Definition and Revision of the Orthrius-group of genera (Coleoptera, Cleridae, Clerinae)

Roland Gerstmeier†, Jonas Eberle‡

Technische Universität München, Department für Ökologie und Ökosystemmanagement, Lehrstuhl für Tierökologie, Hans-Carl-von-Carlowitz-Platz 2, 85350 Freising, Germany

† urn:lsid:zoobank.org:author:03727426-842C-4C2F-9703-613CCADC305D
‡ urn:lsid:zoobank.org:author:3A048DFB-D6E1-4F17-9705-9B2EB2753B94

Corresponding author: Roland Gerstmeier (r.gerstmeier@googlemail.com)

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Abstract

An “Orthrius-group” of genera is proposed, and defined to include Aphelochroa Quedenfeldt, 1885; Cardopus Schenkling, 1908; Dozocolletus Chevrolat, 1842; Gyponyx Gorham, 1883; Languropilus Pic, 1940; Orthrius Gorham, 1876; Pieleus Pic, 1940; Xenorthrius Gorham, 1892; plus three new genera Neorthrius gen. n., Nonalatus gen. n. and Pseudoastigmus gen. n. A phylogeny of the 11 constituent Orthrius-group genera (analysis of 22 morphological characters using Clerus Geoffroy as the out-group taxon was performed with TNT v1.1) is proposed. Four genera are synonymised: Burgeonus Pic, 1950, syn. n. (with Aphelochroa Quedenfeldt, 1885); Brinckodes Winkler, 1960, syn. n. and Quasibrinckodes Winkler, 1960, syn. n. (both with Dozocolletus Chevrolat, 1842); and Dedana Fairmaire, 1888, syn. n. (with Orthrius Gorham, 1876). The genera Falseorthrius Pic, 1940 and Mimorthrius Pic, 1940 are transferred from Clerinae to the subfamily Tillinae.

Keywords

Cleridae, genus-group, synonymy, phylogeny

Introduction

The checkered beetles (Cleridae and Thanerocleridae) contain approximately 3600 described species, which are classified into seven subfamilies (Lawrence and Newton Jr. 1995) and involve 303 genera. By far, the Clerinae is the most specious subfamily with
approximately 45% of the species of the family. Checkered beetles are largely tropical insects with an approximate faunal distribution as follows: 1030 species in the Afro-tropics, 840 in the Neotropics, 690 in the Orientalis, 510 in the Australis and 490 in the Palaearctis (Gerstmeier 2000).

The higher classification of the Cleridae has undergone considerable categorical oscillations (Opitz 2002, 2010). Several landmark publications of Crowson (1955, 1964, 1966, 1970) form the basis for a modern classification of Cleroidea, while some nomenclatural amendments were made by Lawrence and Newton Jr. (1995). More recently, significant contributions dealing with suprageneric taxa include the elevation of Thanelorcerinae (Kolibáč 1992, 2004) and Metaxina Broun, to family rank (Kolibáč 1992, 2004), the proposition of two subfamily classifications (Kolibáč 1997, Opitz 2010) plus revisions of the genera and species of Epiphloeinae (Opitz 1997, 2004, 2005, 2006, 2007, 2008a, 2008b, 2008c), the genera of Hydnocerinae (which included a tribal classification for that subfamily) (Kolibáč 1998) and the Australian Korynetinae (Kolibáč 2003). Nevertheless, some discontinuities are obvious and not all changes made at the subfamily-level are universally accepted among cleridologists. From a world viewpoint, much remains to be done with clarification of generic concepts and zoogeographic relationships at superspecific levels (Opitz 2002). In our opinion, Opitz’s (2010) concept of 12 subfamilies seems to result in the best system.

The Clerinae is the largest of all subfamilies of the Cleridae and the most difficult in which to define generic limits (Chapin 1924). Furthermore, the paucity of clearly defined morphological gaps among these genera renders their generic delimitation very difficult. A paper dealing with genera related to Clerus Geoffroy (Gerstmeier 2002) represents an initial step in clarifying generic limits within Clerinae. After an extensive review of Indo-Australian clerid material, a generic concept of clerine genera such as Clerus Geoffroy, 1762, Omadius Laporte, 1836, and Stigmatium Gray, 1832 became apparent and resulted in a preliminary concept of “Clerus-series” (Gerstmeier 2002).

A recent revision of the genus Xenorthrius Gorham (Gerstmeier and Eberle 2010) represents besides Mawdsley’s (1994) revision of the genus Aphelochroa the second in a series of papers dealing with the genera of a so-called “Orthrius-group”. In the Xenorthrius revision 11 species were transferred from Orthrius to Xenorthrius, and 22 new species were described, so that the genus Xenorthrius now includes 50 species (from 20 species formerly listed in Corporaal 1950). The aim of the present paper is to define the characters for a generic group, to determine those genera constituting the Orthrius group and examine the relationships among those genera. The following genera have been taken into consideration: Aphelochroa Quedenfeldt, 1885, Caridopus Schenkling, 1908, Dozocolletus Chevolat, 1842, Gyponyx Gorham, 1883, Languropilus Pic, 1940, Neorthrius gen. n., Orthrius Gorham, 1876, Pieleus Pic, 1940, Nonalatus gen. n., Pseudoastigmus gen. n., Xenorthrius Gorham, 1892, Falsoorthrius Pic, 1940 and Mimorthrius Pic, 1940 (during this study, the latter two genera were discovered to belong to the subfamily Tillinae).
Historic overview

Gorham (1876) described the genus *Orthrius* for *Orthrius cylindricus* and noticed the relationship to *Thanasimus*, and, on the basis of the tarsal structure, to *Clerus*. Seven years later, the same author (Gorham 1883) established the genus *Gyponyx* and mentioned its relationship to *Thanasimus* and *Axina*. Chevrolat (1842) described the species “oblongus”, drawing attention to its flightlessness and established the genus *Dozocolletus*, without a generic diagnosis; a diagnosis was given later by Lacordaire (1857). Quedenfeldt (1885) described the genus *Aphelochroa* (with *A. carneipennis* as type species) comparing it with *Opilo* and *Natalis*. Later, Gorham (1892) established the new genus *Xenorthrius* for three new species (*X. balteatus*, *X. mouhoti* and *X. subfasciatus*). For another two wingless species Schenkling (1908) erected the genus *Caridopus* and in the same publication, described the species *Apteroclerus brevis* from the Kilimanjaro, though with reservations about its generic placement. In two different publications Pic (1940a, 1940b) respectively described the genera *Languropilus* and *Pieleus*, while in an earlier paper (Pic 1933), he had expressed his view that the flightless *Astigmus pygidialis* differs greatly from all other *Astigmus* species.

Material and methods

Abbreviations

| Abbreviation | Description |
|--------------|-------------|
| A            | Antennomere |
| CuA2         | Cubitus anterior 2 |
| MNHN         | Museum National d’Histoire Naturelle, Paris, France |
| MRAC         | Musée Royal de l’Afrique Central, Tervuren, Belgium |
| MSNG         | Museo Civico di Storia Naturale “Giacomo Doria”, Genova |
| MZLU         | Museum of Zoology, Lund University, Sweden |
| RGCM         | Roland Gerstmeier Collection, Munich (deposited in the collection of the Technical University Munich, Animal Ecology), Germany |
| r3, r4       | Radial cross vein 3 and 4 |
| RP2          | Radius posterior 2 |
| SDEI         | Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany |
| T            | Tarsomere |

Cladistic analysis

23 characters with their respective states (Tab. 1) were analysed. Character polarity was determined by the outgroup method (Nixon and Carpenter 1993); no ancestral states were forced. The genus *Clerus* Geoffroy, 1762, was considered the outgroup taxon. The data matrix (Tab. 2) was analysed with the Willi Hennig Society edition of TNT 1.1
from September 2009 (Goloboff et al. 2003, 2008). To receive an exact solution, every possible tree was computed by using the “implicit enumeration” routine. For characters with more than one state per genus, multiple character states were used; they appear enclosed by square brackets in the matrix. Characters that were ambiguous, or missing in the available specimen, appear as a question mark. All characters were chosen to be nonadditive and none were weighted. Implied weighting was also turned off. The species were sorted alphabetically within the input file.

Diagnosis
Species of the Orthrius-group are readily distinguished from other Clerinae by the presence of the following characters (in combination):
– Eyes distinct, more or less protruding laterally, coarsely facetted
– Eyes separated by more than one eye width
– Labrum bilobed to broadly V-shaped (Fig. 1)
– Terminal segment of labial palpi securiform (Fig. 2)
– Terminal segment of maxillary palpi cylindrical (to digitiform) (Fig. 3)
– Antennal flagellum more or less filiform (Fig. 4)
– Antennomere 2 shorter than antennomere 3 (except Langiropilus)
– Procoxal cavities broadly open posteriorly (Figs 5, 6)
– Pro-intercoxal process not (or only slightly) dilated distally (Figs 5, 6)
– Metendosternites without anterior tendons, furcal arms distinct, furcal laminae mostly distinct, furcal stalks mostly of normal length or very short in wingless genera (Figs 11–20)
– Elytra without sharply-defined basal margin
– Typical wing venation (if winged), with open wedge cell, r3, r4 and CuA2 (except Pieleus) present, RP2 absent (Figs 21–28)
– Pro- and meso-tarsi each with four pulvilli (number of metatarsal pulvilli variable) (Fig. 8)
– Hind tarsi: T2<T3 + T4 (Tarsomere 2 smaller than tarsomeres 3 and 4 together)
– Spiculae of spicular fork more or less dilated (Figs 29–37)

Key to genera
1 Pronotum with six gibbosities on disc.................................................. Caridopus
– Pronotum without six gibbosities on disc.............................................. 2
2 Wingless species.................................................................................. 3
– Species with wings ................................................................................ 5
3 Antennomeres of flagellum from A4 dilated, antennal club absent........... 4
– Flagellum filiform, antennal club with 3 antennomeres......................... Dozocolletus
4 Tarsal pulvillar formula 4-4-2 .............................................................. Nonalatus gen. n.
Figures 1–10. 1–4 Labrum, labium, maxille and antenna of *Orthrius sepulcralis* 5 Pro-intercoxal process of *Xenorthrius robustus* 6 Pro-intercoxal process of *Orthrius sepulcralis* 7 Anterior mesosternal process of *Xenorthrius robustus* 8–9 Tarsus and claws of *Orthrius sepulcralis* 10 Claws of *Xenorthrius robustus*. 
Description of genera

**Aphelochroa** Quedenfeldt, 1885
http://species-id.net/wiki/Aphelochroa
Figs 11, 21, 29, 38, 47, 58

*Burgeonus* Pic, 1950 syn. n.; Pic 1950: 158.

**Type species:** *Aphelochroa carneipennis* Quedenfeldt, 1885. Quedenfeldt 1885: 267; Kraatz 1899: 86; Schenkling 1902: 326; Schenkling 1903: 29, 57; Mawdsley 1994: 128; Mawdsley and Sithole 2010: 1.

**Distribution:** Aethiopian region.

**Material examined:** *Aphelochroa sanguinea* (Thomson, 1857), Kenya, Voi, Sagala Region, 12.1991, leg. K. Werner. *Aphelochroa sanguinalis* (Westwood, 1852), Congo, VIII.1959, Albertville. *Aphelochroa fulva* Kraatz, 1899, Kenya, Meru Distr., Materi (Mitunguu), mt. 800, R. Mourglia legit; and several other specimens of this genus (all RGCM). *Burgeonus freynei* Pic, 1950 (Holotype), Coll. Mus. Congo, Lulua: Luashi, XI-1938, F. Freyne; R. DET, X., 5621; desire; Burgeonus freynei n sp [handwritten by Pic](MRAC).

**Head:** Eyes strongly protruding, only slightly emarginate at antennal insertion; interocular space more than one eye width; gular sutures converging, gular process broad; A1 large, stout, almost twice as long as A2, A2 shorter than A3, A3-A8 filiform, antennomeres becoming shorter, A9 dilated distally, A10 broader than long, A11 subovate, apical third pinched, terminal three antennomeres forming a loose club.

**Thorax:** Proepimeron short, not acute; anterior mesosternal process absent; proepimeron short; metendosternite with normal furcal stalk, short, normal furcal
Figures 11–20. Metendosternites of 11 Aphelochroa sp. 12 Caridopus sp. 13 Dozocolletus discophorus 14 Gyponyx sp. 15 Languropilus fortipes 16 Neorthrius sp. 17 Nonalatus brevis 18 Orthrius sepulcralis 19 Pseu-

doastigmus pygidialis 20 Xenorthrius loricus. Scale bars 0.5mm.
Figures 21–28. Wings of 21 Aphelochroa sp. 22 Caridopus sp. 23 Gyponyx sp. 24 Languropilus sp. 25 Neorthrius sp. 26 Orthrius sp. 27 Pieleus sp. 28 Xenorthrius sp. Scale bars 5mm.

arms and very slightly emarginate stalk base (Fig. 11). Elytra long, subparallel, broadest behind middle, apices broadly rounded, elytral punctation not arranged into striae.

Legs: Of normal size, stout; tarsal pulvillar formula 4-4-3, tibial spur formula 1-2-2; tibiae with longitudinal carinae; claws simple.
**Abdomen:** Apical margin of male ventrite 6 distinctly emarginate (Fig. 47); tegmen slender, tapering to a curved acumination distally, phallic struts acuminate, not fused, phallobasic apodeme slightly dilated distally (Fig. 38).

*Caridopus* Schenkling, 1908  
[http://species-id.net/wiki/Caridopus](http://species-id.net/wiki/Caridopus)  
Figs 12, 22, 30, 39, 48, 59

**Type species:** *Caridopus monstruosus* Schenkling, 1908. Schenkling 1908: 71.  
**Distribution:** Aethiopian region.

**Material examined:** *Caridopus monstruosus* (Type), Kilimanj., Sjösted; Kibonoto, kulturz.; 30. April; *Caridopus monstruosus*, Typus! (NRM). *Caridopus affinis* Schenklng, 1908 (Type), Meru, Regenwald; Meru, Sjöstedt; *Caridopus affinis* Schklg., Typus! (NRM).

**Head:** Eyes strongly protruding, only slightly emarginate at antennal insertion; interocular space more than 1.5 eye widths; gular sutures converging, gular process broad; antennae long, A2 shorter than A3, A3-A8 filiform, antennomeres becoming shorter, A9 and especially A10 dilated distally, A10 shorter than A9, A11 sub-ovate, apical third pinched, without club.

**Thorax:** Conspicuously longer than broad, with six gibbosities on disc; pro-intercoxal process narrow, linear; proepimeron short, acute to slightly rounded; anterior mesosternal process present; metendosternite with normal furcal stalk length, furcal arms acute distally, stalk base conspicuously emarginate (Fig. 12). Elytra compact (broadest behind middle), conspicuously constricted at base and strongly dilated apically in wingless species, apices broadly rounded, elytral punctuation arranged into ten more or less regular striae; wingless or with hindwings.

**Legs:** Long, very stout, femora conspicuously thickened; tarsal pulvillar formula 4-4-4, tibial spur formula 1-2-2; tibiae without longitudinal carinae; claws simple.

**Abdomen:** Apical margin of male ventrite 6 deeply emarginate (Fig. 48); phallobasic struts fused, phallic struts very broad, phallobasic apodeme strongly dilated distally (Fig. 39).

*Dozocolletus* Chevrolat, 1842  
[http://species-id.net/wiki/Dozocolletus](http://species-id.net/wiki/Dozocolletus)  
Figs 13, 31, 40, 49, 60

*Brinckodes* Winkler, 1960 syn. n.; Winkler 1960: 130.  
*Quasibrinckodes* Winkler, 1960 syn. n.; Winkler 1960: 134.

**Type species:** *Dozocolletus oblongus* Chevrolat, 1842. Chevrolat 1842: 278; Lacordaire 1857: 442; Schenkling 1903: 28, 38.  
**Distribution:** Aethiopian region (southern Africa).
Figures 29–37. Spicular forks of 29 Aphelochroa sp. 30 Caridopus monstruosus 31 Dozocolletus discophorus 32 Gyponyx sp. 33 Neorthrius sp. 34 Nonalatus brevis 35 Orthrius sepulcralis 36 Pseudoastigmus pygidialis 37 Xenorthrius simplex. Scale bars 0.5mm.
Material examined: *Dozocolletus discophorus* (Boheman, 1851) (Type), Caffraria, J. Wahlb, Type. *Dozocolletus puberulus* (Boheman, 1851) (Type), Caffraria, J. Wahlb, Type. *Dozocolletus oblongus* Chevrolat, 1842, Pretoria, 2.XII.1963, leg. A.L. Capener (all NRM). *Brinckodes apterus* Winkler, 1960 (Holotype and two Paratypes), S. Afr. Transvaal, 16 miles NE of Pretoria, Oct.-Nov. 1954, G. Rudebeck; *Brinckodes apterus* n.g., n.sp., Det. J.R. Winkler 1959. *Brinckodes apterus ab. ater* Winkler, 1960 (Holotype), S. Afr. Transvaal, 16 miles NE of Pretoria, Oct.-Nov. 1954, G. Rudebeck; *Brinckodes apterus* n.g., n.sp., n.ab., Det. J.R. Winkler 1959. *Quasibrinckodes pictus* Winkler, 1960 (Holotype), 8200 ft.; S. Afr. Cape Prov., Drakensbergen, 8 miles ENE Rhodes, 10.III.51, No 223; Swedish South Africa Expedition, 1950–1951, Brinck-Rudebeck; *Quasibrinckodes pictus* n.g., n.sp., Det. J.R. Winkler 1959, Holotypus (all MZLU).

**Head:** Eyes protruding, very slightly emarginate at antennal insertion; interocular space two to three eye widths; gular sutures converging, gular process broad; antennae long, A1 large, stout, almost twice as long as A2, A2 shorter than A3, A3–A8 filiform, antennomeres becoming shorter, A9 short, transverse, A10 larger than A9, transverse, A11 approximately equal in length to A9+A10, sub-ovate, apical half pinched, terminal three antennomeres forming a distinct club.

**Thorax:** Pronotum conspicuously constricted towards base, without transverse impression, proepimeron short to medium-sized, not acute; anterior mesosternal process present, broadly bent, proepimeron broad, short; metendosternite with very short furcal stalk, stalk base broad, with a deep emargination, furcal arms long, acute distally (Fig. 13). Elytra short, elytral base strongly constricted, broadest behind middle, apexes rounded, elytral punctuation arranged into ten striae; wingless.

**Legs:** Relatively short, stout; femora conspicuously thickened (especially profemora); tarsal pulvillar formula 4-4-4, tibial spur formula 2-2-2; tibiae with longitudinal carinae; claws simple, stout.

**Abdomen:** Apical margin of male ventrite 6 not emarginate (Fig. 49); tegmen relatively broad, phallobasic struts fused, phallic struts broad, dilated distally, phallobasic apodeme not dilated distally (Fig. 40).

*Gyponyx* Gorham, 1883
http://species-id.net/wiki/Gyponyx
Figs 14, 23, 32, 41, 50, 61

**Type species:** *Notoxus chinensis* Fabricius, 1794. Gorham 1883: 604; Schenkling 1900: 14; Schenkling 1903: 29, 45; Schenkling 1907: 199.

**Distribution:** Aethiopian region.

**Material examined:** *Gyponyx apicalis* (Chevrolat, 1842), Südafrika, SE 3130AA, Umtanvuma 3.1.1989, leg. T. Beyers; *Gyponyx signifer* (Boheman, 1851), Tanzania, Nufindi Dist., Nafinga 1000m, 21.11.-4.12.1989, leg. R. Mourglia; and several further specimens of this genus (all RGCM).
Head: Eyes strongly protruding, broadly but not deeply emarginate at antennal insertion; interocular space more than 1.5 eye widths; gular sutures converging, gular process broad; A1 large, stout, almost two times longer than A2, A2 shorter than A3, A3-A6 filiform, A7-A10 slightly dilated distally, antennomeres becoming shorter, A11 sub-ovate, apical third pinched, without club.

Thorax: Proepimeron medium-sized, more rounded than acute; anterior mesosternal process present; metendosternite with normal furcal stalk, short, normal furcal arms and very slightly emarginate stalk base (Fig. 14). Elytra long, subparallel, strongly dilated apically (broadest behind middle), apices broadly rounded, elytral punctation arranged into ten more or less regular striae.

Figures 38–46. Aedeagi of 38 Aphelochroa sp. 39 Caridopus sp. 40 Dozocolletus discophorus 41 Gyponyx sp. 42 Neorthrius sp. 43 Nonalatus brevis 44 Orthrius sepulcralis 45 Pseudoastigmus pygidialis 46 Xenorthrius simplex. Scale bars 1mm.
Figures 47–57. Terminal abdominal segments of 47 Aphelochroa sp. 48 Caridopus sp. 49 Dozocolletus discophorus 50 Gyponyx sp. 51 Languropilus fortipes 52 Neorthrius sp. 53 Nonalatus brevis 54 Orthrius sepulcralis 55 Pieleus irregularis 56 Pseudoastigmus pygidialis 57 Xenorthrius simplex. Scale bars 1 mm.
Legs: Of normal size; tarsal pulvillar formula 4-4-4, tibial spur formula 2-2-2; tibiae with longitudinal carinae; claws simple.

Abdomen: Apical margin of male ventrite 6 very slightly emarginate (Fig. 50); tegmen broad, phallobasic struts fused, phallic struts and phallobasic apodeme broad, but not conspicuously dilated distally (Fig. 41).

**Languropilus Pic, 1940**
http://species-id.net/wiki/Languropilus
Figs 15, 24, 51, 62

*Type species:* *Languropilus fortipes* Pic, 1940. Pic 1940a: 3.

*Distribution:* Aethiopian region (East Africa).

*Material examined:* *Languropilus fortipes* (females), Tanzania, Shinyanga Prov., Serengeti Sopa L., 19.XI.93, LF., Heiss (RGCM).

Head: With weakly protruding eyes, only very slightly emarginate at antennal insertion; interocular space about two times one eye width; gular sutures long, converging, gular process broad; antennae short, A1 large, stout, almost two times longer than A2, A2=A3 or A2>A3, A3-A8 filiform, antennomeres becoming shorter, A8 almost spherical, A9 and A10 transverse, A11 ovate, terminal three antennomeres forming a distinct club.

Thorax: Proepimeron medium-sized, more rounded than acute; anterior mesosternal process absent; metendosternite with normal furcal stalk length, stalk slender, base almost straight, furcal arms of more or less normal length, acute distally (Fig. 15). Elytra long, broadest behind middle, apices broadly rounded, elytral punctuation arranged into ten striae.

Legs: Of normal size, stout; tarsal pulvillar formula 4-4-3, tibial spur formula 1-2-2; tibiae without longitudinal carinae; claws simple.

**Neorthrius Gerstmeier & Eberle, gen. n.**
urn:lsid:zoobank.org:act:37980052-1760-48A2-8AA8-F677612AA8AE
http://species-id.net/wiki/Neorthrius
Figs 16, 25, 33, 42, 52, 63

*Type species:* *Neorthrius monticola* Schenkling, 1906 Schenkling 1906: 267.

*Distribution:* Indo-Australian region.

*Material examined:* *Neorthrius monticola* (Holotype), Kina-Balu-Geb., 1500m, Coll. Waterstrad; Schenkling det (SDEI); and several unidentified specimens of this genus.

Head: Eyes strongly protruding, conspicuously emarginate at antennal insertion; interocular space at least more than one eye width; gular sutures converging, gular process broad, compact, only slightly emarginate at middle; antennae long, A1 about two times longer than A2, A2 shorter than A3, A3-A8 filiform, A9 and A10 slightly dilated distally, A3-A5 more or less equal in length, A6-A8 becoming shorter, A11 sub-ovate,
apical half pinched, sometimes without club, sometimes terminal three antennomeres forming a loose club.

**Thorax:** Proepimeron short to medium-sized, more rounded than acute; anterior mesosternal process absent; metendosternite with normal furcal stalk length, furcal arms
normal, stalk base slightly emarginate (Fig. 16). Elytra long, subparallel, sometimes constricted apically, apices rounded separately, elytral punctuation arranged into ten striae.

**Legs:** Of normal size, sometimes with thickened femora; tarsal pulvillar formula 4-4-3, tibial spur formula 1-2-2; tibiae with longitudinal carinae; claws simple.

**Abdomen:** Apical margin of male ventrite 6 sometimes deeply emarginate (Fig. 52); phallobasic struts not fused, phallic struts and phallobasic apodeme dilated distally (Fig. 42).

*Nonalatus* Gerstmeier, gen. n.
urn:lsid:zoobank.org:act:4331C030-7A93-4F7D-A6F1-D896965CF99D
http://species-id.net/wiki/Neorthrius
Figs 17, 34, 43, 53, 64

**Type species:** *Apteroclerus brevis* Schenkling, 1908, comb. n. Schenkling 1908: 71.

**Distribution:** Aethiopian region (Kilimanjaro).

**Material examined:** *Apteroclerus brevis* (Type), Kilimandj., Sjöstedt; Kiboscho, 3’-4000m; 15. febr.; Bärqs-ägarne; Typus; Bergwiesen, Ericinella-Region, In den trockenen Blumenständen von Lobelia deekeni (NRM).

**Head:** Eyes protruding, emarginate at antennal insertion; interocular space two to three eye widths; gular sutures strongly diverging, gular process broad; antennae long, A2 shorter than A3, from A4 slightly dilated apically, A3-A7 becoming shorter, A9 and A10 more or less equal in length, A11 longer than A10, A11 sub-ovate, apical third pinched, without club.

**Thorax:** Proepimeron short, not acute; anterior mesosternal process present, broadly bent; metendosternite with very short furcal stalk, stalk base deeply emarginate, furcal arms acute distally (Fig. 17). Elytra ovate, short, compact, strongly constricted at base and towards apex, broadest behind middle, apices broadly rounded, elytral punctuation arranged into ten irregular striae; wingless.

**Legs:** Relatively long, stout; tarsal pulvillar formula 4-4-2, tibial spur formula 1-2-2; tibiae without longitudinal carinae; claws simple, with a very small, acute basal denticle.

**Abdomen:** Apical margin of male ventrite 6 distinctly emarginate (Fig. 53); tegmen very broad, parameres expanded laterally, tapering to an acumination distally, phallobasic struts not fused, phallic struts and phallobasic apodeme not dilated distally (Fig. 43).

*Orthrius* Gorham, 1876
http://species-id.net/wiki/Orthrius
Figs 1–4, 6, 8–9, 18, 26, 35, 44, 54, 65

*Dedana* Fairmaire, 1888, syn. n.; Fairmaire 1888: 26; Schenkling 1903: 4, 23.

**Type species:** *Orthrius cylindricus* Gorham, 1876. Gorham 1876: 74.
**Definition and Revision of the Orthrius-group of genera (Coleoptera, Cleridae, Clerinae)**

**Distribution:** Indo-Australian region.

**Material examined:** *Orthrius cylindricus* (Type), NSW; *Orthrius Gorh., cylindricus* G., Type; Museum Paris, Coll. Gorham, 1914 (MNHN); and several other specimens of this genus. *Dedana rufodorsata* Fairmaire, 1888 (Type), Fokien; *Dedana rufodorsata* Fairm.; ExMusaeo Arm. David, 1900 (MNHN).

**Head:** Eyes strongly protruding, only slightly emarginate at antennal insertion; interocular space more than one eye width; gular sutures converging, gular process broad;

**Figures 64–68.** Habitus of 64 *Nonalatus brevis* 65 *Orthrius sepulcralis* 66 *Pieleus irregularis* 67 *Pseudoastigmus pygidialis* 68 *Xenorthrius moubati.*
antennae long, A2 shorter than A3, A2-A8 filiform, A10 broadest, A11 sub-ovate, apical half pinched, terminal three antennomeres forming a more or less conspicuous club.

**Thorax:** Proepimeron short to medium-sized, not acute; anterior mesosternal process absent; metendosternite with normal furcal stalk length, furcal arms normal, stalk base very slightly emarginate (Fig. 18). Elytra long, subparallel, sometimes dilated apically (broadest behind middle), apices rounded, elytral punctuation not arranged into striae.

**Legs:** Long, especially profemora intermediately to strongly thickened; tarsal pulvillar formula 4-4-3, tibial spur formula 0-1-1; tibiae with longitudinal carinae; claws simple.

**Abdomen:** Apical margin of male ventrite 6 straight or slightly emarginate (Fig. 54); tegmen relatively broad, parameres expanded laterally, tapering to a curved acumination distally, phallobasic struts not fused, phallobasic apodeme dilated distally (Fig. 44).

**Pieleus** Pic, 1940
http://species-id.net/wiki/Pieleus
Figs 27, 55, 66

**Type species:** *Pieleus irregularis* Pic, 1940. Pic 1940b: 4.

**Distribution:** China.

**Material examined:** *Pieleus irregularis* (Type female), T’ienmu Shan, Musée Heude; 20.VII.36, O. Piel, coll.; Orthrius irregularis mihi [handwritten by Pic](MNHN).

**Head:** Eyes strongly protruding, conspicuously emarginate at antennal insertion; interocular space about 1.5 eye widths; gular sutures diverging, gular process broad; antennae short, A1 more than two times longer than A2, A2 shorter than A3, A2-A6 filiform, antennomeres becoming shorter, A7 shorter than A6, slightly dilated distally, A11 sub-ovate, apical third pinched, terminal three antennomeres forming a loose club.

**Thorax:** Proepimeron medium-sized, slightly rounded; anterior mesosternal process present; metendosternite missing. Elytra compact, strongly dilated apically (broadest behind middle), apices broadly rounded, elytral punctuation not arranged into striae; without CuA2 in hindwings (Fig. 27).

**Legs:** Of normal size; tarsal pulvillar formula 4-4-4, tibial spur formula 1-1-2; tibiae without longitudinal carinae; claws with basal denticle.

**Pseudoastigmus** Eberle, gen. n.
urn:lsid:zoobank.org:act:56520F10-5440-4188-ACCE-CBA847869133
http://species-id.net/wiki/Pseudoastigmus
Figs 19, 36, 45, 56, 67

**Type species:** *Astigmus pygidialis* Pic, 1933, comb. n. Pic 1933: 257.

**Distribution:** Aethiopian region (Ruwenzori).
Material examined: Astigmus pygidialis (Syntype), Musée du Congo, Ruwenzori (4200m), VII-1932, L. Burgeon; type; Stigmatium (Astigmus) pygidialis n sp [handwritten by Pic], and four additional syntypes (MRAC).

Head: Eyes strongly protruding, conspicuously emarginate at antennal insertion; interocular space about two eye widths; gular sutures subparallel to slightly diverging, gular process of medium width; antennae long, A2 shorter than A3, from A4 onwards slightly dilated distally, A11 sub-ovate, apical half pinched, without club.

Thorax: Proepimeron very short, not acute; anterior mesosternal process present; metendosternite with very short furcal stalk length, furcal arms acute distally, stalk base conspicuously emarginate (Fig. 19). Elytra short, compact, dilated apically (broadest behind middle), apices broadly rounded, elytral punctation arranged into more or less regular ten striae; wingless.

Legs: Long, stout; tarsal pulvillar formula 4-4-3, tibial spur formula 1-2-2; tibiae without longitudinal carinae; claws with basal denticle.

Abdomen: Apical margin of male ventrite 6 deeply emarginate (Fig. 56); tegmen relatively broad, tapering to a curved acumination distally, phallobasic struts not fused, phallic struts and phallobasic apodeme not dilated distally (Fig. 45).

Xenorthrius Gorham, 1892
http://species-id.net/wiki/Xenorthrius
Figs 5, 7, 10, 20, 28, 37, 46, 57, 68

Type species: Xenorthrius mouhoti Gorham, 1892. Gorham 1892: 733, 1893: 575; Schenckling 1903: 46–47.

Distribution: Indo-Australian and Palaearctic region.

Material examined: X. mouhoti, Lectotype (MSNG), Paralectotypes, and additional species (see Gerstmeier and Eberle 2010).

Head: Eyes strongly protruding, conspicuously emarginate at antennal insertion; interocular space larger than one eye width; gular sutures subparallel to divergent, gular process varying in width, from narrow to broad; antennal length interspecifically variable and sometimes sexually dimorphic (longer in males), A2 shorter than A3, A3-A8 more or less filiform, A10 broader than long, A11 sub-ovate, apical half pinched, mostly without club, sometimes terminal three antennomeres forming a loose club.

Thorax: Proepimeron medium-sized, more or less acute; anterior mesosternal process present, with a subtriangular sulcus in the middle (Fig. 7); metendosternite with normal furcal stalk length, furcal arms broad, apically dilated, stalk base very slightly to deeply emarginate (Fig. 20). Elytra subparallel, sometimes broadest behind middle, apices rounded (most species), strongly dehiscent (X. prolongatus and X. furcalis), or dentate (X. truncatus and X. scordalus); elytral punctation arranged into ten striae.

Legs: Mostly relatively short; tarsal pulvillar formula 4-4-4, tibial spur formula 1-2-2; tibiae with or without longitudinal carinae; claws with pronounced basal denticle (Fig. 10).
Table 1. Characters and character states used in the cladistic analysis of the genera.

| Character | Description                                                                 |
|-----------|-----------------------------------------------------------------------------|
| Character 0 | Mesotarsal pulvilli: (0) 4; (1) 3                                               |
| Character 1 | Metatarsal pulvilli: (0) 4; (1) 3; (2) 2                                       |
| Character 2 | Protibial spurs: (0) 2; (1) 1; (2) 0                                          |
| Character 3 | Mesotibial spurs: (0) 2; (1) 1                                                |
| Character 4 | Metatibial spurs: (0) 2; (1) 1                                                |
| Character 5 | Ommatidial facets: (0) coarse; (1) fine                                      |
| Character 6 | Flagellomeres: (0) filiform; (1) dilated                                       |
| Character 7 | Eye’s emargination: (0) absent or weak; (1) conspicuous                     |
| Character 8 | Eye’s separation: (0) more than two eyes width; (1) between one and two eyes width |
| Character 9 | Gular sutures: (0) convergent to subparallel; (1) subparallel to divergent |
| Character 10 | Gular process: (0) broad; (1) narrow                                         |
| Character 11 | Relation between A2 and A3: (0) A2 < A3; (1) A2 = A3 or A2 > A3               |
| Character 12 | Anterior mesosternal process: (0) present; (1) absent                         |
| Character 13 | Metendosternite, furcal stalk length: (0) normal; (1) very short             |
| Character 14 | Metendosternite, furcal arms: (0) normal; (1) acute                          |
| Character 15 | Metendosternite, furcal stalk base: (0) normal; (1) deeply emarginate        |
| Character 16 | Wings: (0) present; (1) absent                                                |
| Character 17 | CuA2: (0) present; (1) absent                                                 |
| Character 18 | RP2: (0) present; (1) absent                                                  |
| Character 19 | Elytral punctation: (0) with 10 regular striae; (1) with 10 irregular striae; (2) with more than 10 irregular striae |
| Character 20 | Tibial carinae: (0) present; (1) absent                                       |
| Character 21 | Claws: (0) simple; (1) with basal denticle                                    |
| Character 22 | Phallobasic struts: (0) not fused; (1) fused                                  |

Abdomen: Apical margin of male ventrite 6 more or less distinctly emarginate (Fig. 57); tegmen mostly elongate, cross-section subrectangular; phallobasic struts not fused, phallic struts acute, phallobasic apodeme not dilated distally (Fig. 46).

Discussion of cladistic results

The cladistic analysis resulted in a single most parsimonious tree with a length of 37 steps (Fig. 69). Common to all taxa of the Orthrius-group are four mesotarsal pulvilli (char. 0-0) and coarse ommatidial facets (char. 5-0) which distinguishes them from the Clerus-series.

Pseudoastigmus gen. n. and Nonalatus gen. n. appear together at the base of the tree. This pair is supported by the acute form of the furcal arms of the metendosternite (char. 14-1) as well as the complete reduction of the hind wings (char. 16-1).

The remaining taxa share the filiform flagellum (char. 6-0). The development of four pulvilli at the metatarsus (char. 1-0) is also synapomorphic at this point, but is
Table 2. Character matrix of 23 adult morphological characters of *Clerus* (outgroup) and genera of the *Orthrius* group.

| Taxa      | Characters |
|-----------|------------|
|          | 0 1 2 3 4 5 6 7 8 9 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 1 1 0 |
| Clerus    | 0 1 1 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 2 0 0 0 |
| Aphelochroa | 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 1 1 1 ? ? 0 1 0 1 |
| Caridopus | 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 |
| Dozocolletus | 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 ? ? 0 0 0 1 |
| Gyponyx   | 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 |
| Languropilus | 0 1 1 0 0 0 0 0 1 0 0 1 1 0 0 0 0 1 0 1 0 1 0 ? |
| Neorthrius | 0 1 1 0 0 0 0 1 1 0 0 0 1 0 0 0 0 1 0 0 0 1 1 1 0 |
| Nonalatus | 0 2 1 0 0 0 1 1 0 1 0 0 0 1 1 1 1 ? ? 1 1 1 0 |
| Orthrius  | 0 1 2 1 1 0 0 0 1 0 0 0 1 0 0 0 0 0 1 2 0 0 0 |
| Pieleus   | 0 0 1 1 0 0 0 1 1 1 0 0 0 ? ? ? 0 1 1 2 1 1 ? |
| Pseudoastigmus | 0 1 1 0 0 0 1 1 1 1 0 0 0 ? 1 ? 1 ? ? 0 1 1 0 |
| Xenorthrius | 0 0 1 0 0 0 0 1 1 1 1 01 [01] 0 0 0 0 [01] 0 0 1 0 [01] 1 0 |
reduced to three pulvilli for the cluster of Neorthrius gen. n., Languropilus, Orthrius and Aphelochroa (char. 1-1).

These four genera also share the loss of the anterior mesosternal process (char. 12-1). Like in Dozocolletus and Caridopus the emargination of the eyes is weak or absent (char. 7-0) in Languropilus, Orthrius and Aphelochroa. For this reason, Neorthrius adopts a basal position in this group. The monophyly of Orthrius and Aphelochroa is supported by their elytral punctation (char. 19-2). Orthrius differs from all other taxa in this revision in its tibial spur formula which is 0-1-1 (chars. 2-2, 3-1 and 4-1).

The aethiopian genera Gyponyx, Dozocolletus and Caridopus have in common, that the phallobasic struts are fused with the phallobasic apodeme (char. 22-1). The monophyly of Dozocolletus and Caridopus is well supported by the weak or absent emargination of the eyes (char. 7-0) and similarities of their metendosternites: the furcal arms are acute (char. 14-1) and the furcal stalk base (char. 15-1) is deeply emarginate.

A common ancestor can be assumed for the latter two clusters of genera. This is supported by two synapomorphies: the gular sutures are convergent to parallel (char. 9-0) and the claws are simple (char. 21-0). The presence of the tibial carinae (char. 20-0) also is apomorphic at this node but reduced in Caridopus and Languropilus. As Solervicens (2007) mentioned, it also may be considered a symplesiomorphy, because it is a common character of the Clerinae.

Figure 69. Cladistic tree of the genera of the Orthrius-group.
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