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Article *in* Systematics and Biodiversity · December 2013

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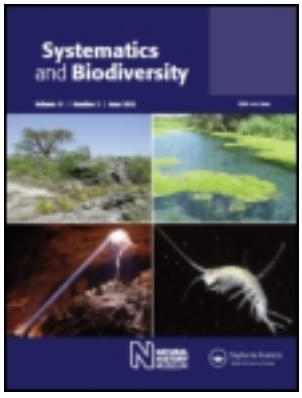

Systematics and Biodiversity
Publication details, including instructions for authors and subscription information:
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Mikael Jeppson[a], R. Henrik Nilsson[b] & Ellen Larsson[b]

[a] Lilla Håjumsgatan 4, SE-461 35 Trollhättan, Sweden

[b] Department of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, SE-405 30 Göteborg, Sweden

Published online: 16 Dec 2013.

To cite this article: Mikael Jeppson, R. Henrik Nilsson & Ellen Larsson (2013) European earthstars in Geastraceae (Geastrales, Phallomycetidae) – a systematic approach using morphology and molecular sequence data, Systematics and Biodiversity, 11:4, 437-465, DOI: 10.1080/14772000.2013.857367

To link to this article: http://dx.doi.org/10.1080/14772000.2013.857367

Systematics and Biodiversity (2013), **11(4)**: 437–465

Taylor & Francis
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Research Article

European earthstars in Geastraceae (Geastrales, Phallomycetidae) – a systematic approach using morphology and molecular sequence data

MIKAEL JEPPSON[1], R. HENRIK NILSSON[2] & ELLEN LARSSON[2]

[1]Lilla Håjumsgatan 4, SE-461 35 Trollhättan, Sweden
[2]Department of Biological and Environmental Sciences, University of Gothenburg, PO Box 461, SE-405 30 Göteborg, Sweden

(Received 14 March 2013; revised 16 October 2013; accepted 16 October 2013)

Phylogenetic relationships among European earthstars were inferred using sequence data from the nuclear ribosomal DNA internal transcribed region (ITS1, 5.8S and ITS2), partial nuclear large subunit (LSU), and partial translation elongation factor 1-alpha (Tef-α). The phylogenetic analyses recovered 11 clades that correlate to 31 morphological species and species groups. A close relationship of *Myriostoma coliforme* and *Geastrum* was supported by the molecular data. The genus *Radiigera* was found to be polyphyletic, and the four species were recovered in different clades within *Geastrum*. *Radiigera bushnellii*, *R. flexuosa*, *R. fuscogleba* and *R. taylori* are therefore combined in *Geastrum*. One of the supported terminal clades is likely to represent an undescribed species that occurs in east central Europe. Notes on the morphology and ecology for each species are given, including a key to the 31 species of earthstars occurring in Europe.

Key words: *Geastrum*, molecular phylogeny, *Myriostoma*, *Radiigera*, *Trichaster*, systematics, taxonomy

Introduction

The genus *Geastrum* was erected by Persoon to cover fungi with gasteroid basidiomata and stellate splitting of the outer peridium at maturity. The Geastraceae are distributed worldwide, and approximately 50 species are known (Kirk *et al*. 2008). The genus has been treated by numerous authors during the 20th century: Lloyd (1902, 1907), Hollós (1904), Cunningham (1944), Bottomley (1948), Staněk (1958), Dissing & Lange (1961, 1962*a*, *b*), Dring (1964), Ponce de León (1968), Nitare (1980), Dörfelt (1989), Sunhede (1989), Jalink (1995) and others. Intensified studies in recent years have indicated the occurrence of a high species diversity particularly in tropical regions, and several new species have been described (e.g. Calonge *et al*., 2000; Baseia & Milanez, 2002; Calonge & Mata, 2004; Douanla-Meli *et al*., 2005; Baseia & Calonge, 2006; Leite *et al*., 2007; Leite & Baseia, 2007; Fazolino *et al*., 2008; Kuhar & Papinutti, 2009). New species have been found also in temperate Europe and Asia (e.g. Gardezi, 2005; Zamora & Calonge, 2007). Recently Jeppson (2013) published a field guide in Swedish including descriptions and photos of all species of Geastraceae currently known to occur in Europe.

Traditionally considered to be closely related to the puffballs (Lycoperdaceae; e.g. Zeller, 1949), molecular phylogenetic studies have shown *Geastrum* to be nested in the gomphoid-phalloid clade (Hibbett *et al*., 1997; Krüger *et al*., 2001). In Hosaka *et al*. (2006) a classification for Geastrales (Phallomycetidae) was proposed, and the authors recognized the families Geastraceae, Sphaerobolaceae, Sclerogastraceae and Pyrenogastraceae. In the present study we have included all currently known European taxa of the family Geastraceae. The aims were to resolve generic boundaries within Geastraceae as represented in Europe and to characterize a majority of the European species using molecular sequence data, macro- and micro-morphological characters, and ecology. Special emphasis is put on the occurrence and distribution of the species in northern Europe.

Materials and methods

Morphology

The main part of the material was collected in northern Europe (Fennoscandia), east central Europe (Hungary, Slovakia), and southwestern Europe (Spain). Additional

Correspondence to: Ellen Larsson. E-mail: ellen.larsson@bioenv.gu.se

ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2013.857367

material was borrowed from several herbaria (BP, BRA, C, MA, PRM and UPS). Dried mature fruiting bodies were used for macro- and microscopic examination. Samples of spores and capillitium were mounted in Lactophenol-cotton blue and heated to boiling temperature. Spore dimensions were measured using the AxioVision 4 software (http://microscopy.zeiss.com). All spore dimensions are exclusive of spore wall ornamentation. Terminology is in accordance with Sunhede (1989). Species identifications were primarily based on Staněk (1958) and Sunhede (1989, 2012). Type materials studied by the authors are marked (!). The investigated specimens have been deposited in Herbarium GB if not otherwise stated. Data on specimens morphologically studied is provided as Appendix 1 (see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2013.857367).

Taxon sampling

In this study, 66 ingroup specimens were sequenced, including the type specimen of *Geaster pseudostriatus* Hollós (BP). They represent the majority of all known described species in *Geastrum*, *Radiigera* and *Myriostoma* that occur in Europe (Sunhede, 1989), with the exception of *G. welwitschii*, but with the addition of *G. xerophilum* (new to Europe, detected in the present study) and the recently described *G. parvistriatum* (Zamora & Calonge, 2007). *Trichaster melanocephalus* is included in accordance with Staněk (1958), Kasuya *et al.* (2012) and Sunhede (2012). Specimens were selected to represent a broad spectrum of morphological characters and ecological traits observed within *G. berkeleyi sensu lato*. Based on results from earlier molecular phylogenetic studies of Phallomycetidae and Geastrales (Hosaka *et al.*, 2006), species in *Sphaerobolus*, *Schenella* and *Sclerogaster* were selected as outgroup. LSU and Tef-1α sequences data for the selected outgroup species were retrieved from GenBank (DQ218519, DQ219232, DQ218607, FJ435984, FJ435978, AY574647, DQ219237, AY439010 and AY487982). In addition, sequence data (ITS, LSU and Tef-1α) representing 14 *Geastrum* and *Radiigera* species were retrieved from GenBank and added to the dataset (JN845105, JN939572, JN845112, JN845230, EU784235, EU784223, DQ218609, DQ219234, JN939555, JN943168, JN845104, JN845222, EU784248, AF336251, DQ21860, DQ219228, JN845093, JN845211, DQ218520, DQ219235, JN845204, JN845329, DQ218608, DQ219233, EU784376 and DQ218606). The selection was based on previous molecular studies of Geastraceae (Hosaka *et al.*, 2006; Kasuya *et al.*, 2012).

DNA extraction, PCR and sequencing

Sequences from three regions were generated for the study: the complete ITS region and about 1400 base pairs of the 5′ end of the nuclear ribosomal LSU DNA, and about 1000 base pairs of translation elongation factor subunit 1 alpha (Tef-1α). DNA extractions, PCR reactions, and sequencing were performed as described in Larsson & Örstadius (2008). Primers used to amplify the complete ITS region and the 5′ end of the LSU region were ITS1F (Gardes & Bruns, 1993) and LR21, LR0R and LR7 (Hopple & Vilgalys, 1999); for Tef-1α we used EF983F and EF2218R (www.aftol.org/pdfs/EF1primer). Primers used for sequencing were ITS1, ITS4 (White *et al.*, 1990), Ctb6 (http://plantbio.berkeley.edu/~bruns/), Lr5 and LR3R (Hopple & Vilgalys, 1999), EF983F, EF2218R and 1567Ra (www.aftol.org/pdfs/EF1primers).

Phylogenetic analyses

Sequences were edited and assembled using Sequencher 4.1 (Gene Codes, Ann Arbor). Alignment of individual genes was performed using the L-INS-i strategy as implemented in MAFFT v. 7.017 (Katoh & Standley, 2013). The alignment was adjusted manually using the data editor in PAUP* 4.0b12 (Swofford, 2003). Sequences have been deposited in GenBank and accession numbers are listed in Table 1.

Phylogenetic analyses were based on the concatenated gene alignments. Heuristic searches for the most parsimonious trees were performed using PAUP*. All transformations were considered unordered and equally weighted. Variable regions with ambiguous alignment, mainly from the ITS region and the flanking gene regions, were excluded (bp 1–59, bp 228–234, bp 576–586, bp 1851–2144, bp 3050–3173) and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates, TBR branch swapping and MulTrees option in effect, were performed. Relative robustness of clades was assessed by the bootstrap method using 1000 heuristic search replicates with 100 random taxon addition sequence replicates and TBR branch swapping, the latter saving at most 100 trees in each replicate.

Bayesian phylogenetic analyses were carried out in MrBayes 3.0 (Ronquist & Huelsenbeck, 2003), with a best-fit model of nucleotide evolution supplied by MrModeltest 2.2 (Nylander, 2004). Eight default-setting Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains were run for 50 million generations with trees sampled every 1000 generations and an initial burn-in of 50%. After discarding the trees prior to the burn-in threshold, a 50% majority-rule consensus phylogram was computed from the remaining 25 000 trees.

For improving the resolution within the *G. berkeleyi* species complex and to be able to use more characters of the ITS region in the phylogenetic analysis, realignment of the sequence data of subclade G, using *G. schmidelii* as outgroup was performed as described above. This subset of the large alignment featured all three molecular

Table 1. Data of specimens sequenced in this study

Species	Coll.ID /Origin	GenBank Acc. No. ITS/LSU	Tef-1α
Geastrum arenarium	MJ9531/Spain	KC581955	KC758596
G. arenarium	Zamora 76/ (MA-Fungi)/Spain	KC581956	KC758597
G. berkeleyi	MJ8673/Slovakia	KC581985	KC758619
G. berkeleyi	MJ5544/Sweden	KC581986	KC758621
G. berkeleyi	MJ8844/Sweden	KC581987	–
G. berkeleyi	RGC06-168/Sweden	KC581988	KC758620
G. campestre	MJ891121/Spain	KC581998	KC758630
G. campestre	MJ&BN061025/Sweden	KC581999	KC758631
G. campestre	MJ9349/Spain	KC582000	–
G. campestre	SÅH08-146/Sweden	KC582001	–
G. cf. pseudostriatum	MJ6413/Sweden	KC581989	KC758622
G. corollinum	MJ2322/Sweden	KC581972	KC758611
G. coronatum	MJ8804/Sweden	KC581965	KC758605
G. elegans	MJ2372/Sweden	KC582013	KC758642
G. elegans	MJ2809/Sweden	KC582014	KC758643
G. flexuosum	JN&SS09-1985 (UPS)/Sweden	KC581970	KC758609
G. fimbriatum	MJ5706/Sweden	KC582015	KC758644
G. fimbriatum	MJ4802/Sweden	KC582016	–
G. floriforme	JJ80330/Sweden	KC581983	KC758617
G. floriforme	MJ5421/Sweden	KC581984	KC758618
G. fornicatum	MJ9532/Sweden	KC582012	KC758641
G. hungaricum	MJ8915/Hungary	KC581963	KC758603
G. hungaricum	MJ9317/Slovakia	KC581964	KC758604
G. kotlabae	MJ6571/Hungary	KC582004	KC758634
G. kotlabae	MJ8821/Hungary	KC582005	KC758635
G. lageniforme	MJ7337/Slovakia	KC581966	KC758606
G. melanocephalum	MJ3385/Sweden	KC581980	–
G. melanocephalum	MJ6516/Sweden	KC581981	–
G melanocephalum	MJ030921/Sweden	KC581982	–
G. minimum	MJ9529/Sweden	KC581957	KC758598
G. morganii	MJ8422/France	KC581971	KC758610
G. pectinatum	MJ9030/Norway	KC581962	KC758602
G. pouzarii	ZítaV20384/Czech Republic	KC582002	KC758632
G. pouzarii	ZítaV20129/Czech Republic	KC582003	KC758633
G. pseudolimbatum	MJ8063/Sweden	KC581973	KC758612
G. pseudolimbatum	SÅH09-014/Sweden	KC581974	KC758613
G. pseudostriatum	MJ8770/Sweden	KC581990	KC758627
G. pseudostriatum	MJ7564/Sweden	KC581991	KC758628
G. pseudostriatum	MJ5738/Sweden	KC581992	KC758629
G. pseudostriatum	MJ050919/Sweden	KC581993	KC758623
G. pseudostriatum	MJ8240/Sweden	KC581994	KC758624
G. pseudostriatum	MJ7573/Sweden	KC581995	KC758625
G. pseudostriatum	MJ9067/Sweden	KC581996	KC758626
G. pseudostriatum	BP22110 (Type BP)/Hungary	KC581997	–
G. pseudostriatum	MJ8933/Hungary	KC758593	–
G. pseudostriatum	SÅH02-0321/Sweden	KC758594	–
G. pseudostriatum	MJ8812/Sweden	KC758595	–
G. quadrifidum	MJ7151/Sweden	KC581958	KC758599
G. quadrifidum	MJ2749/Sweden	KC581959	KC758600
G. rufescens	MJ6268/Sweden	KC582010	KC758639
G. rufescens	VW07-2006 (UPS)/Sweden	KC582011	KC758640
G. rufescens	Adamcik060628/Slovakia	KC582009	KC758638
G. saccatum	MJ090404/Sweden	KC581967	KC758607
G. saccatum	GH000909/Sweden	KC581969	KC758609
G. saccatum	TK950910/Sweden	KC581968	KC758608
G. schmidelii	MJ8449/Sweden	KC582006	–
G. schmidelii	MJ2135/Sweden	KC582008	KC758637
G. schmidelii	MJ8246/Sweden	KC582007	KC758636
G. smardae	TSNielsen/Spain	KC581976	KC758614
G. smardae	AW&MJ100920(O)/Norway	KC581977	–

(*continued*)

Table 1. (*Continued*)

Species	Coll.ID /Origin	GenBank Acc. No. ITS/LSU	Tef-1α
Geastrum sp 1.	MJ8945/Hungary	KC582017	–
Geastrum sp 1.	MJ8969/Hungary	KC582018	KC758645
Geastrum sp 1.	MJ9003/Hungary	KC582019	KC758646
G. striatum	MJ8807/Sweden	KC581960	–
G. striatum	RGC&KAJ070712/Sweden	KC581961	KC758601
G. triplex	MJ8234/Sweden	KC581978	KC758615
G. triplex	MJ8672/Slovakia	KC581975	KC758616
G. xerophilum	MJ9533/Spain	KC581975	–
Myriostoma coliforme	MJ8714/Hungary	KC582020	–

regions. Heuristic searches for the most parsimonious trees and bootstrap analysis were undertaken as detailed above. Bayesian analysis of the restricted dataset was performed identical to the first one, with the exception of differences in the suggested models of nucleotide evolution.

Results

Molecular results

The aligned complete dataset, including sequences downloaded from GenBank, consisted of 88 taxa and 3310 characters. After exclusion of ambiguous regions, mainly from the ITS1 and ITS2, 2653 characters remained for the analysis. Of these, 1729 were constant, 214 were variable but parsimony uninformative and 710 (27%) were parsimony informative.

The maximum parsimony (MP) analysis yielded 69 900 equally parsimonious trees (length = 3265 steps, CI = 0.4049 and RI = 0.6994). One of the equally parsimonious trees is presented as a phylogram in Fig. 1.

The bootstrap analysis recovered *Geastrum* including *Myriostoma* as monophyletic with 92% support. Eleven weakly to strongly supported clades within the ingroup are labelled as subclades A–K in the phylogram of Fig. 1 for discussion. The subclades more or less correspond to morphological species or groups of species; these are further described below.

As suggested by MrModeltest, the nucleotide evolution model GTR+G was used for the ITS1 spacer; SYM was used for the 5.8S gene; HKY+G was used for the ITS2 spacer; and GTR+I+G were used for the nLSU and TEF genes in the Bayesian analysis. The MCMC analysis converged well in advance of the burn-in threshold and chain mixing was found to be satisfactory, as assessed by using Tracer v1.5 (Drummond *et al*., 2012).

Also in the Bayesian analysis, *Geastrum* including *Myriostoma* was recovered as a monophyletic group with strong support (a Bayesian posterior probability (BPP) of 1.00). The Bayesian tree topology is similar to the MP bootstrap tree. The eleven clades, A–K, recovered in the MP analysis were also recovered in the Bayesian analysis, with the minor differences that several clades with moderate or no bootstrap support received a high BPP value (Fig. 1).

The realigned dataset of 24 taxa in the *G. berkeleyi sensu lato,* subclade G, initially comprised 3173 characters. After exclusion of ambiguous regions, 2875 characters remained for the analysis. Of these, 2351 were constant, 138 were variable but parsimony uninformative, and 386 (13%) were parsimony informative. The MP analysis yielded 94 100 equally most parsimonious trees (length = 703 steps, CI = 0.8734 and RI = 0.9235). The topology of the calculated strict consensus tree shows two major clades corresponding to *G. berkeleyi* and *G. pseudostriatum*, including the ITS sequence of the type specimen of *G. pseudostriatum* and a third taxon. The bootstrap analysis recovered the same topology with the two major supported clades *G. berkeleyi* (98%) and *G. pseudostriatum*, including the ITS sequence of the type specimen of *G. pseudostriatum* (62%) and a third taxon. The latter taxon is here named *G. cf. pseudostriatum*, but it is represented by one sequence only and comes out on a separate branch with *G. pseudostriatum* (65%). For the restricted dataset MrModeltest suggested models of nucleotide evolution (ITS1: HKY+G, 5.8S: K80, ITS2: HKY+G, LSU: GTR+I and TEF: GTR+I). The Bayesian analysis gave no support for the *G. pseudostriatum* clade but *G. berkeleyi* received 1.0 BPP, see Fig. 2.

Subclades and morphological characters

Subclade A (65%, 0.92 BPP) comprises two species, the widely distributed and well-known *G. fimbriatum* (syn. *G. sessile*) and the rare *G. arenarium*. They are both characterized by a hypogeous development with a mycelial layer encrusted with soil. However the sequence difference between the two species is rather large and that may be reflected in the rather low support. They are also rather different in morphology, in so far as *G. arenarium* instead shares many macro-morphological characters with *G. minimum* (subclade B).

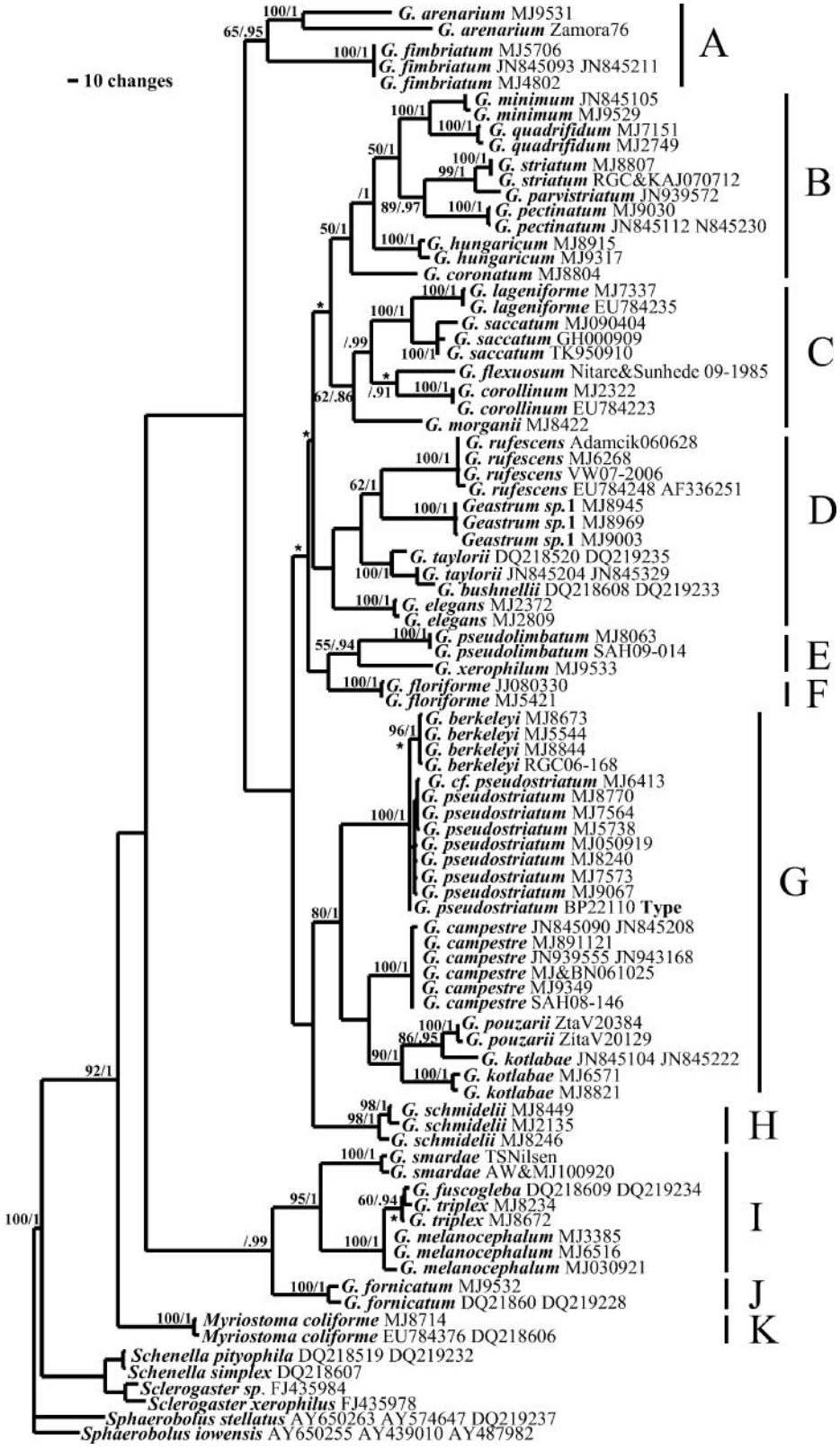

Fig. 1. One of the most parsimonious trees obtained from the MP analysis based on ITS, LSU, and Tef-1α sequence data of the earthstars that occur in Europe. Bootstrap values and BPP are indicated on branches. A star * indicates branches that collapse in the Strict consensus tree. Subclades A–K marked with a scale bar represent species or species groups that are discussed in the text.

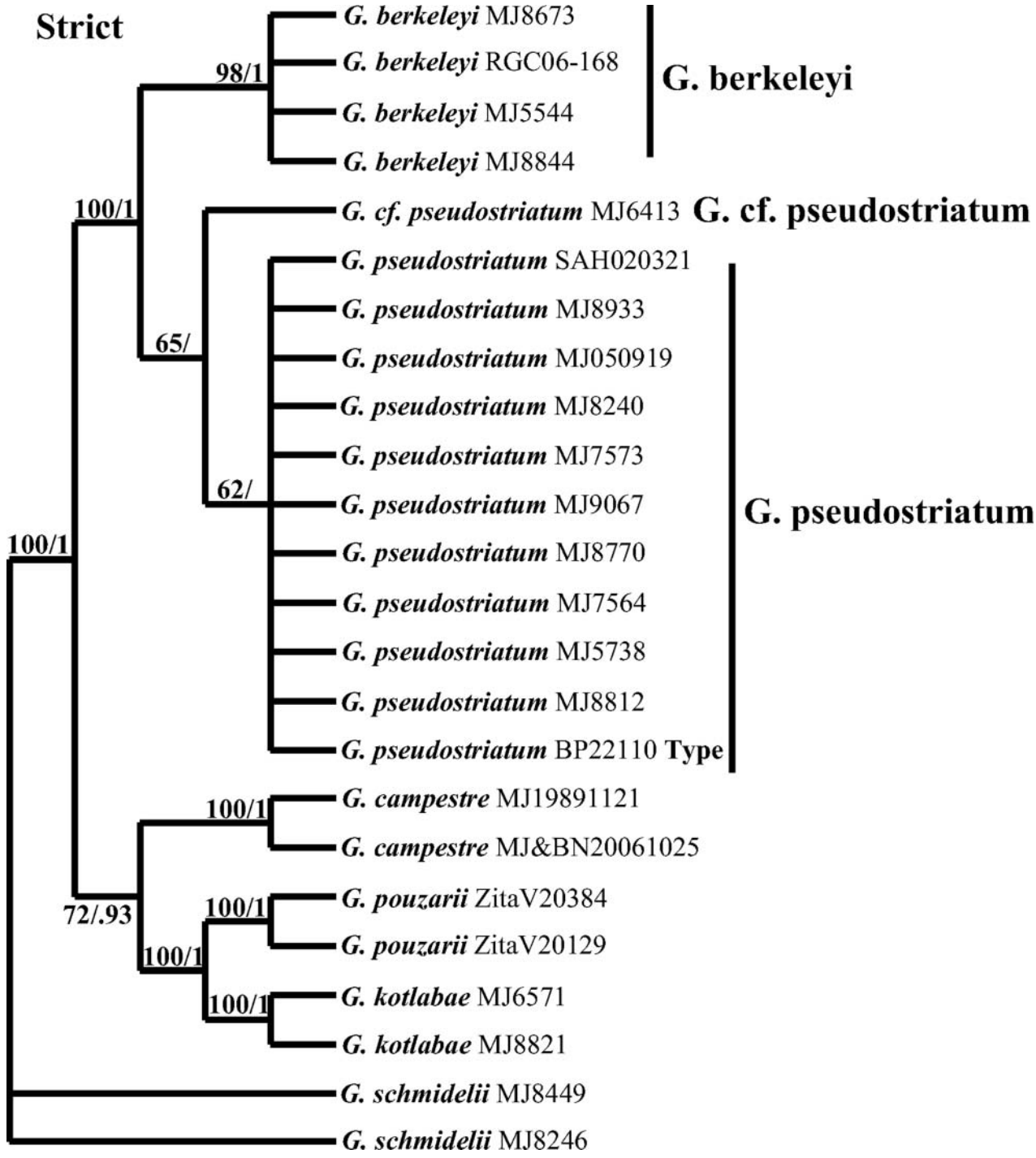

Fig. 2. The Strict consensus tree from the MP analysis of the realigned dataset including ITS, LSU and Tef-1α sequence data of subclade G, including the *G. berkeleyi*/*G. pseudostriatum* species complex, using *G. schmidelii* as outgroup. Bootstrap values and BPP are indicated on branches.

Subclade B (50%, 1.00 BPP) is composed of seven species including *G. coronatum*, the type species of the genus. The fruiting bodies of the species develop hypogeously and have a mycelial layer that encrusts soil particles. *Geastrum quadrifidum* forms fornicate basidiomata. *Geastrum minimum* and *G. quadrifidum* are characterized by a distinctly delimited, almost disc-like, fibrillose peristome and the presence of a crystalline mesoperidium. The related *G. hungaricum* shares a similar type of peristome but has less mesoperidial covering and strongly hygroscopic fruiting

bodies. *Geastrum striatum*, *G. parvistriatum* and *G. pectinatum* have strongly sulcate peristomes and usually abundant mesoperidial covering.

Subclade C (62%, 0.83 BPP) features five species with a more or less epigeous development. The fruiting bodies of one species, *G. flexuosum* (syn. *Radiigera flexuosa*), develop sub-hypogeously and do not split stellately at maturity. The mycelial layer covers at least the lower portion of the exoperidium and partly encrusts soil particles. *Geastrum corollinum* has a smooth mycelial layer, a stellate dehiscence, and strongly hygroscopic exoperidium. *Geastrum saccatum* and *G. lageniforme* have a mycelial layer that never encrusts soil and a distinct central and basal attachment point to the below-ground mycelium. Unexpanded fruiting bodies are ± onion-shaped to lageniform. The two species are also characterized by a delimited and fibrillose peristome. *Geastrum morganii* shares several morphological characters with *G. saccatum* and *G. lageniforme,* but has an undelimited and sulcate peristome.

Subclade D is an unsupported constellation of five species that are grouped in four terminal, highly supported clades. All species in this subclade have a ± hypogeous development and a mycelial layer which at least partly is encrusted with debris. *Geastrum* sp. 1 and *G. rufescens* (62%, 1.0 BPP) are stellate species with plain, undelimited, fibrillose peristomes. *Geastrum* sp. 1 is likely to be an undescribed species that occurs in east central Europe. *Geastrum taylorii* and *G. bushnelli* (100%, 1.0 BPP, not known from Europe) have rounded, non-dehiscing fruiting bodies and were described in the genus *Radiigera*, similar to *G. flexuosum* that clusters in subclade C. The fruiting bodies of *G. elegans* (100%, 1.0 BPP) have a hypogeous development with a mycelial layer encrusted with debris. It is characterized by saccate fruiting bodies with a sessile endoperidial body and a strongly sulcate peristome.

Subclade E contains *G. pseudolimbatum* and *G. xerophilum* (55%, 0.94 BPP). The two species have a hypogeous development and a mycelial layer encrusted with debris. They have a shortly stalked endoperidial body and exoperidial rays which are slightly hygroscopic or permanently curving upwards and inwards under the endoperidial body.

Subclade F is made up by *G. floriforme* (100%, 1.0 BPP) that has a hypogeous development, a mycelial layer which is encrusted with debris, and strongly hygroscopic exoperidial rays.

Subclade G (80%, 1.0 BPP) comprises at least five species, all with a hypogeous development and a mycelial layer that encrusts debris. Species that mainly occur in exposed, xeric habitats are more or less hygroscopic. *Geastrum campestre*, *G. pouzarii* and *G. kotlabae* are characterized by a strongly sulcate peristome and a more or less rugulose – verrucose endoperidial surface. The sequence originating from Japan of *G. kotlabae* is divergent from the European sequences of *G. kotlabae* and instead formed a group together with *G. pouzarii* (86%, 0.95 BPP) indicating that it may represent a separate taxon. Thirteen specimens including the type specimen of *G. pseudostriatum* were grouped in the *G. berkeleyi/G. pseudostriatum* clade (100%, 1.0 BPP). As the representatives in this clade show variation in morphology and the ITS sequence data, the sequence data for this clade were realigned and analysed separately. The bootstrap analysis (Fig. 2) supports *G. berkeleyi* and *G. pseudostriatum* as distinct species and indicates that there may be a third taxon within this clade, here referred to as *G. cf. pseudostriatum* and only represented by one sequence. The Bayesian analysis did not give any support for the *G. pseudostriatum* clade, however *G. berkeleyi* is strongly supported (Fig. 2). The sequence difference in the ITS region between *G. berkeleyi* and *G. pseudostriatum* is seven substitutions and one 8 bp, one 2 bp and two 1 bp insertion/deletion events. The sequence difference between *G. pseudostriatum* and *G. cf. pseudostriatum* is nine substitutions and one 8 bp insertion/deletion event. Average spore size is a morphological character of importance in this group for distinguishing between the similar species pairs *G. campestre* (5.3 μm) – *G. pouzarii* (4.4 μm) and *G. berkeleyi* (4.3 μm) – *G. pseudostriatum* (4.8 μm).

Subclade H (98%, 1.0 BPP) is composed of three sequences of *G. schmidelii*. The species shares morphological characters with *G. pseudostriatum,* but is easily distinguished by its smooth endoperidial surface.

Subclade I (95%, 1.0 BPP) encompasses medium- to large-sized and robust species with epigeous or hypogeous development. The mycelial layer is not encrusted with debris. Although our European material of *G. triplex* and *G. melanocephalum* are clearly distinguished based on morphological features, sequence data show a close relationship (100%, 1.0 BPP). The GenBank sequence of *Radiigera fuscogleba* originating from North America, the generic type of *Radiigera*, with a hypogeous development and an irregular peridial dehiscence, forms a supported clade with *G. triplex* and *G. melanocephalum. Geastrum smarda*e forms pseudofornicate fruiting bodies.

Subclade J (95%, 1.0 BPP) contains two sequences of *G. fornicatum*, a species that has a hypogeous development and fornicate fruiting bodies. It forms a moderately supported (-,0.99 BPP) clade together with clade I.

Subclade K (100%, 1.0 BPP) features two sequences of *Myriostoma coliforme*; this clade forms the sister taxon to the remainder of *Geastrum*. Although a close relationship with *Geastrum* is suggested by the sequence data analyses (92%, 1.0 BPP), we prefer to keep it as a separate genus due to its unique morphological characters until sequence data from more specimens from a broader geographical origin are available.

Taxonomy

An emended circumscription of *Geastrum* and the genera of Geastraceae in Europe.

Geastrum Pers.: Pers., Neues Mag. Bot. 1: 85 (1794).

= *Radiigera* Zeller, Mycologia 36(6): 628 (1944).
= *Trichaster* Czern., Bull. Soc. Imp. nat. Moscou 18(2, III): 149 (1845).

According to our phylogenetic analyses, the European specimens of *Geastrum* are grouped in subclades that more or less correspond to morphologically supported species-groups (Figs 1, 2). Our analyses strongly indicate that the genus *Radiigera* is an artificial assemblage of species that should not be recognized as a genus of its own. A new, emended circumscription of *Geastrum* will include species with a stellately splitting exoperidium as well as those with an irregularly rupturing peridium, with permanently rounded, hypogeous or semiepigeous fruiting bodies. In non-stellate species the endoperidium is lacking or poorly developed.

The genus *Radiigera* comprises species that have subglobose, more or less hypogeous fruiting bodies that may finally split irregularly upon maturity. The genus was described as a member of the Mesophelliaceae by Zeller (1944). Askew and Miller (1977) published a detailed study on the morphology and fruiting body development of the generic type species, *R. fuscogleba*, and compared it with species of *Geastrum*. They concluded that there was a close relationship between the two genera, and that they differed merely in the manner of dehiscence of the fruiting body at maturity. They subsequently transferred *Radiigera* from Mesophelliaceae to Geastraceae. This placement has gained general acceptance and has lately been strongly supported by sequence data (Hosaka *et al*., 2006). In a monographic revision of the genus *Radiigera*, Domínguez de Toledo and Castellano (1996) included four species, viz. *R. bushnellii* L.S. Domínguez & Castellano, *R. flexuosa* L.S. Domínguez & Castellano, *R. fuscogleba* Zeller and *R. taylorii* (Lloyd) Zeller, all with hypogeous–semihypogeous fruiting bodies. In the present study, sequences of all four species attributed to *Radiigera* by Domínguez de Toledo & Castellano (1996) were included, three of them represented by Genbank sequences. In the phylogenetic analysis, the sequences were recovered in different clades within *Geastrum* (Fig. 1), showing that *Radiigera* is polyphyletic. These results suggest that *Radiigera* should not be recognized as a separate genus, which is in accordance with the observations of Gube & Piepenbring (2009). We therefore propose that *R. bushnellii*, *R. flexuosa*, *R. fuscogleba* and *R. taylori* be transferred to the genus *Geastrum*. Domínguez de Toledo & Castellano (1996) distinguished the genus *Pyrenogaster* as distinct from *Radiigera*. It was described by Malençon & Riousset (1977) and was characterized by non-dehiscing, ± hypogeous fruiting bodies that differed from *Radiigera* in the structure of the gleba, which in *Pyrenogaster* develope peridiole-like structures. Two species were attributed to *Pyrenogaster*, viz. *P. pityophilus* Malençon & Riousset and *P. atrogleba* (Zeller) L.S. Domínguez & Castellano (basionym *Radiigera atrogleba* Zeller). Recently, Estrada *et al*. (2005) showed that *Pyrenogaster atrogleba* was identical with the holotype of *Schenella simplex* T. Macbr., up till then known as a myxomycete. Subsequent name changes were introduced, viz. *Schenella simplex* T. Macbr. (syn.: *Radiigera atrobleba* Zeller, *Pyrenogaster atrogleba* (Zeller) L.S. Domínguez & Castellano), *S. pityophila* (Malençon & Riousset) Estrada & Lado (as '*S. pityophilus*', basionym *Pyrenogaster pithyophilus* Malençon & Riousset). *Radiigera romana* Quadraccia (syn.: *Pyrenogaster romana* (Quadraccia) Calonge), a recently described species from Italy, was furthermore transferred to *Schenella* as *S. romana* (Quadraccia) Estrada & Lado. In our analyses two *Schenella* species were represented by GenBank sequences. They came out as a sister clade to *Sclerogaster* – that is, outside *Geastraceae* – thus supporting the results of Hosaka *et al*. (2006).

Czerniaiev (1845) described the genus *Trichaster* (type species *T. melanocephalus*) from Ukraine. It has since been treated as a monotypic genus. The main differentiating character from *Geastrum* is the presence of a naked gleba, which is not surrounded by any endoperidium at maturity. Staněk (1958) combined Czerniaiev's species to *Geastrum* and placed it in the vicinity of *G. triplex*, with which it shares several characters. This relationship was supported by Kers (1975) and Sunhede (1989), who both studied Swedish material. In the phylogeny presented here – as well as in that of Kasuya *et al*. (2012) – *T. melanocephalus* forms a clade together with *G. triplex*. This confirms that the species are very closely related, and that the opinions of Staněk (1958), Ponce de León (1968), Calonge (1998), Kreisel (2001), Kasuya *et al*. (2012) and Sunhede (2012), to consider *Trichaster* a later synonym of *Geastrum* are correct.

Myriostoma Desv., J. Bot. (Desvaux) 2: 103 (1809).

The genus *Myriostoma* was erected to accommodate *Lycoperdon coliforme* Dicks. The genus is considered monotypic (Sunhede, 1989; Kirk *et al*., 2008) with a worldwide distribution. It shares the general macrocharacters with *Geastrum* but differs in having its endoperidium supported by several stalks, one to several, often branching columellae and by having an endoperidium with multiple stomata. In micro-morphology it differs from *Geastrum* by having a capillitium with tapering branches and very strongly ornamented spores, with curved and ramified ridges (cfr SEM-photos in Eckblad, 1971; Calonge, 1975; Sunhede, 1989; Rimóczi *et al*., 2011).

New combinations

Geastrum bushnellii (L.S. Domínguez & Castellano) Jeppson & E. Larss. comb. nov.

Index Fungorum IF 550135
Basionym: *Radiigera bushnellii* L.S. Domínguez & Castellano, Mycologia 88(5): 873. (1996).

Geastrum flexuosum (L.S. Domínguez & Castellano) Jeppson & E. Larss. comb. nov.

Index Fungorum IF 550136
Basionym: *Radiigera flexuosa* L.S. Domínguez & Castellano, Mycologia 88(5): 877 (1996).

Geastrum fuscogleba (Zeller) Jeppson & E. Larss. comb. nov.

Index Fungorum IF 550137
Basionym: *Radiigera fuscogleba* Zeller, Mycologia 36(6): 633 (1944).

Geastrum taylorii (Lloyd) Jeppson & E. Larss. comb. nov.

Index Fungorum IF 550138
Basionym: *Mesophellia taylorii* Lloyd, Mycol. Writ. 7 (Letter 73): 1305 (1924).

Key to the species of Geastraceae occurring in Europe

1a. Peridium rounded, semi-hypogeous or hypogeous, opening irregularly at maturity	*G. flexuosum*
1b. Exoperidium splitting stellately, revealing a rounded endoperidial body	2
2a. Endoperidial body not covered by the endoperidium at maturity	*G. melanocephalum*
2b. Endoperidial body permanently covered by an endoperidium	3
3a. Endoperidium with several stalks and numerous ostioles	*Myriostoma coliforme*
3b. Endoperidium sessile or on a single, distinct stalk; with one apical ostiole	4
4a. With sulcate peristome	5
4b. With smooth to fibrillose/fimbriate peristome	17
5a. Mycelial layer not encrusting soil	*G. morganii*
5b. Mycelial layer encrusts soil	6
6a. Exoperidium hygroscopic – subhygroscopic or with exoperidial rays permanently rolled upwards-inwards under the endoperidial body	7
6b. Exoperidium non-hygroscopic	11
7a. Endoperidial body sessile	*G. kotlabae*
7b. Endoperidial body stalked	8
8a. Endoperidium smooth – felted	*G. xerophilum*
8b. Endoperidium rough	9
9a. Exoperidium weakly hygroscopic or non-hygroscopic; spores 4.3–5.5 μm in diam. (average 4.8 μm)	*G. pseudostriatum*
9b. Exoperidium distinctly hygroscopic	10
10a. Mycelial layer persistent; spores 4.5–5.7 μm in diam. (average 5.3 μm)	*G. campestre*
10b. Mycelial layer detaching and revealing a radially striate fibrous layer; spores 4.0–4.7 μm in diam. (average 4.4 μm)	*G. pouzarii*
11a. Endoperidium sessile	*G. elegans*
11b. Endoperidium stalked	12
12a. Endoperidial surface rough	13
12b. Endoperidial surface smooth or with farinaceous mesoperidium	14
13a. Spores 3.5–4.5 μm in diam. (average 4.3 μm); medium-sized–large species of wooded habitats	*G. berkeleyi*
13b. Spores 4.3–5.5 μm in diam. (average 4.8 μm); small species in dry and open habitats	*G. pseudostriatum*
14a. With little or no farinaceous mesoperidium in newly expanded fruiting bodies; in dry grasslands	*G. schmidelii*
14b. With abundant farinaceous mesoperidium in newly expanded fruiting bodies; in wooded habitats (woodlands, plantations, parks and gardens)	15
15a. Endoperidial body with a radially striate or sharply edged, collar-like apophysis	16
15b. Endoperidial body with a less developed and smooth apophysis	*G. parvistriatum*
16a. Endoperidial body with a sharply edged, collar-like apophysis	*G. striatum*
16b. Endoperidial with an almost smooth to distinctly radially striate apophysis	*G. pectinatum*
17a. Exoperidium ± hygroscopic	18
17b. Exoperidium non-hygroscopic	22
18a. Mycelial layer not encrusted with soil	*G. corollinum*
18b. Mycelial layer encrusted with soil, but may in some species detach soon after expansion to reveal a smooth fibrous layer	19
19a. With a distinctly delimited, disc-like peristome	20
19b. With undelimited peristome	21
20a. Endoperidal body sessile; mycelial layer detaches to reveal a smooth, white exterior of the fibrous layer; very small, strongly hygroscopic species	*G. hungaricum*
20b. Endoperidial body stalked; mycelial layer permanently attached; weakly to distinctly hygroscopic	*G. arenarium*
21a. Exoperidial rays coriaceous, strongly hygroscopic	*G. floriforme*
21b. Exoperidial rays not very firm; only weakly hygroscopic	*G. sp.1*
22a. Endoperidial body sessile	23

(*continued*)

(*continued*)

22b. Endoperidial body stalked	26
23a. Mycelial layer not encrusted with soil; with delimited peristome	24
23b. Mycelial layer encrusted with soil; with undelimited peristome (although sometimes lighter in colour than the rest of the endoperidium)	*G. fimbriatum*
24a. Mycelial layer felted	*G. saccatum*
24b. Mycelial layer smooth – radially fissured	25
25a. Spores 3.5–4.5 μm in diam. (average 3.7 μm); pseudoparenchymatous layer splits to encircle the endoperidial body as a collar	*G. triplex*
25b. Spores 2.5–3.5 μm in diam. (average 3.0 μm); pseudoparenchymatous layer not forming a collar	*G. lageniforme*
26a. Exoperidial rays somewhat hygroscopic or at least curled upwards under the endoperidial body	*G. pseudolimbatum*
26b. Exoperidial rays non-hygroscopic	27
27a. Mycelial layer not encrusted with soil; fruiting body pseudofornicate	*G. smardae*
27b. Mycelial layer encrusted with soil; fruiting body not pseudofornicate	28
28a. With delimited peristome	29
28b. With undelimited peristome	30
29a. Exoperidium fornicate, with four rays	*G. quadrifidum*
29b. Exoperidium not fornicate; with more than four rays	*G. minimum*
30a. Exoperidium fornicate, with four rays	*G. fornicatum*
30b. Exoperidium not fornicate, with more than 4 rays	31
31a. Mature fruiting body reddish brown; endoperidial body grey brown	*G. rufescens*
31b. Mature fruiting body pale greyish ochre; endoperidial body grey to almost black	*G. coronatum*

Notes on European species of *Geastrum* and *Myriostoma*

Geastrum arenarium Lloyd [as '*Geaster*']

The Geastrae (7): 28 (1902).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–10 more or less hygroscopic exoperidial rays; fully expanded 8–25 mm in diameter, ± arched. Pseudoparenchymatous layer pale grey to ochre, with age grey brown to dark grey. Fibrous layer pale grey. Mycelial layer persistent, encrusted with debris. Endoperidial body ± globose, 3–8 mm in diameter, sessile or with a short stalk and a poorly developed apophysis. Endoperidium grey, initially with a delicate, farinaceous pruina, later smooth. Peristome distinctly delimited, silky fibrillose, broadly conical. Basidiospores globose to weakly ellipsoidal, 3.0–4.0 × 3.0–3.5 μm, ornamented with irregular, low warts. Capillitial hyphae up to 7 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, North America, Africa, Australia.

Type specimen. Florida, USA. Holotype BPI.

Habitat. Dry and sandy forests under *Quercus ilex* and *Olea europea*.

Notes. *Geastrum arenarium* was described from Florida and was first reported from Europe (Móstoles, Madrid, Spain) by Calonge & Zamora (2003). It shares many of its morphological characters with *G. minimum*, and was considered a variety of the latter by Cunningham (1944). Distinguishing characters are, however, the somewhat hygroscopic exoperidial rays, the lack of crystalline matter on the endoperidial surface and smaller spores in *G. arenarium*. The material in the present study consisted of a part of the above-mentioned collection from Móstoles and specimens collected in 1985 in a dry and sandy habitat under *Quercus ilex* in El Parque de Casa de Campo in Madrid (Spain). The morphology of our material matches the descriptions in Lloyd (1902), Sunhede (1986), Calonge & Zamora (2003) and Bates (2004). Sunhede (1986) gave a detailed description of Lloyd's type material. Sequence data from the type material of *G. arenarium*, or other specimens of the species from North America, are not yet available for comparison.

Geastrum berkeleyi Massee [as '*Geaster*']

Ann. Bot., Lond. 4: 79 (1889). Fig. 3

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 5–9 non-hygroscopic exoperidial rays; fully expanded 30–80 mm in diameter, arched. Pseudoparenchymatous layer in young specimens pink, with age darkening to reddish brown. Fibrous layer greyish. Mycelial layer persistent, encrusted with debris. Endoperidial body ± globose, 15–25 mm in diameter, stalked and provided with a distinct apophysis. Endoperidium grey to grey brown, distinctly warty. Peristome delimited, sulcate, conically protruding. Basidiospores globose, 3.4–4.5 μm in diameter (average 4.3 μm), verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, with abundant surface debris.

World distribution. Europe.

Type specimen. Nottingham, UK. Lectotype K.

Habitat. Deciduous and coniferous woodlands on calcareous, nutrient-rich, often nitrogen-rich soils.

Notes. In Fennoscandia *G. berkeleyi* is known from scattered occurrences in the southern part of mainland Sweden and from the Baltic Sea islands Öland and Gotland. In our material it was represented from southern Sweden and

Figs 3–8. 3. *Geastrum berkeleyi*. Slovakia, Záhorská nižina, Lakšarska Nová Ves, 3 Sep 2005, leg. *J. & M. Jeppson 7494*. **4**. *Geastrum campestre*. Hungary, Csongrád, Ópuszta szer, Hantháza, 14 Apr 2009, leg. *M. Jeppson 8942*. **5**. *Geastrum corollinum*. Hungary, Bács-Kiskun, Kecskemét, Heténye gyháza, Nyír-erdö, 9 Apr 2009, leg. *M. Jeppson 8978*. **6**. *Geastrum flexuosum*. Sweden, Uppland, Röllingen NR, 1985. Photo Johan Nitare. **7**. *Geastrum floriforme*. Sweden, Öland, Vickleby, 12 Oct 2012. **8**. *Geastrum hungaricum*. Hungary, Bács-Kiskun, Kunadacs, 12 Apr 2009, leg. *M. Jeppson 8915*. Scale bar 10 mm.

Slovakia, showing little variation in morphology and ecology. Our concept of *G. berkeleyi* matches the original description of a collection from England (leg. Massee 1889; lectotype), studied by both Sunhede (1989) and Pegler *et al*. (1995). For the phylogenetic analyses, three new sequences of *G. berkeleyi* were generated. Sunhede (1989), as well as Kotlaba & Pouzar (1987), used a wide concept of *G. berkeleyi*, including also smaller specimens from open, xerothermic habitats. These had originally been described by Hollós (1901, 1904) as *G.*

pseudostriatum and, later, by Staněk (1958), as *G. hollosii*. We included also seven specimens originally labelled *G. berkeleyi* in the wide sense of Kotlaba & Pouzar (1987) and Sunhede (1989), but with small, slightly hygroscopic fruiting bodies from open grassland sites. These samples differed somewhat in sequence data, but were assigned to the same clade as *G. berkeleyi* by the phylogenetic analysis. Based on morphological, ecological and molecular sequence data we thus consider these specimens to be different from *G. berkeleyi* s. str. and represent the closely related species *G. pseudostriatum* Hollós (see species description below). *Geastrum berkeleyi* can be distinguished from *G. pseudostriatum* as it grows in nutrient-rich, wooded or bushy habitats; has larger fruiting bodies; and has on average smaller spores.

Geastrum campestre Morgan [as '*Geaster*']

Am. Nat. 21: 1027 (1887). Fig. 4.

Synonym. *Geastrum asperum* Lloyd [as '*Geaster asper*'], The Geastrae (7): 18 (1902).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–10 hygroscopic exoperidial rays; fully expanded 10–35 mm in diameter, arched. Pseudoparenchymatous layer in young specimens pinkish, with age brown to grey brown. Fibrous layer greyish. Mycelial layer persistent, encrusted with debris. Endoperidial body ± globose, 7–10 mm in diameter, stalked and provided with an apophysis. Endoperidium grey to grey brown, distinctly warty. Peristome delimited, sulcate, conically protruding. Basidiospores globose to subglobose, 4.5–5.7 μm in diameter (average 5.3 μm), verrucose. Capillitial hyphae up to 7 μm in diameter, thick-walled and with abundant surface debris.

World distribution. Europe, Asia, North America, South America, Australia, Hawaii, Africa.

Type specimen. Nebraska, USA. Holotype ISC, isotype K.

Habitat. Dry and warm, more or less steppic sites on both calcareous and acidic ground.

Notes. In our material *G. campestre* was represented by specimens from central Spain, Hungary, Slovakia, Sweden and Norway, with little variation in morphology. Our material matches the concept of *G. campestre,* used by European authors such as Hollós (1904, as Geaster asper), Staněk (1958), Calonge (1998) and Sunhede (1989, 2012). Although generally rare, *G. campestre* has a wide geographical distribution in Europe. In Fennoscandia it is on record from the island Lilla Karlsö in the Baltic Sea (Sunhede, 1989) and from the southermost parts of the Swedish mainland (provinces Skåne and Blekinge), coastal areas in Denmark, and on calcareous islands in the Oslo fiord area (Eckblad, 1955; Sunhede, 1989). Some reports from Sweden (e.g. Jeppson & Knutsson, 2008) have proved to be erroneous and refer to *G. pseudostriatum*. The phylogenetic analyses show a close relationship to *G. berkeleyi* and *G. pseudostriatum*.

Geastrum corollinum (Batsch) Hollós

Gasterom. Ung. 65: 154 (1904). Fig. 5.

Basionym*: Lycoperdon corollinum* Batsch, Elench. fung. (Halle): 151 (1783).
= *Geastrum recolligens* (With.) Desv., J. Bot., Paris 2: 102 (1809).

Description. Immature basidiomata epigeous, ochraceous to yellowish brown, ± onion-shaped; at maturity splitting in 7–10 hygroscopic exoperidial rays; fully expanded 15–40 mm in diameter, ± saccate. Pseudoparenchymatous layer in young specimens pale beige, with age pale brown to dark brown. Fibrous layer beige to brownish. Mycelial layer not encrusted with debris, partially detaching to expose a whitish inner layer. Endoperidial body globose to depressed, 10–20 mm in diameter, sessile. Endoperidium grey to grey brown, smooth. Peristome ± delimited, fibrillose, applanate to broadly conical. Basidiospores globose, 4.0–4.5 μm in diameter, verrucose. Capillitial hyphae up to 7 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, Hawaii, Africa.

Type specimen. Europe. Lectotype: Micheli, 1729, tab. 100, fig. 3. See discussion in Sunhede (1989).

Habitat. In shaded situations in deciduous forests or under bushes, on calcareous soil, often in nitrogen-rich sites. In southern Fennoscandia it is also found close to junipers in dry calcareous grasslands.

Note. *Geastrum corollinum* has a wide European distribution and reaches its northernmost localities in southern Fennoscandia (north to 58°N). The specimens sequenced in our study match the morphological descriptions in Staněk (1958), Sunhede (1989) and others.

Geastrum coronatum Pers.

Syn. meth. fung. (Göttingen) 1: 132 (1801).

= *Geastrum limbatum* Fr. [as '*Geaster*'], Syst. mycol. (Lundae) 3(1): 15 (1829).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–12 non-hygroscopic exoperidial rays; fully expanded 30–110 mm in diameter, arched. Pseudoparenchymatous layer in young specimens pale

greyish brown, with age grey brown. Fibrous layer greyish white. Mycelial layer persistent, encrusted with debris. Endoperidial body globose to irregularly globose, 10–30 mm in diameter, stalked and provided with a distinct apophysis. Endoperidium light grey to grey brown to almost black, smooth. Peristome ± delimited, often indistinctly, silky fibrillose, applanate to broadly conical. Basidiospores globose, 4.5–5.5 μm in diameter, irregularly verrucose. Capillitial hyphae up to 15 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, North America, Central America, Australia, Africa.

Type specimen. Germany. Lectotype: Schmidel, 1793, plate 46 (cfr. Sunhede, 1989).

Habitat. Nitrogen-rich sites in deciduous and coniferous woodlands, parks, and gardens. In southern Fennoscandia also under junipers in dry calcareous grasslands.

Notes. *Geastrum coronatum* is widely distributed in Europe and reaches 61°N in Sweden. The specimen sequenced in this study closely matches the concepts of Hollós (1904), Staněk (1958) and Sunhede (1989). *Geastrum coronatum* is the generic type of *Geastrum*.

Geastrum elegans Vittad. [as '*Geaster*']

Monograph Lyc.: 15 (1842).

= *Geastrum badium* Pers., J. Bot. (Desvaux) 2: 31 (1809).
= *Geastrum umbilicatus* Fr. [as '*Geaster*'], Syst. mycol. (Lundae) 3(1): 14 (1829) sensu auct.

Description. Immature basidiomata hypogeous, at maturity epigeous, splitting in 5–8 non-hygroscopic exoperidial rays; fully expanded 8–35 mm in diameter, ± saccate. Pseudoparenchymatous layer in young specimens pale beige, with age brownish beige to grey brown. Fibrous layer whitish beige to pale ochre. Mycelial layer encrusted with debris. Endoperidial body globose to ellipsoid, 5–10 mm in diameter, sessile and without apophysis. Endoperidium light grey to greyish beige, in newly expanded basidiomata covered with a whitish pruina (mesoperidium). Peristome undelimited, sulcate, conically protruding. Basidiospores globose, 4.5–5.5 μm in diameter, verrucose. Capillitial hyphae up to 7 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, South America.

Type specimen. Italy. Neotype TO.

Habitat. Open dry grassland sites on well-drained base-rich soils; occasionally found also in woodlands.

Notes. *Geastrum elegans* is a widely distributed species in Europe, reaching its northernmost outposts in southern Fennoscandia (north to 60°N). The specimens studied closely match the species concept of Hollós (1904; as Geaster umbilicatus), Staněk (1958; as *Geastrum badium*), and Sunhede (1989). Its intraspecific morphological variation was treated by Sunhede (1974).

Geastrum fimbriatum Fr.

Syst. mycol. (Lundae) 3(1): 16 (1829).

= *Geastrum sessile* (Sowerby) Pouzar, Folia geobot. phytotax. 6: 95 (1971).
= *Geastrum tunicatum* Vittad. [as '*Geaster*'], Monograph Lyc.: 18 (1842).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–9 non-hygroscopic exoperidial rays; fully expanded 20–50 mm in diameter, saccate. Pseudoparenchymatous layer in young specimens almost white to pale beige, with age ochraceous brown to nut brown. Fibrous layer whitish beige. Mycelial layer encrusted with debris. Endoperidial body ± globose, 10–25 mm in diameter, sessile and without apophysis. Endoperidium beige to greyish brown, smooth. Peristome undelimited, silky fibrillose, applanate to broadly conical. Basidiospores globose, 3.0–4.0 μm in diameter, verrucose. Capillitial hyphae up to 9 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, South America, Australia, Africa.

Type specimen. Sweden. Neotype GB (!).

Habitat. Deciduous and coniferous woodlands on calcareous soils; also in dry calcareous grasslands, under or close to junipers.

Notes. *Geastrum fimbriatum* is a widely distributed and well-known species in Europe, its distribution reaching north of the Polar Circle in Fennoscandia (Sunhede, 1989).

Our specimens match the descriptions given by Staněk (1958), Sunhede (1989) and other authors.

Geastrum flexuosum (L.S. Domínguez & Castellano) Jeppson & E. Larss.

Fig. 6.

Basionym: *Radiigera flexuosa* L.S. Domínguez & Castellano, Mycologia 88(5): 877 (1996).

Description. Immature basidiomata hypogeous or semi-epigeous. Mature basidiomata rounded, 20–40 mm in diameter, white to pale brownish, with irregular rupture of the peridium. Fibrous layer white to ochraceous. Mycelial layer basally encrusted with debris. Endoperidium reduced or lacking. Mature gleba dark brown, with a distinct metallic smell (Kers, 1976). Basidiospores globose, 4.0–5.0 μm in diameter, verrucose. Capillitial hyphae 3–5 μm in diameter, thin walled, somewhat tortuous to flexuose, sparsely and irregularly covered with surface debris.

World distribution. Europe (Sweden).

Type specimen. Sweden. Holotype UPS (!).

Habitat. Among leaf litter under deciduous trees.

Notes. *Geastrum flexuosum* is known from a single locality, with one active mycelium, in south central Sweden, where it first was detected by Kers (1976) and published as *Radiigera atrogleba*. In a revision of the genus *Radiigera*, Domínguez de Toledo & Castellano (1996) described it as a new species, choosing an epithet referring to the somewhat tortuose–flexuose capillitial hyphae found in the mature gleba. It is characterized by semihypogeous fruiting bodies splitting irregularly at maturity and not in rays as in a typical earthstar. For detailed morphological descriptions, see Kers (1976) and Domínguez de Toledo & Castellano (1996). The locality in Sweden is an old abandoned farm-site situated in a deciduous forest on an island in Lake Mälaren, not far from Stockholm. It was observed regularly during a period of more than 30 years but, despite annual monitoring, no new fruiting bodies have been observed after 2005. It is on the Swedish Red-list as CR (Critically endangered) and an Action plan for its conservation has been established by the Swedish Environmental Protection Agency (Jeppson, 2009). In the phylogeny, *G. flexuosum* is found in subclade C, affiliated with the widely distributed *G. corollinum*. The sequence data clearly show that *R. flexuosa* is nested in the genus *Geastrum.*

Geastrum floriforme Vittad. [as '*Geaster*']

Monograph Lyc.: 23 (1842). Fig. 7.

= *Geastrum delicatum* Morgan [as '*Geaster*'], Am. Nat. 21: 1028 (1887).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–11 hygroscopic exoperidial rays; fully expanded 20–50 mm in diameter, ± saccate to slightly arched. Pseudoparenchymatous layer in young specimens light beige, with age dark brown. Fibrous layer greyish. Mycelial layer encrusted with debris, soon detaching and exposing the exterior part of the fibrous layer. Endoperidial body globose to depressed globose, 5–15 mm in diameter, sessile and without apophysis. Endoperidium ochraceous to grey brown, finely furfuraceous to smooth. Peristome undelimited, silky fibrillose, applanate to broadly conical. Basidiospores globose, 4.5–5.5 μm in diameter, verrucose. Capillitial hyphae up to 7 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, South America, Australia, New Zealand, Africa.

Type specimen. Italy, but currently no available type specimen. Original Vittadinian material may be present in K (Sunhede, 1989). If no such material exists, Vittadini, 1842, tab. 1, fig. 5, should be selected as lectotype.

Habitat. Mostly in dry, open grasslands, pastures, and sand dunes, but also in shaded, nitrogen-rich habitats; several records from ant-hills (*Formica* spp.) in dry, open grassland areas.

Notes. *Geastrum floriforme* has a wide European distribution and reaches its northernmost localities in the boreal zone of Fennoscandia (north to 63°N). The material at our disposal shows little morphological variation and our concept is in accordance with that of Hollós (1904), Staněk (1958) and Sunhede (1989).

Geastrum fornicatum (Huds.) Hook

Curtis Fl. Londin. 4: 575 (1821).

Basionym: *Lycoperdon fornicatum* Huds. Flora Anglica: 502 – 502 (1762).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 4 (rarely 3 or 5) non-hygroscopic exoperidial rays; fully expanded 30–80 mm in diameter, with a maximum height of 120 mm, fornicate. Pseudoparenchymatous layer initially beige, rather thick, later shrinking and becoming dark brown to almost black, and, partially, peeling off. Fibrous layer beige, with age becoming brown. Mycelial layer encrusted with debris, remaining in the soil as a cup to which the arched exoperidial rays are connected. Endoperidial body ± globose, 10–15 mm in diameter, stalked and provided with an apophysis. Endoperidium ochraceous to grey brown, with age dark brown, smooth. Peristome undelimited, silky fibrillose, conical to shortly tubiform. Basidiospores globose, 3.5–4.5 μm in diameter, finely verrucose. Capillitial

hyphae up to 9 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, South America, West Indies, Australia, Hawaii, Africa.

Type specimen. Great Britain. Lectotype: Watson, 1744, fig. 11–12; cfr. Sunhede (1989).

Habitat. In rich deciduous woodlands on calcareous soil, also churchyards and gardens, often in nitrogen-rich sites. In central Europe in *Robinia* woodlands.

Notes. *Geastrum fornicatum* has a wide European distribution but is rare and declining, and it is on the red-lists of several countries. It reaches its northernmost limits in southern Sweden (north to about 59°N). Our samples, originating from Sweden, France, Germany and Hungary, are in agreement with descriptions in Hollós (1904), Staněk (1958), Sunhede (1989) and others.

Geastrum hungaricum Hollós [as '*Geaster*']

Mathem. Természettud. Közlem. 19: 502 (1901). Fig. 8.

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–11 hygroscopic exoperidial rays; fully expanded 3–8 (–10) mm in diameter, arched or saccate. Pseudoparenchymatous layer persistent, initially beige, later yellowish brown to dark brown. Fibrous layer white, sometimes with a short basal cord. Mycelial layer encrusted with debris, but soon detaches to expose the exterior of the fibrous layer. Endoperidial body ± globose, 1–5 mm in diameter, sessile. Endoperidium ochraceous to grey brown, in newly expanded basidiomata with an evanescent whitish pruina. Peristome delimited, discoid, silky fibrillose, broadly conical. Basidiospores globose, 5.0–5.5 μm in diameter, verrucose. Capillitial hyphae up to 5 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia.

Type specimen. Hungary. Neotype BP, designated by Sunhede (1989).

Habitat. Dry, steppic grasslands, pastures and wastelands.

Notes. *Geastrum hungaricum* was originally described from Hungary by Hollós (1901), and later reported from Russia, Mongolia and Japan (Hollós, 1904; Dörfelt & Täglich, 1990; Rebriev, 2007a, 2007*b*; Kasuya *et al*., 2011). Recent European records include the Czech Republic, Germany, Hungary (several localities) and Poland (Rauschert, 1958; Staněk, 1958; Sunhede, 1989; Rimóczi *et al*., 2011). Records from southern Slovakia are added in this paper. There are no records from the Mediterranean area, nor from the western and northern parts of Europe. It is considered a potentially declining species in eastern Europe (Holec & Beran, 2006; Siller *et al*., 2006). The specimens studied for this paper match the species concept of previous authors.

Geastrum kotlabae V.J. Staněk

Flora ČSR, B-1, Gasteromycetes: 474, 784 (1958). Fig. 9.

= *Geastrum ambiguum* Mont. [as '*Geaster*'], Annls Sci. Nat., Bot., sér. 2 8 (1837) sensu Hollós (1904).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–9 hygroscopic exoperidial rays; fully expanded 8–15 mm in diameter. Pseudoparenchymatous layer persistent, initially beige, with age brown to almost black. Fibrous layer whitish to greyish. Mycelial layer encrusted with debris but soon detaches to expose the exterior of the fibrous layer. Endoperidial body ± globose, 4–10 mm in diameter, sessile. Endoperidium pale grey to greyish brown, initially furfuraceous or finely warty, with age smooth. Peristome undelimited, sulcate, broadly conical. Basidiospores globose, 4.0–5.0 μm in diameter, finely verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, North America, Central America, Asia (?), Australia, Africa.

Type specimen. Hungary. Holotype PRM.

Habitat. Dry grasslands, pastures and wastelands.

Notes. *Geastrum kotlabae* is a rare xerothermophilous species with a wide distribution in south, central, and eastern Europe (Hollós, 1904; Calonge, 1998; Sarasini, 2002; Rebriev, 2007*a*, 2007*b*; Rimóczi *et al*., 2011). There are no records from northern Europe. Our specimens, originating from Hungary, Spain and Slovakia, closely match the concept of this species in Hollós (1904, as G. ambiguum), Staněk (1958) and Sunhede (1989). In the phylogenetic tree it is found with the hygroscopic species *G. pouzarii*, from which it differs in its sessile endoperidial body and the less pronounced spore ornamentation. The sequences of the two samples from Hungary were identical, whereas the GenBank sequence originating from Japan differs and seems to be more closely related to *G. pouzarii*. This sequence may represent a separate taxon.

Geastrum lageniforme Vittad. [as 'Geaster']

Monograph Lyc.: 16 (1842). Fig. 10.

Description. Immature basidiomata epigeous, onion-shaped, brown, smooth, at maturity splitting in 6–9

Figs 9–12. 9. *Geastrum kotlabae*. Hungary, Pest, Nagykörös, Csokáserdö, 12 Apr 2004, leg. *M. Jeppson 6850*. Photo Tommy Knutsson. **10**. *Geastrum lageniforme*. Slovakia, Podunajská nižina, Révayovská pustatina,16 Oct 2004, leg. *M. Jeppson 7337*. Bottom view of exoperidium showing a brownish, smooth mycelial layer. **11**. *Geastrum minimum*. Sweden, Öland, Högby, Högby fyr, 2 Nov 2012. Photo T. Knutsson. **12**. *Geastrum morganii*. France, La Vendée. Longeville, Forêt de Longeville, 25 Jan 2007, leg. *J. & M. Jeppson 8430*. Photo J. Jeppson. Scale bar 10 mm.

non-hygroscopic exoperidial rays; fully expanded 15–50 mm in diameter, saccate. Pseudoparenchymatous layer persistent, initially beige, later ± dark brown. Fibrous layer white to grey. Mycelial layer not encrusted with debris, brown, smooth and radially fissured. Endoperidial body ± globose, 10–15 mm in diameter, sessile. Endoperidium beige to greyish brown, smooth. Peristome delimited, silky fibrillose, broadly conical. Basidiospores globose, 2.5–3.5 μm in diameter (average 3.0 μm), finely verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, South America, Australia, Africa.

Type specimen. Italy. Neotype K (cfr. Sunhede, 1989).

Habitat. Dry deciduous woodlands on calcareous soil.

Notes. *Geastrum lageniforme* is a rare but widely distributed species in Europe. It does not reach Fennoscandia. Our specimens consist of recent collections from Hungary and Slovakia, where it has scattered occurrences, particularly growing amongst leaf litter in *Robinia pseudoacacia*-stands on calcareous, sandy soil. In our experience, the often referred character of the exoperidium, having slender rays, is not a consistent feature of this species. The micro-character in the outer layer of the exoperidium mentioned by several authors (i.e. presence of clamps; Vidal, 1987; Sunhede, 1989) could be confirmed in the material at our disposal, but as noted by Trieveiler-Pereira *et al*. (2011), this character is not always easy to observe. The smooth, brown, thin, radially striate mycelial layer of the exoperidium is an important macro-character distinguishing *G. lageniforme* from the closely related, and morphologically very similar, *G. saccatum*. Spore size is yet another character differentiating *G. lageniforme* from *G. saccatum*. According to Vidal (1987), the spores in *G. lageniforme* are slightly smaller and with less pronounced ornamentation. This is in accordance with our observations. Average spore diameter in our material was 3.5 μm in *G. saccatum*, in contrast to the 3.0 μm observed for *G. lageniforme*. Sunhede (1989) further notes differences in the shape of the basidia, *G. lageniforme* having ± lageniform basidia, whereas they are ± clavate in *G. saccatum*. Basidia were not observed in this study.

Geastrum melanocephalum (Czern.) V.J. Staněk

Česká Mykol. 10(1): 22 (1956).

Basionym: *Trichaster melanocephalus* Czern. Bull. Soc. Imp. nat. Moscou 18(2, III): 149 (1845).

Description. Immature basidiomata epigeous, rounded to onion-shaped, brown, smooth or somewhat cracked or scaly. At maturity splitting in 5–8 non-hygroscopic exoperidial rays; fully expanded 40–200 mm in diameter, arched. Pseudoparenchymatous layer initially beige, with age ± dark brown, shrinking and peeling off, partly covered with the detached endoperidium and parts of the gleba. Fibrous layer brown to greyish brown. Mycelial layer not encrusted with debris, brown, smooth to cracked. Endoperidial body ± globose, 25–60 (–80) mm in diameter, provided with a stout stalk and a prominent columella. Endoperidium detaching from the mature gleba, sticking to the pseudoparenchymatous layer of the exoperidium, leaving the gleba denuded. Remnants of the endoperidium is sometimes seen as a ring on the stalk. Peristome lacking. Basidiospores globose, 3.5–4.5 μm in diameter, verrucose. Capillitial hyphae up to 6 μm in diameter, thick-walled, usually covered with abundant surface debris.

World distribution. Europe, Asia, North America.

Type specimen. Ukraine. Holotype K.

Habitat. Nitrogen-rich sites in forests, but also from under, or adjacent to, shrubs in calcareous grasslands.

Notes. *Geastrum melanocephalum* has a wide distribution in Europe and reaches its northernmost localities in southern Fennoscandia (north to about 60°N), as shown by Sunhede (1989). It is usually considered a Eurasian species, but an additional recent record has been published from Mexico by Esqueda-Valle *et al*. (1995). The studied specimens agree with the descriptions by previous authors (e.g. Staněk, 1958; Sunhede, 1989). *Geastrum melanocephalum* was described as *Trichaster melanocephalus* by Czerniaiev (1845) and later transferred to *Geastrum* by Staněk (1956). Studies by Lohwag (1925), Staněk (1958), Kers (1975) and Sunhede (1989) have demonstrated morphological similarities between *G. melanocephalum* and *G. triplex*, and several authors have chosen to follow Staněk (1958) in considering the genus *Trichaster* a later synonym of *Geastrum*. In the phylogenetic tree it forms a strongly supported clade together with sequences of *G. triplex*, which is in accordance with Kasuya *et al*. (2012), and which confirms the relationship. Although *G. melanocephalum* and *G. triplex* can be readily distinguished on morphological features, the phylogenetic analyses of Kasuya *et al*. (2012) indicated conspecificity between *G. melanocephalum* and European and North American samples of *G. triplex*.

Geastrum minimum Schwein. [as 'Geaster']

Schr. naturf. Ges. Leipzig 1: 58 (1822). Fig. 11.

= *Geastrum marginatum* Vittad. [as '*Geaster*'], Monograph Lyc.: 163 (1842).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–9 non-hygroscopic exoperidial rays; fully expanded 5–30 mm in diameter, ± arched. Pseudoparenchymatous layer in young specimens whitish to beige, with age pale grey. Fibrous layer whitish beige. Mycelial layer persistent, encrusted with debris. Endoperidial body ± globose, 5–10 mm in diameter, stalked, and provided with an apophysis. Endoperidium pale grey to greyish brown, in newly expanded basidiomata with a whitish crystalline pruina. Peristome delimited, ± discoid, silky fibrillose, broadly conical. Basidiospores globose, 4.5–5.5 μm in diameter, verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled and sparsely covered with surface debris.

World distribution. Europe, Asia, North America, Central America, South America, Australia, New Zealand, Africa.

Type specimen. North Carolina, USA. Holotype K.

Habitat. Dry calcareous grasslands, sand dunes, sand steppe vegetation; also in dry, arctic-alpine sites.

Notes. *Geastrum minimum* is a well characterized, small and pale-coloured species with a wide European distribution, reaching the arctic-alpine zone in northern Fennoscandia (Sunhede, 1989). Although on record from Greenland (Lange, 1948), it has to date not been reported from Iceland. In southern regions misidentifications are possible with the somewhat similar *G. arenarium*, known from Central Spain, which, however, is characterized by a ± hygroscopic exoperidium and smaller spores. A Swedish specimen of *G. minimum*, matching the species concept of Sunhede (1989) and Staněk (1958), was used in our molecular analysis. It forms a strongly supported clade together with *G. quadrifidum*.

Geastrum morganii Lloyd [as '*Geaster*']

Mycol. Writ. 1(8): 80 (1901). Fig. 12.

Description. Immature basidiomata epigeous, ± onion-shaped; at maturity splitting in 5–8 non-hygroscopic exoperidial rays; fully expanded 30–60 mm in diameter, ± saccate. Pseudoparenchymatous layer initially pinkish beige or ochre, with age darkening to brown, frequently forming a collar around the base of the endoperidium. Fibrous layer ochraceous. Mycelial layer not encrusted with debris, smooth to furfuraceous, initially pinkish to pale orange brown, later pale grey to grey-brown. Endoperidial body sessile, smooth, brown to grey brown, 8–25 mm in diameter. Peristome undelimited, irregularly sulcate, ± conical. Basidiospores globose, 3.0–4.0 μm, verrucose. Capillitial hyphae up to 7 μm in diameter, thick-walled and sparesly covered with surface debris.

World distribution. Europe, North America, Central America, Canary Islands.

Type specimen. USA. Lectotype: Lloyd, 1901, fig. 45–46, selected by Sunhede (1989).

Habitat. Coastal woodlands on sandy, calcareous soil; in Europe found mainly amongst leaf litter under *Robina pseudoacacia*.

Notes. *Geastrum morganii* is a rare species, first recorded in Europe in 1968, growing in sandy coastal woodlands along the French Atlantic coast (Boiffard, 1976). Later it was also on record from Catalunya (Spain; Vidal, 1987) and Italy (Sarasini, 2002, 2005). There are no reports from northern or central Europe, and Kreisel (2001) considers it an introduced species in Europe. Our specimens, collected in France, agree with the general concept of this species (e.g. Boiffard, 1976; Vidal, 1987; Sunhede, 1989). Calonge (1998) synonymized *G. morganii* with *G. elegans* (as *G. badium*) based on similarities in morphology (e.g. saccate basidiomata with undelimited, sulcate peristomes). Sunhede (1989) compared the two species and concluded that they share several characters, but differ, *inter alia* in the features of the exoperidium and the peristome, and should be kept separate. Our sequence data placed *G. morganii* and *G. elegans* in different subclades in the phylogenetic tree, thus confirming Sunhede's concept.

Geastrum parvistriatum J.C. Zamora & Calonge

Boln Soc. Micol. Madrid 31: 140 (2007).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 5–9 non-hygroscopic exoperidial rays; fully expanded 10–40 mm in diameter, arched. Pseudoparenchymatous layer in young specimens white with a pinkish tinge, with age beige to light brown. Fibrous layer whitish beige to pale ochre. Mycelial layer encrusted with debris. Endoperidial body globose to ellipsoid, 5–16 mm in diameter, stalked and with an apophysis. Endoperidium light grey to dark grey, in newly expanded basidiomata covered with a whitish pruina (mesoperidium). Peristome indistinctly delimited, sulcate, conically protruding. Basidiospores globose, 4.0–5.0 μm in diameter, verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, without, or with sparse surface debris.

World distribution. Europe (Spain).

Type specimen. Spain. Holotype MA-Fungi, isotypes K and PC (!).

Habitat. In dry, Mediterranean vegetation under *Pinus halepensis*, *Olea europea*, *Cupressus arizonica* and *Tamarix*; also in urban parks and gardens.

Notes. *Geastrum parvistriatum* is a small earthstar, recently described from central Spain (Zamora & Calonge, 2007). It shares several morphological features with *G. striatum*, e.g. sulcate peristome and a stalked endoperidial body with farinaceous mesoperidial covering, but it forms smaller fruiting bodies, lacking the sharply edged apophysis of *G. striatum*. The material studied for this paper consisted of a part of the holotype, as well as fresh fruiting bodies collected in a plantation of *Pinus halepensis* on gypsum soil in the vicinity of Alcalá de Henares (Madrid, Spain). Our observations confirm the morphological features as described by Zamora & Calonge (2007). The occurrence of *G. parvistriatum* is to date restricted to the central parts of the Iberian Peninsula.

Geastrum pectinatum Pers.

Syn. meth. fung. (Göttingen) 1: 132 (1801).

= *Geastrum plicatum* Berk. [as '*Geaster*'], Ann. Mag. nat. Hist., Ser. 3: 399 (1839).
= *Geastrum tenuipes* Berk. [as '*Geaster*'], London J. Bot. 7: 576 (1848).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–10, non-hygroscopic exoperidial rays; fully expanded 15–120 mm in diameter, arched. Pseudoparenchymatous layer pale greyish beige to greyish brown, thick in young specimens, gradually drying and shrinking, often covering the endoperidial stalk as a cylinder or a ring-like collar. Mycelial layer persistent, encrusted with debris. Endoperidial body globose to depressed globose, 10–25 mm in diameter, stalked, with a ± radially striate apophysis. Endoperidium greyish brown to dark brown, in newly expanded basidiomata with an abundant farinaceous mesoperidial covering of hyphae and crystalline matter. Peristome indistinctly to distinctly delimited, sulcate, conical. Basidiospores globose, 3.5–4.5 μm in diameter, coarsely verrucose. Capillitial hyphae up to 9 μm with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, Africa.

Type specimen. Germany. Neotype L, selected by Palmer (1959).

Habitat. Coniferous and deciduous rich woodlands (also on base-poor soils), frequently on needle beds or on abandoned ant-hills, also under, or adjacent to bush in dry, open habitats.

Notes. *Geastrum pectinatum* is a fairly frequent species with a wide European distribution, reaching the subarctic vegetation in northernmost Norway (70°N; Bohlin, 1993). In South and Central Europe it is mainly a montane species. The morphology of the studied specimens matches the descriptions by Hollós (1904), Staněk (1958) and Sunhede (1989).

Geastrum pouzarii V.J. Staněk

Česká Mykol. 8: 107 (1954).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 8–10 hygroscopic exoperidial rays; fully expanded 20–30 mm in diameter, arched. Pseudoparenchymatous layer persistent, initially beige to orange brown, with age dark brown. Fibrous layer white to grey, with radial striation on the exterior side. Mycelial layer encrusted with debris, but soon detaches and exposes the fibrous layer. Endoperidial body ± globose, 4–6 mm in diameter, shortly stalked, with a ± developed apophysis. Endoperidium beige to greyish brown, warty. Peristome delimited, sulcate, conical. Basidiospores globose, 4.0–4.7 μm in diameter (av. 4.4 μm), verrucose. Capillitial hyphae up to 5 μm in diameter, thick-walled, with no or sparse surface debris.

World distribution. Europe, North America (Mexico).

Type specimen. Czech Republic. Holotype PRM.

Habitat. Dry rupicolous steppe vegetation in Central Europe; in Spain under *Juniperus thurifera* in dry Mediterranean vegetation.

Notes: *Geastrum pouzarii* is a hygroscopic earthstar with strong morphological affinity with *G. campestre.* It was considered a variety of *G. campestre* by Dörfelt (1989; as G. pedicellatum var. pouzarii) and Calonge (1998). Sequence data confirm it as a distinct species with *G. kotlabae* as the sister species. *Geastrum pouzarii* can be distinguished from *G. campestre* by the evanescent mycelial layer and the significantly smaller spores. In the Czech Republic it forms fruiting bodies in spring, just after the snow has gone (Kotlaba, 1980). There are currently no records from northern Europe. It was recently reported from dry bushland communities and dry tropical forests in Mexico (Esqueda *et al*., 2003). The samples studied for this paper closely match the original description by Staněk (1954) and with that of Sunhede (1989).

Geastrum pseudolimbatum Hollós [as '*Geaster*']

Mathem. Természettud. Közlem. 19: 507 (1901). Fig. 13.

= *Geastrum coronatum* f. *pseudolimbatum* (Hollós) Dörfelt & Müller-Uri, Boletus 7: 15 (1983).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–10 exoperidial rays, which are ± hygroscopic; fully expanded 15–50 mm in diameter, arched. Pseudoparenchymatous layer persistent, initially pinkish beige, with age reddish brown to dark grey-brown. Fibrous layer whitish. Mycelial layer persistent, encrusted with debris, detaching in old specimens. Endoperidial body ± globose, 7–15 mm in diameter, stalked, with a ± distinct apophysis. Endoperidium grey, with minute warts and ridges. Peristome delimited, silky fibrillose, broadly conical. Basidiospores globose, 4.5–5.5 μm in diameter, verrucose. Capillitial hyphae up to 9 μm in diameter, thick-walled and sparsely covered with surface debris.

World distribution. Europe, North America (Mexico).

Figs 13–16. 13. *Geastrum pseudolimbatum*. Sweden, Öland, Sandby, Åby sandfält, 22 Feb 2008, leg. *M. Jeppson 8796*. **14**. *Geastrum pseudostriatum*. Sweden, Öland, Gårdby, 25 Oct 2010, leg. M. Jeppson. **15**. *Geastrum saccatum*. Hungary, Pest, Pustavacsi erdö, 12 Oct 2004, leg. *B. Hägg* & *M. Jeppson 6840*. Bottom view of exoperidium showing a chamois-like, felted mycelial layer. **16**. *Geastrum xerophilum.* Spain, Almería, Venta de Yesos, 6 Apr 2001, leg. *M. Jeppson 9533*. Scale bar 10 mm.

Type specimen. Hungary. Neotype BP, selected by Sunhede (1989).

Habitat. Xerothermic, steppic sites, sand dunes, sand steppe vegetation; sometimes also in nitrogen-rich waste places.

Notes. *Geastrum pseudolimbatum* is a widely distributed, albeit rare species in Europe. It has scattered records in continental regions of the Iberian Peninsula (Calonge, 1998) and littoral habitats in Italy (Sarasini, 2005). It reaches the Atlantic coast in France and the Netherlands (Boiffard, 1976; Jalink, 1995) but seems to have its main distribution in east central Europe (Rimóczi *et al*., 2011). Its northernmost localities are situated in southern Sweden (Sunhede, 1979; Hanson & Jeppson, 2005; Jeppson & Knutsson, 2008). It was reported from Mexico by Esqueda *et al*. (2003). Our specimens show little morphological

variation and are in accordance with the descriptions in Hollós (1904), Staněk (1958) and Sunhede (1989). Although it was considered a mere form of *G. coronatum* by some authors (e.g. Dörfelt & Müller-Uri, 1983; Dörfelt, 1989; Calonge, 1998), both the morphological characters and molecular sequence data confirm it as a distinct species. *Geastrum pseudolimbatum* forms a clade together with *G. xerophilum* in the phylogenetic tree, a species with which it also shares morphological similarities.

Geastrum pseudostriatum Hollós [as '*Geaster*']

Math. Termész. Értes 19: 505–506 (1901). Fig. 14.

= *Geastrum hollosii* V.J. Staněk, Flora ČSR, B1 Gasteromycetes: 467, 790 (1958).
= *Geastrum berkeleyi* Massee [as '*Geaster*'], Ann. Bot., Lond. 4: 79 (1889) sensu auct.

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 5–9 non-hygroscopic (or sometimes slightly hygroscopic) exoperidial rays; fully expanded 15–30 mm in diameter, arched. Pseudoparenchymatous layer persistent, initially greyish pink to pale brownish, later beige-brown to dark brown. Fibrous layer whitish to ochraceous. Mycelial layer persistent and encrusted with debris. Endoperidial body ± globose, 5–10 mm in diameter, stalked, with an apophysis. Endoperidium grey, warty. Peristome delimited, sulcate, conically protruding. Basidiospores 4.5–5.5 μm in diameter (av. 4.8 μm), verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, with abundant surface debris.

World distribution. Europe, Asia.

Type specimen. Hungary. Lectotype BP (!), selected by Sunhede (1989).

Habitat. Open or semi-exposed dry grasslands and steppe-like habitats on calcareous ground.

Notes. *Geastrum pseudostriatum* has been recorded from southern Sweden, southern Slovakia, central Hungary and Turkey. It is characterized by small, non-hygroscopic (or sometimes weakly and irregularly hygroscopic) fruiting bodies with a rough endoperidium and a sulcate peristome. Two species with this morphology have been described from east central Europe: *G. pseudostriatum* Hollós and *G. hollosii* V.J. Staněk, both synonymized with *G. berkeleyi* by Kotlaba & Pouzar (1987) and Sunhede (1989). Since the phylogenetic analyses indicated that *G. berkeleyi* in the sense of Sunhede could be divided in two taxa, the type materials of *G. hollosii* and *G. pseudostriatum* were studied. The morphology of the lectotype of *G. pseudostriatum* was found to be conspecific with our specimens. DNA was extracted and the sequence of the ITS1 region was successfully obtained. The ITS1 was found to be identical with the sequences generated from our own specimens. Furthermore, the holotype of *G. hollosii* was studied and found to agree in morphology with the lectotype of *G. pseudostriatum* and our specimens from open habitats in Sweden. Unfortunately, we did not succeed in generating sequence data from this type specimen, but judging from the morphology we are of the opinion that Hollos's and Staněk's species are mutually identical and also identical with our own specimens. In addition, morphological studies of specimens in Herbarium BRA, labelled *G. pseudostriatum*, originating from the Hurbanovo area (type locality of *G. hollosii*, southern Slovakia), supported our hypothesis. We thus, in accordance with the species concept of Hollós (1901, 1904), recognize *G. pseudostriatum*, with *G. hollosii* as a later synonym, to cover the small forms of '*G. berkeleyi*' from open or semi-exposed, xerothermic habitats. *Geastrum pseudostriatum* can be separated morphologically from *G. berkeleyi* on the basis of its smaller fruiting bodies and slightly larger spores. One sequence in our study (MJ 6413) was found within the *G. pseudostriatum* clade, but the sequence data are divergent. It agrees with *G. pseudostriatum* in morphology and is here tentatively treated as *G.* cf. *pseudostriatum*.

Geastrum quadrifidum Pers.

Neues Mag. Bot. 1: 86 (1794)

= *Lycoperdon coronatum* Scop., Fl. carniol., Edn 2 (Wien) 2: 490 (1772).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 4 arched, non-hygroscopic rays; fully expanded 10–30 mm in diameter and up to 40 mm in height, fornicate. Pseudoparenchymatous layer initially pale beige, with age brownish to almost black, and partially peeling off. Fibrous layer ochraceous to almost white. Mycelial layer encrusted with debris and remains in the soil as a cup, to which the arched exoperidial rays are connected. Endoperidial body ± globose, 5–10 mm in diameter, stalked and provided with an apophysis. Endoperidium grey to grey brown, in young specimens with a greyish pruina of crystalline matter. Peristome delimited, discoid, silky fibrillose, broadly conical. Basidiospores globose, 4.0–5.5 μm in diameter, verrucose. Capillitial hyphae up to 10 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, South America, West Indies, Australia, New Zealand, Africa.

Type specimen. Germany. Neotype L, selected by van Eyndhoven (1937).

Habitat. Rich deciduous and coniferous woodlands; also on needle beds under junipers in calcareous dry grasslands.

Notes. *Geastrum quadrifidum* has a wide European distribution and is one of the more abundant earthstars in some regions. It seems to be rare, or absent, from the Mediterranean vegetation, and shows montane tendencies in eastern Europe. In Fennoscandia it occurs north to about 66°N, preferring older coniferous forests on somewhat basic soils. Our concept of this species matches that of Staněk (1958), Sunhede (1989) and others.

Geastrum rufescens Pers. [as '*Geaster*']

Syn. meth. fung. (Göttingen) 1: 134 (1801).

= *Geastrum schaefferi* Vittad. [as '*Geaster*'], Monograph Lyc. 22 (1842).
= *Geastrum vulgatum* Vittad. [as '*Geaster*'], Monograph Lyc. 20 (1842).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 5–8 non-hygroscopic exoperidial rays; fully expanded 20–90 mm in diameter, arched. Pseudoparenchymatous layer persistent, initially pale pink, with age pinkish to reddish brown. Fibrous layer ochraceous. Mycelial layer encrusted with debris. Endoperidial body ± globose, 10–30 mm in diameter. Endoperidium ochre to pale grey-brown, in young specimens finely pubescent, later smooth. Peristome undelimited, silky fibrillose, applanate to broadly conical. Basidiospores 4.0–5.0 μm in diameter, verrucose. Capillitial hyphae up to 12 μm in diameter, thick-walled, with a dense cover of surface debris.

World distribution. Europe, Asia, North America, Central America.

Type specimen. Germany. Lectotype: Schaeffer 1763, tab. 182, fig. 2, selected by Dörfelt & Müller-Uri (1984).

Habitat. Coniferous and deciduous woodlands on calcareous soils, often adjacent to decaying tree trunks or on ant-hills; also found on sawdust.

Notes. *Geastrum rufescens* has a wide European distribution with northernmost records in southern Fennoscandia (north to 61°N). The studied specimens match the concepts of Hollós (1904), Staněk (1958) and Sunhede (1989).

Geastrum saccatum Fr.

Syst. mycol. (Lundae) 3(1): 16 (1829). Fig. 15.

Description. Immature basidiomata epigeous, onion-shaped to lageniform, ochraceous to yellowish grey brown; at maturity splitting in 5–8 non-hygroscopic exoperidial rays; fully expanded 10–40 mm in diameter, saccate. Pseudoparenchymatous layer initially whitish beige, with age ochre to brown, persistent. Fibrous layer white to pale ochraceous. Mycelial layer not encrusted with debris, ochre to yellowish grey, felted. Endoperidial body ± globose, 10–20 mm in diameter, sessile, beige to greyish brown, smooth. Peristome delimited, silky fibrillose, broadly conical. Basidiospores globose, 3.2–4.5 μm in diameter (av. 3.5 μm), verrucose. Capillitial hyphae up to 10 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, South America, West Indies, Africa, Australia.

Type specimen. Brazil; no type material available (cfr. Sunhede, 1989).

Habitat. Dry deciduous and coniferous woodlands on base-rich soils; also in xerothermic grasslands. In northern Europe sometimes recorded under *Syringa*, in east central Europe often under *Robinia*.

Notes. *Geastrum saccatum* has a wide European distribution and reaches its northernmost outposts in southern Sweden (to appr. 59 °N). It can be distinguished from its look-alike *G. lageniforme*, due to its velvety, chamois-like outer mycelial layer, composed of clamp-less hyphae. The two species can also be distinguished by the slightly larger and more coarsely ornamented spores in *G. saccatum*. According to Sunhede (1989) there are additional differences in the immature gleba, *G. saccatum* having bladder-like to clavate basidia whereas they are lageniform in *G. lageniforme*. The material at our disposal originates from Hungary, Spain and Sweden and complies with the morphological features described by Vidal (1986) and Sunhede (1989). The phylogenetic analysis confirms *G. saccatum* and *G. lageniforme* as sister species. *Geastrum saccatum* is a species with a worldwide distribution. It was described by E. Fries based on specimens from Brazil, but unfortunately no type material was preserved and Sunhede (1989) refrained from selecting a neotype. There are, however, several recent records from Brazil (Baseia *et al*., 2003; Trierveiler-Pereira *et al*., 2011) matching the concept of Sunhede (1989), and a neo- and epitypification should thus be possible.

Geastrum schmidelii Vittad. [as '*Geaster*']

Monograph Lyc.: 12 (1842).

= *Geastrum nanum* Pers. J. Bot (Desvaux) 2: 27 (1809).

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 6–9 non-hygroscopic exoperidial rays; fully expanded 12–40 mm in diameter, arched. Pseudoparenchymatous layer initially pale beige, with age light to dark brown. Fibrous layer whitish to beige. Mycelial layer encrusted with debris. Endoperidial body ± globose, 5–10 mm in diameter, stalked and provided with an apophysis. Endoperidium beige to grey-brown, smooth. Peristome delimited, sulcate, conically protruding. Basidiospores globose, 4.5–5.5 μm, verrucose. Capillitial hyphae up to 9 μm in diameter, thick-walled, with sparse surface debris.

World distribution. Europe, Asia, North America, Central America, Africa, Australia.

Type specimen. Described from Italy, but not yet typified. Species concept based on Vittadini, 1842, tab. I, fig. A-E. Original material from Vittadini may exist in K, according to Bates (2004).

Habitat. Dry grasslands and pastures on calcareous soils; also under junipers in grasslands.

Notes. *Geastrum schmidelii* has a wide European distribution. In the north it reaches the alvar and sand steppe vegetation of southern Fennoscandia, where it is one of the more frequently encountered species (Hanson & Jeppson, 2005; Sunhede, 1989; Hanson, 2010). It is also known from littoral grasslands on shell-rich sand dunes along the south Fennoscandian coastline, north to about 60°N (Sunhede, 1989). Recent findings in subalpine dry grasslands of south central Norway (62°N) have extended its distribution (Jeppson, 2008*a*; Jordal *et al*., 2007). The specimens studied match the concept of this species as conceived by Sunhede (1989). Our material includes specimens with small fruiting bodies from open habitats as well as larger ones found on needle beds under junipers in calcareous grasslands.

Geastrum smardae V.J. Staněk

Česká Mykol. 10(1): 22 (1956).

= *Geastrum limbatum* Fr. [as '*Geaster*'], Syst. mycol. (Lundae) 3(1): 15 (1829) sensu Coker & Couch (1928), Long & Stouffer (1948).

Description. Immature basidiomata epigeous, whitish to ochraceous, rounded, sometimes with an umbo; at maturity splitting in 7–9 non-hygroscopic exoperidial rays; fully expanded 40–60 mm in diameter, pseudofornicate. Pseudoparenchymatous layer initially pinkish white to beige, later brown. Fibrous layer ochraceous to grey. Mycelial layer thick and membranous, ochre to pale brown, not encrusted with debris, partially loosening in the centre, to form a hanging bowl underneath the fibrous layer (pseudofornicate basidiome). Endoperidial body ± globose, 15–20 mm in diameter, shortly stalked and provided with a ± developed apophysis. Endoperidium beige to grey brown, smooth. Peristome ± delimited, silky fibrillose, applanate to broadly conical, often deformed. Basidiospores globose, 3.0–4.5 μm in diameter, verrucose. Capillitial hyphae up to 5 μm in diameter, thick-walled, with sparse to abundant surface debris.

World distribution. Europe, North America, Central America.

Type specimen. Brno, Czech Republic. Holotype PRM.

Habitat. On rich soils in urban parks and gardens; also reported from waste places under *Pinus nigra*, and from temporarily flooded alluvial forest habitats.

Notes. Prior to its formal description based on European type material, this species was known in North America, where Coker & Couch (1928) and Long & Stouffer (1948) considered it to be a light-coloured American form of *G. limbatum* Fr., a later synonym of *G. coronatum* Pers. It was nicely illustrated as *G. limbatum* by Smith (1951: pl. 32: 2–3). In Europe it was first discovered in Czechia in 1955 and was described by Staněk (1956) as a new species, named in honour of the Czech mycologist František Šmarda. Staněk, who was well acquainted with *G. coronatum* in the sense of Persoon, concluded that his new species was not a pale form of Persoon's species. It has since been found on several occasions in Europe, but the occurrences have been ephemeral and almost always in strongly anthropogenic habitats, such as botanical gardens, urban parks and playgrounds with non-indigenous plants and bushes (Winterhoff & Wöldeke, 1981; Kreisel, 1987; Sunhede, 1989). In Fennoscandia it was reported from the Botanical Garden in Copenhagen (Denmark) (Dissing & Lange, 1961, 1962*a*) and, recently, from under *Symphoricarpus* (shrub introduced from North America) on an island near Oslo (Norway; Jeppson *et al*. 2011), on calcareous ground. A further recent European record is from Spain (first record from the Iberian Peninsula), made by members of a Norwegian mycological foray in 2010. Rebriev (2007*b*) reports findings in a temporarily flooded forest in southern Russia. The studied specimens originate from the Czech Republic, Denmark, Norway and Spain; they all agree morphologically with the descriptions in Staněk (1956, 1958), Sunhede (1989) and Bates (2004).

Geastrum striatum DC. [as '*Geaster*']

in Lamarck & de Candolle, Fl. franç., Edn 3 (Paris) 2: 267 (1805).

= *Geastrum bryantii* Berk. [as '*Geaster*'], Outl. Brit. Fung. (London): 300 (1860).

Description. Immature basidiomata hypogeous; at maturity splitting in 6–9 non-hygroscopic exoperidial rays; fully expanded 20–65 mm in diameter, arched. Pseudoparenchymatous layer initially pale beige, later greyish brown to dark brown. Fibrous layer beige to pale grey. Mycelial layer persistent, encrusted with debris. Endoperidial body ± depressed globose, 10–15 mm in diameter, stalked and provided with a prominent, sharply edged, almost collar-like, apophysis. Endoperidium initially covered with a greyish white farinaceous layer of crystalline matter (mesoperidium), later dark brown and smooth. Peristome delimited, sulcate, conical. Basidiospores 4.0–4.5 μm in diameter, verrucose. Capillitial hyphae up to 8 μm in diameter, thick-walled, with sparse to abundant surface debris.

World distribution. Europe, North America, Africa, Australia.

Type specimen. Great Britain. Lectotype: Bryant, 1782, fig. 19, designated by Sunhede (1989).

Habitat. Deciduous and coniferous woodlands as well as parks and gardens; also on compost and rotten sawdust; preference for nitrogen-rich habitats.

Notes. *Geastrum striatum* is widely distributed in Europe and reaches 62°N in Central Sweden. The morphology of the studied specimens matches the descriptions by Hollós (1904), Staněk (1958) and Sunhede (1989).

Geastrum triplex Jungh. [as '*Geaster*']

Tijdschr. Nat. Gesch. Physiol. 7: 287 (1840).

Description. Immature basidiomata epigeous, rounded to onion-shaped, brown, smooth to cracked; at maturity splitting in 5–7 non-hygroscopic exoperidial rays; fully expanded 30–125 mm in diameter, arched or saccate. Pseudoparenchymatous layer pale ochre to light brown, later dark brown, usually forming a collar around the base of the endoperidial body. Fibrous layer ochraceous to greyish brown. Mycelial layer not encrusted with debris, brown, smooth to somewhat scaly. Endoperidial body ± globose, 20–40 mm in diameter, sessile. Endoperidium smooth, greyish beige to grey-brown. Peristome ± delimited, fibrillose, broadly conical. Basidiospores globose, 3.5–4.5 μm in diameter. Capillitial hyphae up to 8 μm in diameter, thick-walled, with abundant surface debris.

World distribution. Europe, Asia, North America, Central America, South America, Africa, New Zealand. See notes below.

Type specimen. Indonesia. Holotype L. See notes below.

Habitat. Forests, gardens, parks and waste places on well-drained alkaline soils, occasionally in semi-open grasslands adjacent to shrubs.

Notes. *Geastrum triplex* is a widely distributed species in Europe with northernmost records at 62°N (Sunhede 1989) in Fennoscandia. Our material agrees with descriptions given by European authors (Staněk, 1958; Sunhede, 1977, 1989). The sequences in our phylogenetic analyses originate from specimens collected in north and east central Europe and formed a clade together with *G. melanocephalum*. The molecular study by Kasuya *et al*. (2012) included specimens with a wide geographical sampling of *G. triplex.* The study showed that this widely spread species is not monophyletic and that several 'collar-forming' taxa may be involved; the signal of the sequence data was more or less correlated with geographical origin. *Geastrum triplex* was described by Junghuhn from Java, Indonesia and is, according to the results of Kasuya *et al*. (2012), not identical with European *G. triplex*. Type studies of European species, which hitherto have been considered synonymous with *G. triplex*, will be needed to find a suitable name for the European species. Kasuya *et al*. (2012) showed that Swedish specimens of *G. triplex* are very closely related to, or conspecific with, *G. melanocephalum*, a result which is confirmed in this study.

Geastrum xerophilum Long ex Desjardin

Pacific Science 65: 32 (2011). Fig. 16.

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–11 non-hygroscopic, often truncated exoperidial rays, which curl upwards; fully expanded 15–20 mm in diameter, ± arched. Pseudoparenchymatous layer beige to grey-brown. Fibrous layer grey ochraceous. Mycelial layer persistent, encrusted with debris. Endoperidial body globose to depressed globose, 10–16 mm in diameter, sessile or shortly stalked, without apophysis. Endoperidium grey to grey brown, minutely felted. Peristome undelimited, sulcate, applanate to broadly conical. Basidiospores globose, 3.5–4.5 μm in diameter, verrucose. Capillitial hyphae up to 6 μm in diameter, thick-walled, without or with very sparse surface debris.

World distribution. Europe (Spain), North America, South America, Hawaii.

Type specimen. New Mexico, USA. Holotype BPI.

Habitat. Xerothermic grassland.

Notes. *Geastrum xerophilum* was described by Long (1942) from New Mexico and has later been reported from Arizona (Bates, 2004), Mexico (Pérez-Silva & Aguirre-Acosta, 1986; Moreno *et al*., 2010), Hawaii (Smith & Ponce de León, 1982; Hemmes & Desjardin, 2011), and Brazil (Silva *et al*., 2011). Long's name, being illegitimate lacking a Latin diagnosis, was recently validated by Hemmes & Desjardin (2011). Our collection consists of a single fruiting body with a morphology matching the descriptions by previous authors. It was collected in a sheep-grazed sloping steppe habitat in the xeric province of Almería in the southeast corner of Spain. This is the first record of *G. xerophilum* from Europe.

***Geastrum* sp. 1.**

Description. Immature basidiomata hypogeous; at maturity epigeous, splitting in 7–9 ± hygroscopic exoperidial rays; fully expanded 18–25 mm in diameter, ± arched. Pseudoparenchymatous layer persistent, initially pale ochraceous, with age nut-brown to dark brown. Fibrous layer whitish to ochraceous. Mycelial layer persistent, encrusted with debris. Endoperidial body globose to depressed globose, 7–10 mm in diameter, sessile. Endoperidium beige to greyish ochre, finely pubescent to smooth. Peristome undelimited, silky fibrillose, applanate to broadly conical. Basidiospores 4–4.5 μm, verrucose. Capillitial hyphae up to 5 μm in diameter, thick-walled, with sparse surface debris.

Notes. This small earthstar was discovered in grazed, alkaline, sand steppe vegetation on two sites in Hungary. In the field it was mistaken for *G. floriforme*, from which it differs in the softer, more papery exoperidial rays. It resembles *G. deylii* Pilát, known from steppe habitats in Mongolia, from where it was described by Pilát (1972) based on a single fruiting body. Dörfelt & Täglich (1989) recorded *G. deylii* on two new localities in Mongolia, and added important morphological data. According to literature, *G. deylii* seems to differ from our samples as it has slightly larger spores, but the original material of *G. deylii* was not studied by us. Our samples were identical in sequence data and formed a strongly supported clade together with *G. rufescens*. The formal description of this species will have to await more material to be collected in Hungary and adjacent steppe regions, adding relevant morphological characteristics.

Myriostoma coliforme (Dicks.) Corda

Anleit. Stud. Mykol., Prag: 131 (1842).

Basionym: *Lycoperdon coliforme* Dicks., Fasc. pl. crypt. brit. (London) 1: 2 (1776)
= *Geastrum coliforme* (Dicks.) Pers. [as '*Geaster*'], Syn. meth. fung. (Göttingen) 1: 131 (1801)

Description. Immature basidiomata epigeous, rounded, brown, smooth to patchy or scaly. At maturity splitting in 6–10 non-hygroscopic rays; fully expanded 70–150 mm in diameter, arched. Pseudoparenchymatous layer initially whitish beige, gradually turning nut-brown to dark brown. Fibrous layer ochraceous to light brownish grey. Mycelial layer not encrusted with debris, brown, smooth to cracked. Endoperidial body globose to depressed globose, 20–50 mm in diameter, with numerous short stalks; apophysis lacking. Endoperidium ± metallic silver grey to grey brown, finely warty, with numerous applanate to slightly elevated, undelimited, fibrillose stomata. Basidiospores 3.5–4.0 μm in diameter, coarsely verrucose, almost reticulate under light microscope. Capillitial hyphae up to 4 μm in diameter, sometimes with dichotomous branching, ± thick-walled, without surface debris.

World distribution. Europe, Asia, North America, South America, Africa, Australia.

Type specimen. Great Britain. Lectotype: Dickson, 1785, p. 24, tab III: 4a, b. (Bates, 2004).

Habitat. Thermophilic deciduous forests, often in glades or along forest tracks, on alkaline soils.

Notes. *Myriostoma coliforme* has a worldwide distribution. In Europe it is a rare and declining species in thermophilic woodlands on alkaline soils. It is fairly frequent in the pannonic vegetation of central Hungary (Rimóczi *et al*., 2011), and reaches the Atlantic coast in France (Boiffard, 1976) and southernmost England (Pegler *et al*., 1995). In Fennoscandia it has two isolated northern outposts in southern Sweden (Kers, 1976, 1982; Sunhede, 1989). On the Swedish localities it grows among leaf litter under shrubs below south-facing cliffs, close to the sea. Our specimens agree with descriptions in Hollós (1904), Staněk (1958), Sunhede (1989) and others. In the phylogenetic analysis it forms the sister taxon to the remainder of *Geastrum* (subclade K). The species was placed in *Geastrum* by Persoon 1801 and its re-incorporation in *Geastrum* would be justified judging from the molecular results.

Discussion

The earthstars of Europe (genera *Geastrum* and *Myriostoma*) comprise 31 species according to current data. The generic concept includes also *Radiigera flexuosa* which does not split stellately at maturity and lacks a well-developed endoperidium. It agrees in other morphological characters with the traditional concept of the genus *Geastrum*. The infrageneric boundaries are still largely unresolved and a subgeneric division is currently premature as new species are frequently described as a result of an increasing interest in gasteroid

fungi worldwide. Our phylogenetic analyses based on European specimens nevertheless show a certain level of congruence with the classification by Staněk (1958) and the species groups (Verwandtschaftskreise) presented by Dörfelt (1989). Characters traditionally used in infrageneric divisions (e.g. Lloyd, 1902; Staněk, 1958; Dissing & Lange, 1961; Ponce de León, 1968; Dörfelt, 1989), e.g. epigeal development with a basal attachment point of the mycelium combined with a non-encrusting mycelial layer as well as the peristomal features (fibrillose vs. sulcate) appear at different levels in the phylogenetic tree (Fig. 1) but are still fairly constant features in relation to the terminal sub-clades, i.e. the species groups. The classification by Lloyd (1902) in sections Rigidae and Non-rigidae is not tenable as the species with coriaceous and hygroscopic exoperidia are distributed in different clades in the phylogenetic tree and the result rather suggests that these characters should be looked upon as adaptations to arid conditions, that is, as having evolved several times. Some species limits are still largely unresolved in current molecular studies. One of these is the *triplex* group, recently explored by Kasuya *et al*. (2012). They found the European population of *G. triplex* to be closely related to *G. melanocephalum* and made suggestions of speciation in the European populations and their ancestors. Our analyses are consistent with the results of Kasuya *et al*. (2012) and indicate a relationship also with the American *G. fuscogleba*, here represented by a GenBank sequence. *Geastrum triplex* was described from Indonesia and according to Kasuya *et al*. (2012) the current species concept is not monophyletic. The supposedly close relationship between *G. triplex* and *G. saccatum/lageniforme* (e.g. Dörfelt, 1989), based on fruiting body morphology, is not supported by our molecular data, as inferred from European material (Fig. 1).

Most species of *Geastrum* have wide distributions in Europe, although some species are rarely encountered. Geographical areas in Europe that are rich in earthstars include Hungary, south Slovakia, the Czech Republic, southern Germany and the Berlin area, the Dutch, Belgian and French Atlantic coasts, continentally influenced parts of Spain, southern Sweden, and the Oslo area in Norway (Hollós, 1904; Andersson, 1950; Eckblad, 1955; Rauschert, 1958; Staněk, 1958; Boiffard, 1976; Winterhoff, 1981; Calonge, 1998; Benkert, 2003; Hanson & Jeppson, 2005; Jeppson, 2008*b*; Jeppson & Knutsson, 2008; Zíta *et al*., 2008; Rimóczi *et al*., 2011). These hotspot areas all have several features in common: more or less alkaline, often sandy soils, warm summers and a low yearly precipitation (cf. Winterhoff, 1981). A number of species reach their northernmost limits in the temperate and hemiboreal zones of southern Fennoscandia (e.g. *G. campestre*, *G. elegans*, *G. melanocephalum*, *G. fornicatum*, *G. saccatum*, *G. corollinum* and *Myriostoma coliforme*). Eight species reach the boreal zone (*G. coronatum*, *G. fimbriatum*, *G. floriforme*, *G. pectinatum*, *G. quadrifidum*, *G. striatum*, *G. minimum* and *G. triplex*). Two species (*G. minimum* and *G. pectinatum*) are known from subalpine habitats, and *G. minimum* is also known from the Arctic. Recent records of *G. schmidelii* in dry calcareous grasslands with a steppic character in the Norwegian mountains (south central Norway) have extended the distributions of this southern species. Four species, traditionally considered American, have scattered occurrences in Europe: *G. arenarium*, *G. morganii*, *G. smardae* and *G. xerophilum*. According to Kreisel (2001), at least *G. morganii* and *G. smardae* could be looked upon as recent introductions. Although earthstars are considered a well-known group, intensified studies, using morphological and molecular sequence data, are now in progress worldwide. This will undoubtedly lead to the discovery of many new species, and help to resolve the infrageneric relationships. In Europe a considerable number of earthstars are on the national red-lists. As shown by Nitare (2000) and Benkert (2003), the occurrence of earthstars might in some areas have an important role as indicator of valuable habitats of great interest for nature conservation.

Acknowledgements

The authors want to express their sincere gratitude to several contributors of valuable material and important discussions: Johan Nitare, Stellan Sunhede, Francisco de Diego Calonge, Gabriel Moreno, Alberto Altés, Signe and Jörgen Jeppson, Anders and Karin Bohlin, Ulla-Britt Andersson and Thomas Gunnarsson, Imre Rimóczi, Lajos Benedek, László Nagy, Sven-Åke Hanson, Elna Hultqvist, Leo Jalink, Juan-Carlos Zamora, Ivona Kautmanová, Slavomir Adamčik, Pierre-Arthur Moreau, Tommy Knutsson, Terje Spolén Nilsen and Vladímir Zíta. Curators Jan Holec (PRM), Gizella Vasas (BP), Margarita Dueñas (MA-Fungi), Svengunnar Ryman (UPS), Ivona Kautmanová (BRA) and Henning Knudsen (C) kindly provided material from their respective herbaria. We are grateful to the anonymous reviewers for their helpful comments in reviewing this manuscript and to Ernest E. Emmett for revising the English. Financial support was received from The Swedish Taxonomy Initiative, ArtDatabanken SLU Uppsala (EL), FORMAS (215-2011-498 to RHN), the Carl Stenholm Foundation (MJ) and Länsstyrelsen i Uppsala län.

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Associate Editor: Karen Hansen