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A new species of *Gomphus* from southeastern United States

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Abstract: *Gomphus ludovicianus* is proposed as a new species. It is described morphologically, placed phylogenetically and compared with *G. crassipes* from the Atlas Mountains of North Africa.

Key words: Gomphales, cantharelloid fungi, taxonomy, phylogeography

Introduction: *Gomphus sensu lato* has been shown to be polyphyletic (Humpert et al. 2001; Hosaka et al, 2006; Giachini et al., 2010), with one result being restriction of *Gomphus sensu stricto* to very few taxa (Giachini et al. 2010). One name, *G. clavatus*, is in use for basidiomata collected around the temperate Northern Hemisphere (Petersen, 1971). Giachini et al. (2011) recognized only two additional names, *G. brunneus* and *G. crassipes*, both from Africa. With such a limited species list, it was surprising to find an undescribed species from southern United States, not usually considered sub-boreal. The literature, however, described and illustrated *G. crassipes*, which must be distinguished if the New World collections are to be proposed as new.

Materials and Methods: Morphological procedures were described in Petersen and Hughes (2010). Tissue response to 3% Potassium hydroxide (KOH) was examined and color changes noted. Microscopic characters were examined with light microscopy as well as phase contrast microscopy (PhC).

Color names enclosed in quotation marks are from Ridgway (1912); those cited alphanumerically are from Konerup and Wanscher (1967).

Procedures for DNA extraction, PCR of the ribosomal ITS and LSU regions and cloning of ITS PCR products was described in Hughes et al. (Hughes et al. 2013). The data set used for alignment was obtained by a blast search of GenBank accessions using *Gomphus ludovicianus* ITS and LSU sequences. This search recovered both *Ramaria* and *Gomphus* sequences, consistent with findings by Giachini (2004) and Giachini and Castellano (2011) that neither genus is monophyletic. PhyML maximum likelihood (Guindon and Gascuel 2008), for the ribosomal LSU dataset was performed in Geneious (Geneious 2005) using the GTR model of evolution with the ratio of

transitions to transversions, the proportion of invariant sites and the gamma distribution parameter estimated. One-hundred bootstrap replicates were performed. Available ITS sequences for *Gomphus* and related *Ramaria* collections generated by this and other studies were too divergent to align easily. LSU sequences also were unusually divergent from each other but were alignable, although small differences in alignments could change observed tree structure considerably. This is reflected by low bootstrap scores at deeper nodes in the phylogeny. Available ITS sequences and LSU sequences used to generate the LSU phylogeny are deposited in GenBank (Table 1).

Reciprocal monophyly of *Gomphus clavatus* and *Gomphus ludovicianus* was tested using Rosenberg's P_{AB} statistic (Rosenberg 2007; Masters et al. 2011) as implemented in Geneious using the Species Delimitation plugin (Masters et al., 2011). This statistic is the probability that a putative species containing 'A' collections is monophyletic with respect to a putative sister clade containing 'B' collections. The ratio of the within-species genetic differentiation to interspecies-genetic differentiation (Intra/Inter ratio) was also examined within Geneious using this plugin.

Results:

Gomphus ludovicianus R.H. Petersen J. Justice and D.P. Lewis Figs. 1-9.

Mycobank no.: 808722

Holotype: Louisiana, Grant Parish, Kisatchie National Forest, Catahoula Dist. vic. Intersection LA 123 & FR 120 & CO 360, 31° 38.524' N, 092° 28.097' W, 6.XII.2013, coll Jay Justice and Carl David, TFB 14476 (TENN 69161; holotype);

Macromorphology: Basidiomata (Figs. 1-4) generally stout, obconical, usually depressed,

subpseudorhizal. Pileus 7-18 cm broad, shallowly convex when young, becoming applanate with down-turned margin, innately coarsely scaly or lumpy (like *Hydnellum imbricatum*, *Turbinellus bonarii*, see Figs. 2, younger basidiome, 4); pileus surface dull “benzo brown” (9D3) to “deep Quaker drab” (17B2) (compare left and right surfaces in Fig. 1), bruising darker. Some surface over center paler. Paradermal scalp of dried basidiome upper surface macroscopically dull cream colored, instantly macro and microscopically red-orange in 3% aqueous KOH. Fresh pileus and stipe flesh (Fig. 6) delicately mottled, “deep Quaker drab” to “ecru drab” (16B2), naturally “yellow ocher” (4C7) when bruised (by rotting or insect damage; Fig. 6). Hymenophore delicately wrinkled (Figs. 3, 5), outward on pileus with radial (longitudinal) ridges higher and dominant, with subordinate anastomosing interveins, “purple gray” (23B3), downward on stipe becoming gyrose without orientation (i.e. merismatoid), finally becoming smooth on upper stipe. Upper stipe surface dull purplish gray mottled in small, ill-defined paler off-white areas, irregularly lumpy in contour, matt. 3% KOH on fresh pileus surface = cherry red, similar on stipe, on hymenium only darker purple. Odor and taste negligible.

Habitat and phenology: Forest of *Quercus*, *Pinus palustris*, *Carya*: known from central Louisiana and southeastern Texas.

Micromorphology: Superficial pileus surface of young basidiomata detersile; hyphae of pileus scales or lumps 2-3.5 μm diam, tightly interwoven, with common hyphal termini emergent and forming a delicate pruina; emergent termini cylindrical but irregular in outline (Fig. 7A), often with suggestions of lobes or branches. Tissue underlying pileus surface a layer of repent, tightly interwoven hyphae without radial orientation; hyphae 2.0-4.5 μm diam, inconspicuously clamped, thin-walled, unornamented; contents heterogeneous, obscuring observation of hyphal walls. Dried

basidiome flesh extremely friable, disarticulating into powder not supporting microscopic examination. KOH applied to intact dried hymenium macroscopically unchanging (merely darkening to deep purple), immersion in KOH with cover slip quickly changing to deep orange-brown. Pileus tissue under subhymenium tightly interwoven, free (not adherent nor with gelatinized matrix); hyphae 3-6 μm diam, thin- to firm-walled, conspicuously clamped.

Hymenium distinctly thickening, often in semidefinable layers, appearing more congested and more pigmented in oldest layers, composed of paraphysoid basidioles, narrowly clavate basidioles and basidia of various stages of maturity. Basidioles (Fig. 8) 2.5-3.5 μm diam, linear, thin-walled, cylindrical, sometimes apically lobed or branched, widening through development to elongate narrow-clavate shapes and developing scattered, small, refringent guttules; mature basidia (Fig. 8) 59-62 \times 9-12 μm , clavate clamped, 4-sterigmate, effete after spore discharge and not totally collapsing or disintegrating and therefore forming succeeding hymenial layers. Basidiospores (Fig. 7B) (12-)14-17 \times (4.5-)5-7 μm ($Q = 1.87-2.82$; $Q^m = 2.46$; $L^m = 14.70 \mu\text{m}$), ellipsoid with slightly depressed suprahilar region, minutely irregular in outline; contents with one or more amorphous, refringent inclusions (not spherical, refringent oil droplets); ornamentation minutely rugulose, hardly definable, weakly cyanophilous.

Upper stipe surface a superficial dense thatch of hyphae; hyphae very slender (2-2.5 μm diam), tightly interwoven, gnarled, thin-walled, copiously branched with common acerose hyphal tips protruding, interwoven portions apparently involving abundant spherical bodies <1 μm diam, obscuring accurate observation. Subtending hyphal layer of strictly parallel, strictly longitudinal hyphae 3-3.5 μm diam, firm-walled, occasionally but conspicuously clamped, perhaps adherent (disarticulating in bundles or sheets). Stipe internal tissue generally longitudinally

interwoven; hyphae 3-8 μm diam, firm- to thick-walled (wall – 0.7 μm thick), conspicuously clamped; ampulliform swellings common, -9 μm diam, thick-walled (wall -1.5 μm thick, refringent; PhC), internally smooth to finely stalactitiformly ornamented.

Commentary: Although 3% aqueous KOH applied to fresh or dried hymenium produces only dark purple coloration, when a small portion of dried hymenium is immersed in KOH a color change is immediate to bright copper-orange. The KOH color change on pileus surface (fresh or dried) is instantaneous and sensational, but differs from cherry red on fresh surface to bright copper-orange on dried surface.

Cyanophilous reaction of spore ornamentation is doubtful. Spores seem to react from acyanophilous to weakly to strongly cyanophilous, probably dictated by exposure to the stain in the crushed mount. The spore width in the proximal area of spore (from spore base distally to 1/4 spore length, including the suprilar area) is weakly cyanophilous to acyanophilous and apparently smooth-walled from hilar appendix upward. Distally over the upper 2/3-3/4 spore surface, the surface becomes very finely rugulose (with almost uniform cyanophily), with spore profile very delicately pebbled. Ornamentation is almost indefinable, not clearly definable as spots or ridges.

Clamp connections are sometimes inconspicuous but universally present. Hyphae are tightly packed, apparently adherent in some areas, and branches arise from clamp connections, all rendering structures difficult to ascertain.

Maire (1914) reported the pileus surface as tomentose and Petersen (1971) also found this in *G. clavatus*, with common, erect, slender hyphae arising from repent hyphae as a short trichodermium. In *G. ludovicianus*, pileus surface is a layer of strictly interwoven, repent hyphae. Whether a tomentose surface is deterrent

or merely absent in basidiomata in the collections examined is unknown, but common spores deposited on the pileipellis indicate that the tissue forms, in fact, the true pileipellis surface.

Especially DPL photos show pileus surface with the same coppery shades as commonly seen in *Gloeocantharellus purpurascens*. KOH reactions are identical, as they are with purple *Ramaria* taxa [*R. fennica* (P. Karst.) Ricken, *R. violaceibrunnea* (C.D. Marr & Stuntz) R.H. Petersen, *R. purpurissima* R.H. Petersen and Scates, *R. fumigata* (Peck) Corner, etc.] and probably *R. cedretorum* (Maire) Malençon.

Specimens examined: Louisiana, Grant Parish, Kisatchie National Forest, Catahoula Dist. vic. Intersection LA 123 & FR 120 & CO 360, 31° 38.524' N, 092° 28.097' W, 6.XII.2013, coll Jay Justice and Carl Davis, TFB 14476 (TENN 69161; holotype); same location, 7.XII.2013, coll David P. Lewis, DPL 11087 (TENN 69174). Texas, Jasper Co., vic. Erin, off FM 1004, 30.802589° N, 93.98233° W, 29.XI.2013, coll. David P. Lewis (as *G. cf. clavatus*), DPL 11067 (TENN 69175).

Separation of *Gomphus crassipes*:

Gomphus crassipes (Dufour) Maire. 1937. Mem. Soc. Sci. Nat. Maroc 45: 81

Basionym: *Cantharellus crassipes* Dufour. 1889. Rev. Gen. Bot. 1: 358.

≡ *Neurophyllum crassipes* (Dufour) Maire. 1914. Bull. Soc. Mycol. France 30: 216.

Dufour's (1889) protologue included a photo of two basidiomata (one photo reproduced by Giachini et al. (2012)). Each shows a stout stipe with a single pileus and a reticulate hymenophore. Although Dufour included an abbreviated description, spores were described as white. Dufour (1889) reported that his original specimens of *Cantharellus crassipes* were gathered at "Teniet-el-Haad (province d'Alger)," (Google earth = 35° 05' 17" N, 2° 01' 43" E) a town

located not far from the Mediterranean coastline. He continued his report of location, however, as “la maison forestière du Rond-Point des Cèdres, par conséquent à une altitude d’environ 4,450 mètres...” on “Le Djebel-Enndate montagne.” The discrepancy is unexplained. Moreau (1914) described the forestry station and its resources.

The “Moyen Atlas” (middle Atlas Mountains) roughly describes the middle portion of the Atlas Mountains, which extend southwest to northeast within present-day Morocco. At one time, a large portion of the Moyen Atlas was considered part of Algeria, a French colony, and it has been from the cedar (*Cedrus*) forests of the higher altitudes of these mountains that material of *C. (Gomphus) crassipes* has been gathered.

Maire (1914) commented at length on *C. crassipes*, furnished a color lithograph and discussed its relationship with the large, fleshy “*Clavaria*” taxa now placed in *Ramaria*. In the same paper, Maire proposed *Clavariella cedretorum* and redescribed *C. versatilis*, both now in *Ramaria* and both exhibiting violet to purple coloration when young, similar to the colors attributed to *Neurophyllum crassipes* (Dufour) Maire. Presciently, he concluded that there were “deux series distinctes”: 1. *Cantharellus-Craterellus-Clavaria*; and 2. *Neurophyllum-Clavariella*. Implicated in the first line was present-day *Clavulina*, and in the second line, present-day *Clavariadelphus*. Maire also corrected Dufour’s report of white spores in *Cantharellus crassipes* to “jaune-ochracé.” Later, Maire and Werner (1937) cited two Algerian specimens of *G. crassipes* “sous Cedres” at Ifrane (Moyen-Atlas Reg.) at 1700 m (leg Borey, Oct. 1937) and Azrou (Moyen-Atlas Reg.) at 1700 m (November, 1937).

A report by Malençon (1957) merely mentioned *G. crassipes*, but by 1970 (Malençon and Bertault 1970: 24) *G. crassipes* was noted as one of several taxa unique to the acid soils surrounding Azrou [33° 26’ 30” N, 5° 13’ 29” E], reminiscent of the

“Hygrophores, des Russules et des Bolets des conifères de l’Europe tempéré et des régions alpines.” Later, however, Malençon and Bertault (1975) included a full description and line drawing for the fungus as they knew it, but from Algeria, not Morocco. Two apparently immature basidiomata were illustrated in color, showing a suggestion of the coarse scaly pileus surface, while a third basidiome was shown in longitudinal section, the flesh showing subtle avellaneous shades (in its legend, the plate is noted as “G.M. no. 1525,” the only reference to a specific herbarium specimen in the literature). Two different basidiomata were illustrated with line drawings as they appeared to be more mature, exhibiting single, central stipes but lobed, mesopodal pileal extensions more typical of the northern *G. clavatus*. Some spores were also represented, with ornamentation generally conforming to that common in the Gomphaceae. Because Dufour’s original description was not in their hands, they reproduced Saccardo’s (1891) Latinized description and their personal experience with the taxon. Spores were described as “argilacé clair” and figured with appropriate nodulose ornamentation.

In the report by Malençon and Bertault (1975: 524-527) there is no evidence that Dufour’s original material was examined, but a fresh collection was gathered at Ràs-el-Mâ (November, 1950). Apparently based on that specimen, numerous details were added to previous descriptions, as follows: 1. basidiomata cespitose, more rarely isolated; 2. pileus surface matt, subtomentose, “ocracé ou roussâtre;” 3. pileus margin often upraised to produce a cyathiform shape; 4. stipe 30-(50)-70 × 10-30 mm, central or occasionally lateral, short or bulbous at base, violet upward and grayish in age; 5. ridges of hymenophore longitudinal, often anastomosed, “beau violet” becoming grayish yellow by sporulation; 6. flesh violet, marbled when sliced; 7. clamp connections at septa; 8. pleurocystidia absent; 9. basidia (2-)4-spored, 80-(100)-115 × 9-10(-12) µm, clavate with significantly elongated

bases; 10. spores $13-15 \times 5.5-6 \mu\text{m}$, “subhyalines ou jaune très pale,” “amygaliformes-allongées, fusoïdes-cambrées à sommet atténué et base fuyante avec apicule lateral saillant et dépression dorsale plus ou moins marquée...”; 11. distributed apparently strictly under cedars; 12. not known from Morocco but only from calcareous soils in Algeria. Basidiome colors were reported using Saccardo’s *Chromotaxia*, with the pileus surface “*cremeus, ochrালেucus et isabellinus*.”

Dufour (1889, reproduced by Giachini et al. 2012), Maire (1914, also reproduced by Giachini et al. 2012) and Malençon and Bertault (1975) all provided illustrations with their reports. Some of those by Dufour (photo) and Malençon and Bertault (particularly Plate 22) represent somewhat immature basidiomata and suggest a rather scaly or lumpy pileus surface. This feature may be suppressed into basidiome maturity, but persists in *G. ludovicianus*.

Giachini and Castellano (2011) and Giachini et al. (2012) reported that specimens of *G. crassipes* were at RAB (Rabat), but were unavailable for loan due to fragile condition. They relied on literature, therefore, to provide illustrations and description. Giachini et al. (2012) also reported the species from Spain, although there was no reference to a specimen, but only to a personal communication. Giachini et al. (2012) designated as lectotype Dufour’s (1889) protologue photo but understandably declined to designate an epitype. Given only bibliographic information, we also decline to establish an epitype for *G. crassipes*.

Our attempt to procure material of *G. crassipes* from RAB was not acknowledged. Index Herbariorum’s listing of Montpellier University Herbarium (MPU) indicates that the collections of R. Maire and G. Malençon are housed there. A request for information and material was not acknowledged. Based on habitat (apparently limited to *Cedrus* forests), basidial dimensions (reported as much longer in *G. crassipes*) and

geographic distance (Morocco-Algeria versus southeast United States), however, it seems efficacious to describe the American material as new.

Molecular Results: A ribosomal LSU phylogeny is given in Fig. 9. At the ribosomal LSU level, *Gomphus ludovicianus* sequences from Louisiana and Texas collections formed a well-supported monophyletic clade, as did *G. clavatus* sequences deposited in GenBank by other workers. Rosenberg’s P statistic for *G. clavatus* and *G. ludovicianus* was $P_{AB}=1.85 \text{ E-}3$ strongly indicating reciprocal monophyly for the two clades. Ross et al. (2008) developed a test based on simulations that determined whether, given an aligned data set, a given species could be correctly identified. He demonstrated that the ratio of the within-species genetic differentiation to interspecies-genetic differentiation (Intra/Inter ratio) was a better predictor of correct identification than the “barcode gap,” a hiatus in barcode sequences. P_{ID} (strict) “is the mean probability of correctly identifying an unknown member of a species with the proviso that it must fall within, but not sister to, the species clade in a tree” (Masters et al. 2011). It is sensitive to the number of reference taxa (3 in this case) and was $P_{ID} = 0.79$ (95% confidence interval 0.62-0.97). P_{ID} (liberal) requires only that the query sequence form a clade with a monophyletic species group, either as sister to the monophyletic group or within the sister group of reference sequences. Here the probability of a correct identification was P_{ID} (liberal) = 1.00. These statistics, together with strong bootstrap support, are supportive of reciprocal monophyly and indicate that *Gomphus ludovicianus* is a distinct species.

Several names in *Ramaria* applied to disparate sequences resulted in putatively clearly polyphyletic “species” based on LSU sequences deposited in GenBank. These were *R. largentii*, *R. maculatipes*, *R. cyaneigranosa*, *R. aurantiiscescens* and *R. araiospora*. This

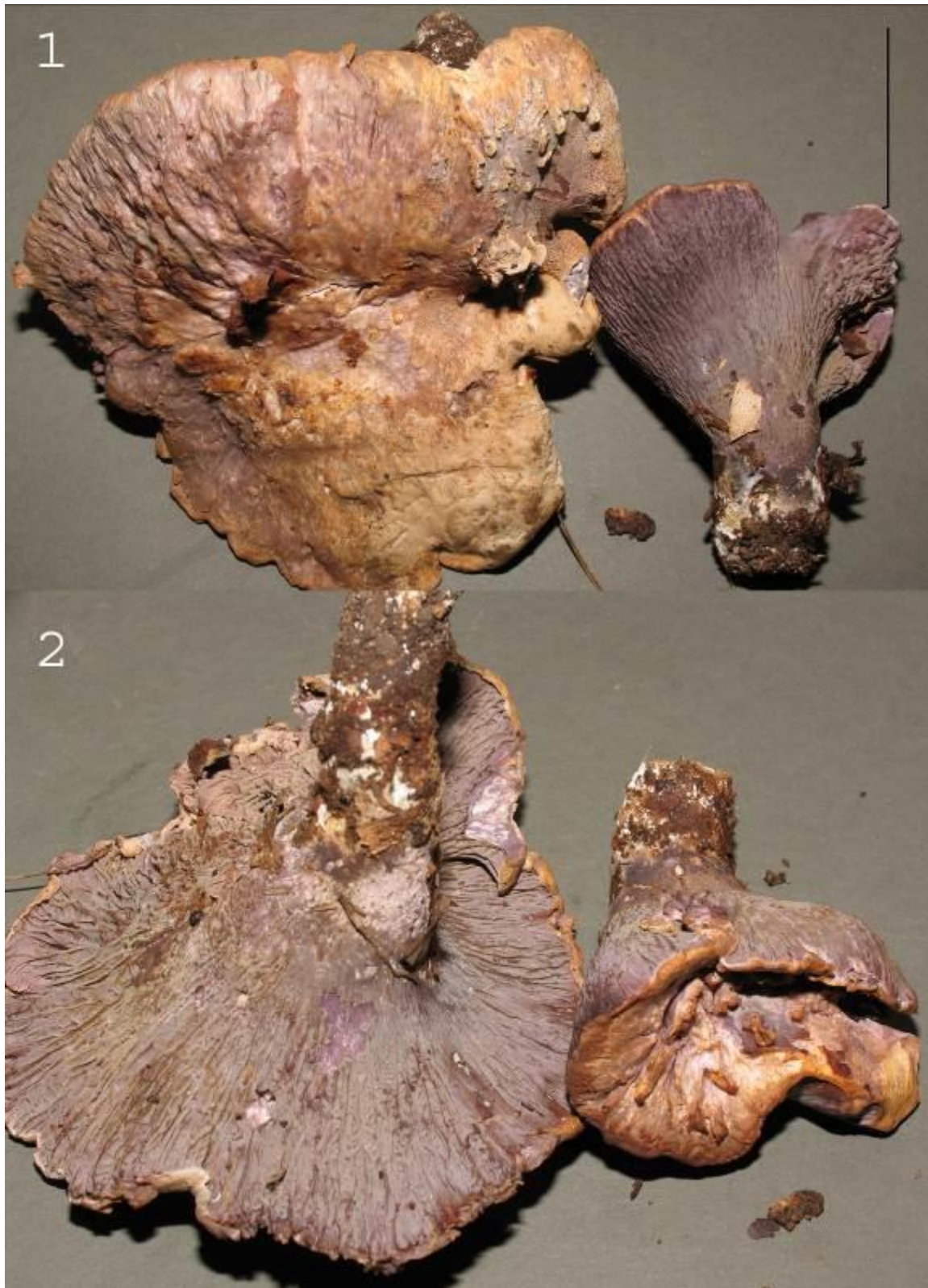
would seem to reflect difficulty in accurate morphological identification in *Ramaria* subg. *Laeticolora*. Giachini et al. (2010) noted that *Ramaria* and *Gomphus* were not monophyletic genera and noted that they were interspersed in phylogenies. That is consistent with findings in this paper again based on GenBank sequences.

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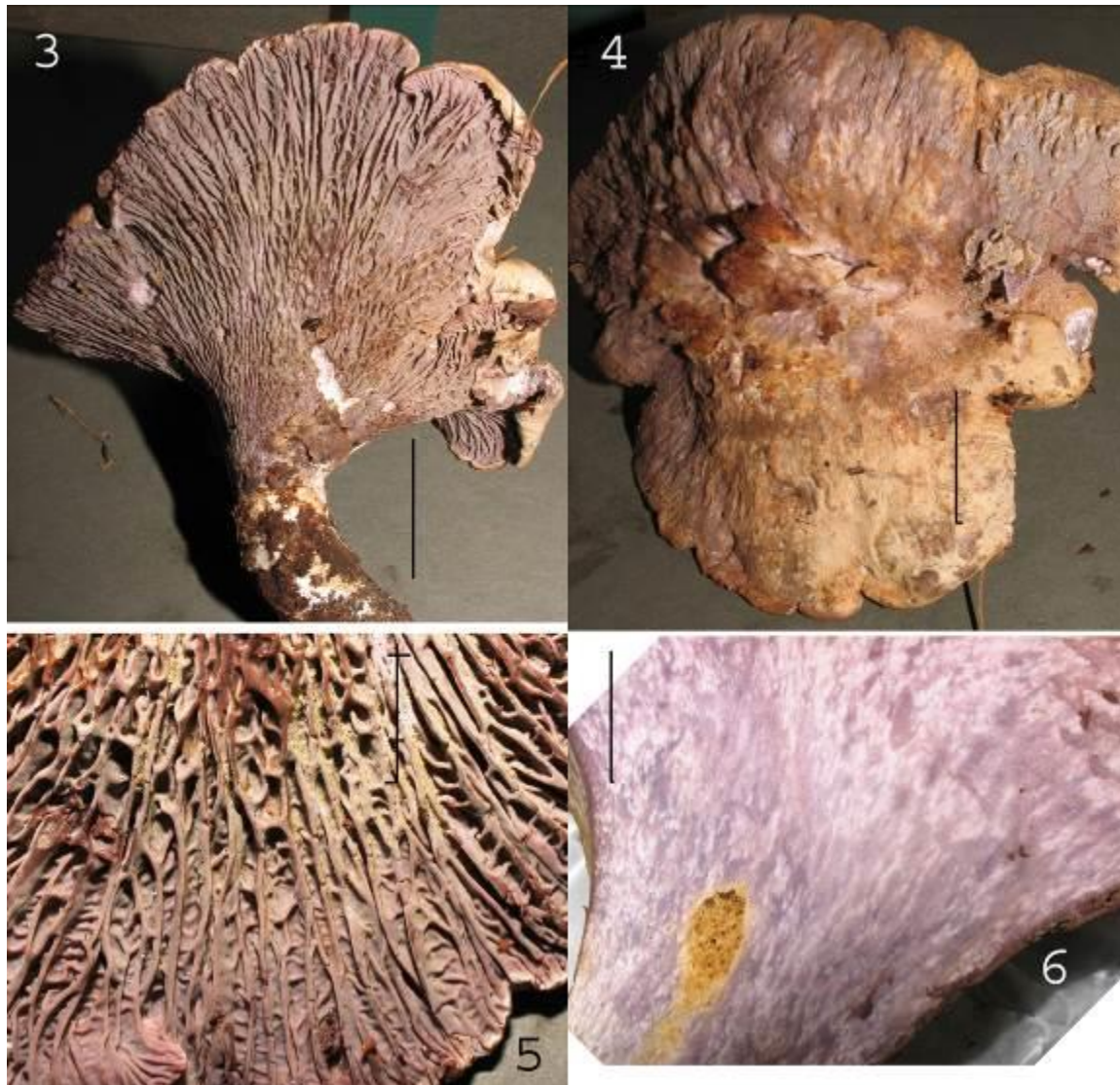
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Figs. 1, 2. *Gomphus ludovicianus*. Basidiomata. Holotype. Standard bar = 5 cm.



Figs. 3-6. *Gomphus ludovicianus*. 3, 4. Basidioma. DPL 11067. 5. Hymenophore showing primary vertical folds and secondary gill-fold anastomoses. Holotype. 6. Flesh of basidioma, showing discoloration of insect wound. Holotype. Standard bars: 3, 4 = 3 cm; 5-6 = 2 cm.

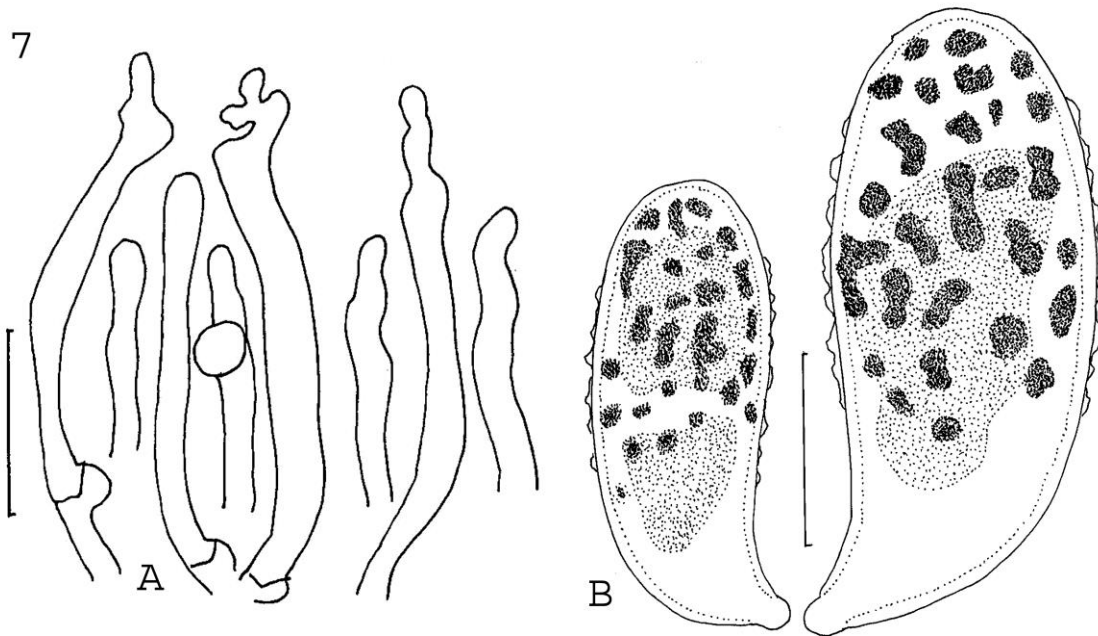


Fig. 7. *Gomphus ludovicianus*. A. Emergent hyphal tips from superficial tomentum. Holotype. Standard bar = 20 μ m. B. Basidiospores. Holotype. Standard bar = 5 μ m.

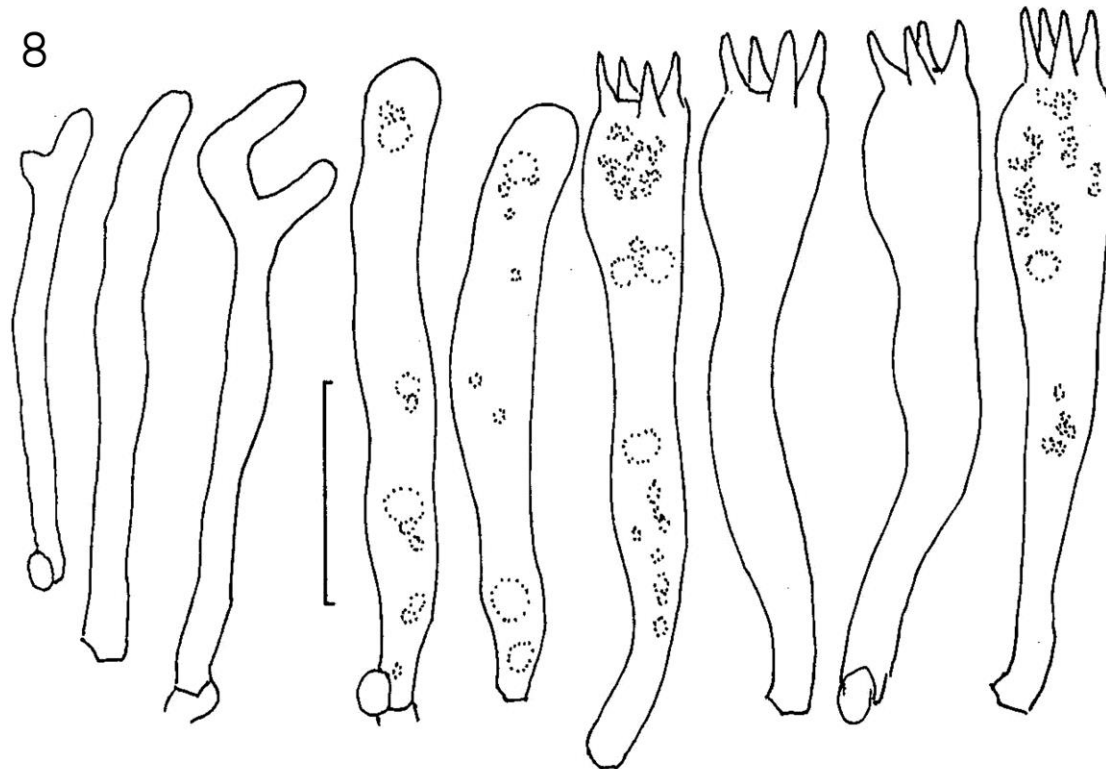


Fig. 8. *Gomphus ludovicianus*. Young basidioles and paraphysoid hyphae (left); maturing basidia (center); fertile basidia (right). Holotype. Standard bar = 20 μ m.

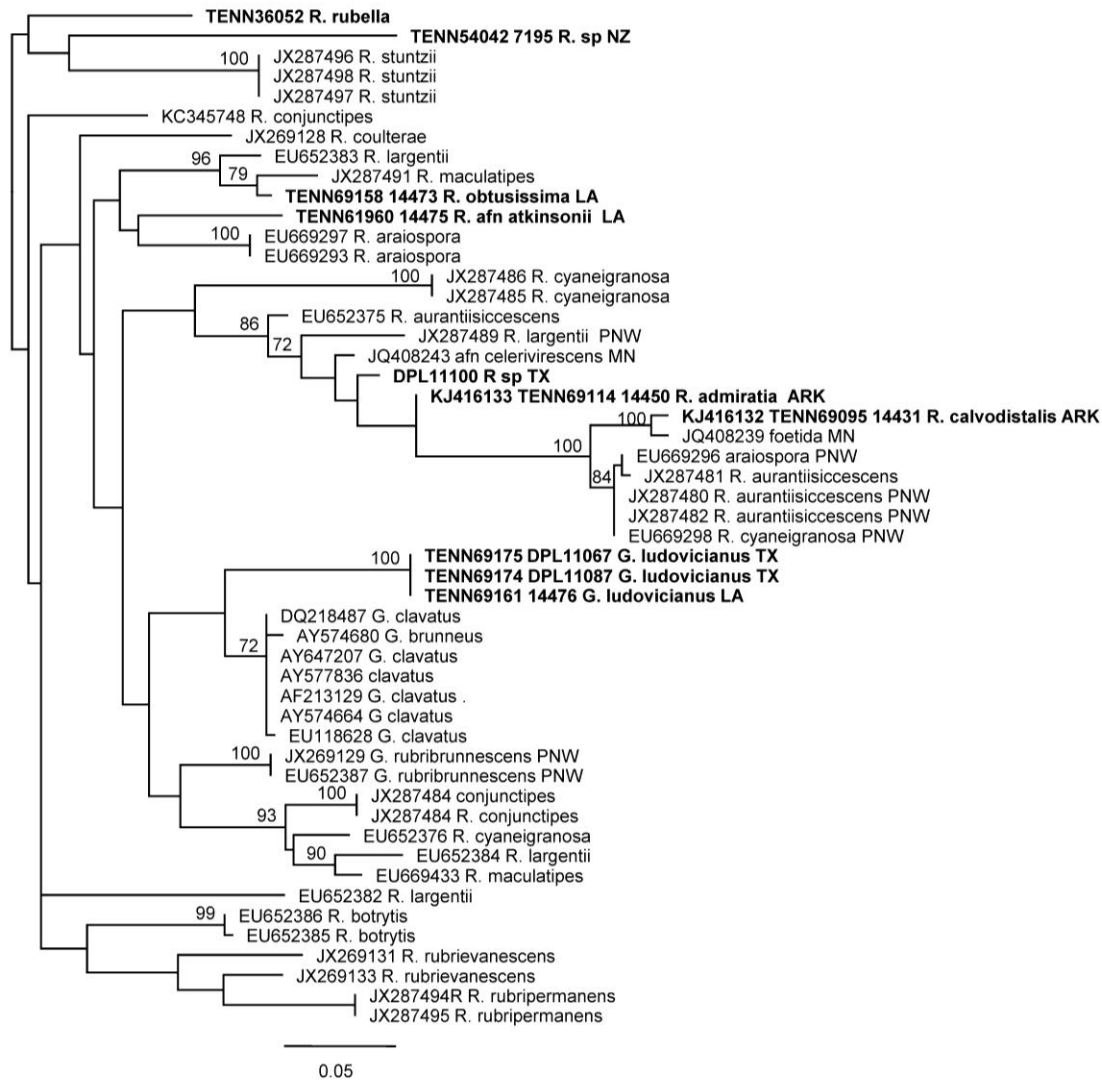


Fig. 9 *Gomphus ludovicianus*. PHYML tree of ribosomal LSU sequences. Bootstrap values greater than 70% are given to the left of the supported node. Data from collections in bold were generated by the authors. PNW=Pacific Northwest, NZ=New Zealand. Other locations are designated by state abbreviations.

Table 1. GenBank numbers for sequences generated in this study

Name	TENN-F number	Collection Number	GenBank Number	Location
<i>Ramaria rubella</i>	TENN-F-036052	RHP36052	No ITS sequence; KJ655573 LSU	USA, Tennessee, GSMNP
<i>Ramaria</i> sp.	TENN-F-054042	TFB7195	No ITS sequence; KJ655574 LSU	New Zealand
<i>Ramaria afn maculatipes</i>	TENN-F-069158	TFB14473	KJ655554 ITS; KJ655575 LSU	USA, Louisiana, Grant Parish
<i>Ramaria afn araiospora</i>	TENN-F-069160	TFB14475	KJ55555-62 ITS; KJ655576 LSU	USA, Louisiana, Grant Parish
<i>Ramaria</i> sp.	TENN-F-069176	DPL11100	No ITS sequence; KJ655577 LSU	USA, Texas
<i>Ramaria admiratia</i>	TENN-F-069114	TFB14450	KJ416133 LSU	USA, Arkansas
<i>Ramaria calvodistalis</i>	TENN-F-069095	TFB14431	KJ416132 LSU	USA, Arkansas
<i>Gomphus ludovicianus</i>	TENN-F-069175	DPL11067	KJ655571 ITS; KJ655578 LSU	USA, Texas, Jasper Co.
<i>Gomphus ludovicianus</i>	TENN-F-069174	DPL11087	KJ655572 ITS; KJ655579 LSU	USA, Louisiana, Grant Parish
<i>Gomphus ludovicianus</i>	TENN-F-069161	TFB14476	KJ655563-70 ITS; KJ655580 LSU	USA, Louisiana, Grant Parish

Table 2. Basidiospore dimensions in *Gomphus ludovicianus*

Collection	Spore Dimensions	Q	Q ^m	L ^m
Holotype (1)	12-16 × 4.5-7 μm	Q = 2.17-2.67	Q ^m = 2.42	L ^m = 14.20 μm
Holotype (2)	14-17 × 5-6.5 μm	Q = 1.87-3.40	Q ^m = 2.48	L ^m = 14.75 μm
DPL 11067 (1)	(13-)14-16 × 5.5-6.5 μm	Q = 2.15-2.64	Q ^m = 2.42	L ^m = 14.40 μm
DPL 11067 (2)	14.5-17 × (5-) 5.5-7 μm	Q = 2.14-2.64	Q ^m = 2.36	L ^m = 15.25 μm
DPL 11087 ¹	(13-)14.5-15.5 × 5-6 μm	Q = 2.42-2.82	Q ^m = 2.61	L ^m = 14.90 μm

¹ approximately 50 m from holotype location.