



CYTOTAXONOMIC STUDIES OF FRESHWATER LIMPETS
(GASTROPODA: BASOMMATOPHORA)

I. THE EUROPEAN LAKE LIMPET, *ACROLOXUS LACUSTRIS*

by J. B. Burch²

ABSTRACT

Acroloxus lacustris (Linnaeus) is a freshwater limpet common to Europe, northern Asia and Caucasasia. It has nearly always been assigned to the basommatophoran family Ancyliidae, and hence is generally regarded as one of the most specialized and phylogenetically advanced basommatophorans.

It is shown in this paper that in regard to certain details of cytology, *A. lacustris* should not be considered closely related to other Ancyliidae, but rather placed in a family by itself, the Acroloxiidae, a conclusion corroborated by other authors on morphological grounds. Indeed, the various cytological differences would tend to further separate *Acroloxus* from other Basommatophora. The differences observed consist in the large size of the various cells of spermatogenesis, the greater volume ratio of chromatin to cytoplasm, the relatively large size of the chromosomes and the morphology of the mature sperm, whose heads are long and thread-like, not bullet- or turnip-shaped like those found in other basommatophoran snails. In addition, the chromosome number (n=18), although characteristic of the Basommatophora in general, is different from that found in other freshwater limpets (x or basic haploid number-45 in the Ancyliinae-Ferrissiinae; n=17 in the Laevapecinae).

The mitotic chromosomes of *A. lacustris* are metacentric as characteristic of all Basommatophora; 6 pairs (including the 2 largest and the smallest) are medianly constricted; the other 12 pairs are submedianly or subterminally constricted. This is the first time the karyotype of any Euthyneuran snail has been accurately determined and figured.

The phylogenetic position of the Acroloxiidae may be close to the base of the Basommatophora as suggested by Bondesen and Hubendick, but at the present state of knowledge the evidence which would tend to support such a conclusion can not be found in details of cytology. But, contrary to earlier views reached on purely anatomical grounds, the position of the Ancyliidae, as determined by their chromosome numbers, should also be near the base of the Basommatophora, but not close to the Acroloxiidae because of the other cytological differences.

INTRODUCTION

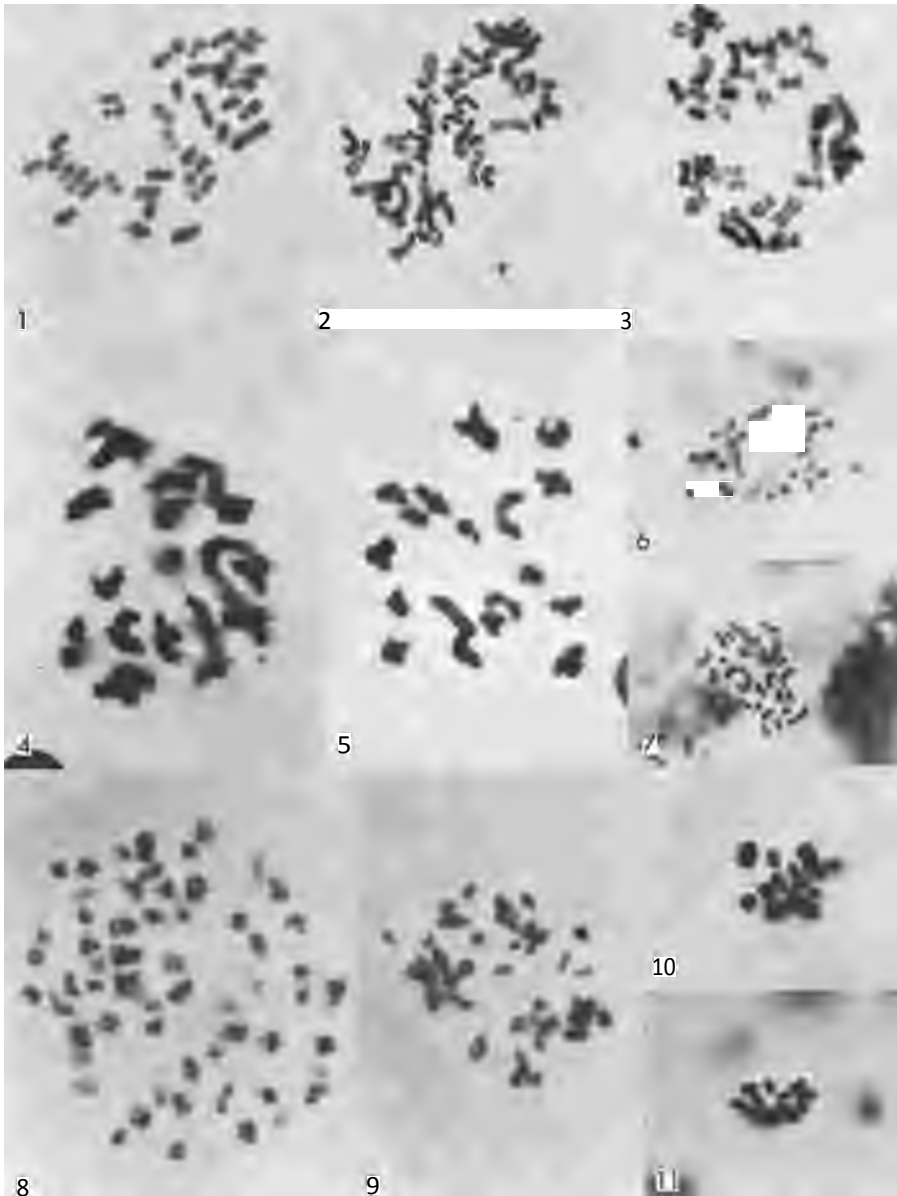
Acroloxus lacustris (Linnaeus) is a freshwater limpet common to Europe, northern Asia and Caucasasia. It is often called the "lake limpet" because of its preference for a lentic environment in contrast to the other common freshwater limpet of its region, *Ancyclus fluviatilis* Muller³, which inhabits rivers.

Most molluscan systematists have placed *Acroloxus* in the basommatophoran family Ancyliidae which originally contained all freshwater limpets. However, Bondeson (1950) and Burch (1961b) have contended that the differences found between *Acroloxus* and other ancyliids in regard to egg-capsule morphology and spermatogenesis are great enough to warrant its separation as a distinct family. These authors were not the first to appreciate

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³Generic designations given here are in accord with Opinion 363 of the International Commission on Zoological Nomenclature (Hubendick, 1952; Hemming, 1955).



FIGS. 1-5. Chromosomes of *Acroloxus lacustris*. Figs. 1-3. Spermatogonial metaphase chromosomes. The chromosomes in Fig. 1 are excessively contracted. A camera lucida drawing of these chromosomes is shown in Fig. 16. The chromosomes in Figs. 2 and 3 have divided. Camera lucida drawings of Figs. 2 and 3 are shown in Figs. 18 and 24. Fig. 4. Late prophase I (diakinesis) chromosomes. Fig. 5. Metaphase I chromosomes.

FIG. 6. Spermatogonial late prophase chromosomes of *Rhodacmea cahawbensis*.

FIG. 7. Spermatogonial metaphase chromosomes of *Laevapex fuscus*. A camera lucida drawing of these chromosomes is shown in Fig. 17.

the differences exhibited by *Acroloxus*, as indicated by Walker's (1923) precedent of placing it in a subfamily by itself among the Ancyliidae. Most recently Hubendick (1962) has also argued for familial status for *Acroloxus* on morphological grounds.

Chromosome studies of freshwater limpets are rather sparse and to date are restricted to only six publications (Le Calvez and Certain, 1950; Burch 1959a, b, 1960a, c; Burch, Basch and Bush, 1960). The present report presents cytological information obtained in our laboratory on the common European limpet, *Acroloxus lacustris*, and discusses the significance of these findings in respect to commonly held concepts of systematics and phylogeny in freshwater limpet-like mollusks.

Grateful acknowledgement is made to Dr. Dorothea Franzen, Illinois Wesleyan University, Bloomington, Illinois, U. S. A., and to Mr. Jack Hayworth, University of Reading, Reading, England, for supplying me with the cytological material of *Acroloxus lacustris*. I am also indebted to Dr. Henry van der Schalie, Museum of Zoology, University of Michigan for facilities and many kindnesses, to Mrs. Elizabeth Poulson, also from our Museum, for technical assistance during part of the work, and to Mrs. Anne Gismann for critically reading the manuscript.

MATERIALS AND METHODS

Specimens used in this study were obtained by Dr. Dorothea Franzen and Mr. Jack Hayworth from two localities in England. The material examined consisted of ovotestes from 3 specimens

taken along the River Thames at Sonning (near Reading) on April 13, 1959, and from 7 specimens collected near East Bergholt, Suffolk, on June 26, 1959. The tissues were killed, fixed and preserved in Newcomer's (1953) fluid and stained by the acetic-orcein squash technique (La Cour, 1941) for chromosome studies, or stained with haematoxylin and eosin for a general histological study of gametogenesis. Tissues for the latter study were washed in absolute alcohol, cleared in chloroform, embedded in paraffin and sectioned at 15 micra. Shells of duplicate specimens (from the Thames River at Sonning) have been deposited in the collection of the Museum of Zoology, University of Michigan (UMMZ cat. no. 207600).

Observations were made with a *Tlyoda-microscope* using a 90X (n.a. 1.25) oil immersion objective and 10-30X oculars. The chromosomes in Figs. 12-26 were drawn with the aid of a camera lucida and reproduced at a table top magnification of 4650X. Photographs (Figs. 1-11) were taken using a 20X ocular, oil immersion objective, a Kodak Wratten 57A (green) filter, and Kodak High Contrast Copy and Ektachrome Type F films.

OBSERVATIONS

1. Cytology of *Acroloxus lacustris*
 - a. Spermatogonial Divisions

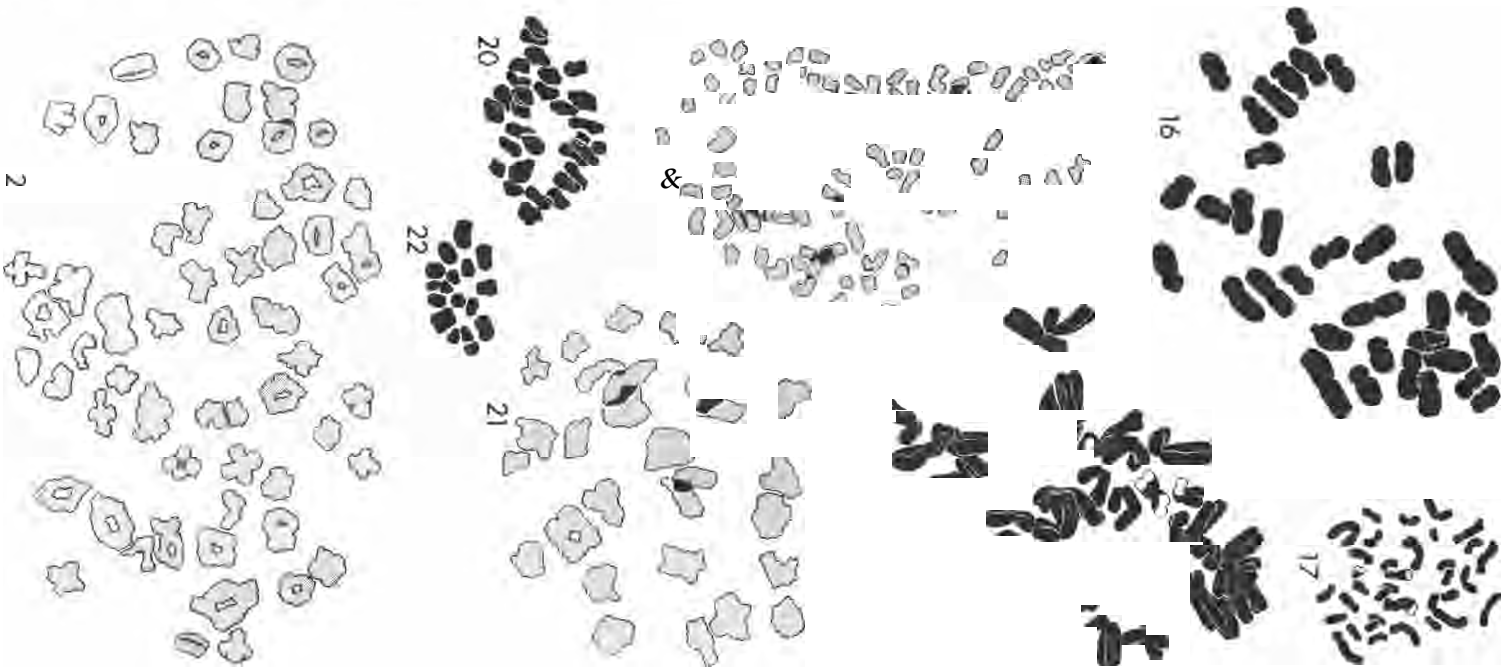
Thirty-six chromosomes are easily counted during metaphase of spermatogonial divisions of *Acroloxus lacustris* (Figs. 1-3, 16, 18, 24). Primary constrictions can easily be observed in these metaphase chromosomes, and in addition

FIG. 8-9. Chromosomes of *Ancylus fluviatilis*. Fig. 8. Late Prophase I (diakinesis) chromosomes. A camera lucida drawing of the chromosomes of a cell similar to this one is shown in Fig. 23. Fig. 9. Metaphase I chromosomes. A camera lucida drawing of these chromosomes is shown in Fig. 26.

FIG. 10. Metaphase I chromosomes of *Rhodacmea cahawbensis*.

FIG. 11. Metaphase I chromosomes of *Laevapex fuscus*. A camera lucida drawing of these chromosomes is shown in Fig. 22.

Figures 1-11 X1470.



to their constrictions they are often also very noticeable because they are non-staining or only lightly staining (Fig. 1; the non-staining character associated with the primary constrictions is not shown in Fig. 16, and only in the shaded chromosomes in Fig. 12).

During their period of maximum contraction, spermatogonial metaphase chromosomes appear to be divided into 6 pairs of medianly or nearly medianly constricted homologues (shaded in Figs. 12-14) and 12 pairs of distinctly submedianly or subterminally constricted homologues (solid in Figs. 12-14). The two largest pairs and the smallest pair of chromosomes are medianly constricted. One pair of chromosomes has secondary constrictions (the 10th pair shown in Fig. 12).

There is considerable variation in the degree of contraction of spermatogonial metaphase chromosomes. The extent of this variability can readily be observed in Figs. 1-3, 12-14, 16, 18, 24. Measurements in micra for the homologous pairs of excessively contracted chromosomes shown in Fig. 1 are as follows (arranged in decreasing order, see also Fig. 12): 4.7, 4.1, 3.4, 3.1, 3.0, 3.0, 2.9,

2.8, 2.7, 2.7, 2.7, 2.5, 2.5, 2.5, 2.5, 2.3, 2.2, 1.9. Similar highly contracted chromosomes have been found in other species of basommatophoran snails and have been discussed by Burch (1960a).

b. Meiotic Divisions

Eighteen bivalents can be readily observed during late prophase (diakinesis) and metaphase of the first meiotic divisions of spermatogenesis. The pairing behavior of the bivalents appeared to be normal, and during diakinesis the paired chromosomes were held together by one or more chiasmata. Details of the chromosome cycle of *Acroloxus lacustris* during meiosis appear to be similar in most respects to that of other basommatophoran snails as described by Burch (1960c).

c. Mature Sperm

The mature sperm of *Acroloxus lacustris* were first described by Retzius (1906) and the present observations do not add additional information but merely confirm his report. The mature sperm as seen in the ovotestis occur in large bundles of many spermatozoa each. The head segment or nucleus is extremely

FIGS. 12-14. Chromosomes of three spermatogonial cells of *Acroloxus lacustris*. The chromosomes are paired and arranged according to decreasing lengths. Medianly constricted chromosomes are shaded. Fig. 12. Aligned chromosomes of Figs. 1 and 16. Fig. 13. Aligned chromosomes of Figs. 2 and 18. Fig. 14. Aligned chromosomes of Figs. 3 and 24.

FIG. 15. Aligned mitotic metaphase chromosomes of *Laevapex fuscus* from Figs. 7 and 17.

FIG. 16. Camera lucida drawing of mitotic metaphase chromosomes of *Acroloxus lacustris* shown in Fig. 1. These chromosomes are shown paired and arranged according to decreasing lengths in Fig. 12.

FIG. 17. Camera lucida drawing of mitotic metaphase chromosomes of *Laevapex fuscus* shown in Fig. 7. These chromosomes are shown paired and arranged according to decreasing lengths in Fig. 15.

FIG. 18. Camera lucida drawing of mitotic metaphase chromosomes of *Acroloxus lacustris* shown in Fig. 2. These chromosomes are shown paired and arranged according to decreasing lengths in Fig. 13.

FIG. 19. Camera lucida drawing of late mitotic prophase chromosomes of *Ancylus fluviatilis*.

FIGS. 20-21. Camera lucida drawing of chromosomes of meiosis I of *Ferrissia parallela*. Fig. 20. Metaphase I. Fig. 21. Late Prophase I (diakinesis).

FIG. 22. Camera lucida drawing of Metaphase I chromosomes of *Laevapex fuscus* shown in Fig. 11.

FIG. 23. Camera lucida drawing of Prophase I (diakinesis) chromosomes of *Ancylus fluviatilis*. A photograph of the chromosomes of a cell similar to this one is shown in Fig. 8.

Figures 12-23 X1940.

long and thin (thread-like), and, in acetic-orcein squash preparations, can hardly be distinguished from the sperm tail segment. The contrast of this sperm morphology to that of other basommatophoran snails will be discussed below.

2. Comparisons with Ancylicids and other Basommatophora.

After looking at many basommatophoran species, representing many groups, I have been struck by the general uniformity of various details of spermatogenesis. This includes the general appearance of the cells at the various stages, the volume ratio of the nuclear material to the cytoplasm, the general size of the chromosomes, and the appearance of the sperm. In *Acroloxus lacustris*, I was surprised to find that these various details were strikingly different.

a. Spermatogonial Chromosomes

All of the cells of spermatogenesis are much larger than those observed in other basommatophoran snails, and the ratio of chromatin to cytoplasm is noticeably greater (although no actual quantitative measurements were made).

The mitotic metaphase chromosomes observed during spermatogonial divisions are noticeably larger than any previously observed in Euthyneuran snails. Normally contracted metaphase chromosomes during these divisions measure from 7.0 micra for the largest chromosomes to 3.5 micra for the smallest. Measurements for spermatogonial chromosomes in similar preparations for other freshwater basommatophoran snails have been given as 3.7 micra for the largest and 0.7 micra for the smallest (Burch, 1960a, c; Burch and Bush, 1960). Thus, in comparative terms, the chromosomes of *Acroloxus lacustris* are approximately twice the size previously found for other species of the order. This size difference can be readily observed, as regards the Ancylicidae, by comparing the chromosomes of *A. lacustris* (Figs. 1-3, 12-14, 16, 18, 24; spermatogonial metaphase) with the corresponding chromosomes of

the ancyline limpets, *Rhodacnæa cabanbensis* (Fig. 6; late spermatogonial prophase) and *Ancylus fluviatilis* (Fig. 19; late spermatogonial prophase), and the laevapeicine⁴ limpet *Laevapex fuscus* (Figs. 7, 15, 17, 25; spermatogonial metaphase).

In comparing the chromosome number of *Acroloxus lacustris* ($n=18$, $2n=36$) with those known from other freshwater limpets (Table I), it is readily apparent that this number, although characteristic of the Basommatophora in general, has not yet been observed in other freshwater limpets. The numbers $n=15$, 30 and 60 ($x=15$) have been reported for the Ancylineae and Ferissiinae (Burch, Basch and Bush, 1960) and the number $n=17$ for the Laevapeicinae⁴ (Burch, 1960a, c) (see Table I).

When the karyotype of *Acroloxus lacustris* (Figs. 12-14) is compared to that of *Laevapex fuscus* (Fig. 15), the most obvious difference between the two (other than sizes of the chromosomes and their number) is that the two largest pairs of chromosomes of *A. lacustris* are medianly constricted, while the two largest pairs of *L. fuscus* are submedianly or subterminally constricted. It would be very interesting to compare the karyotypes of other species of freshwater limpets and to ascertain whether or not the above differences will prove to be significant.

b. Meiotic Chromosomes

The meiotic chromosomes of *Acroloxus lacustris* are considerably larger than those seen by me or reported by others for any other basommatophoran snail. These size differences, as compared to various ancylicid limpets, are illustrated in Figs. 4, 5, 8-11, 20-23, 26. Late prophase I (diakinesis) chromosomes of *A. lacustris* are shown in Fig. 4. As can readily be seen, these are much larger than the chromosomes of the same stage of *Ancylus fluviatilis* (Figs. 8, 23) and

⁴ In this paper the Laevapeicinae are considered as a subfamily of the Ancylicidae (see Footnote 8 and Table I).

TABLE I: Chromosome Numbers In Freshwater Limpets⁵

Species		2n	Source
Acroloxiidae			
<i>Acroloxus lacustris</i>	18	36	England
Ancylidae			
Ancylinae			
<i>Rhodacmea cahawbensis</i> ⁶	15	30	Alabama, U. S. A.
<i>Ancylus fluviatilis</i>	60	ca.120	England
Ferrissiinae			
<i>Ferrissia parallela</i>	30	60	Michigan, U. S. A.
<i>Ferissia tarda</i>	30		Michigan, U. S. A.
Laevapecinae ⁷			
<i>Laevapex fuscus</i>	17	34	Michigan, U. S. A.
	17	34	Virginia, U. S. A.
<i>Burnupia</i> sp.	17		Republic of South Africa

5 From Burch, 1960a, c, 1961a and this report; Burch, Basch and Bush, 1960.

6 *Rhodacmea* is considered here to belong to the Ancylinae, s.s., because of similarities in shell, jaw, radula, and dorsal muscle scars. These and other comparative aspects will be discussed in greater detail in a later paper on systematics of freshwater limpets.

7 Hannibal (1912) created the subfamily Laevapecinae for *Laevapex* s. s., *Fisherola* and *Walkerola*. Gwatkin (1914), Pilsbry (1925) and Baker (1925) have shown that snails of the latter two taxonomic categories should be placed near or with the Lymnaeidae (Lancinae). Despite their divergent chromosome number, the Laevapecinae are provisionally left within the Ancylidae. *Burnupia* is herewith added to the Laevapecinae because of similarities to *Laevapex* in male reproductive structures, dorsal muscle scars and chromosome numbers. Anatomical details of *Burnupia* will be presented in a later paper.

Ferrissia parallela (Fig. 21). Metaphase I chromosomes of *Acroloxus lacustris* are shown in Fig. 5. These are correspondingly much larger than metaphase I chromosomes of *Ancylus fluviatilis* (Figs. 9, 26), *Rhodacmea cahawbensis* (Fig. 10), *Ferrissia parallela* (Fig. 20) and *Laevapex fuscus* (Figs. 11, 22).

Because of their relatively larger size one might expect a higher chiasmata frequency for meiotic chromosomes in *A. lacustris* than in other Basommatophora. However, such a comparison was not attempted in this study.

c. Mature Sperm

In the Basommatophora (with the exception of *Acroloxus*) the sperm head is bullet- or turnip-shaped following fixation in Newcomer's fluid and acetic- or cein staining. In *Acroloxus lacustris* the sperm head is strikingly different. It is a very fine thread of slight diameter and very long. Such sperm would at least

superficially appear to be similar to those described by Tuzet (1950) for *Aplysia* and by Franzen (1955) for various opisthobranchs (e. g., *Acera*, *Cylichna*, *Aplysia*, *Limapontia*).

Retzius (1904) and later Franzen (1956) extensively studied spermiogenesis among invertebrates and both concluded that the various types of mature sperm could be generally placed into two groups, one of "primitive", the other of "modified" sperm. Franzen defines primitive sperm as follows: "The nucleus is short and of rounded or conical shape. Also the middle piece is short, and contains 4-5 mitochondrial spheres arranged in a regular ring around the axial filament. The tail is formed by a thin filament which issues from a centriole at the posterior part of the head, traverses the middle piece, and reaches a length of about 50 micra. The terminal portion of the tail is formed by a set-off thinner portion, the end piece." Sperm deviating from

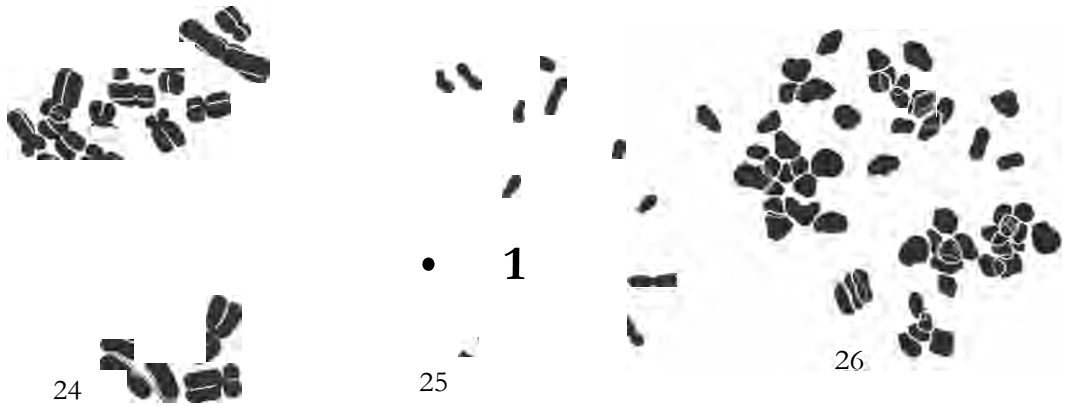


FIG. 24. Camera lucida drawing of mitotic metaphase chromosomes of *Acroloxus lacustris* shown in Fig. 3. These chromosomes are shown paired and arranged according to decreasing lengths in Fig. 14.

FIG. 25. Camera lucida drawing of mitotic prometaphase chromosomes of *Laevapex fuscus*.

FIG. 26. Camera lucida drawing of metaphase I chromosomes of *Ancyclus fluviatilis* shown in Fig. 9.

Figures 24-26 X1940.

this type are considered modified. Primitive sperm, although occurring in the Placophora (=Polyplacophora), Solenogastres (=Aplacophora), Pelecypoda, Scaphopoda and Diotocardia, have not been found in Euthyneura.

The sperm of *Acroloxus lacustris* are highly modified. The nucleus, instead of being short and round or conical, is very long, forming almost 1/4 the length of the spermatozoon. It is thread-like and hardly thicker than the tail piece. The acrosome can hardly be distinguished from the nucleus.

The bullet- or turnip-shaped sperm nuclei of the other Basommatophora would at first sight appear much like that described above as primitive. However, Franzen (1955) considers them to also be highly modified without "... any trace whatsoever of primitive conditions in any of the forms." It is interesting to note that Franzen also reports sperm approaching this second modification from some opisthobranchs (*Actaeon*, *Onchidoris*, *Partulida*, *Tritonia*).

Since the two modified sperm types found in the Basommatophora appear to be found also in the opisthobranchs, it might seem that the Basommatophora are really diphyletic, and that each group was derived independently from different opisthobranch ancestors. According to Franzen (1956): "If within a larger group a subgroup is found which has an entirely different type and genesis of the sperm unaccompanied by any essential differences in the way of fertilization, and if the same type of sperm is found within another group the assumption is justified that the sperm possesses a phylogenetic-taxonomical significance." But after comparing the species he studied with current concepts of Euthyneuran phylogeny (e.g., Boettger, 1955) I was unable to correlate the recurrence of the two types of sperm with any consistency. It would seem therefore that the modified sperm of both orders arose independently; or, that the question of phylogeny and relationships in Euthyneuran snails has not been finally settled.

DISCUSSION

1. Systematics

It seems desirable to present a brief historical account of systematics at the family level for freshwater limpets in general, since some present workers on these snails are either unaware of their classical groupings and of the changes subsequently made, or tend to ignore them. Moreover, since *Acroloxus* has nearly always been placed in the rather inclusive family Ancyliidae, systematic considerations of that family also, in part, involve *Acroloxus*.

In 1923 Bryant Walker, the leading authority on freshwater limpets, made the following observation concerning their taxonomy: "The classification of the Ancyliidae is in a very unsatisfactory condition owing to the fact that . . . practically nothing is known of the soft anatomy. The simple form of the shell not only renders the determination of the species exceedingly difficult, but affords very slight indications of generic relations, and none as to the evolutionary history and affinities of the various groups." Our state of knowledge concerning this perplexing group has advanced surprisingly little since that time. The anatomy of most freshwater limpets is still largely unknown.

It has long been known that all freshwater limpet-like mollusks should not be placed in the single family Ancyliidae Rafinesque 1815 (see also Phylogeny p. 64). Some of the genera formerly included have already been transferred to other families on well founded anatomical grounds. As early as 1882 Hutton designated a separate family Latiidae for the New Zealand genus *Latia* because of the difference in position of its eyes, its peculiar radular teeth and lack of jaws. However, Hutton's paper was overlooked by later authors. For example, Pelseneer (1901) and Walker (1923) both indicated that *Latia* should be put into a separate family, but neither actually made this change. Hannibal (1912) proposed the subfamily Latiinae, "n. sub-f am." and

Thiele (1931) raised it to familial rank. Later, Boettger (1955) reduced Latiinae again to subfamilial rank, but within the Chiliniidae.

Gwatin (1914) pointed out that in radular characters and jaw the west American *Lanx* resembled the Lymnaeidae. Pilsbry (1925) followed up this observation and raised Walker's (1917) subfamily Lancinae to family status. He noted that *Lanx* had "no direct or near relation to Ancyliidae. It belongs to a separate family, related to the Lymnaeidae somewhat as the Ancyliidae are to the Planorbidae." H. B. Baker (1925) showed conclusively that anatomically *Lanx* was indeed a lymnaeid, but retained the family name Lancidae, because of its peculiar modification of the pallial complex. Thiele (1931) again subordinated Lancinae to subfamilial rank, but within the Lymnaeidae.

Pilsbry and Bequaert (1927) placed *Protancylylus* (sole genus of Walker's (1923) subfamily Protancylylinae) with the **Planorbidae** (Bulininae). Hubendick (1958) independently concluded that this change was necessary. Zilch (1959) also considered *Protancylylus* as a planorbid, but retained its subfamilial ranking.

Bondesen (1950) proposed splitting off another limpet, *Acroloxus*, from the **Ancyliidae** and placing it in its own family. In doing this he raised Thiele's (1931) subfamily Acroloxinae (=Ancyliinae Walker 1923) to the family Acroloxidae. The reason for this elevation in the systematic position of *Acroloxus* was its strikingly different egg-capsule morphology. There exist several other reasons for separating the dextral *Acroloxus* from the sinistral Ancyliidae (as understood here) and, more recently Zilch (1959), Burch (1961b) and Hubendick (1962) also considered the Acroloxidae as a distinct family.

The remaining taxa have generally been left with the Ancyliidae or, if raised to familial rank, retained as closely associated families. The elevation of certain groups to family status has not been universally accepted, and the grounds for

these changes are usually not well founded⁸

Hannibal (1914) raised his 1912 subfamily *Laevapecinae* to family rank. Wenz (1938) raised Hannibal's (1912) subfamily *Neoplanorbinae* and Walker's (1917) subfamily *Ferrissiinae* to family status, and also presumably Walker's (1923) *Ancylastruminae* to *Ancylastridae*. Boettger (1955) and Meyer (1955) also treated the *Ferrissiinae* as a separate family. Zilch (1959) recently raised Walker's (1917) subfamily *Rhodacmeinae* to familial rank.

The descriptive cytological details and comparisons shown in this paper strengthen Bondesen's contention that *Acroloxus* should be separated at the family level from other freshwater limpets. This has already been pointed out in a brief abstract by Burch (1961b). Their higher chromosome number ($n=18$) which differs from that of the *Ancylinae* and *Ferrissiinae* ($x=15$), and *Laevapecinae* ($n=17$) is also considered as an additional cytological character speaking for separation. The divergent chromosome number of the *Laevapecinae* would suggest possible basic differences from the *Ancylinae* also, which, if borne out by anatomical detail, might lead to their removal from the *Ancylidae*. As regards *Acroloxus*, such a systematic separation as supported here seems justified also on more gross morphological grounds, since considerable differences in shell, radula and soft anatomy have been demonstrated between *Acroloxus* and other freshwater limpets (e.g., see Walker, 1923; Hubendick, 1960, 1962).

2. Phylogeny

For many years it has been known, or at least suspected, that the freshwater limpets are not monophyletic. For ex-

ample, Walker (1923) stated: "The remarkable differences that have recently been discovered [by Gwatkin] in the radulae of the various groups would certainly tend to strengthen the suggestions that have been made that the family [*Ancylidae*] as now recognized is not of homogeneous origin, but of diverse ancestry, and that the similarity in conchological characters should be considered rather as an example of parallel development than as indicating a common line of descent." Although Walker was perhaps the first to state clearly such views on the polyphyletic origin of freshwater limpets, Hannibal (1914) was apparently earlier thinking along similar lines (although his groupings are largely unnatural ones).

Phylogenetic considerations of freshwater limpets go back many years, to Plate (1894), who considered *Ancylus* to be a tectibranch. Pelseneer (1901) took exception to this and placed *Ancylus* (*A. fluviatilis* + *Acroloxus lacustris*) and *Gundlachia* near *Planorbis* with the *Basommatophora*. His reasons for considering *Ancylus* to be a basommatophoran were: 1) the shape and position of its osphradium, 2) its pallial "gill", 3) its stomach with a pyloric caecum, 4) the position of the ventricle in relation to the auricle in its heart, 5) the separation of its male and female genital openings, and 6) its short second pedal commissure. He showed that *Gundlachia* was similar to *Ancylus* in its basic organization.

In relation to other *Basommatophora*, Pelseneer considered *Ancylus* to be very specialized because of 1) its very concentrated nervous system, 2) its acquisition of a secondary gill, 3) its loss of the lung, 4) the displacement of its heart, and 5) the early division of its hermaphroditic duct and the consequent great length of its oviduct. The position of the *Ancylidae* as now understood (and excluding *Acroloxus*), both in their relation to the *Planorbidae* and in regard to the other *Basommatophora* has not been challenged by subsequent authors (e.g., see Hubendick, 1947; Meyer, 1955; Boettger, 1955).

⁸The *Ancylidae* are here considered to contain the following genera: *Ancylastrum* (*Ancylastruminae*); *Ancylus*, *Brondelia* and *Rhodacmea* (*Ancylinae*); *Ferrissia*, *Gundlachia* and *Hebelancylus* (*Ferrissiinae*); *Anisancylus*, *Burnupia*, *Laevapex* and *Uncancylus* (*Laevapecinae*). This is a modification of Walker's (1923) classification.

Hubendick (1945) and others before him consider Chiliniidae and Amphibolidae to be primitive Basommatophora. Since the more specialized Lymnaeidae appear to him (Hubendick, 1947) to be similar to these two families in type of tentacles and in having a muscle on the ventral side of the kidney, he considers the lymnaeids to be the most primitive of the "higher limnic Basommatophora" (= Branchiopulmonata). In addition, he considers some lymnaeids⁹ and *Chilina* to have similar copulatory organs.

Since among the "Branchiopulmonata" the Ancyliidae and the Planorbidae are most dissimilar to the Lymnaeidae, they appear to Hubendick to be the most specialized. However, he points to certain similarities that the Ancyliidae have with *Amphibola* and *Chaim*, i.e., the presence of an anal lobe, of lobate salivary glands, and of a flagellum (he considers the flagellum of *Ancylus* to be histologically different from that of *Amphibola*; *Chilina* does not have a flagellum). The similarities of the salivary glands he considers unimportant. But the anal lobe he does not so easily dismiss. He (loc. cit.) says: "The homologization of *Ancylus*' lobe with one of those in Planorbidae offers certain difficulties", and "as the shape of the lobe and the course of the rectum in the lobe agree well in Ancyliidae with those in Thalassophila and Chiliniidae, it might be possible for the lobe to be homologous with the anal lobe. . ." thereby indicating greater primitiveness. But Hubendick continues to say that " . . . if Ancyliidae ought to be derived from any recent types of higher limnic Basommatophora" then "the justification for this last argument disappears . . ."

At this point, the nature of the variation of chromosome numbers in Euthy-

neurans snails needs to be mentioned since they have phylogenetic significance. If one disregards erroneous and unreliable cytological reports (for discussion see Burch (1960c)) and considers chromosome numbers in the various Euthyneuran groups for which reliable information is available, in regard to their presumed morphological advancement, one immediately sees that there is a gradual increase in chromosome numbers as one goes up the evolutionary scale. Haploid numbers of the marine "opisthobranchiate" snails are all less than 18 (Fig. 27). The basic haploid number (x) for the freshwater Basommatophora is 18 (Burch 1960c). The haploid numbers of nearly all members of the land-dwelling Stylommatophora are greater than 18. The increase in number is a gradual one as one goes from one closely related larger taxon to the next, indicating that change in chromosome number has resulted by aneuploidy rather than polyploidy. This was first pointed out for pulmonate snails by Husted and P. R. Burch (1946). In those families where polyploidy has been reported (Burch, 1960b, d; Burch, Basch and Bush, 1960) the diploid number basic to the group is readily discerned. The great constancy of chromosome numbers within large taxonomic groups, especially in the lower Euthyneura, suggests that aneuploidy has been a rather rare occurrence, and that, when it occurs, it usually involves a whole major group, e.g., an order or family (sometimes only a genus in the Stylommatophora). Polyploidy is rare, and when it occurs it usually involves species (perhaps genera in the Ancyliidae), and not larger groups. Also, chromosome change by aneuploidy, when relating to higher taxonomic categories seems to be by addition, rather than subtraction, of chromosomes. (For a more detailed discussion of the above concepts see Burch, 1961a; Burch and Heard, 1962).

With the above information at hand it is then difficult to consider that the Ancyliidae as here understood ($x=15$; $n=17$) are highly specialized derivatives of the

⁹He says that *Lanx* differs from other lymnaeids in that it lacks a praeputium, but H. B. Baker (1925) in his excellent detailed treatment of *Lanx* quite clearly describes the praeputium. I have also determined that *Lanx* has a well developed praeputium which seems to differ but little from that of other Lymnaeidae.

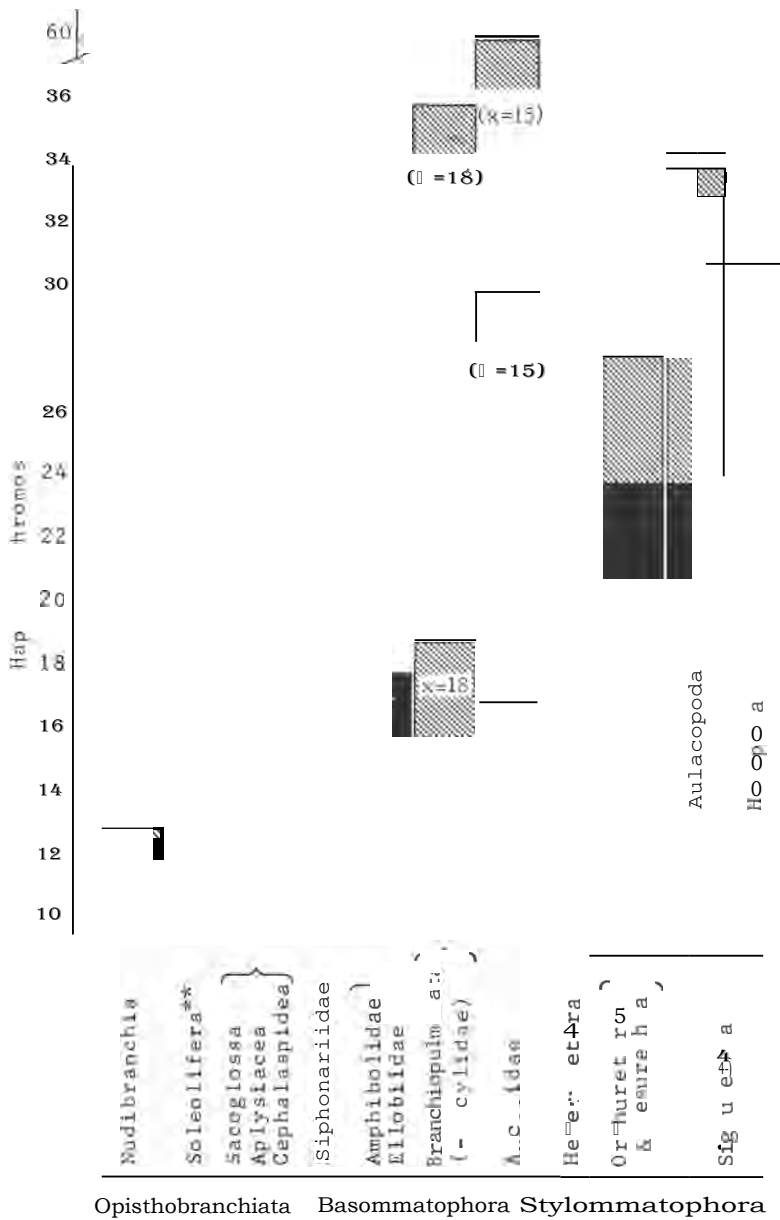


FIG. 27. Histogram of haploid chromosome numbers reported in Euthyneuran snails.* Shaded areas show limits of variation. x refers to the basic haploid chromosome number.

*From Beeson (1960, Nature, 186: 257), Burch (1960b, d; 1961a), Burch, Basch and Bush (1960), Burch and Heard (1962), Husted and Burch (1946; 1953, Virginia J. Sci., 4: 62), Inaba (1953, J. Sci. Hiroshima Univ., 14: 221; 1959, *Ibid.*, 18: 71; 1959, Annot. Zool. Jap.,

32:81), Inaba and Hirota (1958, Jap. J. Zool., 12: 157), Le Calvez and Certain (1950), Perrot (1930, Rev. Suisse Zool., 37: 397; 1938, *Ibid.*, 45: 487), Perrot and Perrot (1938, C. R. Soc. Phys. Hist. nat. Genève, 55: 92).

**J. a Burch, unpublished data.

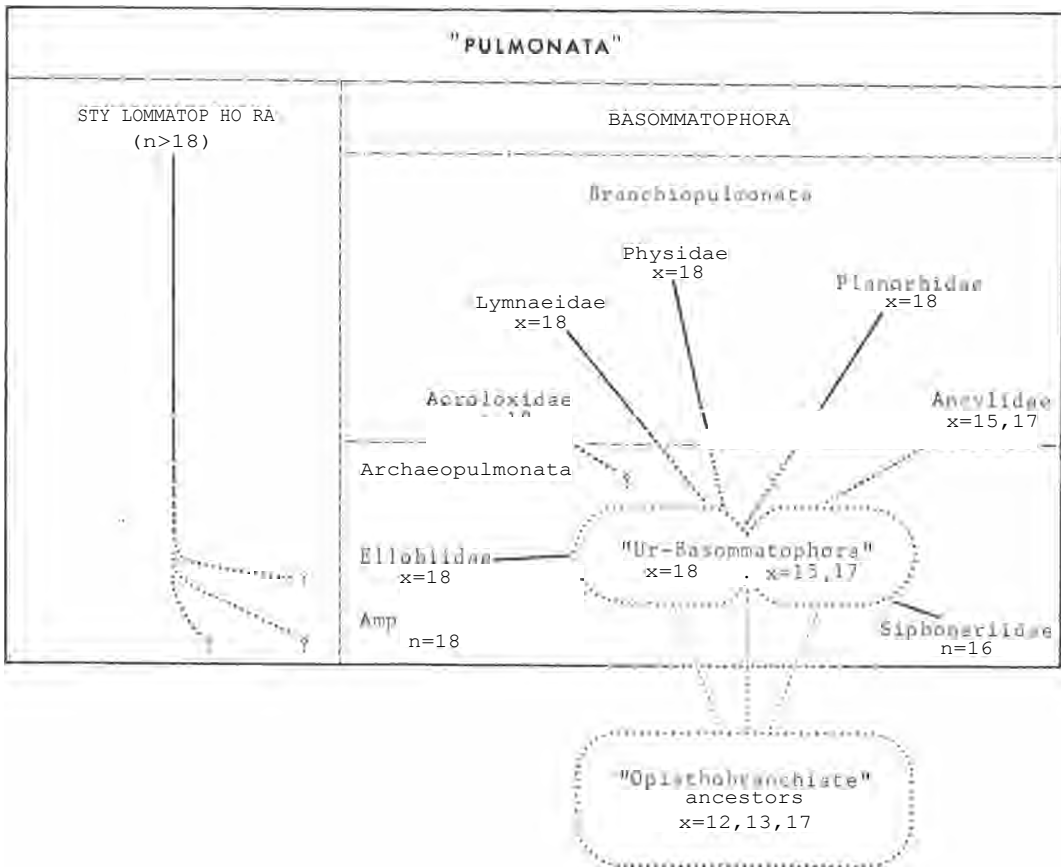


FIG. 28. Possible relationships of various taxa within the subclass Euthyneura based (in part) on haploid chromosome numbers. For phylogenies based on various morphological considerations see Hubendick (1947), Boettger (1955), Meyer (1955) and Morton (1955).

Planorbidae ($x=18$) as contended by Pelseneer (1901), but it would seem that they are perhaps much more primitive in nature. Brief attention has already been called to this possibility by the author (Burch, Basch and Bush, 1960). Even for *Acroloxus*, despite agreement in the chromosome numbers ($n=18$), there seems little justification in leaving its connections with the Planorbidae, when one considers the gross differences in other details of cytology, discussed previously in this paper.

Bondesen (1950), in considering the relationship of *Acroloxus* to other freshwater pulmonates as shown by comparative egg capsule morphology, states that

the origin of the Acroloxiidae "must be . . . sought nearer to more primitive forms within the Basommatophora." Hubendick (1962) most recently has advocated that *Acroloxus* had an origin in common with the primitive and aberrant *Laticostus* of New Zealand. He bases his conclusions on what he considers similarities in the radulae and reproductive tracts of the two genera. However, Pelseneer (1901) who alone has studied the soft anatomy of *Laticostus*, pointed out certain important dissimilarities between *Laticostus* and the ancyliids (including *Acroloxus lacustris*, with which he was familiar) that cannot be overlooked. These differences include the morphology of the nervous

system, the kidney, the lack of flagellum in *Latia*'s male reproductive system (perhaps a superficial character), and the presence of a well-developed pulmonary cavity in *Latia*. Concerning the radula of *Acroloxus* Hubendick (*loc. cit.*) states that it ". . . has certain important similarities with that of *Latia*." But, after carefully examining the radula of *Latia*, I find it very different from *Acroloxus* and cannot understand Hubendick's statement, unless he considers the arched rows of radular teeth of *Latia* and the semi-arched nature of those of *Acroloxus* to be important. The only other author that I know of that has studied the radula of *Latia* is Hutton (1882), and his drawings also do not show the radular teeth of *Latia* to be similar to those reported by other authors for *Acroloxus* (e.g., see Walker, 1925).

The aberrant spermatozoon of *Acroloxus lacustris* has been considered an extreme specialization when compared with *Lymnaea*, *Physa* and *Planorbarius* (see Retzius, 1904; also Boettger, 1944). But if Bondesen's and Hubendick's suggestions are correct in that *Acroloxus* had its origin near to primitive forms within the Basommatophora, and if it might be assumed that such a starting point could be from a group more primitive than those so far studied in respect to spermiogenesis, then perhaps the anomalous sperm morphology might not be in the direction of extreme specialization, but more closely like that of less specialized living groups not yet thoroughly investigated. Or perhaps the aberrant sperm are related to more specialized species of a group less specialized or more primitive than the Basommatophora (i.e., an "opisthobranch" group).

That a critical reevaluation of phylogeny and phylogenetically significant characters in the so-called "higher limnic Basommatophora" or "Branchiopulmonata", indeed, in the entire Euthyneura, is badly needed is readily apparent. But such a reevaluation of relationships must await the proper accumulation of detailed

morphological data, which at present is unavailable for many Euthyneuran groups.

Relationships of freshwater limpets to other Euthyneura as suggested by their chromosome numbers might be illustrated as in Fig. 28.

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ZUSAMMENFASSUNG

ZYTOTAXONOMISCHE STUDIEN UBER DIE NAPFSCHNECKEN
DES SUSSWASSERS (GASTROPODA: BASOMMATOPHORA). I. DIE
EUROPAISCHE BINNENSEENAPFSCHNECKE *ACROLOXUS LACUSTRIS*.

Acroloxus lacustris (Linnaeus) ist eine in Europa, Nordasien und Kaukasien verbreitete Napfschnecke die gewöhnlich der Basommatophorenfamilie Ancyliidae zugerechnet wird und daher auch zu den spezialisiertesten und phylogenetisch am weitesten fortgeschrittenen Basommatophoren.

Es wird hier gezeigt, dass in Anbetracht gewisser Einzelheiten des Zellbaues, *A. lacustris* nicht als eine den anderen Ancyliiden verwandte Schnecke angesehen werden sollte, sondern eher in eine Familie für sich (Acroloxidae) gestellt werden sollte, wie es ja auch bereits von anderen Autoren aus morphologischen Gründen befürwortet wurde. Ja darüber hinaus scheinen die beobachteten zytologischen Unterschiede sogar für einen weiteren Abstand von den übrigen Basommatophoren zu sprechen. Diese Unterschiede bestehen aus der beträchtlicheren Grösse der verschiedenen spermatogenetischen Zellen, aus deren im Verhältnis zum Zytoplasma grösserer Chromatinmasse, aus den verhältnismässig grossen Ausmassen der Chromosome und aus der Gestalt der Spermatozoen, deren Köpfe lang und fadenförmig und nicht geschoss- oder rübenförmig sind wie die der anderen Basommatophoren. Ausserdem ist die Chromosomenzahl ($n=18$) des *Acroloxus*, obwohl für die Basommatophoren kennzeichnend, von der der anderen Napfschnecken des Süsswassers verschieden; die haploide Grundzahl (x) beträgt in den Ancyliinae und den Ferrissiinae 15, während die in den Laevapecinae $n=17$ beträgt.

Wie für sämtliche Basommatophoren charakteristisch, sind die mitotischen Chromosome des *Acroloxus lacustris* metazentrisch. Sechs Paare, darunter die 2 grössten und das kleinste, sind median, die übrigen 12 submedian oder subzentral abgeschnürt. Es wurde hier zum ersten Male die Kariotype einer euthyneuren Schnecke genau festgestellt und abgebildet.

Es könnte wohl sein dass die Acroloxidae, wie es schon Bondeson und Hubendick vertraten, phylogenetisch in die Nähe der Wurzel des Basommatophorenstammes zu stellen wären, doch kann die Zytologie, zumindestens beim heutigen Stand unseres Wissens, noch nicht das Beweismaterial für einen derartigen Schluss liefern.

Auf Grund ihrer Chromosomenzahl wären auch die Ancyliidae, im Gegensatz zur üblichen, auf rein anatomischer Grundlage geschlossenen Folgerung, ebenfalls in die Nähe der Wurzel der Basommatophoren zu versetzen, jedoch in Hinblick auf die anderen zytologischen Unterschiede, nicht in die unmittelbare Nähe der Acroloxidae.

RÉSUMÉ

ETUDES CYTOTAXONOMIQUES SUR LES PATELLIENS D'EAU DOUCE
(GASTROPODA: BASOMMATOPHORA) I. LA PATELLE
LACUSTRE EUROPÉENNE *ACROLOXUS LACUSTRIS*.

L'*Acroloxus lacustris* (Linné) est une patelle lacustre répandue en Europe, en Asie septentrionale et en Caucase, qui a généralement été rangée dans la famille basommatophore des ancyliides et, par là, parmi les basommatophores les plus spécialisés et les plus avancés phylogénétiquement.

Nous montrerons dans cet exposé que, en vue de certains détails cytologiques, *A. lacustris* ne saurait être placée dans le voisinage immédiat des ancyliides, mais plutôt dans une famille séparée, les Acroloxidae, conclusion qui d'ailleurs se trouve aussi corroborée par d'autres auteurs pour raisons morphologiques. Plus que cela, les différences cytologiques observées semblent même indiquer un certain écart entre *Acroloxus* et les autres basommatophores. Ces différences se trouvent dans la grandeur des cellules de la spermatogénèse, dans le volume supérieur de leur chromatine par rapport au cytoplasme, dans les dimensions relativement grandes des chromosomes et dans la morphologie des spermatozoïdes mûrs, dont les têtes

son longues et filiformes, ne montrant point la forme de balle ou de navet rencontrée chez les autres basommatophores. En outre, son nombre de chromosomes ($n=18$), quoique caractéristique pour les basommatophores en général, diffère de celui des autres patelles d'eau douce, dont le nombre haploïde fondamental de chromosomes (x) est 15 pour les *Ancylinae* et *Ferrissinae*, pendant que n , le nombre haploïde, est 17 pour les *Laevapecinae*.

Les chromosomes mitotiques de *A. lacustris* sont métacentriques de façon caractéristique pour tous les basommatophores. Les constrictiones sont médianes dans 6 paires, comprenant les 2 plus grandes ainsi que la plus petite, et submédianes ou subterminales dans les autres 12. C'est d'ailleurs la première fois que le caryotype d'un mollusque euthyneure ait été minutieusement observé et figuré.

Il se pourrait que la position phylogénétique des *Acroloxidae* serait à chercher plutôt près de la base du tronc basommatophore comme l'ont suggéré Bondesen et Hubendick, mais, à l'état actuel de nos connaissances, la cytologie ne peut pas encore fournir les preuves d'une pareille conclusion.

Quant à la position des *Ancylidae*, elle se trouverait, contrairement aux conclusions antérieures basées sur une évaluation purement anatomique, également proche de la base de l'arbre phylogénétique basommatophore relativement à leur nombre de chromosomes, mais pas en proximité immédiate des *Acroloxidae* à cause des autres différences cytologiques.

RE SEÑA

ESTUDIOS CITOTAXONOMICOS SOBRE LAS LAPAS DE AGUA DULCE (GASTROPODA: BASOMMATOPHORA) I. LA LAPA DE LAGO EUROPEO, *ACROLOXUS LACUSTRIS*.

El *Acroloxus lacustris* (Linnaeus) es una lapita de agua dulce común en Europa, norte de Asia y Caucasia. Casi siempre ha sido asignada a la familia basommatophora *Ancylidae*, considerada como una de las mks especiales y filogenéticamente avanzadas.

Se demuestra en este estudio que en base a ciertos detalles de citología *A. lacustris* no debería considerarse muy relacionada a otros *Ancylidae* sino más bien como constituyendo una familia por sí sola, *Acroloxidae*, conclusión que ha sido corroborada por otros autores, en base de conocimientos morfológicos. Ciertamente las varias diferencias citológicas tienden a separar más los *Acroloxus* de los otros Basommatophora. Las diferencias observadas las constituyen el tamaño y mayor volumen de las varias células espermatogénicas, el mayor volumen de cromatina en relación al citoplasma, la relativa mayor medida de los cromosomas y la morfología de la esperma madura cuyas cabezas son largas y en forma de bala o de nabo como se encuentran en los otros caracoles basommatoforos. En suma, el número de cromosomas ($n=18$), aunque característico de los Basommatophora en general, es diferente del que se encuentra en otras lapas de agua dulce (x o número básico = 15 en *Ancylinae-Ferrissinae*; $n=17$ en *Laevapecinae*).

Los cromosomas mitóticos del *A. lacustris* son metacéntricos como es característico de todos los Basommatophora; 6 pares (incluyendo las 2 más grandes y las más pequeñas) que están medianamente ligados. Los otros 12 pares son submedianamente o subterminalmente ligados. Esta es la primera vez que el

La posición filogenética de los *Acroloxidae* puede que este muy cerca de los Basommatophora como sugirió Bondesen y Hubendick. Desafortunadamente al presente estado de conocimiento la evidencia que ayudaría a sostener tal conclusión no puede encontrarse en detalles de citología. Pero al contrario de opiniones antiguas alcanzadas en base a puros conocimientos anatómicos, la posición de los *Ancylidae* determinada por el número de cromosomas debería también estar muy cerca de los Basommatophora, aunque no cerca a los *Acroloxidae* debido a las otras diferencias citológicas.

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АБСТРАКТ

Ancylina (L.) пресноводный щитовидный моллюск распространен в Европе, Азии и на Кавказе. Он всегда относим к басомматофорному семейству Анциллиды и поэтому он считался одним из наиболее специализированных и филогенетически наиболее развитым видом из басомматофора.

В этой работе показано, что в некоторых деталях цитологии *Ancylina* не должен считаться близким к другим видам *Ancylina*, но он должен быть выделен в особое семейство - *Ancylinae*; к тому же заключению пришли и другие авторы на основании морфологических данных. Цитологические различия указывают даже на дальнейшее выделение *Ancylina* из Басомматофора. Замеченные различия состоят из гораздо большего размера разных сперматогенетических клеток, пропорционально большего количества хроматина чем цитоплазмы, в сравнительно более крупных хромосомах, в морфологии зрелой спермы, которая длинная и нитевидная, не в виде пули или луковички, как это наблюдается в других улитках среди Басомматофора. Кроме того, число хромосом ($n=18$), хотя и характерно для Басомматофора вообще, отличается от обычного в других новоявленных щитовидных моллюсков (х или основное гаплоидное число = 15 в *Ancylinae*; $n = 17$ в *Euthyracina*).

Митотические хромосомы *Ancylina* метацентричны, что характерно для всех видов Басомматофора; 6 (включая 2 наибольшие и наименьшие) сужены посредине; другие 12 сужены подале от середины. Тут в первый раз кариотип какой либо улитки из всех видов *Euthyracina* точно иллюстрирован.

Филогенетическое положение *Ancylina* может быть в основе Басомматофора, но полагали Бондэсен и Хюбэндик, но в настоящее время доказательств, подтверждающих такое заключение, в деталях цитологии не найдено. Но, вопреки сложившемуся мнению, основанному на чисто анатомических данных, систематическое положение *Ancylinae*, как это доказано числом хромосом, должно быть в основе Басомматофора, но никак не рядом с *Ancylina* по причине других цитологических различий.