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Trap structure of the carnivorous plant *Genlisea* (Lentibulariaceae)

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Abstract

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The developmental morphology of the trap of five *Genlisea* species (*G. africana, G. hispidula, G. pygmaea, G. repens* and *G. subglabra*) from South America and Africa is described. Studies are based on living and preserved material using scanning electron microscopy. The traps show interspecific differences in types of detentive hairs and the occurrence of stomata. Highly decomposed organisms were found in the traps, especially in the bulb and proximal neck. *Genlisea* and *Utricularia* (Lentibulariaceae) show similarities in early development of the trap and anatomy of external glands.

Key words: carnivory, detentive hairs, developmental morphology, digestion, *Genlisea*, Lentibulariaceae, stomata, trap, *Utricularia*.

1. Introduction

Genlisea A. Saint-Hilaire belongs to Lentibulariaceae (Order Scrophulariales) (Takhtajan 1987). Most literature on *Genlisea* is cited in Taylor (1991). The genus is closely related to *Utricularia* of the same family. The flower of *Genlisea* has a five-parted calyx, while *Utricularia* shows a two-parted calyx (Taylor 1991). *Genlisea* is divided into two sections, depending on the type of capsule dehiscence. Section *Genlisea* has circumscissile dehiscence, while *Tayloria* has longitudinal (Fromm-Trinta 1979). The five species (*G. africana* Oliver, *G. hispidula* Stapf, *G. pygmaea* A. Saint-Hilaire, *G. repens* Benjamin and *G. subglabra* Stapf), examined in this paper, belong to section *Genlisea*, which occurs in both Africa and South America. Eight *Genlisea* species are known from tropical and South Africa and 11 from Central and South America (Taylor 1991). Some species pairs are difficult to identify on floral characters, e.g., *G. repens* and *G. pygmaea,* and *G. hispidula* and *G. subglabra* (Taylor 1991). Trap morphology was considered to be of limited use in the classification of *Genlisea* (Taylor 1991). One aspect of this study was to reexamine the systematic significance of trap morphology.

Genlisea occurs in wet meadows, sandy riverbanks and marshy grasslands and can seasonally be submerged (Cook 1990, Taylor 1991). These habitats are well known for the development of the carnivory syndrome in plants (Heslop-Harrison 1978).

Most *Genlisea* species possess a rosette of green leaves on a short rhizome. Only *G. repens* has a creeping elongated rhizome. Besides the foliage leaves, the rhizome bears whitish subterranean or submerged organs, which were considered by Darwin (1876) to be a trap for catching small invertebrates. Goebel (1891: Fig. 5, Taf. XV) found animals and algae in the bulb of the *Genlisea* trap. Although carnivory sensu stricto (i.e:, attracting, capture and digestion: see Juniper et al. 1989) in *Genlisea* has not been conclusively demonstrated, the term trap is used for convenience to describe this structure. The trap is the only organ of *Genlisea*, which has positively geotropic growth. *Genlisea* lacks a typical root system. The trap seems to have both root and leaf characteristics, so it was therefore called "Wurzelblatt" by Schmucker und Linnemann (1959).

Previous morphological and histological works on the flower and trap of *Genlisea* spp. were provided by Warming (1874: *G. aurea* A. Saint-Hilaire, syn. *G. ornata* Martius), Goebel (1891: *G. aurea*; 1893: *G. violacea* A. Saint-Hilaire), Lloyd (1942: *Genlisea* spp. including *G. filiformis* Benjamin, *G. repens*) and Fromm-Trinta (1979: *G. aurea, G. filiformis, G. pygmaea, G. repens* and *G. violacea*). These studies were restricted to South American species. Juniper et al. (1989, p. 125) stated that early studies were primarily based on dried and fixed material and "therefore any explanation of how the trap works is purely speculative". The present study uses both living and preserved plant material of South American and African species. It aims to provide an understanding of the trap function, focussing on trap histology and morphology, using scanning electron microscopy.

2. Material and methods

The following material of *Genlisea* has been studied (N = fixed material from natural site, ZH = cultivated plants grown at the Botanical Garden of Zurich University, Switzerland).

Species from South America

Genlisea pygmaea A. Saint-Hilaire
N: Trinidad, *Baker & Simmonds et al. 17. Nov. 1951 No. 6* (spirit collection Kew)
ZH: young plants provided by *L. Bütschi s.n.* (origin of seeds: Auyan-Tepui, Estado Bolivar, Venezuela)
Genlisea repens Benjamin
N: Auyan-Tepui, Estado Bolivar (Venezuela), *L. Bütschi s.n.*
ZH: seeds from Auyan-Tepui, Estado Bolivar (Venezuela), *L. Bütschi s.n.*

Species from tropical and South Africa

Genlisea africana Oliver
N: Liberia: *Baldwin 13003* (spirit collection Kew)
Genlisea hispidula Stapf
ZH: plants provided by *R. Fürst s.n.*, source unknown
ZH: plants provided by *L. Bütschi s.n.*, source unknown
Genlisea subglabra Stapf
N: Tanganyika: *Redhead & Taylor 8009* (spirit collection Kew)

In 1988, Lorenz Bütschi (present address: Horticulture, Qu. les Vignaux, B.P. 22, F-83520 Roquebrune sur Argens, France) collected living material of *G. repens* and *G. pygmaea* on the Auyan-Tepui (Venezuela). Cultures of these two closely related species at the Botanical Garden of Zurich are relatively large.

Most fixed material was preserved in a mixture of ethanol and glycerine (Kew mixture). One % glycerine in 70% ethanol solution was fixative for the preparation of *G. repens* (N, ZH) and *G. pygmaea* (ZH). A Hitachi S-4000 field emission scanning electron microscope (SEM) was used for morphological examinations on *Genlisea* spp.

3. Results: Anatomy and development of the Genlisea trap

The trap of *Genlisea* is a complex structure which consists of a footstalk **P1** and an utricle (Fig. 1). The utricle has a hollow bulb **P2**, a tube (neck) **P3**, and two twisted arms **P5** (Fig. 1). There are up to 20 twists in each arm. The arms are tube-like but have a longitudinal slit. The prey enters the trap through the mouth (Lloyd 1942) of the branching zone **P4**, and also through the slits of the arms.

General histology of the trap varies and is well described by Lloyd (1942). The footstalk consists of an epidermis and aerenchyma. The only vascular strand divides at the distal end of the footstalk into a dorsal and ventral vascular strand before entering the bulb. These strands divide once more at the branching zone. Therefore, each arm contains vascular tissue of dorsal and ventral origin. The utricle of the *Genlisea* trap consists of two epidermal layers, sometimes divided by parenchyma.

3.1. The inner epidermis of the trap

The inner epidermis of the *Genlisea* trap contains hairs, glands, supporting cells and occasionally stomata. The supporting cells are of two types underlying basal cells of hairs and pedestal cells of glands. Glands of the inner epidermis generally possess multicellular heads which are one cell-layer thick (Fig. 1a–i).

3.1.1. Detentive hairs

"Detentive hairs" or "bristles" (Lloyd 1942) occur on the inside of the neck and arms of the trap. These hairs are oriented towards the bulb and are thought to have a detaining role. In the arms, there are rows of these hairs, while in the neck they form about 40–60 complete funnels. Detentive hairs seem to be extensions of long narrow supporting cells (Fig. 2), which are part of the inner epidermis of the neck and arms. The detentive hairs are 2–3-celled (Fromm-Trinta 1979). They consist of a basal cell, a terminal cell and, occasionally, a middle cell (Fig. 4). In the species examined, only *G. africana* has 3-celled detentive hairs, which are restricted to the proximal neck.

The zone between two rows of detentive hairs of the same type is referred to as a "segment". The appearence of segments is loosely defined by constrictions of the external wall of the neck.

Detentive hairs in South American *Genlisea* spp. were studied in detail by Fromm-Trinta (1979). She demonstrated that the shape of terminal cells of these detentive hairs is quite variable. The types of terminal cells in *G. repens* and *G. pygmaea* were described by Fromm-Trinta (1979) and studied using SEM in this paper. In the African species (*G. africana, G. hispidula* and *G. subglabra*), different hair types occur from those present in the South American taxa. The hair types differ in the shape of both the terminal and basal cell (Tab. 1). Hair types, not known from South American species (see Fromm-Trinta 1979), are basal cells with an obvious longitudinal furrow, terminal cells with globose apex, and pusticulate basal cells (Figs. 1j–l, n, 3, 4, 5). In South American and

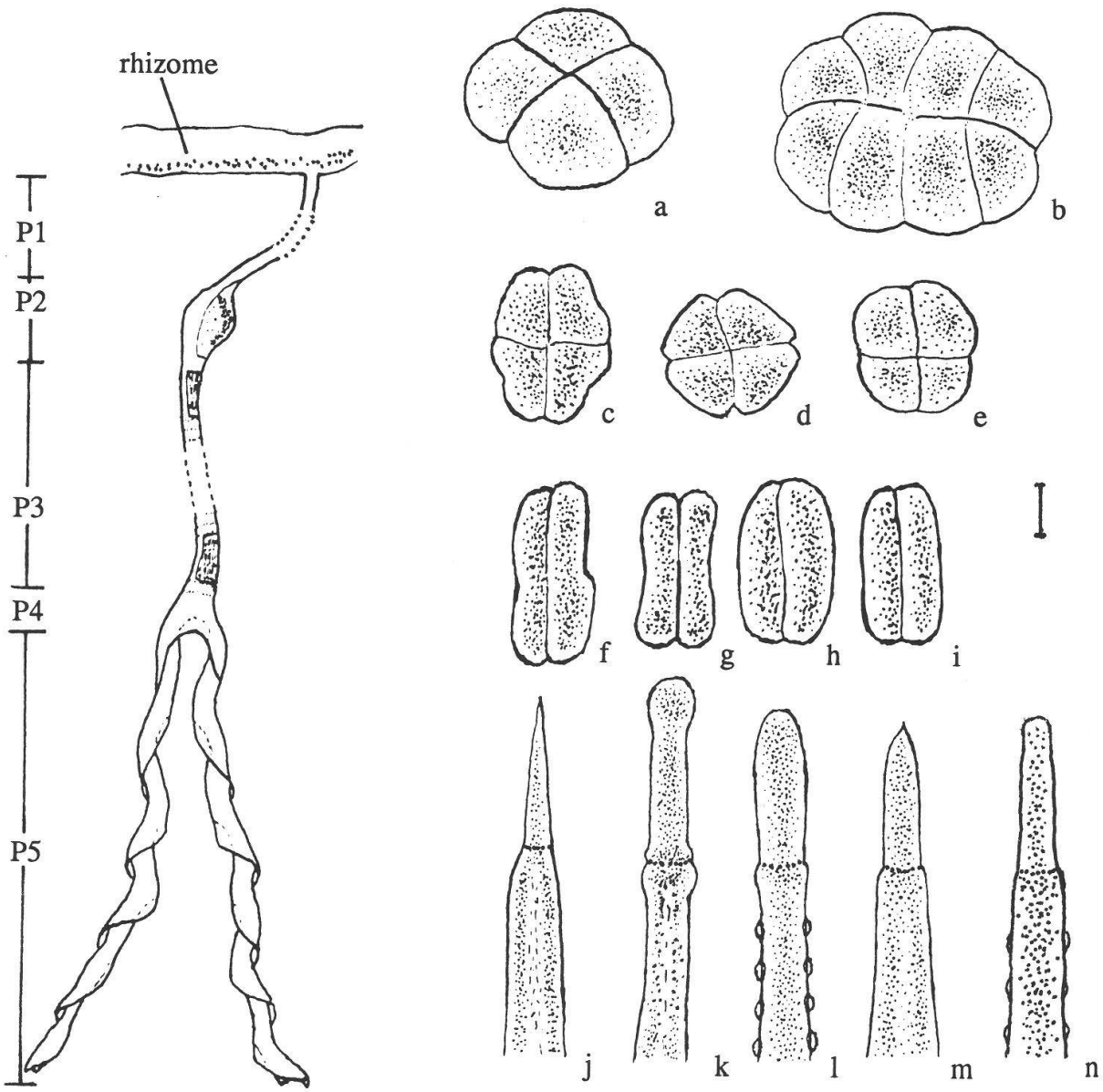


Fig. 1. Trap of *Genlisea*: P1–P5. Trap of *Genlisea*: P1. Footstalk. P2. Hollow bulb. P3. Neck (tube). P4. Branching zone. P5. Arms. a–m. Glands and hairs of inner epidermis of bulb and neck: a–b. Glands in the bulb: a. *G. pygmaea*: 4-celled gland. b. *G. hispidula*: 8-celled gland. c–e: Slightly different shapes of 4-celled glands of the proximal neck: c. *G. hispidula*. d. *G. repens*. e. *G. subglabra*. f–i. 2-celled glands of the distal neck: f. *G. hispidula*. g. *G. subglabra*. h. *G. africana*. i. *G. repens*. j–m. Detentive hairs of the proximal and/or distal neck (definition of the types see Tab. 1): j. *G. hispidula* and *G. subglabra* (type LA). k. *G. subglabra* (type LG). 1. *G. africana* (type PK). m. *G. repens* (type SC). n. *G. hispidula* (type PB). P2 is 2 mm in *G. repens*. Scale bar for a–n is 10 µm.

African species, a slightly developed longitudinal furrow in the basal cell is occasionally present in the smooth cylindrical type (Fig. 1 m).

Tab. 1 shows that different hair types may occur in the various parts of the trap. In the arms of *G. africana*, the middle neck of *G. hispidula*, and the distal neck and arms of *G. subglabra*, two distinct hair types are present within each row of detentive hairs (Tab. 1, Fig. 3). The detentive hairs with pusticulate basal cell and awl-shaped terminal

Tab. 1. Detentive hair types of *Genlisea*

	G. africana				*G. hispidula*				*G. pygmaea*			
	neck			arm	neck			arm	neck			arm
	p	m	d		p	m	d		p	m	d	
hair type	SA_2	PA_3	PK_4	PK_4 SK_3	LA_{2-4}	PA_4 PB_4	PB_4	PB_4 SA_3 SA_1	SC_2	SC_{2-3}	SC_{2-3}	SC_{3-4} SA_1

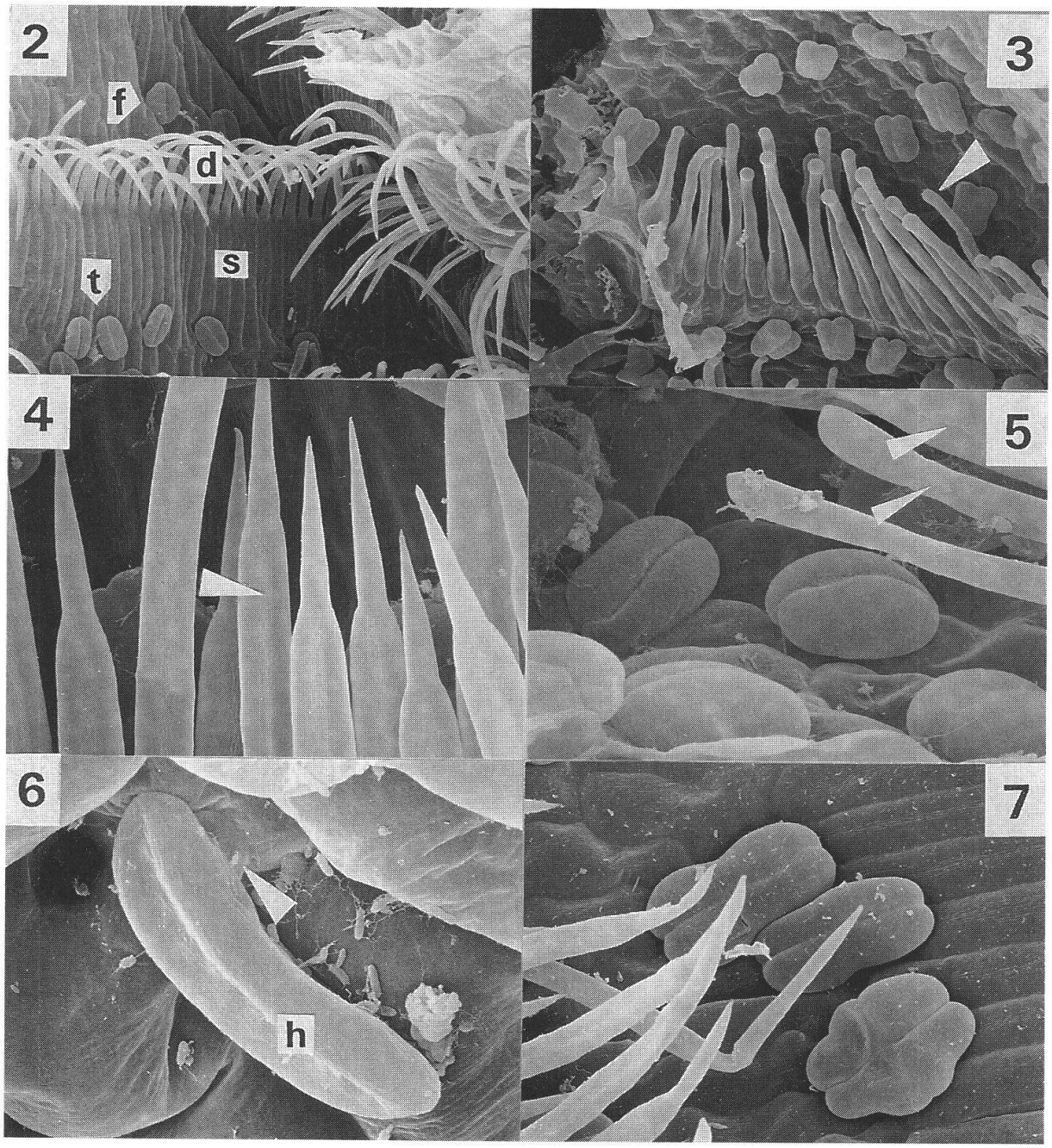
	G. repens				*G. subglabra*			
	neck			arm	neck			arm
	p	m	d		p	m	d	
hair type	SC_2	SC_3	SC_4	SC_{3-4} SA_1	LA_{2-4}	LA_{2-4}	LB_{2-4} LG_{2-3}	LB_{2-3} LG_{2-3}

Part of neck: p, proximal; m, middle; d, distal (including branching zone).
Detentive hair type: Basal/middle cell (1st letter): L, with deep longitudinal furrow and smooth surface. P, ± cylindrical, with pusticulate structure. S, ± cylindrical, with smooth surface. Terminal cell (2nd letter): A, awl-shaped; B, blunt; C, cuspidate; G, distal part globose; K, club-shaped. Index numbers stand for different classes of size or lengths: 1, 40–60 µm; 2, *61–120* µm; 3, 121–150 µm; 4, 151–230 µm.

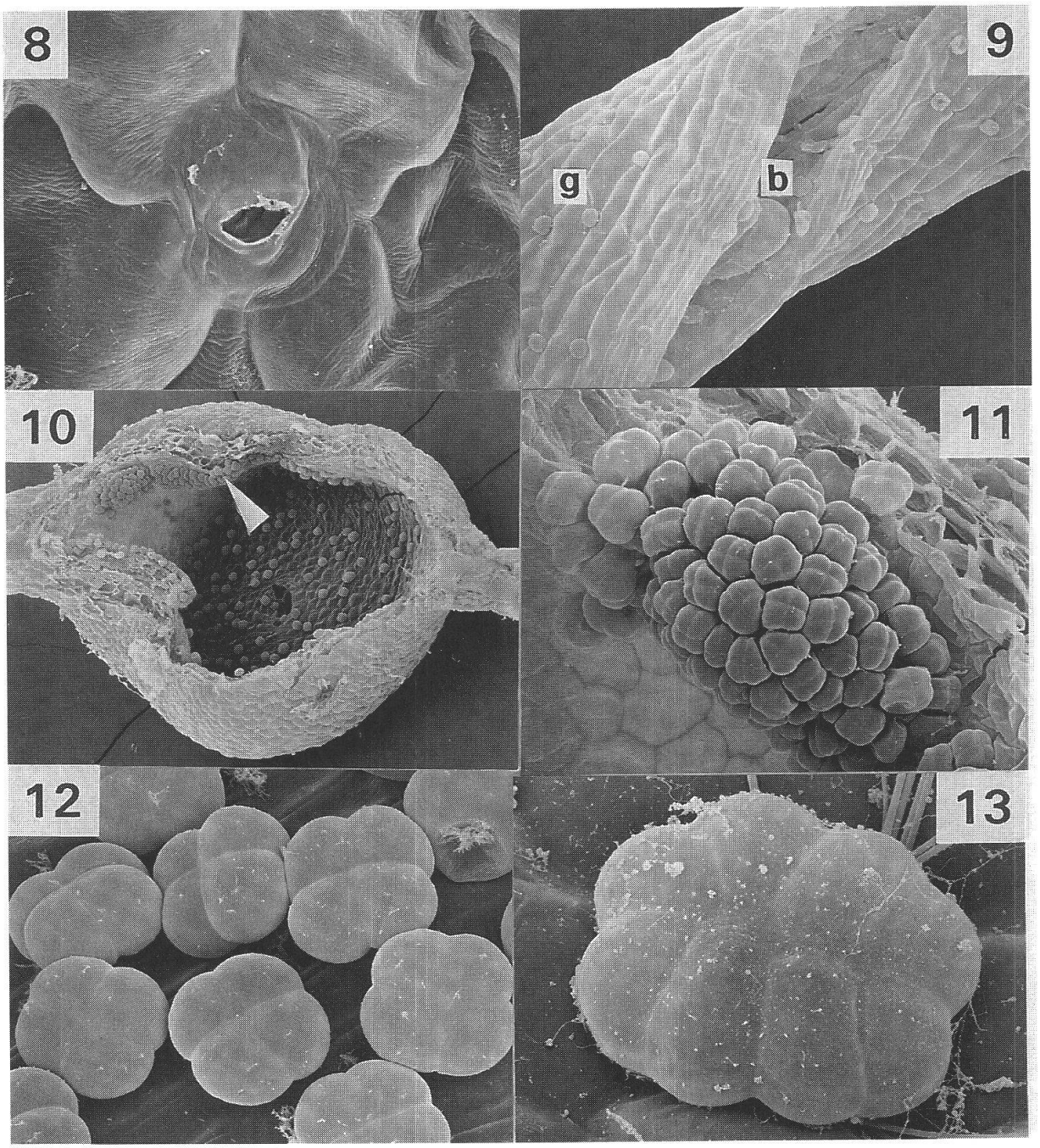
cell in *G. hispidula* and the detentive hairs with longitudinal furrowed basal cell and blunt terminal cell in *G. subglabra* may be viewed as intermediates between two hair types (Tab. 1, Fig. 3). In *G. repens*, up to 3 rows of short hairs of one type occur along the margins of the arm slits (Tab. 1). Normally, *G. pygmaea* has no short hairs on the margins (Fromm-Trinta 1979: Fig. 13A, Reut pers. obs.). One specimen of *G. pygmaea* (ZH), however, showed 3–4, closely spaced rows of short hairs of the same type (Tab. 1). In the arms of *G. hispidula,* one single row of short hairs is present along the margins of the slit, and 2 rows of detentive hairs within a segment. In this species, these rows are closely spaced together, and each row is characterized by a distinct hair type (Tab. 1). This was also shown in *G. aurea* by Fromm-Trinta (1979: Figs. 12B+C).

3.1.2. Other structures of the inner epidermis

In each segment, up to 3 rows of glands occur. These glands are borne on supporting cells with sinuous margins, and consist of a short pedestal cell and a multicellular head (Figs 3, 6). In the arms, the branching zone, and the distal and middle part of the neck, the glandular head is composed of 2 terminal cells (Fig. 6). In the proximal neck, the head consists of 2–4 cells (Fig. 7), rarely 8 cells as occasionally in *G. pygmaea.* The 2-celled glandular head is ventro-laterally attached to the inner epidermis by the pedestal cell (Fig. 6), while the 4-celled head is centrally fixed to the inner epidermis by the pedestal cell. The shapes of 2–4-celled heads are quite variable within the species examined (Fig. 1c–i). These shapes seem to be of little value for the identification of species.



Figs. 2–7. *Genlisea* spp.: Detentive hairs and glands of trap: 2. Proximal neck of *G. repens* showing "supporting cells" (s) of detentive hairs (d), 4-celled glands (f) and 2-celled glands (t) (168 ×). 3. Branching zone of *G. subglabra* showing detentive hairs terminal cells of globose and blunt (arrow) type (233 ×). 4. Middle neck of *G. subglabra* with awl-shaped terminal cell and longitudinal furrow (arrow) of basal cell of detentive hairs (654 ×). 5. Distal neck of *G. africana* showing pusticulate structure (arrow) of detentive hairs (747 ×). 6. Glandular trichome in the arm of *G. repens* with pedestal cell (arrow) and 2-celled head (h) (1867 ×). 7. Proximal neck of *G. hispidula* with 2- and 4-celled glands and awl-shaped terminal cells of detentive hairs (467 ×).



Figs. 8–13. *Genlisea* spp.: Figs 8–9. Details of the trap arm: 8. Stoma of inner epidermis of *G. repens* trap surrounded by cells with sinuous margins (1027 ×). 9. Portion of helically twisted arm of *G. africana* with bridge (b) and external glands (g) (121 ×). Figs 10–11. Bulb: 10. Opened bulb of *G. repens* showing ridge (arrow). Many 4-celled and a few 8-celled glands scattered on the inner bulb surface (37 ×). 11. Detail of Fig. 10 showing ridge with 4-celled glands (233 ×). 12. 4-celled glands on inner wall of bulb of *G. subglabra* (420 ×). 13. 8-celled gland on inner wall of bulb of *G. hispidula* (840 ×)

Goebel (1891) observed stomata on the inner epidermis of the distal neck and arms of *G. aurea*. These internal stomata were found in all species studied, except *G. subglabra*. In *G. repens* and *G. pygmaea*, the stomatal number varies in different parts of the trap. In the neck, up to 2 stomata occur per segment, while in the arms no more than 4 stomata are present in each segment. In *G. hispidula*, normally a single stoma occurs in each segment of the arms. The stomata of the inner epidermis of these three species are anomocytic (see Dilcher 1974) and surrounded by 5 epidermal cells (Fig. 8). The guard cells are raised above the epidermal cells. The long axis of guard cells is parallel to the long axis of the trap.

In the arms and branching zone of the *Genlisea* trap, unusually shaped trichomes occur at regular intervals of about 0.25 mm. Lloyd (1942) called them "distance pieces" or "articulating hairs", because they articulate and support the two margins of the arm slit (Fig. 9), and seem to avoid its collapse. The basal and middle cell of these trichomes separate the margins of the arm slit. They were referred to by Juniper et al. (1989) as a "bridge" or by Lloyd (1942) as a "prop-cell". The basal and middle cell are much enlarged, whilst the apical cell is reduced and button-like in appearance (Lloyd 1942).

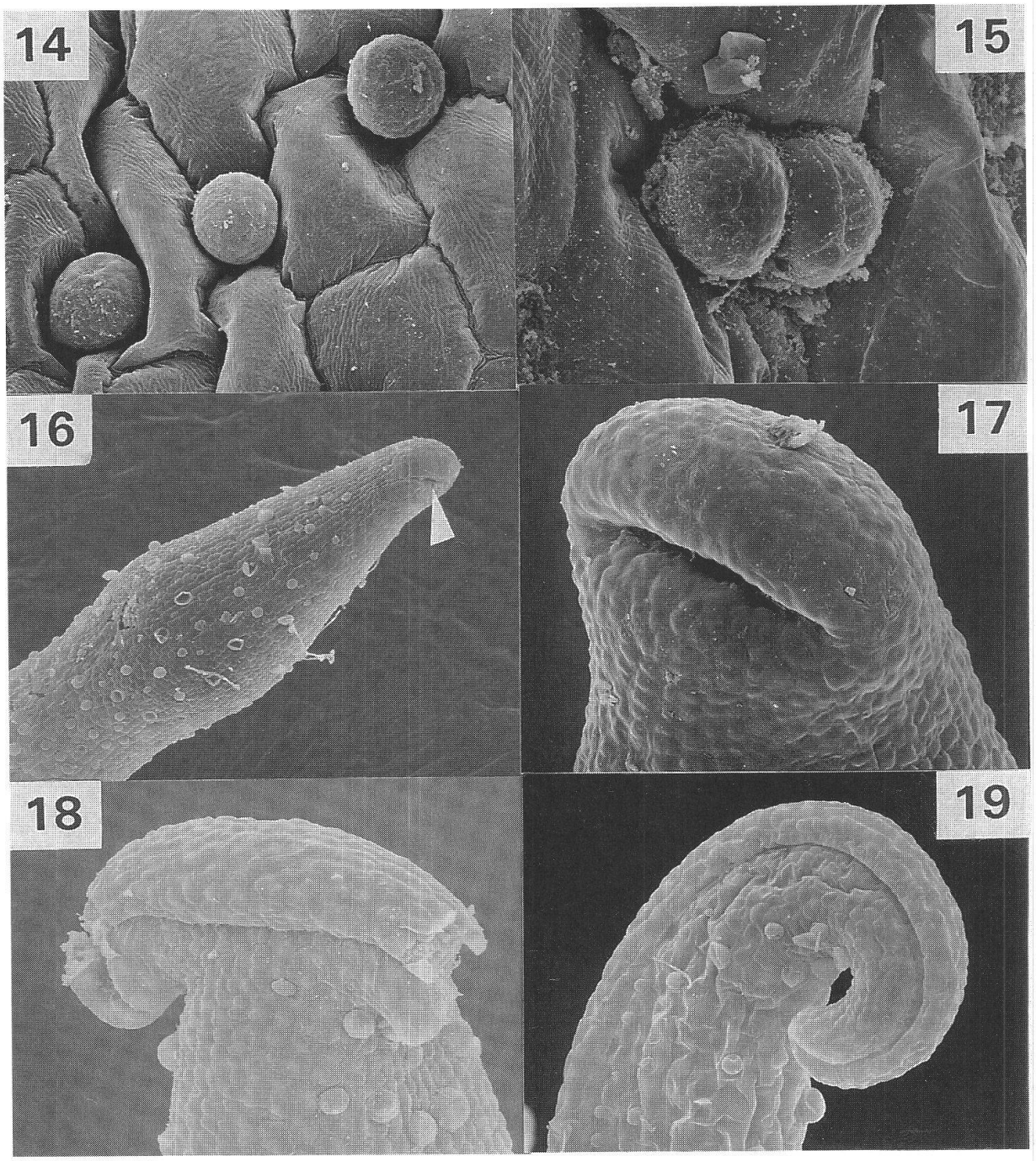
In general, hairs, glands and supporting cells of the distal neck continue into the arms. Glands and supporting cells of detentive hairs of the arms are usually smaller than those of the distal neck.

The inner epidermis of the bulb differs from that of the more distal parts of the *Genlisea* trap. The inner surface of the bulb contains isodiametric, straight-walled cells. Many glands occur irregularly on the inside of the bulb (Fig. 10). These glands consist of a short pedestal cell, supporting 4 to 8 terminal cells (Figs. 12, 13); the 4-celled glands are much more frequent. Many crowded, 4-celled glands are present on the proximal inner side of the bulb and extend ventrally and dorsally on either side above the vascular bundles. In the species examined, these crowded glands are attached to an internal ridge (Figs. 10, 11), except in *G. subglabra*. Whilst the multicellular heads of the glands in the neck are flattened, the terminal cells of the glands in the bulb are more spherical.

3.2. The outer epidermis

Many button-like trichomes (glands) are present irregularly on the outer epidermis of the trap. These trichomes are similar in appearance to the external glands of the *Utricularia* bladder (Juniper et al. 1989). In both genera, they consist of a pedestal cell and a head. The pedestal cell is supported by a basal cell, which is normally surrounded by 4, straight-walled, hexagonal epidermal cells (Fig. 14). Differences between *Genlisea* and *Utricularia* exist in the number of head cells of the external glands. Single-celled heads occur in *G. repens, G. pygmaea, G. africana,* and *G. hispidula* (Fig. 14), and were recorded in *U. dichotoma* by Richter (1990: p. 27, Fig. 3b). Two-celled heads of external glands are present on the bulb of *G. subglabra* (Fig. 15), and were found in *U. minor* by Kristen (1974).

Stomata are absent from the external epidermis of the trap of all examined *Genlisea* species, except *G. africana*. Stomata of *G. africana* are anomocytic, and restricted to the outer epidermis of the neck. Their guard cells are usually surrounded by 4 epidermal cells and raised relative to them. The long axis of the guard cells are oriented parallel to the long axis of the trap.



Figs. 14–19. *Genlisea* spp.: 14–15. Glands on outer epidermis of trap. 14. Single-celled glands of *G. repens* (840 ×). 15. Two-celled glands on *G. subglabra* bulb (934 ×). Figs. 16–19. Trap development of *G. repens*: 16. Young bulb with primordial neck. Arrow points to opening of tubular neck (140 ×). 17. Neck apex with ventral mouth (560 ×). 18. Initiation of arms due to transversal extension of mouth region (373 ×). 19. Young folded arm with coiled tip (280 ×).

3.3. Trap development

Development of the *Genlisea* trap was described by Goebel (1891), Troll (1939), Lloyd (1942), and recently reviewed by Juniper et al. (1989).

Development of the trap initially involves formation of a cylindrical primordium from the rhizome. This stalk grows by an apical meristem. The ventral side of this apical tip then widens by invagination to form a gullet, which enlarges into a hollow structure (Lloyd 1942) (Fig. 16).

The next stage in *Genlisea* trap development is a lateral extension of the apex on both sides, which causes the opening to become a mouth (slit) (Fig. 17). The lateral sides of the mouth bend proximally because cell divisions occur more rapidly on the dorsal side than the ventral (Fig. 18) (Goebel 1891). Helically twisted arms develop on both sides of the mouth. One arm twists clockwise and the other counter clockwise. The tips of the arms are initially coiled (Fig. 19), but straighten by the end of arm development.

The inner and outer epidermis of the trap show differentiated glands and hairs early in development.

4. Discussion

It is sometimes difficult to identify species of *Genlisea* using only floral characters. According to Taylor (1991), there seems to be little floral variability within the genus. Fromm-Trinta (1979) and my results demonstrate that the anatomy of the detentive hairs in the *Genlisea* trap shows interspecific variability. African species, examined in the present study, show hair types which are not present in the South American species described by Fromm-Trinta (1979). The occurrence and number of internal or external stomata of the *Genlisea* trap seems to be characteristic at the level of species. Fromm-Trinta (1979) noted that on the inside of the bulb, only 4-celled glands occur in *G. pygmaea*, and 4–6-celled glands in *G. repens*. In the present study, 4–8-celled glands were observed on the inner wall of the bulb of both species.

The early development of the trap (especially its stalk) is characterized by prolonged apical growth, which is typical for roots in most flowering plants (Goebel 1891, 1913). The morphology of the *Genlisea* trap at the primordial stage is similar to young stolons of several *Utricularia* species (see Brugger and Rutishauser 1989). The mouth development of the *Genlisea* trap (Fig. 17) resembles the early development of the *Utricularia* bladder (see Goebel 1891; Lang 1901: Fig. 8; Brugger und Rutishauser 1989: Fig. 38).

It is not clearly known, why small aquatic organisms enter the *Genlisea* trap (Taylor 1991). Perhaps looking for shelter, animals creep into the slits of the arms. It is unclear, whether the *Genlisea* trap functions by active and/or passive processes. Passive capture of prey is possible as once inside the trap, the prey has little chance to turn back, because the detentive hairs block the exit. There are many rows and funnels of hairs in the mature trap. Each funnel extends into the next. Therefore, the whole *Genlisea* trap functions as a series of traps. This function of the *Genlisea* trap was alluded to by Darwin (1876) as an "eel trap" and by Heslop-Harrison (1975) as a "lobster pot". The only possible movement for the prey is unidirectional and leads directly into the bulb of the trap. Highly disintegrated organisms are found especially in the bulb and proximal neck of the *Genlisea* trap (Lloyd 1942, Reut pers. obs.). Therefore, the glands in these parts of the trap possibly play digestive and absorptive roles.

It is also possible that a suction mechanism exists which results in an active movement of water, soil particles and organisms into the trap. Joel (unpublished obs.) found mud

particles amongst animals in the bulb and neck of *Genlisea* traps (Juniper et al. 1989). This would suggest that either a water current or an active process of suction is responsible for the movement of these particles and organisms into the trap (Juniper et al. 1989). Alternatively, animals could have transported these mud particles into the neck and bulb.

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