

The genus *Gromphas* Dejean, 1836 (Coleoptera, Scarabaeinae): nomenclature, distribution, and conservation, including a contribution to the debate on electronic publications in zoology

Mario CUPELLO



DIRECTEUR DE LA PUBLICATION / PUBLICATION DIRECTOR: Gilles Bloch
Président du Muséum national d'Histoire naturelle

RÉDACTRICE EN CHEF / EDITOR-IN-CHIEF: Laure Desutter-Grandcolas

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Anne Mabilille (zoosyst@mnhn.fr)

MISE EN PAGE / PAGE LAYOUT: Anne Mabilille

COMITÉ SCIENTIFIQUE / SCIENTIFIC BOARD:

Nesrine Akkari (Naturhistorisches Museum, Vienne, Autriche)
Maria Marta Cigliano (Museo de La Plata, La Plata, Argentine)
Serge Gofas (Universidad de Málaga, Málaga, Espagne)
Sylvain Hugel (CNRS, Université de Strasbourg, France)
Marco Isaia (Università degli Studi di Torino, Turin, Italie)
Rafael Marquez (CSIC, Madrid, Espagne)
Jose Christopher E. Mendoza (Lee Kong Chian Natural History Museum, Singapour)
Annemarie Ohler (MNHN, Paris, France)
Jean-Yves Rasplus (INRA, Montferrier-sur-Lez, France)
Wanda M. Weiner (Polish Academy of Sciences, Cracovie, Pologne)

COUVERTURE / COVER:

G. *lemoinei* Waterhouse, 1891, preserved in the MNHN.

Zoosystema est indexé dans / *Zoosystema is indexed in:*

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / *Zoosystema is distributed electronically by:*

- BioOne® (<http://www.bioone.org>)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par /
Articles and nomenclatural novelties published in Zoosystema are referenced by:

- ZooBank® (<http://zoobank.org>)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / *Zoosystema is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonia, Geodiversitas, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie, Comptes Rendus Palevol*.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2024
ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

The genus *Gromphas* Dejean, 1836 (Coleoptera, Scarabaeinae): nomenclature, distribution, and conservation, including a contribution to the debate on electronic publications in zoology

Mario CUPELLO

Laboratório de Sistemática e Bioecologia de Coleoptera, Departamento de Zoologia,
Universidade Federal do Paraná, Caixa Postal 19020, 81531-980, Curitiba, Paraná (Brazil);
and Department of Entomology, Texas A&M University,
College Station, TX 77843 (United States)
mcupello@hotmail.com

Submitted on 11 April 2023 | Accepted on 26 July 2023 | Published on 9 February 2024

urn:lsid:zoobank.org:pub:4B49C1D9-1196-4942-969F-2E923B1FC12C

Cupello M. 2024. — The genus *Gromphas* Dejean, 1836 (Coleoptera, Scarabaeinae): nomenclature, distribution, and conservation, including a contribution to the debate on electronic publications in zoology. *Zoosystema* 46 (2): 23-59. <https://doi.org/10.5252/zoosystema2024v46a2>. <http://zoosystema.com/46/2>

ABSTRACT

Previously overlooked literature now brought to my attention has resulted in the following nomenclatural conclusions: 1) The species known since 2013 as *Gromphas inermis* Harold, 1869 must be called *G. lacordairii* (Oken, 1834), whose original combination was *Coprobium lacordairii*. *Gromphas inermis* is a new junior subjective synonym of *G. lacordairii*; 2) *Gromphas* was made available by Dejean, in 1836, not Brullé, in 1837; the former, therefore, should be credited with the authorship; and 3) the type species of *Gromphas* is *Coprobium lacordairii* Oken, 1834 by original monotypy, not *Onitis aeruginosus* Perty, 1830 by subsequent monotypy. Also discussed is the publication year of *G. jardim* Cupello & Vaz-de-Mello, 2015. This leads me to address the problem of zoological works first published in electronic-only versions with their own pagination and which are later reissued integrated into a journal's volume and repaginated. It is here argued that these two versions – the detached and the volume-integrated ones – should be deemed separate available works, and that new nomenclatural acts can be made available from detached versions. If this is accepted, the later publication of the volume-integrated versions has no bearing on the availability of the earlier detached versions. I also introduce new data on the type series of *Onitis aeruginosus* (currently, *Gromphas aeruginosa*) and *G. inermis*, new specimens of the rare *G. jardim*, mislabelled specimens of *G. amazonica* Bates, 1870, and newly discovered specimens of the vanished *G. dichroa* Blanchard, 1846. The latter include the new record from Santa Catarina state, Brazil. The disappearance of *G. dichroa* since 1954, including the possibility that it might be extinct, is discussed.

KEY WORDS

Gromphas dichroa,
Gromphas lacordairii,
Gromphas lacordairii,
Gromphas inermis,
publication date,
preprint,
available work,
extinction,
disappeared species,
South America.

RÉSUMÉ

Le genre Gromphas Dejean, 1836 (Coleoptera, Scarabaeinae) : nomenclature, distribution et conservation, avec une contribution au débat sur les publications électroniques en zoologie.

La littérature précédemment ignorée et maintenant portée à mon attention a abouti aux conclusions nomenclaturales suivantes : 1) l'espèce connue depuis 2013 sous le nom de *Gromphas inermis* Harold, 1869 doit être appelée *G. lacordairii* (Oken, 1834), dont la combinaison originale était *Coprobium lacordairii*. *Gromphas inermis* est un nouveau synonyme subjectif junior de *G. lacordairii*; 2) *Gromphas* a été rendu disponible par Dejean, en 1836, et non par Brullé, en 1837 ; c'est donc le premier qui doit être crédité de la paternité; 3) l'espèce type de *Gromphas* est *Coprobium lacordairii* Oken, 1834 selon la monotypie originale, et non *Onitis aeruginosus* Perty, 1830 selon la monotypie ultérieure. L'année de publication de *G. jardim* Cupello & Vaz-de-Mello, 2015, est également discutée. Ceci m'amène à aborder le problème des travaux zoologiques publiés pour la première fois en version électronique avec leur propre pagination et qui sont ensuite réédités, intégrés dans le volume d'une revue et repaginé. L'argument avancé ici est que ces deux versions – la version détachée et la version intégrée au volume – devraient être considérées comme des œuvres disponibles distinctes, et que de nouveaux actes nomenclaturaux peuvent être rendus disponibles à partir des versions détachées. Si l'on accepte ce point de vue, la publication ultérieure des versions intégrées au volume n'a aucune incidence sur la disponibilité des versions détachées antérieures. Je présente également de nouvelles données sur les séries types d'*Onitis aeruginosus* (présentement *Gromphas aeruginosa*) et de *G. inermis*, de nouveaux spécimens du rare *G. jardim*, des spécimens mal étiquetés de *G. amazonica* Bates, 1870 et des spécimens nouvellement découverts de *G. dichroa* Blanchard, 1846, qui a disparu. Ces derniers comprennent le nouveau signalement de l'État de Santa Catarina, Brésil. La disparition de *G. dichroa* depuis 1954, y compris la possibilité qu'il soit éteint, est discutée.

MOTS CLÉS

Gromphas dichroa,
Gromphas lacordairii,
Gromphas lacordairei,
Gromphas inermis,
date de publication,
preprint,
travaux disponibles,
extinction,
espèces disparues,
Amérique du Sud.

INTRODUCTION

Some years ago, Fernando Vaz-de-Mello and I published a series of papers dealing with the systematics of the South American dung beetle genus *Gromphas* (Cupello 2013; Cupello & Vaz-de-Mello 2013, 2014, 2015). All the main systematic aspects were addressed, from nomenclature to species delimitation and intraspecific variation to the phylogeny of the genus and its relationships with other scarabaeine groups. Also addressed were the ecology and distribution of the species. Yet, unsurprisingly, new discoveries have accumulated since then and some have made me reconsider a few of the previous conclusions. This paper is a compilation of these new findings.

I shall first address nomenclatural issues that change three aspects of our revision. Firstly, the valid name of the species we called *Gromphas inermis* Harold, 1869, a common element of middle South America, is actually *Gromphas lacordairii* (Oken, 1834). Secondly, the authorship of the genus-group name *Gromphas* does not belong to Brullé (1838) as we said, but to Dejean (1836). Thirdly, the type species of *Gromphas* is not *Onitis aeruginosus* Perty, 1830 by subsequent monotypy by Sturm (1843), but *Coprobium lacordairii* Oken, 1834 by original monotypy. These novelties are all based on my reevaluation of the nomenclatural history of the genus and its species in light of my recent reading of previously overlooked literature. The two key references that had been overlooked are Lacordaire's (1830) memoir of his beetle explorations in South America and Oken's (1834) review of Lacordaire's paper. Both were recently brought to my attention by my colleague and ICZN Commissioner Patrice Bouchard.

In another part of the paper, I shall address the publication date of *Gromphas jardim* Cupello & Vaz-de-Mello, a problem that has to do with the controversy over the availability of electronic-only versions of works that appear with pre-volume pagination (Dubois *et al.* 2013, 2015a, b; Krell 2015). I will offer a solution to this problem that has apparently not been put forward before. In the continuation, I will present data on specimens newly studied by me in collections around the world, including the type series of *Onitis aeruginosus* (currently *Gromphas aeruginosa*), some new specimens of the rare *G. jardim*, mislabelled specimens of *G. amazonica* Bates, 1870, and a few new specimens of the vanished *G. dichroa* Blanchard, 1846. The latter include a new state record for Brazil and the most recent collection date for the species, 1954. The reasons for the disappearance of the species over the past 70 years, including the possibility of extinction, are examined.

MATERIAL AND METHODS

COLLECTIONS

The following collections were visited during the research for this paper (curator or another contact in parentheses):

CAPC	Carlos Aguilar personal collection, Capiatá;
CEAH	Coleção Entomológica Adolph Hempel, Instituto Biológico, São Paulo (Sergio Ide);
CEMT	Coleção Entomológica de Mato Grosso Eurides Furtado, Universidade Federal de Mato Grosso, Cuiabá (Fernando Z. Vaz-de-Mello);
CMNC	Canadian Museum of Nature, Ottawa (François Génier);

CNCI	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (Patrice Bouchard and Serge Laplante);	Material housed in the following collection is included on the list of material examined from label data kindly provided by Patricia González-Vainer:	
DZUP	Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (Lucia Massutti de Almeida);		
FSCA	Florida State Collection of Arthropods, Gainesville, Florida (Paul Skelley);	FCUR	Facultad de Ciencias, Universidad de la República, Montevideo (Enrique Morelli).
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus (Marcio Luiz de Oliveira);		
LSUK	The Linnean Society of London, London (Suzanne Ryder);		
MCNZ	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (Luciano de Azevedo Moura);		
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (Charles Farnum, Crystal Maier and Rachel Hawkins);		
MFNB	Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (Joachim Willers, Bernd Jaeger, and Johannes Frisch);		
MGAP	Museu Anchieta de Ciências Naturais, Colégio Anchieta, Porto Alegre (Fernando Meyer);		
MHNG	Muséum d'Histoire naturelle de Genève, Geneva (Giulio Cuccodoro);		
MNHN	Muséum national d'Histoire naturelle, Paris (Olivier Montreuil and Antoine Mantilleri);	LBEV	Coleção Entomológica do Laboratório de Biologia Evolutiva, Universidade Federal de Santa Maria, Santa Maria;
MNHNP	Museo Nacional de Historia Natural del Paraguay, San Lorenzo (Bolívar Garcete);	MCCR	Acervo entomológico do Museu de Ciências Naturais Carlos Ritter, Pelotas (currently part of the holdings of Laboratório de Zoologia, Departamento de Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Pelotas, Brazil);
MPEG	Museu Paraense Emílio Goeldi, Belém (Orlando Tobias Silveira);	MECB	Coleção do Museu de Entomologia Ceslau Maria Biezanko, Pelotas;
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo (Sonia Casari and Carlos Campaner);	MCTP	Coleção de Insetos do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre;
MZUFPA	Museu de Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém (Fernando A. B. Silva);	MHNU	Coleção do Museu de História Natural da Universidade Católica de Pelotas, Pelotas;
NHM	The Natural History Museum, London (Maxwell Barclay), formerly BMNH;	MRGC	Acervo do Museu Professor Ramiro Gomes Costa, Porto Alegre.
NHMB	Naturhistorisches Museum Basel, Basel (Isabelle Zürcher and Matthias Borer);		
NHMW	Naturhistorisches Museum Wien, Vienna (Harald Schillhammer);		
NMPC	National Museum (Natural History), Prague (Jiří Hájek);		
OUMNH	Hope Entomological Collections, Oxford University Museum of Natural History, Oxford (Darren Mann);		
RBINS	Institut royal des Sciences naturelles de Belgique, Brussels (Alain Drumont);		
RMNH	Naturalis Biodiversity Centre, Leiden (Hans Huijbregts);		
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg (Stephan Blank);		
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main (Andrea Hastenpflug-Vesmanis; current curator: Marianna V. P. Simões);		
SMTD	Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden, Dresden (Olaf Jäger and Klaus-Dieter Klass);		
TAMU	Texas A&M University, College Station, Texas (John D. Oswald, Mario Cupello, and Edward G. Riley);		
ZFMK	Zoologisches Forschungsinstitut Alexander Koenig, Bonn (Dirk Ahrens);		
ZMSC	Zoologische Staatssammlung München, Munich (Michael Balke and Ditta A. Balke);		
ZMUK	Zoologische Museum, Universität Kiel, Kiel (Michael Kuhlmann).		

Finally, the geographical provenance of the *Gromphas* specimens housed in the following collections was compiled by Pedro Giovâni da Silva in 2011 and graciously shared with me in March 2023 for inclusion in this work. These collections are all located in the Brazilian state of Rio Grande do Sul. Note that, in his Herculean effort of cataloguing all the Scarabaeinae from these regional collections, da Silva did not have time to take note of the exact number of specimens existing from each locality and each date. Therefore, this information is not provided in Figure 14 or in Table 1, where it would be expected to be found.

NOMENCLATURE PRINCIPLES

Given the convoluted nomenclature problems associated with *Gromphas* and its species (Cupello 2013; Cupello & Vaz-de-Mello 2013, 2014; herein), I gave special attention to the dating of nomenclature relevant publications. I based this dating primarily on Evenhuis (1997a, b; 2003; 2015; personal communication), Bousquet (2016), and the literature cited therein. For Edgar von Harold's papers published in *Coleopterologische Hefte*, I followed Bouchard *et al.* (2011) and based their dating on when the journal's respective volumes were recorded as received in donation by the Entomological Society of London (current Royal Entomological Society) in the society's *Proceedings*. See in the references section comments on the publication date of each 19th-century publication (and some 20th-century ones) relevant to the nomenclature issues discussed herein. All nomenclature discussions and decisions are based on the provisions of the International Code of Zoological Nomenclature (ICZN 1999), hereafter referred to simply as 'the Code'.

ON THE AUTHORSHIP OF THE GENUS-GROUP NAME *GROMPHAS*, AND THE AUTHORSHIP, ORIGINAL COMBINATION, AND SPELLING OF THE SPECIES-GROUP NAME '*GROMPHAS LACORDAIREI*'

NOMENCLATURAL HISTORY

The nomenclatural history related to the establishment of the names *Gromphas* and '*Gromphas lacordairei*', as the latter has been commonly spelled, can be summarised as follows:

1) Lacordaire (1830) (Figs 1; 2), in a memoir of his South American coleopterological observations (1824-1830), listed, family by family, the many species that he had seen in the southern continent. Following four paragraphs on pages 260 and 261 discussing the species of *Coprobium* Latreille, 1829 (current junior synonym of *Canthon* Hoffmannsegg, 1817), he introduced a new paragraph on a new dung beetle species from Buenos Aires, 'of a rather large size, of metallic color', which Dejean, the person responsible for identifying the Coleoptera that Lacordaire had brought back to Europe (Lacordaire 1830: 187), decided to name after him (Fig. 2). The name of this new species was not expressly given, however. This new species, according to Lacordaire, and certainly writing from information provided by Dejean, 'must belong to a new genus'. Lacordaire ended the paragraph by adding that the new species is 'fairly commonly found in the excrement of horses, and digs, like *Copris*, deep holes in the earth, a habit foreign to the aforementioned *Ateuchus*'. In the following paragraph, he addressed another new species, '*Ateuchus arachnoides*', from Tucumán, which reminded him of a spider and was said to also belong to a new genus.

2) Three years later, Dejean (1833) (Figs 1; 2), in the second edition of his Coleoptera collection's catalogue, the first published after Lacordaire's return, listed on page 143, among several dung beetle groups, the new genus '*Gromphas*. Dejean', with the new species '*Lacordairei* Dej.', from 'Buenos-Ayres' (Fig. 2). Because this is the only Buenos Aires scarabaeine named by Dejean after Lacordaire and, moreover, because it belongs to a new genus, it is obvious that this is the new species that Dejean named after Lacordaire that Lacordaire referred to in 1830. No description or diagnosis was provided by Dejean for either the genus or the species.

3) A review of Lacordaire's memoir was published by Lorenz Oken (1834) (Figs 1; 2). Oken enumerated the species addressed by Lacordaire one by one; in a paragraph on the *Coprobium*, besides several names mentioned for this genus by Lacordaire, Oken (1834: 1117) also included '*lacordairii*, digs deep; *arachnoides*, like spider in cow dung' ('*Coprobium*: [...] *lacordairii*, *gräbt tief*; *arachnoides*, *wie Spinne im Kuhmist*') (Fig. 2). Though Lacordaire expressly explained that they belonged to new genera, not to *Coprobium*, it is clear from the context and the associated biological and morphological information that the two species referred to by Oken as *Coprobium lacordairii* and *C. arachnoides* are, respectively, Lacordaire's new Buenos Aires species and his *Ateuchus arachnoides* from Tucumán.

4) The third and final edition of Dejean's catalogue was published in parts between 1836 and 1837. The page listing '*Gromphas*. Dejean' and '[*Gromphas*] *lacordairei*. Dej.', page 159, appeared in 1836 (Madge 1988; Bousquet 2016) (Fig. 2). Like in the previous edition, no description or diagnosis was provided for either the genus or the species.

5) Brullé (1838: 304-305) (Figs 1; 2) considered '*Gromphas*. Dej.' a subgenus of *Copris* Geoffroy, 1762 and described the taxon by saying: 'This subgenus is composed of one sole species that has the appearance of the Phanées [i.e., the subgenus *Phanaeus* of *Copris*] and their broad sternal plate [i.e., metaventricle], as well as their antennae with arched, cup-shaped club articles; it is distinguished only by the presence of anterior tarsi in males as well as in females' (Fig. 2). Even though Brullé explicitly said that *Gromphas* included only one species, the name of that species was never mentioned by him. While it is evident from the context that he was referring to Dejean's '*Gromphas lacordairei*', this has no nomenclatural bearing. In a footnote to page 304, Brullé added that the subgenus *Gromphas* was still new ('*Sous-genre encore inédit*'), alluding to the fact that Dejean had never described it.

6) Sturm (1843: 108), in a catalogue of his beetle collection, listed '*Gromphas*. Dej.' with a single species, *Onitis aeruginosus* Perty, 1830.

7) Arguing that, although already 'characterised' by Brullé (1838), no species had been described for *Gromphas* until then, Blanchard (1846: 181-182) described '*Gromphas Lacordairei*, Dej., Catal.' from specimens collected in Santa Cruz de la Sierra, Bolivia, and *G. dichroa*, from Montevideo, Uruguay.

8) Harold (1869b), after explaining that the dung beetles described by Blanchard as *G. lacordairei* referred not to Lacordaire's Buenos Aires species, but to the same species as *Gromphas aeruginosa* (= *Onitis aeruginosus*), and that Dejean's name, by not being accompanied with descriptions, could not be accepted, concluded that Lacordaire's species had never been formally named. To fix the situation, he established the name *Gromphas inermis* Harold, 1869 for it. As for the authorship of *Gromphas*, Harold (1869a) credited it to Brullé, the first to describe the genus.

9) Burmeister (1874) disagreed with Harold (1869b) and considered Dejean's names *Gromphas* and *Gromphas lacordairii* (his spelling) available from the latter's 1830s collection catalogues. By being senior to both Blanchard's *G. lacordairei* and Harold's *G. inermis*, *G. lacordairii* Dejean was, in Burmeister's view, the proper valid name of Lacordaire's species, with *G. inermis* as its junior synonym, whereas Blanchard's *G. lacordairei* was a junior synonym of Perty's *G. aeruginosa*.

10) A period of instability reigned during the late 19th and the early 20th centuries, when authors transitioned from using Harold's *G. inermis* (e.g., Preudhomme-de-Borre 1886; Judulien 1899; Gahan & Arrow 1903; Heyne & Taschenberg 1908), to '*G. lacordairei* Dejean' (e.g., Tremoleras 1910), and then to '*G. lacordairei* Brullé' (e.g., Bruch 1911) as the valid name of Lacordaire's Buenos Aires species. With the adoption of the latter name and authorship by Gillet's (1911) and Blackwelder's (1944) catalogues and by d'Olsoufieff's (1924) landmark revision of the phanaeines, a consensus seemed to

A



B



C



D



FIG. 1. — Authors in the early taxonomic history of *Gromphas*: **A**, Jean Théodore Lacordaire (1801-1870), the Belgian-French entomologist who collected in Argentina the first known specimens of the genus. He was also the first to record aspects of its behaviour in the literature (Lacordaire 1830). From an engraving reproduced by Candèze (1872); **B**, Pierre François Marie Auguste Dejean (1780-1845), who recognised that the specimens collected by Lacordaire belonged to a then-new genus and species, which he named – first as a *nomen in litteris* and later as a *nomen nudum* (Dejean 1833) – ‘*Gromphas lacordairei*’. From Wikipedia; **C**, Lorenz Oken (1779-1851), a leader of the *Naturphilosophie* movement in Germany and editor of the journal *Isis*. In a 1834 literature review for the journal, Oken combined the morphological and behavioural information introduced by Lacordaire (1830) with the specific name coined by Dejean (1833) and made the name *Coprobius lacordairii* available. From Ecker (1883); **D**, Gaspard Auguste Brullé (1809-1873), who has been erroneously regarded as the author who made both *Gromphas* and ‘*Gromphas lacordairei*’ available. From Wikipedia.

Un grand nombre d'espèces de moyenne et petite taille, ornées pour la plupart de couleurs métalliques ou non métalliques brillantes, peuvent se ranger dans le genre Coprobius de M. Latreille.

Les suivants : *A. rutilans*, Klug., *smaragdulus*, Fab., *scapularis*, Dupont, *histrion*, *cyanescens*, Dej., *depressifrons*, *emarginatus*, *virescens*, ejusd. *N. Sp.*, etc., toutes du Brésil, où elles sont plus ou moins communes, vivent indistinctement dans les bouses et sur les feuilles. On les trouve souvent rassemblés en assez grand nombre, occupés à sucer la liqueur qui découle des plaies des arbres. Leur vol est assez facile, et il a lieu pendant le jour.

Une espèce, *A. flavicollis*, Dej., *N. Sp.*, qui appartient à cette division, et qui est voisine, par son faciès, de l'*A. 6-punctatus*, Fab., est remarquable par l'odeur infecte qu'elle exhale, et qui a le plus grand rapport avec celle des *Sylpha*, mais plus forte encore. Il est probable qu'elle se nourrit de matières animales

décomposées, habitude que nous retrouverons dans un *Phanæus*.

D'autres, *A. niger*, *sulcatulus*, *congener*, Dej., *lituratus*, Illig., *carbonarius*, *oblongus*, *propinquus*, Dej. (du Brésil), *cupricollis*, *sobrinus*, Dej., *N. Sp.*, *glabricollis*, ejusd. (de Buénos-Ayres et Montevideo), *subsulcatus*, *litigiosus*, Dej., *cæsus*, mihi (Espèces nouvelles du Tucuman), vivent exclusivement dans les bouses. Une seule, *A. carbonarius*, qui fréquente de préférence les endroits sablonneux, y creuse des trous assez profonds. Les autres fouillent simplement la surface du sol sans s'y enfoncer.

Une autre espèce, de Buénos-Ayres, d'assez grande taille, de couleur métallique, et que M. le comte Dejean a bien voulu me dédier, doit constituer un nouveau genre. On les trouve assez communément dans les excréments des chevaux, et elle creuse, comme les *Copris*, des trous profonds dans la terre, habitude étrangère aux *Ateuchus* ci-dessus.

Lacordaire (1830)

GROMPHAS. Dejean.

Lacordairei. Dej. Buenos-Ayres.

I

Dejean (1833)

Annales des sciences naturelles Tom. XIV. 1829.
(Fortsetzung von Seite 1062 Heft 10)

Tome XX, 1830.

S. 185 J. Th. Lacordaire, über die Lebensweise der Käfer im mittäglichen America. Viele Käfer namentlich angeführt.

Coprobius: *A. rutilans*, *smaragdulus*, *scapularis*, *histrion*, *cyanescens*, *depressifrons*, *emarginatus*, *virescens*, in Kuhmist und auf Blättern, fliegen; *flavicollis*, sinkt; *niger*, *sulcatulus*, *congener*, *lituratus*, *carbonarius*, *ablongus*, *propinquus*, *cupricollis*, *sobrinus*, *glabricollis*, *subsulcatus*, *litigiosus*, *cæsus*, im Kuhmist, außer carbonariis, der im Sand gräbt; *lacordairii*, gräbt tief; *arachnoides*, wie Spinne im Kuhmist.

Oken (1834)

GROMPHAS. Dejean.

Lacordairei. Dej. Buenos-Ayres.

I

Dejean (1836)

FIG. 2. — The early taxonomic literature on *Gromphas* Dejean, 1836 and *G. lacordairii* (Oken, 1834). Lacordaire's (1830) was the first publication where the species and genus were ever mentioned (green underline), and where a description was provided, though their names were not given. Notice that the discussion on this new genus and species follows four paragraphs on *Coprobius* (red underlined). In the second edition of his catalogue, Dejean (1833) finally mentioned the names, but did not accompany them with either a description, a diagnosis, or an indication. Oken (1834), in his review of the papers appearing in several volumes of *Annales des sciences naturelles*, including Lacordaire's, listed the name *lacordairii* followed by a short description ('digs deep'), but erroneously assigned it to *Coprobius* Latreille, 1829. This short description, plus the indication of Lacordaire's paper and expanded description, made the species-group name *Coprobius lacordairii* available under Oken's (1834) authorship. When Dejean (1836), in the third edition of his catalogue, combined it with the then-nomen nudum *Gromphas*, he made the latter available and *lacordairii* its type species. See the text for more details.

have been reached and all authors until 2013 adopted '*G. lacordairei* Brullé' as the valid name and treated *G. inermis* as its invalid junior synonym. The authorship of *Gromphas* was likewise consistently attributed to Brullé. And though never expressly addressed in the literature, it is clear that '*G. lacordairei* Brullé', having been supposedly established in the same work as *Gromphas*, was tacitly regarded as the type species.

11) In their revision of *Gromphas*, Cupello & Vaz-de-Mello (2013) argued that Brullé cannot be deemed the author who gave availability to *G. lacordairei* for he did not mention the name in his work. They considered that Blanchard (1846) had been the first author to use *G. lacordairei* in a way that complies with the availability criteria of the Code and that, therefore, the authorship of the name would be his. How-

ever, as Blanchard's name referred to an Amazonian species (namely, *G. aeruginosa*), it was not available to denote the species then known as '*G. lacordairei* Brullé' (i.e., Lacordaire's Buenos Aires species). The oldest available name for the latter was, as far as they were aware, *G. inermis*. Hence, Cupello & Vaz-de-Mello adopted this name for Lacordaire's Buenos Aires species in all of their papers dealing with *Gromphas* (Cupello & Vaz-de-Mello 2013, 2014, 2015). Moreover, because Burmeister (1874) explicitly said that he was using '*G. lacordairii* Dejean' as a different name from '*G. lacordairei* Blanchard', Cupello & Vaz-de-Mello interpreted that he also established a new available name under his own authorship, *G. lacordairii* Burmeister, 1874, a junior synonym of *G. inermis* Harold, 1869. As for the authorship of *Gromphas*, since Cupello & Vaz-de-Mello believed that Brullé had been the first to publish the name in a way to comply with all the availability criteria of the Code, they agreed with the consensus of the time and attributed it to Brullé. Since no nominal species had been originally included in the genus, Cupello & Vaz-de-Mello initially designated one of the two nominal species subsequently assigned to the genus by Blanchard (1846), *G. dichroa*, as the type species. Later, however, they came across Sturm's (1843) earlier inclusion of *Onitis aeruginosus* in the genus and interpreted that this fixed it as the type species by subsequent monotypy (Cupello & Vaz-de-Mello 2014).

12) The following taxonomy and nomenclature resulted from all this activity and have until now been considered valid (only names so far discussed and deemed available included):

Gromphas Brullé, 1837

[sic; see Bousquet (2016) for the correct publication year of Brullé's work, 1838].

TYPE SPECIES. — *Onitis aeruginosus* Perty, 1830, by subsequent monotypy by Sturm (1843: 108).

Gromphas aeruginosa (Perty, 1830)

Onitis aeruginosus Perty, 1830: 39, pl. 8, fig. 8.

Gromphas aeruginosa – Sturm 1843: 108.

Gromphas lacordairei Blanchard, 1846: 181 (subjective synonymy firstly established by Harold (1859)).

Gromphas inermis Harold, 1869

Gromphas inermis Harold, 1869b: 62.

Gromphas lacordairii Burmeister, 1874: 130 (objective synonymy firstly recognised by Cupello & Vaz-de-Mello [2013]).

Gromphas dichroa Blanchard, 1846

Gromphas dichroa Blanchard, 1846: 182.

ANALYSIS OF PREVIOUS HISTORY

Now aware of Lacordaire's (1830) and Oken's (1834) texts, I challenge some of the previous interpretations:

1) Because Lacordaire (1830) mentioned neither the generic name nor the full binomen of his new Buenos Aires species, he did not make either available. Nevertheless, by listing three taxonomic characters – viz., colouration, size, and digging behaviour – and the respective states shown by the species – viz., metallic, 'large', and 'digs deep holes in the earth like *Copris* but unlike any *Ateuchus*' –, he presented what the Code would term a description or definition, however brief it might be considered (the Code cites 'taxonomic characters' in the definition of 'description', but does not explain what the term means, only plain 'character'; I follow Mayr *et al.*'s [1953], Mayr's [1969], and Mayr & Ashlock's [1991] definition). When, four years later, Oken (1834: 1117), in a review of Lacordaire's paper, used the name *Coprobius lacordairii* to refer to this new species of Lacordaire's, he made the name available by a) using it as valid (complying with Article 11.5), b) accompanying it with a rather short description ('it digs deep', '*gräbt tief*') (Art. 12.1), and c) accompanying it with an indication, namely, an indication to Lacordaire's text he was expressly reviewing, where the slightly expanded description can be found (Art. 12.2.1). Therefore, the oldest name available for Lacordaire's Buenos Aires species is neither '*Gromphas lacordairei* Dejean, 1833 [or 1836]', '*Gromphas lacordairii* Dejean', '*Gromphas lacordairei* Brullé, 1837 [or 1834, or 1838]', nor *G. inermis* Harold, 1869, but *Coprobius lacordairii* Oken, 1834.

2) Since every author who has ever used the name *Gromphas lacordairei*, regardless of the spelling employed and the recognized taxonomic limits of the species, has always referred directly or indirectly to the name coined by Dejean and, thus, to the specimens collected by Lacordaire, they were all referring to the same nominal species. For this reason, no one has established new homonyms '*lacordairei*/*lacordairii*' in *Gromphas*, and no separate available name '*G. lacordairei* Blanchard' or '*G. lacordairii* Burmeister' exists as Cupello & Vaz-de-Mello (2013) argued. What we actually have is, in retrospect, in Blanchard's case, an erroneous attribution of the authorship of the name (to Dejean) and identification (i.e., his application to specimens belonging to an Amazonian species, *G. aeruginosa*), and, in Burmeister's, only an erroneous attribution of the authorship (to Dejean). Using Smith & Smith's (1972) apt term, '*lacordairei* Blanchard' and '*lacordairii* Burmeister' are chresonyms, not homonyms, of *Coprobius lacordairii* Oken, 1834 (hetero- and orthochresonyms, respectively; see Dubois 2000), and thus have no separate availability. To make it clear: they are simple subsequent citations of the name originally made available by Oken, not separate available names in their own right. They must be accordingly removed from the synonymic list of the *Gromphas* species.

3) When Dejean (1836) listed '*lacordairei* Dej.' under *Gromphas* in the third edition of his catalogue, he was using the same species-group name that i) had been indirectly mentioned as a *nomen in litteris* by Lacordaire (1830); ii) appeared as a *nomen nudum* in the second edition of his own catalogue

(Dejean 1833); and iii) had been made available two years earlier by Oken (1834). Hence, by including an already available name under *Gromphas*, Dejean (1836) complied with the availability criterion for genus-group names established in Article 12.2.5 and made *Gromphas* available. The authorship of this name does not belong to Brullé (1838), after all, but to Dejean (1836), something rather fitting since it was indeed Dejean who coined the name.

4) *Coprobius lacordairii* (currently, *Gromphas lacordairii*) is the type species of *Gromphas* Dejean, 1836 by original monotypy, since, as just explained, this was the only nominal species included in *Gromphas* (through an indication to its name) when the genus-group name was made available.

5) The type series of *Coprobius lacordairii* is composed of the specimens observed and collected by Lacordaire in Buenos Aires, for they were the ones which provided the characters mentioned in his 1830 description indicated by Oken (1834) and it is clear that Oken himself did not see additional specimens. Where are these specimens? My conclusion is that they are now lost. Lacordaire's Coleoptera collection was sold in parts through the years, and some of its material is currently housed in the Paris (MNHN), Brussels (RBINS), and London (NHM) museums (Horn *et al.* 1990b; Cambefort 2006). Unfortunately, nothing is known particularly about the whereabouts of Lacordaire's scarabs, nor did I find in any of the searched museums a specimen that could have belonged to Lacordaire's Buenos Aires series (see the list of collections studied in the Material and Methods). The specimen illustrated in figure 4, plate 27, of a later work by Lacordaire (1855) (Fig. 3B), which belongs to the species nowadays known as *G. inermis sensu* Cupello & Vaz-de-Mello, is not part of that series, for Lacordaire (1855) mentioned in the 'explanation' on page 10 that this specimen came from Tucumán (Argentina), not Buenos Aires (Fig. 3A).

In addition to the syntypes that may have been housed in Lacordaire's collection, there were also those deposited in Dejean's. We know they existed because, as we have seen, Dejean listed the species as present in his collection in his 1830s catalogues (Dejean 1833, 1836) (but not in the 1821 first edition, preceding Lacordaire's South American travel) and indicated their provenance precisely from the place where Lacordaire collected them, Buenos Aires. Like Lacordaire's, Dejean's beetle collection was sold in parts in 1840 and scattered across Europe (Horn *et al.* 1990a; Cambefort 2006; Bousquet & Bouchard 2013; Maldaner *et al.* 2017). His scarabs seem to have been split mainly between François Thibault de la Carte, marquis de La Ferté-Senectère (1808-1886), in France, and Robert Bakewell (1810-1867), in Britain. Eventually, La Ferté's specimens were mostly (i.e., excluding the Cetoniinae) incorporated into the MNHN via the Oberthür collection in 1952 (Cambefort 2006), whereas Bakewell's were divided in 1867, with one part going to the NHM that same year, while the other (apparently a 'second choice') ended up at the MNHN via the Oberthür collection along with La Ferté's (Horn *et al.* 1990a; Cambefort 2006).

I was unable to recognise any Bakewell specimens in the *Gromphas* material of the MNHN, or Dejean scarabs in general. As for any potential La Ferté *Gromphas*, the only specimen I located there is the *G. lemoinei* Waterhouse, 1891 depicted in Figure 4. But because this species lives only in Colombia and Venezuela (Cupello & Vaz-de-Mello 2013, 2015) (Fig. 5), this specimen cannot be part of the series collected by Lacordaire in Buenos Aires and later acquired by Dejean. As for the NHM, sometimes it is relatively easy to identify Bakewell's Dejean scarabs relying on Dejean's labelling style (see Horn *et al.* 1990b for an example). Unfortunately, however, I found no Dejean or Bakewell *Gromphas* in the museum.

Two further possibilities explored by me were the Oxford University Museum of Natural History, Oxford (OUMNH), and the Museo Regionale di Scienze Naturali, Turin, Italy (MRSN). Drawing from letters exchanged between the two entomologists in the early 1820s, it is known that Frederick William Hope (1797-1862) received, in 1823, around 50 Coleoptera from Dejean (Smith 1986). Even though syntypes of *C. lacordairii* cannot be among these *c.* 50 specimens given that Lacordaire only came back to Europe in 1830, it is possible that Dejean and Hope continued to exchange material over the years. All the specimens received by Hope, if still surviving, must be in the OUMNH, where the Hope-Westwood collection is preserved. Unfortunately, none of the *Gromphas* that Cupello & Vaz-de-Mello (2015) found there bears any link to either Dejean or Lacordaire. Three of them are from areas other than Buenos Aires – two from Brazil and one from Bolivia – another five have no provenance data, and none is from Argentina.

As for the Turin museum, the Dejean material housed there originates from the private collection of Massimiliano Spinola (1780-1857) and, except for some Chrysomelidae still preserved in original Dejean boxes, is now scattered in the general collection among specimens from several other sources (Giachino 1982). Box 94 of the general collection contains two cabinet labels reading 'Gromphos [*sic*] lacordairei', one of them ascribing the authorship of the name to Dejean and standing beside two specimens, the other citing no author and standing beside a single specimen (Giachino 1982). However, because both labels state Brazil as the place of origin of the species, it is unlikely that the specimens associated with them came from Dejean's material and certainly not from Lacordaire.

Having failed to find the specimens, I deem the type series lost. But is the allocation of the name *Coprobius lacordairii* (and, by extension, of *Gromphas*) affected by that? It has been traditionally considered Lacordaire's specimens belonged to the species currently known as *Gromphas inermis* (see Cupello & Vaz-de-Mello 2013). Arguably, the earliest indication that they did belong at least to the genus *Gromphas* as the name is currently applied is from Brullé (1838: 298), who expressly ascribed to this genus – but, as we have seen, without mentioning its name – the species that Lacordaire observed digging deep holes below horse dung.

Yet, the best evidence regarding the identity of Lacordaire's specimens is found in a work by Lacordaire himself (Lacordaire 1855). In this work, Lacordaire recognised (though

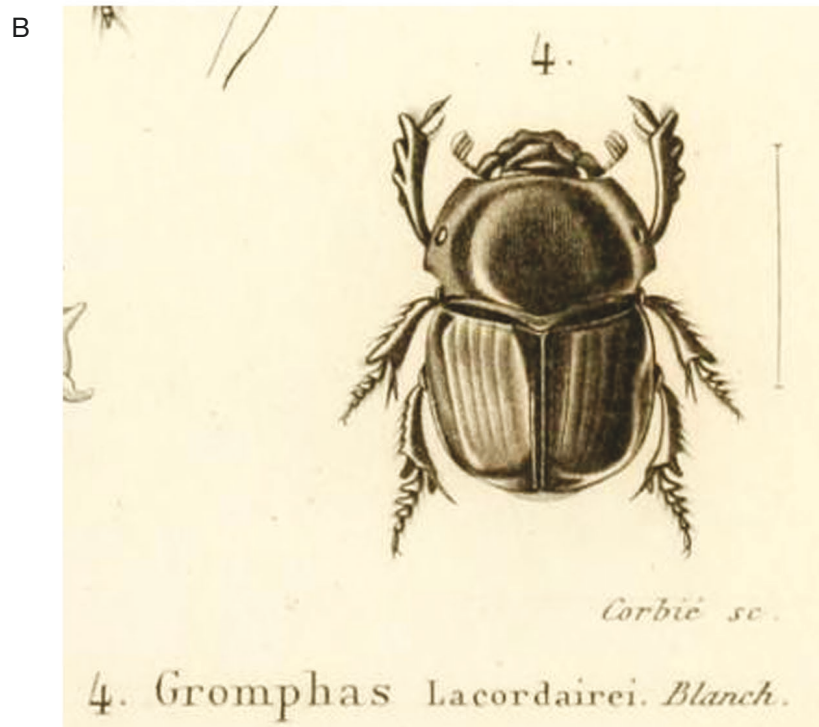
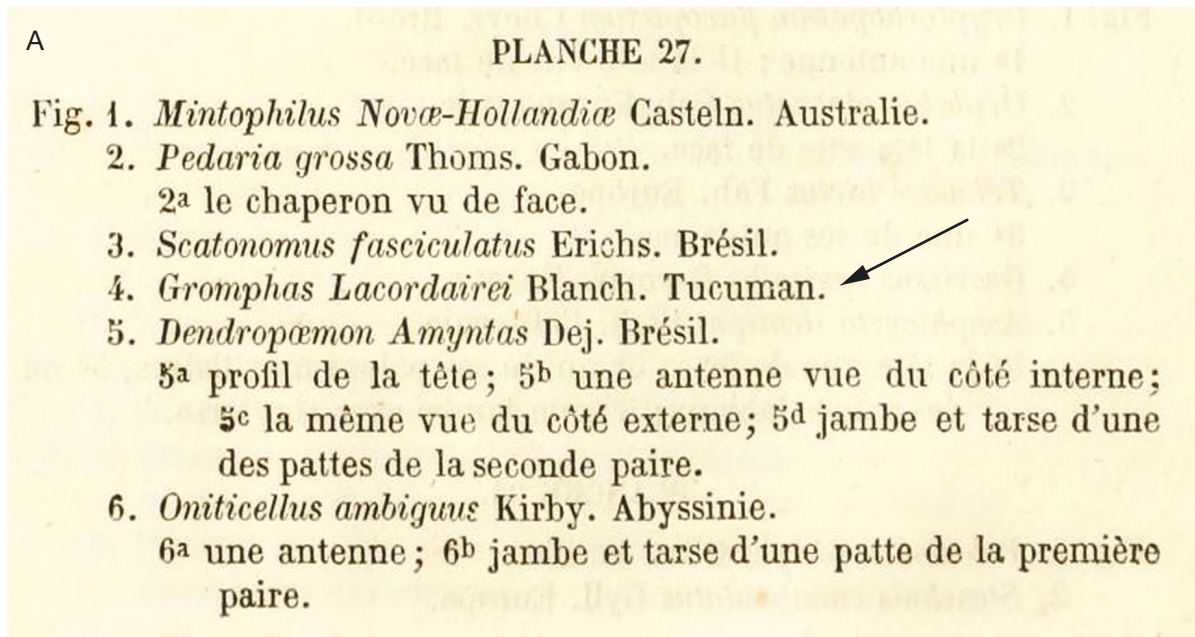


FIG. 3. — Lacordaire's (1855) illustration of '*Gromphas lacordairei* Blanchard'. Note that in the 'explanation' (i.e., the captions) of his plate 27 (A), Lacordaire indicated Tucumán, Argentina, as the locality of origin of *G. lacordairei*. I assume he was referring to the provenance of the individual specimen figured in his plate (B), not of the species as a whole, since, in the text, he said that the species ranged from Peru to Argentina. Being from Tucumán, the specimen cannot be part of the series collected by Lacordaire in Buenos Aires and that later became the type series of *G. lacordairei* (Oken, 1834).

hesitantly) two species for *Gromphas*, *G. dichroa* Blanchard, 1846 and '*G. lacordairei* Blanchard', the latter said to be the one he discovered in Buenos Aires. Since the only *Gromphas* species other than *G. dichroa* to occur in Buenos Aires is *G. inermis sensu* Cupello & Vaz-de-Mello (2013, 2015), and, as said above, this is clearly the species depicted in Lacordaire's

(1855) plate 27 as '*Gromphas lacordairei* Blanch.' (Fig. 3), his Buenos Aires specimens must indeed have belonged to *G. inermis*. That said, Lacordaire's (1855) text clearly shows that what he considered to be '*G. lacordairei*' (i.e., his taxonomic species '*G. lacordairei*') also included specimens of *G. aeruginosa*. This is evident because he says that the distribution

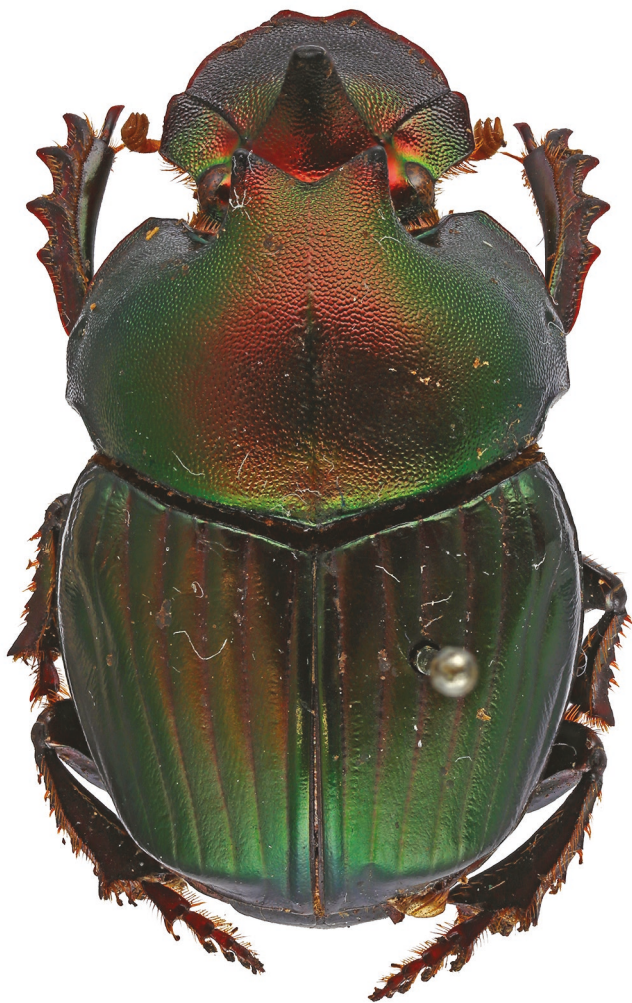


FIG. 4. — The only specimen of *Gromphas* from the La Ferté collection. This specimen, a *G. lemoinei* Waterhouse, 1891, like the majority of the La Ferté specimens, is now preserved in the MNHN. Since La Ferté owned specimens from the Dejean collection, one could suggest that this specimen might be one of the syntypes of *G. lacordairii* (Oken, 1834). But this is not the case. *Gromphas lemoinei* is endemic to Colombia and Venezuela, while the syntypes were all collected in Buenos Aires, Argentina. Photographs courtesy of Christophe Rivier (MNHN). Scale bar: 5 mm.

of ‘*G. lacordairei*’ reaches Peru and males are different from females in bearing cephalic and pronotal horns. It is evident that he mistook real *G. inermis*/*G. lacordairii* (both sexes hornless and lacking in Peru) for females and *G. aeruginosa* specimens (both sexes horned and occurring in Peru) for males of a single species, a common misconception among coleopterists working until the mid-19th century (Cupello & Vaz-de-Mello 2013). But since *G. aeruginosa* does not occur in Argentina, there are no doubts that all the specimens he collected in Buenos Aires did belong to *G. inermis*. As the identity and geographical provenance of the lost syntypes are unambiguous, the allocation of the name is straightforward and no neotype designation is necessary or justified under Article 75.3 of the Code.

6) Having concluded that the syntypes of *G. lacordairii* Oken, 1834 belong to the same species as the lectotype designated by Cupello & Vaz-de-Mello (2013) for *Gromphas inermis* Harold, 1869, the two names are now subjective synonyms, with the former being valid due to its 35-year seniority.

7) The complete revised nomenclature of the genus *Gromphas* and its species is as follows (see the list of references for details on the publication dates).

REVISED NOMENCLATURE OF THE GENUS *GOMPHRAS*

Gromphas Dejean, 1836

Gromphas Dejean, 1836: 159 [30th July 1836].

TYPE SPECIES. — *Coprobium lacordairii* Oken, 1834, by original monotypy.

ETYMOLOGY. — From the Latinisation of the Ancient Greek noun γρομφάς (*gromfás*), meaning ‘an old sow’, feminine in gender (Brullé 1838; Harold 1869a; Bailly 1895; Liddell & Scott 1897; Brown 1954; Cupello & Vaz-de-Mello 2013). The name likely draws a parallel between the stout, hornless body shape of both pigs and the only species originally included in the genus, *G. lacordairii*, while also making a probable reference to the ‘filthy’ coprophagous habits of these dung beetles.



FIG. 5. — Updated distribution map of the six species of *Gromphas*. Data retrieved from Cupello & Vaz-de-Mello (2013, 2015), Damborsky *et al.* (2015), Cajaiba *et al.* (2017), Gámez & Acconcia (2018), Alonso *et al.* (2019), Uchoa & Rodrigues (2019), Bitencourt *et al.* (2019), Noriega *et al.* (2021), and the material examined for this work.

Gromphas aeruginosa (Perty, 1830)

Onitis aeruginosus Perty, 1830: 39, pl. 8, fig. 8 [31st December 1830].

Gromphas aeruginosa – Sturm 1843: 108.

NAME-BEARING TYPE. — Lectotype (male), designated by Scherer (1983: 298), ZMS.

TYPE LOCALITY. — Brazil: the Amazon rainforest, somewhere visited by Spix and Martius along the Amazon River, the Japurá, the lower Madeira, or the Rio Negro (see Papavero 1971 for a map with these places indicated) (see discussion below).

ETYMOLOGY. — A Latin first-class adjective in the nominative case meaning ‘rusty’, ‘covered with verdigris’, and, by extension, ‘green-

ish’, ‘verdigris green’ or ‘dark green’ (Lewis & Short 1891; Brown 1954; Glare 1968-1982; Papavero 1994). Though not originally explained, the name makes an obvious reference to the greenish metallic colouration of many individuals of the species, including those in the type series, a characteristic that Perty (1830) described as ‘*obscurae viridi-metallicus*’.

DISTRIBUTION. — The Amazon Basin in Colombia, Ecuador, Peru, Brazil, and Bolivia, especially in sandbanks, floodplains and natural savannas, with southern incursions into the dry Chiquitano forests of eastern Bolivia and the Bañados de Izozog wetlands (‘Río Parapetí’) of the southern Bolivian Dry Chaco. The species is also known from a sole locality in the upper Magdalena River Valley, the town of Gigante (Huila, Colombia), separated from the Amazon by the Cordillera Oriental, the eastern branch of the Colombian Andes. It

is unclear whether this population is somehow connected to those in the Amazon across the Andes or represents a geographical isolate. If the latter, then the question is raised as to whether this Gigante population is a relict from a time when the species was more widely ranged and skirted the Cordillera Oriental or whether it is somehow the result of jump dispersal across the Andean mountains.

Gromphas lacordairii (Oken, 1834)

Coprobis lacordairii Oken, 1834: 1117 [30th November 1834].

Gromphas inermis Harold, 1869b: 62 [1st November 1869], **n. syn.**

Gromphas lacordairii bipunctata d'Olsoufieff, 1924: 59 [31st December 1924], **n. syn.** [subjective synonymy with *G. inermis* firstly established by Cupello & Vaz-de-Mello (2013: 464); here extended to *G. lacordairii* (Oken, 1834)].

NAME-BEARING TYPE. — *Coprobis lacordairii*: syntypes (unknown sexes), unknown whereabouts, likely destroyed; allocation remains unambiguous (see the text above).

Gromphas inermis: lectotype (male), designated by Cupello & Vaz-de-Mello (2013: 464), MNHN (ex Edgar von Harold and René Oberthür collections).

Gromphas lacordairii bipunctata: lectotype (male), designated by Cupello & Vaz-de-Mello (2013: 464), MNHN (ex René Oberthür collection).

TYPE LOCALITY. — *Coprobis lacordairii* and *Gromphas inermis*: Argentina: either somewhere in the province of Buenos Aires or the adjacent city of Buenos Aires.

Gromphas lacordairii bipunctata: Brazil: Mato Grosso.

ETYMOLOGY. — *Coprobis lacordairii*: the masculine singular genitive of the proper noun *Lacordairius*, the Latinised form of the French surname Lacordaire. It is an eponym after Belgian-French naturalist Jean Théodore Lacordaire (1801-1870), the collector of the type material. The name is spelled as '*lacordairii*', and not '*lacordairei*' as originally intended by its coiner Dejean (1833, 1836) and so far cited in most of the literature, because Oken derived it not directly from Lacordaire's name in modern French as Dejean did (i.e., the name Lacordaire + the Latin masculine genitive suffix *-i*), but, as said, from its Latinized form, *Lacordairius* (i.e., by adding the masculine suffix *-i* to the stem *Lacordairi-*; see Article 31.1.1 of the Code for more details). The '*lacordairei*' spelling is regarded here as an incorrect subsequent spelling in the terms of Article 33.3 of the Code; even though it is in prevailing usage, because this spelling has never been attributed to the publication of the original spelling (i.e., to Oken 1834), it cannot be deemed a correct original spelling under Art. 33.3.1.

Gromphas inermis: A Latin adjective in the nominative case meaning 'unarmed', 'having no weapons' (Lewis & Short 1891; Brown 1954; Glare 1968-1982), a reference to the hornless condition of this species in contrast to the horned congeneric *G. aeruginosa*.

Gromphas lacordairii bipunctata: A New Latin first-class adjective in the nominative case meaning 'bi-punctate', 'bearing two punctures', the combination of the Latin prefix *bi-* for 'two', 'occurring twice', and the New Latin adjective *punctatus* (*-a, -um*) for 'punctate' (Brown 1954; Wiktionary 2019a). It alludes to the pair of tenuous posterior pronotal fossae that characterized the purported variety of *G. lacordairii* for which d'Olsoufieff (1924) established the name and which he knew exclusively from Mato Grosso (Brazil). Cupello & Vaz-de-Mello (2013) observed that specimens bearing this feature are always small and actually found throughout the range of the species, always in polymorphism with the much more abundant smooth individuals of all sizes. Due to this, and in keeping with the authors' taxonomic criteria, they were prompted to invalidate d'Olsoufieff's taxon and name.

DISTRIBUTION. — Open environments of middle South America in Brazil, Bolivia, Paraguay, Argentina, and Uruguay, inhabiting savannas, grasslands, floodplains, river sandbanks, pastures, and restingas as well as associated forest edges and gallery forests.

Gromphas dichroa Blanchard, 1846

Gromphas dichroa Blanchard, 1846: 182 [18th December 1846].

NAME-BEARING TYPE. — Holotype by monotypy (female), MNHN.

TYPE LOCALITY. — Uruguay: Montevideo, 'near the sea' (Blanchard 1846).

ETYMOLOGY. — A New Latin first-class adjective in the nominative case meaning 'having two colours', 'bicoloured' (Wiktionary 2022). The word ultimately derives from the combination of the Ancient Greek prefix *δι-* (*di-*), meaning 'twice', 'double' (Brown 1954; Wiktionary 2023a), and the Ancient Greek noun *χρῶμα* (*khrōma*), meaning 'colour', 'pigment', especially of the skin or body surface (Bailey 1895; Liddell & Scott 1897; Brown 1954), Latinized by the addition of the Latin adjectival suffix *-us* (*-a, -um*) (Wiktionary 2023b). The name makes an obvious reference to the dorsal colouration of the holotype, with a centrally red pronotum and blue elytra, a pattern seen in many – but not all – individuals of the species (Cupello & Vaz-de-Mello 2013, 2015; see more details later in this work). Blanchard (1846) called the species in his vernacular French the '*gromphas bicolore*'.

DISTRIBUTION. — The Pampas biome and peripheral areas of the southern Atlantic Forest (e.g., Itapiranga, Santa Catarina, and Nova Petrópolis, Rio Grande do Sul) in southern Brazil, Argentina, and Uruguay; possibly also present in the southern Humid Chaco of Paraguay. Nothing is known about the habitats occupied by the species in this vast area. One possibility, based on what is known of the biology of the other *Gromphas*, is that the species occupies more humid areas, especially wetlands, including the floodplains and sandbanks of the Uruguay River along the border of Argentina and the Brazilian state of Rio Grande do Sul and other such water bodies like Lake Guaíba (e.g., in Porto Alegre) and the River Plate (e.g., Montevideo and Buenos Aires).

Gromphas amazonica Bates, 1870

Gromphas amazonica Bates, 1870: 175 [30th June 1870].

NAME-BEARING TYPE. — Lectotype (female), designated by Cupello & Vaz-de-Mello (2013: 462), MNHN (ex Henry Walter Bates and René Oberthür collections).

TYPE LOCALITY. — Brazil: Amazonas: Tefé.

ETYMOLOGY. — A New Latin first-class adjective in the nominative case meaning 'Amazonian', 'from the Amazon rainforest' (Wiktionary 2019b). A toponym after the place famously explored by H. W. Bates between 1848 and 1859 (Bates 1863; Papavero 1973), where he collected the type series and where the species is endemic.

DISTRIBUTION. — Floodplains and sandbanks of the Amazon and some of its upper tributaries and headwaters, namely the Juruá, Huallaga, Ucayali, and Pisqui Rivers, across Peru, the southern tip of Colombia, and Brazil.

Gromphas lemoinei Waterhouse, 1891

Gromphas lemoinei Waterhouse, 1891: 60 [1st July 1891].

NAME-BEARING TYPE. — Holotype by monotypy (unknown sex), NHM.

TYPE LOCALITY. — Venezuela: La Guaira: La Guaira.

ETYMOLOGY. — The masculine singular genitive of the proper noun Lemoine, a French surname meaning 'the monk' ('Le Moine'). Waterhouse (1891) did not explain after whom this eponym was formed, but I suspect it may have been the French entomologist Victor Lemoine (b. ?-1897), the only Lemoine who I found associated with entomology in the late 19th century. Alas, apart from the fact that he was based in Paris and was a pioneer in the application of radiography in the study of arthropods (Lemoine 1897), almost nothing is known about Victor Lemoine (Anonymous 1897; Constantin 2012; Groll 2016).

DISTRIBUTION. — Open savannas, pastures and river sandbanks in the Colombian and Venezuelan Llanos and associated areas.

Gromphas jardim Cupello & Vaz-de-Mello, 2015

Gromphas jardim Cupello & Vaz-de-Mello, 2015: 4 [12th October 2015; see discussion below].

NAME-BEARING TYPE. — Holotype by original designation (male), OUMNH.

TYPE LOCALITY. — Bolivia: Beni: Moxos, Río Ichiguita, 155 m, 15°08'S, 65°18'W, savanna habitat.

ETYMOLOGY. — The masculine singular nominative of the proper noun Jardim, a Portuguese surname meaning 'garden', used in apposition. It is an eponym after my beloved maternal grandfather and Brazilian airline pilot Arlindo da Silva Jardim (1923-2014), who died in the same week I realised this species was new while examining specimens at the Oxford and London museums.

DISTRIBUTION. — Open savannas, pastures and perhaps river sandbanks in the Beni Savanna of Bolivia (in the Mamoré River Basin) and the western Brazilian Cerrado (on the northern fringes of the Pantanal wetlands).

ON THE TYPE SERIES OF *GROMPHAS AERUGINOSA* (PERTY, 1830)

For our revision of *Gromphas* (Cupello & Vaz-de-Mello 2013), Vaz-de-Mello and I could examine the lectotype of *Onitis aeruginosus* Perty, 1830 (i.e., *G. aeruginosa*) only through photos provided by Michael Balke, the Coleoptera curator at the Zoologische Staatssammlung München, Munich, Germany (ZSMC), where the specimen has been housed since its arrival in Europe in the early 19th century (Scherer 1983; Cupello & Vaz-de-Mello 2013). The lectotype was designated by Scherer (1983) from a series of eight syntypes, all of which I was able to locate during a three-day visit to the ZSMC in November 2019. As originally suspected by Cupello & Vaz-de-Mello (2013), Scherer (1983), like Perty (1830) before him, mistakenly took every major specimen (i.e., those with well-developed cephalic and pronotal horns) for males and every minor one for females. His information that the type series was composed of four males and four females was consequently bound to be incorrect; in fact, there are three males (including the lectotype, as correctly sexed by Scherer

and five females. Their labels are transcribed below (italics for handwriting, slashes for line breaks). As Scherer (1983) already noted, none of the former syntypes bears original labels in Perty's handwriting, those having been replaced by printed labels by later curators (Scherer 1983).

As explained by Cupello & Vaz-de-Mello (2013), the geographical provenance pointed out by Perty (1830) for *O. aeruginosus*, the then Brazilian provinces and now states of São Paulo and Minas Gerais, is certainly wrong, as the species is exclusively Amazonian. The provenance indicated on the labels of the type specimens, 'Brasilien' or 'Brasilia', is not of great help either for it is already widely known (and, indeed, stated in the work itself) that Perty's (1830) book was based on material collected exclusively in Brazil during Johann Baptist von Spix and Karl Friedrich Philip von Martius' expedition across the country (1817-1820). But where exactly in Brazil did the naturalists find the species? Studying the itinerary of Spix and Martius' journey, especially the list of places visited by them in the Amazon, can at least limit the possibilities. In addition to other areas of Brazil, the two naturalists visited together numerous Amazonian localities along the Amazon River, from its mouth in the Atlantic Ocean upstream to Benjamin Constant, on the border of Brazil, Colombia, and Peru, as well as along the lower Madeira River (Spix & Martius 1823-1831; Papavero 1971). They also explored separately the lower c. 420 km of the Amazon's main left tributary, the Rio Negro, from Manaus to Barcelos (Spix), and the entire Brazilian extension of another mighty left tributary, the Japurá (Martius). *Gromphas aeruginosa* is abundant in many of these places (Cupello & Vaz-de-Mello 2013, 2015), and the type series, and particularly relevant for the type locality, the lectotype, can have been collected in any of them. Following Recommendation 76A.2 of the Code, I correct Perty's erroneous type locality statement ('*Habitat in mediterraneis Prov. S. Pauli et Minarum*') to 'Brazil: the Amazon rainforest, somewhere visited by Spix and Martius along the Amazon River, the Japurá, the lower Madeira, or the Rio Negro'.

TYPE MATERIAL EXAMINED. — **Lectotype** • ♂; ZSMC; designated by Scherer (1983: 298): green disk, 'Brasilien', 'Type von / *gromphas / aeruginosa / Perty*' [Hans Kulzer's handwriting], 'Type', 'alte / Sammlung', 'HOLOTYPUS / *Onitis Perty / aeruginosus / det. Dr.G.Scherer 1981*' [Scherer's handwriting], '*Gromphas / aeruginosus / (Perty) / det. G.Scherer, 1981*' [Scherer's handwriting].

Paralectotypes • ♂; ZSMC: green disk, 'Brasilien', 'alte / Sammlung' [sic; 'l' in both 'Alte' and 'Sammlung' faded], '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr.G.Scherer, 1981*' [Scherer's handwriting] • ♂; ZSMC: '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr. G.Scherer, 1981*' [Scherer's handwriting] • ♂, ZSMC: green disk, 'Brasilien', 'alte / Sammlung', '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr.G.Scherer, 1981*' [Scherer's handwriting] • ♂; ZSMC: green disk bordered in black, 'Brasilia' [unknown handwriting], 'alte / Sammlung', '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr.G.Scherer, 1981*' [Scherer's handwriting] • ♂, ZSMC: green disk bordered in black, 'alte / Sammlung', '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr.G.Scherer, 1981*' [Scherer's handwriting] • ♂; ZSMC: green disk, 'Brasilien', 'alte / Sammlung', '*Lecto- / PARATYPUS / Onitis / aeruginosus / Perty / Dr.G.Scherer, 1981*' [Scherer's handwriting] • ♂; ZSMC: '9. / *Brasilia / O. ♂ ♀ / aeruginosus / P.*' [unknown handwriting; same style as Max Gemminger's labels as shown in Scherer (1983)],

‘*Lecto-* / PARATYPUS / *Onitis / aeruginosus / Perty* / Dr.G.Scherer, 1981’ [Scherer’s handwriting].

ADDITIONAL NON-TYPE MATERIAL EXAMINED. — **Bolivia. Cochabamba** • 1 ♂; [genitalia dissected], 1 ♀; Carrasco, Puerto Villarroel, Valle Sacta; 17°07’S, 64°45’W; 230 m; 9.V.2000; M. Aliaga leg.; human faeces trap; Amazon Forest; TAMU.

Santa Cruz • 1 ♂; 1 ♀; Andrés Ibáñez, Lomas de Arena; 17°55.360’S, 63°09.637’W; 413 m; 5.XII.2008; W. D. Edmonds and T. Vidaurre leg.; human faeces; forest remnant; TAMU • 3 ♂, 3 ♀; Ichilo, Buena Vista; 380 m; XI.1971; F. Steinbach leg.; TAMU • 1 ♂; Ichilo, Buena Vista; 17°27’49”S, 63°35’58”W; 360 m; no date; W. D. Edmonds leg.; horse dung; pasture; TAMU.

Brazil. Acre • 1 ♀; Cruzeiro do Sul; VI.1952; J. Correia leg.; TAMU • 1 ♂, 3 ♀; same data as for the preceding; ex Alvarenga collection; DZUP • 1 ♀; Cruzeiro do Sul; IX.1952; J. Correia leg.; ex Alvarenga collection; DZUP • 3 ♂; Rio Branco; 15-20.XI.1961; F. M. Oliveira leg.; DZUP.

Amazonas • 2 ♂, 1 ♀; Benjamin Constant; IX.1960; L. G. Pereira leg.; DZUP • 2 ♂ [genitalia dissected], 3 ♀; Benjamin Constant; XI.1962; A. Silva leg.; TAMU • 2 ♂, 2 ♀; Borba, ‘Guajará’ (see Lack-Ximenes *et al.* [2005: 60] for a discussion on the dubious identity of this locality recorded on labels of Parko specimens); VII.1943; A. Parko leg.; ex Alvarenga collection; DZUP • 4 ♂, 5 ♀; Careiro, Janauacá; XII.1988; J. Dellone leg.; DZUP • 2 ♂, 3 ♀; Tabatinga; VII.1956; M. Alvarenga leg.; DZUP.

Pará • 1 ♂ [genitalia dissected]; Óbidos; XI.1954; J. Brazilino leg.; ex Alvarenga collection; DZUP • 3 ♀; Óbidos; VIII.1963; no collector; DZUP • 1 ♂, 1 ♀; Óbidos; 4.V.2002; Reinhard F. leg.; CAPC.

Rondônia • 1 ♂; Porto Velho; XII.1955; M. Alvarenga leg.; ex Alvarenga collection; DZUP • 1 ♂, 1 ♀; Porto Velho, Madeira River (‘*Amazonas / P. Velho – Rio / Madeira.*’); XII.1938; no collector; ex F. Justus Júnior collection; DZUP.

Peru. Loreto • 2 ♂; Maynas, Iquitos; 106 m; 1-15.V.1948; C. Bolívar leg.; at light; TAMU.

San Martín • 1 ♀; Juanjuí; 10.III.2010; M. Tafur Novda (?) leg.; CAPC • 1 ♂, 1 ♀; Juanjuí, ‘zona sur’; 7.VIII.2007; no collector; CAPC.

Ucayali • 1 ♀; Coronel Portillo, Pucallpa; 200 m; 22.VIII.1963; J. Schunke L. leg.; under pig dung; TAMU • 1 ♂, 1 ♀; Coronel Portillo, Pucallpa; 200 m; 15.IX.1963; J. Schunke L. leg.; under pig dung; TAMU • 1 ♂; Coronel Portillo, Pucallpa; 200 m; 17.IX.1963; J. Schunke L. leg.; TAMU • 1 ♂, 3 ♀; Coronel Portillo, Pucallpa; 200 m; 17.IX.1963; J. Schunke L. leg.; under pig dung; TAMU • 1 ♂; Coronel Portillo, Pucallpa; 200 m; 18.IX.1963; J. Schunke L. leg.; under cow dung; TAMU • 1 ♀; Coronel Portillo, Pucallpa; 200 m; 20.IX.1963; J. Schunke L. leg.; under cow dung; TAMU • 2 ♀; Coronel Portillo, Pucallpa; 200 m; 21.IX.1963; J. Schunke L. leg.; under cow dung; in meadow; TAMU • 2 ♀; Coronel Portillo, Pucallpa, Pueblo Aguaytia; V.2009; no collector; CAPC • 4 ♂, 5 ♀; Coronel Portillo, Pucallpa, San Lorenzo; 17-20.VII.1992; no collector; TAMU.

Erroneous data Brazil. Minas Gerais • 2 ♂; Manhumirim (‘NANHUMIRIM’ [*sic*]); 30.III.1937; Zellior leg.; DZUP.

THE TYPE SERIES OF *GROMPHAS INERMIS* HAROLD, 1869

Cupello & Vaz-de-Mello (2013) designated the lectotype of *G. inermis* from the only syntype found by them in the MNHN, but failed to illustrate it. I take the opportunity to do this here in Figure 6. Since then, I have located one of the missing paralectotypes. It belongs to the MNHN, but has been on loan to my colleague Federico Ocampo, in Argentina, since the 2000s. Many are the aspects that confirm that this specimen is indeed part of Harold’s type series. Harold (1869b)

described *G. inermis* in a work dealing specifically with the material that he had seen during a visit to the MNHN (see Cupello 2020), and the specimen bears a label identifying it in Harold’s handwriting as *G. inermis* (Fig. 7). Another label borne by the specimen, a rectangular, green one typical of South American specimens collected by Alcide d’Orbigny housed in the MNHN, reads ‘*G. aeneus, / Blanch. / Corrientes / M. D’Orbigny.*’. This *nomen in litteris* was curiously never mentioned by Blanchard (1846) in his study of the d’Orbigny South American material or anyone else in the literature except for Harold (1869b), who cited it as one of the (to use modern jargon) rejected unavailable synonyms of *G. inermis* along with ‘*G. larcordairei* Dejean’. The only way that Harold could have learnt of the existence of this name was from this label, thus making clear that he did examine this d’Orbigny specimen for the description of *G. inermis*.

TYPE MATERIAL EXAMINED. — **Lectotype** • ♂; MNHN (ex Edgar von Harold and René Oberthür collections); designated by Cupello & Vaz-de-Mello (2013: 464): “*Buen. Aires*” [Harold’s handwriting], “*inermis / Harold.*” [Harold’s handwriting], “*Ex-Musæo / E.Harold*”, “LECTOTYPE”, “MNHN, Paris / EC12059 / [QR code]”, “HØ= LØLECTOTYPE / *Gromphas / inermis / Har. / F.Z. Vaz-de-Mello 2013*” [Fernando Z. Vaz-de-Mello’s handwriting] (Fig. 6).

Paralectotype • unsexed; MNHN: green disk [obverse] / not seen, but probably aged white, stating an accession number, likely from 1834 given that it is a d’Orbigny specimen [reverse], “*G. æneus, / Blanch / Corrientes. / M. D’Orbigny.*” [unknown handwriting], “558” [unknown handwriting], “*Gromphas / inermis / Harold*” [Harold’s handwriting] (Fig. 7).

NEWLY DISCOVERED SPECIMENS OF THE RARE *GROMPHAS JARDIM* CUPELLO & VAZ-DE-MELLO, 2015

Cupello & Vaz-de-Mello (2015) described *G. jardim* based on two males and three females from Brazil and Bolivia. These specimens were originally discovered in the collections of the Natural History Museum, London (NHM), the Oxford University Museum of Natural History (OUMNH), and the Universidade Federal de Mato Grosso, Brazil (CEMT). Darren Mann, the OUMNH Coleoptera curator, allowed me to take one of the two OUMNH female paratypes for the museum where I was then based, the Museu Nacional, in Rio de Janeiro (MNRJ). Unfortunately, three years later, this paratype was destroyed. It was consumed along with c. 5 million other insects housed in the MNRJ by the great fire that devastated the main building of the institution on the evening of 2nd September 2018 (Escobar 2018). This would have meant that only four specimens are now known to exist in collections, but this is not the case. A few months earlier, in July 2018, I visited the Florida State Collection of Arthropods, in Gainesville, Florida (FSCA), and there I found a sixth specimen of this rare species, a male (Fig. 8). Then, more recently, after joining Texas A&M University as the new Assistant Curator of Entomology in October 2023, I found in the collection three more specimens, a male and two females. Altogether, rather than decreasing, the number of known specimens has risen to eight, half males, half females.

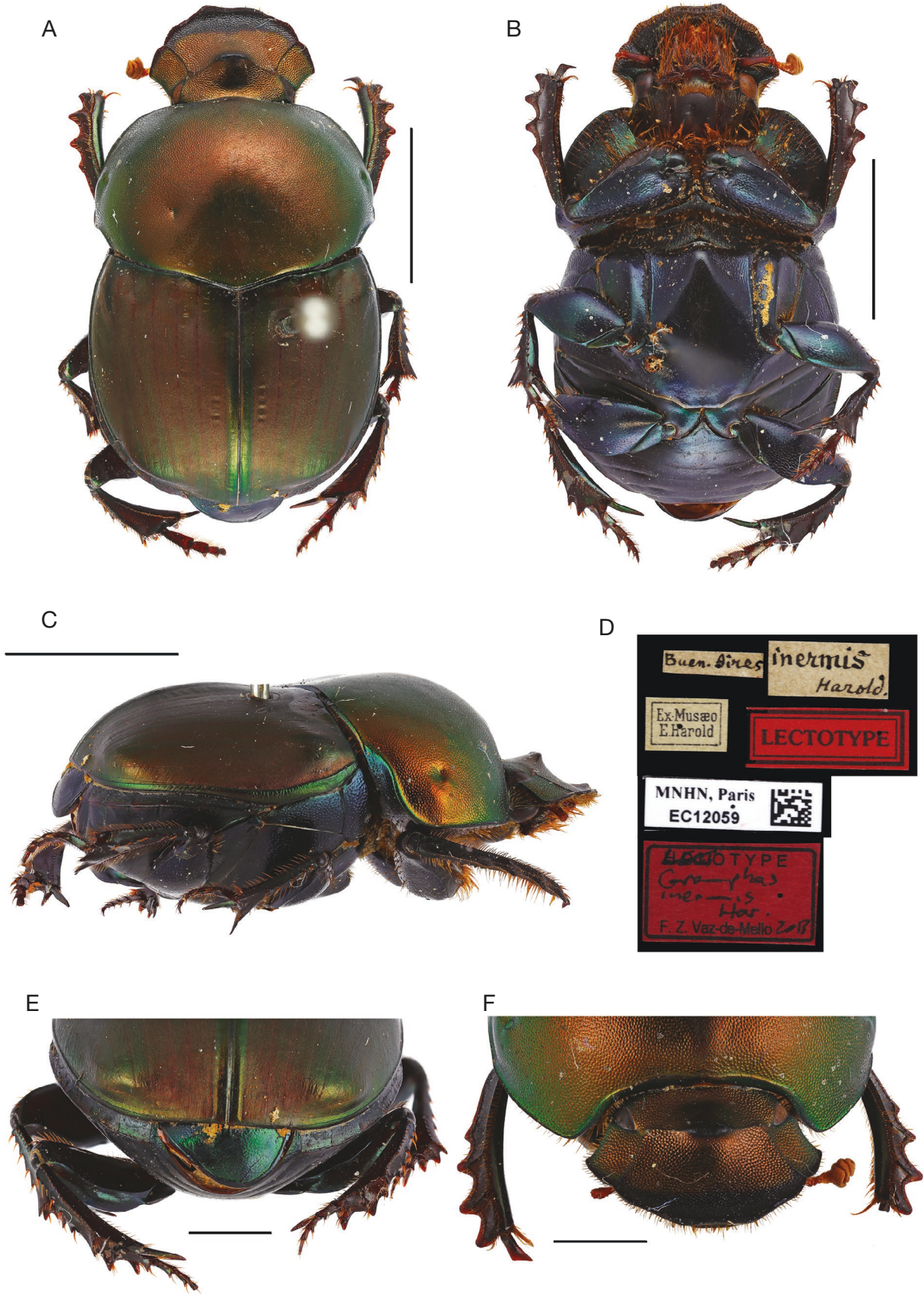


FIG. 6. — The lectotype of *Gromphas inermis* Harold, 1869, a junior subjective synonym of *G. lacordairii* (Oken, 1834): **A**, dorsal view; **B**, ventral view; **C**, lateral view; **D**, labels, note that the 'Buen. Aires' and 'inermis / Harold' labels are in Harold's handwriting; **E**, posterior view; **F**, dorsal view of the head and protibiae. Photographs courtesy of Christophe Rivier (MNHN). Scale bars: A-C: 5 mm; E, F, 2 mm.



FIG. 7. — The labels of the only known (and newly found) paralectotype of *Gromphas inermis* Harold, 1869. Notice that it is a d'Orbigny specimen from Corrientes (Argentina) and bears Blanchard's *nomen in litteris* '*G. aeneus*', which was only mentioned in the literature by Harold (1869b). The label at the top bearing the identification '*Gromphas inermis* / Harold' is in Harold's handwriting. Courtesy of Federico Ocampo.

The TAMU specimens are part of the same series as the OUMNH holotype and paratypes from Bolivia, and originally belonged to the W. D. Edmonds collection; they came to TAMU after Edmonds' material was donated to the university in 2012 (Streit 2012). As explained by Cupello & Vaz-de-Mello (2015), all these specimens were misidentified as *Gromphas lacordairii* (cited as '*lacordairei*') in Hamel-Leigues *et al.*'s (2006, 2009) study of the Bolivian scarabaeine fauna. The male from FSCA, in turn, the second oldest ever recorded for *G. jardim*, was collected in October 1951 in the town of Trinidad (Cercado, Beni, Bolivia), located only about 50 km from the type locality in San Ignacio de Moxos (Moxos, Beni). It is here addressed in the literature for the first time.

Apart from the body size of the FSCA male – it is the largest specimen so far recorded [total length: 17.2 mm (versus 16.3 mm previous maximum); length without head: 15.0 mm (vs 13); pronotal width: 10.1 mm (vs 9 mm); elytral width: 10.5 mm [not measured before]] –, the newly discovered specimens show no noticeable differences from the previously known material and fit the original description of the species well. The sexual dimorphism that Cupello & Vaz-de-Mello (2015), relying on their small original series, suspected to exist in the size and degree of impression of the posterior pronotal fossae – clearly marked and easily visible to the naked eye in males, much less marked and almost imperceptible in females even under the microscope – is also observed in this new material, suggesting that it is indeed a real sexual difference.

The four new specimens also confirm that most of the differences that Cupello & Vaz-de-Mello listed between *G. jardim* and *G. amazonica*, its sister species (Cupello & Vaz-de-Mello 2015), are indeed accurate, particularly in the shape of the cephalic projection and the apical tubercle of the protibiae, as well as the distinctions concerning colouration and the ventral carina of the protibiae (unarmed in *G. jardim*, armed with a row of sharp tubercles in *G. amazonica*). The only main character then deemed distinct between the two species that I now think does not vary in a non-overlapping way between them is the pronotal granulation. Cupello & Vaz-de-Mello (2015) said that, while in *G. jardim* the pronotal granulation, in lateral view, reaches the posterior edge of the pronotum, it is 'absent or rudimentary in [the] posterolateral region after [the] lateral fossa' in *G. amazonica*. This description is accurate enough for *G. jardim*; all known specimens, including the ones from FSCA and TAMU, have the entire lateral region of the pronotum covered with granules. But a reanalysis of the species showed that *G. amazonica* is more variable in this regard than previously considered to be. While most of the specimens are indeed smooth after the lateral fossa of the pronotum, a few may show the integument rugose and, for this reason, may be mistaken for *G. jardim* if no material of the latter is available for comparison. Therefore, I caution readers not to rely solely on this character to tell these species apart. Attention is also needed as to the way that the apical tuft of setae of the male protibiae of *G. amazonica* is described in Cupello & Vaz-de-Mello's identification key. The form described refers to large- and medium-sized individuals only; in small males, the tuft tends to be separated from the apical tubercle in a similar way as in *G. jardim* of all sizes.

ADDITIONAL MATERIAL EXAMINED. — **Bolivia. Beni** • 1 ♂; Cercado, Trinidad ('BOLIVIA - REGION / AMAZONICA / TRINIDAD'); X.1951; no collector; ex E. N. Kellesvig-Waering collection; FSCA • 1 ♀; Moxos, San Ignacio de Moxos, Río Ichiguaita; 15°08'S, 65°18'W; 155 m; 18.V.2005; C. Hamel and T. Vidaurre leg; human faeces trap, savanna; ex W. D. Edmonds collection; TAMU • 1 ♂, 1 ♀; Moxos, San Ignacio de Moxos, Río Ichiguaita; 15°08'S, 65°18'W; 155 m; 19.V.2005; C. Hamel and T. Vidaurre leg; human faeces trap, savanna; ex W. D. Edmonds collection; TAMU.

ON THE PUBLICATION DATE OF *GROMPHAS JARDIM* CUPELLO & VAZ-DE-MELLO, 2015

In a previous publication (Vaz-de-Mello & Cupello 2018a), I followed Dubois *et al.*'s (2013; 2015a, b) arguments and considered that an electronic work is only available for nomenclatural purposes once it is published with the pagination and other bibliographical information of its version issued as part of a journal's volume. For that reason, electronic-only versions of articles that are originally published with their own pagination but are later (re)issued as part of a particular volume of a journal, and, consequently, are given new pagination corresponding to the sequence of works published in that volume, were previously considered unavailable in their 'detached' versions. Nomenclatural novelties contained in



FIG. 8. — The male specimen of the rare *Gromphas jardim* Cupello & Vaz-de-Mello, 2015 newly discovered in the Florida State Collection of Arthropods, Gainesville, Florida, USA. With the destruction of one of the paratypes in the 2018 Museu Nacional fire, it is one of the eight specimens known to survive in collections. Photographs courtesy of Paul Skelley (FSCA).

them – i.e., new names and nomenclatural acts (Dubois *et al.* 2013) – would only be given availability when their volume-integrated versions finally appeared. Nevertheless, after additional thought and reading, I changed my stance on this matter.

My new rationale is that when a work is registered in ZooBank and its first electronic-only ‘detached version’ (i.e., not incorporated into a volume) is clearly intended by its journal to be a proper publication (i.e., not just a ‘preliminary version’, ‘preview’, ‘early version’, ‘uncorrected proof’), this detached version should be deemed the work where new nomenclatural novelties are given availability. In turn, the later, re-paginated version integrated into a journal’s volume should be interpreted in the same way as second printings or second editions of printed works are; i.e., not as a modified version of a previous ‘unfinished’ work, but instead as a new, independent available version of a work that is already available. The detached version with its own pagination and the one with volume pagination should, therefore, be seen as two independent available works; instead of seeing the pagination of the detached version as preliminary and the one of the volume version as definitive, it should be interpreted that the pagination in the former is definitive and the one in the latter is a new version. If this whole argument is accepted, the early electronic-only detached versions comply with Article 8.1.1 and are thus not to be deemed preliminary

versions as referred to by Articles 9.9 and 21.8.3. If they are dated, they can be interpreted as preprints as defined in the Code’s glossary. Provided that they comply with the other demands of Article 8, these preprints, i.e., the detached versions, are available publications and can be the place where nomenclatural novelties are made available.

Evidence that the journal has the intention of effectively publishing the work and not merely posting a preliminary version on its website – i.e., that the journal issued the PDF with the clear ‘purpose of providing a public and permanent scientific record’ of the content of the work (Article 8.1.1 of the Code) – will most usually and clearly come from the journal’s use of the unambiguous expression ‘published online on [date]’ or ‘published on [date]’ instead of alternatives like ‘available on-line since/from [date]’ to refer to the date when the detached version of the work was made public. Likewise, the use of the term ‘Version of Record’ (see Krell 2015) confirms the intention of permanently publishing the work, whereas terms like ‘early view’ may indicate a preliminary version and others such as ‘accepted’ certainly denotes a preliminary version.

This whole argument and my new conclusion are particularly relevant in regard to the paper published by me and Vaz-de-Mello in the *Journal of Natural History* on a new species and the phylogeny of *Gromphas*. Its electronic-only detached version was uploaded to the journal’s website on 12th October 2015,



Fig. 9. — The publication date of *Gromphas jardim* Cupello & Vaz-de-Mello, part I; **A**, the webpage of Cupello & Vaz-de-Mello’s article in the *Journal of Natural History*. Notice that the information mixes data from the detached and the volume-integrated versions. The **green arrow** points to the publication date of the detached version as indicated by the journal, 12th October 2015, whereas the **red arrow** points to the bibliographical information concerning solely the volume-integrated version published in 2016. Note also that the journal uses the expression ‘published online’ (not ‘ahead of print’, ‘early view’, or the like) to refer to the detached version, denoting that it was not considered ‘preliminary’, but a proper publication; **B**, the upper part of the first page of the PDF of the detached version. The **yellow arrow** points to the publication year of the PDF, 2015; the **white arrow** indicates the ‘article history’. Note that, while the full date, including the day and month, of the submission and acceptance are given (**white arrow**), only the year of the publication is mentioned (**yellow arrow**); **C**, the same page in the PDF of the volume-integrated version. The **pink arrow** points to the bibliographical data of this version (publication year, volume, number, and pagination), whereas the **black arrow** shows the updated ‘article history’. Observe that here, the full publication date of the detached version (‘Online’) is given. The full date of the publication of the volume-integrated edition itself, however, is not given anywhere either in the PDF or on the journal’s website. I was able to obtain the date when this version was sent to print, 15th March 2016, through direct inquiry with the publisher.

whilst its volume-integrated version was sent to print on 15th March 2016 (Henrietta Thomson, Taylor & Francis Group, personal communication, 6 February 2020). Considering that the journal uses the expression ‘published online’ to refer to its 2015 detached version (Fig. 9A) and that, according to its Editor in Chief Andrew Polaszek (personal communication, 5th February 2020), this is meant to signify that it is the definitive version of the paper (i.e., in his words, the Version of Record), I follow them and treat the 2015 detached version as definitive (i.e., not ‘preliminary’). It is, therefore, the first available work wherein the species-group name *G. jardim* Cupello & Vaz-de-Mello appeared and where it was made available. The work’s 2016 volume-integrated version is, in turn, a new edition with modified bibliographical information and no special nomenclatural relevance. In conclusion, the publication date of *G. jardim* is that of the detached version: 12th October 2015.

A similar, though not identical, proposal was put forward by ICZN Commissioner Frank-Thorsten Krell a few years ago (Krell 2015). In a few words, applying the NISO/ALPSP Recommendations, Krell sees the detached and volume-integrated versions not as a ‘first’ and a ‘second’ independently available edition of a publication as I do here, but as the very same work and, indeed, the very same version of the work, for changes in pagination and information about volume and issue (‘bibliographical metadata’) are not considered as changes in the content. Similar to my proposal, availability is gained upon the publication of what I call here the detached version provided that it is considered the Version of Record by the publisher and is not further modified without warning. I decided not to follow Krell’s exact proposal, however, because I judge that mine avoids several uncertainties associated with his. These include determining whether a journal follows the NISO/ALPSP Recommendations (e.g., do amateur or small



FIG. 10. — The publication date of *Gromphas jardim* Cupello & Vaz-de-Mello, part II; **A**, footer of the first page of the PDF of the detached version showing the Zoobank link of the article (**yellow arrow**); **B**, footer of the first page of the PDF of the volume-integrated version. Notice that, although this version was published in 2016 (and is dated as such at the upper part of the same page; see Fig. 6C), the footer is dated 2015 (**pink arrow**). The **gray arrow** shows that it is the full date of the detached version that is given in the volume-integrated version; **C**, the webpage of Cupello & Vaz-de-Mello's article in Zoobank. Note that even though the publication date stated on the website correctly refers to the detached version (**green arrow**), the information in the 'Journal Article' section is inaccurate (**red arrow**). It mixes the publication year of the detached edition ('2015') with the bibliographical information of the 2016 volume-integrated version ('50 (15-16): 943-969'). The correct pagination of the 2015 detached version – the one wherein *G. jardim* was made available – is 1-27.

museum or society journals follow them?) or whether a Version of Record has been later modified to produce a Corrected or an Enhanced Version of Record without explicit indication, in which case the original detached version becomes unavailable under Krell's guidelines but not under mine. How can one ever know – and be assured – that a Version of Record will not be later modified without warning and, thereby, make a previously available work unavailable?

Krell's proposal also creates difficulties during the preparation of lists of references and catalogues. How should one cite a work first issued as a detached version? By the pagination and publication date of this detached version or by those of the later volume-integrated version? Take the case of *G. jardim*, for instance: both versions consist of 27 pages of text (the PDF of the volume version has an additional unpaginated cover page containing basically bibliographical information), but their pagination is not the same. While the 2015 detached version is paginated [1]-27, the 2016 volume version is paginated [943]-969. The information making the name available, in particular, appears on pages 4 (information on the holotype) and 7-8 (description) of the detached version, and on pages

946 and 949-950 of the volume-integrated version. When citing the name *G. jardim* in a work, its authorship and year of publication must be given as 'Cupello & Vaz-de-Mello, 2015', for 2015 was the year when the name was made available under Krell's criteria (as well as under mine). But should the paper be dated 2015 or 2016 in the references? If 2015, then this will agree with the year of the authorship of the name as cited in the text; but which pagination to cite in the same reference? If the one of the detached version, then the volume-integrated version will essentially be ignored (just like I propose). But if, instead, the pagination of the volume-integrated version is to be cited, then it will be inconsistent with its publication date being cited as 2015, for this is not the pagination of the PDF published in 2015 (this inconsistency is present, for example, on the Zoobank webpage of Cupello & Vaz-de-Mello's article; see Fig. 10C). If, to fix this problem, one decides to cite the article in the references based entirely on the information of the volume-integrated version, including its year of publication (2016), then the inconsistency will be with the year of publication mentioned in the text for the authorship of the name (2015).

In one way or the other, considering the detached and the volume-integrated versions as the same as proposed by Krell (2015) is, as aptly pointed out by Dubois *et al.* (2015b), an artificial procedure and creates a lot of problems. Under my proposal, in contrast, the date and pagination to be cited on the list of references are unambiguous: those of the detached version, as it was there where the name was made available.

Dubois *et al.* (2015a, b) have already made similar comments and stressed the importance of page citation in taxonomic works, a claim that I fully endorse. The fact that pagination is not regulated by the Code, as Krell (2015) argued, does not make it less relevant for taxonomists and cataloguers or its stability less desirable. On the contrary, anyone who has carried out a taxonomic project, particularly the preparation of catalogues and comprehensive systematic revisions – or, to be more general, anyone who has needed to check in the original publication a quotation or specific information cited by a third author – is aware of the importance of knowing, and being able to cite, the exact and unambiguous place in a publication where a piece of information is to be found.

In contrast to Krell's (2015), my procedure, I believe, is more straightforward and in line with the way the Code and zoologists have been approaching printed publications for decades: once a work has been published in a way to satisfy the Code's criteria of availability, that version is the definitive one where new nomenclatural acts are established, no matter how many new modified versions are later reissued or whether the original version is no longer obtainable from the publisher. Concerning the latter point – *viz.*, the detached version not being publicly obtainable after being replaced by the volume-paginated version on the journal's website –, it could be argued (see, e.g., Dubois *et al.* 2015b) as a difficulty for implementing my proposal. However, if Krell is correct (and I believe he is) that the later volume-integrated versions are almost always identical to the early detached ones except for their bibliographical content (but see Dubois *et al.* 2013), then there should be no problem: in practice, these volume-integrated versions can be used as surrogates for the detached versions when these are not obtainable. Nevertheless, if Dubois is correct and many journals do produce volume-integrated versions with additional modifications, then my procedure will safeguard the availability of the early works, which would become unavailable under Krell's, and avoid the chaos of never knowing whether a work has been – or will be – made unavailable due to modifications included without warning in subsequent versions produced by the publisher.

Despite my new stance on electronic publications, I still consider Dubois *et al.*'s (2013, 2015a, b) arguments to be in most parts quite sensible, as indeed recognised by Krell (2015) himself, and should be taken into consideration by readers. I only prefer my new stance over Dubois *et al.*'s because I consider mine protects more widely the availability and priority of new names and nomenclatural acts and leaves authors less exposed to bad editorial procedures over which they are usually powerless. Under my proposal, editors have to comply with fewer requirements for a work to be available (e.g., they can produce as many modified versions as they like without

threatening the availability of the original work), and so it is easier (and faster) for new names and nomenclatural acts to be available than under Dubois *et al.*'s, and all while still respecting the principle of permanency of the zoological literature.

It must be noted that Dubois *et al.* (2013, 2015a, b) have analysed the alternative that I present here – *viz.*, to treat the detached and volume-integrated PDFs as different works and to deem them independently available –, but came to a different conclusion. While they agree with the first part of the argument – that the two versions are distinct publications, not the same as argued by Krell (2015) –, they consider that the first version, the detached version, is unavailable because, in their opinion, it fails to comply with Articles 8.1.1 and 9.9. Their point is that because the PDF of the detached version is removed from the journal's website and replaced with the volume version once the latter is published, this would indicate that the journal regarded the detached version as only preliminary and so that it did not have the 'purpose of providing a public and permanent scientific record' as demanded by Article 8.1.1. I disagree.

The term 'published', if used by the journal to refer to the detached version, clearly denotes the stated purpose of the editors and publishers that the content of this version is public, citable, and a permanent part of the scientific literature. However, if, in practice, they replace the PDF of the detached version with that of the volume-integrated version and the former thus ceases to be accessible from the journal's website, this does not deny the original intention (the purpose) behind their action. Rather, this only shows either that the editors are bona fide ignorant of the intricacies of the Code (they believe that replacing the original PDF with another nearly identical, differing only in the bibliographical data, would not interfere with the availability of the original work; i.e., it would not interfere with its original purpose of being a permanent scientific record), or that they simply disagree with Dubois *et al.*'s interpretation of what a published work is and that, in their interpretation, replacing the PDFs would not go against Article 8.1.1 (e.g., if they follow Krell's proposal). The point is not whether the PDF of the detached version remains obtainable from the journal's website or not, but rather, what the original intention of the editors was in preparing the PDF of the detached version. Article 8.1.1 does not demand a work to be permanently public, but only that it being permanently public has to be the publishers' original intention¹.

Being, in practice, permanently obtainable from the publisher has indeed never been a requirement for a work to be available or to be regarded as a permanent scientific record in zoology. For instance, is the 10th edition of *Systema Naturae* still obtainable from Lars Salvius? Of course not. It is currently only accessible through original copies in a handful of public and private libraries and a very few antique bookshops around the world, through photocopies or facsimile reproductions, or through digitised copies obtainable online from specialised websites (e.g., Biodiversity Heritage Library, Google Books). This situation is analogous to that of detached versions that have been removed from their respective journals' websites: they remain in existence only on the computers (digital library)



FIG. 11. — Newly (re)discovered specimens of the potentially extinct *Gromphas dichroa* Blanchard, 1846: **A**, labels of the holotype female and oldest known specimen, property of the Muséum national d'Histoire naturelle, Paris. It had been deemed lost in the last revision of the genus (Cupello & Vaz-de-Mello 2013). The **black arrow** indicates a label in Harold's handwriting; Harold (1869b) indeed reported the study of the specimen during his visit to the MNHN, when he confirmed that the species belongs to *Gromphas* – as originally maintained by Blanchard (1846) and Lacordaire (1855) – instead of *Bolbites* as he had previously suggested (Harold 1869a; see Cupello *et al.* 2021). Courtesy of Federico Ocampo; **B, C**, the specimen from the Institut royal des Sciences naturelles de Belgique, Brussels. Courtesy of Alain Drumont (RBINS); **D**, the four-specimen series housed in the Museu Anchieta de Ciências Naturais, Porto Alegre, Brazil. This series includes the most recently collected individual of the species, caught in Santa Catarina (Brazil) in 1954 (second from the left). Courtesy of Luísa Menezes da Silveira (MGAP).

of those who downloaded them before removal, or of those who had the PDF shared with them by colleagues, as well as in physical libraries in the form of house-made printed copies, or stored on academic social networks like *ResearchGate* or *Academia*. In all these cases, modern or old, new copies ceased to be obtainable from the original publisher.

A similar thing could also be said of many printed journals published (currently or in the past) by small amateur societies, small museums, or even privately by amateurs around the world, particularly in Europe. Anyone who has worked on the taxonomy of Coleoptera, for instance, knows how difficult it can be to obtain copies of papers published by many of these small journals. While this situation is far from desirable, rarity and difficulty of obtaining have never prevented a printed work from being available. Why should it be the case for electronic publications? Although it would undoubtedly be preferable for journals to maintain the detached version on their websites alongside the volume-integrated version, I see no reason why them failing to do so would be any different from printed works that ceased to be obtainable from the original publisher, nor why considering otherwise would be a natural (or even desirable) interpretation of the Code and its 2012 Amendment (ICZN 2012). This would only create more uncertainties. So, I disagree with Dubois *et al.* and argue for the proposal that I put forward above.

Yet, I concede that, sometimes, it can be difficult to ascertain the purpose of a detached version uploaded to a journal's website. Such ambiguity may trigger endless quarrels about the publication date of a work under the Code, and detract zoologists from the actual object of their studies, animals and their biology. It would greatly serve stability and universality in zoological nomenclature and the science of zoology overall if journals and their publishers stated fully unambiguously their intention as related to Art. 8.1.1 when posting the PDFs of works containing zoological names and new nomenclatural acts on their websites². Currently, there is nothing in the Code enforcing this. All I can do here is urge editors and publishers to expressly state on the first page of the earliest version of a work that they deem published that it has the 'purpose of providing a public and permanent scientific record'. This will prevent any doubts about the work's compliance with Art. 8.1.1 and, provided that the other criteria established in Chapter 3 of the Code are met, ensure its availability. At the same time, to solve this problem definitively in a formal way, I put forward the following proposal to the Commission: in the forthcoming 5th edition of the Code, Article 8.5.2 should be amended as follows:

8.5. Works issued and distributed electronically

To be considered published, a work issued and distributed electronically must

[...]

8.5.2. state the following sentence on its first or last page: 'This work is issued on [exact date of publication, with day, month, year] for the purpose of providing a public and permanent scientific record as established in Article 8.1.1 of the International Code of Zoological

Nomenclature and is registered in ZooBank under number [exact Zoobank registration number]'. Text between square brackets is to be replaced with information relating to the work in question.

ON SOME MISLABELLED SPECIMENS OF *GROMPHAS AMAZONICA* HOUSED IN THE BRUSSELS MUSEUM (RBINS)

While examining the collection of the Institut royal des Sciences naturelles de Belgique, Brussels (RBINS), for this work, I realised that, quite surprisingly, all the specimens of *G. amazonica* housed there either are certainly mislabelled or bear suspicious provenance data. To prevent future misunderstandings and the potential publication of erroneous geographical records, it is relevant to address these specimens here. Two males gifted along with 759 268 other insects to the RBINS in 1939 or before (one with accession number 12.595) and originating from the collection of the French insect dealer Eugène Le Moul (1882-1967) bear information saying they were collected in the municipality of Uberaba, state of Minas Gerais, in central Brazil and within the Cerrado ecoregion. A series of three males and seven females from the same gift (same accession number) are labelled as if coming from the town of Muzo, in the Colombian department of Boyacá, and within the Magdalena Valley. Finally, a male and a female, these from a lot of 26 488 insects acquired by the RBINS from J. J. Gillet on 5th October 1935 (accession number 10.640), are said to have been caught in Paraguay without further data. Since, based on trustworthy data, *G. amazonica* is known only from localities along the Huallaga, Pisqui, Ucayali, Juruá, and Amazon Rivers, in the Amazon rainforest (Cupello & Vaz-de-Mello 2013, 2015; see Fig. 5), these three records, all of which lying outside that area, are most likely incorrect.

Janssens (1940) examined the two Gillet specimens supposedly from Paraguay and considered that they indicated that *G. amazonica* is much more widely distributed than its previously thought Amazonian restriction (e.g., in Bates 1870; d'Olsoufieff 1924). In my opinion, he was wrong in accepting the label content at face value. In regard to the Muzo (Colombia) record, which could be argued to be the least improbable given the strong biotic influence from Amazonia in the Magdalena Valley, Alejandro Lopera (personal communication to MC, 7th February 2020), a specialist in the Colombian dung beetle fauna, informed me that the area near Muzo and the rest of the Magdalena River Basin 'have been well sampled, so if it were a correct location it should have been reported by now' (see, e.g., Medina *et al.* 2012). This strengthens my confidence that the Muzo record is indeed incorrect. It is noteworthy, however, that *G. aeruginosa*, the other typically Amazonian species of *Gromphas*, is known from reliable specimens to have been collected at least three times between 1979 and 1982 at a locality in the upper Magdalena Valley, the Colombian town of Gigante (Huila) (Cupello & Vaz-de-Mello 2013). Therefore, if, against my expectation, *G. amazonica* does prove to be present there, it will not be unprecedented for an Amazonian *Gromphas*.

MATERIAL EXAMINED. — **Brazil. Amapá** • 1 ♂ [genitalia dissected], 1 ♀; Macapá, BR-156, Km 14; 26.XI.1981 [in cow dung]; I. S. Gorayeb and team leg.; MPEG. — **Amazonas** • 1 ♂ [genitalia dissected]; Benjamin Constant; IX.1955; I. C. Lima leg.; ex Alvarenga collection; DZUP.

Peru. Loreto • 3 ♂ [all with genitalia dissected], 2 ♀; Ucayali, Contamana; XII.2001; no collector; TAMU. **Erroneous data: Brazil.** — **Minas Gerais** • 2 ♂ [both with genitalia dissected]; Uberaba; no further data; ex Le Moults collection (one with accession number 12.595); RBINS. — **Colombia. Boyacá** • 3 ♂ [all with genitalia dissected], 7 ♀; Occidente, Muzo; no further data; ex Le Moults collection (all with accession number 12.595); RBINS. — **Paraguay** • 1 ♂, 1 ♀; no further data; ex J. J. Gillet collection (accession number 10.640); RBINS.

NEW RELEVANT RECORDS FOR THE VANISHED *GROMPHAS DICHROA* BLANCHARD, 1846

Cupello & Vaz-de-Mello (2013, 2015) discussed the rarity of *G. dichroa* in collections. Only 9 males and 9 females were known to us apart from the missing holotype³, the lost six specimens studied by Barattini & Sáenz (1961, 1964), and the two equally lost specimens mentioned by Burmeister (1874). No individuals were known to have been caught since 1947 despite intensive collecting efforts across the species' range from southern Paraguay to the Argentinian province of Buenos Aires⁴. Even Antonio Martínez (1922-1993), who collected and studied the Argentinian dung beetle fauna so extensively through the mid- and late-20th century, never collected a *G. dichroa* or obtained a specimen caught by others after the 1940s. The same is reported by Federico Ocampo (personal communication, 21 June 2021), who has done fieldwork more recently in areas within the historical range of *G. dichroa*, including Uruguay and Buenos Aires. For these reasons, I started to wonder whether *G. dichroa* may have become extinct.

Since the publication of Cupello & Vaz-de-Mello's revision, I had the opportunity to visit several other collections in Europe and the Americas, including all the main ones in southern Brazil and Paraguay, and in just two of them did I find additional specimens of *G. dichroa*. One is the Brussels museum (RBINS), which houses a single specimen. As can be seen in Figure 11B, C, this specimen shows the bicoloured colouration pattern of the species (similar to fig. 14a of Cupello & Vaz-de-Mello 2013) and bears only two labels, neither informing where and when the specimen was collected. But this certainly happened before 1935, for the accession number '10.640' stated on one of its labels refers to material acquired on 5th October that year by the RBINS from the Belgian coleopterist Joseph Jean Edouard Gillet (1865-1937) (Alain Drumont, Coleoptera curator at RBINS, personal communication, 16th March 2020). This same specimen was mentioned five years later by Janssens (1940) in his study of the RBINS phanaeines, a work overlooked by Cupello & Vaz-de-Mello. Regrettably, I did not have time to sex the specimen during my stay in Brussels, nor did Janssens mention it in his paper.

The second collection where I found additional specimens of *G. dichroa* is that of the Museu Anchieta de Ciências Naturais, Colégio Anchieta, Porto Alegre, Brazil (MGAP). There,

I found one male and three females collected between 1928 and 1954 in the Brazilian states of Rio Grande do Sul and Santa Catarina (Fig. 11D). These data represent the most recent record for the species (seven years later than the previous most recent record from 1947) and the first report for Santa Catarina; furthermore, the Rio Grande do Sul specimen caught in Nova Petrópolis represents a new municipality record in the state. These two new records also confirm that the species at least used to occupy areas not only in the Uruguayan Savanna ecoregion (also known as the Pampas), from where most of the specimens are known, but also in the bordering southern fringe of the Atlantic Forest; whether they were caught in the rainforests themselves, in transitional areas, or in deforested farmlands is unclear. The four MGAP specimens encompass much of the colour variation shown by *G. dichroa*: both Rio Grande do Sul females have the typical bicoloured pattern of the species, with a shiny red head and pronotum and blue elytra, whereas the Itapiranga individuals show either the body entirely green (the male) or its head and pronotum red at centre and green over the lateral edges and its elytra uniformly green (the female). As discussed and illustrated by Cupello & Vaz-de-Mello (2013, 2015), this whole variation can occur within a single population, and the bicoloured pattern evolved in parallel in at least two other sympatric lineages of dung beetles, namely *Bolbites onitoides* Harold, 1868 (Cupello *et al.* 2021) and the clade formed by *Canthon lividus* Blanchard, 1846 and *C. auricollis* Redtenbacher, 1868 (Vaz-de-Mello & Cupello 2018b).

The MGAP is only one of the two museums in Porto Alegre, the capital city of the state of Rio Grande do Sul and which is (or was) part of the range of *G. dichroa*, the other being the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCNZ). While the MGAP collection grew rapidly during the first half of the 20th century, it has been mostly inert since the death of its founder, Father Pio Buck (1883-1972), and houses few specimens collected after the 1950s. It is not surprising, therefore, that no *G. dichroa* collected after that decade is held there. On the other hand, the MCNZ was founded as a separate museum only in 1954 (Nedel 2005) and owns scarabaeine material collected mostly thereafter. Its dung beetle collection is particularly rich and includes material collected all over Rio Grande do Sul, including several rare species native to the state and other regions of Brazil (personal observation in 2018). Were *G. dichroa* still living in that region, it would be expected that at least some specimens would be housed in the MCNZ. But this is not the case. Why? This becomes even more intriguing because *Gromphas lacordairii*, a closely related species (Cupello & Vaz-de-Mello 2015), is abundant both in the MGAP and in the MCZN and continues to be commonly caught throughout the region where *G. dichroa* used to be found, including specific localities such as Porto Alegre (last *G. dichroa* from 1928; last *G. lacordairii* from 1993) and the greater Buenos Aires area (1935 and 2006, respectively) (Figs 12-14; Table 1).

But despite its decades-long disappearance and my suspicion of possible extinction, I concede that no formal assessment of the conservation status of *G. dichroa* is currently possi-

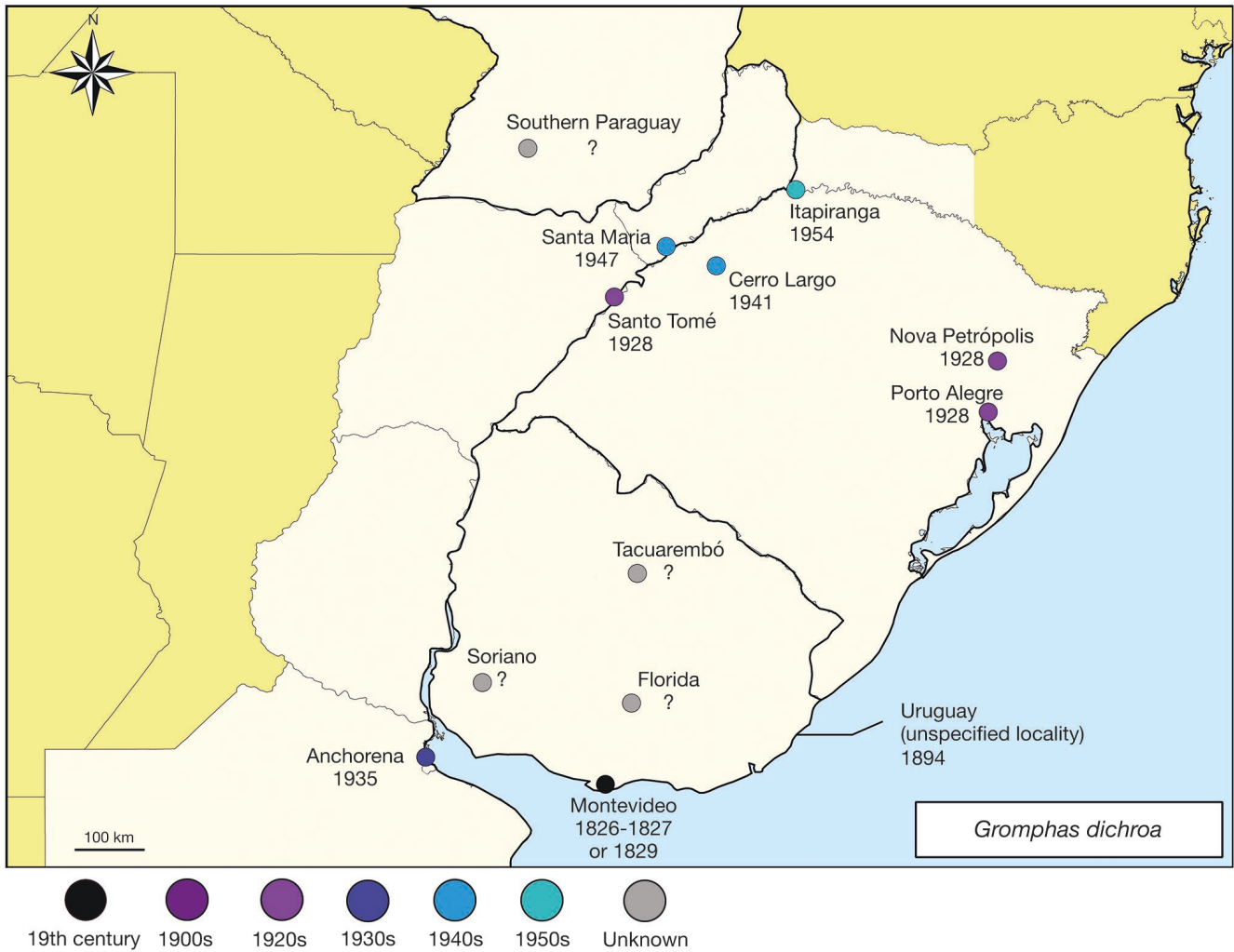


FIG. 12. — The disappearance of *Gromphas dichroa* Blanchard, 1846. The map shows the date of the last record at each known collecting point for the species. The different colours represent the decade of the last record at each locality. Notice that *G. dichroa* has not been found since the 1950s. Compare with the map for *G. lacordairii* in Figure 13. Observe, for instance, that *G. lacordairii* continues to be found even in Porto Alegre and the greater Buenos Aires area, places where *G. dichroa* was last collected in the 1920s and 1930s, respectively. Data gathered from the material examined by Cupello & Vaz-de-Mello (2013, 2015) and herein, as well as from additional records found in the literature (Blanchard 1846; Martínez 1959; Barattini & Sáenz 1961, 1964). See Table 1 for more details.

ble under the criteria set out by the IUCN Species Survival Commission (2012). At least the historical extent of its geographical occurrence, beyond 600 000 km², is way too large for any of the IUCN threatened categories (maximum of 20 000 km² for vulnerable), and nothing in terms of the species' population sizes and trends, habitat preferences, current area of occupancy, and life habits is available for a proper judgement. Formally classifying the species as 'extinct', in particular, would be, for the moment, too precipitate as *G. dichroa* does not match the IUCN's requirement of having been the special target of exhaustive surveys in all places where it is known to have been historically present as well as others where it might be expected to occur. Until these are performed using all the collecting techniques available for dung beetles (not only pitfall traps baited with excrement; see below), the species is better classified as 'data deficient'. Critical localities are those where even *G. lacordairii* has not been recorded over the last decades, for this

denotes a general lack of collection effort. These include, in Argentina, Santo Tomé (last *G. dichroa* from 1928; last *G. lacordairii* from 1926) and Santa Maria (last *G. dichroa* from 1947, no *G. lacordairii*), and, in Brazil, Cerro Largo (1941 and 1949, respectively), Nova Petrópolis (both species last recorded in 1928), and Itapiranga (*idem* in 1954). Also worthy of attention are the Campanha Gaúcha and Serras de Sudeste regions of the Brazilian state of Rio Grande do Sul. Although *G. dichroa* has never been recorded from there, these regions are apparently within its range and still encompass vast extensions of relatively pristine areas of the Pampas, particularly around the nature preserve Área de Proteção Ambiental Ibirapuitá, on the border of Brazil and Uruguay (see Souza *et al.* 2020's map). Should all these future collections be performed and, yet, *G. dichroa* continue failing to appear, then we can finally – and unfortunately – deem the species extinct. Nevertheless, if any of the localities does retrieve the species, a study of the re-discovered populations

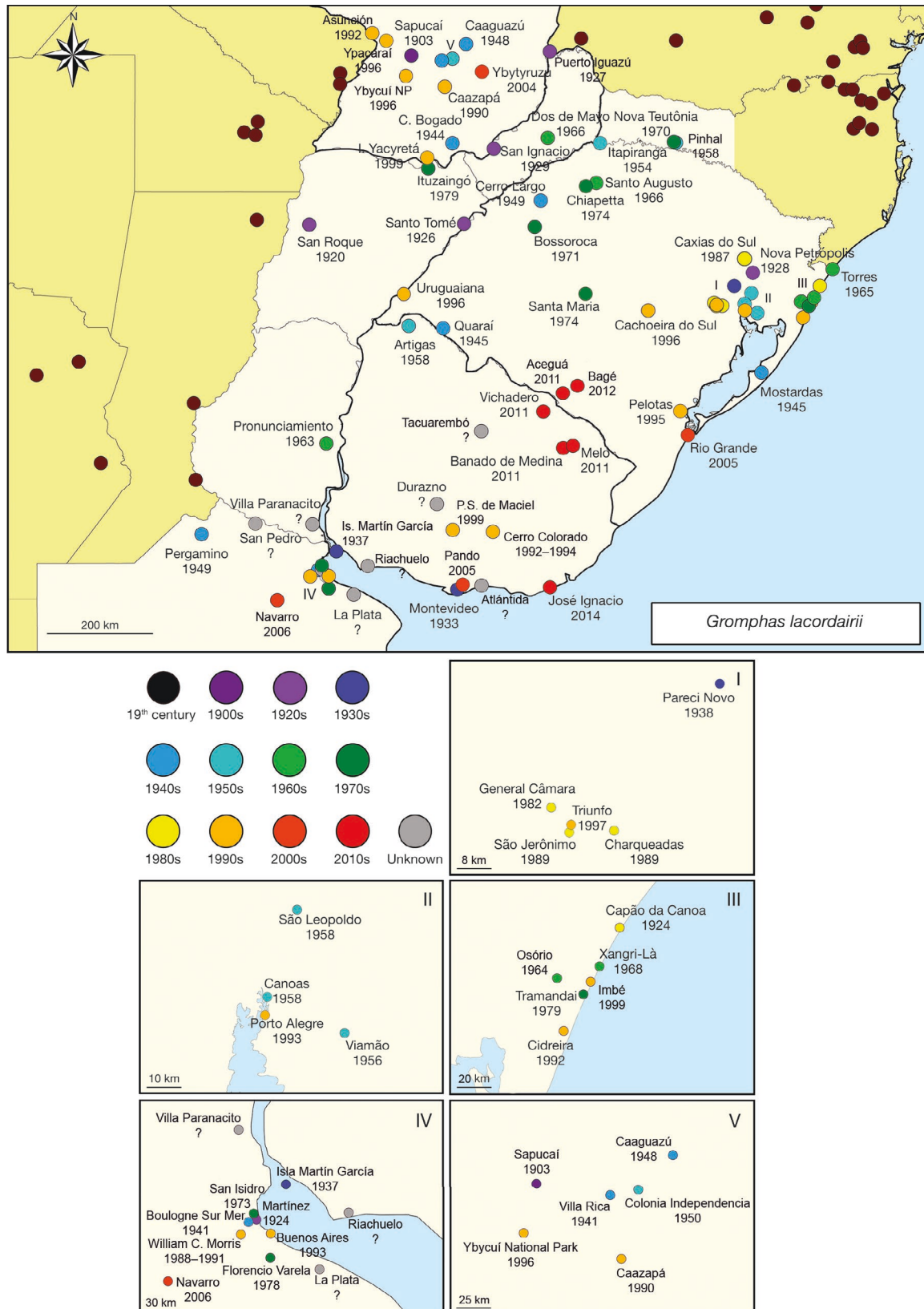


FIG. 13. — *Gromphas lacordairii* (Oken, 1834) records in the general area of occurrence of *G. dichroa*. Like Figure 12 for *G. dichroa*, this map shows the date of the last record at each known collecting point for *G. lacordairii*. The 'general area of occurrence of *G. dichroa*' (the pale yellow area on the maps) is here interpreted to include southern Paraguay, southern Brazil (Rio Grande do Sul and western Santa Catarina), northeastern Argentina (Misiones, Corrientes, Entre Ríos, the Buenos Aires city and northern and northeastern Buenos Aires province), and Uruguay. The different colours of the locality symbols represent the decade of the last record. Data gathered from the material examined by Cupello & Vaz-de-Mello (2013, 2015) and herein, as well as from additional records found in the literature (Barattini & Sáenz 1961, 1964; Cabrera-Walsh & Cordo 1997; Morelli *et al.* 2002; Sánchez & Genise 2008). See Table 1 for more details.

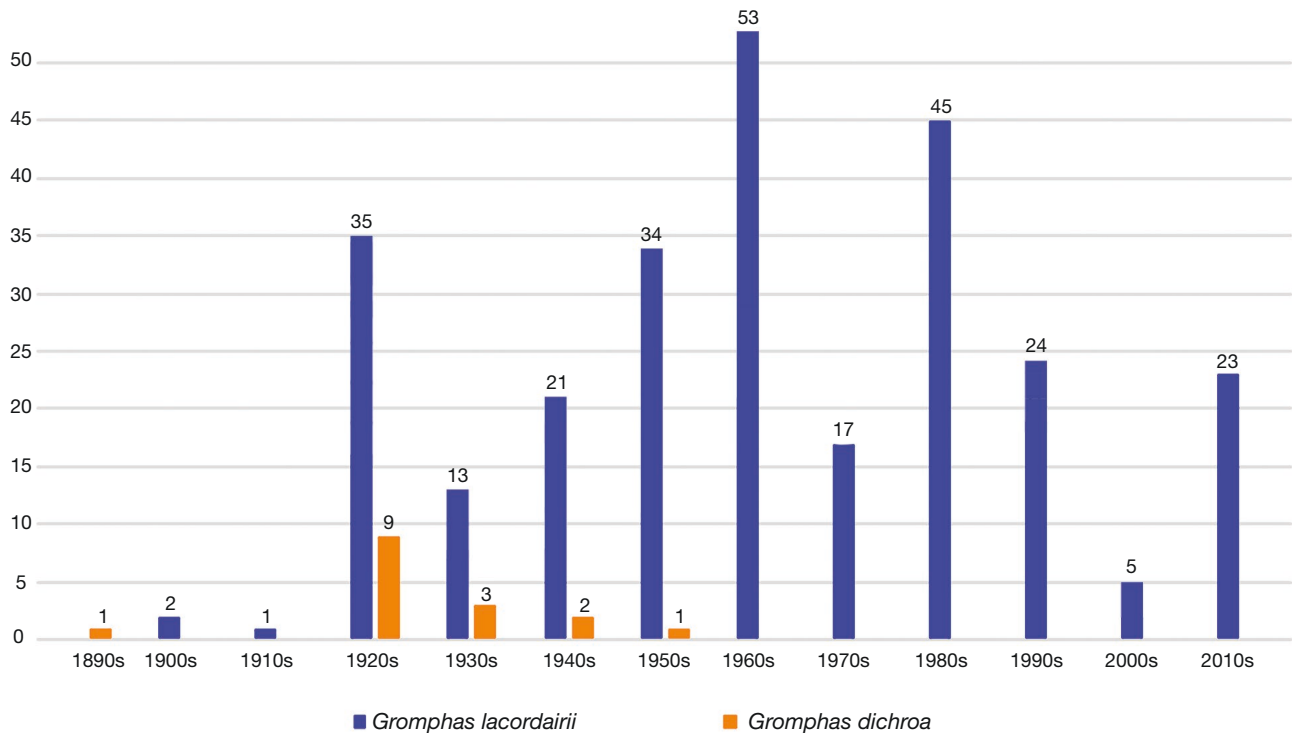


FIG. 14. — Number of specimens of *Gromphas lacordairii* (Oken, 1834) and *G. dichroa* Blanchard, 1846 collected in the 'general area of occurrence of *G. dichroa*' (see captions of Fig. 13 for explanation) in each decade since 1890 (refer to Table 1 for details. Localities in the table from personal communication with P. G. Da Silva not included here; see explanation in 'Material and Methods'). These figures indicate that although never common, *G. dichroa* was consistently collected during the first half of the 20th century. The most recent specimen, however, dates from 1954, 70 years ago (from Itapiranga, Santa Catarina). At the same time, *G. lacordairii* has always been much more common and has never ceased to be collected.

will enable a formal assignment to one of the IUCN categories. Another dung beetle species occupying much the same range as *G. dichroa*, *Anisocanthon pygmaeus* (Gillet, 1911), and which has, too, vanished since the 1950s, has also been classed as data deficient by Vaz-de-Mello *et al.* (2014). My treatment thus follows the established convention.

This prudence is indeed justified. A number of Brazilian dung beetles that, like *G. dichroa*, had vanished during the second half of the 20th century have been recently re-discovered either in new populations or in the same area where they were previously known. A representative of the latter case is *Paracryptocanthon borgmeieri* (Vulcano, Pereira & Martinez, 1976), which until recently was known from just seven females collected in the 1960s and 1970s and which was rediscovered in 2013 through the collection of a large series of specimens of both sexes at the type locality (Pacheco & Vaz-de-Mello 2017). Its almost 40-year disappearance is particularly remarkable because the species' entire range lies in the heart of the heavily collected city of Rio de Janeiro. In turn, a case of a vanished species that was later rediscovered living far from its previously known range is *Sulcophanaeus rhadamanthus* (Harold, 1875). After being known for decades from a few old specimens collected in the Serra da Mantiqueira and Serra dos Órgãos mountain ranges in southeastern Brazil (Edmonds 2000; the author does not provide precise label data of the specimens he examined, but it is likely that they were all collected before

the 1950s), this species was recently rediscovered living about 1000 km farther south in the municipality of Santa Maria in the Rio Grande do Sul state (da Silva *et al.* 2011, 2012a, 2013) and, subsequently, a little farther north in the municipality of Anitápolis, Santa Catarina state (Simões-Clivatti & Hernández 2022). These rediscoveries of long-lost dung beetles are, in fact, not limited to the Brazilian fauna, as recently shown by Deschodt *et al.* (2021) in Madagascar and Hielkema (2023) in Suriname.

But, if not extinction, what else could explain the widespread disappearance of *G. dichroa* whereas *G. lacordairii* continues to be abundant? Part of the explanation may be that the populations of *G. dichroa* have always been naturally small and sparse. The number of specimens collected before the 1950s, for example, was already much smaller than that of *G. lacordairii* (Fig. 14). Kohlmann (1991) and Price & May (2009) have shown that pairs of sympatric phanaeine species with similar body size like the *dichroa/lacordairii* pair usually differ drastically in their local relative abundance, from a ratio of *c.* 3 individuals per 7 to 1/100. A similar proportion was found by Cupello & Vaz-de-Mello (2018) for the deltochilines *Sylvicanthon seag* Cupello & Vaz-de-Mello, 2018 and *S. securus* (Schmidt, 1920) in northern Amazonia, although the exact figures vary from place to place. More impressive still, Feer (2000) observed the same phenomenon across an entire Scarabaeinae community in French Guiana. This persistent pattern may be the result of

the competitive exclusion principle (Hardin 1960). One of the competitors, being more efficient in a given context, multiplies and pushes the other to lower abundances or even complete local extinction. This in itself may already explain why *G. dichroa* has always been rarer: it is less competitive than its close ally and always sympatric *G. lacordairii*.

TABLE 1. — Number of specimens of *G. dichroa* Blanchard, 1846 and *G. lacordairii* (Oken, 1834) collected in the range of *G. dichroa* (see definition in the captions of Fig. 13). Data compiled from the material examined by Cupello & Vaz-de-Mello (2013, 2015) and herein, from information provided by colleagues (F. Ocampo and P. G. da Silva, the latter indicated by the collection abbreviations LBEV, MCCR, MCTP, MECB, MHNU, MRGC), and from additional records found in the literature (Blanchard 1846; Martínez 1959; Barattini & Sáenz 1961, 1964; Cabrera-Walsh & Cordo 1997; Morelli *et al.* 2002; Sánchez & Genise 2008; Canziani & González-Vainer 2022). **Bold** denotes places where both species have been recorded.

Country State/ Department	Locality	Date (number of specimens)
<i>Gromphas dichroa</i>		
Argentina		
Buenos Aires	Anchorena	X.1935 (1)
Corrientes	Santo Tomé	XII.1922 (1), IX.1926 (1), II.1927 (4), X.1928 (1)
Misiones	Santa Maria	XI.1947 (1)
Brazil		
Rio Grande do Sul	Cerro Largo	I.1931 (or 1933?) (1), III.1941 (1)
	Nova Petrópolis	I.1928 (1)
	Porto Alegre	X.1928 (1)
Santa Catarina	Itapiranga	XI.1934 (1), X.1954 (1)
Paraguay ?	Southern Paraguay?	? (unknown number of specimens; reference: Martínez 1959, who merely listed the species for the country. The presence of <i>G. dichroa</i> in Paraguay, either historical or present, still has to be confirmed by physical specimens or any more substantial evidence)
Uruguay		
	No specific locality	? (4), XII.1894 (1)
Florida	No specific locality	? (unknown number of specimens; reference: Barattini & Sáenz 1961, 1964)
Salto (?)		? (1)
Soriano	No specific locality	? (unknown number of specimens; reference: Barattini & Sáenz 1961, 1964)
Montevideo	Montevideo	? (1), 1826-1827 or 1829 (1; reference: Blanchard 1846; this record refers to the holotype, the sole specimen known from Montevideo. Blanchard (1846) stated that the specimen was collected by Alcide d'Orbigny (1802-1857) in Montevideo 'near the sea'. D'Orbigny stayed in Montevideo during three different periods: 1) 29th October to 17th November 1826; 2) 2nd December 1826 to 10th January 1827; and 3) 12th to 27th December 1829 (d'Orbigny 1835, 1839-1843; Papavero 1971). He may have collected the holotype in any of these three periods.)
Tacuarembó	No specific locality	? (unknown number of specimens; reference: Barattini & Sáenz 1961, 1964).
No data		1
<i>Gromphas lacordairii</i>		
Argentina		
Autonomous City of Buenos Aires	Buenos Aires city	IV.1943 (1), I.1993 (1)
Buenos Aires	'17 km south of Buenos Aires'	8.I.1980 (1)
	Boulogne Sur Mer	XI.1941 (1)
	Florencio Varela	I.1978 (1)
	Isla Martín García	IV.1937 (1)
	La Plata	? (9)
	Martínez	16.II.1924 (1)
	Navarro	2006 (6 nests; reference: Sánchez & Genise 2008)
	Pergamino	II.1949 (1)
	San Isidro	14.IV.1956 (1), XII.1967 (1), XI.1973 (1),
	San Pedro	? (1)
	William C. Morris	1988-1991 (unknown number of specimens; reference: Cabrera Walsh & Cordo [1997])
Corrientes	No specific locality	? (11)
	'5 km W Ituzaingó'	IX.1979 (1)
	Ituzaingó	III.1976 (2)
	San Roque	I.1920 (1)
	Santo Tomé	? (10), X.1925 (5), XII.1925 (1), IX.1926 (1)
Entre Ríos	No specific locality	? (2)
	Pronunciamiento	I-III.1963 (23)
	Villa Paranacito	? (1)
Misiones	No specific locality	? (15)
	Dos de Mayo	I.1966 (1)
	Puerto Iguazú	X.1927 (1)
	San Ignacio	1928-1929 (2), 21.X.1929 (1)
	Upper Paraná River	01-18.XI.1933 (1)

Table 1. — Continuation.

Brazil		
Rio Grande do Sul	No specific locality	? (5), III.1915 (1), 7.XI.1959 (1), 20.X.1961 (1), I.1995 (1)
	Aceguá	08-14.XI.2011 (7)
	Bagé	6.XII.2006 (1), 17.I.2007 (1), 07-13.I.2012 (4)
	Bossoroca	III.1971 (LBEV)
	Cachoeira do Sul	II.1996 (4)
	Canoas	3.I.1958 (MRGC)
	Capão da Canoa	22.I.1978 (1), 10.IX.1987 (MCTP), 9.X.1989 (1), 18.XI.1989 (7)
	Caxias do Sul	17.IX.1987 (MECB)
	Cerro Largo	I.1931 (1), I.1939 (1), I.1940 (10), 1949 (2), I.1949 (2)
	Charqueadas	12.I.1989 (26)
	Chiapetta	16.XI.1974 (LBEV)
	Cidreira	2.XI.1992 (4)
	General Câmara	16.IX.1982 (1)
	Imbé	II.1961 (9), II.1973 (2), 6.XI.1999 (1)
	Mostardas	I.1945 (4)
	Nova Petrópolis	28.I.? (MRGC), I.1928 (16)
	Osório	3.I.1950 (5), 24.I.1958 (9), 25.I.1958 (2), 2.II.1964 (1)
	Pareci Novo	20.X.1927 (1), VIII.1935 (1), XI.1938 (1)
	Pelotas	XII.1934 (2), I.1935 (2), XII.1935 (MHNU), 17.II.1941 (MHNU), 10.XI.1953 (1), XII.1955 (MHNU), 1959 (MCCR), 12.II.1962 (MECB), II.1963 (1), II.1968 (MECB), 2.IV.1968 (MECB), 2.I.1970 (MECB), 13.X.1975 (MECB), 16.X.1978 (MECB), 2.IX.1982 (MECB), 14.X.1983 (MECB), III.1988 (MECB), IX.1995 (MCCR), X.1995 (MCCR)
	Porto Alegre	? (1), VI.1927 (1), 16.X.1928 (1), 29.IX.1929 (1), 29.V.1934 (1), 15.XI.1935 (1), 1941 (1), 1943 (1), 25.IX.1949 (1), 3.X.1956 (1), I.1959 (3), 25.XI.1962 (MRGC), 6.XII.1962 (1), 7.X.1963 (1), 22.X.1963 (1), 1964 (1), 26.I.1965 (1), 7.II.1965 (1), 7.X.1965 (1), 26.X.1966 (1), 18.VIII.1970 (1), 8.XI.1993 (1)
	Quaraí	I.1945 (1)
	Rio Grande	26.IV.2005 (MCCR)
	Santa Maria	7.IV.1971 (LBEV), 2.II.1973 (LBEV), 23.X.1973 (LBEV), 1.X.1974 (LBEV), 30.X.1974 (LBEV)
	Santo Augusto	12.X.1966 (1)
	São Jerônimo	13.I.1989 (2), 11.I.1989 (6),
	São Leopoldo	XI.1958 (1)
	Torres	X.1956 (1), 2.II.1960 (MCTP), 9.XII.1964 (1), II.1965 (MRGC)
	Tramandaí	I.1979 (1)
	Triunfo	21.IX.1989 (1), 14-15.I.1997 (1)
	Uruguaiana	18.XII.1996 (2)
	Viamão	X.1956 (2)
	Xangri-Lá	20.I.1968 (1)
Santa Catarina	Itapiranga	IX.1953 (1), V.1954 (1)
	Seara: Nova Teutônia	25.IX.1963 (1), 23.X.1963 (1), 2.I.1964 (1), 30.I.1964 (1), I.1966 (1), II.1970 (1), XII.1970 (6)
	Seara: Pinhal	IV.1958 (1), XII.1958 (1)
Paraguay		
	Caaguazú	XII.1948 (1)
	Caazapá	01-8.XII.1990 (1)
	Capital District	IX.1922-IV.1923 (1), 12.X.1990 (1), 7.I.1991 (1), 26.II.1992 (1)
	Central	Ypacaraí 23.X.1996 (2)
	Guairá	Colonia Independencia I.1950 (1), III.1950 (1)
		Cordillera del Ybytyruzú, 24.XII.1994 (1)
		Carpa Cué
	Cordillera del Ybytyruzú, Cerro Akatí	19.II.2004 (2)
	Villarrica	X.1941 (1)
	Coronel Bogado	I.1944 (1)
	Isla Yacyretá	? (3), 14.XII.1999 (1)
	Parque Nacional Ybycuí	13.I.1996 (1)
	Sapucaí	1903 (2)
Uruguay		
	No specific locality	? (7)
	Artigas	Arroyo Tres Cruces Grande 18.I-20.II.1958 (1)
	Canelones	Atlántida ? (1)
		Campo Experimental Instituto de Higiene 10.XI.2020 (6)
	Pando	10.I.2005 (1)
	Cerro Largo	Bañado de Medina 13-20.XII.2011 (8)
		Melo 13-20.XII.2011 (2)

Table 1. — Continuation.

Colonia	No specific locality	? (1)
	Riachuelo	? (1)
Durazno	No specific locality	? (unknown number of specimens; reference: Barattini & Sáenz 1961, 1964)
Florida	Cerro Colorado	1992-1994 (44; reference: Morelli <i>et al.</i> 2002)
	Puntas de Sauce	107 (1999; reference: Canziani & González-Vainer 2022. Date of collection not stated in the paper, but year informed by Patricia González-Vainer, pers. comm., 13th September 2022)
	de Maciel	
Maldonado	No specific locality	? (unknown number of specimens; reference: Barattini & Sáenz 1961, 1964)
	10 km SW of José Ignácio	l.2014 (unknown number of specimens; reference: Federico Ocampo, pers. comm.)
Montevideo	Montevideo	? (4), 20.XII.1929 (1), 10.X.1933 (1)
Rivera	Vichadero	21-27.XI.2011 (2)
Tacuarembó	near San Gregorio de Polanco	20.X.2019 (1)

And there may be more to this. In evolutionary time, this continuous pressure from competition may eventually lead the rarer, less competitive species to niche specialisation through ecological character displacement (Brown & Wilson 1956; Pfennig & Pfennig 2009). Perhaps the competition with the presumably more efficient *G. lacordairii* drove *G. dichroa* to stenotopy. And if, in this specialisation, *G. dichroa* departed from the usual coprophagous, non-inquiline behaviour of most dung beetles, including *G. lacordairii*, maybe becoming, for example, mycetophagous or an inquiline of insect or vertebrate nests, this would explain why it has not been attracted to regular dung traps. Edmonds (2000) indeed suggested that *S. rhadamanthus*, with a body size similar to its sympatric and possibly sister species *S. menelas* (Castelnau, 1840), was rarer for possibly having such an idiosyncratic biology, and Cupello & Vaz-de-Mello (2018) made a similar suggestion to explain why *S. securus* has been collected so less frequently than *S. seag*. Perhaps this is also the case with *G. dichroa* and *G. lacordairii*. Indicating that *G. lacordairii* is indeed more eurytopic and competitive than *G. dichroa* is that it has a much broader geographical range and inhabits a more diverse set of biomes than its rarer relative (Fig. 5; Cupello & Vaz-de-Mello 2013, 2015).

But low abundance and stenotopy in themselves, while explaining rarity in the field and collections, would still leave unanswered the question of why *G. dichroa* has not been collected since the 1950s as these factors did not prevent the species from being collected before. An explanation could be that early-20th-century collectors applied collection procedures more suitable for the capture of *G. dichroa* than modern collectors do, such as the search for specimens in ant nests. Even though, judging from its morphology, *G. dichroa* does not seem to be a myrmecophilous species, we know, for instance, that the likely collector of the MGAP series, Father Pio Buck, used to search for beetles in ant nests (e.g., the type series of *Ateuchus myrmecophilus* (Boucomont, 1935) was collected by him in an *Acromyrmex lobicornis* (Emery, 1888) nest; see Boucomont 1935). It may also be that *G. dichroa* is a saprophagous species attracted to decaying fruits or fungi, and the current preferred usage of mammalian excrement and carrion as bait (e.g., Morelli *et al.* 2002; da Silva 2017; da Silva *et al.* 2008, 2009; da Silva & Di Mare

2012; Canziani & González-Vainer 2022; but see da Silva 2011; da Silva *et al.* 2012a, b, 2013; da Silva & Bogoni 2014) may have been inefficient in attracting the species. In sum, it may be that the disappearance of *G. dichroa* since the 1950s is simply the consequence of a peculiar biology (this itself a result of the competition with the more ecologically aggressive *G. lacordairii*) that keeps population densities low and spatial presence limited, coupled with the fact that modern collectors are not looking in the right places or applying the right collecting techniques that earlier naturalists, by chance or design, employed.

But having now examined all the difficulties inherent in the idea and explored its alternatives, we can at least recognise the plausibility of my initial hypothesis, extinction. If this is indeed the case, causes that could have driven *G. dichroa* to extinction are certainly multifactorial and likely included at least two of the elements discussed above, competition with sympatric species such as *G. lacordairii* and potential strict ecological specialisations. But chief among the factors is likely the negative impact of the ongoing anthropogenic conversion of habitats in southern and central South America. It may be, as briefly explored by Cupello & Vaz-de-Mello (2013), that the intense human pressure converting the forests and natural grasslands from Paraguay and southern Brazil to Argentina and Uruguay into urban space, pastures, and agricultural fields over the second half of the 20th century, particularly from the 1960s Green Revolution onwards (Roesch *et al.* 2009; Souza *et al.* 2020; Ribeiro *et al.* 2021), impacted the populations of the putatively stenotopic *G. dichroa*, and this drove a specialised and already fragile species to extinction or at least to a drastic reduction in abundance and range. *Gromphas lacordairii*, in turn, a more eurytopic and, thus, adaptable species, has not only resisted but continued to flourish. For the time being, however, the fate of *G. dichroa* will remain uncertain. Future fieldwork may, after all, rediscover the species living in some of the region's last areas of natural grasslands, wetlands, river sandbanks, floodplains, shrublands, and gallery forests, which, based on its widespread presence in the northern Pampas and the biology of congeneric species, are the candidate preferred habitats of *G. dichroa*. This would be an exciting discovery, finally allowing us to better understand the biology and conservation status of this intriguing and beautiful species.

MATERIAL EXAMINED. — *Gromphas dichroa*: **Brazil**. Rio Grande do Sul • 1 ♀; Cerro Largo; III.1941; no collector (but likely Pio Buck leg.); MGAP • 1 ♀; Nova Petrópolis; I.1928; no collector (but likely Pio Buck leg.); MGAP. — **Santa Catarina** • 1 ♀; Itapiranga; XI.1934; no collector (but likely Pio Buck leg.); MGAP • 1 ♂; Itapiranga; X.1954; no collector (but likely Pio Buck leg.); MGAP. No data: • 1 unsexed specimen; ex J. J. Gillet collection; RBINS. *Gromphas lacordairii*: **Argentina**. Autonomous City of Buenos Aires • 1 unsexed specimen; Palermo; IV.1943; no collector; ex Martínez collection; CMNC. — **Buenos Aires** • 1 ♂; Boulogne Sur Mer; XI.1941; no collector; ex Martínez collection; CMNC • 1 unsexed specimen; Florencio Varela; I.1978; Giacomozzi leg.; CMNC • 1 unsexed specimen; San Isidro; 14.IV.1956; H. J. Molinari leg.; CMNC • 1 unsexed specimen; San Isidro; XII.1967; no collector; ex Martínez collection; CMNC • 1 unsexed specimen; San Isidro; XI.1973; no collector; ex Martínez collection; CMNC. — **Chaco** • 1 ♂, 3 ♀; Presidencia de la Plaza; 26°59'S, 59°50'W; 7.X.2006; M. Damborsky leg.; TAMU. — **Corrientes** • 1 unsexed specimen; '5 km W Ituzaingó'; IX.1979; no collector; ex Martínez collection; CMNC • 2 unsexed specimens; Ituzaingó; III.1976; no collector; ex Martínez collection; CMNC. — **Entre Ríos** • 16 ♂, 7 ♀; Uruguay, Molino, Pronunciamento; I-III.1963; J. Foerster leg.; cow dung; TAMU. — **Misiones** • 1 ♀; Caingúas, Dos de Mayo; I.1966; J. Foerster leg.; carrion; TAMU. — **Salta** • 1 unsexed specimen; Embalse de Cabra Corral; 18.I.1984; Bordón leg.; ex Martínez collection; CMNC • Guachipas; I.1948; no collector; ex Martínez collection; CMNC • 1 unsexed specimen; Guachipas, Alemania; III.1973; no collector; ex Martínez collection; CMNC. — **Santiago del Estero** • 2 unsexed specimens; Río Hondo, Termas de Río Hondo; 16.II.1982; Henry Howden and Anne Howden leg.; CMNC. — **Tucumán** • 1 ♂; Yerba Buena, San Javier, 1200 m; 20.I.1970; Mielke leg.; DZUP. **Bolivia**. **Santa Cruz** • 1 unsexed specimen; Chiquitos, Roboré, Santiago de Chiquitos; XI.1959; no collector; ex Martínez collection; CMNC. — **Tarija** • 1 ♀; between Yaguacua and Caiza; 21°50'52"S, 63°36'26"W; 620 m; 3.I.2005; Mann, Hamel and Herzog leg.; horse dung; Chaco transition zone, low lying pasture, open habitat, sandy-loam; TAMU. **Brazil**. **Espírito Santo** • 4 ♂, 1 ♀; Linhares; XI.1965; A. Maller leg.; DZUP • 2 ♂; Linhares; XII.1965; A. Maller leg.; DZUP. — **Mato Grosso** • 1 ♀; Santo Antonio de Leverger; XII.1965; W. D. Edmonds leg.; meat trap; 'capoeira' vegetation; TAMU • 4 ♂ [1 with genitalia dissected], 1 ♀; Santo Antonio de Leverger; 4.XII.1965; W. D. Edmonds leg.; cattle dung; TAMU. — **Mato Grosso do Sul** • 1 ♂; Corumbá; 17.X.1961; F. M. Oliveira leg.; DZUP. — **Paraná** • 1 ♂, 1 ♀; Araucária, Barigui; V.1941; no collector; ex F. Justus Júnior collection; DZUP • 1 ♀; Curitiba; X.1961; S. Laroca leg.; DZUP • 5 ♂, 5 ♀; Curitiba; 25.I.1962; S. Laroca leg.; DZUP • 5 ♂, 5 ♀; Curitiba; 28.X.1964; Sebastião Laroca leg.; DZUP • 1 ♂, 1 ♀; Curitiba; 21.XI.1965; Mitchell and Graf leg.; DZUP • 1 ♂; Curitiba; 11.IV.1968; Gonçalves leg.; DZUP • 1 ♀; Curitiba; 900 m; 2.XI.1963; Departamento de Zoologia da Universidade Federal do Paraná leg. ('Dept. ZOO. leg.'). DZUP • 1 unsexed specimen; Curitiba, Cajuru; X.1938; Claretiano leg.; MGAP • 1 unsexed specimen; Curitiba, Parolin ('Parolim'); I.1937; Claretiano leg.; MGAP • 1 ♀; Guaira; X.1953; C. R. Leite leg.; ex Alvarenga collection; DZUP • 1 ♀; Ponta Grossa; VIII.1942; no collector; ex F. Justus Júnior collection; DZUP • 1 ♂, 3 ♀; São José dos Pinhais; 18.XI.1966; Laroca and Antoni leg.; DZUP. — **Rio de Janeiro** • 1 ♀; Duque de Caxias, São Bento ('S Bento'); XII.1954; P. A. Tâles leg.; ex Alvarenga collection; DZUP • 1 ♀; Rio de Janeiro, Botafogo; X.1957; Alvarenga leg.; ex Alvarenga collection; DZUP • 1 unsexed specimen; Rio de Janeiro, Copacabana; XII.1994; R. L. Vaz de Mello leg.; CMNC. — **Rio Grande do Sul** • 3 ♂, 1 ♀; Cachoeira do Sul; II.1996; H. Schaurich leg.; MCNZ • 1 ♂; Capão da Canoa, Curumim; 22.I.1978; C. J. Becker leg.; MCNZ • 1 ♀; Capão da Canoa; 9.X.1989; M. A. Santos leg.; MCNZ • 3 ♂, 4 ♀; Capão da Canoa; 18.XI.1989; M. A. Santos leg.; MCNZ • 1 unsexed specimen; Cerro Largo; I.1931; no collector; MGAP • 1 unsexed specimen; Cerro

Largo; I.1939; no collector; MGAP • 1 unsexed specimen; Cerro Largo; I.1940; no collector; MGAP • 2 unsexed specimens; Cerro Largo; 1949; no collector; MGAP • 2 unsexed specimens; Cerro Largo; I.1949; no collector; MGAP • 12 ♂, 14 ♀; Charqueadas, Fazenda Águas Claras; 12.I.1989; A. Ferreira leg.; MCNZ • 2 ♂, 2 ♀; Cidreira, Salinas; 2.XI.1992; Lascombe leg.; MCNZ • 1 ♂; General Câmara ('Gen Câmara'); 16.IX.1982; A. Lise leg.; MCNZ • 4 ♂, 5 ♀; Imbé; II.1961; Buckup leg.; MCNZ • 1 ♂, 1 ♀; Imbé, Santa Teresinha Beach; II.1973; M. H. Galileo leg.; MCNZ; • 1 ♂; Imbé, Santa Teresinha Beach; 6.XI.1999; L. Moura and I. Heydrich leg.; MCNZ • 3 unsexed specimens; Mostardas; I.1945; no collector; MGAP • 16 unsexed specimens; Nova Petrópolis; I.1928; no collector; MGAP • 5 unsexed specimens; Osório; 3.I.1950; no collector; MGAP • 8 unsexed specimens; Osório; 24.I.1958; no collector; MGAP • 1 unsexed specimen; Osório; 24.I.1958; Pio Buck leg.; MGAP • 1 unsexed specimen; Osório; 25.I.1958; no collector; MGAP • 1 unsexed specimen; Osório; 25.I.1958; Pio Buck leg.; MGAP • 1 ♀; Osório; 2.II.1964; P. Braun leg.; MCNZ • 1 unsexed specimen; Pareci Novo; 20.X.1927; no collector; MGAP • 1 unsexed specimen; Pareci Novo; VIII.1935; no collector; MGAP • 1 unsexed specimen; Pareci Novo; XI.1938; no collector; MGAP • 1 unsexed specimen; Pelotas; II.1963; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 16.X.1928; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 29.IX.1929; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 29.V.1934; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 15.XI.1935; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 1941; 'T. L.' leg.; MGAP; • 1 unsexed specimen; Porto Alegre; 1943; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 25.IX.1949; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 3.X.1956; no collector; MGAP • 1 ♀; Porto Alegre; 6.XII.1962; P. Braun leg.; MCNZ • 1 unsexed specimen; Porto Alegre; 7.X.1963; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 22.X.1963; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 1964; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 26.I.1965; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 7.II.1965; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 7.X.1965; no collector; MGAP • 1 unsexed specimen; Porto Alegre; 26.X.1966; no collector; MGAP • 1 ♀; Porto Alegre; 18.VIII.1970; no collector; MCNZ • 1 ♂; Porto Alegre; 8.XI.1993; V. L. C. Lascombe leg.; MCNZ • 3 unsexed specimens; Porto Alegre, Belém Novo; I.1959; no collector; MGAP • 1 unsexed specimen; Quaraí; I.1945; no collector; MGAP • 1 unsexed specimen; Santo Augusto; 12.X.1966; O. Roppa leg.; CMNC • 2 ♂; São Jerônimo, Fazenda Santa Hermenêutica; 13.I.1989; A. Ferreira leg.; MCNZ • 3 ♂, 3 ♀; São Jerônimo, Instituto Rio Grandense do Arroz ('IRGA'); 11.I.1989; on dung; A. Ferreira leg.; MCNZ • 1 unsexed specimen; São Leopoldo; XI.1958; no collector; MGAP • 1 ♂; Torres; X.1956; T. de Lema leg.; MCZN • 1 ♂; Triunfo, Braskem plant (stated on the label by its former name 'COPELUL'); 21.IX.1989; M. Hoffmann leg.; MCNZ • 1 ♀; Triunfo, Braskem plant ('COPELUL'); 14-15.I.1997; A. Franceschini leg.; MCNZ • 2 ♀; Uruguaiana, Estância Corumbá; 18.XII.1996; N. S. Macedo leg.; MCNZ • 1 ♂, 1 ♀; Viamão; X.1956; L. Buckup and E. Buckup leg.; MCNZ • 1 ♀; Xangri-Lá, Atlântida Beach; 20.I.1968; no collector; MCNZ. — **Santa Catarina** • 1 unsexed specimen; 'Emboebas' (?); 3.IV.1953; no collector; MGAP • 1 ♀; Canoinhas, Pinhal; XII.1952; A. Maller leg.; ex Campos Seabra collection; TAMU • 1 unsexed specimen; Itapiranga; IX.1953; MGPA • 1 unsexed specimen; Itapiranga; V.1954; no collector; MGAP • 1 unsexed specimen; Joinville; VI.1949; no collector; MGAP • 1 unsexed specimen; São Bento do Sul; I.1989; no collector; CMNC • 1 unsexed specimen; Seara, Nova Teutônia; 25.IX.1963; F. Plaumann leg.; CMNC • 1 unsexed specimen; Seara, Nova Teutônia; 23.X.1963; F. Plaumann leg.; CMNC • 1 unsexed specimen; Seara Nova Teutônia; 2.I.1964; F. Plaumann leg.; CMNC • 1 unsexed specimen; Seara, Nova Teutônia; 30.I.1964; F. Plaumann leg.; CMNC • 6 unsexed specimens; Seara, Nova Teutônia; XII.1970; no collector; CMNC • 1 unsexed specimen; Seara, Nova Teutônia; 300-500 m; II.1970; no collector;

CMNC • 1 ♂; Seara, Pinhal, 700 m; IV.1958; no collector; DZUP • 1 ♂; Seara, Pinhal, 700 m; XII.1958; no collector; DZUP. — **São Paulo** • 1 unsexed specimen; 'CIPO' (?); 6.II.1973; V. N. Alin leg.; CMNC • 1 unsexed specimen; 'CIPO' (?); 12.XII.1973; V. N. Alin leg.; CMNC • São Paulo, Santo Amaro ('S. Amaro'); 20.XII.1953; no collector; MGAP.

Paraguay. Alto Paraguay • 1 ♀; Puerto la Esperanza; 2.XII.2006; C. Aguilar Julio leg.; CAPC. — **Caaguazú** • 1 unsexed specimen; Caaguazú; XII.1948; F. H. Schade leg.; CMNC. — **Caazapá** • 1 unsexed specimen; Caazapá; 1-8.XII.1990; G. Arriagada leg.; CMNC. — **Capital District** • 1 ♂; Asunción; 26.II.1992; J. A. Kochalka leg.; MNHNP • 1 unsexed specimen; Asunción, Mburicaó; 12.X.1990; G. Arriagada leg.; CMNC • 1 unsexed specimen; Asunción, Mburicaó; 7.I.1991; G. Arriagada leg.; CMNC. — **Central** • 1 ♂; Ypacaraí ('1000 Mts. al E. de / YPACARAÍ'); 23.X.1996; D. Moyano leg.; CAPC • 1 ♂; Ypacaraí ('1000 Mts. al E. de / YPACARAÍ'); 23.X.1996; D. Moyano leg.; MNHNP. — **Concepción** • 1 ♀; San Lázaro, Vallemi; 26.XI.2006; C. Aguilar leg.; CAPC. — **Guairá** • 1 ♂; Cordillera del Ybytyruzú, Carpa Cué; 24.XII.1994; Aguilar leg.; MNHNP • 2 ♀; Cordillera del Ybytyruzú, Cerro Akati; 19.II.2004; no collector; CAPC • 1 unsexed specimen; Mbocayaty ('Bcayaty'); 23.IX.1946; Schade leg.; CMNC. • 1 unsexed specimen; Villarrica; X.1941; Schade leg.; CMNC. — **Itapúa** • 1 ♀; eastern portion of Isla Yacyretá, Paraná River [Butia savanna]; 14.XII.1999; J. A. Kochalka leg.; MNHNP. — **Paraguari** • 1 unsexed specimen; Parque Nacional Ybycuí; 13.I.1996; C. Aguilar J. leg.; CMNC. — **San Pedro** • 2 unsexed specimens; Cororo, Río Ypané; II.1979; no collector; Martínez leg.; CMNC • 2 ♂; Nueva Germania; 15-20.I.1992; Aguilar leg.; MNHNP.

Uruguay. Canelones • 1 ♂; Pando; 10.I.2005; no collector; CAPC • 6 unsexed specimens; Ruta 82, Km 46 500, Campo Experimental Instituto de Higiene; 10.XI.2020; unknown collector; cow dung; FCUR. — **Cerro Largo** • 1 ♀; no further locality or date; Sáenz leg.; TAMU. — **Montevideo** • 1 unsexed specimen; no further data; MGAP. — **Tacuarembó** • 1 unsexed specimen; Ruta 43, on the banks of Río Negro near San Gregorio de Polanco; 32°38'43"S, 55°47'45"W; 20.X.2019; unknown collector; cow dung; FCUR. **Likely erroneous data: Bolivia. Santa Cruz** • 1 ♀; Ichilo, Buena Vista; 380 m; XI.1968; F. Steinbach leg.; TAMU.

Unknown wild origin • 1 ♂; reared from a laboratory colony at Texas A&M University, College Station, TX, USA; summer 1981; ex G. T. Fincher collection; TAMU • 1 ♂; same data as for preceding but the date; XI.1981; ex G. T. Fincher collection; TAMU; 1 ♀ • same data as for preceding but the date; 1982; ex G. T. Fincher collection; TAMU.

No data • 2 ♂, 8 ♀; DZUP • 12 unsexed specimens; MGAP.

Acknowledgements

I am especially grateful to Patrice Bouchard for bringing to my attention Lacordaire's memoir of his South American beetle explorations and Oken's review of it. Patrice also had the interest and patience to discuss most of the nomenclatural issues addressed in this paper and to point out my mistakes. Equally appreciated is the help provided by Neal Evenhuis, Miguel Alonso-Zarazaga, and François Génier in interpreting the intricate nomenclatural problems I was dealing with, even though some of them may not agree with my conclusions. Any mistakes are naturally my own. Neal Evenhuis also kindly shared with me his unpublished dating of *Dictionnaire universel d'Histoire naturelle, Voyage dans l'Amérique méridionale*, and *Isis von Oken*. Many other colleagues assisted me in completing this work. Adriano B. Kury and Álvaro Alfredo Bragança Júnior helped me investigate the publication date and editorship of Perty's *Delectus animalium articulorum*. Luciano de Azevedo Moura sent me detailed label data of the

MCNZ *Gromphas* and illuminated my discussion on the disappearance of *G. dichroa* with some important facts about the geography of southern Brazil. Patricia González-Vainer shared information on Uruguayan populations of *G. lacordairii*. Luísa Menezes da Silveira was responsible for digitising the label data of the MGAP *G. lacordairii* and for producing Figure 11D. Paul Skelley is the author of Figure 8, and Olivier Montreuil, Antoine Mantilleri and Christophe Rivier are responsible for Figures 4, 6. Alvaro Mones, Miguel A. Monné and Walter Sosa assisted me in my ultimately fruitless search for the *G. dichroa* specimens studied by Luis Barattini and Aberlado Sáenz for their 1960s revision of the genus. Federico Ocampo was generous enough to allow me to publish data from specimens on loan to him, including the holotype of *G. dichroa*, and to cite his unpublished field notes. Alejandro Lopera confirmed my suspicion about the likely erroneous state of the Muzo record for *G. amazonica*, and Jorge A. Noriega and Juan Pablo Botero clarified some further dubious Colombian records. Stéphane Boucher and Olivier Montreuil advised me on the history of the MNHN collections, while Alain Drumont photographed the sole RBINS *G. dichroa* illustrated in Figure 11B, C and dispelled some of my doubts about Lacordaire's beetle collection. Max Barclay provided information on the possible identity of the eponymous Lemoine of C. O. Waterhouse's *Gromphas lemoinei*. Pedro Giovani da Silva allowed me to use the data of *G. lacordairii* specimens he gathered in small collections across Rio do Grande do Sul state. Finally, Andrew Polaszek (Editor in Chief, *Journal of Natural History*) and Henrietta Thomson (Taylor and Francis Group) are thanked for the information about the publication date of the online and printed versions of my JNH *Gromphas* paper. My travel to Ottawa, when I had the opportunity to meet Patrice Bouchard at the CNCI, was funded by a Canadian Museum of Nature Visiting Scientist Award, and François Génier, Robert Anderson, and Andrew Smith warmly hosted me while at the CMNC. My visits to the MNHN as well as to several other European museums were partly funded by an Ernst Mayr Travel Grant (Museum of Comparative Zoology, Harvard University, USA) and an Oxford University Museum of Natural History Visiting Fellowship. I extend my gratitude to all the curators who received me during my studies of the collections under their care. The librarians at the NHM and CNCI as well as Vinicius S. Ferreira, Alvaro Mones, Juan Pablo Botero, and the Biodiversity Heritage Library are thanked for granting me access to literature that would be otherwise unavailable. I deeply appreciate the careful reading and criticism of different parts and versions of this work by Frank-Thorsten Krell, Patrice Bouchard, Michele Rossini, Auke Hielkema, W. D. Edmonds, Juan Pablo Botero, Victor Moctezuma, Cibele S. Ribeiro-Costa, Pedro Giovani da Silva, Elie Saliba, an anonymous reviewer, and the editor Annemarie Ohler. I was funded by a PhD scholarship granted by the Brazilian *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) during the writing of the manuscript. I am further thankful to my post-doctoral supervisor, prof. Cibele S. Ribeiro-Costa, for allowing me to enjoy the facilities of the *Laboratório de Sistemática e Bioecologia de Coleoptera*, at the Federal University of Paraná.

REFERENCES

- ALONSO C. B. G., ZURITA G. A. & BELLOCQ M. I. 2019. — Live-stock areas with canopy cover sustain dung beetle diversity in the humid subtropical Chaco forest. *Insect Conservation and Diversity* 12 (4): 296-308. <https://doi.org/10.1111/icad.12340>
- ANONYMOUS 1897. — Séance du 14 avril 1897. Présidence M. A. Grouvelle. Nécrologie. *Bulletin de la Société entomologique de France* [year 1897]: [129]. <https://www.biodiversitylibrary.org/page/9210617>
- BAILLY A. 1895. — *Dictionnaire grec-français*. Hachette, Paris, 2193 p.
- BARATTINI L. P. & SÁENZ A. 1961. — Contribución al conocimiento de las especies del género *Gromphas* Brullé 1854 [sic] (Col. Scarab.). *Actas y Trabajos del Primer Congreso Sudamericano de Zoología* 3: 21-29. [publication date according to the colophon: 8th September 1961 (Alvaro Mones, personal communication, 24th April 2021)].
- BARRATTINI [sic] L. P. & SÁENZ A. 1964. — Contribution à l'étude des espèces du genre *Gromphas* (Brullé) [Col. Scarabaeidae]. *Revue française d'Entomologie* 31 (3): 173-181.
- BATES H. W. 1863. — *The Naturalist on the River Amazons, a Record of Adventures, Habits of Animals, Sketches of Brazilian and Indian Life, and Aspects of Nature under the Equator, During Eleven Years of Travel*. John Murray, London, in two volumes, Vol. 1, 351 p., Vol. 2, 423 p. <https://doi.org/10.5962/bhl.title.21335>
- BATES H. W. 1869. — [proceedings from November 1, 1869]. *Proceedings of the Entomological Society of London* [year 1869]: xix-xxiii. <https://www.biodiversitylibrary.org/page/14787693>
- BATES H. W. 1870. — On a new genus and some new species of Copridæ (Coleoptera-Lamellicornia). *The Transactions of the Entomological Society of London* 18: 173-180. [publication date for nomenclatural purposes: 30th June 1870 (dated 'June' on the article's first page; I follow Article 21.3.1 of the Code to determine the precise day of publication for nomenclatural purposes)] <https://www.biodiversitylibrary.org/page/14719377>
- BITENCOURT B. S., DIMAS T. M., DA SILVA P. G. & MORATO E. F. 2019. — Forest complexity drives dung beetle assemblages along an edge-interior gradient in the southwest Amazon rainforest. *Ecological Entomology* electronic-only detached version: 1-10. <https://doi.org/10.1111/een.12795>
- BLACKWELDER R. E. 1944. — Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America. Part 2. *United States National Museum Bulletin* 185: 189-341. <https://www.biodiversitylibrary.org/page/7876519>
- BLACKWELDER R. E. 1957. — Checklist of the coleopterous insects of Mexico, Central America, West Indies and South America. Part 6. *United States National Museum Bulletin* 185: [v]-vii, 927-1492. <https://www.biodiversitylibrary.org/page/7877283>
- BLANCHARD É. 1846. — [livraison 80: 169-184, pl. 31], in BLANCHARD É. & BRULLÉ G. A. 1835-1846. *Voyage dans L'Amérique Méridionale (le Brésil, la République orientale de L'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, par Alcide d'Orbigny. Tome Sixième. 2^e partie: Insectes*. P. Bertrand, Paris, and V^e. Lerrault, Strasbourg, 222 p. [publication date for nomenclatural purposes: 18th December 1846 (Evenhuis, personal communication, 3rd September 2019)] <https://www.biodiversitylibrary.org/page/2531073>
- BOUCHARD P., BOUSQUET Y., DAVIES A. E., ALONSO-ZARAZAGA M. A., LAWRENCE J. F., LYAL C. H. C., NEWTON A. F., REID C. A. M., SCHMITT M., ŚLIPINSKI A. & SMITH A. B. T. 2011. — Family-group names in Coleoptera (Insecta). *Zookeys* 88: 1-972. <https://doi.org/10.3897/zookeys.88.807>
- BOUCOMONT A. 1935. — Description de trois Coprides de l'Amérique du Sud. *Miscellanea Entomologica* 36 (2): 9-10.
- BOUSQUET Y. 2016. — Litteratura Coleopterologica (1758-1900): a guide to selected books related to the taxonomy of Coleoptera with publication dates and notes. *Zookeys* 583: 1-776. <https://doi.org/10.3897/zookeys.583.7084>
- BOUSQUET Y. & BOUCHARD P. 2013. — The genera in the second catalogue (1833-1836) of Dejean's Coleoptera collection. *Zookeys* 282: 1-219. <https://doi.org/10.3897/zookeys.282.4401>
- BROWN R. W. 1954. — *Composition of scientific words. A manual of methods and a lexicon of materials for the practice of logotechnics*. Smithsonian Books, Washington, D. C., 882 p. <https://archive.org/details/compositionofsci00brow>
- BROWN JR. W. L. & WILSON E. O. 1956. — Character displacement. *Systematic Zoology* 5: 49-64. <https://doi.org/10.2307/2411924>
- BRUCH C. 1911. — Catálogo sistemático de los coleópteros de la República Argentina. Pars IV. Familias Lucanidae, Scarabaeidae (Coprini-Cetonini), Passalidae. *Revista del Museo de La Plata XVII (IV)*: 181-225. <https://www.biodiversitylibrary.org/page/53896861>
- BRULLÉ A. 1838. — [livraison 8: p. 225-448], in BRULLÉ A. 1837-1838. *Histoire naturelle des insectes, traitant de leur organisation et de leurs moeurs en général, par M. V. Audouin, et comprenant leur classification et la description des espèces, par M. A. Brullé. Le tout accompagné de planches gravées sur acier, d'après des peintures exécutées pour cette édition sur la collection du Muséum de Paris. Tome VI. Coléoptères III*. F. D. Pillot, Paris, 448 p. + pls. 18, 19, 19bis, 20, 25 [publication date for nomenclatural purposes: 31st of December 1838 (based on Bousquet 2016)] <https://www.biodiversitylibrary.org/page/25546370>
- BURMEISTER H. 1874. — Lamellicornia Argentina. *Entomologische Zeitung* 35: 120-133. [publication date for nomenclatural purposes: 30th June 1874 (based on the range 'April-Juni' provided at the end of the volume on page 444)] <https://www.biodiversitylibrary.org/page/9236010>
- CABRERA-WALSH G. & CORDO H. A. 1997. — Coprophilous arthropod community from Argentina with species of potential use as biocontrol agents against pest flies. *Environmental Entomology* 26 (2): 191-200. <https://doi.org/10.1093/ee/26.2.191>
- CAJAIBA R. L., PÉRICO E., DALZOCCHIO M. S., DA SILVA W. B., BASTOS R., CABRAL J. A. & SANTOS M. 2017. — Does the composition of Scarabaeidae (Coleoptera) communities reflect the extent of land use changes in the Brazilian Amazon? *Ecological Indicators* 74: 285-294. <https://doi.org/10.1016/j.ecolind.2016.11.018>
- CAMBEFORT Y. 2006. — *Des coléoptères, des collections et des hommes*. Paris, Muséum national d'Histoire naturelle, 2006, 375 p. (Archives ; 10).
- CANDEZE [E. C. A.] 1872. — Notice sur J.-Théodore Lacordaire, associé de l'Académie, né à Recey-sur-Ource (France) le 1^{er} février 1801, mort à Liège le 18 juillet 1871. *Annuaire de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 38: unpagéd [Lacordaire's engraving] + [139]-160.
- CANZIANI C. & GONZÁLEZ-VAINER P. 2022. — Structure and composition of dung beetle assemblages (Coleoptera: Scarabaeidae) in a livestock ranch in central Uruguay: Responses of functional groups and species to local habitats and trophic resources. *The Coleopterists Bulletin* 76 (3): 407-418. <https://doi.org/10.1649/0010-065X-76.3.407>
- CONSTANTIN R. 2012. — Mémorial des coléoptéristes français. Retirage de décembre 2012. *Bulletin de Liaison de l'Association des Coléoptéristes de la Région Parisienne* 14 (supplement): [1]-[116].
- CUPELLO M. 2013. — Case 3612. *Onitis aeruginosus* Klug, 1855 (Insecta, Coleoptera, Scarabaeidae): proposed conservation of the specific name. *Bulletin of Zoological Nomenclature* 70: 15-18. <https://doi.org/10.21805/bzn.v70i1.a4>
- CUPELLO M. 2020. — The discovery of Edgar von Harold type material in the Museum of Zoology, Dresden. *Scarabaeus* 1: 15-24.
- CUPELLO M. & VAZ-DE-MELLO F. Z. 2013. — Taxonomic revision of the South American dung beetle genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini: Gromphadina). *Zootaxa* 3722 (4): 439-482. <https://doi.org/10.11646/zootaxa.3722.4.2>

- CUPELLO M. & VAZ-DE-MELLO F. Z. 2014. — Correction of the type species of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Zootaxa* 3790 (2): 399-400. <https://doi.org/10.11646/zootaxa.3790.2.7>
- CUPELLO M. & VAZ-DE-MELLO F. Z. 2015. — A new species and the phylogeny of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Journal of Natural History* electronic-only detached version: 1-27. [publication data for nomenclatural purposes: 12th October 2015 (information available at the journal's website: <https://doi.org/10.1080/00222933.2015.1091099>)] [volume-integrated version published in 2016 – on or after 15th March, the day it was sent to print (Henrietta Thomson, Taylor & Francis Group, personal communication to MC, 6th February 2020) –, as volume 50 (15-16): 943-969] <https://doi.org/10.1080/00222933.2015.1091099>
- CUPELLO M. & VAZ-DE-MELLO F. Z. 2018. — A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), with a reappraisal of the taxonomic history of '*Canthon sensu lato*'. *European Journal of Taxonomy* 467: 1-205. <https://doi.org/10.5852/ejt.2018.467>
- CUPELLO M., RIBEIRO-COSTA C.S. & VAZ-DE-MELLO F. Z. 2021. — The evolution of *Bolbites onitoides* (Coleoptera: Scarabaeidae: Phanaeini): its phylogenetic significance, geographical polychromatism and the subspecies problem. *Zoological Journal of the Linnean Society* electronic-only detached version: 1-62 [volume-integrated version published in March 2022, volume 194 (3): 973-1034.] <https://doi.org/10.1093/zoolinnean/zlab015>
- CUPELLO M., IANNUZZI L. & VAZ-DE-MELLO F. Z. 2022. — On the authorship of *Canthon rutilans cyanescens* 'Harold, 1868' (Coleoptera, Scarabaeidae, Scarabaeinae, Deltochilini): the treatment of varieties and *nomina nuda* by a 19th-century zoologist. *Bionomina* 27: 67-87. <https://doi.org/10.11646/bionomina.27.1.4>
- DAMBORSKY M. P., BOHLÉ M. C. A., POLESEL M. G. I., PORCEL E. A. & FONTANA J. L. 2015. — Spatial and temporal variation of dung beetle assemblages in a fragmented landscape at eastern humid chaco. *Neotropical Entomology* 44: 30-39. <https://doi.org/10.1007/s13744-014-0257-2>
- DEJEAN P. F. M. A. 1821. — *Catalogue de la collection de coléoptères de M. le Baron Dejean*. Crevot, Paris, I-VIII + 136 p. + 2 p. [errata] [publication date for nomenclatural purposes: 12th May 1821 (see Bousquet 2016)] <https://doi.org/10.5962/bhl.title.11259>
- DEJEAN P. F. M. A. 1833. — [livraison 2: 97-176], in Dejean P. F. M. A. 1833-1836. *Catalogue des Coléoptères de la collection de M. le Comte Dejean*. Méquignon-Marvis Père et Fils, Paris, 443 p. [publication date for nomenclatural purposes: 27th July 1833 (see Bousquet 2016)] <https://doi.org/10.5962/bhl.title.8771>
- DEJEAN P. F. M. A. 1836. — [livraisons 1-4: 1-384], in DEJEAN P. F. M. A. 1836-1837. *Catalogue des Coléoptères de la collection de M. le Comte Dejean. Troisième édition, revue, corrigée et augmentée*. Méquignon-Marvis Père et Fils, Paris, v-xiv + 503 p. [publication date for nomenclatural purposes: 30th July 1836 (see Bousquet 2016)]
- DESCHODT C. M., HARRISON J. G. & SOLE C. L. 2021. — Rediscovery of *Scarabaeus sevoistra* Alluaud, 1902 (Coleoptera: Scarabaeinae): biological notes and IUCN Red Listing. *Bothalia* 51 (2): 113-119. https://hdl.handle.net/10520/ejc-bothalia_v51_n2_a10
- DUBOIS A., CROCHET P.-A., DICKINSON E. C., NEMÉSIO A., AESCHT E., BAUER A. M., BLAGODEROV V., BOUR R., DE CARVALHO M. R., DESUTTER-GRANDCOLAS L., FRÉTEY T., JÄGER P., KOYAMBA V., LAVILLA E. O., LÖBL I., LOUCHART A., MALÉCOT V., SCHATZ H. & OHLER A. 2013. — Nomenclatural and taxonomic problems related to the electronic publication of new nomina and nomenclatural acts in zoology, with brief comments on optical discs and on the situation in botany. *Zootaxa* 3735: 1-94. <https://doi.org/10.11646/zootaxa.3735.1.1>
- DUBOIS A. 2000. — Synonymies and related lists in zoology: General proposals, with examples in herpetology. *Dumerilia* 4 (2): 33-98.
- DUBOIS A., BOUR R. & OHLER A. 2015a. — What is an online 'preliminary version' of a publication in the meaning of Article 9.9 of the Code? – One more step on the trail of the Asian elephant. *Bulletin of Zoological Nomenclature* 72 (1): 6-18. <https://doi.org/10.21805/bzn.v72i1.a13>
- DUBOIS A., BOUR R. & OHLER A. 2015b. — Nomenclatural availability of preliminary electronic versions of taxonomic papers: in need of a clear definition. *Bulletin of Zoological Nomenclature* 72 (3): 252-265. <https://doi.org/10.21805/bzn.v72i3.a1>
- ECKER A. 1883. — *Lorenz Oken, a biographical sketch. Or 'in memoriam' of the centenary of his birth read before the fifty-second meeting of the German Association for the Advancement of Science at Baden-Baden, September 20, 1879. With explanatory notes selections from Oken's correspondence and a portrait of the professor*. Kegan Paul, Trench & Co., London, xxiv + 183 + 47 p.
- EDMONDS W. D. 2000. — Revision of the Neotropical dung beetle genus *Sulcophanaeus* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Heyrovskyana, Supplementum* 6: 1-60.
- ESCOBAR H. 2018. — In a 'foretold tragedy', fire consumes Brazil museum. *Science* 361 (6406): 960. <https://doi.org/10.1126/science.361.6406.960>
- EVENHUIS N. L. 1997a. — *Litteratura taxonomica dipterorum (1758-1930). Vol. I. A-K*. Backhuys, Leiden, 426 p.
- EVENHUIS N. L. 1997b. — *Litteratura taxonomica dipterorum (1758-1930). Volume II. L-Z*. Backhuys, Leiden: 427-871.
- EVENHUIS N. L. 2003. — Publication and dating of the journals forming the *Annals and Magazine of Natural History* and the *Journal of Natural History*. *Zootaxa* 385: 1-68. <https://doi.org/10.11646/zootaxa.385.1.1>
- EVENHUIS N. L. 2015. — [dating of] Berliner Entomologische Zeitschrift (1857-1876). Available online at: <http://hbs.bishopmuseum.org/dating/berlentzeit.html> (last accessed on 4th February 2020)
- FEER F. 2000. — Les coléoptères coprophages et nécrophages (Scarabaeidae s. str. et Aphodiidae) de la forêt de Guyane Française: Composition spécifique et structure des peuplements. *Annales de la Société Entomologique de France (N. S.)* 36 (1): 29-43.
- GAHAN C. J. & ARROW G. J. 1903. — List of the Coleoptera collected by Mr. A. Robert at Chapada, Matto Grosso (Percy Sladen Expedition to Central Brazil). *Proceedings of the Zoological Society of London* 1903 (2): 244-258.
- GAMEZ J. & ACCONCIA R. 2018. — Escarabajos coprófagos y necrófagos (Scarabaeidae: Scarabaeinae: Phanaeini) del flanco andino llanero, piedemonte y llanos, con el reporte de nuevos registros para los estados de Barinas y Mérida (Venezuela). *Revista Gaditana de Entomología* 9 (1): 65-75.
- GLARE P. G. W. (ED.) 1968-1982. — *Oxford Latin Dictionary*. Clarendon Press, Oxford, xxiii + 2126 p.
- GIACHINO P. M. 1982. — *Cataloghi III – Collezione Coleotterologica di Massimiliano Spinola*. Museo Regionale di Scienze Naturali, Turin, 616 p.
- GILLET J. J. E. 1911. — *Coleopterorum Catalogus. Pars 38: Scarabaeidae: Coprinae I*. W. Junk, Berlin, 100 p.
- GROLL E. K. 2016. — Lemoine, Victor, in ANONYMOUS (ed.) *Biographies of the entomologists of the world*. Available online at: <https://sdei.senckenberg.de/biographies/>
- HAMEL-LEIGUE A. C., MANN D. J., VAZ-DE-MELLO F. Z. & HERZOG S. K. 2006. — Hacia un inventario de los escarabajos peloterós (Coleoptera: Scarabaeidae) de Bolivia: primera compilación de los géneros y especies registrados para el país. *Revista Boliviana de Ecología y Conservación Ambiental* 20: 1-18.
- HAMEL-LEIGUE A. C., HERZOG S. K., MANN D. J., LARSEN T. H., GILL B. D., EDMONDS W. D. & SPECTOR S. 2009. — Distribución e historia natural de escarabajos coprófagos de la tribu Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae) en Bolivia. *Kempffiana* 5 (2): 43-95.
- HARDIN G. 1960. — The competitive exclusion principle. *Science* 131: 1292-1297. <https://doi.org/10.1126/science.131.3409.1292>

- HAROLD E. 1859. — Beiträge zur Kenntnis einiger coprophagen Lamellicornien. *Berliner Entomologische Zeitschrift* 3: [193]-224. [publication date for nomenclatural purposes: 31st December 1859 (based on Evenhuis 2015)] <https://www.biodiversitylibrary.org/page/9204087>
- HAROLD E. 1869a. — *Catalogus coleopterorum. Hucusque descriptorum, synonymicus et systematicus. Tom. IV. Scarabaeidae*. E. H. Gummi, Munich: 979-1346 + [8]. [publication date for nomenclatural purposes: 27th May 1969 (based on Bousquet 2016)] <https://www.biodiversitylibrary.org/page/9641549>
- HAROLD E. 1969b. — Ueber coprophage Lamellicornien mit besonderer Berücksichtigung der Pariser Sammlungen. *Coleopterologische Hefte* 5: [46]-70. [publication date for nomenclatural purposes: 1st November 1869. This dating is based on the November 1st record by Bates (1869) in the *Proceedings of the Entomological Society of London* of the donation to the society by Edgar von Harold of the fifth volume of *Coleopterologische Hefte*. This donation likely occurred at some point between July and November 1869, as the previous proceedings date from 5th July 1869 (Smith 1869). Had Harold donated the fifth volume of *Coleopterologische Hefte* before July, the volume would have probably been recorded in the 'additions to the library' section of the July proceedings rather than the one from November.] <https://www.biodiversitylibrary.org/page/16069721>
- HEYNE A. & TASCHENBERG O. 1908. — *Die exotischen Käfer in Wort und Bild*. Verlag von J. F. Schreiber, Esslingen and Munich, 262 p. + I-L p. + 39 plates.
- HIELKEMA A. 2023. — Leaf litter deposits in spiny palms: A hideout for "rare" scarabs? *Scarabaeus* 3: 3-6.
- HORN W., KAHLE I., FRIESE G. & GAEDIKE R. 1990a. — *Collectiones entomologicae. Ein Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960. Teil I: A bis K*. Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, Berlin: 1-220.
- HORN W., KAHLE I., FRIESE G. & GAEDIKE R. 1990b. — *Collectiones entomologicae. Ein Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960. Teil II: L bis Z*. Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, Berlin: 221-573.
- JACK-XIMENES G. E., DE VIVO M., PERCEQUILLO A. R. 2005. — A new species of *Echimys* Cuvier, 1809 (Rodentia, Echimyidae) from Brazil. *Papeis Avulsos de Zoologia* 45 (5): 51-60. <https://doi.org/10.1590/S0031-10492005000500001>
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. — *International code of zoological nomenclature. Fourth edition adopted by the International Union of Biological Sciences*. International Trust for Zoological Nomenclature, London, 306 p. <https://www.iczn.org/the-code/the-code-online/>
- IUCN SPECIES SURVIVAL COMMISSION. 2012. — *IUCN Red List categories and criteria. Version 3.1. Second Edition*. International Union for Conservation of Nature, Gland, iv + 32 p. <https://portals.iucn.org/library/node/10315>
- JANSSENS A. 1940. — Contribution à l'Étude des Coléoptères lamellicornes coprophages. II. — Remarques sur quelques Phanaeides. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 16 (34): 1-7.
- JUDULIEN F. 1899. — Quelques notes sur plusieurs coprophages de Buenos Aires. *Revista del Museo de La Plata* 9: 371-380. <https://www.biodiversitylibrary.org/page/9644378>
- KERTESZ G. A. 1986. — Notes on *Isis von Oken*, 1817-1848. *Isis* 77 (3): 497-503. <https://doi.org/10.1086/354208>
- KOHLMANN B. 1991. — Dung beetles in subtropical North America, in HANSKI I. & CAMBEFORT Y. (eds) *Dung beetle ecology*. Princeton University Press, Princeton: 116-132.
- KRELL F.-T. 2015. — A mixed bag: when are early online publications available for nomenclatural purposes? *Bulletin of Zoological Nomenclature* 72 (1): 19-32. <https://doi.org/10.21805/bzn.v72i1.a14>
- KURY A. B., MENDES A. C., CARDOSO L., KURY M. S. & GRANADO A. A. 2020. — *World Catalogue of Opiliones. WCO-Lite: Online world catalogue of harvestmen (Arachnidae, Opiliones). Version 1.0 – Checklist of all valid nomina in Opiliones with authors and dates of publication up to 2018*. Adriano B. Kury, Rio de Janeiro, [ii] + 237 p.
- LACORDAIRE J. T. 1830. — Mémoire sur les habitudes des Insectes Coléoptères de l'Amérique méridionale. *Annales des Sciences naturelles* 20: 185-291. <https://www.biodiversitylibrary.org/page/6069943>
- LACORDAIRE J. T. 1855. — *Histoire naturelle des insectes. Genera des coléoptères, ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome troisième*. Librairie Encyclopédique de Roret, Paris, 594 p. [publication date for nomenclatural purposes: 29th October 1855 (see Bousquet 2016); publication date of plate 27 depicting '*Gromphas lacordairei* Blanch.' is unclear and may have been different from the corresponding text. Here, for the sake of simplicity, I have accepted that both were published together.] <https://www.biodiversitylibrary.org/page/9612631>
- LEMOINE [V.] 1897. — Sur l'application des rayons Roentgen à l'étude des Articulés. *Bulletin de la Société Entomologique de France* [year 1897]: 87-89. <https://www.biodiversitylibrary.org/page/9210571>
- LEWIS C. T. & SHORT C. 1891. — *Harpers' Latin dictionary. A new Latin dictionary founded on the translation of Freund's Latin-German lexicon edited by E. A. Andrews, LL. D. Revised, enlarged, and in great part rewritten*. Harper & Brothers, Franklin Square, New York, and Clarendon Press, Oxford, xiv + [2019] p.
- LIDDELL H. G. & SCOTT R. 1897. — *A Greek-English lexicon. Revised and augmented throughout with the cooperation of professor Drisler, of Columbia College, New York. Eighth Edition*. Harper & Brothers, New York, New York, xvi + 1778 p.
- MADGE R. B. 1988. — The publication dates of Dejean's catalogues. *Archives of Natural History* 15 (3): 317-321.
- MALDANER M. E., CUPELLO M., FERREIRA D. C. & VAZ-DE-MELLO F. Z. 2017. — Type specimens and names assigned to *Coprophanaeus (Megaphanaeus)* d'Olsoufieff, 1924, the largest New World dung beetles (Coleoptera: Scarabaeidae: Phanaeini). *Zootaxa* 4272 (1): 83-102. <https://doi.org/10.11646/zootaxa.4272.1.4>
- MARTÍNEZ A. 1959. — Catálogo de los Scarabaeidae Argentinos. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas* 5: 1-126.
- MAYR E. 1969. — *Principles of systematic zoology*. McGraw-Hill, New York, New York, xi + 428 p.
- MAYR E. & ASHLOCK P. D. 1991. — *Principles of systematic zoology. Second edition*. McGraw-Hill, New York, New York, and various other cities, xx + 475 p.
- MAYR E., LINSLEY E. G. & USINGER R. L. 1953. — *Methods and principles of systematic zoology*. McGraw-Hill Book Company, New York, New York, Toronto and London, 328 p.
- MEDINA C. A. C., MEDINA-URIBE C. A., QUINTERO B. G. M., ESCOBAR-VILLA A. F., CHUAIRE L. M. C. & POSADA N. J. B. 2012. — *Escarabajos coprófagos (Scarabaeinae) del eje cafetero: Guía para el estudio ecológico*. Anonymous editor, Villa María, 196 p.
- MONNÉ M. A. 2005. — Catalogue of the Cerambycidae (Coleoptera) of the Neotropical region. Part II. Subfamily Lamiinae. *Zootaxa* 1023: 1-760. <https://doi.org/10.11646/zootaxa.1023.1.1>
- MORELLI E., GONZALEZ-VAINER P. & BAZ A. 2002. — Coprophagous beetles (Coleoptera: Scarabaeoidea) in Uruguayan prairies: abundance, diversity and seasonal occurrence. *Studies on Neotropical Fauna and Environment* 37 (1): 53-57.
- NEDEL L. B. 2005. — Breviário de um museu mutante. *Horizontes Antropológicos* 11 (2): 87-112. <https://doi.org/10.1590/S0104-71832005000100006>
- NORIEGA J. A., SANTOS A. M. C., CALATAYUD J., CHOZAS S. & HORTAL J. 2021. — Short- and long-term temporal changes in the assemblage structure of Amazonian dung beetles. *Oecologia* 195: 719-736. <https://doi.org/10.1007/s00442-020-04831-5>
- [OKEN L.] 1834. — J. Th. Lacordaire, über die Lebensweise der Käfer im mittäglichen America. Viele Käfer namentlich angeführt.

- Isis von Oken* [volume for the year 1834] (11): 1112-1127. [The authorship of this review is not stated expressly anywhere, as far as I could find, but the context makes clear that the journal's editor, Lorenz Oken (1779-1851), the famous German naturalist of the *Naturphilosophie* movement, was the one who wrote it and the other literature reviews that appeared in the journal. For this reason, Oken should be credited with its authorship under Article 50.1 of the Code. In Cupello *et al.* (2022), we conservatively treated the review as published anonymously, but this seems unjustified. Kertész (1986) tells the details of the history of *Isis von Oken* and confirms that Oken was the one who prepared the literature reviews] [publication date for nomenclatural purposes: 30th November 1834. Neal Evenhuis (personal communication, 26th January 2023) confirmed that *Isis von Oken* appeared in monthly issues. Oken's review of Lacordaire's paper appeared in the 11th issue of 1834, therefore, in November of that year, with no more specific date known to me. Following Article 21.3.1, I take the last day of that month as the publication date]. <https://www.biodiversitylibrary.org/page/27510335>
- D'OLSOUFIEFF G. 1924. — Les Phanaeides (Coleoptera – Lamellicornia), famille Scarabaeidae – tr. Coprini. *Insecta* 13: 4-201. [publication date for nomenclatural purposes: 31st December 1924 (no more precise date than the year was found)]
- D'ORBIGNY A. 1835. — *Voyage dans l'Amérique Méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, par Alcide d'Orbigny. Tome Premier. Partie Historique du voyage dans l'Amérique Méridionale.* Pitois-Levrault et C.e, Paris, and V.e Lerrault, Strasbourg, 672 p. [publication date for nomenclatural purposes: 31st December 1835. Taken in part from the title page, which states only the year, 1835; day and moth determined by Article 21.3.2 of the Code.] <https://www.biodiversitylibrary.org/page/49209075>
- D'ORBIGNY A. 1839-1843. — *Voyage dans l'Amérique Méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, par Alcide d'Orbigny. Tome Deuxième. Partie Historique.* P. Bertrand, Paris, and V.e Lerrault, Strasbourg, 667 p. [publication date taken from the title page; no more precise or reliable dating was found in the specialised literature] <https://www.biodiversitylibrary.org/page/45472755>
- PACHECO T. L. & VAZ-DE-MELLO F. Z. 2017. — Rediscovery of the Neotropical genus *Paracryptocanthon* Howden & Cook, 2002 (Coleoptera: Scarabaeidae: Scarabaeinae) in the Brazilian Atlantic Forest. *Annales de la Société Entomologique de France (N. S.)* electronic-only detached version: 1-7 [publication date for nomenclatural purposes: 11th April 2017 (from the journal's website)] [volume-integrated version published in 2017, volume 53 (2): 99-105.] <https://doi.org/10.1080/00379271.2017.1308809>
- PAPAVERO N. 1971. — *Essays on the history of Neotropical dipterology, with special reference to collectors (1750-1905). Vol. I.* Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil, 216 p. <https://doi.org/10.5962/bhl.title.101715>
- PAPAVERO N. 1973. — *Essays on the history of Neotropical dipterology, with special reference to collectors (1750-1905). Vol. II.* Museu de Zoologia, Universidade de São Paulo, São Paulo, i-iii + [217]-444 p. <https://doi.org/10.5962/bhl.title.101597>
- PAPAVERO N. 1994. — Rudimentos de latim, in PAPAVERO N. (ed.). *Fundamentos práticos de taxonomia zoológica (coleções, bibliografia, nomenclatura).* Editora Unesp, São Paulo:121-150.
- PERTY J. A. M. 1830. — *Insecta Brasiliensia:* 1-60, pls. 1-12, in PERTY J. A. M. 1830-1833. *Delectus animalium articulatum, quae in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto collegerunt Dr. J. B. de Spix et Dr. C. F. Ph. de Martius.* C. F. P. von Martius, Munich ['Monachii'], iii + 44 p. + 224 p. + 40 pls. [publication date for nomenclatural purposes: 31st December 1830 (cf. Sherborn 1922; Evenhuis 1997b; Bouchard *et al.* 2011; Bousquet 2016). The colophon on page 224 is dated 13th December 1833 ('Idibus Decembris MDCCCXXXIII'), but this date must refer only to the printing of the last livraison, not being valid for the publication date of the first livraison where *Onitis aeruginosus* was given availability and which, consequently, concerns us here. The editorship of this book is also disputed. The several individuals and their cities listed by Evenhuis (1997b) as editors were, in fact, purely booksellers, not editors in the sense of those who underwrote the costs of publication, as defined by Bousquet (2016). The one cited by Bouchard *et al.* (2011) and Kury *et al.* (2020), Friedrich Fleischer, as far as I could find, is mentioned only on the 1834 title page as the bookseller in Leipzig, and is also probably incorrect as the editor. Other important works citing Perty's book have simply omitted the editor altogether (e.g., Sherborn 1922; Blackwelder 1957; Scherer 1983; Monné 2005; Bousquet 2016). In my opinion, however, there is no doubt that Carl Friedrich Philipp von Martius (1794-1868) was the editor of this book. The 1834 title page, besides saying that the book was produced at the 'editor's expenses' ('IMPENSIS EDITORIS'), bears the information 'praefatus est et edidit Carol. Frideric. Philip. de Martius' below the title, making it clear the true identity of the person who financed the production of the book, edited it, and was thus ultimately responsible for its publication.] <https://www.biodiversitylibrary.org/page/57932830>
- PFENNIG K. S. & PFENNIG D. W. 2009. — Character displacement: ecological and reproductive responses to a common evolutionary problem. *Quarterly Review of Biology* 84 (3): 253-276. <https://doi.org/10.1086/605079>
- PREUDHOMME-DE-BORRE A. 1886. — Liste des Lamellicornes Laparostictiques recueillis par feu Camille van Volxem pendant son voyage au Brésil et à La Plata en 1872 suivie de la description de dix huit espèces nouvelles et un genre nouveau. *Annales de la Société entomologique de Belgique* 30: [103]-120. <https://www.biodiversitylibrary.org/page/12278849>
- PRICE D. L. & MAY M. L. 2009. — Behavioral ecology of *Phanaeus* dung beetles (Coleoptera: Scarabaeidae): review and new observations. *Acta Zoológica Mexicana (N. S.)* 25 (1): 211-238. https://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S0065-17372009000100022
- RIBEIRO S., MOREIRA L. F. B., OVERBECK G. E. & MALTCHIK L. 2021. — Protected areas of the Pampa biome presented land use incompatible with conservation purposes. *Journal of Land Use Science* 16 (3): 260-272. <https://doi.org/10.1080/1747423X.2021.1934134>
- ROESCH L. F. W., VIEIRA F. C. B., PEREIRA V. A., SCHÜNEMANN A. L., TEIXEIRA I. F., SENNA A. J. T. & STEFENON V. M. 2009 — The Brazilian Pampa: A fragile biome. *Diversity* 1: 182-198. <https://doi.org/10.3390/d1020182>
- SÁNCHEZ M. V. & GENISE J. F. 2008. — Nest and brood chamber structure of two South American dung beetles: *Gromphas lacordairei* Brullé and *Ontherus sulcator* (Fabricius) (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* 62 (1): 49-61. <https://doi.org/10.1649/986.1>
- SCHERER G. 1983. — Die von J. B. v. Spix und C. F. Ph. v. Martius in Südamerika gesammelten Coleopteren. *Spixiana* 9: 295-305.
- SHERBORN C. D. 1922. — *Index animalium sive index nominum quae ab A. D. MDCCCLVIII generibus et speciebus animalium imposita sunt societatis eruditorum adiuvantibus. Sectio secunda. A kalendis ianuariis, MDCCCL usque ad finem Decembris, MDCCCL. Part I. Introduction, bibliography and index A-Aff:* 1-128. 1801-1850. The Trustees of the British Museum, London, cxxxi + 128 p. <https://www.biodiversitylibrary.org/page/36191976>
- DA SILVA P. G. 2011. — Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of two non-native habitats in Bagé, Rio Grande do Sul, Brazil. *Zoological Studies* 50 (5): 546-559.

- DA SILVA P. G. 2017. — Dung beetles (Coleoptera, Scarabaeinae) from high-altitude grasslands in São Joaquim National Park, Santa Catarina, southern Brazil. *Check List* 13 (6): 817-830. <https://doi.org/10.15560/13.6.817>
- DA SILVA P. G., AUDINO L. D., NOGUEIRA J. M., DE MORAES L. P. & VAZ-DE-MELLO F. Z. 2012b. — Escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) de uma área de campo nativo no bioma pampa, Rio Grande do Sul, Brasil. *Biota Neotropica* 12 (3): [1]-8. <https://doi.org/10.1590/S1676-06032012000300024>
- DA SILVA P. G. & BOGONI J. A. 2014. — Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) attracted to rotten eggs in the Atlantic Forest in subtropical southern Brazil. *The Coleopterists Bulletin* 68 (2): 339-342. <https://doi.org/10.1649/0010-065X-68.2.339>
- DA SILVA P. G. & DI MARE R. A. 2012. — Escarabeíneos copro-necrófagos (Coleoptera, Scarabaeidae, Scarabaeinae) de fragmentos de Mata Atlântica em Silveira Martins, Rio Grande do Sul, Brasil. *Iheringia, Série Zoologia* 102 (2): 197-205. <https://doi.org/10.1590/S0073-47212012000200012>
- DA SILVA P. G., GARCIA M. A. R. & VIDAL M. B. 2008. — Besouros copro-necrófagos (Coleoptera: Scarabaeidae *stricto sensu*) coletados em ecótono natural de campo e mata em Bagé, RS. *Ciência e Natura, UFSM* 30 (2): 71-91. <https://doi.org/10.5902/2179460X9839>
- DA SILVA P. G., GARCIA M. A. R. & VIDAL M. B. 2009. — Besouros copro-necrófagos (Coleoptera: Scarabaeidae *sensu stricto*) do município de Bagé, RS (bioma campos sulinos). *Biociências* 17 (1): 33-43.
- DA SILVA P. G., VAZ-DE-MELLO F. Z. & DI MARE R. A. 2011. — Guia de identificação das espécies de Scarabaeinae (Coleoptera: Scarabaeidae) do município de Santa Maria, Rio Grande do Sul, Brasil. *Biota Neotropica* 11 (4): 329-345. <https://doi.org/10.1590/S1676-06032011000400027>
- DA SILVA P. G., VAZ-DE-MELLO F. Z. & DI MARE R. A. 2012a. — Attractiveness of different bait to the Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in extreme southern Brazil. *Zoological Studies* 51 (4): 429-441.
- DA SILVA P. G., VAZ-DE-MELLO F. Z. & DI MARE R. C. 2013. — Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências* 85 (2): 679-697. <https://doi.org/10.1590/S0001-37652013005000033>
- SIMÕES-CLIVATTI T. R. O. & HERNÁNDEZ M. I. M. 2022. — Ecological indication metrics on dung beetles metacommunities in native forests and *Pinus* monocultures. *Frontiers in Ecology and Evolution* 10:972176: 1-13. <https://doi.org/10.3389/fevo.2022.972176>
- SMITH A. B. T. 2006. — A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. *Coleopterists Society Monograph* 5: 144-204. <https://digitalcommons.unl.edu/entomologypapers/122/>
- SMITH A. Z. 1986. — *A history of the Hope Entomological Collections in the University Museum, Oxford, with lists of archives and collections*. Clarendon Press, Oxford, xiii + 172 p.
- SMITH F. 1869. — [proceedings from July 5, 1869]. *Proceedings of the Entomological Society of London* [year 1869]: xvi-xviii. <https://www.biodiversitylibrary.org/page/14787690>
- SMITH H. M. & SMITH R. B. 1972. — Chresonymy ex synonymy. *Systematic Zoology* 21 (4): 445. <https://doi.org/10.1093/sysbio/21.4.445>
- SOUZA JR. C. N., SHIMBO J. Z., ROSA M. R., PARENTE L. L., ALENCAR A. A., RUDORFF B. F. T., HASENACK H., MATSUMOTO M., FERREIRA L. G., SOUZA-FILHO P. W. M., DE OLIVEIRA S. W., ROCHA W. F., FONSECA A. V., MARQUES C. B., DINIZ C. G., COSTA D., MONTEIRO D., ROSA E. R., VÉLEZ-MARTIN E., WEBER E. J., LENTI F. E. B., PATERNOST F. F., PAREYN F. G. C., SIQUEIRA J. V., VIERA J. L., NETO L. C. F., SARAIVA M. M., SALES M. H., SALGADO M. P. G., VASCONCELOS R., GALANO S., MESQUITA V. V. & AZEVEDO T. 2020. — Reconstructing three decades of land use and land cover changes in Brazilian biomes with landsat archive and earth engine. *Remote Sensing* 12 (2735): [1]-27. <https://doi.org/10.3390/rs12172735>
- SPIX J. B. VON & MARTIUS C. F. P. VON. 1823. — *Reise in Brasilien auf Befehl Sr. Majestät Maximilian Joseph I. Königs von Baiern in den Jahren 1817 bis 1820 gemacht und beschrieben. Erster Theil*. Anonymous editor, Munich, x + 412 p. <https://www.biodiversitylibrary.org/page/28880206>
- SPIX J. B. VON & MARTIUS C. F. P. VON. 1828. — *Reise in Brasilien auf Befehl Sr. Majestät Maximilian Joseph I. Königs von Baiern in den Jahren 1817 bis 1820 gemacht und beschrieben. Zweiter Theil*. C. F. P. von Martius, Munich, viii + [413]-884. <https://www.biodiversitylibrary.org/page/28862211>
- SPIX J. B. VON & MARTIUS C. F. P. VON. 1831. — *Reise in Brasilien auf Befehl Sr. Majestät Maximilian Joseph I. Königs von Baiern in den Jahren 1817 bis 1820 gemacht und beschrieben. Dritter und letzter Theil*. C. F. P. von Martius, Munich, viii + [885]-1388 + 40 p. <https://www.biodiversitylibrary.org/page/28885488>
- STREIT B. 2012. Edmonds Phanaeini collection donated to Texas A&M. *Scarabs* 70: 14-15.
- STURM J. 1843. — *Catalog der Kaefer-Sammlung von Jacob Sturm*. Privately published, Nuremberg [Nürnberg], III-XII + 386 p. + pl. I-VI. [publication date for nomenclatural purposes: 27th July 1843 (see Bousquet 2016)] <https://doi.org/10.5962/bhl.title.37837>
- TREMOLERAS J. 1910. — Coleopterologische Skizze von Uruguay. *Entomologische Blätter* 6: 22-28, 39-41. <https://www.biodiversitylibrary.org/page/33946292>
- UCHOA M. A. & RODRIGUES M. M. 2019. — Dung beetles (Coleoptera: Scarabaeoidea) population patterns in three environments in the Midwest of Brazil. *EntomoBrasilis* 12 (1): 19-26. <https://doi.org/10.12741/ebrazilis.v12i1.825>
- VAZ-DE-MELLO F. Z. & CUPELLO M. 2018a. — The type specimens of South American dung beetles. Part I: On the species described in the genus *Canthon* Hoffmannsegg, 1817 by the German entomologist Adolf Schmidt (1856-1923). *Spixiana* 41 (1): 33-76.
- VAZ-DE-MELLO F. Z. & CUPELLO M. 2018b. — The type specimens of South American dung beetles, Part II: The species described by the Austrian coleopterist Ludwig Redtenbacher (1814-1876) in the 1868 part of the 'Reise der österreichischen Fregatte Novara um die Erde' (Insecta: Coleoptera, Scarabaeidae, Scarabaeinae). *Annalen des Naturhistorischen Museums in Wien, B* 120: 42-58.
- VAZ-DE-MELLO F., LARSEN T., SILVA F., GILL B., SPECTOR S. & FAVILA M. 2014. — *Anisocanthon pygmaeus*. The IUCN Red List of Threatened Species 2014: e.T137106A520010. Available online at: <https://doi.org/10.2305/IUCN.UK.2014-1.RLTS.T137106A520010.en>. (last accessed on 28th January 2023).
- WATERHOUSE C. O. 1891. — New Scarabaeidae in the British Museum: a fifth contribution. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology, Sixth Series* 8 (43): 53-61. [publication date for nomenclatural purposes: 1st July 1891 (Evenhuis 2003)] <https://www.biodiversitylibrary.org/page/19244729>
- WIKTIONARY 2019a. — *punctatus*. Available online at: <https://en.wiktionary.org/wiki/punctatus> (last accessed on 23rd May 2023).
- WIKTIONARY 2019b. — *amazonicus*. Available online at: <https://en.wiktionary.org/wiki/amazonicus> (last accessed on 23rd May 2023).
- WIKTIONARY 2022. — *dichrous*. Available online at: <https://en.wiktionary.org/wiki/dichrous> (last accessed on 23rd May 2023).
- WIKTIONARY 2023a. — *di-*. Available online at: https://en.wiktionary.org/wiki/%CE%B4%CE%B9-#Ancient_Greek (last accessed on 23rd May 2023).
- WIKTIONARY 2023b. — *-us*. Available online at: <https://en.wiktionary.org/wiki/-us#Latin> (last accessed on 23rd May 2023).

Submitted on 11 April 2023;
accepted on 26 July 2023;
published on 9 February 2024.

ENDNOTES

1. — Article 16.4.2 provides another, even clearer example in which it is the author's intention, not the actual materialisation of this intention, that determines availability. In this Article, the Code rules that, for a new species-group name published after 1999 to be available, authors must state their intention that the name-bearing types, if extant, are or will be deposited in a collection. This need not actually happen, however. A name whose holotype is a living specimen will not become unavailable if its holotype eventually dies in the wild and fails to end up in a collection. Provided that this was not what the authors originally intended – i.e., if their original vision was that the living holotype would eventually be caught and deposited in a collection –, and that the authors stated in the original description their original intention, then the name will remain available regardless of what actually happens to the holotype.

2. — I say zoological names overall, and not only new names, because the presence of names in available works is relevant for nomenclatural aspects beyond simply establishment of availability, such as defining prevailing usage and reversal of precedence as governed by Art. 23.9.

3. — For our revision of *Gromphas*, Cupello & Vaz-de-Mello (2013, 2015) searched without success for the holotype of *Gromphas dichroa* in the dung beetle collection of the MNHN, where the d'Orbigny South American material, of which the specimen is part, is mostly housed (Horn *et al.* 1990b; but

see Cupello & Vaz-de-Mello 2015). Not finding it there, we deemed the holotype lost. When I was writing this paper, however, I recalled that Federico Ocampo had mentioned to me in an email exchange in early 2012 that he had planned during the 2000s to revise *Gromphas*, but that, eventually, I took over independently the project and he aborted the idea. Recalling this, the suspicion grew in me that Ocampo might have borrowed the holotype from the MNHN during the 2000s and that it could still be with him. I contacted him in June 2021 and he kindly confirmed that this is indeed the case. The holotype, as stated by Blanchard (1846), is a female and bears the labels shown in Fig. 10A.

4. — The presence in Paraguay is still speculative. The only reason I mention the country here is Martínez's (1959) record of Paraguay along with Uruguay and the Argentinian provinces of Buenos Aires and Corrientes as composing the range of *G. dichroa*. The basis for this record was, however, not explained. Since I found no Paraguayan *G. dichroa* in the Martínez collection material at the CMNC or elsewhere, I suspect that this was either a lapse, a guess from the other places where the species was known to occur, or *in litteris* information from Paraguayan collectors. If the record is real, it most likely refers to the savannas, wetlands, or gallery forests of the Humid Chaco of southern Paraguay, given its proximity to the areas in southern Brazil and northeastern Argentina where the species was confirmedly caught.