



A cladistic analysis of Gorytina (Hymenoptera: Crabronidae: Bembicini), with a reclassification of the subtribe

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Abstract

Based on a cladistic analysis of the digger wasp subtribe Gorytina, the subtribes Argogorytina Nemkov and Lelej 1996, **stat. resurr.** (consisting of *Argogorytes* Ashmead 1899, *Neogorytes* Bohart in Bohart and Menke 1976, and *Paraphilanthus* Vardy 1995), and Trichogorytina, **subtrib. nov.** (genus *Trichogorytes* Rohwer 1912 only) are removed from Gorytina. The genus *Pterygorytes* Bohart 1967 is transferred to Handlirschiina. New generic synonyms are: *Pseudoplisus* Ashmead 1899, and *Leiogorytes* Bohart 2000 = *Gorytes* Latreille 1805; and *Malaygorytes* Nemkov 1999 = *Argogorytes* Ashmead 1899. Thirteen species originally described in *Pseudoplisus* are transferred to *Gorytes* (**new comb.**): *P. butleri* Bohart 1969, *P. californicus* Bohart 1969, *P. catalinae* Bohart 1969, *P. claripennis* Bohart 1969, *P. erugatus* Bohart 1969, *P. flavidulus* Bohart 1969, *P. hadrus* Bohart 1969, *P. imperialis* Bohart 1969, *P. nigricomus* Bohart 1969, *P. ocellatus* Bohart 1969, *P. samiatius* Bohart 1969, *P. willcoxi* Ohl 2009, and *P. tanythrix* Bohart 1969. Also transferred to *Gorytes* (**new comb.**) are *Leiogorytes guerrero* Bohart 2000, *Arpactus nyasicus* R. Turner, 1915 and the following twelve species originally described in *Gorytes* but currently placed in *Pseudoplisus*: *G. abdominalis* Cresson 1865, *G. aequalis* Handlirsch 1888, *G. divisus* F. Smith 1856, *G. effugiens* Brauns 1911, *G. fasciatus* W. Fox 1896, *G. montanus* Cameron 1890, *G. natalensis* F. Smith 1856, *G. ranosahae* Arnold 1945, *G. rubiginosus* Handlirsch 1888, *G. rufomaculatus* W. Fox 1896, *G. smithii* Cresson 1880, and *G. venustus* Cresson 1865. *Malaygorytes konishii* (Nemkov 1999) is transferred to *Argogorytes* (**new comb.**). Updated diagnoses of *Gorytes* and *Argogorytes* are provided.

Key words: Argogorytina, Trichogorytina, digger wasps, classification

Introduction

This study began with Nemkov's (1999) examination of *Gorytes ishigakiensis* Tsuneki 1982. This Far East species combines the diagnostic characters of both *Gorytes* Latreille 1805 and *Pseudoplisus* Ashmead 1899. According to Bohart and Menke (1976), these two genera are closely similar, but differ in the sculpture of the propodeal enclosure and the length of gastral segment I. In *G. ishigakiensis*, the propodeal enclosure is all ridged (as in *Gorytes*), but gastral segment I is elongate (as in *Pseudoplisus*). Except for the sculpture of the propodeal enclosure (and some other less important characters), the species is almost identical to the Eurasian *G. kohlii* (Handlirsch 1888). Subsequently, we found an identical situation in the male of the South African *G. jonesi* R. Turner, 1920 (propodeal enclosure all ridged, length of tergum I $1.8 \times$ its apical width), the female of which is unknown. A study of additional material showed that the propodeal enclosure of some *Gorytes* is largely smooth and ridged only basally, e.g., *G. africanus* Mercet, 1905, *G. maculicornis* (F. Morawitz 1889), *G. quinquefasciatus intercedens* Handlirsch 1893, and *G. sulcifrons mongolicus* Tsuneki 1971 (Nemkov 1999). Furthermore, in some species of *Pseudoplisus*, the gaster is sessile (e.g., *P. californicus* Bohart 1969,

P. divisus (F. Smith 1856), and *P. ocellatus* Bohart 1969). These facts cast doubt about the validity of separating *Pseudoplisus* from *Gorytes*.

Subsequently, Nemkov (2007) demonstrated that *Pseudoplisus*, as understood by Bohart (1969a, 1969b) and Bohart and Menke (1976), was highly heterogeneous, and he placed the *phaleratus* group (first recognized by Bohart 1969a) in a new genus that he called *Saygorytes*.

In April 2007, a grant to visit the California Academy of Sciences allowed P.G. Nemkov to examine a number of gorytine genera described by Bohart (2000). It became clear at that point that the existing classification of Gorytina (including the validity of *Gorytes* and *Pseudoplisus*) should be reassessed using a cladistic methodology, and Pulawski joined him in this undertaking.

Descriptive terminology follows Bohart and Menke (1976).

Subtribe Gorytina

Gorytina Lepeletier de Saint Fargeau 1845. Based on *Gorytes* Latreille (stem: *Goryt-*). Originally spelled Gorytites, latinized to Gorytinae by Dalla Torre 1897. Spelled Goritini by A. Costa 1859 (Italian vernacular), and Gorytesii by Acloque 1897.

Arpactina R. Turner 1915. Based on *Arpactus* Panzer 1805 (stem: *Arpact-*).

Hoplisina Rohwer 1916. Based on *Hoplisus* Lepeletier de Saint Fargeau 1832 (stem: *Hoplis-*).

Taxonomic rank. Gorytina are variously ranked. Bohart and Menke (1976) subdivided the subfamily Bembicinae (their Nyssoninae) into six tribes: Heliocausini, Alyssontini, Nyssonini, Gorytini, Stizini, and Bembecini. Bohart (2000) also recognized Gorytini as a tribe. Hanson and Menke 2006 (based on Prentice 1998, unpublished doctoral thesis) recognized only three tribes within Bembicinae: Alyssontini, Bembicini, and Nyssonini, and reduced Gorytini to one of six subtribes of Bembicini. We accept Prentice's proposed classification (Hanson & Menke 2006), as it is based on a much more detailed study of morphological characters and a cladistic analysis, rather than on a purely comparative approach.

Recognition. Gorytina are members of the tribe Bembicini, as demonstrated by the following characters: midcoxae close to each other, metapleuron with greatly reduced ventral area, separated from the propodeum by sulcus, forewing with three submarginal cells, propodeum dorsolaterally without spines or teeth, and gastral sternum I with basomedian ridge.

Gorytina differ from the other subtribes of Bembicini (Bembicina, Exeirina, Handlirschiina, Heliocausina, and Stizina) in having the following character complex: palpal formula 6+4 (5+3, 4+2 or 3+1 in some Bembicina); labrum not or barely exposed or, if prominent, its exposed part at most one-third as long as broad (exposed part one-third or more as long as broad in Bembicina and some Handlirschiina and Stizina); inner eye margins of female almost parallel to conspicuously converging toward clypeus (converging above in Heliocausina and some Bembicina), nearly straight from upper clypeal margin to midocellus level (markedly convex in Exeirina); ocelli not deformed, well developed (deformed, ill defined in Heliocausina and Bembicina); scutellum not overlapping metanotum (overlapping in Bembicina, Stizina and some Handlirschiina); forewing submarginal cell II not petiolate (petiolate in some Exeirina); male sternum II without keel-like elevation (elevation present in Heliocausina and some Bembicina); male sternum VIII apically with one or two prongs (with three prongs in Stizina); male volsella differentiated into cuspis and digitus (not differentiated in some Handlirschiina); female pygidial plate well-defined (ill defined or absent in Heliocausina, Stizina and some Bembicina).

Currently Recognized Genera. *Afrogorytes* Menke 1967, *Allogorytes* Bohart 2000, *Argogorytes* Ashmead 1899, *Arigorytes* Rohwer 1912, *Aroliagorytes* Bohart 2000, *Austrogorytes* Bohart 1967, †*Biamogorytes* Nemkov 1990, *Eogorytes* Bohart in Bohart and Menke 1976, *Epigorytes* Bohart 2000, *Gorytes* Latreille 1805, *Hapalomellinus* Ashmead 1899, *Harpactostigma* Ashmead 1899, *Harpactus* Shuckard 1837, *Hoplisoides* Gribodo 1884, *Leiogorytes* Bohart 2000, *Lestiphorus* Lepeletier de Saint Fargeau 1832, *Leurogorytes* Bohart 2000, *Liogorytes* Bohart 1967, *Malaygorytes* Nemkov 1999, *Megistommum*

W. Schulz 1906, *Neogorytes* Bohart in Bohart and Menke 1976, *Oryttus* Spinola 1836, *Paraphilanthus* Vardy 1995, *Psammaecius* Lepeletier de Saint Fargeau 1832, *Psammaletes* Pate 1936, *Pseudoplisus* Ashmead 1899, *Pterygorytes* Bohart 1967, *Sagenista* Bohart 1967, *Saygorytes* Nemkov 2007, *Stenogorytes* Schrottky 1911, *Stethogorytes* Bohart 2000, *Tretogorytes* Bohart 2000, *Trichogorytes* Rohwer 1912, and *Xerogorytes* Bohart in Bohart and Menke 1976.

Trachogorytes Bohart 2000, treated as a member of Gorytini by its author, was synonymized with *Mellinus* by Pulawski (2007).

Sources of material

This study is based on the material from the following institutions:

Bohart Museum of Entomology, University of California, Davis, California, USA (Steven L. Heydon): various taxa;
California Academy of Sciences, San Francisco, California, USA, various taxa;
Institute of Biology and Soils Science, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia: various taxa;
Naturhistorisches Museum, Wien, Austria (Dominique Zimmermann): *Aroliagorytes imitator*, holotype, *Pseudoplisus rubiginosus*, syntypes;
The Natural History Museum, London, United Kingdom (Christine Taylor): *Leiogorytes guerrero* including holotype, *Pseudoplisus nyasicus* including holotype, *Pterygorytes triangularis* including holotype;
United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (Brian Harris): *Paraphilanthus costaricae*, paratype, *Pseudoplisus fasciatus*, *Pseudoplisus venustus*;
Utah State University, Logan, Utah, USA (Terry L. Griswold): *Allogorytes bifasciatus*;
Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (Vladimir I. Tobias): various taxa;
Zoological Museum, Moscow State University, Moscow, Russia (Alexandr V. Antropov): various taxa.

Species examined

Altogether, the following 242 species and subspecies belonging to 37 genera have been studied:

Afrogorytes Menke 1967: *A. monstrosus* (Handlirsch in Kohl 1894).

Allogorytes Bohart 2000: *A. bifasciatus* (Brèthes 1909)

Argogorytes Ashmead 1899: *A. areatus* (Taschenberg 1875), *A. carbonarius* (F. Smith 1856), *A. fairmairei* (Handlirsch 1893), *A. fargeii* (Shuckard 1837), *A. hispanicus* (Mercet 1906), *A. mystaceus* *mystaceus* (Linnaeus 1761), *A. mystaceus grandis* (Gussakovskij 1932), *A. nigrifrons* (F. Smith 1856), *A. nipponis* Tsuneki 1963, *A. umbratilis* Bohart 2000.

Arigorytes Rohwer 1912: *A. coachellae* Bohart 1971, *A. insolitus* (W Fox, 1896), *A. ruficrus* Bohart 1971, *A. smohalla* Pate 1947.

Aroliagorytes Bohart 2000: *Aroliagorytes imitator* (Handlirsch 1901).

Austrogorytes Bohart 1967: *A. bellicosus* (F. Smith 1862).

Eogorytes Bohart in Bohart and Menke 1976: *E. fulvohirtus* (Tsuneki 1963).

Epigorytes Bohart 2000: *E. flavidalis* Bohart 2000.

Exeirus Shuckard, 1838: *E. lateritius* Shuckard 1838.

Gorytes Latreille 1805: *G. foveolatus* group: *G. foveolatus* Handlirsch 1888, *G. procrustes* Handlirsch 1888; *G. hebraeus* group: *G. hebraeus* de Beaumont 1953; *G. kohlii* group: *G. kohlii* Handlirsch 1888, *G. ishigakiensis* Tsuneki 1982; *G. jonesi* (R. Turner 1920); *G. laticinctus* group: *G. albidulus* (Lepeletier de Saint Fargeau 1832), *G. ambiguus* Handlirsch 1888, *G. atricornis* Packard 1867, *G. atrifrons* W. Fox 1892, *G. canaliculatus* Packard 1867, *G. laticinctus laticinctus* (Lepeletier 1832), *G. laticinctus koreanus* Handlirsch 1888, *G. nevadensis* W. Fox 1892, *G. planifrons* (Wesmael 1852), *G. prosopis* Bohart 1971, *G. tricinctus* Pérez 1905, *G. umatillae* Bohart 1971; *G. neglectus* group: *G. aino* Tsuneki 1963, *G. limbellus* Bohart 1971,

G. neglectus Handlirsch 1895; *G. pleuripunctatus* group: *G. pleuripunctatus pleuripunctatus* (A. Costa 1859), *G. pleuripunctatus barbarus* de Beaumont 1953; *G. quinquecintus* group: *G. angustus* (Provancher 1895), *G. maculicornis* (F. Morawitz 1889), *G. mcateei* Krombein and Bohart in Krombein 1962, *G. nigrifacies* (Mocsáry 1879), *G. quinquecintus* (Fabricius 1793), *G. schlettereri schlettereri* Handlirsch 1893, *G. schlettereri ponticus* de Beaumont 1967, *G. schmiedeknechti* Handlirsch, 1888 *G. sulcifrons sulcifrons* (A. Costa 1869), *G. sulcifrons mongolicus* Tsuneki 1971; *G. quinquefasciatus* group: *G. africanus* Mercet 1905, *G. deceptor* Krombein 1958, *G. fallax* Handlirsch 1888, *G. pieli* Yasumatsu 1943, *G. provancheri* Handlirsch 1895, *G. quinquefasciatus quinquefasciatus* (Panzer 1798), *G. quinquefasciatus levantinus* Pulawski 1961, *G. simillimus* F. Smith 1856, *G. tobiasi* Nemkov 1990.

Handlirschia Kohl 1897: *H. scoliaeformis* (Arnold 1929).

Hapalomellinus Ashmead, 1899: *H. albitomentosus* (Bradley 1920), *H. pulvis* Bohart 1971, *H. teren* Pate 1946.

Harpactostigma Ashmead 1899: *H. velutinum* (Spinola 1851)

Harpactus Shuckard, 1837: *H. affinis* (Spinola 1808), *H. alvaroi* Gayubo 1992, *H. annulatus* Eversmann 1849, *H. arenarum* (de Beaumont 1953), *H. betpakdalensis* Kazenas 1988, *H. clypeatus* (Bohart 1980), *H. coccineus* (Balthasar 1954), *H. consanguineus* (Handlirsch 1888), *H. creticus* (de Beaumont 1965), *H. croaticus* Vogrin 1954, *H. dimorphus* (Pulawski 1979), *H. elegans* (Lepeletier de Saint Fargeau 1832), *H. exiguus* (Handlirsch 1888), *H. fertoni* (Handlirsch in Kohl and Handlirsch 1910), *H. formosus formosus* (Jurine 1807), *H. formosus ferrugatus* (Gussakovskij 1928), *H. guichardi* (de Beaumont 1968), *H. gyponae* F. Williams 1914, *H. hissaricus* (Gussakovskij 1952), *H. histrio* (de Saussure 1892), *H. immaculatus* (Pulawski 1979), *H. kazakhstanicus* Nemkov 1996, *H. kazenasi* Nemkov 1994, *H. kohli* Nemkov 1994, *H. laevis laevis* (Latreille 1792), *H. laevis aegyptiacus* (W. Schulz 1904), *H. leucurus* (A. Costa 1884), *H. lunatus* (Dahlbom 1832), *H. mendicus* (Handlirsch 1893), *H. montanus* Kazenas 1992, *H. morawitzi* Radoszkowski 1884 (= *moravicus* Šnoflak 1946), *H. mundus* (de Beaumont 1950), *H. obscurus* (de Beaumont 1969), *H. octonotatus* Kazenas 1992, *H. pictifrons* (W. Fox 1894), *H. pollux* (Handlirsch 1898), *H. pulchellus* (A. Costa 1859), *H. pyrrhobasis* (Morice 1911), *H. quadrisignatus quadrisignatus* (Palma 1867), *H. quadrisignatus ifranensis* (Nadig 1933), *H. quinquefasciatus* Kazenas 1989, *H. rufithorax* (Brauns 1911), *H. rugosus* Nemkov 1994, *H. rugulosus* (Bohart 1980), *H. russulus* (Bohart 1980), *H. schwarzi* (de Beaumont 1965), *H. tauricus* Radoszkowski 1884, *H. tjanshanicus* Kazenas 1992, *H. transbaikalicus* Nemkov 1994, *H. transcaspicus* (Kokujev 1909), *H. transcaucasicus* Nemkov 1994, *H. tumidus tumidus* (Panzer 1801), *H. tumidus dimidiatus* Kazenas 1989, *H. walteri* (Handlirsch 1888).

Hoplisoides Gribodo, 1884: *H. alaya* (Pate 1947), *H. carinatus* Bohart 1968, *H. cazieri* Bohart 1968, *H. confertus* (W. Fox 1896), *H. craverii* (A. Costa, 1867), *H. dentatus* (W. Fox 1893), *H. denticulatus* (Packard 1867), *H. diversus* (W. Fox 1896), *H. ferrugineus* (Spinola 1839), *H. fuscus* (Taschenberg 1875), *H. gazagnairei gazagnairei* (Handlirsch 1893), *H. gazagnairei distinguendus* (Yasumatsu 1939), *H. glabratus* Bohart 1968, *H. hamatus* (Handlirsch 1888), *H. iheringii* (Handlirsch 1893), *H. iridipennis* (F. Smith 1856), *H. jordani* (Handlirsch 1895), *H. latifrons* (Spinola 1808), *H. metapleura* Bohart 2000, *H. ovatus* Bohart 2000, *H. parkeri* Bohart 1997, *H. placidus placidus* (F. Smith 1856), *H. placidus nebulosus* (Packard 1867), *H. punctifrons* (Cameron 1890), *H. punctuosus* (Eversmann 1849), *H. pygidialis* (W. Fox 1896), *H. quedenfeldti* (Handlirsch 1895), *H. ruficeps* Bohart 2000, *H. semipunctatus* (Taschenberg 1875), *H. spiloferus* (Handlirsch 1888), *H. splendidulus* (Bradley 1920), *H. thalia* (Handlirsch 1895), *H. tricolor* (Cresson 1868), *H. vespoides* (F. Smith) 1873.

Leiogorytes Bohart 2000: *L. guerrero* Bohart 2000.

Lestiphorus Lepeletier de Saint Fargeau 1832: *L. bicinctus* (Rossi 1794), *L. bilunulatus* A. Costa 1869, *L. cockerelli* (Rohwer 1909), *L. egregius* (Handlirsch 1893), *L. oreophilus* (Kuznetzov-Ugamskij 1927), *L. pacificus* (Gussakovskij 1932), *L. piceus* (Handlirsch 1888), *L. pictus* Nemkov 1992.

Leurogorytes Bohart 2000: *L. stangei* Bohart 2000.

Liogorytes Bohart 1967: *L. cordobensis* (Fritz 1964), *L. polybia* (Handlirsch 1895), *L. schrottkyi* (Fritz 1964), *L. uncinatus* (Brèthes 1913).

Malaygorytes Nemkov 1999: *M. konishii* Nemkov 1999.

Megistommmum W. Schulz 1906: *M. evansi* Bohart 2000, *M. politum* (F. Smith 1873), *M. procerus* (Handlirsch 1888), *M. splendidum* (Handlirsch 1888).

Neogorytes Bohart in Bohart and Menke 1976: *N. hansonii* Bohart 2000.

Olgia Radoszkowski 1877: *O. helena* de Beaumont 1953, *O. maracandica* (Radoszkowski 1877), *O. modesta* Radoszkowski 1877, *O. spinulosa* de Beaumont 1953.

Oryttus Spinola 1836: *O. concinnus* (Rossi 1790), *O. cribratus* (F. Morawitz 1892), *O. dives* Nemkov 1992, *O. gracilis* (Patton 1879), *O. infernalis* (Handlirsch 1888), *O. kaszabi* Tsuneki 1971, *O. laminiferus* (W. Fox 1896), *O. umbonatus* (C. Baker 1907).

Paraphilanthus Vardy 1995: *Paraphilanthus costaricae* Vardy 1995.

Psammaecius Lepelletier de Saint Fargeau 1832: *P. luxuriosus* (Radoszkowski 1877), *P. punctulatus* (Vander Linden 1829), *P. versicolor* (de Beaumont 1959).

Psammaletes Pate 1936: *P. bigeloviae* (Cockerell 1897), *P. costaricae* Bohart 2000, *P. mexicanus* (Cameron 1890), *P. schlingeri* Bohart 2000.

Pseudoplisus Ashmead 1899: *P. abdominalis* (Cresson 1865), *P. aequalis* (Handlirsch 1888), *P. californicus* Bohart 1969, *P. catalinae* Bohart 1969, *P. divisus* (F. Smith 1856), *P. effugiens* (Brauns 1911), *P. erugatus* Bohart 1969, *P. fasciatus* (W. Fox 1896), *P. montanus* (Cameron 1890), *P. natalensis* (F. Smith 1856), *P. nigricornis* Bohart 1969, *P. nyasicus* (R. Turner 1915), *P. ocellatus* Bohart 1969, *P. ranosahae* (Arnold 1945), *P. rubiginosus* (Handlirsch 1888), *P. rufomaculatus* (W. Fox 1896), *P. samiatius* Bohart 1969, *P. smithii* (Cresson 1880), *P. tanythrix* Bohart 1969, *P. venustus* (Cresson 1865), *P. willcoxi* Ohl 2009.

Pterygorytes Bohart 1967: *P. triangularis* (F. Smith 1873).

Sagenista Bohart 1967: *S. brasiliensis* (Shuckard 1838), *S. cayennensis* (Spinola 1841), *S. kimseyorum* Bohart 2000, *S. pilosa* Bohart 2000, *S. scutellaris* (Spinola 1841).

Saygorytes Nemkov 2007: *S. phaleratus* (Say 1837), *S. tritospilus* (Bohart 1969).

Sphēcicus Dahlbom 1843: *S. antennatus* (Klug 1845), *S. conicus conicus* (Germar 1817), *S. conicus syriacus* (Klug 1845), *S. lutescens* (Radoszkowski 1877), *S. nigricornis* (Dufour 1838), *S. persa* Gussakovskij 1933, *S. uljanini* (Radoszkowski 1877).

Stenogorytes Schrottky 1911: *S. bruchi* (Schrottky 1909), *S. facilis* (F. Smith 1873), *S. foxii* (Handlirsch 1901), *S. notabilis* (Handlirsch 1888), *S. porteri* Bohart 2000, *S. specialis* (F. Smith 1873).

Stethogorytes Bohart 2000: *S. volcano* Bohart 2000.

Tretogorytes Bohart 2000: *T. sinuosus* Bohart 2000.

Trichogorytes Rohwer 1912: *T. argenteopilosus* Rohwer 1912, *T. cockerelli* (Ashmead 1899).

Xerogorytes Bohart in Bohart and Menke 1976: *X. anaetis* (Pate 1947).

Cladistic Analysis

Terminal taxa. In most cases, genera have been selected as terminal taxa, because they are either monotypic or homogenous. However, the species groups in *Gorytes* and the species in *Pseudoplisus* have been recognized as terminal taxa because these two genera consist of diverse elements whose generic affiliation needed confirmation.

To recognize phylogenetic affinities of *Pseudoplisus*, *Gorytes*, and other genera of Gorytina, and to test their subtribal position, we selected as the ingroup the following 59 taxa: *Afrogorytes*, *Allogorytes*, *Argogorytes*, *Arigorytes*, *Aroliagorytes*, *Austrogorytes*, *Eogorytes*, *Epigorytes*, *Gorytes foveolatus* group, *Gorytes hebraeus* group, *Gorytes kohlii* group, *Gorytes laticinctus* group, *Gorytes neglectus* group, *Gorytes pleuripunctatus* group, *Gorytes quinquecintus* group, *Gorytes quinquefasciatus* group, *Hapalomellinus*, *Harpactus*, *Harpactostigma*, *Hoplisoides*, *Leiogorytes*, *Lestiphorus*, *Leurogorytes*, *Liogorytes*, *Malaygorytes*, *Megistommmum*, *Neogorytes*, *Oryttus*, *Paraphilanthus*, *Psammaecius*, *Psammaletes*, *Pseudoplisus abdominalis*, *Pseudoplisus aequalis*, *Pseudoplisus californicus*, *Pseudoplisus catalinae*, *Pseudoplisus divisus*,

Pseudoplisus erugatus, *Pseudoplisus fasciatus*, *Pseudoplisus montanus*, *Pseudoplisus natalensis*, *Pseudoplisus nigricornis*, *Pseudoplisus nyasicus*, *Pseudoplisus ocellatus*, *Pseudoplisus ranosahae*, *Pseudoplisus rubiginosus*, *Pseudoplisus rufomaculatus*, *Pseudoplisus smithii*, *Pseudoplisus samiatu*, *Pseudoplisus tanythrix*, *Pseudoplisus venustus*, *Pseudoplisus willcoxi*, *Pterygorytes*, *Sagenista*, *Saygorytes*, *Stenogorytes*, *Stethogorytes*, *Tretogorytes*, *Trichogorytes*, and *Xerogorytes*.

As outgroups, we chose four genera from two subtribes related to Gorytina: *Exeirus* (Exeirina), *Olgia* (Exeirina), *Handlirschia* (Handlirschiina), and *Sphecius* (Handlirschiina).

Characters. Forty-one binary and multistate characters of adult female and male external morphology were coded for analysis, all treated as unordered and unweighted. The following is a list of characters examined in this study:

1. Labrum: 0. not or barely exposed, 1. prominent, exposed part nearly half as long as broad.
2. Female mandible: 0. one-toothed, 1. two-toothed, 2. three-toothed.
3. Female inner eye margins: 0. nearly parallel (distance at level of antennal socket at least $0.9 \times$ that at level of midocellus), 1. moderately converging toward clypeus ($0.8-0.7 \times$ that at level of midocellus), 2. strongly converging toward clypeus (0.6 or less \times that at level of midocellus).
4. Female antennal sockets: 0. positioned next to clypeus, 1. one diameter or nearly so above clypeus.
5. Male four apical flagellomeres: 0. not modified, 1. one or more modified (concave, curved, etc.).
6. Acetabular carina: 0. absent, 1. present, short (not longer than three midocellus diameters), not elevated medially, 2. present, short (not longer than three midocellus diameters), elevated medially, 3. present, long (much longer than three midocellus diameters).
7. Episternal sulcus: 0. absent, 1. present, continued downward almost vertically, 2. present, curving backward.
8. Omaulus: 0. absent, 1. present, not toothed below, 2. present, toothed below.
9. Subomaulus: 0. absent or obscure, without projections, 1. well defined, continued below in nearly straight line to ventral middle carina, next to it somewhat bent and projecting, almost tooth-shaped.
10. Sternaulus: 0. absent, 1. present.
11. Metapleuron: 0. gradually tapering below or nearly parallel-sided, 1. broadening below.
12. Admedian scutal lines: 0. broadly separated, 1. joining to form median carina.
13. Posterolateral oblique scutal carina: 0. absent, 1. present.
14. Oblong depression on admedian side of oblique scutal carina: 0. absent, 1. present.
15. Axilla: 0. small (space between axillae much more than their width), 1. large (space between axillae not more than their width).
16. Anterior scutellar sulcus: 0. efoveate, 1. foveate.
17. Scutellum: 0. not overlapping metanotum, 1. overlapping metanotum.
18. Female scutellum: 0. without depression, 1. with posteromedian pubescent depression.
19. Metapleural posterior suture: 0. simple, 1. simple below and foveolate above, 2. foveolate.
20. Propodeal enclosure: 0. entirely smooth or punctate, without rugae, 1. mostly smooth, rugose anteriorly, 2. mostly or entirely rugose.
21. Propodeal enclosure median line: 0. absent, 1. present.
22. Lateral sulcus of propodeal enclosure: 0. shallow, seamlike, 1. deep, furrowlike.
23. Spiracular groove: 0. absent, 1. present.
24. Propodeal posterior surface: 0. unsculptured or punctate, 1. at least partly rugose or areolate.
25. Body pubescence: 0. not concealing integument, 1. largely concealing integument.
26. Female arolia: 0. nearly equal in size, 1. enlarged on foreleg, markedly larger than on midleg and hindleg, 2. enlarged on foreleg and midleg, markedly larger than on hindleg.
27. Female foretarsal rake: 0. absent, 1. present, outer margin of basitarsus without long spines before apex, 2. present, outer margin of basitarsus with two long preapical spines, 3. present, outer margin of basitarsus with three or more long preapical spines (regarded as apical are one spine at the very end of the forebasitarsus and one adjacent to it).

28. Forewing stigma: 0. moderately large, 1. minute.
29. Forewing submarginal cell I: 0. without remnant of *Ir*, 1. with short remnant of *Ir*.
30. Forewing submarginal cell II: 0. not petiolate, 1. petiolate.
31. Forewing marginal cell: 0. not bent away from wing margin, 1. bent away from wing margin.
32. Hindwing media: 0. diverging well beyond *cu-a*, 1. diverging at or before *cu-a*.
33. Hindwing jugal lobe: 0. smaller than outline of tegula, 1. larger than outline of tegula.
34. Gastral segment I: 0. sessile, 1. slightly elongate (length about $1.5 \times$ apical width), 2. distinctly elongate (length of more than $1.5 \times$ apical width).
35. Gastral tergum I: 0. not nodose apically, 1. nodose apically.
36. Gastral terga II-IV: 0. simple, 1. double edged.
37. Male gaster: 0. with six visible terga, 1. with seven visible terga.
38. Male sterna III-VI: 0. simple, 1. III and IV and in some species V with dense apical fimbriae, 2. III-V with velvety setal mats.
39. Male sternum VIII: 0. one-pronged apically, 1. two-pronged apically.
40. Female pygidial plate (shape): 0. moderately wide, semielliptical, 1. moderately wide, triangular, with convex lateral edge, 2. moderately wide, triangular with straight lateral edge, 3. moderately wide, triangular, with concave lateral edge, 4. narrow, almost parallelsided.
41. Female pygidial plate (sculpture): 0. sparsely punctate, punctures several diameters apart, 1. moderately punctate, punctures approximately one diameter apart, 2. densely punctate, punctures practically contiguous, 3. longitudinally ridged.

Analysis. The data matrix is given in Table 1. It was constructed using the WinClada version 1.00.08 (Nixon 2002), where missing characters are represented by a question mark (?), and polymorphous characters are indicated by an asterisk (*).

The data were analyzed using the NONA version 2.0 (Goloboff 1993), with the following options: unconstrained heuristic search, maximum trees to keep (hold) = 10000, number of replications (mult*N) = 9999, starting trees per rep (hold/) = 1, random seed = 0, search strategy of multiple TBR + TBR (mult*max*). The program generated 900 equally parsimonious trees, each with 218 steps, consistency index of 27, and retention index of 62. The strict consensus tree, with 249 steps, consistency index of 23, and retention index of 54, is presented in Fig. 1.

Conclusions

Based on the resulting cladogram (Fig.1), we have drawn the following conclusions:

1. The genera described by Bohart (2000) are all valid, except for *Trachogorytes*, which is a synonym of *Mellinus* as demonstrated by Pulawski (2007), and *Leiogorytes*, which is herein synonymized with *Gorytes* (see below).

2. *Gorytes* Latreille 1805.

= *Pseudoplisus* Ashmead 1899, **syn. nov.**

= *Leiogorytes* Bohart 2000, **syn. nov.**

The genera *Pseudoplisus*, *Leiogorytes*, and *Gorytes* are not supported by any unique synapomorphy and are therefore paraphyletic. Furthermore, they cannot be clearly separated as they blend into each other (in particular, it is impossible, for the reasons explained above, to construct a key separating *Gorytes* from *Pseudoplisus*). We therefore synonymize *Pseudoplisus* and *Leiogorytes* with *Gorytes*. Thirteen species originally described in *Pseudoplisus* are transferred to *Gorytes* (**new comb.**): *P. butleri* Bohart 1969, *P. californicus* Bohart 1969, *P. catalinae* Bohart 1969, *P. claripennis* Bohart 1969, *P. erugatus* Bohart 1969, *P. flavidulus* Bohart 1969, *P. hadrus* Bohart 1969, *P. imperialis* Bohart 1969, *P. nigricomus* Bohart 1969, *P. ocellatus* Bohart 1969, *P. samiatius* Bohart 1969, *P. tanythrix* Bohart 1969, and *P. willcoxi* Ohl. Also

TABLE 1. Data matrix for the 63 taxa and 41 characters used in cladistic analysis.

Taxa	Characters				
	0	1	2	3	4
	1	1	1	1	1
<i>Sphecius</i>	10011321000011011000000000300001100010002				
<i>Handlirschia</i>	11011000000010000000100101310001100010012				
<i>Exeirus</i>	01010011000000000000101000300101100010022				
<i>Olgia</i>	00010011000000000000000000101000100011022				
<i>Afrogorytes</i>	01211322011111010022111000200001120010021				
<i>Allogorytes</i>	11211301110011010011110002300001101012121				
<i>Argogorytes</i>	010103110000000101121111000000001000100**				
<i>Arigorytes</i>	01111111010011010012111*00300001100012021				
<i>Aroliagorytes</i>	1121?0110100100100011111023000011000???33				
<i>Austrogoorytes</i>	01111011010011010002111101201000000010120				
<i>Eogorytes</i>	01111311010011010012111001200001110010020				
<i>Epigorytes</i>	01211311010011010011111000300001110010033				
<i>Gorytes foveolatus</i> group	02110111010011010012111100200001100010031				
<i>Gorytes hebraeus</i> group	02110111010011010012111100200001100010022				
<i>Gorytes kohlii</i> group	0221031101001001001*111100201001110010020				
<i>Gorytes laticinctus</i> group	02010111010011010012111100200001100010021				
<i>Gorytes neglectus</i> group	02110111010011010012111100200001100010021				
<i>Gorytes pleuripunctatus</i> group	02110311010011010012111100200001100010023				
<i>Gorytes quinquecintus</i> group	0211011101001101001*111*00200001100010023				
<i>Gorytes quinquefasciatus</i> group	02*1011101001101001*111*00200001100010021				
<i>Hapalomellinus</i>	01*10*100000110100001000003000001*1010020				
<i>Harpactus</i>	01011*1101001101001*111*00300000100010021				
<i>Harpactostigma</i>	01011111010011010022111101300001120010021				
<i>Hoplisoides</i>	0100131*010011010012111100300001100000021				
<i>Leiogorytes</i>	02100001000011010001111001200001111010020				
<i>Lestiphorus</i>	010010110*00100100121111013000011*1010121				
<i>Leurogorytes</i>	01211111010011010011111000300001110010123				
<i>Liogorytes</i>	01111011010011010020111000300001110000123				
<i>Malaygorytes</i>	0101?3110000000100121111000010001001???40				
<i>Megistommum</i>	02210111010011000000101000200001121010020				
<i>Neogorytes</i>	01010311010000000100111000000000120010023				
<i>Oryttus</i>	01011011010010010012111101300001110010122				
<i>Paraphilanthus</i>	0??10111000000000?0011100??000001000110??				
<i>Psammaecius</i>	011*1020110011010012111*0030000110001002*				

continued on next page

TABLE 1. (continued)

Taxa	Characters				
	0	1	2	3	4
	1	1	1	1	1
<i>Psammaletes</i>	0	1	0	0	0
<i>Pseudoplisus abdominalis</i>	0	2	2	0	0
<i>Pseudoplisus aequalis</i>	0	2	0	0	0
<i>Pseudoplisus californicus</i>	0	2	2	0	0
<i>Pseudoplisus catalinae</i>	0	2	2	0	0
<i>Pseudoplisus divisus</i>	0	2	2	0	0
<i>Pseudoplisus erugatus</i>	0	2	2	0	0
<i>Pseudoplisus fasciatus</i>	0	2	2	0	0
<i>Pseudoplisus montanus</i>	0	2	2	0	0
<i>Pseudoplisus natalensis</i>	0	2	2	0	0
<i>Pseudoplisus nigricornis</i>	0	2	2	0	0
<i>Pseudoplisus nyasicus</i>	0	1	0	0	0
<i>Pseudoplisus ocellatus</i>	0	2	2	0	0
<i>Pseudoplisus ranosahae</i>	0	2	2	0	0
<i>Pseudoplisus rubiginosus</i>	0	2	2	0	0
<i>Pseudoplisus rufomaculatus</i>	0	2	2	0	0
<i>Pseudoplisus samiatius</i>	0	2	2	0	0
<i>Pseudoplisus smithii</i>	0	2	2	0	0
<i>Pseudoplisus tanythrix</i>	0	?	?	?	?
<i>Pseudoplisus venustus</i>	0	1	2	0	0
<i>Pseudoplisus willcoxi</i>	0	2	2	0	0
<i>Pterygorytes</i>	1	1	1	0	2
<i>Sagenista</i>	0	1	0	0	0
<i>Saygorytes</i>	0	2	2	0	0
<i>Stenogorytes</i>	1	1	2	0	0
<i>Stethogorytes</i>	0	1	2	0	0
<i>Tretogorytes</i>	0	1	1	?	?
<i>Trichogorytes</i>	0	1	0	0	0
<i>Xerogorytes</i>	0	1	1	0	0

transferred to *Gorytes* (**new comb.**) are *Leiogorytes guerrero* Bohart 2000, *Arpactus nyasicus* R. Turner 1915, and the following 12 species originally described in *Gorytes* but currently placed in *Pseudoplisus*: *G. abdominalis* Cresson 1865, *G. aequalis* Handlirsch 1888, *G. divisus* F. Smith 1856, *G. effugiens* Brauns 1911, *G. fasciatus* W. Fox 1896, *G. montanus* Cameron 1890, *G. natalensis* F. Smith 1856, *G. ranosahae* Arnold 1945, *G. rubiginosus* Handlirsch 1888, *G. rufomaculatus* W. Fox 1896, *G. smithii* Cresson 1880, and *G. venustus* Cresson 1865.

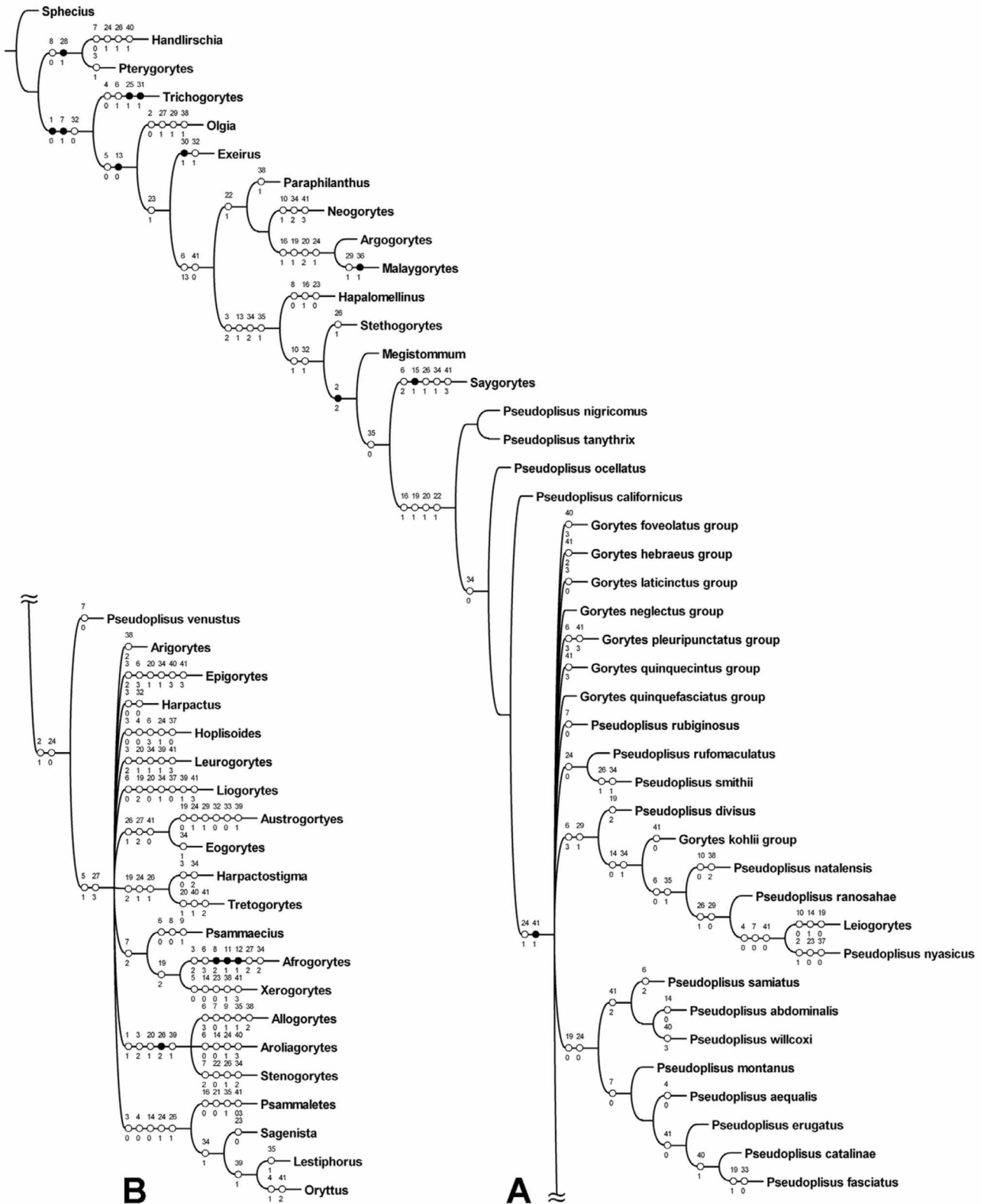


FIGURE 1. Strict consensus tree (249 steps, CI= 23, RI=54) of 900 equally parsimonious trees (each with 218 steps, CI=27, RI= 62). Character-state changes optimized as unambiguous.

Diagnosis for *Gorytes* (after Bohart & Menke 1976, with modifications): medium-sized to fairly large wasps; inner eye margins converging below, in several species conspicuously so; mandible in most species three-toothed; labrum inconspicuous; male flagellomeres in many species with tyli but four apical articles not

especially modified; pronotal collar rather thin, rounded, nearly even all across, not closely adherent to scutum; posterolateral oblique scutal carina present, oblong depression on admedian side of oblique scutal carina present in most species; axilla small, space between axillae much greater than their width; anterior scutellar sulcus foveate; episternal sulcus, when well impressed, ending on scrobal sulcus which is continued forward in nearly a straight line to omaulus; acetabular carina present, short or long, not elevated medially; sternaulus present in most species; propodeum in most species with spiracular groove, enclosure variably sculptured, with well defined median groove; female foretarsal rake well developed, forebasitarsus with two long setae before apex, female arolia in most species nearly equal in size; midtibia with two apical spurs; forewing media diverging before *cu-a*, stigma moderate, veinlet of submarginal cell II between recurrens about one-fourth posterior length of submarginal cell I, jugal lobe considerably larger than tegula; hindwing media in most species diverging before *cu-a* but in some species at *cu-a* or a little beyond it; gaster tapering toward base, in some species nearly pedunculate, tergum I somewhat constricted but not at all nodose; male with seven terga normally exposed, sterna without fimbriae, sternum VIII narrowly blade-like; female pygidial plate variable, flat, in most species long.

3. *Pseudoplisus venustus* is placed separately from the remaining *Pseudoplisus*, together with the *Argogorytes*–*Oryttus* genus complex, forming a single clade supported by characters 2(0) and 24(0). This placement suggests that it should be raised to a separate genus, but we think such an action is unwarranted: the two supporting characters are of little value, as 2(0) is shared with *Pseudoplisus nyasicus* and 24(0) with most *Pseudoplisus*. We conclude that *Pseudoplisus venustus* should be transferred to *Gorytes*, together with the remaining *Pseudoplisus*.

4. *Argogorytes* Ashmead, 1899.

= *Malaygorytes* Nemkov, 1999, **syn. nov.**

Argogorytes and *Malaygorytes* are sister taxa, and are strongly supported by characters 16, 19, 20, and 24. *Argogorytes*, however, has no supporting synapomorphy and is thus paraphyletic with respect to *Malaygorytes*. To remove the paraphyly, we synonymize *Malaygorytes* with *Argogorytes*. *Malaygorytes konishii* (Nemkov, 1999) is transferred to *Argogorytes* (**new comb.**).

Diagnosis for *Argogorytes* (after Bohart & Menke 1976, with modifications): medium-sized to fairly large wasps; inner eye margins sinuate, frons broad but a little narrowed toward clypeus, breadth at level of midocellus less than that short distance below; mandible two-toothed; labrum in most species slightly exposed; male antenna simple, last four articles not specially modified; pronotal collar elevated, not appressed to scutum; lateral margin of scutum a thin flange with no oblique carina; axilla small, space between axillae much greater than axillar width; anterior scutellar sulcus foveate; female scutellum in most species (except former *Malaygorytes* and, presumably, several South Asian species) with posteromedian pubescent depression; omaulus strongly developed throughout; episternal sulcus a vertical pitted groove that ends ventrad on omaulus; scrobal sulcus ending on episternal sulcus at right angle; acetabular carina present, well developed, not elevated medially; sternaulus absent; propodeum without spiracular groove or only a slightly defined one, enclosure mostly or entirely rugose, with deep median groove; female foretarsus without rake; midtibia with two apical spurs; forewing media diverging before, at, or beyond *cu-a*, stigma relatively large, marginal cell tapering to moderate point distally, both recurrens received by submarginal cell II, distance between their ends more than one-third posterior length of submarginal cell I; hindwing media diverging at obtuse angle well beyond *cu-a*, jugal lobe larger in outline than tegula and about twice as long; gaster sessile or slightly, and broadly pedunculate, sternum II humped; terga II-IV in most species simple (except former *Malaygorytes* in which these terga are double edged and a little thickened laterally); male with seven visible terga, male sternum VIII slender apically, sword shaped, upturned; female pygidial plate with dense fine bristles toward apex in most species, bare in several species.

5. *Pterygorytes* is transferred to subtribe Handlirschiina, because this genus is similar in its basic features to *Handlirschia*. The two genera share characters 8(0) and 28(1).

6. Three genera (*Argogorytes*, *Neogorytes*, and *Paraphilanthus*) do not cluster with the rest of the Gorytina, and should be placed in their own subtribe, the Argogorytina Nemkov and Lelej, 1996, **stat. resurr.**,

which is supported by character 22(1). This subtribe is characterized by the following: female inner eye margins nearly parallel, male four apical flagellomeres not modified, posterolateral oblique scutal carina absent, body pubescence not concealing integument, female foretarsal rake absent, forewing marginal cell not bent away from wing margin, hindwing media diverging well beyond *cu-a*.

7. *Trichogorytes* does not cluster with the remaining Gorytina and can be distinguished by characters 4(0), 6(1), 25(1), and 31(1). We place it in its own subtribe, Trichogorytina, **subtrib. nov.** This new subtribe is characterized by the following: female inner eye margins nearly parallel, male four apical flagellomeres modified, posterolateral oblique scutal carina present, body pubescence largely concealing integument, female foretarsal rake present (outer margin of basitarsus with three long preapical spines), forewing marginal cell bent away from wing margin, hindwing media diverging well beyond *cu-a*.

8. The subtribe Gorytina, after exclusion of Argogorytina and Trichogorytina, is supported by characters 3(2), 13(1), 34(2), and 35(1), and is characterized by the following: female inner eye margins nearly parallel or converging toward clypeus, male four apical flagellomeres modified or not modified, posterolateral oblique scutal carina present, body pubescence not concealing integument, female foretarsal rake present (outer margin of basitarsus with two or three long preapical spines), forewing marginal cell not bent away from wing margin, hindwing media diverging at, before or well beyond *cu-a*.

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