

Ultra-thin surface structure of elytra in the identification of species of the genus *Morychus* Erichson, 1840 (Coleoptera, Byrrhidae)

Ультратонкая структура поверхности надкрылий в идентификации видов рода *Morychus* Erichson, 1840 (Coleoptera, Byrrhidae)

S.E. Tshernyshev
С.Э. Чернышёв

* Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Frunze Str. 11, Novosibirsk 630091 Russia; Tomsk State University, Lenina Prospekt 36, Tomsk 634050 Russia. E-mail: sch-sch@mail.ru.

* Институт систематики и экологии животных СО РАН, ул. Фрунзе 11, Новосибирск 630091 Россия; Томский государственный университет, проспект Ленина 36, Томск 634050 Россия.

Key words: Pill beetle, morphology, elytral surface, species identification.

Ключевые слова: жуки-пиллюльщики, морфология, поверхность надкрылий, идентификация видов.

Abstract. Analysis of the ultrafine structure of the surface of the elytra in species of the genus *Morychus* Erichson, 1840 has revealed characteristics that can be used for species identification. Identification based on the shape of the elytra is possible through the presence or absence of indentation before the apex, the type of apical notch, the angle of inclination of the notch, the proneness of the external basal angle and the ratio of the width of the sutural and epipleural areas. The type and size of the dots, their density (i.e. the distance between them) and uniformity (i.e. the presence of 'rows' or the random arrangement of the dots), as well as the size and location of the hairs, can be used to identify species based on the sculpture of their surface. These characteristics and patterns can be applied to the analysis of damaged deposits that are often lacking in pubescence.

Резюме. Анализ ультратонкой структуры поверхности надкрылий у видов рода *Morychus* Erichson, 1840 позволил выявить дополнительные признаки, которые возможно использовать для видовой идентификации по надкрыльям. Наличие или отсутствие вдавления перед вершиной надкрылий, тип прищепковой выемки, угол её наклона, выраженность внешнего базального угла, соотношение ширины пришовной и эпиплевральной половин позволяет проводить определение по форме надкрылий. Вид и величина точек пунктировки, густота (по расстоянию между точками) и равномерность пунктировки (наличие «рядов» или спутанность точек) и размер и расположение волосков — по скульптуре их поверхности. Выявленные признаки и закономерности их проявления могут быть использованы при анализе образцов из отложений, претерпевших повреждения, а часто и лишённых опушения.

Introduction

Pill beetles (Byrrhidae) are well known in palaeontological research and are common in Quaternary deposits. To date, 31 species belonging to seven genera and two subfamilies have been found. While this representation

is small compared to more abundant families such as ground beetles, weevils and rove beetles, it is quite significant given the low overall diversity of the family. The presence of pill beetles in Quaternary deposits enables to characterise the type of biocenosis that they inhabited in the past.

The species of the genus *Morychus* Erichson, 1840 inhabit tundra-steppe biotopes; therefore, this group of Coleoptera can be used as a model or marker in the study and reconstruction of palaeolandscapes [Berman, 1990; Muratova et al., 1993; Sher et al., 2005; Elias et al., 2006; Kuzmina, Sher, 2006; Kirillova et al., 2016; Tshernyshev, 1997, 2006, 2012, 2017, 2021; Tshernyshev et al., 2013; Zinovyev et al., 2016; Dudko et al., 2022; Gurina et al., 2019, 2023, 2024]. In the Quaternary deposits of North Asia, fragments of beetles are often found that have been subjected to mechanical pressure and have lost a number of structures, such as bristles and hairs. Remains of this quality do not permit accurate species identification using existing identifiers based on comparisons of the external appearance of adults and male genitalia. The genus *Morychus* Erichson currently includes nine species [Tshernyshev, 1997, 2000, 2006, 2012, 2021; Tshernyshev, Pütz, 1999]: *M. aeneolus* (LeConte, 1863), *M. aeneus* (Fabricius, 1775), *M. dud-korum* Tshernyshev, 1997, *M. oblongus* (LeConte, 1857), *M. ostasiaticus* Tshernyshev, 1997, *M. subparallelus* (Motschulsky, 1845), *M. tibeticus* Tshernyshev, 2000, *M. viridis* Kuzmina, Korotyaev, 1987, and *M. yamalus* Tshernyshev, 1999. Two of these species are only found in North America: *M. aeneolus* (LeConte) and *M. oblongus* (LeConte). The remaining species are found in the Palearctic region from Tibet to Chukotka and Central Europe. The elytra of each species are shown in Figures 1–7 and 9–10. Due to the difficulty of identifying species in fossil remains, a microscopic study of the elytra of

different *Morychus* species was conducted. This revealed features that can be used to identify taxa based on the external morphology of these beetle body parts.

Materials and methods

The left elytra of the males from the type series were used for comparison, paratypes: *M. viridis*, *M. ostasiaticus*, *M. dudkorum*, *M. yamalus*, *M. tibeticus*, and topotypes of *M. subparallelus* and *M. aeneus*. Only Palaearctic species underwent ultra-thin microscopy.

Microscopy was performed on a Hitachi TM-1000 scanning microscope with magnifications of x60, x400 and x800. Digital photographs of elytra were taken using a Carl Zeiss Stemi 2000 trinocular microscope and the AxioVision programme.

The present work is registered in ZooBank (www.zoobank.org) under urn:lsid:zoobank.org:pub:61C47A0D-4009-4ADC-8331-24755FCE7D30.

Results

EXTERNAL APPEARANCE OF THE ELYTRA

The beetle's elytra are difficult to describe as they are convex and have a complex curve. When removed and laid flat, their complex structure becomes apparent, with individual characters that appear to be species-specific. Figures 1–10 illustrate the variations in elytra size and shape, the configuration of individual areas, colouration, and pubescence.

The length and width of the elytra reflect the size of the beetles and the overall size of the species. While some individuals in the population may be slightly larger or smaller, on average, the size corresponds to that of the specimens shown in the photographs. The shortest elytra are found in *M. yamalus* (3.25 mm; Fig. 7) and *M. dudkorum* (3.35 mm; Fig. 2), while the longest are found in *M. viridis* (4.25 mm; Fig. 1), *M. subparallelus* (4.15 mm; Fig. 5), and *M. aeneolus* (4.0 mm; Fig. 9). The remaining species fall within the average range of 3.5–3.75 mm. These include *M. tibeticus* (3.7 mm, Fig. 6), *M. aeneus* (3.5 mm, Fig. 3), *M. ostasiaticus* (3.7 mm, Fig. 4) and *M. oblongus* (3.5 mm, Fig. 10). The widest elytra are found in *M. viridis* (2.0 mm; Fig. 1), *M. subparallelus* (2.1 mm; Fig. 5) and *M. aeneolus* (2.0 mm; Fig. 9), while the narrowest are found in *M. yamalus* (1.55 mm; Fig. 7) and *M. dudkorum* (1.75 mm; Fig. 2). The width of the elytra of the other species falls within the average range of 1.75–1.95 mm: These include *M. ostasiaticus* (1.75 mm, Fig. 4), *M. oblongus* (1.85 mm, Fig. 10), *M. aeneus* (1.9 mm, Fig. 3) and *M. tibeticus* (1.95 mm, Fig. 6). The ratio of the elytra's length to width determines the beetles' overall appearance. Some species are elongated and oval: *M. viridis* (2.12 mm, Fig. 1), *M. ostasiaticus* (2.11 mm, Fig. 4), *M. yamalus* (2.09 mm, Fig. 7), *M. aeneolus* (2 mm, Fig. 9), *M. subparallelus* (1.97 mm, Fig. 5) and *M. dudkorum* (1.91 mm, Fig. 2). Others are rounded oval,

such as *M. tibeticus* (1.89 mm, Fig. 6), *M. oblongus* (1.89 mm, Fig. 10) and *M. aeneus* (1.84 mm, Fig. 3). *M. tibeticus* (1.89 mm, Fig. 6), *M. oblongus* (1.89 mm, Fig. 10), and *M. aeneus* (1.84 mm, Fig. 3).

The sutural side of the elytra indicates the degree of convexity of the disc. Thus, in *M. yamalus*, which is almost flat with no bend at the apex, there is dorsoventral flattening of the top, indicating slight flattening in *M. ostasiaticus* and *M. viridis*. In *M. aeneus*, *M. subparallelus*, *M. dudkorum*, *M. aeneolus* and *M. oblongus*, the sutural side curves strongly towards the apex and the apex elongates into a small tail, which compensates for the strong slope of the elytra. In *M. tibeticus*, the curvature is less pronounced, which also indicates slight flattening.

The metallic lustre of the elytra varies considerably among different species. In *M. aeneus* (Fig. 3), *M. subparallelus* (Fig. 5), *M. tibeticus* (Fig. 6), *M. oblongus* (Fig. 10) and *M. aeneolus* (Fig. 9), a bronze tint prevails with varying degrees of green or bluish background. The surface of *M. aeneus* (Fig. 3), *M. subparallelus* (Fig. 5) and *M. tibeticus* (Fig. 6) has a green tint, while *M. oblongus* (Fig. 10) and *M. aeneolus* (Fig. 9) have a bluish or greenish-bluish tint. The background of the elytra of *M. viridis* and *M. yamalus* has a greenish-bluish metallic lustre, *M. dudkorum*, *M. oblongus* and *M. aeneus* have a bluish-greenish lustre, and *M. ostasiaticus* has a greenish lustre with a slight bronze tinge.

The surface of the elytra in all *Morychus* species is covered with adpressed hairs, but their width and colour vary amongst species. In *M. viridis*, for example, the main part of the elytral disc is covered with sparse, inconspicuous, thin hairs, while the sides and apices are covered with more conspicuous, white, thin hairs. In contrast, the sympatric *M. subparallelus* is uniformly covered with strong, short, conspicuous white hairs over almost the entire upper surface. *M. aeneus* is densely covered in thin, adpressed brownish hairs and sparser, thinner white hairs, whereas *M. ostasiaticus* is sparsely covered with thin brownish and white hairs. *M. yamalus* is almost exclusively covered with rare, thin brown hairs. *M. dudkorum* has long, thin, brown hairs that are noticeable, as well as rare, thin, white hairs around the periphery of the elytra. *M. tibeticus* is densely covered with thick brown and white hairs interspersed throughout the upper surface. *M. oblongus* is evenly covered with appressed brown and white hairs that create a banded pattern. *M. aeneolus* is also densely covered with tangled brown and white pubescence similar to *M. tibeticus*, but it differs in that its hairs are shorter and straighter.

Scanning the elytra enables the shape of the individual sections to be examined, particularly the tips of the elytra and the pronotum. In *M. viridis*, the elytra are broadly oval without any noticeable narrowing at the base or apex (see Fig. 11). The end of the elytra is not elongated or notched; it is almost uniformly narrowed with an almost oval-rounded shape (see Fig. 19). The scutellar area is noticeable, but it is almost straight without a notch and slopes to one side (see Fig.

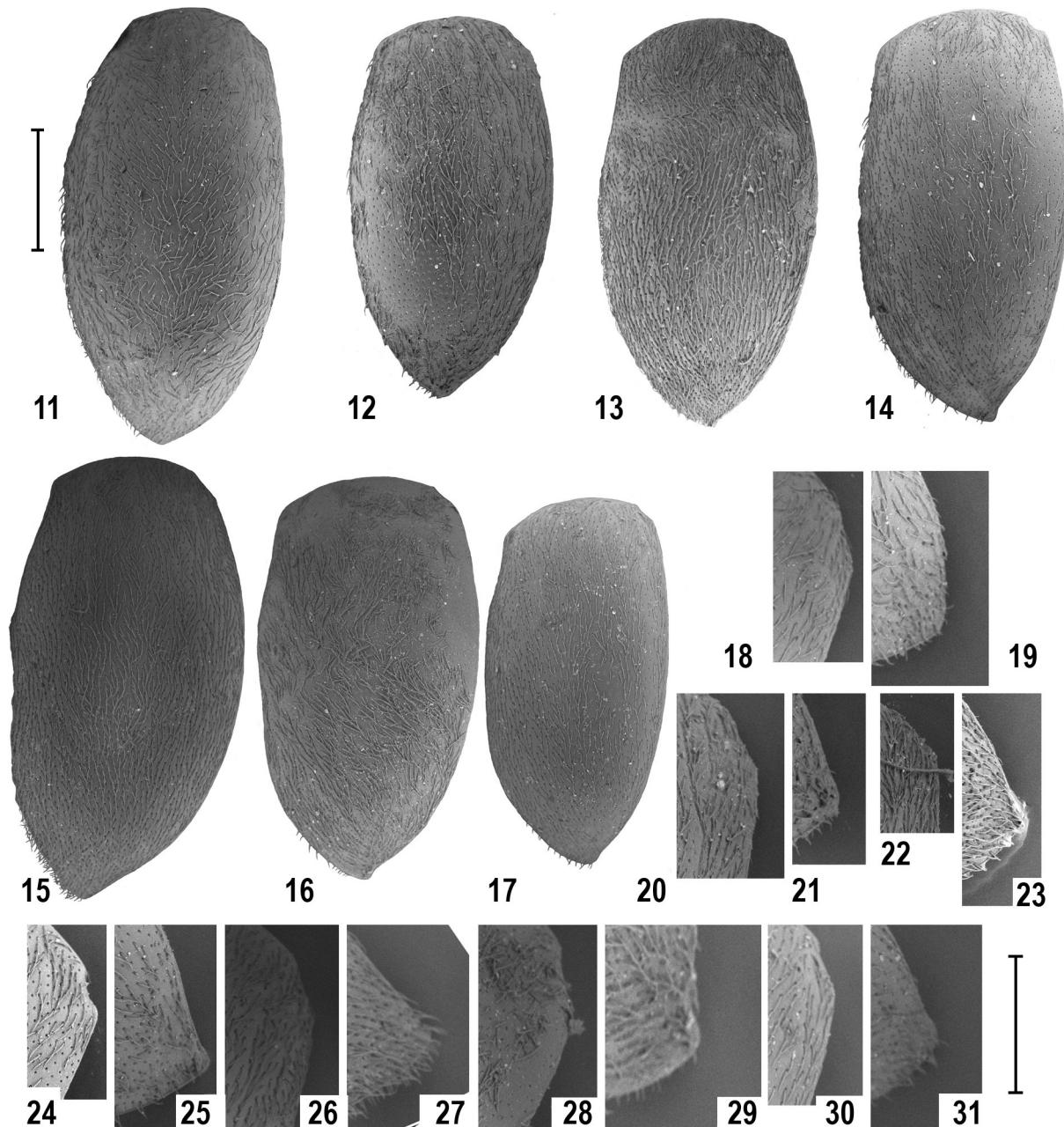


Figs 1–10. Photographs of left elytra of species of the genus *Morychus* Er. 1 — *M. viridis*; 2 — *M. dudkorum*; 3 — *M. aeneus*; 4 — *M. ostasiaticus*; 5 — *M. subparallelus*; 6 — *M. tibeticus*; 7 — *M. yamalus*; 8 — *M.* sp. fossil remains from North America; 9 — *M. aeneolus*; 10 — *M. oblongus*. Scale bar 1 mm.

Рис. 1–10. Фотографии левого надкрылья видов рода *Morychus* Er. 1 — *M. viridis*; 2 — *M. dudkorum*; 3 — *M. aeneus*; 4 — *M. ostasiaticus*; 5 — *M. subparallelus*; 6 — *M. tibeticus*; 7 — *M. yamalus*; 8 — ископаемые останки *M.* sp. из Северной Америки; 9 — *M. aeneolus*; 10 — *M. oblongus*. Масштаб: 1 мм.

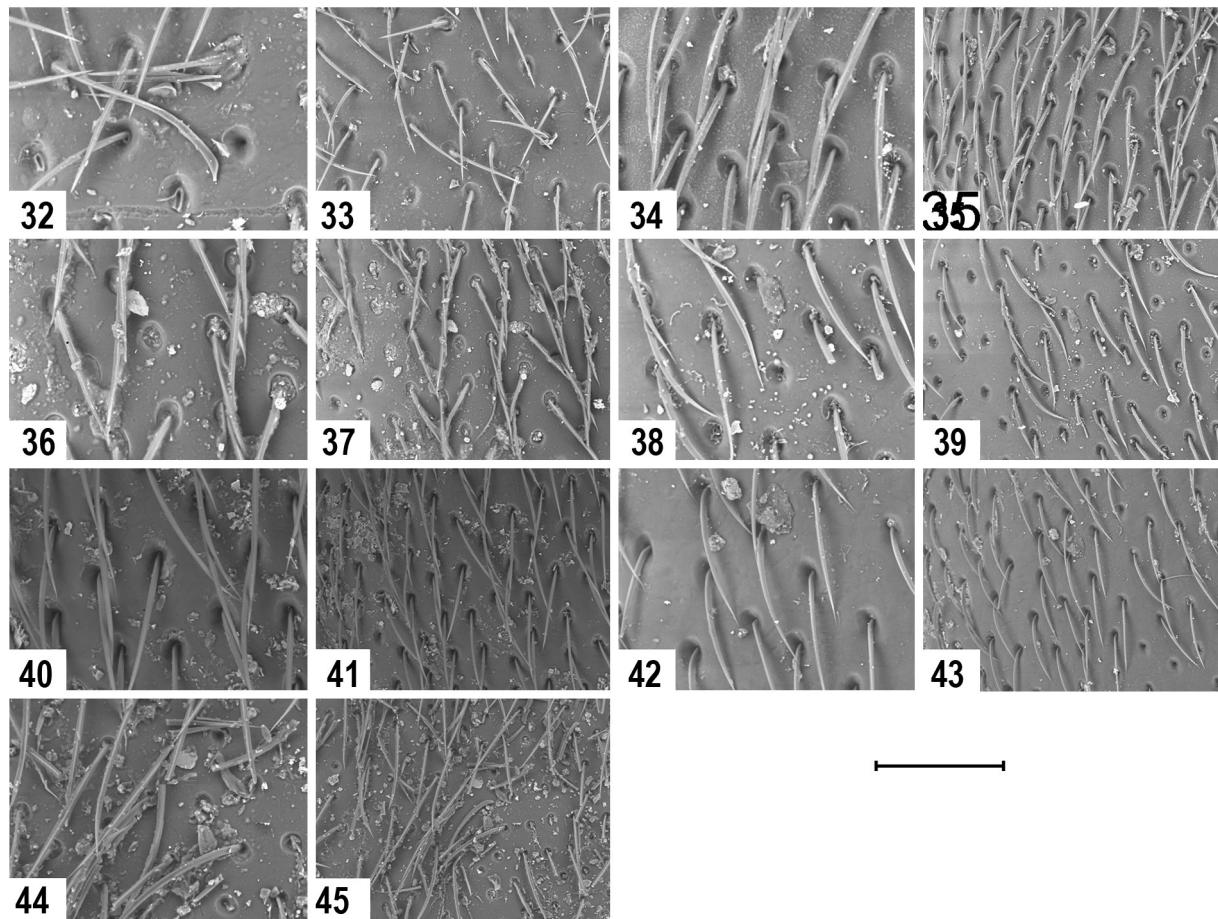
18). By contrast, the elytra of the commonly occurring *M. subparallelus* are narrowed at the tips and indented slightly before the end (Fig. 15), with a sharp rather than rounded tip (Fig. 27). The scutellar notch is faint, straight and slightly slanted (Fig. 26). In general, the elytra of *M. subparallelus* are noticeably more «swollen» in the half closest to the suture, indicating a more convex shape of the beetle. *M. dudkorum*, which is found in the Altai highlands, has a similar shape to these two

species. Its smaller size and less convexity compared to *M. subparallelus* (see Fig. 14) and the presence of a small depression in front of the apex (see Fig. 25) place this species in a transitional position between the aforementioned two species. The closely related species *M. aeneus* and *M. ostasiaticus* can be distinguished by the indentation of the scutellum in *M. ostasiaticus* (Fig. 24), which is noticeable and extends the end into a sharp tail, and by the strong indentation at the elytral



Figs 11–31. Morphology of scanned left elytra of species of the genus *Morychus* Er.: general shape (11–17), scutellar incisure (18, 20, 22, 24, 26, 28, 30) and elytral apex (19, 21, 23, 25, 27, 29, 31). 11, 18, 19 — *M. viridis*; 12, 20, 21 — *M. dudkorum*; 13, 22, 23 — *M. aeneus*; 14, 24, 25 — *M. ostasiaticus*; 15, 26, 27 — *M. subparallelus*; 16, 28, 29 — *M. tibeticus*; 17, 30, 31 — *M. yamalus*. Magnifications 1–17 — $\times 60$, 18–31 — $\times 80$. Scale bars 1 mm.

Рис. 11–31. Морфология сканированных левых надкрылий видов рода *Morychus* Er.: общая форма (11–17), прищипковая выемка (18, 20, 22, 24, 26, 28, 30) и вершина надкрылий (19, 21, 23, 25, 27, 29, 31). 11, 18, 19 — *M. viridis*; 12, 20, 21 — *M. dudkorum*; 13, 22, 23 — *M. aeneus*; 14, 24, 25 — *M. ostasiaticus*; 15, 26, 27 — *M. subparallelus*; 16, 28, 29 — *M. tibeticus*; 17, 30, 31 — *M. yamalus*. Увеличение: 1–17 — $\times 60$, 18–31 — $\times 80$. Масштаб: 1 мм.



Figs 32–45. Ultra-thin surface structure of scanned left elytra of species of the genus *Morychus* Er.: 32, 33 — *M. viridis*; 34, 35 — *M. aeneus*; 36, 37 — *M. dudkorum*; 38, 39 — *M. ostasiaticus*; 40, 41 — *M. subparallelus*; 42, 43 — *M. yamalus*; 44, 45 — *M. tibeticus*. Magnifications 33, 35, 37, 39, 41, 43, 45 — $\times 400$, 32, 34, 36, 38, 40, 42, 44 — $\times 800$. Scale bar 33, 35, 37, 39, 41, 43, 45 — 0.2 mm, 33, 35, 37, 39, 41, 43, 45 — 0.1 mm.

Рис. 32–45. Ультратонкая структура поверхности сканированных левых надкрыльев видов рода *Morychus* Er.: 32, 33 — *M. viridis*; 34, 35 — *M. aeneus*; 36, 37 — *M. dudkorum*; 38, 39 — *M. ostasiaticus*; 40, 41 — *M. subparallelus*; 42, 43 — *M. yamalus*; 44, 45 — *M. tibeticus*. Увеличение: 33, 35, 37, 39, 41, 43, 45 — $\times 400$, 32, 34, 36, 38, 40, 42, 44 — $\times 800$. Масштаб: 33, 35, 37, 39, 41, 43, 45 — 0,2 мм, 33, 35, 37, 39, 41, 43, 45 — 0,1 мм.

apex (Fig. 25). In *M. aeneus*, the scutellar area is almost horizontal and without indentation (Fig. 22), and the elytral apex is triangular and not extended (Fig. 23). As can be seen in Fig. 13, *M. aeneus* is convex at the suture, while *M. ostasiaticus* is more or less flattened (Fig. 14). In addition to its size, the small species *M. yamalus* is notable for a small indentation in front of the apex, giving this part of the elytra the appearance of a slight 'tail' (Fig. 31). It also has a noticeable narrowing at the base, making the beetle appear more rounded in the middle than other closely related species (Fig. 17). The scutellar notch is short and clearly defined (see Fig. 30). In *M. tibeticus*, which inhabits areas far from North Asia, the notch is weakly defined and rounded (Fig. 28). This species has a well-defined notch in front of the apex of the elytra (Fig. 29), as well as a flattened and elongated outer angle of the elytral bases due to the strongly convex shoulder tubercles (Fig. 16). Of all the species found in North Asia, only *M. subparallelus* has a well-pronounced outer angle (Fig. 15), and it is also present in the European *M. aeneus* (Fig. 13).

THIN MICROSCOPY OF THE SURFACE OF THE ELYTRA

Fine microscopy at 400x and 800x magnification revealed the nature of the pubescence, the shape and frequency of the punctures, and how uniformly they were distributed. In the *M. viridis* species, the punctuation is fine and sparse, with intervals between punctures 2–2.5 times their diameter. It does not form any rows and is irregular (Fig. 33). The surface is covered with very fine, short hairs. The punctures are rounded and not elongated, with a flattened, cone-shaped rim that is deepened (Fig. 32). In *M. subparallelus*, the punctuation is noticeably more frequent (the distance between the punctures is 1.5 times their diameter), with no clear rows visible. Instead, separate areas can be seen where the punctures are arranged evenly, forming uneven rows (Fig. 41). The surface is covered with thin, longer hairs, with separate, thicker bristles visible on the sides. The punctures are slightly elongated oval, without a conical rim, deeply gaping (Fig. 40). In *M. dudkorum*, the

punctuation is more frequent (the distance between the punctures is about 1 diameter of the punctures), tangled, and does not form any rows (Fig. 37). The hairs are thin and short, as in *M. viridis*, but slightly longer bristles appear on the sides. The punctures are flat, rounded, slightly oval, completely closed, as if covered by a flat membrane that does not descend in a cone but lies on the surface (Fig. 36). In *M. aeneus*, the punctuation is very clearly expressed and frequent (the distance between the punctures is about 1 diameter, and between the peculiar rows — 1.5 diameters of the puncture), due to the difference in distances between neighbouring punctures, the arcuate ‘rows’ are clearly distinguishable (Fig. 35). The hairs are short and strong, with thickened bristles clearly visible among them. The punctures resemble those of *M. viridis*, but are slightly more oval with a rounded opening in the centre and a conical rim on the sides (see Fig. 35). In *M. ostasiaticus*, the punctures are smaller and more rounded. They are spaced further apart (approximately two to two-and-a-half puncture diameters) and, although there is no marked difference between neighbouring punctures, arc-shaped ‘rows’ of punctures are clearly visible (Fig. 39). The hairs are thin and short, with thicker bristles rarely found among them. The punctures are similar to those of *M. viridis* but are noticeably smaller in diameter (Fig. 38). The punctuation of *M. yamalus* is also well pronounced (distance 1–2 dot diameters), forming arcuate ‘rows’ (Fig. 43). The hairs are thin and short, interspersed with longer ones. The punctures are very similar in shape to those of *M. subparallelus*: slightly oval with an almost imperceptible cone and arranged more sparsely (see Fig. 42). *M. tibanicus* has a different surface sculpture on the elytra. The punctures are very small and completely intermingled. The distance between closely spaced punctures is approximately one puncture diameter and the distance between more widely spaced punctures is approximately 1.5–2 puncture diameters. The punctures do not form rows (Fig. 45). The surface is densely covered with long, thin hairs and shows no traces of thickened bristles. The punctures are so small that they are barely visible at 800x magnification. They are rounded with a faint conical inner rim that is almost flat and a thin, rounded opening in the centre that is gaping (Fig. 44).

Discussion and conclusion

Species of the genus *Morychus* Erichson inhabit landscapes with elements of tundra-steppe and characterise phytocommunities of this type. This group of Coleoptera can be used as a model or marker in the study and reconstruction of palaeolandscapes. Remains of this group are often found in Quaternary deposits of North Asia, mainly in its northern part. However, they are quite difficult to identify based on isolated fragments. Previously, all remains from the northern regions of North Asia were attributed to only one species — *M. viridis* [Berman, 1990; Muratova et al., 1993; Sher et al., 2005; Elias et al., 2006; Kuzmina, Sher, 2006;

Kirillova et al., 2016]. Later, beetle remains from other regions of North Asia were also attributed to this species [Zinov'yev, 2011].

In the north, *M. subparallelus* co-occurs with *M. viridis* [Berman, Zhigul'skaya, 1989; Tshernyshev, 1997; Kuzmina, 2025], but as one moves southwest, it is replaced by other species [Tshernyshev, 1997, 2006, 2012, 2017, 2021; Tshernyshev et al., 2013; Zinov'yev et al., 2016; Dudko et al., 2022; Gurina et al., 2019, 2023, 2024]. Distinguishing them based on their remains is difficult, as these are usually incomplete elytra or pronota. Other characteristics are used to identify species of recent fauna, such as the analysis of male reproductive organs, the shape of antennae clubs, the nature of elytral and scutellar pubescence, and leg colouration. Studying the shape and microsculpture of the elytra of different *Morychus* species should facilitate the subsequent identification of palaeofossil beetles. The punctuation on the elytra is particularly important as, in specimens from deposits, the elytra are often completely hairless. The shape and colouring of the hairs and bristles are species-specific. In their absence, characteristics such as the type and shape of the punctuation must be used for identification purposes.

When identifying *Morychus* species based on their elytra in palaeofossils, the following characteristics should be considered: the presence or absence of indentation before the apex of the elytra; the type of scutellar notch and its angle of inclination; the proneness of the external basal angle; the ratio of the width of the suture and epipleural halves of the elytra relative to an imaginary line drawn from the apex to the middle of the base; the shape and size of the punctures; and the density and uniformity of the punctures (i.e. the presence of ‘rows’ or tangles of punctures). Differences in the shape and size of the punctures and the nature and frequency of their distribution can be observed in all species and can be used in the analysis of specimens from deposits lacking pubescence. These additional morphological characteristics can be used to identify *Morychus* Er. species based on their elytra in palaeofossils.

Preliminary analysis of the available material indicates that deposits from north-eastern regions contain fragments of at least two species: *M. viridis* and *M. subparallelus* [Kuzmina, 2025]. The southern regions of North Asia, meanwhile, are dominated by the remains of *M. ostasiaticus* and *M. dudkorum*, while the deposits in northern Western Siberia contain remains of *M. yamalus*, as well as forms similar to *M. ostasiaticus* and *M. dudkorum*.

The morphology of the species *Morychus aeneolus* (LeConte, 1863) and *M. oblongus* (LeConte, 1857) is common in America and requires further study of the ultrafine surface structure, as well as a comparison of the remains found in deposits. One of the fragments found in Quaternary deposits in Canada (see Fig. 8) does not resemble any known American species (see Figs 9–10) and bears a closer resemblance to *M. yamalus* (see Fig. 7), a species not recorded in America.

Acknowledgements

I am sincerely grateful to Drs B.A. Korotyaev (Saint Petersburg), S.A. Kuzmina (Moscow) and V.I. Alekseev (Kalinin-grad) for loan of species and fossil remains, Drs R.Yu. Dudko (Novosibirsk), O.A. Khruleva (Moscow) and V.K. Zinchenko (Novosibirsk) for collection beetles in different regions of North Asia and loan them for this study, Dr. A.A. Legalov for help in research and valuable discussion. My special thanks are due to Dr. R.Yu. Dudko (Novosibirsk) for help in preparation of photomicrographs, and continuous assistance during Byrrhidae research.

This study was funded by the Federal Fundamental Scientific Research Program (grant No. 1021051703269-9-1.6.12; FWGS-2021-0004).

References

Berman D.I. 1990. The phenomenon of mass beetle genus *Morychus* from Pleistocene deposits in northeastern Asia // Current Research in the Pleistocene. Vol.7. P.101–103.

Berman D.I., Zhigulskaya Z.A. 1989. [About differences of the pill beetles *Morychus aeneus* Fabr. and *M. viridis* Kuzm. et Korot. (Coleoptera, Byrrhidae) and description of their larvae] // Entomologicheskoe Obozrenie. Vol.68. No.3. P.612–619. [In Russian].

Dudko R.Yu., Danukalova G.A., Gurina A.A., Ivanov A.V., Mikhailov Yu.E., Osipova E.M., Prosvirov A.S., Solodovnikov A.Yu., Legalov A.A., Zinov'yev E.V. 2022. Insects and molluscs of the Late Pleistocene at the Gornovosite (Southern Ural foreland, Russia): New data on palaeoenvironment reconstructions // Quaternary International. No.623. P.154–177. <https://doi.org/10.1016/j.quaint.2021.10.003>

Elias S.A., Kuzmina S., Kiselyov S. 2006. Late Tertiary origins of the Arctic beetle fauna // Palaeogeography, Palaeoclimatology, Palaeoecology. Vol.241. P.373–392. <http://dx.doi.org/10.1016/j.palaeo.2006.04.002>

Gurina A.A., Dudko R.Yu., Ivanov A.V., Kotov A.A., Mikhailov Yu.E., Prokin A.A., Prosvirov A.S., Solodovnikov A.Yu., Zinov'yev E.V., Legalov A.A. 2023. New Data on the Distribution of Southern Forests for the West Siberian Plain during the Late Pleistocene: A Paleoentomological Approach // Diversity. Vol.15. No.1. Art.56. P.1–23. <https://doi.org/10.3390/d15010056>

Gurina A.A., Dudko R.Yu., Mikhailov Yu.E., Prokin A.A., Solodovnikov A.Yu., Zinov'yev E.V., Legalov A.A. 2024. First record of insects from the oldest and older Dryas of Altai (Russia). Coleoptera assemblages from Lebed River // Palaeoentomology. Vol.007. No.1. P.112–131. <https://doi.org/10.11646/palaeoentomology.7.1.8>

Gurina A.A., Dudko R.Yu., Tshernyshev S.E., Zinov'yev E.V., Legalov A.A. 2019. Late Pleistocene insects from the Dubrovino site at Ob River (West Siberia, Russia) and their paleoenvironment significance // Palaeontologia Electronica. Art.22.1.2A. P.1–18. <https://doi.org/10.26879/914>

Kirillova I.V., van der Plicht J., Gubin S.V., Zanina O.G., Chernova O.F., Lapteva E.G., Trofimova S.S., Zinov'yev E.V., Zharov A.A., Fadeeva E.O., van Kolfschoten T., Shidlovskiy F.K., Kotov A.A. 2016. Taphonomic phenomenon of ancient hair from Glacial Beringia: perspectives for palaeoecological reconstructions // Boreas. Vol.45. No.3. P.455–469. <https://doi.org/10.1111/bor.12162>

Kuzmina S., Sher A. 2006. Some Features of the Holocene Insect Faunas of North-Eastern Siberia // Quaternary Science Reviews. Vol.25. No.15. P.1790–1820. <https://doi.org/10.1016/j.quascirev.2006.01.013>

Kuzmina S. 2025. Pleistocene steppe-tundra insect communities of Beringia // Arctic, Antarctic, and Alpine Research. Vol.57. No.1. Art.2494353. P.1–32. <https://doi.org/10.1080/15230430.2025.2494353>

Muratova M.M., Serebryanny L.R., Denissenko O.V., Kiselev S.V. 1993. Climate and Vegetation changes in the Northern Eurasia during the Younger Dryas // Geographica Helvetica. No.3. P.111–119.

Sher A.V., Kuzmina S.A., Kuznetsova T.V., Sulerzhitsky L.D. 2005. New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals // Quaternary Science Reviews. Vol.24. P.533–569. <https://doi.org/10.1016/j.quascirev.2004.09.007>

Tshernyshev S. 1997. Towards the Knowledge of the Genus *Morychus* Er. (Coleoptera, Byrrhidae) in Russia // Entomologica basiliensis. Vol.20. P.115–132.

Tshernyshev S.E. 2000. Two new species of pill beetles (Coleoptera: Byrrhidae) from Tibet // Russian Entomological Journal. Vol.9. No.2. P.133–137.

Tshernyshev S.E. 2006. [A review of pill beetles (Coleoptera, Byrrhidae) of the fauna of Russia and the adjacent territories. Taxonomic composition] // [Proceedings of the Russian Entomological Society] (Trudy Russkogo Entomologicheskogo Obshchestva). Vol.77. P.287–293. [In Russian].

Tshernyshev S.E. 2012. [A review of pill beetle fauna (Coleoptera, Byrrhidae) of North Asia] // Euroasian Entomological Journal. Vol.11. No.5. C.437–447. [In Russian].

Tshernyshev S.E., Tsepelev K.A., Dudko R.Yu., Zinov'yev E.V., Legalov A.A. 2013. Pill beetles (Coleoptera, Byrrhidae) in Late Neo-Pleistocene and Pleistocene deposits in the south of the West Siberia // Euroasian Entomological Journal. Vol.12. No.2. C.109–119. [In Russian].

Tshernyshev S.E. 2017. Pill beetles (Coleoptera, Byrrhidae) in paleontological studies of North Asia // XV Congress of the Russian Entomological Society. Russia, Novosibirsk, July 31 – August 7, 2017. P.530–531. [In Russian].

Tshernyshev S.E. 2021. *Morychus* (Coleoptera, Byrrhidae) in the Himalayas, North Asia, Europe and North America: a phenomenon of distribution or a misunderstanding? Cenozoic faunogenesis as evidence of an independent distribution and evolution of *Morychus* Erichson and *Byrrhobolus* Fiori // Biodiversität und Naturausstattung im Himalaya. Bd.7. P.445–456.

Tshernyshev S.E., Pütz A. 1999. New data on the fauna of pill beetles (Coleoptera, Byrrhidae) of Russia // Russian Entomological Journal. Vol.8. No.1. P.15–22.

Zinov'yev E. 2011. Sub-fossil beetle assemblages associated with the «mammoth fauna» in the Late Pleistocene localities of the Ural Mountains and West Siberia // Kotze D.J., Assmann T., Noordijk J., Turin H., Vermeulen R. (eds): Carabid Beetles as Bioindicators: Biogeographical, Ecological and Environmental Studies. ZooKeys. Vol.100. P.149–169. <https://doi.org/10.3897/zookeys.100.1524>

Zinov'yev E.V., Dudko R.Yu., Gurina A.A., Prokin A.A., Mikhailov Yu.E., Tsepelev K.A., Tshernyshev S.E., Kireev M.S., Kostyunin A.E., Legalov A.A. 2016. First records of sub-fossil insects from Quaternary deposits in the southeastern part of Western Siberia, Russia // Quaternary International. Vol.20. P.221–232. <http://dx.doi.org/10.1016/j.quaint.2015.09.023>

Поступила в редакцию 28.11.2025