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On the natural history and ecology of Meinertellidae (Archaeognatha, Insecta) from dryland and inundation forests of Central Amazonia

by

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Abstract

The life-cycle and ecology of four nocturnal species of Meinertellidae are given and their adaptation from Amazonian dryland to inundation forests is discussed. In primary and secondary dryland forests, *Neomachilellus scandens, N. amazonicus* and *Meinertellus adisi* are arboricolous, show no defined reproduction period and juveniles are found throughout the year. In inundation forests of the Rio Negro valley, which are annually flooded for 5 - 6 months, *N. scandens, N. adisi* and *M. adisi* have one generation per year. Annual inundation is considered as the main reason for the acquisition of a seasonal development. In *N. scandens,* juveniles hatch from previously submerged eggs on the forest floor at the beginning of the non-inundation period and reach maturity after 3 months. Adults propagate in the litter, where females deposit their eggs which are subject to the next flooding. Both sexes subsequently migrate into the trunk/canopy area and perish. *N. adisi* is restricted to inundation forests and lives on tree trunks where eggs undergo facultative flooding.

Keywords: **Archaeognatha, Amazon, Brazil, flood-resistance, inundation forest.**

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1. Introduction

Archaeognatha (Microcoryphia) are represented in South America only by Meinertellidae. First data regarding the natural history and ecology of this family can now be presented, as studies on the development of four species from Central Amazonia, representing two genera (*Neomachilellus* and *Meinertellus*) have been completed (STURM & ADIS 1984). In the vicinity of Manaus, Meinertellidae are found in primary and secondary dryland forests (= non-inundated forests). They also inhabit inundation forests in the Rio Negro valley, which are flooded annually for 5 - 6 months to a depth of several metres (ADIS 1984). This area was originally dryland forest until the first flooding occurred several million years ago (IRION & ADIS 1979; ADIS & SCHUBART 1984). Arthropods of these inundation forests are believed to originate either from the former dryland forests and from dryland forests presently extending behind the inundation forests, with examples reported for Pseudoscorpiones and Archaeognatha (ADIS & MAHNERT 1985; ADIS & STURM 1987), or from non-forested wetlands located between rivers and the inundation forests, with examples given for Carabidae (ERWIN & ADIS 1982). In addition, some populations may have undergone extensive evolution within inundation forests, due to forest isolation caused by climatical shifts and microgeographic changes (ADIS 1984) as indicated for Pseudoscorpiones, Symphyla and Opiliones (ADIS & SCHUBART 1984). In all cases, arthropods which now inhabit inundation forests had to evolve strategies to compensate for the periodic loss of their terrestrial habitat. Means of achieving this include: (1) staying near the water line and moving in advance of the ascending flood (IRMLER 1979), (2) moving to non-flooded trunk and canopy areas in the inundation forest (ADIS 1977, 1981, 1982; FRIEBE & ADIS 1983; ADIS & SCHELLER 1984; ADIS & MAHNERT 1985), (3) flying to adjacent dryland biotopes during inundation (ADIS et al. 1986), (4) evolving adaptations for remaining in flooded terrestrial areas (BECK 1969, 1976; IRMLER & FURCH 1979; SCHELLER & ADIS 1984; SMITH & ADIS 1984; ADIS 1986; ADIS & ARNETT 1987), and (5) combining one or more of these features (ADIS & STURM 1987 and this study).

In this paper we present data on the natural history and ecology of *Neomachilellus scandens* WYGODZINSKY, 1978 and *Meinertellus adisi* STURM, 1983 from primary and secondary dryland forests near Manaus and adaptation of the species to inundation forests in the Rio Negro valley. Ecological data are also given for *N. amazonicus* STURM, 1983 which inhabits primary and secondary dryland forests, and for *N. adisi* WYGODZINSKY, 1978 which was only found in inundation forests.

2. Study area and methods

Meinertellidae were collected between 1975 and 1985 in the course of ecological studies on Central Amazonian arthropods from three previously investigated and fully described forest types, all within 30 km of Manaus: (1) in a primary dryland forest at Reserva Florestal A. Ducke (2° 55'S, 59° 59'W) on the Manaus-Itacoatiara highway (AM-010 at km 26), study area of ADIS & SCHUBART (1984), ADIS et al. (1984), MORAIS (1985), PENNY & ARIAS (1982) and others; (2) in a blackwater inundation forest at Rio Tarumã Mirím (03° 02'S, 60° 17'W), a tributary of the Rio Negro, study area of ADIS (1981, 1984), ADIS et al. (1979, 1986), BECK (1976), ERWIN (1983), IRMLER (1975, 1979),

WORBES (1985) and others; (3) in a cut but unburned secondary dryland forest adjacent to the inundation forest, study area of ADIS & SCHUBART (1984), RODRIGUES (1986). All forests were subject to a rainy season (December - May: average precipitation 1,550 mm) and a dry season (June - November: average precipitation 550 mm; cf. RIBEIRO & ADIS 1984).

2.1. Inundation forest

The soil of the inundation forest consisted of clay, silt and sand material and had an organic layer of 5 - 10 cm thickness. Its fine humus was penetrated by a matting of roots and supported up to 3 cm leaf litter (cf. ADIS et al. 1986). The study site was covered annually by up to 3.35 m of floodwater from March/April until August/September. Meinertellidae were collected between December, 1975 and May, 1977. On the forest floor 28 pitfall traps (aperture diametre 5.6 cm; cf. BARBER 1931) and 8 ground photo-eclectors (= emergence traps with a basal area of 1 m^2) provided data on activity densities during the non-inundation period (September, 1976 - April, 1977). Trunk ascents and descents of Meinertellidae were detected with arboreal photo-eclectors on three tree trunks each, throughout the collecting period. The killing-preserving agent used in all traps was aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of atraction or repellence in temperate zones (ADIS 1979). The material in traps was collected at 1 - 2 week intervals. All capture devices are fully described by ADIS (1981) and FUNKE (1971, 1977) who also explain their mode of utilization and function. The presence of Meinertellidae in the soil was studied between September, 1981 and February, 1982 (non-inundation period). Once a month, six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges, diameter 21 cm, length 33 cm), which was driven into the soil by a mallet. Each sample of 7 cm depth was then divided into two soil discs of 3,5 cm thickness. Animals were extracted from these subsamples following a modified method of KEMPSON (ADIS 1987).

The presence of meinertellid eggs in the flooded soil was studied at the end of each inundation period in 1983 - 1985. Twelve soil samples were taken in 3-weekly intervals under water with a split corer as described above. Each subsample of 3.5 cm thickness was kept moist for 10 - 14 days on a grid inside a bucket, which was covered by a cotton screen (sealed up by a plastic snap ring) and contained aqueous picric acid at its bottom. Hatched animals were subsequently extracted from subsamples.

2.2. Dryland forest

The yellow latosoil of the primary and secondary dryland forest supported a 2 - 3 cm thick humus layer, interspersed with fine roots, and a thin, surface covering leaf litter. One ground photo-eclector and one arboreal photo-eclector for trunk ascents were set up in both forests from December, 1981 to January, 1983 (cf. ADIS & SCHUBART 1984). MORAIS (1985) and RODRIGUES (1986) provided data on the presence of Meinertellidae in the soil. Once a month, they took twelve soil samples from each forest type between September, 1982 and August, 1983 and extracted the animals, as described above.

In addition, Meinertellidae were collected from tree crowns by fogging canopies with pyrethrum. Sampling was realized during the early dry season in the completely flooded inundation forest (July, 1977, 1979) and in the primary forest under study (August 1977; cf. ADIS et al. 1984; ERWIN 1983). Complementary material was obtained from a second dryland forest (2° 30'S, 60° 15'W) were canopy was fogged during the rainy season (February, 1979; MONTGOMERY & ERWIN, unpubl.) and during the early dry season (August, 1979; cf. ERWIN 1983).

All Meinertellidae collected were identified to species (cf. STURM 1983; WYGODZINSKY 1978) and classified as juveniles and subadults or adults (males and females), according to size classes suggested by STURM & ADIS (1984). The taxonomic work for this paper was done by H. STURM and the collection and evaluation of field data by J. ADIS. The influence of weather conditions on meinertellid activity on trunk and soil surfaces was statistically investigated with the linear correlation-test (CAVALLI-SFORZA 1972), using the original field data.

3. Results

3.1. Species spectrum and biotopes

About 1,400 Meinertellidae were evaluated for this study. They represented four species: *Neomachilellus scandens* WYGOD. (60 % of the total material), *Meinertellus adisi* STURM (25 %), *Neomachilellus amazonicus* STURM (13 %) and *N. adisi* WYGOD. (2 %). Three species occurred in the two dryland forest types: *N. amazonicus, N. scandens* and *M. adisi*. They were mostly caught on trunks (Figs. 1, 2) and in the canopy. *N. amazonicus* dominated in the primary forest (Fig. 1) and *M. adisi* in the secondary forest (Fig. 2). Two of these species occurred in the inundation forest as well: *N. scandens* dominated on trunk and forest floor, *M. adisi* was captured during trunk descents and in the canopy (Fig. 3). A third species, *N. adisi,* was exclusively caught on tree trunks, mainly during trunk ascents (Fig. 3).

3.2. Life-cycles and ecology

Neomachilellus scandens WYGODZINSKY, 1978

This species showed no defined reproduction period in dryland forests. Juveniles and subadults were caught throughout the year (Fig. 4) and when canopies were fogged in August. *N. scandens* is considered arboricolous, as no animals were extracted from soil samples and as the few specimens captured in ground photo-eclectors were mostly adults. Catch data from the secondary dryland forest are similar, although low in number. Another study supports our conclusion: 20 baited pitfall traps which were set up for one year in the primary forest under study did not catch any meinertellids (PENNY & ARIAS 1982). However, the two scaleless juveniles recorded for this species were obtained by soil extraction in the secondary forest in August. Sex ratio (adult males to females) of *N. scandens* from arboreal photo-eclectors was 1.2 : 1 in the primary forest. No correlation was found between catch numbers on the trunk and the abiotic parameters of this forest.

In the inundation forest, *N. scandens* showed a defined reproduction period. At the beginning of the non-inundation period, juveniles were observed to hatch from eggs previously submerged for 5 - 6 months. When soil and wood samples were taken under water during forest inundation and kept moist for 10 - 14 days, 2nd to 4th instars of *N. scandens* were obtained in the following extraction (cf. ADIS & STURM 1987). For this reason we presume a quiescence in egg development during forest inundation and that hatching depends on a dry forest floor. This was also reported for Collembola from the same habitat (BECK 1976). Hatching may be caused by changing abiotic factors (e. g. decreasing humidity, increasing oxygen values, oscillation of soil and air temperatures) and needs further study. As the first instar of *N. scandens* was never collected, it may be inactive or last a short time only. Up to 60 second instars of *N. scandens* were counted per m² litter surface at night, 1 - 2 weeks after the forest floor had dried. They were caught in pitfall traps, ground photo-eclectors (Fig. 5, 6) and sporadically extracted from soil samples. In 1976, the first subadult males were captured in early October, only 3 - 4 weeks after the

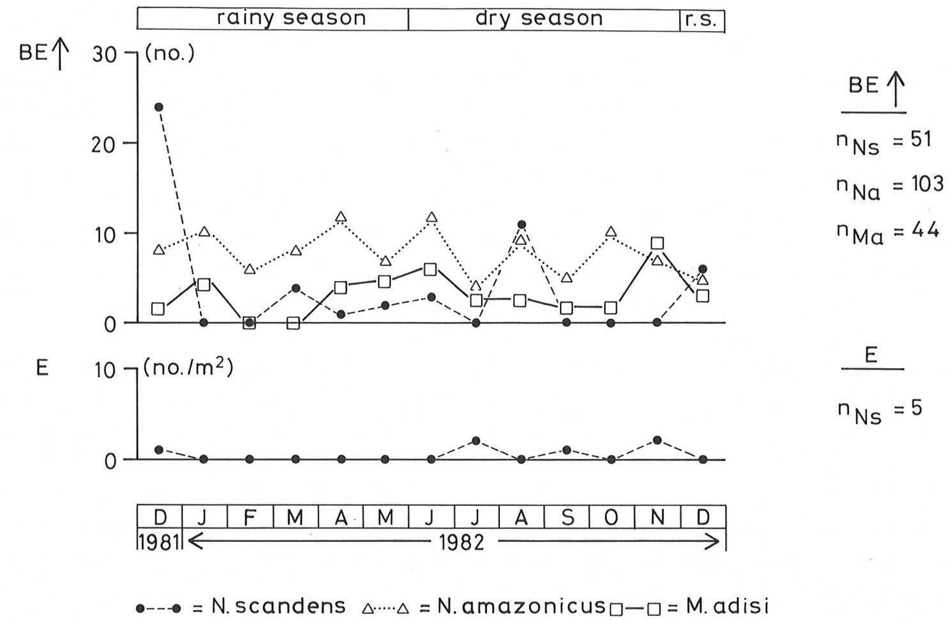

Fig. 1:
Activity density of Meinertellidae on the forest floor (E = 1 ground photo-eclector) and on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a primary dryland forest near Manaus. Catches collected between December, 1981 and December, 1982. n = total number per species and trap type.

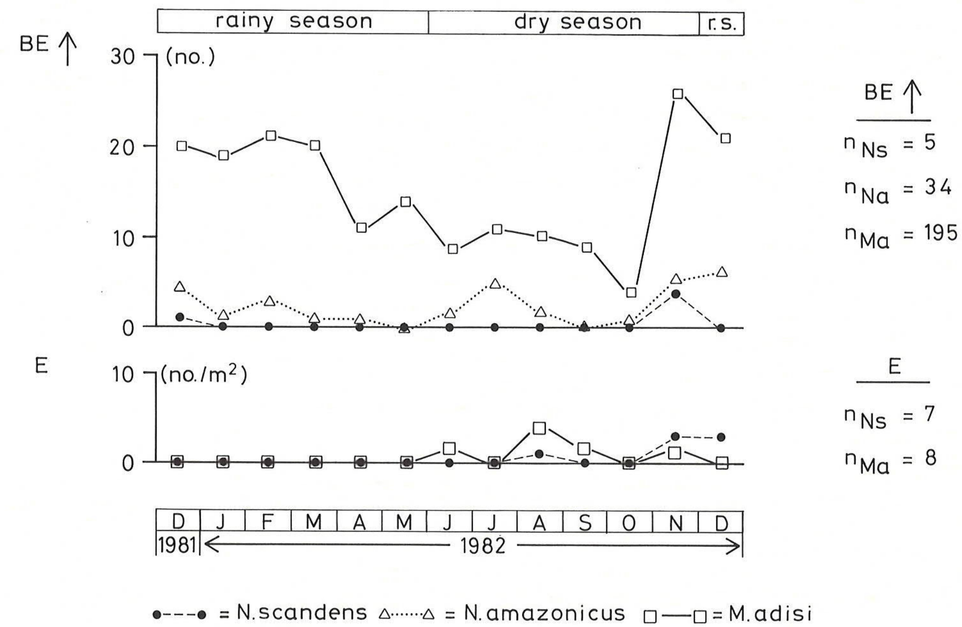

Fig. 2:
Activity density of Meinertellidae on the forest floor (E = 1 ground photo-eclector) and on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a secondary dryland forest near Manaus. Catches collected between December, 1981 and December, 1982. n = total number per species and trap type.

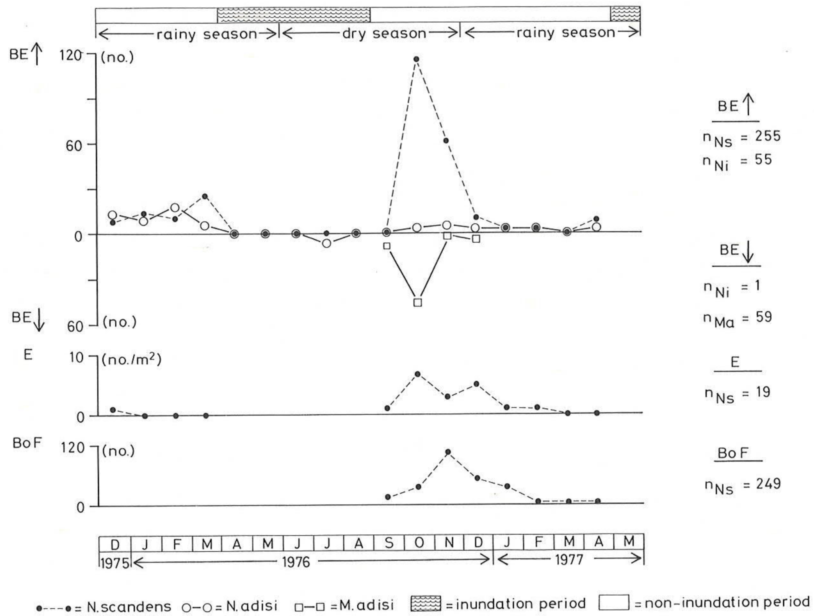

Fig. 3:
Activity density of Meinertellidae on the forest floor (BoF = 28 pitfall traps; E = 8 ground photo-eclectors) and on tree trunks (BE ↑, BE ↓ = 3 arboreal photo-eclectors for trunk ascents and trunk descents, respectively) in a blackwater inundation forest near Manaus. Catches collected between December, 1975 and May, 1977. n = total number per species and trap type.

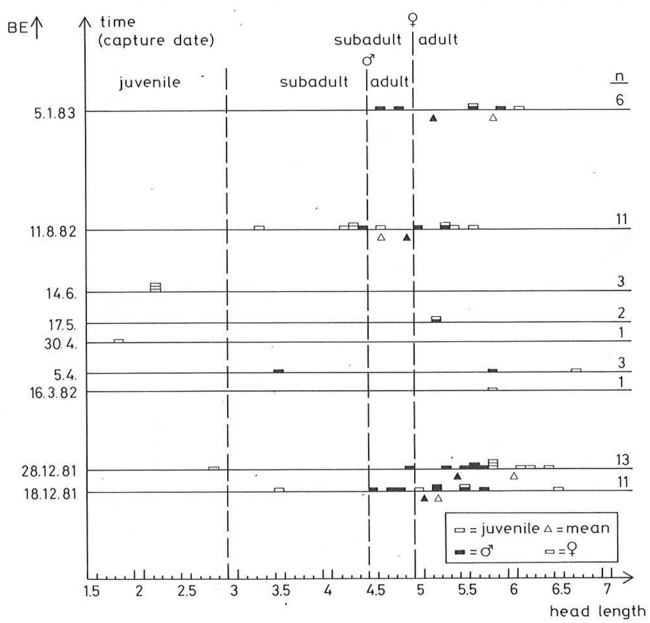

Fig. 4:
Developmental stages of *Neomachilellus scandens* caught on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a primary dryland forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture data. Catches collected every two weeks between December, 1981 and January, 1983.

flood water had receded. First subadult females were recorded two weeks later. Maturity in males was first observed in late October and in females in mid-November (Fig. 6). The highest activity density of *N. scandens* on the forest floor was registered in late October with ground photo-eclectors (7 ind./m^2; Fig. 3) and in mid-November with pitfall traps (Fig. 6). The presence of fungal hyphae and spores, and of algae and leaf material in the gut indicated that the animals were grazing on leaf litter. Capture rates in ground photo-eclectors in October/November were elevated, when the relative humidity of the air was low ($p < 0.05$; $r > +0.9816$, $n = 4$) and when the difference between day/night temperatures of the air was high ($p < 0.05$; $r > +0.9899$, $n = 4$). This suggests a greater activity of *N. scandens* on the forest floor during periods of low precipitation. Strong single rainfalls during the dry season, however, increased the water saturation of the soil sporadically (cf. ADIS 1981; RIBEIRO & ADIS 1984). Under these conditions, subadults and adults moved temporarily to the lower trunk area (in October/November) and were caught in higher numbers in arboreal photo-eclectors (Fig. 7: $p < 0.01$; $r > 0.9986$, $n = 3$). From December onwards, all animals caught on the forest floor had reached maturity. This indicates, that development from hatching animals to adults lasted 10 - 12 weeks at most and was concluded within the dry season. By the end of November, the nocturnal adults propagated on the forest floor. Females deposited eggs in leaf litter and dead wood, where they were subject to the next inundation (in 1977 from April onwards). Sex ratio (adult males to females) was 1 : 1.3 in ground photo-eclectors and 2.6 : 1 in pitfall traps, which suggests a greater activity of males on the forest floor. After propagation, and probably due to the beginning rainy season, both sexes migrated into the trunk/canopy area (cf. Fig. 7: 25.11. & 8.12.1976). Animals grazed on tree trunks and intestinal tracts contained algae, fungal hyphae and spores along with bark and moss material. Low catch numbers in ground photo-eclectors and pitfall traps indicated, that only few animals remained on the forest floor (Figs. 5, 6). They were caught on tree trunks after the forest was flooded (Fig. 7: in April). *N. scandens* presumably perished in the trunk/canopy area, as -1) no specimens were caught with canopy fogging during high-water in July; -2) either did animals occur in arboreal photo-eclectors which recorded trunk descents during and after the inundation period (Fig. 3), nor was *N. scandens* ever collected from epiphytes in the canopy.

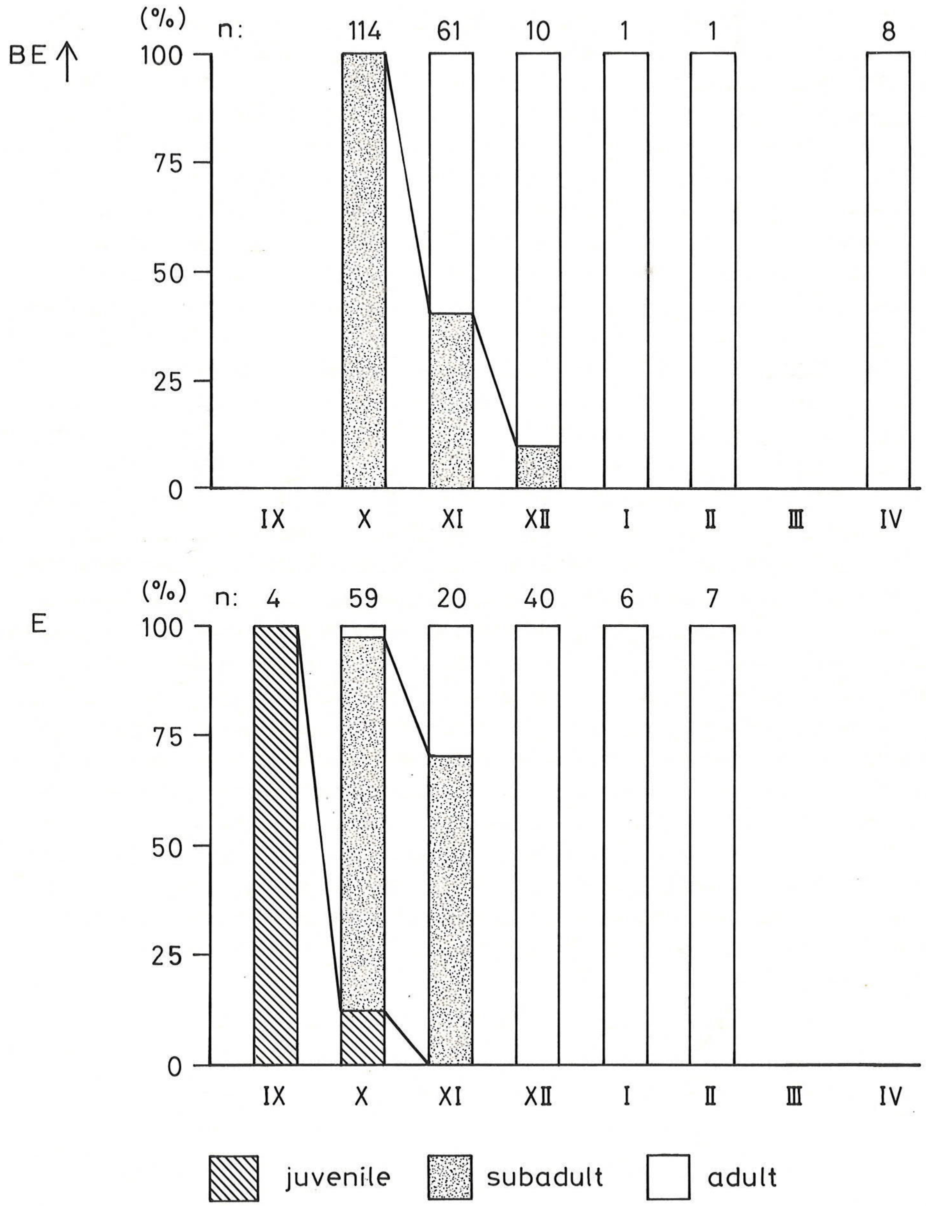

Fig. 5:
Developmental stages of *N. scandens* captured per month (in %) on the forest floor (E = 8 ground photo-eclectors) and on tree trunks (BE ↑ = 3 arboreal photo-eclectors for trunk ascents) in a blackwater inundation forest near Manaus. Catches collected between September, 1976 and April, 1976 (non-inundation period); total catch per month = 100 %; n = total number of specimens caught per month.

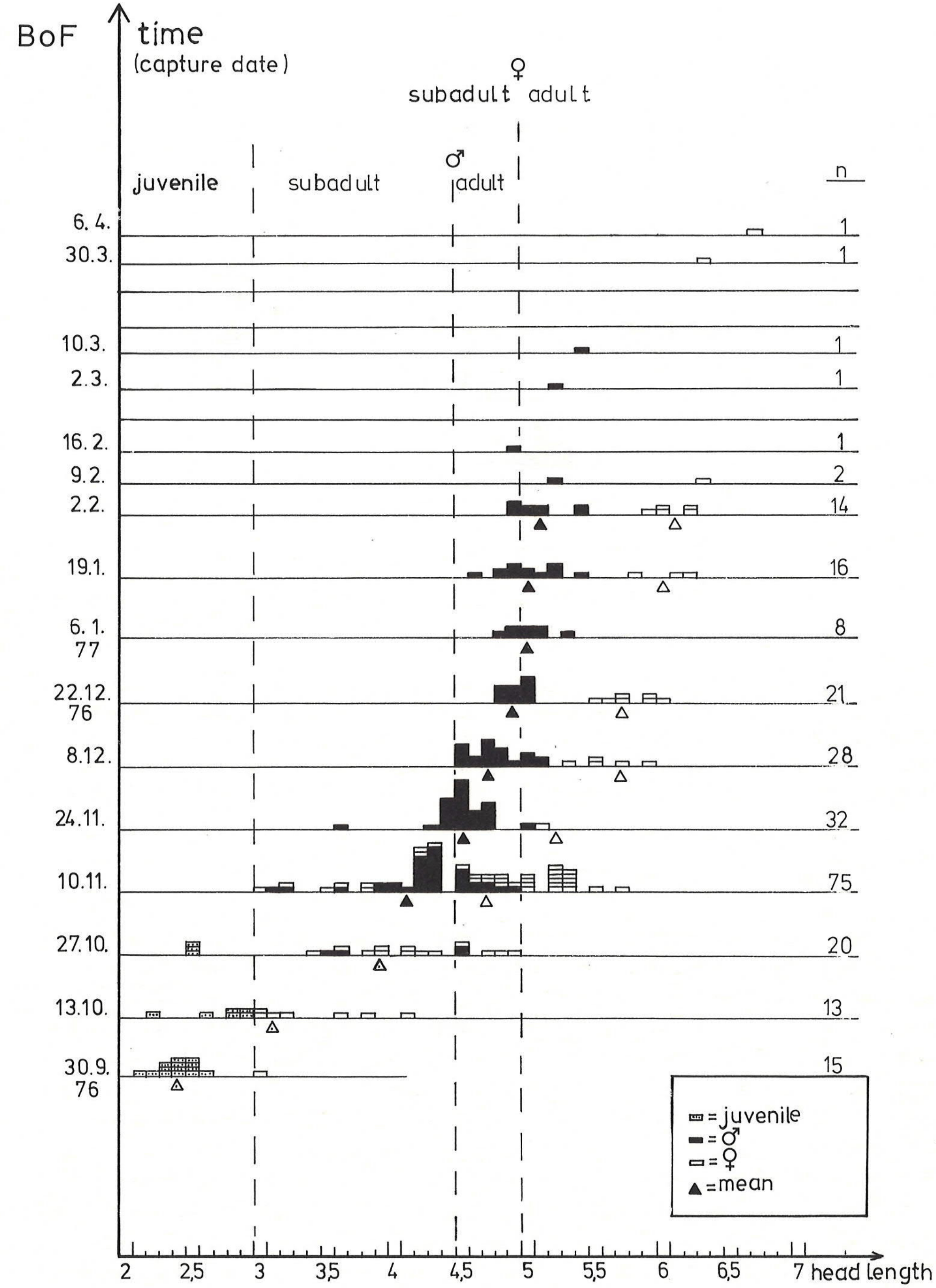

Fig. 6:
Developmental stages of *Neomachilellus scandens* caught with 28 pitfall traps (BoF) in a blackwater inundation forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between September, 1976 and January, 1977 and weekly from February until April, 1977 (non-inundation period). Data from STURM & ADIS (1984), complemented.

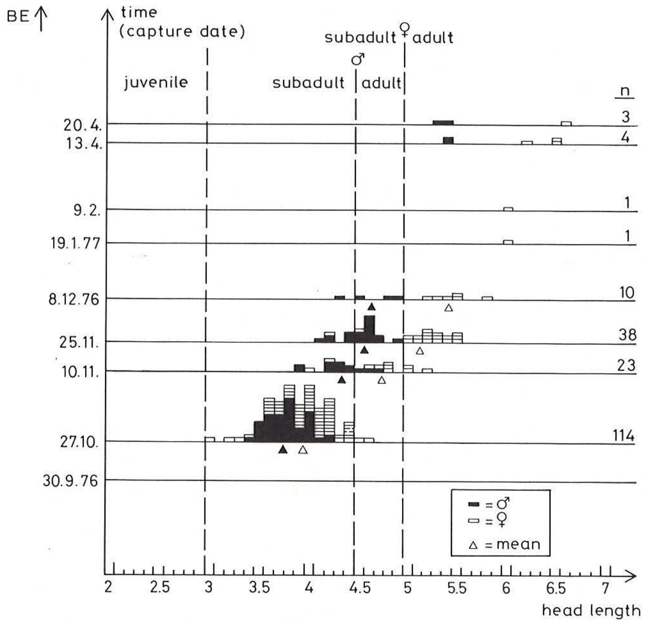

Fig. 7:
Developmental stages of *Neomachilellus scandens* caught on tree trunks (BE ↑ = 3 arboreal photo-eclectors for trunk ascents) in a blackwater inundation forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between July, 1976 and January, 1977 and weekly from February until April, 1977. Forest inundated until September 16, 1976 and from April 9, 1977 onwards. Data from ADIS & STURM (1987).

Neomachilellus amazonicus STURM, 1983

This species was restricted to dryland forests, is considered arboricolous and showed no defined reproduction period (Fig. 8). In the primary and secondary dryland forest, juveniles and subadults were captured throughout the year in arboreal photo-eclectors (Figs. 9, 10) and during canopy fogging in August. Scaleless juveniles were only found in trunk catches and represented the second instar (STURM & ADIS 1984). The presence of scales was correlated with a certain head length of animals (Figs. 9, 10). No animals were ever recorded on the forest floor with the sampling methods applied (ground photo-eclectors, soil extraction, pitfall traps). This supports our conclusion, that reproduction of *N. amazonicus* takes place in the trunk/canopy area. Throughout the year, the activity density of *N. amazonicus* was higher in the primary forest. About four times more animals were caught on the trunk (103 specimens) when compared to the secondary forest (34 specimens, cf. Figs. 1, 2). Juveniles dominated, representing 62 % of the total catch in the primary forest (Figs. 8, 9) and 68 % in the secondary forest (Fig. 10). Sex ratio of males to females (subadults and adults) was 1 : 1.2 in the primary forest. No correlation was found between catch numbers on the trunk and the abiotic parameters of this forest.

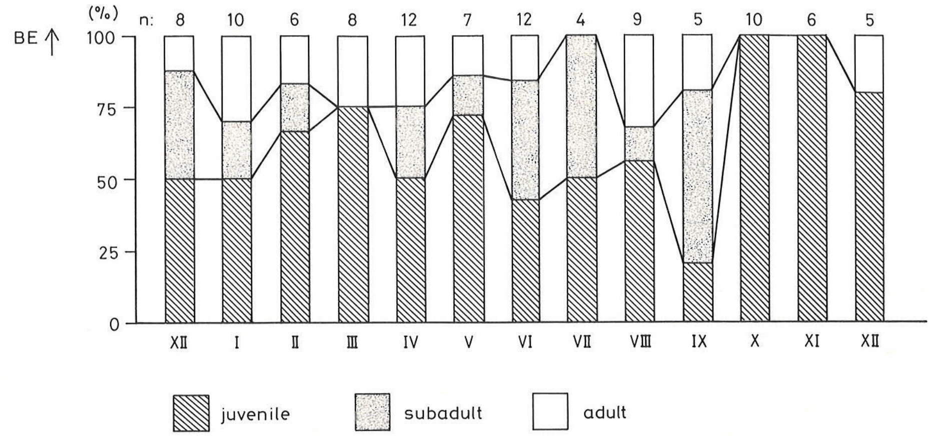

Fig. 8:
Developmental stages of *Neomachilellus amazonicus* captured per month (in %) on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a primary dryland forest near Manaus. Catches collected between December, 1981 and December, 1982; total catch per month = 100 %; n = total number of specimens caught per month.

Meinertellus adisi STURM, 1983

M. adisi was obtained in large numbers from the canopy of primary dryland forests during fogging studies. Like in other meinertellid species from dryland forests, there was no definded reproduction period. Juveniles were present throughout the year (Fig. 11) and reproduction presumably took place in the canopy/trunk region. *M. adisi* represented the largest meinertellid in the Central Amazon (cf. STURM & ADIS 1984). All developmental stages were highly active. They frequently came to the lower trunk area and were caught in arboreal photo-eclectors (Figs. 12, 13). In the secondary forest, activity density on trunks was somewhat higher during the dry season (Fig. 2). Sex ratio (adult males to females) was 1 : 1.1, and 1 : 1 when subadults were included. On the forest floor, animals were only recorded during the dry season and in low numbers. They were captured in ground photo-eclectors and represented advanced juvenile stages and subadults. No animals were obtained by soil extractions. In the primary forest, activity of *M. adisi* was limited to the canopy/trunk area (Fig. 1). About four times fewer animals (44 specimens) were caught there as compared to the secondary forest (195 specimens; Figs. 1, 2). Gut contents of animals from trunks contained heavily fragmented plant material, many fungi and parts of arthropods, but few algae and moss fragments. In addition, mandibles and scales of ingested exuviae were found. The fungus flora on trunks seems to change with the season: during the dry season many non-pigmented fungal spores, few conidiophorous fungi and few hyphae were found in digestive tracts, whereas in the rainy season few hyaline fungal spores, many conidiophorous fungi and many hyphae were present (KATZ, pers. commun.). Changing food sources might explain different activity densities of *M. adisi* on trunks between seasons and the temporal occurrence of animals on the forest floor (Fig. 2).

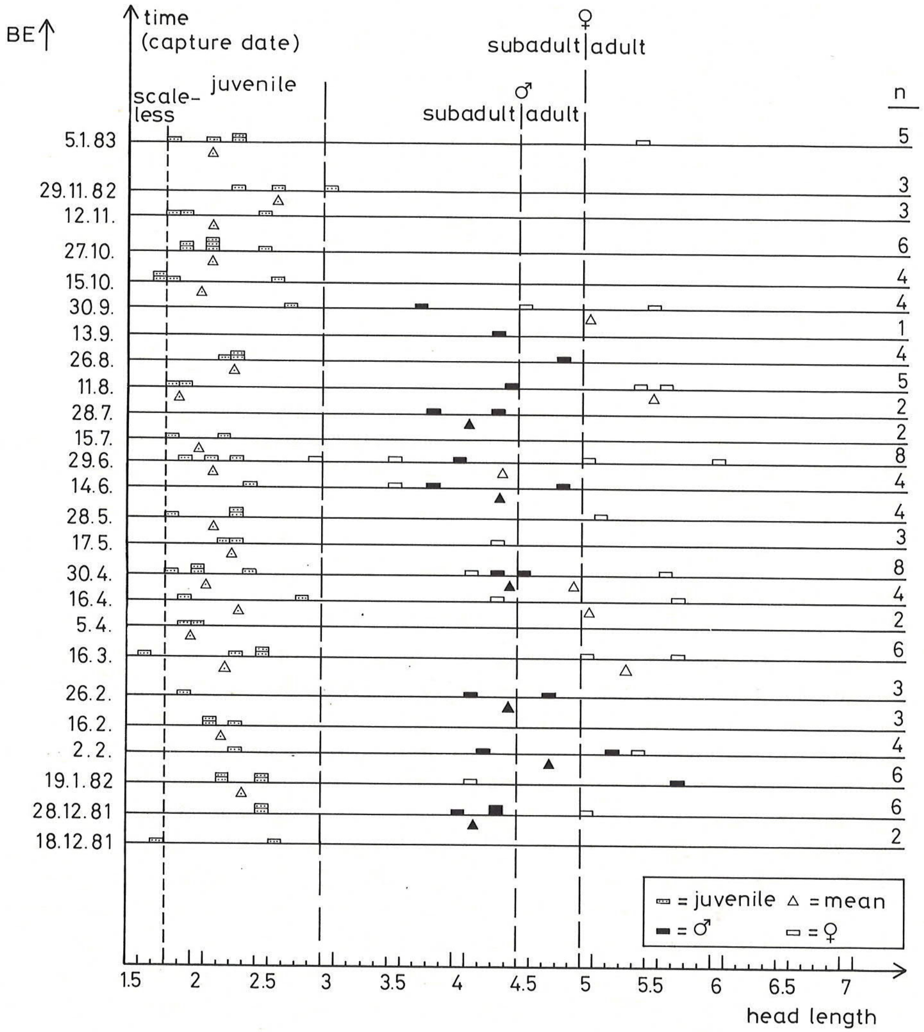

Fig. 9:
Developmental stages of *Neomachilellus amazonicus* caught on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a primary dryland forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between December, 1981 and January, 1983.

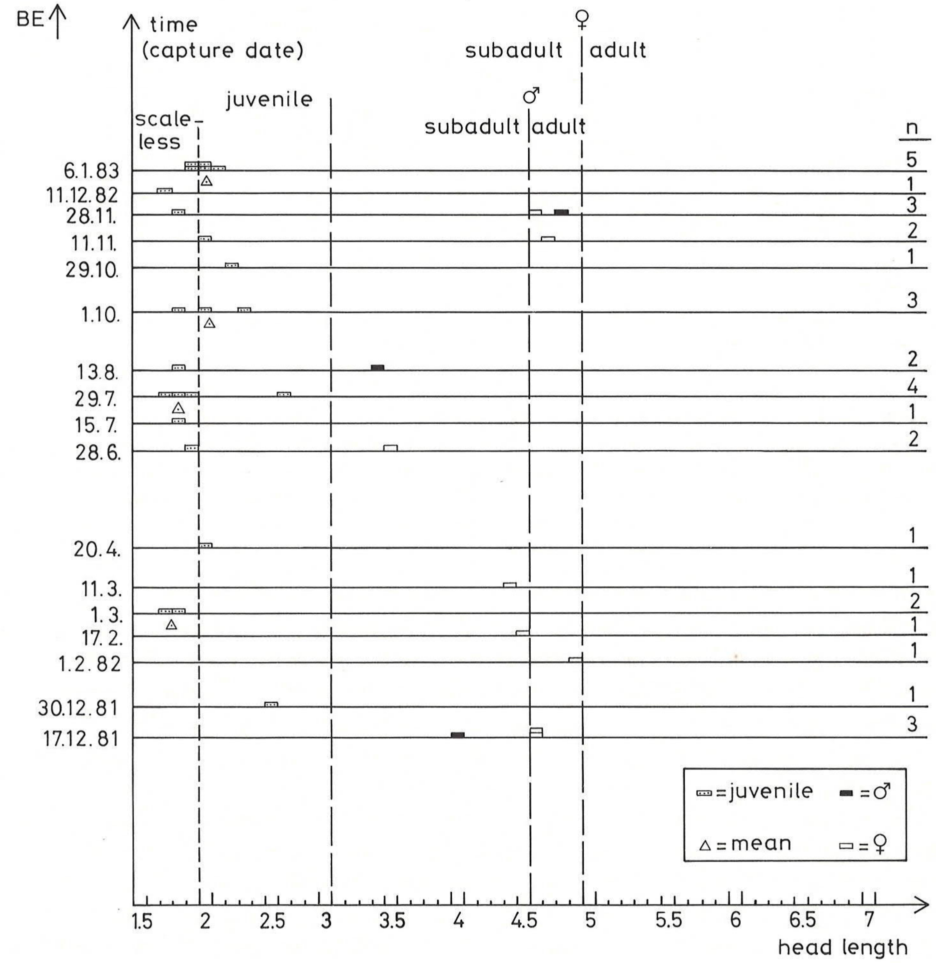

Fig. 10:
Developmental stages of *Neomachilellus amazonicus* caught on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a secondary dryland forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between December, 1981 and January, 1983.

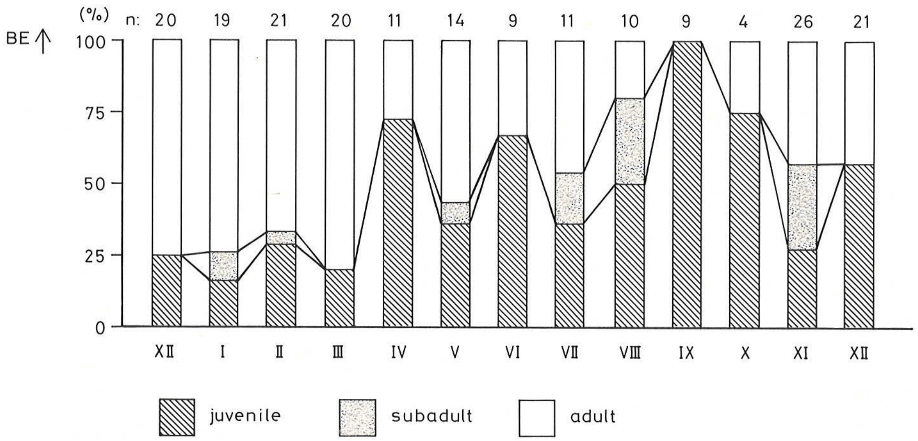

Fig. 11:
Developmental stages of *Neomachilellus adisi* captured per month (in %) on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a secondary dryland forest near Manaus. Catches collected between December, 1981 and December, 1982; total catch per month = 100 %; n = total number of specimens caught per month.

In the inundation forest, the activity of *M. adisi* was limited to the canopy and upper trunk area, from which specimens were collected during fogging studies. Only during the dry season did animals temporarily come to the lower trunk area of the non-flooded forest (Fig. 3). The presence of small scaleless juveniles and the steady increase in size of specimens, which were subsequently caught during trunk descents (Fig. 14), indicates a defined reproduction period. As in *N. scandens*, these animals are believed to represent one generation.

The possibility that additional reproduction occurred in the upper trunk and canopy area cannot be excluded since collecting data were fragmentary. This idea is supported by material from another fogging study in March, 1979, where scaleless and small juvenile specimens of *M. adisi* were obtained, together with adults, in an inundation forest on the opposite side of the Rio Tarumã Mirím (MONTGOMERY & ERWIN, unpubl.).

Neomachilellus adisi WYGODZINSKY, 1978

This species was restricted to the inundation forest and lived on tree trunks (Fig. 3). It was neither collected on the forest floor nor in the canopy. As in *N. scandens* from the same biotope, we observed one generation per year. During field work in September, small juveniles were caught in the lower trunk area, shortly after forest inundation. Larger juveniles were captured during trunk ascents in October and subadults in November (Fig. 15). Females developed somewhat faster than males (cf. *N. scandens*). Adults were recorded

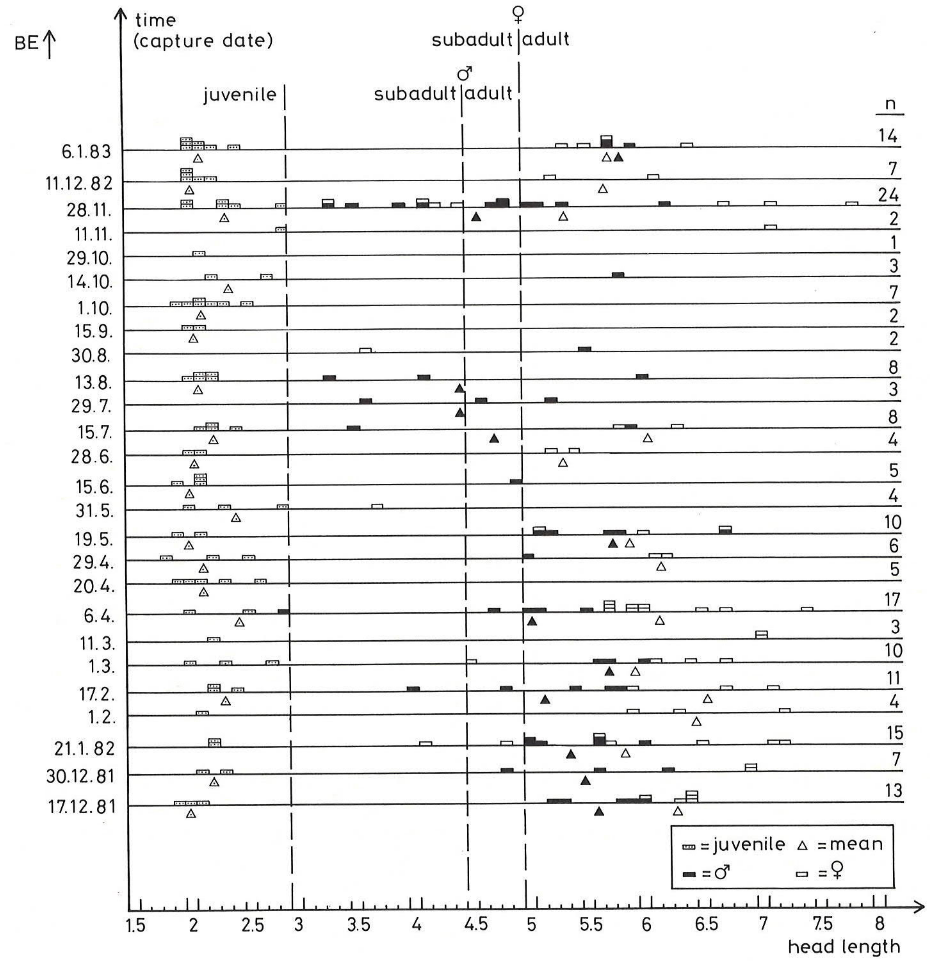

Fig. 12:
Developmental stages of *Meinertellus adisi* caught on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a secondary dryland forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between December, 1981 and January, 1983.

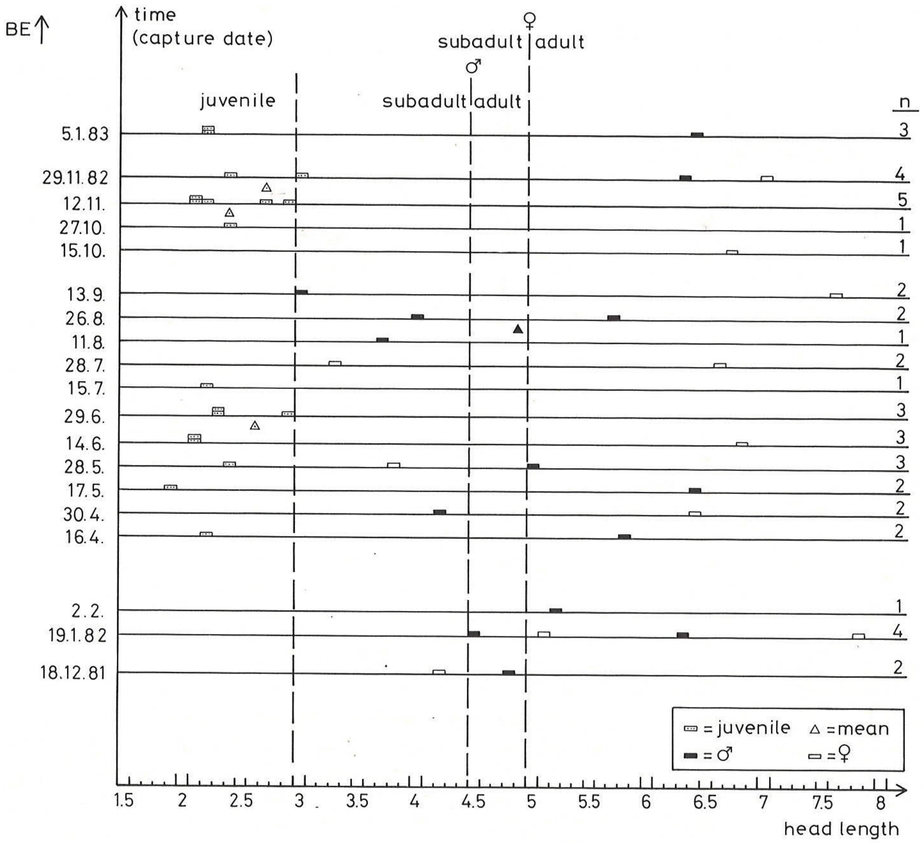

Fig. 13:
Developmental stages of *Meinertellus adisi* caught on a tree trunk (BE ↑ = 1 arboreal photo-eclector for trunk ascents) in a primary dryland forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between December, 1981 and January, 1983.

from December onwards. At this time *N. adisi* was observed to graze in the lower trunk area at night (1 - 4 m height), together with *N. scandens*. Intestines contained mostly algae, fungal hyphae and bark material. Animals of laboratory cultures fed on green algae. When disturbed, e. g. during our capturing efforts, *N. adisi* jumped up and down on the trunk without falling to the forest floor. Propagation was never observed in the field. Eggs might have been deposited under loose bark in the lower trunk area, where animals hid during the day. They were facultatively flooded during subsequent forest inundation (cf. *N. scandens*). This assumption is supported by fogging studies during forest inundation (July, 1977, 1979) in which no specimens of *N. adisi* were obtained. However, the only female captured in arboreal photo-eclectors for trunk descents during flooding (Fig. 3: July) still carried two eggs.

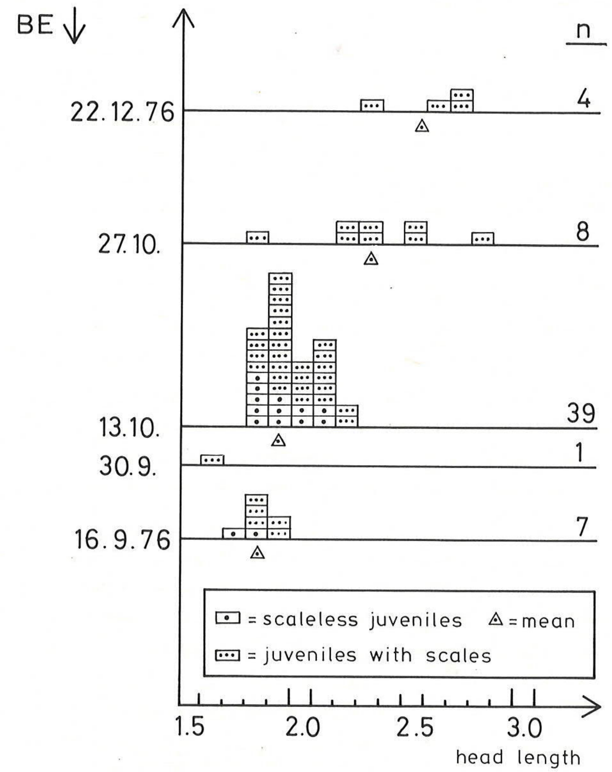

Fig. 14:
Developmental stages of *Meinertellus adisi* caught in 3 arboreal photo-eclectors for trunk descents (BE↓) in a blackwater inundation forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between September and December, 1976. Forest inundation until September 16, 1976.

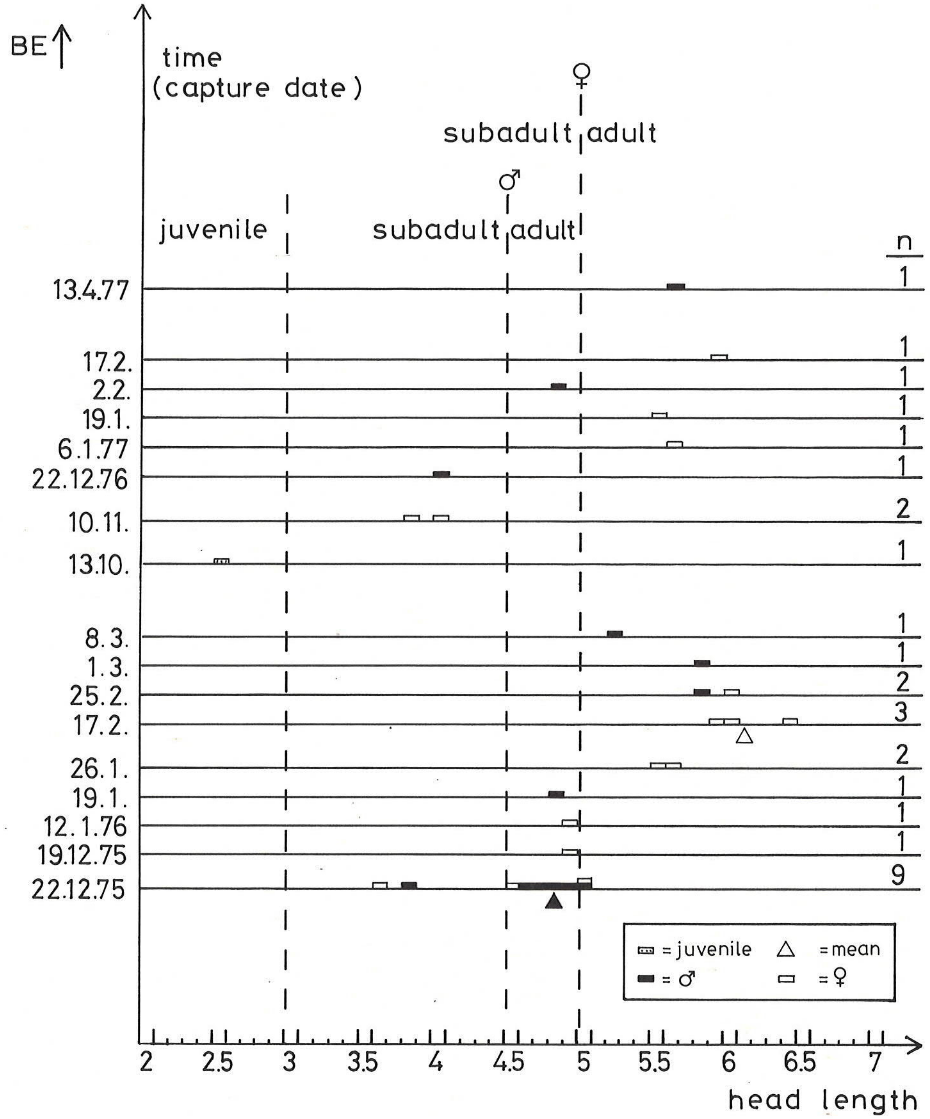

Fig. 15:
Developmental stages of *Neomachilellus adisi* caught in 3 arboreal photo-eclectors for trunk ascents (BE ↑) in a blackwater inundation forest near Manaus. Data arranged by head length of specimens (1 graduation = 0.272 mm) and capture date. Catches collected every two weeks between December, 1975 and March, 1976 as well as between February and April, 1977 and every two weeks from July, 1976 to January, 1977. Forest inundated until September 16, 1976 and from April 9, 1977 onwards. Specimens caught between December, 1975 and March, 1979 (cf. Fig. 3) were only in part available for evaluation.

4. Discussion

Our taxonomic knowledge of Meinertellidae from Central Amazonia is still fragmentary and interpretation of life-cycles is tentative to some extent since data depended on the catch effectiveness of traps, i. e. sampling methods (cf. ADIS 1981). We have to admit, for example, that trunk descending meinertellids surmounted the arboreal photo-eclector for upward migrations to some extent and were erroneously caught during trunk ascents. Some animals certainly did not represent inhabitants of the lower trunk region but were caught on forest floor and trunk while returning to the upper trunk and canopy region from which they had fallen, especially during strong wind and rainfall. Despite these and other deficiencies, some general conclusions can be drawn from this study:

The genera *Meinertellus* and *Neomachilellus* originated in tropical regions (STURM 1984). In South America, they have been recorded from tropical rain- and mountain forests. In Central Amazonia, meinertellids inhabit the canopy and trunk region of forests (*M. adisi, N. amazonicus, N. adisi*) in contrast to other, mostly petrophilous Archaeognatha. They adapted from the life on the ground to the canopy/trunk habitat also by acquisition of a vertical jumping ability. In the inundation forest, they colonized the leaf litter as well (*N. scandens*). The flood resistance of eggs in *N. scandens* (and probably *N. adisi*) and the regulation of their development time by the waterbody (= quiescence duration) are conditions for a potential distribution via waterways (e. g. on driftwood, floating macrophytes). *N. adisi* which was also reported from an inundation forest above Leticia (STURM, unpubl.) could have reached Central Amazonia via the Rio Solimões-Amazonas. Likewise, the *Neomachilellus* species which are today recorded from the Caribbean and the coastal zones of the USA (cf. STURM 1984) could have been transported from the mouth of the Orinoco and the Amazon by ocean-currents to these regions. The practically unpermeable blastoderm cuticula of their eggs and a possibly long developmental time in eggs (one year and more; cf. LARINK 1979) certainly favoured a distribution via waterways. An interruption of the quiescence in egg development caused by desiccation of the transporting vehicle, a subsequently fast hatching of juveniles and a rapid attainment of their maturity (cf. *N. scandens*) would facilitate the new colonization of a biotope. This is also true for the ability to swim and to temporarily stay on the water surface, as reported for several species of Machilidae (cf. STURM 1984).

N. scandens seems to be widerspread in dryland forests of the Central Amazon. Until now, it has been collected at various localities up to 100 km distant from Manaus (ADIS & MORAIS, unpubl.). The species apparently has colonized inundation forests in the Rio Negro valley secondarily, where it is presently recorded as far as the arquipelago Anavilhanas (2°42'S, 60°45'W). We consider the annual flooding as the main reason for the acquisition of a seasonal development in *N. scandens* (one generation per year) and the waterbody as the actual timer for the quiescence in eggs. The development strategy of eggs and the structure of their shell need further study. Furthermore, the life-cycle of *N. scandens* in the inundation forest is so synchronized with water-level fluctuations, that the development "hatching juvenile to adult" on the forest floor takes 10 - 12 weeks at most, half the time of the non-inundation period. The flood resistance of eggs enables the species to persist in a harsh environment. *N. scandens* thus represents an ecological transition between terrestrial invertebrates which move to non-flooded areas prior to inundation and terrestrial invertebrates which have evolved adaptations for remaining in flooded terrestrial areas (see Introduction). Further examples for a seasonality achieved in Neotropical wetlands were found in terrestrial Pseudoscorpiones (ADIS et al. 1987) and in aquatic shrimps (WALKER, pers. commun.; cf. WALKER & FERREIRA 1985). Specimens of *N. scandens* from dryland forests and inundation forests are morphologically indistinguishable. Preliminary studies by electrophoresis showed, however, that specimens from dryland forests represent a different stock when compared to inundation forests (biotope-specific races or even subspecies; WOLF, unpubl.). This would explain, why populations of the inundation and secondary dryland forest are clearly separated with respect to microhabitat, behaviour and life history, although study sites were separated from each other by only 100 m. Further studies should focus on interbreeding experiments in the laboratory and on the reaction of eggs from the primary and secondary dryland forest to artificial flooding.

5. Resumo

O ciclo de vida e a ecologia de quatro espécies noturnas de Meinertellidae são dados e suas adaptações da floresta de terra firme à floresta de inundação na Amazônia são discutidas. Em florestas primárias e secundárias de terra firme, *Neomachilellus scandens, N. amazonicus* e *Meinertellus adisi* são arboricolas, não mostram um período de reprodução e seus juvenis são coletados ao longo do ano. Em florestas de inundação no vale do Rio Negro, as quais são alagadas por 5 até 6 meses, *N. scandens, N. adisi* e *M. adisi* têm uma geração por ano. A inundação anual é considerada a razão principal para a aquisição de um desenvolvimento sazonal. Em *N. scandens*, os juvenis eclodem, no início do período não-inundado, de ovos anteriormente submersos no chão da floresta e atingem a sua maturidade 3 meses depois. Adultos propagam-se na liteira onde as fêmeas depositam seus ovos, os quais estão sujeitos à próxima inundação. Ambos os sexos migram a seguir para a área de tronco e da copa e morrem. *N. adisi* é restrito à florestas inundàveis e vive nos troncos onde os ovos passam por uma inundação facultativa.

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