

Columnar Galls on *Platimeliphyllum snatolense* N. Maslova (Angiospermae) Leaves from the Upper Paleocene of Western Kamchatka Peninsula

D. V. Vasilenko and N. P. Maslova

Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia

e-mail: vasilenko@paleo.ru

Received December 24, 2014

Abstract—A type of damage to fossil *Platimeliphyllum snatolense* N. Maslova leaves, fusiform galls attached to the lower surface of leaves, is described. This type of damage is new to the Late Paleocene plant communities. Classification and interpretation of columnar galls are discussed.

Keywords: insect galls, new species, *Antronoides*, *Platimeliphyllum*, Paleocene, Kamchatka

DOI: 10.1134/S0031030115050147

INTRODUCTION

The genus *Platimeliphyllum* N. Maslova (Maslova, 2002) was established for entire leaves with craspedodromous venation (occasionally camptodromous in the lower part of the lamina), variously developed basal veins, and dentate margin. Five species of the genus are known to date from the Paleocene and Eocene of Russia (Western Kamchatka Peninsula and Amur Region) and Kazakhstan. In addition, leaves from the Eocene of the Northeast and South China (Manchester et al., 2005; Kodrul et al., 2012) and North America (Krassilov et al., 2009) have also been assigned to the genus *Platimeliphyllum*.

Leaves of the genus *Platimeliphyllum* are distinguished by a peculiar combination of morphological characters found in both Platanaceae and Hamamelidaceae. Epidermal characters known for the species *P. palanense* N. Maslova (Maslova, 2002), *P. valentinii* Kodrul et N. Maslova (Kodrul, Maslova, 2007), and *P. reznikoviorum* N. Maslova (Maslova et al., 2014), are typical for Platanaceae.

As shown by studies, the leaves of *Platimeliphyllum* are associated with reproductive structures principally different from those of the recent *Platanus* L. For instance, *P. palanense* and *P. snatolense* N. Maslova have been found together with staminate inflorescences *Chemurnautia* N. Maslova (family Platanaceae; Maslova, 2002); *P. valentinii* was found together with two genera of staminate inflorescences (*Archaranthus* N. Maslova et Kodrul, family *Bogutchanthaceae*; Maslova and Kodrul, 2003, and *Bogutchanthus* N. Maslova, Kodrul et Tekleva, family *Bogutchanthaceae*; Maslova et al., 2007). Leaves of *P. reznikoviorum* are associated with capitate infructescences that combine

characters of the families Platanaceae and Hamamelidaceae (Maslova et al., 2014).

MATERIAL AND METHODS

The fossil material described here was collected by L.I. Fotyanova (Borissiak Paleontological Institute, Russian Academy of Sciences) and given for study to N.P. Maslova in 2002. The material originates from the Napana Formation (Upper Paleocene) outcropped along the Snatol River, Western Kamchatka Peninsula. The plant assemblage includes *Trochodendroides speciose* (Ward) Berry, *Acer arcticum* Heer, *Aesculus magnificum* (Knowlton) Iljinskaja, *Magnolia basicordata* Fotyanova et Lavrenko, *Nyssa budantsevii* Fotyanova, *Parrotiopsis shimanskiana* N. Maslova, *Sassafras* sp., *Rhus* sp. (Lavrenko and Fotyanova, 1994).

The collection of plant fossils from the Snatol River includes 30 specimens of differently preserved *Platimeliphyllum snatolense* leaves. In 14 of these specimens traces of damage have been found.

Photographs of leaves were taken with a Nikon D200 camera; the damage was studied using a Leica M165C stereomicroscope with a DFC 420C digital camera and a Tescan scanning electron microscope (SEM) under low vacuum conditions without coating.

The collection, no. 4256, is stored in the Paleontological Institute, Russian Academy of Sciences (PIN).

ISSUES OF NOMENCLATURE AND DESCRIPTION OF DAMAGE TO *PLATIMELIPHYLLUM SNATOLENSE* LEAVES

The structures that we interpret as leaf galls are situated in all specimens on the lower surface of the leaf. Breaks in leaf tissues, often stellate, are clearly visible

Table 1. Composition of the formal genus *Antronoides* Waggoner et Poteet

Formal species	Plant	Age, region
<i>A. oregonensis</i> Erwin et Schick, 2007	<i>Quercus simulata</i>	KZ: Middle Miocene, United States
<i>A. cyanomontanus</i> Erwin et Schick, 2007	<i>Quercus simulata</i>	KZ: Middle Miocene, United States
<i>A. polygonalis</i> Waggoner et 1999	<i>Quercus simulata</i>	KZ: Middle Miocene, United States
<i>A. schorni</i> Waggoner et Poteet, 1996	<i>Quercus hannibali</i> (<i>Q. pollardiana</i> in Erwin and Schick, 2007)	KZ: Middle Miocene, United States
<i>A. krassilovi</i> sp. nov.	<i>Platimeliphyllum snatolense</i>	KZ: Upper Paleocene, Russia
<i>A. ovatus</i> (Krassilov et al., 2008) comb. nov.	<i>Dewalquea gerofitica</i>	MZ: K ₂ , Turonian, Israel
<i>A. mucronatus</i> (Krassilov et al., 2008) comb. nov.	<i>Dewalquea gerofitica</i> <i>Platydebeya papilionacea</i>	MZ: K ₂ , Turonian, Israel

at the site of gall attachment on the opposite (upper) surface of the lamina; threads of a carbonaceous substance are clearly visible through these breaks, often coinciding with veins of the lamina. The new structures themselves are covered with a carbonaceous film. In some leaves we have recorded only the characteristic stellate breaks, which were probably left on the leaf after natural detachment of the gall.

Krassilov et al. (2008) described elongate oval and conical galls *Ceratoneon ovatum* Krassilov, Silantjeva et Lewy and *C. mucronatum* Krassilov, Silantjeva et Lewy on leaves *Dewalquea gerofitica* (Dobruskina) Krassilov and *Platydebeya papilionacea* Krassilov from the Turonian of Israel. Similar galls are also known from the Miocene of Nevada, United States (Waggoner and Poteet, 1996). They are conical galls, similar in shape to *Ceratoneon mucronatum*, on leaves of *Quercus hannibali* Dorf; they were described as a new formal genus and species, *Antronoides schorni* Waggoner et Poteet, in the hymenopteran family Cynipinae Ashmead. This illustrates two different approaches to the classification of galls (for more details on the principles of classification, see Vassilenko, 2005). Several other formal gall species and their traces on *Quercus simulata* Knowlton leaves were described later in the formal genus *Antronoides* Waggoner et Poteet from the Miocene of Oregon, United States (Waggoner, 1999; Erwin and Schick, 2007) (Table 1).

Formal genera and species have been used for recent galls in the literature since the 19th century. In most cases the gall-maker has been reliably determined; therefore, formal genera are usually assigned to particular families or even tribes of the natural system. This approach is justified if it is applied to recent forms. However, if it is applied also to fossil forms, it can raise some problems. The older are the deposits, the more questions emerge about the reliability of interpretations. The number of fossil galls collected in deposits of different ages has considerably increased recently, and if galls found in the Miocene or Eocene could somehow be assigned to the galls of a recent hymenopteran tribe or a particular group of mites based on external similarity and on the taxon of the host plant, assigning similar galls from earlier—e.g.,

Cretaceous—deposits to recent arthropod taxa is against common sense. The most objective way of recording data would probably be to describe all fossil forms without exceptions in a formal system, independently of the gall-making taxon or of the plant. This would make it possible to analyze the stratigraphic distribution of formal taxa, taxonomic diversity, etc.

Renunciation of classifying fossil galls in natural taxa of supposed gall-makers and unification of the system are necessary for the following reasons. First, for many fossil galls and other biodamages there are no reasons for unambiguous interpretation of particular forms. Columnar galls can be made either by mites or by some insects. In some particular cases interpretation can be quite reliable, but it should not be raised to taxonomic rank. It is important to identify the gall-maker, but such identifications should be taken out of classification, as well as the taxon of the host plant, the taxonomic assignment of which sometimes disagrees with natural classification. Second, description of formal genera and species of biodamages in natural taxa of insects according to various notions of different authors complicates analysis and on the whole compromises the reliability of conclusions. Therefore, in our opinion, classification of fossil galls should be purely formal. Morphological parameters of a new structures and specifics of its position on the leaf, association with veins or the margin of the lamina, etc., can be used as main objective characters in such a classification.

Krassilov et al. (2008) used the name *Ceratoneon* for conical and horn-shaped galls. However, the name *Ceratoneon* has always been used in formal morphological classifications for galls of extant mites (e.g., Massalongo, 1891). Non-taxonomic usage of the name “ceratoneon” is also sometimes found in the literature, for instance for galls made by thrips (e.g., Krishnamurthy et al., 1975). Therefore, it appears inappropriate to use this formal genus for naming fossil forms. One of the reasons is that it is impossible to compare recent formal species described earlier with newly described fossil species by some characters because of specifics of paleontological material.

The formal genus *Antronoides* Waggoner et Poteet and species *A. schorni* Waggoner et Poteet were originally described for Miocene galls with the following diagnosis: “elongated fusiform galls with annulate bases on leaves of *Quercus hannibali*” (Waggoner and Poteet, 1996, p. 1081). The diagnosis of the genus *Antronoides* was soon re-formulated to include a direct indication of fossil galls (Waggoner, 1999). The generic character used in this diagnosis is the non-attachment of galls to veins. It seems to us that such a detailed specification of topography for the genus is superfluous, as well as specification of the area in which the gall is attached to the leaf. In addition, the provided photograph (Waggoner, 1999, text-fig. 5) shows that some of the numerous galls can be situated on or adjacent to leaf veins.

In accordance with priority of the name, it seems appropriate to us to assign the formal species described by Krassilov et al. (2008) to the genus *Antronoides*. The diagnosis of *Antronoides* should therefore be enlarged, and the genus itself should be transferred from the natural taxon Cynipini to a formal taxon.

Following Vyalov (1975), the formal family Paleogallidae Vjalov and genus *Paleogallus* Vjalov, with a simple and rather all-embracing diagnosis, were used earlier for fossil galls (Vassilenko, 2005, 2007; Aristov et al., 2013). At present we believe that it is appropriate to retain the formal genus *Paleogallus* for local leaf galls of flattened, hemispherical, or nearly hemispherical shape and use the genus *Antronoides* for various versions of columnar and elongate forms of new structures independently of their assignment to any particular group of gall-makers or taxonomic identity of the plant.

SYSTEMATIC PALEONTOLOGY

Family Paleogallidae Vjalov, 1975

Genus *Antronoides* Waggoner et Poteet, 1996

Antronoides: Waggoner and Poteet, 1996, p. 1081; Waggoner, 1999, p. 9.

Ceratoneon: Krassilov et al., 2008, p. 87.

Type species. *A. schorni* Waggoner et Poteet, 1996.

Diagnosis. Fossil new structures on plant leaves, appearing as galls of conical, columnar, horn-shaped, or fusiform shape. Length of new structures greater than diameter (width) of base.

Species composition. In addition to type species, five species: *A. oregonensis* Erwin et Schick,

2007, *A. cyanomontanus* Erwin et Schick, 2007, *A. polygonalis* Waggoner, 1999, *A. ovatus* (Krassilov et al., 2008) comb. nov., *A. mucronatus* (Krassilov et al., 2008) comb. nov., *A. krassilovi* sp. nov.

Comparison. This genus is distinguished from the genus *Paleogallus* Vjalov in the elongate shape of the new structures.

Antronoides krassilovi, sp. nov.

Plate 11, figs. 1–6, Plate 12, figs. 1–3

Etymology. In memory of the distinguished scientist Prof. Valentin Abramovich Krassilov (1937–2015).

Holotype. PIN, no. 4256/30, gall and traces of detached galls on leaf *Platimeliphyllum snatolense*; Western Kamchatka Peninsula, natural outcrops along Snatol River; Upper Paleocene, Napana Formation.

Description. Gall. Fusiform structure up to 2 mm wide and 8–9 mm long, attached with short end (base) to lower surface of lamina near a vein or in an intercostal area of the leaf, narrowing basally and distally.

Attachment area (trace of detached gall). On upper leaf surface, stellate gaps with galls' remains formed by a carbonaceous substance are clearly visible (Pl. 12, fig. 6).

Measurements, mm. Gall length, up to 9; gall width, up to 2; width of distorted part of lamina in area of gall attachment, up to 4.

Remarks. In paratype PIN, no. 4256/31, the gall was fossilized parallel to the lamina; it is somewhat shorter and narrower. At the base of the gall, dense fibers are visible, connecting the body of the gall to the lamina. The attachment areas (stellate breaks) vary in size within a small range in different leaf specimens and between different galls on the same leaf. In some cases (paratype PIN, no. 4256/31, Pl. 11, figs. 5, 6), if the gall is adjacent to a vein, the vein is visibly diverted towards the gall. The rounded depression about 0.7 mm in diameter visible on the body of the gall (holotype PIN, no. 4256/30, Pl. 11, figs. 1, 3, 4) could be the outlet opening.

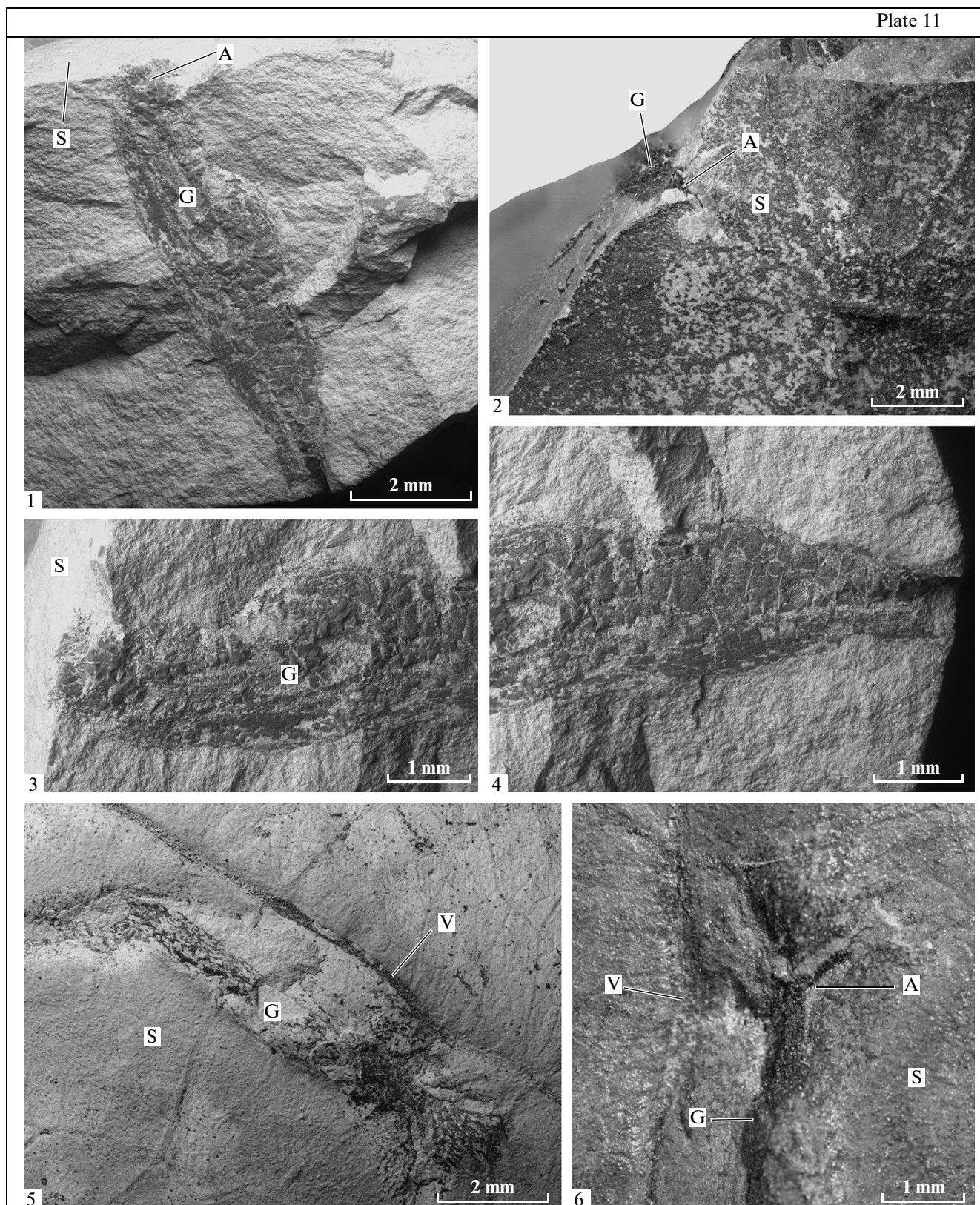
Material. In addition to holotype, paratypes PIN, nos. 4256/31, 33, 302, and damage on ten specimens of leaves *Platimeliphyllum snatolense* from the same locality.

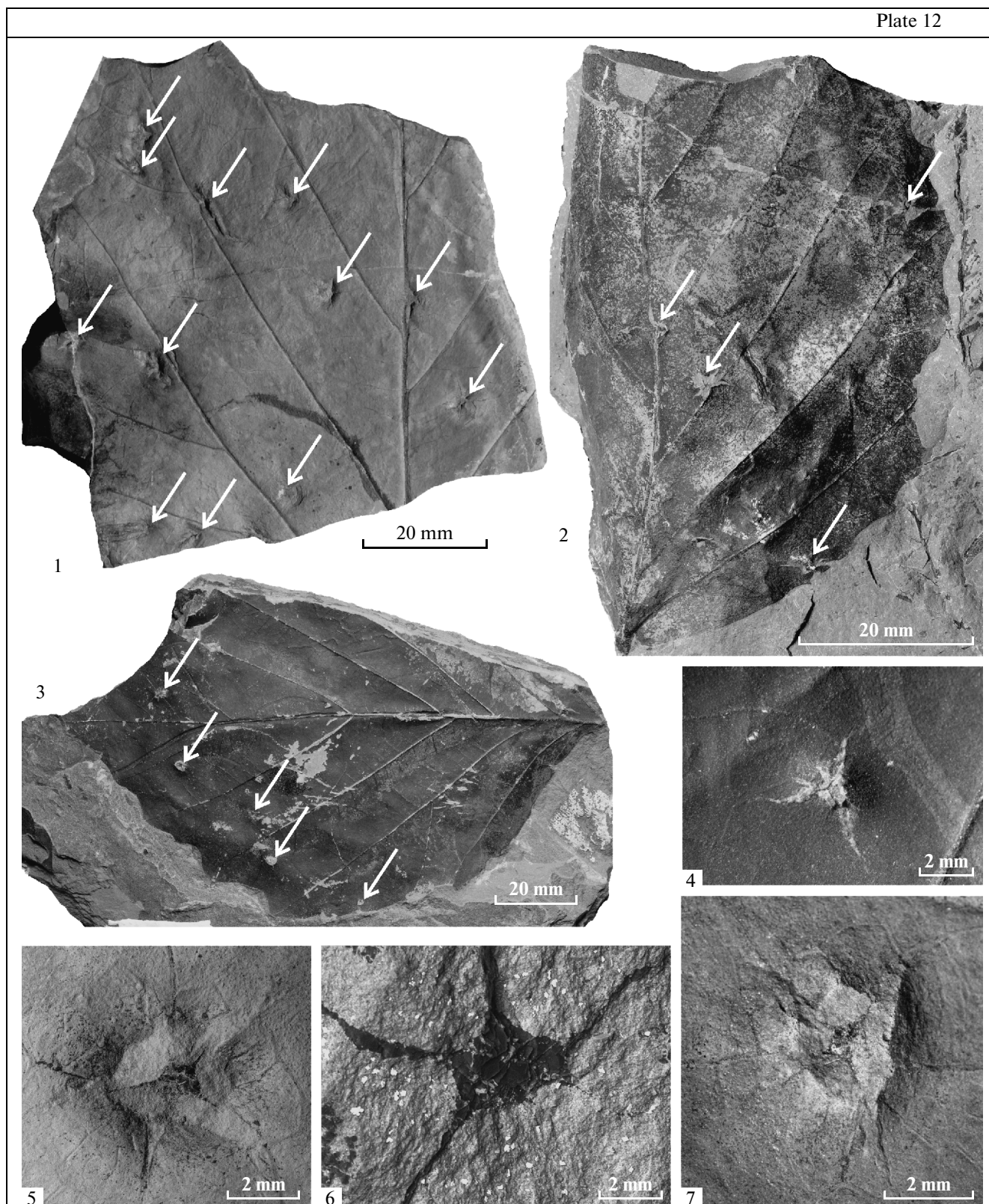
Explanation of Plate 11

Figs. 1–4. *Antronoides krassilovi* sp. nov., holotype PIN, no. 4256/30, gall on *Platimeliphyllum snatolense* leaf, fossilized perpendicular to lamina (as in life): (1) general view of gall (SEM); (2) area of attachment of gall to lamina viewed from leaf surface; (3) proximal part of gall (SEM); (4) distal part of gall (apex missing) (SEM).

Figs. 5 and 6. *Antronoides krassilovi* sp. nov., paratype PIN, no. 4256/31, gall on *Platimeliphyllum snatolense* leaf, fossilized parallel to lamina: (5) general view (SEM); (6) area of attachment of gall to lamina (fibers and leaf vein diverted towards gall). Notation: (S) lamina surface; (G) gall body; (A) area of attachment of gall to lamina; (V) leaf vein.

Plate 11





Explanation of Plate 12

Figs. 1–3. Position of galls *Antronoides krassilovi* sp. nov. and their traces on *Platimeliphyllum snatolense* leave: (1) paratype PIN, no. 4256/31; (2) holotype PIN, no. 4256/30; (3) paratype PIN, no. 4256/33.

Figs. 4–7. Traces of attachment of galls *Antronoides krassilovi* sp. nov., stellate breaks of tissues on upper surface of *Platimeliphyllum snatolense* leaves: (4) paratype PIN, no. 4256/302; (5, 7) paratype PIN, no. 4256/31 (SEM); (6) holotype PIN, no. 4256/30 (SEM).

DISCUSSION

To date, seven formal fossil species of columnar and horn-shaped galls are known from the stratigraphic interval from the Upper Cretaceous (Turonian) to Middle Miocene (table). Recent galls of such shapes can belong to mites of the family Eriophyidae or to some hymenopterans of the family Cynipidae. It is difficult to reliably determine the gall-maker of the fossil forms. The Miocene forms could belong to hymenopterans of the tribe Cynipini, judging by their external similarity and by the taxon of the host plant (Waggoner and Poteet, 1996; Waggoner, 1999; Erwin and Schick, 2007). The Turonian damage should probably be interpreted as mite-made. We leave the question of interpreting the new gall species from the Paleocene of the Kamchatka Peninsula open for the time being; these galls could belong to mites or to some insects.

One of the characteristic features of the galls in question is their position on the leaf. For instance, marginal position on the lamina is typical of the Turonian *Antronoides mucronatus* and *A. ovatus*. They are probably pathological new structures developed from denticles of the lamina margin. The process of such overgrowing of denticle tissues resulting in the emergence of two stable morphological forms of new structures could indicate either two different biochemical agents (and thus, in essence, two different gall-makers) or species-specific response of the plant. Since *A. ovatus* has been found only on leaves *Dewalquea gerofitica*, and *A. mucronatus* has been found on both *D. gerofitica* and *Platydebeya papilionacea*, the former possibility seems more likely.

In the Miocene species, the galls are typically distributed either more or less evenly over the lamina (as in *A. cyanomontanus*, *A. polygonalis*, and *A. schorni*) or more densely in the area of the central vein (as in *A. oregonensis*). Of all Miocene forms, *A. oregonensis* is the most specialized, distinguished from the others not only by the preference for the central vein, but also by shape and mutual position of the galls (Erwin and Schick, 2007, text-fig. 6).

The galls of the new species have not been found to be particularly associated with any areas of the lamina. They can be situated near veins as well as in intercostal spaces (Pl. 12, figs. 1–3). If they are situated near veins, the vein is occasionally diverted towards the gall (Pl. 11, figs. 5, 6).

The structure of the area of attachment of the galls to the lamina is known in all species except *A. mucronatus* and *A. ovatus*. A distinct stellate break of tissues remains visible on the upper surface of the lamina in the area of attachment of the gall *A. krassilovi* sp. nov. (Pl. 12, figs. 4–7), whereas in all Miocene forms the structure of this area is different, appearing as round holes with a ridge along their perimeter or flattened rounded ridges on the leaf surface.

The galls *A. cyanomontanus*, *A. polygonalis*, *A. schorni*, *A. oregonensis* and *A. krassilovi* sp. nov. could probably easily become detached from the lamina after dying, whereas this might not be the case in *A. mucronatus* and *A. ovatus*, judging by the material available. The possibility of such detachment is probably associated also with the presence of the peculiar ring-shaped thickening or fibers in the area of “contact” between the gall and the leaf surface; such structures are distinct in *A. krassilovi* sp. nov., *A. schorni* and *A. oregonensis*.

A. krassilovi sp. nov. is especially similar in position on the leaf to *A. cyanomontanus* and differs in the type of attachment to the lamina. The new species especially strongly differs from the Turonian *A. mucronatus* and *A. ovatus*, which are distinguished by a number of characters from any fossil galls known to date.

ACKNOWLEDGMENTS

We are grateful to T.M. Kodrul (Geological Institute, Russian Academy of Sciences) and R.A. Rakitov (PIN) for constructive discussions of the results of this study and to A.G. Ponomarenko and A.P. Rasnitsyn (PIN) for useful comments on the manuscript at the stage of peer-reviewing.

This study was supported by the Russian Foundation for Basic Research, project no. 14-04-00800.

REFERENCES

- Aristov, D.S., Bashkuev, A.S., Golubev, V.K., Gorochov, A.V., Karasev, E.V., Kopylov, D.S., Ponomarenko, A.G., Rasnitsyn, A.P., Rasnitsyn, D.A., Sinitshenkova, N.D., Sukatshева, I.D., and Vassilenko, D.V., Fossil insects of the Middle and Upper Permian of European Russia, *Paleontol. J.*, 2013, vol. 47, no. 7, pp. 641–832.
- Erwin, D.M. and Schick, K.N., New Miocene oak galls (Cynipini) and their bearing on the history of cynipid wasps in western North America, *J. Paleontol.*, 2007, vol. 81, no. 3, pp. 568–580.
- Kodrul, T.M., Jin Jian-hua, Aleksandrova, G.N., Herman, A.B., Feng Xin-xin, Song Yun-sheng, and Liu Xiaoyan, Phytogeographical relationships of the low-latitude Eocene floras of South China (Changchang Basin, Hainan Province and Maoming Basin, Guangdong Province), in *Proc. 2nd Sino-Russian Seminar on Evolution and Development of Eastern Asian Flora Based on Palaeobotanical Data (November 5–10, 2012, Guangzhou, China)*, Guangzhou, 2012, pp. 37–46.
- Kodrul, T.M. and Maslova, N.P., A new species of the genus *Platimeliphyllum* N. Maslova from the Paleocene of the Amur region, Russia, *Paleontol. J.*, 2007, vol. 41, no. 11, pp. 1108–1117.
- Krassilov, V.A., Silantieva, N., and Lewy, Z., Part I, in *Plant-arthropod interactions in the Early Angiosperm history. Evidence from the Cretaceous of Israel*, Krassilov, V. and Rasnitsyn, A., Eds., Sofia: Pensoft Publishers, 2008, pp. 1–187.
- Krassilov, V.A., Kodrul, T.M., and Maslova, N.P., Plant systematics and differentiation of species over Trans-Beringian land connections including a new species of cupressaceous

- conifer *Ditaxocladus* Guo et Sun, *Bull. Geol. Sci.*, 2009, vol. 85, no. 1, pp. 95–110.
- Krishnamurthy, K.V., Raman, A., and Ananthakrishnan, T.N., On the morphology of the ceratoneon thrips galls of *Schefflera racemosa* Harms. (Araliaceae), *Marcellia*, 1975, vol. 38, nos. 2/3, pp. 179–184.
- Lavrenko, O.D. and Fot'janova, L.I., Some Early Paleogene species from western Kamchatka, in *Cenozoic Plants and Climates of the Arctic*, Boulter, M.C. and Fischer, H.C., Eds., NATO ASI Series, vol. 27, Berlin: Springer-Verlag, 1994, pp. 315–325.
- Manchester, S.R., Chen Zhi-duan, Geng Bao-yin, and Tao Jun-rong, Middle Eocene flora of Huadian, Jilin Province, Northeastern China, *Acta Palaeobot.*, 2005, vol. 45, no. 1, pp. 3–26.
- Maslova, N.P., A new plant of the family Platanaceae from the Early Paleogene reconstructed on the basis of leaves and inflorescences, *Paleontol. J.*, 2002, vol. 36, no. 2, pp. 207–218.
- Maslova, N.P. and Kodrul, T.M., New platanaceous inflorescence *Archaranthus* gen. nov. from the Maastrichtian–Paleocene of the Amur region, *Paleontol. J.*, 2003, vol. 37, no. 1, pp. 89–98.
- Maslova, N.P., Kodrul, T.M., and Tekleva, M.V., A new taxon of staminate inflorescences *Bogutchanthus* gen. nov. (Hamamelidales) from the Paleocene of the Amur region, *Paleontol. J.*, 2007, vol. 41, no. 5, pp. 564–579.
- Maslova, N.P., Kodrul, T.M., Tekleva, M.V., and Aleksandrova, G.N., *Platimeliphyllum reznikoviorum* N. Maslova, sp. nov. (Angiospermae) and associated infructescence from the Paleogene of central Kazakhstan, *Paleontol. J.*, 2014, vol. 48, no. 6, pp. 688–700.
- Massalongo, C.B., Acarocecidii nella flora veronese: ulteriori osservazioni ed aggiunte, *Nuovo Giorn. Bot. Ital.*, 1891, vol. 23, pp. 68–119, 469–488.
- Vasilenko, D.V., Damages on Mesozoic plants from the Transbaikalian locality Chernovskie Kopi, *Paleontol. J.*, 2005, vol. 39, no. 6, pp. 628–633.
- Vasilenko, D.V., Feeding damage on Upper Permian plants from the Sukhona River, *Paleontol. J.*, 2007, vol. 41, no. 2, pp. 207–211.
- Vyalov, O.S., Fossil remains of insect feeding, in *Paleontol. sborn. No. 12. Vyp. 1–2* (Collection of Paleontological Papers, Vol. 12, No. 1–2), L'vov: L'vovsk. Gos. Univ., 1975, pp. 147–155.
- Waggoner, B.M. and Poteet, M.F., Unusual oak leaf galls from the Middle Miocene of northwestern Nevada, *J. Paleontol.*, 1996, vol. 70, no. 6, pp. 1080–1084.
- Waggoner, B.M., Fossil oak leaf galls from the Stinking Water paleoflora of Oregon (Middle Miocene), *PaleoBios*, 1999, vol. 19, no. 3, pp. 8–14.

Translated by P. Petrov