Basidiospore measurements are based on at least 20 basidiospores from each collection; numbers in square brackets refer to the number of basidiospores measured, the number of basidiocarps, and the collections they originate from, respectively. Spore measurements are given as follows: length range × breadth range × width range. Q_1 and Q_2 values were calculated as follows: Q_1 = length divided by breadth; Q_2 = length divided by width. Measurements of basidia included sterigmata. The calculation of the proportion of 4-, 3-, or 2-spored basidia was made according to the methods of C. Bas (pers. comm.) and Schmidt-Stohn (2012): an even, ripe piece of lamella is placed on a piece of moist paper tissue on a microscope slide. The basidia are then observed on the face of the lamella with 40× or 400× magnification, and the number of basidiospores per basidium is counted. Pleurocystidia and cheilocystidia were observed and measured by cutting the lamellae edge from the rest of lamella to avoid blending of the two types of cystidia.

RESULTS

Phylogenetic analyses.—We generated 28 new sequences from 12 species. The concatenated alignment comprised 77 specimens with 2166 nucleic acid sites (ITS: 785 sites, 28S: 1381 sites) and 167 binary characters coded from indels in the ITS alignment. The ITS alignment comprised 77 specimens with 785 nucleic acid sites, and the 28S alignment consisted of 58 specimens with 1381 nucleic acid sites. Phylogenetic trees reconstructed using ML and Bayesian methods were largely congruent with each other and reflected current views on the phylogeny of the genus (FIG. 1; SUPPLEMENTARY FIGS. 1–4; Nagy et al. 2009). Briefly, both inference strategies recover *Parasola conopilus, P. auricoma, P. setulosa*, and *P. malakandensis* as basal groups with strong support and grouping species of section *Parasola* in a "crown" *Parasola* clade. *Parasola malakandensis* (Hussain et al. 2017) grouped closely to the crown group of *Parasola* (1.00/81) occupying an intermediate position between species of section *Auricomi* and those of section *Parasola*. The phylogeny indicated three species-level groups that could not be assigned to known species, and they are described here as *P. crataegi, P. ochracea*, and *P. plicatilis-similis. Parasola crataegi* was inferred basal to a clade formed by *P. misera* and *P. lactea. Parasola plicatilis-similis* was inferred sister to the clade including *P. megasperma* (P.D. Orton) Redhead, Vilgalys & Hopple and *P. schroeteri* (P. Karst.) Redhead, Vilgalys & Hopple (1.00/75). Specimens of the third species, *P. ochracea*, nested within *P. lilatincta* complex (0.96/68). Although its position within *P. lilatincta* was strongly supported by Bayesian analyses, constraint analyses indicated that a monophyletic *P. lilatincta* with *P. ochracea* as a sister species cannot be rejected ($P = 0.102$–0.103, au-test). Our analyses indicate the existence of further four species that we tentatively named *Parasola* sp. 1–4. *Parasola* sp. 1 forms a monophyletic group with *P. plicatilis* with strong support (1.00/97). *Parasola* sp. 2 groups together with *P.* cf. *lilatincta* in a weakly supported clade (0.67/47) close to the clade that contains the true *lilatincta* group. *Parasola* sp. 3 forms a clade with *P. lilatincta* and *P. ochracea*, but this is only supported in ML analyses (—/99). *Parasola* sp. 4 forms a monophyletic group with *P. misera* in both the Bayesian and ML analyses (1.00/98).

TAXONOMY

Parasola crataegi Schmidt-Stohn, sp. nov.

FIGS. 2A, B, 3A, 4A, B

MycoBank MB817192

Typification: GERMANY. SCHLESWIG-HOLSTEIN: Lübeck-Travemünde, Dummersdorfer Ufer (nature reserve), on grazed pasture under *Crataegus monogyna*, 29 Oct 2008, *G. Schmidt-Stohn, SSt08-154* (**holotype**, M 0280274). GenBank: KY928605.

Etymology: The epithet refers to the main habitat under *Crataegus*.

Pileus 4–6 × 2–3 mm when still closed, ellipsoidal to cylindrical, then convex to hemispherical and plano-convex to applanate when expanded, up to 15 mm wide, gray-brown with an ochraceous-brown center when young and moist, grayish to grayish white when mature, sulcate-striate almost up to the center. Lamellae free, up to 30 reaching the stipe at a distance of 0.5–1 mm, additionally 15–20 lamellules, crowded, ventricose, <2 mm broad, whitish to grayish, finally blackish, with an indistinct fimbriate edge. Stipe 15–40 × 0.5–1 mm, cylindrical, fistulose, translucent grayish, slightly flocculose when young, later glabrous; smell and taste not distinctive.

Basidiospores [41, 2, 2] 6.5–8.5 × 5.5–7.5 × 4–5.5 µm, avg 7.4 × 6.5 × 4.8 µm, Q_1 = 1.00–1.35, Q_{1avg} = 1.15, Q_2 = 1.35–1.77, Q_{2avg} = 1.49, rounded triangular to heart-shaped and also ovoid, flattened, ellipsoidal in lateral view, with eccentric germ pore. Basidia in the majority (ca. 80%) 4-spored, but some (10–20%) also 2- or 3-spored, clavate, 31–48 × 10–14 µm. Cheilocystidia fairly densely packed, oblong, ellipsoidal, narrowly to broadly utriform, some also spheropedunculate, 23–40 × 10–17 µm. Pleurocystidia scattered, predominantly near the edge of lamellae, not easily detected, utriform, 48–62 × 17–24 µm. Pileipellis a hymeniderm, pileo- and sclerocystidia lacking.

Habitat: Grazed grasslands, almost always in close vicinity to single *Crataegus monogyna* or in scrubs of this species, basidiocarps solitary.

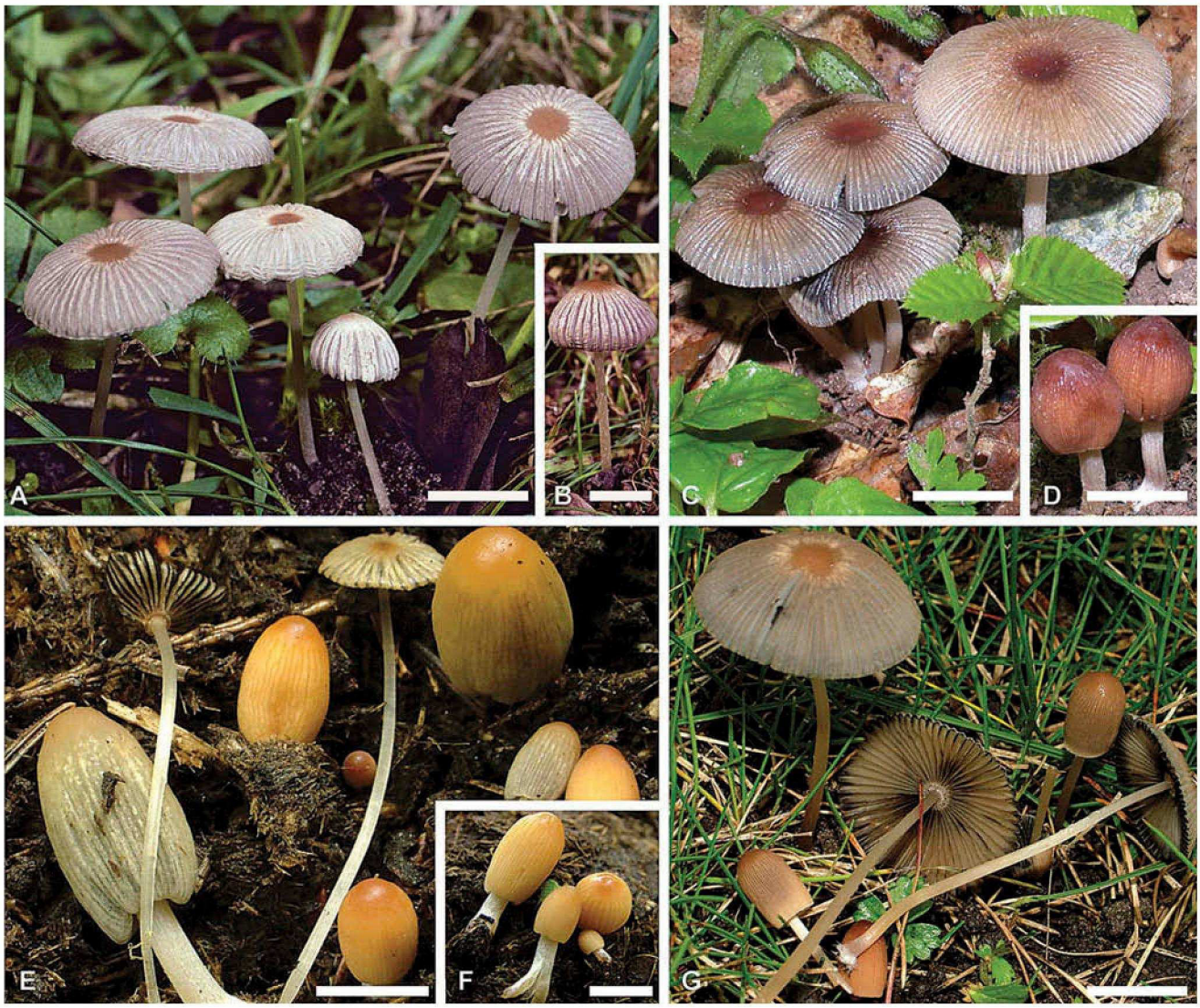

Figure 2. Macromorphology of *P. kuehneri* and the newly described *Parasola* species. A, B. *P. crataegi*. C, D. *P. kuehneri*. E, F. *P. ochracea*. G. *P. plicatilis-similis*. Photos: A–D: G. Schmidt-Stohn; E, G: L. Nagy. Bars = 1 cm.

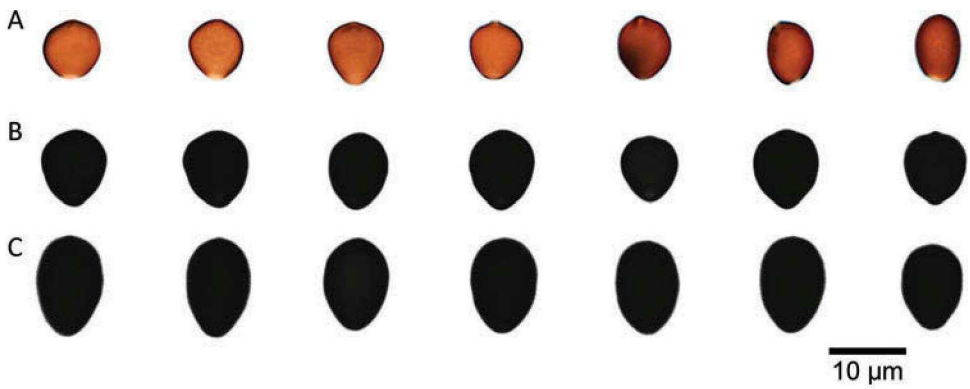

Figure 3. Illustration of the diversity of basidiospore shapes and sizes in the newly described species. A. *Parasola crataegi*. B. *P. ochracea*. C. *P. plicatilis-similis*.

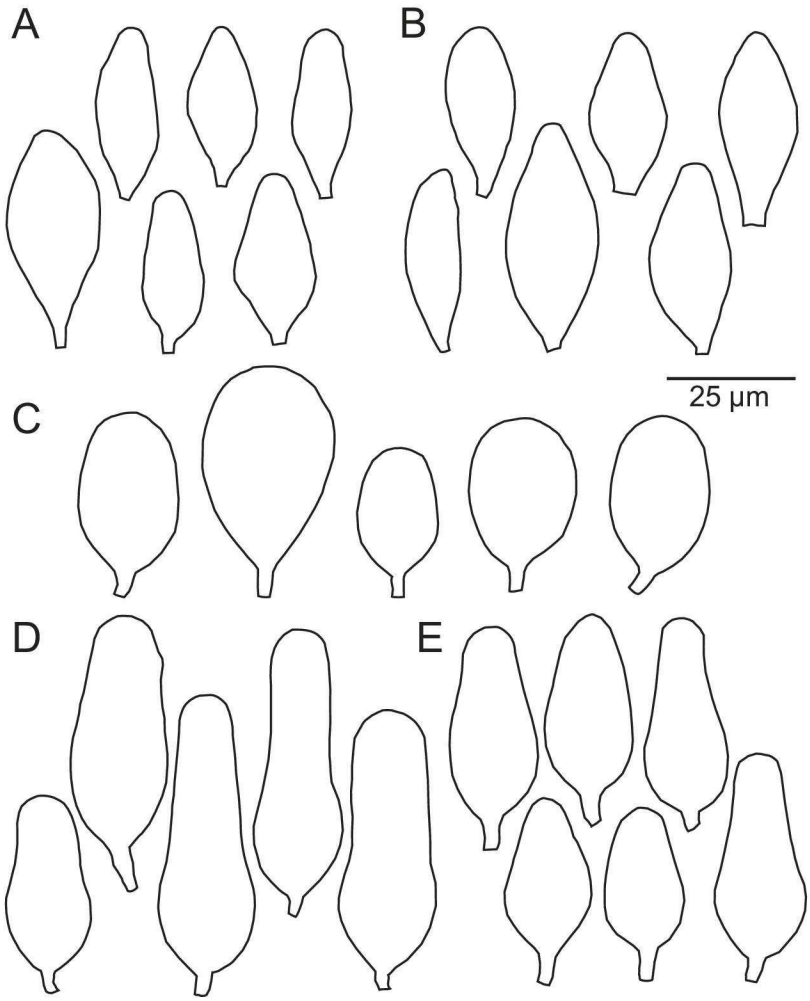

Figure 4. Cheilo- and pleurocystidial characters of *Parasola* species. A, B. *P. crataegi*. A. Cheilocystidia. B. Pleurocystidia. C. *P. ochracea* cheilocystidia. D, E. *P. plicatilis-similis*. D. Pleurocystidia. E. Cheilocystidia.

Distribution: Germany, Hungary.

Other specimens examined: GERMANY. SCHLESWIG-HOLSTEIN: Lübeck-Travemünde, Dummersdorfer Ufer (nature reserve) on grazed pasture under *Crataegus monogyna*, 21 Oct 1995, *G. Schmidt-Stohn, SSt95-113* (M 0280273); same location, 24 Oct 2009, *G. Schmidt-Stohn, SSt09-105* (M 0280275); SACHSEN-ANHALT: Huy, north of Halberstadt, Paulskopfwarte, on naked soil under *Corylus* and *Crataegus*, 29 Sep 1998, *G. Schmidt-Stohn, SSt98-239*; NIEDERSACHSEN: Heeseberg west of Jerxheim on grazed pasture under *Crataegus monogyna*, 17 Jul 2000, *G. Schmidt-Stohn, SSt00-018a*. HUNGARY. BÁCS-KISKUN: Fülöpháza (Kiskunság National Park), *Robinia pseudoacacia* plantation with *Crataegus* and *Ailanthus*, on leaf litter, 12 Oct 2008, *L.G. Nagy*, herb. *NL-4175*.

Notes: Before the description of *P. crataegi*, the only known species in *Parasola* with such small basidiospores was *P. kuehneri*. Therefore, our new species was usually identified as *P. kuehneri* using existing keys. Considering other morphological and ecological characters, confusion of the two species is impossible: *P. kuehneri* has a distinctly darker pileus of <3.5 cm diam and usually grows in forests and shrubs along trails on naked, mineral, alkaline soil rather than in poorly manured grasslands like *P. crataegi*. Moreover, the basidiospores of *P. kuehneri* average 9.4 µm long, whereas those of *P. crataegi* are only 7.4 µm. Genetically, *P. crataegi* is closest to *P. lactea* (formerly *P. leiocephala*), forming two well separated clades. However, both the basidiospores (avg 10.7 × 8.8 × 6.7 µm) and the basidiocarps of *P. lactea* are much larger than those of *P. crataegi*.

Parasola crataegi is so far known from three sites in Germany, mostly found repeatedly in different years, and one in Hungary. The habitat is almost always in grasslands/open landscape and usually in close proximity to *Crataegus monogyna*, as emphasized with the epithet "crataegi." Nevertheless, we suspect that *P. crataegi* is more widespread because of confusion with *P. kuehneri* in the past. The only previous reference to our new species is from

Bender (1989; also pers. comm.), who when commenting on *Coprinus kuehneri* mentioned "a deviating form under *Crataegus monogyna* with smaller and ± ovoid basidiospores." His collection may be our *P. crataegi*.

Parasola ochracea L. Nagy, Szarkándi & Dima, sp. nov.

FIGS. 2D–E, 3B, 4C

MycoBank MB817193

Typification: NORWAY. NORD-TRØNDELAG: Steinkjer, Skrattåsen, on cow dung, 5 Sep 2009, *L.G. Nagy & T. Knuttson, NL-3621* (**holotype**, BP). GenBank: JN943134.

Etymology: Ochracea refers to the orange to ochraceous color of the basidiocarp.

Pileus 4–20 × 3–9 mm when still closed, ellipsoidal to cylindrical, campanulate to flat with an umbo when expanded, up to 35(40) mm wide, vivid orange to ochraceous, grayish orange to brownish when mature, sulcate and grooved up to the center. Lamellae free, crowded, ventricose, <3 mm broad, whitish to grayish, finally blackish, with a fimbriate edge. Stipe 30–90 × 0.5–2 mm, cylindrical, fistulose, pure white, slightly silky when young, later glabrous, smell and taste not distinctive.

Basidiospores [40, 1, 1] 10–11 × 6–8.5 µm, avg 10.8 × 7.4 µm, Q = 1.25–1.58, Q_{avg} = 1.46, rounded triangular to ovoid with rounded angles, sometimes almost hexagonal, lentiform, ellipsoid in lateral view, with eccentric germ pore. Basidia 4-spored, clavate, 35–47 × 11–13.5 µm. Cheilocystidia densely packed, clavate, ellipsoidal, ovoid to balloon-shaped, some utriform, 42–75 × 25–38 µm. Pileipellis hymeniderm, pileo- and sclerocystidia lacking.

Habitat: On cow dung or dung mixed with straw in wet grazed meadows.

Distribution: Norway, Sweden.

Other specimens examined: SWEDEN. ÖLAND: Möckleby/Gardstorp, on cow dung and dung mixed with straw, 10 Sep 2008, *L.G. Nagy & T. Knuttson, NL-3623*; ÖLAND: Ned-Västerstad, on cow dung, 10 Sep 2008, *L.G. Nagy & T. Knuttson, NL-3167*.

Notes: Parasola ochracea is morphologically close to *P. schroeteri, P. misera*, and *P. cuniculorum*, with which it shares the habitat and spore shape. However, *P. schroeteri* has darker-colored basidiocarps and pleurocystidia, whereas *P. misera* and *P. cuniculorum* have much smaller basidiocarps and smaller basidiospores.

Parasola plicatilis-similis L. Nagy, Szarkándi & Dima, sp. nov.

FIGS. 2F, 3C, 4D–E

MycoBank MB817194

Typification: SWEDEN. ÖLAND: Mörbylanga parish, Södra Barspunkten, north of the road, in alvar vegetation, 28 Sep 2007, *L.G. Nagy & T. Knuttson, NL-2125* (**holotype**, BP). GenBank: KY928620.

Etymology: Similis (Latin) = like, referring to the similarity of the new species to *Parasola plicatilis*.

Pileus 6–20 × 4–10 mm when still closed, cylindrical to ellipsoidal or ovoid, expanding to campanulate then flat, 15–45 mm when expanded, honey-colored, ochre-brown when young, becoming sordid, grayish upon ageing, with a pale ochre-brown button when mature, sulcate-striate up to the center. Lamellae free, crowded, ventricose, up to 4 mm broad, at first whitish, then grayish and black. Stipe 40–90 × 1–2 mm, slender, fistulose, glabrous, pale ochre-brownish, slightly strigose at the base. Smell and taste not distinctive.

Basidiospores [38, 2, 1] 10.5–13.5 × 8–11.5 µm, avg 11.8 × 9.7 µm, Q = 1.1–1.4, Q_{avg} = 1.2, broadly ellipsoidal to broadly hexagonal, sometimes ovoid or almost rounded triangular, lentiform, ellipsoid in lateral view, with eccentric germ pore. Basidia 4-spored, clavate, 30–45 × 10–14 µm. Cheilocystidia utriform, clavate, sometimes broadly lageniform, 35–80 × 12–20 µm, pleurocystidia utri- to lageniform, often quite narrow and slender 75–90 × 24–35 µm. Pileipellis hymeniderm, pileo- and sclerocystidia lacking.

Habitat: Grazed meadows and pastures, once found in alvar vegetation.

Distribution: Sweden, Slovakia.

Other specimens examined: SLOVAKIA. RIMAVSKÁ SOBOTA: Drňa, on grazed pasture with *Festuca*, 3 Oct 2008, *L.G. Nagy, NL-3980*. SWEDEN. ÖLAND: Langlöt parish, 500 m NNW Astad, on grazed meadow, 22 Sep 2006, *L.G. Nagy & T. Knuttson, NL-0287*.

Notes: The species is highly similar to *P. plicatilis*, differing mostly in spore shape and to a smaller extent by the presence of many narrow, lageniform pleurocystidia as opposed to mostly utriform-ellipsoidal in *P. plicatilis*. The basidiospores of *P. plicatilis-similis* are mostly broadly ellipsoidal, whereas those of *P. plicatilis* are mostly ellipsoidal or hexagonal (Q = 1.15–1.5 vs. 1.25–1.6). The spore shape of *P. plicatilis-similis* is transitional between that of earlier diverging ellipsoid-spored species (*P. plicatilis, P. auricoma*) and more derived species with rounded triangular basidiospores (e.g., *P. schroeteri, P. lactea*). Accordingly, the species present a continuum in spore shape and their identification should rely on the shape of the majority of basidiospores and measurements of 10–20 individual basidiospores.