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**DEVELOPMENT OF DIAPAUSE IN PYRRHOCORIS APTERUS FEMALES
IN THE MIDDLE PERIOD OF WINTER DORMANCY (HETEROPTERA)**

Ivo HODEK

Received June 25, 1973

Abstract: Between mid-November and late February, six samples of hibernating *Pyrrhocoris apterus* adults were transferred from the nature to short day conditions (L12, D12), 25° C and ample food. It has been proved that even under this diapause inducing photoperiod all females start ovipositing if they are transferred to the laboratory after mid-December. During the subsequent two months, however, the preoviposition period still keeps shortening (it does not achieve its normal values before January or February), and particularly the fecundity grows and the unproductive end of life shortens.

This increase of the reproductive activity during January and February shows that the inner inhibition of reproduction is not yet quite overcome at the time of the hundred-per-cent incidence of ovipositing adults in December. Although this criterion of the end of diapause is not correct on principle, its further use is not rejected. This methodically advantageous qualitative criterion is widely used and is comparable with the resumption of development in insects with other types of diapause.

P. apterus females, which had survived two months after ceasing ovipositing under short day, were transferred to long day (L18, D6). Many of them resumed oviposition there. It was thus demonstrated that in the middle period of diapause *P. apterus* females lose their sensitivity to the diapause inducing photoperiod only temporarily.

INTRODUCTION

Two criteria have been used to reveal when the diapause (or the refractory period of diapause)¹⁾ is terminated in nature. One is the *potentiality* to resume the morphogenetic development, i.e. in the case of imaginal diapause the potentiality in females to complete vitellinization of oocytes and to start the oviposition. This potentiality may be realised after a transfer of the insects from the open to adequate laboratory conditions.²⁾ Another criterion is the

1) The term "end of diapause" or "termination of diapause" is used in the sense common for most ecologists: diapause ends when the development in the open starts to be inhibited only directly by environmental conditions, e.g. by low temperature, insufficient humidity, lack of essential food. This period of dormancy is usually designated by a neutral term "post-diapause", or by a rather confusing term "quiescence". By some workers, however, it is assumed that diapause lasts over the whole period of inactivity of the neuro-endocrine mechanisms regulating development, an inactivity *due to whatever cause*; for example, in temperate climates it lasts until the rise temperature in spring. Then the first period of diapause, when the animal cannot yet respond to favourable conditions, may be denominated as the "refractory" phase (of diapause) and the next period as the "activated" phase (Mansingh, 1971) or a "competent" phase (Watson, Smallman, 1971).

2) In the species which can be reactivated right at the onset of diapause by a photoperiod adverse to diapause, it is, of course, necessary to use a diapause inducing photoperiod (or a neutral photoperiod) if we attempt to reveal the end of diapause by such a transfer.

shortening of the duration of the preoviposition period to the "normal" value, after the reactivation by a photoperiod adverse to diapause. According to these two characteristics also the "development" of diapause (or the diapause termination) in *P. apterus* was evaluated in the previous paper (Hodek, 1971a).

Some of our recent results have indicated that the mere onset of reproduction is not a sufficient sign of the physiological state of a female. Therefore the bugs in the critical period, when the diapause approaches its end (i.e. from mid-November to late February), were observed over a long period of time after transfer to the laboratory. The experiment was not discontinued before all experimental specimens died, and thus the intensity and the duration of the oviposition, and also the duration of the post-oviposition period could be ascertained. In the last mentioned period attempts at a further stimulation were made with females with higher longevity by transferring them to long day.

The aim of this paper has been¹⁾ to check by the above mentioned characteristics a) the relationship between the mere onset of reproduction and the end of diapause, b) the suitability of the length of the pre-oviposition period at the laboratory activation as an indicator of the diapause intensity; ²⁾ to verify whether the end of diapause in *P. apterus* females is combined with the irreversible disappearance of the sensitivity to photoperiod

MATERIAL AND METHODS

The method of sampling and breeding was described in the previous paper (Hodek, 1971a). All seven samples were collected in a lime-tree alley near the castle of Veltrusy (N. Bohemia) between early November and late February. They were reactivated under short day (L12, D12) and 25° - 15° C. From each sample thirty isolated pairs and thirty pairs in a group culture were reared in the laboratory till their death. Thus the duration of the pre-oviposition, oviposition and post-oviposition period, as well as the total number of eggs laid was ascertained. The index of the reproductive activity (i) was calculated according to the following formula:

$$i = \frac{\text{total amount of eggs laid}}{\text{longevity in the laboratory (in days)}}$$

RESULTS

Incidence of ovipositing females

Only a little more than half of the females of the mid-November and early December samples (57 and 64% resp.) began to lay eggs, whereas as many as 90% of the females of mid-December oviposited. Since late December the whole population was reproductive after the transfer to short day (L12, D12) and 25° (Fig. 1). In this regard the new results confirm the previous ones (Hodek, 1971a).

Fecundity

The average number of eggs kept increasing gradually, even though not quite regularly (Fig. 2). The females from the first sample still had a comparatively low oviposition rate: 202 eggs in 3.9 batches. The females sampled 2 weeks later laid many more eggs: 276 in 5.2 batches. Further increase of the average fecundity was recorded in January when about 300 eggs in approximately 6 batches were laid, the same as in February.

When the average numbers were calculated for all the females, i.e. including even the non-ovipositing ones, naturally the average amount of eggs was substantially lower in the first samples and its later rise was steeper and more regular (Fig. 1).

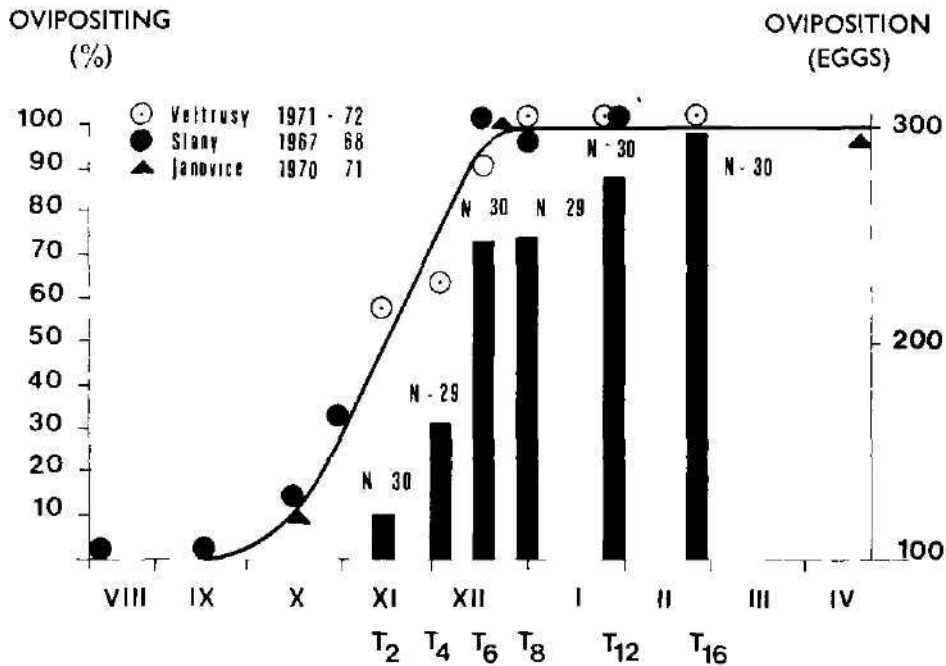


Fig. 1. Reactivation of *Pyrrhocoris apterus* under L 12, D 12. — Symbols: incidence of ovipositing females (%), columns: aver. amount of eggs laid (average calculated from both ovipositing and non-ovipositing females); abscissa: time of sampling.

Duration of the main life-periods

The total longevity under experimental conditions kept gradually shortening in the course of experiment. The longevity decreased rather steeply by 25 days during 4 weeks between samples T₄ and T₈, later it fell only by 8–10 days within 4 weeks (Fig. 2). The decrease of the overall longevity was mainly due to the shortening of the post-oviposition period. The pre-oviposition and oviposition periods taken together (with the exception of sample T₆) had quite a steady length — within the total 14 weeks they got shorter by 11 days only. In the last sample, in late February, the pre-oviposition period shortened to values which are common in non-diapausing bugs at the same temperature. Also this last finding conforms to the previous experiment (Hodek, 1971a).

Intensity of the reproductive activity

The intensity of the reproductive activity, i.e. the rate of reactivation of hibernating females, is apparently indicated not only by the number of eggs laid, but also by the duration of both-oviposition and post-oviposition

period. Index i , which is obtained by dividing the total number of eggs by the longevity in experiment, involves all these 3 features. This index of the intensity of reproduction grows very regularly (Fig. 2) with the exception of the sample of late December where it was affected by a relatively low fecundity.

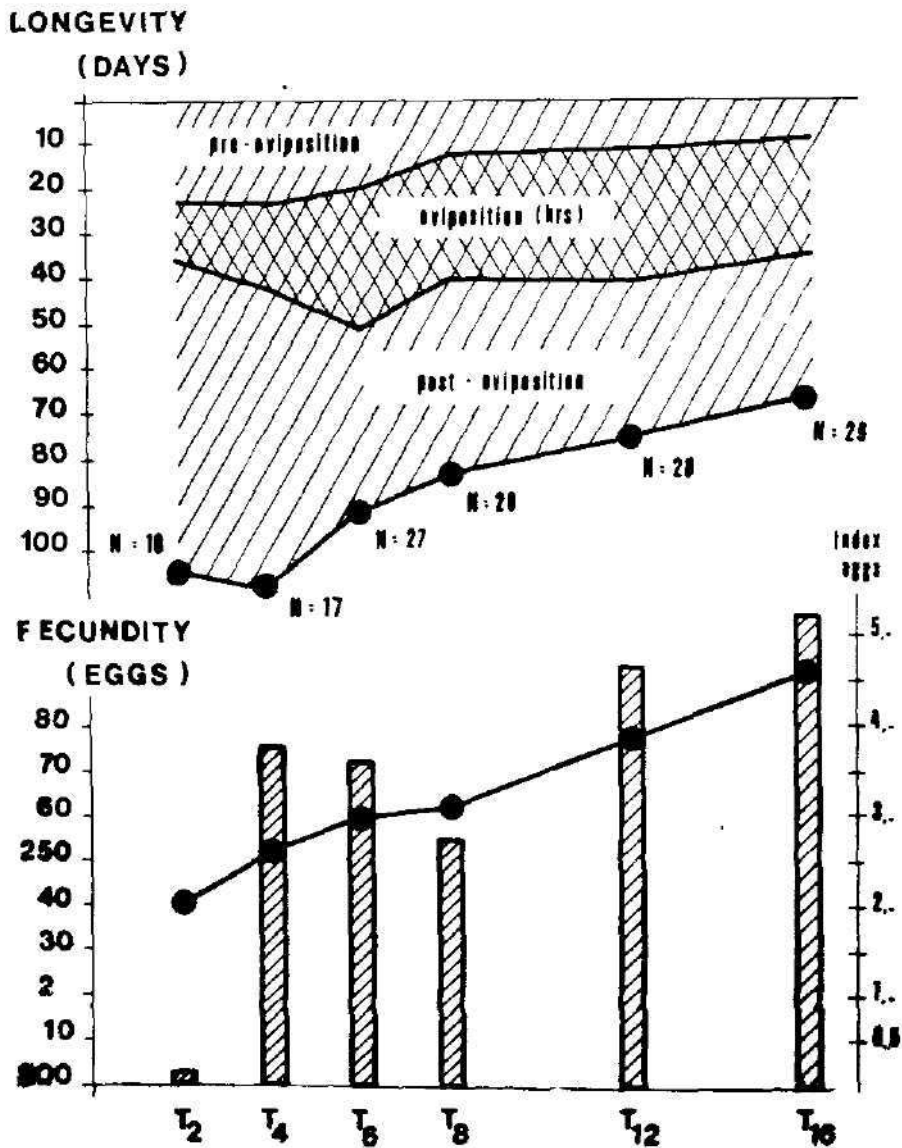


Fig. 2. Fecundity and longevity of females ovipositing after the transfer from the open to L12, D12. — Upper part: longevity divided into three periods, the pre-oviposition, oviposition and post-oviposition period; lower part — columns: fecundity of ovipositing females (number of eggs per day); — circles: index of reproductive activity (fecundity divided by longevity); abscissa: time of sampling.

Tab. 1. Resumption of oviposition after the additional transfer from L12, D12 to L18, D6

Sample	Date of transfer to the laboratory (short day)	Number of females		Number of egg batches			Duration of the pre-oviposition period under long day
		transferred to long day ¹⁾	which resumed egg laying	females which later resumed egg laying	under short day	under long day	
T ₂	15. 11.	10	5	4.0 (1-9)	4.0 (2-6)	2.4 (1-4)	31.2 (19-51)
T ₄	2. 12.	7	5	5.0 (4; 6)	2.3 (1-4)	4.0 (2-7)	37.0 (20-46)
T ₆	16. 12.	6	6	—	6.0 (5-7)	2.2 (1-4)	23.3 (16-32)
T ₈	31. 12.	8	4	6.0 (3-8)	4.5 (3-6)	2.7 (2-4)	22.8 (19-26)
T ₁₂	27. 1.	7	6	7	4.7 (4-6)	2.2 (1-5)	21.0 (16-30)
T ₁₈	23. 2.	9	5	5.8 (5-7)	6.4 (5-9)	1.0 (1)	15.6 (7-28)
		47	31				

¹⁾ The bugs were first transferred from the open to the laboratory short day (L12, D12) and 26° ± 1.5°C. The females which stopped ovipositing were kept for 8 weeks under the same conditions and then the females still alive were transferred, this time under long day (L18, D6) and 28° C ± 1.5° C.

Additional transfer to long day conditions

A rather large percentage of females survived for a long time after the last egg-laying. In individual samples, 6–10 females (i.e. 20–33%) were still living 8 weeks after having ceased ovipositing under short day (L12, D12). These females were transferred to long day (L18, D6) while maintaining the same temperature conditions ($25 \pm 1.5^\circ\text{C}$). In individual samples, 50–100% of these transferred females resumed egg-laying after the second pre-oviposition period which, on the average, lasted 4 weeks in the samples of November, about 3 weeks in the samples of December and January and little over 2 weeks in the February sample. Individual variability was always considerable (Tab. 1).

After the transfer to long day the females usually (with the exception of sample T₄) laid, on the average, substantially fewer batches than after the first transfer from the open to short day (Tab. 1). Except the first two samples (from the period before diapause termination in the whole population), those were females which under short day had already laid at least 3 batches and 4.5–6.4 batches on the average.

Relation between the duration of the pre-oviposition period and the number of egg-batches under short day

In the samples of the period November–January there was shown no correlation between the shortening of the pre-oviposition period and the increase of the number of batches under short day. Thus, in the sample of mid-November, with the average duration of the pre-oviposition period, there were obtained both a very low number of batches (3 females laid 1 batch each) and a very high number (9–10 batches), and the maximum number of batches was laid by that female which had a very long pre-oviposition. Similarly, a great range of numbers of batches (1–9 batches) was ascertained in the sample of early December, with the pre-oviposition period of medium length, and two females laid 9 batches each after the maximum pre-oviposition (24 days). In the samples of middle and late December, the number of batches was always the highest in the connection with only a medium length of the pre-oviposition period (15–16 and 11–12 days resp.) and it was rather lower after a shorter duration of pre-oviposition.

Only the results in the last sample, that of late February, indicate some correlation between the maximum number of batches and a short pre-oviposition period.

DISCUSSION

Completion of diapause development

Many authors, who have studied winter adult diapause in the insects of the temperate zone, have reported that already in the middle of winter (i.e. at the astronomical onset of winter) an essential qualitative change of inhibition occurs in hibernating adults. The insects which up to this time could not be reactivated by suitable temperature and food, are now able, under those conditions, to resume reproduction even at an unfavourable photoperiod (see Introduction). If this criterion is used, it might be assumed for *Pyrrho-*

coris apterus that diapause (or, the refractory period of diapause)¹⁾ ends at the latest in late December because later all females begin to oviposit after the transfer to 25°C and short day.

The bugs were kept at a stimulating temperature, but under a short photophase, until they died; if they stopped ovipositing, they were additionally stimulated by a transfer to long day. The use of this procedure uncovered a problem which remains concealed if the mere *onset* of oviposition is recorded.

Even if at the end of year oviposition starts in all females, the reproductive activity increases further on: fecundity increases, the duration of both the pre-oviposition and post-oviposition periods shortens and the index of the intensity of reproduction rises distinctly. This evidence indicates that the attainment of oviposition at short day conditions is not a sign of a qualitative change in the level of diapause inhibition. A comparison with data from literature for other insects cannot be made because the experiments are discontinued by most authors soon after the onset of oviposition.

The diapause inhibition of reproduction disappears gradually and it is difficult to find a safe criterion for its total absence. If obtaining one egg batch even under an adverse photoperiod is deprived of the function of the qualitative threshold criterion, there is no substitution for it. All the other criterions are only quantitative. Most of them (amount of eggs laid, longevity, etc.) are coupled with the level of vitality.

In many types of diapause the result of the resumption of development is a transient process — eclosion of larvae, emergence of adults, pupation. Then even a very short-term resumption of the appropriate physiological mechanisms may be sufficient to lead to this end. The use of an analogous criterion enables to compare adequately the termination of diapause in females with the termination of diapause of other types.

Therefore, in spite of the above mentioned limitations which must be borne in mind, we recommend that the mere onset of oviposition after the transfer to a reactivating temperature but to diapause inducing photoperiod be further used as a criterion of the end of diapause. Two advantageous criterions giving more precision are the shortening of the pre-oviposition period to the "normal" length and the increase of fecundity to the maximum.

The resumption of sensitivity to diapause inducing factors

Imaginal diapause differs from the other types of diapause by the fact that the process which is inhibited by it, i.e. reproduction, requires otherwise a constant stimulation. For that reason the imaginal diapause is the most suitable type of diapause for the study of the reversibility of sensitivity to diapause inducing signals after the termination of diapause.

Two thirds of the females resumed egg-laying, if transferred to long day 8 weeks after the last batch laid under short day. This response probably could not be recorded in the rest of the females only because they were less vital, so that after a long rearing at a rather high temperature they had been already exhausted and died without ovipositing.

¹⁾ See remark 1) on page 161

The females which resumed oviposition after the transfer to long day had laid several batches (4.5—6.4) under short day. Therefore the subsequent cessation of oviposition under short day can hardly be considered as a sign of an incomplete termination of diapause; it is most likely a result of the resumption of sensitivity to photoperiod after a certain time of egg laying. The loss of sensitivity to diapause inducing photoperiod caused by the completion of diapause development appears to be reversible in *P. apterus*.

The case of *P. apterus* is not exceptional. In spring, *Aelia acuminata* keeps ovipositing under a diapause inducing photoperiod (L12, D12) only 12 to 23 days (18 days on the average). By a subsequent transfer to the diapause averting photoperiod (L18, D6) oviposition is achieved after 10—20 days (aver. 14 days) (Hodek, 1971b). Similarly, Pener and Broza (1971) and Broza and Pener (1972) ascertained for the grasshopper *Oedipoda miniata* that the ovipositing post-diapause females, brought from the field to the laboratory, stopped egg laying within a few weeks. The authors also state that "though reproductive diapause had been terminated in the field, the grasshoppers returned under laboratory conditions to a state of reproductive inactivity, comparable to reproductive diapause". The laboratory conditions were constant light and temperature varying between 24—38°C, i.e. they were diapause inducing for a short-day insect *O. miniata*. No attempts were made to stimulate the resumption of egg laying by the change of rearing conditions.

The resumption of sensitivity to diapause inducing environmental signals after a certain time of egg laying subsequent to the termination of diapause apparently is an advantageous adaptive feature. Generally there is little probability that under normal circumstances the females encounter the diapause inducing conditions at that time. And in the case of an unfavourable season, not enabling a fullfilment of the normal cycle, such a mechanism will render possible a secondary induction of diapause for the next hibernation.

Relation between the speed and rate of perfection of activation

No correlation between the shortening of the pre-oviposition period and the increase of fecundity has been found at the reactivation of diapausing females of *P. apterus* under short day (L12, D12) and 25°C. Both characteristic, however, may be supposed to be affected by the level of activity of the neuroendocrine system governing the egg laying. The share of variability of the vitality of females in the number of batches does not appear to be substantial, since the bugs laid the minimum of batches not due to low longevity; they often had a long postoviposition period.

It appears that there need not be any correlation between the *speed* of activation, whose criterion is the duration of the pre-oviposition period, and the *rate of perfection* of activation, manifested by the endurance of oviposition under an adverse photoperiod. The speed of activation after the transfer from the open to the laboratory seems to be affected to a certain degree by a varying sensitivity of the females to the stimulation by a sudden, substantial increase in temperature, rise of light intensity, presence of food, presence of a male, etc. The females which laid only a small number of batches, although they had started ovipositing after a short pre-oviposition period,

apparently were very sensitive to such a substantial amelioration of environment, but their diapause had not yet been completely overcome.

The intensity of diapause cannot, therefore, be measured by the duration of the pre-oviposition period at the activation, as this is also influenced by the variable sensitivity of the insects to stimulating factors.

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CONTRIBUTION TO THE FURTHER KNOWLEDGE OF OLIGOCHAETA
FROM LAKE TELECKOJE IN THE ALTAI MOUNTAINS

SERĚJ HRABĚ

Received October 10, 1973

Abstract The collection of Oligochaeta from Lake Teleckoje, collected by doc. Dr. O. Štěrba, includes *Haplotaxis ascaroides* Mich., known up to date only from Lake Baikal. The paper contains also remarks to the description of *Rhyacodrilus altaianus* Mich., *Rhyacodrilus lepnevae* Mal. emend. Hrabě and *Pelodrilus ignatovi* Mich.

Lake Teleckoje in the Altai Mountains, situated between 51°—52° N. lat. and 87°—88° E. long. at 436 m above sea level, is 325 m deep.

The Oligochaeta from this lake were treated by Michaelsen (1903) and Malevič (1949).

Michaelsen (1903) described a new species, *Pelodrilus ignatovi*, and determined *Haplotaxis gordioides* (Hart.) (no adult specimens!), *Peloscolex ferox* Eis. and *Limnodrilus udekemianus* Clap.

Malevič (1949) found, among the Oligochaeta collected by S. G. Lepneva, 7 species of Naididae, *Rhyacodrilus lepnevae* n. sp., *Tubifex tubifex* (Müll.), *Peloscolex ferox* Eis., *Bythonomus lemani* (Grube), *Pelodrilus ignatovi* Mich. and *Haplotaxis gordioides* (Hart.) (no adult specimens too!). This author had also mature specimens of *Rhyacodrilus altaianus* Mich. whose reproductive organs he described, but he determined these specimens as *Rhyacodrilus lepnevae*, the genital organs of which, according to my findings are quite different from those of *Rhyacodrilus altaianus* Mich.

In the collection of Oligochaeta from Lake Teleckoje collected by doc. Dr. O. Štěrba on 11—19 Aug. 1972 and submitted to me for determination, I found the following mature species *Rhyacodrilus altaianus* Mich., *Rhyacodrilus lepnevae* Mal., emend. Hrabě, *Haplotaxis ascaroides* Mich. and *Pelodrilus ignatovi* Mich.

Rhyacodrilus altaianus Michaelsen, 1935

Prof. Dr. W. Michaelsen described a new *Rhyacodrilus altaianus* from Lake Sredne-Kočurlinskoje in the Central Altai according to several macerated, in most cases broken specimens, and thus the description of this species does not conform in some respects, to my material from Lake Teleckoje.

One non-injured specimen, examined by Michaelsen, was 10 mm long, 0.5 mm wide and consisted of 70 segments. Also among my 45 specimens, only a few non-mature individuals are intact. One not quite mature specimen without the posterior segments is 455 μm wide in segment 10 and 490 μm in segment 11.

The prostomium of Michaelsen's worms is simply rounded as that of mine specimens.

Michaelsen observed only 2-3 forked setae in the ventral bundles, with nearly equally long prongs. In my specimens they are up to 6 in the

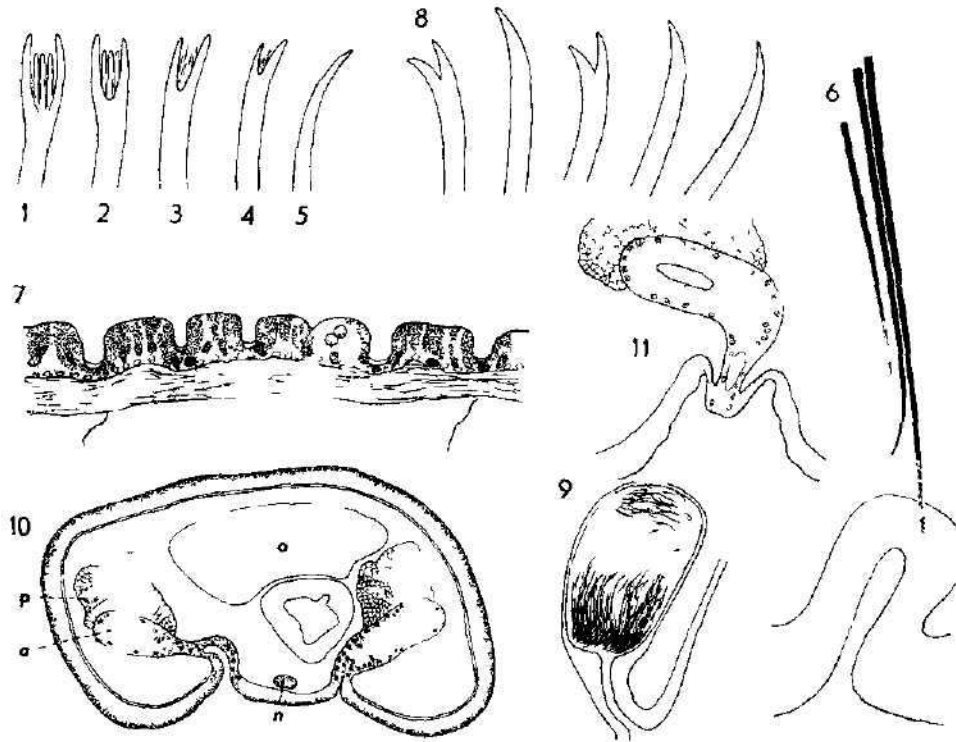


Fig. 1-6 *Rhyacodrilus altaianus* Mich.: 1 - Ectal end of dorsal seta of segment 3; 2 - of segm. 7, 3 - of segm. 14, 4 - of segm. 23; 5 - of segm. 30; 6 - Penial seta Fig 1-5 $\times 995$, fig. 6 $\times 475$
 Fig 7-11 *Rhyacodrilus lepnevae* Mal 7 - Epidermis of segm. 5, $\times 440$, 8 - Five setae of ventral bundle of segm. 6, $\times 1240$; 9 - Spermatheca, $\times 170$; 10 - Transverse section of segm. 11, a - atrium, n - nerve-cord, o - ovum, p - prostate glands, $\times 132$, 11 - Ectal end of male duct of second specimen, $\times 158$

bundles of the anterior part of the body, with the upper prong somewhat longer than the lower one in the anterior segments. In the postclitellial segments the upper prong is equally long or shorter than the lower one.

In the dorsal bundles there are, according to Michaelsen, 1-3 hair and 1(2?) forked seta. The hair setae are smooth, and of different length in one and the same bundle. The part of the hair setae protruding from the body is nearly as long as the diameter of their segment. The forked dorsal setae end with two equally long prongs diverging at an acute angle. No intermediate comb-teeth were observed.

In my material, the hair setae do not differ from the description of *Rhyacodrilus altaianus*. I found 2-3 hair setae in the antecitellial segments and two, posterior one seta in the postclitellial segments. They are up to 550 μm long in segment 7, and only 200 μm in segment 30-40.

The forked dorsal setae of the specimens from Lake Teleckoje are different in shape and form one continuous series of transitions from forked setae to simple pointed ones (fig. 1—5).

In the 17 anterior segments there are, roughly speaking, 2—3 (4) pectinate and 1—3 hair setae in each dorsal bundle. The pectinate setae end by two very long prongs bent inwardly a little. The prongs are equally long. The intermediate comb distinct. These setae resemble the comb-like setae of *Peloscolex ferox*, as shown in fig. 13 a₃ on table IV in the monograph of Štolc (1888). From segment 18 the upper prong of the pectinate setae shortens gradually in comparison with the lower one. This difference increases toward the posterior segments. In segment 25 only one forked seta remains in the bundle, the upper prong of the second one disappears and the seta changes into a simple-pointed one with an acutely bent ectal end. One double-pronged seta, one simple-pointed and one hair-like occur still in segment 32.

The penial setae are very characteristic of *Rhyacodrilus altaianus*. They protrude from the deep slit-like male pore in a number of 1—2. Michaelsen could not describe their form from specimens mounted in Canada balsam. He only stated that they are about 120 μm long, straight and hair-shaped on the ectal end. Malevič observed 2—3 penial setae up to 170 μm long, nearly straight, with ectal end simple-pointed, slightly bent, gradually narrowing to the ectal end in the specimens determined as *Rhyacodrilus lepnevae*.

I found 3 penial setae on each side in segment 11 (fig. 6). They are 150 to 175 μm long, stick-shaped, gradually tapering to the arched ectal end. These setae protrude in the distal portion of the male duct.

The clitellum was not developed in my specimens and those available to Michaelsen. The dissepiments are thin. Coelomocytes 17—18 μm. Chromophil (not chlorophyll) cells (= pharyngeal glands), badly preserved occur in segment 4—6 of my specimens.

One pair of testes in segment 10 on dissepiment 9/10, one pair of ovaria in segment 11 on dissepiment 10/11.

One pair of very small, flat, male funnels on the anterior side of dissepiment 10/11 in segment 10. The spermducts moderately long, not regularly winding, lying rolled up in the anterior half of segment 11. They open in the ental ends of atria. The atria are long, tubular, bent 3 or 4 times. Their diameter measures 55 μm. They are covered with pear-shaped prostatic cells (diffuse prostatic glands), 40 μm long, so that the total diameter of atria measures 135 μm (not 185 μm). The atria end directly by a shorter, thinner, bare discharging duct in the deep slit-like male pore. This is Michaelsen's description of the male duct of *Rhyacodrilus altaianus*.

The specimens studied by Malevič showed long sac-like atria, only slightly dilated in apical part. At the male pores there occur 2—3 penial setae lying in special sacs (?).

My specimens are not fully mature, with atria 130 μm long, cylindrical, covered by diffuse prostatic glands, 12.8 μm long. No ripe spermatozoa or ova are present but the penial setae mentioned are quite developed. The diameter of atrial ampulla measures $12.8 + 25.7 + 12.8 = 51.3$ μm.

Spermathecae with long pear-shaped ampulla filled with spermatozoa in

specimens examined by Michaelsen (1935, fig. 1, page 299). Some of my specimens have, besides, empty cylindrical ampullae.

Note. The specimens from Lake Teleckoje differ in some features from the description of individuals from Lake Sredne-Kočurlinskoje; I explain these differences by the insufficient preservation of scarce material studied by Michaelsen. The dimension of the body, the significant length of the hair setae, the presence and the form of the penial setae are the argument for the identity of Michaelsen's, some of Malevič's and my own specimens. The form of the penial setae, but not the form of the anterior ventral setae, is the most characteristic feature of *Rhyacodrilus altaianus*.

Localities: 1. The Central Altai. Lake Sredne-Kočurlinskoje, 15. Aug. 1933 L. N. Žinkin leg., W. Michaelsen det. (Kočura 52°40 N. lat., 87°50 E. long.). 2. Lake Teleckoje, district of Kobuchta-Airataš and Korbu, depth 130–325 m S. G. Lepneva 1928–1931 leg., I. I. Malevič as *Rhyacodrilus lepnevae* part. 1949 det. 3. Bay Kangi, in the depth of 38 m S. G. Lepneva 1928 to 1931 leg., I. I. Malevič 1949 as *Rhyacodrilus lepnevae* part. det. 4. Lake Teleckoje at Jajlu, depth 220 m doc. Dr. O. Štěrba, ing. J. Štetina leg. (Collectio Hrabě: Hr. 1876–1). 5. Lake Teleckoje, at the waterfall Korbu, 15. Aug. 1972 doc. Dr. O. Štěrba leg. (Collectio Hrabě Hr. 1876–3). 6. Lake Teleckoje, 15 km from the mouth of the lake into the river Bija 11. Aug. 1972 O. Štěrba leg. (Hr. 1876–4). 7. Lake Teleckoje, 50 km from the mouth of the lake 11. Aug. 1972. Doc. Dr. O. Štěrba leg. (Hr. 1876–6). 8. The River Bija, 130 km from Lake Teleckoje 19. Aug. 1972 doc. Dr. O. Štěrba leg. (Hr. 1876–5).

Rhyacodrilus lepnevae Malevič, 1949 emend. S. Hrabě

In the sample from the depth of 220 m also 3 anterior parts of mature worms occurred belonging to *Rhyacodrilus lepnevae*, described by I. I. Malevič from Lake Teleckoje. According to Malevič, this species is 8–12 mm long and consists of 50–60 segments. The diameter of the body in segment 8 measures 0.5 mm. Prostomium short, rounded.

The anterior fragments of the body studied by me are distinguished by the reddish-brown coloration caused by the granular secretion in all epidermal cells as well as the prostomium, as I observed in the sections (Fig. 7). According to Malevič, this remarkable coloration serves to distinguish readily *Rhyacodrilus lepnevae* from the other species in the sample. I can confirm this statement of my colleague and add that the not numerous specimens of the other coloration determined by Malevič also as *Rhyacodrilus lepnevae* belong actually to *Rhyacodrilus altaianus*. Malevič described, probably just from these discoloured specimens, the genital organs similar to the organs of *Rhyacodrilus altaianus* and different from the sexual organs of *Rhyacodrilus lepnevae*. The brown coloured *Rhyacodrilus lepnevae* has one pair of spermathecal pores in segment 9 (!) and one pair of male pores in segment 11 without exception in all my 3 mature specimens. The penial setae are absent in *Rhyacodrilus lepnevae*. In discoloured *Rhyacodrilus altaianus*, the spermathecae lie in segment 10, the male pores in segment 11. The very characteristic penial setae of *Rhyacodrilus altaianus* are missing in *Rhyacodrilus lepnevae*.

Epidermis is plicated, as observed by Malevič (Fig. 7). Chloragogen cells cover the digestive tube from segment 6. Pharyngeal glands (chromophil cells) are in segment 4–6. I cannot find the coelomocytes and study the

*) I transliterate the Russian alphabet according to the International normalization commission (Kent Fr. L., 1956: Progrès internationaux dans le domaine de la translittération. Bull. Unesco Bibl., vol. 10, No 5–6 : 135–141.)

blood and nephridial system in my unfortunately not well preserved material. In the ventral bundles of segment 3–6 there are 3, 4, 5, 5, setae from which 1, 1, 2, 2, are forked with the upper prong slightly shorter than the lower one and 2, 3, 3, 3 setae simple pointed with sharp ectal end (Fig. 8). In

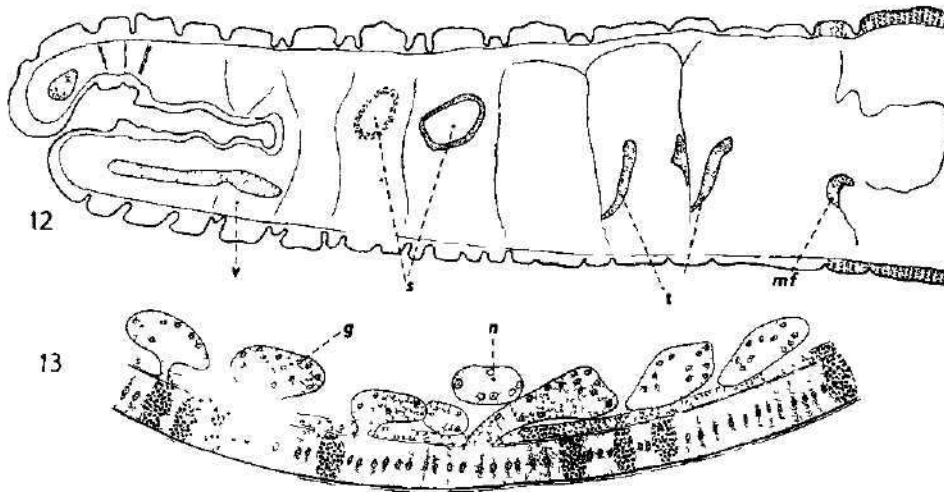


Fig. 12–13. *Pelodrilus ignator* Mich 12 – Longitudinal section of the anterior segments, v – segm. 5, f – male funnel, s – spermatheca, t – testis, $\times 39$; 13 – Transverse section of ventral body wall, g – copulatory glands, n – nerve-cord, $\times 172$.

segment 11, the ventral setae are absent. In the postclitellial segments, according to Malevič, there are only forked ventral setae.

On segment 2–6 of one mature specimen, I found 1, 2, 3, 2, 3 hair setae and 2, 3, 3, 2, 3 comb like setae. The non-feathered hair setae are up to 550 μm long. I did not find awn-like protuberances either on the bent setae or on the end of the broken ones. The comb-like setae of the anterior segments are like those of *Rhyacodrilus altaianus*.

Clitellum on segment 10–11. One pair of spermathecal pores in segment 9 posterior and much median from the ventral setae. One pair of male ducts open in the place of the ventral setae of segment 11.

One pair of testes in segment 10 on dissepiment 9/10, one pair of ovaria in segment 11 on the dissepiment 10/11.

Spermathecae, with oval ampullae and short duct, filled with a lot of spermatozoa (Fig. 9). Ampullae do not communicate with the digestive tract similar as at *Rhyacodrilus altaianus*.

One pair of small male funnels covered with spermatozoa on dissepiment 10/11. Atria cylindrical, covered with diffuse prostate glands. Atrial ampullae of one specimen are 110 μm long and their diameter measures 50 μm (Fig. 10). The ectal part of male duct in one specimen is 65 μm long, it is not everted out of the body (Fig. 10), the atrial duct in other two individuals form the interior portion of a conical pseudopenis, also 50 μm long, lying in a deep sac (Fig. 11) The specimens are fully mature.

Locality: Lake Teleckoje, at Jajlu, depth 220 m Doc. Dr. O. Štěrba, Al. Drevnikov, ing. J. Štětina leg. (Collectio Hrabé 1876-1).

Note. Most *Rhyacodrilus* spp. have the reproductive organs in a normal position (spermathecae in segment 10, male pores in segment 11), only in *Rhyacodrilus riabuschinskii* Mich. from Kamchatka spermathecae occur in

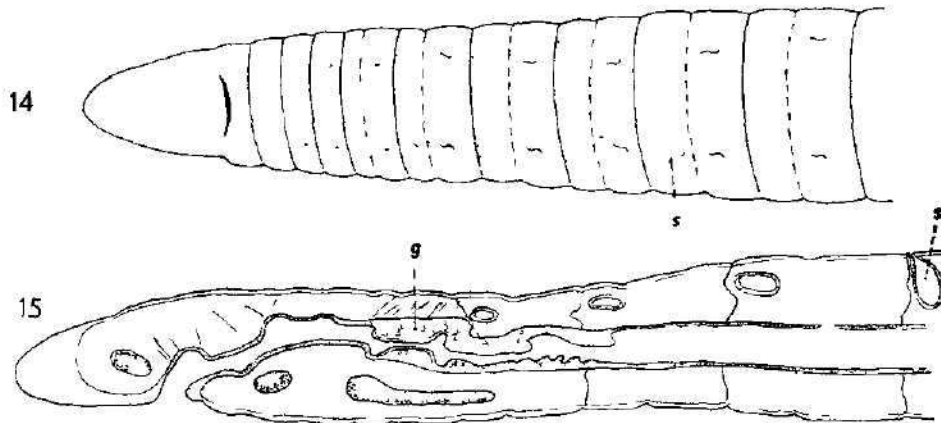


Fig. 14-15. *Haplotaxis ascaroides* Mich. 14 - Anterior part of body, from the ventral side, s - spermatheca, $\times 55$, 15 - Longitudinal section through anterior segments, g - gizzard, s - spermatheca, $\times 100$.

segment 8 and male pores in segment 9 and 11. In *Rhyacodrilus lepnevae*, these organs are also aberrant in segment 9 and 11. It is possible that *Rhyacodrilus lepnevae* belongs to a separate genus and not to the genus *Rhyacodrilus* from which it differs by the position of spermathecal pores, absence of coelomycetes (') and modified penial setae. Further investigations in this interesting species are required.

Pelodrilus ignatovi Michaelsen, 1903

In the sample from the depth of 220 m, I determined mature specimens of this species. The worms were insufficiently fixed and I could not study some of the systems of organs, to which earlier authors had paid no attention. I have the following notes to the description of *Pelodrilus ignatovi*, published by Michaelsen.

The segments are secondarily segmented from segment 5 or 6, as evident from the longitudinal sections (Fig. 12).

The setae are equally long only in the anterior segments, the dorsal setae are much shorter and thinner in the other parts of the body than the ventral ones. The dorsal setae of segment 2 of one adult specimen are 65 and 68 μm long, in segment 5, 151 and 158 μm . The ventral setae of the same segment measure 158 and 162 μm ; in segment 11 the dorsal and ventral setae are 171 and 193 μm long. In segment 22 the dorsal setae measure 175 μm , the ventral ones 223 μm . In segment 23, the dorsal setae measure 162 μm , the ventral ones 214 μm . The other specimen has the dorsal seta in the posterior part of the body (in segment 38 from the posterior end of the body) 184 μm

long, the ventral one 291 μm ; in segment 8 from the posterior end the dorsal seta measures 193 μm , the ventral one 257 μm .

The significant difference between Michaelsen's and my own observations is in the number and position of the spermathecae. *Pelodrilus ignatovi* has 2 pairs of spermathecae in segment 8 and 9 according to Michaelsen (1903) while I found 2 pairs of these organs in segment 7 and 8 in 3 specimens, their apertures are in the intersegmental furrow 6/7 and 7/8 exactly in the line lateral; only 1 spermatheca in segment 7 and one pair of spermathecae in segment 8 of 3 specimens (on the opposite side in segment 7 there are no vestiges of these organs); 2 specimens have only the posterior pair of spermathecae in segment 8.

The other components of the genital organs are disposed similar to the observations of Michaelsen: 2 pairs of testes in segment 10 and 11, one pair of ovaria in segment 12, the pubertal glands on the ventral side of segment 11, male funnels on dissepiment 10/11 and 11/12, the female ones on dissepiment 12/13.

I cannot explain the differences mentioned in the number and position of the spermathecae in my own and Michaelsen's specimens. After the regeneration of the genital organs, all their components vary, whereas in the specimens of *Pelodrilus ignatovi* examined by myself, only the spermathecae do so.

The copulatory glands are only 90–130 μm long and occur on the whole ventral side of segment 11 (Fig. 13). They are very different from the setal glands of *Pelodrilus bureschi* Mich. and *Pelodrilus leruthi* Hr. which I have in my collection of Oligochaeta.

Localities: 1. Lake Teleckoje, opposite to river Bolšaja Korbu, depth of 106 m, 22. Juni 1901, 2. opposite to Kopša, depth of 203 m, 21. Juni 1901, 3. southward of river Čečensk, depth 319 m, 4. At Jajlu, depth of 38 m, 26. Mai 1901. Nr. 1–4 Ignatov leg. and W. Michaelsen det. 5. At Jajlu from the depth of 220 m doc. Dr. O. Štěrba et soc. leg., Collectio Hrabě Hr. 1876–1.

Haplotaxis ascaroides Michaelsen, 1905

In the sample from the depth of 220 m there occurred one not quite mature specimen of *Haplotaxis ascaroides* Mich. with 4 pairs of spermathecae opening on the dorsal side of the body in the intersegmental furrows 5/6, 6/7, 7/8 and 8/9 (Fig. 15).

This species was known only from Lake Baikal (Michaelsen, 1905; Michaelsen and Vereščagin, 1930) and its occurrence in Lake Teleckoje is of great zoogeographical interest. *Haplotaxis ascaroides* is probably very common in this lake, but mature specimens were not present in the collections determined by Michaelsen and Malevič. These authors therefore determined the immature worms as *Haplotaxis gordioides* (Hartm.) which is very similar in appearance.

Localities: Lake Baikal, in all parts of the lake, depth 10.5 – 1300 m Al. Korotnev 1900 to 1902 leg., W. Michaelsen 1905 det. 2. Lake Baikal, in the Selenga-river area depth 74 and 125 m. G. Vereščagin 1925 leg., W. Michaelsen 1930 det., 3. Lake Teleckoje, depth 220 m (one not quite mature specimen) doc. Dr. O. Štěrba et soc. leg. (Collectio Hrabě Hr. 1876–1) 4. Lake Teleckoje, depth 40 m, doc. Dr. O. Štěrba leg. (Collectio Hrabě Hr. 1876–9) (immature specimens).

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**PSEUDANOPHTHALMUS PILOSELLUS POLONINENSIS SSP. N.
(COL.: CARABIDAE: TRECHINAE)**

KAREL HŮRKA

Eingegangen am 5. August 1973

Abstrakt: *Pseudanopthalmus pilosellus poloninensis* ssp. n. wurde von der slowakischen und polnischen Seite der Waldkarpaten beschrieben und von den Unterarten *P. p. pilosellus* (Miller) und *P. p. stobieckii* (Csiki) unterschieden.

In den letzten Jahren wurde sowohl auf der slowakischen (1962, 1963, 1970), als auch auf der polnischen Seite (1965, 1967) der Waldkarpaten* eine Population der Art *P. pilosellus* (Miller) gefunden, die sich von der östlichen Unterart *P. p. pilosellus* (Mill.) und auch von der westlichen Unterart *P. p. stobieckii* (Csiki) unterscheidet. Dieser Fund führte uns zu einer Revision der ganzen vorherigen Gattung *Duvaliopsis* Jeannel (Hůrka, im Druck), die zahlreiche Probleme sowohl der taxonomischen und synonymischen (*D. pilosellus beskidensis* Hlisnikowski, 1942 = *P. pilosellus stobieckii* [Csiki, 1907]), als auch der zoogeographischen Natur löst. Im folgenden bringe ich die Beschreibung der gefundenen Population als einer neuen Unterart, die durch ihre Gesamtgröße und durch lange Fühler und Tarsen auffällig ist.

Pseudanopthalmus pilosellus poloninensis ssp. n.

(Abb. 1, 2)

Beschreibung: Die Fühler sehr gestreckt (Abb. 2 I), ihre Gesamtlänge beträgt bei den Männchen 2,15—2,35 mm (durchschnittlich 2,23 mm), bei den Weibchen 2,05—2,30 mm (durchschnittlich 2,10 mm). Der Index Fühlerlänge: Flügeldeckenlänge = 1,1. Die Hintertarsen gestreckt (Abb. 2 L), nicht unter 0,80 mm lang (durchschn. 0,82 mm). In der Halsschildform erinnert die neue Unterart mehr an *P. pilosellus stobieckii*, da die Halsschildseiten meistens nur in der vorderen Hälfte gerundet sind und die Ausschweifung vor den Hinterecken länger erscheint (Abb. 2 A, B, C). Der Index Halsschildbreite: Halsschildlänge beträgt 1,28. Auch in der Ausbildung des Apikalstreifens der Flügeldecken nähert sich die neue Unterart mehr dem *P. p. stobieckii*, da der Apikalstreifen mit dem dritten Streifen der Flügeldecken meistens nicht vereinigt ist (Abb. 2 O, P). In der Ausbildung des

* Für die Möglichkeit das polnische Material zu studieren bin ich Herrn Doz. Dr. J. Pawłowski aus Kraków zum Dank verpflichtet.

Innensackes des Aedoeagus zeigt die neue Unterart dagegen eine deutliche Beziehung zu *P. p. pilosellus*, da die zahnartigen Strukturen an der Basis des Innensackes zahlreicher sind und in den 2 oder 3 basalen Reihen dicht nebeneinander stehen und nicht isoliert sind (Abb. 1 E); der Index Körper-

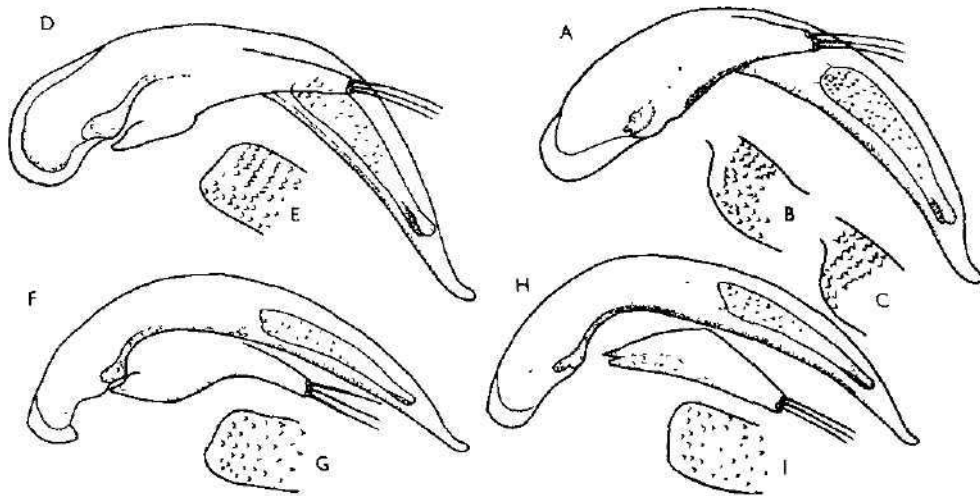


Abb. 1. Aedoeagus: A — *P. pilosellus pilosellus* aus Mármaros, B — Basis des Innensackes, C — Basis des Innensackes bei einem anderen Exemplar; D — *P. pilosellus poloninensis*, Holotypus, E — Basis des Innensackes; F — *P. pilosellus stobieckii* von Vysoké Tatry, G — Basis des Innensackes, H — *P. p. stobieckii* von den Beskidy, I — Basis des Innensackes.

länge: Aedoeaguslänge beträgt 5,8. Grösser als die beiden übrigen Unterarten, die Länge bei den Männchen 3,2—3,8 mm (Mittelwert von 8 Exemplaren 3,6 mm), bei den Weibchen 3,3—4,0 mm (Mittelwert von 16 Exemplaren 3,7 mm).

Holotypus (♂): Slov. or., Poloninské Karpaty (Waldkarpaten)*, Stužica, 650 m, 6. VII. 1970, leg. Hürka. In der Sammlung K. Hürka, Praha.

Paratypen: 3 ♂♂, 2 ♀♀, leg. Hürka, 4 ♂♂, 4 ♀♀, leg. Bílý, dieselben Angaben wie beim Holotypus; 1 ♀, dieselbe Lokalität, Sommer 1962, leg. Honeč; 3 ♀♀, Slov. or., Poloninské Karpaty, Nová Sedlica, Baskyd, 500—550 m, 17. VII. 1963, leg. Hürka. In den Sammlungen Bílý, Honeč, Hürka und der Entomologischen Abteilung des Nationalmuseums Praha-Kunratic.

Weiteres Material (Polska Akademia Nauk Kraków): 3 ♀♀, Polonia mer. or. Bieszczady, Wielka Rawka 1290 m, 10. VI. 1965, leg. A. Szujewski; 3 ♀♀, dieselbe Lokalität, 9.—10. VI. 1966, leg. J. Pawlowski; 1 ♀, Polonia mer. or. Bieszczady Mt., am Ufer eines Baches im Buchenwald, 16. V. 1967, leg. J. Pawlowski.

Derivatio nominis: Der Name stammt vom slavischen Wort polonina, das für die Bezeichnung des Gebirgszuges Poloninské Karpaty benutzt wurde.

Differentialdiagnose: *P. p. poloninensis* ssp. n. unterscheidet sich von *P. p. pilosellus*, mit dem sie die Ausrüstung des Innensackes gemeinsam hat (Abb. 1 B, C), durch die grössere Gestalt (bei *P. p. pilosellus* sind die Männchen 3,1—3,5 mm lang, durchschn. 3,3 mm, die Weibchen 3,2—3,7, durchschn. 3,4 mm), durch die längeren Fühler (*P. p. pilosellus* — Männchen

* Waldkarpaten: tschechisch Poloninské Karpaty, polnisch Bieszczady, ein Teil des Karpatenbogens, der zoogeographisch schon zu den Ostkarpaten gehört.

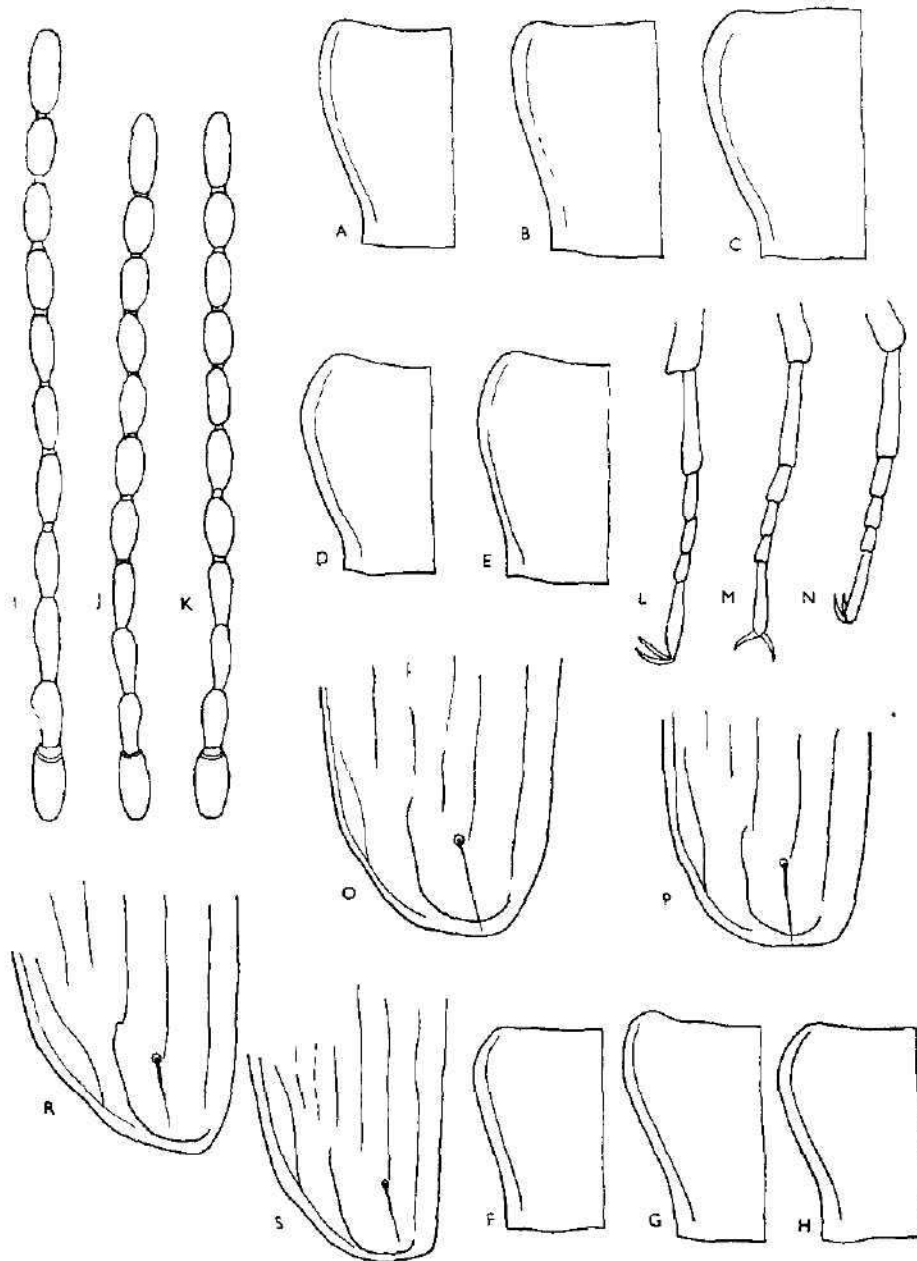


Abb. 2. Halschildform: A, B, C - *P. p. poloninensis*, ein Männchen von Stuzica, zwei Weibchen von Beskyd; D, E - *P. p. pilosellus* von Czernahora; F, G, H - *P. p. stobieckii*, zwei Weibchen, ein Männchen von Vysoké Tatry. Fühler von Männchen: I - *P. p. poloninensis*, J - *P. p. pilosellus*, K - *P. p. stobieckii*. Hintertarsen von Männchen: L - *P. p. poloninensis*, M - *P. p. stobieckii*, N - *P. p. pilosellus*. Flugeldeckenspitze: O, P - *P. p. poloninensis* (O ist typisch), R - *P. p. pilosellus*, S - *P. p. stobieckii*.

1,85–2,00 mm, durchschn. 1,93 mm; Weibchen 1,85–2,20 mm, durchschn. 1,95; Index Fühlerlänge: Flügeldeckenlänge = 1,03) und Tarsen (Hintertarsen bei *P. p. pilosellus* nur ausnahmsweise über 0,8 mm, durchschn. 0,76 mm), durch die verschiedene Form des Halsschildes und den mit dem 3. Streifen der Flügeldecken nicht verbundenen Apikalstreifen. Von *P. p. stobieckii*, mit dem die neue Unterart die Halsschildform und den Verlauf des Apikalstreifens der Flügeldecken gemeinsam hat, unterscheidet sie sich durch die verschiedene Ausrüstung des Innensackes des Aedoeagus (Abb. 1 G, I), durch die grössere Gestalt (bei *P. p. stobieckii* sind die Männchen 3,0–3,8 mm lang, durchschn. 3,4 mm, die Weibchen 3,0–3,8 mm, durchschn. 3,5 mm), durch die deutlich längeren Fühler (*P. p. stobieckii* – Männchen 1,90 bis 2,10 mm, durchschn. 1,98 mm; Weibchen 1,80–2,20 mm, durchschn. 1,98 mm; Index Fühlerlänge: Flügeldeckenlänge = 1,04) und Tarsen (Hintertarsen bei *P. p. stobieckii* nicht über 0,8 mm, durchschn. 0,71 mm).

Chorologie: Die Vertreter der neuen Unterart wurden in der unteren Waldzone des tschechoslowakischen Teils der Waldkarpaten in der Höhe von 500–700 m unter tief im Boden eingesenkten Steinen, in der Gesellschaft von *Duvalius subterraneus* (Mill.) gesammelt. Alle Exemplare wurden im Juli erbeutet, am 6. VII. 8 ♂♂, 6 ♀♀, am 17. VII. 3 ♀♀. Die Exemplare aus der polnischen Seite der Waldkarpaten – bisher nur die Weibchen – wurden jedoch auch auf dem waldlosen Gipfel des höchsten Berges Wielka Rawka, in der Höhe von 1290 m unter tief eingebetteten Steinen, gefunden. Das Material wurde am 16. V. (Ufer eines Baches im Buchenwald) und am 10. VI. (W. Rawka) gesammelt.

Verbreitung: Die Gesamtverbreitung der Art reicht von den West-Beskiden über Malá Fatra, Babia góra, Nízké Tatry, Vysoké Tatry, Pieniny, Beskid Sadecki und Poloninské Karpaty bis in das Czernahora-Gebirge in der Ukraine. Die westliche Unterart *P. p. stobieckii* ist von den West-Beskiden in der Tschechoslowakei in as Beskid Sadecki in Polen verbreitet. Die neu beschriebene Unterart *P. p. poloninensis* kommt in den Waldkarpaten (Poloninské Karpaty, Bieszczady) vor. Die östliche Unterart *P. p. pilosellus* ist mit Sicherheit nur vom Czernahora Gebirge bekannt.

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**THE INFLUENCE OF Mg^{2+}/Na^+ ON THE ISOENZYME SPECTRUM
OF THE MIDGUT ESTERASES OF *GALLERIA MELLONELLA* PREPUPAE
(LEPIDOPTERA)**

MILAN MAREK

Received July 23, 1973

Abstract: Incubation of *Galleria mellonella* midgut pieces for 24 hr in two hypertonic NaCl/MgCl₂ media (120/120 mM and 160/160 mM) caused the simultaneous appearance of three to five new esterase bands and the disappearance of several others.

The regulation of gene activity and enzyme synthesis in the insects is an old problem that has not been solved satisfactorily yet. In spite of the genes being equally present in all tissue cells during the whole development of individuals, only some genes are active and only in certain tissue or organs and only in a certain stage of development. The principal question remains how the gene activity and the enzyme synthesis are regulated in this case and to what extent they can be influenced by the incubation media of cations.

The chromosomes in cells are under the influence of a certain milieu of karyoplasma and cytoplasma which also regulate their biochemical-biological condition. There are certain factors which have a special effect on the DNA-histones complex in karyoplasma. Ionic bond between the anions of DNA molecule and the cations of histone molecules is predominantly dependent on the ionic strength of karyoplasma (Katchalski, 1964).

Kroeger (1963) demonstrated that changes in the ratio of Na^+/K^+ -ions in incubation media of explanted salivary glands of the *Chironomus* larvae can induce a certain activity of genetic loci. Lezzi and Gilbert (1970) in their experiments with isolated chromosomes also demonstrated that Na^+ and K^+ -ions exert a direct effect on the condensation state of genetic loci. Kroeger and Lezzi (1966) postulate that in the influence of cations no artefacts are involved, but that the functional state of a certain gene in a certain course of development is regulated by the contents of ions in karyoplasma, which is under the influence of cytoplasma.

Marek (1970) in his *in vivo* experiments at the temperature $+4^{\circ}C$ demonstrated an acceleration of the synthesis of "cooling protein" by injecting K^+ and Na^+ -cations into the *Galleria mellonella* pupae. Shigematsu (1958 and 1960) studied the influence of certain cations on the proteosynthesis in *Bombyx mori* tissues in his "in vitro" experiments. Price (1967) was successful in studying the problem of the influence of certain cations of incubation media on the synthesis of released protein and retained protein.

MATERIALS AND METHODS

Midgut of *Galleria mellonella* prepupae in the first day of development were chosen for our experiments. The wax moth larvae were reared at 30°C and fed with standard Haydak food.

The preparation of the midguts was carried out under a stereomicroscope in Ringer solution for insect. After the preparation, five pieces of the midguts were transferred into the incubation

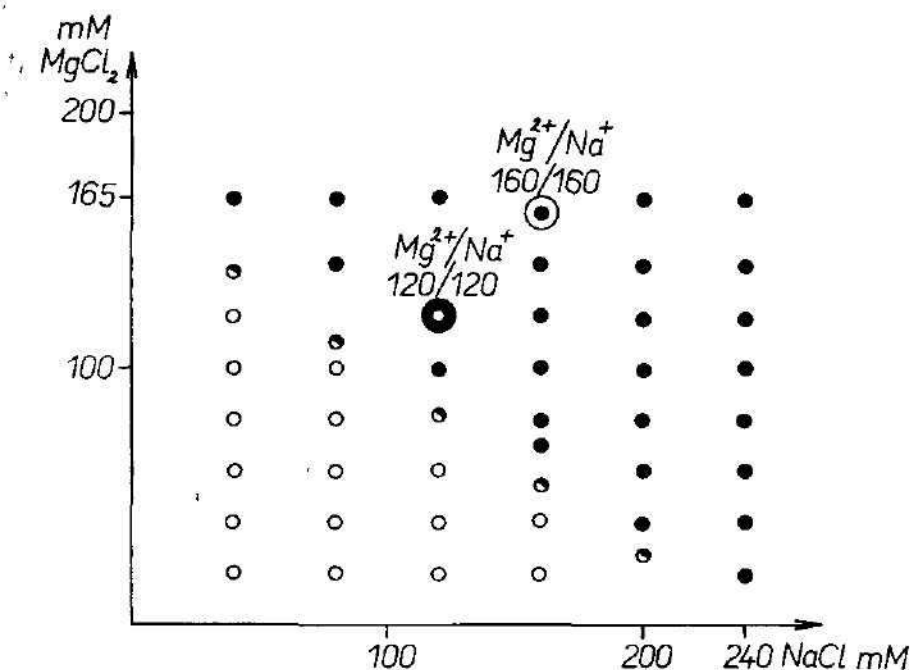


Fig. 1. Concentrations of $MgCl_2/NaCl$ -incubation media employed in experiments with the midgut of *Galleria mellonella*. \odot , denotes isotonic incubation media; \bullet , denotes hypertonic incubation media; \circ , denotes hypotonic incubation media. Points with special marks for concentration of 120/120 and 160/160 mM $MgCl_2/NaCl$ denote incubation media which induced activity of esterase isoenzymes (more precisely marked in Fig. 2). All incubation media were buffered with 10 mM Tris-HCl at pH 7.2.

media with the volume of 0,05 ml + 2 phenyl thiourea crystals (antimelanizant) and incubated at 30°C for 24 hours. Mixtures of Mg^{2+}/Na^+ -ions in the range of concentration of 20 mM–240 mM in various ratios were used as incubation media (Fig. 1). Osmolarity in the haemolymph and in all the incubation media was determined by Knauer semi-microosmometer and expressed in mOsm. The value of 424 ± 53 mOsm ($n = 9$) was determined for *Galleria mellonella* haemolymph and an isotonic solution of the incubation medium of 240 mM NaCl or 165 mM $MgCl_2$ corresponds directly to this value. All solutions were buffered with Tris-HCl (10 mM) at pH 7.2. After incubation, the tissues of midguts were removed, rinsed with the Ringer solution and homogenized with Potter-Elvehjem homogenizer. The incubation medium with released enzyme and the supernatant from the gut homogenate with retained enzyme were separately used for the separation by starch-gel electrophoresis. The electrophoresis was performed at 4°C, 500 V and 20 mA in Tris-boric acid buffer at pH 8.6. After 6 hr the starch gel was submerged for 30 min. in 100 ml phosphate buffer at pH 6.9 to which 2 ml of an 1% acetone solution of α -naphthyl-butyrate with 250 mg of the diazonic salt of Fast Blue BB were added. Each experiment was repeated 3 times. In these experiments 525 prepupae of *Galleria mellonella* were used. The percentage of the isoenzymes was determined by means of a densitometerintegrator (ERI 10, Zeiss, Jena).

RESULTS

The incubation of tissues in Ringer physiologic solution for insects and the incubation medium of Jones and Cunningham (1961) induced almost no changes in the spectrum of esterase enzymes in comparison with the isoenzymes obtained from tissues in "in vivo" experiments (Fig. 2). Great changes in the isoenzyme spectrum of *Galleria mellonella* midgut were however, induced above all by the hypertonic incubation media containing Mg^{2+}/Na^{+} -ions. A hypertonic incubation medium of 120 mM Mg^{2+} /120 mM Na^{+} caused an inactivation of five isoenzymes occurring on the electroforogram in region No 1, i.e., closely behind the place of origin with isoenzymes migrating toward the anode. On the other hand, the newly activated isoenzymes of esterases were found in region No 2. These do not appear in the *Galleria mellonella* midgut during the whole normal development. In the place of the inactivation of the five isoenzymes (in region No 1), we succeeded

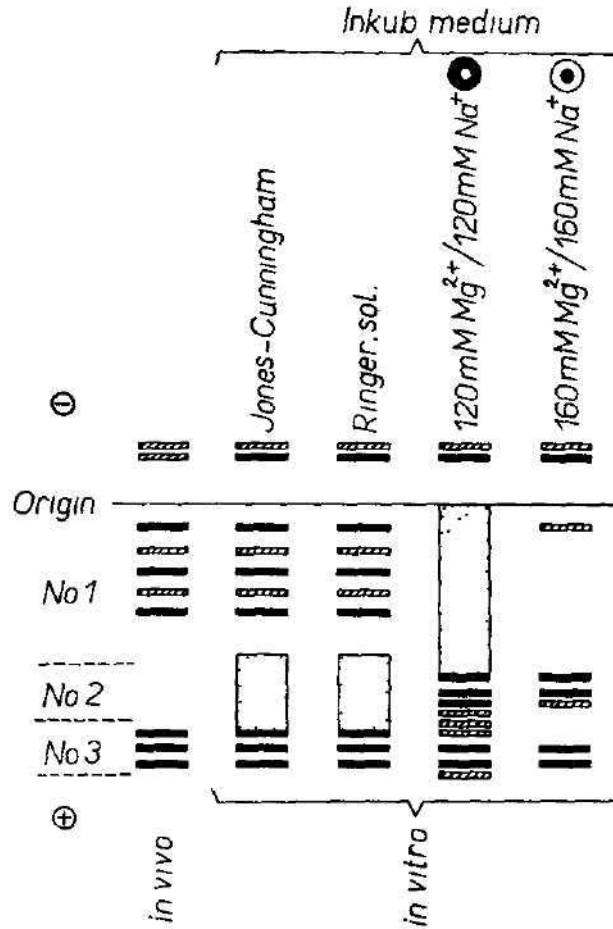


Fig. 2. Esterase isoenzyme patterns from untreated "in vivo" and from prepupal midgut pieces of *Galleria mellonella* after incubation for 24 hr in artificial media. Solid bands = heavy staining; hatched bands = light staining; point bands = "veil".

in identifying a sort a "veil" of esterase, as a trace after the preceding five isoenzymes, suggesting that some more esterases are present, but the separation of their protein part on the starch gel is not feasible. Another "veil" of esterases was observed in region No 2 on the electrophoretogram in the in vitro experiments with the Ringer solution and with the Jones-Cunningham medium. The hypertonic solution of 160 mM Mg^{2+} /160 mM Na^+ did not lead to the formation of the "veil", but created conditions for activation of isoenzymes in region No 2.

From the physiological point of view the finding is important that more than 60% of activated enzymes do not stay in the midgut tissue, but are secreted as a released enzyme into all the employed media, namely hypertonic, hypotonic and isotonic ones.

DISCUSSION

On the strength of the presumption that one isoenzyme band determined on the electrophoresis corresponds to one genetic locus of a chromosome, the influence of the outer milieu on the gene activity of chromosome in the midgut cells of *Galleria mellonella* prepupae was studied by means of electrophoresis.

By means of starch electrophoresis, the isoenzymes of the midgut were separated into three regions. Three to five isoenzymes of esterases occur in each region. It is also interesting that various concentrations of incubation media led to activation of at least 3—5 genes carrying a common function, i.e., the esterase activity.

According to our results it is apparent that isoenzymes of the midgut cells in region No 1 are induced by genetic loci activated only in isotonic incubation media, including the midgut cells obtained from "in vivo" experiments. The increase of the concentration of Mg^{2+}/Na^+ -cations towards the hypertonic region led to a gradual disappearance of isoenzymes in region No 1, in spite of their so called "veil". Genetic loci of the chromosomes of the midgut cells, which by their activity influence the activation of esterases in region No 2, are — in comparison with the region No 1 — quite inversely sensitive to a concentration of incubation media in which the hypertonic concentration of Mg^{2+}/Na^+ -cations causes induction of the esterase isoenzymes. We cannot overlook the fact that the isoenzymes of esterases in region No 3 and isoenzymes migrating towards the cathode are almost always activated in the same way, both in isotonic and hypotonic and hypertonic incubation media.

The veil of esterases, determined by means of starch-gel electrophoresis in region No 2 in vitro experiments with the incubation medium of Ringer solution for insects, became of interest owing to the fact that it disappears when a hypertonic solution of 120 mM $Mg^{2+}/120mM Na^+$ -incubation medium is used and in its site well separable isoenzyme bands are formed and on the other hand another "veil" occurs in region No 1.

The problem of secretion of proteins from the incubated tissue into the medium was first studied by Shigematsu (1958 and 1960) in tissue *Bombyx mori* and later by Price (1967). Both authors came to the conclusion that the major volume of synthesized protein is secreted from the cell into the incubation medium and only a part of it remains in the tissue cells. Our results agree with the results of the above authors. It is perhaps paradoxical

that the increased concentration of Mg^{2+}/Na^{+} -ions in the incubation media is not a decisive factor for the secretion of isoenzymes into the incubation media. It is more likely that a certain threshold content of the retained enzyme in the cell is decisive, which the cell is "trying" to retain.

SUMMARY

Incubation of *Galleria mellonella* midgut in hypertonic Mg^{2+}/Na^{+} incubation media in the range of 120 mM/120 mM and 160 mM/160 mM caused a simultaneous activation of three to five isoenzymes of esterases.

After 24 hr incubation about 60% of the enzyme activity were found in the incubation medium.

Acknowledgments

We gratefully acknowledge the help extended by Dipl. Natw. N. U. Bosshard in the development of media and in osmolarity determinations.

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**ON THE SYSTEMATICS OF THE EUROPEAN GRAYLING,
THYMALLUS THYMALLUS (LINNAEUS, 1758)
(OSTEICHTHYES: THYMALLIDAE)**

OLGA OLIVA and ASHOK S. NAIKSATAM

Dedicated to 60th birthday of Prof. MVDr Václav Dyk, D.Sc.

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Abstract: 75 specimens of the European grayling, *Thymallus thymallus* (Linnaeus, 1758) were biometrically studied. 26 specimens of them were from the upper Vltava river (Labe water system) and the remaining 49 were from the river Danube drainage, amongst them 9 were juvenile specimens. The results obtained were compared chiefly with the sample of 100 specimens studied by Svetovidov (1936), originating from the river Mesna, Kanin peninsula, the USSR, and with 27 specimens from Sweden (Smitt, 1886, 1887). A few differences were found; e.g. the Danube sample had the shortest distance between V—A, whereas the Mesna sample the longest; the depth of the posterior part of D was the highest in the Vltava sample while it was the lowest in the Mesna sample. The depth of anal fin of the Mesna sample was lower than in the samples from the Vltava and the Danube. The values for both upper and lower caudal fin lobes were higher in juveniles than in adult specimens. The length of the middle caudal fin rays was smaller in the Mesna sample than in the Danube and the Vltava rivers. These differences are probably due to food conditions, sexual maturity, size and nonhomogeneity of samples. Having added the meristic data, the authors have completed the description of the Central European grayling. In general, the grayling does not show any apparent variability on its large distribution, inspite of the fact that the geographical conditions in which it lives vary considerably. The Central European grayling is supposed to be a typical glacial relict form.

INTRODUCTION

With the exception of the data published by Smitt (1886, 1887, 1895), Vladykov (1931), Andrijašev (1954), Solewski (1960), Zinovev (1963), Oliva (1963) and Banarescu (1964), there is no other information concerning the morphometrical variability of the grayling in its wide distribution (for this see Berg, 1948). Most interesting is the fundamental monograph by Svetovidov (1936), because it deals with the richest material and the known forms of Euro-Asiatic graylings are revised with great precision. Graylings from the territory of Czechoslovakia have not been studied from the systematic point of view. Only Oliva (1963) measured 10 specimens from the present sample, which are included here. Vladykov (1931) studied 12 specimens from the basin of the river Tisza on the territory of Karpathian Ukraina. Therefore, a more thorough taxonomical revision of the specimens from Central Europe seems to be necessary, especially when we take into

account that the river Mesna,¹⁾ from where Svetovidov's sample (1936) originated is on the northern border of Europe — in the tundra region which cannot be considered typical of the European territory. The graylings occurring here and in the river Kara (Andrijašev, 1954; Berg, 1948)²⁾ certainly belong to the northern border of their distribution. Unfortunately, a more exact "terra typica" for the European grayling is not given by Linnaeus, 1758 (*Salmo thymallus*, 1758, 311: In Europae fluviis Maritimis). Similarly Gronovius (in Gray, 1854): "Habitat in Europae fluminibus, longe a mari remotis". It is very interesting that the grayling belongs to fish species enumerated already by Balbín (1679) among the Bohemian fishes (cited after Frič, 1859) in chapter 54 of "Miscellanea Regni Bohemiae". He wrote about "the multitude of trouts and graylings in Bohemian rivers". But according to Frič (1859, 1872) graylings occur in Bohemia less frequently than the trout and he supposed it would be very useful to publish solid data about their distribution. Frič (1859) mentioned 2 specimens which he received from his assistant Mr. Prach from the river Jizera near the town of Trutnov. These specimens weighed about 1 pound each and reached to about 1 foot in length. It was only after the gap of 70 years, however, that the collection of such data was resumed, when Dyk (1932) published an outline concerning the Bohemian grayling; the same author returned to this problem in 1938, and published another valuable paper in 1958. But a precise systematic redescription of this species on the territory of Czechoslovakia was still lacking, although Dyk (1958) noted that "altitude above the sea level, the length of feeding period, water regime have influence on exterior of graylings", naturally the study of this problem was not the aim of his paper. Dyk devoted a lot of energy in broadening the knowledge of graylings on the Czechoslovak territory. His papers concern the problem of the so called "grayling zone" of our rivers (1932, 1932a) and biological aspect of the life of graylings viewed from the point of fishery biology; he summarised his experience in a book (1956). Unfortunately the systematics of grayling was not among the aims of his work (with the exception of some measurement data from 1937, published in 1957, concerning the grayling from the river Belá) that is why the authors take the opportunity and dedicate this study to him on the occasion of his 60th birthday in 1972.

MATERIAL AND METHOD

Altogether 75 specimens were examined, out of which 26 were from the upper part of the river Vltava (Moldau), a left tributary of the river Labe (Elbe) in Bohemia (17/18-9-1955), the upper Vltava near the town Volary along the stream up to Černý Kříž, leg. doc. dr. Rudolf Šrámek Hušek, purchased in 1966¹⁾. They are catalogued in our laboratory under the cumulative name of "Labe drainage" (No. Cat. Lab. Ichthyol. Zool. Inst. Fac. Sci. 30966—998). Remaining 49 specimens, under the cumulative name of "Danube drainage" come from the Slo-

¹⁾ The river Mesna has about 60 kms. of length, emptying itself into the Beloe more on the west shore of Kanin peninsula. It is situated on 68° of north. lat. and between 44°30'—45°30' of west. length.

²⁾ The river Kara is the last European river originating on the most northern part of the Ural mountains between the hills Gora Ošenyrd (1363 m) and Gora Chojdype (1240 m) and emptying itself into the Karskoe more (= sea), part of the Arctic Ocean. It is situated between 68°—69° of west. length. The European grayling, *Thymallus thymallus* (Linnaeus) lives here together with the Siberian grayling, *Thymallus arcticus arcticus* (Pallas, 1776), but the former species predominates. In one sample of 300 specimens of the European grayling, only 10 specimens of the Siberian grayling were found.

vakian tributaries of the Danube: 12-8-1951, the river Váh near Liptovský Mikuláš, 5 sp., No. Cat. of Ichthyol. Lab. Zool. Inst. Fac. Sci. Charles Univ. 8391—94; 14-8-51, the Mutňanka nad Brezou, 5 sp., Nos. 8422—26; 14-8-51, the Polhoranka at Raběn, 6 sp. Nos. 8076—77

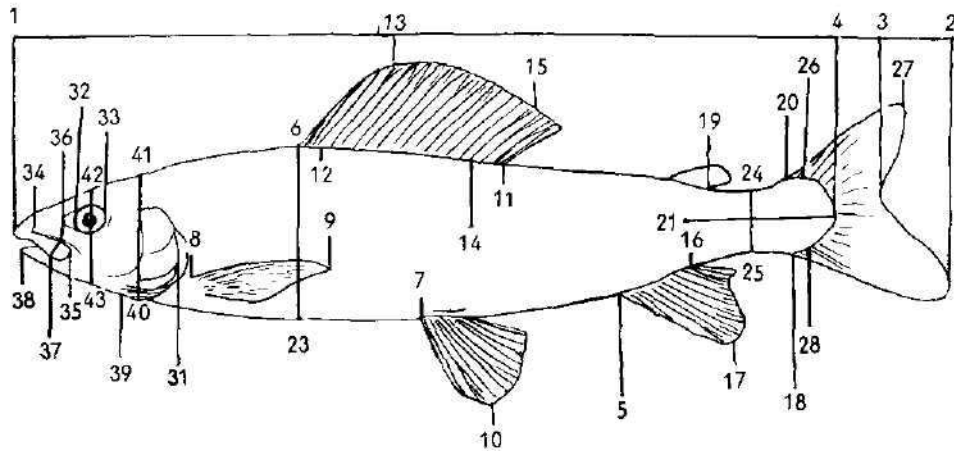


Fig. 1. Explanations to the table of measurements in the grayling, *Thymallus thymallus* (Linnaeus, 1758).

Explanation to the table of measurements:

- 1— 2 total length
- 1— 3 standard length (Smitt's length, 1886, 1887)
- 1— 4 body length
- 1— 5 preanal distance (anteanal distance)
- 1— 6 predorsal distance (antedorsal distance)
- 1— 7 preventral distance (anteventral distance)
- 8— 9 P—V distance — distance between the insertion of pectoral and ventral fins
- 7— 5 V—A distance — distance between the insertion of anterior margins of ventral and anal fins
- 8— 9 length of pectoral fin
- 7—10 length of ventral fin
- 6—11 length of dorsal fin
- 12—13 D₁ depth of anterior part of dorsal fin measured along the length of last unbranched ray
- 14—15 D₂, depth of posterior part of dorsal fin measured along the length of 4th branched ray from the end
- 5—16 length of anal fin
- 5—17 depth of anal fin
- 16—18 distance between A—C, (between base of the anal fin and base of the caudal fin)
- 19—20 distance between adipose fin and the base of the caudal fin
- 21— 4 length of caudal peduncle
- 6—23 maximum depth of body
- 24—25 minimum depth of body
- 26—27 length of upper caudal lobe
- 28— 2 length of lower caudal lobe
- 4— 3 length of middle caudal rays
- 1—31 length of head
- 1—32 preorbital distance
- 33—31 postorbital distance
- 32—33 longitudinal diameter of eye
- 34—35 length of maxilla
- 36—37 width of maxilla
- 38—39 length of lower jaw
- 40—41 depth of head (occipital region)
- 42—43 depth of head (orbital region)

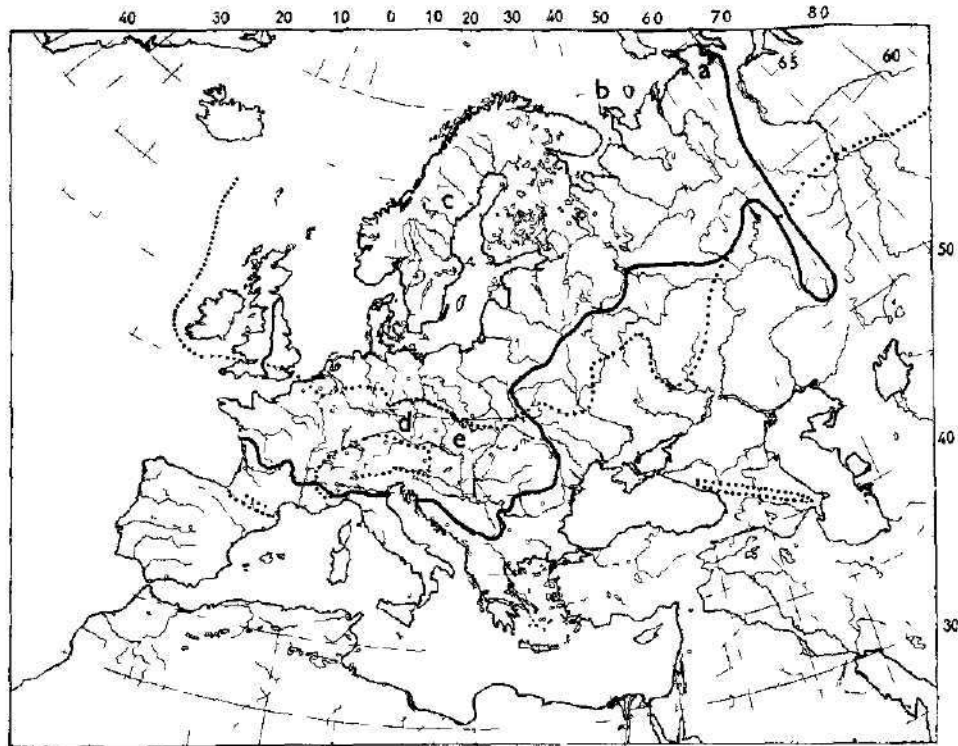


Fig.2. Geographical distribution of the grayling, *Thymallus thymallus* (Linnaeus, 1758) in Europe a — river Kara, b — river Mesna, Kamun Peninsula, c — Sweden (Smitt's localities), d — upper Vltava, Elbe system, Bohemia, e — Slovakian localities, Danube system. With the dotted line the boundaries of maximum glaciation in Europe, with dots is also marked glaciation in Pyreneans, Alps and Caucasus. With full line, the distribution of *Thymallus thymallus*, where from the technical reasons some regions where the grayling does not occur are not marked, e.g. lowlands of France, Belgium, Holland, North Germany, East Jutland, southern Sweden, most part of western Norway, Pommerania, north Poland and its lacking in most part of stream's course in Middle European rivers is also not shown. The same concerns where this species was artificially introduced, e.g. in Scotland. (The boundary of ice cover after Holdhaus and Lindroth, 1939, Wolstedt 1929, Ekman 1922 from Thienemann, 1950).

and 8456—57; 29-4-1952, the Revúca above the mouth of the Trlenský potok (brook), 13 sp., Nos. 9948, 10068—078; 30-4-1952, the Zazrivá near its mouth into the river Orava, Párnica, 2 sp., Nos. 10256—57; 29-4-1952, the river Belá at Pribylina, the mill-race, 3 sp., Nos. 10122—24; 29-4-1952, the river Váh near Lubčanský most (bridge) above Ružomberok, 3 sp., Nos. 9956—5; 25-7-1951, No. 7970, the trout hatchery in the town of Jablunkov, the breeding specimen purchased from Mr Nieslanik;¹⁾ 14-8-1951, the river Bílá Orava above Námestovo, 1 sp., No. 8035; 26-4-52, the Revúca, Podsúcha, hatchery, 2 sp., Nos. 16222, 16582 from the Morávka (Silesia) were also added to the "Danube system", similarly as 1 sp. from the river Moravice (Dec. 1951, No. 24567). Finally, 6 specimens from the Danube drainage, without more exact designation of locality. All numbers must be referred to the Fish Collection of Laboratory of Ichthyology, Zoological Institute, Faculty of Science, Charles University, Prague. The so called "grayling region" in the upper part of the Vltava river, called here "Studená Vltava" (the Cold Vltava) was known to Dyk (1958) already from 1936. According to this author the region is 6 km long, the upper part of the occurrence of the grayling lies here 779 m above the sea level while the

¹⁾ It is interesting that Woldřich (1858) did not know the grayling from this region

lower part near the mouth of the Studená Vltava into the Teplá Vltava lies 770 m above the sea level. The hills around this region reach up to 1058 m. According to Ing. Jiří Vostradovský, C.Sc. (personal communication) of 17-1-1973), who knows the locality from where our sample was collected from late doc. dr. Šrámek Hušek, the river is about 15—20 m wide, the bottom is covered with gravel and sand, and the whole part is a typical "grayling zone". The banks are grassy with some bushes of *Carex*, but in some parts the banks are hollowed. The maximum depth reaches up to 150 cm; the colour of water is brownish because the river flows here through the large peaty area. The grayling here diminished slowly after 1960, when the Lipno dam was built on the Vltava river and this part of the river closely adhered to the riverine lake of Lipno, from where carnivorous fishes like pikes and perch migrated upstream to the above described grayling zone. But recently graylings became more frequent again, which can be explained by the diminishing number of the carnivorous fishes in this zone. By the stocking of new material from the nearby fish hatchery in Stožec the endemic grayling population was enlarged here also before 1960. These released fry originated from the parents of aboriginal stock. Some fish were brought here also from the neighbouring hatcheries of Southern Bohemia, e.g. from the town of Sušice. This locality may be also known to Frič (1872) ("Vltava in the neighbourhood of Vimperk", p. 121; but the Vltava does not flow closely to the town Vimperk — through Vimperk another river is running, the Volyňka).

The fishes were measured by means of a ruler with the accuracy of ± 0.5 mm, the measurements being levelled up to the nearest full mm. All the measurements were carried out according to the scheme given by Smitt (1886, 1887) for Salmons. For more details see the explanation to the table of measurements and Discussion.

RESULTS

The average standard length of the specimens from the upper Vltava river is a little higher than that from the drainage of the Danube. Ecological conditions, e.g. water and temperature, may be more suitable for the grayling in the upper Vltava river. Juveniles from the Danube drainage, however, have the smallest average standard length.

The percentage values of standard length show some differences in the two localities studied. The predorsal distance of the specimens from the Danube drainage is a little higher than that from the upper Vltava river (Table 1). But the V—A distance for the specimens from the upper Vltava river is higher than that from the Danube drainage (Table 1). The depth of posterior part of dorsal fin of the upper Vltava river specimens is far greater than that from the Danube drainage (Table 1). The maximum body depth is higher in the specimens from the Danube drainage (with particular reference to female specimens) than in the other locality studied (Table 2). It is interesting that the juveniles from the drainage of the Danube have higher values for length of upper caudal lobe, length of lower caudal lobe and length of middle caudal rays than the adult specimens from both the localities studied. Similarly, longitudinal diameter of eye is also higher than that of the adult specimens from both the localities (Table 2).

Similarly, the percentage values of head length also show some differences in the two localities studied. The length of the middle caudal rays of the specimens from the upper Vltava river is higher than that from the drainage of the Danube (Table 3). But specimens from the upper Vltava river have lower values for preorbital distance and length of maxilla than that from the drainage of the Danube (Tables 3, 4). Similarly, the specimens from the upper Vltava river also show the lower values for occipital and orbital depth of head as compared with the values of the Danube drainage (Table 4).

¹⁾ According to Dyk (in litt. 25.3.1973) the graylings in Jablunkov were brought from Slovakia.

Table 1. Morphometric characters of *Thymallus thymallus*

Systematic characters	Sex	Authors (Vitava river)				Authors (Danube drainage)			
		No.	M	±	m	No.	M	±	m
Standard length	M	12	251.0	3.49	10.09	17	252.0	14.25	58.73
	F	14	245.0	3.18	11.03	23	216.0	7.90	37.85
	M&F	26	248.0	2.07	10.56	40	234.0	7.65	48.28
	Juv	—	—	—	—	9	157.0	8.39	25.18
As % of standard length body length	M	12	91.83	1.25	4.34	17	91.20	1.19	4.96
	F	14	91.57	2.00	7.50	23	91.65	0.30	1.46
	M&F	26	91.70	1.16	5.92	40	91.44	0.50	3.18
	Juv	—	—	—	—	9	90.72	0.38	1.18
preanal distance	M	12	68.75	1.49	5.18	17	69.00	0.57	2.35
	F	14	69.00	1.32	4.95	23	70.00	0.94	4.00
	M&F	26	68.87	0.99	5.06	40	69.50	0.54	3.42
	Juv	—	—	—	—	9	68.00	1.71	5.15
predorsal distance	M	12	33.95	0.85	3.20	17	34.61	0.37	1.52
	F	14	33.94	1.16	4.36	23	35.60	0.35	1.70
	M&F	26	33.94	0.73	3.75	40	35.10	0.25	1.61
	Juv	—	—	—	—	9	35.16	0.57	1.71
preventral distance	M	12	45.29	1.30	4.87	17	46.00	0.53	2.17
	F	14	45.32	1.01	3.76	23	46.86	0.82	3.92
	M&F	26	45.31	0.85	4.31	40	46.43	0.48	3.05
	Juv	—	—	—	—	9	46.33	1.63	4.99
P—V distance	M	12	26.62	1.11	3.85	17	27.50	0.35	1.46
	F	14	27.48	1.00	3.74	23	28.11	0.25	1.20
	M&F	26	27.17	0.74	3.79	40	27.80	0.21	1.33
	Juv	—	—	—	—	9	25.00	1.16	3.48
V—A distance	M	12	25.16	1.14	3.94	17	23.51	0.93	3.85
	F	14	25.14	0.98	3.67	23	23.62	0.32	1.55
	M&F	26	25.15	0.75	3.80	40	23.56	0.43	2.70
	Juv	—	—	—	—	9	22.83	0.34	1.03
length of P	M	12	15.50	0.88	3.04	17	16.15	0.31	1.27
	F	14	15.13	0.25	0.94	23	16.16	0.24	1.13
	M&F	26	15.32	0.39	1.99	40	16.16	0.19	1.20
	Juv	—	—	—	—	9	16.22	0.19	0.57
length of V	M	12	15.51	0.21	0.74	17	15.44	0.84	3.45
	F	14	14.50	0.12	0.46	23	14.84	0.16	0.78
	M&F	26	15.00	0.12	0.60	40	15.16	0.34	2.13
	Juv	—	—	—	—	9	15.33	0.25	0.74
length of D	M	12	22.80	1.18	4.10	17	22.70	0.87	3.57
	F	14	21.71	0.22	0.84	23	21.46	0.30	1.24
	M&F	26	22.25	0.48	2.45	40	22.08	0.39	2.45
	Juv	—	—	—	—	9	20.43	0.47	1.40
depth of D ₁	M	12	13.80	0.32	1.10	17	13.91	0.36	1.26
	F	14	13.40	0.39	1.44	23	13.29	0.27	1.27
	M&F	26	13.57	0.26	1.25	40	13.60	0.20	1.24
	Juv	—	—	—	—	9	13.67	0.40	1.29
depth of D ₂	M	12	16.25	0.37	1.29	17	12.95	1.03	4.23
	F	14	12.00	0.34	1.28	23	10.52	0.26	1.24
	M&F	26	14.13	0.25	1.28	40	11.74	0.44	2.75
	Juv	—	—	—	—	9	9.80	0.27	0.89

No.	Smitt (1886, 1887) (Sweden)			No.	Svetovidov (1936) (Mesna river)		
	M	±	m		M	±	m
11	311.27	—	—	50	215.20	3.69	26.09
16	187.56	—	—	50	222.80	3.92	27.70
27	249.41	—	—	100	219.00	2.72	27.20
—	—	—	—	—	—	—	—
—	—	—	—	50	95.43	0.09	0.63
—	—	—	—	50	95.26	0.07	0.48
—	—	—	—	100	95.38	0.06	0.70
—	—	—	—	—	—	—	—
11	71.37	—	—	50	71.34	0.15	1.07
16	71.40	—	—	50	71.36	0.16	1.11
27	71.39	—	—	100	71.35	0.11	1.10
—	—	—	—	—	—	—	—
11	34.34	—	—	50	32.38	0.12	0.82
16	35.82	—	—	50	32.64	0.16	1.03
27	35.08	—	—	100	32.51	0.09	0.94
—	—	—	—	—	—	—	—
11	46.61	—	—	50	45.56	0.16	1.13
16	46.93	—	—	50	45.92	0.17	1.16
27	46.77	—	—	100	45.74	0.17	1.16
—	—	—	—	—	—	—	—
11	28.40	—	—	50	27.90	0.16	1.11
16	28.43	—	—	50	28.07	0.16	1.13
27	28.41	—	—	100	27.98	0.11	1.13
—	—	—	—	—	—	—	—
11	26.40	—	—	50	26.60	0.15	1.04
16	25.86	—	—	50	26.38	0.16	1.07
27	26.16	—	—	100	26.49	0.11	1.06
—	—	—	—	—	—	—	—
11	15.45	—	—	50	14.44	0.08	0.58
16	14.26	—	—	50	14.61	0.08	0.54
27	14.83	—	—	100	14.53	0.06	0.57
—	—	—	—	—	—	—	—
—	—	—	—	50	14.03	0.06	0.45
—	—	—	—	50	13.99	0.08	0.58
—	—	—	—	100	14.01	0.05	0.52
—	—	—	—	—	—	—	—
11	22.23	—	—	50	22.22	0.14	0.96
16	19.73	—	—	50	22.08	0.14	0.96
27	20.98	—	—	100	22.15	0.10	1.00
—	—	—	—	—	—	—	—
11	16.48	—	—	50	14.25	0.11	0.74
16	12.80	—	—	49	13.73	0.12	0.85
27	14.64	—	—	99	13.98	0.08	0.84
—	—	—	—	—	—	—	—
—	—	—	—	49	10.31	0.17	1.18
—	—	—	—	49	9.74	0.15	1.05
—	—	—	—	98	10.02	0.12	1.15
—	—	—	—	—	—	—	—

Table 2. Morphometric characters of *Thymallus thymallus*

Systematic characters	Sex	Authors (Vltava river)				Authors (Danube drainage)			
		No.	M ± m		No.	M ± m			
As % of standard length length of A	M	12	9.60	0.176	0.61	17	9.65	0.706	2.91
	F	14	9.28	0.231	0.80	23	9.30	0.139	0.87
	M&F	26	9.44	0.133	0.70	40	9.47	0.233	1.79
	Juv	—	—	—	—	9	9.17	0.973	2.92
depth of A	M	12	13.46	0.184	0.64	17	13.80	0.754	3.11
	F	14	13.07	0.200	0.75	23	14.43	0.632	3.27
	M&F	26	13.26	0.136	0.69	40	14.11	0.504	3.19
	Juv	—	—	—	—	9	14.44	0.253	0.76
distance between A and C	M	12	11.29	1.086	3.76	17	11.91	0.218	0.90
	F	14	11.10	0.368	1.38	23	11.70	0.649	3.11
	M&F	26	11.20	0.504	2.57	40	11.80	0.316	2.00
	Juv	—	—	—	—	9	11.93	0.223	0.67
distance between adipose fin and C	M	12	11.55	0.231	0.80	17	10.67	0.783	3.23
	F	14	11.37	0.181	0.68	23	10.45	0.187	0.90
	M&F	26	11.46	0.145	0.74	40	10.56	0.328	2.06
	Juv	—	—	—	—	9	10.81	0.383	1.15
length of caudal peduncle	M	12	14.37	0.184	0.64	17	14.37	0.235	0.97
	F	14	14.11	0.858	3.21	23	13.88	0.304	1.46
	M&F	26	14.24	0.378	1.92	40	14.03	0.192	1.21
	Juv	—	—	—	—	9	14.17	0.280	0.84
maximum body depth	M	12	20.54	1.068	3.69	17	21.00	1.145	4.72
	F	14	20.47	0.173	0.65	23	23.17	0.300	1.44
	M&F	26	20.51	0.256	2.17	40	22.09	0.487	3.08
	Juv	—	—	—	—	9	20.32	0.396	1.19
minimum body depth	M	12	7.12	0.095	0.33	17	7.24	0.123	0.51
	F	14	7.06	0.104	0.39	23	7.00	0.089	0.43
	M&F	26	7.09	0.070	0.36	40	7.12	0.074	0.47
	Juv	—	—	—	—	9	6.14	0.126	0.38
length of upper caudal lobe	M	8	19.36	1.202	4.16	16	17.53	1.104	4.18
	F	11	19.00	0.259	0.97	18	18.60	0.258	1.24
	M&F	19	19.18	0.503	2.59	34	18.06	0.424	2.71
	Juv	—	—	—	—	9	19.95	0.410	1.23
length of lower caudal lobe	M	8	18.93	1.106	3.83	14	18.26	1.004	4.14
	F	14	18.80	0.227	0.85	21	19.21	0.206	0.99
	M&F	22	18.86	0.459	2.34	35	18.73	0.405	2.56
	Juv	—	—	—	—	9	20.69	0.526	1.58
length of middle caudal rays	M	12	8.37	0.257	0.89	17	8.11	0.262	1.08
	F	14	8.30	0.157	0.59	23	8.35	0.242	1.16
	M&F	26	8.33	1.145	0.74	40	8.23	0.177	1.12
	Juv	—	—	—	—	9	9.06	0.360	1.08
length of head	M	12	20.79	1.057	3.66	17	20.52	0.796	3.28
	F	14	20.39	0.149	0.56	23	21.15	0.582	2.79
	M&F	26	20.59	0.414	2.11	40	20.83	0.480	3.03
	Juv	—	—	—	—	9	21.91	1.146	3.44
preorbital distance	M	12	5.79	0.566	1.96	17	5.71	0.160	0.66
	F	14	5.66	0.237	0.89	23	5.69	0.201	0.49
	M&F	26	5.72	0.279	1.42	40	5.70	0.090	0.57
	Juv	—	—	—	—	9	5.63	0.113	0.34

No.	Smitt (1886, 1887) (Sweden)			No.	Svetovidov (1936) (Mesna river)		
	M	\pm	m		M	\pm	m
11	9.36	—	—	50	9.06	0.079	0.56
16	8.45	—	—	50	9.05	0.073	0.52
27	8.90	—	—	100	9.05	0.064	0.54
—	—	—	—	—	—	—	—
11	10.92	—	—	50	11.17	0.134	0.95
16	10.28	—	—	50	11.22	0.137	0.97
27	10.60	—	—	100	11.20	0.096	0.96
—	—	—	—	—	—	—	—
11	11.01	—	—	50	9.41	0.077	0.54
16	11.33	—	—	50	9.51	0.088	0.53
27	11.17	—	—	100	9.46	0.059	0.59
—	—	—	—	—	—	—	—
11	11.44	—	—	50	8.97	0.080	0.56
16	11.71	—	—	50	9.04	0.100	0.71
27	11.51	—	—	100	9.01	0.065	0.65
—	—	—	—	—	—	—	—
11	15.10	—	—	50	16.19	0.098	0.69
16	14.82	—	—	50	16.24	0.084	0.59
27	14.96	—	—	100	16.22	0.065	0.65
—	—	—	—	—	—	—	—
—	—	—	—	50	19.86	0.149	1.04
—	—	—	—	50	19.50	0.160	0.16
—	—	—	—	100	19.68	0.111	1.10
—	—	—	—	—	—	—	—
11	7.29	—	—	50	6.58	0.048	0.34
16	6.96	—	—	50	6.71	0.045	0.32
27	7.12	—	—	100	6.65	0.034	0.34
—	—	—	—	—	—	—	—
10	15.71	—	—	46	16.27	0.101	0.70
12	15.63	—	—	38	16.35	0.113	0.70
22	15.67	—	—	84	16.31	0.077	0.70
—	—	—	—	—	—	—	—
—	—	—	—	44	15.94	0.099	0.66
—	—	—	—	41	16.01	0.125	0.80
—	—	—	—	85	15.97	0.079	0.73
—	—	—	—	—	—	—	—
11	5.57	—	—	50	5.29	0.075	0.53
16	5.98	—	—	50	5.11	0.072	0.51
27	5.77	—	—	100	5.20	0.053	0.53
—	—	—	—	—	—	—	—
11	19.36	—	—	50	18.81	0.077	0.54
16	19.56	—	—	50	18.85	0.085	0.60
27	19.46	—	—	100	18.53	0.057	0.57
—	—	—	—	—	—	—	—
—	—	—	—	50	4.35	0.032	0.23
—	—	—	—	50	4.43	0.036	0.26
—	—	—	—	100	4.39	0.025	0.25
—	—	—	—	—	—	—	—

Table 3. Morphometric characters of *Thymallus thymallus*

Systematic characters	Sex	No.	Authors (Vltava river)			Authors (Danube drainage)			
			M	±	m	No.	M	±	m
As % of standard length postorbital distance	M	12	10.41	0.109	0.38	17	10.44	0.167	0.69
	F	14	9.97	0.090	0.34	23	10.58	0.106	0.51
	M&F	26	10.19	0.070	0.36	40	10.51	0.094	0.60
	Juv	—	—	—	—	9	10.80	0.193	0.58
long. diameter of eye	M	12	4.46	0.265	0.92	17	4.61	0.128	0.53
	F	14	4.60	0.004	0.15	23	5.02	0.116	0.56
	M&F	26	4.52	0.105	0.53	40	4.81	0.086	0.54
	Juv	—	—	—	—	9	5.61	0.156	0.47
length of maxilla	M	12	5.13	0.080	0.28	17	5.61	0.131	0.54
	F	14	5.32	0.427	1.60	23	5.95	0.073	0.35
	M&F	26	5.22	0.184	0.94	40	5.73	0.070	0.44
	Juv	—	—	—	—	9	5.95	0.220	0.66
width of maxilla	M	12	2.33	0.063	0.22	17	2.48	0.550	0.23
	F	14	2.46	0.034	0.13	23	2.53	0.064	0.31
	M&F	26	2.39	0.034	0.17	40	2.50	0.042	0.27
	Juv	—	—	—	—	9	2.86	0.220	0.66
length of lower jaw	M	12	8.86	0.286	0.99	17	9.70	0.169	0.70
	F	14	9.54	0.085	0.32	23	9.85	0.129	0.62
	M&F	26	9.20	0.128	0.65	40	9.77	0.104	0.66
	Juv	—	—	—	—	9	10.63	1.093	3.28
interorbital distance	M	12	6.33	0.606	2.10	17	6.21	0.123	0.51
	F	14	6.00	0.098	0.37	23	6.19	0.091	0.44
	M&F	26	6.16	0.242	1.23	40	6.20	0.075	0.47
	Juv	—	—	—	—	9	6.12	0.193	0.58
occipital head depth	M	12	13.45	0.982	3.40	17	14.14	0.111	0.46
	F	14	13.12	0.104	0.39	23	14.59	0.175	0.84
	M&F	26	13.28	0.372	1.89	40	14.36	0.102	0.65
	Juv	—	—	—	—	9	14.65	0.193	0.58
orbital head depth	M	12	9.58	0.274	0.95	17	10.35	0.099	0.41
	F	14	9.70	0.139	0.52	23	10.75	0.177	0.85
	M&F	26	9.64	0.144	0.73	40	10.55	0.099	0.63
	Juv	—	—	—	—	9	10.34	0.163	0.49
As % of head length minimum body depth	M	12	34.37	1.228	4.25	17	34.82	0.837	3.45
	F	14	35.42	1.197	4.48	23	33.52	0.492	2.36
	M&F	26	34.76	0.857	4.36	40	34.17	0.459	2.90
	Juv	—	—	—	—	9	31.57	0.840	2.52
length of middle caudal rays	M	12	43.73	0.430	1.49	17	39.55	1.121	4.62
	F	14	41.00	1.411	5.28	23	39.21	1.344	6.44
	M&F	26	42.36	0.665	3.38	40	39.38	0.875	5.53
	Juv	—	—	—	—	9	41.33	1.913	5.74
preorbital distance	M	12	20.04	0.702	2.43	17	27.23	0.509	2.10
	F	14	27.17	1.032	3.86	23	26.28	0.384	1.84
	M&F	26	23.60	0.617	3.14	40	26.75	0.311	1.97
	Juv	—	—	—	—	9	25.45	0.416	1.25
postorbital distance	M	12	50.33	0.286	0.99	17	50.30	0.378	1.56
	F	14	49.42	0.823	3.08	23	50.00	0.588	2.82
	M&F	26	49.88	0.399	2.03	40	50.15	0.346	2.19
	Juv	—	—	—	—	9	49.10	1.636	4.91

Smitt (1886, 1887) (Sweden)				Svetovidov (1936) (Mesna river)			
No.	M	±	m	No.	M	±	m
—	—	—	—	50	9.64	0.044	0.31
—	—	—	—	50	9.73	0.044	0.31
—	—	—	—	100	9.68	0.031	0.31
—	—	—	—	—	—	—	—
—	—	—	—	50	4.76	0.041	0.29
—	—	—	—	50	4.84	0.046	0.31
—	—	—	—	100	4.80	0.030	0.30
—	—	—	—	—	—	—	—
11	5.83	—	—	50	5.35	0.031	0.22
16	6.18	—	—	50	5.31	0.039	0.28
27	6.00	—	—	100	5.33	0.025	0.25
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	1.73	0.016	0.11
—	—	—	—	50	1.76	0.018	0.13
—	—	—	—	100	1.75	0.012	0.12
—	—	—	—	—	—	—	—
11	9.83	—	—	49	9.65	0.042	0.29
16	10.18	—	—	50	9.72	0.050	0.36
27	10.00	—	—	99	9.68	0.032	0.32
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	4.37	0.026	0.18
—	—	—	—	50	4.47	0.037	0.26
—	—	—	—	100	4.42	0.023	0.23
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	12.75	0.071	0.50
—	—	—	—	50	12.69	0.075	0.53
—	—	—	—	100	12.72	0.052	0.52
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	8.82	0.060	0.42
—	—	—	—	50	8.91	0.050	0.36
—	—	—	—	100	8.87	0.039	0.39
—	—	—	—	—	—	—	—
11	37.81	—	—	50	35.00	0.301	2.13
16	35.73	—	—	50	35.52	0.243	1.72
27	36.77	—	—	100	35.26	0.196	1.95
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	27.72	0.374	2.64
—	—	—	—	50	26.64	0.402	2.84
—	—	—	—	100	27.18	0.218	2.80
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
11	27.89	—	—	50	23.20	0.185	1.31
16	26.35	—	—	50	23.52	0.196	1.39
27	27.12	—	—	100	23.36	0.136	1.36
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	50	51.36	0.237	1.67
—	—	—	—	50	51.56	0.214	1.51
—	—	—	—	100	51.46	0.160	1.80
—	—	—	—	—	—	—	—

Table 4. Morphometric characters of *Thymallus thymallus*

Systematic characters	Sex	Authors (Vltava river)				Authors (Danube drainage)			
		No.	M ± m		No.	M ± m			
As % of head length. long. diameter of eye	M	12	21.61	0.612	2.12	17	22.11	0.186	0.77
	F	14	22.91	0.727	2.72	23	23.65	0.540	2.59
	M&F	26	22.27	0.475	2.42	40	22.88	0.265	1.68
	Juv	—	—	—	—	9	25.35	0.266	0.80
length of maxilla	M	12	24.66	0.667	2.31	17	26.55	0.939	3.87
	F	14	25.96	0.887	3.32	23	27.76	0.910	4.36
	M&F	26	25.62	0.553	2.81	40	27.15	0.650	4.11
	Juv	—	—	—	—	9	27.03	0.800	2.40
width of maxilla	M	12	11.32	0.205	0.71	17	11.78	0.327	1.35
	F	14	10.95	0.502	1.88	23	12.03	0.254	1.22
	M&F	26	11.13	0.254	1.29	40	11.90	0.203	1.28
	Juv	—	—	—	—	9	12.82	0.600	1.80
length of lower jaw	M	12	46.00	1.303	4.51	17	46.61	0.512	2.11
	F	14	47.10	0.997	3.73	23	46.47	0.872	4.18
	M&F	26	46.50	0.809	4.12	40	46.54	0.497	3.14
	Juv	—	—	—	—	9	48.00	1.770	5.51
interorbital distance	M	12	30.37	0.664	2.30	17	29.79	0.366	1.51
	F	14	29.64	0.443	1.66	23	29.31	0.352	1.69
	M&F	26	30.00	0.389	1.98	40	29.55	0.253	1.60
	Juv	—	—	—	—	9	27.88	1.620	4.86
occipital head depth	M	12	63.58	1.283	4.44	17	67.35	0.910	3.75
	F	14	64.35	0.759	2.84	23	68.95	1.045	5.01
	M&F	26	63.96	0.715	3.64	40	68.15	0.693	4.38
	Juv	—	—	—	—	9	67.13	2.313	6.94
orbital depth of body	M	12	46.33	1.667	5.77	17	49.51	0.927	3.32
	F	14	46.53	1.208	4.52	23	51.72	1.010	4.34
	M&F	26	46.43	1.010	5.14	40	50.61	0.685	4.33
	Juv	—	—	—	—	9	47.22	1.673	5.02
gill rakers	M	12	23.75	0.500	1.73	17	22.35	0.373	1.54
	F	14	23.64	2.336	8.74	23	21.78	0.465	2.23
	M&F	26	23.69	1.028	5.23	40	22.06	0.298	1.88
	Juv	—	—	—	—	9	22.33	0.470	1.41
branchiostegals	M	12	10.25	0.213	0.74	17	9.94	0.109	0.45
	F	14	10.14	0.096	0.36	23	9.65	0.173	0.83
	M&F	26	10.19	0.108	0.55	40	9.79	0.101	0.64
	Juv	—	—	—	—	9	9.66	0.173	0.52
lateral line scales	M	12	84.41	1.323	4.58	17	81.23	0.652	2.63
	F	14	85.64	0.748	2.80	23	80.34	0.933	4.47
	M&F	26	85.02	0.724	3.69	40	80.78	0.561	3.55
	Juv	—	—	—	—	9	81.77	0.680	2.04
nonramified rays in D	M	12	6.92	0.138	0.48	17	7.11	0.070	0.29
	F	14	7.00	—	—	23	7.00	—	—
	M&F	26	6.96	—	—	40	7.05	—	—
	Juv	—	—	—	—	9	7.00	—	—
ramified rays in D	M	12	13.16	0.254	0.88	17	13.82	0.14	0.58
	F	14	12.85	0.176	0.66	23	13.56	0.15	0.72
	M&F	26	13.00	0.151	0.77	40	13.69	0.102	0.65
	Juv	—	—	—	—	9	14.33	0.233	0.70

Smitt (1886, 1887) (Sweden)				Svetovidov (1936) (Mesna river)			
No.	M	±	m	No.	M	±	m
--	--	--	--	50	25.34	0.180	1.27
--	--	--	--	50	25.38	0.208	1.47
--	--	--	--	100	25.36	0.137	1.37
--	--	--	--	--	--	--	--
11	30.08	--	--	50	28.22	0.111	0.78
16	31.26	--	--	50	28.08	0.157	1.11
27	30.67	--	--	100	28.16	0.085	0.85
--	--	--	--	--	--	--	--
--	--	--	--	50	9.15	0.088	0.62
--	--	--	--	50	9.34	0.091	0.65
--	--	--	--	100	9.24	0.064	0.64
--	--	--	--	--	--	--	--
11	50.83	--	--	--	--	--	--
16	51.90	--	--	--	--	--	--
27	51.36	--	--	--	--	--	--
--	--	--	--	--	--	--	--
--	--	--	--	50	23.22	0.181	1.14
--	--	--	--	50	23.54	0.199	1.41
--	--	--	--	100	23.38	0.129	1.29
--	--	--	--	--	--	--	--
--	--	--	--	50	65.76	0.534	3.77
--	--	--	--	50	65.12	0.392	2.77
--	--	--	--	100	65.44	0.332	3.32
--	--	--	--	--	--	--	--
--	--	--	--	50	46.76	0.334	2.36
--	--	--	--	50	47.24	0.324	2.29
--	--	--	--	100	48.00	0.234	2.34
--	--	--	--	--	--	--	--
--	--	--	--	50	23.88	0.199	1.41
--	--	--	--	50	24.32	0.220	1.55
--	--	--	--	100	24.10	0.150	1.50
--	--	--	--	--	--	--	--
--	--	--	--	50	9.70	0.081	0.57
--	--	--	--	50	9.68	0.066	0.47
--	--	--	--	100	9.69	0.052	0.52
--	--	--	--	--	--	--	--
11	84.81	--	--	49	88.31	0.477	3.34
16	79.37	--	--	50	88.12	0.407	2.87
27	82.09	--	--	99	88.21	0.313	3.11
--	--	--	--	--	--	--	--
11	5.33	--	--	50	6.48	0.081	0.57
16	5.06	--	--	49	6.46	0.071	0.50
27	5.19	--	--	99	6.47	0.054	0.54
--	--	--	--	--	--	--	--
11	14.63	--	--	50	14.94	0.087	0.61
16	14.50	--	--	49	15.12	0.085	0.59
27	14.56	--	--	99	15.03	0.061	0.61
--	--	--	--	--	--	--	--

The meristic characters also show a few differences. The number of gill rakers is higher for the specimens of the upper Vltava river than it is in the other locality studied. Interesting is the difference in the number of lateral line scales. The specimens from the upper Vltava river have larger numbers of lateral line scales (4.24 on average) than that from the drainage of Danube (Table 4).

Specimens studied were in normal condition, and the sample from the upper Vltava river was homogenous and collected during two days in 1955.

Sexual Dimorphism

Authors found a well defined sexual dimorphism in the graylings studied. The preanal, predorsal, preventral and P—V distance is larger in females than in the males. But the length of the ventral fin and the length of the base of dorsal fin is greater in males than in females. It is well known that the depth of dorsal fin (particularly from the posterior side) is always greater in males than in females. This fact applies very well also to the graylings studied.

Sexual dimorphic characters in the specimens studied

In % of standard length:	the upper Vltava river		the Danube drainage	
	Males	Females	Males	Females
preanal distance	68.75	69.00	69.00	70.00
predorsal distance	33.95	33.94	34.61	35.60
preventral distance	45.29	45.32	46.00	46.86
P—V distance	26.62	27.48	27.50	28.11
length of V	15.51	14.50	15.44	14.84
length of base of D	22.80	21.71	22.70	21.46
depth of D ₁	13.80	13.35	13.91	13.29
depth of D ₂	16.25	12.00	12.95	10.52

Vladykov (1931) showed clear sexual dimorphism in grayling. It is characterised by the longer preorbital part of head (males — 27.7—29.5 % of head length, females — 26.2—26.9 % of head length/28.1/%), higher dorsal fin in males (14.4—15.0 % of standard length in males, 11.7—12.9 % of the same length in females), lower ventral (/14.4/ 15—16.9 % of standard length in males, 13.3—13.5 in females), and the length of the ventral fins is 61.0—67.2 % of V—A distance in males while 54.1—57.2 % of the same distance in females.

Schäferna (1939) published two photographs of an adult pair of graylings from the upper part of river Vltava in Sušice where the sexual dimorphism is clearly visible. In his comments pointed out that the males have a more pointed rostral part of the head and the posterior part of the dorsal fin is prolonged while in females it is rounded. The ventral part of the body is generally blackish in males and their ventral fins are longer than in females. Solewski (1960) found slightly larger predorsal distance in males. Zinovev (1963) drew attention to the shape and size of unpaired fins, but these characters are distinct only in fish of more than 30—35 cm of body length. According to Zinovev (l. c.), the shape and size of the dorsal fin is the best character for the sex recognition.¹⁾ The depth of the dorsal fin in 38 males

¹⁾ The pointed end of the dorsal fin in males can be observed in specimens closely before the first spawning, up to three years of age it is not possible to recognise sex in graylings from the river Belá (Dyk, 1957).

Table 5. Morphometric characters of *Thynnalus thynnus*

Systematic characters	Sex	Authors (Vlava river)			Authors (Danube drainage)			Smitt (1886, 1887) (Sweden)			Svetovidov (1936) (Mesna river)					
		No.	M	± m	No.	M	± m	No.	M	± m	No.	M	± m			
meristic characters total rays in D	M	12	20.50	0.257	0.89	17	20.94	0.162	0.67	11	20.00	—	50	21.42	0.090	0.64
	F	14	19.85	0.176	0.66	23	20.60	0.160	0.72	16	19.55	—	49	21.37	0.126	0.88
	M&F	26	20.18	0.152	0.77	40	20.77	0.109	0.69	27	19.78	—	99	21.39	0.081	0.81
	Juv	—	—	—	—	9	21.33	0.166	0.50	—	—	—	—	—	—	—
ramified rays in P	M	12	13.83	0.095	0.33	17	13.88	0.092	0.38	11	14.27	—	50	13.92	0.120	0.84
	F	14	13.85	0.096	0.36	23	13.86	0.075	0.36	16	13.87	—	50	13.70	0.121	0.85
	M&F	26	13.84	0.087	0.34	40	13.87	0.058	0.37	27	14.07	—	100	13.81	0.085	0.85
	Juv	—	—	—	—	9	14.00	—	—	—	—	—	—	—	—	—
ramified rays in V	M	12	9.83	0.112	0.39	17	9.82	0.140	0.58	11	10.20	—	50	9.16	0.091	0.84
	F	14	9.78	0.112	0.42	23	9.86	0.070	0.34	16	10.12	—	50	9.24	0.080	0.87
	M&F	26	9.80	0.079	0.40	40	9.84	0.072	0.46	27	10.16	—	100	9.20	0.061	0.81
	Juv	—	—	—	—	9	10.00	—	—	—	—	—	—	—	—	—
ramified rays in A	M	12	9.83	0.095	0.33	17	10.12	0.094	0.39	11	9.72	—	50	9.62	0.093	0.86
	F	14	10.16	0.141	0.53	23	10.04	0.075	0.36	16	9.55	—	50	9.72	0.092	0.85
	M&F	26	10.00	0.084	0.43	40	10.80	0.059	0.37	27	9.63	—	100	9.69	0.065	0.86
	Juv	—	—	—	—	9	10.00	—	—	—	—	—	—	—	—	—

Table 7. Morphometric characters of *Thymallus thymallus*

Authority	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors
Locality	Vitava river	Danube drainage	Danube drainage	Danube drainage	Danube drainage	Danube drainage	Denube river	Denube drainage
Sex	males and females	males and females	males and females	males and females	juveniles	males and females	males and females	males and females
N. o. of specimens	26	40	9	27	9	27	12	25

	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges
As % of head length								
minimum body depth	30.50-37.50	26.50-28.60	25.70-34.50	29.60-46.70	25.70-34.50	29.60-46.70	31.50-40.80	—
length of middle caudal rays	32.00-48.00	25.50-47.50	37.00-52.50	—	37.00-52.50	—	21.60-36.30	—
postorbital distance	22.00-31.00	24.50-33.60	23.00-37.00	20.50-31.20	23.00-37.00	20.50-31.20	20.80-26.60	26.20-32.10
long. diameter of eye	47.05-53.00	47.50-52.60	47.60-50.00	—	47.60-50.00	—	46.20-57.00	—
length of maxilla	21.00-24.00	16.25-26.60	23.75-27.60	—	23.75-27.60	—	21.70-29.10	26.70-37.80
width of maxilla	23.50-27.00	24.50-30.60	23.75-28.50	27.30-35.60	23.75-28.50	27.30-35.60	26.00-31.60	25.80-28.60
length of lower jaw	8.50-13.80	10.60-14.00	10.30-15.60	—	10.30-15.60	—	8.10-10.80	—
inner orbital distance	43.00-49.00	42.00-52.00	45.00-50.00	47.60-57.10	45.00-50.00	47.60-57.10	48.00-58.00	42.60-50.00
occipital head depth	27.00-33.00	23.60-33.20	26.70-31.00	—	26.70-31.00	—	20.40-27.80	—
orbital head depth	50.00-70.00	55.00-76.00	61.00-76.00	—	61.00-76.00	—	60.70-74.00	—
	42.50-49.00	39.50-64.00	42.00-55.00	—	42.00-55.00	—	42.80-53.20	—
Meristic character:								
gill rakers	21-28	19-26	21-25	—	21-25	—	20-27	21-27
branchiostegals	10-11	8-11	9-10	—	9-10	—	9-11	6-10
lateral line scales	80-92	75-95	80-86	63-93	80-86	63-93	82-96	76-91
nonramified rays in D	VI-VII	VII-IX	VII	III-VI	VII	III-VI	V-VIII	IV-VI
ramified rays in D	12-14	12-16	13-15	13-16	13-15	13-16	14-16	15-17
total rays in D	19-21	19-22	21-22	17-21	21-22	17-21	19-23	19-23
ramified rays in P	13-14	13-14	14	11-16	14	11-16	12-16	12-14
ramified rays in V	9-11	9-10	10	9-11	10	9-11	9-11	—
ramified rays in A	9-11	9-11	10	8-11	10	8-11	8-11	9-11

Table 6. Morphometric characters of *Thymallus thymallus*

Authority	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors	Authors
Locality	Vihava river	Danube drainage	Danube drainage	Sweden	Mesma river	Tisza river	Danube drainage	Sweden	Mesma river	Tisza river	Danube drainage	Danube drainage
Sex	males and females	males and females	males and females	males and females	males and females	males and females	males and females	males and females	males and females	males and females	males and females	males and females
No. of specimens	26	40	9	27	100	12	25	27	100	12	25	25
	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges	ranges
Standard length	230-279	158-378	130-188	66.0-510.0	178.1-283.7	—	99.0-280.0	—	—	—	—	—
As % of standard length												
body length	90.00-95.00	90.00-95.00	88.50-92.00	—	93.50-96.50	—	—	—	—	—	—	—
preanal distance	66.00-74.00	63.00-74.00	66.50-69.50	63.80-74.40	69.00-73.60	—	—	—	—	—	—	—
predorsal distance	28.00-36.50	31.00-38.00	32.00-37.00	32.40-38.10	31.00-35.40	—	—	—	—	—	—	—
preventral distance	42.00-48.00	42.00-50.00	45.50-48.50	44.60-48.90	43.70-48.70	—	—	—	—	—	—	—
P-V distance	24.00-30.00	25.60-30.50	25.50-30.00	25.80-32.50	25.10-30.50	—	—	—	—	—	—	—
V-A distance	23.00-28.00	17.70-26.50	21.00-24.50	22.70-29.20	24.10-29.30	—	—	—	—	—	—	—
length of P	14.00-17.60	13.30-18.30	15.50-17.00	12.40-17.10	13.20-16.00	—	—	—	—	—	—	—
length of V	13.60-17.00	12.30-17.30	14.00-16.10	—	12.70-16.10	—	—	—	—	—	—	—
length of D	20.00-23.50	18.30-27.00	18.40-22.00	15.80-25.60	20.10-24.80	—	—	—	—	—	—	—
depth of D (D ₁)	12.00-15.80	10.70-16.50	12.20-16.10	11.00-23.90	11.60-15.60	—	—	—	—	—	—	—
depth of D (D ₂)	9.90-18.60	8.50-19.60	7.90-10.70	—	8.10-13.20	—	—	—	—	—	—	—
length of A	8.60-10.70	7.80-12.20	8.40-10.20	7.00-11.00	7.70-10.80	—	—	—	—	—	—	—
depth of A	11.20-14.00	10.60-16.00	12.90-15.40	8.00-13.60	10.16-12.40	—	—	—	—	—	—	—
distance between A and C	9.50-14.00	9.80-14.10	10.70-12.50	9.90-12.50	8.10-11.30	—	—	—	—	—	—	—
dist. between adipose fin and C	10.00-12.80	8.60-13.00	10.00-11.60	10.50-13.80	7.50-11.00	—	—	—	—	—	—	—
length of caudal peduncle	12.80-15.60	11.80-16.80	13.00-15.40	12.00-16.10	14.50-17.00	—	—	—	—	—	—	—
maximum body depth	18.60-21.50	17.80-24.50	18.00-21.80	—	17.80-21.80	—	—	—	—	—	—	—
minimum body depth	6.40-7.80	6.30-8.30	6.20-7.60	5.80-8.00	5.70-7.50	—	—	—	—	—	—	—
length of upper caudal lobe	17.00-21.00	12.70-21.00	18.00-22.00	13.70-19.90	14.70-18.10	—	—	—	—	—	—	—
length of lower caudal lobe	17.00-21.00	15.00-22.00	18.40-23.00	4.10-7.60	4.20-6.60	—	—	—	—	—	—	—
length of middle caudal rays	6.70-10.00	5.50-9.90	8.10-11.40	4.10-7.60	4.20-6.60	—	—	—	—	—	—	—
length of head	19.60-21.50	16.20-24.00	20.00-23.70	18.50-21.20	17.10-20.10	—	—	—	—	—	—	—
preorbital distance	5.00-6.60	4.70-7.00	5.00-6.20	—	3.90-4.99	—	—	—	—	—	—	—
postorbital distance	9.20-11.00	9.00-12.00	9.90-11.50	—	8.94-10.60	—	—	—	—	—	—	—
long. diameter of eye	4.10-5.00	3.35-5.70	4.80-6.30	—	4.08-5.70	—	—	—	—	—	—	—
length of maxilla	4.80-5.70	4.70-6.70	4.80-7.00	5.10-7.30	4.62-5.97	—	—	—	—	—	—	—
width of maxilla	2.00-2.70	1.90-2.90	2.10-3.50	—	1.44-2.03	—	—	—	—	—	—	—
length of lower jaw	7.30-10.00	8.40-11.40	9.00-12.30	8.80-12.10	8.63-10.50	—	—	—	—	—	—	—
interorbital distance	5.50-6.70	5.10-7.30	5.50-7.00	—	3.97-5.10	—	—	—	—	—	—	—
occipital head depth	12.40-14.20	11.60-16.70	13.50-15.40	—	11.69-13.89	—	—	—	—	—	—	—
orbital head depth	8.60-10.80	8.90-12.00	9.70-11.00	—	8.00-9.88	—	—	—	—	—	—	—

Table 8. Meristic characters of *Thymallus thymallus* given by different authors

Authors	Locality	No. of specimens	Dorsal rays		Anal rays		No. of lateral line scales	No. of gill rakers
			hard rays	soft rays	hard rays	soft rays		
Banarescu (1964)	Romania	25	IV-VII	15-17	II-IV	9-11	76-91	21-27
Svetovidov (1936)	USSR	100	V-VIII	14-16	-	8-11	82-96	20-27
Vladykov (1931)	Karp. Ukraina	12	IV-VI	15-17	III-IV	9-11	83-90	21
Siebold (1863)	Germany	-	V-VII	14-17	III-IV	9-10	86-88	-
Solewski (1960)	Poland	50	III-VII	13-15 ^a	II-IV	9-12	75-86	(20-23) 24-25
Andrijašev (1954)	USSR	-	IV-VII (XI)	13-17	II-IV (VI)	8-11	74-96 (98)	(20-21) 22-29
Tortoneso (1970)	Italy	13	V-VII	14-17	III-V	9-11	80-90	-
Vuković (1971)	Yugoslavia	-	IV-VIII	13-17	III-V	9-10	86-90	-
Roule (1925)	France	-	-	-	-	12-15 ^b	75-85	-

a - by an error III-XV.

b - apparently all rays.

Table 9. Comparative table showing the differences in the measurement of *Thymallus thymallus* by the use of two different schemes employed by authors (Oliva, Naiksatam) in the same material, from Vltava river. A — standard length measured from the tip of snout to the posterior margin of middle caudal rays, B — the same according to Svetovidov (1975), i.e. the standard length measured from the begin of maxilla to the posterior margin of middle caudal rays.

Systematic characters	A		B		A		B		averages	
	males	and females	males	and females	males	and females	males	and females	males	and females
Standard length	233.00	— 254.00	231.00	— 252.00	245.80	237.40	241.60	244.00	255.20	239.60
As % of standard length										
body length	90.00	— 94.00	90.00	— 93.50	92.00	91.60	91.80	92.10	91.50	91.80
predorsal distance	32.50	— 34.50	33.00	— 34.50	33.46	34.16	33.81	33.86	34.34	34.10
V — A distance	24.00	— 27.00	24.25	— 27.25	25.80	24.80	25.30	26.14	25.30	25.72
depth of D (D ₂)	11.30	— 17.14	11.50	— 17.40	15.56	12.20	13.88	15.76	12.36	14.06
depth of A	13.00	— 13.60	13.10	— 13.80	13.04	13.44	13.24	13.32	13.60	13.46
distance between A and C	9.60	— 13.20	9.70	— 13.20	11.50	11.00	11.25	11.80	11.14	11.47
distance between adipose fin and C	10.60	— 12.40	10.80	— 12.50	11.36	11.20	11.28	11.64	11.40	11.52
length of caudal peduncle	11.20	— 15.40	12.60	— 15.60	13.75	13.96	13.86	14.20	14.08	14.14
maximum body depth	18.60	— 21.50	18.80	— 22.00	20.62	20.20	20.41	20.76	20.42	20.59
length of middle caudal rays	6.60	— 9.90	6.60	— 9.90	8.12	8.42	8.27	8.20	8.32	8.36
length of head	19.60	— 21.50	19.60	— 21.30	20.70	22.22	21.46	20.05	20.30	20.17
orbital head depth	12.80	— 14.20	12.90	— 14.50	13.44	13.40	13.42	13.66	13.52	13.59
orbital head depth	8.60	— 10.80	8.90	— 11.00	9.54	9.62	9.58	9.64	9.78	9.71
interorbital space	5.50	— 6.70	5.90	— 6.70	6.34	6.18	6.26	6.33	6.30	6.34
As % of head length										
length of middle caudal rays	32.00	— 48.00	33.00	— 49.00	39.40	40.00	39.70	40.40	40.40	40.40
preorbital distance	24.00	— 29.00	23.80	— 29.20	26.66	26.60	26.63	27.10	26.68	26.89
long. diameter of eye	21.00	— 23.50	21.50	— 24.00	22.60	23.00	22.80	21.70	23.60	22.65
length of maxilla	23.00	— 27.00	24.00	— 28.00	24.70	25.80	25.25	25.44	26.64	26.04
interorbital space	28.50	— 33.00	29.00	— 34.75	30.70	30.80	30.75	31.30	31.76	31.53
orbital head depth	43.50	— 56.00	43.00	— 56.00	46.10	48.00	47.05	48.00	48.90	48.45
occipital head depth	61.00	— 70.00	62.50	— 71.50	65.20	66.20	65.70	67.00	67.70	67.35

Table 10. Comparative table showing the differences in the measurement of *Thymallus thymallus* by the use of two different schemes employed by authors (Oliva, Narkisam) in the same material from Danubio drainage. A — standard length measured from the tip of the snout to the posterior margin of middle caudal rays, B — the same according to Svetovidov (1936), i.e. the standard length measured from the begin of maxilla to the posterior margin of middle caudal rays.

Systematic characters	ranges		averages			
	A males and females	B males and females	A males	A females	A males and females	B males and females
Standard length	191.00—270.00	189.00—269.00	234.00	235.20	234.60	232.00
As % of standard length						
body length	90.00—92.00	90.00—92.50	91.30	90.50	90.90	91.40
predorsal distance	33.50—38.00	33.80—38.50	34.90	35.50	34.20	35.22
V—A distance	22.00—26.00	22.10—26.50	24.10	23.70	23.90	24.34
depth of D (D ₂)	9.40—13.20	9.50—13.40	11.62	11.96	11.79	11.84
depth of A	12.00—16.00	12.20—16.10	13.32	15.28	14.30	13.50
distance between A and C	10.60—12.20	10.70—12.20	11.62	11.28	11.45	11.76
distance between adiposo fin and C	9.70—11.80	9.70—11.90	10.80	10.40	10.60	10.90
length of caudal peduncle	11.80—14.70	12.00—14.80	13.80	13.64	13.72	13.90
maximum body depth	17.80—23.00	18.00—23.50	20.74	20.92	20.83	20.94
length of middle caudal rays	8.00—9.90	8.10—10.00	8.84	9.32	9.80	8.92
length of head	18.00—22.00	18.40—21.50	19.86	20.78	20.32	19.78
occipital head depth	11.50—16.00	11.60—16.00	13.10	15.10	14.10	13.28
orbital head depth	8.90—11.60	9.00—11.70	9.64	10.76	10.20	9.70
interorbital space	5.20—6.70	5.10—6.50	5.72	6.14	5.93	5.96
As % of head length						
length of middle caudal length	37.50—47.50	38.00—49.00	44.40	44.80	44.60	45.60
preorbital distance	24.50—32.50	24.00—33.00	26.50	27.90	27.20	27.38
long. diameter of eye	16.25—25.00	17.00—26.20	23.10	22.56	22.89	24.24
length of maxilla	24.50—29.00	25.50—29.00	25.70	26.80	26.25	26.80
interorbital space	25.50—30.50	25.50—31.00	29.10	29.30	29.20	28.72
orbital head depth	45.50—56.50	46.50—57.00	48.14	51.40	49.77	52.70
occipital head depth	61.00—75.00	63.00—77.00	65.90	71.50	68.70	73.30
						70.40

of 26.5–46.5 cm body length (Smitt's length) was 12.0–14.9 % of body length while in the same number and same size of females it represented 11.9–12.8 % of body length. He also stated that in males the highest depth of dorsal fin is situated with its increasing growth towards the posterior part, but in females the highest depth can be measured in the first (oral) part of the fin. During the maturation of the males an intensive growth of the last rays (from the third up to the seventh from the end) is observable. The base of the dorsal fin is also longer in males (20.0–21.0 % of body length) in comparison with the females (19.9–20.4 % of body length). The length of the base of the anal fin is greater in males (8.5–9.8 % of body length, while in females it is about 8.6 % of body length). But the depth of the anal fin decreases in males as well as females with their size. The specimens having the body length up to 250–300 mm have concave margin of the anal fin, but in larger specimens it is convex as the distal part of the last ray is lost and the fin is mutilated. This is probably caused by the movements of the fin in the gravel on the bottom during the spawning act of both the sexes, but in females the mutilation of the anal fin appears sooner than in the males.

DISCUSSION

Unfortunately, our results are not so simply comparable with the data given by other authors as could be supposed. Svetovidov (1936) used Smitt's scheme (1887) of measurement "in corrected sense of Pravdin" as he wrote, "for measuring the white fish genus *Coregonus* . . . , and the length of the body, head length, preorbital distance and other measurements were performed from the beginning of the maxillare, but not from the tip of the snout". Svetovidov (l. c.) (p. 185) supposed that this would be in many cases useful and precise, as the upper lip in graylings is sometimes bent downwards, especially in *Thymallus thymallus*. In the English summary of his paper (1936), he repeats (p. 294) that "Smitt's scheme was employed, i.e. the body length was measured from the beginning of the maxillary (not from the tip of the snout) to the extremity of the middle caudal rays, the length of the head from the beginning of the maxillary also." Unfortunately, Smitt's scheme brings out difficulties concerning the fact that there are two "Salmonid schemes". The first one, "Figura Salmonis", in Smitt 1887, tab. metrica I–VI, demonstrates the method of measurements in Salmon (genera *Salmo*, *Salvelinus*, *Oncorhynchus*, *Hucho*), the second series, tables VII–XIII demonstrates the method of measuring in the genera *Coregonus*, *Osmerus*, *Mallotus*, *Argentina*, *Thymallus*, *Stenodus*, *Brachymystax*. The difference is in the concept of the "standard" of "fork" length, taken in the first series (tabl. V–VI) from the tip of the snout to the posterior margin of central caudal fin rays (the same method was used by Pravdin, 1931 and Berg, 1948). However, in the second series of tables (VII to XIII) it is measured from the beginning of maxillare (used also by Pravdin, 1931, Svetovidov, 1936 and Berg, 1948). But we have the reason to suppose that most of the ichthyologists who used the Smitt's scheme when measuring Salmonids, overlooked the scheme given in the last cited tables (Smitt's length Nr. 2) and used the first concept (Smitt's length Nr. 1, from salmon's figure of Smitt, 1887). This is used by Vladykov (1931), Balon (1953, 1962) and also by the present authors. Our measure-

ments, as it is clearly shown in the Figure 1, were made with regard to the standard or fork length being the distance between the tip of the rostrum up to the posterior margin of the central caudal fin rays. The head length is measured from the tip of the snout to the posterior margin of opercular bone excluding the width of the branchiostegal membrane.

For comparison, we selected sample and did measurements using the scheme of Smitt (1887) for *Coregonus* in the same sense as Svetovidov (1936) did his measurements. In these two measurements there is some difference, but it is not much significant. We demonstrated this by selecting certain characters (Table nos. 9 and 10) which are measured according to Smitt (1887) as well as to Svetovidov (1936). In some cases the standard length is greater by about 2 mm, which is the distance between the tip of the mouth and the beginning of the maxilla. But the percentage values of standard length and of head length do not show much difference. In certain cases the difference is not greater than of 1 mm. Considering this negligible difference we compared our results with those given for the graylings from the river Mesna.

Serious mistake appeared in the paper of Solewski (1960), where the body length is measured from the tip of the snout to the beginning of the caudal fin rays as in cyprinids and not according to Smitt's scheme used for salmonids by almost all authors. Another problem lies in the fact that the specimens studied by Solewski were classified according to their age into the age classes (II, III, IV), which makes the material uncomparable with the material of all other authors, where such division is not made. In taxonomical papers simultaneous division of material into age groups occurs very rarely. Dyk (1952) published some measurements of 29 specimens giving the absolute metrical values and only the total length but not the length of the body. Zinovev (1963) divided his material into age classes (I-V) in a similar way as Solewski (1960), but apparently the length of the body given by him coincides with the original paper of Smitt (1887) and Svetovidov (1936). Unfortunately, the data of both the authors becomes uncomparable as their material is divided into age classes. Only the data of meristic characters can be utilised from Solewski (1960) and Zinovev (1963) for comparison with our data. Similarly, it is not possible to compare the data of Solewski (1960) with those of Smitt (1886, 1887) because Solewski did not take into account that the measurements by Smitt were based on a different concept of "standard length". Therefore the part of Solewski's paper (1960) devoted to such comparison is without any use. Solewski (l. c.) did not utilise the data of Smitt (1887), which can be easily obtained from tables of measurements, although he operated with them. The necessity of comparing the specimens of the same size is quite obvious in graylings, and several authors showed differences in body form coloration of juveniles, subadults and adult specimens (see, e.g., Dyk 1953, 1956; Nikolski, 1954; Solewski, 1960; Zinovev, 1963). Therefore we respected this fact in our comparison.

Linnaeus (1758) described graylings as follows: "S. maxilla superior longiore, pinna dorsi radiis 23, *Salmo thymallus*, p. 311. Fauna Svec. 314, idem, B. 10, D 23, P 16, V 12, A 14, C 19. Habitat in Europae fluviis maritimis". According to Linnaeus, Artedi also characterised the grayling by the presence of 23 rays in the dorsal fin. Bloch (1783) repeated the same

diagnosis: — Kh. 10, Br. 16, B. 12, A. 14, S. 8, R. 23. (Kh = brachioistegal membrane, Br. = pectoral fins, S = caudal fin, B = ventral fin, R = dorsal fin). Hamilton (1843) gave these data: D 20, P 15, V 10, A 13, C 20. When compared the values given by Solewski (1960) (D, hard rays $M = 5.10 \pm 0.146$, $s = 1.035$, D, soft rays $M = 14.08 \pm 0.124$, $s = 0.876$) with the data given in our Table 8, it is clearly observed that the low number of hard (non-ramified) dorsal rays of the grayling from southern Poland resembles the description of the grayling from Sweden studied by Smitt (1886, 1887). This is also true with the soft rays of the dorsal fin where the number decreases from north to south. The average number of soft rays in the anal fin given by Solewski (1960, $M = 9.63$) is the same as that for the Mesna river population given by Svetovidov (1936). But it is interesting that the "Danube" graylings showed the largest number of soft anal rays ($M = 10.12$). Pectoral (P) fin has generally 14 rays (I 12–14). Solewski's data (1960, $M = 13.30 \pm 0.111$, $s = 0.789$) agree with this number and other authors (Table 7) did not find any differences, either. The number of lateral line scales decrease in the localities of southward direction. The greatest values given by Andrijašev (1954) and Svetovidov (1936) are in agreement with this generally known law.

Zinovev (1963) showed a clear variability of meristic characters during the growth of the studied specimens from the river Vishera (between 60° to $61^{\circ}30'$ of north lat. and 56° – 59° west. length). He demonstrated it by defining three groups of different standard length (Smitt's length). In the first group there were 29 specimens with 169 mm of standard length while the average number of gill rakers was 24.93 ± 0.27 ; in the second group there were 30 specimens with 237 mm of standard length where the average number of gill rakers was 26.35 ± 0.22 ; and in the third group of average standard length 351 mm, the same number was 27.14 ± 0.15 (M diff. = 7.13). The number of pyloric caeca was 16.33 ± 0.23 , 17.40 ± 0.36 and 20.00 ± 0.41 (M diff. 7.94), respectively, with the three groups mentioned above. The number of lateral line scales with reference to the above groups was 85.23 ± 0.49 , 87.13 ± 0.39 , and 86.78 ± 0.34 (M diff. 2.58), respectively. Solewski (1960), unfortunately did not pay attention to the growth variability of meristic characters.

It is interesting to note that in the northern populations of graylings, the length of maxilla seems to be longer than in the southern ones, e.g. Andrijašev (1954) found it to be 29–30 % of the head length, rarely exceeding 30 %. Also the snout seems to be longer (up to 38 % of head length); Banarecu (1964) nozed values up to 36 %.

Balon (1962) studied the life of graylings in the riverine lake of Hnílec (Slovakia) and in comparatively smaller span of time transformed into a limnophil form, which migrated into the river during spawning period. The life in the riverine lake, which forms the Hnílec valley water reservoir, provoked the changes of body dimensions. Graylings here became more robust, and thus they are believed, analogous to trouts, bleaks, coregonids and others, to be a different reversible ecotype, namely *Thymallus thymallus lacustris* (see also Balon, 1966). Unfortunately, Balon (1962, 1966) does not offer any further descriptive data. When we measured the specimens considered as "normal" by Balon (1966, Photo No. 29, p. 266) the maximum depth was 17.6 % (Smitt's scheme), while in the elevated specimen, designat-

ed by Balon as *morpha lacustris* (photo — 30, p. 267), the value was 21.5 %. In Balon's (1966) concept of the "normal" grayling (fig. on p. 163), the body depth was 23.5 %, and in "lacustrine" form it was 24 %. His description is thus not precise, as such more or less elevated specimens can be found in the other samples as well especially in those from the Danube and Tisza drainage.

NOTE TO THE GEOGRAPHICAL DISTRIBUTION OF THE GRAYLINGS IN EUROPE

We believe it is necessary to add some notes on the geographic distribution of the graylings in Europe, which is very curious especially in the European part of the USSR as it coincides mostly with the greatest distribution of glacial cover (see also Dyk, 1956). In Europe, the grayling does not occur in the Iberian Peninsula, the central and southern Italy, Macedonia, Bulgaria, the southern part of Russia, the southern part of Sweden, the western part of England, Ireland, Scotland, the lowlands of the Netherlands and the Polish and German drainages of the Baltic sea, but it is present in the upper part of the streams of western Jutland, in the Baltic drainage of Finland, in Bucovina (see Bloch, 1783; Selys-Longchamps, 1842; Hamilton, 1843; Otterström, 1914; Karaman, 1924; Roule, 1925; Thienemann, 1925, 1950; Ziemiankowski, 1925; Svetovidov, 1936; Redeke, 1941; Helling, 1943; Drenski, 1948, 1952; Müller, 1961). The distribution in Europe is characterised by the isolation of single localities where the fish occurs; this was known to many authors, e.g. Svetovidov, 1936; Ladiges, -Vogt, 1965). But it remains vague and recently the natural distribution has been changed by the artificial planting into the rivers where the grayling did not occur previously (see e.g. Thienemann, 1950, 519). Its presence in the upper part of streams in the southern area of its distribution, e.g. in Italy, and its absence in the lowland parts of the rivers within the area of its natural distribution (e.g. in most parts of southern Sweden, see Thienemann, 1950) may have time connection with the fact that the grayling is the member of the glacial relict fauna of Europe, as supposed by Ekman, 1922 (see also Müller, 1961). The occurrence of grayling in the upper Volga can be explained by the adjoining of a part of the water system which formerly belonged to the Arctic Ocean (Berg, 1933; Thienemann, 1950) to the Volga drainage. The occurrence of the grayling in northern Italy (the Po and its right side tributaries: the Adige, the Brenta, the Piave, the Tagliamento, the Isonzo — Tortonese, 1970) could be explained only by its stenotopic character and boreo-alpine distribution. Nybelin (1936, see Thienemann, 1950) showed that the geographical distribution of the sculpin *Cottus poecilopus* Heckel, 1843, is in many respect similar to that of the grayling, *Thymallus thymallus* (Linnaeus, 1758). Gronovius' note (see Gray, 1814) is very interesting: he says that the grayling lives in rivers "longe a mari remotis", from where it is obvious as the old authors knew that the grayling does not enter the sea, and thus salt water is a barrier against its distribution: e.g., for a *Salmo salar* Gronovius gave a different characteristic: "Habitat in Mari Europaeo flumina adscendens", which is true.

According to the present distribution of graylings throughout Europe Thienemann (1950) supposed that the fish is "ein genuiner Europäer, Sie wird also präglazial bei uns vorhanden gewesen sein, und zwar vor allem

im Süden. Hier, besonders in der Umgebung der Alpen, aber auch im Südosten, hielt sie sich während der Eiszeit. Das Überdauern der Eiszeit im Süden gab ihr die Möglichkeit, schon vor der Litorinassenkung in Nordwesteuropa die Küstenländer zu erreichen und so nach England zu gelangen. Nach Nordskandinavien kam sie postglazial von Nordosten." The localities of graylings in "Lüneburger Heide", west of the mouth of the Elbe and western Jutland in northern Germany are explained as relicts of the last interglacial period or by immigration of the fish during the last (3rd) glacial period (this is Vistula = Würm = Wisconsin glacial period) through the river beds of that time in this territory. Against the concept of the primeval habitat of graylings in Europe (term genuiner Europäer of Thienemann, 1950) tests the fact that most representatives of this genus live in Central Asia (northern Mongolia and surrounding parts of Siberia, see Svetovidov, 1936), and the past history of European fish fauna as explained better through a number of arguments by Lindberg (1955). Müller (1961) found that in the river Lule Älv in Swedish Lapland the grayling's zone "has the length of about 340 km" (this is 75 % from its total length), while the percentage of this zone in the river Fulda (from 250 km of its length only 5 km is the grayling region, which is only about 2.2 % of the river's length) is remarkably small. In northern Scandinavia the grayling is not confined to certain "zone" of the river and occurs in rivers and lakes, filled with snow and ice water from surrounding glaciers, in rivers and lakes, filled with snow and ice water from surrounding glaciers, in rivers and lakes rich in humus and in weedy or swampy regions, and also in the brackish water in the mouth of the river Lule Älv. According to Dyk (1958), from the whole length of the river Vltava (435 km) only about 20 km is the "grayling zone", this is about 2.2 % of the river's length. In the river Labe (the whole length within Bohemian frontiers 396 km, total 1122 km), the grayling zone has the length of 15 km, this is 2.7 % of the total river's length in Bohemia and only 0.9 % of the total length.

In agreement with the definition of "glacial relicts" as they are summarised by de Beaufort (1951) and with Svetovidov (1936) we suppose that in Central Europe the grayling is the true glacial relict.

There is no doubt that the grayling is a stenotopic animal, and this blocks its wider extension in the present time. It is of full interest that its occurrence, spreading from rivers and lakes of tundra regions up to the Po river drainage south of the Alps, is not accompanied by any remarkable changes in the fish. According to de Beaufort (1951) Ch. Darwin was the first to give the explanation of this "boreo-alpine distribution" of some plants and animals. As regards the fish fauna, it must be added that all main European rivers were several times united after the rise of temperature and retreat of ice cover following each glaciation (Aridt, 1938, see also Banareescu, 1960; Lindberg, 1955). The river basins of the northern slope of Europe were coverpartially or fully by ice during glacial periods. This explains sufficiently the scarcity of this typical fresh water fish fauna (Lindberg, 1955). The present fish fauna of Europe is composed of immigrants partly Ponto-Caspian rayon and partly from the north-east of Asia. The penetration of some faunal elements as *Cottus poecilopus* (Heckel, 1843), *Phoxinus phoxinus* Pallas, 1811 and *Hucho hucho* (Linnaeus, 1758) and most probably also the grayling into Central Europe seems to be an obvious document of the varia-

bility of this theory. Naturally, the influence of every glacial and interglacial period on composition of the European fish fauna remains to be a matter of open discussion.

SUMMARY

1. 32 plastic measurements and 8 meristic measurements were studied in 75 specimens of *Thymallus thymallus* (Linnaeus, 1758) from the territory of Czechoslovakia (samples from the Labe system and the Danube drainage).
2. Compared with the results of other authors, graylings from the Central Europe (Czechoslovakia) show the following differences: They differ from the graylings from Northern Europe, the Mesna river, Kanin Peninsula, by having smaller body length and preanal distance, while the depth of the posterior part of the dorsal fin (D_2), the depth of the anal fin and the length of the middle caudal rays is greater. The number of gill rakers, lateral line scales and ramified rays of the dorsal fin (particularly from the upper Vltava river) is found to be comparatively smaller. When compared with the graylings from Scandinavia, our graylings have smaller preanal distance and greater depth of the anal fin, while the length of the upper caudal rays and middle caudal rays is greater. From the graylings of Poland, where only some meristic characters could be compared, our graylings differ by increased number of hard and soft anal rays and smaller number of soft dorsal rays.
3. In general, following characters are found to be the same throughout the whole territory of distribution of the grayling: preanal distance, P-V distance, length of dorsal fin, depth of anterior part of dorsal fin (D_1), length of anal fin, minimum depth of body, length of head, preorbital distance, postorbital distance, longitudinal diameter of eye, length of maxilla, width of maxilla, length of lower jaw, number of branchiostegal rays, number of non-ramified rays of dorsal fin, pectoral fin, ventral fin and anal fin.
4. On the wide area of its distribution the European grayling shows apparently small intraspecific variability.

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**VERÄNDERUNGEN DER KÖRPERPROPORTIONALITÄT
WÄHREND DES WACHSTUMS IM POPULATIONSMUSTER
DES WASSERFROSCHES RANA ESCULENTA (LINNAEUS, 1758)
(AMPHIBIA: RANIDAE)**

ZBYNĚK ROČEK

Eingegangen am 9. April 1973

Abstrakt: In der Arbeit werden die Veränderungen der Körperproportionen des Wasserfrosches während des Wachstums verfolgt. Als Material sind 109 Exemplare aus einer Lokalität unweit der Stadt Týnště nad Orlicí im nordöstlichen Böhmen angewendet. Auf Grund der Resultate wird eine Möglichkeit diskutiert, manche Indexe als Charakteristiken der ganzen Population zu benutzen.

EINLEITUNG

Bei der Beurteilung der Interpopulationsvariabilität und der geographischen Variabilität ist es sehr wichtig, die Veränderungen der Körperproportionen während des Wachstums des Einzelwesens zu kennen. Im entgegengesetzten Fall mag es werden, dass man bei der Festlegung der verschiedenen Grössengruppen zu Fehlschlüssen kommt (darauf hat schon vor längerer Zeit Terentjev aufmerksam gemacht — z. B. Terentjev & Černov, 1949). Deswegen ist es überraschend, dass die Aufmerksamkeit auf dieses Problem nur von seltenen Autoren, die sich mit der Taxonomie von Amphibien beschäftigt haben, gerichtet worden ist. Unter den Verfassern, die in ungleichartigem Masse, von verschiedenen Standpunkten und oft auch nach verschiedenartigen Methoden die proportionellen Veränderungen des Wachstums vom Wasserfrosch oder Seefrosch gewertet haben, ist es möglich z. B. Berger (1966), Günther (1968), Kauri (1959), Lác (1959), Opatrný (1966, 1970b), Terentjev (1962) u. a. zu nennen. Ausführlicheren Verlauf des Wachstums im Inneren einer Population kennt man aber bisher nicht.

Die unterbreitete Arbeit sollte wenigstens zum Teil den Umfang und den Verlauf der Körperproportionalität während des Wachstums erklären und auf dieser Basis feststellen, ob man irgendwelche Kennzeichen als Charakteristiken der ganzen Population benutzen kann, oder, ob man bei der Beschreibung der Interpopulationsunterschiede immer das System der Grössenklassen bewahren muss. Es ist notwendig hervorzuheben, dass die Grössenstruktur der Population der Alterstruktur nicht entsprechen muss und dass die Kurven des Wachstums auf den Veränderungen der Körpergrösse und keineswegs auf dem Alter des Einzelwesens gegründet sind. Die Beziehungen des Wachstums eines Einzelwesens zu seinem Alter kann man vorläufig nicht genau festsetzen.

Für eine lebenswürdige Durchsicht des Manuskripts und für die kritischen Bemerkungen danke ich besonders Doc. Dr. O. Ohva CSc. aus der Karlsuniversität in Prag und Dr. E. Opatrný aus der Palacký Universität in Olomouc.

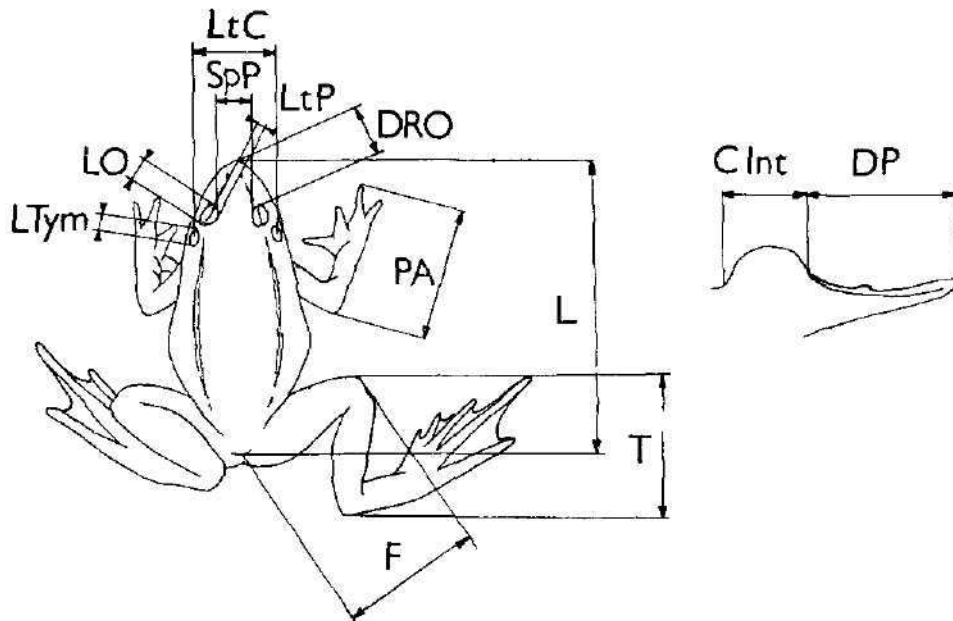


Abb. 1. Das Schema der abgenommenen Dimensionen.

MATERIAL UND METHODIK

Im ganzen wurden 109 Exemplare (49 ♀♀, 37 ♂♂ und 23 Juv.) als ein Muster einer Population aufgearbeitet. Das Sammeln wurde im Zeitabschnitt von 15. bis 22. 6. 1972 auf der Lokalität „Novoveský rybník“ — etwa 3 km SW von der Stadt Týniště nad Orlicí, nordöstliches Böhmen — durchgeführt. Dieser Teich ist ein verhältnismässig grosses Wasserbassin am Rande der ausgedehnten Walder mit Seehöhe von 262 m. In der Serie des Populationsmusters ist ein Exemplar vorgekommen, das sich in der relativen Grösse des inneren Metatarsalhockers von den übrigen einzelnen Individuen unterschieden hat. Die Stellenwerte, die bei dem kritischen Einzelwesen abgemessen worden sind, haben den Kurvenverlauf nicht beeinflusst; im Text wird es auf sie von mir immer aufmerksam gemacht. Alles Material ist mit der Formaldehydlosung von 4% fixiert worden.

Es sind diese Merkmale gemessen worden (Abb. 1) — L (Körperlänge), DRO (Entfernung des Auges vom Vorderkorperrand), LO (Augendurchschnitt), LtP (Augenlidbreite), SpP (Gegentfernung beider Augenhöhlen), LTym (Trommelfelldurchschnitt), F (Femurlänge), T (Tibiallänge), DP (Länge der ersten Zehe), CInt (Länge des Forshockers). Beim Abnehmen dieser Masse habe ich mich an der von Terentjev & Černov (1949) empfohlenen Massmethodik gehalten. Ausserdem habe ich einen Teil der Länge der vorderen Gliedmassen (PA — Entfernung vom Ende der längsten Zehe bis zur Gelenkverbindung Ulna-Humerus) und die Kopfbreite (LtC — hier wird sie durch die gegenseitige Entfernung der Trommelfelldurchmitten repräsentiert) gemessen. Die einzelnen Masse sind mit der Genauigkeit von 0,1 bis 0,5 mm mit einer Abhängigkeit von der Grösse des gemessenen Merkmales und von den zutreffenden Materialdeformationen abgenommen worden.

*) Mit dem Begriff „Population“ meine ich hier eine Gesamtheit von den Einzelwesen in einer bestimmten Lokalität, d. h. in einem Wasserbassin und in seiner Umgebung, die hinreichend räumlich oder anders von einer anderen solchen Gesamtheit abgeteilt ist. Eine so begriffene Population wird manchmal mit dem Termin „Lokalpopulation“ bezeichnet und als eine Gesamtheit von den potentiell beiderseitig kreuzenden Einzelwesen in einer gegebenen Lokalität definiert (Mayr, 1963; Mayr, Linsley & Usinger, 1953).

ERGEBNISSE

Histogramm auf der Abbildung 2 stellt die Grösseneinteilung vom son-
dierten Populationsmuster. Es ist offenbar, dass die Indexwerte in höchstem
Masse dem wirklichen Zustand in meist frequentierten Grössenklassen ent-
sprechen. Die Werte der weniger frequentierten Klassen können nicht für
entsprechenden Repräsentanten der Beziehungen in einer Population ge-
halten werden.

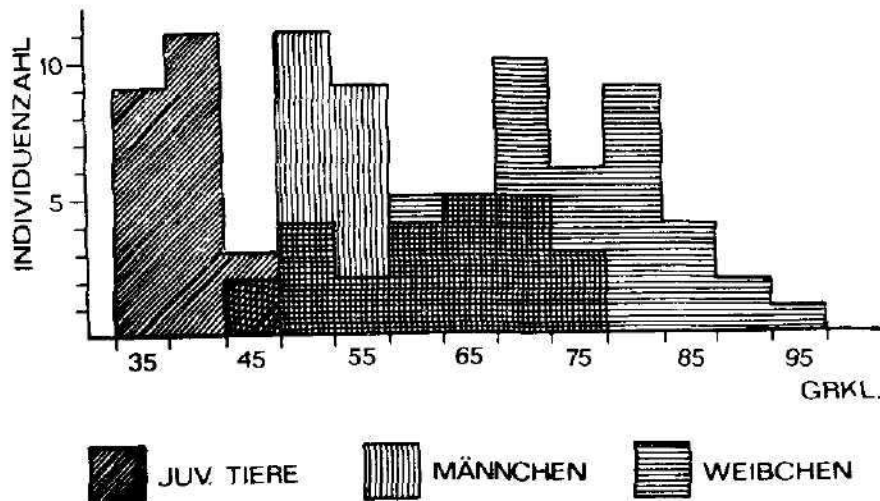


Abb. 2. Histogramm, der Grösseneinteilung des Musters der untersuchten Population.

a) Relative Tibialänge (T)

Es zeigt sich, dass dieses Merkmal innerhalb einer Population verhältnis-
mässig zu variabel ist (Abb. 3; *siehe Berger, 1966*). Bei den *Jugendeinzel-*
wesen wächst Tibia relativ schneller als der Körper. Ähnlich ist es möglich,
auch die Veränderungen dieses Indexes bei den Männchen zu bewerten,
obwohl die Situation hier nicht so eindeutig ist. Bei den Weibchen scheint es,
dass Tibia bei den niedrigeren Grössenklassen relativ länger wird, später
aber, während des Körperwachstums wird sie kürzer. Vom Variabilitätsgrad
dieses Merkmales innerhalb einer Population zeugt auch eine Variations-
spannung: 1,86–2,25 bei Juv., 1,89–2,35 bei ♂♂ und 1,82–2,44 bei ♀♀.
Es zeicht sich, dass ein auf Grund der mittelmässigen absoluten Werte
konstruiertes Schaubild zur Illustration der Wachsenveränderungen un-
passend ist, weil es in hohem Masse die wirkliche Variabilität verschleiert
(Abb. 4).

b) Verhältnis Femur zu Tibia (F:T)

Das Verhältnis von diesen zwei Grössen wird oft in den taxonomischen
Studien angeführt. Schon bei einem fluchtigen Blick auf die Abb. 5 ist es klar,
dass der Wert dieses Indexes während des Wachstums eines Einzelwesens kon-
stant ist und dass gegenseitige Beziehung F:T in allen Wachsenkategorien also
unveränderlich bleibt; es schwankt nur unscheinbar um den Wert 1,00. Die

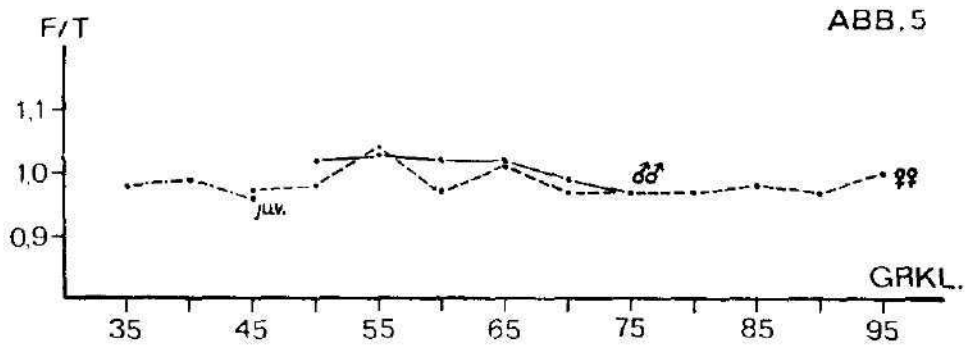
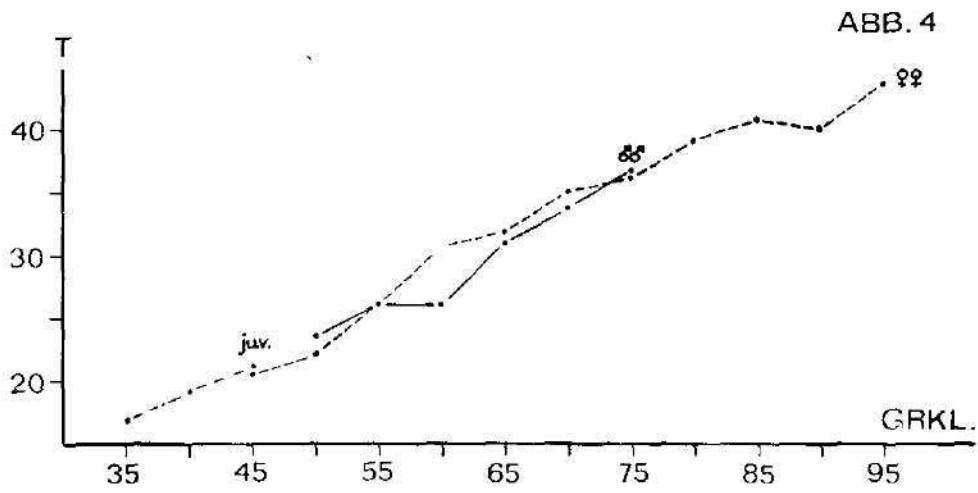
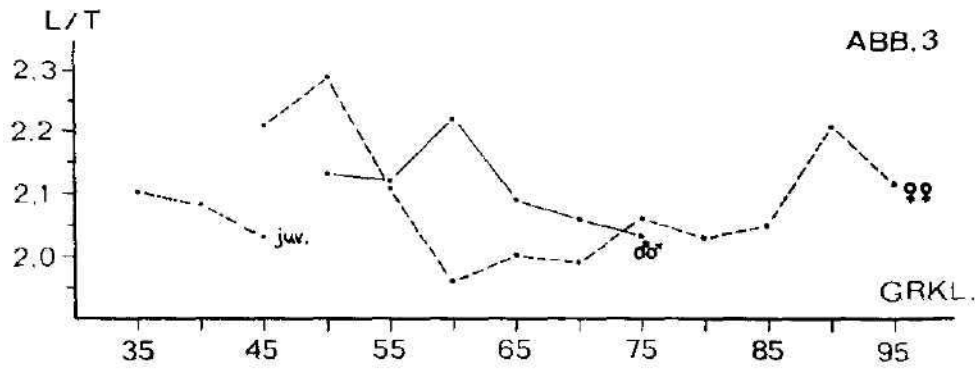


Abb. 3. Die Veränderungen der relativen Tibiallänge während des Wachstums. Vertikale – relative Tibiallänge, Horizontale – Grossenklassen.
 Abb. 4. Die Veränderungen der Tibiallänge während des Wachstums. Das Schaubild wurde auf

Variationsbreite ist bei Juv. 0,88—1,07, bei Weib. 0,89—1,09 und bei Männ. 0,93—1,12.

c) Relative Länge der vorderen Gliedmassen (PA)

Die relative Länge der vorderen Gliedmassen ist wieder ein zu variables Merkmal und man kann nur schwer die vorherrschende Wachstentendenz feststellen. Es ist möglich mit einer bestimmten Wahrscheinlichkeit zu konstantieren, dass sie bei den Männchen die mässig aufsteigende Tendenz hat; bei den Weibchen sinkt sie zuerst und steigt später langsam. Die vorderen Gliedmassen wachsen also bei den kleineren Weibchen relativ schneller; nach der Erreichung der Körperlänge von 60 mm kommt ein Bruch und bei den meisten Einzelwesen bleibt die Wachstumsgeschwindigkeit der vorderen Gliedmassen hinter dem Wachsen des ganzen Körpers zurück. Wenn wird das Tibiawachsen (siehe höher) wenigstens für ein ungefähr repräsentationsfähiges Wachsen der ganzen hinteren Gliedmassen halten, ist es interessant, dass wir die prinzipielle Veränderungen der Wachstentendenz auch bei der Grössenklasse von 60 mm konstantieren können. Die Variationsbreite ist bei den Juv. 2,10—3,18, bei den Weibch. 2,16—2,57 und bei den Männ. 2,13—2,59.

d) Relative Kopfbreite (LtC)

Bei den Jugendindividuen und Männchen sind die Veränderungen dieses Indexes den meisten übrigen hier angeführten Merkmalen gegenüber sehr eindeutig (Abb. 7). Aus ihnen geht hervor, dass der Kopf während des Wachstums relativ enger wird; das Verhältnis des Kopfwachsens in die Breite zum Wachsen der Körperlänge ändert sich aber fließend. Bei den Weibchen wird der Kopf den allen Voraussetzungen in den niedrigsten Grössenklassen gegenüber gelind breiter, nach der Erreichung der Körperlänge von 60 bis 65 mm kommt ein Bruch, und während des weiteren Wachstums wird der Kopf wieder relativ enger. Die Grösse um 60 mm weist also bei den Weibchen wieder einen Wachsenbruch auf, ähnlich wie bei den Merkmalen T und PA. Die Variationsspannung ist 2,85—3,35 bei Juv., 3,14—3,79 bei den Männ. und 3,17—3,81 bei den Weibchen.

e) Relative Entfernung des Auges vom Vorderkörperperrand (DRO)

Nach der Abb. 8 ist es klar, dass bei den Weibchen und auch bei den Männchen dieser Index während des Wachstums eines Einzelwesens verhältnismässig ständig ist und dass es sich hier um ein isometrisches Wachsen handelt. Bei näherer Beurteilung der Weibchenkurve kommen wir aber zum Schluss, dass die relative Geschwindigkeit des Wachstums sich vom vorderen Kopfteil ändert: bei den kleinsten Weibchen (bis 50 mm) wird sie während des Wachstums relativ kürzer (ähnlich wie bei den Jugendexemplaren), in einem Intervall von 50 bis 60 mm wächst dieser Teil schneller und bei den grösseren Einzelwesen (über 60 mm) bleibt sie gelind zurück. Im Vergleich mit den ausdrucksvollen Veränderungen der relativen Wachstumsgeschwindigkeit von manchen anderen Merkmalen sind diese Veränderungen

Grund der absoluten Werte konstruiert. Vertikale — absolute Tibialänge, Horizontale — Grössenklassen.

Abb. 5. Die Veränderungen des Verhältnisses Tibia zu Femur während des Wachstums. Vertikale — Index Femur zu Tibia, Horizontale — Grössenklassen.

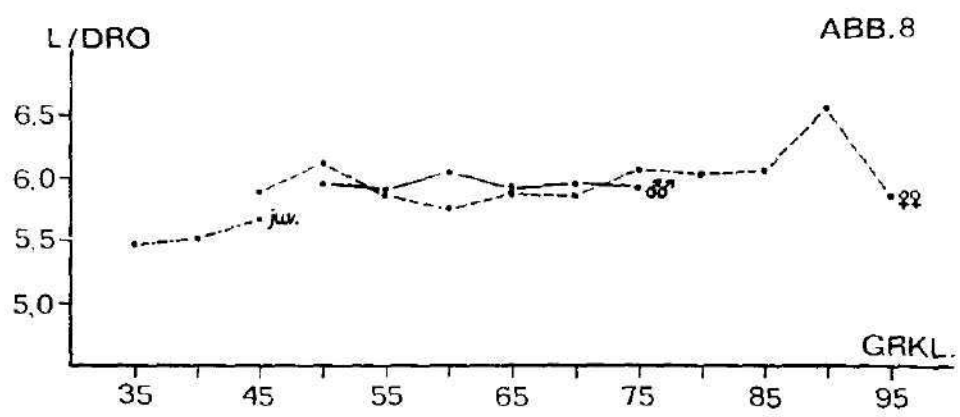
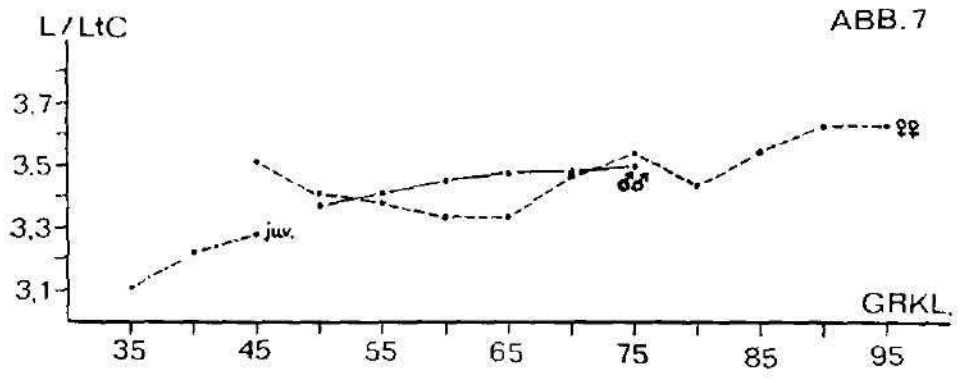
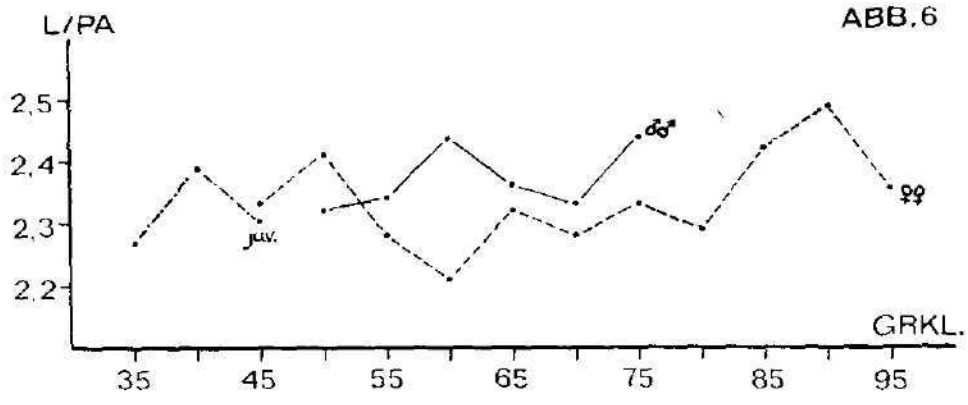


Abb. 6. Die Veränderungen der relativen Länge der vorderen Gliedmassen während des Wachstums. Vertikale — relative Länge der vorderen Gliedmassen, Horizontale — Grossenklassen.

bei den Weibchen aber nicht erheblich, obwohl man sie bei der Bewertung nicht unterlassen kann. Variationsamplitude: 4,84—5,83 bei Juv., 5,57—6,71 bei Männ. und 5,42—6,81 bei Weib.

f) Verhältnis von der Augenlidbreite und Gegenentfernung beider Augenlider (LtP/SpP)

Diese beiden Indexe sind untersucht worden, weil sie (nicht nur bei den Wasserfröschen) von manchen Autoren für die Schlüsselbestimmungsmerkmale gehalten werden und gleichzeitig, gemeinsam mit dem vorgehendem Merkmal LtC, über die Proportionalitätsveränderungen des Kopfteles während des Wachsens informieren.

Bei den Männchen und Weibchen ist eine ausdrückvolle Variabilität von diesem Merkmal festgestellt worden und aus dem unregelmässigen Verlauf beider Wachsenkurven ist es unmöglich, auf jede beliebige Wachstendenz zu schliessen (Abb. 9). Nur die Kurve für die Weibchen hat in den Mittelgrössen-kategorien einen verhältnismässig ruhigeren Verlauf und das ist von der grösseren Frequenz der Fälle verursacht. Bei den Jugendeinzelwesen ist es möglich aus dem Verlauf der Veränderungen von diesem Index abzuleiten, dass der interpalpebrale Raum im Verhältnis zur Lidbreite relativ zuerst schneller, später langsamer kleiner wird. Die Variationsbreite ist 1,17 bis 1,94 bei Juv., 1,37—2,85 bei Männ. und 1,13—2,48 bei Weib.

g) Verhältnis von dem Augen- und Trommelfelldurchschnitt (LO/LTym)

Die verhältnismässig bedeutenden Unterschiede unter den einzelnen Grössen-kategorien machen sich durch den unregelmässigen Verlauf der Wachsenkurve bemerkbar (Abb. 10). Mit einem gewissen Grad der Wahrscheinlichkeit ist es möglich zu konstatieren, dass es sich augenscheinlich bei den Männchen und den Weibchen um eine Wachsenisometrie handelt. Bei den juvenilen Exemplaren wird der Trommelfelldurchschnitt sichtlich um etwas schneller als der Augendurchschnitt grösser. Die Variationsbreite ist 1,08—1,45 bei Juv., 1,05—1,50 bei Mann. und 1,03—1,49 bei Weib.

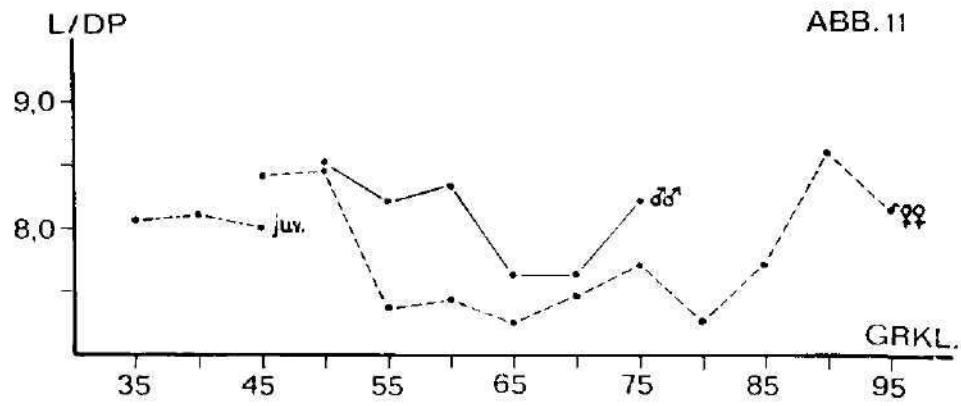
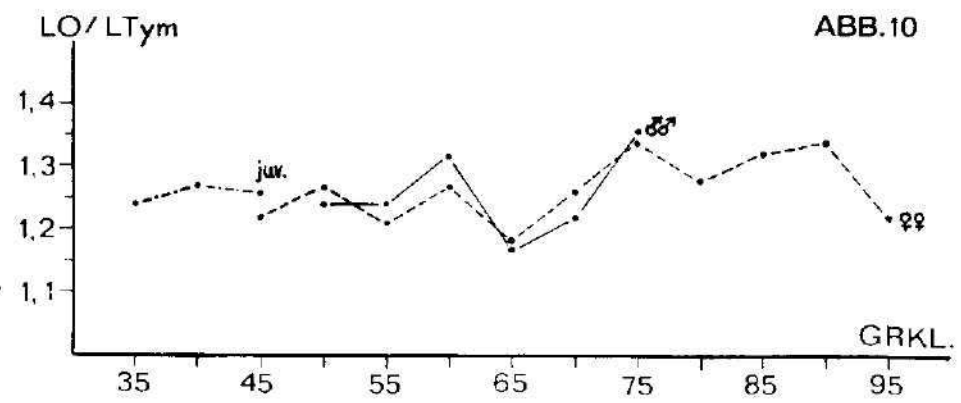
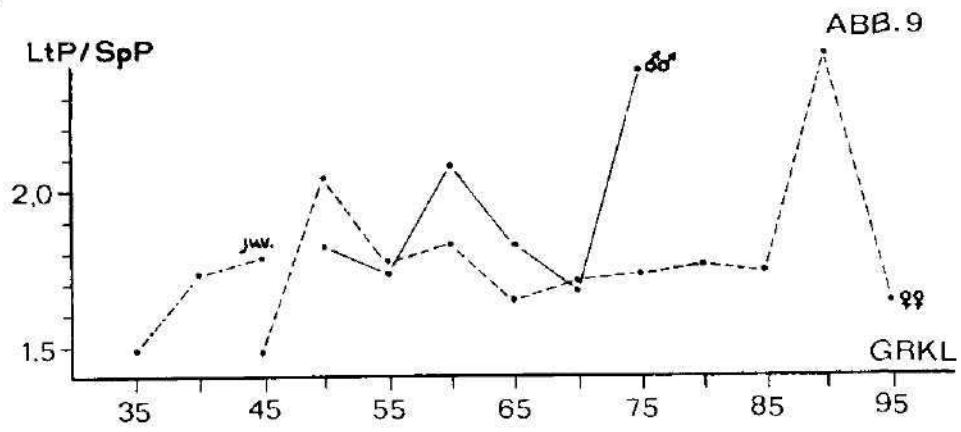
h) Relative Länge der ersten Zehe (DP)

Die relative Länge der ersten Zehe L/DP, die relative Grösse des inneren Fersenhockers L/CInt, das gegenseitige Verhältnis von beiden diesen Merkmalen (DP/CInt) und das Verhältnis vom inneren Fersenhöckers zur Tibia (T/CInt) sind von wichtigsten Determinationsmerkmalen, nach den die Art-sangehörigkeit bei *Rana esculenta*, *R. ridibunda* und *R. lessonae* festgestellt wird. Die Feststellung von Veränderungen dieser Indexe während des Wachsens eines Einzelwesens ist deshalb sehr wichtig.

Während die durchschnittlichen Werte des Indexes L/DP bei den Jugendeinzelwesen sich in allen drei Grössen-kategorien voneinander nur sehr unbedeutend unterscheiden, und deswegen man voraussetzen kann, dass die Wachsengeschwindigkeit der ersten Zehe im Verhältnis zum Wachsen des

Abb. 7. Die Veränderungen der relativen Kopfbreite während des Wachstums. Vertikale — relative Kopfbreite, Horizontale — Grössenklassen.

Abb. 8. Die Veränderungen der relativen Entfernung zwischen dem Auge und dem vorderen Kopfrand während des Wachstums. Vertikale — relative Entfernung zwischen dem Auge und dem vorderen Kopfrand, Horizontale — Grössenklassen.



ganzen Körpers steht (Abb. 11), bei den Männchen und den Weibchen ist die Situation weit komplizierter. Nach der Kurve für die Männchen ist es möglich zu deduzieren, dass die erste Zehe bei ihnen zuerst schneller als der ganze Körper wächst. Nach der Erreichung der Körperlänge von 65–70 mm wird das relative Wachsen aber langsamer und in den höchsten Grössenklassen bleibt sie hinter der Körperlänge zurück. Die gleiche Situation gibt es auch bei den Weibchen, wo ein ähnlicher Wachsenbruch nach der Erreichung der Körperlänge von 65 mm erscheint. Die Variationsspannung ist 7,02–9,85 bei Juv., 6,55–9,39 bei Männ. und 6,53–9,18 bei Weib.

i) Relative Grösse des inneren Fersenhöckers (CInt)

Im allgemeinen ist es möglich zu sagen, dass das innere Fersenhöcker bei allen drei Mustern während des Körperwachstums relativ kleiner wird (Abb. 12). Am besten ist es wieder bei den Jugendeinzelwesen bemerkbar; der Verlauf der übrigen zwei Kurven wird ziemlich durch die Innerpopulationsvariabilität kompliziert, die Wachsentscheidung ist aber evident. Die Variabilitätsstufe wird hier gewiss auch durch die Wirklichkeit beeinflusst, dass es sich um ein Verhältnis von dem kleinsten und dem grössten gemessenen Werte handelt (siehe Berger, 1966). Die Variationsspannung ist 13,38 bis 19,77 bei Juv., 12,80–19,88 bei Männ. und 13,46–19,28 (30,21) bei Weib. Der in der Klammer angeführte extreme Wert bei Weibchen gehört dem Exemplar, von dem wir schon im Abschnitt Material und Methodik gesprochen haben.

j) Verhältnis vom inneren Fersenhöcker zur Länge der ersten Zehe (DP/CInt)

Nach dem Verlauf der Kurven (Abb. 13) ist es möglich zu konstatieren, dass das innere Fersenhöcker bei den Jugendeinzelwesen im Verhältnis zur Länge der ersten Zehe während des Wachstums relativ kleiner wird. Bei den Männchen und den Weibchen gibt es zu Beginn eine ähnliche Wachsentscheidung, bei beiden Geschlechtern entsteht aber eine Gegentendenz, d. h. — das innere Fersenhöcker wächst relativ schneller als die erste Zehe. Die Variationsamplitude ist 1,61–2,57 bei Juv., 1,46–2,70 bei Männ. und 1,56–2,51 (4,10) bei Weib. Die zweite von den angeführten extremen Werten bei den Weibchen gehört wieder dem Exemplar, das ich im Abschnitt Material und Methodik berührt habe.

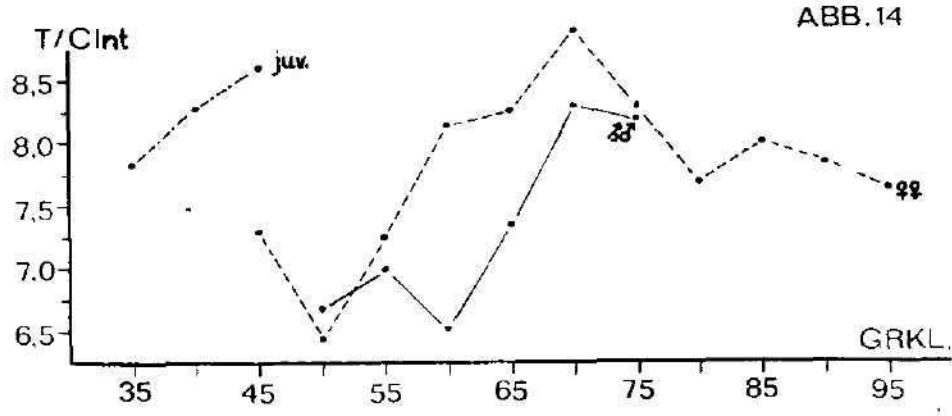
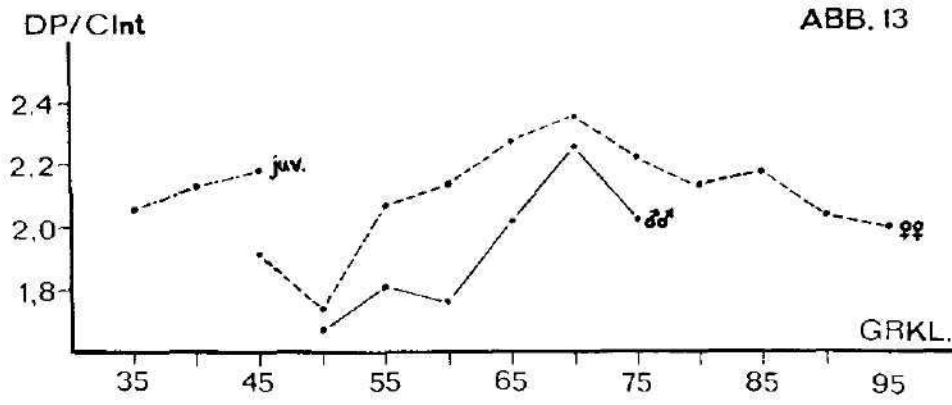
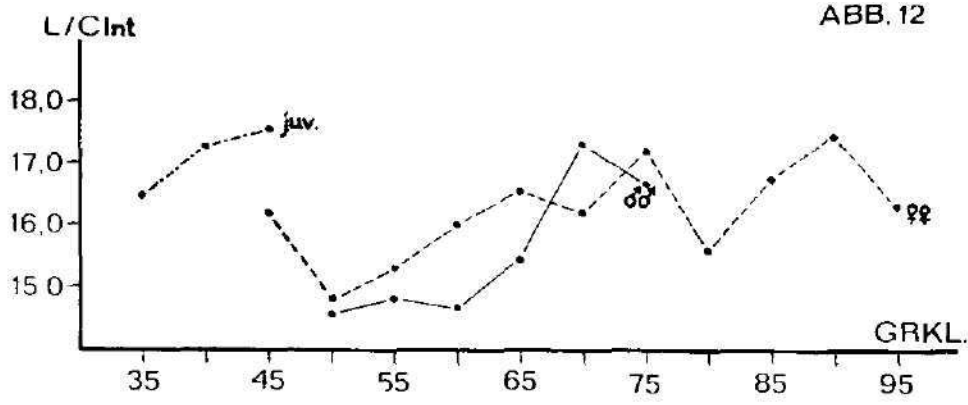
k) Verhältnis vom inneren Fersenhöcker zur Tibiallänge (T/CInt)

Bei der Bewertung dieses Indexes entsteht dieselbe Situation wie im vorstehenden Fall. Auch hier bleibt das Fersenhöcker mit seinem Wachsen hinter Tibia relativ zurück und auch bei den Männchen und auch bei den Weibchen kommt ein Wachsenbruch bei der Erreichung der ungefähren Körperlänge von 70 mm. Die Kurven auf der Abb. 13 und 14 haben beachtenswert viele

Abb. 9. Die Veränderungen des Verhältnisses von der Entfernung beider Augenlider zur Lidbreite während des Wachstums. Vertikale — Index Augenlidbreite zur gegenseitigen Entfernung der Augenlider, Horizontale — Grössenklassen.

Abb. 10. Die Veränderungen des Verhältnisses vom Trommelfells zum Augendurchschnitt während des Wachstums. Vertikale — Index Augendurchschnitt zum Trommelfellsdurchschnitt, Horizontale — Grössenklassen.

Abb. 11. Die Veränderungen der relativen Länge der ersten Zehe während des Wachstums. Vertikale — relative Länge der ersten Zehe, Horizontale — Grössenklassen.



Ähnlichkeiten miteinander, und was die Wachsntendenzen betrifft, kann man fast dasselbe, wie im Falle des Indexes DP/CInt, konstatieren. Die Variationsspannung ist 6,61—9,90 bei Juv., 5,88—9,36 bei Männ. und 6,12 bis 9,47 (16,52) bei Weib. Der zweite extreme Wert bei den Weibchen gehört wieder dem vorerwähnten Exemplar (siehe Material und Methodik).

DISKUSSION

Aus den angeführte Ergebnissen geht hervor, dass man die Wachsenveränderungen fast bei allen beurteilten Werten eindeutig nur beim Muster von Jugendeinzelwesen interpretieren kann. Es bezieht sich auf die Merkmale L/T, L/LtC, L/DRÖ, LtP/SpP, L/CInt, DP/CInt, T/CInt. Eine streitigere Situation gibt es bei den Merkmalen F/T, LO/LTym und L/DP, wo sich die Wachsntendenz, obwohl nur in unerheblichen Masse, ändert. Nur beim Merkmal L/PA ist es möglich wirklich einen ausdrückvollen Wachsenbruch zu konstatieren, den wir aber nicht der Variabilität beimessen können. Den verhältnismässig ruhigen Verlauf der meisten Wachsenkurven bei diesem Muster von den Jugendeinzelwesen ist es möglich der bisher ausdruckslosen Proportionalvariabilität in den kleinsten Grössenklassen beizumessen (man kann voraussetzen, dass die kleinsten ergriffenen Exemplare in ganzem Populationsmuster die Metamorphose im Sommer des vorigen Jahres durchgemacht haben und dass man die kleinste Grössenklassen wenigstens im allgemeinen mit der niedrigsten Alterskategorie identifizieren kann). Während des Weiterwachsens wird jedes Einzelwesen den verschiedenen Modifikationsfaktoren (z. B. Nahrung, Temperatur usw.) ausgesetzt, und die Folge davon ist eine ungleichartige Stufe von der Interpopulationsvariabilität. Diese Variabilität kann bei verschiedenen Merkmalen ungleich ausdrückvoll sein und zwar danach, wie jedes Merkmal den vorerwähnten Modifikationsfaktoren untersteht.

Schon eingangs habe ich erwähnt, dass das Wachsenproblem oft von verschiedenen Gesichtspunkten gelöst worden ist. Wenn ich meine Ergebnisse, die sich auf die Proportionalitätsveränderungen des Wasserfrosches beziehen, konfrontieren will, kann ich mich nur an Lác (1959) wenden; es gibt hier aber ein bestimmter Mangel in seiner Arbeit werden beide Geschlechter zusammenbetrachtet, was nach meinen Ergebnissen in manchen Fällen zu entstellten Schlüssen führen kann. Dieser Verfasser hat auch seine Schlussfolgerungen beträchtlich generalisiert und diese Wirklichkeit erschwert wesentlich einen Vergleich. Láces Angaben konstatieren einen auffallenden Bruch von der Wachsengeschwindigkeit bei *Rana esculenta* in einem Intervall von 55 bis 60 mm (bei meinem Material ist diese Erscheinung vor allem auf Abb. 13 und 14 auffallend, aber bei der Grössenklasse von 70 mm). Dieser Bruch wird durch die Erreichung der geschlechtlichen Reife erklärt. Aus weiteren Schlüssen dieses Autors geht hervor, dass die Werte des Indexes T/CInt bei

- Abb. 12. Die Veränderungen der relativen Länge des inneren Fersenhockers während des Wachstums. Vertikale — relative Länge des inneren Fersenhockers, Horizontale — Grössenklassen.
 Abb. 13. Die Veränderungen des Verhältnisses von der Länge des inneren Fersenhockers zur Länge der ersten Zehe während des Wachstums. Vertikale — Index Länge der ersten Zehe zur Länge des inneren Fersenhockers, Horizontale — Grössenklassen.
 Abb. 14. Die Veränderungen des Verhältnisses von der Länge des inneren Fersenhockers zur Tibialänge während des Wachstums. Vertikale — Index Tibialänge zur Länge des inneren Fersenhockers, Horizontale — Grössenklassen.

den Jugendeinzelwesen niedriger sind. Sie steigen während des weiteren Wachsens. Nach meinen Ergebnissen gilt es ungefähr bis zur Grössengränze von 70 mm; in den grösseren Kategorien hat der Index im Gegenteil eine niedersinkende Tendenz. Bei der Beurteilung des Indexes L/T konstantiert der besagte Verfasser eine fallende Tendenz während des Wachsens. Im Vergleich mit meinen Ergebnissen gilt es wieder nur zum Teil, weil dieser Index bei den Weibchen nach der Erreichung der Körperlänge ungefähr von 60 mm eine niedersteigende Tendenz hat. Bei den Kopfmassen ist es möglich nur die relative Kopfbreite zu vergleichen (Index L/LtC): nach Lác wird die relative Kopfbreite während des Wachsens kleiner, was im Männchen- und Jugendeinzelwesenfall auch meinen Schlüssen entspricht. Bei den Weibchen ist es möglich diese Behauptung nur auf die grösseren Grössenkategorien (über 65 mm) zu beziehen. Gesamt ist es möglich zu sagen, dass Lács Angaben im allgemeinen meinen Ergebnissen entsprechen; durch eine vereinfachte Interpretation werden aber die wirklichen Verhältnisse von diesem Verfasser zum Teil verzerrt.

Eine grössere Aufmerksamkeit ist auf die Veränderungen von Körperproportionen bei *Rana ridibunda* gerichtet worden. Terentjev (1962) hat z. B. festgestellt, dass der Index D/CInt während des Wachsens eines Einzelwesens heftig sinkt, später, in den grösseren Grössenklassen, gleichen sich die Wachsendgeschwindigkeiten ungefähr aus und der Index schwankt unerheblich um den Wert von 3,00. Das zeigte auf eine völlig entgegengesetzte Wachsentscheidung, als es bei *R. esculenta* (siehe Abb. 12) erhoben worden ist. Ausserdem wurde es von diesem Verfasser festgestellt, dass die relative Geschwindigkeit des Wachsens sich von verschiedenen Körperproportionen bei *R. ridibunda* mit einer Abhängigkeit von der geographischen Lage ausdrucksvoll (z. B. Merkmal L/CInt) unterscheiden kann. Falls wir Terentjews Schlüsse auch auf andere Arten von Fröschen beziehen, geht daraus hervor, dass alle Populationen theoretisch voneinander im Wachsen der Körperproportionen abweichen könnten, und zwar nicht nur in den Einzelheiten vom Kurvenverlauf, sondern auch in der grundsätzlichen Wachsentscheidung. Es geht daraus hervor, dass es notwendig sein wird, die Wachsenverhältnisse in gegenseitig fernliegenden Populationen gründlich zu bearbeiten, um diese Annahme zu bestätigen oder zu widerlegen.

Manche Autoren (Berger, 1966; Günther, 1968; Kauri, 1959 u. a.) haben das Wachsen von einzelnen Körperproportionen bewertet, insbesondere die sehr variablen Merkmale, auf einer Grundlage der empirisch gewonnenen absoluten Werte. Die Anwendung dieser Methode leitet zwar zu einer Elimination der störenden Einflüsse, mit den die Variabilität in den Verlauf von Wachsenkurven eingreift, doch unterrichtet sie auf keine Weise über die relative Wachsendgeschwindigkeit (siehe Abb. 3 und 4 — Kurve für die Weibchen).

ZUSAMMENFASSUNG

1. In der Arbeit sind die 109 Exemplare (44 ♀♀, 37 ♂♂ und 23 Juv.) von *Rana esculenta* aus einer Population „Novoveský rybník“ (Týniště nad Orlicí — nordöstliches Böhmen) für das Messen angewandt worden.

2. Bei jedem Einzelwesen sind 12 Merkmale gemessen worden. Die Ergebnisse sind auf den Veränderungen von 11 verhältnismässigen Werten (Indizes) in einzelnen Grössenkategorien begründet.

3. Ein isometrisches Wachsen des Körperteils im Verhältnis zur Länge des ganzen Körpers ist beim Merkmal $L/DR0$ — Männchen und F/T — Weibchen festgestellt. In beiden Fällen ist es möglich diese Merkmale als Charakteristiken der ganzen Population zu benutzen.

4. Bei den übrigen Merkmalen sind die Wachsengeschwindigkeiten des untersuchten Körperteils und des ganzen Körpers voneinander abweichend, meistens bei der Erreichung der Körpergrösse von 60—70 mm. In diesen Fällen ist es möglich bei der Beurteilung der Zwischenpopulationsvariabilität nur die gegenseitig entsprechend Grössenkatégorien zu vergleichen.

5. Benützung der absoluten Werte bei der Konstruktion der in dieser Arbeit angewandten Wachsenkurven ist in einem Falle als ein Nachteil demonstriert worden. Diese Kurven bieten keinesfalls einen Überblick über die wirklichen Veränderungen der Körperproportionalität während des Wachsens.

6. Die auf den Wachsenveränderungen der Körperproportionalität begründeten Arts-Übereinstimmung und Unterschieden zwischen *Rana esculenta* und *Rana ridibunda* sind unter Berücksichtigung des Mangels an älteren Angaben nur im allgemeinen diskutiert worden.

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**BIOLOGY OF THE REPRODUCTION OF THE COMMON HAMSTER,
CRICETUS CRICETUS (L.)**

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Abstract: The biology of the Common hamster was studied using 15 animals trapped in Moravia and Bohemia, and 28 litters of the young bred from them (206 specimens). The methods of and experiences with hamster rearing in the laboratory are described. We studied the period of reproduction, of attaining sexual maturity, the duration of pregnancy, the number of litters, the size of litters, the sex ratio in the newborn and several other problems concerned with the biology and ethology of the Common hamster.

INTRODUCTION

Although the first comprehensive monograph on *Cricetus cricetus* (Linnaeus, 1758) dates back to the 18th century (Sulzer, 1774), our present knowledge of its biology is still incomplete. A review of the older literature on this subject was given by Petzsch (1936); more recent data on the biology of reproduction of this species were published in papers by Petzsch (1943, 1968), Eibl-Eibesfeldt (1953), Saint Girons et al. (1968). It is surprising how little information is available on the period of reproduction, on the number of the young in the litter, on the number of litters within one season, on the attainment of sexual maturity etc. Except for the limited records on the number of the young, exact information on the reproduction of the hamster in the field is still scarce.

We have attempted to contribute to the solution of these problems by studying animals reared in the laboratory. In view of the fact that recently the hamster has been frequently used in physiological research, numerous attempts have been made to breed it in the laboratory. The results, however, have often been unsatisfactory and therefore a description of our rearing experience may be helpful.

MATERIAL AND METHODS

Our breeding experiments with the Common hamster were started with 15 animals (6 ♂♂ and 9 ♀♀), trapped in 1968 in various localities of Moravia and Bohemia. From these animals and from the young of generation F₁ and F₂ born in captivity during the years 1968—1971, we obtained a total of 28 litters (206 specimens). Two additional litters of the young were trapped in August 1968 and 1970 in the field (Zábřeh, Moravia).

The adult animals were housed in cages measuring 60 × 50 × 40 cm; during hibernation several of these animals were placed in smaller cages of a similar construction measuring 35 × 30 × 25 cm. The walls of the cages were made of glass, the lid of metal netting. The floor was made either of tin or glass and was covered with a layer of peat (3—5 cm thick).

During the period of reproduction the cages of the females were fitted with wooden boxes with a detachable lid. The inner size of these boxes was 28 × 20 × 13 cm, the front wall having an opening (8 × 7 cm) at one of the bottom corners. The hamsters lined these boxes with hay and they served for rearing the young. The remaining animals made their own nests with hay.

During the active period (from the beginning of April to the end of October) the hamsters were kept in a room where the temperature ranged from 18°–25°C, relative air humidity from 65–70%. From the beginning of November till the end of March, the hamsters were kept in a room with a relative air humidity from 85–95%. In November the temperature was 6–10°C, in December, January, February and March it ranged from 2–6°C, in the middle of April it was 13°C. Artificial lighting during summer was consistent with the rhythm in nature, the winter quarters were lighted by a window in the ceiling.

During the period of activity (i.e., except hibernation) the hamsters were fed once a day in the late afternoon or evening hours. Their diet consisted mainly of dandelion leaves (*Taraxacum officinale*) with an addition of various plantain (*Plantago* sp.) leaves, sugar beet, kohlrabi and an occasional cabbage leaf. In the summer and above all in the spring months they were fed with carrots and wheat moderately germinated, in the autumn also with fallen apples. The animal component in their diet (served mainly in the spring) consisted of cockroaches (*Periplaneta americana*), crickets (*Gryllus domesticus*), larvae and pupae of meal worms (*Tenebrio molitor*), an occasional freshly killed frog (*Rana* sp.) and field mouse (*Apodemus sylvaticus*).

In the spring an oil solution of vitamin E "Erevit" (Slovakofarma n. p. Hlohovec) was added to their diet once a week.

In the winter the hamsters were fed once every second day. They received moistened wheat and oats, a thick porridge of Larsen's diet, carrots, potatoes and sugar beet. Of these food items they stored approximately 0.5–1 kg for winter stores.

Water was never given and water levels in the body were kept up by the water contained in the food. Only the females were given milk several days before and after parturition.

RESULTS AND DISCUSSION

Rearing of the Common hamster in the laboratory

We know of several successful attempts at rearing the Common hamster in captivity: Petzsch (1943, 1968), Hediger (1944), Eibl-Eibesfeldt (1953), Saint Girons et al. (1968). Various authors (Sulzer 1774; Petzsch 1936, 1952b; Eöry, 1959) tried to obtain the young from pregnant females captured in the field, but the results were unsatisfactory because the females always killed their young sooner or later. Successful rearing depends evidently on the fact that the females have, first to get used to life in captivity and to the presence of man before giving birth to the young.

Since the hamster is used to a solitary mode of life, each animal has to have its own cage. Outside the rutting period, adult hamsters attack each other immediately and the weaker animal is killed frequently because there is no escape. Exceptions are rare.

From April till August, the males were paired with the females in the female cages for 2–3 days and this was repeated until copulation occurred. The best hours for attempting mating were from 8–10 p. m. Usually we tried several combinations of partners during one evening. The nesting boxes were removed from the female cages.

When the male is with the female, their behaviour is to be watched. The situation may often develop that the male approaches the female and starts to sniff; mostly the female tries to escape and the male chases her. Although the behaviour of the hamsters shows considerable variability evidently due to individual character and to the influence of the varied factors of the external environment, two basic situations can be distinguished:

1. If the female squeaks in sharp, high tones, runs wildly and tries to jump out of the cage, the male has to be caught immediately and taken away,

otherwise the female will soon be caught by the male and a fight will start with ferocious biting often causing wounds several cm long. These are generally not too dangerous and heal up quickly, but sometimes, they may be fatal.

2. If the female is on heat, she starts to run in circles with the male close behind her. If contact is interrupted, the female stops running and waits for the male to approach her, or approaches him herself, turns round close to him and again escapes. Both animals let off a typical, snuffle-like noise (see "oestrus of the females, mating") and copulate shortly after.

The male is taken away after repeated copulation but it may be quite safe to leave both animals together for several days. If the female is on heat, she is immediately ready to copulate with several other males in succession.

The claws of the hamsters grow very long when kept for a prolonged period in captivity. Therefore, the claws of the females have to be clipped to the normal length before parturition to avoid injuring the newborn, because these injuries may be sometimes fatal. For this purpose the animals are narcotized with ether to which they respond quite satisfactorily.

The nesting boxes have been found very convenient not only for rearing the young, but also for taking them away from the females. To be able to measure and weigh almost daily the young, we proceeded in the following way: the detachable lid of the box was removed and placed at an angle against the side of the nesting box with the entrance hole in order to provide a shady and partly closed space. The female almost immediately left the box and got in to the space between the box and the lid. At any other procedure the females started to hide themselves under the hay and often injured the young with their claws. The box with the young was removed from the cage as soon as the female had left it, the young were measured and then returned in the box to the cage. In this way the disturbance of the animals was reduced to a minimum and losses due to a daily destruction of the nest were avoided. In addition, it is most difficult to remove the female from the nest by force.

An important component of the hamster's diet, particularly of the young, were leaves of *Taraxacum officinale*. The hamsters preferred these to any other food and the young fed on them from the age of 6–7 days.

The young were kept with the female up to an age of 30–40 days. At an age of approximately 30 days the young started to molest the female by their continuous playing around and fighting, and frequently threatening to exhaust their mother by their constant demand for sucking. In one instance, a mother with 34 day-old young was found dead in her cage. Examination of the extremely cachectic animal disclosed that the death cause was a sepsis due to teats torn to shreds by the young through consistent demands for sucking. In order to avoid fatalities the young were removed from the mother at the age of 30 days.

The young were kept together in one cage mostly up to the beginning of September, because at this time they started to attack seriously one another. If these fights started at an earlier time, the initiator, mostly a male, was removed from the cage. It seemed not advisable to leave the animals together in one cage until the late autumn. The hamster evidently requires his own nest for hibernation and this accounts for the hard fights and attacks to which the weaker animal often succumbs. If one of the animals fell into winter lethargy, it was eaten by the rest.

Breeding season

According to information in the literature, the mating of the Common hamster in the field starts in the second half of April (Petzsch 1952a; Stroganova, 1954; Popov, 1960), the first litters appear at the beginning

Table 1. Duration of pregnancy and litter size

Litter reference	Female reference	Date of mating	Birth	Duration of pregnancy (in days)	Number of young			Total
					♂♂	♀♀	?	
1	1	—	29. 6. 1968	—	3	6	1	10
2	2	14. 6. 1968	1. 7. 1968	17	3	4	—	7
3	1	14. 7. 1968	2. 8. 1968	18,5	6	1	—	7
4	1	12. 8. 1968	30. 8. 1968	18	5	4	—	9
5	II	15. 4. 1969	2. 5. 1969	17	2	6	—	8
6	C(1)	30. 4. 1969	17. 5. 1969	17	4	4	2	10
7	XII	10. 5. 1969	27. 5. 1969	17	3	4	2	9
8	C(2)	11. 5. 1969	28. 5. 1969	17	3	2	—	5
9	1	18. 5. 1969	4. 6. 1969	17	4	4	1	9
10	C(1)	18. 5. 1969	12. 6. 1969	25	3	4	—	7
11	X'(4)	15. 6. 1969	2. 7. 1969	17	3	2	2	7
12	VI	15. 6. 1969	2. 7. 1969	17	3	4	—	7
13	IX	15. 6. 1969	2. 7. 1969	17	4	5	1	10
14	X'(4)	4. 7. 1969	10. 8. 1969	37	—	—	—	?
15	C(1)	11. 7. 1969	8. 8. 1969	28	3	5	—	8
16	IV	1. 8. 1969	19. 8. 1969	17,5	2	4	—	6
A	D(2)	—	26. 5. 1969	—	3	7	—	10
B	5(2)	29. 5. 1969	15. 6. 1969	17	2	3	—	5
C	XIV	30. 5. 1969	16. 6. 1969	17	—	8	—	8
D	6(I)	3. 6. 1969	20. 6. 1969	17	2	5	—	7
E	I'(1)	12. 8. 1969	29. 6. 1969	17	4	4	—	8
F	D(2)	28. 5. 1969	29. 6. 1969	32	5	4	—	9
17	I'(1)	18. 6. 1970	5. 7. 1970	17	4	3	—	7
18	A(12)	—	2. 7. 1970	—	4	1	—	5
19	IV	20. 6. 1970	7. 7. 1970	17	7	3	—	10
20	K(11)	11. 7. 1970	28. 7. 1970	17	5	4	—	9
21	IV	9. 7. 1970	14. 8. 1970	36	1	4	—	5
22	I'(20)	9. 6. 1971	26. 6. 1971	17	4	—	—	4
Σ					92	105	9	206

of May. Studies on hamster burrows opened up in the autumn disclosed that reproduction continues until the end of August (Dukelskaja and Stepanova, 1932; Petzsch, 1936).

Although this information was obtained from very different geographical areas (Germany, the Moscow-, Saratov- and Kujbyšev areas of the U.S.S.R.) it is consistent with our findings in the laboratory-bred animals. The first successful mating occurred on April 15, the last on August 12. Before, during and after this period we recorded a number of unfertile copulations. First parturition occurred on May 2, the last on August 30.

This indicates that the period of reproducing in our stock lasted 4 months, i.e., from the beginning of May till the end of August. Exact data on copulation and parturition are given in Table 1.

Attaining sexual maturity

No exact data are available in the literature about the time when the Common hamster attains sexual maturity. Saint Girons et al. (1968) inferred that the reproduction season of this animal is too short to allow the female born in the current year to attain a state of body development, which could make it fit for reproduction, normal lactation after parturition and to allow it to accumulate sufficient fat reserves before the beginning of hibernation. By contrast Sulzer (1774) and Petzsch (1936, 1952a) suggested that reproduction of young hamsters is already possible before their first hibernation. Petzsch (1952a) writes "Die Weibchen des ersten Jahreswurfes, der etwa zwischen dem 20. Mai bis 10. Juni geboren wird, können bereits wieder gegen Ende August desselben Jahres ihren ersten Wurf bringen". However, he did not confirm this statement by concrete data. Also Popov (1960) believes that young females can reproduce at as early an age as 3 months, if conditions are satisfactory, the males, however, mature at a somewhat later period.

In our laboratory breed we observed in several males a scrotal position of the testes at the age of 23–25 days. At the age of 50–60 days, the testes of almost all males were in the scrotal position. At this time the males frequently tried to copulate with females from the same litter, but these remained entirely indifferent to the approaches. In one instance only we tried to pair a male born in the current year with a mature, one year-old female. On August 1, 1969, we paired a well-developed, 65 day-old male with ♀IV which was in rut and had copulated shortly before with a two year-old male. Copulation with the young male was repeated several times and its course was normal. The female produced a litter 17.5 days later, but this could not be taken as a confirmation of fertility of the young male, because the female had previously been covered by an adult.

We did not inspect regularly the opening of the introitus vaginae in the females, but occasional inspection disclosed it once in 60 and 90 day-old females. We did not record parturition in the females of the current year's production.

The possibility of producing the young during the first season has been confirmed by the following finding. On August 22, 1968, we opened near Zábřeh, Moravia a burrow inhabited by a female and 9 young aged 21 to 23 days. We assessed their age by comparison with material from our stock (Vohralík, in press). The female was small, weighing only 160 g on September 1, 1968. According to the values obtained from our stock this excludes the possibility that this female had overwintered. The animal was killed on November 5, 1968, weighing 169 g. Her measurements were (in mm): body length — 200; length of tail — 58; length of hind foot — 32.7; condylobasal length — 44.3; zygomatic breadth — 24.6; height of mandible — 13.5; length of mandible — 27.6. The values of skull measurements indicate that the female was produced in the current year. This was confirmed also by an evaluation of the degree of wear on the teeth suggesting an age of 4–5 months

and considerably different from what was observed in overwintering hamsters killed at the beginning of October (i.e., at the age of 13–17 months). All comparative material was obtained from our laboratory stock (Vohralík, in press).

If the female under consideration were of this year's litter, than she must have become pregnant approximately on July 15 (assuming that parturition occurred between July 30 and August 1, and pregnancy lasted for 17 days), i.e. at age of 2.5 months at the outside.

As regards this subject, an interesting finding has been made by Kryštal (1929) who on August 4, 1928, in the Berdičev province of the Ukraine (U.S.S.R.) trapped a very small female hamster with embryos. Although the author doubted that this female was produced in the same year, we confirmed that this was the case by comparing its body- and skull measurements (body length — 175 mm; condylobasal length — 39.0 mm) with the values assessed in our stock.

Oestrus of the female; mating

The time of oestrus in the female was established by placing the males into the female cages at 2–3 day intervals. Fertile mating was considered as the confirmation that oestrus had taken place. The first fertile mating was recorded on April 15, the last on August 12. A number of unfertile matings was recorded before, during and after this period.

In females, we observed also the occurrence of oestrus postpartum, i.e., 1–2 days after parturition. Fertile mating was observed at these intervals after parturition: one day (twice), two days (three times), 10, 15, 29 days. For exact data see Table 1.

A detailed description of the mating behaviour of the Common hamster was given by Petzsch (1943) and Eibl-Eibesfeldt (1953). Our observations are consistent with theirs except for a few details:

The authors observed in rutting males a special kind of snuffling which the males made shortly before copulation. In Eibl-Eibesfeldt (l.c.) description... "Dieses ffff ffff ffff drückt immer sexuelle Kontaktbereitschaft aus und wirkt stark werbend". We observed these sounds with both males and females, although they were stronger and more frequent with the males. The hamsters made these noises mainly close to copulation but often they were heard also from rutting animals placed separately in the individual cages.

If a female started to make these noises, the fertile mating followed in the absolute majority of cases. We observed frequently that several males started to make these noises and tried to escape from their cages if a female on heat was present in one of the nearby cages (sometimes up at a distance of 3 m).

These findings may carry practical implications for rearing hamsters in the laboratory, because the time of female rut may be registered without having to undergo the prolonged and risky procedure described in the method of rearing.

No information is available as yet as to the actual cause of these sound effects. They may be either a purely acoustic manifestation associated with the mating behaviour (in this case evidently evoked by an olfactory sti-

mulus), or only a secondary acoustic effect caused by hard breathing and drawing in the air through the nostrils in order to catch the smell of the animal of the opposite sex. Our observations are in favour of the latter suggestion. The importance of olfactory signals in the mating behaviour of hamsters has been pointed out by Lipkow (1954) who experimented with the closely related species *Mesocricetus auratus* and disclosed in her studies the importance of the glandular flank organ. This organ and also the cutaneous umbilical glandular organ are well-developed in the Common hamster and a sexual function is ascribed to both of them (Vrtiš, 1930 a, b; 1931, 1932).

Duration of pregnancy

The duration of pregnancy as referred to in the literature lasts generally approximately 20 days. Already Heck (in: Brehm, 1914) writes that... "Die Tragzeit beträgt 20 Tage, das ist im Berliner Zoologischen Garten durch wiederholte Beobachtung sicher festgestellt worden". Petzsch (1943) gave a period of 20—21 days. Kirchshofer (1950) recorded a period of 20 days. Later Petzsch (1952a) gave for the average duration of pregnancy a period of 19—20 days. Eibl-Eibesfeldt (1953) found considerable variability in the duration of pregnancy. By carefully recording the time of mating and of parturition, he obtained these values: once 17 days, 5 times more than 19 days, once 20 days, once 21 days.

In our stock we observed that pregnancy lasted in 17 cases 17 days; in one case each 17.5; 18; 18.5; 25; 28; 32; 36; 37 days. We divided these greatly varying values into two main groups:

1. Pregnancy lasting for 17—17.5 days occurred always with the first litter of the female in the pertinent production period. This represents the normal length of time for the Common hamster.
2. All cases in which pregnancy lasted longer were concerned with the second or third litter during the same season. It is possible that this is a special case of prolonged pregnancy in lactating females as recorded, e.g., for the house mouse (*Mus musculus*), and for several species of the genus *Peromyscus* (Asdell, 1946). The examples of prolonged pregnancy in the Common hamster may be again divided into two groups:
 - a) In cases of pregnancy lasting for 18 and 18.5 days mating had occurred 10 or 15 days after previous parturition.
 - b) In the remaining cases (duration of pregnancy from 25—37 days) mating had occurred on day 1—2 after parturition, i.e., during the post-partum rut of the female. Only with ♀ C(1) (duration of pregnancy 28 days) did mating occur as late as 30 days after parturition. An explanation of this greatly prolonged period of pregnancy may be found in the fact that it was the third litter of a relatively weak female in one season and the period of pregnancy of the second litter had been prolonged to 25 days (Table 1, Fig. 1).

The mechanism involved in the prolongation of the period of pregnancy in the Common hamster is unknown. Kirkham (1916) studied the cause of this phenomenon in white mice and found that in the lactating females, cleaved eggs at the blastula stage remained unattached in the lumen of the uterus for a considerable length of time. Implantation occurred much later than in nonsuckling females. It will have to be confirmed in experiments whether the situation is similar in the Common hamster.

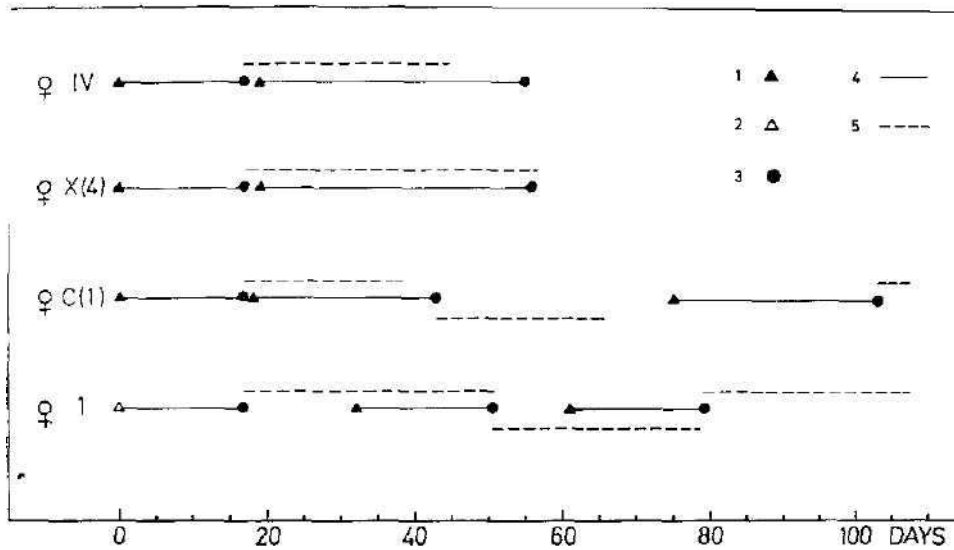


Fig. 1. Pattern of reproduction of females in which the prolonged pregnancy occurred. — Explanation: 1. Copulation. 2. Supposed copulation. 3. Parturition. 4. Duration of pregnancy. 5. Presence of the young together with the mother.

In view of the occurrence of oestrus post-partum, prolongation of the period of pregnancy carries a certain biological importance. According to Petzsch (1952a) young hamsters in the field leave the maternal burrow at the age of 25 days. If the duration of pregnancy were to be normal, the young of the second litter would be produced one week before the young of the first litter had left the burrow. Our observations on the laboratory stock indicate that the simultaneous presence of two litters of different age in the nest must lead to the killing of the younger animals by their older siblings.

Parturition

In our stock, parturition occurred mostly in the afternoon. Out of 16 more carefully observed cases, it occurred in 8 cases between 4–6 p.m., the remaining females produced their litters at various times of the day or night.

In female IX (litter no. 13) we observed delivery. The female had no nesting box placed in her cage and had made its nest of hay. Delivery occurred between 6.46–7.24 p.m., 10 young in the litter. The female sat partly erect on her hind legs during parturition in a position similar to hibernation and helped the young with her teeth (see also Petzsch, 1943). She released the newborn from their foetal membranes, bit of the navel cord and stuffed everything including the placenta into her cheek pouches. During parturition of the first, and after giving birth to the third young, the female left the nest, ran actively in the cage and drank milk. She continued to concentrate the foetal membranes in her cheek pouches. Since they were not found later, she must have eaten them.

Number of litters

The literature does not supply exact data on the number of litters during one reproduction season. Several authors, e.g., Pidoplička (1928), Dukelskaja and Stepanova (1932) suggested that the hamster reproduced only once a year, and that the reproduction period covers several months. A number of other authors suggested two litters per year (Krištal, 1929; Stroganova, 1954; Popov, 1960). The possibility of a third litter was discussed in detail by Petzsch (1936) who concluded that this was possible above all in areas with satisfactory climatic conditions.

Petzsch (1968) and Saint Girons et al. (1968) both observed, in hamsters kept in captivity, one instance only where a female had two litters per year.

Females of our stock produced two litters per year in three instances (Table 1), three litters per year in two instances, i.e., in 1968 ♀ 1 produced litters on June 29, August 2, August 30; in 1969 female C(1) produced litters on May 17, June 12, August 8. Having regard to the fact that ♀ 1 produced her first litter as late as June 29, i.e., at a time when ♀ C(1) had already the young of the second litter aged one week, it may be possible theoretically to produce 4 litters per year.

Petzsch (1952) suggested that the young of the last litter, born in the second half of August, may often be unable to store sufficient food for the winter and, therefore, cannot survive hibernation. This assumption is correct particularly in view of the fact that, nowadays, the fields are ploughed generally by the end of August. Consequently, the majority of the young of later litters, apparently, do not survive the winter and, hence, cannot participate markedly in the population dynamics of this species.

From three females (no. 1, IV and I'[1]) we obtained litters within two consecutive seasons. Their age was 2 years in the second reproduction season. Another two females trapped in the field and kept in captivity for some time (no. 2, XII) produced litters at the age of at least 2 years. Since rearing of our laboratory stock was discontinued we could not establish the maximum number of fertile seasons.

Size of litter

In our stock, the number of young in the 27 litters ranged from 4–10, with an average of 7.6. The frequency of the individual values of the size of litter and comparable literary data are given in Table 2.

Our results are similar to those obtained by Petzsch (1943, 1956, 1968) who recorded from 17 litters of the young produced in captivity an average size 7.5 (original material: Thüringen, Dresden, Halle/Saale). In 10 litters of the young collected in the field near Dresden (Petzsch, 1936) the average size of litter was 7.8. For Germany Nehring (1901) recorded an average size of 7–8, with a maximum of 12 embryos; the author referred to a written communication by W. Schüter from Halle on the finding of 8 times 5–8, once 9 and once 10 embryos.

From Czechoslovakia information on the size of litter for the Common hamster in the field is not available apart from our limited material (Table 2) and data by Bartoš (1959).

Although the material mentioned is very limited and of different origin, it indicates that both in Germany and in the Czech Lands the number of the

Table 2. Incidence of litter size

Author	Locality of observation	Litter size																	Note
		3	4	5	6	7	8	9	10	11	12	13	14	15	20	\bar{x}			
Petzsch (1943, 1956, 1968)	Thüringen, Dresden, Halle/Saale	-	-	3	-	8	-	4	1	1	-	-	-	-	-	-	7.5	born in captivity	
Petzsch (1936)	Dresden	-	-	-	4	1	3	-	-	1	1	-	-	-	-	-	7.8	field, 1-25 days old	
present study	Moravia and Bohemia	-	1	4	1	7	4	5	6	-	-	-	-	-	-	-	7.6	born in captivity	
present study	Zábřeh (Moravia)	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	field, young	
Bartoš (1959)	Prague	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	field, young	
Krištal (1929)	Ukraine (mostly from the environs of Žitomir)	1	-	1	2	1	2	4	3	-	-	-	1	1	-	-	8.6	*	
Pidoplička (1928)																			
Gershenson, Polevoi (1941)	Ukraine (Černigov province)																n = 73	8.5	field, young
Dukejskaja, Stepanova (1932)	Moskva region	1	1	-	-	4	-	2	2	3	-	-	-	-	-	-	8.1	field, young	
Popov (1960)	Confluence of the Volga and Kama rivers (USSR)	-	1	-	2	-	1	1	2	2	4	2	-	1	-	-	10.2	field, embryos	
Stroganova (1954)	Kujbyšev and Saratov area (USSR)																n = 7	1	field, embryos
Kirikov (1952)	South Ural area (USSR)	-	-	-	-	-	-	-	-	-	1	3	2	-	-	-	13.2	field, probably embryos	

* From Pidoplička (i.e.) only verified data were recorded, from Krištal (i.e.) only embryos and cases in which the female together with the young were caught in the burrow.

young in the litter of the Common hamster ranges mostly from 5–10, and values above 12 young are, apparently, an exception.

It can also be seen from Table 2 that the number of the young in the litter increases eastwards from the areas under consideration both in average value and in the maximum size of the litter. Although samples small in several instances, the increase mainly in the maximum size of litter is marked in areas East of the Volga River (Popov, 1960; Stroganova, 1954; Kirikov, 1952). We cannot say as yet whether there are decreasing trends in the size of litter in the opposite direction, i.e., towards the western border of the area of distribution of the Common hamster, because more numerous samples from the area of N. E.-France, Belgium and Holland are not available.

A similar eastward increase in the size of litter was observed by Zejda (1966) for *Clethrionomys glareolus*, and by Pelikán (1972) for *Arvicola terrestris*.

In the case of the Common hamster, however, we have to distinguish between values based on the number of embryos or newborn, and values established in litters of the older young. Petzsch (1936) noticed that in the field the number of seeing young in the litter (i.e., older than 14 days) was seldom greater than 8, which is in accord with the number of teats of the female hamster, while the number of newborn was frequently higher. He explained this difference by the fact that the stronger individual pushed the weaker ones away from the teats, these did not get sufficient nourishment, their development was retarded and they were eaten by the mother and the other young.

We observed a similar situation in our stock especially if the litter was more numerous. On day 2–3 after parturition one or two (total 7) young disappeared without traces. We cannot say as yet whether this phenomenon commonly occurs in the field or whether it was induced by unnatural conditions.

Sex ratio

Of the 206 young born in our stock, 92 were males, 105 females. In 9 young the sex could not be determined, because they died shortly after birth and were eaten by their mother or the other young in the litter. The ratio of males to females was 1 : 1.14. It differs from theoretical assumption of 1 : 1, but the difference is statistically insignificant ($\chi^2 = 0.858 < \chi^2_{0.05} = 3.8$).

A larger number of females of the Common hamster was observed also by Petzsch (1936). He writes: "Soweit ich beobachten konnte, war das Verhältnis der Geschlechter unter den Junghamstern durchschnittlich etwas über fünf Weibchen auf vier Männchen."

Popov (1960) observed in one litter of bare and blind young, and in 3 females in which he determined the sex of the embryos, a total ratio of 18 ♂♂ 23 ♀♀, i.e., 1 : 1.27.

Adoption of the unrelated young

Nursing females of our stock carried in to their own nests and accepted readily the unrelated young of the same species. E. g., we exchanged repeatedly the individual young of the same age (from 1–20 days) among litters no. 11, 12, 13 and these were always accepted by the females and

treated as their own. Also Eibl-Eibesfeldt (1953) observed that the female brings unrelated young to her nest.

In one instance, a female hamster reared successfully the young of a white rat (*Rattus norvegicus* f. *alba*) placed at the age of 5 days among her litter of 3 day-old hamsters.

FINAL REMARKS

In conclusion we should like to stress that several aspects of the biology of reproduction of the Common hamster may have been influenced by the artificial conditions of rearing in the laboratory and, therefore, may differ slightly from conditions in the field. While in studies on the duration of pregnancy we shall evidently have to rely solely on data obtained from animals held in captivity, several other problems concerned with the breeding season, the attaining of sexual maturity, the number of litters and the size of the litter should be studied using field material.

SUMMARY

The biology of reproduction of the Common hamster was studied using 15 animals trapped in the field and 28 litters bred from them (206 animals).

1. A detailed description is given of the methods and of the experience of rearing hamsters in captivity.

2. The period of reproduction was 4 month in our stock (from the beginning of May to the end of August). This is consistent with information in the literature.

3. It appears that in the field an occasional female of *Cricetus cricetus* attains sexual maturity prior to her first hibernation.

4. We recorded the occurrence of oestrus post-partum.

5. The normal period of pregnancy of the Common hamster is 17 days. With the second and third litter produced within one season, pregnancy was prolonged from 18–37 days.

6. We obtained, during one reproduction season, on three occasions two and twice 3 litters from one female. Fertility of the females was established to be maintained up to at least 2 years of age.

7. The average number of the young in the litter was 7.6 (minimum 4, maximum 10). The number of the young in the litter increased eastwards within the area of distribution of this species.

8. The total sex ratio of the newborn was $92 \text{ ♂♂} : 105 \text{ ♀♀} = 1 : 1.14$. The difference is statistically insignificant.

9. Several other observations on the biology and ethology of the Common hamster are recorded.

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