Arch. Moll. | 99 | (1/2) | 55—67 | Frankfurt a. M., 25. 4. 1969

The Baikal limpets and their phylogenetic status.

By

Bengt Hubendick,
Naturhistoriska Museet, Gothenburg.

With 39 figures.

The fresh-water limpets of Lake Baikal have been classified first as *Ancylus*, later as *Pseudancylastrum*. Their true taxonomical position has never been properly worked out. An examination of their morphology clearly shows that they all belong to the family Acroloxidae.

In this paper the Baikal Acroloxidae will be reviewed and their phylogenetic relationships discussed. It has been possible to carry out the study only thanks to the helpfulness of the late Dr. M. M. Kozov, Department of Zoology, the State University, Irkutsk, Dr. S. M. Popova, Limnological Institute, Irkutsk, and Dr. Y. Starobogatov, Zoological Institute, Academy of Sciences, Leningrad, who have generously provided preserved material. Shell material has been borrowed from the British Museum (N. H.) through Mr. J. F. Peake. I wish to express my sincere gratitude to them. I am also indebted to Mrs. H. Revay, who has skilfully drawn my figures in Indian ink.

Acroloxus troscheli (Dybowski 1875).

Description. The cicumference of the shell (Fig. 1) is roundish elliptical, slightly blunter anteriorly than posteriorly. The apex is located almost medially and well behind the middle of the shell. The rather high shell (Fig. 2) slopes steeply from the apex to the margin posteriorly. The anterior slope is more gradual and slightly convex. Below the apical region there is no radial sculpture, only a somewhat irregular and coarse growth sculpture. The rather blunt apex has a small shallow pit (Fig. 3). Outside this pit there is an extremely fine microsculpture of radial and concentric blunt ridges leaving minute depressions between them. This can be seen only in perfectly intact shells. The shell material is normally comparatively thick. The periostracum is very pale yellowish. The material available to the author does not allow any conclusion about the variability of the species. In full-grown specimens the shell length reaches 7-8, the width 5-6, and the height 4-5 mm.

In the material examined the mantle is almost black inside the unpigmented mantle collar and outside the shell adductors (Fig. 4). Inside the adductors the pigmentation is less dense and somewhat uneven. A pale grayish colour occurs on the head and sparcely on the sides of the foot.

The pseudobranch is reduced to a papilla penetrated by the rectum. The mantle cavity is completely reduced. The two anterior shell adductors are comparatively small. The posterior adductor is not restricted to the right side but is thin, arch-shaped and almost bilaterally symmetrical.

In the radula (Fig. 29) the central is assymetrical with one small cusp besides the dominating main cusp. The laterals, 12-17 in number on either side, are bicuspid. The innermost marginal is unicuspid, the remaining 8-10 marginals have no cusp at all. In an earlier paper (HUBENDICK 1962) I figured half a radula row of this species. This looks rather different from the figure reproduced here (Fig. 29). There is apparently a certain intraspecific variation in the radula of *A. troscheli.* This conclusion is supported by the drawing presented by DYBOWSKI (1884). However, the aberrant look of the radula figured by me 1962 is partly due to displacement of the teeth and to wear of the cusps.

The male copulatory organ has a comparatively short, thick-walled preputium with a narrow lumen, and a long constricted neck between the preputium and the penis sheath (Fig. 36). The penis is comparatively short and has a terminal pore. The lumen of the penis sheath continues into that of a long glandular flagellum.

Nomenclature. The species has been presented under the following names:

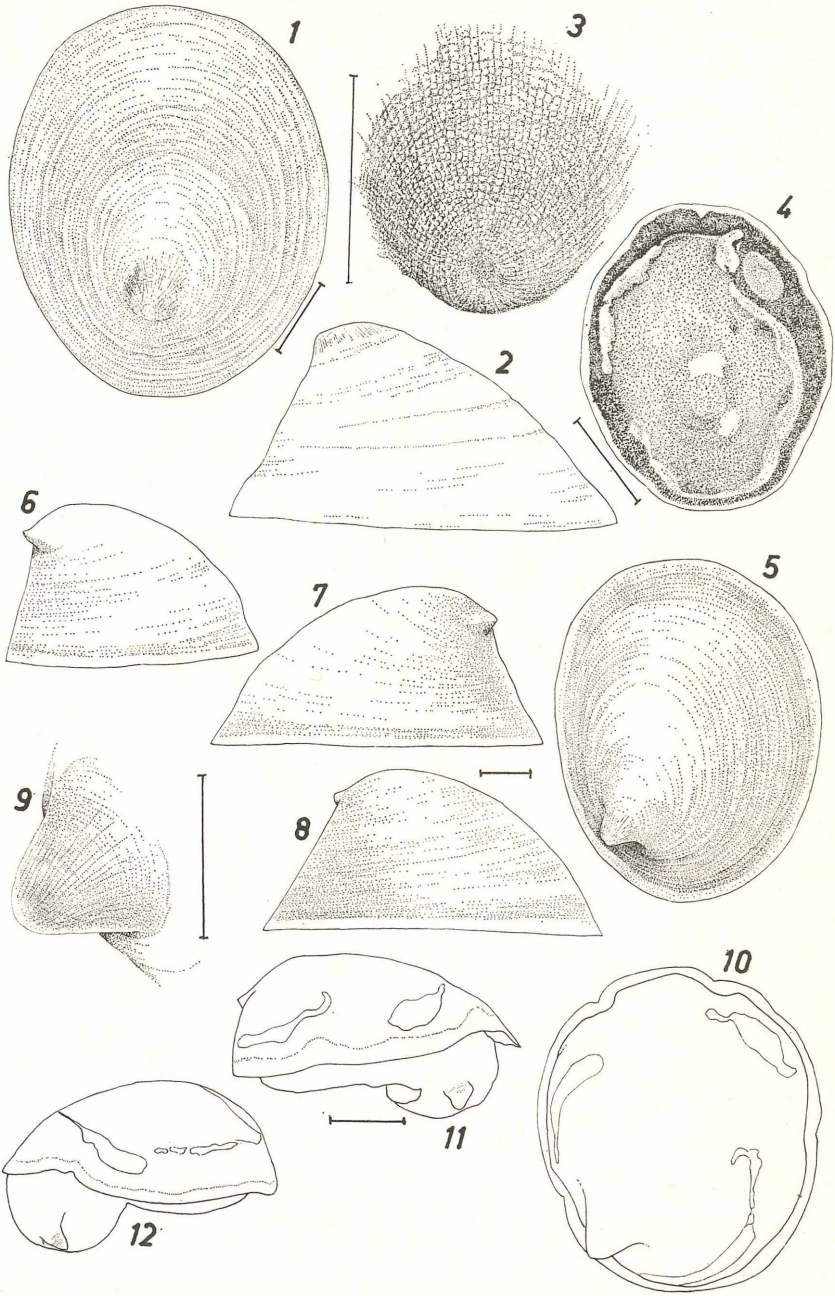
1875 *Ancylus troscheli* DYBOWSKI, Mém. Acad. imp. Sci. St.-Pétersbourg, (7) 22 (8): 64.
1884 *Ancylus Renardii* DYBOWSKI, Bull. Soc. imp. Nat. Moscou, 60: 157.
1909 *Ancylus (Pseudancylastrum) troscheli* DYB., LINDHOLM, in Wiss. Ergebn. zool. Exped. Baikal-See, 4: 28.
—— *Pseudancylastrum troscheli* DYB. in litt., e. g. KOŽOV 1936 and SHADIN 1952.

Discussion. *Acroloxus troscheli* is well distinguished from the other *Acroloxus* species by its almost bilaterally symmetrical shell. The from described by DYBOWSKI (1884) as *Ancylus renardii* was, according to him, conchologically distinguished from *A. troscheli* merely by a blunter apex in a median position and with a small, shallow pit. However, such an apex characterizes also *Acroloxus troscheli.* DYBOWSKI pointed out radular differences between the forms as well; slightly sharper cusps of the first and second laterals and slightly less elongate and more squarish marginals. These differences may be due merely to different degree of wear or to a slight difference in the position of the radula and teeth in the mounts. They can hardly be regarded as significant. KOŽOV (1936) and ZHADIN (1952) have also evaluated *renardi* as conspecific with *troscheli.*

Acroloxus troscheli is known only from Lake Baikal, where it lives on stones and sandy bottoms at a depth of 1·5-40 meters (ZHADIN 1952). It is probably the most common *Acroloxus* species in the lake.

▶

Figs. 1-4. *Acroloxus troscheli* (DYBOWSKI). In Fig. 3 the apical region only is shown. Fig. 4 shows a dorsal view of the animal without shell. — Figs. 5-12. *A. sibiricus* (GERSTFELDT) from Lake Baikal. In Fig. 6 seen from behind, in 7 from the left and in 8 from the right. Figs. 10-12 shows the animal without the shell from above, the right and the left respectively. — When not otherwise stated the scale corresponds to one mm in all figures.


1
3
4
2
6
7
5
9
8
10
11
12

Acroloxus sibiricus (GERSTFELDT 1859).

Description. The circumference of the shell (Figs. 5 and 13) is elliptical. The anterior end is blunter than the posterior end. The apex is located at the left side and well behind the middle of the shell. The rather high shell slops steeply posteriorly and laterally (Figs. 6-8, 14). The top of the shell continues evenly in the less steeply sloping anterior side of the shell. The apex, which may reach beyond the vertical projection of the shell margin but mostly lies inside this, is bluntly pointed and dorsally flattened (Fig. 9). Thist last-mentioned characteristic means that the apex shows a slight dorsal concavity at its base. The whole apical region has a fine radial sculpture, which is often hidden by overgrowth. The groves between the tiny ridges contain series of shallow, indistinctly delimited pits. This structure is reveiled only under high power. The radial sculpture disappeares gradually below the apical region. The rest of the shell does hardly show any sculpture at all. The periostracum extends beyond the calcified part of the shell. Its colour is pale yellowish brown. The measurements of an ordinarily sized shell are: length 6·5, width 5·1, and height 3·4 mm. ZHADIN (1952) gives 6-8, 4-7, and 4-5 mm respectively.

The mantle, inside the mantle collar, is densely and fairly evenly dark, almost black (Fig. 16). The head-foot complex is pale gray dorsally and on its sides. The pseudobranch is shaped as but a small papilla transversed by the rectum. The papilla forms a ventral tip on a part of the visceral sac which hangs down betweeen the foot and the mantle collar on the right side (Fig. 15). The mantle cavity is completely reduced. The anterior shell adductors are rather extended in a posterial direction. The posterior adductor consists of several disconnected parts which together form a largely horseshoe-shaped arch (Figs. 10-12).

In the radula (Fig. 30) the central is bicuspid but in the examined material the cusps are small and of different size. The three first laterals are bicuspid, the fourth unicuspid. The marginals, about nine in number, lack cusps completely, except the innermost marginal. DYBOWSKI's (1884) drawing of this radula seems to depict it from an older specimen with a worn radula.

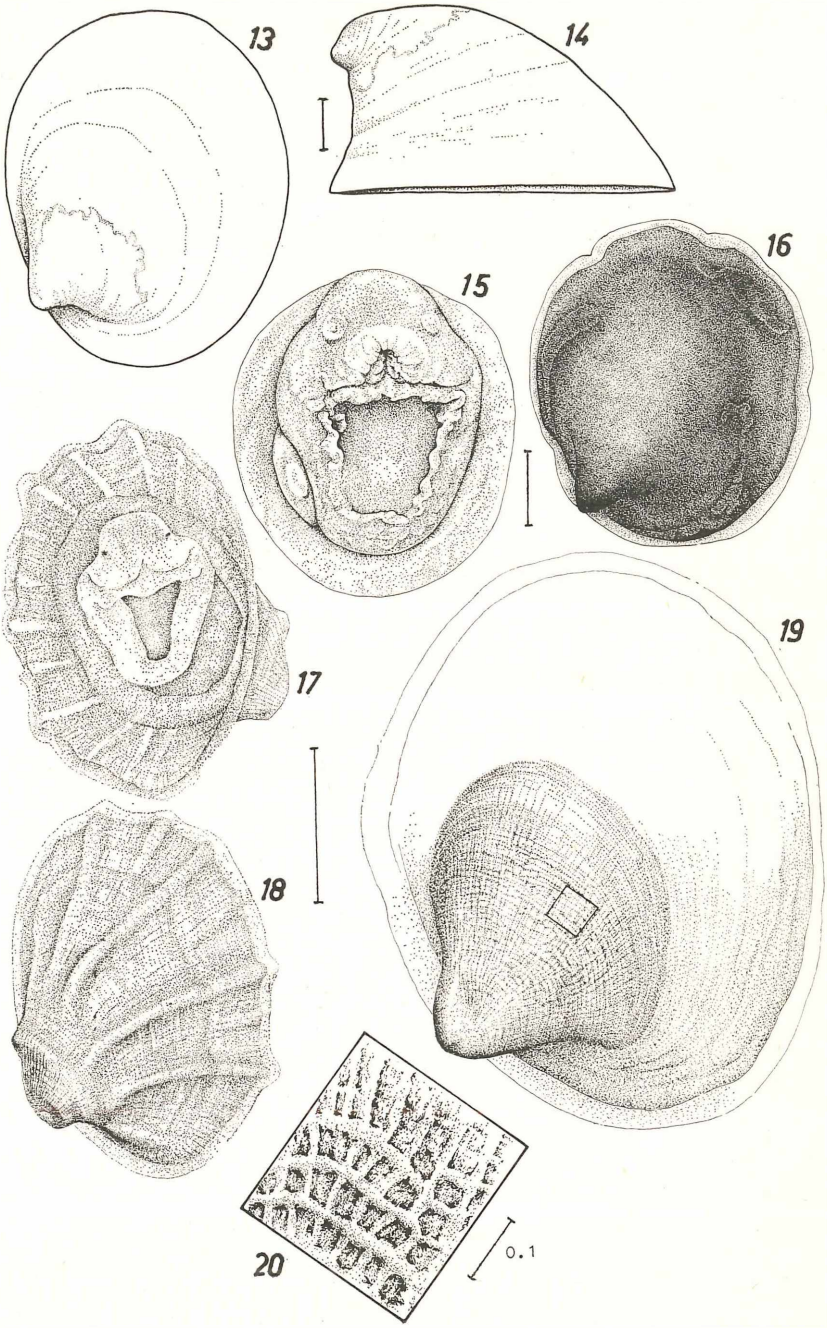
The male copulatory organ (Fig. 37) has, relatively, a still smaller preputium than *A. troscheli*. The penis pore is lateral and the terminal portion of the penis is irregular in shape. The lumen of the penis sheath continues into a glandular flagellum.

Nomenclature. The species has been presented under the following names:

1859 *Ancylus sibiricus* GERSTFELDT, Mém. Sav. étrang., 9: 326 (p. 23 in reprint).
1882 *Ancylus Dybowskii* CLESSIN, in MARTINI & CHEMNITZ: Syst. Conch.-Cab., 1 (6): 38.

►

Figs. 13-16. *Acroloxus sibiricus* from the river Angara near Irkutsk. Figs. 15 and 16 shows the animal without the shell from below and above respectively. — Figs. 17-20. *A. boettgerianus* (LINDHOLM) from Cape Ireksokon, Lake Baikal. Ventral, dorsal and dorsal view respectively. In Fig. 20 the framed area in Fig. 19 is shown under higher magnification.


13
14
15
16
17
18
19
20
0.1

1909 *Ancylus (Pseudancylastrum) sibiricus* (GERSTF.), — LINDHOLM, in Wiss. Ergebn. zool. Exped. Baikal-See, 4: 27.
1909 *Ancylus (Pseudancylastrum) ? dybowskii* CLESS., — LINDHOLM, in Wiss. Ergebn. zool. Exped. Baikal-See, 4: 28.
—— *Pseudancylastrum sibiricum* (GERSTFELDT) in litt., e. g. KOŽOV 1936 and ZHADIN 1952.

Discussion. *Acroloxus sibiricus* is clearly distinguished from the other Baikal species by its left-hand position of its apex in combination with its size. When CLESSIN described *Ancylus dybowskii* he put some effort in explaining that his new form was distinct from *A. troscheli.* He did not, however, give reasons for its being distinct from the much more similar *A. sibiricus.* In the description of *A. dybowski* CLESSIN did not present any characteristics which do not fit *A. sibiricus.* As CLESSIN's types were destroyed during the second world war the identity of *A. dybowski* cannot he checked.

A. sibiricus is known from Lake Baikal and the upper part of the river Angara which drains the lake. It is reported from depths between 2 and 20 meters. A single specimen in the British Museum (N. H.) il labelled to be from Amur. The origin has to be considered doubtful untill confirmed by further findings.

Acroloxus boettgerianus (LINDHOLM 1909).

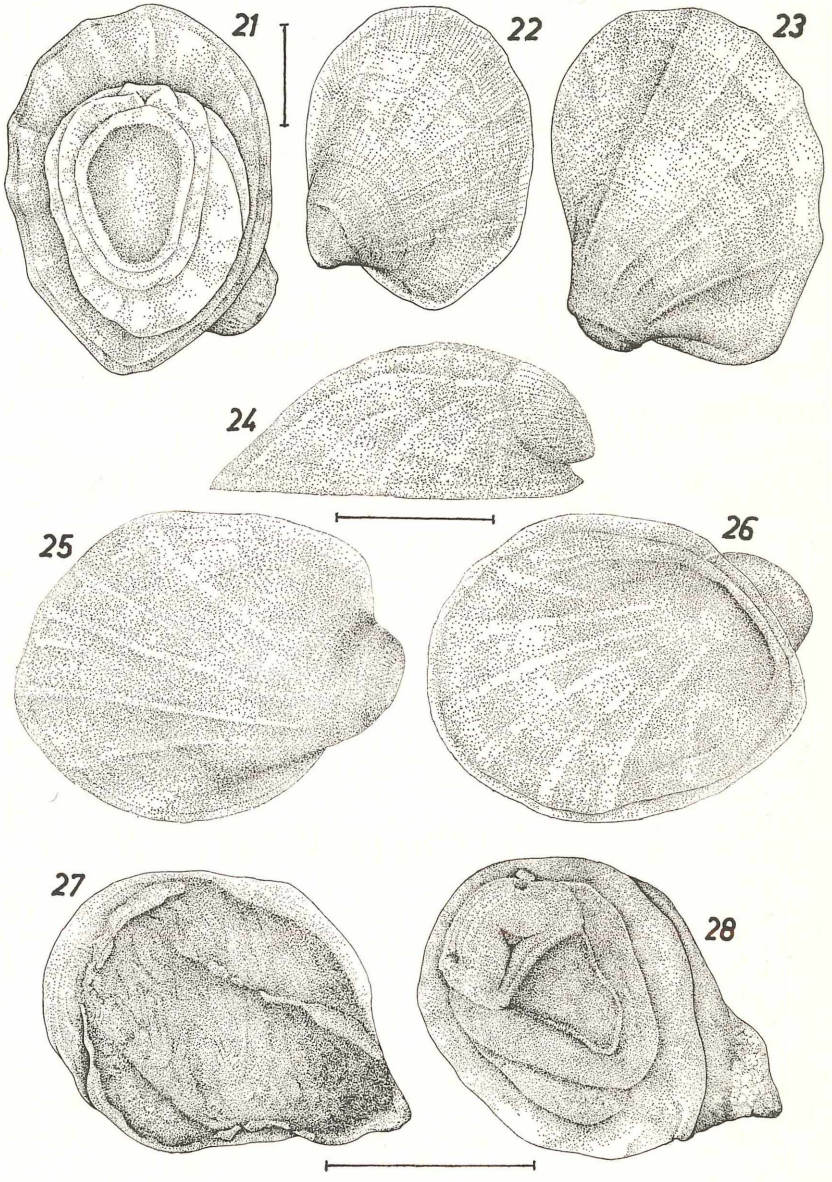
Description. The cicumference of the shell is slightly elongate (Figs. 17-19, 21-23). The anterior end is blunt, the posterior end bluntly pointed. The shell margin may be even or slightly undulating with projections corresponding to the radial ribs of the shell surface. The apex is located to the left, often projecting beyond the projection of the left shell margin. The apex reaches posteriorly to less than one fifth of the shell length from the posterior shell margin. The apical region is curved downwards and the highest part of the shell is normally to the right of and anterior to the apex. The left side of the shell is pronounced concave posteriorly, the right side is convex. Anteriorly the shell forms an almost straight slope. Beyond the apical region the shell often has more or less distinct radial ribs, up to about twelve in number. The ribs vary considerably in strength, from non-existence to very well pronounced. Minute radie are sometimes visible between the ribs. Traces of a concentric growth sculpture may sometimes occur. The apex has a dense but minute radial striation (Figs. 17-18). In some shells there is also a still finer concentric striation. Both together form a kind of lattice pattern in some specimens (Figs. 19-20). The very blunt tip of the apical region is sometimes set off from the rest of the shell by a circular impression (Figs. 17-18, 22-23). Dorsally the apical region has often a slight concavity. The thin periostracum is almost colourless and transparent. It projects well beyond the calcareous layer of the shell. The shell measures in length 3·9, in width 3·1 and in height 1·4 mm. Corresponding measure-

▶

Figs. 21-23. *A. boettgerianus* from Lake Baikal. — Figs. 24-28. *A. kobelti* (DYBOWSKI) from Lake Baikal. Figs. 27 and 28 show the animal without the shell seen from above and below respectively.

ments of other specimens are 4·3, 3·2 and 2·0, and 2·9, 2·6 and 1·8 (LINDHOLM 1909). ZHADIN (1952) gives 2·0-4·3, 1·0-3·2 and 0·8-2·0 mm respectively.

The mantle is gray or dark gray inside the mantle collar. The head-foot complex as well as the ventral side of the mantle collar are gray or very pale grayish.



The pseudobranch is probably still smaller than in the other species. It has not been possible to examine to what extent the mantle cavity is reduced.

The radula (Fig. 31) is slender with only 19 longitudinal rows in the examined specimen. The central has three very small cuspes. The four laterals on either side are bicuspid, the fourth one with two minute cusps. The squarish marginals have no cusps at all.

The available material of this species has not sufficied for examination of the male copulatory organ.

Nomenclature. The species has been presented under the following names:

1909 *Ancylus (Pseudancylastrum) boettgerianus* LINDHOLM, Wiss. Ergebn. zool. Exp. Baikal-See, 4: 28.

—— *Pseudancylastrum kobelti* (DYBOWSKI) in litt., e. g. DYBOWSKI 1912, KOŽOV 1936 and ZHADIN 1952.

Discussion. This species is well distinguished from the other Baikal species by its extremely left-handed apex, its small size and, normally, its radially ribbed shell. The species has been found only in Lake Baikal in shallow water.

Acroloxus kobelti (DYBOWSKI 1886).

Description. The circumference of the shell (Figs. 25-26) is irregularly elliptical and broadest just anterior to the middle of the shell. The anterior end is more evenly rounded than the posterior end, which is slightly angular. The apex is located at the posterior end and slightly to the left of the median line. It may project beyond the vertical projection of the posterior shell margin. The apical region is curved downwards and its tip is pointed but not sharp (Fig. 24). The highest point of the shell is slightly behind its middle. The slopes are gentle anteriorly and on the right side, more abrupt on the left and behind, even concave below the apical region. There are 8-12, rather weak, radial ribs from the apical region towards the periphery of the shell. On the apical region there is a very faint sculpture of minute radial striae. The colour of the shell is pale yellowish brown. The measurements of one specimen are: length 2·5, width 2·0 and height 1·0 mm.

The mantle is gray inside the mantle collar. The head-foot complex as well as the ventral side of the mantle collar are gray or pale grayish (Figs. 27-28).

The pseudobranch seems to be still smaller than in *A. troscheli* and *sibiricus*. It has not been possible to examine to what extent the mantle cavity is reduced. Judging from the arrangement of the shell adductors (Fig. 27) it seems probable that it is almost completely reduced. The left anterior and the posterior shell adductors form together an almost complete, but in several places interrupted ring. The right anterior adductor fills in most of the main gap. (Due to the very scant material available this description has been based practically on one specimen only, apart from on DYBOWSKI's original description.)

DYBOWSKI mentioned that the small size of the radula made observations difficult. According to his observations there are nine laterals and seven marginals on either side. He has indicated only one cusp on the central and two on the laterals. The marginals are more or less rectangular and the two innermost ones have three cusps, which are slender and sharp.

Nomenclature. This species was originally described as *Ancylus kobelti* DYBOWSKI 1886 in SB. naturf. Ges. Univ. Dorpat, *7*: 313. What has subsequently been called *Ancylus kobelti* or *Pseudancylastrum kobelti* has probably been identical with *Acroloxus boettgerianus.*

Discussion. *A. kobelti* is of the same order of size as *A. boettgerianus* but is well distinguished from this by the more posterior position of its apex.

Despite the posteriorly located apex the general shape of the shell indicates a dextrorse torsion. The arrangement of the shell adductor muscles and the visceral mass clearly demonstrate that the species belongs to *Acroloxus* and is not an Ancylid.

DYBOWSKI (1886) reported the species from the river Angara, which drains Lake Baikal. In the collection of the zoological museum of Leningrad there is a small sample from Lake Baikal itself. These are the only safe records of *A. kobelti.*

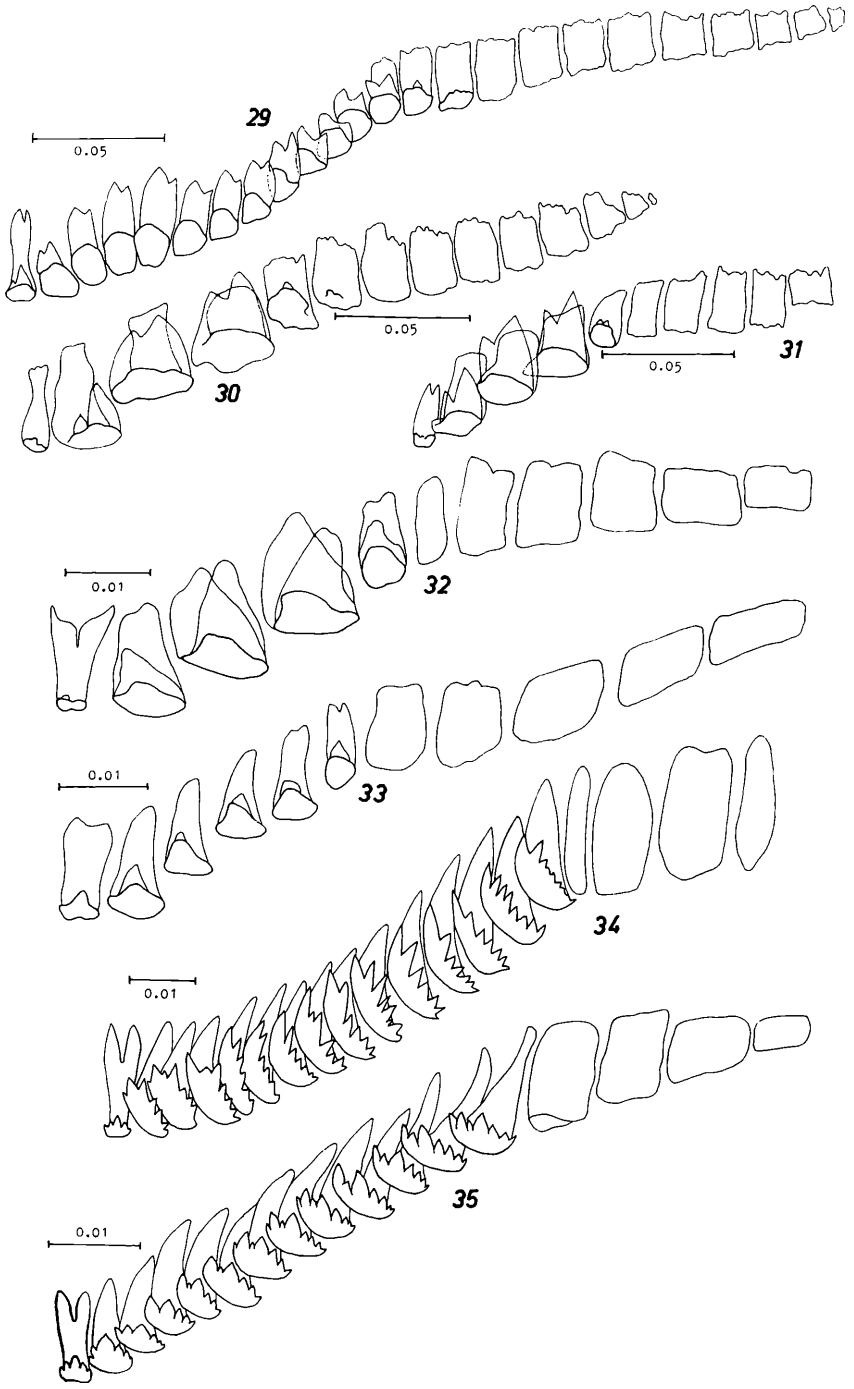
Acroloxus lacustris (LINNÉ 1758).

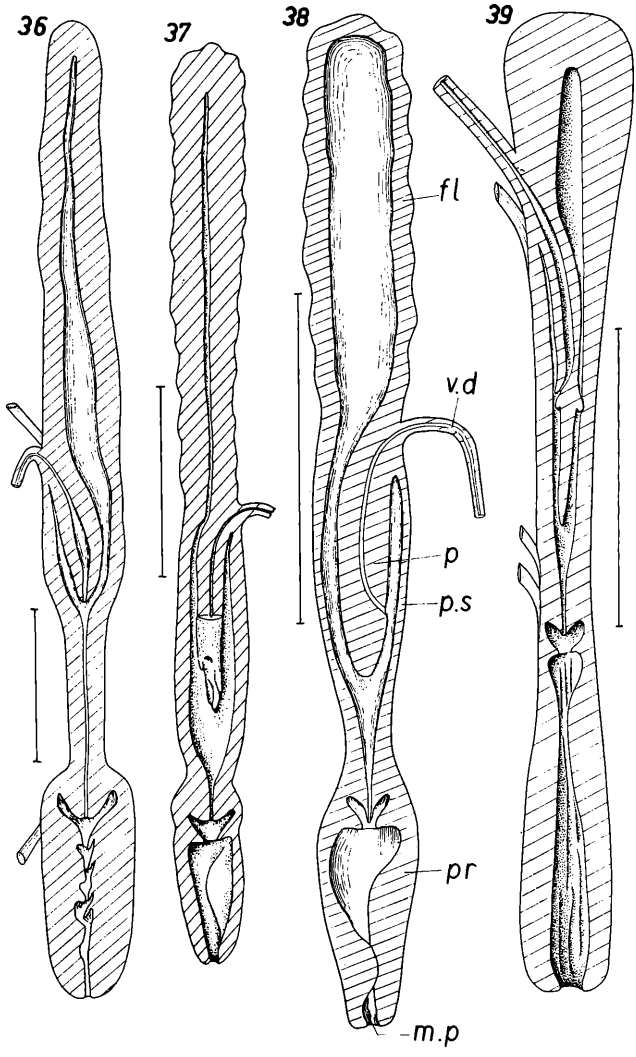
This species was reported from the Čivyrkuisk Bay of Lake Baikal by Kožov (1936), where only one specimen was found 1932. No more specimen has been reported from the Baikal area since then. Kožov described what he called a new variety, *baicalensis,* on the basis of this single specimen. The specimen might as likely have represented a bird-dispersed individual. It is hardly possible to state that *A. lacustris* is an established species in the area out from this single observation.

Phylogenetic status of the Baikal *Acroloxus* species.

The *Acroloxus* species of the world can be devided up into three groups. The first comprises the genotype *A. lacustris* (LINNÉ) and *A. coloradensis* (HENDERSON), a palearctic and a nearctic species respectively, making the distribution of the group holarctic. The second group comprises the species of Lake Ochrid and, possibly, the cave species *A. tetensi* (KUŠČER), all from Jugoslavia. The third group comprises the Lake Baikal species. The last group has been given the name *Pseudancylastrum* and has obviously been considered a taxonomically distinct unit. For a critical revaluation of this it is necessary to distinguish primitive and advanced characteristics within *Acroloxus.*

Due to its wide geographical range it is a priori reasonable to assume that *A. lacustris* and *A. coloradensis* represent a more original type than the Ochrid and Baikal forms, which have obviously evolved through local speciation (cf. HUBENDICK 1960). However, the radula of the Ochrid and Baikal *Acroloxus* is simpler and more similar to the general radula type of Planorbidae and Ancylidae and thus could seem to be primitive. We must remember, though, that *Acroloxus* is not closely related to the Planorbidae and Ancylidae but to Latiidae (HUBENDICK 1962, 1965). In *Latia* the details of the radula are peculiar but its general type can well have its origin in common with that of *Acroloxus lacustris* (Fig. 34) or coloradensis (Fig. 35). From this point of view the simple structures of the radula in the Ochrid and Baikal species can be assumed to be secondary. The rudimentary mantle cavity in these species in comparison with


29
0.05
30
0.05
31
0.05
32
0.01
33
0.01
34
0.01
35
0.01



Figs. 36-39. Longitudinally sectioned male copulatory organ of: Fig. 36, *A. troscheli.* — Fig. 37, *A. sibiricus.* — Fig. 38, *A. improvisus* POLINSKI from Lake Ochrid, Jugoslavia. — Fig. 39, *A. lacustris* from Sweden. — *fl* = flagellum; *mp* = male genital pore; *p* = penis; *pr* = preputium; *ps* = penis sheath.

◀

Figs. 29-35. Half a radula row from: Fig. 29, *Acroloxus troscheli.* — Fig. 30, *A. sibiricus.* — Fig. 31, *A. boettgerianus.* — Fig. 32, *A. improvisus* POLINSKI from Lake Ochrid, Jugoslavia. — Fig. 33, *A. macedonicus* HADŽIŠČE from Lake Ochrid, Jugoslavia. — Fig. 34, *A. lacustris* (LINNÉ) from Sweden. — Fig. 35, *A. coloradensis* (HENDERSON) from Montana, USA.

in *A. lacustris* and *coloradensis* must necessarily be secondary. *Latia* has a well-developed mantle cavity.

In the male copulatory organ the only important differences between the *Acroloxus* species (Figs 36-39) relate to the position of the penis pore and to the degree of development of the flagellum. It is hardly possible to decide what is primitive or advanced in this connection. The fact that both a terminal and a lateral penis pore occur among species of the Baikal fauna indicates that an evolution in either direction has probably occurred independently within this fauna and that this fauna is secondary in relation to *A. lacustris* or their common ancestors.

It is true that the Baikal species on the one hand and the Ochrid species on the other show certain similarities in the radula. In both groups the teeth have been simplified in a similar way alhough this process has resulted in mostly bicuspid laterals in the Baikal species and unicusped laterals in the Ochrid species. The evolution has obviously run parallelly in the two groups. A tendency to parallel evolution in the two groups can be observed also in the shell form when *A. macedonicus* HADŽIŠČE and *A. kobelti* are compared.

To summarize, the most probable conclusion to be drawn from the structural and distributional facts is that the Baikal species have evolved within the Baikal area as the Ochrid species have evolved within the Ochrid area. Both groups originate from an ancentral type of *Acroloxus* with wide distribution. *A. lacustris* and *A. coloradensis* have probably retained more structural characteristics of this ancestral form than have the Baikal and Ochrid *Acroloxus* species.

As a further conclusion it can be stated that there is nothing wrong, as a principle, to distinguish the Baikal group of species as a certain subgenus. Then the Ochrid group should be distinguished as another subgenus and *lacustris* and *coloradensis* represent *Acroloxus* s. str. However, I cannot find it practical to add another unneccessary name to the malacological nomenclature.

Summary

The Baikal fresh-water limpets all belong to the genus *Acroloxus*. They have been reviewed in some detail. Comparison with other *Acroloxus* species makes it reasonable to assume that the Baikal species have evolved within the Baikal basin parallelly with the evolution of the Ochrid species in the Ochrid basin. *A. lacustris* (LINNÉ) and *A. coloradensis* (HENDERSON) probably represent a morphological type, which is closely related to the ancestral form from which the Baikal and Ochrid species have evolved.

References

CLESSIN, S. (1882): Die Familie der Ancylinen. In MARTINI & CHEMNITZ, Syst. Conc.-Cab., 1 (6).

DYBOWSKI, W. (1875): Die Gastropoden-Fauna des Baikal-Sees, anatomisch und systematisch bearbeitet. — Mém. Acad. imp. Sci. St. Pétersbourg, (7) 22 (8): 11-73.

— — — (1884): Ein Beitrag zur Kenntnis der im Baikal-See lebenden *Ancylus*-Arten. — Bull. Soc. imp. Nat. Moscou, 60: 145-159.

— — — (1886): Beschreibung einer neuen sibirischen *Ancylus*-Art. — SB. naturf.-Ges. Univ. Dorpat, 7: 312-315.
— — — (1912): Mollusken aus der Uferregion des Baikalsees. — Ann. Mus. Zool. Acad. imp. Sci. St. Petersbourg, **17** (1): 123-142.

GERSTFELDT, G. (1859): Über Land- und Süßwasser-Mollusken Sibiriens und des Amur-Gebietes. St. Petersburg.

HUBENDICK, B. (1960): The Ancylidae of Lake Ochrid and their bearing on intralacustrine speciation. — Proc. zool. Soc. London, **133** (4): 497-529.
— — — (1962): Studies on *Acroloxus*. — Göteborgs K. Vetenskaps- & Vitterhets-Samh. Handl., **9** (2): 1-68. (Medd. Göteborgs Mus. Zool. Avd., 133.)
— — — (1965): Patelliform shape and classification. — Proc. First Europ. Malac. Congr., : 61-67.
— — — (In press): A note on *Acroloxus coloradensis* (HENDERSON). — J. de Conch.

KOŽOV, M. M. (1936): Mollusques du Lac Bajkal. (In Russian).

LINDHOLM, W. A. (1909): Die Mollusken des Baikal-Sees systematisch und zoogeographisch bearbeitet. — Wiss. Ergebn. zool. Exp. Baikal-See, **4**. Kiew und Berlin.

ZHADIN, V. I. (1952): Molluscs of fresh and brackish waters of the U.S.S.R. (In Russian. English edition 1965).