Thuranthos: notes on generic status, morphology, phenology and pollination biology

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ABSTRACT

The generic status of *Thuranthos* C. H. Wr. is discussed. A key separating the two species is provided. The genus is reported to occur in Natal for the first time. Field studies in Natal have yielded additional information on the habitat, phenology, fruit morphology and pollination biology of *T. macranthum* (Bak.) C.H. Wr. Phalaenophily is reported for the second time in the South African Liliaceae. The relationship of *T. macranthum* with the moth *Diaphone eumela* (Cramer)—Noctuidae, Hadeniae, is discussed.

Résume

THURANTHOS: NOTES SUR LE STATUT GÉNÉRIQUE, MORPHOLOGIQUE, PHENOLOGIQUE ET BIOLOGIQUE DE LA POLLINISATION

Le statut générique de Thuranthos C. H. Wr. est discuté. Une clef séparant les deux espèces est fournie. Le genre est signalé du Natal pour la première fois. Des études sur le terrain au Natal ont fourni des informations additionnelles sur l'habitat, la phenologie, la morphologie du fruit et la biologie de la pollinisation du T. macranthum (Bak.) C.H. Wr. La phalaenophilie est signalée pour la seconde fois dans les Lileaceae d'Afrique du Sud. La relation di T. macranthum avec l'alène Diaphone eumela (Cramer)—Noctuidae, Hadeniae, est discutée.

INTRODUCTION

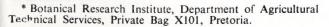
Thuranthos C.H. Wr. provides an example of the difficulties and controversies encountered in the delimitation of genera in the Liliaceae. Wright (1916a) established Thuranthos to accommodate the species Thuranthos macranthum (Bak.) C.H. Wr. which had been anomalously referred to the genera Ornithogalum L. and Drimia Jacq. respectively (Fig. 1). A second species T. nocturnale was described by R. A. Dyer in 1964 (Fig. 2). The generic name Thuranthos is derived from θvpa , an opening, and $av\theta os$, a flower, in allusion to the interspaces between the lower parts of the filaments (Wright, 1916b).

GENERIC STATUS OF THURANTHOS

In a recent study Jessop (1973) sinks *Thuranthos* C.H. Wr., *Urginea* Steinh. and *Urgineopsis* Compton under *Drimia* Jacq. This decision is clearly based on the relationship between *Urginea* and *Thuranthos* on the one hand and between *Urginea* and *Urgineopsis* on the other. Field studies suggest, however, that the two species of *Thuranthos* have very distinct features separating them from all species of the other three genera.

Like other authors (Wright 1916a, 1916b; Dyer, 1964) I consider the structure of the filaments of *Thuranthos* to be an outstanding feature, which is of particular significance with respect to pollination biology. The structure of the filaments only becomes visible once the perianth segments have reflexed and for this reason is scarcely apparent in herbarium specimens.

The filaments are clearly divisible into two regions. Fig. 3.1 shows the basal parts which are flattened and convex. This region resembles a paper lantern with longitudinal slits. In the upper region (Fig. 3.2) the filaments are mostly terete and straight but often arch near the anthers (Fig. 3.3) and at the point of connivence (Fig. 3.4). The basal region is a drab yellow-green, like the perianth segments, whereas the upper region is white. The green anthers produce white lanceolate pollen grains (Fig. 3.5).



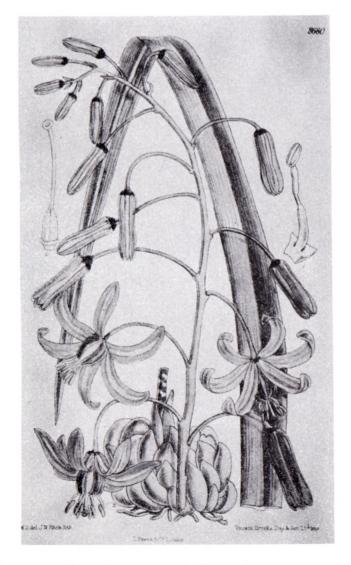


Fig. 1.—Thuranthos macranthum (Bak.) C.H. Wr., photograph from Bot. Mag. CXLII. t. 8680 (1916).

FIG. 2.—Thuranthos nocturnale R. A. Dyer, photograph from Flow. Pl. Afr. 36. t. 1439 (1964).

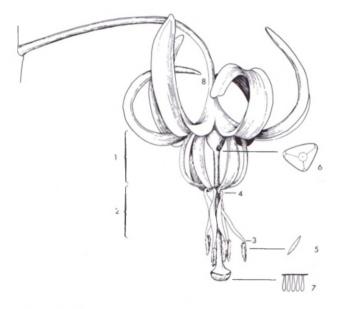


Fig. 3.—Thuranthos macranthum, showing open flower. 1, basal region of androecium; 2, upper region of androecium; 3, arching base of upper filament region; 4, arching apex of upper filament region; 5, pollen grain; 6, T/S near apex of ovary, gland position indicated in corners, style position shown in centre; 7, papillae of stigma.

None of the species of *Urginea*, *Urgineopsis* or *Drimia* has such a complex filament structure. Until detailed field studies on the *Drimia—Thuranthos* relationship (sensu Jessop, 1973) have been undertaken it seems best to maintain *Thuranthos* as a genus.

SPECIES OF THURANTHOS

1. Thuranthos macranthum (*Bak.*) *C.H. Wr.* in Kew Bull. 1916: 213 (1916); C.H. Wr. in Bot. Mag. CXLII. t. 8680 (1916).

Ornithogalum macranthum Bak. in J. Linn. Soc. (Bot). 13: 280 (1873). Types: Cape Province, Drège 2204, 3531. Drimia macrantha (Bak.) Bak. in Bot. Jahrb. 15 (3): 7 (1892) Urginea macrantha (Bak.) Phill. in Ann. S. Afr. Mus. 16: 305 (1917).

2. Thuranthos nocturnale R. A. Dyer in Flow. Pl. Afr. 36: t. 1439 (1964). Type: Cape Province, Grootfontein, Acocks 18650 (PRE, holo!).

In the past these two species have been separated on the shape of the leaves and capsules, the presence or absence of pubescence on the stigma and the length of the peduncle. The following key incorporates additional characters observed during field studies.

Scape 50-140 cm high, peduncle $1\frac{1}{2}$ to $2 \times longer$ than inflorescence, not noticeably thickened at base; flowers pendulous, pedicels of reflexed flowers arched, only inner perianth segments tightly reflexed; stigma glabrous; capsule (3,4)4,0-5,0 cm long, 1,5-2,0 cm broad, ovate oblong, twice as long as broad, upright on vertical pedicel, surface smooth...... macranthum

BIOLOGY OF T. MACRANTHUM IN NATAL POPULATIONS

Distribution

Two populations of *T. macranthum* have been found in Natal and seem to constitute the second record for the Province. Ross (1972) cited Taylor 29750 (NH), from the Natal Midlands, as *T. macranthum*. I have not seen this specimen. The additional Natal localities are Edendale, Pietermaritzburg (2931 CB) and Mkondeni (2931 CB).

Habitat

The Edendale population occurs in an annually burnt vlei. This area holds surface water in shallow depressions throughout the summer but gradually dries out with the onset of winter by which time very little vegetation is photosynthesizing. Plants were found to grow on raised tussocks.

The Mkondeni population occurs along the edge of a well-grassed donga (eroded gulley) which, although drier than the Edendale population, generally holds more water than the surrounding area.

The Edendale locality has a soil belonging to the Rensburg series whereas the Mkondeni locality has a soil of the Clovelly Series. These soils differ markedly in PH value, base saturation and the sum total of exchangeable cations (Van der Eyk, Macvicar & De Villiers, 1969). From this information one could conclude that this species is plastic as to its general edaphic requirements.

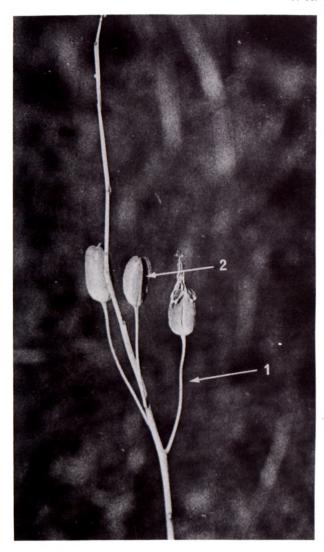


FIG. 4.—Thuranthos macranthum, rhachis bearing fruits 1, erect pedicel; 2, upright deeply angled fruit. Note the remains of the perianth segments on the right hand fruit. The centre fruit is atypical in form.

Phenology

Scapes are produced during October and November. The erect 50–140 cm scapes emerged about three months before the leaves. Nineteen scapes emerged in the Edendale locality during 1973, and over sixty-five scapes were counted during 1974. This seems to indicate a seasonal flowering periodicity and needs further study. In both localities the scapes emerged in a flush with no recorded stragglers appearing at a later date. An average of 15 to 24 flowers were produced per plant in both populations. Leaves appeared during late January after the capsules had dehisced and the scapes had died back.

Fruit morphology

Capsules were unknown to Jessop (1973). A short description, however, did appear in Bot. Mag. CXLII t. 8680 (1916): "Capsula longa, laevis, 3,5 cm longa, I cm diametro, pedicillis suberectus instructa". Based on a population of 135 capsules, from two populations, this description is amended as follows. Capsule upright on erect pedicel (Fig. 4.1) deeply 3-angled (Fig. 4.2), (3.4) 4,0-5,0 cm long, 1,5-2,0 cm broad, narrowing from base to apex, base slightly cordate to truncate, apex emarginate-truncate, more than twice as long as broad, carpels with slight groove down angle (Fig. 5.1), surface smooth (Fig. 5.2), green with a faint white bloom, turning brown with age, basipetal tricarpellar dehiscence. Seeds 10-12 mm long, 6-8 mm wide, black.

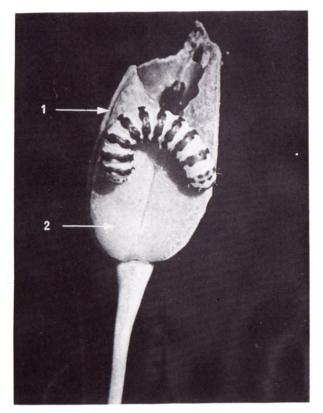


Fig. 5.—Fruit of *Thuranthos macranthum*. The fruit shows feeding damage by the caterpillar *Diaphone eumela* (Cramer) shown in the foreground. 1, slight groove down angle; 2, smooth surface of capsule.

Pollination biology

Important features of the flower of *T. macranthum* as shown below agree with those given by Faegri & Van der Pijl (1971) as typical of phalaenophily (moth pollination).

Nocturnal anthesis

Diurnal closure

Drab colour

Copious secretion of strongly scented nectar

Versatile anthers

Deeply divided perianth segments (reflexing upwards)

Lattice like structure of basal region of androecium and of reflexed perianth segments

Partly obscured nectar.

Field studies have shown that the Noctuid moth Diaphone eumela (Cramer), Fig. 6, is closely associated with T. macranthum. The relationship is discussed after a short description of the floral mechanism of T. macranthum.

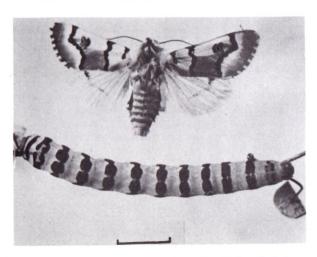


Fig. 6.—Diaphone eumela (Cramer), moth and larval stages.

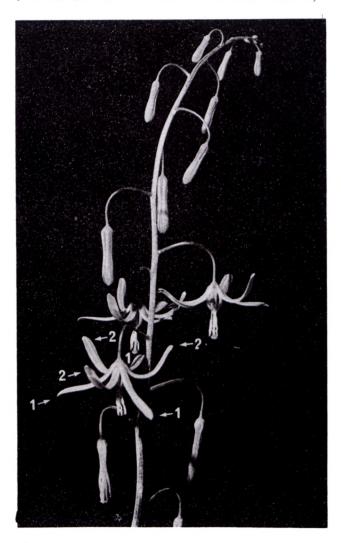


Fig. 7.—Thuranthos macranthum, flowers in the process of opening. 1, outer perianth segments; 2, inner perianth segments. Compare the position of the filaments with the later stage shown in figure 8.

Flowers opened at dusk between 1730 and 1800 hours and closed at dawn between 400 and 500 hours. Laboratory and field observations strongly suggest that a circadian rhythym is involved. This phenomenon needs further study by physiologists.

Fig. 7 shows flowers in the process of opening. The outer perianth segments are the first to spread outwards and upwards (Fig. 7.1). They are followed closely by the inner perianth segments (Fig. 7.2) which curl rapidly and tightly inwards until the tips almost touch the apex of the pedicel (Fig. 8.3). The pedicel itself stiffens and arches so that it lies above the horizontal. This movement forces the open flower away from the rhachis (Fig. 3). In this aspect *T. macranthum* differs markedly from *T. nocturnale*. In the latter the pedicel is patent and only curves downwards slightly at the tip. This forces the flower well away from the rhachis and at about an angle of 20°-30° off the vertical (Fig. 2). It is worthwhile to note that as far as the reflexure of perianth segments is concerned both Fig. 1 and 2 are incorrect. These paintings were probably made during the late afternoon or early evening before the perianth segments had completely reflexed. Mrs A. A. Obermeyer confirms this for Fig. 2. Coloured negatives of the open flowers of the type specimen of T. nocturnale (in PRE) show that all the perianth segments reflex tightly towards the apex of the pedicel. This is not shown in Flow. Pl. Afr. 36. t. 1439 (1964).

Open flowers exude strongly perfumed nectar which saturates the ambient atmosphere. The nectar is produced by three glands, one each at a corner of the triangular apex of the ovary (Fig. 3.6). A drop of nectar is visible in Fig. 8.1. Note also the shiny inner surface of the perianth segments which could be due to some secretion (Fig. 8.2).

Flowers open only once. After closing in the early morning the flowers dry out and by evening they become mucilaginous owing to the breakdown of tissue of the inner walls of the perianth segments. No more than three flowers were ever seen open on any one plant at the same time. The flowering period of individuals extended from six to nine days depending on the number of flowers produced per inflorescence.

The moth Diaphone eumela (Cramer) belongs to the family Noctuidae, sub-family Hadeniae (Fig. 6). It lays its eggs on the youngest buds of the inflorescence of *T. macranthum* usually at a time when the first flower opens. The young larvae feed on the flower buds. It was found that the first opened flowers had produced sizeable fruits by the time the larvae, which had undergone a number of instars, had reached these fruits. Fruits and ovaries appeared to be the main diet of grown larvae (Fig. 5). No more than fifteen of these yellow and black caterpillars were seen on any one plant, and were found on only 6 per cent of the total number of scapes produced in both populations. On maturity the caterpillars crawl down the scape and pupate beneath the soil, forming mud cocoons. Laboratory reared caterpillars formed chrysali without spinning a cocoon if no substrate was provided, otherwise they pupated like the "wild specimens". Moths emerged from the chrysali after a period of three weeks under laboratory conditions.

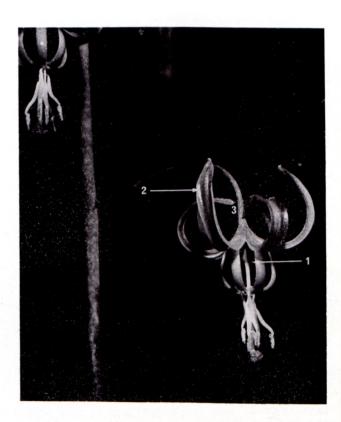


Fig. 8.—Thuranthos macranthum, flowers open. 1, drop of exuded nectar; 2, shiny undersurface of perianth segments; 3, tips of inner perianth segments reflexed tightly towards the apex of the pedicel.

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Diaphone eumela (Cramer) pollinates T. macranthum as follows: The moth lands on the filament cage with its head pointing upwards. The movement of its feet as it attempts to maintain this position causes the

independant filaments to move. These filaments push against the style at the point of connivence then slip off (similar to pushing a pencil against a thin cylinder). The moth usually slides down until it hangs beneath the anther cage. This causes the moth's abdomen to rub against the anthers and sticky stigma. Some moths were observed to land on the top of the perianth segments, head downwards. The effect of their movements resulted in the ready release of pollen. In such cases very little pollen fell on the stigma as only the apical part is receptive i.e. the half-circle facing the ground. Note the stigmatic papillae in Fig. 3.7.

Apart from *D. eumela* (Cramer) no other pollinators were observed. Autogamy may occur but seems unlikely in view of the small number of capsules produced per plant. Moths were noted to visit most open flowers, often returning to the same flower on a number of occasions to feed on the nectar. There is no record of pollination in *T. nocturnale*.

Stuckenberg (1975) informed me that *D. eumela* had been recorded to have the following host plants: *Ornithogalum virosa* Lindl. (=0. ecklonii Schlecht.), *Dipcadi viride* (L.) Moench [=D. umbonatum (Bak.) Bak.] and *Albuca setosa* Jacq. (=A. pachychlamus Bak.). *T. macranthum* is a new host plant record. Davidson (1975) has observed at least three further Liliaceous genera on which the larvae of *D. eumela* also feed. It would be most interesting to have further information of the relationship, if any, of the moth to the flowers of these various genera.

DISCUSSION

Judging by the existing literature and by my own observations phalaenophily seems to be a rarely recorded type of pollination in the South African flora. Vogel (1954) records phalaenophilous flowers for only one South African member of the Liliaceae, namely a species of *Dipcadi*. This report constitutes, to the best of my knowledge, the second such case. The meagre knowledge of this phenomenon could undoubtedly be due to the nocturnal behaviour of both plants and insects, as opposed to the diurnal closure of botanists and entomologists. Future

pollination studies in the South African flora could conceivably be based on a critical assessment of structural morphology with subsequent extrapolation to the field.

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UITTREKSEL

Die generiese status van Thuranthos C.H. Wr. word behandel. 'n Sleutel vir die onderskeiding van die twee species word verskaf. Vir die eerste keer word aangeteken dat die genus in Natal voorkom. Veldwerk in Natal het addisionele inligting oor groeiplek, fenologie, vrugmorfologie en bestuiwingsbiologie van T. macranthum (Bak.) C.H. Wr. aan die lig gebring. Motbestuiwing word vir die tweede keer in die Suid-Afrikaanse Liliaceae aangeteken. Die verwantskap tussen T. macranthum en die mot Diaphone eumela (Cramer)—Noctuidae, Hadeniae, word bespreek.

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