ASPECTS OF THE BIOLOGY OF *AUTOLYTUS ALEXANDRI* MALMGREN 1867 (POLYCHAETA, SYLLIDAE).

by

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Résumé

Aspects biologiques d'*Autolytus alexandri* Malmgren 1867 (Polychète Syllidé).

Malgré les indications anatomiques apportées par Gidholm en faveur de l'hypothèse selon laquelle *Autolytus alexandri* n'est que le stade épitoque du Ver Polychète benthonique *A. longeferiens,* on manquait encore de vérifications biologiques. Elles sont présentées ici : il paraît fort probable que l'espèce est bisannuelle dans les eaux côtières du Norfolk (Grande-Bretagne) et qu'elle est la seule du type *longeferiens-alexandri* dans l'Atlantique-Nord. Les observations taxonomiques et statistiques sont discutées ; l'accouplement, observé pour la première fois, est semblable à celui des autres espèces du genre. Le mode de nutrition demeure inconnu.

Introduction

From time to time, there has been discussion as to whether the planktonic *A. alexandri* Malmgren (1867) and the benthonic *A. longeferiens* de Saint-Joseph (1887) are distinct species or merely phases in the life-cycle of the same animal. Both species have been recorded from arctic and boreal European waters (including the British Isles and the North Sea), and each is much larger than the corresponding phase of any other autolytoid in those areas; but, although *A. longeferiens* is frequently dredged, no specimens have ever been found bearing stolons (the stoloniferous "*A. alexandri*" of Hartman (1945) is almost certainly mis-identified), which greatly increases the difficulty of tracing the life-cycle from preserved material. From the examination of a few preserved specimens of one or both phases Augener (1933), Friedrich (1939) and Southern (1914) each suspected that *A. alexandri* and *A. longeferiens* were identical, but without being able to establish the connection beyond reasonable doubt; Malaquin (1893, p. 348) suggested that *A. longeferiens* might have direct reproduction (epitoky, as in many other syllids but not in other autolytoids, that is, members of the sub-family Autolytinae:

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see Gidholm, 1966b) and quotes (1893, p. 6) Malmgren's work, but saw no connection between his own *longeferiens,* which has become epigamous in the laboratory, and the *alexandri* of Malmgren, probably because his epigamous specimen was not sufficiently developed for the resemblance to be obvious. Malaquin's supposition that *A. longeferiens* also produced stolons by budding has been refuted by Gidholm (1966a, pp. 140-141), whose anatomical work makes it clear beyond a doubt that atoquous benthonic individuals of the *longeferiens* type metamorphose into epitoquous specimens of the *alexandri* type. Precisely how many species there are of each type is, however, still not known, nor which benthonic "species" metamorphoses into which planktonic "species"; the present paper is an attempt to answer these questions as regards North Atlantic material, based on information derived from living animals.

In some species of autolytoid, the stolons are much more variable than the stocks (own observations) and it is therefore unwise to describe new species of autolytoids solely from the reproductive phase; however, the reproductive phase in the present species is so distinct from that of any other species occurring in the same area that an exception may be made in favour of the two names applied to it by Malmgren (1867), both of which were given to planktonic females. Of these two names, *A. newtoni* has page priority but is without a figure, whereas *A. alexandri* is well figured and is clearly the animal dealt with here; later authors have all used the name *alexandri* as against *newtoni,* which is an additional argument for the retention of the former name. Marenzeller's (1892) arguments for using yet another specific name, *verrilli,* are not in line with current taxonomic procedure and also fail to allow for variability in the reproductive phase. In the following account the names *alexandri* and *longeferiens* are used for the epitoquous planktonic phase and the atoquous benthonic phase respectively, until the point where it can be shown that they are synonymous.

Material and methods

Specimens of *A. longeferiens* were dredged (Hamond, 1966a) in the neighbourhood of the Blakeney Overfalls Buoy ("the Buoy") and elsewhere (Hamond, 1963, 1966b); specimens of *A. alexandri* were taken in the plankton both near the Buoy and in Blakeney Harbour, being immediately separated into the sexes. The three categories of worms were placed in separate litre beakers, each containing about 0.8 litre of seawater which was continually aerated in a controlled-temperature enclosure (ambient sea-temperature ± 1°C); the *longeferiens* died after about ten days (probably because I was unable to find suitable food for them [Hamond, in press]), while the *alexandri* seldom lived for more than a week after capture (their ages at capture being unknown).

Specimens were studied either living or after narcotisation (in a one per cent. solution of benzamine hydrochloride in distilled water) followed by fixation (Bouin or Zenker). A few males of *alexandri* were sectioned (paraffin wax, 8 microns, Heidenhain's Azan after Bouin or Cason's single-stage Mallory after Zenker), but the results did not throw any fresh light on Gidholm's (1966a) findings, with which they agreed closely and will not be considered further here.

Growth

As already mentioned, *A. longeferiens* would not feed in culture, so that growth could not be observed directly. The lengths of *A. longeferiens* dredged at various times are shown in Fig. 1; the results, especially the presence of half-grown individuals during and immediately after the breeding season, appear to indicate that the species is biennial. The individuals grow most rapidly from June to September, probably because their food is most plentiful at that time; conversely, growth in winter and early spring is very slow. Although the rate of growth at any given season in Norfolk waters is roughly proportional to the offshore sea-temperature (Fig. 1, and Hamond, 1967), it cannot be assumed that rate of growth is causally related to temperature until similar investigations have been made on this species in other parts of its range, for instance, in Arctic waters, where the annual range of sea-temperature is quite different and where the duration of the life-span is unknown.

The formation of epitoquous stages in relation to sea-temperature.

At no time of year have I ever found *A. longeferiens* bearing stolons, although the other Norfolk species are all known to produce them either in Norfolk waters (Hamond, 1966b and unpubl.) or elsewhere (Gidholm, 1966b). On the other hand, an *A. longeferiens* was seen, with what may have been ova inside it, on 4.8.1957 (53°10' N. 01°04' E.; station W.33, Hamond, 1963), and another (definitely containing ova) on 22.3.1961 (53°03' N. 00°59' E.; station W.38), both among whelkpot rubbish; finally, three atoquous specimens in process of becoming epitoquous were dredged about one kilometre east of the Buoy (station D.54) on 10.2.1967 and none of them showed any signs of stolonisation. These findings agree with those of Gidholm (1966a) and make it seem certain that:

(1) *A. longeferiens* reproduces, not by stolonisation, but by some other method, very probably epigamy;

(2) the breeding adults approach maturity in February and March.

The nearly epitoquous specimens from D.54 had already begun to form swimming setae behind the 14th setiger (a condition at once ruling out the planktonic phases of all Norfolk autolytoids except *A. alexandri*), but were otherwise inseparable from the two found in whelkpots, which were completely atoquous and externally agreed with *A. longeferiens* in every way.

At about the time when *A. longeferiens* might be expected to become epitoquous, specimens of the *alexandri* type appear in the

Norfolk plankton (Fig. 1); they agree well with the descriptions and figures of Malmgren (1867, as *A. alexandri*; females only) and of Wesenberg-Lund (1947, as *A. verrilli*; both sexes) and are most abundant off Norfolk between late March (water temperature 5.0°C) and early May (10.0°C), although ten males were taken on 10.2.1967 (3.5°C) and two males on 1.6.1966 (10.8 to 11.2°C), all near the Buoy. Very few autolytoids are found budding at this time either intertidally or offshore and all their stolons can easily be recognised as being quite distinct from *A. alexandri.*

A search of the literature reveals records of *alexandri*-type planktonic stages from the north coast of France and from Massachusetts northwards to the Arctic (Table 1); nearly all the records fall within the range of temperature recorded above (3.5 to 11.2°C.), except for certain Arctic records (down to approximately 1.5°C.) and the Plymouth specimen taken by Okada (see below). It appears that, in waters where the lowest winter temperature is below 11°C., *alexandri*-type specimens appear as soon as the sea temperature has attained, or has begun to rise from, its annual minimum; along North Atlantic coasts the 11°C. isotherm for minimum annual sea temperature lies somewhere on the west coast of France and on the coast of North Carolina near Cape Hatteras, south of which limits *alexandri*-type specimens are not likely to occur. North of these limits, however, and in depths of usually less than 100 fathoms, their geographical distribution seems to be continuous to and including Arctic waters (references in Table 1); the records do not indicate discrete populations breeding over different temperature ranges (cf. the two forms of *Polydora ciliata* at Whitstable; Dorsett, 1961), and it is thus practically certain that there is but one species of the *alexandri*-type in the area under consideration. This area includes the entire known distribution both of *A. alexandri* and *A. longeferiens,* which may therefore be considered to be the pelagic and benthonic phases respectively of one and the same species, for which the name *alexandri* should be used.

To the above scheme, there is one outstanding exception, the female taken off the Eddystone on 17.9.1928. From the very clear figure by Okada (1933, fig. 1, as *A. roseus*) it seems certain that this specimen belonged to *A. alexandri* as understood here; since it had ovulated (passed its eggs from the body cavity to the eggbag, which is possible only after mating; Gidholm 1965, own observations), at least one male was probably nearby, but is not recorded as having been captured. What is exceptional about this female is that it was taken at a water temperature of about 14°C., far above the limits demonstrated above for *A. alexandri* (although in an area from which this species is recorded; Plymouth Marine Fauna, 1957, p. 121), and at a time of year when the sea-temperature was falling instead of rising; this specimen probably represents a population, near the southern limit for *A. alexandri* in European waters, which has been able to raise the breeding temperature in the way suggested by Orton (1920) and has thus become potentially capable of colonising areas far to the south of the southern limit for this species as known at present. I have not been able to find any records of *A. alexandri,* either in plankton or among benthos, from the coasts of Spain, Portugal, or western France; it is common offshore at Roscoff

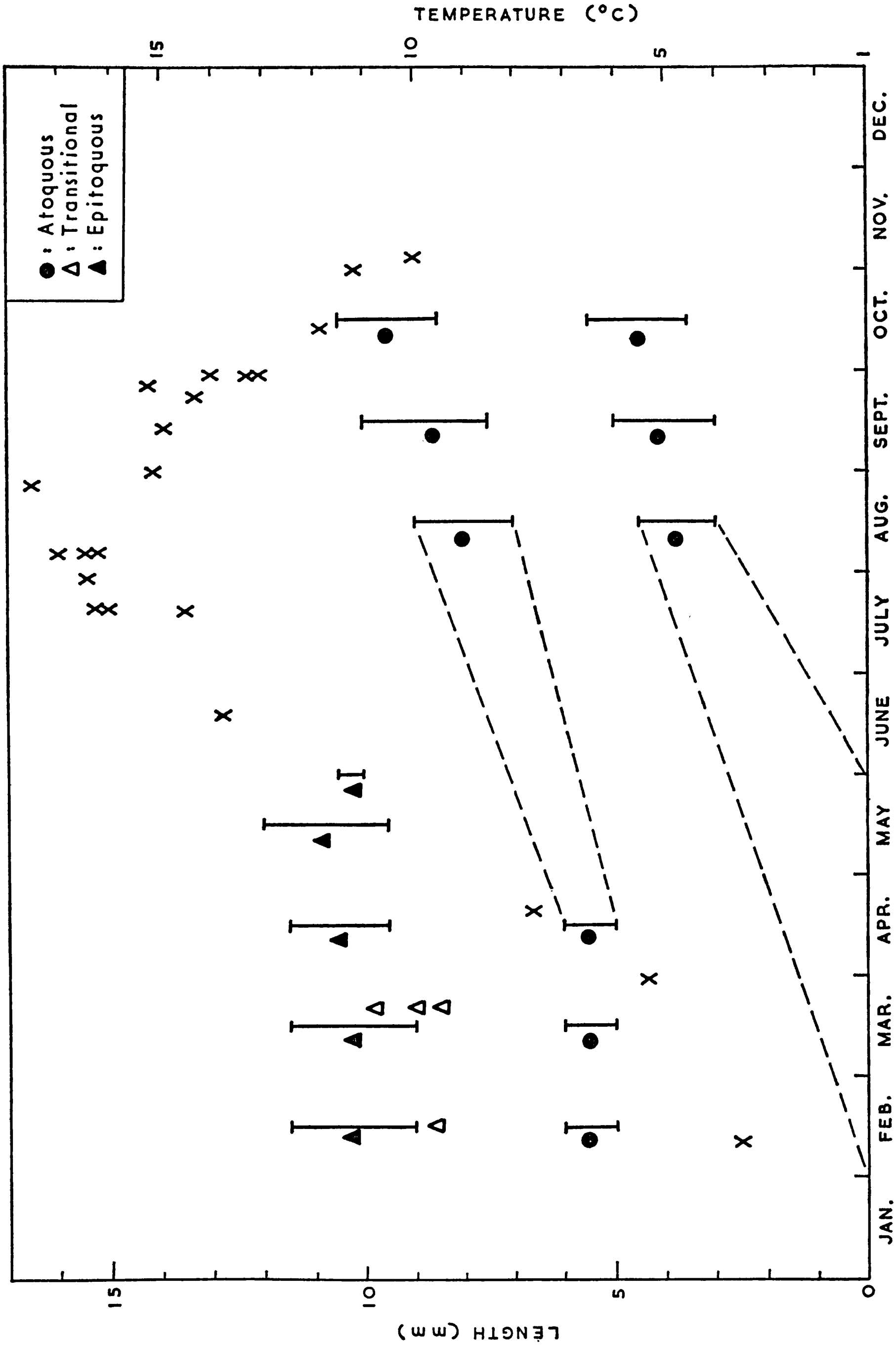

Fig. 1.

Seasonal variation in length (vertical lines represent total variation for all the samples of that month) of atoquous, transitional, and epitoquous *A. alexandri.* The extents of the vertical lines are approximate, owing to the contractile nature of the worms; a moderate state of extension is assumed, as for slow unimpeded crawling or swimming. Pairs of dashed lines represent conjectural rates of growth during periods when specimens were not obtained.

Crosses represent offshore temperature readings; at any given time the water-temperature near the Buoy is the same to within 0.05° C from the surface to the bottom (24 metres).

(Cognetti, 1961), which is fairly near the southern limit, but seems to be unknown from warmer waters, so perhaps Okada's specimen was "a flash in the pan".

Okada's determination of the above specimen as *A. roseus* appears to be mistaken, mainly because it had fourteen setigers in the front region as against only eight setigers for the original *A. roseus* of Claparède (1964). The latter should be regarded as a doubtful species until more specimens are found and the life-cycle is known in all its stages.

Surface swarming of *A.alexandri*

On 29.3.1965, a calm and brilliantly sunny day, at about 7.30 a.m., during slack water near the Buoy, I saw a male *alexandri* swimming rapidly at the very surface, causing a bow wave as it rushed hither and thither just like a centipede, at about 10 cm/second. A few minutes later, a second male, behaving in the same way, was caught in a glass jar and the identification confirmed, after which the plankton net was towed slowly round and round in circles within a hundred metres or so of the Buoy from 7.50 to 8.10 a.m., the mouth of the net being half immersed so as to sample the maximum amount of surface water. This haul took seventy-eight males (but no females) of *A. alexandri,* five hyperiid amphipods (*Parathemisto gracilipes*), two copepods (*Calanus helgolandicus*), and large numbers of drowned or drowning insects and spiders. The end of this haul coincided with the end of slack water; after this a plankton haul near the bottom (8.20-9.20 a.m.) secured five, and a surface haul (9.30-10.30 a.m.) took one, male *A. alexandri.*

The probable significance of surface swarming in this and other species of autolytoid will be assessed in a future paper; there is no published record of surface swarming in any autolytoid, nor of such a large number of any species being taken in a single haul. Owing to navigational hazards, I have not been able to work offshore at night; whether this swarming takes place at the surface in darkness, or by moonlight or by artificial light, is therefore unknown.

The habits of epitoquous stages in captivity

To the anatomical reasons given by Gidholm (1966a, pp. 137-140) must be added a behavioural reason for supposing that epigamy, as against stolonisation, is the rule in this species. During the next four days, after which they were preserved, the males from the above sample were kept in about a litre and a half of seawater in a glass bowl, with periodic aeration; a few individuals (not always the same ones) swam intermittently at low speed, but at any given moment the majority were lying or crawling on the glass. They crept very slowly, with their front halves walking on the glass exactly in the manner of the atoquous forms and with the rear part of the swimming region and the entire tail region raised clear of the substratum. This remnant of benthonic behaviour is most difficult to explain by stolonisation, since the behaviour of stolons is strikingly different from their stocks (and in fact, among hundreds of stolons of other species reared by me in culture, none have been seen to crawl in this way), but is simply explained if the pelagic *A. alexandri* is a transformed benthonic individual in which vestiges of old habits still linger. Four females, observed on different occasions, swam continuously and, in general, towards the light; in this respect they were much more like true stolons.

Mating

The day after the above sample of males was taken, a female of the *alexandri*-type was caught in Blakeney Harbour plankton; although post-ovulatory, and therefore presumably less sexually attractive than a virgin female, when put in the bowl with males she was mated with by one and elicited signs of sexual response (spasms of high-speed swimming; erection of flicking of the head appendages) from some ten or fifteen others. This is the first experimental proof that the male and female planktonic autolytoids, both ascribed to the present species on morphological grounds (Wesenberg-Lund, 1947, figs. 14, 15), do in fact belong together. Mating appeared to be more like that of *Proceraea cornuta* (own observations) than that of *A. edwardsi* (Gidholm, 1965), in that during rotation the female rolls up into

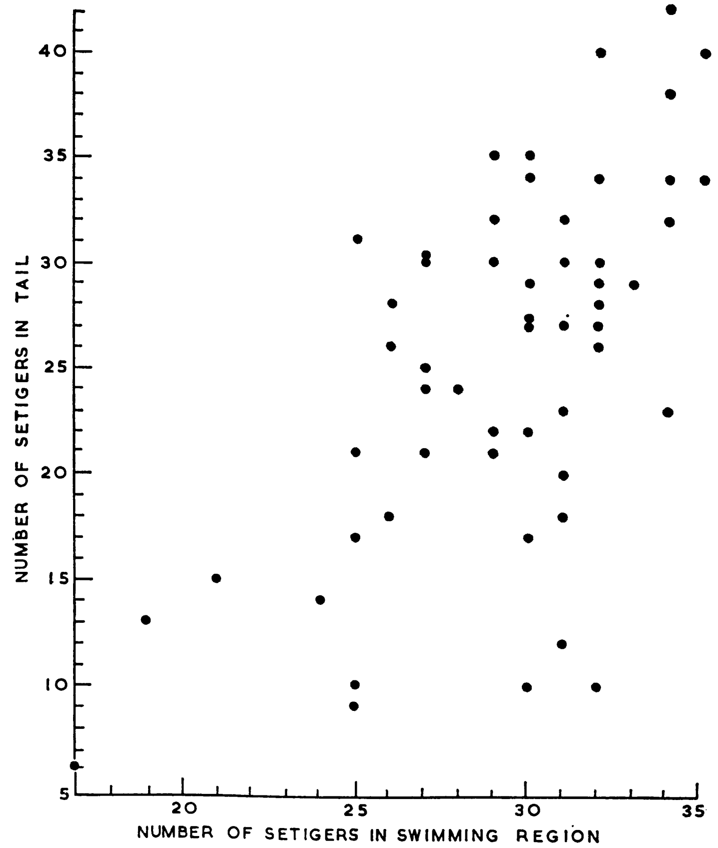

Fig. 2

a ball instead of being spun on her long axis; the speed of rotation (about 150 to 180 r.p.m.) is substantially slower than in either of these species.

Variability of the epitoquous stages

The numbers of setigers in the front, swimming, and tail regions of the epitoquous phase may be denoted by a, b, and c respectively (Gidholm, 1966b, p. 173), and the setiger formula for an individual is thus $a+b+c$. In *A. alexandri*, a is usually 14, but may be 13 or 12, while b and c vary widely (Table 1). To find whether b and c were related in any way, the fifty-four complete examples from the rich haul of males on 29.3.1965 were plotted on a graph of b against c (Fig. 2); the correlation coefficient between b and c was $r = 0.6$, which for this size of sample is highly significant (for $r = 0.35$, $P = 0.01$). It appears that both b and c tend to be highest in those individuals which, prior to becoming epitoquous, had attained the largest size and the greatest total number of setigers, although neither b nor c appear to be under strict numerical control. Females were not obtainable in sufficient numbers for statistical work.

TABLE 1.

Records of planktonic *Autolytus*, presumably *A. alexandri*. In each case the record comprises the name of the author, the date of publication, the sex and setiger formula of each specimen, the locality and date of capture, and the water-temperature at that date and place at the surface (from Anon, 1954); water-temperatures for the North Norfolk samples, however, were taken at the times of the hauls themselves (own unpublished records).

Malmgren (1867, as *A. alexandri*); one female, 14+ca.30+ (22 or more); Davis Strait, no date (water-temperature unknown).

Malmgren (1867, as *A. newtoni*); females, 13+(22-26)+(10-30 or more); Spitsbergen, in Hornsund on 2.8.1864 and in Storfjord on 21.8.1864 (from 1.5°C to 4.5°C).

Pettibone (1963, as *A. alexandri*); females 14+(18-30)+(10-63), males 14+(27-37)+(11-23); Canadian Arctic, June, July, August (2.0°C or less); Gulf of St.Lawrence, June (7.0°C to 10.0°C); Massachusetts, March, April (4.5°C to 7.0°C).

Wesenberg-Lund (1947, as *A. verrilli*); females 14+(20-25)+(40-50), males 14+35+2; 65°29' N, 24°36' W, 22.4.1904 (ca. 4.5°C); 64°45' N, 52°52' W on 19.6.1925, 63°56' N, 52°41' W on 8.6.1925, 60°45' N, 52°45' W on 23.6.1925, and in Godthaabsfjord on 15.6.1939 (these four records from 1.5°C to 4.5°C).

Fauvel (1923, as *A. longeferiens*); both sexes, no formulae; north coast of France in January and February (Pas-de-Calais, 5.0°C to 7.0°C; Dinard, 8.0°C to 8.5°C).

Okada (1933, as *A. roseus*); female, 14+25+65, near the Eddystone, 17.9.1928 (ca. 14.0°C).

Plymouth Marine Fauna (1957):—

as *A. roseus*. — Female, no formula, February 1929, near the Eddystone (ca. 9.0°C);

as *A. longeferiens*. — Both sexes, no formulae, Plymouth area in general, February (8.5°C to 9.0°C).

Sexton (unpublished sketches in the Library of the Marine Biological Association at Plymouth); a female, 14+20+35, and two males, 14+32+39 and 13+32+30, all three near the Eddystone on 18.2.1914 (ca. 9.0°C).

Author's unpublished records from North Norfolk waters:—

Females. — 14+18+(40-50), 14+18+37, and 14+19+40, all on 19.4.1963 (7.5°C); 12+19+40, on 6.5.1963 (9.9°C); 12+18+25, 14+14+11, 13+16+18, 14+17+43, and 12+19+30, all on 7.5.1963 (9.2°C);

Males. — 14+33+32 on 8.4.1963 (5.5°C); 14+29+22 and 14+29+24, both on 23.3.1964 (5.5°C); those taken on 29.3.1965 (5.3°C), see text; two males, no formulae, 1.6.1966 (10.8°C to 11.2°C); ten males, no formulae, 10.2.1967 (3.5°C).

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Summary

The relationship between the planktonic *A. alexandri* and the benthonic *A. longeferiens* was formerly uncertain, although Gidholm had produced strong anatomical evidence to show that the former is the epitoquous stage of the latter. Biological data support this verdict, and show that there is but one species of autolytoid of this type in the North Atlantic, *A. alexandri* (of which *A. longeferiens* is a synonym), which in Norfolk waters is biennal. Taxonomic and statistical observations are discussed; the food is still unknown, but mating is recorded for the first time in this species.

Zusammenfassung

Die Annahme, dass *A. alexandri* nur das epitökische Stadium von *A. longeferiens* sei, die sich zunächst auf anatomische Beobachtungen stützte, scheint nun durch biologische Beobachtungen weiter gefestigt. Die letzterer zeigen, dass im Nord-Atlantik nur eine Art dieses Typus innerhalb der Gattung *Autolytus* lebt, deren Lebenszyklus in Norfolkschen Gewässern zweijährig ist. Es werden Beobachtungen über Taxonomie, Statistik und Paarung angestellt ; letztere wurde erstmals beobachtet und ist identisch mit der Paarung anderer Arten dieser Gattung. Die Art der Nahrung bleibt noch unbekannt.

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