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A TAXONOMIC STUDY OF SOME SPECIES OF *SEMISULCOSPIRA* IN JAPAN (MESOGASTROPODA: PLEUROCERIDAE)

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ABSTRACT

The purpose of this paper is to establish basic taxonomic concepts for 10 distinct species-group taxa of the freshwater snail genus *Semisulcospira*. Over 30 species and subspecies of this genus had been named from Japan, including the Ryukyu and Ogasawara Islands. In the current study, topotypes of the most prominent of the previously described species were obtained. Two taxa are described here as new, *Semisulcospira habei habei* and *S. habei yamaguchi*.

Topotypes were analyzed in terms of the largest 10% of each population. Data were collected on adult shell morphology, embyro shell characters and intra-brood pouch development of embryo shells. Data were analyzed and presented to permit the reader to understand natural variation in the parameters measured or counted. Data were correlated with the cytological findings of Burch & Davis (1967) and Burch (1968) in order to establish species concepts.

The taxa are relegated to 2 species groups, the *Semisulcospira libertina* group and the *S. niponica* groups. The former is characterized by having a chromosome number of n=18 or 20, adult shells have 7 or more basal cords, and there are numerous (100 or more) young in the female brood pouch (modified pallial oviduct). *S. libertina* and *S. reiniana* are the main species in the complex. *S. kurodai* is placed in the group because the taxon's chromosome number is n=18; the species is, however, considered transitional between the 2 species groups as the adult shells average 5.1 basal cords and there are 35.5 ± 15.4 embryos per female brood pouch.

The *Semisulcospira niponica* species group is characterized by species having low chromosome numbers, n=7 to 14; adult shells have 2 to 6 basal cords and there are few embryos per brood pouch (an average of 25.2 ± 9.8 maximum to 5.2 ± 3.4 minimum, depending on the species). Taxa included in this group are endemic in Lake Biwa and its drainage; they are: *S. niponica, S. decipiens, S. reticulata, S. habei habei, S. habei yamaguchi, S. nakasekoae and S. multigranosa.*

A key to the species is provided to aid in the identification. The utility of traits used in describing the taxa is discussed. Characters of basic importance in defining the species are chromosome numbers, number of basal cords on the adult shell, number of embryos carried by the female, ontogeny of shell sculpture, number of ribs and nodes on the adult shell, embryo size and shape, growth patterns of the embryos in the brood chamber, whorl size attained by the embryo in the female, embryo sculpture and color patterns.

Several traits seem to be particularly subject to inter-population variation. These are adult shell width, spire angle, length of body whorl, embryo microsculpture, apical whorl measurements and adult color patterns. In the *Semisulcospira libertina* species group the presence or absence of ribs and embryo sculpture is subject to such variation. Spire angle is, however, useful in differentiating between several species. The number of whorls and adult shell length are subject to environmental control.

Semisulcospira habei yamaguchi, S. decipiens and *S. multigranosa* are sibling species. Further, *S. multigranosa* is polymorphic by having smooth and ribbed morphs, and 3 color patterns. When data from cytological studies and embryo morphology were correlated, it became evident that these are distinct species. Further distinguishing shell features were then recorded. In Lake Biwa the following species are sympatric: *S. habei yamaguchi, S. decipiens, S. multigranosa, S. reticulata* and *S. niponica*.

The majority of species studied here are endemic to the Lake Biwa area, Shiga Prefecture, Honshu. Several conditions for speciation have been present in Lake Biwa. The lake is ancient (Tertiary) and has had about 1 million years stability; it has an immense lacustrine volume divided into numerous niches. Endemism and sympatry perhaps resulted when the lake level dropped with subsequent elevation of barriers preventing immigration or emigration. The shrinking lake forced the association of numerous organisms within the limits of the current lake basin and the single drainage system of the Setagawa River. Other populations were excluded from the lake or perished. *Semisulcospira kurodai* may be an example of such exclusion. A million years of stability probably allowed further speciation or incipient speciation, e.g. *S. habei habei* and *S. habei yamaguchi*.

CONTENTS

I. INTRODUCTION

The freshwater snail genus *Semisulcospira* is widespread in Japan, Korea, Taiwan and China. Although the genus is extremely common and certain of the taxa within the genus are among the most frequently encountered aquatic snails in the Orient, there is little useful biological information for adequately defining subgeneric categories. There has been great uncertainty in the interspecific systematics and species discrimination.

Over 30 species and subspecies of this genus have been described from Japan including the Ryukyu and Ogasawara (=Bonin) Islands. Kuroda (1963) lists most of these species in his catalog of the non-marine mollusks of Japan. The species definitely named or reported from the main Japanese Island of Honshu, the area from which most of the snails of this study came, are listed in Table 1. The plethora of names evidently resulted from describing local populations which are not only widespread in canals, rivers and lakes of Japan, but also exhibit great variability in shell size, shape, color patterns and sculpture.

Problems faced when working with this confusing and complex genus are many. Several of the major problems are: (1) any one "species" seems to grade into several others when adult shell features of numerous populations

TABLE 1. Species of *Semisulcospira* named or reported from the main island of Honshu, Japan*

Species group name	Original generic designation	Author and Publication
libertina	*Melania*	Gould, 1859, Proc. Bost. Soc. natur. Hist., 7: 42
*japonica***	*Melania*	Reeve, 1859, Conch. Icon., Monog. *Melania,* sp. 129, pl. 17, fig. 125
tenuisulcata	*Melania*	Dunker, 1860, Malakozool. Blätt., 6: 229
*rufescens***	*Melania*	Martens, 1860, Ibid., 7: 47
*ambidextra***	*Melania*	Martens, 1860, Ibid., 7: 46
*martensi***	*Melania*	Brot, 1862, Matér. Fam. Mélaniens, Cat. Syst. p 48
*reiniana***	*Melania*	Brot, 1876, Jahrb. Deut. Malakozool. Ges., 3: 277, pl. 8, fig. 4
niponica	*Melania*	Smith, 1876, Quart. J. Conch., 1: 124
libertina var. *decussata*	*Melania*	Martens, 1877, Sitz.-Ber. Ges. naturforsch. Freunde Berlin, 1877: 114
libertina var. *plicosa*	*Melania*	Martens, 1877, Ibid., 1877: 114
libertina var. *irrigua*	*Melania*	Martens, 1877, Ibid., 1877: 116
biwae	*Melania*	Kobelt, 1879, Senckenberg. Natur. Ges., 11: 132, pl. 19, fig. 9
niponica var. *decipiens*	*Melania*	Westerlund, 1883, Nachrichtsb. Deut. Malakozool. Ges., 15: 56
japonica var. *ornata*	*Melania*	Westerlund, 1883, Ibid., 15: 57
niponica var. *trachea*	*Melania*	Westerlund, 1883, Ibid., 15: 57
andersoni	*Melania*	Smith, 1886, J. Conchol., 5: 58
*mariesi***	*Melania*	Smith, 1886, Ibid., 5: 59
multigranosa	*Melania*	Boettger, 1886, Jahrb. Deut. Malakozool., 13: 7
yokohamensis	*Melania*	Hartman, 1897, Nautilus, 11: 41
reiniana var. *hidachiensis*	*Melania*	Pilsbry, 1902, Proc. Acad. natur. Sci. Phila., 54: 119, pl 9, fig. 2
libertina var. *latifusus*	*Melania*	Pilsbry, 1902, Ibid., 54: 120, pl. 9, fig. 8
libertina var. *gigas*	*Melania*	Pilsbry & Hirase, 1904, Nautilus, 18: 9
kawamurai	*Semisulcospira*	Kuroda, 1929, Venus, 1: 189, pl. 5, fig. 29-30
nakasekoae	*Semisulcospira*	Kuroda, 1929, Ibid., 1: 189, pl. 5, fig. 37-41
libertina nassaeformis	*Semisulcospira*	Kuroda & Kanamura, 1929, Ibid., 1: 188, pl. 5, figs. 25-26
decipiens reticulata	*Semisulcospira*	Kajiyama & Habe, 1961, Ibid., 21: 171, fig. 6
kurodai	*Semisulcospira*	Kajiyama & Habe, 1961, Ibid., 21: 173, figs. 1-3

* The list does not include nomen nuda or erroneous names. However, most of these nominal species are considered synonyms of *S. libertina* (Gould) (see Kuroda, 1963).

**Type locality, "Japan"; not definitely known from Honshu.

are studied; (2) Almost no morphological information has been added in recent years to that of the original papers, which described numerous species in few, brief paragraphs utilizing the "adult" shell alone, e.g., Gould (1859), Brot (1874), Kobelt (1879), Martens (1877), Westerlund (1883), etc. Morphological data on the soft anatomy of the genus are non-existent, except for the gross anatomy of *Semisulcospira libertina* (Itagaki, 1960), and Kajiyama & Habe's (1961) use of embryo shell characters in distinguishing *Semisulcospira* species. (3) There has been a recent trend to "lump" species, thus creating a list of synonyms without adequate justification or data. For example, Kuroda (1963) subordinated *Semisulcospira libertina* and 14 other named taxa to *S. bensoni* (Philippi, 1851). Most recently, Habe (1965) considered the genus *Semisulcospira* in Japan to be comprized of 4 species; *S. bensoni*, *S. niponica*, *S. kurodai* and *S. decipiens*. He reduced *S. multigranosa*, *S. nakasekoae* and *S. reticulata* to subspecies of *S. decipiens*.

Confusion will continue until an attempt is made to define basic genetic units within the genus. Characters must be brought forth which serve to objectively characterize taxa. Therefore, a program was initiated at the 406th Medical Laboratory to establish criteria for defining fundamental, biologically distinct groups within the genus. The basic approach was to locate topotype populations and study these using different methods and techniques. The populations sought and located were those of species which appeared quite distinctive in the original descriptions and figures. Data were correlated from cytological investigations (Burch & Davis, 1967; Burch, 1968) and studies on shell morphology, embryo shell characters and intra-brood pouch development patterns of the embryo shells.

The purpose of this paper is to present detailed descriptions of the 10 taxa of *Semisulcospira* from Honshu, Japan which appear to be very distinct. Two of the 10 taxa are new. The taxa were analyzed and compared using numerous characters previously unused or not used uniformly in collating the numerous named forms of *Semisulcospira* from Japan. The utility of different characters in defining taxa is discussed.

Of primary importance is the fact that topotype populations were used to establish expanded concepts of the species by studying hitherto unrecorded ranges of variability in characters. Within the framework of cytological findings it has been possible to untangle problems involving sibling species and polymorphic forms which had escaped the notice of early authors dealing with very limited segments of the type populations.

With an expanded central or core concept of the species based on topotype populations it is more easily possible to understand the wide range of variability exhibited by other populations. Populations may be relegated to a particular species group and trends in variability may be seen for a number of characters and how these fit into an overall unified species concept.

II. MATERIALS AND METHODS

Living specimens were collected in large numbers, generally 300 to 1000 of each shell type from each population studied, in order to establish limits of variability within populations. In a few cases, a given population yielded few individuals, 3 to 20 of a desired shell type. Specimens were split into 3 groups when large numbers were available; each group had the same composition of size range of individuals. One group was placed in 70% alcohol, another was placed in culture in the laboratory, and the 3rd was boiled in commercial Clorox (5.25% sodium hypochlorite). Living adults maintained in the laboratory were used for the cytological studies mentioned previously.

Fully adult animals were desired to

obtain adequate estimates of young in the pallial brood pouch as well as adult shell characteristics and upper limits of shell size. Abbott (1952) used the largest 10% of each population in his study of *Thiara granifera*, because there was no distinctive way of telling when a snail had reached full limits of growth. He stated, "Since growth is continuous throughout the life of the individual, two factors will delimit the length of the shell - genetic and environmental." I also chose the largest 10% of the populations to characterize each taxon in terms of adult characters and to obtain embryonic shells. Measurements and observations involving adult snails were made using a series of snails selected at random from the largest 10%. The selection of an arbitrary cut-off point of 10% will be discussed later.

In almost every population a number of apical whorls were eroded from the adults. Therefore, measurements of length of shell are limited in application. Size is best discussed in terms of length of body whorl and shell width. I used the length of the body whorl to determine which specimens were in the largest 10% of the population.

All shells, adult or embryos, were treated with Clorox when only the shell characters were to be studied (a valuable method of Walter, 1962). Since adult shells were frequently covered with algae or caked with hard, black deposits, such treatment aided in removal of the periostracum with adhering artificial deposits, and all animal remains. This treatment left a perfectly clean shell where all details of sculpture, shell banding and true color could be clearly seen.

Lengths and widths of shells were recorded along with spire increment angles, numbers of whorls, ribs and basal cords, lengths and widths of apertures, lengths of body whorls, presence or absence of nodes on the ribs and shell color patterns. Methods of measuring several of these characters are presented below.

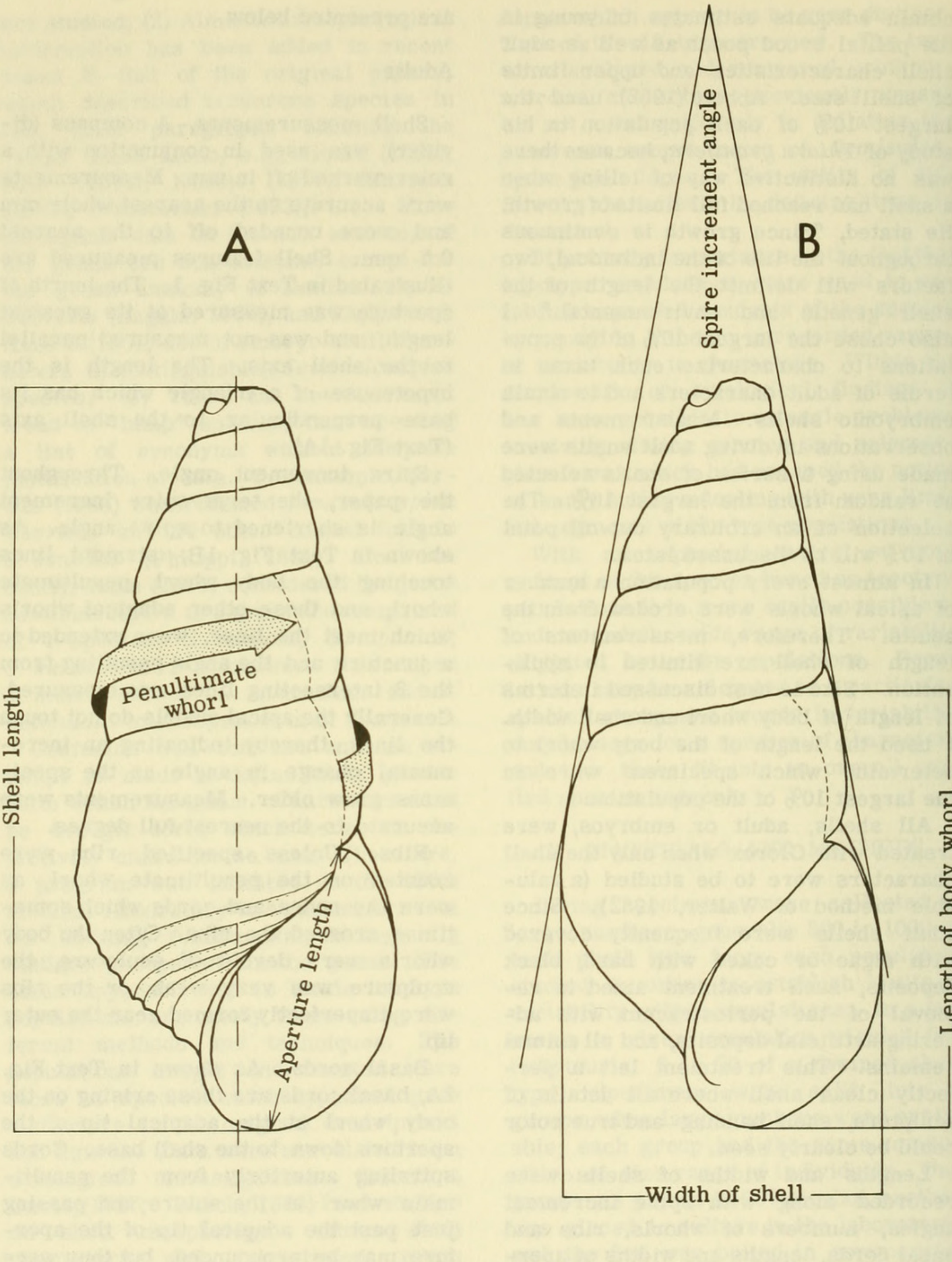
Adults

Shell measurements. A compass (divider) was used in conjunction with a ruler marked off in mm. Measurements were accurate to the nearest whole mm and were rounded off to the nearest 0.5 mm. Shell features measured are illustrated in Text Fig. 1. The length of aperture was measured at its greatest length, and was not measured parallel to the shell axis. The length is the hypotenuse of a triangle which has its base perpendicular to the shell axis (Text Fig. 1A).

Spire increment angle. Throughout the paper, the term spire increment angle is shortened to spire angle. As shown in Text Fig. 1B, straight lines touching the body whorl, penultimate whorl, and those other adapical whorls which meet the lines, were extended to a juncture and the angle resulting from the 2 intersecting lines was measured. Generally the apical whorls do not touch the lines, thereby indicating an incremental change in angle as the specimens grow older. Measurements were accurate to the nearest full degree.

Ribs. Unless specified, ribs were counted on the penultimate whorl, as were the nodes and cords which sometimes crossed the ribs. Often the body whorls were devoid of sculpture, the sculpture was very weak, or the ribs were imperfectly formed near the outer lip.

Basal cords. As shown in Text Fig. 1A, basal cords are those arising on the body whorl at the adapical tip of the aperture down to the shell base. Cords spiraling anteriorly from the penultimate whorl at the suture and passing just past the adapical tip of the aperture may be pronounced, but they were considered to belong to the cords counted on the penultimate whorl. Basal cords were counted at magnifications of 6× and 16×.



TEXT FIG. 1. Diagrams illustrating methods of making adult shell measurements of Japanese *Semisulcospira* species.

Embryos

The study of embryonic shells involved establishing the number of young per pallial brood pouch, i.e., young per female, and finding the percentage of young at each whorl stage. In addition, shell lengths and widths, as well as lengths of body whorls were measured, and the points on the apical whorls where ribs first started, as well as the number of ribs per first ribbed volution, were recorded. Also, features of shell sculpture and the color patterns of the shells were analyzed.

To obtain the young, specimens were chosen at random from the largest 10% of the populations which had been preserved in alcohol. The individual adult shells were cracked off and the pallial brood pouches were dissected out entire, care being taken not to lose any of the embryos. The individual brood chambers were placed in separate vials filled with Clorox. This resulted in the oxidation of all tissues and eggs, leaving only the shells from the earliest to the later stages. The cleaned embryonic shells were washed in alcohol and stored in clear water (slightly basic) until they were studied.

Embryos were studied under the dissecting microscope at magnifications of 16× and 40×. Measurements were made with a standard ocular micrometer and were accurate to 0.024 mm.

Whorls were counted, as discussed by Davis (1967a), to the nearest 0.5 whorl. Shells appearing to be an intermediate +.25 or +.75 whorls were not used for measurements. Embryos were not studied or measured from just 1 female of a taxon, but from as many as possible.

III. HABITATS AND FAUNAL ASSOCIATIONS

Collection sites are shown in Text Figs. 2-4. I attempted to obtain as many topotypes as possible from the Lake Biwa region because this area is noted for its high endemicity and because several species of *Semisulcospira* described from this area appeared to be quite distinct.

Station 1 (Text Fig. 2). Topotypes of *Semisulcospira niponica*.

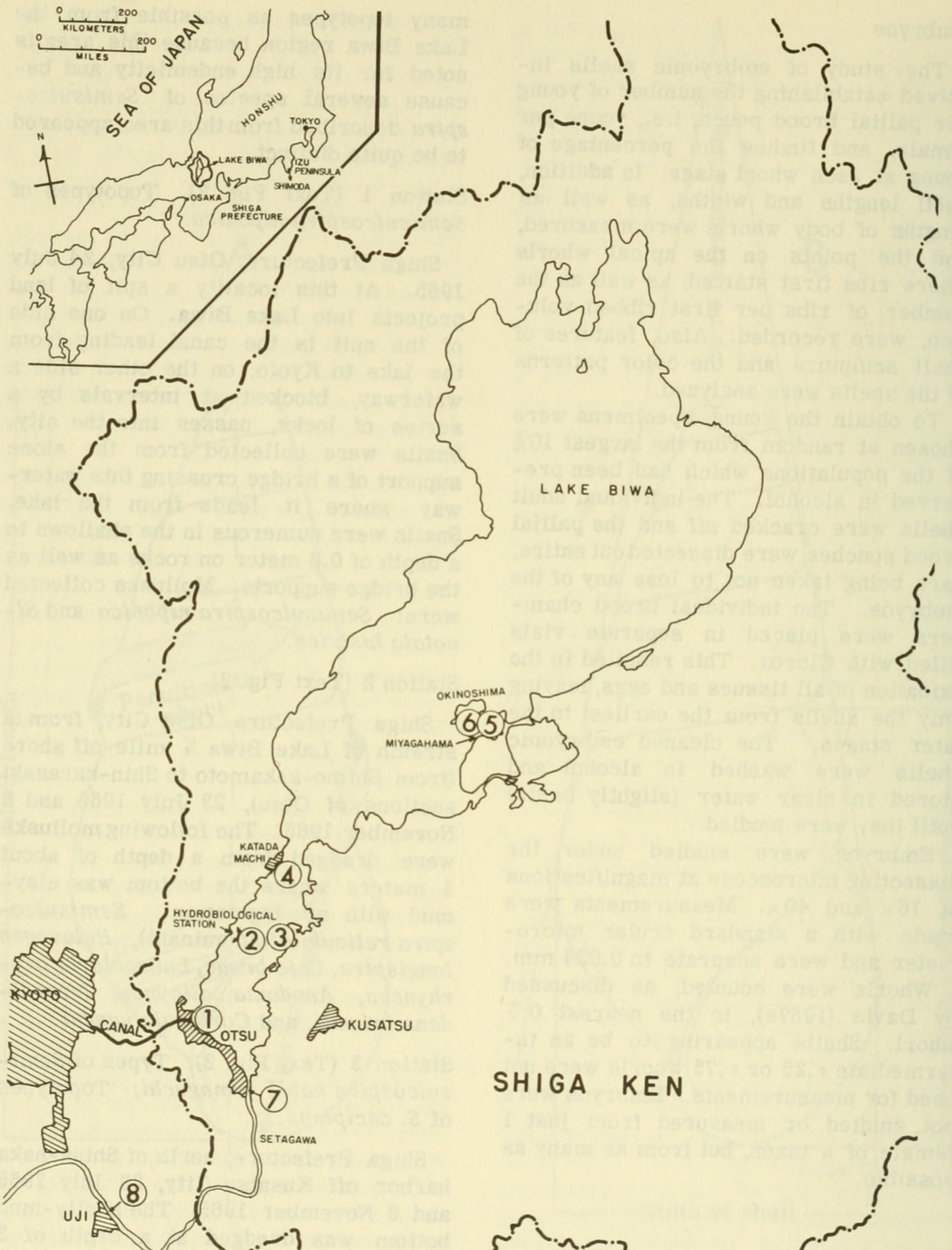
Shiga Prefecture, Otsu City, 24 July 1965. At this locality a spit of land projects into Lake Biwa. On one side of the spit is the canal leading from the lake to Kyoto; on the other side a waterway, blocked at intervals by a series of locks, passes into the city. Snails were collected from the stone support of a bridge crossing this waterway where it leads from the lake. Snails were numerous in the shallows to a depth of 0.6 meter on rocks as well as the bridge supports. Mollusks collected were: *Semisulcospira niponica* and *Sinotaia histrica*.

Station 2 (Text Fig. 2).

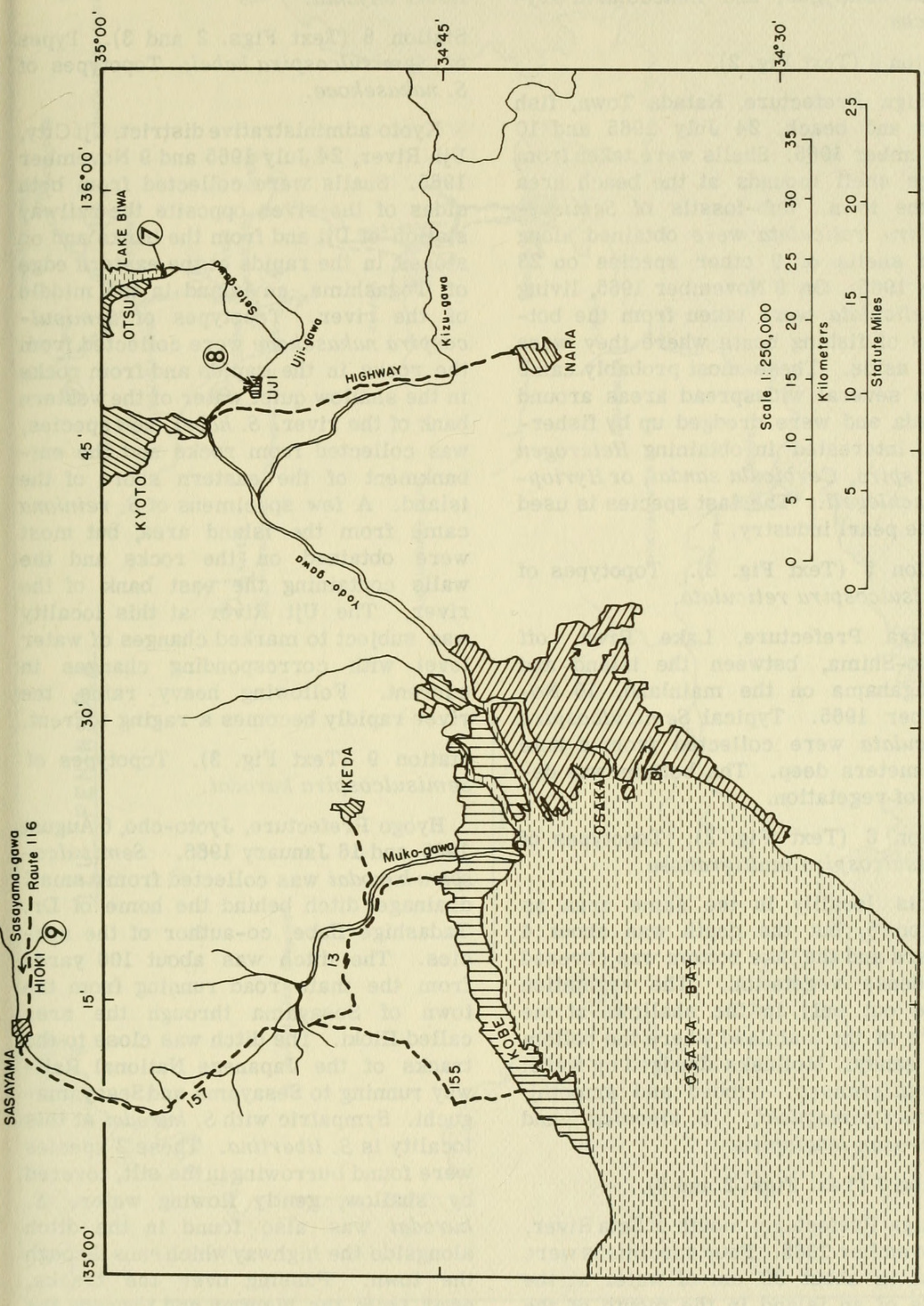
Shiga Prefecture, Otsu City, from a stretch of Lake Biwa ¼ mile off shore (from Shimo-sakamoto to Shin-karasaki sections of Otsu), 23 July 1965 and 8 November 1965. The following mollusks were dredged from a depth of about 4 meters where the bottom was clay-mud with no vegetation: *Semisulcospira reticulata* (dominant), *Heterogen longispira*, *Unio biwae*, *Lanceolaria oxyrhyncha*, *Anodonta calipygos*, *Inversidens brandti*, and *Corbicula sandai*.

Station 3 (Text Fig. 2). Types of *Semisulcospira habei yamaguchi;* Topotypes of *S. decipiens*.

Shiga Prefecture, north of Shina-naka harbor off Kusatsu City, 23 July 1965 and 8 November 1965. The shelly-mud bottom was dredged at a depth of 3 meters. Vegetation was sparse. Mollusks collected were: *Semisulcospira decipiens* (dominant), *S. habei yamaguchi*, new subspecies (sparse), *S. multigranosa* (smooth form), *Corbicula sandai* (dominant), *Unio biwae* (dominant),



TEXT FIG. 2. Map of Shiga Prefecture and surrounding area showing collecting stations in and near Lake Biwa. The heavy broken line shows the limits of the prefecture. The location of this prefecture on Honshu I. is shown in the inset.



TEXT FIG. 3. Map of the area southwest of Lake Biwa showing collecting stations 7, 8 and 9.

Inversidens reiniana, *I. brandti*, *Anodonta calipygos*, and *Lanceolaria oxyryncha*.

Station 4 (Text Fig. 2).

Shiga Prefecture, Katada Town, fish pier and beach, 24 July 1965 and 10 November 1965. Shells were taken from large shell mounds at the beach area of the town. Sub-fossils of *Semisulcospira reticulata* were obtained along with shells of 9 other species on 23 July 1965. On 8 November 1965, living *S. reticulata* were taken from the bottoms of fishing boats where they were cast aside. These most probably came from several widespread areas around Katada and were dredged up by fishermen interested in obtaining *Heterogen longispira*, *Corbicula sandai*, or *Hyriopsis schlegeli*. The last species is used in the pearl industry.

Station 5 (Text Fig. 2). Topotypes of *Semisulcospira reticulata*.

Shiga Prefecture, Lake Biwa, off Okino-Shima, between the island and Miyagahama on the mainland, 10 November 1965. Typical *Semisulcospira reticulata* were collected from a hole 6-7 meters deep. The bottom was devoid of vegetation.

Station 6 (Text Fig. 2). Topotypes of *Semisulcospira multigranosa*.

This locality is the same area as Station 5, but the depth was about 4 meters and the lake bottom was covered by dense vegetation. The vegetation faded out only in the shallows at the shore of the mainland where the bottom was sandy. Mollusks dredged up were: *S. multigranosa* (ribbed and smooth), *S. habei yamaguchi*, *S. niponica* and *Heterogen longispira*.

Station 7 (Text Figs. 2 and 3).

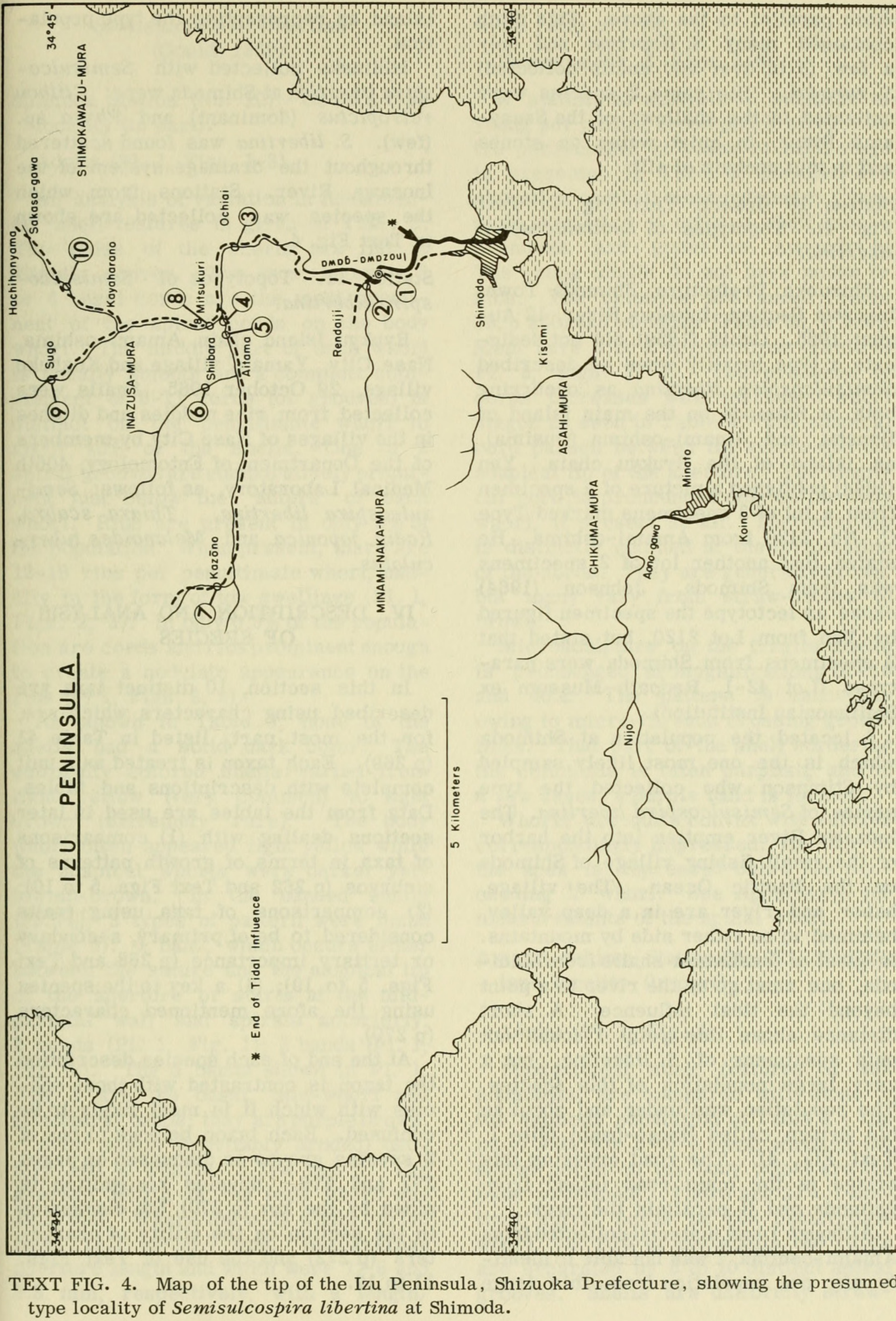
Shiga Prefecture, mouth of Seta River, 9 November 1965. Four specimens were found in about 30 cm of water at the banks of an island in the mouth of the river. Three of these were *Semisulcospira habei yamaguchi*, the 4th was *Radix onychia*.

Station 8 (Text Figs. 2 and 3). Types of *Semisulcospira habei;* Topotypes of *S. nakasekoae*.

Kyoto administrative district, Uji City, Uji River, 24 July 1965 and 9 November 1965. Snails were collected from both sides of the river opposite the railway station of Uji and from the banks and on stones in the rapids at the eastern edge of Togashima, an island in the middle of the river. Topotypes of *Semisulcospira nakasekoae* were collected from the rocks in the rapids and from rocks in the shallow quiet water of the western bank of the river. *S. habei*, new species, was collected from rocks and the embankment of the eastern shore of the island. A few specimens of *S. reiniana* came from the island area, but most were obtained on the rocks and the walls containing the east bank of the river. The Uji River at this locality was subject to marked changes of water level with corresponding changes in current. Following heavy rains, the river rapidly becomes a raging torrent.

Station 9 (Text Fig. 3). Topotypes of *Semisulcospira kurodai*.

Hyogo Prefecture, Jyoto-cho, 6 August 1965 and 16 January 1966. *Semisulcospira kurodai* was collected from a small drainage ditch behind the home of Dr. Tadashige Habe, co-author of the species. The ditch was about 100 yards from the main road running from the town of Sesayama through the area called Hioki. The ditch was close to the tracks of the Japanese National Railway running to Sesayama and Sesayama-guchi. Sympatric with *S. kurodai* at this locality is *S. libertina*. These 2 species were found burrowing in the silt, covered by shallow, gently flowing water. *S. kurodai* was also found in the ditch alongside the highway which runs through the town. Passing over the tracks, away from the highway and towards the Sesayama River, is another drainage



TEXT FIG. 4. Map of the tip of the Izu Peninsula, Shizuoka Prefecture, showing the presumed type locality of *Semisulcospira libertina* at Shimoda.

ditch parallel to the above. This ditch contained many *S. libertina* and only a few (3 in over 100 snails collected) *S. kurodai*. The same 2 species were collected in the shallows of the Sesayama River, in quiet water on stones and in thin pockets of silt.

Station 10 (insert, Text Fig. 2; Text Fig. 4). Topotypes of *Semisulcospira libertina*.

Shizuoka Prefecture, Shimoda Town, Inozawa Section, Inozawa River, 12 August 1965. Gould (1859) did not designate a type locality when he described *Semisulcospira libertina* as occurring both at Shimoda on the main island of Honshu, and Amami-oshima (Ousima), an island of the Ryukyu chain. Yen (1944) published a picture of a specimen from a lot of 3 specimens marked Type C, No. 2120 from Amami-oshima. He stated that another lot of 2 specimens was from Shimoda. Johnson (1964) chose as lectotype the specimen figured by Yen from Lot 2120, but stated that 2 specimens from Shimoda were paratypes (Lot 42-1, Redpath Museum ex Smithsonian Institution).

I located the population at Shimoda which is the one most likely sampled by Stimpson who collected the type series of *Semisulcospira libertina*. The Inozawa River empties into the harbor of the small fishing village of Shimoda on the Pacific Ocean. The village, habor and river are in a deep valley, hemmed in on either side by mountains. In quest of freshwater snails from Shimoda, one must go up the river to a point beyond the tidal influence. A short distance above this point I found not only specimens of *S. libertina*, but a very large population of this species. The population was under and about an old bridge called Hongo-bashi (Site 1, Text Fig. 4). The road crossing this bridge is the main road inland from Shimoda and it parallels the river.

Although I had material collected from Amami-oshima, I was not able to identify any one population from this large island as representing the type population.

Mollusks collected with *Semisulcospira libertina* at Shimoda were: *Clithon retropictus* (dominant) and *Physa* sp. (few). *S. libertina* was found scattered throughout the drainage system of the Inozawa River. Stations from which the species was collected are shown in Text Fig. 4.

Station 11. Topotypes of *Semisulcospira libertina*.

Ryukyu Island chain, Amami-oshima, Nase City, Yamato village and Koshuko village, 29 October 1965. Snails were collected from rice paddies and ditches in the villages of Nase City by members of the Department of Entomology, 406th Medical Laboratory, as follows: *Semisulcospira libertina*, *Thiara scabra*, *Radix japonica* and *Melanoides tuberculatus*.

IV. DESCRIPTION AND ANALYSIS OF SPECIES

In this section, 10 distinct taxa are described using characters which are, for the most part, listed in Table 41 (p 269). Each taxon is treated as a unit complete with descriptions and tables. Data from the tables are used in later sections dealing with (1) comparisons of taxa in terms of growth patterns of embryos (p 262 and Text Figs. 5 to 10); (2) comparisons of taxa using traits considered to be of primary, secondary or tertiary importance (p 268 and Text Figs. 5 to 19); (3) a key to the species using the afore mentioned characters (p 270).

At the end of each species description the taxon is contrasted with those species with which it is most likely to be confused. Each taxon belongs to one of 2 species groups as discussed on pages 272 and 279. Species recognition is aided by the key (p 270), the discussion in the section on the utility of characters (p 272) and the use of Text Figs. 11 to 19.

Semisulcospira libertina (Gould, 1859)

Shimoda Station (No. 10) - Gould's type locality (in part).

Adults (Pl. 1, Figs. 1-3)

An analysis of variation in fundamental shell features is given in Table 2. The sides of the whorls are flat to slightly convex. The most anterior 3 or 4 basal cords are the most prominent of the spiral cords on the body whorl. The middle part of each whorl is usually smooth and a complete complement of 8-11 cords (or grooves) is distinct on the penultimate whorl in about 10% of the shells. One or 2 spiral grooves are comparatively prominent just below the suture of each whorl. Ribs are present in only 3% of the population. When present, there are 12-18 ribs per penultimate whorl, usually in the form of low swellings (Pl. 1, Figs. 2, 3). In only 0.5% of the population are cords and ribs prominent enough to create a nodulate appearance on the ribs (Pl 1, Figs. 2, 3).

As shown in Table 3, none of the shells had a solid dark color. The uniformly colored shells varied from light yellow (very common) to light brown (extremely rare). The body whorl often appeared light yellow while the adapical whorls were darker yellowish-brown. In the banded shells (39.5%), 3 types of pattern were found (Table 3): 1 band, which occurs either between the suture and the adapical tip of the aperture or starts at the mid-parietal wall and spirals anteriorly; 2 bands (Pl. 1, Fig. 1); 3 bands (Pl. 1, Fig. 2). The 3 bands shown in Pl. 1, Fig. 2 are the basal, mid-whorl and subsutural bands; they are purple brown.

Adult shells (inevitably eroded) usually had 4 whorls, a few had 5. The average length of the body whorl was 19.2 mm. Where the body whorl varied from 18.7 to 19.7 mm, the average aperture length and width were 12.8 and 7.3 mm, respectively, with a length/width ratio of 1.75.

Embryos (Pl. 8, Figs. 1-5)

A statistical analysis of numbers of young per pallial brood pouch along with the percentages of young at each stage is presented in Table 5; included are statistics on shell measurements. Complete statistics of embryo shell measurements are given in Appendix 1. The young shells do not have nodes or ribs. The embryos are small (Table 38, p 260) and elongate (Table 40, p 266). Most have 1 or 2 spiral cords (Table 4; Pl. 8, Figs. 2, 3). The presence of cords increases with increased whorl stages as seen in Table 4. The adapical cord passes between the suture and the adapical tip of the aperture. The abapical cord is pronounced only on the body whorl, if present at all. The outer lip is distinctly notched at the termination of the cords. They are generally brown, but many vary from straw-yellow to brown.

Microsculpture on the fragile shells is pronounced at magnifications of 16 and 40X. The pattern is cancellate owing to micro-threads crossing growth lines. That part of the shell bordering the columella is often purplish, and in a few cases, a purple band is formed.

Whorls are quite convex with sutures correspondingly impressed. The tip of the apex is depressed below the succeeding ¼ whorl. See Appendix 2 for measurements of the apical whorl.

Amami-oshima Station (No. 11) - Gould's type locality (in part).

Adults (Pl. 1, Fig. 4)

Fundamental shell features of this population are compared with those of the Shimoda population in Table 2. The most anterior 3 or 4 basal cords of the spiral cords on the body whorl are the most prominent. There are 11 ± 1 distinct spiral cords on the penultimate whorl. In 20% of the shells the cords are separated by 8 to 10 distinct spiral grooves. Shells are uniformly straw-

PLATE 1. Adult shells of 2 species of *Semisulcospira*. The measurement line is in mm.

FIGS. 1-3. *Semisulcospira libertina* (Gould) from Shimoda. Note faint ribs on the specimen in Fig. 1.

FIG. 4. *Semisulcospira libertina* (Gould) from Amami-oshima. The spiral cords are more pronounced than in specimens of the same species from Shimoda.

FIGS. 5, 6. *Semisulcospira reiniana* (Brot).

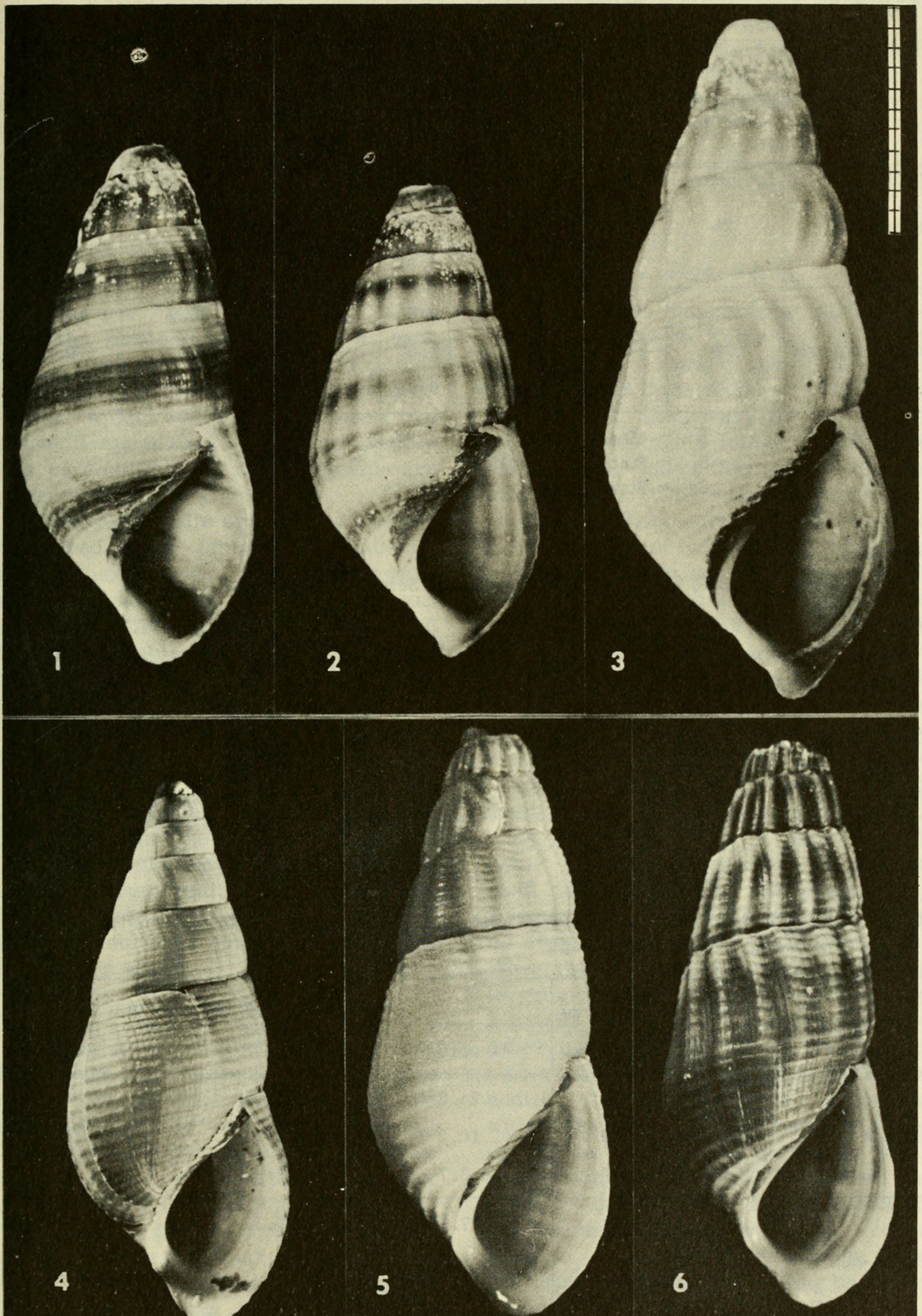

1
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TABLE 2. Adult shells; a statistical analysis of shell features of *Semisulcospira libertina*

Locality	Number specimens examined	Statistic	Feature measured or counted					
			Spire angle	Ribs	Basal cords	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
Shimoda	25	$\bar{X}$	22.2°	*	9.2	19.2	28.6	13.0
		S	3.1		1.6	1.7	--	1.3
		Se	0.63		0.31	0.33	--	0.26
Amami-oshima	25	$\bar{X}$	22.6	0	9.5	16.3	26.0	11.0
		S	2.3	—	1.3	0.9	--	0.7
		Se	0.46	--	0.03	0.19	--	0.15

* see text

$\bar{X}$ = Mean
S = Standard deviation
Se = Standard error of the mean

TABLE 3. Color patterns of adult *Semisulcospira libertina*

Locality	Number specimens examined	Color pattern (% of shells)				
		Uniform yellow	Uniform purple	1 band	2 bands	3 bands
Shimoda	200	60.5	0	9.0	15.5	15.0
Amami-oshima	50	100	0	0	0	0

TABLE 4. The number and frequency of occurrence of cords on embryos of *Semisulcospira libertina* at each whorl stage

Locality	Whorl stage	No. embryos examined	% of shells		
			0 cords	1 cord	2 cords
Shimoda	2.0	1271	24.3	47.0	28.7
	2.5	629	10.2	29.1	60.7
	3.0	27	3.7	25.9	70.4
Amami-oshima	2.0	441	27.9	72.1	0.0
	2.5	101	8.9	91.1	0.0
	3.0*	--	--	--	--

* insufficient embryos for study

yellow (Table 3); no banded shells were found.

Adult shells (eroded) had 5 ± 1 whorls. The average length of the body whorl was 16.3 mm. Where the body whorl varied from 18.7 to 19.7 mm, the average length and width of their apertures was 11.1 and 6.4 mm, respectively, with a length/width ratio of 1.73.

Embryos (Pl. 8, Figs. 6-10)

A statistical analysis of the numbers of young per pallial brood pouch, along with the percentages of young at each whorl stage, is presented in Table 5, including statistics on shell measurements. Apical whorl measurements are given in Appendix 2. Complete statistics of embryo shell measurements are given in Appendix 1.

Embryonic shells are similar to those described from females at Shimoda, with the exception of details concerning cords, apical whorl measurements and microsculpture. None of the shells had 2 cords (Table 4). The single cord becomes more evident on shells of 2½ to 3 whorls. The apical whorl has an average diameter of 0.47 mm, which is significantly smaller than that of the Shimoda snails (P = 0.01). The tip of the apex is either emergent or suppressed below the following ¼ whorl. The microsculpture is limited to growth lines (at magnification of 16 and 40X). The distinct spiral threads described for the embryos from the Shimoda population are absent.

Comparison of species

Semisulcospira libertina may be confused with *S. reiniana*. The populations of the former which have nodulate ribs (see p 270) appear very much like adult *S. reiniana*. The taxa differ in that the former has a chromosome number of n=18 while the latter has n=20. The embryos of the former are very significantly smaller than are those of the latter (Table 38). It is evident in Text Fig. 5 that the taxa differ in the slope of the curve for shell length per whorl. Embryos of *S. libertina* are smooth or with nodes (p 274), while those of *S. reiniana* have pronounced ribs. Further differences are evident in Text Figs. 7 and 9 involving growth characteristics of the embryos.

Semisulcospira reiniana (Brot, 1876)

Station 8

Adults (Pl. 1, Figs. 5 & 6)

Statistics on fundamental shell features are given in Table 6. The most anterior 3 or 4 basal cords of the spiral cords on the body whorl are especially pronounced. Ribs vary in prominence from low to highly folded pleats; they are nodulate where they are crossed by spiral cords. The suture is scalloped where the whorl curves around the rib of the adjacent adapical whorl. The ribs tend to fade out on the body whorl near mid-whorl (indicating full adult status); they are not prominent for about ½ whorl back from the aperture.

There are 11.0 ± 1.66 (mean and standard deviation) spiral cords on the penultimate whorl. In 8% of the population raised cords are not as pronounced as inter-cord grooves, of which there are 8-11 on the penultimate whorl.

As seen in Table 7, there are 5 color patterns. Generally, when the shell is uniform blue or blue-purple, 2 bands, the apical one the wider, can be seen on the inside of the outer lip. When the external shell has 1 band, it is generally found at mid-whorl. When 2 purple bands are seen they are separated by a narrow yellow belt above mid-whorl. In the case of 3 bands, in addition to the subsutural band, the wide basal band (of the 2-banded condition) is divided by a yellow belt.

Following the shell coil back from the aperture one observes that the bands do not become evident for ⅕ to ⅓ of a volution. The yellow of the lip edge protrudes between the 2 fading bands as a V-shaped wedge or squarish notch. Spiral cords stand out white against the

TABLE 5. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira libertina*

Locality	Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl counts				
				<2.0	2.0	2.5	3.0	3.5
Shimoda	11	X̄, 351.6	Shell length		0.95	1.16	1.35	--
		S, 241.7	Shell width		0.74	0.84	0.93	--
		Se, 72.9	Body whorl L.		0.78	0.90	0.99	--
			Ratio L/W		1.28	1.38	1.45	
		Range 168-979	% total embryos	47.6	35.6	16.1	0.7	
Amami-oshima	11	X̄, 229.4	Shell length		0.92	1.18	1.39	--
		S, 84.4	Shell width		0.74	0.84	0.99	--
		Se, 25.5	Body whorl L.		0.78	0.96	1.08	--
			Ratio L/W		1.24	1.40	1.40	
		Range 137-384	% total embryos	76.6	18.3	4.9	0.2	

X̄ = mean
S = standard deviation
Se = standard error of the mean
L = length
W = width

TABLE 6. Adult shells, a statistical analysis of shell features of *Semisulcospira reiniana*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords*	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
25	X̄	20.6°	16.0	8.3	17.9	26.1	11.1
	S	3.36	1.63	1.23	1.43	--	0.74
	Se	0.67	0.33	0.25	0.29	--	0.15

X̄ = mean
S = standard deviation
Se = standard error of the mean

TABLE 7. Color patterns of adult *Semisulcospira reiniana*

Number specimens examined	Uniform blue or purple-blue	Uniform yellow	1 band	2 bands	3 bands
110	21.8%	26.4%	1.8%	36.4%	13.6%

TABLE 8. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira reiniana*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl counts				
			< 2.0	2.0	2.5	3.0	3.5
10	X̄, 138.0	Shell length		0.93	1.28	1.64	1.89
	S, 53.0	Shell width		0.78	0.97	1.19	1.29
	Se, 16.8	Body whorl L.		0.79	1.03	1.21	1.37
		Ratio L/W		1.19	1.32	1.38	1.47
	Range 74–225	% total embryos	[<2.5 (57.5)]		23.9	14.3	4.3

X̄ = mean
S = standard deviation
Se = standard error of the mean

L = length
W = width

TABLE 9. Color types of *Semisulcospira reiniana* embryos from 10 females

Embryos from each female		% of females	Color of embryos	% of embryos
All embryos 1 color		30	yellow	33
			brown	67
Embryos with 2 color types	embryos predominantly yellow	70	yellow	68
			brown	32
	embryos predominantly brown		yellow	29
			brown	71

dark bands or uniformly dark shells. This gives the ribs a white-nodulate appearance.

Shells were predominantly 4 whorled (eroded) although a few had 3 or 5 whorls. The average shell length and width was 26.1 and 11.1 mm, respectively. The body whorl averaged 17.9 mm in length. Where the length of body whorl varied from 17.4 to 18.4 mm, the average aperture length and width were 11.7 and 6.3 mm respectively, with a length/width ratio of 1.85.

Embryos (Pl. 8, Figs. 11-15)

Statistics on numbers of young per pallial brood pouch along with the percentage of young at each whorl stage are presented in Table 8; included are statistics on shell measurements. Data of use for performing analyses of variance of shell measurements are given in Appendix 1. Measurements of the apical whorl are given in Appendix 2.

Shells reach 3.5 whorls in the brood pouch, are predominantly ribbed and have a pronounced cord at mid-whorl. They are medium sized (Table 38, p 260) and elongate (Table 40, p 266). Ribs (Appendix 2) first appear at 2¼ to 2½ whorls. In 2% or less, ribs appear as early as 1¾ whorls or as late as 3¼ whorls. Early ribs have a diameter of 0.12 - 0.17 mm; they are more pronounced at mid-whorl where they are thicker and jut out more. Ribs at mid-whorl generally have pronounced nodes. Twenty per cent of the shells of 3 or more whorls lacked ribs.

On dark shells, the cords stand out as a darker purple-brown. On lighter shells the cords are slightly darker than the background color. The frequency of occurrence of cords on embryos of different whorl stages is given in Table 10. Two spiral cords are more in evidence in shells of 2½ whorls than in those of later whorl stages. The first indication of ribs is generally seen as nodes on the adapical cord. This adapical cord at the whorl shoulder disappears at 3 to 3½ whorls. The cord at mid-whorl on the body whorl may be nodulate owing to the termination of ribs on this cord. In a few cases (in shells of 3.0 - 3.5 whorls) nodes on the ribs, 0.16 to 0.17 mm above the cord at mid-whorl, are connected by a cord.

Two classes of shell color were evident; (1) brown to dark reddish-brown, (2) light straw yellow to light yellow-brown. Banding patterns on the embryos were not found. In the light shells, the apical 2 whorls were generally yellowish-brown with later whorls much lighter. In light colored shells a purple patch twisted along the columella at the shell base. As shown in Table 9, all young from each female in 30% of the females were of a uniform color (brown or yellow) while young from each female in 70% of the females were mixed in color. When the embryos were mixed in color, the ratio was about 3 to 1, with one or the other color predominant. Where young from a female were uniform in color, 2/3 of the cases had dark embryos. Shells are fragile and the tip of the apex is emergent or suppressed.

Comparison of species.

See the section under *Semisulcospira libertina*.

Semisulcospira kurodai Kajiyama & Habe, 1961

Station 9, Topotypes

Adults (Pl. 2, Figs. 1-3)

Statistics on basic shell features are given in Table 11. The most anterior 2 to 4 basal cords of the spiral cords on the body whorl are generally the most pronounced. The shells are fragile and smooth with ribs occurring on only the 1 or 2 most apical whorls of the adult. When erosion of the spire of the adult shell is minimal, ribs are seen (Pl. 2, Figs. 1, 2) and these average 15 (standard deviation of 1.75 and standard error of the mean of 0.49) on the whorl where they begin to fade out. On this whorl the ribs measure 0.39 -

TABLE 10. The number and frequency of occurrence of cords on embryos of *Semisulcospira reiniana*

Whorl stage	No. embryos examined	% of shells		
		0 cords	1 cord	2 cords
2.5	25	8	48	44
3.0	25	4	76	20
3.5	25	0	80	20

TABLE 11. Adult shells; a statistical analysis of features of *Semisulcospira kurodai*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length	Shell length (mm)	Shell width (mm)
25	X̄	16.6	see text	5.1	15.2	25.6	9.1
	S	3.08		1.02	0.89	--	0.60
	Se	0.62		0.20	0.18	--	0.12

X̄ = mean
S = standard deviation
Se = standard error of the mean

TABLE 12. Color patterns of adult *Semisulcospira kurodai*

Number specimens examined	Uniform white or pale yellow	Uniform dark color	1 band*	2 bands**	3 bands***
73	15%	0	17.8%	15.1%	52.1%

* of the 17.8%, 15.0% was type 2 banding, 2.8% was type 5 (see text).
** of the 15.1%, 12.3% was type 3 banding, 2.8% was type 4 (see text).
*** of the 52.1%, 49.3% was type 1 banding, 2.8% was type 6 (see text).

0.43 mm in diameter; the whorl has an average mid-whorl diameter of 5.0 mm (with a standard deviation of 0.65 and a standard error of the mean of 0.18). The ribs rise rather abruptly from the shell surface.

Shells of this species are remarkably smooth abapical to the region of ribs. In about 56% of the population, 1 to 3 faint cords were observed just abapical to the suture (at magnifications of 5-6 ×).

As seen in Table 12, 85% of the shells were banded. The basic shell color varied from white to pale yellow. The bands varied from brown to purple-brown. Six banding patterns were encountered. (1) 3 bands (basal, mid-whorl, subsutural) as shown in Pl. 2, Fig. 1. The subsutural band was usually a very thin brown one. Often the bands at mid-whorl and base were weak and interrupted. (2) An indication of a spiral streak of brown was observed here or there on the shell at mid-whorl, subsutural area, or base. (3) Subsutural and basal bands only were found. (4) Only the subsutural and mid-whorl bands were found. (5) A distinct band at the suture spiraled anteriorly onto the mid-body whorl. (6) A subsutural band was added to the one described under 5.

Shells (eroded) had 5 ± 1 whorls. The average length and width were 25.6 and 9.1 mm, respectively. The average length of the body whorl was 15.2 mm. Where the body whorl length varied from 14.7 to 15.7 mm, the average length and width of the aperture were 9.9 and 5.6 mm, respectively, with a length/width ratio of 1.77.

Embryos (Pl. 8, Figs. 16-20)

Statistics on numbers of young per pallial brood pouch along with the percentages of young at each whorl stage are presented in Table 13; included are statistics on shell measurements. Data of use for performing analyses of variance of shell measurements are given in Appendix 1. Measurements of the apical whorl are given in Appendix 2.

Shells are glassy to opaque white; they are medium in size (Table 38) and elongate (Table 40). They typically have 2 pronounced spiral cords and are nodulate, not ribbed. The tip of the apex is not emergent but generally suppressed. The adapical cord appears at 1½ whorls on the shoulder of the whorl. Nodulation begins on this cord at 1¾ to 2 whorls and nodes average 15 on the first volution (Appendix 2). Looking down on the apex, the nodes are expanded laterally so that the cord has a scalloped appearance. On the shoulder of the whorl between the suture and the noded cord are 2 or 3 spiral threads or grooves (seen at 16× magnification). Only rarely does a node elongate into a low rib. The noded cord spirals anteriorly to form a distinct outpocketing on the outer lip about ⅓ the aperture height from the adapical tip (Pl. 8, Figs. 16-20).

In shells of 2½ whorls the abapical cord is evident only on the last half of the body whorl about 0.19 mm below the adapical cord. This also causes an outpocketing of the outer lip. In shells of 3 whorls, the 2 cords are very distinct, 0.24 - 0.31 mm apart. The abapical cord at this later whorl stage arises at the adapical tip of the aperture and spirals anteriorly (Pl. 8, Fig. 19). In 14% of the shells, a 3rd minor cord was seen between the 2 main cords; this cord was nodulate, the nodes being in line with those on the adapical cord. In a few cases the series of nodes was connected by a very low rib.

At a magnification of 16×, spiral threads or grooves are seen at mid-body whorl and near the base. These are crossed by fine growth lines. Under water and direct illumination, about 5 distinct spiral threads may be seen, looking through the aperture, on the basal portion of the body whorl, towards the outer lip. These will later become the pronounced basal cords in the adult.

A yellow or brown basal band was observed on 48% of the embryonic shells of 3 whorls; it was rarely seen on

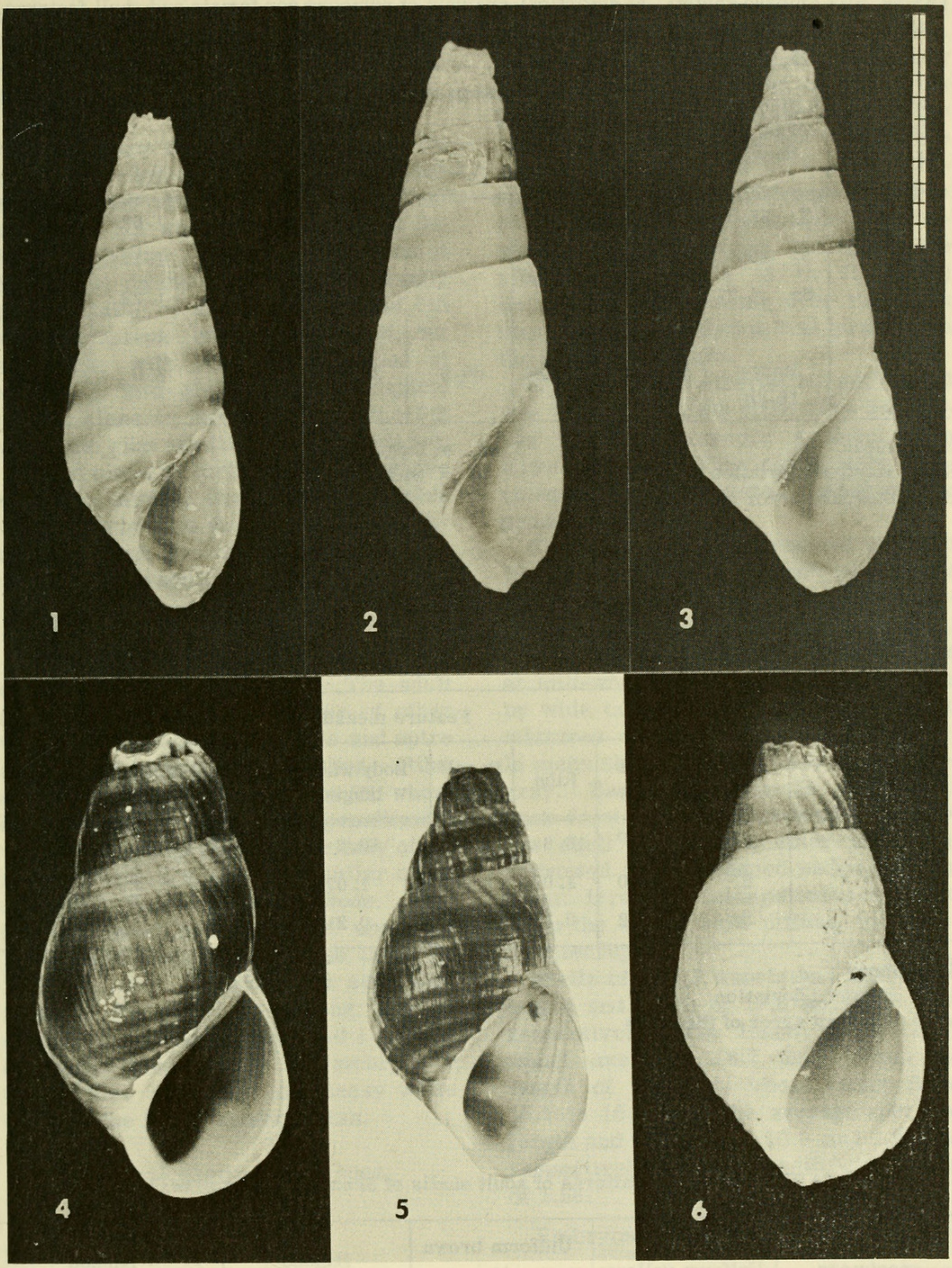

PLATE 2. Adult shells of 2 species of *Semisulcospira*. The measurement line is in mm.

FIGS. 1-3. *Semisulcospira kurodai* Kajiyama & Habe. Note how the ribs fade out on the apical whorls.

FIGS. 4-6. *Semisulcospira nakasekoae* Kuroda. The finely noded ribs of this species fade out on the penultimate whorl of fully mature specimens.

TABLE 13. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira kurodai*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl counts				
			< 2.0	2.0	2.5	3.0	3.5
13	X̄, 35.5	Shell length		0.96	1.25	1.62	--
	S, 15.4	Shell width		0.83	0.99	1.15	--
	Se, 4.27	Body whorl L.		0.81	1.02	1.23	--
		Ratio L/W		1.16	1.26	1.41	
	Range 18-66	% total embryos	60.6	20.3	13.1	6.0	0

X̄ = mean
S = standard deviation
Se = standard error of the mean
L = length
W = width

TABLE 14. Adult shells; a statistical analysis of features of *Semisulcospira nakasekoae*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length	Shell length (mm)	Shell width (mm)
25	X̄	29.1°	16.8	4.6	16.2	19.8	10.9
	S	4.10	1.07	0.86	1.07	--	0.85
	Se	0.82	0.38	0.17	0.21	--	0.17

X̄ = mean
S = standard deviation
Se = standard error of the mean

TABLE 15. Color patterns of adult shells of *Semisulcospira nakasekoae*

Number specimens examined	Uniform yellow	Uniform brown to purple-black	Banded (normal)	Banded (irregular patterns)
111	13.5	10.8	66.6	9.1

shells of 2.5 whorls although many shells of the latter had a tinge of yellow at the columellar base.

Ontogeny of Sculpture

Ribs never develop on the shells of some post-embryonic young. In these cases, nodes are present at mid-whorl up to the 5th whorl, but fade out on the 6th. In another variation, the nodes at mid-whorl on the 4th whorl are actually the summits of low ribs. By the 5th whorl ribs are more pronounced, but still low, with one spiral series of nodes at mid-whorl and an adapical series close to the suture. In the 6th whorl the ribs are the most pronounced.

A 3rd class of variants is found where ribs are narrow, long pronounced folds from whorls 5 to 8. Nodes fade out by the 7th whorl and the ribs fade out as described for adult shells.

Comparison of species

Semisulcospira kurodai is a member of the *S. libertina* complex. The adult shell is different from those of other taxa when the ontogeny of ribs and spire angle are considered together. Ribs do not develop past the 6th to 8th whorl and are not present on the penultimate whorl of mature snails. The only other species with a somewhat similar ontogeny of ribs is *S. nakasekoae*. The former taxon has a spire angle of 16.6° ± 3.08° while that of the latter is 29.1° ± 4.10°. *S. kurodai* is separated from *S. libertina* by having significantly fewer basal cords (5.10 ± 1.02 as compared to 9.2 ± 1.6). The embryos of the former are white or glassy while those of the latter are brownish.

Semisulcospira nakasekoae
Kuroda, 1929

Station 8, Topotypes

Adults (Pl. 2, Figs. 4-6)

Statistics on basic shell features are given in Table 14. Shells were very sturdy, short and with a large spire angle (29.1° ± 4°). In over 60% of the population the adults had only 2 whorls. Ribs were observed and countable only on the most apical whorl in 32% of the population. The ribs faded out on the body-whorl and often on the penultimate whorl; they averaged 0.19 mm in diameter, were low, and frequently slanted from left to right (adapical to abapical). In some young specimens the ribs were nodulate (8 to 10 nodes) owing to cords passing over them. In some cases, nodulation was present in the absence of cords.

In 28% of the shells the mid-whorl was smooth. Cords often were depressed so that intercord grooves were more evident. When cords were pronounced, 8 to 10 were counted on the penultimate whorl.

Color patterns are presented in Table 15. In "uniformly yellow" shells the apical whorl was often a darker yellow-brown than the body whorl (Pl. 2, Fig. 6). In normal banded shells a yellow stripe at mid-whorl was flanked on either side by wide colored bands (purple-brown to mixtures of blue, green and brown). In many shells the bands appeared blue-gray. Bands faded out ⅕ to ½ whorl back from the aperture where the yellow shell background color of the lip narrowed to a U-shaped wedge between them. Irregular color patterns occurred when the bands were diffuse, indistinct or interrupted.

Shells of 2 or 3 whorls had an average length and width of 19.8 and 10.9 mm, respectively. The length of the body whorl averaged 16.2 mm. When the length of the body whorl varied from 15.7 to 16.7 mm, the average aperture length and width were 10.9 and 6.9 mm, respectively, with a length/width ratio of 1.58.

Embryos (Pl. 9, Figs. 1-5)

Statistics on numbers of young per pallial brood pouch and the percentages of young at each whorl stage are given in Table 16; included are statistics on shell measurements. More complete

TABLE 16. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira nakasekoae*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count				
			< 2.0	2.0	2.5	3.0	3.5
	$\bar{X}$, 19.7	Shell length		1.14	1.59	2.28	2.99
	S, 10.1	Shell width		1.05	1.38	1.86	2.40
17	Se, 2.4	Body whorl L.		1.05	1.42	2.01	2.57
		Ratio L/W		1.09	1.15	1.23	1.25
	Range 1-35	% total embryos	56.0	15.5	15.2	11.0	2.3

$\bar{X}$ = mean L = length
S = standard deviation W = width
Se = standard error of the mean

TABLE 17. Color patterns of *Semisulcospira nakasekoae* embryo shells

Embryo whorl stage	No. embryos examined	Color type (% of embryos)			
		(1) uniform light yellow	(2) uniform dark brown	(3) sutural band weak and basal band	(4) sutural band strong and wide basal band
2.0	25	100.0	0	0	0
2.5	21	14.2	4.8	81.0	0
3.0	24	8.3	0	41.7	50.0
3.5	9	11.1	0	11.1	77.8

TABLE 18. Shell measurements (mm) of the type series of *Semisulcospira habei*

Type series	Shell		Aperture		Body whorl length	Spire angle	Ribs
	Length	Width	L	W			
Type specimen	25.5	9.8	10.7	6.3	16.3	21°	13
Paratypes 1	23.3	9.5	9.8	5.5	14.5	22°	22
2	23.8	9.6	10.3	5.6	15.2	24°	23
3	24.5	9.2	10.0	5.2	15.4	18°	22
4	27.0	10.7	10.9	7.0	17.8	16°	12

L = length
W = width

data are given in Appendix 1.

Embryo shells are large (Table 38) and globose (Table 40). The apical whorl is flat with the tip emergent, level with the whorl or suppressed. Measurements of the apical whorl are given in Appendix 2. Ribs (Appendix 2) are present but not cords. Low ribs begin at 1¾ to 2 whorls and do not become pronounced until 2½ to 3 whorls; they are not nodulate. Five to 6 spiral grooves may be seen on the base of the shell. There are 4 color patterns (Table 17); the frequency of a particular pattern definitely changes as the whorl stages increase. The light yellow shell at 2.0 whorls changes at 2.5 whorls when a faint purple band starts at the suture and spirals abapically but does not continue out on the mid-body whorl. A 2nd purple-brown basal band is seen. At 3.0 whorls and later the sutural band continues out into the mid-body whorl, the intensity in band color increases, and both bands become wider. From 8 to 14% of the shells remain yellow (Tables 15, 17). A uniformly dark embryo shell is rare.

Comparison of species

This species is a member of the *Semisulcospira niponica* species complex. It is distinguished from other species by having an extremely great spire angle ($\bar{X}$, 29.1°; Text Fig. 18), ribs which fade out on the penultimate whorl of fully mature snails, and embryos which are globose at 3.5 whorls (at which time they are liberated from the pallial brood chamber).

Semisulcospira habei, new species

Station 8, Type Population

Type series (Pl. 3, Figs. 1-3)

The type specimen (Pl. 3, Fig. 1) is a female (UMMZ 220236) with a brood pouch that contained 31 young. There are 13 paratypes (UMMZ 220237), of which 4 were cleaned in Clorox. This series is deposited in the Museum of Zoology, University of Michigan. Statistics on the type and selected paratypes are given in Table 18. The description that follows is based on data from the type series plus 12 additional snails of the same population.

Adults

Statistics on prominent adult features are given in Table 19. Ribs are more prominant than spiral cords. They are distinctly nodulate, the nodes corresponding to the points where spiral cords pass over the ribs. In many specimens cords are not present; when cords are absent, intercord spiral grooves are often seen passing over the ribs. Generally, there are 6 ± 1 spiral cords. The 3 or 4 basal cords on the body whorl are all distinct.

As shown in Table 20, there are 2 color patterns. Dark colored shells are uniform blue to blue-purple. The body whorl may be purple. In dark shells, ribs stand out owing to their white nodes (on cleaned shells). Banding is masked by the dark background color in dark shells. The outer lip is white to yellow-white. The clear area narrows like the point of a V at mid-whorl and extends back along the whorl from the outer lip often as far as ½ whorl. This divides the dark shell into 2 bands on the body whorl near the outer lip.

Looking into the aperture at the inside wall of the outer lip (sometimes seen on the exterior body whorl at the base near the lip), it can be seen that the abapical dark band is frequently split into 3-5 brown bands, each following along one of the cords (Pl. 3, Figs. 2, 3).

Most shells had 4 whorls, but a few had 3 or 5. They averaged 25.3 and 10.5 mm in length and width, respectively. The length of the body whorl averaged 16.9 mm. Where the length of body whorl varied from 16.4 to 17.4 mm, respectively, the average length and width of the aperture were 10.7 and 6.2 mm, respectively, with a length/

TABLE 19. Adult shells; a statistical analysis of features of *Semisulcospira habei*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length	Shell length (mm)	Shell width (mm)
	$\bar{X}$	18. 0	20. 8	4. 0	16. 9	25. 3	10. 5
17	S	2. 84	3. 9	0. 15	1. 70	--	1. 08
	Se	0. 68	0. 95	0. 05	0. 47	--	0. 26

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

TABLE 20. Color patterns of adult and embryo shells of *Semisulcospira habei*

% of 30 adults		% of 200 embryos*		
		yellow	dark	banded
yellow	40	58	0	42
dark	60	18	0	82

* 100 embryos from yellow adults, 100 from dark adults.

TABLE 21. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira habei*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count				
			<2. 0	2. 0	2. 5	3. 0	3. 5
	$\bar{X}$, 25. 2	Shell length		1. 21	1. 63	2. 23	2. 59
	S, 9. 85	Shell width		1. 11	1. 44	1. 79	2. 00
13	Se, 2. 73	Body whorl L.		1. 09	1. 43	1. 86	2. 09
		Ratio L/W		1. 09	1. 13	1. 25	1. 30
	Range 5-41	% total embryos	18. 0	24. 8	30. 1	17. 2	9. 8

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

width ratio of 1.73.

Embryos (Pl. 9, Figs. 6-10)

Statistics on numbers of young per pallial brood pouch and the percentages of young at each whorl stage are given in Table 21; included are statistics on shell measurements. More complete data are given in Appendix 1.

Embryo shells are sturdy, large (Table 38) and globose (Table 40). The columella has a distinctive twist at the end of the parietal wall. Abapical to this twist the columella is thickened and reflected. Apical whorl measurements are given in Appendix 2.

Ribs are prominent (Appendix 2). They begin at 1¼ whorls and are strongly nodulate or spinose on the whorl shoulder. In shells of 2½ whorls the shoulder is sharp. Beneath the spiny process on the shoulder, each rib decreases in height and generally disappears before reaching the abapical suture. In shells of 3 or more whorls, the whorls are less shouldered and more convex. On these later whorls each rib has 2 to 4 nodes, the height of each rib is 0.13 to 0.18 mm and their diameters average 0.23 mm. The greatest rib height and most pronounced node are just adapical to mid-whorl. On the body whorl, ribs fade out abruptly at mid-whorl as a node or on a spiral cord. The cord, when present, is smooth or nodulate.

The color pattern of the young appears to be influenced by the color pattern of the adult (Table 20). Embryos are either uniform yellow or banded. When bands are extremely pronounced the shells take on a purple-red shade. Some white-yellow shells have a slight purple-brown tinge to the columella and shell next to the columella.

There are 3 bands in the majority of the banded shells (Pl. 9; Figs. 9, 10): a distinct purple-brown band at the suture (0.12 mm wide); one crossing the body whorl over the ends of the ribs (or cord when it is present); and an extremely wide basal band. In some rare cases the band at mid-whorl is very faint or missing.

Discussion of the species

The low number and large size of the embryos in each pallial brood pouch and the low number of basal cords on the adult shell separate this taxon from *Semisulcospira libertina* and *S. reiniana*.

Semisulcospira habei has pronounced nodulate ribs on the penultimate whorl of the strong adult shell and embryos. *S. nakasekoae* has a shorter and stouter shell, and ribs are not pronounced on the adult body whorl or embryos. *S. kurodai* is fragile and smooth, and its embryos are without colored bands and ribs (they only have nodes). One of the morphs of *S. multigranosa* is smooth and more slender.

Semisulcospira habei adult shells have 16 to 25 ribs on the penultimate whorl (68% of the population) and each rib has 5 to 7 nodes. *S. niponica* has only 10 to 12 ribs (68% of the population), with each bearing only 3 to 4 large pustulate nodes.

Semisulcospira habei is separated from *S. reticulata* and *S. multigranosa* by a number of fundamental differences. The latter taxa have 2 to 8 embryos per brood pouch (68% of the population), while the former has 15 to 35 (68% of the population). As seen in Table 38, *S. reticulata* has much larger embryos. Adult shells of *S. reticulata* have more ribs on the penultimate whorl than *S. habei* (26 or more in 68% of the former, while 25 or less in 68% of the latter; significant difference, $P = <0.01$). Embryos of *S. multigranosa* are elongate, while those of *S. habei* are globose (Table 40). The ribbed morph of *S. multigranosa* is significantly more slender and has more ribs ($P=0.01$) than *S. habei*.

Semisulcospira habei has a mean spire angle of 18° and *S. decipiens* has a mean spire angle of 12.4° (significant difference, $P=0.01$). The former has globose embryos where the majority are banded and the latter has elongate yellow-white embryos. The embryos of *S. habei* are larger than those of *S. decipiens* (Table 38).

Semisulcospira habei is contrasted to *S. habei yamaguchi* under that subspecies (see below).

Semisulcospira habei yamaguchi, new subspecies

Station 3, Type Population; Stations 6 and 7

Type series.

The type specimen is a female (Pl. 3; Fig. 4). The shell was broken, as were the shells of the entire type series, to obtain the gonad for cytological studies. The shell, prior to breaking, consisted of 4 whorls and measured 27.5 mm long and 9.5 mm wide. The apex was eroded. There are 23 ribs on the penultimate whorl with 6 nodes per rib. The spire angle is 14°. The type series, comprising the type (UMMZ 228801) and 4 paratypes (UMMZ 228802), is deposited in the Museum of Zoology, University of Michigan. The description that follows is based on the type series and 6 additional specimens from Stations 6 and 7.

Adults (Pl. 3; Figs. 4-6)

Statistics on fundamental shell features are given in Table 22. The 2-3 basal cords of the spiral cords on the body whorl are prominent, shells are slender, and each rib on the penultimate whorl has 5 to 6 pronounced nodes. As shown in Table 23, shells are a uniform yellow or banded. Banded shells have 2 patterns: (1) a sutural band spirals out onto the mid-body whorl, (2) the same as 1, but with an additional basal band and a wide, dark sub-sutural band.

Shells had 5 ± 1 whorls with an average length and width of 27.1 and 8.7 mm, respectively. The average length of the body whorl was 13.9 mm. The whorls are slightly convex. In older adults, sculpture on the body whorl is faint or absent.

Embryos (Pl. 9, Figs. 11-15)

Statistics on numbers of young per pallial brood pouch and the percentages of young at each whorl stage are given in Table 24; included are data on shell measurements. More complete statistics on shell measurements are given in Appendix 1.

Embryo shells were found in only 3 of the 11 available snails. Shells were medium in size (Table 38) and intermediate in shape (Table 40); they were fragile. Measurements of the apical whorl are given in Appendix 2. There were spinose ribs at the whorl shoulders which began at the 1¼ to 1¾ whorl stage. There were 14 ± 1 spinose nodes on the first volution (Appendix 2); when ribs were present they faded out by mid-whorl. Several minute spiral threads or grooves passed over the ribs.

Shells were uniform glassy to white or banded (Table 23). Banding started with a sutural brownish-purple band at 2 to 2½ whorls, which spiraled anteriorly to form a distinct band at mid-body whorl. There was also an accompanying basal band appressed to the columella.

Discussion of the species

This taxon was initially confused with both *Semisulcospira decipiens* and *S. multigranosa*, with which it is sympatric. It was first distinguished when it was found that snails appearing to be *S. decipiens* had the same low chromosome number as *S. habei* (2n=17 to 20 contrasted with 2n=25 or 26 for *S. decipiens* [Burch & Davis, 1967; Burch, 1968]).

The embryos of this taxon and *Semisulcospira decipiens* were quite different than those of *S. multigranosa*. When one compares the embryos of *S. habei yamaguchi* (Pl. 9; Figs. 11-15), *S. decipiens* (Pl. 10; Figs. 6-9) and *S. multigranosa* (Pl. 11; Figs. 5-8), it is evident those of *S. multigranosa* are

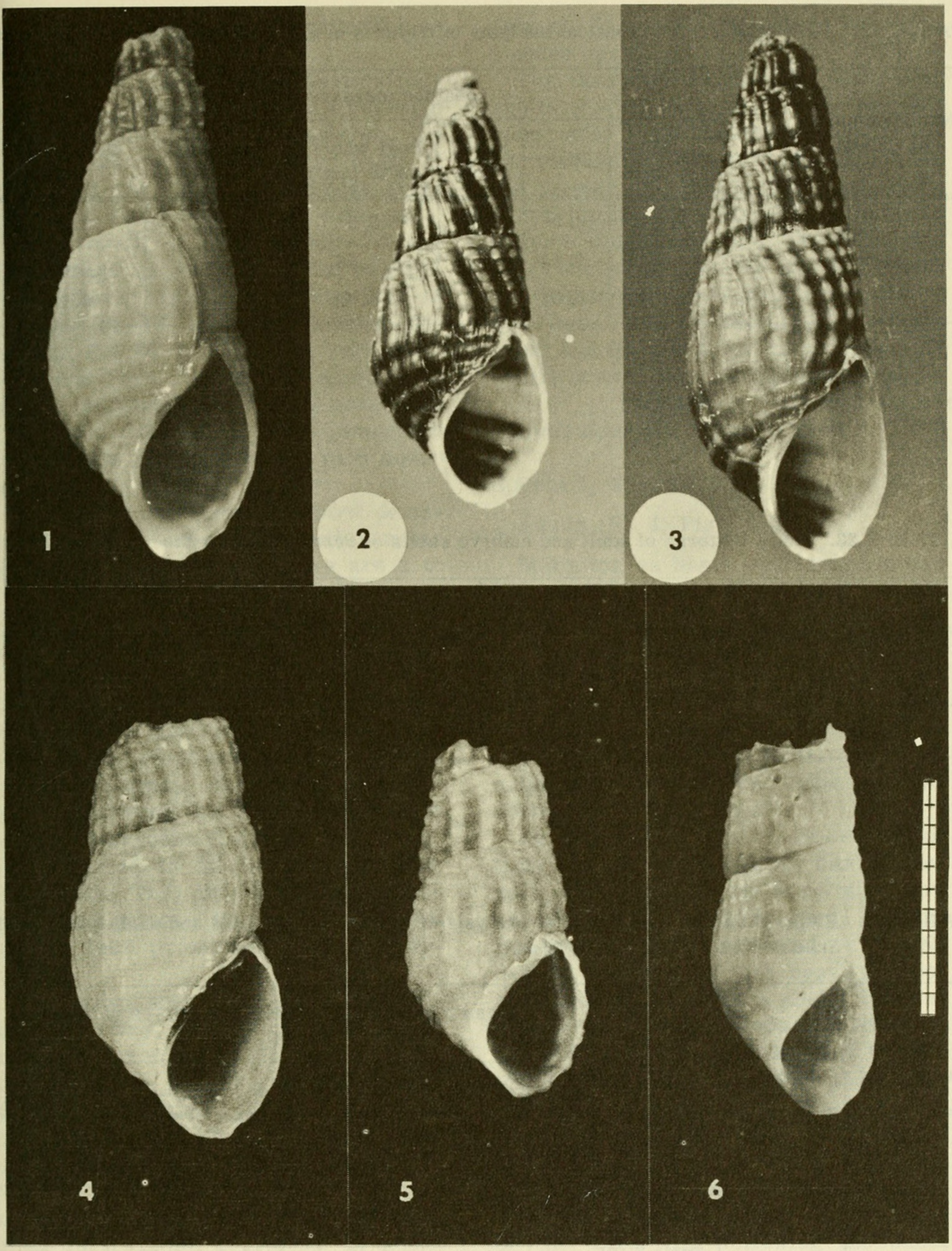

PLATE 3. Adult shells of 2 new taxa of *Semisulcospira*.
Measurement line is in mm.

FIGS. 1-3. *Semisulcospira habei* new species. Fig. 1, Holotype; Figs. 2-3, Paratypes.

FIGS. 4-6. *Semisulcospira habei yamaguchi* new subspecies. Fig. 4, Holotype; Figs. 5-6, Paratypes. Apical whorls were removed to gain access to the gonad for cytological studies (Burch & Davis, 1967).

TABLE 22. Adult shells; a statistical analysis of features of *Semisulcospira habei yamaguchi*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
11	$\overline{X}$	14.5°	18.0	2-3	13.9	27.1	8.7
	S	2.25	3.14	--	1.58	--	0.87
	Se	0.71	0.94	--	0.52	--	0.27

$\overline{X}$ = mean
S = standard deviation
Se = standard error of the mean

TABLE 23. Color patterns of adult and embryo shells of *Semisulcospira habei yamaguchi*

Adults (%)			Embryo (%)		
No.	Uniform yellow	Banded	No.	Uniform glassy-white	Banded
11	64	36	50	74	26

TABLE 24. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira habei yamaguchi*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count				
			< 2.0	2.0	2.5	3.0	3.5
3	$\overline{X}$, 17 ± 3	Shell length		1.06	1.35	1.78	2.15
		Shell width		0.96	1.15	1.35	1.56
		Body whorl L.		0.96	1.16	1.47	1.68
		Ratio L/W		1.10	1.17	1.32	1.38
		% total embryos	36.5	26.9	11.15	11.5	13.5

$\overline{X}$ = mean
L = length
W = width

much larger and more elongate (Tables 38, 40).

Adult shell features of *Semisulcospira habei yamaguchi* appear to overlap those of *S. decipiens*. However, the former has an average spire angle of 14.5° and the latter an average spire angle of 12.4° (significant difference, P=0.01 level). *S. habei yamaguchi* has an average of 18 ribs on the penultimate whorl, while *S. decipiens* has an average of 16 (not significantly different, P=0.10 level). The ribs of *S. decipiens* are, however, smooth to weakly nodulate with 7 to 8 nodes per rib, while ribs of *S. habei yamaguchi* are heavily nodulate with 5 to 6 nodes per rib.

Embryos of *Semisulcospira decipiens* and this taxon appear quite similar in size and structure. There are 2 to 3 significant differences. *S. habei yamaguchi* has a wider shell, as shown by the length/width ratios for different whorl stages (Table 40, Text Figs. 9, 10). *S. h. yamaguchi* has more ribs on the first volution of the embryonic shell (13 to 15 as compared to 10 to 12 for *S. decipiens*). Not only are the ribs more numerous, but they begin earlier on the embryonic shell (1¼ to 1¾ whorl as compared to 1¾ to 2 whorls on *S. decipiens*). They are also sharp, prominent and spinose as contrasted to the flatter, less prominent ribs of *S. decipiens*.

Until more specimens are made available for study, I am reluctant to designate this taxon as a full species. It is closely allied to *Semisulcospira habei habei* on the basis of chromosome number (2n=17 to 20) and by being present in the same drainage system (allopatric). Certain adult features appear to overlap. The spire angle of *S. h. habei* varies from 15° to 21° in 68% of the population, while that of *S. h. yamaguchi* varies from 12° to 17° in 68% of the population. However, the spire angles in the 2 populations are very significantly different (P=0.01 level). *S. h. habei* has significantly more ribs (P only at .05 level). Both taxa have 5 to 6 nodes per rib.

The taxa differ in that the embryonic shells of *Semisulcospira h. habei* are globose while those of *S. h. yamaguchi* are intermediate (Table 40). The embryos of the former are larger than those of the latter (Table 38). The columella of the latter's embryonic shell is not twisted as in the former, nor do the shells have the pronounced heavy banding peculiar to *S. h. habei*. No adult shells of *S. h. yamaguchi* had the purple or dark blue-purple shells seen in 60% of adult *S. habei*.

Semisulcospira niponica (Smith, 1876)

Station 1, Topotypes

Adults (Pl. 4; Figs. 1-3)

Statistics on basic shell features are presented in Table 25. The extremely sturdy shell has 2 basal cords on the body whorl in 92% of the population studied (77 specimens). There are 3-4 very large pustulate nodes on each rib of the penultimate whorl. Spiral cords are not in evidence except towards the outer lip, where one can count 6-8 faint cords for the body whorl.

As shown in Table 26, there were no light colored shells. In the mixed category, the apical whorls were often purple-black and the body whorl brown. Banding was not prominent or clearly defined because of the heavily noded ribs and generally dark shell. Banding was most pronounced on shells in the mixed category. Three dark brown bands (sutural, mid-whorl and basal) crossed the body whorl when banding was evident. The sutural bands on the penultimate whorl were divided by a yellow central band. Looking into the aperture, brownish bands on the inside of the outer lip following the basal cords, and 1 or 2 brownish-purple bands toward the suture (Pl. 4, Fig. 2) frequently could be observed.

Adult shells were eroded at the apex, had 3 or 4 whorls and averaged 22.8 and 10.1 mm in height and width, respec-

TABLE 25. Adult shells; a statistical analysis of features of *Semisulcospira niponica*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
	X̄	20.0	11.4	2-3	15.4	22.8	10.1
25	S	2.80	1.23	--	0.80	--	0.50
	Se	0.56	0.25	--	0.16	--	0.10

X̄ = mean
S = standard deviation
Se = standard error of the mean

TABLE 26. Color patterns of adult and embryo shells of *Semisulcospira niponica*

Adults (%)				Embryos (%)		
No.	Light-brown	Purple-black	Mixed	No.	Unbanded	3 bands
77	12.9	38.9	48.2	300	5	95

TABLE 27. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira niponica*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count				
			<2.0	2.0	2.5	3.0	3.5
	X̄, 21.6	Shell length		1.14	1.59	2.35	2.83
	S, 11.68	Shell width		1.08	1.44	1.87	2.11
14	Se, 3.12	Body whorl L.		1.04	1.42	2.01	2.30
		Ratio L/W		1.06	1.10	1.26	1.34
	Range 2-49	% total embryos	38.3	21.4	17.5	13.5	9.2

X̄ = mean
S = standard deviation
Se = standard error of the mean
L = length
W = width

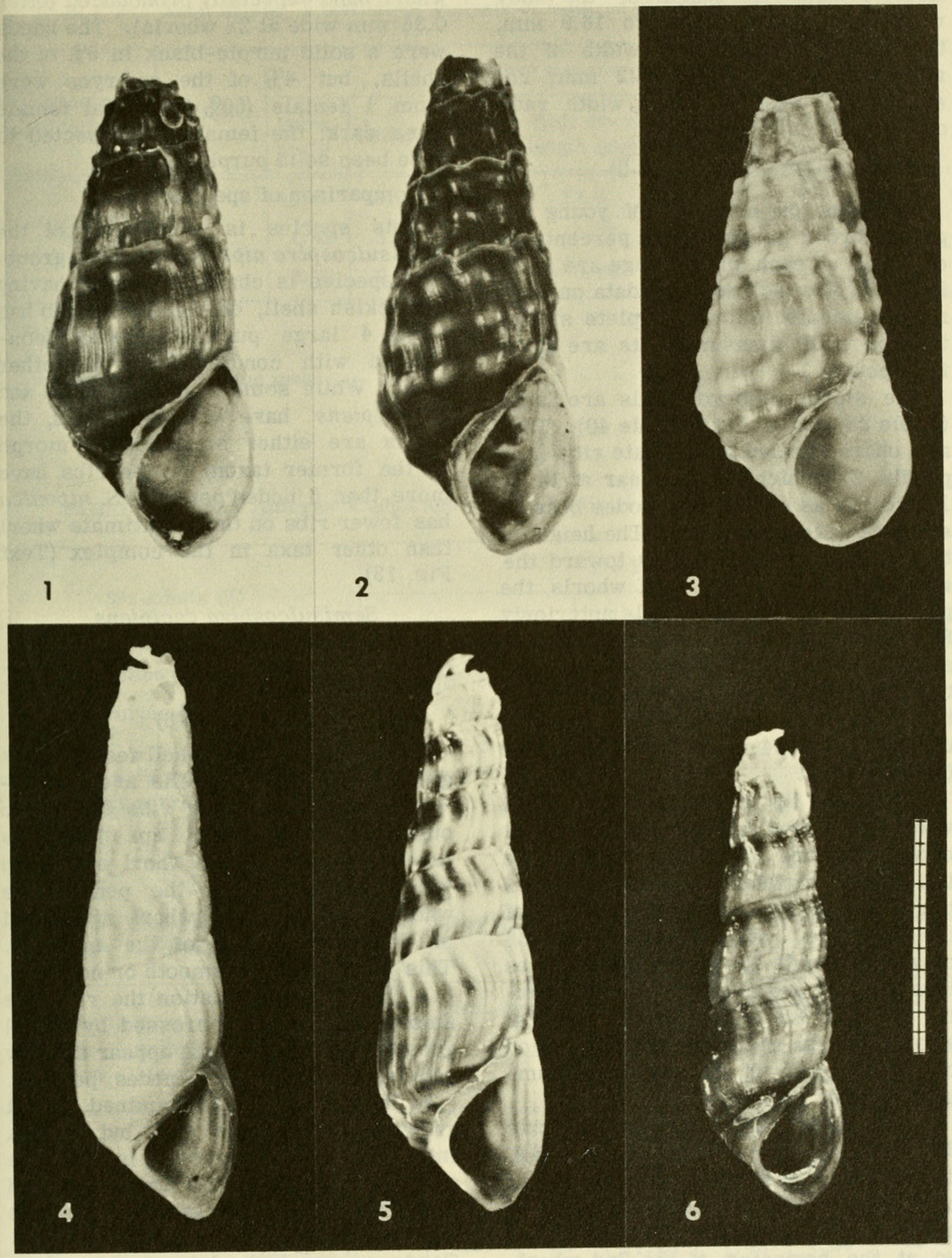

PLATE 4. Adult shells of 2 species of *Semisulcospira*. Measurement line in mm.

FIGS. 1–3. *Semisulcospira niponica* (Smith).

FIGS. 4–6. *Semisulcospira decipiens* (Westerlund).

tively. When the length of the body whorl varied from 14.9 to 16.9 mm, the average length and width of the aperature were 9.7 and 6.2 mm, respectively, with a length/width ratio of 1.56.

Embryos (Pl. 10, Figs. 1-5)

Statistics on numbers of young per pallial brood pouch and the percentages of young at each whorl stage are given in Table 27; included are data on shell measurements. More complete statistics on shell measurements are given in Appendix 1.

The sturdy embryo shells are large (Table 38) and globose (Table 40). They are characterized by nodulate ribs (Appendix 2), which first appear at 1¼ to 1½ whorls as nodes. The nodes become elongate at the 2nd whorl. The height of the ribs decreases rapidly toward the abapical whorl. In later whorls the position of the nodes spirals anteriorly from the shoulder to a mid-whorl position. In shells of 3 or more whorls, the rib is most swollen transversely at the mid-whorl region, where it has a diameter of 0.24 mm. Ribs terminate on a low cord.

The outer lip of shells with 2 to 2½ whorls is flared out and especially bent outward where the cord reaches the lip. This outfolding occurs about 1/3 the distance from the adapical tip of the aperture. Where shells have 3½ or more whorls the outfolding becomes less distinct and is often absent. Looking down on the shoulder of the apical whorls, spiral grooves can be observed on the shoulder of the whorls and running between the ribs.

Shells of 2½ whorls and larger have 3 distinct purple-brown bands (95%, Table 26); these are sutural, a slight one at mid-whorl, and a pronounced basal band. The sutural band shows up at the beginning of the 2nd whorl. The 2 apical whorls are light brown. In later whorls the shell background is white to yellow-white. In a few cases, the background is brown with the mid-whorl band especially pronounced (often 0.36 mm wide at 2½ whorls). The bands were a solid purple-black in 5% of the shells, but 4% of the embryos were from 1 female (50% from that female were dark; the female is suspected to have been solid purple-black).

Comparison of species

This species is a member of the *Semisulcospira niponica* species group. The species is characterized by having a blackish shell, on which each rib has 3 to 4 large pustulate nodes (contrasted with conditions in all other taxa). While some *S. multigranosa* and *S. decipiens* have blackish shells, the shells are either smooth (one morph of the former taxon) or the ribs have more than 6 nodes per rib. *S. niponica* has fewer ribs on the penultimate whorl than other taxa in the complex (Text Fig. 13).

Semisulcospira decipiens (Westerlund, 1883)

Station 3, Topotypes

Adults (Pl. 4; Figs. 4-6)

Statistics on basic shell features are given in Table 28. Shells are characteristically ribbed, the ribs tending to curve with the outer lip. The ribs terminate on the body whorl on a cord which spirals from the penultimate whorl onto the body whorl at a level of the adapical tip of the aperture. This cord is either smooth or nodulate. In 11% of the population the ribs are smooth and are not crossed by spiral grooves; in 89% the ribs appear slightly nodulate, with 7 or 8 nodes per rib.

In 20% of all shells examined, spiral grooves crossed the ribs, but not the inter-rib shell surface. In 69% the grooves passed across both ribs and inter-rib shell. The grooving over the ribs causes the ribs to appear nodulate. Cords appear to be lateral expansions of the nodes on the ribs. These are, on any whorl, irregularly positioned, i.e., a cord may not complete a whole volution, or all nodes on a rib may not

TABLE 28. Adult shells; a statistical analysis of features of *Semisulcospira decipiens*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs	Basal cords	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
	$\bar{X}$	12.4	16.0	2-4	13.8	26.3	8.30
20	S	1.42	3.00	--	0.73	--	0.59
	Se	0.32	0.67	--	0.16	--	0.13

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

TABLE 29. Color patterns of adult and embryo shells of *Semisulcospira decipiens*

	389 Adults (%)	173 Young* (%)		
		Uniform yellow	Uniform black	Banded
Uniform yellow	84.0	92.0	0	8.2
Uniform purple-black	3.0	43.5	0	56.5
Banded	13.0	60.0	0	40.0

* analyzed by correlation with adult color

TABLE 30. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira decipiens*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count					
			< 2.0	2.0	2.5	3.0	3.5	4.0
	$\bar{X}$, 13.8	Shell length	--	--	1.35	1.83	2.23	--
	S, 7.67	Shell width	--	--	1.08	1.28	1.42	--
31	Se, 1.38	Body whorl L.	--	--	1.30	1.53	1.85	--
		Ratio L/W	--	--	1.25	1.43	1.54	--
	Range 2-33	% total embryos	[(2.5)	32.1]	37.1	17.5	11.6	1.6

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

L = length
W = width

have lateral expansions into cords.

Shell color patterns are given in Table 29. In the category of uniform yellow, a few specimens varied from light yellow through brownish-yellow to uniform light brown. Such brown shells without banding are rare (less than 1%). Banded shells have a yellow stripe at mid-whorl flanked on either side by purplish-brown bands. The basal band on the penultimate whorl is closely appressed to the abapical suture; it continues onto the body whorl as a single band which expands to the shell's base. Variation in banding results from the varying degree in the width of each band. In some cases the central yellow stripe is very wide; in others, this spiral band is almost obliterated by the very wide flanking bands, with the result that the shell appears black. The extreme condition is a totally purple-black shell resulting from fusion of bands.

The eroded adult shells had 5 ± 1 whorls. When the length of the body whorl varied from 13.1 to 14.1 mm, the average length and width of the aperture were 8.5 and 5.0 mm, respectively, with a resulting length/width ratio of 1.70.

Embryos (Pl. 10, Figs. 6-9)

Statistics on numbers of young per pallial brood pouch and the percentage of young at each whorl stage are given in Table 30; included are data on shell measurements. More complete statistics on shell measurements are given in Appendix 1. Measurements of the apical whorls are given in Appendix 2.

The shells are characteristically medium in size (Table 38), elongate (Table 40) and fragile. Ribs are present, appearing first as low nodes on the shoulder at 1¾ whorls (Appendix 2). The nodes become elongated into ribs at the 2nd whorl. In shells of 2½ to 4 whorls the ribs do not pass across the periphery as a bar of uniform height; they are most pronounced at the shoulder where they are swollen but not spinose. Just below mid-whorl the ribs are interrupted by a distinct spiral groove 0.05 to 0.07 mm wide. The height of the rib decreases markedly, or is absent below the groove (abapically). In a few shells, ribs below the spiral groove are nodulate, the nodes expanding laterally into a spiral cord. This last feature is more characteristic of adult shells. Spiral grooves are seen at 6 to $16\times$ magnifications crossing the ribs and inter-rib shell.

The percentage of young of a given color pattern depends upon the pattern in the parent (Table 29). The darker the adult shell (banded to uniform purple-black) the greater the frequency of banded young. Banding is variable: (1) some shells have only a brownish basal band, or (2) some shells have basal and mid-whorl bands, the latter circling just abapical to the point where the ribs terminate. Some shells are uniformly brown with a darker purple-brown basal band. Where young are obtained from purple-black adults, 61% have a decidedly brown shell.

Comparison of species

Semisulcospira decipiens is a member of the *S. niponica* species group. Because of the slender shell (spire angle $12.4° \pm 1.42°$) and ribs, it may be confused with *S. multigranosa* and *S. habei yamaguchi*. It differs from the former by having fewer ribs (16.0 ± 3.0 as compared to 23.2 ± 2.4) and smaller embryos (medium size against large; Table 38, p 260). The nature of the ribs on the embryos also is different (Compare Pl. 10, Figs. 6-9 to Pl. 11, Figs. 5-8). Both taxa are polymorphic in color pattern; however, no embryos of *S. decipiens* have been found which are uniform black, which is not the case for *S. multigranosa*. *S. decipiens* does not have smooth morphs as does *S. multigranosa*.

Semisulcospira decipiens was contrasted with *S. habei yamaguchi* in the section on the latter taxon.

Semisulcospira reticulata Kajiyama and Habe, 1961

Station 5, Topotypes; Stations 2 and 4

The species concept for *Semisulcospira reticulata* described here was derived from 3 different populations. Too few specimens were collected at the type locality (Station 5) to permit adequate analysis of shell or embryos. Populations of a size adequate for analysis were sampled at stations 2 and 4. Two different growth forms were found at station 4, the differences of which are discussed below.

Adults (Pl. 5, Figs. 1 and 2; Pl. 6, Figs. 1 and 2)

There are 2 different growth forms. Type 1 is identified by shells with moderately convex whorls, where the body whorl swells noticeably outside the angle formed by preceding whorls (Pl. 6, Fig. 1). The body whorl at the suture often appears crimped inwardly, giving the shell outline an angular to undulate appearance. In this crimped area, 2 to 4 spiral cords may be rather pronounced. The body whorl often appears lighter in color, and in older specimens advanced age is shown by the lack of clearly defined sculpture.

Type 2 growth form (Pl. 6, Fig. 2) closely resembles the figured type (Kajiyama & Habe, 1961). The whorls are flat sided with only the body whorl showing a slight convexity in some cases. Sculptured ribs are pronounced on the body whorl nearly the same length as that of type 1 shells where clearly defined sculpture is lacking.

Statistics on fundamental shell features are given in Table 31. Shells of both types are extremely sturdy. Ribs are numerous, pronounced and highly nodulate, with 6 ± 1 nodes per rib. The nodes correspond to cords, which vary in prominence from pronounced to absent.

Adult color patterns are given in Table 32. Banded shells had a purplish-brown band at mid-whorl (Pl. 6, Fig. 2). The band generally fades out or is missing on the body whorl. In some older specimens, the band is missing on the penultimate whorl. A basal band is present in some younger specimens (length of body whorl, 13.5 mm).

Shells from station 2 were all Type 1; they had 4.5 ± 1 whorls. With the length of the body whorl averaging 17.0 mm, the average length and width of the aperture were 10.5 and 6.8 mm, respectively, with a length/width ratio of 1.54. Collections at station 4 were made on 24 July and 10 November, 1965. In the former collection shells were recovered from shell mounds and were sub-fossils; 76% were type 2 and 24% were type 1. These sub-fossils were considerably larger than those from station 2. Those of shell type 2 averaged 7.5 whorls. When the body whorl length varied from 17.8 to 18.8 mm, the average length and width of the aperture were 11.5 and 7.9 mm, respectively, with a length/width ratio of 1.46. Those of shell type 1 had 6 whorls. When the body length varied from 21 to 22 mm, the average length and width of the aperture were 13.5 and 4.0 mm, respectively, with a length/width ratio of 1.50.

Living material was collected from the bottoms of fishing boats at station 4 on 10 November, 1965. These were type 1 only and had 5.5 ± 1 whorls. When the length of the body whorl ranged from 18.2 to 19.2 mm, the average length and width of the aperture were 12.2 and 7.4 mm, respectively, with a length/width ratio of 1.65.

Embryos (Pl. 10, Figs. 10, 11; Pl. 11, Figs. 1-4)

Embryos from parental stock collected at station 2 were studied in detail. Statistics on numbers of young per pallial brood pouch and the percentages of young at each whorl stage are given in Table 33; included are data on shell measurements. More complete statistics on shell measurements are given in Ap-

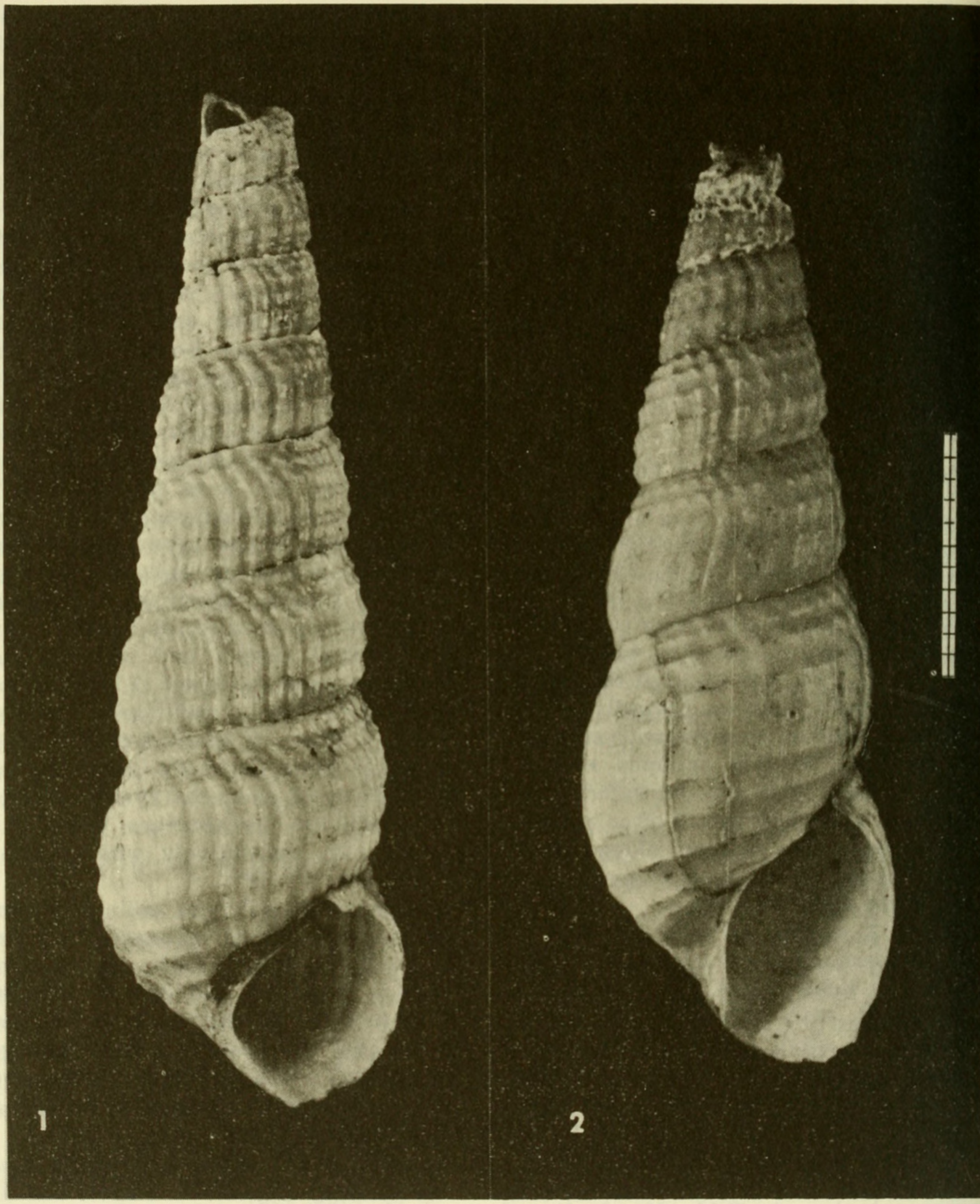

PLATE 5. Adult shells of *Semisulcospira reticulata* Kajiyama & Habe. The measurement line is in mm.

FIG. 1. Shell type 2 conforms to the "type."

FIG. 2. Shell type 2. The specimen shown is larger than that in Fig. 1 as determined by the greater length of the body whorl. Irregularity of sculpture on the body whorl indicates advanced age, as does the increased convexity of the body whorl relative to the most apical 4 whorls.

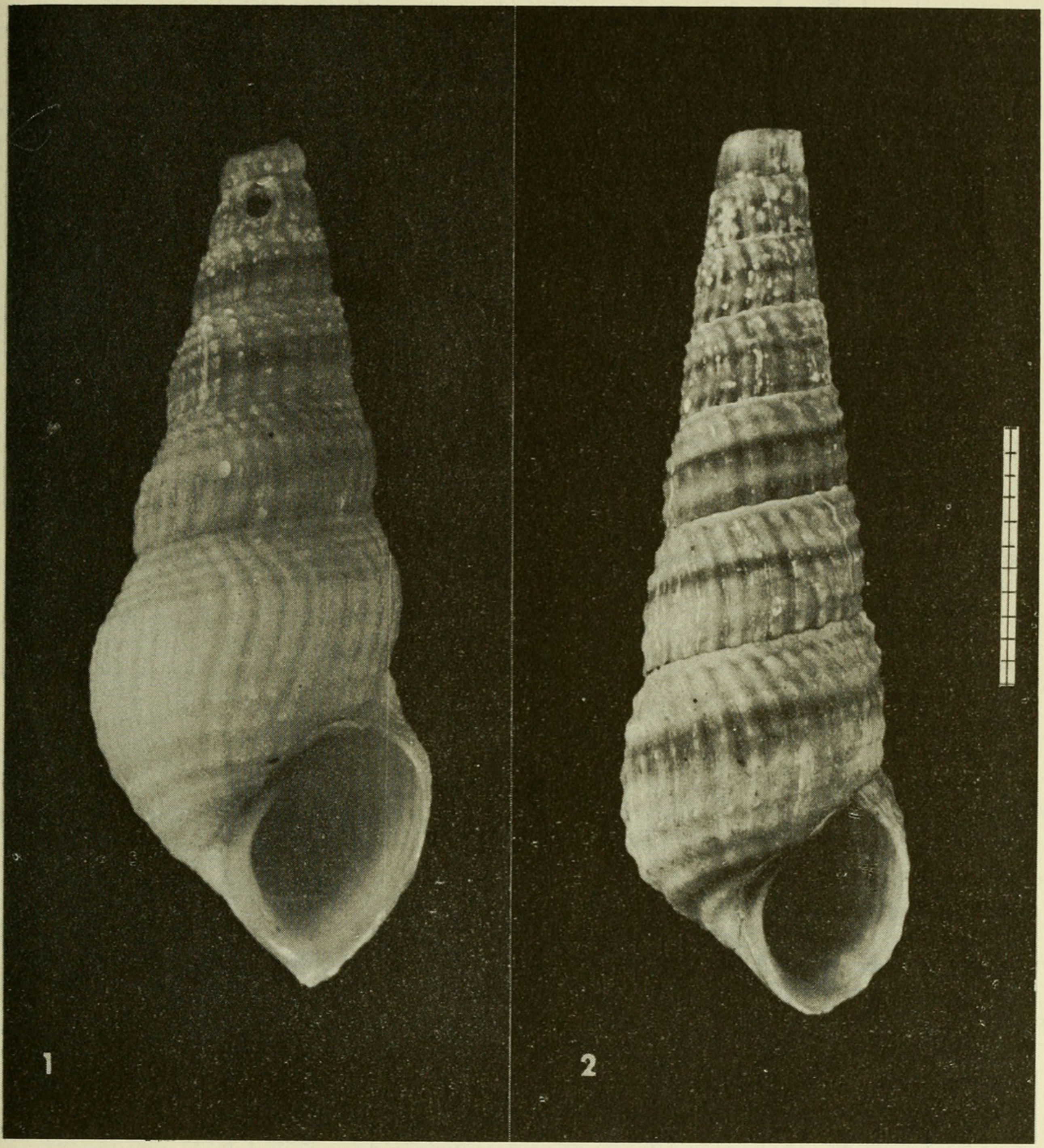

PLATE 6. Adult shells of *Semisulcospira reticulata* Kajiyama & Habe.
The measurement line is in mm.

FIG. 1. Shell type 1. Note the convex whorls starting with the 4th whorl from the apex. The body whorl is markedly convex, yet the sculptural pattern is clear and regular.

FIG. 2. Shell type 2 conforms to the "type." Note the flatsided whorls.

TABLE 31. Adult shells; a statistical analysis of features of *Semisulcospira reticulata* collected from 2 populations

Station (Collecting site)	Statistical measurement	Feature measured or counted								
		Spire angle	Ribs	Basal cords	Nodes on ribs	Body whorl length (mm)	No. of whorls	Shell length (mm)	Shell width (mm)	No. specimens examined
Site 2	$\bar{X}$	17.3°	31.0	3-4	6.6	17.0	4.5	30.2	11.8	
Living shell	S	3.35	3.70	-	0.83	1.3	±1.0	-	1.15	36
type 1	Se	0.67	0.65	-	0.13	0.21	-	-	0.19	
Site 4	$\bar{X}$	16.4°	29.1	3-4	6.0	21.5	6.0	42.7	14.9	
Sub-fossil shell	S	1.15	2.48	-	0.65	1.18	0.0	-	0.94	8
type 1 (July 24)	Se	0.41	0.94	-	0.23	0.42	0.0	-	0.33	
	$\bar{X}$	15.8°	29.0	3-4	6.0	18.3	7.5	43.0	13.6	
Shell type 2	S	1.52	3.00	-	0.68	1.0	0.96	-	0.79	20
	Se	0.34	0.67	-	0.15	0.22	0.21	-	0.18	
Site 4	$\bar{X}$	18.1°	30.5	3-4	6.2	18.7	5.5	35.3	12.9	
Living shell	S	3.29	5.48	-	0.98	1.06	0.80	-	0.77	15
type 1 (Nov. 10)	Se	0.85	1.56	-	0.27	0.27	0.22	-	0.20	

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

TABLE 32. Color patterns of adult and embryo shells of *Semisulcospira reticulata*

%	Population	No. of specimens	Uniform yellow or brown	Banded
Adults	Site 2 Living shell type 1	428	74	26
	Site 4 Living shell type 1	19	63	37
	Site 4 Sub-fossil shell type 1	28	54	46
	Site 4 Sub-fossil shell type 2	115	55	45
Embryos	Site 2 From living adults of shell type 1	100	48	52

TABLE 33. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira reticulata* from population 2 with adults of shell type 1

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count							
			<2. 0	2. 0	2. 5	3. 0	3. 5	4. 0	4. 5	5. 0
21	$\bar{X}$, 4. 8	Shell length		1. 24	1. 82	2. 59	3. 60	4. 71	5. 65	-
	S, 3. 40	Shell width		1. 19	1. 64	2. 07	2. 61	3. 12	3. 57	-
	Se, 0. 74	Body whorl L.		1. 18	1. 59	2. 24	2. 98	3. 64	4. 27	-
		Ratio L/W		1. 04	1. 11	1. 25	1. 38	1. 51	1. 58	-
	Range 1-13	% total embryos	20. 0	14. 0	24. 0	12. 0	17. 0	7. 0	4. 0	2. 0

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

L = length
W = width

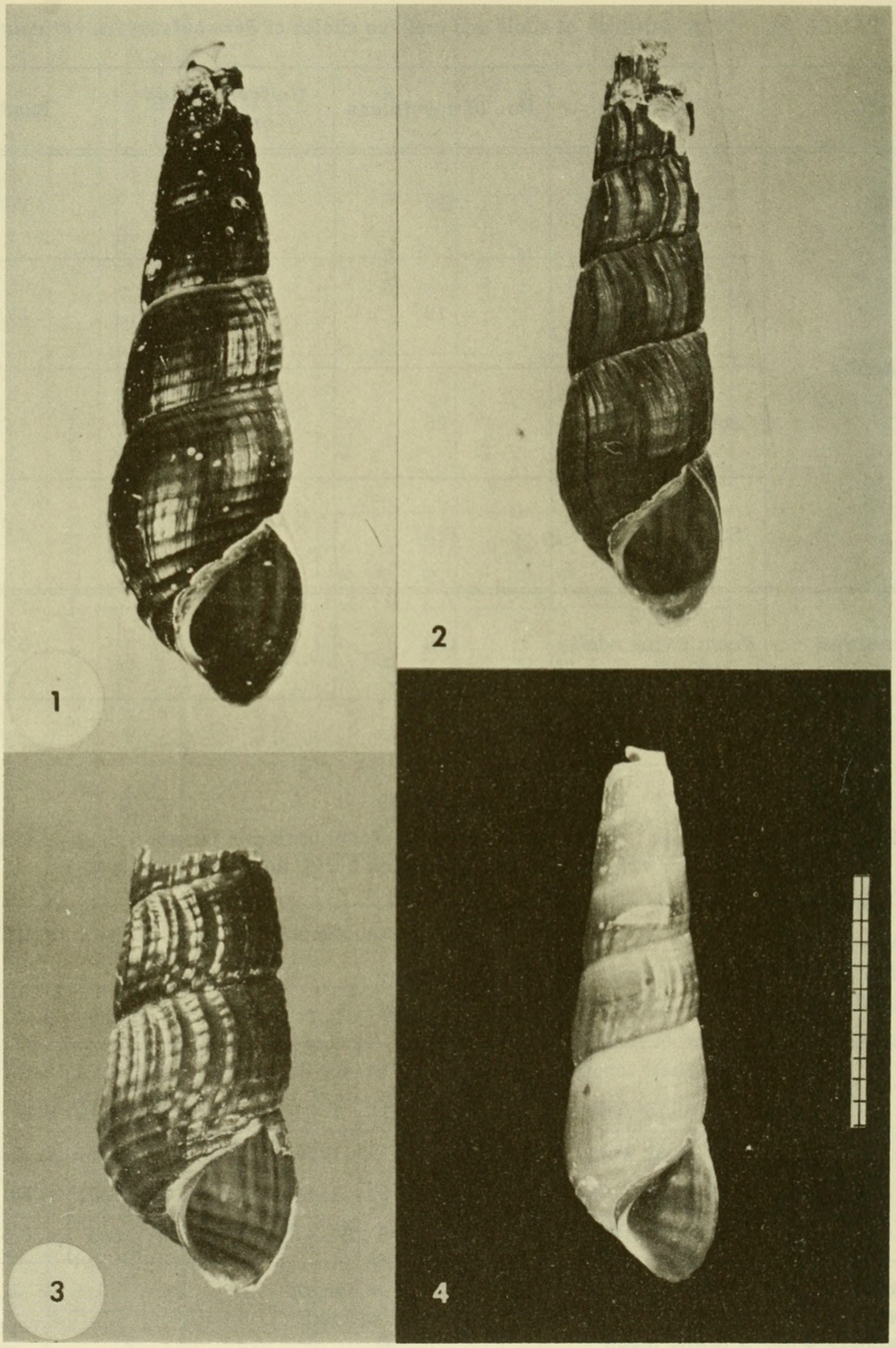

PLATE 7. Adult shells of *Semisulcospira multigranosa* (Boettger). The measurement line is in mm.

FIGS. 1,2,4. Three examples of the smooth morph are shown. Ribs are obsolete in Fig. 2, and only very faint elongate folds are seen in Figs. 1 and 4.

FIG. 3. An example of the ribbed morph showing the pronounced nodes on the rib. The apical whorls were removed to permit access to the gonad for cytological studies (Burch & Davis, 1967).

pendix 1. Measurements of the apical whorls are given in Appendix 2.

The shells are large (Table 38) and globose (Table 40); they are strong and ribbed. Ribs are first noticeable as low nodes at 1½ to 1¾ whorls. In early whorls (2 to 3) the ribs are often nodulate at the shoulders; in later whorls (3½) the ribs are smooth. Data on the ribs are given in Appendix 2. They are relatively wide, 0.30 - 0.48 mm in width on the second whorl. Cords do not show up until late in ontogeny, i.e., beyond 6 whorls where they cause the characteristic nodulation. At a magnification of 16×, a few faint spiral threads or grooves cross the ribs (found in some specimens of 3 to 5 whorls).

As shown in Table 32, about half of the embryos (3 whorls or larger) were uniform yellow. There were 4 banding patterns in the other embryos: (1) with subsutural, basal and sutural bands, the latter being faint and emerging at the mid-body whorl; (2) as in 1, but without the band on the mid-body whorl; (3) with only a basal band (rare); (4) only the sutural band which spirals onto the body whorl was present.

Young were removed from 27 females of shell Type 2, station 4 (24 July 1965 collection). These did not vary significantly from those discussed above in dimension per whorl or color. They had, however, more pronounced ribs.

Particularly noticeable in this species was the great variation in size of snails at the same whorl stage. For example, embryos of 4 whorls from females at station 2 measured 3.87, 4.38, 5.37 and 5.75 mm in length. As shown in Table 33, the average length was 4.71 mm for shells of 4 whorls and 5.65 mm for shells of 4½ whorls. This great variability was generally absent in other species (Appendix 1, a standard deviation for shell length, at 3.0 whorls, of about 0.1 or 0.2 mm for other species as compared to 0.3 mm for *Semisulcospira reticulata*). Many young shells looked distorted as a result of disproportionate growth.

Comparison of species

This taxon is a member of the *Semisulcospira niponica* species group. Because of the size of this species and the large number of highly noded ribs, it is not easily confused with other species. It has been compared with *S. multigranosa* in the preceeding section. The large embryos which are globose at 3 whorls are characteristic. This species has been contrasted with *S. habei* and *S. habei yamaguchi* in the sections dealing with those taxa.

Semisulcospira multigranosa (Boettger, 1886)

Stations 3 and 6

Adults (Pl. 7, Figs. 1-4)

Statistics on basic shell features are given in Table 34. The species is polymorphic. There is shell dimorphism in that some shells are very smooth with ribs obsolete or entirely absent (Pl. 7, Figs. 1, 2, 4); or other shells prominent nodulate ribs occur (Pl. 7, Fig. 3). When the ribs are obsolete, irregularly placed low folds are observed on just 1 or 2 whorls and these fade out into elongate creases, lines or ripples, which are regularly positioned on the whorls where the ribs would normally occur. Spiral cords (7 to 8) may be pronounced, faint, or absent in the case of the smooth morphs. When absent, spiral grooves are often seen. In the multigranulate morphs the numerous ribs ($\bar{X}$, 23.2) have 7-8 distinct nodes where cords cross the ribs.

As shown in Table 35, 3 color patterns are found. These occur on both smooth and multigranulate morphs. In banded shells a central or mid-whorl stripe of yellow is flanked on either side by wide brownish-purple bands. The suture is yellow to yellowish-white.

Embryos (Pl. 11, Figs. 5-8)

Statistics on numbers of young per pallial brood pouch and the percentage

PLATE 8. Embryo shells from the pallial brood chambers of 3 species of *Semisulcospira*. The length of the scale line is 1 mm.

FIGS. 1-5. *Semisulcospira libertina,* Shimoda. Two cords are evident on the inside of the outer lip of embryos in Figs. 2 and 5. The adapical cord is the strongest.

FIGS. 6-10. *Semisulcospira libertina*. Amami-oshima. None of the embryos observed had 2 cords. One faint cord is evident in Fig. 8. About 91% of the embryos of 2. 5 whorls had 1 cord. The specimen in Fig. 9 has 2. 5 whorls.

FIGS. 11-15. *Semisulcospira reiniana*. Note the large size relative to embryos of *S. libertina.* The ribs terminating on a cord is characteristic.

FIGS. 16-20. *Semisulcospira kurodai*. Note the nodes on the adapical cord. The specimen in Fig. 20 has 3 whorls and 2 cords are quite evident.

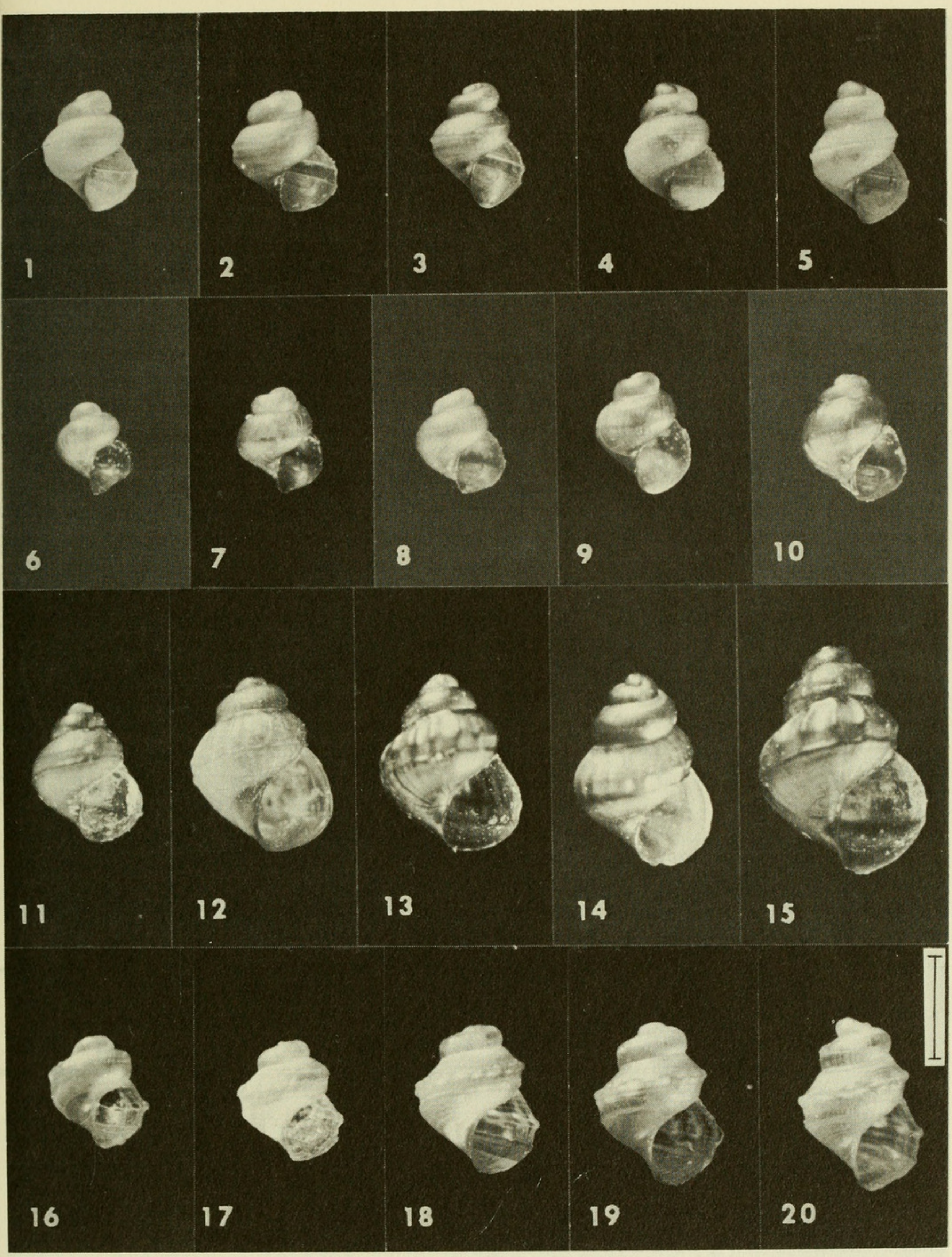
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TABLE 34. Adult shells; a statistical analysis of features of *Semisulcospira multigranosa*

No. specimens examined	Statistic	Feature measured or counted					
		Spire angle	Ribs*	Basal cords	Body whorl length (mm)	Shell length (mm)	Shell width (mm)
25	$\bar{X}$	14.2	23.2	2-3	13.1	26.0	8.3
	S	3.11	2.42	--	1.24	--	0.60
	Se	0.64	0.67	--	0.25	--	0.12

* only multigranulate forms

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean

TABLE 35. Shell color patterns of adult *Semisulcospira multigranosa*

No. of specimens	Uniform yellowish-white (%)	Banded (%)	Uniform purple-black (%)
54	40.7	9.3	50.0

TABLE 36. Shell color patterns of embryo *Semisulcospira multigranosa*

Color of adult	No. of embryos	Uniform yellowish-white (%)	Banded (%)	Uniform purple-black (%)
Smooth morph				
yellow	16	32	25	43
banded	3	67	33	0
black	39	28	26	46
Multigranulate morph				
yellow	2	100	0	0
banded	0	0	0	0
black	0	0	0	0

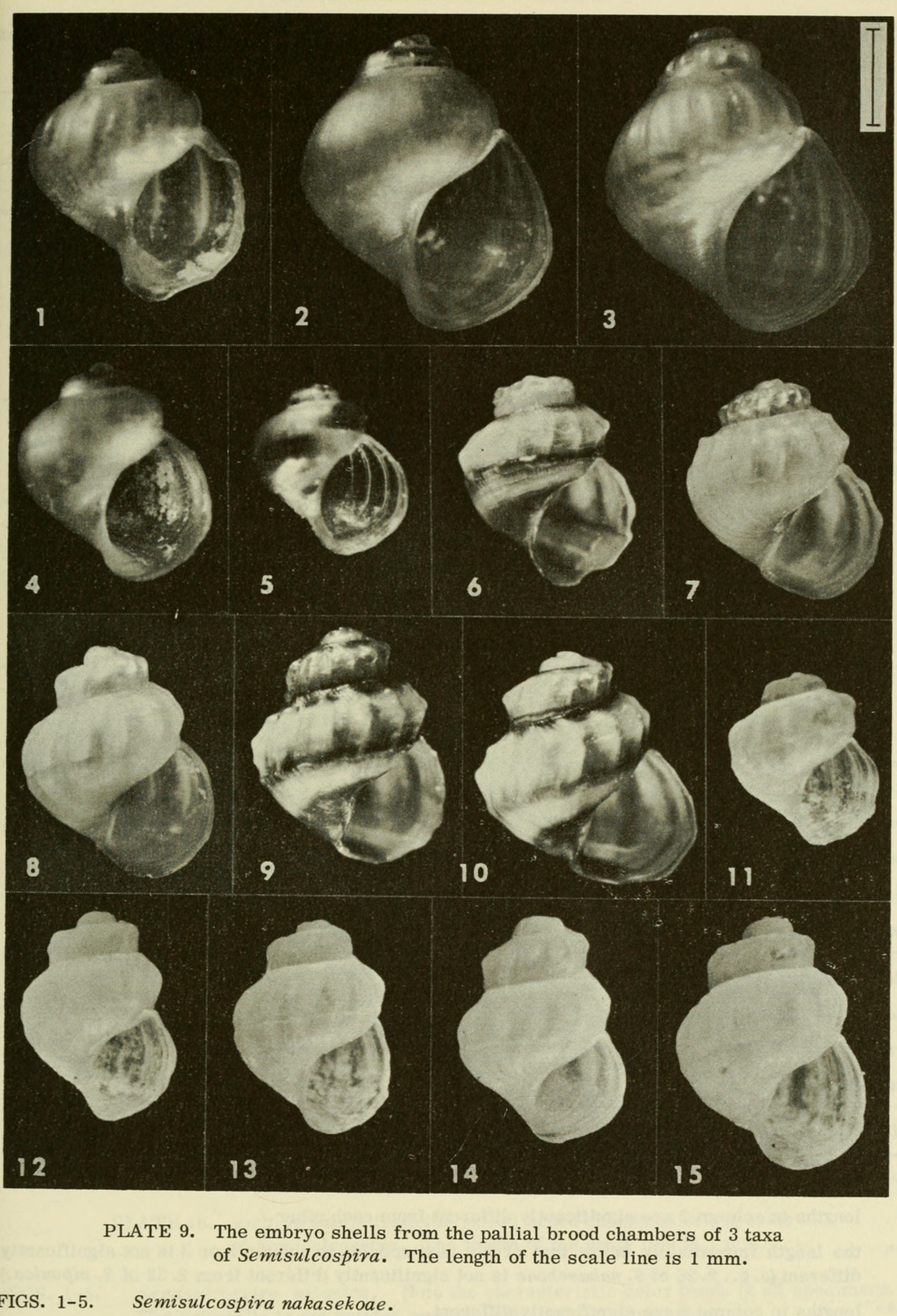


PLATE 9. The embryo shells from the pallial brood chambers of 3 taxa of *Semisulcospira*. The length of the scale line is 1 mm.

FIGS. 1-5. *Semisulcospira nakasekoae*.

FIGS. 6-10. *Semisulcospira habei*, new species. The columellar twist is particularly evident in Figs. 7, 9, 10.

FIGS. 11-15. *Semisulcospira habei yamaguchi*, new subspecies.

TABLE 37. Embryo shells; a statistical analysis of numbers per female and shell features of *Semisulcospira multigranosa*

Number females examined	Number young per female	Feature studied	Mean measurements (mm) of embryos of different whorl count							
			<2.0	2.0	2.5	3.0	3.5	4.0	4.5	5.0
	$\bar{X}$, 5.2	Shell length			1.52	2.22	2.77	3.53	4.67	-
	S, 3.41	Shell width			1.25	1.51	1.84	2.09	2.54	-
16	Se, 0.85	Body whorl L.			1.33	1.85	2.28	2.85	3.66	-
		Ratio L/W			1.22	1.47	1.51	1.69	1.84	-
	Range 2-12	% total embryos	[(<2.5)26.0]		18.7	10.5	17.5	9.3	16.3	1.7

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean
L = length
W = width

TABLE 38. Comparison of embryo shell length of *Semisulcospira* species at 3 whorls

Species of *Semisulcospira*	Shell length at 3 whorls			Size class
	*	**	***	
reticulata	2.59			Large
niponica	2.32(P = <.01)			
nakasekoae		2.28		
habei habei	2.23(P=<.05)	2.23		
multigranosa		2.22		
decipiens	1.83(P=<.01)			Medium
habei yamaguchi		1.78	1.78	
reiniana	1.64(P=<.01)		1.64(P = <.02)	
kurodai		1.62		
libertina	1.39(P=<.01)			Small

P = probability

* lengths in column 2 are significantly different from each other.

** the length immediately below that of the next species in column 2 or 3 is not significantly different (e.g., 2.28 of *S. nakasekoae* is not significantly different from 2.32 of *S. niponica*.)

*** lengths in column 4 are significantly different.

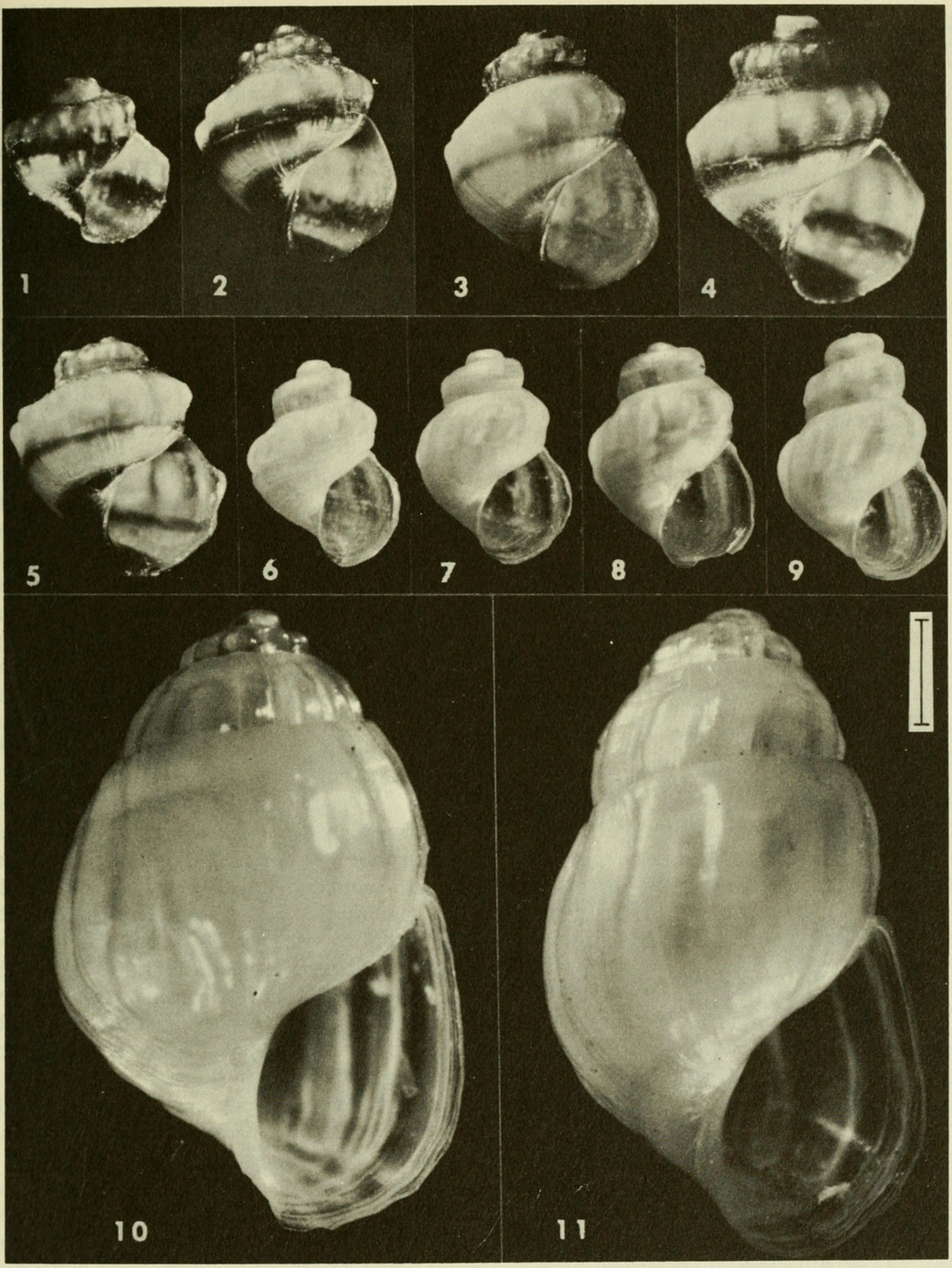


PLATE 10. Embryo shells from the pallial brood chambers of 3 species of *Semisulcospira*. The length of the scale line is 1 mm.

FIGS. 1–5. *Semisulcospira niponica*. Note the characteristic color bands in all specimens. The columella is not twisted as in *S. habei* (Pl. 9, Figs. 6–10).

FIGS. 6–9 *Semisulcospira decipiens*.

FIGS. 10, 11. *Semisulcospira reticulata*.

of young at each whorl stage are given in Table 37; included are data on shell measurements. More complete statistics are given in Appendix 1. Apical whorl measurements are given in Appendix 2.

Shells are compartively large (Table 38) and elongate (Table 40). The sturdy shells have wide ribs (Appendix 2) which are not nodulate. Shells are characterized by the absence of cords and the great increase in length of body whorl after 3 whorls. The latter results in a shell with long, straight-sided whorls. Ribs first appear as low swellings on the shoulder at 1⅔ to 2 whorls. They are not nodulate and are most pronounced on the 3rd whorl. The diameter of the ribs at 4 to 4½ whorls varies from 0.29 to 0.42 mm; they are widest at mid-whorl. Shells of 4 whorls and larger have 7 ± 1 spiral grooves passing over the shells and ribs.

Embryo color patterns are given in Table 36. Too few multigranulate adults were found to determine adequately the percentage of young of each color type correlated with adult color pattern. Data for embryos from smooth as well as multigranulate adults are not sufficient to give generalities about correlation of embryo color in relation to adult color. In banded shells either a single thin basal band is present, or both sutural and basal bands occur.

Comparison of species

This species is a member of the *Semisulcospira niponica* complex. With polymorphism of this taxon in mind, it is necessary to point out criterea for contrasting this species with *S. decipiens* (done in the preceeding section), *S. habei yamaguchi* (done in the section on that taxon) and *S. reticulata*. As shown in Text Fig. 13, *S. multigranosa* has fewer ribs than *S. reticulata* (23.2 ± 2.4 as compared to a minimum of 29.0 ± 3.0). The length of the body whorl of mature *S. multigranosa* (13.1 ± 1.24 mm) is considerably shorter than that of *S. reticulata* (17.0 ± 1.3 mm), which indicates the great size differences between the taxa. There is also a vast difference in the 2 taxa when the size of the embryos at 3 whorls is compared (Table 38); *S. multigranosa* averages 2.22 mm and *S. reticulata* 2.59 mm. While some adult shells of *S. multigranosa* are black, no black *S. reticulata* shells have been found. As shown in Text Fig. 10, the embryos of *S. multigranosa* become elongate at 3 whorls, while those of *S. reticulata* are not clearly elongate until 4 whorls.

V. ANALYSES OF SHELL GROWTH PATTERNS

Species of *Semisulcospira* are characterized by shells which are elongate and conical. If the shells were true cones in the mathematical sense, the spire angle would be constant, as would be the ratio of length to width at any stage in growth. Since the shell is a coiled tube, increase in the length of the "cone" may be arithmetic or exponential; the latter because the length of the body whorl increases at a constant rate with growth.

It is clearly evident from casual observations of *Semisulcospira* that shell morphology departs from a pure cone and that increase in shell length is exponential. A series of measurements of embryonic shells from the brood pouch were taken to determine if certain departures from the ideal cone were species specific. The assumption made is that the brood pouch environment represents the most stable environment that the snail experiences, and within it occur the most uniform and regular growth processes.

With the above in mind, the following information was plotted or tabulated from data presented in the description of each species: (1) length of shell per whorl stage, (2) length of body whorl at each whorl stage, (3) the length-width ratio at each whorl stage. A number of comparisons were carried out with embryos at 3 whorls because: (1) the

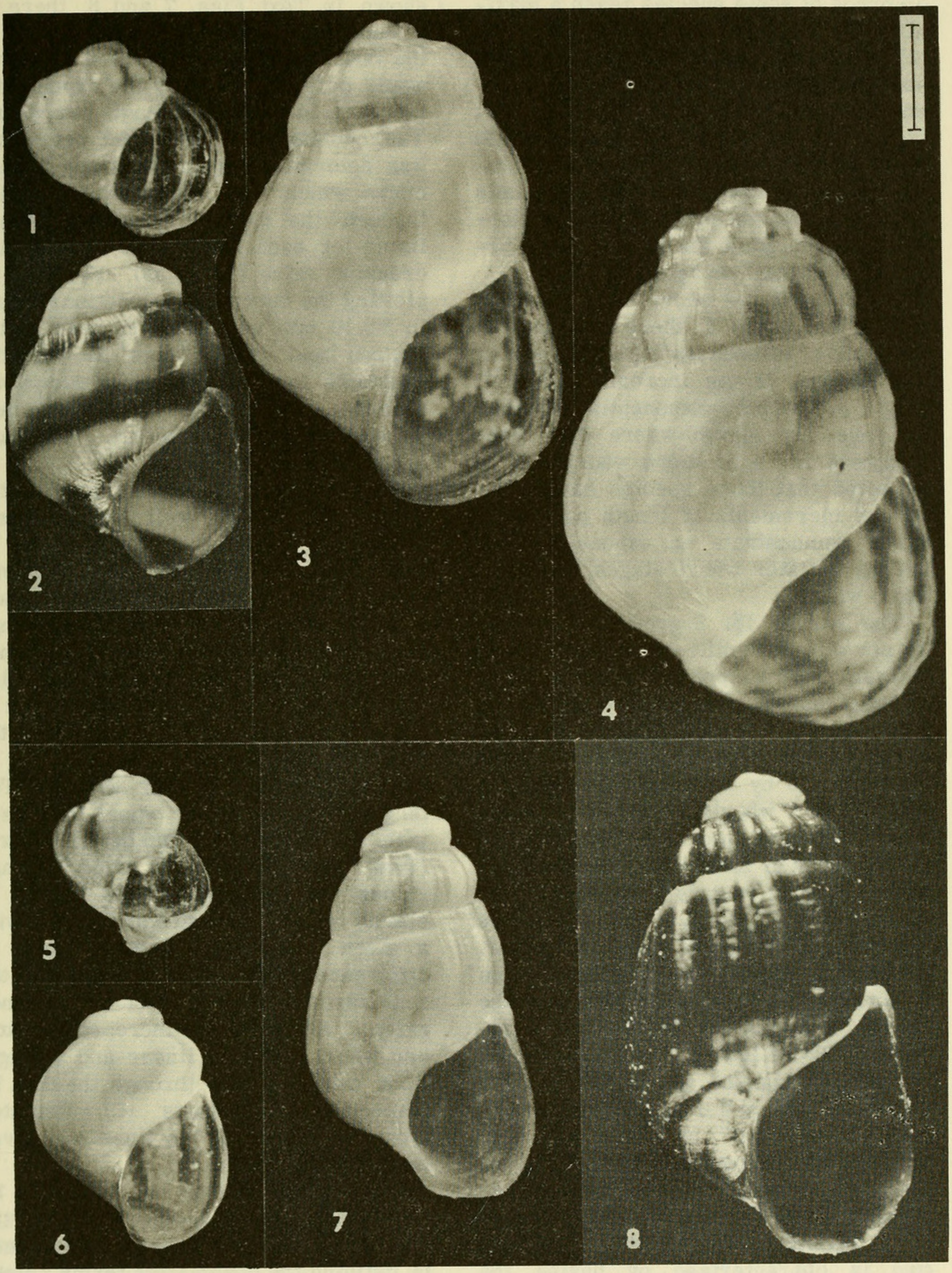


PLATE 11. Embryo shells from the pallial brood chambers of 2 species of *Semisulcospira*. The length of the scale line is 1 mm.

FIGS. 1–4. *Semisulcospira reticulata*.

FIGS. 5–8. *Semisulcospira multigranosa*.

embryos of some species reach a maximum of 3 whorls in the brood pouch, (2) this size of embryo is easily handled and measured, (3) size differences become more accentuated at this whorl stage than at lower whorl stages; (4) at 3 whorls growth is beyond the embryonic 1 or 2 whorls and the shells begin to assume progressive development to the adult shell, e.g., they become "elongate" or "globose."

Shell length per whorl. As shown in Text Figs. 5 and 6, there are, indeed, distinctive differences between some of the species in the increment of shell length per whorl. Exponential increase is generally shown where data were complete for 4 or more whorls. It is expected that those species having the lowest increments of length per whorl would demonstrate an exponential increase at later whorl stages, e.g., 4.5 and 5 whorls.

The curves for 2 groups of species do not differ significantly; these are 1) *Semisulcospira niponica*, *S. nakasekoae*, *S. habei* and *S. multigranosa* on the one hand; and 2) *S. kurodai* and *S. reiniana* on the other. The species are ranked in Table 38 by decreasing mean shell lengths at 3 whorls. They were arbitrarily grouped into size categories of large, medium and small; the divisions were indicated by gaps in the data. Data in columns 2 and 4 are for species significantly different from each other. *S. habei* is significantly different from *S. niponica* at 3 whorls and likewise the curves of length per whorl differ significantly (P=.05 level).

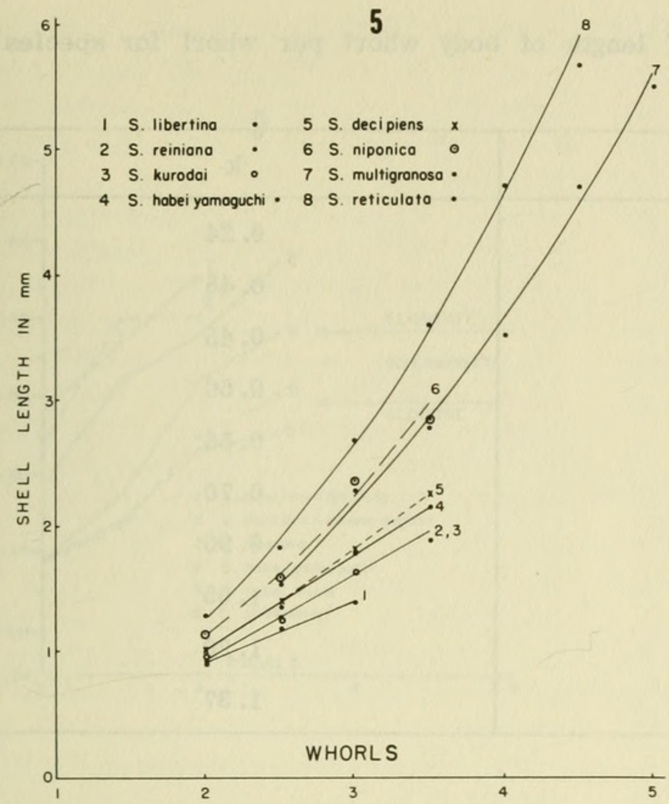
Embryos classed as "large" are 2.0 mm or longer at 3.0 whorls, those considered "medium" in length are 1.60 to 1.85 mm; those less than 1.45 mm long are "small." *Semisulcospira reticulata* is in a class by itself because of its pronounced size, while *S. libertina* is characterized by having the smallest embryos. Note the pronounced differences in size between *S. habei* and *S. habei yamaguchi*.

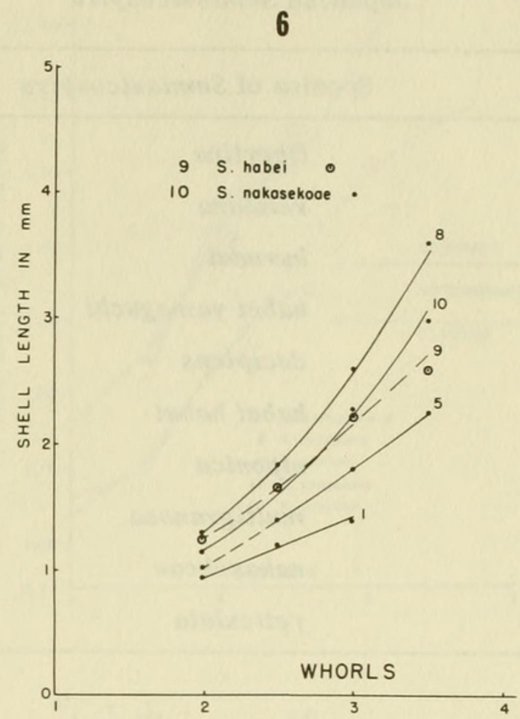
Length of body whorl per whorl. As shown in Text Figs. 7 and 8, there is a constant increment in the length of the body whorl at each whorl stage, as would be expected from the exponential increase in total shell length per whorl. The constant (K) increment per whorl was determined from the slope of each curve which was drawn by inspection through the data. The constants are listed for each species in order of increasing value (Table 39). Variation in plotting the curves by inspection is within ±0.10 mm/whorl. It is seen in the figures and from Table 39 that the constants for *Semisulcospira decipiens*, *S. habei yamaguchi*, *S. reiniana* and *S. kurodai* are very similar. There are at least 6 distinct slopes.

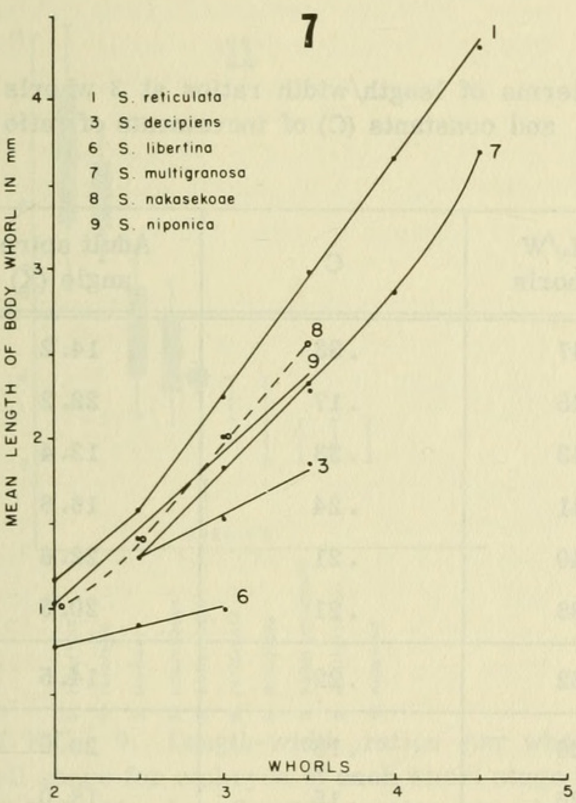
The curves fit the mean values plotted (in the figures) very well in most cases. Exceptions are the curved portions of the otherwise straight lines of *Semisulcospira nakasekoae*, *S. reticulata* and *S. multigranosa*. The slope of the lines may be altered in a significant manner due to drawing the lines by inspection only in the case of *S. nakasekoae;* it is possible that this species may have the 7th distinct slope.

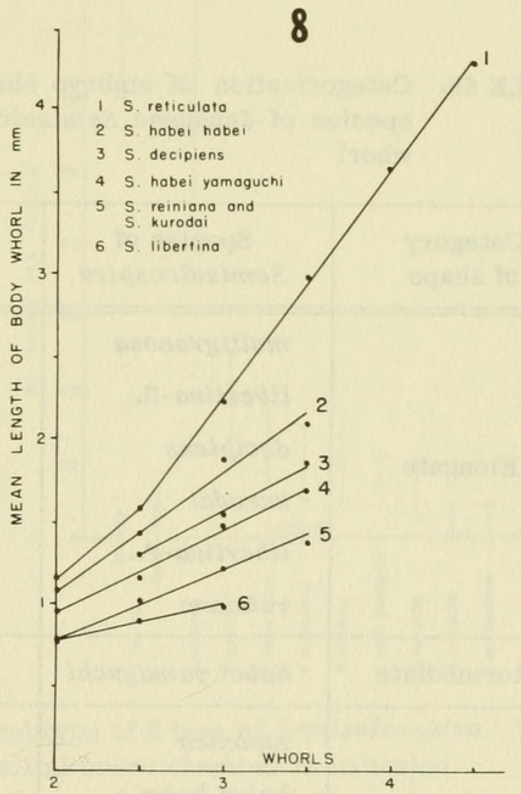
Length/width ratio per whorl. The length/width ratio per whorl increases with the increasing number of whorls (Text Figs. 9 and 10). The average values are connected in the figures to clarify which points are associated with a given taxon. The reduced scale of difference between whorls accentuate the departure of points from strict linearity. Actually, the increase in ratio per whorl is fairly linear and straight lines can be drawn through the data by inspection. Constants (C) calculated from the slopes of the lines are given in Table 40.

Species are ranked in Table 40 by decreasing length/width ratios of the shells at 3 whorls. These data are used in defining the descriptive terms "elongate" and "globose." For embryos within the brood pouch, *Semisulcospira multigranosa* is an extreme form in being "elongate" with a ratio of 1.47 at 3









TEXT FIG. 5. Shell length per whorl for 8 taxa of *Semisulcospira*.

TEXT FIG. 6. Shell length per whorl for 2 species of *Semisulcospira* compared with similar data for 3 species shown in Text Fig. 5.

TEXT FIG. 7. Mean length of body whorl per whorl for embryos from 7 taxa of *Semisulcospira*.

TEXT FIG. 8. Mean length of body whorl per whorl for embryos from 3 species of *Semisulcospira* compared with 3 species shown in Text Fig. 7.

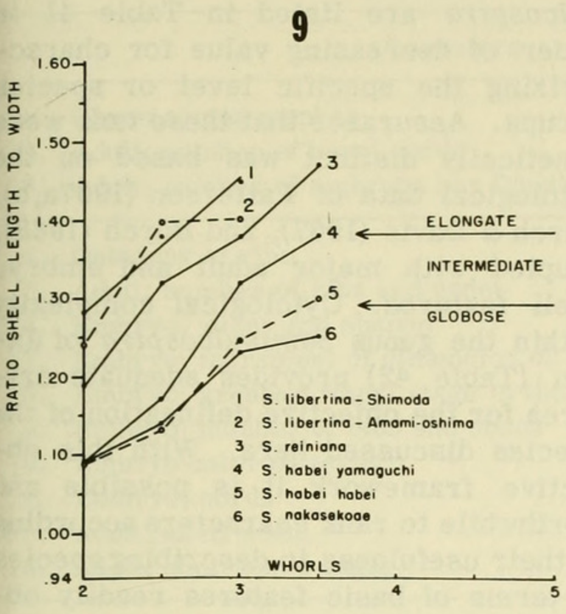
TABLE 39. The constant (k) increment of length of body whorl per whorl for species of Japanese *Semisulcospira*

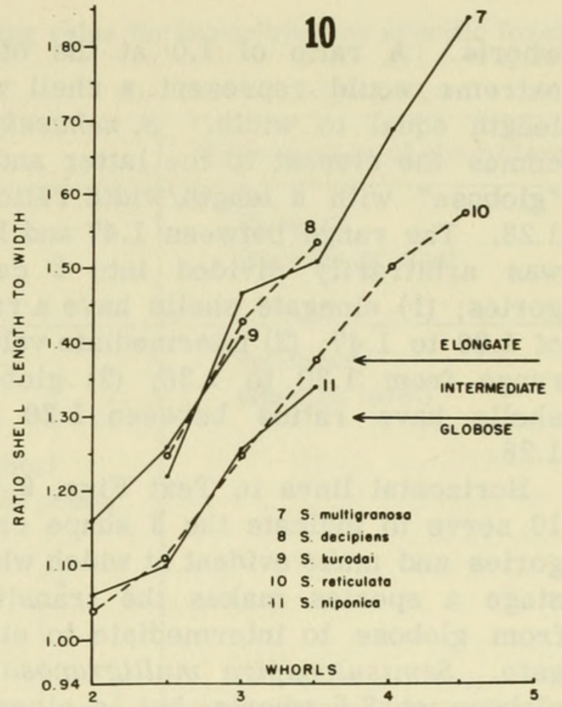
Species of *Semisulcospira*	k
libertina	0.24
reiniana	0.45
kurodai	0.45
habei yamaguchi	0.50
decipiens	0.56
habei habei	0.70
niponica	0.90
multigranosa	1.05
nakasekoae	1.20
reticulata	1.37

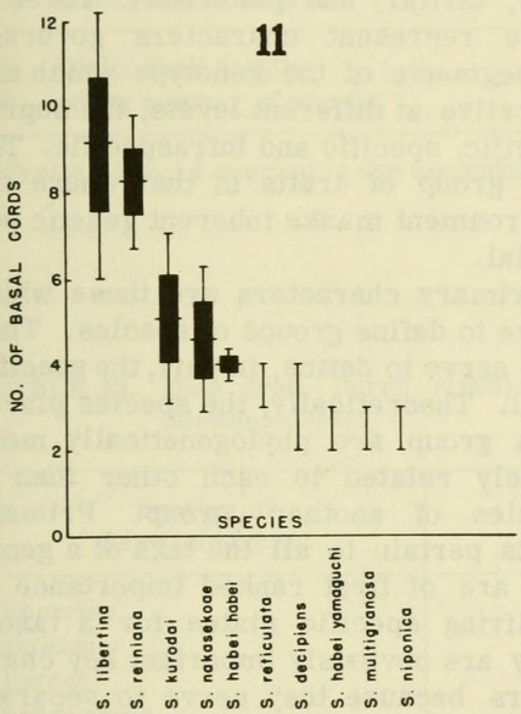
TABLE 40. Categorization of embryo shape in terms of length/width ratios at 3 whorls for species of Japanese *Semisulcospira*, and constants (C) of increments of ratio per whorl

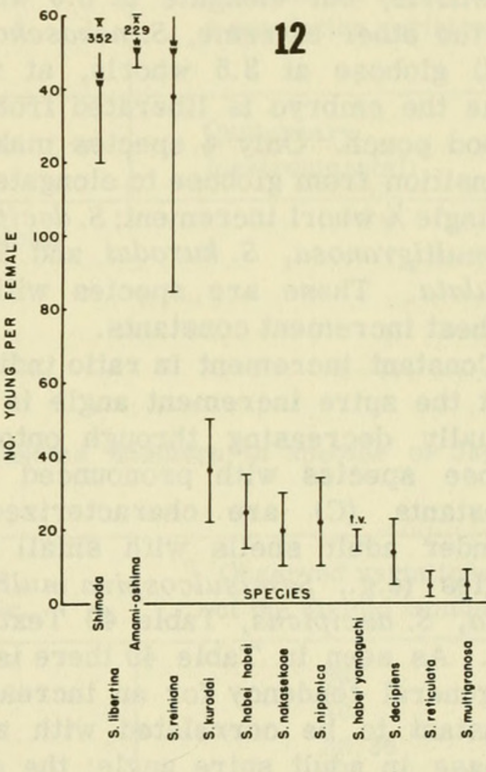
Category of shape	Species of *Semisulcospira*	Shell L/W at 3 whorls	C	Adult spire angle ($\bar{X}$)
Elongate	*multigranosa*	1.47	.33	14.2
	libertina-S.	1.45	.17	22.2
	decipiens	1.43	.33	12.4
	kurodai	1.41	.24	16.6
	libertina-A.	1.40	.21	22.6
	reiniana	1.38	.21	20.6
Intermediate	*habei yamaguchi*	1.32	.22	14.5
Globose	*niponica*	1.26	.18	20.0
	habei habei	1.25	.15	18.0
	reticulata	1.25	.23	17.0
	nakasekoae	1.23	.13	29.1

S. = Shimoda
A. = Amami-oshima
$\bar{X}$ = mean
L = length
W = width
C = constant for increment in length/width ratio per whorl









TEXT FIG. 9. Length-width ratios per whorl for embryos of 5 taxa of *Semisulcospira*. The shell shape for embryos of each whorl stage in the pallial brood chamber is indicated.

TEXT FIG. 10. Length-width ratios per whorl for embryos of 5 species of *Semisulcospira* not given in Fig. 9. The shell shape for embryos of each whorl stage in the pallial brood chamber is shown.

TEXT FIG. 11. The 10 taxa of *Semisulcospira* compared in terms of the number of basal cords on the adult shell. The mean and 2 standard deviations are shown for the 5 taxa on the left; the total range is given for the 5 taxa on the right.

TEXT FIG. 12. The 10 taxa of *Semisulcospira* compared in terms of the number of young found per pallial brood chamber. The mean and 1 standard deviation are given.

whorls. A ratio of 1.0 at the other extreme would represent a shell with length equal to width. *S. nakasekoae* comes the closest to the latter and is "globose" with a length/width ratio of 1.23. The range between 1.47 and 1.23 was arbitrarily divided into 3 categories; (1) elongate shells have a ratio of 1.38 to 1.47; (2) intermediate values range from 1.30 to 1.36; (3) globose shells have ratios between 1.20 and 1.28.

Horizontal lines in Text Figs. 9 and 10 serve to indicate the 3 shape categories and make evident at which whorl stage a species makes the transition from globose to intermediate to elongate. *Semisulcospira multigranosa* is globose at 2.5 whorls, but is elongate at 3 whorls. *S. reticulata* is globose at 3 whorls, but elongate at 3.5 whorls. At the other extreme, *S. nakasekoae* is still globose at 3.5 whorls, at which time the embryo is liberated from the brood pouch. Only 4 species make the transition from globose to elongate with a single ½ whorl increment; *S. decipiens*, *S. multigranosa*, *S. kurodai* and *S. reticulata*. These are species with the highest increment constants.

Constant increment in ratio indicates that the spire increment angle is continually decreasing through ontogeny. Those species with pronounced large constants (C) are characterized by slender adult shells with small spire angles (e.g., *Semisulcospira multigranosa*, *S. decipiens*, Table 40 Text Fig. 10). As seen in Table 40 there is only a general tendency for an increase in constant to be correlated with a decrease in adult spire angle; the coefficient of correlation, r, is -0.66 and is significant ($P=<.05$).

VI. DISCUSSION ON THE UTILITY OF CHARACTERS, WITH A KEY TO THE SPECIES

Grouping characters in terms of importance

The characters or traits used in this paper to describe 9 species and 1 subspecies on the Japanese genus *Semisulcospira* are listed in Table 41 in order of decreasing value for characterizing the specific level or species groups. Assurance that these taxa were genetically distinct was based on the cytological data of Patterson (1967a,b), Burch & Davis (1967), and Burch (1968), coupled with major adult and embryo shell features. Cytological complexity within the genus *Semisulcospira* of Japan (Table 42) provides adequate criterea for the objective delineation of the species discussed here. With this objective framework it is possible and worthwhile to rank characters according to their usefulness in describing species in terms of basic features readily observed.

The characters are placed in 4 groups, referred to here as primary, secondary, tertiary and quaternary. Three of these represent characters governed by segments of the genotype which are operative at different levels; the supraspecific, specific and infraspecific. The last group of traits is that where the environment masks inherent genetic potential.

Primary characters are those which serve to define groups of species. They also serve to define, in part, the specific level. Theoretically, the species placed in a group are phylogenetically more closely related to each other than to species of another group. Primary traits pertain to all the taxa of a genus and are of first ranked importance in justifying specific status for a taxon. They are obviously important key characters because they serve to separate taxa in terms of non-overlapping variation (i.e., mean and standard deviation).

Secondary characters are of use in defining the species and also provide good key characters. Secondary characters, while naturally variable, should not be subject to such inter-population variation that there is confusion in species recognition. For example,

TABLE 41. Characters ranked in order of decreasing value for describing the specific level of species groups

Characters	Major groups of characters
1. Chromosome number 2. Adult; number of basal cords 3. Adult; number of embryos per female	Primary (species groups)
4. Ontogeny of ribs 5. Adult; number of ribs and nodes 6. Embryo, sizes and shapes 7. Embryo; increment of dimension or ratio per whorl 8. Embryo; greatest whorl stage in the pallial brood pouch 9. Embryo; number of ribs and nodes 10. Embryo color patterns 11. Embryo; cords * 12. Adult; shell width 13. Adult; shell spire angle	Secondary (species level)
14. Adult; length of body whorl 15. Embryo; microsculpture 16. Embryo; apical whorl measurements 17. Adult; color patterns	Tertiary (subspecific level) = population variation
18. Adult; shell length 19. Adult; number of whorls	Quaternary (environmental)

*Traits 11 to 14 overlap in the secondary-tertiary grouping

TABLE 42. Data from Burch (1968) on the chromosome numbers of species of Japanese *Semisulcospira*

Species of *Semisulcospira*	Inferred basic haploid number	Observed variations of the diploid number
libertina	18	36
reiniana	20	40
kurodai	18	35,36
nakasekoae	13	26
**habei habei*	7	17-20
**habei yamaguchi*	7	17-20
niponica	12	25-27
decipiens	12	25,26
reticulata	12	25,26
multigranosa	14	28-31

*These were not discussed by name in Burch, 1968 the "presence or absence of ribs" would make a poor secondary character. This is shown in *Semisulcospira libertina* where populations from Amami-oshima had no evidence of ribs while the same species from Shimoda had shells with ribs in 3% of the population. In more recent studies (Davis 1967b, 1969), I investigated a population from Ashino Lake in the Hakone mountain range, Kanagawa Prefecture where all the snails had distinct ribs. This population is considered conspecific with *S. libertina* because of its agreement with topotypes of *S. libertina* in primary and secondary characters (also electrophoretically and immunologically, Davis, *loc. cit.*). Martens (1877) noted the gradation from shells with no ribs to those with pronounced ribs when he studied populations of *S. libertina* and he accordingly gave variety names to the stages, such as *tenuisulcata*, *ambidextra*, *decussata* and *plicosa*.

A species is defined in terms of unique mixtures of secondary traits, grouped within the framework of primary characters. Traits ranked closer to the primary characters in Table 41 indicate where more distinct breaks in the data occur when all the taxa are compared using a single trait. For example, when the taxa are compared in terms of numbers of ribs on the penultimate whorl (Text Fig. 13) more distinct groups of data are seen than when data for spire angles are compared (Text Fig. 18).

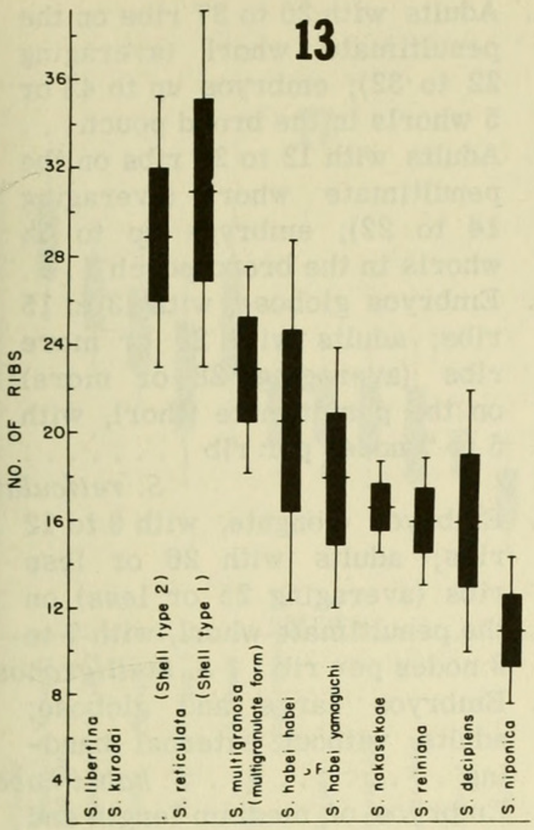
Tertiary characters are those which vary a great deal from population to population. As shown by the bracket-line in Table 41, traits 11 to 14 tend to be affected by population variation. While, for example, it is clear that *Semisulcospira nakasekoae* and *S. decipiens* are distinct when they are compared on the basis of spire angle (Text Fig. 18), the degree to which the environment affects growth patterns of snails of different populations of the same species is not clear, and, in particular, how shell width and spire angle are affected. In the case of cords on the embryo, *S. multigranosa* has none, while *S. libertina* is characterized by their presence. Yet, *S. libertina* from Shimoda had 2 cords (in 70% of the individuals with 3 whorls), while embryos of the same species from Amami-oshima had only 1 (in 91% with 2.5 whorls). The number of cords varies between populations.

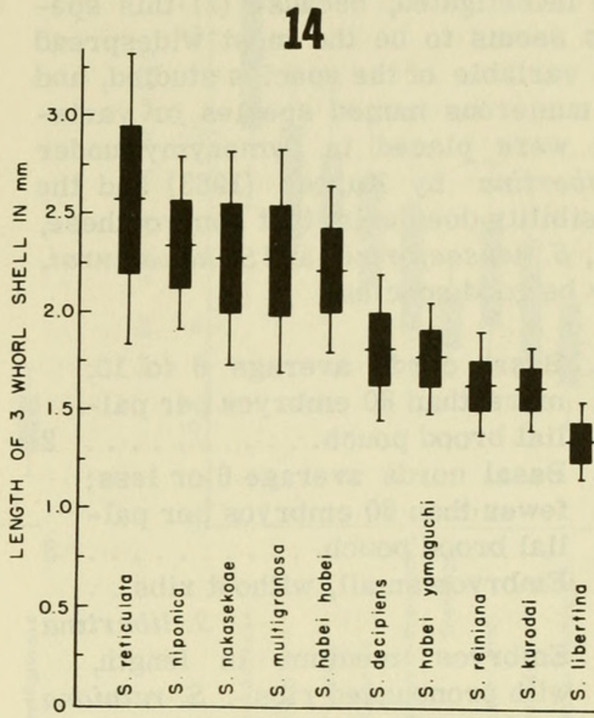
A character in this group may have similar types of expression in many taxa yet serve to characterize 1 species. The color patterns of adult shells for several taxa vary from uniform yellow to banded in similar patterns; however, *Semisulcospira niponica* is characterized by having a dark brown-black to purple black shell.

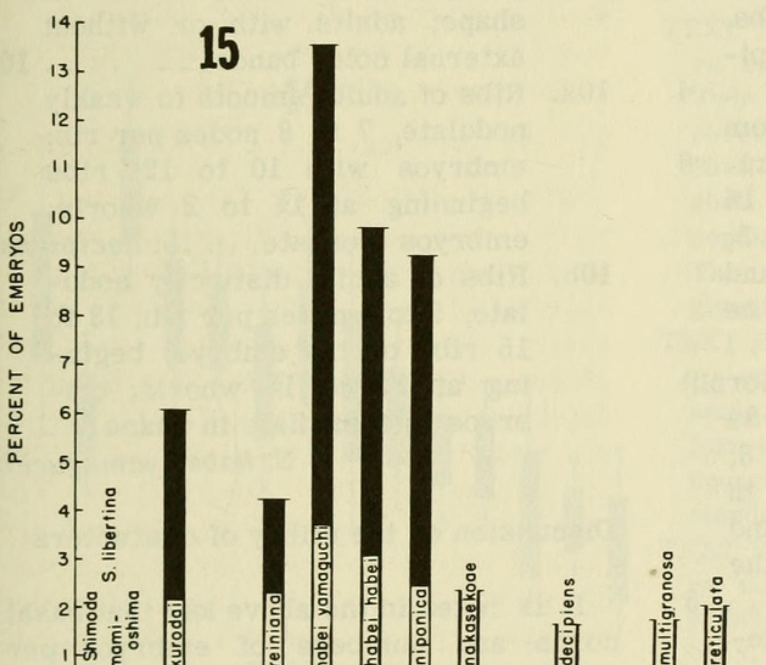
Quaternary characters are those which are acted on by the environment to the extent that the genotype is not expressed. Characters involving adult shell size are generally poor because of lack of information on how different environments affect growth.

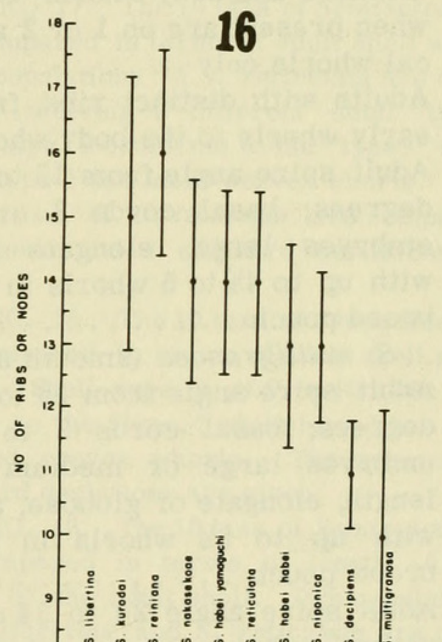
Key to the species of *Semisulcospira*

The following key is presented to show how groups of primary and secondary characters serve to distinguish the species of this study. Only the most easily observed characters are employed. By necessity the key must be used in connection with data provided in the tables for each species, and Tables 38 and 40 and Text Figs. 5 to 19. At least 10 to 25 adult specimens are needed and these must be in good condition; embryos from 5 or more females are needed; and, averages of data should be used. Traits of chromosome numbers and indexes of increment of length per whorl for the embryos are not used because they are comparatively difficult and/or tedious to work out, thereby offsetting the purpose of the key which is the rapid and efficient identification of species. The key serves to show which groups of readily observed characters are indicative of distinctive









TEXT FIG. 13. The 10 taxa of *Semisulcospira* compared in terms of the number of ribs on the penultimate whorl of adult shells. The mean and 2 standard deviations are given. Shell type 2 of *S. reticulata* conforms to the type; shell type 1 has the convex body whorl. [*S. libertina* does not have ribs on shells from the populations studied; *S. kurdoai* does not have ribs on the penultimate whorl of mature adults.]

TEXT FIG. 14. A comparison of the 10 taxa of *Semisulcospira* in terms of embryo shell length at 3 whorls. The mean and 2 standard deviations are given.

TEXT FIG. 15. The maximum embryo whorl size found in the brood chamber of each taxon of *Semisulcospira* and the % of embryos attaining that size.

TEXT FIG. 16. The number of ribs or nodes on the most apical whorl of the embryo having these structures is given for each taxon of *Semisulcospira*. The mean and 1 standard deviation are given for 8 taxa while the total variation (t.v.) is given for 1 taxon.

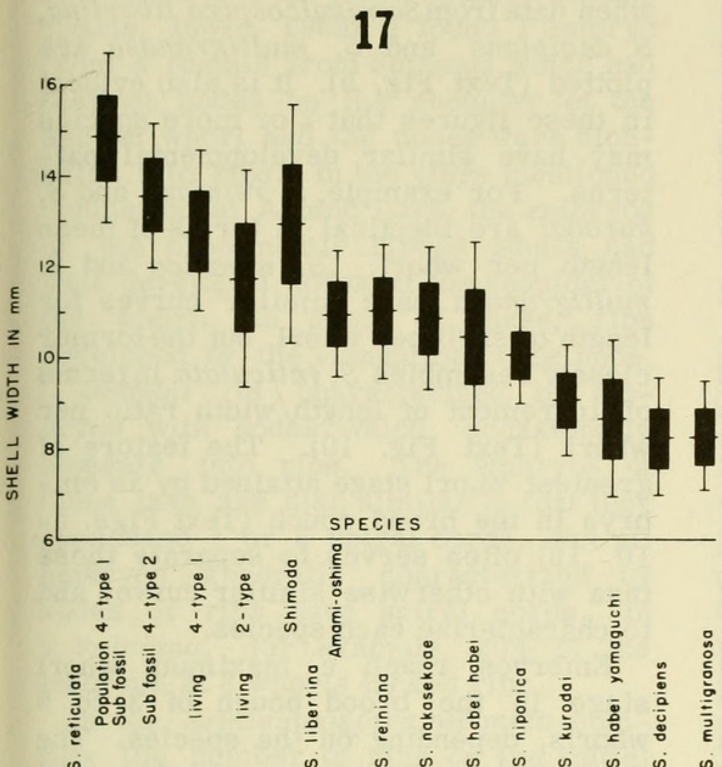
genotypes.

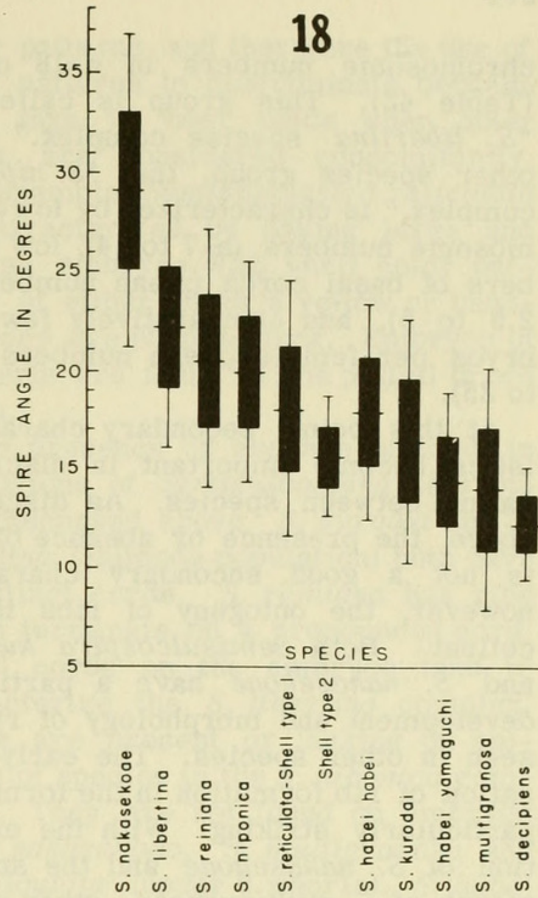
The key is limited in use until more populations of *Semisulcospira libertina* are investigated, because (1) this species seems to be the most widespread and variable of the species studied, and (2) numerous named species or varieties were placed in symonymy under *S. libertina* by Kuroda (1963) and the possibility does exist that some of these, e.g., *S. nassaeformis* and *S. kawamurai*, may be good species.

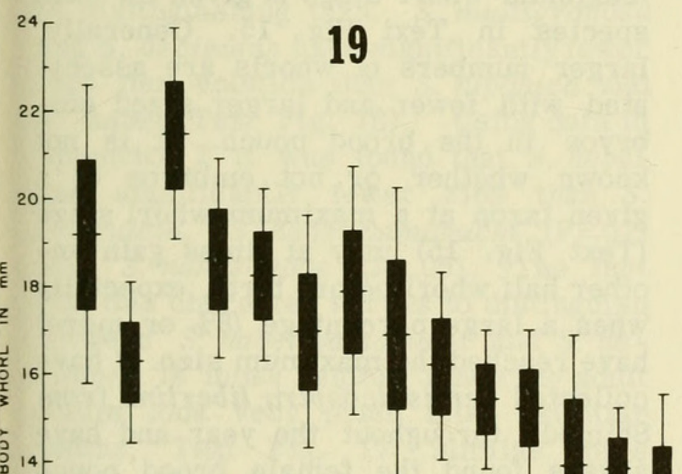
1a. Basal cords average 8 to 10; more than 80 embryos per pallial brood pouch. 2
1b. Basal cords average 6 or less; fewer than 60 embryos per pallial brood pouch. 3
2a. Embryos small, without ribs . . *S. libertina*
2b. Embryos medium in length, with pronounced ribs . *S. reiniana*
3a. Adults without ribs on the penultimate and body whorls; ribs, when present are on 1 or 2 apical whorls only 4
3b. Adults with distinct ribs, from early whorls to the body whorl. 6
4a. Adult spire angle from 12 to 16 degrees; basal cords 2 or 3; embryos large, elongate and with up to 4½ to 5 whorls in the brood pouch . . . . *S. multigranosa* (smooth morph)
4b. Adult spire angle from 15 to 34 degrees; basal cords 3 to 6; embryos large or medium in length, elongate or globose, and with up to 3½ whorls in the brood pouch 5
5a. Adult spire angle 24 to 34 degrees; embryos large and globose . . . . *S. nakasekoae*
5b. Adult spire angle 14 to 21 degrees; embryos medium in length and elongate. . . .*S. kurodai*
6a. Ribs on adults 9 to 13 with 3 or 4 large pustulate nodes on each . . . . *S. niponica*
6b. Ribs on adults 13 to 37 with 5 or more nodes per rib 7
7a. Adults with 20 to 37 ribs on the penultimate whorl (averaging 22 to 32); embryos up to 4½ or 5 whorls in the brood pouch. . . 8
7b. Adults with 12 to 24 ribs on the penultimate whorl (averaging 14 to 22); embryos up to 3½ whorls in the brood pouch 9
8a. Embryos globose, with 13 to 15 ribs; adults with 26 or more ribs (averaging 28 or more) on the penultimate whorl, with 5 to 7 nodes per rib . . . . *S. reticulata*
8b. Embryos elongate, with 8 to 12 ribs; adults with 26 or less ribs (averaging 25 or less) on the penultimate whorl, with 7 to 8 nodes per rib . . *S. multigranosa*
9a. Embryos large and globose; adults without external banding . . . . *S. habei habei*
9b. Embryos of medium length and elongate or intermediate in shape; adults with or without external color bands. 10
10a. Ribs of adults smooth to weakly nodulate, 7 to 8 nodes per rib; embryos with 10 to 12 ribs beginning at 1¾ to 2 whorls; embryos elongate. . . .*S. decipiens*
10b. Ribs of adults distinctly nodulate, 5 to 6 nodes per rib; 13 to 15 ribs on the embryo, beginning at 1¼ to 1¾ whorls; embryos intermediate in shape. . . *S. habei yamaguchi*

Discussion on the utility of characters

It is noted in the above key that basal cords and numbers of embryos per brood pouch separate *Semisulcospira libertina* and *S. reiniana* from the remaining species. As seen in Text Figs. 11 and 12, further gaps in the data for these traits are seen in other species. *S. kurodai* is clearly in an intermediate category when both basal cord number and numbers of young per female are concerned. The above 3 taxa are united into a group by having similarly high







TEXT FIG. 17. The 10 taxa of *Semisulcospira* compared in terms of adult shell width. Two populations of *S. reticulata* are compared involving 2 different shell types. Shell type 2 conforms to the "type," while shell type 1 has more convex whorls. Two populations of *S. libertina* are compared. The mean and 2 standard deviations are given.

TEXT FIG. 18. The 10 taxa of *Semisulcospira* compared in terms of adult shell spire angle. Shell type 2 of *S. reticulata* conforms to the "type," while type 1 has pronounced convex whorls. The mean and 2 standard deviations are given.

TEXT FIG. 19. The 10 taxa of *Semisulcospira* compared in terms of length of body whorl of the adult shell. Two populations of *S. libertina* and *S. reticulata* are compared. The latter involved type 2 shells conforming to the "type," and type 1 shells with pronounced convex whorls. The mean and 2 standard deviations are given.

chromosome numbers of n=18 or 20 (Table 42). This group is called the "*S. libertina* species complex." The other species group, the "*S. niponica* complex," is characterized by low chromosome numbers (n=7 to 14), low numbers of basal cords (mean numbers of 2.5 to 5), and comparatively few embryos per female (mean numbers of 5 to 25).

At this point, secondary characteristics become important in discriminating between species. As discussed above, the presence or absence of ribs is not a good secondary character; however, the ontogeny of ribs is excellent. Both *Semisulcospira kurodai* and *S. nakasekoae* have a particular development and morphology of rib not seen in other species. The early cessation of rib formation in the former is particularly striking. With the exception of *S. nakasekoae* and the smooth morph of *S. multigranosa*, other members of the *S. niponica* complex have well developed ribs throughout ontogeny.

As seen in Text Fig. 13, the number of ribs on the penultimate whorl serves to distinguish several species of the *Semisulcospira niponica* group. It is evident at a glance that *S. reticulata* has significantly more ribs than *S. multigranosa*, and that *S. niponica* has significantly fewer ribs than *S. decipiens*. Similarly, *S. multigranosa* has significantly more ribs than *S. habei yamaguchi*, *S. nakasekoae* and *S. decipiens*. The number of nodes on the ribs of these species characterizes some of the species. *S. niponica* has 3 or 4; *S. decipiens* and *S. multigranosa* have 7 or 8; *S. habei* and *S. habei yamaguchi* have 5 or 6.

Embryo size and shape vary considerably between species, as shown in Tables 38 and 40, and Text Fig. 14. These differences are accentuated when plots are made of increments of dimension per whorl (Text Figs. 5 to 8). The curves in these figures demonstrate significantly different patterns of development in the female brood pouch. Consider the very significant difference between the curves for length of shell per whorl when data from *Semisulcospira libertina*, *S. decipiens* and *S. multigranosa* are plotted (Text Fig. 5). It is also evident in these figures that 2 or more species may have similar developmental patterns. For example, *S. reiniana* and *S. kurodai* are identical in terms of mean length per whorl. *S. niponica* and *S. multigranosa* have similar curves for length of shell per whorl, but the former closely resembles *S. reticulata* in terms of increment of length/width ratio per whorl (Text Fig. 10). The feature of greatest whorl stage attained by an embryo in the brood pouch (Text Figs. 5-10, 15) often serves to separate those taxa with otherwise similar curves and to characterize each species.

Embryos reach a maximum whorl stage in the brood pouch of 3 to 5 whorls, depending on the species. The percentages of embryos reaching the maximum whorl stage is given for each species in Text Fig. 15. Generally, larger numbers of whorls are associated with fewer and larger sized embryos in the brood pouch. It is not known whether or not embryos of a given taxon at a maximum whorl stage (Text Fig. 15) may at times gain another half whorl before birth, expecially when a large percentage (8% or more) have reached the maximum size. I have collected *Semisulcospira libertina* from Shimoda throughout the year and have always found the female brood pouch full of embryos no larger than 3 whorls. However, as it may be possible for a species such as *S. habei yamaguchi* to have embryos with 4 whorls, I have used this character to separate taxa on the basis of at least 1 whole whorl difference.

Gross sculpture on the embryos is an important secondary character. There are taxa with no nodes or ribs, taxa with nodes, and taxa with ribs (Text Fig. 16). Taxa without ribs are prominent in the *Semisulcospira libertina* complex, but *S. reiniana* is the exception with well developed embryonic ribs. *S. libertina* from both localities has smooth embryos. In later studies (Davis, 1967b, 1969), I found 1 embryo from a female from Shimoda which had distinct nodes on the shoulder of the second whorl and the nodes were elongated into ribs. In the afore mentioned population at Ashino Lake, the embryos of the prominently ribbed adults had well developed nodes at the shoulder of the whorl. In some of these, ribs developed by the elongation of the node. *S. kurodai* is characterized by embryos with nodes which occasionally elongate into ribs. The embryos of these taxa are also similar in that they possessed 1 or 2 spiral cords. Not all embryos generally characterized by nodes or ribs have spiral cords. In *S. reiniana*, for example, 20% of the embryos at 3 whorls lacked ribs.

In the *Semisulcospira niponica* complex the number of ribs on the initial ribbed whorl of the embryo shell helps in distinguishing taxa. *S. multigranosa* and *S. decipiens* have significantly fewer ribs per volution than *S. niponica* and *S. habei* (Text Fig. 16). Using data in Appendix 2 it was found that *S. habei* has significantly fewer ribs than *S. reticulata*, *S. habei yamaguchi* (P=.01) and *S. nakasekoae* (P=.05). The fact that this character serves to distinguish between *S. habei yamaguchi* and *S. decipiens* is most helpful, since the adult shells look very much alike (similar widths, Text Fig. 17; similar spire angles, Text Fig. 18; similar lengths of body whorls, Text Fig. 19; etc.).

Embryo color patterns are useful in characterizing several species. Brownish embryos characterize *Semisulcospira libertina* and *S. reiniana*. *S. kurodai* has glassy or opaque white shells which may have a yellow or brown basal band on shells of 3 whorls. *S. niponica* has a globose shell with 3 very distinct purple-brown bands. Some embryos of *S. multigranosa* are a uniform purple-black.

Embryos of most taxa have variable color patterns, and therefore the use of color patterns to discriminate between such taxa is best made when other traits are considered concomitantly. For example, *Semisulcospira reticulata* is characterized by having large and globose embryos with shell color patterns of either uniform yellow or banded; none are purple-black. Embryos of 5 whorls are found in the pallial brood pouch.

The presence or absence of cords in populations of *Semisulcospira libertina* was discussed above. *S. kurodai* and *S. libertina* (Shimoda population) both have 2 distinct cords. *S. reiniana* has ribs which terminate on a pronounced cord. Spiral cords on the embryos tend to characterize the *S. libertina* complex. Cords are present or lacking on embryos of species in the *S. niponica* complex. They are not found on embryos of *S. nakasekoae*, *S. multigranosa* and *S. reticulata* (under 6 whorls). *S. habei habei* may or may not have a cord, which, when present, may be either smooth or nodulate. A low cord is found on *S. niponica*. A noded cord is frequently found on embryos of *S. decipiens*.

Traits used to delineate the specific level become less useful when they vary qualitatively from population to population, or when quantitative characters are based on significant differences where P is at the .05 level and/or measurements vary by very small amounts (e.g., apical whorl measurements). With the exception of *Semisulcospira nakasekoae*, statistical analyses must be used to test for significant differences between taxa ranked next to each other by decreasing spire angle, width, or length of body whorl (Text Figs. 17-19). The characters of spire angle or shell width (Text Figs. 18 and 17) are useful as key characters where extremes are separated, e.g., in separating *S. multigranosa* or *S. decipiens* from *S. habei* or *S. niponica*.

It is important to note that shell types 1 and 2 (shells of living shell type 1, and shells of subfossil type 2, station 4) of *Semisulcospira reticulata* had significantly different spire angles (P=.02) and widths (P=.02), although there were no significant differences in lengths of body whorl (i.e., size), numbers of ribs, or nodes on the ribs. Differences in length of body whorl between populations of *S. libertina* and populations of *S. reticulata* indicate differences in degree of growth (population differences). The same holds true for differences in width between populations of *S. libertina* and populations of shell type 1 of *S. reticulata* (Text Fig. 17).

Adult color patterns are extremely variable between populations of the same species. For example, *Semisulcospira libertina* from Amami-oshima all had uniform yellow shells, while those from Shimoda had either uniform yellow or banded shells. *S. libertina* from Ashino-lake had uniform purple-blue, uniform yellow, and banded shells. The banding patterns are variations of a basic pattern of basal, mid-whorl and subsutural bands, where 1 or more bands are often missing or vague. The bands may be a brighter red-purple in some and brown-purple in other populations. Similar banding patterns are seen in other species, e.g., *S. reiniana*, *S. kurodai*, *S. habei yamaguchi*.

A few species have distinctive color patterns. For example, there are no light colored shells in *Semisulcospira niponica*, and the general purple-black or brown-black shell color tends to mask the banding present on some shells. *S. reticulata* has shells that are either uniform yellow or banded. The banded shells are distinct in having a purplish-brown band at mid-whorl.

Semisulcospira multigranosa and *S. decipiens* not only look quite similar, but also both have shells of 3 color patterns: uniform yellow, banded and uniform purple-black. In both species, banded shells have a yellow stripe at mid-whorl flanked on either side by purplish-brown bands.

Microsculpture appears to vary, partly with the population. For example, *Semisulcospira libertina* from Shimoda has a distinct cancellate microsculpture not seen on specimens from Amami-oshmia.

Apical whorl measurements are listed in Appendix 2. Unless the measurements are made exactly as demonstrated by Davis (1967a), the mean values may vary significantly from those given. As the order of magnitude of difference between taxa is not very great, and as the measurements are tedious to make, as well as subject to great variation if not done as described, I consider this character of somewhat limited value. The populations of *Semisulcospira libertina* did differ significantly in the width of the apical whorl. The difference between the diameters of the apical whorls of *S. nakasekoae* and *S. reticulata* was 0.14 mm, and the standard error of the mean of each did not exceed 0.009 mm; it is therefore evident that a distinct order of magnitude of difference exists between these two species. Significant differences exist between the mean values for a number of taxa, but I do not consider these differences especially relevant as diagnostic characters, because the order of magnitude of difference between the means is so small.

Characters environmentally controlled.

The length of the shell and the number of whorls have little meaning when the degree of erosion of the apical whorls is clearly associated with environment. Populations of *Semisulcospira libertina* from numerous areas have been observed and shells from these varied habitats have ranged from nearly entire with 7 to 8 whorls, to severely eroded shells with only the last 3 whorls remaining. It would seem desirable to investigate the relationships between environmental water pH, chemical composition of the water, and growth phenomena in *S. libertina* (rate of growth, degree of shell erosion, width of shell, spire increment angle and length of the body whorl).

VII. CONCLUDING DISCUSSION

Taxa not studied.

This paper probably covers most of the species of *Semisulcospira* found on the 4 main islands of Japan, even though 17 nominal taxa listed in Table 1 are not discussed here. Nevertheless, several of the latter may be distinct species. In this regard, *S. libertina nassaeformis* Kuroda & Kanamura (in Kuroda, 1929), *S. kawamurai* Kuroda (1929) and *Melania reiniana* var. *hidachiensis* Pilsbry (1902) should be studied because of their interesting adult shell characters. In fact, each named taxon should be properly accounted for by studying the topotype population to ascertain if it is a valid species or merely a synonym of another species, and if synonymy is justified, then adequate reason should be given. A number of the nominal species which were not studied were those for which no type locality is known. Others were varieties considered by their authors to be within the species concept of *S. libertina* (e.g. varieties *decussata, plicosa,* and *irrigua* of von Martens, 1877). In the future, I plan to study as many of these nominal taxa as possible.

Identification of species

Concepts for the species presented here were taken from their original descriptions, and expanded on from a study of topotype populations (except for *Semisulcospira reiniana*). Dr. T. Habe, Natural Science Museum, Ueno Park, Tokyo, pointed out to me the topotype populations for *S. kurodai*, *S. nakasekoae* and *S. reticulata.*

The polymorphic nature of *Semisulcospira multigranosa* is noted here for the first time. Specimens of the ribbed morph were sent to Dr. Zilch, Senkenberg Museum, Frankfurt am Main, Germany, who compared them with the type material and thus verified the identification. *S. multigranosa* corresponds, in part, to the ribbed morph figured and discussed by Kajiyama & Habe (1961). The species figured by Kawamura (1918) as this species actually conforms to the type of *S. reticulata.*

Semisulcospira libertina (Gould) was readily located and identified at the Shimoda locality. *S. niponica* (Smith) and *S. biwae*[1] (Kobelt) were readily obtained and identified from Lake Biwa (see figures in Brot, 1874, Pl. 34, Fig. 10; Kobelt, 1879, Pl. 19, Fig 9). *S. decipiens* discussed here corresponds to the specimen figured by Kajiyama & Habe (1961).

Semisulcospira reiniana was described by Brot but the description was first published by Kobelt (1876). No type locality was given. Brot (1874)[2] gives the type locality as "Yokohama (v. Martens)." Martens (1877) described *S. libertina* var. *irrigua* from Yokohama, Japan and this taxon is discussed by Kobelt (1879) under *"Melania Reiniana."* Boettger (1886) studied what he considered to be *S. reiniana* from a brook near Lake Biwa, and which he considered to agree with Brot's illustration of *S. reiniana* (Brot, 1874, Pl. 34, Fig. 14, 14a); Boettger stated that to his knowledge *S. reiniana* previously was known only from "Yokohama (Rein)." The specimens of the population I studied agreed with the original description and the figures given by Kobelt (1876, Pl. 8, Fig. 4; 1879, Pl. 18, Fig. 2).

Reasons for studying the largest 10% of each population.

I have described the species I studied

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[1]This variety is synonymous with *Semisulcospira niponica,* it is simply an extreme form in which the nodules are remarkedly pronounced.

[2]Brot evidently wrote his "Die Melaniaceen" in sections, the last parts apparently were written after the Kobelt paper in 1876 describing *S. reiniana.*

in terms of adult shells and embryos. I used the largest 10% of the population collected to represent the adult condition because (1) material currently present in museums is comprized of the largest examples of a population (for the most part), (2) classical descriptions involve the largest specimens, and (3) criteria for establishing the adult or mature condition in *Semisulcospira* have not been adequately established. The main reason is the latter one. No data have been published which give information on the population structure of any species of *Semisulcospira* so that the following are known: (1) the growth rate of newly born individuals, (2) mortality schedules for the young born, (3) the size and age at which the snails become sexually mature, (4) the sex ratio of the population, and (5) the production of young per female per unit time.

Over a 3 year period, I have observed that many populations of *Semisulcospira* in Japan appear to be in a steady state with regard to the size composition of the population and the maximum size of individuals. When one rapidly collects by hand-picking 1000 specimens from a large population, it is inevitable that the largest individuals are included and that small or embryo snails are few or lacking. If the largest 10% is sorted from the rest on the basis of length of body whorl, and a series of adults (e.g., 25) is chosen at random from these large snails, it then is evident that there is not a great amount of variability in ensuing conchological measurements. For example, the mean length of body whorl of large *S. libertina* from Shimoda was 19.2 mm, with a standard error of the mean of 0.33 mm (Table 2). I subsequently found that this mean length did not change significantly in this population for a 2-year period. I consider the largest 10% of a population to represent the mature condition of the population.

Adult-hood may be defined as that age and size where reproduction is achieved. The problem of using this criterion is that embryos are often found in females which are less than ¾ grown. If adults are characterized by these snails that are in the reproductive state, then the various traits such as spire angle and ribs, etc., must be analyzed in terms of different size classes, and the description for a species then becomes very cumbersome. Additionally, it is of little help to consider as mature snails only those which have stopped growing. There are no objective methods for determining if the snail has stopped growing by simply observing the shell. No varix is formed at the end of growth, as in some hydrobiid snails, although an indication of the slowing-down of growth is often seen in the change in sculpture or color pattern on the body whorl near the outer lip. Ribs which are regularly positioned on the apical whorls, may become irregularly positioned on the body whorl, or they may fade out altogether. Spiral cords may fade out on the body whorl, which often becomes thickened and wrinkled. However, these sculpture conditions resulting from slower growth may persist for a whorl or more (seen in *Semisulcospira reticulata*), which involves a considerable increase in shell length during the period.

No post reproductive stage has been observed in any of the species studied. The largest adult females have had full complements of embryos in their brood chambers. Because of this, and the above factors, it is reasonable to discuss the characteristics of adult and mature snails in terms of the largest 10% of the population. In the absence of knowledge on population structure, this arbitrary level allows for an objective comparison of different populations. It is particularly valid when 300 or more specimens are easily collected from a large and prominent population, which is usually the case. Only *S. habei yamaguchi* and *S. multigranosa* of this study appeared to be rare and diffuclt to locate and collect.

Species groups, characters and the discrimination of taxa.

It is useful to create species groups or complexes within *Semisulcospira* based on the primary characters given in Table 41. The validity of considering the *S. libertina* and *S. niponica* complexes genetically distinct depends upon (1) further studies in cytogenetics as well as future investigations in biochemistry, and (2) further morphological and cytological data from numerous other populations of *Semisulcospira*, including named taxa from Japan not included in this study.

The *Semisulcospira libertina* group is characterized by taxa with a chromosome number of n=18 or 20, adult shells with 7 or more basal cords, and numerous young in the female brood pouch (generally 100 or more). *S. libertina* and *S. reiniana* seem to occupy central positions in the complex, while *S. kurodai* is considered marginal and transitional. *S. kurodai* has a chromosome number of n=18, although the numbers of basal cords ($\bar{X}$ of 5.1) and embryos per brood pouch ($\bar{X}$ of 35.5) are intermediate between the 2 species groups (observe Text Figs. 11 and 12).

The *Semisulcospira niponica* complex is comprized by taxa with chromosome numbers ranging from n=7 to n=14. The adult shells have 2 to 6 basal cords, and there are few embryos per brood pouch (less than 50, usually 35 or less). Species of this complex are endemic to Lake Biwa or its tributaries, and include *S. niponica*, *S. decipiens*, *S. reticulata*, *S. multigranosa*, *S. habei habei*, *S. habei yamaguchi* and *S. nakasekoae*.

Semisulcospira niponica is distinct by both its shell characters and its ecology. It belongs to the "rupicolous" association described for Lake Biwa by Annandale (1922), i.e., those animals habitually clinging to rocks or stones of either shallow or deep water. Typical *S. reticulata* is also distinct in regard to shell characters of adults and embryos, and it is characterized ecologically by being a deep-water (but not profundal) species. *S. decipiens*, *S. multigranosa* and *S. habei yamaguchi* are sympatric; they have an immediate association in their habitats. In the broader sense, 5 species of this complex (excluding *S. nakasekoae* and *S. habei habei*) are sympatric in Lake Biwa, i.e., they live in the same general area. *S. decipiens*, *S. multigranosa* and *S. habei yamaguchi* are sibling species, in that they are difficult to distinguish on shell characters (e.g., they have overlapping ranges of spire angles and rib numbers, and variable strength of nodes on the ribs). It was only when distinct chromosomal differences were found that they could be clearly separated and the limits of shell sculpture variability established. But once they were clearly separated by cytological differences, other specific features became evident. My results here agree with Simpson's (1962) statement that "there are extremely few examples in which species called sibling did not prove to be anatomically distinct when studied more carefully and with simultaneous consideration of all available anatomical characters."

Chromosome number and karyotype data (Burch & Davis, 1967; Burch, 1968) serve to distinguish most of the taxa discussed in this paper. For instance, Burch (1968) stated that *Semisulcospira kurodai* differed from *S. libertina* in that the former had relatively large numbers of acrocentric and subterminally constricted chromosomes, while the latter had mostly metacentric chromosomes (2n=36 in both). It is fortunate that cytological data are so useful in distinguishing taxa in this difficult group where conchological characters are notoriously variable. However, certain limitations and problems relating to the cytological data should be considered when using this information to characterize lower taxa such as species. For example, chromosome number variability probably due to supernumery elements, is present in certain taxa discussed here, and it is not known if taxa separated by a small difference in chromosome number can hybridize. Hybridization, however, is probably not likely when different karyotypes are involved, e.g., a snail with metacentric small chromosomes probably cannot produce offspring with a snail having acrocentric large chromosomes. A difference in chromosome number would further complicate potential for pairing of these structurally different elements. Further, two or more distinct species may have the same chromosome number and seemingly similar karyotypes. It is important therefore to establish criteria in addition to cytological data for distinguishing between lower taxa.

When taxa are compared in terms of classical conchological features it is evident that inter-population variability exists where ranges of values about the mean overlap very much (e.g., spire angle of adult shells, Text Fig. 18). Comparisons of taxa in terms of many of these shell features thus involves statistical treatment. Because of this variability it is evident that a given species has relatively few traits which clearly serve to set it off from other species (i.e., presence of features with non-overlapping variation). Traits associated with adult shell size are particularly variable and unreliable in discriminating between species, e.g., total shell length, shell width, length of the body whorl and (in part) spire angle. Because of the usual erosion of the shell, counts of whorl number are of little use. As has been discussed above (p 270) the presence or absence of ribs does not serve to distinguish between species, and ribbing may vary from population to population, particularly in *Semisulcospira libertina*.

Potentially reliable criterea for defining species are found in the primary traits (Table 41), coupled with embryo size, morphology and intrabrood pouch developmental patterns. Developmental sequences of the embryos help in understanding the ontogeny of shell features basic to the species. The ontogeny of ribs in *Semisulcospira nakasekoae* (p 235) and *S. kurodai* (p 235) are cases in point; also, the globose condition of the embryos of *S. nakasekoae* at 3.5 whorls is correlated with the great spire angle of the adult shells (p 235). Finally, added to the above features are selected traits associated with the ribs on the adult shell, such as numbers of nodes and ribs (especially pertinent in the *Semisulcospira niponica* complex).

The full use of embryo characters for providing reliable traits for species discrimination is dependent on future results of studies involving many more populations of a species such as *Semisulcospira libertina*. For example, embryos of topotypes of *S. libertina* do not have nodes or ribs, according to my initial investigations in 1965. Later, in 1967 I found 1 of 1000 embryos from females of the Shimoda population which had nodes on the shoulder of the body whorl of a 3 whorl embryo. Recently (Davis; 1967b, 1969) I studied topotypes of so-called *S. trachea* (Westerlund) from Ashino Lake, Hakone Mountains, Kanagawa Prefecture, Japan, and as a result of the investigation placed this taxon in synonymy under *S. libertina*. The decision was based on data involving cytology, morphological studies similar to those of this paper, immunology and electrophoresis of proteins from foot muscle extract. The embryos of "*S. trachea*" uniformly had nodes on the shoulder of the whorls. The type of question which arises and which future investigations should answer is: Does some population exist where the embryos have distinct ribs yet all other features fit the present concept of *S. libertina* presented here and in Davis (1967b, 1969)?

Endemism of *Semisulcospira* in Lake Biwa.

With the exception of *Semisulcospira libertina* and *S. kurodai*, all the species which are thus far considered to be distinct valid species come from the immediate Lake Biwa area. *S. reiniana* has been observed living along the shores of the lake. The question naturally asked is: Why are so many species found in such close association? Such speciation as evidenced in Lake Biwa can be understood in part, when one considers the unique features of this lake. As summed up by Annandale (1922), Lake Biwa lies towards the northern fringe of the extension of the Oriental region where extensions of southern faunas characteristic of South China are found. The abyssal fauna of the lake appears to be a relic of a period when the Palearctic fauna extended farther south than it does currently. These ideas are reiterated by Ueno (1937) and again by Horie (1961). Kawamura (1918) gives evidence for a wide belt of overlap in faunas from the Oriental and Palearctic regions (based on fishes and a few invertebrates). Most of Korea is in this belt, as are Kyushu Island, and Honshu Island to a point north of Tokyo.

Lake Biwa is the largest lake in Japan. It has a maximum depth of 104 meters (Horie, 1962) with an area of 674.4 km^2. Horie (1961, 1962) reviews other morphometric features of the lake, and the antiquity of Lake Biwa is discussed by Horie (1961) in light of the available literature. The lake dates back to the Tertiary Period, and its basal deposits are probably pre-Pliocene in origin. In these ancient times, the lake was 60 to 290 meters above its present level, and it extended considerably south (50 km or more) of its present position. With downwarping of the Tertiary peneplain accompained by faulting, the lake level was considerably lowered and the basin has been relatively isolated by barriers for about 1 million years without marked geological disturbances (Horie, 1961).

Endemicity in the lake was discussed by many writers (e.g., see Annandale, 1922; Horie, 1961). As stated by Matsushita (1963), "frequent land connections with the East Asian continent probably from some age of the Mesozoic to the Pleistocene" were characteristic for the geology of Japan.

Semisulcospira is a part of the Oriental fauna characteristically found in abundance in the belt of regional overlap discussed by Kawamura (1918), i.e., throughout Honshu, Kyushu, Korea, and the Ryukyu Islands, as well as Taiwan (Formosa) and mainland China. Quite possibly, *Semisulcospira* invaded Japan from East Asia several times with 1 or 2 representatives of different genetic stock (i.e., the *S. niponica* and *S. libertina* groups?).

Several conditions for speciation have been present within the lake: an immense lacustrine volume divided into numerous niches in the accompanying drainage systems, and a long period of time. Endemism and sympatry have probably resulted because of the drop in lake level with subsequent appearance of elevated barriers preventing immigration or emigration. The shrinking lake forced the association of numerous forms within the limits of the present lake basin and the present single drainage system of the Setagawa River. The drop in lake level possibly resulted in other populations perishing or being excluded to other drainage systems. One such example of possible exclusion is *Semisulcospira kurodai*.

A million years of relative geological stability probably allowed further speciation or incipient speciation such as evidenced by *Semisulcospira habei habei* and *S. habei yamaguchi*. The former is found within the Setagawa River system and the latter is spread throughout Lake Biwa and is sympatric with populations of other species of *Semisulcospira* living in the lake.

The *Semisulcospira libertina* complex is associated with a genetic potential permitting invasion of the Palearctic region of Japan, i.e., northern Honshu and southern Hokkaido. Members of this complex are well represented throughout the belt of regional faunal overlap, as well as north of that belt.

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APPENDIX 1

Statistics of embryo shell dimensions for each whorl stage for species of Japanese *Semisulcospira*

Species	No. specimens	Embryo whorl stage	Shell feature measured	Statistic		
				$\overline{X}$	S	Se
S. libertina		2.0	L	0.95	0.048	0.010
Shimoda	25		W	0.74	0.055	0.011
			LBW	0.78	0.069	0.014
	24	2.5	L	1.16	0.301	0.061
			W	0.84	0.058	0.012
			LBW	0.90	0.067	0.014
	16	3.0	L	1.35	0.094	0.023
			W	0.93	0.050	0.013
			LBW	0.99	0.059	0.015
Amami-oshima	25	2.0	L	0.92	0.081	0.016
			W	0.74	0.060	0.012
			LBW	0.78	0.075	0.015
	25	2.5	L	1.18	0.077	0.015
			W	0.84	0.087	0.017
			LBW	0.96	0.062	0.012
	4	3.0	L	1.39	0.078	0.039
			W	0.99	0.026	0.013
			LBW	1.08	0.035	0.018
S. reiniana	25	2.0	L	0.93	0.102	0.020
			W	0.78	0.078	0.016
			LBW	0.79	0.108	0.022
	25	2.5	L	1.28	0.116	0.023
			W	0.97	0.097	0.019
			LBW	1.03	0.082	0.016
	25	3.0	L	1.64	0.119	0.024
			W	1.19	0.086	0.017
			LBW	1.21	0.104	0.021

Appendix 1 (cont'd)

Species	No. specimens	Embryo whorl stage	Shell feature measured	Statistic		
				X̄	S	Se
S. reiniana (cont'd)	23	3.5	L	1.89	0.118	0.025
			W	1.29	0.072	0.015
			LBW	1.37	0.088	0.018
S. kurodai	25	2.0	L	0.96	0.073	0.015
			W	0.83	0.083	0.017
			LBW	0.81	0.086	0.017
	25	2.5	L	1.25	0.135	0.027
			W	0.99	0.114	0.023
			LBW	1.02	0.149	0.030
	25	3.0	L	1.62	0.110	0.022
			W	1.15	0.067	0.013
			LBW	1.23	0.110	0.022
S. nakasekoae	25	2.0	L	1.14	0.093	0.019
			W	1.05	0.089	0.018
			LBW	1.05	0.088	0.018
	25	2.5	L	1.59	0.197	0.039
			W	1.38	0.148	0.030
			LBW	1.42	0.179	0.036
	25	3.0	L	2.28	0.274	0.055
	24		W	1.86	0.286	0.058
	25		LBW	2.01	0.247	0.049
	9	3.5	L	2.99	0.344	0.115
			W	2.40	0.210	0.070
			LBW	2.57	0.278	0.093
S. habei	17	2.0	L	1.21	0.157	0.050
			W	1.11	0.136	0.044
			LBW	1.09	0.131	0.042
	25	2.5	L	1.63	0.198	0.040
			W	1.44	0.141	0.028
			LBW	1.43	0.156	0.031

Appendix 1 (cont'd)

Species	No. specimens	Embryo whorl stage	Shell feature measured	Statistic		
				X̄	S	Se
S. habei (cont'd)	25	3.0	L	2.23	0.212	0.042
			W	1.79	0.139	0.028
			LBW	1.86	0.158	0.032
	25	3.5	L	2.59	0.162	0.032
			W	2.00	0.123	0.025
			LBW	2.09	0.189	0.038
S. habei yamaguchi	10	2.0	L	1.06	0.088	0.028
			W	0.96	0.079	0.025
			LBW	0.96	0.066	0.021
	5	2.5	L	1.35	0.099	0.044
			W	1.15	0.055	0.025
			LBW	1.16	0.073	0.033
	6	3.0	L	1.78	0.128	0.052
			W	1.35	0.078	0.032
			LBW	1.47	0.095	0.039
	7	3.5	L	2.15	0.161	0.061
			W	1.56	0.181	0.068
			LBW	1.68	0.051	0.019
S. niponica	25	2.0	L	1.14	0.136	0.027
			W	1.08	0.104	0.021
			LBW	1.04	0.129	0.026
	25	2.5	L	1.59	0.200	0.040
			W	1.44	0.177	0.035
			LBW	1.42	0.170	0.034
	25	3.0	L	2.35	0.156	0.031
			W	1.87	0.121	0.024
			LBW	2.01	0.146	0.029
	20	3.5	L	2.83	0.222	0.050
			W	2.11	0.149	0.033
			LBW	2.30	0.183	0.041

Appendix 1 (cont'd)

Species	No. specimens	Embryo whorl stage	Shell feature measured	Statistic		
				X̄	S	Se
S. decipiens	25		L	1.35	0.115	0.023
	25	2.5	W	1.08	0.256	0.051
	9		LBW	1.30	0.074	0.025
	25		L	1.83	0.173	0.035
	25	3.0	W	1.28	0.107	0.021
	9		LBW	1.53	0.103	0.034
	25		L	2.23	0.202	0.040
	25	3.5	W	1.45	0.119	0.024
	9		LBW	1.85	0.106	0.035
S. reticulata			L	1.24	0.307	0.085
Station 2	13	2.0	W	1.19	0.160	0.044
Shell type 1			LBW	1.18	0.150	0.042
			L	1.82	0.257	0.054
	20	2.5	W	1.64	0.024	0.051
			LBW	1.59	0.029	0.061
			L	2.59	0.36	0.108
	11	3.0	W	2.07	0.21	0.063
			LBW	2.24	0.27	0.081
			L	3.60	0.51	0.128
	16	3.5	W	2.61	0.367	0.093
			LBW	2.98	0.688	0.173
			L	4.71	0.39	0.13
	9	4.0	W	3.12	0.32	0.107
			LBW	3.64	0.39	0.13
			L	5.65	0.37	0.140
	7	4.5	W	3.57	0.228	0.087
			LBW	4.27	0.27	0.102
S. multigranosa			L	1.52	0.224	0.085
	7	2.5	W	1.25	0.162	0.061
			LBW	1.33	0.170	0.064

Appendix 1 (cont'd)

Species	No. specimens	Embryo whorl stage	Shell feature measured	Statistic		
				X̄	S	Se
S. multigranosa (cont'd)	6	3.0	L	2.22	0.165	0.067
			W	1.51	0.252	0.103
			LBW	1.85	0.161	0.066
	11	3.5	L	2.77	0.341	0.103
			W	1.84	0.137	0.041
			LBW	2.28	0.242	0.073
	4	4.0	L	3.53	2.94 - 4.18 (range)	
			W	2.09	1.88 - 2.31 (range)	
			LBW	2.85	2.25 - 3.31 (range)	
	10	4.5	L	4.67	0.227	0.072
			W	2.54	0.178	0.056
			LBW	3.66	0.193	0.061

L = length
W = width
LBW = length of the body whorl

X̄ = mean
S = standard deviation
Se = standard error of the mean

APPENDIX 2

Embryo shell features of Japanese *Semisulcospira* measured or counted

Species	Statistics	Apical diameter		Number of ribs
		Apical whorl (mm)	Tip of apical whorl (mm)	
S. libertina				
Shimoda	X̄	0.51	0.19	0
	S	0.03	0.018	-
	Se	0.006	0.004	-
	No.	25	25	-
Amami-oshima	X̄	0.47	0.18	0
	S	0.03	0.02	-
	Se	0.006	0.004	-
	No.	25	25	-

Appendix 2 (cont'd)

Species	Statistics	Apical diameter		Number of ribs
		Apical whorl (mm)	Tip of apical whorl (mm)	
S. reiniana	$\bar{X}$	0.46	0.20	16.0
	S	0.05	0.05	1.60
	Se	0.007	0.007	0.32
	No.	49	49	25
S. kurodai	$\bar{X}$	0.46	0.16	15.0*
	S	0.039	0.027	2.26
	Se	0.005	0.004	0.54
	No.	51	51	17
S. nakasekoae	$\bar{X}$	0.44	0.17	14.0
	S	0.051	0.023	1.63
	Se	0.008	0.003	0.45
	No.	46	46	13
S. habei	$\bar{X}$	0.51	0.16	13.0
	S	0.066	0.018	1.60
	Se	0.008	0.002	0.17
	No.	68	57	88
S. habei yamaguchi	$\bar{X}$	0.47	0.16	14.0
	S	0.040	0.02	1.45
	Se	0.009	0.004	0.34
	No.	22	22	18
S. niponica	$\bar{X}$	0.47	0.16	13.0
	S	0.065	0.025	1.17
	Se	0.009	0.004	0.19
	No.	48	48	36
S. decipiens	$\bar{X}$	0.45	0.15	11.0
	S	0.028	0.019	0.85
	Se	0.005	0.004	0.15
	No.	31	31	31

Appendix 2 (cont'd)

Species	Statistics	Apical diameter		Number of ribs
		Apical whorl (mm)	Tip of apical whorl (mm)	
S. reticulata	$\bar{X}$	0.58	0.17	14.0
Station 2	S	0.077	0.031	1.43
	Se	0.009	0.003	0.24
	No.	61	61	35
S. multigranosa	$\bar{X}$	0.51	0.016	10 ± 2
Station 3	S	0.060	0.03	-
	Se	0.01	0.006	-
	No.	24	23	-

$\bar{X}$ = mean
S = standard deviation
Se = standard error of the mean
No. = number of observations

*generally there are only 15 ($\bar{X}$) nodes which are rarely elongated into ribs.

RÉSUMÉ

UNE ÉTUDE TAXONOMIQUE SUR QUELQUES ESPÈCES DE *SEMISULCOSPIRA* DU JAPON (MESOGASTROPODA: PLEUROCERIDAE)

G. M. Davis

Le but de cette étude est d'établir les concepts taxonomiques de base pour 10 taxa du groupe-espèce concernant les mollusques dulcicoles du genre *Semisulcospira*. Plus de 30 espèces et sous-espèces de ce genre ont été décrites du Japon, y compris les îles Ryuku et Ogasawara. On a obtenu pour la présente étude, les topotypes des espèces précédemment décrites les plus remarquables. Deux taxa sont décrits comme nouveaux, *Semisulcospira habei habei* et *S. habei yamaguchi*.

Les topotypes ont été analysés dans la proportion de plus de 10% de chaque population. Des critères ont été établis sur la morphologie de la coquille adulte, de la coquille embryonnaire et de la poche incubatrice. Les critères ont été analysés et présentés de façon à permettre au lecteur de comprendre les variations naturelles du paramètre mesuré ou compté. On a établi une corrélation avec les études cytologiques de Burch & Davis (1967) et Burch (1968), en vue d'établir des critères spécifiques.

Les taxa ont été réduits à deux groupes-espèces, le groupe de *Semisulcospira libertina* et le groupe *S. niponica*. Le premier est caractérisé par un nombre de chromosomes n=18 ou 20, des coquilles adultes ayant des bourrelets basaux au nombre de 7 ou plus, et par les nombreux jeunes (100 ou plus) se trouvant dans la poche incubatrice (oviducte modifié) de la femelle. *S. libertina* et *S. reiniana* sont les principales espèces de ce complexe. *S. kurodai* est placé dans ce groupe à cause de nombre de chromosomes de ce taxon, qui est n=18; cependant, cette espèce est considérée comme intermédiaire entre les 2 groupes-espèces du fait que, en moyenne, la coquille adulte a 5,1 bourrelets basaux et qu'il y a 35,5 ± 15,4 embryons par poche incubatrice chez la femelle.

Le groupe espèce *Semisulcospira niponica* est caractérisé par un faible nombre de chromosomes, n=7 à 14; par des coquilles adultes ayant 2 à 6 bourrelets basaux et par un faible nombre d'embryons par poche incubatrice (une moyenne de 25,2 ± 9,8 maximum à 5,2 ± 3,4 minimum, selon les espèces). Les taxa compris dans ce groupe sont des endémiques du lac Biwa et de son bassin hydrologique; ce sont: *S. niponica, S. decipiens, S. reticulata, S. habei habei, S. habei yamaguchi et S. nakasekoae.*

Une clé des espèces est fournie pour faciliter l'identification. L'utilité des critères utilisés dans la description des taxa est discutée. Les caractères fondamentaux pour définir les espèces sont: le nombre de chromosomes, le nombre de bourrelets basaux de la coquille adulte, le nombre d'embryons portés par la femelle, l'ontogénie de l'ornementation de la coquille, le nombre de stries et de nodosités sur la coquille adulte, la taille et la forme de l'embryon, les modes de croissance des embryons dans la poche incubatrice, le nombre de tours de spire atteint par l'embryon dans la femelle, la texture et la coloration de l'embryon.

Plusieurs caractères semblent être sujets à variation à l'intérieur d'une population. Ce sont la largeur de la coquille, l'angle de la spire, la longueur du dernier tour de spire, la microtexture de l'embryon, les mesures du tour apical, et la coloration de l'adulte. Dans le groupe-espèce *Semisulcospira libertina,* la présence ou l'absence de stries et la texture de l'embryon sont sujets à de telles variations. L'angle de spire, cependant, est utile pour la différenciation de plusieurs espèces. Le nombre de tours de spire et la longueur de la coquille adulte sont sous la dépendance du milieu.

Semisulcospira habei yamaguchi, S. decipiens et *S. multigranosa* sont des espèces morphologiquement semblables. De plus, *S. multigranosa* est polymorphe ayant des formes lisses et striées, et 3 types de coloration. Quand les résultats d'études cytologiques et de la morphologie embryonnaire sont mis en corrélation, il devient évident que ce sont des espèces distinctes. De nouveaux caractères de coquilles décelables ont alors été notés. Dans le lac Biwa, les espèces suivantes sont sympatriques: *S. habei yamaguchi, S. decipiens, S. multigranosa, S. reticulata* et *S. niponica.*

La majorité des espèces étudiées sont endémiques dans l'aire du lac Biwa, Préfecture de Shiga, Honshu. Plusieurs des conditions requises pour la spéciation sont présentes dans le lac Biwa. Le lac est ancien (Tertiaire) et a eu environ 1 million d'années de stabilité; il a un immense volume lacustre divisé en nombreuses niches. Endémisme et sympatrisme résultent peut être de ce que, lorsque le niveau du lac s'abaisse, des barrières apparaissent qui empêchent l'émigration et l'immigration. La rétraction du lac oblige les associations de nombreux organismes à demeurer à l'intérieur des limites du bassin hydrographique du lac et du seul système de drainage de la rivière Setagawa. Les autres populations ont été exclues du lac ou ont péri. *Semisulcospira kurodai* peut être un exemple d'une telle exclusion. Un million d'anneés de stabilité ont problement permis une nouvelle spéciation ou une speciation naissante, par ex. *S. habei habei* et *S. habei yamaguchi.*

RESUMEN

ESTUDIO TAXONOMICO DE ALGUNAS ESPECIES DE *SEMISULCOSPIRA* EN JAPON (MESOGASTROPODA: PLEUROCERIDAE)

G. M. Davis

El objeto de este trabajo es el de establecer conceptos taxonómicos básicos para 10 "grupos de especies" diferentes, del género de gastropodos dulceacuícolas *Semisulcospira.* Más de 30 especies y subespecies de este este género han sido denominadas para el Japón, incluyendo las islas Ryukyu y Ogasawara. Para el estudio se obtuvieron topotipos de las especies previamente descriptas más prominentes. Dos se describen aqui como nuevas: *Semisulcospira habei habei* y *S. habei yamaguchi.*

Los topotipos fueron analizados en términos del 10% de los más grandes en cada población. Se reunieron todos los datos sobre la morfología de la concha adulta, caracteres conchológicos embrionarios y el desarrollo de los embriones incubados en el saco marsupial. Los datos se analizan y se presentan en tal forma que puedan permitir al lector estimar la variación natural en los parámetros medidos y contados; tambien se correlacionaron con los descubrimientos citológicos de Burch & Davis (1967) y Burch (1968), para establecer conceptos de las especies.

Los taxa se ubicaron en 2 grupos, el de *Semisulcospira libertina*, y el de *S. niponica*. El primer grupo se caracteriza por tener un número cromosomático de n=18 o 20, conchas adultas con 7 o mas cordones basales, y gran cantidad (100 o mas) de juveniles en el saco marsupial (oviducto paleal modificado). *S. libertina* y *S. reiniana* son las especies principales del complejo. *S. kurodai* se coloca en este primer grupo porque su número cromosomático es n=18; sin embargo, la especie se considera como de transición entre los 2 grupos de especies, ya que el adulto tiene por término medio 5,1 cordones basales y 35,5 ± 15,4 embriones en el saco marsupial de cada hembra.

El grupo de *Semisulcospira niponica* está caracterizado por el número cromosomático n=7 a 14, conchas adultas con 2 a 6 cuerdas basales, y pocos embriones en la marsupia (25,2 ± 9,8 maximo, a 5,2 ± 3,4 mínimo, dependiendo de la especie). Los taxa incluídos, en este grupo endémico en el Lago Biwa y su desague, son: *S. niponica*, *S. decipiens*, *S. reticulata*, *S. habei habei*, *S. habei yamaguchi* y *S. nakasekoae*.

Se da una clave para ayudar a la identificación de las especies. Se discute la utilidad de los rasgos usados en las descripciones. Caracteres de importancia básica para definir las especies son: número cromosomático, número de cuerdas basales de la concha adulta, cantidad de embriones llevados por la hembra, ontogenia de la escultura conchológica, número de costulaciones y nudos en la concha adulta, forma y tamaño del embrión, patrón de crecimiento de los embriones en el saco marsupial, tamaño que alcanza el anfracto embrionario dentro del saco, escultura embrional y diseño de color.

Algunos rasgos parecen estar particularmente sujetos a variación intra-poblacional. Estoa son, el ancho de la concha adulta, ángulo espiral, longitud del último anfracto, microescultura embrional, medidas del anfracto apical y diseños de color en el adulto. En el grupo de especies de *S. libertina* la presencia o ausencia de costillas y escultura embrional están sujetas a mucha varación. El ángulo apical es, sin embargo, útil para la diferenciación entre varias especies. El número de anfractos y longitud de la concha adulta están sometidos al control del ambiente.

Semiculcospira habei yamaguchi, *S. decipiens*, y *S. multigranosa* son especies gemelas (sibling). *S. multigranosa* es polimórfica por tener tanto formas lisas como costuladas, y tres patrones de color distintos. Cuando se correlacionaron los datos de estudios citológicos con la morfología embrional, se puso en evidencia las diferencias entre esas especies. Se distinguieron entonces otros caracteres conchológicos. En el lago Biwa las siguientes especies son simpátricas: *S. habei yamaguchi*, *S. decipiens*, *S. multigranosa*, *S. reticulata* y *S. niponica*. La mayoría de las especies aquí estudiadas son endémicas en el área del lago Biwa, Prefectura de Shiga, Honshu. Varias condiciones para la especificación estan presentes en el lago. El lago es antiguo (terciario) y se ha estabilizado hace un millon de años; tiene un volúmen lacustre inmenso dividido en numerosos nichos. Endemismo y simpatría comenzaron quizá cuando el nivel del lago bajó, con la subsecuente elevación de barreras que no permitieron inmigración o emigración. El estrechamiento del lago forzó la asociación de numerosos organismos dentro de los límites del lago corriente y el único sistema de desague del lago Setagawa. Otras poblaciones fueron excluídas del lago o perecieron. *Semisulcospira kurodi* puede ser un ejemplo de tal exclusión. Un millon de años de estabilidad permitió probablemente mayor o incipiente especiación, por ejemplo *S. habei habei* y *S. habei yamaguchi*.

АБСТРАКТ

ТАКСОНОМИЧЕСКОЕ ИЗУЧЕНИЕ НЕКОТОРЫХ ВИДОВ ***SEMISULCOSPIRA*** **(MESOGASTROPODA, PLEUROCERIDAE)** ЯПОНИИ

Г.М.ДЕВИС

В работе рассматриваются некоторые основные концепции для установления систематического положения 10 различных групп видов пресноводных моллюсков из рода ***Semisulcospira***. Более 30 видов и подвидов этого рода было найдено в Японии, включая острова Рюкю и Огасавара. Во время исследования были найдены топотипы наиболее известных из ранее описанных видов. Описываются два новых таксона: ***Semisulcospira habei habei*** и ***S. habei yamaguchi***. Топотипы анализировались в количестве 10% от каждой популяции. Собраны данные по морфологии раковины взрослых форм и эмбрионов и по развитию эмбриональной раковины внутри выводковой камеры. Полученные данные анализировались и представлены в статье для получения естественных вариаций измеренных или подсчитанных параметров. Эти данные согласованы с цитологическими открытиями, полученными Бёрчем и Девисом (1967) и Бергом (1968), чтобы установить видовую специфику.

Таксоны распадаются на 2 группы: ***Semisulcospira libertina*** и ***S. niponica***. Первая группа характеризуется наличием числа хромосом n=18 или 20, семью или более базальными ребрами (**cords**) на взрослой раковине; молодь в выводковой сумке самки (модифицированном мантийном яйцеводе) - многочисленна (100 или более экземпляров).

Основные виды этой группы ***S. libertina*** и ***S. reiniana***. ***S. kurodai*** отнесен к этой группе, т.к. число хромосом у него равно 18; однако этот вид рассматривается как переходный между двумя группами видов, поскольку взрослая раковина у него имеет в среднем 5,1 базальных ребер, а количество эмбрионов в выводковой сумке каждой самки составляет 35,5± 15,4.

Группа видов ***Semisulcospira niponica*** характеризуется меньшим числом хромосом n=от 7 до 14; взрослая раковина имеет от 2 до 6 базальных **cords**, а количество эмбрионов в выводковой сумке каждой самки очень мало (в среднем наиболвщее число 25,2 ± 9,8, минимум, 5,2 ± 3,4 что зависит от вида). Виды, отнесенные к этой группе являются эндемиками озера Бива и его притоков Это - ***S. niponica***, ***S. decipiens***, ***S. reticulata***, ***S. habei habei***, ***S. habei yamaguchi*** и ***S. nakasekoae***.

Имеется ключ для определения видов. В работе обсуждаются валидность тех или иных признаков, употребляющихся при видовом описании. Основными признаками считаются: число хромосом, количество базальных ребер на взрослой раковине, количество эмбрионов в выводковых сумках, онтогения скульптуры раковины, количество и форма эмбрионов, особенности роста эмбрионов в выводковой камере и размер оборотов раковины находящихся в ней эмбрионов, их скульпт у ра и окраска. Некоторые признаки видимо подвержены межвидовой изменчивости. Это ширина взрослой раковины, угол макушки, длина основного завитка, микроскульптура эмбрионов, изменения апикального оборота и окраска взрослых форм. У группы ***Semisulcospira libertina*** ь наличии или отсутствии ребер и скульптуры у эмбрионов имеются также вариации. Угол вершины макушки может служить для различия между некоторыми видами. Количество оборотов и длина взрослой раковины зависит от условий среды. ***Semisulcospira habei yamaguchi***, ***S. decipiens*** и ***S. multigranosa*** являются родственными видами. Последний очень полиморфный вид, имеющий гладкие и ребристые морфы, 3 цветных пятна. После сравнения цитологических данных и морфологии эмбрионов стало очевидным, что это разные виды. В дальнейшем были получены и различия в раковинах. В озере Бива обитают вместе ***S. habei yamaguchi***, ***S. decipiens***, ***S. multigranosa***, ***S. reticulata*** и ***S. niponica***.

Большая часть изученных видов эндемичны для области озера Бива, префектура Шига, Хонсю. Некоторые условия озера способствуют видообразованию. Озеро весрма древнее (третичное) и мало менялось втечение последнего млн. лет; оно имеет огромный объем, распадющийся на многочисленные ниши. Эндемизм и симпатрия возможно возникли, когда уровень озера понижался и возникали барьеры и поднятия, затруднявшие иммиграцию или эмиграцию. Усыхающее озеро приводило к образованию многих групп организмов в бассейне проточного озера с единственным стоком ввиде реки Сетагава. Остальные популяции населения исчезли из озера или погибли. ***Semisulcospira kurodai*** может служить примером такого исчезновения. Миллионы лет стабильности возможно привели к дальнейшему видообразованию или к его начальным стадиям, как в случае ***S. habei habei*** и ***S. habei yamaguchi***.