



Short communication

Taimyraphes gen. nov., the first glandulariine ant-like stone beetle from Santonian Taimyr amber (Coleoptera: Staphylinidae: Scydmaeninae)

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ABSTRACT

The Glandulariini includes 78 genera comprising over 70% of the extant nominal species of Scydmaeninae. Extant members of this tribe are ubiquitous in forests of all continents. Because of small size of most species (often below 2 mm), taxonomic problems accumulated over the past 200 years, and scarcity of fossils with exposed ventral structures that are crucial for generic diagnoses, Glandulariini are rarely subjects of palaeontological studies. Consequently, only five Cretaceous genera have been described, mostly those that can be diagnosed by conspicuous, often bizarre autapomorphies. We report a finding of the first Santonian member of Glandulariini, *Taimyraphes microscopicus* gen. et sp. nov., based on a specimen in Taimyr amber from Yantardakh. This is also the smallest described Cretaceous glandulariine beetle, with the body length merely ~0.8 mm. The fossil preservation state allows for examination of mesoventral structures, rarely exposed in such small specimens. We conclude that *Taimyraphes* does not show any novel character states; it is defined, as many extant Glandulariini, by a unique combination of synapomorphies that, separately or in different sets, can be found in its extant relatives. The Santonian *Taimyraphes* of Taimyr shares a similar body form with the extinct Eocene *Rovnoscydmus* of Ukraine, and with the extant Neotropical *Amimoscydmus* and *Heteroscydmus*, Nearctic *Delius* and *Neladius*, cosmopolitan *Microscydms*, or Western Palaearctic *Leptocharis*. As most Cretaceous Glandulariini are known from Cenomanian, and only one from Turonian, the first Santonian fossil is important to fill gaps in our knowledge of the evolution of Scydmaeninae, a group of beetles that apparently diversified into the extant tribes in or before Early Cretaceous.

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1. Introduction

The staphylinid subfamily Scydmaeninae or ant-like stone beetles includes a large tribe Glandulariini (Schaufuss, 1889 (=Cyrtyoscydmini (Schaufuss, 1889) that comprises over 70% of all species. Currently seventy-one extant genera are classified in Glandulariini; their distribution is worldwide, but they are most common and abundant in tropical and subtropical regions (e.g., Jałoszyński, 2016a, with numerous later additions). These

scydmaenines can be easily recognized by their maxillary palps, which have the palpomere 3 enlarged, fusiform with a truncate apex, and the palpomere 4 subconical, much narrower and shorter than 3. Adults of most genera show the typical 'ant-like' body form and predominantly inhabit leaf litter, soil, rotten wood and similar habitats rich in small invertebrates that constitute their diet. Some species are specialized predators that feed exclusively or predominantly on heavily sclerotized mites (e.g., Jałoszyński and Olszanowski, 2013; Jałoszyński, 2016b), but feeding preferences of most taxa remain unknown. These are typically very small beetles, with the body length of adults rarely exceeding 2 mm, and frequently not even reaching 1 mm; forms as small as 0.7 mm are not uncommon (e.g., Jałoszyński, 2014a). Morphological structures of adult Glandulariini are relatively well known, as this group is a long-term subject of systematic study of the first author, who has

Abbreviations: PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow.

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verified the placement and status of most genera and subgenera in a series of over 100 papers focused on the systematics, morphology of adults and larvae, behaviour and palaeontology of this group. However, our knowledge of extinct Glandulariini is still very fragmentary.

Extinct genera of Scydmaeninae described by older authors (summarized by Jałoszyński and Perkovsky, 2016a) are hardly diagnosable, as the descriptions lack important details and many type specimens have been lost or destroyed; in many cases even placement in tribe is currently impossible to clarify. Recent renaissance in studies of extinct Scydmaeninae is characterized by a strong bias toward Glandulariini that show some unusual, often bizarre autapomorphies, as such taxa are more easily diagnosable and identifiable than most of the 71 extant genera, which include inconspicuous beetles that show differences mainly in the arrangement and shapes of fine ventral structures. Recent years brought descriptions of several Cretaceous (Cenomanian and Turonian) glandulariines from Burmese (Myanmar) and French ambers, and two much younger, Priabonian genera from Rovno amber deposits. *Scydmbisetia* Jałoszyński and Yamamoto, 2016 (Cenomanian of Myanmar) has a pair of conspicuous setae on the vertex (Jałoszyński et al., 2016); *Nuegua* Yin et al., 2018a (Cenomanian of Myanmar) has an enormously elongate, bizarre 'snout' (Yin et al., 2018a); *Pangusyndicus* Yin et al. 2018b (same deposit) has a conspicuous, presumably glandular cavity in the pronotal disc and strongly reduced terminal antennomere; *Hyperstenichnus* Jałoszyński and Perrichot, 2017 (Turonian of France) has strongly modified mouthparts with a pair of giant sucking discs on its prementum (Jałoszyński et al., 2017a). Only *Cenomaniola* Jałoszyński and Yamamoto, 2017 (Cenomanian of Myanmar) does not have any striking, easily noticeable or bizarre structures, but this genus is very similar to only one of the extant glandulariine taxa, making it easy to provide a clear-cut diagnosis (Jałoszyński et al., 2017b). The Eocene (Priabonian of Ukraine) fossils of *Glaesoconnus* Jałoszyński and Perkovsky, 2016a and *Rovnoscydmus* Jałoszyński and Perkovsky, 2016a are the least conspicuous extinct genera of Glandulariini, both defined rather by a unique combination of synapomorphies than by any unusual autapomorphies (Jałoszyński and Perkovsky, 2016a). Among extant Glandulariini such inconspicuous forms predominate, and it can be expected that fossils, when better studied, will also yield plethora of tiny specimens representing taxa important to reconstruct the evolution of this group, but technically extremely difficult to examine in detail and to compare with all their numerous extant relatives.

In the present study we report for the first time an occurrence of a definite Glandulariini genus in the Santonian amber of Taimyr Peninsula. This is also the smallest ever described specimen of Cretaceous Glandulariini, which, due to its good preservation, offers an insight into the morphology of ancient miniaturized ant-like stone beetles.

2. Geographic and geological context

The specimen used in this study was found in Yantardakh, Taimyr Peninsula, northern Siberia (Fig. 1). The finding site is a cliff on the right bank of the Maimecha River, three km upstream from its confluence with the Kheta River (Yantardakh Hill, about 200 m long and 30 m high; 71°18'26.54"N E99°33'46.51"E). The amber piece was collected in 2012 by PIN expedition.

The amber at Yantardakh is deposited in the Kheta Formation of Coniacian-Santonian age (Saks et al., 1959). All amber in Yantardakh comes from the upper horizons of the formation, and is consequently thought to be Santonian (Zherikhin, 1978) or even upper Santonian, based on the presence of marine bivalves of the genus *Inoceramus* Sowerby, 1814 (Praecardioida: Inoceramidae) in the overlying (upper Santonian-lower Campanian) Mutino formation (Saks et al., 1959; Zherikhin and Sukacheva, 1973; Zherikhin and Eskov, 1999). The Mutino Formation conformably overlays the amber-bearing horizon without visible breaks (Rasnitsyn, 1980). Geological and palaeontological data concerning the Kheta formation and Yantardakh were recently summarized by Rasnitsyn et al. (2016); the biostratigraphic evidence supports the late Santonian age of the horizon.

A warm-temperate, humid climate was reconstructed for the Mutino and Turonian/Coniacian Ledyanaya formations that overlay and underlay the Kheta Formation, respectively (Golovneva, 2012). Inclusions of Taimyr Santonian localities are hypothesized to have been rapidly buried in deltaic sediments and reflect the fauna that inhabited an area directly adjacent to the river bank (Zherikhin and Sinitshenkova, 2002; Perkovsky et al., 2018) or to the river valleys (Nadein and Perkovsky, 2018).

3. Material and methods

The fossil specimen here described is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN); collection number 3311/666. The inclusion is in a tiny, polished irregular piece of amber about 4.0 × 1.5 × 1.2 mm. The specimen was

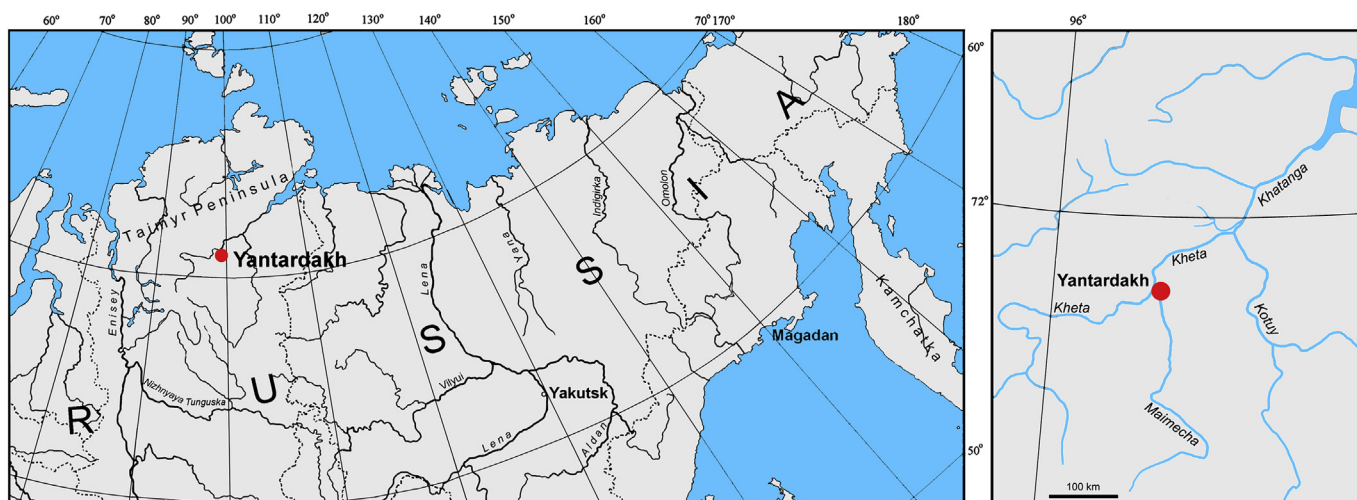


Fig. 1. The location of Santonian amber deposits of Yantardakh in Taimyr Peninsula, northern Siberia.

observed as dry and submerged in cedar oil, in order to enhance visibility. Photographs were taken using a KY-F75U (JVC) camera mounted on a Leica M205 C microscope. Images were edited with Corel PhotoPaint 9.397. Morphological structures were figured by freehand drawing, with exact proportions and general shapes sketched from photographs. Measurement convention and the terminology of morphological structures follow those of Jałoszyński (2012) and Jałoszyński and Perkovsky (2016a). The map in Fig. 1 is based on that published previously by Jałoszyński and Perkovsky (2016b). The work is registered in ZooBank under urn:lsid:zoobank.org:pub:B1F2EB13-7D17-4AA2-A6A3-E495B67FA8C2.

4. Systematic palaeontology

Suborder Polyphaga Emery, 1886

Superfamily Staphylinoidea Latreille, 1802

Family Staphylinidae Latreille, 1802

Subfamily Scydmaeninae Leach, 1815

Tribe Glandulariini Schaufuss, 1889

Genus *Taimyraphes* Jałoszyński and Perkovsky gen. nov.

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Figs. 2–3

Derivation of name. The name is a combination of the toponym Taimyr and the ending *-aphes* commonly used in names of Glandulariini. Gender masculine.

Type species. *Taimyraphes microscopicus* Jałoszyński and Perkovsky (here designated).

Diagnosis. *Taimyraphes* is a glandulariine genus showing a unique combination of characters, that separately or in different configuration, occur also in other genera: body constricted between head and pronotum and between pronotum and elytra, lacking thick bristles; head short, transverse, with eyes nearly equally distant from mandibular bases and occipital constriction; frons and vertex confluent and together subtrapezoidal; antennal insertions broadly separated; occipital constriction only slightly narrower than vertex; mandibles subtriangular, broadly falciform, planar; maxillary palpomere 3 less than 2.5 times as long as broad, palpomere 4 evenly subconical with pointed apex; hypostomal ridges strongly bent mesad, running parallel to anterior margin of submentum and connected at middle; submentum most likely lacking lateral sutures (this area is poorly visible); antennae slender with distinct trimerous club; pronotum elongate, bell-shaped, broadest in front of middle, with distinct but diffuse transverse antebasal impression as broad as pronotum at base; sides of pronotum lacking defined edges or carinae; prosternum most likely laterally fused with prothoracic hypomera (i.e., notosternal sutures not observable, most likely largely obliterated); coxal part of prosternum demarcated by anterior bisinuate carina; mesoscutellum not exposed; each elytron with distinct humeral callus and basal impression, basal elytral foveae not visible; mesoventrite lacking mesoventral intercoxal carina, its precoxal region with indistinct, diffuse median longitudinal elevation far from anterior margins of mesocoxal rests; meta-ventral intercoxal process subtriangular, not separating metacoxae; femora distinctly but moderately clavate.

Description. Body (Figs. 2A–D, 3A–D) strongly elongate and only slightly flattened, strongly constricted between head and pronotum and between pronotum and elytra. Vestiture of setae sparse, short, suberect to erect. Head capsule divided into large and exposed anterior part and smaller posterior 'neck' region largely retracted into prothorax and demarcated by occipital constriction (Fig. 3A; *occ*), the latter only slightly narrower than vertex; anterior part of

head in dorsal view (Fig. 3A) subhexagonal; vertex (Fig. 3A; *vt*) strongly transverse, with well-defined arcuate posterior margin, evenly convex; tempora (Fig. 3A, C; *tm*) slightly longer than eye in dorsal view, evenly but weakly rounded and strongly convergent posterad; frons (Fig. 3A; *fr*) posteriorly confluent with vertex, broadly subtrapezoidal; frontoclypeal groove most likely absent; antennal insertions broadly separated and located in large antero-lateral antennal cavities; composite eyes (Fig. 3A, C; *ce*) large and located near middle of anterior part of head capsule, nearly equally distant from mandibular bases and occipital constriction; eyes weakly convex, in lateral view bean-shaped, with the long axis of eye oblique in relation to the coronal plane of head. Head lacking thick bristles. Antennae slender but not conspicuously long, with distinctly delimited trimerous club and proximal flagellomeres distinctly shorter and narrower than scape (Fig. 3C; *sc*) and pedicel (Fig. 3C; *ped*). Mouthparts only partly visible; mandibles falciform, subtriangular, with slender and strongly curved apical portion, most likely lacking preapical teeth; maxillary palp composed of barely noticeable, minute palpomere 1, strongly elongate and broadened distally palpomere 2 (Fig. 3C; *mxp2*), large, fusiform with truncated apex palpomere 3 (Fig. 3C; *mxp3*) which is stout, less than 2.5 times as long as broad, and strongly elongate, subconical, slender and pointed palpomere 4 (Fig. 3C; *mxp4*).

Prothorax distinctly elongate and slightly flattened, about as broad as head and much narrower than elytra; pronotum broadest near anterior third, lacking lateral and sublateral carinae, with its anterior corners broadly rounded and posterior corners distinct, slightly obtuse-angled; pronotal base with a distinct but diffuse transverse antebasal impression (Fig. 3A, C; *abi*). Prothorax lacking lateral or dorsal bristles. Prosternum with its basisternal part (Fig. 3B; *bst*) appears subequal in length to coxal part, the latter demarcated by distinct bisinuate anterior carina (Fig. 3B; *ac*); notosternal sutures not discernible, most likely largely or completely obliterated and prosternum laterally fused with hypomera (Fig. 3B; *hy*), the latter showing indistinct traces of hypomeral ridges only in their posterior portions. Intercoxal region poorly visible, procoxae anteriorly separated by a subtriangular and pointed process of anterior carina, at middle procoxae not separated.

Elytra complete, oval, elongate and slightly flattened; humeral calli (Fig. 3A; *huc*) distinct; base of each elytron with distinct elongate basal impression (Fig. 3A; *bei*), but elytral foveae indiscernible (absent?); elytra lacking striae.

Mesoscutellum not exposed between elytral bases, most likely hidden under the posterior pronotal margin. Mesoventrite (Fig. 3B; *v2*) nearly entirely exposed in the studied specimen, its median area lacking mesoventral intercoxal process or carina, so that mesocoxae are not separated; weakly elevated and diffuse median longitudinal convexities between mesocoxae and near anterior mesoventral margin can be seen. Mesocoxal projections (Fig. 3B; *mscp*) moderately large, with rounded external (lateral) margins, lacking tufts of long setae.

Metaventrite (Fig. 3B; *v3*) elongate, broadening posterad, lacking any particular structures, evenly convex. Meta-ventral intercoxal process (Fig. 3B; *mtvp*) short and subtriangular, not separating metacoxae.

Hind wings not exposed, but prominent humeral calli indicate that wings are developed.

Abdomen with six visible sternites (Fig. 3B; *s3–8*), sternites 3–6 slightly reducing in length, sternite 7 about as long as 3, suture between sternites 7 and 8 distinct; pygidium only partly exposed (but not visible in dorsal view), declines at an angle of about 45°.

Legs moderately long and slender, not deviating from the generalized structures of all Glandulariini; metacoxae most likely

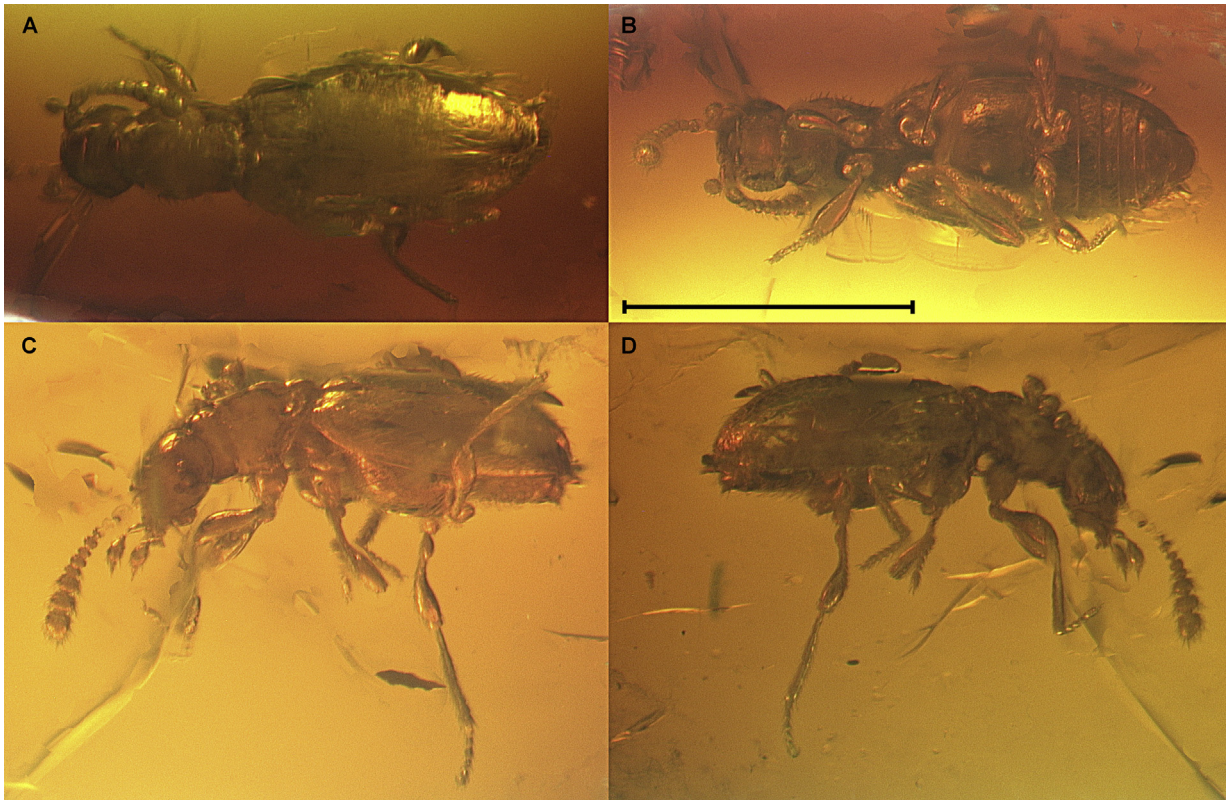


Fig. 2. Holotype (PIN 3311/666) of *Taimyraphes microscopicus* gen. et sp. nov. **A.** Dorsal habitus. **B.** Ventral habitus. **C.** Left lateral habitus. **D.** Right lateral habitus. Scale bar: 500 μ m.

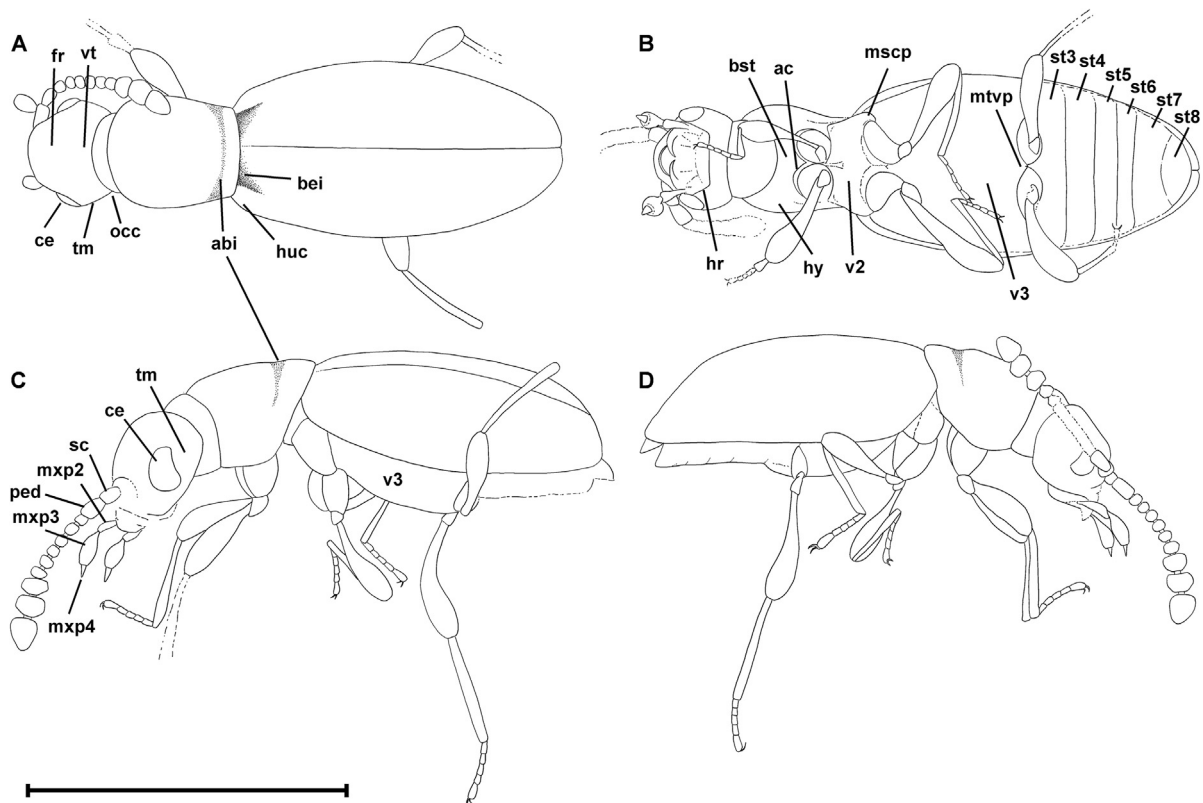


Fig. 3. Holotype (PIN 3311/666) of *Taimyraphes microscopicus* gen. et sp. nov. **A.** Dorsal habitus. **B.** Ventral habitus. **C.** Left lateral habitus. **D.** Right lateral habitus. Abbreviations: abi, antebasal impression; ac, anterior carina of coxal rests; bei, basal elytral impression; bst, basisternal part of prosternum; ce, composite eye; fr, frons; hr, hypostomal ridge; huc, humeral callus; hy, hypomeron; mscp, mesocoxal projection; mtvp, metaventral intercoxal process; mxp2–4, maxillary palpomere 2–4; occ, occipital constriction; ped, pedicel; sc, scape; st3–8, sternite 3–8; tm, temple; vt, vertex; v2, mesoventrite; v3, metaventrite. Scale bar: 500 μ m.

reaching laterally to margins of metaventrite (in ventral view hidden by femora, but in lateral view lateral corners of metacoxae seem to be visible and not separated from sides of metaventrite); all trochanters small and subtriangular, all femora distinctly, gradually but moderately strongly clavate; tarsi slender but not very long, with all tarsomeres at least slightly elongate.

Remarks. *Taimyraphes* is unambiguously placed in Glandulariini on the basis of the autapomorphy of this tribe, the maxillary palpomere 4 subconical, elongate and pointed, much smaller than the palpomere 3, the latter broadened and elongate (Fig. 3C). Additional characters typical of Glandulariini and clearly observable in *Taimyraphes* are: the ant-like body form, i.e., the body deeply constricted between the head and pronotum and the pronotum and elytra (shared with Mastigitae, Scydmaenini, Chevrolatiini and Leptoscydmini, all of which have broadly separated metacoxae); and the antennae not geniculate (i.e., the scape lacking the apical emargination that allows for bending the antennae ventrad or dorsad; shared with Cephenniitae, which are suboval beetles with very shallow or absent occipital constriction and feebly marked constriction between the pronotum and elytra, and with some Scydmaenini, that have the metacoxae broadly separated).

Currently seventy-one extant genera of Glandulariini are known. Three of them, the Neotropical *Napochomorphus* Franz, 1980a, Afrotropical *Neuraphomorphus* Reitter, 1882 and Australian *Psepharobius* King, 1864 are ill-defined, and since their descriptions have never been studied again. All of them are monospecific, and the depositories of the type material of the sole species included in the latter two genera remain unknown. *Napochomorphus* is the only Neotropical genus not seen by the first author. However, *Napochomorphus* was described as having the pronotum broadest at base and strongly narrowing anterad, and consequently it should not be possible to confuse the Cretaceous *Taimyraphes* with its bell-shaped pronotum with the extant *Napochomorphus*. Also the depository of the type specimen(s) of the only species included in the Nearctic *Taphrosydmus* Casey, 1897 remains unknown. However, it was described as having a deep impression on the vertex, and with the pronotum with lateral carinae and a pair of deep lateral antebasal pits, which makes *Taphrosydmus* clearly distinguishable from *Taimyraphes*. All the remaining extant genera of Glandulariini have been studied by the first author and their morphological structures can be compared with those of *Taimyraphes*.

Taimyraphes has a subtriangular and very short metaventral intercoxal process, so that its metacoxae are contiguous. This character alone differentiates the new genus from the extant cosmopolitan *Euconnus* Thomson, 1859, Neotropical *Euconnomorphus* Franz, 1980a, Neotropical *Homococcus* Sharp, 1887, Australian *Leascydmus* Jałoszyński, 2014b, Australian *Kangarooconnus* Jałoszyński, 2017 (in Jałoszyński and Newton, 2017), Madagascan *Madagassococcus* Franz, 1986, Afrotropical *Oneila* Peringuey, 1899, Neotropical *Plaumanniola* Costa Lima, 1962, and *Stenichnoteras* Scott, 1922 of the Seychelles. These glandulariine genera all have the metacoxae clearly separated. *Taimyraphes* has neither the mesoventral intercoxal process nor the anterior metaventral process; and it does not have a sharply, step-wise delimited median longitudinal carina in front of mesocoxae (only a faint and diffuse longitudinal convexity near the anterior mesoventral margin). These structures, if present, would be well-visible in the exposed intermesocoxal region and on the metaventrite of the specimen. This feature allows for distinguishing *Taimyraphes* from further 54 extant genera, adults of which either have one, or all of these carinate processes. This leaves only four extant glandulariine genera that have the ventral pterothoracic structures similar to those of *Taimyraphes*, i.e., the metacoxae contiguous or subcontiguous (i.e., hardly separated, nearly

touching), and the meso- and metaventrite lacking sharply defined median carinae between, in front of, or behind the mesocoxae. These are: the New Caledonian *Austrostenichnus* Franz, 1971, Nearctic *Neladius* Casey, 1897, Australian *Scydmeplitoxis* Jałoszyński, 2014c, and *Stenichnaphes* Franz, 1980b of New Zealand. *Taimyraphes* differs from *Austrostenichnus* in the trimerous antennal club (antennae gradually thickened in *Austrostenichnus*), a short head with eyes placed in its anterior half, and long tempora (in *Austrostenichnus* the head is elongate, eyes nearly touching the posterior margin of the head and consequently the tempora are vestigial), the maxillary palpomere III stout, less than $2.5 \times$ as long as broad (in *Austrostenichnus* conspicuously slender, over $3 \times$ as long as broad); the pronotum with its lateral margins in the posterior half straight (in *Austrostenichnus* sides are distinctly constricted in front of base); and the mesoventrite in front of mesocoxae lacking a pair of large lateral impressions filled with dense setae (in *Austrostenichnus* such impressions are present). *Taimyraphes* differs from *Neladius* (to which it is very similar in the general shape and size of the body, the antennal structure, the shape of the head and pronotum, the shape of the maxillary palpomere III and ventral pterothoracic structures) in the pronotum with a transverse antebasal impression (lacking in *Neladius*); in the mesoscutellum not exposed between elytral bases (in *Neladius* the scutellum is well-visible); and in the short, subtriangular metaventral intercoxal process (in *Neladius* the process is composed of two elongate, pointed spines separated at middle by a narrow and long notch). *Scydmeplitoxis* is conspicuous in having a deeply and narrowly constricted pronotum, which in dorsal view is nearly hourglass-shaped, with two pairs of antebasal pronotal pits, and with the tempora, sides of pronotum and mesanepisterna bearing tufts of thick and dense bristles. None of these characters can be found in *Taimyraphes*. Finally, *Taimyraphes* differs from *Stenichnaphes* in a short head with eyes in its anterior half and long tempora (in *Stenichnaphes* the head is elongate, eyes close to the posterior margin of the head and the tempora are vestigial), the pronotum lacking lateral carinae (in *Stenichnaphes* sides of pronotum carinate at least in the posterior third); and the coxal part of the prosternum demarcated from the basisternal part by a distinct bisinuate carina (in *Stenichnaphes* such a carina is absent and a much shorter basisternum is marked off only by a transverse row of setae).

Taimyraphes differs also from all currently known extinct genera of Glandulariini. The Cenomanian *Cenomaniola* has thick bristles on the tempora and sides of the prothorax; the anterior mesoventral process, the lateral pronotal carinae, the median pronotal longitudinal carina (or at least a distinct trace of it), and densely setose posterior margins of mesocoxae; none of these features can be found in *Taimyraphes*. The Cenomanian *Scydmobisetia* has a pair of conspicuously thick and long lateral setae on the vertex, eyes adjacent to the antennal insertions and the pronotum with a pair of lateral antebasal pits, lacking a transverse impression. In *Taimyraphes* no such setae occur, the eyes are distant from the antennal insertions, and the antebasal pronotal structures are clearly different. The bizarre Cenomanian *Nuegua* has an enormously elongate, snout-like preocular portion of the head capsule, a character not known in any other, extant or extinct, Scydmaeninae; it differs from *Taimyraphes* also in having a long median pronotal carina and a carinate mesoventral intercoxal process, both structures absent in *Taimyraphes*. The most recently described *Pangusyndicus* from Burmese amber has, among other features, two unique characters not known in *Taimyraphes*: a conspicuously large, possibly glandular cavity that occupies a large portion of the pronotal disc, and a reduced, minute antennomere 11 inserted into the antennomere 10 without a separating constriction.

Other than Cenomanian, Cretaceous Glandulariini are represented only by the Turonian *Hyperstenichnus*. *Taimyraphes* differs from this conspicuous genus in the antennae with trimerous club

(gradually thickened and with distal antennomeres strongly elongate in *Hyperstenichnus*), the prosternum presumably fused with hypomera (distinctly demarcated from hypomera by complete notosternal sutures in *Hyperstenichnus*), and presumably unmodified labrum (this region of mouthparts is poorly visible in the studied specimen, but in *Hyperstenichnus* the mouthparts are dominated by a conspicuously enlarged and strongly modified prementum; no structures even slightly indicating a similar modification can be found in *Taimyraphes*).

The remaining fossils of Glandulariini are much younger than *Taimyraphes*. The Priabonian *Glaesoconnus* has the antennae gradually thickened, the pronotum bearing two pairs of antebasal pits, densely setose posterior margins of mesocoxal rests and the metacoxae narrowly separated by a metaventral intercoxal process that has a short median notch, which are characters not found in *Taimyraphes*. The Priabonian *Rovnoscydmus* is very similar to *Taimyraphes* in the small body, general shape, the antennal and ventral thoracic structures, but it clearly differs in having a short median transverse antebasal impression on the pronotum, which is only as broad as about 1/3 of the pronotal base, whereas in *Taimyraphes* there is a diffuse and shallow transverse impression extending from side to side. Moreover, in *Rovnoscydmus* the subtriangular meso-scutellum is visible between elytral bases, whereas in *Taimyraphes* this structure is not exposed.

Species ***Taimyraphes microscopicus*** Jałoszyński and Perkovsky sp. nov.

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Figs. 2–3

Material studied. Holotype (PIN 3311/666), from Taimyr amber, sex unknown; collected in 2012 during a PIN expedition.

Derivation of name. The name *microscopicus* refers to the very small body of this species.

Type locality and horizon. Russia: Krasnoyarsk Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: right bank of the Maimecha River 3 km upstream of its confluence with the Kheta River (a left source of the Khatanga River), Yantardakh Hill; Upper Cretaceous, Santonian (Kheta Formation).

Diagnosis. As for the genus (*vide supra*).

Description. Body (Figs. 2, 3) slender, length 0.81 mm, pigmentation light brown, body covered with sparse, short and suberect to erect setae (well visible on left side of pronotum in Fig. 2B). Anterior (i.e., exposed) part of head slightly transverse, length 0.13 mm, width 0.15 mm; tempora (Fig. 3A; *tm*) weakly and evenly rounded, strongly convergent toward occipital constriction; vertex (Fig. 3A; *vt*) much broader than long, posteriorly demarcated by transverse arcuate ridge, anteriorly confluent with strongly transverse frons; supraantennal tubercles weakly elevated, barely discernible; composite eyes (Figs. 3A, C; *ce*) large but weakly convex, bean-shaped, each with shallow emargination in its posterior margin. Punctures on frons and vertex indiscernible, setae very short, sparse and suberect. Antenna moderately long, slender, length 0.25 mm, scape and pedicel (Fig. 3C; *sc*, *ped*) each distinctly elongate, antennomere 3 indistinctly transverse, 4–6 each about as long as broad; 7 slightly, 8 distinctly transverse, 9 and 10 each much broader and longer than 8, strongly transverse, 11 slightly shorter than 9–10 combined, indistinctly narrower than 10, about 1.3 times as long as broad, with subconical, blunt apex. Most flagellomeres with exposed basal stalks; all antennomeres covered with sparse and moderately long suberect and erect setae.

Pronotum distinctly elongate, length 0.19 mm, width 0.15 mm; broadest near anterior third. Anterior margin evenly rounded,

laterally confluent with lateral margins, sides rounded in anterior half and distinctly narrowing posteriorly, nearly straight in posterior half; posterior pronotal corners slightly obtuse-angled and well defined; posterior margin weakly arcuate; pronotal disc evenly convex; pronotum with distinct but shallow and diffuse transverse antebasal impression (Fig. 3A, C; *abi*). Disc and sides of pronotum covered with sparse suberect to erect short setae; punctures indiscernible.

Elytra slender, oval, length 0.50 mm, width 0.25 mm; dorsal surface slightly flattened, apices rounded together. Elytral punctures barely discernible, not arranged in rows; setae short and suberect, inconspicuous.

Abdomen about as long as metaventrite, unmodified, completely covered by elytra except for the posterior portion of pygidium, which is exposed (Fig. 3D).

Legs lacking any peculiar characters.

5. Discussion

A relatively small number of described extinct Glandulariini (and Scydmaeninae in general) is not a result of scarcity of fossils (Jałoszyński, unpublished obs.), but rather a consequence of problems to properly diagnose amber inclusions and compare their morphological details with extant taxa. The Scydmaeninae are very small beetles and until recently most of world genera (especially those of Glandulariini) were impossible to identify. This was a result of inadequate or dubious diagnoses, descriptions based primarily on easily observable but often insufficient or even misleading dorsal characters, and accumulation of morphological misinterpretations in vast literature on the ant-like stone beetles. A large part of the most recent literature on Glandulariini is focused on detailed morphological descriptions, emending diagnoses and correcting placement of many taxa. As not all world genera of Glandulariini have been redefined yet, it is still difficult to properly diagnose a new, extant genus. Such a task requires comparing its characters with all members of the tribe, and this is not yet possible. A natural consequence is that extinct taxa are being described mainly in better studied groups of Scydmaeninae that include beetles with markedly larger adults (Mastigitae, for instance; e.g., Cai and Huang, 2016; Jałoszyński et al., 2017c, 2018; Yin et al., 2017a, b, 2018c). Another systematic bias is due to reporting mainly 'the oldest' members of tribes previously not known in fossil record or known from relatively young deposits, which are most desirable findings (e.g., Eutheini, Cephenniini, Scydmaenini; Jałoszyński and Peris, 2016; Jałoszyński, 2018; Yin et al., 2018d), or most conspicuous, most bizarre morphological forms that, although equally difficult to compare with extant genera, nevertheless show some unusual apomorphies that increase the probability of establishing a new valid generic name and not a junior synonym (e.g., Jałoszyński et al., 2016, 2017a; Yin et al., 2018a, b). The latter strategy currently predominates in Glandulariini and most of the described Cretaceous genera are morphologically in some way unusual, showing structures as monstrous as the extraordinary 'snout' of *Nuegua*, a deep pronotal cavity of *Pangusyndicus* or the conspicuous premental discs of *Hyperstenichnus* (Jałoszyński et al., 2017a; Yin et al., 2018a, b). However, the majority of Cretaceous fossils of Glandulariini seen by the first author (several hundred specimens) represent small (up to 1.5 mm), inconspicuous, 'generalized' beetles that seem to differ from their extant relatives by unique combinations of characters known in other taxa, and not by some striking autapomorphies that allow them to be identifiable at the first sight. Unfortunately, these fossils are either poorly preserved or only some of their body parts are exposed, making detailed morphological studies difficult. Advanced visualization methods as the synchrotron tomography

are not yet so widely and commonly available to significantly contribute to morphological and phylogenetic studies.

In this study we describe a modest-looking and tiny fossil that does not show any unusual apomorphies, one among many accumulated in various institutional and private collections (Jałoszyński, unpublished obs.). Yet this fossil is unique in representing the second known scydmaenine, and the first member of the now ubiquitous tribe Glandulariini, found in Santonian deposits (the first being the extant eutheine genus *Eutheia* Stephens, 1830 recorded by Jałoszyński and Perkovsky (2016b)). All but one previously known Cretaceous fossils of Glandulariini are Cenomanian, the only exception is the Turonian *Hyperstenichnus vendeanus* Jałoszyński and Perrichot, 2017. In order to understand the evolution of this successful tribe, fossils from more diverse horizons should be studied. *Taimyraphes* in its 'ordinariness' is most interesting as a beetle that, if not embedded in amber, could easily pass for an extant form, similar to many genera that presently inhabit the forest floor of all continents. The body form and small size of *Taimyraphes* resemble those of the extant Neotropical *Amimoscydmus* Jałoszyński, 2013 and *Heteroscydmus* Franz, 1980a, Nearctic *Delius* Casey, 1897 and *Neladius* Casey, 1897, cosmopolitan *Microscydmus* Saulcy and Croissandeau, 1893, or Western Palaearctic *Leptocharis* Reitter, 1887 (morphological structures of these genera were illustrated by Jałoszyński (2013; 2014a, 2015; 2017)). *Taimyraphes* clearly differs from all of them in a combination of cephalic and thoracic structures, as it differs in a similar way from most other 'ant-like', small and slender extant Glandulariini. This combination of character states (given in the diagnosis) allows for unambiguous discrimination between *Taimyraphes* and all remaining Glandulariini (extant and extinct, inasmuch as their characters are known), but none of them taken separately is a novel morphological transformation. The shape of body parts and all their (observable) fine structures are not different from those known in extant Glandulariini, among which there are numerous genera with antennae, hypostomal ridges, pronotal and prosternal structures, mesoventral, metaventral and elytral characters similar to those in the Santonian *Taimyraphes*.

The currently available morphological evidence clearly demonstrates that Scydmaeninae (at least Mastigini, Clidicini, Eutheini, Cephenniini, Scydmaenini and Glandulariini) that constituted components of Late Cretaceous ecosystems did not differ in much detail from their extant relatives. These major tribes must have differentiated during Early Cretaceous or even earlier. However, the Cretaceous fauna of Scydmaeninae is still so poorly known that drawing any more precise conclusions is not yet possible.

To date, only two specimens of Scydmaeninae have been found in Taimyr ambers, in a sample comprising several thousand inclusions (over 6500 from Yantardakh). This intriguing scarcity of scydmaenines in Taimyr ambers that are otherwise rich in invertebrates (Rasnitsyn et al., 2016) is congruent with a rarity of other common components of soil and leaf litter communities. For instance, other staphylinids are represented by five specimens only, including four from Yantardakh (a micropepline record of Zherikhin (1978) was based on a misidentification); ptiliids by one specimen; oribatid mites by merely seven inclusions (Sidorchuk, pers. com.). Springtails have not been found so far, only a single moss specimen is known (Ignatov et al., 2016), and liverworts remain unknown. In Campanian Canadian amber, the other Lagerstätte of the '*Baeomorpha* realm' (a term recently introduced by Gumovsky et al. (2018) and comprising northern, Laurasian territory and biota characterized by a temperate or warm temperate climate and very abundant aphid and rotoitid fossils), nine springtail families are represented by common and diverse specimens, and also oribatids are frequent (at least nine families vs. only two in Kheta Formation ambers (Rasnitsyn et al., 2016)). This

phenomenon may be associated with peculiarities of Taimyr amber forests, which are still poorly understood (Nadein and Perkovsky, 2018; Perkovsky et al., 2018).

6. Conclusions

For the first time, a Santonian genus of the tribe Glandulariini is described and characterized. *Taimyraphes microscopicus* does not show any unique apomorphies; it rather represents a 'generalized' body structures that, in different combinations or in a different set, can be found in extant Glandulariini. It is also the smallest so far described Cretaceous member of this tribe (~0.8 mm), similar in size and shape to some species in the extant genera *Amimoscydmus*, *Heteroscydmus*; *Delius*, *Neladius*; *Microscydmus* or *Leptocharis*, and to the extinct Eocene *Rovnoscydmus*.

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