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Direct development, no diapause, in *Taeniopteryx nebulosa* (Plecoptera, Taeniopterygidae)

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With 6 Figures and 1 Table

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Like its congeners, *Taeniopteryx nebulosa* (Linné) has a very early flight period. Egg development is direct and completed within about one month. Despite this, larvae are almost exclusively first recorded in autumn, so that a larval diapause like the one known for an American species appeared probable. However, we found direct development and continues larval growth when rearing *T. nebulosa* from eggs in the laboratory. Larval size in the laboratory colony matched size of specimens collected in the field at the same time. Growth continuous steadily over winter, but wing pad development during the last three instars may give the incorrect impression of exceptionally fast growth. Some morphological and behavioural details supporting the monophyly of the family Taeniopterygidae are emphasized.

1 Introduction

Nine of the ten nominal European species of genus *Taeniopteryx* are endemic to restricted areas in southern and central Europe between the Pyrenees and the Caucasus. Only *T. nebulosa* (Linné) is widespread, ranging from southern France to the Carpathians and across England and Scandinavia to the Russian Far East (Zhiltzova 1980). There are additional species of the genus in North America, mainly in the east, i.e., the genus exhibits an amphi-atlantic disjunction apparently caused by the opening of the Atlantic Ocean. The genera *Leuctra* and *Oemopteryx* provide similar examples (Zwick 2000).

The monophyly of *Taeniopteryx* is well documented by unique features, the telescoping coxal gills and several microscopic cuticular structures described for North American species (Kapoor 1985) but present also in European representatives, see below. However, the disjunct Palaearctic and Nearctic species groups are pronouncedly distinct in their appearance. The Nearctic nymphs possess a striking pale median band along their dorsum (see, for example, Stewart & Stark 1988), while the dull European species have prominent median abdominal teeth, and several also horned pronota (see, for example, Illies 1955).

A common biological feature of *Taeniopteryx* is the very early flight period, at ice break on rivers or at snow melt. The North American representatives are prime targets of "Winter Stonefly Clubs". The life histories of the North American *T. nivalis* Fitch and *T. burksi* Ricker & Ross are known (Harper & Hynes 1970, 1972). Egg development is direct, but there is a nymphal diapause in about the fourth instar, involving hypermetamorphosis. At the moult to the immobile diapausing stage nymphs undergo considerable morphological change. They shed their setae, lose their cerci and their appendages become appressed to the body; the diapausing specimens resemble little beetle pupae. Diapausing nymphs in the laboratory were attached to corners between leaf ribs or the like and therefore difficult to find; in the field, they were discovered deep in the hyporheos (Harper & Hynes 1970).

Unfortunately, the life history of no single European species is completely known. *T. nebulosa* (Brittain 1977, Elliott 1988) and *T. auberti* Kis & Sowa (Schmidt 1991) are known to have direct egg development. Information on nymphal growth is scanty but the lack of records during spring and early summer in Central Europe is striking. Mertens (1923) reported nymphs of *T. schoenemundi* Mertens and *T. nebulosa* only between November and March, and Brandt (1994) collected *T. nebulosa* only from September to March. Elvang & Madsen (1973) stated that *T. nebulosa* nymphs grow in autumn and winter; however, their graph indicates that nymphs found in October were not small but had a head capsule width of about 0.8 mm. Khoo (1964) raised nymphs from eggs in the laboratory but presented no information beyond the fourth instar. Langford & Bray (1969) found tiny nymphs in July but stressed their scarcity from March to July and Langford (1971) stated that nymphs "did not reappear until September". Svensson (1966) shows no data between adult emergence which occurs at ice-break and begins in mid April until September when mean body length was 4-5 mm; subsequent autumnal growth was rapid.

To clarify if *T. nebulosa* passes through a diapausing nymphal stage it was raised in the laboratory at Schlitz, from eggs obtained from adults collected at Zerbst. Laboratory data were compared with field benthic collections at Zerbst.

2 Study Area

Field work was done in Saxony-Anhalt at Zerbst, along the Lindauer Nuthe at the Buschmühle (ca. 12°10'O, 52°00'N), a tributary of the Zerbster Nuthe which in turn enters the middle Elbe river. At the sampling site, the slow-flowing stream runs through pastures. The stream is bordered by alders (*Alnus glutinosa*). Occasional readings (in mid April, late May and mid October) indicate the stream is circumneutral to slightly alkaline (pH 7.1-7.5), temperature

ranged from 5.6-11.4 °C, conductivity from 680-871 $\mu\text{S}/\text{cm}$, and oxygen content from 8.4-9.0 mg/l, corresponding to 73-92 % saturation.

3 Material and Methods

Numerous adults were collected on 11.03.2000. At this time, no nymphs were left in the stream and most females were already spent. During the next two days, specimens were kept in a gauze cage at low room temperature. Several specimens mated and some females produced small eggs masses, most of less than 100 eggs. Apparently, these were residual egg masses produced by largely spent females because full clutch size is far over 1000 eggs (Khoo 1964).

In the field, larval samples were taken monthly, beginning in late August 2000. At each date, kick-samples were taken for 30-90 minutes, using a hand net with a 30*23 cm opening and 0.5 mm mesh size. Because larvae had previously been noticed to avoid exposition to current, sampling was mainly in quietly flowing reaches with alder roots, dead wood and depositions of dead leaves. Samples were inspected in a white tray, specimens picked manually, and preserved in 70 % ethanol.

Adults were not again collected but the emergence pattern in 2001 was determined by counting exuviae on tree trunks on a 28 m strip along the banks.

Laboratory breeding was performed at Schlitz/Hesse. Eggs were incubated as described by Zwick (1996), at various constant temperatures between 4 and 20 °C. We determined mean incubation period, the number of days until 50 % of all larvae that eventually hatched had actually hatched. Hatchlings and eggs about to hatch were transferred to a simple, efficient sprinkler rearing system (Zwick & Teslenko 2003) (Fig. 1). Most hatchlings were kept in two 2-l-polyethylene boxes with 0.2 mm gauze windows, a bottom layer of coarse sand and fine gravel, and alder roots, where specimens are sometimes found in the field. Several groups of small nymphs were kept in 125-ml-polyethylene freezer boxes with 0.2 mm gauze windows, larger nymphs in 1-l-containers with 0.5 mm mesh screens and with only a mineral bottom.

First instar nymphs were fed a mixture of very fine detritus (mainly fragments of conditioned *Alnus glutinosa* leaves) and feces of shredders (*Gammarus* spp. and of a colony of *Pteronarcys* spp. nymphs). In April, nymphs were additionally offered epilithon brushed off stones in the Breitenbach at Schlitz but later, they were exclusively fed detritus. Inspections were at irregular intervals, about once or twice a week. Each time, exuviae were collected and single nymphs preserved and slide-mounted in Euparal. Nymphal size was variously determined as body length (BL), head capsule width (HCW), or labrum width (LW).

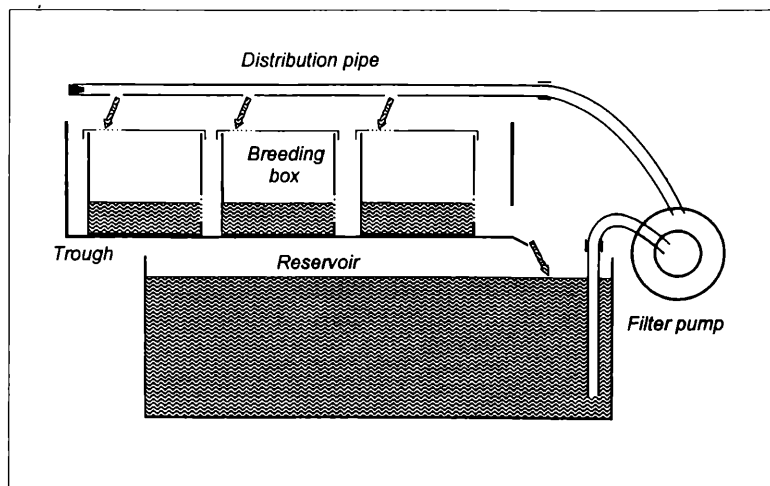


Fig. 1: Diagram of the sprinkler rearing apparatus used

Water temperature (daily mean °C) and photoperiod during laboratory breeding are shown in Fig. 2. Daily amplitude of temperature varied from 0.5 °C in winter to at most 2 °C during summer. Dim indirect light was from a fluorescent light tube.

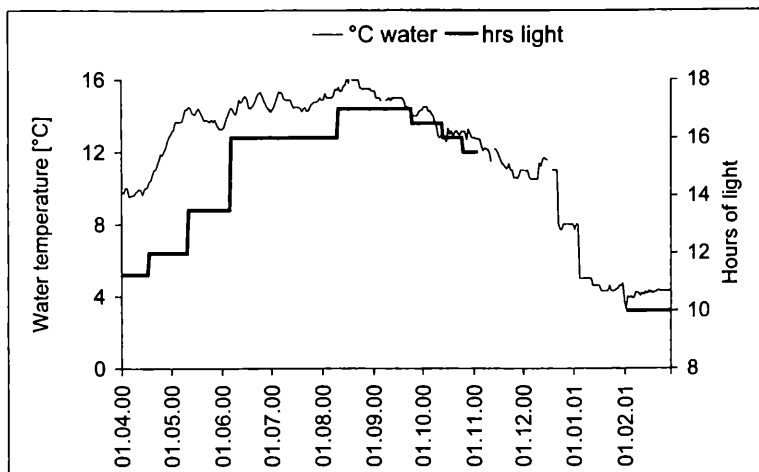


Fig. 2: *Taeniopteryx nebulosa*, daily mean water temperature and photoperiod during laboratory breeding

4 Results

Egg development. Our data for mean hatch (Fig. 3) agree well with those for Scandinavian and British populations (Brittain 1977, Elliott 1988). In the present study, hatching success at 20 °C was only about 20 %; at all other study temperatures success exceeded 90 %.

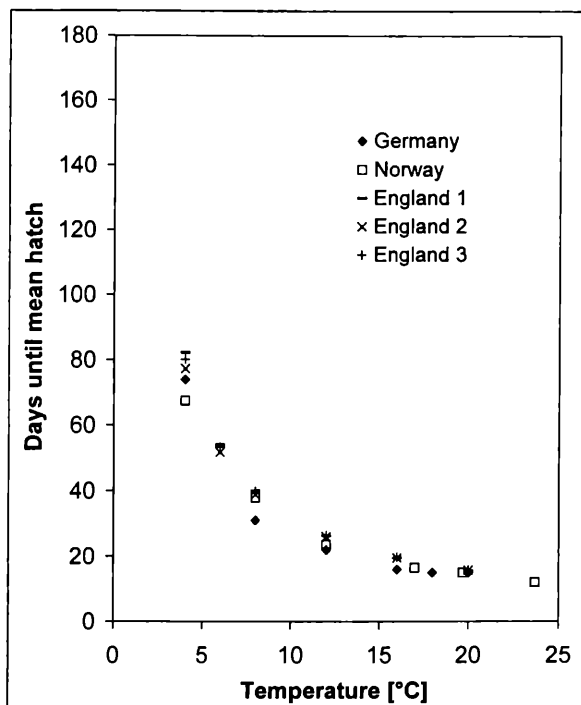


Fig. 3: *Taeniopteryx nebulosa*, mean incubation period (number of days until 50% hatch) at various constant temperatures; data on Norwegian material from Brittain (1977), on populations in three English rivers back-calculated from Elliott (1988)

First larval instar

The animals have simple flat terga and resemble long-legged Nemouridae but do have short simple coxal gills. Antennal and cercal segment numbers are standard, i.e., 9 and 3 (Zwick 1980), respectively, as described by Khoo (1964). The tiny tibiae of first instar *T. nebulosa* (and also of *T. auberti*; Zwick unpublished) have an exceptional appearance because the "hemispheroidal structures" described in detail by Kapoor (1985) are so relatively large and prominent that they make the legs look bumpy and deformed.

Subsequent instars

The 2nd instar has 9 antennal and 3 cercal segments like the first instar but the basal cercal segment carries a supernumerary ring of setae. Segment numbers increase at moults but not in a stepwise fashion permitting the identification of subsequent instars by counting segments. Gills become two- and eventually three-segmented at a head width of approximately 0.5 mm. Distinct median crests and tergal serrations were first apparent in nymphs of about 3.5 mm BL and became increasingly larger at moults.

Nymphal development

The very small nymphs of *T. nebulosa* are slow-moving and tend to remain immobile when disturbed. They are therefore easily overlooked. Slightly larger nymphs curl up upon slight disturbance. When touched they quickly run or swim by laterally undulating body movements and move upward and slightly backward until their antennae and mouthparts get caught in the surface film. All nymphal instars were active, fed and grew, there was no retardation or even arrest of development.

Growth was recorded in various ways. Because of abdominal telescoping, head width and labrum width were the preferred measurements for entire nymphs and exuviae, respectively. Measurements of exuvial labrum width could easily be transformed to head width because the two measurements are closely correlated:

$$\text{HCW} = 2.702 * \text{LW} + 0.001$$

$$(r^2 = 0.985; n = 67; p < 0.005 \text{ for slope, n.s. for intersect})$$

Several specimens were kept singly to compare size of successive instars. At moults, linear measurements increased by factors between 1.05 and 1.21 (mean \pm STABW = 1.13 ± 0.05) but the number of readings was low ($n = 16$).

When body size (as head width) was plotted against calendar date, the size spectra in the laboratory colony and the field population matched reasonably (Fig. 4). The comparison was discontinued after October 2000, because of low numbers of survivors in captivity; the last reared specimen died, in the last larval instar, in February 2001. After October, the laborious analysis of the field population structure via head width measurements of every specimen was replaced by visual assignment of larvae to instars by degree of wing development, see below.

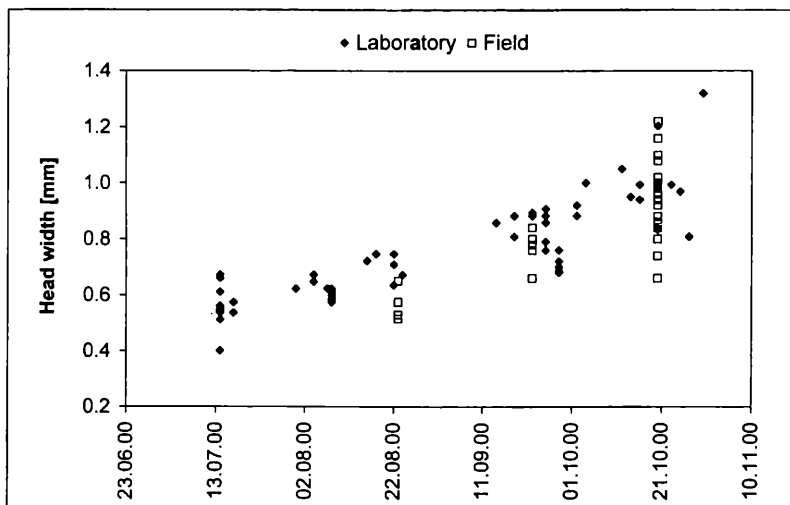


Fig. 4: *Taeniopteryx nebulosa*, change of larval size (as head width) with time, in a laboratory colony and in the field (Lindauer Nuthe)

Wing development

The last three instars bear wing pads whose size falls into three groups, i.e., wing development follows the common pattern in the order (Zwick, submitted). The relation between wing length and head width is approximately the same within each instar, over a wide size range. Members of the different instars overlap in size but are separate for wing length. From one group to the next, wing length more than doubles while head width increases much less (Tab. 1).

Tab. 1: *Taeniopteryx nebulosa*, ranges of head width (HW), wing length (WL) and the proportion WL/HW from the antepenultimate (Ln-2) to the last larval instar (Ln)

Instar	min HW	max HW	min WL	max WL	min WL/HW	max WL/HW
Ln-2	0.80	1.22	0.16	0.46	0.19	0.40
Ln-1	1.12	1.50	0.64	0.94	0.54	0.69
Ln	1.36	1.76	1.50	2.32	1.07	1.32

In the field population in the Lindauer Nuthe, the first specimen with wing pads was found in late September, at about the same time when wing development began in the laboratory colony. Field population structure during late larval life changed quickly, by late January all specimens were in the last instar (Fig. 5).

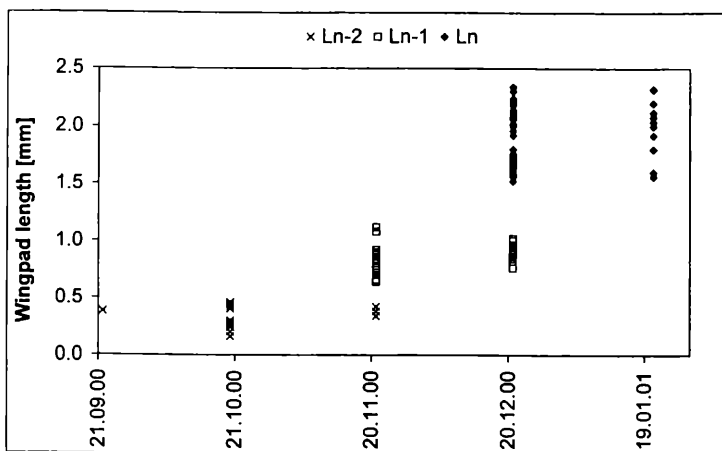


Fig. 5: *Taeniopteryx nebulosa*, population structure in the field, during late larval life. By their wing length, the last three instars can be clearly distinguished

Adult emergence

Instead of collecting adults, exuviae were removed from emergence supports once a week, beginning in January 2001. Exuviae were found from 7 February to 28 March, the largest number was observed in late February (Fig. 6). Most were found on alder trunks, on the side facing the water, usually 5-30 cm above water level but some were found 1 m high. With no exception, exuviae were positioned with their head down.

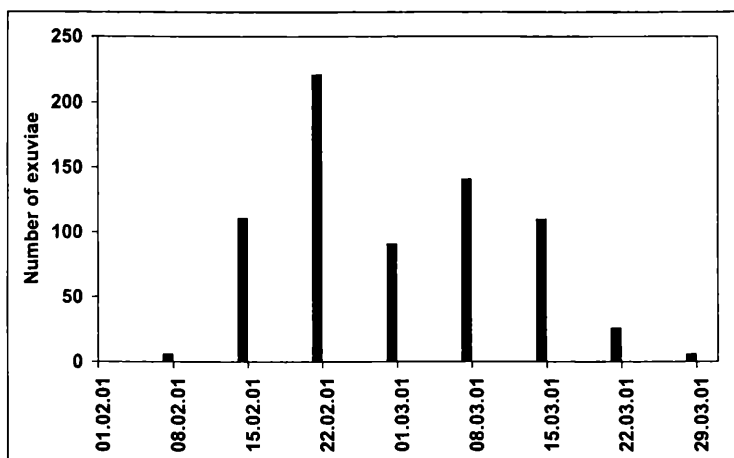


Fig. 6: *Taeniopteryx nebulosa*, numbers of exuviae on emergence supports along the Lindauer Nuthe in early spring, 2001

5 Discussion

Nymphal avoidance behaviour (curling), the backwardly curved path of *Taeniopteryx* larvae swimming in standing water, and the way in which specimens become trapped in the surface film by their antennae and mouthparts, agree completely with *Brachyptera* spp.; they also agree in that the adult moult is exclusively performed with the head down. Curling of disturbed larvae occurs also in Pteronarcyidae (Zwick 2000) but the last three features are unique among Plecoptera. Since the monophyly of family Taeniopterygidae is based on only a small number of morphological details (Zwick 2000) these traits are interesting additions to the list of shared characters.

Egg development is direct, like in *T. auberti* and the American species studied (Zwick in Schmidt 1991, Harper & Hynes 1970, 1972). The pattern of temperature dependence of mean incubation period agrees with Scandinavian and British populations (Brittain 1977, Elliott 1988). Slight differences, mainly an earlier hatch of the German specimens at low temperatures and low hatching success at 20 °C may not be significant, as only very limited German material was studied.

The species is apparently tolerant of warm and even mildly polluted waters; we also found it under such circumstances. There is a rather large stable population of *T. nebulosa* in the river Schwarze Elster in eastern Saxony-Anhalt, where summer temperatures may attain 27 °C (Hohmann & Gohr, unpublished).

Attempts to simulate the natural nymphal habitat in the breeding trays by introducing alder roots were detrimental: despite great care, a few larvae of Polycentropodidae (Trichoptera) were overlooked and quickly ate most specimens. In contrast, losses were negligible in standard breeding boxes with only mineral bottom and only conditioned alder leaves as food.

Small European *Taeniopteryx* nymphs were rarely observed in the field, most records are of larger nymphs in autumn and winter. However, the lack of records of small larvae in spring and summer is no consequence of nymphal diapause, *T. nebulosa* develops directly. The failure to observe young nymphs in spring and summer is probably explained by the smallness of the early instars and by their sluggish habits. The absence of the striking tergal modifications distinctive of larger nymphs and the inconspicuousness of the initially short retractile coxal gills may also have lead to confusion with Nemouridae.

Our observations of early instar morphology partly disagree with earlier descriptions; the first instar does have coxal gills (contra Hynes 1941) and the antennal segment number does not increase at the moult to second instar; we can also not confirm characteristic segment numbers for subsequent instars, as suggested by Khoo (1964). These differences are easily explained by the smallness

and delicate nature of the structures involved, and by general problems of identifying and counting nymphal instars from size distributions in field samples that were recently discussed in detail (Zwick & Teslenko 2003). Figures of first instar *T. burksi* (Harper 1978) do not show the distinctive "hemispheroidal structures" (Kapoor 1985) which are conspicuous in both *T. nebulosa* and *T. auberti*.

Rapid or important growth during late development was sometimes reported (Langford 1971, Svensson 1966). However, students apparently mainly observed the last few instars where the rapid development of the wing pads (Fig. 5) may suggest an exceptional increase of body size, which is, in fact, much less than growth of wings and is only average (Tab. 1).

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