ISSN 0031-0301, Paleontological Journal, 2010, Vol. 44, No. 4, pp. 468–474. © Pleiades Publishing, Ltd., 2010
Original Russian Text © S.V. Naugolnykh, A.G. Ponomarenko, 2010, published in Paleontologicheskii Zhurnal, 2010, No. 4, pp. 105–110.

Possible Traces of Feeding by Beetles in Coniferophyte Wood from the Kazanian of the Kama River Basin

S. V. Naugolnykh[a] and A. G. Ponomarenko[b]

[a]*Geological Institute, Russian Academy of Sciences, Pyzhevsky per. 7, Moscow, 109017, Russia*
e-mail: naugolnykh@rambler.ru
[b]*Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia*
e-mail: aponom@paleo.ru

Received September 7, 2009

Abstract—Possible traces of feeding by wood-boring beetle larvae (Coleoptera, ?Permocupedidae) are described from the Middle Permian locality Tikhie Gory (Tatarstan, right bank of the Kama River, Kazanian Stage). The traces in the form of perpendicular tunnels and shafts were left in picnoxylic wood of some coniferophytes s.l. (the orders Pinales, Cordaitales, or Vojnovskyales).

Key words: wood, beetle, Coleoptera, coniferophyte, Permian, paleoecology, trace-fossils.

DOI: 10.1134/S0031030110040131

INTRODUCTION

Elucidation of interactions between components of terrestrial ecosystems is one of the prime goals of various paleoecological studies, from classification of diverse trace fossils to quantification of components of the biogeochemical cycle. Of particular importance is documentation of such cases of interaction between producers, consumers, and decomposers where information on both the taxonomy of the participating organisms and the exact nature of their interactions (trophic or non-trophic) is preserved. This task is highly demanding because it requires that the fossil material is both well preserved and well documented geologically and stratigraphically.

In this paper we describe feeding traces of beetle larvae in the form of tunnels and shafts with xenoglyphs (for terminology, see Mikuláš and Dronov, 2006) and the mineralized wood containing these traces.

MATERIAL AND METHODS

The specimen described in this paper comes from the locality Tikhie Gory (Fig. 1), which is situated on the right bank of the Kama River 2 km downstream of the town of Mendeleevsk, Tatarstan and is well known among paleontologists and stratigraphers. The deposits exposed there belong to the Sheshma Horizon of the Ufimian Stage (on the status of the Sheshma Horizon and its type sections, see Netschajew, 1915 and Naugolnykh, 2004) and the Baitugan beds of the Lower Kazanian Substage of the Kazanian Stage. Sandstones and slabby siltstones and mudstones of the Baitugan beds contain occasional plant macrofossils and a rich fauna of fossil insects. The specimen described here, GIN no. 4856/242, comes from the same layer.

This is a 73 × 30 × 15 mm fragment of mineralized wood (Pl. 13, figs. 1–3). The wood is replaced by amorphous silica, preserving the structure of the conductive tissue. For study under a CamScan scanning electron microscope small (5 × 3 × 1 mm) fragments were fixed to specimen stages with acrylic glue.

Structure of Wood

Due to the good preservation of the specimen we were able to characterize some of its microanatomical details (Fig. 2, Pl. 13, figs. 4–6, Pl. 14, figs. 1–7). Because one side of the fragment contains peridermal (i.e., bark) layers, the fragment as a whole represents an outer portion of a tree trunk and comprises secondary xylem and wood rays composed of parenchyma.

The secondary xylem is composed of tracheids with distinct araucarioid pitting. The average tracheid diameter is 25–30 μm. The tracheid pits (outside the ray crossfields) are bordered, regularly circular (Pl. 14, figs. 3, 6) or, more rarely, oval; in the latter case, the major axis of the pit can be oriented along (Pl. 14, fig. 4) or perpendicular (Pl. 13, figs. 5, 6) to the tracheid. The average diameter of the pit including the border is 8–11 μm. The apertures of pits are visible in only a few areas (Pl. 13, fig. 5, on the right; Pl. 14, fig. 4); their diameter is 4–5 μm. The pits are closely set, but their borders are usually not contacting each other. The pits are arranged into one (Pl. 13, figs. 5, 6; Pl. 14, figs. 1, 2) or, more rarely, two (Pl. 14, fig. 4)

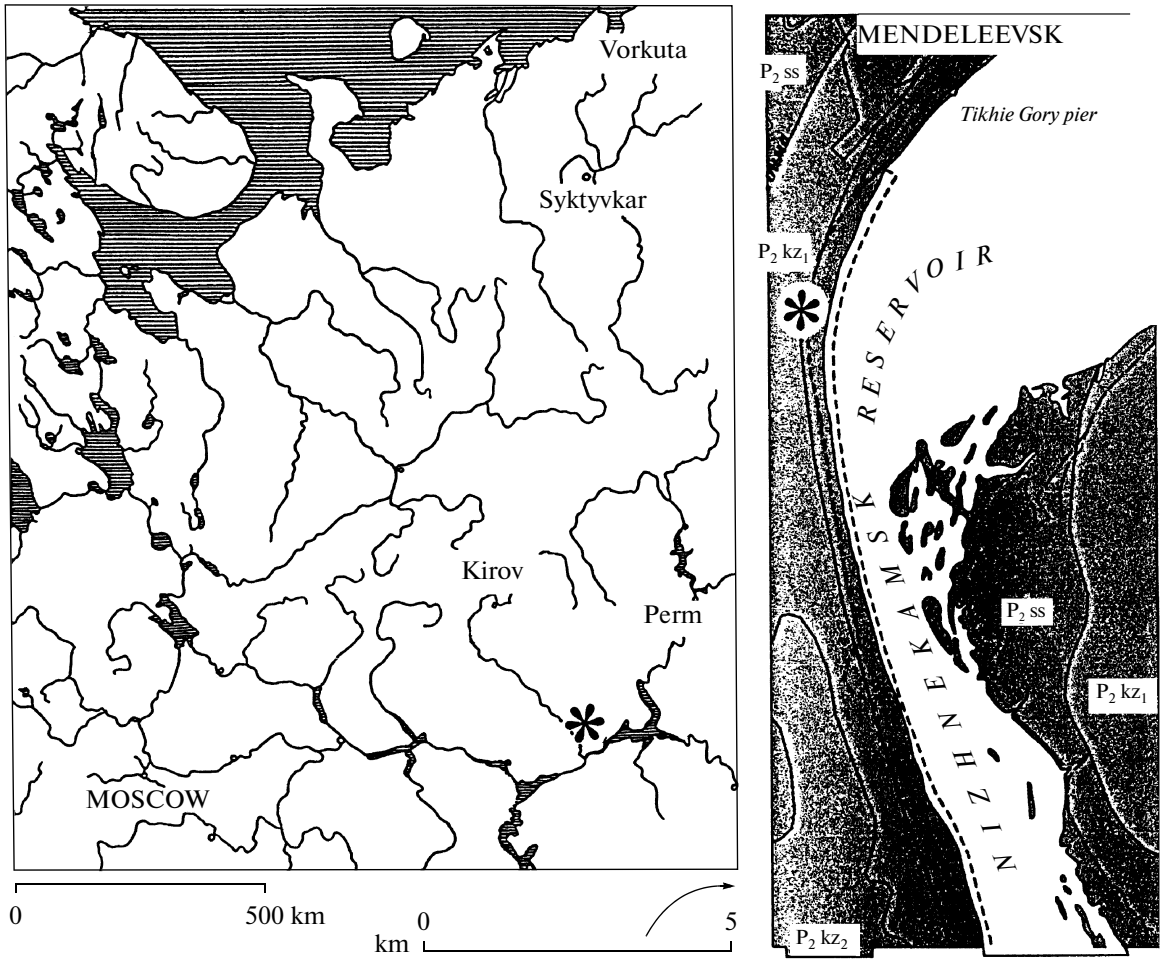


Fig. 1. The geographic location (left) and the geological map (right) of Tikhie Gory (asterisked). The geological map is from Silantiev et al., 2007.

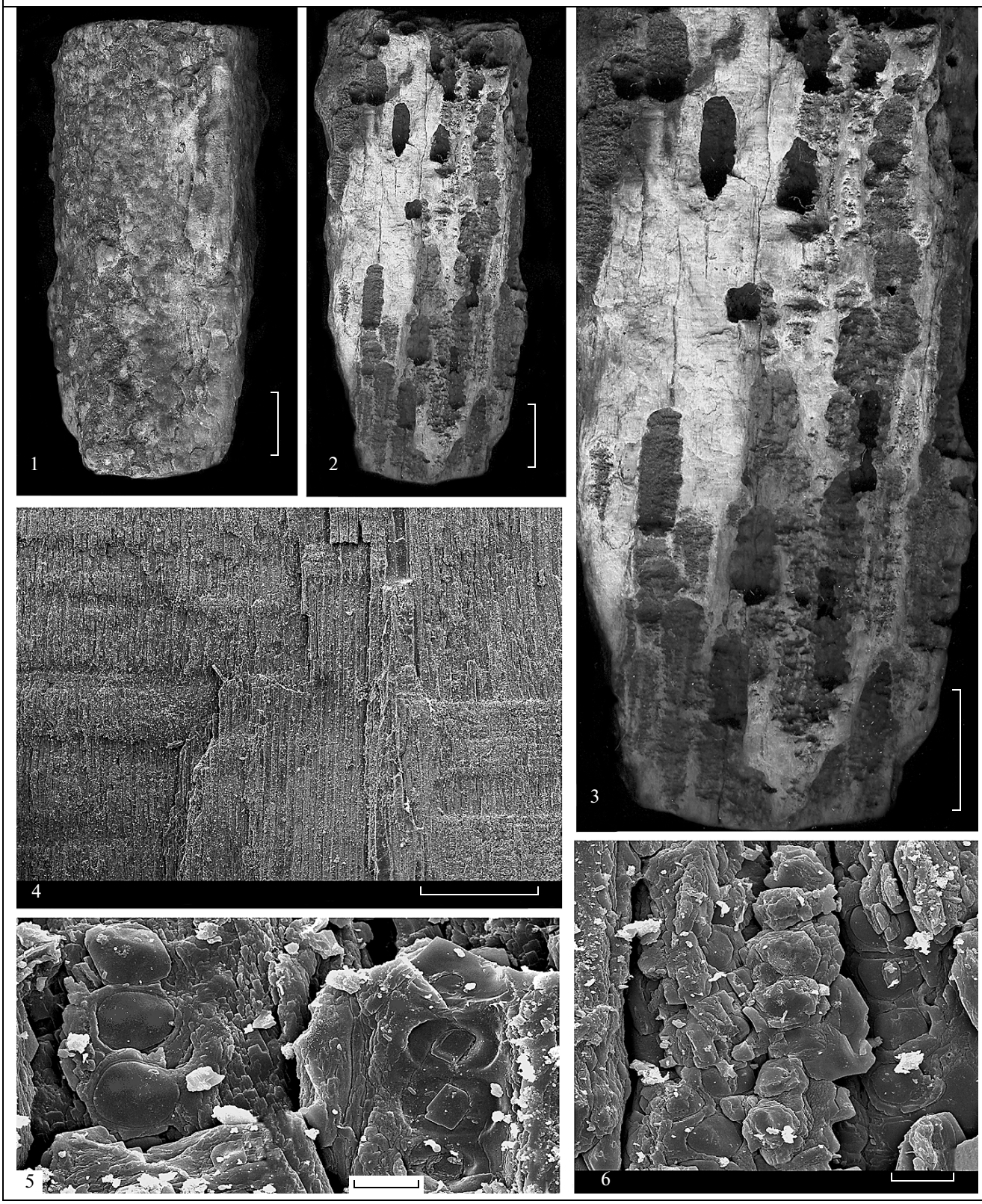
rows; tracheids with such alternative types of pitting can be observed within the same area, close to each other (Pl. 14, fig. 6). On expanded segments of tracheids the uniseriate pitting can become curved (Pl. 14, fig. 3) and transformed into the biseriate one. Pits in the crossfields are usually four in number, arranged one pair above another; sometimes their mutual arrangement is not perfectly symmetrical. The apertures of crossfield pits are slitlike, oblique, 6–7 μm long and 1.5–2.0 μm wide (Pl. 14, figs. 5, 7). No crassulae are present on the tracheids. The wood rays are rather numerous (Pl. 13, fig. 4). All the observed wood rays are uniseriate and homocellular, comprising 2–11 vertical rows (layers) of cells. The cell walls of the tracheids are much thicker than those of the rays.

The structure of pits in the wood specimen from Tikhie Gory is similar to that in the fossil wood from cupriferous sandstones of the Cis-Urals, tentatively identified as *Dadoxylon* sp. (Naugolnykh, 2002: pl. 9, fig. 3 and pl. 10, figs. 2, 6). Wood of a very similar anatomical structure occurs in the Sheshma deposits of the Kama Regions (the Yug Formation and its analogs, see Naugolnykh, 2004). Fossil wood of this type, traditionally classified in the genus *Dadoxylon* Endlicher and allied with coniferophytes, is rather common in the Upper Carboniferous and Lower Permian of western and central Europe (for example, see Reymanowna, 1962), but also occurs in the Permian of the Russian Platform and Cis-Urals (Zalessky, 1927; Naugolnykh, 2007).

Unlike the wood from Tikhie Gory, the older European and the coeval North American woods (Wilson, 1963) possess as a rule wider tracheids with mostly biseriate (and occasionally triseriate) pitting.

Superficially similar fragments of mineralized wood have been illustrated and briefly characterized from the Blaine formation (Pease River Group), dated by the Kungurian or Ufimian (DiMichele et al., 2004). Yet, unlike in our specimen from Tikhie Gory, tracheid pits in the wood from the Blaine Formation are diagonally asymmetrical, elliptical. Similar wood with diagonally asymmetrical pits has also been illustrated from cupriferous sandstones of the Cis-Urals (Naugolnykh, 2002: pl. 10, figs. 1, 3).

Plate 13



Explanation of Plate 13

Figs. 1–3. Macromorphology of the fragment of mineralized wood, GIN no. 4856/242, from Tikhie Gory, Kazanian Stage, Lower Kazanian Substage, Baitugan beds. Scale bar 1 cm.

Figs. 4–6. Microstructure of the fragment of mineralized wood: (4) general view, the wood rays are visible; scale bar, 500 μm; (5, 6) structure of the tracheids; scale bar 10 μm.

The mineralized wood, apparently of a coniferophyte, described from the Lower Permian of Morocco and identified as *Scleromedulloxylon* cf. *aveyronense* Doubinger et Marguerier (Aassoumi et al., 1995) is similar to the specimen from Tikhie Gory in several aspects, such as the presence of wood rays comprising 2–19 vertical layers of cells in the same area of the specimen and both uniseriate and biseriate pitting occurring in neighboring tracheids. These woods share numerous characteristics with woods of the formal genus *Walchiopremnon* Florin, found associated with leaf-bearing branches of walchian conifers (Florin, 1940).

The anatomical characteristics of the wood specimen examined and its comparison with the most similar mineralized fossil woods of the Permian age given above clearly indicate that it belonged to a conifer (the order Pinales or Coniferales s.s.) or a closely related taxon (for example, Cordaitales or Vojnovskyales; due to its unique morphology the latter order may actually deserve elevation to the rank of a class, see Naugolnykh, 2008). These plants are often treated together as the informal group of coniferophytes or Coniferae s.l.

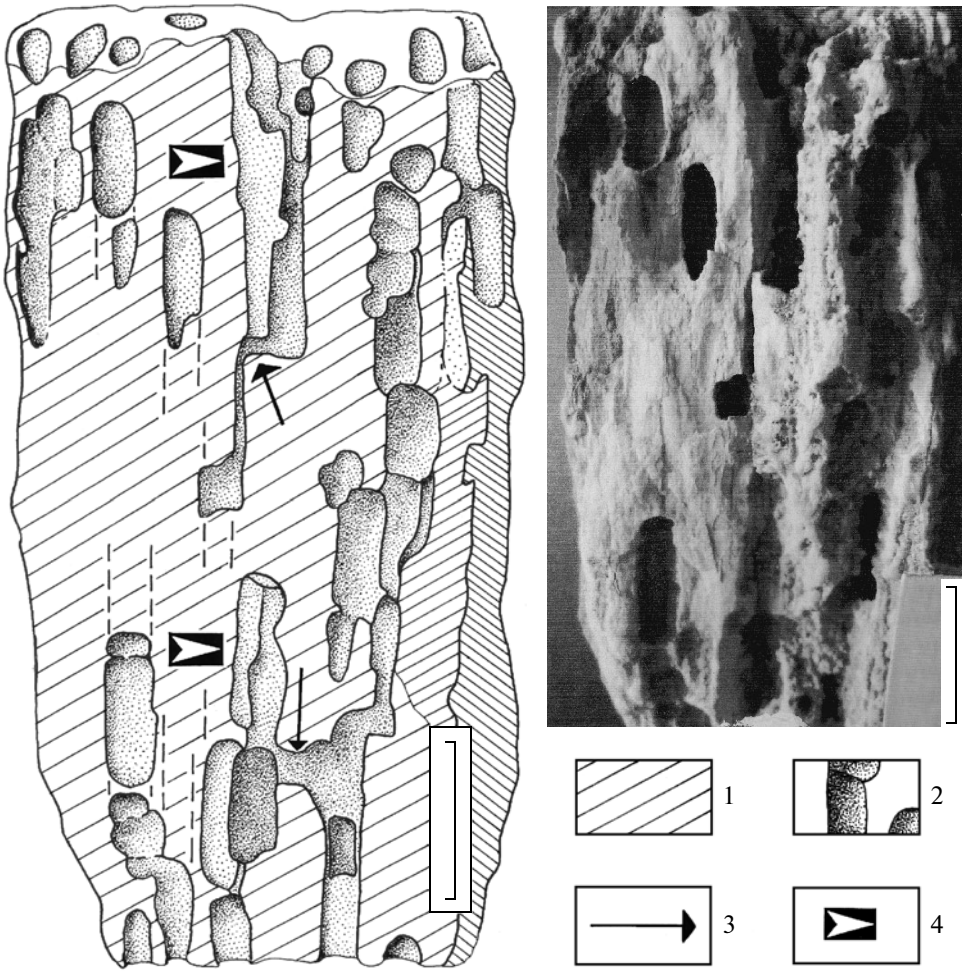
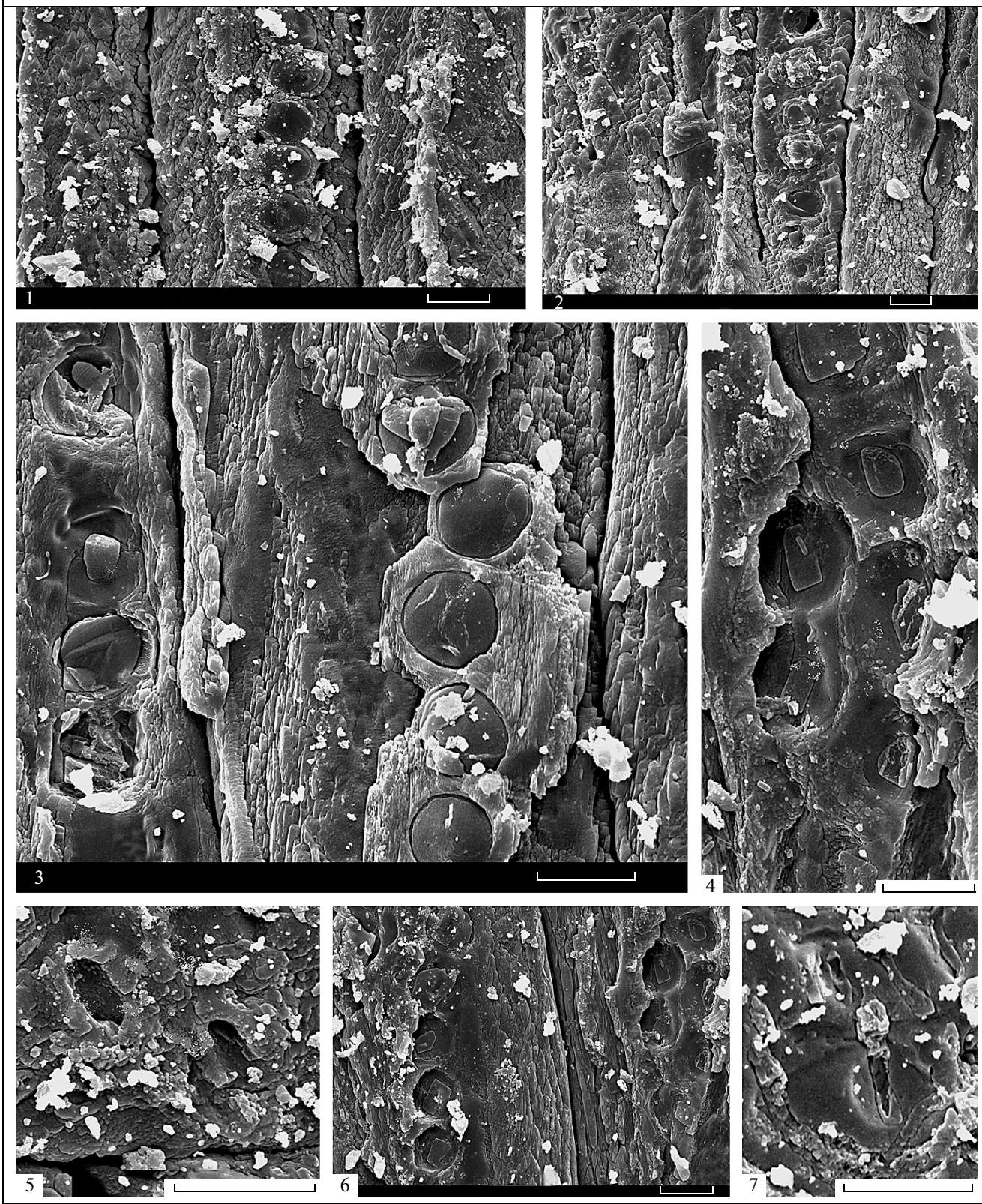


Fig. 2. A drawing showing relative positions of the tunnels and shafts (left) and a photograph of the examined wood fragment, GIN no. 4856/242, taken in oblique light (right). Key: (1) longitudinal section of the fragment, (2) cavities within the wood, (3) tunnels, (4) shafts. Scale bar 1 cm.

Plate 14



Explanation of Plate 14

Figs. 1–7. Microstructure of the fragment of mineralized wood, GIN no. 4856/242, from Tikhie Gory, Kazanian Stage, Lower Kazanian Substage, Baitugan beds. Scale bar 10 μm. See text for details.

("cone-bearing"), which is widely used in modern botany and palaeobotany despite its unofficial status (Aassoumi et al., 1995; Rothwell et al., 1997; Bobrov et al., 2001; Singh et al., 2003).

It remains not fully clear into which formal genus the wood specimen from Tikhie Gory has to be placed. Classification of isolated mineralized woods from the Paleozoic and Mesozoic has traditionally been very difficult (see, for example, Kräusel, 1932; Lepekhina, 1972; Philippe and Bamford, 2008) because many genera that have the priority status had been established with violations of the rules of nomenclature and because the fossil material is by definition incomplete, i.e., all the characters necessary for precise identification can only rarely be observed in one specimen. Therefore, to avoid nomenclatural difficulties, we refrain from placing this specimen into any formal (morphological) genus.

Structure of Feeding Traces

The feeding traces preserved in the examined specimen form a system of tunnels and shafts oriented perpendicularly to each other and ornamented with xenoglyphs inheriting their texture from wood fibers. Because it is impossible to determine the orientation of the wood at the time when it was being eaten by the beetles we use the terms "tunnel" and "shaft" provisionally. The more numerous shafts are oriented along the wood fibers, their diameter is 2.8 mm. The shafts are interconnected by short bridges, referred to as tunnels, of the same shape and diameter. The maximum length of the shafts observed in this specimen equals the length of the specimen itself, 73 mm. Apparently, the actual shafts were longer. The length of the tunnels does not exceed 5 mm.

DISCUSSION

Records of traces of insect feeding, including that by beetles, in fossil wood are extremely rare (Labandeira, 2002). Because only a single such instance has been reported so far from the Permian, the traces found in fossil woods from Antarctica (Weaver et al., 1997), the new record is of considerable interest. Similar records from the Mesozoic are also few. The feeding traces in the Mesozoic woods are traditionally attributed to beetles from the family Cupedidae, the most common and widespread family of the Mesozoic wood-inhabiting beetles. Cupedids are known from the Anisian and are still surviving as relicts in the Recent fauna. During the Mid-Permian the larvae of two beetle families could possibly feed inside wood and leave traces of the size we observed: Permocupedidae and Tshekardocoleidae. The latter family is mostly Early Permian, with only a single record from the Kazanian (Ponomarenko, 2000). Therefore, the traces most likely belonged to larvae of Permocupedidae, a family very closely related and apparently ancestral to Cupedidae. Permocupedidae are represented in the Baitugan beds by relatively numerous (given the overall extreme scarcity of beetle records from that time) beetles from the genus *Permocupes* (see Fig. 3 for a reconstruction). Inevitably, it cannot be completely ruled out that the tunnels and shafts have been made not by beetle larvae but by some other wood-boring organisms.

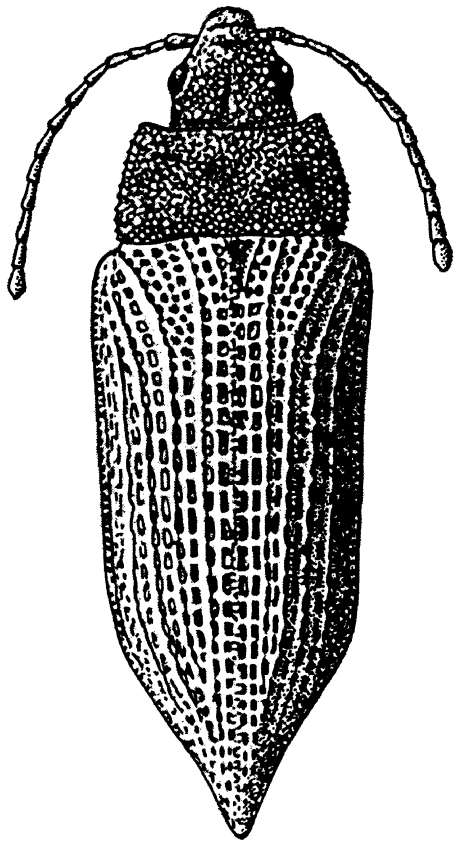


Fig. 3. A reconstruction of a beetle from the genus *Permocupes* (according to Ponomarenko, 2003). Size 5 mm.

ACKNOWLEDGMENTS

The study was supported by the Program of the Presidium of the Russian Academy of Sciences, subprogram 15, "Evolution of the Biosphere," and the Russian Federal Program of Support of Leading Scientific Schools (grant no. NSh-4185.2008.5).

REFERENCES

1. H. Aassoumi, J. Broutin, N. Youbi, et al., "Découverte de *Scleromedulloxylon* cf. *aveyronense*, bois fossile de coniférophyte, dans le complexe volcanique permien du bassin de Khnifra (Maroc): intérêt stratigraphique et floristique," Ann. Paléontol. **81** (1), 1–16 (1995).
2. A. V. Bobrov, M. S. Romanov, and A. N. Sorokin, "Position of the Family Feruglіocladaceae in the Phylogenetic System of Coniferae s.l.," in *Paleobotany at*

the Turn of the Century: Results and Prospects: Abstracts of IV Lectures in Commemoration of A.N. Kryshtofovich (Bot. Inst. Ross. Akad. Nauk, St. Petersburg, 2001), pp. 10–12 [in Russian].

3. W. A. DiMichele, R. W. Hook, W. J. Nelson, and D. S. Chaney, "An Unusual Middle Permian Flora from the Blaine Formation (Pease River Group: Leonardian–Guadalupian Series) of King County, West Texas," J. Paleontol. **78** (4), 765–782 (2004).
4. R. Florin, "Die Koniferen des Oberkarbons und des Unteren Perms," Palaeontogr. B **85** (5), 244–363 (1940).
5. R. Kräusel, "Relation of *Pinoxylon dakotense* Knowlton to *Protopiceoxylon* Gothan," Bot. Gazette **94** (2), 419–420 (1932).
6. C. C. Labandeira, "The History of Associations between Plants and Animals," in *Plant–Animal Interactions: An Evolutionary Approach*, Ed. by C. M. Herrera and O. Pellmyr (Blackwall Sci., London, 2002), pp. 26–74.
7. V. G. Lepekhina, "Woods of Palaeozoic Pycnoxylic Gymnosperms with Special Reference to North Eurasia Representatives," Palaeontogr. B **138** (1–4), 44–106 (1972).
8. R. Mikuláš and A. Dronov, *Palaeoichnology—Introduction to the Study of Trace Fossils* (Inst. Geol. Acad. Sci. Czech Republic, Prague, 2006).
9. S. V. Naugolnykh, "Fossil Flora of Cupriferous Sandstones (Upper Permian of the Cis-Urals)," VM-Novitates, Novosti Geol. Muz. im. V.I. Vernadskogo, No. 8, 48 (2002).
10. S. V. Naugolnykh, "Yugovskaya Flora (Ufimian Stage, Upper Permian) Cis-Urals," in *Problems of Regional Geology: Museum Perspective*, Ed. by G. V. Kalabin, Z. A. Bessudnova, M. N. Kandinov, and I. A. Starodubtseva (Akropol', Moscow, 2004), pp. 168–172 [in Russian].
11. S. V. Naugolnykh, *Permian Flora of the Urals: Proceedings of the Geological Institute of the Russian Academy of Sciences, Vol. 524* (Geos, Moscow, 2007) [in Russian].
12. S. V. Naugolnykh, "The Great Break in History of the Plant World," Mineralogical Almanac **13c**, 36–50 (2008).
13. A. V. Netschajew, "Kazanian and Ufimian Stages of the Permian System," Geol. Vestn. **1** (1), 4–6 (1915).
14. M. Philippe and M. K. Bamford, "A Key to Morphogenera Used for Mesozoic Conifer-Like Woods," Rev. Palaeobot. Palynol. **148** (2–4), 184–207 (2008).
15. A. G. Ponomarenko, "New Beetles from the Permian of European Russia," Paleontol. J. **34** (Suppl. 3), S312–S316 (2000).
16. A. G. Ponomarenko, "Ecological Evolution of Beetles (Insecta: Coleoptera)," Acta Zool. Cracov. **46** (Suppl. Fossil Insects), 319–328 (2003).
17. M. Reymanowna, "On *Dadoxylon schrollianum* with Pith and Other Dadoxyla from the Upper Carboniferous in South Poland," Acta Palaeobot. **3** (1), 3–20 (1962).
18. G. W. Rothwell, G. Mapes, and R. H. Mapes, "Late Paleozoic Conifers of North America: Structure, Diversity, and Occurrences," Rev. Palaeobot. Palynol. **95** (1–4), 95–113 (1997).
19. V. V. Silantiev, Yu. P. Balabanov, G. A. Galushin, et al., *Geological Natural Monuments of the Republic of Tatarstan* (Akvarel'-Art, Kazan, 2007) [in Russian].
20. K. J. Singh, G. W. Rothwell, G. Mapes, and S. Chandra, "Reinvestigation of the Coniferophyte Morphospecies *Buriadia heterophylla* Seward and Sahni, with Reinterpretation of Vegetative Diversity and Putative Seed Attachments," Rev. Palaeobot. Palynol. **127** (1–2), 25–43 (2003).
21. L. Weaver, S. McLoughlin, and A. N. Drinnan, "Fossil Woods from the Upper Permian Bainmedart Coal Measures, Northern Prince Charles Mountains, East Antarctica," AGSO J. Austral. Geol. Geophys. **16**, 655–676 (1997).
22. L. R. Wilson, "A New Species of *Dadoxylon* from the Seminole Formation (Pennsylvanian) of Oklahoma," Oklahoma Geol. Notes **23**, 215–220 (1963).
23. M. D. Zalessky, "Flore permienne des limites ouraliennes de l'Angaride. Atlas," Mém. Comité Géol., Nouv. Sér. **176**, 5–52 (1927).