

CYTOTAXONOMIC STUDIES OF LYMNAEID SNAILS¹Akihiko Inaba²

ABSTRACT

The chromosomes of 16 species of lymnaeid snails from 22 localities were observed during spermatogenesis, as well as during oögenesis and mitotic divisions. The chromosomes of 7 species and subspecies are reported for the first time in this paper. In the other species new knowledge of chromosomes in spermatogonia, oöcytes, polar bodies and somatic mitoses is added to previous reports. The chromosome numbers determined are compared with those previously reported. In the Lymnaeidae, chromosome numbers now have been reported for 41 species and subspecies belonging to 7 genera. Based on cytological features, various taxonomic points are discussed in each group with different chromosome numbers.

Lymnaea (4 subspecies), *Stagnicola* (15 species and subspecies), *Acella* (1 species), *Pseudosuccinea* (1 species) and *Bulinnea* (1 species) all have the haploid chromosome number 18. No obvious morphological difference or remarkable characteristics were found to distinguish caryotypes among or within these genera. Three species of *Fossaria* have the haploid number 18, but *F. rustica* has 19. This suggests that the latter should be raised to the rank of species, although many authors in the past considered this snail as a form or subspecies of *F. modicella*. The additional chromosome pair is small and often rather weakly staining during spermatocyte diakinesis.

Radix (11 species and subspecies) has 17 haploid chromosomes. "*Lymnaea*" *natalensis* from Liberia also has $n=17$, which suggests that it is a *Radix* species. Anatomical features confirm this. Three lymnaeid species have only 16(n) chromosomes: "*L.*" *ollula* (= *viridis*?), "*L.*" *tomentosa* and "*L.*" *lessoni*. They have been included in various nominal generic groups, mainly by their conchological features. However, a new group name may be needed for those 16(n) species.

Somatic chromosomes were observed in 5 species (*Stagnicola palustris wyomingensis*, *S. exilis*, *S. catascopium*, *Bulinnea megasoma* and *Fossaria rustica*). Generally, all chromosomes in somatic mitoses of young embryos were meta- or submetacentric in nature. These chromosomes may be very useful for caryotype analyses of lymnaeid snails, but more detailed observations are needed before reliable conclusions can be drawn from comparative studies.

A phylogenetic consideration of Lymnaeidae based on cytotaxonomic, cytological and paleontological information is presented.

INTRODUCTION

The basommatophoran Lymnaeidae are one of the most extensively studied

groups of mollusks in regard to their chromosome numbers. Nevertheless, only a few caryotype studies have been undertaken on this family. Perrot &

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Perrot (1938) studied the chromosome numbers in 6 species of lymnaeid snails and postulated that 3 subgenera (*Radix*, *Stagnicola* and *Lymnaea* s.s.) should be grouped into 2: *Radix* (n=17) and *Stagnicola-Lymnaea* (n=18); but this has not been widely accepted among taxonomists. Inaba & Tanaka (1953) reported the chromosome numbers of 2 lymnaeid snails in Japan, but recently Burch, et al. (1964) and the author (1965) corrected these earlier chromosome reports. Natarajan (1960) reported on the chromosomes of a species of *Radix* from India.

Burch (1960a) reported on the shapes of mitotic chromosomes in aquatic pulmonate snails which included 2 lymnaeids, and, more extensively, he (1960b) studied 18 species and subspecies of the Lymnaeidae. Burch, et al. (1964) studied the chromosomes of 3 *Radix* species and a *Fossaria* from Japan. They found the lowest chromosome number of lymnaeid snails in "*Lymnaea*" *ollula* (n=16), and suggested that this species should be placed in the genus *Radix* because of its cytological features, instead of the genus *Fossaria*, where it had been previously placed. Burch (1965) presented the possible relationships of various genera of the Lymnaeidae, based on their chromosome numbers, in his general review of cytotaxonomy in euthyneuran snails.

MATERIALS AND METHODS

Sixteen species and subspecies of lymnaeid snails from 22 localities were used in this investigation. The chromosomes in 9 of these species were reported previously by Burch (1960a,b). A list follows to indicate the species studied here as well as to give exact localities for obtaining the snails. An asterisk (*) indicates the species previously reported, and a double asterisk (**) indicates that the specimens were from the same locality as those studied by Burch (1960a, b). Shells of specimens from populations of the current study are shown in Figs. 83-102.

List of species and localities

Stagnicola palustris wyomingensis Baker, 1927. Giggey Lake, Boulder Co., Colorado, U.S.A., by George W. Bryce, June 25, 1967; "Lodge of the Pines," Boulder Co., Colorado, by George W. Bryce, June 25, 1967.

**Stagnicola umbrosa* (Say, 1832). **Roadside pond, 3 miles Northeast of East Tawas on US 23, Iosco Co., Michigan, U.S.A., May 18, 1967.

**Stagnicola exilis* (Lea, 1837). Small pond at junction of Dancer Rd. and Trinkle Rd. near Dexter, Sec. 11, Lima Township, Washtenaw Co., Michigan, U.S.A., by J. B. Burch, May 2, 1967; Small pond at junction of Dancer Rd. and Jackson Rd., Sec. 15, Lima Township, Washtenaw Co., Michigan, by J. B. Burch, May 10, 1967.

**Stagnicola catascopium* (Say, 1817). **Au Sable River, public fishing site, just off highway M-72, 4 miles east of US 27, near Grayling, Crawford Co., Michigan, U.S.A., May 18, 1967; Beach pool at Hammond Bay, Presque Isle Co., Michigan, by R. H. Russell, Sept. 4, 1967.

**Stagnicola emarginata serrata* (Halderman, 1842). Southwest side of Higgins Lake, Roscommon Co., Michigan, U.S.A., May 18, 1967.

Stagnicola hinkleyi (Baker, 1906). NW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 26, T. 39 N., R. 116 W., Snake River, Teton Co., Wyoming, U.S.A., by D. W. Taylor, Aug. 29, 1959.

Stagnicola idahoensis (Henderson, 1931). NW $\frac{1}{4}$, Sec. 25, T. 21 N., R. 1 E., Little Salmon River, Idaho Co., Idaho, U.S.A., by D. W. Taylor, Sept. 29, 1959.

Stagnicola cf. *bonnevillensis* (Call, 1884). SW $\frac{1}{4}$, Sec. 36, T. 42 N., R. 116 W., Spring at base of Cobble gravel terrace, Teton Co., Wyoming, U.S.A., by D. W. Taylor and J. D. Love, Aug. 24, 1959.

**Pseudosuccinea columella* (Say, 1817). Bass Lake, Unadilla Township, Livingston Co., Michigan, U.S.A., by J. B. Burch, May 1, 1967.

**Bulimnea megasoma* (Say, 1824). **Roadside drainage ditch, highway

M-55, about 2 miles West of Houghton Lake, Roscommon Co., Michigan, U.S.A., May 18, 1967.

**Fossaria parva* (Lea, 1841). Small roadside drainage ditch, 1 mile West of Clio, Genesee Co., Michigan, U.S.A., by R. H. Russell, July 15, 1967.

**Fossaria modicella* (Say, 1825). Fleming Creek, at Parker's Mill, 2 miles East of Ann Arbor, Washtenaw Co., Michigan, U.S.A., by J. B. Burch, May 9, 1967; Burnt Cabin Point, Huron Co., Michigan, by J. B. Burch, June 27, 1967; Comstock, Kalamazoo Co., Michigan, by J. B. Burch, July 7, 1967.

**Fossaria rustica* (Lea, 1841). **Mill pond on highway M-132, Sec. 5, Scio Township, Dexter, Washtenaw Co., Michigan, U.S.A., Aug. 16, 1967; Pond, Willys Park, Toledo, Ohio, U.S.A., by R. H. Russell, Sept. 4, 1967.

Radix natalensis (Krauss, 1848). Liberia, West Africa, by Dr. Z. H. Abedi, Sept. 4, 1963. University of Michigan Laboratory stock.

"*Lymnaea*" *tomentosa* (Pfeiffer, 1855). South Australia, by Dr. J. C. Boray; received Feb. 13, 1967. University of Michigan laboratory stock.

"*Lymnaea*" *lessoni* (Deshayes, 1831). Small stream, 3 miles from Popondetta on Oro Bay Road, Papua, by J. B. Burch, Sept. 7, 1966.

The materials examined consisted of 1) ovotestes in active stages of gametogenesis and 2) egg masses within 2 or 3 days after spawning. Ovotestes dissected from living material were fixed in Newcomer's (1953) fluid and stained by the acetic-orcein squash technique (La Cour, 1941). A few species collected from Papua, South Pacific, Idaho and Wyoming (U.S.A.) were fixed and preserved in Newcomer's fixative for 1-9 years. Their ovotestes were also examined by squash preparations. In those species that chromosomes were studied from egg masses, the living embryos were taken out of the egg mass, and after breaking their individual cap-

sules, the embryos were stained on a microscope slide with acetic-orcein either directly or after fixation in Newcomer's fluid. Observations were made with a Nikon microscope using a 100× immersion objective, 15× oculars, and achromatic condensor (n.a. 1.25). The chromosomes were drawn with the aid of a camera lucida and reproduced at a table-top magnification of 3,200×.

OBSERVATIONS

Chromosome numbers determined in this investigation are given in Table 1.

I. Chromosomes in spermatogenesis.

1. *Stagnicola*

Eight species collected from 11 localities were investigated. All of the species of *Stagnicola* observed in this study have the same chromosome number ($n=18$), the same number found for this genus in previous reports. There seems to be very little difference between *Stagnicola palustris wyomingensis* (Figs. 1-4) and 3 subspecies of *S. palustris* observed by Burch (1960b).

Stagnicola umbrosa (Figs. 5-7) and *S. catascopium* (Figs. 10, 11), collected from the same localities as Burch (1960b), and *S. exilis* (Figs. 8, 9), *S. catascopium* (Figs. 12, 13) and *S. emarginata serrata* (Figs. 14, 15), collected from different localities, also show the same appearance in meiosis as Burch (1960a,b) reported. The chromosome figures of *S. hinkleyi* (Figs. 16, 17), and *S. sp.* (cf. *bonnevillensis*) (Fig. 20) are also similar in appearance to the other *Stagnicola* species. In gonial cells of *S. umbrosa* (Fig. 5), *S. catascopium* (Fig. 12), *S. emarginata serrata* (Fig. 14), *S. idahoensis* (Fig. 18) and *S. cf. bonnevillensis* (Fig. 19), 36 meta- or submetacentric chromosomes were observed. No remarkable differences were found between them.

2. *Pseudosuccinea*

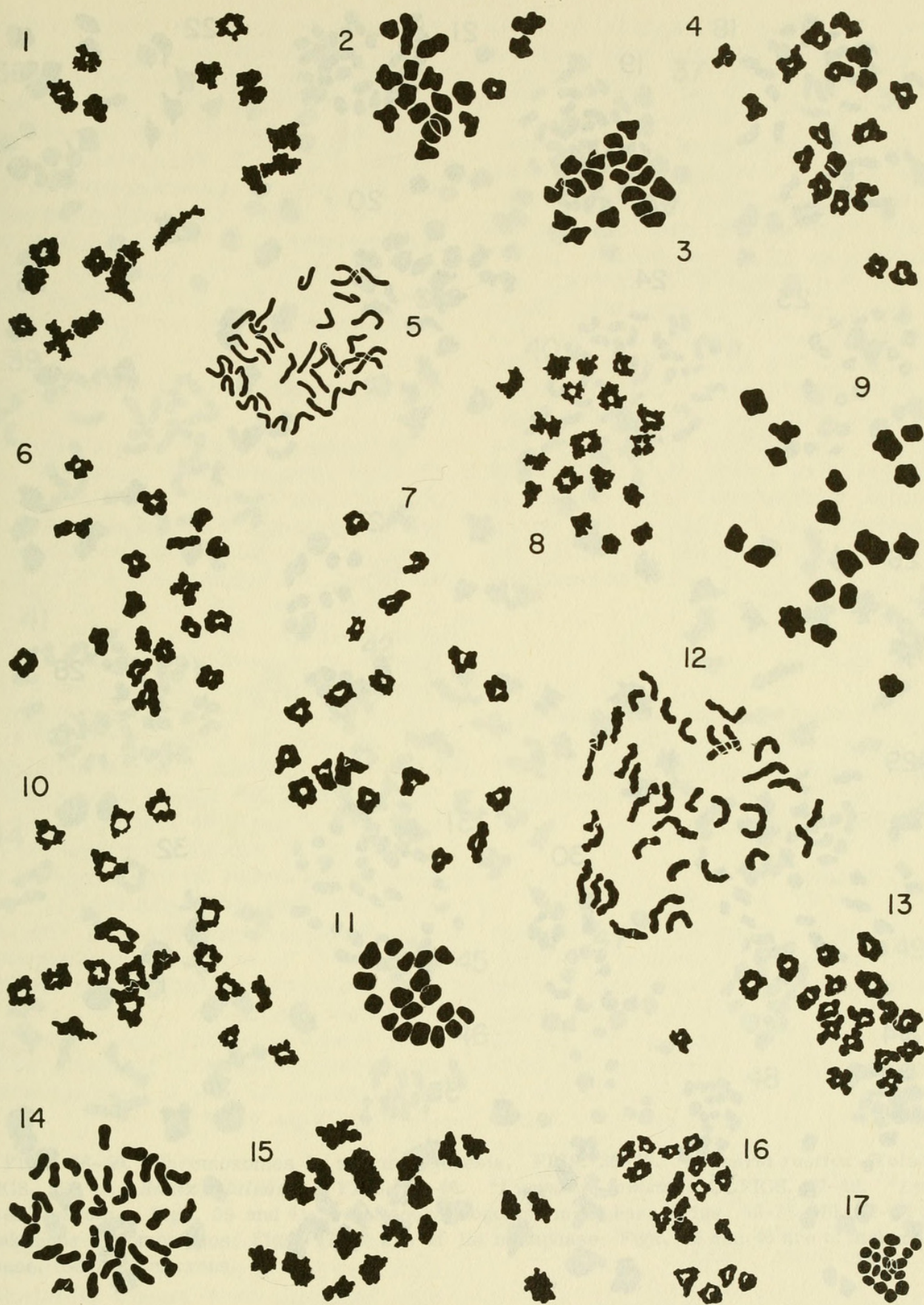
The caryotype of *Pseudosuccinea columella* from Michigan (Figs. 21, 22)

TABLE 1. The chromosome numbers determined in this investigation

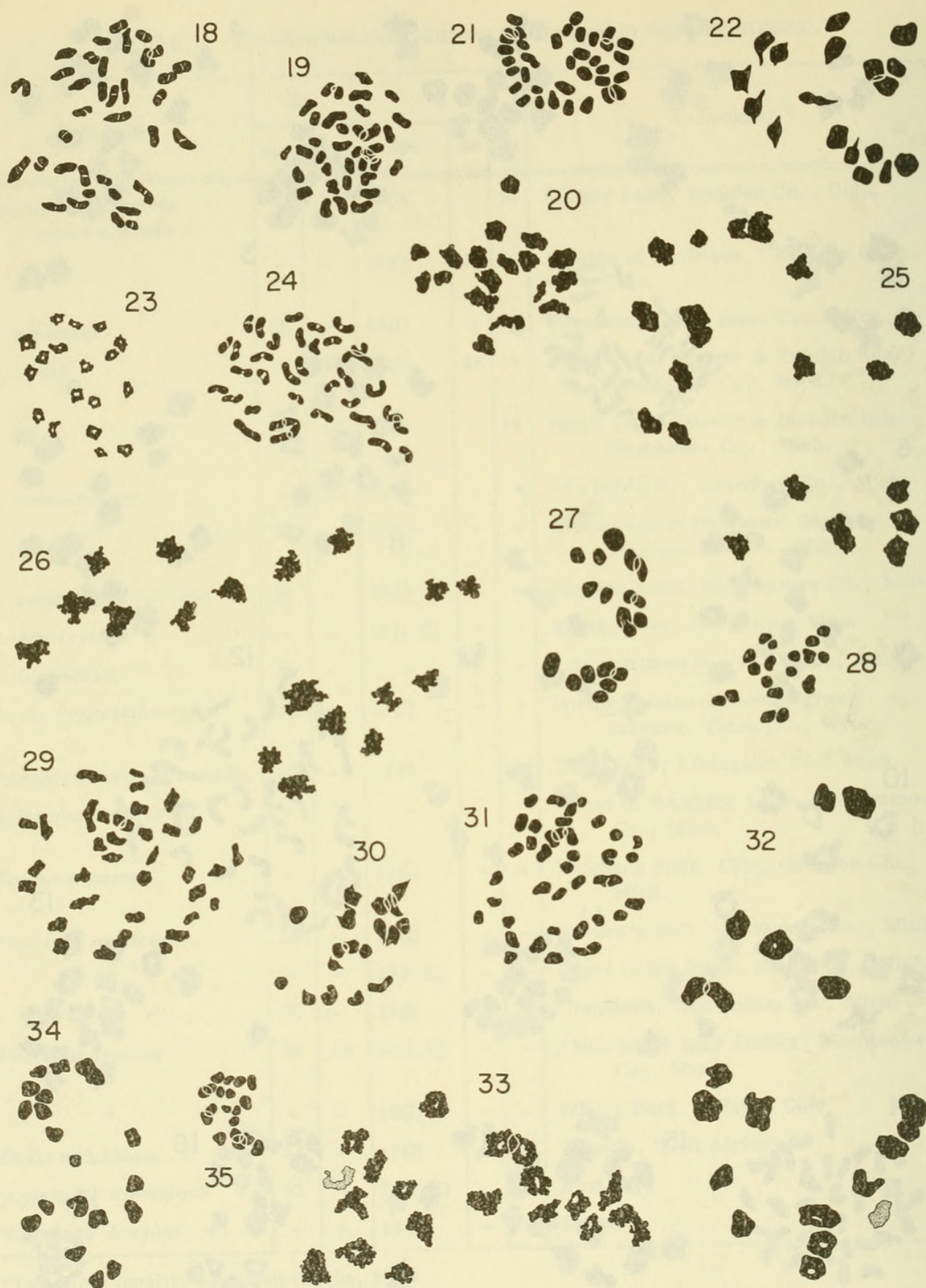
Species	2n		n			Locality
	spg	som	spc	oc	pb	
<i>Stagnicola palustris wyomingensis</i>	—	36	18(I)	—	18	Giggey Lake, Boulder Co., Colo.
"	—	—	18(I)	18	18	"Lodge of the Pines," Boulder Co., Colo.
<i>S. umbrosa</i>	36	—	18(I)	—	—	*Roadside pond, Iosco Co., Mich.
<i>S. exilis</i>	—	36	18(I)	18	—	Small pond, Dancer & Trinkle Rds., Washtenaw Co., Mich.
"	—	36	18(I)	—	18	Small pond, Dancer & Jackson Rds., Washtenaw Co., Mich.
<i>S. catascopium</i>	—	36	18(I)	—	—	*Au Sable R., Crawford Co., Mich.
"	36	—	18(I)	—	—	Beach pool at Hammond Bay, Presque Isle Co., Mich.
<i>S. emarginata serrata</i>	36	—	18(I)	—	—	Higgins Lake, Roscommon Co., Mich.
<i>S. hinkleyi</i>	—	—	18(I, II)	—	—	Snake River, Teton Co., Wyo.
<i>S. idahoensis</i>	36	—	—	—	—	Little Salmon R., Idaho Co., Ida.
<i>S. cf. bonnevillensis</i>	36	—	18(I)	—	—	Spring at base of Cobble gravel terrace, Teton Co., Wyo.
<i>Pseudosuccinea columella</i>	36	—	18(I)	—	—	Bass Lake, Livingston Co., Mich.
<i>Bulinnea megasoma</i>	—	36	—	—	—	*West of Houghton Lake, Roscommon Co., Mich.
<i>Fossaria parva</i>	—	—	18(I)	—	—	Roadside ditch, Clio, Genesee Co., Mich.
<i>Fossaria modicella</i>	36	—	18(I)	—	—	Parker's Mill, Washtenaw Co., Mich.
"	—	—	18(I, II)	—	—	Burnt Cabin Point, Huron Co., Mich.
"	36	—	18(I)	—	—	Comstock, Kalamazoo Co., Mich.
<i>Fossaria rustica</i>	38	38	19(I, II)	—	—	*Mill pond, near Dexter, Washtenaw Co., Mich.
"	—	—	19(I)	—	—	Willys Park, Toledo, Ohio
<i>Radix natalensis</i>	34	—	17(I)	—	—	Liberia, West Africa
' <i>Lymnaea</i> ' <i>tomentosa</i>	32	—	16(I, II)	—	—	Australia
' <i>Lymnaea</i> ' <i>lessoni</i>	—	—	16(I)	—	—	Papua

*The same locality as Burch (1960a, b).

note: spg = spermatogonia. som = somatic mitosis. spe = spermatocyte. oc = oöcyte. pb = polar body.



FIGS. 1-17. Chromosomes in spermatogenesis. FIGS. 1, 2. *Stagnicola palustris wyomingensis* (Giggey Lake). FIGS. 3, 4. *S. p. wyomingensis* ("Lodge of the Pines"). FIGS. 5-7. *S. umbrosa*. FIG. 8. *S. exilis* Dancer & Trinkle Rds.). FIG. 9. *S. exilis* (Dancer & Jackson Rds.). FIGS. 10, 11. *S. catascopium* (Au Sable R.). FIGS. 12, 13. *S. catascopium* (Hammond Bay). FIGS. 14, 15. *S. emarginata serrata*. FIGS. 16, 17. *S. hinkleyi*. Figs. 5, 12 and 14 are of spermatogonial metaphase; Figs. 1, 4, 6-8, 10, 13, 15 and 16 are diakinesis chromosomes; Figs. 2 and 9 are 1st prometaphase chromosomes; Figs. 3 and 11 are of 1st metaphase; Fig. 17 is 2nd metaphase. Scale: 5 microns.



FIGS. 18-35. Chromosomes in spermatogenesis. FIG. 18. *Stagnicola idahoensis*. FIGS. 19, 20. *S. cf. bonnevillensis*. FIGS. 21, 22. *Pseudosuccinea columella*. FIG. 23. *Fossaria parva*. FIGS. 24, 25. *F. modicella* (Parker's mill). FIGS. 26-28. *F. modicella* (Burnt Cabin Point). FIGS. 29, 30. *F. modicella* (Comstock). FIGS. 31-35. *F. rustica* (Dexter). Figs. 18, 19, 21, 24, 29 and 31 of spermatogonial metaphase; Figs. 20, 23, 25, 26, 32 and 33 are diakinesis chromosomes. Figs. 22, 27, 30 and 34 are of 1st metaphase; Figs. 28 and 35 are of 2nd metaphase. Scale: 5 microns.



FIGS. 36-49. Chromosomes in spermatogenesis. FIGS. 36-38. *Fossaria rustica* (Toledo). FIGS. 39, 40. *Radix natalensis*. FIGS. 41-46. "*Lymnaea*" *tomentosa*. FIGS. 47-49. "*Lymnaea*" *lessoni*. Figs. 39 and 41 are of spermatogonial metaphase; Figs. 36-38, 40, 42-44 are diakinesis chromosomes; Figs. 47-49 are of 1st metaphase; Figs. 45 and 46 are of 2nd metaphase. Scale: 5 microns.

show the same appearance as those studied from Virginia (Burch, 1960b).

3. *Fossaria*

The chromosomes of 3 *Fossaria* species from 6 localities were observed. *Fossaria parva* (Fig. 23) and *F. modicella* (Figs. 24-30) have chromosome numbers of $n=18$ and $2n=36$. But *F. rustica* has 19 haploid chromosomes and 38 chromosomes in gonial cells. Burch (1960b) reported the same chromosome number for this species from Michigan. The author confirmed it in the materials collected from the same locality (Figs. 31-35), and found in addition that this species from Toledo, Ohio also has 19 haploid chromosomes (Figs. 36-38). In diakinesis of *F. rustica*, one small bivalent was observed (Figs. 32, 33, 36-38). Generally this chromosome stained weakly.

4. *Radix*

Radix natalensis has 34 chromosomes in its spermatogonia (Fig. 39) and 17 chromosomes in meiotic cells (Fig. 40). This is the same number previously reported in *Radix*.

5. Others

This is the group which has 16 pairs of chromosomes. "*Lymnaea*" *tomentosa* from Australia and "*Lymnaea*" *lessoni* from Papua are included in this group. "*L.*" *tomentosa* (Figs. 41-46) has 32 chromosomes in spermatogonial divisions and 16 chromosomes in the 1st and 2nd meiotic divisions. In "*L.*" *lessoni* (Figs. 47-49), 16 haploid chromosomes were also observed. The karyotypes of these 2 species are similar to "*Lymnaea*" *ollula* (= *viridis*?) (Burch, et al., 1964; Inaba, 1965).

II. Chromosomes in oögenesis.

Chromosomes during oögenesis have been studied in 2 species of *Stagnicola*. Within half an hour after spawning, the

extrusion of the polar body could be seen. In *S. palustris wyomingensis* 18 chromosomes were observed in the 1st oöcyte (Fig. 50) and the 1st polar body (Figs. 51, 52), as well as in the spermatocytes (Figs. 1-4). These chromosomes are all meta- or submetacentric in nature. In *S. exilis*, 18 chromosomes were also determined in the oöcyte (Fig. 53) and 1st polar body (Fig. 54). These chromosomes are also meta- or submetacentric in shape.

III. Chromosomes in somatic mitoses.

The mitotic chromosomes of 3 species of *Stagnicola*, *Bulimnea megasoma* and *Fossaria rustica* have been studied during egg cleavage. Eighteen pairs of V- or J-shaped chromosomes were observed in *S. palustris wyomingensis* (Fig. 55), *S. exilis* (Figs. 56-59) and *S. catascopium* (Figs. 60-63). There is no significant observable difference among these 3 karyotypes. Two or 3 pairs are metacentric chromosomes, and the rest are submeta- or subtelocentric. However, it is difficult to consistently determine the exact nature of each chromosome, because the size and shape of chromosomes sometimes appear to be changed somewhat by the pressure of squashing (Figs. 56-57 and 60-61).

In *Bulimnea megasoma* (Fig. 64), 18 pairs of V- or J-shaped chromosomes were observed similar to those seen in *Stagnicola* species.

In *Fossaria rustica*, one more pair of chromosomes, i.e., 19 pairs, were recognized in the mitotic divisions of the embryos (Figs. 65-67).

DISCUSSION

In the Lymnaeidae, chromosome numbers have now been reported for 41 species belonging to 7 genera (Table 2). *Lymnaea*, *Stagnicola*, *Acella*, *Pseudosuccinea* and *Bulimnea* have the haploid chromosome number 18. The species of *Fossaria* have mostly the haploid



FIGS. 50-54. Chromosomes in oögenesis. FIGS. 50-52. *Stagnicola palustris wyomingensis* ("Lodge of the Pines"). FIG. 53. *S. exilis* (Dancer & Trinkle Rds.). FIG. 54. *S. exilis* (Dancer & Jackson Rds.). Figs. 50 and 53: 1st metaphase. Figs. 51, 52 and 54: 1st polar body chromosomes. In Fig. 50, the lower figure shows the whole nuclear plate (side view) in lower magnification. Lower scale: 5 microns. Upper scale (only for lower part of Fig. 50): 10 microns.

TABLE 2. Chromosome numbers reliably reported in Lymnaeidae

Species	Chromosome number				Source	Reference
	2n		n			
	spg	som	spc	oöc		
<i>Lymnaea</i>						
<i>L. stagnalis</i>	-	-	18	-	England	Burch, 1965
<i>L. s. lacustris</i>	36	-	18	-	Switzerland	Perrot, 1930
<i>L. s. rhodani</i>	36	-	18	-	Switzerland	Perrot, 1930, 1934
<i>L. s. jugularis</i>	36	-	18	-	Michigan, USA	Burch, 1960b
<i>Stagnicola</i>						
<i>S. palustris</i>	-	-	18	-	Switzerland;	Perrot & Perrot, 1938;
	-	-	18	-	Sweden	Burch, 1960b
<i>S. p. elodes</i>	36	-	18	-	Michigan, USA	Burch, 1960b
<i>S. p. desidiosa</i>	36	-	18	-	Michigan, USA	Burch, 1960b
<i>S. p. wyomingensis</i>	-	36	18	18	Colorado, USA	Inaba (this paper)
<i>S. umbrosa</i>	36	-	18	-	Michigan, USA	Burch, 1960b; Inaba (this paper)
<i>S. exilis</i>	-	36	18	18	Michigan, USA	Burch, 1960b; Inaba (this paper)
<i>S. catascopium</i>	-	36	18	-	Michigan, USA	Burch, 1960b; Inaba (this paper)
<i>S. reflexa</i>	-	-	18	-	Ohio, USA	Burch, 1960b
<i>S. lanceata</i>	-	-	-	18	Minnesota, USA	Burch, 1960b
<i>S. emarginata serrata</i>	36	-	18	-	Michigan, USA	Burch, 1960a,b; Inaba (this paper)
<i>S. hinkleyi</i>	-	-	18	-	Wyoming, USA	Inaba (this paper)
<i>S. idahoensis</i>	36	-	-	-	Idaho, USA	Inaba (this paper)
<i>S. cf. bonnevillensis</i>	36	-	18	-	Wyoming, USA	Inaba (this paper)
<i>S. (Hinkleyia) caperata</i>	-	-	18	-	Ohio, USA	Burch, 1960b
<i>S. (H.) montanensis</i>	36	-	18	-	Idaho, USA	Burch, 1963
<i>Acella</i>						
<i>A. haldemani</i>	36	-	18	-	Michigan, USA	Burch, 1960b
<i>Pseudosuccinea</i>						
<i>P. columella</i>	36	-	18	-	Va., Mich., USA	Burch, 1960b; Inaba (this paper)

spg = spermatogonia; som = somatic mitosis; spc = spermatocyte; oöc = oöcyte.

Table 2 (cont.)

Species	Chromosome number				Source	Reference
	2n		n			
	spg	som	spc	oöc		
<i>Bulinnea</i>						
<i>B. megasoma</i>	36	36	18	-	Michigan, USA	Burch, 1960a,b; Inaba (this paper)
<i>Fossaria</i>						
<i>F. parva</i>	-	-	18	-	Michigan, USA	Burch, 1960a,b; Inaba (this paper)
<i>F. modicella</i>	36	-	18	-	Ohio, Mich., USA	Burch, 1960b; Inaba (this paper)
<i>F. truncatula</i>	36	-	18	-	Japan	Burch, et al., 1964
<i>F. sp. (= truncatula)</i>	-	-	18	-	Japan	Burch, 1965
<i>F. rustica</i>	38	38	19	-	Mich., Ohio, USA	Burch, 1960b; Inaba (this paper)
<i>Radix</i>						
<i>R. auricularia</i>	-	-	17	-	Switzerland	Perrot & Perrot, 1938
<i>R. a. swinhoei</i>	-	-	17	-	Formosa	Burch & Natarajan, 1965
<i>R. a. japonica</i>	34	-	17	-	Japan	Burch, et al., 1964; Inaba, 1965
<i>R. ovata</i>	-	-	17	-	Switzerland	Perrot & Perrot, 1938
<i>R. peregra</i>	-	-	17	-	Switzerland	Perrot & Perrot, 1938
	34	-	17	-	Turkey	Burch, 1960b
<i>R. onychia</i>	34	-	17	-	Japan	Burch, et al., 1964
<i>R. luteola</i>	34	-	17	-	India	Natarajan, 1960
<i>R. hovarum</i>	-	-	17	-	Madagascar	Burch, 1965
<i>R. sp.</i>	-	-	17	-	Italy	Burch, 1965
<i>R. natalensis</i>	34	-	17	-	Liberia	Inaba (this paper)
" <i>R. limosa</i> "	36	-	18	-	Europe	La Calvez & Certain, 1950
" <i>Lymnaea</i> "						
" <i>L.</i> " (" <i>Radix</i> ") <i>ollula</i> (= <i>viridis</i> ?)	32	-	16	-	Japan	Burch, et al., 1964; Inaba, 1965
" <i>L.</i> " <i>tomentosa</i>	32	-	16	-	Australia	Inaba (this paper)
" <i>L.</i> " <i>lessoni</i>	-	-	16	-	Papua	Inaba (this paper)

number 18, but *F. rustica* has 19. All species of *Radix* have 17 pairs of chromosomes. "*Lymnaea*" *tomentosa* and "*L.*" *lessoni* have the same chromosome number, $n=16$ as "*L.*" *ollula* (= *viridis*?).

The use of spermatogonial or spermatocyte chromosomes as taxonomic characters at the level of the lower taxonomic categories is very difficult because these chromosomes are small and do not show remarkably diverse characters. The majority or all of the spermatogonial metaphases of all the species examined had elongate chromosomes that were medianly or submedianly constricted. However, the chromosomes of the mitotic divisions in early development of the embryos are very useful for caryotype analysis because their size and shape are larger and longer than the spermatogonial chromosomes. Since the size and shape of the chromosomes are changed rather easily by the pressure of squashing (see Figs. 56-57 and 60-61), it is very difficult at present to get constant figures of chromosomes. But this variability seems to be controlled by the time of fixation or staining. At any rate, such studies show considerable promise as an aid toward clarifying systematics in the lower taxonomic categories.

In the following paragraphs, I wish to discuss some taxonomic points based on cytological studies in each chromosome number group, and possible phylogenetic relationships within the Lymnaeidae.

I. Cytotaxonomic considerations in Lymnaeidae.

1. *Stagnicola* and others, 18(n) groups (except *Fossaria*).

Stagnicola is the most extensively studied generic group. The chromosomes of 15 species and subspecies have been observed. All of them have 18 pairs of chromosomes. *Lymnaea*, *Acel-*

la, *Pseudosuccinea* and *Bulinnea* also have 18 pairs of chromosomes. No distinct morphological difference or remarkable characteristics have been found between the caryotypes of these genera. It is difficult to analyze spermatogonial caryotypes, but from observations on somatic chromosomes, it may be possible to use the latter caryotype for comparisons at the species level. However, in order to critically analyze such caryotypes, more detailed and numerous observations are desirable. At present, in comparing the somatic caryotypes of 3 *Stagnicola* species, the author wishes to point out only the following few features: (1) Generally, most of the chromosomes are meta- or submetacentric in nature, but in *S. palustris wyomingensis*, the 11th chromosome is more or less subtelocentric; (2) The chromosomes decrease gradually in length from the 2nd down to the last (18th), but the 1st chromosome is noticeably longer than the rest. The 2nd chromosome is 83% of the length of the 1st one in *S. palustris wyomingensis*, but only 80% in *S. exilis* and 72% in *S. catascopium* (Figs. 68-70).

Stagnicola species have bicuspid lateral radular teeth (Figs. 71-74). The genus *Lymnaea* also has bicuspid laterals, but the 1st lateral occasionally has 3 cusps. Other genera, e.g., *Acella*, *Pseudosuccinea* and *Bulinnea*, have tricuspid lateral teeth. Hubendick (1951) considers that there is nothing with definite taxonomic importance among these generic names. However, I find it convenient to classify the $n=18$ group into the above genera on characters of the shells, and morphology of the radulae and genitalia.

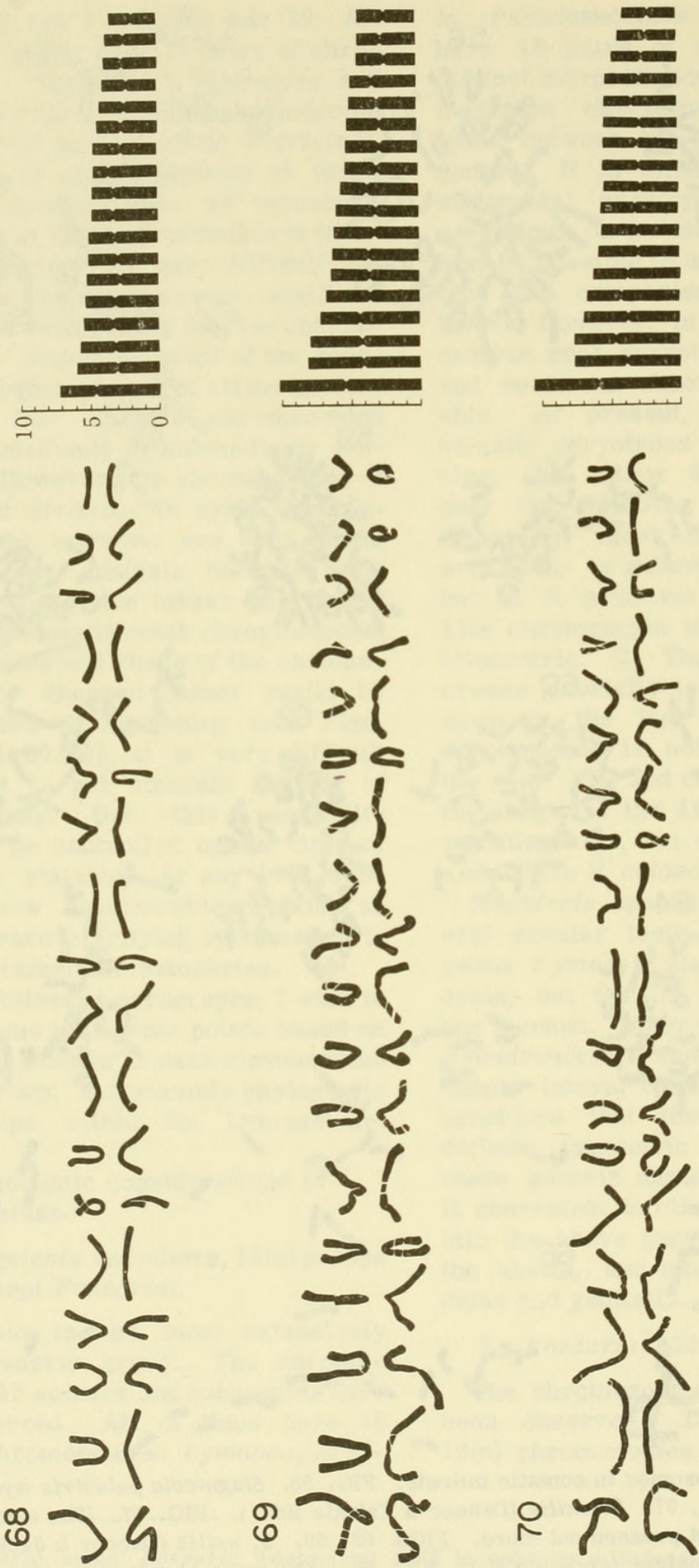
2. *Fossaria*³, 18(n), 19(n) group.

The chromosomes of 5 species have been observed. These species have 18(n) chromosomes as in the preceding

³The generic name *Fossaria* Westerlund 1885 is used here instead of *Galba* Schranck 1803, according to the opinion of Baker (1928).



FIGS. 55-67. Chromosomes in somatic mitosis. FIG. 55. *Stagnicola palustris wyomingensis* (Giggey Lake). FIG. 56, 57. *S. exilis* (Dancer & Trinkle Rds.). FIG. 57. The same chromosomes as in Fig. 56, but pressed out more. FIGS. 58, 59. *S. exilis* (Dancer & Jackson Rds.). FIGS. 60-63. *S. catascopium* (Au Sable R.). FIG. 61. The same chromosomes as in Fig. 60, but pressed out more. FIG. 64. *Bulinnea megasoma*. FIGS. 65-67. *Fossaria rustica* (Dexter).



FIGS. 68-70. Serial arrangement and schematic representation of the somatic metaphase karyotypes of 3 *Stagnicola* species. FIG. 68. *Stagnicola palustris wyomingensis* (chromosomes shown in Fig. 55). FIG. 69. *S. exilis* (chromosomes shown in Fig. 56). FIG. 70. *S. catascopium* (chromosomes shown in Fig. 63). Scale: 10 microns.

group, with only one known exception (*Fossaria rustica*, $n=19$). Morphological differences in the chromosomes could not be found between *Fossaria* (except *F. rustica*) and the other 18(n) group. These small lymnaeid snails have tricuspid lateral teeth, without exception (Figs. 78-81).

Burch (1960b) observed that *Fossaria modicella rustica* has the haploid chromosome number 19 and considered it to have gained 1 bivalent in addition to the 18 of an original species, *F. modicella*. My studies on this species collected from the same locality confirm his observations, and in addition, I found that this same species from Ohio also has 19(n) chromosomes. The additional 19th chromosome was small and rather weakly stained in the 1st spermatocyte diakinesis. These cytological features indicate that *F. rustica* is not a variety of *F. modicella*, but a new species which originated (probably) from *F. modicella* by the addition of 1 bivalent, i.e., by natural aneuploidy (hyperploidy). As such, *F. rustica* seems to be a species that has appeared rather recently. It originally had been described by Lea (1841) as *Lymnea rustica*; Baker (1928) considered it as a variety of *F. modicella*. Body features, genitalia, jaw and radula seem to be similar in all respects to those of *F. modicella*. The ecological habitat is also similar to *F. modicella*. Hubendick (1951) stated that "*L. parva* Lea, "*L. humilis modicella* Say, "*L. humilis rustica* Lea, and similar fossarid species in Baker's (1911) monograph must probably be linked to

"*Lymnaea*" *humilis* Say, according to characteristics of the shell, radula and genitalia. But he mentioned in his preceding part that the first laterals of "*L. humilis*" were bicuspid (in his figure, the 2nd lateral is also bicuspid). Therefore, it would seem that his material, at least that from California, was probably small specimens of some *Stagnicola* species.

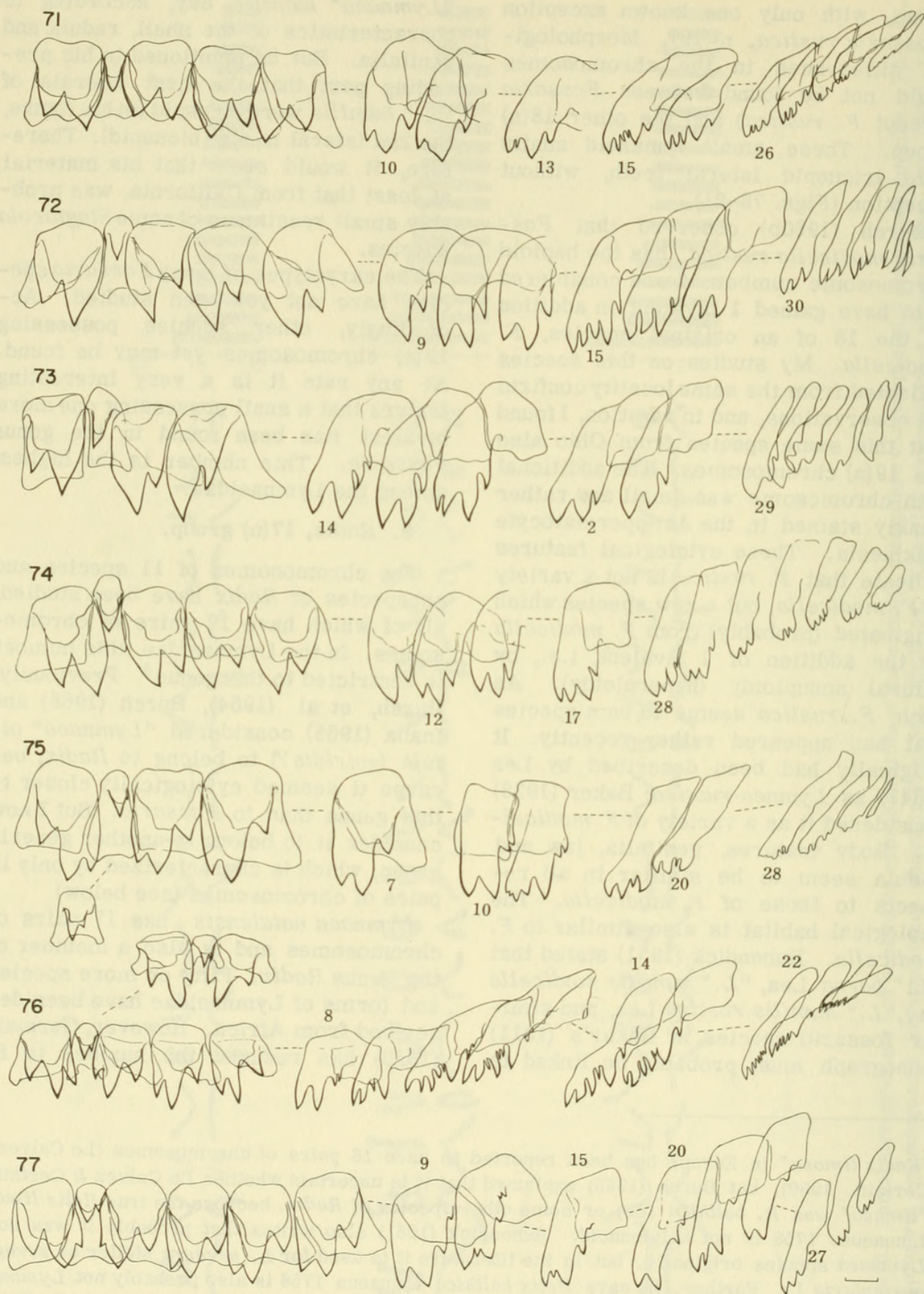
The caryotypes of many *Fossaria* species have not yet been studied. Accordingly, other species possessing 19(n) chromosomes yet may be found. At any rate it is a very interesting feature that a snail possessing one more bivalent has been found in the genus *Fossaria*. This number is the highest among the Lymnaeidae.

3. *Radix*, 17(n) group.

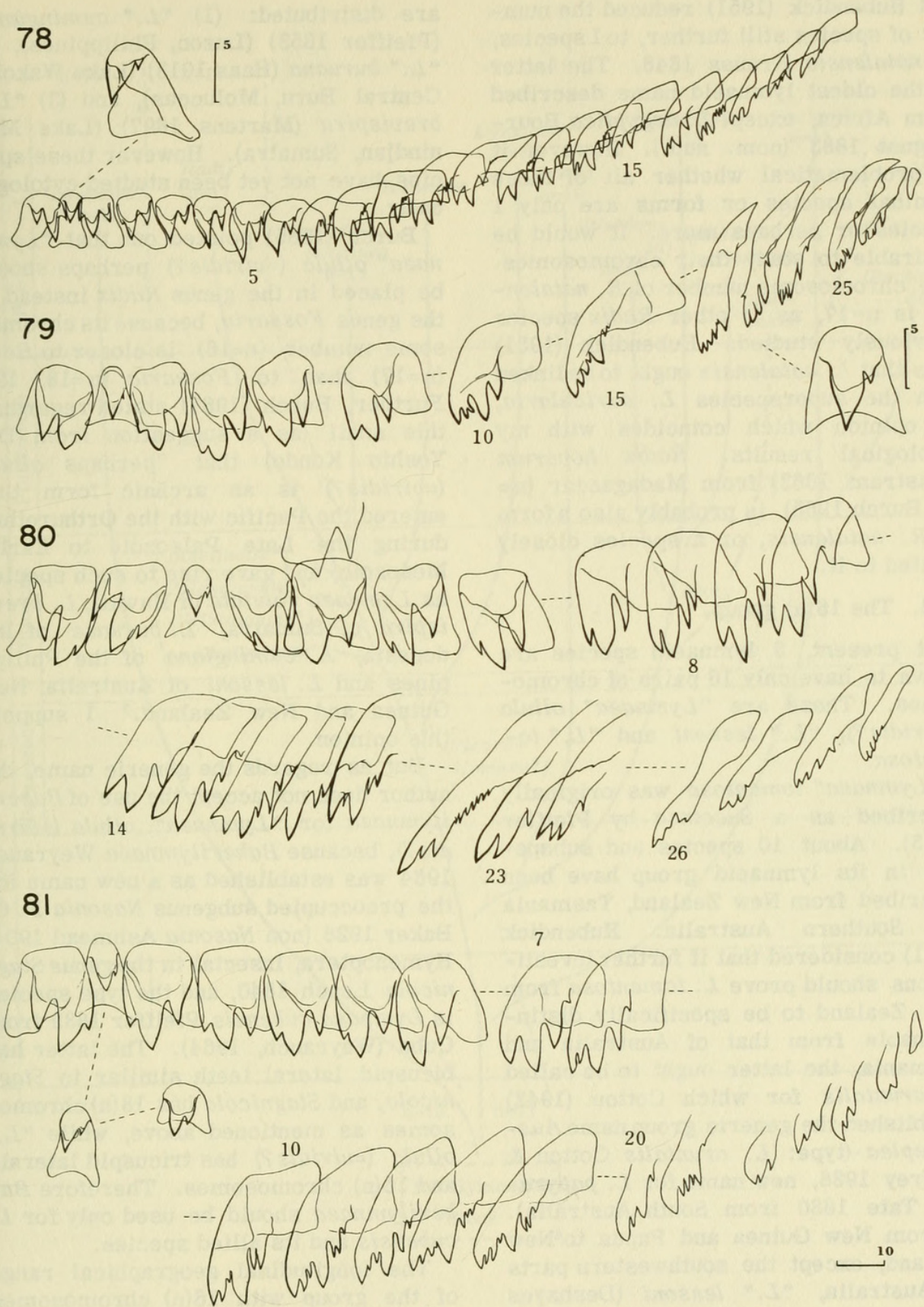
The chromosomes of 11 species and subspecies of *Radix* have been studied, all of which have 17 pairs of chromosomes. In the Lymnaeidae, this number is restricted to this genus⁴. Previously, Burch, et al. (1964), Burch (1965) and Inaba (1965) considered "*Lymnaea*" *olulula* (= *viridis*?) to belong to *Radix*, because it seemed cytologically closer to this genus than to *Fossaria*. But I now consider it to belong to another generic group, which is characterized by only 16 pairs of chromosomes (see below).

Lymnaea natalensis has 17 pairs of chromosomes and is also a member of the genus *Radix*. Fifty or more species and forms of Lymnaeidae have been described from Africa. However, Germain (1919) has reduced the number to 6,

⁴"*Radix limosa*" in Europe has been reported to have 18 pairs of chromosomes (Le Calvez & Certain, 1950), but Burch (1965) explained that it is uncertain whether Le Calvez & Certain's "*limosa*" was *R. balthica* (L.) or some other species of *Radix*, because the true *Helix limosa* Linnaeus, 1758 is not a lymnaeid. Hubendick (1951) also writes that probably it was not a *Lymnaea* species originally, but in the literature it is used for *L. peregra* Müller or *peregra auricularia* L. Further, he says *Helix balthica* Linnaeus 1758 is also probably not *Lymnaea*, but used for *P. peregra* by mistake in the literature. At any rate, Le Calvez and Certain's species, whatever it is, should be re-examined.



FIGS. 71-77. Radulae of Lymnaeidae. FIG. 71. *Stagnicola palustris wyomingensis* (Giggey Lake). FIG. 72. *S. catascopium* (Au Sable R.). FIG. 73. *S. emarginata serrata*. FIG. 74. *S. hinkleyi*. FIG. 75. *Radix natalensis*. FIG. 76. "*Lymnaea*" *tomentosa*. FIG. 77. "*Lymnaea*" *lessoni*. Scale: 10 microns.



FIGS. 78-81. Radulae of Lymnaeidae. FIG. 78. *Fossaria parva*. FIG. 79. *F. modicella* (Burnt Cabin Point). FIG. 80. *F. rustica* (Dexter). FIG. 81. *F. rustica* (Toledo). Scale: 10 microns, except the figures of 2 central teeth in Figs. 78, 79.

and Hubendick (1951) reduced the number of species still further, to 1 species, *L. natalensis* Krauss 1848. The latter is the oldest lymnaeid name described from Africa, except *L. aegyptica* Bourguignat 1883 (nom. nud.). However it is problematical whether all of those nominal species or forms are only 1 species or perhaps more. It would be desirable to study their chromosomes. The chromosome number of *R. natalensis* is $n=17$, as in other *Radix* species previously studied. Hubendick (1951) says that *L. natalensis* ought to be linked with the superspecies *L. auricularia*, an opinion which coincides with my cytological results. *Radix hoverum* (Tristram 1863) from Madagascar ($n=17$, Burch 1965) is probably also a form of *R. natalensis*, or a species closely related to it.

4. The 16(n) group.

At present, 3 lymnaeid species are known to have only 16 pairs of chromosomes. These are "*Lymnaea*" *ollula* (=viridis?), "*L.*" *lessoni* and "*L.*" *tomentosa*.

"*Lymnaea*" *tomentosa* was originally described as a *Succinea* by Pfeiffer (1855). About 10 species and subspecies in its lymnaeid group have been described from New Zealand, Tasmania and Southern Australia. Hubendick (1951) considered that if further investigations should prove *L. tomentosa* from New Zealand to be specifically distinguishable from that of Australia and Tasmania, the latter ought to be called *L. aruntalis* for which Cotton (1942) established the generic group name *Austropeplea* (type: *L. aruntalis* Cotton & Godfrey 1938, new name for *L. papyracea* Tate 1880 from South Australia).

From New Guinea and Papua to New Zealand, except the southwestern parts of Australia, "*L.*" *lessoni* (Deshayes 1831) occurs. About 20 forms have been reported in this species group.

Between the geographical distributions of the above 2 species groups and "*Lymnaea*" *viridis*, at least 3 species

are distributed: (1) "*L.*" *cumingiana* (Pfeiffer 1853) (Luzon, Philippines), (2) "*L.*" *buruana* (Haas 1913) (Lake Wakolo, Central Buru, Moluccas), and (3) "*L.*" *brevispira* (Martens 1897) (Lake Manindjan, Sumatra). However these species have not yet been studied cytologically.

Burch (1965) pointed out that "*Lymnaea*" *ollula* (=viridis?) perhaps should be placed in the genus *Radix* instead of the genus *Fossaria*, because its chromosome number ($n=16$) is closer to *Radix* ($n=17$) than to *Fossaria* ($n=18, 19$). Further, Burch (1967) stated regarding this snail (as a suggestion from Dr. Yoshio Kondo) that "perhaps *ollula* (=viridis?) is an archaic form that entered the Pacific with the *Orthurethra* during the Late Paleozoic to Early Mesozoic, and gave rise to such species as *Lymnaea volutata* of Hawaii, *L. brevispira* of Sumatra, *L. buruana* of Indonesia, *L. cumingiana* of the Philippines and *L. lessoni* of Australia, New Guinea and New Zealand." I support this opinion.

But as regards the generic name, the author does not accept the use of *Bakerilymnaea* for "*Lymnaea*" *ollula* (=viridis?), because *Bakerilymnaea* Weyrauch 1964 was established as a new name for the preoccupied subgenus *Nasonia* F. C. Baker 1928 (non *Nasonia* Ashmead 1904; Hymenoptera, Insecta) in the genus *Stagnicola* Leach 1840, and the type species is *Lymnaea cubensis* Pfeiffer 1839 from Cuba (Weyrauch, 1964). The latter has bicuspid lateral teeth similar to *Stagnicola*, and *Stagnicola* has 18(n) chromosomes as mentioned above, while "*L.*" *ollula* (=viridis?) has tricuspid laterals and 16(n) chromosomes. Therefore *Bakerilymnaea* should be used only for *L. cubensis* and its allied species.

The longitudinal geographical range of the group with 16(n) chromosomes extends from the eastern part of Asia to Australia. It is a very interesting problem as to whether or not this unique distribution occurred for geological reasons. Further cytological studies on

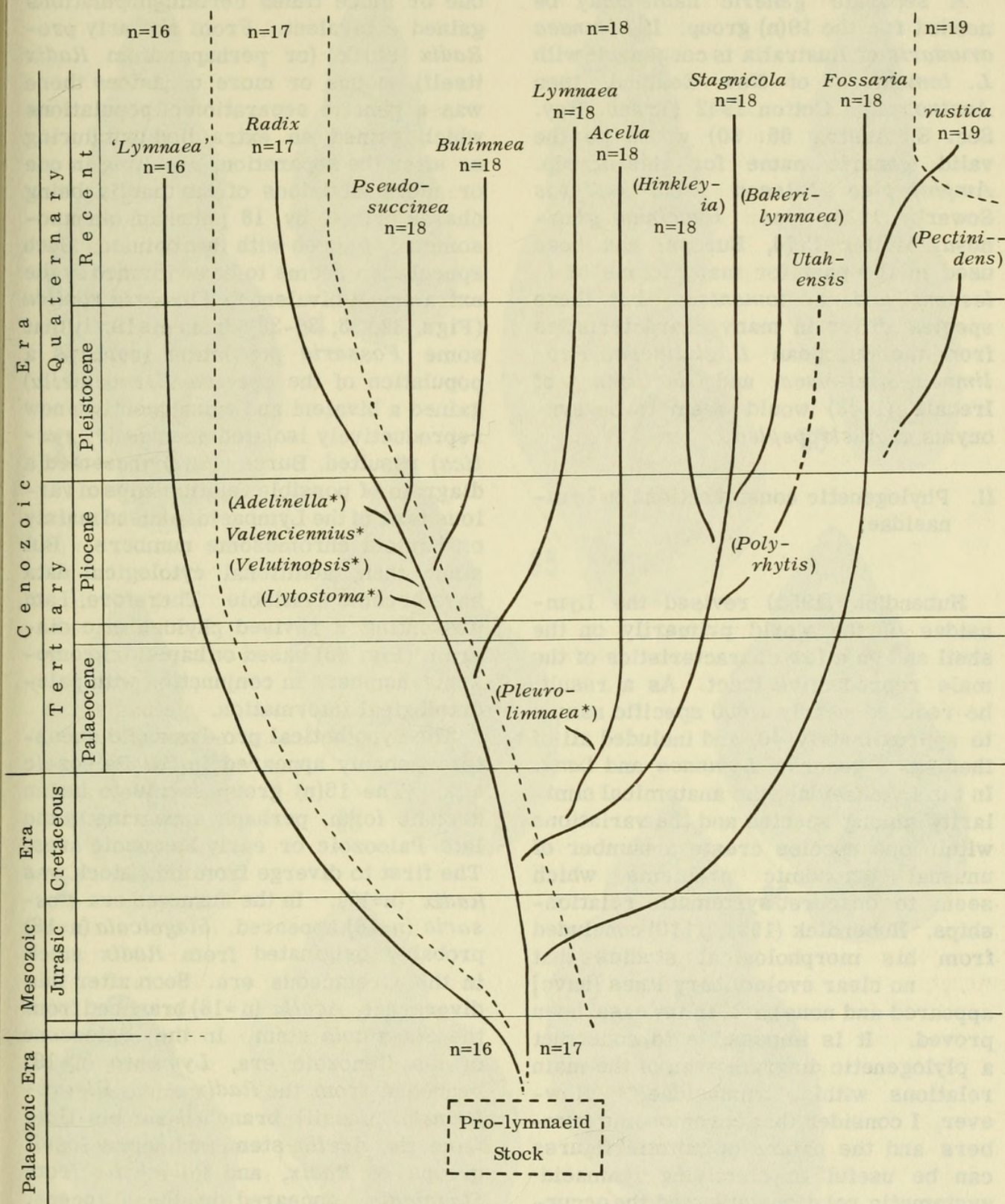


FIG. 82. Hypothetical phylogenetic diagram of the lymnaeid genera and subgenera based partly on haploid chromosome numbers, with consideration of fossil groups and geological data. * marks fossil groups not found in the Recent. Paleontological information from Zilch (1959-60, Gastropoda, Teil 2, Euthyneura, In: Schindewolf, Handbuch der Paläozoologie, v. 6, Borntraeger, Berlin, xii + 834 p (p 91-102)).

these geographical groups are desirable.

A separate generic name may be needed for the 16(n) group. If *Lymnaea aruntaris* of Australia is congeneric with *L. tomentosa* of New Zealand, then *Austropeplea* Cotton 1942 (Trans. Roy. Soc. S. Austr., 66: 80) would be the valid generic name for this group. *Amphipeplea* Nilsson 1822 (= *Myxas* Sowerby 1822; type: *Buccinum glutinosa*, Müller 1774, Europe) has been used in the past for many forms of *L. lessoni* and *L. tomentosa*, but these species differ in many characteristics from the European *L. glutinosa*. *Pep- limnea*, *Simlimnea* and *Glacilimnea* of Iredale (1943) would seem to be synonyms of *Austropeplea*.

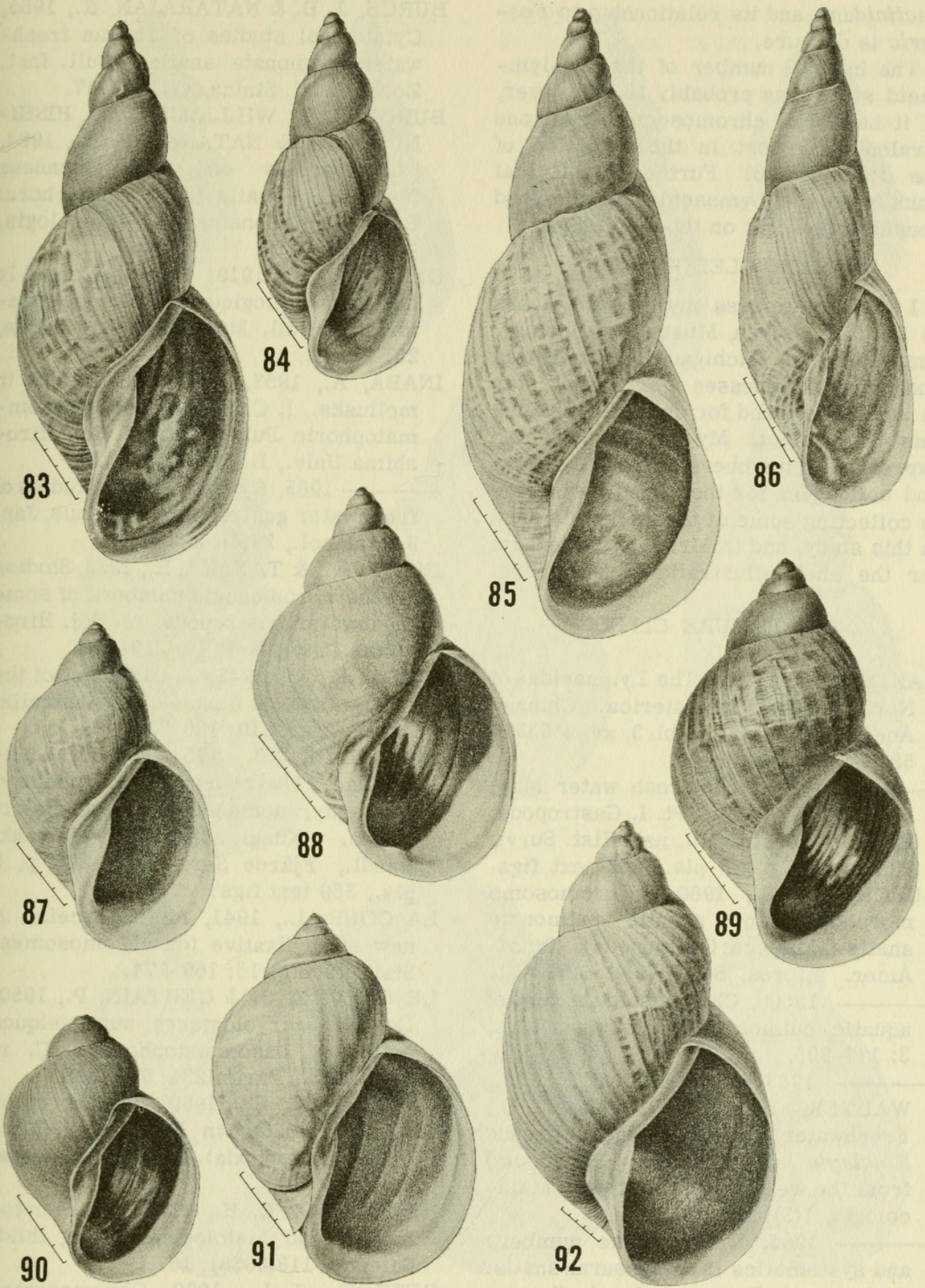
II. Phylogenetic considerations in Lymnaeidae.

Hubendick (1951) revised the Lymnaeidae of the world primarily on the shell and on a few characteristics of the male reproductive tract. As a result, he reduced nearly 1,800 specific names to approximately 40, and included all of them in 2 genera: *Lymnaea* and *Lanx*. In the Lymnaeidae, the anatomical similarity among species and the variations within one species create a number of unusual taxonomic problems which seem to obscure systematic relationships. Hubendick (1951, p 110) concluded from his morphological studies that "... no clear evolutionary lines [have] appeared and none have, in any case, been proved. It is impossible to construct a phylogenetic diagram even of the main relations within Lymnaeidae." However, I consider that chromosome numbers and the nature of mitotic figures can be useful in clarifying lymnaeid systematic relationships, and the occurrence of 3 different chromosomal groups verifies this.

Burch (1965; 1967, p 122) considered that "the original pro-limnaeid stock had less than 18 chromosomes, and that this stock gave rise to *Radix* which gained wide geographic distribution re-

taining 17 pairs of chromosomes, but one or more times certain populations gained a bivalent. From an early pro-*Radix* stock (or perhaps from *Radix* itself) on one or more occasions there was a genetic separation of populations which gained an extra bivalent during or after the separation, resulting in one or more divisions of the family being characterized by 18 pairs of chromosomes." I agree with this opinion. Such speculation seems to be confirmed by the extra small bivalent in *Fossaria rustica* (Figs. 32, 33, 36-38). It seems likely that some *Fossaria* population (perhaps a population of the species *L. modicella*) gained a bivalent and subsequently a new reproductively isolated species (*F. rustica*) resulted. Burch (1965) presented a diagram of possible relationships of various taxa of the Lymnaeidae based mainly on haploid chromosome numbers. But since then, additional cytological data have become available. Therefore, I am presenting a revised phylogenetic diagram (Fig. 82) based on haploid chromosome numbers in conjunction with paleontological information.

The hypothetical pro-lymnaeid ancestor probably appeared in the Paleozoic era. The 16(n) group seems to be an archaic form, perhaps appearing in the late Paleozoic or early Mesozoic eras. The first to diverge from this stock was *Radix* (n=17). In the Jurassic era *Fossaria* (n=18) appeared. *Stagnicola* (n=18) probably originated from *Radix* stock in the Cretaceous era. Soon after this divergence, *Acella* (n=18) branched from the *Stagnicola* stem. In the Paleocene of the Cenozoic era, *Lymnaea* (n=18) branched from the *Radix* stem. *Pleurolimnaea* (fossil) branched in this time from the *Acella* stem, and many fossil groups of *Radix*, and *Polyrhytis* from *Stagnicola*, appeared in the Pliocene. From the middle to late Pliocene, *Hinkleyia* and *Bakerilymnaea* branched from the *Stagnicola* stem. At almost the same time, *Bulimnea* and *Pseudosuccinea* appeared, probably from the *Radix* stem. Recently a 19(n) species originated within the *Fossaria* group. The origin of



FIGS. 83-92. Shells of snails used in this study. FIG. 83. *Stagnicola palustris wyomingensis* (Giggey Lake). FIG. 84. *S. p. wyomingensis* ("Lodge of the Pines"). FIG. 85. *S. umbrosa*. FIG. 86. *S. exilis* (Dancer and Trinkle Rds.). FIG. 87. *S. catascopium* (Au Sable R.). FIG. 88. *S. cf. bonnevillensis*. FIG. 89. *S. hinkleyi*. FIG. 90. *S. idahoensis*. FIG. 91. *S. emarginata serrata*. FIG. 92. *Bulinnea megasoma*. Measurement lines in mm.

Pectinidens and its relationship to *Fossaria* is obscure.

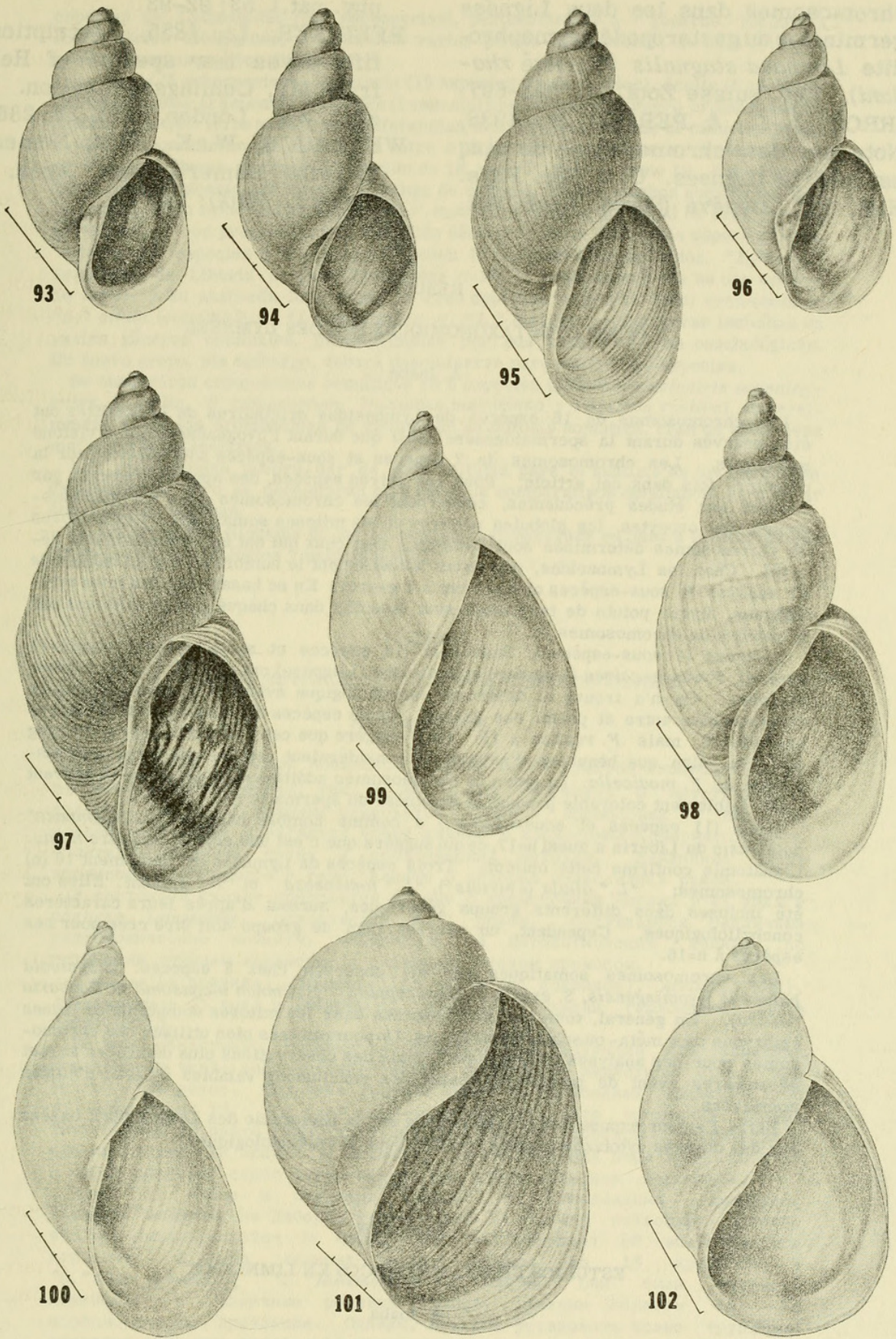
The haploid number of the pro-lymnaeid stock was probably 16. However, if it had 17(n) chromosomes, then one bivalent was lost in the evolution of the 16(n) group. Further cytological studies on the Lymnaeidae should shed considerable light on this subject.

ACKNOWLEDGEMENT

I wish to express my sincere thanks to Dr. J. B. Burch, Museum of Zoology, University of Michigan, for facilities and many kindnesses during my stay in Ann Arbor, and for critically reading this manuscript. My gratitude is also expressed to members of his laboratory and colleagues for their kind assistance in collecting some of the materials used in this study, and to Mr. J. L. Tottenham for the shell illustrations used here.

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FIGS. 93-102. Shells of snails used in this study. FIG. 93. *Fossaria parva*. FIG. 94. *F. modicella* (Parker's mill). FIG. 95. *F. rustica* (Toledo). FIG. 96. *F. modicella* (Comstock). FIG. 97. *F. rustica* (Dexter). FIG. 98. *F. modicella* (Burnt Cabin Point). FIG. 99. *Radix natalensis*. FIG. 100. *Pseudosuccinea columella*. FIG. 101. "*Lymnaea*" *lessoni*. FIG. 102. "*Lymnaea*" *tomentosa*. Measurement lines in mm.

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RÉSUMÉ

ETUDES CYTOTAXONOMIQUES SUR DES LYMNÉES

A. Inaba

Les chromosomes de 16 espèces de Lymnaeidae originaires de 22 localités ont été observés durant la spermatogénèse ainsi que durant l'ovogénèse et les divisions mitotiques. Les chromosomes de 7 espèces et sous-espèces sont décrits pour la première fois dans cet article. Pour les autres espèces, des apports nouveaux par rapport aux études précédentes, concernent les chromosomes dans les spermatogonies, les ovocytes, les globules polaires et les mitoses somatiques. Les nombres de chromosomes déterminés sont comparés avec ceux qui ont été précédemment décrits. Chez les Lymnaeidae, on connaît actuellement le nombre de chromosomes de 41 espèces et sous-espèces appartenant à 7 genres. En se basant sur des faits cytologiques, divers points de taxonomie sont discutés dans chaque groupe différant par le nombre de chromosomes.

Lymnaea (4 sous-espèces), *Stagnicola* (15 espèces et sous-espèces), *Acella* (1 espèce), *Pseudosuccinea* (1 espèce) et *Bulinnea* (1 espèce) ont tous 18 comme nombre haploïde. On n'a trouvé ni différence morphologique évidente, ni caractéristiques remarquables entre et parmi ces genres. Trois espèces de *Fossaria* ont le nombre haploïde 18, mais *F. rustica* a 19. Ceci suggère que cette dernière mérite le rang d'espèce, bien que beaucoup d'auteurs la considéraient comme une forme ou sous-espèce de *F. modicella*. La paire de chromosomes additionnelle est petite et souvent assez faiblement colorable pendant la diacinèse du spermatocyte.

Radix (11 espèces et sous-espèces) a comme nombre haploïde 17. "*Lymnaea*" *natalensis* du Libéria a aussi $n=17$, ce qui suggère que c'est une espèce du genre *Radix*. L'anatomie confirme cette opinion. Trois espèces de Lymnées ont seulement 16 (n) chromosomes: "*L.*" *ollula* (= *viridis*?), "*L.*" *tomensosa* et "*L.*" *lessoni*. Elles ont été incluses dans différents groupes génériques, surtout d'après leurs caractères conchyliologiques. Cependant, un nouveau nom de groupe doit être créé pour ces espèces à $n=16$.

Les chromosomes somatiques ont été observés chez 5 espèces: (*Stagnicola palustris wyomingensis*, *S. exilis*, *S. catascopium*, *Bulinnea megasoma* et *Fossaria rustica*). En général, tous les chromosomes dans les mitoses somatique de jeunes embryons sont méta- ou submétacentriques. On pourrait très bien utiliser ces chromosomes pour des analyses caryotypiques, mais des observations plus détaillées seront nécessaires avant de pouvoir esquisser des conclusions valables à partir d'études comparées.

Enfin, l'auteur expose des considérations sur la phylogénie des Lymnaeidae, basées sur des données cytotaxonomiques, cytologiques et paléontologiques.

RESUMEN

ESTUDIOS CITOTAXONOMICOS EN LIMNEIDOS

A. Inaba

Se observaron los cromosomas en 16 especies de limneidos, durante sus espermatogenesis, ovogensis y divisiones mitóticas. Se informa por primera vez acerca de los cromosomas de 7 especies y subespecies, y para otras se agrega nuestro conocimiento a los ya previamente informados de la espermatogenesis, oocitos, cuerpos polares y mitosis somática. Se conoce hasta ahora el número cromosómico de 41

especies de Lymnaeidae (con subespecies), pertenecientes a 7 géneros. En base a los aspectos citológicos, se discuten varios puntos taxonómicos, en cada grupo de número cromosómico diferente.

Lymnaea (4 subespecies), *Stagnicola* (15 especies y subespecies), *Acella* (1 especie), *Pseudosuccinea* (1 especie), *Bulinnea* (1 especie) tienen todas el número cromosómico haploide o de 18. No se encontraron diferencias morfológicas obvias, ni características notables, para distinguir cariotipos entre o dentro de esos géneros. Tres especies de *Fossaria* llevan el número haploide de 18, pero *F. rustica* tiene 19. Esto sugiere que la última debería ser elevada al rango de especie, aunque muchos autores previos la consideraban como una subespecie de *F. modicella*. El par adicional de cromosomas es pequeño y con frecuencia tinte más bien débil durante la diakinesis espermatocita.

Radix (11 especies y subespecies) tienen 17 cromosomas haploides. "*Lymnaea*" *natalensis* de Liberia también tiene $n=17$, lo cual sugiere que es una especie de *Radix*, y su anatomía lo confirma. Tres especies tienen sólo 16(n) cromosomas: "*L.*" *ollula* (= *viridis*?), "*L.*" *tomentosa* y "*L.*" *lessoni*; estas fueron incluidas en varios géneros nominales, principalmente por sus características conchológicas. Un nuevo grupo, sin embargo, deberá denominarse para estas 16(n) especies.

Se observaron cromosomas somáticos en 5 especies (*Stagnicola palustris wyomingensis*, *S. exilis*, *S. catascopium*, *Bulinnea megasoma* y *Fossaria rustica*). Generalmente, todos los cromosomas de embriones en mitosis somática, eran de naturaleza meta- o submetacéntrica.

Los cromosomas pueden ser de gran utilidad para el análisis de los cariotipos de limneidos, pero se necesitarán más estudios comparativos detallados, para sacar conclusiones seguras.

Se presenta una filogenia de los Lymnaeidae, considerada en base a la información citotaxonómica, citológica y paleontológica.

АБСТРАКТ

ЦИТОТАКСОНОМИЧЕСКОЕ ИССЛЕДОВАНИЕ МОЛЛЮСКОВ-ЛИМНЕИД

АКИХИКО ИНАБА

Хромо-сомы 16 видов моллюсков лимнеид из 22 пунктов наблюдались как в течение сперматогенеза, так и во время овогенеза и митотического деления. В статье впервые приводятся данные о хромосомах 7 видов и подвидов, а также излагаются новые данные о хромосомах в сперматогониях, ооцитах, полярных телах и соматических митозах. Найденные числа хромосом сравниваются с теми, данные о которых приводились ранее.

В настоящей статье приводятся данные о хромосомных числах у 41 вида и подвида Lymnaeidae, относящихся к 7 родам. Обсуждаются различные таксономические моменты, основанные на цитологических данных по различным группам моллюсков с различным числом хромосом.

Lymnaea (4 подвида), *Stagnicola* (15 видов и подвидов), *Acella* (1 вид), *Pseudosuccinea* (1 вид) и *Bulinnea* (1 вид) - все имели гаплоидное число хромосом 18.

Не было обнаружено никаких морфологических различий или заметных характерных черт, достаточных, чтобы различить карiotипы среди или внутри этих родов. Три вида *Fossaria* имеют 18 гаплоидных хромосом, но *F. rustica* имеет 19. Это дает основание думать, что последний должен быть поднят до ранга вида, хотя многие авторы в прошлом рассматривали его как форму или подвида *F. modicella*. Дополнительная пара хромосом мала и часто довольно слабо окрашивается при сперматоцитном диакинезе.

Radix (11 видов и подвидов) имеет 17 гаплоидных хромосом, "*Lymnaea*" *natalensis* из Либерии также имеет $n=17$, что позволяет думать, что она тоже относится к *Radix*, что подтверждает её анатомическое строение. 3 вида лимнеид имеют только по 16 хромосом: 4 "*L.*" *ollula* (= *viridis*?), "*L.*" *tomentosa* и "*L.*" *lessoni*. Они были включены номинально в различные родовые группы, главным образом по их морфологическим признакам. Однако, следует установить новые групповые названия для этих видов с 16 хромосомами.

Соматические хромосомы наблюдались у 5 видов (*Stagnicola palustris wyomingensis*, *S. exilis*, *S. catascopium*, *Bulinnea megasoma* и *Fossaria rustica*). В общем, все хромосомы в соматических митозах молодых эмбрионов были мета-или субметацентрическими по своей природе. Эти исследования хромосом могут быть очень полезными при анализе кариотипа лимнейд, но для получения более достоверных данных необходимы более детальные сравнительные наблюдения.



Inaba, Akihiko. 1969. "Cytotaxonomic studies of lymnaeid snails." *Malacologia* 7, 143–168.

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