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A REASSESSMENT OF THE BRITISH SPECIES OF HYMENOGASTER (BASIDIOMYCOTA:CORTINARIALES)

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ABSTRACT. Descriptions, illustrations and a key are provided to eleven British species of *Hymenogaster*. The genus is subdivided into three sections, *Hymenogaster, Lutei* and *Vulgares* on the basis of the presence or absence of a loose myxosporium, and the mucronate spore apex. *Hymenogaster albus* is recognized as an exotic species and placed in the genus *Hymenangium*. A detailed analysis of spore structure within *Hymenogaster* is provided on the basis of light, SEM and TEM observation.

Hymenogaster is a hypogeal basidiomycetous genus of world-wide distribution, although more commonly occurring in the temperate–subtemperate regions, similar to other genera and families of the Cortinariales. It remains to be determined, however, whether or not the species described from south-east Asia and Australasia are congeneric with the North temperate species.

The genus was originally proposed by Vittadini (1834), with the following diagnosis: *Uterus subglobosis, laevis, arrhizus, basi tamen radicali instructus, clausus, indehiscens. Substantia interna viz venosa; homogenea, manifeste cellulosa; cellulae cavae, intus hymenio retiformi obductae. Sporidia ovato-fusiformia, majuscula, subpedicellata, ascis cylindraceis inclusa.* Eight species were described, namely *H. bulliardi, H. citrinus, H. griseus, H. luteus, H. lycoperdineus, H. niveus,* and *H. olivaceus,* most with excellent coloured illustrations. Dodge & Zeller (1934) selected *H. bulliardi* as the lectotype species, a species not found in the British Isles. The exchange of information between Vittadini, Berkeley and Tulasne from 1840–1850 led to the recognition of many additional species, and the publication of the classical monograph on hypogeal fungi by Tulasne & Tulasne (1851), together with accounts on British species by Berkeley (1844) and Berkeley & Broome (1846). A further account of British species was provided by Massee (1889), but the standard work to date, based on detailed collecting and personal observation was published by Hawker (1954, 1974). Further monographic accounts, dealing with the North temperate species, have been produced by Zobel (1854), Hesse (1891), Dodge & Zeller (1934), Svrček (1958), Soehner (1962), and Gross (1980).

The reduced structure of the hypogeal and subepigeal gasterocarps, together with the near uniformity of the bisporic basidia and the total absence of cystidia within the genus, has increasingly placed an emphasis on the spore form and structure in the infrageneric classification. Apart from the section *Lutei* Svrček, the brown, thick-walled spores are

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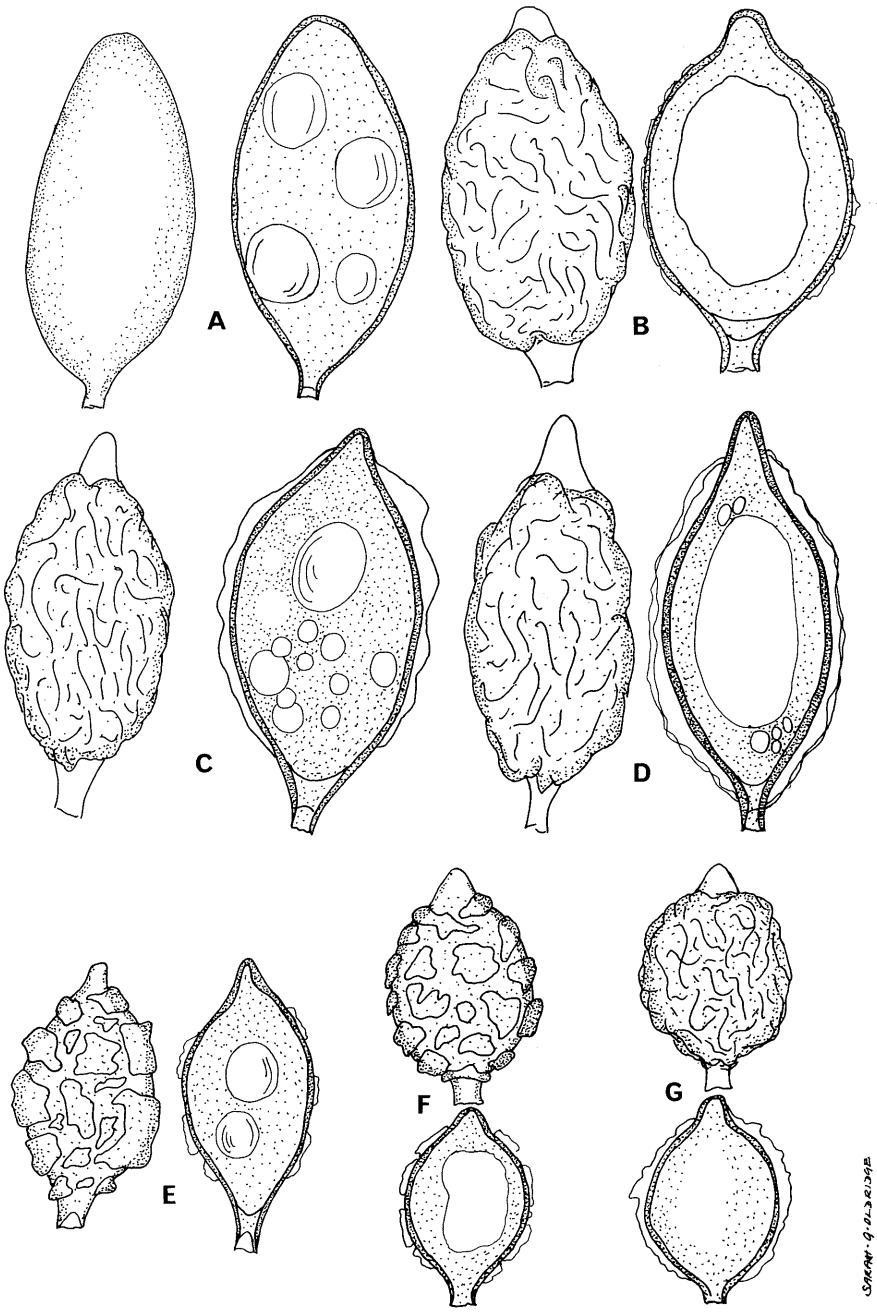

FIG. 1. Spores of *Hymenogaster*. A, Sect. Lutei, *H. luteus*. B–G, Sect. Hymenogaster. B, *H. bulliardii*; C, *H. citrinus*; D, *H. olivaceus*; E, *H. sulcatus*; F, *H. tener*; G, *H. arenarius*. All ×1750.

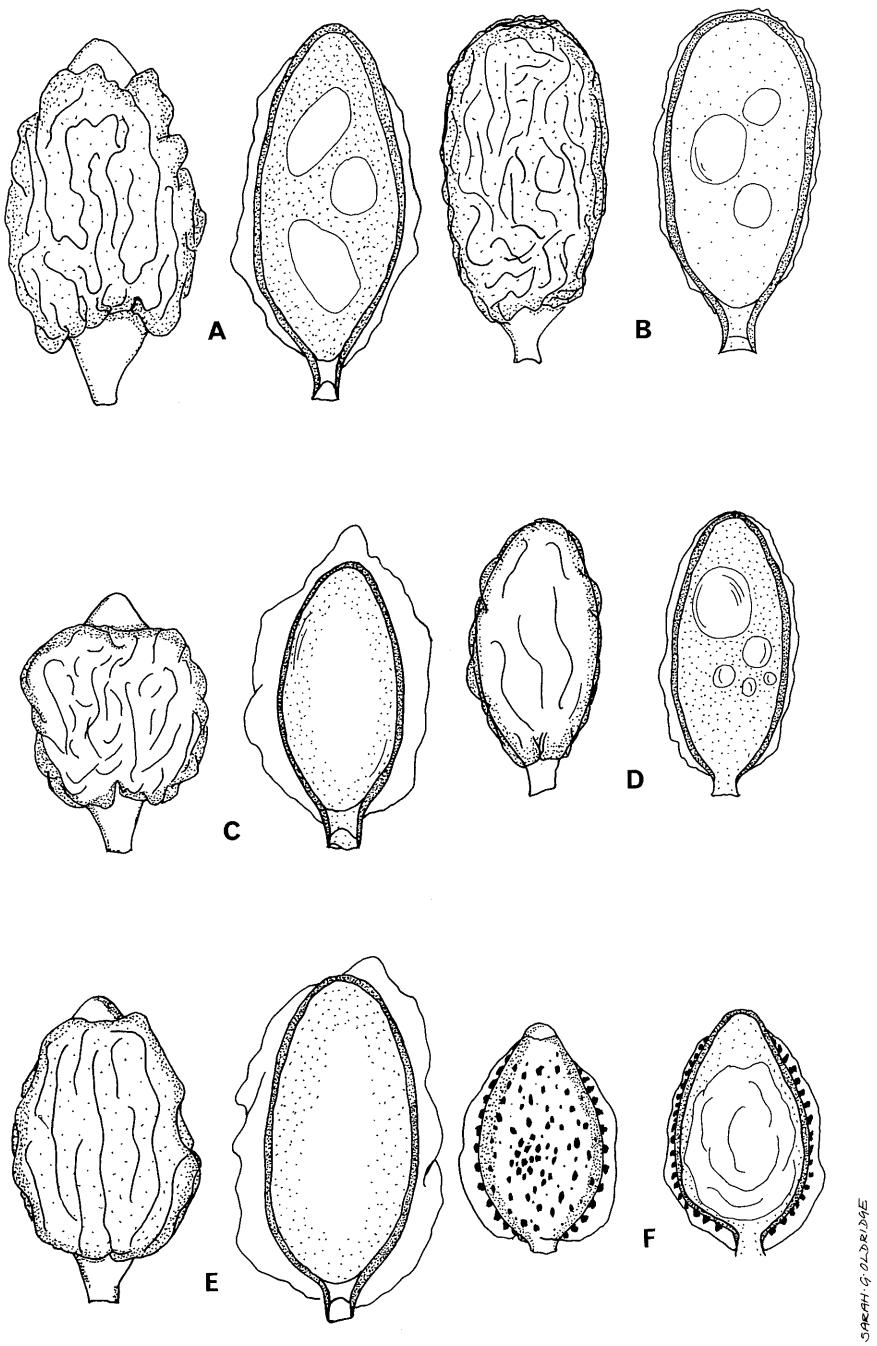

FIG. 2. A–E, Spores of *Hymenogaster*. A, *H. vulgaris*; B, *H. muticus*; C, *H. thwaitesii*; D, *H. griseus*; E, *H. hessei*. F, Spores of *Hymenangium album*. All ×1750.

enveloped by a loosened, thin-walled, hyaline myxosporium. The wrinkling or fragmentation of this myxosporium has often been wrongly interpreted as exosporial ornamentation, resulting in inadequate descriptions of the spores and confusion in the classification of species.

Basidiospore Structure in Hymenogaster

Hymenogaster species are characterized by large, brown, ovo-ellipsoid to mucronato-fusoid basidiospores, usually retaining all or part of a loosened, hyaline myxosporium. The spores are frequently described as verrucosely ornamented but this has been the result of a misinterpretation of the fragments of myxosporium closely applied to the surface. The spore wall contains a golden brown to ferruginous pigment in the majority of species, although paling to sulphur yellow in *H. luteus* and darkening to fuscous brown in *H. griseus*. Spores retained for some time in old gasterocarps may appear more darkly pigmented, largely owing to the myxosporium acquiring brownish tints.

Spore form segregates the genus into two major groups, for several species develop a prominent, mucronate apical outgrowth. This is most conspicuous in *H. citrinus* (Fig. 4D) and *H. olivaceus* (Fig. 4G), in which spores exceeding 45μm in length may be found. The remaining species have spores which lack this mucronate projection although the apex may be more or less acute. The two most common British species, namely *H. tener* (13–17 × 8–12μm) and *H. olivaceus* (30–47 × 13–19μm) represent the range of spore size found in the genus. One of the major distinguishing features lies in the final appearance of the persistent myxosporium, ranging from a very loose saccate structure in *H. hessei* and *H. thwaitesii,* closely applied yet strongly wrinkled in *H. muticus,* longitudinally ridged in *H. vulgaris,* and breaking down into plate-like fragments in *H. tener* and *H. sulcatus*. In *H. luteus* the myxosporium is closely appressed to the eusporium at maturity and is not discernible with the light microscope.

Ultrastructurally, the outer layer of the spore wall in *Hymenogaster* comprises a fine, persistent, electron-opaque, smooth myxosporium. The myxosporium is appressed to the thick episorium in *H. luteus* (Fig. 3A), an exosporium is absent and the spore wall appears smooth in surface view. The exosporium is a thin, continuous electron-opaque layer in *H. bulliardii* (Fig. 4B), appearing areolate in *H. olivaceus* and *H. tener*. The exosporial condensation which forms a well-defined, electron-dense layer over the episporium in *H. tener* (Fig. 5E), less strongly so in *H. olivaceus,* retains connections with the myxosporium and is responsible for the irregular, coarse verrucosities in *H. tener* and rugosities in *H. olivaceus,* observed in surface view. The spore surface in *H. vulgaris* displays prominent, irregular, incomplete, approximately longitudinal ridges derived from the well-developed, electron-dense, irregular exosporial condensation with electron-opaque interstitial material (Fig. 6C). The exceptionally thick wall of the *Hymenogaster* spore (Fig. 4A), and that of *Hymenangium album* (Fig. 7E–F), is due mainly to the very strong development of the fibrillar episporium. In *Hymenangium album,* the saccate, electron-dense, myxosporial layer, which appears smooth in surface view, fragments at maturity revealing the verruculose exosporial

layer. In ultrathin section, the exosporial condensation, a well-defined electron-dense, extensively lacunose layer appears irregularly but distinctly columnar (Fig. 7F).

TAXONOMY

Hymenogaster Vittad., Monogr. Tuberac.:20(1831).

Syn.: *Dendrogaster* Bucholtz in Hedwigia 40:316 (1901). Type: *H. connectens* Bucholtz.

Hymenogaster subg. *Dendrogaster* (Bucholtz) A. H. Smith in Mycologia 58:104 (1966).

Gasterocarp mostly more than 1cm diam., globose, ellipsoid, lobate or irregularly tuberous, frequently depressed at the base, sessile, indehiscent. *Peridium* thin to very thick, whitish, yellow, brownish, or with purplish to violaceous tints, often mottled, viscid or dry, smooth to finely velutinate, often becoming wrinkled, but generally not separable from the gleba. *Gleba* soft-fleshy to cartilaginous, labyrinthoid, mostly white when young becoming yellowish, lilaceous, violaceous, rusty brown finally darker, consisting of small chambers, round or elongate, empty or partially filled, more or less radially arranged with a small sterile base. *Tramal plates* thin. *Hyphal system* monomitic, with thin-walled, inflated generative hyphae; clamp-connections often present, occasionally absent. *Columella* mostly absent but sometimes visible as fine strands radiating from the sterile base, never percurrent. *Sterile base* usually present but small in young gasterocarps. *Spores* statismosporic, orthotropic, 10–20μm or more long, ovo-ellipsoid, amygdaliform or fusoid, at times apically mucronate, with a thickened, compound wall, yellow, ochraceous brown or rusty brown, mostly smooth, sometimes bearing a verrucose to ridged ornamentation, and more often with a gelatinized myxosporium which frequently becomes loosened and wrinkled; hilar appendix small with a terminal hilar pore, sometimes retaining a sterigmal appendage. *Basidia* clavate then elongating at maturity to cylindric, bearing usually 2, rarely 1, 3 or 4 well-developed, straight sterigmata. *Cystidia* none. *Hymenophoral trama* regular, hyaline to brown. *Subhymenial layer* pseudoparenchymatous. *Peridiopellis* a repent epicutis. *Development* angiocarpic.

Habitat and Distribution: Hypogeal to subepigeal, forming ectotrophic mycorrhizal associations with forest trees world-wide.

Lectotype species (Dodge & Zeller, 1934: 629): *Hymenogaster bulliardii* Vittad.

KEY TO BRITISH SPECIES

1. Peridiopellis an epithelium; spores rugulose, 14–17 × 7·5–11·5μm, citriform, with a closely appressed myxosporium; gasterocarp 0·5–2cm diam., whitish to pale yellowish brown; gleba ferruginous; exotic, in botanic gardens, usually associated with *Eucalyptus*
Hymenangium album

\+ Peridiopellis a repent epicutis of narrow hyphae; spores smooth but often overlain by a wrinkled myxosporium (*Hymenogaster*) . . . 2

2. Spores lacking a loosened myxosporium, 19–23 × 9–12μm, narrowly citriform, sulphur yellow; gasterocarp 0·5–1·5cm diam., snow white

then yellowish brown; gleba greenish to sulphur yellow; odour sweetish, recalling vanillin or phenol; common under conifers, occasionally deciduous trees (Sect. 1. *Lutei*) . . . **1. H. luteus**

\+ Spores enveloped in a loose, wrinkled or fragmenting myxosporium 3

3. Spores with a pronounced and persistent mucronate apex (Sect. 2. *Hymenogaster*) 4

\+ Spores more or less fusoid, with an obtusely rounded apex, never mucronate (Sect. 3. *Vulgares*) 8

4. Spores more than 25μm long, fusoid-citriform 5

\+ Spores less than 25μm long, citriform 7

5. Gasterocarp 1–2(–4)cm diam., soon becoming bright lemon yellow to golden yellow, finally nigrescent; gleba red-brown to umbrinous; spores 20–40 × 14–19μm, with a loose myxosporium; odour 'cheese-like' or phenolic; common . . . . . **2. H. citrinus**

\+ Gasterocarp not bright yellow, rather off-white discolouring brownish; odour slight 6

6. Spores elongate, 30–47 × 13–19μm, with a wrinkled myxosporium; gasterocarp 0·5–2·5(–4)cm diam., with olivaceous tints; gleba creamy brown to dull brown; most common species, often in large numbers **3. H. olivaceus**

\+ Spores 24–32 × 12–15μm, citriform, with myxosporium fragmenting into irregular patches; gasterocarp 0·5–1cm diam., often with a basal groove; gleba yellowish to golden brown; rare . . **4. H. sulcatus**

7. Gleba soon acquiring pale pinkish tints, finally grey brown; spores 13–17 × 8–12μm, with myxosporium fragmenting into irregular patches; gasterocarp 0·5–2cm diam., off-white bruising reddish, often with a white rhizomorph; fungoid; common . . . **5. H. tener**

\+ Gleba pale brown to greyish black, variegated; spores 16–22 × 12–17μm, with a closely applied but very strongly wrinkled myxosporium; gasterocarp 0·2–1cm diam., pure white to greyish; odour none; uncommon . . . . . **6. H. arenarius**

8. Spores more than 26μm long 9

\+ Spores 19–26 × 10–14μm, ellipso-fusoid. 10

9. Spores 22–37 × 11–14μm, fusoid, with a longitudinally wrinkled myxosporium; gasterocarp 0·5–1·5cm diam., whitish to dull yellowish brown; gleba soon darkening to fuscous-black; common **7. H. vulgaris**

\+ Spores 19–32 × 12–16μm, with a closely applied but irregularly wrinkled myxosporium; gasterocarp 0·5–1·5cm diam., off-white to very dark brown, peridium often cracking; gleba ferruginous to dark fuscous. . . . . **8. H. muticus**

10. Spores with a very loose, wrinkled myxosporium, sometimes giving a more or less globose outline; gasterocarp small, less than 5mm diam., whitish staining brown; known only from type locality **9. H. thwaitesii**

\+ Spores with a closely applied, wrinkled myxosporium . . . 11

11. Gleba dark greyish brown; spores fuscous brown; gasterocarp 0·5–1·5cm diam., whitish soon cinnamon brown, with a thick peridium; odour sweet . . . . . **10. H. griseus**

\+ Gleba dark fuscous brown to black; gasterocarp 1–3cm diam., white to greyish; odour rancid . . . . . **11. H. hessei**

Section 1. **Lutei** Svrček apud Pilát, Flora ČSR ser. B, 1 [Gasteromycetes]: 151 (1958).

Syn.: *Hymenogaster* sect. *Leves* Soehner in Beih. Nova Hedwigia 2:17 (1962).

Spores fusoid to narrowly citriform but lacking a mucronate apex; lacking myxosporial remnants at maturity.

1. H. luteus Vittad., Monogr. Tuberac.: 22 (1831). Figs 1A, 3A–F.

Syn.: *Splanchnomyces luteus* (Vittad.) Corda, Icon. Fung. 6:40 (1854).
S. berkeleyanus Corda, loc. cit.: 43.
Hysterogaster luteus (Vittad.) Dodge apud Gaumann, Comp. Morph. Fungi: 488 (1928).

Gasterocarp 0·5–1·5cm diam., subglobose becoming irregular, often with a depressed base, often with a white to yellow rhizomorph. Peridium thin, at first snow white then yellowish brown, smooth, silky. Gleba soft, initially white soon greenish to sulphur yellow; chambers small, numerous, full; sterile base minute, conical. Tramal plates thin, 10–20μm thick, of narrow hyphae, 2–7μm diam.; odour becoming sweetish, recalling vanillin or phenol. Spores 19–23(–26) × 9–12(–14)(21 ± 1·5 × 10 ± 1·0)μm, $Q = 2{\cdot}1$, ovoid to fusoid, with an acute apex, often abnormal in form, sulphur yellow, smooth, thick-walled, with a conspicuous hilar appendix, lacking a loose myxosporium. Basidia 20–30 × 4–6μm, clavato-cylindric, bisporic, with short sterigmata. Subhymenial layer not conspicuous. Peridiopellis 40–50μm thick, with narrow, radially repent hyphae, 2–5μm diam.
ITALY: Lombardy, Milan, *Vittadini* (**holo.** K).

A species commonly found in southern Britain, and numerous collections were cited by Hawker (1954: 527) from Gloucestershire, Gwynedd, Kent, Oxfordshire, Somerset, Surrey, and Wiltshire. Gasterocarps are found in the humus or buried up to 5cm deep in the underlying soil. British collections have been associated with Fagaceae (*Fagus, Quercus*), Oleaceae (*Fraxinus*), Pinaceae (*Abies, Larix, Picea, Pinus*) and Taxaceae (*Taxus*). The species is easily recognized by the pale colour of the gleba and the distinctive smooth spores. The latter character formed the basis of the section *Lutei,* proposed by Svrček (1958: 726). Scanning electron micrographs also reveal wrinkled remains on the young, attached spores (Hawker, 1975: pl. 34, 35). A colour plate was published by Tulasne & Tulasne (1851: pl. 1, fig. 3).

Section 2. **Hymenogaster**

Spores mucronate-citriform, with a pronounced apex, enveloped in a loosened, wrinkled or fragmented myxosporium at maturity.

2. H. citrinus Vittad., Monogr. Tuberac.: 21 (1831). Figs 1C, 4C–D.

Syn.: *H. decorus* Tul. in Ann. Sci. Nat., Bot. sér. 2, 19:374 (1843).
Splanchnomyces citrinus (Vittad.) Corda, Icones Fung. 6:43 (1854).
H. citrus Tul., Fungi Hypog., edit. 2:74 (1853).
S. citrus (Tul.) Corda, loc. cit.
H. tomentellus Hesse, Hypog. Deutschl. 1:112 (1891).
H. pisomyces Fr. in Herb.

Gasterocarp 1–2cm diam., exceptionally up to 4cm diam., irregularly globose, often sulcate and deformed. Peridium thin, initially white soon lemon yellow to golden yellow, finally dingy and rufous nigrescent, silky, smooth, brittle when dry. Gleba firm but soft, reddish brown finally fuscous to umbrinous; chambers small to medium, solid, no clear orientation; sterile base initially present but soon obliterated. Tramal plates 60–80μm thick; context hyphae much inflated, 8–15μm diam., hyaline, thin-walled; odour none then 'cheese-like' or phenolic. Spores 26–40 × 14–19(32 ± 3·0 × 17 ± 2·0)μm, $Q = 1{\cdot}88$, elongate fusoid with a mucronate apex, golden brown then dark umbrinous, smooth, thick-walled, with a persistent, hyaline, much wrinkled myxosporium. Basidia 27–36 × 5–9μm, cylindric-tapering, bisporic occasionally monosporic, with large, stocky sterigmata. Subhymenial layer broad, pseudoparenchymatous. Peridiopellis 80–150μm thick, of uninflated, loosely woven, subagglutinated hyphae. Clamp-connections present.

ITALY: Lombardy, *Vittadini,* Herb. Berk. (**holo.** K).

FRANCE: Bois de Boulogne, vi 1942, *Tulasne,* Herb. Berk. (K, type of *H. decorus*).

SWEDEN: Upsala, *Fries,* Herb. Berk. (K, type of *H. pisomyces*).

ENGLAND: Somerset, Batheaston, *Broome,* Herb. Berk. (K, type of *H. citrus*).

A fairly common species, occurring throughout the year when climatic conditions are suitable. It is recognized macroscopically by the bright yellow gasterocarps of the younger specimens, and microscopically by the exceptionally large, fusoid spores with a smooth wall and a wrinkled myxosporium. The large, mucronate spores indicate a relationship with *H. bulliardii* Vittad. (the type species of the genus), *H. olivaceus* and *H. sulcatus*. Gasterocarps may be found either on the soil surface below the humus layer or buried 2–5cm deep, usually in calcareous soils. The species is most commonly found associated with Fagaceae (*Fagus*) but is also known to grow with Juglandaceae (*Juglans*) and Pinaceae (*Larix, Picea, Pinus*). British records include Dorset, Gloucestershire, Gwynedd, Kent, Oxfordshire, Somerset and Wiltshire. Coloured illustrations were provided by Vittadini (1831: pl. 3 fig. 2); Tulasne & Tulasne (1851: pl. 1 fig. 1, 10 fig. 3), Berkeley (1860: pl. 20 fig. 2), and Massee (1889: pl. 1 fig. 8).

3. H. olivaceus Vittad., Monogr. Tuberac.: 24 (1831). Figs 1D, 4E–H.

Syn.: *H. olivaceus* var. *modestus* Berk. & Br. in Ann. Mag. Nat. Hist. ser. 1, 18:74 (1846).
H. pallidus Berk. & Br., loc. cit.
H. calosporus Tul., Fung. Hypog.: 70 (1851).
Splanchnomyces cordaeanus Zobel apud Corda, Icon. Fung. 6:42 (1854).
S. olivaceus (Vittad.) Corda, op. cit.: 44.
S. broomeanus Corda, op. cit.: 44, pl. 13 fig. 107, pro syn.

Gasterocarp 0·5–2·5(–4)cm diam., subglobose to irregularly flattened. Peridium thin, 0·2–0·3cm thick, whitish to very pale brownish soon discolouring dingy olivaceous brown, finally fuscous, cracking to expose

the gleba. Gleba soft, pale watery brown to creamy brown, finally dull brown, drying snuff brown; chambers small, irregular; sterile base visible only in young specimens. Tramal plates 20–30μm thick, whitish; context of narrow, non-inflated, gelatinized hyphae, 2–5μm diam.; odour slightly fungoid (mushroom). Spores large 30–47 × 13–19(41 ± 2·5 ± 15 ± 1·0)μm, $Q = 2.5$, lanceolate fusoid with a mucronate apex and a conspicuous tapering hilar appendix, golden brown, smooth, thick-walled, with a hyaline, wrinkled myxosporium. Basidia 23–30 × 4–7μm, short cylindric, bisporic. Subhymenial layer poorly developed. Peridiopellis of thin-walled, semi-agglutinated, inflated hyphae, 4–19μm diam. Clamp-connections present.

ITALY: Lombardy, Milan, *Vittadini,* Herb. Berk. (**holo.** K, type of *H. olivaceus*).

FRANCE: Vincennes, October, *Tulasne,* Herb. Berk. (K, type of *H. calosporus*).

ENGLAND: Wiltshire, Hartham Park, autumn 1845, *Broome,* Herb. Berk. (K, type of *H. olivaceus* var. *modestus*); Northamptonshire, Cotterstock, x 1845, *Berkeley* (K, type of *H. pallidus*).

It has long been argued that the type collection of *Hymenogaster decorus* represents the mature condition of *H. olivaceus,* whilst the type collections of *H. olivaceus, H. olivaceus* var. *modestus, H. pallidus,* and *H. calosporus* represent young material. The spores of *H. decorus,* however, are very distinct from those of *H. olivaceus,* having only a short mucronate apex in the vast majority of cases, the main body of the spore is wider and more deeply pigmented, and there is a much more pronounced wrinkled myxosporium. These spores, combined with the dark fuscous brown colour of the gleba would indicate synonymy with *H. citrinus* Vittad. to be more appropriate than with *H. olivaceus.*

Hymenogaster olivaceus is probably the most common species of *Hymenogaster,* and may occur in large numbers during dry periods. Gasterocarps may be relatively large for the genus, although variable, and occur almost at the soil surface or up to 10cm deep in the humus. Known associates include Fagaceae (*Fagus, Quercus*), Tiliaceae (*Tilia*) and Pinaceae (*Larix, Picea*). It is known from Buckinghamshire, Gloucestershire, Hereford & Worcester, Northamptonshire, Perthshire, Somerset, and Wiltshire.

The species is very close to *H. citrinus* Vittad. but with duller peridial pigmentation. It is easily recognized microscopically by the exceptionally large spores with a pronounced mucronate apex. Scanning electron micrographs of the spores were first published by Hawker (1974: pl. 35 figs 29, 30). Lange (1956: 73) recognized *H. decorus* Tul. as a small-spored form of *H. olivaceus,* with spores measuring 17·5–25 × 10–14μm.

4. H. sulcatus Hesse, Hypog. Deutschl. 1:111 (1891). Figs 1E, 4I–J.

Gasterocarp 0·5–1cm diam., more or less globose, at times flattened, often with a basal groove. Peridium 0·3mm thick, dingy white to yellowish finally dark reddish brown. Gleba soft and spongy, yellowish brown to golden brown; chambers fairly large, mostly full; sterile base indistinct. Tramal plates 25–40μm thick; context of loosely woven,

thin-walled, inflated hyphae 3–9μm diam.; odour slight. Spores 24–32(–36) × 10–16(29 ± 1·5 × 13 ± 1·0)μm, $Q = 2{\cdot}2$, ovoid to citriform with a short but constant mucronate apex and a conspicuous hilar appendix, pale golden brown to rusty brown, smooth, thick-walled, covered with fragmenting myxosporial remnants. Basidia 25–32 × 5–7μm, cylindrico-clavate, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis 80–100μm thick, formed by a non-agglutinated, repent epicutis of radially parallel hyphae 2–4μm diam., with a slightly thickened wall. Habitat under *Fagus, Quercus, Tilia*; North temperate.
GERMANY: Kirchdirmold, v 1889, *Hesse* (**holo.** MB, n.v.).
NORTH WALES: Nant y Glyn, x 1880, Herb. Broome (K).
ENGLAND: Somerset, Bristol, Stoke Bishop, 19 xi 1951, *Fraymouth* 138 in *Hawker* 558 (K).

A rare species in western Europe but apparently more common towards the east. Microscopically it is distinguished by the characteristic fragmenting of the spore myxosporium. The spore form and structure indicates that the affinity of the species lies with *H. bulliardii* Vittad., *H. citrinus,* and *H. olivaceus* Vittad.

5. H. tener Berk. & Br. in Ann. Mag. Nat. Hist. ser. 1, 13:349 (1844). Figs 1F, 5A–F.
Syn.: *H. lilacinus* sensu Berk., Brit. Fung. Fasc., 4: no. 305, non *H. lilacinus* Tul. in Ann. Sci. Nat., Bot. sér. 2, 19:374 (1843).
H. argenteus Tul. in Giorn. Bot. Ital. 1(2):55 (1844).
Splanchnomyces tener (Berk. & Br.) Corda, Icon. Fung. 6:44 (1854).
Gasterocarp 0·5–2cm diam., globose, sometimes arising from a white rhizomorph. Peridium thick, off white bruising reddish, silky, smooth. Gleba soft, initially white becoming pale pinkish lilac then greyish pink, finally greyish brown; chambers relatively large, often appearing empty; sterile base more or less pronounced in young specimens, white; columella sometimes visible as fine strands radiating from base. Tramal plates 30–40μm thick; context of inflated, thin-walled hyphae 2–11μm diam.; odour unpleasant, fungoid. Spores 13–17 × 8–12(16 ± 1·0 × 10·5 ± 1·0)μm, $Q = 1{\cdot}52$, ovo-citriform with a small but persistent mucronate apex and a short truncate hilar appendix, ferruginous, smooth, thick-walled, with large irregular fragments of a disintegrating hyaline myxosporium adhering to the surface. Basidia 22–28 × 6–7μm, clavate, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis a fairly thick epicutis of agglutinated, thin-walled hyphae, 2–6μm diam.
ENGLAND: Wiltshire, Rudloe, 2 v 1843, *C. E. Broome,* Herb. Berk. (**holo.** K, type of *H. tener*).
FRANCE: Bois de Boulogne, ix 1844, *Tulasne,* Herb. Berk. (K, type of *H. argenteus*).

The spores appear coarsely verrucose owing to an irregular exosporial ornamentation. The relatively small spores, combined with the delicate pinkish tints of the gleba in fresh specimens, distinguish this species. The spores of *Hymenogaster tener* show the smallest size range within the section *Hymenogaster*.

It is a common and widespread species in the British Isles, and is recorded from Derbyshire, Durham, Gloucestershire, Hereford & Worcester, Hertfordshire, Kent, Perthshire, Somerset, Surrey, Sussex, Wiltshire, Yorkshire, and also Dublin, Kildare (Eire). Gasterocarps mostly occur in surface litter but may occur up to 5cm below the surface usually associated with *Quercus* or *Fagus* (Fagaceae) but also with Betulaceae (*Betula*), Tiliaceae (*Tilia*), Pinaceae (*Larix, Picea*) and Taxaceae (*Taxus*).

The species is characterized by the small size, the smooth, silky-white peridium, the pinkish tinge to the young, pale gleba, and the small spores. *Hymenogaster arenarius* is closely related but less common, and distinguished by the dull brown peridium, the darker and variegated appearance to the gleba, and larger spores. *Hymenogaster niveus* Vittad. is dubiously distinct with differences limited to a duller white peridium, a more violaceous tint to the gleba and paler spores. The latter species is not confirmed from Britain.

Excellent coloured illustrations were published by Tulasne & Tulasne (1851: pl. 1 fig. 4, 10 fig. 1), and Lange & Hora (1963: 215).

6. H. arenarius Tull. in Giorn. Bot. Ital. 1(2):55 (1844). Figs 1G, 5G–K.
Syn.: *H. pusillus* Berk. & Br. in Ann. Mag. Nat. Hist. ser. 1, 18:75 (1846).

Gasterocarp 0·2–1cm diam., subglobose, lobate or depressed. Peridium pure white to greyish white, unchanging, yellowish brown when dry, matt and smooth. Gleba white then tan, appearing variegated, finally greyish black; chambers large, angular, radiating from the base; sterile base at first present then inconspicuous. Tramal plates 70–100μm thick, greyish. Odour none to slight. Spores $16–22 \times 10–17(20 \pm 1{\cdot}5 \times 12 \pm 1{\cdot}0)\mu$m, $Q = 1{\cdot}5$, ellipsoid to fusoid-citriform, reddish brown, thick-walled, smooth but enveloped by a closely applied yet strongly wrinkled myxosporium so as to appear coarsely verrucose. Basidia $25–30 \times 6–7\mu$m, cylindric, bisporic. Subhymenial layer broad. Hymenophoral trama of thin-walled hyphae, 3–5μm diam. Peridiopellis 200–300μm, thin-walled hyphae, 2–6μm diam. Clamp-connections present.

(**lecto.** K—Dodge & Zeller, 1934:674).

FRANCE: Seine, Bois de Boulogne, *Tulasne,* Herb. Berk.

ENGLAND: Northamptonshire, Rushton, The Wilderness, 8 x 1845, *Berkeley* (K, type of *H. pusillus*).

A small, pale species, with a sterile base present in the early stages. *Hymenogaster pusillus,* which was described from England, is merely young and largely immature material of this species. Although Lange (1965: 69) reported the species as common in *Fagus* woods in Denmark, it has been only rarely collected in Britain, being known from Gloucestershire, Northamptonshire, Oxfordshire and Somerset. It occurs in the soil to a depth of 2–5cm. The species is closely related to *H. tener,* differing in the dull coloured peridium, the darker gleba, and the slightly larger spores. Whereas the myxosporium of the spores of *H. tener* breaks down into small, irregular adhering fragments, that of *H. arenarius*

remains more closely applied but becomes densely wrinkled. The spores of both species are described as 'verrucose'.

Section 3 **Vulgares** Svrček apud Pilát, Flora ČSR ser. B, 1 [Gasteromycetes]: 726 (1958).

Syn.: *Hymenogaster* sect. *Involuti* Soehner in Beih. Nova Hedwigia 2:17 (1962).

Spores ovo-ellipsoid to fusoid, sometimes with an acute apex but not mucronate; enveloped in a loosened, wrinkled or fragmented myxosporium at maturity.

7. H. vulgaris Tul. apud Berk. & Br. in Ann. Mag. Nat. Hist. ser. 1, 18:74 (1846). Figs 2A, 6A–D.

Syn.: *Rhizopogon albus* Bull.: Fr., Syst. Mycol. 2:293 (1823), non *R. albus* Berk. apud J. E. Smith, Engl. Fl. 5(2):229 (1836).

H. griseus Tul. in Ann. Sci. Nat., Bot. sér. 2, 19:374 (1843), non *H. griseus* Vittad., Monogr. Tuberac.: 23 (1831).

H. albus (Bull.: Fr.) Fr., Summa Veg. Scand. 2:436 (1849), non *H. albus* (Klotzsch) Berk. in Ann. Mag. Nat. Hist. ser. 1, 13:349 (1844).

Splanchnomyces tulasneanus Zobel apud Corda, Icon. Fung. 6:43 (1854).

Hysterangium australe Speg. in An. Soc. Cient. Arg. 11:242 (1881).

Hymenogaster campester Becker in Natur 35:355 (1886).

H. australis (Speg.) Speg. in An. Soc. Cient. Arg. 29:124 (1887).

H. limosus Hesse, Hypog. Deutschl. 1:133 (1891).

H. tener Berk. & Br. var. *arbuticola* P. Henn. in Verh. Bot. Ver. Prov. Brandenb. 40:146 (1898).

Gasterocarp 0·5–1·5cm diam., globose, often irregular or lobate. Peridium up to 1mm thick, off-white to dull yellowish-brown, smooth and silky, at times cracking but not separable. Gleba soft and spongy, white, at times with lilaceous tints, soon becoming dark fuscous brown to blackish; chambers small, variable, often labyrinthoid; sterile base often present but base of gasterocarp depressed. Tramal plates 40–50μm thick, subgelatinized, consisting of inflated, thin-walled hyphae, 4–12μm diam.; odour slight, finally rancid. Spores $22–37 \times 11–14(30 \pm 2{\cdot}0 \times 12 \pm 0{\cdot}8)\mu$m, $Q = 2{\cdot}5$, fusoid with a tapering apex, but not mucronate, and a tapering base, ferruginous, smooth, thick-walled, enveloped in a persistent, membranous, longitudinally wrinkled myxosporium. Basidia $25–34 \times 5–8\mu$m, cylindrico-clavate, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis an agglutinated epicutis of narrow, repent hyphae, 2–4μm diam., with a slightly thickened wall.

(**lecto.** K—Dodge & Zeller, 1934: 664).

FRANCE: Bois de Boulogne, 17 iv 1846, *Tulasne,* Herbs Berk. & Broome.

ENGLAND: Somerset, Stapleton Grove, x 1845, *Broome,* Herb. Berk. (K); Apethorpe, 15 vii 1845, Herb. Berk. (K).

Although the species was described by Tulasne (1846) and Dodge & Zeller (1934: 664) chose the Bois de Boulogne collection as the lectotype, both the British collections, from Apethorpe, Northamptonshire and Stapleton Grove, Somerset, were cited in the original description. All have identical spores. The species is distinguished microscopically by the elongate fusoid spores, enveloped in a persistent myxosporium with longitudinal wrinkling. It is closely related to *H. hessei* and *H. thwaitesii,* but has significantly larger spores. It differs from the other large-spored species, *H. citrinus* and *H. olivaceus,* in not having a distinctly mucronate apex to the spores, a feature emphasized by Berkeley & Broome (1846). The non-mucronate spore form is judged sufficient to place *H. vulgaris* and allied species in a section separate from the type section, namely sect. *Vulgares* Svrček. The characteristic ridges of the myxosporium, due to exosporial ornamentation, was first illustrated by Hawker (1975: pl. 35 fig. 28).

This is a common species in Britain producing small, whitish to pale yellowish-brown gasterocarps, growing up to 12cm deep in the soil. It is usually associated with Fagaceae (*Fagus, Quercus, Castanea*), but is also found under Tiliaceae (*Tilia*), Pinaceae (*Larix, Picea*) and Taxaceae (*Taxus*). Collections are known from Buckinghamshire, Gwynedd, Durham, Gloucestershire, Hereford & Worcester, Perthshire, Somerset, and also Kildare (Eire).

8. H. muticus Berk. & Br. in Ann. Mag. Nat. Hist. ser. 2, 2:267 (1848). Figs 2B, 6E–F.

Gasterocarp 0·5–1·5cm diam., globose to pulvinate, occasionally irregular. Peridium dull white soon discolouring dark brownish-black, smooth but cracking and separable. Gleba reddish-brown to dark fuscous; chambers small, full, crowded; sterile base absent. Tramal plates 50–100μm thick, of broadly inflated, thin-walled hyphae, 5–18μm diam.; odour slight. Spores large, 19–32 × 12–16(24 ± 1·5 × 14 ± 1·0)μm, $Q = 1{\cdot}7$, oboboid to broadly ellipsoid, with an obtuse apex, occasionally subacute but never mucronate, with a ferruginous brown, thick wall, smooth, enveloped in a closely applied yet very wrinkled, hyaline myxosporium. Basidia 20–25 × 4–6μm, cylindric, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis 150–250μm thick, formed by a repent epicutis of radially parallel, repent, agglutinated, thin-walled hyphae, 2–5μm diam.
ENGLAND: Somerset, Stapleton Grove, *Broome* (**holo.** K).

This is a poorly known species, the type collection being the only definite record from Britain. A collection cited from Tring, Hertfordshire is found on examination to represent *H. tener* Berk. & Br. The spores of the type collection are very characteristic with an ovo-ellipsoid outline lacking any indication of a mucronate apex. This places the species in the section *Vulgares,* close to the common *H. vulgaris,* the latter species having longer and more fusoid spores. Published drawings of the spores of this species have proved misleading. The illustrations provided by Massee (1899: p. 1 fig. 20), Dodge & Zeller (1934: pl. 18 fig. 22), and Lange (1956: fig. 19) show mucronate spores typical of either *H. tener* or *H. arenarius* Tul., whilst Tulasne & Tulasne (1851: pl. 10 fig. 7), Svrček

(1958; fig. 37/8), and Hawker (1954: fig. 28q) correctly depict an ellipsoid outline.

Macroscopically, the gasterocarps have been compared with *H. olivaceus* Vittad.

9. H. thwaitesii Berk. & Br. in Ann. Mag. Nat. Hist. ser. 1, 18:75 (1846). Figs 2C, 6G–H.

Gasterocarp small, less than 5mm diam., more or less globose. Peridium thin, off-white staining brown, smooth. Gleba whitish becoming brown; chambers elongated; sterile base none. Tramal plates white, thin, consisting of loosely woven, inflated, thin-walled hyphae 2–12μm diam. Spores 19–26 × 10–14(23 ± 1·5 × 12 ± 1·0)μm, $Q = 1{\cdot}9$, obovoid to subfusoid with a tapering but not mucronate apex and a pronounced hilar appendix, dark reddish-brown, thick-walled, enveloped in a persistent, loose and strongly wrinkled myxosporium. Basidia 22–27 × 5–7μm, cylindrico-clavate, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis 110–120μm thick, formed by a repent epicutis of radially parallel, hyaline, narrow hyphae, 2–4μm diam.

ENGLAND: Somerset, Portbury, 29 ix 1845, *Thwaites* (**holo.** K).

The type collection is extremely fragmentary and the species remains incompletely known. Berkeley & Broome emphasized the 'globose' appearance of the spores but this is a misleading description. The spore proper is ovo-fusoid and quite typical of those found in the genus *Hymenogaster,* although not distinctly mucronate as in the section *Hymenogaster*. The persistent myxosporium, however, is very loosely attached, and strongly wrinkled, inflating in a liquid mount to give an overall globose outline.

On the basis of the available information this species differs from *H. hessei* in the smaller size of the gasterocarp and the loosely attached myxosporium.

10. H. griseus Vittad., Monogr. Tuberac.: 23 (1831). Figs 2D, 6I–K.

Gasterocarp small, 0·5–1·5cm diam., subglobose to flattened or lobate. Peridium exceptionally thick, up to 1mm, pruinose, glabrescent, initially whitish soon cinnamon brown. Gleba grey fuliginous to dark fuscous brown; chambers very small to medium, full; sterile base minute, whitish in young specimens. Tramal plates 30–40μm thick, white; context hyphae much inflated, 5–30μm diam., hyaline, thin-walled; odour sweet. Spores 19–26 × 10–14(23 ± 1·5 × 11·5 ± 1·0)μm, $Q = 2{\cdot}0$, ellipsoid to subfusoid but not mucronate, dark fuscous brown, thick-walled, smooth, with a persistent wrinkled myxosporium, and a small hilar appendix. Basidia 35–40 × 6–7μm, cylindric-tapering, bisporic. Subhymenial layer pseudoparenchymatous. Peridiopellis of densely woven, narrow hyphae, 2–7μm diam. Clamp-connections present.

ITALY: Lombardy, Milan, *Vittadini* (type n.v.).

ENGLAND: Gloucestershire, Dursley, 15 viii 1973, *Reyner* 41 in *Hawker* 763 (K).

The epithet refers to the dark greyish-brown colour which characterizes the gleba. A colour plate was published by Vittadini (1831: 3, fig. 15),

who described the species from Milan, Italy. It differs from *H. hessei* Soehner in the brown, very thick peridium which gives a firm texture to the gasterocarp. The spores range from ellipsoid to subfusoid but are never mucronate, thus the species represents a member of the closely related group within the section *Vulgares*.

According to Hawker (1954: 53), the species is either uncommon or locally common in western England, with all the records restricted to Gloucestershire and Somerset. Gasterocarps occur either near the surface or up to 15cm deep in humus, on calcareous soils, under Fagaceae (*Fagus*) and Pinaceae (*Larix, Picea*).

11. H. hessei Soehner in Zeitschr. f. Pilzk. 2:158 (1923). Figs 2E, 7A–B.

Syn.: *H. vulgaris* sensu Hesse, Hypog. Deutschl. 1:114 (1891); non Tulasne (1851).

H. vulgaris Tul. var. *hessei* Soehner in Kryptog. Forsch. 6:396 (1924).

Gasterocarp 1–3cm diam., irregularly globose to lobate. Peridium thin, white to greyish, eventually darkening, shiny, smooth. Gleba initially whitish soon becoming dark fuscous brown to blackish; chambers large, irregular, giving a soft-spongy texture; sterile base minute, only visible in very young specimens. Tramal plates 20–40μm thick; context of much inflated, thin-walled hyphae, 8–30μm diam.; odour rancid. Spores 19–26 × 10–13(22 ± 1·5 × 12 ± 1·0)μm, $Q = 1{\cdot}83$, ellipsoid to ellipso-fusoid, with or without an acute apex but not mucronate, ferruginous brown, smooth, thick-walled, with a distinct hilar appendix, and a loose, wrinkled, hyaline myxosporium. Basidia 25–32 × 5–8μm, clavate to cylindric, bisporic. Subhymenial layer broad, pseudoparenchymatous. Peridiopellis 10–30μm thick, formed of a repent epicutis of radially parallel hyphae, 3–5μm diam., with a slightly thickened wall.

GERMANY: Hessen-Nassau, Marburg, 6 x 1886, *Hesse* (**holo.** MB, n.v.).

ENGLAND: Somerset, Burrington, Mendip Lodge Wood, 28 ix 1953, *Hawker* 848 (K).

A species, described from Germany, which is very closely related to *H. vulgaris,* with similar macrocharacters, but less common, and differing microscopically by having broader and more deeply pigmented spores. It was first reported for Britain by Hawker (1952: 283, fig. 2J–L) who emphasized the spore differences between the two species. The spores of *H. hessei* bear a loosely attached myxosporium, approaching that found in *H. thwaitesii,* which frequently forms three or four longitudinally arranged folds, visible both in light and scanning electron microscopy. A scanning electron micrograph of the spores of this species was published by Hawker (1975: pl. 35 fig. 27). A coloured illustration, under the name *H. vulgaris,* was published by Hesse (1891: pl. 2 figs 14–17).

Gasterocarps occur up to 8cm deep in humus, usually of Fagaceae (*Fagus, Quercus*), or sometimes Pinaceae (*Larix, Picea*).

Hymenangium album Klotzsch apud Dietr., Fl. Regn. Boruss. 7: no. 466 (1839). Figs 2F, 7C–F.

Syn.: *Rhizopogon albus* Berk. apud J. E. Smith, Engl. Fl. 5(2):229 (1836), non Bull.: Fr., Syst. Mycol. 2:293 (1823).

Hymenogaster albus (Klotzsch) Berk. in Ann. Mag. Nat. Hist. ser. 1, 13:349 (1844).
H. klotzschii Tul., Fungi Hypog.: 64 (1851).
Splanchnomyces albus (Klotzsch) Zobel apud Corda, Icon. Fung. 6:40 (1854).

Gasterocarp 0·5–2cm diam., subglobose to piriform, basally attached. Peridium thin, dingy-white to pallid yellowish-brown, glabrous, at times cracking, floccose and partially detersile. Gleba pale brown to ferruginous, loculate, of irregular, empty or partially filled chambers, very variable in size, lacking any radial arrangement; sterile base small or none. Tramal plates up to 175μm thick, white, with a narrow hymenophoral trama and very broad subhymenial layers; clamp-connections present on all hyphae. Spores 14–17(–19·5) × 7·5–11·5(16 ± 1 × 10 ± 0·5)μm (excl. myxosp.), $Q = 1{\cdot}6$, limoniform, deep golden-brown to fuscous brown, with a thickened wall, bearing a coarsely rugulose exosporial ornamentation, overlain by a loose membranous, hyaline myxosporium. Basidia 28–33 × 9–11μm, clavate, bearing two short sterigmata, and forming a regular palisadic hymenium. Hymenophoral trama regular, hyaline, of inflated, thin-walled hyphae, 3–18μm diam. Subhymenial layer very well developed, 20–30μm wide, pseudo-parenchymatous. Peridiopellis an agglutinated, stratified epithelium, of hyaline, thin-walled elements, 26–40 × 13–30μm, globose to piriform.
(lecto. K—Dodge & Zeller, 1934: 641).
SCOTLAND: Glasgow, Botanic Garden, x 1830, *Hooker f.*

Berkeley (1836: 229) gave the name '*Rhizopogon albus* Bull.' to material collected by J. D. Hooker at the Botanic Garden, Glasgow, and this material was examined by Klotzsch. Klotzsch (1839) matched this to material gathered in the Botanic Garden at Grunewald, near Berlin, and redescribed it as *Hymenangium album* Klotzsch, the type species of the genus *Hymenangium* Klotzsch. The Glasgow specimens, labelled '*Hymenangium album*' by Klotzsch are now located in the Kew Herbarium, whilst the Grunewald material is lost. Dodge & Zeller (1934: 641) recorded collections from many North temperate localities, in both Europe and North America, commenting that it was usually collected in pots of cultivated plants in greenhouses, often associated with *Eucalyptus*, and Hawker (1954: 533) did not regard this species as indigenous to Western Europe.

Hymenogaster albus is an Australian species, definitely confirmed from south Queensland and Victoria, and represents the most reduced form in the series including the agaricoid *Descolea* Singer, and the secotioid *Setchelliogaster* Pouzar, and should be known as *Hymenangium album* Klotzsch, being the type species of *Hymenangium* Klotzsch. All genera in the series have an epithelial pellis; submucronate spores with a finely verruculose exosporial ornamentation overlain by a loosely applied myxosporium; and usually form an ectotrophic mycorrhizal relationship with eucalyptus. A detailed description of Australian material was provided by Beaton, Pegler & Young (1985: 190).

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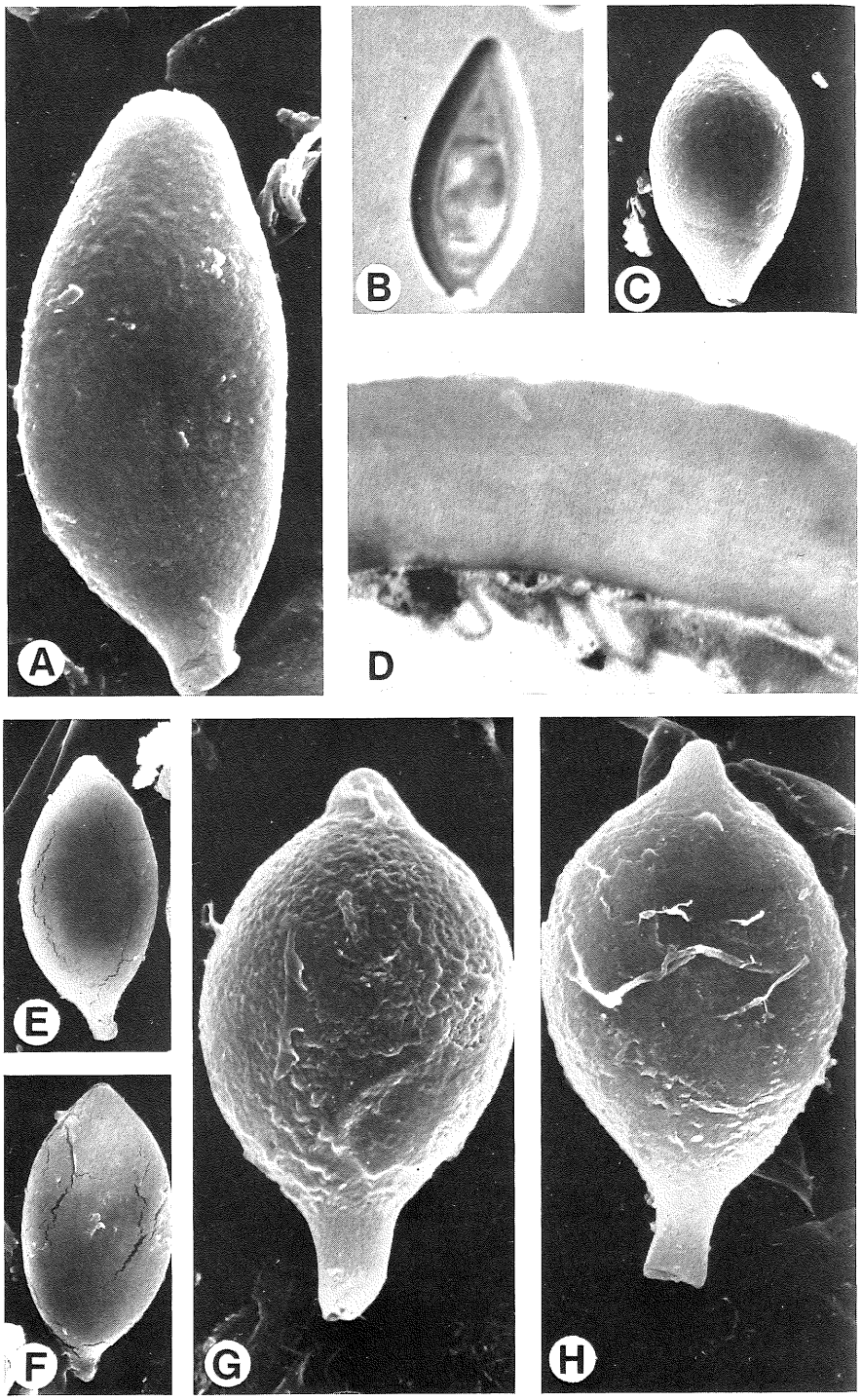

FIG. 3. *Hymenogaster* spores. A–D, *H. luteus,* type. A, SEM ×3500; B, LM ×1600; C, SEM ×1800; D, TEM ×28000. E–F, *H. luteus,* Apethorpe ×1800. G–H, *H. bulliardii,* type, SEM ×28000.

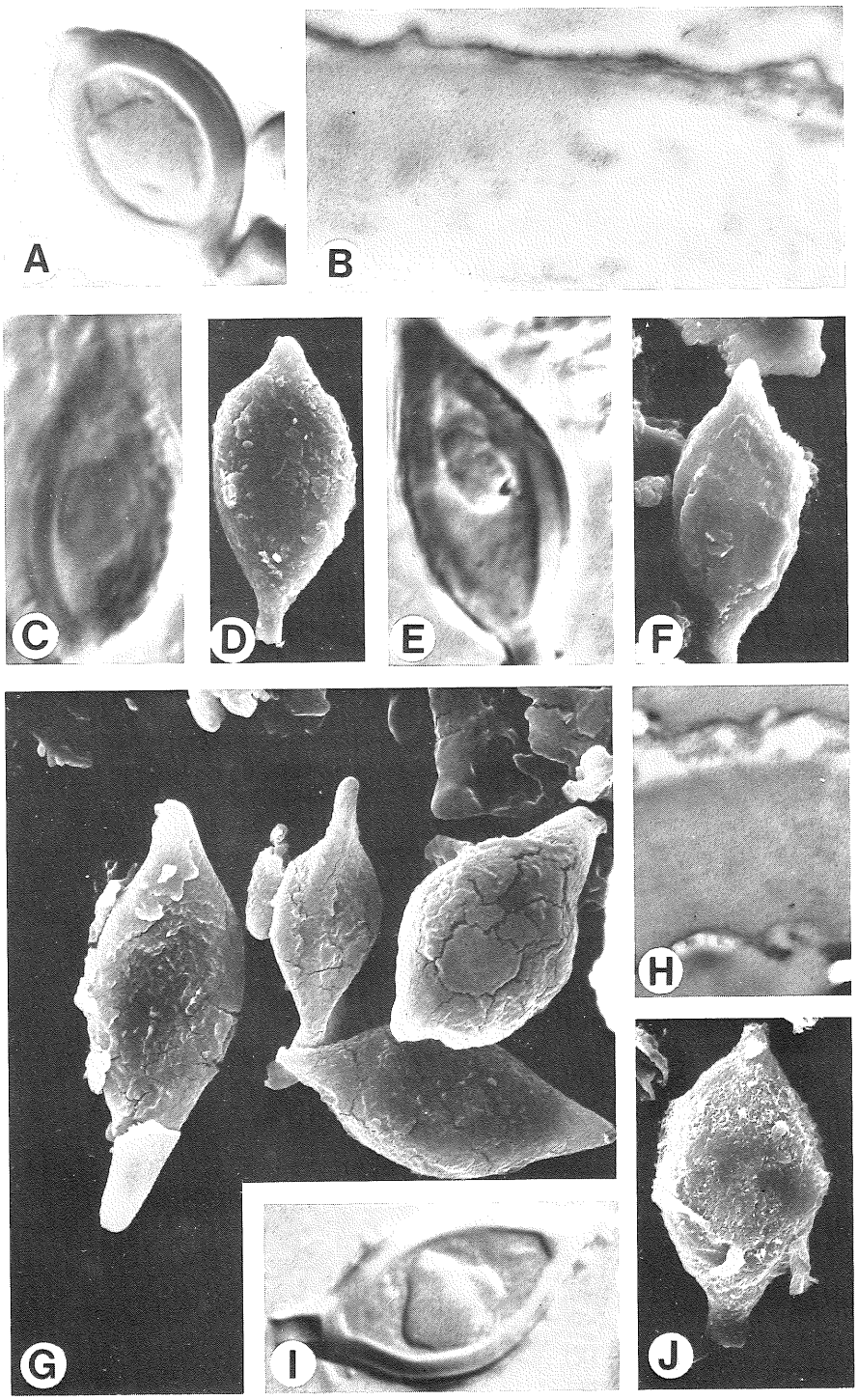

FIG. 4. *Hymenogaster* spores. A–B, *H. bulliardii,* type. A, LM ×1600; B, TEM ×22000. C–D, *H. citrinus,* type. C, LM ×1600; D, SEM ×1250. E–H, *H. olivaceus,* type. E, LM ×1600; F, SEM ×1000; G, SEM ×1200; H, TEM ×19600. I–J, *H. sulcatus, Hawker* 558. I, LM ×1600; J, SEM ×1500.

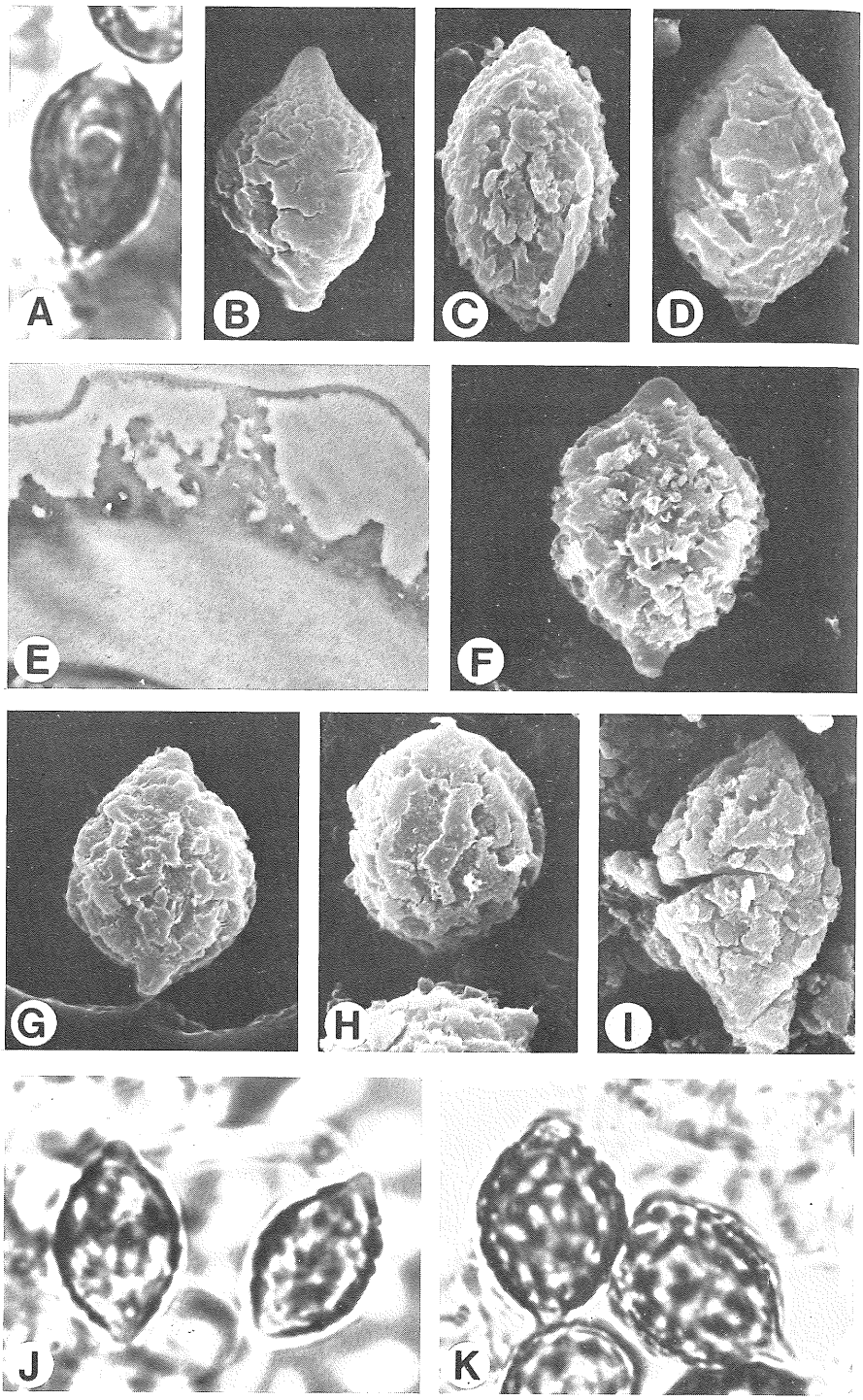

FIG. 5. *Hymenogaster* spores. A–C. *H. tener,* type A, LM ×2250; B–C, SEM ×2250, ×2500. D–F, *H. tener, Hawker* 692. D, SEM ×2500; E, TEM ×18000; F, SEM ×2500. G–K, *H. arenarius*. G–I, Type, SEM ×2000. J–K, *H. pusillus,* type, LM ×1600.

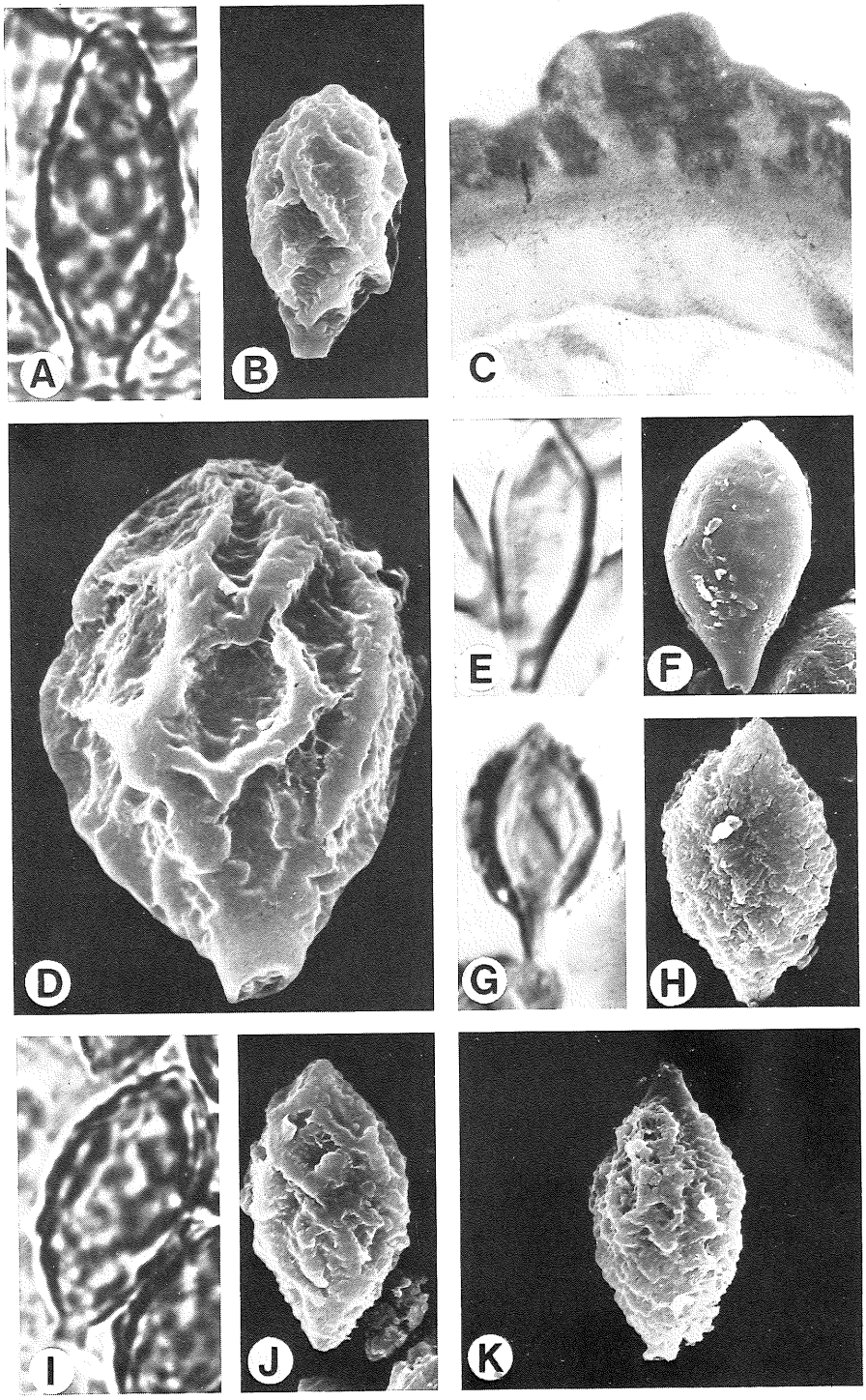

FIG. 6. *Hymenogaster* spores. A–D, *H. vulgaris,* type. A, LM ×1600; B, SEM ×1250; C, TEM ×22000; D, SEM ×2500. E–F, *H. muticus,* type. E, LM ×1600; F, SEM ×1500. G–H, *H. thwaitesii,* type. G, LM ×1600; H, SEM ×1750. I–K, *H. griseus, Hawker* 657. I, LM ×1600; J–K, SEM ×1750.

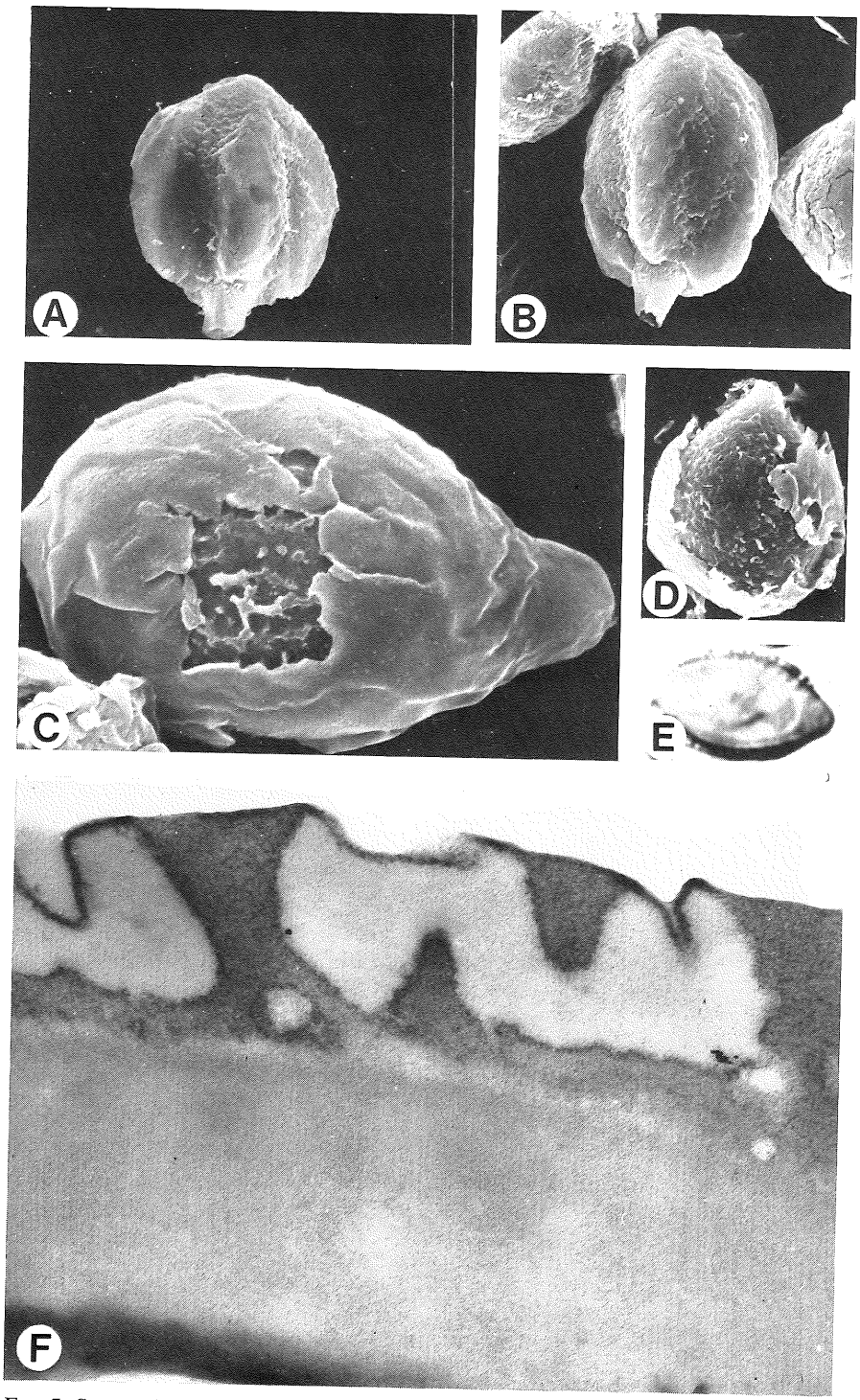

FIG. 7. Spores. A–B, *Hymenogaster hessei, Hawker* 848, SEM ×1800. C–F, *Hymenangium album,* type. C, SEM ×5250; D, SEM ×2300; E, LM ×1600; F, TEM ×49000.