The Biology of *Terebra gouldi* Deshayes, 1859, and a Discussion of Life History Similarities among Other Terebrids of Similar Proboscis Type[1]

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ABSTRACT: Although gastropods of the family Terebridae are common in sub-tidal sand communities throughout the tropics, *Terebra gouldi*, a species endemic to the Hawaiian Islands, is the first terebrid for which a complete life history is known.

Unlike most toxoglossan gastropods, which immobilize their prey through invenomation, *T. gouldi* possesses no poison apparatus and captures its prey with a long muscular proboscis. It is a primary carnivore, preying exclusively on the enteropneust *Ptychodera flava*, a nonselective deposit feeder. The snail lies completely buried in the sand during the day, but emerges to search for prey after dark. Prey are initially detected by distance chemoreception, but contact of the anterior foot with the prey is necessary for proboscis eversion and feeding.

The sexes in *T. gouldi* are separate, and copulation takes place under the sand. Six to eight spherical eggs are deposited in a stalked capsule, and large numbers of capsules are attached in a cluster to coral or pebbles. There is no planktonic larval stage. Juveniles hatch through a perforation in the capsule from 30–40 days after development begins and immediately burrow into the sand. Growth is relatively slow. Young individuals may grow more than 1 cm per year, but growth rates slow considerably with age. Adults grow to a maximum size of 8 cm and appear to live 7–10 years.

Natural predation on adults 3 or more years old is insignificant, but the sand crab *Calappa hepatica* and the gastropod *Natica gualteriana* successfully prey on younger individuals.

Other terebrids with a proboscis nearly identical in structure to that of *T. gouldi* exhibit similar life history aspects, including habitat preference and prey choice. It is suggested that proboscis types may be useful in predicting basic life history aspects throughout the family.

TEREBRID GASTROPODS are among the most abundant mollusks found in tropical and subtropical sand environments, ranging from the intertidal to depths of several hundred meters. No complete life history has been published for any terebrid species, despite their abundance and relative ease of collection. This study is the first detailed report on feeding, reproduction, and growth for any member of the Terebridae.

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Terebra gouldi Deshayes, 1859, was described from the Hawaiian Islands, and apparently is endemic. It has been recorded from Midway Island to Maui, but no specimens have been reported from the island of Hawaii.

Specimens of *T. gouldi* occur in sand from depths slightly below mean low water to deeper than 100 m. The areas in which it is found are characterized by little or no wave action, soft sand of variable sorting coefficient, and essentially open ocean conditions of salinity and temperature throughout most of the year.

The most distinctive feature of *T. gouldi* is the nature of the foregut, for it belongs to a specialized group of terebrids that lack the typical toxoglossan feeding apparatus and utilize a modified proboscis in prey capture. I call this proboscis the type IA polyembolic
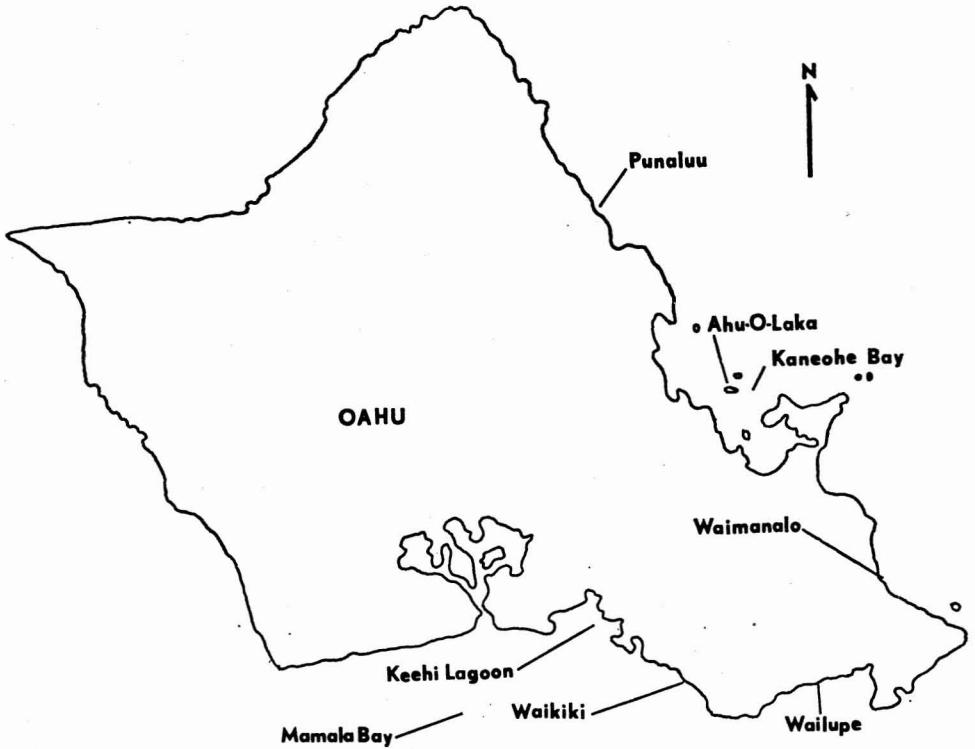
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FIGURE 1. Map of Oahu, Hawaii, showing location of collection sites of *Terebra gouldi*.

(Miller 1970), this term being based on the terminology of Smith (1967). Distinctive behavior patterns are associated with the occurrence of this type of proboscis.

Studies on the ecology and life history of *T. gouldi* were conducted between June 1968 and June 1969 on Oahu. Observations in the field and laboratory were primarily concerned with locomotion, food and feeding, reproduction, development, growth, and predation. Using standard skin- and SCUBA-diving gear, I observed and collected animals from six shallow sites and dredged them from two sites 50 to 100 m in depth. Study sites are indicated in Figure 1. Work was concentrated in two areas: (1) shallow (less than 3 m) sand channels off the coast of Waikiki, and (2) extensive sand flats surrounding Ahu-o-Laka Island in Kaneohe Bay.

GENERAL MORPHOLOGY

The shell is thin, axially ribbed, and reaches a maximum length of approximately 80 mm.

As with many species of terebrids, *T. gouldi* exhibits considerable variation in shell pigmentation, its color ranging from the light tan of specimens in shallow sand flats around Oahu to the very dark brown of specimens in deeper waters leeward of Maui (Figure 2).

The animal (Figure 3) has a large, fleshy foot, short eyestalks, and a long siphon which can be extended to the sand surface when the snail is buried. The mantle cavity contains a small osphradium, gill, and hypobranchial gland. The large, coiled, digestive gland nearly fills the length of the shell spire, surrounding the stomach anteriorly and the diffuse gonad ventrally.

LOCOMOTION

Except for a note by Pearse, Humm, and Wharton (1942) on reburrowing in *Terebra dislocata* from North Carolina and a brief discussion by Mollick (1973) on locomotion in the same species, nothing has been reported in the literature concerning locomotion in the genus
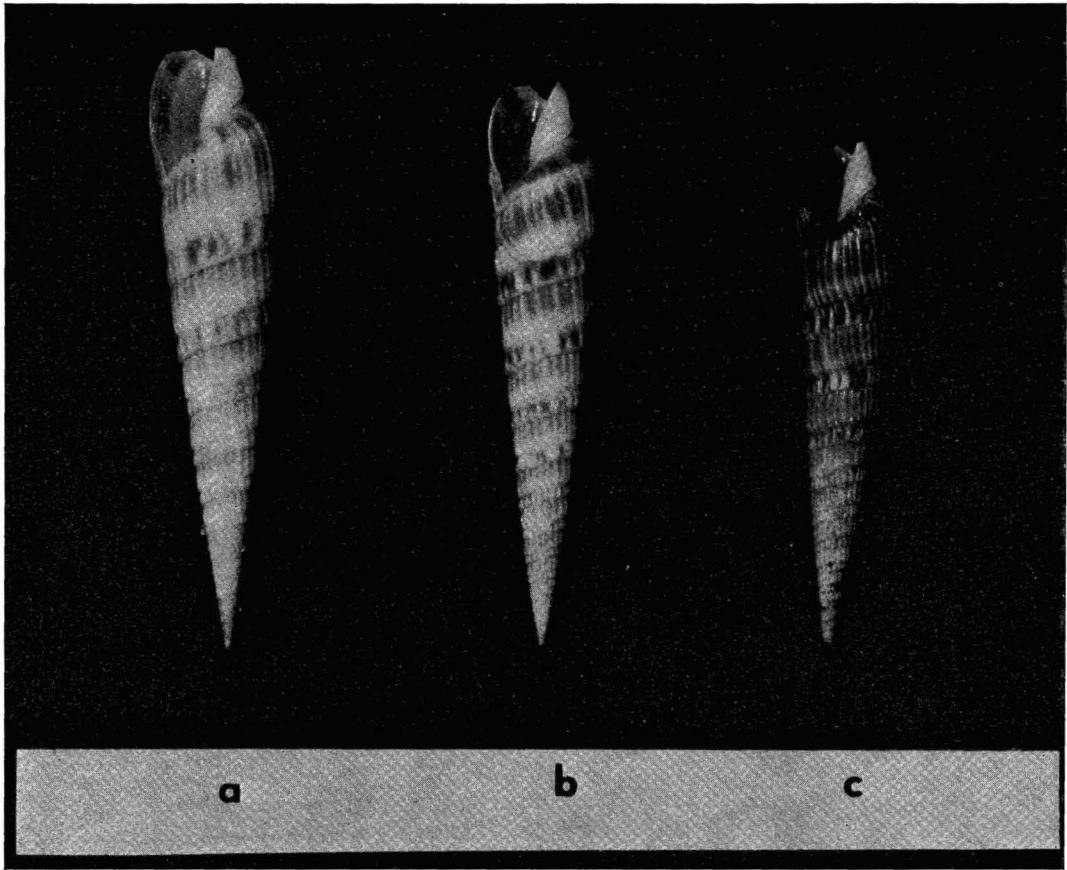
FIGURE 2. Variations in shell pigmentation of *Terebra gouldi* from Hawaii.

Terebra. Observations on locomotory behavior of *T. gouldi* were conducted in the laboratory during winter 1966 and in the field from June 1968 through February 1969. Basic locomotory movements were studied in black sand substrata placed at the bottom of a narrow glass aquarium 30×10 cm on a side. The black sand formed a contrasting background for the crawling animals, and details of locomotion were observed through the glass. Other aspects of locomotory activity were studied in the laboratory in a seawater table exposed to natural light and constantly illuminated by a 25-watt red light, and in the field during daylight hours around the Ahu-o-Laka study area.

From the above observations, behavior under natural conditions can be reconstructed. When *T. gouldi* is not crawling, it lies buried in the sand with the foot fully extended. At this time only the siphon and apex of the shell project to the surface. During daylight hours the tip of the siphon protrudes just above the sand surface, but with the approach of darkness it extends to several centimeters.

When crawling, the snail moves with a loping gait consisting of two distinct movements. First the base of the foot undulates forward with the highly innervated propodium probing the sand, the shell remaining motionless (Figure 4A). When the foot is fully extended, the propodium ceases undulating and is thrust downward into the sand (Figure 4B). Then, with the propodium acting as an anchor, the pedal retractors contract, lifting the shell and pulling it forward (Figure 4C). In this position the propodium begins to undulate again, moving
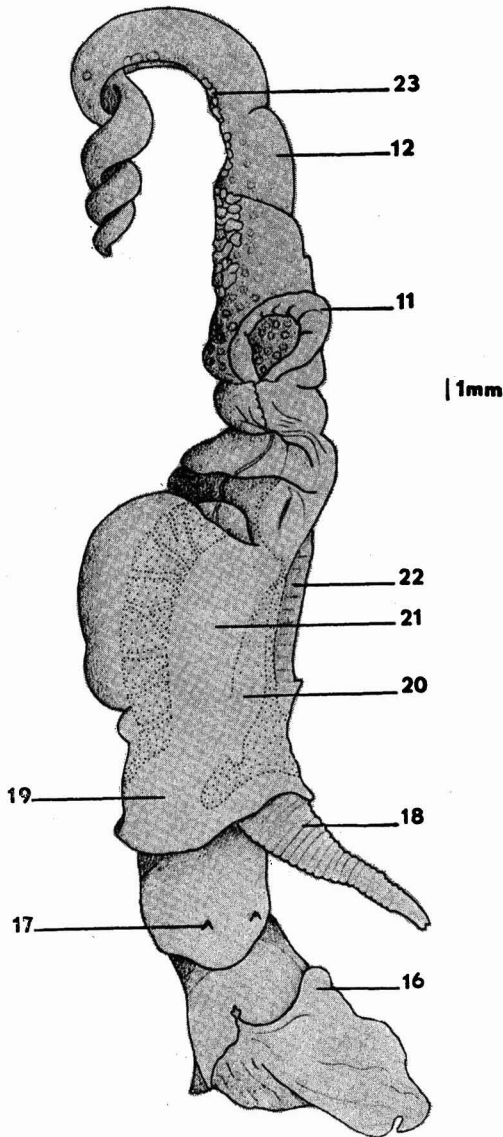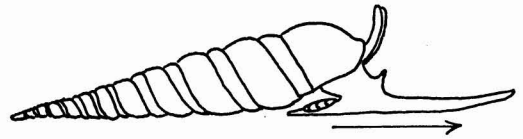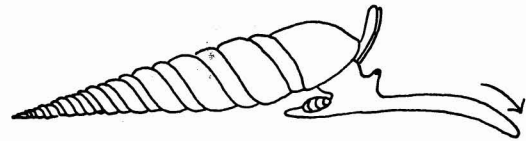
FIGURE 3. Gross morphology of *Terebra gouldi* with the animal relaxed and removed from the shell (dorsal view). *11*, Stomach; *12*, digestive gland; *16*, foot; *17*, eyestalk; *18*, siphon; *19*, mantle; *20*, osphradium; *21*, ctenidium; *22*, columellar muscle; *23*, gonad.

FIGURE 4. *A–C*, sequence of movements of *Terebra gouldi* during locomotion.

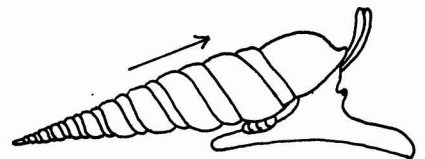forward until the next contraction of the pedal muscles. In the following discussions one complete cycle is considered a step.

The snail usually begins to move about after sunset. When emerging from the sand, the animal first begins to undulate the propodium upward and then it lifts its anterior end out of the sand by a series of forward thrusts until only the foot remains buried. Emergence usually requires less than 1 minute and may involve from six to eight steps.

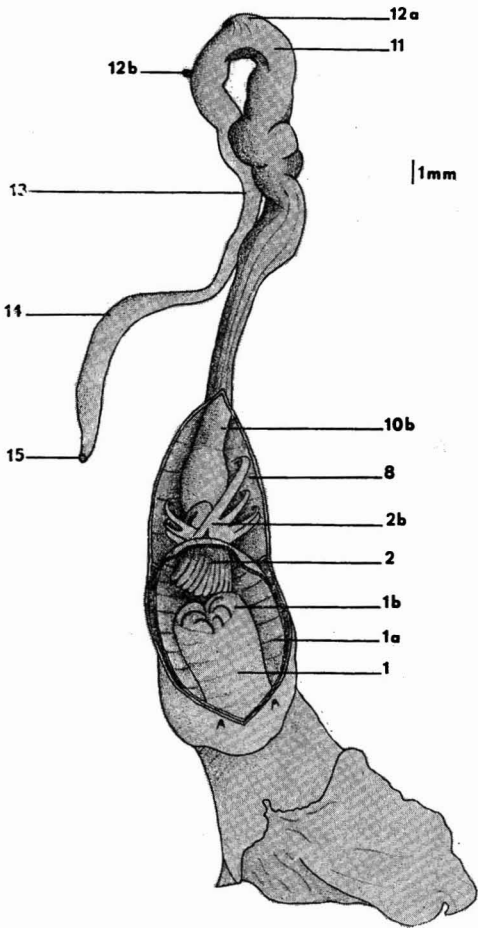Forward locomotion proceeds at a fairly

FIGURE 5. Gross morphology of the digestive system of *Terebra gouldi*. The proboscis, exposed by a cut through the dorsal mantle and body wall, is retracted. *1*, Labial tube; *1a*, labial cavity; *1b*, sphincter of the labial tube; *2*, buccal tube; *2b*, longitudinal retractor muscles of the buccal tube; *8*, cephalic hemocoel; *10b*, postganglionic esophagus; *11*, stomach; *12a*, anterior duct of the digestive gland; *12b*, posterior duct of the digestive gland; *13*, intestine; *14*, rectum; *15*, anus.

Reburrowing in soft sand generally requires from 1 to 3 minutes. The propodium digs downward into the sand at approximately a 45° angle, and pedal contractions similar to those involved in forward locomotion pull the anterior part of the animal below the sand surface until only the siphon and the apex of the shell are exposed.

Periods of activity are sporadic; in the laboratory an individual emerges, crawls, and reburrows several times in an evening. Individuals do not crawl every night, but generally alternate several days of activity with several days of quiescence. During the summer and early fall at the Ahu-o-Laka study site, when wind and wave action are minimal, an average of approximately 50 percent of the individuals in a population crawl in one evening (Miller and Croker 1972). The percentage drops from November through March, when the trade winds periodically cease and strong southerly gusts create substantial wave action and resultant sand disturbance. At these times the animals burrow deeper and locomotion is reduced. If conditions are severe, locomotion of most animals in a population may cease for several weeks.

FOOD AND FEEDING

Data on food and feeding of *T. gouldi* were obtained through gut and fecal analyses and by observations in the field and laboratory. I collected animals by sieving and by following trails during the morning hours, and I worked out details of the anatomy of the feeding apparatus by dissecting fresh specimens that had been removed from the shell after quick freezing.

Gross Morphology of the Alimentary Tract

The alimentary tract of *T. gouldi* is shown in Figure 5 with the proboscis retracted and in Figure 6 with the proboscis everted. As is the case for all terebrids with the type IA polyembolic proboscis (Miller 1970), the primary functional components utilized in prey capture of *T. gouldi* are a long, eversible, labial tube which terminates in an anterior sphincter, and a short retractile buccal tube. The cephalic hemocoel contains the longitudinal retractor

constant pace of 5 to 10 steps per minute. Variations in distances traveled are dependent on animal size and the nature of the terrain. In the field, specimens of average size (40 to 50 mm) in soft sand crawl a distance of from 1 to 3 m in a night. This distance is considerably reduced in substrata other than soft sand. Locomotion is generally directional, and there is evidence of positive orientation into a current (to be discussed later).
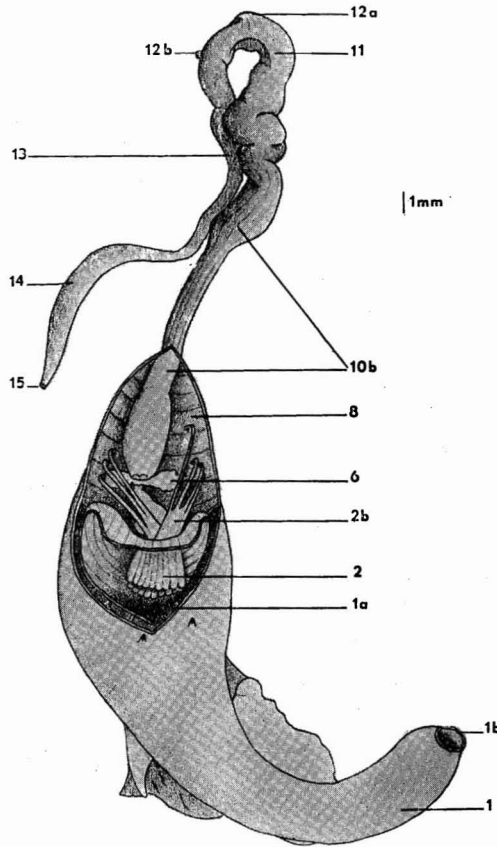
FIGURE 6. Gross morphology of the digestive system of *Terebra gouldi*. The proboscis, exposed by a cut through the dorsal mantle and body wall, is everted. *1*, Labial tube; *1a*, labial cavity; *1b*, sphincter of the labial tube; *2*, buccal tube; *2b*, longitudinal retractor muscles of the buccal tube; *6*, salivary gland; *8*, cephalic hemocoel; *10b*, postganglionic esophagus; *11*, stomach; *12a*, anterior duct of the digestive gland; *12b*, posterior duct of the digestive gland; *13*, intestine; *14*, rectum; *15*, anus.

muscles of the buccal tube, the small bipartite salivary gland which opens into the muscular buccal cavity, and the short, thin-walled, preganglionic esophagus. The distensible, thin-walled, postganglionic esophagus expands in diameter posterior to the cephalic hemocoel and enters into the tubular stomach. The stomach receives two ducts from the digestive gland. Posterior to the point of entrance of the first duct, the stomach curves anteriorly, receives the second duct, then constricts and enters into a narrow, thin-walled intestine. The intestine passes onto the right wall of the mantle and opens anteriorly near the mantle edge.

Diet and Feeding Behavior

Gut contents of 120 specimens collected from June through September 1968 at the Ahu-o-Laka habitat and of 30 animals collected periodically from other study sites around Oahu were analyzed. Fecal remains of 20 animals collected by sieving at Ahu-o-Laka in December 1968 were examined, and the proboscis contents of 80 *T. gouldi* collected from the same area in April 1969 were studied. Animals ranged in length from 28 to 64 mm. These examinations showed that *T. gouldi* of all sizes feed exclusively on the enteropneust *Ptychodera flava* (Table 1), a nonselective deposit feeder that burrows just beneath the sand surface.

Feeding behavior appears to consist of three separate activities: emergence, search, and capture, each being guided by a different set of stimuli.

During the day the animals lie buried in sand

TABLE 1

ANALYSIS OF PREY CHOICE OF *Terebra gouldi** AT AHU-O-LAKA ISLAND

DATE	NUMBER OF SPECIMENS EXAMINED	COLLECTION METHOD	TYPE OF ANALYSIS	PREY	NUMBER OF SPECIMENS WITH PREY	POSITION OF PREY IN GUT		MAXIMUM NO. OF PREY/ *Terebra*
						FORE	HIND	
Summer 1968	62	following trails	gut	*Ptychodera flava*	27	20	7	1
Summer 1968	58	sieving	gut	*P. flava*	6	0	6	1
December 1968	20	trails and sieving	fecal	–	0	0	0	0
April 1969	80	following trails	labial tube exam	*P. flava*	14	14	†	†

* Individuals of all sizes.
† Data not applicable for this type of analysis.

TABLE 2

RESULTS OF FEEDING EXPERIMENTS TO DETERMINE THE METHOD OF PREY LOCATION
BY *Terebra gouldi*

| POSITION OF *Ptychodera* IN THE CHAMBER	NUMBER OF *Terebra* PER TRIAL	LOCATION OF *Terebra* AFTER 14 HOURS		
		LEFT	RIGHT	NEITHER
Left Chamber	10	8	1	1
	10	7	3	0
Right Chamber	10	2	8	0
	10	3	6	1
Neither Chamber	10	5	4	1
	10	4	4	2

with the siphon fully retracted. As darkness falls, the siphon extends and the animals emerge. This action is probably endogenous (Miller 1966), but may also be signalled by the effect of reduced light intensity on siphonal photoreceptive cells. That the siphon contains photoreceptors is indicated by the observation that a flash of light on the siphonal tip causes immediate retraction.

The search for prey begins after the snail has emerged from the sand and appears to be facilitated by distance chemoreception, a hypothesis supported both by observations in the field and by the results of simple choice-chamber tests. When *Ptychodera* are macerated during the evening in the field, the terebrids repeatedly orient into the current and begin moving upstream toward the prey. Results of feeding experiments conducted in a simple Y-chamber (Table 2) further show that animals are consistently attracted to the chamber containing the prey, perhaps in response to some chemical released into the water.

Although distance chemoreception is involved in locating prey, it is not sufficient to elicit labial tube eversion and prey capture, a behavior never observed in the field and difficult to achieve in the laboratory. Freshly captured terebrids placed in a seawater tank containing *Ptychodera* do not feed, no matter how many prey may surround them. However, the feeding response can be elicited in a paraffin-bottom aquarium when animals, starved for several weeks, are placed under low light intensity. Feeding begins only if one end of a worm is wedged into the paraffin substratum when the labial tube is everted, and as the propodium of the foot comes into direct contact with the partially buried prey (Figure 7*A*). Marcus and Marcus (1960) reported that the propodium of the foot of *Hastula cinerea* is a highly innervated sense organ, and the same appears to be true for *Terebra gouldi*.

From the above observations and from others made in laboratory and field, prey capture under natural conditions can be reconstructed. The terebrid slowly crawls up-current over the surface of the sand, attracted by a chemical stimulant released into the water by the *Ptychodera*. When the propodium touches a buried *Ptychodera*, propodial undulations cease, crawling stops, and the foot arches slightly, slowly probing the area. Relaxation of the retractor muscles, along with contraction of the circular muscles, leads to eversion of the labial tube and extension of the buccal tube. As soon as the labial tube is fully everted, the anterior end bearing the sphincter begins "searching" in the vicinity of the propodium for the *Ptychodera* (Figure 7*B*). When contact is made, the sphincter relaxes, and the labial tube completely everts, engulfing the prey (Figure 7*C*). The sphincter then contracts and the labial tube slowly inverts, bringing the worm into close proximity with the fully extended buccal tube (Figure 7*D*). The circular muscles of the buccal tube grasp the worm when contact is made, and the seven retractors inserted around the buccal tube contract, pulling the worm in farther. Immediately the sphincter again relaxes, the labial tube everts full-length to further engulf the prey (Figure 7*E*), and then inverts (Figure 7*F*). At this point, the prey fills nearly the entire labial
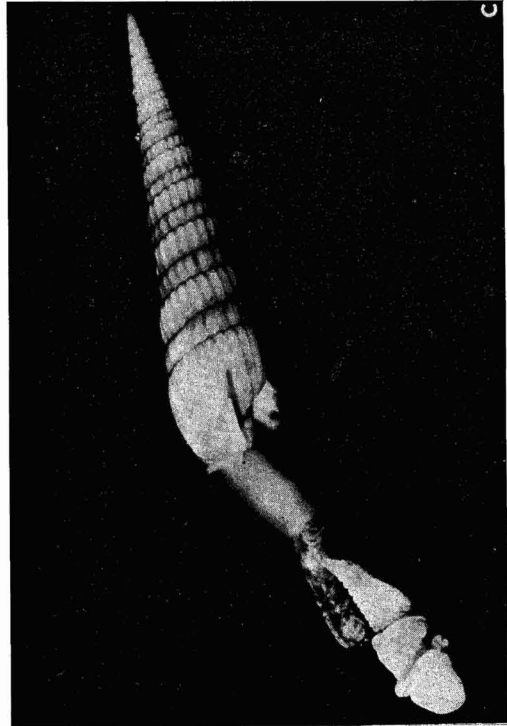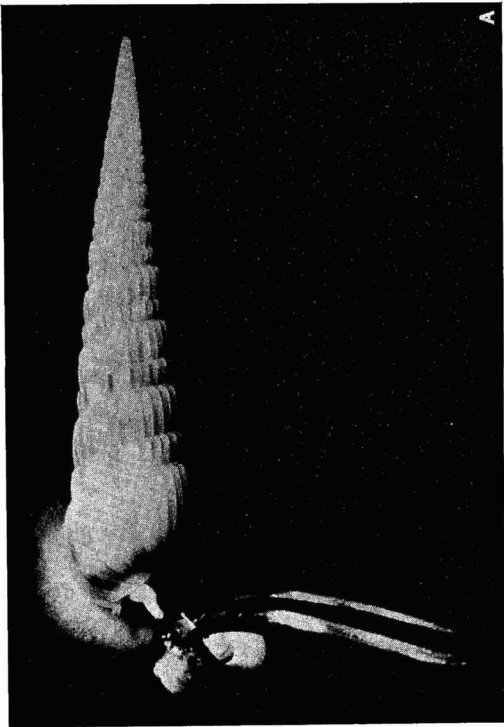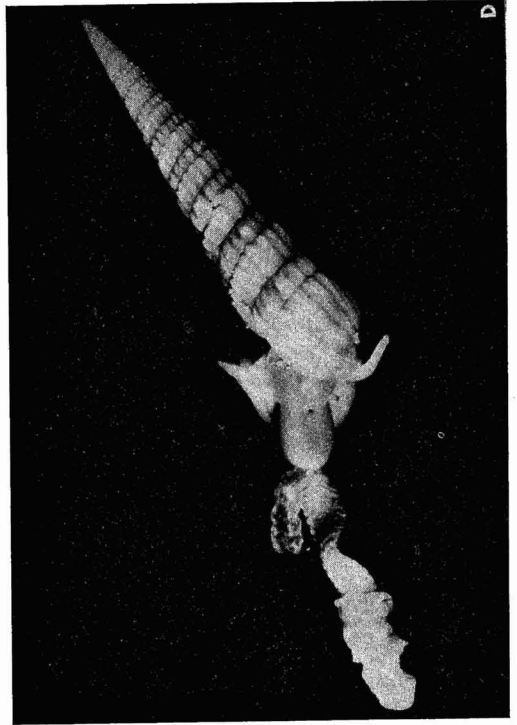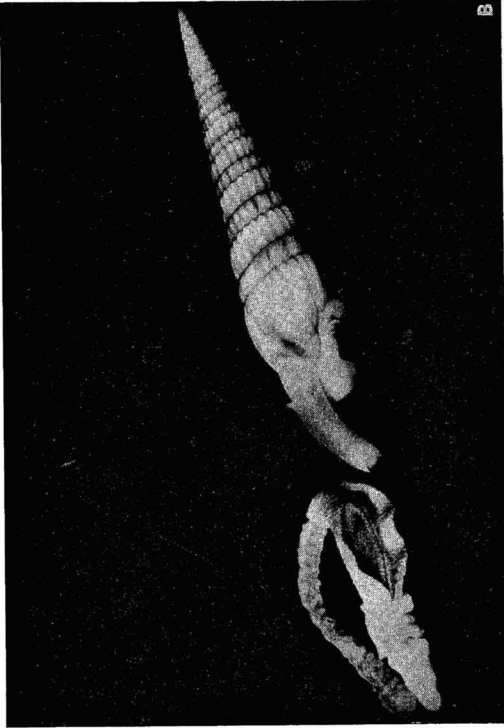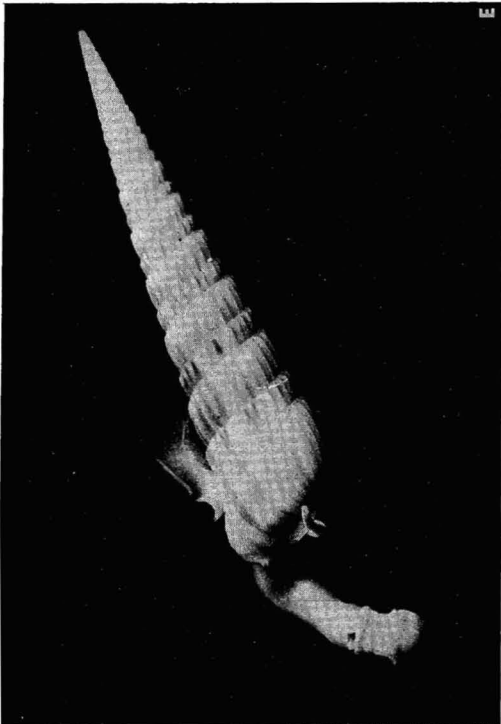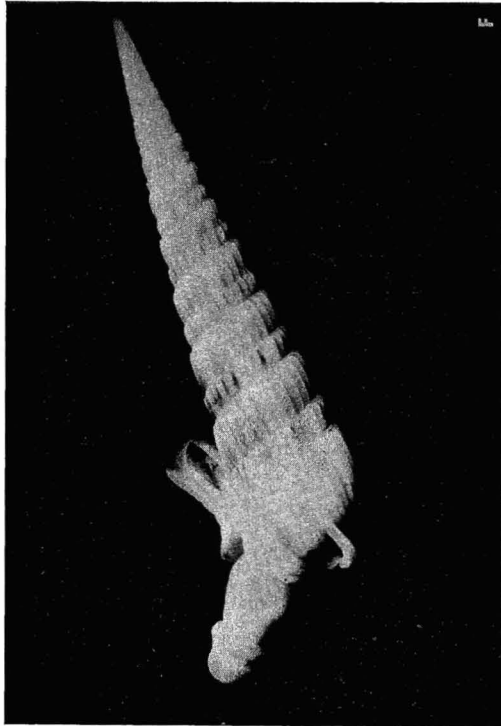
FIGURE 7. *A-F, Terebra gouldi* feeding on the enteropneust *Ptychodera flava*. The sequence depicts the rapid ingestive phase of feeding behavior.

cavity, and the terebrid slowly digs into the sand, remaining there while ingestion and digestion continue at a slower rate.

Ingestion and Digestion

Estimates on the duration of ingestive and digestive processes were obtained by gut analyses of animals fed in the laboratory and dissected at intervals of from 4 to 40 hours after feeding, and by observation on the amount of time elapsed between ingestion and defecation.

Prey capture normally occurs at night, but ingestion usually continues into the daylight hours. In marked contrast to the rapid rates of ingestion noted in turrids (Pearce 1966) and conids (Kohn 1959), the rate of complete ingestion of *Ptychodera* by *Terebra gouldi* is slow, averaging from 8 to 12 hours; and 15 hours may pass before a large worm is fully contained in the esophagus.

Little digestion occurs in the upper esophagus, but prey in the lower esophagus show signs of partial digestion. Digestion fluids from the stomach may be carried anteriorly to the esophagus, as in other toxoglossans. The digestive process is relatively slow and feces are usually not voided until 30 to 40 hours after prey capture. Feces are not compacted, but voided as an amorphous mass of sand and mucuslike material.

Feeding Rates

Feeding rates were studied at the Ahu-o-Laka habitat from June 1968 to April 1969. I collected 62 animals from June through September 1968 by following trails in selected areas during early morning. Because the animals only crawl at night and sand trails are rapidly erased in a short time by water disturbance, the collection represents those animals that had searched for prey the preceding night. The same areas were then thoroughly sieved to collect any remaining animals that had not left trails. Fifty-eight individuals were recovered, this collection representing those animals that had not crawled for at least 1 day. Accordingly, approximately 50 percent of the population sampled during the summer at Ahu-o-Laka had crawled and searched for prey each evening.

The data in Table 1 indicate that none of the animals collected by sieving contained prey in the foregut, and the fecal matter found in the rectum of six of these animals represents remains of *Ptychodera* eaten more than 24 hours before sieving. Twenty-seven of the 62 animals collected when trails were followed contained partially digested *Ptychodera* in the foregut. Thus, approximately 43 percent of the crawling population but only 22 percent of the total population in any one area was successful in capturing prey the previous night. The rate of feeding is considerably lower during stormy winter months when wave turbulence may inhibit locomotion of the entire population for as long as several weeks. Only 20 animals could be located when trails were followed and the sand sieved around Ahu-o-Laka from December through March, and none of these showed evidence of feeding.

Individual feeding rates thus appear to be low. Because prey ingestion takes from 8 to 12 hours, it is probable that a maximum of one *Ptychodera* can be consumed in an evening, and gut analyses have verified this. Based on a maximum feeding rate of 22 percent of the total population of *Terebra* feeding per night, the rate for an individual would appear to average slightly more than one *Ptychodera* per week.

REPRODUCTION AND DEVELOPMENT

Mating

The sexes are separate in terebrids, and fertilization is internal. Mating of *Terebra gouldi* was observed in the field on several occasions, and represents the first reported observation of mating in any toxoglossan gastropod. The mating season of *T. gouldi* is long; copulating individuals were found in the field from mid-March through the end of August.

During March 1969, a typical mating process was observed in shallow water to the leeward of Ahu-o-Laka Island, the description being representative of all succeeding observations. A slight current was flowing along the axis of the island, and two trails were noticed in the sand. The trail of one *T. gouldi*, later found to be female, led into the current, and the animal was observed partially covered with sand and in the process of ingesting a large *Ptychodera*. The second animal, the male, slowly approached from downstream until it contacted the sand trail produced by the female. The male then changed direction and slowly crawled along the trail made by the female until the propodium of its foot touched the apex of the female's shell. The male then slowly crawled along the right side of the shell, stopping when the propodium came in contact with the female's extended foot. The female continued feeding activity for a few minutes, then moved slightly and forcefully regurgitated the prey. Movement of both animals ceased when the male was situated to the right of and slightly above the female and did not begin again for 10 minutes. When both animals were removed from the sand, the distended penis of the male was found to be inserted into the mantle cavity of the female.

Mating in *T. gouldi* always occurs with the male situated above and to the right of the female (Figure 8). As occurs in other gastropods (Fretter and Graham 1962), the normally folded penis becomes distended by hemostatic pressure, unfolds, and enters the mantle cavity. Morphological considerations indicate that the penis is not inserted into the vaginal aperture, but rather that the sperm are transferred by way of the papillary opening of the vas deferens. The penis can be rapidly retracted by a reduction of hemostatic pressure and by contraction of the large penial muscles. Duration of the copulatory process is not known since mating animals were disturbed and returned to the laboratory.

No experimental evidence exists to indicate the method by which one sex is attracted to another, either in the terebrids or in any other toxoglossan. Kohn (1961) discussed the function of chemoreception in the mating of gastropods and reported seeing several aggregates of males and females in *Conus*. Hancock (1959) found large aggregations of *Urosalpinx cinerea* in mass spawning and suggested that some form of chemotaxis may be active in spawning behavior.
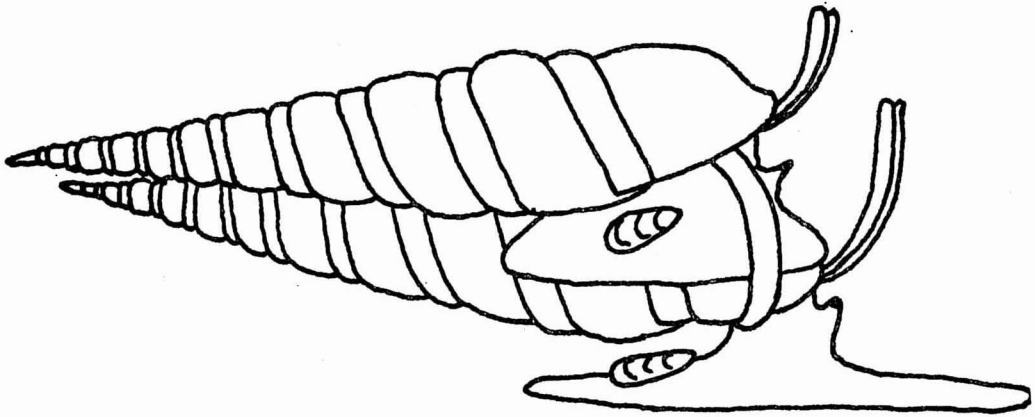
FIGURE 8. Characteristic posture of *Terebra gouldi* during mating.

Egg Capsules

Six copulating pairs of *T. gouldi* found in the field in mid-June 1968 were brought back to the laboratory and placed in an aquarium with running seawater. One cluster of small oblong egg capsules, 1.5 mm in length, was found 27 days later. Each capsule contained from six to eight spherical eggs, 0.5 mm in diameter, and was attached by a thin thread, 2 to 3 mm in length, to several central strands. These strands in turn were attached directly to sand grains and bits of coral rubble. The entire egg mass consisted of 140 capsules, all of which were located above the sand surface.

Development

The egg capsules were placed in a large beaker of filtered seawater supplied with continuous aeration and maintained at a constant temperature of 25° C. When they were first observed, most of the developing eggs were in a late stage of gastrulation. The trochophore stage was passed rapidly, and by the end of the 9th day the embryos were elongate veligers with an extended head vesicle. There were no nurse eggs, and most of the eggs showed normal development. The veligers possessed a relatively small, four-lobed velum, and rotated freely in the capsule. By the end of 30 days the young, having a shell of 2.5 to 3 whorls, had reached the veliconch stage. They measured 0.65 to 0.75 mm in length and nearly filled the
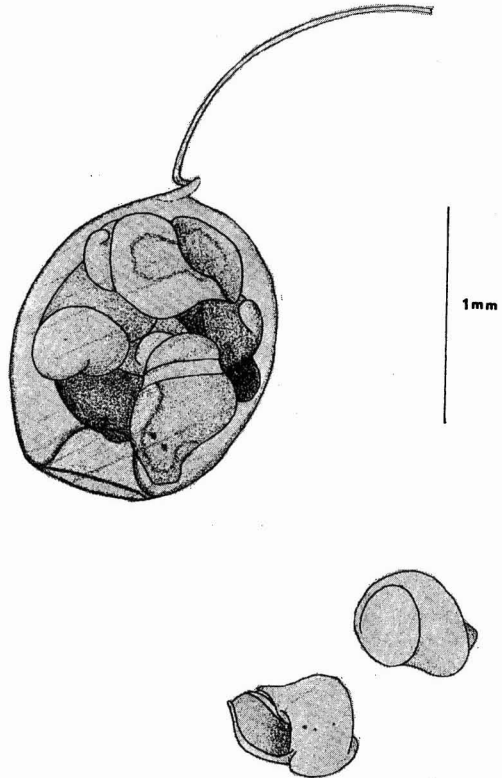

FIGURE 9. Top: a single egg capsule of *Terebra gouldi* containing veliconchs. Bottom: two isolated veliconchs.

egg capsules (Figure 9). The capsular plug was eroded away by the 35th day and juveniles emerged.
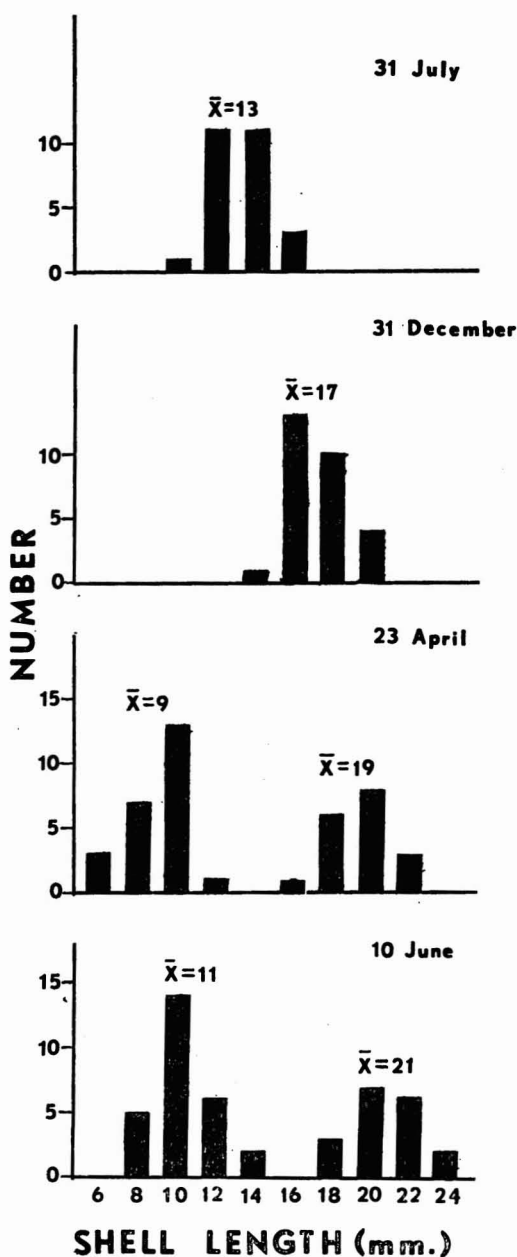
Most known toxoglossan species have a

FIGURE 10. Length-frequency distribution of juvenile *Terebra gouldi* from leeward Ahu-o-Laka Island, 31 July 1968–10 June 1969.

planktonic stage of at least several days, but there is none in *T. gouldi*. The juveniles on emerging immediately dropped to the sand and burrowed in. They remained buried in the sand during the day and crawled at night. Loosely compacted sand appears to be essential for successful settling. Juveniles were kept in shallow petri dishes filled with filtered seawater and sand from the natural habitat, but no feeding was observed and few survived.

GROWTH

Observations on growth in toxoglossans are difficult to make because most species do not feed normally in the laboratory and tagged specimens can rarely be recovered after release in the field. No published data on growth exist for the turrids and terebrids, but Kohn (1959) has made brief observations on the postlarval development of *Conus pennaceus*.

Several unsuccessful approaches were attempted to obtain data on the postlarval growth of *Terebra gouldi*, but the only conclusive data on growth rates were obtained through periodic collecting and measuring of the first and second year classes. A 0.25-inch mesh sieve was used to make collections in July and December 1968 and April and June 1969 to the leeward of Ahu-o-Laka Island. As shown in Figure 10, the peak in the 12.0 to 14.0 mm range probably represents those animals hatched during the summer of 1967 (for reference, termed the 1967 year class). Between July and December the mean shell length of the 1967 year class changed from 13.0 mm to 17.0 mm, an average growth rate of 0.8 mm/month for the first 5 months. Between December 1968 and April 1969, mean shell length of the 1967 year class changed from 17.0 mm to 19.0 mm, an average growth rate of 0.5 mm/month for the 4 winter months. The 1968 age class (spawned in the summer of 1968) appeared in the sieve samples for the first time in April 1969 and had a mean shell length of 9.0 mm. It is possible that this age class would have appeared in the December sampling, but heavy rainfall and high waves made detection of the small sizes in the sieve extremely difficult.

Between April and June 1969, mean shell length of the 1967 year class changed from 19.0 to 21.0 mm, for an average growth rate for the 2 spring months of 0.5 mm/month. During the same period of time, mean shell length of

the 1968 age class changed from 9.0 to 11.0 mm, an average growth rate of 0.5 mm/month.

Growth rates appear to be similar for both the 1st and 2nd year classes, and average 8 to 10 mm in total length per year. The highest growth rates occurred during the summer and fall months when weather conditions were moderate, and the lowest occurred during the stormy winter and early spring.

Adult *T. gouldi* reach a maximum shell length of 70 to 80 mm. Animals of this size may be considerably older than their early rates of growth would indicate, for evidence from other species reveals that growth rates slow considerably in older individuals. Adult *T. maculata* from Enewetak grow very slowly, and large individuals 100 to 150 mm in length appear to add no more than 2 to 4 mm in shell length per year (Miller, unpublished).

PREDATION

Nothing is known concerning predation on the egg capsules or juveniles of *T. gouldi*, but it can be assumed that both are ingested along with the sand by *Ptychodera flava* and other non-selective deposit feeders and perhaps by flounders and other fish foraging over the sand flats.

Most predation in young *Terebra gouldi* results from the action of the sand crab *Calappa hepatica*. Successful predation by this animal was observed in the laboratory on two occasions, and attempts at predation were observed in the field.

Calappa usually lies buried in soft sand, but periodically emerges and slowly walks over the surface, poking the tips of the walking legs deeply into the sand. When potential prey such as a *Terebra* is located, the crab grasps it with the chelae and reburies into the sand. Thus buried, *Calappa* begins chipping away the thin shell lip, gradually rotating the shell as it is cracked, and feeding on the soft parts of the animal when reached. Because shells become considerably thicker with age, predation is usually successful only in younger individuals. After unsuccessful attempts, the lip gradually reforms, but an irregularity on the shell remains that can be used to measure predation attempts throughout the life of each animal.

Calappa predation on young *Terebra gouldi* under 1 cm in length appears to be successful at certain times of the year. Newly hatched juveniles are not attacked by *Calappa* during the fall and winter for, from the time of emergence in late summer until early the following spring, individuals in the *Calappa* population are probably too large to prey on small shells. However, in mid-April significant numbers of *Calappa* 2 to 3 mm in length were observed in the sand, and by June they had grown to 5 to 10 mm in length. Although no cracks were found in the young *Terebra* in April, nearly 50 percent of the 1st year class showed evidence of recent predation attempts in June, several of them successfully completed.

Most of the *T. gouldi* longer than 1 cm showed signs of *Calappa* attack, with less than 5 percent free from any cracks. Most specimens had withstood an average of two to four attacks. However, to prey successfully on *Terebra*, *Calappa* must necessarily break open from 1.5 to 2 whorls, and this rarely occurs. Of 208 *Terebra* longer than 1 cm, only 9 showed sufficient fractures to indicate successful predation.

A few *T. gouldi* shells contained small bore holes, the result of predation by *Natica gualteriana*, a common gastropod in the subtidal sand community. A low rate of predation is indicated, with only 2 out of 219 specimens of *Terebra* examined showing *Natica* attacks.

Kohn (1959) reported that *Conus pennaceus* feeds on *Terebra gouldi* in the laboratory, but it is unlikely that these two species occur together naturally. Because no mollusk-eating cones have been found in association with *T. gouldi*, mortality in those shells lacking cracks or bore holes may be assumed to result from causes other than predation.

Human predation appears to be a significant cause of adult mortality. During low tide when the sand flats at Ahu-o-Laka are barely covered with calm water, many shell collectors wander over the area and collect large numbers of live animals.

DISCUSSION

In addition to *T. gouldi*, four other terebrids with the type IA feeding apparatus are common in Hawaiian waters (Figure 11). *Terebra gouldi*
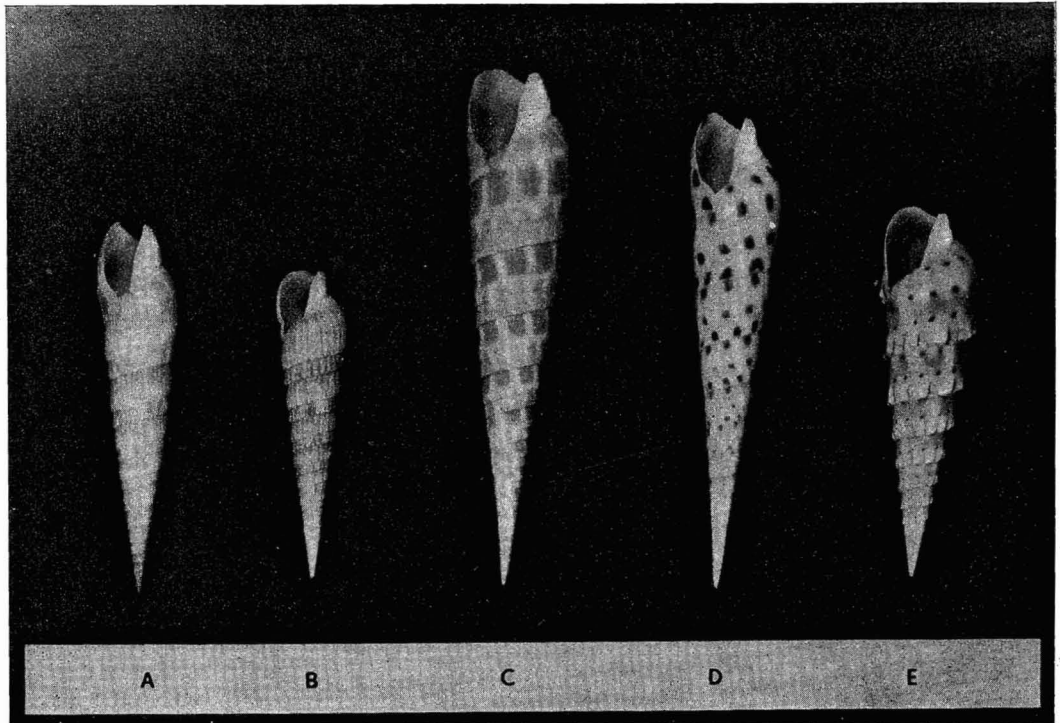
FIGURE 11. Hawaiian species of Terebridae with the type IA polyembolic proboscis (.75 ×). *A, Terebra gouldi* Deshayes, 1859; *B, Terebra thaanumi* Pilsbry, 1920; *C, Terebra dimidiata* (Linnaeus, 1758); *D, Terebra areolata* (Link, 1807); *E, Terebra crenulata* (Linnaeus, 1758).

and *T. thaanumi* Pilsbry, 1920, are endemic, whereas *T. areolata* (Link, 1807), *T. crenulata* (Linnaeus, 1758), and *T. dimidiata* (Linnaeus, 1758) are Indo-Pacific in distribution. All are similar in internal morphology and in many aspects of life history. These terebrids generally live in extensive sand flats protected from strong wave action. They crawl and burrow slowly, feed at night, and rarely emerge from the sand during the daylight hours.

The most striking similarities are observed in the method of feeding and the choice of prey. Because of the lack of a radular apparatus and the short buccal tube present, they would presumably have difficulty in capturing rapidly moving polychaetes, the prey of many radular feeding toxoglossans. I suggest that species with this feeding apparatus are restricted in prey and are specialized such that they feed only on slow-moving, shallowly buried prey.

To determine the prey preference of the other type IA species, I made gut analyses on

T. thaanumi dredged off the coast off Waikiki, on *T. dimidiata* and *T. areolata* from Enewetak, and on *T. crenulata* from Hawaii and Enewetak. *Terebra thaanumi* is conchologically similar to *T. gouldi*, but lives in considerably deeper water. Like *T. gouldi*, it feeds exclusively on *P. flava*. *Terebra areolata* and *T. dimidiata* also feed on *P. flava* at Enewetak. Both species live in beds of medium to find sand at a depth of 3 to 6 m. *Terebra crenulata* lives in shallow sand bars at Enewetak, usually in coarse sand and gravel where it feeds exclusively on *Ptychodera flava*. In Hawaii, *Terebra crenulata* is often found living in the same habitat as *T. gouldi*, and hence the animals compete for the same prey species. *Terebra crenulata* also lives in coarse sand pockets in the reef and feeds on a large, as yet unidentified hemichordate. All of the species except *T. areolata* have fed on *Ptychodera flava* in the laboratory.

These observations tempt one to speculate on the prey choice of other type IA terebrids.

Terebra dislocata, a type IA species found along the southeastern coast of the United States, has been studied by Stewart (personal communication). He had no success in feeding the animal but observed that it lives in close association with a hemichordate. Pearse, Humm, and Wharton (1942) indicated that *T. dislocata* in North Carolina is commonly found in the same habitat as the hemichordate *Balanoglossus* sp. Mollick (1973) confirmed this observation, but his speculation that *Terebra dislocata* and other terebrids may lack carnivorous habits and possibly feed on organic detritus is unfounded. It is more probable that *T. dislocata* feeds on *Balanoglossus*.

It is too early to reach definite conclusions on the taxonomic relationships of terebrids with the type IA feeding apparatus. It is possible, however, that all species of this feeding type have evolved along parallel lines from one ancestral stock and are specialized to exploit the large number of hemichordates occurring throughout the tropics. The study of more species should make it possible to determine the diagnostic significance of this feeding type in a reclassification of the family. I would expect that all species with the type IA proboscis eventually will prove to have similar feeding habits. Similarity in feeding habits and obvious similarities in the morphology of the shell and feeding apparatus may serve to place the type IA species in a separate genus.

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