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**A MICROSPORIDIAN INFECTION IN OTIORRHYNCHUS EQUESTRIS
(COLEOPTERA, CURCULIONIDAE)**

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Received October 18, 1978

Abstract: Two microsporidian infections were found in one infected *Otiorrhynchus equestris* Richter: *Nosema adjuncta* sp. n. infects the ovaries, *Nosema equestris* sp. n. infects the connective tissue, Malpighian tubes, oenocytes and the fat body. The infection was transferred to *Gastroides viridula* and *Leptinotarsa decemlineata* where it infected the same tissues and caused larval mortality.

In an attempt to find microsporidians capable of holding the Colorado beetle in check, we examined various chrysomelid beetles which might act as hosts of a suitable microsporidian. It was of interest that microsporidians commonly found in other chrysomelids caused in the Colorado beetle either an acute, lethal infection or an infection which was so light that it could be eliminated prior to pupation by regeneration of damaged cells of the intestinal epithelium.

A comparison of the frequency of the incidence of microsporidians in various chrysomelids (Hostounský, Weiser, 1973, 1975, 1978) and of that in the Colorado beetle provided conclusive evidence that the latter was an extrinsic element in Europe which had not become adapted as yet to local pathogens. The barrier was constituted partly by an inadaptability of microorganisms to the insect, partly by an ecological barrier between the infection and the host. In spite of these facts we did not give up hope that one of these microsporidians might have become adapted to the Colorado beetle and thus be capable of holding the population of this pest in check.

An abundance of microsporidian species and small differences in developmental stages of the various species caused frequent difficulties in determination of their taxonomic position and in differential diagnosis. Therefore, various similar species of the material examined were frequently regarded as one species and, in reverse, wider groups separated into several species. The present situation calls for a better understanding of the taxonomy of microsporidia in order to complement a number of incomplete descriptions.

MATERIAL AND METHODS

A solitary female of *O. equestris* with well developed ovaries was found on the wall of a house at Holovousy, Eastern Bohemia, in July 1975. Postmortem examination disclosed infection with two different microsporidian species. A spore suspension was made of cuticular remnants and administered to other hosts. A small portion of the ovary, the Malpighian tubules and the fat body were fixed with Bouin and embedded in paraffin. Sections cut to a thickness of 4 µm were stained with Giemsa or Hedenhain's haematoxylin. Dried smears of the material were stained either with Giemsa or, for the detection of nuclei, they were hydrolyzed in 8% heated HCl (suggested by Weiser 1976) prior to staining.

Substitute hosts used in our experiments were *Gastroidea viridula* from our laboratory stock and the Colorado beetle *Leptinotarsa decemlineata*. *G. viridula* was kept on leaves of *Rumex obtusifolia* in plastic boxes. The boxes were covered with fine netting for airing. Groups of eggs were collected daily and isolated. Hatched larvae were infected with the spore suspension placed on a platinum loop. The spores had been purified by repeated centrifugation. The number of spores used for the infection ranged from 300–500/1 mm³ in order to prevent the larvae from dying before the infection could develop. Infected larvae were kept in plastic boxes with a daily change of food. Progress in the infection was studied on individuals taken from day 5–6 p.i. for microscopic inspection.

A similar procedure was used for larvae of *Leptinotarsa decemlineata*. The development of the infection was studied on fresh material from day 5 p.i. onwards. Infected individuals were fixed with Bouin and embedded in paraffin for histological treatment in the same way as the original material.

The yield of infection was studied on a total suspension of tissues of the host, spores per 1 mm³ were counted in Burker's chamber. The spores were stored as a purified suspension in water at 4 °C.

RESULTS

The two microsporidian species recovered from *O. equestris* differed in the shape and size of their spores, the organisation of spores, and in the type of tissues attacked by them. Treatment of the primary material was impeded by the fact that most of it had been used up in infection experiments.

Nosema adjuncta sp. n. (Fig. 1a–g)

The infection of this species in *Otiorrhynchus equestris* Richter was concentrated in the ovary and in maturing eggs. We did not find it in other tissues. Typical of the development of this microsporidian was the small number of schizonts of which several attained a size of 5 µm; they were spherical and contained up to 8 nuclei. They produced bi-nucleate sporoblasts measuring 3 × 5 µm. Spores matured individually. They were elongately ovoid and measured 4–4.8 × 1.5–1.8 µm (average 4.2 × 1.8 µm); they did not stain well with Giemsa. The sporoplasm was conical with a vacuole in the anterior pole. The wall of the spore did not stain and, sometimes, a kidney-shaped deformation appeared on it during drying and fixation. In several spores, the metachromatic granule situated at the very end of the spore became stained. After hydrolysis with HCl, the two nuclei became clearly visible. They were spherical, measured 0.4 µm in diameter, and were situated in tandem position close to the wall in the second half of the spore. Hydrolysis dissolved the metachromatic granule and its former space was occupied by a posterior vacuole. Occasionally, three spherical nuclei stained in longer spores, which evidently were teratospores.

The microsporidian attacked the egg follicles, entered them and formed diffuse centres in the developing oocytes. These were present throughout the cutting plane of the egg. The groups were connected with single developmental stages and spores.

In its organisation, the spore of this microsporidian was conform to that of other typical *Nosema* species such as *N. apis* or *N. bombycis*. It was close in its size to *N. otiorrhynchi*, but differed from it in the length of spores and in its distribution in the host tissues, particularly in that it was absent from the fat body.

Nosema equestris sp. n. (Fig. 1h–n)

In the original host, *Otiorrhynchus equestris*, the microsporidian attacked the connective tissue, the Malpighian tubules and the oenocytes which were considerably enlarged. A small number of spores were present in the fat body. Shizonts were

infrequent, we recovered mainly spores and an occasional sporoblast. Sporogony was bi-nucleate. Mature spores were widely ovoid in shape and attenuated towards the anterior pole they measured $4-5 \times 3 \mu\text{m}$. A posteriorly located vacuole was visible in fresh spores. The sporoplasm stained fairly well and so did part of the spore surface. After HCl hydrolysis, the two nuclei stained inside the spore. They evidently continued in their development as the spore matured. Sometimes, we observed two spherical nuclei ($0.5-1 \mu\text{m}$) in tandem position similar to that of nuclei

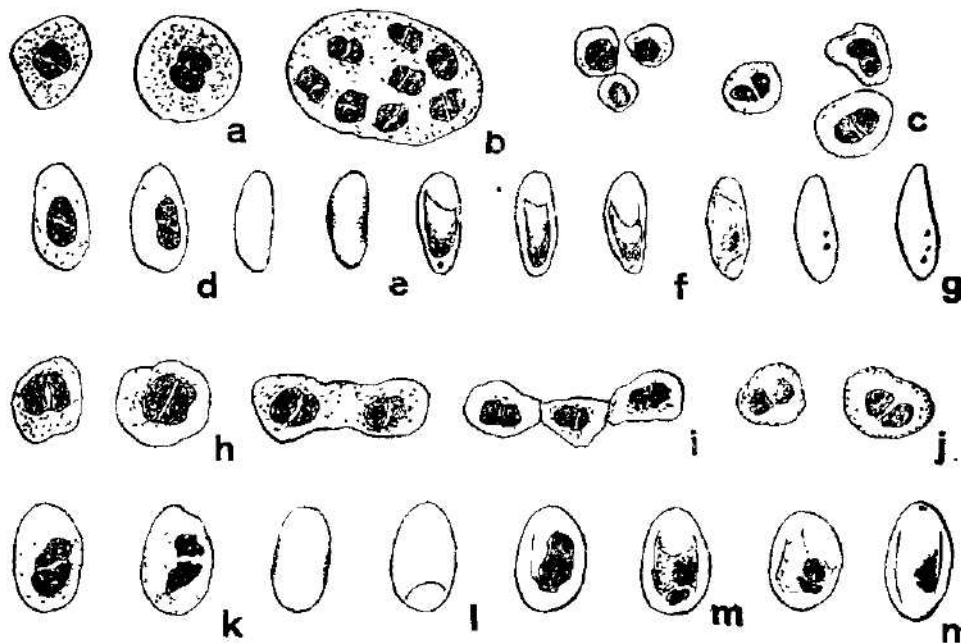


Fig. 1. *Nosema adjuncta* (a-g) and *Nosema equestris* (h-n) in the cecidionid *Otiorrhynchus equestris*: a - schizonts, b - late schizont before merogony, c - development of meronts into sporonts, d - sporoblasts, e - fresh spores, f - Giemsa stained spores with the cone of the sporoplasm and the dotlike posterosome, g - spores with stained nuclei, h - schizonts, i - merozoites formed in rows, j - early sporonts, k - sporoblasts, l - fresh unstained spores, m - Giemsa stained spores with sporoplasm and the large posterosome, n - nuclei stained inside the spores.

in sporoblasts. More frequently, however, the posterior nucleus which in normally stained spores was lying close above the posterosome, was flattened or disk-shaped; the second, more anteriorly situated nucleus was extending into the first. The second nucleus stained less intensively and was often triangular, passing anteriorly into a tapering protrusion. This nuclear structure, atypical of the genus *Nosema*, will have to be studied in detail in other material in order to disclose conformities and differences among the species inside the genus *Nosema*.

Developmental stages and spores of the microsporidian were found to concentrate in the connective tissue, lymphocytes, Malpighian tubules and the fat body of the original host.

Similar spores have been described from various other coleopterans (Lípa, 1968a, b, Lípa, Steinhaus, 1959) such as *N. coccinellae*, *N. hippodamiae*, *N. lep-*

tinotarsae or *N. longifilum*, but the organisation of spores and especially of nuclei differed from that in our species. The new species differs from earlier described species in the location of the metachromatic posterosome in the posterior vacuole of the spore, and in the distribution of the infection in the organs of the host.

The development of an infection with *N. equestris* in a substitute host

In *Gastroidea viridula*, the microsporidian attacked first the Malpighian tubules and infected them gradually throughout their length. At first, spores attacked and filled individual cells which increased in volume, ruptured and released spores into the lumen. The number of infected cells increased until the infection spread to almost the majority of cells in the lumen of the Malpighian tubules. Infected tubules still contained urate crystals. A gradual, sac-like swelling of the attacked parts was followed by a reduction in the number of urate crystals and finally by their complete disappearance. This damage caused to the Malpighian tubules evidently affected both their excretory and resorptive parts, and it was possible to observe the ceasing of the process of resorption and the production of crystals from the watery excreta. The absence of crystals indicated that both the process of secretion and that of water resorption had been disturbed.

In the fat body of the host, the infection was first disseminated in the form of small islets, later it affected whole lobes and finally the entire fat body. A lighter colour of the infected parts indicated the presence of microsporidia.

The infection became generalized in *Gastroidea viridula*, and the oenocytes known as the seat of infection in the primary attack in *O. equestris* disappeared in *G. viridula* as a result of their rupture under the pressure of the parasite in the first phase of infection. Later, the infection spread to the muscle fibres of the kinetic muscles and to the intestinal muscles, but the intestinal epithelium was not attacked by the parasite.

In spite of progressing infection, the activity of larvae of *G. viridula* was not greatly affected by the presence of the parasite. Although slightly retarded in their development, they pupated and developed into normal adults which fed normally and copulated. However, distinct changes occurred in fertilized females. As the eggs developed, their abdomen did not increase in size as much as it did in normal females. Also the number of eggs laid by infected females was smaller than that of normal females. As feeding conditions worsened in the autumn, lightly infected imagoes survived while all the other infected individuals died. No mortality was recorded among healthy individuals, the females laid eggs. An appreciable number of spores was recovered from dead animals.

In the Colorado beetle, the course of the infection was acute. However, the pattern of the development of infected larvae was most ununiform. The highest rate of mortality occurred in the prepupal stage. After a normal preparation for pupation, the larvae stopped responding to touch, their body shortened and desiccated. In soil with a higher relative humidity, dead larvae began to decompose. A disseminated infection was found in the Malpighian tubules at the time of larval development of the Colorado beetle. The Malpighian tubules of infected last-instar larvae were densely packed with spores, infected lobes of the fat body contained white masses of spores, a focally disseminated infection was found in kinetic muscles of the legs and in the muscle layer of the intestine. Although an occasional individual attained the adult stage in cage experiments, it was much smaller in size than a healthy individual, and no oviposition occurred in the female.

DISCUSSION

The new microsporidian species differed from other microsporidia obtained from related host species in many morphological features.

The newly described *Nosema adjuncta* differed from *Nosema otiorrhynchi* (Weiser, 1951) (host *Otiorrhynchus ligustici*) in that it developed at a considerably slower rate especially in the ovaries of the host. Also a comparison of the course of infection in the eggs showed a very different picture, e.g. in the absence of digested foci and widely ovoid stages of the parasite common to *N. otiorrhynchi*.

N. equestris differed from the related species *N. longifilum* (host *Otiorrhynchus fuscipes*) in its distribution in the host tissues and in a more widespread infection than that caused by *N. longifilum* attacking only the fat body. Spherical cysts in the fat body observed and described by Hesse (1905) for an infection on with *N. longifilum*, which were surrounded by a sheath of connective tissue inside which the spores were destroyed, were not observed with our species.

If the production of cysts is to be regarded as a reaction of the host to an "unadapted" parasite, we expected to obtain interesting results from a comparison of the reaction of two substituting hosts, *G. viridula* and *L. decemlineata* to the two newly described microsporidians. The results indicated that *Nosema adjuncta* did not develop too well in these hosts, the production of islets was sporadic and they were surrounded neither by connective tissue nor by lymphocytes of the host, and there was no indication of a further spreading. The same applied to *N. equestris* to which the substitute hosts did not react in any form resembling cysts produced as a reaction to *N. longifilum*. A substitution of hosts (*G. viridula* and *L. decemlineata*) was manifested solely in a more acute course and in a difference in the number of spores produced in an individual or in relation to the mg/weight of the host.

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The plates (Tab. 1, 2) will be found at the end of this issue.

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**LARVAE AND THE BREEDING TYPE OF THE CENTRAL EUROPEAN
SPECIES OF THE SUBGENERA BRADYTUS AND PSEUDOBADYTUS
(COLEOPTERA, CARABIDAE, AMARA)**

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Received January 15, 1979

Abstract: The larvae of *Amara* (*Bradytus*) *apricaria* (Paykul) (L I, L II, L III), *Amara* (*Bradytus*) *consularis* (Duftschmidt) (L I, L II), *Amara* (*Bradytus*) *fulva* (O. F. Müller) (L I, L II, L III), *Amara* (*Bradytus*) *majuscula* (Chaudoir) (L I, L II) and *Amara* (*Pseudobradytus*) *crenata* Dejean (L I) are described, illustrated and keyed, *A. majuscula* and *A. crenata* for the first time. In *A. (B.) fulva* the egg is described. The diagnosis of *Bradytus* Stephens and the preliminary diagnosis of *Pseudobradytus* Csiki in larval stage are given. Larval characters suggest the separation of *A. crenata* into the different subgenus *Pseudobradytus* Csiki. *A. (B.) majuscula* belongs to another species-group of *Bradytus* Steph. than *A. apricaria*, *A. consularis* and *A. fulva*. All the species are of a breeding type characterized by larval diapause during the winter period. The duration of individual developmental stages under laboratory conditions is mentioned.

The taxonomic definition of the subgenera *Bradytus* Stephens, 1828 and *Pseudobradytus* Csiki, 1908 as well as of most other subgenera of *Amara* Bonelli is insufficient and not entirely clear. Therefore also the inclusion of individual species of *Amara* Bon. into the subgenera is not uniform with various authors.

Among about 50 species of the subgenus *Bradytus* Stephens (sensu Csiki, 1908) there only six are known as larvae: *A. (B.) apricaria* (Payk.) (Schjødte, 1867; Larsson, 1941, 1968; Emden, 1942; Šarova, 1958, 1964), *A. (B.) batesi* Csiki (Gardner, 1937), *A. (B.) consularis* (Duft.) (Boldori, 1935; Larson, 1968; Emden, 1942; Šarova, 1958, 1964), *A. (B.) exarata* Dej. (Emden, 1942; Kirk, 1973), *A. (B.) fulva* (O. F. Müller) (Boldori, 1935; Emden, 1942; Larsson, 1941, 1968; Šarova, 1958, 1964; Raynaud, 1976) and *A. (B.) simplicidens* Morawitz (Habu, Sadanaga, 1965).

The one known species of the subgenus *Pseudobradytus* Csiki, *A. crenata* Dej. has not been described as a larva.

Four species of the subgenus *Bradytus* Steph. live in central Europe: *A. (B.) apricaria* (Payk.), *A. (B.) consularis* (Duft.), *A. (B.) fulva* (O. F. Müller) and *A. (B.) majuscula* (Chaud.), as well as *A. crenata* Dej. The specimens of all these species were reared in laboratory and the larvae of all species mentioned were thus obtained.

MATERIAL AND METHODS

The larvae were reared during 1964–1975 under laboratory conditions in the Department of Systematic Zoology, Charles University, Praha, at the technical assistance of Ms. Vlaslová (*A. apricaria*: 10 L I, 4 L II, *A. consularis*: 6 L I, 4 L II, *A. fulva*: 26 L I, 15 L II, *A. majuscula*: 3 L I, 2 L II, *A. crenata*: 5 L I). The origin of the reared adults was as follows: *A. apricaria* — Boh. c. Praha-Petřín, 28. 9. 1964; Boh. c. Praha-Jinonice, 21. 8. 1974; *A. consularis* —

Boh. mer. Vlkov n. Veselí n. L., 19. 7. 1965; Boh. c. Praha-Jinonice, 13. 8. 1974, 4. and 21. 4. 1975. *A. fulva* — Boh. mer. Vlkov n. Veselí n. L., 19. 7. 1965. *A. majuscula* — Russia sept. Leningrad, 12. 8. 1968. *A. crenata* — Boh. c. Praha-Jinonice, 13. and 21. 8. 1974, 19. 8. 1975.

Larvae found in the field (leg. Hůrka) were of the following origin: *A. apricaria* 1 L III, Boh. c. Praha-Dívčí Hrad, 28. 10. 1970; *A. fulva* 2 L III, Boh. c. Čelákovice, 14. 10. 1968.

The method of laboratory rearing was described by Hůrka, 1972. Daily checks on the reared larvae made possible to observe and ascertain the duration of the developmental rate of individual stages at the temperatures given.

The description of larval instar III (or II, if L III is not available) is the most detailed, that of L II and L I comprehends only the differences from the preceding instar.

Larval diagnosis of the subgenus *Bradytus* Stephens

Head wider than long. Clypeus, only slightly conspicuous, bears six minute teeth, more or less of the same size. Frontale in L I with spinous egg burster (Figs. 3, 21, 33, 49) which may be sometimes doubled or tripled (*A. fulva*). Epicranial sulcus absent or practically absent, dot-shaped (Fig. 32), or very short, as long as the egg burster (Fig. 48). The first antennal segment short, occupying less than one third of antennal length. Retinaculum short and obtuse, lying more or less in the mid part between apex and base of mandible (Figs. 6, 7); outer margin of mandible bears in L I one, in L II and L III two setae. Cervical grooves absent. Chaetotaxy of the head in L I is shown in Fig. 32. In L II and L III the number of setae increases, mainly between setae O_2 and L_1 on epicranium and in the area of clypeal setae (Cl) on frontale. Ninth abdominal sternum with one or several pairs of distinct setae (Fig. 57) at middle of its length.

Amara (Bradytus) apricaria (Paykull. 1790)

(Figs. 1–19)

Schiodte, 1867: 530; Larson, 1941: 333, 336, Fig. 52i; Emden, 1942: 11, 71; Šarova, 1958: 69, Figs. 54, 58, 126b; Šarova, 1964: 181, Figs. 110–2, 112, 158–9; Larsson, 1968: 393, 400, Fig. 57i.

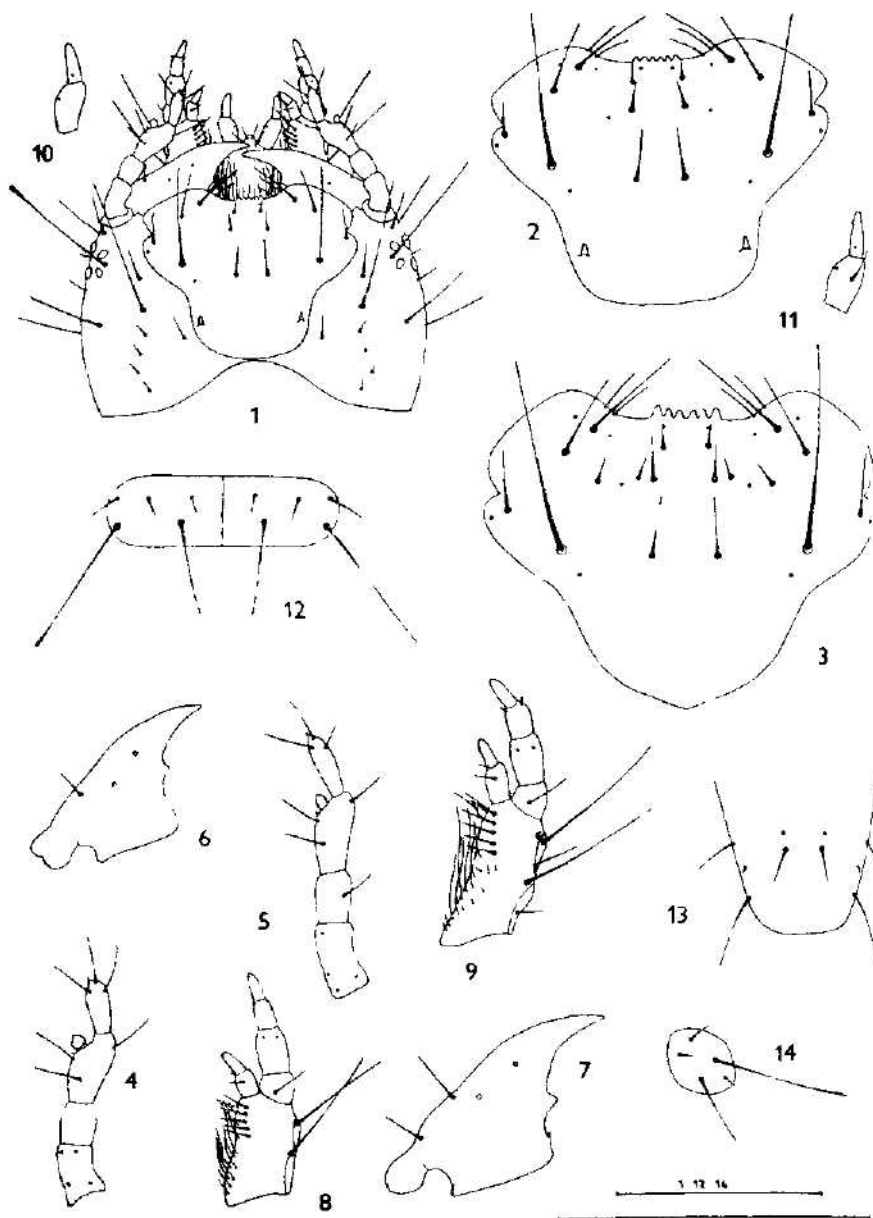
Material: 10 L I, 2 exuviae L I, 4 L II, 1 L III.

Description

Larval instar III: Head — wider than long, ratio of head capsule to length of frontale 2.1 : 1. Epicranial sulcus dot-shaped. Anguli frontales rounded, clypeal teeth minute, of almost equal length, the outer being slightly greater; ratio of width to length of frontale 1.4 : 1; pars alboralis frontalis obtusely pointed caudad (Fig. 15), its width to length ratio 2.5 : 1. Length ratio of antennal segments (I : II : III : IV) 1.5 : 1 : 1.6 : 1.2; second segment with one seta, third and fourth segments with three setae each (Fig. 16). Mandibles (Fig. 17) with two setae on the outer margin, its length : width ratio = 1.6 : 1. Stipes maxillaris (Fig. 18) 2.4 times longer than wide and 1.1 times as long as maxillary palp; length ratio of segments of maxillary palps (with the palpiger) 1.2 : 2 : 1.5 : 1, that of galeal segments 1.3 : 1. First segment of labial palps with two short setae, ratio of segments (I : II) 1.5 : 1. There are two short setae between setae L_1 and O_2 . Width of head capsule 1.41 mm (Emden, 1942 gives in 40 specimens 1.27–1.43, average 1.38 mm).

Thorax — pronotum 1.4 times wider than long, both meso- and metatergum about 3.1 times wider than long. Trochanter with 7–8 spines, two longer and several shorter setae, femur with 9–10 spines and short setae, tibia with 4 spines and 2 setae, tarsus with 2 spines; tarsus 1.2 times as long as tibia.

Abdomen — terga 1–7 approximately 2.9 times wider than long, with 3 pairs of short setae in anterior row and with 2 pairs of long setae in posterior row. Ster-



Figs. 1--14. *Amara (Bradytus) apricaria* (Payk.) L I, L II: 1 — head of L I; 2, 3 — frontal view of L I, L II; 4, 5 — antenna of L I, L II; 6, 7 — mandible of L I, L II; 8, 9 — maxilla of L I, L II; 10, 11 — labial palpus of L I, L II; 12 — abdominal tergum 4 of L I; 13 — ventral view of abdominal segment 10; 14 — 4th epipleurite of L II. Scale = 0.5 mm.

num 9 with one pair of setae at middle of its length, ventral side of segment 10 with 2 pairs of setae. Ratio of length of cercus to width of tergum 9 at base of cerci 1.3 : 1; each cercus with 9 setae.

Body length 10.6 mm, body width 1.7 mm.

Larval instar II: Head — ratio of width of head-capsule to length of frontale 2 : 1. Epieranal sulcus absent. Ratio of width to length of frontale (Fig. 3) 1.3 : 1; that of pars aboralis frontalis 2.2 : 1. Length ratio of antennal segments 1.6 : 1 : 1.8 : 1.2 (Fig. 5). Mandible (Fig. 7) 1.5 times longer than wide at base. Stipes (Fig. 9) as long as maxillary palp, length ratio of individual segments of palp 1 : 1.5 : 1.1 : 1.1. Basal segment of labial palps 1.2 times longer than second segment (Fig. 11). Width of head capsule 0.90–0.99 mm, average in 4 specimens 0.94 mm.

Thorax — trochanter with 6 spines, 2 long and several short setae, femur with 9 spines, tibia with 6 spines and one seta at base, tarsus with several short spines and 2 strong spines apically.

Abdomen — as in larval instar III.

Body length in 3 specimens 5.4–6.2 mm, body width 0.9–1.0 mm.

Larval instar I: Head — width to length ratio of pars aboralis frontalis 2 : 1; this forms caudally a broad arch (Fig. 2), egg bursters spinous. Length ratio of antennal segments 1.5 : 1 : 1.8 : 1.3 (Fig. 4). Mandibles (Fig. 6) with only one seta on the outer margin. Stipes broader (Fig. 8) 1.7 times as long as wide and a little shorter than palpus (0.9 : 1); the length ratio of palpal joints = 1 : 1.4 : 1 : 1; both segments of galea of equal length. Labial palps without setae (Fig. 10), ratio of segments 1.1 : 1. Width of head capsule in 10 specimens 0.74–0.86 mm (average 0.77 mm).

Thorax — trochanter with 4 spines, 2 long and several short setae, femur with 4 spines and 2 short setae, tibia with 6 spines and 1 seta at base, tarsus with 2 strong and several slender spines; tarsus 1.3 times longer than tibia.

Abdomen — terga 1–7 as in Fig. 12. Sternum 9 as well as ventral side of segment 10 (Fig. 13) with one pair of setae at middle. Ratio length of cercus to width of tergum 9 at base of cerci 1.2 : 1; each cercus with 5 setae.

Body length in 5 specimens 3.9–4.6 mm (average 4.1 mm), body width 0.9 mm in all specimens.

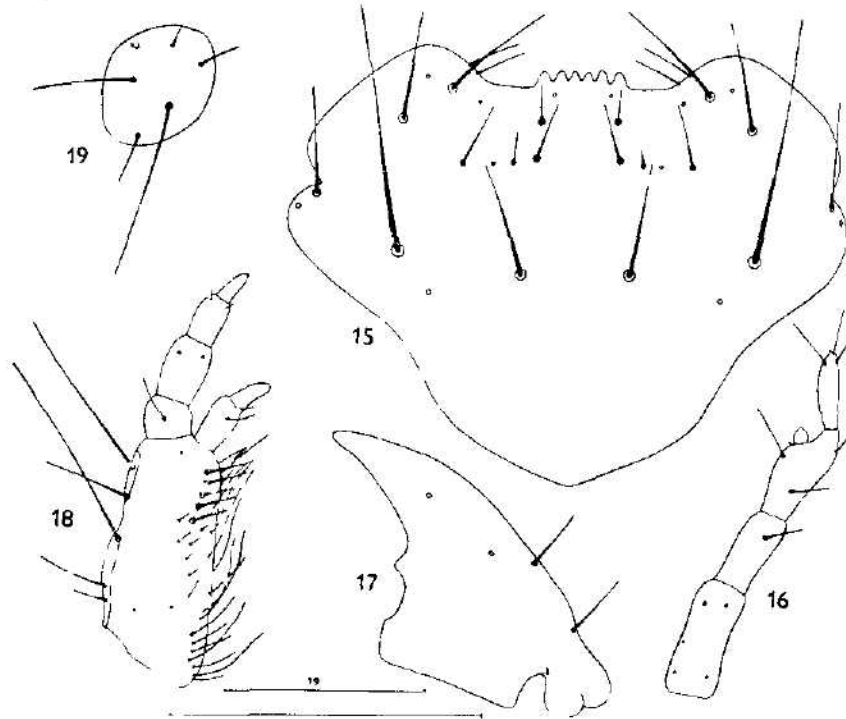
Our descriptions agree with the brief characterization of larvae by Schiødte (1867), Larsson (1941, 1968) and Šarova (1958, 1964), with the only exception of Larsson giving 2nd antennal segment as being a little longer than the fourth; our findings show quite the reverse.

Bionomic notes

Rearing. The females laid eggs from the end of August to mid-October. The eggs (10 specimens) developed 7–8 days at mean temperature 18.5°C (mortality 9%), larval instar I (4 specimens) 11–16 days (mean temperature 20°C) and one specimen of larval instar II 13 days (mean temperature 20.8°C). Mortality in both instars I and II was about 50%. The only larva of instar III died after 10 days (fungal infection).

In natural conditions of Czechoslovakia the occurrence of adults reaches its peak in August, mating was observed in August and September (Pulpán, personal communication). The females lay eggs probably from May to October, with the maximum in August (according to dissected females from the environs of Prague —

Formánková, 1973). We found one L III in Prague on 28. 10. 1970 (leg. Hůrka). Emden (1942) mentions the finding of 40 L III in April and May 1936 in Riesa (Saxonia), Larsson (1939) found larvae in Denmark from September to May, pupae and immature adults from June to August. Pulpán (pers. comm.) found immature adults in Czechoslovakia from May to August, with the peak occurrence in May.



Figs. 15–19. *Amara (Bradytus) apricaria* (Payk.) L III: 15 – frontale; 16 – antenna; 17 – mandible; 18 – maxilla; 19 – 4th epipleurite. Scale = 0.5 mm.

It follows from the above data that *A. apricaria* belongs to the species of the breeding type characterized by the larval diapause (Hůrka, 1973). Adults (at least of two generations) overwinter with the larvae.

Amara (Bradytus) consularis (Duftschmidt, 1812)

(Figs 20–31)

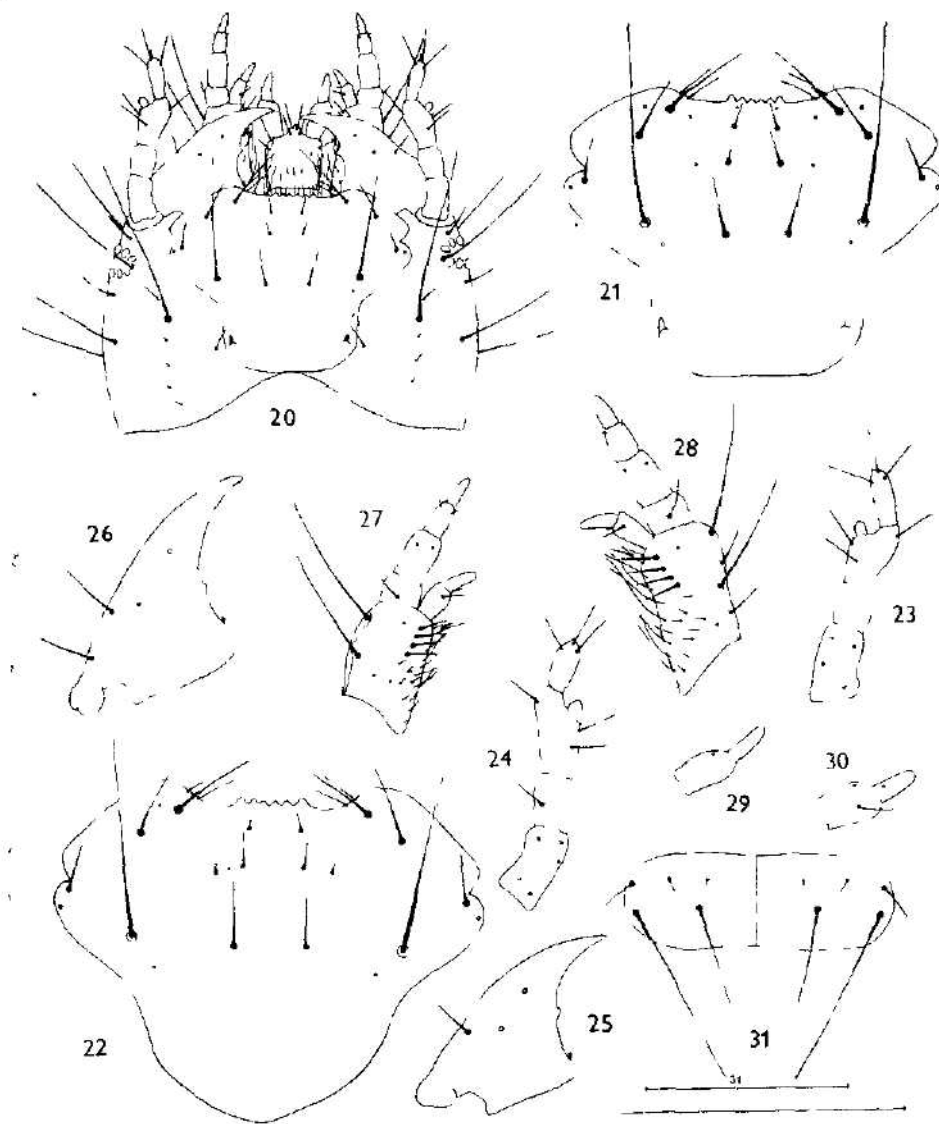
Boldori, 1935: 151, Fig. 2; Emden, 1942: 11, 71, Fig. 57; Šarova, 1968: 69; Šarova, 1964: 180–181; Larson, 1968: 393, 400.

Material: 6 L I, 6 exuviae L I, 4 L II, 1 exuvia L II.

Description

Larval instar II: Head – width of head capsule to length of frontale 2:1. Epicranial sulcus absent. Frontale (Fig. 22) 1.3 times wider than long, with rounded anguli frontales; clypeal teeth minute, of almost equal length (the outer slightly

greater); pars aboralis frontalis 2.3 times wider than long. Length ratio of antennal segments 1.5 : 1 : 1.7 : 1 (Fig. 24), second antennal segment with one seta. Mandibles (Fig. 26) 1.5 times as long as wide, 2 setae on the outer margin. Ratio of length to width of stipes 2.1 : 1 (Fig. 28) stipes of equal length as palpus; ratio of segments of palp 1.1 : 1.8 : 1.1 : 1, that of segments of galea 1.1 : 1. Basal segment of labial palps with one seta (Fig. 30), ratio of segments 1.2 : 1. There are no setae



Figs. 20-31. *Amara (Bradytus) consularis* (Duft.) L I, L II. 20 - head of L I; 21, 22 - frontale of L I, L II; 23, 24 - antenna of L I, L II; 25, 26 - mandible of L I, L II; 27, 28 - maxilla of L I, L II; 29, 30 - labial palp of L I, L II; 31 - abdominal tergum 4 of L I. Scale = 0.5 mm.

between L_1 and O_2 . Width of head-capsule in 4 specimens 1.03—1.16 mm (average 1.08 mm).*)

Thorax — pronotum 1.4 times wider than long, meso- and metatergum about 3 times as wide as long. Trochanter with 6 spines, 2 long and several short setae, femur with 9 spines (and 2 very short setae), tibia with 6 spines (and 1 seta at base) tarsus with 2 strong and several shorter and slender spines. Tarsus 1.1 times longer than tibia.

Abdomen — terga 1—7 3 times wider than long, with one pair of medium setae, 1 pair of short setae and one pair of minute setae in anterior row; posterior row with 2 pairs of long setae, another pair of short setae on segments 1—5. Sternum 9 with 1 pair of setae at middle, 2 pairs of setae on the ventral side of segment 10. Cerci short, length equal to the width of tergum 9 at base of cerci; each cercus with 9 setae.

Body length in 4 specimens 6.2—6.7 mm, body width 1.0—1.3 mm.

Larval instar 1: Head — twice wider than the length of frontale (Fig. 20). Epicranial sulcus absent. Frontale with un conspicuous anguli frontales, clypeal teeth minute, outer pair being the largest; pars aboralis frontalis of rectangular form, lateral margins being parallel (Fig. 21), its width to length ratio 21:1, egg bursters spinous. Length ratio of antennal segments 1.8 : 1 : 1.8 : 1.4, second segment bare (Fig. 23). Mandibles (Fig. 25) with one seta on the outer margin. Stipes broader (Fig. 27) 1.7 times longer than wide, shorter than palpus (0.9 : 1); ratio of segments of maxillary palp 1 : 1.7 : 1.1 : 1.1; both segments of galea of equal length. First joint of labial palp 1.1 times longer than the second (Fig. 29). Width of head capsule in 6 specimens 0.88—0.96 mm (average 0.91 mm). Emden (1942) gives in 3 specimens 0.90, 0.92, 0.94 mm.

Thorax — pronotum 1.6 times wider than long. Trochanter with 4 spines, 2 long and several short setae, femur with 4 spines and 2 very short setae, tibia with 4 spines and several setae, tarsus with 2 spines and several setae; tarsus 1.3 times as long as tibia.

Abdomen — terga 1—7 about 2.7 times wider than long, with 3 pairs of shorter setae on the anterior margin and with 2 pairs of long setae on the hind margin (Fig. 31). One pair of setae at middle of sternum 9 and one pair of setae on the ventral side of segment 10. Each cercus with 5 setae.

Body length in 4 specimens 3.8—5.3 mm, body width 0.9—1.1 mm.

Šarova (1958, 1964) and Larsson (1968) give brief characterizations of larvae. Our observations agree with both, with the exception of the relative size of the 2nd and 4th antennal segments by Larsson. Šarova gives the length of epicranial sulcus to be as long as the diameter of antennal segment 4. Epicranial sulcus is absent in our larvae of instars II and I.

Bionomic notes

Rearing. Mating was observed on October 19 (in adults collected on July 19), egg laying from the end of August to the end of October. The eggs (16 specimens) developed on average 7.5 (6—9) days at mean temperature 21.7° C (mortality 6%), larval instar I (9 specimens) on average 21 (11—33) days at mean temperature 21.4° C (mortality 40%). Only one larva of instar II hatched after 17 days (mean

*)Emden (1942) reports 1.70 mm in one specimen of L. III.

temperature 20.8° C) in third instar; the larva pupated after 16 days (mean temperature 21.5° C), and a defective adult emerged after 13 days (mean temperature 20.6° C). The entire development of this specimen from the egg lasted 79 days at mean temperature 21.2° C (min. 15° C, max. 28° C). The mortality rate in larval instar II was 86%.

In natural conditions of Czechoslovakia the occurrence of adults reaches its peak in August and September (Pulpán, pers. comm.). Emden (1942) gives 1 L III from Great Britain in April 1930; Larsson (1939) found larvae in Denmark in August, pupae and immature adults from June to August; in Czechoslovakia, immature specimens were found from May to November with the peak occurrence from June to August (Pulpán, p.c.). According to data by Formánková (1973) (based on dissected females) most newly hatched females reproduce in Central Bohemia till after hibernation.

A. consularis therefore also belongs to the breeding type with the larval diapause (in all probability to the variation with imaginal diapause).

Amara (Bradytus) fulva (O. F. Müller, 1776)

(Figs. 20–33, 67)

Boldori, 1935: 151, Figs. 3, 5, Larsson, 1941: 333, 336; Emden, 1942: 11, 71, Fig. 10; Šárova, 1958: 70, Fig. 130; Šárova, 1964: 181, Fig. 160; Larsson, 1968: 393, 400; Raynaud, 1976: 19–24.

Material: 26 L I, 17 exuviae L I, 15 L II, 2 L III.

Description

Larval instar III (Fig. 67): Head — distinctly wider than long, ratio of width of head-capsule to length of frontale 2.3 : 1. Epicranial sulcus dot-shaped. Frontale (Fig. 34) 1.6 times wider than long; teeth of clypeus minute, almost of equal size; pars aboralis frontalis obtusely pointed caudad, its width to length ratio 2.7 : 1. Length ratio of individual antennal segments 1.6 : 1.3 : 1.8 : 1, second segment with 2–4 setae (Fig. 38). Mandibles (Fig. 41) 1.5 times longer than wide at base, with 2 setae on the outer margin. Stipes (Fig. 47) nearly elongate, 2.3 times longer than wide and 1.2 times longer than maxillary palpus, length ratio of individual segments of maxillary palps 1.5 : 2 : 1.3 : 1. Basal joint of galea 1.6 times longer than joint 2. Length ratio of segments of labial palps 1.5 : 1 (Fig. 47). One pair of longer setae between setae L_1 and O_2 . Width of the head capsule 1.83 and 1.87 mm, Emden (1942) gives 1.60–1.84 (average 1.74 mm) in 10 specimens.

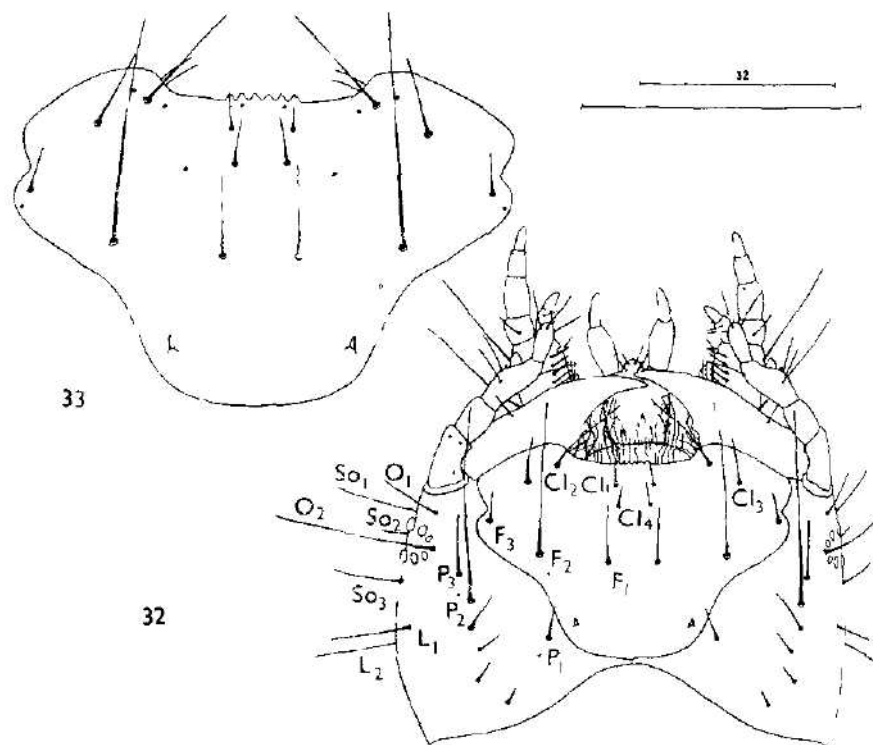
Thorax — pronotum 1.6 times wider than long, its surface abundantly covered with setae. Both terga of meso- and metathorax about 3 times wider than long. Trochanter with 6 spines, 2 long and several short setae, femur with 9–13 spines and 2 setae, tibia with 6 spines and one seta, tarsus apically with 2 strong spines and 4 short setae; tarsus 1.1 times longer than tibia.

Abdomen — terga 1–7 about 2.5 times wider than long, with higher number of setae in anterior row and with 5 pairs of setae in posterior row. Several pairs of setae at middle of sternum 9 as well as on the ventral side of segment 10. Cerci short, shorter than width of tergum 9 at base of cerci (0.8 : 1); 12 setae on each cercus.

Body length 11.0 and 11.1 mm, body width 2.3 and 2.5 mm.

Larval instar II: Head — Frontale as in Fig. 35. Epicranial sulcus dot-shaped. Length ratio of antennal segments 1.6 : 1.1 : 1.7 : 1, 1 or 2 setae on the second

segment (Fig. 37). Mandibles (Fig. 40) 1.6 times longer than wide. Stipes (Fig. 40) 2.2 times longer than wide and as long as palpus; length ratio of palpal joints 11 : 1.4 : 1.2 : 1, first segment of galea 1.1 times longer than segment 2. One seta on the first segment of labial palpus (Fig. 46), ratio of both segments 111 (one shorter and one longer setae between setae L_1 and O_2). Width of head capsule in 15 specimens 1.27–1.47 mm (average 1.34 mm); Emden (1942) gives 1.31 mm in one specimen.



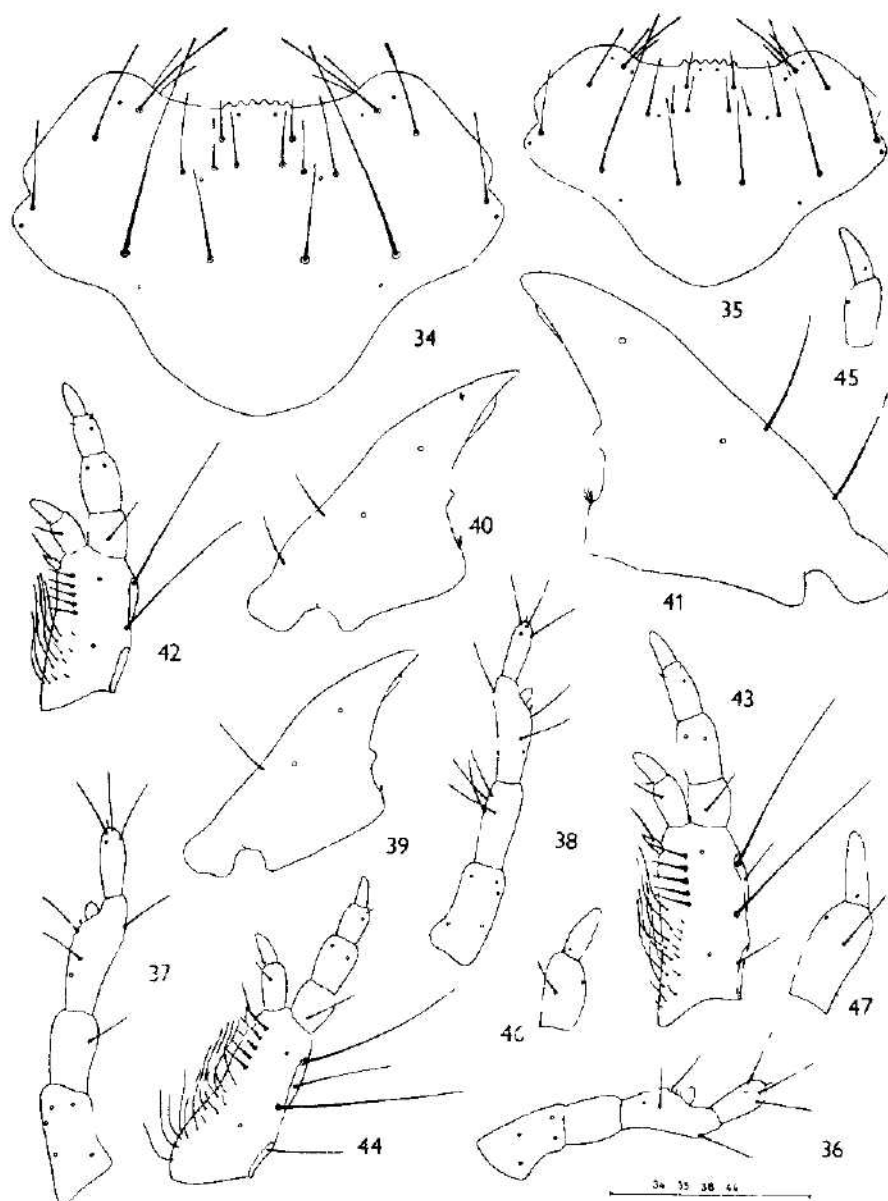
Figs. 32–33. *Amara (Bradytus) fulva* (O. F. Mull.) L I: 32 — head; 33 — frontal. Scale = 0.5 mm.

Thorax — pronotum 1.8 times wider than long. The chaetotaxy of the legs and the length ratio of tarsus and tibia are the same as in L III.

Abdomen — terga 1–7 about 2.8 times wider than long, with 3 pairs of longer setae and several pairs of shorter ones in both anterior and posterior rows. Sternum 9 with one pair of setae at middle of its length and the ventral side of segment 10 with several pairs of setae. Cerci short, as long as the width of tergum 9 at base of cerci; each cercus with 9–10 setae.

Body length 6.5–10.5 mm (average in 6 specimens 8.3 mm), body width 1.5 to 1.9 mm (average 1.7 mm).

Larval instar I: Head (Fig. 32) — epicranial sulcus dot-shaped. The form of



Figs. 34-47. *Arara (Bradytus) fulva* (O. F. Mull.) L I, L II, L III: 34, 35 - frontale of L II, L III; 36, 37, 38 - antenna of L I, L II, L III; 39, 40, 41 - mandible of L I, L II, L III; 42, 43, 44 - maxilla of L I, L II, L III; 45, 46, 47 - labial palp of L I, L II, L III. Scale = 0.5 mm.

frontale similar to that of L III, pars aboralis frontalis not obtusely pointed (Fig. 38), ratio of width to length of pars aboralis frontalis 2.5 : 1; egg bursters spinous sometimes doubled or tripled. Length ratio of antennal segments 1.6 : 1 : 1.6 : 1 (Fig. 36). Mandibles (Fig. 39) slender, length to width ratio 1.5 : 1, with one seta on the outer margin. Stipes (Fig. 42) twice longer than wide and as long as palpus; length ratio of palpal joints: 1.2 : 1.5 : 1.1 : 1; length ratio of segments of galea as in L₂. Palpi labiales without setae (Fig. 45), ratio of segments 1.2 : 1. Width of head capsule in 26 specimens 0.97—1.20 mm (average 1.10 mm).

Thorax — width to length ratio of individual segments as in L₂. Trochanter with 4 spines and with several shorter and 2 long setae, femur with 4 spines and 2 short setae, tibia with 6 spines and 1 seta, tarsus with 2 strong spines and 4 small ones, length ratio of tarsus and tibia 1.4 : 1.

Abdomen — terga 1—7 approximately 2.7 times wider than long, with 3 pairs of short setae in anterior row and with 2 pairs of long setae and one pair of minute setae in posterior row. Sternum 9 with one pair of setae at middle of its length, ventral side of segment 10 with 3 pairs of setae. Cerci as long as the width of tergum 9 at base of cerci; each cercus with 5 setae.

Body length 4.4—6.8 mm (average in 13 specimens 5.6 mm), body width 1.1 to 1.4 mm (average 1.3 mm).

The egg is elongate, oval in shape, pale yellowish in colour; average size in 5 specimens 1.8×1.1 mm. Sculpture of chorion: circular, more or less regular areas of 9—15 μ m.

The brief characterization by Larsson (1941, 1968) and Šarova (1958, 1964) agree with our findings.

Bionomic notes

Rearing. Mating was observed from the end of August to the end of September (in adults collected on July 19), the egg laying at the same time (28. 8.—29. 9.). The eggs (44 specimens) developed on average 8 (6—10) days at the mean temperature 19.5° C (mortality 17%), the larval instar I (19 specimens) on average 20 (12—30) days at the mean temperature 20° C (mortality 56%). Mortality in larval instar II was 100%.

In natural conditions reaches the occurrence of adults in Czechoslovakia its peak (Pulpán, p.c.) in June (hatching of the new generation), and in August—September (reproduction). We found 2 L III (Hôrka lgt.) in Central Bohemia on 14. 10. 1968. Emden (1942) reports 1 L II and 6 L III from Poland (Czernowitz) on 8. 11. 1936, 4 L III from Germany (Riesa, Saxonia) in April and May 1935; Larsson (1939) mentions in Denmark findings of larvae in December and May, that of pupae and immature adults in June and July. In Czechoslovakia, immature adults were found from April to August, with the peak occurrence in June (Pulpán, p.c.).

Considering all available data, the species belongs to those characterized by the breeding type with the larval diapause.

Amara (Bradytus) majuscula (Chaudoir, 1850)

(Figs. 48—59, 68)

Material: 3 L I, 2 L II

Description

Larval instar II: Head — Ratio of width of head capsule to length of frontale 1.7 : 1. Epicranial sulcus dot-shaped. Clypeal teeth minute, pars aboralis frontalis

pointed caudad; ratio of width to length of frontale 1.2 : 1 (Fig. 50), that of pars aboralis frontalis 1.8 : 1. Length ratio of antennal segments 1.5 : 1 : 1.7 : 1, second segment with one seta (Fig. 52). Mandibles (Fig. 54) with 2 setae on the outer margin, 1.4 times longer than wide. Stipes (Fig. 56) 2.2 times longer than wide and of equal length as the palpus; ratio of segments of palps 1.1 : 1.6 : 1.1 : 1, that of segments of galea 1 : 1. Between setae L_1 and O_2 there is one long and one short seta. Width of head capsule 1.03 and 1.07 mm.

Thorax — pronotum 1.5 times wider than long; meso- and metaterga about 3 times wider than long. Trochanter with 6 spines, 2 long and several short setae, femur with 9 spines and several short setae, tibia with 4 thick and 2 slender spines, tarsus with 2 spines and several setae; tarsus 1.1 times longer than tibia.

Abdomen — terga 1—7 about 3 times wider than long, with 3 pairs of short setae on the anterior margin and 3 pairs of longer setae on the posterior margin (on terga 7 and 8 the outer pair is short). Sternum 9 with one pair of setae at middle, ventral side of segment 10 with 2 pairs of setae. Cercus 1.4 times longer than the width of tergum 9 at base of cerci; each cercus with 9 setae.

Body length 5.6 and 6 mm, body width 1.1 mm.

Larval instar I (Fig. 68): Head (Fig. 48) — ratio of width of head capsule to length of frontale 2 : 1. Epicranial sulcus distinct, about as long as egg burster. Ratio of width to length of frontale 1.3 : 1, that of pars aboralis frontalis 1.8 : 1 (Fig. 49); egg burster spinous. Length ratio of antennal segments 1.7 : 1 : 1.8 : 1.3, second segment bare (Fig. 51). Mandibles (Fig. 53) with one seta on the outer margin. Stipes twice longer than wide (Fig. 55), shorter than palpus (0.9 : 1); ratio of segments of palpi 1.1 : 1.5 : 1 : 1; both segments of galea of equal length. Labial palpi without setae, ratio of segments 1.1 : 1. Width of head capsule in 3 specimens 0.81, 0.81 and 0.89 mm.

Thorax — trochanter with 5 spines, 2 long and several short setae, femur with 4 spines and 2 setae, tibia with 4 strong and 2 slender spines, tarsus with 2 strong spines; tarsus distinctly longer than tibia (1.5 : 1).

Abdomen — terga 1—7 with 3 pairs of setae on the anterior margin and with 2 pairs of long setae on the posterior margin. At middle of sternum 9 there is 1 pair of setae (Fig. 57), 1 pair of setae also on the ventral side of segment 10. Ratio of length of cerci to width of tergum 9 at base of cerci 1.2 : 1; each cercus with 5 setae.

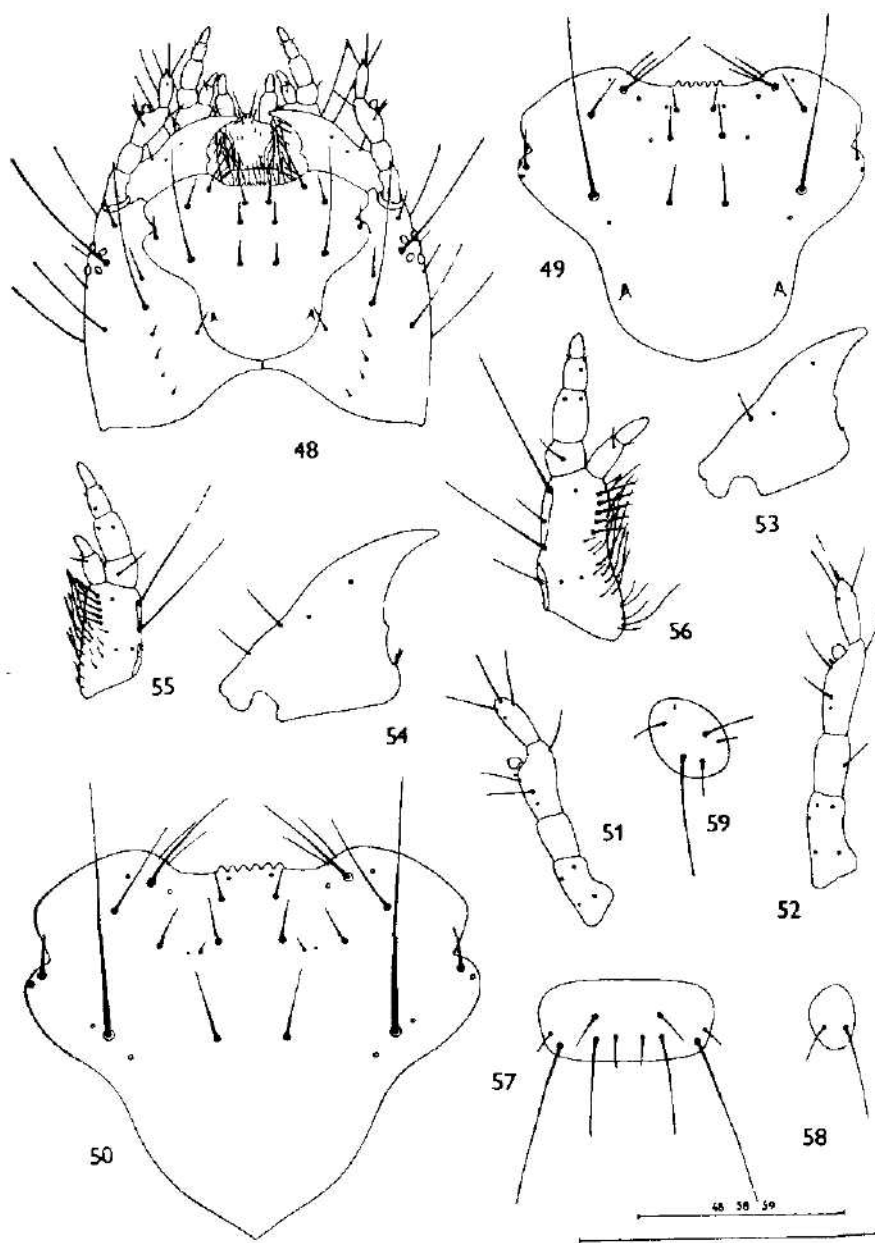
Body length 4.0—5.6 mm, body width 0.9 mm.

Bionomic notes

Rearing. Two pairs of adults found on August 12, 1968 in a park in Leningrad laid eggs immediately after being placed in the rearing room. Only 2 specimens of larval instar I hatched in to second instar (after 16 and 23 days at the mean temperature 22° C — mortality in L I = 75%); the mortality in L II was 100%.

In Czechoslovakia, adults were found from March to October, with the peak occurrence in July, immature specimens occur from April to June, most frequently in May (Pulpan, p.c.).

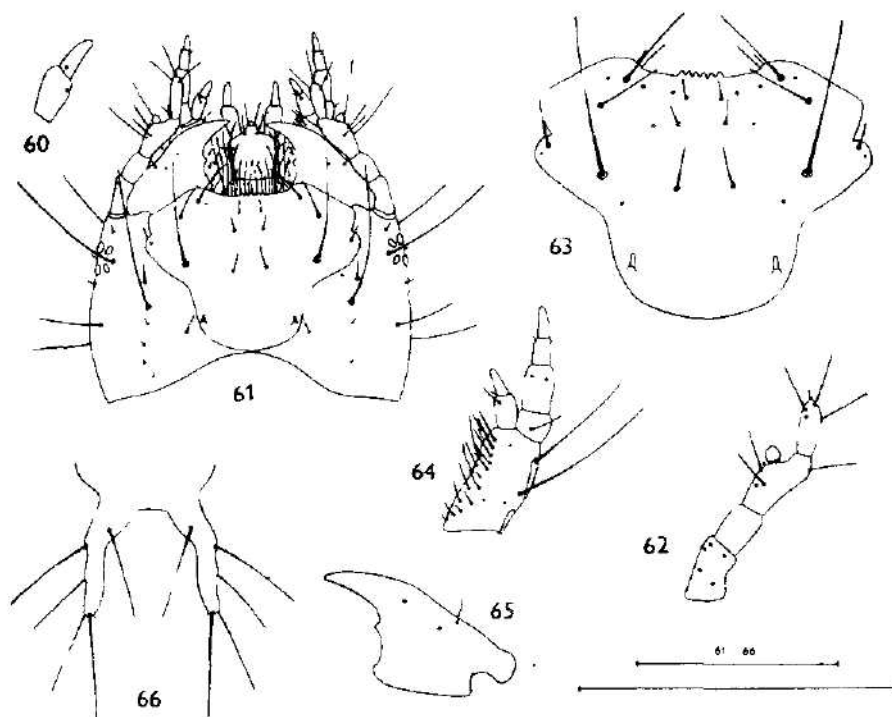
According to these scarce data it seems that *A. majuscula* also belongs to the species with the larval diapause in the breeding cycle.



Figs. 48-59. *Amara (Bradytus) majuscula* (Chaud.) L I, L II: 48 - head of L I, 49, 50 - frontale of L I, L II; 51, 52 - antenna of L I, L II; 53, 54 - mandible of L I, L II; 55, 56 - maxilla of L I, L II; 57 - abd. sternum 9 of L I; 58, 59 - 4th epipleurite of L I, L II. Scale = 0.5 mm.

Preliminary larval diagnosis of the subgenus *Pseudobradytus* Csiki

Head wider than long. Clypeus with 6 minute teeth; frontale in L I with spinous egg burster (Fig. 63). Epicranial sulcus absent. Mandible with short obtuse retinaculum at middle of inner part. Cervical grooves absent. Ninth abdominal sternum without a pair of distinct setae at middle of its length.



Figs. 60–66. *Amara (Pseudobradytus) crenata* (Dej.) L I: 60 — labial palp; 61 — head; 62 — antenna; 63 — frontale; 64 — maxilla; 65 — mandible; 66 — cerci. Scale = 0.5 mm.

Amara (Pseudobradytus) crenata Dejean, 1828

(Figs. 60–66)

Material: 5 L I

Description

Larval instar I: Head (Fig. 61) — ratio of width of head capsule to length of frontale 2 : 1. Epicranial sulcus dot-shaped as absent. Anguli frontales flat, clypeal teeth minute, of about equal size; ratio of width to length of frontale 1.3 : 1, that of pars aboralis frontalis 2 : 1 (Fig. 63); egg burster spinous. Length ratio of antennal segments 1.6 : 1 : 1.9 : 1.4 (Fig. 62). Mandibles 1.4 times longer than wide, with a small retinaculum and with one seta on the outer margin (Fig. 65). Stipes (Fig. 64) twice as long as wide and shorter than palpus (0.9 : 1); length ratio of segments of palpi 1 : 1.6 : 1 : 1; basal joint of galea 1.1 times longer than second joint. Labial palpi without setae (Fig. 60), ratio of segments 1.2 : 1. Width of head capsule in 5 specimens 0.73–0.84 mm (average 0.78 mm).

Thorax — pronotum 1.8 times wider than long. Meso- and metathoracic terga about 3 times as wide as long. Trochanter with 4 spines, 2 long and several short setae, femur with 4 spines and several short setae, tibia with 4 strong and 2 slender spines, tarsus with 2 spines and several setae; tarsus 1.4 times longer than tibia.

Abdomen — terga 1–7 about 2.6 times wider than long, with 3 pairs of short setae on the anterior margin and with 2 pairs of long setae on the posterior margin. There are no setae at middle of sternum 9; ventral side of segment 10 with 1 pair of setae. Cerci 1.1 times longer than the width of tergum 9 at base of cerci, each cercus with 5 setae (Fig. 66).

Body length 3.5–3.7 mm, body width 0.9 mm.

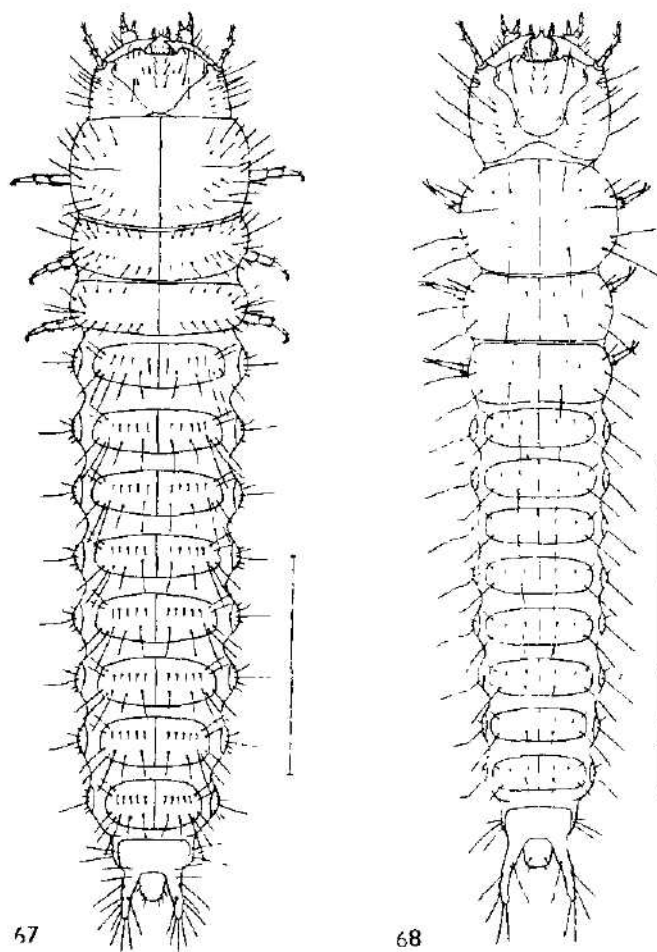


Fig. 67. *Amara* (B.) *fulva* (O. F. Müll.) L III, scale = 3 mm; Fig. 68. *Amara* (B.) *mojavensis* (Chaud.) L I, scale = 2 mm.

Bionomic notes

Rearing. The larvae of instar I were found in the rearing vessels during the first half of September (adults had been found in the second decade of August), their mortality was 100%.

The peak occurrence of adults in Czechoslovakia was observed in May and in August and September, immature adults were found from April to August, most frequently in May (Pulpan, p.c.). Formánková (1973) dissected some females from the Central Bohemia in March and April. She ascertained that females of two generations overwinter; the ovaries of all specimens examined were inactive and most females had not yet reproduced.

A. crenata apparently also belongs to the species characterized by the breeding type with the larval diapause.

TAXONOMIC NOTES AND KEYS

Csiki, 1908 separated *A. crenata* Dej. into the subgenus *Pseudobradytus* described by him. Jeannel (1942) and Burakowski et al. (1974) accepted this subgenus sensu Csiki as a monogenetic taxon; Kult (1947) also included *A. majuscula* (Chaud.) into this subgenus according to the chaetotaxy of the hind tibiae of males. Lindroth (1945), Kryžanovskij (1965) and Hieke (1976) consider *Pseudobradytus* Csiki a synonym of *Bradytus* Stephens.

The larval characters (absence of a pair of setae at middle of sternum 9) confirm the separation of *A. crenata* Dej. into the subgenus *Pseudobradytus* Csiki. *A. majuscula* (Chaud.) evidently belongs to another species-group of the subgenus *Bradytus* Steph. than the species *A. apricaria* (Payk.), *A. consularis* (Duft.) and *A. fulva* (O. F. Müller).

Key to larval instar I

- 1 (8) One pair of setae at middle of abdominal sternum 9 (Fig. 58) *Bradytus* Stephens
- 2 (7) Epierianial sulcus absent; pars aboralis frontalis at least twice wider than long (Figs. 3, 16, 33)
- 3 (4) Two or more pairs of longer setae on the ventral side of abdominal segment 10 *A. (B.) fulva* (O. F. Müll.)
- 4 (3) One pair longer setae on the ventral side of abdominal segment 10 (Fig. 10)
- 5 (6) Two inner pairs of setae in anterior row of abdominal terga of subequal length (Fig. 5); cerci a little longer (1.2 times) than width of tergum 9 at base of cerci *A. (B.) apricaria* (Payk.)
- 6 (5) The inner pair of setae in anterior row of abdominal terga distinctly shorter than second pair (Fig. 31); cerci about as long as width of tergum 9 at its base *A. (B.) consularis* (Duft.)
- 7 (2) Epierianial sulcus present, short, as long as egg burster (Fig. 48); pars aboralis frontalis less than twice wider than long (Fig. 49) *A. (B.) majuscula* (Chaud.)
- 8 (1) No pair of setae at middle of abdominal sternum 9 *Pseudobradytus* Csiki, *A. (P.) crenata* Dej.

Key to larval instars II and III

- 1 (6) Pars aboralis frontalis more than twice wider than long, obtusely rounded caudad (Figs. 6, 17, 26, 34, 35)
- 2 (3) Ventral side of abdominal segment 10 with numerous setae; two or more pairs of setae at middle of abdominal sternum 9; more than 3 pairs of setae in posterior row of abdominal terga 1-5 *A. (B.) fulva* (O. F. Müll.)
- 3 (2) Ventral side of abdominal segment 10 with two pairs of setae; one pair of setae at middle of abdominal sternum 9; 2-3 pairs of setae in posterior row of abdominal terga 1-5
- 4 (5) Only 2 pairs of setae in posterior row of abdominal terga 1-5 *A. (B.) apricaria* (Payk.)

- 5 (4) 3 pairs of setae in posterior row of abdominal terga 1–5 . . . *A. (B.) consularis* (Duf.)
 6 (1) Pars aboralis frontalis less than twice wider than long, pointed caudad (Fig. 54).
 *A. (B.) majuscula* (Charad.)

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GROWTH OF RUFFE, *ACERINA CERNUA* (PISCES, PERCIFORMES) IN CZECHOSLOVAKIA

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Abstract: Growth rate of Ruffe or stone perch, *Acerina cernua* (Linnaeus, 1758), collected during the years 1949–1963 from six ponds, four rivers, two rivulets, three backwaters and three valley water reservoirs of Czechoslovakia has been studied from the scales of 553 specimens. Stone perch of eight classes were recorded. Lee's disk was used for the back-calculations of lengths at the formation of different respective annuli. Specimens from the ponds grow at higher rate in between the age classes 1+ to 4+ and in the latter classes from the valley water reservoirs. The rate of growth is similar from the populations of rivers and rivulets.

INTRODUCTION

Literature regarding the growth of *Acerina cernua* (Linnaeus) is scarcely available. Järnefelt (1921) studied the growth of stone perch from the lakes of Finland, Berg (1949) from Ubinskoe lake of U.S.S.R., Talčanov (1951) from four ponds of U.S.S.R., Bauch (1954) from the Baltic sea, rivers and 24 lakes of Germany and Oliva-Vostradovský (1960) from Slapy and Pastviny Valley Water reservoirs of Czechoslovakia.

MATERIAL AND METHODS

553 specimens of *Acerina cernua* were collected from the different localities. Table 1 gives the details of material studied as far as locality, number of specimens, date of collection and the name of the collector is concerned.

Whole material was deposited in the ichthyological collections of Department of Systematic Zoology, Charles University, Prague, Czechoslovakia.

Three to five scales were removed from the first, second very rarely from the third row, below the 2nd–4th dorsal ray of the dorsal fin above the lateral line. For the measurement of the scales "Documator" (microprojector, Carl Zeiss, Jena, magnification 17.5) was used using diagonal scale radius and on this radius the distance of different annuli was measured. All the scales were studied in dry mounts. Lee's disk was used for the back-calculations of the body lengths at the respective annuli with a correction factor of 19 mm (Fig. 1).

All the measurements were taken to the nearest millimeter.

For the calculation of specific rate of linear growth, the following formula was used:

$$Cl = \frac{L_2 - L_1}{L_1} \cdot 100$$

where Cl = Specific rate of linear growth

L_1 and L_2 = Computed standard lengths at the successive years of life.

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Table 1. Details of the material of *Acerina cernua* collected for the present studies

S. No.	Locality	Date of collection	No. of specimens	Collected by
Ponds				
1.	Opatovický rybník	Oct. 1963	161	O. Oliva
2.	Ponědražský rybník	Oct. 1954	48	O. Oliva
3.	Millrow to pond Rožmberk	July, 1956	60	O. Oliva
4.	Kaňov at Třeboň	Nov. 1953	43	O. Oliva
5.	Dvořiště	Nov. 1954	1	O. Oliva
6.	Máchovo jezero	Oct. 1951	25	O. Oliva
Rivers				
7.	Vltava, Prague	May, 1949	5	O. Oliva
8.	Berounka at Revnice	Oct. 1949	22	J. Materna
9.	Labe at Čelákovice	Sept. 1951,	1	O. Oliva
	Labe at Kersko	Aug. 1951	3	A. Romanovsky
10.	Dyje at Znojmo and Tasovice	Oct. 1957	29	Angling Soc. Znojmo
Valley Water Reservoirs				
11.	Vranovská	July, 1957	10	O. Oliva
12.	Pastvinská	Aug. 1957	13	O. Oliva and Angling Soc. Prague
13.	Slapská near villages Bučily and Živohošť	Nov. 1957	97	O. Oliva
Rivulets				
14.	Stropnice at Borovany	April, 1953	9	J. Čihař
15.	Výmola at Čelákovice	Oct. 1952	2	O. Oliva
Backwaters				
16.	Hrad, inund. area of river Labe	Nov. 1949	16	J. Hrbáček
17.	Řeháková bouda, middle Bohemia, river Labe	Feb. 1954	1	O. Oliva
17.	Řeháková bouda, middle Bohemia, river Labe	Sept. 1950	1	
18.	Poltruba	May 1952	2	O. Oliva
		Aug. 1952	4	

RESULTS AND DISCUSSION

The body length/diagonal scale radius relationship (Fig. 1) shows linear relationship and the scale formation appeared at 19 mm of body length. The back calculated lengths using 19 mm as a correction factor indicate that the first annulus was formed when the stone perch attained the average size of 53.8 mm from ponds, 55.2 mm from rivers, 53.8 mm from valley water reservoirs, 55.2 mm from rivulets and 53.8 mm from backwaters of Czechoslovakia. Maximum age classes has been recorded from Ponědražský rybník among ponds (7+ age classes), from the river Dyje among rivers (8+ age classes), valley water reservoir Pastvinská among valley water reservoirs (7+ age classes) and from backwater Řeháková, middle Bohemia among backwaters (5+ age classes).

The observations from the different ponds are presented in the Table 2 from Opatovický rybník and Table 3 from Ponědražský rybník.

From the millrow to Rožmberk 60 specimens were collected, out of which 51 belong to 0+ age class with body length ranging between 35–60 (45) mm and 9 specimens to the age class 1+ ranging between 64–76 (70.2) mm; $l_1 = 45-60$ (50.4) mm

From the pond Kaňov at Třeboň in south Bohemia, 43 specimens were collected belonging to five age classes. In the age class 0+, 14 specimens ranging between 42–63 (50.3) mm; in the age class 1+, 17 specimens ranging between 75–85 (80.3) mm, $l_1 = 50$ –60 (54.3) mm; in the age class 2+, 9 specimens ranging between 88–98 (91.2) mm, $l_1 = 54$ –60 (54) mm, $l_2 = 75$ –85 (77.2) mm; in the age class 3+, 3 specimens ranging between 91–102 (97.6) mm, $l_1 = 49$ –57 (54) mm, $l_2 = 65$ –80 (71.6) mm, $l_3 = 85$ –94 (90.6) mm.

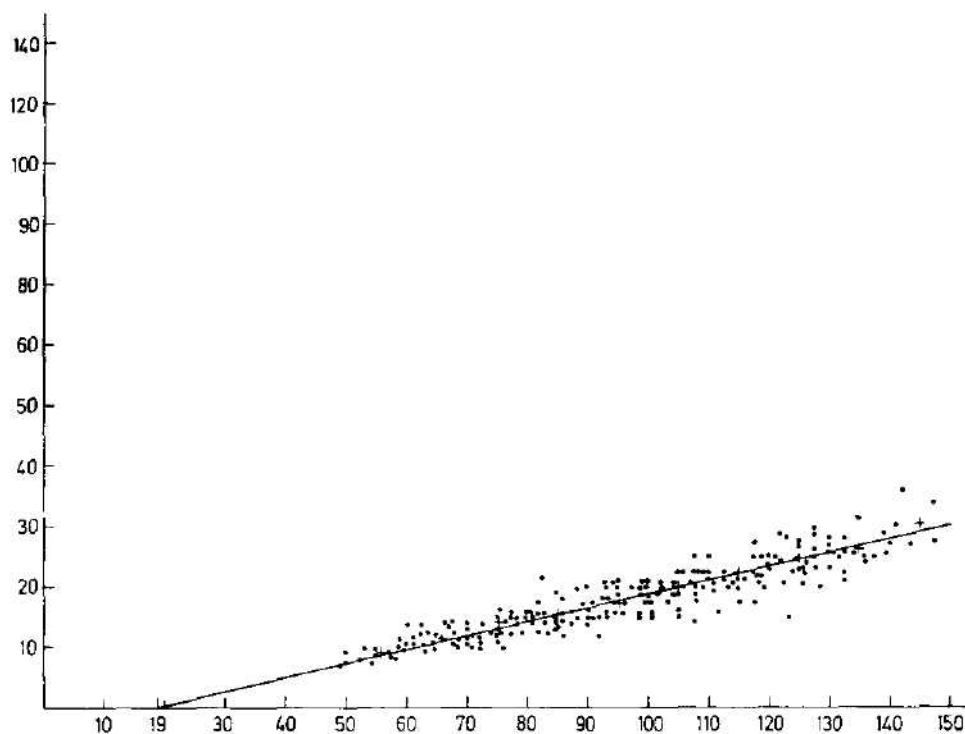


Fig. 1. Relationship between body length and scale radius in *Acerina cernua*. Body length (in mm.) is along abscissa and scale radius (in mm.) is along ordinate. Thick circles = original readings, crosses = average readings at 10 mm. interval.

Table 2. Growth of *Acerina cernua* from Opatovický rybník collected during the year 1963

Age class	No. of specimens	Body length at the time of capture in mm	Average back-calculated length in mm	
			l_1	l_2
0+	32	45	—	—
1+	106	40–54	—	—
		71	50	—
2+	23	63–68	45–60	—
		82	52	73
Total	161	80–86	48–60	70–75
			51	73
			45–60	70–75

Table 3. Growth of *Acerina cernua* from Pončdravský rybník at Třeboň collected during the year 1954

Age Class	No. of specimens	Body length at the time of capture in mm	Average back-calculated lengths in mm						
			l ₁	l ₂	l ₃	l ₄	l ₅	l ₆	l ₇
1+	5	75 71-81	54 50-58	—	—	—	—	—	—
3+	7	101 95-109	55 50-62	80 73-86	93 84-108	—	—	—	—
4+	16	112 104-120	52 48-59	73 70-77	87 76-95	102 93-111	—	—	—
5+	14	122 118-130	52 48-67	72 66-82	84 75-97	100 94-114	112 108-120	—	—
6+	4	129 127-130	48 45-49	70 66-75	81 78-85	93 90-97	108 100-110	118 115-120	—
7+	2	132	51 50-52	71 70-72	77 76-78	89 88-90	98.5 97-100	109 108-110	119 118-120
Total	48		52 45-62	73 66-86	84 75-108	96 88-114	105 97-110	113 108-120	119 118-120
Annual increment in mm.			21	11	12	9	8	6	
Specific rate of linear growth (Cl)			41.2	16.6	13.7	9.3	7.9	4.8	

Table 4. Growth of *Acerina cernua* from river Dyje at the towns Znojmo and Tasovce collected during the year 1957

Age class	No. of specimens	Body length at the time of capture in mm	Average back-calculated lengths in mm									
			l ₁	l ₂	l ₃	l ₄	l ₅	l ₆	l ₇	l ₈	l ₉	l ₁₀
1+	3	73 71-75	57 55-59	—	—	—	—	—	—	—	—	—
2+	1	87	60	71	—	—	—	—	—	—	—	—
4+	3	118 115-120	55 54-58	79 79-80	91 90-93	109 108-110	—	—	—	—	—	—
5+	6	123 116-126	57 51-61	75 74-80	90 85-94	102 100-107	113 108-117	—	—	—	—	—
6+	7	131 126-136	57 53-60	75 70-82	87 80-97	98 96-108	112 105-118	122 118-127	—	—	—	—
7+	8	135 130-140	52 50-56	71 70-74	82 80-85	91 85-98	106 98-110	115 116-125	126 120-129	—	—	—
8+	1	132	48	70	80	90	108	118	123	126	—	—
Total	29		55 50-61	74 70-82	86 80-94	98 85-110	109 98-118	119 116-127	124 120-129	126	—	—
Annual increment in mm			19	12	12	12	11	10	5	1		
Specific rate of linear growth (Cl)			33.2	16.9	14	14	11.4	8.2	5	0.3		

From the pond Dvořiště (south Bohemia) only one specimen was caught with body length 83 mm and has completed two years of age with $l_1 = 62$ mm, $l_2 = 74$ mm.

From the pond Máchovo jezero (north Bohemia) 25 specimens were caught belonging to 4 age classes. In the age class 1+, 4 specimens ranging between 61–76 (67.7) mm of body length, $l_1 = 53$ –60 (56.5) mm, in the age class 2+, 12 specimens ranging between 82–92 (87.6) mm, $l_1 = 50$ –66 (58) mm, $l_2 = 71$ –82 (74.9) mm; in the age class 3+, 8 specimens ranging between 93–105 (97.1) mm, $l_1 = 50$ –58 (53) mm, $l_2 = 75$ –85 (80.8) mm, $l_3 = 80$ –91 (86.2) mm; in the age class 4+ only one specimen was collected with body length 113 mm, $l_1 = 51$ mm, $l_2 = 81$ mm, $l_3 = 98$ mm, $l_4 = 108$ mm.

Results of the river Dyje (south Moravia) at the town Znojmo and village Tasovice are given in the Table 4.

From the river Vltava, Prague, 5 specimens were caught belonging to 3 age classes from 1+ to 3+. In the age class 1+, 2 specimens ranging between 66–76 (71) mm, $l_1 = 47$ –55 (51) mm; in the age class 2+, only one specimen with body length 82 mm, $l_1 = 49$ mm, $l_2 = 71$ mm; in the age class 3+, 2 specimens ranging between 100–113 (102.5) mm, $l_1 = 54$ (54) mm, $l_2 = 70$ –80 (78.5) mm, $l_3 = 90$ –96 (94.5) mm.

From the river Berounka at Řevnice (Middle Bohemia) 22 specimens were collected belonging to 4 age classes from 0+ to 3+. In the age class 0+, 5 specimens ranging between 60–65 (62.9) mm; in the age class 1+, 6 specimens ranging between 60–72 (64.5) mm, $l_1 = 47$ –56 (52) mm, in the age class 2+, 7 specimens ranging between 84–95 (91.2) mm, $l_1 = 58$ –61 (59.5) mm, $l_2 = 72$ –88 (81.5) mm, in the age class 3+, 4 specimens ranging between 97–112 (105.7) mm, $l_1 = 48$ –61 (54.7) mm, $l_2 = 74$ –81 (76.4) mm, $l_4 = 84$ –102 (93.7) mm.

From the river Labe at the village Čelákovice (middle Bohemia) only one specimen was caught with body length 105 mm and belongs to the age class 4+, $l_1 = 57$ mm, $l_2 = 72$ mm, $l_3 = 80$ mm, $l_4 = 96$ mm.

From the river Labe at village Kersko (middle Bohemia), 3 specimens were collected belonging to 2 age classes 1+ and 2+ respectively. In the age class 1+ specimens ranging between 68–72 (70) mm, $l_1 = 59$ –65 (62) mm, in the age class 2+, only one specimen with body length 85 mm, $l_1 = 55$ mm, $l_2 = 77$ mm.

Results of the valley water reservoir Slapská near the villages Bučily and Žárohošť (middle Bohemia) are presented in the Table 5.

From the Valley Water reservoir Vranovská přehrada, 10 specimens were collected belonging to 5 age classes from 1+ to 5+. In the age class 1+, 2 specimens ranging between 67–68 (67.5) mm, $l_1 = 52$ –57 (54.5) mm; in the age class 2+, 3 specimens ranging between 80–91 (84.6) mm, $l_1 = 50$ –56 (53) mm, $l_2 = 73$ –80 (76) mm; in the age class 3+, only one specimen with body length 101 mm, $l_1 = 57$ mm, $l_2 = 80$ mm, $l_3 = 90$; in the age class 4+, 3 specimens ranging between 112–113 (112.4) mm, $l_1 = 50$ –61 (55.3) mm, $l_2 = 70$ –83 (77.3) mm, $l_3 = 87$ –94 (90) mm, $l_4 = 103$ –106 (104) mm; in the age class 5+, only one specimen with body length 118 mm, $l_1 = 53$ mm, $l_2 = 73$ mm, $l_3 = 85$, $l_4 = 90$ mm, $l_5 = 108$ mm.

From the Pastvinská Valley Water reservoir (northeastern Bohemia), 13 specimens were collected belonging to 3 age classes 4+, 5+ and 7+ respectively. In the age class 4+, 7 specimens ranging between 105–125 (110) mm, $l_1 = 47$ –55 (52.4) mm, $l_2 = 69$ –74 (72.4) mm, $l_3 = 84$ –93 (87.5) mm, $l_4 = 95$ –110 (99.1) mm, in the age class 5+, 3 specimens ranging between 122–127 (124) mm, $l_1 = 60$ –63 (56.6) mm, $l_2 = 65$ –84 (74.6) mm, $l_3 = 84$ –95 (91) mm, $l_4 = 100$ –110 (106.6) mm.

Table 5. Growth of *Acerina cernua* from Slapy Water Reservoir at the villages Bačův and Živočov collected during the years 1957 and 1958

Age class	No. of specimens	Body length at the time of capture in mm	l_1	l_2	Average back-calculated lengths in mm	l_4	l_5
1+	12	73 64-80	56 50-60	—	—	—	—
2+	26	87 80-96	56 47-60	77 65-83	—	—	—
3+	38	101 94-109	54 43-60	77 65-90	93 82-104	—	—
4+	17	109 102-114	52 48-58	73 70-78	87 80-93	101 92-106	—
5+	4	121 117-124	52 49-55	70 68-72	87 85-90	99 95-102	113 110-114
Total	97		54 43-60	73 65-83	89 80-90	101 92-106	113 110-114
Annual increment in mm			19	16	12	12	12
Specific rate of linear growth (Ct)			35.2	21	12.8	12.8	12.8

$l_3 = 110-120$ (115.3) mm; in the age class 7+, 3 specimens ranging between 142-148 (143) mm, $l_1 = 49-51$ (50) mm, $l_2 = 69-70$ (69.5) mm, $l_3 = 80-82$ (81) mm, $l_4 = 91-95$ (93) mm, $l_5 = 105-113$ (109) mm, $l_6 = 117-126$ (121) mm, $l_7 = 135-136$ (135.5) mm.

From the rivulet Stropnice at the village Borovany (southern Bohemia), 9 specimens were collected belonging to 2 age classes, 1+ and 2+ respectively. In the age class 1+, 9 specimens were collected ranging between 70-80 (76.6) mm, $l_1 = 50-68$ (60.1) mm; in the age class 2+, 3 specimens ranging between 82-85 (84) mm, $l_1 = 52-54$ (53.3) mm, $l_2 = 69-75$ (73.6) mm.

From the rivulet Výmola at the village Čelákovice (central Bohemia), 2 specimens were caught belonging to the age class 2+ with body length 82-90 (86) mm, $l_1 = 54$ (54) mm, $l_2 = 75-78$ (76.5) mm.

From the backwater Hrad, inundation area of river Labe (central Bohemia), 16 specimens were collected belonging to 4 age classes 1+ to 4+. In the age class 1+, 7 specimens ranging between 64-72 (67.8) of body length, $l_1 = 52-61$ (58.4) mm; in the age class 2+, only one specimen with 90 mm of body length, $l_1 = 54$ mm, $l_2 = 78$ mm; $l_3 =$ in the age class 3+, 4 specimens ranging between 102-107 (104.5) mm, $l_1 = 60-67$ (62.7) mm, $l_2 = 79-87$ (83.7) mm, $l_3 = 94-98$ (95.5) mm, in the age class 4+, 4 specimens ranging between 100-107 (104.3) mm, $l_1 = 44-56$ (52) mm, $l_2 = 66-75$ (71) mm, $l_3 = 80-90$ (85) mm.

From the backwater Řeháková bouda at the river Labe (central Bohemia), 2 specimens were caught and all of them belong the age class 5+, with body length 124-126 (125) mm, $l_1 = 57-60$ (58.5) mm, $l_2 = 72-80$ (75.5) mm, $l_3 = 90$ (90) mm, $l_4 = 102-104$ (102) mm, $l_5 = 116-118$ (117) mm.

In the backwater Poltruba, 6 specimens were collected belonging to 2 age classes 2+ and 3+ respectively. In the age class 2+, 5 specimens ranging between 78-92 (85.7) mm, $l_1 = 50-53$ (52) mm, $l_2 = 70-85$ (75.5) mm; in the age class 3+, only one specimen was caught with body length 94 mm, $l_1 = 50$ mm, $l_2 = 78$ mm, $l_3 = 90$ mm.

The relationship between body length/scale radius has been found to be linear and the correction factor was 19 mm, whereas Oliva-Vostradovský (1960) described the correction factor 23 mm. This difference is due to the fact that the smaller material studied by Oliva-Vostradovský (1960) and only belongs to valley water reservoirs, whereas the more numerous material from ponds, rivers, rivulets, valley water reservoirs and backwaters has been studied by me.

The growth of stone perch from the different ponds has indicated that the maximum rate of growth has been observed from the ponds Kaňov at Třeboň (56 mm) and Máchovo jezero (54.9 mm) during the age class 1+, during the age class 2+ from the pond Kaňov at Třeboň (79 mm) during the age classes 3+ and 4+ from the pond Máchovo jezero (92 mm and 108 mm). Specimens from the pond Máchovo jezero apparently were found to be with relatively higher rate of growth. One specimen from the pond Dvořiště has got the higher rate of growth (62 mm), due to very low number it can not be compared with the specimens from other ponds.

Tolčanov (1951) studied the growth of stone perch from four ponds of the U.S.S.R. Average growth of different years from the observations of Tolčanov (1951) are as follows:

$$l_1 = 42 \text{ mm}, \quad l_2 = 69.5 \text{ mm}, \quad l_3 = 89 \text{ mm}.$$

While comparing the present investigations (Table 7) with the findings of Tolčanov (1951) it has been observed that during age classes 1+ and 2+, the specimens

Table 6. The growth of *Acerina cernua* from different localities of Czechoslovakia (in mm). Total length calculated by the conversion factor:
Total length = 1.21 standard or body length

Locality	No. of	Total/body length								
		l ₁	l ₂	l ₃	l ₄	l ₅	l ₆	l ₇	l ₈	
Ponds										
Opatovický rybník	161	62/51	88/73	—	—	—	—	—	—	—
Ponědražský rybník at Třeboň	48	63/52	88/73	102/84	116/96	127/105	137/113	144/119	—	—
Mlýnský náhon to pond Rožmberk at Třeboň	50	60/50	—	—	—	—	—	—	—	—
Kaňov at Třeboň	43	66/55	96/79	110/91	—	—	—	—	—	—
Dvořiště	1	75/62	89/74	—	—	—	—	—	—	—
Máchovo jezero	26	65/55	95/79	111/92	131/108	—	—	—	—	—
Rivers										
Vltava, Prague	5	62/51	90/74	114/94	—	—	—	—	—	—
Berounka	22	66/55	95/79	114/94	—	—	—	—	—	—
Labo at village Čelákovice	1	69/57	87/72	97/80	110/96	—	—	—	—	—
Labo at Kersko	3	70/58	—	—	—	—	—	—	—	—
Dyje at towns Znojmo and Tasovice	29	66/55	90/74	104/86	118/98	132/109	143/119	150/124	151/125	—

Table 7. The growth of *Acerina cernua* from different localities of Czechoslovakia (in mm)

Locality	No. of specimens	Total/body length						
		l ₁	l ₂	l ₃	l ₄	l ₅	l ₆	l ₇
Valley water reservoir								
Vranovská přehrada	10	65/64	93/77	107/89	—	—	—	—
Pastvinská přehrada	13	64/53	87/72	104/86	120/99	135/112	145/120	157/130
Slapské near villages Bučily and Živoň	97	63/54	88/73	107/89	121/100	137/113	—	—
Rivulets								
Stropnice at Borovany	9	69/57	90/74	—	—	—	—	—
Výmola at Čelákovice	2	65/54	92/76	—	—	—	—	—
Backwaters								
Hrad, inund. area of Labe middle Bohemia	16	63/52	86/71	103/85	116/96	—	—	—
Reháková bouda of river Labe middle Bohemia	2	70/58	91/75	109/90	123/102	141/117	—	—
Poltruba	6	62/51	92/76	109/90	—	—	—	—

from the Czechoslovak ponds show higher rate of growth whereas in the age class 3+ same rate of growth has been observed. It can be concluded that the pope fish from the ponds of Czechoslovakia grow at higher rate than the ponds of the U.S.S.R.

Among rivers, three specimens from the river Labe at Kersko showed maximum rate of growth during the age class 1+, but due to small number of specimens, it is not advisable to include this population in the present discussion. In the age class 1+ the maximum rate of growth has been observed from the population of the river Dyje (55 mm) and the river Berounka (55.4 mm), in the age class 2+ from the river Berounka (79.1 mm), in the age class 3+ from river Vltava (94.5 mm) and in the age classes 4+ to 8+ from the river Dyje (Table 6). Among rivers the specimens from the river Dyje apparently grow at higher rate. Bauch (1954) studied the rate of growth of pope fish from the German river Br. Lucin bei Feldberg/Mekl. Bauch (1954) did not mention about the age classes 1+ and 2+ respectively. In the age class 3+ Bauch's (1954) sample showed higher rate of growth and in the age classes 4+ and onwards the specimens from the Czechoslovak rivers showed higher rate of growth.

Out of the three valley water reservoirs, in the age class 1+ the specimens from the Vranovská Valley Water reservoir and Slapská Valley Water reservoir showed maximum rate of growth (54 mm), in the age classes 2+ and 3+ again from the Vranovská Valley Water reservoir (77.8 mm). In the age classes 4+ and onwards specimens from the Slapská Valley Water reservoir were found to grow at higher rate.

While comparing the present results with the observations of Oliva-Vostradovský (1960), from Slapská Valley Water reservoir similar rate of growth has been recorded in the age classes 1+ and 2+ respectively. In the age class 3+ the present sample showed lower rate of growth whereas in the age classes 4+ and 5+ the present sample showed higher rate of growth. (Calculated average growth values from the data of Oliva-Vostradovský, 1960: $l_1 = 55$ mm, $l_2 = 73.9$ mm, $l_3 = 93.3$ mm, $l_4 = 94.3$ mm, $l_5 = 103$ mm, $l_6 = 107$ mm).

From the Pastviny Valley Water reservoir, Oliva-Vostradovský (1960) described erroneously the average growths in the age classes 2+ 69 mm instead of 74.6 mm, in the age class 3+ 80 mm instead of 90 mm. While comparing the results of the present investigations with Oliva-Vostradovský (1960) from Pastviny Valley Water reservoir, the present sample showed higher rate of growth in the age classes 1+, 4+, 5+ and 6+, low during the age classes 2+ and 3+ respectively.

Out of the two rivulets, in the age class 1+ the specimens from the Stropnice at Borovany and in the age class 2+ from Výmola at Čelákovice showed maximum rate of growth.

Among three backwaters, in the age class 1+, the specimens from the backwater Řehákova bouda, river Labe (58.5 mm), in the age class 2+ specimens from Poltruba backwater (76 mm), in the age class 3+ from Řehákova bouda and Poltruba and in the age classes 4+ and 5+ from Řehákova bouda showed higher rate of growth. Apparently the specimens from the backwater Řehákova bouda have got higher rate of growth in all age classes except age class 2+, but at the same time very small number of specimens from this backwater is one of the limiting factor for final conclusion.

While comparing the growth of *Acerina cernua* from five different type of water bodies of Czechoslovakia (Table 7 and Fig. 2), it has been observed that in the age class 1+, the specimens from all type of water bodies grow at the same rate, in

Table 8. The growth of *Acerina cernua* from different type of water bodies of Czechoslovakia

Type of water body	No. of specimens	1. Body length		l ₁	l ₂	l ₃	l ₄	l ₅	l ₆	l ₇	l ₈
		2. Total length									
Ponds	338	1	54	54	76	89	102	106	113	119	
		2	66	66	91	107	123	127	136	144	
Rivers	60	1	56	56	75	88	97	109	118	125	125
		2	66	66	91	107	117	132	143	151	151
Valley Water reservoirs	120	1	53	53	74	88	99	112	120	130	
		2	64	64	89	106	120	136	145	157	
Rivulets	11	1	55	55	75						
		2	66	66	91						
Backwaters	24	1	53	53	74	88	99	117			
		2	64	64	90	107	120	141			

Total length and body length in mm.

Total length calculated by the conversion factor: Total length = 1.21 standard or body length.

the age classes 2+ to 4+ specimens from the ponds and in the age classes 5+ to 7+ the specimens from the valley water reservoirs grow at higher rate. Only in the age class 5+ the specimens from the backwaters indicated the higher rate of growth. The specimens from the rivulets and rivers have shown the similar rate of growth in the age classes 1+ and 2+, as there are no specimens in the age classes 3+ to 8+ from rivulets, therefore I can not comment the rate of growth in the latter years. In the valley water reservoirs and backwaters the tempo of growth between the age classes 1+ to 4+ was almost the same.

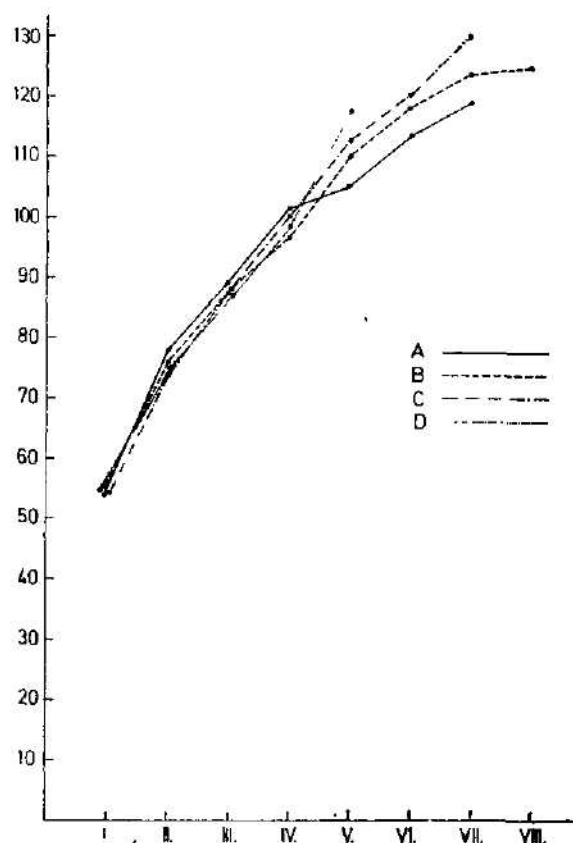


Fig. 2. Graphical representation of rate of growth of *Acerina cernua* in different water bodies of Czechoslovakia in different age classes. Body length (in mm.) is along ordinate and age classes (in years) is along abscissa. A — — — Ponds., B Rivers., C - · - · - · Valley Water Reservoirs., D Backwaters.

The maximum rate of growth of Ruffe has been reported from the Lake Ubinskoe in the U.S.S.R. (Berg, 1949) in the age classes 2+ to 4+, similarly the minimum rate of growth has been described from the Lake Sorvaslakti in Finland by Järnefelt (1921) among fresh water bodies.

Bauch (1954) described the rate of growth of Ruffe from the Baltic sea, Drasser Boden and Oderhaff. The populations of the Baltic sea and Drossen Boden grow

slower than Ubinskoe lake populations but higher than in other type of fresh water bodies. The populations from Oderhaff grow at higher rate in the age classes 1+ than the different populations of Czechoslovakia, in the age classes from 2+ to 4+ the rate of growth slowed down and is similar to the populations of valley water reservoirs.

Berg (1949) observed higher rate of growth in females, my material was not sexed therefore I can not confirm this statement.

In the present sample the rate of growth decreased gradually with the increase in body length. Similar observations have been made by Tolčánov (1951), Bauch (1954) and Oliva-Vostradovský (1960).

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SUMMARY

The growth of 553 specimens of Ruffe from 19 different water bodies in Czechoslovakia was studied using scale method.

In general the growth is slow and the observed specimens had not exceed the age of 8+ years.

The best growth was found in ponds from the age classes 1+ to 4+ and from valley water reservoirs in the age classes 5+ to 7+ and worstest from backwaters.

The total length-standard length conversion factor has been found out to be:

$$\text{Total length} = 1.21 \text{ standard length.}$$

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KEY CHARACTERS OF LARVAE OF TWO EUROPEAN LAMPREY SPECIES (CYCLOSTOMATA)

Dedicated to the 80th birthday of Professor Vadim D. Vladykov, DSc

Mohinder Singh JOHAL*) and Ota OLIVA

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Abstract: Seventeen larvae of *Lampetra planeri* (Bloch, 1784) from the environs of the town Tábor (drainage of the river Vltava) and 63 larval specimens of *Eudontomyzon mariae* from the river Raba (drainage of the upper Vistula, Poland) are described. Three age classes of the larvae (ammocoetes) of *Lampetra planeri* and four age classes of *Eudontomyzon mariae* are recorded. With an increase in size, the dorsal fin is drawn near to the head, anal opening shifts towards the middle part of the body and the length of the gill-apparatus is considerably reduced. The number of trunk myomeres varies and therefore could not be used for the identification of larvae of both species of lampreys. A difference in the pattern of pigmentation of the caudal part is described. The shape of the caudal part and character of its pigmentation are considered more reliable for identification. The Raba specimens from Poland were determined as *Eudontomyzon mariae* (Berg, 1931), and the larvae of this species are described in detail for the first time.

INTRODUCTION

Very little is known about the characters for identification of larvae of lampreys from Europe as well as from the U.S.A. and Canada. Owing to the fact that European lampreys are diminishing species it is considered important to distinguish larvae of the few species occurring in Europe. (For their list see Berg, 1948.)

Some important data are available on different biological aspect of *Lampetra planeri*, from Czechoslovakia and other parts of the world, such as those by Dyk (1951), Balon (1957), Berg (1939, 1948), Holčík (1970), Holčík and Nalbant (1974), Ivanova-Berg (1962), Kux (1967, 1969), Lohniský (1965, 1967, 1975), Penczak (1967), Šulc (1923), Vladykov and Follet (1967), Zanandrea (1958).

Šulc (1923) described the pigmentation of *L. planeri* from the river Labe, but Vladykov (1950) was the first to give special attention on the characters of pigmentation of the caudal part with regard to the shape of the caudal fin as an important key character for the identification of larvae of lampreys. The method was followed by Kux (1965, 1969) and Kux-Steiner (1971-1972). In the present paper we attempt to elucidate the possibility of correct identification of unknown larval lampreys from the upper Vistula drainage in Poland, where two species of lampreys, *L. planeri* and *Eudontomyzon mariae*, have been recorded (Oliva and Hensel, 1962; Oliva, 1966).

No data are available on the larval characters of *Eudontomyzon mariae* (Berg,

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1931), suitable for distinguishing them from other species. Oliva and Hensel (1962) reported the occurrence of adult specimens of this species in Poland.

Zanandrea (1961) reported that *E. mariae* is restricted to the Danube and all Russian tributaries of the Black Sea, Grossu, Homei, Barbu & Popescu (1962) found this species in Rumania in the drainage of the river Olt (near Sibin-Cabul). Žukov (1965) described different spawning periods of *L. planeri* and *E. mariae* in the river Neman belonging to the Baltic system. He observed that larval as well as adult specimens of *E. mariae* are bigger than *L. planeri*, but gave no description concerning the taxonomic characters of the larvae of *E. mariae*. Rembiszewski (1967) similarly reported the occurrence of this species in the river Jeziorka (tributary of the Vistula below Warsaw), belonging to the Baltic Sea drainage. The literature concerning the distribution of *E. mariae* shows that Zanandrea's (1961) assumption limiting the distribution of *E. mariae* only to the Black Sea rivers is apparently wrong.

Newly, Hubbs and Potter (1971) described the distribution of *E. mariae* from the tributaries of the Black Sea, from the basin of the Danube to the Kuban as well as the Vistula and Neman of the Baltic drainage.

Earlier workers described the species as *Lampetra (Eudontomyzon) mariae* Berg, 1931 (who, however, surmised "perhaps, *Eudontomyzon* is a valid genus"), *Lampetra mariae*, Kux (1966, 1967), Kux-Steiner (1971-72), *Lampetra (Eudontomyzon) mariae*, Oliva and Hensel (1962). We follow the classification by Vladykov and Kott (1967) and Vladykov and Follet (1967), listing *Eudontomyzon* Regan, 1911 as a valid genus, not subgenus of *Lampetra*. Zanandrea (1961) also described it as *Eudontomyzon mariae*. Similarly, Hubbs and Potter (1971) also considered *Eudontomyzon* a valid genus. Weisz and Kux (1966) described the pattern of pigmentation in *Eudontomyzon mariae* and *Lampetra planeri* and both authors felt the necessity of further revision of both species of lampreys from southern Poland, especially those belonging to the Vistula drainage system of the Black Sea.

Because they were not able to find *E. mariae* in the tributaries of the upper Vistula in southern Poland, they challenged the older data of Oliva & Hensel (1962) on the occurrence of the species there, but the occurrence of 3 specimens collected again in the brook Rudawa near Cracow has confirmed previous data (Oliva, 1966).

MATERIAL AND METHODS

For our study we used 17 larvae of the brook lamprey *Lampetra planeri* presented to the Department of Systematic Zoology, Charles University by Dr. Svorad. They had been collected in brooks in the environs of the town Tábor, central Bohemia, from the drainage of the river Vltava in the spring 1952. We also used 63 larvae of the "Ukrainian" or "South Russian" lamprey, *Eudontomyzon mariae*, collected by the second author (O.) on 30-31 August 1960 in a millrow in the town Dobzyce on the river Raba, which is the right side tributary of the upper Vistula, about 30 km south of Cracow in Poland.

Three specimens, 2 metamorphosing amocoetes and 1 subadult from the brook Rudawa, tributary of the Vistula near Cracow, Poland, collected in 1965-6, were also used for the study.

All the material was preserved in 4% solution of formalin and deposited in the ichthyological collections of the Department of Systematic Zoology, Charles University, Prague.

Our studies were made following the scheme for the study of larvae of lampreys given in the papers of Balon (1957), Lohniský (1967), Schultz (1930), Vladykov (1950) and Kelberg (1922).

All measurements and counts were performed on the left side of the specimens and rounded to the nearest mm. They were expressed in body length and total length. The following abbreviations are used:

a-c Tail length, the distance from the posterior edge of the cloacal slit to the end of the dorsal fin

B₇-a: Trunk length, the distance from the posterior edge of the last (7th) branchial opening to the anterior edge of the cloacal slit.

B₁-B₇: Branchial length, the distance from the anterior edge of the first branchial opening to the posterior edge of the last (7th) branchial opening.

d-B₁: Prebranchial length, the distance from the anterior edge of the upper lip to the anterior edge of the first branchial opening.

d-D₁: Predorsal distance, the distance from the anterior edge of the upper lip to the anterior edge of the base of first dorsal fin.

d-a: Preanal distance, the distance from the anterior edge of the upper lip to the anterior edge of the cloacal slit.

Body length indicates the distance from the anterior edge of the upper lip to the end of the tail (excluding tail fin), and total length includes the tail fin.

The number of trunk myomeres is counted from the posterior edge of the last branchial cleft (7th) to the anterior edge of the cloacal slit.

For the determination of different age classes of larvae, Peterson's method (Ricker, 1962) of length frequency is used. For a detailed study of pigmentation of the tail camera lucida diagrams had been drawn, using Carl Zeiss (Jena) binocular with $\times 4$ eye piece and 0.63 objective.

RESULTS AND DISCUSSION

1. Growth

By plotting length frequency distribution graphs, three age classes 1+ to 3+ of larvae of Czechoslovak brook lampreys, *Lampetra planeri* (Fig. 1) and four age classes, from 1+ to 4+, of Polish lamprey larvae of *Eudontomyzon mariae* have been recorded. In the case of Czechoslovak lamprey larvae the first peak (Fig. 1) was observed at 94 mm of total length, second peak at 115 mm of total length, the third peak consisting of three points (128 mm, 133 mm and 133 mm) of total length. In the Polish lampreys (Fig. 2) the first peak was recorded at 94 mm of total length, second peak at 107 mm, of total length, third at 145 mm and fourth at 153 mm of total length. The range of different age classes of these two larvae is given below.

Age class	Brook lamprey, <i>Lampetra</i> from Bohemia (17)*	Ukrainian lamprey, <i>Eudontomyzon</i> <i>mariae</i> , from Poland (63)*
I	73 - 94 (81)	58 - 84 (65)
II	87 - 115 (92)	70 - 107 (86)
III	94 - 133 (119)	97 - 145 (119)
IV	—	110 - 153 (132)

Balon (1957) studied the growth of larvae of *Lampetra planeri* from the river Lučina in Moravia Silesia (river Odra drainage, Baltic Sea system) in different age classes from 0+ to 4+. While comparing the present sample of the brook lamprey *Lampetra planeri* from Bohemia (river Vltava drainage, Northern Sea system), it was observed that the present sample showed a higher growth rate in age class 1+, whereas a lower rate of growth was observed in age classes 2+ and 3+.

Polish larvae of another lamprey genus, *Eudontomyzon mariae*, showed a lower rate of growth in all age classes.

2. Plastic characters

Balon (1957) and Holčík (1970) describing larvae of *Lampetra planeri* observed that the dorsal fin moves towards the head, the anal opening moves towards the

*) = Number of specimens

Figures given in brackets indicate the mean values

middle part of the body and branchial apparatus is reduced with progressing growth. The Bohemian specimens confirm the observations of Balon (1957) and Holík (1970), but in the case of Polish larval lampreys the branchial apparatus increases proportionately to the increasing body length.

Lohniský (1967) described the morphometric characters in different size groups of *Lampetra planeri* from the Vltava. Comparing the present sample of *Lampetra*

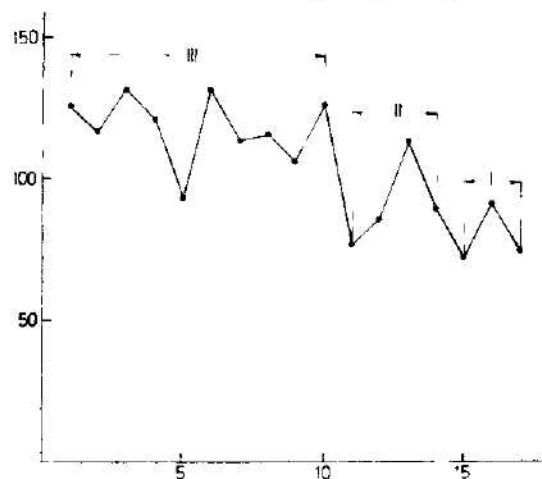


Fig. 1. Determination of age classes and growth of larvae of *Lampetra planeri* from Bohemia (Czechoslovakia). Abscissa: number of specimens, ordinate: total length (in mm).

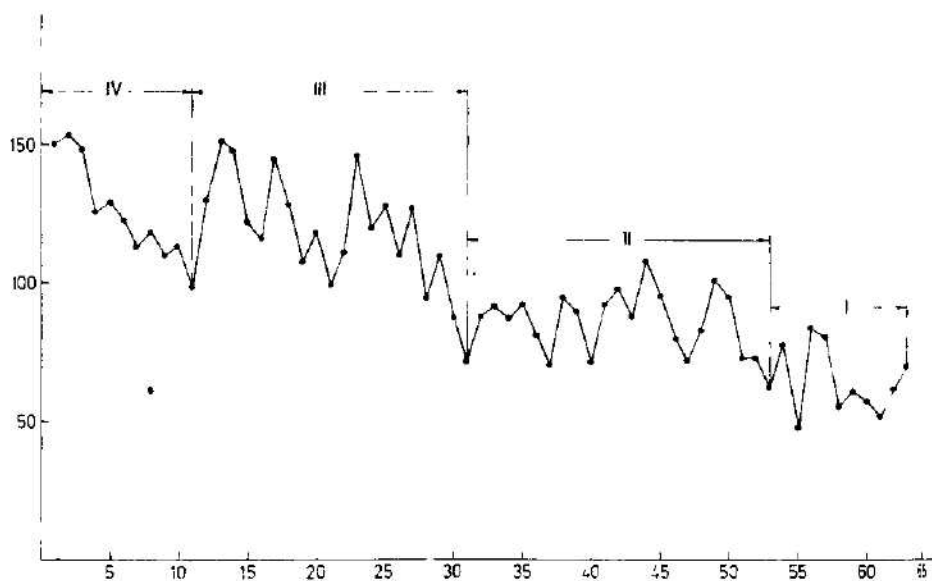


Fig. 2. Determination of age classes and growth of larvae of *Eudontomyzon mariae* from Poland. Abscissa: number of specimens; ordinate: total length.

planeri with the observations of Lohniský (1967), the postnatal distance is shorter in smaller size groups and the same in larger size groups, the trunk length shows no difference, the branchial apparatus shows a wider range; the prebranchial distance shows narrower ranges in small size groups, but no difference was seen in larger size groups.

Table 1. *Lampetra planeri*, larval form. Plastic characters.

Age class		In the percentage of body length		
		I	II	III
Body length in mm.	1.	80	91	118
	2.	72	76	93
	3.	93	114	132
Predorsal distance	1.	49	51	50
	2.	47	49	47
	3.	51	53	52
Preanal distance	1.	73	72	70
	2.	72	71	65
	3.	75	74	72
Postanal distance	1.	24	25	26
	2.	22	24	20
	3.	26	26	29
B ₁ —B ₇	1.	13	12	11
	2.	12	11	11
	3.	13	14	13
Body depth	1.	5	5	5
	2.	4	5	4
	3.	5	6	6
Number of specimens		3	4	10

1. Mean. 2. Minimum. 3. Maximum. Body proportions in % of body length in different age classes of the larvae of *Lampetra planeri* from Czechoslovakia.

Comparing the present sample agewise with the observations of Balon (1957), the percentage of predorsal distance in body length was higher in the present sample, preanal distance lower in all age classes, postanal distance was the same, prebranchial apparatus was lower in age classes 2+ and 3+ and the same in age class 1+, body depth was found to be less in all age classes.

The minor differences observed are probably due to small samples, different localities and time of collection. Our observations confirm the observations of Lohniský (1967) and Balon (1957).

3. Trunk myomeres

As regards the number of trunk myomeres in *Lampetra planeri*, Lohniský (1967) cited 61, Holčík (1970) — 64. Penczak (1967) 62 from Poland, ranging from 61—66; 62 from Estonia and Sweden. 63 from Czechoslovakia and 62 from France and England. Kus and Steiner (1971—72) counted 63 myomeres from Bohemia. Rembiszewski (1967) stated 65 myomeres in *Eudontomyzon mariae* from the river Jeziorka (tributary of the Vistula below Warsaw). In our material there are 59 trunk

myomeres in Czechoslovak brook lampreys and 61 in Polish lampreys. Žukov (1969) counted 66 myomeres ranging from 63—70 in *E. mariae*. The variation in the number of trunk myomeres in both species of lampreys is apparent and therefore this character cannot be considered a valid character for identification.

Vladykov (1950) did not consider the number of trunk myomeres to be one of important characters for identification of North American lamprey larvae. The considerable range of variation in the number of trunk myomeres (57—66) in the larvae of individual species of *Lampetra planeri* (Table 3) from different parts of Europe shows the problematic significance of this character for purposes of determination.

Table 2. Body proportions in number of the percentage of total length in different size groups of the larvae of *Lampetra planeri* from Czechoslovakia.

Total length in mm.	Mean	1.	76	92	112	122	133
	Minimum	2.	73	87	106	116	133
	Maximum	3.	77	94	115	128	133
Number of specimens in each group			3	4	3	5	2
a—c		1.	24	24	27	27	26
		2.	23	20	25	25	25
		3.	25	26	30	29	27
B ₇ —a		1.	54	51	53	50	52
		2.	53	46	51	46	52
		3.	55	53	55	53	52
B ₁ —B ₇		1.	13	13	12	13	12
		2.	12	13	11	12	12
		3.	13	14	13	13	13
d—B ₁		1.	6	6	6	7	6
		2.	6	6	6	6	6
		3.	7	7	7	8	7
Number of trunk myomeres		1.	58	59	59	59	59
		2.	56	55	54	54	59
		3.	60	60	60	61	59

4. Pigmentation

Vladykov (1950) was the first to prove that the pigmentation of the tail region in the larval lampreys can be used as an important diagnostic character. Similar studies were carried out by Vladykov, Kott, Pharand (1975) and Vladykov & Kott (1976).

A comparison of the patterns of distribution of melanophores on the tails of our material showed that Polish specimens are different from Bohemian ones.

The caudal fin of the larvae of lampreys from Bohemia, doubtless *Lampetra planeri*, is transparent, without any pigmentation and the fin rays are clearly visible in all age classes. In age class 1+ there are melanophores, in bases of the caudal fins (both dorsal and ventral), but in the higher age classes, for example in the present sample in age classes 2+ and 3+, their intensity decreases. On the tail the concentration of melanophores is higher in the dorsal part and at the end of

Table 3. Variability in the number of trunk myomeres of the larvae of *Lampetra planeri* from different localities.

Locality	Year of collection	Range of total length	Mean total length	58	59	60	61	62	63	Mean	Range	Number of specimens
Salerno, Italy												
i) Scafti ¹⁾	1889	98-108	104.3					2	1	61	61-62	3
ii) S. Valentino-Tor ¹⁾	1953-55	61-151	101.4	2	7	8	9	8	1	60	58-63	35
Sweden ¹⁾	1954	56-144	100.9	1	7	13	8	5		60	58-62	34
France ¹⁾	?	136	136			1				60	—	1
Biela Voda, brook, Czechoslovakia ²⁾	1967	22-131	—							64	60-68	19
Vltava river, Czechoslovakia ³⁾	1957, 1958, 1961	63-168	—							61	57-64	62
Authors, drainage of the Vltava river, Tábor, Czechoslovakia		73-133	106							59	54-61	17

Quoted from ¹⁾ Zanandrea (1958) ²⁾ Holčík (1970) ³⁾ Lohniský (1967)

Table 4. Predorsal distance in the percentage of body length in the larvae of *Eudontomyzon mariae* from Poland in different age classes.

Age class	Predorsal distance in the percentage of body length															Mean	No. of specimens	Ranges
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58			
I	1			1				1	2	1	1	1	1	2		52	11	44-57
II	1			1	1		1	4	4	6					3	53	21	44-58
III					1	2	6	4	3	4	1	1				51	22	48-63
IV			2	2	1	2	2	1	1	1						50	10	47-52

Table 5. Preanal distance in the percentage of body length in different age classes in the larvae of *Eudontomyzon mariae* from Poland.

Age class	Preanal distance in the percentage of body length																			sub;	No. of specimens	Ranges
	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80					
I							2	2	2	2		1	1				1			73	11	70-80
II	1			1		3	4	2	5	3	1	1								71	21	64-75
III				1	1	5	7	5	1	1	1									70	22	67-74
IV				1		2		1	3	2				1						70	10	65-75

Table 6. Postanal distance in the percentage of body length in the larvae of *Eudontomyzon mariae* in different age classes from Poland.

Age class	Postanal distance in the body length								Mean	No. of specimens	Ranges
	20	21	22	23	24	25	26	27			
I	1	2		5	2	1			23	11	20—25
II	1		3	3	3	2	6	3	24	21	20—27
III					2	4	6	10	26	22	24—27
IV						1	5	4	26	10	25—27

the tail. On the lateral sides of the tail, melanophores are present in rows along myomeres of the tail region (Figs, 7, 8, 9).

Šulc (1923) was the first who described pigmentation in the larvae of *L. planeri* from the river Labe. He observed a band of pigment cells below and above the tail region and single dispersed pigment cells located in transverse rows in the cauda fin. His observations were also based on histological studies. Zanandrea (1958), Ivanova-Berg (1962), Kux and Steiner (1971—72), Holčík & Nalbant (1974), Vladykov & Follet (1965) and Weisz and Kux (1966) presented similar observations. Vladykov & Follet (1965) further mentioned that during spawning the individuals of *L. planeri* develop "peppered" pigmentation in the caudal fin. Our present observations agree with those of the earlier workers. None of them described pigmentation in the different age classes.

The caudal pigmentation of larvae of Polish lampreys is different from the brook lamprey larvae of Bohemia. The caudal fins are translucent, with light yellowish or cream-coloured tinge, fin rays are not visible at all and the fins are thicker than the caudal fin of Bohemian lamprey larvae. In age class I+, clear pigment granules

Table 7. Distance B₁—B₇ in the percentage of body length in different age classes in the larvae of *Eudontomyzon mariae* from Poland.

Age class	B ₁ —B ₇ in the percentage of body length						Mean	No. of specimens	Ranges
	11	12	13	14	15	16			
I		3	2	3	2	1	13	11	12—16
II		4	12	4	1		13	21	12—15
III	3	9	6	4			13	22	11—14
IV		3	4	3			13	10	12—14

Table 8. Body depth in the percentage of body length in the larvae of *Eudontomyzon mariae* in different age classes from Poland.

Age class	Body depth in the percentage of body length			Mean	No. of specimens	Ranges
	5	6	7			
I	4	5	2	6	11	5—7
II	5	16		6	21	5—6
III	10	10	2	6	22	5—7
IV	2	8		6	10	5—6

are irregularly present up to the lower half of the dorsal and ventral caudal fins. Dorsal and ventral sides of the tail are more conspicuously pigmented than the lateral sides. The tip of the tail fin is less pigmented.

Live specimens had the dorsal part of the body brown-greenish, the sides white-yellowish, with unclear marbling of the brownish colour, the keel in the middle of the dorsal body side was remarkably yellow but the colour appeared only in larger ammocoetes, over 10 cm in length, the smaller ones were greyish all over

Table 9. *Eudontomyzon mariae*, plastic characters of larval form.

Total length (in mm.)	1.	59	77	93	109	123	141	150
	2.	52	71	87	106	116	134	147
	3.	70	84	99	113	130	145	151
Number of specimens		9	11	14	10	12	3	5
a—C	1.	22	24	25	26	26	28	26
	2.	20	22	24	25	26	27	26
	3.	24	27	28	28	28	28	28
B ₇ —a	1.	48	51	50	50	51	52	51
	2.	44	48	47	48	48	52	50
	3.	51	52	51	52	52	52	53
B ₁ —B ₇	1.	14	13	13	13	12	13	12
	2.	12	12	13	13	11	12	11
	3.	16	14	13	14	13	13	12
d—B ₁	1.	7	8	8	7	6	6	6
	2.	6	7	6	6	5	6	6
	3.	9	8	8	8	7	6	7
Number of myomeres	1.	61	60	61	60	62	61	60
	2.	60	55	57	58	60	59	56
	3.	63	64	68	63	65	63	63

1. Mean value, 2. Minimum value, 3. Maximum value.

Body proportions in the percentage of total length in different size groups in the larvae of *Eudontomyzon mariae* from Poland.

There is no difference regarding pigmentation, in age classes 2+, 3+ and 4+. The conspicuous melanophores are restricted only to the basal portions of the dorsal and ventral sides of the caudal fin, but the caudal fin is pale yellow with a light brown tinge, which is more apparent in its basal part and less in the peripheral part. The ventral and dorsal sides of the tail are heavily pigmented as compared with the lateral parts. Definite rows of melanophores are lacking. The living large ammocoetes had apparent pigmentation on the base of the whole length of caudal fin, but most parts of the fin margin seem to be transparent (without the use of a microscope).

While studying the distribution of melanophores in 2 metamorphosing specimens and 1 subadult of *Eudontomyzon mariae* from the brook Rudawa near Cracow (the same locality from where Oliva & Hensel (1962), Oliva (1966) reported the occurrence of this species in Poland), the tail fin is pigmented in various degree (Figs. 10–12). The intensity of the pigmentation of the tail fin is comparatively

greater in the specimens from Rudawa as compared to those from Raba, but undoubtedly they belong to the same species.

Kux and Steiner (1971-72) observed melanophores in the caudal fin (more in the lower part and fewer in the upper part) in adult female specimens of *E. mariae* from the river Dniepr, USSR. Rembiszewski (1967) also described a black dot at the end of the tail in adults as well as juveniles of this species. Similarly Weisz and Kux (1966) also noted dots on the caudal fin (disappearing from preserved specimens) in *E. mariae* from the rivulet Strwiaż near the southeastern frontier of Poland with USSR.

Table 10. *Eudontomyzon mariae*, larval form. Plastic characters.

Age class		I	II	III	IV
In the percentage of body length	Body length in mm	1. 64 2. 51 3. 83	85 62 106	118 76 150	130 110 152
	Predorsal distance	1. 52 2. 44 3. 57	53 44 58	51 48 55	50 47 53
	Precanal distance	1. 73 2. 70 3. 80	71 64 75	70 67 74	70 65 75
	Postnatal distance	1. 23 2. 20 3. 25	24 20 27	26 24 27	26 25 27
	B ₁ -B ₇	1. 13 2. 12 3. 16	13 12 15	13 11 14	13 12 14
	Body depth.	1. 6 2. 5 3. 7	6 5 6	6 5 7	6 5 6
	No. of specimens	11	21	22	10

1. Mean value, 2. Minimum value, 3. Maximum value.

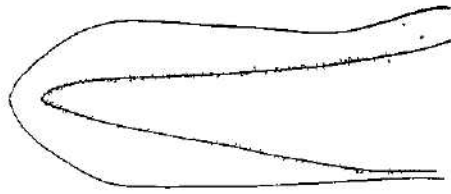
Body proportions in the percentage of body length in different age classes in the larvae of *Eudontomyzon mariae* from Poland.

The prebranchial spot and pigmentation of the upper lip are absent from both Bohemian and Polish larvae.

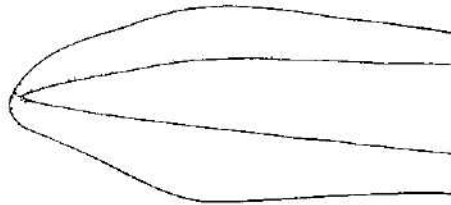
The pattern of pigmentation on the trunk portion is the same in both.

5. Shape of tail

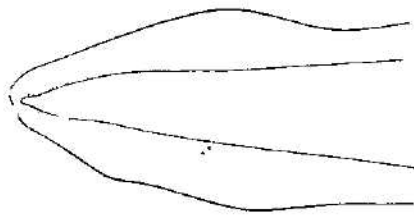
As regards the shape of the tail and tail fin in Bohemian larvae of brook lampreys, the caudal fin of smaller specimens is rounded, a roughly triangular shape is observed in bigger specimens belonging to age class 1+. In age classes 2+ and 3+ the triangular shape is very pronounced (Figs. 7, 8, 9).



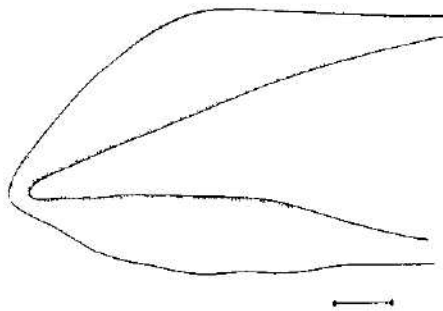
1



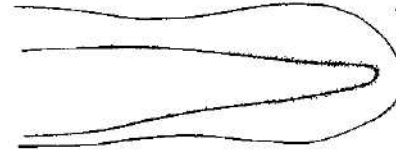
2



3



5



6



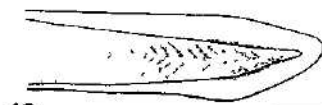
7



8



9



10

In the Polish lamprey larvae of all age classes the tail fin is rounded and beaver-like (this term is given by Vladyskov (1950) for larvae of Eastern American lampreys). See Figs. 3, 4, 5, 6.

The tail is straight in Bohemian larvae and slightly curved downward in Polish larvae of lampreys (both compared in formalin preservation).

The shape of the tail in age class I+ and smaller specimens appears to be the same in both larvae excepting the pattern of melanophores and the visibility of fin rays (Figs. 3, 7).

Regarding the shape of the tail fin of *Lampetra planeri* and *Eudontomyzon mariae* our observations are in conformity with the description given by Kux and Steiner (1971-72), Weisz and Kux (1966), Berg (1931) and Hrabě, Oliva and Opatrný (1973).

6. Notes on the distribution of *Eudontomyzon*

Concerning the distribution of *Eudontomyzon mariae*, Berg (1931) reported it from the basins of the Dniestr, Dniepr, Don and Kuban. Zanandrea (1961) similarly ascertained the distribution of *E. mariae* is restricted to "lower Danubian and all Russian tributaries of the Black Sea system". He broadened the distribution by adding the lower Danube system. Grossu, Homei, Barbu (1967) reported with certainty this lamprey from Rumania, Žukov (1965) reported it from the upper drainage of the river Neman in the Soviet Union, from the Baltic drainage, Oliva and Hensel (1961) earlier from the Vistula system in Poland, and Rembiszewski (1967) from the river Jeziora (tributary of the Vistula below Warsaw), as well as from the Baltic Sea system.

Kux (1965, 1966, 1967, 1969), Kux and Steiner (1971-72), Hubbs (1971), Vladyskov (1950, 1973), Vladyskov and Kott (1976a, 1976b, 1976c), Vladyskov and Follet (1965b), Vladyskov, Kott and Pharand-Coad (1975), Hrabě, Oliva and Opatrný (1973) should be especially mentioned for using the character

Plate I. 1 - Ammocoete of *Eudontomyzon mariae* from Poland, size 148 mm, age class IV. Rounded tail fin with conspicuous melanophores at the base. The intensity of melanophores decreases from basal part of the tail fin. 2 - Subadult specimen of *Eudontomyzon mariae* from brook Rudawa at Mydlniki near Cracow, Poland, tributary of the upper Vistula, collected in 1966, size 163 mm, tail rounded, heavily pigmented. 3 - Ammocoete of *Eudontomyzon mariae* from brook Rudawa, size 159 mm, tail rounded, melanophores are distributed only in the basal half of the dorsal and ventral parts of the tail fin. End of the tail fin without melanophores. 4 - Ammocoete of *Eudontomyzon mariae* from brook Rudawa, size 214 mm, tail rounded, dorsal and ventral parts with richly distributed melanophores but with colourless patches in the posterior part of the ventral part of the tail fin. Concentration of melanophores is increasing on the basal parts of the tail fin. 5 - Ammocoete of *Eudontomyzon mariae* from Poland, size 53 mm, age class I. Tail fin rounded without any depression, melanophores are concentrated only in the basal part of the tail fin. 6 - Ammocoete of *Eudontomyzon mariae* from Poland, size 78 mm, age class II. Tail fin is apparently rounded. More melanophores at the base of the tail fin, fewer on the periphery. 7 - Ammocoete of *Eudontomyzon mariae* from Poland, size 120 mm, age class III. Pigmentation and the shape of the tail fin are similar to the specimens belonging to age class II. 8 - Ammocoete of *Lampetra planeri* from Bohemia (Czechoslovakia), size 65 mm, age class I. Tail fin without melanophores, rounded in appearance. Melanophores are present on the tail in rows along the tail muscles. 9 - Ammocoete of *Lampetra planeri* from Bohemia (Czechoslovakia), size 126 mm, age class II. Tail fin without melanophores, triangular in shape, ventral part bigger than dorsal. Melanophores on the tail in rows, heavy concentration at the base of the caudal fin. 10 - Ammocoete of *Lampetra planeri* from Bohemia (Czechoslovakia), size 130 mm, age class III. The pigmentation and shape of the tail are similar to the specimens of age class II. Scales = 1 mm.

of pigmentation for the identification of lampreys. The literature concerning the pigmentation of *Eudontomyzon mariae* is scarce. Kux and Steiner (1971—72) described the larvae of *Lampetra planeri* and *L. lanceolata* as dirty brownish with a paler belly and without spots, whereas in *Eudontomyzon mariae* and *E. vladykovi* dots are very conspicuous on the lateral sides. The present observations confirm the findings of Kux and Steiner (1971—72).

Vladykov and Kott (1976), while reestablishing the genus *Eudontomyzon* Regan, 1911 described the same distribution of the following species from the Danube and drainages of the Black and Baltic Seas: *Eudontomyzon danfordi* Regan, 1911; *E. mariae* (Berg, 1931); *E. vladykovi* (Oliva and Zanandrea, 1959) and *E. gracilis* (Kux, 1965) from Slovakian waters.

The occurrence of *E. mariae* has been recently reported from Poland by Oliva and Hensel (1962), Oliva (1966), Rembiszewski (1967), from Rumania by Grossu, Homei, Barbu and Popescu (1962) and from the river Neman in the Soviet Union by Žukov (1965). As the distribution of these four species of *Eudontomyzon* Regan, 1911, shows similarities, we propose, on the basis of our observations and those of Kux (1965, 1976), Kux & Steiner (1971—72) and Weisz and Kux (1966), the following key to these four European species of the genus *Eudontomyzon*.

7. Key to larval forms of *Eudontomyzon*

- 1 (2) Tail fin rounded with melanophores, sides marbled *E. mariae* and *E. vladykovi*
- 2 (1) Tail fin triangular, without melanophores, sides not marbled *E. danfordi* and *E. gracilis*

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SUMMARY

- 1 Three age classes were distinguished in larvae of *Lampetra planeri*, and four in *Eudontomyzon mariae*. One-year-old larvae of *Lampetra planeri* attained the average total length 81 mm, 92 mm at two years, 119 mm at three years. In *Eudontomyzon mariae*, the total length of one-year-old larvae was 65 mm, 86 mm at two years, 119 mm at three years and 132 mm at four years.
2. The average values of plastic characters are given in Tables. It has been observed that in Bohemian *L. planeri* as well in Polish *E. mariae* larvae, the dorsal fin shifts towards the head with increasing age, the anal opening is shifted towards the middle of the body, and the gill apparatus, when measured externally, is reduced. But in *Eudontomyzon mariae* the percentage of the gill apparatus in the body length remains the same in all age classes.
3. On the basis of plastic characters and the number of trunk myomeres it has been found that these two different larval forms of both species of lampreys can not be separated.

4. The pigmentation of the caudal part of the body is more valid for the distinguishing of *Lampetra planeri* from *Eudontomyzon mariae*. It is transparent, without any melanophores, and the fin rays are clearly visible in *Lampetra planeri*. In *Eudontomyzon mariae*, it is translucent, with melanophores of varying degree in different age classes, and fin rays are not visible. In *Lampetra planeri*, melanophores on the tail are arranged in rows.
5. The shape of the caudal fin is triangular in *Lampetra planeri* and rounded in *Eudontomyzon mariae*. In smaller specimens the caudal fin appears to be the same in both species.

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FILTERING STRUCTURES OF CLADOCERA AND THEIR ECOLOGICAL SIGNIFICANCE I. DAPHNIA PULICARIA

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Abstract: In *Daphnia pulicaria* Forbes the filtration area (3rd and 4th thoracic limbs) grows approximately with the second power of the body length, the mean number of setae in the filtration comb is independent of the size of the animal and the intersetal distance grows proportionally with the body. The density of setules is inversely proportional to the body size and partly depends on the amount of food available.

INTRODUCTION

The morphology of thoracic limbs and especially the functional analysis of the 3rd and 4th limbs of Cladocera have been intensively studied since the second half of the last century (for references see Eriksson, 1935 and Smirnov, 1971). The first quantitative treatment of setules covering filtratory setae was mentioned, according to our knowledge, by Coker and Hayes (1940), while Johnson (1952) measured intersetal distance in seven species of the genus *Daphnia*. However, not earlier than in the sixties was the functional morphology of thoracic limbs used for differentiation on species level (Fryer, 1968, 1974 and Smirnov, 1966, 1968 and 1971). The last two authors devoted their interest to the families Chydoridae and Macrothricidae. Egloff and Palmer (1971) found a difference in the relation between the filtration area and body size in *Daphnia magna* and *Daphnia rosea*.

During a comparative study of possible mechanisms of food particles selectivity in the species of the genera *Daphnia* and *Ceriodaphnia*, we have concentrated on the evaluation of differences in the structure of filtering combs of the 3rd and 4th thoracic limbs. The results dealing with the species *Daphnia pulicaria* Forbes are presented here with preliminary notes on *Daphnia galeata* Sars and *Ceriodaphnia dubia* Richard.

MATERIAL AND METHODS

The study is focused on the following parameters of the filtering combs: (a) the filtering area of the combs, (b) the number of setae in the comb, (c) the intersetal distance, and (d) the density of secondary ciliation of setae (e.g. number of setules per unit of setal length). As the last parameter is probably not homogeneous throughout the comb (Storch, 1926), its central part was used for measurements.

Specimens of species *Daphnia pulicaria* from the Czech carp pond Velký Pálenec were used for measurements sub (a) to (c): preserved specimens sampled in the pond for large size group above 1.5 mm, and a laboratory culture of the same population for size groups below 1.5 mm. About 30 individuals of each size group were dissected under a stereomicroscope. The intersetal distance was measured in the distal portion of the seta, just behind the nodule. The filtering area was measured on drawings of the combs made with a Visopan (Reichert, Austria) with a polar planimeter (Riess). Differences in the density of setules were studied in material gathered

across the range of the species distribution (Tab. 4). The setules were counted on photographs of the 3rd limb: 1 to 2 pictures per each limb, 5 adult females per locality. A Peraval (Zeiss Jena) with Interphaco equipment was used for microphotography. Material for the study of other species was sampled in carp ponds in the vicinity of Blatná Hydrobiological Station.

RESULTS

The number of setae in filtering combs is nearly size-independent. A small but significant increase in the number of setae was found in the combs of the 3rd thoracic limbs but not in the 4th (Tab. 1). The mean intersetal distance therefore grows with the body length as well as the area of the combs. The total filtering area grows approximately with the second power of the body length, proportionality constant $b = 2.23$ (Fig. 1, 2). In adult females of *Daphnia galeata* (1.5 to 2.0 mm), the num-

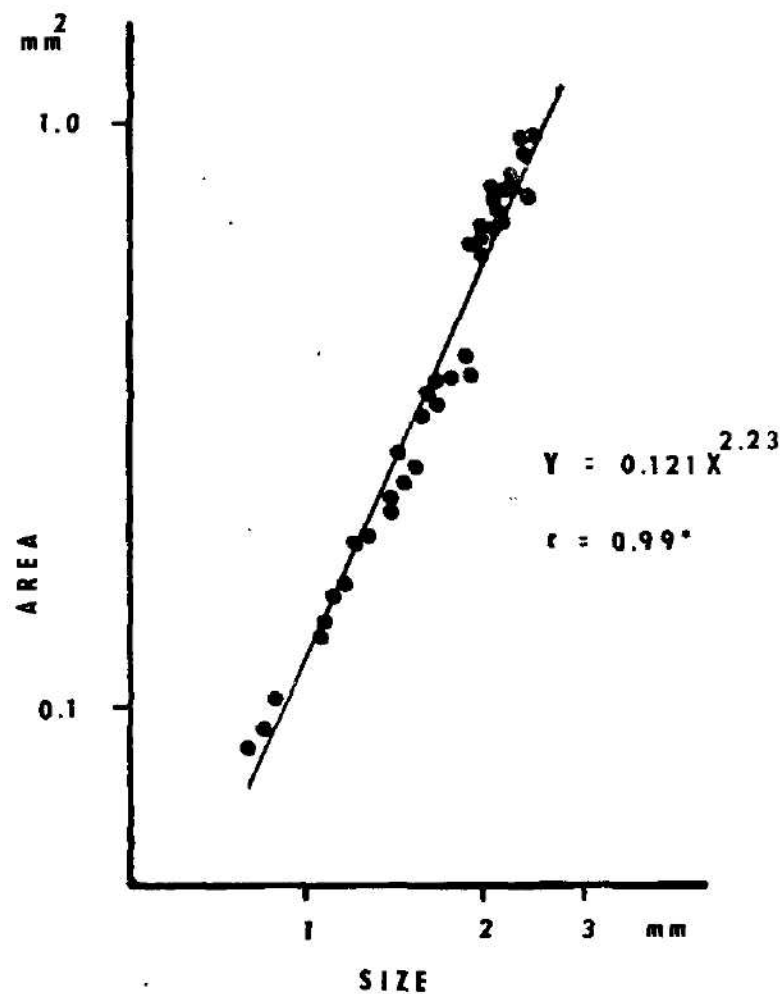


Fig. 1. Relation between the total filtration area and the body length in *Daphnia pulicaria* Forbes. Each point represents several measurements, $N = 90$.

Tab. 1. Parameters of the filtering combs of *Daphnia pulicaria*: 1. mean intersetal distance (in μm), 2. mean number of setae per one comb, 3. mean size of the filtering area of both pairs of limbs (in mm^2). Confidence limits at 95% conf. level added.

Mean size of females (mm)	Parameter	Limb 3	Limb 4
1.0 ± 0.05	1	3.1 ± 0.2	2.6 ± 0.1
	2	84 ± 1	76 ± 1
	3	0.08 ± 0.003	0.04 ± 0.004
1.6 ± 0.2	1	4.9 ± 0.2	4.1 ± 0.2
	2	85 ± 1	75 ± 1
	3	0.19 ± 0.01	0.11 ± 0.01
2.3 ± 0.1	1	6.5 ± 0.2	5.3 ± 0.2
	2	88 ± 1	77 ± 1
	3	0.5 ± 0.02	0.3 ± 0.01

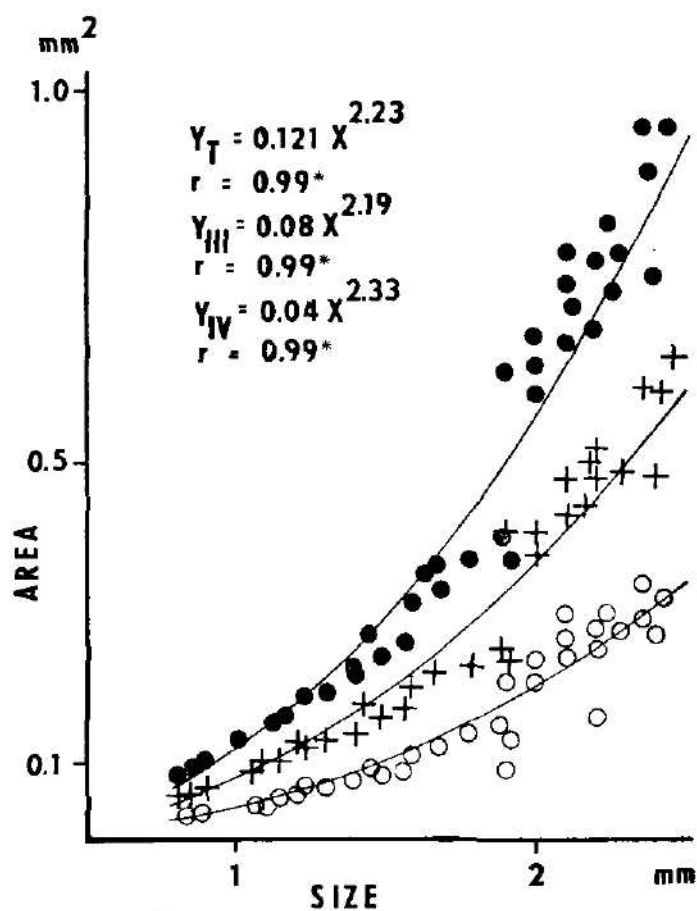


Fig. 2. Relation between the filtration area of the 3rd pair (Y_{III} , crosses) and 4th pair (Y_{IV} , circles) of thoracic limbs, and the body length in *Daphnia pulicaria*. Dots (Y_T) — the same relation of total filtration area of both pairs of thoracic limbs ($N = 90$).

ber of setae in the comb is smaller, the intersetal distance being approximately the same, so that the filtration area is smaller than in the same size group of *Daphnia pulicaria*. In *Ceriodaphnia dubia* (0.7 to 1.0 mm), the number of setae in the comb is small and the mean intersetal distance larger than in *Daphnia pulicaria*. The relation of the total filtering area to the body length in *Ceriodaphnia dubia* nevertheless seems to be similar to that of *Daphnia pulicaria* species (Tab. 2, 3).

Tab. 2. Parameters of filtering combs of *Daphnia galeata*. Size group $1.8 \text{ mm} \pm 0.05$, $N = 50$ confidence limits at 95% conf. level added.

Parameter	Limb 3	Limb 4
Intersetal distance (μm)	5.1 ± 0.15	4.7 ± 0.2
Number of setae in the comb	61 ± 1	51 ± 1
Mean filtering area (mm^2)	0.15 ± 0.006	0.09 ± 0.003

Tab. 3. Parameters of filtering combs of *Ceriodaphnia dubia*. Size group $0.8 \text{ mm} \pm 0.02$, $N = 50$. conf. limits at 95% conf.

Parameter	Limb 3	Limb 4
Intersetal distance (μm)	3.5 ± 0.1	3.4 ± 0.1
Number of setae in the comb	48 ± 1	29 ± 1
Mean filtering area (mm^2)	0.06 ± 0.003	0.03 ± 0.001

The mean density of setules measured on individuals from the laboratory culture of *Daphnia pulicaria* was 195, 117 and 101 setules per $100 \mu\text{m}$ of setal length for size groups 1.4, 2.0 and 3.0 mm, respectively. Therefore we consider it to be inversely proportional to the body size. Using scanning electron microphotography, we have found that both the acuteness of the angle of insertion of setules as well as their length are decisive for the size of intersetal gaps and thus, in addition to the distance of setules, also affect the size distribution of filtered food particles (Figs. 3 and 4). A detailed analysis of the variation in the distance of setules revealed that the density of setules in populations living in lakes and reservoirs with a low amount of seston in water (measured as chlorophyll-a concentration and/or Secchi disk transparency) is smaller than in those living in ponds and laboratory cultures with a high content of seston (we have no such supporting data for Alkaline lake, U.S.A.) (Tab. 4).

Using an oil immersion and Interphaco equipment, we were not able to see setules in the first instar, except on the tips of setae.

DISCUSSION AND CONCLUSIONS

Comparing our data with those of Egloff and Palmer (1971) we have found that the relation between body size and the total filtering area of the 3rd and 4th limbs of *Daphnia pulicaria* does not differ significantly from that of *Daphnia rosea* (sensu Brooks, 1957). We expected small differences as the measurement of the area had probably not been quite exact. The two-dimensional projection of the comb is not identical with the real filtering area. The comb is arched, the filtering setae oriented with their convex side carrying setules to the median food groove. Moreover, neither the convexity of combs on both limbs nor the proportionality of their projection are the same.

Tab. 4. Mean density of setules per 100 μm of setal length in *Daphnia pulicaria*. Confidence limits at 95% conf. level added.

Locality Date	Secchi disk (m)	Chlorophyll ($\mu\text{g.l}^{-1}$)	Size of ♀♀ (mm)	Density of setules
Alkaline lake USA, June, 1968	×	×	2.2	190 ± 10
V. Pálenec Pond lab. cult.	×	over 10^2	2.1	149 ± 17
Smyslov Pond May, 1961	0.6	50	2.1	167 ± 21
West Blue Lake Canada, lab. cult.	×	over 10^2	2.1	152 ± 4
West Blue Lake, one year lab. cult.	×	over 10^2	2.0	149 ± 13
Lake Tahoe USA, March, 1968	25	×	2.1	93 ± 23
Hanabanilla Res. Cuba, Apr., 1966	5.5	1.3	2.2	129 ± 16
Tchata Lake, USSR	×	×	2.3	104 ± 15
Smyslov Pond June, 1972	2.5	2 to 5	2.1	139 ± 17
Hubenov Res. Feb., 1977	5.5	2	2.1	138 ± 24
Hubenov Res. Sept., 1976	5.5	3.4	2.0	102 ± 31
V. Pálenec Pond June, 1975	2.5	2	2.1	94 ± 32

The nearly constant number of setae in combs during individual growth means that the filtration area grows in consequence of the elongation of setae and growth of the basal part of the endopod. Behning (1912) found a greater range in the number of setae, but the variation was not estimated.

Information on the density of setules is scarce. Their importance for the size limitation of particles screened out of the water is however evident. Coker and Hayes (1940) did not find a significant difference in the density of setules between *Daphnia pulex* (very probably not specifically different from *Daphnia pulicaria*) and *Diaphanosoma brachyurum*. Our material from several localities and laboratory cultures allowed us to establish different densities of *Daphnia pulicaria* filtration screen in various habitats. In our opinion, this variation could be connected with previous data on slower postembryonic development of populations from oligotrophic lakes (Hrbáčková, 1971; Kořínek, 1970, 1979). The mechanism of the adjustment of a population to the changing availability of food is not clear. The natural selection of individuals with a denser or thinner filter is probable as there

is considerable variation in this respect. An analogous switch in feeding behavior, based on the morphological change of the animal, was already reported for *Tetrahymena patula* complex, especially *Tetrahymena paravorax* (Corliss, 1973).

In newborns and probably early juveniles, the setules seem to be poorly developed and there is no detailed information on the feeding behavior of the first juvenile instar.

Acknowledgement

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The Figures 3 and 4 will be found at the end of this issue.

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**A CONTRIBUTION TO THE SYSTEMATICS OF EUROPEAN RANID
FROGS (AMPHIBIA, RANIDAE) ON THE BASIS OF THE INCRASSATIO
FRONTOPARIETALIS**

Zbyněk ROČEK

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Abstract: On the basis of the *incrassatio frontoparietalis*, which is a thickened, well limited part of the frontoparietal bone, covering in ranids three openings in the dorsal wall of the endocranium, and thus substituting missing parts of the wall, it is possible to hypothesize phylogenetic relationship of the European green and brown ranids. It is shown that the *incrassatio frontoparietalis* can be satisfactorily used on the taxonomical level of species.

INTRODUCTION

European ranids were classically divided into two main groups on the basis of external characters, but the evolutionary relationships of species in each of these groups is still poorly understood. Classical taxonomic methods restricted to the description of external body features (e. g. coloration and proportion) and ecology, behaviour, etc. are not always sufficient for hypothesizing the phylogeny of the species. When taking into account only the above attributes, sufficient attention is not given to the selection of examined characters, so that characters influenced by the adaptability of animals are judged equivalently to characters reflecting phylogenetic relations. Modern systematics bases taxonomic classification on true phylogenetic relations, and attempts to minimize the utilization of adaptive characters because they may more often reflect parallel or convergent evolution. Moreover, the evaluation and choice of characters suitable for taxonomic study is complicated by the more conspicuous nature of adaptive characters over phylogenetic characters.

Externally, frogs are conspicuously uniform because of adaptive characters. When searching for phylogenetic characters, the most conservative structures, i.e. these which remain relatively stable during the course of evolution are preferred. Therefore, many papers have been recently published which hypothesize frog systematics from genetical data (karyotype analysis, electrophoresis of blood proteins, DNA hybridization, immunological reaction). Osteological characters are considered among the most conservative and are thus excellent predictors of phylogeny. As the majority of the fossil record are bones, using osteological material of different ages, changes of the skeleton at different stages of evolution can be followed. The chosen osteological character can then be evaluated as one of phylogenetic or only adaptive value.

The *incrassatio frontoparietalis* is a suitable character. It is defined by a thickened part of the frontoparietale projecting from its ventral surface and covering the openings in the dorsal wall of the endocranium. This character

fortunately indicates the size and extent of the dorsal openings of the endocranium, as the latter are not always preserved and are of different size in higher frog taxa. In the course of vertebrate evolution the endocranium underwent various changes (e.g. its dorsal wall was being gradually reduced, so that in advanced mammals it is limited only to the base of the skull). The reason for these changes is not clear, it is evident, however, that they cannot be caused by adaptive answer of an organism. Therefore, the *incrassatio frontoparietalis* can be considered a valuable phylogenetic character, i.e. it can be used for ascertainment of vertebrate phylogenetic relationships.

The question arises, to which taxonomical level (familial, generic, specific) this character is useful. Špínar (1975, 1976) drew attention to considerable morphologic differences between frontoparietal *incrassations* of various frog families and of species within the family Pelobatidae. The aim of this paper is to decide: (i) to which taxonomical level the *incrassatio frontoparietalis* can be used, (ii) whether *incrassatio frontoparietalis* enables us to satisfactorily hypothesize the phylogenetic relationship of European representatives of the family Ranidae.

NOMENCLATURE AND DESCRIPTION OF THE INCRASSATIO FRONTOPARIETALIS IN THE RANIDAE*)

The frontoparietale of ranids is a paired dermal-cranial bone elongated in rostral-caudal direction and divided by a sagittal suture (*sutura sagittalis* Bolkey). It forms a substantial part of the dorsal wall of exocranium between orbits. Rostrally, it contacts the nasale forming the *sutura transversalis* Bolkey. Laterally, it forms a part of the orbit margin (*margo orbitalis* Bolkey), latero-caudally, it contacts the prootic bone (*margo prootica* Bolkey) and caudally the occipitale laterale (*margo occipitalis* Bolkey). At the level of the rostral two-thirds (approximately *margo orbitalis*), the lateral margin of the frontoparietale is bent slightly ventrally (*lamina perpendicularis* Bolkey), so that the *processus orbitalis* projecting from this margin is better visible when viewed laterally.

The *incrassatio frontoparietalis* is comprised of a *facies cerebralis anterior* and two *facies cerebrales posteriores*. The *facies cerebralis anterior* is divided by sagittal suture, and fills the opening in the endocranium (*fenestra frontalis*). *Facies cerebrales posteriores* are conspicuously inward projecting oval plates filling the *fenestrae parietales* of the endocranium. *Facies cerebralis anterior* either is projecting entirely or only rostrally, while the caudal part is an indentation. The third pattern is that the entire *facies* is a depression in the bone. For detailed nomenclature see Text Fig. 1.

Description of the *incrassatio frontoparietalis* in individual species

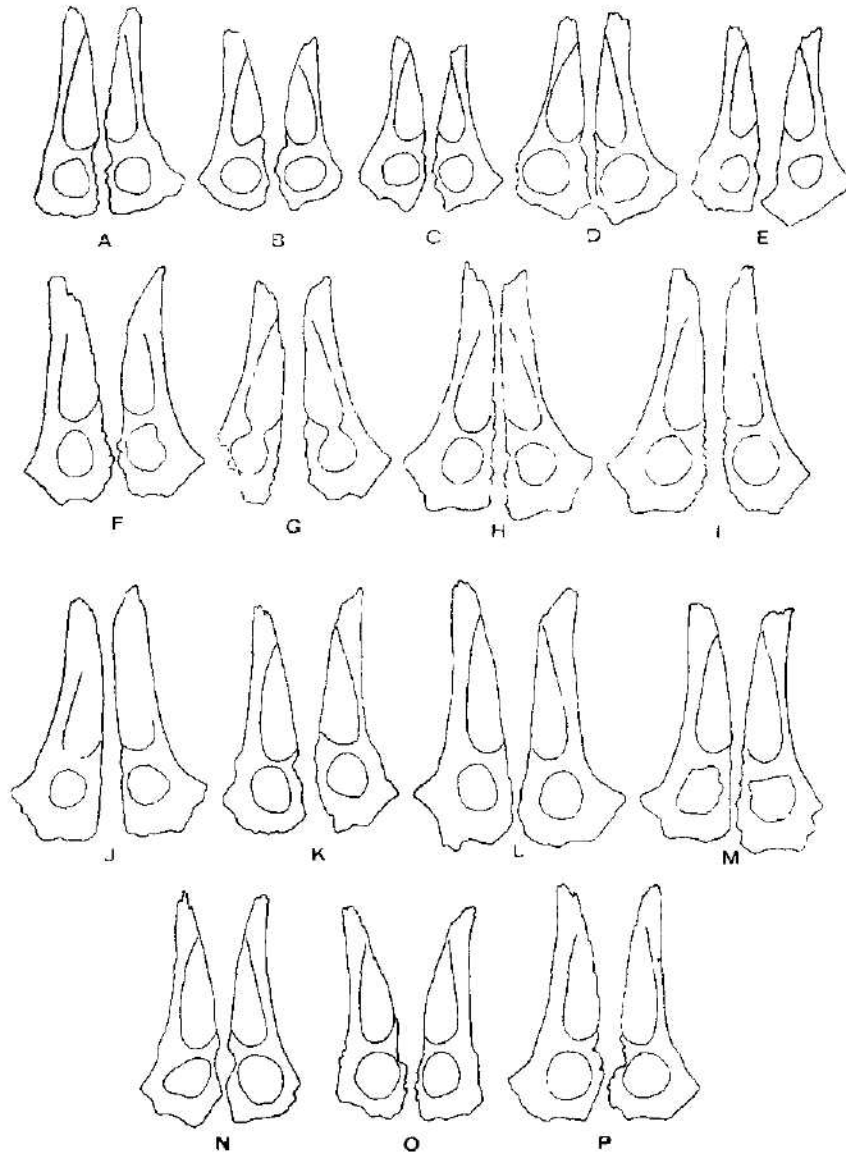
The basic configuration of the pattern is identical in all ranid species and is described above. The following text mentions only differing features between species. In all cases, both left and right frontoparietals were examined. The material is deposited in the collections of the Department of Paleontology, Faculty of Natural Science, Charles University, Prague.

*) When naming parts of the frontoparietale, I have mostly followed the terminology of Bolkey (1919), although not always anatomically correct. The adopted names are followed by the author's name.

Rana esculenta L. (Text Fig. 2, Pl. Fig. 1)

Sixteen specimens were examined (8 ♂♂, 8 ♀♀; loc. Malý Horusický Pond, leg. Roček, June 1972).

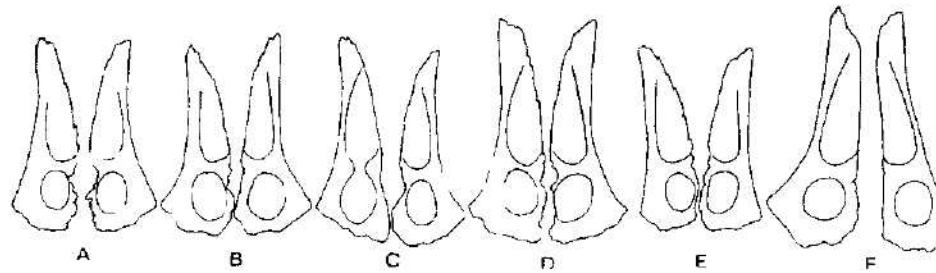
In most cases, the margo sagittalis of the frontoparietale transcends arch-like into the margo anterior, so that both margins are not sharply separated from each other. Only rarely do both margins form an obtuse angle. In all cases, however, the



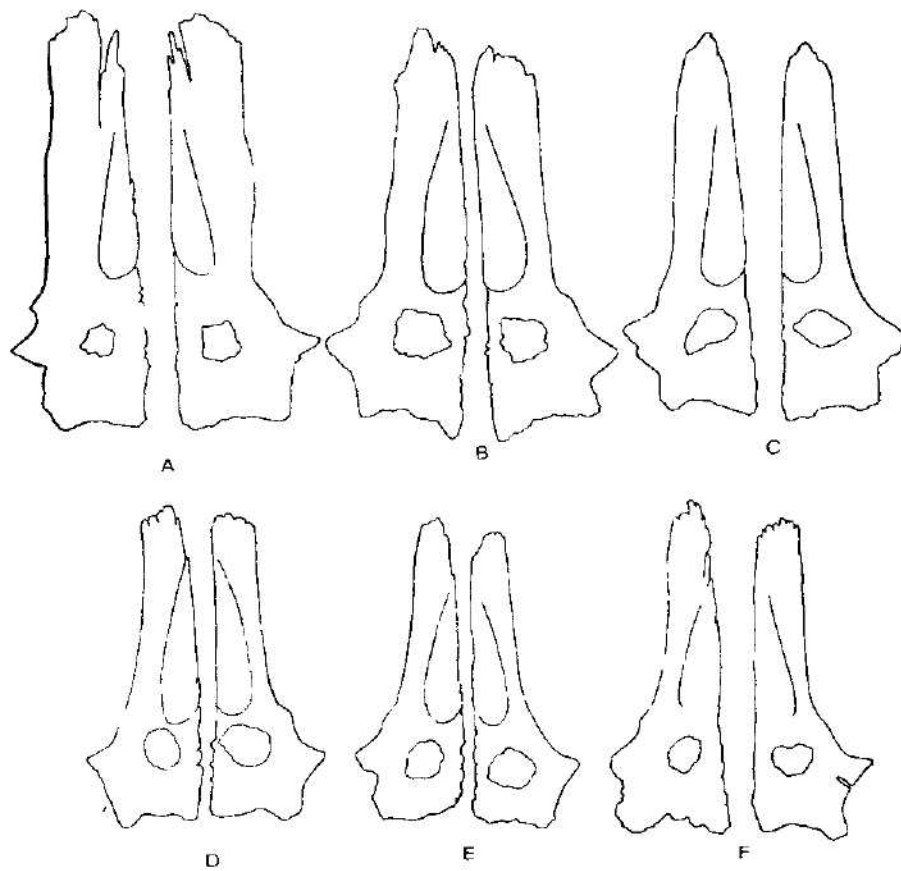
Text Fig. 2. Variability of the incrementatio frontoparietalis in *Rana esculenta*.

lateral margin of the facies cerebialis anterior is directed antero-medially, and terminates at the margo sagittalis.

The facies cerebrales posteriores are separated from the facies cerebialis anterior by the gap spatium interfaciale, corresponding with the taenia tecti transversalis of the endocranium. However, anomalous cases do occur where the facies cerebrales



Text Fig. 3. Variability of the incrassatio frontoparietalis in *Rana esculenta lessonae*.



Text Fig. 4. Variability of the incrassatio frontoparietalis in *Rana ridibunda*.

anterior is connected with the facies cerebrales posteriores by bridges (see Text Fig. 2 G), indicating that the taenia tecti transversalis is partly interrupted. Also between the facies cerebrales posterior and margo sagittalis lies a strip of unthickened bone, separating both facies cerebrales posteriores from each other (corresponding to the taenia tecti medialis of endocranium).

The facies cerebrales anterior is defined by a slight indentation of the ventral surface of the anterior portion of the frontoparietale. In contrast, the facies cerebrales posteriores are raised areas, projecting into the cranial cavity and thus filling fenestrae parietales in the endocranium.

The variability of shape, and proportional relation of both parts of the pattern and the space between them are shown in Text Fig. 2. No sexual differences of this character were observed. Sexual dimorphism was also not observed in the other species although insufficient numbers were examined for a statistical statement.

Rana esculenta lessonae Camerano (Text Fig. 3)

Six specimens were examined (3 ♂♂, 3 ♀♀: loc. Ruda near the town Veselí nad Lužnicí, leg. Roček, June 1972).

No marked character can be found in the configuration of the incrassatio frontoparietalis in *R. e. lessonae* that differs from any in *Rana esculenta*. Specimens with anomalously formed frontoparietal incrassation do occur (see Text Fig. 3 C), some asymmetrically.

Rana ridibunda Pall. (Text Fig. 4, Pl. Fig. 2)

Six specimens were examined (1 ♂, 5 ♀♀: loc. Constanta, Roumania, leg. Roček, July 1971 — Text Fig. 4 A, B; loc. Navodari, Roumania, leg. Roček, July 1975 — Text Fig. 4C; loc. Lozenec, Bulgaria, leg. Roček, July 1975 — Text Fig. 4D; loc. Hostivice near Prague, leg. Špinar, May 1970 — Text Fig. 4E, F).

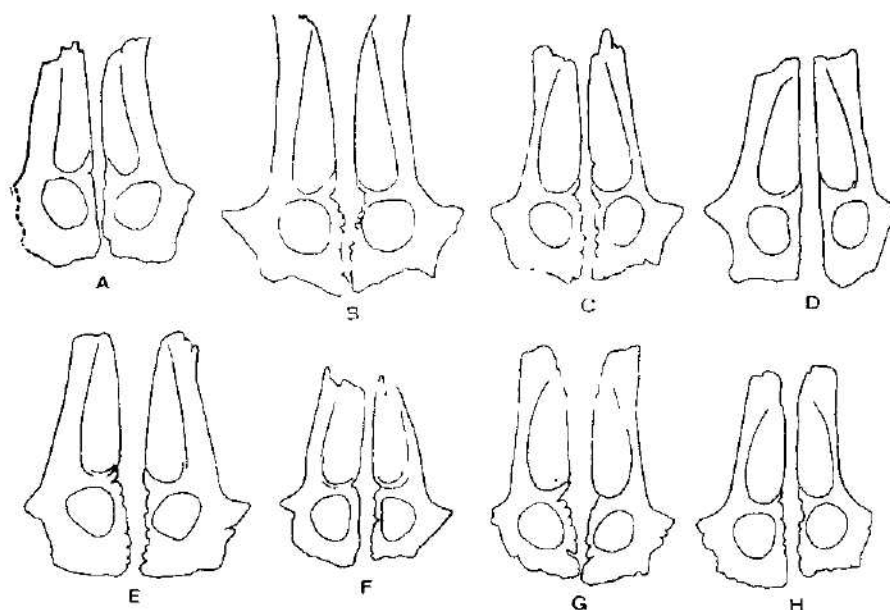
The lateral margin of facies cerebrales anterior is directed either towards the margo sagittalis or toward the point where the margo sagittalis and margo anterior intersect. Unlike the condition in *Rana esculenta*, the facies cerebrales anterior is convex, not an indentation into the bone. However, this projection is not very conspicuous rostrally.

The facies cerebrales posteriores are separated from the rostral part of the pattern by the wide spatium interfaciale. In most cases they are irregularly shaped, with sharp margins and projecting considerably into the openings of the endocranium.

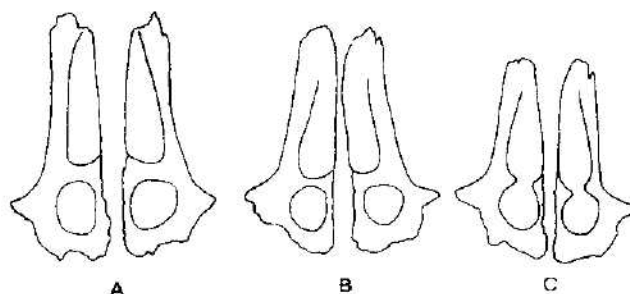
Rana temporaria L. (Text Fig. 5, Pl. Fig. 3)

Eight specimens were examined (1 ♂, 7 ♀♀: loc. Žofín, Novohradské Mts., leg. Andára & Vohralík, May 1971 — Text Fig. 5A, B, C; loc. Miedzygórze, Poland, leg. Roček, August 1972 — Text Fig. 5D, E, F; loc. Horní Albeřice, Rýchory Mts., leg. Lipenský, June 1975 — Text Fig. 5G, H).

For this species the incrassatio frontoparietalis cannot be unambiguously defined. For example, for both specimens from Horní Albeřice the frontoparietale and the incrassatio frontoparietalis are identical but differ from all other examined *Rana temporaria* specimens. The margo sagittalis of their frontoparietals forms a right angle with the margo anterior, and the latter again forms an approximately right angle with the margo orbitalis. The lateral margin of the rostral part of the incrassatio frontoparietalis in the two above-mentioned specimens turns rostro-medially and terminates at the margo sagittalis. In all other specimens the lateral margin



Text Fig. 5. Variability of the incrassatio frontoparietalis in *Rana temporaria*.



Text Fig. 6. Examples of the incrassatio frontoparietalis in *Rana dalmatina*.

of facies cerebialis anterior is directed to or terminates at the margo anterior, or at the common intersection of margo anterior and margo sagittalis.

In the rostral part, the border of facies cerebialis anterior sharply projects internally, a feature typical of all examined specimens. Caudally the facies cerebialis anterior is depressed, and its projecting caudal margin is rounded, not sharp.

Unlike green ranids, a more or less conspicuous incisura medialis is formed in most but not all specimens. The facies cerebrales posteriores are similar to those of *Rana esculenta*. The spatium interfasciale is very narrow in some specimens.

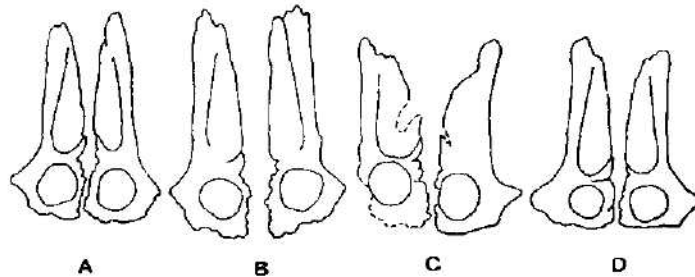
Rana dalmatina Bon. (Text Fig. 6)

Three specimens were examined (1 ♂, 2 ♀♀: loc. Lozenec, Bulgaria, leg. Roček, July 1975 - Text Fig. 6A, B, loc. Putnok, Hungary, leg. Roček, May 1971 - Text Fig. 6C).

The basic shape of the incrassatio frontoparietalis is identical with *Rana temporaria*. In all three specimens, the lateral margin of the facies cerebialis anterior is

directed toward the margo anterior. The facies cerebialis anterior is also depressed in the caudal part and projecting in the rostral part.

Remarkably, the facies cerebialis anterior is connected with the facies cerebialis posterior in one specimen (see Text Fig. 6 C).

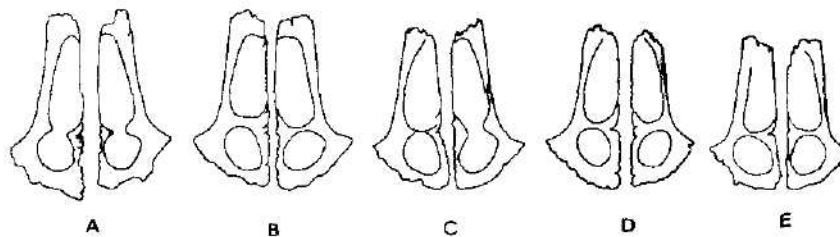


Text Fig. 7. Examples of the incassatio frontoparietalis in *Rana arvalis* and *Rana arvalis wolterstorffi*.

Rana arvalis Nills, *Rana arvalis wolterstorffi* Fejervary (Text Fig. 7)

Four specimens were examined (2 ♂♂, 2 ♀♀: loc. Bohemia (specific locality unknown. From Frič's collections of the National Museum, Prague) — Text Fig. 7A, loc. Soroksár, Hungary, leg. Kovács, 1957 — Text Fig. 7B, C; loc. Osa, Hungary, leg. Kovács, 1957 — Text Fig. 7D).

The frontoparietale and the incassatio frontoparietalis are similar to the previously described brown ranid species. In some cases (Text Fig. 7 B) the incassatio frontoparietalis can be very indistinct.



Text Fig. 8 Examples of the incassatio frontoparietalis in *Rana iberica*.

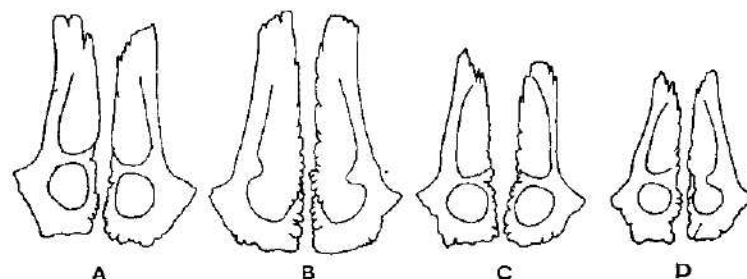
Rana iberica Boul. (Text Fig. 8)

Five specimens were examined (1 ♂, 4 ♀♀: loc. Arroyo de San Juan, Villa Franca del Biergo, provincia de León, Spain, leg. Knoepfner, September 1976).

The lateral margin of the facies cerebialis anterior is directed toward the margo anterior. In most cases, however, it does not reach the margo. Either this part of the incassatio frontoparietalis ends rostrally in a distinct arch-like border (a specific character of this taxon — see Text Fig. 8 A, B), or the lateral margin of facies cerebialis anterior becomes rostrally indistinct. The facies cerebialis anterior in the rostral part projects internally, the margin being very acute, but in the caudal part it is depressed and lacks a rounded projecting border, as in *Rana temporaria*, except on the medio-caudal margin of facies cerebialis anterior.

The facies cerebralis posterior is oval-shaped and surrounded by a rounded and projecting margin. The remainder is depressed to the level of the surrounding bone.

When compared with the entire incrassatio frontoparietalis, spatium interfaciale is relatively narrow. In some specimens the anterior and posterior parts of the pattern closely touch or are connected by a bridge. This phenomenon need not occur symmetrically (see Text Fig. 8 C).



Text Fig. 9. Examples of the incrassatio frontoparietalis in *Rana macrocnemis*.

Rana macrocnemis Boul. (Text Fig. 9)

Four specimens were examined (4 ♂♂: loc. Azau, Caucasus, leg. Lipenský, July 1974).

The caudal part of the facies cerebralis anterior is depressed and separated from the spatium interfaciale either by a rounded ridge (as is the case with brown ranids) or by a sharp ridge. The facies cerebralis posterior projects into the endocranium openings, and the margin is sharp. The lateral part of facies cerebralis posterior is concave, the medial part is flat.

In two of the four investigated specimens both parts of the incrassatio frontoparietalis would be probably connected either symmetrically or only on one side. This connection can be so extensive that the taenia tecti transversalis of the endocranium is developed only slightly laterally (see Text Fig. 9 B).

Rana graeca Boul. (Text Fig. 10)

Two specimens were examined (1 ♂, 1 ♀: loc. Pirin, Bulgaria; precise locality not available; collections of the National Museum, Prague).

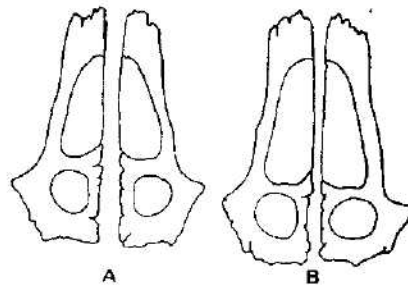
The facies cerebralis anterior is distinct rostrally and the margin terminates at the margo sagittalis. Caudally it is slightly depressed and can transcend without any border into the lateral part of the spatium interfaciale (Text Fig. 10 A).

The facies cerebralis posterior is projecting internally, and has a reticulation of grooves on its surface.

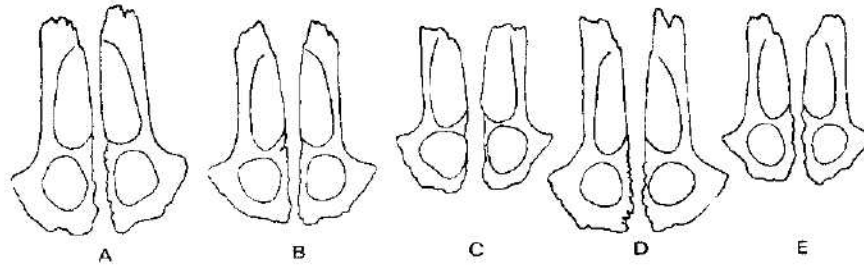
Rana latastei Boul. (Text Fig. 11)

Five specimens were examined (2 ♀♀; the other 3 were eviscerated: loc. Como, Italy, leg. Pozzi, 1977).

The incrassation is typical of other taxa of brown ranids. Specific features are depression of the caudal part of facies cerebralis anterior is bordered laterally, caudally and medio-caudally by a sharp ridge, slanting inwards. A similar sharp ridge forms the margin of facies cerebralis posterior forming a cup-like concavity. These features, however, are not equally conspicuous in all specimens and cannot be used as diagnostic characters for the species of brown ranids.



Text Fig. 10. Examples of the incrassatio frontoparietalis in *Rana graeca*.



Text Fig. 11. Examples of the incrassatio frontoparietalis in *Rana latastei*.

DISCUSSION

The above observations reveal that the incrassatio frontoparietalis of green ranids markedly differs from that of brown ranids. Differences are: (i) The lateral margin of the facies cerebialis anterior is straight or slightly bent in green ranids, directed rostro-medially, and terminates at the margo sagittalis. In all species of brown ranids the lateral margin is directed toward the margo anterior where it either terminates or becomes indistinct. In several individuals of different species it is sharply bent (often at an angle less than 90° — see Text Fig. 8 A, B, C and Text Fig. 10). To generalize, the outline of the rostral part of the incrassatio frontoparietalis is approximately triangular in green ranids, while in brown ranids it is approximately oblongated. (ii) In all species of brown ranids, the facies cerebialis anterior projects internally and the margin is sharply defined. In the caudal part it is depressed, and separated from the spatium interfasciale by a rounded projecting ridge. In both species of green ranids this part of the incrassation is differently shaped, as is described in the following text.

Both species of green ranids are conspicuously different in frontoparietal incrassation. In *Rana esculenta* the facies cerebialis anterior is slightly indented into the frontoparietale, and has a rounded margin. The facies cerebrales posteriores are oval-shaped. The facies cerebialis anterior in *Rana ridibunda* is flat or even slightly convex, projecting away from the level of the surrounding bone. In some specimens this part becomes inconspicuous or lacking. The facies cerebrales posteriores are irregularly shaped with broken outlines. The incrassatio frontoparietalis in the *Rana esculenta lessonae* does not differ from that in the nominate form.

The differences between the different brown ranid species are not great, and the range of variation of frontoparietal incrassations is so wide that it is difficult to find

diagnostic characters. Therefore, *Rana temporaria*, *Rana dalmatina*, *Rana arvalis* (including *Rana arvalis wolterstorffi*) and *Rana macrocnemis* cannot be distinguished from each other. In some individuals of *Rana iberica* the facies cerebralis anterior is conspicuously bordered rostrally where the lateral margin sharply bends and terminates on margo sagittalis. The only diagnosable species is *Rana graeca* which has a reticulation on the surface of facies cerebralis posterior. Unfortunately, I had only two specimens at my disposal making this conclusion unreliable. *Rana latidorsalis* had a distinct morphology for most but not all specimens.

When hypothesizing the phylogeny of the European ranids on the basis of the character *incrassatio frontoparietalis*, we must argue that both species of green ranids have not speciated much sooner than the several geographical populations of brown ranids which are considered by some to be good species. It results from the considerable differences between the *incrassatio frontoparietalis* in *Rana esculenta* and *Rana ridibunda*.

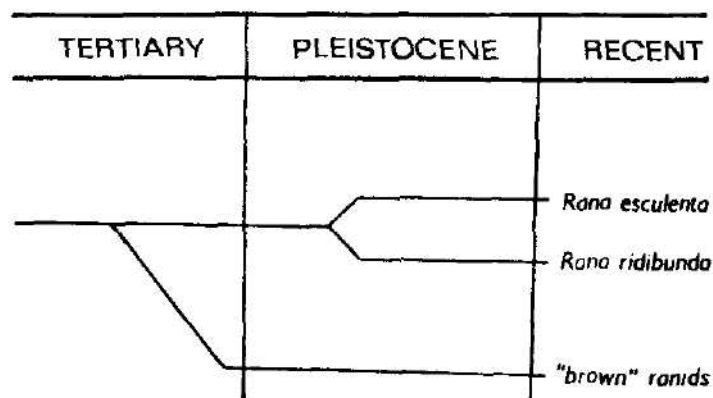
On the contrary the brown ranids, although forming a well defined group, cannot be well distinguished specifically owing to the wide variability of the *incrassatio frontoparietalis*. In my opinion the European species of brown ranids have not reached the sufficient genetic isolation, and their taxonomical status as a species should be reviewed.

These facts enable us to reconstruct the phylogenetic history of the European ranids. Although the first ranid fossils are known from the Upper Cretaceous of Africa (Vergnaud-Grazzini 1974), the first known European ranid is from the Lower Eocene, *Rana plicata* Filhol, 1876/7. The newly described *Rana strausi* from the Upper Pliocene of Willershausen (German Federal Republic) (Špinar, in press) possesses characters of both green and brown ranids. Špinar (l. cit.) considers this fossil a representative of the common ancestor of the ranids from which developed the two species of green ranids and later all forms of brown ranids. However, according to Terentjev (1950), the Oligocene *Rana aquensis* Coq. is supposedly a typical representative of the green ranids. The ancestors of European ranids may have been morphologically more similar to green ranids and the divergence of green and brown ranids has resulted in greater morphological change in the brown ranid lineage (Text Fig. 12). Undoubtedly, two main groups evolved: green and brown ranids (in the literature they sometimes are named *Rana esculenta* species group and *Rana temporaria* species group). Fossils of brown ranids are younger, suggesting that the brown ranids split off the main green ranid lineage sometime between the Miocene and the end of the Tertiary. In the Recent, both groups are distinguished morphologically and ecologically, and their species are reproductively isolated.

Rana esculenta and *Rana ridibunda* are well-defined species on the basis of the character *incrassatio frontoparietalis* as well as by other morphological and osteological characters and to a certain extent also ecologically. The reproductive isolation, however, does not prevent mutual breeding. As for *Rana esculenta lessonae*, the *incrassatio frontoparietalis*, other morphological characters and its ecology suggest that this taxon is only an ecological variant and not a subspecies.

As for single forms of brown ranids, considered species in the literature, it can be stated that some of them are more ancient (e.g. *Rana graeca*), better defined morphologically and ecologically, and others are of younger age, and less genetically isolated. It was mentioned above that only one or two forms differ markedly from the basic *incrassatio frontoparietalis*. Therefore, it can be supposed that Recent forms of European brown ranids are much younger than the forms of green ranids.

The question arises, whether there is adequate ground for classifying these forms as species. Not only the results of study of the *incrassatio frontoparietalis*, but also the instability and wide variability of other morphological characters and insufficient degree of reproductive isolation contradict such classification.



Text Fig. 12. Hypothesized phylogeny for the ranids of Europe.

SUMMARY

1. Three basic types of the *incrassatio frontoparietalis* can be distinguished in European representatives of the family Ranidae: *Rana esculenta* type, *Rana ridibunda* type and a type common to all species of brown ranids (with the exception of *Rana graeca*, for which insufficient information was available).

2. The major differences are found in the rostral part of the *incrassatio*.

3. No sexual dimorphism was ascertained for this character.

4. Some specimens have an anomalously shaped *incrassatio* as the rostral and caudal parts are fused together in various degrees.

5. On the basis of the *incrassatio frontoparietalis* and other taxonomically important characters we hypothesize that the lineage of green ranids has been the main stem, from which the lineage of brown ranids diverged at the end of Tertiary. Both species of European green ranids are more ancestral than the species of brown ranids, whose taxonomic status should be reviewed.

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**THE MOST IMPORTANT FACTORS AFFECTING THE LARVAL
DEVELOPMENT OF CESTODES OF THE FAMILY HYMENOLEPIDIDAE
IN CRUSTACEANS (COPEPODA)**

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Abstract: The effects of temperature, size of an intermediate host and intensity of infection on the course of larval development of 11 cestode species parasitic in water birds were experimentally studied. The most important factor is temperature, and it must be considered in all mentioned relations. The intensity of infection has a special position among the factors under study; it affects the larval development and at the same time it is dependent on other factors, temperature and size of the intermediate host. The temperature is a generally valid factor with all studied cestode species, affecting the length of larval development, size of cysticercoids and intensity of infection. The size of the intermediate host is a factor of limited validity. It affects the size of cysticercoids of *Diorchis inflata*, *D. ransomi*, *Microsomacanthus compressa*, *M. paracompressa*, *M. paramicrosoma*, *Sobolevicanthus gracilis*, *S. krabbeella*, *S. octacantha* (group I) and the intensity of infection with *Dicranotaenia coronula*, *Diorchis nyrocae* and *Fimbriaria fasciolaris* (group II). The intensity of infection also has a limited validity, since it affects the length of larval development and the size of cysticercoids of group II only.

The present paper summarizes the results of investigations on the effects of temperature, size of an intermediate host and intensity of infection on the course of larval development of 11 cestode species parasitic in water birds (Table I). The experiments were carried out in 1964—1972. The relationship between the larval stages of cestodes and crustaceans as intermediate hosts was dealt with in papers by Kisiełewska (1957) and Ryšavý (1961, 1962). Kisiełewska described the effect of intensity of infection on the length of larval development of *Drepanotaenia lanceolata* Bloch, 1782, whereas Ryšavý studied the effect of the size of intermediate host on the size of cysticercoids of *Fimbriaria fasciolaris* (Pallas, 1781). Nadakal et al. (1970) compared the size of cysticercoids of *Raillietina tetragona* (Molin, 1858) in relation to various species of beetles serving as intermediate hosts.

MATERIAL AND METHODS

The crustaceans were kept in 5—10 l aquaria with pond water, sand, mud, minute aquatic plants and some snails, usually *Lymanaea peregra ovata* (Draparnaud) and *L. stagnalis* Linnaeus feeding on decaying plant and animal residues. Tap water, previously left to stand for 6—10 days, was added when necessary and pond water was added two or three times a month. The aquaria with crustaceans were placed on a light site without direct sunshine to prevent rapid processes of decay and intensive growth of bacteria which the crustaceans could not destroy. The amount of oxygen was sufficient for the life of crustaceans and artificial oxidation of water was unnecessary, because the crustaceans died more rapidly.

Cestode eggs used in the experiments were obtained from cestodes at dissections of *Anas platyrhynchos domestica* L., *A. platyrhynchos* L., *A. crecca* L., *A. querquedula* L., *A. streperus* L., *Aythya ferina* L., *A. fuligula* L., *A. nyroca* L. and *Fulica atra* L. The eggs had to be examined

Table 1. Survey of cestodes and their intermediate hosts in our material

Cestode	Intermediate host, length of body without furcal setae
<i>Dicranotaenia coronula</i> (Dujardin, 1845)	<i>Acanthocyclops viridis</i> (Jurine) 1.5—3.0, <i>Cyclops strenuus strenuus</i> Fischer 1.4—2.4, <i>Mesocyclops (Thermocyclops) crassus</i> (Fischer) 0.9—1.4
<i>Diorchis infata</i> (Rudolphi, 1819)	<i>Acanthocyclops vernalis</i> (Fischer) 1.5—1.9, <i>Macrocyclops albidus</i> (Jurine) 1.7—2.5
<i>D. nyrocae</i> Yamaguti, 1935	<i>A. vernalis</i> , <i>A. viridis</i> , <i>C. strenuus</i> , <i>M. crassus</i> , <i>Mesocyclops</i> (s. str.) <i>leuckarti</i> Claus 0.9—1.9
<i>D. ransomi</i> Schultz, 1940	<i>A. vernalis</i> , <i>A. viridis</i> , <i>C. strenuus</i>
<i>Fimbriaria fascioluris</i> (Pallas, 1781)	<i>A. vernalis</i> , <i>A. viridis</i> , <i>C. strenuus</i> , <i>M. albidus</i> , <i>M. crassus</i> , <i>M. leuckarti</i> , <i>Paracyclops poppei</i> (Rehberg) 0.7—1.0
<i>Microsomacanthus compressa</i> (Linton, 1782)	<i>A. viridis</i> , <i>C. strenuus</i> , <i>Eucyclops</i> (s. str.) <i>serrulatus</i> (Fischer) 0.7—1.4, <i>M. albidus</i> , <i>M. crassus</i>
<i>M. paracompressa</i> (Czapliński, 1956)	<i>A. viridis</i> , <i>M. albidus</i> , <i>M. crassus</i>
<i>M. paramicrosoma</i> (Gasowska, 1931)	<i>A. viridis</i> , <i>M. crassus</i>
<i>Sobolevicanthus gracilis</i> (Zeder, 1803)	<i>E. serrulatus</i> , <i>M. crassus</i>
<i>S. krabbeella</i> (Hughes, 1940)	<i>E. serrulatus</i> , <i>M. crassus</i>
<i>S. octacantha</i> (Krabbe, 1869)	<i>E. serrulatus</i> , <i>M. crassus</i>

microscopically before the experiment, because we had found that morphologically fully differentiated eggs are capable of further development in intermediate hosts only in the case that they contain mobile oncospheres.

Proglottids with eggs containing mobile oncospheres were torn up with preparation needles and put into crystalization dishes with tap water. The whole contents were left for 24—48 hrs at the temperature of 4—10° C. During that time the oncosphere envelopes swelled up in the water so that the eggs added into the dishes with experimental crustaceans were dispersed at various heights of the water column which enhanced the possibility of infection.

Cestode proglottids with eggs containing immobile oncospheres were first left for 24—48 hrs in tap water at the temperature of 18—20° C. After that time, most of the oncospheres were mobile so that the eggs could be pressed out from the proglottids, the proglottids were torn up with preparation needles and left for 12—24 hrs in tap water at 4—10° C. Samples with bacterial contamination were discarded. Antibiotics were not used, because the increased mortality of crustaceans would have distorted the results of the experiments.

Only crustaceans of the family Cyclopidae were used in order to obtain a homogeneous material. They are the most common intermediate hosts of the cestode species applied. The experiments were performed at water temperatures of 8—10° C, 18—20° C, 24—26° C, 28—30° C, and 33—35° C. Under natural conditions, the temperatures of 8—10° C and 28—30° C represented the minimum and maximum values and larval development most frequently occurred at the temperatures of 18—26° C. No cysticercoids were obtained experimentally at a temperature lower than 8° C and neither in nature larvae developed at such a low temperature. The temperature of 33—35° C was unsuitable both for the life of crustaceans and for the development of cysticercoids. The results obtained at these temperatures were not included in the tables, since 50—70% of the crustaceans died.

The water temperature in experimental aquaria was measured with immersion thermometers and regulated in thermostats. The temperature in thermostats could not be kept exactly and we are therefore giving a range of 3° C for every temperature applied. Control measuring showed a slight variation in water temperature of ± 0.3 — 0.8 ° C. pH of water was maintained within the range of 6.8—7.0 by regular adding of pond water (2—3 times monthly, pH 7.0—7.2), because if only tap water was added (pH 5.8—6.2) the pH values decreased to 6.2—6.4.

Cestode eggs and corresponding species of crustaceans serving as intermediate hosts (Table 1) were studied in 432 experiments. The eggs of one cestode species and one crustacean species were studied in 12 experiments, i.e., 3 experiments for each temperature. One hundred crustaceans of the same species were used in each experiment. They were placed in a 1-litre aquarium with eggs of the studied species of cestodes, on the average 50 eggs per crustacean. After 12 hrs the crustaceans were transferred into larger aquaria (5-litre) where they were left till the end of the experiment. During the development of the oncosphere into the cysticercoid the crustaceans were examined with a microscope after 1, 2, 3, 4, 6, 8, and 12 hours and later i

necessary, but at least once a day. Individual phases of larval development are described in a paper by Neradová-Valkounová (1971).

The crustaceans died only rarely during the experiments and we assume that their death was not caused by the cestode larvae. The reason was, e.g., infection with protozoans, age of the crustacean, unsuitable temperature etc. In no case was infection with a larger number of larvae found to cause the death of crustaceans. In such cases the number of larvae was reduced (see Conclusions and Discussion). The crustaceans infected with cestode larvae differed from other specimens in that they moved more slowly, in various anomalies in the formation of egg sacs and spermophore sterility or shorter life-span (3–6 weeks). Owing to these facts the incidence of infection was not considered. The mortality was 1–13% (only in two cases 20%) of the total number (100) of crustaceans used in individual experiments. Of the total number of dead crustaceans, 1–8% were positive and 1–5% negative to cestode larvae. Of the 100 experimental crustaceans, 1–7% of the specimens were negative to cestode larvae and 80% of the specimens positive to cestode larvae survived. Only those which survived and were infected with cestode larvae were evaluated in the results. All measurements are given in millimeters.

RESULTS

The larval development of the studied cestode species is markedly affected by the following factors: 1) water temperature, 2) size of intermediate host, and 3) intensity of infection. The most important factor is temperature which must be considered in all mentioned relationships. The intensity of infection, which also affects the development of larvae, is at the same time affected by the other two factors, temperature and size of intermediate host.

1. Temperature

1a. The effect of temperature on the length of larval development (Tables 2, 3)

The length of larval development was proportional to water temperature with all 11 cestode species under study. The time necessary for the development of the oncosphere into the cysticercoid shortened with increasing temperature from 8°C to 30°C. At the temperature of 33–35°C the length of larval development was approximately the same as at 18–20°C. This relation is valid if we consider the length of larval development at a certain temperature without any regard to the species of the intermediate host (Table 2), but also if we compare the relation between the length of larval development and temperature in individual crustacean species (Table 3).

1b. The effect of temperature on the size of cysticercoids

The size of cysticercoids of all cestode species examined was related to temperature. A direct relation was observed at the temperature of 8–26°C. At the temperature of 8–10°C the cysticercoids were smaller on the average by 0.035–0.055 than at 18–20°C; at the temperature of 18–20°C they were smaller by 0.026 to 0.050 than at 24–26°C and 28–30°C. At the temperature of 33–35°C the cysticercoids were of almost the same size as at 18–20°C.

1c. Effect of temperature on the intensity of infection (Table 2)

In our experiments, the intensity of infection with oncospheres was always higher than the intensity of infection with cysticercoids (see Conclusions and Discussion – withering of oncospheres). The intensity of infection with oncospheres of all 11 cestode species and intensity of infection with cysticercoids of *Dicranotaenia coronula*, *Diorchis nyrocae* and *Fimbriaria fasciolaris* increased with temperature increasing from 8°C to 26°C, but at 28–30°C it started to decrease and reached values lower by 12–33% than at the temperature of 18–20°C. At 33–35°C the intensity of

Table 2. Effect of temperature on intensity of infection and length of larval development

Cestode	Temperature °C	Intensity of infection		Length of larval development in days
		Oncospheres	Cysticercoids	
<i>Dicranotaenia coronula</i>	8—10	1) 3—10 2) 5	1—6 3	27—31
	18—20	7—17 8	1—10 7	13—18
	24—26	9—21 11	1—12 8	11—14
	28—30	5—15 8	1—8 4	9—12
<i>Diorchis nyrocae</i>	8—10	2—18 6	1—10 4	28—34
	18—20	11—34 22	1—27 15	13—19
	24—26	10—37 27	1—31 19	12—16
	28—30	10—23 20	1—17 11	10—13
<i>Fimbriaria fasciolaris</i>	8—10	1—13 5	1—10 8	20—37
	18—20	1—43 26	1—32 18	13—28
	24—26	1—48 29	1—37 18	11—19
	28—30	1—33 22	1—24 13	9—17
<i>Diorchis inflata</i>	8—10	3—7 3	1	29—32
	18—20	4—13 8	1—4	14—16
	24—26	3—20 12	1—4	11—13
	28—30	2—10 8	1—4	9—12
<i>Diorchis ransomi</i>	8—10	2—6 3	1	30—33
	18—20	5—13 7	1—4	18—24
	24—26	3—19 12	1—4	15—17
	28—30	2—12 8	1—4	11—13
<i>Microsomacanthus compressa</i>	8—10	1—3 1	1	27—32
	18—20	3—18 6	1—4	18—23
	24—26	5—20 7	1—4	15—17
	28—30	5—14 5	1—4	11—16
<i>Microsomacanthus paracompressa</i>	8—10	4—10 5	1	30—33
	18—20	6—17 9	1—4	18—20

Cestode	Temperature °C	Intensity of infection		Length of larval development in days
		Oncospheres	Cysticercoids	
<i>Microsomacanthus paracompressa</i>	24—26	3—21 10	1—4	13—16
	28—30	2—13 7	1—4	11—12
<i>Microsomacanthus paramicrosoma</i>	8—10	2—9 6	1	29—30
	18—20	4—17 11	1—4	20—22
	24—26	3—22 16	1—4	17—19
	28—30	7—15 13	1—4	12—15
<i>Sobolevicanthus gracilis</i>	8—10	2—5 3	2	30—32
	18—20	2—18 5	1—4	13—17
	24—26	4—22 9	1—4	12—13 ¹
	28—30	3—11 7	1—4	9—12
<i>Sobolevicanthus krabbeella</i>	8—10	1—8 4	1	18—29
	18—20	2—17 10	1—4	16—18
	24—26	2—24 16	1—4	13—16
	28—30	2—13 10	1—4	10—13
<i>Sobolevicanthus octacantha</i>	8—10	2—7 5	1	31—34
	18—20	1—16 12	1—4	18—21
	24—26	2—19 15	1—4	16—18
	28—30	3—13 9	1—4	12—14

¹) minimum—maximum value

²) average value in round numbers

infection was approximately half of that at 18—20° C. The intensity of infection with cysticercoids of the remaining cestode species was, as follows: 1 cysticercoid at 8—10° C, 1—4 cysticercoids at 18—30° C and 1 cysticercoid at 33—35° C. The effect of the number of eggs on the intensity of infection was excluded using a sufficient (experimentally verified) and standard number of eggs in the experiments (see Material and Methods).

2. Size of intermediate host

2a. Effect of the size of intermediate host on the size of cysticercoids at a given temperature (Table 4)

Table 3. Effect of temperature on length of larval development of *Fimbraria fasciolaris* in various species of crustaceans serving as intermediate hosts

Intermediate host	Temperature °C	Length of larval development in days
<i>Acanthocyclops viridis</i>	8—10	30—37
	18—20	14—28
	24—26	15—19
	28—30	12—17
<i>Macrocyclus albidus</i>	8—10	23—29
	18—20	14—22
	24—26	13—18
	28—30	9—15
<i>Cyclops strenuus</i>	8—10	23—25
	18—20	14—18
	24—26	12—15
	28—30	11—13
<i>Mesocyclops leuckarti</i>	8—10	20—24
	18—20	13—15
	24—26	11—14
	28—30	10—13
<i>Paracyclops poppei</i>	8—10	20—23
	18—20	14—15
	24—26	11—15
	28—30	10—13

A relation between the size of cysticercoids and the size of the crustaceans was observed in *Diorchis inflata*, *D. ransomi*, *Microsomacanthus compressa*, *M. paramicrosoma*, *Sobolevicanthus gracilis*, *S. krabbeella* and *S. octacantha*. The larger was the crustacean the larger were the cysticercoids of individual cestode species, irrespective of the intensity of infection which was 1—4 cysticercoids per crustacean. This was verified by comparing both individual species and individual specimens of a single species. However, this relation was not found in the remaining cestode species.

2b. Effect of the size of intermediate host on the intensity of infection at a given temperature (Table 5)

The intensity of infection with cysticercoids of *D. coronula*, *D. nyrocae* and *F. fasciolaris* was proportional to the size of crustacean. The larger was the crustacean the higher was the intensity of infection. This relation was observed by comparing

Table 4. Effect of size of intermediate host on the size of cysticercoids of *Microsomacanthus compressa* at temperature of 18—20° C

Intermediate host	length of body without furcal setae	Size of cysticercoids	
		length	width
<i>Acanthocyclops viridis</i>	1.5—2.9	0.214—0.393	0.176—0.282
<i>Macrocyclus albidus</i>	1.9—2.5	0.240—0.386	0.220—0.276
<i>Cyclops strenuus</i>	1.9—2.4	0.238—0.360	0.220—0.265
<i>Eucyclops serrulatus</i>	0.7—1.4	0.189—0.280	0.145—0.237
<i>Mesocyclops crassus</i>	0.9—1.1	0.201—0.250	0.183—0.196

both individual crustacean species of different size and individual specimens within the population of one species. It was therefore evaluated with respect to the size of the crustacean and regardless of its species. Table 5 shows this relation expressed in minimum and maximum values of intensity of infection, forming an almost ideal succession on one hand, and in average values of intensity of infection stated in round numbers on the other hand. The differences in the intensity of infection were small at the temperature of 8–10° C. For example, in *F. fasciolaris* the intensity of infection was 1–6 cysticeroids in *Cyclops strenuus* (measuring 1.900 to 2.400 in our material), *Acanthocyclops vernalis* (1.500–1.800) and *Mesocyclops leuckarti* (0.900–1.700). In the remaining eight cestode species the intensity of infection was 1–4 cysticeroids irrespective of the size of the crustacean.

3. Intensity of infection

3a. Effect of the intensity of infection on the length of larval development at a given temperature (Table 6)

Table 5. Effect of size of intermediate host on intensity of infection at a given temperature

Cestode	Intermediate host, length of body without furcal setae		Intensity of infection (cysticeroids) at a temperature (°C)			
			8–10	18–20	24–26	28–30
<i>Dicranotaenia coronula</i>	<i>Acanthocyclops viridis</i>	2.5–2.9	¹⁾ 1–6 ²⁾ 3	1–10 5	1–12 6	2–8 3
	<i>Cyclops strenuus</i>	1.8–2.1	1–5 3	1–8 4	1–10 5	1–6 2
	<i>Mesocyclops crassus</i>	0.9–1.2	2–3 2	1–5 3	1–7 3	1–4 2
<i>Diorchis nyrocae</i>	<i>Acanthocyclops viridis</i>	2.4–3.0	1–10 5	1–27 9	1–31 12	1–17 8
	<i>Cyclops strenuus</i>	1.9–2.3	1–7 3	1–13 5	1–15 6	1–11 4
	<i>Acanthocyclops vernalis</i>	1.5–1.9	1–6 3	1–11 4	1–14 4	1–8 3
	<i>Mesocyclops leuckarti</i>	1.3–1.9	1–4 2	1–9 3	1–12 4	1–7 3
	<i>Mesocyclops crassus</i>	0.9–1.1	1–4 1	1–8 3	1–10 3	1–6 2
<i>Fimbriaria fasciolaris</i>	<i>Acanthocyclops viridis</i>	2.0–2.9	1–10 4	1–32 13	1–37 15	1–24 10
	<i>Macrocyclus albidus</i>	1.9–2.5	1–6 4	1–29 8	1–33 9	1–22 7
	<i>Cyclops strenuus</i>	1.9–2.4	1–6 4	1–27 6	1–29 9	1–22 6
	<i>Acanthocyclops vernalis</i>	1.5–1.8	1–6 3	1–19 5	1–22 6	1–15 3
	<i>Mesocyclops leuckarti</i>	0.9–1.7	1–6 2	1–17 5	1–20 6	1–13 3
	<i>Mesocyclops crassus</i>	0.9–1.2	1–5 2	1–14 3	1–11 5	1–7 3
	<i>Paracyclops poppei</i>	0.7–0.9	1–3 1	1–5 2	2–5 3	2–3 2

¹⁾ minimum—maximum value

²⁾ average value in round numbers

The length of larval development was proportional to the intensity of infection with *D. coronula*, *D. nyrocae* and *F. fasciolaris*. This relation was apparent only at the intensity higher than 4 cysticeroids and was found at all temperatures investigated. No similar relation was observed in the remaining cestode species.

3b. Effect of the intensity of infection on the size of cysticeroids at a given temperature (Table 7)

Table 6. Effect of intensity of infection on the length of larval development at a given temperature

Cestode	Intermediate host	8—10 °C		18—20 °C		24—26 °C		28—30 °C	
		I	L	I	L	I	L	I	L
<i>Diorchis nyrocae</i>	<i>Cyclops strenuus</i>	1—2	28	1—3	13	1—3	12	1—3	10
		1—2	29	4—5	14	1—5	14	4—6	11
		2—4	30	3—7	15	7—8	14	5—11	12
		4—6	31	7—9	16	10—13	15		
		7	32	9—13	17				
<i>Fimbriaria fasciolaris</i>	<i>Acanthocyclops viridis</i>	1—2	30	1—2	14	1—5	15	1—3	12
		1—3	31	1—2	15	8—13	16	1—5	13
		1—3	32	2—3	16	10—18	17	7—10	14
		4—5	33	3—6	17	20—25	18	12—17	15
		5	34	7—10	18	32—34, 37	19	17—19	16
		6—7	35	10—22	19			20—24	17
		7	36	13—26	20				
		10	37	30—32	26—28				
		10	38						
	<i>Cyclops strenuus</i>	1—2	23	1—2	14	1—3	13	1	9
		1—2	24	1—3	15	4—8	14	1—3	10
		1—3	26	1—5	16	10—15	15	4—6	11
		4—5	27	3—9	17	18—20	16	6—11	12
		4—5	28	8—13	18	25	17	10—14	13
		8	29	12—15	19	27, 29	18	16—19	14
				17—19	20			18—22	15
				21—23	21				
				23—27	22				

I — Intensity of infection (cysticeroids)

L — Length of larval development (in days)

An indirect proportion between the intensity of infection and size of cysticeroids was observed in *D. coronula*, *D. nyrocae* and *F. fasciolaris*. The size of cysticeroids decreased with increasing intensity of infection. This relation was not observed in the remaining cestode species.

CONCLUSIONS AND DISCUSSION

The factors studied in our experiments affected a) the length of larval development, b) the size of cysticeroids, and c) the intensity of infection.

a) The length of larval development, which is completed by invagination of the scolex into the cyst cavity (= cysticeroid), was related to temperature and the intensity of infection. In the case of *D. coronula*, *D. nyrocae* and *F. fasciolaris* it was affected by temperature and the intensity of infection, whereas in the remaining cestode species it was affected only by temperature. In our experiments, in which

the infection of crustaceans with cestode eggs lasted 12 hours, the length of larval development of one cestode species in the population of one crustacean species differed by 24–48, in some cases even by 72 hours at the same temperature and intensity of infection.

The relation between the length of larval development and intensity of infection was studied by Kisielewska (1957a) who used the cestode *D. lanceolata*. The author described this relation in crustaceans infected with more than 7 larvae.

b) The size of cysticercoids was related to temperature, the size of crustacean and intensity of infection. In *D. coronula*, *D. nyrocae* and *F. fasciolaris* it was affected by temperature and the intensity of infection, whereas in the remaining cestode species it was affected by temperature and the size of the crustacean serving as the intermediate host.

Table 7. Effect of intensity of infection on the size of cysticercoids of *Fimbriaria fasciolaris* in *Cyclops strenuus* and *Mesocyclops crassus* at the temperature of 18–20 °C

Intensity of infection cysticercoids	Size of cysticercoids in crustaceans			
	<i>C. strenuus</i>		<i>M. crassus</i>	
	Length	Width	Length	Width
1	0.168–0.184	0.155–0.170	0.188–0.198	0.177–0.185
2	0.170–0.174	0.150–0.155	0.170–0.190	0.134–0.164
3	0.161–0.173	0.147–0.155	0.168–0.189	0.129–0.173
4	0.159–0.170	0.140–0.148	0.167–0.185	0.126–0.169
5	0.155–0.169	0.139–0.148	0.164–0.179	0.119–0.162
6	0.153–0.165	0.135–0.148	0.159–0.178	0.117–0.159
7	0.150–0.161	0.135–0.146	0.156–0.173	0.113–0.156
8	0.148–0.159	0.135–0.144	0.151–0.169	0.108–0.150
9	—	—	0.147–0.166	0.104–0.140
10	0.141–0.155	0.132–0.140	0.144–0.165	0.103–0.140
11	0.138–0.149	0.130–0.137	0.141–0.159	0.102–0.137
12	0.135–0.140	0.127–0.134	0.140–0.159	0.102–0.134
13	—	—	0.139–0.154	0.102–0.126
14	—	—	0.137–0.150	0.098–0.124
15	0.131–0.136	0.116–0.129	—	—
16	0.126–0.136	0.114–0.127	—	—
17	0.120–0.129	0.111–0.125	—	—
18	0.116–0.125	0.106–0.120	—	—
19	0.111–0.123	0.104–0.119	—	—
22	0.105–0.122	0.104–0.117	—	—
24	0.102–0.123	0.100–0.115	—	—
27	0.100–0.123	0.098–0.115	—	—

Ryšavý (1961, 1962) described the relation between the size of cysticercoids and size of infected crustaceans using the cestode species *F. fasciolaris*. In *Acanthocyclops viridis* (according to the author "larger of the two") the cysticercoids measured 0.128×0.104 , whereas in *Eudiaptomus vulgaris* (Schmeil) they measured $0.083–0.098 \times 0.075–0.082$. His results cannot be compared with ours, because the intensity of infection and size of crustaceans were not given. Nadakal et al (1970) observed the effect of various species of beetles serving as intermediate hosts on the size of cysticercoids of *R. tetragona*. Their results are consistent with our finds of cysticercoids of various sizes in crustaceans of various sizes.

c) The intensity of infection was related to the temperature and the size of the intermediate host. The intensity of infection with oncospheres was affected only by temperature in all 11 cestode species. The intensity of infection with cysticercoids

of *D. coronula*, *D. inflata* and *F. fasciolaris* was affected by temperature and the size of the crustacean. The intensity of infection with cysticercoids of the remaining cestode species was also affected only by temperature.

The greatest reduction of larval stages occurred in the stage of moving oncosphere. The mechanism of this phenomenon has not yet been elucidated. Most probably those oncospheres died which had been damaged in some manner or which had begun developing too late. The dying oncospheres were not very motile, their hooks were irregularly distributed on the periphery of the body and the content of their middle cells was vacuolized. Later the cells structure was completely damaged and only embryonic hooks were found in body cavities of the crustaceans. The death of the subsequent larval stages (elongated and differentiating larvae) was mainly related to a sudden decrease in temperature. If temperature decreased from 28–30° C to 14–16° C and from 18–20° C to 8–10° C, there occurred larvae which were retarded in their development and gradually died (e.g., elongated larvae without tail anlage of differentiating larvae with undeveloped scolex, neck or body cavity). In some cases there was mortality in the stage of elongated or differentiating larva even if the temperature was quite sufficient and the larvae had developed normally. Probably the effects of other parasites as protozoans, or complicated parasite-host relationships were involved in that case. No dying of differentiated larvae or cysticercoids were observed.

Dubinina (1950) described the dying of procercoids of the cestode *Ligula colymbi* Zeder, 1803 in *Cyclops gracilis* Lilljeborg on day 13 after the beginning of the experiment. Kisielewska (1957b) observed the dying of all larval stages of *D. langeolata* in 8 species of crustaceans. Ryšavý (1962) found dying oncospheres of some cestode species studied in our experiments.

In a standard number of cestodes, maximum intensity of infection was 4 cysticercoids in group I (*D. inflata*, *D. ransomi*, *M. compressa*, *M. paracompressa*, *M. paramicrosoma*, *S. gracilis*, *S. krabbeella*, *S. octacantha*) and more than 4 cysticercoids in group II (*D. coronula*, *D. nyrocae*, *F. fasciolaris*). This intensity of infection was encountered both under experimental and natural conditions and it can therefore be considered an original phenomenon not affected by laboratory conditions, which cannot be explained fully and unambiguously. We assume that it is closely related to the size of cysticercoids which is given by the size of hooks in individual cestode species. During their development and growth the hooks load the metabolic processes of crustaceans proportionally to their size, since they consist of proteins with disulphide groups (Valkounová and Prokopič, 1978). Cestodes of group I have large hooks (in our material, *D. inflata* 0.066–0.077, *D. ransomi* 0.039–0.045, *M. compressa* 0.053–0.063, *M. paracompressa* 0.054–0.063, *M. paramicrosoma* 0.034–0.044, *S. gracilis* 0.075–0.087, *S. krabbeella* 0.060–0.064, *S. octacantha* 0.036–0.039), whereas those of group II possess hooks approximately 2–3 times smaller (in our material, *D. coronula* 0.018–0.022, *D. nyrocae* 0.021–0.024, *F. fasciolaris* 0.018–0.024).

Our results were compared with those obtained during the study of larval development under natural conditions (Neradová-Valkounová 1971, Valkounová 1972a, b, c). It was found that the relation observed under laboratory conditions also occur in nature. There was only one difference in the intensity of infection in cysticercoids of group II. The highest intensity of infection was found under laboratory conditions, lower in duck farms and the lowest in other parts of the pond. The differences in the intensity of infection resulted from the concentration of infection in the environment. Under experimental conditions, the intensity was

on the average 50 cestode eggs per crustacean. In duck farms there was a rather high concentration of definitive hosts in a limited area (300–350 *Anas platyrhynchos dom.* on the average) and, consequently, the concentration of eggs of the above-mentioned cestode species was also high. In other parts of the ponds the intensity of infection was lowest with respect to a great dispersion of definitive hosts, intermediate hosts and eggs of cestodes. In contrast to experimental conditions, under natural conditions the intensity of infection may also be affected by the stage of maturity of cestode eggs released into the environment, concentration of eggs in water, possibility of contact of the eggs with crustaceans, density of intermediate host populations, height of water column, size of water reservoir, weather conditions and many other factors which cannot be either influenced or changed.

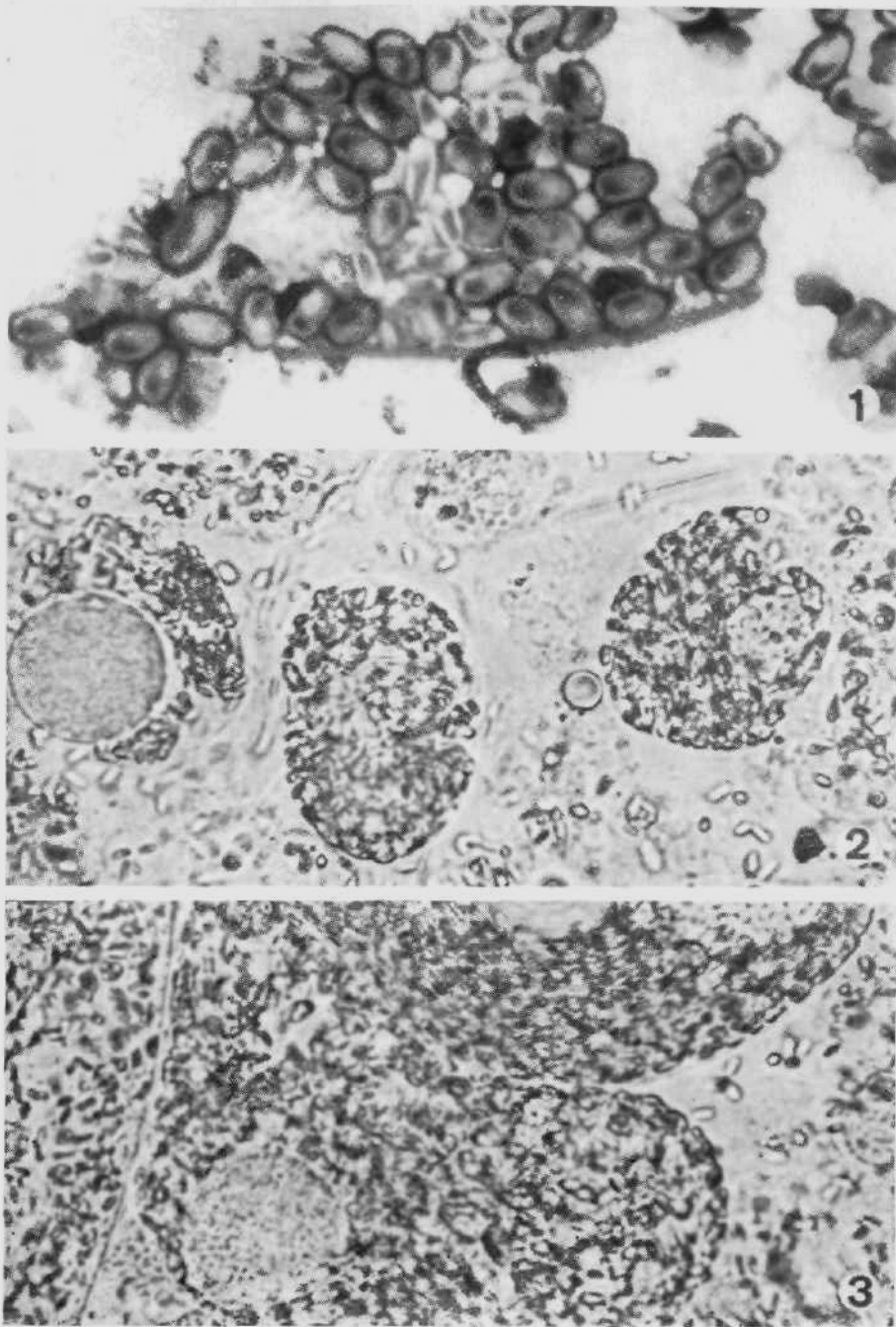
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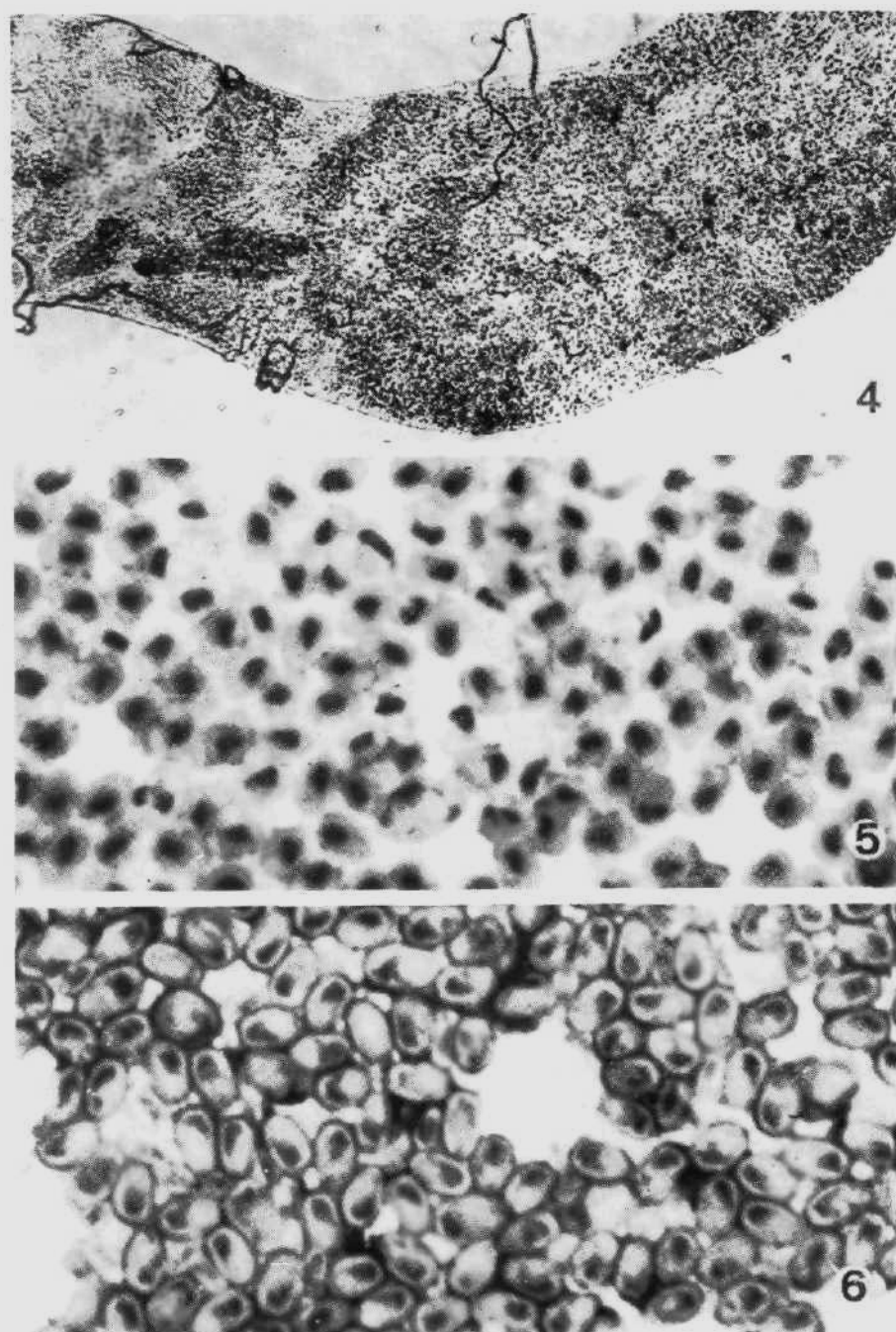
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Tab. 1. *Nosema adjuncta*. 1. Smear with Giemsa stained spores of *N. adjuncta* (minor, less stained ones) and *N. equestris*. 2. Oenocytes filled with spores of *N. adjuncta*. 3. Spores of *N. adjuncta* in gonads. Magn. $\times 1,200$, (1) and $\times 500$ (2, 3).



Tab. 2. *Nosema equestris*. 4. Malpighian tube with spores of *N. equestris* spread over the wall. 5. Giemsa stained spores with dark posterosome prominent in the sporoplasm. 6. Spores of *N. equestris* with visible nuclei, the posterior flat, the anterior protruding in a flare. Magn. $\times 200$ (4) and $\times 1,200$ (5, 6).

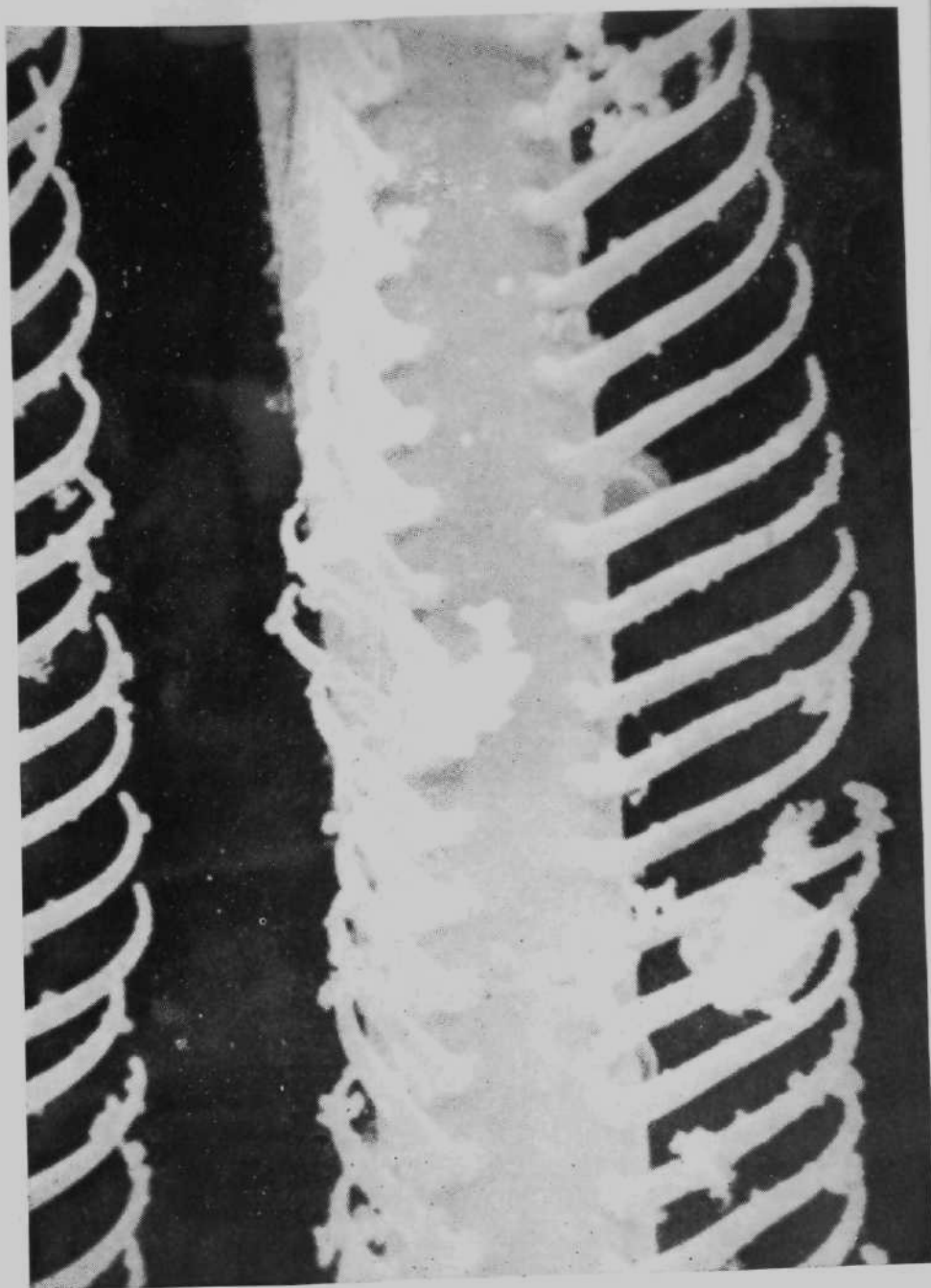


Fig. 3. *Daphnia pulex* from a laboratory culture, filtering setae of the 3rd thoracic limb distal part. $\times 6600$, SEM.

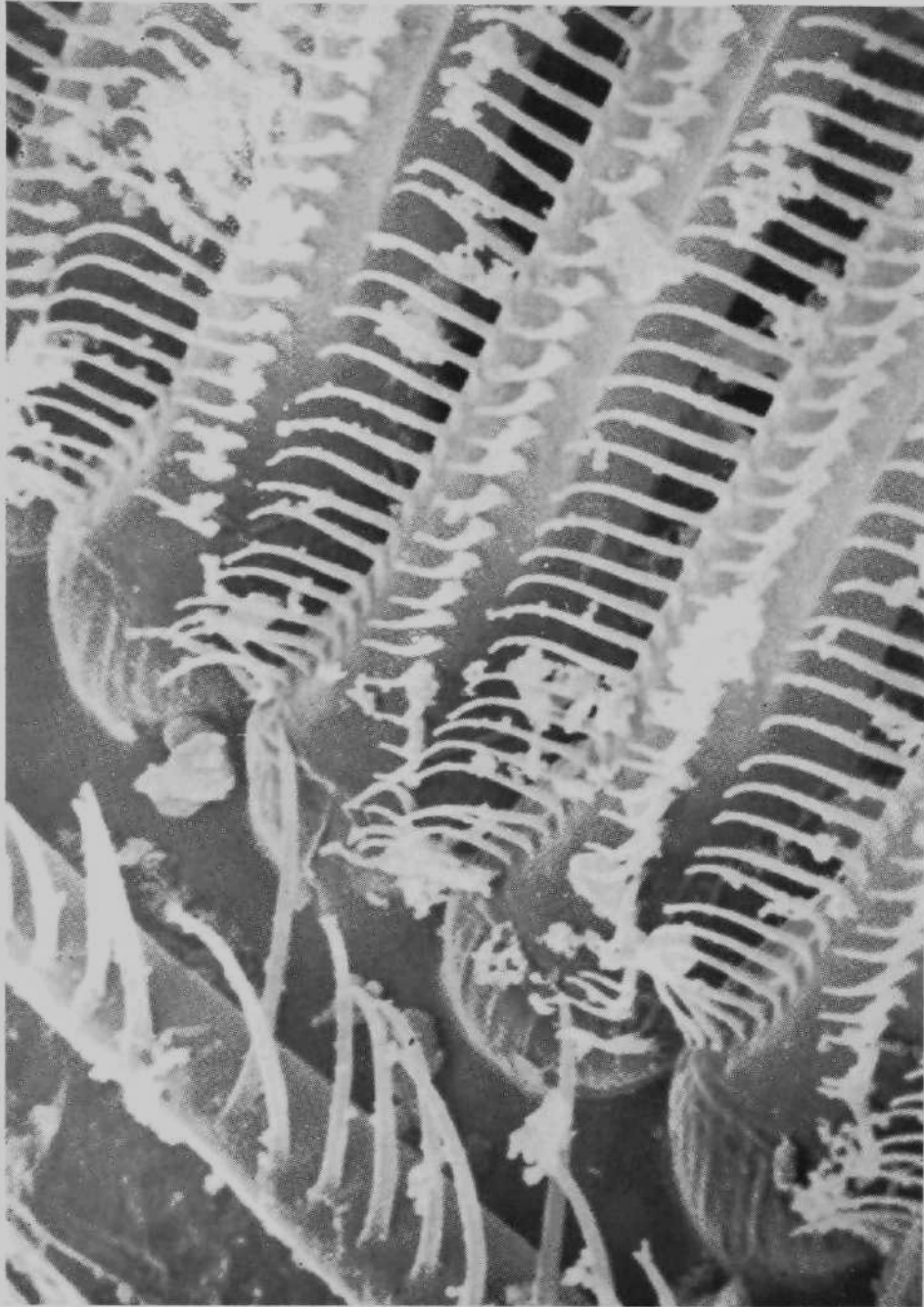
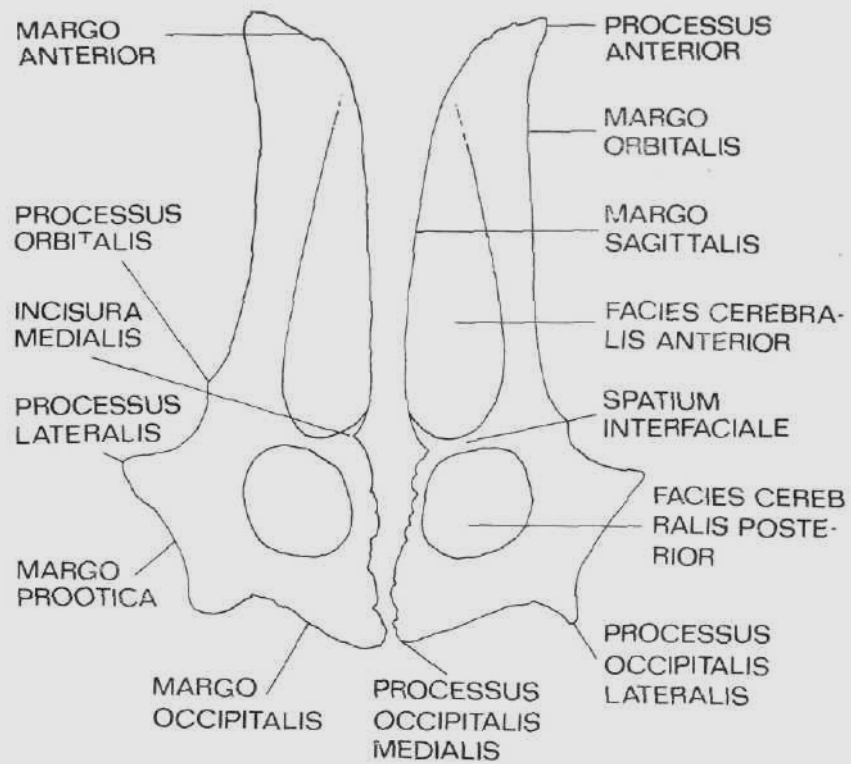
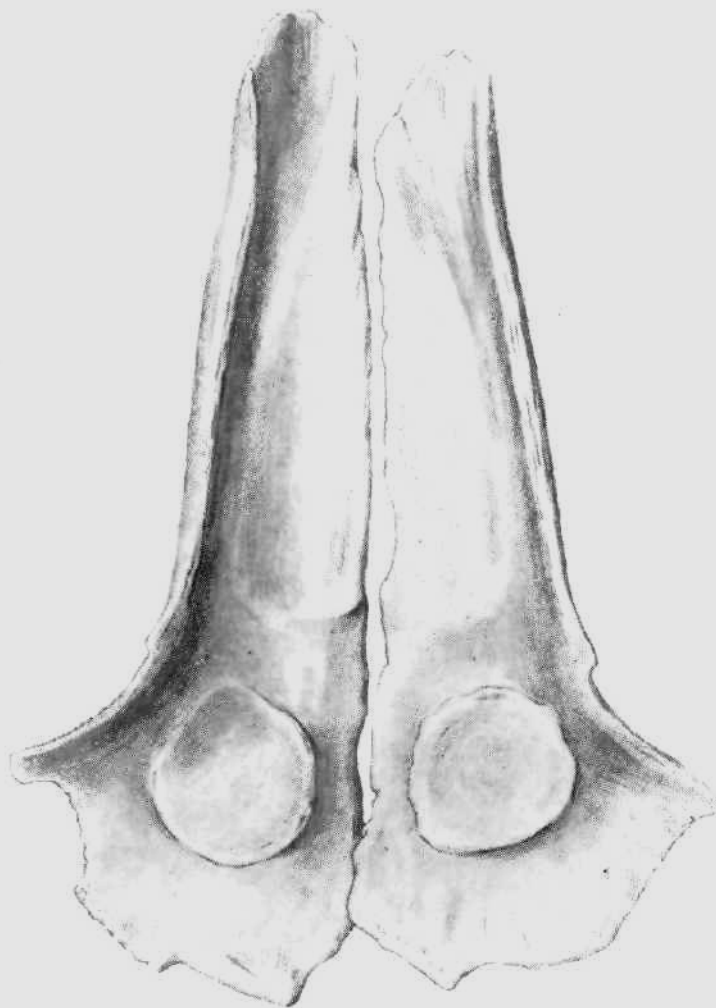


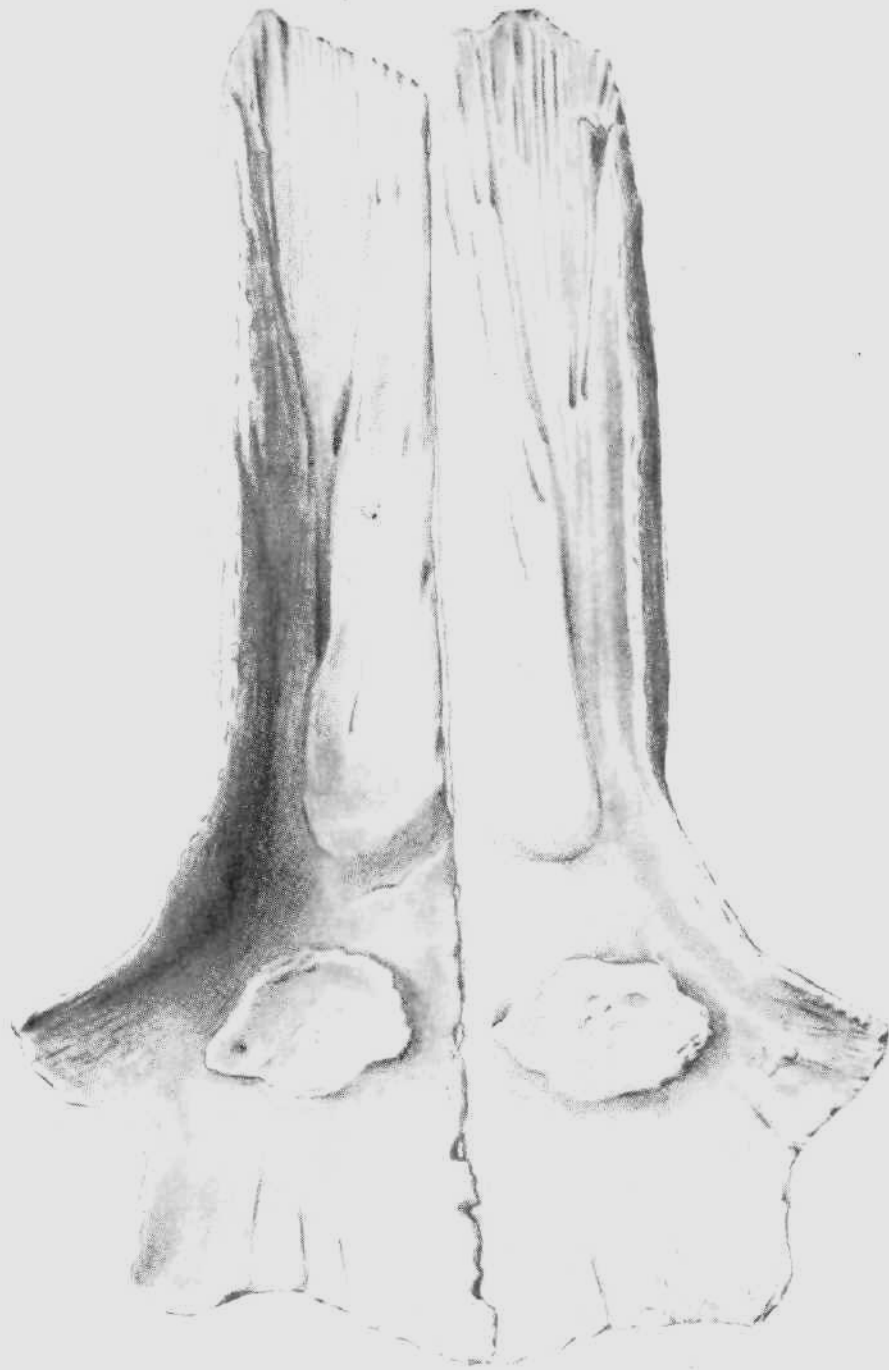
Fig. 4. Basal part of the filtering comb of the 3rd thoracic limb. *Daphnia pulicaria*, laboratory culture. $\times 2500$, SEM.



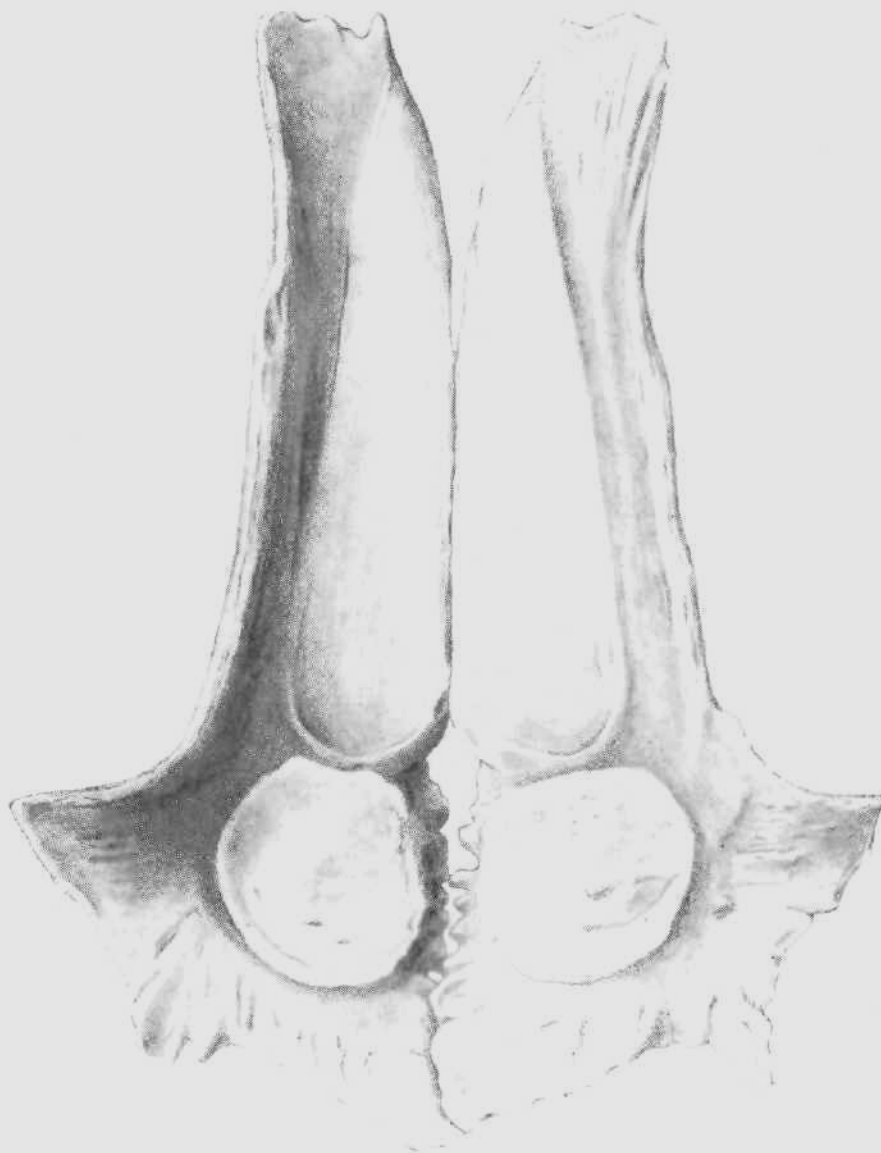
Text Fig. 1. Ventral surface of the frontoparietals of generalized ranid, together with a terminology for the *incrassatio frontoparietalis*.



Pl. Fig. 1. The *incrassatio frontoparietalis* type of *Rana esculenta*.



Pl. Fig. 2. The incrassatio frontoparietalis type of *Rana ridibunda*.



Pl. Fig. 3. The incrassatio frontoparietalis type common to brown ranids.

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