

The taxonomic position of *Trypophloeus grandis* Schedl, 1964 (Coleoptera, Curculionidae, Scolytinae) and comments on the species-groups

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In total, only five specimens of *Trypophloeus grandis* Schedl, 1964 are known in entomological collections. *T. grandis* is the last of the valid species in the genus to have the DNA sequence studied. The results of these DNA analyses are presented in this study. Our analyses of COI sequences combined with morphological characters place this species in a separate monophyletic species-group. It is named *Trypophloeus grandis* species-group. In addition, a more detailed study of the morphology is presented, including pictures of specimens from the type series. A discussion and a general conclusion of the species-groups in the genus *Trypophloeus* is also presented. A compilation and discussion of the biology of *T. grandis* is based on information from literature.

Key words: Coleoptera, Curculionidae, Scolytinae, *Trypophloeus grandis*, taxonomy, morphology, DNA sequence, species groups.

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Introduction

The genus *Trypophloeus* Fairmaire, 1864 (Curculionidae, Scolytinae, former Cryphalini) has a very problematic taxonomy, strongly in need of a modern revision including both classical taxonomic studies as well as analyses with DNA sequences. Already Wood (1982) highlighted the taxonomic chaos within Cryphalini: “*The generic classification of this tribe is in chaos*”. Later work by e.g., Johnson *et al.* (2020) have moved forward the phylogenetic knowledge in Cryphalini. Johnson *et al.* (2020) resurrected

the subtribe Trypophloeini Nüsslin, 1911 including the genera *Afrocosmoderes* Johnson & Jordal, 2020, *Atomothenus* Bright, 2019, *Cosmoderes* Eichhoff, 1878, *Hypothenenus* Westwood, 1834, *Macrocryphalus* Nobuchi, 1981, *Microcosmoderes* Johnson & Jordal, 2020, *Microsomus* Bright, 2019, *Pygmaeoborus* Bright, 2019 and *Trypophloeus* Fairmaire, 1860. Only 16 species are known within the genus *Trypophloeus* (Johnson *et al.* 2020, Kvamme *et al.* 2021). Four species are known from Nearctic and 12 from Palearctic. All species except *Trypophloeus grandis* Schedl, 1964 have been subjected to DNA

barcoding. The latest example is *Trypophloeus borealis* Kvamme, Mandelshtam, Salnitska, Ojeda & Lindelöw, 2021. *T. borealis* was found to be a cryptic species, first determined as *Trypophloeus dejevi* Stark, 1936 (Lindelöw 2009).

However, there are still many more unanswered taxonomic problems in *Trypophloeus* that needs to be studied, but they are outside the scope of the present paper. The nomenclature of the species is partly inconsistently used (cf. Lindelöw & Kvamme 2013, Kvamme & Lindelöw 2014). The objective of this paper is to present a DNA barcoding data on *T. grandis* and suggest a taxonomic position of this species within the genus *Trypophloeus*.

Material and methods

The nomenclature in the presented study is based on Wood (1982), Knížek (2011) and Kvamme *et al.* (2021).

Studies of the morphological characters were based on traditional studies of two paratypes in the Schedl collection using a stereo microscope. *Trypophloeus grandis* is only known from a total of five specimens:

The **holotype** and one **paratype** are in the collection of the National Natural History Museum in Paris (France), both have the label details: Alger, Fevrier 1850. Coll. H. Lucas (cf. Schedl 1964). These specimens have not been examined in this study but were examined from photos provided by the museum (Figure 1 and 2). The two **paratypes** (one female and one male) from the Schedl collection in Vienna (Austria) are from the same series as the holotype and labelled; Alger 1850 ♀. Coll. H. Lucas 78-49. Paratype *Trypophloeus grandis* K. E. Schedl. Museum Paris. These specimens have been examined in this study and are shown on figure 3 and 4.

In addition, one specimen is in the collection of the Natural History Museum in Helsinki (Finland), carrying the label information: Maroc. Aït-Melloul pr. Oued Sous. 27.ii – 2.iii 1961 collected by Håkan Lindberg (cf. Schedl 1964). This specimen was kindly sent by our colleagues in Finland to the University of Guelph, Canada for

non-destructive extraction of DNA.

Håkan Lindberg's fieldnotes and his correspondence with Karl E. Schedl can be found digitalized on the website of the Natural History Museum in Helsinki (<http://digit.luomus.fi/fi/node/1118>).

Taxon sampling, sequencing, and phylogenetic analysis

A DNA sequence from the single specimen of *T. grandis* collected in Morocco in 1961 by Lindberg has been included in the present study. It was analyzed together with additional 63 specimens of *Trypophloeus*, representing all 15 currently recognized species within the genus *Trypophloeus* (Johnson *et al.* 2020, Kvamme *et al.* 2021). The *T. grandis* COI sequence used in this study was provided us by the Natural History Museum in Helsinki, Finland. Other sequences included were downloaded from GenBank, the Barcode of Life Data System (Ratnasingham & Hebert 2007: www.barcodinglife.org), and from a previous study (Johnson *et al.* 2018, Kvamme *et al.* 2021) (Table 1). The COI matrix was aligned with AliView (Larsson 2014) and we obtained summary statistics with AMAS (Borowiec 2016). A maximum likelihood (ML) analyses with IQ-TREE (Nguyen *et al.* 2015) was performed using the best model obtained and 500 bootstrap replicates. Three species of the genus *Hypothenemus* were used as outgroups. This genus is one of the closest genera to *Trypophloeus* according to the most recent phylogenomic analyses (Johnson *et al.* 2020, 2018). All trees were visualized and edited using FigTree v1.4.3 (Rambaut 2016). Sequence divergence of sequences of COI was estimated with the Maximum Composite Likelihood model as implemented (Tamura *et al.* 2004) in MEGA ver. 11 software package (Tamura *et al.* 2021).

Ancestral area reconstruction

The ancestral area reconstruction was performed using the dispersal-extinction-cladogenesis (DEC) approach on the consensus tree derived from the ML IQ-TREE analysis. RASP v.4.2 (Yu *et al.* 2015) was used for both analyses using the two main areas in the distribution of *Trypophloeus*, Nearctic and Palearctic. The distribution area for



FIGURE 1. Holotype of *Trypophloeus grandis* Schedl, 1964 in the collection of the National Natural History Museum in Paris shown from different views and the labels attached to the specimen. Photos: Christophe Rivier, National Natural History Museum, Paris.

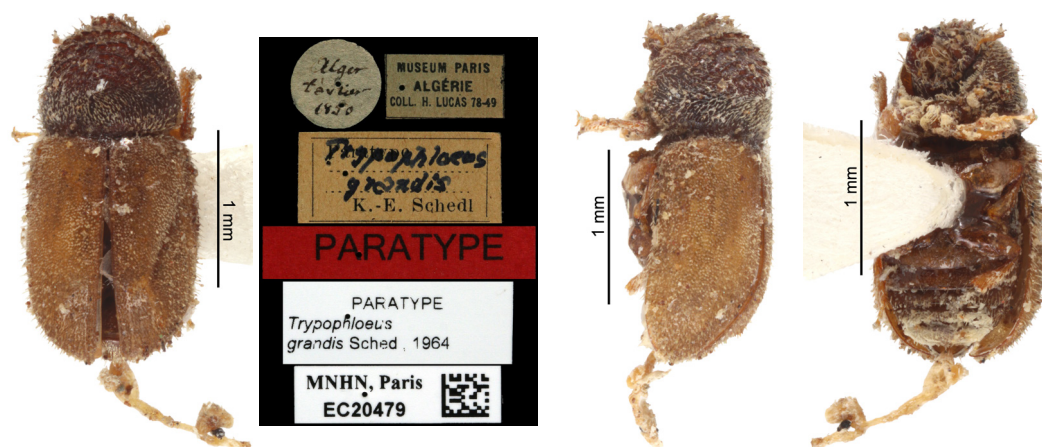


FIGURE 2. The paratype of *Trypophloeus grandis* Schedl, 1964 in the collection of the National Natural History Museum in Paris shown from different views and the labels attached to the specimen. Photos: Christophe Rivier, National Natural History Museum, Paris.

each species was collected from the literature. For these analyses only one specimen per species were included.

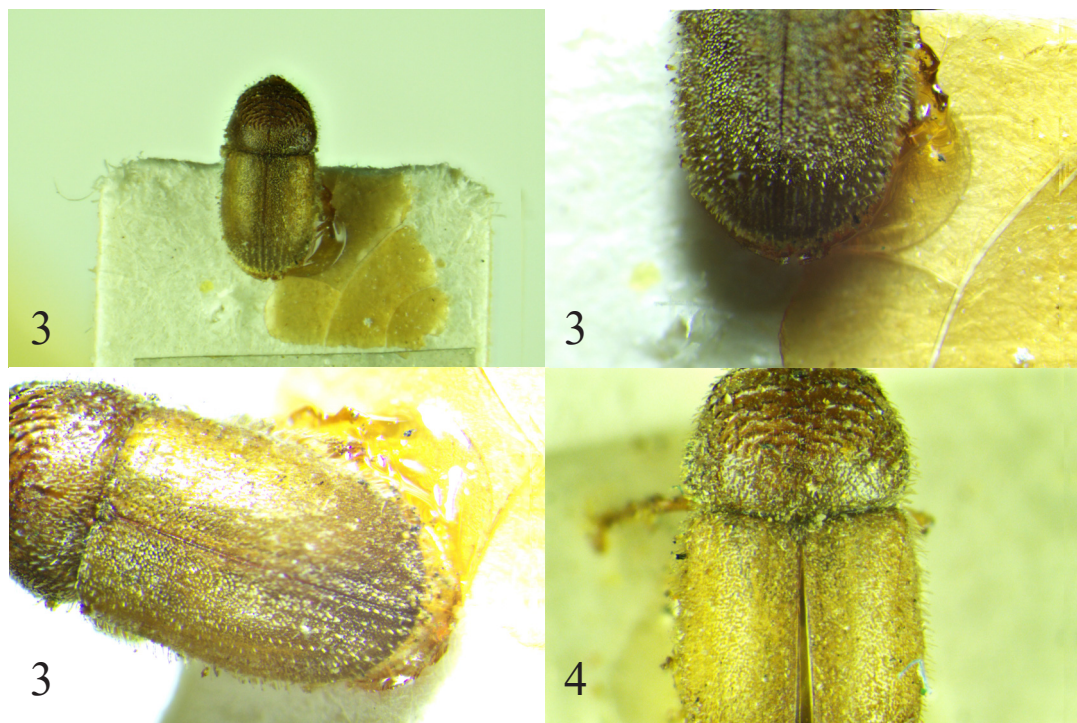
Results

Morphology of *T. grandis*

The original description of *T. grandis* by Schedl (1964) is translated from German and interpreted. The nomenclature is as used by Karl E. Schedl except that auctor is written in full text and description years are added:

Female. Dirty yellowish brown (“schmutzig gelbbraun”). Body 2.3 mm long, and 2.25 times longer than wide. The largest known species of the genus *Trypophloeus* Fairmaire, 1864, more stout built compared to *T. granulatus* (Ratzeburg, 1837) and *T. asperatus* (Gyllenhal, 1813) especially expressed in the proportion of the elytra, the central parts of elytra without visible stria and densely covered with short, flat, and broad scales, on the posterior part of elytral declivity the interstria 1 and 2 are depressed and the suture is elevated.

Frons shining, flat, densely, and rather



FIGURES 3 & 4. Paratypes of *Trypophloeus grandis* Schedl, 1964. **3.** Details of one of the paratypes of *T. grandis* in the Schedl Collection in Vienna. Photos: Åke Lindelöw. **4.** Details of the second paratype of *T. grandis* in the Schedl Collection in Vienna. Photos: Åke Lindelöw.

strongly punctured. The punctures with fine erect, small setae, setae are visibly longer along the slightly curved epistomal line. Antenna club long and slender.

Pronotum broader than long (29:25), broadest near the posterior edge. The hind angles are obtuse angled. The side edge posteriorly divergent and then tapered anteriorly. Anterior margin with 6 spines, the largest in the middle, the outermost rudimentary; the highest point is just behind the middle point, apical part strongly arched and with concentric ridges of asperites, posteriorly forming an obtuse pattern, posterior part, and sides with very fine and dense punctation. Side margin with dense, but fine punctures and covered with fine scales.

Elytra Hardly broader than long (30:29) and 1.6 times as long as pronotum. Apex of elytra from above broad rounded and muzzle shaped. The side parallel up to the middle. Apex broadly rounded and sloping down from the middle,

without obvious stria, densely covered with flat, depressed scales. The density of scales similar in all interstria, but show four irregular rows, towards and on the declivity all interstria have a row of slender, slanting erect scales; on the steep sloping part of declivity the 1st and 2nd interstria are clearly depressed as lines; suture slightly erased towards apex, side bulges slightly implied, the basic scale pattern as on the dorsal part of elytra, the medial longer scales slightly stronger.

Male. Elytra side bulges anterior more obvious and in the third interstria with a sharp spine.

Our studies show that *T. grandis* is separated from the other Palearctic *Trypophloeus* species by the total body length up to 2.3 mm (*cf.* Pfeffer 1995) and the very robust body shape. According to Pfeffer (1995) the other species have a size up to 2,2 mm. The length/width of the two paratypes in the Schedl Collection in Vienna were measured. The proportion was 2.0 and 2.07 which is less than 2,26 that Schedl (1964) mentioned.

TABLE 1. List of data from BOLD and new data used in this paper. COI = GenBank and Barcode of Life (BOLD) COI accessions. * = Natural History Museum, Helsinki (Finland). ** = (GAC.33850_LEFIJ28026-22)

Name	Location and host	Voucher	COI
OUTGROUP			
<i>Hypothenemus hampei</i>	USA, Puerto Rico	UPR13Hypham	MK622712
<i>Hypothenemus seriatus</i>	USA, Puerto Rico	UPR66Hypseriatus	MK622767
<i>Hypothenemus obscurus</i>	USA, Puerto Rico	UPR58Hypobsc	MK622758
<i>Trypophloeus asperatus</i>	Ukraine, Carpathians	10064509	KU144883
	Ukraine, Carpathians	10064538	KU144884
	UK	BMNH 1046450	NC_036285
	UK	BMNH 1046450	KX035204
INGROUP			
<i>Trypophloeus alni</i>	Russia, Orzhitsy, Lomonosov district, Leningrad Prov.,9.V.2001, host Alnus incana, Leg et det. M. Mandelshtam. Ethanol preserved	No. 10	MT672002
	Russia	CrTry01	JX263805
	Russia, Leningrad Prov, Orzhitsy	CrTry01	KU144900
<i>Trypophloeus asperatus</i>	Germany, Thuringia, Erfurt, Noeda, Auwald	ZFMK-TIS-2535593	KU913568
	Norway, More og Romsdal	BHJ316	-
	Norway, More og Romsdal	BHJ315	-
	Norway, More og Romsdal	BHJ318	-
	Norway, More og Romsdal	BHJ320	-
	Norway, More og Romsdal, Nesset	BHJ315	KU144911
<i>Trypophloeus binodulus</i>	Norway, More og Romsdal, Nesset	BHJ318	KU144910
	Norway, More og Romsdal, Nesset	BHJ317	KU144912
<i>Trypophloeus bispinulus</i>	Finland, northern Ostrobothnia, Kiiminki	ZMUO/FIN:003978	KJ965579
	Russia, Leningrad Prov, Lomonosov, Old Peterhof	GBCL49834-19	KU144913
	Russia, Leningrad Prov, Kuznechnoye	10064516	KU144892
	Russia, Leningrad Prov, Kuznechnoye	10064523	KU144891
	Russia	CrTry02	KC845440
	Russia, Pskov Prov, Astratovo	10064525	KU144894
	Russia, Pskov Prov, Astratovo	10064514	KU144893
	Norway	BHJ317	SCOL303-12
	Russia, Saint Petersburg	BHJ225	SCOL214-12
	Norway, Fi Karasjok, Jergul (EIS 166)	No. 12	MT672003
	3.VII.2012 host Salix myrsinifolia	No.12B	MT672007
	Leg. et det. Å. Lindelöw. Etanol conserved		

TABLE 1. continued

Name	Location and host	Voucher	COI
<i>Trypophloeus dejevi</i>	Russia, Vladivostok, 16.VIII.2000, host: Populus tremula. Leg et det. M. Mandelshtam. Dry mounted	No. 7	MT672000
		No. 8	MT672001
		No. 9	MT672006
	Russia, Primorsky Krai, Arseniev	BHJ283	KU144914
	Russia, Primorsky Krai, Anisimovka	CrTry09_4	KU144903
	Russia, Primorsky Krai, Anisimovka	CrTry09_3	KU144902
	Russia	AJJ_64	MG051184
	Russia, Primorskiy Kray	BHJ279	SCOL266-12
<i>Trypophloeus discedens</i>	Russia	UFIFAS_UFFE_13677	-
	Ukraine, Kharkov Prov, Gaidary	10064510	KU144885
	Sweden, Up Fiby	CrTry08	KU144904
	Russia, Yaroslavl Prov, st Molot	10064512	KU144895
<i>Trypophloeus grandis</i>	Ukraine, Kharkov Prov, Gaidary	10064519	KU144886
	Morocco, Aït-Melloul pr. Oued Sous.	NHMH*, Lindberg 1961	PP437870 **
<i>Trypophloeus granulatus</i>	Norway, Aust-Agder	BHJ56	SCOL054-12
	Ukraine, Carpathians	CrTry05_2	KU144906
	Norway, More og Romsdal	BHJ319	SCOL305-12
	Ukraine, Carpathians	10064536	KU144889
	Ukraine, Carpathians	10064529	KU144890
	Ukraine, Carpathians	CrTry05_1	KU144905
	Norway, More og Romsdal	BHJ321	-
	Tajikistan, Pamirs, Gishun	10064503	KU144898
<i>Trypophloeus klimeschi</i>	Tajikistan, Pamirs, Gishun	10064502	KU144899
<i>Trypophloeus nitidus</i>	USA, Alaska. 1996. Salix alaxensis. Leg. et det. M.M.Furniss. Dry mounted	No. 14	MT672004
		No. 14B	MT672005
		No. 14C	MT672008
		No. 14D	MT672009
<i>Trypophloeus rybinski</i>	Ukraine, Crimea, Demerdzhi	CrTry06_1	KU144907
<i>Trypophloeus salicis</i>	USA	I10239	-
		UFIFAS_UFFE_13951	-
<i>Trypophloeus nitidus</i> (= <i>striatulus</i>)	USA, Alaska, Chandalar Shelf	UAM:Ento:111009	KU876418
	USA, Alaska, Chandalar Shelf	UAM:Ento:111008	KU876419
<i>Trypophloeus thatcheri</i>	USA	10064484	KU144897
	USA	10064482	KU144896
<i>Trypophloeus tremulae</i>	Ukraine	CrTry04	KC845442
	Ukraine, Crimea, Magabi	CrTry04_1	KU144908
	Russia, Krasnodar	10064500	KU144887

General morphology of the species-groups

The morphologic characters have been studied to see if the morphology on the species-group level is different so they can be identified based on morphology alone. The species-groups follow mainly the definition in Kvamme et al. (2021).

***T. salicis* species-group.** *T. salicis* Hopkins, 1915, *T. populi* Hopkins, 1915 and *T. thatcheri* (Wood, 1954) are restricted to the Nearctic region. Thus, we do not treat the members of the group on species level here.

***T. grandis* species-group.** Based on the DNA study *T. grandis* is placed separately in a monophyletic species-group. Thus, the morphological species characters also separate this species-group from the other groups.

The very robust habitus of *T. grandis* as Schedl (1964) mentions is alone enough to distinguish it from the species of the other species groups. Other characters include pronotum broader than long and with 6 spines on the anterior edge, although one specimen from the Schedl Collection had only 4 spines. Posterior part of pronotum densely punctured. Stria on elytra have small punctures not impressed, with recumbent scales. On declivity interstria are depressed and suture erased.

***T. granulatus* species-group.** Only *T. granulatus* (Ratzeburg, 1837) and *T. binodulus* (Ratzeburg, 1837) are included in this species-group. Punctures of the stria on elytra are not impressed and with fine punctures on posterior part of pronotum disc.

***T. alni* species-group.** *T. alni* species-group consist of *T. borealis* Kvamme, Mandelshtam, Salnitska, Ojeda & Lindelöw, 2021, *T. nitidus* Swaine, 1912, *T. dejevi* Stark, 1936 and *T. alni* (Lindemann, 1875).

These species are in general characterized by slender appearance, elytra longer than 1.5 times the width (cf. Pfeffer 1995). The main characters are the frontal micro sculpture and reticulated upper part of frons and vertex. The other *Trypophloeus* have aciculation (cf. Kvamme et al. 2021).

This is the only species-group including species from both the Nearctic and Palaearctic regions.

***T. discedens* species-group.** The group includes the following species: *T. rybinskii* Reitter,

1895, *T. klimeschi* Eggers, 1915, *T. tremulae* Stark, 1952, *T. discedens* Palm, 1950 and *T. bispinulus* Eggers, 1927.

This species-group is uniform considered the main morphological characters, with coarse punctures at the posterior parts of the pronotum and distinct striae on the elytra. However, *T. rybinskii* has a very slender body appearance, more like *T. alni*. Data from the DNA studies clearly support to include the species in the *T. discedens* species-group.

The name for the species-group was earlier proposed as *T. rybinskii* species-group (Kvamme et al. 2021). *T. discedens* has a more representative body shape for the species-group compared to *T. rybinskii*. Consequently, the name should be changed to the *T. discedens* species-group.

Phylogenetic analyses and sequence divergence estimates

The COI matrix consisted of 521 bp with 7.24% missing data, 192 variable sites and with a proportion of 0.28 parsimony informative sites. The average pairwise difference among *Trypophloeus* species was 0.1600 (excluding samples of *T. asperatus*). These analyses were based on material from one single specimen of *T. grandis*, already >50 years old. Access to fresh material is desirable as well as observations on breeding galleries and choice of host trees. Five major groups were recovered with support (>75 bootstrap) within *Trypophloeus* with also high resolution and support among the species within each group. The only exception was the *T. salicis* group, where the position of *T. salicis* is not supported with respect to *T. populi* and *T. thatcheri* (Figure 4). Three taxonomic species-groups (*T. granulatus*, *T. grandis*, and *T. discedens*) consist of species with only a Palearctic distribution, while all species within the *T. salicis* contain Nearctic species. Only one taxonomic species-group, *T. alni*, has species from both the Nearctic and Palearctic regions. Our results from the ancestral area reconstruction using DEC suggests that *Trypophloeus* likely originated in the Palearctic and expanded into Nearctic on two occasions. In one instance in the *T. salicis* species-group, and another into the Nearctic within the *T. alni* species-group (Figure 5).

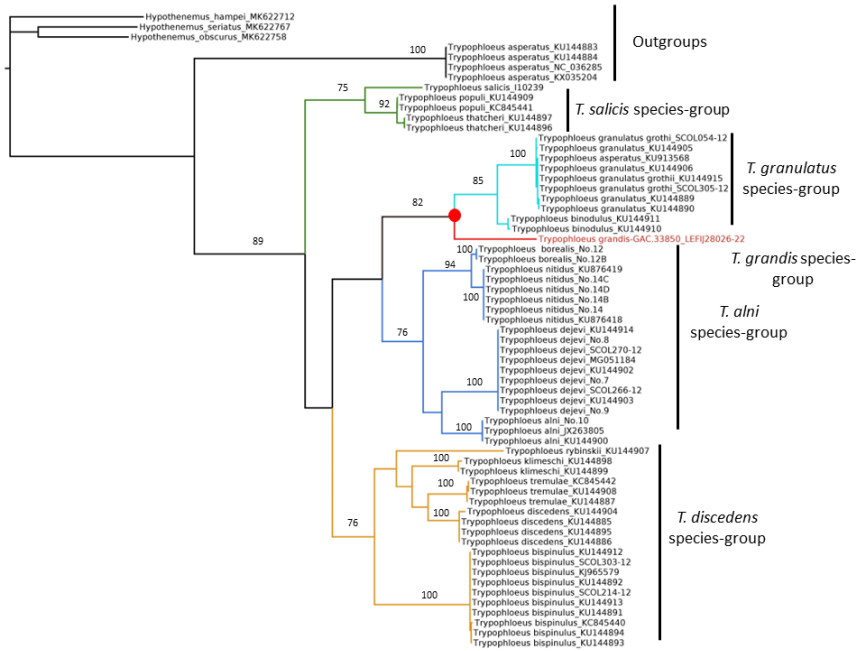


FIGURE 5. Consensus tree obtained with IQ-TREE using COI sequences in *Trypophloeus* species. The different colors represent the different taxonomic groups. Values next to the branches indicate bootstrap support. The name *T. asperatus* in *T. granulatus* species-group is an obvious misnaming.

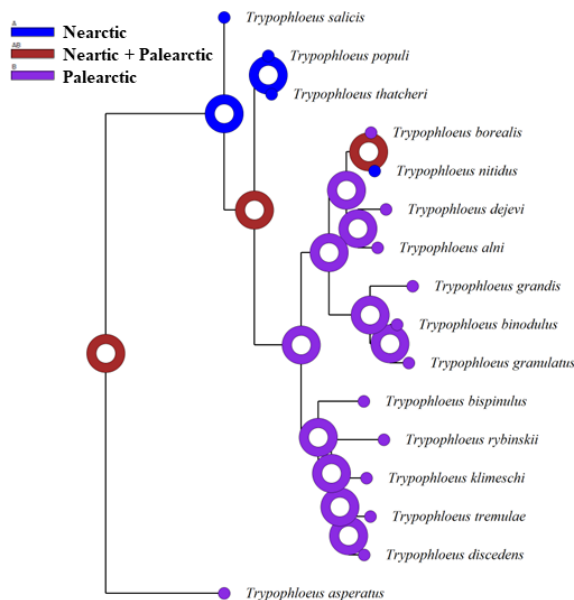


FIGURE 6. Ancestral area reconstruction of the main distribution of *Trypophloeus* species using dispersal-extinction-cladogenesis (DEC) on the consensus tree as implemented in RASP.

Discussion

Morphology

The description by Schedl (1964) is very extensive. The color of elytra is mentioned as yellow brown, which can be questioned since specimens collected from host trees may be teneral and all other species are black when fully colored. More material is required before an answer can be given.

Species-groups

The DNA based phylogenetic tree clearly shows that species are grouped in five distinct species-groups. However, this is only partly supported by morphological characters. Some characters overlap between the species-groups. As a conclusion we interpret the grouping of species as more solid when based on the DNA than on more confusing morphological characters.

T. salicis species-group includes three species, all Nearctic and clearly different from the other groups. The *T. granulatus* species-group and the *T. discedens* species-group contain only Palearctic species. Only the *T. alni* species-group have species from both Nearctic and Palearctic regions since *T. nitidus* Swaine, 1912 is a Nearctic species (Kvamme et al. 2021).

T. grandis is a well separated species and rather distant from the nearest relatives in the *T. granulatus* species-group, based on the phylogenetic and divergence analyses of COI sequences (Figure 4). Thus, *T. grandis* is placed in its own monophyletic species group. All five groups have high bootstrap support, and the average sequence divergence between *T. grandis* species-group and the other four groups is similar (ranges from 0.1989-0.1359). This does justify our recognition of five groups within *Trypophloeus*.

The DNA-analysis of *T. grandis* is only made from material from one single specimen, already >50 years old. Access to fresh material is desirable.

Pfeffer (1995) placed *T. grandis* in his “*T. asperatus* species-group”, based on morphological studies alone. *Trypophloeus asperatus* (Gyllenhal, 1813) is not a valid name anymore (cf. Knížek 2011) and has been transferred to the genus

Cryphalus (Erichson, 1836). According to Justesen et al. (2023) *C. asperatus* was included in the genus *Trypophloeus* due to a mistake by Stephen Wood, based on a specimen of *Cryphalus saltuarius* Weise, 1891. The type species of the genus *Trypophloeus* is *Bostrichus asperatus* Gyllenhal, 1813. *Bostrichus asperatus* Ratzeburg, 1837 is a homonym and therefore unavailable. It is synonymous with *C. saltuarius*, which is the valid name for the species (cf. Knížek 2011). Consequently, there can be no *T. asperatus* species-group.

Pfeffer (1995) also named a *T. granulatus* species-group. But *T. granulatus* do not belong in the group with *T. rybinskii* Reitter, 1895, *T. klimeschi* Eggers, 1915, *T. tremulae* Stark, 1952, *T. bispinulus* Eggers, 1927 and *T. discedens* Palm, 1950. Kvamme et al. (2021) proposed the renaming of this species-group as *T. rybinskii* species-group. However, species-group names are not regulated by the code (ICZN 1999). Morphologically *T. rybinskii* “belongs” to the *T. alni* species-group. Since *T. discedens* is a more representative species of the group according to the body shape and the name *T. discedens* species-group should replace the name *T. rybinskii* species-group.

According to the DNA results the *T. granulatus* species-group includes only the two Palearctic species *T. granulatus* and *T. binodulus* (Ratzeburg, 1837). There are still some unanswered questions concerning the names *T. grothii* (Hagedorn, 1904) and *T. spiculatus* Eggers, 1927. They are listed as synonyms of *T. binodulus* (e. g. Knížek 2011), but these questions are outside the scope of this paper. The *Trypophloeus* species do not have very clear morphological differences, which the taxonomic history and all the misidentifications show. The DNA studies are consequently considered a better basis for grouping the species compared to morphology. An ancestral area reconstruction (cf. Figure 5) of the distribution of *Trypophloeus* species shows that the ancestors of *Trypophloeus* arrived Nearctic at two different occasions.

One is the ancestor of the *T. salicis* species-group and the other is the ancestor of *T. nitidus*. This clearly shows the connection between the fauna in the Nearctic and Palearctic regions. Wood (1982; 850) wrote that the genus *Trypophloeus* and

other genera in the tribus Cryphalini originated in Eurasia and reached North America recently. On what basis Wood made this conclusion is unknown, but our results indicate that Wood was correct.

Biology

Schedl (1964) does not mention any host tree in his paper. Schedl asked Lindberg for information on host tree information (letters from Schedl to Lindberg 20.i.1964 and 20.i.1964 (Natural History Museum, Helsinki, cf. <http://digit.luomus.fi/fi/node/1118>). No letter from Lindberg to Schedl answering the question has been found. Nor do Lindberg's field notes give any information on host tree. However, other beetle species mentioned in the field notes indicate that Lindberg collected from *Populus* species in Morocco, and he also mention collecting on *Populus alba* (Natural History Museum, Helsinki, cf. <http://digit.luomus.fi/fi/node/1118>). Pfeffer (1995) mentioned *Populus* sp. as a host tree. So far, we have not been able to trace where he got this information from, but he might have been in contact with Lindberg personally. It is reasonable to think that *T. grandis* has *Populus* sp. (spp.) as host tree(s) since many other species in the genus live in *Populus* spp. The following *Populus* species are indigenous species in North-Africa: *Populus alba* L., *P. euphratica* Olivier, *P. nigra* L. and *P. tremula* L. (only in Algeria) (Kew 2023). In addition, many exotic species, hybrids etc. have been introduced for forest use in the region (FAO 1979). The conditions in the region are thus good for species using *Populus* species as host trees. To document *Populus* spp. as host trees for *T. grandis* new observations are needed.

Many of the remaining challenges with the species names in the genus *Trypophloeus* are outside the scope of this study. Therefore the nomenclature considered valid for the species in the genus follow Knížek (2011) and Kvamme *et al.* (2021). The only exception is *T. discedens* which is not mentioned by Knížek (2011, cf. Kvamme & Lindelöw 2014). Thus, we use the name as used by Silfverberg (2010) and Rassi *et al.* (2015) without discussing the validity of the name.

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