THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE PHYLOGENY OF AMERICAN LAND SNAILS WITH EMPHASIS ON THE POLYGYRIDAE, ARIONIDAE, AND AMMONITELLIDAE

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

GLENN ROBERT WEBB

1960

THE PHYLOGENY OF AMERICAN LAND SNAILS WITH EMPHASIS ON THE POLYGYRIDAE, ARIONIDAE, AND AMMONITELLIDAE

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGMENTS

Many persons aided this study by sending specimens. Thus I am indebted to Dr. Wendell O. Gregg of Los Angeles, California for *Glyptostoma gabrielense* Pilsbry; Curator Emory P. Chace of San Diego, California for paratypes of *Ammonitella yatesi allyni* Chace and *Micrarionta tryoni* (Newcomb); Dr. Harold W. Harry of Ida, Louisiana for *Humboldtiana* and *Ariolimax columbianus* (Gould) and others; Commander W. D. Miller of Port Hueneme, California for *Allogona* species, *Cryptomastix*, *Polygyrella polygyrella* and others; Dr. Henry van der Schalie of Ann Arbor, Michigan for Puerto Rican specimens; Curator Allyn G. Smith of Berkeley, California for *Monadenia* and *Vespericola armigera* (Ancey); and Mr. Robert Talmadge of Willow Creek, California for *Trilobopsis loricata sonomaensis*. I am also indebted to the late Dr. A. O. Weese, Dr. J. Teague Self, and Dr. Carl D. Riggs for aiding the continuance of this study at the University of Oklahoma, to Dr. Harley P. Brown for acting as director of the dissertation, and to the University of Oklahoma Chapter of Sigma Xi for financial aid.

TABLE OF CONTENTS

THE PHYLOGENY OF AMERICAN LAND SNAILS WITH EMPHASIS ON THE POLYGYRIDAE, ARIONIDAE, AND AMMONITELLIDAE

CHAPTER I. INTRODUCTION

The family Polygyridae is composed of the large, active North American land-snails in which shell growth is terminated at sexual maturity by the addition of a thickened reflected-lip or peristome, which have no dart, and which in most species bear denticles within the aperture and on the peristome in a characteristic pattern. This paper annexes thereto the slug genus Prophysaon. East of the great prairies the Polygyridae constitute the dominant snails of the forests, where ubiquity, as well as the interestingly varied forms of genera and species, raises the tantalizing problem of their evolutionary history.

Because of their size and diversity, the polygyrid snails early became my favorites, being readily subject to anatomical and other types of studies without elaborate optical equipment, all of which has combined to make phylogenetic studies of this group both expedient and pleasurable.

The present study began when I chanced to observe the mating habits of several species after I had just completed

conventional study on the genitalia of non-mating individuals. Being quite unable to understand the mating process as simply observed, I decided to try to kill the snails at the instant of mating by plunging them into boiling water so that the exserted organs would be fixed in the functional position. The procedure was successful. The mating-anatomies so obtained revealed how the various parts of the genitalia functioned, indicated the relative import of diverse parts, and exhibited new structures and details. The organs which are usually concealed within the lumen of the non-functioning sex-organs and anatomical parts often are revealed conspicuously, both anatomically and functionally, by this method.

The data proved to be exceptionally useful in the recognition of homology and in revealing trends in the evolution of the genitalia. Gradually a pattern of phylogeny became apparent and the research broadened into an overall study of relationships rather than a series of detailed anatomic studies of individual genera.

The study progressed to the point that in 1948 the phylogeny of the Triodopsinae, one of the two original subfamilies of the Polygyridae, was made the basis of a Master's Thesis at the University of Illinois. These data were extended slightly and published in 1954 (Webb, 1954b). This study is intended primarily to explore the snail families which, from either geographic distribution or from

traditional taxonomic status, might be or have been considered as ancestral or related to the Polygyridae. It was also necessary to make an extended survey of the arionid slugs, since one of these, Prophysaon, seemed to be a polygyrid. This was an important point to confirm, for if a family of snails is so old that it has had time in a given region to develop a slug-type, the datum is quite important phylogenetically.

The present study thus embraced the following main points:

1. A study of the Sagdidae and Thysanophorinae.

2. A study of all the obtainable American Arionidae.

3. A study of the Oreohelicinae and Ammonitellinae of Pilsbry, 1939.[1]

4. Supplementary studies on genitalial development of Haplotrematidae and Philomycidae.

The results are significant but not strictly comparable because materials available in the various groups have not been equivalent. I do not consider this survey to be exhaustive; indeed, it cannot be expected to be, yet the results do seem to delimit more accurately than has been possible heretofore all the taxa considered. It is not a

---

[1] C. B. Wurtz (1955) presents an evaluation of the family Camaenidae and formally rejects the Oreohelicinae and Ammonitellinae as being allied to the Camaenidae.

final word, but rather suggests interesting new lines of research on the phylogeny of these snails.

CHAPTER II. HISTORICAL REVIEW

The Sagdidae, Polygyridae, and Ammonitellidae (Camaenidae of Pilsbry) were initially all grouped in the family Helicidae and the Arionidae were lumped with the Limacidae (Woodward, 1856). The concept of the Polygyridae as a subfamily unit of helicoid snails was initiated by Pilsbry (1895) when he equated his informal group, Protogona, with the term Polygyrinae. In this important paper he also outlined a new classification of helicoid snails as follows:

1. Protogona: supposedly the most primitive group, composed of Praticolella, Polygyra, Polygyrella, Polygyratia, all American; Coxia, Papuan; and Dorcasia, South African.

2. Macroogona: a mixed group, important here in that some may be allied to our Ammonitellinae.

3. Teleophallogona: the Sagdidae and Thysanophorinae.

4. Epiphallogona: a seemingly mixed group including Camaena and some helicoids.

5. Belogona Eudenia: Helminthoglyptidae, Cepolidae, Xanthonycidae, and some Eurasian helicoids (and Glyptostoma).

6. Belogona Siphonadenia (supposedly the most highly evolved Helicidae): Helicidae and Jacostidae.

Pilsbry (1898) was able to study the anatomy of Glyptostoma and found it belonged in his Belogona Eudenia (5). Later Pilsbry (1939) shifted it and the other Ammonitellinae into his Epiphallogona under the family Camaenidae. To this I shall give more consideration later.

When Pilsbry (1930) studied the anatomy of Ammonitella yatesi and found it and Polygyroidea akin to Glyptostoma and not the Polygyridae, he erected for them the subfamily Ammonitellinae. Earlier, H. B. Baker (1930) had described a new genus of a supposed zonitid snail as Megomphix and had made it the type of a new subfamily, the Megomphicinae. The group at best seems only subgenerically distinct from Glyptostoma and is thus a subjective prior homonym which cannot be used as a prior family unit.

Pilsbry (1932) studied the anatomy of Polygyrella and found that it also would have to be removed from the Polygyridae and put in the Ammonitellinae.

Pilsbry (1895) in discussing the evolution of the Polygyridae stated (Manual of Conchology IX, p. 70):

> The white-lipped Helices of North America form a very distinct and homogeneous genus, well distinguished by characters of shell and still more by those of the soft parts. The group, in practically its present limits, was first defined in 1889, by the writer [Pilsbry]; subsequently the European forms supposed by former authors to be allied to Triodopsis were shown to differ generically. . . .

> No snails referable to Polygyra have been found in any part of the Old World, or in South America, either living or fossil. It is therefore highly probable that the genus arose and developed its peculiarities upon eastern North American soil. The West Indian species are to be regarded as stragglers from the continental fauna, just as Hemitrochus, Cepolis, Liguus and Thysanophora in Florida are emigrants from the Antillean fauna. . . .
>
> The question of relationships of Polygyra are beset with difficulties. I had formerly grouped the genus with Pyramidula, etc. but the characters of the foot peremptorily forbid such association. Dr. von Ihering suggests the possibility that it may be either a modified branch of Arionta [Helicidae] in which the genitalia have become simple by degeneration, or a further development of Patula [Endodontidae]. The latter hypothesis is untenable. The former has as yet no facts to support it.
>
> No fossils now known throw light upon the problem. From what we know of the living forms of Polygyra, it is likely that their common ancestor possessed a shell with tridentate aperture, reflected lip, and a color-band above the periphery. It is not unlikely that the group represents an early stage of the true Helix phylum, which did not share the evolution of the accessory organs of the genitalia [darts and associated glands] now characteristic of the Pentataenia, Campylaea, Cochlostyla, etc.

Pilsbry's latest concept of the phylogeny of the Polygyridae finds gradual expression in the two volumes of his Land Mollusca of North America, particularly volume 1, parts 1 and 2. The latter part is a monograph on the family, exclusive of Mexican and Antillean species. Thus, in 1940, he placed the family after the Camaenidae (which contained the Ammonitellinae and Oreohelicinae) and included the Sagdidae with the superfamily Polygyracea. At that time he stated:

> The main evolution of Polygyridae appears to have been in the temperate zone, only two genera, Polygyra and Giffordius, being represented in the tropics. . . .

> As fossils, Polygyridae appeared in the Upper Cretaceous of Alberta. Several species are known from the Miocene in Oregon and Florida.
>
> Although the family is allied to the group I defined as Epiphallogona, it is rather divergent from that stock, and apparently is not directly related to the Ammonitellinae or Oreohelicinae, or to any tropical American Camaenidae. It will probably turn out to be a very old group in America.

In discussing the Triodopsinae, Pilsbry added:

> It is now believed that the genera having an epiphallus and flagellum retain earlier structures of the family, which have been lost in most of the Polygyrinae and of a few Triodopsinae; these being the more highly evolved stocks, though secondarily simplified in penial structure. When I segregated the Polygyras as a group "Protogona". . . the anatomy was known in only the simplified forms, then thought to be primitive; an opinion now relinquished.

At that time (August, 1940) Pilsbry suggested an affinity between the Polygyridae and Sagdidae:

> The Sagdidae have no known relatives in the Eastern Hemisphere, and apparently arose from a primitive helicid stock which may also have given birth to the exclusively American family Polygyridae.

H. B. Baker (October, 1940) augmented this concept by tentatively removing the Thysanophorinae from the Sagdidae and putting them in the Polygyridae with a question mark. In this paper Baker seemed particularly impressed by the resemblance of the unusual Puerto Rican endemic, Mcleania, to the Polygyridae.

Webb (1954) considered the Polygyridae to have evolved in some northern continental area and thence to have spread southward into California and Eastern North America. He erected the subfamily Ashmunellinae for the most conservative types and stated:

. . . . The presence of the most conservative genus of Ashmunellin in the southern Rockies with an apparent evolution center in the Northwest prohibits belief that the Ashmunellinae and Triodopsinae arose in eastern North America. . . . Of the Ashmunellinae, Cryptomastix probably arose from northern stocks of Ashmunella, while Allogona is a more pronounced deviant with Allogona s. str. being evolved from the Dysmedoma type by a loss of one "stimulator" lobe and the reduction in size of the mid-penis, perhaps subsequent to the invasion of eastern North America by ancestral verge-bearing triodopsins. These . . . seem to be now invading southward along the Gulf Coast.

The Polygyrinae have undoubtedly evolved from some large basal-penised Ashmunellinae, but the details of their phylogeny remain to be worked out.

CHAPTER III.

MATERIALS AND METHODS

Most of the specimens used in this study were secured during two special field trips made for the purpose. One trip extended through the Northwestern United States, the other through Texas. The source of all figured material is given in the explanations as an aid to re-identification as the nomenclature changes, especially that of Creohelix. The two new slugs discovered during this fieldwork have been described elsewhere (Webb, 1959).

Living specimens were kept under observation whenever possible, mating habits were noted, and mating-anatomies were obtained as has been described above and in earlier papers (Webb, 1947). In addition, size-series of snails were dissected to determine the pattern of development of the genitalia from youth to sexual maturity.

In 1952 concrete cages were constructed to take the place of the temporary cardboard carton cages of previous years. These measured 13 x 9 x 4½ inches in outer dimensions. The concrete was about one-half inch thick. The rectangle was poured first and when set (but not dry) the

forms were removed and the bottom poured so that it fused with the sides. The cages would be improved by being about one and one-half inches deeper. The cage-weight of about twenty pounds is objectionable.

The figures are projection-tracings with details added free-hand from a microscopic examination of the slides. The specimens were outline-stained with aceto-carmine and then dehydrated in alcohol, cleared, and mounted in resin. The dissected organs were dehydrated in petri dishes. It is sometimes advantageous to place the genitalia between two slides spaced by chips of suitably wide glass. The entire procedure has been described in detail in an earlier paper (Webb, 1954a). Such permanently preserved dissections are to be recommended, despite the tedious processing required; they yield figures more detailed than those taken from semiopaque or opaque dissections because one can see into the organs involved. It is a particularly desirable method for treating specimens of new species or rare dissected material.

Because formalin- or alcohol-hardened material is brittle, the following technique may be of use to other anatomists. Place the hardened specimen in water, add some trisodium phosphate crystals and keep testing the specimen for softening. Often when starting to dissect, one will find the inner organs of the specimen still hard. When

this occurs, by judiciously adding crystals of trisodium phosphate among the tissues exposed, one can proceed with the dissection within an hour or less, and finally secure a specimen nearly as well expanded as one from fresh material. Very hard material sometimes can be treated with stronger hydroxide-forming substances. I have used sodium hydroxide successfully for this. Vigilance is required not to over-soften the specimen. The color pattern of the skin is often abnormalized in material so softened, but the genitalia can be dissected beautifully. Vinegar will help overcome excess or latent softening which may occur. No longer are dust-dry alcoholic specimens, sometimes the fate of type material in museums, totally worthless. They can be restored to dissectability or to a fairly normal-appearing rehydrated condition.[1]

Many of the seemingly abundant snails, such as Oreohelix, actually are very slow-growing and long-lived. Some specimens taken in October 1954 were still alive at the end of 1958. When weather conditions are suitable such snails often can be taken in numbers. In a few moments one can harvest mature specimens which have developed slowly over three or four years, and may be the main reproductives in the colony. Such material in the past was hastily removed

---

[1] Wurtz, 1955, cites using a 1% solution of sodium hydroxide.

from the shell and the extracted animals discarded or summarily preserved in fluid. Most of this material has long since dried up or otherwise become valueless from age. Because modern roads and vehicles give easy access to many type localities, such places (if quite local) can easily be deprived of the very resource which makes them noteworthy. By judicious, parsimonious collecting, aided by dissections made in the field, much better data can be obtained than can be accumulated by working over a discolored, malodorous mass of pickled material. A dozen or fewer specimens alive may yield much more information for modern malacology than a hundred haphazardly-preserved specimens. Habits can be observed and sometimes more specimens can be obtained by the reproduction of the specimens. For example, the more than a dozen Glyptostoma gabrielense used in this study were derived from the original pair of adults sent by Dr. Gregg.

In the present work a binocular dissecting lens set (worn like spectacles) was taken into the field, so that when some of the mountain species (Hemphillia, Gliabates, Zacoleus, Udosarx, and others) started to expire in the lowlands, it was possible to dissect them without risking all to preservatives. For dehydration, a series of wide-mouth jars of alcohols was used. An additional advantage in dissecting in the field is that the puzzling forms can be dissected on the spot, and if they prove worthwhile more can be sought.

In the past, the emphasis in gastropod taxonomy was on shell-characteristics; more recently much stress has been placed on preserved series. My research experience, however. leads me to believe that the study of the living mollusk may prove a key to major advances in malacology. Investigators will also find that merely keeping some species alive in captivity is an intricate research challenge and that dying material is more dissectable than some preserved material. The shells of captive snails are not reliable, however, since the conditions of captivity favor atypical growth and the shell may "age" faster (from erosion) than its occupant.

CHAPTER IV.

AULACOPODY VERSUS HOLOPODY

Pilsbry (1894) outlined a new classification of the Helicidae and related groups, using foot characteristics as follows:

> In the Endodontidae and Zonitidae a deep longitudinal furrow runs parallel to the foot-edge on each side, a short distance above it. These are parapodial or pedal grooves. . . .

He used the pedal grooves taxonomically in a key to families as follows:

> I. Foot-edges with no trace of pedal grooves; no tail gland; sole undivided. . . . SELENTIDAE. II. Foot margin defined by a pedal groove. . . . (a). . . . Tail gland often present, and sole frequently tripartite, ZONITIDAE. (b). . . . [no added pedal data], ENDODONTIDAE. III. Foot-edges without pedal grooves; no tail gland. . . . HELICIDAE.

Two years later Pilsbry (1896) erected two superfamilies in the Stylommatophora: (1) Aulacopoda, having pedal grooves, and (2) Holopoda, lacking pedal grooves. Fifty years later Pilsbry (1946) elaborated further on the Aulacopoda and indicated some of the difficulties experienced in detecting aulacopody (v. 2, pt. 1, pp. 231-232):

> In the Stylommatophora a groove, the pedal groove, marks the boundary where the smooth ciliated integument of the sole joins the tuberculate side walls of the foot. This pedal groove is usually rather inconspicuous and in or close to the angle of the foot (the "holopod" condition . . .), but in aulacopod snails it is situated higher, leaving a distinct band of the sole above the lateral angle. . . . Above the pedal groove there is a second parallel groove in the lateral integument of the foot, which Wachtler has termed the suprapedal groove. This is often close to the pedal groove and inconspicuous or irregular, but rarely it is rather widely separated from the pedal groove and deeper than that. When this is the case, holopod snails sometimes have the superficial appearance of Aulacopoda, as in Ferussacia. . . ., Glyptostoma . . . and some other genera.

Whereas initially Pilsbry stated that in Holopoda the pedal grooves are absent, he later found (as the result of a continued study) that they were present in the Holopoda as well as in the Aulacopoda, and that holopody must be differentiated from aulacopody by the relative distance of the pedal furrow above the edge of the sole, that part of the foot where the sole ends or turns upward. Thus, holopody, under continued study, has proven to be an uncertain, lesser kind of aulacopody. If, in evolution, the pedal line should move down slightly in an aulacopod genus, or up slightly in a holopod genus, can the taxonomist still place it in the proper superfamily? Pilsbry mentions this difficulty:

> On the other hand, some aulacopod snails appear to have assumed the holopod foot structure, the only such case known to me [Pilsbry] being the Bermudan Poecilozonites. In this genus the pedal groove is visible as a thin impressed line where it begins at the end of the sinus between head and foot; this line soon descends to

> the lateral angle of the foot, where it becomes only very faintly or not visible (in alcoholic preparations). A suprapedal groove is irregularly and quite weakly developed. . . .

This quotation exactly describes the condition of the pedal groove as I see it in living specimens of Otala lactosa Muller which is placed in the family HELICIDAE; Monadenia mormonum (Pfeiffer) which is placed in the family XANTHONYCIDAE; Micrarionta tryoni (Newcomb) which is placed in the family HELMINTHOGLYPTIDAE; Cryptomastix mullani (Bland and Cooper), Mesodon kiowaensis (Simpson), Mesodon thyroidus bucculentus (Gould) and others of the family POLYGYRIDAE. Under the circumstances of his observations, Pilsbry regarded the condition of Poecilozonites (ZONITIDAE) as unusual: ". . . . there are a few exceptional cases where the distinction between the aulacopod and holopod patterns is obscured." But my living material always seems to show some degree of aulacopody. In cases of ambiguous foot-structure Pilsbry suggests: "Other structures, such as radula and genitalia, leave no doubt about the actual relationships." Since foot-structure is ambiguous, the only possible conclusion seems to be the abandonment of superfamilies based on such characteristics. We may then turn to these other criteria, as Pilsbry has suggested.

Lest my conclusions seem critical of Pilsbry's observations, it should be understood that I have been espe-

cially favored by having a diverse collection of living land-snails of varied ages. I made my observations by allowing the snails to crawl on a slide or plate of glass which was strongly illuminated from various angles. Only when the specimens were so observed were the pedal grooves and the fringe-grooves (next to be discussed) strongly evident. By holding the slide against the lamp-shade so that part of the snail is shaded and the edges of the foot are intensely illuminated, and yet shading the observer's eyes from glare, one can see most clearly the fringe-grooves and contrasting central area when present. Many snails believed to be of uniform or non-tripartite sole will thus be revealed to be tripartite.

The true importance of pedal grooves is not in groovedness[1] but in the functionally important adjacent zone they delimit. This zone is the one bearing the fringe-grooves which are grooves which run at oblique or right angles to the pedal groove and, when the grooves are pigmented differently from the interspaces, they give a fringe-like color effect. In tripartite snails the fringe-zone ends at the central zone in some cases, partially so in others, but is seemingly entire (Anguispira) or very nearly entire in others (Ventridens). The fringe-zone extends up

---

[1] Haplotrema concavum (Say) has a ridge in place of a groove. If the ridge is truly homologous to the pedal groove, the species is nearly as aulacopod as Glyptostoma.

over the sides of the foot in obvious aulacopods, but in nominal holopods it is almost or entirely ventral (except near the labial palps where it is highest). In the tripartite sole, the central area bears and seems to be the zone of origin of the muscular waves (not to be confused with coordinated ciliary waves). Muscular waves seem either not to involve or only passively to involve the fringe-zones (except in Haplotrema).

The area below the pedal grooves (the fringe-zone) is ciliated (Pilsbry, 1946) and provides ciliary motility as well as fossoriality. The width of the lateral part of the obliquely grooved zone of the foot seems to determine fossorial adeptness, being wider in those snails that are persistent diggers and in snails which probe through encompassing detritus for their food, shelter, or mates. Would a holopod snail, with a vestigial or reduced lateral part to the fringe-zone, in evolving into a slug-type, develop a more obvious aulacopody? So far as my personal experience goes, all stylommatophoran slugs are aulacopod, but do not have equally wide lateral parts of the fringe-zone.

In the holopods, which probably evolved from aulacopods as Baker (1955, p. 111) has suggested, the lateral part of the fringe-zone has seemingly either been almost lost or mainly shifted to the ventral surface where it is

protected from desiccation. The retention of a remnant just behind the head may be because this is the most contractile part which initiates the slime-track for the rest of the foot, and because the foremost part of the foot is commonly used in excavating holes in the earth as nests for eggs. Holopods tending toward a slug-type are known among the Mexican xanthonycid snails (Baker, 1942, pp. 37-40).

The obvious aulacopods (exclusive of slugs) are soil-dwelling or leaf-litter-inhabiting snails. Such snails feed, mate, and carry on the entire life cycle buried completely or partially in duff (comminuted leaf-litter) or soil.

The holopods, in contrast, feed, mate and actively move predominantly on top of the soil or duff, or amid very loose leaves or detritus, a habitat presenting some of the qualities of a talus-habitat. Thus, because of their behavior, they are more exposed to dessiccation than aulacopods. Large desert snails are mainly holopods.

Very small aulacopods which inhabit logs, rock-crevices, or talus all live essentially as holopods because they are amply surrounded by space and are not intimately embedded in duff or detritus. Duff-dwelling aulacopods do share the talus habitat, but this does not deny their specialization for embedded living. The above ecologic generalizations are not solely my observations but

are almost common knowledge and are expressed and implied by the writings of many collectors and ecologists. Soil-flooding or sogginess brings up most ground-dwellers, subfossorial or otherwise, but this constitutes an emergency behavior. Sporadic exceptions probably occur, but not in significant numbers except in the case of stylommatophoran slugs (Philomycidae, Limacidae, Zonitidae, Arionidae, and others).

CHAPTER V.

ARIONIDAE AND SO-CALLED ARIONIDAE

The genus Arion Ferussac comprises a conspicuous, abundant West Palaearctic group (Pilsbry, 1948a) of moderate to large slugs, often with lateral stripes and other markings such as are shown in the Nearctic genera Prophysaon, Anadenulus, and others. The characteristics of true arionids are: jaw somewhat ribbed; mantle oval, anterior; mucous pore often conspicuous, caudal; aulacopod sole sometimes strikingly colored laterally. Initially, the Arionidae were differentiated from the Limacidae by having a less conspicuous shell plate, ribbed jaw, caudal mucous pore, and by lacking a tail-keel.

A basically Arion-colored slug was found in the region near Port Townsend[1], Jefferson County, Washington. It was subsequently named Arion foliatum in 1851 by Gould. As other species and genera were discovered and named, they were regarded as arionids due to coloration, lack of the smooth jaw of limacids, or lack of the elongation of the

---

[1] Pilsbry, 1948a, p. 690.

mantle of the philomycids (which usually have ribbed jaws). Being slugs, these forms were linked taxonomically only with slugs, and never with the endemic, sympatric, shelled snails. Little was known then of the genitalia of true Arionidae or of our slugs. As the North American slugs were dissected, they were placed in new genera of their own and never in non-endemic or Old World genera.

Initial studies of the genitalia, unfortunately, revealed the true Arionidae as being misleadingly like the North American genera, even to the extent of a supposed absence of a penis-retractor in both Arion and Prophysaon (Pilsbry and Vanatta, 1896; 1898; Pilsbry, 1948a). It was also wrongly believed that in these genera the oviduct everted and functioned as a penis. Quick corrected this error for Arion in 1952 and showed that the organ involved is actually a part of the upper atrium (he regards it as atrial but I believe it actually homologous to parts of the vagina) which contains a ligula or stimulator; in species like A. hortensis Ferussac the stimulator is proximal to the oviduct and seems to be a part of it. Only the stimulator is everted during mating--the oviduct passively descending inside the stimulator (see figures in Quick, 1947, and Webb, 1950). Earlier, Pilsbry (1948a) had regarded the elongate structure in Geomalacus as an atrial extension as also does Quick (1952).

In all the prior data on the genitalia of Arion, however, there is one point of common error: that the penis is replaced functionally by the epiphallus, and that the penis and penis-retractor are absent. The failure of anatomists to note the true penis homolog and the penis-retractor probably results from the excessive shortening of the penis in Arion. This shortening has caused the verge (or remnant in some species) to open almost directly into the vaginal upper atrium (see fig. 15). The true penis appears as an encompassing ring about the verge (fig. 16). In mating (as in most helicids and verge-bearing snails), the verge is exserted and engages the expanded basal spermathecal duct and the epiphallus-molded spermatophore egresses through the verge or its relict into the spermathecal duct. Careful dissection will show a penis-retractor to insert adjacent to the verge on the epiphallus, but unless the muscle is stained the insertion may not be obvious. The penis-retractor is ample to retract the small verge but is less massive than the spermathecal or oviducal retractors. Clearly, we cannot continue to call the male organ of Arion an epiphallus since it has a verge associated with a penis-retractor exactly as in some helicoids and zonitids. The absence of a flagellum where the vas deferens inserts on the epiphallus is an occasional condition in both taxa.

The two ubiquitous characteristics of the genitalia of typical Arionidae are the long, glandular atrium and the

stimulator which attains extreme length in the genus Geomalacus. In the genitalially less evolved forms such as Arion ater (Linnaeus) the position of the stimulator is homologous with the vaginal disk of helicoids (with which it may prove to be homologous). This organ seems absent in North American forms, but it is simulated by the functionally and developmentally unknown organ of one subgenus of Binneya, in which the oviduct is said to open at its tip (Pilsbry, 1948a). The organ thus may be an ovipositor rather than a stimulator. The extremely short atrium of Binneya is certainly a non-arionid feature. In having a long, glandular atrium, short spermatheca, short epiphallus, and a short vas deferens, arionids could be derived from a zonitid sequence. The ribbed jaw of Arion is the main feature indicative of a helicoid derivation but such is not totally unknown in zonitids (Baker, 1955). The verge (when present) is within the usual size-range of the organ in Zonitidae. These data may now be compared with the following data on the so-called Arionidae of the New World.

Ariolimax is known anatomically from the work of Pilsbry and Vanatta (1896) and Mead (1943). In contrast to these authors, however, I find the verge of Ariolimax columbianus (Gould) to be structurally as in most xanthonycids, except that the outer epithelial layer of the verge is more prominent (figs. 8, 9). The verge develops almost exactly as in xanthonycid snails. See figures 7-10.

The courting behavior also seems basically xanthonycid (Heath 1916; Mead, 1943), and agrees basically with that of Monadenia fidelis (Gray) as described by Webb (1952a), and occurs from a head-on position (Heath, 1916, p. 23). No species of Arion is known which indulges in head-arching biting duels but some species of Arion are known which entwine the foreparts and gnaw (Webb, 1950). In Arion and Ariolimax (as in most snails) a pursuit stage has been observed (Mead, 1943; Webb, 1950).

The pattern of development of the genitalia in Ariolimax seems more like that of Monadenia and Leptarionta (fig. 12) than like the patterns of any other snails I have studied.[1] As shown by Quick (1952) and my own partial series, the pattern of Arion is much like that of zonitid snails. In the developmental pattern of Ariolimax, the atrium is rather short, the penis exceptionally long and distally expanded. The verge develops very early. At first the spermatheca exhibits proportions similar to that of a xanthonycid, but it shortens with maturity. No enlargement of the basal part of the spermathecal duct was ever noted. The vagina is long and with a xanthonycid-like expansion retained even in the adult.

---

[1] Possibly the American camaenids of Wurtz (1955) have a similar pattern. Unfortunately, data are lacking.

All the available data would seem to indicate that Ariolimax is allied to the xanthonycid snails much more closely than to the true Arionidae of the Old World. That the xanthonycids have in fact evolved toward a slug-like type is well known from such genera as Xanthonyx and Bunnya (Baker, 1942).

Hemphillia has been considered more primitive than Ariolimax on the basis of its more snail-like structure (Pilsbry, 1948a). The shell is still discernibly convex and, at least in some species, it protrudes dorsally where the mantle does not cover it. The viscera are not embedded in the foot, but remain in the general region below the shell-plate. Unfortunately, I was unable to keep alive the specimens of the two species of Hemphillia I collected in 1954 and thus had no opportunity to observe the mating or other habits of any of the specimens. The material obtained, however, has given some data on the pattern of development of the genitalia (see figs. 3-5). The general character of the developmental pattern of the genitalia is similar to that of Ariolimax, but the early development of the penis-pilaster and verge is striking. If we compare the penis characteristics of Hemphillia with xanthonycids such as Humboldtiana, especially with species such as H. nuevoleonis Pilsbry (1948b) or H. fortis Pilsbry (ibid.) we again have an example of an endemic snail with both a small verge and fleshy bodies in the basal penis. Baker

(1942) has already pointed out that:

> . . . . in its genitalia, Bunnya appears to approach Humboldtiana, which occurs with it in the temperate zone, although tropical Xanthonyx has more in common with Averellia.

At one time I considered a possible affinity of Hemphillia with those polygyrids which have a disk in the penis, but the proper relationships of talon, penis-retractor and retentor were not exhibited, nor is the genitalial development similar enough.

In my nearly adult specimen of Hemphillia danielsi Vanatta the epiphallus is curiously adnate and looped about the tip of the penis-evagination which seems to bear a tear-shaped internal body which I cannot be sure is not an artifact (fig. 5). In contrast, the organ in the lower part of the penis of H. glandulosa Bland and Binney bears a discoid pilaster (figs. 3, 4, 6). Magnipelta mycophaga Pilsbry (1953) may represent a more highly slug-like relative. Pilsbry and Brunson (1954) do not state how far into the pedal extremity the viscera extend. The penis is shown to have a basal pilaster but no verge. They stated that the intestinal loops are not as in Ariolimax.

The slugs of the types just considered, if one supposes a further simplification of the penis with retention of the pilaster but loss of the verge and considerable shortening of the epiphallus, could produce a type like the slug, Hesperarion hemphilli (W. G. Binney). If this inter-

pretation of phylogeny is correct, H. hemphilli should be placed in a separate genus from the type species H. niger (J. G. Cooper). This was done in a separate paper (Webb, 1959), in which the generic name Gliabates was proposed for a new slug, G. oregonia Webb, from Oregon (fig. 98). As Mead (1943) has stated:

> The phylogenetic relationships are now practically self-evident. The Hesperarion type [he discusses only H. niger] is prototypic; the columbianus type is essentially an amplification with greater attenuation of the penis papilla. . .

True Hesperarion is thus the more primitive relative of Ariolimax, at least in regard to the characters of the genitalia.

The data on Zacoleus are more nearly adequate. This slug, too, might appear to be allied to this sequence of slugs which bear penis-pilasters and tend toward an enlargement of the vaginal and spermathecal regions. Such seems decidedly not to be the case. All freshly-dissected non-preserved specimens of Z. idahoensis which I have dissected as adults show the inside surfaces of the tremendously inflated, pilaster-bearing basal spermathecal duct to bear strong, calcareous teeth (figs. 17, 18, 25). Only Philomycus of the Philomycidae has such a calcareous structure, but the single spike or dart of Philomycus happens to be on the vaginal side, whereas in Zacoleus idahoensis the somewhat more than a dozen curved denticles are in the basal

spermatheca. In homology, however, the oviduct of Philomycus inserts laterally on the vagina, which merges continuously with the spermathecal duct and is functionally part of it (figs. 13, 14 and 19-24). If the oviduct of Philomycus were to insert further down, the area would be considered an expanded basal spermathecal duct as it is in related species of the genera Pallifera and Eumelus. Functionally, coitus in Eumelus Rafinesque occurs in the vagina and expanded part of the basal spermathecal duct (Webb, 1951b). In Philomycus, coitus occurs mostly in the vagina, but the penis tip does enter the expanded basal spermathecal duct (fig. 14). The dart of Philomycus probes against the inserted organ of its mate.[1] Unfortunately, the mode of functioning of the denticles and pilasters of the basal spermathecal expansion of Zacoleus is not yet known.

The supposed pilaster of the penis of Zacoleus is actually the invaginated apex of the penis above the insertion of the epiphallus (fig. 18). No verge seems present. In the immature genitalia, the penis-retractor inserts on the epiphallus where it enters the penis (figs. 1, 2). The retractor I assume to atrophy, for I have never found any trace of the retractor in adults. Internally, the walls of the penis are finely tuberculate. At the base of the penis is a philomycid-like sheath (fig. 18). This is easily over-

---

[1] Details of the sexology of Philomycus are being presented in a separate paper (Webb, in press).

looked. Such a sheath has never been noted in Ariolimax, Arion, or Hemphillia; likewise unknown in these genera are denticles in either vagina or spermathecal duct. Despite the small size of the mantle of Zacoleus idahoensis and the tripartite sole, it seems to have more in common with the philomycids than with these other slugs. For this reason, I placed the species with Udosarx lyrata Webb (fig. 73) in a special subfamily, Zacoleinae, with Z. idahoensis as the type (Webb, 1959).

To make clear my present concept of the phylogeny of the Arionidae and the New World forms heretofore supposed to be arionid relatives, the diagrams of Mead (1943) and of Pilsbry (1948a) are given in contrast to mine (figs. 26, 27, 28). We still know too little about all the forms involved for a final evaluation, but this hypothesis, added to those of others, may at least aid the research. The status of Prophysaon is reserved for discussion in a later chapter. Without more data than the literature now affords, the status of our genus Anadenulus is uncertain (possibly it belongs near Hemphillia) and the non-endemic Anadenus seems best forgotten until malacologists have more nearly adequate data on its several species. Because A. beebei is said to have fleshy filaments within the penis, while others are implied to have calcareous spines (Cockerell, 1913), one might speculate that the genus is closest to the Zacoleinae.

CHAPTER VI.

THE AMMONITELLIDAE AND ALLIES

According to Pilsbry (1939, 1948a) five genera are present in this family: Ammonitella, Megomphix, Polygyrella, Polygyroidea, and Glyptostoma. New representatives may yet be discovered. Of the known members, I have been able to study Polygyrella and Glyptostoma as living captives, with the bulk of the data pertaining to the latter. Live paratypes of Ammonitella yatesi allyni sent by Emory P. Chace arrived dead, but provided anatomical data (fig. 60).

Aside from regarding them as allied equivalent groups, Pilsbry seems never to have united the Oreohelicinae and Ammonitellinae under a common family but subordinated them to the Camaenidae. Thus, in 1939 he wrote:

> This group of helices [Camaenidae] has been accepted by systematists in the sense of the original definition, though it has been enlarged by the inclusion of genera unknown or not dissected at the time it was instituted and various family names have been used for it. In 1895 these snails were termed Epiphallogona. . . .
>
> While the Epiphallogona apparently form a natural group, several subordinate structural types are included, and further investigation is required to show whether all of its genera are to be retained in the single family Camaenidae, or divided among several families. In case further division is made, our genera shall form the families Ammonitellidae and Oreohelicidae. Pending

> further study of Asiatic and East Indian epiphallogonous helices our West American representatives are here left in the Camaenidae as subfamilies. . . .
>
> Helices of this stock seem to have had an early radiation in Mesozoic time, reaching Australia . . . and spreading to Europe. . . .

The status of these two families has been surveyed by Wurtz (1955) during the course of his studies of the Camaenidae. In his study, he formally deleted the Ammonitellidae and Oreohelicidae from the snails to be considered as camaenids. He rejected these two families on the basis of their having alveoli of the ovotestis disposed in clumps in the digestive gland instead of being formed as a single mass in or adjacent to the liver. A second difference he cited involves the shape of the talon--flagelliform in Ammonitellidae; tusk-shaped and darkly pigmented in Oreohelicidae. To these criteria of differences I propose adding those of dissimilar genitalial development and mode of functioning of the sex-organs, as well as structural details of these same organs.

The first generic recognition of any member of these families was Polygyrella, W. G. Binney, 1863. Others were recognized as follows: Ammonitella, Cooper, 1868; Glyptostoma, Bland and Binney 1873; Oreohelix, Pilsbry 1904; Polygyroidea, Pilsbry 1930; and Megomphix, Baker 1930, for Macrocyclis hemphilli W. G. Binney 1879.

In initially recognizing affinity between an ammonitellid and a haplotrematid (then termed Macrocyclis instead

of Haplotrema), W. G. Binney (1879) seems to have been more nearly correct than he or later authors have supposed. It is true that the teeth of the lingula of known ammonitellids do not resemble the aculeate-cusped type of the snail-eating Haplotrematidae, but the entire genitalial development and mode of functioning of the various parts of the sex-organs of the Ammonitellidae, Oreohelicidae, and Haplotrematidae are similar. To this triad must be added the Philomycidae for similar reasons, so that we seem to have a slug-line of evolution from the ancestral ammonitellid-oreohelicid stocks. Instead of only one such divergence, it is possible that the Zacoleinae represent a second later divergence. The evidence in favor of this latter view is the retention of a well-formed shell in the two known species of Zacoleinae.

Such a dualistic phylogeny is further indicated by the fact that all traces of a shell in the Philomycidae are either a membraneous scale or a solid, calcareous granule located in the posterior end of the copious mantle-sac. Such structures were first noted by Clapp (1920). I find them frequently in dissections of Pallifera, Philomycus, and Eumelus Rafinesque. The posterior location of these vestigial structures indicates that the shell of ancestral philomycids was also in a posterior location relative to the body, much perhaps as in present day Testacella, the carnivorous slug.

The available data do not support the view that Am-

monitellidae and Philomycidae are most closely allied to Haplotrematidae. Existent but incomplete anatomic data of exotic groups of South America and of Australia show even a more pronounced anatomical similarity to the Ammonitellidae than do the Haplotrematidae (i. e., the Australian Pedinogyra and its allies, substantially Pilsbry's group Macroogona or Acavinae).

The spermatophores (figs. 57, 67-69, 77) and sex-organs (figs. 67-69, 76-84) as well as the pattern of development of the genitalia (figs. 29-35, 49-52) of the Oreohelix species studied were found to be basically similar to those of the Haplotrematidae (figs. 41-48, 53-54). A strong possibility exists, therefore, that in the Oreohelicidae we have a surviving and presumably further evolved member of the basic stock from which, by snail-eating and other specializations, the Haplotrematidae have evolved.

I do not believe that the pedal and dentitional differences between the Oreohelicidae and the Haplotrematidae confute the viewpoint that they have a common origin. For the special uses of the haplotrematid foot--capturing snail-prey, disintegrating parts of the shells of the prey, and plugging the aperture in defense--are as likely specializations contingent upon the snail-eating evolutionary theme as is the form of their dentition. Mammalogists have long recognized the common ancestry of certain carnivores and herbivores despite their dissimilar dental and pedal spe-

cializations. That snail evolution could have produced allied families of carnivorous and non-carnivorous types is not surprising and could be expected. Inasmuch as several other diverse groups of snail-eating snails exist in various parts of the world, the possibility of independent origin of some of these should be considered rather than expecting a common ancestry (Baker, 1930). Thus, if comparisons of snail-eating groups and sympatric non-snail-eating groups be made, some new points of phylogenetic affinity may be revealed.

In 1873 when Binney created the genus Glyptostoma as a zonitid genus, and in 1930 when Baker erected Megomphix (Glyptostoma-ally) as a zonitid genus, both authors may have been recognizing a valid affinity of the ammonitellids and zonitids. Certainly in some respects such Zonitinae as Oxychilus and Mesomphix anatomically resemble Glyptostoma and Megomphix. Thus, the naturalness of the assemblage grouped in the Zonitidae is open to question, especially if the unlikeness of sex-organ functioning between the genus Ventridens, Gastrodontinae, and Mesomphix, Zonitinae, (Webb, 1948, 1952b) are considered. The courtship of the few species of Mesomphix I have observed is much like that of Glyptostoma, while that of Oxychilus strongly resembles that of Haplotrema. Perhaps only a remote relationship of common ancestry of Ammonitellidae, Oreohelicidae, Haplotrematidae, and Zonitinae is involved.

Historically, the oreohelicids have also been associated with endodontids. In anatomy and shell characteristics, the Ammonitellidae and Oreohelicidae are, in my opinion, definitely closer to endodontids than to helicoid families like the Camaenidae. Initially described as species of the genus Helix, Oreohelix was transferred by W. G. Binney (1878) to the endodontid genus Patula (a name now superseded by Anguispira). In 1893 Pilsbry proposed to unite all patuloid snails under Pyramidula. In reviewing this in 1939, Pilsbry concludes:

> It was an unfortunate idea, for further research has shown that neither Pyramidula or Oreohelix are related to the "Patulae" (Endodontidae).

It would be interesting to know what Pilsbry's conclusion would be now if he could review the sexological data of both oreohelicids and endodontids. The courtship behavior of such endodontids as I have happened to observe [Anguispira alternata ssp. (Say), A. kochi (Pfeiffer), and Discus rotundatus (Muller)] is Haplotrema-like, with one snail clinging to the shell of the other. Mating in each was effected by a nearly instantaneous entwining of the penises with a polygyrin-like exchange of semen. No moulding of the ejected semen was noted. In this regard, these species are more like the genus Polygyra than like Mesodon. If this type of sexology is typical of all or most of the endodontids, then those supposed endodontids with a verge are of questionable status as endodontids.

I have sometimes suspected that our Helicodiscus might be a diminutive ammonitellid, but have not been able to gain any corroboratory sexological or developmental data. That question is still unsolved. At one time I also entertained the idea that some affinity might exist between Polygyridae and Endodontidae, but the total unlikeness of the genitalial development, as well as my failure to be able to homologize penis-structure, between the two groups failed to support the idea. Meanwhile, sexological study of various polygyrids showed that they formed a natural transition series back to Ashmunella. The endodontid type of organ does not fit into this series. Close conchological affinity was never present between the two groups. Because limacid slugs also have penis-entwining types of mating procedure, they too were compared with polygyrids and were also found lacking in real homology. They and the Endodontidae have perhaps a very close relationship, but since some zonitid groups seem also to have a penis-entwining type of mating, these too will have to be evaluated relative to the Limacidae.

CHAPTER VII. THE SAGDIDAE:

PRIMITIVE SURVIVORS, DWARFS OR POLYGYRIDS?

Since I was able to study only one of the members of the smallish snails currently allocated to the family Sagdidae, my data will not much increase our understanding of these snails as a group. Since my purpose was to seek evidence of supposed affinity of the Sagdidae with the Polygyridae, my observations are not applicable to an evaluation of the naturalness of the assemblage of snails currently tallied as sagdids. Pilsbry (1940) suggested that the Sagdidae and Polygyridae have had a common helicid ancestral stock. Baker (1940) credited the sagdid, Mcleania, with a closer affinity to Polygyridae than to other Sagdidae.

My specimens of Lacteoluna selenina (Gould) were derived from specimens taken near the "Old Biology Building," University of Miami, Coral Gables, Florida. In shell structure I find this species to be quite unlike the polygyrids. The shell striae are more of the character of those of ammonitellids than of polygyrids. The simple lip of the known species is also not polygyrid-like, although the interesting Mcleania darlingtonii from Puerto Rico does have a kind of

reflected lip similar to that of the zonitid Trochomorphinae and the nodal swellings on the periphery of its shell are also matched only in the Trochomorphinae. If the genitalia of Mcleania are considered to be of the polygyrid type, a new subfamily would be necessitated to do it justice, for the vas deferens opens into a capacious epiphallus, an essentially abbreviated ammonitellid type of caecum and flagellum. Again, a like anatomical feature is presented in the Trochomorphinae. Present data indicate that to ally Mcleania with the Polygyridae creates more problems than it solves.

Unfortunately, sexological data could not be secured from Lacteoluna. Serious courtship seems to be effected from a head-on position. The stage of dilated atrial pores was as far as I ever noted such affairs to progress. My anatomical material, however, presents the following important details: The tubular mucous gland constricts to a ductile portion which seems to end in a muscular expansion containing a small dart (this may be artifactual, fig. 75). This body is located on a neophore as in the west coast Helminthoglyptidae except that the neophore arises from the penis-limb rather than from the atrial-pore region. The long dentate flagellum clearly molds very spiny spermatophores and has an accessory lobe much as some camaenids. This nodular body, located below the point of insertion of the vas deferens, may possibly aid the spermatophore tip to

be formed, or perhaps it is a gland assisting in the passage of the spermatophore. The epiphallus proper is stout below the accessory body and receives a retractor muscle on its lower one-fourth. The epiphallus seems to terminate just above a small verge which projects into the upper part of the penis above its union with the neophore lobe. The very digitiform tubules composing the prostate are confined to a very short segment of the oviduct and are not distributed the entire length as in polygyrids. The vagina is about as long as the penis below the verge and would seem to receive the latter by insertion as in helicids. The tip of the spermathecal duct ends in a blunt limb, which may be an atrophied diverticulum; the other, more ductile part ascends to the ovoid spermatheca. The presence of a mucous gland ending by a seeming dart and dart-sac complex clearly differentiates this genus from any polygyrid. For example, in the polygyrin, Praticolella, the glandular body of the penis has no trace of a dart-sac and functions to help anchor the semen-mass received from the penis of the mate-animal.

The penis-structure of Lacteoluna is more helicid-like than otherwise and seems to indicate an aberrant group, certainly not one ancestral to the polygyrids.

CHAPTER VIII.

PROPHYSAON AND THE POLYGYRIDAE

In the discussion of the Arionidae I proposed to defer consideration of Prophysaon to the present chapter in which I will present evidence which seems to justify annexing this genus formally into the Polygyridae. The sexology of Prophysaon seems to differ little from the ashmunellin type and Prophysaon is transferred into that polygyrid subfamily.

By good fortune, I was able to secure mating-anatomies of one species in the field (figs. 89, 90). The specimens were found in a woodlot at Olympia, Washington, in coitus. The bodies were in crescentic contact anteriorly, free posteriorly. Only the position of the animals and the disk of slime on the moss indicated that they were probably mating. The anatomies show coitus had been essentially completed with a reciprocal exchange of long, vermiform spermatophores which have the semen dispersed nearly throughout the entire spermatophore as in Ashmunella. Slightly greater quantity was present in the thicker end of the spermatophore. In the mating-anatomies there was not a conspicuous atrial

clasping disk as in Ashmunella. Instead, a smooth, slightly prominent atrial zone bore the short papilla-sized penis outward. The vagina was also slightly everted as a low prominence and into this, in life, the papilloid penis probably had been inserted. It is to be noted that the atrium is not expanded in the subgenus Prophysaon s. str. as it is in the subgenus Mimetarion, and that the penis and penis-loop are much larger. In Mimetarion, a strong clasping disk occupies the large atrium and the penis has a short vergic extension into the atrial chamber. This seeming verge relict is very short but technically seems properly so homologized. Apparently in Mimetarion the clasping disk is the main organ uniting the genitalia during mating and the short penis-papilla with its very abbreviated vergic-tip is thrust into the lumen of the vagina. While he has indicated it in some of his drawings, Pilsbry (1948a) has not stressed the expansion of the atrial region in the subgenus Mimetarion. The organ duplicates the condition in many species of Ashmunella.

The mode of development and of functioning of the sex-organs of Prophysaon is as in Ashmunella of the Polygyridae. As in that genus, in Prophysaon the penis bears a large epiphallus which is thrown into a short loop (fig. 91). The retractor muscle inserts on the upper limb of the loop, then continues to the lower segment of the loop as a penis-retentor muscle. In the juvenile Prophysaon

these muscles are as prominent as in Ashmunella. However, Prophysaon has evolved somewhat from the exact condition in Ashmunella. In the more conservative of the two subgenera, Mimetarion, we have a condition shown by some species of Ashmunella in which the clasping disk of the penis is mainly situated in the atrium. At the same time, that part of the upper penis just below the loop, which functions as the intromittent organ by eversion, has become reduced in size. Mimetarion has the beginnings of a verge in a button-like disk projecting into the cavity of the atrium. In my studies on Ashmunella, I noticed that some individuals showed a tendency for the upper part of the penis where it is conjoined by the epiphallus to project dome-like into the lumen of the upper penis. The condition was somewhat more slight than in Mimetarion, but a little increase in developmental emphasis of the tissues at the penis-epiphallus junction could easily give rise to the button-like verge of Mimetarion. This evolutionary development is not shared by the subgenus Prophysaon s. str. which retains a larger penis-loop and the upper penis functioning as in Ashmunella. The clasping disk of Mimetarion and of Ashmunella seems atrophied into non-existence in Prophysaon s. str.

It may be recalled that Pilsbry failed to find a penis-retractor muscle in Prophysaon or Mimetarion. By looking for the retractor muscle in its approximate ashmu-

nellin position, I have found it in many dissections of adult Mimetarion. In a few instances, but not all, it was found in adult Prophysaon s. str. It is invariably present in the juvenile condition. Its function in the adult has been supplanted by the very dense sheet of penis-retentor muscle, which is ample to retract the slight lower penis in Prophysaon s. str., and in Mimetarion it seems to help retract the descended loop. In both subgenera of Prophysaon, the loop-like part of the epiphallus straightens out during coitus and thus functions exactly as it does in Ashmunella.

In distribution, it is interesting to note that Prophysaon and Mimetarion do not occur beyond the limits of distribution of the western Polygyridae (Pilsbry, 1948a). The absence of Prophysaon in the area of distribution of the species of Ashmunella might at first sight seem to prohibit its having evolved from this genus. However, when it is realized that Cryptomastix makes a reasonable transition from Ashmunella, that its simpler members have the ashmunellin type of clasping disk, and that the shells also are transitional, there seems no question but that an ashmunellin ancestral type was present in the Northwest.

Malacologist are faced by one more question. Why has the Northwestern region been the cradle of several distinct slug lineages? Ariolimax apparently demonstrates a xanthonycid slug line. Hemphillia seems to demonstrate a second xanthonycid slug line of evolution. The Zacoleinae

appear to represent an ammonitellid-oreohelicid slug line; and a polygyrid slug line is represented by Prophysaon. This orgy of slug-evolution from a snail prototype seems not shared with the endemic snails of the more eastward portion of the continent. We have a native limacid slug which is clearly a prehistoric immigrant from Europe; there is a strong galaxy of philomycid species and genera but this family is not confined to North America. Perhaps in the complicated geology of the Northwest has existed a factor which may have favored slug evolution. What that factor may be is not apparent to me.

CHAPTER IX. CONCLUSIONS

The main conclusions reached during the present study are:

1. The Sagdidae are not directly related to the Polygyridae, but do seem to be helicoid derivatives.

2. True Arionidae are not endemic in the New World. Our supposed arionids are polyphyletic, representing two separate derivations of slugs from xanthonycid snails, one derivation from primitive polygyrids, and two derivations from the ancestral ammonitellid-oreohelicid complex--first the Philomycidae, and more recently the Zacoleinae.

3. The Ammonitellidae are more closely related to exotic snails than to the Oreohelicidae.

4. The Oreohelicidae seem to be related to the Haplotrematidae.

5. The zonitids such as Mesomphix and Oxychilus and the endodontids may have some phylogenetic relationship to the ammonitellid-oreohelicid-haplotrematid complex.

6. The segregation of snails into the superfamilies Holopoda and Aulacopoda is not valid, as the holopods show variable degrees of aulacopody, and the aulacopods show varying degrees of holopody.

CHAPTER X. SUMMARY

Studies of the development of the genitalia, mating-behavior, and functioning of the sex-organs were made on several snail families which from geographic or taxonomic position might be expected to have a relationship to the polygyrid land-snails. As the study progressed, other groups were surveyed when considered pertinent. Ultimately, representatives of the Sagdidae, American Arionidae (so-called), Oreohelicidae, Ammonitellidae, Haplotrematidae, Philomycidae and Zonitidae were evaluated.

The living snails were confined in concrete cages, and observations were made on the living snails whenever possible. The study was aided by the dissection of specimens in the field, and by preserving the dissections as permanent slides. Trisodium phosphate and sodium hydroxide were used as softening agents for alcoholic and over-hardened tissues. Dry specimens, which would have shattered into fragments during manipulation, were dissected intact after being rehydrated and softened in solutions of these substances.

Pilsbry's superfamilies, Holopoda and Aulacopoda, based on the supposed presence or absence of pedal grooves,

were found to be ambiguous due to the presence of a more or less prominent pedal groove in both groups.

The true Arionidae were demonstrated to have a true penis, penis-retractor muscle, and traces of a verge. The stimulator-like organ of Arion, formerly considered an eversible portion of the oviduct, is suggested to be homologous to the vaginal pilasters and stimulators of helicids. The long atrium of the Old World true arionids is contrasted to the short atrium of the so-called New World arionids, which are believed to be of a distinct and multiple phylogeny not involving the Old World arionids. The mechanism of mating of the true arionids is quite unlike that of the sexologically known New World supposed arionids.

The New World slugs formerly assigned to the Arionidae are re-distributed to the following basic groups or families. Ariolimax and Hesperarion are considered slug types derived from one group of xanthonycid snails; Bunnya, Hemphillia, Magnipelta possibly, and Gliabates are believed to represent a second, later evolution from xanthonycids like Humboldtiana.

Prophysaon is transferred to the polygyrid subfamily Ashmunellinae, with which its sexology and pattern of genitalial development were found to be almost identical--especially in the subgenus Mimetarion (less so in Prophysaon s. str.). A trace of a verge was noted in Mimetarion, and a penis-retractor is usually to be found even in adults.

The penis-retractor was noted to develop as in Ashmunella, but tends to be lost in adults of Prophysaon s. str.

Zacoleus and Udosarx, a new genus discovered during the study, were transferred to the Philomycidae (Webb, 1949), but are believed to represent a secondary evolution to a slug type from the ammonitellid-oreohelicid snail group whereas the Philomycidae are believed to be a much earlier slug line derived from this group. During the study spermathecal denticles were noted in Zacoleus, a feature which heretofore has apparently escaped malacological notice. The sexology of Philomycus is contrasted with that of the ammonitellid, Glyptostoma, and the patterns of genitalial development are compared with Glyptostoma and Haplotrema.

Additional differences among the Ammonitellidae, Oreohelicidae, and Camaenidae were found in the patterns of genitalial development and in the mode of sex-organ functioning. The North American Ammonitellidae are believed to have family if not generic relatives in both South America and Australia (Pedinogyra and its allies). Oreohelicidae are believed more intimately related to the Haplotrematidae than to the Ammonitellidae, and are proposed as representing a surviving plant-eating relative of the snail-eating Haplotrematidae. A possible relationship of these snails to the zonitids, as characterized by Mesomphix and Oxychilus, is recognized, and also with the endodontids.

The Sagdidae are evaluated in relationship to the

Polygyridae. The recently proposed affinity suggested by Baker (1940) could not be substantiated on the basis of anatomical and conchological grounds. A dart-organ and verge were found to be present in Lacteoluna selenina. The sagdids are concluded to be related to helicids rather than to polygyrids.

The most important results of general interest are:

1. A new outline of arionid phylogeny and rejection of the concept that arionids are endemic to the Americas.

2. Establishment of the probability that all sigmurethra are aulacopod (holopody being obscured aulacopody--a matter of degree but not of absolute difference). Thus, neither the characteristics (holopody, aulacopody) nor the groups based upon them are of basic taxonomic validity.

3. The relationships of the Arionidae, Ammonitellidae, Endodontidae, Zonitidae, Sagdidae, and Rhiomycidae are discussed on the basis of their sexological and other characteristics.

LITERATURE CITED

BAKER, H. B. 1930. The Land Snail Genus Haplotrema. Proc. Acad. Nat. Sci. Philadelphia, 82: 405-425.

_____ 1940. Some Antillean Sagdidae or Polygyridae. Naut. 54 (2): 54-62. pls. 4-5.

_____ 1941. Zonitid Snails from Pacific Islands, Parts 3 and 4. Bernice P. Bishop Museum Bull. 166: 205-370 pls. 43-65.

_____ 1942. A New Genus of Mexican Helicids. Naut. 56 (2): 37-40.

_____ 1955. Heterurethrous and Aulacopod. Naut. 68 (4): 109-112.

_____ 1956. Family Names in Pulmonata. Naut. 69 (4): 126-128.

BECQUAERT, J. and W. J. CLENCH. 1939. Mcleania, a New Genus of Land Mollusks from Puerto Rico. Mem. Soc. Cub. Hist. Nat. 13 (5): 283-284, figs. 4-6, pl. 36.

BINNEY, W. G. 1878. The Terrestrial Air-Breathing Mollusks of the United States. Vol. 4. Cambridge, Harvard University, Museum of Comparative Zoology.

CLAPP, G. H. 1920. The Shell of Philomycus carolinianus Bosc. Naut. 33:83.

COCKERELL, T. D. A. 1913. A New Slug from the Himalaya Mountains. Bull. Amer. Mus. Nat. Hist., 32, art. 41, 617-619, figs. 1-7.

HEATH, H. 1916. The Conjugation of Ariolimax californicus. Naut. 30(2):22-24.

JONES, D. T. 1940. A Study of the Great Basin Land Snail Oreohelix strigosa depressa (Cockerell). Bull. Univ. of Utah. 31(4):1-43.

KONDO, Y. 1943. Anatomical Studies of Three Species of Ouagapia (Pulmonata, Agnatha, Paryphantidae). Occ. Pap. B. P. Bishop Mus. 42(19):229-248.

MEAD, A. R. 1943. Revision of the Giant West Coast Land Slugs of the Genus Ariolimax Morch (Pulmonata: Arionidae). Amer. Midland Nat. 30(3):675-717, figs. 1-29.

ODHNER, N. H. J. 1932. New or Little Known African Land Shells. Proc. Mala. Soc. 20(1):19-40.

PILSBRY, H. A. 1892. On the Anatomy of Sagda, Cysticopsis, Aegista and Dentellaria. Proc. Acad. Nat. Sci. Philadelphia, pp. 213-215, pl. 13.

_____ 1893-95. Manual of Conchology. Second series, vol. 9. Guide to the Study of Helices. Philadelphia, Academy of Natural Sciences.

_____ 1896. The Aulacopoda; a Primary Division of the Monotremate Land Pulmonates. Naut. 9:109-111.

PILSBRY, H. A. 1898. Revision of the North American Slugs: Binneya, Hemphillia, Hesperarion, Prophysaon, and Anadenulus. Proc. Acad. Nat. Sci. Philadelphia, pp. 219-262, pls. 9-16.

_____ 1916. Notes on the Anatomy of Oreohelix, with a Catalogue of the Species. Proc. Acad. Nat. Sci. Philadelphia, 68: 340-359, pls. 19-22.

_____ 1927. The Structure and Affinities of Humboldtiana and Related Helicid Genera of Mexico and Texas. Proc. Acad. Nat. Sci. Philadelphia, 79: 165-192, pls. 11-14.

_____ 1928. Studies on West Indian Mollusks: The Genus Zachrysia. Proc. Acad. Nat. Sci. Philadelphia, 80: 581-606, pls. 28-30.

_____ 1930. Anatomy and Relationships of Some American Helicidae and Polygyridae. Proc. Acad. Nat. Sci. Philadelphia, 82; 303-327, pls. 23-27.

_____ 1932. The Land Snail Genus Polygyrella. Proc. Acad. Nat. Sci. Philadelphia, 84: 15-19, figs. 1-8.

_____ 1939, 1940, 1946 1948a. Land Mollusca of North America (North of Mexico). 2 vols. Philadelphia, Academy of Natural Sciences of Philadelphia.

_____ 1948b. Inland Mollusks of Northern Mexico. I. The Genera Humboldtiana, Sonorella, Oreohelix and Ashmunella. Proc. Acad. Nat. Sci. Philadelphia, 100; 185-203, pls. 12-14.

PILSBRY, H. A. and R. B. BRUNSON. 1954. The Idaho-Montana Slug, Magnipelta (Arionidae). Notulae Naturae 262:1-6, figs. 1-10. Philadelphia, Academy of Natural Sciences.

PILSBRY, H. A. and E. G. VANATTA. 1896. Revision of the North American Slugs: Ariolimax and Aphallarion. Proc. Acad. Nat. Sci. Philadelphia, pp. 339-350, pls. 12-14.

PILSBRY, H. A. and E. G. VANATTA. 1898. Anatomical Notes on Certain West American Helices. Proc. Acad. Nat. Sci. Philadelphia, pp. 67-71, pl. 1.

QUICK, H. E. 1947. Arion ater (L.) and A. rufus (L.) in Britain and Their Specific Differences. Jour. of Conch. 22(10):249-261.

_____ 1952. Rediscovery of Arion lusitanicus Mabille in Britain. Proc. Mala. Soc. London 29(2-3):93-101.

SMITH, A. G. 1957. Snails from California Caves. Proc. Calif. Acad. Sci. 29(2):21-46, pls. 1-2.

WEBB, G. R. 1943. The Mating of the Landsnail Haplotrema concavum (Say). Amer. Midland Nat. 30(2):341-345.

_____ 1947. The Mating-Anatomy Technique as Applied to Polygyrid Landsnails. Amer. Nat. 81:134-147.

_____ 1948. Notes on the Mating of Some Zonitoides (Ventridens) Species of Landsnails. Amer. Midland Nat. 40(2):453-461.

_____ 1950. Comparative Study of Mating in Two Species of Arionid Mollusks. Jour. of Ent. and Zool., Pomona College, 42(1):28-37.

WEBB, G. R. 1951a. Sexological Notes on the Landsnail Oreohelix. Chicago Acad. Sci. Nat. Hist. Misc. 78:1-5.

_____ 1951b. Notes on the Sexology of Philomycid Slugs of the Genus Eumelus Rafinesque. Jour. Tenn. Acad. Sci. 26(1):73-78.

_____ 1952a. Pulmonata, Xanthonycidae: Comparative Sexological Studies of the North American Land-Snail Monadenia fidelis (Gray). Gast. 1(1):7-8.

_____ 1952b. Sexological Notes on Mesomphix cupreus and M. subplanus. Trans. Amer. Micro. Soc. 71(4):408-410.

_____ 1954a. Additions to the Pulmonate Snails of Oklahoma. Proc. Okla. Acad. Sci. 34:81-84.

_____ 1954b. The Life-History and Sexual Anatomy Data on Ashmunella with a Revision of the Triodopsin Snails. Gast. 1(2):19-20.

_____ 1959. Two New North-Western Slugs, Udosarx lyrata and Gliabates oregonia. Gast. 1(3):22-23, figs. 37, 39.

WOODWARD, S. P. 1856. A Manual of the Mollusca; or, Rudimentary Treatise of Recent and Fossil Shells. Parts I and II. London, John Weale.

WURTZ, C. B. 1955. The American Camaenidae (Mollusca: Pulmonata). Proc. Acad. Nat. Sci. Philadelphia, 117:99-143, pls. 1-19.

PLATE 1
(Figs. 1-12)

Fig. 1. Zacoleus idahoensis Pilsbry. Immature genitalia of a specimen from Lolo Pass, route 11, near the conjunction of Clearwater and Idaho county lines, Idaho.

Fig. 2. Z. idahoensis. Slightly older specimen from the Esley C. Hankins farm, Kootenai County, Idaho, near the Big Spokane River. Note the pronounced spermathecal-duct expansion in comparison with Hemphillia.

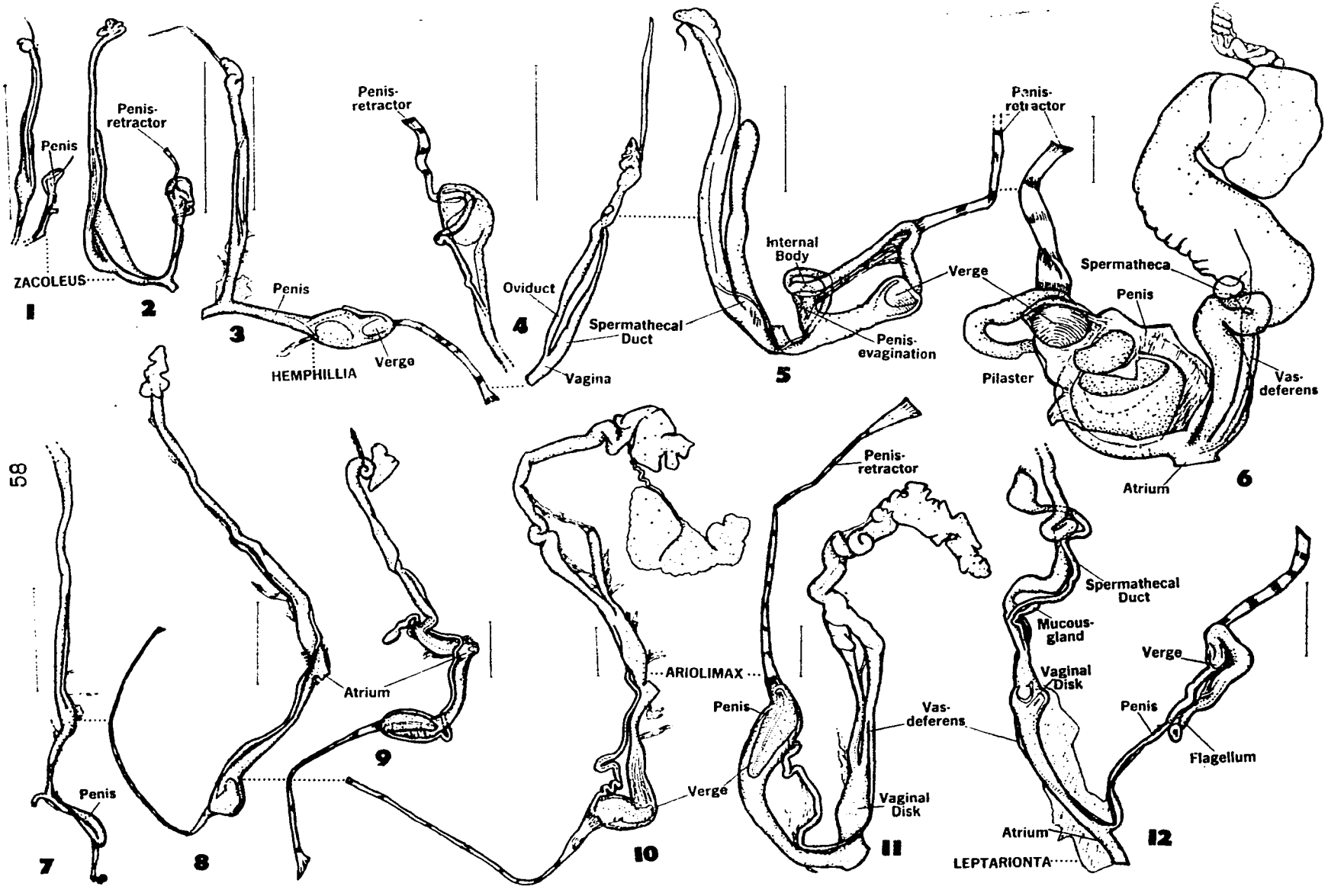
Figs. 3-4. Hemphillia glandulosa Bland and Binney. Immature specimens from Priest Point, Olympia, Washington.

Fig. 5. H. danielsi Vanatta. (Same location as fig. 1). Note the teardrop-shaped body in the penis-evagination. (The atrium has become twisted upward from the usual configuration).

Fig. 6. H. glandulosa. An adult from the same locality as specimens of figs. 3-4.

Figs. 7-11. Ariolimax columbianus (Gould). A progressively older series of immature genitalia. Note the development of the verge. The specimens are from Olympia, Washington.

Fig. 12. Leptarionta sp. The immature genitalia of a specimen taken "4 miles north of El Candelaria, Oaxaca, Mexico, July 10, 1949" by Dr. W. Leslie Burger.


Penis
ZACOLEUS
1
Penis-
retractor
2
Penis
HEMPHILLIA
Verge
3
Penis-
retractor
Oviduct
Spermathecal
Duct
Vagina
4
Internal
Body
Verge
Penis-
evagination
5
Penis-
retractor
Spermatheca
Penis
Pilaster
Vas-
deferens
Atrium
6
Penis
7
Atrium
8
9
ARIOLIMAX
Verge
10
Penis-
retractor
Penis
Vas-
deferens
Vaginal
Disk
11
Spermathecal
Duct
Mucous-
gland
Vaginal
Disk
Verge
Penis
Flagellum
Atrium
LEPTARIONTA
12

58

PLATE 1

PLATE 2
(Figs. 13-25)

Fig. 13. Philomycus carolinianus Bosc. The dissected vagina and spermathecal system of the other specimen of fig. 14.

Fig. 14. P. carolinianus. X 3.25. The mating-anatomies of a pair of specimens from Big Bureau Creek, north of Princeton, Bureau County, Illinois.

Fig. 15. Arion hortensis Ferussac. A specimen from Bury St. Edmunds, England, showing the penis, atrium, and spermathecal duct.

Fig. 16. Arion sp. Another specimen from Bury St. Edmunds showing penis and atrium only. Note the verge homologue and the penis-retractor.

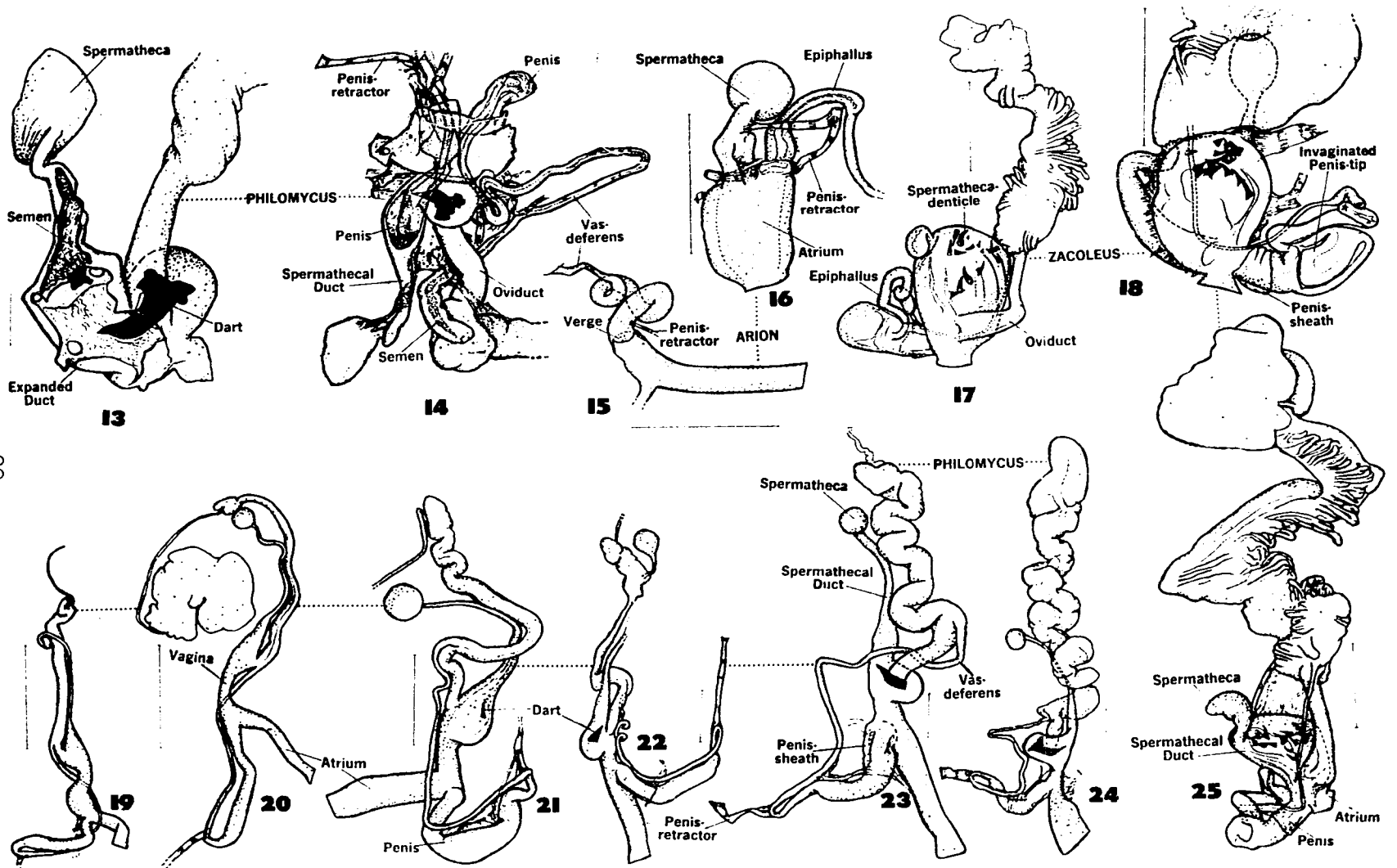
Fig. 17. Zacoleus idahoensis Pilsbry. The nearly mature genitalia.

Fig. 18. Z. idahoensis. The mature sex-organs of a specimen from the Esley C. Hankins farm, Kootenai County, Idaho. Note the spermathecal duct denticles.

Figs. 19-23. P. carolinianus. A series showing genitalial maturation. Specimens from Brownfield's Woods, near Urbana, Illinois.

Fig. 24. P. carolinianus. A nearly adult anatomy. Specimen from Trelease Woods, near Urbana, Illinois.

Fig. 25. Z. idahoensis. The mature genitalia of a specimen from Lolo Pass, route 11, near the common boundary of Clearwater and Idaho counties, Idaho.


Spermatheca
Semen
PHILOMYCUS
Dart
Expanded Duct
13
Penis-retractor
Penis
Penis
Spermathecal Duct
Oviduct
Vas-deferens
Verge
Penis-retractor
Semen
14
15
Spermatheca
Epiphallus
Penis-retractor
Atrium
ARION
16
Spermatheca-denticle
ZACOLEUS
Epiphallus
Oviduct
17
Invaginated Penis-tip
Penis-sheath
18
Vagina
Atrium
Penis
19
20
21
Dart
22
PHILOMYCUS
Spermatheca
Spermathecal Duct
Vas-deferens
Penis-sheath
Penis-retractor
23
24
Spermatheca
Spermathecal Duct
Atrium
Penis
25

60

PLATE 2

PLATE 3
(Figs. 26-28)

Fig. 26. The phylogeny of the Arionidae as indicated by Mead (1943).

Fig. 27. The phylogeny of the Arionidae as indicated by Pilsbry (1948) with the inclusion of his data on Magnipelta (Pilsbry, 1954).

Fig. 28. The phylogeny of the Arionidae and other snails discussed in the present thesis. Generic and other groups not discussed are not shown; thus, only a few xanthonycids, one sagdid, and one endodontid are shown although many genera are known to exist. Note that the diagram indicates three radiating stocks which may be connected by the Zonitidae, but this is not yet proven to be correct. Where appreciable uncertainty exists as to the position of a branch, a ? is inserted in the lineage. In view of the absence of extensive fossil series, it has seemed more nearly correct to show higher genera being derived from yet existing genera than from a common ancestor, such as is probably often the case. The diagram is presented to show possible phylogeny rather than an an outline of verified taxonomy.

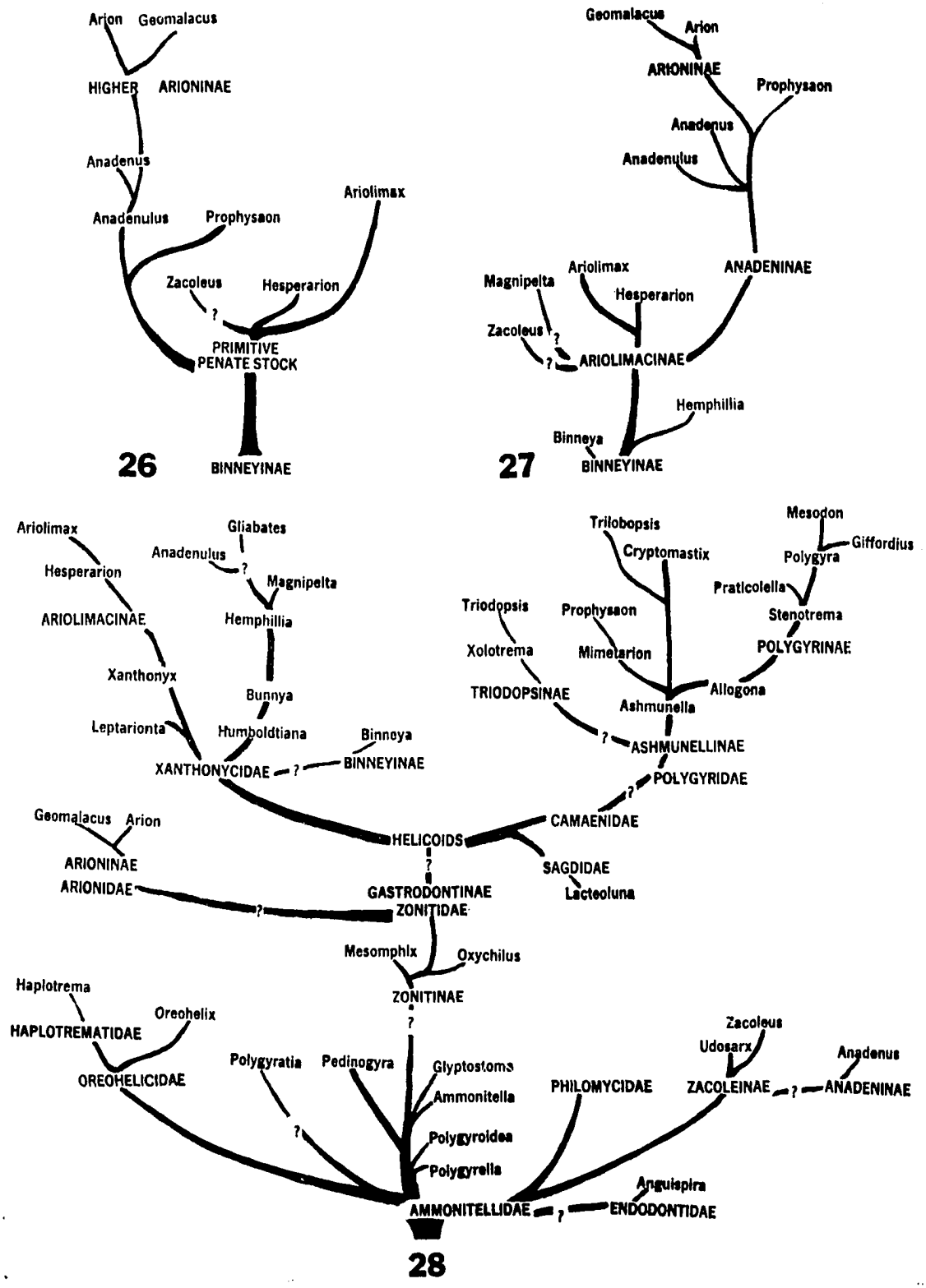

Arion
Geomalacus
HIGHER
ARIONINAE
Anadenus
Anadenulus
Prophysaon
Ariolimax
Zacoleus
Hesperarion
?
PRIMITIVE
PENATE STOCK
BINNEYINAE
26
Geomalacus
Arion
ARIONINAE
Prophysaon
Anadenus
Anadenulus
ANADENINAE
Magnipelta
Ariolimax
Hesperarion
Zacoleus
?
?
ARIOLIMACINAE
Hemphillia
Binneya
BINNEYINAE
27
Ariolimax
Gliabates
Anadenulus
?
Hesperarion
Magnipelta
ARIOLIMACINAE
Hemphillia
Xanthonyx
Bunnya
Leptarionta
Humboldtiana
Binneya
XANTHONYCIDAE
?
BINNEYINAE
Trilobopsis
Cryptomastix
Mesodon
Giffordius
Polygyra
Praticolella
Triodopsis
Prophysaon
Stenotrema
Xolotrema
Mimetarion
POLYGYRINAE
TRIODOPSINAE
Allogona
Ashmunella
?
ASHMUNELLINAE
?
POLYGYRIDAE
Geomalacus
Arion
ARIONINAE
ARIONIDAE
?
HELICOIDS
?
CAMAENIDAE
SAGDIDAE
Lacteoluna
GASTRODONTINAE
ZONITIDAE
Mesomphix
Oxychilus
ZONITINAE
?
Haplotrema
Oreohelix
HAPLOTREMATIDAE
OREOHELICIDAE
Polygyratia
Pedinogyra
Glyptostoma
Ammonitella
?
Polygyroidea
Polygyrella
AMMONITELLIDAE
Zacoleus
Udosarx
Anadenus
PHILOMYCIDAE
ZACOLEINAE
?
ANADENINAE
Anguispira
?
ENDODONTIDAE
28

PLATE 3

PLATE 4
(Figs. 29-40)

Fig. 29. Oreohelix strigosa depressa (Cockerell). Genitalia of a juvenile from Granite Pass, U. S. 14, Sheridan County, Wyoming.

Fig. 30. O. subrudis ("Pfeiffer", Reeve). Unlocalized. Genitalia of a juvenile.

Fig. 31. O. subrudis. Specimen from stream-side bushes a mile south of Taraghee Pass, Fremont County, Idaho.

Fig. 32. O. subrudis. Unlocalized. Slightly more mature than the next specimen.

Fig. 33. O. subrudis. Another specimen from Taraghee Pass. See fig. 31.

Fig. 34. O. subrudis. Unlocalized. The nearly mature genitalia.

Fig. 35. O. haydeni (Gabb). Immature genitalia. Specimen from 19 miles west of Drummond, Granite County, Montana, taken under rocks amid open stand of pines. Note penis-invagination in both this specimen and in fig. 34.

Figs. 36-40. Genitalial development of Glyptostoma gabrielense Pilsbry. Laboratory generation of parent material collected June 24, 1950 by Dr. Wendell O. Gregg at Monrovia Canyon, San Gabriel Mountains, Los Angeles County, California.

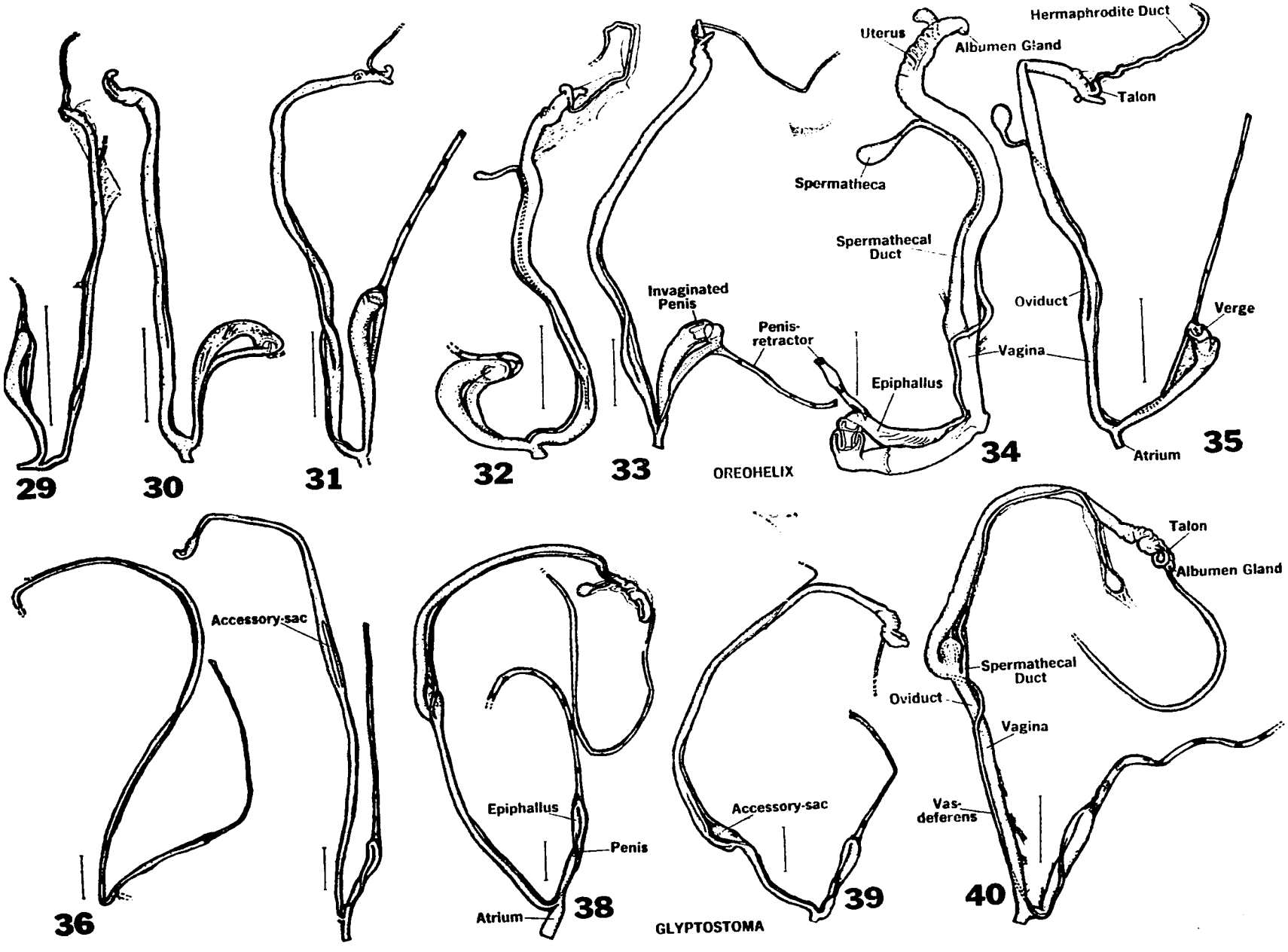

29
30
31
32
33
Uterus
Albumen Gland
Hermaphrodite Duct
Talon
Spermatheca
Spermathecal Duct
Invaginated Penis
Penis-retractor
Epiphallus
Vagina
Oviduct
Verge
Atrium
34
35
OREOHELIX
36
Accessory sac
38
Epiphallus
Penis
Atrium
39
GLYPTOSTOMA
40
Talon
Albumen Gland
Spermathecal Duct
Oviduct
Vagina
Vas-deferens

PLATE 4

PLATE 5
(Figs. 41-56)

Fig. 41. Haplotrema vancouverense (Lea). The immature genitalia of a specimen from Bellevue, near Seattle, Washington.

Figs. 42-47. H. concavum (Say). Genitalial development as illustrated by a series of specimens from Big Bureau Creek, 1 mile north of Princeton, Bureau County, Illinois.

Fig. 48. H. sportella hybridum (Ancey). Mature genitalia. Note the hypertrophy of the medial section of the penis-retractor muscle which also envelops the caecum-epiphallus complex of the penis.

Figs. 49-50. Oreohelix strigosa (Gould). Topotypes. Mouth of Entiat River at Entiat, Washington. A quite immature specimen and a nearly adult specimen.

Figs. 51-52. O. pygmaea Pilsbry. The immature genitalia of specimens from 13 miles northeast of Shell, on U. S. 14, Big Horn County, Wyoming, in the general region of the type locality.

Figs. 53-54. Haplotrema sportella (Gould). The immature genitalia of specimens collected by Dr. Harold W. Harry at Cascade Locks, Oregon.

Figs. 55-56. Polygyrella polygyrella (Bland and Cooper). Immature specimens from Lolo Pass, Idaho.

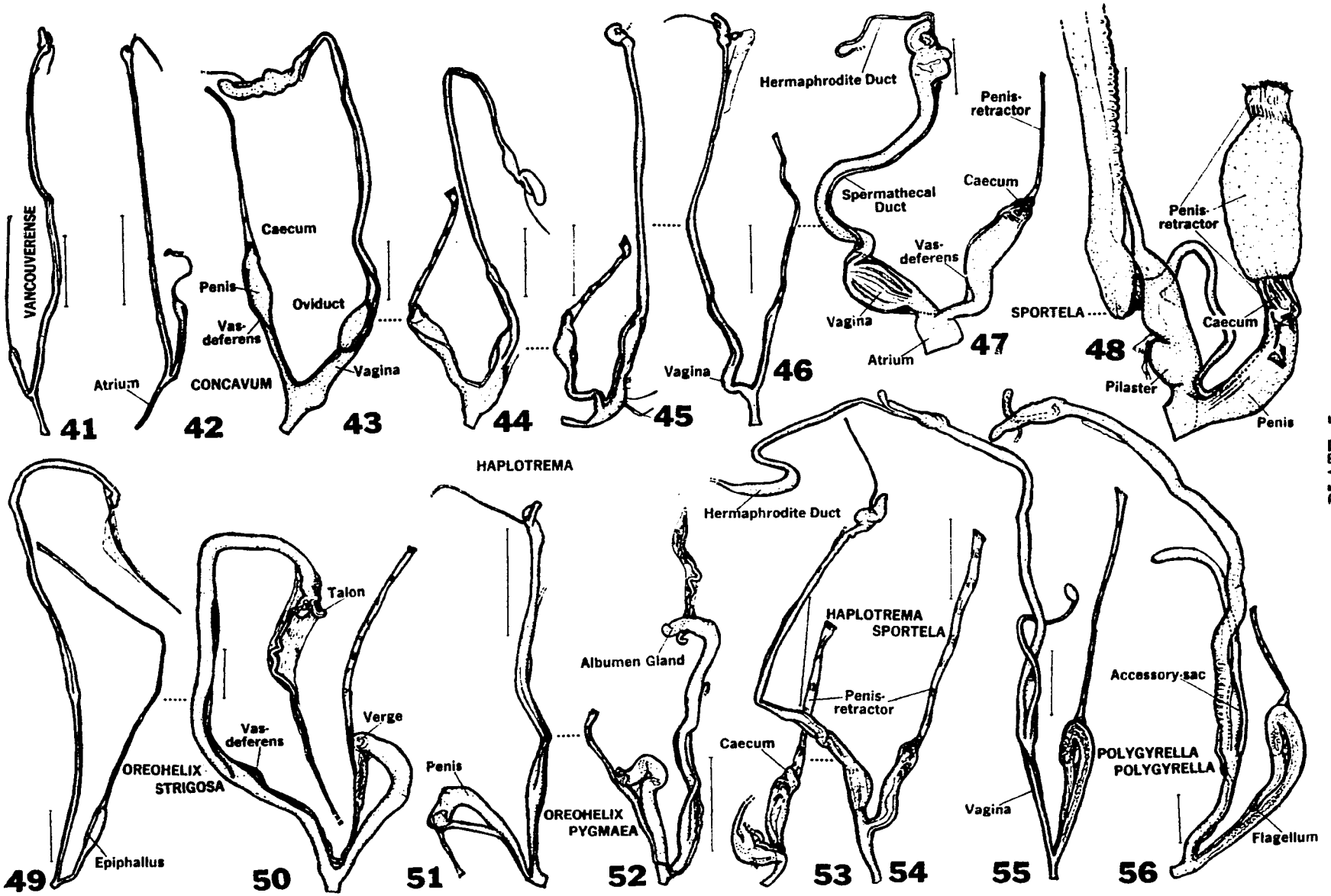

VANCOUVERENSE
Atrium
41
Caecum
Penis
Oviduct
Vas-deferens
CONCAVUM
Vagina
42
43
44
Vagina
45
Hermaphrodite Duct
Penis-retractor
Caecum
Spermathecal Duct
Vas-deferens
Vagina
Atrium
46
47
SPORTELA
Penis-retractor
Caecum
Pilaster
48
Penis
HAPLOTREMA
Talon
Verge
Vas-deferens
OREOHELIX STRIGOSA
Epiphallus
49
50
Penis
Albumen Gland
OREOHELIX PYGMAEA
51
52
Hermaphrodite Duct
HAPLOTREMA SPORTELA
Penis-retractor
Caecum
53
54
Vagina
55
Accessory sac
POLYGYRELLA POLYGYRELLA
Flagellum
56

PLATE 5

PLATE 6
(Figs. 57-66)

Fig. 57. Haplotrema sportella (Gould). Cascade Locks, Oregon, collected by Dr. Harold W. Harry.

Fig. 58. Glyptostoma gabrielense Pilsbry. Laboratory generation adult.

Fig. 59. Polygyrella polygyrella (Bland and Cooper). Lolo Pass, Idaho.

Fig. 60. Ammonitella yatesi allyni Chace. Paratype. Note the gland-like nodules on the epiphallus.

Fig. 61. Oreohelix pygmaea Pilsbry. An adult from 13 miles northeast of Shell, Big Horn County, Wyoming.

Fig. 62. O. strigosa depressa (Cockerell). East side of Granite Pass, Big Horn Mountains, Big Horn County, Wyoming, on U. S. 14.

Fig. 63. Haplotrema keepi (Hemphill). Hillside on Dog Creek, U. S. 99, about 25 miles south of Dunsmuir, Shasta County, California.

Fig. 64. Oreohelix carinifera Pilsbry. Topotype. Under bushes amid sparse juniper, Garrison, Powell County, Montana.

Fig. 65. Haplotrema vancouverense (Lea). Collected by Ross T. Bell, "3 miles below Humboldt River (Camp ground), Olympic National Park, Washington.

Fig. 66. Ariolimax columbianus (Gould). Adult collected at Olympia, Thurston County, Washington.

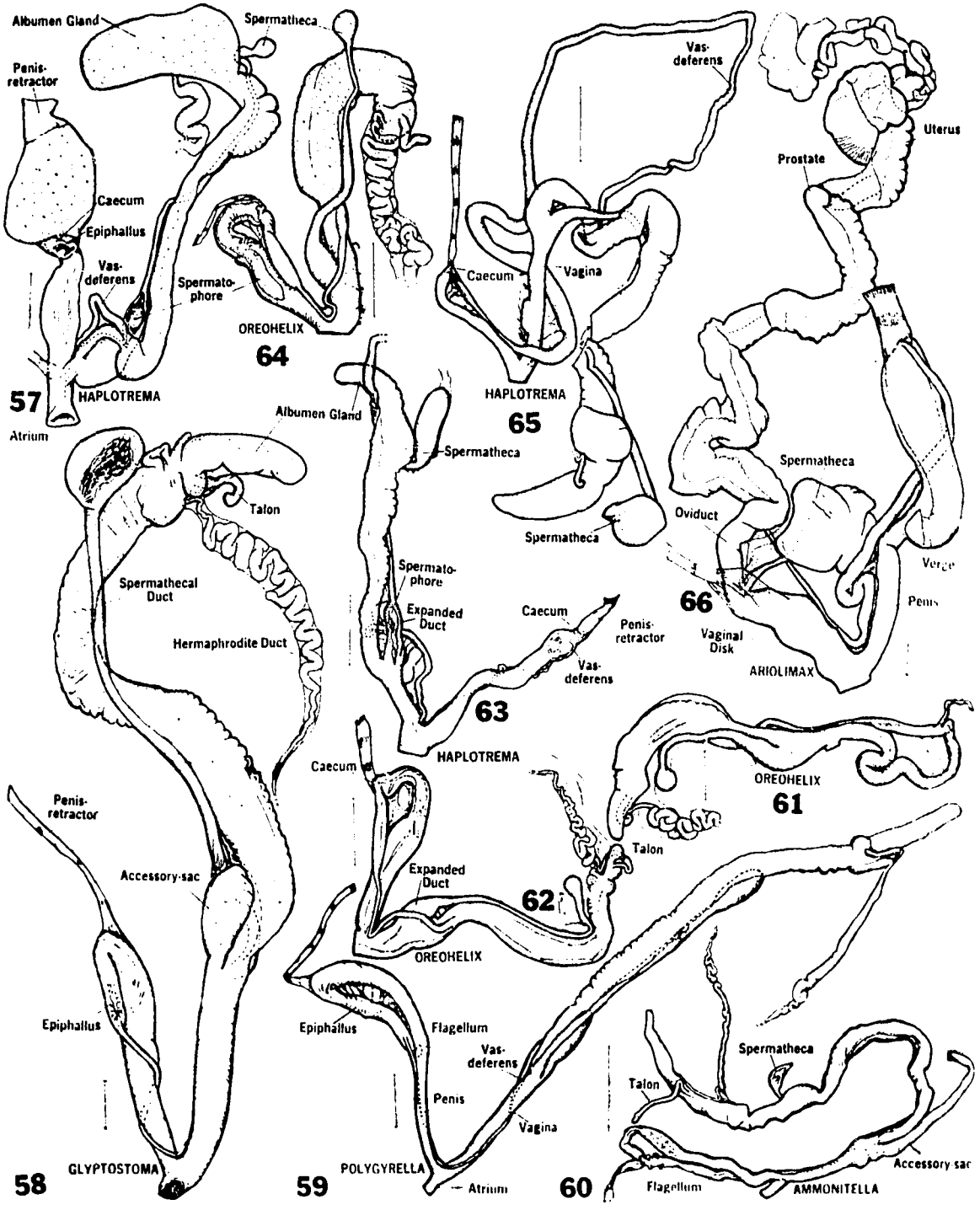

Albumen Gland
Spermatheca
Penis-retractor
Caecum
Epiphallus
Vas-deferens
Spermato-phore
OREOHELIX
64
57
HAPLOTREMA
Atrium
Vas-deferens
Uterus
Prostate
Caecum
Vagina
HAPLOTREMA
65
Spermatheca
Albumen Gland
Spermatheca
Oviduct
Talon
Spermathecal Duct
Hermaphrodite Duct
Spermato-phore
Expanded Duct
Caecum
Penis-retractor
Vas-deferens
66
Vaginal Disk
ARIOLIMAX
Verge
Penis
63
HAPLOTREMA
Caecum
OREOHELIX
61
Penis-retractor
Accessory sac
Talon
Expanded Duct
62
OREOHELIX
Epiphallus
Epiphallus
Flagellum
Vas-deferens
Penis
Vagina
Spermatheca
Talon
Accessory sac
Flagellum
AMMONITELLA
58
GLYPTOSTOMA
59
POLYGYRELLA
Atrium
60

PLATE 6

PLATE 7
(Figs. 67-75)

Figs. 67-68. Oreohelix strigosa (Gould). A pair of mating-anatomies of topotypic specimens from the hills at the mouth of the Entiat River, Washington.

Fig. 69. O. strigosa. Showing the engaged sex-organs.

Fig. 70. Glyptostoma gabrielense Pilsbry. A pair of dissected mating-anatomies. The vagina-accessory-sac complex has been opened to free the penis which was inserted into it. Laboratory generation.

Fig. 71. G. gabrielense. Spermatophore ejected by one of the specimens.

Fig. 72. G. gabrielense. Another mating-anatomy.

Fig. 73. Udosarx lyrata Webb. The new slug discovered at Lolo Pass, Idaho. The species is a relative of Zacoleus.

Fig. 74. Gliabates oregonia Webb. The new slug from under leaves under bushes on the east bank of the Long Tom River adjacent to Alderwood State Park, Lane County, Oregon. The species may be related to Hesperarion hemphilli (W. G. Binney); if so, the latter species becomes congeneric.

Fig. 75. Lacteoluna selenina (Gould). Near the old Biological Laboratory Building, University of Miami, Coral Gables, Florida. The presumed dart is indicated by the dark line in the dart-sac. Miami is cited by Pilsbry as the type locality.

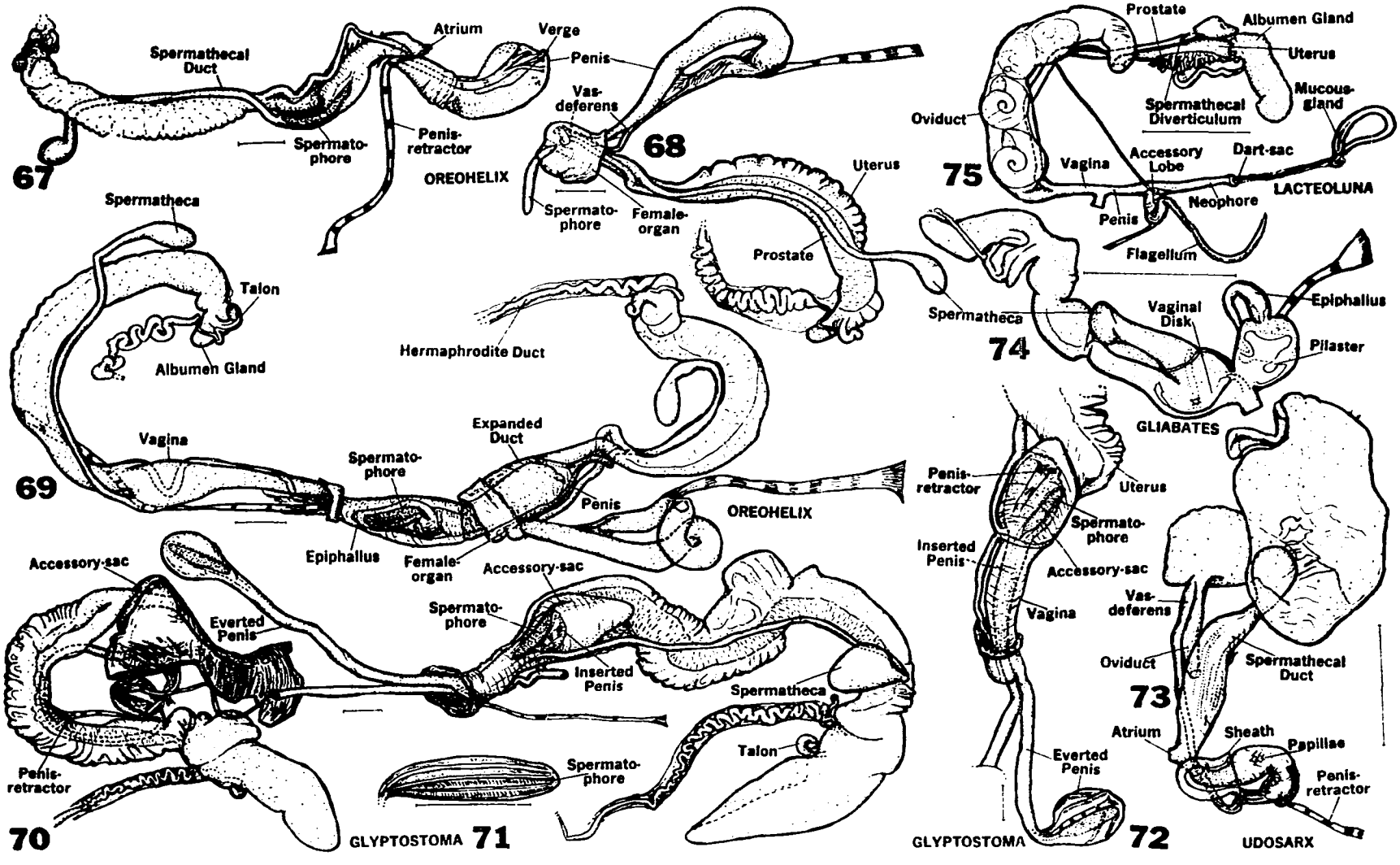

Spermathecal Duct
Atrium
Verge
Penis
Penis-retractor
Spermato-phore
67
OREOHELIX
Vas-deferens
68
Uterus
Spermato-phore
Female-organ
Prostate
Spermatheca
Talon
Albumen Gland
Hermaphrodite Duct
Vagina
69
Expanded Duct
Spermato-phore
Penis
OREOHELIX
Epiphallus
Female-organ
Accessory-sac
Accessory-sac
Spermato-phore
Everted Penis
Inserted Penis
Spermatheca
Talon
Penis-retractor
Spermato-phore
70
GLYPTOSTOMA
71
Prostate
Albumen Gland
Uterus
Oviduct
Spermathecal Diverticulum
Mucous-gland
Vagina
Accessory Lobe
Dart-sac
75
LACTEOLUNA
Penis
Neophore
Flagellum
Spermatheca
Vaginal Disk
Epiphallus
Pilaster
74
GLIABATES
Penis-retractor
Uterus
Spermato-phore
Inserted Penis
Accessory-sac
Vas-deferens
Vagina
Oviduct
Spermathecal Duct
73
Atrium
Sheath
Papillae
Everted Penis
Penis-retractor
GLYPTOSTOMA
72
UDOSARX

PLATE 8
(Figs. 76-84)

Figs. 76-77. Oreohelix strigosa depressa (Cockerell). Note that one of the pair has assumed the role of male and the other that of female. This is true in every mating of this genus I have noted. The presence of received spermatophores in male-acting specimens indicates that they had functioned a short time previously as the female-acting specimens. East side of Granite Pass, U. S. 14, Wyoming.

Fig. 78. O. strigosa (Gould). Penis of male-acting topotypic specimen.

Fig. 79. O. s. depressa. Another specimen, unlocalized.

Fig. 80. O. subrudis ("Pfeiffer", Reeve). Route 1, Gallatin National Forest, northwest of Hebgen Lake Dam, at intersection with Beaver Creek Road, Gallatin County, Montana.

Fig. 81. O. pygmaea Pilsbry. Male-acting specimen from east side of Granite Pass, U. S. 14, Sheridan County, Wyoming. The spermatophore in the spermathecal duct indicates that this specimen has recently functioned as a female in another mating.

Fig. 82. O. subrudis. The incompletely everted penis and the everted female-organ of an unlocalized pair of specimens.

Fig. 83. O. haydeni (Gabb). U. S. 10, 27 miles west of Garrison, near Bearmouth, Granite County, Montana. Female-acting specimen.

Fig. 84. O. haydeni. Male-acting specimen of another pair. Same locality.

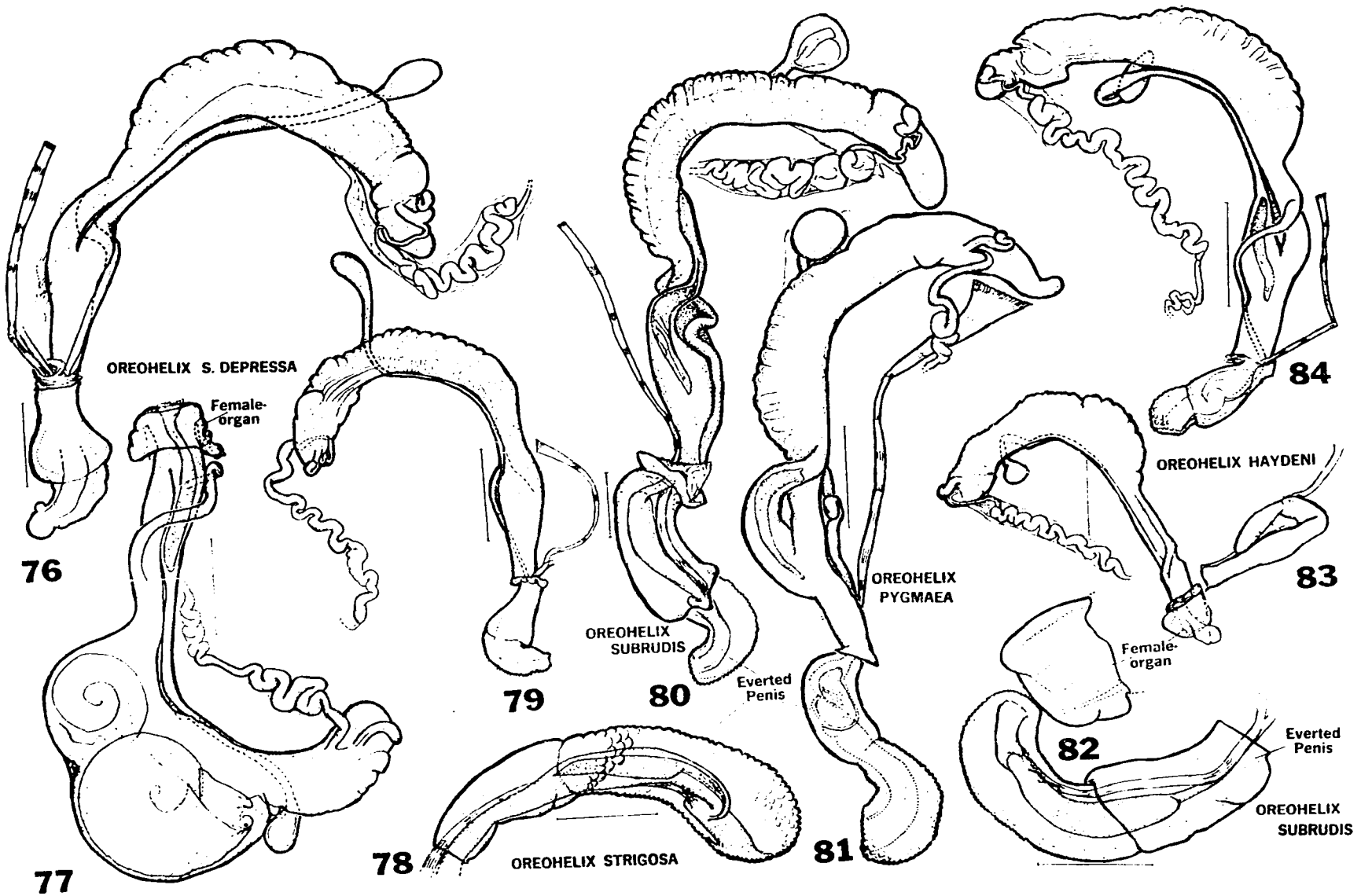

OREOHELIX S. DEPRESSA
Female-organ
76
77
79
OREOHELIX SUBRUDIS
80
Everted Penis
78
OREOHELIX STRIGOSA
OREOHELIX PYGMAEA
81
84
OREOHELIX HAYDENI
83
Female-organ
82
Everted Penis
OREOHELIX SUBRUDIS

PLATE 8

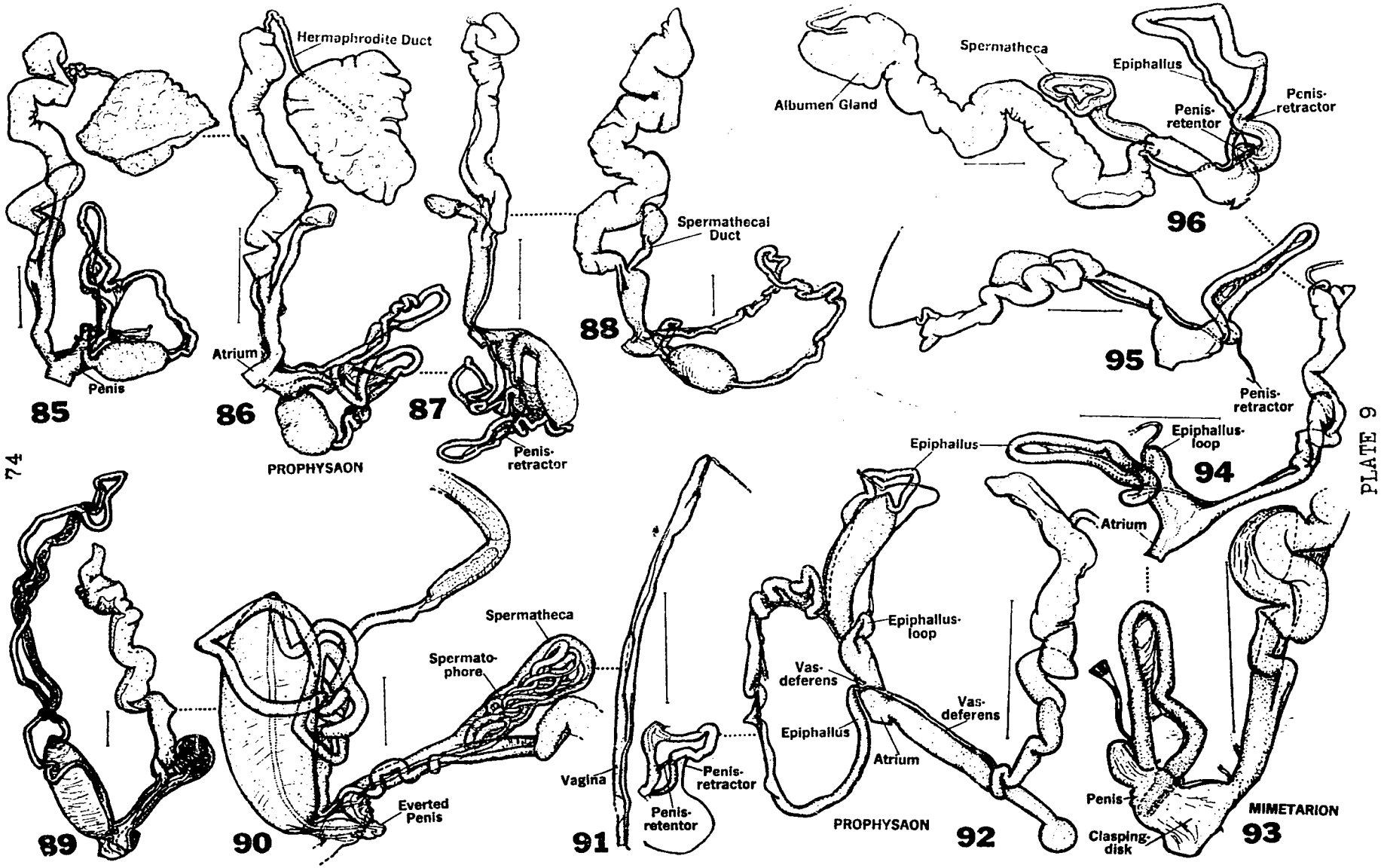
PLATE 9
(Figs. 85-96)

Figs. 85-88, 92. Prophysaon sp. Site of Mormon Island settlement about one-half mile west of Folsom Penitentiary limits. Downstream of the former bridge. Area is now inundated as a reservoir. Sacramento County, California.

Figs. 89-90. Prophysaon sp. Pair of mating-anatomies. The spermatophores exchanged have semen uniformly dispersed as in Ashmunella. Collected in coitus in the field, Oct. 6. 1954, Olympia, Washington.

Figs. 91, 96. Prophysaon (Mimetarion) sp. Fig. 91. very immature specimen. The structure labeled retractor muscle may in actuality be a bit of fiber and not the true organ. Specimen of fig. 96 is nearly adult. Both specimens are from the Esley C. Hankins farm, Kootenai County, Idaho.

Figs. 94, 93 and 95. Prophysaon (Mimetarion) sp. The specimens increase in size in the order of listing. Specimens from Bellevue, near Seattle, Washington.


Hermaphrodite Duct
Penis
Atrium
Spermathecal Duct
Albumen Gland
Spermatheca
Epiphallus
Penis-retractor
Penis-retentor
Epiphallus-loop
Vas-deferens
Vagina
Spermato-phore
Everted Penis
PROPHYSAON
MIMETARION
Clasping-disk
85
86
87
88
89
90
91
92
93
94
95
96

74

PLATE 9