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Taxonomic position of two fossil social bees (Apidae)

by

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Abstract: Numerical taxonomic methods were used to localize two fossil bees: *Meliponorytes devictus* and *Electrapis proava.* The results indicate that both bees belong to the tribe Meliponini (Apidae). *M. devictus* was confirmed as *Tetragona devicta. E. proava* is strongly associated to the superior trigonas *(Trigona, Scaptotrigona, Oxytrigona),* and according to the different existing taxonomic schools it should be renamed either *Trigona (Roussyana) proava* or simply *Roussyana proava.*

In 1962 one of us (WEK) had the opportunity to examine and take some measurements of two fossils in the British Museum of Natural History. About 70 characters of each bee were measured, but due to the position of the fossils in the amber, only 51 were coincident. Numerical taxonomic techniques were used to assess the taxonomic position of these two fossils.

MATERIAL AND METHODS

The two fossils measured were *Electrapis proava* (Oligocene, Baltic) and *Meliponorytes devictus* (Miocene, Burma). The latter has been renamed *Trigona (Tetragona) devicta* (Cockerell) according to **Kerr & Maule** (1964). Both are in the collection of the British Museum of Natural History. The other bees are deposited in the collection of the Department of Genetics, Faculdade de Medicina de Ribeirao Preto, Brazil. Both fossils and present species studied are in the following list.

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Fossil species:

Apidade

01. *Trigona (Tetragona) devicta* (Cockerell)
02. *Electrapis proava* Cockerell

Present species

Apidae

03. *Trigona (Tetragona) iridipennis* Smith (6)
04. *Melipona quadrifasciata* Lepeletier (1)
05. *Melipona scutellaris* Latreille (2)
06. *Melipona puncticollis* Friese (3)
07. *Scaptotrigona postica* (Latreille), a male, (4)
08. *Scaptotrigona tubiba* (Smith) (1)
09. *Oxytrigona tataira* (Smith) (1)
10. *Trigona (Trigona) hyalinata* (Lepeletier) (4)
11. *Meliponula bocandei* (Spinola) (5)
12. *Apis mellifera* Linné (4)
13. *Bombus (Fervidobombus) atratus* Franklin (6)
14. *Eulaema (Apeulaema) nigrita* Lepeletier (4)
15. *Euglossa (Euglossa) cordata* Linné (4)

Anthophoridae

16. *Xylocopa (Shoenherria) muscaria* (Fabricius) (4)
17. *Centris (Hemisiella) tarsata* Smith (4)
18. *Epicharis (Epicharitides) cockerelli* Friese (4)
19. *Melitoma segmentaria* (Fabricius) (4)

Megachilidae

20. *Megachile (Leptorachis) paulistana* Schrotkyi
21. *Anthidium (Anthidium) manicatum* (Linné) (6)

Halictidae

22. *Augochloropsis cupreola* Cockerell (4)

Andrenidae

23. *Oxaea flavescens* (Klug) (4)

The numbers in parentheses refer to the location of the specimens: (1) Pocinhos do Rio Verde, M.G.; (2) Riachuelo, S.E.; (3) Obidos, P.A.; (4) Rio Claro, S.P.; (5) Luanda, Angola (Africa); (6) Serra Negra, S.P.; (6) British Museum of Natural History 2-94; Bingham Collection 96-3, Tenasserim, Burma. Except for the bees numbered 01, 02, 03, and 11, the others are from Brazil.

Fifty-one characters were measured under a Zeiss Stereoscope and are shown in Table 1.

Eight bees, numbers 16 to 23 belonging to the distantly related families Anthophoridae, Megachilidae, Halictidae and Andrenidae were included in the analysis as "taxonomic indicators". If the fossil species cluster with some of a family that is not Apidae, it would mean that the similarity coefficients reached low values, that is, distantly related.

TABLE 1

List of characters used in the analysis of fossil bees by the numerical taxonomic method

01. Length of head
02. Width of head
03. Length of clypeus
04. Maximum width of clypeus
05. Length of eye
06. Width of eye
07. Diameter of median ocellum
08. Distance between median and marginal ocellum
09. Distance from median ocellum to eye margin
10. Diameter of antennal basis
11. Distance from antennal basis to eye margin
12. Distance from antennal basis to posterior head margin
13. Distance between antennal basis
14. Distance from upper eye margin to head margin
15. Inner distance between upper margin of eyes
16. Length of malar area
17. Length of mandible
18. Width of mandible basis
19. Width of mandible apex
20. Length of first segment of flagellum
21. Diameter of fourth segment of flagellum
22. Length of forewing
23. Width of forewing
24. Length of pterostigma
25. Width of pterostigma
26. Length of marginal cell
27. Length of free segment of radius
28. Number of submarginal cells
29. Number of hamulli
30. Length of thorax
31. Width of thorax
32. Length of scutum
33. Width of scutum
34. Length of scutellum
35. Width of scutellum
36. Length of tibia (III)
37. Width of tibia (III)
38. Length of the first tarsal segment (III)
39. Width of the first tarsal segment (III)
40. Length of tibia (II)
41. Width of tibia (II)
42. Length of the first tarsal segment (II)
43. Width of the first tarsal segment (II)
44. Length of tibia (I)
45. Width of tibia (I)
46. Length of the first tarsal segment (I)
47. Width of the first tarsal segment (I)
48. Types of hairs on tibia (III)
49. Types of pollen carriers
50. Length of corbicula
51. Maximum width of abdomen

(I) : First pair of legs
(II) : Second pair of legs
(III) : Third pair of legs

Gower's coefficient of similarity was calculated in order to have a similarity matrix among operational taxonomic units (OTU's) and this matrix used to construct dendrograms illustrating the relationship among OTU's. Four different clustering techniques were used in the construction of the dendrograms: Weighted Average Linkage; Unweighted Average Linkage; Single Linkage; and a Weighted Pair-Group method using arithmetic averages. Cophenetic correlations were also obtained **(Sneath & Sokal,** 1973). Part of the analysis was performed using programs written by M.J. Sakin, Medical Research Council, University of Leicester, and implemented to the set of programs in Numerical Taxonomy by A.M.F. Cadete of the Centro de Cálculo Científico, of the Gulbenkian Science Foundation, Oeiras, Portugal.

RESULTS

The results are summarized in Fig. 1 (Weighted Average Linkage), Fig. 2 (Unweighted Average Linkage), Fig. 3 (Single Linkage) and table 2 (Reduced Matrix of Similarity Coefficients).

TABLE 2

Matrix of similarity coefficients for 10 selected OTU's (The similarity values are the same as those in the initial similarity matrix)

OTU Nº	01	02	03	05	06	07	08	09	10
02	.758								
03	.947	.757							
05	.649	.652	.782						
06	.682	.695	.806	.869					
07	.814	.818	.816	.752	.840				
08	.764	.774	.822	.809	.888	.899			
09	.843	.853	.840	.759	.808	.879	.863		
10	.745	.771	.821	.796	.862	.837	.882	.862	
11	.707	.702	.795	.854	.872	.807	.863	.818	.837

Fig. 1 shows that the group with the species *Apis mellifera* (12), *Euglossa cordata* (15), *Melitoma segmentaria* (19), *Megachile paulistana* (20), *Centris tarsata* (17), *Epicharis cockerelli* (18), *Bombus atratus* (13), *Xylocopa muscaria* (16), *Anthidium manicatum* (21). *Oxaea flavescens* (23) and *Eulaema nigrita* (14) should be discarded for two reasons: it did not contain any of two fossil bees; and, on the other hand, it contained 7 of the 8 "indicators". In this case the group: *Trigona devicta* (01), *Trigona iridipennis* (03), *Electrapis proava* (02), *Melipona quadrifasciata* (04), *Melipona scutellaris* (05), *Melipona puncticollis* (06), *Meliponula bocandei* (11), *Scaptotrigona postica* (07), *Scaptotrigona tubiba* (08), *Augochloropsis cupreola* (22), *Oxytrigona tataira* (09), and *Trigona hyalinata* (10) is left for futher analysis. From Fig. 2 the following group, not discarded, contains bees: 01, 02, 03, 07, 08, 09, 10 and one "indicator" (22). Finally, in Fig. 3 the non-discarded group contains the bees 01, 03, 04, 05, 06, 07, 08, 10, 09, 12, 11, 15, 02 plus the "indicators" 22 and 19. Taking this information into account the species in Table 2, were clustered using the "Weighted Pair-Group Method" **(Sneath & Sokal,** 1973). Fig. 4 shows the dendrogram obtained by this method; it gives the final position of both fossils, *Tetragona devicta* and *Electrapis proava*.

DISCUSSION

According to **Nelson** (1972) the systematist faces three positions: a) the classification should closely express the group phylogeny; b) the classification is an artifice, useful for the phylogenetic studies and; c) phylogeny and classification should be undertaken independently. Our position is the second, especially in this case where we are trying to determine the positon of two fossil bees.

The final result of this study (Fig. 4) confirms **Kerr** and **Maule** (1964) as far as the position of the Miocene fossil *Tetragona devicta* is concerned, that is, that it is very close to the present *Tetragona iridipennis* which still inhabits the same area. The similarity coefficient between these two species is 0.947.

Electrapis proava possesses the greatest similarity coefficient with *Oxytrigona tataira* (0.840) followed by *Scaptotrigona tubiba* (0.822) and *T. hyalinata* (0.821). The two species of *Melipona* have among themselves a coefficient of similarity of 0.869, and the two of *Scaptotrigona* a coefficient of similarity of 0.899. These values suggest that *Electrapis proava* is a Meliponini associated to superior South American *Trigonas,* all of which possess communication by trail marking.

Manning (1960) divided the fossil genus *Electrapis* in three subgenera: *Electrapis (Electrapis)* Cockerell (1909), *Electrapis (Protobombus)* Cockerell (1909), and *Electrapis (Roussyana)* Manning (1960) to which *E. proava* belongs. Since Manning attributes *Apis*-like characters to the first subgenus and *Bombus*-like body and *Apis*-like venation to the second, it is obvious that after the present results *E. proava* should be included in the Meliponini and called *Trigona (Roussyana) proava,* according to the classification of Moure (**Wille** & **Michener,** 1973). Probably the Oligocene fossil *Apis palmnickenensis* Roussy, that is considered by **Manning** (1960) as belonging to the subgenus *Roussyana,* is also a *Trigona (Roussyana) palmnickenensis.* This conjecture is supported by plate 13 of **Roussy** (1937) which shows that *Apis palmnickenensis* has many *Trigona*-like characteristics.

ACKNOWLEDGMENTS

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RESUMEN

Los resultados de ubicación de dos abejas fósiles, usando métodos de taxonomía numérica, indican que ambas, *Meliponorytes devictus* y *Electrapis proava,* pertenecen a la tribu Meliponini (Apidae). Se confirmó a *M. devictus* como *Tetragona devicta.* Por su fuerte asociación con las trigonas superiores *(Trigona, Scaptotrigona, Oxytrigona)* y de acuerdo con las diferentes escuelas taxonómicas existentes, *E. proava* debería llamarse *Trigona (Roussyana) proava,* o simplemente *Roussyana proava.*

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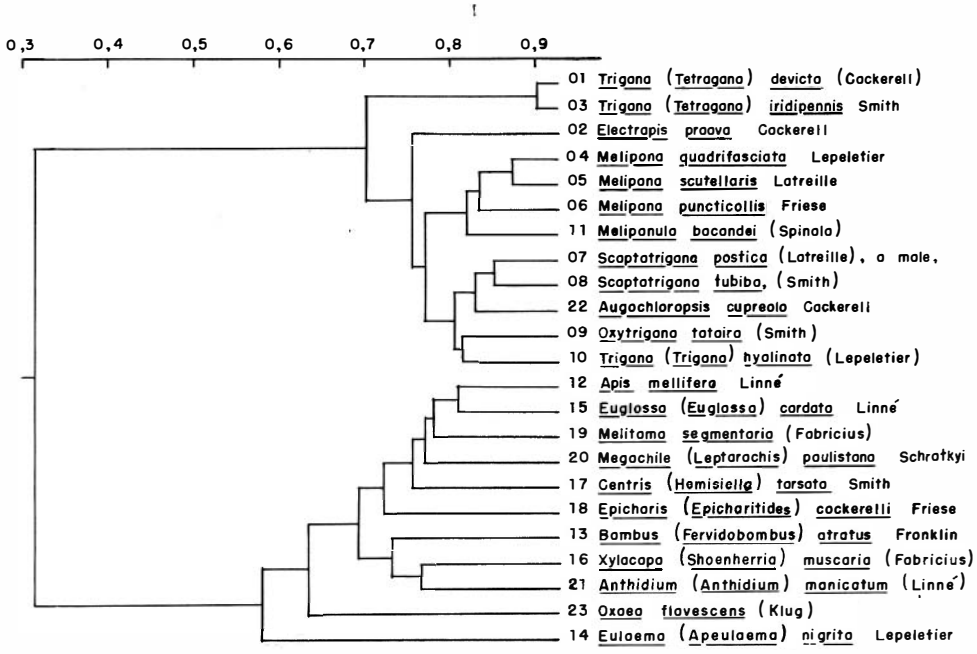
Fig. 1. Diagram of relationship for the 23 OTU's obtained by the Weighted Average Linkage method.
Cophenetic correlation: r = 0.52.

Fig. 2. Diagram of relationships for the 23 OUT's obtained by the Unweighted Average Linkage method.
Cophenetic correlation: r = 0.73.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01 Trigona (Tetragona) devicta (Cockerell)
03 Trigona (Tetragona) iridipennis Smith
02 Electrapis praeva Cockerell
04 Melipona quadrifasciata Lepeletier
05 Melipona scutellaris Latreille
06 Melipona puncticollis Friese
11 Meliponula bocandei (Spinola)
07 Scaptotrigona postica (Latreille), a male,
08 Scaptotrigona tubiba, (Smith)
22 Augochloropsis cupreola Cockerell
09 Oxytrigona tataira (Smith)
10 Trigona (Trigona) hyalinata (Lepeletier)
12 Apis mellifera Linné
15 Euglossa (Euglossa) cordata Linné
19 Melitoma segmentaria (Fabricius)
20 Megachile (Leptorachis) paulistana Schrottkyi
17 Centris (Hemisiella) tarsata Smith
18 Epicharis (Epicharitides) cockerelli Friese
13 Bombus (Fervidobombus) atratus Fronklin
16 Xylocopa (Shoenherria) muscaria (Fabricius)
21 Anthidium (Anthidium) manicatum (Linné)
23 Oxaea flavescens (Klug)
14 Eulaema (Apeulaema) nigrita Lepeletier

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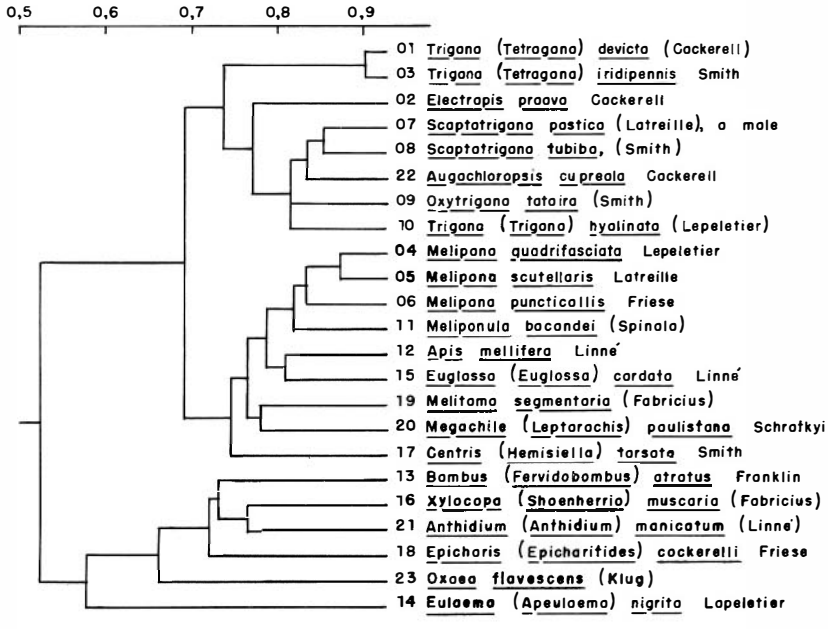
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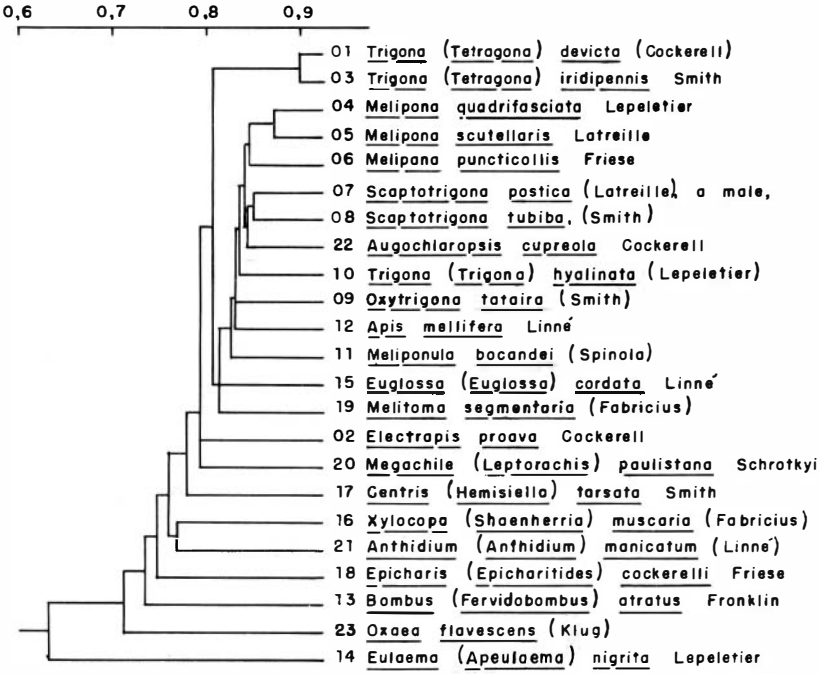
20 Megachile (Leptorachis) paulistana Schrottkyi
17 Centris (Hemisiella) tarsata Smith
13 Bombus (Fervidobombus) atratus Fronklin
16 Xylocopa (Shoenherria) muscaria (Fabricius)
21 Anthidium (Anthidium) manicatum (Linné)
18 Epicharis (Epicharitides) cockerelli Friese
23 Oxaea flavescens (Klug)
14 Eulaema (Apeulaema) nigrita Lepeletier

2

Fig. 3. Diagram of relationships for the OTU's obtained by the Single Linkage method. Cophenetic correlation: $r = 0.78$.

Fig. 4. Diagram of relationships for 10 selected OTU's obtained by the Weighted Pair Group method using aritmethic averages.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17 Gentris (Hemisiella) tarsata Smith
16 Xylocopa (Shaenherria) muscaria (Fabricius)
21 Anthidium (Anthidium) manicatum (Linné)
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13 Bombus (Fervidobombus) atratus Fronklin
23 Oxaea flavescens (Klug)
14 Eulaema (Apeulaema) nigrita Lepeletier

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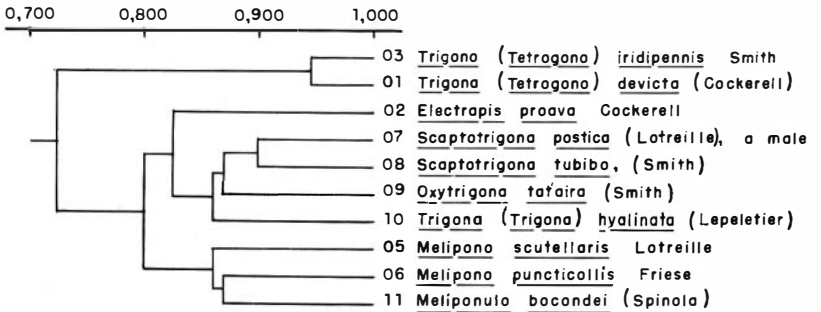
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