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Phylogeny of the cleptoparasitic bee genus *Exaerete* (Hymenoptera: Apidae)*

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Abstract – Relationships among the species of *Exaerete* Hoffmannsegg (Apinae: Euglossini) were explored based on new morphological data and including new taxa described since the study of Engel (Am. Mus. Novit. 3272, 1–14, 1999). Analysis of the data matrix was undertaken in NONA using the *WinClada* interface and resulted in a single topology of length 39, CI 0.66, RI 0.78. Three principal clades were identified in the genus, resulting in interrelationships among the species as: (((*E. smaragdina* + (*E. frontalis* + *E. lepeletieri*)) + ((*E. trochanterica* + *E. guaykuru*) + (*E. azteca* + *E. dentata*))). Biogeographic patterns are briefly discussed in light of the recovered phylogeny and *Exaerete lepeletieri* Oliveira & Nemésio is newly considered a synonym of *E. frontalis* (Guérin-Méneville).

cleptoparasitism / Euglossini / orchid bees / phylogeny / *Exaerete* / biogeography

1. INTRODUCTION

Species of the tribe Euglossini are frequently robust, brightly colored bees commonly referred to as orchid bees owing to the collection of fragrant oils from flowers of Orchidaceae. The tribe comprises five genera, two of which are cleptoparasitic on other orchid bees – *Aglae* Lepeletier de Saint Fargeau and Audinet-Serville and *Exaerete* Hoffmannsegg. The former genus is monotypic, although significant variation exists across the large range of the species and more

than one taxon may ultimately be recognized (Engel, unpubl. data). *Exaerete* presently includes seven species, ranging from southern Mexico to northern Argentina (Anjos-Silva and Rebêlo, 2006). All species are brilliant metallic green, blue-green, or purple and range in size from 18 to 28 mm in total length (Fig. 1). Aside from the usual suite of parasitic features, the genus can be most readily recognized by the strongly dentate metafemora and the convex mesoscutellum (not flattened and bladelike as in *Aglae*) bearing sublateral welts. *Exaerete* victimize the nests of species in the genera *Eulaema* and *Eufriesea* (e.g., Zucchi et al., 1969; Bennett, 1972; Pereira-Martins, 1991; Garófalo and Rozen, 2001).

The first attempt at elucidating the phylogeny of *Exaerete* was undertaken by Engel (1999) in combination with a study of the relationships among genera of Euglossini. That study included five species – two species were discovered and described subsequent to

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An appendix is available online at
<http://www.apidologie.org>

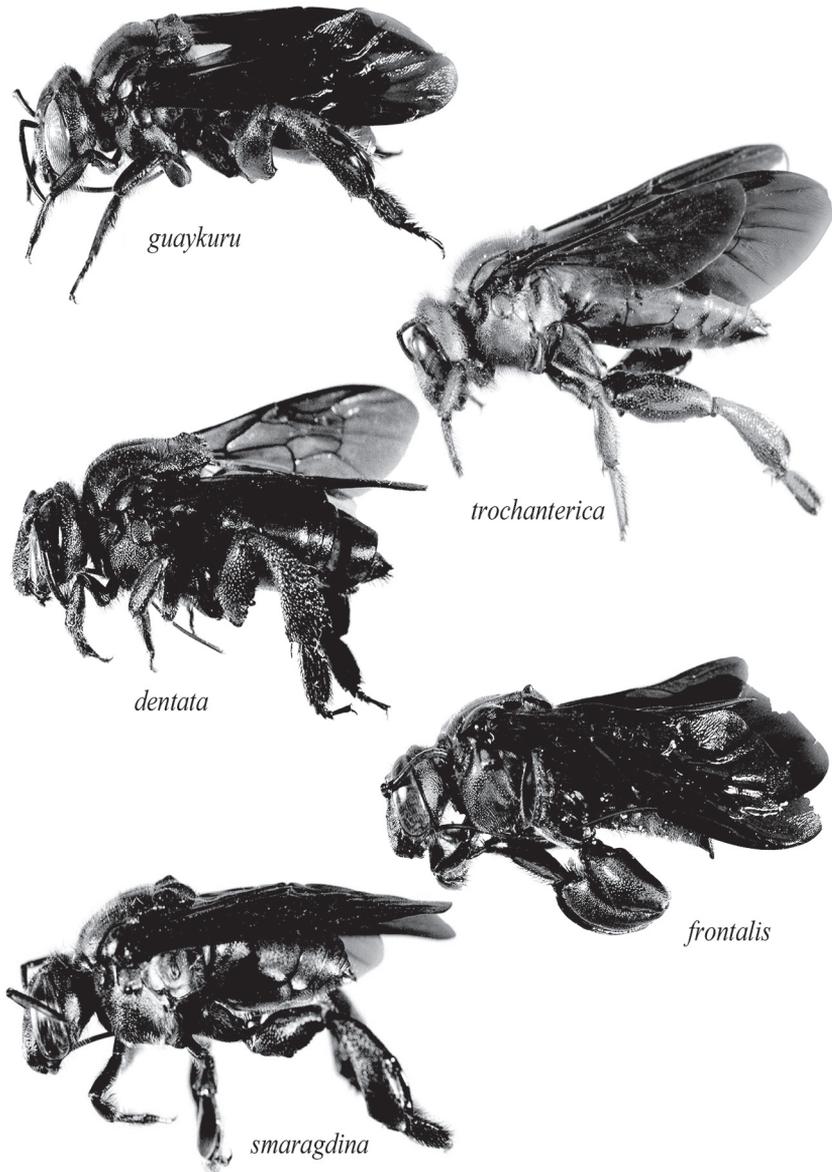


Figure 1. Representative species of *Exaerete* (Euglossini).

Engel's work (Oliveira and Nemésio, 2003; Anjos-Silva and Rebêlo, 2006) – and corroborated two ideas: that the genus was monophyletic and appeared related to the much larger and non-parasitic genus *Euglossa* (Engel, 1999). Herein we expand upon the study of Engel (1999) to include the more recently described species and to include eight

new morphological characters resulting from the discovery of additional taxa.

2. MATERIALS AND METHODS

Specimens were studied in the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto,

Universidade de São Paulo (Ribeirão Preto, Brazil) and the University of Kansas Natural History Museum (Lawrence, Kansas, USA) and obtained, in addition to material resident in these institutions, from the collections of Museu de Zoologia da Universidade de São Paulo, Universidade Federal do Maranhão, Universidade Federal de Mato Grosso, Universidade do Estado de Mato Grosso, Instituto Nacional de Pesquisas da Amazônia, and the American Museum of Natural History. Localities for those specimens examined since Engel (1999) are provided in the online Appendix (<http://www.apidologie.org>). Measurements, where pertinent, were taken using a Leica MZ7.5 Stereomicroscope and imaged (e.g., Fig. 1) using a Leica DFC280 digital camera and the Leica IM50 software package. A key to the identification of species in *Exaerete* was provided by Anjos-Silva and Rebêlo (2006).

The characters and data matrix of Engel (1999) formed the nucleus of the present study. Those original characters were coded for the species *E. guaykuru* and *E. lepeletieri*, unknown in 1999. We were particularly interested to include *E. lepeletieri* given that this species is exceedingly similar to the more widespread *E. frontalis* and even the original authors noted that there was little to distinguish this species from the latter taxon (Oliveira and Nemésio, 2003). Although we ultimately conclude that *E. lepeletieri* is a synonym of *E. frontalis* (refer to Discussion, *infra*), for the purposes of the analysis we took a conservative stance and coded this variant separately so as to confirm that it ultimately grouped with *E. frontalis*. Therefore, *E. lepeletieri* conservatively appears as a separate coding in our matrix and topology. To Engel's matrix were added five additional characters from the male genitalic sclerites and three additional characters from other regions of the male. Additional features were identified but proved to be autapomorphic and, therefore, uninformative for cladistic analysis. The final list of characters is provided in Table I and the resulting matrix in Table II (figures of the characters and their characters states can be found in Anjos-Silva and Rebêlo, 2006).

Analysis of the data matrix was undertaken in *NONA* (Goloboff, 1997: analysis followed the procedures employed in Engel, 1999, 2004) using the *WinClada* interface (Nixon, 2002). The characters were treated as non-additive and with equal weights. Characters were polarized by outgroups (Nixon and Carpenter, 1993), represented herein by the distantly-related genera *Xylocopa* (used for

rooting), *Apis*, and *Bombus* as well as the other four genera of Euglossini as more closely-related outgroups (Tab. II). No attempt was made to evaluate relationships among outgroup genera and, as such, only relationships within Euglossini and *Exaerete* were focused upon.

3. RESULTS AND DISCUSSION

Analysis of the matrix resulted in a single topology of length 39, consistency index 0.66, and retention index 0.78 (Fig. 2). Relationships among the genera were those recovered by Engel (1999) while there was some minor rearrangement within *Exaerete* resulting from the inclusion of the newly described taxa resulting in the interrelationships among the species as: (((*E. smaragdina* + (*E. frontalis* + *E. lepeletieri*)) + ((*E. trochanterica* + *E. guaykuru*) + (*E. azteca* + *E. dentata*))) (Fig. 2). Three principal clades were found within *Exaerete*, character support for which is depicted on the cladogram. A branch, here referred to as the *frontalis* group, consisting of *E. frontalis*, *E. smaragdina*, and the dubious *E. lepeletieri* (see discussion of its status, *infra*). The remaining species belong to the *dentata* group which is itself split into two distinctive clades – the *dentata* subgroup (*E. dentata* and *E. azteca*) and the *trochanterica* subgroup (*E. trochanterica* and *E. guaykuru*). In the study by Engel (1999) only *E. trochanterica* + *E. smaragdina* formed a clade as there were too few taxa and characters at that time to resolve the base of *Exaerete*. Moreover, the matrix of Engel (1999) was principally designed to resolve relationships among euglossine genera and test the monophyly of *Exaerete* rather than provide a definitive analysis of relationships within genus. The eight characters newly added to the matrix, along with the newly recognized taxa, have permitted complete resolution of relationships within the genus, partially corroborating the informal groups employed by Moure (1964) in his artificial, dichotomous key. More than half of the species are relatively widely distributed, the most extensive being *E. smaragdina* which occurs from northern Argentina to Mexico. *Exaerete dentata*, type species of the genus, is similarly distributed

Table I. Characters used in phylogenetic analysis of *Exaerete* [1–15 extracted from Engel (1999), 16–23 newly employed herein.]; morphological terminology follows that of Engel (1999).

1.	Labial palpus: (0) tetramerous; (1) dimerous.
2.	Mesoscutellum in profile: (0) convex, depressed medially; (1) flat, bladelike.
3.	Mesoscutellar tuft: (0) absent; (1) present.
4.	Sternal groove: (0) absent; (1) present.
5.	Male mesotibial carina: (0) absent; (1) incomplete; (2) complete.
6.	Male metatibial slit: (0) broad, ovoid; (1) narrow, curved.
7.	Male metatibial slit: (0) reaching apex; (1) not reaching apex.
8.	Male metatibial shape: (0) round apical margin; (1) pointed apical margin.
9.	Gonocoxal projection: (0) absent; (1) present.
10.	Volsella: (0) ovoid; (1) linear, setose; (2) fused.
11.	Hypoepimeral knob: (0) absent; (1) present.
12.	Male metafemoral dentition: (0) absent; (1) present.
13.	Male mesobasitarsal tooth: (0) absent; (1) present.
14.	Male metatibial slit: (0) absent; (1) present.
15.	Jugal comb: (0) absent; (1) present.
16.	Clypeal profile: (0) prominent; (1) not prominent.
17.	Genal width: (0) less than 1/2 compound eye width; (1) greater than 1/2 compound eye width.
18.	True mesoscutellar, sublateral tubercles: (0) absent; (1) present.
19.	Broad, medial production of VII sternal margin: (0) absent; (1) present.
20.	Notch in apical margin of sternum VII: (0) absent; (1) present (notch shallow but present in <i>E. guaykuru</i>).
21.	Gonocoxal, ventroapical projection along gonostylar base: (0) short, pointed; (1) elongate.
22.	Discal setae of sternum VII: (0) absent; (1) present as submarginal band; (2) present as submarginal band but interrupted medially and extended laterally.
23.	Minute, medial process on apical margin sternum VII: (0) absent; (1) present (makes margin appear weakly trilobed).

Table II. Data matrix for phylogenetic analysis of *Exaerete*¹. Codings for outgroup genera are composites and apply across all included species. Locality data for *Exaerete* newly studied since Engel (1999) are provided in Appendix I.

	1111111112222
	12345678901234567890123
<i>Aglae</i>	11002000010001111000000
<i>Eufriesea</i>	00011001110001111010*0*
<i>Euglossa</i>	00111110000001100010*0*
<i>Eulaema</i>	11102001110001110010*0*
<i>Exaerete azteca</i>	0001111000011111?000010
<i>Exaerete dentata</i>	00011110000111111100010
<i>Exaerete frontalis</i>	10011100001111111110001
<i>Exaerete smaragdina</i>	10011100001111111110000
<i>Exaerete trochanterica</i>	00011100000111111111110
“ <i>Exaerete lepeletieri</i> ”	10011100001111111110001
<i>Exaerete guaykuru</i>	00011100101111101111120
<i>Apis</i>	00000 -- 0020000001000--00
<i>Bombus</i>	00000 -- 00200000010*0*--*
<i>Xylocopa</i>	00000 -- 00200000110*0*--*

¹ Inapplicable states are coded with a dash (–), complete polymorphisms with an asterisk (*), and missing data with an interrogative mark (?).

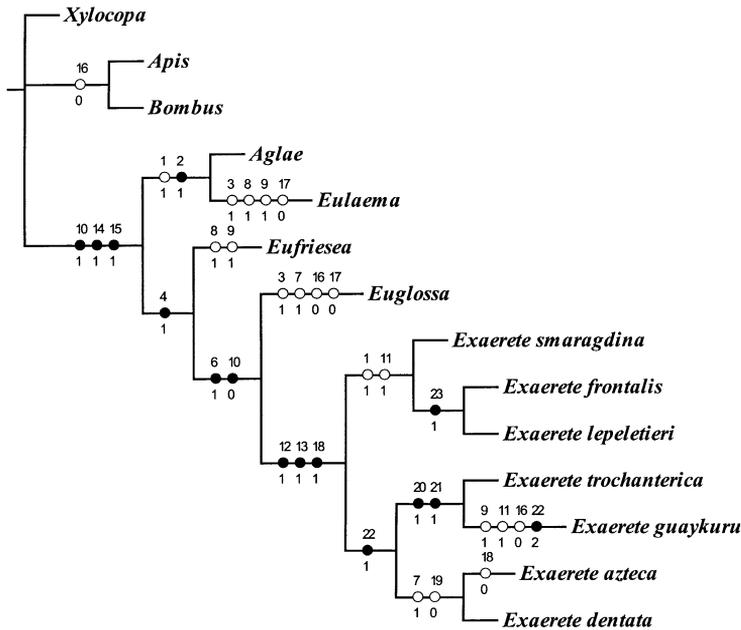


Figure 2. Phylogeny of species of *Exaerete* (length = 39, CI 0.66, RI 0.78); black points denote unique and unambiguous changes; white point indicate reversals and convergences.

from northern Argentina to at least Costa Rica, while *E. trochanterica* and *E. frontalis* occur from Brazil to Panama and Mexico, respectively. Only *E. azteca*, *E. guaykuru*, and the dubious *E. lepeletieri* have more restricted occurrences in Mexico for the first, and Brazil for the latter two. It would appear that the genus originated in central South America and then speciated and expanded its distribution from there, with subsequent differentiation in Central America to give rise to *E. azteca* (within the *dentata* subgroup) and localized specialization in specific areas of Brazil to form *E. guaykuru* and *E. lepeletieri*. The last “species” scarcely differs from *E. frontalis* (Tab. II) and is united with this taxon in our tree (Fig. 2). In the specimens studied in this work, the diagnostic morphological features of *E. lepeletieri* presented by Oliveira and Nemésio (2003) in relation of *E. frontalis* (e.g., frons with small median tubercle vs. strongly pronounced; median low longitudinal tubercle present on the mesoscutellum vs. absent; metafemur slightly depressed basally vs. basally depressed) seem to be merely regional variations. According to Oliveira and Nemésio (2003), only two addi-

tional characters separate *E. lepeletieri* from the other two species of the clade, mesoscutellum with straight posterior margin and a longitudinal impunctate stripe on the seventh metasomal tergum. These characters were the reason for its segregation as a separate species. Nonetheless, Oliveira and Nemésio (2003) noted that their material might represent a hybrid between *E. smaragdina* and *E. frontalis*, given the intermediary morphological characters. Therefore, the phylogeny proposed by these authors, based on Engel’s matrix (1999) only added *E. lepeletieri* in the polytomy comprising *E. smaragdina* and *E. frontalis*, leaving this clade unresolved.

We must take into account the fact that *E. lepeletieri* has a restricted geographic distribution, found only in the northern region of Brazil (specifically the Amazon Basin), while *E. frontalis* has a wide distribution encompassing the range of the former taxon (see above). The shape of the seventh metasomal sternum (trilobed) might be a feature to distinguish the species – the apical margin of *E. frontalis* has a strong median lobe while that of *E. lepeletieri* is relatively weak in comparison to the lateral

lobes. Beyond this relatively minor difference, these taxa are unique in sharing setae only on the apical margin. Furthermore, no differences were found in the shape or setation of the gonostylus, in both species this structure is subtriangular laterally and completely clothed in dense setae. In our matrix (see Tab. II) all characters were coded identically for both species and were accordingly recovered as sister groups. We accordingly consider *E. lepeletieri* as a synonym of *E. frontalis*.

It would be interesting to document whether the distributional gap within the *dentata* subgroup is a real phenomenon. For example, the distribution of *E. azteca* may be larger than presently understood owing to poor sampling in intervening countries such as Honduras and Nicaragua (alternatively the distribution of *E. dentata* may eventually be discovered to extend further northward). The occurrence of *A. caerulea*, a species that was presumed to occur only in the Amazon Basin, may prove to be analogous to *E. azteca*. Recently the range of *Aglae* was newly documented in the Platina Basin (Mato Grosso State, Brazil), increasing its known geographical distribution by approximately 2400 kilometers southward in South America (Anjos-Silva et al., 2006). Such a large geographical extension, for what are otherwise well documented bees indicates that the wider distribution of *E. azteca* suggested herein may be plausible and additional sampling should be undertaken.

Unfortunately too little information exists about host associations among species of *Exaerete* to extract patterns from the resulting phylogeny. However, given the apparently labile host usage exhibited by the more completely studied *E. smaragdina* and *E. dentata* (the former attacking species in two genera) it would seem that no such patterns exist. Nonetheless, further biological studies on the species will either confirm or refute this suspicion. Although the differences in body size between *Exaerete* and *Euglossa* species may be seen as a limitation for such interaction, it will be particularly interesting to discover whether or not some *Exaerete* are capable of victimizing species of *Euglossa*, their apparent non-parasitic sister group.

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Phylogénese du genre *Exaerete* (Hymenoptera: Apidae), abeille cleptoparasite.

Euglossini / cleptoparasitisme / phylogénese / *Exaerete* / biogéographie

Zusammenfassung – Phylogenie der kleptoparasitischen Bienengattung *Exaerete* (Hymenoptera: Apidae). Die kleptoparasitische Prachtbienengattung *Exaerete* Hoffmannsegg (Apinae: Euglossini) umfasst 7 Arten (Abb. 1) die sich andere Gruppen der Prachtbienen zum Opfer machen. Die evolutionären Beziehungen zwischen den 7 Arten wurden anhand von Daten über die externe Morphologie adulter Bienen untersucht. Eine frühere Studie von Engel (1999) wurde um mehrere neue für eine phylogenetische Analyse nutzbare morphologische Eigenschaften erweitert und darüber hinaus die seit 1999 neu beschriebenen Arten einbezogen. Unter Benutzung von NINA wurde eine parsimonische Analyse durchgeführt, die zu einer einzigen Topologie führte. Innerhalb des Genus wurden drei Hauptgruppen der Arten identifiziert. Die Beziehungen zwischen den Arten können folgendermassen zusammengefasst werden: ((*E. smaragdina* + (*E. frontalis* + *E. lepeletieri*)) + ((*E. trochanterica* + *E. guaykuru*) + (*E. azteca* + *E. dentata*))) (Abb. 2). Die Gattung besiedelt einen geografischen Bereich von Argentinien bis Mexico, wobei einige Arten in der neotropischen Region weit verbreitet sind. Nur wenige biogeografische Muster sind als solche erkennbar, aber es scheint dass die Gattung ihren Ursprung in Südamerika genommen hat, mit lokalisierten Arealen einer Artbildung in Mexico (for *E. azteca*) und Brasilien (for *E. guaykuru*). Aus den wenigen zur Verfügung stehenden Daten zur Biologie von *Exaerete* konnte kein Muster der Wirtspreferenz abgeleitet werden. *Exaerete lepeletieri* Oliveira & Nemésio wird neu als ein Synonym von *E. frontalis* (Guérin-Méneville) angesehen.

Kleptoparasitismus / Euglossini / Prachtbienen / Phylogeny / *Exaerete* / Biogeographie

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Online Materials

Appendix. Localities for specimens of *Exaerete* studied since Engel (1999) (specimens studied by Engel in 1997–1999 are in the Division of Entomology, University of Kansas Natural History Museum and the Division of Invertebrate Zoology, American Museum of Natural History).

Exaerete azteca: Mexico, Queretaro 26.5 km W San Luis Potosí, Queretaro border on Hwy 120, 1270 m; Mexico, Queretaro, 43 km E Jalpan, 1300 m; Mexico, Hidalgo, 38 km NE Jacala, 3100 m (holotype). Specimens in the Division of Entomology, University of Kansas Natural History Museum.

Exaerete dentata: Brazil, Mato Grosso State, Pantanal de Cáceres bordered on Paraguai River, 110 m; Brazil, Mato Grosso State, 23 km SE Cáceres, Serra do Quilombo border on BR 364 km 777, Jacobina Farm, 300 m; Brazil, Água Milagrosa sinkhole, Província Serrana de Mato Grosso, 20 km NE Cáceres, 390 m; Brazil, Maranhão State, Barreirinhas 270 km E São Luís, 4 m. Specimens in Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Universidade Federal do Maranhão and Universidade do Estado de Mato Grosso.

Exaerete frontalis: Brazil, Amazonas State, Jaú National Park, 220 km W Manaus, 100 m; Brazil, Maranhão State, Buriticupu 320 km SW São Luís, 200 m. Specimens in Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo and Universidade Federal do Maranhão.

Exaerete guaykuru: Brazil, Mato Grosso State, Coxipozinho Stream, Chapada dos Guimarães National Park, MT 251 km 50, 600 m (holotype).

Specimens in Museu de Zoologia, Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo and Universidade do Estado de Mato Grosso (paratypes).

Exaerete lepeletieri: Brazil, Amazonas State (further locality data not provided with specimen). Specimen in the Instituto Nacional de Pesquisas da Amazônia, Manaus.

Exaerete smaragdina: Brazil, Mato Grosso State, Pantanal de Cáceres bordered on Paraguai River, 110 m; Brazil, Mato Grosso State 23 km SE Cáceres, Serra do Quilombo border on BR 364 km 777, Jacobina Farm, 300 m; Brazil, Água Milagrosa sinkhole, Província Serrana de Mato Grosso 20 km NE Cáceres, 390 m; Brazil, Mato Grosso State, Coxipozinho Stream, Chapada dos Guimarães National Park, MT 251 km 50, 600 m; Brazil, Mato Grosso State, Cuiabá border on Cuiabá River, 185 m; Brazil, São Paulo State, Cajuru, Santa Carlota Farm, 700 m; Brazil, Maranhão State, São Luís, 24 m; Brazil, Maranhão State, Alcântara, 32 m; Brazil, Maranhão State, Buriticupu 320 km SW São Luís, 200 m; Brazil, Maranhão State, Barreirinhas 270 km E São Luís, 4 m; Specimens in Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Universidade Federal do Maranhão, Universidade Federal de Mato Grosso and Universidade do Estado de Mato Grosso.

Exaerete trochanterica: Brazil, Mato Grosso State, Cuiabá, Serra de São Vicente 80 km SE Cuiabá bordered on BR 364 km 329, 780 m. Specimen in the Universidade Federal de Mato Grosso.