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by Arthur H. Clarke

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Résumé

On a découvert récemment, au Centre-Nord du Québec et au Nord-Est de l'Ontario, une patelle (*Acroloxus coloradensis*) dont on n'avait jusqu'ici constaté la présence que dans quatre lacs des montagnes Rocheuses. On en rencontre des populations éparses sur des roches et sur des coquilles vides d'Anodontes, dans les eaux peu profondes qui bordent la rive de certains lacs mésotrophes. Le présent ouvrage donne quelques détails d'écologie, ainsi que des observations sur la morphologie des adultes et de l'enveloppe des oeufs. On y trouvera enfin des remarques sur la zoogéographie de ce mollusque et sur une présumée relation entre les coquilles de moules et les patelles d'eau douce.

Summary

Acroloxus coloradensis, a limpet previously known only from four lakes in the Rocky Mountains, has been discovered in north-central Quebec and north-eastern Ontario. Sparse populations occur on cobbles and on empty *Anodonta* shells in shallow near-shore habitats in mesotrophic lakes. Observations on ecology and on the morphology of egg capsules and adults are presented. Also included are remarks on zoogeography and on a presumed relationship of mussel shells and freshwater limpets.

Introduction

The Superfamily Acroloxacea (freshwater limpets) contains one Family (Acroloxidae), one Genus (*Acroloxus*), and seven living species, six in Eurasia and one in North America. The group exhibits many unique features of cytology, reproduction, and anatomy, especially the dextral organization of the organs, which sets them apart from other higher Basommatophora, i.e., the Lymnacea and Ancylacea (*see* Hubendick 1962; Bondesen 1950; Burch 1962). Shell characters are also unique, particularly the prominent, extended, and (in some species) acutely pointed apex, located posteriorly and on the left. In Ancylidae, the major family of freshwater limpets, the apex is also principally posterior but in the midline or on the right.

Acroloxidae are recorded from deposits as old as Upper Cretaceous in Europe (subgenus *Pseudancylastrum* Lindholm) and Paleocene in North America (*Palaeancylus* Yen). The Recent Eurasian species are — *Acroloxus lacustris* (L.), found throughout Europe and northern Asia; *A. improvisus* (Polinski) and *A. macedonicus* (Hadzisce), endemic in Lake Ochrid, Yugoslavia; and *A.* (*Pseudancylastrum*) *kobelti* (Dybowski), A. (P.) *sibiricum* (Gerstfeldt, and A. (P.) *troscheli* (Dybowski), endemic in Lake Baikal, U.S.S.R.

The single North American Recent species, *Acroloxus coloradensis* (Henderson), is apparently rare and has been recorded alive from only four lakes, all high in the Rocky Mountains. These are — Eldora Lake, Boulder County, Colorado, collected by Junius Henderson in 1925; Lake Iris and "lake north of Geikie Station," both in the Miette Valley, Jasper National Park, Alberta, collected by Alan Mozley in 1925 and 1926 (*see* Basch 1963); and Lost Lake, Glacier National Park, Montana, collected by R. H. Russell and R. B. Brunson in 1966 (*see* Russell and Brunson 1967) and by R. H. Russell in 1968. *A. coloradensis* is also known from Pleistocene deposits of Nebraskan or Aftonian age in Brown County, Nebraska and Kingman County, Kansas (Taylor 1960: 61).

While studying freshwater molluscs collected from 1959 to 1967 in connection with another work I was much surprised to find *Acroloxus coloradensis* among an unsorted collection of freshwater limpets. Two preserved specimens with soft parts and one empty shell were present. According to field notes these had been collected in 1960 from a lake in north-central Quebec and from a pond in northeastern Ontario, respectively. These locations are about 1600 and 1340 mi. distant from Eldora Lake, Colorado, the closest and most easterly Recent locality previously known.

As soon as weather would permit, in June 1968, another trip was made to north-central Quebec with the hope of confirming the presence of *A. coloradensis* there. The effort was a success. Living *Acroloxus* were found at two additional localities, ecological observations were made, and living specimens were brought back to the laboratory for observation.

Acknowledgments

My assistant, Mrs. M. F. I. Smith, helped greatly in our efforts to culture *A. coloradensis* in the laboratory and assisted in several other ways. Comparative specimens of *A. coloradensis* from Alberta and Montana were generously made available by Dr. R. Tucker Abbott, Philadelphia Academy of Natural Sciences, and by Richard H. Russell, University of Arizona. The algae were identified by Dr. R. K. Lee, Curator of Algology; the Hirudinea by Mrs. Fahmida Rafi, Assistant in Invertebrate Zoology (both of the National Museum of Natural Sciences); and the Trichoptera by Dr. F. Schmidt, Entomology Research Institute, Canada Department of Agriculture. Mr. Benjamin Korda, Department of National Health and Welfare, took the excellent photographs of *Acroloxus coloradensis* used in Figure 1. Field and laboratory work by the author were supported by the National Museum of Natural Sciences, National Museums of Canada.

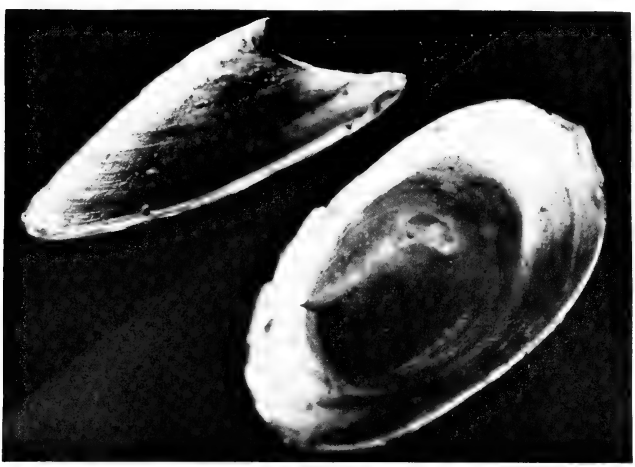

FIGURE 1—Two views of a preserved specimen (NMC 22323) of *Acroloxus coloradensis* from Lac Gabrielle, Quebec (station 115). Length 4.7 mm.

Collecting Sites

The eastern Canadian localities that yielded *Acroloxus* are as follows. Precise locations for the Quebec sites are taken from National Topographic Series Map 32G, Edition 2ASE, Series A501 (scale 1:250,000) and for the Ontario site from Map 42A/8 west, Edition 1ASE (scale 1:50,000), both published by the Department of Energy, Mines and Resources, Surveys and Mapping Branch, Ottawa, Canada.

Station 115. Lac Gabrielle, the northern bay of the lake near provincial highway 58, about 10 mi. S. of Chibougamau, Quebec. Precise location: lat. 49°47′38″N, long. 74°25′32″W, elevation 1,246 ft. Two living specimens from rocks, July 17, 1960.

Station 177. Unnamed pond, 6 mi. S. of Matheson, Ontario. Precise location: lat. 48°27′30″N, long. 80°29′10″W, elevation about 1,125 ft. One empty shell among debris, August 29, 1960.

Station 946. Lac Caché, south half of lake, at rocky point ¼ mi. N of Fecteau Air Base, within sight of highway 58 and about 8 mi. (by road) S. of Chibougamau, Quebec. Precise location: lat. 49°49′42″N, long. 74°25′-16″W, elevation about 1,260 ft. Three living specimens from a water depth of about 12 in. and 4 to 6 ft. from shore, two from empty *Anodonta* shells, and one from a 4-inch rock, June 17, 1968.

Station 947. Lac Doré, north half of lake, about 4 mi. due SE of Chibougamau. Precise location: lat. 49°52′50″N, long. 73°16′30″W, elevation 1,246 ft. One living specimen from a 6-inch rock in about 1½ ft. of water and about 3 ft. from shore, June 18, 1968.

Habitats

Station 115 was not revisited in 1968 because it had been altered during road improvement. Other localities in the vicinity (stations 946, 947, and several found to be unproductive) were therefore searched. Station 177 and its vicinity are yet to be revisited.

Station 946 is at the edge of a small, rounded, exposed rocky point within an open bay in Lac Caché — an irregular, *C*-shaped, mesotrophic lake of about 2 sq. mi. in area. The habitat is shown in Figures 2 and 3. The

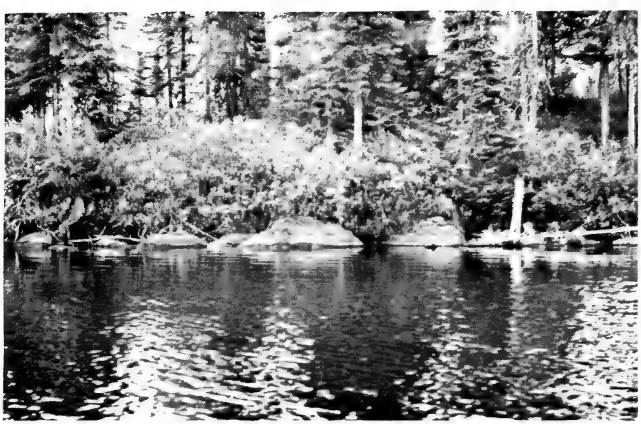

FIGURE 2—A general view of station 946 at Lac Caché, Quebec, photographed on June 17, 1968. The dominant terrestrial plants shown are Labrador Tea (*Ledum groenlandicum*) along the shore and Black Spruce (*Picea mariana*) with some Eastern White Cedar (*Thuja occidentalis*) on higher ground.

three *Acroloxus* specimens represent the total number that could be found by examining all movable submersed rocks (about 200) and all empty *Anodonta* shells (about 150 valves) seen in the area in depths of from about 6 in. to 2½ ft. and at distances of about one to 10 ft. from shore. The submersed rock and shell surface areas examined are estimated to total about 12 sq. metres.

There are no submersed vascular plants at this station. Rocks at the 2-foot depth are coated with algae, however; and this algae (as later observed in the laboratory) is fed upon by *Acroloxus*. This algal community is dominated by the blue-green algae *Tolypothrix*. *Oscillatoria* is also abundant, and some *Calothrix* (both blue-green algae) also occurs along with isolated unicellular green algae (Chlorococcales) and diatomes (Cymbellacea). The mussel shells serve as substrate for small colonies of unicellular blue-green algae (Chroococcacea).

Surface water temperature at noon, June 17, at station 946 was 16°C. Alkalinity and chlorinity were found[1] to be 35 p.p.m. (as $CaCO_3$) and 15 p.p.m. (as NaCl), respectively.

Station 947, an exposed rocky area along the shore of Lac Doré, is ecologically very similar to station 946 at Lac Caché. Lac Doré is large, elongate, and mesotrophic and varies between ½ and 1 mi. in width over its 30-mile length. The shore and shelf at station 947 is composed principally of boulders and cobbles. Submersed vascular plants are absent, and algae coats the rocks in shallow water. This algae is similar in colour and macroscopic appearance to that at station 946. The boulder-cobble shelf is more gently sloping than that at station 946; about 25 ft. from shore the water is only 3 ft. deep. No mussel shells were seen. The surface area of submersed boulders and cobbles examined is estimated to be about 6 sq. metres.

Analysis of water quality at station 947 produced results for alkalinity and chlorinity that were identical to those at station 946.

Stations 115 and 947 are about 10 mi. apart, and station 946 is between them. All are on connected bodies of water that are adjacent to and confluent with Lac Chibougamau, a major lake in the Nottaway River System. Station 177 is approximately 275 mi. WSW of the Lac Chibougamau area and is in the Moose River System. The Nottaway and the Moose river systems are divergent and are separated by the Harricanaw River System, all three of which flow into the southern end of James Bay.

Stations 115 and 177 were sampled for all available mollusc species, and the collections were made from several microhabitats. Stations 946 and 947 were examined specifically for *Acroloxus* and associated organisms occurring in the same microhabitat. A meaningful list of associated molluscan species therefore can only be given for the two latter stations. This is presented in Table I.

[1]A Hach water analysis kit was used, Model 39-AP, manufactured by the Hach Chemical Company, Ames, Iowa.

TABLE 1—Associated Epifaunal Molluscs

Species	Station 946		Station 947	
	Total Specimens	Spec./M²	Total Specimens	Spec./M²
Acroloxus coloradensis (Henderson)	3	0.25	1	0.17
Amnicola limosa (Say)	–	–	1	0.17
Ferrissia parallela (Say)	–	–	2	0.33
Gyraulus deflectus (Say)	11	0.92	1	0.17
Physa gyrina (Say)	1	0.08	2	0.33
Totals	15	1.25	7	1.17

Other associated epifaunal macro-invertebrates were as follows:

Station 946. Trichoptera: *Helicopsyche borealis* Hagen (pupae and larvae) and *Limmephilus submonilifer* Walker (?) (larvae).

Station 947. Hirudinea: *Nephelopsis obscura* Verrill, *Glossiphonia complanata* L., and *G. stagnalis* L. Trichoptera: *Helicopsyche borealis* Hagen (pupae and larvae), *Limnephilus* (sp.?) (larval cases) and *Psilotreta indecisa* Walker (pupae).

FIGURE 3—A closer view of the microhabitat at station 946 (Lac Caché) in which the *Acroloxus coloradensis* were collected. The three large boulders in the centre are each about 24 inches long and are submerged in about 12 inches of water. A few empty *Anodonta* shells are faintly visible in the top centre of the picture.

The Shell

Ancylus coloradensis Henderson, 1939 (now *Acroloxus*) was proposed as a replacement name for *Ancylus hendersoni* Walker, 1925, preoccupied by *Ancylus hendersoni* Walker, 1908. Walker's 1925 description of a specimen from Eldora Lake, Colorado, is as follows:

"Shell oval, slightly wider anteriorly, very much depressed, light horn color; anterior and posterior margins regularly rounded, lateral margins about equally curved, the right somewhat more than the left; anterior, posterior and right lateral slopes straight, left lateral slope slightly incurved; apex very acute, almost spine-like, eccentric, turned towards the left side, situated at about $\frac{2}{3}$ of the length from the posterior margins and at about $\frac{1}{3}$ of the width from the left margin, radially striate, the striae continuing over the surface of the shell from the apex to the margins; surface with fine and regular lines of growth and delicately radially striate.

Length 5, width 3, alt. 1 mm." (Walker 1925: 1).

The specimens collected in eastern Canada match this description very closely. They are also similar to specimens of *A. coloradensis* collected near Geikie Station, Alberta, by Alan Mozley in 1926 (ANSP 152666) and to specimens collected in Lost Lake, Montana, by R. H. Russell in 1968 (NMC 47401). Measurements of the eastern Canadian specimens (in mm) are given in Table II.

TABLE II—Measurements

Length	Width	Height	L/W	L/H	W/H	A-PM/L[1]	A-LM/W[1]
Pond 6 mi. S of Matheson, Ont. (Sta. 177, NMC 22322):							
4.5	3.0	1.0	1.5	4.5	3.0	.27	.37
Lac Gabrielle, 10 mi. S of Chibougamau, Que. (Sta. 115, NMC 22323):							
4.7	2.7	1.2	1.7	3.9	2.2	.31	.28
5.0	2.9	1.1	1.7	4.5	2.6	.34	.28
Lac Caché, 8 mi. S of Chibougamau (Sta. 946, NMC 47402):							
3.3	1.8	0.7	1.8	4.7	2.6	.27	.39
3.2	1.9	0.7	1.7	4.6	2.7	.28	.32
Lac Doré, 4 mi. SE of Chibougamau (Sta. 947, NMC 47403):							
4.6	2.9	1.2	1.6	3.8	2.4	.28	.38

[1]A-PM is the distance from the apex to the posterior extremity measured parallel to the midline of the aperture. A-LM is a similar measurement taken from the apex to the left marginal extremity and perpendicular to A-PM.

The Living Animal

One of the four *Acroloxus* collected on June 17 and 18 was lost, but the other three and two *Ferrissia parallela* from station 947 were carried alive to Ottawa. On June 22 they were installed in two Petri dishes, which were three-quarters filled with water from Lac Doré. All limpets from station 946 were placed in one dish, and those from station 947 in the other. A small algae-covered stone from Lac Caché was also placed in each dish along with a piece of *Anodonta* shell from that locality.

Acroloxus coloradensis was seen to move slowly, about half as rapidly as *Ferrissia parallela*. Both species moved away from strong light, but neither appeared to be predominantly nocturnal. All the limpets ranged freely over the immersed surfaces of the dish, stone, and *Anodonta* shell, the mouth and radula in constant feeding activity. Much time was also spent immobile, often on the stone or the shell.

When in motion *A. coloradensis* does not protrude beyond the edge of its shell. Some of the anatomy is visible through the translucent, horn-coloured shell, i.e., a continuous, prominent blackish band along the mantle edge, close to the shell margin, the orange to brownish-purple visceral mass (there is colour variation between specimens), the dusky head, and the two black eyes. Viewed from beneath, the dark mantle band is seen to bear approximately 100 small, bright blue, elongate processes (apparently papillae) lying across the mantle band and directed toward the mantle edge. The foot and head are of moderate width, flecked with grey on a pale purplish-brown background, and not unlike the foot and head of a *Ferrissia parallela* from Lac Doré. In general the body appears similar to that of *Acroloxus lacustris* as figured by Hubendick (1962, Figure 3).

On the fourteenth day after installation in Petri dishes the large *Acroloxus* from station 947 (Lac Doré) deposited one oval egg capsule on the side of the dish. The egg capsule measured 3.4 x 3.0 mm and contained three elliptical eggs, 1.2, 1.1, and 1.0 mm long. The adult died on the same day. From the fourteenth to nineteenth days the two smaller specimens from station 946 deposited two and three egg capsules respectively, each containing two or three eggs. These adults died on the twenty-seventh day. Some of the embryos in the egg masses grew for a few days, but none completed development.

Although detailed observations of the *A. coloradensis* egg masses were not made, the following rather superficial comments may be of some value. The capsules were lenticular-ovate, from 1.9 to 3.4 mm long, with double transparent walls and pale yellow lumen, and with two or three eggs in each capsule. The eggs, which measured from 0.5 x 0.8 to about 0.6 x 1.2 mm, were ovate and colourless or faintly whitish. The egg capsules and eggs resemble those of *Acroloxus lacustris* figured by Bondesen (1950: 64) in general shape and in that the eggs are loosely packed. They appear to differ in having yellow lumen (not mentioned for *A. lacustris*) and a smaller number

of eggs in each capsule. Surface striae of the capsules, as mentioned for *A. lacustris* by Bondesen, were not observed through the walls of the dishes.

A short statement on the observed behaviour of *Ferrissia parallela* is also appropriate. One of the *F. parallela* from station 947 died on the day of installation in the Petri dish, but the other remained active. Between the seventh and eleventh days after installation, it deposited eight egg capsules on the sides of the dish. It was then transferred to another dish, where it deposited a few additional capsules before it died on the twenty-fifth day. The egg capsules contained from one to three closely packed eggs, about the same size and colour as the *Acroloxus* eggs. The outer capsule membrane in *Ferrissia* was much more closely appressed to the eggs than in *Acroloxus,* and the lumen was white, not yellow. Embryonic development proceeded rapidly, and about five days after ovoposition young *Ferrissia,* each about 1.0 mm long, began to emerge.

The scanty available evidence indicates that under laboratory conditions *Acroloxus coloradensis* shows significantly less activity and lower fecundity than *Ferrissia parallela.* The four presently known eastern localities for *A. coloradensis* are all near the northern edge of the geographical range of *F. parallela,* and the two species were collected together at only one of these localities. Direct competition between the two species may therefore occur only in a minority of localities where *Acroloxus* now lives.

Zoogeography

The Recent distribution of *A. coloradensis* in North America, i.e., with populations in the Rocky Mountains from Colorado to Alberta and in north-central Quebec (and probably in northeastern Ontario), is indicative of a much wider geographical range in previous time. The early Pleistocene records in Kansas and Nebraska support this. The similarities between *A. coloradensis* and *A. lacustris* imply that the two species are closely related. There is no direct evidence available to indicate whether or not *Acroloxus* utilized the Pleistocene Beringian land bridge.

It is quite possible that *A. coloradensis* is even now more widely distributed in North America than the Recent records indicate. As reported by Henderson (*in* Basch 1963: 413), by Russell and Brunson (1967: 33), and in some detail by the present study, it occupies a seemingly inhospitable habitat and one which is not searched thoroughly by most collectors. In the Quebec localities visited, adults that had overwintered also occurred in low densities, i.e., about one individual in 5 sq. metres of substrate. It appears probable that this primitive species may be adapted to survive in specialized habitats where predator pressures are low and competition from more advanced limpets and other molluscs is less intense.

The relationship of empty unionid shells and of algae that concentrate calcium carbonate in providing shell-building material for limpets, especially in soft-water habitats, needs to be investigated. For example, in a thoughtful paper Russell-Hunter *et al.* (1967) have shown that a population of *Ferrissia rivularis* in Black Creek, New York, has a higher concentration of calcium carbonate in its shells than some other populations studied. This seemed anomalous because Black Creek water has the lowest concentration of dissolved calcium carbonate of the seven *F. rivularis* habitats examined. This lack of correlation was presumed to be indicative of physiological races in *F. rivularis*. Black Creek has (or had, in 1957) a dense population of the soft-water but long-lived mussel *Margaritifera margaritifera* (Clarke and Berg 1959: 18), however, and the abundant shells of that species might well have been an important supplementary source of calcium carbonate for the limpets.

Addenda

While this paper was in press, three additional adult specimens of *Acroloxus coloradensis* (two collected alive) were received from Dr. John G. Oughton, Department of Zoology, Ontario Agricultural College, University of Guelph, Guelph, Ontario. These were collected by Dr. Oughton and Mr. D. G. S. Wright on September 1, 1967, from a small pond 1½ miles north of the village of Arkell, Nassagawaya Township, Halton County, Ontario. This find considerably extends the known range of *A. coloradensis*.

Dr. Oughton's field notes state that the pond basin is five to ten acres in area but that encroachment by *Typha* has reduced open water to about 75 x 100 feet. The pond bottom is mud and plant detritus, and the pond is heavily vegetated. Yellow water lily is dominant, and *Riccia, Lemma, Carex,* and *Nympha* were also noted. Other molluscs found during a half-hour search by both men are *Lymnaea stagnalis* (not common); *Helisoma trivolvis* (few); *Lymnaea elodes* (very few); sparse empty and immature shells of *Physa, Planorbula,* and *Gyraulus;* three specimens of *Sphaerium;* and one of *Pisidium*.

I am grateful to Dr. Oughton for permission to include this information, and to Dr. Jorgen Knudsen, Zoological Museum, Copenhagen for generously providing specimens of *Acroloxus lacustris* for comparison.

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