

**THE NEOTROPICAL WEEVIL GENUS *ENTIMUS* (COLEOPTERA:
CURCULIONIDAE: ENTIMINAE): CLADISTICS, BIOGEOGRAPHY, AND
MODES OF SPECIATION**

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Abstract

The weevil genus *Entimus* Germar is a monophyletic taxon, recognized by a combination of the following characters: large size (12–45 mm); presence of green, blue, and gold iridescent scales; antennae reaching base of prothorax, with second funicular article scarcely longer than first; widened frontal groove; pronotum as wide as long, granulate; elytra triangularly shaped; tibiae not crenulated or dentate within; scutellum protruding; and aedeagal apex slightly acute. It includes seven species, which are endemic to the Neotropics, ranging from Mesoamerica to northeastern Argentina. A cladistic analysis was carried out using 16 characters from external morphology, body vestiture, and male genitalia. The analysis yielded four equally parsimonious cladograms, each with 33 steps, a consistency index of 0.60, and a retention index of 0.53. After successive weighting, a single cladogram resulted, with 105 steps, a consistency index of 0.89, and a retention index of 0.90. According to this cladogram, the species of *Entimus* follow the sequence: *E. arrogans* Pascoe, *E. granulatus* (Linnaeus), *E. imperialis* (Forster), *E. fastuosus* (Olivier), *E. sastrei* Viana (= *E. formosus* Viana, **syn. nov.**), *E. nobilis* (Olivier), and *E. excelsus* Viana. According to predictions based on phylogenetic and distributional information available, the most likely mode of speciation for four species of the genus is sympatric, whereas *E. arrogans* and *E. granulatus* have followed an allopatric mode of speciation, and *E. sastrei* has followed the centrifugal mode of speciation.

Entimus Germar, belonging to the subtribe Entimina of the tribe Entimini (Curculionidae: Entiminae), is distributed in the Neotropical region, from Mesoamerica to northeastern Argentina (Morrone 1999a). Species of *Entimus* are easily identified by their typical body shape (Fig. 1), and by the green, blue, and gold iridescent scales covering their integument (with the exception of *E. arrogans*, which has only whitish seta-like scales). Vaurie (1952) reviewed the genus, established the main differences with its closely related genera, and provided a key to its five known species. Viana (1958, 1968) described three further species, two from Argentina and one from Brazil.

Examination of specimens collected by myself in Punta Lara (Buenos Aires province, Argentina) led me to suspect that *E. sastrei* Viana and *E. formosus* Viana (1958), from Argentina, were conspecific. In addition, when analyzing the distribution of this species, it appeared that it may have arisen through the formation of a peripheral isolate, namely, a small isolated or semi-isolated population, distributed around the periphery of a large central portion of a species' range (Mayr 1963). A cladistic hypothesis analyzed together with distributional maps of the species, may allow us to distinguish between this mode of speciation and the centrifugal mode of speciation (Frey 1993).

My objectives are to provide a synopsis of the species of *Entimus*, to review the synonymy of *E. sastrei* and *E. formosus*, present a cladistic analysis of the

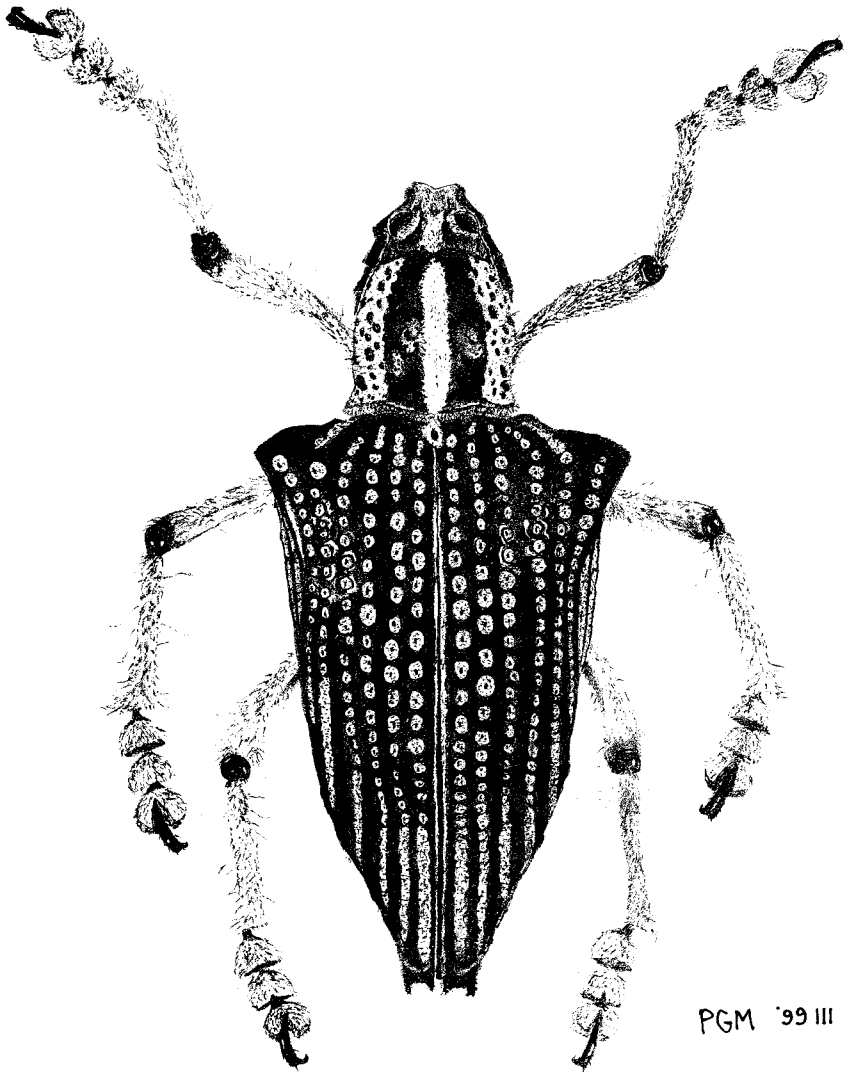


Fig. 1. *Entimus imperialis*, habitus drawing.

genus, and to discuss the geographic distribution of the species and the modes of speciation possibly involved.

Material and Methods

The specimens examined in this study are from the following collections: American Museum of Natural History, New York, U.S.A. (AMNH); Natural History Museum, London, England (BMNH); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBio); Museo Argentino de Ciencias

Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN); Museo de La Plata, La Plata, Argentina (MLP); and Museo de Zoología, Facultad de Ciencias, UNAM, Mexico D.F., Mexico (MZFC).

A total of 16 characters used for the phylogenetic analysis were derived from the external morphology (6), body vestiture (8), and male genitalia (2). Although females of all the species were dissected, no useful characters could be obtained from their genitalia. Table I contains the data matrix and the list of characters analyzed; all multistate characters were treated as additive. Analysis was carried out with Hennig86 1.5 (Farris 1988), applying the implicit enumeration option and the successive weighting procedure. Cladograms were rooted with the closely related genus *Phaedropus* (Fig. 2) (Vanin 1983).

Results and Discussion

Entimus Germar

Entimus Germar 1817:341 (type species: *Curculio imperialis* Forster, subsequent designation by Schönherr 1823).

Curculio Duponchel [1843]:398 (misidentification, not Linnaeus 1758).

Curculio Blanchard 1845:99 (misidentification, not Linnaeus 1758).

Curculio Gistel 1848:134 (misidentification, not Linnaeus 1758).

Entimnus Handlirsch 1907:808 (lapsus).

Entymus Jacob [1936]:155 (lapsus).

Diagnosis. Species of *Entimus* are easily identified by their large size (12–45 mm) and the presence of green, blue, and gold iridescent scales. In addition, the combination of the following characters is diagnostic: antennae reaching base of prothorax, with second funicular article scarcely longer than first; widened frontal groove; pronotum as wide as long, granulate; elytra triangularly shaped; tibiae not crenulated or dentate within; scutellum protruding; and aedeagal apex slightly acute.

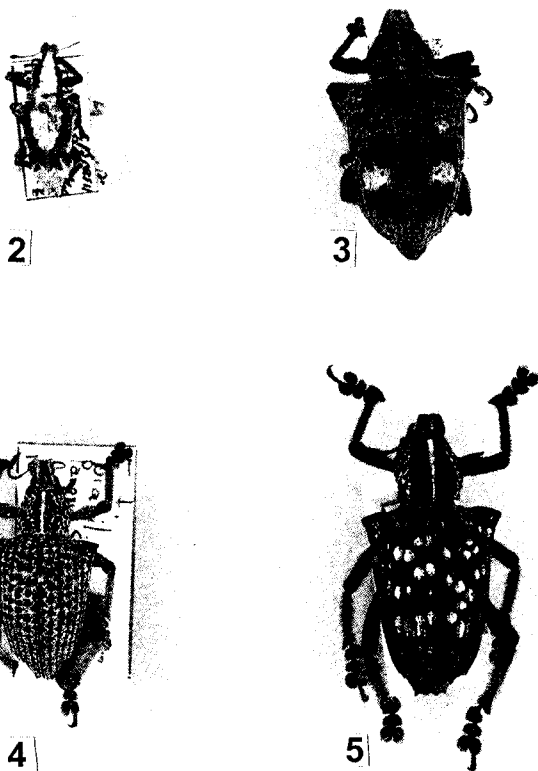
Key to Species of *Entimus*

- 1 Body vestiture with green, blue, and gold iridescent, elongate to ovate scales 2
- 1' Body vestiture with whitish, seta-like scales. Colombia, Costa Rica, Nicaragua, and Panama *E. arrogans* (Fig. 3)
- 2 Prementum as wide as long, with longitudinal median impression; postocular lobes acute; scales elongate (more than twice as long as wide) 3
- 2' Prementum conspicuously wider than long, lacking longitudinal median impression; postocular lobes rounded; scales ovate (less than twice as long as wide). Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Panama, and Peru *E. granulatus* (Fig. 6)
- 3 Interstriae with rounded tubercles 4
- 3' Interstriae lacking rounded tubercles 5
- 4 Interstriae lacking scales; male legs with abundant, long, whitish setae. Brazil *E. nobilis* (Fig. 8)
- 4' Interstriae with scales; male legs with few, long, whitish setae. Brazil *E. excelsus* (Fig. 4)
- 5 Elytral humeri acute; striae with scales not spreading outside punctures. Argentina, Brazil, and Paraguay *E. imperialis* (Figs. 1, 7)

Table 1. Data matrix and list of characters used in the cladistic analysis of *Eritimus*. 0 = plesiomorphic; 1 and 2 = apomorphic.

<i>Phaetropus</i>	0000000000000000
<i>E. arrogans</i>	1101112000000001
<i>E. excelsus</i>	1211011110100102
<i>E. fastuosus</i>	1211101201100111
<i>E. granulatus</i>	1101000200111011
<i>E. imperialis</i>	0211001201110101
<i>E. nobilis</i>	0211111111100102
<i>E. sasstri</i>	1210101101101111

1. Frontal groove: [0] shallow; [1] widened.
2. Pronotum shape: [0] subcylindrical; [1] as wide as long; [2] wider than long.
3. Postocular lobes: [0] rounded; [1] acute.
4. Scutellum: [0] flat; [1] protruding.
5. Elytral humeri: [0] angulate and projecting; [1] rounded.
6. Interstriae: [0] lacking rounded tubercles; [1] with rounded tubercles.
7. Scales: [0] ovate; [1] elongate-ovate; [2] seta-like.
8. Scales: [0] uniformly covering elytra; [1] uniformly covering striae; [2] only covering punctures.
9. Elytral scales: [0] imbricate; [1] contiguous to slightly overlapping.
10. Scales on interstriae: [0] present; [1] absent.
11. White bands on elytra: [0] present; [1] erect.
12. Pronotal setae: [0] decumbent; [1] erect.
13. Elytral setae: [0] abundant; [1] scarce to absent.
14. Long setae on male legs: [0] scarce; [1] abundant.
15. Aedeagal relative length: [0] longer than apodemes; [1] shorter than apodemes.
16. Aedeagal apex: [0] rounded; [1] slightly acute; [2] strongly acute.



Figs. 2–5. *Phaedropus togatus* and *Entimus* spp., habitus photographs. 2) *Phaedropus togatus* (13 mm length); 3) *Entimus arrogans* (30 mm length); 4) *E. excelsus* (25 mm length); 5) *E. fastuosus* (35 mm length).

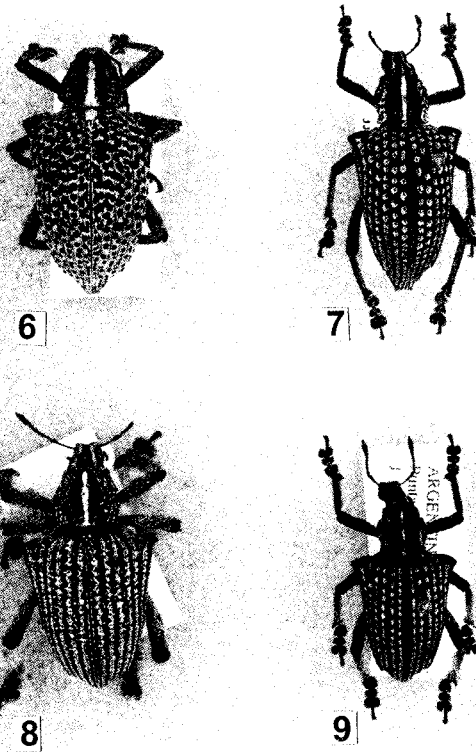
- 5' Elytral humeri rounded; striae with scales spreading over two or more puncturesm 6
 6 Striae with green scales, in regular rows. Argentina *E. sastrei* (Fig. 9)
 6' Striae with golden and/or green scales, irregularly placed. Brazil
 *E. fastuosus* (Fig. 5)

E. arrogans Pascoe
(Fig. 3)

Entimus arrogans Pascoe 1872:448.

Entimus plebejus Roelofs 1875:XXXVIII; Champion 1911:301 (= *E. arrogans*).

Diagnosis. Frontal groove widened; pronotum as wide as long, with rounded postocular lobes, and decumbent setae; scutellum protruding; elytra with rounded humeri, interstriae with rounded tubercles, and abundant setae; seta-like scales uniformly covering elytra, imbricate, present on intestriae; elytra



Figs. 6-9. *Entimus* spp., habitus photographs. **6)** *E. granulatus* (30 mm length); **7)** *E. imperialis* (28 mm length); **8)** *E. nobilis* (29 mm length); **9)** *E. sastrei* (22 mm length).

with white bands; and male legs with scarce setae. Total length (pronotum + elytra): 24-30 mm.

Distribution. Colombia, Costa Rica, Nicaragua, and Panama.

Material Examined. **COSTA RICA.** **Limón:** Est. Hitoy Cerere, R. Cerere, Res. Biol. Hitoy, 100 m, 6/16-V-1992, G. Carballo coll., 1 (INBio). **Puntarenas:** Est. La Casona, Res. Biol. Monteverde, 1,520 m, III-1992, N. Obando coll., 1 (INBio). Without more precise data, 1 (BMNH). **PANAMA.** Without more precise data, 1 syntype of *E. arrogans* (BMNH).

E. excelsus Viana
(Fig. 4)

Entimus excelsus Viana 1968:103.

Diagnosis. Frontal groove widened; pronotum wider than long, with acute postocular lobes, and decumbent setae; scutellum protruding; elytra with angulate and projecting humeri, interstriae with rounded tubercles, and abundant setae; scales elongate-ovate, uniformly covering striae, contiguous to slightly

overlapping, present on intestriae; elytra lacking white bands; and male legs with abundant setae. Total length (pronotum + elytra): 13–31 mm.

Distribution. Brazil.

Material Examined. BRAZIL. **Espirito Santo:** Linhares, Parque Sooretama, XI-1967, A. Martínez coll., 3 paratypes (MACN).

E. fastuosus (Olivier)

(Fig. 5)

Curculio fastuosus Olivier 1790:524; Latreille 1804:158 (*Brachyrhinus*); Dejean 1821:92 (*Entimus*).

Curculio splendidus Fabricius 1792:448; Olivier 1807:294 (= *C. fastuosus*); Germar 1817:341 (*Entimus*).

Diagnosis. Frontal groove widened; pronotum wider than long, with acute postocular lobes, and decumbent setae; scutellum protruding; elytra with rounded humeri, interstriae lacking rounded tubercles, and abundant setae; scales elongate-ovate, only covering punctures, imbricate, absent on intestriae; elytra lacking white bands; and male legs with abundant setae. Total length (pronotum + elytra): 16–45 mm.

Distribution. Brazil.

Material Examined. BRAZIL. **Rio Grande:** without more precise data, 1 (BMNH). **Santa Catarina:** Corupá, XII-1961, 2 (BMNH). **Without more precise data.** 3 (BMNH).

E. granulatus (Linnaeus)

(Fig. 6)

Curculio granulatus Linnaeus 1758:386; Dejean 1821:92 (*Entimus*).

Curculio sumptuosus Olivier 1790:525; Dejean 1821:92 (*Entimus*); Schönherr 1826:84 (= *E. granulatus*).

Entimus speciosus Erichson 1847:127; Marshall 1930:572 (= *E. granulatus*).

Diagnosis. Frontal groove widened; pronotum as wide as long, with rounded postocular lobes, and erect setae; scutellum protruding; elytra with angulate and projecting humeri, interstriae lacking rounded tubercles, and scarce to absent setae; scales ovate, only covering punctures, imbricate, present on intestriae; elytra lacking white bands; and male legs with scarce setae. Total length (pronotum + elytra): 21–31 mm.

Distribution. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Panama, and Peru.

Material Examined. BOLIVIA. Without more precise data, 3 (MACN). BRAZIL. Hohenau, Alto Paraná, 1 (BMNH). GUYANA. A. W. Bartlett coll., 1 (BMNH). ECUADOR. **Morona-Santiago:** Río Cuangos, near Cuevas de los Tayos, 7-VII-1976, A. M. Huston coll., 1 (BMNH). PERU. Without more precise data, 3 (BMNH). **Without more precise data.** 2 (BMNH).

E. imperialis (Forster)

(Figs. 1, 7)

Curculio imperialis Forster 1771:34; Latreille 1804:158 (*Brachyrhinus*); Germar 1817:341 (*Entimus*).

Diagnosis. Frontal groove shallow; pronotum wider than long, with acute postocular lobes, and erect setae; scutellum protruding; elytra with angulate

and projecting humeri, interstriae lacking rounded tubercles, and abundant setae; scales elongate-ovate, only covering punctures, imbricate, absent on intestriae; elytra lacking white bands; and male legs with abundant setae. Total length (pronotum + elytra): 16–33 mm.

Distribution. Argentina, Brazil, and Paraguay.

Material Examined. BRAZIL. Bahia: Bahia, X-1981, 1 (BMNH). Espirito Santo: Jetibá, II-1964, 1 (MACN). Minas Gerais: Ipatinga, 1988, 1 (MZFC), X-1993, E. J. Grossi coll., 5 (MZFC). Rio de Janeiro: Mendes, Hno. Eufrasio coll, 2 (MACN). Without more precise data. 4 (3 BMNH, 1 MACN).

E. nobilis (Olivier)

(Fig. 8)

Curculio nobilis Olivier 1790:525; Dejean 1821:92 (*Entimus*).

Diagnosis. Frontal groove shallow; pronotum wider than long, with acute postocular lobes, and decumbent setae; scutellum protruding; elytra with rounded humeri, interstriae with rounded tubercles, and abundant setae; scales elongate-ovate, uniformly covering striae, contiguous to slightly overlapping, absent on intestriae; elytra lacking white bands; and male legs with abundant setae. Total length (pronotum + elytra): 12–25 mm.

Distribution. Brazil.

Material Examined. BRAZIL. Bahia: Bahia, 1 (BMNH). Rio de Janeiro: without more precise data, 1 (BMNH). Santa Catarina: 1850, Sahlberg coll., 1 (BMNH). Without more precise data. 3 (BMNH).

E. sastrei Viana

(Fig. 9)

Entimus sastrei Viana 1958:6 (= *E. nobilis* of authors, misidentification, not Olivier 1790).

Entimus formosus Viana 1958:2, **syn. nov.**

Initially, I supposed that the specimens from Punta Lara (Buenos Aires province, Argentina) belonged to the species *E. sastrei* Viana, however, when I compared them with those of *E. formosus* Viana I found that they all belonged to a single species. The few differential characters given by Viana (1958), e.g., development of pronotal granules, presence of scales on the elytral suture, or depth of elytral punctures, represent intraspecific variation.

Diagnosis. Frontal groove widened; pronotum wider than long, with acute postocular lobes, and decumbent setae; scutellum flat; elytra with rounded humeri, interstriae lacking rounded tubercles, and scarce to absent setae; scales elongate-ovate, uniformly covering striae imbricate, absent on intestriae; elytra lacking white bands; and male legs with abundant setae. Total length (pronotum + elytra): 15–36 mm.

Distribution. Argentina and Uruguay.

Material Examined. ARGENTINA. Buenos Aires: Punta Lara, I-1928, C. Bruch coll., holotype of *E. sastrei* (MACN), 20-II-1938, M. Bruzzone coll., 1 (MLP), 1939, C. Bruch coll., 4 paratypes of *E. sastrei* (MACN), II-1953, 1 (MLP), 30-X-1987, J. J. Morrone coll., 5 (MZFC); Zárate, I-1935, 1 (MLP), II-1955, 2 (MLP). Corrientes: Santo Tomé, Pellerano coll., 10 paratypes of *E. formosus* (MACN). Entre Ríos: Río Martínez, II-1953, 2 (MLP). Misiones: Depto. Concepción, Santa María, II-1945, M. J. Viana coll., 1 (MACN), X-

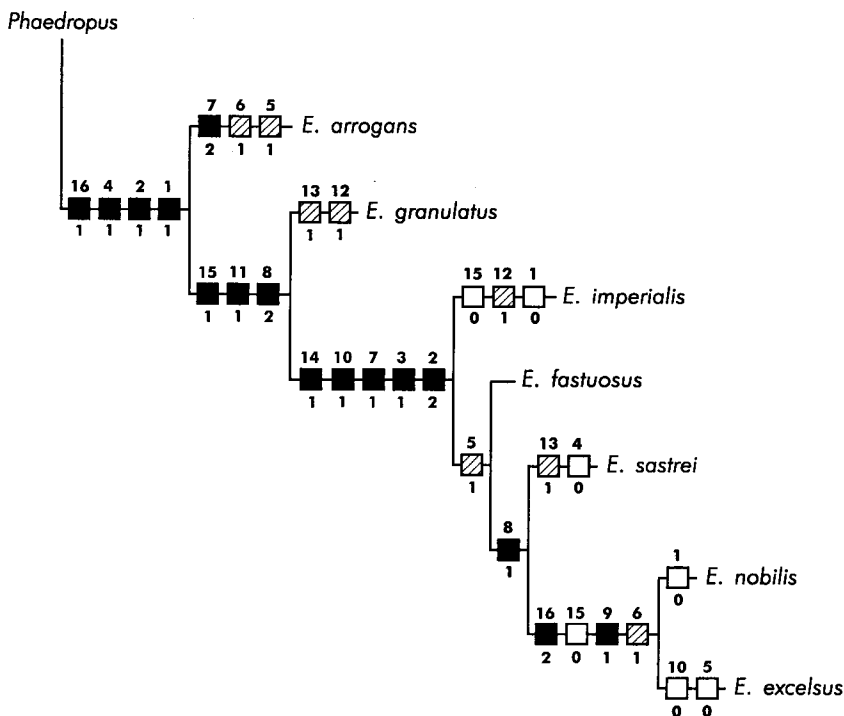


Fig. 10. Cladogram of the species of *Entimus*. Black squares = synapomorphies; dotted squares = parallelisms; open squares = reversals.

1947, M. J. Viana coll., holotype and two paratypes of *E. formosus* (MACN), X-1952, M. J. Viana coll., 1 (MACN). **Without more precise data.** 1 (MLP).

The cladistic analysis yielded four equally parsimonious cladograms, each with 33 steps, a consistency index of 0.60, and a retention index of 0.53. After successive weighting, a single cladogram resulted, with 105 steps, a consistency index of 0.89, and a retention index of 0.90. According to this cladogram (Fig. 10), the species follow the sequence: *E. arrogans*, *E. granulatus*, *E. imperialis*, *E. fastuosus*, *E. sastrei*, *E. nobilis*, and *E. excelsus*. The clade including the latter five species is strongly supported by five synapomorphies and the species included in it are very similar.

In spite of the small number of specimens examined in this study, there are several localities reported by Vaurie (1952) and Viana (1958, 1968) which may be taken into consideration when speculating on the modes of speciation and analyzing the geographical distribution of the species of *Entimus* (see Fig. 11). According to the available data, *E. arrogans* (Mesoamerican), *E. granulatus* (basically Amazonian), and *E. sastrei* (from northeastern Argentina) are allopatric, whereas the remaining four species are sympatric in southeastern Brazil. By comparing these distributions with their phylogenetic relationships, I hypothesize that *E. arrogans* and *E. granulatus* probably followed an allopatric mode of speciation, whereas the most likely mode for the latter four species is sympatric.

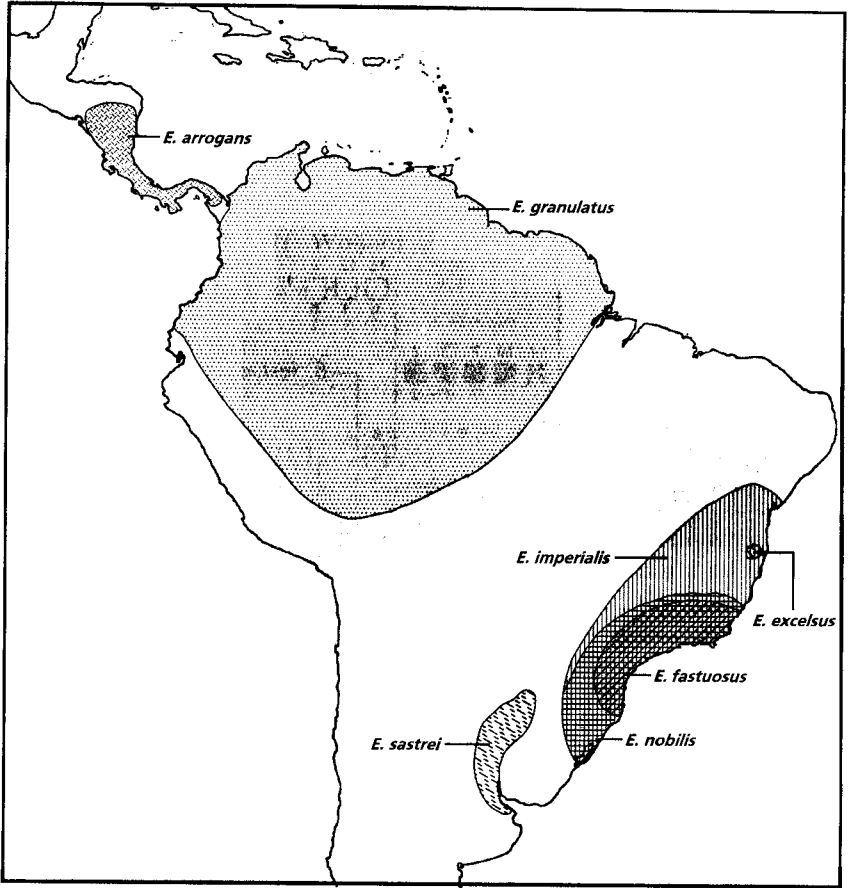


Fig. 11. Geographical distribution of the species of *Entimus* (modified from Vaurie 1952).

The isolated distribution and relatively small range of *E. sastrei* may imply that it evolved through either the peripheral isolate mode or the centrifugal mode of speciation. Predictions of the peripheral isolate model (either by waif dispersal, microvicariance, or range retraction) imply that the peripheral isolate possesses the symplesiomorphic character states that were present in the original population and autapomorphies that arose independently of other populations after isolation, whereas predictions of the centrifugal mode of speciation imply that the peripheral isolate should remain relatively plesiomorphic while the greater number of apomorphic character states should be present in the central population (Frey 1993). If we consider the ancestor of *E. nobilis* + *E. excelsus* as the "central population" from which *E. sastrei* arose, the centrifugal mode of speciation seems to be the most plausible. Although *E. excelsus* also has a restricted range, based on the cladistic and biogeographic information available, it is not clear whether it also may have followed the latter mode of speciation.

The first dichotomy in the cladogram, separating the Mesoamerican species *E. arrogans* from the South American taxa, agrees with the results of Lanteri's (1995) analysis of the weevil genus *Ericydeus*, also belonging to the tribe Entimini. This could be due to the vicariance between the Caribbean subregion (*sensu* Morrone 1999b) from the rest of the Neotropical region, as postulated by Amorim and Pires (1996) and Ron (2000). The second dichotomy, separating *E. granulatus* from the rest, agrees with a vicariant event between the Amazonian and the Parana + Chacoan subregions.

Within the clade including the remaining species, *E. sastrei* is distributed in the Parana flooded savannas ecoregion (*sensu* Dinerstein *et al.* 1995), considered as a part of the Pampean province of the Chacoan subregion (Morrone 2000). Usually Pampean taxa exhibit closer relationships with those of other Chacoan provinces, although there are cases where they show closer biotic links with the Parana subregion, for example the Entimini *Cyrtomon* and *Priocyphus* (Lanteri 1990a, b; Lanteri and Morrone 1991). Species of the latter two genera, however, are absent from the Parana flooded savannas ecoregion, so no biogeographic congruence is present. This lack of congruence also agrees with the biogeographic predictions of the centrifugal mode of speciation (Frey 1993).

Acknowledgments

I thank Lee Herman (AMNH), Chris Lyal (BMNH), Ángel Solís (INBio), Axel Bachmann (MACN), and Juan Schnack (MLP) for the loan of specimens; Fernando Vaz-de-Mello (Universidade de Viçosa, Viçosa, Brazil) for the gift of specimens of *E. imperialis*; Chris Carlton and two anonymous reviewers for their useful comments; Pablo Gesundheit for the habitus drawing; and Alejandro Martínez Mena for the habitus photographs. Economic support by National Geographic grant 6590-99 is gratefully acknowledged.

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(Received 7 February 2001; accepted 13 June 2001)