

***GANODERMA APPLANATUM* (POLYPORALES, BASIDIOMYCOTA)  
AT THE SAINT PETERSBURG AREA**

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**Abstract**—*Ganoderma applanatum* is one of the most common polypores in the world. However, due to the variability of its macro- and even micro-characters, it is rather difficult to compile an exact picture of the distribution of this fungus both in the world as a whole and in its different regions. At the same time, in cities all the *Ganoderma* representatives are subject of control, because the pathogenesis of parkland is often associated with these species. Therefore, an exact identification of the pathogen is not only a subject of basic scientific, but also of practical importance. The aim of this paper is molecular testing of *G. applanatum*-coll. representatives to understand one or more phylospesies are distributed over area in question. In the present study, we analyzed 20 model samples collected in various St. Petersburg localities. The analysis of ITS sequences has showed that only one phylospesies (*G. applanatum*) characterized by significant biomorphological plasticity is distributed over St. Petersburg area. It has shown that, according to the ratio of pileus diameter to basidiome thickness, two basic morphotypes can be distinguished: subfomitoid one (the ratio of the pileus radius to its thickness  $\leq 2$ ) and applanate one (the ratio of the cap radius to its thickness  $\geq 2$ ). A severity of this character depends on basidiome age, and on the content of easily immobilized metabolites in host tree. According to their substrate location, basidiomes can be grouped onto laterally attached on vertical surfaces and complex rosette-shaped mantle formations on buried wood. Variability of basidiomes associated with interaction with insects or vertebrates was separately noted. It was found that the age structure of model St. Petersburg population of *G. applanatum* is characterized by predominance of 1–2-years-old basidiomes, whereas the largest age of basidiomes doesn't exceed 7 years. It has been suggested that relatively young age of perennial basidiomes is rather constitutional feature of the species in boreal zone, characterized by mycelium freezing in marginal zones of basidiome. Variability of *G. applanatum* basidiospores was considered, too. It was shown that specimens with longest (and partly widest) basidiospores are confined to living trees. *G. applanatum* combines two trophic strategies, a pathogenic saprotroph growing on living trees and causing chronic rot, and a pure saprotroph, which continues to develop on dead trunks as well as stumps, dead and buried wood. As a pathogen, the species manifests itself by colonizing the frost holes of the butt area, characteristic of broad-leaved species under conditions of degradation of artificial drainage of broadleaf stands. As a pathogen control measure, furrowing of the bark of spring shoots of broad-leaved seedlings was proposed to prevent increased formation of frost cracks as well as the prevention the degradation of drainage systems of broad-leaved stands. A modern diagnosis of the species was given taking into account the data obtained on its boundaries and variability at St. Petersburg areas.

**Keywords:** modification variability, frost cracks, *Ganoderma*, ITS phylogeny

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## INTRODUCTION

*Ganoderma applanatum* (Polyporales, Basidiomycota) is one of polypores the most common in the world. It grows on deciduous and coniferous species, causing a lump, roots, or stems white rot, and is able to begin its

development on living trees, but continue also a dead wood colonization (Bondartsev, 1953; Ryvarden, Gilbertson, 1993; Bondartseva, 1998; Ryvarden, Melo, 2017). However, due to its huge variability of macro- and even micro-characters, which was a reason for repeated re-descriptions of this species, an exact picture

of distribution of this polypore is rather difficult to establishing both for the global space and for its different regions.

The species has been described as *Boletus applanatus* by Persoon (1800). An authentic type specimen of this species is kept in the Leiden herbarium (Steyaert, 1967). Authentic material was not preserved for *B. lipsiensis*, which was described a little earlier (Batsch, 1786), while contemporaries doubted the identity of *B. applanatus* with *B. lipsiensis* (Persoon, 1801), therefore, this second name should be considered today rather as avoidable (Moncalvo, Ryvarden, 1997).

Later, the species *Polyporus leucophaeus* (Montagne, 1856) was described in North America. The lectotype of this species was tested and recognized as pale variety of *Ganoderma applanatum* (Ryvarden, 1982). The situation with *G. australe* (type *Polyporus australis*) (Fries, 1828) is more complicated, because for this species in Kew kept an associated European specimen, apparently unrelated to the original collection (Steyaert, 1975). In Europe, this species is understood either widely (Ryvarden, Gilbertson, 1993; Bondartseva, 1998), or narrowly and then referred to *Ganoderma europaeum* (Steyaert, 1961) or *G. adpersum* (Donk, 1969). This latter, due to the lack of molecular testing of type material till now, is very often mixed with *G. applanatum* in European guides.

In Saint Petersburg, located in the softwood zone, but covered with a broad-leaved plantations on artificially drained grounds, in principle, there are conditions for meeting both a ubiquitous *G. applanatum* and more southern Central European taxa of the genus, such as *G. adpersum* or *G. pfeifferi*. *G. applanatum* was reported for Saint Petersburg areas in a range of papers (Bondartseva et al., 2014; Zmitrovich et al., 2018; etc.). *G. adpersum* was also preliminary indicated for this territory (Zhukova et al., 2017) in accordance with widespread morphological concept of the species. However, the morphological concept of *Ganoderma* spp. is very unreliable issue due to huge variability of macro- and micro-morphological characters over wide range even for one species (Steyaert, 1980; Wasser et al., 2006). At the same time, *Ganoderma* representatives in cities are subject to control, since the pathogenesis of parkland is associated with these species, therefore, an exact identification of pathogen has not only basic scientific, but also applied importance.

Taking into account aforementioned, the aim of the present paper is a molecular testing of Saint Petersburg *G. applanatum*-coll. representatives in order to understand one or more phyllopecies we are dealing with in area in question. In case of successful solution of this problem it would help reassess the morphological boundaries of the units previously described in the literature as well as streamline the understanding of measurements of morphological intraspecific variability of *G. applanatum* and clarify the diagnosis of this species.

## MATERIALS AND METHODS

The present study has involved an isolation of DNA from field material coupled with morphological testing of the same samples. A total of 20 samples were selected, covering the range of morphological variability of basidiomes as much as possible, main areas of St. Petersburg, and substrates on which the species was recorded most often.

Table 1 shows a geographic coordinates of each find, the herbarium documentation (voucher specimens) and GenBank number under which the obtained nucleotide sequence is defended.

The material collection involved both remnants of the zonal vegetation of Saint Petersburg Region (such as Piskarevskiy Forest Park) as well as old broadleaf stands, namely the Summer Garden, Mikhailovskiy Garden, Engineering Square, Peter the Great Botanical Garden, St. Petersburg University Botanical Garden.

Material collection and herbarization were carried out according to standard methods (Bondartsev, Singer, 1950).

DNA was extracted from small pieces of dried basidiocarps using NucleoSpin® Plant II (Macherey-Nagel, Germany). The ribosomal ITS1–5.8S–ITS2 region was amplified with the fungal specific primers ITS1F and ITS4B (Gardes, Bruns, 1993). PCR products were visualized using agarose gel electrophoresis and Gel Red staining, and subsequently purified with the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific, MA, USA). Purified PCR products were sequenced on an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). Raw data were edited and assembled in MEGA 6 (Tamura et al., 2013). Newly generated sequences have been deposited in the GenBank.

For this study, 15 ITS sequences were generated and additional 12 ITS sequences of other species including *Amauroderma sprucei* JX982568 chosen as outgroup were retrieved from GenBank ([www.ncbi.nlm.nih.gov/genbank/](http://www.ncbi.nlm.nih.gov/genbank/)). Sequences were aligned with the MAFFT version 7 web tool (Kato, Toh, 2008; <http://mafft.cbrc.jp/alignment/server/>) using the G-INS-1 option. The final ITS alignment contained 624 characters (including gaps). ML analysis was performed in the RAxML BlackBox, v0.9.0 (Kozlov et al., 2019), under a GTR + G model with 100 rapid bootstrap replicates. Bootstrap (BS) values  $\geq 70\%$  are considered significant.

The macroscopic descriptions were based on study of fresh and dried specimens. The materials of the herbarium of Komarov Botanical Institute (St. Petersburg, Russia, LE) were studied. Microscopic preparations were mounted from dried material in Melzer's solution, 10% ammoniacal Congo Red and 5% aqueous solution of KOH, using a LOMO Micmed-6 light microscope. The hyphal system was revealed and described according to updated technique (Zmitrovich

**Table 1.** Geographical coordinates and other documentation of *Ganoderma applanatum* specimens studied

OSU*	Field number**	Coordinates	Locality	GenBank accession number	Voucher - specimen number
1	IZ 1	59°58'12"N, 30°19'31"E	Peter the Great Botanical Garden	MN435132	LE 287658
2	IZ 2	59°58'12"N, 30°19'31"E	»»	MN435133	LE 287659
3	IZ 3	59°58'12"N, 30°19'31"E	»»	–	LE 287660
4	IZ 4	59°58'12"N, 30°19'31"E	»»	–	LE 287661
5	IZ 5	59°58'12"N, 30°19'31"E	»»	MN435134	LE 287662
6	IZ 6	60°00'57"N, 30°24'27"E	Grazhdanka green space	MN435135	LE 287663
7	IZ 7	60°00'57"N, 30°24'27"E	»»	MN435136	LE 287664
8	IZ 8	59°59'59"N, 30°24'26"E	Piskarevskiy forest park	–	LE 287665
9	IZ 9	59°59'21"N, 30°23'43"E	Bogoslovskoye Cemetery	–	LE 287667
10	IZ 10	59°59'21"N, 30°23'43"E	»»	MN435137	LE 287668
11	EZ 13-35	59°94'63"N, 30°33'26"E	Summer Garden	MN435138	LE 287669
12	EZ 12-24	59°94'55"N, 30°33'66"E	»»	MN435139	LE 287670
13	EZ 98	59°94'37"N, 30°33'51"E	Engineering Square	MN435140	LE 287671
14	EZ 698	59°94'85"N, 30°33'58"E	Mikhailovskiy Garden	MN435141	LE 313851***
15	EZ 893	59°94'53"N, 30°33'71"E	»»	MN435142	LE 287672
16	MS 3	59°41'54"N, 30°28'16"E	Pavlovskiy Park	MN435143	LE 287673
17	MS 11	59°55'56"N, 30°16'56"E	St. Petersburg University Botanical Garden	–	LE 287674
18	MS 7	59°41'54"N, 30°28'15"E	Pavlovskiy Park	MN435144	LE 287675
19	MS 6	59°41'54"N, 30°28'17"E	»»	MN435145	LE 287676
20	MS 10	59°55'56"N, 30°16'56"E	St. Petersburg University Botanical Garden	MN435146	LE 287677

Note. \*OSU – operational sample units; \*\*Field numbers abbreviations: EZ – E.A. Zhukova, IZ – I.V. Zmitrovich, MS – M.V. Sidelnikova; \*\*\*The specimen kept in LE Herbarium under name *G. adspersum*.

et al., 2009). The size of mature spores was measured on 30 spores in distilled water and Melzer's solution. The variability of basidiospores was studied according to the methods proposed by Parmasto et al. (1987).

Visualization and graphing were performed using the programming language R 3.3.3 (R Core Team, 2012) in the software environment RStudio 1.0.136 (R Studio Team, 2017). The graphs were performed using the packages Ggplot2 (Wickham, 2009), Scales (Scales, 2019), Ggpubr (R Packages 2019), as well as the online program Sankey Diagram Generator v1.2 (Sankey, 2019).

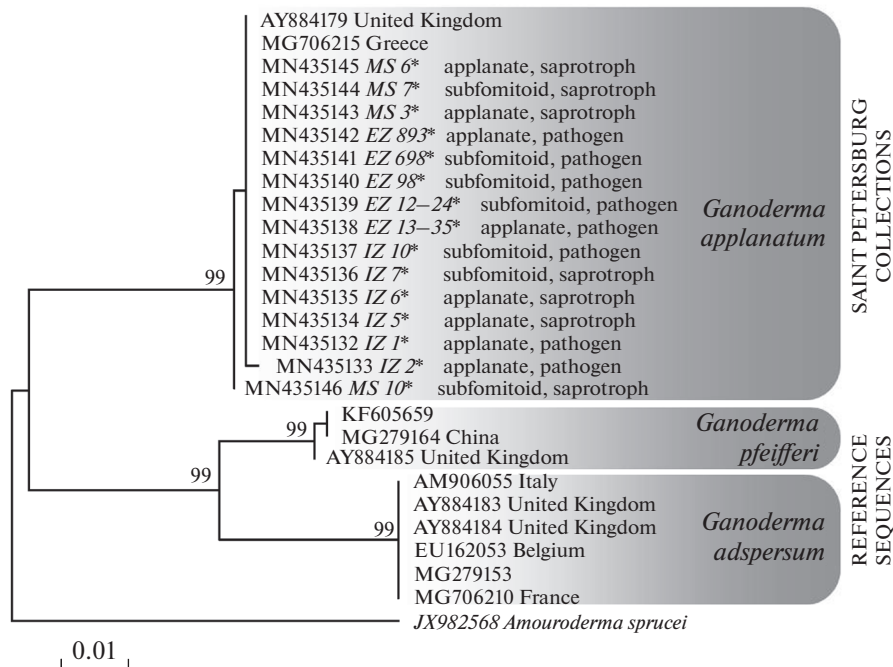
## RESULTS AND DISCUSSION

**Phylogenetic analysis.** Since approximately 2/3 of tested fungal organisms have an intraspecific variability of ITS1–ITS2 sequences lies in the range 0–1% and approximately 3/4 of fungi have their intraspecific variability ca 1–2%. Therefore, in fungi this region can be used as a marker of species divergence (Nilsson et al., 2008). This region we used in this study. 15 of the 20 samples involved in the study succeeded in amplifying this region. Five samples (IZ3, IZ4, IZ8, IZ9, MS11) have produced dubious products and we excluded them from further analysis, all the more so be-

cause all of them had a typical morphology of “neutral *applanatum* type”.

The analysis of ITS region of all 20 operational sample units (OSUs) showed that all differences between the lines are absent, or (MS-10) lie within a few hundredths of the expected changes per site (noise is possible due to intragenomic rDNA variability) which is typical for a single phyllospecies. We did not set the task of populations marking by microsatellite polymorphisms, but our task was to identify whether several deeply diverging species were hiding behind the morphologically motley conglomerates of the *G. applanatum* collective. In the Fig. 1, all OSUs are marked with a rough morphobiological characteristic and it turns out that the distribution of morphobiotypes through phylogenetic multifurcation is quite random. It is obviously that here we can talk about the age and modification variability of basidiomes, that will be described in more detail in the next section of the paper.

It should also be noted that the more divergent sequences introduced into the topology, such as *G. adspersum* or *G. pfeifferi*, although represent separate lineages of the species level, are in no way correlated with nomenclatural types of these taxa. This represents the main problem of the *Ganoderma* taxonomy. With the exception of a few common ubiquitous species, the au-



**Fig. 1.** Phylogenetic tree derived from Maximum Likelihood analysis, based on nrITS1–5.8S–ITS2 data. Bootstrap values (BS > 70%) are shown to the left of a node (field numbers abbreviations – see Table 1). Scale bar – a number of expected changes per site.

thenticity of which does not cause doubts, the identification of most other ganodermas without resorting to type material and a few standard revisions is impossible – for this reason such names as “*G. lucidum*”, “*G. resinaceum*”, “*G. tsugae*”, “*G. australe*” can be found in different clusters of the same molecular cladogram, and the question of their relation to the corresponding types remains to be open (Zmitrovich, 2018). We guess that in the future it will be necessary to provide a critical type study of *G. adspersum* with the corresponding epitypification procedures (in case it is impossible to obtain a holotype DNA) in order to understand in which part of the *Ganoderma*-tree this taxon is really nested.

The fact of belonging of samples identified by key-books as *G. australe* – *G. adspersum*, allows us to outline new approaches to differentiating the boundaries of these taxa, but this issue should also be addressed in connection with the molecular critical type studies.

**Overview of morphological variability.** As can be seen from Table 2 and Fig. 2, the variability spectra of the individual features of model samples intersect, and, as a result, there is the impression of a fine species differentiation. Particularly noteworthy are fungi infesting living trees and having wide white margin that sometimes really want to associate with some southern *Ganoderma* taxa. In fact, we are dealing with an incubation of the age and modification variability of basidiomes, in which the following directions can be distinguished.

According to the ratio of the cap diameter to the thickness of the basidiome, two basic morphotypes can

be distinguished: subfomitoid one (the ratio of radius of the pileus to its thickness  $\leq 2$ ), and applanate one (the ratio of radius of the pileus to its thickness  $\geq 2$ ). A severity of this trait depends on basidiome age (perennial pilei have an applanate tendency) and the content of easily immobilized metabolites in host tree (on living trees, the sterile layer is thicker, which marks a subfomitoid tendency) (Zmitrovich, Spirin, 2005).

Another variability dimension is connected with a substrate location of basidiomes. In addition to classic case of laterally attached pilei, this species is characterized by the formation of rosette-shaped mantle structures, rooted in roots buried wood. Sometimes individual marginal pilei rise on stalk-like base resembling representatives of the *G. lucidum*-complex.

It should also be noted the variability of basidiomes associated with interaction with insects or vertebrates. Insects form galls and capsules, channels and external deposits of processed fungal tissue. Vertebrates (including humans) can affect the growing edge and surface of the pileus, causing the growing felt part of anamixoderm to collapse and an obliterated surface to remain polished spots, with a hint of the *G. lucidum*-complex and *G. pfeifferi*, but this is impression only, because true pileocystidia are absent into *G. applanatum* crust.

It is interesting, but the age population structure of *G. applanatum* is characterized by predominance of basidiomes of the first year or biennial ones, while the maximum age of basidiomes in Saint Petersburg model population does not exceed 7 years (Fig. 3). At the

**Table 2.** Substrates and morphological features of studied *Ganoderma applanatum* operational sample units (OSU)

OSU	Basidiome age (year layers)	Pileus radius (cm)	Pileus radius/base thickness	Basidiospores (1 × w limits, μm)	Qm	Host	State*
1	1	4.5	3.0	7.8–10.4 × 5.2–6.2	1.65	<i>Tilia platyphyllos</i>	1
2	2	3.8	2.5	7.8–10.6 × 5.2–6.2	1.57	<i>Ulmus glabra</i>	1
3	5	12.5	3.2	7.8–10.4 × 5.2–6.5	1.59	<i>Sorbus aucuparia</i>	1
4	1	3.5	1.8	7.0–8.5 × 4.4–5.7	1.50	<i>Salix alba</i>	1
5	2	5.5	2.5	7.8–10.4 × 4.4–6.5	1.52	»»»	2
6	3	11.2	2.1	7.8–9.1 × 5.2–6.2	1.48	<i>Betula pendula</i>	5
7	2	9.0	1.9	7.8–10.4 × 4.9–6.2	1.52	<i>Populus nigra</i>	3
8	2	4.0	2.8	7.8–8.5 × 5.2–5.9	1.52	<i>Betula pubescens</i>	3
9	7	35.0	2.3	7.5–10.4 × 4.9–6.2	1.55	<i>Populus nigra</i>	2
10	1	4.0	1.7	7.0–9.1 × 4.4–5.7	1.44	<i>Sorbus aucuparia</i>	1
11	1	9	2.3	7.8–10.9 × 5.2–5.9	1.73	<i>Tilia cordata</i>	1
12	1	4	2.0	7.8–10.1 × 5.2–5.9	1.56	»»»	1
13	2	5.5	1.7	5.7–8.5 × 4.6–5.7	1.43	<i>Fraxinus excelsior</i>	1
14	1	3	1.2	7.8–11.1 × 5.2–7.8	1.44	<i>Tilia cordata</i>	1
15	1	4.5	3.0	7.8–9.1 × 5.2–5.9	1.47	<i>Fraxinus excelsior</i>	1
16	5	12	3.1	7.5–8.3 × 4.9–5.7	1.49	<i>Tilia cordata</i>	3
17	4	14	2.0	7.8–10.4 × 4.9–6.2	1.53	? <i>Ulmus glabra</i>	3
18	1	6	1.1	7.2–10.4 × 5.2–5.9	1.55	<i>Tilia cordata</i>	3
19	4	8	3.2	7.8–10.4 × 5.2–5.9	1.51	»»»	3
20	7	15	2.0	5.9–8.3 × 4.9–5.7	1.51	<i>Salix alba</i>	3

Note. \*Substrate state: 1 – living trees, 2 – dead trees, 3 – stumps, 4 – fallen logs, 5 – buried wood.

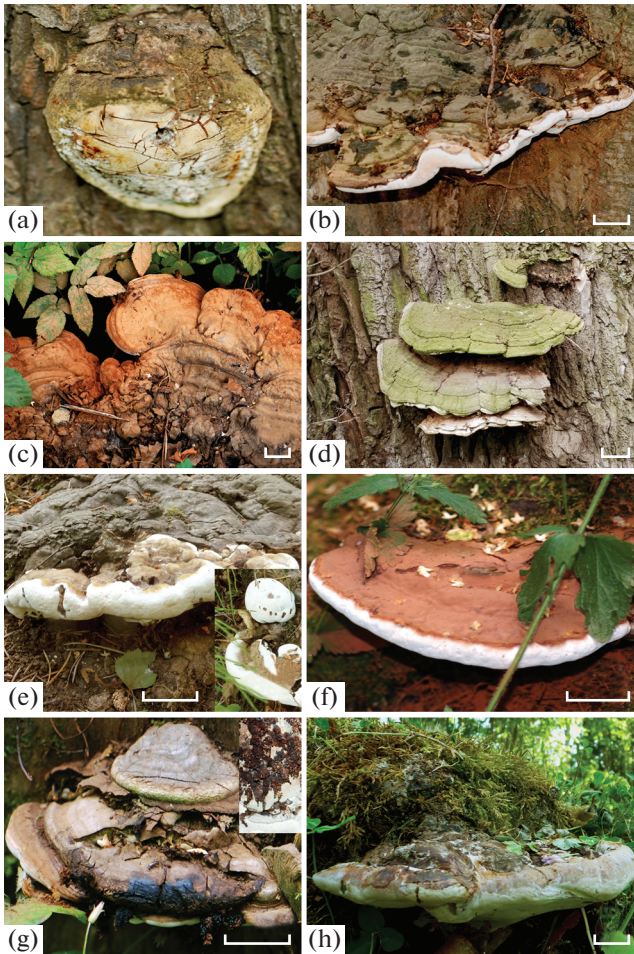
same time, species of the genera *Phellinus* and *Fomes* in the surrounding boreal forests often reach 25–30 years. Dr. M. Szczepka (personal communication) has reported the presence of 20-year-old *G. pfeifferi* basidiome found in Southern Poland. The cause of the short-lived state of *G. applanatum* basidiomes may be the same insects and vertebrates, leading to their destruction. Parasitic mycophilous fungi, e.g. *Sporophagomyces chrysostomus* (Donk, 1974), may play some role, too. However, the general basidiome design of the fungus seems to be not in perfect harmony with boreal environments and, possibly, like *Fomitopsis pinicola*, short-lived state of *Ganoderma applanatum* basidiomes is incorporated structurally (the impossibility of preserving mycelial nests in marginal zones after overwintering). As a result, the basidiomes of small age with wide zone of hypertrophy (subfomitoid) in the Saint Petersburg areas prevail over mature applanate ones, characterized by maximum ages (Fig. 4).

The visualization of spore variability of *G. applanatum* model population is presented on Fig. 5. The samples with the longest (and partly widest) basidiospores are mainly associated with living trees. This can also be partly explained by better supply of mycelium with easily immobilized metabolites, which leads to hypertrophy and hyperplasia of elements of aerial mycelium.

**The modern diagnosis of *G. applanatum*.** In view of our new data on the boundaries and morphological variability of *G. applanatum* based on Saint Petersburg material, below we provide an updated diagnosis of this taxon. Outside the scope of this paper, the molecular type revision of southern *applanatum*-like polypores remains. Only after such revision it would be possible to compose any species keys in boreal guides.

*Ganoderma applanatum* (Pers.) Pat., Hyménomyc. Eur.: 143, 1887. — *Boletus applanatus* Pers., Observ. Mycol. 2: 2, 1800; *Polyporus merismoides* Corda in Sturm, Deutschl. Fl. 4: 139, 1837; *P. stevenii* Lév., Ann. Sci. Nat. Bot. 2: 91, 1844; *P. megaloma* Lév., Anns Sci. Nat., Bot., 1846; *P. leucophaeus* Mont. (ut '*leucophaeum*'), Syll. Gen. Sp. Crypt.: 157, 1856; *P. incrassatus* Berk., J. Linn. Soc. Bot. 16: 41, 1878; *P. concentricus* Cooke, Grevillea 9: 13, 1880; *Fomes gelsicola* Berl., Malpighia 3: 373, 1889; *F. longoporus* Lloyd, Mycol. Writ. 6: 940, 1920.

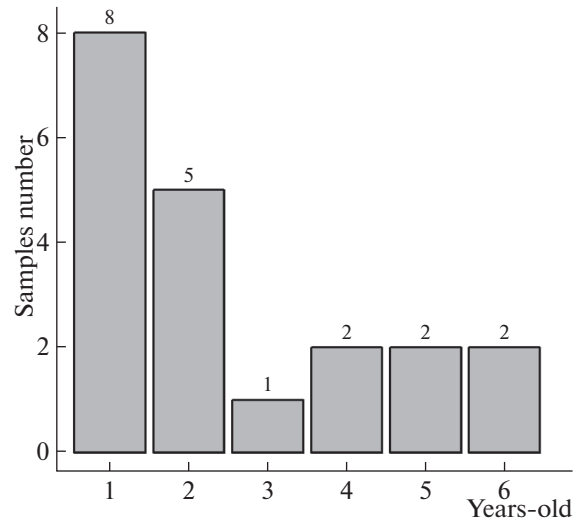
Basidiocarps perennial (up to 7 years in boreal forests), subfomitoid to applanate, sessile of arising from buried wood, woody to corky, in section triquetrous or unguulate; up to 70 cm in diam. and 10 cm thick near the base. The pilei often clustered, radiating, with orthotropic tendency on rosette-like formations. Upperside crustose, cinnamon, grayish or brown, some cracking and protruded insect pores, usually covered with rusty-



**Fig. 2.** The age and modification variability of *Ganoderma applanatum*. The first range – basic morphotypes: subfomitoid (a), applanate (b); the second range – substrate location: with an orthotropic tendency on submerged wood (c), lateral on standing trees (d); the third range – basic ecades: eutrophic ecade of the first year with hypertrophic margin (e), mesotrophic ecade of the second year with thinning margin (f); the fourth range – morphological changes due to interaction with environmental factors: channel penetration from insect activity (g), collapse of anamixoderm with formation of polished surface under impact of vertebrates (h).

brown spore deposits, appearing dusty, irregular to scrupose, radially zonate. Margin round, white, bolster-like, firstly thick, later more slender. Context corky, purplish-brown, usually mottled with whitish streaks and patches, with weak fruit odour. Hymenophore stratified: tube layers concolorous with context, separated by a layer of context tissue, each layer up to 1 cm thick. Pore surface white on fresh specimens, quickly bruising brown when handled, becoming dull buff with age, pores circular, 4–7 per mm.

Hyphal system dimitic with sympodially branched sclerohyphae (according to Zmitrovich, 2018) or trimitic (Corner, 1983). Generative hyphae 2–5  $\mu\text{m}$  in diam., thin-walled, with clamps. Skeletal hyphae 3–

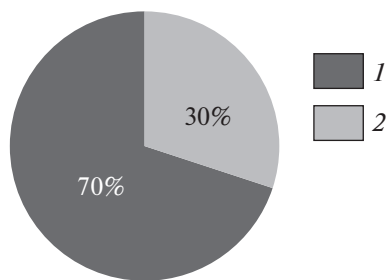


**Fig. 3.** Distribution of St. Petersburg *Ganoderma applanatum* model samples by age of basidiomes.

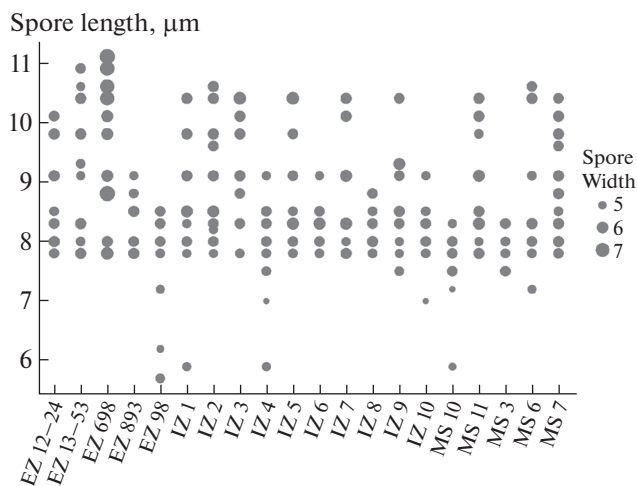
6.5  $\mu\text{m}$  in diam., thick-walled, brown, non-septate, occasionally branched, the extremities tapering to acute apices. Cystidia none. Basidia mostly 18–25  $\times$  8–10  $\mu\text{m}$ , but occasionally with elongated bases, broadly clavate, 4-spored, some tapering abruptly to a narrow base, arising from intercalary positions on the subhymenial hyphae, with a basal clamp. Basidiospores 5.9–10.4  $\times$  4.4–6.2  $\mu\text{m}$ , ovoid, truncate at the distal end, with ornamented exosporium enveloping with transparent perisporium, inamyloid, faintly cyanophilous. Specimens associated with living trees usually have, on average, larger basidiospores.

**Pathogenicity and control.** *G. applanatum* combines two trophic strategies. It can grow as pathogenic saprotroph (Zmitrovich et al., 2015) which infests living trees and causes a chronic rot and as pure saprotroph which continues its development on dead trunks as well as stumps, dead and buried wood. As pathogen, *G. applanatum* is subject for control (Tura et al., 2016).

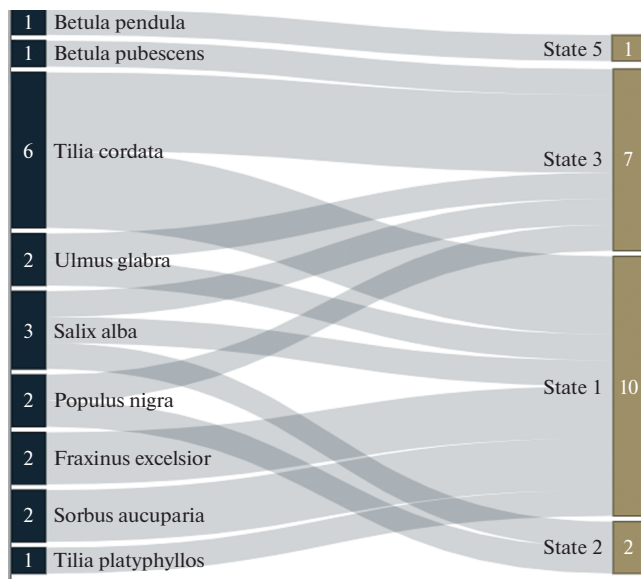
The Fig. 6 shows the Sankey-visualization of relationship of species belonging to tree hosts inhabited by model *G. applanatum* samples and state of the wood substrate (living trees, dead trees, stumps, fallen logs, buried wood). From this diagram, in particular, it can be seen that only as a saprotroph does the species manifest itself on zonal stand-formers (*Betula* spp.), while it exhibits pathogenic properties in broadleaf stands reproduced in Saint Petersburg under conditions of anthropogenic ground drainage. Prior to testing the (subsequently rejected) two-species hypothesis, there was a great temptation to associate the pathogenic populations with some southern *Ganoderma* species, whereas the saprotrophic ones with autochthonous boreal one. However, since it was turned out that only one species is widespread in Saint Petersburg areas, some other explanations are needed. One of them boils down to the fact that broadleaf species on water-rich soils are prone



**Fig. 4.** Distribution of St. Petersburg *Ganoderma applanatum* model samples on basic morphotypes: subfomitoid (1), applanate (2).



**Fig. 5.** Variability in the sizes of basidiospores of St. Petersburg *Ganoderma applanatum* model samples (field numbers abbreviations – see Table 1).



**Fig. 6.** Sankey-visualization of relationship between species attribution of host trees inhabited by model specimens and the state of wood substrate. Substrate states: 1 – living trees, 2 – dead trees, 3 – stumps, 4 – fallen logs, 5 – buried wood.

to ripening of wood and the formation of frost cracks at the base, where *G. applanatum* rushes. We studied frost-cracks in the model objects of Peter the Great Botanical Garden (Firsov et al., 2018). When a frost-crack is infested by ganodermas in the buttress area, the pathogen quickly captures the sapwood and core wood, and such a tree becomes threatening due to its tendency to easy windfall. As control measures, we proposed the furrowing the bark of spring shoots of broadleaf seedlings to prevent increased formation of frost-cracks as well as the preventing a degradation of drainage systems of broadleaf stands (Zmitrovich, Volobuev, 2019).

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## ***GANODERMA APPLANATUM* (POLYPORALES, BASIDIOMYCOTA) НА ТЕРРИТОРИИ САНКТ-ПЕТЕРБУРГА**

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*Ganoderma applanatum* является одним из самых распространенных в мире трутовиков. Однако в силу вариабельности его макро- и даже микропризнаков, точную картину распространения этого трутовика как в мире в целом, так и в различных регионах, составить довольно трудно. Вместе с тем, виды рода *Ganoderma* в городах являются объектом контроля, поскольку с ними связан патогенез парковых насаждений, а точная идентификация возбудителя имеет не только общенаучное, но и прикладное значение. Целью данной работы было молекулярное тестирование представителей *G. applanatum*-coll. чтобы понять, один или несколько филовидов распространены на данной территории. В настоящей работе проанализировано 20 модельных образцов, собранных в различных районах Санкт-Петербурга. Анализ маркерной последовательности ITS показал, что на территории Санкт-Петербурга распространены один филовид (*G. applanatum*), характеризующийся значительной биоморфологической пластичностью. Поскольку спектры вариабельности отдельных признаков модельных образцов значительно перекрываются, возникает впечатление наличия тонкой видовой дифференциации. Было показано, что по отношению диаметра шляпки к толщине базидиомы можно выделить 2 базовых морфотипа – субфомитоидный (отношение радиуса шляпки к ее толщине  $\leq 2$ ) и плоский (отношение радиуса шляпки к ее толщине  $\geq 2$ ). Выраженность этого признака зависит от возраста базидиомы и содержания в дереве легко иммобилизуемых метаболитов. По субстратной локализации базидиомы делятся на латерально-прикрепленные на вертикальных поверхностях и сложные розетковидные многошляпочные образования на погребенной древесине. Отдельно отмечена изменчивость базидиом, связанная с взаимодействием с насекомыми и позвоночными животными. Было выяснено, что возрастная структура модельной макропопуляции *G. applanatum* характеризуется преобладанием базидиом первого года и двухлетних базидиом, в то время как максимальный возраст базидиом не превышает 7 лет. Высказано предположение, что относительно малый возраст многолетних базидиом – конституциональная особенность вида в таежной зоне, характеризующейся промораживанием мицелия в маргинальных зонах базидиомы. Рассмотрена вариабельность базидиоспор *G. applanatum*. Показано, что образцы с наибольшей длиной (и отчасти наибольшей шириной) базидиоспор приурочены к живым деревьям. *G. applanatum* совмещает две трофические стратегии – патогенного сапротрофа, растущего на живых деревьях и вызывающего хронические гнили, и “чистого сапротрофа”, продолжающего развиваться на мертвых стволах, а также пнях, валежной и погребенной древесине. В качестве патогена вид проявляет себя, колонизируя морозобоины комлевой области, характерные для широколиственных пород в условиях деградации искусственного дренажа насаждений. В качестве мер контроля патогена было предложено бороздование коры весенних побегов саженцев широколиственных пород для предотвращения повышенного образования морозобойных трещин, а также предотвращение деградации дренажных систем широколиственных древостоев. Составлен современный диагноз вида, учитывающий полученные данные о границах вида и его вариабельности на территории Санкт-Петербурга.

**Ключевые слова:** модификационная изменчивость, морозобойные трещины, *Ganoderma*, ITS-филогения