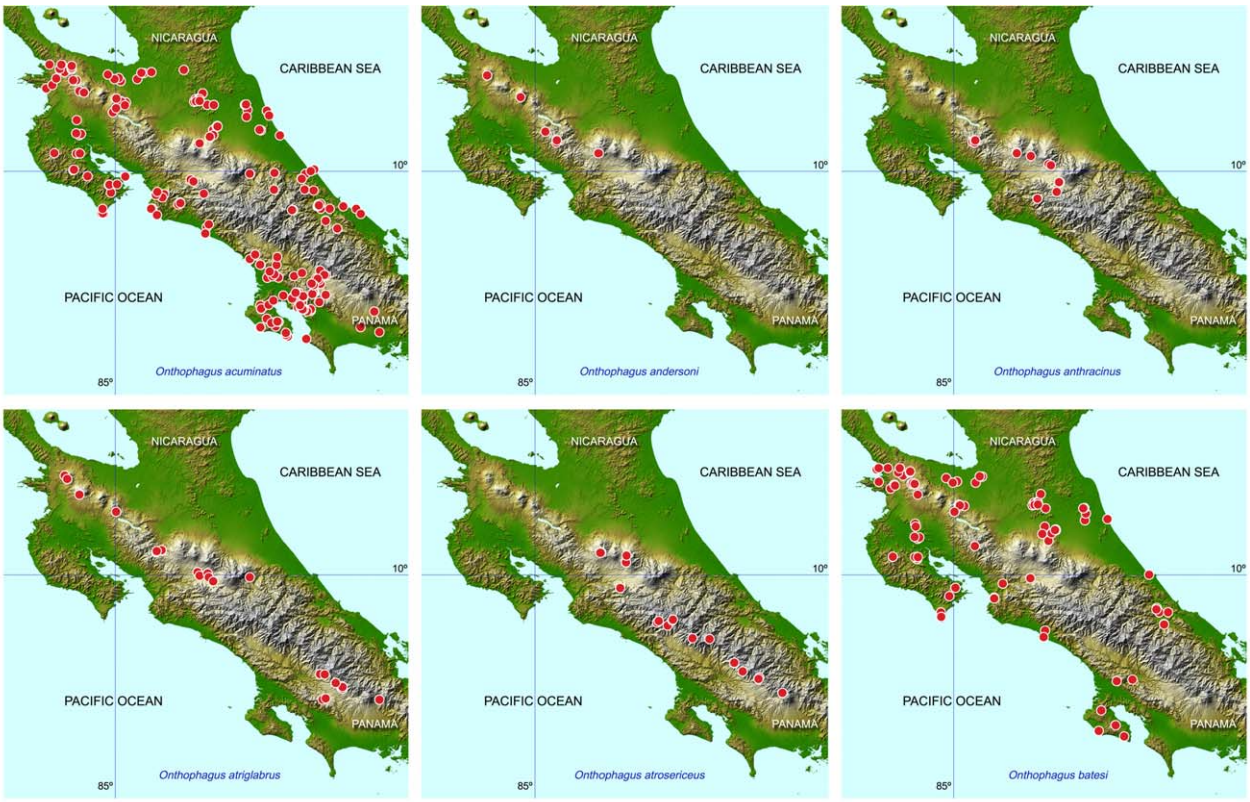

NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Deltochilum acanthus
Deltochilum gibbosum panamensis
Deltochilum lobipes
Deltochilum mexicanum
Deltochilum parile
Deltochilum pseudoparile

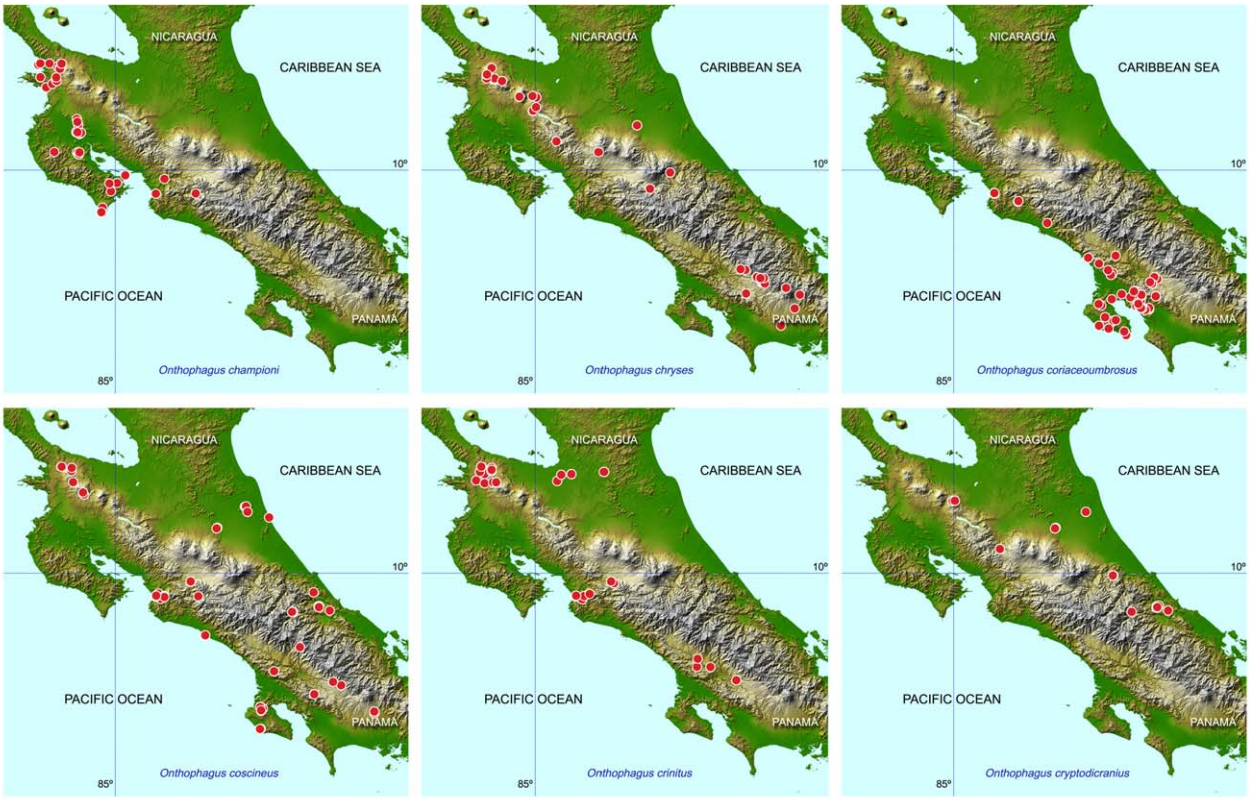

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Deltochilum scabriusculum
Deltochilum valgum acropyge
Dichotomius agenor
Dichotomius amicitiae
Dichotomius annae
Dichotomius centralis

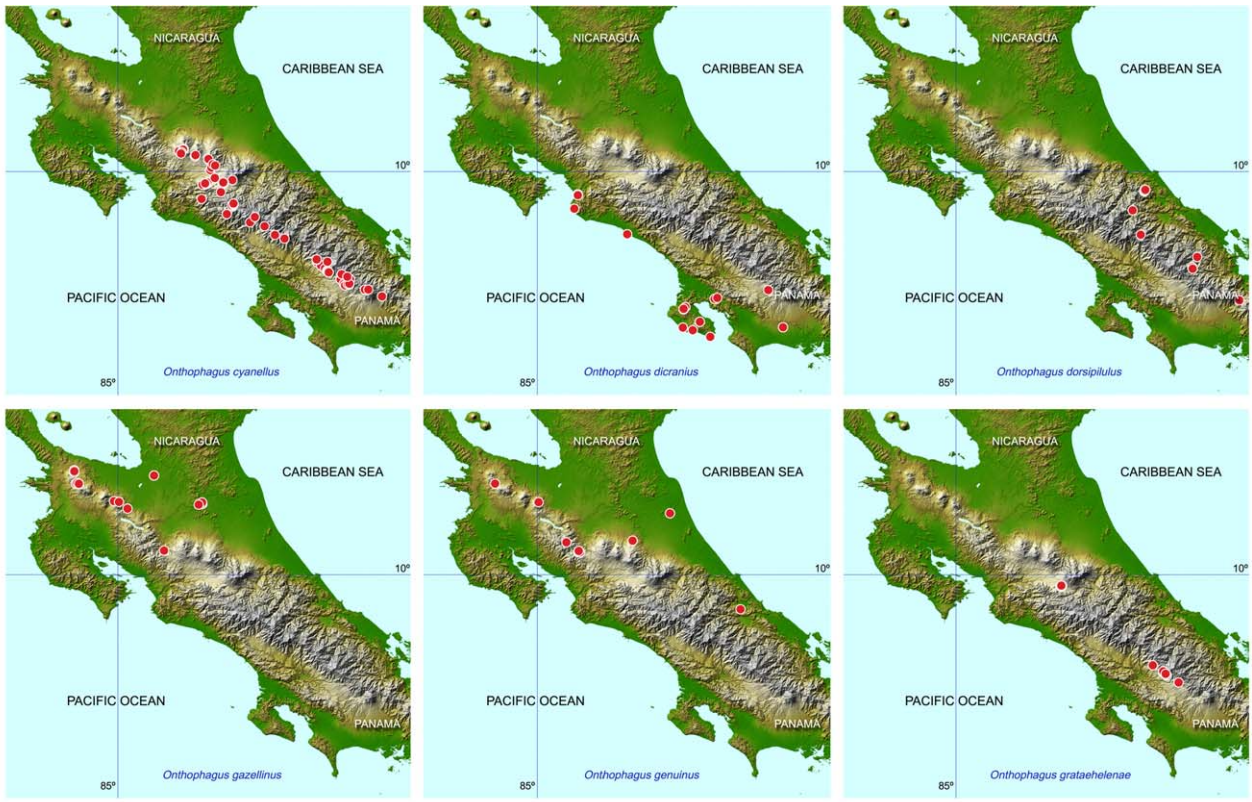

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Dichotomius danieli
Dichotomius favi
Dichotomius femoratus
Dichotomius rodrigoi
Dichotomius satanas
Dichotomius yucatanus

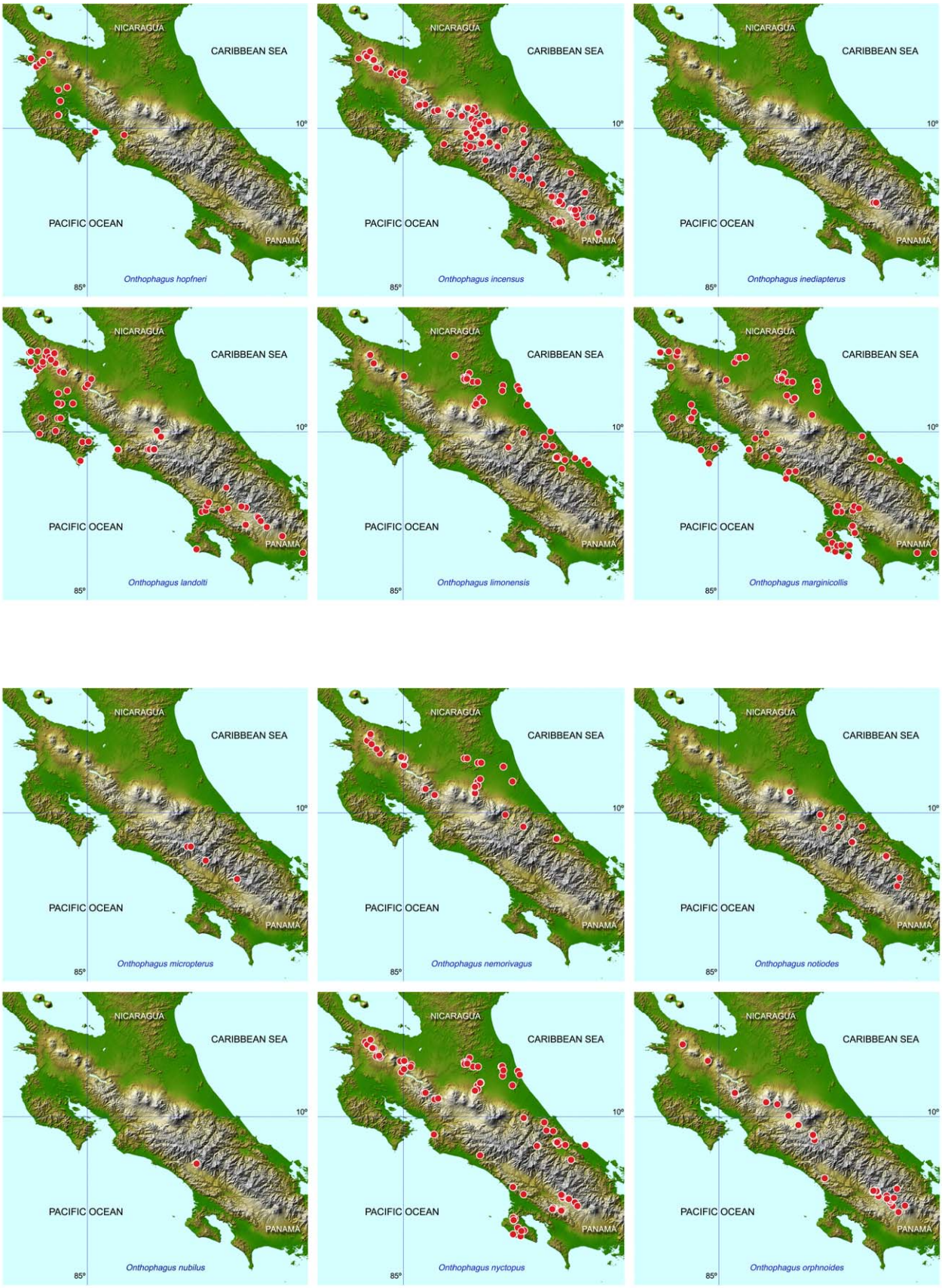

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Euoniticellus intermedius
Eurysternus caribaeus
Eurysternus foedus
Eurysternus hamaticollis
Eurysternus magnus
Eurysternus mexicanus
Eurysternus olivaceus
Eurysternus plebejus
Eurysternus streblus
Eurysternus velutinus
Eutrichillum arcus
Malagoniella astyanax yucateca

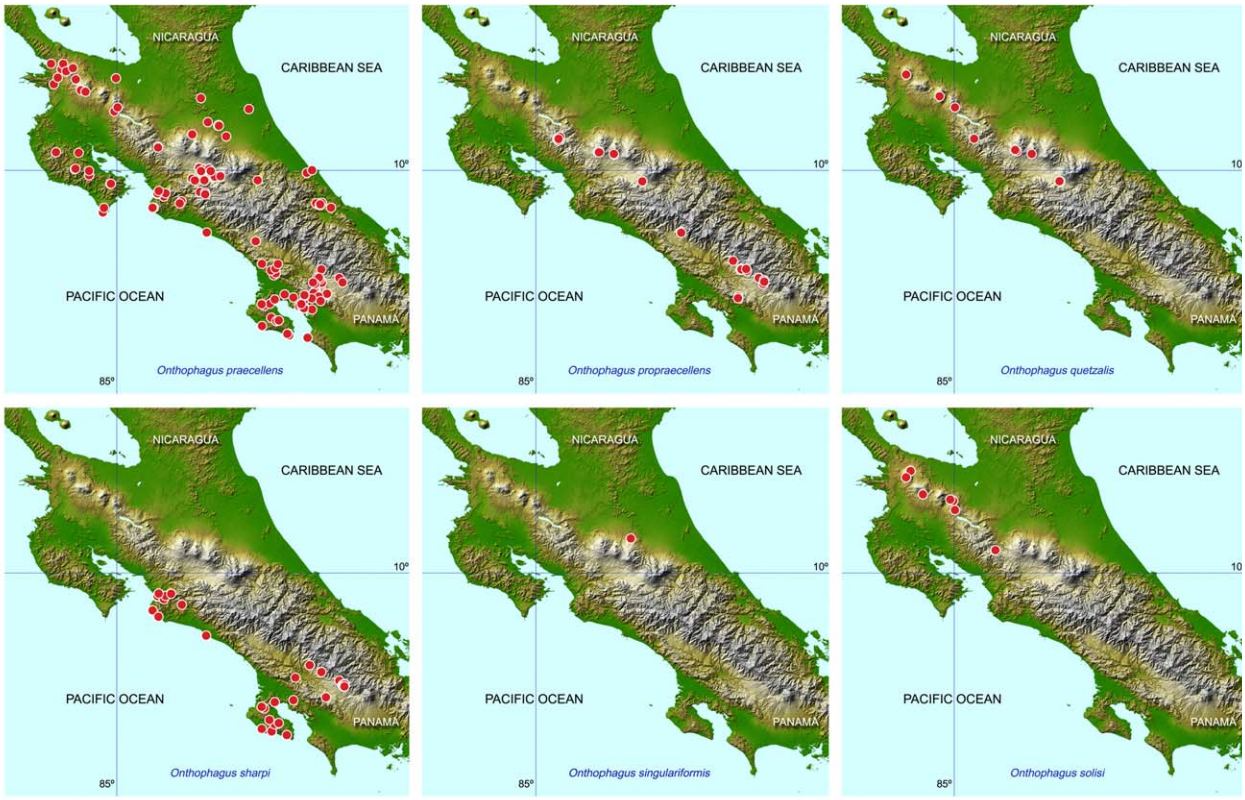

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Megathoposoma candezei
Onoreidium bottimeri
Ontherus azteca
Ontherus brevipennis
Ontherus pseudodidymus
Ontherus sextuberculatus

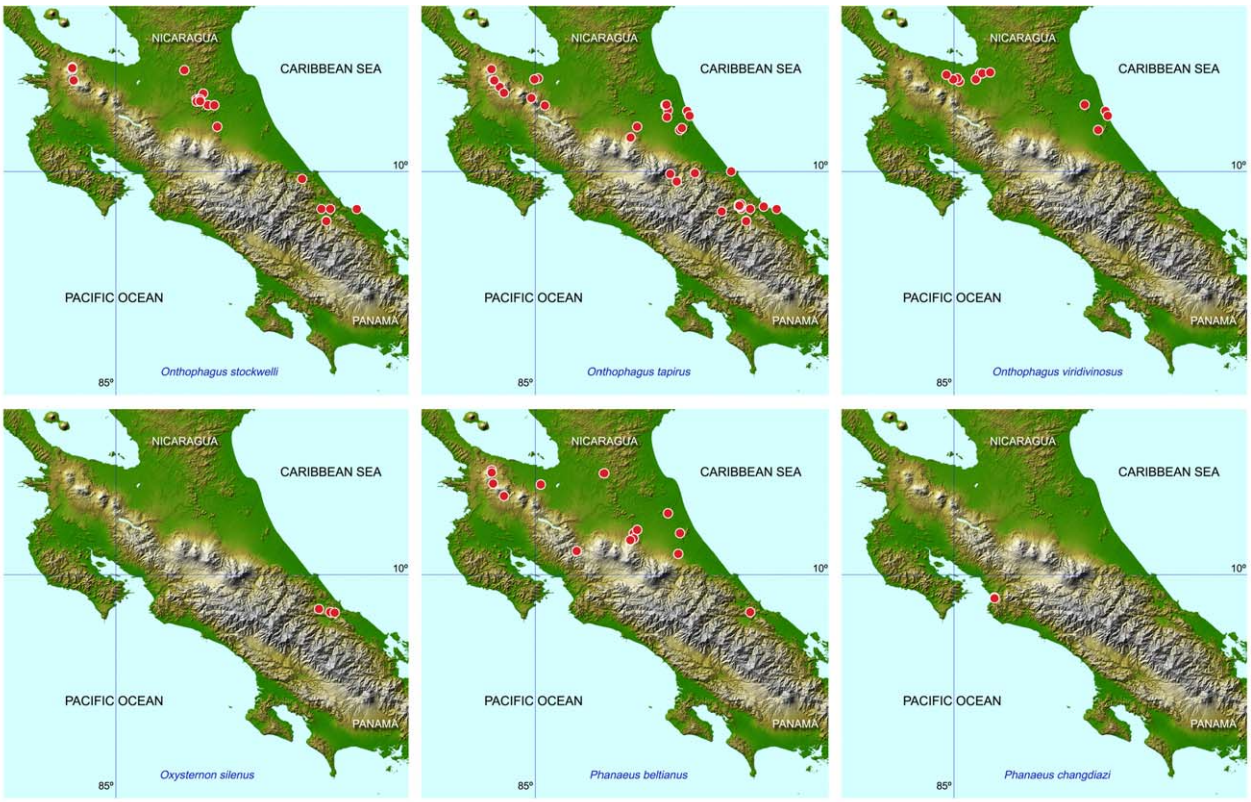

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Onthophagus acuminatus
Onthophagus andersoni
Onthophagus anthracinus
Onthophagus atriglabrus
Onthophagus atrosericeus
Onthophagus batesi


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Onthophagus championi
Onthophagus chryses
Onthophagus coriaceoumbrosus
Onthophagus coscineus
Onthophagus crinitus
Onthophagus cryptodicranius

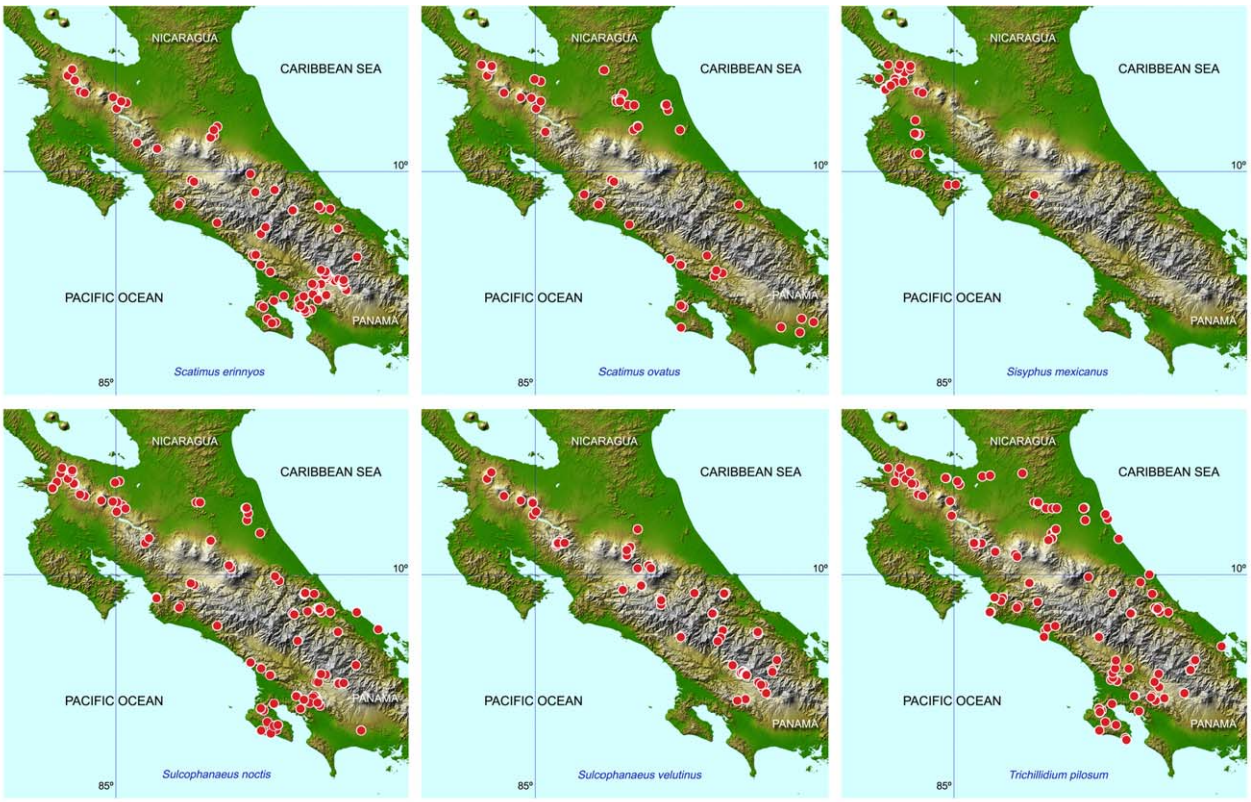

NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Onthophagus cyanellus
Onthophagus dicranius
Onthophagus dorsipilulus
Onthophagus gazellinus
Onthophagus genuinus
Onthophagus grataehelenae


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10°
85°
Onthophagus hopfneri
Onthophagus incensus
Onthophagus inediapterus
Onthophagus landolti
Onthophagus limonensis
Onthophagus marginicollis
Onthophagus micropterus
Onthophagus nemorivagus
Onthophagus notiodes
Onthophagus nubilus
Onthophagus nyctopus
Onthophagus orphnoides


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Onthophagus praecellens
Onthophagus propraecellens
Onthophagus quetzalis
Onthophagus sharpi
Onthophagus singulariformis
Onthophagus solisi


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Onthophagus stockwelli
Onthophagus tapirus
Onthophagus viridivinosus
Oxysternon silenus
Phanaeus beltianus
Phanaeus changdiazi


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Phanaeus excelsus
Phanaeus eximius
Phanaeus hermes
Phanaeus pyrois
Phanaeus malyi
Phanaeus wagneri wagneri
Pseudocanthon perplexus


NICARAGUA
CARIBBEAN SEA
PACIFIC OCEAN
PANAMA
10º
85º
Scatimus erinnyos
Scatimus ovatus
Sisyphus mexicanus
Sulcophanaeus noctis
Sulcophanaeus velutinus
Trichillidium pilosum


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys boneti


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys deavilai


NICARAGUA
CARIBBEAN SEA
10
PACIFIC OCEAN
PANAMA
85°
Uroxys dybasi


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys gatunensis


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys gorgon


NICARAGUA
CARIBBEAN SEA
10
PACIFIC OCEAN
PANAMA
85°
Uroxys metagorgon


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys microcularis


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys micros


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys nebulinus


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys pauliani


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys platypyga


NICARAGUA
CARIBBEAN SEA
10°
PACIFIC OCEAN
PANAMA
85°
Uroxys transversifrons