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A NEW PLEISTOCENE FAUNULE FROM MEADE COUNTY, KANSAS

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ABSTRACT

A molluscan faunule of Kansan age, here named the Silage Pit faunule, containing 31 species, is reported from Meade County, Kansas. The stratigraphic sequence at the Silage Pit, and the geologic ranges of the assemblage suggest a Kansan age for the sediments from which the faunule was collected. The faunule, assigned to the Cudahy fauna, contains one species, *Strobilops affinis (?)* not previously reported from other Cudahy assemblages. The habitats inferred from the molluscan assemblage consist of a marsh, probably bordering a small pond, and surrounded by tall grass, brush, and scattered trees.

The climate at the time the faunule lived was probably characterized by cooler summers than those of the present. Precipitation was probably more effective, due to less evapotranspiration, or greater in amount than at present.

INTRODUCTION

The present paper describes a Kansan molluscan faunule from a new locality of the Cudahy fauna. The material was collected by Dr. B. B. Miller and members of the Kent State University Geology Department field party, during the summer of 1971, from a silage storage pit located approximately one mile NNE of the Sunbrite Ash mine, NE ¼ sec. 23, T. 32, S., R. 28 W., Meade County, Kansas (Figure 1). Assignment of this fossil material to the Cudahy fauna is based on the identification and study of the 31 species of mollusks recovered from the sample, and the stratigraphic position of the sediments from which the matrix was collected.

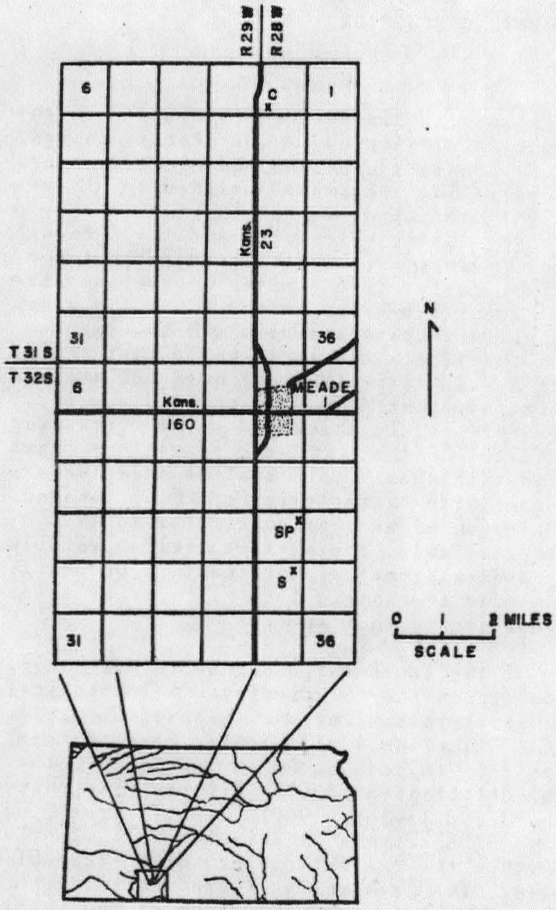


FIGURE 1. Index map showing location of the Silage Pit, Sunbrite Mine and Cudahy Mine localities of the Cudahy fauna, Meade County, Kansas.

THE SILAGE PIT FAUNULE

The Silage Pit faunule consists of 31 species of mollusks. A complete list of the species and their geologic ranges, based on data from Taylor (1960), Hibbard and Taylor (1960), and Miller (1966), is presented in Table 1, along with the corresponding Kent State University Paleontological Collection catalogue numbers for each. Identifications were based on the morphological discussions of Baker (1911, 1928, 1945). Franzen and Leonard (1947), Hibbard and Taylor (1960), Leonard (1959), and Pilsbry (1948).

FAUNAL DISCUSSION

Taxonomic discussion is warranted of the materials assigned to *Deroceras aenigma*, *Gastrocopta tappaniana*, and *Strobilops affinis*. The specimens assigned to *D. aenigma* presented a problem in that only 4 of the shells were large and thick enough to be definitively referred to that species. Taylor (1954) cites an average size of about 5 by 3 mm, with a thick and heavy shell as characteristic of the species. On the other hand, it is noted that shells of *D.* cf. *laeve* (Müller) have an average size of about 4 by 2.5 mm, and the shell is very rarely thickened. The remaining shells in the lot were of various sizes and thicknesses, all smaller than the average size characteristic of *D. aenigma*. Based on an assumption similar to that of Taylor (1954), the smaller shells probably represent immature specimens of *D. aenigma*, and the entire lot of 17 specimens was assigned to that species.

Of the specimens assigned to *Gastrocopta tappaniana*, 9 displayed morphological characters similar to those of *G. pentodon*. The shell differences used to separate *G. tappaniana* from *G. pentodon* intergrade (Leonard, 1959); Pilsbry, 1948; Hibbard and Taylor, 1960). Twenty-three of the 32 specimens in this lot fall clearly within the characteristics of *G. tappaniana*. The remaining 9 are similar to *G. pentodon* based on the shape of the shell and characteristics of the lamellae within the aperture. Of the 9 questionable specomens, 3 were complete. The general shape of the shell appeared to be more oblong-conic than ovate-conic, the latter shape being more typical of *G. tappaniana*. Most of the 9 specimens had 5 lamellae within the aperture, 4 of which were dominant: the parietal, upper palatal, lower palatal,

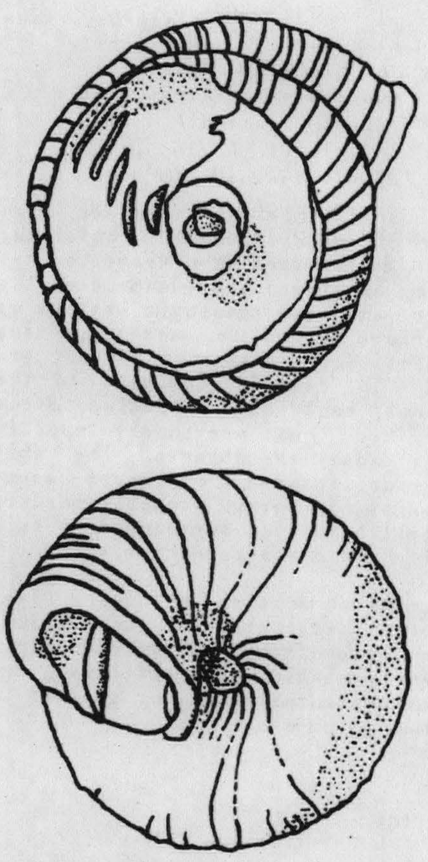


FIGURE 2. *Strobilops affinis* (?) from the Silage Pit faunule of Meade County, Kansas. Above, apical view of dissected specimen showing relative size and position of basal lamellae. Below, basal view showing parietal lamella and lack of the infraparietal and interparietal lamellae.

TABLE 1. Molluscan assemblage comprising the Silage Pit faunule, Meade County, Kansas. All specimens are in the Paleontological Collection, Department of Geology, Kent State University, Kent, Ohio.

NAME	KSU Cat. #	GEOLOGIC RANGE
Pelecypoda		
Sphaeriidae		
Sphaerium sp. (immature)	2951	---
Pisidium casertanum (Poli)	2949	(Early Pliocene to Holocene)
Pisidium compressum Prime	2950	(Kansan to Holocene)
Gastropoda		
Carychiidae		
Carychium exiguum (Say)	2952	(Late Pliocene to Holocene)
Lymnaeidae		
Fossaria dalli (Baker)	2954	(Early Pliocene to Holocene)
Stagnicola caperata (Say)	2953	(Middle Pliocene to Holocene)
Stagnicola sp.		
Planorbidae		
Omalodiscus pattersoni (Baker)	2955	(Late Pliocene to Illinoian)
Gyraulus circumstriatus (Tryon)	2956	(Kansan to Holocene)
Gyraulus deflectus (Say)	2957	(Kansan to Holocene)
Gyraulus parvus (Say)	2958	(Late Pliocene to Holocene)
Promenetus umbilicatellus (Cockerell)	2959	(Late Pliocene to Holocene)
Physidae		
Aplexa hypnorum (Linnaeus)	2960	(Aftonian to Holocene)
Strobilopsidae		
Strobilops affinis Pilsbry (?)	2961	(uncertain)
Strobilops sp. (incomplete)	2962	---
Pupillidae		
Gastrocopta contracta (Say)	2963	(Early Pliocene to Holocene)
Gastrocopta tappaniana (Adams)	2964	(Late Pliocene to Holocene)
Pupoides albilabris (Adams)	2967	(Early Pliocene to Holocene)
Pupilla blandi (Morse)	2968	(Kansan to Holocene)
Pupilla muscorum (Linnaeus)	2969	(Kansan to Holocene)
Vertigo elatior Sterki	2970	(Kansan to Holocene)
Vertigo milium (Gould)	2971	(Late Pliocene to Holocene)
Vertigo ovata Say	2972	(Early Pliocene to Holocene)
Valloniidae		
Vallonia cyclophorella Sterki	2973	(Late Miocene to Holocene)
Vallonia gracilicosta Reinhardt	2974	(Late Pliocene to Holocene)
Vallonia pulchella (Muller)	2975	(Late Pliocene to Holocene)
Succineidae		
cf. *Succinea*	2966	(Pliocene to Holocene)
Endodontidae		
Discus cronkhitei (Newcomb)	2976	(Kansan to Holocene)
Limacidae		
Deroceras aenigma Leonard	2977	(Late Pliocene to Sangamon)
Zonitidae		
Euconulus fulvus (Müller)	2978	(Kansan to Holocene)
Nesovitrea electrina (Gould)	2979	(Late Pliocene to Holocene)
Hawaiia minuscula (Binney)	2980	(Late Pliocene to Holocene)

and columellar The fifth basal, was weak when present. In the specimens with more than 5 folds, the same lamellae were dominant. These 9 specimens were, however, assigned to *G. tappaniana* rather than to *G. pentodon*. The morphological characters appear to fall within the limits of variation discussed in the literature for *G. tappaniana* Further, the two species are not often found living in association since *G. pentodon* occupies a considerably drier ecological niche than *G. tappaniana* (Hibbard and Taylor, 1960).

Of the 10 specimens belonging to the genus *Strobilops*, eight were assigned to *S. affinis* Pilsbry (two specimens were incomplete). *S. affinis* has not, to this author's knowledge, been heretofore reported in the Cudahy fauna. Assignment to this species is predicated on the following morphological characters which are consistent with the description in Pilsbry (1948). The first half of the base is smooth, or almost so, with the ribs barely passing over the peripheral angle, and passing weakly over the umbilical half. The ribs reappear more strongly within the umbilicus itself. The parietal lamella extends to the edge of the callus, but the infraparietal lamella, unlike that in *S. labyrinthica*, is low, weak, wanting, or is not visible in apertural or basal view. The interparietal lamella is also not visible in apertural or basal view. Dissection of two of the specimens revealed a series of 5 obliquely radial basal lamellae, about a third of a whorl behind the aperture, which were short and subequal; these differ from those typical of *S. labyrinthica*, which are characteristically longer and more conspicuously unequal, the inner two being much larger than the rest (Pilsbry, 1948).

TABLE 2. Habitat indications of the mollusks from the Sunbrite, Cudahy, and Silage Pit localities, Meade County, Kansas The habitat categories follow those of Miller (1966). The following abbreviations are used to denote the three localities. S: Sunbrite C: Cudahy; SP: Silage Pit The faunal lists of the mollusks from the Cudahy and Sunbrite localities are from Miller (1968). The values in the column 'percentage by habitat group' were obtained by dividing the total number of species in each of the groups by the total number of specimens picked for each of the three faunules. The totals used are: Sunbrite, 2,095; Cudahy, 2,647; Silage Pit, 450.

Habitat	**Species**	**Locality**			**Percentage by habitat group**		
		S	C	SP	S	C	SP
Shaded areas, under & on moist to wet ground-debris; usually not far from water.	*Carychium exiguum*	X	X	X	30.9%	36.8%	32.0%
	Vertigo elatior	X	X	X			
	V. milium	X	X	X			
	V. ovata	X	X	X			
	Gastrocopta tappaniana	X	X	X			
	*Deroceras aenigma**	X	X	X			
Woodland: dense shade; damp areas beneath ground debris; under leaf litter; among tall marsh grass.	*Cionella lubrica*		X		5.1%	42.6%	8.2%
	Discus cronkhitei	X	X	X			
	Euconulus fulvus	X	X	X			
	Nesovitrea electrina	X	X	X			
	Punctum minutissimum		X				
	Strobilops labyrinthica	X	X				
	*Strobilops affinis**			X			
	Stenotrema leai		X				
	Zonitoides arboreus	X	X				
Sheltered areas: among rocks, shrubs, grass; timbered situations.	*Gastrocopta armifera*	X			1.2%	0.3%	1.8%
	G. contracta			X			
	G. holzingeri	X	X				
Sheltered situations: scattered trees, brush, grass; damp to dry habitat; these species not restricted to woodlands and can tolerate drier conditions.	*Hawaiia minuscula*	X	X	X	6.0%	11.8%	28.7%
	Pupilla blandi			X			
	P. muscorum	X	X	X			
	Pupoides albilabris	X		X			
	Vallonia cyclophorella	X		X			
	V. gracilicosta	X	X	X			
	V. pulchella	X	X	X			

Table 2 - *(Continued)*

Habitat	Species	Locality			Percentage by habitat group		
		S	C	SP	S	C	SP
Marginal situations: wet mud, sticks, stones, or other debris along water's edge; shallow pools, other protected spots.	*Fossaria dalli*	X	X	X	0.8%	1.4%	8.0%
Semiaquatic: among vegetation and debris near water's edge	*Oxyloma sp.*	X	X		0.7%	0.3%	0.0%
Shallow quiet water: small ponds, streams, sloughs or marsh that may become dry during part of the year.	*Pisidium casertanum*	X		X	6.5%	9.6%	9.1%
	Stagnicola caperata	X	X	X			
	S. exilis	X					
	Gyraulus circumstriatus	X	X	X			
	G. deflectus	X	X	X			
	Promenetus umbilicatellus	X	X	X			
	Aplexa hypnorum	X	X	X			
Shallow quiet water: small ponds, streams, sloughs or marsh, with no current or areas of rooted vegetation. Soft sand or mud bottoms; not subject to significant seasonal drying.	*Gyraulus parvus*	X	X	X	38.6%	2.6%	0.4%
	Helisoma trivolvis	X					
	Planorbula campestris	X	X				
	P. cf. P. armigera		X				
	Promenetus exacuous kansasensis	X					
	Physa skinneri	X					
	Ferrissia paralella	X					
	Pisidium obtusale	X					
Perennial water: stream, lake with slow to moderate current; areas of still water; shallow spots with soft sand or mud substrate; not affected by seasonal drying.	***Pisidium compressum***			X	0.0%	0.0%	0.6%
Uncertain: material not identified satisfactorily to specific level, or specimens which are broken or immature. In the case of an extinct species, only an implied habitat is possible by its association with other living species.	*Sphaerium sp.* (immature)			X	4.2%	0.3%	11.1%
	Stagnicola sp. (lost)			X			
	Omalodiscus pattersoni (extinct)	X	X	X			
	Physa sp. (immature)	X					
	Strobilops sp. (incomplete)			X			
	cf. Succinea			X			

** These specimens were questionably referred to species.*

PALEOECOLOGY

Of the mollusks recovered from the Silage Pit faunule, 18 are terrestrial, 9 are aquatic, and 5 are uncertain. A summary of the local habitats represented at the Silage Pit, Sunbrite Mine, and Cudahy Mine is given in Table 2. The arrangement of habitat categories is somewhat arbitrary, since many of the species are not necessarily restricted to the one category to which they have been assigned. It is believed, however, that these habitat groupings probably reflect the fact that each species does have a preferred niche where it most commonly occurs (Miller, 1966).

Ecological interpretations are based on the requirements of extant species (Pilsbry, 1948; Taylor, 1960; Hibbard and Taylor, 1960; Miller, 1966), and the habitat categories follow those of Miller (1966). Many of the conclusions reached are generalities since the exact ecological requirements and distributional patterns are not fully known (Getz and Hibbard, 1965).

The Silage Pit faunule contains a large proportion of terrestrial species which are commonly found living at present in a relatively dry environment among tall grass and shrubbery. That moist conditions also existed is suggested by a slightly larger percentage of species which are found living on moist to wet ground, under debris, or near water. In addition, the presence of *Fossaria dalli* in the faunule suggests either a marginal situation or small pools of standing water typical of marshes. The Silage Pit faunule suggests a marshy environment bordering a small pond, situated in a relatively open grassland. The pond may have been subject to seasonal fluctuations in water level. The presence of *Pisidium compressum* suggests that fluctuations in water level allowed a few aquatic forms to be washed into the flooded marsh during periods of high water. On the other hand, these specimens may have been washed in by the flooding of a nearby stream. The species requiring moist to wet ground conditions probably existed among clumps of grass, hummocks, or logs, while those requiring drier conditions were probably washed in by runoff from higher elevations. That some brush or clumps of trees existed at least nearby, is indicated by the small propertion of woodland species in the faunule.

Climate

Taylor (1960) has summarized the conditions under which the Cudahy fauna lived. The generally accepted interpretation in agreement with the stratigraphic sequence in Kansas is that the Cudahy fauna lived in a lateglacial stage (Kansan) with summers considerably cooler than at present in Kansas, and with winters which were no more severe than those of the present, and probably less so. In addition, it is postulated that the precipitation was greater or at least more effective because of cooler summers, with less evapotranspiration. Maximum precipitation was probably during the summer months (Getz and Hibbard, 1965).

The climatic interpretations for the faunule are based on the species present which have been considered to be of climatic significance, and follow the assumptions of Taylor (1960) and Miller (1966, 1970) which are: (1) that climatic factors are the primary agents controlling the distribution of non-marine mollusks; (2) and, that the north-south and east-west distributions of some groups of mollusks appear to be controlled mainly by extremes of temperature and available moisture.

That the climate at the time the Silage Pit faunule lived was colder than at present is, in part, supported by the presence of the following species, all of which today have a predominantly northern distribution: *Gyraulus circumstriatus*, *G. deflectus*, *Stagnicola caperata*, *Vallonia gracilicosta*, *V. pulchella*, *V. cyclophorella*, *Discus cronkhitei*, *Nesovitrea electrina*, and *Pupilla muscorum* (Taylor, 1960; Miller, 1966). In addition, two species, *Gastrocopta contracta* and *Vertigo elatior*, have an eastern or northeastern distribution, not including Meade County, *V. elatior* having the stronger northerly dispersion of the two. Therefore, it is suggested that there was greater and/or more effective precipitation in Meade County at the time the faunule lived. The presence of *Pupilla blandi* in the faunule adds additional weight to the above assumptions, as this species is restricted today to the Rocky Mountains, from New Mexico at high elevations to southern Alberta; also on the northern Great Plains only as far east as western North Dakota (Miller, 1966).

The absence in the Silage Pit faunule of such southern forms as *Helicodiscus* *singleyanus*, *Gastrocopta procera*, and *G. cristata*, implies either a climate with an average temperature too low to allow a northward dispersal of these species, or a slightly different age. These forms do occur in the Vera faunule of the Cudahy fauna, from the Seymour Formation of Baylor and Knox Counties, Texas, reported by Getz and Hibbard (1965)

Further, while the absence in the Silage Pit faunule of several of the species which occur in the Sunbrite and Cudahy faunules may be explained in part by the small sample size of the Silage Pit sample, *Pupilla blandi* does occur in the Silage Pit faunule but not in the Sunbrite and Cudahy faunules. It therefore seems a reasonable suggestion that the Silage Pit faunule represents a slightly different age and probably colder climate (cold 'pulse within the Kansan) than either of the other two faunules. The other species present in the Silage Pit faunule, but not the Sunbrite or Cudahy faunules is *Gastrocopta contracta*. However, this species appears not to be as thermally significant as *P. blandi*.

STRATIGRAPHIC OCCURRENCE

The sample from the Silage Pit was collected from a silt containing abundant caliche nodules Just above the silt is a lens of Pearlette like ash It is assumed in this report that the stratigraphic sequence at the Silage Pit is equivalent to that represented at the Cudahy Ash Mine, SE ¼ sec. 2, T. 31 S., R 28 W., and the Sunbrite Ash Mine, NE ¼ sec. 26 T. 32 S., R. 28 W, Meade County, Kansas (Figure 1) A regional stratigraphic column has been presented in additional publication (Miller 1966; Skinner and Hibbard 1972)

AGE AND CORRELATION

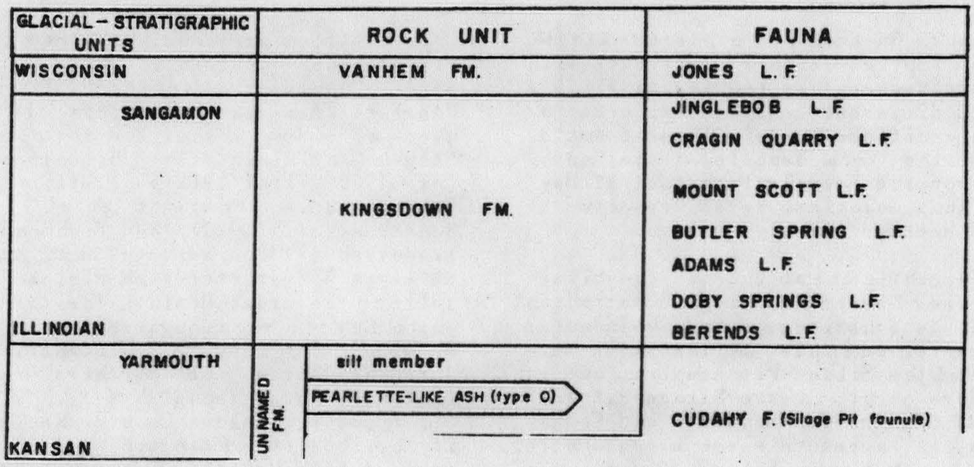
The geologic ranges of the species comprising the Silage Pit faunule (Table 1) bracket the age of the assemblage between the Kansan and Illinoian *Pisidium compressum*, *Gyraulus deflectus* *Pupilla blandi*, *P. muscorum*, *Vertigo elatior*, *Vallonia pulchella*, *Discus cronkhitei*, and *Euconulus fulvus* have ranges extending only as far back as the Kansan on the High Plains. *Omalodiscus pattersoni* is known in the southern Great Plains from the late Pliocene, Rexroad local fauna (Taylor 1965) to the Illinoian, Butler Spring local fauna (Hibbard and Taylor, 1960).

It has been previously assumed that all Pleistocene occurrences of ash in the Meade County area were coeval with the Pearlette Ash and therefore, the ash was used as a key marker bed for the Kansan Stage of the Pleistocene Hibbard and Taylor 1960, Flint 1972 551, Miller 1966) Recent studies by Izett *et al.* (1971) Naeser *et al.* (1971), and Richmond and Obradovich (1972) indicate that there are at least 3 Pearlette-like Pleistocene ash falls in the Great Plains. The three types which have been recognized are: (1) Type *B*, about 2.0 m. y BP identified thus far only from the Borchers Gravel Pit (Borchers local fauna), N ½ sec. 21, T. 33 S., R. 28 W., Meade County, Kansas; this is the locality of the type section of the Atwater Silt Member of the Crooked Creek Formation (Hibbard 1956); (2) Type *S*, about 1.2 m. y. B.P., at the type locality of the Sappa Formation (described in Frye and Leonard, 1952: 87), and other localities in Nebraska and Colorado, but not thus far recognized in Meade County, and (3) Type *O*, about 0.6 m. y. B.P., at many localities on the Great Plains including the Cudahy Ash Mine, where the ash directly overlies the silt containing the Cudahy fauna.

Based on these studies, the Cudahy fauna at the Cudahy Mine and Sunbrite Mine localities does not occur in the Atwater Silt Member of the Crooked Creek Formation. The sediments containing the Cudahy fauna apparently belong to a younger, hitherto unnamed rock unit Although the ash at the Silage Pit locality is unstudied, the molluscan assemblage and the stratigraphic position of the silt containing the faunule suggest a Kansan age and assignment to the Cudahy fauna (Figure 3).

CONCLUSIONS

Based on the several means of correlation presented, it appears a reasonable assumption that the Silage Pit faunule be assigned to the Cudahy fauna, and to a Kansan age The assemblage contains a significant proportion of species with a present northern distribution or northeastern distribution, implying a cooler and moister climate in Meade County during the time the faunule lived, than at the present. The presence of *Pupilla blandi* in this faunule, but not in the Sunbrite or Cudahy faunules suggests the possibility that the Silage Pit faunule is representative of a relatively cooler period and hence slightly different age within



GLACIAL – STRATIGRAPHIC UNITS	ROCK UNIT	FAUNA
WISCONSIN	VANHEM FM.	JONES L. F.
SANGAMON ILLINOIAN	KINGSDOWN FM.	JINGLEBOB L. F. CRAGIN QUARRY L. F. MOUNT SCOTT L. F. BUTLER SPRING L. F. ADAMS L. F. DOBY SPRINGS L. F. BERENDS L. F.
YARMOUTH KANSAN	UNNAMED FM.: silt member PEARLETTE-LIKE ASH (type O)	CUDAHY F. (Silage Pit faunule)

FIGURE 3. Late Cenozoic stratigraphic sequence and faunal succession in southwestern Kansas, modified from Hibbard (1972).

the Kansan stage than that represented by the Sunbrite and Cudahy faunules. The absence of such southern forms as *Helicodiscus singleyanus*, *Gastrocopta procera*, and *G. cristata* apparently does, by negative evidence, add strength to the above assumption. However, these species are reported in the Vera faunule of the Cudahy fauna in Texas, and it might be suggested that the faunules are contemporaneous and that a warmer climate prevailed at the time in Texas than in the Meade County, Kansas area.

While further study of the foregoing stratigraphic interpretation appears to be warranted, it is suggested that the Atwater Silt containing the Borchers local fauna should be reassigned a pre-Nebraskan age correlative with type *B* ash, rather than a Yarmouth age. The Cudahy fauna would then be assigned to a new silt member of a hitherto unnamed formation correlative with the type *O* ash.

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PSEUDOGASTROPODS

Valvata arenifera turned out to be a caddis case and is well known to collectors of freshwater gastropods working in lakes with sandy bottoms. There is another group of well known pseudogastropods belonging to the genus *Spirorbis* that is familiar to marine malacologists and students of fossil gastropods. Occasional notes on fossil *Spirorbis* appear in the paleontological literature but no mention is made, to my knowledge, of the operculum, at least in North American references. A paper by Knight-Jones and Walker (1972) on spirorbids from the South Orkney Islands includes fine drawings of these structures which may be of interest to students of fossiliferous sediments both Recent and ancient. At first sight, the opercula of spirorbids would suggest a barnacle plate, albeit a very unusual one, and reference to the above paper may solve the problem of identity of these structures, whether they occur in Recent or Paleozoic sediments.

In passing, Knight-Jones and Walker cite several papers on spirorbids which are of interest. These are, among others, one by J.M. Gee (1964) on British Spirorbinae, another by Harris (1969) on species from the South Atlantic, two by Pixell (1912 snd 1913) bearing on the west coast of North America and the Antarctic, and finally a monographic study by Zibrowius (1968) on morphology, systematics, and ecology of the species of the Marseille region.

A. L.

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ANNOUNCEMENTS

STERKIANA NO. 50

This number set records not only for size but also for lateness in appearance. It should have been out in June but was not mailed until July 20, 21, and 23. The delay was due to breakdown of machinery which is now happily corrected.

Since it is a double number, single copies of No. 50 are priced at $1.00 postpaid. Subscribers have received their copy at no extra charge.

The index for Sterkiana 41-50 will be ready soon. Those who bind Sterkiana in volumes of 10 numbers should wait until the index is received before binding.

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THE TERRESTRIAL SLUGS OF NORTHEASTERN NORTH AMERICA

LYLE F. CHICHESTER and LOWELL L. GETZ[1]

INTRODUCTION

The term 'slug' is applied to those gastropod mollusks in which there has been a distinct trend towards the loss of the external shell. With one exception, all the terrestrial slugs which have been recorded from, or could be expected to be found in northeastern North America have entirely lost the external shell. Some forms still retain a small, plate-like remnant of the shell under the fleshy mantle; in others only granules or spicules of calcium carbonate buried in the mantle remain. The loss of the shell reduces the need for calcium and permits the animals to move through narrow spaces.

Associated with the loss of the coiled shell has been the assumption of a partial anteroposterior, external bilateral symmetry. The foot is lengthened to accommodate the viscera which lie in an elongated body cavity. In all genera except *Testacella*, the unpaired openings of the lung, excretory, genital system, and digestive tract are on the right side near the anterior end of the body. In *Testacella* the openings of the lung, excretory system, and digestive tract are located posteriorly under the right edge of the external shell; the reproductive pore opens below the right upper tentacle.

The arrangement of the internal structures still resembles the general pattern found in the shelled relatives. Most systems still display the asymmetry resulting from the process of torsion, a characteristic feature of the class Gastropoda. Except in certain primitive groups, the digestive system extends posteriorly to fill the elongate body cavity over the foot.

As a result of the loss of the shell, the entire body of the slug is naked. The body surface contains numerous slime glands scattered over its entire surface. These exude a copious flow of slime, particularly when the slug is disturbed. The slime aids the animal in removing noxious substances from the body surface and may serve as a protective device against potential predators. The slime does not afford protection from desiccation, however. The consistency and color of the slime vary among species and are aids in their identification.

A pedal gland whose pore is located anteriorly just below the mouth produces a particularly large amount of slime. This provides the foot with a layer of slime over which the slug travels. The slime formed by the pedal gland is left as a distinct trail on the substrate. One can frequently determine prior activity of slugs by observing the slime trails on the surface over which they have traveled.

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NORTHEASTERN NORTH AMERICAN FAUNA

An outline of the classification of slugs recorded from or of possible occurrence in northeastern North America is as follows:

- CLASS GASTROPODA
  - SUBCLASS Pulmonata (Euthyneura)
    - ORDER Stylommatophora
      - SUBORDER Sigmurethra
        - DIVISION Aulacopoda
          - Superfamily Endodontacea
            - Family Arionidae
              - Subfamily Arioninae
                - *Arion subfuscus*
                - *Arion intermedius*
                - *Arion ater*
                - *Arion hortensis*
                - *Arion fasciatus*
                - *Arion circumscriptus*
                - *Arion silvaticus*
            - Family Philomycidae
              - *Philomycus carolinianus*
              - *Pallifera dorsalis*
          - Superfamily Zonitacea
            - Family Limacidae
              - Subfamily Limacinae
                - *Limax maximus*
                - *Limax flavus*
                - *Lehmannia valentiana*
                - *Deroceras laeve*
                - *Deroceras reticulatum*
              - Subfamily Parmacellinae
                - *Milax gagates*
          - Superfamily Oleacinacea
            - Family Testacellidae
              - *Testacella haliotidea*

Both species of Philomycids and *Deroceras laeve* (Limacidae) are native to North America and occur throughout northeastern North America. All the remaining species have been introduced into North America from Europe. Although seven genera of Arionidae are native to the western regions of North America, none of these has been reported from eastern North America.

Of the introduced species, *Deroceras reticulatum, Arion subfuscus,* and *A. fasciatus* have become widespread and very abundant in the northeast in general. *Limax maximus* may be locally abundant, but is more spotty in its distribution. *Arion hortensis, A. intermedius, A. silvaticus,* and *A. circumscriptus* have been reported from several localities but normally are not found in large numbers in these colonies. The remaining species are found in greenhouses or as isolated individuals; no established colony of these species has been found in northeastern North America.

BIOLOGY

Habitats.—The presence of an exposed moist integument restricts slugs to relatively damp situations. Most species are relatively intolerant of submersion in water, however. The evaporation of water from the skin as well as that lost in slime production (by the pedal gland in particular) is compensated for by water in the food and by cutaneous absorption of dew, rain, or other free water.

The most favorable places for slugs are: under leaf litter; beneath the bark of dead trees; under logs, boards, rocks, paper, or other debris; at the base of grasses and sedges; in the soil (especially in gardens and truck farms); and in cellars and damp sites under outbuildings.

The three native species are more or less solitary in habits; they normally are encountered as isolated individuals; Only in exceptionally favorable sites does one find more than a few individuals together. The introduced species are in general more gregarious than are the native species. They are frequently encountered in dense colonies in natural situations as well as in cultivated gardens and fields.

Activity patterns.—Since slugs are relatively intolerant of desiccation and ultraviolet radiation, most species are nocturnal in habits. A few species *(Arion subfuscus* and *Deroceras reticulatum* in particular) are found active above the surface even on relatively clear days, however.

Seasonal activity is influenced by temperature, moisture, and food availability. During the winter most species burrow into the substrate and hibernate under logs or other objects on the ground. Some species may become active in sheltered places during warm periods in the winter; most are inactive in the northeast from December to March, however. Some species may have short periods of inactivity (or aestivation) during the more extremely hot, dry periods in the summer. Such periods of inactivity may also be partially related to unavailability of succulent food. The slugs immediately become active again after a rainy period.

Life history.—Eggs are laid in clusters of up to several dozen eggs in moist places under leaf litter, logs or debris. The eggs may be connected by thin gelatinous threads which adhere together in compact masses or they may form loose, unconnected aggregations. The eggs are gelatinous in appearance; they vary from clear to brownish opaque in color. They range from 2 to 5 mm in size and from round to oval in shape.

Newly hatched individuals may be somewhat lighter in color than adults, in some the color pattern of the young may differ from that of the adults. Young individuals are active and begin feeding immediately after hatching.

Rate of growth varies among species and is dependent upon temperature, moisture and food availability. Under normal conditions adult size and sexual maturity is usually attained between 3 to 9 months. Many species die soon after completing egg laying. The enlargement of the reproductive system during the breeding period results in a rather sudden increase in the size of many species during their final month or two of life.

All species of terrestrial slugs that occur in northeastern North America are hermaphroditic. Cross fertilization is normal; when two individuals mate there is usually a mutual exchange of sperm. In some matings an individual may function only as a male or a female but not both. Self-fertilization has been reported in *Arion ater*, *A. subfuscus*, *A. intermedius*, *Milax gagates*, and *Deroceras reticulatum*. Self fertilization can occur with or without self-copulation. Parthenogenesis has not been recorded in slugs.

Most species have rather elaborate courtship displays, usually consisting of some sort of a circular 'dance' preceding copulation. In *Deroceras* a penial accessory organ, the sarcobelum, is used to stimulate the partner during the final stages of the 'dance.' *Milax* has an atrial accessory organ which functions as a stimulator. *Arion hortensis* everts the distal portion of the oviduct which also serves as a stimulatory structure. *Limax maximus* has been observed to mate while hanging from mucus threads below a ledge or tree branch.

Arion and *Milax* form a spermatophore which contains the sperm; this structure is deposited in the seminal receptacle of the mating partner. The other genera transfer the sperm as a viscous mass.

Food habits.—In the wild, slugs feed primarily on fungi, decaying organic matter, paper, fecal material, and carrion. In greenhouses and gardens a variety of fresh plant food is consumed; succulent plants, including roots, stems, and fruits as well as leaves are especially favored. *Testacella* feeds on earthworms and slugs while others display cannibalistic tendencies when in crowded conditions.

Enemies.—Slugs are preyed upon by various species of amphibians, reptiles, birds, and small mammals. Some insects are also known to feed on slugs.

METHODS OF DISPERSAL

Slugs are readily dispersed from place to place by the activities of man. Both eggs and adult slugs are transported with greenhouse plants and soil. Movement of nursery plants with associated soil and organic material from one region to another is an important method of dispersal. Other related methods of dispersal include packaged food items such as fruits and vegetables, garden settings, and floricultural cuttings. When the above items are either planted or discarded the slugs or eggs on them are liberated and the species may become established in a new region.

The method in which plants are maintained in greenhouses (in wooden flats, moist pots, in soil beds, etc.) and the requirement of warm, uniform temperatures, and frequent watering of the tables (with the resulting high humidities) afford an ideal habitat for slugs. If there is any excess debris in the greenhouse the conditions are even more suitable.

Greenhouses therefore may serve as a source of sporadic records for species that do not become established in natural conditions. The removal or discarding of potted plants and cuttings may result in slugs being liberated in the wild, especially in such places as cemeteries and garbage dumps. Although these species may not be able to form established colonies because of unfavorable environmental conditions, individuals may thus be frequently collected away from greenhouses. While such a process could result in the establishment of permanent colonies there is no evidence that this is happening in northeastern North America at the present time. Except for *Deroceras reticulatum*, the wild are not normally abundant in greenhouses

Transportation of logs (with bark attached), sod, and any material or machinery which has been on the ground and on which soil sticks and remains moist during movement are potential dispersal means for slugs. During the early days of commerce ballast carried in ocean-going ships may have also been a ready means of transporting European species on small, isolated, uninhabited islands where ballast was dumped indicate some of the early introductions may have been via ballast. Later introductions into North America have obviously been by way of horticultural and floricultural materials. Present inspection practices by plant and animal quarantine personnel have reduced such introductions.

ECONOMIC IMPORTANCE

The native slugs are seldom abundant enough under natural conditions to be considered serious pests in the northeast. *Deroceras laeve* is often abundant in greenhouses, however and can do considerable damage.

Introduced species, especially because of their tendency to be gregarious and locally very abundant, as well as their association with man's activities, can become serious pests. In addition to greenhouse damage, they are locally problems in gardens and flower beds; damage to commercial crops is not particularly significant in the northeast. In addition to destruction, injury, or aesthetic damage to plants and fruits, they are somewhat of a nuisance when abundant in lawns or other places where they are stepped on or when encountered in one's lettuce salad.

Parasites.—Relatively little work has been done concerning the importance of slugs as intermediate hosts for parasites of significance to man or his domestic animals. Malek (1962) gives a list of Trematodes and Nematodes that have been found to use slugs as intermediate, transport, or definitive hosts. Taylor (1907) cites *Limax maximus* as a host of the fowl tapeworm, *Davainea proglottina*.

Control measures.—Numerous commercial poisons are available; only those containing metaldehyde have proven to be effective, however. Baits (1.75% metaldehyde, 5.0% tricalcium arsenate, and 93.25% inert material) are most effective in greenhouses and small garden plots. Since such baits mold easily, they must be changed frequently. Liquid (20% metaldehyde) or dust (15% metaldehyde) are more effective in larger areas such as lawns or fields (they may also be used on greenhouse benches and in small gardens, however). Care must be taken to get the spray on the ground below the plants; if sprayed on the surface of plants, it will be ineffective.

Steam sterilization of greenhouse tables is also an effective method of slug control. Removal of debris and other hiding places for slugs will aid greatly in reducing the number of slugs in greenhouses.

PRESERVATION

The simplest method of preserving slugs is to place them directly in 70% ethyl alcohol or in 2% phenoxyethanol; isopropyl ('rubbing') alcohol will also suffice. The volume of alcohol should be approximately 3 to 4 times the volume of the slugs in the container to prevent undue dilution of the alcohol by the body fluids of the slugs. The slugs should be covered sufficiently to prevent drying out. As a safety procedure, vials can be stoppered with cotton plugs and then the individual vials placed in a large container of alcohol. This will reduce maintenance to a minimum.

When placed directly in alcohol the slugs preserve in a contracted condition. If it is desirable to have the slugs in a more relaxed state to facilitate dissection, they can be drowned before preservation. This is done by placing them in vials completely filled with water and stoppered so that no air bubble is present. The vials should be maintained at room temperature and the slugs observed at frequent intervals to determine when movement ceases (24 to 48 hours). The slugs will die in a somewhat extended position; they can then be preserved in 70% alcohol.

A more satisfactory method of relaxation is by the use of nembutal (pentobarbital sodium) or menthol crystals. A maximum of 10 to 15 slugs should be placed in approximately 100 cc of water in a dish provided with a cover. Ten cc of a 10% solution of nembutal or 2 or 3 small crystals of menthol are then added to the water. The slugs should be observed at periodic intervals to insure that they remain in the water and to determine when they are completely relaxed. Additional relaxing agent may be added as needed. When using nembutal a pin prick may be used to determine when the animals are unable to contract; when menthol is used, the slugs should not be disturbed as once they contract, they may not completely extend again. Once thoroughly relaxed, the slugs can be preserved in 70% alcohol.

Since the color of slugs soon fades in alcohol, detailed descriptions of the color of the live animals (including the slime produced when handled) should be recorded in the collection notes. When preserved, the mucus of most species forms an opaque layer over the body. This slime should be carefully rubbed off to permit examination and identification of the animals.

Labels should be written in pencil or permanent ink (not ballpoint!) on good quality paper and placed *in* the vial with the animals from each collection site. Information on the label should include date, exact location of the collection site, collector, general habitat, and color of the animals and slime. It is also desirable to include a collection number and repeat the above information with a more detailed description of the habitat in a collection log book.

Preserved specimens can either be shipped in vials packed in shipping containers or the slugs can be tightly tied in plastic freezer bags with a small piece of cotton saturated with alcohol; the bag can be sealed in an envelope. Specimens should not be maintained more than a few days in plastic bags, however, as the alcohol will eventually dissolve the bags.

A KEY TO THE TESTACELLID, ARIONID, PHILOMYCID AND LIMACID SLUGS OF NORTHEASTERN NORTH AMERICA

1. **EXTERNAL** abalone-shaped shell present on posterior end (Fig. 8d) .... (Testacellidae) *Testacella haliotidea*
   EXTERNAL shell absent (see footnote 1 for exceptions) 2
2. **MANTLE** covers more than 2/3 of the back (Fig. 1b) ... (Philomycidae) 3
   MANTLE covers less than ½ of the back (Fig. 1a) 4
3. **HEAD** covered by anterior lip of mantle; slime milky when animal is irritated; mantle covered with many dark pigmented spots, some of which may coalesce to form paired and/or unpaired longitudinal bands or streaks; adults more than 50 mm long ...... *Philomycus carolinianus*
   HEAD not covered by anterior lip of mantle; slime clear when animal is irritated; mantle either without spots or with a mid-dorsal line plus faint lateral spot rows; adults less than 35 mm long .... *Pallifera dorsalis*
4. **BREATHING PORE** in posterior half of mantle (Fig. 1e); jaw smooth (Fig. 1c). .... (Limacidae) 5
   BREATHING PORE in anterior half of mantle (Fig. 1f); jaw ribbed (Fig. 1d) .... (Arionidae, Arioninae) *Arion* .. *10*
5. **DORSAL KEEL** extends to posterior margin of mantle; mantle subdivided by a horseshoe shaped groove. (Fig. 1g) .... (Parmacellinae) *Milax gagates*
   DORSAL KEEL does not extend forward to posterior margin of mantle; mantle not subdivided by a groove (Fig. 1h) .... (Limacinae) ... 6
6. **TAIL TRUNCATED** when viewed from the side (Fig. 1k); posterior margin of mantle rounded (Fig. 1i); nucleus of concentric mantle ridges lies on right side of mantle (Fig. 1i) ... *(Deroceras)* . *7*
   TAIL POINTED when viewed from the side (Fig. 1l); posterior margin of mantle obtusely angular (Fig. 1j); nucleus of concentric mantle ridges lies mid dorsally (Fig. 1j) 8
7. **BREATHING PORE** with a pale border (Fig. 1m); slime milky when animal is irritated; rectal caecum present (Fig. 1o); penial appendix multifid and crenulate (Fig. 2b); ovotestis exposed .... *Deroceras reticulatum*
   BREATHING PORE not pale bordered (Fig. 1n); rectal caecum absent; penial appendix simple, smooth and tubular (Fig. 2c); ovotestis hidden by digestive gland .... *Deroceras laeve*
8. **MANTLE** bears at least one pair of dark longitudinal bands; penial appendix present (Fig. 2e) .. *Lehmannia valentina*
   MANTLE bears either yellow spots, black spots or blotches, or bears no markings at all; penial appendix present (Fig. 2a) ... *(Limax)* 9
9. **MANTLE** with black spots, blotches or no markings at all; rectal caecum absent; slime clear .... *Limax maximus*
   MANTLE yellow spotted; rectal caecum present (Fig. 1p); slime yellow .... *Limax flavus*

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[1] An external, anteriorly located shell is found in the New World *Binneya* and the Old World *Parmacella*. Neither has been reported in eastern North America.

10\. **TUBERCLES** conically shaped with hyaline apices when animal contracts (Fig. 1q); adults less than 25 mm long .... *Arion intermedius*

TUBERCLES not conically shaped and without hyaline apices when animal contracts (Fig. 1r); adults more than 25 mm long 11

11\. **FOOT FRINGE** wide; foot fringe bears numerous dark vertical lines at least posteriorly; lateral dark bands present or absent 12

FOOT FRINGE not conspicuously wide; foot fringe without dark vertical lines; lateral dark bands always present .. 13

12\. **COARSE, ELONGATE TUBERCLES** on side and back; adult animals lack bands on mantle; slime usually clear; free oviduct of constant diameter throughout its length and very short (Fig. 2H) .... *Arion ater*

TUBERCLES not conspicuously coarse or elongate; adult animals may or may not have lateral bands; slime usually yellow; free oviduct slender proximally, swollen distally and long (Fig. 2g) ... . *Arion subfuscus*

13\. **BREATHING PORE** located below lateral mantle band; mid-dorsal, post mantle tubercles raised and enlarged to form longitudinal ridge (may be faint or lost in some adults) (Fig. 4a); sole white to gray in life; free oviduct slender through its length; seminal receptacle pear shaped (Fig. 2i) .... *Arion fasciatus* complex[2]

BREATHING PORE located within lateral mantle band; mid-dorsal tubercles not enlarged, no ridge is discernible; sole bright yellow to orange in life (color disappears in alcohol); free oviduct swollen distally; seminal receptacle ball shaped (Fig. 2j)...*Arion hortensis*

SUPERFAMILY ENDODONTACEA

Family Arionidae Gray, 1840

Description

Slugs with an internal shell in the form of an oval plate or a mass of granules, except in the genus *Binneya* in which the shell is external. The jaw is ribbed (Fig. 1d). The kidney surrounds the pericardium. An epiphallus is always present. The foot sole may be uniform or tripartite.

Distribution

Europe, Africa, Asia, North America. Members of the genus *Arion* have been introduced into North and South America, Polynesia, Australia, New Zealand, Tasmania, and South Africa.

Origin

The family appears to have originated from an Endodontid stock. The most primitive subfamily, Binneyinae, has an external, depressed, spiral shell, a common origin of the retractor muscles, and a solid 'tail.' See Pilsbry (1948) for further evolutionary discussion.

Subfamily Arioninae Binney, 1864

Slugs with a shell in the form of a flat plate *(Geomalacus)* or discrete granules *(Arion)*. Foot fringe wide. A caudal mucus gland is present. A penis is absent. The left and right tentacular retractor muscles and the buccal retractor muscle originate separately at or beyond the posterior margin of the diaphragm.

Genus *Arion* Férussac, 1819

Arion Férussac, 1819, Hist. Nat. Moll., p. 53.

Slugs with shell reduced to discrete granules. Breathing pore located in the anterior half of the mantle on the right side. Reproductive opening below lateral margin of the mantle in the vicinity of the breathing pore.

EXPLANATION OF FIGURE 1 (OPPOSITE PAGE)

FIG. 1. Diagnostic characters used in key and text. a, generalized slug; s, retractor muscles in typical Limacids; t, retractor muscles in typical Arionids; u, radular teeth of *Lehmannia valentiana* (position of teeth in transverse row is indicated by number, except median tooth which is labeled c; ect., ectocone; end, endocone, mes, mesocone); v, radular teeth of *Lehmannia marginata*.

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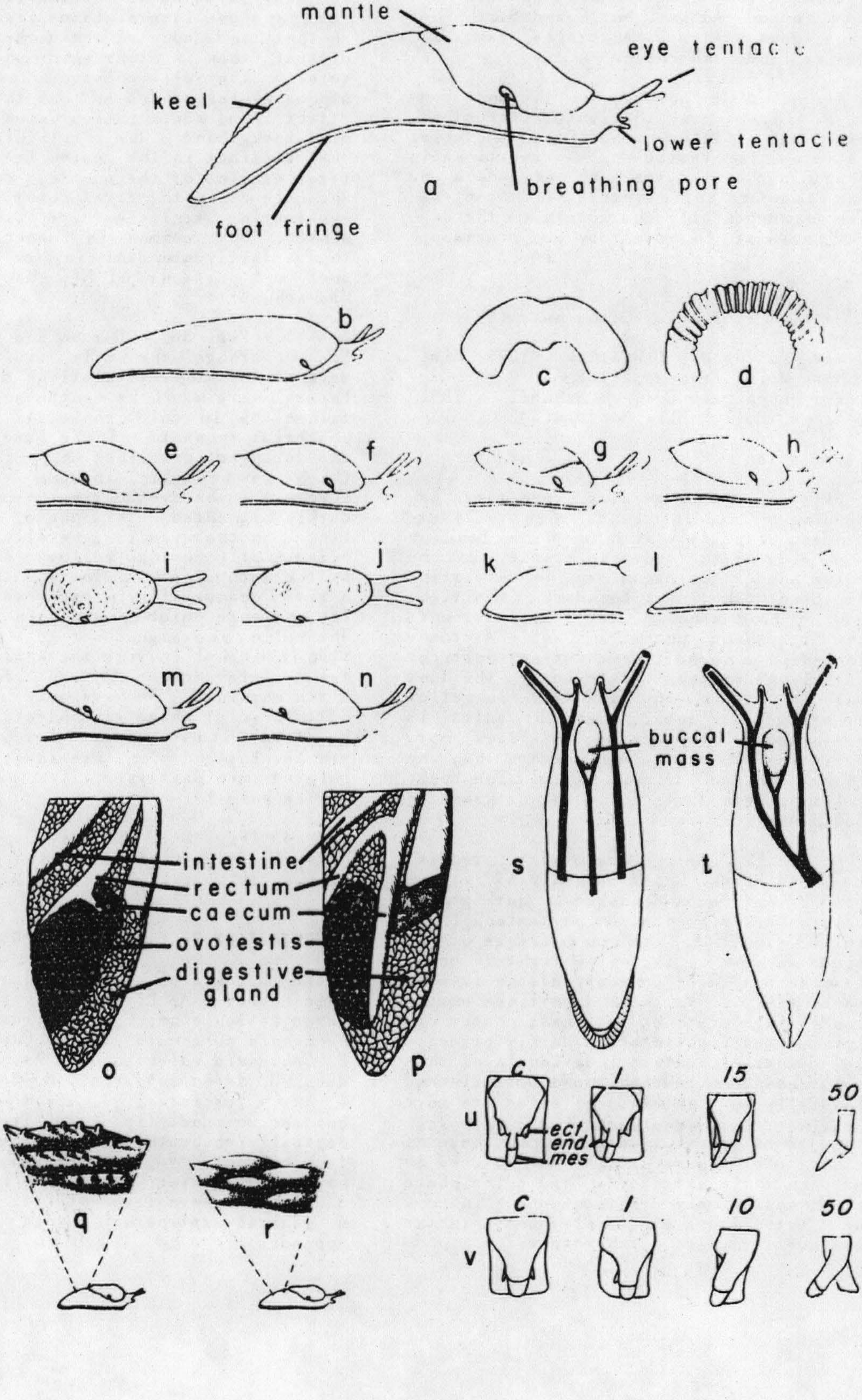
[2] Some European workers believe that *Arion fasciatus* as previously conceived by older workers is a complex of three species. See text for discussion and key to the component species.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The genus is native to the western Palearctic Region. One or more species have been introduced into North and South America, South Africa, Australia, Tasmania, New Zealand, and Polynesia.

Arion is perhaps one of the more complex slug genera; the systematics of the group are still unsolved. Color and color patterns are variable; the traditionally dependable characters such as radula and jaw are not reliable systematic characters. The most dependable characters are the distal parts of the accessory sex organs.

Arion subfuscus (Draparnaud, 1805)

Limax subfuscus Draparnaud, 1805, Hist. Nat. Moll. France, 2:125.
Arion subfuscus Drap., Scharff, 1891, Trans. Roy. Dublin Soc., 4:542.

Description

External. A large slug, some forms exceeding 80 mm in length when fully extended. Typically with a black band on each side of the body and mantle; in some color phases the bands may be very faint or absent. The lower boundary of the right mantle band usually diffusely surrounds the breathing pore. The well-developed foot fringe normally has distinct vertical dark lines, at least posteriorly, the foot sole is whitish gray. The slime is yellow or orange, at least when the animal is disturbed. This species displays more variation in color and pattern than any other imported Arionid slug. The basic color pattern forms found in northeastern North America are:

1. (Fig. 3a). Dorsum dark reddish brown to black. Upper boundary of lateral band or entire band masked by dark ground color. Dark pigmentation may extend laterally almost to the foot fringe or the sides may be sufficiently light in color to make the lower boundary of the lateral bands visible. Vertical dark lines on the foot fringe distinct, at least posteriorly. Eye-bearing tentacles darkly pigmented. Sexually immature individuals of this color phase are reddish brown dorsally and laterally so that lateral bands are more distinct. Individuals of this color phase tend to be somewhat larger than those of other color phases; adults may exceed 80 mm when fully extended. This color phase is the most widely distributed one in Connecticut. It is especially common in the southwestern part of the state.

2. (Fig. 3b). Dorsum brown to brownish gray, mottled with black pigment. Area just above lateral bands lighter brown so that bands appear much darker and more distinct than in other color phases. Laterally, the valleys between the tubercles are darkly pigmented so that the over-all effect is of a dark reticulum on a whitish gray background. These reticulations are most distinct in the region below the lateral margins of the mantle. Foot fringe and sole as in the first color phase. The eye-bearing tentacles are darkly pigmented. Not common in Connecticut, although fairly abundant in New York, Vermont and portions of New Hampshire and Massachusetts.

3. (Fig. 3d). Dorsum and sides yellow to orange, the only indications of dark pigment are reticulations between the lateral margins of the mantle and the foot fringe (as in color phase 2), indistinct posterior remnants of the lateral bands, and dark vertical lines on the foot fringe (these may be lacking in some individuals, however). The eye-bearing tentacles are darkly pigmented. This phase, when collected in the wild is generally yellow or occasionally orange-yellow. When reared in the laboratory on lettuce they become a vivid orange after a few weeks. The yellow or orange color is mainly in the slime. The yellow or orange color goes into solution in alcohol leaving the animal a light tan to gray color, except for the few black markings. We have only one record of this color phase in Connecticut (North Branford); it is abundant in much of northern New England. Immature individuals are colored and patterned like the sexually mature animals.

4. (Fig. 3c). Dorsum light brown to brownish yellow; lateral bands usually very

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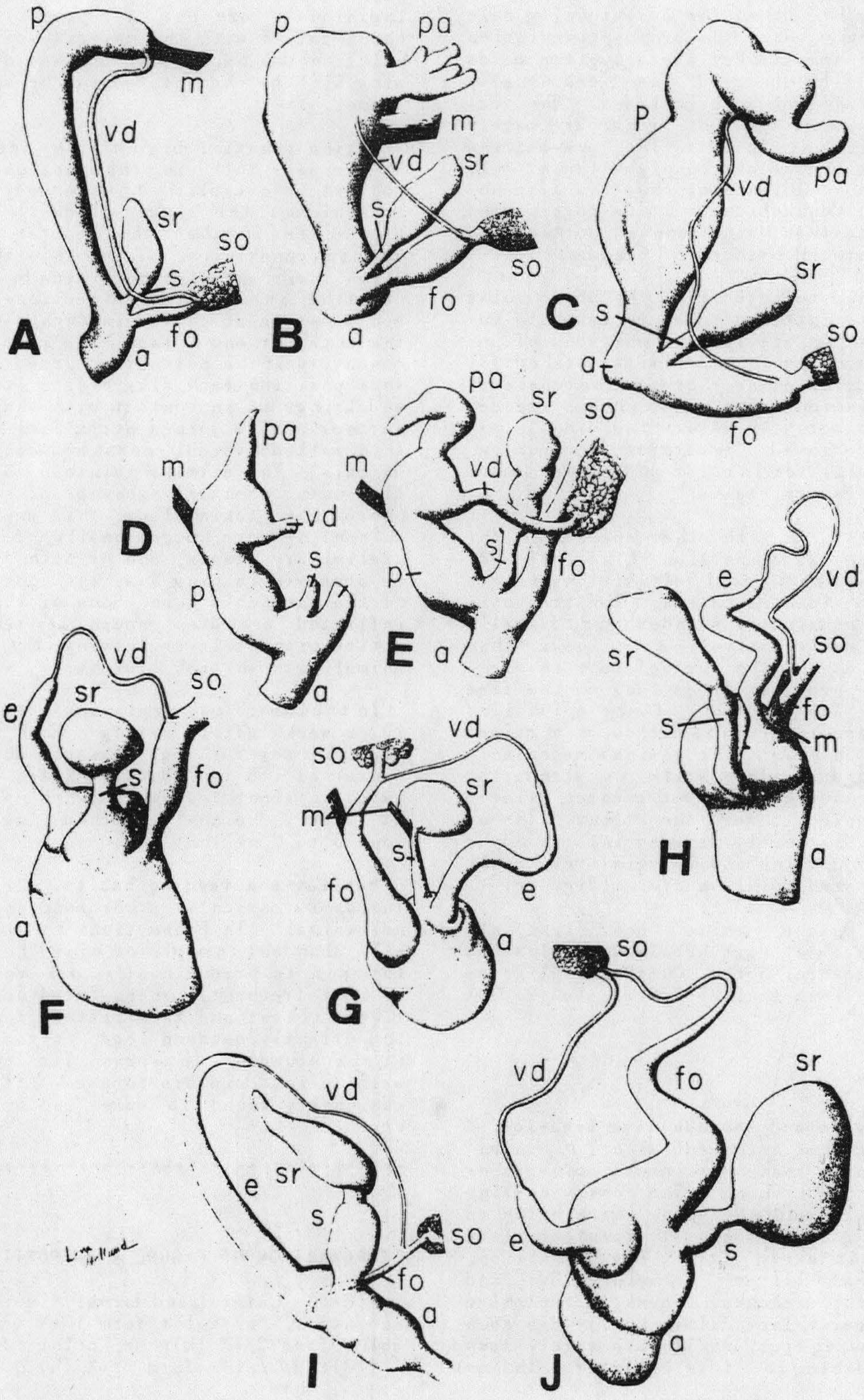
EXPLANATION OF FIGURE 2 (OPPOSITE PAGE)

FIG. 2. Distal genitalia (not drawn to same scale). A, *Limax maximus;* B, Deroceras reticulatum; C, *Deroceras laeve;* D, *Lehmannia marginata* (after Quick, 1960); E, *Lehmannia valentiana;* F, *Arion intermedius;* G, *Arion subfuscus;* H, *Arion ater;* I, *Arion fasciatus;* J, *Arion hortensis;* *so,* spermoviduct (in some figures shown partially ensheathed by prostate); fo, free oviduct; vd, vas deferens; e, epiphallus; p, penis; sr, seminal receptacle; s, stalk of seminal receptacle; a, atrium; m, genital retractor muscle; pa, penial appendix.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faint, being most distinct on the mantle. The bands are brown (or occasionally pale gray); hence, when the brown pigmentation of the dorsum extends laterally, the bands are virtually obscured. The sides usually are whitish and unreticulated. The vertical lines of the foot fringe are barely discernible or absent. The eye-bearing tentacles are usually unpigmented or only faintly so. This color phase is also not common in Connecticut. It is more common in southeastern Maine and in portions of the Atlantic Provinces of Canada.

It should be noted that the above color phases are intended to apply to whole populations or significant portions of populations. Within the limits defined for any one color phase there can be considerable variations The color phases are defined for sexually mature individuals except where noted. Immatures are usually somewhat lighter in color and possess more distinct lateral bands.

Internal. As with other species in the genus, the distal portion of the accessory sex organs are the most reliable characters to use for identification. The free oviduct is proximally slender and distally dilated and relatively much longer than in *Arion ater*. The vas deferens is slender and approximately as long as the free oviduct. The junction of the epiphallus with the upper atrium is marked by a raised ring or annulus. The seminal receptacle is spheroidal. The stalk is slender at its receptacular end, but becomes dilated as it proceeds toward the atrium. The atrium is distinctly divided into an upper and lower portion and is relatively small when compared to *Arion ater*. (Fig. 2g).

Eggs. Opaque, white, pearl-like, almost spheroidal eggs are laid in clusters of up to several dozen. Quick (1960) gives the dimensions as 2.25 X 2.25 to 2.25 X 3.25 mm.

BIOLOGY

Life cycle and reproductive behavior.— In Connecticut *Arion subfuscus* is an annual species that overwinters as eggs or newly hatched young. The overwintering individuals and the young which hatch in the spring become sexually mature by late summer and early fall. Egg deposition, under leaf litter, decaying logs, and rocks, etc., reaches a peak in September and October. The adults usually die soon after laying eggs. Adults are rarely found in the field in late November. In most populations it appears that at least a few individuals are out of reproductive synchronization with the majority of the population; an occasional egg mass or mature slug will be encountered in the spring or summer.

Mating behavior begins with one member of the pair following the other until body contact is established. Once body contact is achieved the slugs gradually orient themselves so that the genital openings are in opposition. To do this the slugs align their anterior ends side by side but pointing in opposite directions. Their bodies are also curved in such a way that the anterior end of each slug rests in the concavity of the partner's curved body. In this position each slug everts its atrium and brings it in contact with that of its partner's. The joined atria form a bluish, thin walled ovoidal mass between the two animals. The animals maintain this position until a mutual exchange of spermatophores has taken place; this may require an hour or more. Occasionally, during the preliminary stages, one or both slugs may be observed rasping away the upper layers of the partner's skin. Some of the wounds inflicted are deep enough to remove the entire pigment layer leaving the injured animal with whitish blotches.

In the laboratory egg laying begins within a week after mating Each slug may produce several egg masses during the course of its reproductive life. The eggs hatch in about four weeks when maintained at 15° C. The newly hatched slugs are about 5 to 7 mm long.

Habitat and feeding habits. *Arion subfuscus* is basically a woodland and ecotonal animal. In Connecticut it is especially abundant in maple or mixed hardwoods, but not in predominantly oak woods. It is most frequently encountered under thin layers of leaf and twig litter, loose bark and slightly decayed logs. Farther north, it is abundant in spruce-fir forrsts as well as in deciduous forests. It is occasionally found in dumps and cultivated areas.

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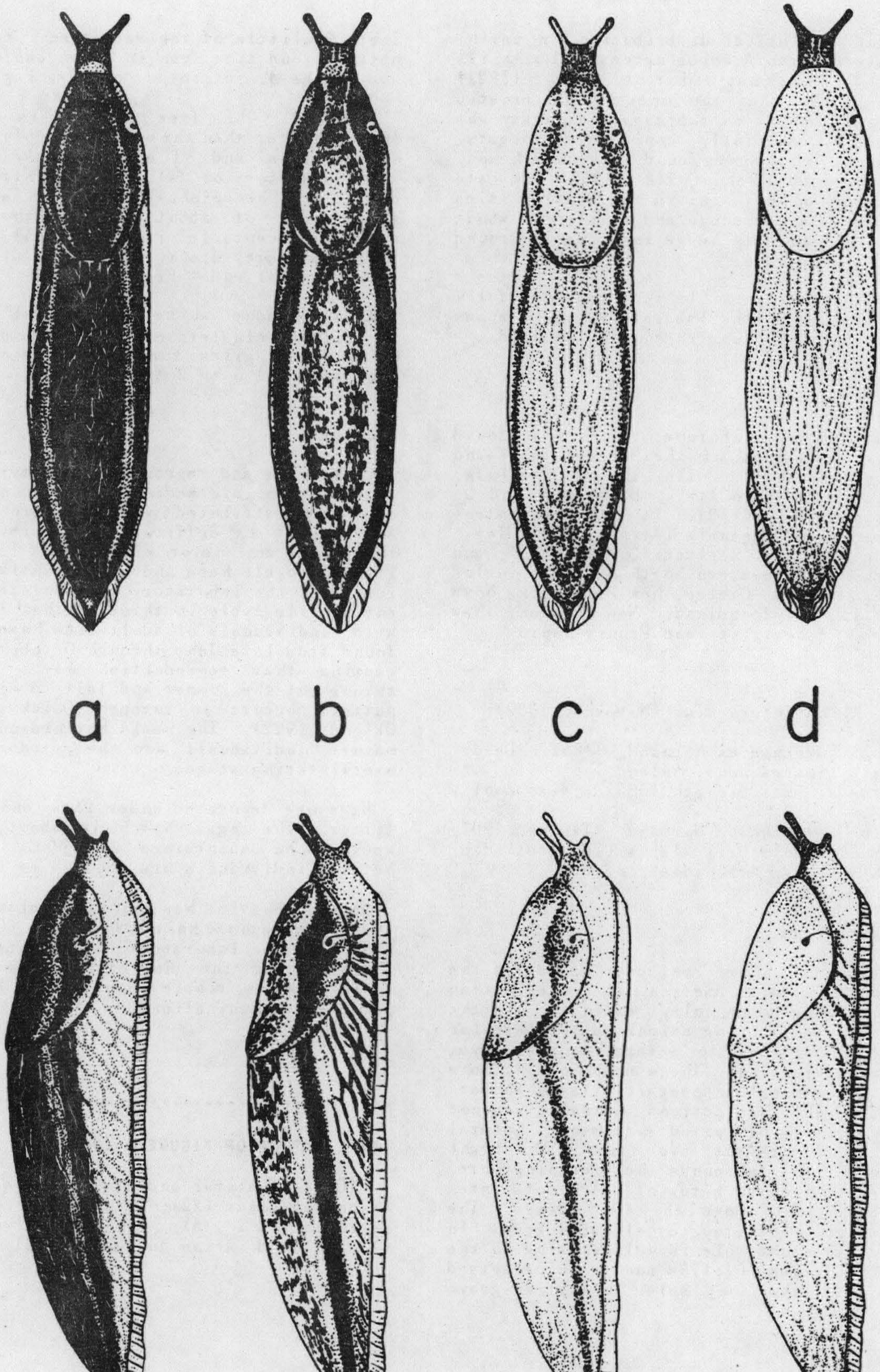
EXPLANATION OF FIGURE 3 (OPPOSITE PAGE)

FIG. 3. Lateral and dorsal views of *Arion subfuscus*. a, color form 1 (X 1 1/3); b, color form 2 (X 1½); c, color form 4 (X 1 1/3); d, color form 3 (X 1½).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Schaefer

The ecological distribution in northeastern North America agrees well with its ecology in its native Europe. Økland (1922) considered that the most characteristic habitat of *Arion subfuscus* in Norway was forests, especially coniferous forests, although it also was found in refuse heaps. Taylor (1907) and Quick (1960) indicate that *Arion subfuscus* in the British Isles resides in deciduous and coniferous woods as well as damp hedge rows, waste ground and some gardens.

Although it can be reared successfully on lettuce in the laboratory, it is apparently mainly fungivorous in the wild.

Distribution

A native of Europe, it is now found throughout most of the British Isles and Europe north of a line through Orenburg, Odessa, northern Italy, Bsrcelona and Oporto (Quick, 1960). It has been introduced into Venezuela (Arias, 1959), Iceland and New Zealand (Quick, 1949), and much of northeastern North America, including Ontario, Quebec, New Brunswick Nova Scotia, Newfoundland, New England, New York, Connecticut, and Pennsylvania.

Arion intermedius (Normand, 1852)

Limax intermedius Normand, 1852. Descr. six limaces nouv. Valenc., p. 6.

Arion minimus Simroth, 1885, Z. Wiss. Zool., 42(2):237.

Arion intermedius Normand, Taylor, 1907, Monogr. Moll. Brit. Isles (Testacellidae, Limacidae, Arionidae), p. 240.

Description

External. The smallest member of the genus in North America, it is less than 25 mm long when fully extended. In the contracted, living animal each tubercular ridge bears one to several conical, hyaline projections. These unique projections give the animal an overall bristly appearance. The projections normally are not apparent in preserved specimens. Lateral bands, if present, are faint. The right mantle band surrounds the breathing pore. There is often a row of black dots anteriorly just above the foot fringe The body color is gray to yellowish gray. In life the foot sole is yellow owing to the accumulation of yellow mucus. In preserved animals, the foot sole is whitish gray. There is little of the variation in color, pattern, and size seen in *Arion subfuscus* and in the *A. fasciatus* complex. Fig. 5c.

Internal. The free oviduct is short (much shorter than the epiphallus plus the vas deferens) and of approximately constant diameter or slightly constricted distally. The epiphallus and the vas deferens are of about equal length. The seminal receptacle is spheroidal. Its stalk is short, stout, and widely dilated at its atrial end. Fig. 2f.

Eggs. Opaque white, ellipsoidal eggs are laid in clusters of one to two dozen. Quick (1960) gives the dimensions of the eggs as 2 X 1.5 to 2 X 2 mm.

Biology

Life cycle and reproductive behavior. Because *Arion intermedius* is not abundant or widely distributed in northeastern North America, it is difficult to determine if there are any major differences between its life cycle here and in its native Europe. In the laboratory it completes the entire life cycle in three months. In the wild, individuals of adult size have been found from late June through October suggesting that reproduction may occur throughout the summer and fall. A similar pattern occurs in Europe (Quick 1960; Økland 1922). The newly hatched and immature individuals are the predominant overwintering stages.

Eggs are deposited under logs and leaf litter. The eggs hatch in about three weeks when maintained at 15° C. Newly hatched individuals are about 4 mm long.

Mating behavior has not been observed. The spermatophore has not been seen (Quick, 1960). In the laboratory individuals kept isolated from the time of hatching commonly produce viable eggs (Jerry Franz, personal communication).

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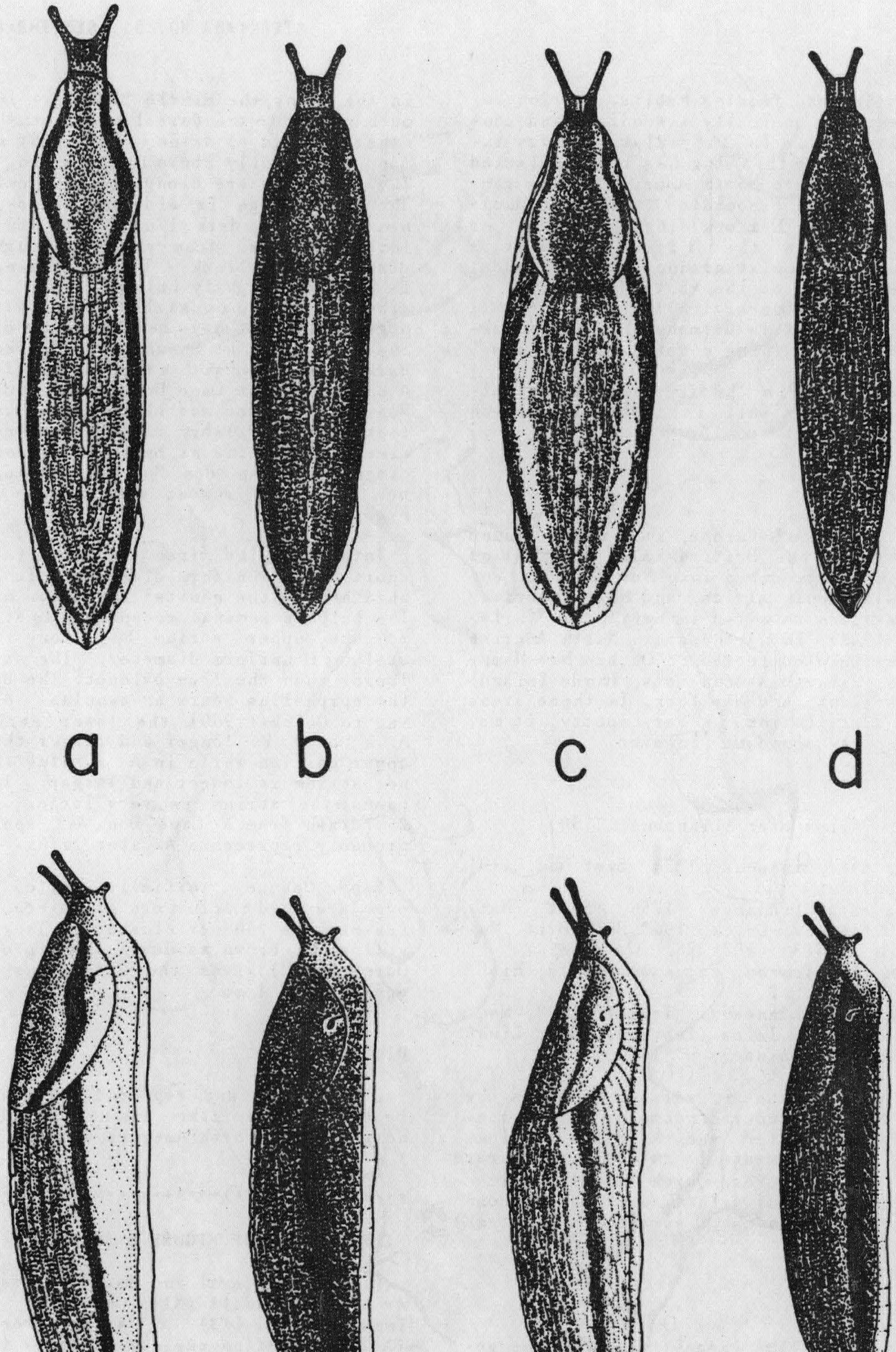
EXPLANATION OF FIGURE 4 (OPPOSITE PAGE)

FIG. 4. Lateral and dorsal views of a, *Arion fasciatus* (X2); b, *Arion circumscriptus* (X 2 1/3); c, *Arion silvaticus* (X 2 1/3), d, *Arion hortensis* (X2).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Habitat and feeding habits. *Arion intermedius* is basically a woodland and ecotonal animal. In the relatively few instances where this slug has been collected in northeastern North America it has generally been associated with deciduous woods (other than oak), shrub thickets or hedgerows. In the British Isles it is common in the moist ground litter of woods, thickets, and at the roots of grass in open fields (Quick, 1960). Taylor (1907) indicates that in Germany the slug is associated with 'pine covered, heathy land.'

The animal is chiefly fungivorous although it does well in the laboratory on a lettuce diet.

Distribution

A native of Europe; it is now found throughout the British Isles and most of Europe. Introduced into New Zealand, Polynesia, South Africa, and North America. It has been reported in California (Pilsbry, 1948). In northeastern North America it has been collected in Quebec, New Hampshire, Maine, Massachusetts, Rhode Island, Connecticut, and New York. In these areas its distribution is very spotty; it may be locally abundant however.

Arion ater (Linnaeus, 1758)

Limax ater, Linnaeus, 1758, Syst. Nat. (10), 1:652.
Limax rufus Linnaeus, 1758, Syst. Nat. (10) 1: 652; Quick, 1960, Bull. Brit. Mus. (N.H.), 6(3): 103-226.
Arion empiricorum Férussac 1819, Hist. Nat. Moll., 2.
Arion ater (Linnaeus), Taylor, 1907, Mon. Moll. Brit. Isles (Testacellidae, Limacidae, Arionidae), p. 167.

Arion ater has at various times in the past been considered a complex of two species, *Arion ater* and *A. rufus*. Quick, (1947, 1949) treats *A. rufus* as a separate species. However, Quick (1960) again grouped *A. rufus* with *A. ater* and now considers *A. rufus* as a subspecies of *A. ater*.

Description

External. The largest slug in the genus, its extended length may exceed 150 mm. Adults lack lateral bands. When present in the young, the mantle bands are located much closer to the dorsal mid-line than in other species of *Arion*. The right mantle band lies wholly above the breathing pore. The tubercles are elongate and prominent. The foot fringe is wide and bears prominent vertical dark lines The adult coloration ranges from yellow through reddish brown to black. The foot fringe may be dark or brightly colored. The sole is gray. The slime is usually clear, although occasionally it may be yellow or orange. Specimens seen at Sherbrooke, Quebec were dark olive brown with a reddish foot fringe. A specimen from Cape Bon Ami (near Cap des Rosiers), Quebec was black with a reddish foot fringe. Pilsbry (1948) reported specimens from Maine as being black and specimens from Cap des Rosiers, Gaspé, Quebec as being 'russet with orange foot.' Fig. 5a, b.

Internal. The free oviduct is very short and of uniform diameter. It is ensheathed by the genital retractor muscle. The bulbous seminal receptacle is attached to the upper atrium by a long slender stalk of uniform diameter. The stalk is longer than the free oviduct. The base of the epiphallus bears an annulus. According to Quick (1960) the lower atrium of A. a. ater is longer and larger than the upper portion while in A. a. rufus the upper atrium is longer and larger. In both cases the atrium is very large. Figure 2h, drawn from a Cape Bon Ami specimen, probably represents A. ater rufus.

Eggs. Opaque, initially white, oval eggs are laid in clusters of several dozen (as many as 250 per cluster). They turn yellow to brown as development proceeds. Quick (1960) gives the dimensions of the eggs as 5 X 4 mm.

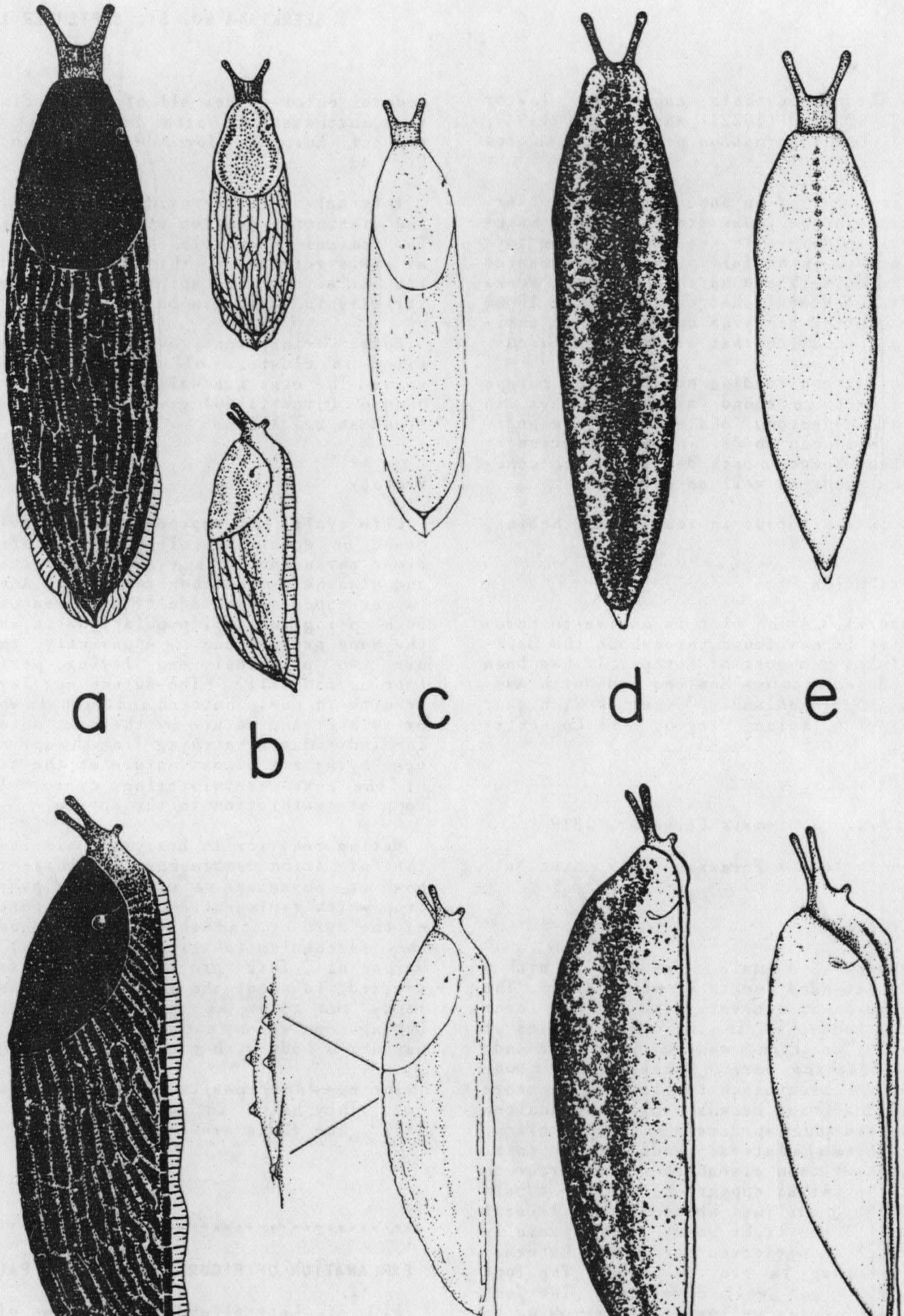
Biology

Life cycle and reproductive behavior. Because *Arion ater* is not abundant in northeastern North America, we must depend

* * *

EXPLANATION OF FIGURE 5 (OPPOSITE PAGE)

FIG. 5. Lateral and dorsal views of a, *Arion ater,* adult (X1); b, *Arion ater,* immature (X 1 1/3), c, *Arion intermedius* (X 2½); d, *Philomycus carolinianus* (X 1¼); e, *Pallifera dorsalis* (2 1/3).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upon European authors, especially Taylor (1907), Økland (1922) and Quick (1949, 1960) for information pertaining to its life cycle.

Arion ater is an annual slug that overwinters in the young stage. Sexual maturity is attained in the summer. Egg laying occurs inthe fall. Eggs are deposited in the soil. These hatch four to six weeks later. The newly hatched slugs are 10 mm long. Mating behavior apparently is basically similar to that of *Arion subfuscus*.

Habitat and feeding habits. In Europe *Arion ater* is found along roadways, in fields, hedgerows, and woodlands, especially deciduous woods. In North America it has been found in both deciduous and coniferous woods as well as gardens.

It is omnivorous in its feeding habits.

Distribution

General. *Arion ater* is native to Europe. It is now found throughout the British Isles and most of Europe. It has been introduced into New Zealand and North America (Newfoundland, Quebec, Michigan, Washington, Maine, Oregon, and Connecticut).

Arion hortensis Férussac, 1819

Arion hortensis Férussac, 1819, Hist.Nat. Moll. 2:65.

Description

External. A small, slender slug with a fully extended length of about 40 mm. The lateral bands are very dark and are lower on the body than in the other species of *Arion*. The right mantle band surrounds the breathing pore. Dorsally the body color is blue-black to black in immature individuals and brownish black in adults; preserved adult specimens are bluish black. Just above the lateral bands the body color is lighter than elsewhere on the dorsum so that the animal appears to possess a pair of light bands just above the dark lateral bands. These light bands are especially distinct in preserved specimens. Laterally the body is gray to brown. The foot fringe is not well developed. The foot sole in life is yellow or orange owing to the accumulation of colored mucus. In preserved specimens the foot sole is white. Although in Europe this slug exists in several color phases, all of the specimens from northeastern North America fit the typical European form described above. Fig 4d.

Internal. The free oviduct is very long and distinctly swollen at its atrial end. The seminal receptacle is spheroidal; its stalk is very short, thick and swollen at its atrial end. The epiphallus terminates atrially in a swollen bulb. Fig 2j.

Eggs. Transparent, oval eggs are deposited in clusters of up to three dozen eggs. The eggs gradually turn yellow and opaque. Quick (1960) gives the egg dimensions as 2.5 X 2 mm.

Biology

Life cycle and reproductive behavior. Based on specimens collected at various times throughout the year in Connecticut and elsewhere in northeastern North America, it appears that adults are present in both spring and fall populations in about the same proportions. Apparently there are two principal egg laying periods (spring and fall). The autumn egg laying results in newly hatched individuals which overwinter and mature by the next autumn. The individuals hatching from the spring egg laying are almost mature at the start of the next overwintering cycle. They complete maturation in the spring.

Mating behavior is basically similar to that of *Arion subfuscus*. *A. hortensis*, however, possesses a club-shaped projection which represents an everted portion of the oviduct and which is analogous to the sarcobelum (a stimulatory organ) of *Deroceras*. This projection, when fully everted, is about the same size, transparency and color as the everted atrium. During copulation each slug strokes its partner's body with the everted oviduct.

The eggs are deposited under ground litter. They hatch in about four weeks at 15°C. The young are 4 to 5 mm long.

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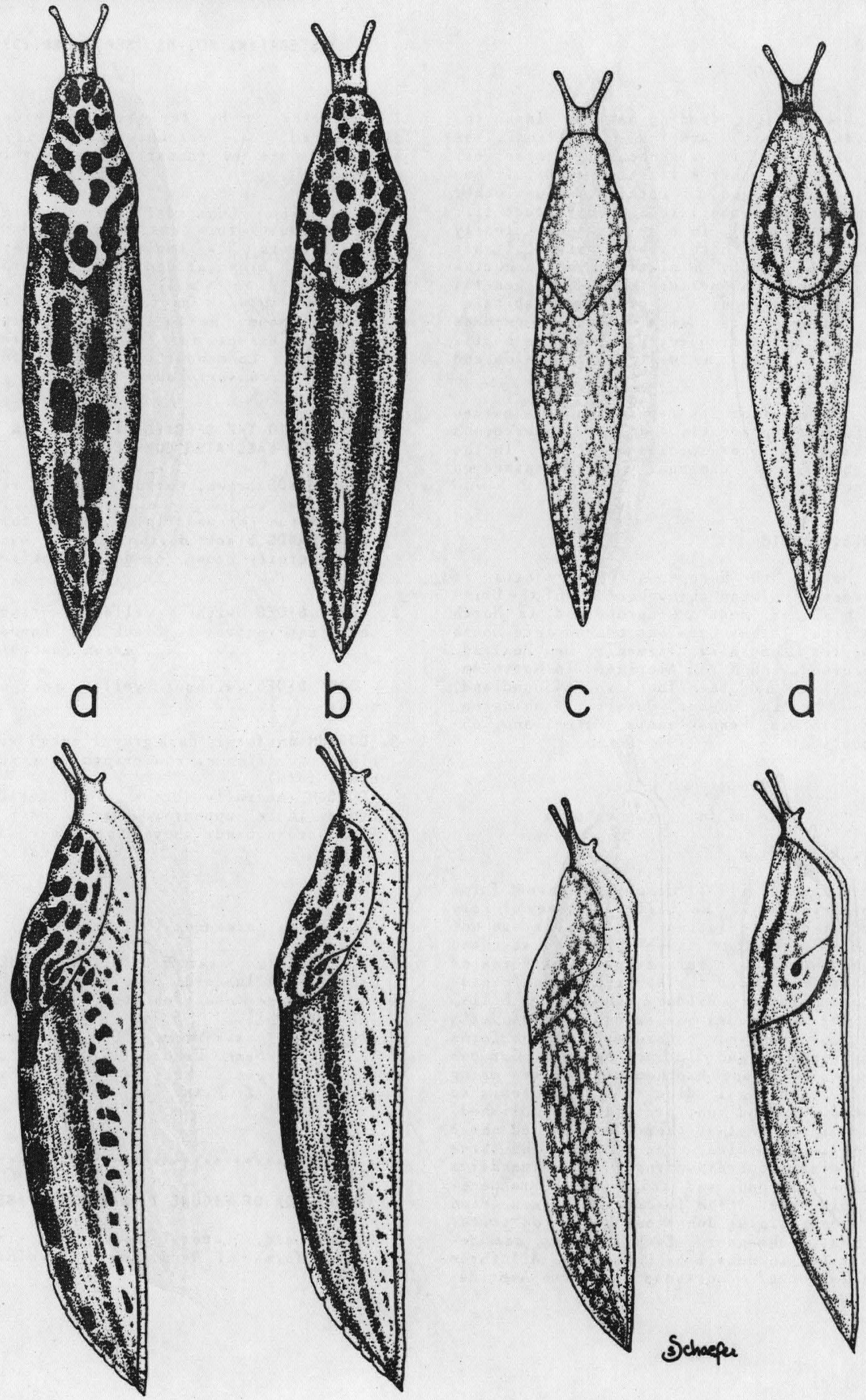
EXPLANATION OF FIGURE 6 (OPPOSITE PAGE)

FIG. 6. Lateral and dorsal views of a, b, *Limax maximus* (X 1); c, *Limax flavus* (X 1); d, *Lehmannia valentiana* (X 1)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Habitat and feeding habits. In northeastern North America *A. hartensis* has been found in greenhouses, nurseries, parks, and other cultivated areas. It has also been found in both deciduous (other than oak) and coniferous woods (spruce-fir, in particular), in some cases not closely associated with cultivated areas. It has far too spotty a distribution in northeastern North America to make any general statements about its preferred habitats. In Europe it is commonly found in gardens (where it is frequently a serious horticultural pest) as well as in fields and woodlands.

Judging from its reputation as a garden slug it apparently is less fungivorous than most other species of *Arion*. In the laboratory it can easily be maintained on lettuce.

Distribution

Native to Europe, *Arion hortensis* is presently found throughout all of the British Isles, most of Europe and in North Africa. It has been introduced into South Africa, Australia, Tasmania, New Zealand, Iceland, and North America. In North America it has been found in Newfoundland, Nova Scotia, Quebec, Ontario, Washington, California, Pennsylvania, Maine, and Connecticut.

Arion fasciatus complex

I. Definition

Lohmander (1937) described three forms of *Arion* which he believed were closely related, but distinct. Lohmander was not certain whether these forms constituted good species or were simple subspecies or varieties under the species *Arion fasciatus* Nilsson. Wwlden (quoted by Ellis, 1966) in Sweden has extended Lohmander's research and now considers the three forms as separate and distinct species. Our own anatomical and biochemical studies using acrylamide gel disc electrophoresis to study egg and foot proteins (unpublished) convince us that there are indeed three distinct species in the complex. The three species, corresponding to Lohmander's first, second, and third forms, respectively, are: *Arion fasciatus* Nilsson, *Arion circumscriptus* Johnston, and *Arion silvaticus* Lohmander. Each species was described in detail by Lohmander. All three forms occur in northeastern North America. *A. fasciatus* is by far the most widely distributed. *A. circumscriptus* and *A. silvaticus* are by comparison relatively uncommon.

In addition to Lohmander's three distinct forms a fourth form has been introduced into southern New England. This form, with reddish brown ground color and brown lateral bands is simply a color form of *A. circumscriptus*. On the basis of its internal anatomy as well as its external appearance, except for color, it agrees exactly with Lohmander's 'second' form (i.e., *A. circumscriptus*).

II. KEY TO THE SPECIES OF THE ARION FASCIATUS COMPLEX

1. **BODY BANDS** brown; dorsum and sides reddish brown .... *Arion circumscriptus* (brown form)
   BODY BANDS black; dorsum medially black and laterally brown, or dorsum entirely gray 2

2. **BODY SIDES** with a yellow or orange band just ventral to black body bands.. .... *Arion fasciatus*

   BODY SIDES without yellow oror nge bands 3

3. **DORSUM** uniformly dark gray flecked with black ... *Arion circumscriptus* (typical black form).
   DORSUM medially black and laterally brown (there appears to be a pair of light brown bands above the black body bands) *Arion silvaticus*

Arion fasciatus (Nilsson, 1822)

Limax fasciatus, var. γ, Nilsson, 1822, Historia Molluscorum Sveciae, p. 4.
Arion circumscriptus Johnston, 1828, Edinb. New Phil. J., 5:76.
Prolepis hortensis Malm, 1868, Goteborgs Vet. Vitt. Samh. Handl., 10:49.
Arion bourguignati Mabille, 1868; Simroth, 1885, Z. Wiss. Zool., 42(2).

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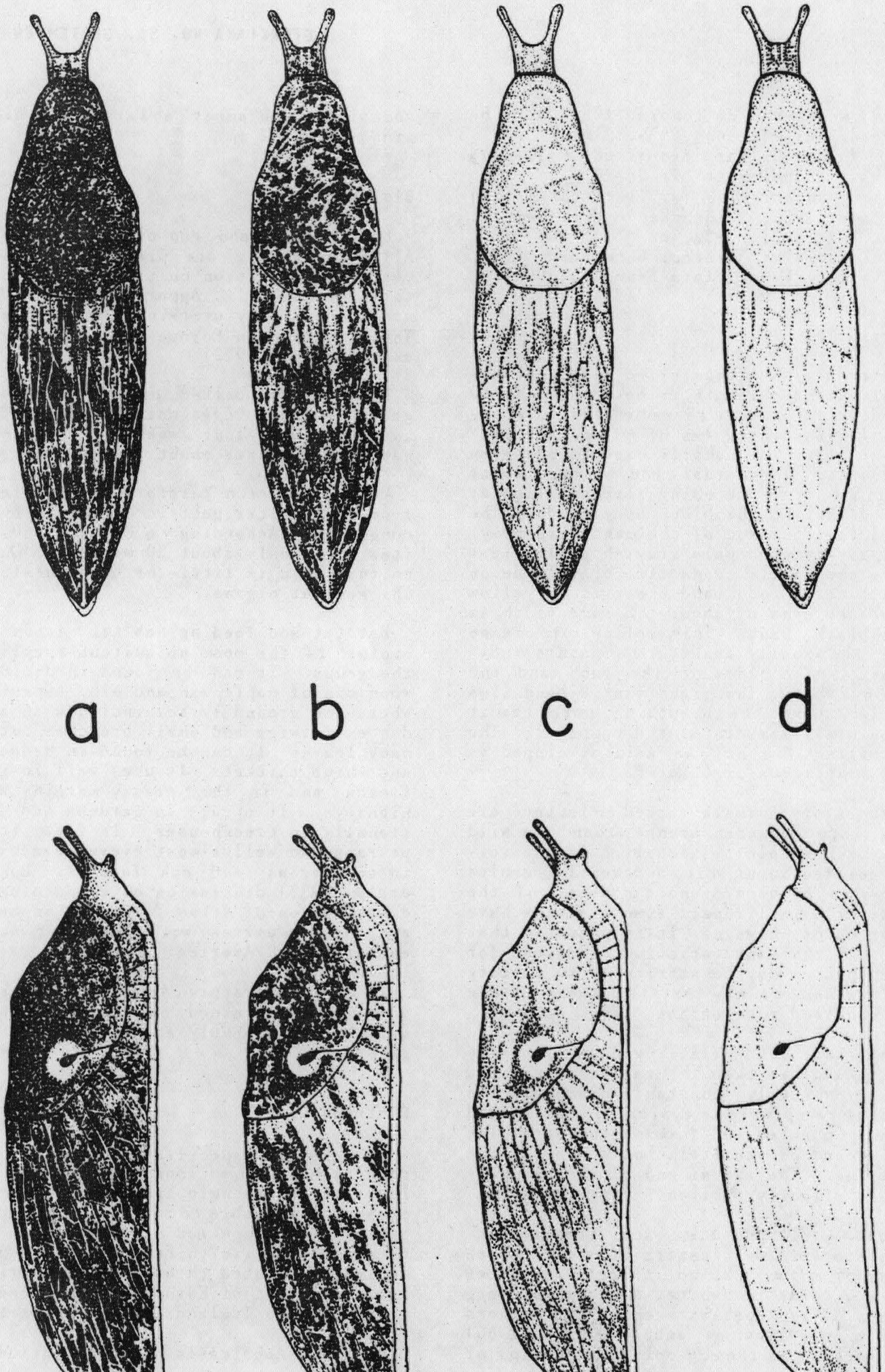
EXPLANATION OF FIGURE 7 (OPPOSITE PAGE)

FIG. 7, a-d, Lateral and dorsal views of color forms of *Deroceras reticulatum* (X 2).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Arion nilssoni Pollonera, 1887, Atti R. Accad. Sci. Torino, 22½5.
Arion fasciatus, var. *flavescens* Collinge, 1893. Conchologist, 2: 26-27.
Arion circumscriptus, var. *circumscripta* Økland, 1922, Videnskap. Skrifter, I. Mat.-Nat., Kl. 1922, no. 5:32-40.
Arion fasciatus Nilsson; Lohmander, 1937, Acta Soc. Fauna Flora Fenn., 60:90-112.

Description

External. A medium sized slug, the typical extended length is between 40 to 50 mm; some laboratory reared individuals attain lengths in excess of 60 mm. The middorsal ridge is usually conspicuous even in adults. The dorsal body ground color is light gray becoming slightly lighter just dorsal to the black body bands. The mid dorsal portion of the mantle is gray. The gray fades to pale grayish yellow just above the mantle bands. Immediately below each lateral body band there is a yellow or orange band of about the same width as the black band. This yellow or orange band is usually absent in immature individuals. The sides of the foot and the sole are white. The right mantle band lies wholly above the breathing pore (as it does in all members of the complex). The foot fringe is not as well developed as in *A subfuscus* or *A. ater*.

Laboratory animals reared on lettuce are much more brownish orange than the wild forms This color is acquired from a yellow colored mucus which apparently results from the high carotenoid content of the food. Wild individuals almost always have clear mucus, however. It is possible that some of the many varieties described for this species may be attributed to dietary differences as may exist between garden and woodland populations. Fig. 4a.

Internal. The free oviduct is very short (shorter than the vas deferens) and of approximately constant diameter. The seminal receptacle is typically tear-shaped with the pointed end forming the apex. The atrial end of the stalk bears a bulb like swelling. The atrial end of the epiphallus is slightly swollen. Fig. 2i

Eggs. Ellipsoidal, semi-translucent eggs are laid in clusters of one to three dozen or more. Økland (1922) describes the egg color as white although all egg masses of the species seen by the authors have been yellow or amber. Quick (1960) also describes the egg color as 'yellow or sometimes dark amber' and gives the dimensions as 3 X 2 mm.

Biology

Life cycle and reproductive behavior. All size classes are present through the year. Reproduction continues from spring through the fall. Apparently all stages can successfully overwinter in our region. The situation in Europe is apparently the same (Økland, 1922).

Eggs are deposited on the soil under ground litter. Eggs maintained at 15° C hatch in about four weeks. The newly hatched slugs are about 5 mm long.

Mating in *Arion fasciatus* is different from the typical pattern displayed by its congeners. According to Quick (1960) coitus lasts only about 20 minutes. During coitus there is little or no eversion of the genital organs.

Habitat and feeding habits. *Arion fasciatus* is the most ubiquitous species of the genus. It can be found in deciduous woodlots of maple, ash, and elm, especially where the ground litter includes an abundance of twigs and small branches, but not many leaves It can be found in hedgerows and shrub thickets. It does well in grass fields and in the grassy margins along highways It occurs in gardens and occasionally in greenhouses. In fact, it appears to do well almost everywhere except in coniferous and oak forests. Lohmander's (1937) discussion of the ecological distribution of *Arion fasciatus* in Sweden and Norway agrees with that for northeastern North America.

In the laboratory *Arion fasciatus* can easily be maintained on lettuce. In the wild it is probably at least partly fungivorous.

Distribution

Because the specific components of the complex have for so long been treated collectively as a single species, it is not presently possible to decide which records apply to each species of the complex The complex is native to Europe. It is presently distributed throughout the British Isles and most of Europe. It has been introduced into Iceland and North America.

In North America it has been introduced

into most of Canada and the United States. It is undoubtedly the most widely distributed of the introduced Arionids. In northeastern North America *Arion fasciatus* is by far the most widely distributed species in the complex. Both *A circumscriptus* and *A. silvaticus* are relatively uncommon, although there are scattered populations throughout the region.

Arion circumscriptus Johnston, 1828

Arion fasciatus, var. ? Nilsson, 1822, Historia Molluscorum Sveciae, p. 4.
Arion circumscriptus Johnston, 1828, Edinb. New Phil. J., 5:76.
Arion bourguignati Mabille, 1868; Pollonera, 1887, Atti R. Accad. Sci. Torino, 22:5.
Arion ambiguus var. *armoricana* Pollonera, 1889, Atti R. Accad. Sci. Torino, 24:13.
Arion fasciatus var. *grisea* Collinge, 1892, Conchologist, 2(3).
Arion circumscriptus var. *nigra* Økland, 1922, Videnskap. Skrifter, I. Math.-Nat. Kl. 1922, no. 5:32-40.
Arion circumscriptus Johnston; Lohmander, 1937, Acta Soc. Fauna Flora Fenn., 60: 90-112.

Description

External. Typicsl black form. A small slug, the extended length usually does not exceed 40 mm. The dorsal and lateral ground color is gray (ranging from light steel gray through a bluish gray to a blackish gray). The dorsum and mantle are distinctly flecked with black spots of various shapes and sizes. Because of these black spots fully contracted animals appear almost black. Lateral black body bands are present. In Lohmander's (1937) description the lower boundary of each band is said to be less distinct because the sides are a darker gray than that portion of the dorsum immediately adjacent to the bands. This is not the case, however, in the relatively few populations that we have been able to sample in our region. The sides are not darker than the area immediately above the bands. The weakly developed foot fringe is faintly peppered with black spots. The foot sole is bluish-white. The slime is clear. Fig. 4b.

Brown form. The dorsal and lateral ground color is reddish brown. The dorsum and mantle are distinctly flecked with brown spots of various shapes and sizes. The lateral bands are brown. No black pigment is present. In all other respects it is like the typical form described above.

Internal. Because the differences between this form and the other species in the complex are quite subtle and not entirely consistent, interested readers are referred to Lohmander's original paper (1937).

Eggs. Differences from *A. fasciatus*, if any, are not known.

Life cycle and reproductive behavior. Differences from *A. fasciatus*, if any, are not known.

Habitat and feeding habits. In Connecticut, all records are for mixed hardwoods adjacent to or very near cultivated lands. Lohmander (1937) stated that *A. circumscriptus* shares many sites in common with both other forms. He also indicated that it occurs in more moist and shady habitats than does *A. fasciatus*.

Differences in feeding habits from *A. fasciatus* are not known.

Distribution

See discussion under *Arion fasciatus*.

Arion silvaticus Lohmander, 1937

Arion fasciatus var. ? Nilsson, 1822, Historia Moll. Sveciae, p. 4.
Arion circumscriptus Johnston, 1828, Edinb. New Phil J., 5:76.
? *Arion neustriacus* Mabille, 1868, ev. Mag. Zool., (2) 20:138.
Arion fasciatus var. *neustriaca* Mabille; Collinge 1892, Conchologist, 2(3).
Arion circumscriptus var. *sylvatica* Lohmander, 1937, Acta Soc. Fauna Flora Fenn. 60:90-112.
Arion silvaticus Lohmander; Walden, 1966 (Quoted by A. Ellis in Conchologists' Newsletter, No. 17).

Description

External. In size, it is comparable to *A. circumscriptus*; its extended length is less than 40 mm. The lateral bands are broad and darkly pigmented. The mid-dorsal portions of the body and mantle are also darkly pigmented. Because the area just above the lateral bands is lightest in color there appears to be a pair of light bands present between the dark mid-dorsum and the dark lateral bands. The dorsum has a distinctly chocolate brown tinge that is not lost in preservation. There is apparently no brown pigment present however. The brownish color results from a combination of orange and black pigments in a gray, semi-translucent matrix. The body sides are slightly paler than the dorsum. The valleys between the lateral tubercles are darkly pigmented producing a distinctly reticulated appearance. The two ventralmost rows of tubercles contain an abundance of white pigment flecks which greatly contributes to the overall paler appearance of the sides. The foot fringe is dark spotted almost to the extent of being lineolate. The foot sole is a pale yellowish white The slime is clear. Fig. 4c.

Internal. See Lohmander 1937.

Eggs. Differences from *A. fasciatus*, if any, are not known.

Biology

Life cycle and reproductive behavior. Differences from *A. fasciatus*, if any, are not known.

Habitat and feeding habits. In Connecticut, all records are for mixed hardwood woodlots adjacent to or very near cultivated lands. Lohmander (1937) stated that *A. silvaticus* shares many sites in common with both other forms. He also indicated that it tends to occur in even more moist habitats than *A. circumscriptus;* for example, he found it in bogs.

Distribution

See discussion under *Arion fasciatus*.

Family Philomycidae Keferstein, 1866

Description

Slugs in which the mantle covers almost the entire body. A shell is absent The jaw is ribbed or striated The foot sole is undivided. The tentacular and buccal muscles have separate origins. The breathing pore lies near the right anterior margin of the mantle.

Distribution

Native to Asia, North America, and Central America south to Colombia. It has been introduced into Hawaii.

Origin

Apparently arose from an Endodontid stock which also gave rise to the Arionidae.

Genus *Philomycus* Rsfinesque, 1820

Philomycus Rafinesque, 1820, Annals of Nature, 1.1-16.

Description

A vaginal, calcareous stimulator is present The jaw is striated (rather than ribbed). The mantle covers most of the head.

Distribution

Eastern North America from Canada to Florida and Texas.

Philomycus carolinianus (Bosc, 1802)

Limax carolinianus Bosc, 1802, Hist. Nat. Vers, 1 80.
Philomycus flexuolaris Rafinesque, 1820, Annals of Nature 1 10
Tebennophorus caroliniensis Binney, 1842. Boston Jour. Nat Hist. 4:171.

Description

A large slug, the extended length is usually about 70 to 80 mm; occasionally it may reach 100 mm The mantle covers the entire body, including most of the head. The mantle ground color is tan. Except for the lateral margins, however, the tan color is usually almost obliterated by a wide dark (black or brown) mid-dorsal band with diffuse margins, two narrower lateral bands that are so irregular they may appear as discontinuous blotches, and by numerous spots between these bands. Irritated individuals produce a milky slime. Fig. 5d.

Biology

P. carolinianus is a relatively inactive slug. It is widespread but rarely locally abundant. Although native to our region, its biology is not well known. It inhabits both deciduous and coniferous woods where it is usually found in decaying logs. It is more common in deciduous forests, especially beech and basswood.

It is fungivorous in the wild.

Distribution

Eastern half of North America from Canada south to Florida and Texas.

Genus *Pallifera* Morse, 1864

Pallifera Morse, 1864, Jour. Portland Soc. Nat. Hist., 1:1-63.

Description

Slugs in which the mantle covers all of the body except the head. The genus includes several species; except for one species in Arizona, all are confined to eastern North America. Only one species occurs in Connecticut.

Pallifera dorsalis (Binney, 1842)

Philomycus dorsalis Binney, 1842, Boston Jour. Nat. Hist. 4:174.
Tebennophorus dorsalis Binney, 1851, Terr. Moll., 2:24.

Description

A small slug about 25 mm long when fully extended. Externally similar to *Philomycus* except that the head is not covered by the mantle and the tail is more tapered. The slime is more watery than that of *Philomycus*. The mantle ground color is light to bluish gray. There is usually a faint row of dots, or a broken line, extending mid-dorsally down the mantle. Occasionally a fainter, paired, lateral set of bands may also be present. The foot fringe and sole, especially toward the anterior end, may be rust red. Fig. 5e.

Biology

The life history and reproductive habits of this species are not well known. It is widespread and more abundant than is *Philomycus carolinianus*. It is a woodland form which typically is found beneath the bark of decaying logs and under the leaf litter. It is more likely to be in ecotonal and semi-cultivated areas than is *Philomycus*.

Distribution

It has been recorded from eastern Canada, New England, New York, Pennsylvania, Virginia, and the northern midwestern United States

SUPERFAMILY ZONITACEA

Family Limacidae Gray, 1824

Description

Slugs in which the shell is almost always a flat plate enclosed wholly within the mantle. The jaw is smooth. The foot sole is tripartite. The breathing pore is located behind the mantle cleft in the right, rear quadrant of the mantle. The tentacular and buccal retractor muscles all arise from a common origin just behind the posterior margin of the mantle (Fig. 1t). Usually there is a dorsal keel present, at least posteriorly.

Distribution

The family is primarily a native of Europe and adjacent portions of North Africa and Asia. Only the genus *Deroceras* has a world-wide distribution. Other members of the family have been introduced into South Africa, Australia, Tasmania, New Zealand, Polynesia, Japan Iceland, and South and North America.

Origin

The family is believed to have arisen from a Zonitid stock, probably in Europe.

Subfamily Limacinae

The mantle is concentrically ridged but lacks a subdividing horseshoe-shaped groove. The dorsal keel terminates before reaching the posterior margin of the mantle. There is no caudal gland. An epiphallus and spermatophore are absent. The stimulator, if present, is associated with the penis.

Genus *Limax* Linnaeus, 1758

Limax Linnaeus, 1758, Syst. Nat. (10), 1: 652.

Description

The concentric ridges of the mantle have their nucleus on the dorsal midline (Fig.

1j). The posterior end is pointed rather than truncated as in *Deroceras* (Fig. 11). A penial appendix and a rectal caecum may be present or absent (no penial appendix is present in any *Limax* species known to be introduced into North America). The right tentacular retractor muscle passes forward between the penis and the oviduct.

Distribution

Native to Europe and adjacent parts of Africa and Asia. Some species have been spread by commerce throughout much of the world, including Africa, North and South America, and Australia.

Limax maximus Linnaeus, 1758

Limax maximus Linnaeus, 1758, Syst. Nat. (10) 1:652.

Description

External. A latge slug, its extended length is 100 to 200 mm. The dorsal keel extends less than half the distance between the posterior margin of the mantle and the 'tail'. The keel is slightly crenate. The body color is some shade of gray or brown. There are numerous dark spots, blotches, or stripes present in a variable pattern. There may be up to 20 small irregular black spots on the mantle or there may be less than a dozen brownish, black bordered blotches; there are no regular mantle bands. On the body proper there may be several rows of black spots or blotches which may coalesce to form body bands or the body may be uniformly dark and unspotted. The tentacles are uniformly brown. The foot sole is whitish gray. The slime is clear. (Fig. 6a, b) A closely related form, *L. cinereoniger* Wolf, which has not been reported from North America, is distinguished from *L. maximus* by its dark spotted tentacles, a black body with a white keel, and its coarser tubercles (Quick, 1960).

Internal. Fig. 2a. The penis is quite large and contorted. It lacks an appendix. The free oviduct is relatively long. The distal part of the slender stalk of the seminal receptacle runs parallel and adjacent to the free oviduct; the stalk may arise from either the free oviduct or the atrium. A rectal caecum is absent.

Eggs. The transparent, colorless, oval eggs are deposited in clusters of one to several dozen. Quick (1960) gives the dimensions as 5.0 X 5.5 mm.

Biology

Life cycle and reproductive behavior. In Connecticut the eggs are deposited under rocks, logs and leaf litter, chiefly in the fall. Eggs maintained at 15° C hatch in three to four weeks. *L. maximus* lives at least three to four years (Quick, 1960); two years are required for it to reach sexual maturity in the laboratory (Simpson, 1901). It is probable that all stages overwinter in our region.

Mating behavior in *L. maximus* has been described in detail by Adams (1898). Mating usually involves the suspension of the mating pair by a thick mucus thread attached to an overhang. The pair, while suspended in mid-air intertwine their bodies and finally their penes. While in this position viscous masses of semen are exchanged.

Habitat and feeding habits. All Connecticut records for *L. maximus* are from cultivated areas such as gardens and parks or from cellars, retaining walls, etc. associated with human dwellings. In Europe *L. maximus* occurs in woods as well as in cultivated areas.

In the laboratory this species can be reared on a diet of lettuce. In the wild they are omnivorous.

Distribution

Native to Europe, it is now widely distributed throughout the British Isles, Europe and adjacent Asia and Africa. It has been introduced into South Africa, Australia, Twsmania, New Zealand, South America and throughout much of North America.

Limax flavus Linnaeus, 1758

Limax flavus Linnaeus, 1758, Syst. Nat. (10) 1:652.

Description

External. A large slug, its extended length is 70 to 100 mm. The ground color ranges from yellowish gray to green. Adults have the body irregularly blotched or spotted with yellow. Lsteral bands are absent. The tentacles are blue. The foot sole is pale yellow. The slime is yellow. Fig. 6c.

Internal. The penis is quite large and contorted. It lacks an appendix. A long rectal caecum is present.

EGGS. The lemon-shaped, amber colored eggs are deposited in clusters of up to two dozen eggs. Quick (1960) gives the egg dimensions as 6 X 4 mm.

BIOLOGY

Life cycle and reproductive behavior. Because it is extremely rare in natural areas in our region we must depend upon accounts provided by European workers and upon greenhouse observations such as those provided by Karlin and Bacon (1961). In the British Isles egg laying lasts from late summer to February. The eggs hatch in three to six eeeks at 20° C. Newly hatched slugs are 10 to 13 mm long.

Mating occurs on a substrate (rather than in mid-air as in *L. maximus)*. Entwined penes exchange viscous seminal masses as in *L. maximus*. The actual copulation takes less than a minute.

Habitat and feeding habits. In Europe, *L. flavus* is occasionally found in woods; it is much more common in gardens and around buildings, however.
It is omnivorous.

Distribution

Native to Europe, it occurs throughout the British Isles, most of Europe and adjacent parts of Africa and Asia. It has been introduced into South Africa, Australia, South America, and in many localities in North America.

Genus *Lehmannia* Heynemann, 1861

Lehmannia Heynemann, 1861, Malakozool., 8:85-105.

Description

The penis is short; it bears a well developed appendix. There is a long rectal caecum present which extends posteriorly almost to the apex of the visceral mass (Fig. 1p). The body frequently becomes translucent and swollen owing to the absorption of water from moist surroundings (especially in *Lehmannia marginata)*. The nucleus of the concentric mantle ridges is mid-dorsal (Fig. 1j). Walden (1961) suggests that *Lehmannia* be provisionally treated as a subgenus under the genus *Limax*. Since *Lehmannia* is such a well established generic name in both the North American and European literature and because its taxonomic status is still in doubt we choose to retain *Lehmannia* as a separate genus for the present.

Distribution

Native to Europe and adjacent parts of Africa and Asia, it has been introduced into South Africa, Australia, and North and South America.

Lehmannia valentiana (Férussac 1823)

Limax valentianus Férussac 1823, Hist. Nat. Moll., Suppl. Fam. Limaces, p. 96.
Limax poirieri Mabille, 1883, Bull Soc. Philom. Paris (7) 7:39-53; Walden 1961, Arkiv Zoologi, (15) 3:71-95.
Lehmannia poirieri Mab., Quick, 1960, Bull. Brit. Mus. (N.H.), 6(3):197.

There has been more nomenclatural confusion about this slug than any other imported Limacid. This confusion springs from two sources First, only recently has it become clear that *L. poirieri* and *L. valentiana* are conspecific (Walden, 1961). Secondly, this slug has been referred to by many American authors as *L. marginata* in the mistaken belief that *L. valentiana* was conspecific with *L. marginata*, the forest-dwelling species of Europe. Walden (1961) discusses the problem in detail.

Description

External. A medium sized slug, the extended length is about 60 mm. The keel is very weakly developed and may occasionally be absent. The breathing pore is surrounded by a whitish area. The ground color is light brown dorsally, fading gradually to light tan laterally. The mantle bears a pair of gray to black lateral bands and usually a single, less well-defined mid-dorsal band. Only paired bands are present on the back where they are situated close together near the dorsal midline. Often the mantle bears pale yellow spots which may occasionally disrupt the dark bands. Individuals in which the spots are distinct and the bands faint may be mistaken for *Limax flavus* The foot sole is whitish. The concentric mantle ridges are especially distinct. The slime is clear.

Internal. The penial appendix is a large, slightly contorted cylinder with a blunt to rounded terminus (Fig. 2e). The long rectal caecum is a fairly wide, flat band lying on the dorsal surface of the visceral mass (Fig. 1p). The radula is distinctly different from that of adult *L. marginata* in that the central tooth is distinctly tricuspid, as are the first dozen or more lateral teeth. (Fig 1u).

Eggs. The oval transparent eggs are deposited in loose aggregations of up to several dozen eggs. The eggs are usually colorless and 2.25 X 1.5 mm in size.

There are two other Limacid slugs which may be confused with *L. valentiana* and which have been reported from North America:

Lehmannia marginata (Müller, 1774). This woodland slug of Europe is slightly larger than *L. valentiana*. It is banded as in *L. valentiana*. Positive identification depends upon internal characters of which the most dependable are: the presence of a conical penial appendix (Fig. 2d as opposed to a cylindrical one in *L. valentiana*, and the presence of a specialized radula (in adults) in which the central tooth has a large mesocone and only vestiges of the ectocones while the inner lateral teeth have large mesocones, no ectocones, and except for the first two rows, no endocones (Fig. 1v). Apparently the only valid record for North America is from Newfoundland.

Limax nyctelius Bourguignat, 1861. Externally this North African slug looks very much like *L. valentiana*. It differs from *L. valentiana* in possessing a long penis without an appendix. This greenhouse slug has been introduced into Washington, D.C. (Quick, 1960).

Biology

Life cycle and mating behavior. In northeastern North America *L. valentiana* is essentially a greenhouse slug. Under greenhouse conditions it breeds throughout the year. The eggs are deposited on, or partially in the soil. Eggs maintained at 15° C hatch in about four weeks. The newly hatched young are 3 to 5 mm long.

Mating behavior has not been recorded.

Habitat and feeding habits. Although it apparently occurs in a variety of habitats in California throughout the rest of North America *L. valentiana* appears to be confined to greenhouses and their environs.

It is probably omnivorous. In the laboratory it can easily be maintained on lettuce.

Distribution

L. valentiana is a native of the Iberian Peninsula (Walden, 1961). It has spread, through commerce, to other parts of Europe and the British Isles. It has been introduced into North and South America, South Africa, Australia, and several Atlantic and Pacific Islands. In North America it has been recorded from natural areas as well as greenhouses in California and from greenhouses in many other states and provinces.

Genus *Deroceras* Rafinesque, 1820

Deroceras Rafinesque, 1820. Annals of Nature, 1: 1-16.

Description

The concentric ridges of the mantle have their nucleus near the breathing pore (Fig. 1i). The posterior end is truncated when viewed in profile (Fig. 1k). A penial appendix is present. A short rectal caecum may be present. The right tentacular retractor lies medial to both the penis and the oviduct. Lateral bands are usually absent.

The name *Agriolimax* Mörch has been used for this genus by some European workers. The genus includes a number of species which are quite similar in external morphology but distinct in internal anatomy. Positive identification usually requires dissection.

Distribution

The genus is native to North and South America, northern Asia and Europe. Several species are restricted to western North America.

Deroceras laeve (Müller, 1774)

Limax laevis Müller, 1774. Verm. Terr. et Fluv. Hist., 2:1.
Limax gracilis Rafinesque 1820, Annals of Nature, 1:52.
Limax campestris Binney, 1842, Proc. Boston Soc. N. H., 1:52.

Description

External. A small slug, its extended length is about 25 mm. The ground color varies from light brown through light gray to black. Black, irregular spots or reticulations may be present on the body.

Extensively reticulated individuals may resemble *D. reticulatum,* especially preserved specimens where slime color is not available and where the normal dark bordered breathing pore of *D. laeve* may appear pale. When the animal is extended the mantle appears almost centrally located because of its long neck. The slime is clear and watery Fig. 8 a, b.

Internal. Fig. 2c. The ovotestis is usually completely buried in the visceral mass. The slightly contorted and relatively large penis bears a large tubular appendix There is no rectal caecum. Some individuals may lack a penis; still others may lack both a penis and vas deferens.

Another European slug, *Deroceras caruanae* Pollonera, which has been introduced into California and eastern Canada, may be easily confused with *D. laeve.* This slug is somewhat larger than *D. laeve.* It lacks a rectal caecum. Apically, the penis bears a pair of diverging club-like processes at the junction of which arises a penial appendix consisting of several fine thread-like projections. In our region, large *D laeve*-like slugs found in greenhouses and gardens should be examined internally to insure correct identification.

Eggs. The eggs are deposited in very loose aggregations or in small. scattered clusters. The eggs are oval and transparent They may turn yellow several days after deposition. Quick (1960) gives the egg size as 1.8 X 1.5 to 2 X 1.3 mm.

Biology

Life cycle and reproductive behavior. Egg laying occurs throughout most of the year. Eggs are deposited on, or slightly under, the soil under logs, stones, and ground litter. They hatch in about 4 weeks at 15° C. The newly hatched slugs are 3 to 4 mm long. All stages probably overwinter in our region.

D. laeve does not engage in the preliminary 'following and circular dances' of *D. reticulatum* Also the copulatory position is maintained for a longer period (up to an hour; Gerhardt, 1939).

Habitat and feeding habits. *D. laeve* is undoubtedly the most ecologically ubiquitous slug in northeastern North America. It can be found in greenhouses gardens, fields, marshes and deciduous and coniferous woods. In cultivated areas population sizes approach those of some colonial, imported slugs. In wild areas population sizes are generally small. In Connecticut it is one of the few slugs found in oak forests.

Distribution

This species is native to North America and perhaps also Central and South America. It also occurs in Europe and northern Asia, from where it presumably spread to North America in late Pleistocene or postglacial times (Pilsbry, 1948). In North America it is distributed throughout Canada, the United States, and Mexico. In Connecticut it is widely distributed throughout the state.

Deroceras reticulatum (Müller, 1774)

Limax reticulatus Müller, 1774, Verm. Terr. et Fluv. Hist., 2:10.
Limax agrestis Schrenck, 1848, Land und Süssw. Moll. Livlands.
Agriolimax reticulatus Müller; Luther, 1915, Acta Soc. Fauna Flora Fenn., 40 (2): 1-42.

This slug was referred to by older authors as *Agriolimax agrestis* (L). Luther (1915) showed that *A. agrestis* as it was defined by earlier authors encompassed two species, *A. reticulatus* and the less widely distributed *A. agrestis. Deroceras agreste* has not been recorded from North America. However since it closely resembles *D. reticulatum* it may have been overlooked. It is smaller than *D reticulatum.* Internally, the ovotestis lies farther forward. The penial appendix is a short, slender unbranched tube. A short rectal caecum is present as in *D. reticulatum.*

Description

External. A larger and more robust slug than *D. laeve,* its extended length may exceed 45 to 50 mm The dorsal keel is short but distinct The breathing pore is surrounded by a white border. The ground color varies from almost solid black through mottled black or brown to light tan or grayish white. As its name implies the body usually appears distinctly reticulated because of the presence of black or brown pigment in the valleys between the tubercles Occasionally dark, irregular spots will more or less completely hide the reticular pattern. The sides are normally paler than the dorsum. The foot sole is gray. The mantle is located more anteriorly in fully extended *D reticulatum* than it is in active *D. laeve.* The slime is clear in undisturbed animals but milky white and very sticky in irritated animals (owing to the incorporation of calcareous particles in the slime). Fig. 7 a-d.

Internal. A short rectal caecum is present. The ovotestis lies near the apex of the visceral mass and is exposed dorsally (Fig. 1o). The penis bears a multifid penial appendix (Fig. 2b).

Eggs. The transparent ovoidal eggs are deposited in close aggregations of up to several dozen eggs. They normally remain colorless throughout development. Quick (1960) gives the egg dimensions as 3 X 2.5 mm.

Biology

Life cycle and reproductive behavior. In northeastern North America egg laying occurs chiefly in the late summer and fall; a few eggs may be found throughout the spring and summer, however. The adults die in the fall after egg laying. The overwintering populations consist primarily of newly hatched individuals from the fall hatching. Adult size and sexual maturity are not attained until late summer. In greenhouses and other protected habitats egg laying usually occurs throughout the year. Also, more southern localities with milder winters may have a spring egg laying peak in addition to the fall peak. In this case spring hatched individuals mature in the fall and fall hatched individuals mature in the spring.

The eggs are deposited on the soil under ground litter. The eggs hatch in three to four weeks at 15° C. The newly hatched slugs are 3 to 4 mm.

Mating involves a preliminary 'courtship dance in which the animals follow each other in a circle. This may be performed either on a vertical or horizontal surface. Each slug moves its sarcobelum over the body of its partner as it circles. After 30 minutes or more of 'following' and circling, the animals align themselves so as to bring the reproductive openings into opposition. The atria and penes are everted. Finally, the penial appendices are also everted and the viscous seminal masses are exchanged.

Habitat and feeding habits. *D. reticulatum* is found in greenhouses, gardens, fields, pastures, in the grassy margins of highways, dumps, and occasionally in deciduous woods (especially maple or ash). It is rarely found in coniferous woods. It has the potential for being a serious pest of field crops, truck gardens, and pasture lands because of the extremely high population densities which it can attain.

It apparently feeds on succulent vegetation to a greater extent than do most slugs. In the laboratory it can be maintained on lettuce.

Distribution

Native to all of the British Isles and most of Europe. It has been introduced into almost all parts of the world. In North America it probably occurs in every state and province. In Connecticut it is distributed throughout the state.

Subfamily Parmacellinae

The shell is either flat and completely enclosed in the mantle or spiral and partially exposed. The mantle is subdivided by a horseshoe-shaped groove. The keel extends forward to the posterior margin of the mantle. Both an epiphallus and penis are present. Copulation involves the mutual exchange of spermatophores.

Genus *Milax* Gray, 1855

Milax Gray, 1855, Cat. Pulmonata Brit. Mus. 1:174.

Description

The shell is a flat plate, completely enclosed in the mantle. A stimulator, if present, is associated with the atrium rather than the penis.

Distribution

A native of Europe and North Africa, it has been introduced into Australia, North and South America, New Zealand, and South Africa.

Milax gagates (Draparnaud, 1801)

Limax gagates Draparnaud, 1801, Tabl. Moll. France, p. 100.

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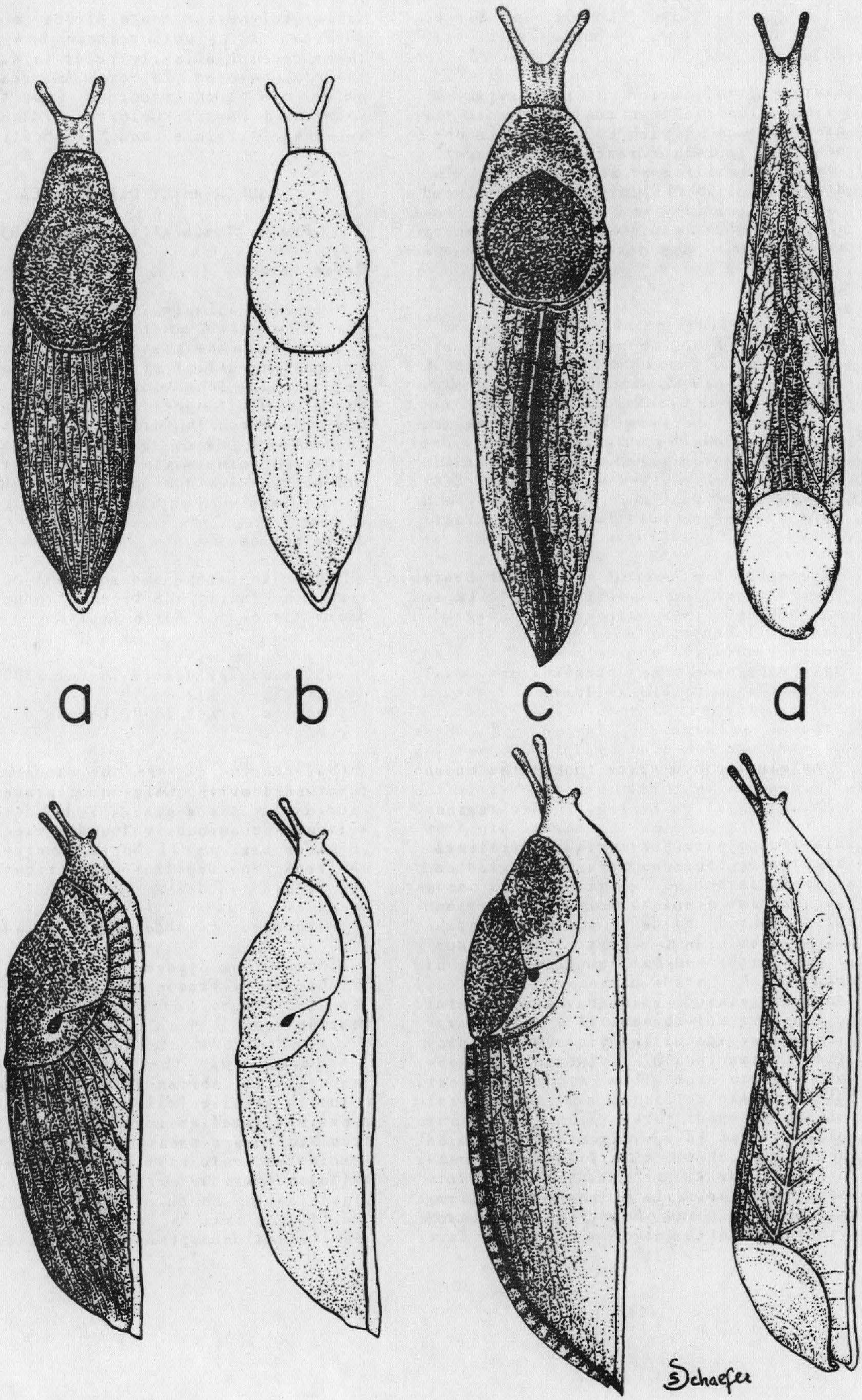
EXPLANATION OF FIGURE 8 (OPPOSITE PAGE)

FIG. 8. Lateral and dorsal views of a, b *Deroceras laeve* (X 2 2/3); c, *Milax gagates* (X 1 2/3); d, *Testacella haliotidea* (X 1).


a
b
c
d
Schaefer

Milax gagates Drap.; Lovell and Black, 1920, Oregon Agric. Coll. Exper. Sta. Bull. 170, p. 37.

Two separate species, *M. gagates* and *M.* cf *insularis* have been confused under the name *M. gagates* (Quick, 1960). It is possible that some references to *M. gagates* in North America may be erroneous. The atrial stimulator is abundantly papillated in *M.* cf. *insularis* and sparsely papillated or without papillae in *M. gagates* (Quick, 1960). The description below applies to *M. gagates*.

Description

External. A medium sized slug; the extended length is about 50 mm. The dorsal keel and horseshoe-shaped mantle groove are very distinct. The body surface appears smooth because the tubercles are flat. The animal is gray to black. The dorsal keel is usually darker than the back which in turn is usually darker than the sides. The foot sole is pale gray and distinctly tripartite. The slime is clear. Fig. 8c.

Internal. The atrial stimulator bears either a few small papillae distally or none at all. (See Quick, 1960, Fig. 8, page 152).

Eggs. The eggs are transparent, oval and 2 X 1.5 mm (Taylor, 1907).

Biology

M. gagates is so rare in northeastern North America that it is not possible to say much about its biology in our region. All records for the northeast are from greenhouses, parks, or private dwellings *M. gagates* in Europe is a slug of gardens, 'wild places,' and cliffs; it is more common along sea coasts than inland regions (Quick 1960). Because of its subterranean habits it can be a pest of root crops. It apparently breeds throughout much of the year.

During mating the animal uses its atrial stimulator to stroke the body of its partner. Apparently mating is a lengthy process (Karlin and Bacon, 1961).

Distribution

A native of Europe, it occurs throughout most of the British Isles and northwestern Europe. The closely related form *M.* cf. *insularis* occurs in the Mediterranean region. *M. gagates* has been introduced into Australia, New Zealand, Tasmania, Polynesia, South Africa and North America; it is not certain how many of these records actually refer to *M.* cf. *insularis*, however. In North America *M. gagates* has been recorded from the West Coast and Hawaii, Colorado, Idaho, Pennsylvania, Virginia, and Nova Scotia.

SUPERFAMILY OLEACINACEA

Family Testacellidae Gray, 1833

Description

Slug-like animals in which an abalone-shaped vestige of the shell is located externally on the posterior end. The shell covers the pallial organs. The body wall is scored by longitudinal, lateral grooves which give off upper and lower transverse branches which, in turn, ramify into finer grooves. A jaw is absent. They are subterranean forms which feed on earthworms and slugs *Testacella* is the only genus in the family.

Distribution

Native to Europe and adjacent North Africa; the family has been introduced into South Africa and North America.

Genus *Testacella* Cuvier, 1800

Testacella Cuvier, 1800, Leçons d'anatomie comparée, 1.

Characteristics are the same as those for the family. Only one representative species in the genus will be described. Although occasionally found in greenhouses in other regions of North America, none has been recorded from Connecticut.

Testacella haliotidea Draparnaud, 1801

Testacella haliotidea Draparnaud, 1801, Tabl. Moll. France p. 99.

Description

A large slug; the extended length may reach 120 mm; the shell is 7 X 5 mm. The color is grayish yellow. The presence of a penial flagellum separates this species from *T. maugei* which is the only other species known to have been introduced into North America. Fig. 8d.

Biology

T. haliotidea spends much of its existence burrowing underground, although individuals may be found crawling on the soil surface at night. It feeds mainly upon earthworms and slugs. The species is most frequently encountered in cultivated areas. The white, ellipsoidal eggs are deposited in the soil. The egg dimensions, given by Quick (1960), are 7 X 4 mm.

Distribution

Native to the British Isles, Europe, and adjacent North Africa; it has been introduced into North America and Cuba. In North America it has been recorded from greenhouses in Tennessee, Philadelphia, Illinois, and California.

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around the free margin. At the hinge margin two denser areas may be observed, which, when examined from the inner face of the valve, are found to be continuous with the border around the free margin (fig. 13, pl. VIII). The test with acid shows that this entire border is calciferous and that there is a thinner layer of carbonate of lime over the whole surface and beneath the cuticle. This layer is often cracked, as one might break the shell of a hen's egg, when preserved specimens are slightly crushed under a cover glass, and it is then seen to be distinct from the cuticle which may wrinkle but does not break. Upon the loss of the lime, the cuticle is no longer firm enough to preserve the shape of the shell and successful permanent mounts must therefore avoid acids at any stage of the preparation.

Along the ventral border of the shell is a flange, formed of cuticle only, and so transparent that it is easily overlooked in a ventral view of the open glochidium (fig. 15, pl. VIII). Viewed laterally (fig. 14, pl. VIII), this flange has at a certain focus the appearance of a hook and may easily be mistaken for one when seen under a low magnification. It is, however, a continuous flange, as shown in the figures, and not a hook; and since its edge is very fine it must, when the glochidium closes its valves, cut into and hold to a delicate tissue like that of the gill filament, thus performing much the same function as the hook in the other type of glochidium. The general spoon-like character of the valves is shown clearly by the figures. The adductor muscle is well seen in the living specimen, being a conspicuous object from whatever angle it is examined. Viewed laterally (fig. 13, pl. VIII), or from the ventral aspect (fig. 15, pl. VIII), the adductor is seen to lie nearer the shell margin at one end of the hinge than at the other, a fact which enables one to recognize at a glance the future anterior border of the shell. There is also in this glochidium of *Lampsilis subrostrata* a slight difference in outline by which these anterior and posterior borders of the shell may be distinguished (fig. 13, pl. VIII), while in the hooked type of glochidium (fig. 10, pl. VIII, and text fig. 1, A, B, and C) this difference is even more pronounced and one recognizes the anterior border of the future adult by its slightly greater length.

The two outer pairs of sensory cells with their fine projections (fig. 14 and 15, pl. VIII) are readily seen in the living glochidium; the two inner pairs, in which the cells project but a short distance from the surface, are more easily found in specimens which have been properly preserved and stained. The position of the two outer pairs may also be seen in the closed glochidium (fig. 13, pl. VIII). Little can be seen of the rudiments of the various organs of the adult without the careful staining of well fixed material. In the living glochidium they appear as a slightly denser area on either side of the median line and posteriorly to the adductor muscle (fig. 13, pl. VIII). The cells of the larval mantle (fig. 15, pl. VIII), which occupy the greater part of the surface exposed within the valves, appear in the living glochidium as a dense mass in which cell outlines can not be recognized.

Further details in the structure of this glochidium can only be studied in specimens which have been properly fixed and stained. After trying various reagents, we have found that they may be stupefied in a few moments by the addition of several small crystals of hydrochlorate of cocaine to the water in a watch glass, after which they may be fixed with no serious shrinkage by using the solution of plain corrosive sublimate obtained by diluting a saturated solution two or three times with water. Acids should be avoided throughout the whole process. Alum cochineal, Delafield's hæmatoxylin, and borax carmine, alone or with Lyon's blue, have been used as stains, each being more suitable for the demonstration of certain structures. In this stained material the shell shows a slight wrinkling of its ventral flange and is the only part not shown to better advantage than in the living specimens.

The lateral pairs of sensory cells (fig. 14 and 15, pl. VIII) are tall chimney-like structures expanded at the base and terminated by several very fine motionless processes. A denser border where these processes are inserted in the cell is presumably due to their continuation within the cytoplasm which has been observed in sections of these and other glochidia. The two median pairs of sensory cells (fig. 14, pl. VIII) project only a short distance and have short processes. The anterior pair is located ventral to the median portion of the larval adductor muscle, the posterior pair near the outer ends of the rudiments of the adult organs (fig. 15, pl. VIII). The designation of these cells as "sensory" by all writers rests upon their structural features as described by the earlier investigators, and upon the fact, recorded by Lillie (1895), of their staining reaction with methylene blue. The actual connection of the cells with the larval muscle fibers has been sought for by investigators, but never discovered. We have not attempted a further demonstration of the function of these cells by the methods practiced in recent experimentation upon the protozoa and other minute organisms, although such a study might yield some interesting results.

Lining the greater part of the surface between the valves, are the large cells composing the larval mantle (fig. 15, pl. VIII). They are filled with fine granules, which, since these cells actually digest the tissue of the host during the early stages of the parasitism, are probably the zymogen granules from which the digestive enzymes originate. The absence of these cells over the area of flexure ventral to the adductor muscle will be noted in figure 15. In this area the ectoderm is thinner and there is no granulation. The adductor muscle is composed of fibers having elongated nuclei and often seen to branch toward the ends where they are attached to the valves. In a glochidium of *Lampsilis subrostrata*, which has been carried over the winter in the parent gills and which has therefore reached the highest stage of differentiation possible for this glochidium, we can identify the rudiments of foot, stomodæum and enteron, and of the heart, pericardium, and kidney, as described by Harms (1909) in his accounts of the structure and organogeny in the hookless type of glochidium. Reference to figure 15, plate VIII, will make clear the following account of these rudiments.

In the median region, just posterior to the adductor, is a triangular area, the oral plate; behind this a narrow band of closely set nuclei extending well out into the valves, where it becomes wider. The ectoderm in the median part of this area becomes the covering of the foot, while the deeper part of the area is endoderm, the rudiment of the enteron. The lateral expansions of this general mass are mesodermal cells which are closely applied to the endoderm and in which are found the rudiments of the kidney, heart, and pericardium. A backward curve in the posterior outline at either side of this mass appears to represent imperfectly developed lateral pits, from the outer borders of which Schierholz (1888), Schmidt (1885), and Harms (1909) agree that the first rudiments of the gills originate, and which are very conspicuous structures in the glochidia of the hooked type. We have never observed any structure resembling the larval thread or its rudiment in the fully formed glochidia of species of the genera *Lampsilis* and *Quadrula*, the glochidia of which we have studied most extensively; and the larval thread is not present in functional condition in any of the species we have studied from the genera listed on page 145, with the exception of *Anodonta* and *Unio*. A discussion of this organ, which has heretofore been assumed to occur in all glochidia, is given after the account of the hooked glochidium which follows.

THE HOOKED TYPE.

Our first infections were performed with the hooked glochidium of *Anodonta cataracta*, which is essentially like the *Anodonta* type of glochidium described for European species, and which has been described in a detailed manner by Lillie (1895). Our later work has been with the young of *Symphynota complanata* and *S. costata*, the glochidia of which resemble one another in structure, as shown by their outlines in text figure 1, A and B, and figures 9 and 10, plate VIII; so that here, as elsewhere noted in the case of hookless glochidia, the outline appears to be a characteristic of the genus, which enables one at once to distinguish the glochidia of *Anodonta* from those of *Symphynota*. There is, however, a marked size difference between the glochidia of these two species of *Symphynota* (text fig. 1, A and B).

In both *Anodonta* and *Symphynota* glochidia, the slightly greater length of one border of the valve between hook and hinge is indicative of the future anterior region. In most hookless glochidia there is a similar slight difference in the anterior and posterior marginal outlines (fig. 13, pl. VIII), but it is more difficult to detect, and in any case the safest guide is the larval adductor muscle, which is always recognizably nearer the anterior end, a position to be correlated with the location of the rudiments of the adult organs in the posterior region. In the living glochidium of *S. complanata* the shell shows calcification beneath the cuticle and is marked as though the calcareous layer were porous.

The external appearance of these hooked glochidia is like that shown for *S. costata* in figure 10, plate VIII. The hooks, with their spines, the fibers of the larval adductor, and the sensory cells are seen when turned in profile view (fig. 9, pl. VIII); but the cellular structure is so obscure in living specimens that the rudiments appear only as a denser area and even the fibers of the adductor muscle are not very distinct. There is no sign of a larval thread or a thread gland, nor do sections of preserved glochidia reveal such a structure. A conspicuous feature of the whole mass of glochidia in *Symphynota*, as taken from the gill of the parent, is the thick, ropy mucus in which they are embedded. This holds them so firmly together that when stirred up in a dish they remain suspended and quite evenly distributed through the water, settling to the bottom only very slowly over a period of four or five minutes. During this suspension in the water the sucking of a pipette will draw in glochidia over a wide area, as they are pulled by the invisible strands into which the mucus has been divided. The significance of this mucus and the absence of the thread gland are discussed under another heading of this paper. The mucus is dissolved by the water in a short time, so that after 24 hours the glochidia are found entirely free and snapping actively upon the bottom. We find that these glochidia can be freed from the mucus by repeated washing, and that it is desirable to do this at once if one wishes to keep them alive for the maximum period. When thus set aside it is possible for them to remain alive for as long a time as two or three weeks.

In killing this glochidium we have used successfully crystals of chloral hydrate or hydrochlorate of cocaine added to the water of a watch glass containing the glochidia, and fixation with Merkel's fluid, or with weak corrosive sublimate, as described for the hookless type.

Stained specimens show the same rudiments of stomodæum, enteron, and mesodermal structures, as described by Lillie (1895) and Harms (1909) for the glochidium of *Anodonta*. The lateral pits are conspicuous and the cells of the larval mantle are well developed laterally, though thinning out over the median part of the larval adductor, where their boundaries are not clear and only a few nuclei are discernible. Sections show two kinds of granules within the larval mantle cells, one staining deeply with iron hæmatoxylin and the other with acid-fuchsin. Near each corner of each valve is a cell which stains deeper than the rest and seems to contain more of the granules. The significance of these six cells we can not determine. The sensory cells (fig. 9, pl. VIII) are slightly different in position from those in *Anodonta*. Lying along a line drawn across from hook to hook are three large cells in line beneath the hooks and a smaller one on either side between the larval adductor and the lateral pit.

THE PROPTERA OR AXE-HEAD TYPE.

This glochidium possesses hooks which are not homologous with those of the *Anodonta* type and is to be regarded as more nearly related to the hookless forms, an interpretation which is borne out by the fact that the "axe-head" can be readily imagined as a modification of the glochidial outline seen in some species of *Lampsilis*, the glochidia of which, like those of *subrostrata* (fig. 13, pl. VIII), show some approach to a rectangular form. Its four hooks are so arranged that those of one valve pass inside the opposite ones, thus bringing the ventral margins close together and giving a very firm hold upon the host's tissue. In other respects it does not show marked differences from the hookless type, and the few experiments we have made with it indicate its attachment to the gills rather than to the fins.

Recently Coker and Surber (1911) have observed "an almost exactly similar glochidium" in *Lampsilis capax*, while in *Lampsilis* (*Proptera*) *lævissima* they find an axe-head glochidium which is of a somewhat different outline and lacks the hooks. They point out the fact that in *Lampsilis gracilis*, a species which in its adult features (form of shell) seems almost to intergrade with *lævissima*, the glochidium is of the ordinary hookless type, although the outlines of the two glochidia are very similar when seen on edge, as in their figures 1a and 2a of plate 1. With respect to the significance of these facts when applied "to a relationship between *lævissima* and *capax*," they conclude that "there would be strong corroborative evidence in adult characters alone" for the closer union of these three species, and this "in spite of the fact that *lævissima* and *capax* are the two extremes in the degree of inflation." The similar degree of inflation of *capax* and *ventricosa* offers, they believe, "only a striking instance of convergence in one character."

THE LARVAL THREAD.

Our observations upon the occurrence of the larval thread (formerly erroneously termed the byssus) are of importance, since the current accounts in textbooks and literature lead one to believe that this structure is a conspicuous feature of all glochidia. Such an assumption is natural because the organ is conspicuous in the European anodontas and unios and in the American species of these genera examined by Lillie (1895).

We find the larval thread present in the species of *Unio* and *Anodonta* which we have been able to examine with care, and the thread is undoubtedly a characteristic of these genera. We have never seen any sign of such a structure in the ripe glochidia of the other genera, above listed, which possess hookless glochidia, nor in the hooked forms of the genus *Symphynota*. Lillie (1895, p. 52) considers the thread a condensed excretory product, which, accepting the account of Schierholz (1888), he thinks has also become an organ which is of use in bringing the glochidium in contact with the fish. This latter function is the one commonly ascribed to the thread. We have not studied the pre-glochidial stages in the development of those species which show no thread-gland in the mature glochidium, although it is important that this should be done with a view to determining whether a homologue of the thread gland is present at any time. We have, however, made repeated examinations of glochidia, either ripe or well along in their development, in several species of *Lampsilis*, particularly in *ligamentina*, *recta*, *anodontoides*, *ventricosa*, *luteola*, and *subrostrata*, and to a lesser extent in species of the other genera mentioned, without finding any trace of the thread which is so conspicuous a feature of the glochidium of *Unio complanatus*.

We have also examined the glochidia of *Symphynota complanata* many times with the same negative results, and a smaller number of observations confirm this for *S. costata*. Since many species thus have no thread in any way functional for attachment to the fish, the question arises whether the thread when present has as important a function in this respect as has been supposed. Our observations upon the glochidia of *Anodonta cataracta* confirm the descriptions of Schierholz (1888) and others who have studied the European species of *Anodonta* as to the tangling of the glochidia into masses by means of their extruded threads, and in this genus the threads do seem effective in drawing other glochidia into contact with the fish when a single one has become attached. This is not, however, effective during the greater part of the period in which the glochidium may remain alive upon the bottom, for the threads are dissolved within a day or two and the glochidia then become entirely free from one another. When taken from the parent gill the glochidia of *Symphynota* are entangled in a ropy mucus, and this acts in a manner similar to the threads of *Anodonta*, but it is usually dissolved after a few hours in the water. In the ripe glochidium of *U. complanatus* the threads are extruded immediately after the glochidia are removed from the parent and placed in water, and, according to Harms (1907b, p. 819), the minute glochidia of *Margaritana margaritifera* extrude their threads while still within the egg capsule.

When this extrusion has taken place in *Unio complanatus* the glochidia and broken egg membranes become united into globular masses from which it is difficult to separate individual specimens, and from observing such glochidia in contact with the fish we are forced to conclude that they are not so likely to become attached to the gills or fins as they are later, when they have been separated by the disintegration of the threads. The glochidia of *Lampsilis*, which when fully ripe fall apart into masses of entirely unconnected individuals, appear much better able to attach to the gills of fishes immediately after their discharge from the parent. We believe therefore, that the thread is something to be gotten rid of rather than an organ of great importance in the attachment to fish, and this is in agreement with Lillie's interpretation of this organ as an excretory product. It is possible that some homologue of the thread exists in these threadless glochidia, and a comparative study of the pre-glochidial stages might yield material for interesting comparisons.

BEHAVIOR AND REACTIONS OF GLOCHIDIA.

At the time of spawning the glochidia, already freed from the egg membranes, and usually held together in slimy strings, are discharged at irregular intervals. Being heavier than water, they sink rapidly to the bottom, coming to rest with the outer surface of the shell directed downward and the valves gaping widely apart. The belief was formerly general that they "swim" about by rapidly opening and closing the valves, after the manner of *Pecten*, and, in spite of frequent denials by Schierholz (1888), Latter (1891), and others, the same statement is still occasionally encountered. In the recent volume on Mollusca in the Treatise on Zoology, edited by Lankester, this inexcusable error is repeated. "The glochidia," we are again informed, "swim actively by clapping together the valves of the shell" (p. 250). They are, on the contrary, as is now well known, entirely incapable of locomotion and remain in the spot where they happen to fall, although it is true that they may exhibit from time to time spasmodic contractions of the adductor muscle, which cause the valves to snap or wink, each contraction being immediately followed by relaxation and opening of the shell. These movements of the valves, however, are never so vigorous as to cause the glochidium to move from place to place in the water.

The glochidia remain in this helpless situation until they die, unless they happen to come in contact with the host on which they pass through the post-embryonic development as parasites. The stimulus which causes the contraction of the muscle and results in attachment to the host is, in the case of hookless glochidia, usually a chemical one, but in that of the hooked forms it is mechanical. The latter may be readily imitated and glochidia of this type made to grasp firmly the point of a needle or the edge of a piece of paper by simply touching them between the open valves. When once closed in this manner they do not relax, but remain attached to the object until they die.

The following statement made by Latter (op. cit., p. 56) has been frequently quoted, especially in textbooks, but it has apparently never been verified or disproved.

> The Glochidia are evidently peculiarly sensitive to the odor (?) [sic] of fish. The tail of a recently killed Stickleback thrust into a watch glass containing Glochidia throws them all into the wildest agitation for a few seconds; the valves are violently closed and again opened with astonishing rapidity for 15–25 seconds, and the animals appear exhausted and lie placid with widely gaping shells, unless they chance to have closed upon any object in the water (*e. g.*, another Glochidium), in which case the valves remain firmly closed.

Although it is not stated that the tail which caused such a commotion among the glochidia had been cut off from the fish, it is probable that such was the case. We have repeatedly tested glochidia in the same manner both with fins and gills of different fishes, and, providing that a bleeding surface is not brought in contact with the water containing the glochidia, absolutely no response on the part of the latter takes place. The result, however, is much as Latter describes if a little of the fish's blood gets into the water in the neighborhood of the glochidia, except that our experience has shown that after snapping for a few seconds they come to rest in permanent closure. It therefore seems possible that the contractions seen by Latter were due to the introduction of some blood with the tail of the fish, as otherwise agitation of the glochidia under similar conditions has not been observed by us.

Since the hooked and hookless glochidia, whose reactions to blood and to certain salts we have studied, show important differences in their behavior, they are referred to separately below.

REACTIONS OF HOOKLESS GLOCHIDIA.

It was first observed that glochidia of the hookless type, in marked contrast with the hooked forms, only occasionally exhibit spontaneous contractions and respond either not at all or only sluggishly to tactile stimuli, and the question at once arose as to what causes their closure when they become attached to fish. If the stimulus which brings about a contraction of the adductor muscle in attachment is not a mechanical one, it presumably is chemical in nature, but we were completely in the dark in the matter until it was cleared up by the following experiments, the first of which were made with the glochidia of *Unio complanatus* at Woods Hole, Mass.

When a small drop of blood of either the killifish, *Fundulus diaphanus*, or the white perch, *Morone americana*, was placed over the glochidia contained in a small amount of water in a watch glass, the effect was immediate and very striking. Every glochidium was thrown into rapid and violent contractions, alternating with relaxations, the edges of the valves either quite or nearly touching with each snap. Where the stimulus was strongest—that is, immediately under the drop of blood—the glochidia exhibited two or three strong contractions and then remained closed, but, proceeding outward to zones of diminishing intensity, the snapping occurred intermittently for from 10 to 50 seconds. Here the contractions were quite rapid at first, one or two every second, but soon the intervals became longer, until finally the activity was ended by the closure of the valves. In some cases it was observed that after the first few snaps the muscle did not completely relax, and each subsequent contraction caused the valves to describe a shorter arc. This experiment was repeated time and time again, with invariably the same result, and it was astonishing to see what a small quantity of the fish's blood was required to produce the reaction. It should be emphasized, furthermore, that after the stimulus had caused the final contraction of the muscle the valves remained permanently closed.

The experiment was later performed a great many times with the glochidia of *Lampsilis ligamentina* and *subrostrata*, and identically the same reaction was obtained with the blood of several different fishes and that of the frog, *Necturus*, and man.

Since the hookless glochidia, which are essentially gill parasites and, when taken into the mouth of the fish lodge among the gill filaments, produce abrasions of the delicate epithelium covering the latter, a more or less extensive hemorrhage from the blood capillaries occurs, as may be readily seen from a microscopic examination. It is therefore evident that blood exuding from the gill filaments in the immediate neighborhood of the glochidia must have the same effect as in our experiments, and, by exciting vigorous contractions of the adductor muscle, furnish an efficient stimulus in bringing about a firm and permanent attachment to the filaments. It is true that hookless glochidia will occasionally secure an attachment to the edge of the fins and other external parts of the fish, but it is quite evident that they are not adapted to such locations, as they rarely succeed in remaining there. It is possible that when they do become attached to the fins the closure of the valves is due to the presence of blood on the latter; but, since hookless glochidia occasionally close when touched repeatedly, the attachment in these situations is probably brought about by a sluggish response to contact with the edges of the fins. Their characteristic place of attachment, however, is the gill filaments, and this definite reaction to the fish's blood constitutes a most striking functional adaptation to the special habit of hookless glochidia as gill parasites.

Although the matter has not been exhaustively studied, it is in all probability the salts of the blood that are responsible for these reactions. A series of experiments, however, has been undertaken for the purpose of determining the reactions of glochidia of this type to solutions of several different salts, and, although the investigation has not yet been completed, a brief statement may be made here. Diluted sea water and solutions varying in strength from 0.5 to 1 per cent of $NaCl$, KCl, KNO_3, and NH_4Cl have exactly the same effect as fish's blood, although the intensity of the reaction varies somewhat in certain cases. Weak solutions of $MgCl_2$ and $MgSO_4$, however, as would be expected, inhibit contractions, and glochidia, after treatment with these salts, may be killed in an expanded condition, if allowed to remain in the solutions for a sufficient length of time.