The biology of the millipedes *Aporodesmus zaria* Hoffman, 1967 and *A. aestivus* Hoffman, 1972 in Nigeria (Diplopoda: Polydesmida: Pterodesmidae)

Биология двупарноногих многоножек *Aporodesmus zaria* Hoffman, 1967 и *A. aestivus* Hoffman, 1972 в Нигерии (Diplopoda: Polydesmida: Pterodesmidae)

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ABSTRACT: The life histories of two sympatric species of the flat-backed millipede, genus Aporodesmus, in northern Nigeria are described. Both species complete their life cycles in one year. A. zaria Hoffman, 1967 lays eggs in May, at the beginning of the rainy season: the early larval stadia are presumably soildwelling. The next generation of adults appears towards the end of the rains in August or September and must survive the dry season in the soil, an exception for savannah polydesmoids in Nigeria. Adult A. aestivus Hoffman, 1972 appear in the litter in July and the early larval stadia in August. The species presumably passes the dry season as larvae in the soil. These become adult the following year. The phasing of the life histories means that similar developmental stadia of these species do not coincide in the litter at the same time.

РЕЗЮМЕ: Описана биология двух симпатрических видов плоскоспинных многосвязов рода Арогоdesmus в Северной Нигерии. Оба вида завершает жизненный цикл за год. Вид A. zaria Hoffman, 1967 откладывает яйца в мае, в начале сезона дождей, а ранние личиночные стадии, вероятно, обитатели почвы. Следующее поколение взрослых появляется к концу сезона дожей в августе или сентябре и должно пережить засушливый период в почве. Это исключительный случай среди многосвязов саванн Нигерии. Взрослые A. aestivus Hoffman, 1972 появляются в подстилке в июле, а ранние личинки в августе. Этот вид переживает засушливый сезон, видимо, в стадии личинки в почве. Взрослые появляются на следующий год. Фенология жизненных циклов такова, что сходные стадии онтогенеза этих видов в подстилке гетерохронны.

Introduction

Northern Nigeria has a varied fauna of polydesmoid millipedes [Hoffman, 1967]. The gomphodesmids *Tym*-

bodesmus falcatus (Karsch) and Sphenodesmus sheribongensis Schiøtz are large round-backed millipedes with moderately developed lateral keels. The first six or seven of the eight stadia are unpigmented soil-dwellers, whilst the adults, and in particular the males, are found on the soil surface [Lewis, 1971a]. The paradoxosomatids Habrodesmus duboscqui Brolemann, Xanthodesmus sp. and Xanthodesmus physkon (Attems) are also round-backed but are soil surface dwellers at all stadia except the first [Lewis, 1971b]. The lateral keels are reduced and the animals burrow into the soil before moulting and egg laying.

In the present paper the biology of two litter-dwelling species of the flat-backed genus *Aporodesmus* (Family Pterodesmidae) which was briefly summarised by Lewis [1974] is described and discussed.

The species investigated

Aporodesmus zaria Hoffman has only been recorded from Zaria, Nigeria. Hoffman [1967] described the species from material collected by Dr. S. A. Toye in "spring 1965". At an early stage in the study here reported it appeared that there were two similar species of Aporodesmus in the habitat, differing in their seasonal activity and in the proportions of the adults. Material was sent to Dr R. L. Hoffman who described a second species Aporodesmus aestivus Hoffman [Hoffman, 1972]. Adult males of A. zaria measure 17.8 to 21.2 mm in length and 4.0 to 4.6 mm in width, females 18.2 to 22.4 mm in length and 4.2 to 4.7 mm in width. Adults of A. aestivus are somewhat shorter and wider than A. zaria, males measuring 15.4 to 20.3 mm in length and 4.4 to 5.5 mm in width, females 15.4 to 19.2 mm in length and 4.3 to 5.8 mm in width.

Both species have strongly developed lateral keels, which cover the head and almost or completely obscure the legs (Fig. 1).

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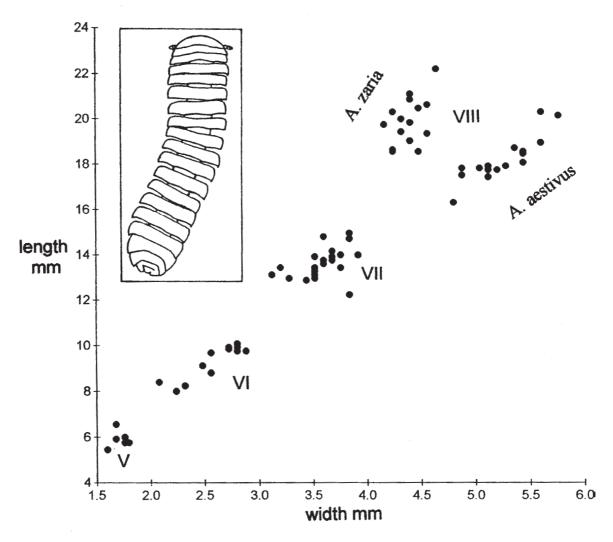


Fig. 1. Plot of body length against width for stadia V-VIII male *Aporodesmus* spp. in 1968. Inset *Aporodesmus zaria*. Рис. 1. Биплот соотношения длины и ширины тела для самцов стадий V-VIII у *Aporodesmus* spp. в 1968 году. На врезке — *Aporodesmus zaria*.

Materials and methods

The investigation was carried out on the campus of Ahmadu Bello University, Zaria, Nigeria. Zaria is situated in the northern guinea savanna vegetation zone. It has a mean annual rainfall of 1,220 mm. The rainfall is seasonal, there being five months (November to March) which have less than 25 mm of rain. The rains are normally fairly continuous after the end of May and until the end of September.

Specimens were collected from litter (mainly of *Cassia siamea* Lam.) in the gardens of houses on campus and from mixed deciduous litter in the University Botanical Garden.

Collections were made throughout the rainy seasons of 1968 and 1969. In 1968, specimens were hand-sorted from litter in the field at intervals of between two and three weeks. In 1969 the collections were made at

approximately ten-day intervals.

Larvae were extracted from litter collected from the Botany Garden using Tullgren funnels. Three samples of approximately $0.14~{\rm m}^{-3}$ each were extracted for 14 days in funnels 240 mm in diameter with floors of 1.7 mm wire mesh. In 1968 samples were taken at approximately three-weekly intervals. In 1969 they were taken once a fortnight.

In *Aporodesmus* as in most polydesmoids there are eight post-embryonic stadia (instars). These are easily separated, as there is a constant increment in the number of body rings at each moult. Thus stadia I to VIII have 7, 9, 12, 15, 17, 18, 19 and 20 rings respectively. Plots of body length against width for the fifth to eighth stadia for males (Fig. 1) in 1968 show two groups in the eighth stadium. The longer, narrower specimens are *A. zaria*. Similar data were obtained for females. Earlier stadia did not show these two size groups.

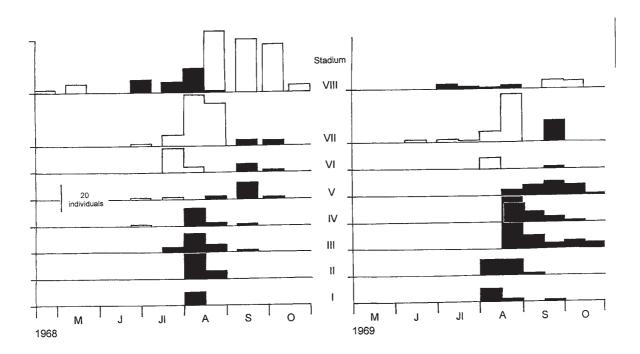


Fig. 2. The succession of stadia in *Aporodesmus* spp. in 1968 and 1969. Black columns *A. aestivus*, open columns *A. zaria*. Stadia V–VII have been ascribed to species on the basis of their time of appearance in the habitat (see text).

Рис. 2. Смена стадий у Aporodesmus spp. в 1968 и 1969 годах. Черные столбцы — A. aestivus, пустые столбцы — A. zaria. Стадии V-VII привязаны к видам на основе времени появления в биотопе (см. текст).

Life cycles

Aporodesmus zaria

In 1968, adult A. zaria were present in the litter in late April and early May and then disappeared. Newly moulted adults appeared in numbers in the litter at the end of August but were uncommon when sampling was discontinued at the end of October (Fig. 2). Five females collected on 15 May 1968 contained large ova, mean diameter 0.32-0.39 mm. No ova could be identified in five newly moulted females collected on 29 August 1968 nor in a further five collected on 3 October. The most probable explanation of these observations is that adults died after a period of oviposition in late May. The individuals of stadia VI and VII that were very common in the litter in late July and preceded the newly moulted adult A. zaria that appeared in August were presumably of this species. Apart from single individuals of stadium IV and V, earlier stadia did not precede stadia Vl and Vll in the litter, suggesting that the earlier stadia were soil dwelling. Large numbers of stadia I-IV appeared, however at the beginning of August. These were probably the larvae of A. aestivus (see below).

No adult *A. zaria* were found in April or May 1969 but, stadium VI and VII appeared at the beginning of August to be followed by newly moulted adults in September (Fig. 2). These adults had disappeared from the litter by mid-October.

The above data suggest that A. zaria lays eggs at the end of May and then dies. The early stadia are soil

dwelling. Stadium VI is reached by the end of July and enters the litter. Stadium VII moults to the adult at the end of August or later. These adults survive the dry season to lay eggs after the beginning of the next rains.

Aporodesmus aestivus

In 1968, adult *A. aestivus* were present in the litter from the end of June until the beginning of August (Fig. 2). The stadium I–IV larvae that appeared in the litter in the first half of August had presumably hatched from eggs laid by *A. aestivus* in June or July. Stadium VI larvae appeared at the beginning of September together with a few stadium VII probably of *A. aestivus*. These late instars must aestivate in the soil to emerge as adults the following June/July. In 1969 the pattern was similar: adults appeared in the litter in July and August, stadia I and II, presumably of this species, at the beginning of August, followed rapidly by stadia III to VI and VII.

Food

The gut contents of 17 adult and six stadium VII *A. zaria* were examined. In 4 of the adults (females with large ova) the gut was empty but 11 of the remaining 13 contained fragments of dead plant material and one, fungal conidia. In addition, nine contained mineral particles. All the stadium VII larvae contained fragments of dead plant material, one, in addition, contained mineral particles. Six stadium III larvae examined contained fragments of dead plants and mineral particles.

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Discussion

In Zaria the rainy season lasts from April to October. Initially, in April and May, the rains are spasmodic and the soil may dry out several times. In the paradoxosomatids *Habrodesmus duboscqui* and *Xanthodesmus* sp., which are surface dwellers characteristic of open habitats, adults first appear several weeks after the first rains and earlier stadia emerge from the soil later (in mid June) by which time the rains are established [Lewis, 1971b].

Lewis [1974] suggested that the delay in the appearance of some species or of particular stadia might be due to the slow speed at which rainwater penetrates the soil. Water will not reach animals deep in the soil until the middle of the rains. The depth at which the animals aestivate may therefore control the time at which they emerge.

The gomphodesmid *Tymbodesmus falcatus* and the three paradoxosomatids in Zaria survive the dry season as diapausing larvae in moulting chambers in the soil. Lewis [1971a] suggested that these chambers are important in restricting water loss in the dry season. The adults cannot construct moulting chambers and are relatively shortlived, dying before the end of the rains. Like gomphodesmids and paradoxosomatids, *A. aestivus* appears to have short-lived adults and survives the dry season as larvae. Adult *A. zaria*, on the other hand, appear in the latter part of the rainy season and unlike the other polydesmoids investigated in Zaria, survive the dry season to lay eggs at the beginning of the next rains. Since they do not produce moulting chambers, the adults must reach permanently damp soil or are very resistant to desiccation.

Adult A. zaria are present in April and May and again from late August to October, whereas adult A. aestivus are present from July to mid-August. The two species are not, therefore, present in the litter at the same time of the year. Neither are other instars of similar developmental stadia of the two species present in the habitat at the same time.

Other work on the life histories of tropical polydesmoids has been carried out on three species of Indian paradoxosomatids. Bellairs et al. [1983] investigated Streptogonopus phipsoni (Pocock) in a thinly wooded area in Poona (Pune), Maharashtra, India. Here, there are three major seasons, summer, monsoon and winter. The species probably has a life cycle of one year. Adults emerge from the soil at the onset of the monsoon, mate and lay their eggs and shortly afterwards die. The first two stadia are spent in the soil but the larvae of stadium III aggregate into swarms above ground. They reach stadium VII at the end of the monsoon and probably overwinter at this stage, undergoing a final moult at the onset of the next monsoon. The pattern is therefore resembles that of the Nigerian paradoxosomatids. The statement of Bellairs et al. [1983] that "in African species [Lewis 1971]... egg-laying continues during a period of four to seven months" is incorrect.

In contrast, the adults of *S. phipsoni* from grassland in West Bengal occur throughout the year [Bhakat,

1987]. The author suggested that there were two breeding periods a year, the life cycle taking one or two years. Similar life histories are described by Bhakat [1989a] for *Orthomorpha coarctata* (Humbert) and for *Chondromorpha kelaarti*(Humbert) in West Bengal [Bhakat, 1989b]. In these species too, older larval stadia and adults overwinter and life cycles take one or two years. Both have two periods of egg laying which overlap in *O. coarctata*. The fact that these three species in West Bengal overwinter as adults suggests that conditions are less severe in the winter there than in the dry season in northern Nigeria where the paradoxosomatids aestivate as larvae. *S. phipsoni* appears to have a variable life cycle or, alternatively there may be two closely related species with different life cycles.

Lewis [1971b] pointed out that most Temperate Zone millipedes have long lived adults, which overwinter. In the savanna of Northern Nigeria most polydesmoid millipedes have short-lived adults and this seems to be necessitated by the harsh dry season conditions. *Aporodesmus zaria* is a notable exception and data on its method of surviving the dry season would be of considerable interest.

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