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ON SYSTEMATICS OF THE SUBFAMILY CYBOCEPHALINAE (COLEOPTERA: NITIDULIDAE) WITH DESCRIPTION OF NEW SPECIES AND GENERIC TAXA

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ABSTRACT

This paper describes a new species, *Hierronius madeiraensis* sp. nov., from Madeira belonging to the wingless group of the family Nitidulidae, together with the description of new cybocephalin genera from Japan (*Apastillus* gen. nov., type species: *Pastillus eminentithorax* Sadatomo Hisamatsu, 2013), South America (*Amedissia* gen. nov., type species: *Pycnocephalus argentines* Bréthes, 1922) and Micronesia (*Pacicephalus* gen. nov., type species: *Cybocephalus gressitti* Endrödy-Younga, 1971). A key to all recent and fossil genera of the subfamily is provided. *Theticcephalus* Kirejtshuk, 1988 is regarded as a separate genus (stat. nov.). The genera with species having partly or completely reduced hindwings (*Apastillus* gen. nov., *Hierronius* Endrödy-Younga, 1968, *Pastilodes* Endrödy-Younga, 1968, *Pastillus* Endrödy-Younga, 1962, and probably the fossil *Pastillocenicus* Kirejtshuk et Nel, 2008), characterized by a short metaventrite, are considered as independent lineages. The systematics and phylogeny of the family are discussed in regards to recent publications affecting the position of the subfamily Cybocephalinae and proposing changes in the general system of the family Nitidulidae.

Key words: Coleoptera, Nitidulidae, Cybocephalinae, *Hierronius*, new species, new genera, key to genera

О СИСТЕМАТИКЕ ПОДСЕМЕЙСТВА СУВОСЕРНАЛИНАЕ (СОЛЕОПТЕРА: НИТИДУЛИДАЕ) С ОПИСАНИЕМ НОВОГО ВИДА И НОВЫХ РОДОВ

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РЕЗЮМЕ

В настоящей статье описывается новый вид, *Hierronius madeiraensis* sp. nov., из Мадейры, относящийся к бескрылой группе семейства Nitidulidae, вместе с описанием новых родов цибоцефалин из Японии (*Apastillus* gen. nov., типовой вид: *Pastillus eminentithorax* Sadatomo Hisamatsu, 2013), Южной Америки (*Amedissia* gen. nov., типовой вид: *Pycnocephalus argentines* Bréthes, 1922) и Микронезии (*Pacicephalus* gen. nov., типовой вид: *Cybocephalus gressitti* Endrödy-Younga, 1971). Предложен ключ для всех современных и вымерших родов. *Theticcephalus* Kirejtshuk, 1988 рассматривается как самостоятельный род (stat. nov.). Роды с видами, имеющими полностью или частично редуцированные задние крылья (*Apastillus* gen. nov., *Hierronius* Endrödy-Younga,

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1968, *Pastillodes* Endrödy-Younga, 1968, *Pastillus* Endrödy-Younga, 1962 и, вероятно, вымерший *Pastillocenicus* Kirejtshuk et Nel, 2008) характеризуются коротким метавентритом и рассматриваются независимыми линиями. Обсуждаются систематика и филогения семейства в связи с последними публикациями, затрагивающими положение подсемейства Cybocephalinae и предлагающими изменения в общей системе семейства Nitidulidae.

Ключевые слова: Coleoptera, Nitidulidae, Cybocephalinae, *Hierronius*, новый вид, новые роды, ключ для родов

INTRODUCTION

The subfamily Cybocephalinae is a very specialized group within Nitidulidae, sometimes regarded as a separate family (Endrödy-Younga 1968, 1976; Tian and Ramani 2003; Sadatomo Hisamatsu 2011; etc.). However it was never demonstrated that this group has synapomorphies with any group beyond Nitidulidae, although some structural apotypic peculiarities in the antennae, male aedeagus, and also number of tarsomeres, were well known. The structural characters of these and other organs can be found in different groups of the nitidulin lineage (Kirejtshuk 2008), mostly in the tribe Cyllochini Everts, 1898 of the subfamily Nitidulinae. Finally, the analogous parasitoid mode of life is characteristic of both Cybocephalinae and Cychramptodini Kirejtshuk et Lawrence, 1992 (Nitidulinae). If we consider this group (Cybocephalinae) as a family we are obliged to raise the taxonomic ranks for all the subgroups within both carpophilin and nitidulin lineages or at least regard these lineages as separate families together with “Cybocephalidae”. Recently Cline et al. (2014) made a more radical proposal, joining the Cybocephalinae with Sphindidae and putting both in the “Cerylonid series”. Such an innovation is not fully grounded and is considered unreasonable (see Discussion below). The classification of the subfamily under consideration is still poorly defined and the diagnoses of many genera are still not clear. This paper describes a new species of the genus *Hierronius* Endrödy-Younga, 1968 and provides a key to the genera of the subfamily. Three new genera are proposed, viz. *Apastillus* gen. nov. for *Pastillus eminentithorax* Sadatomo Hisamatsu 2013 from Japan, *Amedissia* gen. nov. for *Pycnocephalus argentines* Bréthes, 1922 from South America and *Pacicephalus* gen. nov. for *Cybocephalus gressitti* Endrödy-Younga, 1971. In addition, the ranks of supraspecific taxa, structural features, and trophic interactions of this group are discussed.

MATERIAL AND METHODS

Holotype and part of paratypes of described species are housed in the collection of the Zoological Institute RAS, Saint Petersburg, Russia (ZIN) and further paratypes in the private collection of Marion Mantič (MM) and Museum National d’Histoire Naturelle in Paris (MNHN). Male genitalia after the standard preparation procedure were dipped in a drop of Euparal and placed on a plastic card below the beetle. The digital color photographs were taken from dry specimens with a Leica MZ16 stereo microscope equipped with a Leica DFC290 digital camera and were combined using the Helicon Focus software. Additional studies were made with usage stereomicroscopes MBS-12.

SYSTEMATICS

Family Nitidulidae Latreille, 1802

Subfamily Cybocephalidae Jacquelin du Val, 1858

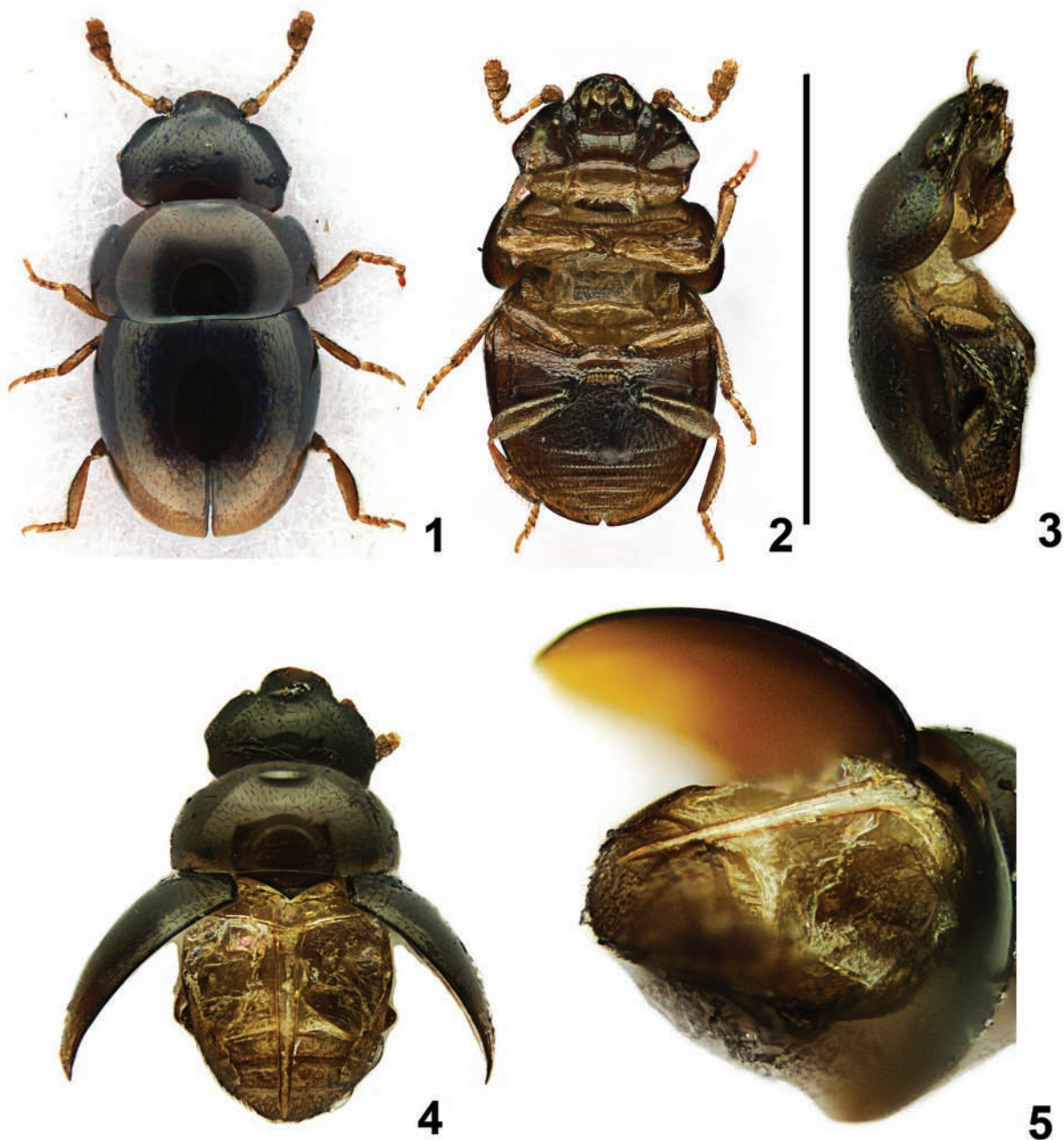
Genus *Hierronius* Endrödy-Younga, 1968

Type species: *Cybocephalus laevis* Wollaston, 1864, recent, Canary Islands, original designation.

Hierronius madeiraensis sp. nov.

(Figs. 1–11)

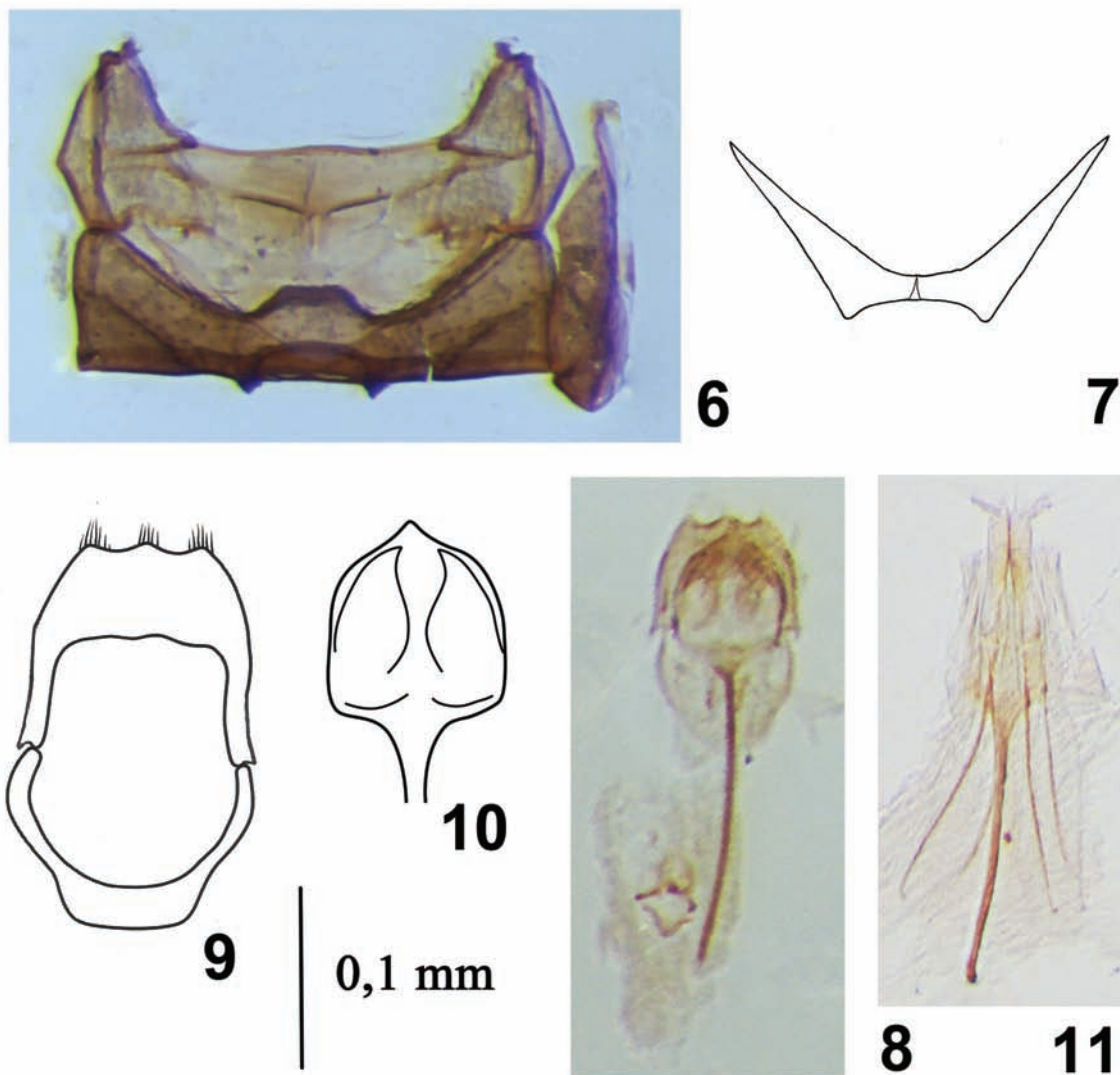
Type material. *Holotype, male* (ZIN) and 260 *paratypes* (ZIN, MM, MNHN), “Portugal, Madeira c., Bica da Cana env., 5 km S of Sao Vicente, 21.05.2013, Mantič lgt., 32°45′20″N, 17°03′30″W, 1600 m n.m., Erica sp., meadows, fern – sifting”; 10 *paratypes* (MM), “Madeira c., Loiral env.-Levada do Paul, 4,5 km N of Canhas, 16.05.2013, Mantič lgt., 32°44′19″N, 17°06′03″W, 1300 m n.m., Erica sp. – sifting”; 3 *paratypes* (MM), “Madeira c., Achada da Teixeira, 4,5 km SSW of Ilha, 23.05.2013, Mantič lgt.,



Figs. 1–5. *Hierronius madeiraensis* sp. nov.: 1 – body, dorsal view; 2 – idem, ventral view; 3 – idem, lateral view; 4 – paratype with open elytra, dorsal view; 5 – idem, dorsolateral view. Scale bar = 1.0 mm.

32°45'54''N, 16°55'16''W, 1650 m n.m., *Erica* sp., *Ulex* sp. – sifting"; 3 *paratypes* (MM), "Madeira c., Queimadas env.- Levada do Caldeirao Verde, 2,5 km S of Ilha, 23.05.2013, Mantič lgr., 32°47'02''N, 16°54'23''W, 900 m n.m., *Erica* sp., *Laurus* sp. –

sifting"; 1 *paratype* (MM), "Madeira c., Pico do Arieiro, 4 km NE of Curral das Freiras, 17.05.2013, Mantič lgt., 32°44'08''N, 16°55'43''W, 1700 m n.m., *Erica* sp. – sifting"; 1 *paratype* (MM), "Madeira c., Poiso, 2,5 km N of Monte, 17.05.2013, Mantič lgt.,



Figs. 6–11. *Hierronius madeiraensis* sp. nov.: 6 – pterothoracic sclerites (with metendosternite), inner (dorsal) view; 7 – metendosternite, dorsal view; 8 – aedeagus, ventral view; 9 – tegmen, ventral view; 10 – penis, dorsal view; 11 – ovipositor, ventral view. Width of metaventricle 0.3 mm. Scale bar for Figs. 10, 11 = 0.1 mm.

32°42′42″N, 16°53′46″W, *Erica* sp., *Vaccinium* sp. – sifting, 1400 m n.m.”; 1 *paratype* (MM), “Madeira occ., Pombais, 3 km SWW of Porto Moniz, 24.05.2013, Mantič lgt., 32°51′34″N, 17°12′11″W, moss on the terrace by the levada – sifting, 400–450 m n.m.”.

Description. *Male* (*holotype*). Length 1.0 mm (with not deflected head), width 0.4 mm, height 0.4 mm. Elongate oval and rather convex; elytra and eyes dark brown to blackish; anterior part of head, metaventricle and base of abdomen brownish;

appendages, base of head, prosternum, mesoventrite and abdominal apex reddish; rather convex dorsally and suflattened ventrally; dorsum moderately shining and underside with a slight shine; dorsum with very sparse, very fine and hardly conspicuous hairs, somewhat shorter than distance between their insertions; underside with denser and more conspicuous hairs, slightly longer than their insertions on head and thorax, and 3–4 times as long as distance between their insertions. Dorsum nearly alutaceous and

with extremely fine and sparse punctation. Pygidium and underside with very fine, shallow and nearly indistinct punctures; interspaces between them on pygidium and distal ventrites about as greater as eye facet and becoming sparser anteriorly irregularly to almost cellularly microreticulated.

Head rather large and wide, weakly convex, with a frons moderately projecting anteriorly, widely rounded temples, slightly and narrowly excised at antennal insertions and without visible submarginal line before eyes; eyes very small, located at widest part of head and represented only by few large facets not reaching lateral edge and not extending on underside. Labrum scarcely exposed from under frons. Mandibles well exposed at sides and slightly exposed before frons. Antennae 11-segmented, their scape subglobular, pedicel subconical and about twice as long as thick, their elongate three-segmented club about twice as long as wide and obliquely truncate at apex. Pronotum nearly twice as long as wide and slightly wider than elytra at the middle, rather and evenly convex at disc and strongly sloping at sides, its anterior edge bisinuate, lateral edges widely rounded, posterior edge shallowly emarginated at rounded posterior angles. Scutellum widely subtriangular and with widely rounded apex. Metanotum far extended behind as a long narrow flat median process under elytra congruent their curve along suture and reaching midlength of pygidium. Elytra somewhat less than twice as long as pronotum and slightly shorter than wide combined, rather convex at disk and steeply sloping laterally, their sides slightly arcuate and apices nearly forming a joint arc. Hindwings absent. Pygidium widely truncate at apex and anal segment clearly exposed from under it.

Labial palpi penultimate palpomere subconical and rather widened apically (about as long as thick at apex) and ultimate palpomere subconical and narrowed apically (somewhat shorter than thick at base). Mentum about 1.5 times as wide as long. Maxillary palpi with ultimate palpomere gradially narrowing to subacute apex. Hypostomal sinuses very narrow and not extended behind level of posterior edge of mentum. Antennal grooves arcuate and continued by divergent gular sutures. Prosternum very short and forming collar-like stripe along anterior edge, its process very narrow and not extended behind procoxae. Metaventricle distinctly shorter than mesoventricle, with weakly expressed premetacoxal lines arcuately outlined and ended at anterior

third of metepisterna. Distance between metacoxae nearly as great as that between mesocoxae and about 2/3 as great as length of metatibia. Abdominal ventrite 1 about twice as long as metaventricle and 3.5 times as long as hypopygidium and about twice as long as ventrites 2–4 combined. Submetacoxal lines arcuately deviating and disappearing at the middle of ventrite 1. Hypopygidium widely emarginate at apex. Epipleura moderately narrow and steeply sloping downwards laterally.

Legs well developed. Protibia subtriangular and scarcely curved, at apex markedly narrower than antennal club and with clear outer angle; mesotibiae subtriangular, slightly narrower than protibia and with arcuate outer angle; metatibia rather narrow (slightly wider than mesotibia) and narrowing in distal half; all tibiae with a row of moderately long hairs along outer edge. Femora of usual shape; pro- and mesofemora somewhat less than twice as wide as corresponding tibiae; metafemur somewhat more than twice as wide as metatibia and about three times as long as wide. Tarsi of moderate length and rather narrow, tarsomeres 1–3 narrowly lobed.

Aedeagus moderately sclerotized.

Female. Externally differs from the male in the widely rounded apices of pygidium and hypopygidium. Ovipositor weakly sclerotized.

Variations. Length 0.8–1.1 mm (up to 0.6 mm with rolled head and prothorax). The punctation and pubescence are somewhat variable: sometimes dorsal hairs are not visible, the color of the underside is also variable and some paratypes are rather light.

Etymology. The epithet of this new species is formed from the name of island where it was collected.

Comparison. Three species of this genus known before this study are recorded from Canary Islands; two of them described from females and one from both sexes. This new species is somewhat similar to *H. angulosus* Endrödy-Younga, 1968 by the elytral outline (viewing laterally) and comparatively short antennal flagellum, and also to *H. nanus* Endrödy-Younga, 1968 by the comparatively small eyes. *H. madeiraensis* sp. nov. differs, however, from the congeners by its sculpture (not completely smooth) and conspicuous pubescence of the dorsum, widely arcuate pronotal sides (viewing laterally), smallest eyes, shape of protibia (subtriangular and widened apically), antennal scape (larger and wider), pedicel (comparatively narrow) and segments of club, and also from *H. nanus* by the peculiarities of structure of an aedeagus.

Remarks. The senior author had opportunity to have a look at all specimens described (Endrödy-Younga 1968), except type series of *H. angulosus*, however the authors had not at their disposal them while the description of new species was fulfilling and, therefore, they decided to prepare a more detailed description of the new species including both species and group (generic) characters. The process of metanotum discovered in the new species could be found also in other congeners.

Notes on bionomy. This new species is collected by sifting of soil at roots of different bushes (Figs. 12–15). It can be supposed that it is associated some coccids inhabited at roots most probably of *Erica arborea*, unless at roots of *Ulex europaeus* or under some other bushes from Viciaceae.

Genus *Amedissia* gen. nov.

Type species: *Pycnocephalus argentinus* Bréthes, 1922, recent, Argentine.

Diagnosis. Body ca. 1.5 (with not deflected head mm long and ca. 1.0 mm wide; elongate oval and extremely convex; subunicolourous dark coloured and shining with metallic hue. Head comparatively narrow, with a frons shortly projecting anteriorly; eyes rather large dorsally and ventrally. Mentum subtriangular and rather narrowing anteriorly. Ultimate maxillary palpomere subconical, narrowing apically and slightly longer than subcylindrical ultimate labial palpomere. Antennae 10-segmented and with elongate club consisting of three antennomeres (ultimate subequal in length to each previous segments of club); scape very short and antennomere 2 longest. Lateral edge of pronotum emarginate. Scutellum subpentagonal and widest at base. Elytra of usual shape. Hindwings apparently present. Abdominal ventrite 1 not longer than each of ventrites 2–4; each of 1–4 ventrites with a row of stout setae along their posterior edge; “palplike process” of each lateral side of ventrite 4. Mesofemur strongly dilated and with a dorsal depression to receive mesotibia (which can be completely concealed). Metafemur moderately dilated and with a dorsal depression to receive metatibia (which is only partly concealed). Tarsomeres 1–3 strongly lobed.

Species included: The type species only.

Comparison. This new genus is alone cybocephalins taxon with incomplete elytra leaving uncovered last abdominal segments, emarginated lateral edges

of pronotum, subtriangular mentum and very characteristic setae on abdominal ventrites. It can be diagnosed after the below key to the genera. Besides, *Amedissia* gen. nov. is characterized by the subpentagonal scutellum, rather short abdominal ventrite 1 with scarcely visible submetacoxal line, processes at the sides of abdominal ventrite 4 and rather dilated meso- and metafemora with elongate depression to receive the correspondent tibiae.

Remarks. Bréthes (1922) described “*Pycnocephalus*” *argentines* mentioned only few structural characters. Parker (1951) identified this species after the mentioned characters and mostly thanks to the specific habitat of this species [association with *Ceroplastes* scales (Coccidae) of *Baccharis platensis* (Asteraceae)]. Both coleopterists probably meant the same species which according to Bréthes (1922) is characterized by 10-segmented antennae and “les élytres tronquées en arc à l’extrémité” (Bréthes 1922: 265), un unique combination within cybocephalins. However, the type species of the new genus shares only few external similarities with *Pycnocephalus* but many characters of the former shows a great distinctness among the members of the subfamily. This is a reason to propose a new genus. The body size of its type species (*Amedissia argentina* comb. nov.) is somewhat smaller than that in the *Pycnocephalus*. The similar characters of the latter and *Amedissia* gen. nov. are mostly plesiotypic, however, the flattened meso- and metafemora with an elongate depression for receipt of correspondent tibia could be inherited from a common ancestor.

Etymology. The name of this new genus is formed from the first letters of the name America and generic name “*Dissia*” proposed in Cybocephalinae and synonymised with *Cybocephalus*. The gender is feminine.

Genus *Apastillus* gen. nov.

Type species: *Pastillus eminentithorax* Sadatomo Hisamatsu, 2013, recent, Japan.

Diagnosis. Body ca. 1.8 (with not deflected head) mm long; elongate oval and extremely convex; subunicolourous dark brown with light appendages; dorsum finely and sparsely punctured, rather smoothed, shining and subglabrous; underside with more clear sculpture and more conspicuous pubescence. Head large and wide, with a frons moderately projecting anteriorly, distinctly bordered and with deep emarginations for reception of antennal scape; eyes rather



12



13



14



15

Figs. 12–15. Portugal, Madeira, sites of collecting of the type species of *Hierronius madeiraensis* sp. nov.: 12, 13, 15 – Bica da Cana; 14 – Achada da Teixeira.

large dorsally and indistinctly visible ventrally. Labrum slightly exposed from under frons and truncate at apex. Mentum slightly wider than long. Antennae 10-segmented and with elongate club consisting of two antennomeres (penultimate much shorter than ultimate one with subacute at apex). Pronotum along the middle about three times as long as along arcuate sides, its anterior edge bisinuate, lateral edges widely rounded, posterior edge gently convex. Scutellum widely subtriangular and with angular apex. Elytra somewhat less than twice as long as pronotum and rather convex at disk and steeply sloping laterally, their sides arcuate and apices subvertically sloping and nearly forming a joint arc. Hindwings present. Antennal grooves arcuate and continued by divergent angular sutures. Prosternum with carinate process. Metaventrite distinctly shorter than mesoventrite, with weakly expressed premetacoxal lines suboblique

and ended at the middle of metepisterna. Metacoxae narrowly separated and distance between metacoxae much smaller than that between mesocoxae. Abdominal ventrite 1 longest and with submetacoxal lines rectilinearly reaching the posterior edge at outer apical angles of ventrite 1. Legs well developed. Pro- and mesotibiae very narrow, with arcuate outer angle, not crenellate outer edge and with long setae; metatibia wide and flat, curved at base, subparallel-sided in distal 2/3 and with a row of moderately long hairs along outer edge. Femora of usual shape; metafemur somewhat wider. Tarsi of moderate length and rather narrow, tarsomeres 1–3 narrowly lobed. *Aedeagus* moderately sclerotized, with short penis trunk subtruncate at apex.

Female. Externally differs from the male in the widely rounded apices of both pygidium and hypopygidium. Ovipositor weakly sclerotized.

Species included: The type species only.

Comparison. This genus is distinct among all members of the subfamily by extremely convex body, very short lateral edges of pronotum, elytral apices subvertically sloping and posterior edge of abdominal ventrite 1 distinctly emarginate. This new genus is easily recognized after the below key. Besides, it differs from other genera with short metaventrite also in the following characters:

- from *Hierronius* Endrödy-Younga, 1968 in the narrowly separated both meso- and metacoxae, strongly relief premetacoxal and submetacoxal lines;
- from *Pastillodes* Endrödy-Younga, 1968 in the narrowly separated mesocoxae and not concave metaventrite;
- from *Pastillus* Endrödy-Younga, 1962 in the strongly relief submetacoxal lines and markedly longer abdominal ventrite 1;
- from *Pastillocenicus* Kirejtshuk et Nel, 2008 in the narrowly separated both meso- and metacoxae, strongly relief submetacoxal lines.

Etymology. The new generic name is formed from the generic name “*Pastillus*” and the negative prefix “*a*”. The gender is masculine.

Genus *Pacicephalus* gen. nov.

Type species: *Cybocephalus gressitti* Endrödy-Younga, 1971, recent, Micronesia.

Diagnosis. Body ca. 1.0–1.6 (with not deflected head) mm long; elongate oval and extremely convex; subunicolorous dark brown. Head comparatively narrow, with a frons moderately projecting anteriorly, distinctly bordered and with deep emarginations for reception of antennal scape; eyes rather large dorsally and indistinctly visible ventrally. Antennae 10-segmented and with elongate club consisting of three antennomeres (ultimate subequal in length to each previous segments of club); scape very short and antennomere 2 longest. Elytra of usual shape. Hindwings present. Metaventrite much longer than prosternum and mesoventrite combined. Abdominal ventrite 1 longest. Pro- and metatibiae rather wide and dilated, their outer edge not crenellate. Tarsi of moderate length and rather thick, tarsomeres 1–3 rather wide but not lobed. *Aedeagus* moderately sclerotized and comparatively short, tegmen with arcuate apex, penis trunk pointed at apex.

Species included: The type species only.

Comparison. This new species is distinct from all genera with 10-segmented antennae by the very short scape and longest pedicel. It can be diagnosed after the below key to the genera.

Remarks. This new genus is proposed after the original description of its type species in order to reach an equilibrium group disposition in the system of the subfamily Cybocephalinae. Nevertheless a re-examination of specimens of its type species would be very important to provide this taxon with a complete set of characters. Other cybocephalin genera including the species with 10-segmented antennae and long metaventrite have ranges very distant from the area of the type species of this new genus (*Theticephalus* Kirejtshuk, 1988, stat. nov.: Old Mediterranean; *Horadion* Endrödy-Younga, 1976: Equatorial Africa (Afrotropical Region) and *Amedissia* gen. nov.: South America (Neotropical Region)), but the type species of this new genus is quite distinct from members of the mentioned groups.

In the original description of the types species of *Pacicephalus* gen. nov. Endrödy-Younga (1976) wrote that this species is “without close relation to the 10 segmented species of Palearctic Region” (now *Theticephalus*), although later describing *Horadion* (Endrödy-Younga, 1976) he pointed out that “*Cybocephalus gressitti* E.Y. has to be transferred to this new genus (*Horadion*) and a further species yet to be described from Mindanao will be also classified to it”. Nevertheless, at least the type species of *Pacicephalus* gen. nov. differs from both members of *Horadion* (see below) in the structure of antennae (scape, pedicel and club), longer and narrower head. Taking also into consideration the disruption in the distribution of these groups their separation into two taxa seems to be rather reasonable.

Etymology. The name of this new genus is formed from the Pacific Ocean and root “*cephalus*” referring to other generic names in the subfamily Cybocephalinae (“*Cybocephalus*” and “*Theticephalus*”). The gender is masculine.

Key to the genera of the subfamily Cybocephalinae

1. Antennae 10-segmented 2
 - Antennae 11-segmented 6
2. Meso- and metacoxae very narrowly separated; metaventrite very short (markedly shorter than abdominal ventrite 1); elytral apices subvertically sloping; antennal club two-segmented; metatibia strongly dilated;

- submetacoxal lines with high relief and reaching posterior edge of abdominal ventrite 1. Japan; recent (Sadamoto Hisamatsu 2013: p. 255, fig. 1D; p. 256, fig. 2A; p. 265, fig. 8) *Apastillus* gen. nov.
- Mesocoxae moderately and metacoxae widely separated; metaventrite moderately long (longer than abdominal ventrite 1 or comparable with it); elytral apices very gently sloping; antennal club three-segmented 3
3. All tibiae and femora of usual in shape and moderately narrow; tarsomeres 1–3 comparatively narrow and bilobed or nearly simple; ultimate antennomere well raised and exposed; submetacoxal lines moderately expressed and usually reaching posterior edge of abdominal ventrite 1. Old Mediterranean (North Africa – Sahara, “Kaukasus”, Middle Asia, Mongolia); recent (Kirejtshuk 1988: 94, figs. 133–138) *Theticephalus* Kirejtshuk, 1988, stat. nov.
- All tibiae or at least some tibiae (and femora frequently widely dilated): combination of other characters different 4
4. Ultimate antennomere very small and slightly exposed (almost concealed into previous one) and penultimate antennomere longest; scape longer than antennomere 2; dorsum without metallic shine; scape of usual shape (enlarged); tarsomeres 1–3 more or less thickened but without lobes; all tibiae and femora except profemur rather dilated. Kenya and Republic of the Congo (Congo-Brazzaville); recent (Endrödy-Younga 1976: 114, fig. 1) *Horadion* Endrödy-Younga, 1976
- Ultimate antennomere comparable in size or larger than penultimate one; protibia moderately dilated ... 5
5. Elytra long, nearly complete and with conjointly rounded apices leaving at most a part of pygidium uncovered; abdominal ventrite 1 about twice as long as each of ventrites 2–4; dorsum without metallic shine; pronotum with somewhat projecting anterior angles and straight (not emarginate) lateral edge; scutellum subtriangular; scape of usual shape and shorter than antennomere 2; tarsomeres 1–3 more or less thickened but without lobes; pro- and metatibiae widely dilated, but all femora of usual shape. Micronesia (Caroline Is.); recent (Endrödy-Younga 1971: 284, fig. 3) *Pacicephalus* gen. nov.
- Elytra short, with widely and separately rounded apices leaving three last abdominal segments uncovered; abdominal ventrite 1 about as long as each of ventrites 2–4; dorsum with strong metallic shine; pronotum with anterior angles not projecting and emarginate lateral edge; scutellum subpentangular; scape extended externally and longer than antennomere 2; tarsomeres 1–3 strongly dilated; only metatibiae dilated, and mesotibia could be completely concealed into the depression (invisible ventrally); femora strongly dilated. South America (Argentina, Uruguay); recent (Bréthes 1922: 265, fig. 1; Parker 1951: 38, figs. 9–10; p. 40, figs. 11–17) *Amedissia* gen. nov.
6. Metaventrite shorter than mesoventrite; submetacoxal lines expressed or not 7
- Metaventrite at least comparable in length or longer than mesoventrite; submetacoxal lines moderately expressed and usually reaching posterior edge of abdominal ventrite 1 10
7. Metaventrite with a distinct transverse excavation before posterior edge; eyes with facets only on dorsal side; submetacoxal lines moderately expressed and not reaching posterior edge of abdominal ventrite 1. Canary Islands, Madeira; recent (Figs. 1–11) *Hierronius* Endrödy-Younga, 1968
- Metaventrite subflattened along the middle. ... 8.
8. Metacoxae widely separated – distance between them smaller than that between mesocoxae; abdominal ventrite 1 much longer than metaventrite; eyes with facets on both dorsal and ventral sides; submetacoxal lines on abdominal ventrite 1 not expressed. Lowermost Eocene Oise amber; fossil (Kirejtshuk and Nel 2008: 428, figs. 28–33; p. 430, figs. 35–37; p. 431, figs. 39–46) *Pastillocenicus* Kirejtshuk et Nel, 2008
- Metacoxae very narrowly separated – distance between them comparable with or greater than that between mesocoxae 9
9. Metaventrite concave; eyes with facets on both dorsal and ventral sides; abdominal ventrite 1 much longer than metaventrite and with submetacoxal lines well exposed; intermediate and posterior legs of usual structure, and mesotibia cannot be completely concealed into the depression on dorsal side of mesofemur. Western areas of North Africa; recent (Endrödy-Younga 1968: 37, fig. 1C; p. 38, fig. 2C; p. 38, Fig. 3C; p. 113, fig. 30) *Pastillodes* Endrödy-Younga, 1968
- Metaventrite convex; eyes with facets only on dorsal side; abdominal ventrite 1 much longer than metaventrite and with submetacoxal lines not expressed; meso- and metafemora dilated and with a large depression on ventral surface to receipt tibiae, metatibia dilated, and mesotibia could be completely concealed into the depression (invisible ventrally). Afrotropical and Capean Regions (Republic of Sierra Leone, Ruanda, Republic of South Africa); recent (Endrödy-Younga 1962: 272, Fig. 2; p. 273, Figs. 10–12; p. 275, Figs. 13–20) *Pastillus* Endrödy-Younga, 1962
10. Protibia crenellate along outer edge 11
- Protibia with smooth outer edge 12
11. Body at least twice as long as wide and with nearly black dorsum; metaventrite about as long as prosternum and mesoventrite combined; scape of usual shape and somewhat longer than subcylindrical antennomere 2; mentum distinctly convex; meso- and metatibiae as well as meso- and metafemora of usual structure. Vietnam; recent (Figs. 20–22; Kirejtshuk 1994: 120, figs. 86–90) *Taxicephomerus* Kirejtshuk, 1994
- Body less than twice longer than wide and with metallic

- lustre on dorsum; metaventrite longer than prosternum and mesoventrite combined; scape extended outwards and at least twice as long as subglobular antennomere 2; mentum somewhat concave; meso- and metatibiae somewhat dilated, femora strongly dilated with depression on dorsal surface for receipt of correspondent tibiae. Central and South America (Guatemala, Panama, Brazil, Trinidad and Tobago, Venezuela); recent (Figs. 16–19; Sharp 1891: Pl. 11, fig. 23)
 *Pycnocephalus* Sharp, 1891
- 12 (10). Posterior femur and tibia strongly dilated; eyes very large and with facets completely represented only from above. Madagascar; recent (Endrödy-Younga 1962: 272, fig. 2, 4)
 *Endroediellus* Endrödy-Younga, 1962
- Posterior femur and tibia not strongly dilated; eyes more or less moderately large and with facets represented from above and from below. All large zoogeographic regions (except Antarctic, New Caledonia and New Zealand Regions or Provinces); recent and Upper Eocene (Baltic amber), fossil (Sadatomo Hisamatsu 2013: 255, fig. 1A–C; p. 256, fig. 2B; p. 258, fig. 4; Kurochkin and Kirejtshuk 2010: Pl. 9; p. 541, fig. 3; p. 542, fig. 4; p. 544, fig. 5) *Cybocephalus* Erichson, 1843

DISCUSSION

The *Cybocephalites* Jacquelin du Val, 1858 or *Cybocephalidae* Thomson, 1862 after Sharp (1891) was included during a long time in the family Nitidulidae. In the second half of XX century some researchers treated this group separately (Endrödy-Younga 1962, 1968; Tian and Ramani, 2003; Smith and Cave 2006; Sadatomo Hisamatsu 2013; etc.). Recently Cline et al. (2014) revised the family Nitidulidae based on a comparison of some nucleotid sequences of different representatives of the family. They concluded that the Cybocephalinae belong together with Sphindidae to the lineage, which in turn was placed far from other groups of Nitidulidae. This grouping was quite different from that based on morphological evidence. In particular, Cline et al. (2014) restored the subfamily Prometopiinae Böving et Craighead, 1931, which previously had been considered at the divergence of the carpophilin and nitidulin lineages. Such a phylogenetic hypothesis strongly conflicts with classification based on structures and supported by fossil evidence (Kirejtshuk 2008). On the other hand, the above mentioned phylogenetic tree does not agree with the one published for the nitidulids based on nucleotide sequences (Brown et al. 2012), which was not cited by Cline et al. (2014). Unfortunately most

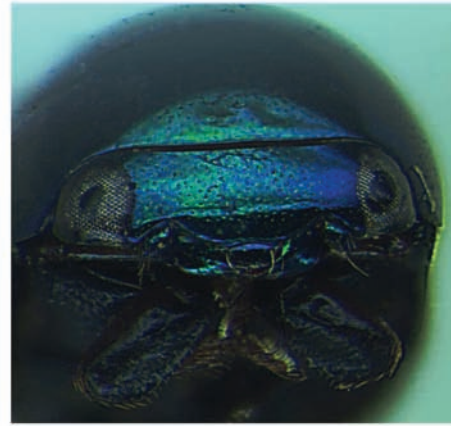
branches of both trees are not characterized by a high level of resolution and, therefore, it would be reasonable to regard both of them as rather premature and not conclusive enough to change the present system arrangement of Nitidulidae. In this connection it is necessary to consider a complete ambiguity in the phylogenetic position of the Cybocephalinae (support of the branch with this subfamily is less than an acceptable threshold of reliability). As to the molecular comparison of “Prometopiinae”, their joining can be regarded as statistically supported, but the isolation of the branch with this group with other groups of Nitidulinae needs further analysis with more data. A similar problem of using the modifications of the traditional system of Meligethinae by some authors (Audisio et al. 2009) without morphological definition but with many taxonomic innovations was discussed earlier (Kirejtshuk 2011; Kirejtshuk and Kirejtshuk 2012).

Here it is important to remember that Sharp (1891) placed the Cybocephalinae “between” the Nitidulinae and the Cryptarchinae Thomson, 1859 (= “Ipsinae”) with notes “there can be very little doubt that such a position is correct.” (Sharp 1891: 372). Crowson (1955: 98) insisted on the correctness of this interpretation and warned against: “*Cybocephalus* could be regarded, both in adult and larval characters, as annectent from the present family to Coccinellidae; according to the concept of Cucujoid phylogeny here envisaged, the latter family can hardly have any direct relationship to Nitidulidae, so that one or other of apparent affinities of *Cybocephalus* may be expected to prove illusory... *Cybocephalus* is a really Nitidulid owing its resemblance to ladybirds to parallel adaptation”. Later Kirejtshuk (1986) showed that the Cybocephalinae is a member of the nitidulin lineage that was differentiated after the divergence of a common ancestor of sap beetles into two lineages (carpophilin and nitidulin lineages). Thus, the recognition of the Cybocephalidae as a separate family needs the automatic lifting as least of the Epuraein-lineage to the family rank. Otherwise the general system of the family Nitidulidae is not phylogenetic in a strict sense.

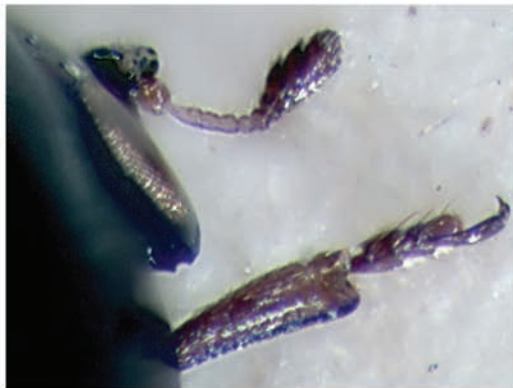
Cline et al. (2014) did not considered these systematic and phylogenetic concepts, but mentioned in their diagnosis: “Cybocephalidae adults can be differentially diagnosed by the following combination of character states: a 4–4–4 tarsal formula; five visible abdominal ventrites (excluding the male ‘anal



16



17



18

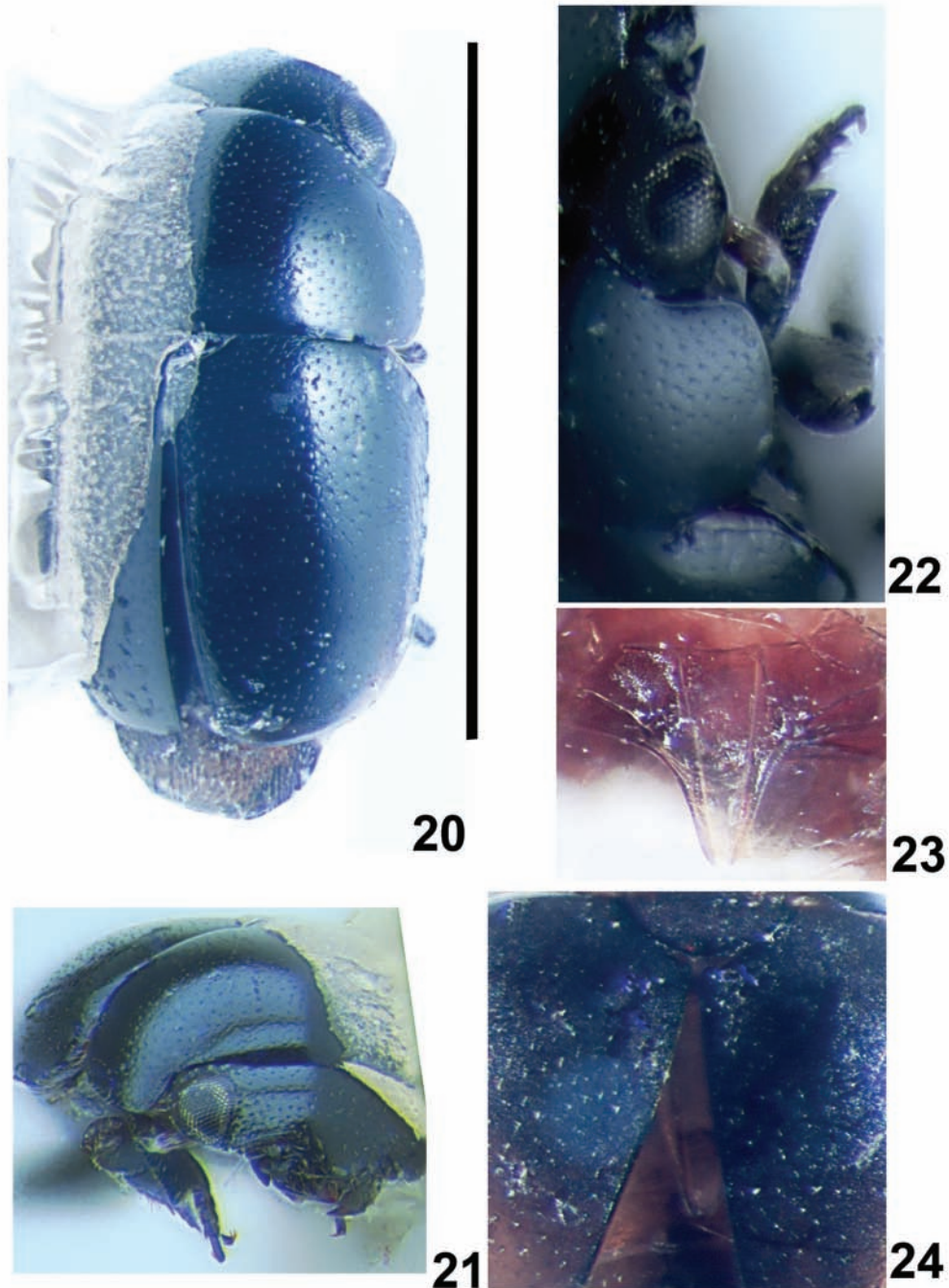


19

Figs. 16–19. *Pycnocephalus* sp.: 16 – body, dorsal view; 17 – head, anterior view; 18 – antenna, protibia and tarsus, dorsal view; 19 – head and thorax, ventral view. Fig. 16 of specimen from “Santa Cathirina, Nova Teutonia, Basil, 12.1938, Fr. Plaumann” with length 1.8 mm (Natuhistoriska Riksmuseet, Stockholm); Figs. 17–19 of specimen “Rio.Jan”, “F. Sahlb.” with length 1.4 mm (Natuhistoriska Riksmuseet, Stockholm). Scale bar for Fig. 16 = 1.8 mm.

plate’); and five pairs of abdominal spiracles; body contractile (capable of conglobulation) allowing the mandibles in repose to rest against the metasternum (Fig. 1). The larvae of Cybocephalidae (Fig. 2) can be differentially diagnosed by the following combination of characters: head without dorsal sutures; pregomphi and urogomphi absent on abdominal tergite XI; hypostomal rods present with divergent hypostomal ridges posteriorly; hypopharynx without a sclerome or bracons; mandibles without mola;

mandibles without prostheca; peculiarly long seta present on last antennomere (nearly as long as the whole antennae); and annular spiracles with two lateral air tubes. Cybocephalidae pupae differ from Nitidulidae and other Cucujoidea, in the shape and composition of the terminal abdominal segment (Fig. 3A, B).” (Cline et al. 2014: 762). It should be noted that these authors did not define any morphological synapomorphies of the Cybocephalinae with other cucujoids but repeated features tradi-

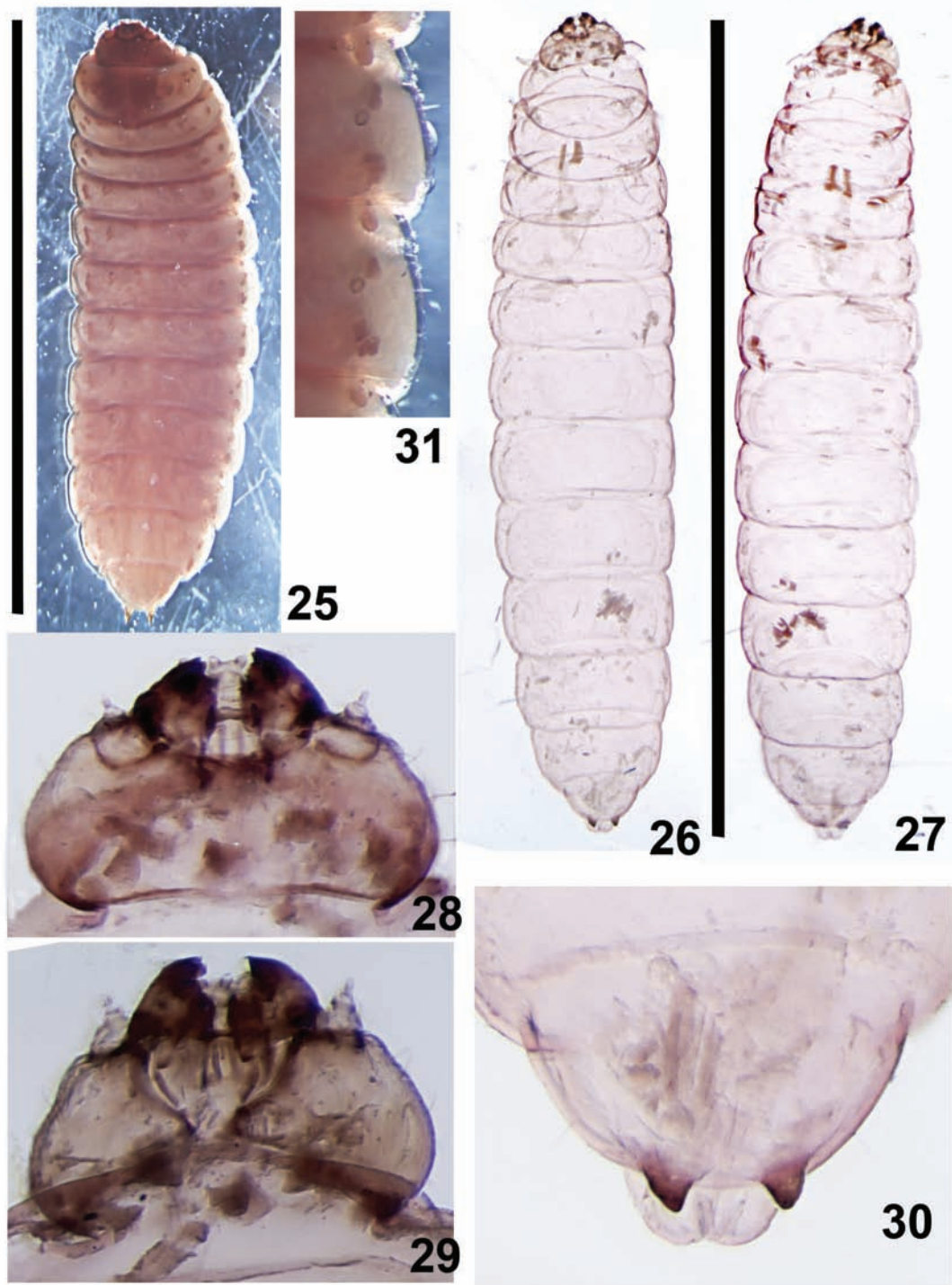


Figs. 20–24. Species of Cybocephalinae: 20 – body of *Taxicephomerus porrectus* Kirejtshuk, 1994, dorsal view (holotype “Vietnam, Tam Dao, pr. Vinh Phu, 1000 m, forest, 10–16.11.1990, Belokobylskij”; ZIN); 21 – idem, anterior view; 22 – side of head and pronotum with anterior and intermediate legs of the same specimen, dorsolateral view; 23 – metanotum of *Cybocephalus turanicus* Endrödy-Younga, 1968 (specimen “Alashan, dolina Gaytzo, nachalo peskov, 1–10.IV.1908, P. Kozlov”; ZIN), dorsal view; 24 – partly open elytra with exposed metascutellum of *Cybocephalus fodori* Endrödy-Younga, 1968 (specimen “Tbilisi, 28.viii.64, Yasnosh, na *Lepidosophes ulmi* (L.)”; ZIN), dorsal view. Length of *Taxicephomerus porrectus* 1.8 mm; width of *Cybocephalus turanicus* 2.1 mm; width of *C. fodori* 1.1 mm. Scale bar for Fig. 20 = 1.8 mm.

tionally regarded as having independent origins (tarsi 4–4–4, lack of larval pre- and urogomphi, predation on hemipterous insects). As to the above-mentioned diagnostic characters, “five visible abdominal ventrites” are characteristic of all nitidulids and most cucujoids; larval “head without dorsal sutures” reflects a general trend in the transformation of larval epicranium of many nitidulid groups (in some members of different groups the frontal sutures are absent or hardly traceable); “pregomphi and urogomphi absent on abdominal tergite XI” needs to be modified since the pregomphi are absent in many nitidulid larvae; and urogomphi at least in all Meligethinae, if raised, are only represented by slightly traceable tubercles. However, there are some species of *Epuraea* Erichson, 1843 with raised pregomphi and urogomphi and also species where they are scarcely raised (f.e., *Epuraea laeviuscula* (Gyllenhal, 1827)); pupae of *Cybocephalus* are very similar to those of the other nitidulids, with processes on the head, pronotum, wide lateroventrites and also urogomphi, which are always present in pupae even in those larvae that lack them (Böving and Rozen 1962; Rosen 1963; Kurochkin and Kirejtshuk, 2003; Kurochkin 2005). On the other hand, the pictures of pupa of *Cybocephalus niponnicus* Endrödy-Younga, 1971 in Cline et al. (2014: 746, Fig. 3A) demonstrate one outstanding character in the structure of the metanotum (long median process), which separates the subfamily from the other nitidulid groups (see below). Finally, Böving and Craighead (1931) illustrated their monograph with drawings of the larva of *Cybocephalus californicus* Horn, 1879 showing not only small urogomphi but also lateral conical projections on the abdominal segments 8 and 9 (Böving and Craighead, 1931: pl. 37 G).

Cline et al. (2014) did not consider probable synapomorphies of the Cybocephalinae and other Nitidulidae. In spite of the likelihood of parallel reduction (f.e. in structure of adult mouthparts, including the reduction of galea, number of tarsomeres; etc.), the symmetric and flattened male genitalia are absolutely characteristic of Nitidulidae, while the tendency toward asymmetric male genitalia is characteristic of the cerylonid lineage as a whole, including Sphindidae, and also of Kateretidae (Kirejtshuk 2000). The structure of the male genitalia and genital capsule of the cybocephalins completely corresponds to those in the other groups of the nitidulin lineage, although their penis trunk is rather wide,

with a complex curve along its length and with very long lobes above its apical orifice (Endrödy-Younga 1962, 1968; Sadatomo Hisamatsu 2013; etc.). The nitidulid adult mouthparts have only one maxillary lobe (like those in some groups consisting of species with small bodies, f.e., Ptiliidae, Latridiidae and Corylophidae) but their one-lobe demonstrates rather peculiar shape indicating a particular similarity. The fossil Libanopsinae Kirejtshuk, 2014 (Kirejtshuk et al. 2014) with one maxillary lobe, shows the general structure of their maxilla as in the other members of Sphindidae (Burakowski and Slipinski 1987; McHugh 1993; etc.) but different from those in the nitidulids (with reduction of lacinia). The capacity to roll into a sphere can be observed in different groups (Ceratocanthidae, Clambidae, Scirtidae, Eucinetidae, Leiodidae, etc.) and in different nitidulid subfamilies (Cyllodini and Cychramptodini Kirejtshuk et Lawrence, 1992 of Nitidulinae, Cybocephalinae and Arhinini Kirejtshuk, 1981 of Cryptarchinae), which is accompanied by the similar transformations in their head and thoracic sclerites (Crowson 1955, 1979; Endrödy-Younga 1960; Kirejtshuk 1981; Kirejtshuk and Lawrence 1992; etc.), and significance of these parallel transformations for systematics and phylogenetics should be regarded as rather limited. It is possible that the conclusions on larval structures used by Cline et al. (2014) were taken mostly from data published by Böving and Craighead (1931) and Hayashi (1978) and without personal observations of larvae of different groups. The cybocephalin larvae as well as those of all nitidulids are characterized by peculiar mouthparts with a narrow and longitudinal cardo, maxillary mola frequently with a spur on its inner edge and also one-segmented labial palpi. *Cychramptodes* Reitter, 1878, demonstrating predation on coccids like cybocephalins, have a strongly convex adult body, similar transformations of the head and thoracic sclerites that provide them with the capacity to roll into a ball, comparatively long mentum with a concave apex and 10-segmented antennae (Kirejtshuk and Lawrence 1992). Also their larvae have very soft bodies without appendages (except sparse long setae and short urogomphi) and lack frontal sutures on the epicranium (as in *Cybocephalus*) (Figs. 25–31). As an important comment to the proposals of Cline et al. (2014), it can be noted that only a few larvae of *Cybocephalus* living on coccids have short spatulate setae intermixed with long and very thin setae dispersed on dorsal body integuments (Silvestri



Figs. 25–31. *Cychramptodes murrayi* Reitter, 1878: 25 – mature larva after alcohol solution, dorsal view; 26 – idem after KOH, dorsal view; 27 – idem after KOH, ventral view; 28 – head after KOH, dorsal view; 29 – idem after KOH, dorsal view; 30 – apex of abdomen after KOH, dorsal view; 31 – side of abdominal base (segments 1 and 2) with spiracles, dorsal view. Specimen “Australia, ACT, Oxley, Canberra, 28.11.1990, A. Kirejtshuk, *Cryptes baccatus* on *Acacia floribunda*”; ZIN. Specimen after alcohol 7.0 mm and that after KOH 8.8 mm. Scale bar for Fig. 25 = 7.0 mm., for Fig. 26, 27 = 8.8 mm.

1910; Hayashi 1978). However larvae of *Cybocephalus* from Australia preying on aleyrodids support only very long setae (Kirejtshuk et al. 1997). In addition, the species of *Amedissia argentina* comb. nov. also feeding on coccids in Central and South America are sparsely covered with long setae intermixed with short “microscopic wedge-shaped spines”. This distinguishing larval character was emphasized by Parker (1951). Thus, at the moment there is no serious reason to regard the subfamily Cybocephalinae separately from the other subfamilies of the family Nitidulidae.

Comments on many other phylogenetic suggestions of Cline et al. (2014) can be omitted in this paper, except one, which gives reason for these authors to propose an important systematic change. They restored the subfamily Prometopiinae Böving et Craighead, 1931 with included genera: *Axyra* Erichson, 1843, *Pseudoplatychora* Grouvelle, *Megauchenia* MacLeay, 1833, *Platychora* Erichson, 1843, *Prometopia* Erichson, 1843, *Parametopia* Reitter, 1884, *Palaeometopia* Kirejtshuk et Poinar, 2007, *Taraphia* Audisio et Jelínek, 1993, and *Megaucheniodes* Audisio et Jelínek, 1993, with the following diagnosis: “Prometopiinae taxa can be differentiated by the following combination of characters: (i) presence of a shallow or deep sulcus (often delimited by a raised line) along lateral margin of head adjacent and typically posterior to each eye (faint in *Prometopia*); (ii) presence of deeply diverging metacoxal lines (Fig. 5A, B) on abdominal sternite I (reduced in *Taraphia*); (iii) meso- and metacoxae widely separated (Figs. 5, 7C); (iv) tarsomeres simple, never bilobed or with densely setose ventral empodium; (v) antennomere 3 \geq 2 \times length of antennomere 2; (vi) mycangium often present near prosternal suture or basal region of metacoxal axillary line (absent in *Prometopia*, *Parametopia* and *Platychora*). To date, only larvae of *Prometopia* have been described (Fig. 6A–D). However, *Prometopia* possesses urogomphi unlike any nitidulin taxon in that the urogomphi are oriented in a laterally flattened arrangement (Fig. 6D). Likewise, the presence of a multi-lobed mandible with deep central groove and bispinose mesal margin (Fig. 6B) are unlike other nitidulid larvae. These larvae also lack adhesive tarsungular seta. These were the characters that Böving and Craighead (1931) originally used to delimit the subfamily.” (Cline et al. 2014: 763). It is necessary to mention that the character “(i)” is present not in all species

of *Platychora* and absent in *Axyra*, *Megauchenia*, and *Pseudoplatychora*; the character “(ii)” occurs in other nitidulid genera aside from the proposed “Prometopiinae” (f.e., *Stelidota* Erichson, 1843 in some cybocephalin genera, etc.); the character “(iii)” occurs widely beyond the mentioned genera (f.e. almost all Amphicrossinae, some Epuraeinae, many Cyllodini, etc.); the character “(iv)” includes the simple tarsomeres 1–3 of all legs, which is also diagnostic for the genera *Somatoxus* Sharp, 1891 (Cyllodini) and *Taxicephomerus* (Cybocephalinae). Also, the simple meso- and metatarsomeres 1–3 are characteristic of many members of the genera related to the genus *Pallodes* Erichson, 1843 and the bisetose empodium is usual for many nitidulids with large body size, while it is reduced to a short membranous process between tarsal claws or absent in smaller representatives. The character “(v)” is known also in some genera of Epuraeinae and Meligethinae with long antennae and at least in *Ceratochramus* Kirejtshuk, 1996 in the Nitidulinae. The doubtful meaning of the character “(vi)” was explained by the authors themselves (see above). As to the above mentioned larval characters, the three-toothed mandibles are usual in many nitidulids and the forked oblique apices of urogomphi are characteristic of many Cryptarchinae. Thus, the Prometopiinae has no real morphological base and the genera included in it by Cline et al. (2014) would be better placed in different complexes of the tribe Nitidulini (Kirejtshuk 2008).

The important aspect of the systematics of Cybocephalinae is the distribution of genera with reduced hindwings among the recent fauna, which makes it possible to consider that the reduction or even lack of hindwings in these groups could appear independently. These groups are easy to recognize based on the shortening of metaventrite (like that in other coleopterous families), and this feature is supposed for the recent members of *Apastillus* gen. nov., *Hierronius*, *Pastillus*, and *Pastillodes*. Besides, some level of reduction or lack of hindwings can also be assumed for fossil species of *Pastillocenicus* with a comparatively short metaventrite. This transformation is accompanied by lengthening other sclerites of the underside (mesoventrite or both mesoventrite and abdominal ventrite 1). It is interesting to note that shortening of metaventrite and metendosternite was recorded in wingless species of *Rioneta* Johnson, 1975 from Ptiliidae (Grebennikov 2008). The metendosternite of the new species of *Hierronius* examined (Fig. 7) is

rather similar to that in winged Ptiliidae (like species of *Oligella* Rossau et al., 1987 etc.: Hall 2014) but very different from that in other Nitidulidae (Kirejtshuk 1998). In contrast to all other nitidulids with examined metendosternite, this structure in *Hierro-nius* is characterized by the strongly reduced median part and lack of anterior tendons, its lateral arms are very widely separated and gradually narrow to acuminate apices (as frequently occurs in Ptiliidae). It is interesting to note that such a tendency in structural transformations can be traced to other staphyliniformians (see the metendosternite of *Cercyon* and *Hister* in Crowson 1938: Pl. 3, Fig. 4 and Pl. 9, Fig. 9). Thus, the similarity in transformations of this inner sclerite seems to coincide with the shortening of the metaventricle, but it could scarcely be associated with an inability to fly. These parallel transformations of metathoracic structures make reconstructions of cybocephalin phylogeny more complex. Taking into consideration significant migratory restrictions of species with short or absent hindwings, the assumption of a possible independent appearance of the set of accompanying characters of the thoracic and abdominal sclerites as a sequence of hindwing reduction could be assumed. At least *Apastillus* gen. nov. could scarcely be related to those groups with a short metaventricle from the Afro-Madagascan regions and West Mediterranean. Such a parallelism is also apparent for the groups with wide and flattened meso- and metafemora, and also wide and flattened meso- and metatibiae.

Variation of some characters is rather broad and in some cases similar variability can be traced in different groups. The recent species of *Theticephalus* show some variability in structure of the tarsi. *Theticephalus palmarum* (Peyerimhoff, 1931), comb. nov. and *T. salsus* (Kirejtshuk, 1988), comb. nov. have all tarsi rather narrow and with nearly simple tarsomeres 1–3, while *T. nigriceps* (Sahlberg, 1908), comb. nov. and *T. decamerus* (Endrödy-Younga, 1976), comb. nov. demonstrate lobed pro- and mesotarsi but simple metatarsi. Finally, all tarsi of *T. aurocupreus* (Reitter, 1900), comb. nov. are narrowly lobed.

A very unusual type of interlocking of elytra was found in the new species here described. It is formed by elytra having no structural difference along the suture (folds for fixation of both elytra), however beneath the elytral suture in the closed position there is a long narrow and flat process of the metanotum restricted by lateral ridges (metascutellum) which

seems to assist in maintaining the elytra in a fixed position (not allowing them to be lowered) (Fig. 7). Other members of the subfamily have also demonstrate a long process of the metanotum which, however, is much shorter than that in *Hierro-nius madeiraensis* sp. nov. (Figs. 23, 24). The pupae of almost all known nitidulids have an angular projection of the metanotum (Rosen 1963; Kurochkin and Kirejtshuk 2003; Kurochkin 2005; Cline et al. 2014; etc.), although in species of the genus *Conotelus* Erichson, 1843 the metanotum has only a slightly projecting posterior edge (Rosen 1963). Pupae of other coleopterous families rarely demonstrate this feature to such an extent, although it can be found in different groups of different infraorders. Thus, this projection seems to be characteristic but not an apotypic character of the family Nitidulidae, however the further development of it in Cybocephalinae can be regarded as an apomorphy and treated as additional evidence of a close relationship of the latter.

Cybocephalinae are characterized by feeding on armored scales (Diaspididae), soft scales (Coccidae) and whiteflies (Aleyrodidae). It can be supposed that members of this group are similar in appearance due to their adaptation to a parasitoid mode of life. The oldest records of the Cybocephalinae are Lowermost Eocene (Kirejtshuk and Nel 2008), although taking into consideration the distribution of recent representatives throughout all continental areas except circumpolar territories, it is supposed that this subfamily could have originated at least in the Upper Cretaceous (Kirejtshuk 1994). However, their prey are known from the Lower Cretaceous (Coccoidea: Tosolini and Pole 2010) and even Jurassic (Aleyrodidae: Shcherbakov 2000) and, therefore, these Mesozoic hemipterans could have been attacked by some parasites and parasitoids earlier. The oldest known nitidulids (both nitidulin and carpophilin lineages: Kirejtshuk and Ponomarenko 1990) are from the Lower Cretaceous.

Genera of the subfamily Cybocephalinae

– with short metaventricle in adults:

1. Genus *Apastillus* gen. nov.: *A. eminentithorax* (Sadatomo Hisamatsu, 2013), comb. nov. [*Pastillus*] (type species).
2. Genus *Hierro-nius* Endrödy-Younga, 1968: *H. laevis* (Wollaston, 1864) [*Cybocephalus*] (type

species), *H. angulosus* Endrödy-Younga, 1968, *H. madeiraensis* sp. nov. and *H. nanus* Endrödy-Younga, 1968.

3. Genus *Pastillus* Endrödy-Younga, 1962: *P. basilewskyi* Endrödy-Younga, 1962 (type species), *P. conflexus* Endrödy-Younga, 1962 and *P. pusio* Endrödy-Younga, 1962.

4. Genus *Pastilodes* Endrödy-Younga, 1968: *P. agathidioides* (Peyerimhoff, 1927) [*Cybocephalus*] (type species) and *P. areolatus* (Norman, 1940) [*Cybocephalus*].

5. Genus *Pastillocenicus* Kirejtshuk et Nel, 2008: *P. grandiclavis* Kirejtshuk et Nel, 2008 (type species), *P. polyaki* Kirejtshuk et Nel, 2008 and *P. longifrons* Kirejtshuk et Nel, 2008.

– with moderately long metaventrite in adults:

1. *Amedissia* gen. nov.: *A. argentina* Bréthes 1922, *comb. nov.* [*Pycnocephalus*] (type species).

2. Genus *Cybocephalus* Erichson, 1843: *C. politus* (Gyllenhal, 1813) [*Nitidula*] (= *exguus* C. Sahlberg, 1834) [*Anysotoma*] (type species) and about 140 recent and fossil species.

3. Genus *Endroediellus* Endrödy-Younga, 1962 [Endrödiellus]: *E. speciosus* Endrödy-Younga, 1962 (type species).

4. Genus *Horadion* Endrödy-Younga, 1976: *H. villiersi* Endrödy-Younga, 1976 (type species) and *H. aphrodite* (Endrödy-Younga, 1969), *comb. nov.* [*Cybocephalus*].

5. Genus *Pacicephalus* gen. nov.: *P. gressitti* Endrödy-Younga, 1971, *comb. nov.* [*Cybocephalus*] (type species).

6. *Pycnocephalus* Sharp, 1891: *P. deyrollei* (Reitter 1875) [*Cybocephalus*] and *P. metallicus* Sharp, 1891 (type species).

7. Genus *Taxicephomerus* Kirejtshuk, 1994: *T. porrectus* Kirejtshuk, 1994 (type species).

8. Genus *Theticephalus* Kirejtshuk, 1988, *stat. nov.*: *T. aurocupreus* (Reitter, 1900), *comb. nov.* [*Cybocephalus*] (type species), *T. decamerus* (Endrödy-Younga, 1968), *comb. nov.* [*Cybocephalus*], *T. mesopotamicus* (Endrödy-Younga, 1968), *comb. nov.* [*Cybocephalus*], *T. nigriceps* (Sahlberg, 1908), *comb. nov.* [*Cybocephalus*], *T. palmarum* (Peyerimhoff, 1931), *comb. nov.* [*Cybocephalus*] and *T. salsus* (Kirejtshuk, 1988), *comb. nov.* [*Cybocephalus*].

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