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The autecology of *Battarrea stevenii* in ephemeral rivers of southwestern Africa

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In September 1990, 74 sporocarps of *Battarrea stevenii* were observed on the floodplain of the ephemeral Kuiseb River in western Namibia. Herein we report subsequent studies of the distribution, abundance, nutritional role, phenology, and sporocarp development of this fungus in the hyper-arid Namib Desert. Included are full descriptions of developing and mature sporocarps. *B. stevenii* is a common associate of riparian forests on silty floodplain terraces, but does not form mycorrhizal associations with the dominant woody species, *Faidherbia albida* or *Tamarix usneoides*. Rather, clamped mycelium extends throughout floodplain soils decomposing coarse and fine particulate organic material (4–7% of soil dry weight). Sporocarp production occurs 4·5–12 mo post-flooding in response to soil desiccation at depths of 20–35 cm. The extensive mycelium, duration of vegetative growth post-flooding, and large size and abundance of *B. stevenii* sporocarps suggest that it is an important component of the subsurface decomposer community in the Namib's ephemeral rivers. Given that the fungus has also been recorded from floodplain soils of Angola, Hungary, and New Mexico (U.S.A.), and is known to have a world-wide distribution, we predict that further biogeographical studies will reveal that *B. stevenii* is a characteristic element of the riparian biota in dryland rivers, which drain approximately one-third of the earth's land surface.

In September 1990, 74 sporocarps of a *Battarrea* species were observed in a 200 m^2 area of floodplain along the ephemeral Kuiseb River in the Namib Desert (Figs 1, 2). Thereafter, through April 1991, additional large populations of the fungus were found along a 70 km reach of the lower river. The abundance of large woody sporocarps suggested the fungus was an important component of the subsurface decomposer community, and raised questions about abiotic and biotic factors that stimulate growth and sporocarp development, as well as the nutritional role, habitat preferences, phenology and biogeography of this fungus.

A review of the literature revealed that little is known regarding the autecology of the genus. The aim of this paper is, therefore, to document sporocarp development, phenology, habitat and substrate preferences, and distribution of the fungus in the Namib Desert. *Battarrea* species are known to associate with various desert plants, including grasses, *Acacia*, *Atriplex*, *Artemisia*, *Eucalyptus*, *Euphorbia*, *Juniperus*, *Pinus*, *Prosopis*, *Sarcobatus*, *Tamarix*, and *Yucca* (Welwitsch & Currey, 1870; Maublanc & Melancon, 1930; Long, 1943; Dring & Rayner, 1967; Miller, 1969; Trueblood, 1975; Moreno *et al.*, 1984; Calonge, 1990; States, 1990). The exact nature of the association of the fungi with these plants was not reported. Miller & Miller (1988) provide the only exception, reporting the genus decomposing roots of *Atriplex*, *Artemisia*, and *Purshia* in Idaho, U.S.A. The possibility of a mycorrhizal association between *Battarrea* and associated vegetation has never been examined, however, and was thus investigated in this study.

Battarrea species are reported to have a preference for xeric habitats (Cunningham, 1944; Pilat, 1970; Miller & Miller, 1988; Calonge, 1990). Large numbers of sporocarps (20–100) are known from single locations (Long, 1943; Guzman & Herrera, 1969), and repeated fruiting may occur at a site over many years (Maublanc & Melancon, 1930; Miller, unpublished data). Zak (1993) hypothesized that fungal activity in deserts is temporally and spatially limited by substrate and moisture availability. The unique physiographic characteristics of Namib Desert habitats provided an opportunity to explore the abiotic and biotic parameters affecting the widespread, yet patchy distribution of *Battarrea*.

The Namib Desert, defined as the region of southwestern Africa with mean annual rainfall less than 100 mm (Fig. 1), is one of driest deserts in the world. A pronounced rainfall gradient, ranging from near zero at the coast to approximately 100 mm some 150 km inland, allowed us to determine how rainfall affects the distribution of *Battarrea*, including the minimal rainfall required for sporocarp production and the effects of variable moisture inputs on fruiting phenology. Physiographic differences among habitat types within the Namib Desert also provided information regarding the habitat and substrate preferences of the fungus.

MATERIALS AND METHODS

Study sites

Searches for *Battarrea* during the first two years of the study were conducted in the three habitats which characterize the

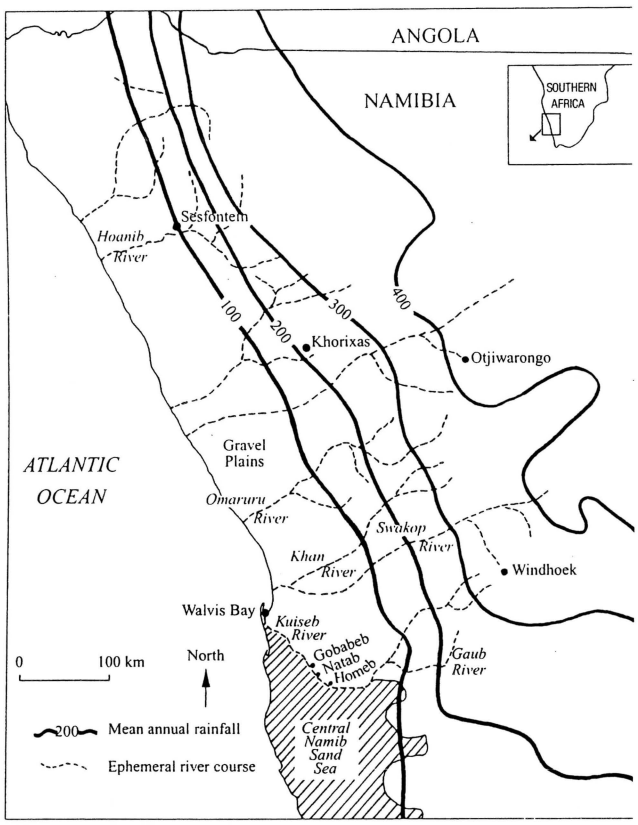


Fig. 1. The Namib Desert, the region of western Namibia where rainfall is less than 100 mm, is characterized by three main habitat types – gravel plains, sand seas and ephemeral rivers.

Central Namib Desert; the Kuiseb River, the sand sea south of the river, and the gravel plains north of the river (Figs 1, 2). The Central Namib Sand Sea consists of dunes and inter-dune valleys, composed of sandy substrates of varying depths. Vegetation communities are dominated by perennial and annual grasses adapted to the constraints imposed by abiotic factors, particularly moisture and stability (Yeaton, 1988; Seely, 1991; Jacobson, 1997). Plant cover along the eastern margin of the sand sea averages 3·5–4·5%, decreasing towards the coast in response to the marked decrease in rainfall (Boyer, 1989).

Similar trends characterize the vegetation communities of the gravel plains, although the limited infiltration and retention capacity of the compacted gravel substrate restricts perennial vegetation to rills and washes filled with coarse gravelly alluvium. The perennial vegetation of the washes is composed of patchy perennial grasses, woody shrubs, and trees. Following occasional rains, the gravel plains exhibit a cover of annual grasses.

Ephemeral rivers are perhaps the most dramatic of the three habitat types found in the Namib Desert (Fig. 2). The river channels are typically dry for more than eleven months of the year, flowing only for short periods in response to summer convective storms in their upper catchments. Twelve rivers cross the Namib Desert between the Central Namib Sand Sea in the south and the border with Angola, some 900 km to the north. Riparian forest communities along the river channels create linear oases spanning the width of the desert. These forests are entirely dependent on brief seasonal floods, characterized by significant inter-annual variability (Jacobson, Jacobson & Seely, 1995). For example, while the Kuiseb River flows an average of 18 d y^{-1} at Gobabeb (n = 33; 1963–5), in 1974 it flowed for 102 d, and did not flow at all from 1980–3. Woody tree species that dominate the riparian forests include *Faidherbia albida* (Del.) A. Chev., *Tamarix usneoides* E. Meyer ex Bunge, *Euclea pseudebenus* E. Meyer ex A. DC., and *Acacia erioloba* E. Meyer (Theron, van Rooyen & van Rooyen, 1980). Bank and floodplain soils are composed of interstratified layers of sands and organic-rich silts, regularly reworked by floods (Jacobson, P., 1997). Active river channels are characterized by gravel or cobble substrates in their upper reaches, grading to coarse to fine sands towards the coast.

From 1992–4 the study focused primarily on ephemeral river habitats, and was expanded to include other ephemeral rivers, the Swakop, Khan, Omaruru and Hoanib Rivers, as well as the main tributary of the Kuiseb River, the Gaub (Fig. 1). Five locations in the Kuiseb River provided the majority of specimens used for descriptions of sporocarp morphology and development:

(1) *Gobabeb* (23° 33′ 50″ S, 15° 02′ 30″ E): a silty floodplain terrace below the Desert Research Foundation of Namibia (DRFN) Research Station, with 5–10 cm diam. breast height (dbh) *T. usneoides* and *F. albida*.
(2) *0·5 km east of Natab* (23° 35′ 48″ S, 15° 05′ 24″ E): a silty bank with 80–100 cm dbh *F. albida* trees.
(3) *5 km east of Homeb* (23° 38′ 24″ S, 15° 13′ 00″ E): a silty floodplain terrace with 5–10 cm dbh *T. usneoides* and 30–80 cm dbh *F. albida*.
(4) *10 km east of Homeb* (23° 38′ 48″ S, 15° 15′ 21″ E): a silty floodplain terrace with 10–20 cm dbh *T. usneoides* and 10–30 cm dbh *F. albida*.
(5) *2 km east of Gobabeb* (23° 34′ 00″ S, 15° 03′ 42″ E): a silty floodplain terrace with 10–20 cm dbh *T. usneoides* and 30–80 cm dbh *F. albida*.

Data collection

During 1990–1, rainfall was monitored with a network of gauges distributed throughout the study area. Collecting was conducted in all three habitats at weekly intervals over a two month period following a single widespread rain event that occurred in April 1991. Searches were conducted within a square kilometre surrounding each gauge. Temporal and spatial fruiting patterns within the lower Kuiseb River were monitored in response to seasonal floods from 1990–4. Hydrological records from the Namibian Department of Water Affairs were used to quantify the discharge and volume of recorded floods.

Data obtained from *Battarrea* populations included the total number of sporocarps, the approximate area covered by the population, associated vegetation, and soil composition. Excavations of specimens were conducted to depths up to 1 m to assess the nutritional relationships of the fungus. The presence or absence of mycelium in association with sporocarps and roots was visually assessed, and soils were collected to confirm identity of the mycelium microscopically.

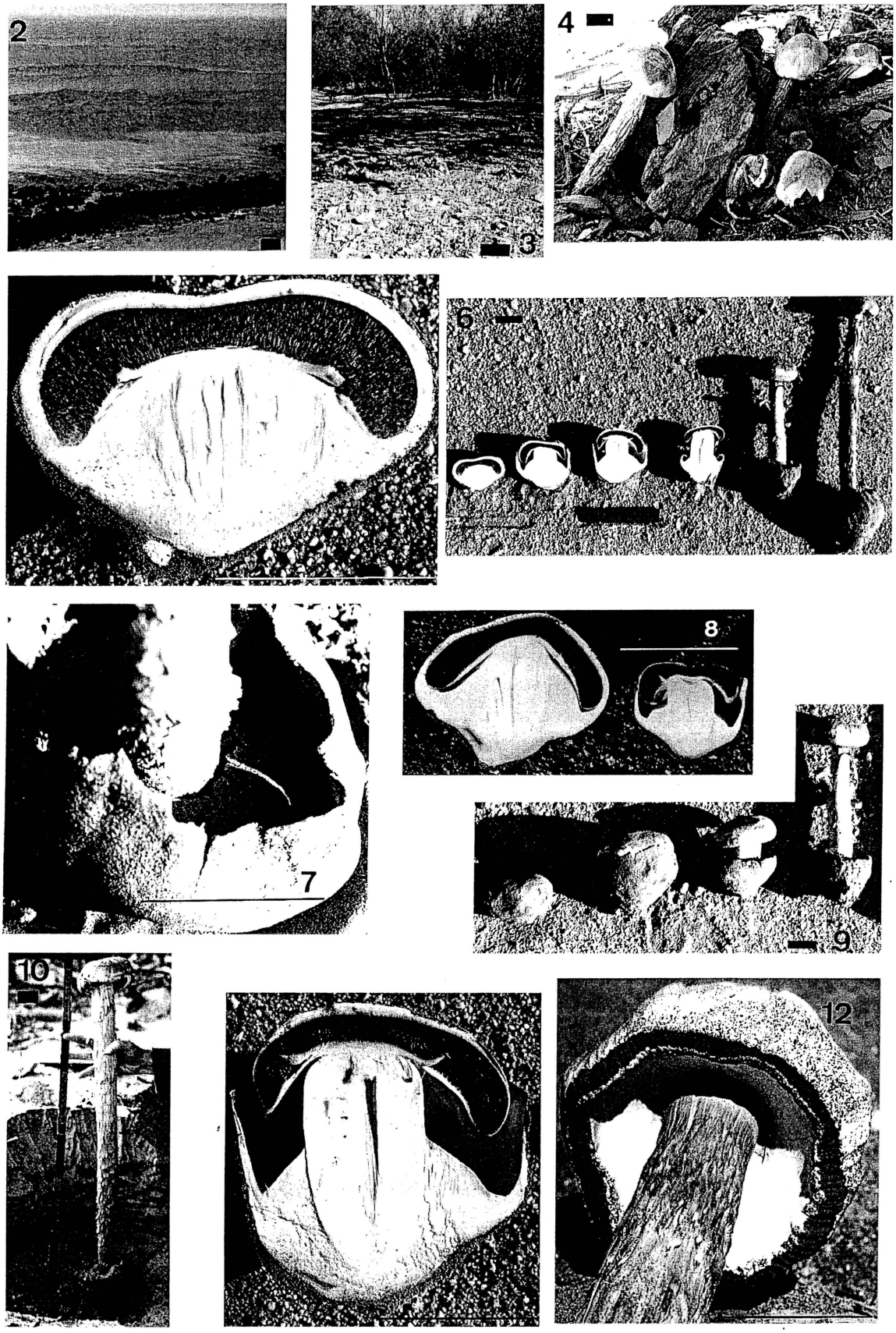


Fig. 2. The Kuiseb River in the Central Namib Desert separates the gravel plains to the north from the sand sea to the south. Bar = 50 m. **Fig. 3.** The riparian forest on the Kuiseb River floodplain, showing *Battarrea* habitat. Bar = 1 m. **Figs 4–12.** *Battarrea stevenii* from the Kuiseb River, Namibia. Bars = 50 mm.

Mycorrhizal associations of *Battarrea* with putative hosts *F. albida* and *T. usneoides* were examined in 1990. Roots were washed free of adhering soil and the external surfaces observed for mycorrhizal colonization at 60 × magnification. Thereafter, roots were cleared and stained with trypan blue (Koske & Gemma, 1989) to assess internal colonization.

Depending on their maturity at the time of observation, 5–20 representative sporocarps from each population were carefully excavated for in-field measurements that included sporocarp dimensions, depth of stipe burial, depth of visibly moist soil relative to the sporocarp base, soil moisture content at the sporocarp base, soil organic content, and soil temperatures to a depth of 50 cm.

Sporocarps in various stages of development were found by excavating the upper 40 cm of soil within a 1 m radius of sporocarps breaking through surface silts. Developing sporocarps were cut in half to reveal developmental stages for photography. Fresh material was stored at 15 °C for travel. In the laboratory a full macro- and microscopic description was completed on all collections within 4 h of collecting. The Methuen Handbook of Colour (Kornerup & Wanscher, 1984) was used as the standard reference for describing tissue and gleba colours. Reagents used for the microscopic examination of peridial tissues and gleba were lactophenol cotton blue, Melzer's reagent, 10% KOH, and Congo Red. Segments of immature gleba were cut from fresh sporocarps and fixed in 70% ethanol for further detailed examination of fascicles and basidia. All remaining fresh material was dried in a ventilated oven at 60°.

RESULTS

Taxonomy

Battarrea stevenii (Libosch.) Fr., *Systema Mycologicum* **3**: 7, 1829. (Figs 3–19)

Sporocarps 16–48 (−70) cm long, 4–11 cm broad at the apex, with creamy-white endoperidium enclosing a rusty-brown, powdery gleba, that splits by circumsessile dehiscence into upper and lower endoperidia (Fig. 12). The upper endoperidium may be lost, exposing the gleba borne on the thickened lower endoperidium, which is centrally and firmly attached to the stipe. The woody, hollow *stipe* is generally equal to slightly tapering at the apex, 15–45 (−67) cm long, 1–4 cm broad. Outer stipe texture is smooth or flaking, with small to large, flat, bark-like elements (Figs 4, 6, 9, 10, 12), wax yellow to yellowish-brown, often exfoliating in age. Stipe base (Figs 7, 10) is enclosed by an *outer volva*, 3–10 cm long, 4–12 cm broad, composed of sand-encrusted exoperidium, and a white inner volva (Fig. 7). Exoperidial remains may also be visible on the upper endoperidium, as a thin, sand-encrusted tissue layer. All inner tissues other than gleba are uniformly white to yellowish-white and do not stain when cut or exposed to air.

The *lower endoperidium* is composed of densely interwoven, frequently branching, acyanophilic binding hyphae (5–7·5 µm broad, walls < 1 µm) with clamp connections. The *upper endoperidium* is composed of similar hyphae but with less branching, resulting in a more friable texture. *Gleba* is arranged in loosely connected fascicles with a longitudinal arrangement (Fig. 5). *Fascicles*, 523–1235 µm long, 360–475 µm broad and 350–450 µm thick, are composed of thin layer of loosely interwoven, thin-walled *paracapillitium* (Fig. 13) which also loosely connects adjacent fascicles. The acyanophilic, clamped paracapillitial hyphae, 3–5 (−7) µm wide, do not stain in 3% KOH or Melzer's reagent and are best observed with Congo Red. *Elaters* (Fig. 13) are 3·5–6 µm wide and 45–125 µm long (mean: 5·3 × 81·4 µm, $n = 36$), with walls up to 1 µm thick, and an irregular spiral thickening along the length. Elaters do not stain with any of the reagents used. *Plectobasidia*, 19–30 µm long, 5–8 µm wide at the apex, 1–3 µm wide at the neck, are not present in mature gleba (see description of developing sporocarps below). *Spores*, 5–7 × 6–8 µm, are round to globose, with a short, broad pedicel, verrucose or warty ornamentation (Fig. 13), and do not stain with any of the reagents used.

Material examined: Namibia: Erongo Region, Kuiseb River; 23° 33′ 50″ S, 15° 02′ 30″ E, 11 Sep. 1990, Jacobson, KJ90091101 (VPI); 23° 35′ 80″ S, 15° 05′ 40″ E, 24 Jan. 1993, Jacobson, KJ93012401 (VPI); 8 May 1993, Jacobson & Miller, OKM 25975 (VPI); 23° 38′ 40″ S, 15° 13′ 00″ E, 19 May 1994, Jacobson, KJ94051901 (VPI); 23° 38′ 80″ S, 15° 15′ 35″ E, 30 May 1994, Jacobson, KJ94053001 (VPI); 23° 34′ 00″ S, 15° 03′ 70″ E, 30 May 1994, Jacobson, KJ94053003 (VPI).

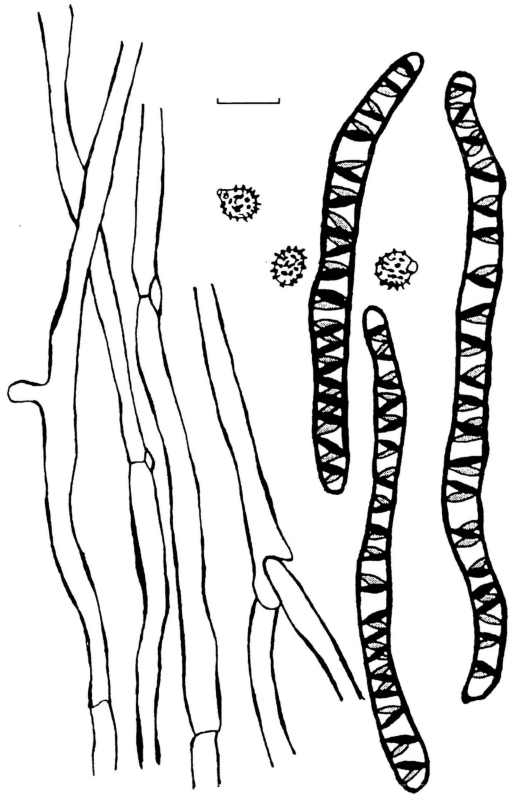
Spatial and temporal distribution in the Namib Desert

Throughout the Namib Desert *B. stevenii* was restricted to ephemeral rivers, and was never found in adjacent upland sand seas or gravel plains. *B. stevenii* was found at least once in silty banks (Fig. 3) of all large ephemeral rivers and tributaries examined during the 4 yr study (Kuiseb, Gaub, Khan, Omaruru, and Hoanib Rivers). During this period more than 400 sporocarps, comprising 35 observations of 3–76 specimens per population, were observed. (We assume herein that all specimens from a single location are from a single population). Fruiting was only observed following seasons of overbank flooding, and not with rainfall events ranging from 4–46 mm. Fruiting occurred 4·5–12 months post-flooding, but the start date and duration of fruiting was not correlated with flood volume or peak discharge (Table 1). Rather, the size of the floods determined where fruiting occurred in relation to the active channel. Large floods resulted in sporocarp production on the banks and floodplain. Small floods, which did not moisten the floodplain, produced fruiting only along the river banks.

Habitat preferences

B. stevenii showed no preference for full sun versus shade. It was only found in soils with a high silt fraction (> 15%) (Jacobson, P., 1997), and never occurred in pure sand or gravel substrates. Fruiting depth ranged from 20–35 cm below surface, where soils were warm (26·5–28·5°) and exhibited minimal daily fluctuation, despite daytime air temperatures ranging from 30–44°. Fresh sporocarps consistently formed at the visibly discernible dry-moist soil interface. The gravimetric moisture content of visibly moist soil was 4·3–7·0% versus < 2·5% for visibly dry soil.

B. stevenii was found exclusively on silty floodplain terraces (Fig. 3) and river banks inundated by flood waters during the



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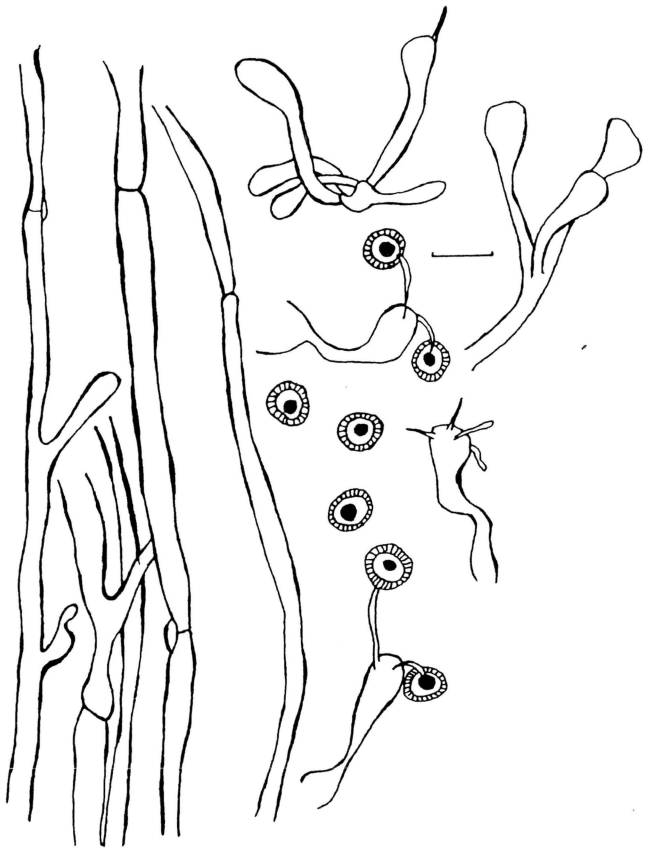

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Fig. 13. Elements of the mature gleba. **Fig. 14.** Elements of the immature gleba. Bars = 10 μm.

Table 1. Fruiting of *B. stevenii* in the Kuiseb River (1990–4) in relation to river flow (as recorded at the Gobabeb Weir)

Flow duration	Flood volume (m^3)	Peak discharge (m^3 sec^{-1})	First fruiting date	Period post-flooding (months)	Location
7–9 Feb. 1990	$3{\cdot}36 \times 10^6$	40	11 Sep. 1990	7	Mid floodplain
24–25 Jan. 1991	$0{\cdot}55 \times 10^6$	10	No collections	—	—
5–6 Jan. 1992	$0{\cdot}18 \times 10^6$	9	24 Jan. 1993	12	Channel edge
24–25 Feb. 1993	$4{\cdot}60 \times 10^6$	57	21 Nov. 1993	9	Mid floodplain
9–13 Jan. 1994	$2{\cdot}30 \times 10^6$	51	20 May	4·5	High floodplain
9–13 Jan. 1994	$2{\cdot}30 \times 10^6$	51	2 Dec.	11	Mid floodplain

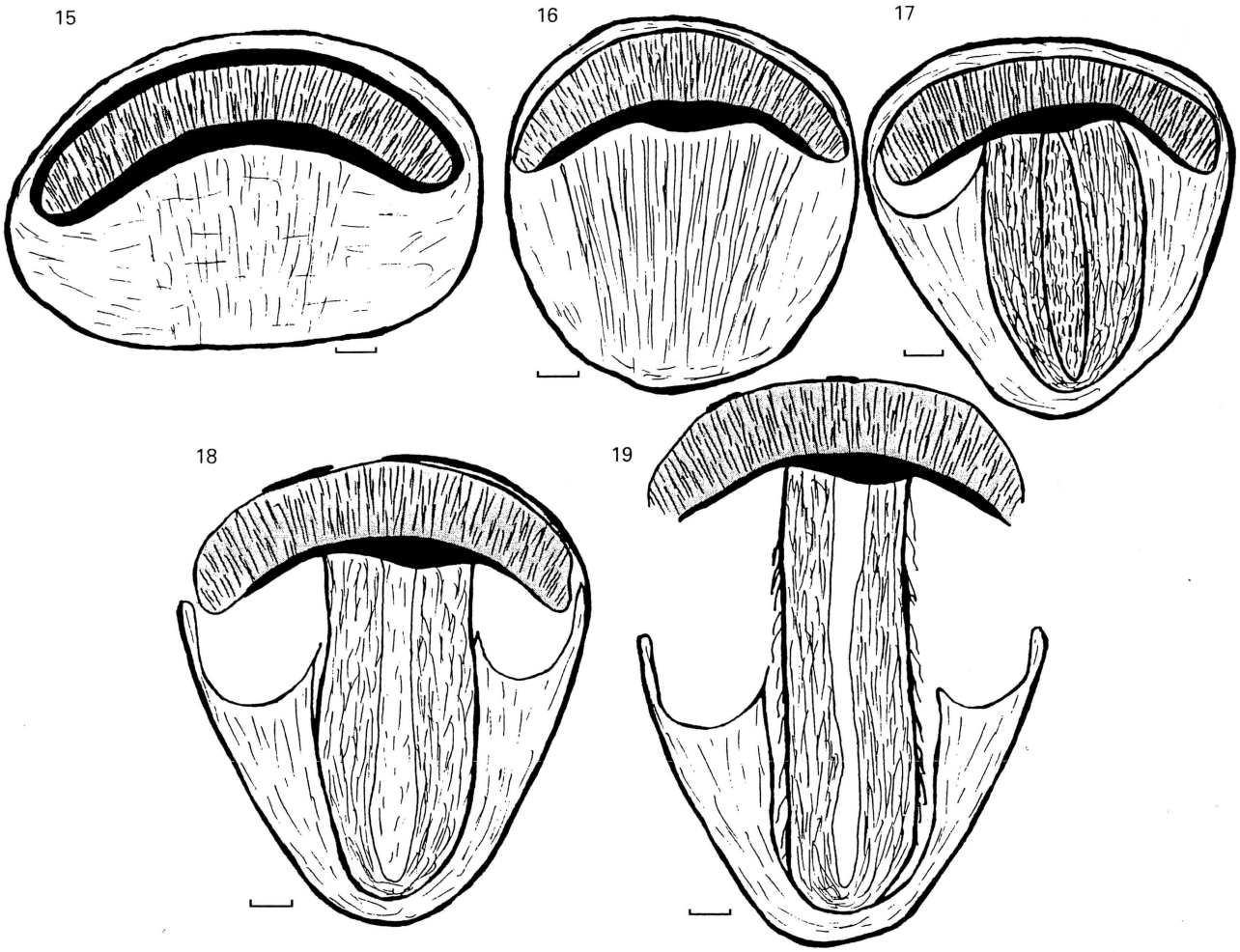
previous flood season, and was not associated with any particular component of the vegetation community. Soils were often covered by a thick layer of silt, deposited during flood recession. This 3–10 cm thick silt capping (Fig. 4) is impermeable to moisture loss, but is readily permeable to oxygen (D. Mitchell, unpublished data), maintaining a moist, aerobic environment suitable for subsurface fungal activity for extended periods after surface substrates have dried (up to 45 d at 10 cm, and 12 mo at 35 cm).

Nutritional mode

Roots of *T. usneoides*, *F. albida* and *A. erioloba* growing in association with *B. stevenii* sporocarps exhibited no mycorrhizal colonisation. In addition, buried woody substrates were never found in association with sporocarps. Rather, all fresh sporocarps observed during this study were associated with a white mycelium, with clamp connections, which permeated moist soils for distances up to 1 m from sporocarps. Based on these observations, we conclude that *B. stevenii* is not involved in mycorrhizal or parasitic relationships with woody vegetation along the Kuiseb River, nor is the fungus deriving its nutrition from buried wood. Rather, soil organic material, comprising 3·6–7·0% of soil DW, appears to be the principal nutritional source. The high organic matter content of these soils is derived from receding floods as particulate organic matter and organic-rich silts deposited on floodplain surfaces. Subsequent fluvial or aeolian sedimentation incorporates these layers into the soil profile. Floods thus provide not only the moisture, but also the organic substrates used by *B. stevenii*.

Sporocarp development

Sporocarp development occurs entirely below-ground. The following description is based on four collections which exhibited various stages of development (KJ90091101 (VPI),



Figs 15–19. Development of *B. stevenii* sporocarps. Bars = 10 mm.

74 sporocarps; KJ93012401 (VPI), 20 sporocarps; KJ94051901 (VPI), 26 sporocarps; and KJ94053001 (VPI), 45 sporocarps). Sporocarps with expanding stipes were found growing from depths of 20–35 cm. Their presence was revealed by cracks in the surface silt crust.

The earliest developmental stages observed were round to flattened-oblong, becoming longitudinally oval or egg-shaped (Figs 6, 9). At this stage the entire sporocarp is covered by a sand-encrusted exoperidium which eventually splits, approximately 4–7 cm from the base, such that a base, stipe, and head are discernible (Figs 8, 11). The base, which is enclosed by the volva, remains at the level of initial sporocarp development, 15–35 cm below the soil surface (Fig. 10). The stipe continues to elongate (Figs 6, 9), pushing the head containing the mature gleba, through the surface silts, to 15–30 cm above the soil surface. As the stipe elongates it becomes narrower (Fig. 6), as a result of expansion and drying upon exposure to the desert air.

Cross-sections of buttons at various stages of development are shown in Figs 15–19. In the earliest stage observed (Fig. 15), the light-yellow gleba is already fully-formed, and enclosed within a well-differentiated continuous endoperidium. The upper endoperidium is of uniform thickness but the lower endoperidium is thickened at the centre (up to 7 mm) and tapers towards the lateral edges (approximately 2 mm). The entire endoperidium has a tough texture and is discrete from the adjacent gleba and mesoperidium. The lower endoperidium has a rubbery texture and is slightly darker in colour than the white upper endoperidium. The upper and lower endoperidia, in turn, are completely enclosed within white mesoperidium, which even in the youngest material examined shows evidence of the developing stipe. The exoperidium, with outer surface silt-encrusted, surrounds the entire mesoperidium.

Despite the large number of sporocarps observed, only two were sufficiently immature to yield basidia. Light-yellow gleba, organised in fascicles, contains thin-walled plectobasidia, paracapillitium, and spores (Fig. 14). Plectobasidia are enlarged terminal cells arising singly or multiply from a central plexus or simple hypha without clamps, borne on paracapillitium that extends throughout the fascicle. Plectobasidia do not stain in 3% KOH, Melzer's reagent, or lactophenol cotton blue, and were best observed in Congo Red. Cyanophilic spores borne on 2–4 sterigmata (4–12 µm long), arise from anywhere on the basidium apex. These immature spores appear smooth at 1000 × magnification, with outward radiating wall laminations.

As the stipe differentiates from the mesoperidium, the sporocarp develops a more longitudinally elongate shape (Fig. 16). The mesoperidium above the gleba becomes progressively thinner and indistinguishable between the upper endoperidium

and exoperidium, as the endoperidium pushes against it. As the spores mature, they lose the cyanophilic staining reaction and develop brown ornamented cell walls, causing the gleba colour to change from light yellow to greyish-yellow to brownish-orange to the mature gleba colour, rust brown, by the time the stipe has developed fully, but not yet expanded lengthways (Fig. 17). Stipe tissue that has differentiated from the mesoperidium can be distinguished from the remaining mesoperidium by colour (brilliant white as opposed to drab white), and by the orientation of the hyphal tissue (longitudinal versus homogeneous, e.g. Figs 16, 17). Basidia degenerate very rapidly and were not observed in greyish yellow gleba. Elaters do not appear until the gleba is brownish orange. Glebal development is homogeneous. When the stipe begins to elongate (Fig. 17), the gleba is mature and is composed of spores, elators, and paracapillitium.

The elongating stipe is composed of longitudinally arranged hyphae surrounding a core of more loosely woven hyphae that may remain as a stuffed inner stipe for some time or rapidly become hollow (Fig. 18). In mature specimens, however, with stipe fully extended, the stipe is hollow. As the stipe lengthens and narrows, it separates entirely from the mesoperidium (Figs 17, 18), which forms a collar-like inner volva around the base of the stipe, within the sand-encrusted exoperidium or external volva (Figs 8, 11, 18, 19). The form of the inner volva is highly variable in mature specimens. It may be a well-formed collar as illustrated here, or simply a thin layer of ragged tissue through which the stipe has extended. Our observations suggest that the different forms of the inner volva are a function of the proportion of mesoperidium which is committed to stipe tissue, and that this can vary substantially depending on the depths at which the sporocarp develops and subsequently extends to reach the soil surface.

As the stipe continues to expand (outer stipe tissue is white to yellowish-white, concolorous with inner tissue of the base and head), the exoperidium splits irregularly around the endoperidium (Fig. 18), revealing the creamy-white upper endoperidium. In sporocarps where the mesoperidium is still thick and well-developed after stipe extension, it may remain soft and fleshy for as long as a week after the sporocarp has pushed through the surface silts. Cultures have been made from the mesoperidium when upper stipe material was completely dry (e.g. the specimen illustrated in Fig. 10). Insects (termites, tenebrionid beetles, and larvae) are frequently seen eating this material, and yeasts often cause the entire base to rot. It is thus common to find specimens which have no base or only various remnants thereof. Approximately 50 *Gonocephalum* sp. beetles were observed at the base of sporocarps (Fig. 4) in Jan. 1993.

The endoperidium breaks in a ragged to highly uniform manner (circumsessile dehiscence), but always around the lower perimeter of the gleba at an obvious juncture between the thicker lower and thinner upper endoperidial layers (Figs 12, 19). Circumsessile dehiscence may happen as early as when the sporocarp is pushing through the surface silts. The expanding stipe, which initially may be quite smooth (Fig. 9), becomes increasingly lacerate with flakes of stipe tissue drying on the outer layers and therefore no longer expanding with the inner tissue. Alternatively, the entire stipe tissue may expand quite uniformly resulting in a relatively smooth stipe.

DISCUSSION

Taxonomic and nomenclatorial issues relevant to Namib Desert Battarrea

While 15 species of *Battarrea* have been recognized from various regions of the world (Maublanc & Melancon, 1930; Cunningham, 1944), there is now general agreement that no more than two species are known (Cunningham, 1944; Rea, 1942; Pilat, 1970); *Battarrea phalloides* (Dicks.) Pers. described in 1801, and *B. stevenii* described in 1829. Nonetheless, whether these two species are in fact true taxonomic or biological species remains unresolved. According to Pilat (1970), the principle characters which distinguish the two species are the presence of a gelatinous volva and sporocarp size. While Martin & Llimona (1994) have observed both species in Spain, other taxonomists question the nature of the gelatinous volva, suggesting there is only one highly variable species with a world-wide distribution (Calonge, 1990; Reijnders, pers. comm.).

Based upon our descriptions of developing and mature sporocarps, all specimens from the Namib Desert have been identified as *B. stevenii*. The lack of any gelatinous component to the volva was of primary importance in making this decision because of the variation in sporocarp size. While most sporocarps were large, hence fitting the description of *B. stevenii*, a number of smaller sporocarps were well within the range of *B. phalloides*. In emphasising the importance of the gelatinous volva as a distinguishing character, we follow a convention established by Rea (1942), Guzman & Herrera (1969), Dring & Rayner (1967), and Calonge (1990). Having noted the size variation in their collections, these authors relied on the absence of the gelatinous volva as the distinguishing feature for identifying their material as *B. stevenii*.

We believe that effective resolution of the *Battarrea* species problem will only be achieved by using independent character sets (i.e. molecular markers, mating studies) that may provide insights into the taxonomic relevance of characters such as the gelatinous volva and size variation. The Namibian collections provide the most complete series of developmental stages of any *Battarrea* material collected to date, and provide an important basis for such studies. The following additional attributes of the mature and developing sporocarps are thus particularly noteworthy in relation to previous descriptions of *Battarrea* species:

1. The lower endoperidium is firmly attached to the stipe, even in material that has been exposed for two years. This is contrary to descriptions of North American material, in which the lower endoperidium frequently becomes detached with age (Rea, 1942; Long, 1943).

2. Elater size of the Namib material is a consistent character of all sporocarps examined and is generally greater than that reported for *B. stevenii* or *B. phalloides*. Based on North American material, Rea (1942) suggested that elater size could be used as generic character, with *Battarreoides* having elaters in excess of 100 µm, versus *Battarrea* with elaters less than

80 µm long. Our observations suggest that this is not a reliable generic character and support observations of Bottomley (1948) of large elater size from South African *Battarrea* material.

3. Maublanc & Melancon (1930) first described the fascicular organization of the gleba that we observed. In contrast, however, to their reports of an organized hymenium within the fascicles, we observed plectobasidia borne throughout the fascicles, lacking any organized hymenium.

4. We hypothesize that the previously undescribed cyanophilic reaction of immature spores is due to the presence of perisporium that is shed as the spores mature, revealing the ornamented, acyanophilic exosporium illustrated by Coetzee & Eicker (1994).

5. The elaters arise from the paracapillitium in the Namibian material, and are not degenerate spores, as reported by Maublanc & Melancon (1930).

6. Development of the Namibian sporocarps clearly showed that the volva is composed of two distinct tissue layers: the exo- and mesoperidium. While the mesoperidium has been illustrated or noted by other authors (Maublanc & Melancon, 1930; Cunningham, 1944; Miller & Miller, 1988), it has not been identified as a distinctive tissue. Our studies show that the mesoperidium is the tissue which gives rise to the stipe and as such, varies substantially in thickness, depending on the proportion of tissue committed to the expanding stipe.

The autecology of Battarrea stevenii *in the Namib Desert*

Within the Namib Desert, *B. stevenii* is known only from the banks and floodplains of ephemeral rivers. We attribute this limited distribution to the low rainfall (< 100 mm) that characterises the region. *B. stevenii* is known from semi-arid regions of Namibia where annual rainfall is greater than 200 mm (W. du Plessis & C. Hines, pers. comm.), where its distribution is not limited to riparian habitats. Similarly, *Battarrea* have been collected in semi-arid and temperate grasslands and savannah in Congo, Kenya, Mozambique, South Africa, and Tunisia (Berkeley, 1843; Maublanc & Melancon, 1930; Bottomley, 1948; Dring, 1964; Dring & Rayner, 1967). It thus appears that annual flooding creates an environment conducive to *B. stevenii*, in a xeric habitat which would otherwise be unsuitable. As with a number of other organisms (Seely & Griffin, 1986), ephemeral rivers are habitats which create a substantial range extension for *B. stevenii* well into one of the driest deserts of the world.

An essential component of the hydrologic regime that supports *B. stevenii* is the deep penetration of soil moisture in the silty soils of the banks and floodplains. Vegetative growth and sporocarp development occur at depths of 15–30 cm, requiring moist soils for periods of at least 4·5 mo prior to sporocarp production. Rainfall is insufficient in the Namib Desert to create such conditions, and hence the fungus is only found within the inundation zone of the previous season's flood, 4·5–12 mo post-flooding.

The fact that fresh sporocarps were always collected from the wet/dry soil interface suggests that sporocarp production occurs in response to declining soil moisture. This hypothesis is supported by detailed observations of macro-fungal fruiting in the Namib Sand Sea (Jacobson, 1996; Jacobson & Jacobson, 1998). Here, smaller macro-fungi fruit within 3–70 d after rains ranging from 8–62 mm. All species are stipitate, and decompose buried material at depths related to sporocarp size. Small species, such as *Montagnea arenaria* and *Schizostoma laceratum*, fruit early in association with lignocellulose substrates at depths not exceeding 10 cm. In contrast, larger species, such as *Podaxis pistillaris* and *Gyrophragmium delilei*, fruit later from substrates buried at 12–20 cm by aeolian deposition. Fruiting phenology in the dunes correlates well with soil desiccation patterns that vary as a function of rainfall amount. As in the riparian habitats, fresh sporocarps are always found at the moist/dry soil interface, suggesting that fruiting occurs in response to soil desiccation.

Floods not only provide moisture, triggering fungal decomposition, but also create the organic-rich soils (Abrams *et al.*, 1997; Jacobson, P., 1997) that support the tremendous production of sporocarps observed in the Kuiseb River. The abundance and size of the *B. stevenii* sporocarps, and the associated abundance of mycelium in the surrounding soils, suggests that these fungi are an important component of the subterranean decomposer community in the silty, organic-rich soils of Namib ephemeral rivers. The moist, aerobic soil environment maintained within the alluvial sediments is conducive to periods of decomposition which greatly exceed those achieved by rainfall.

B. stevenii possesses a unique set of characters which allow effective use of resources in floodplain soils created by hydrologic disturbance. The massive size of the sporocarps permits use of rich organic soils at depths where soil moisture persists for significant periods post-flooding. Spore production is completed long before the woody stipe extends, forcibly breaking through the thick silt crust and exposing the gleba to the desiccating surface environment. The thick-walled, darkly pigmented spores are wind-dispersed during the dry season when surface materials are being eroded and buried by aeolian disturbance. In subsequent floods, these materials may be buried in-situ or mobilised and transported downstream to be redeposited elsewhere within the dynamic soils of the bank or floodplain. *Battarrea* decomposes woody substrates in other habitats, and is also known to produce laccase which is involved in lignin decomposition (Miller, unpublished data). We thus suspect that the lack of association of this fungus with buried wood in the Namib simply reflects its ability to make effective use of the fine particulate organic material readily available in the moist soils, rather than an inability to decompose woody substrates.

In addition to our observations demonstrating that *B. stevenii* is an important component of the subsurface decomposer community in Namib ephemeral rivers, there are at least three other reports of *Battarrea* from riparian habitats subject to periodic flood disturbance. *B. stevenii* was originally collected by Liboschitz from the Volga River (White, 1901), and States (1990) reports extensive fruiting of *Battarrea* in *Tamarix* thickets of the Rio Grande and Colorado Rivers of North American deserts. In addition, Welwitsch found *Battarrea* along the Caroca River, in southern Angola in

September 1859, 'in sandy thickets, composed chiefly of *Tamarix*, on the banks of the river... about 12 miles [19 km] from the sea' (Welwitsch & Currey, 1870). Based on the world-wide distribution of the fungus, and its documented presence in other riparian habitats, we predict that further biogeographical studies will reveal that *Battarrea* is a common component of the decomposer community in dryland river systems which drain approximately one-third of the earth's surface.

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REFERENCES

Abrams, M. M., Jacobson, P. J., Jacobson, K. M. & Seely, M. K. (1997). Survey of soil chemical properties across a landscape in the Namib Desert. *Journal of Arid Environments* **35**, 29–38.

Berkeley, M. J. (1843). Enumeration of fungi collected by Herr Zeyher in Uitenhage. *The London Journal of Botany* **2**, 507–527.

Bottomley, A. M. (1948). Gasteromycetes of South Africa. *Bothalia* **4**, 473–810.

Boyer, D. C. (1989). Some characteristics of the plant communities of three dunes situated across a climatic gradient in the Namib Desert. *Madoqua* **16**, 141–148.

Calonge, F. D. (1990). Check-list of the Spanish Gasteromycetes (Fungi, Basidiomycotina). *Cryptogamic Botany* **2**, 33–55.

Coetzee, J. C. & Eicker, A. (1994). *Battarreoides diguetii* (Gasteromycetes, Tulostomatales) in southern Africa. *Mycotaxon* **50**, 19–25.

Cunningham, G. H. (1944). *Gasteromycetes of Australia and New Zealand*. Dunedin, New Zealand.

Dring, D. M. (1964). Gasteromycetes of west tropical Africa. *Mycological Papers* **98**, 1–60.

Dring, D. M. & Rayner, R. W. (1967). Some gasteromycetes from Eastern Africa. *Journal of the East African and Uganda Natural History Society* **24**, 5–46.

Guzman, G. & Herrera, T. (1969). Macromicetos de las zonas aridas de Mexico, II Gasteromicetos. *Anales del Instituto de Biologia Universidad Nacional Autonoma de Mexico Ser Botanica* **40**, 1–92.

Jacobson, K. M. (1997). Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. *Journal of Arid Environments* **35**, 59–76.

Jacobson, K. M. (1996). Macrofungal ecology in the Namib Desert: a fruitful or futile study? *McIlvainea* **12**, 21–32.

Jacobson, K. M. & Jacobson, P. J. (1998). Rainfall regulates decomposition of buried cellulose in the Namib Desert. *Journal of Arid Environments* **38** (in the press).

Jacobson, P. J. (1997). *An Ephemeral Perspective of Riverine Ecosystems: Viewing Ephemeral Rivers in the Context of Current Lotic Ecology*. Ph.D. Dissertation, Virginia Polytechnic Institute and State University: Blacksburg, Virginia.

Jacobson, P. J., Jacobson, K. M. & Seely, M. K. (1995). *Ephemeral Rivers and their Catchments: Sustaining People and Development in Western Namibia*. Desert Research Foundation of Namibia and Department of Water Affairs: Windhoek, Namibia.

Kornerup, A. & Wanscher, J. H. 1984. *Methuen Handbook of Colour*. Westinghouse: New York.

Koske, R. & Gemma, J. (1989). A modified procedure for staining roots to detect VA mycorrhizas. *Mycological Research* **92**, 486–488.

Long, W. H. (1943). Studies in the Gasteromycetes VIII. *Battarrea laciniata*. *Mycologia* **35**, 546–556.

Martin, M. P. & Llimona, X. (1994). Gasteromycetes checklist of the northeastern Iberian Peninsula and Balearic Islands. *Mycotaxon* **51**, 289–312.

Maublanc, M. A. & Melancon, G. (1930). Recherches sur le *Battarraea guicciardiniana* Ces. *Bulletin Trimestriel de la Societe Mycologique de France* **46**, 43–73.

Miller, O. K. Jr (1969). Notes on gasteromycetes of the Yukon Territory and adjacent Alaska. *Canadian Journal of Botany* **47**, 247–250.

Miller, O. K. Jr & Miller, H. H. (1988). *Gasteromycetes: Morphological and Development Features with Keys to the Orders, Families and Genera*. Mad River Press: Eureka, California.

Moreno, G., Honrubia, M., Calonge, F. D. & Wright, J. E. (1984). Apartacion al conocimiento de los Hongos del S.E. de Espana. V. Tulostomatales (Gasteromycetes). *Boletín Sociedad Micólogica Micol. Castellana* **8**, 93–106.

Pilat, A. (1970). Uber *Battarrea stevenii* (Lib.) Fr. *Zeitschrift für Pilzkunde* **36**, 2.

Rea, P. M. (1942). Fungi of southern California. I. *Mycologia* **34**, 563–574.

Seely, M. K. (1991). Sand dune communities. In *The Ecology of Desert Communities* (ed. G. A. Polis), pp. 348–383. University of Arizona Press: Tucson, Arizona.

Seely, M. K. & Griffin, M. (1986). Animals of the Namib Desert: interactions with the physical environment. *African Journal of Zoology* **100**, 47–63.

States, J. S. (1990). *Mushrooms and Truffles of the Southwest*. University of Arizona Press: Tucson, Arizona.

Theron, G. K., van Rooyen, N. & van Rooyen, M. W. (1980). Vegetation of the lower Kuiseb River. *Madoqua* **11**, 327–345.

Trueblood, E. (1975). Notes on fungi of the Owyhee Region. *Nova Hedwigia* **6**, 311–318.

Welwitsch, F. & Currey, F. (1870). Fungi Angolenses. – A description of the fungi collected by Dr F. Welwitsch in Angola during the years 1850–1860. *Transactions of the Linnean Society of London* **26**, 279–294.

White, V. S. (1901). The Tylostomataceae. *Bulletin of the Torrey Botanical Club* **28**, 421–445.

Yeaton, R. I. (1988). Structure and function of the Namib dune grasslands: characteristics of the environmental gradients and species distributions. *Journal of Ecology* **76**, 744–758.

Zak, J. C. (1993). The enigma of desert ecosystems: the importance of interactions among the soil biota to fungal biodiversity. In *Aspects of Tropical Ecology* (ed. S. Isaac, J. C. Frankland, R. Watling & A. J. S. Whalley), pp. 59–72. Cambridge University Press: Cambridge, UK.

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Two types of basidia in *Urocystis hypoxis* and the implications for smut taxonomy

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Germinating spore-balls of *Urocystis hypoxis* produce both unicellular basidia, crowned with 4—6 basidiospores, and what appear to be transversely septate, 3-celled, prostrate basidia with conjugation, through a conjugation tube, between top and bottom cells. This most unusual situation is discussed in relation to the taxonomy of smut fungi.

After 15 years studying teliospore germination in both ustilaginaceous and tilletiaceous smuts, it seemed time to end this line of work recently summarized (Ingold, 1997, 1998). Casual examination of *Urocystis hypoxis* Thaxt., however, revealed such an unusual situation during the germination of its spore-balls that a more thorough study was clearly desirable.

MATERIALS AND METHODS

The sample of *U. hypoxis* on *Hypoxis acuminata* Baker used was collected by Dr K. Vánky at Golden Gate Highlands National Park, Orange Free State Province, South Africa, in December 1996 and is HUV 18403 in his herbarium.

To induce germination, spore-balls were scattered on 0·2% malt agar in Petri dishes kept at 20 °C. All drawings were made from living materials with the aid of a *camera lucida*.

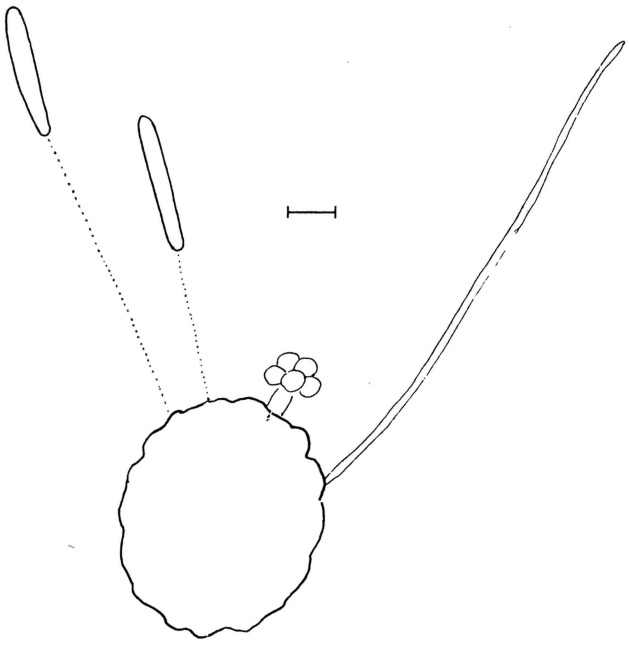

Fig. 1. *Urocystis hypoxis*. Products of germination from a spore-ball (in outline) showing: a basidium with basidiospores; a narrow hypha that is still elongating; and two spore-like bodies formed from surface hyphae, the dotted line indicating the probable course of the autolysed regions of the hyphae. Hyphal contents not shown. Bar = 10 μm.

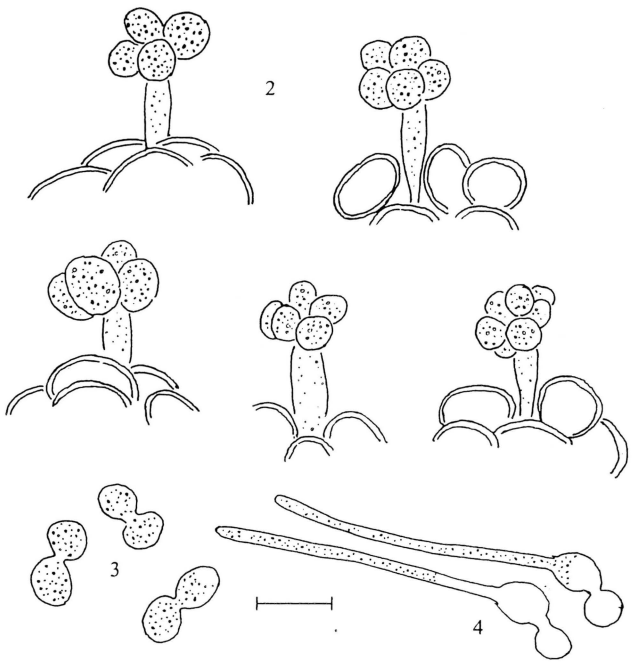

Fig. 2–4. *Urocystis hypoxis*. **Fig. 2.** Five basidia together with portions of the spore-ball. **Fig. 3.** Conjugating basidiospores. **Fig. 4.** Two pairs of conjugated basidiospores with a hypha arisen from one member of each pair. Bar = 10 μm.