

THE TROPICAL LIANA *TRIPHYOPHYLLUM PELTATUM* (DIONCOPHYLLACEAE): FORMATION OF CARNIVOROUS ORGANS IS ONLY A FACULTATIVE PREREQUISITE FOR SHOOT ELONGATION

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Summary

The complete life cycle of *Triphyophyllum peltatum* (Dioncophyllaceae) has been observed under greenhouse conditions. Without passing through the carnivorous stage, the plant reached maturity and, after flowering abundantly, developed the unusual seeds. This cultivation success permitted valuable observations on floral and fruit biology of *T. peltatum*.

Introduction

The palaeotropical plant family Dioncophyllaceae (Airy Shaw 1951) consists of three species: *Triphyophyllum peltatum* (Hutch. & Dalz.) Airy Shaw, *Habropetalum dawei* (Hutch. & Dalz.) Airy Shaw, and *Dioncophyllum thollonii* Baillon. Of these, only *Triphyophyllum* is known to bear carnivorous glandular leaves, and this only occurs during a certain period of its life. The systematic position of the Dioncophyllaceae was very unclear for a long time. At the time of the discovery of *Triphyophyllum peltatum* (originally called *Dioncophyllum peltatum*) in Sierra Leone in 1927, the describers placed it in the Flacourtiaceae (Hutchinson & Dalziel, 1927). Since then many authors expressed their opinions on the relationships of the Dioncophyllaceae to other plant families, based on morphological evidence. Recently, genetic investigations confirmed its placement within the Caryophyllidae as a sister clade of the noncarnivorous Ancistrocladaceae and as a close relative of the carnivorous Drosophyllaceae (Meimberg *et al.*, 2000). This placement is chemotaxonomically supported by the presence of naphthylisoquinoline alkaloids both, in the Dioncophyllaceae and in the Ancistrocladaceae (Bringmann & Pokorny, 1995) and by the occurrence of structurally and biosynthetically closely related naphthoquinones in most of the closely allied families (Nepenthales) within the Caryophyllidae (Hegnauer, 1989).

Among carnivorous plant enthusiasts *Triphyophyllum peltatum* is particularly famous for its “part-time carnivorous” habit (Bringmann *et al.*, 1996), which distinguishes it from all other known carnivorous plants. In this paper we complete our observations on this intriguing species based on further observations on greenhouse grown plants.

Materials and Methods

In April 1996 juvenile *T. peltatum* plants, which had not been carnivorous before, were received from the Centre National de Floristique in Abidjan, Ivory Coast. The plants had been grown there for a time after having been legally collected in the Parc de Taï.

The plants were grown in the greenhouse of the Botanical Garden in Würzburg propagation chambers as described previously (Bringmann *et al.*, 1999). Slow release fertilizer (Osmocote®, NPK 14/14/14, Urania Agrochem GmbH, Hamburg, Germany) was added to the substrate. When the plant started to elongate it was repotted in a 65 liter vessel in hydroponic substrate and was placed outside the chamber in the greenhouse.

Results and Discussion

1. Stem Elongation of Rosetted Plants: Possible without Carnivorous Stage

In our previous communication (Bringmann *et al.*, 1999) we reported on the germination of *Triphyophyllum peltatum* and the development of rosetted plants in the greenhouse. Our expectation that the plants would develop glandular leaves (Marburger, 1979) capable of catching and digesting prey was not fulfilled.

Field studies (Schmid, 1964; Green *et al.*, 1979) suggested that the development of *T. peltatum* proceeds through two distinct phases, as is known in many other tropical lianas. Juvenile plants remain small for a considerable period of time (up to several years), and the leaves are separated from each other by very short internodes, so they are arranged in rosettes or short shoots. It is only then, right after the unique carnivorous stage, that a marked change occurs: The internodes elongate considerably, and the resulting elongated shoots start climbing into the canopy of high trees, which, in the case of *Triphyophyllum*, is facilitated by hooked leaves that are formed on elongated shoots. The two lateral subapical hooks are positively thigmonastic (coiling in the direction of contact) and anchor the slender climbing shoots on their way up.

In contrast to these observations in the field, in October 1998 one plant (two and a half years old, 35 cm high with a rosette of 30 mature lanceolate leaves 20 to 40 cm in length, which had not been carnivorous before) elongated by producing new leaves which were separated by much larger internode length (see back cover) and formed the characteristic hooked leaves (Figure 1), which account for the familial name "Dioncophyllaceae." Within a few weeks the shoot reached nearly 2 m in height. Because of limited greenhouse space the shoot was trained to a horizontally fixed wire (1.5 m high). In the lower part of the plant the stem exhibited a clearly visible secondary growth. Then signs of lignification became visible and the outer bark started bursting (Figure 2). From the point of the first attachment to the wire, the elongated shoot grew for another 2 m in the horizontal direction. About every fifth leaf was attached manually to the wire by its hooks because the free end of the shoot tended to grow obliquely upwards.

These observations prove for the first time that carnivory is not a prerequisite for shoot elongation in *T. peltatum*.

2. Flower Development and Morphology

Surprisingly the *Triphyophyllum* plant began to produce numerous inflorescences. On June 5, 1999, several flower buds were observed on specialized short flowering shoots formed in the axils of the elongated shoot leaves. The total inflo-

rescence comprised 34 consecutive nodes at the apical portion of the elongated shoot. The flowering branches had 1 to 5 buds arranged in a cymose cluster, the bud on the longest branch usually opening first. Within two weeks the buds enlarged from 3 mm diameter (spherical) to a size of 2 cm length \times 6 mm width (elliptical). On June 20, 1999 two flowers of *T. peltatum* opened, to the best of our knowledge the first ever obtained in cultivation.

All parts of the flower are glabrous (Figure 3). The flowering pedicel is 2.5-4 cm long and *ca.* 2 mm wide, terete, and dull red. It is usually subtended by a small bract 1-10 mm long. The flower is actinomorphic. The 5 persistent sepals remain short (*ca.* 2 mm long, 1 mm thick), triangular, acute, spreading, and form a star-shaped calyx. The petals are contorted in bud, coriaceous, whitish, *ca.* 20 mm long and 5 mm wide, slightly involute, and narrowly elliptical. The petals are fragrant (pores on the adaxial surface), and the fragrance lasts as long as the flowers are open (just one day, see below). It is pronouncedly sweet and is reminiscent of ripe fruit or carnations. The 10 stamens consist of short stout, white filaments and acute, narrowly triangular anthers *ca.* 2 mm long (Figure 4), bearing yellow pollen, located in two series alternating with and opposite the petals, respectively. Apart from their insertion, there is no pronounced difference between the stamens of the two series. The ovary is globose, green, 5-carpellate, and *ca.* 3 mm in diameter. The 5 white styles are *ca.* 6 mm long, separate from their base and repeatedly divided in their apical, stigmatic portion. The stigmatic area is minutely papillose (Figure 5). The up to 25 spherical ovules are borne on 5 parietal placentae and arranged in two rows on each placenta so that ovules from neighboring placentae are stacked alternately above each other in 5 columns, parallel to the longitudinal axis of the ovary.

The flowers opened at sunrise and started withering in the evening of the very same day. The petals, stamens, and styles turned brown and usually dropped off 2-7 days later, the styles being somewhat more persistent than the petals and stamens. A total of 47 flowers opened on 5 consecutive days (Figure 6a). None of the buds present after this first period of anthesis produced any more flowers. Half of the flowers were pollinated with pollen from freshly opened flowers of the same plant, and a few flowers were pollinated with pollen of *Drosophyllum lusitanicum*, *Nepenthes* \times *mixta*, and *Ancistrocladus abbreviatus*, plants from families that are phylogenetically closely related to Dioncophyllaceae. The short stamens that do not reach the stigma at any time of anthesis make autogamy unlikely. Several hovering flies were observed to visit the open flowers in the greenhouse. It is not known if these insects effect pollination of *T. peltatum* at natural habitats (hovering flies do occur there, as proved by the investigation of prey caught by *T. peltatum* in its carnivorous phase (Bringmann *et al.*, 2001)). Anyway, the pollinating agent is most likely a diurnal animal, as judged from the timing of anthesis.

3. For the First Time in a Greenhouse: Fruit Ripening

Whether manually pollinated or not, within 10 days after anthesis the ovary of each flower enlarged into an obovoid capsule 1.5-2.5 cm long and 6 mm wide. All fruits split open 2-3 weeks after anthesis, but only 4 of them produced a cumulative total of 5 seeds. All ovules, whether fertilized or not, were flattened (most of them 3 mm in diameter, only the fertilized ones being larger) so they had a mushroom- or nailhead-like appearance, supported on the funicle attached to the center of the ovule (Figure 7). The developing seeds (from fertilized ovules, Figure 8) showed a rapid growth of both the circular wing surrounding the embryo and the funicle. Most of the ovules ceased growth at some stage (the largest undeveloped seed produced a wing 1 cm in diameter and a funicle 1.5 cm in length).

None of the flowers pollinated with pollen from other species produced any seeds. The low number of seeds produced from selfed flowers indicates *T. peltatum*



Figure 1: *T. peltatum*. Hooked adult leaf. (Photo: H. Rischer)



Figure 2: *T. peltatum*. Stem showing signs of secondary growth. (Photo: H. Rischer)

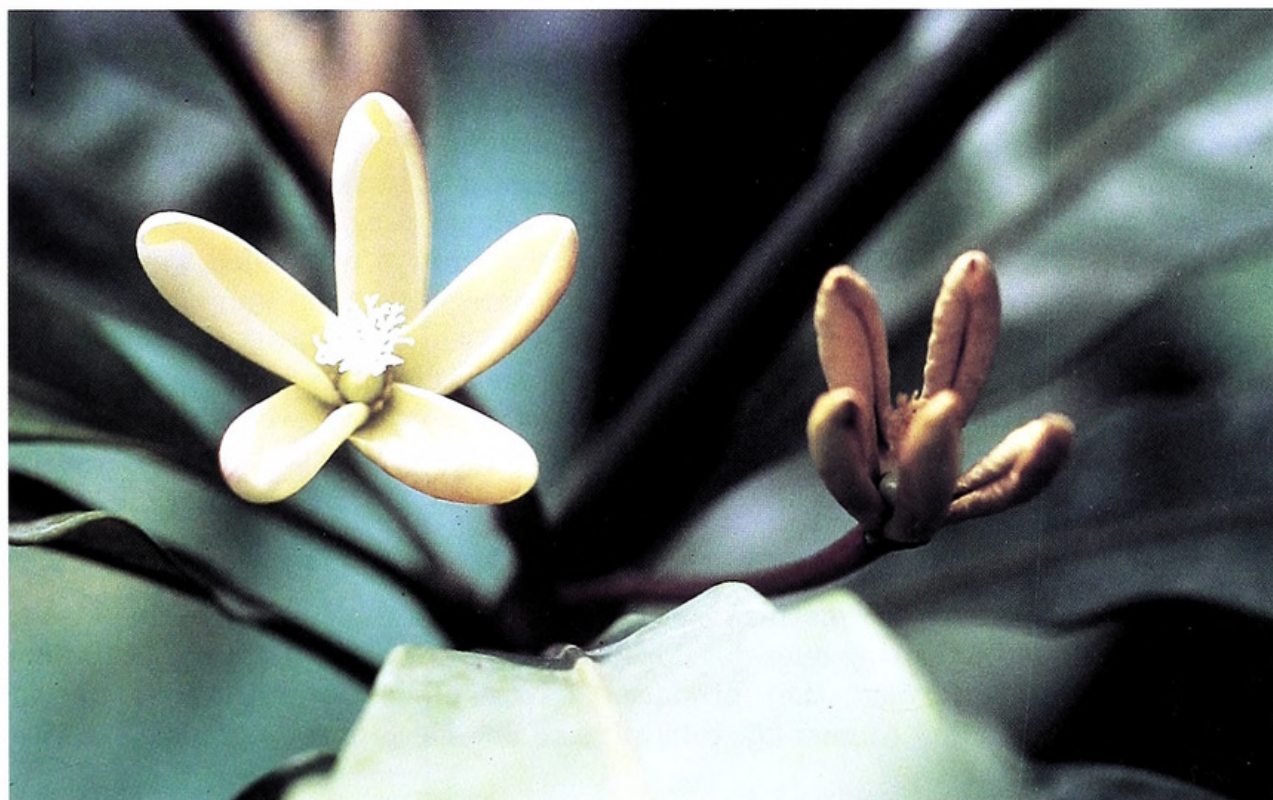


Figure 3: *T. peltatum*. Details of flowers—mature (left), withered (right). (Photo: H. Rischer)

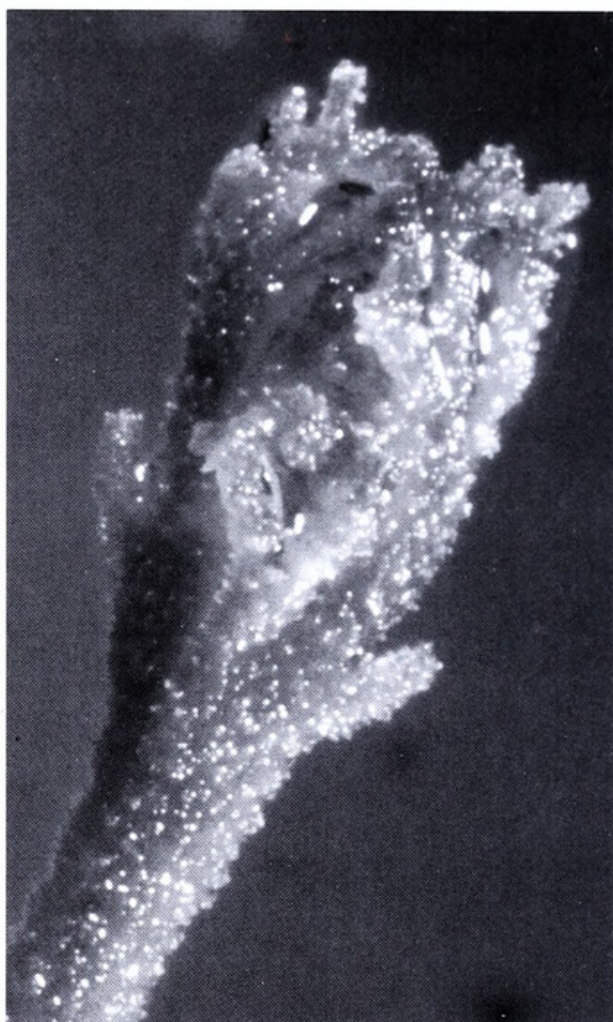


Figure 4: *T. peltatum*. Flower with petals and ovary removed to show the arrangement of anthers. (Photo: H. Rischer)

Figure 5: *T. peltatum*. Stigmatic area of style. (Photo: H. Rischer)

to be moderately self-fertile, if at all.

The opening of the capsule long before the seeds are fully developed presents a unique opportunity to study seed development and maturation, in a noninvasive and nondestructive way. The funicles of the developing seeds became *ca.* 4.5 cm long and 2 mm thick, resembling the pedicels in all respects, including a red coloration. This coloration was lacking in the funicles of non-developing ovules. The seed wing reached an ultimate diameter of 10 cm with the embryo embedded in a disk of endosperm positioned in the center. The seeds were first green and then became reddish from the centre. After maturation, *ca.* 8 weeks after anthesis, the wing dried and became brown and brittle (Figure 9) and the seeds detached from the apical end of the funicles. In relation to their size (see above) the seeds were light (*ca.* 0.45 g each) and they floated gently in the air, the funicular pole pointing downwards, sinking with a constant speed of (0.9-) 1.5 (-2.3) m/sec.

4. Second Flowering Period

Simultaneous with the maturation of the seeds from the June flowering event, the nodes above the fruiting ones developed new flower buds. This time, 14 flowering branches were formed; they produced a total of 24 flowers, which opened between August 22 and August 26, 1999 (Figure 6b). Despite selfing, none of these flowers yielded seeds.

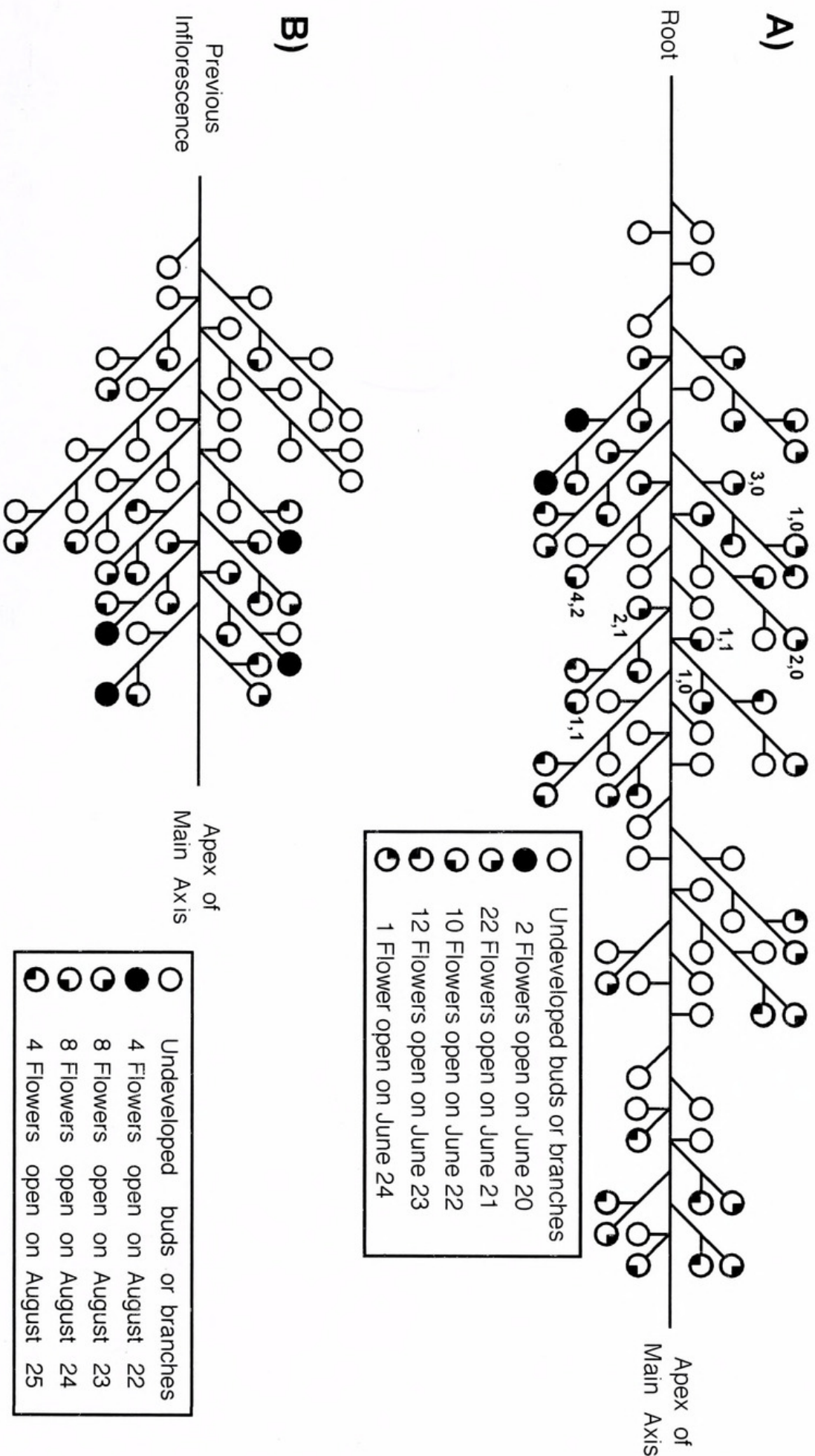


Figure 6: (a) Schematic representation of first inflorescence; the branching pattern of the short flowering shoots is simplified in order to visualize the relative positions of flowers. The pairs of numbers by eight flowers indicate the number of seeds that began to form, and the number of seeds that did not abort. (b) Schematic representation of second inflorescence. No seeds developed.



Figure 7: *T. peltatum*. Cross-section of young fruit. (Photo: H. Rischer)



Figure 8: *T. peltatum*. Opening young fruit. (Photo: H. Rischer)



Figure 9: *T. peltatum*. Almost ripe seeds on open fruits. (Photo: H. Rischer)

5. Further Flowering Periods

Three further flowering periods occurred in 2000. The first and longest one in May lasted 5 days and yielded 125 flowers, the second one was in July and the third one was in September. The September flowering period yielded two fruits from self-flowers, which produced one seed each.

6. Ecological Implications

Field observations on *T. peltatum* are scarce, with only five reports in the literature: (Airy Shaw, 1951; Schmid, 1964; Green *et al.*, 1979; Lamb, 1991; and Bringmann *et al.*, 2001). Because of the inaccessible habitats of the plants observations depend on cultivated plants. This study provides the first long-term observation on the life cycle of *Triphyophyllum*.

The flexibility of *T. peltatum* with respect to the formation of carnivorous glandular leaves seems to be greater than previously noticed. The fact that mature specimens are able to develop glandular leaves when chopped was already noted by Green *et al.* (1979). It seems that glandular leaves are only formed when the plants run into a deficiency of special nutrients for the building of the large biomass associated with the elongated growth. These nutrients (Green *et al.* (1979) especially mention K) are probably deficient in the natural soils, especially during certain climatic periods (e.g. the transition from the dry to the wet season). For this or other reasons, the uptake of existing nutrients by the plants may be too low during these periods, so the carnivorous phase would have great benefit to the plant at this time. Meanwhile, the absence of the carnivorous phase in our cultivated plants may be due to the fact they were well-fertilized. It is nonetheless astonishing that only one plant elongated although all plants were of the same age and virtually the same size. It might be that the other Dioncophyllaceae species, which have never been observed to be carnivorous, might likewise develop insect-trapping organs under nutrient-deficient conditions. The actual trigger remains unknown.

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