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STUDIES ON THE BIOLOGY AND ECOLOGY OF SOME INDO-PACIFIC *Terebra* FROM ENIWETOK ATOLL

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ABSTRACT

Some aspects of the biology and ecology of fourteen species of Indo-Pacific *Terebra* collected at Eniwetok Atoll have been studied.

Locomotion in the terebrids is intermittent, and specific differences among species are found in the depth at which crawling occurs in the sand, the effect of the substratum on locomotion, and the nature of the trails produced.

Terebra exhibit both external and internal sexual dimorphism. Mating was observed and described, and differences in the sex ratio and spawning season are discussed.

Terebra are negatively photosensitive to white light, but are unaffected by low intensity red light. Endogenous rhythms of locomotory activity are exhibited by the species of *Terebra* studied. Activity is greatest from 2100 to 0900, and least from 0900 to 2100. The rhythmicity is decreased by continuous illumination from white or red light, and can be reestablished by changes in light intensity.

The functional anatomy of the terebrid digestive system is presented, and the feeding process is described. Differences are noted between *T. maculata* and *T. crenulata* in the nature of the prey, the time of feeding, and the percent of the population feeding each day. Duration of the feeding and digestive processes is discussed.

The shallow water sand community structure of Eniwetok

Atoll is examined. Several factors may lead to ecological isolation among sympatric species of Terebra. These factors include selective differences in substratum preference, specific prey preferences, and differences in the depth at which crawling occurs in the sand.

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I. INTRODUCTION

Members of the gastropod family Terebridae comprise a significant component of tropical and sub-tropical marine sand bottom communities. Nevertheless, practically nothing is known of the habits and life history of these animals.

The family has been thoroughly studied by systematists on the basis of shell characteristics, but no satisfactory classification has been devised. For years it was assumed that all species in the family possessed the typical Toxoglossan structures exhibited by the Conidae, namely the presence of a poison gland and modified harpoon-like radular teeth. According to Tryon (1885), Troschel attempted a dissection of several species of *Terebra*, only to find that there are important differences in the buccal apparatus among species. Troschel would have separated them into three families based on the following characters, had he not been deterred by a lack of sufficient material:

(1) mouth mass at the end of a proboscis furnished with arrow-like teeth, as in *Conus*, and a poison gland

(2) no teeth and no poison gland

(3) mouth with a true radula and no poison gland

Much controversy has arisen as a result of Troschel's observations, some systematists preferring to split the family into several genera, while others are more cautious, restricting the family to the genus Terebra.

Early descriptions of the functional anatomy of the terebrids by Bouvier (1887) led to considerable debate, both among his contemporaries and among those working in the field more recently, such as Risbec (1953), who found some of Bouvier's observations difficult to accept. Past discussion notwithstanding, most current authors cite the generalized characteristics of the Terebridae as established in the late 1800's. The most useful approach at present appears to be that of Rippingale and McMichael (1961), who state that the taxonomy of the family is in such confusion that they avoid the use of generic names other than Terebra until the family is properly studied and monographed.

Interest in the present work on terebrids was not stimulated so much by the confused taxonomic picture as by the paucity of information on the biology of the family. Thorough literature search and discussion with people working on related Toxoglossans indicate that little has been published to date on the general biology of any species of the Terebridae. Several research notes have appeared on aspects of locomotion in terebrids, notably those by Kornicker (1961) on T. salleana, and Marcus and Marcus (1960) on Hastula cinerea, while brief observations *on terebrids have appeared in work by Pearse, Humm, and*

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Wharton (1942) and Hedgpeth (1953).

Because the terebrids are a major molluscan component of tropical marine sand communities, this work is presented in the hope that it will provide for the first time an integrated approach to the biology of the family Terebridae, and that it will lead to a more definitive study of the family, as well as provide more information on the structure of tropical marine sand communities.

II. THE HABITAT OF *Terebra* AT ENIWETOK ATOLL

Location and physical features of the study areas

Studies were done on material from Eniwetok Atoll, one of 29 atolls and 5 islands in the Marshall Islands. Located in the western Marshalls, Eniwetok Atoll consists of 38 small low islets with a total land surface of 2.5 square miles at high tide. The enclosed lagoon, 25 miles long by 20 miles wide, has an average depth of 49 m (Emery, Tracey, and Ladd, 1954).

Collections were made on the lagoon side of 18 islets lying in an arc from Rigili to Aranit, indicated in FIGURE 1, and on the ocean side at Rigili and Eniwetok. All lagoon observations were restricted to tne 24 m terrace, stretching from 300 to 900 m to the lagoon of each islet. Slope in this area is barely perceptible, the bottom dropping to 3.7 m at the edge of each islet, then gently sloping to 7.2 m before again dropping to a greater depth. The bottom is composed predominantly of sand. The chief components are foraminiferan tests, coral fragments, shells, coralline algae, and lesser components. In wave affected areas such as the 2 m sand bar off of Eniwetok Islet, the sediment is coarse, while in the majority of the areas it is fine and chalky. The sand area is interspersed with coral knolls and patches of broken coral, the knolls ranging in size from 2 to 20 m in length, and reaching to within less than 1.8 m of the surface at low tide.

There is no exposure of the sand substratum at the lowest tide, and currents, while generally slight, flow consistently from the NE to SW, except in time of SW storm, when there may be a temporary reversal.

Annual temperature in the ocean near Eniwetok ranges from 26° to 30°C, and generally remains within this 4° range in the shallows of the lagoon.

Collecting areas on the ocean side are similar in physical features. The area off of Rigili is on the leeward side of the islet. It is protected by a fringing reef and appears to differ little from the lagoon side. Ocean collecting at Eniwetok Islet was in a man-made quarry cut into the windward reef flat, 3 m deep and protected by the reef edge from disruptive wave action. The bottom is composed of fine sand, with isolated coral knolls reaching close to the surface. The pool is subject to slightly greater temperature fluctuations than the lagoon, due to heating of the reef flat at low tide. Total sand area of the quarry was calculated to be 640 m^2, dispersed in patches of varying size. Major collection areas at Eniwetok Islet are shown in FIGURE 2.

The family Terebridae from Eniwetok Atoll

Members of the family Terebridae are widely distributed throughout tropical and sub-tropical seas. The species in this study range over much of the Indo-Pacific faunal region from Japan and the Hawaiian Islands to the Indian

Ocean. Because no definitive study of the Eniwetok Atoll bottom community has been published, it is not known how many species are represented in the fauna of the region. Of the approximately 50 or more valid terebrid species named in the Pacific, 14 were found in extensive collections made from June through September and in December 1965 (TABLE I). All of the animals were collected from areas less than 12 m in depth. The classification is according to the key proposed by Kay (unpublished 1966), and the mean shell length is based on the total number of specimens collected.

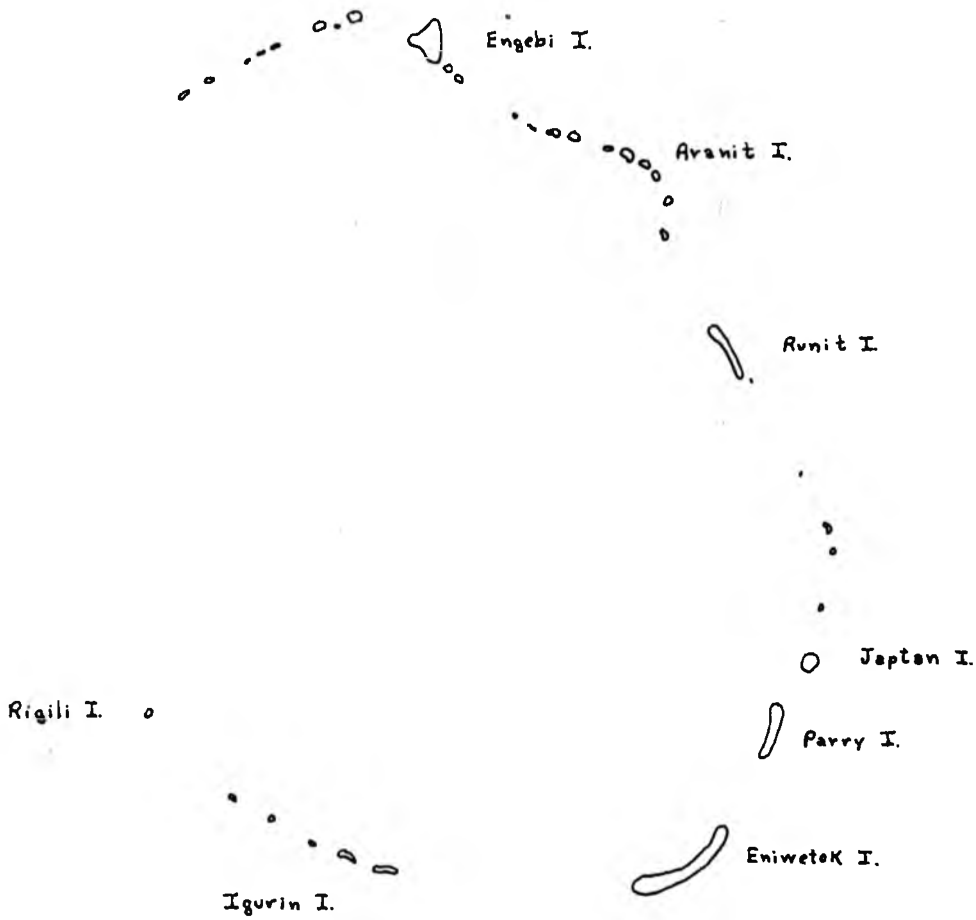


FIGURE 1. ENIWETOK ATOLL, MARSHALL ISLANDS

FIGURE 2. AERIAL VIEW OF ENIWETOK ISLET SHOWING MAIN COLLECTION AREAS IN THE QUARRY AND LAGOON

TABLE I. *Terebra* COLLECTED AT ENIWETOK ATOLL

SPECIES	LENGTH (av. in cm)	TOTAL
Terebra maculata Linne	10.73	845
Terebra crenulata Linne	9.66	229
Terebra subulata Linne	8.32	47
Terebra guttata Roding	7.91	15
Terebra dimidiata Linne	6.98	4
Terebra tigrina Gmelin	6.70	1
Terebra argus Hinds	6.00	1
Terebra cinguilifera Lamarck	5.35	4
Terebra babylonica Lamarck	5.30	2
Terebra laevigatus Gray	4.00	2
Terebra affinis Gray	2.95	82
Terebra picta Hinds	2.81	21
Terebra cancellata Quoy-Gaimard	2.67	4
Terebra solida Deshayes	2.36	14

III. MOVEMENT AND LOCOMOTION IN THE TEREBRIDS

Previous literature on terebrid locomotion

The literature on movements and locomotion of the terebrids is sparse. Pearse et al (1942) mention that specimens of *T. dislocata* from North Carolina burrow back into the sand in less than two minutes after being removed and placed on the surface. Keen (1958) reports that the terebrids crawl about just under the surface, hidden by a mound of sand, although she cites no evidence to support this idea. Marcus and Marcus (1960) briefly discuss the habitat of *Hastula cinerea*, a species that is chiefly intertidal, and mention its movements when exposed to the surface by wave action. Kornicker (1961) reports from field observations in the Gulf of Mexico that *T. salleana* uses its large foot as a sail to repidly accomplish transport to deeper water on a receding tide. Morton (1964) states that most species of *Terebra* trail over the sand and mud, while a few can burrow. Weaver (1959) has observed the tracks of several species of Hawaiian terebrids, and recorded their characteristics for the benefit of shell collectors. The detailed observations in this study are intended to present an integrated picture of the mechanics and characteristics of movement and locomotion in several species of *Terebra*.

<u>Field observations on horizontal traverse in Terebra</u>

<u>Observational techniques</u>. From July 1st to September 6th, 1965, the horizontal traverse of <u>Terebra</u> was observed in the field on 45 days, at various times from 0645 to 2400 hours. Most of the observations were done in 3 to 5 m of water in the lagoon leeward of Eniwetok Islet, and in the quarry windward of the Islet. All observations were performed with the aid of standard skin-diving equipment, and data were recorded underwater on a fiberglass slate.

Experiments were carried out in the field to determine time and frequency of locomotion, distances traversed, and direction of locomotion over a period of time. Several methods of tagging the specimens were attempted until one was found that would withstand tidal action and yet permit freedom of movement for the animals. A small rubber band was placed around the first spire of the shell, and a 38 cm length of string was tied onto the rubber band at the dorsal side (FIGURE 3). Flat pieces of cork, 1 cm in diameter, were tied onto the string, which was consequently buoyed up and kept free from coral and stones. Each cork was numbered with India Ink. Thin plexiglass rods .5 cm in diameter were cut into 25 cm sections, and numbered metal tags were wired to the end of each rod.

Two areas were chosen for observations, a large sandy patch 30 m to the leeward of Eniwetok Islet in 3 to 5 m of water, and a sandy plot in 3 m of water in the quarry. Twenty <u>T. maculata</u> were selected in a length range from

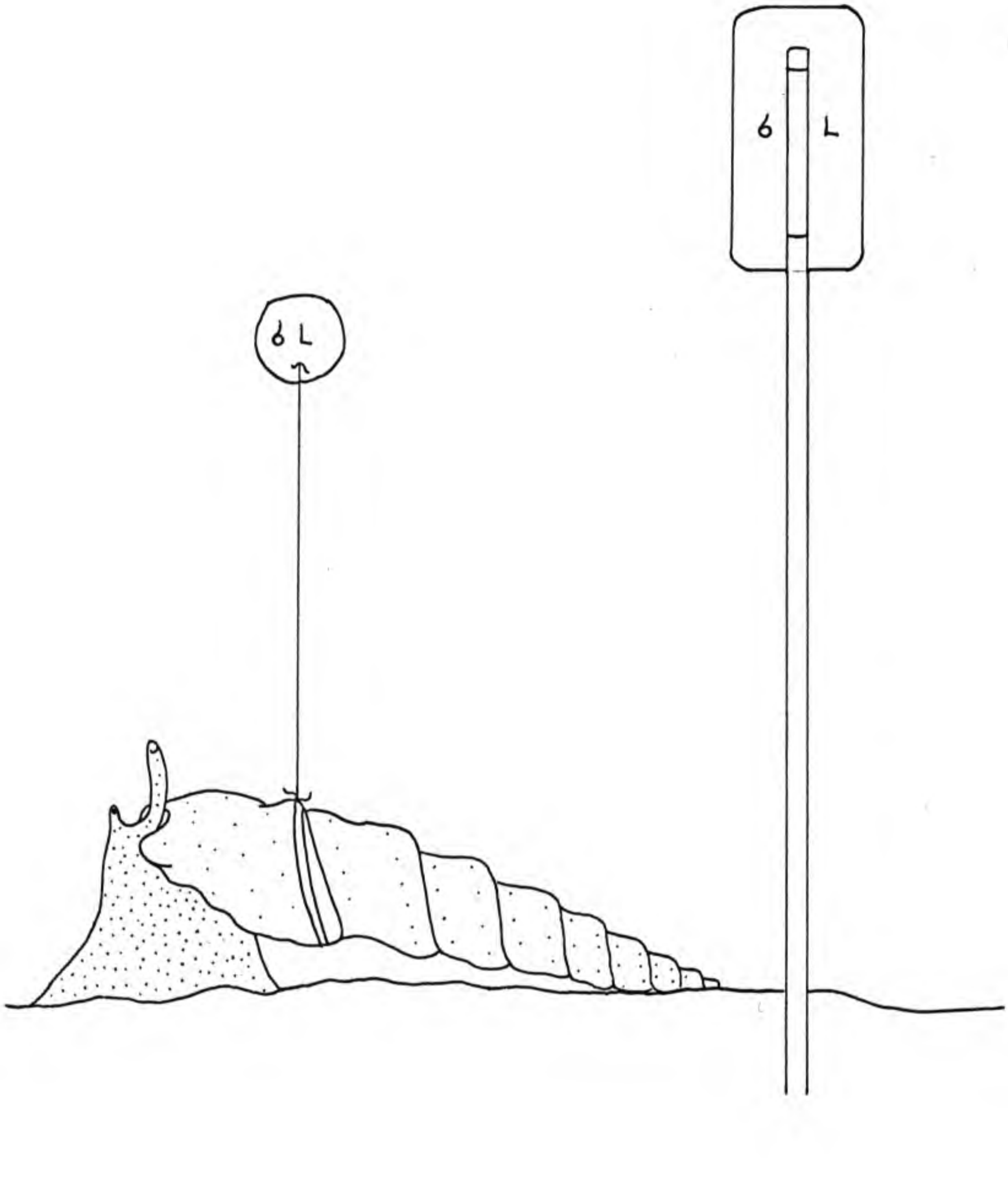


FIGURE 3. TAGGING TECHNIQUE
FOR LOCOMOTION STUDIES

6.4 to 17.0 cm, six _T. crenulata_ in a length range from 8.2 to 11.5 cm, and four _T. subulata_ and two _T. guttata_ in a length range from 7.6 to 13.0 cm.

The first group of tagged animals was placed in the quarry on August 2nd, and the remainder were distributed between the quarry and the lagoon on August 6th. Each animal was placed in the sand, with the fiberglass marking rod inserted in the sand at the apex of the shell. Observations were taken each day at 0900 and at 1600 hours. Paths traversed were determined by following trails in the sand, and the distance of each trail was measured by placing a string, knotted at 1 m intervals, over the trail from the marker to the animal. Each path was drawn to scale on the fiberglass slate, and later transferred to a master sheet in the laboratory.

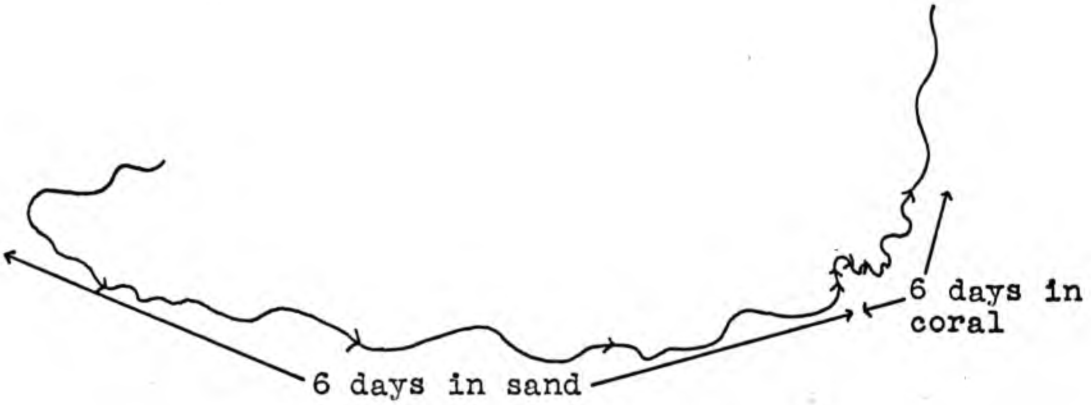
Results and discussion

T. maculata. Trails of _T. maculata_ are best seen in the field from 0700 to 1000 hours. The trail is clearly distinguishable from those of all other species. The range in width is from 6 to 12 cm, depth is from 1 to 3 cm, and termination is in a distinct mound of sand. Although Weaver (1959) has mentioned that _T. maculata_ can be tracked from trails 15 m in length, out of 181 measurements on 21 animals, the greatest length was 6.7 m. Average distance traversed by each specimen per day was 1 m, this average including the days when no locomotion occurred.

In FIGURE 4 the 13 day path is traced and the distance traversed per day is recorded for a specimen of <u>T. maculata</u> moving through alternating patches of sand and coral rubble. Direction of locomotion is random, in that there appears to be no orientation to current or the direction of light. However, there is an avoidance of both coral rubble and coarse sand. The trail of an individual becomes quite erratic when it is in an area of scattered debris, and locomotion through the area may slow considerably.

There are fewer individuals of <u>T. maculata</u> in areas of coarse sand than in equivalent areas of fine sand, but the reason for this is not clear. Because the coarse sand patches are located in shallow areas affected by wave action, it is possible that the animals avoid these conditions. <u>T. maculata</u> has not been found intertidally at Eniwetok, and rarely occurs in areas less than 2 m below low tide level. However, the animals are reported to have been collected from the deepest points of Eniwetok lagoon (59 m), and they have been reported from dredged samples in the Hawaiian Islands at a depth of 64 m.

Data found in TABLE II indicate that locomotion in <u>T. maculata</u> does not occur every day, but rather is intermittent. Considering all 24-hour observations, an average of 35% of the individuals showed no change in horizontal traverse each day. Periods of inactivity ranged from one to five days, although in most cases they were no more than two days in duration. Only one specimen out of twenty showed traverse



DAY NO.	DISTANCE TRAVERSED (in m)	SUBSTRATUM
1	4.0	sand with some coral
2	3.1	" " " "
3	0	" " " "
4	6.0	" " " "
5	6.7	" " " "
6	5.5	" " " "
7	.3	coral rubble
8	.2	" " " "
9	.4	" " " "
10	3.6	coral rubble and sand
11	0	sand with some coral
12	0	" " " "
13	4.1	" " " "

FIGURE 4. THE INFLUENCE OF SUBSTRATUM COMPOSITION ON THE HORIZONTAL TRAVERSE OF A SPECIMEN OF *T. maculata* AT ENIWETOK ATOLL

SPECIMEN LENGTH (cm)	TOTAL DISTANCE TRAVERSED (m)	DAYS WITH NO TRAVERSE	TOTAL DAYS OBSERVED
T. maculata			
17.0	16.8	2	13
15.0	8.8	6	13
13.5	19.5	5	13
11.9	17.6	5	11
10.6	12.2	5	15
10.5	33.9	3	13
10.2	18.9	2	13
10.2	11.0	4	10
10.0	27.1	0	10
10.0	10.1	5	13
9.5	18.8	2	14
9.5	5.5	1	7
8.7	7.3	1	3
8.4	7.3	4	8
8.2	.6	5	7
8.2	7.3	2	13
8.0	3.7	5	13
7.3	5.2	2	11
7.1	2.1	9	11
6.4	2.7	6	9
6.4	2.1	7	11
		81	231
T. crenulata			
11.5	8.8	5	10
10.4	4.3	5	10
8.9	30.5	2	10
8.6	7.9	2	10
8.4	12.2	3	10
8.2	4.9	2	10
		19	60
T. subulata			
13.0	16.5	1	7
12.6	14.8	2	7
12.0	12.5	2	7
11.6	14.2	2	7
		7	28
T. oculata			
11.5	15.9	1	7
7.6	16.5	0	0
		1	7

TABLE II. OBSERVATIONS ON FIELD TRAVERSE OF *Terebra* AT ENIWETOK ATOLL every day.

Field observations on the time of locomotion show that there is very little activity from 0900 to 1600 hours, although on occasion a specimen will crawl in this period. Two evening dives at 1800 and 1900 hours, just before sunset, showed several individuals beginning to crawl, as evidenced by freshly made trails.

T. crenulata. The trails of *T. crenulata* are readily distinguishable from those of *T. maculata* by their narrow width (2-3 cm) and noticeable depth (1-2 cm) in relation to width. They also terminate in a distinct sand mound. Average horizontal distance traversed for the specimens studied was 1.1 m per day. The maximum recorded distance in one day was 7.6 m. Direction of locomotion is random, and is not noticeably affected by either rubble or coarse sand. The animals will crawl over both stones and coral, and the trails often lead into and out of coral patches. *T. crenulata* has occasionally been found at low tide level in Hawaii, and is found in wave disrupted areas at Eniwetok. There is a greater concentration of this species in coarse sand patches, possibly correlated with a greater concentration of its food source, as will be explained later.

Considering all 24-hour observations, an average of 33% of the individuals showed no change in horizontal traverse each day. None of the specimens showed locomotion every day. Periods of quiescence ranged from one to five days, and no locomotion was seen in the field between sunrise and sunset.

T. subulata and *T. guttata*. Trails of these species are very narrow, 1-2 cm, and shallow, .5-1 cm. They seldom terminate in a sand mound. Data on field locomotion in these animals were difficult to obtain, because large specimens are rare, and marking tags were often lost. Locomotion is intermittent, but records are not complete enough to generalize. Average distance traveled for *T. subulata* was 2.1 m per day, and 2.3 m per day for *T. guttata*. The maximum recorded distance traveled in one day for both species was 7.6 m. The paths appear to be rather directional, but this is not certain, for the animals often crawled over coral rubble, and trails were not recognizable. No locomotion was recorded during the hours from 0700 to 2000, which is the same as that recorded for *T. crenulata*.

Laboratory observations on movement and locomotion

Orientation of the animals when buried in the substratum. All species of *Terebra* lie buried in the sand when they are not actively crawling. The foot and head remain relaxed and extended, and the siphon in all cases protrudes through the sand. As will be elaborated later, the position of the siphon is affected by intensity of light. Siphons of those animals kept in the dark may be fully extended, and will reach a considerable distance above the sand surface, while those in light of daytime intensity are noticeably shortened, and in most cases extend only to the sand surface.

The small (less than 3 cm in length) species, such as *T. picta* and *T. solida*, are barely covered by a layer of sand, and at times the dorsal portion of the shell may show through to the surface. The foot is small, and does not dig deeply into the substratum. In spite of their small size, a noticeable mound of sand usually marks the location of the animal.

T. guttata and *T. subulata* are larger species, both exhibiting many similarities in locomotion. The foot of animals of this group extends 2-3 cm below the sand surface, while the base of the shell lies from 1-2 cm under the sand. In the resting position the base of the shell is lower than the spire, and on most occasions part of the apex is exposed at the surface. Consequently most of the shells are badly eroded at the tip, and covered with a coating of green algae on the dorsal surface.

T. crenulata is occasionally found with the tip of the spire exposed, but on most occasions the base of the shell is at least 2 cm below the sand surface, and the foot 3 cm below, so that the shell is covered. As with the above species, the tip of the spire is tilted above the base of the shell.

In *T. maculata*, the largest Indo-Pacific terebrid, the foot may extend from 4 to 10 cm below the sand surface, and the base of the shell lies from 3 to 6 cm below the surface.

The apex of the shell of T. maculata was observed to be exposed only in highly deformed specimens, and observations indicate that even a small specimen of this species lies more deeply in the sand than the other species. The animal possesses an extremely long siphon, and can maintain contact with the surface from a considerable depth.

Mechanics of pedal locomotion in Terebra. Both Fretter and Graham (1962) and Wilbur and Yonge (1964) present detailed accounts of the functional anatomy of the prosobranch muscular system, particularly stressing the pedal musculature. Dissections of Terebra and studies of muscular movement in the laboratory indicate that these animals conform closely to the general prosobranch scheme. The basic muscular components of the foot of Terebra are the longitudinal muscles of the sole, and the muscles of the body stalk and side of the foot, which are continuous with the columellar muscle. The central part of the foot is highly vascularized and filled with a hemocoelic blood supply, hence probably functioning as an efficient hydrostatic skeleton.

Specimens of T. maculata, T. crenulata, T. subulata, and T. guttata were studied to determine the mechanism involved in locomotion. A trough was constructed along one side of a ten gallon aquarium by placing a glass plate parallel to and 5 cm from the side. Fine black lava sand was placed in the trough, and specimens of each species were individually introduced at the end of the trough. The black sand formed a contrasting background for the moving foot, and the entire process could be observed through the aquarium glass. The basic movements are the same for all species observed, the only variations resulting from differences in depth of movement in the sand. While in many gastropods the shell is actively lifted from the substratum in locomotion, the pointed shell of Terebra is only raised at the base where the maximum weight is sustained, while the major length of the shell is dragged along in the sand.

From these observations two basic movements are postulated for locomotion: 1. undulation of the sole of the foot, and 2. contraction of the longitudinal and circular muscles of the body stalk. The movement of the sole is smooth and continuous, with the propodium passing anteriorly through the sand by undulating waves of muscular contractions. When the sole of the foot is fully extended and located anterior to the visceral mass, the undulations of the propodium cease, and the longitudinal muscles of the column contract, forming an elevated stalk. With the propodium as a base, the shell and animal are lifted and pulled forward. Thus the columellar muscles serve not only to control the position of the animal in the shell, but also to return the visceral mass and the shell to the normal position dorsal to the sole. In this position the propodium begins to undulate again, sliding forward until the next contraction of the column. One complete cycle is termed a step.

For purposes of correlation with field observations on excursions, laboratory studies were made under controlled conditions. A bin filled with sand to a level of 10 cm and supplied with constantly running sea water was used for the studies. Forty specimens, ten each of _T. maculata_, _T. crenulata_, _T. subulata_, and _T. guttata_, were introduced and observations between the hours of 2000 and 2400 were made for each species during the month of October.

T. subulata and _T. guttata_ are similar in their locomotory characteristics. Locomotion is usually preceded by a noticeable extension of the siphon, after which the propodium begins to undulate upwards. The animal lifts its anterior end out of the sand by a series of forward thrusts until only the sole of the foot remains buried. The emergence usually requires less than 1 minute and may involve from six to eight steps. Forward locomotion proceeds at a fairly constant pace of from four to ten steps per minute, and the animal covers a distance of from 3 to 5 cm per minute. Variations in distances traveled are associated with animal size and the nature of the terrain. The body stalk is relatively long, and this results in the complete clearance of the main part of the shell from the sand, with only the posterior spire dragging. The foot itself causes little disturbance in the sand, and the resulting trail which is produced by the spire is thin and shallow. Crawling is not markedly hindered by coral in the sand, nor by an absence of sand.

Burrowing requires from 1 to 3 minutes, and is usually initiated after the animal has ceased forward locomotion. The propodium digs downward into the sand, and pedal contractions similar to those involved in forward locomotion pull the anterior part of the shell below the sand surface until only the siphon and the tip of the shell are exposed. With each thrust the shell is slowly twisted forward and to the right, and then rapidly returned to the left. When the animal is below the surface, forward locomotion ceases, but sporadic movement of the shell may continue for several minutes.

Methods of locomotion and burrowing of T. crenulata and T. maculata are similar to those observed for T. subulata and T. guttata. However, some variations are evident. T. crenulata crawls at a rate similar to that of the other species. The principal difference is that the sole of the foot remains deeper in the sand during locomotion. Consequently, more of the shell is dragged, producing a wider, deeper trail. Burrowing into the sand requires more time, and because the animal enters at a lesser angle, it produces a groove terminated by a sand mound. Obstructions in the path normally do not hinder locomotion.

The rate of locomotion for T. maculata is similar to that for the other species, but the mechanism of locomotion differs considerably. Small specimens (1-4 cm in length) often crawl with the sole of the foot shallowly placed into the sand, and with the shell and most of the body above. However, some specimens of the same size were found to crawl with the shell completely covered, or with only the anterior of the shell and the head exposed. Specimens of greater size (5-21 cm in length) were usually found crawling under the s and.

T. maculata has a greatly expanded fleshy foot, as do many gastropods that crawl beneath the sand. The large fleshy foot and bulky shell produce a wide trail and a sizeable mound marking the location of the animal. The animal rarely crawls over obstructions in its path such as coral rubble or stones, but rather circumvents them.

Righting behavior. Many specimens of Terebra in the lagoon were found rooted from the sand and turned on their dorsal side by foraging fishes. To determine methods of righting, ten specimens each of T. maculata, T. crenulata, and T. subulata were removed from the sand and turned on their dorsal surface in an aquarium, with the aperture of the shell directed away from the substratum. All of the animals righted themselves within 24 hours, the process of righting, once initiated, taking from 1 to 3 minutes.

Direction of righting apparently depends on the position of the animal in relation to the substratum. If the animal is placed with the lip of the shell inclined toward the sand, the righting movements will proceed from that side. If the lip is slightly elevated above the horizontal, righting movements will begin on the columellar side. If the animal is placed with the foot perpendicular to the substratum, the direction of righting occurs at random.

Righting over the lip begins with a contraction of the circular columellar muscles. This forces the foot out, and shortly the propodium begins moving in a ventral direction over the lip. When the propodium comes in contact with the substratum, it rapidly displaces the particles of sand and digs in. Shortly thereafter it flexes and the animal uses it as a base to push outward from the body against the sand by further contraction of the circular muscles. If this thrust is successful, the shell begins to rotate on the column, with the lip directed ventrally. Two or three thrusts are necessary to bring the shell around to its normal position. The process is essentially the same for righting over the columellar side.

IV. SEX AND REPRODUCTION

Sexual dimorphism in the *Terebra* population at Eniwetok Atoll

A characteristic of the prosobranch neogastropods is that they are dioecious. Terebrids are no exception, and like other prosobranchs they show varying degrees of external sexual dimorphism. The shell of the male tends to be more acute and the aperture is less round than in the females. The male shell in many cases is more dull than that of the female, and appears to be of slightly greater thickness.

Wilbur and Yonge (1964) state that in a population of gonochoristic gastropods the female is usually larger than the male. They attribute this to a slower growth rate and shorter life span for the males. The results from randomly selected, measured, and sexed *T. maculata* (309 specimens) and *T. crenulata* (53 specimens) collected from the lagoon are shown in FIGURE 5. In both species the females were found to be longer in shell length than the males.

Male reproductive system of *T. maculata* (FIGURE 6)

The cream to yellow colored testis (T), covered with an epithelial membrane, occupies the ventral portion of the visceral mass, extending anteriorly in the mass from the tip of the spire to a position just ventral to the stomach. The testis is many branched, and depending upon the reproductive state, may occupy a greater or lesser portion of the visceral area.

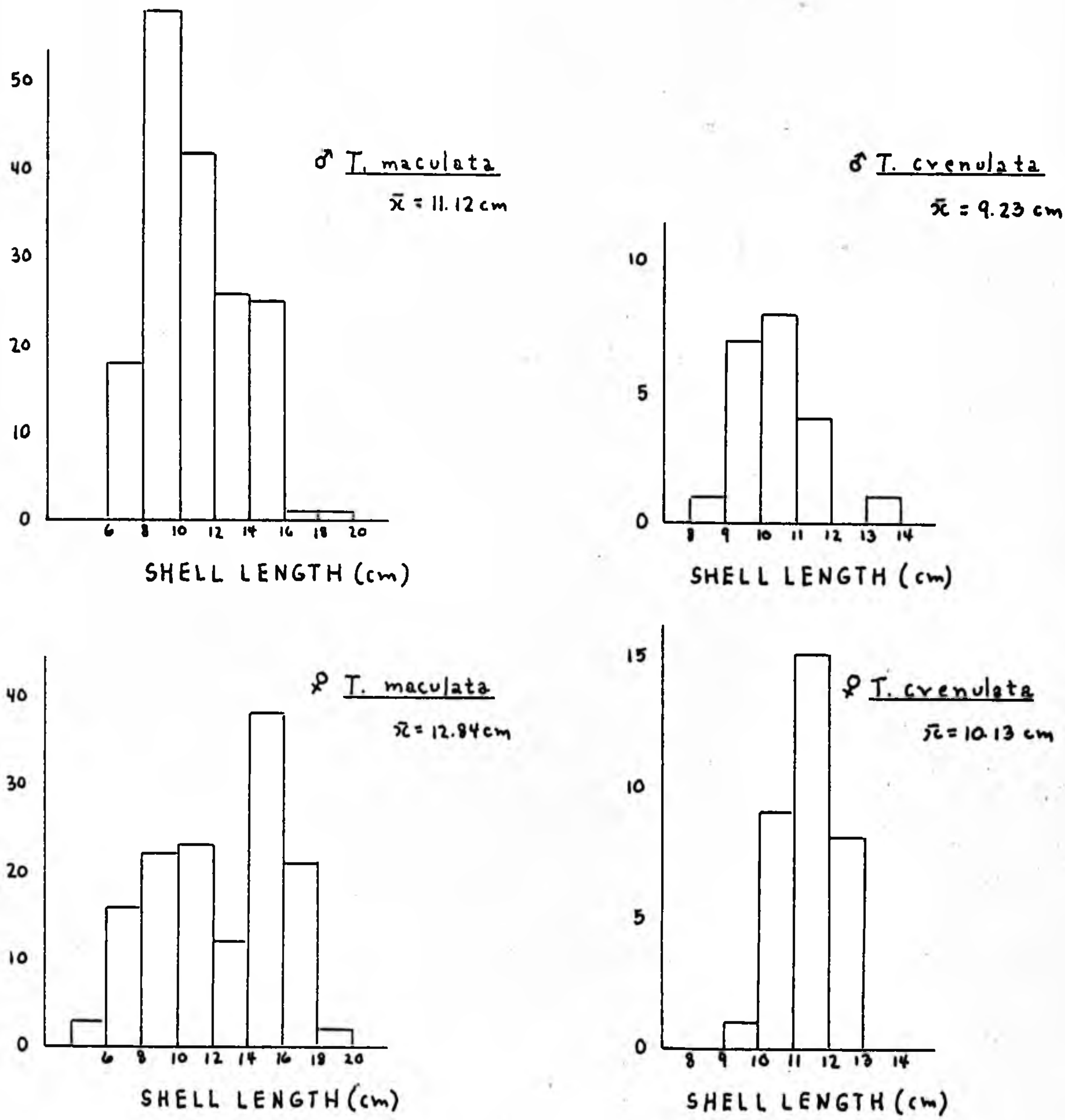


FIGURE 5. COMPARISON OF LENGTH-FREQUENCY DISTRIBUTION BETWEEN MALES AND FEMALES OF TWO SPECIES OF *Terebra* FROM ENIWETOK ATOLL

FIGURE 6. MALE REPRODUCTIVE SYSTEM

OF _T. maculata_

GD.....genital duct (in transparency)

P......penis

PP.....penial papilla

PGL....prostate gland

RVD....renal vas deferens

SD.....seminal duct

T......testis

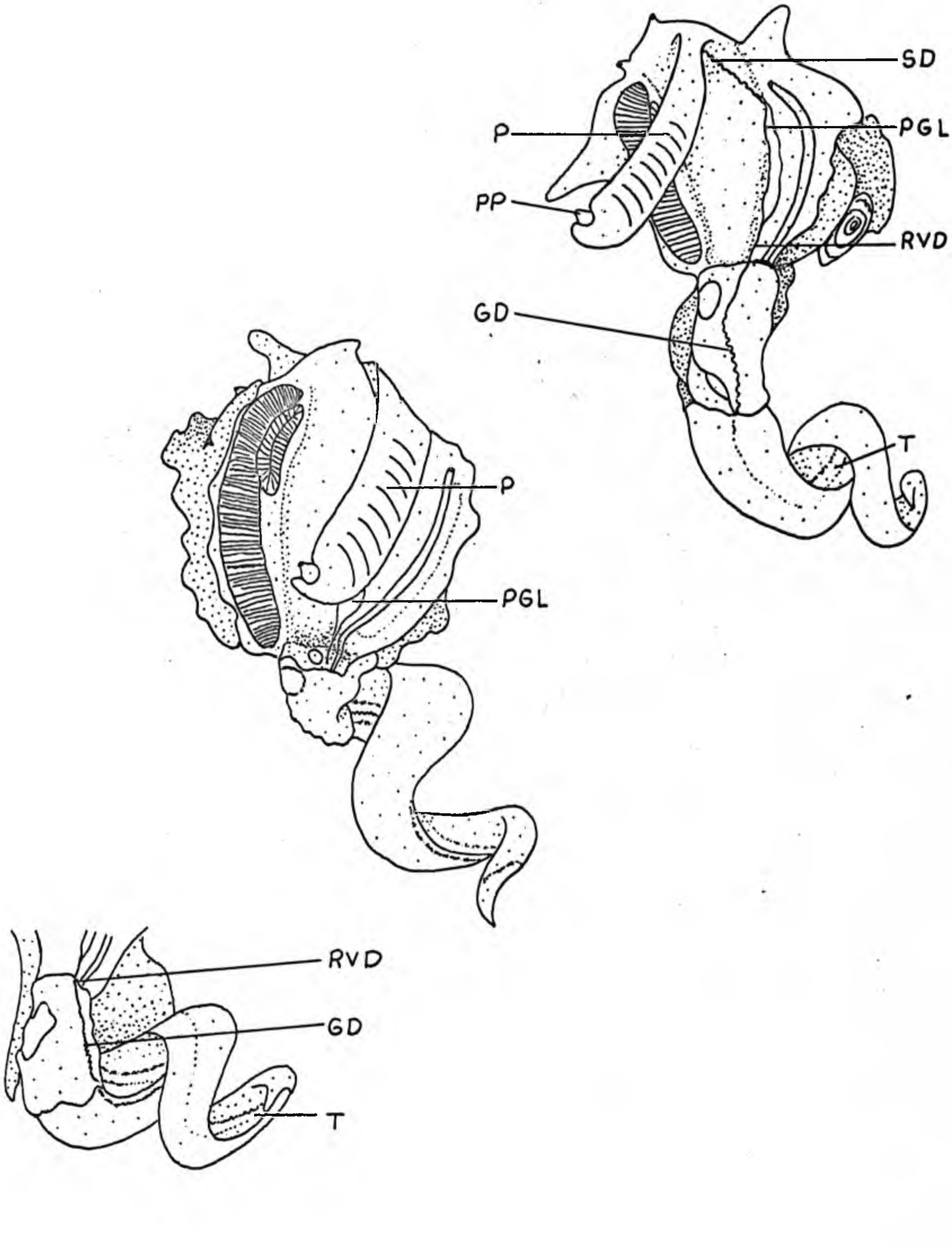


FIGURE 6. MALE REPRODUCTIVE SYSTEM

OF <u>T. maculata</u>

The testis leads into a prominently coiled genital duct (GD) situated ventral to the origin of the small intestine. This duct, functioning as a seminal vesicle, passes anteriorly and ventrally under the small intestine to the pericardial area. It then straightens into a slender duct, the renal vas deferens (RVD), which passes ventral to the intestine on the right posterior portion of the mantle wall. On the mantle wall the renal vas deferens expands into a thin-walled prostate gland (PGL). At the level of the anus, the prostate narrows and passes anteriorly onto the right side of the body wall, forming a closed seminal duct (SD) which leads into the penis (P) at the anterior part of the mantle cavity.

The penis in the mature males is a large structure (5 cm) which fully occupies most of the mantle cavity when in its usual position i.e. folded back and passing posteriorly to the renal region. It is strongly compressed laterally, and grooved on the dorsal surface. The seminal duct enters the penis at the fold, passing along the ventral edge to the distal end. The vas deferens opens at the apex of a short papilla (PP) situated ventral and posterior to the distal end of the penis.

Female reproductive system of *T. maculata* (FIGURE 7)

The ovary (OV) varies in color from cream to light yellow, and occupies a position in the ventral portion of the visceral mass similar to that occupied by the testis,

FIGURE 7. FEMALE REPRODUCTIVE SYSTEM

OF <u>T. maculata</u>

AGL....albumen gland

CGL....capsule gland

OO.....oviduct opening

OV.....ovary

POD....pallial oviduct (in transparency)

VO.....vaginal opening

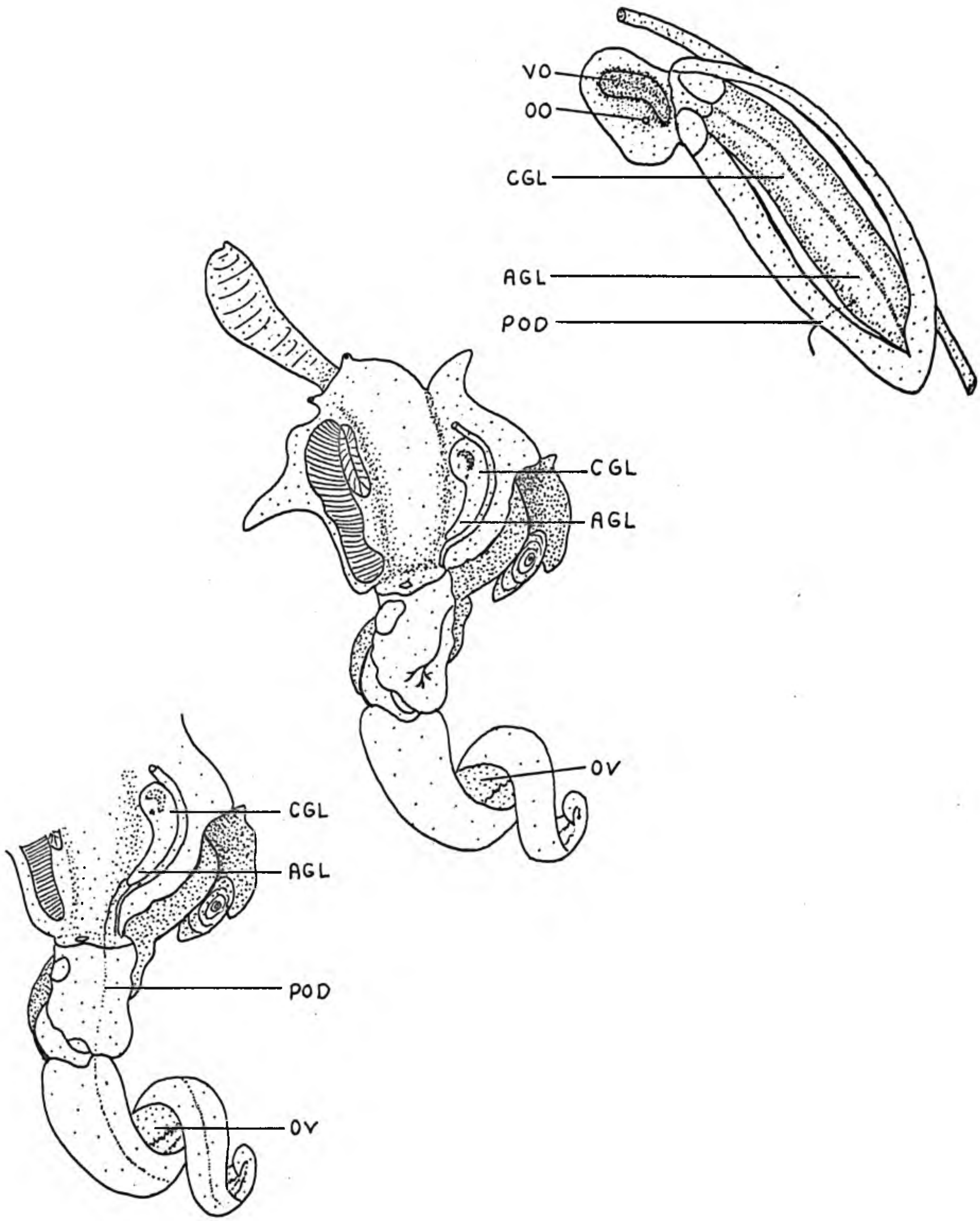


FIGURE 7. FEMALE REPRODUCTIVE SYSTEM OF T. maculata

extending from the apex of the spire anteriorly to terminate just ventral and posterior to the duct of the digestive gland. However, when the ovary is ripe it occupies a much greater area of the visceral mass than does the testis, filling spaces around the digestive gland and at certain points extending onto the dorsal surface. Its over-all effect is that of a branched structure, and it may appear granulated.

The pallial oviduct (POD) emerges from the ovary and is directed anteriorly on the right ventral surface of the kidney and onto the right posterior wall of the mantle cavity. The pallial oviduct turns dorsally shortly after entering the mantle cavity, and opens into the ventral surface of the albumen gland (AGL), one of the glandular components of the oviduct. This gland and its anterior extensions lie on the right lateral wall of the mantle cavity, terminating just ventral and posterior to the anus. The main postion of the pallial oviduct anterior to the albumen gland is the capsule gland (CGL), composed of three distinct parts which are defined macroscopically by color differences. The lateral walls of the capsule gland vary in thickness with reproductive state, and the entire gland may be up to 0.6 cm in diameter in a ripe female. The gland is divided dorso-ventrally by a slit-like duct, and laterally by a longitudinal fold.

The vaginal channel is separated from the pallial oviduct anteriorly, and the female consequently has two openings into the mantle cavity. The vaginal opening (VO), anterior to the opening of the oviduct (OO), is shaped such that it receives the penial papilla of the male. Connections between the vaginal duct and the pallial oviduct could not be established macroscopically.

Mating in Terebra

Copulation has been observed in relatively few higher prosobranchs, and nothing has been written on the process in the terebrids. Mating was observed on four occasions between pairs in four different species at Eniwetok.

On August 30th at 0645 T. guttata were observed mating in fine sand and 3 m of water, 30 m to the lagoon side of Eniwetok Islet. The male, 11.2 cm in length, was on top of the sand; the female, 12.0 cm in length, was below the male.

On September 2nd at 1100 T. subulata were seen mating in fine sand and 4.5 m of water, 50 m from Eniwetok Islet. Both of the shells were buried except for the tips of the spires. The male, 5.8 cm in length, was on the right of the female, 6.2 cm in length.

On December 28 from 0930 to 1030 both T. maculata and T. crenulata were observed mating. These species were in 3 m of water 28 m from Eniwetok Islet. The male T. maculata, 14.0 cm in length, was on the right of the female, 14.5 cm, while the male T. crenulata, 8.0 cm, was on the right of the female, 11.0 cm.

Since the mating patterns are similar for the four species, a generalized description is set forth. Field observations show that the sand paths of two mating individuals begin to run parallel when the animals are 2-3 cm apart, and then merge into one broad track. This track may continue for several centimeters, and terminates in an area of considerable sand disturbance.

Copulation can begin when the animals are oriented in the same direction, with the male to the right of the female. As in other higher gastropods (Fretter and Graham, 1962), the folded penis apparently becomes distended by hemostatic pressure and passes anteriorly out of the mantle cavity. In the unfolding process the papilla of the vas deferens becomes oriented so that it can curve into the mantle cavity of the female, becoming situated in the vaginal aperture. Indications are that the penis is not inserted into the female duct, but that the sperm are transferred by way of the papilla.

Duration of copulation is not known, but most likely lasts at least several hours. At the termination of copulation the penis is probably retracted by a reduction of hemostatic pressure and by contraction of the large penial muscle, by which it is attached to the body.

There is no experimental evidence to suggest any method by which one sex attracts the other, either in the terebrids or in any of the Toxoglossans. However, it seems likely that some attraction is present. Because mating pairs of animals (judged by ovary size) were found in 33 female *T. crenulata* collected from June through December, although a greater number of females had eggs in the oviduct in September than in either June or December. As could best be ascertained by qualitative judgment on 141 female *T. maculata*, 35% had ripe ovaries in June, 40% in August, and 15% in December. No comparative studies could be done on *T. subulata* and *T. guttata*, species which were observed mating in August, because few animals could be found.

Data for *T. crenulata* and *T. maculata* thus indicate that the time of spawning extends over a period of several months, and possibly may occur throughout the year, with a peak in late summer and early fall. Kohn (1961) reports from studies of capsule frequency that the spawning season for *Conus rattus* is at least seven months, and is of similar duration for several other species of *Conus*. Until studies are done to identify the egg capsules of the Terebridae, conclusions relative to the spawning season will be limited.

Shell enthusiasts from Hawaii have long noted that there is an abundance of large *T. maculata* in shallow water during the summer months, and that these tend to disappear in the fall and winter, only to be found in deeper sandy areas. It has been proposed that these animals may come into shallow water to breed, returning to the deeper water at the end of the spawning season.

Data from Eniwetok certainly would not dispute these observations. As shown in FIGURE 8, from June to September there were more females than males in a random sample of 127 T. maculata from the lagoon, $\bar{x}$= 11.75. In December, however, the situation was reversed, and there were nearly twice as many males as females in a random sample of 182 animals, $\bar{x}$= 11.43. These results would seem to indicate that there is some form of differential seasonal migration taking place between the males and females, but whether the females or males do the migrating is a matter of conjecture.

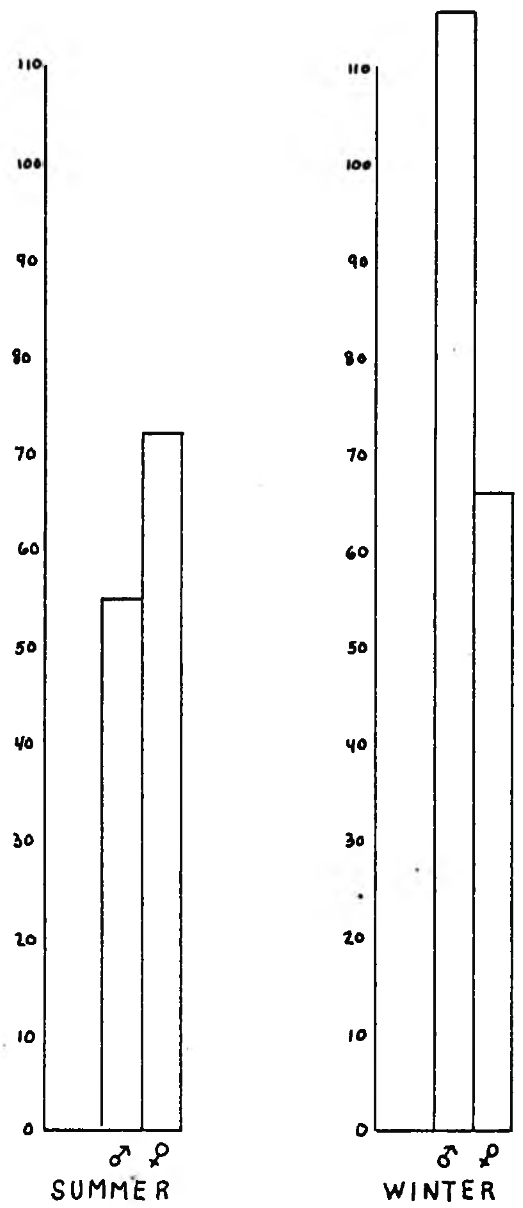


FIGURE 8. COMPARISON OF THE SEX RATIOS BETWEEN SUMMER AND WINTER POPULATIONS OF T. maculata at Eniwetok

V. BEHAVIORAL STUDIES ON PHOTOSENSITIVITY AND RHYTHMICITY

It has been observed that several species of *Terebra* are rarely if ever seen crawling in the daylight hours, while they are exposed and crawling when observed in the evening. *T. crenulata*, *T. subulata*, and *T. guttata* were never seen crawling from 0700 to 1900 hours, roughly the time from sunrise to sunset at Eniwetok, while *T. maculata* was found crawling on occasion in mid-morning, and only twice in the afternoon. That some type of rhythmicity exists for these species is readily apparent. Cloudsley-Thompson (1961) states that living organisms may show several kinds of periodicity which are frequently quite unrelated, although simultaneously apparent in the same individual. Field observations on the terebrids led to the conclusion that there may be two controlling mechanisms operational in the periodism: negative photosensitivity, and a persistent endogenous rhythm set to the daily dark-light cycle.

Photosensitivity

Prosser and Brown (1962) mention that a great range of photoreceptive mechanisms is displayed by the molluscs, some of them having a diffuse light sensitivity in addition to eyes. Light (1930) showed that the sand clam *Mya arenaria* possesses a diffuse light sensitivity confined primarily to the siphon. When under constant conditions of illumination this structure was fully extended, but increase in light intensity would cause a rapid withdrawal. Kennedy (1958) has shown that siphonal branches of the mantle nerves in the clam _Mactra_ are directly sensitive to light. In the gastropods, Arvanitaki and Chalazontis (1960) have demonstrated light responses of genital ganglia in _Aplysia_. The terebrids possess a pair of stalked eyes, and it is believed from field and laboratory observations that they may also possess a diffuse light sensitivity on parts of the body, specifically the siphon.

The sensitivity of terebrids to quality and quantity of light was studied for purposes of determining whether these factors play any role in the diurnal excursions observed in the field and laboratory. The following procedures were employed. Ten specimens of each species were placed in sand tanks in a controlled light room supplied with running sea water. A single 100-watt bulb was placed 30 cm from the water surface, and the terebrids were allowed to burrow into the sand. The position of the siphon of each animal was recorded at four-hour intervals for 24 hours. The white light was then replaced by a 50-watt red bulb, followed by observations of siphon positions.

In a comparable experiment the animals were first exposed to darkness. After six hours of dark adaptation the white light was turned on for one minute at four hour intervals for a period of 48 hours. Observations on the position of the siphons of buried animals and of the behavior of actively crawling animals were made at each time. The same procedure was followed using the red light in place of the white.

All species exposed to continuous illumination of the white light were found to have the siphons contracted at every observation. With illumination from the red bulb the siphons of most animals were observed above the sand surface during the hours from 0700 to 1900. The siphons of all animals extended even further during the period from 1900 to 0700.

The illumination of the surface after a period of darkness resulted in a rapid contraction (within one second) of the siphons of buried animals. This was frequently followed by a movement of the entire body, presumably the contraction of the foot. If the animals were actively crawling at the surface of the sand, the reaction was a rapid siphonal contraction. This was followed by cessation of locomotion, usually within less than one minute. After an inactive period from approximately one-half to several minutes, there followed burrowing into the sand. This was not terminated until orientation in the resting position was accomplished, with the siphons at the surface of the sand. Conversly, dark adapted animals exposed to red illumination exhibited no contraction of the siphon. Furthermore, no indication of cessation of locomotion or burrowing was recorded, even in the presence of prolonged illumination.

From these observations it is tentatively postulated that light sensitive receptors are located on the siphon of terebrids. This hypothesis seems reasonable because siphonal retraction occurs upon increase in light intensity, even when the eyes are buried under several centimeters of sand. It is also presumed that the animals are negatively photosensitive to sustained white light. They are apparently unaffected by red light.

Studies on endogenous activity cycles

Endogenous rhythms which persist under constant conditions in the laboratory have been reported for a number of animals. Work with molluscs has shown that such rhythms exist in several classes. Gompel (1937) has shown that Patella, Haliotus, and Mytilus maintain persistent rhythms of oxygen consumption under laboratory conditions. According to the investigations of Brown (1954) on Crassostrea virginica, and Bennett (1954) on Venus mercenaria, these bivalve molluscs exhibit tidal rhythms of siphonal contraction that are persistent in the laboratory without tidal fluctuations. Endogenous activity in the Toxoglossa has been demonstrated by Kohn (1959) for several species of Conus. He mentions that at night the animals are on the surface of the marine bench actively crawling about, and that the rhythmic activity persists when the animals are kept under artificial illumination in the laboratory. Greater movement of the siphon, degree of foot expansion, and locomotion of the animals are evidenced at night than during the day.

Because the previous experiments showed that the activity of the terebrids investigated is directly inhibited either by continuous or intermittent artificial illumination, testing for evidence of an endogenous activity cycle was performed under conditions of constant artificial illumination and constant darkness. This procedure provides an opportunity to state whether one can expect the effects of light on the daily activity cycle to be initiated by stimulus of a specific photosensitive receptor or to be inherent and persistent.

The following procedure was used to make preliminary studies of possible endogenous activity cycles in several terebrids. Two sand tables with running sea water similar to those previously described were used for observations on locomotion. One table was placed in a room free from all external light source, and a 50-watt red light was placed 30 cm above the water. Each table was provided with a grid composed of strings set at 10 cm intervals resulting in divisions of 100 cm^2. Each square was numbered, and was correspondingly indicated as a 1 cm^2 on the data work sheet. Each experimental animal was tagged with a numbered cork suspended from a thin copper wire 20 cm in length attached to the spire of the shell. Four species of <u>Terebra</u> were employed in two experiments.

Effect of continuous illumination from white and red light on the activity cycle of four species of Terebra

Twelve *T. maculata*, five *T. crenulata*, five *T. subulata*, and three *T. guttata* were marked and introduced into the sand table illuminated by the 50-watt red bulb. The tank illuminated by the 100-watt white bulb was provided with the same number of species as those under continuous illumination from the red bulb, and both groups of animals remained undisturbed for 24 hours. At 0900 the position of each animal was recorded on the data sheet, and similar records were made at 2100. Observations were made for a period of seven days.

The results of twelve hour observations are shown in FIGURE 9. This figure indicates the frequency of animals observed crawling to the surface of the sand and reburrowing at 12 hour intervals, termed an excursion period. Animals crawling at the time of observation were counted with the period in which movement ceased. This figure represents composite data for all species. It shows that 26 excursions were recorded during the daylight hours (approximately 0900 to 2100), and 73 excursions were recorded during the hours of darkness (approximately 2100 to 0900). This is an average of 4.3 excursion periods in the day, and 10.5 excursion periods in the night.

Because the results from continuous artificial illumination showed a correlation of inherent rhythm with diurnal illumination, it was deemed appropriate to investigate how

Total no. excursions in period 0900-2100 (D): 26

Total no. excursions in period 2100-0900 (N): 73

Average no. excursions/ period 0900-2100 (D): 4.3

Average no. excursions/ period 2100-0900 (N): 10.5

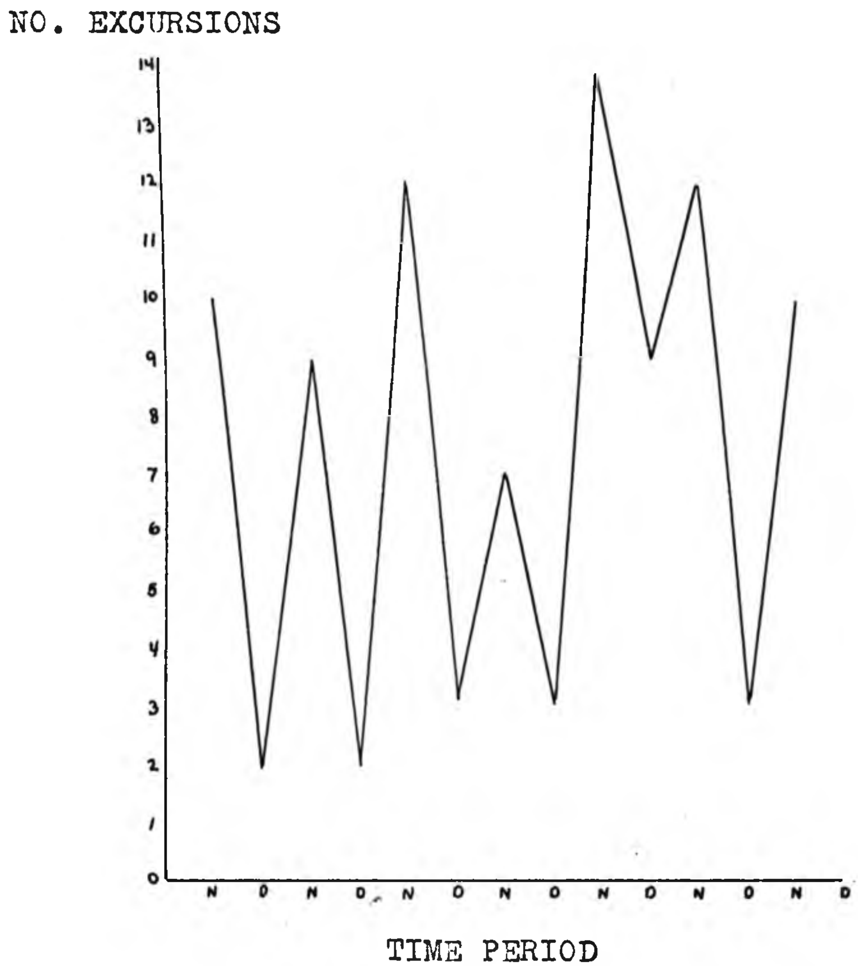


FIGURE 9. COMPOSITE FREQUENCY OF EXCURSIONS OF FOUR SPECIES OF Terebra RECORDED OVER 12-HOUR INTERVALS UNDER SEVEN DAYS OF CONTINUOUS ILLUMINATION FROM RED AND WHITE LIGHT (RED LIGHT = DARKNESS)

this rhythm would be affected by subjecting the animals to intermittent periods of artificial illumination for an extended period of time.

Fourteen T. maculata, six T. crenulata, four T. subulata, and three T. guttata were marked and placed in the dark room equipped with the 100-watt tungsten bulb and the 50-watt red bulb. Readings were taken at 0900 and 2100 each day for 23 days. The white light was used first. After eight days of continuous white light, the room was then illuminated by the red light for eight days, simulating darkness for the animals. This was followed by four more days of continuous light, and three days of continuous darkness.

The results of twelve hour observations taken over a 23 day period on the same individuals subjected to alternating phases of light and dark are shown in FIGURE 10. As in FIGURE 9, considering all species, more animals crawled during the night period than during the day, with a total of 68 excursions from 0900 to 2100, an average of 3.0 per day, and a total of 105 excursions from 2100 to 0900, an average of 4.6 per night.

The composite frequency of excursions for all four species at 12 hour intervals for a period of 23 days is plotted in FIGURE 10. The data show an inherent constant diurnal rhythm for the first six days. By seven to eight days under continuous artificial illumination it can be seen that the amplitude of the cycle is decreased. This is consistent with findings by Bunning (1964) that an

Total no. excursions in period 0900-2100 (D): 68
Total no. excursions in period 2100-0900 (N): 105
Average no. excursions/ period 0900-2100 (D): 3.0
Average no. excursions/ period 2100-0900 (N): 4.6

NO. EXCURSIONS

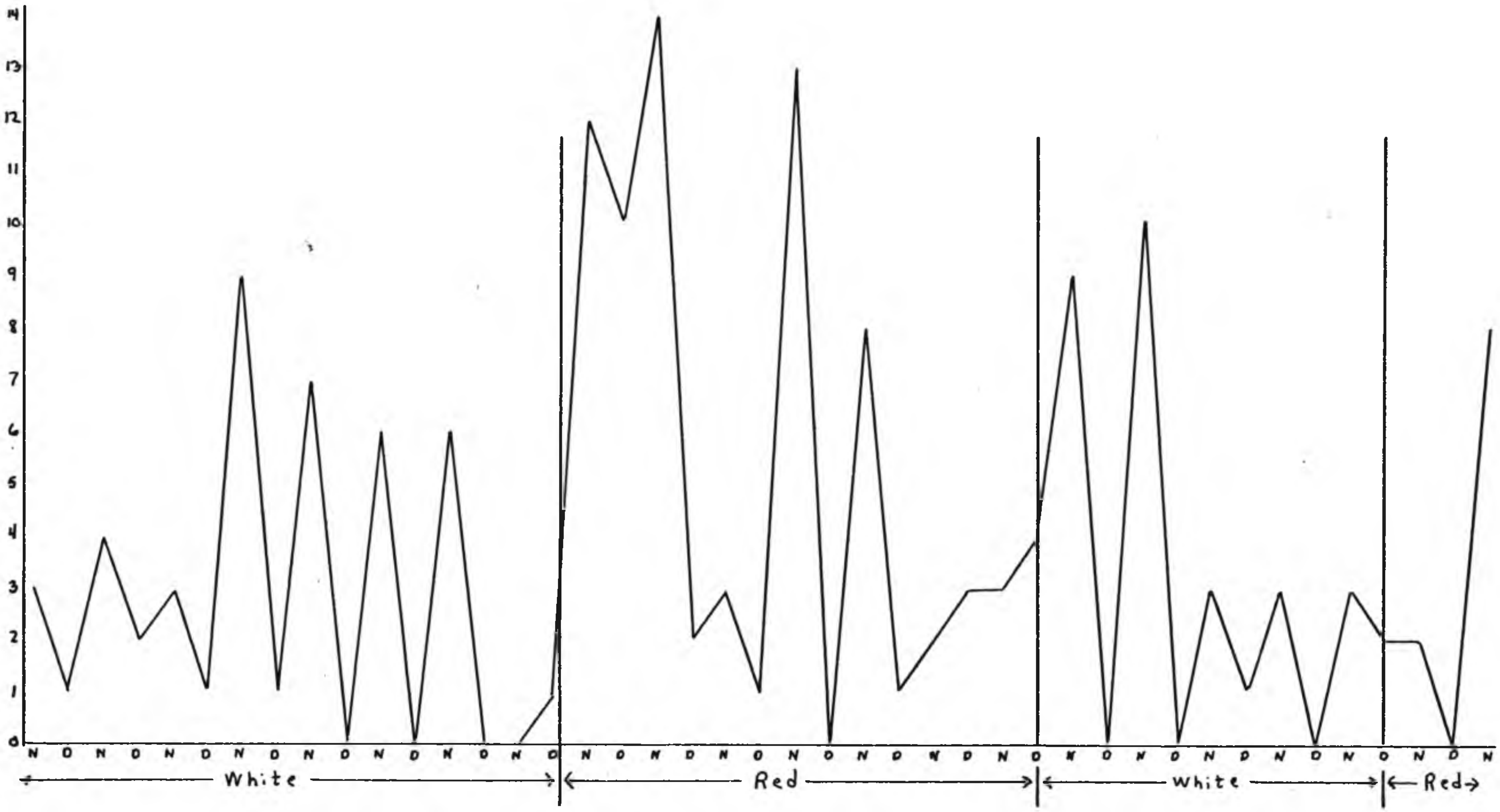


FIGURE 10. COMPOSITE FREQUENCY OF EXCURSIONS OF FOUR SPECIES OF Terebra RECORDED OVER 12-HOUR INTERVALS UNDER 23 DAYS OF INTERMITTENT ILLUMINATION FROM RED AND WHITE LIGHT (RED LIGHT = DARKNESS)

endogenous rhythm will fade out after a varying length of time under constant conditions. On the eighth day at 2100 hours the illumination was turned off and activity was recorded. This resulted in increased frequency of activity in the following hours, but lower frequencies were still evident for daylight hours. By ten days the cycle was reestablished and continued for four days. At this time activity again became arhythmic. At the completion of sixteen days the tank was again illuminated from the 100-watt bulb. This stimulus resulted in the recording of increased frequency of activity at seventeen days as shown in the figure. It is evident from the records of the reactions observed that locomotory activity in Terebra is endogenous, and active periods are approximately correlated with periods of natural darkness (2100-0900).

We cannot dispute that locomotory activity does occur throughout the day. However, as Cloudsley-Thompson (1961) has indicated, in most of the reported cases of endogenous rhythm, the data show that the majority of the animals are rhythmic, while lesser numbers may have periods of arhythmicity.

It was observed that the rhythmic activity cycle in Terebra after several days of continuous illumination or continuous darkness becomes damped (see FIGURE 10). It was also found that the rhythm was reestablished if an interruption of the constancy of illumination occurred. The stimulus for this was either removal of illumination or by introduction of light in darkness.

In his review of the physiological clock, Bunning (1964) notes that most rhythms fade out if the animals are kept under constant environmental conditions for a length of time. This is well shown in the experiments with Terebra. Furthermore, Webb (1949) found that endogenous clocks can be reset by changes in illumination at sensitive times of the daily cycle. Fiddler crabs kept under very bright conditions of continuous illumination for about ten days remained consistently black, while they normally change color rhythmically. If the crabs were placed in darker conditions either at 1200 or 1800, the normal rhythm of color change occurred at once.

In TABLE III the data are presented by species and distance traveled by each species, under seven days of continuous illumination and darkness. First examination of the total number of excursions is misleading, for it shows that the light had little effect on the movement of the animals. There were 45 excursions recorded in the light, and 55 in the dark, Chi Square 1.2, P 0.25. However, when the data are presented by species and distances traveled, two points become evident. 1. Every species shows a higher frequency of activity when exposed to continuous darkness than when exposed to continuous illumination. 2. The average locomotion for all species in continuous darkness is almost twice that under continuous illumination (31 cm and 18 cm respectively). The most striking differences were found in T. subulata and T. guttata. Only two excursion periods were recorded in the light (60 cm in length), while under continuous darkness 23 excursion periods were recorded (850 cm in length).

The activity of species under intermittent illumination are presented in FIGURE 11. The results from observations of T. subulata and T. guttata are combined because of their uniformity, while those for T. maculata and T. crenulata are presented independently. In TABLE IV the data are presented by species and distances traveled by the same individuals under 23 days of intermittent conditions of light and darkness. The data show results similar to those found for records of continuous illumination and darkness. There were more individuals crawling in the dark than in the light, and there was a higher frequency of activity among the animals under continuous darkness. An average of 26 cm per excursion was measured for all species under continuous darkness as compared to 18 cm per excursion under continuous illumination. This agrees with the results presented in FIGURE 9 and TABLE III for animals not given periods of intermittent light and darkness. Furthermore, the records for T. subulata and T. guttata are also indicative of a low threshold to illumination, while those for T. maculata indicate a higher threshold to illumination than for the other species.

SPECIES	TOTAL EXCURSIONS		TOTAL DISTANCE (cm.)		DISTANCE PER EXCURSION (cm.)	
	WHITE	RED	WHITE	RED	WHITE	RED
T. maculata	25	18	320	320	13	18
T. crenulata	17	14	430	560	27	40
T. subulata	2	16	60	590	30	37
T. guttata	0	7	0	260	0	33
TOTAL	44	55	810	1730	18	31

TABLE III. EXCURSIONS UNDER SEVEN DAYS OF CONTINUOUS ILLUMINATION BY RED AND WHITE LIGHT (RED LIGHT - DARKNESS)

SPECIES	TOTAL EXCURSIONS		TOTAL DISTANCE (cm.)		DISTANCE PER EXCURSION (cm.)	
	WHITE	RED	WHITE	RED	WHITE	RED
T. maculata	50	54	940	1290	19	24
T. crenulata	12	34	190	1080	16	32
T. subulata	2	5	20	180	10	36
T. guttata	4	12	40	240	10	20
TOTAL	68	105	1190	2790	18	26

TABLE IV. EXCURSIONS UNDER TWENTY-THREE DAYS OF INTERMITTENT ILLUMINATION BY RED AND WHITE LIGHT

(RED LIGHT - DARKNESS)

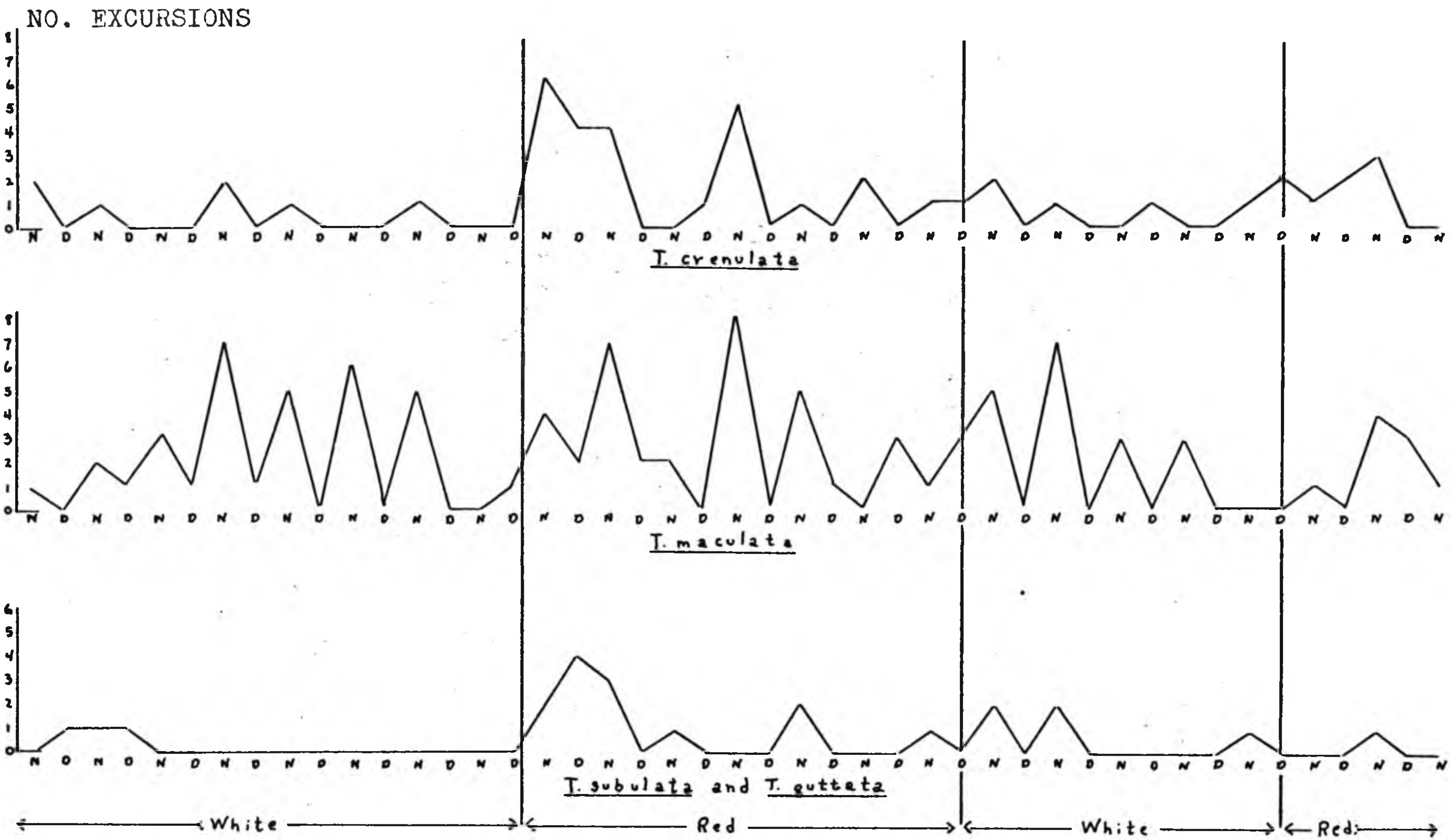


FIGURE 11. FREQUENCY OF EXCURSIONS OF FOUR SPECIES OF <u>Terebra</u> RECORDED OVER 12-HOUR INTERVALS UNDER 23 DAYS OF INTERMITTENT ILLUMINATION FROM RED AND WHITE LIGHT

(RED LIGHT = DARKNESS)

VI. OBSERVATIONS ON FOOD AND FEEDING MECHANISMS IN *Terebra*

Functional anatomy of the terebrid digestive system as shown by T. maculata

While much discussion has centered on the functional anatomy of the generalized Toxoglossan digestive system, only Kohn has attempted a definitive study of both feeding mechanisms and prey preferences in living animals. His work has contributed much toward a better understanding of the biology of the Toxoglossan family Conidae. Even though the terebrids are Toxoglossans, there apparently is little uniformity in the foregut of the animals. Hence, generalizations on the structure and function of the buccal apparatus made for the conids cannot be extended to the terebrids.

No observations on the feeding process in the terebrids have been published, although several workers have suggested possible prey. Hedgpeth (personal communication) believes that the terebrids from the Gulf Coast may prey on *Donax*, although he failed to mention if he observed the actual feeding process. Marcus and Marcus (1960) found partly decomposed bits of polychaetes in the stomach of *Hastula cinerea*, and polychaete setae in the feces, although they observed no feeding in the animals. Stewart (personal communication) mentions that he had no success in feeding *T. dislocata*, *T. salleana*, *T, protexta*, or *T. concava* in the laboratory. Because of the paucity of detailed information about the food and mechanisms of feeding in the terebrids, an investigation of some of these parameters has been made for two species.

The anatomy of T. maculata and T. crenulata is similar, and structures and functions found applicable to T. maculata can be extended to T. crenulata as well. Results of dissections of T. maculata of various sizes are drawn in FIGURE 12 and FIGURE 13. The stomodeum opens into an elongate muscular tube called the proboscis sheath (PBS), which when introverted consists of outer longitudinal muscles and inner circular muscles. The proboscis sheath terminates in the mouth. Fretter and Graham (1962) state that the proboscis apparatus of all Stenoglossans is of the type called pleurembolic, in which the structure is only partly invaginated when in the buccal cavity of the animal, thus allowing for accommodation of a longer proboscis in the same space. Retraction in Toxoglossans is generally brought about by contraction of two retractor muscles inserted on the side of the proboscis. In T. maculata, however, the proboscis is not of the pleurembolic type, but rather of a modified acrembolic type, in which the entire introverted proboscis sheath is accommodated in the buccal cavity. It is folded upon itself several times, the end which corresponds to the mouth when everted lying at various locations in the posterior of the buccal cavity. No muscles of any type were found connected to this part of the sheath, although the entire structure is contained within a thin membrane.

Posterior to the proboscis sheath is the proboscis (PB). This structure differs from that normally found in the acrembolic type apparatus because it is not connected to the proboscis sheath directly, but only indirectly by the membranous sheath covering both structures. It tapers to a funnel at the posterior end, opening into an oral tube (OT) or anterior esophagus. This tube passes forward to the nerve ring (NR), curves ventrally around it, and then turns posteriorly, continuing as a straight tube to a position just ventral to the proboscis.

As a functional unit the feeding apparatus leaves many questions to be answered. Because there is no direct communication between the proboscis and the proboscis sheath, mechanisms for movement of these structures are open to speculation. Bouvier (1887) and Risbec (1953) discuss problems involved in the functioning of the buccal apparatus of terebrids, but they present no hypotheses on the possible mechanisms involved. In <u>T. maculata</u> the proboscis sheath is completely everted at the time of feeding (FIGURE 13), often to as great a length as the shell. The mechanism of eversion is not certain, but probably is by hemostatic pressure and muscular contraction. Indications are that the proboscis sheath everts posterior end first, since it would be structurally impossible for the anterior part to evert over the entire folded length inside the buccal cavity. In the everted proboscis sheath

FIGURE 12. DORSAL DISSECTION OF _T. maculata_ TO SHOW PRINCIPAL PARTS OF THE DIGESTIVE SYSTEM

A........anus

CR.......crop

DDGL.....duct of the digestive gland

DGL......digestive gland

ES.......esophagus

I........intestine

M........mouth

NR.......nerve ring

OT.......oral tube

PB.......proboscis

PBS......proboscis sheath

RS.......radula sac

S........stomach

SGL......salivary gland

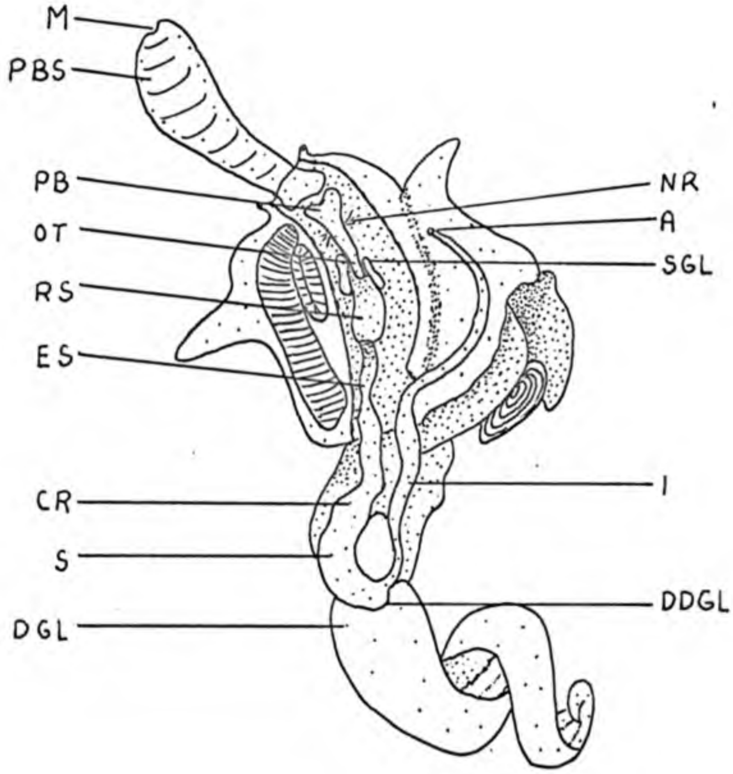


FIGURE 12. DORSAL DISSECTION OF <u>T. maculata</u>

TO SHOW PRINCIPAL PARTS OF THE DIGESTIVE SYSTEM

FIGURE 13. BUCCAL APPARATUS OF *T. maculata*

1. Buccal apparatus with the proboscis and proboscis sheath introverted.
2. Buccal apparatus with the proboscis sheath removed to show the underlying structures.
3. Lateral view of the introverted proboscis showing the relation of the associated structures.
4. Buccal apparatus with the proboscis and proboscis sheath everted.

ES........esophagus

M.........mouth

NR........nerve ring

OT........oral tube

PB........proboscis

PBS.......proboscis sheath

RS........radula sac

SGL.......salivary gland

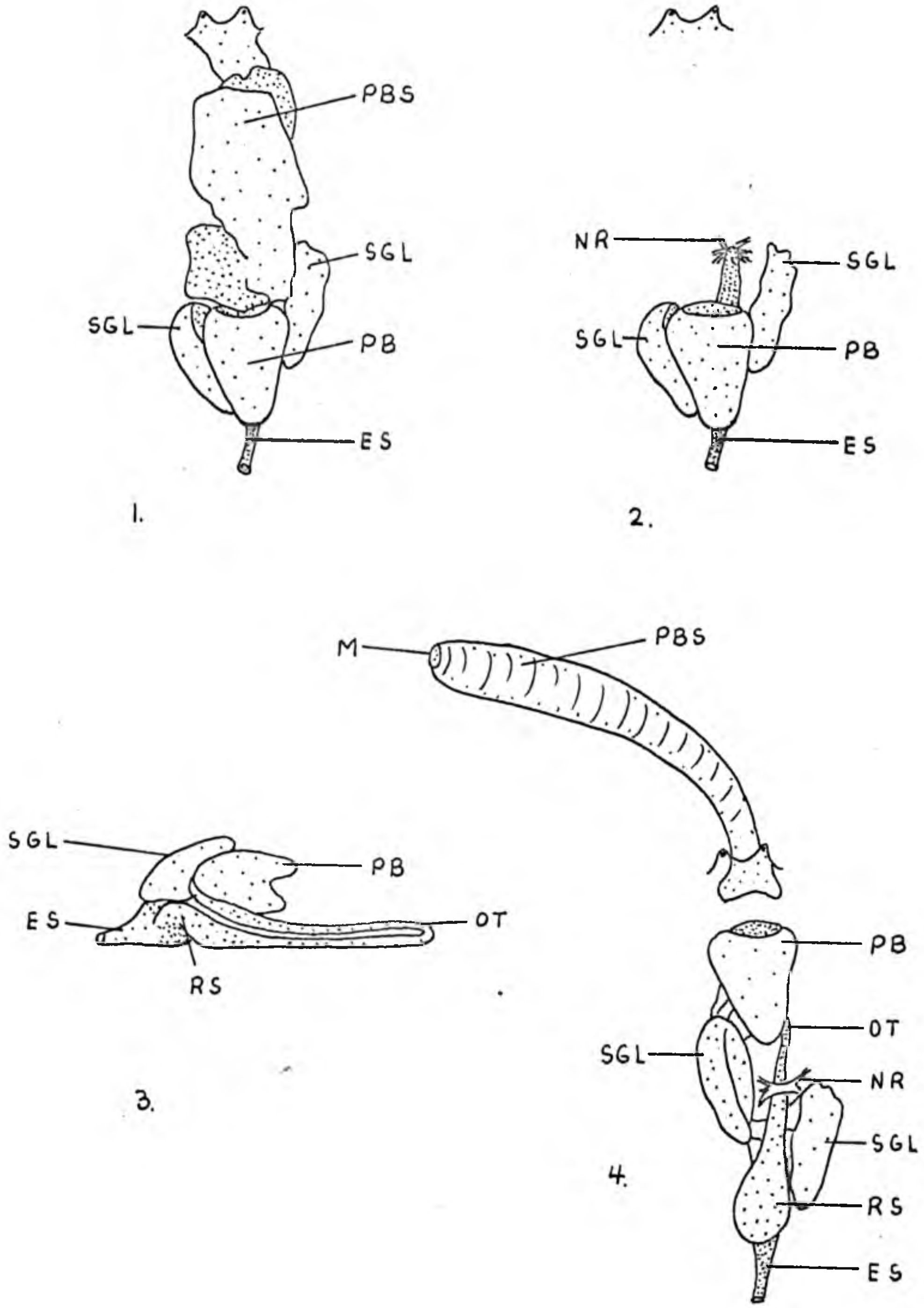


FIGURE 13. BUCCAL APPARATUS OF <u>*T. maculata*</u>

the longitudinal muscles surround the lumen, and the circular muscles are beneath the epidermis, forming a sphincter around the mouth (M) at the anterior end.

Retraction of the proboscis sheath in many of the species of _Terebra_ can be explained simply by contraction of a set of retractor muscles, one located on each side of the proboscis. In _T. maculata_ there are no retractor muscles, and hence some different method is postulated. It appears as if the anterior part of the proboscis sheath introverts initially and passes anteriorly, probably by a contraction of the anterior longitudinal muscles pulling on the sphincter. Introversion can best be explained by a reduction in hemostatic pressure and by some form of peristalsis which carries the proboscis sheath back into the buccal cavity. Longitudinal muscles located on the body wall posterior to the proboscis sheath and connected to it may account for the final introversion to the level of the eyes.

In a discussion of several species possessing radular teeth, Clench (1946) states that neither turrids nor terebrids are known to bite or sting their prey as the conids do. From studies on the anatomy of several species of _Terebra_, Risbec (1953) has concluded that if the radular teeth are used at all, this must be done in the buccal tube or oral cavity, and not by direct capture of the prey, which is presumably engulfed by the muscular proboscis sheath. Neither _T. maculata_ nor _T. crenulata_ possess radular teeth or poison glands, so they can hardly feed as would normally be expected for the Toxoglossans. T. maculata grasps its prey by the sphincter muscle at the terminus of the proboscis sheath, and then ingests the food whole. The prey apparently is then carried posteriorly to the buccal cavity by peristaltic action.

How the proboscis comes into position to receive the prey is another matter of conjecture. Risbec states that the proboscis of T. cancellata is not fixed by muscle attachments to the proboscis sheath, and he is at a loss to explain how it slides in the sheath and projects to the exterior. Alpers (1931), in his review of the prosobranch proboscis, is also uncertain of the mechanics of the terebrid proboscis. In T. maculata and T. crenulata it is postulated that the proboscis may be moved anteriorly by hemostatic pressure, thus achieving close proximity with the proboscis sheath at the anterior part of the buccal cavity. The proboscis apparently grasps the prey whole as it is carried into the buccal cavity from the proboscis sheath, for animals dissected while in the process of feeding contained prey that extended across the gap between the proboscis and proboscis sheath.

Just ventral to the proboscis, the oral tube expands into a Y-shaped radular sac (RS) and the anterior part of the esophagus. On either side of the radular sac, and connected to it and the proboscis by long narrow ducts, lie the large white salivary glands (SGL). The esophagus then passes ventrally and posterior through the body wall, expanding slightly into a distensible tube lying just dorsal to the columellar muscle. This structure serves as a crop (CR) which receives the ingested prey, and can be greatly distended when full. At the posterior border of the kidney the stomach (S) appears on the surface of the first visceral spire, imbedded in the mass of the digestive gland. As mentioned by Morton (1964), the Toxoglossan stomach is reduced to a simple sac, thin-walled and serving as a chamber for the reception of the digestive enzymes. Enzymes of the digestive gland (DGL) enter through the ventral side of the stomach by way of a duct (DDGL), which is internally grooved and opens toward the intestine. Internal walls of the stomach are distinctly grooved, as they are in the esophagus. No caecum is present. At its most posterior position, the stomach constricts greatly and curves to the right around the anterior lobe of the digestive gland. This constriction marks the termination of the stomach and the beginning of the intestine.

The intestine (I) is a thin-walled tube of more or less uniform diameter, passing anteriorly from the stomach under the kidney. At the limits of the mantle cavity it turns slightly toward the esophagus, then curves back and onto the right lateral wall of the mantle, to which it is attached by a thin membrane. The intestine continues anteriorly dorsal to the genital duct, and terminates as the anus (A) lying just posterior to the edge of the mantle. Feces are not consolidated into pellets, but rather pass out as an amorphous mass.

<u>Laboratory and field studies on the food and methods of feeding in Terebra</u>

Because of their availability and relatively large size, <u>T. maculata</u> and <u>T. crenulata</u> were used for investigating the time of feeding, the nature of the prey, the frequency of feeding in the population, and the time required for digestion in terebrids. Collections from June to September and again in December, chiefly in the lagoon leeward of Eniwetok Islet, were the principal source for this information. Before it was known that the animals possess rhythmic activity cycles, collections were made from 0630 to 2330 at two hour intervals. From five to twenty specimens per hour were collected by diving at depths of from 2 to 5 m. Subsequent collections were confined to the morning hours from sunrise to 1030.

Animals were immediately placed in an ice bath (ice buckets suspended from the collecting tubes) in order to decrease the rate of the digestion of material in the gastro-intestinal tract. The entire animal was removed from the shell, and dissections and gross macroscopic examination of the entire gastro-intestinal track from the mouth to the anus were made. Location and nature of gut contents were recorded along with the time of collection for each specimen. A total of 229 <u>T.maculata</u> and 58 <u>T. crenulata</u> were used.

Time required for the digestive process was determined by retaining the animals collected with prey in their proboscis sheaths in aquaria in the laboratory. Dissection from two to eight hours after initial collection presented some index of the rate of digestion. Undigested prey from the esophagus and stomach was sent to Dr. Alan Kohn for specific identification.

Food items of *T. maculata* and *T. crenulata*

The gut analyses from 58 *T. crenulata* in collections from 0630 to 1030 show that an enteropneust, *Ptychodera sp.*, comprises the only source of food. According to Kohn (personal communication) the species is probably *P. flava*, as this has been reported from similar sand habitats. Nine worms still alive were found in the proboscis sheath of animals collected between 0630 and 1030 hours, and nineteen remains of enteropneusts, mostly fleshy particulate matter and lime sand, were found in the stomach and intestine of other animals collected during the same time.

Results of 229 dissections of *T. maculata* indicate that the diet consists of at least two species of prey, the enteropneust *P. flava*, and a species of polychaete worm belonging to the family Capitellidae. Because the anterior end of the polychaete had been digested in every case before the posterior was completely engulfed, identification could not be made to genus and species, even though the posterior segments were in good condition. Six capitellids and two enteropneusts were found still alive in the proboscis sheaths during collecting periods, and ten remains of enteropneusts, essentially lime sand, were found in the stomach and intestine.

Time of feeding

Determination of the time of feeding by locating the position of food in the gut was not entirely successful, although Kohn (1959) used this procedure for the conids. Specimens feeding on worms were collected from 0630 to 1030 and examined, but no significant differences in position of the prey in the gut could be noted. The observations on movement indicate that T. crenulata probably feeds sometime between 2000 and 0700, Specimens in the collection were all found buried in the sand, and it is presumed that feeding had occurred sometime before 0700. This assumption seems reasonable, because the animals do not crawl under the sand, and they only crawl above the sand surface from 2000 to 0700 hours.

The slow rate of digestion renders determination of the peak period of feeding difficult to establish. Sand was found in the intestines of some animals at every period of collecting. The sand is either ingested with the food or it represents material in the gastro-intestinal tract of the prey (i.e. Ptychodera). Consequently, it cannot be established whether the sand is indicative of food for one day, or whether it is left from the previous day.

While observations indicate that T. maculata crawls mainly at night, they also show that some specimens are prone to locomotion in the early sunlight hours from 0700 to 1100. Most of the food was found in the digestive tract between 0930 and 1030, with a few worms being eaten as late as 1330. As with T. crenulata, all specimens of T. maculata were buried in the sand when located, but because this species normally crawls under the sand, no estimate of the time at which locomotion ceased can be ventured. It can be assumed, however, that initial capture of prey takes place at night or early morning, with the feeding process continuing into the late morning.

Duration of the feeding and digestive processes

When several terebrids were found in the process of feeding long after locomotion has normally ceased, questions were raised as to the length of time involved in the feeding and digestive processes. Dissections show that after the prey has moved through the proboscis and anterior esophagus it is passed into the large distensible crop, stretching the organ to several times its normal size when empty. In several instances Terebra maculata feeding on large capitellid worms were collected. In these cases the posterior part of the living worm was still in its tube, while the anterior end was ingested. Dissection and examination of the prey indicates that the effects of digestion become visibly apparent in the posterior crop.

The worms were of natural red color in the anterior crop, but were maroon in the posterior crop and in the stomach. An amorphous black-red mass was located in the intestine, and the feces were passed as a black liquid. Thus the entire digestive process from ingestion to egestion can occur on part of the prey before the entire prey is ingested.

Other feeding terebrids were placed in salt water aquaria, and the prey being engulfed by the proboscis sheath were severed at the mouth level of the terebrids. From two to eight hours after the prey were no longer visible at the mouth, the terebrids were dissected to determine the amount of digestion on the prey and their location in the gut. After three hours the prey were still in the region of the anterior crop. They were not found to be in the region of the intestine until the sixth hour. Because complete digestion (ingestion to passage of feces) can occur on the anterior of the prey before the feeding is completed on the posterior, it is postulated from these observations that the process of feeding may take from six to twelve hours, especially when large prey are being ingested. This would explain why feeding individuals of <u>T. maculata</u> are often found after the peak period of locomotion should have ceased.

<u>Percentage of the population feeding each day</u>

From a collection of 58 <u>T. crenulata</u> obtained during the morning hours, 28 were found with either whole worms or sand particles in their guts. Hence it was deduced that feeding had taken place in 48% of the population during the preceding 24 hours. It was not possible to determine the number of prey ingested per day. However, no specimen of T. crenulata was found to contain more than one enteropneust.

Data for T. maculata indicate that the feeding rate is considerably lower than for T. crenulata. From an examination of 229 specimens, 18 were found with either whole worms or sand particles in their guts. This suggests a successful predatory rate of 8% within the population in a 24 hour period. Two Ptychodera were found in one specimen of T. maculata, while only one specimen of prey was found in all others.

Attraction to prey

Kohn (1961) consolidates the available information on chemoreception in gastropods, and concludes that both distance chemoreception (smell) and contact chemoreception (taste) are used in the attraction to prey. No evidence exists to indicate that Terebra locate potential prey by distance chemoreception. However, when sea water containing oyster extract and polychaete extract was introduced into a tank containing Terebra, activity for several of the specimens increased significantly.

When large polychaetes were placed in the sand they were not preyed upon, even though the terebrids crawled directly over the worms. It is possible that the worms have to be normally oriented in the sand before predation will commence, but introduction of undisturbed sand containing polychaetes in tubes also failed to elicit the feeding response in terebrids.

VII. SOME ASPECTS OF THE ECOLOGY OF *Terebra* AT ENIWETOK

The composition and structure of tropical marine sand communities is poorly understood. Thorson (1957) reviews the literature on sand communities and states that more information is needed before the community relationships can be fully elucidated. Kohn (1959) has done some studies on the shallow marine communities of Hawaii, principally on the reefs and marine benches, although a few sand habitats are mentioned.

The sand communities of Eniwetok Atoll are rich in the number of infaunal species, as is typical for tropical areas. By sieving sand from areas ($3m^2$) in the quarry, the following average counts of macrofauna were obtained:

Cerithidae (33 specimens)

11 different species

Terebridae (33 specimens)

T. affinis	19	*T. cancellata*	1
T. solida	5	*T. guttata*	1
T. maculata	4	*T. subulata*	1
T. picta	2		

Conidae (6 specimens)

C. pulicarius	5	*C. arenatus*	1

Mitridae (7 specimens)

Mitra mitra	1	*Vexillum exasperata*	4

Mitra sp. 2

Olividae (2 specimens)

Oliva erythrostoma 1 *Olivella sp.* 1

Strombidae (3 specimens)

Strombus gibberulus 2 *Strombus sp.* 1

Naticidae (1 specimen)

Polinices pyriformis 1

Cardidae (1 specimen)

Echinoidea (4 specimens)

Holothuroidea (1 specimen)

Polychaeta (no quantitative data)

For all areas studied in the quarry, the predominant macrofauna were the terebrids, cerithids, and the filter-feeding polychaetes. This community corresponds quite closely to the *Cerithium-Turitella* community mentioned by Thorson (1957) from deeper tropical areas. The proportions of species vary from area to area in the quarry, and between the quarry and the lagoon, but the general community structure remains similar in all areas, where the predominant molluscan families are the Terebridae, Conidae, Cerithidae, and Mitridae.

Predation on the terebrids

Very little has been learned concerning predation on the terebrids. Although the animals are abundant in most shallow areas of the lagoon, few empty shells were found in the collection periods from June to December. Most of these contained hermit crabs, and were extensively covered with calcareous algae. *T. maculata*, *T. crenulata*, *T. subulata*, and *T. dimidiata* were observed with holes bored in the shell such as those produced by *Polinices* or *Natica*. *Polinices pyriformis* is found in most areas occupied by the terebrids, and this large mollusc may account for the borings.

Several species of *Conus* living in association with the terebrids may contribute to the predation. Kohn (1959) reports that *Conus textile* and *Conus marmoreus* feed entirely on molluscs.

Marcus and Marcus (1960) note that many shells of *Hastula cinerea* contain many local breaks that are irregularly repaired, but they propose no cause for this. The same has been found for specimens of *Terebra*. From an examination of 171 shells of *T. maculata* from both Eniwetok lagoon and quarry, 76 shells were found cracked at from one to several places and consequently repaired. It is believed that some cracks may result from wave action, although the greater number is believed to be contributed by xanthid crabs and foraging eagle rays. Xanthids have been observed by Kohn (1959) to crack the lip of *Conus* shells, and terebrids were found dug from the sand at Eniwetok with freshly made cracks in the shell after foraging by the rays.

Nothing is known on larval predation and parasitism.

Ecological isolation

Kohn (1959) indicates that a large number of species of *Conus* are found in a restricted reef habitat in the Hawaiian Islands. This phenomenon prompted studies to determine the mechanisms by which these animals can survive sympatrically and retain their identity as species. Similar conditions exist for the Terebridae of Eniwetok Atoll, where 14 species have been found in the same macrohabitat. Although studies such as those conducted by Kohn were beyond the scope of the present work, several preliminary observations are recorded.

Terebrids are motile, and attempts were made to determine the number of sympatric species living in a closed community. One area of sand, a depression completely contained by coral reef, was thoroughly sieved to remove all terebrids. Below are listed the species and number of each found in the enclosed area.

T. affinis	68	*T. crenulata*	3
T. maculata	30	*T. laevigatus*	2
T. subulata	7	*T. picta*	2
T. guttata	6	*T. cinguilifera*	1
T. cancellata	3	*T. babylonica*	1

As demonstrated by Kohn (1959), there are subtle differences occuring among the ecological niches of _Conus_. This permits them to survive sympatrically. It is suggested that the same phenomenon can be used to explain the existence of numerous terebrids in the same restricted area. While more data are needed before definite conclusions can be reached, preliminary evidence for isolation among species does exist.

This can best be demonstrated from the data for _T. maculata_ and _T. crenulata_. A series of mechanisms, closely interrelated, appear to be operational in the isolation of these species.

1. _Nature of the substratum_

T. maculata is rarely if ever found in wave affected areas, and usually occurs in fine sand, while _T. crenulata_ is seen in areas of coarse sand often affected by wave action. Because the quarry is free from wave affected coarse sand, a comparison of the total number of animals collected in both the quarry and the lagoon should give some indication of habitat preference.

	T. maculata	_T. crenulata_
lagoon	632	220
quarry	213	5

It is quite evident that selection has occurred, for with no active selection the expected number of _T. crenulata_ in the quarry should have been 74.

2. Food preference

It is postulated that the substratum preference may be correlated with the availability of prey. *T. crenulata* feeds exclusively on the enteropneust, *P. flava*, which is normally found in shallow patches of coarse sand. *T. maculata* has a catholic diet, consisting of at least two species from different phyla, the enteropneust and the capitellid polychaete. This species is normally found in fine sand, but is on occasion located in coarse patches. Thus it is probable that the animals may exhibit not only substratum preference, but also a food preference related to the types of substratum.

3. Depth of locomotion in the substratum

Food selection may also be related to depth of locomotion in the sand. Large *T. maculata* usually crawl under the sand surface with the foot buried deeply in the sand, where they encounter the tubes of the prey, capitellid polychaetes. None of the large *T. maculata* were found with ingested enteropneusts, although smaller specimens contained mainly enteropneusts. *T. crenulata* crawls over the surface, as do some of the smaller *T. maculata*, and these feed exclusively upon the enteropneust.

VIII. SUMMARY AND CONCLUSIONS

1. Fourteen species of Terebra were studied at Eniwetok Atoll, Marshall Islands, from June through September and in December, 1965. Specimens were collected from sandy areas adjacent to 18 islets in water less than 12 m deep. No species of Terebra were found intertidally, nor in less than 0.5 m of water.

2. Movement and locomotion in T. maculata, T. crenulata, T. subulata, and T. guttata were studied in the field and laboratory.

a. All these species lie buried in the sand when they are not actively crawling. The foot and head are relaxed and extended, and the siphon protrudes through the sand to the surface. T. maculata is usually found buried deeper in the sand than are the other species.

b. Two basic movements are postulated for locomotion: 1. continuous undulations of the sole of the foot, and 2. contraction of the longitudinal and circular muscles of the body stalk, resulting in distinct forward thrusts of the body and shell.

c. T. crenulata, T. subulata, and T. guttata emerge to the sand surface when they are crawling, and burrow back into the sand prior to cessation of locomotion. T. maculata usually crawls beneath the surface, although small specimens sometimes crawl at the surface. The rate of forward locomotion is from four to ten steps per minute for all species.

d. Trails produced in the sand exhibit species specific differences in width and depth which can be correlated with the depth at which locomotion occurs, shell shape, and the angle at which the shell is dragged across the sand.

e. Forward locomotion is generally slowed by the presence of coral rubble and stones in the substratum, and by a total absence of sand. *T. crenulata*, *T. subulata*, and *T. guttata* crawl over such obstacles; *T. maculata* crawls around them.

f. Locomotion is intermittent, with periods of inactivity ranging from one to five days. Little or no locomotion was seen in the field from 0900 to 1800 hours.

3. Terebrids from Eniwetok show varying degrees of external sexual dimorphism. The shells of males tend to be more acute, shorter in length, of greater thickness, duller in finish, and possess a less rotund aperture than female shells.

4. Four species of *Terebra* were observed mating in the field. During copulation both partners are oriented in the same direction, with the male to the right of the female. Copulation probably lasts several hours. It is postulated that chemoreception is utilized in the attraction of one sex to the other.

5. Spawning in *T. maculata* and *T. crenulata* probably

extends over a period of several months, and possibly may occur throughout the year, with a peak in late summer and early fall. Some form of differential seasonal migration appears to occur between males and females of _T. maculata_. In June females are more abundant than males in shallow waters, while in December males outnumber females by almost two to one.

6. The larger species of _Terebra_ rarely crawl during the daylight hours, but they are exposed and crawling at night. Two major controlling factors may be operational in the periodism: negative photosensitivity, and a persistent endogenous rhythm set to the daily dark-light cycle.

7. Specimens of several species of _Terebra_ were observed under conditions of white and red illumination in the laboratory. _Terebra_ are negatively affected by white light of constant or changing intensity, but neither movement nor locomotion are visibly affected by red light. White light leads to cessation of locomotion and contraction of the siphon. Terebrids appear to possess light sensitive receptore on the siphon, contraction of this structure occuring in white light even when the eyes of the animal are buried under several centimeters of sand.

8. _T. maculata_, _T. crenulata_, _T. subulata_, and _T. guttata_ exposed to varying periods of continuous illumination and continuous darkness (illumination by red light) in the laboratory show a correlation of

inherent locomotory rhythm with diurnal illumination.

a. Greater locomotory activity was noted in the time period from 2100 to 0900 than from 0900 to 2100 hours.

b. Each species showed a greater average distance of traverse when exposed to continuous darkness than when under continuous illumination. T. subulata and T. guttata appear to have a low threshold to illumination. while T. maculata shows a higher threshold to illumination.

c. The rhythmic activity cycle of Terebra was suppressed after several days of continuous illumination and continuous darkness, but the rhythm was reestablished when an interruption of the constancy of conditions occurred.

9. The anatomy of the digestive system of T. maculata and T. crenulata was examined.

a. Both species lack a radula and poison gland. although a radula sac is present.

b. The proboscis apparatus is of a modified acrembolic type in which the entire proboscis and proboscis sheath, when introverted, are contained in the buccal cavity. The proboscis is only indirectly connected to the proboscis sheath by a membranous tissue covering both structures.

c. The proboscis sheath is probably everted by hemostatic pressure. Prey is grasped by the sphincter muscle at the terminus of the proboscis sheath, and apparently carried posteriorly by peristalsis to the buccal cavity.

d. The proboscis sheath is believed to be introverted by reduction in hemostatic pressure and by peristalsis.

e. The digestive system posterior to the buccal cavity is similar to that found in the other Toxoglossans.

f. Feces are passed out as an amorphous mass.

10. Observations on feeding were obtained from dissections and gut analyses of T. maculata and T. crenulata.

a. T. crenulata was found to only feed on an enteropneust, Ptychodera sp., while T. maculata feeds on both the enteropneust and a polychaete worm belonging to the family Capitellidae.

b. The process of feeding begins sometime between the hours of 1800 and 0700, and may take from six to twelve hours, often extending into the late morning.

c. Approximately 48% of the population of T. crenulata appears to feed once in 24 hours, while only 8% of the population of T. maculata feeds in the same time period. The maximum number of prey located in the gut of T. crenulata was one worm, while one specimen of T. maculata contained two worms, and the rest one.

d. Attraction to and location of prey by Terebra may be by chemoreception. Introduction of oyster extract and polychaete extract into the laboratory aquaria resulted in significantly increased activity among the *Terebra*, but no feeding could be induced by introduction of living oysters or polychaete worms.

11. Terebrids form a major component of the sand communities at Eniwetok Atoll. Other predominant groups represented in the sand communities are the cerithids, mitrids, conids, and the filter-feeding polychaetes.

12. Little evidence exists to demonstrate significant predation on the adult terebrids, although spotted eagle rays and xanthid crabs may account for the large number of cracked shells. Predation appears to be restricted to gastropods such as *Polinices* and *Conus*.

13. Fourteen species of *Terebra* at Eniwetok Atoll were found to exist sympatrically. Evidence for *T. maculata* and *T. crenulata* indicates that ecological differences exist which may permit these and the other terebrids to live in the same restricted habitat:

a. *T. maculata* rarely crawls in wave affected areas, usually occuring in fine sand; *T. crenulata* is seen in areas of coarse sand, often affected by wave action.

b. *T. crenulata* feeds exclusively on enteropneusts; *T. maculata* feeds on both the enteropneust and a polychaete.

c. *T. crenulata* crawls on the surface, while *T. maculata* usually crawls under the sand.

BIBLIOGRAPHY

Abbott, R.T. 1955. American Seashells. New York, D. Van Nostrand Co. 541 pp.

Allen, J. 1950. Australian Shells. Melbourne, Georgian House. 470 pp.

Alpers, F. 1931. Zur Kenntniss des Anatomie von Conus lividus Brug. besonders des Darmkanals. In Risbec, J. 1953. Observations sur l'anatomie des Terebridae neocaledoniens. Bull. Mus. Hist. Nat., Paris. 25: 576-583.

Amaudrut, A. 1898. La partie anterieure du tube digestif et la torsion chez les mollusques gasteropodes. Ann. Sci. Nat. Zool. 7 (8): 1-291.

Arvanitaki, A., and N. Chalazonitis 1960. Photochemical excitation and inhibition of Aplysia neurons. Bull. Inst. Oceanog. Monaco 87: 1-83.

Bennett, M.F. 1954. The rhythmic activity of the quahog, Venus mercenaria, and its modification by light. Biol. Bull. 107: 174-191.

Bouvier, L. 1887. Systeme nerveux, morphologie generale et classification des gasteropodes prosobranches. Ann. Sci. Nat. Zool. 7 (3): 1-510.

Brown, F.A. Jr. 1954. Persistent activity rhythms in the oyster. Amer. J. Physiol. 178: 510-514.

Bryan, W.A. 1915. Natural History of Hawaii. Honolulu, The Hawaiian Gazette Co., Ltd.

Calhoun, J.B. 1944. Twenty-four hour periodicities in the animal kingdom. Part I. The invertebrates. J. Tenn. Acad. Sci. 19 (2): 179-200; 19 (3): 252-262.

Clench, W.J. 1946. The poison cone shell. Occ. Pap. Mollusks Harv. I: 49-80.

Cloudsley-Thompson, J.L. 1961. Rhythmic Activity in Animal Physiology and Behavior. New York and London, Academic Press. 236 pp.

Emery, K.O., J.L. Tracey Jr., and H.S. Ladd. 1954. Geology of Bikini and nearby atolls. Geol. Sur. Prof. Pap. 260-A. Washington, U.S. Govt. Printing Office. 265 pp.

Fretter, V. 1941. The genital ducts of <u>Theodoxus</u>, <u>Lamellaria</u>, and <u>Trivia</u>, and a discussion on their evolution in the prosobranchs. J. Mar. Biol. Ass. U.K. 26: 312-351.

Fretter, V., and A. Graham 1962. British Prosobranch Molluscs: Their functional anatomy and ecology. London, The Ray Society. 755 pp.

Gompel, M. 1937. Recherches sur la consommation d'oxygene de quelquex animaux aquatiques littoraux. C.R. Acad. Sci., Paris. 205: 816-818.

Graham, A. 1941. The esophagus of the Stenoglossan prosobranchs. Proc. Royal Soc. Edinburgh LXI Part I (1): 1-23.

Graham, A. 1949. The molluscan stomach. Trans. Royal Soc. Edinburgh. LXI Part III (27): 737-778.

Hancock, D.A., 1959. The biology and control of the American whelk tingle _Urosalpinx_ _cinera_ (Say) on English oyster beds. Fish. Invest., London. (II) 22 (10): 1-66.

Hanna, G.D., and L.G. Hertlein 1961. Large species of _Terebra_ (Mollusca) from the eastern Pacific. Proc. Calif. Acad. Sci. 30 (3): 67-80.

Hedgpeth, J. 1953. Zoogeography of the Gulf of Mexico. Publ. Inst. Mar. Sci. Texas 3(1): 186.

Hedgpeth, J., ed. 1957. Treatise on Marine Ecology and Paleocology. V. 1. Ecology. Washington, D.C. The Geological Society of America. 1296 pp.

Kaicher, S. 1956. Indo-Pacific Sea Shells: Toxoglossa. Published by the author.

Keen, A.M. 1958. Sea Shells of Tropical West America. Stanford Univ. Press, Stanford, California.

Kennedy, D. 1958. Nerve response to light in molluscs. Biol. Bull. 115: 338.

Kira, T. 1955. Colored Illustrations of the Shells of Japan. Hoikushu, Osaka. 204 pp.

Kohn, A.J. 1959. The ecology of Conus in Hawaii. Ecol. Monogr. 29: 47-90.

-----------1961a. Studies on spawning behavior, egg masses, and larval development in the gastropod genus Conus, Part I. Observations on nine species in Hawaii. Pac. Sci. 15 (2): 163-179.

-----------1961b. Spawning behavior, egg masses, and larval development in Conus from the Indian Ocean. Bull. Bingham. Ocean. Coll. 17 (4): 1-51.

-----------1961c. Chemoreception in gastropod molluscs. Am. Zoologist 1: 291-308.

Kornicker, L.S. 1961. Tidal responses of Terebra salleana. Ecol. 42: 207.

Korringa, P. 1947. Relations between the moon and periodicity in the breeding of marine animals. Ecol. Monogr. 17: 347-381.

Lankester, E., ed. 1906. A Treatise on Zoology. Part V. Mollusca. London, Adam and Charles Black. 355 pp.

Light, V.E. 1930. Photoreceptors of Mya. J. Morph. Physiol. 49: 1-42.

Marcus, E., and E. Marcus 1960. On Hastula cinerea. Biol. Fac. Fil., Univ. S. Paula Zoologia. 23: 25-66.

Morton, J.E. 1964. Mollusca. London, Hutchinson University Press. 232 pp.

Ohba, S. 1952. Analysis of activity rhythm in the marine gastropod, Nassarius festivus, inhabiting the tide pool. I. On the effect of tide and food in the daytime rhythm of activity. Annot. Zool. Japon. 25: 289-297.

----------1954. Analysis of activity rhythm in the marine gastropod, Nassarius festivus, inhabiting the tide pool. II. Nocturnal activity and its artificial control by light. Biol. J. Okayama Univ. I: 209-216.

Pearse, A.S., H.J. Humm, and G.W. Wharton 1942. Ecology of sand beaches at Beaufort, N.C. Ecol. Monogr. 12 (2): 135-190.

Prosser, C.L., and F.A. Brown 1962. Comparative Animal Physiology. Philadelphia and London, W.B. Saunders Co. 688 pp.

Reeve, L.A. 1860. Conchologia Iconica. V. XII. London. 155 pp.

Rippingale, O.H., and D.F. McMichael 1961. Queensland and Great Barrier Reef Shells. Brisbane, The Jacaranda Press.

Risbec, J. 1953. Observations sur l'anatomie des Terebridae neocaledoniens. Bull. Mus. Hist. Nat., Paris. 25: 576-583.

Robinson, E. 1960. Observations on the toxoglossan gastropod Mangelia brachystoma (Philippi). Proc. Zool. Soc. London 135 (3): 319-338.

Rogers, J.F. 1908. The Shell Book. New York, Doubleday, Page, and Co. 485 pp.

Thorson, G. 1956. Marine level bottom communities of recent seas, their temperature adaptation and their "balance" between predators and food animals. Trans. N.Y. Acad. Sci. 18: 693-700.

Thorson, G. 1957. Bottom Communities. In Hedgpeth, J., ed. 1957.

Tinker, S. 1958. Pacific Sea Shells. Vermont and Tokyo, Charles E. Tuttle Co. 240 pp.

Tryon, G.W., Jr. 1885. Manual of Conchology. V. VIII. Philadelphia, published by the author.

Weaver, C. 1959. The tracks of the sand dwellers. Haw. Shell News. VII (3): 25-27.

Weaver, C.,ed. 1960. Hawaiian marine mollusks, recent and new species. Haw. Shell News. I (1-9): 1-36.

Wilbur, K.M., and C.M. Yonge, ed. 1964. Physiology of Mollusca. New York and London, Academic Press. 473 pp.

Zenberg, D. 1935. Gasteropodes Marins. 1. Famille Terebridae. 2. Famille Mitridae. Mem. Mus. Roy. d'Hist. Nat. de Belgique. 24 pp.