Aliso: A Journal of Systematic and Evolutionary Botany

Volume 12 | Issue 2 Article 9

1989

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ALISO
12(2), 1989, pp. 317–326

TAXONOMY AND NATURAL HISTORY OF *HYDNORA* (HYDNORACEAE)

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ABSTRACT

Hydnora is a genus of subterranean holoparasitic herbs found in arid and semiarid regions of Africa, Madagascar, and the southwestern part of the Arabian peninsula. Results from field and herbarium studies suggest the genus consists of four or five species, although more than 12 have been described. The recent rediscovery of *H. triceps,* a plant that had remained uncollected for a century, supports the need for additional field work. Taxonomic research has been impeded by a paucity of collections, which are often fragmentary in nature and poorly preserved. Supraspecific classification, species complexes, floral biology, and uses are discussed.

Key words: *Hydnora,* root holoparasite, parasitic angiosperm.

INTRODUCTION

The two genera of the Hydnoraceae, *Hydnora* and *Prosopanche,* include some of the strangest plants in the world. The vegetative plant body is highly reduced and the plants are entirely subterranean except when flowering. *Prosopanche* is found in South America (Kuijt 1969); a new species has recently been described from Central America (Gomez 1984). *Hydnora* is essentially an African genus, although two species are found in the southern Arabian peninsula. Little information on *Hydnora* is available due to its furtive nature and often seasonal appearance.

This paper reviews the infrageneric taxonomy of the group and provides notes on the natural history of *H. johannis* Becc. and *H. africana* Thunb., two species we have studied intensively during the past several years. We have drawn heavily upon earlier papers (Musselman 1984; Musselman and Visser 1987) in preparing this work.

The most recent monograph of *Hydnora* is that of Harms (1935), a work based largely on the studies of Vaccaneo (1934), who worked with material collected in East Africa. Kuijt (1969) reviews the biology of the genus. Visser discusses the biology of *H. africana* (Visser 1981) and *H. triceps* (Visser 1988) while Musselman (1984) and Musselman and Visser (1987) treat *H. johannis.*

MATERIALS AND METHODS

Hydnora was studied in the field in Sudan, Zimbabwe, Botswana, South Africa, and Namibia. Specimens from the following herbaria were examined: BM, BR, C, E, K, L, LISC, M, MO, P, PRE, RO, SRGH, UPS, and WIND. Work towards a monograph of this genus has been severely hindered by insufficient and poorly preserved herbarium material. Very few of the type specimens could be located; several were at Berlin and destroyed during the Second World War. Herbarium specimens are usually of poor quality and fragmentary, since the plants are very fleshy and often decay while drying. After drying, the material is very brittle. We estimate that there are fewer than 100 usable *Hydnora* specimens in the world's major herbaria.

RESULTS AND DISCUSSION

Distribution

Hydnora is largely an African genus. Two species, *H. africana* and *H. johannis,* are widespread. Distribution data, however, are very spotty (Fig. 1).

Description

Hydnoraceae are the only angiosperm family entirely devoid of leaflike structures, lacking even scales (Kuijt 1969). The following description of the genus follows Musselman (1984) except that "root" is used for the underground portion of the plant in the sense of Visser (1981) rather then "rhizome" (Musselman 1984).

Subterranean holoparasitic herbs with often massive root systems spreading laterally from the host. Roots up to 1 dm wide, 4–5 angled, terete or sometimes flattened. Periderm well developed, brick-red except at the tip of the root. Fresh roots pink to flesh-red with sticky exudate, extremely bitter and astringent. Entire root (except for the tip) covered with warty outgrowths of haustoreogenic capacity which may be regularly distributed and up to 0.8 cm long or irregularly distributed and less than 0.5 cm long. Latent and active buds scattered along the roots, usually in clusters of 2–4. Buds tubular with valvate lobes. Flowers 3-, 4-, or 5-merous. Perianth lobes patent and resting on the soil, or lobes not reflexed and flower opening by a separation of the lobes. Flowers variable in size from 5 to 25 cm, the length depending on the depth of the root, pedicel 4–9 cm. Ovary inferior, unilocular, with numerous infolded, pendant placentae. Stigmas sessile and with distinct grooves on the surface. Stamens basifixed, anthers 2.5–3 × 2–2.5 cm. Pollen very sticky, adhering to anthers. Perianth lobes 6–8 cm; in some species, "bait bodies" are present between the inner margins of the lobes; in other species a well-developed osmorphoric region ("cucullus") is present. Fruit entirely subterranean, fleshy, globose, 10–15 cm wide, many-seeded, often splitting irregularly after maturation. Fruiting pedicel very short and easily separated from the root. Pericarp with scaly outer periderm; the inner layer mealy, white, very sweet. Fruiting placentae similar to inner layer of pericarp in taste and texture. Seeds brown, very hard, irregularly shaped, oblong to globose, 1–1.8 mm. Seedlings unknown.

Representatives of the genus are illustrated in Figure 2, 3, and 4.

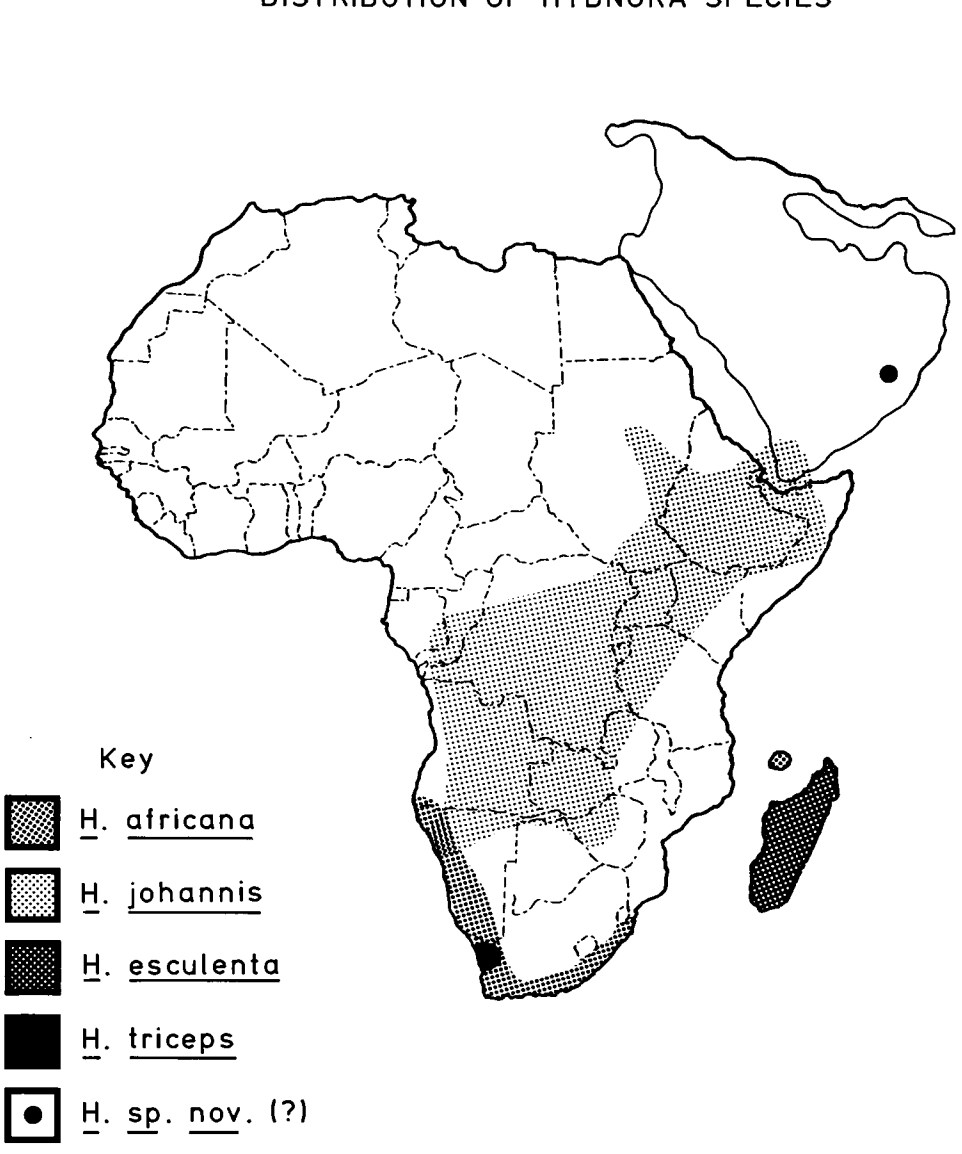

Fig. 1. Distribution of *Hydnora* species based on herbarium specimens, literature, and field work. Ranges are approximate.

Hosts

Hydnora species have a narrow host range. *Hydnora africana* and *H. triceps* are restricted entirely to *Euphorbia* species, with one report of *Zygophyllum* as a host (Table 1), whereas other species of *Hydnora* parasitize only species of *Acacia* and related trees. A report of *H. johannis* on *Kigelia africana* (Lam.) Benth. has been shown to be erroneous. The hosts of *Hydnora* are given in Table 1.

Host-parasite relationships have received very little attention. Since the parasite

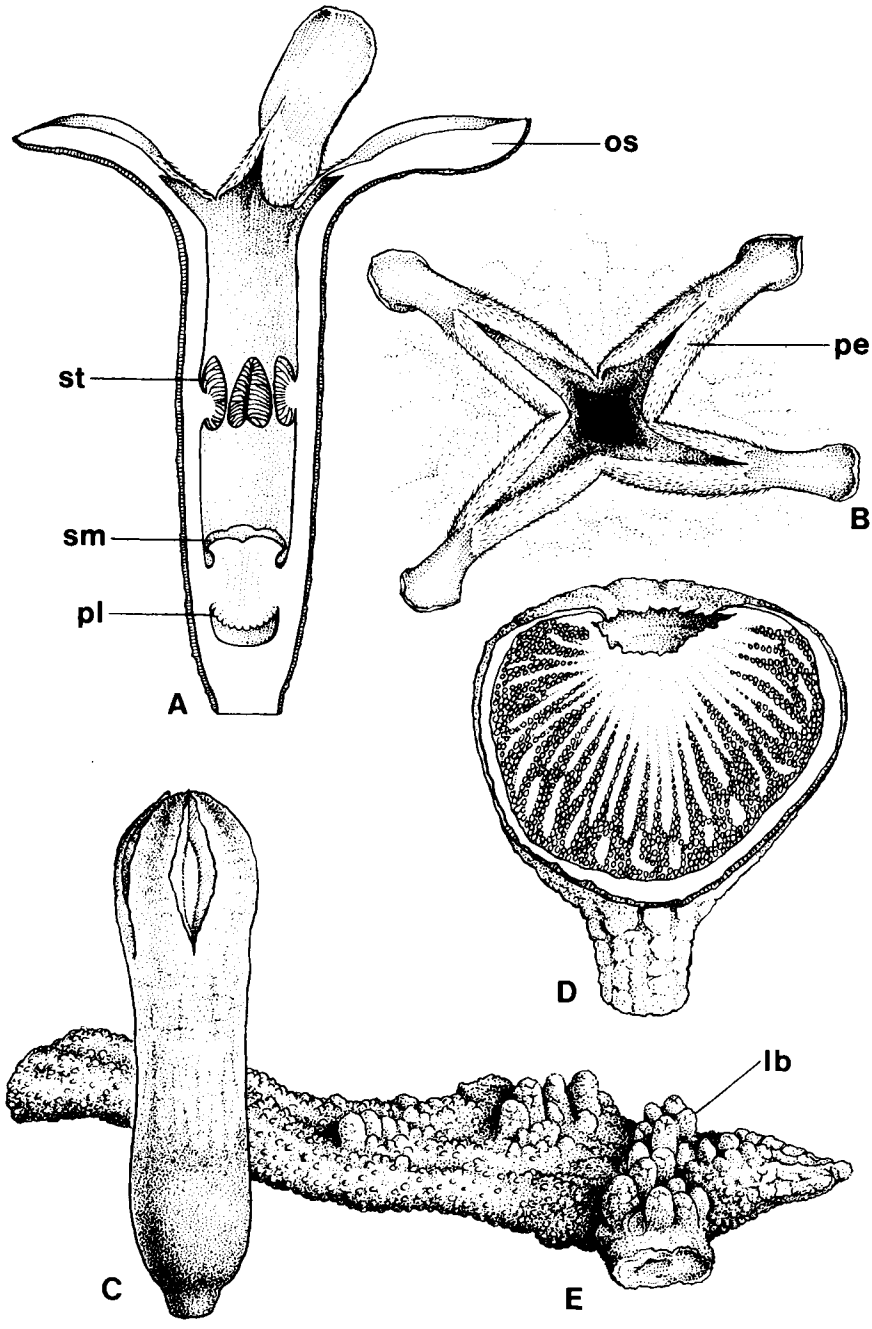

Fig. 2. *Hydnora johannis.*—A. Half-flower (os: osmophoric region; pl: placenta; sm: stigma; st: stamen).—B. Open flower on soil surface showing spreading perianth lobes (pe).—C. Flower showing only slight separation of perianth lobes at anthesis due to lack of moisture.—D. Half-fruit.—E. Portion of root (lb: latent bud). (A and B, approximately ⅔ life size; C, D, and E approximately ½ life size.) (From Musselman [1984] in Notes Roy. Bot. Gard. Edinburgh 42[1]. Reproduced with the permission of the controller of Her Britanic Majesty's Stationery Office.)

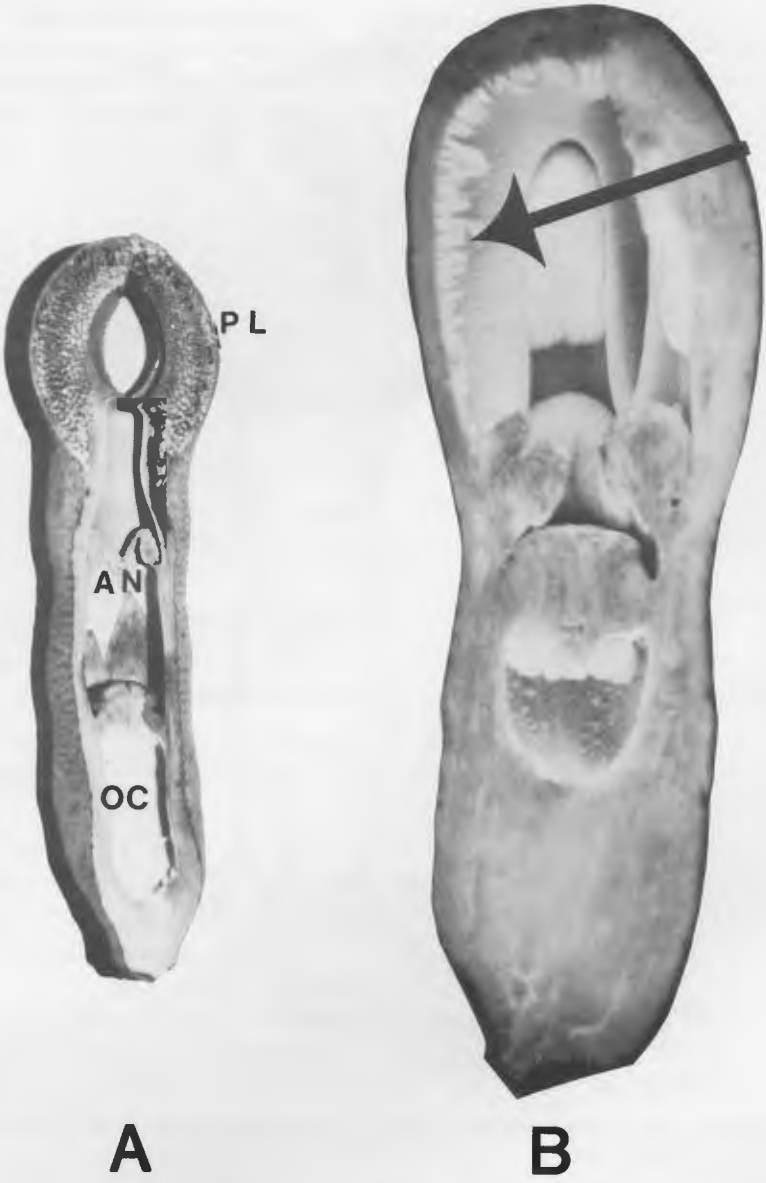

Fig. 3. *Hydnora africana.*—A. Half-flower (an: anthers; oc: ovary; pl: perianth lobes). Note the curved lobes, connivent only at the tip.—B. Perianth lobes showing "bait bodies" (arrow). (A, approximately ½ life size; B. life size.)

has no obvious transpiration, how are materials moved from the host to the parasite? In times of water stress, can water move from the parasite to the host? The answer to these and other questions requires additional research.

Taxonomy

Decaisne (1873) first suggested that subgeneric classification be based on the number of floral parts. In his scheme, subgenus *Dorhyna* contained plants with

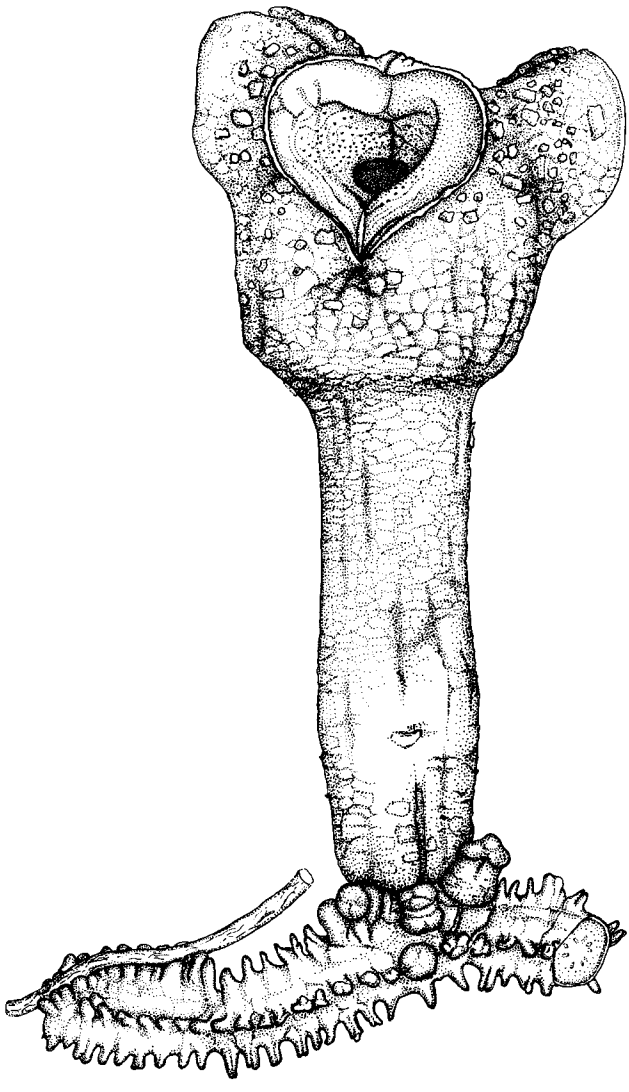

Fig. 4. *Hydnora triceps.* Flower and root; host root at left. (From Visser [1988]). (Three-fourths life size.)

four-parted perianth parts, stigma lobes, and stamens. The subgenus *Hydnora,* on the other hand, contained species with trimerous perianth parts, stigma lobes, and stamens. We have found, however, that individuals in any population of *H. africana* can have four stigma lobes, although this species usually has three stigma lobes. Later, Vaccaneo (1934) amended Decaisne's subgeneric classification to include features of the roots. In this classification, Vaccaneo's subgenus *Hydnora* included species with angled roots and large protuberances and subgenus *Dorhyna* those plants with more or less terete roots and smaller protuberances. Harms (1935) established four sections. One of these, sect. *Tricephalohydnum* Harms, was monotypic and included the poorly known *H. triceps,* which we tentatively place in the now sectionless subg. *Hydnora* due to its 3-merous flowers, the

Table 1. Recorded hosts for *Hydnora*.

Species	Host	Reference
H. africana	*Albizzia lebbek* (L.) Benth.	Harms 1935
	Euphorbia caputmedusae L.	This paper
	E. decussata E. Meyer	Visser 1981
	E. gregaria Marloth	Harms 1935
	E. gummifera Boiss.	Harms 1935
	E. karroensis (Boiss.) N.E. Br.	This paper
	E. lignosa Marloth	Harms 1935
	E. mauritanica L.	Visser 1981
H. cornii	*Albizzia lebbek* (L.) Benth.	Vaccaneo 1934
H. esculenta	"*Acacia* and other legumes"	Jumelle and Perrier de la Bathie 1912
	Tamarindus indica L.	Fide *Humbert 19805*, P
	Casuarina (this needs documentation)	Fide *Schlieben 8260*, P
H. johannis	*Acacia albida* Del.	Fide *Guy 139469*, C
	A. cyanophilla Lindl.	Dinter 1909
	A. karoo Hayne (as *A.* "*horrida*")	Dinter 1909
	A. luederitzii Engl.	Musselman and Visser 1984
	A. nilotica (L.) Willd.	Musselman 1984
	A. seyal Del.	Musselman 1984
	A. tortilis (Forssk.) Hayne (as *A.* "*heteracantha*")	Dinter 1909
	A. "*uncinata*"	Dinter 1909
H. triceps	*Euphorbia dregeana* E. Meyer ex Boiss.	Visser 1988
	Zygophyllum orbiculatum Wel.	Welwitsch 1869

presence of "bait bodies," and its angled warty roots. Our preliminary taxonomic treatment of the group follows. Listed species follow Harms (1935) and Musselman and Visser (1987).

HYDNORA Thunberg, Kongl. Vetensk. Acad. Handl. 36:69. 1775.
TYPE: *H. africana* Thunberg.
Aphyteia Linnaeus, Pl. Aphyteia, p. 7. 1776. [TYPE: *H. africana*]
Subg. *Hydnora*.
Flowers 3-merous; perianth with "bait bodies" on the margins; roots 3- to 4-angled.
H. aethiopica Decaisne
H. africana Thunberg
var. *longicollis* Welwitsch
H. triceps Drège et Meyer
Subg. *Dorhyna* Decaisne, Bull. Soc. Bot. France 20:75–77. 1873.
TYPE: *H. angolensis* Decaisne
Flowers 4- or 5-merous; perianth margins with hairs; roots angled or not angled.
Sect. *Dorhyna*
Flowers 4-merous, perfect; roots not angled.
H. johannis Beccari

H. abyssinica A. Braun
var. *quinquefida* Engler
H. angolensis Decaisne
H. bogoensis Beccari
H. cornii Vaccaneo
H. gigantea Chiovenda
H. hanningtonii Rendle
H. michaelis Peter
H. ruspolii Chiovenda
H. solmsiana Dinter

Sect. *Neohydnora* Harms, Die natürl. Pflanzenf., ed. 2, 16b:282. 1935.
TYPE: *H. esculenta* Jumelle & Perrier de la Bathie.
Flowers 5-merous, imperfect; pistillate flower with well-developed ovary and fleshy staminodes, staminate flower with vestigial ovary; roots angled.
H. esculenta Jumelle & Perrier de la Bathie

Hydnora angolensis, known only from a fruit presumably collected in Gabon, was placed by Decaisne (1873) in subgenus *Hydnora.* We know of no other collections of *Hydnora* from Gabon, so the status of this species is unclear.

Decaisne (1873) described *H. aethiopica* based on a specimen from Sabatier's expedition to find the source of the White Nile. This name also appears to be based on an incomplete specimen. If it represented subg. *Hydnora,* it would provide the basis for a significant range extension for this essentially southern African group.

Lastly, there is a noteworthy collection from the Dhofar region of Oman, *Miller 7619* (E), that has been determined as *H. africana,* a species known only from the southernmost part of Africa; a collection from Arabia would represent a considerable disjunction. The specimen resembles *H. africana* but the label data indicates that it was growing beneath *Acacia.* Although no reference to parasitism is made, this *Hydnora* may have been parasitic on *Acacia.*

Uses

Human uses.—The fruits of *H. johannis* are edible, even delectable (Vaccaneo 1934; Musselman 1984; Musselman and Visser, 1987). *Hydnora africana* fruits are also sought after as food (Visser 1981). Less well known is the medicinal use of the roots (Vaccaneo 1934; Musselman 1984). These have been used as an antidiarrheal agent, probably due to the high concentration of tannin, imparting a strong astringency to the dried roots. The high tannin content also renders the roots useful for tanning leather (Musselman and Visser 1987). In Sudan, the dried roots are used like charcoal (Musselman 1984). Parker (1988) reports that in the Dire Dawa region of Ethiopia, *H. johannis* damages asphalt streets by breaking through the surface to flower.

Animal uses.—The fruits of *Hydnora johannis* are eagerly sought and eaten by monkeys (Musselman 1984), whereas those of *H. africana* are eaten by various other mammals (Visser 1981). According to one herbarium label, *Gilbert & Thulin 1534* (UPS), flower buds of *H. johannis* are eaten. We assume that animals are

implied here, for goats are known to eat the buds of *H. johannis* in Sudan. Because the roots contain large quantities of water, they are often excavated and eaten by animals during the dry season. In the Namib Desert, evidence of foraging for *H. africana* by small mammals is often found. We have observed extensive excavations of *H. johannis* by elephants in Etosha Pan National Park (Musselman and Visser 1987). Rhinoceroses are reported to forage for *H. johannis,* according to the herbarium label for *Bally 7694* (K).

Culture

Kuijt (1969) wrote, regarding the Hydnoraceae: "A fascinating story awaits the botanist who is fortunate enough to have access to viable seeds." Seeds are abundantly produced by *Hydnora* but we know of only one person who has grown these plants in cultivation. We are indebted to this "fortunate botanist," Sherwin Carlquist, for sharing his "fascinating story."

Seeds of *H. africana* were collected in 1973 from plants growing on *Euphorbia mauritanica* L. at Worcester, South Africa. Carlquist planted the seeds in a pot of *Euphorbia caputmedusae* L. in Claremont, California. For four years the *Euphorbia* was repotted as it grew, the *Hydnora* parasite not yet evident. The plant was then transplanted to Carlquist's garden where, three years later, a flower of *Hydnora* appeared! Other *Euphorbia* species were added and they, too, were parasitized. No fruits have been produced, however.

Floral Biology

The structure of the *Hydnora* flower is simple. The perianth lobes, and sometimes part of the tube, are the only portions of the plant emerging above the soil. References to the fetid smell of the flower are numerous, but little information on the floral biology and no information on the breeding system of the parasite are available.

The flowers of *H. africana* and *H. triceps* are apparently unique in possessing "bait bodies" ("Koderkörpen"), first described by Harms (1935) for *H. africana.* These are strong-smelling particles on the perianth lobe margins (Fig. 2). These bait bodies attract beetles, often dermestids, which enter the flower and harvest the pollen. Carrion flies have also been collected in the flowers. Since the stigma is below the anthers, pollen falls onto it. The beetles sometimes crawl onto the stigmatic surface, which is receptive a few days before anthesis. Because beetles bearing pollen have been trapped before anthesis, *H. africana* may be an outcrossing species. This hypothesis is also supported by the fact that flies are sometimes found inside the flower buds. These observations on floral visitors are our own.

The floral biology of *H. johannis* is different. Bait bodies are not present but there is a well-developed osmophore ("cucullus," sensu Vaccaneo 1934) at the tip of each perianth lobe (Fig. 1). *Hydnora johannis* is pollinated by scarab beetles, rather than dermestid beetles.

Blow flies, as well as dermestid beetles, have been found in the flowers of *H. triceps.* The flowers of this species seldom emerge from the soil; insects enter them through cracks in the soil, cracks that form as the flowers grow (Visser 1988).

Further Work

These plants require more attention if we are to understand their biology and their relationship to other groups of angiosperms. Further work is needed to obtain additional information about their floral biology, distribution, phenology, and hosts. For example, *H. triceps,* first described in 1888 from a collection of Dinter, was known from only two herbarium specimens; both collections were from the vicinity of Okiep in western Namaqualand. One of the specimens is not easily identified as this species due to the disfiguration and degradation of the material that attended the drying process. Prior to the discovery of a population occurring in an area of nearly five square kilometers about 60 km north of Springbok, we assumed *H. triceps* to be synonymous with *H. africana,* based on our herbarium studies. For this reason, we caution against taxonomic decisions in the genus *Hydnora* without field experience.

ACKNOWLEDGMENTS

We wish to thank Sherwin Carlquist for providing data on the cultivation of *Hydnora.* The first author (LJM) also expresses appreciation to Dr. Carlquist for the invitation to participate in the 1988 systematics symposium at Rancho Santa Ana Botanic Garden.

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FOOTNOTE

[1] Based on a lecture presented by Lytton J. Musselman at the Fourth Annual Southwestern Botanical Systematics Symposium, *Systematics, Evolution, and Adaptation in the American Southwest,* 20–21 May 1988.