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Discovery of a Nitidulidae in Cretaceous Burmese amber (Coleoptera, Cucujoidea) with description of a new genus and taxonomic notes



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ABSTRACT

The present paper describes a new genus and species, *Sorodites angustipes*, that represents the first nitidulid found in Cretaceous Burmese amber. It is assigned to the *Soronia*-generic complex (subfamily Nitidulinae, tribe Nitidulini). This specimen differs from all known members of the family by its sub-cylindrical to cylindrical tarsomere 3 (not lobed as in most members of the family), the pro- and mesotarsi with lobed tarsomeres 1 and 2, and also from all members of the subfamily Nitidulinae by its antennal club having a weak dorsoventral compression. The exuvium described as probable *Sorodites angustipes* represents a first Mesozoic remains of preimaginal instar of the family Nitidulidae. The *Soronia*- and *Phenolia*-complexes are re-defined and clarified, and attribution of the genus *Cacconia* Sharp, 1890 to the second complex is confirmed.

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1. Introduction

The sap beetles (Nitidulidae Latreille, 1802) represent a rather diverse group in the Recent fauna but remain poorly known in fossils (in the fossil record only 31 genera, including 17 extinct ones have been recorded and 52 species have beed described so far: Kirejtshuk and Ponomarenko, 2018; Kirejtshuk and Nel, 2018). A generic classification was proposed by Kirejtshuk (2008) with later systematic additions and corrections (Kirejtshuk, 2009, 2011a, 2011b; Kirejtshuk and Kurochkin, 2010; Kurochkin and Kirejtshuk, 2010; Kirejtshuk and Kirejtshuk, 2012; Kirejtshuk and Mantič, 2015; Kirejtshuk and Kovalev, 2016, 2017). New data, still unpublished, will require additional modifications. The principal taxonomic combinations and synonymies used in the present paper are explained and clarified in the latter publications. The fossil record of this family based on the web-catalogue by Kirejtshuk and Ponomarenko (2018) was recently updated by Kirejtshuk and Nel (2018). The first author found numerous nitidulid specimens in Burmese amber, and at the moment has at his disposal more than ten new species awaiting description. Most of them were obtained

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from the collection of Carsten Gröhn (Hamburg, who forwards holotypes to the Institute and Museum of Geology and Palaeontology at Hamburg University) and from Anders Damgaard (Copenhagen, with holotypes deposited in the Zoological Museum in Copenhagen). These undescribed species from Burmese amber are rather different from the groups of the Recent fauna and can be assigned to new genera in both Nitiduline- and Carpophilinelineages. Their study brings important information on late Mesozoic diversification of nitidulids and will provide modifications of the current systematics of the family based on new phylogenetic reconstructions. The present paper describes a new fossil from Burmese amber dated near the boundary between the early and late Cretaceous. No member of the Nitidulidae was previously described from this resource, although this family was mentioned earlier from this amber site (Rasnitsyn and Ross, 2000).

2. Material and methods

The holotype of *Sorodites angustipes* **gen. et sp. nov.** (GPIH 4592, coll. Gröhn no. 11022) and a syninclusion of larval exuvium are deposited in the Institute of Geology and Palaeontology and Museum (Geologo-Paläontologisches Institut u. Museum), University of Hamburg. These specimens were examined using a Leica MZ 12.0 stereomicroscope with a DFC290 digital camera at the

Zoological Institute of the Russian Academy of Sciences (St. Petersburg) and an Olympus SCX9 stereomicroscope equipped with an Olympus camera at the Muséum national d'histoire naturelle (Paris). In addition, these specimens were also studied with a Leica TCS SP2 confocal laser scanning microscope (CLSM) in St. Petersburg State University as described previously (Kireitshuk et al., 2015) with slightly modified adjustments of the confocal microscope system: excitation wavelength was 405 nm (blue laser, 80% intensity), emission wavelength range was of 415-800 nm, acquisition resolution 1024×1024 pixels, level of gain 350–400, frame average 1 or 2, and zoom range of 1.2-3.0 times. Between 20 and 98 optical slices were recorded from each specimen examined. The digital images of the confocal stacks were processed using Fiji Open Source Image Processing Package to obtain the maximum intensity projections (MIP). Three-dimensional representations of the insect surface topography were carried out using Amira 5.3.2 software. All 3-dimensional images were recorded using "PrintScreen" keyboard function or "Snapshot" command embedded in Amira. Finally, the specimens were investigated under Nikon TE300 fluorescent microscope with the excitation: 475-490 nm (blue), emission: 506–533 nm (green) and some reconstructions were made using Helicon Focus Pro 4.60 software. For comparisons with other members of the family, the authors used fossil and recent species from the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), and Muséum national d'histoire naturelle (Paris).

2.1. Geological setting

The amber pieces with inclusions originated from mines in the Hukawng Valley in the state of Kachin in Myanmar. The fossil resin has been dated stratigraphically and radiometrically from late Albian to early Cenomanian in the present century (Cruickshank and Ko, 2003; Jarzembowski et al., 2017; etc.). A probably Cenomanian radiometric age of Burmese amber has been proposed; however, the amber tested was from sedimentary beds, indicating that it had been re-deposited (Shi et al., 2012). Thus, the age of this amber remains unclear, although its concentration of amber with inclusions in a certain geological layers gives evidence that its deposition occurred under peculiar conditions and during definite term. Nuclear magnetic resonance spectra and the presence of araucaroid wood fibres in amber samples from the Noije Bum 2001 Summit site indicate an araucarian (possibly Agathis) tree source for the amber (Poinar et al., 2007; Legalov, 2018; etc.).

3. Systematic palaeontology

Family Nitidulidae Latreille, 1802 Subfamily Nitidulinae Latreille, 1802 Tribe Nitidulini Latreille, 1802

Genus Sorodites Kireitshuk, gen. nov.

Type species. Sorodites angustipes sp. nov.

Notes 1. The new genus is a member of the tribe Nitidulini sensu str. not only because of its general resemblance to members of the genus *Soronia* Erichson, 1843 and closely related taxa (*Soronia* complex), but also because of the characteristic sculpture of the integument, structure of the antennae, outline of thoracic and abdominal sclerites, visible shape of coxae and their disposition, structure of tarsi as well as other characters (see the Diagnosis and Discussion below). Nevertheless, *Sorodites* gen. nov. is very different from all taxa of this tribe by its antennal club weakly dorsoventrally compressed and subcylindrical to cylindrical tarsomere 3 (while most members of the family with lobed tarsi have tarsomere 3 more widely lobed than tarsomeres 1 and 2). Besides, in contrast to other genera of this clade, the new genus is characterized by the pronotum

with a shallowly excised anterior edge and rather deep sinuations along posterior edge at each side of the scutellum and the male protibia with proximal dilatation along its inner edge. Finally, the new genus has its elytral apices widely rounded, while the remainding groups of this complex are characterized by the conjointly subacuminate elytral apices and at most only with a small sutural angle. Some important structural characters of the fossil are not observable in the holotype, such as peculiarities of the upper surface of the head and structure of mouthparts, but other characters, which are clearly visible, make it possible to show the distinct characters that support the erection of a new genus and species.

Notes 2. The new genus is represented by only one species and, therefore, the diagnosis of both are similar ("*descriptio generica specifica*").

Etymology. The name of this new genus is formed from the generic names *Soronia* and *Lordites*; masculine gender.

Diagnosis. Sorodites **gen. nov.** should be regarded as belonging to the *Soronia*-complex of genera (defined by Kirejtshuk (2003, 2008; etc.): Amphotis Erichson, 1843; Annachramus Kirejtshuk, 1995; Hisparonia Kirejtshuk, 2003; Lobiopa Erichson, 1843; Macleayania Kirejtshuk, 2003; Microsoronia Kirejtshuk et Kurochkin, 2010; Omosiphila Kirejtshuk, 1990; Ornosia Grouvelle, 1899; Pleoronia Kirejtshuk, 2003; Sebastianiella Kirejtshuk, 1995; Soronia; Stenoronia Kirejtshuk, 2003 Temnoracta Kirejtshuk, 1988). However, except for the above-mentioned characters of the antennal club, pro- and mesotarsi, pronotal structural peculiarities and male protibia, the new fossil genus differs from:

- *Amphotis* in the not enlarged (to moderately enlarged) scape, pronotum somewhat narrowing posteriad and with obtuse posterior angles, lack of a trace of both longitudinal ribs and longitudinal rows of punctures associated with hairs on the elytra, short antennal grooves, a submetacoxal line deviating from the posterior edge of cavity and subcylindrical meta-tarsomeres 1–3;
- Annachramus in the subflattened dorsum, subunicolorous body coloration (without a pattern of spots on elytra), weakly developed subuniform and recumbent pubescence with lack of longitudinal rows on elytra, pronotum with widely explanate sides, distinct sutural angle between elytral apices, not enlarged (to moderately enlarged) scape, lack of interfacetal hairs, submetacoxal line deviating from the posterior edge of the cavity and subcylindrical metatarsomeres 1–3;
- Hisparonia in the subflattened dorsum, surface of pronotum and elytra not tuberculate, pronotum somewhat narrowing posteriad and with obtuse posterior angles, distinct sutural angle between elytral apices, the not very coarsely sculptured dorsal integument, lack of interfacetal hairs, weakly developed subuniform and recumbent pubescence with the absence of strong and long setae on the dorsum, submetacoxal line deviating from the posterior edge of the cavity and subcylindrical metatarsomeres 1–3;
- Lobiopa in the distinct sutural angle between elytral apices, weak dilatation above antennal insertions, lack of longitudinal rows of punctures and associated hairs on elytra, short antennal grooves, submetacoxal line deviating from the posterior edge of the cavity and subcylindrical metatarsomeres 1–3;
- Macleayania in the subunicolorous body, dorsum without both squamose hairs and longitudinal rows of hairs on elytra, not enlarged (to moderately enlarged) scape, pronotum somewhat narrowing posteriad with obtuse posterior angles, short antennal grooves, distinct sutural angle between elytral apices, submetacoxal line deviating from posterior edge of cavity and markedly narrower femora;
- Microsoronia in the subflattened dorsum, markedly finer and denser dorsal puncturation, somewhat narrower explanation

along pronotal and elytral sides, and distinct sutural angle between elytral apices, subcylindrical and longer metatarsomeres 1–3;

- *Omosiphila* in the subunicolorous body with subflattened and finely punctured dorsum, pronotum with obtuse posterior angles, elytra without adsutural lines, distinct sutural angle between elytral apices, submetacoxal line deviating from the posterior edge of cavity, subcylindrical and longer metatarsomeres 1–3;
- Ornosia in the subunicolorous body, dorsum without longitudinal rows on elytra, pronotum an evenly convex disk with obtuse posterior angles, elytra with distinct sutural angle between apices and without adsutural lines, submetacoxal line deviating from the posterior edge of cavity and subcylindrical metatarsomeres 1–3;
- Pleoronia in the subunicolorous body, dorsum without both squamose hairs and longitudinal rows of hairs on elytra, not enlarged (to moderately enlarged) scape, pronotum somewhat narrowing posteriad, elytra without adsutural lines and distinct sutural angle between elytral apices, submetacoxal line deviating from the posterior edge of cavity;
- Sebastianiella in the subunicolorous body, dorsum with markedly finer puncturation and without both longitudinal ribs and longitudinal rows of hairs on elytra, distinct sutural angle between elytral apices, submetacoxal line deviating from the posterior edge of cavity and subcylindrical metatarsomeres 1–3;
- Soronia in the lack of longitudinal rows of hairs on elytra, elytra without distinct sutural angle between apices and without visible adsutural lines, submetacoxal line deviating from the posterior edge of cavity and subcylindrical metatarsomeres 1–3;
- Stenoronia in the much smaller and wider body, widely explanate pronotal and elytral sides, pronotum and elytra markedly wider than head, longer antennae, pronotum without depressions on disk, elytra with sutural angle between apices and without adsutural lines, wider apex of prosternal process without isolated median plate, and moderately wide epipleura;
- Temnoracta in the much smaller and wider subunicolorous body, lack of both interfacetal setae and squamose setae on dorsum, longer antennae, widely explanate pronotal and elytral sides, pronotum and elytra markedly wider than head, pronotum without depressions on disk, elytra without both longitudinal ribs and longitudinal rows of setae, elytra with sutural angle between apices and without adsutural lines, submetacoxal line deviating from the posterior edge of cavity and lobed pro- and mesotarsomeres 1–2.

Members of the large genera Soronia and Phenolia sensu lato show a rather high level of variability in dorsal characters, which can make identification difficult for some species of both genera. Besides, some genera of both Soronia and Phenolia complexes show some individual characters that are not shared with other members of the complexes and, therefore, it is reasonable to compare Sorodites gen. nov. with members of the Phenolia-complex (defined by Kirejtshuk (Kirejtshuk and Kvamme, 2002; Kirejtshuk, 2008; etc.)) together with Cacconia Sharp, 1890 (Cacconia, Gaulodes Erichson, 1843; Ostomarcha Kirejtshuk, 2006; Phenolia Erichson, 1843 with subgenera Aethinodes Blackburn, 1891; Lasiodites Jelínek, 1999; Phenolia sensu str. and Plesiothina Kirejtshuk, 1990; Stelidota Erichson, 1843; Ussuriphia Kirejtshuk, 1992). In addition to the above-mentioned characters in antennal club, pro- and mesotarsi, pronotal structural peculiarities and male protibia, Sorodites gen. **nov.** differs from:

- *Cacconia* in the more elliptic, subflattened and slender body, dorsum with fine and dense puncturation, elytra without a both

trace of longitudinal ribs and longitudinal rows on hairs on elytra, elytra with sutural angle between apices and without adsutural lines at apices, submetacoxal lines deviating from posterior edge of cavity, short antennal grooves, lack of basal median projection of abdominal ventrite 4 and subcylindrical metatarsomeres 1–3;

- Gaulodes in the elliptic, subflattened and slender body, dorsum with fine and dense puncturation, elytra without of both trace of longitudinal ribs and longitudinal rows on hairs, elytra with sutural angle between apices and without adsutural lines, short antennal grooves, apex of prosternal process wider and closer to the surface of mesoventrite, protibia not strongly widened at apex and subcylindrical metatarsomeres 1–3;
- Ostomarcha in the sublattened and slender body, elytra without longitudinal rows on hairs, elytra with sutural angle between apices and without adsutural lines at apices, short antennal grooves, apex of prosternal process wider and closer to the surface of mesoventrite, protibia not strongly widened at apex and subcylindrical metatarsomeres 1–3;
- Phenolia in the elliptic and slender body, dorsum with fine and dense puncturation, elytra without of trace of both longitudinal ribs and longitudinal rows on hairs, elytra with sutural angle between apices, apex of prosternal process wider and closer to the surface of mesoventrite, submetacoxal lines deviating from posterior edge of cavity (except for the subgenus Aethinodes), subcylindrical metatarsomeres 1–2 (see also the Discussion below);
- Stelidota in the elliptic and slender body, dorsum with fine and dense puncturation, elytra without of trace of both longitudinal ribs and longitudinal rows on hairs on elytra, pronotum somewhat narrowed at base and without distinct border along entire posterior edge, elytra with sutural angle between apices, short antennal grooves, apex of prosternal process wider and closer to the surface of mesoventrite, and subcylindrical metatarsomeres 1–3;
- Ussuriphia in the comparatively convex dorsum with fine and dense puncturation, elytra without of both trace of longitudinal ribs and longitudinal rows on hairs, elytra with sutural angle between apices and without adsutural lines at apices, short and apparently moderately deep antennal grooves, prosternal process markedly narrower but with wider apex closer to the surface of mesoventrite, submetacoxal lines deviating from posterior edge of cavity, and subcylindrical metatarsomeres 1–3.

Sorodites angustipes Kirejtshuk, sp. nov. Figs 1–3

Etymology. The epithet of this new species is formed from two Latin words "angustus" (narrow, thin, slender, tight) and "pes" (tarsus, tarsi, foot, feet).

Holotype. "GPIH 4592" - "11022"; late Albian to early Cenomanian (boundary early and late Cretaceous); a complete and probably somewhat dorsoventrally compressed specimen with head somewhat extended forwards and bent downwards is included in a very thin and flat piece of clear amber with a subtriangular shape $(13 \times 6 \times 16 \text{ mm})$ with the longest side widely arcuate. This amber piece contains also many small irregular pieces of different darkish organic matter and many transparent and opaque (milk yellowish) gas bubbles (beneath the holotype are many bubbles making it rather difficult to see structural details), some remains of the larval exuvium of the same specimen (near the posterior half of the holotype) making it possible to distinctly observe details of the mouthparts, antennae, abdominal apex and parts of the lateral integument. The many small larval remains apparently originated from different specimens.



Fig. 1. Sorodites angustipes gen. et sp. nov., holotype and syninclusions of remains of larval exuvium (GPIH 4592 - "11022"), Institute of Geology and Palaeontology and Museum, University of Hamburg; Burmese amber, Cretaceous, late Albian to early Cenomanian; photographed under Leica MZ 12.0 stereomicroscope with a DFC290: A: body of holotype and remains of larval exuvium, from above; **B:** idem, from below; **C:** median anterior part of pronotum and head of holotype, from above; **D:** protibia and protarsus of holotype, from below; **E:** mesotibia and mesotarsus of holotype, from below; **F:** metatibia and metatarsus of holotype, from below. Length of holotype 3.0 mm.

Note. This specimen could be a male because its abdominal apex has the widely rounded posterior edge of both dorsal and ventral sclerites, with an anal sclerite exposed.

Description of holotype, male. Body length 3.0, width 1.4 mm. Body elongate oval to subelliptical, weakly convex dorsally and ventrally, nearly dull to feebly shining; with very fine, comparatively short and moderately dense hairs on body (without trace of longitudinal rows on elytra); tibiae and tarsi with more raised hairs and setae (particularly raised along outer edge of tibiae).

Dorsal integument apparently uniformly sculptured, with punctures subequal in size with eye facets, interspaces between them about as great as one puncture diameter and apparently coarsely microreticulated; ventral integument with punctures about twice as small as those on dorsum and sparser with interspaces between them apparently somewhat smoother.

Head apparently subpentagonal and weakly convex dorsally, apparently with weak dilatations over areas of antennal insertions, eyes round, moderately prominent and moderately facetted; anterior edge of frons and mouthparts not visible. Antennae moderately long; scape moderately swollen, 3-segmented club somewhat loose and elongate, comprising about 2/5 of total antennal length, and only weakly dorsoventraly compressed. Pronotum about 3/4 as long as wide, vaulted at disk and regularly and very gently sloping with widely explanate sides (explanate stripes nearly as wide as metatibia); its anterior edge slightly trapeziumlikely excised; posterior edge very broadly arcuate and with comparatively deep sinuations at each side of scutellum, sides arcuately narrowing anteriad rather than posteriad, anterior angles widely rounded and posterior ones obtuse and with more or less expressed top. Scutellum subtriangular to subsemicircular, somewhat wider than long. Elytra 1 and 1/5 as long as wide combined,



Fig. 2. Sorodites angustipes gen. et sp. nov., holotype (GPIH 4592 - "11022"), Institute of Geology and Palaeontology and Museum, University of Hamburg; Burmese amber, Cretaceous, late Albian to early Cenomanian; photographed – **A** under Leica MZ 12.0 stereomicroscope with a DFC290 and **F** under fluorescent microscope Nikon TE300, and **B-E** under confocal laser scanning microscope Leica TCS SP2: **A**: pronotum, from above, with visible trace of border along posterior edge between sinuations indicated by arrows; **B**: anterior leg, right part of head and antenna, from below; **C**: antenna, from below; **D**: protarsus, from below; **E**: apex of metatibia and metatarsus, from below; **F**: abdominal apex, from below. Length of holotype 3.0 mm.

longest at suture and widest about at shoulders, slightly convex and gently sloping with widely and clearly explanate sides (explanate stripes nearly as wide as those of pronotum or as wide as metatibia), adsutural lines not expressed, their apices widely rounded and with slightly expressed and shallow sutural angle. Widely rounded pygidial apex exposed from under elytral apices.

Antennal grooves rather short and apparently curved inwards. Prosternum not clearly visible, prosternal process somewhat curved along procoxae and strongly widened behind procoxae, its apex subtruncate and closely approached surface of mesoventrite, separation between procoxae apparently comparable with that between mesocoxae. Distance between metacoxae probably twice as great as that between procoxae or that between mesocoxae. Metaventrite subflattened, with median suture (discrimen) and with posterior edge between metacoxae angularly excised. Abdominal ventrite 1 with a clear submetacoxal line extending to basal fourth of ventrite and returning to posterior edge of outer part of metacoxae. Abdominal ventrite 1 longest and about 1.5 times as long as each of ventrites 2 and 3, ventrite 4 somewhat shorter than each of ventrites 2 and 3, hypopygidium somewhat shorter than ventrite 1 and widely rounded at apex. Epipleura rather wide at base (about 1 and 1/3 as wide as metafemur), gradually narrowing posteriad.

Legs moderately narrow and long. Tibiae moderately narrow and dorsoventraly compressed, subparallel-sided and slightly widening posteriad (particularly protibia); protibia with triangularly dilated inner edge at basal third and outer subapical angle somewhat projecting, subarcuate at top and with two very stout



Fig. 3. Sorodites angustipes gen. et sp. nov., holotype (GPIH 4592 - "11022"), Institute of Geology and Palaeontology and Museum, University of Hamburg; Burmese amber, Cretaceous, late Albian to early Cenomanian; thorax, ventral. Scale bar = 0.5 mm.

setae; meso- and metatibiae with two rows of setae along outer edge; each tibia with one rather strong and one rather weak apical spur. Femora about twice as wide as corresponding tibiae, widest at proximal half and narrowing in distal half, although somewhat widened at apex. Tarsi moderately long and rather thin, tarsomere 5 about as long as tarsomeres 1–4 combined and with very long simple claws, two long setae located between bases of claws (giving evidence of presence of empodium); protarsi with subequally long protarsomeres 1–4, tarsomere 1 widest and lobed, protarsomere 2 somewhat narrower and lobed, protarsomere 3 subcylindrical, protarsomere 4 narrowest and cylindrical; tarsomeres 1–4 of mesotarsus somewhat similar to those in protarsus but with narrower mesotarsomeres 1 and 2; metatarsomeres 1–4 simple (cylindrical); all tarsomeres 1–3 with a pair setal brushes at apex.

Male anal sclerite clearly exposed and widely rounded at apex.

Larva ? Sorodites angustipes gen. et sp. nov. Figs 1, 4

Notes. The larval remains under description should be interpreted as parts of an exuvium of a nitidulid larva as they demonstrate the peculiar nitidulid mouthparts with a narrow and comparatively long cardo, maxillary mola with a spur on its inner edge, and a onesegmented labial palpi. Other visible characters of these remains also correspond with those of known nitidulid larvae. It is impossible to interpret these remains as belonging to the same species as the adult holotype of Sorodites angustipes gen. et sp. nov.. Nevertheless such interpretation can be regarded as more or less probable, and both specimens (represented by adult and exuvium) could have been together when fluid resin was dropped on the location of larval development of Sorodites angustipes gen. et sp. nov. However, the size of sclerites in the remains of the exuvium suggests that the latter could belong to a much smaller larva than a probable mature larva of the holotype specimen after corresponding molting pupal instar and adult emergence.

Description of remains of larva. Urogomphi 0.5 mm long. Mouthparts 0.3 mm wide. Abdominal segments prominently lobed laterally and each lobe with rather long seta at apex; abdominal segment 9 with pair of very long, slightly curved and simple (not branched) urogomphi with pointed and gradually curved apex, and also apparently with quite raised and simple pregomphi. Epicranium apparently suboval, about 0.4 mm wide and 0.4 mm long; frontal sutures not visible; very sparse and moderately long setae spread in different places and one very long seta located at each side behind mandibles. Antennae 3-segmented and comparable long, with ultimate antennomere subcylindrical, almost twice as long as two previous ones combined, with three setae in distal half and with apical sensory appendices extremely short (scarcely visible). Labrum appearing as narrow slightly convex stripe with small microtrichia along anterior edge. Mandibles rather wide, bidentate apically; cutting edges furnished with many very small teeth continuing by mola. Maxillae 3-segmented and with ultimate palpomere narrowest and somewhat longer than others. Labium with palpi moderately separated from each other, about 1.5 times as long as wide; ligula moderately produced; suture between mentum and submentum distinct.

4. Discussion

Sorodites gen. nov. should be certainly assigned to the Soroniacomplex in spite of its antennal club weakly dorsoventrally compressed and subcylindrical tarsomere 3. The posterior pronotal edge in most genera of the complex, in contrast to the new genus, has a more or less raised border, although not infrequently this border becomes thinner to almost obsolete at the sides (Annachramus, Hisparonia, Macleayania, Sebastianella). The metatarsomeres 1–3 of Macleayania and Pleoronia are nearly as those in Sorodites gen. nov., but with a more or less visible trace of paired brushes of setae (nearly as those in the new genus). Annachramus has almost simple metatarsomeres and sutural angles almost absent, but its pygidial apex is clearly exposed. The interfacetal setae are rather variable in the large genera of this complex, like Lobiopa and Soronia, demonstrating variability as specific peculiarities of members in each genus as in intraspecific variability of some common species. Many species of Soronia usually have almost simple metatarsomeres 1-3 (also with a pair of small subapical brushes of hairs on lower side), a very clear border along the entire pronotal base in large-sized species and with a rather thin one in small-sized species. Their elytra have adsutural lines following closely to the suture, but distinctly somewhat separated from the latter. It is worthwhile to mention that Stenoronia librodoriformis Kirejtshuk et Cline, 2003, a definite member of Soronia-complex (after the characters of head, prosternal process, tibiae etc.), with a Librodor-like appearance, has a subflattened prosternal process (not curved along procoxae) with sides of its apex far expanded on each side, i.e. looking something like the prosternal process in Librodor species, but not like that of other members of Soroniacomplex.

The Soronia-complex seems to be rather closely related to Phenolia-complex, however, both complexes have a distinct hiatus, expressed mostly in the structure of the protibial apex and prosternal process. The protibial apex of members of the Soroniacomplex is more or less rounded at the outer angle, while the members of Phenolia-complex have a more or less distinct top at the apical angle of the protibia, while the protibia of Cacconia obscura Sharp, 1890 is narrow and its outer angle has an intermediate outline between that in members of Soronia-complex and that in members of Phenolia-complex. The prosternal process of members of the Soronia-complex is more or less curved between the procoxae and widely broadened at the apex, which is closer to the surface of the mesoventrite, while that in the Phenolia-complex is flat, narrow and vertically abrupt posteriorly (with its main plane not approaching the surface of the mesoventrite and extended far beyond the posterior edge of the procoxae). The prosternal process in Cacconia and Ostomarcha has an intermediate condition: it has a curved and rather wide apex of its prosternal process, and the



Fig. 4. ? Sorodites angustipes gen. et sp. nov., remains of larval exuvium (GPIH 4592 - "11022"), Institute of Geology and Palaeontology and Museum, University of Hamburg; Burmese amber, Cretaceous, late Albian to early Cenomanian, photographed – A under Leica MZ 12.0 stereomicroscope with a DFC290, and – B-E under confocal laser scanning microscope Leica TCS SP2: A: remains of larval exuvium at posterior part of holotype Sorodites angustipes gen. et sp. nov., from above; B–C: ibid, from below; C, D: mouthparts, from below.

second has a rather narrow apex and is curved along the procoxae approaching the surface of the mesoventrite. The prosternal process of *Ussuriphia* is rather wide (widest among both members of *Soronia*- and *Phenolia*-complexes), subflattened (not curved along procoxae), slightly widened at apex and with a vertically abrupt posterior wall. The prosternal process within species of the genus *Phenolia* sensu lato is extremely variable but almost never with so wide an apex as that in groups of the *Soronia*-complex. The exceptions are present in *Phenolia* (*Phenolia*) grossa Fabricius, 1801, *Phenolia* (*Lasiodites*) spornraftorum Kirejtshuk et Kvamme, 2002 and some other species whose prosternal apex is nearly shaped as that in some members of the *Soronia*-complex, although the proportion of their prosternal process apex is somewhat smaller than generally found in members of the *Soronia*-complex. The genus *Phenolia* sensu lato is very variable in the presence of postocular fossae and interfacetal setae, development of antennal grooves (from very long and very deep to very short and rather shallow) and adsutural lines (obsolete or not visible in some species) and this genus includes some subgenera distinguished by structural features characteristic of other genera of the *Soronia*- and *Phenolia*-complexes. In particular, the submetacoxal line deviating from the posterior edge of the metacoxae is known in species of the subgenus *Aethinodes*, while representatives of other subgenera have these lines following closely to the posterior edge of the metacoxae.

Remarks on probable bionomy. Like many recent species of the Soronia-complex, Sorodites angustipes gen. et sp. nov. could be associated with some substrates of plant origin infected by fungi, probably including places with concentrated fungal tissues, such as under bark, fermented tree juice, decayed fruits, etc.

Systematics and evolution. Sorodites gen. nov. is the unique representative of the family Nitidulidae with a subcylindrical to cylindrical tarsomere 3 (not lobed as in most members of the family) together with pro- and mesotarsi with lobed tarsomeres 1 and 2. and also the only member of the subfamily Nitidulinae with the antennal club very weakly dorsoventrally compressed. The first feature seems to be secondary, because the basal diversification of the family into two nitidulid lineages (Carpophiline- and Nitiduline-lineages) occurred at least not later than the beginning of the early Cretaceous since modern species of both these lineages have similar principal structures of 5-or 4-segmented tarsi, including three first tarsomeres more or less lobed, tarsomere 4 smallest and cylindrical (usually slightly visible between lobes of the preceding tarsomere) or reduced (in the subfamily Cybocephalinae Jacquelin du Val, 1858). The important argument supporting this interpretation is the presence of paired brushes of setae at the apex of each of tarsomeres 1-3. The second feature concerning the dorsoventral compression of the antennal club could also be secondary because a weak compression of the comparatively long (sometimes nearly loose) antennal club is more characteristic of members of the Carpophiline-lineage, but many groups of both subfamilies Carpophilinae Erichson, 1843 and Epuraeinae Kirejtshuk, 1986, and all representatives of the subfamily Amphicrossinae Kirejtshuk, 1986 have a rather compact and compressed antennal club. At the same time, all groups of the Nitiduline-lineague have a dorsoventrally compressed antennal club, even in the groups with strongly modified clubs.

5. Taxonomic notes

The genus Cacconia should not be placed in the Prometopiacomplex (how it was preliminarily listed in Kirejtshuk (2008)), as the current study of some specimens of Cacconia obscura from Mexico in the Canadian National Collection of Insects, Arachnids, and Nematodes in Ottawa ("MEX., 3 mi N. San Cristobal, Chis, V.29.1969, J.M. Campbell") reveals of its similarity with groups of the Phenolia-complex (Kirejtshuk and Kvamme, 2002) because of the comparatively small mentum, trace of longitudinal costae, seriate puncturation and distinct longitudinal rows of hairs on the elytra, however it has a rather wide apex of the prosternal process curved along its procoxae and closely approachs the surface of the mesoventrite (as in groups of the Soronia-complex). The protibia of Cacconia obscura is simple, i.e. it is not arcuately rounded at the outer apical angle (as usually in members of Soronia-complex) and does not project at the outer apical angle (as is characteristic of members of the Phenolia-complex).

6. Concluding remarks

The specimen given as a base for description of new species and new genus is very important for understanding the Mesozoic evolution of the family and particularly that *Sorodites angustipes* **gen. et sp. nov.** had the tarsal structure with (sub) cylindrical tarsomere 3 is completely different from its relatives of the *Soronia*complex of genera represented in the modern fauna and in other modern members of Nitidulidae. This structural feature is in conflict with the traditional set of diagnostic characters of this family, although all other peculiarities of this new species testify a good accordance of the new species with other groups of the *Soronia*complex. The described exuvium of larva represents the first Mesozoic fossil remains of Nitidulidae. It could be from a specimen conspecific with the holotype of *Sorodites angustipes* **gen. et sp. nov.** It demonstrates a great similarity to modern nitidulid larvae in all visible characters, particularly in the quite characteristic mouthparts. This fact is evidence that main larval morphotype of nitidulids has a rather ancient origin.

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