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Pollination Biology of *Welwitschia mirabilis* Hook. f. (*Welwitschiaceae, Gnetopsida*)

By

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With 12 Figures

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Summary

Wetschnig W. & Depisch B. 1999. Pollination biology of *Welwitschia mirabilis* Hook. f. (*Welwitschiaceae*, *Gnetopsida*). – Phyton (Horn, Austria) 39 (1): 167–183, with 12 figures. – English with German summary.

Observations and experiments on the pollination biology of *Welwitschia mirabilis* were carried out on six days between 6. and 14. February 1997, on a male and a female plant from the Welwitschia-plain in the Namib-Naukluftpark of Namibia. On the basis of the development of flowers, we can conclude, that the flowering period of *Welwitschia* lasts for about 8 weeks, from about mid January to about mid March. Only two flowers open every second day on the male cones. Due to its nectar production each male flower is attractive for insects for about four days but usually the pollen was harvested rightaway on the first or the second day by visiting insects. On most of the days, the production of micropylar drops of the male cones started at 11 a.m. and there is no resorption of the drops. If removed they regenerate in about an hour. About 20 female flowers of each cone produced a micropylar drop every day. Each female flower produces a new micropylar drop for about ten consecutive days in a diurnal rhythm. The production did not start before 12 a.m. and normally reached its peak at about 2 p.m. At 5 p.m. all drops were gone. They were either collected by the insects or reabsorbed by the plant. The beginning of the nectar drop production on the female plant was at least an hour later than that on the male plant.

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The experiments with pollen traps showed that the wind is only responsible for the distribution of a small number of pollen grains in a radius of 6 m around the male plant. Pollen traps at the female plant growing 25 m away from the next male specimen did not receive a single pollen grain within six days. Pollination by wind is not impossible but we consider the effect of the wind as rather unimportant for the pollination of *Welwitschia*.

Eight species of flies carrying *Welwitschia*-pollen were observed at the female cones and are therefore regarded as pollinators. These were: Bengalia depressa WALKER, 1858 (Calliphoridae), Chrysomya albiceps WIEDEMANN, 1819 (Calliphoridae), Musca domestica L., 1758 (Muscidae), Physiphora demandata FABRICIUS, 1798 (Ulidiidae), Rhyncomya spec. (Calliphoridae), Ulidia spec. (Ulidiidae), Wohlfahrtia pachytyli TOWNSEND, 1919 (Sarcophagidae) and two unidentified species of the Bombyliidae. The most common and active visitor was Wohlfahrtia pachytyli, whose participation in pollinating *Welwitschia* was experimentally proved. Ceratitis capitata WIEDEMANN, 1824 (Tephritidae) and Ischiodon aegypticus WIEDEMANN, 1830 (Syrphidae) were also observed at the female cones but could not be caught to check if they were carrying *Welwitschia*-pollen. At least two further species of flies were observed at the female cones but could not be collected for identification and for screening for pollen.

One species of bees (Allodape spec., Anthophoridae) and one wasp species (Oxybelus spec., Sphecidae) were observed at the female cones and also seen to carry *Welwitschia* pollen, thus making them prime suspects as pollinators.

Our observations of Probergrothius sexpunctatus (Heteroptera) provided no indications of any activities of this insect being relevant to the pollination of *Welwitschia*.

Zusammenfassung

WETSCHNIG W. & DEPISCH B. 1999. Bestäubungsbiologie von *Welwitschia mirabilis* HOOK. f. (*Welwitschiaceae*, *Gnetopsida*). – Phyton (Horn, Austria) 39 (1): 167–183, mit 12 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In der Zeit vom 6. bis zum 14. Februar 1997 wurden an insgesamt sechs Tagen blütenbiologische Beobachtungen und Experimente an einer männlichen und einer weiblichen Pflanze von *Welwitschia mirabilis* auf der sogenannten Welwitschiafläche des Namib-Naukluft Nationalparkes in Namibia durchgeführt. Aufgrund der Blütenentwicklung nehmen wir eine Gesamtblühdauer von etwa 8 Wochen an, die ungefähr Mitte Jannuar beginnt und etwa Mitte März endet. Am männlichen Zapfen erblühten nur jeden zweiten Tag jeweils zwei Blüten. Jede männliche Blüte konnte bis zu 4 Tage lang zur Bestäubung beitragen aber normalerweise wurde der Pollen schon am ersten oder zweiten Tag von Insekten entfernt. An den meisten Beobachtungstagen begann die Nektarproduktion an den männlichen Zapfen etwa um 11 Uhr. Die Mikropylartropfen wurden nicht mehr resorbiert. Wurden Tropfen entfernt, wurden sie in etwa einer Stunde wiedergebildet. Von den Blüten der weiblichen Zapfen bildeten 20 zum Untersuchungszeitpunkt täglich einen Mikropylartropfen. Die weiblichen Blüten produzierten etwa 10 Tage lang Nektartropfen. Die Bildung dieses Tropfens folgte einem täglichen Rhythmus. Sie begann nicht vor 12 Uhr und erreichte etwa um 14 Uhr das Maximum. Um 17 Uhr waren alle Tropfen

verschwunden. Sie waren entweder von Insekten entfernt worden oder sie wurden von der Pflanze resorbiert. Jedenfalls gab es eine zeitliche Verzögerung von mindestens einer Stunde zwischen dem Beginn der Nektarbildung der männlichen und der weiblichen Pflanze.

Versuche mit Pollenfallen ergaben, daß der Wind nur eine geringe Anzahl von Pollenkörnern bis zu 6 m weit transportieren konnte. Pollenfallen an unserer weiblichen Pflanze – die 25 m weit von der nächsten männlichen entfernt war – zeigten, daß während sechs Tagen kein einziges Pollenkorn per Wind angeweht worden war. Windbestäubung ist zwar nicht unmöglich, wir halten allerdings die Bedeutung des Windes für die Bestäubung von *Welwitschia* für unbedeutend.

Acht Fliegenarten, die Pollen von *Welwitschia* mit sich führten, wurden an weiblichen Zapfen nachgewiesen und können daher als Bestäuber betrachtet werden. Es waren dies: Bengalia depressa WALKER, 1858 (Calliphoridae), Chrysomya albiceps WIEDEMANN, 1819 (Calliphoridae), Musca domestica L., 1758 (Muscidae), Physiphora demandata FABRICIUS, 1798 (Ulidiidae), Rhyncomya spec. (Calliphoridae), Ulidia spec. (Ulidiidae), Wohlfahrtia pachytyli TOWNSEND, 1919 (Sarcophagidae) und zwei unbestimmte Bombyliidae. Der häufigste und aktivste Blütenbesucher war Wohlfahrtia pachytyli. Für diese Art konnte auch experimentell bewiesen werden, daß sie die Bestäubung von *Welwitschia* durchführte. Ceratitis capitata WIEDEMANN, 1824 (Tephritidae) und Ischiodon aegypticus WIEDEMANN, 1830 (Syrphidae) wurden ebenfalls an den weiblichen Zapfen beobachtet, konnten aber nicht gefangen werden um zu überprüfen ob sie *Welwitschia*-Pollen transportierten. Mindestens zwei weitere Fliegenarten konnten an den weiblichen Zapfen beobachtet werden, es gelang aber nicht, sie für Bestimmungszwecke und den Nachweis von Pollen zu fangen.

Eine zu den Anthophoridae gehörige Bienenart (Allodape spec.) wurde an einem weiblichen Zapfen beobachtet. Da an ihr auch Pollen von *Welwitschia* nachgewiesen werden konnte, kann sie als Bestäuber betrachtet werden.

Eine kleine Wespenart (Oxybelus spec., Sphecidae) die reichlich Welwitschiapollen transportierte konnte ebenfalls am weiblichen Zapfen beobachtet werden und wird als Bestäuber betrachtet.

Unsere Beobachtungen an Probergrothius sexpunctatus (Heteroptera) ergaben keinerlei Hinweise auf eine Bestäubungsfunktion für *Welwitschia*.

1. Introduction

Since *Welwitschia mirabilis* was discovered in 1859 by Friedrich WELWITSCH (WELWITSCH 1861), this extraordinary plant has been subject of more than 250 articles. However, we were quite surprised to see that it is still not clear if the pollination is zoo- or anemophilous. Most of the statements about pollination were based on theoretical considerations rather than actual field observations. Only one publication (WETSCHNIG 1997) dealt exclusively with the pollination biology of *Welwitschia*.

Mainly three opinions about the pollination of *Welwitschia* can be found in recent literature:

1. Pollination by various insect species (but not by Probergrothius sexpunctatus).
2. Pollination by wind.
3. Pollination by Probergrothius sexpunctatus (Heteroptera).

When HOOKER 1863 provided the first detailed description of *Welwitschia mirabilis* he stated (p. 31): "It is reasonable to suppose that impregnation is effected by insect agency. . .". This opinion found acceptance by many of the consecutive authors and some field observations of insects visiting the flowers of *Welwitschia* confirmed this statement. Flower visitations by ants, bees, flies, mosquitos and wasps has been reported in literature up to now.

As far as we know STRASBURGER 1872: 271, 272 was the first who proclaimed that *Welwitschia* is pollinated by wind. This opinion also found acceptance by a lot of authors. It became rather popular through the works of BORNMAN – especially BORNMAN 1978 – and is still widely distributed in recent literature.

SCHINZ 1896 reported that he regularly found Odontopus (= Probergrothius) sexpunctatus (Heteroptera) at the inflorescences of *Welwitschia* and that this proof enough for a relationship between the plant and the insect. If he really meant pollination is hard to say but most authors interpret it so. PEARSON, who first strictly denied pollination by this bug (PEARSON 1906), changed his mind and than regarded Probergrothius to be the main pollinator of *Welwitschia mirabilis* (PEARSON 1907), which is still supported by some authors.

When the first author visited the *Welwitschia* in February 1995 he observed at least three species of bees visiting male and female plants (WETSCHNIG 1997). Unfortunately the schedule of that journey did not allow to spend more than one day at the *Welwitschia*. But plans were made to come again and study the pollination biology of this plant more thoroughly. These plans were realized in 1997 when we spent six days at the Welwitschiavlakte. It was intended to achieve a better knowledge of the pollination biology of *Welwitschia mirabilis* by continuous observations and some experiments.

2. Material and Methods

Our studies were performed in Namibia, in the Namib-Naukluft Park at the Welwitschiavlakte between the Swakop river and the Khan river. Two plants (a male and a female one) were choosen, approximately 700 m away from the famous "Big Welwitschia". The geographical coordinates are: 22°40′S/15°1′~40′E. The male plant was located at the base of a NNW-facing slope of approximately 16° inclination at about 355 m above sea level. The female one was located on the same slope about 25 m away from the male at about 360 m above sea level.

The male plant (Fig. 1) was 40 cm high and the stem measured 75 cm in diameter.

Fig. 1. *Welwitschia mirabilis*: The male plant of the actual study.

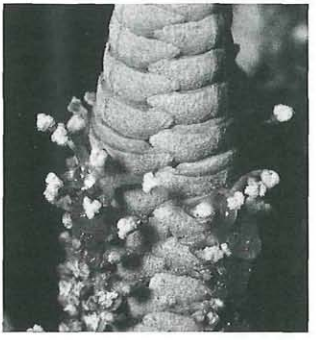

Fig. 2. *Welwitschia mirabilis*: Male cone with freshly opened male flower (left).

The female plant (Fig. 3) was 70 cm high and had a stem-diameter of 130 cm.

Observations and experiments were undertaken from 6. to 14. February 1997 with a gap from 10. until 12. February. The gap was caused by floodings of the Swakop which made it impossible for us to reach the designated plants. Observations started at 7:00 a.m. and lasted until 7:00 p.m. Every plant was visited at least once every hour, during the periods of presentation of pollen and nectar we stayed near the plants. During two nights the plants were visited every two hours.

For determination and scanning electron microscopy (SEM) studies some insects were caught with an entomological net. This proved to be rather difficult as most of the insects were very fast and very shy and they had to be caught at a safe distance from the plant as the inflorescences were rather brittle and vulnerable and any damage to the plants had to be avoided.

The flies were identified by Mr. Wolfgang SCHACHT at the Zoologische Staatssammlung München, while the bee and the wasp were identified by Mr. FRITZ

Fig. 3. *Welwitschia mirabilis*: The female plant of the actual study.

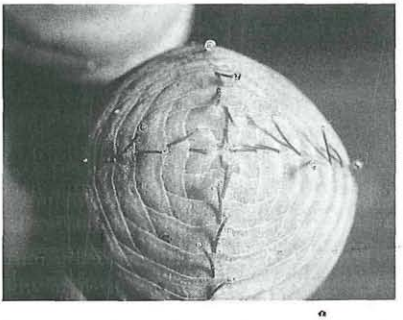

Fig. 4. *Welwitschia mirabilis*: Female cone with female flowers presenting nectar drops

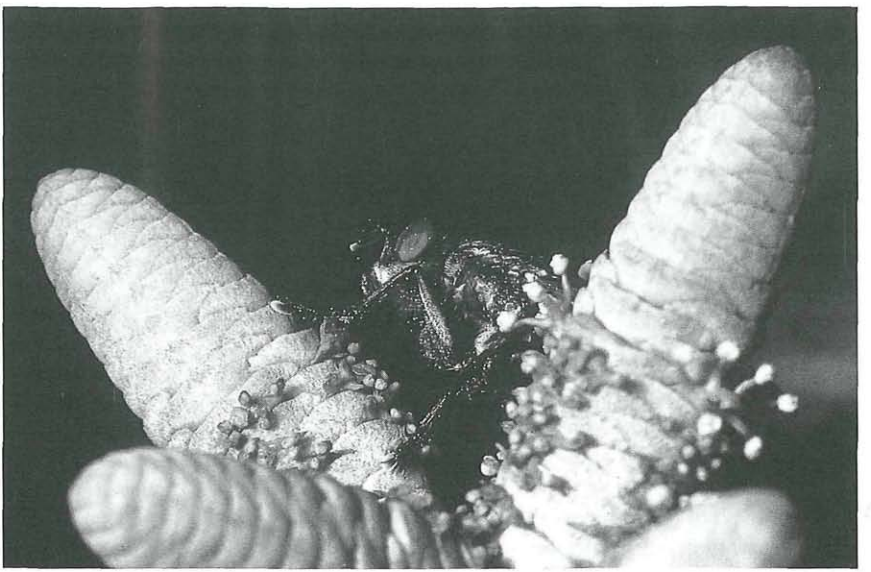

Fig. 5. Wohlfahrtia pachytyli at the male cone.

GUSENLEITNER at the Biozentrum of the OÖ Landesmuseum in Linz. Vouchers of the insects are deposited at the respective institutions.

Photographs of insects visiting *Welwitschia*-flowers were made with a Contax Camera, a 100 mm macro lens (Zeiss) on a bellows and an electronic flashlight. Video sequences of pollinating insects were made with a Sony video camera.

Scanning electron microscopic (SEM) observations and pictures were carried out at the Kärntner Landesmuseum in Klagenfurt. Insects were sputtered with gold and than observed with an JEOL (JSM-35C) scanning electron microscope.

For studies of duration of anthesis, particular cones were marked by coloured sewing thread. Particular flowers were marked by marking pen signs on their bracts.

If it was necessary to avoid insect visitation inflorescences were bagged with mosquito netting.

Microscopic slides covered with Vaseline were used as sticky pollen traps. These traps were bagged with mosquito netting to avoid insects from depositing pollen on them. Pollen traps were placed at the female *Welwitschia* plant and at certain distances (0, 1, 2, 6, 10 and 16 m) from the male plant in the major directions of the local winds. Traps were changed daily. For detection of pollen grains, hot glycerine gelatine was applicated to the sticky surface of the slide and covered with a 50×22 mm cover slip. Then the whole cover slip area (11 cm^2) was screened carefully with the help of a Reichert Polyvar microscope.

For the detection of flower fragrance whole and dissected cones were left in closed petri dishes for 15 to 30 minutes. The concentrated scents were investigated several times and compared with parts of the leaf treated the same way.

3. Results

3.1. Male Plant

The male plant of our study (Fig. 1) had 38 inflorescences and about 830 male cones. Each cone consisted of 48–72 flowers. The male flower (Fig. 2) shows in the middle of six synangia a rudimentary ovule, on whose micropyle the nectar drop is presented. Considering a mean number of 60 flowers per cone the whole plant must have produced about 49800 flowers in the 1997 flowering season. Since on every male cone only two flowers opened every second day, we had about 830 fresh opened flowers at our disposal every day. These flowers were the ones which were the most attractive to insects since they presented the maximum number of pollen and fresh nectar. Beside these flowers, there are about equal numers of 1, 2, 3 and 4 day old flowers. Depending on the individual history of each of these flowers they can present pollen (normally a very reduced number) and some nectar (normally less quantities, mixed with pollen and much more concentrated). Flowers older than 4 days were generally not at all interesting for the insects.

Within the cones, the flowers are arranged in a decussate manner. Two flowers of each node therefore develop simultaneously. Young floral buds are completely hidden by their bracts. Three days before the flower opens, a narrow brownish-red fimbris appears at the apical part of the bract (Fig. 2). This fimbris is the apical part of the perianth. If not examined carefully this fimbris may be considered as a part of the bract. Two days before the flower opens, the perianth elongates, which broadens the fimbris, making it rather conspicious. The day before the flower opens, the tips of the synangia may become visible.

On most of the days of our study the time schedule for flower opening was as follows:

9 a.m.: The synangia were just visible.

10 a.m.: The synangia were fully developed and spreading. No nectar was visible on the sterile ovule.

11 a.m.: A clear colourless nectar drop produced by the sterile ovule was fully developed and the synangia began to open. If not harvested by animals the nectar drop persisted the whole afternoon and the following night. This fact was experimentally proved by bagging male inflorescences. If removed the nectar drop was completely substituted after about an hour.

12 a.m.: The synangia were completely open and pollen presentation was at its peak.

On second day of the open flower, the synangia had lost most of their pollen grains. The nectar drop had lost volume, transparency and had become yellowish. The synangia may retain some of their pollen grains till

the fourth day. At this stage the nectar drop was highly concentrated, often mixed with pollen grains and had turned brownish in colour.

During the whole period of our studies the male cones had freshly opened flowers only every second consecutive day. This fact was proved by observing four marked cones of our particular male plant and one marked cone of five other plants. We could not verify if this time schedule is valid for the entire flowering period. But if so, the 1997 flowering period must have started about mid January and would have lasted until about mid March.

3.2. Female Plant

The female plant of our study (Fig. 3) had 52 inflorescences and about 290 female cones. Each cone consisted of 32–46 flowers. Considering a mean number of 39 flowers per cone, the whole plant must have produced about 11310 female flowers in the 1997 flowering season. An average number of 20 flowers per cone are producing a micropylar drop on a given day (Fig. 4). This means that every day about 5800 flowers of our specimen were able to be pollinated. Compared to the male flowers, the female ones had a distinctly higher longevity. During our nine days observation period only four flowers withered and four freshly opened at the particular female cones. We therefore believe that each flower produces a micropylar drop for about nine to ten consecutive days and then withers. This assumtion corresponds well with the beginning and end of anthesis of the male plant as postulated above.

On most of the days of our study the micropylar drops did not appear before 12 a.m. At about 2 p.m. all viable flowers had already produced a micropylar drop and the drops attained their maximum size. If removed, the micropylar drop appeared again but never attained its former size for the rest of the afternoon. At about 4 p.m. most of the micropylar drops had vanished or were reduced and till 5 p.m. all drops had disappeared. When the inflorescences are bagged, the resorption of the micropylar drop takes place as well, but with a postponement of about half an hour.

3.3. Fragrance

Especially when the weather was hot a very specific, somewhat resinous fragrance was evident from the male and female inflorescences. Our experiments prove, that this fragrance is not specially produced for attracting insects. We were not able to distinguish between the fragrance of male and female flowers and parts of the leafs or the stems of inflorescences. Vegetative parts of the plants do not emit any noticeable fragrance until injured.

3.4. The Effects of Wind for Pollination

The pollen grains of *Welwitschia* are ellipsoid with a length of about 45 µm and a diameter of about 21 µm (Fig. 6). They have no pollenkitt but are nevertheless sticky. If you blow on male flowers that are presenting their pollen you will not succeed in removing high numbers of single pollen grains, maybe some clusters of grains will be removed but these clusters do not fly any noteworthy distance. On the leaves of the male plants several of these clusters that have been removed by wind or by vibrations of the inflorescences can be found. The sticky pollen traps that were exposed at distances of 0, 1, 2, 6, 10 and 16 meters from the male plant showed that only very limited numbers of pollen grains are transported by the wind more than a few meters away. Over a period of six days we found the following mean numbers of pollen grains per day and per trap: 0 m: 890; 1 m: 17; 2 m: 4; 6 m: 2; 10 m and 16 m: 0. These results were also confirmed by the pollen traps between the inflorescences of our female plant. During the six days of observation, with wind every morning and evening, not a single pollen grain found its way to the four traps near the female plant (the nearest male plant was 25 m away). Four traps were also arranged between the inflorescences of a small female plant, with a distance of 4 m and 8 m separating it from the nearest male plants. During six days an average

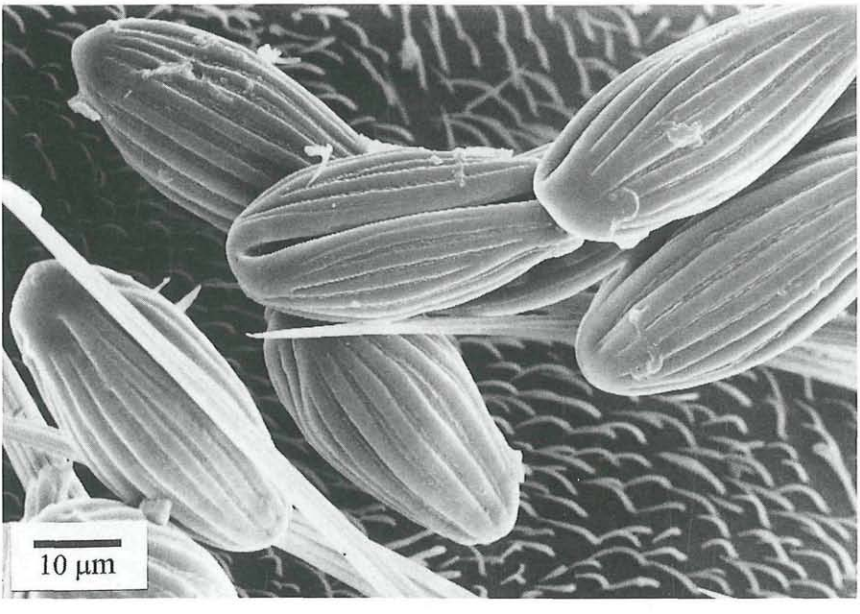

Fig. 6. SEM of *Welwitschia* pollen grains at Wohlfahrtia pachytyli. Photography: K. ALLESCH

number of 3 grains per day per trap were registered. This small female plant had about 120 female cones and about 2400 flowers producing micropylar drops during the five days of our pollen trap studies. With a mean diameter of the micropylar drop of about 1 mm and taking into account the whole surface of the drop, the total surface area of the micropylar drops of this plant would be about 75 cm^2. This would mean that an approximate number of up to 15 pollen grains per day could be received by the micropylar drops of this plant. But these estimations are purely theoretical as our traps were exposed for a whole day whereas the micropylar drops of the female flowers are only evident for some hours each day. During these hours there normally are soft winds or no winds. Furthermore the individuals of a *Welwitschia*-population normally grow rather scattered. So altogether, we think that the wind plays a rather unsignificant role in the pollination of *Welwitschia*.

3.5. The Effects of Animals for Pollination

During our study *Welwitschia*-specimens were visited by a variety of animals ranging from vertebrates like the namaqualand chamaeleon to insects (ants, bees, bugs, flies, moths, scale insects) and spiders. But only flies, bees and a wasp were observed to be acting as pollinators.

3.5.1. Flies

Flies were the most important pollinators by far. They were found in considerable numbers (3 to 10 individuals at one time) at our male and female plant for some hours every day. The following species were observed at the female plant: Bengalia depressa WALKER, 1858 (Calliphoridae), Chrysomya albiceps WIEDEMANN, 1819 (Calliphoridae), Musca domestica L., 1758 (Muscidae) (Fig. 7), Physiphora demandata FABRICIUS, 1798 (Ulidiidae), Rhyncomya spec. (Calliphoridae), Ulidia spec. (Ulidiidae), Wohlfahrtia pachytyli TOWNSEND, 1919 (Sarcophagidae). We observed at least two species of Bombyliidae (Fig. 8) at the male and female cones; two specimens were collected at the female cones but we were unable to get them identified. All these species of flies collected at the female plant carried moderate to high numbers of *Welwitschia* pollen grains (Fig. 6). Two further species of Diptera – Ceratitis capitata WIEDEMANN, 1824 (Tephritidae) (Fig. 9) and Ischiodon aegyptiacus WIEDEMANN, 1830 (Syrphidae) (Fig. 10) – were observed and photographed at the female cones but we were not able to catch them and check if they were carrying *Welwitschia*-pollen. At least two further species of flies were observed at the female cones but could not be collected for identification and for screening for pollen.

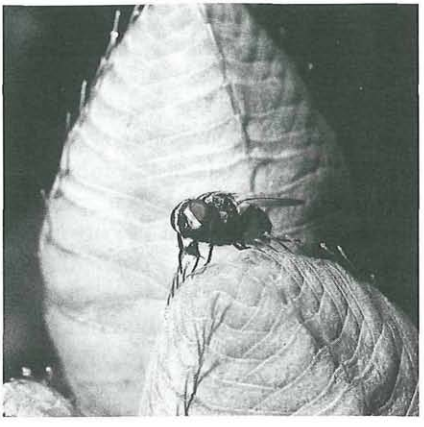

Fig. 7. Musca domestica at the female cone.

Fig. 8. Undetermined species of Bombyliidae at the female cone.

Among all the observed species of Diptera Wohlfahrtia pachytyli (Fig. 5) was the most common and active visitor of *Welwitschia*.

Flies normally appeared at the male inflorescences at about 11 a.m. At this time the nectar drops appeared and pollen presentation started. On cool or very windy days there was a delay of up to 2 hours, the flies then did not appear before 1 p.m. The flies were very busy, visiting lots of male cones and harvesting the available nectar. Doing so they became loaded with considerable numbers of the sticky pollen grains. Most of the pollen grains were located on the dorsal side of thorax and abdomen and on their legs. At about 3 p.m. the number of flies decreased and after 5 p.m. we did

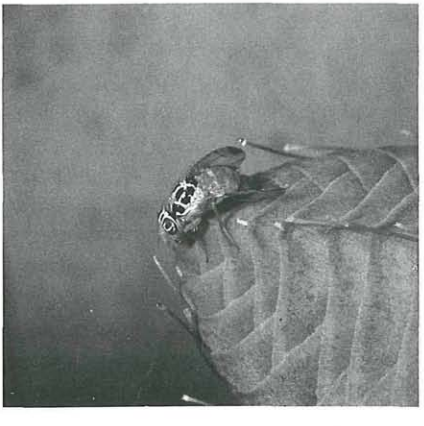

Fig. 9. Ceratitis capitata at the female cone.

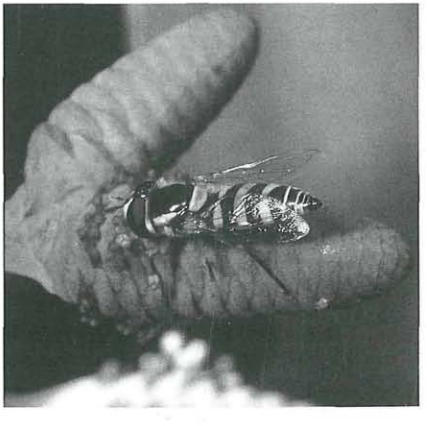

Fig. 10. Ischiodon aegypticus at the male cone.

not observe any flies at the male plants. At the female plant, flies normally arrived at about 2 p.m. when nectar production had reached its peak. We always registered lower numbers of flies at the female plant than at the male plant. At the female cones also, the flies exploited the nectar (Fig. 7) rather systematically, in course of doing so, the pollen grains were deposited on the micropyles. To prove this fact we performed the following experiment. We rinsed one female cone with water in the late afternoon. This cone was then bagged until micropylar drops appeared the next day. After observing the visit of Wohlfahrtia pachytyli to this cone, all (20) micropyles that had produced micropylar drops were collected. The microscopic observation showed that 3–10 pollen grains were adherent to 9 of the 20 micropyles. The number of flies decreased at about 4 p.m. and after 5 p.m. we did not see any flies at the female plant.

3.5.2. Bees

In contrast to the observations of 1995 (WETSCHNIG 1997) bees were only infrequently seen during the period of the actual study. We observed the honeybee Apis mellifera L. (Apidae) on 13. and 14. Feb. at 2 p.m. collecting pollen at our male plant. On 14. February we saw two specimens of a small bee-species collecting the nectar of the female flowers. This species belonged to the genus Allodape (Anthophoridae). Microscopic observations of one specimen showed that the insect carried *Welwitschia*-pollen on the ventral side of the thorax and abdomen and on the legs. While harvesting the micropylar drop on the female cones the behaviour of the animal makes it very likely that it deposits pollen on the micropyles.

3.5.3. Wasps

On 14. February, a single specimen of Oxybelus spec. (Sphecidae) collected the micropylar drops of a female cone. As the animal carried a high number of *Welwitschia*-pollen on the ventral side of thorax, abdomen and on the legs it is very likley that it contributed to pollination.

3.5.4. Probergrothius sexpunctatus (Heteroptera)

Up to five specimens of this bug were seen together on the male and the female plant. We did not see any juvenile Probergrothius on our plants but there were some on other specimens. We were not able to see any actions of the adult bugs that would be relevant for pollination. In fact only once did we see an adult at a cone (a male cone). Normally they remained on the leaves of the plants. Their favorite place for feeding were the stems of the inflorescences. During the present study, we never saw an adult Probergrothius feeding on a female cone. But the first author had seen them doing it rather frequently on previous visits (Fig. 11). We did not

observe any signs, that these bugs leave their "homeplant" by foot or by wings. We never saw these insects making any use of their wings. We tried to irritate them so as to stimulate flight and once we released them 50 m away from the next *Welwitschia* but they never used their wings to escape or to get back to their plant. We examined 20 adult specimens from 10 different male and female plants with a 20× magnifying glass before releasing them, none of them showed any adhering pollen. Close examinations (also by SEM) showed no adhering pollen grains on the three specimens collected at the female plant. One specimen collected at the male plant showed four *Welwitschia* pollen grains on the ventral side of the thorax.

3.5.5. Ants

Two different species of ants frequently visited our plants. They were observed at the female plant definitely more often than at the male plant. At the female plants the ants stood near the micropyles and harvested the nectar without touching any other micropyle (Fig. 12). We could not find pollen grains adherent to any of the ants collected at the female plant. We were not able to observe where the ants were living and how far they went for food. Considering the behaviour and the size of these ants we do not consider them as pollinators of *Welwitschia*.

Fig. 11. Probergrothius sexpunctatus at the female cone. The photograph was taken at the location of the actual study but at a previous visit at 8. February 1995.

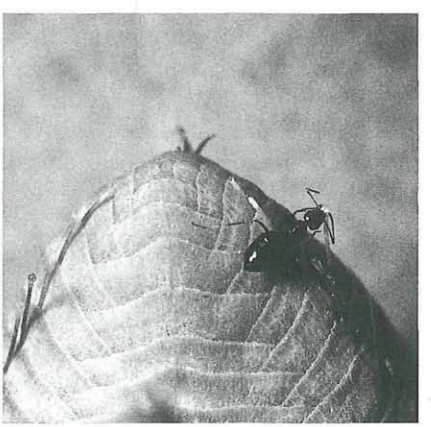

Fig. 12. Undetermined species of ant exploiting the micropylar drop of a female flower.

4. Discussion

Our observations on the development of male and female flowers lead us to the conclusion that in 1997 the flowering period of *Welwitschia* started about mid January and ended about mid March. This corresponds with PEARSON 1906 who discovered the first flowers when he visited *Welwitschia* on the 12. and 13. January 1904. SONG 1980 who observed cultivated plants in a greenhouse noticed a flowering period of 6–8 weeks for the male plants and about 6 weeks for the female ones. JAARSFELD 1990 who also observed cultivated plants, stated that flowering at Kirstenbosch commenced in March and lasted till May. Contrary to our observations he says that in habitat the female cones become receptive to pollen in May.

We observed, that the female flowers produce a micropylar drop day after day for a period of about ten consecutive days. As far as the length of the period is concerned, this agrees with CARAFA, CARRATU & PIZZOLONGO 1992 who observed plants in a greenhouse. But contary to our observations they did not find a diurnal rhythm in the production of the drop. They only state about the drops that ". . .their bulk slightly increasing in the warmer hours of the day when atmospheric humidity is lower" and that "hand pollination does not produce rapid withdrawal of the drop, which is formed again when removed manually". PEARSON 1907 observed plants at their natural habitat and found that the micropylar drop at female flowers "was not observed earlier than 9 a.m. but was common at 9.30 a.m. It remained there until 3 p.m. but disappeared before sunset". This supports our observations of a diurnal rhythm but we never observed micropylar drops on the female flowers that early in the morning. Unfortunately PEARSON 1907 did not mention the time when micropylar drops were produced on the sterile ovules of the male flowers. PEARSON 1909: 344 stated that a micropylar drop is produced by the female flower day after day for two or three days at least. SONG 1980 wrote ". . . the pollination droplet is produced and may disappear and reappear daily for about a week or may persist".

As already mentioned published field observations of flower visitors or pollination of *Welwitschia* are rather scarce. SCHINZ 1896 reported that he always found Odontopus sexpunctatus (= Probergrothius sexpunctatus) at the inflorescences of *Welwitschia* and as this insect already attracted the attention of BAINES 1864 he stated that the idea of a relationship between *Welwitschia* and that insect is obvious.

PEARSON 1906 who visited the *Welwitschia* on the 12. and 13. January 1904 at a very early stage of the flowering period (most of the female cones had no protruding micropyles) reported that "At times the whole inflorescence is surrounded by a swarm of small flying insects which seem to be very definitely attracted to the cones. Insects, apparently of the same species, were seen on the cones and also around the female inflorescences.

Attempts to capture specimens were unsuccessful." About Odontopus (= Probergrothius) he wrote: "It seems to avoid the pollenshedding cones, and a large number of specimens examined for adherent pollen were found to be quite free from it." This agrees with our observations. Three years later PEARSON visited the *Welwitschia* again (PEARSON 1907). The cones then were considerably more advanced as he observed them from 22. January onwards. He captured fourteen specimens of Odontopus "sexpunctulatus" from male and female plants, examined them microscopically and found that all of them carried pollen. The pollen adhered singly or in masses to the smooth surface of the abdomen or were caught up among the short hairs on the limbs. This observation is definitively contrary to our recent findings and to the previous observations (WETSCHNIG 1997) when 30 adults were taken from female plants and only very low numbers of pollengrains on some of them were observed. We can only explain this inanity with the assumption of a striking change in the behaviour of Probergrothius. Maybe there are times in the life cycle of this bug (mating, egg-laying) when they can act as a pollinator of *Welwitschia*. Like PORSCH 1957 we too can not explain what PEARSON meant with "the short hairs of the limbs" of Probergrothius. We found no hairs on this insect where pollen could be caught. PEARSON 1907 also explained the pollination by the bug: "I have observed that as the insect walks over the cone the abdomen is touched by the exserted anthers in the one case and by the fluid-tipped micropyle in the other." PEARSON 1907 states that Odontopus is an important pollen-carrier but not the only one. He also noticed a fly which sometimes was present in considerable numbers and at least two species of Hymenoptera.

GIESS 1969 reports the observations of two scientists: JOUBERT observed bees, which visited *Welwitschia* in the morning and in the evening and carried thick corbiculae of *Welwitschia*-pollen. Bees observed at the male plants were also observed visiting female cones. JOUBERT was therefore convinced that pollination is done by bees. FAGERLIND who spent some days at the Welwitschia-plain north of the Swakop confirmed that *Welwitschia* is visited by flying insects at morning and at evening and that pollination is done by these insects.

KUBITZKI 1990: 389 says that *Welwitschia* may be ambophilous. He further mentioned a personal communication by IHLENFELDT who observed different insects, including Hymenoptera and mosquitos as flower visitors, obviously in search of liquid.

JAARSVELD 1990 suspects that a small wasp which was seen amongst male flowers at Springbokwasser acts as a pollinating agent.

SEELY 1992: 64 reported about investigations at the Desert Ecological Research Unit at Gobabeb which have ". . . fairly conclusively established that wind could not blow the large, sticky pollen grains between the scat-

tered individual plants." No details about the methods of these investigations were given but the result is confirmed by our study. The size of the pollen grains of *Welwitschia* should not be an obstacle for pollination by wind as many wind-pollinated species have pollen grains of similar and even bigger sizes. So it seems that mainly the stickiness of the pollen hinders the distribution by wind. This stickiness is not caused by pollenkitt as HESSE 1984 has shown. If it is caused by tapetal cytoplasma debris as he suspected, is still unknown. SEELY 1992 suspected that instead of the wind different insects probably several species of wasps are responsible for the pollination of *Welwitschia*.

LOVEGROVE 1993: 174 observed ". . . flies carrying substantial deposits of pollen on their legs and bellies while clambering about the male 'flowers'. If they had reason to alight on female 'flowers' they could well be acting as pollinators, although we don't yet know what may attract them to either reproductive organ in the first place." He also gave a good photograph showing a male cone with a fly carrying pollen at her legs. It is not possible to determine the fly of this picture for sure but it is very likely to be Wohlfahrtia pachytyli, the species most often found at *Welwitschia* in the course of our study.

WETSCHNIG 1997 observed three bee-species visiting the *Welwitschia*. Apis mellifera and an Anthophora species were observed on the male cones whereas a member of the Nomiinae was found visiting both, male and female cones. Furthermore some flies, ants and Probergrothius sexpunctatus were observed but bees were the most common visitors of *Welwitschia* by far. When we carried out our recent study at the same place and at the same time of the year as the previous study (WETSCHNIG 1997) we were rather surprised by the missing bees. It was only on the last two days of the recent study that we registered Apis mellifera. On the very last day of the recent study we also observed a second bee-species (Allodape spec.) and the only wasp that we were able to see (Oxybelus spec.). Compared to SEELY 1992 the scarcity of wasps in our study is remarkable. We were not able to find an actual food source in the near vicinity of our location that could be more attractive to bees or wasps than *Welwitschia*. But as bees and wasps are able to fly noticeable distances to attractive food sources it is easily possible that they were busy exploiting other plants growing in the area. The long flowering period of *Welwitschia* certainly provides chances for a wide range of possible pollinators and allows variations in the yearly development of animal populations and in their food source preferences.

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