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**WING POLYMORPHISM IN NOTIOPHILUS BIGUTTATUS IN BOHEMIA
(COLEOPTERA, CARABIDAE)**

Alois HONĚK

Received December 18, 1979

Abstract. The proportion of wing morphs (brachypters and macropters) in the populations of *N. biguttatus* (F.) was investigated at a number of localities in Bohemia and western part of Moravia. In lowland populations there are less than 15% of brachypters. In general, the proportion of brachypters increases with altitude. This trend is more conspicuous in some mountain systems than in others. Often the brachypterous populations are found near the peat-bogs. No environmental factors unequivocally associated with the increase of proportion of brachypters in a population have been found.

Wing polymorphism in Carabidae has been extensively studied, particularly in tropical and arctic faunas (Lindroth, 1963; Darlington, 1971). Also with Central European fauna we have several observations (e. g. Mařan, 1927, Witzke, 1977). A detailed investigation of geographic differences in proportion of brachy- and macropterous forms in local populations of Bohemia has been perphas lacking. We have investigated the ratio of morphs in a common species, *Notiophilus biguttatus* (F.).

MATERIAL AND METHODS

N. biguttatus is a small (5–6 mm long) carabid species living on the ground surface of both forest and field habitats. It is a predator with daily activity (cf. Bauer et al., 1977) which feeds predominantly on various species of Collembola (Ernsting, 1977). The beetles prefer humid but at least partly insolated habitats. The species appears most abundant in pine plantations (to which most Bohemian forests were converted), and may be easily collected on their bare ground surface. The beetles have either fully developed hind wings (longer than elytra), or reduced ones (narrow scales shorter than $\frac{1}{2}$ of the length of elytra). The winged morph has never been observed flying (Bauer, 1975; Pulpán, in prep., cf. den Boer, 1971, p. 191).

The beetles were collected in ca 150 localities in Bohemia and the adjacent western part of Moravia, in 1975–1979 (from April to October). Each sample originated from a small area of known altitude. All samples were collected in pine forests. In this paper the localities are designated usually by the name of nearest human settlement, sometimes by other geographic names, such as prominent hills at which the beetles were sampled etc.

RESULTS

The populations of *N. biguttatus* in Bohemia are mostly macropterous. In lowland localities and in most localities of medium altitude there are less than 15% of brachypters (Fig. 1). Usually the proportion of brachypters increases with increasing altitude (Fig. 2). This general trend, however, is differently expressed in different mountain systems. The highest proportion of brachypters (about 95%) was found in highland populations from the peat-bogs of the Ji-

zerské hory Mountains (number of sample, n. s. 34—42), near Smědava. In these Mountains also the increase of percentage of brachypters with increasing altitude is most conspicuous (Fig. 3). Populations with high proportion of brachypters were observed also in the western part of the Krušné hory Mountains (n. s. 6—19), and in the Sumava Mountains (n. s. 91—104). In other mountain systems

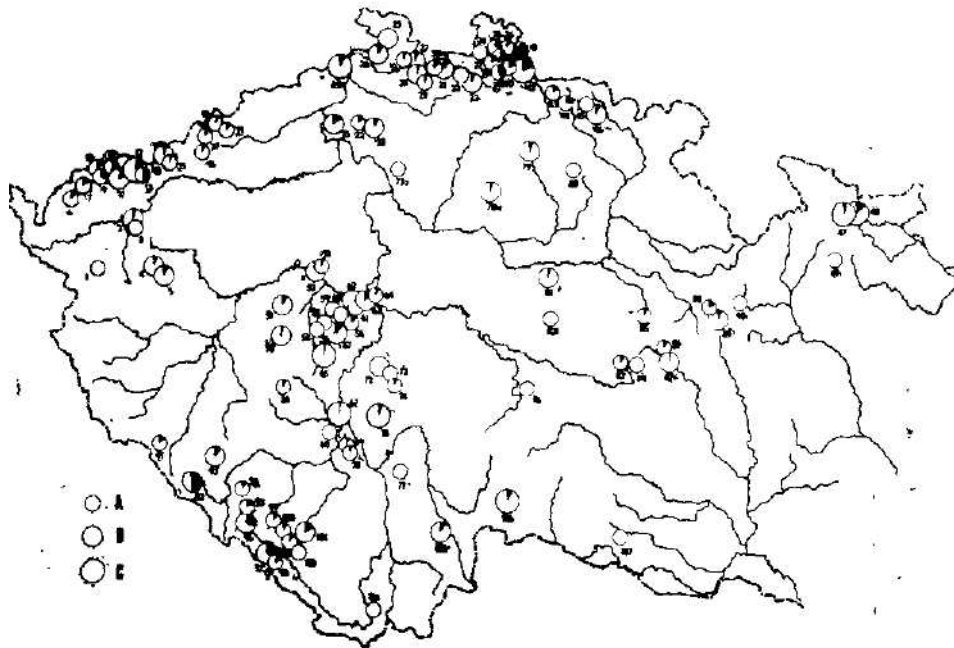


Fig. 1 — The proportion of macropters (open sector) and brachypters (black sector) in Bohemian and Moravian populations of *N. biguttatus*. A — samples of 15—29 individuals; B — 30—49 ind.; C — 50 and more ind.

Localities: 1 — Kladská; 2 — Karlovy Vary — Kolová; 3 — Pila; 4 — Třebouňský vrch; 5 — Bezděrov; 6 — Čtyřdomí; 7 — Hatě; 8 — Jelení; 9 — Jelení; 10 — Horní Blatná; 11 — Horní Blatná; 12 — Abertamy; 13 — Hřebečná — Mrtvý rybník; 14 — Přísečnice; 15 — Měděnec; 16 — Vysoká Lideň; 17 — Nový Dům; 18 — Rudoltice v Horách; 19 — Svahová; 20 — Maxičky; 21 — Němčí; 22 — Trnoblany; 23 — Rašovice; 24 — Na Tokáni; 25 — Vlčí Hora; 26 — Jedlová; 27 — Nová Huť; 28 — Mařenický; 29 — Jablonné v Podještědí; 30 — Petrovice-Falkenštejn; 31 — Petrovice — Loupežnický hrad; 32 — Kryštofovo údolí; 33 — Ptačí kameny; 34 — Lysé skály; 35 — Raspenava; 36 — Lázně Libverda; 37 — Olivetská hora; 38 — Poledník; 39 — Bedřichov; 40 — Bedřichov; 41 — Smědava; 42 — Souš; 43 — Horní Rokytnice; 44 — Šerín; 45 — Jánský vrch; 46 — Staré Buky; 47 — Rejvíz; 48 — Kobrštejn; 49 — Skřítek; 50 — Strašice; 51 — Zebrák; 52 — Nižbor; 53 — Nižbor; 54 — Běřín; 55 — Hostomice pod Brdy; 56 — Dobříš; 57 — Dobříš; 58 — Voznice; 59 — Nesvačily; 60 — Stožec; 61 — Halouny; 62 — Revnice; 63 — Dobřichovice; 64 — Všerory; 65 — Příbram; 66 — Třemšín; 67 — Zvíkov; 68 — Vráž u Písku; 69 — Písek; 70 — Písek; 71 — Zálší; 72 — Sedlčany; 73 — Prčice; 74 — Zvěřinec; 75 — Milevsko; 76 — Želiv; 77 — Dolní Zimor; 78 — Jabkenice; 79 — Jičín; 80 — Hořice; 81 — Zdechovice; 82 — Golčův Jeníkov; 83 — Velké Dářko; 84 — Tisůvka; 85 — Bor u Skutče; 86 — Podlesí; 87 — Sněžné; 88 — Brlenka; 89 — Mladějov; 90 — Česká Třebová; 91 — Hadrava; 92 — Šmauzy; 93 — Velhartice; 94 — Kašperské Hory; 95 — Churáňov; 96 — Kvilda-Františkov; 97 — České Zleby; 98 — Stožec; 99 — Lipka; 100 — Boubín; 101 — Libínské Sedlo; 102 — Bobík; 103 — Volary; 104 — Rožmberk; 105 — Třeboň; 106 — Kunžak; 107 — Znojmo.

(perhaps with the exception of the Krkonoše Mountains, n. s. 43—45) populations with a high proportion of brachypters were not observed even when some small samples were collected as high as in the 1300 m altitude. Two populations where brachypters are abundant live closely to mountain peat-bogs. In Jizerské hory Mountains the largely brachypterous population lives in the surroundings of peat-bog near Smédava (about 900 m altitude). In the Krušné hory Mountains they were observed near the peat-bogs of Boží Dar and near Horní Blatná (950 m). On the other hand in the Šumava Mountains the localities

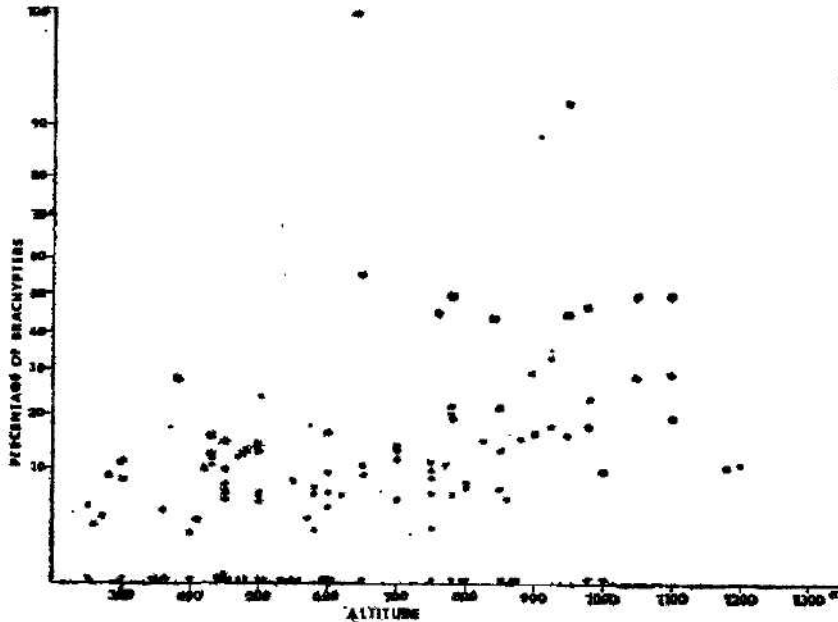


Fig. 2 — The percentage of brachypters (angular transformation) in relation to altitude in populations of *N. biguttatus* (from the same localities as in Fig. 1).

of largely brachypterous populations were found not too close to the peat-bogs. There are also peat-bogs, both lowland and mountain ones, where no increase in proportion of brachypters was observed, e. g. Třeboň (430 m, n. s. 105), Velké Dářko (650 m, n. s. 83), Rejviz (780 m, n. s. 47), Kladská (780 m, n. s. 1), Nový Dům (800 m, n. s. 17), Skřítek (875 m, n. s. 49). A slight increase in the percentage of brachypters was observed also in some localities in the sandstone massive of northern Bohemia (n. s. 20, 30, 31) and in the volcanic České Středohoří Mountains (n. s. 21—23).

The brachypterous populations are always rather local. Therefore their finding is rather a matter of chance. It cannot be excluded that they could be found also at low altitudes. Two mountain systems were sampled more intensively: the low Hřeben Mountains (n. s. 54—64, highest peak 690 m), and the higher Jizerské hory Mountains (n. s. 34—42, highest peak 1124 m). With approximately the same sampling effort paid to both areas, no population with large proportion of brachypters were found in the Hřeben Mountains while several

largely brachypterous samples were collected in the Jizerské hory Mountains. Thus the occurrence of largely brachypterous populations in low mountain systems is at least far less probable than their occurrence in high ones.

The composition of *N. biguttatus* populations was stable in time. In some localities, both with low and high proportion of brachypters, the sampling was repeated in successive seasons. The ratio of forms did not change significantly with time at any locality.

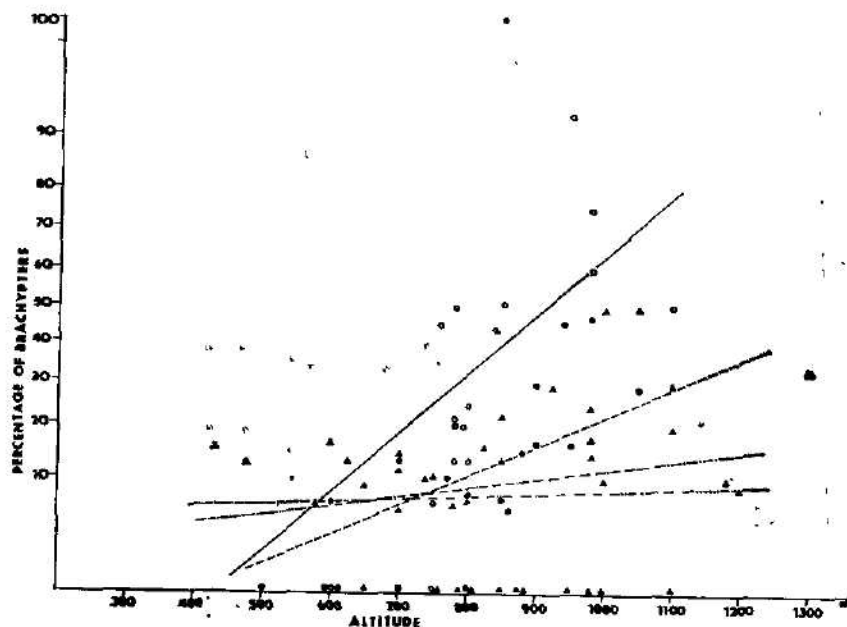


Fig. 3 — The percentage of brachypters (angular transformation) in relation to altitude in different mountain systems. —, ○ Jizerské hory Mountains; ---, ● Krušné hory Mountains; - · - ·, △ Sumava Mountains; · · · ·, ▲ other mountain systems whose highest peaks surpass 800 m altitude. Data from Fig. 1, some samples of 8–14 individuals added

DISCUSSION

Several studies on Coleoptera have revealed complete genetic control over wing polymorphism (Jackson, 1928, Lindroth, 1946; Stein, 1973). In all these cases the brachypters were dominant over macropters. This genetic mechanism has been supposed general for Carabidae (Lindroth, 1963), and this generalization has been confirmed even by recent studies (Carter, 1976). In *N. biguttatus* the regulation of wing polymorphism has not been studied. The temporal stability of spatial pattern of the wing morph distribution in natural populations of *N. biguttatus* indicates some environmentally not easily flexible, probably genetic, control of wing polymorphism.

Supposing the genetic background of *N. biguttatus* wing polymorphism, we may speculate about its adaptive value and the forces regulating the ratio of forms. Several hypotheses have been proposed to explain adaptive significance

and local differences in morph ratio in Coleoptera. The brachypters are thought to have an advantage in stable habitats while the macropters can make better use of temporary ones (den Boer, 1970, 1971). This advantage of brachypters is greater when the favourable habitats are small, surrounded by large areas of unfavourable environment, and free from negative influences (Darlington, 1971). Local differences in the ratio of morphs within a species may arise from different rate of migration of both forms into newly colonized habitats, either in historical past (Lindroth, 1963), or at present times (den Boer, 1970, 1971; Haeck, 1971; Stein, 1977), though not all differences are explicable in this way (Meijer, 1974). Since both wing morphs in *N. biguttatus* are incapable of flying, these ratiocinations cannot apply to our case. Published information about the colonization of newly founded polders (den Boer, 1970; Haeck, 1971) support this view. There, in active fliers local differences in morph frequency arised between newly colonized and old areas. due to different rate of migration of both wing forms. In *N. biguttatus*, however, no such differences were observed.

Accordingly, geographic differences in morph proportion in *N. biguttatus* populations should be maintained in another way. There are two conspicuous features of the morph distribution of this species in Bohemia: (1) The brachypterous populations are very local. (2) The largely brachypterous populations allways live in higher mountains, often near peat-bogs. However, there is but a statistical connection between brachyptery and these habitats: both mountain and peat-bog inhabiting, and at the same time largely macropterous populations were found. Moreover, outside the area studied, populations with relatively high proportion of brachypters (about 30 %) live also at low altitudes (den Boer, 1970, Haeck, 1971). Thus high altitude and/or the vicinity of peat-bog probably does not directly promote the increase of the brachypter frequency in a population.

The phenomen of patchy distribution with abrupt changes of frequency at the boundary, of the genetic morphs of a species ("area effects") has been intensively studied in molluscs. For example, the situation in some types of genetic polymorphism in *Cepaea* (Jones, 1973; Jones and Irving, 1975) has much similarity with our case: local differences persist with weak or no association with environmental conditions. The explanations usually proposed in such cases can be suggested also for *N. biguttatus*: (1) The gene(s) for polymorphism can be strongly linked with other loci subjected to selection at some particular habitats. (2) Some habitats may permit the evolution of brachypterous populations, which thereafter can arise by random genetic diversification (e.g. genetic drift) in natural populations. Clearly much further research has to be done in order to elucidate the subject.

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FOOD AND FEEDING HABITS OF SOME FISHES OF PUNJAB

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Abstract: Food and feeding habits of *Puntius stigma* (Ham.), *Puntius chrysopterus* (McClelland), *Discognathus lamta* (Ham.), *Heteropneustes fossilis* (Bloch) and *Mastacembelus pancalus* (Ham.) have been described. It has been observed that *Puntius stigma* (Ham.) and *Puntius chrysopterus* (McClelland) are herbivorous. *Discognathus lamta* (Ham.) is insectivorous and bottom feeder, whereas *Heteropneustes fossilis* (Bloch) and *Mastacembelus pancalus* (Ham.) are purely carnivorous and bottom feeders.

INTRODUCTION

Puntius chrysopterus (McClelland), *Discognathus lamta* (Ham.) *Heteropneustes fossilis* (Bloch) and *Mastacembelus pancalus* (Ham.) constitute miscellaneous fisheries of Punjab and do not form major catches. All these fishes inhabit standing waters such as ponds, lakes and small ditches along the river beds and canals. *Heteropneustes fossilis* (Bloch) is usually found in marshy places with small amount of oxygen. *Mastacembelus pancalus* (Ham.) is very common in the river beds with stones due to its eel-like body.

For the rational management of the fishery, it is essential to collect information on the various aspects of biology and feeding habits and these form one of the major parts of such studies. Our knowledge about the biology of these fishes and allied species is derived from the works of Chacko and Kurian (1948), Chitray (1964), Job (1941), Khan (1934), Menon and Chacko (1958), Mukerjee, Sen Gupta, Chandhary (1940), Quayyam and Quasim (1964a; 1964b; 1964c), Raj (1916) and Tandon, Johal and Dhawn (1972).

Since the ecological conditions are different at different places influencing directly the abundance of plankton populations, hence the results of the present investigations are somewhat different from the earlier workers.

MATERIAL AND METHODS

Samples of these fishes were collected from Ferozepur, Jullundur, Amritsar and Ropar districts of Punjab State by using cast nets, rod and line and pot method in different months of the years 1969-1971.

170 stomachs (40 for *P. stigma*, 29 for *P. chrysopterus*, 37 for *H. fossilis*, 42 for *D. lamta*, 22 for *M. pancalus*) were examined for the present studies. The total length of each fish was measured in the fresh specimens. The intestine was taken out in a polythene bag containing 4% formalin and were later brought to the laboratory for detailed analysis.

The percentage composition of each food item in all the fishes examined and calculated by alloting points (Froast, 1946; Hynes, 1950; Johal, 1969) based on

the relative volume determined by visual estimation. While allotting the points, the degree of fullness of the stomach and the size of fish were also taken into consideration. The degree of feeding was expressed by recording the stomach as full, $\frac{3}{4}$ full, $\frac{1}{2}$ full, $\frac{1}{4}$ full and empty. The full stomach was allotted twenty points, three quarter full fifteen, half-full ten, quarter-full five and empty zero (empty stomach, however does not mean a complete absence of food organisms in it) The percentage frequency occurrence of each food item was determined by occurrence method. It is very difficult to identify the algae, crustaceans, rotifers, insect larvae even up to genera because they were always in semi-digested state. Before the collection of fishes, mostly water samples were also taken in order to study the presence of different types of planktons in which the fishes were living.

In the present collection almost all the species of fishes belong to the same size group in adult condition, except *D. lamta* where it has been categorised into small sized groups ranging from 1.5–3.0 cm and large size ranging between 3.0–6.0 cm in total length. Four fishes with more than 6.0 cm of total length were also included in the present collection.

For the purpose of identification of these fishes Day (1878), Munro (1955) and "Fishes of Punjab State" by Johal and Tandon (in press) were consulted.

OBSERVATIONS

The alimentary canals of *P. stigma*, *P. chrysopterus*, *D. lamta* are coiled and in *H. fossilis* and *M. pancalus* elongated with prominent stomach indicating their respective feeding habits (Mohsin, 1962). In the present investigations only the contents of the stomach part have been studied, because the digestion is less advanced, which makes the identification of the food materials easier. For the purpose of the simplicity the food items have been categorised as follows.

1. Desmids: — They were represented by *Closterium* sp. and *Comerium* sp. in the gut contents of *P. stigma* and *P. chrysopterus*.
2. Diatoms: — They were represented by *Pinnularia* sp. and *Surirella* sp. and occurred only in the gut contents of *P. stigma* and *P. chrysopterus*.
3. Algae: — *Spirogyra* sp., *Ulothrix* sp., *Volvox* sp. and *Nostoc* sp. were the dominant algae in the gut contents in all the species. In the gut contents of *P. chrysopterus* and *P. stigma* algae constituted the major food items. These algae were present in the negligible amount in the gut contents of *D. lamta*, *H. fossilis* and *M. pancalus*.
4. Higher plants: — They were represented by the leaves of the aquatic plants and their tender stems. Sometimes the branches of other delicate plants were also observed in the gut contents. They were present in all the species except *D. lamta*, where complete absence of higher plants has been recorded. Their percentage frequency was maximum in the months of November to January, when the availability of planktons was minimum. In all the species, higher plants did not form the major food items.
5. Rotifers: — Rotifers were not identified even up to genera due to the non-availability of authentic key, Their occurrence has been recorded in all the species in varying degree but did not form the major food item in any of the species (Tables 1 and 2).
6. Crustaceans: — They were represented by *Daphnia* sp., *Diaptomus* sp., *Cyclops* sp., *Gammarus* sp., *Cypris* sp. and other crustaceans. They were entirely absent in the gut contents of *P. stigma* and *P. chrysopterus*. In *D. lamta*, *H. fossilis* and *M. pancalus* their occurrence has been observed in large amounts and formed major food item. In *D. lamta* liking for crustaceans has been observed in the lower size group but as the size increased, liking showed

Tab. 1. Percentage volume of different food items in the gut contents of different fishes

Food items	<i>Puntius stigma</i> (40)	<i>Puntius chrysopterus</i> (29)	<i>Discognathus lamta</i> (42)	<i>Heteropneustes fossilis</i> (37)	<i>Mastacembelus pancalus</i> (22)
Algae	41.00	60.00	10.00	4.00	10.00
Desmids	10.50	7.00	—	—	—
Plant matter	11.50	11.00	20.00	2.00	—
Rotifers	10.50	12.00	0.50	3.00	2.00
Higher plants	—	—	—	4.00	9.00
Diatoms	26.50	10.00	—	—	—
Crustaceans	—	—	25.50	20.00	9.00
Insects and insect larvae	—	—	10.00	11.00	26.00
Nematodes	—	—	—	4.00	—
Oligochaetes	—	—	10.00	28.00	—
Fish and fish scales	—	—	—	24.00	30.00
Miscellaneous food items	—	—	24.00	—	—
Sand particles	—	—	—	—	14.00

Figures in parenthesis indicate the total number of fishes examined.

downward trend. In *H. fossilis* and *M. pancalus* crustaceans were present in the gut contents of all the specimens but definitely not as the major food items. 7. Insects and insects larvae — They were represented by aquatic beetles, *Notonecta* sp., *Ranatra* sp., *Hydrometra* sp., *Gerris* sp., mosquitoes and other insects. The insect larvae were represented by the larvae of aquatic beetles, dragon flies, caddis flies, mosquito larvae and the larvae of Hemiptera. It has been observed that the insects and insect larvae were completely absent in the gut contents of *P. stigma* and *P. chrysopterus*. In *D. lamta* the occurrence has been observed in all the size groups in varying degree. In *H. fossilis* and *M. pancalus* insect and insect larvae were present in higher amounts in the small sized specimens as compared to bigger ones.

Tab 2. Percentage frequency occurrence of different food items in different fishes

Food items	<i>Puntius stigma</i> (40)	<i>Puntius chrysopterus</i> (29)	<i>Discognathus lamta</i> (42)	<i>Heteropneustes fossilis</i> (37)	<i>Mastacembelus pancalus</i> (22)
1. Algae	100.00	100.00	28.57	10.81	22.72
2. Desmids	62.57	93.10	—	—	—
3. Plant matter	75.00	68.96	100.00	8.10	—
4. Rotifers	100.00	100.00	4.76	27.02	13.63
5. Higher plants	*25.00	*100.00	—	24.30	13.63
6. Diatoms	90.00	72.44	—	—	—
7. Crustaceans	—	—	78.57	100.00	50.00
8. Insects and insect larvae	—	—	57.14	51.32	100.00
9. Nematodes	—	—	—	8.10	—
10. Oligochaetes	—	—	—	100.00	—
11. Fish and fish scales	—	—	—	21.62	100.00
12. Miscellaneous food items	—	—	50.00	*8.10	*22.72
13. Sand particles	—	—	—	—	90.00

* These items are only present in micro-quantities, therefore these items are omitted in Table 1.

Tab. 3. Intensity of feeding (in percentage) in different fishes

Name of fish	Number of specimens	Full	3/4 full	1/2 full	1/4 full	Empty
<i>Puntius stigma</i>	40	35.00	27.50	12.50	—	5.00
<i>Puntius chrysopterus</i>	29	31.72	17.24	13.73	—	17.24
<i>Discognathus lamta</i>	42	30.95	19.04	35.71	—	14.20
<i>Heteropneustes fossilis</i>	37	56.77	24.32	13.52	—	5.41
<i>Mastacembelus pancalus</i>	22	31.82	45.45	22.73	—	—

8. Oligochaetes: — They were represented by *Dero* sp. and *Nais* sp. in the gut contents of *H. fossilis* and constituted the major food items.

9. Fish and fish scales: — Very small fishes, cycloid and ctenoid scales were present in the gut contents of *H. fossilis* and *M. pancalus* only in the bigger specimens.

10. Miscellaneous food items: — These items were represented by the eggs of crustaceans, insects, molluscs, amphihibians and other food items which are not included in the above categories such as strach grains and small plastic pieces occurred only in the gut contents of *H. fossilis* and *M. pancalus* in negligible amounts and in the gut contents of *D. lamta* as major food item.

11. Sand particles: — Sand particles were recorded from the gut contents of *M. pancalus*.

Table 3 indicates the intensity of feeding in different species of fishes. In almost all the species the maximum feeding intensity has been observed in the month of April, May, June, October and in the first two weeks of November. The medium feeding intensity was observed in the months of February, March and September. In the months of July, August, December and January poor feeding intensity has been recorded.

DISCUSSION

Several workers have studied the food and feeding habits of *P. stigma* and *P. chrysopterus* and other allied species (Chacko and Kuriyan, 1938; Das and Moitra, 1955; Moitra, 1956; Qayyam and Quasim, 1964b; Khan, 1934; Mukerjee, Sen Gupta and Chandhary, 1940; Tandon, Johal and Dhawn, 1972). The present investigation is almost in conformity with the results of earlier workers except minor differences. Present studies indicated that *P. stigma* had much liking for diatoms and algae in the adult (Tables 1 and 2). The percentage volume of desmids, rotifers and plant matter remained the same in the gut contents. The maximum feeding intensity was observed in the months of March, April, May, September; medium in the months of October and November; and poor in the months of December, January, February and August.

P. chrysopterus undoubtedly were found to be algae feeder and herbivorous in the true sense. The other food materials such as desmids, plant matter, rotifers and diatoms (Tables 1 and 2) were present in minor quantities. Active

feeding took place in the months of March, April, May and September, medium in the months of November and January and poor in the month of February. There is no data available for comparison as far as feeding habits of this species are concerned.

Concerning the bionomy of *Discognathus lamta* and *Heteropneustes fossilis* the literature is scarce because they do not form the table fishes category. Food and feeding habits of these fishes are studied for the first time. Present investigations revealed that *D. lamta* had liking for algae, rotifers and crustaceans in the lower size groups and with the increase in size liking for insects and insect larvae was observed. The occurrence of miscellaneous food items in the gut contents of *D. lamta* indicated that it is bottom feeder and other food items (Tables 1 and 2) proved its insectivorous nature in the adult stage. Medium feeding intensity was observed throughout the year (only two stomachs were found to be empty in the month of February). Active feeding was noticed in the months of August, September and October.

Heteropneustes fossilis preferred animal diet such as crustaceans, oligochaetes, fish, fish scales, insects, insect larvae. Algae, plant matter, rotifers and higher plants were present in negligible amounts (Tables 1 and 2). The occurrence of oligochaetes in the gut contents prove that the fish is bottom feeder and other contents confirm its carnivore nature. During the period of investigations the intensity of feeding was (Table 3) found to be high except that two stomachs were found to be empty in the month of December 1970. Medium intensity of feeding was noticed in the months October, November and March.

The present studies relating to the feeding habits of *Mastacembelus pancalus* confirm the observations of Khan (1934) and Job (1941). The feeding habits of this species are very similar to that of *M. armatus* (Tandon, Johal and Dhawan, 1972) as both these species occupy the same ecological niche. The presence of sand particles in the gut contents shows, that this fish inhabits the running waters. The occurrence of insects, insect larvae, small fishes and fish scales proved its carnivorous (Tables 1 and 2) nature. Medium intensity of feeding was recorded throughout the period of investigation: maximum in the months of August and September. The specimens of *M. pancalus* were collected using rod and line method, therefore only very few specimens were represented in the present studies.

Present studies have revealed that there was active feeding during the summer months and post breeding months; poor in the winter months and breeding periods. In case of herbivorous and insectivorous fishes empty stomachs were found in winter months indicating the poor availability of planktons. The occurrence of miscellaneous food items were mostly related with starvation condition, because in three stomach of *Discognathus lamta* only miscellaneous food items were present.

In the present investigations, minor differences have been observed in all the fishes as compared with the results of earlier workers. These differences are attributed to the small number of specimens in the present collection and due to the change in the ecological conditions. Most of the collections of the earlier workers were from the southern part of India, whereas the present author had collected these fishes from the northern part of India.

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SUMMARY

1. Food and feeding habits of *Puntius stigma* (Ham.), *Puntius chrysopterus* (McClelland), *Discognathus lamta* (Ham.), *Heteropneustes fossilis* (Bloch) and *Mastacembelus pancalus* (Ham.) have been worked out.
2. The material was collected from different water bodies of the State of Punjab during the years 1969—1971. Punjab lies in the extreme north part of India.
3. Only stomach part was analysed. For percentage composition point method was used and the intensity of feeding has been expressed by recording the stomach as full, $\frac{3}{4}$ full, $\frac{1}{2}$ full, $\frac{1}{4}$ full and empty.
4. The present investigations have proved that *Puntius stigma* and *Puntius chrysopterus* are herbivorous.
5. Food and feeding habits of *Discognathus lamta* and *Heteropneustes fossilis* are described for the first time and it is observed that *D. lamta* is a bottom feeder and insectivorous and *H. fossilis* is also a bottom feeder and carnivorous.
6. *Mastacembelus pancalus* is found to be carnivorous feeding mainly on fishes in the adult stage.

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**STUDIES IN THELOHANELLUS JIROVECI SP. N., A NEW MYXOSPORIDIAN
PARASITIC IN A COMMON TELEOST FISH**

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Abstract. The communication records a new species of myxosporidia, *Thelohanellus jiroveci* sp. n. from the gills of *Labeo bata* (Hamilton) a common edible carp of India. It is characterized by the presence of two distinct type of spores namely macro- and microspores occurring together in the same cyst of the same host fish. A thorough comparison of the parasite has been made with those described previously from *Labeo*- hosts in India.

The genus *Thelohanellus* Kudo, 1933 (Cnidospora : Myxosporidia) includes those protozoan parasites having a single polar capsule. The literature available reveals that only a few species of this genus are reported from Indian fishes. Chakravarty (1943) obtained *T. rohita* (Southwell and Prasad, 1918) from the branchiae of *Labeo rohita* (Hamilton) while Chakravarty and Basu (1948) described *T. catla* sp. n. and *T. seni* (Southwell and Prasad, 1918), both from the branchiae of *Catla catla* (Hamilton)*. Later, Tripathi (1952) described *T. mrigalae* between the eyes and near the snouts of *Cirrhina mrigala* (Hamilton). *T. calbasui* from the scales of *Labeo calbasu* (Hamilton) and *T. gangeticus* from a tumorous growth on the pectoral muscles of *Chela bacaila* (Hamilton). Qadri (1962a, 1962b) noted *T. boggoti* from *Labeo boggot* and *T. andhrae* from *L. fimbriatus*; Qadri (1967) also recorded *T. shortii* from *L. fimbriatus*. Lalitha Kumari (1969) observed five species of *Thelohanellus* namely *T. batae* from the gills of *L. bata*, *T. potaili* from the fins of *L. potail*, *T. chelae* from the gall bladder of *Chela bacuila*, *T. qadrii* from the gill contents of *L. potail* and *T. chrysopomati* from the gills of *Barbus chrysopoma* and *B. sarane*. Recently Hargari et al. (1978) have obtained *T. rodgii* from *Labeo calbasu* (Hamilton). In the course of our studies on the protozoan parasites of fishes, we came across a form having a single polar capsule from the branchiae of *Labeo bata* (Hamilton), a major carp, and thus could identify it as belonging to the genus *Thelohanellus* Kudo. However, the parasite differs from the previously known organisms of the genus in the presence of macro- and microspores occurring simultaneously within the same cyst as well as in other features and, therefore, is described here as *Thelohanellus jiroveci* new species. It may be interesting to note that Karamchandani (1970) described *Myxobolus batae* from the same host fish.

* Southwell and Prasad (1918) collected fishes from Turag River, Mirpur. Dacca, which, at that time was, a part of Undivided British India. Presently, Dacca is the capital of the separate sovereign state of Bangladesh.

MATERIALS AND METHODS

The fishes were purchased alive from dealers at Ranaghat, West Bengal (about 70 Km north of Calcutta), brought to the Laboratory and examined thoroughly for their myxosporidian parasites. Cysts containing the mature spores were carefully removed from the gill filaments, placed on slides containing physiological saline solution, slightly pressed and covered with a cover slip.

Immediately thereafter, these were observed under microscope. For obtaining spores at the same level, Lom's (1969) agar layer method was followed. Lugol's iodine was employed for iodophilous vacuole. India ink (Lom and Vávra, 1963) was employed for observing the mucous envelope of spores. A number of chemicals and techniques were employed for determining their efficacy in the extrusion of polar filament. Permanent preparations of Schaudinn's fluid-fixed materials were made with Heidenhain's iron alumhaematoxylin. The spores were stored using a capillary-tube (Lom, 1975).

OBSERVATIONS

Thelohanellus jiroveci sp. n. (Figs. 1 to 11)

Host: *Labeo bata* (Hamilton) (family Cyprinidae).

Type locality: Ranaghat, West Bengal, India.

Site of infection: Branchiae.

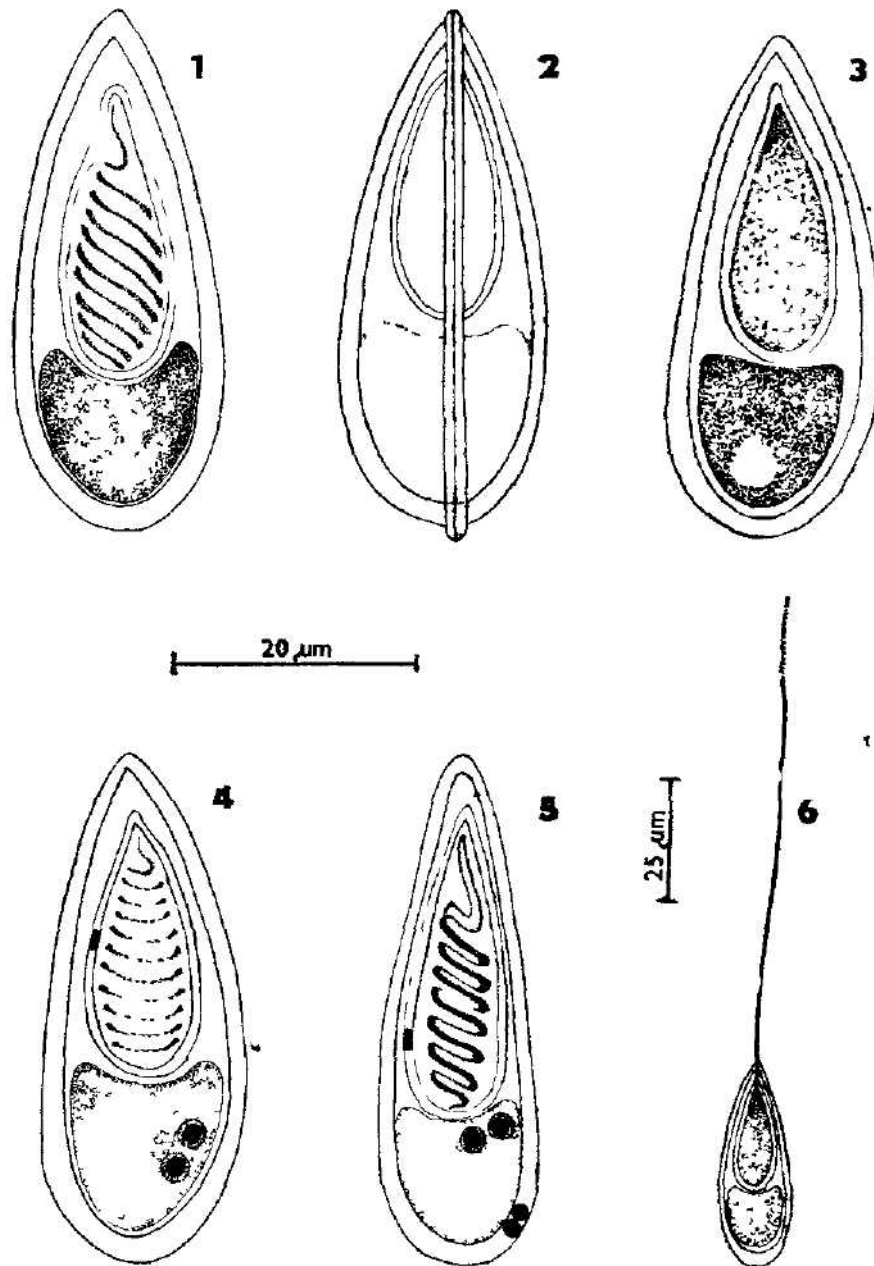
Incidence: Six out of 75 fishes examined have been found to be infected.

Cyst: The cysts are large, oval bodies and creamy white in colour. These measure 1.5—2.0 mm in length and 0.5 mm in breadth. Any developmental stages have not been encountered by us so far; cysts reveal the presence of mature spores only.

Spore: The most striking feature of the parasite is the presence of two distinct type of spores namely macrospores and microspores. They occur simultaneously within the single cyst of the same host fish. Since they vary in morphology and measurements they are described separately below:

Macrospores (Figs. 1—6): These are pyriform in shape with gradually pointed anterior and rounded posterior extremities. In lateral view (Fig. 2) these are more or less spindle shaped. Spore valves are moderately thick and the suture line is distinct. Markings of any type or notches are not seen in the wall of the spore, but the two valvular nuclei are prominent in some spores (Fig. 5). There is a single polar capsule of the same shape as that of the spore itself, situated at the anterior end. There are two capsulogenous nuclei (Figs. 4 and 5). A distinct polar filament with 10—12 coils (Figs. 1, 4 and 5) can be easily discerned inside the capsule. The extruded filament is exceedingly long and is of uniform thickness (Fig. 6). Granular crescentic sporoplasm fills the extra-capsular region. Two distinct round sporoplasmis nuclei are present lying close to one another. A large, more or less round iodophilous vacuole is present below the nuclei of each mature spore (Fig. 3). This stains readily with iodine. There is no mucous envelope outside the spore as revealed by a negative stain with India ink.

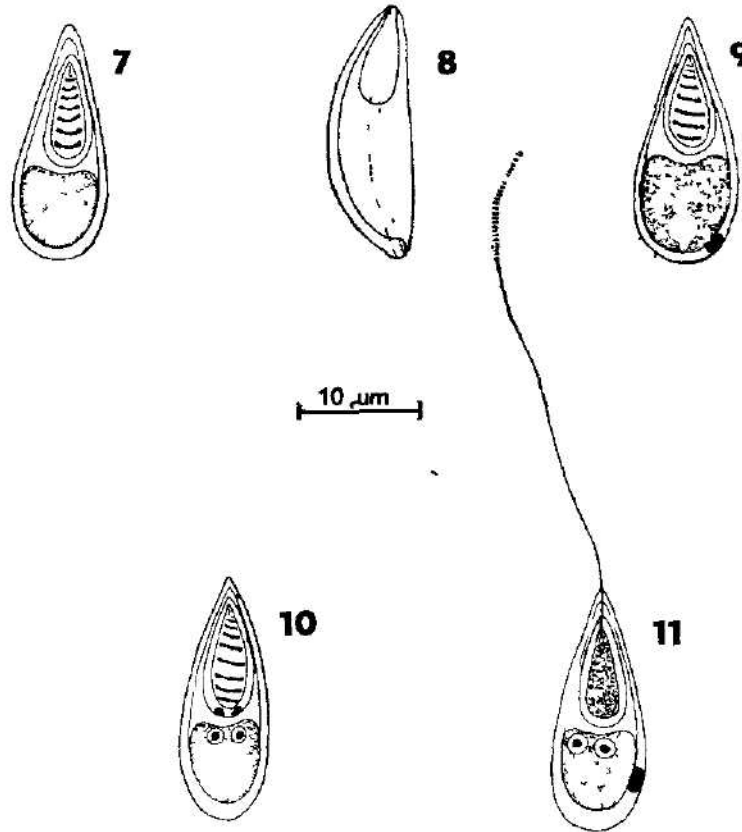
Microspores (Figs. 7—11): The general shape of the microspores resembles that of the macrospores. In side view (Fig. 8) one end is slightly lenticular. The suture line is faintly marked. The two valvular nuclei are clearly seen in some spores (Figs. 9 and 11) but markings of any type are not noted. The polar capsule is of the same appearance as that of the spore and possesses two capsulo-



Figs 1-6 Camera lucida drawings of *Thelohanellus proveci* sp. n. (macrospores)
 1 - fresh spore 2 - side view of a fresh spore, 3 - mature spore, treated with Lugol's iodine, 4 - spore stained with Haematoxylin, 5 - spore stained in Giemsa, where the coils of the filaments can be nicely observed, 6 - spore with fully extruded polar filament, treated with H_2O_2 and stained in Giemsa. The filaments not fully shown in the diagram

genous nuclei (Fig 10) The filament makes about eight coils inside the capsule (Figs. 7, 9 and 10) The extruded filaments have an almost uniform diameter (Fig 11) The characters of the sporoplasm, nuclei and the vacuole are similar to those of the macrospores

The measurements of 20 macrospores and 20 microspores are summarised in Tables 1 and 2



Figs 7-11 Camera lucida drawings of *Thelohanellus jiroveci* sp. n. (microspores) 7 - fresh spore 8 - side view of a fresh spore 9 - mature spore treated with Lugol's iodine 10 - spore stained with Haematoxylin showing the capsulogenous nuclei, 11 - spore with extruded polar filament, Giemsa stained. The filaments not fully shown in the diagram

Extrusion of polar filaments Several reagents have been tried for the extrusion of polar filament of *Thelohanellus jiroveci* sp. n. It has been observed, however, that no single reagent causes one hundred percent extrusion of the polar filament. While H_2O_2 treatment shows the extrusion in 88% of the spores 10% KOH solution gives positive reaction in about 65% of the spores and 100% urea solution in 59% only. Lom (1964) however could obtain 100% extrusion after adding saturated urea solution. Excellent staining of the filament is possible after the method described by Chakravarty

Table 1. Measurements (in microns) of the macrospores of *Thelohanellus jiroveci* sp. n.

Structure	Range	Mean
Length of spore	31.0— 36.1	35.0
Breadth of spore	11.1— 13.8	13.0
Length of polar capsule	15.5— 19.9	18.4
Breadth of polar capsule	5.5— 7.7	7.0
Length of extruded polar filament	194.2—222.0	214.8
Diameter of iodophilous vacuole	3.3— 4.4	3.5
Diameter of nucleus	2.2— 2.7	2.3

(1939) who treated the spores with methyl alcohol followed by staining in Giemsa.

Material: Holotype, on slide No. LB/1, obtained from the branchiae of the carp, *Labeo bata* (Hamilton), collected by T. K. Kundu on 18 Jan., 1978 from Ranaghat, West Bengal, India. Paratypes, many, on the above numbered and other slides. Rest of the particulars are same as for the holotype material.

DISCUSSION AND SYSTEMATIC POSITION

It appears from the descriptions of the features of the spores that the organism can be allocated to the genus *Thelohanellus* Kudo, 1933. A very striking feature of this species is the occurrence of macro- and microspores. The existence of macro- and microspores itself is a unique feature in myxosporidia (Lom, personal communication). Walliker (1969) obtained a similar feature in spores of *Myxobolus serratalmi*, who considered as unlikely the possibility of a double infection. The fact that the macro- and microspores occur simultaneously within the same cyst in the same host specimen rule out the possibility of giving them two separate specific status.

Table 2. Measurements (in microns) of the microspores of *Thelohanellus jiroveci* sp. n.

Structure	Range	Mean
Length of spore	15.5—17.7	16.3
Breadth of spore	6.1— 8.3	6.8
Length of polar capsule	7.2—7.7	7.3
Breadth of polar capsule	3.8— 4.4	4.1
Length of extruded polar filament	66.6—77.7	74.1
Diameter of iodophilous vacuole	2.2	2.2
Diameter of nucleus	1.1— 1.6	1.4

It will not be out of place here to give a thorough comparison of the present species and the species recorded from the *Labeo*- hosts from India thus far. Of the 15 species of *Thelohanellus* described from Indian fishes nine are from *Labeo*- hosts. These are *Thelohanellus rohita* (Southwell and Prasad, 1918) from *Labeo rohita*, *T. calbasui* Tripathi, 1952 from *L. calbasu*, *T. boggoti* Qadri, 1962 from *Labeo boggot*, *T. andhrae* Qadri, 1962 from *L. fimbriatus*, *T. shortti* Qadri, 1967 from *L. fimbriatus*, *T. batae* Lalitha Kumari, 1969 from *L. bata*, *T. potaili* Lalitha Kumari, 1969 from *L. potail* and *T. qadrii* Lalitha Kumari, 1969 from the same host and *T. rodgii* Hagargi, Kundu and Haldar, 1978 from

Table 3. The comparative measurements (in microns) of the ten species of *Thelekanthius* described from *Labeo*-hosts in India

Myxosporidia	Spore		Polar capsule		Length of Polar filament
	Length	Breadth	Length	Breadth	
<i>T. shortii</i>	11.4-12.8	6.4-7.1	6.4-7.9	3.5-4.2	38.4-47.4
<i>T. andhrae</i>	11.3-14.5	4.5-5.5	6.0-8.0	2.0-2.5	100.0-108.0
<i>T. boggsii</i>	11.0-12.0	6.0-7.5	5.5-7.0	3.6-4.0	95.0-108.0
<i>T. rohita</i>	30.0-33.0	10.0-13.0	16.0-20.0	7.0-8.0	208.0
<i>T. balar</i>	11.4-13.6	4.3-7.9	6.4-8.6	2.9-3.6	168.0-185.0
<i>T. petonis</i>	12.1-16.0	7.9-9.5	5.8-8.0	3.6-5.7	60.0-71.0
<i>T. gedrii</i>	14.3-17.1	5.0-6.0	7.5-8.6	2.9-3.9	155.0-204.5
<i>T. calbasui</i>	9.0-10.8	7.2	5.4	3.4	—
<i>T. jiroveci</i> sp. n.	31.0-41.0	10.0-15.0	15.0-20.0	7.0-8.0	—
Macrospores	31.0-36.1	11.1-13.8	15.5-19.9	5.5-7.7	194.2-222.0
Microspores	15.5-17.7	6.1-8.3	7.2-7.7	3.8-4.4	66.6-77.7

L. calbasu. In *T. rohita* the spores are elongated pyriform in shape with acutely pointed anterior and rounded posterior extremities. The valves are thick and the sutural ridge is very prominent. The polar capsule has the same form as the spore. It has a highly coiled filament inside. When extruded it reaches upto a length of 206 μm . The polar capsule of *T. boggoti* is flask-shaped with a short or long neck. The filaments touch the inner side of the capsule and each when extruded measures 194.2 to 220.0 μm in length. In *T. andhrae* there are irregular folds in the shell wall, and the polar capsule always adheres to the inner side of the spore. The extruded polar filament is 100.0 to 108.0 μm in length. The mature spores of *T. shortti* are generally narrow, tapering at the anterior end, broad in the middle and rounded posteriorly. The sutural ridge is curved. The polar filament remains in the form of 3—4 fine loose coils. The fully extended filament is long and its anterior end is rounded. The fully developed spores of *T. batae* are pyriform, whose middle portion is the widest. The valves are thin and smooth. The polar capsule is also pyriform, shifted to one side of the spore. In *T. potaili*, the spores are elongated oval; the polar capsule is broad and oval in which the filament makes 7—9 coils. The mature spores of *T. qadrii* is arched in lateral view and the polar capsules are pear-shaped with a constriction a bit above the middle region. *T. rodgii* is characterized in having pyriform spores. The spore valves are thick and the sutural ridge is prominent. The polar capsule has the same shape as that of the spore. The filament makes about 9—10 double coils inside the capsule.

It will appear from the descriptions of the spores of different *Thelohanellus* species from Indian *Labeo*- hosts that the presently described parasite has a close affinity with *T. rohita* (Southwell and Prasad, 1918) in general shape but differs in measurements. It distinctly differs from *T. batae* Lalitha Kumari, 1989 also described from *L. bata* in Andhra Pradesh in measurements. Furthermore, no one is known to have macro- and microspores. It is therefore, believed to be a new taxon for which the name *Thelohanellus jiroveci* n. sp. is proposed. The specific trivial name is given in honour of Late Prof. Otto Jirovec.

The comparative measurements of the ten species of *Thelohanellus* described from different *Labeo*- hosts in India are summarised in Table 3.

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ON THE LAST BOHEMIAN SALMONS (SALMO SALAR)

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Dedicated to the Memory of Doc. Ing. Dr. F. Volf (1898–1979)

Abstract: The age and biometrical characters of 21 salmon parrs collected around 1930 in the river Otava (drainage of the Vltava in southern Bohemia) and 5 parrs collected here during 1884 were studied. All examined salmon parrs were true salmon, they were ripe, very slow growing. The occurrence of dwarf, "neotenic" form of salmon, previously known from some rivers of Northern Europe, was confirmed also in the upper part of the Labe drainage.

INTRODUCTION

As was known and summarized by Berg (1935, 1937, 1948), sexual maturation of salmon without preliminary marine migration is an exception. But dwarf males of salmon were found undoubtedly in the Vltava by Frič (1879, 1894) and in the river Otava by Schäferna (1933). In Bohemia small salmon males were formerly used for fertilization of stripped eggs of large females at the end of the last century (Frič, 1894), and this fact was cited (Otterström, 1933, 1938, Alm, 1943, Berg, 1935, 1937, 1948). But scarce data as to their age are available (e.g. only Berg, 1937, M. Berg, 1953). The repeated discoveries of "the last Bohemian" salmon in the river Otava made by Volf (1954), proclaimed as "parrs", were of interest and offered the possibility to compare Volf's (1954) statements with previous Schäferna's data and material in his collection, still preserved, and to revise his material. It must be noted here that the last salmon "parr" was captured in the Otava at Sušice by F. Ritter in 1953. It measured 23 cm (Andreska, 1973). Very interesting is the letter note of K. Liška, dated May 23, 1932 (see Dyk, 1940), that the "Fisheries School" at Vodňany determined the age of the river Otava parrs, which are frequent here and apparently not returning into the sea, as 7 years. Dyk (letter comm., Jan. 7, 1980) supposes that apparently the late V. J. Štěpán or Ing. J. Votrubec, who were at that time qualified fishery biologists at Vodňany, determined the age of mentioned parrs. In the year 1878–9 the experiment with fertilizing of salmon eggs with milt of trout was made and this experiment was successful (Frič, 1879). It probably suggested to other fishery biologists that the ripe salmon parrs in the Otava are the hybrids between trout and salmon.

While going through the literature we found that nobody had noticed Frič's observations with regard to the material deposited in the collection of the Na-

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Table 1 — Meristic characters of the salmon (*Salmo salar*)

Character	Specimens examined by us	Berg, 1948	Smitt, 1886, 1895
Nonramified rays in D	III	III-IV	III-IV
Ramified rays in D	9-11	9-12	7-12
Nonramified rays in A	III	III-V	II-IV
Ramified rays in A	9-10	7-9 (10)	7-9
Nonramified rays in V	I	I-II	I
Ramified rays in V	8-10	8-9 (10)	7-8
Lateral line scales	112-124 (118)	114-130	120-140
Scales above l.l.	22-25 (23)	22-26	57-60
Scales below l.l.	18-21 (20)	18-23	
Gill rakers	19-22 (20)	17-24	more than 17
Branchiostegal rays	11-13 (12)	(9) 11-12	—
Nonramified rays in P	I	—	I
Ramified rays in P	11-14	—	10-11/12-14

tional Museum in Prague. Similarly, the salmon material collected by the late Professor Schäferna († 1950) remained unnoticed, although Schäferna (1933) promised that he would make further studies on “dwarf salmon, with ripe eggs, resembling parrs”. Therefore we considered it appropriate to study this material from recent aspects.

MATERIAL AND METHODS

The material of 21 salmon parrs was collected by the late Prof. Dr. K. Schäferna around 1930 in the river Otava, tributary of the river Vltava in southern Bohemia. 5 parrs were loaned from the samples of the late Professor Dr. A. Frič from 1884 and deposited now in the National Museum, Prague.

We studied 1 specimen 149 mm of body length, male, captured in the river Otava in Sušice, Jan 23, 1884 (No. 4 of Frič's protocole); this male had well developed gonads. 4 other specimens captured, apparently at the same place, June 6, Nov. 6, 1884, are sexually ripe males, measured 137-160 mm (ave: 155).

For measuring Pravdin's (1931) (Smitt's 1886-7) scheme was used.

The age determination was proved on selected scales from the middle part of body below dorsal fin base and lateral line scales; from several scales one was selected with clearest annuli and used for study. The back-computed total lengths (L) were ascertained by use of Lea's method on Lea's desk with the intercept 32 mm, using Lohniský's 1966 intercept for brown trouts originating from parts of the river Labe drainage, near of late spawning places of salmon (Tab. 4). For comparison also the uncorrected back-calculated lengths were used, because most of salmon investigators use these lengths for their calculations (Tab. 5).

The lengths of the first year obtained by Dahl's method (= Lea's method) without correction seemed naturally “rather short” to M. Berg (1953).

RESULTS AND DISCUSSION

1. Taxonomical aspects

Results of the study of meristic characters in “dwarf” salmon from Schäferna's samples with data of Berg (1948) and Smitt (1886, 1895) are summarized in Tab. 1.

In 5 ripe salmon parrs of Frič's collection from the Otava we found in D III 10-11 rays, A III 8-9, 12-13 scale rows between the end of adipose fin and lateral line. The scale row number agrees well with the same character found in Scandinavian salmon (Andrijašev, 1954).

Table 2 — Selected proportionate characters in salmon following Nikolskij (1947)

Authority, locality, age	Nikolskij Peshora parrs	dwarf males	Otava dwarf specimens		Frič Otava Parrs	Berg, 1948 Vig dwarf male
Body length (after Smitt) in mm	120	144	212	195.3	155	83.8
In % of body length						
head	20.6	21.0	19.0	22.5	22.1	18.5
max. body depth	18.2	21.5	21.0	18.3	19.6	22.8
Min. body depth	7.0	7.1	7.1	7.8	8.2	6.2
Predorsal distance	40.9	42.9	40.0	41.6	42.3	40.4
Preventral distance	47.4	46.9	39.5	48.4	47.6	48.6
Postdorsal distance	31.7	33.0	36.0	36.4	38.6	—
Caudal ped. length	18.2	19.4	21.6	16.1	19.0	19.4
P length	17.2	15.6	15.5	18.2	18.5	11.4
V length	12.0	11.7	10.4	13.7	13.6	9.3

Using Smitt's schemes (1886, 1887) of measurements and Nikolskij's criteria (1947) in salmon "parrs" we have received results shown in Tab. 2.

In 39 specimens of dwarf salmon from the river Namsen M. Berg (1953) found 14—18 (ave. 16.8) gill rakers, in 8 normal parrs from the river Kjerringneselva 14—18 (ave. 17.2).

Finally, it is necessary to cite Berg's (1953) results of a study of meristic characters in salmon. In 1103 specimens from the drainages of the White, Barents and Baltic Seas, separately males and females, the differences were not found, in average the number of gill rakers is 19.1 or 20.8. In D: 10.1—11.2 (females & males, 1093 sp.) rays were found, in A: 7.9—8.2 (females & males, 1091 sp.) rays were counted.

2. Ecological aspects

In salmon there are males of two "forms"; some are entering the freshwater for spawning (anadromous) and they reach large size, others never descend to the sea, live in freshwater and remain dwarfed maturing sexually. Thus Berg (1948) rightly pointed out the phenomenon of dwarf "complemental" males. Precocious maturation of male salmon is, according to Berg, to a certain extent, analogous to neoteny in some urodeles, with the difference that in salmon this "neoteny" was observed only in males, not in females. Our discovery of matured dwarf female in Schäferna's material, confirmed also by previous observations of Volf (1954), supports Berg's view more decidedly than he was able to do at his time. Zarnecki (1960) erroneously identified land-locked salmon (*Salmo salar* morpha *sebago* Girard, 1853) with the dwarf one. Dwarf salmon males were found and ascertained as such by Frič (1879, 1894) in the Vltava and latter by Schäferna (1933). Normally salmon parrs of Bohemia migrated seawards before reaching the size of 30 cm (Frič, 1894).

Very interesting is the note of Frič (1879) that the males of span length (= 9 inches, 22.8 cm) are ripe with "living sperm". His further note, that they are also feeding herbivorously, is apparently an error.

It is interesting that Willoughby as early as in 1686 (cited Day, 1887) considered salmon parrs as hybrids between salmon and trout and pointed out that they occur only in places where also salmon occur. All examined specimens

Table 3 — Dwarf salmon ("parrs") of Prof. Schäferna's (1933) collection, river Otava

	Ave.	Ranges
Smitt's length of body in mm	195	172—223
In % of body length:		
Head length	23.1	21—25
Width of interorbital space	6.2	6—7
Length of snout	8.5	6—7
Length of maxilla	7.2	7—8
Length of lower jaw	8.4	7—10
Longitudinal diameter of eye	3.0	4—6
Vertical diameter of eye	3.5	3—5
Predorsal distance	41.2	37—44
Length of base of dorsal fin	10.1	9—12
Height of dorsal fin	14.0	10—16
Length of pectoral fin	16.0	15—18
Preabdominal distance	29.4	28—33
Postabdominal distance	19.8	18—24
Preventral distance	48.8	47—52
Length of ventral fin	12.9	12—14
Length of base of anal fin	8.4	7—10
Height of anal fin	13.7	12—13
Dorsal length of caudal peduncle	9.5	7—13
Ventral length of caudal peduncle	11.3	9—13
Maximum body depth	18.1	15—20
Minimum body depth	7.6	6—12
Length of shortest caudal ray	9.2	8—10
Length of longest caudal ray	16.8	15—19

from the river Wye (Herefordshire, England) were males (!), the same was observed also by Ray (after Day l. c.).

According to Vacek (1924) yearlings of salmon in pond reached 27—32 cm of length after 2 years; in females ovaria were not fully developed, but males were ripe. Another trout breeder Bába (1929) reported that male salmon "two years" old are sexually ripe, and they were used formerly for artificial fertilization. Such males resemble normal parrs ("strdlice" in Czech); this is also confirmed by Schäferna (1933).

Sexual maturation of salmon in pond was proofed by Otterström (1933), Kulmatycki (1933). Schäferna (1933) found the weight of ripe "wild" dwarf salmon to be 180—210 g, total length 20—22 cm. With its juvenile "parr" coloration they resemble brown brook trouts (*Salmo trutta m. fario*). Schäferna (1933) and Dyk (1944) found them on the previous spawning places of migratory salmon in the river Otava, but Frič (1879) found such ripe dwarf males also in the lower part of the Vitava in Prague (Holešovice). In the rivers of the Soviet North young salmon spend not less than two years in fresh water (Berg, 1948), in Bohemia formerly female parrs after 2 years of freshwater life migrated downstream; with the overflow of the "third year", most males follow females (Bába, 1929). But from the above cited observations of Frič, Bába and Schäferna it is obvious that a considerable part of male population in Bohemia did not descend to the sea. This confirms statements of Berg (1948). Also Nikol'skij et al. (1947) found, in the upper part of the river Petshora, dwarf salmon males which lost their migratory instinct and, apparently, remained permanently in fresh water. In the river Petshora, spawning places were 1650—1750 km upstream of the river's

mouth. Migrating male spawners compose here 37 % of all specimens. Dwarf males play an important role in spawning. As a rule, dwarf males reach maturity here at the age of 2+, only insignificant number of largest specimens mature at the age of 1+ (Vadimirskaja, 1958, in Nikolskij, 1958).

According to Zarnecki (1960) some dwarf males which matured sexually in fresh water can later migrate seawards, and after a period of fastened growth in the sea they can enter the rivers again and resemble then the "normal" salmon males, but we have not found any source where this opinion would be experimentally confirmed. According to Nikolskij (1947) dwarf males were adult after 3 years and the length of 110 mm. Morphometrically they could be somewhat different from seaward migrating parrs, but the material of the late Professor Schäferna does not permit showing eventual differences. In dwarf males the juvenile coloration persists (Nikolskij, 1947); this we can also confirm. The size of parrs in the river Petshora ranged from 90—180 mm (ave. 129.7 in 25 specimens), the size of dwarf males was 110—210 mm (ave. 150.8 mm in 19 specimens). The age in normal parrs ascertained by Nikolskij was as follows: 2+ (17 sp.), 3+ (15 sp.), 4+ (2 sp.), from dwarf males most (11 sp.) were 3+, 7 sp. 4+, 1 sp. reached the age 5+.

M. Berg (1953) brought a full description of the "relict salmon" of the river Namsen, which looks "very much like a salmon parr".

The biggest specimen of the relict salmon examined by M. Berg (1953) weighed 160 g (maximum is given at 200 g), normally the weight is 100 g, maximum length 240 mm, very few specimens measured more than 200 mm. Spawning in 5th and sometimes in 4th year of life. When the relict salmon is mature it looks as if the growth will stop. In his samples M. Berg (1953) found few females with unreabsorbed eggs and "it looks as if the relict salmon usually spawn only once".

The river Namsen is a comparatively great river (drainage about 6300 km²), salmon may pass from the sea 72 km from the river mouth up to the great fall Fiskemfoss, which is almost vertical and about 40 m high. Higher upstream the relict salmon occurs in the river bed 90 km up to another high fall (M. Berg, 1953).

Three falls in the middle part of the river Namsen hinder now the penetration of the salmon from the sea, and the migration up to the springs of the river is hindered by two other falls. Therefore, seen from the point of recent occurrence, the immigration has probably taken place in the boreal stage some 8—9000 years ago.

Dwarf salmon of Schäferna (1933), dealt with again by us, resemble specimens figured by Berg, 1935, 1937, 1948, Nikolskij, 1971, Dyk, 1944, 1956. It is interesting that Frič (1894) ascertained only 2—3 % females at the parrs in the Otava; in our opinion this is a good proof that the dwarf salmon males were very frequent here and apparently the large migratory males reached the spawning places in small numbers. In *Salmo trutta trutta* one of us (O.) observed identical situation repeatedly during 1959—67 in the southern tributaries of the Vistula in Poland. It seems evident that in the end of the last century the dwarf salmon of the Otava matured normally, because the fertilizing of females of migratory salmon by dwarf salmon males was confirmed by Frič (1894) and was in common use. A similar situation was found in the river Petshora (Nikolskij, 1947), where dwarf males prevailed. The statement concerning the fertilization of eggs using dwarf males in artificial

Table 4 - *Salmo salar*, dwarf specimens of Prof. Schaferna's collection, river Otava. Beck calculated total lengths (L) in mm, with correction factor of 32 mm (R. Lee's method), in brackets ranges. Conversion factor total length = 1.04 Smit's length.

Age class	No of sp.	Mean	Weight in g.	l ₁	l ₂	l ₃	l ₄	l ₅	l ₆
II	1	176	50	97	170	—	—	—	—
III	4	186	70	97	150	197	—	—	—
		(170-203)	(68-83)	(86-120)	(130-166)	(187-211)	—	—	—
IV	6	187	77	80	129	169	177	—	—
		(170-194)	(65-100)	(64-95)	(103-148)	(146-182)	(180-206)	—	—
V	7	198	82	82	132	162	188	209	—
		(174-223)	(68-100)	(71-110)	(116-146)	(141-182)	(164-211)	(181-230)	—
VI	2	206	82	84	122	167	177	194	213
		(203-209)	(80-84)	(79-90)	(117-127)	(156-158)	(174-180)	(192-196)	(210-216)
Total	19	Mean	Mean	88	140	171	180	201	213
				(64-120)	(103-166)	(141-211)	(164-211)	(181-230)	(210-216)

Table 5 - *Salmo salar*, dwarf specimens, river Otava. Beck calculated total lengths (L) without correction (E. Lea's method), in brackets ranges, all measurements in mm. Conversion factor: Total length = 1.04 of Smit's length.

Age class	No of. sp.	Mean	l ₁	l ₂	l ₃	l ₄	l ₅	l ₆
II	1	170	80	164	—	—	—	—
III	4	186	79	141	193	—	—	—
		(170-203)	(62-106)	(119-160)	(180-211)	—	—	—
IV	5	187	58	119	166	198	—	—
		(170-194)	(39-74)	(89-140)	(140-184)	(180-206)	—	—
V	7	198	60	119	156	185	207	—
		(174-223)	(43-95)	(98-154)	(134-202)	(177-220)	(181-236)	—
VI	2	206	61	105	147	170	189	214
		(203-209)	(55-68)	(100-111)	(145-149)	(167-174)	(186-193)	(212-216)
Total	19	Mean	67	130	165	184	194	214
			(39-106)	(89-160)	(134-211)	(167-220)	(181-236)	(212-216)

breeding were cited by Berg, 1937, Otterström, 1938, Berg, 1948, but was known already to Shaw around 1835 (Hamilton, 1843). Shaw made experiments of this kind around 1835.

The life of dwarf salmon in fresh water was not known (Berg, 1948, Nikolskij, 1947, Vovk, 1954). Volf supposed (but without evidence!) that they finally also migrate seawards. Whereas the large migratory males after spawning mostly perish, dwarf males seem to take part in spawning repeatedly (Nikolskij, 1947); similarly Zukov (1965) mentioned that the great mortality in males is recompensed by occurrence of dwarf males ripening in fresh water without the necessity of sea life. According to Volf (1954), dwarf males of salmon occurred regularly in the Otava up to 1939, after 1948 they disappeared. The closing of the Bohemian Elbe for salmon by Sřekov dam was performed in 1935. This shows an apparent relationship between the simultaneous occurrence of the migratory and dwarf population of salmon. It is possible that dwarf salmon of the river Otava were outfished Hamilton (1843) noted that "parrs, preferring clear sunning streams with gravelly bottom, unlike the trout, their frequent companion, they seem to feed at all times, and are ever ready to take a bait". Dyk (in litt. June 21, 1979) observed on common salmon and trout biotops in the river Otava at Žichovice that parrs were more active in searching for food, also during conditions not optimal for trouts (e. g. at higher summer temperatures). Comparing activity of trouts and salmonons gave practical fisherman a rough idea about the relationship of both species at certain places. Šmidt (1947) cited two opinions about the bionomy of dwarf males: either they perish after 1—2 spawnings, or they finally migrate seawards (see Volf, 1954). Šmidt (1947) cited also the possibility that all salmon males mature already during life in the upper part of their native river. He drew attention also to the "total lack" of dwarf females, this is not true according to our observations. Volf (1954) was probably the first to notice that the artificial spawning of dwarf salmon females is not easy because the diameter of eggs is of such a size that the ova are extruded with much difficulty. In the dwarf female of salmon from the Otava Volf (1954) found 76 ripe eggs and 146 resorbed eggs in the right ovary, 61 ripe and 137 resorbed eggs in the left ovary, their diameter was 6 mm. The size of female is not given, but apparently it was within the range of 18.5—23.5 cm. The fertilization of eggs obtained was possible with the combination of brown brook trout and dwarf matured salmon males, but according to Volf (1954) "incomplete results showed that descendants obtained from "parr's eggs" had small life ability".

Volf (1954) studying dwarf salmon from the Otava had 20 specimens (19 males, 1 female), the sample of Professor Schäferna (20 males, 1 female) is almost of the same size. Also Frič (1894) stated that 95% of salmon parrs in the river Otava are males.

Otterström (1937) cited Frič's observations (1893) that among the Elbe parrs ("Struwitzen") 95% were males, and he gave a review of authors who observed similar mature parr's males in other European rivers. The male:female ratio corresponds well with Frič's view (1894) that normal parrs before reaching 30 cm migrated seawards. All Volf's (1954) dwarf salmonons were 3 years old (3 summers and 3 winters, or 3 summers and 2 winters, respectively), dwarf salmonons of Schäferna were older (from 3 summer and 3 winter seasons up to 6).

Although the occurrence of salmon in Bohemia belongs to the past, Frič's determination of Bohemian salmon as "true salmon", *Salmo salar*, was right. In Poland mos "salmons" belong to *Salmo trutta*, which reaches here a great weight, over 10 kg (sometimes even 15 kg, Zarnecki, 1960). For their meristic characters see Chelkowski (1970), biology Zarnecki (1960). Also Dyk (1944, 1956) recognized true salmon parrs living in the river Otava; in 1944 he brought a documentary photo of one specimen caught by M. Hlavsa in the Otava at Zichovice, another specimen, figured in 1956, was caught after 1945 (Dyk in litt. Jan. 7, 1980).

The differences between salmon and trout were noted by Frič (1894) and by Otterström (1935) and lately by Chelkowski (1970).

Young salmon usually spend from one to five years in rivers and then descend to the sea. In the rivers of the Soviet North, salmon usually spend three years in rivers. In countries with milder climate, the parr usually remain in rivers for only two years. Young males tend to remain in rivers for longer periods than females (Berg, 1948, Žukov, 1965). Sarmach (1951) stated that parrs migrate to the sea in their second year of life, having the length of 11–18 cm. He does not mention the presence of dwarf males. Muus and Dahlström (1968) estimated the length of salmon's river life as 1–5 years, longer in northern rivers, 1–2 years in the Rhine; "a part of future males remains in freshwater, these dwarf males are mature already when having 10–15 cm of length". Interesting is the note of Bade (1901) who cited that male parrs after finishing one year of life, 10–15 cm in length, had ripe milt in sufficient quantity. Walter (1913) noted "the relative sexual maturity" in many males of 1–2 years during seaward migration. Bauch (1954) estimated that the length of the river life of parr was 1–3 years, in Scandinavia 3–5 years. Otterström (1938) stated that in West Jutland young salmon most often emigrate after one year of the river life. Staff (1950) designated (1) 2–3 (4–5) years for the same period, Hamilton, more than a century before (1843), stated that "the first migration to the sea takes place in spring in the second season after birth".

Andrijašev (1954), in contrast with the common agreement found above, believes the river life of salmon in the Soviet North to be shorter, usually 3 years, but the range of this period is 1–5 years. After Žukov (1965) the length of the river life period is generally 2 years, with the range of 1–5 years; the migration begins in spring and continues in summer, parrs having the body length of 9–18 cm.

Scott-Crossman, 1973 give 2–3 years as the length of the river life for Canadian salmon, but in Ungava region, parrs do not go to the sea until at least 180 mm in length and at the age of 4–8 years. The existence of dwarf salmon males is mentioned by Hamilton (1843), Muus-Dahlström (1968), Bade (1901), Šmidt (1947), Žukov (1965), but not mentioned by Floericke (1913); here there is an evident error, because normally parrs do not migrate into the sea in the length of 40 cm!, Bauch (1954), Sarmach (1951), Staff (1950). Roule (1925) noted that males in the length of 15–18 cm after three years "prepare themselves to sexual maturity". According to Šmidt (1947) dwarf males are ripe at the age from 9 months to 3 years; in the North later, after 2–3 years.

According to Scott & Crossman (1973) there are taxonomical differences between freshwater and normal anadromous populations of the sal-

mon. "Landlocked" or freshwater salmon is usually smaller on the average than the sea-run salmon, but one specimen weighing 16.1 kg was caught in Sebago Lake, Maine, many years ago and salmon specimens weighing up to 20.4 kg were reported from Lake Ontario. The average weight of landlocked salmon is probably about 0.9—1.8 kg, but Lake St. John (Quebec) fish reached a maximum weight of about 3.5 kg. In Ladoga lake *Salmo salar* morpha *sebago* reaches 75.5 cm on the average (P r a v d i n, 1956). But we suppose that there are evident differences between the "landlocked" or "freshwater" salmon populations and dwarf, "neotenic" populations. "Landlocked" salmon, known as morpha *sebago*, migrates between lake and its tributaries at the time of spawning, whereas "normal" salmon between the sea and its tributaries. The lake habitats of morpha *sebago* can be compared with the sea habitat of anadromous. However dwarf, "neotenic" form is represented chiefly by males (this is not known in morpha *sebago*) and apparently due to space and food conditions it remains very small in size; its growth is also slow. In morpha *sebago* the growth accelerates after emigration of parrs into the lake similarly as it is observable in parrs emigrating into the sea in anadromous form (Tab. 6). Therefore they are two forms of freshwater salmon, the dwarf one (examples from the upper Vltava, the upper Petshora, the upper part of river Namsen, Norway), and the freshwater "relict" salmon, or *Salmo salar* morpha *sebago*, known from Lake Ladoga (USSR), Lake Vänern (Sweden), Lake Sebago (Maine, USA), the river Otra and Lake Byglandsfjorden (Norway, according to D a h l, 1928, cited by M. B e r g, 1953).

A review of "relict forms" of salmon in Norway, Sweden, the Soviet Union and Northeast America is given by M. B e r g (1963). Very interesting is the fact cited by M. B e r g (1953) that the salmon acclimatized on the southern island of New Zealand (population in the lake Te Anan) transformed in the majority into the landlocked form, in spite of the fact that there is a large river Waiau, flowing without any serious obstructions from the lake to the sea. The landlocked salmon migrates here between the lake, where it feeds, and the river, where it spawns.

The dwarf salmon resembles the brook population of brown trout (*Salmo trutta* morpha *fario*). It differs by prevailing number of males. The "sebago" salmon could be compared with the lacustrine form of brown trout (*Salmo trutta* morpha *lacustris*) migrating between lake and its tributaries, with changed growth after descending into the lake, natural or artificial. From Czechoslovakia we have examples from the Klíčava valley water reservoir in central Bohemia, F r a n k (1959). The nominal form of brown trout, *Salmo trutta trutta*, is migratory and its habits are similar to those of anadromous salmon and therefore it is often confused with the latter, *Salmo salar* (e. g. by professional fishermen in Poland until recently). Outstanding accounts about the life history of the salmon in the last century are those of D a y, 1887 and S m i t t, 1895, recently those of B e r g, 1935, 1937, 1948.

G r o w t h

Numerous papers deal with the growth of the salmon, and it is impossible to review them here. Generally, the growth of the salmon is slow in the river and on the contrary very fast in the sea. The "landlocked salmon" grows more slowly and makes little additional growth after the first spawning. The "dwarf" salmon grows very slowly during the whole freshwater life and additional

Table 6 — The growth of dwarf and landlocked salmon, *Salmo salar*, from different selected localities (in mm).

Locality	author	No of sp.	1 ₁	1 ₂	1 ₃	1 ₄	1 ₅	1 ₆	1 ₇	1 ₈
Orava	authors	19	88	140	171	180	201	213	—	—
Upper Petshora dwarf males	Nikolskij et al. 1947	18	45	85	115	—	—	—	—	—
Upper Petshora normal parrs	Nikolskij et al. 1947	24	52	94	127	—	—	—	—	—
Tuloksa, drainage of lake Ladoga (3 years of river life), landlocked	Volkova, 1948, Fide Prozorova, 1951	—	50	108	136	386	495	602	698	755
River Šuja, drainage of Lake Omega, landlocked	Prozorova, 1951	38	52	132	330	490	632	760	864	—
Astray Lake, Ungava, (landlocked)	Power, 1958 Fide Scott-Crossman, 1973	—	63	114	174	248	328	412	508	—
River Nansen, Norway, 1948, dwarf	M Berg, 1953	15	34	67	105	140	163	168	185	—
River Nansen, Norway, 1950, dwarf	M Berg, 1953	15	33	80	127	158	181	—	—	—
River Melingselva Norway, 1950, dwarf	M. Berg, 1953	31	27	82	134	165	176	—	—	—
Terra Nova River System, New Foundl landlocked	Andrews, 1966 Fide Scott-Crossman, 1973	—	99	113	176	217	250	281	320	385

growth after sexual maturity is not observed. As regards growth, the landlocked form of the salmon represents an intergrade between the sea-run salmon and the dwarf one (see Tab 6). From these results analogies between sea-trout (*Salmo trutta trutta*) and salmon (*Salmo salar*) are evident. Both have "dwarf" forms, living in freshwater and their growth after sexual maturity is slow. Both have landlocked forms. In trout they are very frequent and occur in lakes (lacustrine form or morpho *lacustris* in the trout) or now also in large valley water reservoirs in central Europe. They have transformed here from populations of "dwarf" trouts from brooks, trouts from affluents of riverine lakes, or as in Czechoslovakia, they have also been planted artificially using eggs of "original" lacustrine form from some European lakes. Finally, both salmon and trout have anadromous, sea-run forms. In trout the accommodation to the full freshwater life is better than in salmon.

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SUMMARY

1. The morphometric characters and growth were studied in 21 salmon parrs from the river Otava, collected around the year 1932 by the late Professor K. Schaferna, and 5 additional parrs from the year 1884 from the material of the late Professor A. Frič.

2. In 21 salmon parrs of the body length (according to Smitt) 172—223 (ave. 195) mm following meristic characters were found: D III 9—11, A III 9—11, P I 11—14, V I 8—10, 11 scales 112—124 (118), 22—25 (23) scales above lateral line, 18—21 (20) scales below it, 19—22 (20) branchial spines (gillrakers) on the first branchial arch, 11—13 (12) branchiostegal rays. Moreover, 22 plastic characters were studied.

3. All examined salmon parrs were found to be ripe sexually, males prevailing.

4. Growth study using scale structure showed slow growth (Smitt's length of body was following 1₁-88, 1₂-140, 1₃-171, 1₄-180, 1₅-201, 1₆-213).

5. Ripe status of gonads, small size and small growth, especially after 2nd or 3rd year of life, appear to identify the Otava salmon parrs with dwarf ("neotenic") race of salmon in the sense of Berg, 1935, 1937, 1948 and Nikolskiĭ et al., 1947.

6. This investigation confirmed that Bohemian salmon belonged to the true salmon and not the sea-trout, and that also the Labe (Elbe) salmon was characterized by both races, large anadromous and dwarf, neotenic. This dwarf race was later found in the rivers of northern Europe, e.g. in the river Petshora.

7. The existence of population of dwarf salmon in the river Otava was connected with regular migrations of anadromous salmon stock towards its breeding places. Although the way for the sea-run salmon was closed in 1934, the dwarf population of salmon disappeared totally only after 1948.

8 It is not clear if the disappearance of dwarf salmon was caused by the missing population of the sea-run stock or owing to human activity (angling)

9 There are evident analogies between the anadromous population of the sea trout (*Salmo trutta trutta*) in the river Vistula existing until 1968, with almost absolutely prevailing migratory females and anadromous population of the Atlantic salmon (*Salmo salar*) entering until 1934 through the Labe and the Vltava the affluent of the latter, the river Otava in southern Bohemia, where also large anadromous females prevailed

10 With regard to Berg's concept of taxonomical units in ichthyology, and evident analogies between the sea-trout (or salmon trout, *Salmo trutta trutta*) and the salmon (*Salmo salar*), we propose to designate the purely riverine dwarf salmon sporadically occurring together with anadromous form of the salmon, as *Salmo salar* morpha *pygmaea*, n m Their habits occurrence and size are different from another freshwater form of the salmon previously described namely *Salmo salar* morpha *sebago* Girard, 1853 (= *Trutta salar* var *relicta* Malmgren, 1863 called "lake Atlantic salmon, landlocked salmon Sebago salmon")

11 The reports of the late Professor A Frič († 1913), one of the most outstanding investigator into salmon biology in the last quarter of 19th century, who at first pointed out the occurrence of ripe salmon parrs in Bohemia were fully confirmed as well as a preliminary note to this problem by the late Professor K Schaferna († 1950)

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The plates will be found at the end of this issue.

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**REPRODUCTIVE RATE AND LONGEVITY IN SEMIADALIA UNDECIMNOTATA
AND COCCINELLA SEPTEMPUNCTATA (COCCINELLIDAE, COL.)**

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Abstracts. In Czech populations, longevity and fecundity were distinctly lower in *Semiadalia undecimnotata* Schneider than in *Coccinella septempunctata* L., when reared after hibernation on *Acyrtosiphon pisum* Harris under two laboratory regimens (12 L : 12 D and 20–24 °C or 18 L : 6 D and 21–24.5 °C). In both species, longevity of males was considerably higher than that of females. The hatchability of eggs in *S. undecimnotata* was lower than that of *C. septempunctata* under both regimens.

The ovipositional response to the abiotic conditions proved to be more heterogeneous and plastic in the population of *C. septempunctata* than in *S. undecimnotata*. This makes possible considerable modifications of the course of oviposition of *C. septempunctata* by photoperiod. In *S. undecimnotata* where the majority of females had a continuous oviposition analogical modifications can not be provoked.

The total fecundity of *S. undecimnotata* in France in active beetles collected in hills and in activated dormant beetles from hibernation sites in mountains was similar. Dormant coccinellids had a higher oviposition rate in the first half of the oviposition period. The fecundity of beetles from France was slightly higher than that in the Czech sample. The relation of the reproductive rate and survival to the reproductive strategies of both species is compared.

INTRODUCTION

For biological control of aphids their predators are required in large quantities. Attempts to use aphidophagous coccinellids in greenhouses have been made (Gurney, 1971; Hämäläinen, 1977 a; Markkula, Tiittanen, Hämäläinen, 1972). The possibility of permanent mass production of e.g. *C. septempunctata* in the laboratory is hampered by gradual decrease in vigour (Hodek, Čerkasov, 1961; Hämäläinen, Markkula, 1972 a) and after several successive generations the culture must be renewed with coccinellids collected in nature. The course of oviposition and the fecundity are among the most important parameters of the predators used in inundative releases.

Collections of beetles in their dormancy sites provide us with a high initial number of females at a similar physiological state. Both coccinellids *Semiadalia undecimnotata* Schneider and *Coccinella septempunctata* L. have a very long period of inactivity lasting from late August for about nine months. In Central Europe the intensity of diapause during the second half of their inactive period can be concerned as low in both species. Low level of the primary photoperiodic response was found in *C. septempunctata* (Hodek, 1977) From our experiment (Hodek, Růžička, 1977; 1979) we could conclude that *S. undecimnotata* is less sensitive to photoperiod than *C. septempunctata*.

The survival of dormant *C. septempunctata* is poor when the beetles collected in nature at the beginning of their hibernation are stored under low constant temperature (Hämäläinen, 1977 b). Also the eggs of this species can't be stored for more than one week (Hämäläinen, Markkula, 1977).

The coccinellids may be collected in their hibernation quarters in early spring for their most probable use in greenhouses. We studied the influence of two rearing conditions on the course of oviposition, fecundity, hatchability of eggs and longevity of both sexes of overwintered *S. undecimnotata* and *C. septempunctata*. The fecundity of active females of *S. undecimnotata* from hills and dormant females from the high mountains was compared in France.

MATERIALS AND METHODS

Czech samples of *Semiadalia undecimnotata* Schneider and *Coccinella septempunctata* L. were transferred from their dormancy sites at the volcanic Louny hills (northern Bohemia) to experimental conditions at the onset of their dispersal on 16th May 1974 and 11th May 1975 respectively. From the following day series of individual pairs of each species were reared under the photoperiod of 12 L : 12 D at a temperature alternating daily between 20 and 24 °C, or under 18 L : 6 D at 21—24.5 °C (later short and long day). 35 pairs of *S. undecimnotata* and 30 pairs of *C. septempunctata* were reared at each regimen.

The beetles were kept in 100 ccm containers and provided in surplus with *Acyrtosiphon pisum* Harris on seedlings of *Vicia faba* and with water. Food was supplied every day, exceptionally in two day intervals. At the same time the eggs were counted including the remains from cannibalised eggs and the beetles were transferred to new containers. Females were given substitute males for the dead ones. Under fecundity we understand the total number of eggs laid by a female during the experiments.

The recorded egg hatching rate of both coccinellids must be considered as approximate due to unavoidable cannibalism of eggs by adults and newly hatched larvae. For control of the egg hatching rate samples of the egg batches were used in 15 day intervals. We considered as unhatching only batches in which the percentage of the hatched eggs decreased below 20. The mortality recorded in the samples and shown also on our histograms was then related to the total number of eggs laid in corresponding 15 day periods and thus the approximate total mortality was calculated.

French samples of *S. undecimnotata* were collected either in hills or high mountains. The first sample included 27 pairs of young and active beetles collected near Digne (625 m) in the last decade of July 1975. The second sample was taken immediately after the arrival to the hibernation quarters in the first decade of August 1975. This sample included 16 pairs of young and dormant beetles from Mount Saint Michel de Cousson (1515 m). Activation of the second sample was performed at 25 ± 1 °C, 60—70 % r. h. under long day during 15 days. Then the temperature was slightly lowered to 21—24 °C while the other conditions remained unchanged. The beetles were supplied with a surplus of *Aphis fabae* Scop. and the oviposition was recorded daily.

RESULTS

Pre-, inter- and postoviposition periods

The recording of oviposition by individual females revealed considerable polymorphism in the ovipositional pattern under both regimens particularly in

C. septempunctata. We divided the females arbitrarily into two groups according to their continuity of oviposition. Oviposition was considered as continuous when it was not arrested for more than two days in *S. undecimnotata* or more than three days in *C. septempunctata*. Females with longer interoviposition arrest were denoted as females with inter-OA.

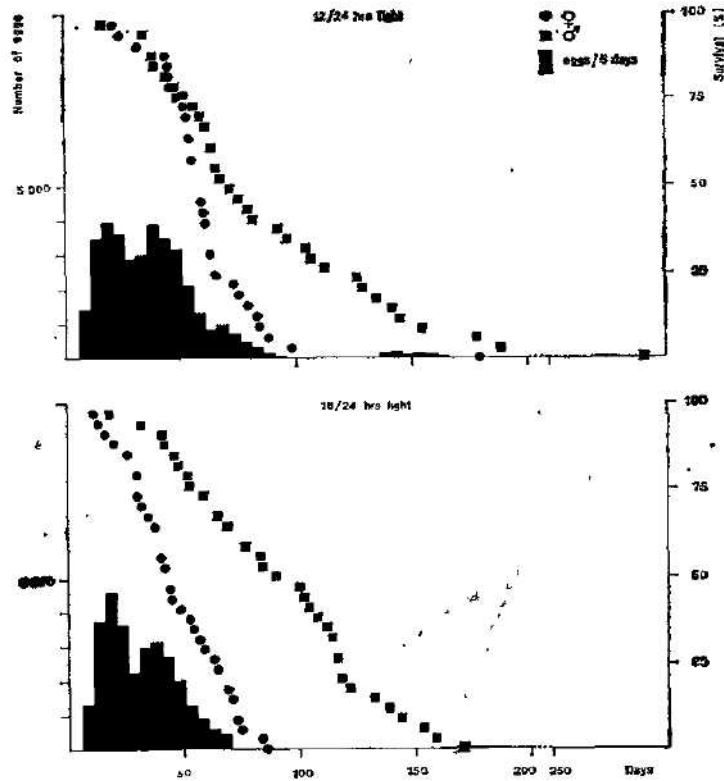


Fig. 1. Course of oviposition and longevity in *Semiadalia undecimnotata*.

As the first ovipositional period in *C. septempunctata* was in a few cases considerably reduced to three or one day only, also those females which revealed one undivided period of egg laying after unusually long preoviposition period were included into the group of females with inter-OA, as well as one aberrant female which laid few eggs at the beginning of the experiment, but later did not oviposit at all, though her life span was the longest one.

In *C. septempunctata* the continuously ovipositing females started to lay eggs after 6 days, the females with inter-OA after 16 days under short day and after 3 and 15 days under long day. We can see a similar difference also in the length of the postoviposition period. Under short day the continuously ovipositing females of *C. septempunctata* survived 5 days, the females with inter-OA 10 days after the last egg was laid. (One female with the longest life span, small early oviposition and very long postoviposition period was excluded.) Under long day the females died almost immediately after they stopped egg

laying. The mean duration of inter-OA differed a little between short and long day amounting to 50 and 42 days.

Females of *C. septempunctata* with inter-OA laid under short day during the 1st oviposition period only 18 % of all eggs and 30 % under long day. When we compare the daily oviposition in continuously ovipositing females and females with inter-OA over the period during which the eggs were ac-

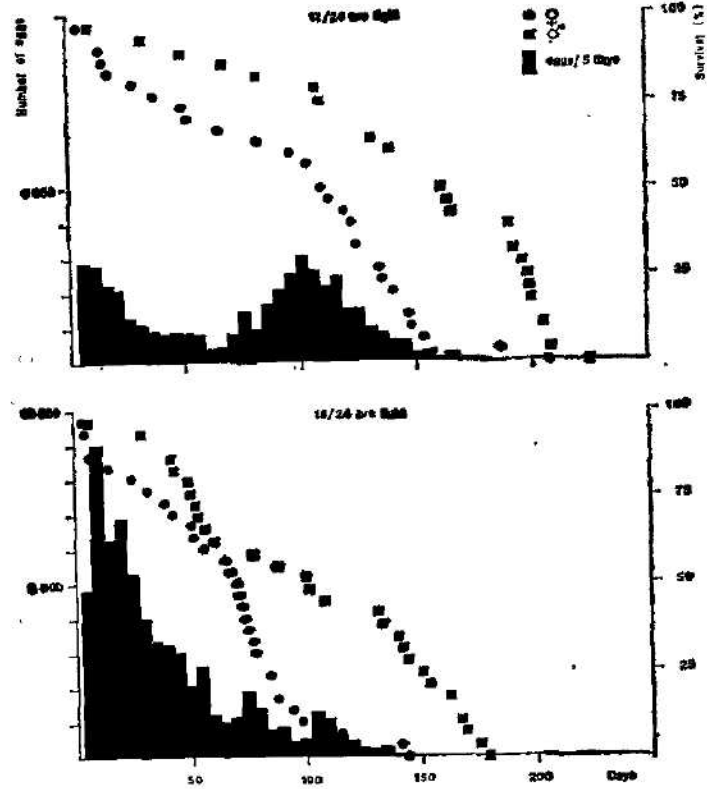


Fig. 2. Course of oviposition and longevity in *Coccinella septempunctata*.

tually laid, we can see in continuously ovipositing females a higher oviposition rate both under short (46 to 38 eggs/day) and long day (51 to 46 eggs/day).

On the contrary the differences in duration of preoviposition period and postoviposition period were small in *S. undecimnotata* and the mean inter-OA dropped from 17 days under short day to 5 days under long day regimen. The inter-OA was exceptionally longer than 30 days and this only under short day.

Longevity

The laboratory posthibernation longevity of both sexes was shorter in *S. undecimnotata* than in *C. septempunctata* under both conditions (Figs 1 and 2). A great difference has been found between longevity of females with continuous as discontinuous oviposition in *C. septempunctata* under short day. Mean

Table 1 — Longevity of *Semiatlata undecimnotata* and *Coccinella septempunctata* adults reared after diapause under two different laboratory conditions

Species	Photoperiod	Type of numer. data	Longevity in females with inter-ovipositional arrest lasting 0-2 days	> 2 days*	Longevity in all ovipositing females	Longevity in non-ovipositing females	Longevity in all females	Longevity in males
<i>Semiatlata undecimnotata</i>	12L : 12D	Mean ± SD	55.5 ± 16.0	81.8 ± 39.7	62.6 ± 26.8	—	62.6 ± 26.8	91.3 ± 55.6
		range (median) n	21-88 24	52-179 9	21-179 33	— 0	— 33	21-179 (59) 16-291 (73)
	18L : 6D	Mean ± SD	47.9 ± 20.2	54	48.3 ± 19.8	11	47.2 ± 20.5	92.1 ± 39.3
		range (median) n	16-86 31	45-63 2	16-86 33	— 1	— 34	11-86 (44) 18-171 (95)
<i>Coccinella septempunctata</i>	12L : 12D	Mean ± SD	51.1 ± 40.5	130.8 ± 37.4	107.5 ± 52.0	02.8	101.1 ± 55.2	150.5 ± 58.9
		range (median) n	14-112 7	51-207 17	14-207 24	4-124 4	4-207 (116) 28	4-225 (162) 9-225 (162)
	18L : 6D	Mean ± SD	58.2 ± 26.9	95.5 ± 34.8	69.7 ± 33.7	24.3	63.6 ± 37.3	103.3 ± 55.1
		range (median) n	6-98 18	50-144 8	6-144 26	3-84 4	3-144 (69) 30	6-205 (101) 29

*) Interovipositional arrest in *C. septempunctata* 0-3 and > 3 days due to longer life span of this species.

longevity of continuously ovipositing females was 51 days while females with inter-OA lived on average 131 days. This difference was less pronounced in females of *C. septempunctata* under long day and in females of *S. undecimnotata* under both day lengths (Table 1).

The males of both species survived under both conditions distinctly longer than the females. While in both species longevity of females was distinctly higher under short day it was not so with *S. undecimnotata* males. Under both conditions the life span of the females of *S. undecimnotata* represented approximately 2/3 of the time recorded in females of *C. septempunctata*. In the longevity of *C. septempunctata* males a similar picture was found under short day.

Under the long day laboratory conditions 50% of *S. undecimnotata* females collected in their dormancy sites at the beginning of August in France survived twice longer than 50% of overwintered females collected in the hibernation quarters in early spring in Bohemia. The difference between dormant and active females in France was small (Fig. 3).

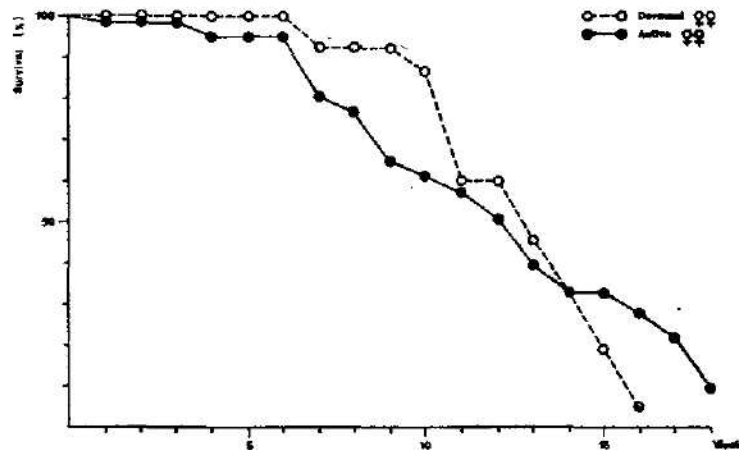


Fig. 3. Longevity of *Semiadalia undecimnotata* in France.

Egg hatching rate

Changes in hatchability during the egg laying period are given in Fig 4. Generally the hatchability was lower in *S. undecimnotata* than in *C. septempunctata*. We did not follow whether (and to what degree) the hatchability depended on females or males. The approximate total mortality did not differ very much under short and long day. It was 15% under short day and 17% under long day in *C. septempunctata*, 27% under short day and 22% under long day in *S. undecimnotata*.

Fecundity and oviposition rate

The average total fecundity of the smaller females of *S. undecimnotata* was markedly lower than in *C. septempunctata* (Table 2). Under long day it represented only 37% and under short day 59%.

While in the thermophilous *S. undecimnotata* collected at the northern limit

of its distribution area the average fecundity did not differ distinctly under the two conditions, the females of the euryoek *C. septempunctata* produced a much higher number of eggs when reared under long day. Oviposition of *S. undecimnotata* was slightly lower under long day (87 %) while, on contrary, oviposition in *C. septempunctata* was significantly suppressed under short day: it amounted to 72 % of the value of the long day.

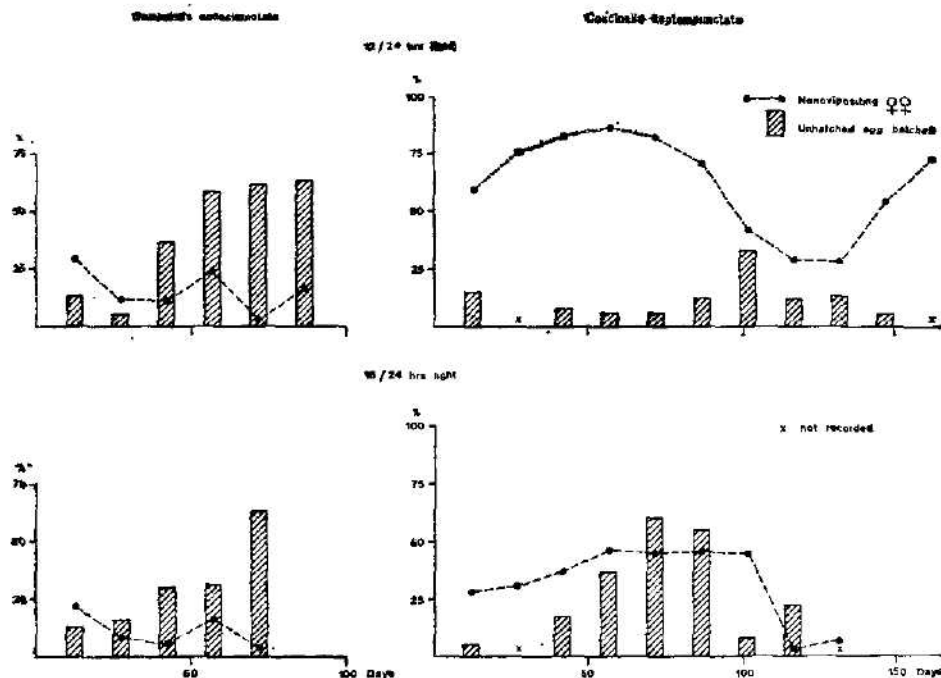


Fig. 4. Hatchability of eggs and degree of nonovipositing females in 15 day intervals in *Semiadalia undecimnotata* and *Coccinella septempunctata*.

In both species the highest fecundity was recorded under long day. The highest fecundity under short day was, however, only a little lower (Table 2 — range of fecundity).

There is the possibility to modify the oviposition rate over the egg laying period in *C. septempunctata* by abiotic conditions, particularly by the photoperiod. This, however, does not apply to *S. undecimnotata* (histograms on Figs 1 and 2).

The fecundity of females of *C. septempunctata* and *S. undecimnotata* with inter-OA varied a little under long day. The fecundity of individual females with inter-OA was close to the total average of fecundity and their highest fecundity was near to 50 % of the highest fecundity observed in the continuously ovipositing females.

The relation between longevity and fecundity shows that under both conditions the population of *C. septempunctata* splits into two considerably different groups. In *S. undecimnotata* this may be seen only in a low proportion

Table 2 — Fecundity of *Semiadalia undecimnotata* and *Coccinella septempunctata* reared after diapause under two different laboratory conditions

Species	Photoperiod	Type of numer. data		Fecundity in females with inter-ovipositional arrest lasting		Total average of fecundity
		Mean \pm SD range (median) n	0-2 days	> 2 days*		
<i>Semiadalia undecimnotata</i>	12L : 12D	Mean \pm SD range (median) n	1096 \pm 508 180-2228 24	911 \pm 415 151-1358 9	1046 \pm 485 161-2228 (1058) 33	
	18L : 6D	Mean \pm SD range (median) n	913 \pm 565 19-2258 31	926 818-1034 2	914 \pm 548 19-2258 (850) 33	
<i>Coccinella septempunctata</i>	12L : 12D	Mean \pm SD range (median) n	1837 \pm 1727 201-4793 7	1758 \pm 1251 4-3516 17	1781 \pm 1367 4-4793 (1911) 24	
	18L : 6D	Mean \pm SD range (median) n	2674 \pm 1515 70-4918 18	1999 \pm 363 1517-2520 8	2467 \pm 1304 70-4918 (2203) 26	

*) Interovipositional arrest in *C. septempunctata* 0-3 and > 3 days due to longer life span of this species — see longevity in Table 1.

of population under short day; the females with inter-OA were found exceptionally under long day (Figs 5 and 6).

The test of difference between the regression coefficients of the continuously ovipositing females and females with inter-OA in *S. undecimnotata* is significant at $p < 0.001$ under short day (Fig. 5). There is no significant difference between regressions of continuously ovipositing females under short and long day.

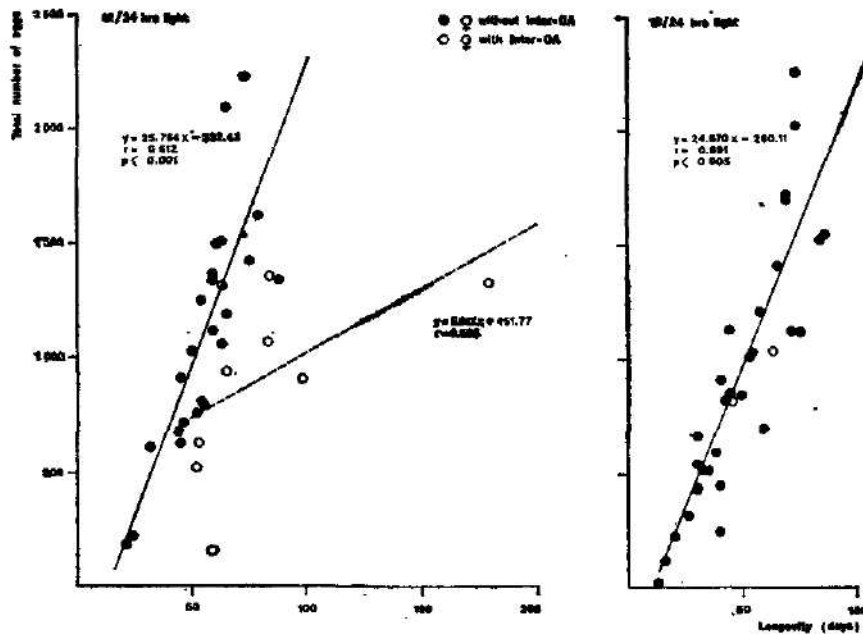


Fig. 5. Relation between longevity and oviposition in *Semiadalia undecimnotata*.

The test of difference between the regression coefficients of the continuously ovipositing females and the females with inter-OA in *C. septempunctata* is significant at $p < 0.05$ under short day and at $p < 0.01$ under long day (Fig. 6). There is neither a significant difference in regressions of continuously ovipositing females under short and long day, nor in regressions of females with inter-OA under these two light regimens.

Females with inter-OA seemed to form two main groups under short day conditions. The first group formed females which laid less than 1100 eggs, the second females with the fecundity higher than that. The difference between the average longevity of these two groups is negligible (128 and 132 days). The regression equation for the first group of females with inter-OA is $y = 17.708x \pm 197.95$, $r = 0.707$ and $p < 0.02$, for the second group it is $y = 0.747x \pm 224.63$, $r = 0.108$ and nonsignificant. The test of difference between the regressions of these two groups of females with inter-OA is significant at $p < 0.05$.

The test of difference between the regression coefficients of continuously ovipositing females and the first group of females with inter-OA is significant

at $p < 0.001$. The analogous test of difference for the second group shows significance at $p < 0.005$. The test of difference between regressions of each of the two groups of females with inter-OA under short day and the regression of females with inter-OA under long day conditions are nonsignificant.

A successful development of the parasite *Perilitus coccinellae* Schr. does not have to cause always an early death of the female of *C. septempunctata*. The

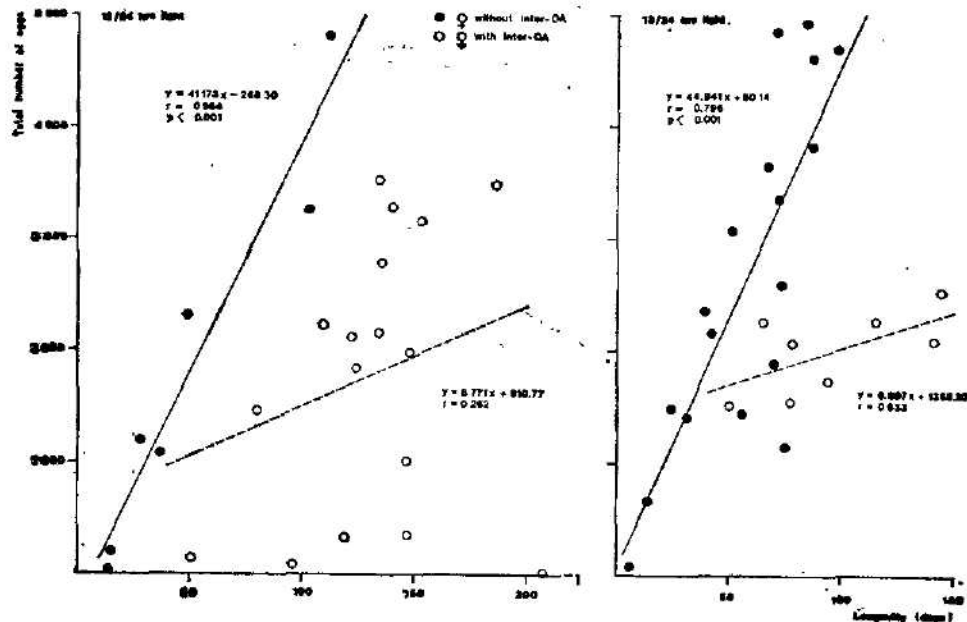


Fig. 6. Relation between longevity and oviposition in *Coccinella septempunctata*.

first oviposition has been observed in one of the parasitized females of this species 67 days after the parasite emerged. This female survived 82 days under short day regimen. The fecundity of this female was 308 eggs.

The comparison of fecundity between active hill population and dormant high mountains population of *S. undecimnotata* in France and comparison of their fecundity with that observed in the experiments with Czech populations of this species are given in Fig. 7. The high mountains females oviposited on an average of 1233 eggs and maximum longevity was 16 weeks. The females from hills oviposited on an average of 1121 eggs and lived 18 weeks at the longest. The difference between the total fecundity of the two groups is statistically not significant. During the first six weeks high mountains females oviposited about 30% more than the females from hills (Fig. 8).

DISCUSSION

Discontinuous oviposition of *C. septempunctata*

A high proportion of females interrupted oviposition for periods longer than three days; under short day about 2/3 of females displayed such an arrest of

oviposition and under long day this proportion amounted to about 1/3. The markedly higher longevity of females displaying such an arrest, particularly under short day, indicates, that a second diapause was entered by these females.

The percentage of ovipositing females of *C. septempunctata* reported by Härmäläinen (1976) who reared them also under 18 hrs light and 6 hrs

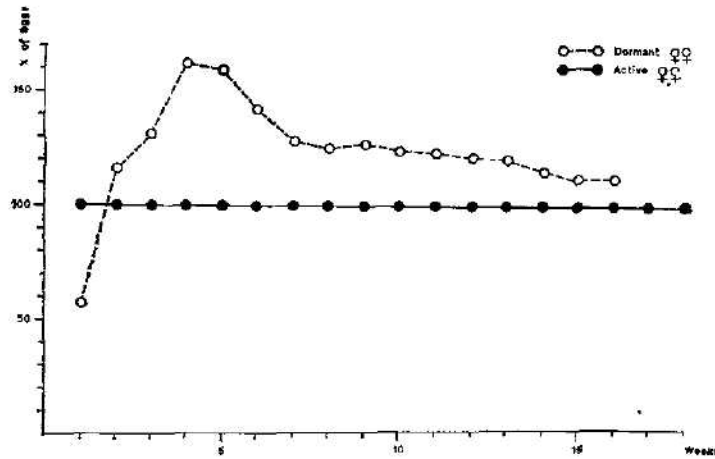


Fig. 7. Fecundity of *Semiadalia undecimnotata* in France and Bohemia.

darkness photoperiodic cycle and constant 24 °C over 11 generations is in accordance with our results. Those four generations where he observed the highest average fecundity accompanied by high hatchability of eggs and also relatively high mortality are most likely generations in which prevailed continuously ovipositing females.

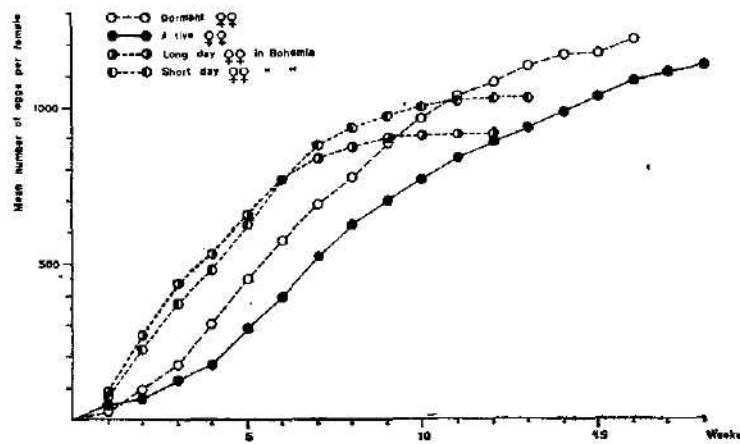


Fig. 8. Comparison of fecundity between active and dormant *Semiadalia undecimnotata* in France.

The females which entered the second diapause even at transfer to extreme high laboratory temperature conditions in our experiment might be in the field those, which would normally remain diapausing over spring and summer and next winter or lay only few eggs and enter a new dormancy. The importance of the recurrent photoperiodic response for this phenomenon and the polymorphism in diapause tendencies are discussed elsewhere (Hodek, Růžicka, 1979).

Longevity

The longevity of males was found to be considerably higher in both species studied. No consistent difference has been found in the longevity between males and females of *Harmonia axyridis* Pallas regardless of the aphid species consumed (Hukusima, Kamei, 1970), on contrary, in overwintered populations of *Propylaea japonica* Thunberg the longevity of males appeared to be shorter than that of females (Hukusima, Komada, 1972).

Fecundity and egg mortality

The ascertained fecundity of *C. septempunctata* was slightly higher than in a Finnish population fed on the same aphid. When other aphid species were used as prey (*Macrosiphum rosae* and *Myzus persicae*), the fecundity was much lower (Hämäläinen, Markkula, 1972 b, Hämäläinen, Markkula, Raij, 1975). Also the highest fecundity of *C. septempunctata* (3765 eggs recorded by Bagal, Trehan (1945)) is much lower than the maximum value from our experiment. The higher fecundity, as well as the proportion of hatched eggs, in our experiment can be explained by steady surplus of essential prey and besides that, probably also by the fact, that in some of the earlier studies the eggs which were destroyed partially by the adults or the first instar larvae were not counted.

The slight difference between the fecundity of two populations from south-eastern France may be due to different physiological conditions of coccinellids in the two samples. The higher fecundity of females which were collected at the very beginning of dormancy was apparently caused by the presence of fat and glycogen reserves which are very abundant in this species (Hodek, 1973, pp. 155—160). It is possible, however, to explain it also by introducing a genetic factor. On high mountains coccinellids from several locations accomplish their migratory flight while the population from hills is from a single location. The genetic variability of high mountains population is higher and the heterosis phenomenon might play a role.

Overwintered adults of *Propylaea japonica* were reported to have a much higher fecundity than the previous nonhibernating generations (Hukusima, Komada, 1972). The oviposition of females in the experiments which were carried out in France could be affected by a similar factor.

The importance of copulation after hibernation has been reported for *P. japonica* (Hukusima, Komada, 1972). In our experiments we have received quite a similar degree of egg mortality for the abundant *C. septempunctata* in comparison with that found for *P. japonica* copulating after the hibernation. In the rather rare *S. undecimnotata* we can presume that the probability of meeting outside the overwintering place is rather low and therefore the copu-

lation in hibernation quarters is important. Under the given laboratory conditions regular copulation was enabled and perhaps responsible for the lower degree of egg mortality than was recorded in *C. septempunctata*.

Fecundity of the two coccinellids in relation to their reproductive strategies

The number of eggs produced by *C. septempunctata* under long day was about three times as large as in *S. undecimnotata*. This difference is in accordance with the general presumption that the reproductive rate of animals grows within one taxonomic group with the increase in latitude (Price 1975, p. 151). The thermophilous *S. undecimnotata* is a species restricted in its occurrence to warmer temperature regions; Bohemia lies in the most northern border of its distribution area, while in Germany and Poland this species is absent (Bielański, 1959). On contrary, the ubiquitous *C. septempunctata* occurs abundantly also in the northernmost areas of the Palaearctic region.

C. septempunctata is a coccinellid with extreme ecological plasticity, which ranges from the wide eurytopy both during the active period and hibernation, to the considerable polymorphism in photoperiodic response and hence in life-cycle (Hodek, Růžicka, 1979). This species sacrifices a part of its population in order to make use of periods uncertain for development, and was therefore once denoted as a "daring" coccinellid, in contrast to "cautious", less plastic species, e.g. *S. undecimnotata* (Hodek, 1966). According to the theory of reproductive strategies (MacArthur, Wilson, 1967; Pianka, 1970) these features shift *C. septempunctata* in the direction of r-selection, whereas *S. undecimnotata* to k-selection. The large difference in fecundity found under long day (which was similar to natural photoperiods) ruling in the course of the reproductive period, is in full accordance with the above anticipation.

The relation between the longevity and the fecundity of the two species studied does not follow another assumption of the theory on reproductive strategies. The species with larger fecundity per season should have lower survivorship (Price, 1975, p. 159). On contrary, *C. septempunctata*, which has about three times higher fecundity than *S. undecimnotata*, has also about 50 % higher longevity. The above rule, valid e.g. in lizards and Carabidae, does not hold true for Coccinellidae in our studies for evident reasons. The interrelationship is assumed to be mostly caused by the higher vulnerability by predators of females loaded with eggs or laying eggs. This dependence may generally be limited in Coccinellidae as they are supposed to be unpalatable to at least some predators (Hodek, 1973, p. 197). It was, of course, totally excluded in our laboratory cultures.

Acknowledgements

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Kreismuseum in Tachov

**QUALITATIVE UND QUANTITATIVE ZUSAMMENSETZUNG
VON NISTSYNUSIEN DER VÖGEL IN DER STADT TACHOV
(SÜDWESTBÖHMEN)**

Pavel ŘEPA

Eingegangen am 18 Januar 1980

Abstract: The author made in the years 1974–1978 an investigation of both qualitative and quantitative composition of bird synusiae in the little town Tachov (14 000 inhabitants). The method of mapping the nesting territories was used. Several biotopes were distinguished hereby, viz. a new housing quarter, a cottage quarter in the town centre, a cottage quarter in the outskirts, the town parks and the parks neighbouring on the town. For each biotope the total density, the species number, the synusia diversity and the representation of individual species were ascertained. By comparison with the data from other Central European towns it was found that the composition of bird nesting synusiae was not different from the same biotopes in big towns.

EINLEITUNG

In dieser Arbeit lege ich eine Übersicht von Nistsynusien der Vögel in einzelnen Biotopen der Umwelt einer Kleinstadt von landlichen Typ (Tachov in Südwestböhmen). In der Literatur sind viele ähnliche Angaben aus mitteleuropäischen Mittel- und Großstädten zu finden (siehe die Literaturübersichten bei Er z 1964 und H u d e c 1976). Die Angaben über Kleinstädte sind weit seltener (K o r o m p a i 1964–5, Z e n k e r 1974).

BESCHREIBUNG DER UNTERSUCHTEN STADT TACHOV

Tachov (14 000 Bewohner) liegt am Flusse Mže, am Ostfuss des Gebirges Český les (= böhmische Seite des Oberpfalzer Waldes) in Südwestböhmen, in einer Seehöhe von 490–540 m. Die Stadt besteht aus einem alten Teil (vorwiegend Villen und Einfamilienhäuser) und aus zwei neuen Wohnsiedlungen. Die städtische Gassenverbauung mit zusammenhängenden mehrstöckigen Häuserblöcken ist nur auf den Platz beschränkt. Die Industriebetriebe werden durch kleine, über die Stadt zerstreute Objekte repräsentiert. Im alten Stadtteil befinden sich einige Parke und zerstreute Gruppen von alten Bäumen. Die Stadt ist vorwiegend von einer landwirtschaftlich ausgenutzten Gegend umgeben, nur im Westen grenzt sie an einen Kiefernwald und im Süden an die stadtnahen Parke.

Das Klima ist ziemlich rau. Die jährliche Durchschnittstemperatur beträgt 6–7 °C, die Durchschnittstemperatur während der Vegetationsperiode 11–12 °C, durchschnittliche Jahressumme der Niederschläge 700–800 mm (S y r o v ý 1958).

In Abb. 1 sind im schematischen Plan die Abschnitte bezeichnet, in denen die Vogeluntersuchungen in der Stadt vorgenommen wurden. Unter Berücksichtigung der Typisierung von Stadtumwelt nach S a e m a n n (1968) wurden folgende Biotope abgegrenzt, die für Tachov am wichtigsten sind: neue Siedlungen, Villenverbauung, Villenverbauung am Stadtrand, Stadtparke, stadtnahe Parke.

Neue Siedlung: Fläche 31,6 ha. Sie liegt am Stadtrand, in ihrer Nachbarschaft befindet sich die Villenverbauung und die Felder. Sie besteht aus 12 Wohnblöcken (8 und 12 Stocke), unter diesen liegen Rasen und Fahrwege. Die Bäume werden gegenwärtig erst angepflanzt und für die Vögel sind einstweilig ohne Bedeutung.

Zur Zeit der Untersuchungen befanden sich noch manche Gebäude im Bau. In die untersuchte Fläche wurden auch die aus dem ursprünglichen Bestand zurückgebliebenen Reste von Strauchgruppen am Rand eingeschlossen

Villenverbauung: Fläche 89,7 ha Einstockige Gebäude, Einfamilienhäuser mit Obstbaumgärten An einigen Stellen sind die Gärten verwildert, mit dichtem Gebusch bewachsen Die Strassen sind mit Asphalt bedeckt, zumeist mit einer schwa-

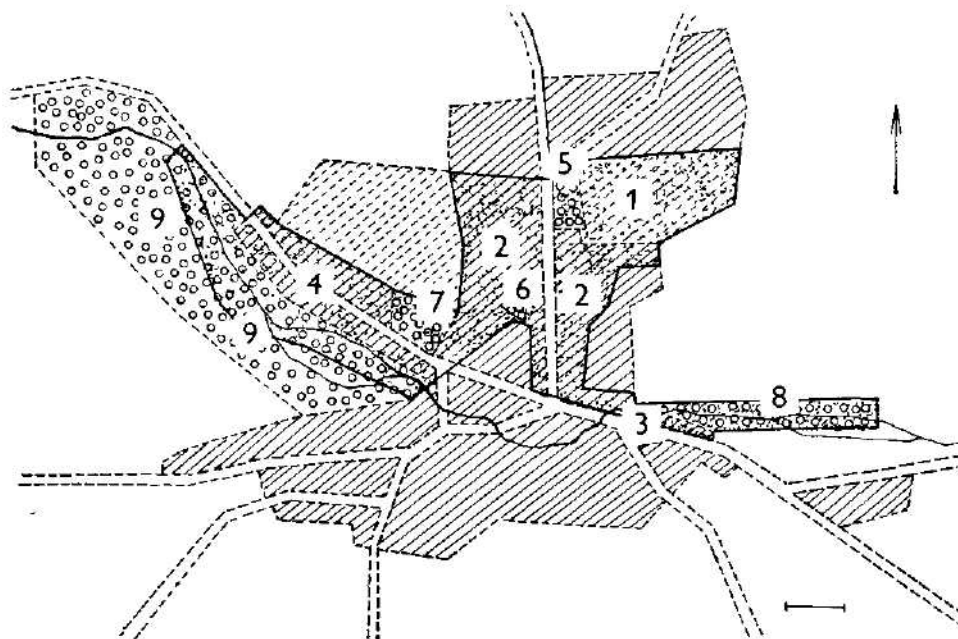


Abb 1 Schematische Karte der Stadt Tachov.

Erklärungen: unterbrochen schraffiert – neue Siedlungen, schraffiert – die übrigen verbauten Stadtteile (durchwegs Villenverbauung mit kleinen Abschnitten des Industriebiotops und der mehrstöckigen Wohnblöcke), kleine Ringe Parke.

Der untersuchte Stadtteil ist punktiert und durch eine stärkere volle Linie umrahmt. 1 – neue Siedlung Ost, 2. – untersuchter Teil der Villenverbauung innerhalb der Stadt, 3 – Miru-Strasse – Villenverbauung am Stadtrand, 4. – Prokop-Holy-Strasse – Villenverbauung am Stadtrand, 5 – Horni-Park, 6. – Václavský-Park, 7 – Park Oddechu, 8 – Park an der Mineralquelle, 9. – Světecký-Park.

Der Liniensegment im rechten Winkel unten entspricht 200 m Länge, der Pfeil bezeichnet den Norden

chen Verkehrsfrequenz. Hier und da befinden sich auf den Strassen Alleen und Baumgruppen. Am Rand der untersuchten Fläche steht ein hohes Gebäude der Stadthauptkirche. Der untersuchte Abschnitt grenzt überall an eine Villenverbauung von demselben Charakter.

Villenverbauung am Stadtrand. Fläche 18 ha. Es handelt sich um zwei am Stadtrand verlaufende Gassen, die erste befindet sich zwischen der neuen Siedlung und dem stadtnahen Park, die andere zwischen der Villenverbauung und den Ruderalflächen am Stadtrand. Die Häuser und Kleingärten sind von demselben Charakter wie im vorhergehenden Biotop, häufiger kommen hier Kleinbauten in den Gärten (Schuppen, Hühnerställe) vor. Auf dieser Fläche befindet sich ein kleines Industrieobjekt und eine Kirche.

Stadtparke: 1. Horni-Park. Fläche 7,7 ha, in der Nachbarschaft befindet sich eine Villenverbauung, ein kleineres Industrieobjekt und eine neue Siedlung. Am Parkrand steht ein grosses Gebäude des Kreisnationalausschusses, und durch den Park

läuft eine Fahrbahn. Es gibt hier einen Omnibusbahnhof des Tschechoslowakischen Staatl. Kraftverkehrs (= ČSAD). Die eigentlichen Parkflächen bestehen aus Rasen mit Asphaltwegen, die durch Reihen von mittelalten Bäumen (Rosskastanien, Berg- und Spitzahorne, Linden, Eschen usw.) gesäumt sind. Auf den Rasen wachsen nur einige zerstreute Sträucher. Eine starke Frequenz sowohl des Kraftwagen- als auch des Passantenverkehrs.

2. Václavský-Park: Fläche 3,4 ha, inmitten der Villen; im Park steht eine kleine Kirche. Bestehend aus Rasen mit einem zerstreuten Bestand von alten mächtigen Bäumen (Eichen, Buchen, Linden, Bergahorne, Fichten u. a.). Sträucher nur vereinzelt. Frequenz des Strassenverkehrs in den anliegenden Strassen mässig, die des Passantenverkehrs stark.

3. Park Oddechu: Fläche 16,0 ha, von einer Villenverbauung umgeben. Etwa 100 m weit vom Südrand befindet sich der Rand eines grossen stadtnahen Parkes. Im Park stehen zwei Wohnhäuser und ein Sommerkino. Der Park besteht vor allem aus alten Bäumen (Linden, Ahorne, Eichen, Pappeln u. a.), jüngere Bäume (Birken, Fichten) und Sträucher (vor allem Jasmin) wachsen nur an einigen Stellen. Frequenz des Kraftfahrverkehrs in den anliegenden Strassen schwach, die des Passantenverkehrs im Park mittelmässig.

Stadtnahe Parke: 1. Světecký-Park: Fläche etwa 100 ha. Mit der Stadtverbauung, mit Wiesen und Feldern und auch mit einem Kiefernwald benachbart. Er wird von dem Fluss Mže durchflossen. Den Park bilden Alleen alter Bäume (Erlen, Ulmen, Berg- und Spitzahorne, Eichen usw.), die das Wegnetz säumen. Unter ihnen befinden sich kleine feuchte Wiesen und an einigen Orten junge Espen-, Erlen- und Birkenbestände. Die Sträucher wachsen in den Alleen vereinzelt oder zerstreut. Im Park befinden sich ein Schwimmbad und ein Winterstadion. Im Sommer wird der Park an Wochenendtage häufiger besucht, sonst ist er verhältnismässig ruhig. Zur Untersuchung wurde ein 33 ha einnehmender Abschnitt erwählt (siehe Abb. 1).

2. Park an der Mineralquelle. Fläche 13,7 ha. Er ist gebildet durch eine Allee alter Bäume (von einem ähnlichen Charakter wie die Alleen im oben erwähnten Park) an dem durch ein Feld von der Stadt laufenden Weg. In die Untersuchung schloss

Tab. 1: Zusammensetzung der Nistsynusie der Vogel in der neuen Siedlung. Die Zahlangaben werden nur für die dominanten und influenten Arten angeführt.

Art	Durchschnittl. Paaranzahl in einem Jahr	Densität (Paare pro 10 ha)	Dominanz
<i>Passer domesticus</i>	56,6	17,8	55,1
<i>Phoenicurus ochruros</i>	10,0	3,2	9,8
<i>Carduelis chloris</i>	9,4	3,0	9,1
<i>Galerida cristata</i>	6,0	1,8	5,9
<i>Turdus merula</i>	5,4	1,6	5,2
<i>Hirundo rustica</i>	4,0	1,2	3,9
<i>Motacilla alba</i>	3,4	1,0	3,3
<i>Emberiza citrinella</i>	2,0	0,6	2,0
<i>Streptopelia decaocto</i>	2,0	0,6	2,0
Insgesamt	102,0	32,2	100,0

Artenzahl: 12

Diversität: 1,47

Äquabilität: 0,59

Akzessorische Brutvögel: *Delichon urbica*, *Carduelis cannabina*, *Serinus serinus*.

Die auf die Fläche während der Brutperiode herbeifliegenden Arten: *Larus ridibundus*, *Falco tinnunculus*, *Corvus monedula*, *Corvus corone corone*, *Sturnus vulgaris*, *Parus major*, *Carduelis carduelis*.

ich auch den Erlen- und Weidenbusch entlang eines Seitenarmes des Flusses Mže ein, das parallel mit der Strasse läuft. Zwischen beiden Beständen liegt eine schmale, stellenweise durch Gebusch und Ruderalvegetation unterbrochene Wiese. Der West-

rand des Parkes grenzt an die Stadtverbauung an, sonst ist der Park von Feldern umgeben.

METHODIK

Die Untersuchungen wurden in den Jahren 1974–1978 durchgeführt. In den Parks und in der Villenverbauung innerhalb der Stadt wurden die Zählungen in den Nistperioden der Jahre 1974–1977 in der neuen Siedlung und in der Villenverbauung am Stadtrand in den Jahren 1975–1978 vollbracht.

Tab. 2: Zusammensetzung der Nistsynusie der Vögel in der Villenverbauung am Stadtrand. Die Zahlangaben werden nur für die dominanten und influenten Arten angeführt.

Art	Durchschnittl. Paaranzahl in einem Jahr	Densitat (Paare pro 10 ha)	Dominanz
<i>Passer domesticus</i>	62,6	46,1	41,3
<i>Carduelis chloris</i>	12,6	9,0	8,1
<i>Hirundo rustica</i>	12,0	8,6	7,7
<i>Fringilla coelebs</i>	8,6	6,2	5,5
<i>Streptopelia decaocto</i>	6,0	4,2	3,8
<i>Turdus merula</i>	5,4	3,8	3,4
<i>Delichon urbica</i>	5,4	3,8	3,4
<i>Parus major</i>	4,0	2,8	2,6
<i>Motacilla alba</i>	4,0	2,8	2,6
<i>Sternus serinus</i>	4,0	2,8	2,6
<i>Passer montanus</i>	4,0	2,8	2,6
<i>Apus apus</i>	3,4	1,4	2,1
Insgesamt	156,0	111,8	100,0

Artenzahl: 26

Diversität: 2,31

Äquitabilität: 0,71

Akzessorische Brutvögel: *Coccyz ciconia*, *Dendrocopos major*, *Parus caeruleus*, *Sturnus vulgaris*, *Turdus philomelos*, *Erithacus rubecula*, *Phoenicurus phoenicurus*, *Hippolais icterina*, *Phylloscopus collybita*, *Ph. trochilus*, *Sylvia curruca*, *Emberiza citrinella*.

Die auf die Fläche während der Brutperiode herbeifliegenden Arten: *Dendrocopos minor*, *Pica pica*, *Sitta europaea*, *Prunella modularis*, *Sylvia atricapilla*, *Pyrrhula pyrrhula*.

Ich benutzte die Methode von Kartierung der Nistterritorien (Enemär 1959, Staštný 1974). Auf jeder Fläche wurden in dem Zeitabschnitt zwischen 15. 4. und 15. 6. jedes Jahr 10 Kontrollen durchgeführt. Bei der Arbeit nutzte ich auch die Erkenntnisse von Tomialojc (1968) und Lenz (1971) zur Kartierung der Nistterritorien im urbanen Biotop. Aus Z. B. ging ich die untersuchten Flächen schon im März und Anfang April durch und stellte die Positionen von singenden Männchen irgendwelcher Arten vorläufig fest, wie es von Lenz (1971) empfohlen wird. Bei einigen Arten (*Passer domesticus*, *Sturnus vulgaris*, *Apus apus*, *Delichon urbica* und *Hirundo rustica*) zählte ich die Nester (oder Stellen an Gebäuden, bei denen das Verhalten der Vögel nachwies, dass sich darin ein Nest befindet). Bei vielen anderen Arten gelang es mir wenigstens bei einem Teil der Paare ihr Vorkommen auch durch Fund des Nestes zu bekräftigen (z. B. bei *Phoenicurus phoenicurus*). Bei *Turdus merula*, *Fringilla coelebs*, *Streptopelia decaocto* und *Carduelis chloris* bewährte sich das Nachsuchen von verlassenen Nestern nach dem Laubabfall (Turček 1956).

Die ermittelte Paaranzahl rechne ich auf die Densität und Dominanz um (Palmgren 1930). Ferner stellte ich auch die Diversität und Äquitabilität der Synusie fest (Bezzel, Reichholf 1974) fest. Der gegenseitige Vergleich zweier Synusien nach der qualitativen Zusammensetzung wurde mittels des Sørensen'schen Indexes, auch der quantitativen Zusammensetzung mittels des Renkonen'schen Indexes voll-

Tab. 3. Zusammensetzung der Nistsynusie der Vogel in der Villenverbauung innerhalb der Stadt. Die Zahlangaben werden nur für die dominanten und influenten Arten angeführt.

Art	Durchschnittl. Paaranzahl	Densität (Paare pro 10 ha)	Dominanz in einem Jahr
<i>Passer domesticus</i>	285,8	45,6	47,7
<i>Carduelis chloris</i>	66,4	10,6	11,0
<i>Turdus merula</i>	35,4	5,6	5,8
<i>Fringilla coelebs</i>	29,0	4,6	4,7
<i>Streptopelia decaocto</i>	28,0	4,4	4,6
<i>Sturnus vulgaris</i>	24,4	3,8	4,0
<i>Apus apus</i>	20,0	3,2	3,3
<i>Phoenicurus ochruros</i>	17,0	2,6	2,8
<i>Serinus serinus</i>	16,0	2,6	2,6
Insgesamt	611,0	97,6	100,0

Artenzahl: 29

Diversität: 2,07

Äquabilität: 0,62

Akzessorische Brutvögel: *Falco tinnunculus*, *Picus viridis*, *Lynx torquilla*, *Pica pica*, *Parus major*, *P. caeruleus*, *Turdus philomelos*, *Phoenicurus phoenicurus*, *Sylvia curruca*, *Hippolais icterina*, *Phylloscopus collybita*, *Muscicapa striata*, *Motacilla alba*, *M. flava*, *Hirundo rustica*, *Delichon urbica*, *Galerida cristata*, *Carduelis carduelis*, *C. cannabina*, *Passer montanus*.

Die auf die Fläche während der Brutperiode herbeifliegenden Arten: *Larus ridibundus*, *Prunella modularis*, *Turdus pilaris*, *Phylloscopus trochilus*.

bracht (Schwerdtfeger 1973). Bei der Berechnung des Renkonenschen Index ziehe ich nur die dominanten und influenten Arten in Betracht (vgl. Jabłoński 1964). Nach Dominanz teile ich die Arten in Sinne Palmgrens (1930) in dominante (Dominanz über 5%), influente (2–5%) und akzessorische (unter 2%) ein.

EIGENE ERGEBNISSE

In Tab. 1–5 sind die Angaben über die Zusammensetzung von Vogelsynusien in den untersuchten Stadtbiotopen vorgelegt. Von allen vier Jahren der Untersuchungen wurden die Durchschnittszahlen berechnet. Die Parke wurden jeder für sich bewertet, da in der Zusammensetzung von Nistsynusien unter ihnen grosse Unterschiede bestanden.

Die niedrigste Densität, Artenzahl und Diversität der Synusien wurden in der neuen Siedlung ermittelt (Tab. 1), wobei in die untersuchte Fläche auch die Randgebüsche eingeschlossen wurden. Innerhalb der Siedlung nisteten eigentlich nur 6 Arten (*Phoenicurus ochruros*, *Motacilla alba*, *Hirundo rustica*, *Delichon urbica*, *Galerida cristata* und *Passer domesticus*).

In der Villenverbauung beträgt die Densität von Nistsynusie etwa 50 Paar pro 10 ha. An den Rändern ist die Densität etwas höher als im Stadttinneren (Tab. 2 u. 3), da hier in grösserer Anzahl vor allem *Hirundo rustica* und *Delichon urbica* nisten. In den Abschnitten der Villenverbauung innerhalb der Stadt ist im Gegenteil die Anzahl nistender Arten höher. Dies ist jedoch offensichtlich nur die Folge des Umstandes, dass hier eine grössere Fläche als am Stadtrand untersucht wurde.

Die Stadtparke wiesen grosse Unterschiede in der Densität der Nistsynusie auf. Am geringsten ist die Densität im Park Oddechu, wo sie sogar niedriger ist als in der Villenverbauung. Dies ist offensichtlich durch den Umstand ver-

Tab. 4. Zusammensetzung der Nistsynusie der Vögel in den Stadtparken. Die Zahlangaben werden nur für die dominanten und influenten Arten angeführt.

Art	Horní-Park			Václavský-Park			Park Oddechu		
	n	De	Do	n	De	Do	n	De	Do
<i>Passer domesticus</i>	44,0	56,6	38,5	7,4	27,4	19,0	3,4	2,0	2,5
<i>Fringilla coelebs</i>	12,6	16,1	11,0	5,4	15,6	10,8	24,6	15,4	18,5
<i>Carduelis chloris</i>	22,6	29,2	20,0	8,0	22,7	16,2	13,4	8,1	10,0
<i>Streptopelia decaocto</i>	9,4	12,0	8,1	5,4	15,6	10,8	9,4	5,8	7,0
<i>Turdus merula</i>	6,6	8,6	5,8	3,4	9,8	6,7	13,4	8,1	10,0
<i>Parus major</i>	4,0	5,2	3,5	2,6	7,8	5,4	11,4	7,0	8,5
<i>Sturnus vulgaris</i>	—	—	—	2,6	7,8	5,4	8,6	5,4	6,5
<i>Parus caeruleus</i>	2,6	3,4	2,3	2,0	5,8	4,0	6,0	3,6	4,5
<i>Carduelis carduelis</i>	3,4	4,2	2,9	—	—	—	2,6	1,6	2,0
<i>Ph. phoenicurus</i>	—	—	—	—	—	—	3,4	2,0	2,5
<i>Phylloscopus trochilus</i>	—	—	—	—	—	—	5,4	3,4	4,0
<i>Ph. collybita</i>	—	—	—	1,4	3,8	2,7	2,6	1,6	2,0
<i>Erithacus rubecula</i>	—	—	—	—	—	—	2,6	1,6	2,0
<i>Sitta europaea</i>	—	—	—	—	—	—	2,6	1,6	2,0
<i>Sylvia curruca</i>	—	—	—	1,4	3,8	2,7	—	—	—
<i>Serinus serinus</i>	2,6	3,4	2,3	—	—	—	3,4	2,0	2,5
<i>Passer montanus</i>	—	—	—	4,2	13,6	9,5	—	—	—
Insgesamt	114,0	146,2	100,0	49,4	145,0	100,0	132,6	82,8	100,0
Artenzahl	14			16			29		
Diversität	1,90			2,07			2,51		

Akzessorische Brutvögel: Horní-Park: *Iynx torquilla*, *Ph. phoenicurus*, *Ph. ochruros*, *Hippolais icterina*, *Carduelis cannabina*.

Václavský-Park: *Certhia brachydactyla*, *Ph. phoenicurus*, *Ph. ochruros*, *Ph. collybita*, *C. carduelis*.

Park Oddechu: *Strix aluco*, *Dendrocopos major*, *I. torquilla*, *Picus viridis*, *Parus palustris*, *C. brachydactyla*, *Prunella modularis*, *Turdus philomelos*, *Ph. ochruros*, *Sylvia borin*, *S. curruca*, *S. communis*, *S. atricapilla*, *Motacilla alba*, *Passer montanus*.

Erklärungen: n — durchschnittliche Paaranzahl in einem Jahr

De — Densität (Paare pro 10 ha)

Do — Dominanz

ursacht, dass im Park keine Sperlinge (*Passer domesticus*) nisten. Dagegen ist die Nistsynusie in diesem Park am artenreichsten. Die Nistsynusie im Horní-Park ist weit artenärmer, dank der grossen Anzahl nistender Paare von *P. domesticus* ist jedoch die Densität wesentlich höher. Im Václavský-Park ist die Artenzahl nur unbedeutend höher als im Horní-Park; *P. domesticus* nimmt jedoch hier nicht mehr eine so ausgeprägte dominante Stellung ein, die Diversität der Synusie ist schon höher. Die Densität ist dieselbe wie im Horní-Park, es setzt sich offensichtlich auch der Einfluss der kleinen Fläche von Václavský-Park durch.

In den stadtnahen Parks kommen Arten hinzu, die die ausgesprochen urbanen Biotope meiden, und die Artenzahl in der Synusie nimmt zu. Der Světecký-Park ist wesentlich ausgedehnter, es überrascht daher nicht, dass hier eine höhere Artenzahl festgestellt wurde. Die Diversität der Synusien von beiden stadtnahen Parks ist fast dieselbe, die Densität im Světecký-Park ist wesentlich höher, was in der Anwesenheit einer grossen Nistkolonie von *Sturnus vulgaris* seine Ursache hat. Einen gewissen Einfluss auf die Densität übt auch

Tab. 5. Zusammensetzung der Nistsynusien der Vogel in den stadtnahen Parken.
Die Zahlangaben werden nur für die dominanten und akzessorischen Arten angeführt.

Art	Park an der Mineralquelle			Svëtecký-Park		
	n	De	Do	n	De	Do
<i>Fringilla coelebs</i>	22,0	16,0	13,6	78,4	20,3	14,3
<i>Sturnus vulgaris</i>	90,	6,6	5,5	51,0	14,6	10,9
<i>Turdus philomelos</i>	9,0	6,6	5,5	34,0	10,1	7,0
<i>Carduelis chloris</i>	11,0	8,0	6,7	12,0	3,6	2,5
<i>Phylloscopus collybita</i>	5,0	3,6	3,0	27,0	8,0	5,6
<i>Turdus merula</i>	7,0	5,2	4,3	26,4	8,0	5,5
<i>Phylloscopus trochilus</i>	6,0	4,4	7,6	24,0	7,2	5,0
<i>Passer montanus</i>	10,4	8,0	6,4	—	—	—
<i>Parus major</i>	7,4	5,4	4,6	22,7	7,0	4,6
<i>Turdus palustris</i>	6,4	4,8	4,2	12,4	3,8	2,6
<i>Sitta europaea</i>	6,4	4,8	4,2	11,0	3,2	2,3
<i>Carduelis carduelis</i>	5,0	3,6	3,0	—	—	—
<i>Passer domesticus</i>	5,0	3,6	3,0	—	—	—
<i>Erithacus rubecula</i>	3,4	2,6	2,1	15,0	4,4	3,1
<i>Phylloscopus subulatrix</i>	4,0	3,0	2,4	14,4	4,4	3,0
<i>Sylvia atricapilla</i>	5,0	3,6	3,0	11,0	3,2	2,3
<i>Sylvia curruca</i>	4,0	3,0	2,4	10,4	3,2	2,3
<i>Parus caeruleus</i>	—	—	—	12,4	3,8	2,7
<i>Certhia familiaris</i> + <i>C. brachydactyla</i>	3,4	2,6	2,1	10,0	3,0	2,1
<i>Troglodytes troglodytes</i>	—	—	—	10,4	3,2	2,3
<i>Sylvia borin</i>	—	—	—	9,4	2,8	2,0
<i>Sylvia communis</i>	4,0	3,0	2,4	—	—	—
Insgesamt	163,0	118,8	100,0	479,5	144,0	100,0
Artenzahl		38			46	
Diversität		3,37			3,2	
Äquitabilität		0,93			0,84	

Akzessorische Brutvogel:

Park an der Mineralquelle: *Dendrocopos major*, *Picus viridis*, *Iynx torquilla*, *Parus caeruleus*, *P. palustris*, *P. montanus*, *Cinclus cinclus*, *Prunella modularis*, *Phoenicurus phoenicurus*, *Locustella fluviatilis*, *Sylvia borin*, *Hippolais icterina*, *Muscicapa striata*, *Motacilla alba*, *M. flava*, *M. cinerea*, *Carduelis cannabina*, *Serinus serinus*, *Emberiza citrinella*.

Svëtecký-Park: *Streptopelia decaocto*, *D. major*, *D. minor*, *Picus viridis*, *I. torquilla*, *Cuculus canorus*, *Pica pica*, *Aegithalos caudatus*, *Parus palustris*, *P. montanus*, *C. cinclus*, *P. modularis*, *Ph. phoenicurus*, *Ph. ochruros*, *Sylvia communis*, *H. icterina*, *Ficedula hypoleuca*, *M. striata*, *M. alba*, *M. flava*, *M. cinerea*, *C. carduelis*, *Pyrrhula pyrrhula*, *S. serinus*, *E. citrinella*, *Passer montanus*, *Carduelis spinus*.

die Tatsache aus, dass im Park an der Mineralquelle die Strauchschicht schwächer entwickelt ist, so dass im Svëtecký-Park vor allem die im Gebüsch nistenden Arten (*Turdus merula*, *T. philomelos*, *Phylloscopus collybita*, *Ph. trochilus* — vgl. Tab. 5) eine höhere Densität aufweisen.

Tab. 6 gibt die Vertretung von ökologischen Gruppen nach der Nistungsweise in verschiedenen Biotopen an. Die Anzahl der an Gebäuden nistenden Arten ist in der neuen Siedlung am höchsten, sie sinkt in der Villenverbauung und noch wesentlich mehr in den Stadtparken (auch diese sind untereinander sehr unterschiedlich), und am geringsten ist sie in den stadtnahen Parken.

Die in Baumhöhlen nistenden Arten sind in der neuen Siedlung überhaupt nicht vertreten. Etwa 10% dieser Arten haben ihre Nistsynusien in der Villenverbauung und in dem Horní-Park. Die beiden übrigen Stadtparke und die

beiden stadtnahen Parke haben in ihren Nistsynusien einen wesentlich höheren Anteil der in Baumhöhlen nistenden Arten. Der überraschend kleine Anteil der in Baumhöhlen nistenden Vögel wird offenbar durch den Umstand verursacht, dass die ältesten Bäume (Rosskastanien) sich am frequentiertesten Orte des Parkes, am Omnibusbahnhof, befinden.

Tab. 6: Zusammensetzung der Nistsynusien der Vogel von einzelnen Biotopen nach ökologischen Gruppen.

	Nistungsweise der Arten:									
	an Gebäuden		in Höhlen		auf Bäumen		in Sträuchern		am Boden	
	n	%	n	%	n	%	n	%	n	%
Neue Siedlung	4	67,4	—	—	4	18,3	1	1,3	3	11,2
Villenverbauung am Stadtrand	5	55,5	7	10,6	7	25,9	6	4,5	2	3,0
Villenverbauung innerhalb der Stadt	5	54,7	8	10,9	8	30,6	5	1,9	3	0,9
Stadtparke:										
Horní-Park	2	39,0	4	8,9	6	50,1	2	1,8	—	—
Václavský-Park	2	19,3	7	28,2	5	45,9	3	6,6	—	—
Park Oddechu	2	3,0	11	31,0	7	52,0	8	13,5	1	0,5
Stadtnahe Parke:										
Tachov-Světce	1	0,5	15	35,0	11	36,3	12	27,0	6	5,7
Park an der Mineralquelle	2	3,5	11	27,9	7	38,9	12	22,7	6	6,3

Die in Gebüsch nistenden Arten sind nur in den stadtnahen Parken und teilweise auch im Park Oddechu von einer grösseren Bedeutung. Die am Boden nistenden Arten sind in den urbanen Biotopen allgemein sehr selten vertreten (vgl. z. B. Erz 1964). In Tachov bilden einen erkennbaren Anteil der Nistsynusie einerseits in der neuen Siedlung, andererseits in den stadtnahen Parken.

Die auf Bäumen nistenden Arten haben ihren grössten Anteil in den Parken. In den Stadtparken ist ihr Prozent in gesamtter Paaranzahl am höchsten, was jedoch eher durch den hohen Anteil von Höhlen- und Gebüscharten in stadtnahen Parken als durch die höhere Densität von baumbewohnenden Arten in den Stadtparken verursacht ist.

In Abb. 2 und 3 sind die Werte von Sørensen'schen und Renkonen'schen Indexe, die zur Bewertung der gegenseitigen Ähnlichkeit von Nistsynusien einzelner Biotope dienen, graphisch dargestellt.

In beiden Fällen ist die Lage analog. Sowohl qualitativ als auch quantitativ ähneln einerseits die Synusien beider stadtnahen Parke, andererseits die Synusien der Villenverbauung am Stadtrand und innerhalb der Stadt. Die Synusien von drei Stadtparken bilden einen allmählichen Übergang zwischen diesen zwei Paaren. Die Synusie der neuen Siedlung weicht von allen übrigen Biotopen am stärksten ab, qualitativ erinnert sie ein wenig an die Synusie der Villenverbauung (Abb. 3).

Tab. 7 fasst das Nistvorkommen einzelner Arten übersichtlich zusammen und Tab. 8 führt die Densitäten der Nistpopulationen von wichtigsten Arten in vier Grundbiotopen (d. h. neue Siedlung, Villenverbauung, Stadtparke und stadtnahe Parke) an. Diese Angaben ermöglichen eine Auswertung der Urbanisierungsstufe einzelner Arten durchzuführen, weil die Biotope in einer Reihe von

dem am meisten zu dem am wenigsten anthropisch beeinflussten angeordnet sind. Die erste Nistvogelgruppe besteht aus sieben Arten, die in allen Biotopen auftraten. Einige von ihnen bevorzugten jedoch ein Biotop (*Phoenicurus ochruros* — neue Siedlung, *Passer domesticus* — Villenverbauung, *Carduelis chloris* und *Streptopelia decaocto* — Stadtparke). *Turdus merula*, ausser neuen Siedlungen, nistet dagegen in allen Biotopen bei einer annähernd gleichen Den-

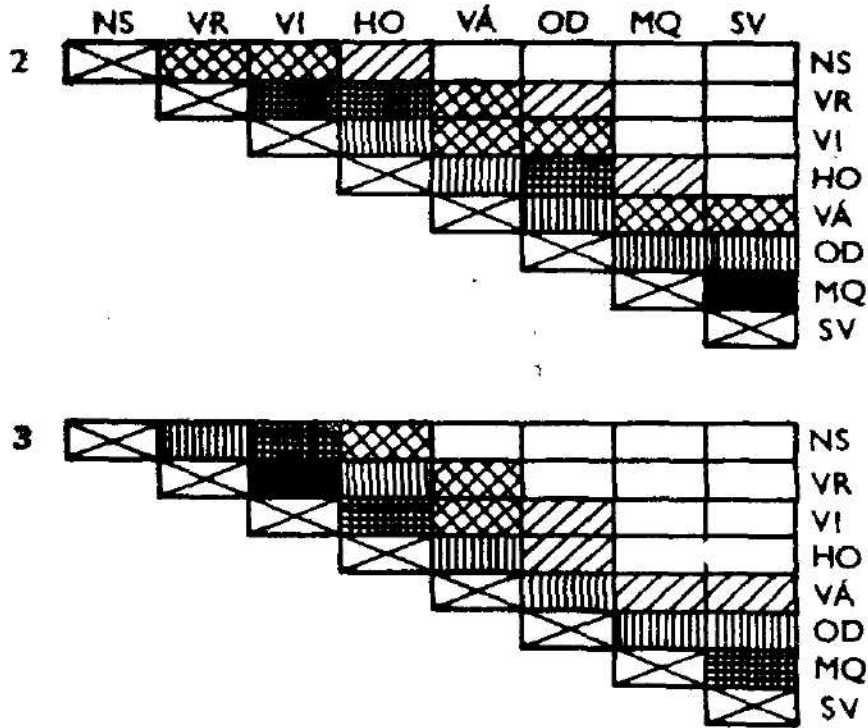


Abb. 2: Sørensen'sche Indexe, durch die die qualitativen Zusammensetzungen der Nistsynusien der Vögel unter den untersuchten Stadtbiotopen von Tachov verglichen werden.

Erklärungen: NS — neue Siedlung, VR — Villenverbauung am Stadtrand, VI — Villenverbauung innerhalb der Stadt, HO — Horní-Park, VÁ — Václavský-Park, OD — Park Oddechu, MQ — Park an der Mineralquelle, SV — Světecký-Park.

Deutung der Werte von Sørensen'schen Indexen: volle Rechtecke — 91–100 %, dicht karierte Rechtecke — 81–90 %, dicht schraffierte Rechtecke — 71–80 %, dünn karierte Rechtecke — 61–70 %, dünn schraffierte Rechtecke — 51–60 %, leere Rechtecke — bis 50 %.

Abb. 3: Renkonen'sche Indexe zum Vergleich der quantitativen Zusammensetzung der Nistsynusien der Vögel unter einzelnen Biotopen von Tachov. Erklärungen siehe bei Abb. 2

sität. *Motacilla alba* und *Carduelis cannabina* kommen zwar auch in allen untersuchten Stadtbiotopen vor, jedoch nur in kleiner Anzahl an Lokalitäten, wo ihre spezifischen Anforderungen erfüllt werden (*M. alba* — Nähe des Wassers, *C. cannabina* — dichte, von Ruderalflächen umgebene Gebüsche).

Tab. 7: Vertretung einzelner Arten in den Nistsynusien der vier städtischen Grundbiotop.

Art	NS	VV	SP	SnP
<i>Galerida cristata</i> , <i>Hirundo rustica</i> und <i>Delichon urbica</i>	+	+	-	-
<i>Apus apus</i> und <i>Falco tinnunculus</i>	-	-	-	-
<i>Passer domesticus</i> , <i>Phoenicurus ochruros</i> , <i>Streptopelia decaocto</i> , <i>Carduelis chloris</i> , <i>Turdus merula</i> , <i>Motacilla alba</i> , <i>Carduelis cannabina</i>	+	+	+	+
<i>Serinus serinus</i> , <i>Phoenicurus phoenicurus</i> , <i>Passer montanus</i> , <i>Picus viridis</i> , <i>Lynx torquilla</i> , <i>Sturnus vulgaris</i> , <i>Parus major</i> , <i>P. caeruleus</i> , <i>Turdus philomelos</i> , <i>Hippolais icterina</i> , <i>Phylloscopus collybita</i> , <i>Sylvia curruca</i> , <i>Fringilla coelebs</i> , <i>Carduelis carduelis</i> , <i>Dendrocopos major</i> , <i>Erithacus rubecula</i> , <i>Phylloscopus trochilus</i>	-	+	+	+
<i>Pica pica</i> , <i>Muscicapa striata</i> , <i>Motacilla flava</i> , <i>Emberiza citrinella</i>	-	+	-	+
<i>Certhia brachydactyla</i> , <i>Sitta europaea</i> , <i>Prunella modularis</i> , <i>Sylvia communis</i> , <i>S. atricapilla</i> , <i>S. borin</i> , <i>Parus palustris</i>	-	-	-	+
<i>Certhia familiaris</i> , <i>Troglodytes troglodytes</i> , <i>Turdus pilaris</i> , <i>Phylloscopus sibilatrix</i> , <i>Dendrocopos minor</i> , <i>Cuculus canorus</i> , <i>Aegithalos caudatus</i> , <i>Parus montanus</i> , <i>Cinclus cinclus</i> , <i>Locustella fluviatilis</i> , <i>Ficedula hypoleucos</i> , <i>Motacilla cinerea</i> , <i>Pyrrhula pyrrhula</i> , <i>Carduelis spinus</i>	-	-	-	+

Erklärungen: NS — neue Siedlung, VV — Villenverbauung SP — Stadtparke, SnP — stadtnahe Parke.

Eine weitere Gruppe bilden jene Arten, die nur in Biotopen mit Gebäuden nisten und in Parken fehlen. Hierher gehören die an Gebäuden nistenden Vogel (*Apus apus*, *Hirundo rustica*, *Delichon urbica*), ferner auch *Galerida cristata*.

Alle diese Arten (mit Ausnahme *C. cannabina*) können als typisch städtisch bezeichnet werden. Diesen kann man auch die Art *Serinus serinus* beordnen, die in allen Biotopen ausser der neuen Siedlung nistete und die höchste Densität in der Villenverbauung aufwies. Ferner können hierher auch *Passer montanus* und *Phoenicurus phoenicurus* eingeschlossen werden, die ihre maximale Densität in den Stadtparken aufweisen und in geringerer Anzahl sowohl in der Villenaufbauung als auch in den stadtnahen Parken nisten.

Weitere Arten, die in allen untersuchten Biotopen mit Ausnahme der neuen Siedlungen vorkommen (*Parus major*, *P. caeruleus*, *Sturnus vulgaris*, *Turdus philomelos*, *Picus viridis*, *Lynx torquilla*, *Hippolais icterina*, *Phylloscopus collybita*, *Sylvia curruca*, *Carduelis carduelis* und *Fringilla coelebs*), weisen die niedrigste Densität in der Villenaufbauung, etwas höhere in den Stadt- und die höchste in den stadtnahen Parken auf. Es handelt sich um Arten, die eher für die freie Landschaft typisch sind, doch dabei über die Fähigkeit, in die Stadt vorzudringen, noch in beträchtlichem Mass verfügen. Diesen können auch einige Arten beigeordnet werden, die in die Villengärten nur am Stadtrand vordringen (*Dendrocopos major*, *Erithacus rubecula*, *Phylloscopus trochilus*)

Tab. 8: Vergleich der Densität von einigen wichtigsten Arten während der Brutperiode in den Biotopen der Stadt Tachov.

Art	Biotop							
	NS	VR	VI	HO	VÁ	OD	MQ	SV
<i>Streptopelia decaocto</i>	0,3	2,2	2,1	6,0	7,8	2,9	—	0,8
<i>Sturnus vulgaris</i>	—	1,9	3,8	—	3,9	2,7	3,3	7,6
<i>Parus major</i>	—	1,0	1,4	2,6	3,9	3,5	2,7	3,5
<i>Turdus merula</i>	0,8	2,8	1,9	4,3	4,9	4,1	2,6	4,0
<i>Phoenicurus ochruros</i>	1,6	1,3	0,7	0,4	1,0	0,4	—	0,2
<i>Hirundo rustica</i>	0,5	4,3	0,7	—	—	—	—	—
<i>Carduelis chloris</i>	1,5	5,3	4,5	14,6	11,7	4,1	4,0	1,8
<i>Fringilla coelebs</i>	—	2,3	3,1	8,1	7,8	7,7	8,0	10,3
<i>Passer domesticus</i>	8,9	22,8	23,1	28,3	13,7	1,0	1,8	—
<i>Passer montanus</i>	—	1,4	0,5	—	6,8	0,6	—	0,1

Erklärungen:

Die Nummern geben die Anzahl nistender Paare pro 10 ha der untersuchten Fläche an.

Bezeichnung der Biotope: NS — neue Siedlung, VR — Villenverbauung am Stadtrand, VI — Villenverbauung innerhalb der Stadt,

Stadtparke: HO — Horní-Park, VÁ — Václavský-Park, OD — Park Oddechu

Stadtnahe Parke: MQ — Park an der Mineralquelle, SV — Světecký-Park

oder die in der Villenverbauung nur ganz vereinzelt nisten (*Emberiza citrinella*, *Pica pica*, *Muscicapa striata* und *Motacilla flava*).

Andere Arten dringen in die Stadt nur über die Stadtparke vor, sonst besiedeln sie häufig die stadtnahen Parke (*Certhia brachydactyla*, *Sitta europaea*, *Parus palustris*, *Prunella modularis*, *Sylvia communis*, *S. borin*, *S. atricapilla*).

Die letzte Gruppe bilden die nur in stadtnahen Parken nistenden Arten, von denen einige hier häufig sind (*Phylloscopus sibilatrix*, *Certhia familiaris*, *Turdus pilaris*), andere auch hier nur in beschränkter Anzahl nisten (*Parus montanus*, *Dendrocopos minor*, *Cuculus canorus*, *Aegithalos caudatus*, *Cinclus cinclus*, *Locustella fluviatilis*, *Ficedula hypoleucos*, *Pyrrhula pyrrhula*, *Carduelis spinus*).

DISKUSSION

Da die Literaturangaben über die Vogelwelt der Städte, die nach ihrer Grösse Tachov entsprechen (d. h. bis zu 20 000 Bewohner), sehr selten sind, benutze ich zum Vergleich auch die Angaben aus grösseren und grossen Städten. Selbstverständlich nehme ich zum Vergleich nur die Angaben aus den Biotopen, die den von mir untersuchten entsprechen.

Der einzige vergleichbare Wert der Densität von Nistsynusie in einer neuen Siedlung stammt aus Karl-Marx-Stadt in der DDR (Saemann 1973) und steht in guten Einklang mit meinen eigenen Erkenntnissen.

Beim Vergleich des in Tachov ermittelten Wertes von Densität der Nistsynusie mit den Angaben aus anderen Städten (Čáslav — Šrámek-Hušek 1944, Kerpen in Rheinland — Zenker 1974, Hamburg — Haarmann 1968 u. 1972, Bonn — Wink 1971, Kiel und Dortmund — Erz 1974, Karl-Marx-Stadt — Saemann 1969, Legnica in Polen — Tomialojc 1970) geht hervor, dass dieser Wert in den mitteleuropäischen Durchschnitt gut passt.

Die Densität in Stadtparken kann mit den Angaben aus Deutschland (Dortmund und Kiel — Erz 1964, Karl-Marx-Stadt — Saemann 1973), Polen

(Kleinstädte in Ostpolen — Luniak 1974, Kraków — Tomek 1969, Tomialojc 1970) und Ungarn (Debrecen — Božko 1967) verglichen werden. Nimmt man beim Vergleich in Erwägung, dass mit zunehmender Parkgröße die Densität von Vogelwelt in Stadtparken niedriger ist (Tomialojc 1970), dann passen die Parke Václavský und Oddechu gut in die in Vergleichsparken ermittelten Werte. Der Horni-Park weist eine höhere Densität auf, als es seiner Fläche und der Größe von Tachov entspräche. Dies ist offensichtlich verursacht durch eine sehr starke Nistpopulation von *Passer domesticus* in diesem durch menschliche Tätigkeit stark beeinflussten Park.

Die in stadtnahen Parks festgestellte Densität verglich ich mit den Angaben aus der Tschechoslowakei (Čáslav — Šrámek-Hušek 1944), Deutschland (Brackwede — Conrads 1957) und Polen (Toruń — Dubicka 1957, Lanciuc — Kulczycki 1966, Legnica — Tomialojc 1970, Storzek Lugowski — Luniak 1974). Die in Tachov ermittelten Werte passten wiederum gut in den mitteleuropäischen Durchschnitt.

Die Zusammensetzung der Nistsynusie in der neuen Siedlung lässt sich mit den Angaben aus Olsztyn (Okulewicz 1971), Karl-Marx-Stadt (Saemann 1973) und Rostock (Plath 1975) vergleichen. Die Zahlen von nistenden Arten stimmen beiläufig überein. Von den in Tachov ermittelten dominanten Arten fehlte an anderen Lokalitäten *Phoenicurus ochruros*, in Karl-Marx-Stadt war dagegen auch *Apus apus* dominant, welche Art in Tachov fehlt.

Die Zusammensetzung der Nistsynusie in der Villenverbauung verglich ich mit Angaben über 17 Abschnitte aus den Städten in der Tschechoslowakei, Polen und Deutschland (Šrámek-Hušek 1944, Strawinski 1963, Erz 1964, Haarmann 1969 u. 1972, Tomialojc 1970, Wink 1971, Okulewicz 1971, Saemann 1973, Zenker 1974). Von den auf mehr als 50 % von verglichenen Flächen festgestellten Arten fehlten in Tachov nur zwei. *Sylvia atricapilla* nistet jedoch in den Parks von Tachov, nur *Columba palumbus* kommt in der Stadt überhaupt nicht vor. Die Art begann sich zwar in der ČSR schon zu synanthropisieren (Hudec et coact. 1977), für eine echte synanthrope Art, wie sie in Polen oder Österreich ist, kann sie jedoch hier noch nicht gehalten werden. Gleichzeitig wurde in Tachov in der Villenverbauung keine nistende Art festgestellt, die in diesem Biotop mindestens in einer der verglichenen Städte nicht nistete.

Wird die Quantität des Vorkommens in Betracht gezogen, überwiegt hier — im Einklang mit den meisten verglichenen Städten — *Passer domesticus* (Ausnahmen nur Bonn — Wink 1971 und Hamburg — Haarmann 1969, wo *Turdus merula* häufiger ist). Auch weitere Arten, die in den meisten Städten dominant sind (*Turdus merula*, *Streptopelia docaecto*, *Carduelis chloris*), gehören in Tachov ebenso zu dominanten oder wenigstens zu influenten Arten.

Die Zusammensetzung der Nistsynusien in Stadtparken vergleiche ich mit Angaben über 28 Parke in Polen, Deutschland und vereinzelt auch in England (Sokolowski 1957, Strawinski 1963, Erz 1964, Tomek 1969, Tomialojc 1970, Saemann 1973, Luniak 1974, Wallace 1974, Wiehe 1976). Von den Arten, die in mehr als einer Hälfte der verglichenen Parke nisten, fehlen in Tachov wieder *Columba palumbus* und *Muscicapa striata*; die letztere nistete jedoch in Tachov in den stadtnahen Parks und in der Villenverbauung. Die in den meisten verglichenen Stadtparken dominanten Arten waren in Tachov auch dominant. Von den anderen Arten, die in mehr als 50 % der Fälle dominant waren, erreichten in Tachov folgende Arten diese Stellung

nicht: *Columba palumbus* und *Corvus monedula* (ganz fehlend) und *Parus caeruleus* und *Sylvia curruca* (in den Parken von Tachov influent).

Was die Zusammensetzung der Nistsynusien in den stadtnahen Parken von Tachov anbelangt, können diese mit Angaben über 15 Parken aus tschechoslowakischen, polnischen und deutschen Städten verglichen werden (Šrámek-Hušek 1944, Conrads 1957, Gerber 1961, Dubicka 1957, Truszkowski 1963, Pawłowski 1965, Kulczicki 1966, Kuhn 1968, Tomialojc 1970, Saemann 1973, Luniak 1974). Von 13 Arten, die in fast allen verglichenen Parken festgestellt wurden, fehlte keine einzige in Tachov. Von den Arten, die mindestens in einer Hälfte der verglichenen Parke festgestellt wurden, fehlten nur *Columba palumbus*, *Coccothraustes coccothraustes* und *Oriolus oriolus*. Die Arten, welche in den Parken von Tachov die dominante Stellung einnahmen, erreichten dieselbe Stellung nur in einigen Parken (*Phylloscopus trochilus* war sogar in keinen der verglichenen Parke dominant). Diese Tatsache hat ihren Grund darin, dass die Zusammensetzung von Synusien dieser Parke weit variabler ist als in den Stadtparken oder Villenstadtvierteln.

Zum Abschluss dieser Vergleiche kann man daher sagen, dass die Nistsynusien der Kleinstadt Tachov keine merklichen Abweichungen von den Synusien analoger Biotope in grösseren und grossen Städten des mitteleuropäischen Raumes zeigen.

ZUSAMMENFASSUNG

1. In den Jahren 1974—1978 wurde die Durchforschung der qualitativen und quantitativen Zusammensetzung von Nistsynusien in der Stadt Tachov (14 000 Bewohner) vollbracht; die Stadt befindet sich in Südwestböhmen am Fuss des Český Les-Gebirges, ihre Seeöhe beträgt 490—540 m.

2. Zu Untersuchungen wurde ein etwa 220 ha Fläche einnehmender Stadtteil erwählt. In diesem Teil wurden folgende Biotope abgegrenzt: neue Siedlung (Untersuchungsjahre 1975—1978), Villenverbauung innerhalb der Stadt (1974—1977), Villenverbauung am Stadtrand (1975—1978), Stadtparke und stadtnahe Parke (1974—1977).

3. Die Zusammensetzung der Nistsynusien wurde mittels der Kartierung von Nistterritorien im Zeitabschnitt von 15. 4. bis 15. 6. untersucht. Bei einigen Arten wurde ihre Anzahl durch direkte Zählung von Nestern ermittelt.

4. In Tab. 1—5 werden die Angaben über die Zusammensetzung von Nistsynusien einzelner Biotope vorgelegt. Die durchschnittliche Densität der Nistsynusie in der neuen Siedlung beträgt 32,2 Paar pro 10 ha, in der Villenverbauung am Stadtrand 111,8 Paar pro 10 ha, in der Villenverbauung innerhalb der Stadt 97,6 Paar pro 10 ha, in den Stadtparken 82,8—146,2 Paar pro 10 ha, in den stadtnahen Parken 118,8 und 144 Paar pro 10 ha.

5. In der neuen Siedlung sind folgende Arten dominant: *Passer domesticus*, *Phoenicurus ochruros*, *Carduelis chloris*, *Galerida cristata*. In der Villenverbauung dominieren *P. domesticus*, *C. chloris*, *T. merula* und *Fringilla coelebs*, in den Stadtparken *Streptopelia decaocto*, *Sturnus vulgaris*, *Parus major*, *T. merula*, *C. chloris*, *F. coelebs*, *P. domesticus* und *Passer montanus*. In den stadtnahen Parken dominieren *F. coelebs*, *St. vulgaris*, *Turdus philomelos*, *T. merula*, *Phylloscopus trochilus*, *Ph. collybita*, *C. chloris* und *P. montanus*.

6. Durch Vergleich der Ergebnisse mit Angaben verschiedener Autoren, die die Zusammensetzung von Nistsynusien der Vögel in mitteleuropäischen Städ-

ten untersuchten, wurde festgestellt, dass die Zusammensetzung der Nistysynusien von einer Kleinstadt in der Landumwelt von der Zusammensetzung der Synusien von analogen Biotopen auch in grösseren Städten nicht unterschiedlich ist.

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**MORPHOMETRISCHE UNTERSUCHUNGEN AN GEHIRNEN DER WIEDERKÄUER
(RUMINANTIA, ARTIODACTYLA, MAMMALIA)*
I. MAKROMORPHOLOGIE DES GEHIRNS DER HIRSCHFERKEL
(TRAGULIDAE)****

Leo SIGMUND

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Abstract: Differences in the shape of brain and in the course of gyrification are examined in three species of ruminants, *Hyemoschus aquaticus*, *Tragulus meminna* and *T. javanicus* (Tragulidae). The structure of the brain of the mouse deer is uniform and primitive from the macromorphological point of view. It is elongate, with large, prefrontal bulbi olfactorii and an extensive palaeopallium separated from the neopallium by a markedly dorsally situated sulcus rhinalis lateralis. The tectum mesencephali, dorsally covered by the telencephalon and cerebellum, is partly uncovered seen in lateral view. The brain of the mouse deer resembles most the endocranial casts of fossil Cervidae (*Dremotherium* and *Dicrocerus*) as well as the brain of recent primitive representatives of the family (*Moschus moschiferus*) by number and longitudinal course of the sulci.

Our findings, which are in agreement with palaeontological results in the mouse deer (*Dorcatherium*) as well as with results of ecological and behavioral studies in *Tragulus napu* and *Hyemoschus aquaticus*, support the view that the tragulids are the last primitive artiodactyls surviving from the Eocene and can be considered as ancestors of all recent ruminants, especially cervids. In accordance with these findings is also the view that the large-sized relict genus *Hyemoschus* of the African branch of the tragulids apparently is plesiomorphic and more generalized while the smaller sized genus *Tragulus* of the Asian branch of the tragulids is apomorphic and more specialized. However, a relationship between tragulids and tayassuids (Dicotylidae) cannot be confirmed.

EINLEITUNG

Dem Gehirn, das durch seine Koordinations- und Assoziationsfähigkeiten die Organisationsstufe eines Säugers am besten widerspiegelt, wird seit langem eine hohe morphologische Wertigkeit zuerkannt (Portmann 1962, Starck 1962 und dort weitere Literatur).

Ziel der vorliegenden Arbeit ist es das Gehirn der Hirschferkel in seinem Bau näher kennen zu lernen und die Erkenntnisse für die Hirnevolution sowie stammesgeschichtliche Beziehungen innerhalb der Artiodactyla auszunützen.

Die Familie Tragulidae repräsentiert körperkleine Wiederkäuer, die gegenwärtig nur durch eine Art- *Hyemoschus aquaticus* im westafrikanischen und durch drei Arten der Gattung *Targulus* (*T. javanicus*, *T. napu* und *T. meminna*) im asiatischen Raum vertreten ist. Alle Hirschferkel sind vorwiegend solitär lebende, nachtaktive Bewohner des tropischen Regenwaldes. Sowohl nach pa-

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laentologischen Befunden (Thenius 1969) als auch nach vergleichend-ökologischen und ethologischen Beobachtungen (Dubost 1975, 1978 und Ralls et. al. 1975) dürfen wir in ihnen bereits aus dem Eozän überlebende Reste der primitiven Vorfahren aller Wiederkäuer sehen. Damit kommt auch dem Gehirn der Hirschferkel eine Schlüsselposition zu, von der bei vergleichend-anatomischen Untersuchungen am Gehirn der Wiederkäuer ausgegangen werden muss.

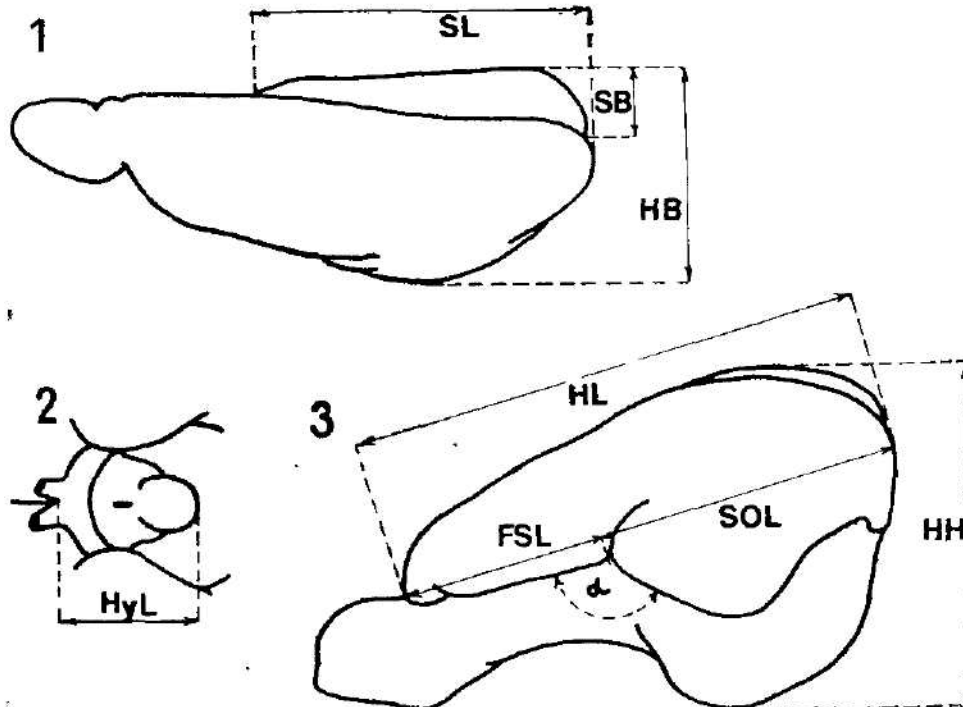


Abb 1: Masse an den Gehirnen von Hirschferkeln.
 Die linke Endhirnhemisphäre von dorsal (1) und lateral (3) und die Hypothalamus-Region von ventral (2) dargestellt HL = grösste Hemisphärenlänge; HB = grösste Hemisphärenbreite; HH = grösste Hemisphärenhöhe; SL = Länge des von dorsal sichtbaren Sulcus splenialis; SB = Breite des von dorsal sichtbaren Gyrus cinguli; HyL = Hypothalamus-Länge; FSL = Entfernung zwischen Polus frontalis und Fissura sylvia, SOL = Entfernung zwischen Fissura sylvia und Polus occipitalis; α = Winkel zwischen Sulcus rhinalis lateralis, Pars rostralis und rostralem Arm des Sulcus rhinalis lateralis, Pars caudalis.

Obwohl Gehirne und Schadelausgüsse der Hirschferkel vereinzelt schon beschrieben worden sind (Dareste 1854, Milne-Edwards 1864, Owen 1868, Gerwais 1872, Krueg 1878, Kohlbrugge 1902) wurden sie bislang noch nicht vermessen und miteinander verglichen. Fragen nach artspezifischen Unterschieden in Gestalt und Furchung der Traguliden-Gehirne liegen diesem Beitrag zugrunde.

MATERIAL UND METHODE

Über Herkunft, Art der Fixierung und Qualität der Gehirne gibt Tabelle 1+ Auskunft. Für die nachstehenden Untersuchungen wurden die fixierten Gehirne ent-

Tabelle 1: Übersicht über die zur Verfügung stehenden Gehirne

Art	Abk	Kat. Nr.	Sex	Herkunft	Fixation	Bemerkung
			Alter			
<i>Hymenochirus aequosicus</i>	Ha 1	si no	†	Zool. Garten Berlin, 11. 9. 1909. Coll.: Zool. Mus. der Humboldt-Univ., Berlin. Erhalten: 16. 10. 1966.	Alkohol immersion	Gut erhalten, cytoarchitektonisch ausgewertet.
<i>Tragulus meminna</i>	Tm 2	XV/4/1 V 32 1935	†	Vorder-Indien, Ceylon, Coll.: Max-Planck-Inst. Hirnf., Frankfurt/M. Erh.: 16. 8. 1967.	Formol immersion	Gut erhalten, cyto- architektonisch ausgewertet.
<i>Tragulus meminna</i>	Tm 3	XV/4/2 2914	†	Vorder-Indien, Ceylon Coll.: Max-Planck-Inst. Hirnf., Frankfurt/M. Erh.: 16. 8. 1967.	Formol immersion	Gut erhalten, cytoarchitektonisch ausgewertet.
<i>Tragulus meminna</i>	Tm 4	M-911	♂ ad	Zoo København, 1905. Coll. Univ. Zool. Mus., København. Erhalten: Oktober 1966.	Alkohol immersion	Gut erhalten, cyto- architektonisch ausgewertet. CBL = 87 mm.
<i>Tragulus javanicus</i>	Tj 5	M-1680	† ad	Bandon, S. Siem. Leg.: R. Haymiller. Coll.: Univ. Zool. Mus. København Erhalten: Oktober 1966.	Alkohol immersion	Gehirn mazeriert. CBL = 88 mm.
<i>Tragulus javanicus</i>	Tj 6	OM 242	♂ ad	Zoo Praha. Coll.: Inst. syst. Zool., Karls Univ Praha. Preparation: 1976.	Formol immersion	Gehirn stark mazeriert.

CBL = C ondylobasallänge

häutet, gewogen und von dorsal, lateral und ventral fotografiert und gezeichnet (Abb. 3 bis 5). Die Beschreibung der Gehirne erfolgte nach der NAV (1968). Die mit einer Noniusschublehre den Fotos entnommenen Masse sind in Tab. 2 zusammengefasst. Die Messstrecken gehen aus Abb. 1 hervor. Am Endhirn wurde stets nur eine (die linke) Hemisphäre ausgemessen. Dies bewährte sich besonders beim Entnehmen der Breitenmasse, da so der Einfluss der artefiziell verschieden gedehnten Fissura longitudinalis cerebri ausgeschlossen werden konnte. Zur Analyse der grossenbedingten Proportionsunterschiede der Gehirne wurden die Hirnmasse auf die hirnumformabhängige Kubikwurzel des Hirnvolumens bezogen, das die Hirngrösse am besten repräsentiert. Die so entstandenen Relativwerte (Indices) sind in Tab. 3 zusammengefasst (Ausführlicheres über Vorteile dieser Methode siehe Herr e und Stephan 1955 und Stephan et al. 1977).

Bei univariater Analyse wurde mit dem geometrischen Mittel

$$GM = \sqrt[n]{x_1 \cdot x_2 \cdot x_3 \cdot \dots \cdot x_n} \quad (1)$$

und dem geometrischen Variabilitätskoeffizienten

$$GVK = \exp \left(\sqrt{\frac{n \cdot \sum_{i=1}^n (\log x_i)^2 - (\sum_{i=1}^n \log x_i)^2}{n \cdot (n-1)}} \right) 100 - 100 \quad (2)$$

gearbeitet (dazu siehe Helmuth und Remp e 1968), da die auf Grund der Logarithmen bestimmten Mittelwerte weniger durch Extremwerte beeinflusst sind als beim Berechnen des arithmetischen Mittels (AM).

BESCHREIBUNG UND GESTALT DER GEHIRNE

Das Gehirn der Hirschferkel wurde schon im vergangenen Jahrhundert beschrieben (Dareste 1854, Owen 1868, Gerwais 1872, Krueg 1878, Kohlbrugge 1902). Im Hinblick darauf, dass sich Gehirne von Traguliden nur selten in Sammlungen finden lassen und im Hinblick auf zukünftige vergleichende Untersuchungen an Gehirnen anderer Wiederkäuer, sollen die makromorphologischen Ergebnisse, die wir an unserem Material erarbeitet haben, neu zusammengefasst werden.

A. Das Wassermoschustier, *Hyemoschus aquaticus* (Ogilby, 1841), Abb. 3, Tab. 1

Es stand uns nur ein Gehirn dieser Art zur Verfügung (Ha 1), das einem Zootier unbekanntes Geschlechtes und Alters entnommen wurde*.

a) Die Hirnform

Das Gehirn ist durch gut entwickelte, seitlich abgeplattete Bulbi olfactorii gekennzeichnet, die von lateral gesehen fast kreisförmig erscheinen. Dem Bulbus schliesst sich der mächtige palaeopalliale Endhirnanteil an, dessen rostraler Abschnitt, der Pedunculus olfactorius, den Bulbus mit dem kaudal und

* Ich danke für die grosszügige Überlassung des Gehirns von *Hyemoschus aquaticus* Frau Dr. R. Angermann, Zoologisches Museum der Humboldt-Universität, Berlin und für die Überlassung zweier Gehirne von *Tragulus meminna* Herrn Dr. H. Stephan, Max-Planck-Institut für Hirnforschung, Frankfurt/M. Herrn Dr. F. W. Braestrup, Universitetets Zoologiske Museum, Kopenhagen bin ich für Überlassung je eines Gehirnes von *Tragulus meminna* und *Tragulus javanicus* mit bestem Dank verpflichtet. Herrn Doz. Dr. D. Kruska, Tierärztliche Hochschule Hannover, danke ich für seine Ratschläge und orthographische Korrektur des Manuskripts.

Tabelle 2. Hirnmass (in mm) von Gehirnen der Hirscherkel aus Tab. 1

Abk.	HL	HB	HH	SL	SB	FB	FSL	SOL	Hyl	BB	CBB	α
Ha 1	35,5	14,8	24,4	22,3	7,9	10,6	14,0	21,5	11,0	14,1	18,9	118°
Tm 2	29,4	13,9	20,4	19,5	6,4	9,2	9,1	20,3	8,9	13,3	16,0	139°
Tm 3	28,5	12,9	19,7	17,9	5,6	9,8	9,2	19,3	8,9	12,3	16,4	135°
Tm 4	33,6	14,7	22,6	22,3	5,2	11,0	13,7	19,9	9,1	12,3	17,4	139°
Tm GM	30,4	13,8	20,9	19,8	5,7	10,0	16,5	18,6	9,0	12,6	16,6	138°
Tm GVK	9,1	6,8	7,4	11,7	11,1	9,6	26,3	2,6	1,3	4,6	4,4	1,7
Tj 6	30,3	12,8	21,6	13,5	5,5	8,2	10,2	20,1	8,7	12,1	16,7	125°
Tj 6	34,5	14,4	24,4	—	6,3	9,6	13,3	21,2	8,1	—	18,3	111°
Tj GM	32,3	13,6	23,0	—	5,9	8,9	11,6	20,6	8,4	—	17,6	118°

GM = geometrisches Mittel; GVI = geometrischer Variabilitätskoeffizient; BB = Breitenbreite; CBB = Cerebellumbreite. Die übrigen Messstreckensymbole siehe Abb. 1.

Tab. 3. Relativverhältnis von Hirnmassen aus Tab. 2 ausgedrückt in % der Kubikwurzel des fixierten Hirnvolumens ($\sqrt[3]{HV}$)³

Abk.	HL	HB	HH	SL	SB	FB	FSL	SOL	Hyl	BB	CBB	HV	$\sqrt[3]{HV}$
Ha 1	138	58	95	87	31	41	54	84	43	55	73	17 085	26,76
Tm 2	121	57	84	80	26	38	37	84	37	55	66	14 382	24,32
Tm 3	121	55	83	76	24	41	39	82	38	52	69	13 234	23,65
Tm 4	143	63	96	95	22	47	68	85	39	52	74	12 934	23,47
Tm AM	128	58	88	83	24	42	44	83	38	53	70	13 481	23,80
Tj 5	136	57	97	61	25	37	46	90	39	54	75	11 100	22,31
Tj 6	146	61	103	—	27	41	56	90	34	—	77	13 320	23,70
Tj AM	140	59	100	—	26	39	50	90	37	—	76	12 167	23,00

AM = arithmetisches Mittel; spez. G. der Hirnmassen = 1,036 (Stephan, 1960). HV = Hirnvolumen in mm³; Messstreckensymbole siehe Abb 1 und Tab. 2.

basal entfalteten Lobus piriformis zusammenfügt. Basal verläuft oberflächlich am Pedunculus der Tractus olfactorius lateralis, der das umfassende Tuberculum olfactorium von lateral abgrenzt. Die Endhirnhemisphären nehmen von lateral und dorsal eine birnenförmige Gestalt ein. Der Polus frontalis ist abgestumpft, der Polus occipitalis breit angelegt. Der Polus pseudotemporalis ist im Lobus piriformis lokalisiert. Am Cerebellum sind Vermis, Hemisphäria und Parafloculi gut entwickelt. Vom Tectum mesencephali, das von dorsal gesehen von Endhirn und Kleinhirn vollständig bedeckt ist, sind in Lateralansicht nur die Colliculi caudales sichtbar. Gut entwickelt ist basal auch die Hypothalamus-Region mit relativ grossem Chiasma opticum und Corpus mamillare. Weiter caudal schliessen sich die Crura cerebri des Mittelhirns an, die sich noch weiter caudal in den Pons einlagern. Hinter der Brücke heben sich Corpus trapezoideum und Pyramidenbahnen vom Hirnstamm deutlich ab.

b) Das Furchenmuster

Der Sulcus rhinalis lateralis (Srh), in dessen Tiefe auch die palaeo-neocorticale Grenze liegt, ist durch die Fissura sylvia (Fs) in einen Sulcus rhinalis lateralis, Pars rostralis (Srrh) und einen S. rh. l., Pars caudalis (Srhc) getrennt. Die Fs ist relativ kurz und weist keine Nebenzweige auf. Im Ursprungsgebiet der Fs ist der Srh nach dorsal geknickt, sodass Srrh und Srhc in einem Winkel von cca 118° konfluieren (Tab. 2). Nicht weit vom Ursprungsgebiet der Fs entfernt verläuft nach rostral auch ein gut entwickelter und relativ tiefer Sulcus praesylvius (Sps). Über der Fs liegt der bogenförmige Sulcus suprasylvius (Sss), an den sich von rostral ein kurzer Sulcus coronalis (Sc) anschliesst. Caudal gabelt sich der Sss in einen zum Occipitalpol führenden und einen anderen, zum Pseudotemporalpol gerichteten Nebenast. Den dorsocaudalen Teil der Facies convexa nimmt der mächtige Gyrus cinguli ein, der vom Gyrus marginalis durch den Sulcus splenialis (Sspl) getrennt ist. Der Sspl hat seinen Ursprung auf der medialen Fläche des Frontallappens. Anfangs in der Fissura longitudinalis cerebri versenkt verläuft er hinter dem Frontallappen oberflächlich und erstreckt sich bis auf die caudale Hemisphärenfläche. Er nimmt oberflächlich 87 % der $\sqrt[3]{HV}$ ein (Tab. 3). Der Sulcus marginalis (Sm) ist kurz und erscheint nur angedeutet. Von den quer orientierten Sulci ist nur der Sulcus ansatus (Sa) entwickelt. Von den Sulci der medialen Hemisphärenfläche, die wir nur an Frontalschnitten verfolgen konnten (Abb. 2), sind ausser dem Sspl noch ein Sulcus rhinalis medialis (Srhmed) und ein Sulcus corporis callosi (Scc) zu erwähnen.

B. Der Fleckenkantschil, *Tragulus meminna* (Erxleben, 1777), Abb. 4. Tab. 1

Von dieser Art konnten wir zwei Gehirne unbekanntes Geschlechtes und Alters (Tm 2 und Tm 3) und das Gehirn eines adulten Mannchens (Tm 4) untersuchen

a) Die Hirnform

Der Bulbus olfactorius ist nur bei Tm 4 unbeschädigt erhalten geblieben. Er nimmt bei diesem Exemplar eine tropfenförmige Gestalt ein. Pedunculus olfactorius und Lobus piriformis sind auch bei dieser Art stark entwickelt. Der Lobus frontalis endet rostral mit einer breiten Basis. Das Tectum mesencephali ist von lateral nur in Form der Colliculi caudales sichtbar.

Dank des grösseren Material (n = 3), ist der Fleckenkantschil die einzige Traguliden-Art bei der wir auch orientierende Aussagen über die innerartliche

Variationsbreite des Gehirns machen könnten Aus Tab. 2 ist zu entnehmen, dass Tm 4 das grösste Gehirn besitzt, während Tm 2 und Tm 3 kleinere, jedoch fast gleich grosse Gehirne haben. Die Relativwerte in Tab. 3 deuten einen Gestaltunterschied der Gehirne an. Dieser kommt insbesondere zum Ausdruck in einem relativ schmalen Gyrus cinguli (durch SB gekennzeichnet), durch relativ längere HL, HH, SL sowie Frontallappenlänge (FSL) bei Tm 4 im Vergleich mit Tm 2 und Tm 3. Aus Tab. 2 ist auch die grösste Variationsbreite bei den Massen FSL, SL, SB, HL und HH ersichtlich.

b) Das Furchenmuster

Ausser einem Sa sind beim Fleckenkantschil alle Furchen entwickelt, die wir bei *Hyemoschus* schon beschrieben haben. Srhr und Srhc bilden untereinander im Durchschnitt einen Winkel von ca. 138° (Tab. 2). Die Fs ist kurz und ohne Seitenzweige. Bei Tm 4 liegt ihr Ursprung stärker caudal ($FSL = 58 \frac{0}{0}$ der $\sqrt[3]{HV}$ gegenüber $37 \frac{0}{0}$ bei Tm 2 und $39 \frac{0}{0}$ bei Tm 3), sodass der Srhr und auch der Frontallappen relativ länger als bei Tm 2 und Tm 4 ausfallen. Einer gewissen Variabilität sind auch Sss und Sc ausgesetzt. Während der Sc bei Tm 2 und Tm 3, also wie bei Ha 1 und Tj an den Sss Anschluss findet, ist sein caudales Ende bei Tm 4 nach medial vom Ursprung des Sss verlagert (siehe Abb. 2B, Schnitt Nr. 810 und Abb. 4). Der Occipitalast des Sss biegt bei Tm 4 nach ventral ab und geht in den Srhc über, während er bei Tm 2 und Tm 3 ähnlich dem von Ha 1 blind auf dem Occipitallappen endet. Bei allen drei Exemplaren tritt caudal der Fs eine kleine, verschieden orientierte Nebenfurche auf. Der Sspl erscheint bereits in der vorderen Hemisphärenhälfte auf der Oberfläche und nimmt $83 \frac{0}{0}$ der $\sqrt[3]{HV}$ ein (Tab. 3). Aus dem soeben Geschilderten geht hervor, dass auch das Furchenmuster des Fleckenkantschil einer individuellen Variabilität unterliegt, deren Ursache und Grenzen nur an grösserem, vor allem altersbestimmten (juv., subad., ad. ?) und nach Geschlechtern getrennten Material geprüft werden können.

C. Der Kleinkantschil, *Tragulus javanicus* (Osbeck, 1765). Abb. 5, Tab. 1

Wir konnten zwei Gehirne untersuchen. Tj 5 war ein ausgewachsenes Tier, unbekanntes Geschlechtes und Tj 6 ein adultes Männchen, dessen Gehirn aber nur mit grosser Vorsicht zum Vergleich herangezogen werden darf, da es beschädigt und stark mazeriert dem Schädel entnommen wurde

a) Die Hirnform

Das Gehirn vom Kleinkantschil spitzt sich zum Frontalpol stark zu. Das geht besonders aus der Lateralansicht (Abb. 5) hervor. Die dorsale Kantenlinie der Hemisphären fällt vom Scheitel- zum Frontallappen ausserordentlich steil ab. Zusätzlich ist der Frontallappen vor der Fs deutlich eingeengt. Er nimmt nur $39 \frac{0}{0}$ der $\sqrt[3]{HV}$ ein (Tab. 3). Besonders auffallend ist die starke Ausbildung caudaler Hemisphärenbereiche im Vergleich mit den relativ kleinen, rostral der Fs gelegenen Anteilen. Die tropfenförmigen Bulbi olfactorii, sowie das Palaeopallium mit basal auslaufendem Lobus piriformis und zugespitztem Polus pseudotemporalis sind mächtig entwickelt. Vergleichen wir die Masse von beiden Gehirnen (Tab. 3) so stellen wir fest, dass das etwas grössere Gehirn von Tj 6 besonders in seiner HL ($= 146 \frac{0}{0}$ der $\sqrt[3]{HV}$) von Tj 5 ($= 136 \frac{0}{0}$) abweicht.

Dieser Längenunterschied ist nur durch den längeren Frontallappen bei Tj 6 im Vergleich zu Tj 5 zu erklären (vergleiche die Messstrecken FSL und SOL). Vom Tectum mesencephali sind von lateral nicht nur die Colliculi caudales sondern auch ein Teil der Colliculi rostrales sichtbar.

b) Das Furchenmuster

Die Furchen konnten nur bei Tj einwandfrei verfolgt werden. Aus Abb. 5 geht hervor, dass alle Hauptfurchen, die schon bei Ha und Tm beschrieben worden sind, auch bei Tj auftreten. Die Fs teilt den Srh auch bei Tj in einen kürzeren Srhr und einen längeren Srhc. Der Sss ist mit dem Sa und dieser wiederum mit dem Sc verbunden. Der Occipitalast des Sss biegt auf die Caudalfläche des Endhirns um, sodass der Scheitellappen wie eine Mutze auf der darunter gelegenen Hirnmasse aufsitzt. Der Temporalast des Sss verläuft zuerst ventral und biegt bei Tj 5 nach caudal, bei Tj 6 hingegen nach ventral und rostral ab. Der Sps ist weit rostral am Frontallappen nur angedeutet. Der Gyrus cinguli erscheint erst in der hinteren Hemisphärenhälfte an der Oberfläche, sodass der Sspl nur 61 % der $\frac{3}{4}HV$ einnimmt (gegenüber 83 % bei Tm und 87 % bei Ha, siehe Tab. 3)

DIE VERGLEICHENDE BETRACHTUNG

Den Tab. 2 und 3 und den Abb. 2 bis 5 ist zu entnehmen, dass nur unwesentliche artspezifische Unterschiede in der Gestalt der Gehirne festgestellt werden konnten. Das Gehirn von Ha und Tj ist im Vergleich mit Tm in der Inselregion etwas stärker geknickt, sodass das Endhirn vom Scheitellappen zum Frontallappen bei Ha und Tj steiler abfällt als bei Tm. In Zusammenhang mit dem unterschiedlichen Knickungsgrad der Gehirne ist auch der Winkel zwischen dem Srhr und dem rostralen Abschnitt des Srhc bei Ha und Tj kleiner (118°) als bei Tm (138°). Das Gehirn von Tj ist am Frontalpol stärker zugespitzt als das Gehirn von Ha und Tm. In der HH konnten wir eine leichte Abflachung der Gehirne von Tj (100 % der $\frac{3}{4}HV$) über Ha (95 %) zu Tm (88 %) vermerken.

Die grossen, bei Ha in der Seitenansicht kreisförmigen, bei Tm und Tj tropfenförmig gestalteten und vor dem Frontallappen gelegenen Bulbi olfactorii, sowie ein mächtiger Pedunculus olfactorius und ein grosser Lobus piriformis deuten einen gut entwickelten palaeopallialen Riechhirnanteil an, der vom Neopallium durch den relativ hoch verlaufenden Srhr und Srhc abgesetzt ist. Diese Verhältnisse spiegeln sich schon in den Seitenabbildungen bei D a r e s t e (1854) und Milne-Edwards (1864) wider, obwohl die Abbildungen des Gehirns von Tj bei D a r e s t e (1854) stilisiert und offensichtlich ohne Bulbus gezeichnet sind und die Abbildungen bei Milne-Edwards (1864) nur Schadelausgüsse von *Tragulus napu* und Ha darstellen. Ein relativ hoher palaeopallialer Anteil an der Endhirnrinde, der noch cytoarchitektonisch überprüft werden muss, ist für Makrosmatiker typisch und charakterisiert gering cerebralisierte, wenig evoluierte, also relativ primitive Hirnträger (Starck 1962). Mit diessen Ergebnissen korrespondiert nicht einwandfrei das dorsal von Endhirn und Kleinhirn bedeckte Tectum mesencephali. Dies lässt auf eine stärkere Entfaltung beider Hirnteile schliessen (Starck 1963). Den Seitenaufnahmen der Gehirne ist aber zu entnehmen, dass dieser Prozess bei den Traguliden nur angedeutet ist, da das Tectum von lateral teilweise noch frei liegt

und die caudale Endhirnfläche mit der rostralen Kleinhirnfläche nicht vollständig in Kontakt sind. Das illustriert besonders gut die Seitenaufnahme von Tj 5, auf der im Vergleich mit Tm 4 und Ha 1 nicht nur der Colliculus caudalis sondern auch ein Teil des Colliculus rostralis sichtbar ist. Auf dieselben Verhältnisse kann auch von den schon erwähnten Darstellungen bei Dareste (1854) geschlossen werden.

b) Das Furchenmuster

Einen primitiven Eindruck macht auch das Furchenmuster der Endhirnhemisphären, die fast nur mit längs orientierten Furchen und Windungen ausgestattet sind. Alle Hauptfurchen sind leicht zu identifizieren und zwischenartiglich zu homologisieren. Interspezifische Unterschiede sind vorläufig nur mit Vorsicht zu äussern, da unsere Ergebnisse auf geringem Material basieren. Auch in der Literatur finden sich u. W. nur wenige Anhaltspunkte für einen ausführlicheren Vergleich (Krueg 1878, Kohlbrugge 1902).

Die Fs ist bei den untersuchten Arten kurz, ohne Seitenzweige entwickelt, bei Ha und Tm nach caudal, bei Tj nach dorsal orientiert. Dieselbe Richtung behält auch der sich um die Fs biegende Gyrus sylvius. Unsere Ergebnisse stimmen mit den von Dareste (1854) und Kohlbrugge (1902) bei Tj und von Milne-Edwards (1864) bei Tn abgebildeten Verhältnissen gut überein. Ohne irgendwelche verwandtschaftliche Beziehungen anzubahnen stellen wir fest, dass auch Kruska (1970) eine kurze Fs bei den Suina-Gehirnen gefunden hat. In der Lage des Ursprunges der Fs konnten wir eine Verschiebung nach caudad von Tm ($\frac{SOL}{FSL} = 1.9$) über Tj (1,8) zu Ha (1.6) vermerken (siehe Tab. 3).

Der Sss hat bei allen drei Arten den typischen, bogenartigen Verlauf. Ihm schliesst sich rostral bei Ha und Tj der kurze Sc an. Bei Tm verläuft der Sc vom Sss isoliert. Vereinigung von Sss mit Sc fanden auch Milne-Edwards (1864) bei Tn und Ha und Owen (1868) bei *Tragulus* sp. Dareste (1864) und Alessandrini (ex Kohlbrugge 1902) beschrieben dagegen bei Tj einen vom Sss getrennten Sc. Sehr variabel im Verlauf fanden wir den caudalen Teil des Sss, der meist als Sulcus suprasylvius caudalis beschrieben wird (Brauer und Schober, 1970). Er gabelt sich bei allen von uns untersuchten Arten in einen dorsalen und einen ventralen Ast, deren Längen und Richtungen verschieden sein können. Ob der ventrale Ast des Sss caudalis mit dem von Kohlbrugge (1902) erwähnten Sulcus ectosylvius posterior identisch ist oder der S. ectosylvius posterior von Kohlbrugge (1902) der kleinen akzesorischen Furche entspricht die wir nur bei Tm gefunden haben, muss vorläufig offen bleiben. Nach Dareste (1854) und Milne-Edwards (1864) verläuft dieser Sulcus nur angedeutet.

Der Sm ist am Gyrus marginalis bei allen drei Arten kurz und leicht angedeutet. Dies steht im Einklang mit Dareste (1854), Milne-Edwards (1864) und Kohlbrugge (1902). Durch die laterale Ausbuchtung des caudalen Teiles des Sss verbreitet sich am Occipitallappen der Gyrus marginalis beträchtlich, sodass er bei Ha 35⁰/₀, bei Tm 37⁰/₀ und bei Tj 42⁰/₀ der $\frac{3}{HV}$ einnimmt.

Die Hauptfurchen der medialen Hemisphärenkante ist der Sspl, dessen Verlauf bei unserem Material mit den Abbildungen von Milne-Edwards (1864), Owen (1868), Krueg (1878), Kohlbrugge (1902) und Friant

(1971) übereinstimmt. Er kommt in Richtung von der *Facies medialis* des Frontallappens zur Oberfläche und nimmt bei Ha 87%, bei Tm 83% und bei Tj nur 61% der $\sqrt[3]{HV}$ ein. Der Gyrus cinguli, der durch den Sspl vom lateral gelegenen Gyrus marginalis isoliert ist, verschmälert sich im Bereich des Occipitalpoles von Ha (SB = 31% der $\sqrt[3]{HV}$) über Tj (26%) zu Tm (24%). Es findet also eine leichte laterale Verschiebung des Gyrus cinguli bei der grösseren Art Ha statt. Zu diesem, von Krueg (1878) als Pronation beschriebenen und grössenabhängig gedeuteten Prozess haben wir auch in der Arbeit über das Gehirn der Schliefer Stellung genommen (Sigmund 1968). Wir konnten zeigen, dass die Pronation bei den Schliefern nicht körpergrössenabhängig sondern offensichtlich mit der Vergrösserung optischer Zentren zusammenhängt, also funktionell zu deuten ist. Die cytoarchitektonische Analyse innerhalb der Traguliden, aber besonders ein Vergleich mit Cerviden soll eine ausführlichere Betrachtung dieses Phänomens möglich machen.

Verlauf und Lage des Sps sind von der Vorwölbung der Inselregion abhängig. Diese erscheint im Bereich des Srhr an der Oberfläche. Bei Tm und Tj ist der Sps relativ kurz und zum Frontalpol verschoben, was auch mit der Abbildung von Dareste (1854) und Kohlbrugge (1902) übereinstimmt. Bei Ha, bei dem die Inselregion in stärkerer Masse an der Oberfläche sichtbar wird (siehe Abb. 3), beschreibt der Sps einen längeren Bogen, der seinen Ursprung fast in der Fs findet.

Ein Sulcus diagonalis tritt nach Kohlbrugge (1902) bei Tj im Bereich des Frontallappens, konnte jedoch von uns sowohl bei Ha als auch bei Tm und Tj nicht gefunden werden.

Von den Sulci der medialen Hemisphärenhälfte haben wir, ausser den schon erwähnten Sspl, obligatorisch den Srhm und den Scc ohne zwischenartige Differenzen im Verlauf gefunden. Der Sulcus genualis ist nur angedeutet und wurde aus diesem Grunde auf den Abbildungen nicht dargestellt.

Von den quer orientierten Furchen konnten wir bei Ha 1 und Tj 5 im Bereich des Frontallappens nur eine kurze Furche beobachten, die wir der Lage nach und im Vergleich mit dem von Brauer und Schöber (1970) abgebildeten Gehirn des Moschustieres als Sa identifiziert haben. Diese Furche fehlt Tm und wurde auch von Dareste (1854), Owen (1868) und Krueg (1878) nicht vermerkt. Nach Kohlbrugge (1902) könnte diese Furche auch als ein Gefässabdruck gedeutet werden.

Die Schädelausgüsse der beiden grösseren Arten — *Tragulus napu* und *Hymoschus aquaticus* lassen bei Milne-Edwards (1864) auf einen grösseren Reichtum quer orientierter Furchen schliessen. Körpergrössenabhängigkeiten sind noch zu prüfen. Da sich im endocranialen Schädelrelief nicht nur Furchen, sondern auch Gefässe und Knochenleisten imprimieren können, sind Rückschlüsse auf Furchenverlauf an Schädelausgüssen nur mit Vorsicht zu ziehen (Thenius und Hofer 1960).

DISKUSSION

Fassen wir unsere Ergebnisse zusammen, so stellen wir fest, dass die Gehirne aller drei untersuchten Traguliden-Arten in Gestalt und Furchenmuster recht einheitlich sind. Praefrontal sind grosse Bulbi olfactorii entfaltet. Sie beteiligen sich gemeinsam mit dem mächtigen Pedunculus olfactorius und dem Lobus piriformis bedeutend am Aufbau der palaeopallialen Riechhirnrinde. Durch den stark ausgebildeten Lobus piriformis ist am Endhirn ein Polus pseudotemporo-

ralis entstanden Die Insel-Region ist langgestreckt und vorgewölbt, sodass sie teilweise im Srhr an die Oberfläche hervorragt Das Tectum mesencephali liegt zwar von dorsal bedeckt aber von lateral noch teilweise frei Der Gyrus cinguli ist auf der caudalen Hemisphärenhälfte gut sichtbar Insgesamt erscheint der neocorticale Anteil am Vorderhirn im Vergleich mit palaeocorticalen Regionen auffallend klein

Alle diese Merkmale des Säugetierhirns werden von verschiedenen Autoren als primitiv bewertet (Pilleri 1960, Starck 1962, 1963, Stephan 1967, Kruska 1970) Sie charakterisieren demnach eine relativ niedere Evolutionsstufe der Hirntrager

Auch vergleichend-okologische und ethologische Untersuchungen an *Tragulus napu* (Ralls et al 1975) und *Hyemoschus aquaticus* (Dubost 1975, 1978) untermauern die Einheitlichkeit dieser Huftiergruppe und bestätigen deren morphologische Primitivität

Diese Ergebnisse stimmen gut mit den stammesgeschichtlichen Vorstellungen überein nach denen die rezenten Traguliden den Rest einer aus dem Eozän stammenden Säugetiergruppe darstellen In ihr dürfen wir sehr wahrscheinlich Vorfahren aller Wiederkäuer, vor allem der Cerviden, sehen (Therius 1969)

Suchen wir unter den Wiederkäuern Hirntrager mit ähnlichen Hirnen, so finden wir sie tatsächlich unter den Cerviden Besonders die Hirnschadelausgüsse der ausgestorbenen *Dremotherium* und *Dicrocerus* (Pivetau 1961) ähneln in Gestalt und Furchenmuster sehr den Gehirnen der Traguliden Viele Gemeinsamkeiten mit dem Traguliden-Gehirn zeigt auch das Gehirn des primitiven rezenten Hirsches *Moschus moschiferus* (vergleiche dazu Abbildungen des *Moschus*-Gehirns bei Brauer und Schöber 1970) Diese Ansicht ist nicht neu und bestätigt nur die Ergebnisse von Flower (1875) und Krueg (1878)

Sowohl *Hyemoschus* als auch *Tragulus* füllen eine sehr alte und offensichtlich auch konstante ökologische Nische des tropischen Regenwaldes aus, in der sie sich durch solitäres und nachtaktives Leben seit Millionen Jahre fast unverändert erhalten haben Ihre Art der Nahrungssuche sowie die innerartliche Kommunikation mit Hilfe von Markierung (Ralls et al 1975, Dubost 1975, 1978) lassen auf ein gut entwickeltes Riechvermögen schliessen Damit korrespondieren unsere Beobachtungen am Bulbus olfactorius und der palaeopallialen Grosshirnrinde die jedoch noch quantitativ zu überprüfen sind

Die afrikanische Relikt-Art *Hyemoschus aquaticus* lebt bereits seit dem Miozän von der asiatischen Gattung *Tragulus* getrennt und unterscheidet sich nur unwesentlich vom geologisch ältesten *Dorcatherium* aus dem Alt-Miozän Eurasiens“ (Therius 1969) Nach Untersuchungen von Schmidt (1911) an Magen von Traguliden und nach Carlsson (1926) steht *Hyemoschus* nicht nur durch seine Körpergrösse sondern auch durch einige Merkmale am Skelett, Verdauungstrakt und Muskelsystem *Dorcatherium* näher als *Tragulus* und ist daher „auf einem mehr primitiven Stadium als *Tragulus* stehengeblieben“ Diese Annahmen werden durch das Verhaltensinventar der Traguliden bekräftigt In dieser Beziehung soll *Hyemoschus* „mehr Schwein als Wiederkäuer“ und *Tragulus* „schon ein wenig mehr Wiederkäuer“ sein (Dubost 1975)

Eine Affinität zu Schweinen (besonders zu den Dicotylidae) wird von Duwe (1969) durch Antigengehalt der Skelettmuskeln hervorgehoben, konnte aber bezüglich der Hirngestalt und des Furchenmusters, ausser der „schweineartigen“ *Fissura sylvia*, von uns nicht bestätigt werden

Die Annahme, dass *Hyemoschus* primitiver und *Tragulus* abgeleiteter sein konnte, steht in Einklang mit unseren makromorphologischen Ergebnissen am Gehirn der Traguliden. Obwohl alle drei untersuchten Traguliden-Arten sich in der Körpergrösse beträchtlich unterscheiden (H_a = Körpergewicht ca. 12 500 g, T_m = ca. 2100 g und T_j = ca. 1600 g), hat diese auf Furchenmuster und Furchenreichtum der Gehirne kaum bedeutenden Einfluss. Danach mussten die kleineren Arten wie *Tragulus javanicus* und *T. meminna* in Abhängigkeit von ihrem Körpergewicht relativ mehr Hirnmasse besitzen als die viel grössere Reliktart *Hyemoschus aquaticus*. Ob ein Verzweigungsprozess des asiatischen Traguliden-Zweiges, der als Spezialisierung auf das kryptische Leben im Gebüsch des tropischen Regenwaldes gewertet werden kann (Ralls et al. 1975), mit parallel, im Sinne von Rohrs (1959) und Kruska (1973), verlaufender Retardation der Hirngrösse dafür verantwortlich gemacht werden kann, muss vorläufig noch dahingestellt bleiben, da zuerst die artspezifischen Hirn- und Körpergewichte bestimmt und zwischenartlich sorgfältig abgeschätzt werden müssen. Diese Untersuchungen sind von uns in Angriff genommen worden.

ZUSAMMENFASSUNG

Die Gehirne von *Tragulus javanicus*, *Tragulus meminna* und *Hyemoschus aquaticus* wurden neu beschrieben und in Gestalt und Furchenmuster untereinander verglichen.

Die Gehirne aller drei untersuchten Arten sind einheitlich gebaut. Sie sind langgestreckt und zeichnen sich durch grosse und präfrontal gelegene, stark entfaltete Bulbi olfactorii sowie einen hoch verlaufenden Sulcus rhinalis aus, der den relativ grossen palaeopallialen Anteil von der Grosshirnrinde abgrenzt.

Das Tectum mesencephali liegt von dorsal bedeckt, von lateral teilweise frei.

Das einfache Furchenmuster ist langs orientiert und ähnelt dem Furchenmuster der ausgestorbenen (*Dremotherium* und *Dicrocerus*) sowie dem primitivsten lebenden (*Moschus moschiferus*) Cerviden.

Alle beschriebenen Hirnmerkmale der Traguliden charakterisieren primitive Hirntrager. Das stimmt mit palaeontologischen Befunden sowie mit den Vorstellungen über die Lebens- und Verhaltensweise der Traguliden gut überein.

Im Einklang damit wurde die Ansicht vertreten, dass die afrikanische Gattung *Hyemoschus* wahrscheinlich ursprünglicher und primitiver, die asiatische Gattung *Tragulus* hingegen starker abgeleitet und spezialisiert ist.

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Die Abbildungen 2–5 sind am Ende des Heftes zu finden

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**NOTES ON THE ULTRASTRUCTURE OF THOMINX AEROPHILUS
(NEMATODA: CAPILLARIIDAE)**

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Abstract: Head part, bacillary bands, spicule sheath and egg shell surface of *T. aerophilus* have been studied by scanning electron microscopy. The ultrastructure of these organs could have specific characters

INTRODUCTION

The family Capillariidae Neveu-Lemaire, 1936 is represented by numerous species divided by Skrjabin et al. (1957) into four genera. According to these authors, a characteristic feature of species belonging to the genus *Thominx* Dujardin, 1845 is the presence of a relatively well developed spicule and spines on spicule sheath in males. Members of this genus have in general very fine and filiform bodies.

The nematodes of the family Capillariidae have been only little studied by SEM (Wright 1974, 1978; Ishii et al. 1974). The authors used *Capillaria hepatica* (Bancroft 1893) as a model species and studied particularly the ultrastructure of the head end, copulatory apparatus of male and egg surface.

However, the stability or variability of morphological features can be evaluated only on the basis of a wider spectrum of specimens of the same species and series of more species of a certain systematical group. Therefore we studied another species of the same family, *Thominx aerophilus* (Creplin, 1893) particularly its head part, bacillary bands, surface of spicule sheath and egg shell surface. Although the results are only partial and concern a single species, they supplement the known data on the ultrastructure of nematodes of the family Capillariidae. It should be noted that no other species of the genus *Thominx* has so far been studied by SEM.

MATERIAL AND METHODS

Adult specimens of *Thominx aerophilus* obtained from the collection of Central Helminthological Laboratory of the Bulgarian Academy of Sciences in Sofia have been used in our studies. The nematodes originated from naturally infected definitive hosts, *Vulpes vulpes* L. and *Felis sylvestris* Schr., from the localities Mikhailov, Gradsko and Vrachansko (Bulgaria). A total of 22 specimens have been studied, of them 4 males (body length 22.10-25.30 mm, maximum body width 0.072-0.038 mm) and 18 females (body length 28.62-31.58 mm, maximum body width 0.104-0.118 mm). Their sites of localization were trachea and bronchi of the hosts.

All specimens were studied and determined by a light microscope prior to the SEM studies. Their classical morphology and measurements are not described in

this paper, since they conform to the diagnosis of this species published in many original papers, and monographs (e. g., Skrjabin et al. 1957).

For the SEM studies, the nematodes were dehydrated through an ethanol series and subjected to ultrasound for one minute while in absolute ethanol. The specimens were the critical point dried, mounted on double sided tape, coated with gold and examined in a JEOL JSM-SI microscope. The ultrastructure of individual morphological details is shown in figures (Plates I and II).

RESULTS

Head end

The head part of body is hemispherical and is covered with a smooth cuticle (Plate I, Fig. 1). It is distinctly separated from the cervical part of body, which has a transversely striated cuticle. The cephalic part measures 0.010—0.013 mm at its base and is 0.008 mm high. The mouth is terminal and oval, surrounded by two low lateral lips (or lip-like elevations) with rounded margins. Their maximum height is 0.001 mm. Near the base of the cephalic part, there are small papillae the total number of which could not be determined (Plate I, Fig. 1.).

Bacillary bands

These specialized surface structures begin at the level of the nerve ring and run along the entire length of body of both sexes. The ventral bacillary band and dorsal bacillary band are very wide and cover a great part of the body (Plate I, Figs. 2, 3). The lateral bacillary band is distinctly narrower, its width usually not exceeding 0.006—0.010 mm (Plate I, Figs. 4, 5). The ventral and dorsal bacillary bands are of the same structure, distinctly differing from the remaining part of body cuticle. Their surface includes the opening of cuticular pores, each with an underlying hypodermal gland cell. As the bacillary band extends posteriorly it gets wider and the density of the pores of the hypodermal gland cells increases. The gland openings are rounded and protrude slightly above the body surface. The cuticle between these pores is either smooth or longitudinally undulated (Plate II, Fig. 1.).

The lateral bacillary band includes few pores and sparse hypodermal gland cells (Plate II, Figs. 1, 2). Similar to the other bacillary bands, the pores of the bands are rounded and protrude slightly above the body surface. The cuticle between the openings of glands is irregularly transversely striated and irregularly longitudinally undulated. The pores of the hypodermal glands of all bacillary bands measure 0.001—0.002 mm in diameter.

Spicule sheath

The spicule sheath is tubular and 0.017—0.020 mm wide when evaginated. Its cuticle is irregularly transversely striated and armed with spines. The spines are sparse and quite irregularly distributed on its surface (Plate II, Fig. 3). They are finger-shaped or conical and their tips are always distinctly rounded. The length of spines is 0.0010—0.0016 mm and their width at base is 0.0004—0.0008 mm.

Egg shell

The eggs are lemon-shaped, measuring 0.072—0.078 × 0.034—0.038 mm (Plate II, Fig. 4) and with an operculum at each pole. Around the opercula, the shell

forms a slightly elevated ring (Plate II, Fig. 5) with a smooth or only indistinctly undulated surface. The operculum measures 0.006—0.007 mm in diameter and protrude moderately above the surface of the egg shell. The surface structure of the operculum differs from that of the egg shell proper, which is covered with shallow depressions in the form of an irregular network.

DISCUSSION

Comparable data on the ultrastructure of the head end of nematode of the family Capillariidae have been published only by Wright (1974). The author described the so-called liplike elevations around the mouth opening of *Capillaria hepatica*. We also observed these structures in *T. aerophilus* (Plate I, Fig. 1). In our opinion (Baruš et al. 1980), these are the real lateral lips similar to those observed in species of the family Trichocephalidae. As in *C. hepatica*, the head part of *T. aerophilus* is covered with a smooth cuticle, distinctly separated from the remaining, transversely striated part of body. The mouth opening of *T. aerophilus* is surrounded by a circle of papillae, but further studies are necessary to ascertain their number and topography.

As to bacillary bands, their ultrastructure is very marked and characteristic. Since only few species of the suborder Trichocephalata have been studied by SEM, it cannot be said to what extent the surface structure of these organs is characteristic of individual systematic categories (species, genera and families). However, a preliminary comparison of the known data on the species of the genera *Trichocephalus* (see Tenora et al. 1980), *Trichinella* (see Baruš et al. 1979) and *Thominx* (see the above data) suggests that the ultrastructure of the surface of cuticle of bacillary bands is characteristic and in relation with systematical categories of the suborder Trichocephalata.

Comparable data on the ultrastructure of the spicule sheath were published only in the paper by Wright (1978) who described and documented this organ in *Capillaria hepatica*, where the spicule sheath was evidently unarmed and covered with a highly wrinkled cuticle. The spicule sheath of *T. aerophilus* is armed with spines, which are much finer and sparser than in the species of the genus *Trichocephalus*, which were studied from this aspect by Baruš et al. (1975, 1977, 1980) and Wright (1978). As in the genus *Trichocephalus*, the ultrastructure of the spicule sheath can be an important taxonomic feature for species of the genus *Thominx* and perhaps other genera of the family Capillariidae.

The ultrastructure of the egg shell surface in *Capillaria hepatica* was described by Ishii et al. (1974). No other data on the family Capillariidae could be traced in the literature, though the SEM method has been used in the studies of the egg shell of several nematode species belonging to other families (Ishii and Myazaki 1970, 1971; Ishii 1972; Ishii and Habe 1973; Baruš et al. 1979). According to the figures published by Ishii et al. (1974), the ultrastructure of the egg shell is net-like (which seems to be associated with the exchange of substances with the outer environment). Also in *T. aerophilus* studied by us the egg shell surface is distinctly divided, but its form differs from that of *C. hepatica*. On the basis of the data obtained on both species of the family Capillariidae it may be deduced that the ultrastructure of the egg shell surface of nematodes of this family is more complicated and more characteristic than that of the species belonging to the related family Trichocephalidae

(Baruš et al. 1975, 1980). In the species of the latter family, the egg shell surface is smooth or only slightly and indistinctly undulated. Consequently, the ultrastructure of the egg shell surface of nematodes of the family Capillariidae will be a very significant taxonomic character applicable for the differentiation of individual species.

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The plates will be found at the end of this issue.

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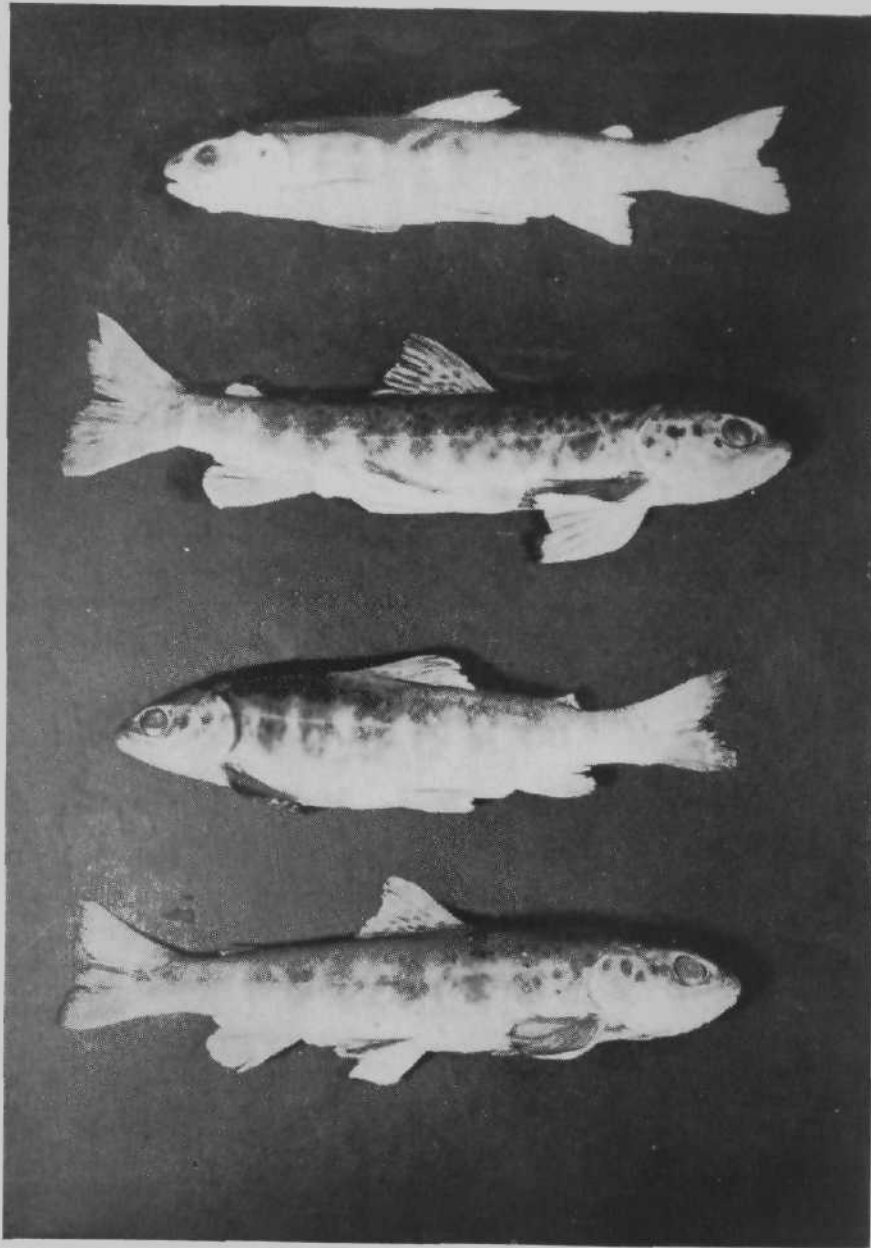


Plate 1:

From above: The dwarf salmon female, river Otava, collection of the late Professor K. Schäferna, now in the Department of Systematic Zoology, Faculty of Sciences, Charles University, Prague. Gonads are ripe. Total view. Below the same female, frontal part of the body. Age 3+, total length (TL) 245 mm, fork length (= Smitt's length, FL) 225 mm, standard length ("urostyle length"), SL 203 mm. The calculated lengths (TL) $L_1 = 126$, $L_2 = 197$, $L_3 = 234$ mm (Lee's method used, correction factor = 32 mm), without correction the same lengths 107, 187, 232 mm (Lea's method). Below: Total view of dwarf male salmon from the same locality. Last photo shows the frontal part of the same specimen. Age 4+, back calculated length using Lee's



Plate 2:
Selected specimens of dwarf salmons from the river Otava. From above below:
No 24260 (Fish Cat. of the Dept. Syst. Zool. Fac. Sci. Charles University, Prague),
TL = 197 mm, age 4, No. 24264, TL = 230 mm, age 5+, No. 24265, TL = 194 mm,
age 5, No. 24268, TL = 212 mm, age 5.

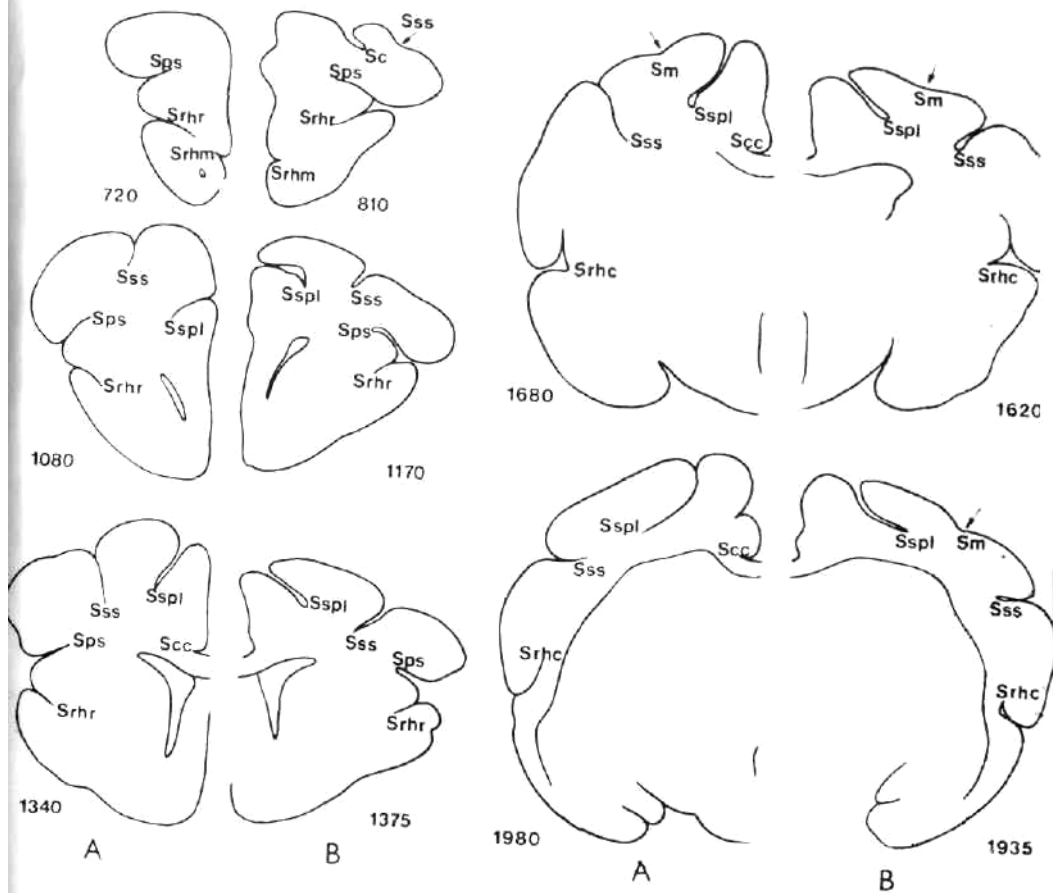


Abb. 2: Schematische Darstellung der Sulci auf ausgewählten Frontalschnitten der Schnittserie durch die rechte Hemisphäre von *Hyemoschus aquaticus* (A) und die linke Hemisphäre von *Tragulus meminna* (B).
 Srhr = Sulcus rhinalis lateralis, Pars rostralis; Srhc = Sulcus rhinalis lateralis, Pars caudalis; Sps = Sulcus praesylius; Sss = Sulcus suprasylivius; Sspl = Sulcus splenialis; Scc = Sulcus corporis callosi; Sm = Sulcus marginalis; Srhm = Sulcus rhinalis medialis; Sc = Sulcus coronalis.

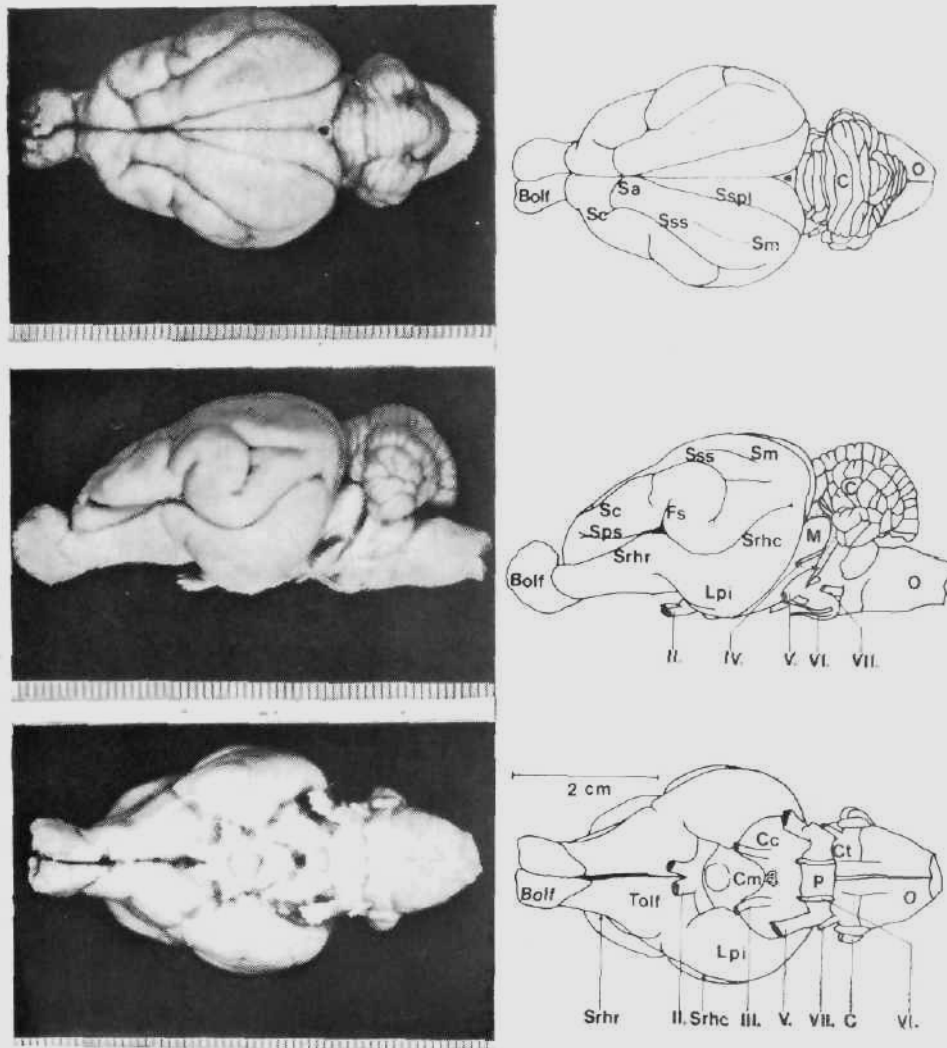


Abb. 3: Das Gehirn von *Hyemoschus aquaticus* in Dorsal-, Lateral- und Ventralansicht.

Unter den Gehirnen ist der Millimeterabstand angegeben. Bolf = Bulbus olfactorius; Lpi = Lobus piriformis; M = Mesencephalon; C = Cerebellum; O = Medulla oblongata; Tolf = Tuberculum olfactorium; Cm = Corpus mamillare; Cc = Crus cerebri; P = Pons; Ct = Corpus trapezoideum; Sa = Sulcus ansatus; Fs = Fissura sylviae; II. bis VII. = Kopfnerven. Weitere Beschreibung siehe Abb. 2.

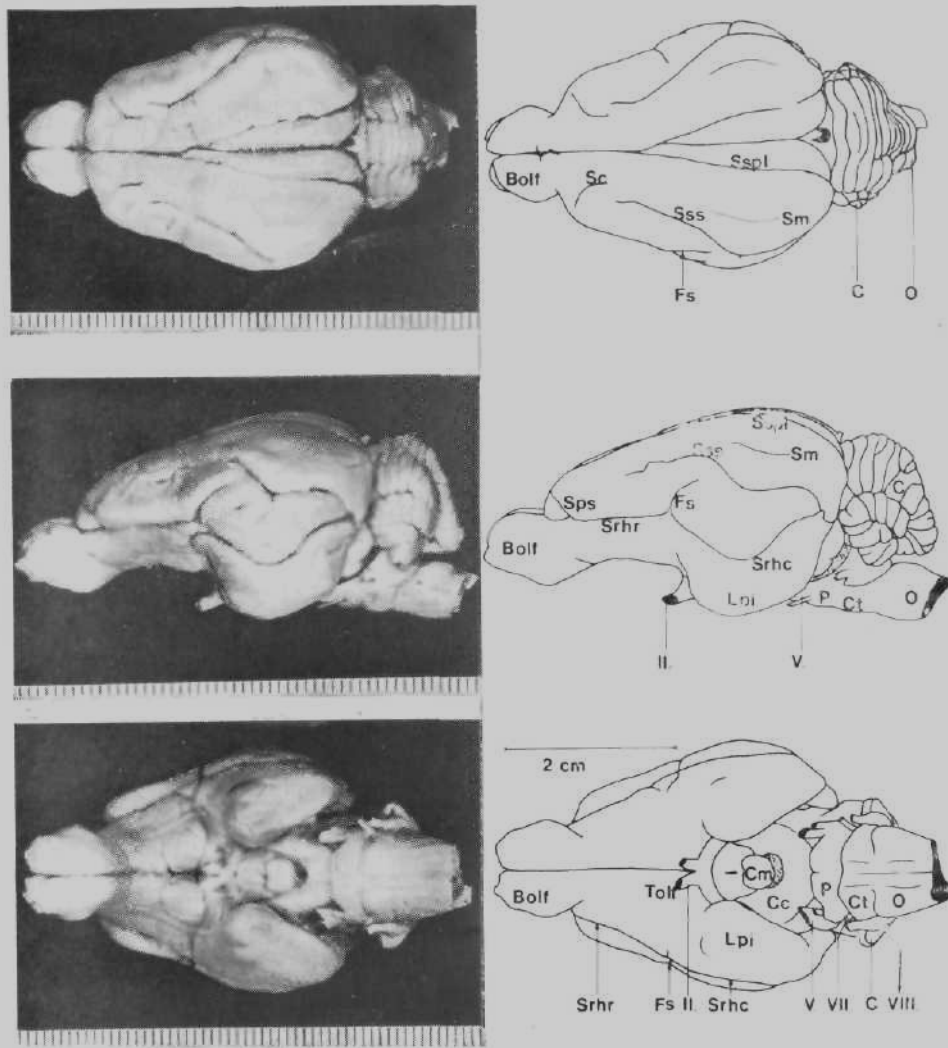


Abb. 4: Das Gehirn von *Tragulus meminna* (M-911) in Dorsal-, Lateral- und Ventralansicht.
Beschreibung der Gehirne wie Abb. 2 und 3.

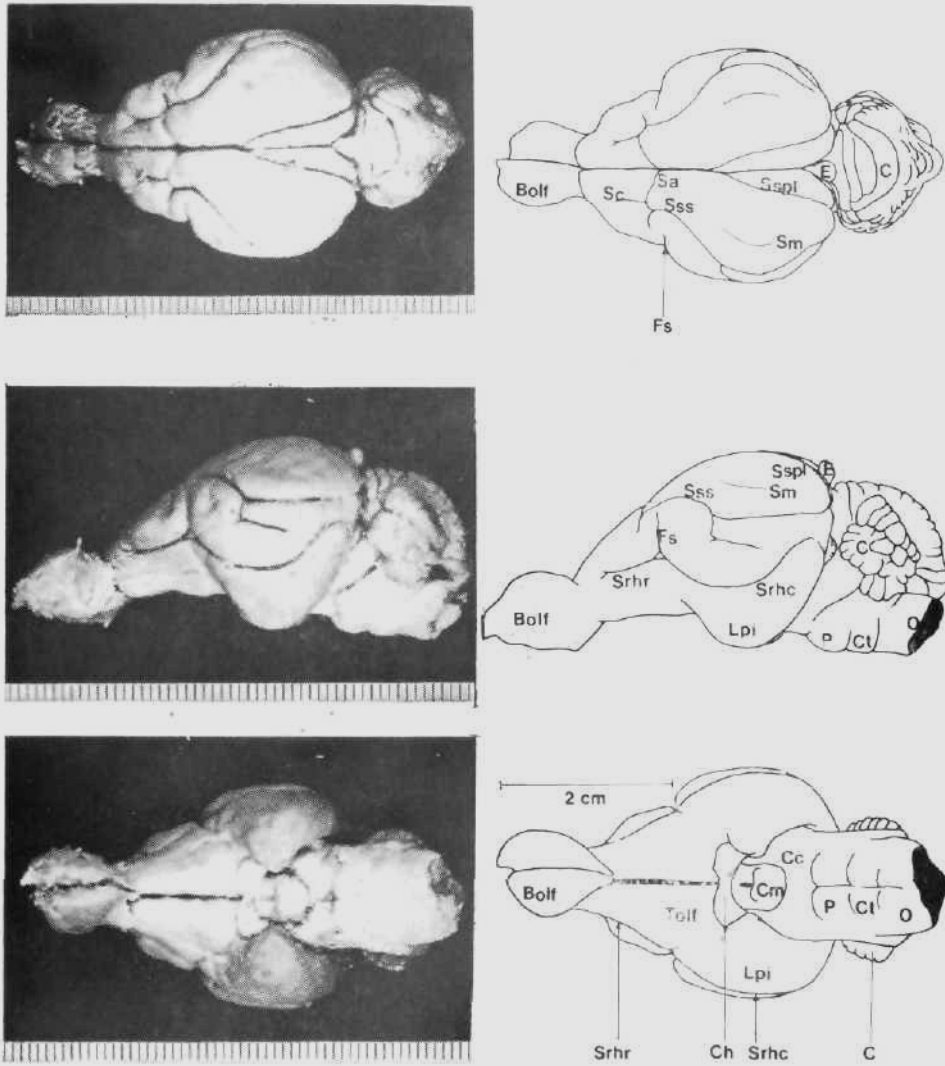


Abb. 5: Das Gehirn von *Tragulus javanicus* (M-1580) von dorsal, lateral und ventral dargestellt.
 E = Corpus pineale; Ch = Chiasma opticum; weitere Beschreibung wie Abb. 2 und 3.

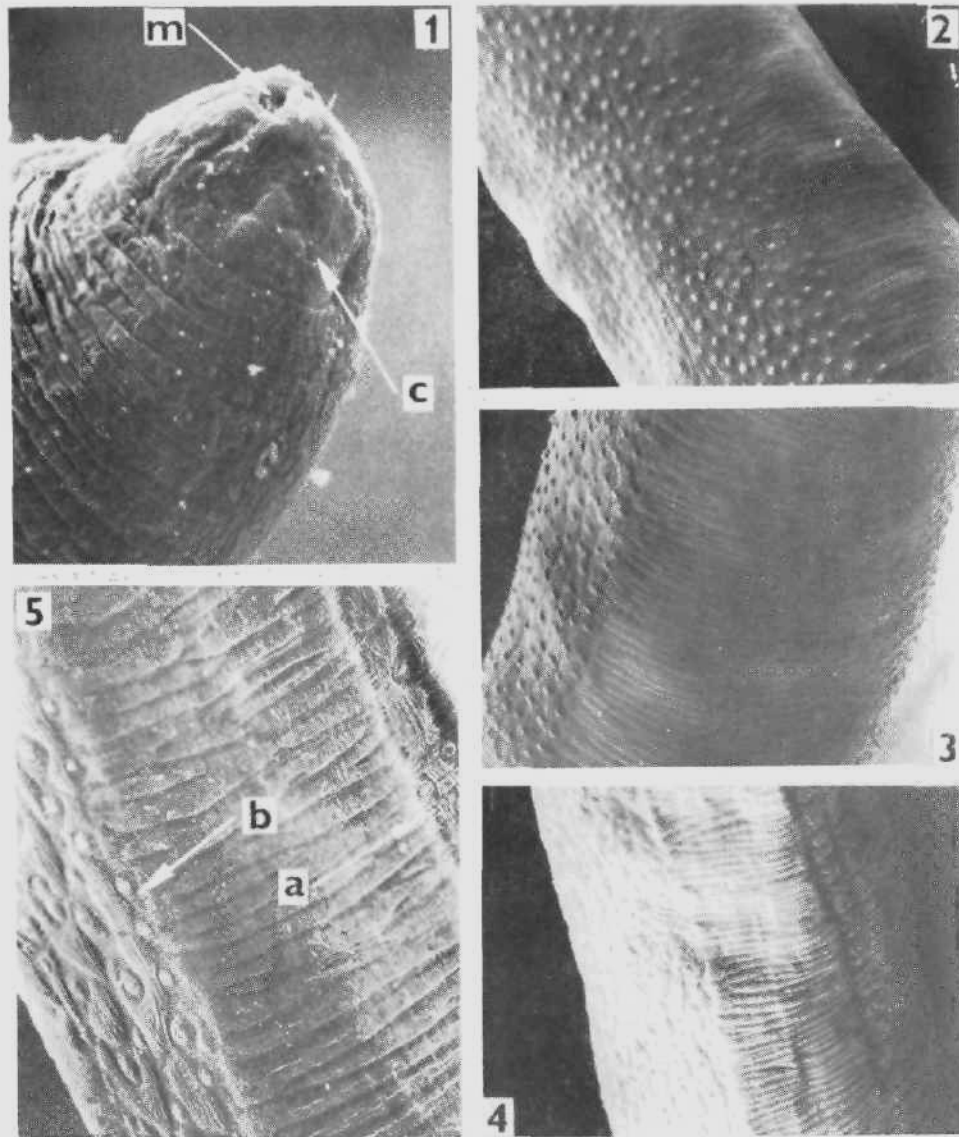


Plate I

Figs 1–5. Scanning electron micrographs of *Thominx aerophilus* (Creplin, 1839). Fig. 1. Head part of female (dorsal view), m – mouth opening, c – cephalic papilla ($\times 5000$); Fig. 2. Oesophageal part of female body – region of ventral bacillary band ($\times 1000$); Fig. 3. Oesophageal part of female body – two wide bacillary bands – ventral and dorsal ($\times 600$); Fig. 4. Posterior part of female body – wide ventral bacillary band (left) and narrow lateral bacillary band (right) ($\times 600$); Fig. 5. Surface of cutice in posterior part of female body (detail), a – narrow lateral bacillary band, b – wide ventral bacillary band ($\times 2000$).

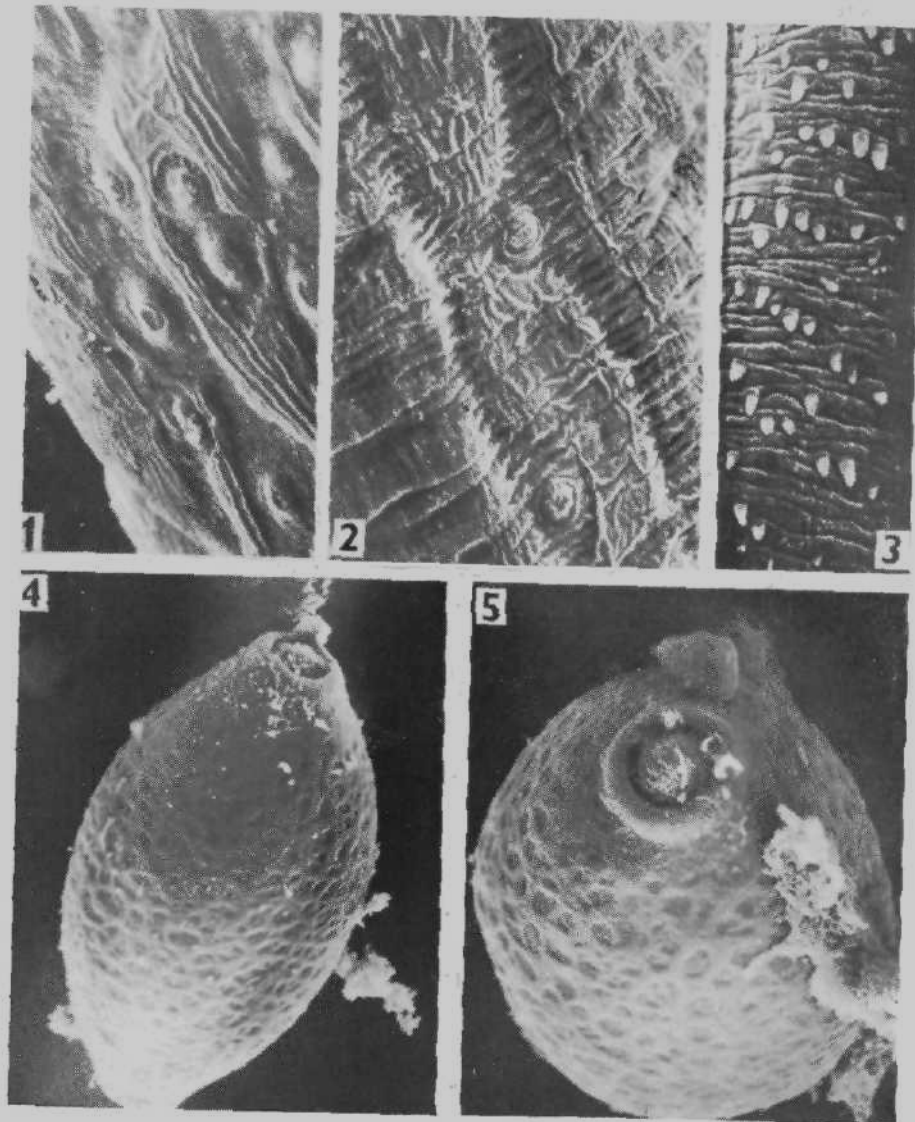


Plate II
Figs. 1-5. Scanning electron micrographs of *Thominx aerophilus* (Creplin, 1839).
Fig. 1. Ultrastructure of the surface of wide ventral bacillary band - typical longitudinal wrinkles of the cuticle ($\times 6000$); Fig. 2. Ultrastructure of the surface of narrow lateral bacillary band ($\times 6000$); Fig. 3. Ultrastructure of the surface of middle part of spicule sheath - characteristic shape of spines ($\times 5000$); Fig. 4. Ultrastructure of the egg shell surface (general view) ($\times 2000$); Fig. 5. Egg shell surface in region of operculum (detail) ($\times 3000$).

POKYNY PRO AUTORY

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Hlavička práce: 1. Název pracoviště. 2. Název práce (u prací taxonomických v závorce za názvem systematické zařazení druhu nebo skupiny – např. Ostracoda: Cyprinidae), obojí v řeči, v níž je práce psána. 3. Jméno a příjmení autora.

Vlastní práce: 1. Velmi stručný abstrakt, v rozsahu nejvýše 15 řádek, v angličtině. 2. Úvod do problematiky (stručně). 3. Materiál a metodika (u známých metod pouze odkaz). 4. Vlastní část experimentální nebo popisná. 5. Diskuse. 6. Závěr. 7. Seznam citované literatury (nikoliv bibliografie!). 8. Adresa autora. 9. Tabulky, texty k obrázkům a grafům. Celý rukopis je průběžně stránkovan.

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Přepis cyrilice proveďte podle mezinárodních pravidel vědecké transliterace (nikoliv fonetické transkripce) – viz ISO Recommendation R 9. International System for the transliteration of cyrillic characters 1. Ed. October 1955 nebo Zekalle R., 1964: *Pedobiologia*, 4: 88–91, Jena.

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V taxonomických pracích dodržujte zásady, ustanovení a doporučení mezinárodních pravidel zoologické nomenklatury.

V rukopisu nepředpisujte zásadně žádně typy písma, označte pouze tužkou po straně části, které mají být vysazeny petitem.

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