

Splitting of the polyphyletic genus *Passalus* Fabricius, s. auct. I. (Coleoptera, Passalidae)

by Stéphane BOUCHER

Muséum national d'Histoire Naturelle, Département Systématique & Évolution, Entomologie,
C. P. 50, 57 rue Cuvier, F – 75231 Paris cedex 05 <sbl@mnhn.fr>

Abstract. – A research on the homologies of various characters of the body and of the complete ectodermic male genitalia has been made on all the nomenclatural genus-group taxa included in the polyphyletic genus *Passalus* Fabricius, 1792, of the American tribe Passalini Leach, 1815. This work allows a re-evaluation of the typological systematics. The splitting of *Passalus*, s. auct., is a requirement for a phylogenetic reality with monophyletic species groups. In this first issue seven genera have a new status: four belong to the “*Passalus-Paxillus* lineage” and three to the “*Pertinax* lineage” sensu Boucher (2006). For each genus are given diagnostic characters, the main endemism and a preliminary number of representative species. The 21 synonyms of these genera are identified (on a number of 40 previous subgenera, or “sections”, including synonyms). None of the six subgenera or “sections” of *Passalus*, s. auct., is maintained in its former acceptance. Genera of the “*Passalus* lineage” are *Passalus* Fabricius, 1792 [n. syn.: *Neleus* Kaup, 1869, *Zosterothrix* Zang, 1905, *Lucilius* Kuwert, 1891, *Pertinacides* Kuwert, 1891, *Oeneus* Kuwert, 1896, *Ptychotrichus* Kuwert, 1896, *Calidas* Kuwert, 1896, *Lasioperix* Zang, 1905], *Toxeutotaenius* Kuwert, 1896, n. stat., *Scalmus* Zang, 1905, n. stat. [n. syn.: *Neleuops* Kuwert, 1891], *Rhagonocerus* Kaup, 1871, n. stat. [n. syn.: *Macrolobus* Zang, 1905, *Ninoides* Kuwert, 1891, *Manlius* Kuwert, 1891, *Phoronaeosomus* Kuwert, 1891, *Epiphoroneus* Arrow, 1907], *Epipleurothrix* Zang, 1905, n. stat. Genera of the “*Pertinax* lineage” are *Pertinax* Kaup, 1869, n. stat. [n. syn.: *Epipertinax* Kuwert, 1891, *Valerius* Kuwert, 1891, *Psilomus* Zang, 1905], *Rhodocanthopus* Kaup, 1871, n. stat. [n. syn.: *Phaulothorax* Zang, 1905, *Polyacanthopus* Kuwert, 1896], *Aponelides* Kuwert, 1896, n. stat. [n. syn.: *Severus* Kuwert, 1896, *Lophocephalus* Kuwert, 1896]. The tribe Passalini has now fourteen genera for seven in the late nomenclature.

Résumé. – Scission du genre polyphylétique *Passalus* Fabricius, s. auct. I. (Coleoptera, Passalidae). Une recherche sur les homologies de divers caractères du corps et des genitalia mâles ectodermiques complets a été réalisée sur tous les taxons nomenclaturaux du groupe-genre du genre polyphylétique *Passalus* Fabricius, 1792, tribu américaine des Passalini Leach, 1815. Ce travail permet de reconsidérer la systématique typologique. La scission de *Passalus*, s. auct., est une condition requise pour une réalité phylogénétique avec des groupes d'espèces monophylétiques. Dans cette première étape sept genres ont un nouveau statut : quatre dans la “lignée *Passalus-Paxillus*” et trois dans la “lignée *Pertinax*” sensu Boucher (2006). Pour chacun d'eux sont donnés des caractères diagnostiques, l'endémisme général et un nombre préliminaire d'espèces représentatives. Les 21 synonymes de ces genres sont identifiés (sur un total des 40 précédents sous-genres, ou “sections”, synonymes inclus). Aucun des six sous-genres ou “sections” de *Passalus*, s. auct., n'est maintenu comme tel. Les genres de la “lignée *Passalus*” sont *Passalus* Fabricius, 1792 [n. syn. : *Zosterothrix* Zang, 1905, *Lucilius* Kuwert, 1891, *Pertinacides* Kuwert, 1891, *Oeneus* Kuwert, 1896, *Ptychotrichus* Kuwert, 1896, *Calidas* Kuwert, 1896, *Lasioperix* Zang, 1905], *Toxeutotaenius* Kuwert, 1896, n. stat., *Scalmus* Zang, 1905, n. stat. [n. syn. : *Neleuops* Kuwert, 1891], *Rhagonocerus* Kaup, 1871, n. stat. [n. syn. : *Macrolobus* Zang, 1905, *Ninoides* Kuwert, 1891, *Manlius* Kuwert, 1891, *Phoronaeosomus* Kuwert, 1891, *Epiphoroneus* Arrow, 1907], *Epipleurothrix*, Zang, 1905, n. stat. Les genres de la “lignée *Pertinax*” sont *Pertinax* Kaup, 1869, n. stat. [n. syn. : *Epipertinax* Kuwert, 1891, *Valerius* Kuwert, 1891, *Psilomus* Zang, 1905], *Rhodocanthopus* Kaup, 1871, n. stat. [n. syn. : *Phaulothorax* Zang, 1905, *Polyacanthopus* Kuwert, 1896], *Aponelides* Kuwert, 1896, n. stat. [n. syn. : *Severus* Kuwert, 1896, *Lophocephalus* Kuwert, 1896]. La tribu Passalini compte désormais quatorze genres, contre sept auparavant.

Keywords. – Passalini, Neotropical, genera, nomenclature, *Passalus*, *Toxeutotaenius*, *Scalmus*, *Rhagonocerus*, *Epipleurothrix*, *Pertinax*, *Rhodocanthopus*, *Aponelides*.

The polyphyletism of the large genus *Passalus* Fabricius, 1792, s. auct., has been recently discussed and affirmed on the base of a study of comparative morpho-anatomy, testing homologies and phylogenetics of the family Passalidae (BOUCHER, 2006: chapter I). The highlighted homologies of characters from various external or internal parts (especially the head capsule, mandibles and complete ectodermic genitalia in both sexes) allowed a substantial phylogenetic reconstruction of family groups and genera. However, if most genera of Passalids from Asia and Australasia seem to be relatively well established — and to a lesser extent among those from Africa and Madagascar — the situation of one of the two American tribes, the Passalini Leach, 1815,

remains problematic. In fact, none of the current genera of Passalini is monophyletic, except four: *Spasalus* Kaup, 1869, *Ptichopus* Kaup, 1869, *Ameripassalus* Jiménez-Ferban & Reyes-Castillo, 2014, and *Antillanax* Boucher, 2015. *Passalus*, although nominotypical, is extremely heterogeneous since the first extended subdivisions of the family (KAUP, 1868, 1869, 1871). This is one of the paradoxes of the systematics of the genus-group level in the family, as the American fauna has been the most studied for the last decades. Which means since the reference date currently followed, the last *Coleopterorum Catalogus* by HINCKS & DIBB (1958). The main mistake at the origin of this situation is very probably the supported and almost permanently application, during this long period, of a typological methodology in the systematic frameworks. This context is discussed in BOUCHER (2006: chapters I-II).

Looking for homologies, the author followed a phylogenetic objective in the study of the family. For this occasion, the terms used by taxonomists for the sclerites and other small dorsal structures of the head capsule, which are so important in every systematic interpretation in the family, were stated as giving difficult or erroneous the historical reconstructions of many lineages. A similar observation has been made on the ectodermic genitalia. Moreover, these structures were partially known and poorly used by taxonomists. Consequently, a majority of the terminology for the concerned homologous structures has been also reconsidered. In practice (BOUCHER, 2006: chapter II), an analysis has been made including the whole second American tribe, the Proculini Kaup, 1868. This analysis has been followed by a second, detailed until the infra-specific populations: the diversified complex, unequalled in the American fauna, supported by the genus *Veturius* Kaup, 1871, with near 75 species, and its closely allied, but very small genus *Arrox* Zang, 1905, with two relictual species (BOUCHER, 2006: chapter III).

The study of these various taxonomic levels in the Passalids, especially among the Proculini, proved the phylogenetic interest of the methodology, together with presumptive evidences in ecology, paleobiogeography and biogeography.

THE TRIBE PASSALINI AND THE GENUS *PASSALUS*

With regard to the Passalini, after the justified revalidation of the genus *Spasalus* (REYES-CASTILLO, 1970), the genera have been kept up to date as proposed by HINCKS & DIBB (1935, 1958). For *Passalus*, that means with the same subgenera and a peculiar infra-subgeneric level, the “*section*”, *sensu* LUEDERWALDT (1931) (and erroneously attributed to this author after him). Subgenera and “*sections*” are three and three (authors corrected): *Passalus* Fabricius, 1792 (“*sections*” *Phoroneus* Kaup, 1869, *Petrejus* Kaup, 1869, *Neleus* Kaup, 1869), *Pertinax* Kaup, 1869, and *Mitrorhinus* Kaup, 1871. These nomenclatural taxa are strongly typological and obviously polyphyletic. They are also unsuitable, or partially suitable, with respect to the ICZN (1999).

In this scheme, in Passalini are the three genera currently recognized as valid since HINCKS & DIBB (1935, 1958): *Passalus*, *Paxillus* Mac Leay, 1819, and *Ptichopus* (although the last corrected by BOUCHER 2006: chapter I), with the addition of *Spasalus* and lately with the new genera *Passipassalus* Fonseca & Reyes-Castillo, 1993, *Ameripassalus* and *Antillanax*. However, *Passalus*, *Paxillus* and *Passipassalus* still remain polyphyletic.

Since the 1970's, only a short contribution (BOUCHER 1990) re-opened the implicit idea of a required splitting of *Passalus*, *s. auct.*, after the study of some species closely related to *Pertinax convexus* (Dalman, 1817). Then BOUCHER (2006: chapter I) enforced this idea for other species or species groups. In this work four genera (or species groups) have been clearly indicated to be redefined and separated, or revalidated: *Passalus s. str.*, *Pertinax*, *Rhodocanthopus* Kaup, 1871, and the “*guatemalensis* group” [inferred from *Passalus guatemalensis* (Kaup, 1869), since then becoming *Ameripassalus*].

In the present paper a first step is made toward the splitting of *Passalus*, *s. auct.*, with *Pertinax* and *Rhodocanthopus* of course, but also with five of the other genus-group taxa within

the appropriate nomenclature: *Toxetotaenius* Kuwert, 1896, *Scalmus* Zang, 1905, *Rhagonocerus* Kaup, 1871, *Epipleurothrix* Zang, 1905, and *Aponelides* Kuwert, 1896.

Toxetotaenius and *Scalmus* belong without any doubt to the “*Passalus-Paxillus* lineage”, *sensu* BOUCHER (2006: chapter I; 2015a). *Spasalus*, *Ameripassalus*, *Passipassalus*, *Epipleurothrix* and *Rhagonocerus* probably belong also to this lineage, but as derived groups. BOUCHER (2015a) has shown that *Antillanax* belongs to the “*Pertinax* lineage”, *sensu* BOUCHER (2006: chapter I). *Rhodocanthopus* and *Aponelides* may also belong to this lineage.

Now the tribe Passalini is gathering 14 genera, but this diversity is not exhaustive. It should be increased with the precise study of numerous species, among which several are in need to be revalidated. Moreover, other species, although described since a long time, are poorly known, if they are not like *nomina oblita*. The new examination of these species will probably suggest the transfer of some of them to other genera. It is, therefore, all a conception of the systematics of the family which is reflected on the genus *Passalus*, *s. auct.* KUWERT (1891, 1896, 1897, 1898) was a splitter, creating an incongruous number of taxa in all supra-specific levels. In contrast, GRAVELY (1914, 1918) was merging an excessive number of taxa created by Kuwert, and in some occasions those created by KAUP (1868, 1869, 1871). The true phylogenetic scheme of the tribe Passalini seems to take place between both the interesting, but often opposite, conceptions of Kuwert and Gravely (see BOUCHER, 2006: chapter I).

In addition, the synonymies in the genus-group including *Passalus s. auct.* were not clearly attributed to their respective valid name in HINCKS & DIBB (1935, 1958). This increased the confusion. At least a number of original type-localities are erroneous.

Unless otherwise stated, the designations of type-species of genera are the species indicated by HINCKS & DIBB (1935, 1958). These authors took over *partim* from the clear or inherent previous basic literature, especially ZANG (1905a, b), ARROW (1907), GRAVELY (1914, 1918) and LUEDERWALDT (1931).

The species checked for each genus are a representative sample among the species currently considered as valid. The type-species of each genus has been studied.

The terminology used for the head capsule is that revisited or established by BOUCHER (2006). The total length of specimens is taken from apex of elytra to anterior border of evaginated labrum.

Genus *Passalus* Fabricius, 1792

Passalus Fabricius, 1792. Type-species: *Lucanus interruptus* Linnaeus, 1758.

Neleus Kaup, 1869, not Rafinesque, 1814: Malacostraca. Type-species: *Lucanus interruptus* Linnaeus, 1758.

Lucilius Kuwert, 1891, **n. syn.** Type-species: *Lucilius petrejoideus* Kuwert, 1891.

Pertinacides Kuwert, 1891, **n. syn.** Type-species: *Passalus affinis* Percheron, 1835.

Oeneus Kuwert, 1896, **n. syn.** Type-species: *Neleus pauxillus* Kuwert, 1891.

Ptychotrichus Kuwert, 1896, **n. syn.** Type-species: *Passalus coniferus* Eschscholtz, 1829.

Calidas Kuwert, 1896, **n. syn.** Type-species: *Neleus transvaalensis* Kuwert, 1891.

Zosterothrix Zang, 1905, **n. syn.** (replacement name for *Vatinius* Kaup, 1869, not Stål, 1865: Hemiptera). Type-species: *Passalus toriferus* Eschscholtz, 1829.

Lasioperix Zang, 1905, **n. syn.** (replacement name for *Flavius* Kuwert, 1896, not Stål, 1862: Hemiptera). Type-species: *Passalus unicornis* Lepeletier & Serville, 1825.

This natural group, previously discussed by BOUCHER (2006: chapter I; 2015a), is characterized as follows.

Total length medium to very large (28-55 mm). Body a little convex but flat to depressed on the elytral disk. Frontal structure complete (*sensu* BOUCHER, 2006: chapter I) of the “*interruptus*” type, with a pair of developed secondary mediofrontal tubercles. This structure has some convergent exceptions (see below). Frontal area concave, short and transverse. Anterior and posterior frontal ridges more or less marked, blunted. Lacinia bidentate. Antennal club long, with three articles slightly curved inward. Metasternum pubescent on the sides, the disk delimited with a marked crest. Elytra: calli and proximal part of first interstria more or less, often widely, covered with dense setae. Membranous wings normally coloured, hyaline. Meso- and metatibiae with, or without, small spine(s); the apical fork normal. Male genitalia: more or less quadratic, angular, never

elongated, the tegument well to strongly sclerotized; phallus quite symmetrical, not clearly, or not at all, twisted; internal sac large to voluminous, more or less widely pubescent, the setae long and dense as a brush, dark to clear and orange (these characters, as well as others from the genitalia in both sexes, are considered homologous with *Paxillus*; the two genera should be sister-groups or equivalent (see BOUCHER, 2006: chapter I).

Distribution. – From N Mexico to the southern limits known for the family (see SCHUSTER, 1978; BOUCHER, 2006: chapters I-III), including part of the Antilles (Hispaniola and the Lesser Arc, from Guadeloupe to Grenada; see BOUCHER, 2015a, b); also present in Trinidad & Tobago.

Species diversity. – Some presumably well-known American Passalids of lowlands and foothills belong to *Passalus*, as *P. interruptus* (Linnaeus, 1758), *P. punctiger* Lepeletier & Serville, 1825, *P. coniferus* Eschscholtz, 1829, *P. toriferus* Eschscholtz, 1829, etc., or less known species as *P. coarctatus* Percheron, 1835, *P. geometricus* Percheron, 1835, *P. languidus* (Kuwert, 1891), *P. pauxillus* (Kuwert, 1891), *P. petrejoides* (Kuwert, 1891), *P. humericrinitus* (Kuwert, 1891), *P. pubicostatus* (Kuwert, 1898), *P. gladiator* (Kuwert, 1898), *P. inundulifrons* (Kuwert, 1898), *P. opacus* Gravely, 1918, *P. bucki* Luederwaldt, 1931, *P. michaeli* Boucher, 1986, *P. reyesi* Fonseca, 1989, etc. However, most of the species are often mixed up with others, described or not. An exception in the genus is the convergent *P. affinis* Percheron, 1835, from Hispaniola, which is proved to be not at all a *Pertinax*, as stated since a long time (BOUCHER, 2015a).

Genus *Toxeutotaenius* Kuwert, 1896, **n. stat.**

Toxeutotaenius Kuwert, 1896. Type-species: *Epiphanus schaufussi* Kuwert, 1891.

This natural group is the most closely allied to *Passalus*, from which it is clearly separated as follows.

Total length smaller to much smaller (21-32 mm). Frontal structure complete, of the “*schaufussi*” type, with some convergent exceptions (see below). Frontal area quite flat and less transverse to long. Elytral calli with a stronger, more prominent, tuft of dense setae. Antennal club shorter, not curved inward. Genitalia in both sexes with exactly same characteristics than *Passalus*.

Distribution. – Wide, but limited to South America, from the eastern side of the Andes to the Atlantic; present in the Cordillera Costale of Venezuela and Trinidad; absent from the Antilles; southern limits in South America like *Passalus*.

Species diversity. – *Toxeutotaenius schaufussi* (Kuwert, 1891), *T. beilingi* (Kuwert, 1891), *T. peruvianus* Kuwert, 1898, *T. elfriedae* (Luederwaldt, 1931), *T. barrus* (Boucher & Reyes-Castillo, 1991), etc. There are about ten species, described or not, most of them being mixed up in the literature. *T. barrus* is somewhat convergent with its peculiar, fused and prominent, secondary mediofrontal tubercles, which seem to belong to other genera far from the *Passalus* lineage.

Genus *Scalmus* Zang, 1905, **n. stat.**

Scalmus Zang, 1905 (replacement name for *Ninus* Kaup, 1871, not Stål, 1859: Hemiptera). Type-species: *Passalus interstitialis* Eschscholtz, 1829.

Neleurops Kuwert, 1891, **n. syn.** Type-species: *Neleurops rhodocanthopoides* Kuwert, 1891.

This natural group is closely allied to the two previous, from which it is clearly separated as follows.

Total length small to medium (20-36 mm). Body totally depressed. Frontal structure of the “*interstitialis*” type, with some convergent exceptions (see below). Frontal area concave and longer, triangular, never transverse. Anterior and posterior frontal ridges very marked, never blunted, but often acute. Genitalia in both sexes with exactly same characteristics than *Passalus*.

Distribution. – Like *Passalus*, but including Cuba and Jamaica; absent from the Lesser Antilles.

Species diversity. – *Scalmus interstitialis* (Eschscholtz, 1829) is one of the most common or abundant American Passalid, with a high ecological range. It is also of the best known in this fauna,

presumably. In fact there is some confusion between a small number of species. *S. huebneri* (Kuwert, 1898), and probably *S. kaupi* (Boucher, 2004) for examples, belong to this genus.

S. rhodocanthopoides (Kuwert, 1891) is an exception in the genus, the species having three remarkable apomorphies: the loss of the anterior frontal ridges, with a deep digging in the place of the laterofrontal areas and two overdeveloped inner tubercles; the loss of the secondary mediofrontal tubercles; the antennal club tetraphylous. With the help of these characters and those of the genitalia in both sexes, the phylogenetic position of the species has been discussed (BOUCHER, 2006: chapter I). Notwithstanding the authors, this species has nothing of a *Pertinax*; the loss of the secondary mediofrontal tubercles is convergent with the basal scheme of *Pertinax*.

Genus *Rhagonocerus* Kaup, 1871, n. stat.

Rhagonocerus Kaup, 1871. Type-species: *Passalus armatus* Perty, 1831.

Ninoides Kuwert, 1891, n. syn. Type-species: *Ninoides simulans* Kuwert, 1891.

Manlius Kuwert, 1891, n. syn. Type-species: *Phoroneus rugifrons* Kaup, 1869.

Phoronaesomus Kuwert, 1891, n. syn. Type-species: *Passalus binominatus* Percheron, 1841.

Macrolobus Zang 1905, n. syn. (replacement name for *Phoroneus* Kaup, 1869, not Rafinesque, 1815: Mollusca). Type-species: *Passalus quadricollis* Eschscholtz, 1829.

Epiphoroneus Arrow, 1907, n. syn. Type-species: *Passalus occipitalis* Eschscholtz, 1829.

This natural group is characterized as follows.

Total length medium to very large (33-54 mm). Body robust, glabrous and rather convex, except the disk of elytra, which is depressed as in *Passalus*. Frontal structure complete and diversified on the base of the “*armatus*” type, with closely disposed secondary mediofrontal tubercles, sometimes small and regressed. Frontal area long and wide, very smooth to granular. Lacinia bidentate. Antennal club long with three articles, a little curved inward. Metasternum glabrous, or pubescent with setae not numerous nor dense, the disk delimited with a marked crest. Meso- and metatibiae with or without small spine(s); the apical fork normal. Elytra: calli glabrous or not; proximal part of first interstria glabrous. Membranous wings normally coloured, hyaline. Male genitalia: aedeagus well distinct from the *Passalus* type, but with similarities with the *Pertinax* type; tegument well to strongly sclerotized; sometimes clearly asymmetrical-twisted on the phallus (as in *R. armatus* and *R. sarryi*); phallobase and parameres totally fused (phallosome) or just a few separated; phallus long; internal sac rather short but wide, obscure and coarse, without setae as a brush, with numerous micro-spicules.

Distribution. – South America, E of the Andes, with two known penetrations N of Amazonia (*R. armatus*, *R. sarryi*). Other species are endemic of SE South America (SE Brazil, N Argentina, Paraguay, N Uruguay, E Bolivia), reaching the southern limits known for the family (see *Passalus*). *Rhagonocerus* forms with *Passalus* the second group of large Passalini in southern South America.

Species diversity. – As a consequence of the morpho-cephalic heterogeneity of the species, this genus was mixed up in various and well distinct lineages. Nine species are listed as valid: *R. occipitalis* (Eschscholtz, 1829), *R. quadricollis* (Eschscholtz, 1829), *R. armatus* (Perty, 1831), *R. rusticus* (Percheron, 1835), *R. binominatus* (Percheron, 1841), *R. denticollis* (Kaup, 1869), *R. simulans* (Kuwert, 1891), *R. frontidivisus* (Kuwert, 1891) and *R. sarryi* (Boucher, 1986).

Genus *Epipleurothrix* Zang, 1905, n. stat.

Epipleurothrix Zang, 1905 (replacement name for *Trichopleurus* Kuwert, 1896, not Motschulsky, 1845: Scarabaeidae). Type-species: *Neleides punctulatus* Kaup, 1869.

This natural group is characterized as follows.

Total length small to large (20-40 mm). Body totally depressed or a little convex, but flat on the elytral disk. Frontal structure incomplete of the “*punctulatus*” type, with loss of the secondary mediofrontal tubercles. Frontal area long and wide, flat and often granular. Inner and mediofrontal tubercles closely disposed and connected by a short ridge. Lacinia bidentate. Antennal club with 3-4 articles moderately long. Elytral calli and proximal part of the epipleura pubescent, sometimes just a few; the same epipleura wide and flat, or curved upward. Metasternum glabrous or pubescent, the setae not dense nor coarse as in *Passalus*. Meso- and metatibiae with or without small spine(s); the apical fork normal. Membranous wings

normally coloured, hyaline. Male genitalia: aedeagus well distinct from the *Passalus* type, but with similarities with the *Pertinax* type; general aspect moderately sclerotized; symmetrical or a few asymmetrical on parameres and phallus; phallobase and parameres well separated; phallus long; internal sac rather short but wide, without setae as a brush, with or without micro-spicules, hyaline to obscure, but fine.

Distribution. – From Nicaragua to the Andes of Bolivia and the Cordillera Costale of Venezuela. Probably absent outside of the Andes. The group seems to be restricted to the low mountains and mountains, reaching 2600 m in Colombia-Ecuador-Peru.

Species diversity. – *Epipleurothrix punctulatus* (Kaup, 1869), *E. incertus* (Percheron, 1841), *E. gracilis* (Kaup, 1869), *E. stultus* (Kuwert, 1891) and *E. sulcatipons* (Kuwert, 1891) belong to, and are well representative, of this genus. There are many other species. Their nomenclature is very muddled, numerous species being introduced and dispersed in various groups of species, including in the recent descriptions as “*Passalus (Pertinax)*”. Some erroneous synonyms of species from SE South America, like “*Passalus anguliferus* (Percheron, 1835) and “*Passalus morio* (Percheron, 1835), belong in fact to *Epipleurothrix*.

Genus *Pertinax* Kaup, 1869, n. stat.

Pertinax Kaup, 1869. Type-species: *Passalus convexus* Dalman, 1817.

Epipertinax Kuwert, 1891, n. syn. Type-species: *Passalus pelliculatus* Perty, 1831.

Valerius Kuwert, 1891, n. syn. Type-species: *Valerius dimidiatifrons* Kuwert, 1891.

Psilomus Zang, 1905, n. syn. (replacement name for *Phanocles* Kuwert, 1896, not Stål, 1865: Phasmatoidea). Type-species: *Phanocles nudus* Kuwert, 1898.

This natural group, discussed by BOUCHER (1990, 2006, 2015a), is characterized as follows.

Total length small to large (28-48 mm). Body quite totally convex, glabrous. Frontal structure incomplete (*sensu* BOUCHER, 2006: chapter I) of the “*convexus*” type, with loss, more or less totally, of the secondary mediofrontal tubercles. Metasternum glabrous or only a little pubescent near the mesocoxa. Antennal club with three articles moderately long, not curved inward. Lacinia bidentate. Meso- and metatibiae with or without small to strong spine(s); the apical fork normal to enlarged. Membranous wings normally coloured, hyaline. Elytral calli glabrous. Male genitalia: aedeagus of the *convexus* type, phallus more or less asymmetrical-twisted; internal sac typically phallic, long and strait, tubular, glabrous or a little pubescent, the setae short and dense, not as a brush, obscure to black, with presence or not of spicules and sclerotized apparatus like wings (see BOUCHER, 2006: chapter I).

Distribution. – From Nicaragua to the southern limits known for the family (see above *Passalus*); present in Grenada in the Lesser Antilles and Trinidad; absent from the Great Antilles.

Species diversity. – *Pertinax convexus* (Dalman, 1817), *P. latifrons* (Percheron, 1841), *P. aequatorialis* Kirsch, 1885, *P. epiphanooides* Kuwert, 1891, *P. ruehli* Kuwert, 1891, *P. brevifrons* (Kuwert, 1891), *P. radiatus* Kuwert, 1898, *P. sulcifrons* Kuwert, 1898, *P. antillarum* (Arrow, 1907), *P. beneshi* Hincks, 1950, *P. umbriensis* (Hincks, 1950), *P. pseudoconvexus* Boucher, 1990, etc. *P. antillarum* is an endemic of Grenada and the only one species known in the Lesser Antilles. *P. venerabilis* (Kuwert, 1898), which is a good species, has been recently cited (BOUCHER, 2006: chapter I) as belonging to the species-group of *P. hylaius* (Fonseca & Reyes-Castillo, 1994), but it is in fact a true *Pertinax*, near *P. epiphanooides*. On the other hand, contrary to BOUCHER (2006), who transferred *P. hylaius* and *P. carajaensis* (Fonseca & Ribeiro, 1993) from *Ptichopus* to *Pertinax*, these species do not belong to *Pertinax*, but to another species group under study.

Despite some cephalic appearances, *P. jansoni* (Bates, 1886) seems to belong to *Pertinax*. In this species, thus possibly the only *Pertinax* known N to the Depression of Nicaragua, the secondary mediofrontal tubercles are relictual, but marked; in other respect the species looks like some species of *Rhagonocerus*, but by convergences. A similar plesiomorphy of the front is found in *P. umbriensis* from southern Central America and also, but polymorphic, in South-American species, as *P. ruehli* or *P. pseudoconvexus*.

Among the species lately described or cited (REYES-CASTILLO & IBÁÑES-BERNAL, 2008; JIMÉNES-FERBAN *et al.* 2012, 2014), in fact none belongs to *Pertinax*, but at least to five genera, mixed up.

Genus *Rhodocanthopus* Kaup, 1871, **n. stat.**

Rhodocanthopus Kaup, 1871. Type-species: *Passalus caelatus* Erichson, 1847.

Polyacanthopus Kuwert, 1896, **n. syn.** Type-species: *Passalus maillei* Percheron, 1841.

Phaulothorax Zang, 1905, **n. syn.** (replacement name for *Microthorax* Kuwert, 1896, not Englemann, 1862: Ciliophora). Type-species: *Rhodocanthopus stultus* Kuwert, 1891.

This natural group is characterized as follows.

Total length small to very small (13-28 mm). Body glabrous, convex except the disk of elytra. Frontal structure incomplete, of the “*caelatus*” type, marked and angulous to thorny, with loss, more or less completely, of the secondary mediofrontal tubercles (often relictual and transverse). Eyes reduced, including in macropterous species. Lacinia bidentate, the inferior tooth often reduced. Antennal club with three articles rather short to short. Metasternum glabrous or a few pubescent near the mesocoxa. Meso- and metatibiae with 2-4 spines, often strong and acute; the apical fork strong and large. Elytra: calli glabrous; infra-anterior angle and proximal part of epipleura prominent to sharp; external edge enlarged and prominent throughout. Membranous wings coloured or bicoloured clear/obscure. Male genitalia: aedeagus more related to the “*Pertinax*” type, more or less asymmetrical, especially on parameres; phallus large and rather short and broad, without setae as a brush, covered with numerous spicules, the tegument obscure and coarse almost all over.

Distribution. – From Mexico N of the Isthmus of Tehuantepec to Central Peru. Otherwise absent in South America E of the Andes, as well as in the Cordillera Costale of Venezuela. The group inhabits from the coast level up to the mountains, reaching easily 2300 m in Meso-America and near 3000 m in the Andes of Colombia-Ecuador-Peru.

Species diversity. – *Rhodocanthopus maillei* (Percheron, 1841), *R. caelatus* (Erichson, 1847), *R. cognatus* (Truqui, 1857), *R. spiniger* Bates, 1886, *R. clypeoneleus* Kuwert, 1891, *R. spinosus* Kuwert, 1898, *R. perparvulus* Kuwert, 1898, *R. spinipes* Gravely, 1918. In fact there are more than 24 species, among which a part includes erroneous synonyms in the current nomenclature. The examination of all type-specimens and of an extended material confirms these facts.

Genus *Aponelides* Kuwert, 1896, **n. stat.**

Aponelides Kuwert, 1896. Type-species: *Passalus punctatostratus* Percheron, 1835.

Severus Kuwert, 1896, **n. syn.** Type-species: *Severus manlioides* Kuwert, 1898.

Lophocephalus Kuwert, 1896, **n. syn.** Type-species: *Rhodocanthopus mirabilis* Kuwert, 1898.

This small natural group is characterized as follows.

Total length small to medium (20-37 mm). Body glabrous, convex except the disk of elytra. Frontal structure incomplete of the “*punctatostratus*” type, blunt, with loss more or less complete of the secondary mediofrontal tubercles. Inner and mediofrontal tubercles closely disposed, sometimes almost fused, and near the front. Eyes reduced to globulous. Antennal club with three articles rather short. Lacinia bidentate. Metasternum glabrous or a little pubescent near the mesocoxa. Meso- and metatibiae with or without small spine(s); the apical fork normal, not enlarged. Membranous wings normally coloured, hyaline Elytra: calli glabrous; infra-anterior angles and epipleura just a few prominent and blunt; external border normal, straight throughout. Male genitalia: aedeagus close to the “*Pertinax*” type, but clearly asymmetrical on all sclerites; phallus long, without setae as a brush, covered with numerous spicules, the tegument obscure and coarse more or less all over.

Distribution. – From N Mexico to Panama, its penetration in northern Colombia being uncertain. Consequently, *Ameripassalus* is probably not the only genus of Passalini to be Meso-American. *Aponelides* inhabits from the coast level up to the mountains, reaching 2400 m.

Species diversity. – There are four described species recognized as valid and belonging in fact to *Aponelides*: *A. punctatostratus* (Percheron, 1835), *A. glabristernus* (Kuwert, 1891), *A. manlioides* (Kuwert, 1898) and *A. mirabilis* (Kuwert, 1898). In the literature these species are

permanently mixed up under the name of *punctatostriatus*, probably since PERCHERON (1835). There are indeed, at least, four distinct species. A strong confusion exists for this group and apparently only KUWERT (1896) recognized them in closely allied genera (and) with a higher diversity in species. Kuwert was erroneously overlooked by all the authors.

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