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STUDIES ON THE BIOLOGY OF INDO-PACIFIC TEREBRIDAE

BRUCE A. MILLER

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TEREBRIDAE.

University of New Hampshire, Ph.D., 1970
Zoology

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**STUDIES ON THE BIOLOGY OF
INDO-PACIFIC TEREBRIDAE**

by

BRUCE A. MILLER

B. A., Lafayette College, 1964

M. S., University of Hawaii, 1966

A DISSERTATION

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

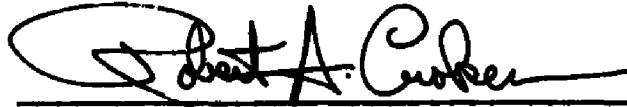
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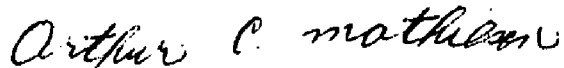
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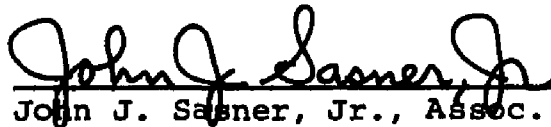
Chairman, Robert A. Croker, Asst. Prof. of Zoology



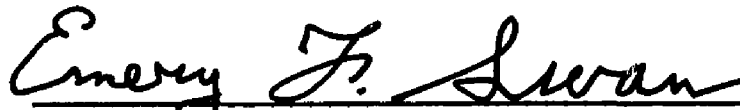
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ABSTRACT

STUDIES ON THE BIOLOGY OF

INDO-PACIFIC TEREBRIDAE

by

BRUCE A. MILLER

Although species of Terebridae are one of the most abundant molluscan components of tropical marine sand communities, they are the least studied of three families included in the gastropod superfamily Toxoglossa. They all have an augur-shaped shell, are similar in external morphology, and have some variety of the basic polyembolic proboscis. The terminology used to describe structural components of the toxoglossan proboscis is not consistent, and a revised terminology is suggested for the terebrid polyembolic proboscis that can be used consistently for the probosces of other toxoglossans. The main functional components of this proboscis are an outer eversible labial tube and an inner retractile buccal tube.

The Terebridae are separated into three primary feeding types based on significant differences in the structure and function of the buccal tube and associated buccal organs. The method of feeding shows great variability, although all species feed on polychaetes or hemichordates. Species with

the Type I polyembolic proboscis have a short buccal tube and lack a radular apparatus. They feed by grasping the prey with the anterior of the labial tube and engulfing it whole. Species with the Type II polyembolic proboscis have a long buccal tube and a functional radular apparatus consisting of a poison bulb, poison gland, and radular sac containing harpoon-like radular teeth. Species of this feeding type impale the prey with a radular tooth, immobilize it with poison secreted from the poison gland, and then grasp it with the sphincter of the labial tube and engulf it. Types I and II have been further subdivided on the basis of variations in shell shape and sculpture, correlated with distinct differences in the relative lengths of the labial and buccal tubes. Species with the Type III polyembolic proboscis have a short or vestigial buccal tube, lack radular teeth and a salivary gland, and have a previously undescribed accessory feeding organ in the labial cavity. This organ is both glandular and muscular, and appears to function primarily by ingesting tentacles of cirratulid polychaetes.

Species of a particular feeding type are not only similar in morphology and in feeding habits, but they also exhibit similar behavioral characteristics, habitat preferences, and other aspects of life history. Life histories of Terebra gouldi, a typical terebrid from subtidal sand areas

with the Type IA polyembolic proboscis, and of Hastula inconstans, a terebrid with a Type IIA polyembolic proboscis living on surf-washed beaches, are given in detail. Preliminary data on feeding and life history in terebrids with the Types IB, IIB, and III polyembolic probosces are also presented. When species of one feeding type are compared with those of another, important differences are seen in life histories, and I suggest that these differences, along with morphological variation, will prove to be of taxonomic significance and can be used to separate the family into several genera.

Terebrids are found in three types of shallow marine sand habitats, namely surf beaches, reef pockets, and extensive subtidal sand flats. Terebrid species diversity is low on surf beaches and in reef pockets, but is often high in subtidal sand flats, where as many as twenty species may live in close proximity. These subtidal sand areas are superficially uniform, but subtle environmental factors effectively limit each species to a fairly well-defined population center. One species from a subtidal sand flat in Hawaii, Terebra gouldi, is considered in detail, and the physical and biological factors that may effect its distribution around the sand flat are demonstrated.

SECTION I

INTRODUCTION TO THE STUDY OF THE FAMILY TEREBRIDAE

Large areas of marine sandy substrata occur throughout the tropical Central Pacific, ranging from surf washed beaches and reef flats in shallow water to extensive sand beds descending hundreds of meters below the surface. Many of these sandy environments support a dense infaunal population of suspension and detritus feeding worms, which are preyed upon by a large number of vermiverous gastropods, primarily members of the toxoglossan family Terebridae. The terebrids are specialized to live successfully in this environment, and are found in no habitat other than sand.

Although terebrids generally are one of the most abundant molluscan components of tropical marine sand communities, they have been little studied. Tryon (1885), Bouvier (1887), Amaudrut (1898), Risbec (1955), and Marcus and Marcus (1960) have recorded aspects of the morphology of a few species, but still not enough is known to make generalizations on morphological relationships in the family. Brief observations on aspects of terebrid locomotion were reported by Pearse et al (1942) and Kornicker (1961). Marcus and Marcus (1960) worked on some aspects of the biology of Hastula cinerea, and brief mention of terebrids

was made in several papers on the ecology of sandy areas (Macnae and Kalk, 1962; Wade, 1968).

To date, there has been little agreement on a classification for the terebrids. Troschel (1866) attempted to classify the family on the basis of differences in the feeding apparatus, but lacked sufficient material to complete his work. Other schemes have been proposed, some based on shell variation alone (Deshayes, 1859; Tryon, 1885; Bartsch, 1923), and some on both shell variation and anatomical differences (Dall, 1908; Cernohorsky, 1966). The earlier descriptions unfortunately were not accurate, and general inconsistency among the various schemes prompted Kay (1967, unpublished) to include all terebrids in the genus Terebra until the family was studied further.

There are probably more than 150 Recent species of terebrids (Cernohorsky, 1966), and Kay (1967, unpublished) listed 41 species from around the Hawaiian Islands. Most of the species found in Hawaii are widely distributed throughout the Indo-Pacific. They have an augur-shaped shell and are similar in external morphology. All terebrids have some variety of the basic polyembolic proboscis, first described by Smith (1967) for the turrids. In this type of proboscis, the primary functional components utilized in prey capture are an outer eversible labial tube and an

inner retractile buccal tube. A detailed discussion of these terms is included in Section II of this paper.

I have separated the Terebridae into three primary feeding types based on significant differences in the structure and function of the buccal tube and associated buccal organs. Species with the Type I polyembolic proboscis have a short buccal tube and no radular apparatus; those with the Type II polyembolic proboscis have a long buccal tube and a functional radular apparatus; and those with the Type III polyembolic proboscis have a short buccal tube, no radular apparatus, and an accessory feeding organ. Types I and II have been further subdivided on the basis of variations in shell shape and sculpture, correlated with distinct differences in the relative lengths of the labial and buccal tubes.

Species of a particular feeding type are not only similar morphologically, but they also exhibit similar behavioral characteristics, habitat preferences, and other aspects of life history. Important differences, however, are seen in these life histories when species of one feeding type are compared with those of another. I believe that these differences will prove to be of taxonomic significance, and can be used to separate the family into several genera.

The purpose of this study is to present a comprehensive

picture of the biology of the family Terebridae in the Central Pacific. In Section II the toxoglossan proboscis is discussed, including a review of past work, revision of terminology, and a discussion of the specialized terebrid probosces. In Section III detailed aspects of the life history of terebrid species characteristic of each feeding type are considered. The life histories of Terebra gouldi, a typical terebrid from subtidal sand areas with a Type I polyembolic proboscis, and of Hastula inconstans, a terebrid with a Type II polyembolic proboscis typically found on surf-washed beaches, will be emphasized. Preliminary ideas on feeding in terebrids with the Type IB, Type IIB, and Type III polyembolic probosces will also be presented.

Three types of sand habitats are typically found in water less than 15 meters deep, namely surf beaches, reef pockets, and extensive subtidal sand flats. Species diversity is low on surf beaches and in reef pockets, but is often high in subtidal sand flats, where as many as 20 species may be found living in close proximity. These subtidal sand areas are superficially uniform, but subtle environmental factors effectively limit each species to a fairly well defined population center. In Section IV, one species from a subtidal sand flat in Hawaii, Terebra gouldi, will be examined to show the physical and biological factors

effecting its distribution pattern.

SECTION II

THE TOXOGLOSSAN PROBOSCIS: A REVIEW OF PREVIOUS WORK,
REVISION OF TERMINOLOGY, AND DISCUSSION OF
THE SPECIALIZED TEREBRID PROBOSCES

Introduction

The toxoglossan alimentary tract is unique, and differs significantly in structure and function from those of other prosobranch gastropods. Various workers have described aspects of the toxoglossan feeding apparatus. Shaw (1914), Alpers (1931), Clench and Kondo (1943), Hermitte (1946), Jackel (1952), and Kohn (1959) worked on conids; Troschel (1866), Bouvier (1887), Risbec (1955), and Marcus and Marcus (1960) studied the terebrids; while Robinson (1960) and Smith (1967) worked with the turrids. The greatest differences among species occur in the nature of the foregut, and because most workers have concentrated their research on one family and have had insufficient material for a comprehensive study of a large number of species, the resulting terminology used to describe homologous structures of the foregut in the conids, turrids and terebrids generally lacks consistency.

Much of the inconsistency arises through the error of

basing terminology on function rather than structure. By combining my studies on the Terebridae with earlier work on the Conidae and Turridae, it can be shown how the highly specialized toxoglossan proboscis is derived from the acremental and pleurental probosces characteristic of many other prosobranchs. To clarify the discussion, I propose a new terminology for the functional components of the toxoglossan proboscis that is consistent for all toxoglossan families and can be readily used in a comparative study involving other prosobranchs.

Significant structural differences occur among the probosces of the Terebridae, particularly in the morphology of the buccal tube and in the number and type of buccal organs present. I have used these differences to separate the family into three primary feeding types, and suggest that they are of potential use as diagnostic characters for a new classification of the family.

Review of previous work

The prosobranch proboscis

Fretter and Graham (1962) have synthesized much of the work published on the alimentary tract of prosobranch gastropods, and have discussed the development of the

prosobranch foregut associated with various changes in the method of feeding. Archaeogastropods and most mesogastropods rasp their food from the surface, and the mouth opens directly at the end of a short snout on the underside of the head. However, many higher prosobranchs feed on material not immediately accessible on the surface, and the progressive development of a proboscis has occurred. In these animals the aperture visible on the underside of the head is not the true mouth, but the opening of a proboscis sac within which the proboscis lies. The proboscis occurs in such groups as the Muricacea which bore into other animals to find their food, in carrion feeders such as the Buccinacea which use their probosces to reach or probe into the body of the prey, in the Cerithiacea and Cypraeacea which extend their probosces into the body of their prey through natural apertures, and in specialized feeders such as the Pyramidellidae and species of the superfamily Toxoglossa.

Regardless of the function of the proboscis, it is basically a retractible elongation of that part of the snout lying anterior to the tentacles. Fretter and Graham have described two types of probosces based on differences in the method of retraction and in the way the elongated snout is held within the body on retraction. The simpler type is the

acrembolic (Fig. 1), found in the families Scalidae, Aclididae, Eulimidae, Pryamidellidae, Naticidae, Lamellariidae, and Eratoidae. This proboscis is essentially an in-turned part of the outer body surface with retractor muscles inserted at the tip. During retraction the tip is introverted and pulled to the base of the proboscis sac. The pleurembolic proboscis (Fig. 2), found in higher Mesogastropoda and most Stenoglossa, is mechanically more efficient. The retractor muscles are inserted nearer to the base of the proboscis, and during retraction the tip of the proboscis is elevated from the base, thus partly filling the proboscis sac. This enables a longer proboscis to be accommodated in the proboscis sac.

The toxoglossan proboscis

As Smith (1967) pointed out, in the Stenoglossa both the Muricacea and Buccinacea have pleurembolic probosces. In these groups the buccal tube originates at the tip of the proboscis and dilates into the buccal cavity, which receives the esophagus dorsally and the radular sac ventrally. The esophagus extends throughout a considerable length of the proboscis, passes through the cephalic hemocoel, and enters the stomach.

The foregut is significantly different among the

Fig. 1. Diagram of the neogastropod acrembolic proboscis (After Fretter and Graham, 1962). In this proboscis type the retractor muscles are inserted at the tip. During retraction the tip is introverted and pulled to the base of the proboscis sac.

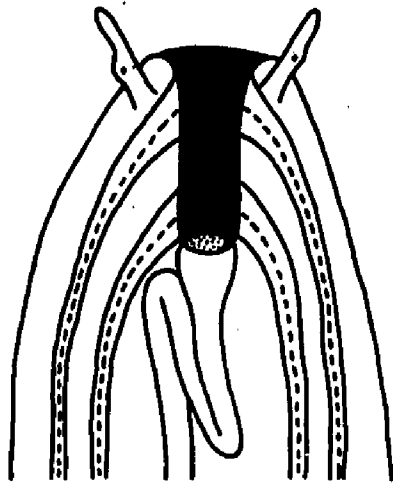
A. Retracted position.

B. Extended position.

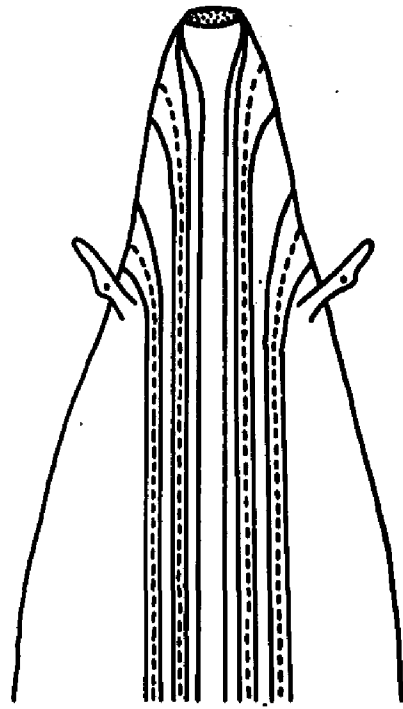
Fig. 2. Diagram of the neogastropod pleurembolic proboscis (After Fretter and Graham, 1962). The retractor muscles are inserted nearer to the base of the proboscis, and during retraction the tip of the proboscis is elevated from the base, thus partly filling the proboscis sac.

A. Retracted position.

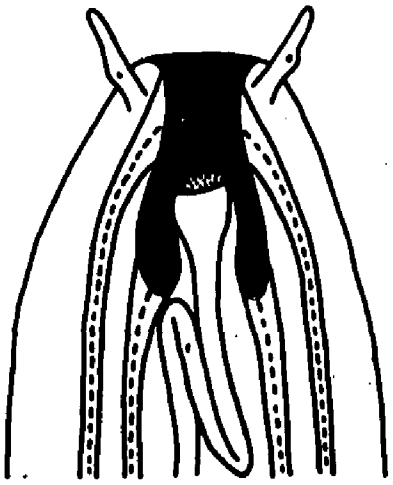
B. Extended position.



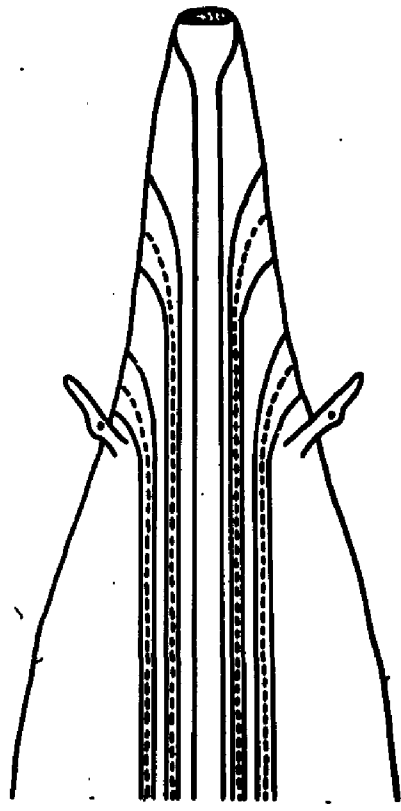
A



B



A



B

Toxoglossa, and it has proved difficult to determine the homology of its functional components. Smith's study (1967) on the functional morphology of the feeding apparatus of turrids is the most complete to date. He proposed two new types of probosces for the turrids, the intraembolic and polyembolic. In the intraembolic proboscis (Fig. 3) the rhynchodaeum (rostrum of Shaw, proboscis sac of Bouvier) is not an integral part of the proboscis but merely forms a sac within which the proboscis extends and retracts. When the proboscis is extended the rhynchodaeum remains intact, and when it is retracted the proboscis does not introvert completely but in a series of co-axial annular folds. The retractor muscles insert near the tip of the proboscis, and the buccal cavity and the esophagus do not extend with the proboscis as they do in acrembolic and pleurembolic types. In the polyembolic proboscis as described by Smith (Fig. 4), the introvert is formed by extension of the walls of the rhynchodaeum, along which the retractor muscles are attached. Retraction occurs by the infolding of the rhynchodaeum walls, while the buccal cavity and esophagus remain at the base of the rhynchodaeum and do not extend and retract.

Fig. 3. Diagram of the toxoglossan intraembolic proboscis (Modified from Smith, 1967, by addition of retractor muscles around the buccal cavity. The terminology is that of Smith). The rhynchodaeum (Proboscis sac) is not an integral part of the proboscis but merely forms a sac within which the proboscis extends and retracts.

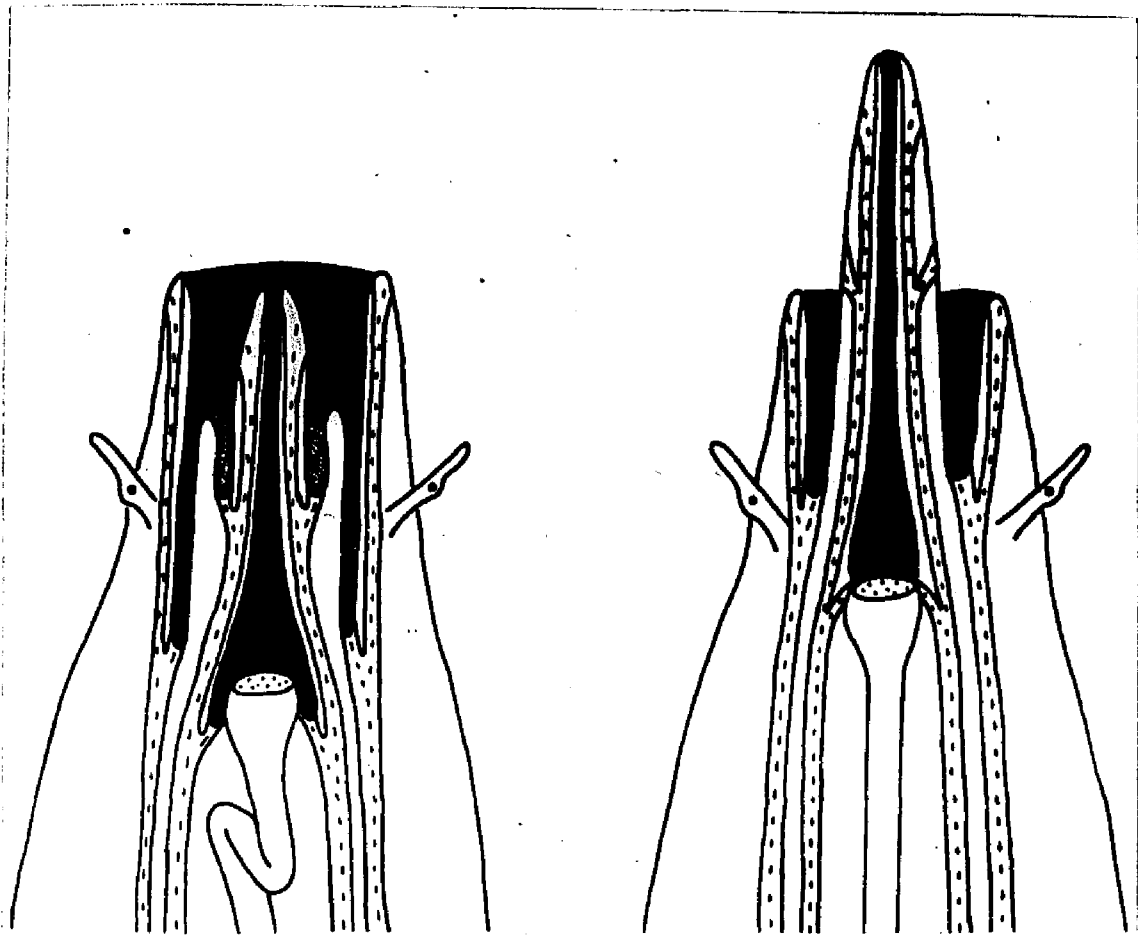
A. Retracted position.

B. Extended position.

Fig. 4. Diagram of the toxoglossan polyembolic proboscis (Modified from Smith, 1967, by addition of retractor muscles along the buccal tube and buccal cavity. The terminology is that of Smith). In this proboscis type the introvert is formed by extension of the walls of the rhynchodaeum, along which the retractor muscles are attached.

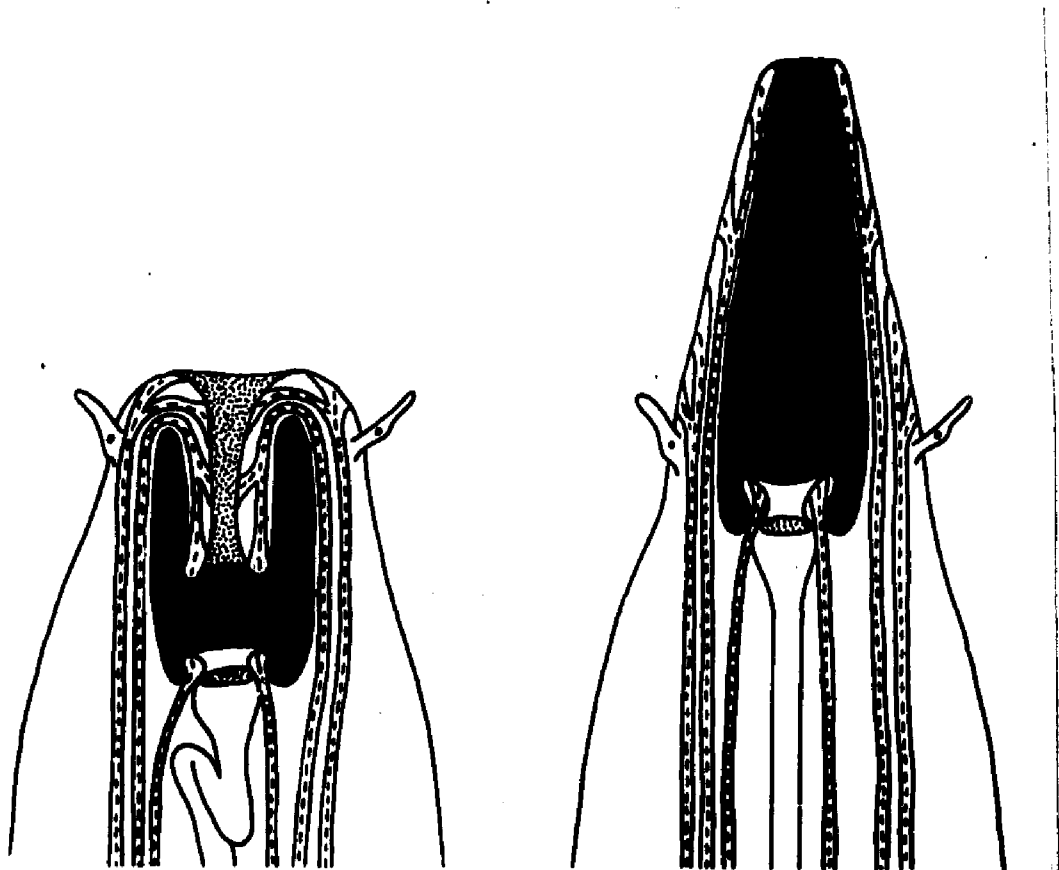
A. Retracted position.

B. Extended position.



A

B



A

B

Revision of terminology for components
of the toxoglossan foregut

As Smith suggested, the intraembolic proboscis described for some turrids is also characteristic of the conids. However, contrary to his interpretation, the intraembolic is not found in the Terebridae. All terebrids that I have studied possess some modification of the basic polyembolic type. Smith's descriptions of the two proboscis types are basically valid, but I cannot fully agree with his interpretation of the functioning of particular structures in the probosces, nor with his terminology. Much of the ambiguity involved in comparing the anatomy of the foregut of the three toxoglossan families arises from the fact that the term proboscis was originally intended for use in animals of acriembolic and pleurembolic type possessing a single introvert. In the Toxoglossa the intraembolic and polyembolic proboscis does not consist of one introvert, but has been completely divided into two separate functional components, both of which may serve as an introvert. It is my contention that the term proboscis should not be used to describe either one or the other of these functional components, but rather should serve as a general term encompassing both components. I would then call the anterior

structure the labial tube, and the posterior structure the buccal tube. The foregut of a generalized prosobranch with the acrembolic or pleurembolic proboscis is shown in Figure 5A with the main structural components labelled. Figures 5B through D illustrate probosces characteristic of the *Toxoglossa*. The terminology proposed for the component parts of these probosces is indicated on the figures. Table I lists the comparable terms used by other workers.

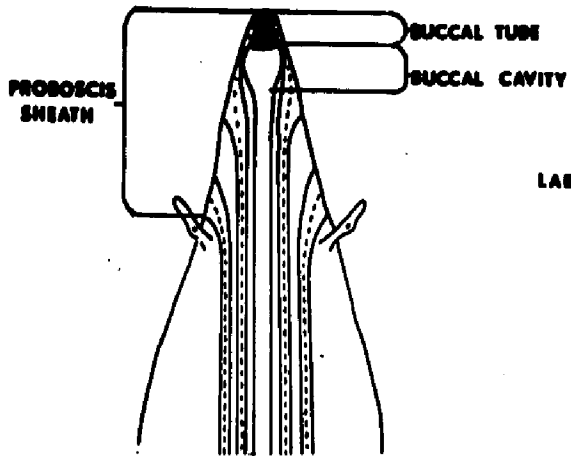
The labial tube

In all prosobranchs with acrembolic and pleurembolic probosces there is only one introvert. The buccal tube and buccal cavity extend to its anterior tip, and are surrounded by a heavy muscular sheath. In the *Toxoglossa* the buccal tube and buccal cavity have been completely separated from their muscular sheath. The buccal cavity has moved posteriorly into the cephalic hemocoel, and the extremely variable buccal tube remains attached to the anterior of the buccal cavity.

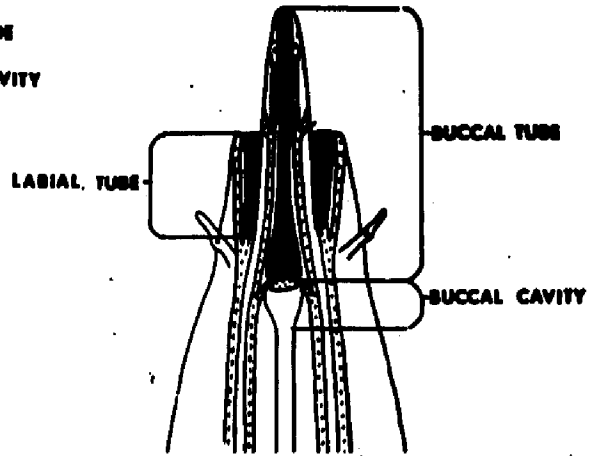
The muscular sheath which has been separated from the buccal tube and buccal cavity has been referred to by several names, generally based on function and not on a clear understanding of structural relationship. Conids characteristically have the intraembolic proboscis, and

Fig. 5. Diagrams of three generalized toxoglossan proboscis types compared with a diagram of the generalized acrembolic or pleurembolic proboscis, indicating the homology of structural components.

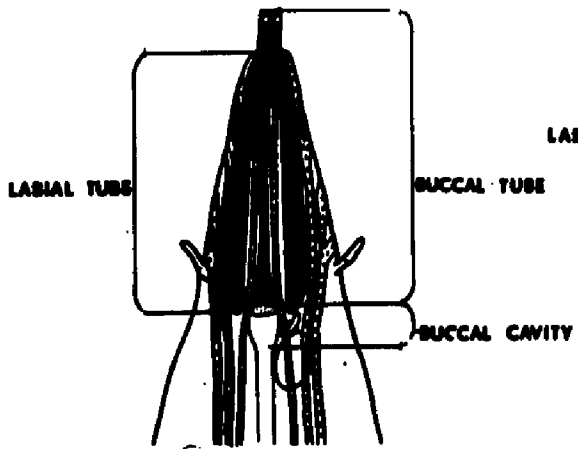
- A. The acrembolic or pleurembolic proboscis characteristic of most higher prosobranchs.
- B. The intraembolic proboscis of conids and some turrids.
- C. A variety of the polyembolic proboscis characteristic of some turrids and terebrids.
- D. A variety of the polyembolic proboscis characteristic of some turrids and terebrids.



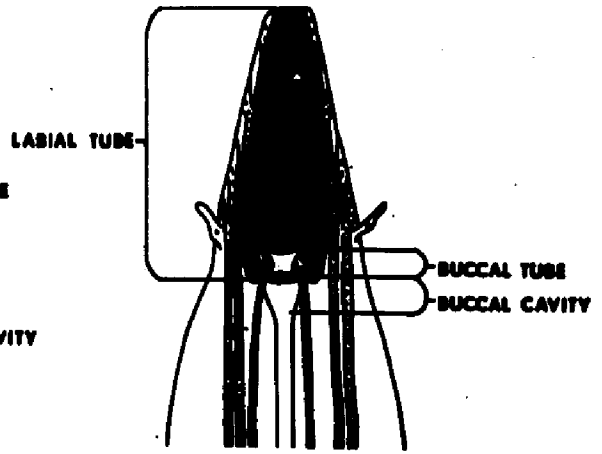
A



B



C



D

Table I. Terminology for components of the toxoglossan foregut used by other workers.

| <u>Worker</u> | <u>Family</u> | <u>Proboscis Type</u> | <u>Labial tube</u> | <u>Buccal tube</u> |
|-------------------------|---------------|---------------------------|---------------------|--------------------|
| Bergh, 1896 | Conidae | Intraembolic | rostrum | proboscis |
| Clench & Kondo, 1943 | Conidae | Intraembolic | rostrum | proboscis |
| Kohn, 1955 | Conidae | Intraembolic | rostrum | proboscis |
| Shaw, 1914 | Conidae | Intraembolic | rostrum | proboscis |
| Bouvier, 1897 | Terebridae | Polyembolic | proboscis sheath | proboscis |
| Marcus, 1960 | Terebridae | Polyembolic | anterior tube | proboscis |
| Risbec, 1953 | Terebridae | Polyembolic | proboscis sheath | proboscis |
| Smith, 1967 | Turridae | Intraembolic | rhynchodaeum | proboscis |
| Smith, 1967 | Turridae | Polyembolic (Type I) | proboscis | buccal sheath |
| Smith, 1967 | Turridae | Intraembolic (Type II) | proboscis | inner proboscis |

the retractile but not eversible sheath has been called the rostrum (Shaw, 1914; Alpers, 1931). It does not function directly in prey capture in most species. Terebrids all have the polyembolic-type proboscis. The fully eversible muscular sheath has been called the proboscis sheath by Bouvier (1887) and Risbec (1953), and the anterior tube by Marcus and Marcus (1960). The turrids have either the intraembolic or the polyembolic proboscis, and it is in this family that the error of basing the name on function is most clearly apparent. Smith called the non-eversible muscular sheath among the intraembolic turrids the rhynchodaeum, but calls the eversible structure in polyembolic turrids the proboscis. Some polyembolic turrids have a long retractile sheath and a long buccal tube, and on the basis of function Smith is then required to name the sheath the outer proboscis and the buccal tube the inner proboscis.

It is my belief that use of the term proboscis in this context should be avoided, for strictly speaking, the proboscis should include the buccal tube and the buccal cavity as well. Similarly, the use of the term proboscis sheath, suggested by Bouvier for the terebrids, implies that the structure surrounds a functional proboscis, which is not necessarily true for many turrids and terebrids. Finally the term rhynchodaeum suggested by Smith for some turrids

has little descriptive value.

The muscular sheath is the most anterior of the functional units of intraembolic and polyembolic probosces, and is unique to the Toxoglossa. It consists of an inner and outer layer of circular muscles, a median layer of longitudinal and diagonal retractors, and terminates in an anterior sphincter. The sheath is innervated by labial nerves (Marcus and Marcus, 1960) and hence corresponds to outer lips. Use of the term labial tube clearly indicates that the structure is an anterior elongation of the lips, and even though the tube is variable in function it is similar in structure throughout the Toxoglossa. Since it is only characteristic of the conids, terebrids, and turrids, general acceptance of this term lends consistency to any comparative description of the feeding apparatus of species in these groups.

The buccal tube

According to Fretter and Graham (1962) the structure located between the mouth and the expanded muscular buccal cavity in all prosobranchs is called the buccal tube. As mentioned above, the buccal cavity and the buccal tube are normally covered by a muscular sheath in the acremental and pleuremental type probosces. In the intraembolic and polyembolic probosces the buccal cavity has been completely

separated from the muscular sheath but it still resembles the buccal cavity of other prosobranchs. However, the structure that corresponds to the buccal tube varies significantly in length and function among different toxoglossan species, and has not been satisfactorily defined. In conids it is considerably longer and more retractile than the labial tube, is used in prey capture, and has generally been called the proboscis (Shaw, 1914; Kohn, 1955). In some turrids and terebrids it is longer than the labial tube and is generally extended out of the labial tube during feeding. In this situation it has been called the inner proboscis (Marcus and Marcus, 1960; Smith, 1967). In other turrids and terebrids the structure is short, consists of a circlet of muscles attached to the anterior of the buccal cavity, and is not extended out of the labial tube during feeding. Hence it does not function in prey capture, and should not be called a proboscis.

Regardless of length and function, the entire structure located between the mouth and the buccal cavity is homologous to the buccal tube of other prosobranchs as defined by Fretter and Graham. Use of the term proboscis should be avoided in this context, and the term buccal tube should be adopted whether the structure is utilized in prey capture or not. The validity of this designation will be discussed

later.

The buccal cavity

The buccal cavity is surrounded by a thick layer of circular muscles. It is bounded anteriorly by the buccal tube, receives the ducts of the salivary glands, and extends posteriorly, as Smith suggests, to include the openings of the radular apparatus and the poison gland when they are present.

In prosobranchs with acrembolic and pleurembolic probosces the functional position of the buccal cavity and the radular teeth is at the tip of the proboscis. Even though the buccal cavity in the toxoglossans is not located at the tip of the proboscis but rather in the anterior part of the cephalic hemocoel, I consider it to be a component of the toxoglossan proboscis. The buccal cavity is not fixed, as Smith has found in the turrids, but is carried anteriorly with the buccal tube for a short distance during feeding. The radular teeth, when they are present, are passed from the radular sac into the buccal cavity. However, they are not utilized here, but rather at the functional position at the tip of the labial tube. Therefore the buccal cavity is never directly used in prey capture.

Terebrid feeding types

All species that I have studied in the family Terebridae possess some variety of the polyembolic proboscis. The family can be divided into three natural groupings on the basis of previously undescribed differences in the structure and function of the probosces and on the number and type of buccal organs present. These groupings are described as having Type I, Type II, and Type III polyembolic probosces.

Methods

All animals were relaxed by quick freezing for 5-10 hours, and were then removed from their shells. The gross anatomy of the feeding apparatus was worked out through dissection of fresh specimens, and specimens dipped in methylene blue. Fine details of the anatomy were studied by microscopic examination of material sectioned on a cryostat and stained with hematoxylin-eosin.

The Type I polyembolic proboscis

Species with the Type I polyembolic proboscis possess an eversible labial tube of variable length, a short muscular buccal tube with limited contractility, and have

no buccal organs other than a bipartite salivary gland.

There are two varieties of the Type I polyembolic proboscis, primarily based on differences in the relative length of the labial tubes.

Type IA.

The Type IA polyembolic proboscis is found in Terebra areolata (Link, 1807); T. crenulata (Linnaeus, 1758); T. dimidiata (Linnaeus, 1758); T. gouldi Deshayes, 1859; and T. thaanumi Pilsbry, 1920. The two primary functional components utilized in prey capture in these species are a long eversible labial tube and a short, slightly retractile buccal tube. The description presented below applies specifically to T. gouldi, but is generally valid for the other species as well.

The labial tube in T. gouldi extends a considerable distance when fully everted and terminates anteriorly in a well-developed sphincter (Fig. 6). In the everted condition the musculature of the labial tube consists of an inner layer of circular muscles covered by a thin epithelium lining the lumen, and an outer layer of circular muscles covered by external epithelium. Well-developed longitudinal and diagonal retractors lie directly beneath the outer circular muscles. They originate in the foot, pass anteriorly in the body wall, and insert around the sphincter. Short

Fig. 6. Terebra gouldi. Diagram of the foregut of the Type IA polyembolic proboscis in the extended position, showing the primary musculature. The cephalic hemocoel is shaded grey.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

1c.....outer circular muscles of the labial tube

1d.....retractor muscles of the labial tube

1f.....inner circular muscles of the labial tube

2.....buccal tube

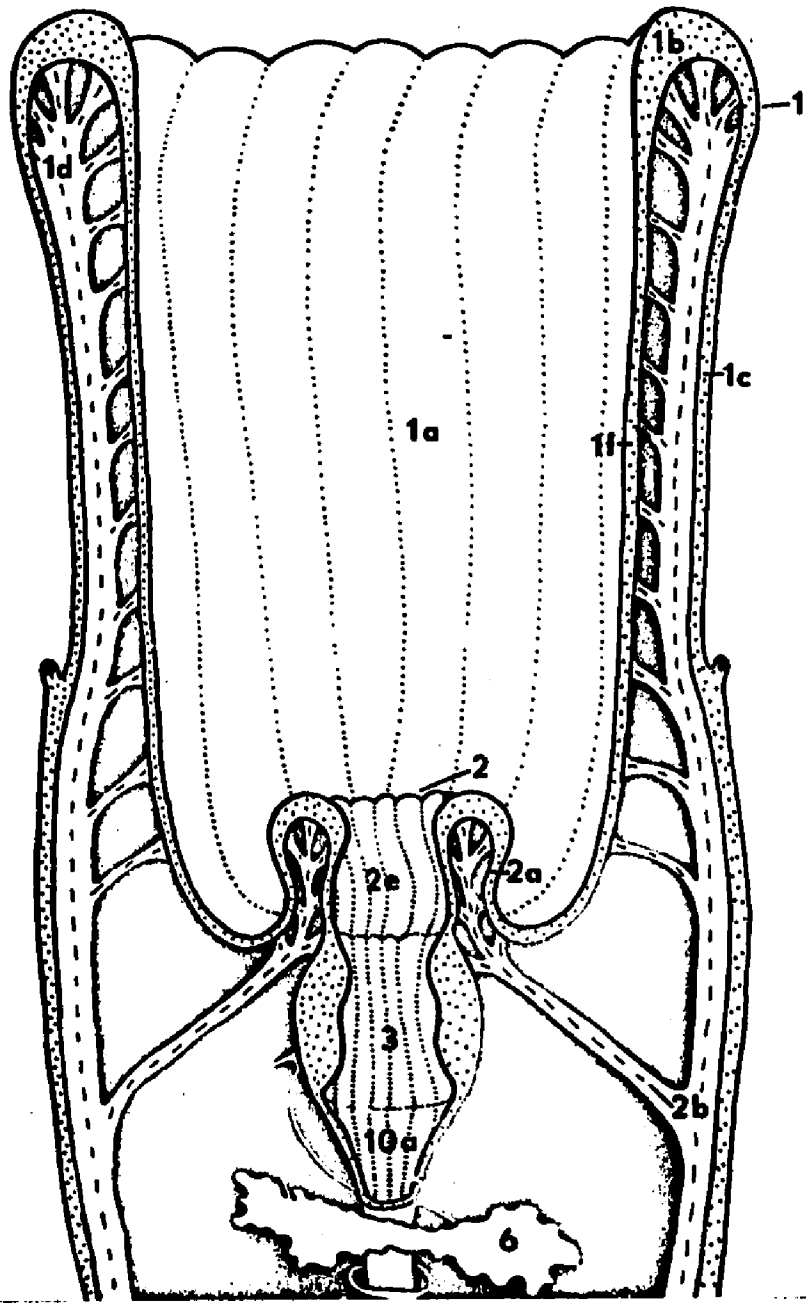
2a.....outer circular muscles of the buccal tube

2b.....retractor muscles of the buccal tube

3.....buccal cavity

6.....salivary gland

10a....pre-ganglionic esophagus



radial muscles connect along the length of the labial tube between the longitudinal retractors and the inner circular layer in a space representing a forward extension of the cephalic hemocoel.

The buccal tube is short, non-eversible, and moderately contractile. The musculature consists of an inner and outer layer of circular muscles joined together by small radial strands. The inner layer of circular muscles is well-developed, and represents an anterior continuation of the thick circular muscles of the buccal cavity. The outer circular layer is thin and is continuous with the inner circular muscles of the labial tube. Each circular layer is covered by epithelium. A space representing a forward extension of the cephalic hemocoel lies between the two muscle layers. This space contains seven bands of longitudinal retractor muscles which originate in the body musculature surrounding the main cephalic hemocoel, insert at the junction between the buccal cavity and the buccal tube, and terminate at the tip of the buccal tube. The buccal cavity contains no longitudinal or diagonal retractors, but is composed of a thick layer of circular muscles continuous with the inner circular muscles of the anterior buccal tube.

The small, bipartite salivary gland lies dorsal to the

nerve ring (Fig. 7). A slender salivary duct arises from each half of the salivary gland, passes ventrally around the pre-ganglionic esophagus, and enters a small sac, termed the buccal sac by Robinson (1960), located on the ventro-posterior side of the buccal cavity.

The pre-ganglionic esophagus commences posterior to the entrance of the salivary ducts. The thick layer of circular muscles surrounding the lumen of the buccal tube terminates, and the esophageal walls are thin and distensible. The pre-ganglionic esophagus is folded upon itself, and then extends anteriorly until it passes through the nerve ring. The long post-ganglionic esophagus leads into a tubular stomach and a narrow thin-walled intestine.

When the proboscis is retracted, the labial tube inverts and the sphincter lies in close proximity to the buccal tube at the posterior of the labial cavity (Fig. 8). The esophagus exhibits a flexure at the nerve ring, and is folded upon itself so that the pre-ganglionic esophagus overlies the salivary gland and the post-ganglionic esophagus. During feeding, hemostatic pressure in the cephalic hemocoel coupled with contraction of the circular muscles and relaxation of the longitudinal retractors, leads to eversion of the labial tube and forward extension of the pre-ganglionic esophagus, buccal cavity, and buccal tube.

Fig. 7. Terebra gouldi. Dorsal view of the buccal organs of the Type IA polyembolic proboscis.

1f.....inner circular muscles of the labial tube

2.....buccal tube

2b.....retractor muscles of the buccal tube

3.....buccal cavity

4a.....buccal sac

6.....salivary gland

6a.....ducts of the salivary gland

9.....nerve ring

10a....pre-ganglionic esophagus

10b....post-ganglionic esophagus

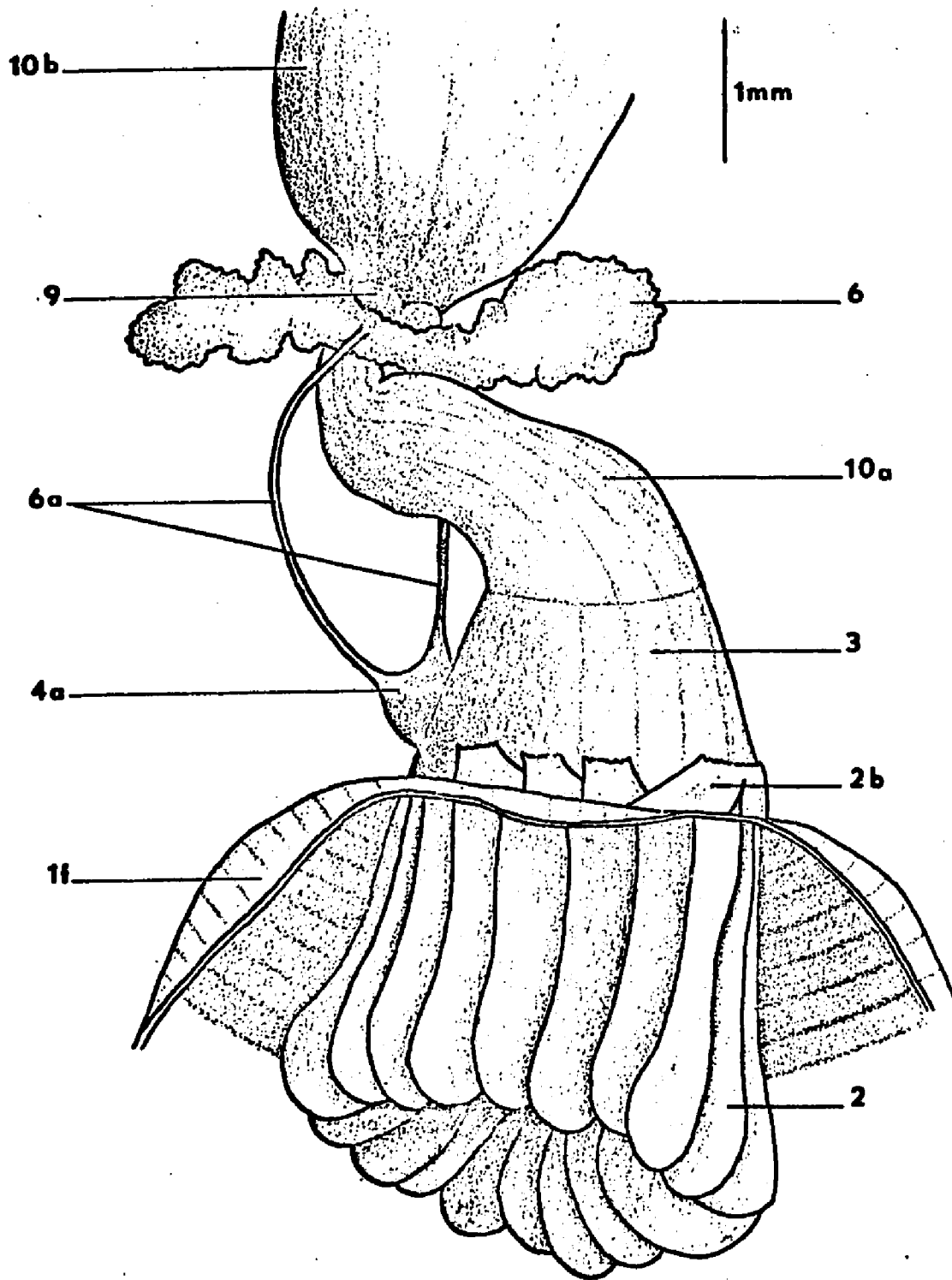
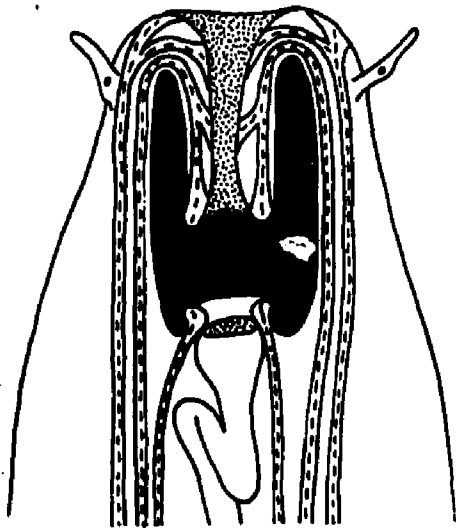
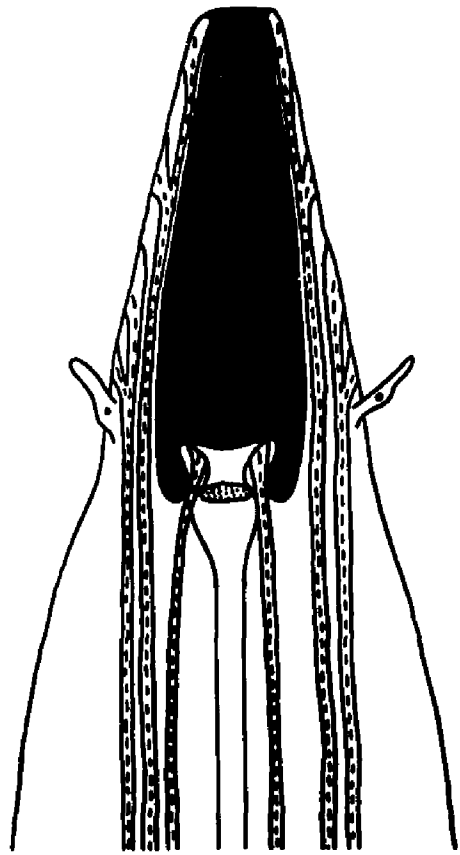


Fig. 8. Diagram of the terebrid Type IA polyembolic proboscis to show the position of component parts while retracted (A) and extended (B).



A



B

The buccal tube is only capable of limited extension, and can not be protruded out of the labial tube.

Type IB

The Type IB polyembolic proboscis is found in Terebra chlorata Lamarck, 1822; T. felina (Dillwyn, 1817); and T. maculata (Linnaeus 1758). Terebrid species of this feeding type are morphologically similar to Type IA terebrids in that they lack a radular apparatus and possess a short non-reversible buccal tube. The arrangement of muscles is nearly identical in both types. However, the everted labial tube in Type IB species is two to three times longer than that of Type IA species, and is folded upon itself several times when inverted within the labial cavity.

The Type II polyembolic proboscis

Species with the Type II polyembolic proboscis are the only terebrids exhibiting typical toxoglossan characteristics. They possess an eversible labial tube of moderate length, a long retractile buccal tube, and in addition to a bipartite salivary gland, contain within the cephalic hemocoel a poison bulb, poison gland, and radular sac equipped with harpoon-like radular teeth. They can be secondarily divided into Type IIA and Type IIB on the basis of differences in the nature of the buccal tube and the

labial cavity.

Type IIA

The Type IIA polyembolic proboscis is found in Hastula albula (Menke, 1843); H. hectica (Linnaeus, 1758); H. inconstans (Hinds, 1844); H. lauta (Pease, 1869); H. penicillata (Hinds, 1844); H. solida (Deshayes, 1857); and H. striqilata (Linnaeus, 1758). The description below pertains specifically to H. inconstans, but applies with minor exception to the other species. The functional components utilized in prey capture, particularly the buccal tube, differ significantly from those found in Type I terebrids, and are similar to those described by Smith (1967) for the turrid Philbertia purpurea (Montagu, 1803).

The labial tube in H. inconstans is long and eversible, and terminates anteriorly in a well developed sphincter (Fig. 9). In the everted condition the musculature of the labial tube consists of an inner layer of circular muscles, covered by a thin epithelium lining the lumen, and an outer layer of circular muscles covered by epithelium. Well-developed longitudinal and diagonal retractors lie directly below the outer circular muscles. They originate in the foot, pass anteriorly in the body wall, and insert around the sphincter. Short radial muscles connect along the length of the labial tube between the longitudinal retractors

Fig. 9. Hastula inconstans. Diagram of the foregut of the Type IIA polyembolic proboscis in the extended position, showing the primary musculature. The cephalic hemocoel is shaded grey.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

1c.....outer circular muscles of the labial tube

1d.....retractor muscles of the labial tube

1f.....inner circular muscles of the labial tube

2.....buccal tube

2a.....outer circular muscles of the buccal tube

2b.....retractor muscles of the buccal tube

3.....buccal cavity

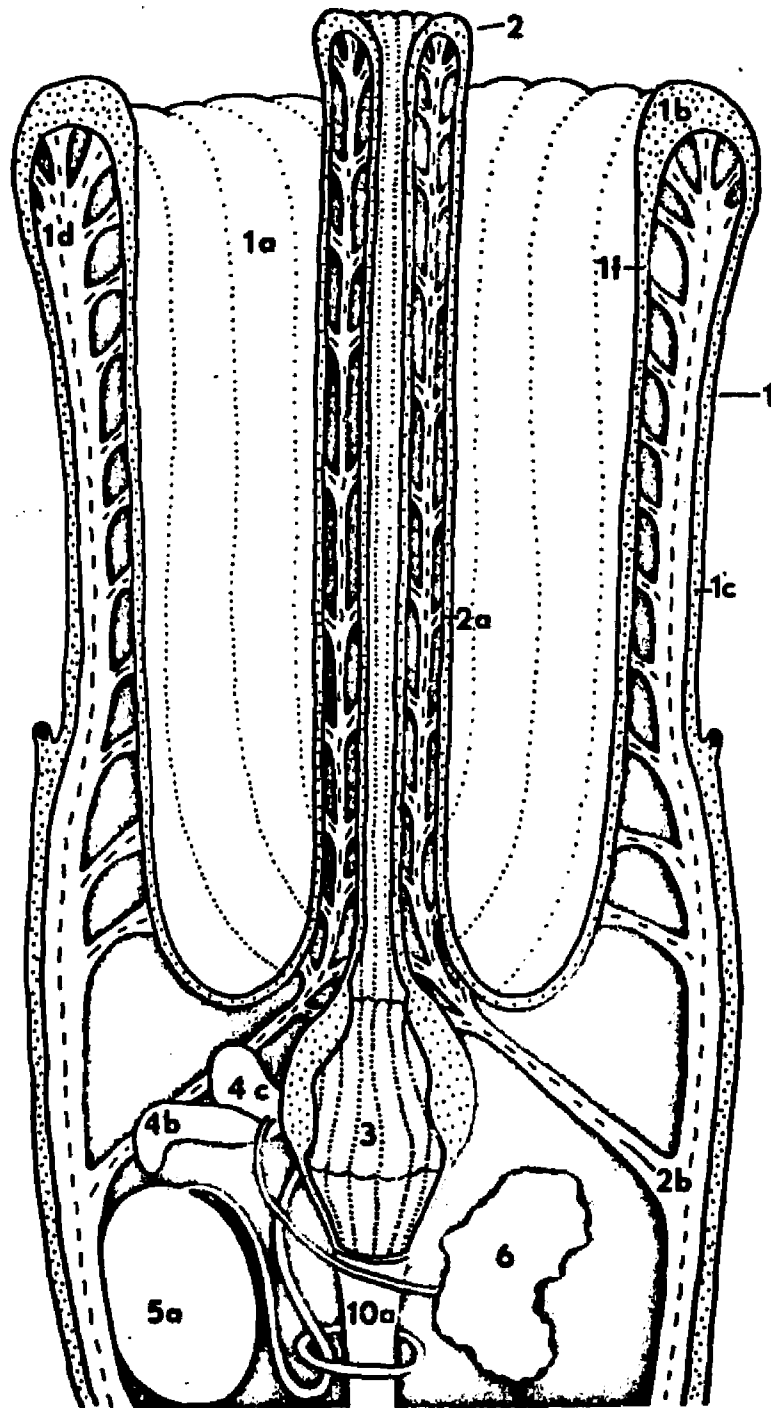
4b.....radular sac

4c.....radular caecum

5a.....poison bulb

6.....salivary gland

10a....pre-ganglionic esophagus



and the inner circular layer in a space representing an anterior extension of the cephalic hemocoel.

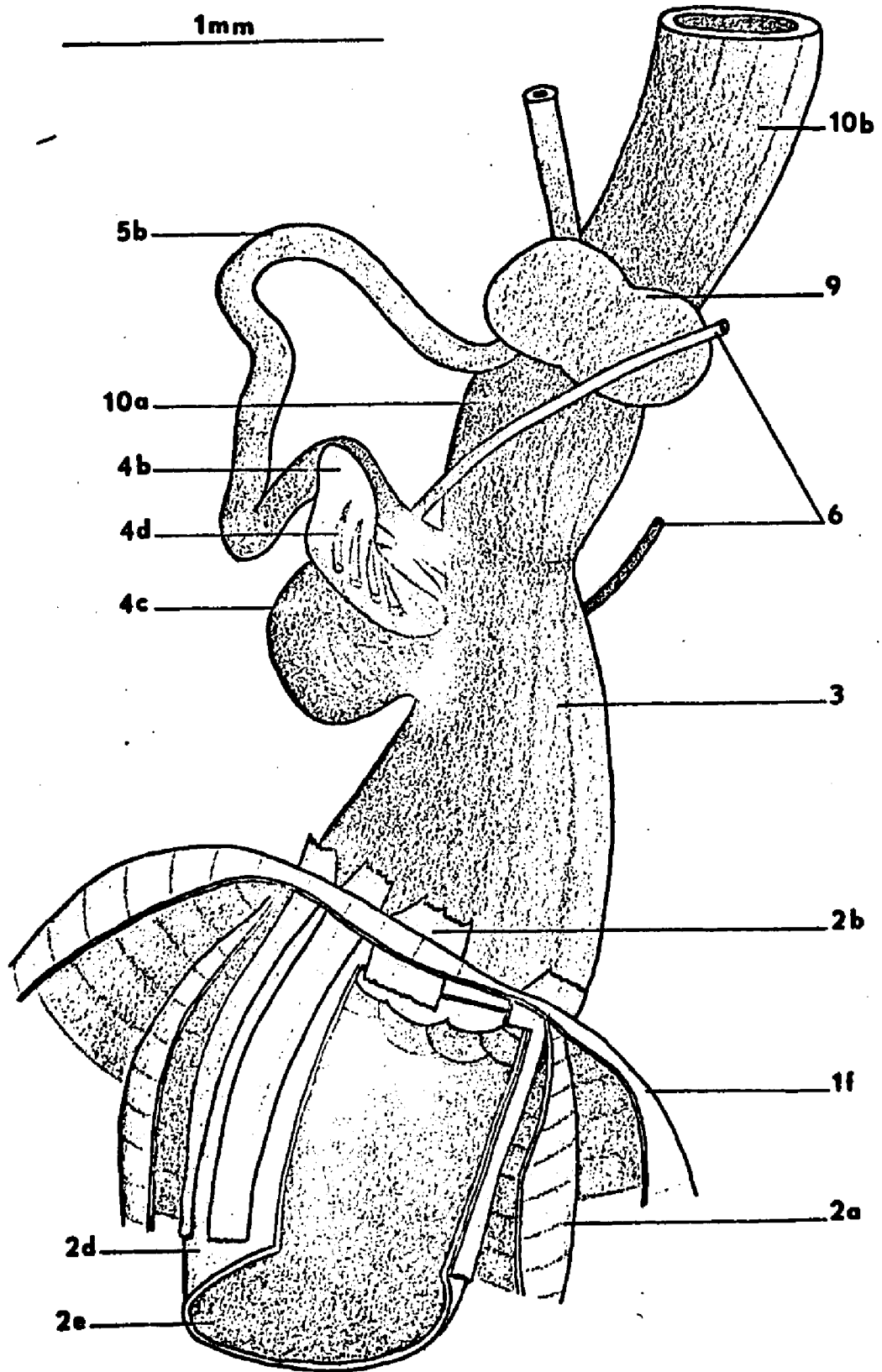
The buccal tube in hastulas is long, slender and retractile. It is attached posteriorly to the buccal cavity at a site demarcated externally by the point of insertion of the buccal retractor muscles, and terminates anteriorly in a small sphincter. The musculature of the buccal tube consists of an inner and outer layer of circular muscles, joined by small radial strands. Each circular layer is covered by a thin layer of epithelium. Between these two layers lies a space representing a forward extension of the cephalic hemocoel. In this space are contained seven bands of longitudinal retractor muscles, originating in the body musculature surrounding the cephalic hemocoel, inserting into the buccal tube at its junction with the buccal cavity, and terminating near the sphincter.

The buccal cavity, termed the pharyngeal bulb by Marcus and Marcus (1960), is homologous with the buccal cavity of the Type I terebrids. It does not contain longitudinal retractors, but rather is surrounded by a thick layer of circular muscles continuous with the inner circular muscles of the anterior buccal tube. This muscle layer is surrounded by an inner and outer layer of epithelium.

Text Figure 10 illustrates the buccal organs contained

Fig. 10. Hastula inconstans. Dorsal view of the buccal organs of the Type IIA polyembolic proboscis.

- 1f.....inner circular muscles of the labial tube
- 2a.....outer circular muscles of the buccal tube
- 2b.....longitudinal retractor muscles of the buccal tube
- 2d.....inner circular muscles of the buccal tube
- 2e.....lumen of the buccal tube
- 3.....buccal cavity
- 4b.....radular sac
- 4c.....radular caecum
- 4d.....radular teeth
- 5b.....poison gland
- 6.....ducts of the salivary gland
- 9.....nerve ring
- 10a....pre-ganglionic esophagus
- 10b....post-ganglionic esophagus



within the cephalic hemocoel of H. inconstans, all of which enter into the buccal cavity. As in all hastulas that have been studied, these organs consist of a muscular poison bulb, a long tubular poison gland, a radular sac, and a small bipartite salivary gland.

The poison bulb is generally large, and is attached by connective tissue to the right side of the cephalic hemocoel, occupying a major part of this cavity. The coiled poison gland commences at the anterior end of the poison bulb, courses ventrally and then anteriorly for some distance, and finally passes through the nerve ring. It enters the ventro-posterior region of the buccal cavity just anterior to the beginning of the pre-gangionic esophagus.

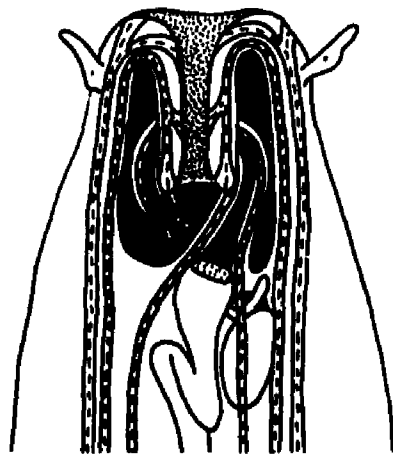
The radular apparatus is composed of two parts, a slender muscular radular sac in which the teeth are secreted in two rows, and a thin-walled structure termed the caecum by Smith (1967). The radular sac contains 20-30 radular teeth, 1-2 mm in length, all of which are pointed away from the opening of the sac. It appears as if the teeth are rotated at the junction between radular sac and caecum, for in the caecum all of the teeth are pointed toward the opening leading into the buccal cavity; The radular caecum opens into a part of the buccal cavity termed the buccal sac by Robinson (1960).

The bipartite salivary gland lies dorsal to the pre-ganglionic esophagus. Two slender salivary ducts, one from each side of the gland, pass ventrally around the esophagus and open into the buccal sac on either side of the opening of the radular caecum.

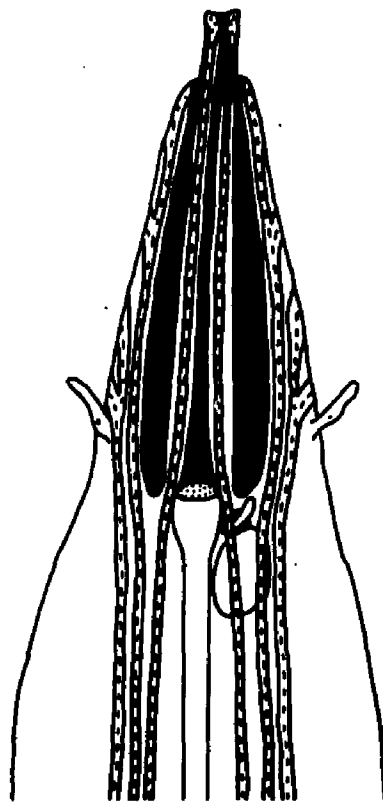
The circular muscles of the buccal cavity terminate just posterior to the opening of the poison gland, and the thin-walled pre-ganglionic esophagus begins. This portion of the esophagus is short and passes ventrally through the nerve ring. The post-ganglionic esophagus is thin-walled, distensible, and occupies a considerable part of the posterior cephalic hemocoel. The remainder of the digestive system consists of a long post-ganglionic esophagus, tubular stomach, and narrow thin-walled intestine.

When the Type IIA polyembolic proboscis is retracted, the labial tube inverts as in the Type I terebrids and the sphincter lies in close proximity to the buccal cavity (Fig. 11). The long slender buccal tube is bent and folded within the labial cavity. The esophagus exhibits a flexure at the nerve ring, and is folded upon itself so that the pre-ganglionic esophagus overlies the post-ganglionic esophagus. During feeding, hemostatic pressure in the cephalic hemocoel, together with contraction of the circular muscles and relaxation of the longitudinal retractors, leads

Fig. 11. Diagram of the terebrid Type IIA polyembolic proboscis to show the position of component parts while retracted (A) and extended (B).



A



B

to eversion of the labial tube and forward extension of the buccal tube, buccal cavity, and pre-ganglionic esophagus. The buccal tube passes out of the labial tube and exhibits searching motions for prey with the radular tooth firmly grasped in the anterior sphincter.

Type IIB

The Type IIB polyembolic proboscis is found in Terebra argus Hinds, 1844; T. babylonia Lamarck, 1822; T. cingulifera Lamarck, 1822; T. funiculata Hinds, 1844; T. guttata (Roding, 1798); T. subulata (Linnaeus, 1767); and T. textilis Hinds, 1844. Terebrid species of this feeding type all have the typical buccal organs exhibited by hastulas, and have the same basic musculature. However, the buccal tube is shorter and thicker, and the labial cavity may be partitioned by a septum not found in other terebrids. The most significant differences are seen in aspects of life history, and are discussed in Section III.

The Type III polyembolic proboscis

Species with the Type III polyembolic proboscis have a labial tube of moderate length, a short buccal tube with little contractility, and a small bipartite salivary gland. The buccal tube and salivary gland are vestigial or lacking entirely in some species. All species have a previously

undescribed accessory feeding organ in the labial cavity.

I have found the Type III polyembolic proboscis in Terebra affinis Gray, 1834; T. columellaris Hinds, 1844; T. conspersa Hinds, 1844; T. flavofasciata Pilsbry, 1921; T. paucistriata (E. A. Smith, 1873); and T. undulata Gray, 1834). The descriptions presented below apply specifically to T. affinis and T. flavofasciata.

As in Type I and Type II terebrids, the labial tube of T. affinis is long and eversible (Fig. 12). However, the anterior of the tube is cleaved and does not terminate in a well developed sphincter, although thick circular muscles surround the tip. When everted, the labial tube musculature consists of an inner layer of circular muscles, covered by a thin epithelium lining the lumen, and an outer layer of circular muscles surrounded by epithelium. Well-developed longitudinal, diagonal, and radial muscles insert along the length of the labial tube, as described for the Type I and Type II probosces.

The accessory feeding organ is extremely variable in size and shape among Type III species. It is composed of two parts, a posterior stalk and a cone-shaped anterior structure consisting of concentric rows of finger-like papillae. The stalk is long and slender in all species and attaches by connective tissue and longitudinal muscles to

Fig. 12. Terebra affinis. Diagram of the foregut of the Type III polyembolic proboscis in the extended position, showing the primary musculature. The cephalic hemocoel is shaded grey.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

1c.....outer circular muscles of the labial tube

1d.....retractor muscles of the labial tube

1f.....inner circular muscles of the labial tube

2b.....retractor muscles of the buccal cavity

3.....buccal cavity

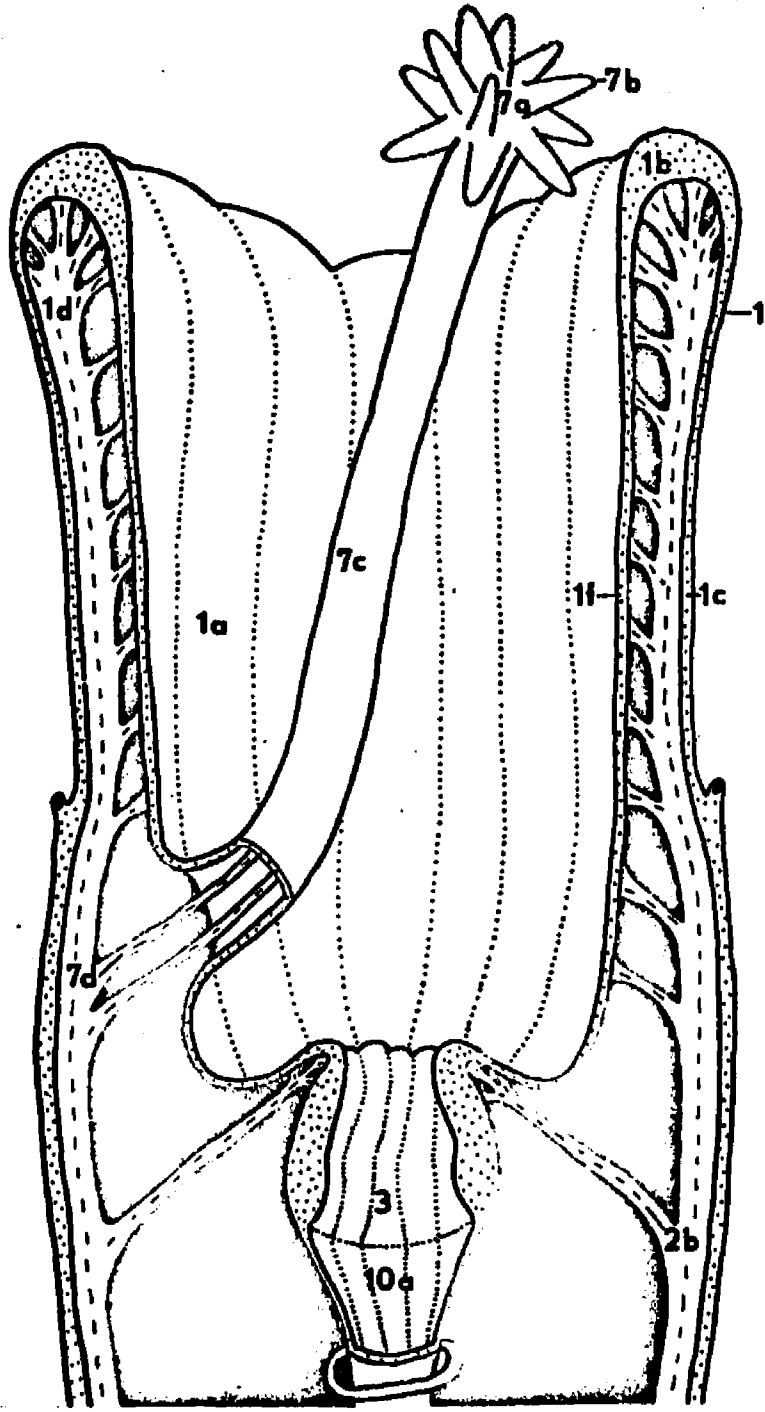
7a.....cone of the accessory apparatus

7b.....papillae of the accessory apparatus

7c.....stalk of the accessory apparatus

7d.....retractor muscles of the accessory apparatus

10a....pre-ganglionic esophagus



the left body wall in the cephalic hemocoel. It protrudes from the cephalic hemocoel into the labial cavity, and is sheathed by the same layer of circular muscles and epithelium which line the lumen of the labial tube. The rest of the stalk appears to be both muscular and glandular. The retractor muscles are arranged in discrete bundles, and pass through the length of the stalk from their posterior insertion in the cephalic hemocoel to the anterior cone. They are surrounded by what appear to be glandular cells, the function of which is unknown. Two small ducts or vessels extend longitudinally through the center of the organ.

I have not studied the morphology of the anterior structure in detail. It appears, however, to be both glandular and muscular. The structure in most species is cone-shaped, with the tip of the cone protruding anteriorly. The concentric rows of finger-like papillae on the cone are capable of muscular extension and contraction. I have not been able to locate the openings of the two ducts passing through the stalk, but they appear to branch just posterior to the cone and may enter into each papillae.

The nature of the buccal tube varies among species, but in all species it is either short or vestigial. In those species with a very small accessory feeding organ, such as T. flavofasciata, the buccal tube is similar in

structure to that of T. gouldi (Type IA polyembolic).

In those species with a well-developed accessory feeding organ, such as T. affinis, the buccal tube is vestigial. The longitudinal retractor muscles insert into the thick circular muscles at the tip of the buccal cavity, and the thin circular muscle layer which usually forms the outer wall of the buccal tube merely inserts around the tip of the buccal cavity distally to the longitudinal retractors.

Salivary glands may or may not be present. When present, they are generally similar in structure to those in other terebrids, with the two slender ducts opening into the ventral wall of the buccal cavity.

When the labial tube is inverted and the accessory feeding organ is retracted, the stalk is bent toward the posterior of the labial cavity, and the anterior cone is inserted into the buccal cavity (Fig. 13). As the labial tube everts the accessory organ swells and extends anteriorly until it passes out of the labial tube. Probably extension is facilitated by contraction of the circular muscles and increase in hydrostatic pressure, while retraction occurs through contraction of the longitudinal and diagonal retractors and reduction in hydrostatic pressure.

Fig. 13. Diagram of the terebrid Type III poly-
embolic proboscis to show the position of component parts
while retracted (A) and extended (B).



A



B

Discussion

Use of the feeding type as a diagnostic character

Species of a particular feeding type are not only similar in the morphology of the feeding apparatus, but they are also remarkably constant in shell morphology and in many aspects of life history. As I will show in Section III, they prefer the same habitats, exhibit nearly identical behavior, and are similar in most other aspects of life history. However, marked differences in life histories are evident when species of one feeding type are compared with those of another.

It is my belief that these morphological and behavioral differences among the feeding types, now known only for Central Pacific species, will prove to be consistent throughout the entire family Terebridae. They are therefore of taxonomic significance, and could serve to separate the family into several genera. The resulting proposed classification based on shell characters, internal anatomy, and life history would be an extension of preliminary taxonomic work begun by Adams and Adams (1858) using terebrid shell characters only and Troschel (1866) using the morphology of terebrid buccal organs.

Significance of length variation
in the terebrid buccal tube

Considering both intraembolic and polyembolic species, it appears that the length of the buccal tube in the Toxoglossa depends primarily on the presence or absence of a functional radular apparatus. The buccal tube is short in those toxoglossan species lacking a functional radular apparatus. This condition is illustrated by terebrids with the Type I and Type III polyembolic probosces and turrids with the Type I polyembolic proboscis. As will be shown in Section III, species with the Type I polyembolic proboscis, such as T. gouldi, capture prey with the muscular labial tube. The prey is not stung, but merely grasped by the sphincter and then transferred to the non-eversible buccal tube. In species such as T. affinis with the highly specialized Type III polyembolic proboscis, the prey is captured by the combined action of the labial tube and the accessory feeding apparatus. In neither case is the buccal tube directly utilized in prey capture.

In those species utilizing a radular tooth in prey capture, the buccal tube is long, highly retractile, and tapered so that the tooth can be effectively grasped by the anterior sphincter. This situation is illustrated by all

intraembolic conids, intraembolic turrids, and Type II polyembolic turrids and terebrids. During feeding the buccal tube holding the radular tooth is extended beyond the labial tube, and the prey is stabbed by the tooth. Poison from the poison gland is forced through the narrow buccal tube into the wound, and the prey is then grasped by the labial tube and ingested.

It appears that the long buccal tube has evolved in the *Toxoglossa* as a specialization for holding the radular tooth. Therefore radular feeding is not possible in species with the short buccal tubes (Type I and Type III) even though a radular apparatus may be present, as reported in some turrids (Smith, 1967).

SECTION III

LIFE HISTORY ASPECTS OF TEREBRID SPECIES

REPRESENTATIVE OF EACH FEEDING TYPE

Part A. The life history of Terebra gouldi Deshayes
1859, and a discussion of feeding in other
species with the Type IA polyembolic proboscis

Introduction

Terebra gouldi, a species having the characteristic Type IA polyembolic proboscis was first described from the Hawaiian Islands and is apparently endemic. It has been reported from Midway Island in the leeward group to Maui in the windwards. No specimens have been collected from the island of Hawaii, although it is possible that they may be present there.

Around the Hawaiian Islands, T. gouldi occurs in sandy areas from depths slightly below mean low water to deeper than 100 meters. These areas are characterized by little or no wave action, soft sand of variable sorting coefficient, and essentially open ocean conditions of salinity and temperature throughout most of the year. Of the five species of terebrids with the Type IA feeding apparatus found in Hawaii, T. gouldi is best suited for a detailed ecological

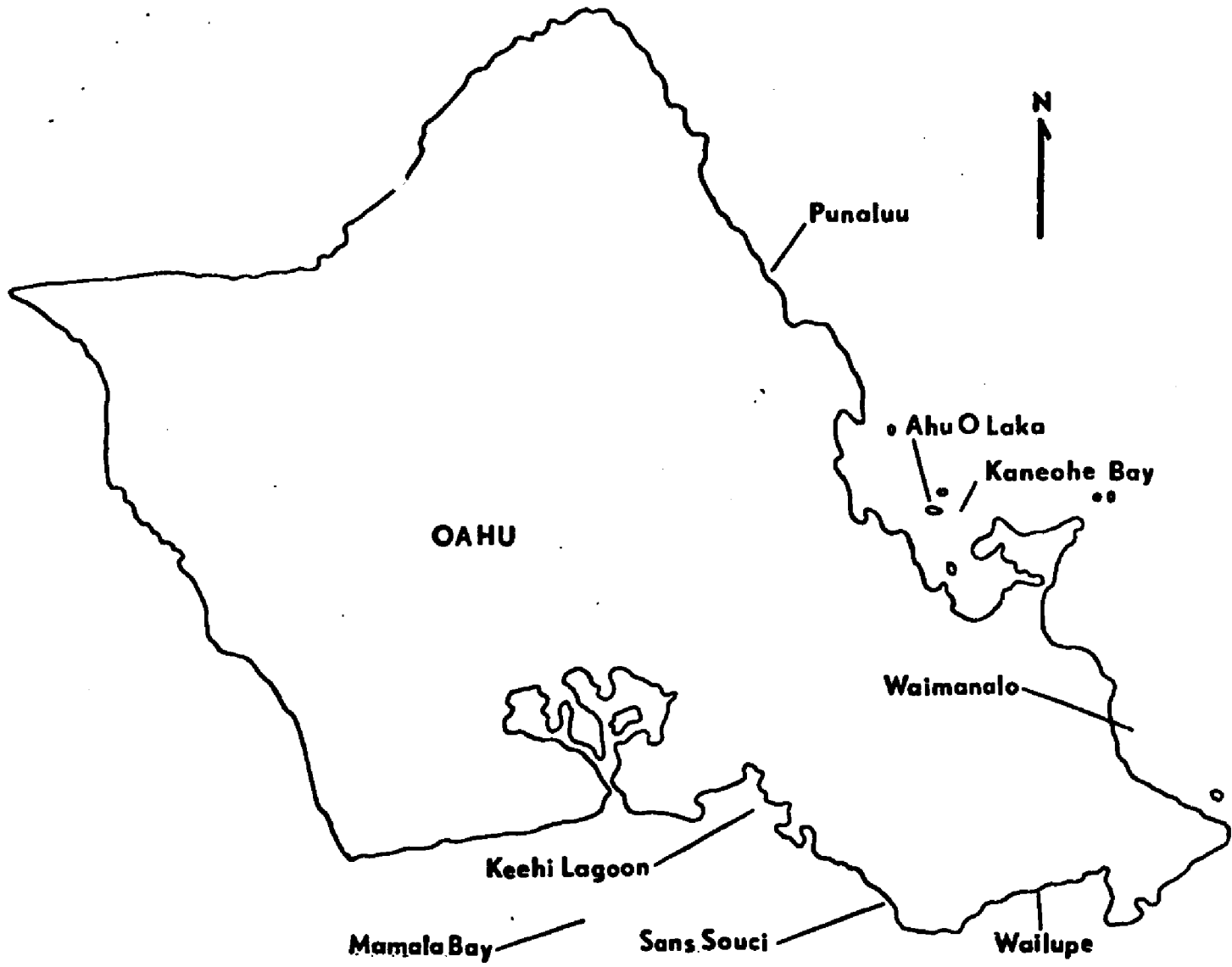
and life history study, since it is abundant and survives well under laboratory conditions. In addition, the animal lives in quiet shallow areas, and so is accessible throughout most of the year.

Studies on the ecology and life history of T. gouldi were conducted over a period of 12 months, from June 1968 to June 1969. Observations in the field and laboratory were primarily concerned with locomotion, food and feeding, reproduction, development, growth and predation. Animals were observed and collected from six shallow sites around Oahu using standard skin and SCUBA diving gear, and were dredged from two sites 50-100 meters in depth. Study sites are indicated in Figure 1. Work was concentrated in two areas: 1) shallow (less than 3 meters) sand channels off the coast at Waikiki, and 2) extensive sand flats surrounding Ahu O Laka Island in Kaneohe Bay. The Ahu O Laka habitat was studied most intensively because of the relatively high population density and accessibility from the Hawaii Institute of Marine Biology.

General morphology

The shell of T. gouldi is thin, axially ribbed, and reaches a maximum length of 80 millimeters. As with many species of terebrids, there is considerable variation in

Fig. 1. Map of Oahu, Hawaii, showing location of collection sites of T. gouldi.



shell pigmentation, color ranging from the light tan of specimens in shallow sand flats around Oahu to the very dark brown of specimens in deeper waters leeward of Maui (Fig. 2).

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

Locomotion

With exception of a note by Pearse et al (1942) on reburrowing in Terebra dislocata from North Carolina, nothing is reported in the literature concerning locomotion for any species of the genus Terebra. Observations on locomotory behavior were conducted on T. gouldi in the laboratory during winter 1966, and in the field from June 1968 through February 1969. Basic locomotory movements were studied in a modified aquarium 30 centimeters long, 10 centimeters high, and 5 centimeters wide. Fine black lava sand was placed in the bottom of the aquarium. It was filled with sea water, and T. gouldi were individually introduced at one end. The black sand formed a contrasting

Fig. 2. Variation in shell pigmentation of T.
gouldi from Hawaii (1.5 X).

- A. Specimen from 5 meters around Oahu.
- B. Specimen from 100 meters around Oahu.
- C. Specimen from 40 meters around Maui.

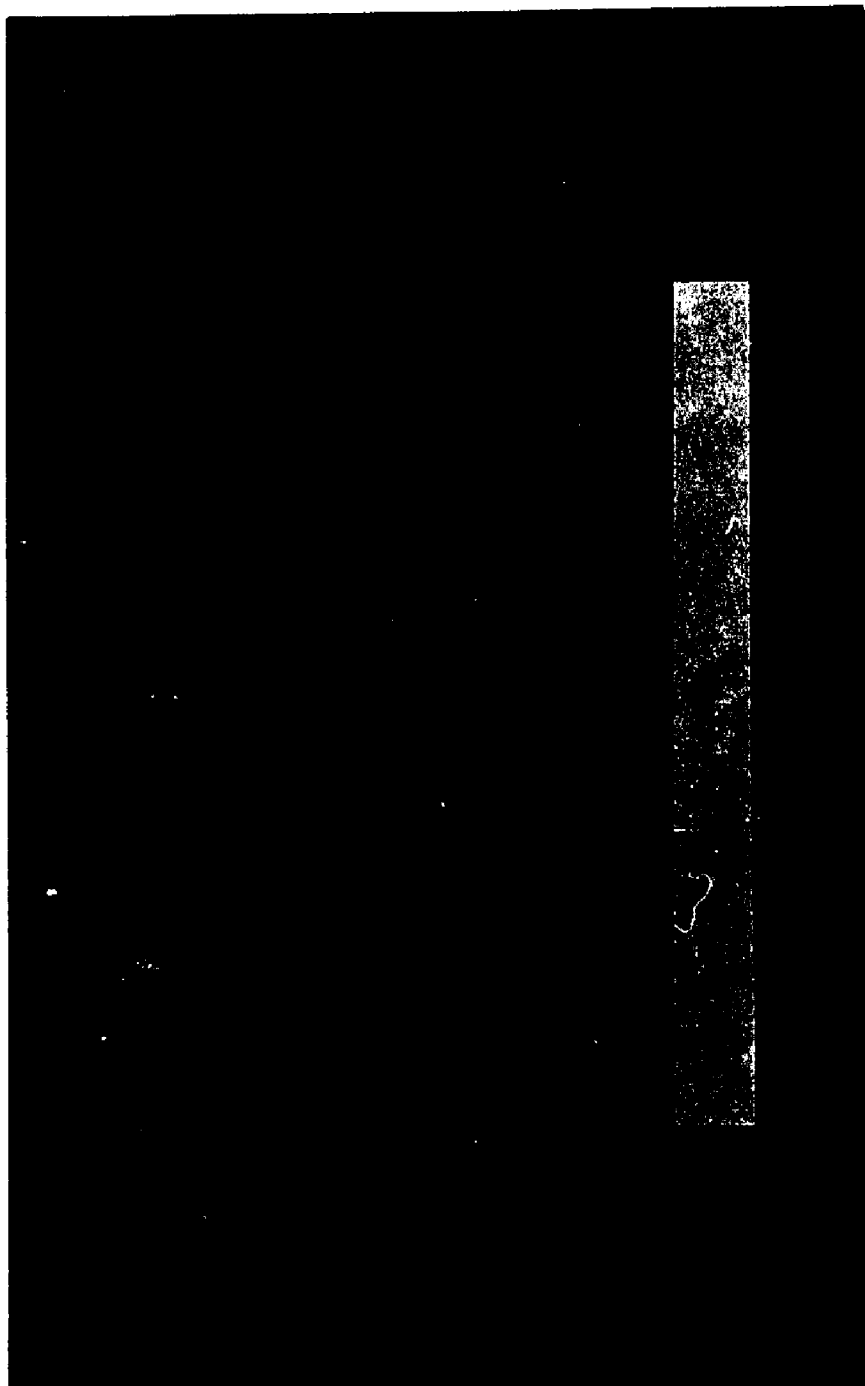
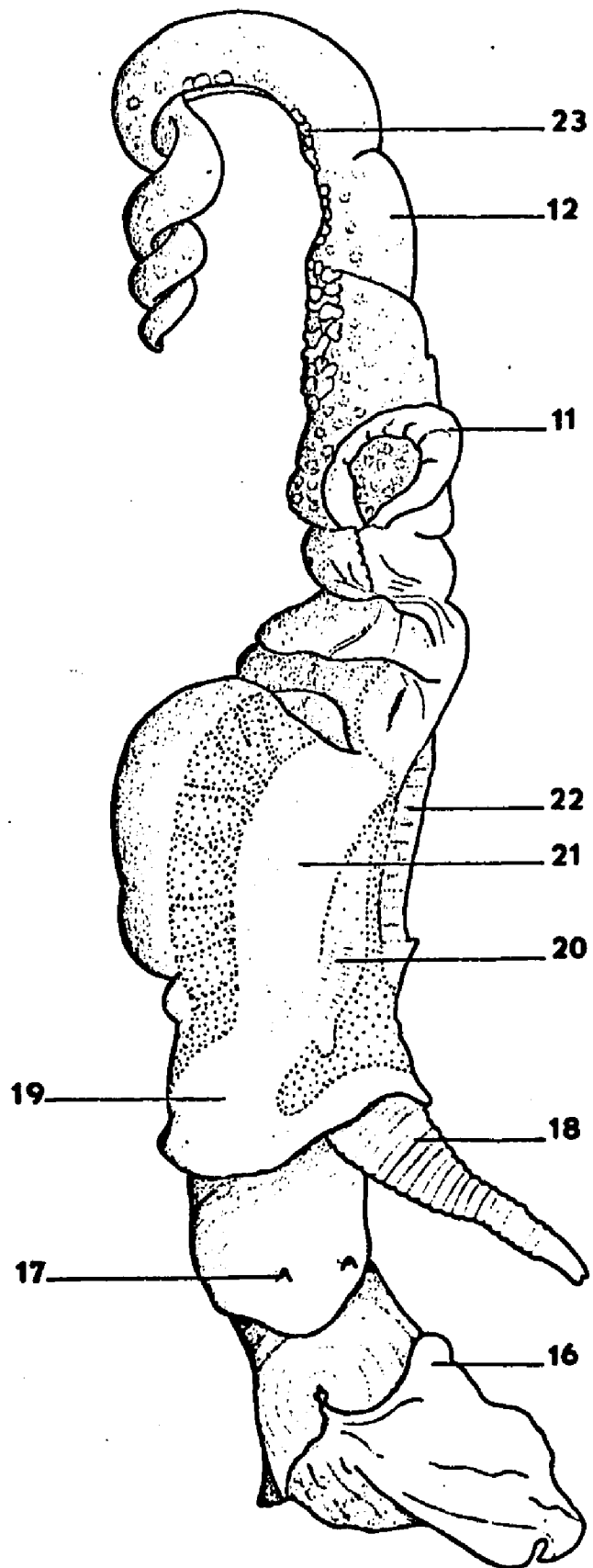


Fig. 3. Gross morphology of T. gouldi with the animal relaxed and removed from the shell (Dorsal view).

- 11.....stomach
- 12.....digestive gland
- 16.....foot
- 17.....eyestalk
- 18.....siphon
- 19.....mantle
- 20.....osphradium
- 21.....ctenidium
- 22.....columellar muscle
- 23.....gonad



| 1mm

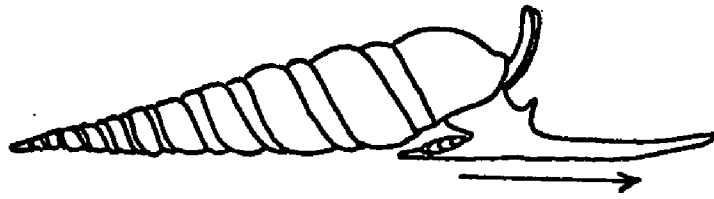
background for the crawling animal, and locomotion could be observed through the glass. Other aspects of activity, such as time of locomotion and distances traversed, were studied in the laboratory in a sea water table exposed to natural light and constantly illuminated by a 25 watt red light. Field observations were primarily made during daylight hours around the Ahu O Laka study area.

When T. gouldi is not crawling, the animal lies buried in the sand and the foot remains fully extended. At this time only the siphon and apex of the shell project to the surface. During daylight hours the tip of the siphon extends just above the sand surface, but in the evening or under conditions of darkness in the laboratory, it extends to several centimeters.

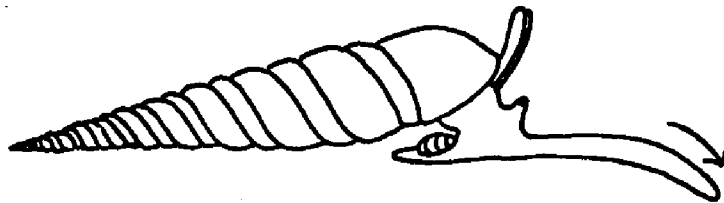
When crawling, the snail does not move with a smooth gliding motion as species of Conus do, but has a loping gait consisting of two distinct movements. First the foot glides forward with an undulating movement, the highly sensitized propodium probing the sand and the shell remaining motionless (Fig. 4A). When the foot is fully extended the propodium ceases undulating and is forced downward into the sand (Fig. 4B). Then with the propodium acting as an anchor, the pedal retractors contract lifting the shell and pulling it forward (Fig. 4C). In this position the propodium begins

Fig. 4. Sequence of movements of T. gouldi during locomotion.

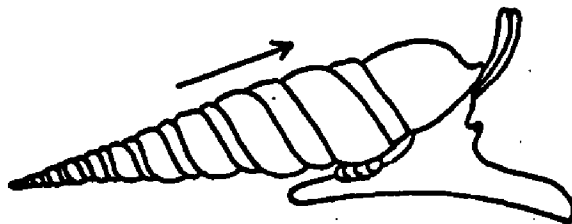
- A. Forward undulation of the foot.
- B. Anchoring of the foot in the sand by the propodium.
- C. Contraction of pedal retractors, resulting in forward movement of the shell.



A



B



C

to undulate again, moving forward until the next contraction of the pedal muscles. In the following discussions one complete cycle is considered a step.

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

Forward locomotion proceeds at a fairly constant pace of five to ten steps per minute. Variations in distances traveled are dependent on animal size and the nature of the terrain. Field observations show that specimens of average size (40-50 millimeters) crawling in soft sand, cover a distance of from one to three meters in a night. Distance traveled is considerably reduced in substrata other than soft sand. Locomotion is generally directional, and there is evidence of positive orientation into a current (to be discussed later).

Reburrowing in soft sand generally requires from one to three minutes. The propodium digs downward into the sand at approximately a 45 degree angle, and pedal contractions similar to those involved in forward locomotion pull the anterior part of the animal below the sand surface until

only the siphon and the apex of the shell are exposed. Reburrowing in substratum other than soft sand is difficult.

Periods of activity occur sporadically and observations in the laboratory indicate that an individual emerges, crawls, and reburrows several times in an evening. Individuals do not crawl every evening, but generally alternate several days of activity with several days of quiescence. Field studies at the Ahu O Laka study site (discussed in Section IV) indicate that during the summer and early fall, when wind and wave action are minimal, an average of approximately 50% of the individuals in a population will crawl in one evening. This percentage drops during the months of November through March, when the trade winds periodically cease and strong southerly gusts create substantial wave action, producing ripple marks in the shallow sand areas. At these times the animals burrow deeper and orient themselves parallel to the ridges of the ripple marks. If conditions are severe, locomotion of most animals in a population may cease for several weeks.

Food and Feeding

Introduction

Nothing has been published on the food and feeding

habits of any species of Terebra. Data on food and feeding of T. gouldi were obtained through gut and fecal analyses, labial tube examination, and observations in the field and laboratory. Animals were collected by sieving and by following trails during the morning hours. Details of the anatomy of the feeding apparatus were worked out through dissection of fresh specimens removed from the shell after quick freezing.

Gross morphology of the alimentary tract

The alimentary tract of T. gouldi is drawn in Figure 5 with the proboscis retracted and in Figure 6 with the proboscis everted. As is the case for all terebrids with the Type I polyembolic proboscis, the primary functional components utilized in prey capture of T. gouldi are a long eversible labial tube which terminates in an anterior sphincter, and a short retractile buccal tube. The cephalic hemocoel contains the longitudinal retractor muscles of the buccal tube, the small bipartite salivary gland which opens into the muscular buccal cavity, and the short thin-walled pre-ganglionic esophagus. The distensible, thin-walled post-ganglionic esophagus expands in diameter after passing out of the cephalic hemocoel dorsally to the columnar muscle, and enters the tubular stomach. The stomach receives

Fig. 5. Gross morphology of the digestive system of T. gouldi with the proboscis retracted, exposed by cutting through the dorsal mantle and body wall.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

2.....buccal tube

2b.....longitudinal retractor muscles of the buccal tube

8.....cephalic hemocoel

10b....post-ganglionic esophagus

11.....stomach

12a....anterior duct of the digestive gland

12b....posterior duct of the digestive gland

13.....intestine

14.....rectum

15.....anus

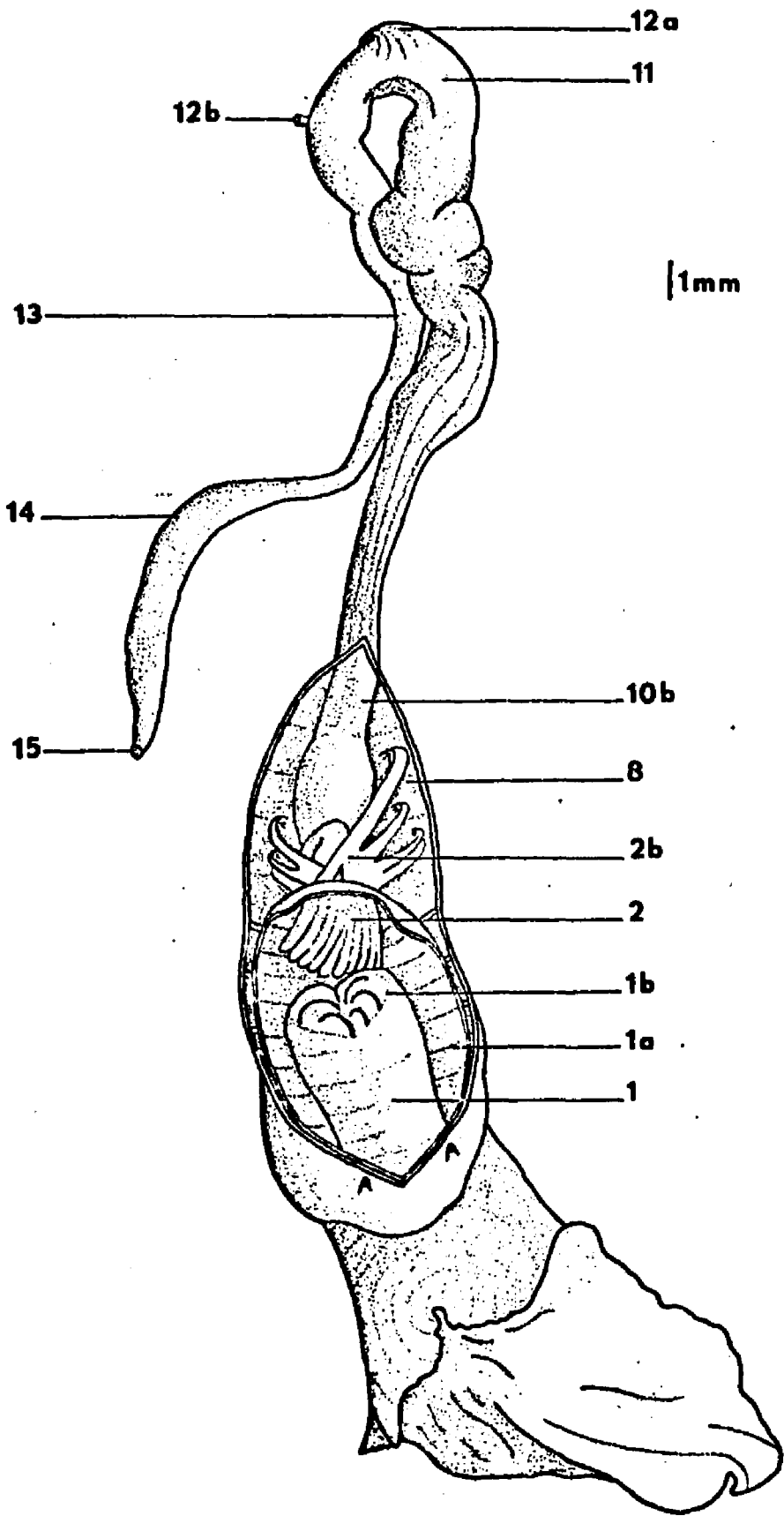


Fig. 6. Gross morphology of the digestive system of T. gouldi with the proboscis everted, exposed by cutting through the dorsal mantle and body wall.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

2.....buccal tube

2b.....longitudinal retractor muscles of the buccal tube

6.....salivary gland

8.....cephalic hemocoel

10b....post-ganglionic esophagus

11.....stomach

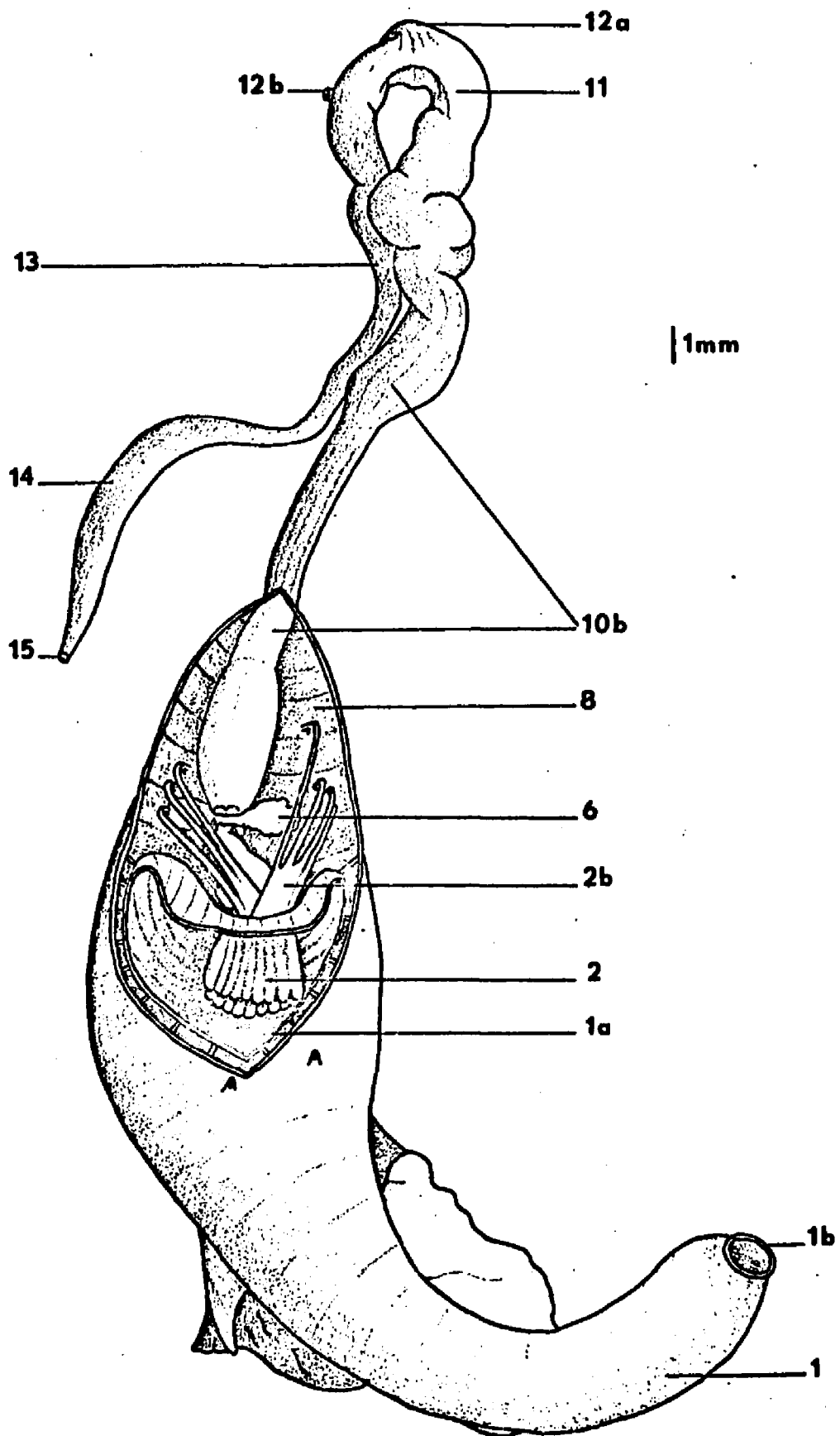
12a....anterior duct of the digestive gland

12b....posterior duct of the digestive gland

13.....intestine

14.....rectum

15.....anus



two ducts from the digestive gland. Beyond the point of entrance of the first duct the stomach curves anteriorly and received the second duct, then constricts and leads into a narrow thin-walled intestine. The intestine passes onto the right wall of the mantle and opens anteriorly near the mantle edge.

Feeding

Analyses of gut contents were made on 120 T. gouldi collected from June to September 1968 at Ahu O Laka habitat, and on 30 T. gouldi from other study sites around Oahu. Animals ranged in length from 28 to 64 millimeters. Examination of fecal remains were made on 20 animals collected at Ahu O Laka by sieving in December 1968, and observations on labial tube contents were made on 80 T. gouldi collected from the same area in April 1969 by following trails. These examinations show that T. gouldi feeds exclusively on the enteropneust Ptychodera flava (Table I). Ptychodera flava is a non-selective deposit feeder which burrows just beneath the sand surface, ingesting large quantities of sand.

Terebra gouldi normally lives buried in the sand during daylight hours with the proboscis retracted and only the siphon extending above the surface. As has been shown in other terebrids (Miller, 1966), the stimulus for emergence

Table I. Analysis of prey choice of Terebra couldi at Ahu O Laka Island

| Date | No. specimens examined | Collection method | Type of analysis | Prey | No. specimens with prey | Position of prey in gut | | Maximum No. of prey/ <u>Terebra</u> |
|-------------|------------------------|-------------------|------------------|-----------------|-------------------------|-------------------------|------|--|
| | | | | | | Fore | Hind | |
| Summer 1968 | 62 | Following trails | Gut | <u>P. flava</u> | 27 | 20 | 7 | 1 |
| Summer 1968 | 58 | Sieving | Gut | <u>P. flava</u> | 6 | 0 | 6 | 1 |
| Dec. 1968 | 20 | Trails & Sieving | fecal | - | 0 | 0 | 0 | 0 |
| April 1969 | 80 | Following trails | Labial tube exam | <u>P. flava</u> | 14 | 14 | * | * |

*Data not applicable for this type of analysis.

is probably endogenous in nature, although photoreceptive cells on the siphon may signal the onset of darkness. Certainly a beam of light flashed on the extended siphon of buried animals will cause rapid siphonal retraction.

I have observed also that strong chemical stimulation from prey extract is sufficient to cause emergence from the sand under low light intensity in the field. At sunset on December 31, 1968, when current flow across Ahu O Laka sand flat was relatively slow, I macerated several hundred Ptychodera through a sieve into the water upstream from the main population concentration of T. gouldi. Although no T. gouldi were observed crawling before the sieving, within five minutes 53 individuals emerged from the sand and began crawling upstream into the area of sieving.

Feeding experiments were conducted in a choice chamber (Fig. 7) to determine if prey are detected by distance chemoreception. Several Ptychodera were contained in front of the left inflow of the chamber for two trials, in front of the right inflow for two trials, and as a control, Ptychodera were not used in two trials. The chamber was thoroughly washed after each trial. Ten T. gouldi were set near the outflow in the late afternoon for each trial, and left in the chamber overnight. Results recorded the following morning (Table II) indicate that after the animals have

Fig. 7. Choice chamber used for determination of the method of prey capture by T. gouldi. Terebra were placed at X for each trial.

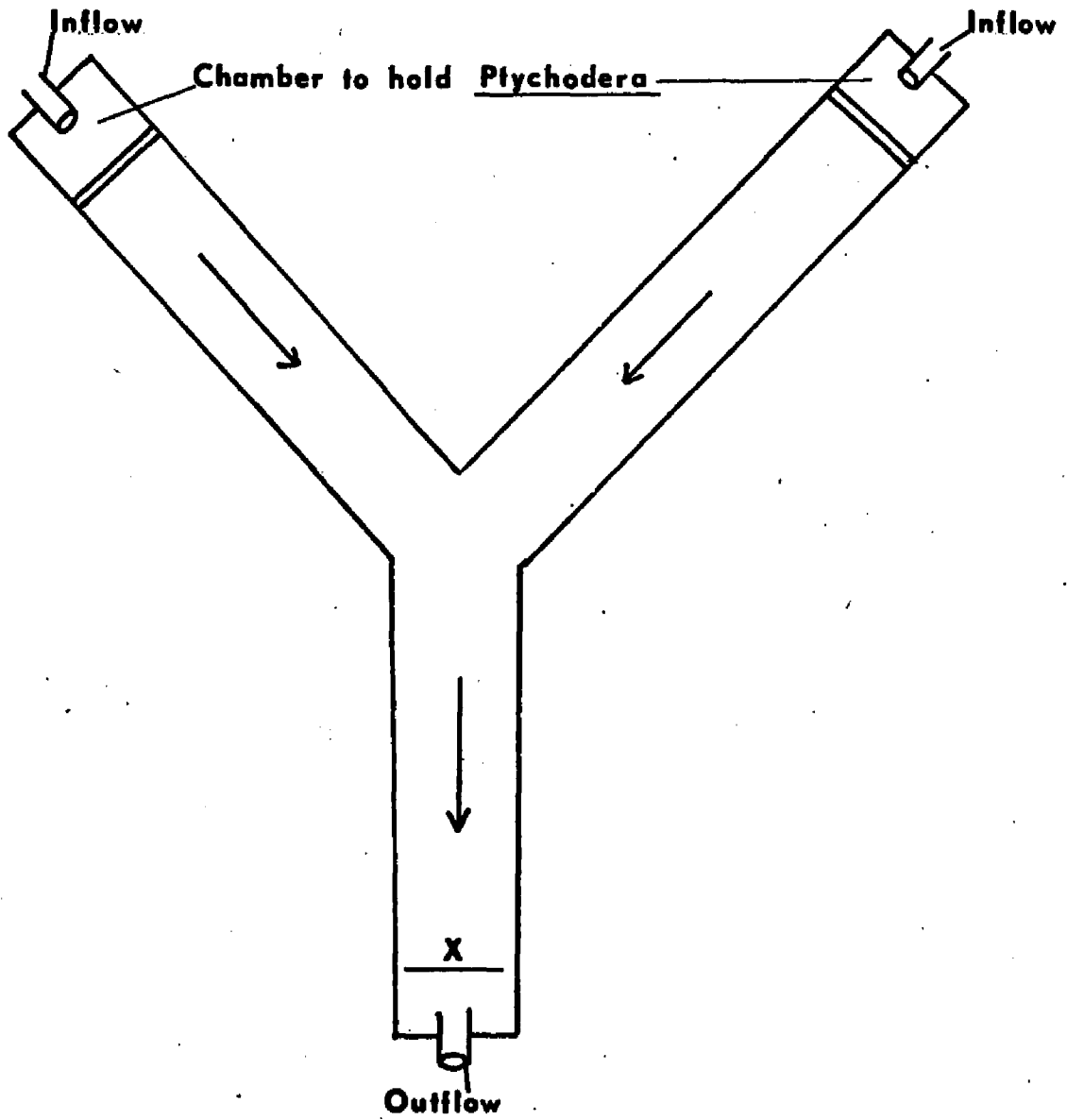


Table II. Results of feeding experiments to determine the method of prey location by T. gouldi

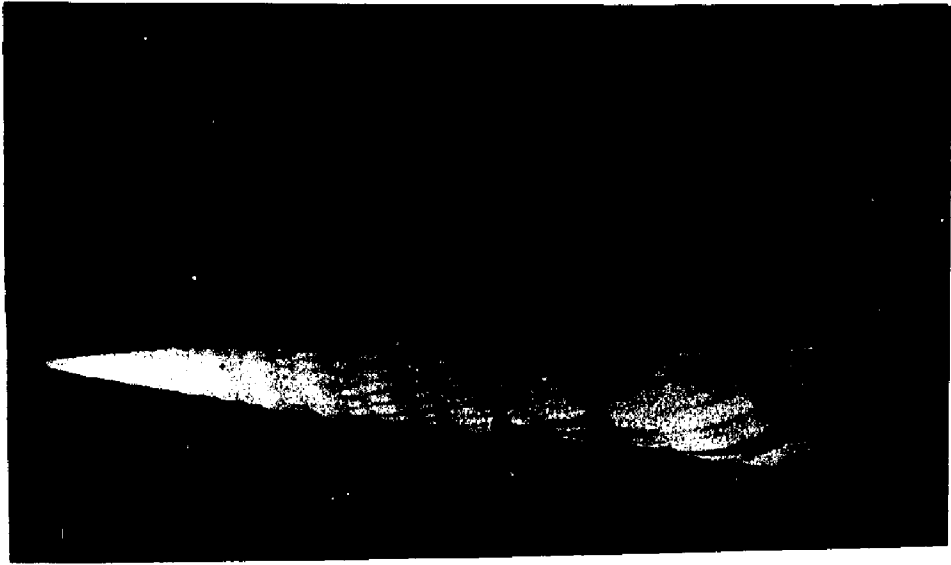
| Position of <u>Ptychodera</u> in the chamber | Number of <u>Terebra</u> per trial | Location of <u>Terebra</u> after 14 hours | | |
|---|---------------------------------------|---|-------|---------|
| | | Left | Right | Neither |
| Left chamber | 10 | 8 | 1 | 1 |
| | 10 | 7 | 3 | 0 |
| Right chamber | 10 | 2 | 8 | 0 |
| | 10 | 3 | 6 | 1 |
| Neither chamber | 10 | 5 | 4 | 1 |
| | 10 | 4 | 4 | 2 |

emerged from the sand, the search for prey is facilitated by distance chemoreception, with the iodoform released from Ptychodera probably providing the chemical stimulus. Emergence from the sand begins with upward undulation of the propodium beneath the sand in a scanning motion, and locomotion commences upstream in the direction of the stimulus. Distance chemoreception was not, however, sufficient to elicit labial tube eversion and prey capture.

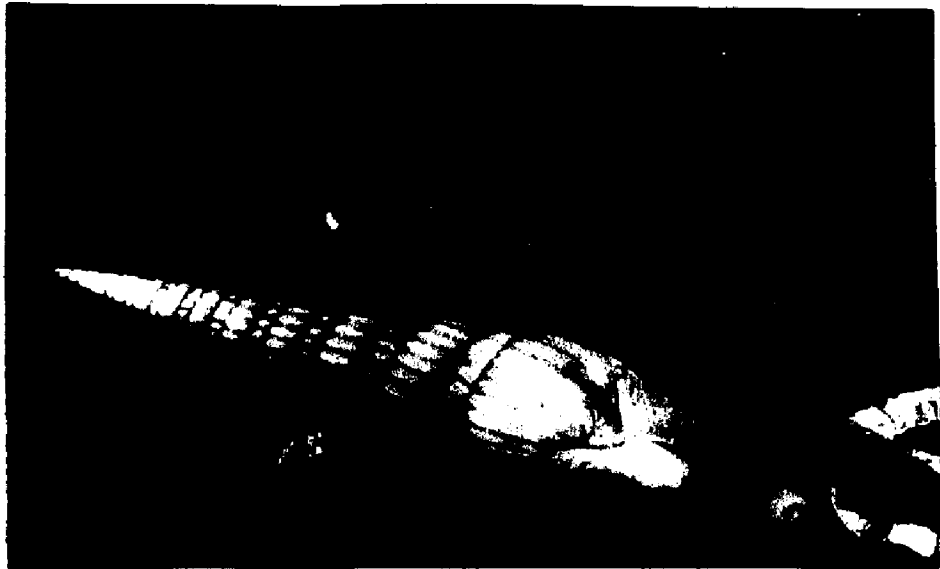
The actual capture of prey has never been observed in the field and is difficult to observe in the laboratory. Freshly captured T. gouldi placed in a sea water tank containing Ptychodera will not feed. However, the feeding response was elicited and observed in an aquarium when T. gouldi, starved for three weeks, were placed under low light intensity in an aquarium with a paraffin bottom. Feeding will not begin if the prey are merely placed on the surface of the paraffin. However if one end of the worm is wedged into the paraffin with forceps, labial tube eversion will occur when the propodium of the foot comes in contact with the partially buried prey (Fig. 8A). Marcus and Marcus (1960) report that the propodium of the foot of Hastula cinerea is a highly innervated sense organ. I have found the same to be true for T. gouldi, and contact of this chemoreceptive area with the prey appears to provide the stimulus for labial

Fig. 8. The rapid ingestive phase of feeding behavior in T. gouldi.

- A. Feeding behavior is elicited by bringing an impaled Ptychodera flava into contact with the propodium of the foot.
- B. After stimulation of the propodium, the labial tube everts and begins searching for the worm.
- C. The worm is rapidly engulfed by the labial tube.
- D. The labial tube then partly inverts, and as the sphincter contracts, the worm is grasped by the buccal tube.
- E. The labial tube again everts to further engulf the worm.
- F. When the labial tube inverts for the second time, the labial cavity is full and further ingestion occurs slowly.



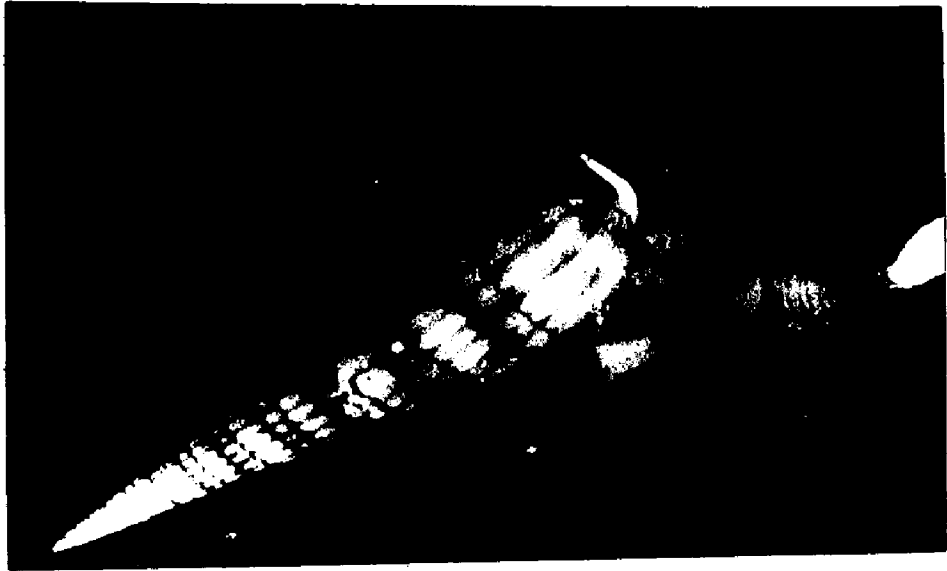
A



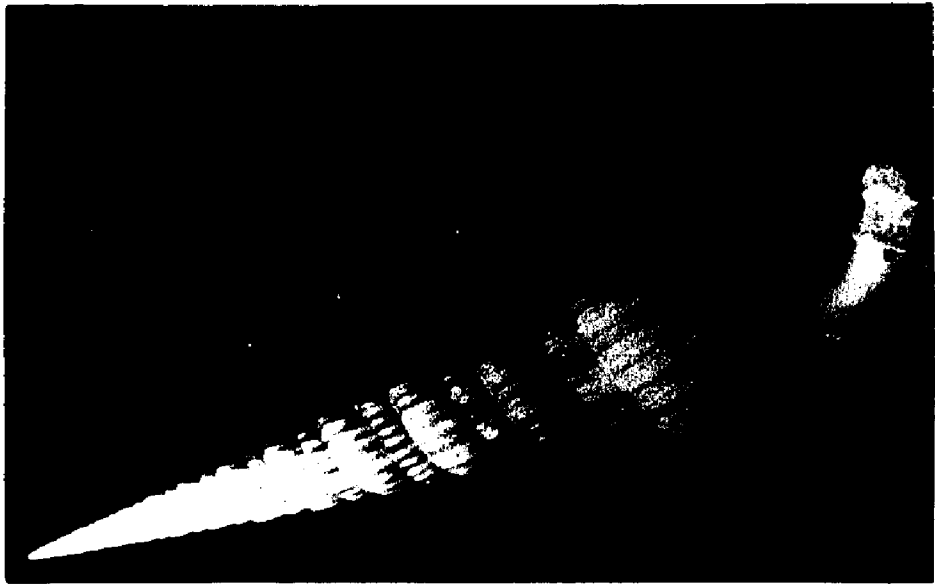
B



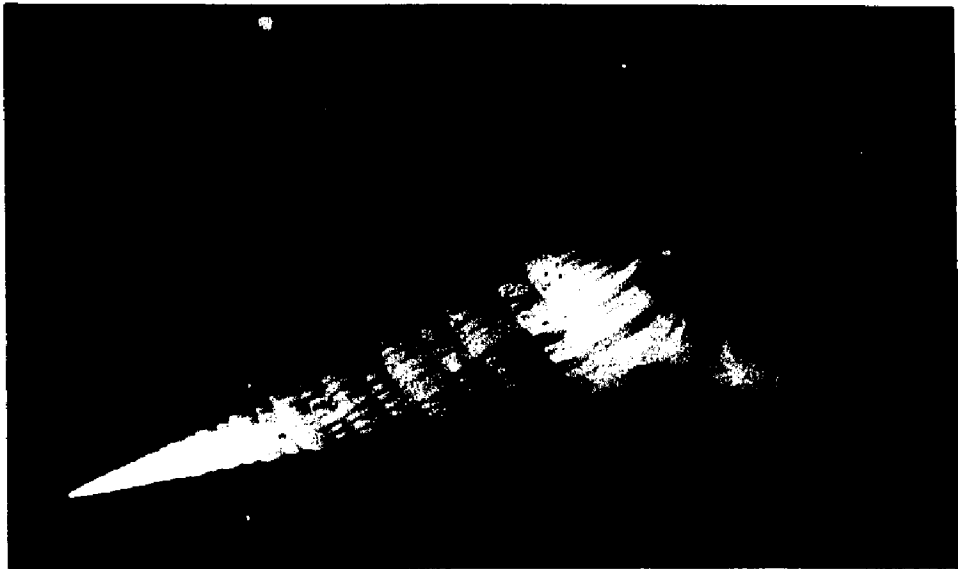
C



D



E



F

tube eversion.

From many observations in the laboratory, feeding under natural conditions can be reconstructed as follows. When the propodium touches a Ptychodera buried in the sand, propodial undulations cease, crawling stops, and the foot arches slightly, slowly probing the area. Relaxation of the retractor muscles, along with contraction of the circulars, leads to eversion of the labial tube and extension of the buccal tube. As soon as the labial tube is fully everted, the anterior end bearing the sphincter begins searching motions around the propodium for the Ptychodera, (Fig. 8B).

The sphincter relaxes when contact is made with the worm, and the labial tube completely everts to engulf the prey (Fig. 8C). The sphincter then contracts and the labial tube slowly inverts, bringing the worm in close proximity to the fully extended buccal tube (Fig. 8D). The circular muscles of the buccal tube grasp the worm when contact is made, and the seven retractors inserted on the buccal tube contract to pull the worm in further. After the buccal tube has grasped the worm, the sphincter again relaxes and the labial tube everts to further engulf the prey (Fig. 8E). When labial tube inversion has occurred for the second time, the prey nearly fills the entire labial cavity, the rapid

ingestive phase of feeding is complete, and ingestion slows considerably (Fig. 8F). Usually at this time, T. gouldi slowly digs into the sand and remains there while the ingestive process continues at a slower rate.

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

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

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

Feeding rates .

Studies on feeding rates were conducted at the Ahu O Laka habitat from June 1968 to April 1969. Sixty-two animals were collected from June to September 1968 by following trails during early morning. Since the animals only crawl at night and sand trails are rapidly erased in a short time by water disturbance, this collection represents those animals that had searched for prey the preceding night. The same areas were then thoroughly sieved to collect any animals that had not left trails. Fifty-eight individuals were recovered, this collection representing those animals that had not crawled for at least one day. Accordingly, approximately 50% of the population of T. gouldi sampled at Ahu O Laka had crawled and searched for prey each evening during the summer months.

As shown in Table I, none of the sieved animals contained prey in the foregut, and the remains found in the rectum of six sieved animals indicate Ptychodera flava eaten more than 24 hours before sieving. Twenty-seven of the 62 animals collected by following trails contained Ptychodera remains in their foregut. Thus approximately 33% of the crawling population, but only 17% of the total population in any one area was successful in capturing prey the previous

night. The rate of feeding is considerably lower during stormy winter months, when wave turbulence may inhibit locomotion of the entire population for as long as several weeks. Only 20 animals could be located by following trails and sieving around Ahu O Laka from December to March, and none of these showed evidence of feeding.

Individual feeding rates thus appear to be low. Since prey ingestion takes from eight to twelve hours, it is probable that a maximum of one Ptychodera can be consumed in an evening, and gut analyses have verified this. Based on a maximum feeding rate of approximately 17% per day for the entire population, it would appear that an individual would average slightly more than one Ptychodera per week.

Reproduction and development

Mating

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

During March 1969, mating was observed in 0.3 meters of water to the leeward of Ahu O Laka Island. The description is representative of all succeeding observations. A slight current was flowing along the axis of the island, and two trails were noticed in the sand (Fig. 9). The trail of one T. gouldi, later found to be female, led into the current, and the animal was observed partially covered with sand and in the process of ingesting a large Ptychodera. The second animal, the male, slowly approached from downstream until it contacted the sand trail produced by the female. The male then changed direction and slowly crawled along the trail made by the female until the propodium of its foot touched the apex of the female's shell. The male then slowly crawled along the right side of the shell, stopping when the propodium came in contact with the female's extended foot. The female continued feeding movements for a few minutes, then moved slightly and forcefully regurgitated the prey. Movement of both animals ceased with the male situated to the right of and slightly above the female, and did not begin again for ten minutes. Both animals were then quickly removed from the sand, and the distended penis of the male was found inserted into the mantle cavity of the female.

Mating in T. gouldi always occurs with the male situated above and to the right of the female (Fig. 10). As in other

Fig. 9. Trails of a mating pair of T. gouldi at Ahu O Laka island. The large arrow indicates current flow; small arrows show the direction of snail locomotion. Site of mating is marked by an X.

Fig. 10. Characteristic posture of T. gouldi during mating. The male is situated above and to the right of the female.

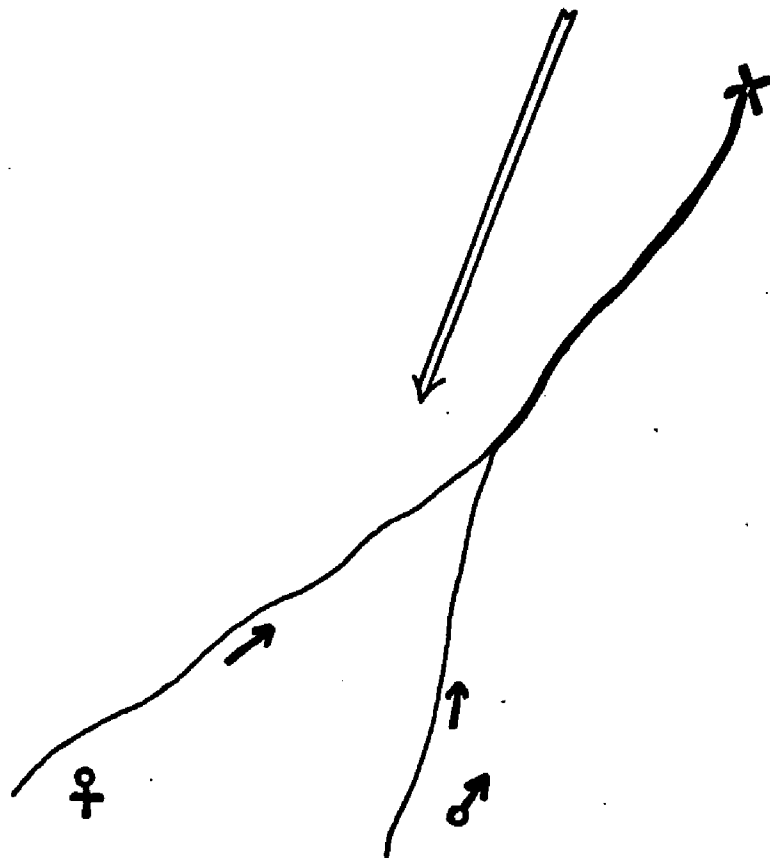


FIG. 9

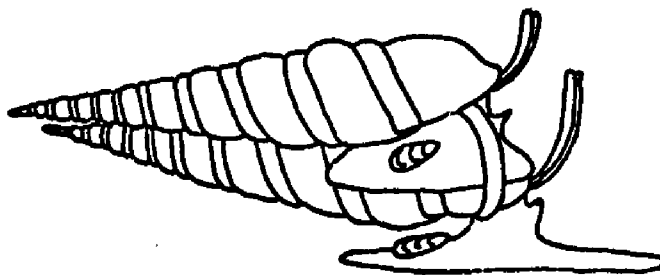


FIG. 10

gastropods (Fretter and Graham, 1962), the normally folded penis becomes distended by hemostatic pressure and unfolds. It enters the mantle cavity of the female where contact is made with the vaginal aperture. Morphological considerations indicate that the penis is not inserted into the female duct, but rather that the sperm are transferred by way of the papillary opening of the vas deferens. The penis can be rapidly retracted by a reduction of hemostatic pressure and by contraction of the large penial muscles. Duration of the copulatory process is not known since mating animals were disturbed and returned to the laboratory.

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

It will be noted (Fig. 9) that the male followed up-current for a considerable distance, and then altered direction to crawl along the trail previously produced by the female. In all instances of mating observed, the two trails were observed to converge and were confluent with each other

for some distance before mating occurred. Preliminary observations in the field thus indicate that mating may involve some form of chemical attractant released by the female into the water and followed upcurrent by the male, as well as a chemical contained in the mucus produced by the female as she crawls through the sand.

Egg capsules

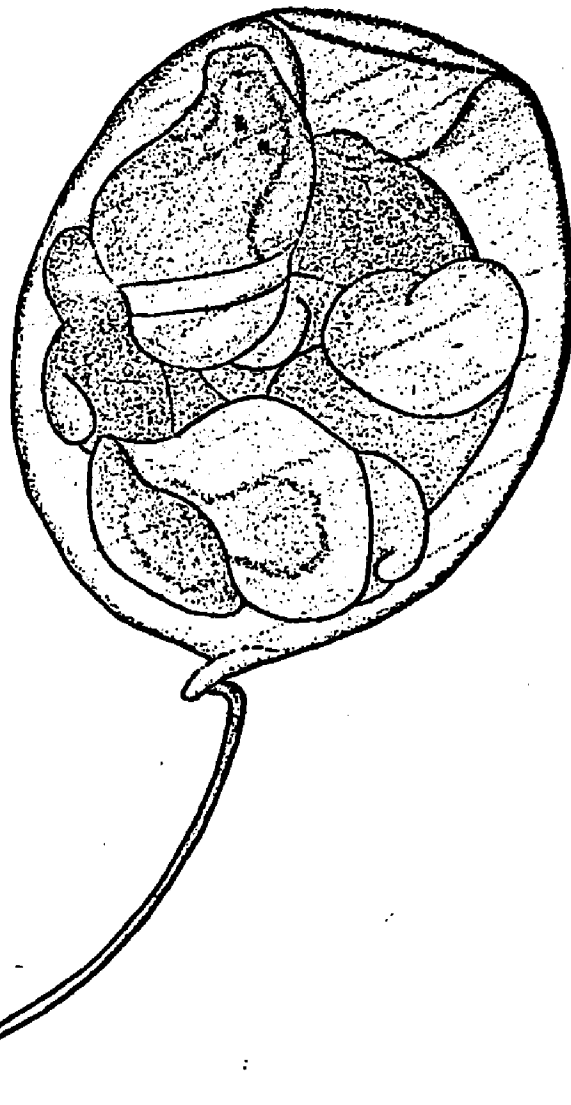
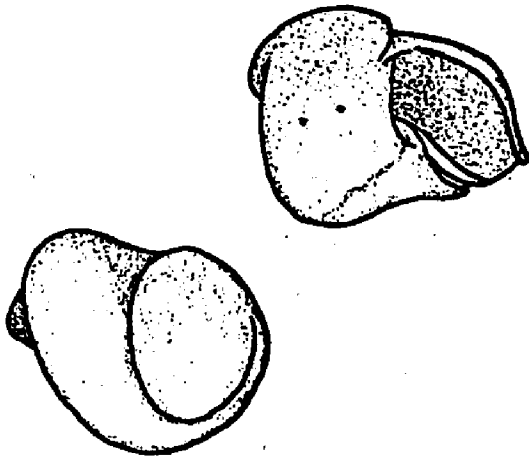
Much information is available on the nature of eggs and egg capsules of other toxoglossans, but nothing has been reported on this subject in the terebrids. Six copulating pairs of T. gouldi were found in the field in mid-June 1968. These animals were brought back to the laboratory and placed in an aquarium with running sea water. One cluster of egg capsules was found 27 days later. Terebra gouldi egg capsules are oblong and small (1.5mm long, 1.2mm wide). Each contains from six to eight spherical eggs, 0.5mm in diameter, and is attached by a thin thread 2-3mm in length to several central strands. These strands are in turn attached directly to sand grains and bits of coral rubble. The entire egg mass consisted of 140 capsules, all of which were located above the sand surface.

Development

The egg capsules were placed in a large beaker of filtered sea water supplied with continuous aeration and maintained at a constant temperature at 25°C. At the time of initial observation, most of the developing eggs were in a late stage of gastrulation. The trochophore stage was passed rapidly, and by the end of the ninth day the embryos were elongate veligers with an extended head vesicle. There were no nurse eggs, and most of the eggs showed normal development. The veligers possessed a relatively small four-lobed velum, and rotated freely in the capsule. By the end of 30 days the young had reached the veliconch stage having a shell of 2½ to 3 whorls. They measured 0.65 to 0.75mm in length, and nearly filled the egg capsules (Fig. 11). The capsular plug was eroded away by the 35th day and juveniles emerged.

Most known toxoglossan species have a planktonic stage of at least several days, but there is none in T. gouldi. The juveniles on emerging immediately drop to the sand and burrow in. They remain buried in the sand during the day and crawl at night. Loosely compacted sand appears to be essential for successful settling. Juveniles were kept in shallow petri dishes filled with filtered sea water and sand

Fig. 11. A single egg capsule of T. gouldi containing veliconchs, and several isolated veliconchs. Large numbers of capsules joined by slender stalks form an egg mass.



1mm

from the natural habitat, but no feeding was observed and few survived. The method of feeding in newly settled carnivorous gastropods is not known, but Fretter (1968, personal communication) believes that the animals are predatory from the time of metamorphosis, and Turner (1970, personal communication) has observed Prunum in the laboratory preying immediately after metamorphosis.

Growth

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

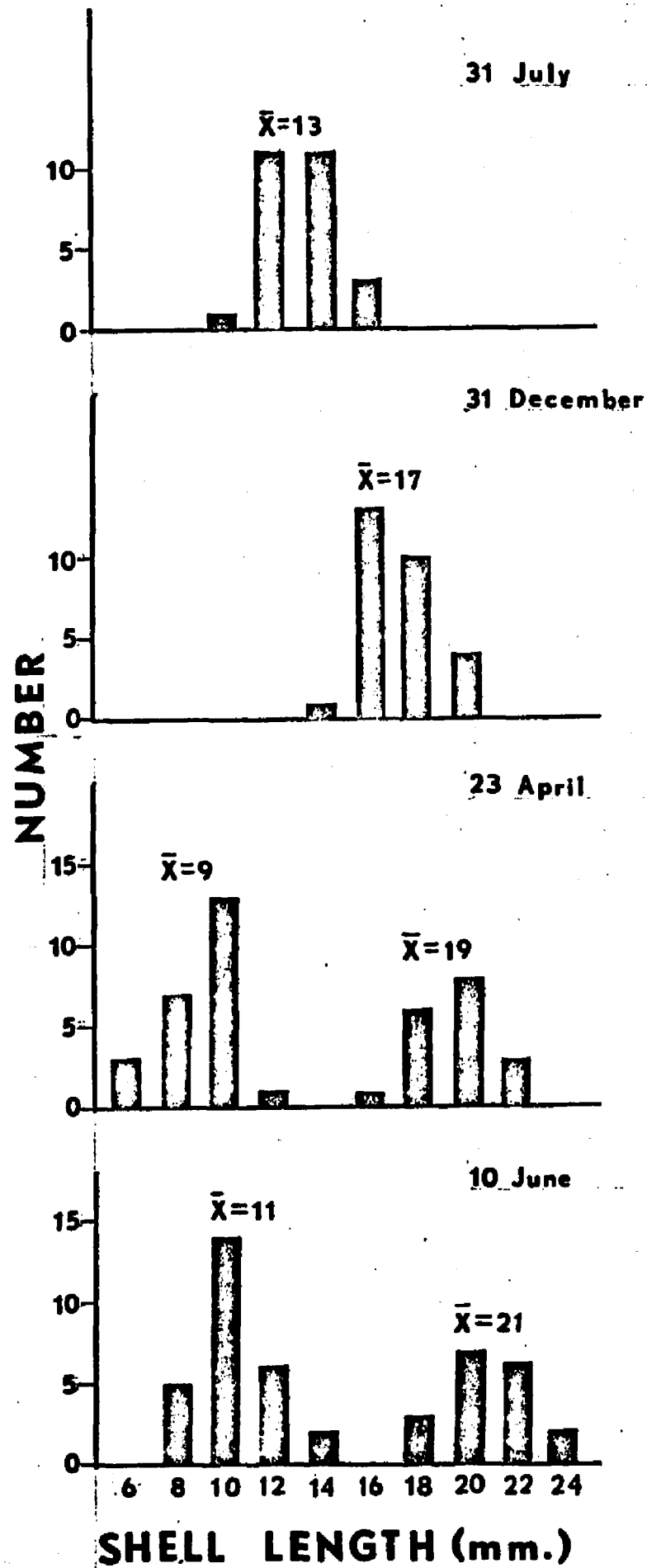
Several techniques were attempted to obtain data on the post-larval growth of T. gouldi. Fifty animals were measured, tagged according to a method developed for deep water terebrids (Miller, 1968) and released in the field. I recovered no animals since the tags unfortunately served as location markers for local shell hunters.

Attempts were made to study growth under laboratory conditions. Twenty-five animals were brought to the labora-

tory, measured, and placed in a sand filled tank supplied with running sea water and a high density of P. flava. The animals were measured monthly from November 1968 until March 1969. Growth was erratic, and only one specimen showed consistent growth, adding one millimeter in total shell length during the time of the observations. Probably the presence of lights and continual disturbance by curious laboratory visitors inhibited normal feeding.

The only conclusive data on growth rates were obtained through periodic collecting and measuring of the first and second year classes. Collections were made using a $\frac{1}{4}$ inch mesh sieve in July and December 1968, and April and June 1969, to the leeward of Ahu O Laka Island. As shown in Figure 12, the peak in the 12.0 to 14.0 millimeter range probably represents those animals hatched during the summer of 1967, and I will call this the 1967 year class. Between July and December the mean shell length of the 1967 year class changed from 13.0mm to 17.0mm, or an average growth rate of 0.8mm/month for the first five months. Between December 1968 and April 1969 the mean shell length of the 1967 year class changed from 17.0mm to 19.0mm, or an average growth rate of 0.5mm/month for the four winter months. The 1968 age class spawned in the summer of 1968 appeared in the sieve samples for the first time in April 1969, and had

Fig. 12. Length-frequency distribution of juvenile T. gouldi from leeward Ahu O Laka Island, 31 July 1968-10 June 1969.



a mean shell length of 9.0mm. It is possible that this age class would have appeared in the December sampling, but heavy rainfall and high waves made detection of the small sizes in the sieve extremely difficult.

Between April and June 1969, the mean shell length of the 1967 year class changed from 19.0mm to 21.0mm, for an average growth rate for the two spring months of 0.5mm/month. During the same period of time, the mean shell length of the 1968 age class changed from 9.0 to 11.0mm, an average growth rate of 0.5mm/month.

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

Adult T. Gouldi reach a maximum shell length of 70-80mm. Animals of this size may be considerably older than their early rates of growth would indicate, for evidence from other species reveals that growth rates slow considerably in older individuals. I have found that adult T. maculata from Eniwetok grow very slowly, and large individuals 100 to 150mm in length appear to add no more than 2-4mm in shell length per year.

Predation

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

Adult T. gouldi live a life free from heavy natural predation. Few empty shells were found after extensive sieving of the Ahu O Laka habitat. I collected 18 shells of recently dead animals throughout the study period. Nine were cracked extensively, two contained bore holes, and seven showed no sign of mechanical injury.

The extensive cracks in the Terebra shells result from the action of the sand crab Calappa hepatica. Successful predation by this animal was observed in the laboratory on two occasions, and attempts at predation were observed in the field. Calappa normally lies buried in soft sand, but periodically emerges and slowly walks over the surface, poking the tips of the walking legs deeply into the sand. When a potential prey is located, the animal grasps it with the chelae and reburies into the sand. If the prey is a Terebra, Calappa begins chipping away the tip of the shell, gradually rotating the shell as it is cracked.

Most of the T. gouldi with shell lengths longer than one centimeter show signs of Calappa attack. Less than 5% are free from cracks, and most specimens average 2-4 attacks. However, to prey successfully on Terebra, Calappa must necessarily break open from $1\frac{1}{2}$ to 2 whorls, and this rarely occurs. In fact out of 208 Terebra longer than ten millimeters that were collected and examined, only nine shells showed sufficient fractures to indicate successful predation.

Calappa predation on young T. gouldi under ten millimeters in length may be more successful. The newly hatched juveniles are not attacked by Calappa during the fall and winter, for from the time of emergence in late summer until early the following spring, most of the Calappa are too large to prey on small shells. However, in mid-April large numbers of Calappa 2-3mm in length were observed in the sand and by June they were 5-10mm in length. Although no cracks were found in the young Terebra in April, nearly 50% of the first year class showed evidence of recent predation attempts in June, several of them successfully completed.

Natica marochiensis is a common gastropod in the sub-tidal sand community and occasionally feeds on T. gouldi, but a low rate of predation is indicated, with only two out of 219 specimens of Terebra showing bore holes. Natica

preys most heavily on the bivalves, particularly Pinguatellina robusta and Ctena bella, as well as on other gastropods.

Kohn (1959) reported that Conus pennaceus fed on T. gouldi in the laboratory, but it is unlikely that these two species occur together naturally. Since no mollusc-eating cones have been found in association with T. gouldi, it is assumed that mortality in those shells lacking cracks or bore holes resulted from causes other than predation.

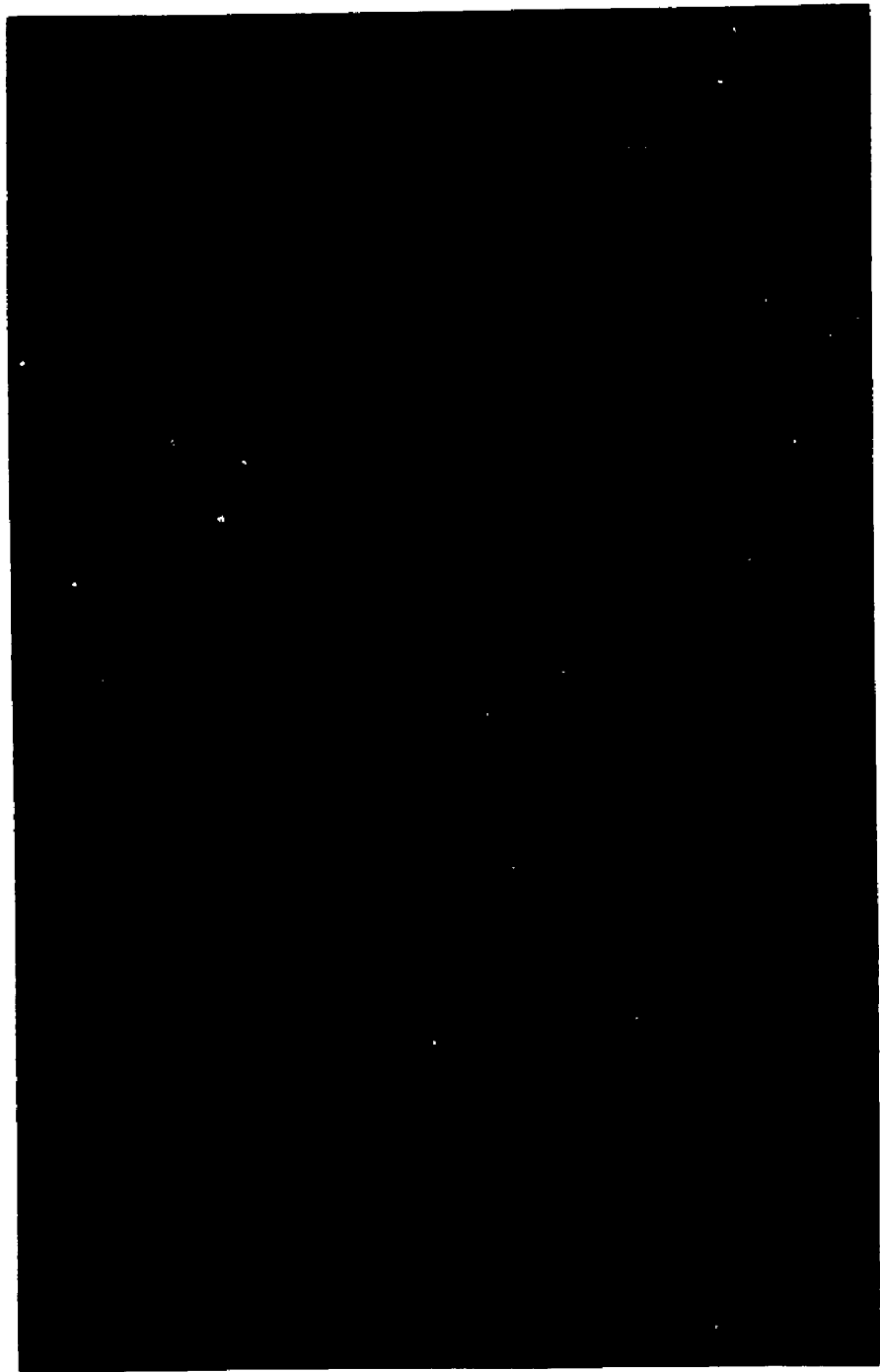
Human predation appears to be the main cause of adult mortality. During low tide when the sand flats at Ahu O Laka are barely covered with calm water, many amateur shell collectors wander over the area and collect large numbers of live animals. In some areas that at one time had large populations of T. gouldi, such as the shallow sands of Waikiki, (Kondo, 1969, personal communication), the species has virtually been eliminated by skin diving tourists.

Discussion

In addition to T. gouldi, four additional species of Terebra with the Type IA feeding apparatus are commonly found in Hawaiian waters (Fig. 13). Terebra gouldi and T. thaanumi Pilsbry 1920 are endemic, whereas T. areolata (Link, 1807), T. crenulata (Linnaeus 1758), and T. dimidata (Linnaeus, 1758) are Indo-Pacific in distribution. All of the species

Fig. 13. Hawaiian species of Terebridae with the
Type IA polyembolic proboscis (.75 X).

- A. Terebra gouldi Deshayes, 1859.
- B. Terebra thaanumi Pilsbry, 1920.
- C. Terebra dimidiata (Linnaeus, 1758).
- D. Terebra areolata (Link, 1807).
- E. Terebra crenulata (Linnaeus, 1758).



are nearly identical in internal morphology and in many aspects of life history. The species generally live in extensive sand flats protected from strong wave action. They all crawl and burrow slowly, feed at night, and rarely emerge from the sand during the daylight hours.

The most striking similarities are observed in the method of feeding and the choice of prey. Terebrids with the Type IA polyembolic proboscis lack the radular apparatus and have a short buccal tube. They would presumably have difficulty in capturing polychaetes, the prey of many radular feeding toxoglossans, because of the rapidity with which a worm can move and the depth to which it can retract into its tube. It is possible that species with this feeding apparatus are restricted in prey choice and are specialized to feed only on slow moving shallowly buried prey.

As discussed earlier, T. gouldi feeds exclusively on Ptychodera flava, a slow moving hemichordate living just beneath the sand surface. To determine the prey preference of the other Type IA species, gut analyses were made on T. thaanumi dredged off the coast off Waikiki, on T. dimidiata and T. areolata from Eniwetok, and on T. crenulata from Hawaii and Eniwetok. Terebra thaanumi is very similar in appearance to T. gouldi, but lives in considerably deeper water. Like T. gouldi, it feeds exclusively on P. flava.

Terebra areolata and T. dimidiata also feed on P. flava at Eniwetok. Both of these animals live in extensive beds of medium to fine sand at a depth of 3-6 meters. Terebra crenulata lives in shallow sand bars at Eniwetok, usually in coarse sand and gravel, where it feeds exclusively on P. flava. In Hawaii, T. crenulata is often found living in the same habitat as T. gouldi, and hence the animals compete for the same prey species. It also lives in coarse sand pockets in the reef and feeds on a large, as yet unidentified hemichordate. All of the species except T. areolata have fed on P. flava in the laboratory.

From this it is tempting to speculate on the prey choice of other Type IA terebrids. Terebra dislocata, a Type IA species found along the southeastern coast of the United States, has been studied by Stewart (1967, personal communication). He had no success in feeding the animal but observed that it lives in close association with a species of hemichordate. Pearse et al (1942) have indicated that T. dislocata from North Carolina is commonly found in the same habitat as the hemichordate Balanoglossus sp.

It is too early to reach definite conclusions on the taxonomic relationship of terebrids with the Type IA feeding apparatus. It is, however, possible that species of this feeding type have evolved from the same ancestral stock along

parallel lines, and have specialized to exploit the large number of hemichordates occurring throughout the tropics. As more species are studied, it should be possible to determine the diagnostic significance of this feeding type in a reclassification of the family. I would expect that all of the species will eventually prove to have similar feeding habits. This fact, correlated with obvious similarities in the morphology of the shell and feeding apparatus, will probably place the Type IA species in a separate genus.

For the present, T. gouldi serves as a representative Type IA species, and can be used with some predictive value to facilitate life history studies on related species of the same feeding type, an important step toward an understanding of the trophic structure of tropical marine sand communities.

Part B. Preliminary data on the biology of T. felina
(Dillwyn, 1817) and other terebrids with the
Type IB polyembolic proboscis

Terebrid species with the Type IB polyembolic proboscis are morphologically similar to Type IA terebrids in that they lack a radular apparatus and possess a short non-eversible buccal tube. However, they differ in several important aspects. Most significantly, the everted labial tube in Type IB species is two to three times longer than that of

Type IA species, and is folded upon itself several times when inverted within the labial cavity. In addition, the shell has a wider aperture, consists of fewer whorls, and is considerably heavier than the shell of Type IA species.

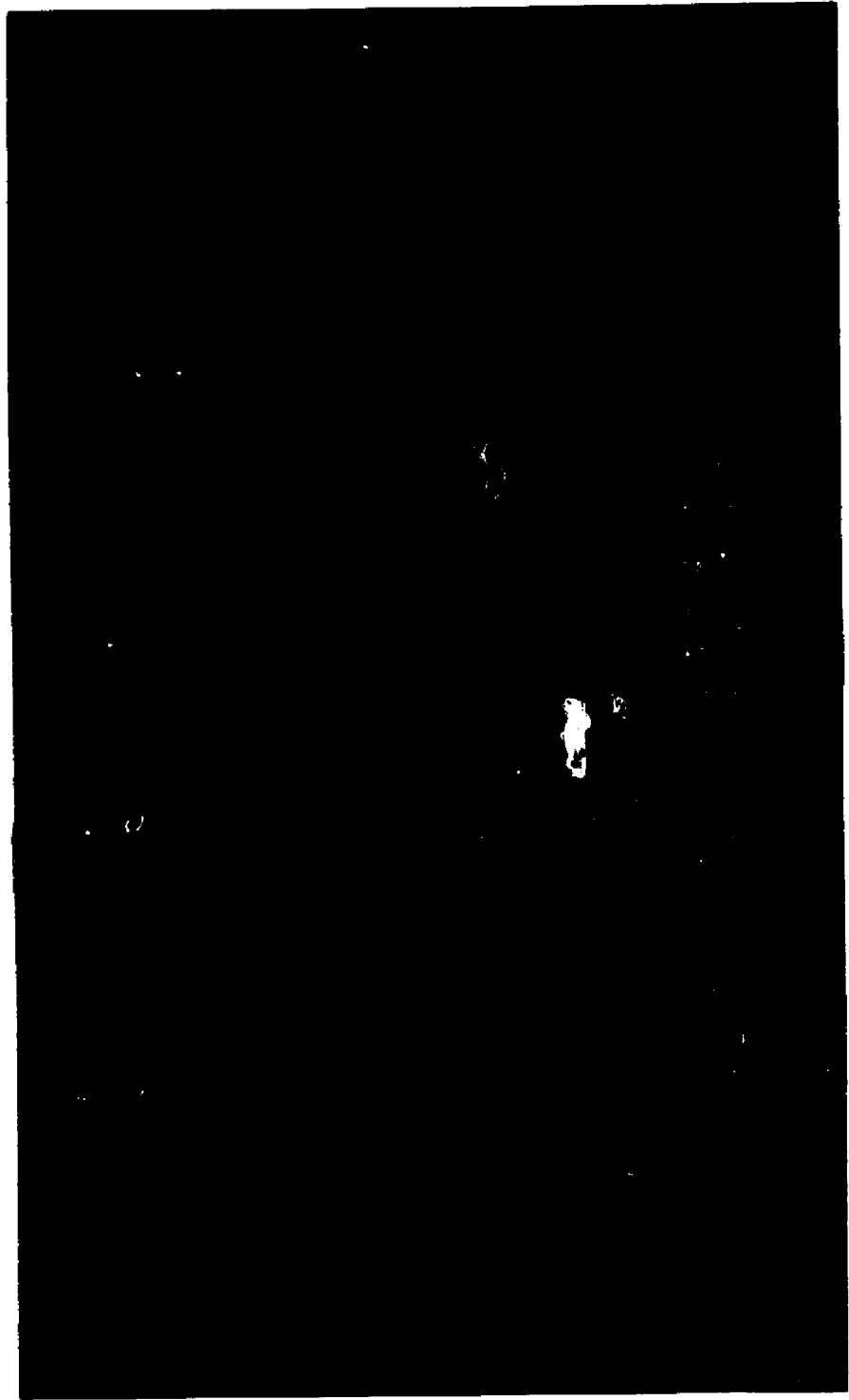
Terebra felina (Dillwyn, 1817) is the most easily collected of three species with the Type IB polyembolic proboscis found in Hawaiian waters (Fig. 1 A & B). The species is distributed throughout the Indo-Pacific and is very abundant around the Hawaiian Islands, where it generally lives in areas of deep coarse sand and gravel. Its behavior is characteristic of all Type IB terebrids that I have studied.

The foot of T. felina is broad, fleshy, and specialized for crawling deeply in the sand. The animal buries itself to a depth of several centimeters during the day, and may crawl during the night with most or all of the shell covered, a behavior not seen in terebrids of other feeding types.

Feeding studies were performed on T. felina from October 1968 to April 1969, and gut analyses were performed on 54 specimens collected during the morning from several sites around Oahu (Table I). Prey were found in the guts of 14 specimens, and all were identified as Dasybranchus caducus (Grube, 1846), a deposit feeding capitellid polychaete living in low density in areas of deep coarse sand.

Fig. 1. Hawaiian species of Terebridae with the Type IB polyembolic proboscis (1 X).

- A. Terebra felina (Dillwyn, 1817). Spotted variety.
- B. Terebra felina (Dillwyn, 1817). White variety.
- C. Terebra maculata (Linnaeus, 1758).
- D. Terebra chlorata Lamarck, 1822.



The method of prey capture is significantly different from that of T. gouldi and other Type IA terebrids, all of which capture slowly-moving prey found just beneath the sand surface. Capitellids generally live in deep vertical burrows, with only the anterior segments exposed to the surface. Terebra felina crawls through the sand, probing for the anterior end of the capitellid with the propodium of the foot. When contact is made, the capitellid rapidly retracts into its burrow. The broad fleshy foot of T. felina then rapidly digs straight down, pulling the shell into the sand at an angle of nearly 90 degrees. At the same time the long slender labial tube everts, enters into the polychaete burrow, and extends until the retracted prey can be grasped by the anterior sphincter. After the prey is grasped by the labial tube, ingestion continues as described for the Type IA species.

In addition to T. felina, two other species with the Type IB polyembolic proboscis are found in the Central Pacific (Fig. 1 C & D). Terebra maculata (Linnaeus, 1758) is commonly found in shallow sand flats at Eniwetok, and in deeper sand channels around the Hawaiian Islands. Terebra chlorata Lamarck, 1822 is usually found living in habitats similar to those occupied by T. felina, but in considerably lower densities. Gut analyses were done on 160 specimens of

T. maculata from Eniwetok, and 22 specimens of T. chlorata from Hawaii. The results are shown in Table I. Both species appear to feed exclusively on Dasybranchus caducus, and feeding behavior is similar to that exhibited by T. felina.

Mating of T. felina was observed in the field on one occasion. Whereas mating in most other terebrids takes place with the male located above the sand surface and the female below, in T. felina both partners were buried deeply in the sand. Nothing is known on the egg capsules, development, or growth of T. felina or of any other Type IB terebrid, and little is known on other life history aspects of these species.

All of the Type IB species studied live in deep, loosely compacted sand and feed on capitellid polychaetes. Since they possess no radular apparatus to immobilize the prey, they consequently require a muscular foot for rapidly burrowing into the deep sand and a long labial tube to reach the prey when it lies retracted in its burrow. Based on the remarkable conformity in the method of feeding and choice of prey shown by the three species, it is possible that they will show similarities in most aspects of life history. A study of Type IB terebrids from other areas is needed before definite conclusions can be reached, but I suggest that these

Table I. Prey organisms consumed by Type IB species of Terebra

| | <u>felina</u> | <u>maculata</u> | <u>chlorata</u> |
|--|-----------------------------|-----------------------------|-----------------------------|
| Collection site | Oahu | Eniwetok | Oahu |
| No. specimens examined | 54 | 160 | 22 |
| No. with prey in guts | 14 | 18 | 2 |
| Unidentified prey | 0 | 10 | 0 |
| Identified prey | 14 | 8 | 2 |
| Prey | <u>Dasybranchus caducus</u> | <u>Dasybranchus caducus</u> | <u>Dasybranchus caducus</u> |
| Max. No. prey eaten per <u>Terebra</u> | 1 | 1 | 1 |

species have evolved from the same ancestral type and are specialized morphologically and behaviorly to feed on deep burrowing polychaetes.

Part C. The life history of *Hastula inconstans* (Hinds, 1844), and a discussion of feeding in other species with the Type IIA polyembolic proboscis

Introduction

Hastula inconstans (Hinds, 1844), a species with the characteristic Type IIA polyembolic proboscis, is Indo-Pacific in distribution and commonly found throughout the Hawaiian Islands. The shell is glossy, reaches a maximum length of 34 millimeters, and exhibits the flared aperture typical of hastulas. Shell color is extremely variable throughout the range, and individuals shade from black through light tan (Fig. 1 A-J).

Around the Hawaiian Islands, *H. inconstans* only occurs on surf washed beaches characterized by fine well-sorted sand, gentle slope, and rolling breakers one to two meters in height. I have never found the species on coarse sand beaches, nor on fine sand beaches protected from wave action. Of the nine species of terebrids with the Type IIA feeding apparatus found in Hawaii, *H. inconstans* is best suited for

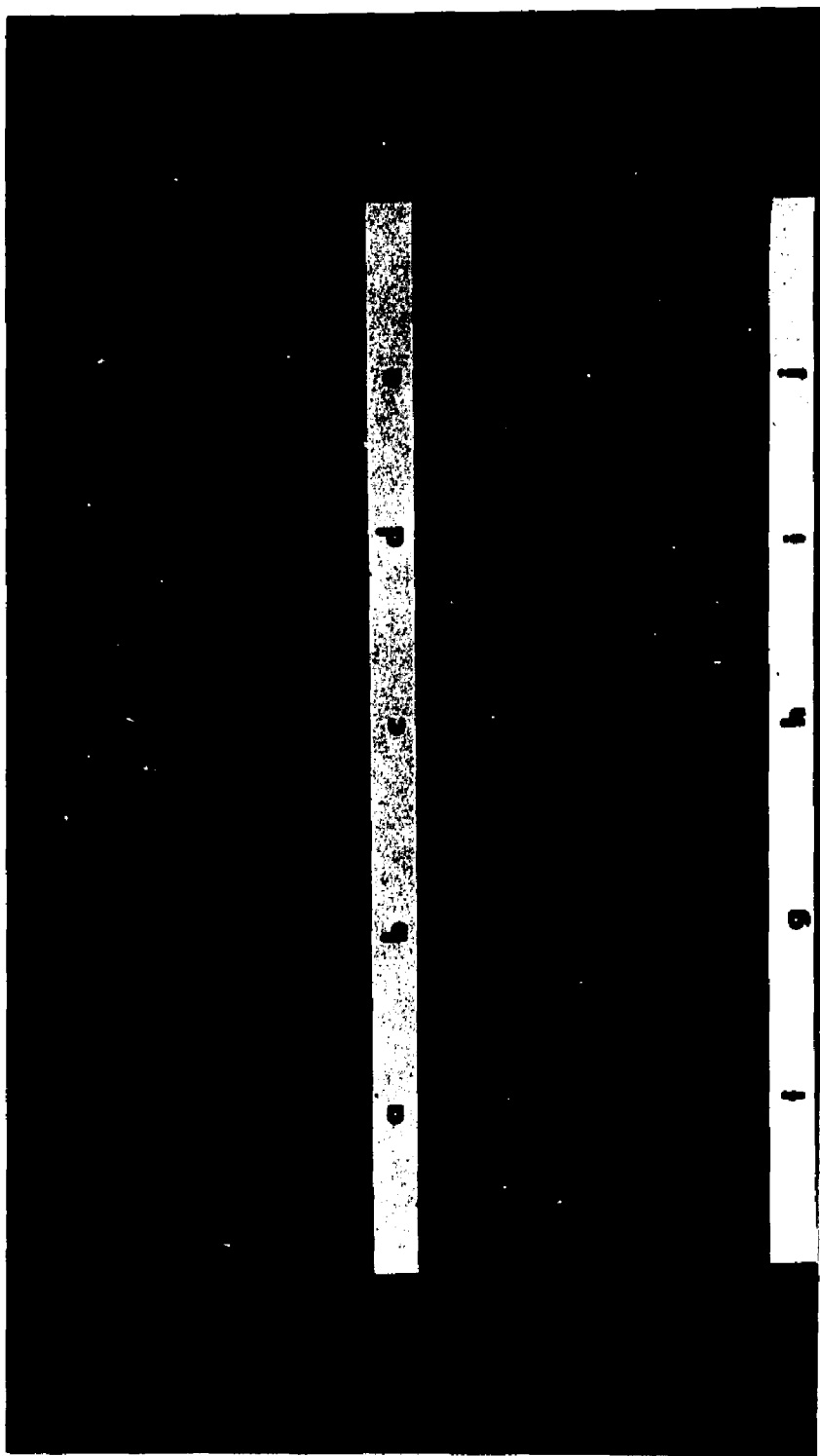
Fig. 1. Variation in shell pigmentation of H.
inconstans from Hawaii (1.5X).

a. Waikiki, Oahu

b-e. Poipu, Kauai

f-h. Kealahou, Hawaii

i-j. Awalua, Maui



a detailed ecological and life history study. The animals are abundant, easily collected, and readily feed under laboratory conditions.

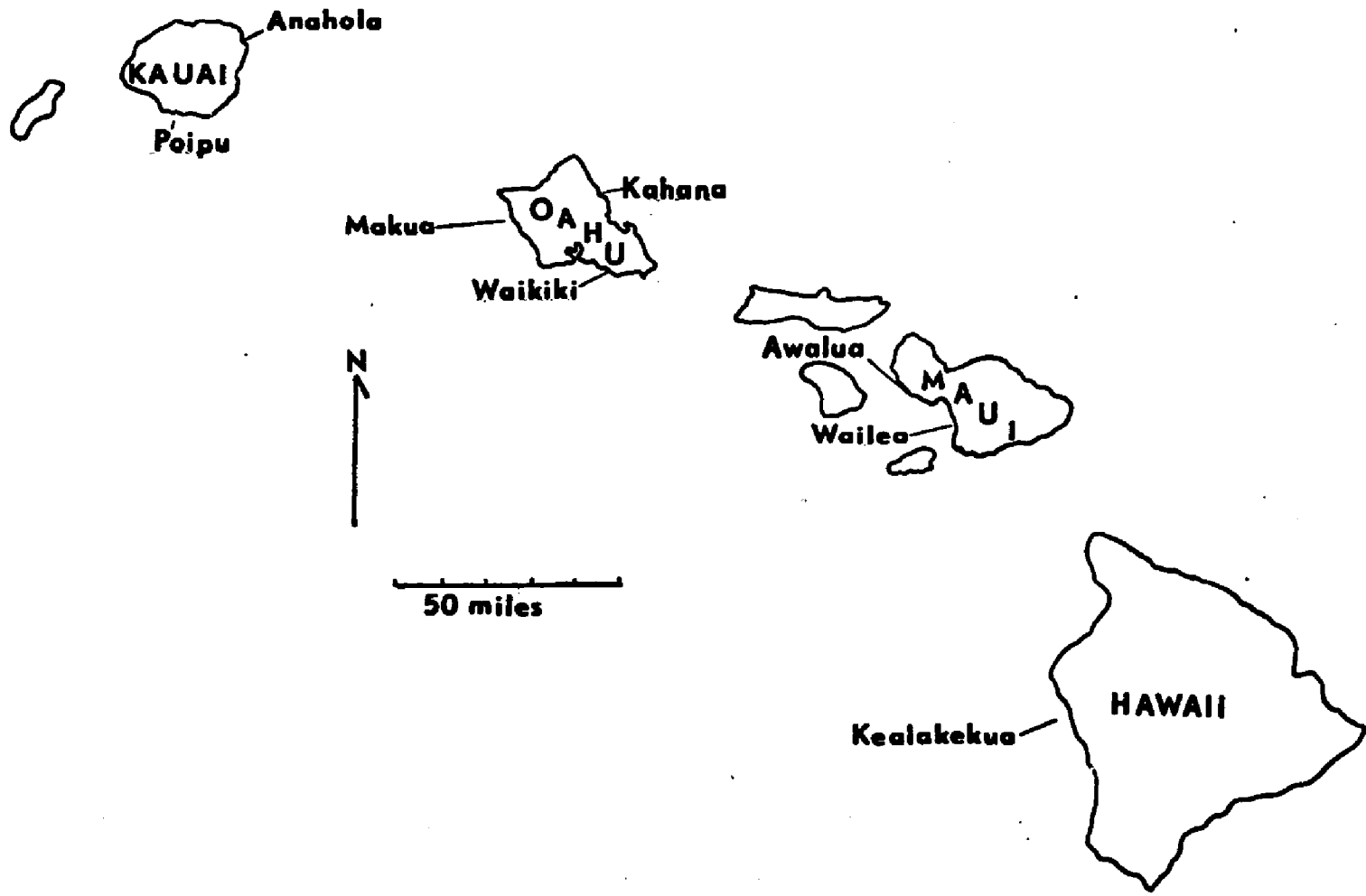
Studies on the ecology and life history of H. inconstans were conducted over a period of ten months from September 1968 to July 1969. Observations on life history in the field and laboratory were primarily concerned with locomotion, food and feeding, reproduction, development, growth, and predation. Animals were observed and collected from twelve surf beaches on the islands of Hawaii, Maui, Oahu, and Kauai using standard skin diving gear and the Johnson Air-Buoy. Study sites are indicated in Figure 2. Most studies were done at Kealakekua, Wailea, and Poipu.

Locomotion

Both the morphology of the foot and general locomotory behavior of hastulas differ markedly from animals of the genus *Terebra*. The foot of H. inconstans is very broad and fleshy. It is capable of rapid contraction and maintains a degree of flexibility not evidenced in other terebrids living in less rigorous habitats.

Locomotory behavior was studied in the field and laboratory using techniques described earlier for Terebra gouldi. As in T. gouldi, there are two basic movements

Fig. 2. Map of the Hawaiian Islands, showing the location of collection sites of H. inconstans.



involved in locomotion; a forward gliding of the foot to a position anterior to the shell, followed by cessation of propodial movements and contraction of the body musculature to advance the shell and visceral mass. I call one complete cycle a step.

Locomotory behavior is dependent both upon the size of the animal and the severity of surf conditions. When the waves are small and the animals are not crawling, they remain deeply buried in the sand, with the long extensible siphon located above the sand surface. In most instances there is an approximate 1:1 ratio between the depth to which the foot is buried in the sand and the length of the shell. Compared with most terebrids locomotion is fast, averaging from 20-30 steps per minute. The process of re-burying in the sand is also rapid, and in most instances dislodged animals will securely anchor the foot before the passage of a succeeding wave, and will be completely buried within 40-60 seconds.

At least during daylight hours, locomotion does not occur in the absence of waves. However, calm conditions are rare, and waves of 0.5-1 meter in height generally break on the beach. Under normal conditions, several millimeters of sand are agitated with the passage of each swell, and the shells of small animals are then exposed to the

surface. The broad foot securely anchors the snail in the sand, and when a wave uncovers the animal, the elongated body permits the shell to rotate with the direction of the surge flow. Following the passage of a wave, the animal may exhibit one of three behavior patterns presumably depending on the presence or absence of prey in the vicinity. In the absence of prey, the snail immediately burrows back into the sand before the passage of the next wave. If prey are present, the snail begins rapid locomotory behavior over the sand, or exhibits the so called "sail effect" first described by Kornicker (1961) (to be discussed later).

With stronger wave action, 5-10mm of sand may be overturned during the passage of each wave, and the smaller specimens are completely dislodged. Under these conditions reburrowing is not successful, but rather the small snails glide back and forth in the surge zone with the foot completely extended. The larger, specimens are rarely completely dislodged, even under extreme wave action.

Since trails cannot be followed in the field, it is impossible to determine the distance an animal crawls each day, or the general direction of locomotion. Specimens of H. inconstans have been observed crawling at all hours of the day. However, evidence to be presented later indicates that the peak period of feeding, and hence locomotion,

takes place during the night and early morning hours.

Food and Feeding

Introduction and methods

Several references exist concerning food and feeding in terebrids of the genus Hastula. Hedgpeth (1953) suggests that H. salleana may prey on the beach clam Donax, although this is not probable. Marcus and Marcus (1960) studied H. cinerea on the beaches of Sal Paulo from Ubatutuba to Cananea. Although they had no success in feeding the animals, setae in the gut suggested that the prey at Ubatuba may be Nerine agilis, while at Cananea the terebrid possibly feeds on an opheleid.

Feeding in H. inconstans was observed both in the field and laboratory on several occasions between October 1968 and July 1969, on animals collected from surf beaches on the islands of Hawaii, Maui, Oahu, and Kauai.

Data on food and feeding were gathered by two methods. Gut analyses were performed on animals collected by sieving in the surge zone with a fine mesh bag. Samples were taken during three periods; 7-10 AM, 2-4 PM, and 6-7 PM to determine the time of feeding, number of prey captured each day, and the per cent of the population feeding each day. Night

samples were not taken due to the presence of observed inshore shark and barracuda. Food preference studies were conducted in the field on each of the four islands. Approximately one square meter of sand in the surge zone at each study site was dug up and sieved through the fine mesh bag. All the polychaetes remaining in the bag were placed in a bucket of sea water containing 50-100 freshly collected H. inconstans. The animals were allowed to feed for five minutes, and then 20 animals from each study area containing prey in their labial tubes were dropped in 70% alcohol, which resulted in immediate regurgitation. Prey were then returned to the laboratory for identification.

Details of the anatomy of the feeding apparatus were worked out through dissection of fresh specimens removed from the shell after quick freezing.

Gross morphology of the foregut

The foregut of H. inconstans is shown in Figure 3 with the proboscis everted. As is the case for all terebrids with the Type II polyembolic proboscis, the primary functional components utilized in prey capture in H. inconstans are a long eversible labial tube that terminates in an anterior sphincter, and a long retractile buccal tube that can be extended out of the labial tube. The cephalic hemocoel

Fig. 3. Gross morphology of the anterior digestive system of H. inconstans with the proboscis everted, exposed by cutting through the dorsal mantle and body wall.

1.....labial tube

1a.....labial cavity

1b.....sphincter of the labial tube

2.....buccal tube

2b.....longitudinal retractor muscles of the buccal tube

3.....buccal cavity

4b.....radular sac

4d.....radular tooth

5a.....poison bulb

6.....salivary gland

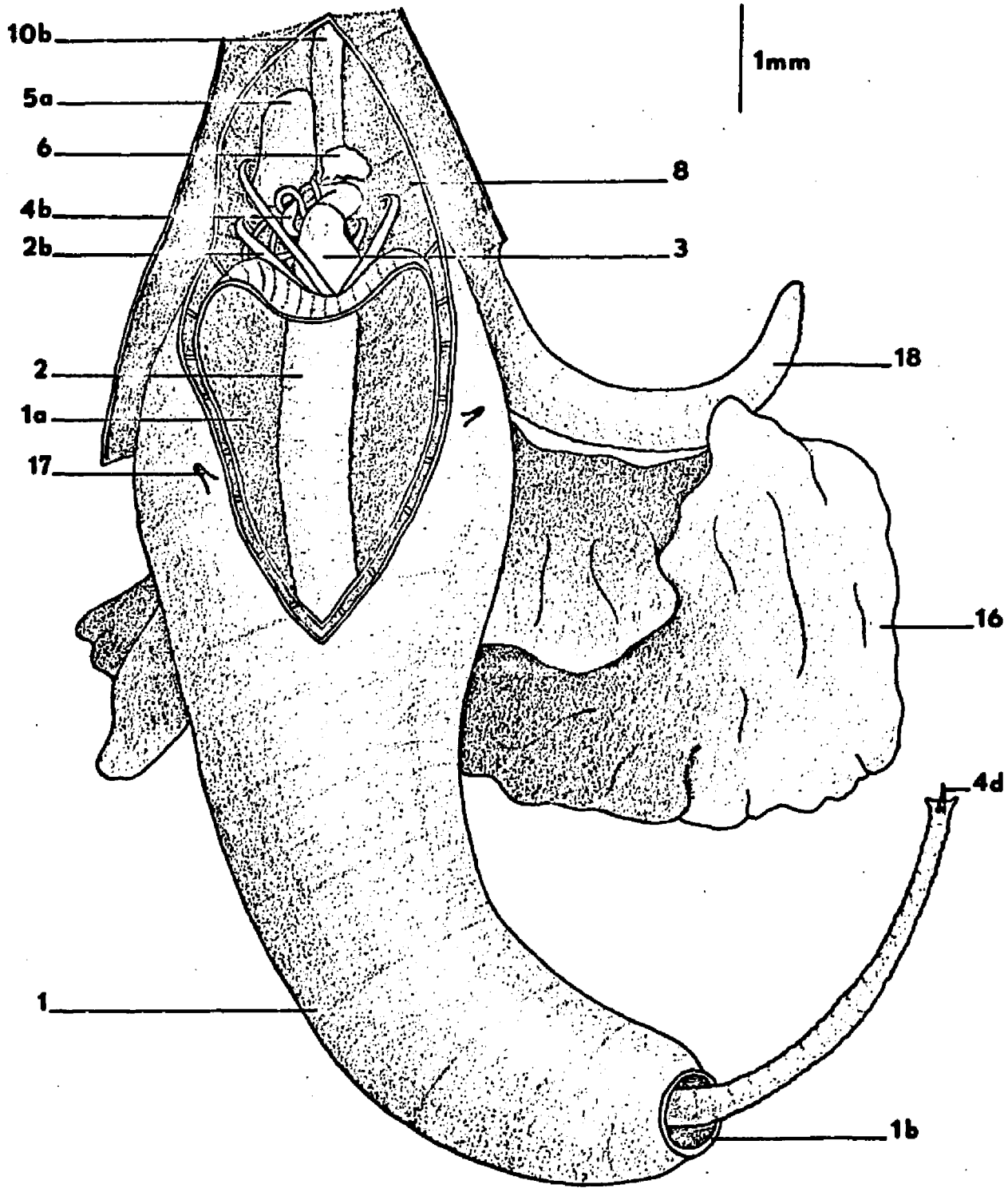
8.....cephalic hemocoel

10b....post-ganglionic esophagus

16.....foot

17.....eyestalk

18.....siphon



contains the longitudinal retractor muscles of the buccal tube and several organs which enter into the muscular buccal cavity (Fig. 4). The radular sac and radular caecum open into the buccal sac on the ventral wall of the buccal cavity. A small bipartite salivary gland overlies the pre-ganglionic esophagus and opens through two ducts into the buccal sac on both sides of the radular caecum. The coiled poison gland leads from a large muscular poison bulb located in the right half of the cephalic hemocoel. It enters the ventral wall of the buccal cavity posterior to the opening of the radular apparatus. The short thin-walled pre-ganglionic esophagus passes through the nerve ring. The remainder of the alimentary tract consists of a long post-ganglionic esophagus, tubular stomach, and slender intestine.

Feeding

Analyses of gut contents were made on 66 H. inconstans from Kealakekua Beach on Hawaii, and prey preference records were obtained for 80 H. inconstans from the four islands studied. The results of gut analyses are shown in Table I. While there are several species of polychaete worms living in the surf beach habitat, both gut analysis and feeding preference records indicate that H. inconstans in Hawaii

Fig. 4. Dorsal view of the organs contained within the cephalic hemocoel of H. inconstans.

- 1f.....inner circular muscles of the labial tube
- 2a.....outer circular muscles of the buccal tube
- 2b.....longitudinal retractor muscles of the buccal tube
- 2e.....lumen of the buccal tube
- 3.....buccal cavity
- 4b.....radular sac
- 4c.....radular caecum
- 4d.....radular teeth
- 5b.....poison gland
- 6.....ducts of the salivary gland
- 9.....nerve ring
- 10a....pre-ganglionic esophagus
- 10b....post-ganglionic esophagus

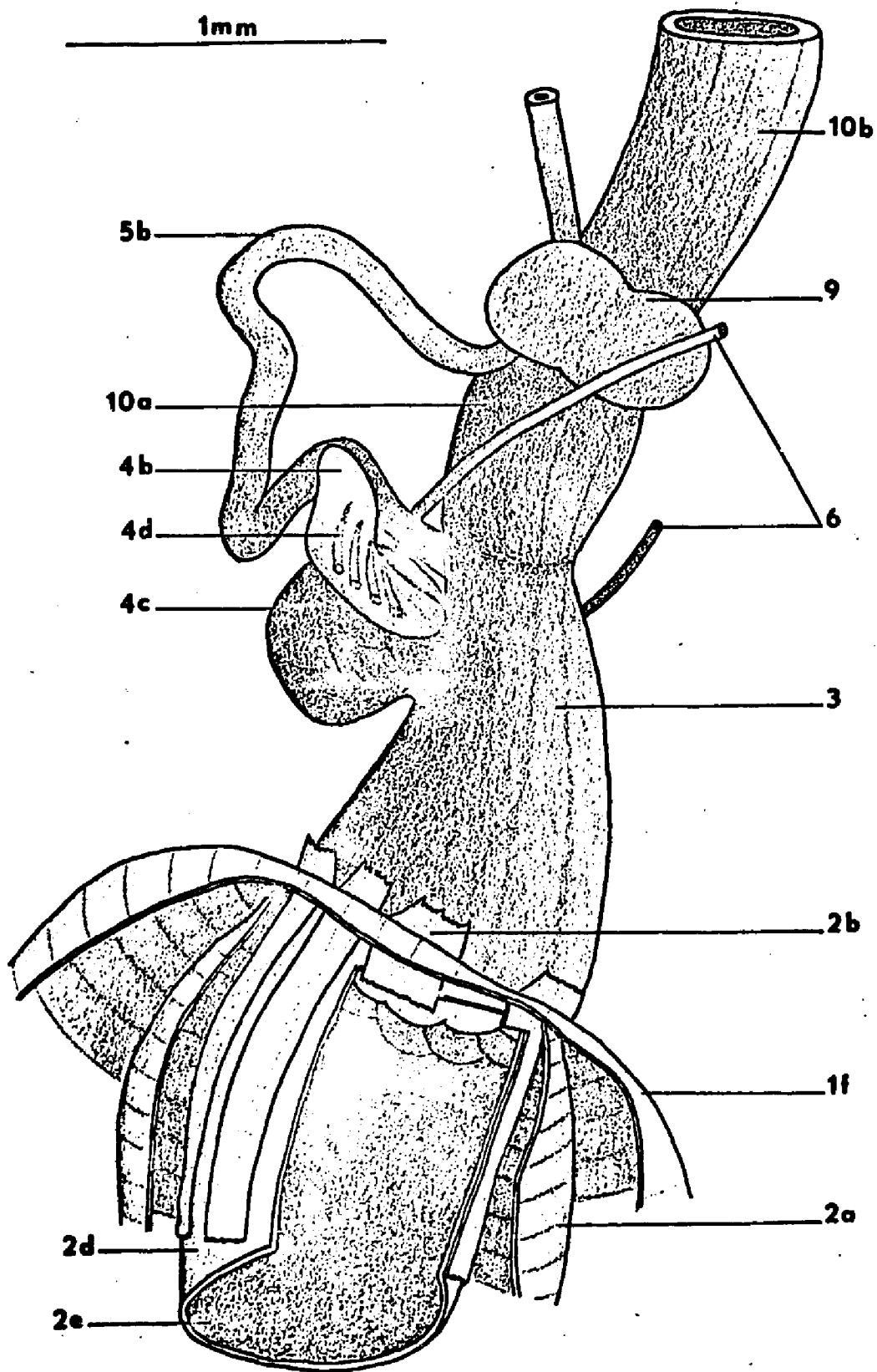


Table I. Analysis of prey choice of H. inconstans from Hawaii.

| Date | No. specimens examined | Collection site | Prey | No. specimens with prey | Position of prey in gut | | Max. No. prey/snail |
|-----------|------------------------|--------------------|---------------------|-------------------------|-------------------------|------|---------------------|
| | | | | | Fore | Hind | |
| 10-13-'68 | 18 | Kealakekua, Hawaii | <u>Dispio magna</u> | 4 | 1 | 3 | 1 |
| 2-18-'69 | 48 | Kealakekua, Hawaii | <u>Dispio magna</u> | 13 | 4 | 9 | 1 |
| 5-3-'69 | 20 | Wailea, Maui | <u>Dispio magna</u> | 20 | - | - | - |
| 6-1-'69 | 20 | Poipu, Kauai | <u>Dispio magna</u> | 20 | - | - | - |
| 6-18-'69 | 20 | Kealakekua, Hawaii | <u>Dispio magna</u> | 20 | - | - | - |

feeds exclusively on the spionid polychaete Dispio magna. This deposit feeder inhabits fine sand on many of the high energy beaches in Hawaii, and utilizes a pair of ciliated palps that stretch over the substratum to gather food particles. Apparently the animals possess a sorting mechanism for removing and ingesting detritus (Day, 1967), but many sand grains as well as detritus are ingested. This species lives buried in the sand to a depth of up to one-half meter in a burrow lined with a fragile mucoid secretion, and is generally found where there is sufficient water agitation to keep the detritus moving. Greatest abundance of the worm occurs in the surge and lower surf zone, and densities of 100-300 animals per square meter are common on fine sand beaches such as Kealakekua on Hawaii, Wailea on Maui, and Poipu on Kauai.

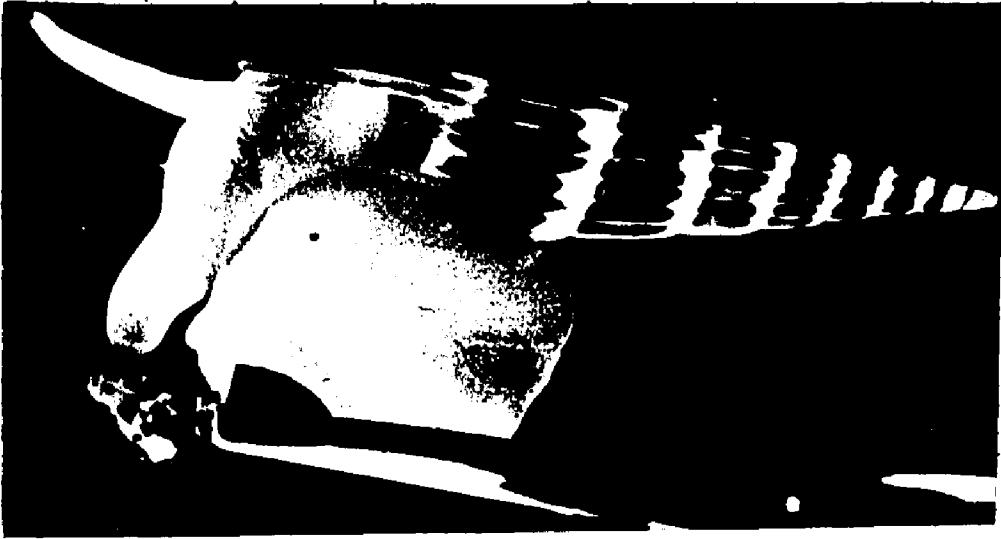
As in other terebrids, feeding appears to be initiated by distance chemoreception. Observations in the laboratory indicate that worm extract will initiate rapid propodial undulation and limited swelling of the cephalic hemocoel. Marcus and Marcus (1960) indicate that the anterior of the foot of H. cinerea is heavily innervated, and serves as an important sensory organ. This is also true for H. inconstans, and under most conditions complete swelling of the cephalic hemocoel will not occur until the propodium of the foot

comes into contact with pieces of prey or sections of the prey tube (Figure 5A). Relaxation of the retractor muscles, along with contraction of the circular muscles, leads to eversion of the labial tube and extension of the buccal tube. It is not known how the radular tooth is moved into position, but Smith (1967) is probably correct when he states that contraction of radular sac muscles moves a tooth into the buccal cavity, and peristalsis moves the tooth to its normal functional position at the tip of the buccal tube.

As the broad foot undulates rapidly through the sand, the sphincter of the labial tube is kept in close contact with the sand surface, and the radular tooth held by the extended buccal tube can be seen darting in and out. When the anterior end of D. magna is sensed by the propodium, the labial tube rapidly swings into position near the worm, and the buccal tube may extend to a considerable distance beyond the sphincter of the labial tube (Fig. 5B). As the buccal tube holding the radular tooth comes into contact with the worm, the poison bulb apparently contracts, and the entire body of the terebrid lunges violently. On several occasions a milky substance could be seen flowing from the tip of the labial tube. The tooth is thus not fired at prey as reported by Jaeckel (1952), but rather is used as Smith suggests, merely to make an opening to admit the poison.

Fig. 5. The rapid ingestive phase of feeding behavior in H. inconstans.

- A. Feeding behavior is elicited by bringing a Dispio magna into contact with the propodium of the foot.
- B. After stimulation of the propodium, the labial tube everts and the long buccal tube bearing the radular tooth searches for the prey.
- C. Following impalement, the buccal tube rapidly retracts and the labial tube extends to engulf the prey.
- D-E. The labial tube retracts, and then extends a second time to further engulf the prey.
- G. When the labial tube inverts for the second time, the labial cavity is full and further ingestion occurs slowly.



A



B



C



D



E



F

As soon as the poison has been injected the labial tube engulfs the worm and the buccal tube rapidly contracts to pull the worm in (Figs. 5C, D, E).

Prey capture is a rapid process, and in the laboratory a section of worm of considerable length may be completely engulfed in less than one minute. As soon as the labial cavity is full, further rapid ingestion cannot occur, and the snail begins crawling (Fig. 5F). In the field, the entire process of prey capture takes place between the passage of successive waves, and as soon as the poison has been injected, H. inconstans begins to burrow into the sand, entering nearly straight down, so that only the spire of the shell is exposed before the next wave passes. The snail continues to reburrow until the shell is completely covered and free from wave disturbance. Feeding then continues at a slower rate until the worm is ingested.

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

Evidence indicates that the entire feeding process in hastulas is of similar duration to that of species of the genus Terebra. Capture and initial ingestion of the prey

are rapid, but when the labial cavity is full, ingestion slows down and continues for five to ten hours after capture. Digestion begins in the upper esophagus, and prey remains are found in the intestine 18 to 24 hours after ingestion. Feces in the form of setae and sand are not voided until considerably later, and may not be found in the rectum until two days after prey capture.

No definite conclusions can be reached concerning the peak feeding period of H. inconstans. Animals will feed in the field and laboratory any time they are presented with prey, and they have been observed feeding throughout the early morning hours in the field. However, gut analyses of 48 animals collected from Kealahou showed a higher percentage of prey in the upper digestive tract at 10 AM (14%) than at 4 PM (5%). William Stewart (1968, personal communication) found that H. cinerea, a surf-dwelling species from Florida, usually feeds at night on the spionid worm Nerine agilis.

Use of the "sail-effect" as a method of prey capture

Hastula inconstans and other surf dwelling hastulas differ from other terebrids in their response to water agitation. As has been shown in certain bivalves (Reese, 1964), hastulas kept in a container of still water show

little or no locomotion. However, upon agitation of the water, the foot is immediately extended and begins rapid locomotory activity. This factor may be of importance in the feeding response.

Feeding of H. inconstans appears to be partially dependent on the degree of surge action. On the rare occasions when wave action on the beach is reduced or absent entirely, no hastulas were seen crawling, and it is probable that little feeding takes place under such conditions. During periods of moderate surge action, sand agitation is sufficiently strong to partially expose both the prey and the hastulas, and the latter begin searching movements as they bury back into the sand.

One of the most curious phenomena associated with locomotion in the hastulas is the so-called "sail-effect" first reported by Kornicker (1961) for H. salleana along the Gulf of Mexico. He claims that the foot of H. salleana is not only used to plough through the sand, but also as a sail to enable an animal to move into deeper water when it is about to be stranded above the swash zone of a falling tide. Assuming that H. salleana is indeed exposed as the tide recedes, this would be a reasonable explanation. However, the "sail effect" is very obvious in H. inconstans, a species that lives well below the swash zone where danger from

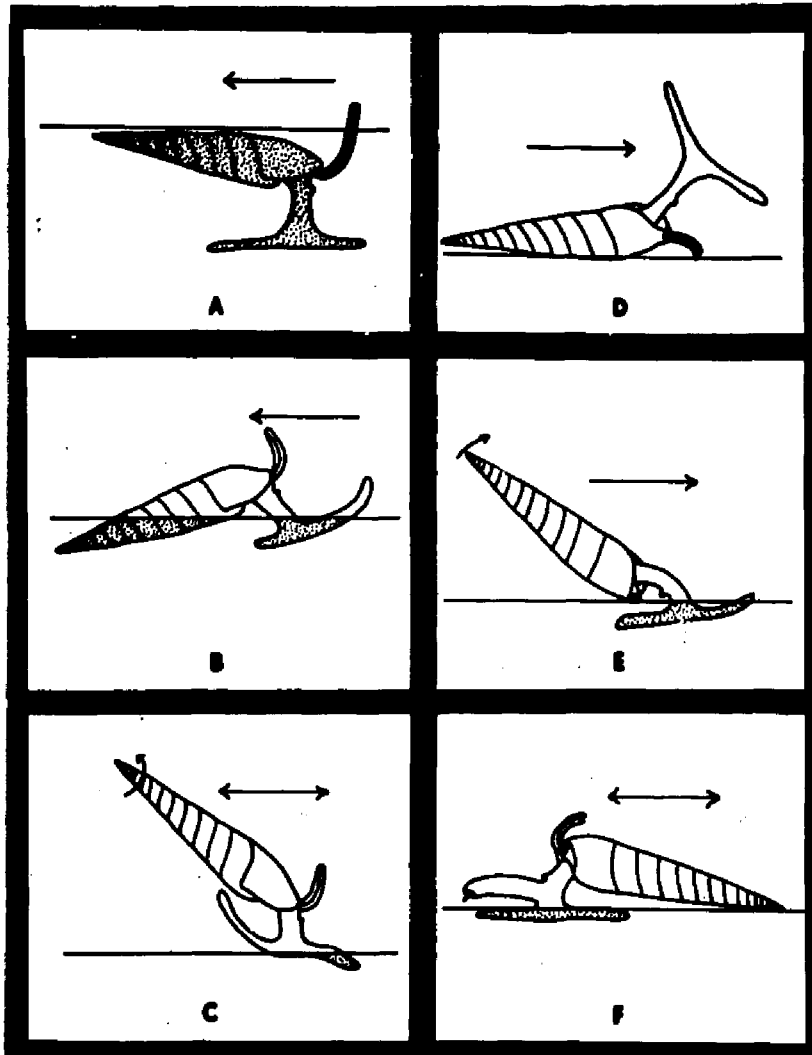
desiccation presents no problem.

The "sail-effect" appears to serve as a behavioral adaptation to feeding in the case of H. inconstans. Most importantly, it permits an animal to move from one part of the beach to another with great rapidity. I was first made aware of this while taking bottom samples in the surge zone, for it was soon obvious that H. inconstans tended to concentrate in the area from which the sample had been removed. By digging a core sample from the sand and then observing the area during the passage of several successive swells, it was clear that the animals are initially attracted to prey by distance chemoreception, and then move into the area of stimulus by the "sail-effect", as diagrammed in Figure 6.

As an incoming swell passes over the bottom from which a sand core had been removed, fragments of the spionid worms are carried shoreward. As the water containing the fragments passes over the hastulas, they crawl to the surface, flip on their side as described by Kornicker (1961), and are carried seaward in the backwash. When the site of agitation is reached, the propodium digs in and the animal flips over. Searching movements immediately begin with the propodium as the labial tube rapidly everts. When a worm is located, feeding ensues before passage of the next incoming swell.

Fig. 6. Sequence of movements of H. inconstans exhibiting the "sail-behavior".

- A. Hastula inconstans buried in the sand as an incoming wave passes.
- B. The snail rapidly crawls to the sand surface.
- C. The apex of the shell is raised at slack wave and thrown to one side.
- D. Using the foot as a sail, the animal is carried seaward by the outgoing wave.
- E. The propodium digs into the sand, and the snail rights itself.
- F. Searching for prey commences at slack water before the passage of the next incoming wave.



Feeding rates

Studies on feeding rates were done on animals collected at Kealakekua Beach from October 1968 to June 1969. Of 66 animals dissected for gut analyses, 9 contained digested or partially digested remains of Dispio magna in the esophagus and stomach, and 9 contained setae and sand grains in the rectum. Since it takes longer than 24 hours for prey to pass through the digestive tract into the rectum, it appears as if the first group represents those animals which had fed less than 24 hours before collection time, and the second group represents those that had fed the previous day. This would indicate a feeding rate of 14% per day for the entire population, a figure that is similar to the 17% feeding rate found for the entire T. gouldi population at Ahu O Laka Island.

Obviously this rate cannot be constant throughout the year, for there are times during the winter months when wave action would be too intense for successful prey capture. Specimens are difficult to locate under extreme surf conditions, and it is probable that they migrate into deeper, calmer waters, although it has been impossible to make meaningful collections in these areas during winter storms. Since the prey species maintain greatest density in the

shallow surge zone, feeding probably slows down or stops during times when migration occurs.

As in T. gouldi, individual feeding rates appear to be low. Because of the relatively long time involved in prey ingestion, it is probable that no more than one prey specimen is eaten per day. Gut analyses failed to show more than one prey specimen in the guts of animals collected in the field, and under no circumstances did any animal feed on more than one prey specimen per day in the laboratory. Based on an approximate feeding rate of 14% per day for the Kealakekua population, it would appear that an individual would average one prey per week.

Reproduction and egg capsules

Mating

Mating in terebrids of the genus Hastula, particularly those species inhabiting surf swept beaches, presents several problems not encountered by Terebra living in less rigorous environments. There is no evidence to indicate the mechanism of sexual attraction. While males of T. gouldi and probably most other terebrids living in calmer areas follow a mucus trail layed down by the female, this is not probable in the case of surf dwelling hastulas, for the

mucus trail would be quickly erased with the passage of each successive wave. Hastula inconstans lives in relatively high densities on most beaches and it is possible that mating results from random contact of sexually ready males and females.

The mating process differs distinctly from that of T. gouldi. In all situations in which mating was observed in the field, the mating pairs were found in the surge zone. They were not buried in the sand, but rather were coupled together and rolled freely back and forth in the surge. The animals remained tightly clasped together, and unlike the response in T. gouldi, did not separate when they were disturbed. Duration of copulation is not known.

Nothing is known on the length of the mating season or the time of juveniles settling. Individuals were found mating every time the habitat was visited, but it is probable that the mating season reaches a peak in the early part of the dry season, as is the case for T. gouldi.

Egg Capsules

Egg capsules were initially found in the field by sieving sand in the surf zone with a fine mesh bag, and later in the laboratory in a sea water table containing a large number of H. inconstans.

Egg capsule deposition differs significantly from the process observed in T. gouldi. Hastula inconstans lives on beaches of moderate wave action and well sorted very fine sand, with a small component of both coarse sand and silt. There are usually no rocks or other stable objects present, and those boulders which do occur on a few of the beaches are generally scoured clean by continual sand abrasion and are periodically buried with changes in the beach profile. Since the animals mate in the surge zone, permanently affixed egg capsules would be impossible.

In the area of surge, just beyond the actual zone where surf breaks, is a region containing litter such as crustacean exuviae, broken shells, leaves, and small bits of basalt rock. This litter is on the surface of the finer sand and rolls back and forth with the successive passage of each wave. Hastula inconstans appears to selectively utilize the small round bits of basalt, generally 1-2mm in diameter, as a base for egg capsule deposition. It is not known whether the deposition is accomplished in the litter zone, with the female exposed to the surface and grasping the small basalt grains, or below the surface of the sand where she contacts a piece of buried basalt. However, all of the egg capsules recorded in the field were found from surface sieving in the litter zone with the use of the fine mesh bag

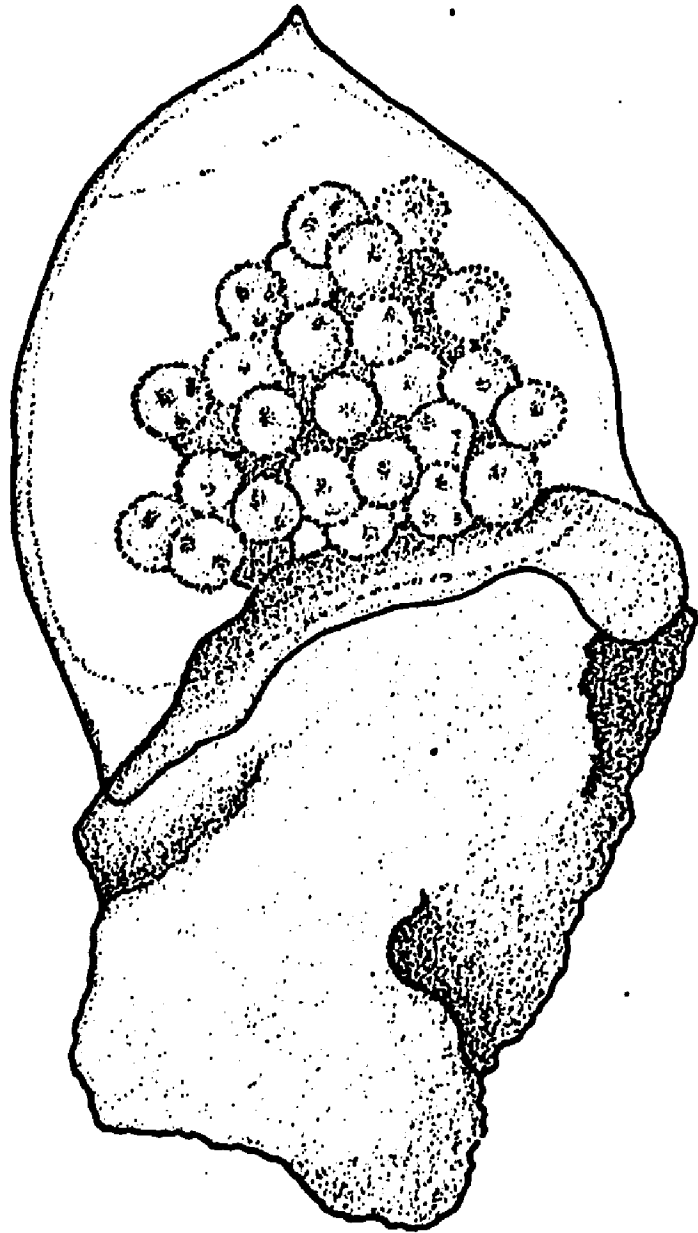
previously described.

As shown in Figure 7, the egg capsules are of approximately the same size as the basalt granules and form a cap-like covering over them. Each capsule contains approximately 40 spherical eggs, 100 μ in diameter. Development beyond this stage has not been observed. Both the extremely small size of the protoconch and the variability in shell color and sculpture among populations from beaches in the Hawaiian Islands and from other Indo-Pacific areas would indicate that the planktonic stage is either greatly reduced or absent entirely (Taylor, 1968, personal communication). If this is true, some of the eggs in the capsule may serve as nurse cells.

Growth

A preliminary survey of H. inconstans at Kealakekua Beach in October 1968 indicated that young individuals 4-11mm in length were very common just below the sand surface. When individuals of all sizes were randomly collected and arranged in a size-frequency histogram, it was apparent that these young individuals probably represented the first year class, and could be used in a study of growth rates. To gather effectively large numbers of small specimens, a nylon bag of 1mm mesh size was attached to a metal scoop and the top

Fig. 7. Egg capsule of H. inconstans containing uncleaved ova. The capsule is attached to a small granule of basalt.

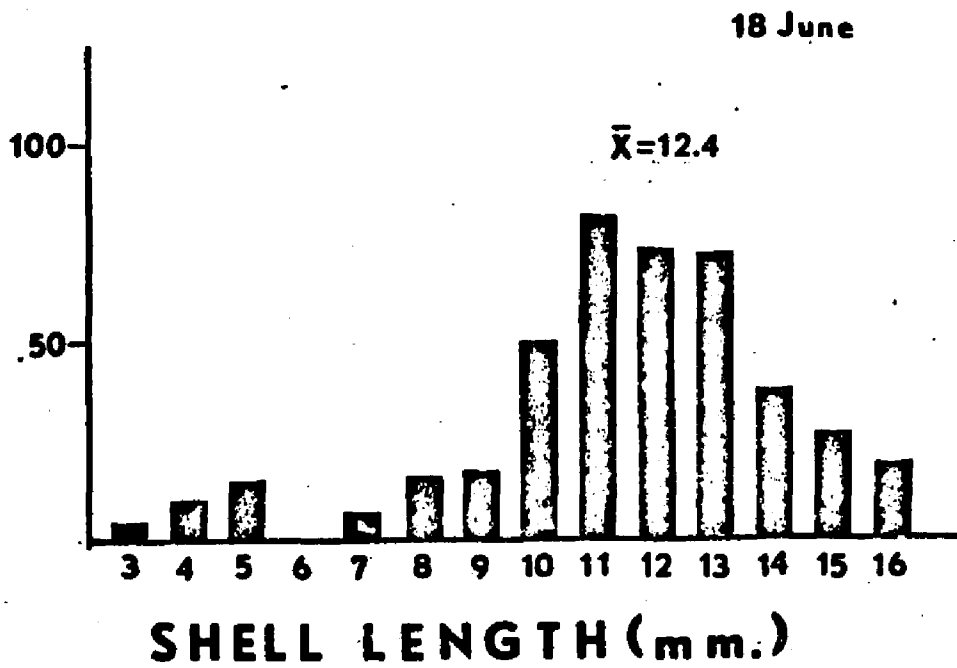
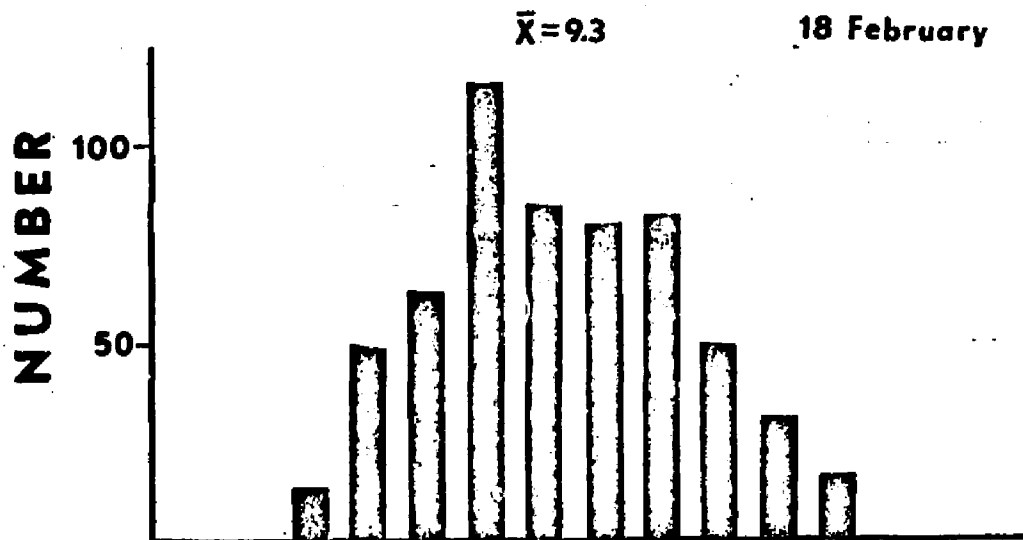
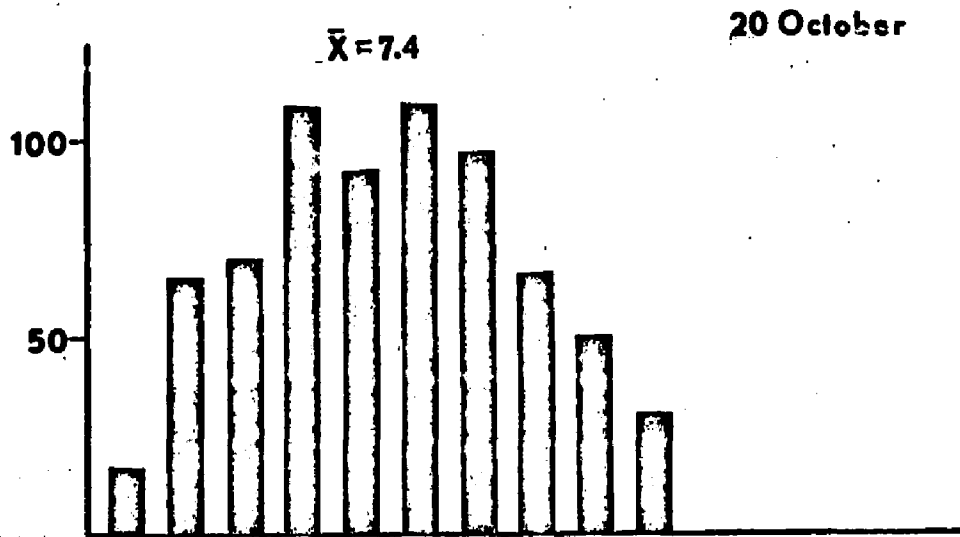


1mm

centimeter of sand was removed by pulling the scoop over the sand between passage of successive breakers. The sand was sieved through the mesh, and sampling was continued until approximately 400 individuals were gathered in each sample. Since larger individuals burrow deeper in the sand, most of them were excluded from the sample. Collections were made in October 1968 and February and June 1969. Shell length was measured with a vernier caliper and animals were returned to the beach after each measurement. The results are shown in Figure 8.

As was shown for T. gouldi, growth rates are considerably slower during the stormy rainy season than in the dry season. Generally, the dry season on the island of Hawaii runs from the end of February until the end of October. This period is characterized by strong NE trades on the windward side of the island, and calm conditions at Kealahou on the leeward side of the island. When the rainy season begins, the winds periodically shift to the SW, generating high surf on the leeward beaches. During the stormy rainy season the average shell length changed from 74mm in October to 93mm in February, an average growth rate of 4.7mm per month. During the first part of the dry season from February to June the average length increased to 124mm, an average growth rate of 8.0mm per month.

Fig. 8. Length-frequency distribution of juvenile
H. inconstans from Kealakekua Bay, Hawaii, 20 October 1968-
18 June 1969.



It is impossible to pinpoint the time of settling by collecting newly settled juveniles, since metamorphosis occurs when the protoconch is approximately 1mm in length, and the sieve would not retain H. inconstans less than 3mm in shell length. However, the individuals collected in October with an average length of 74mm probably represent the 1968 year class, and assuming that the growth rate is 8mm per month or more throughout the summer, the young probably begin metamorphosing in late spring and continue throughout the summer. The 1969 year class only begins to appear in the June collection, when most of the newly settled individuals were under 3mm in length.

Adults reach a maximum length of 33mm, but few individuals longer than 29mm were found. If the growth rate of between 5 and 8mm per month is fairly constant throughout the life span of the species, maximum age would be between 3 and 4 years.

Predation

The effects of predation on H. inconstans are difficult to assess. Members of the crustacean family Calappidae are predators on Terebra in subtidal sand flats, as are several species of Natica. However, neither of these predators are present in surf washed areas. Few empty shells have been

found washed on the beach, and those that have been found exhibit little evidence of predation, thus indicating that predation on the adult population may be negligible.

However, there is a great decline in abundance between the first and second year classes. Two possibilities exist to explain the observed reduction of the first year class. During most of the summer and fall trade winds blow consistently from the northeast, and wave action on the leeward surf beach is slight. With a shift in wind direction during the winter months, waves increase in height and the surf may become extremely heavy, even in the usually placid bays. At this time terebrids smaller than one centimeter in length are usually unable to remain buried in the sand, and are dislodged and tend to accumulate in the litter zone, gliding back and forth over the surface of the sand with each passing wave. It is possible that as wave intensity increases, large numbers of small individuals could be carried into the surf zone and eventually cast high on the beaches.

Another possibility is that predation may act on the young. Small animals dislodged from the sand keep their foot fully extended, presenting a sharp contrast with the generally darker sand. The crustacean Portunus sanguinolentus is abundant on the beach, as is a small species of flounder, Platophys pantherius. Both of these animals frequent the

surge zone, and could quite easily prey on the small hastulas when they are exposed. Sufficient gut analyses were not done, however, to determine the feeding habits of either species.

Discussion

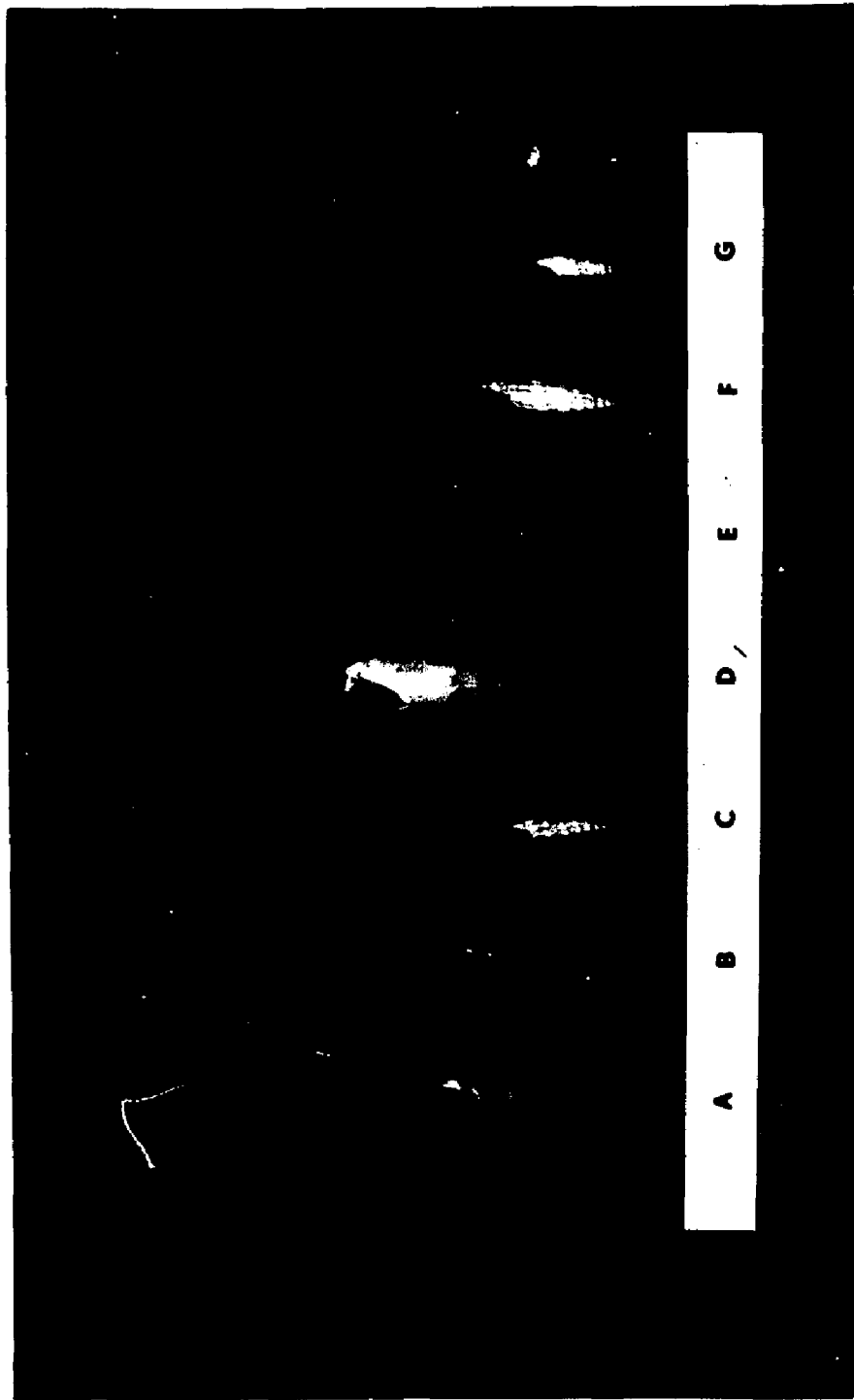
In addition to H. inconstans, I have found four other species with the Type II A polyembolic proboscis commonly living on surf washed beaches, and three living in deeper water (Fig. 9). They all have a small shining shell with few whorls and a wide aperture. All species are nearly identical in internal morphology, with a long slender buccal tube and well-developed radular apparatus.

I have only studied those species living on surf beaches in detail. They all have a broad fleshy foot, crawl and bury rapidly, and show striking similarities in the method of feeding and choice of prey. Gut analyses were performed on three surf species in addition to H. inconstans. All species feed on spionid polychaetes. Both H. hectica (Linnaeus, 1758) and H. strigilata (Linnaeus, 1758) feed on Nerinides sp., although they live in different zones of the beach. Hastula penicillata (Hinds, 1844) feeds on an unidentified spionid.

Spionids apparently are the preferred food of other

Fig. 9. Hawaiian species of Terebridae with the Type IIA polyembolic proboscis (.75X).

- A. Hastula inconstans (Hinds, 1844).
- B. Hastula strigilata (Linnaeus, 1758).
- C. Hastula penicillata (Hinds, 1844).
- D. Hastula hectica (Linnaeus, 1758).
- E. Hastula lauta (Pease, 1869).
- F. Hastula solida (Deshayes, 1857).
- G. Hastula albula (Menke, 1843).



A B C D E F G

species of Hastula as well. Marcus and Marcus (1960) found the remains of Nerinides agilis in the gut contents of H. cinerea at Ubatuba, Brazil, and Stewart (1967, personal communication) found the same species of worm in the guts of H. salleana from Florida.

Considering shell morphology alone, I suggest that Type IIA species show evidence of descent from the same ancestral type. On the basis of similarities of internal morphology and life history aspects as well, I conclude that the animals are sufficiently different to separate them from the genus Terebra, and to include them in the genus Hastula, established by Adams and Adams (1858).

Part D. Preliminary data on the biology of T. textilis
Hinds 1844 and other species with the
Type IIB polyembolic proboscis

All terebrids with the Type IIB polyembolic proboscis that I have studied are similar in morphology. Like the Type IIA hastulas, they have a functional radular apparatus consisting of a large poison bulb, a long convoluted poison gland, and a radular sac containing harpoon-like radular teeth. However, the labial tube is shorter than that of most hastulas, the labial cavity may be divided by a septum, and the buccal tube is shorter and more muscular. Shell

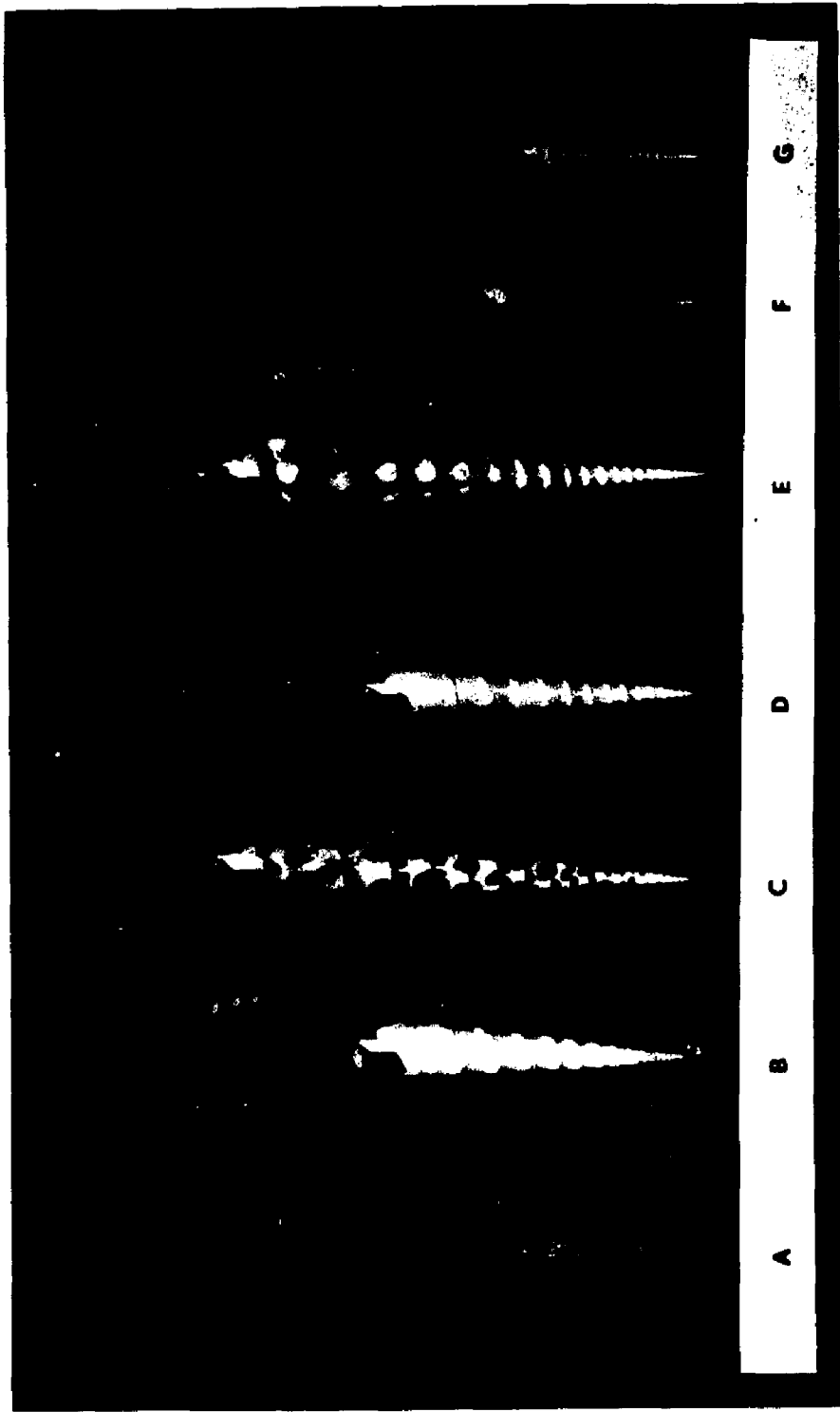
variation between the two types is significant. *Hastulas* possess a small shining shell with 7-10 whorls and a flared aperture, while Type IIB terebrids usually have a large shell which is long and slender, with 15 or more whorls and a constricted aperture. The shells of Type IIB species from Hawaii are shown in Figure 1.

Type IIB terebrids have a small slender foot, and their locomotory behavior is similar to that exhibited by *T. gouldi*. The animals bury shallowly in the sand during the day, and crawl slowly over the surface at night. They respond to water agitation by rapid retraction into the shell, and may remain quiescent for hours after removal from the sand.

Of the seven species with the Type IIB polyembolic proboscis that I have studied, *Terebra textilis* Hinds 1844 is the smallest, and is the only species present in sufficient numbers to permit a study of food and feeding. Most of the specimens were collected during the early morning hours around the Ahu O Laka study area from July 1968 to June 1969. The animals were returned to the laboratory, frozen for 24 hours, and removed from the shells. Gut analyses were done on 71 specimens, and remains of prey were found in 15 animals. Seven prey were undigested in the foregut and were all tentatively identified as the small

Fig. 1. Hawaiian species of Terebridae with the Type IIB polyembolic proboscis (1X).

- A. Terebra textilis Hinds, 1844.
- B. Terebra argus Hinds, 1844.
- C. Terebra subulata (Linnaeus, 1767).
- D. Terebra cinquifera Lamarck, 1822.
- E. Terebra guttata (Roding, 1798).
- F. Terebra babylonia Lamarck, 1822.
- G. Terebra funiculata Hinds, 1844.



red polychaete Prionospio malmgreni Claparede, 1868.

Information on feeding is sketchy. As in other terebrids, locomotion and feeding occur at night, but the animals did not feed in the laboratory and observations in the field were inconclusive. Feeding usually occurs just beneath the sand surface, so I assume that the radular apparatus is used in most instances to immobilize P. malmgreni before it retracts into its burrow. Only once did I observe T. textilis pursuing the prey, and in this instance the shell was partially buried in the sand at a 45 degree angle and the labial tube was everted into the burrow.

Mating individuals were found in the field from April through July. During mating the male was situated above the sand, with the female below and slightly to the left of the male. Probably the sexual attractant is contained in the mucus trail produced by the female. On several occasions the male was observed following the trail of a female downstream, which would indicate that distance chemoreception might not be used in mating in all terebrids, as it appears to be in T. gouldi. Nothing is known about the egg capsules, development, or growth of T. textilis or any other Type IIB species. Both Calappa hepatica and Natica marochiensis prey on adult T. textilis, but the rate of predation is not known.

On the basis of morphological similarities, Type IIB

species appear to be closely related. Until the biology of these secretive animals is understood, no further conclusions can be reached.

Part E. Preliminary ideas on the function of the
accessory feeding organ of Terebra affinis
Gray, 1843, and other terebrids with the Type III
polyembolic proboscis

Introduction

Terebrids exhibit a marked tendency toward a complete loss of radular teeth, correlated with significant changes in feeding from the usual toxoglossan method. When the radular apparatus is lacking, feeding is effected by one of two specialized methods. In species with the Type I polyembolic proboscis the prey is grasped by the anterior sphincter of the labial tube and slowly ingested. Terebrids with a shorter labial tube (Type IA) generally feed on prey living in shallow burrows; those with a long labial tube (Type IB) feed on prey in deep burrows by extending the labial tube for a considerable distance into the burrow. In both cases the prey are ingested whole, and are not immobilized by any chemical means. Terebrids with the Type III polyembolic proboscis may also utilize a labial tube in feeding,

but differ from all other species in that they possess an accessory feeding organ in the labial cavity.

Accessory feeding organs are found in a few other higher prosobranchs. Carriker (1955, 1959) has studied the accessory boring organ in muricids. In Urosalpinx cinerea, the organ normally lies withdrawn into a sac lying in pedal tissue, but when everted it swells into a large rounded projection which facilitates boring through some chemical effect on the shell. Fretter and Graham (1962) reported that an accessory organ located on the lip of some naticids may release an acid or enzyme which helps in boring. The accessory feeding organ of Type III terebrids differs significantly in structure and function from these boring organs. It has not been described in the Terebridae, nor has it been found in any other gastropod family.

I have used Terebra affinis Gray, 1843, for a detailed study of feeding in Type III polyembolic terebrids (Fig. 1A). This species is very abundant in shallow protected areas of sand and coral rubble in Hawaii and other islands in the Central Pacific. Data on food and feeding were obtained through gut and fecal analyses, and observations in the field and laboratory. The gross anatomy of the feeding apparatus was worked out through dissection of fresh specimens removed from the shell after quick freezing.

Fig. 1. Hawaiian species of Terebridae with the Type III polyembolic proboscis (1 X).

- A. Terebra affinis Gray, 1834.
- B. Terebra conspersa Hinds, 1844.
- C. Terebra flavofasciata Pilsbry, 1921.

C

B

A

Gross morphology of the foregut

The foregut of T. affinis is drawn in Figure 2 with the proboscis everted. The long labial tube is cleaved and does not terminate in a well-developed sphincter, although thick circular muscles surround the tip. The buccal tube is vestigial, and the salivary glands are lacking. A considerable part of the labial cavity is occupied by the accessory feeding organ. This organ consists of an anterior cone-shaped structure covered by concentric rows of papillae, and a long posterior stalk with muscular insertions in the body wall of the cephalic hemocoel. The fine structure of the organ is discussed in detail in section II. The cephalic hemocoel contains slender retractor muscles attached to the buccal cavity, and the thin-walled pre-and post-ganglionic esophagus.

Food and feeding

Species with the Type III polyembolic proboscis are secretive, and it has not been possible to directly observe feeding in any species. However, much can be inferred from a careful study of the morphology of the feeding apparatus, correlated with knowledge of the type of prey chosen and of the condition of the prey found in the foregut after gut analysis.

Fig. 2. Gross morphology of the anterior digestive system of T. affinis with the proboscis everted, exposed by cutting through the dorsal mantle and body wall.

1.....labial tube

1a.....labial cavity

2b.....longitudinal retractor muscles of the buccal cavity

3.....buccal cavity

7a.....cone of the accessory proboscis

7c.....stalk of the accessory proboscis

7d.....retractor muscles of the accessory proboscis

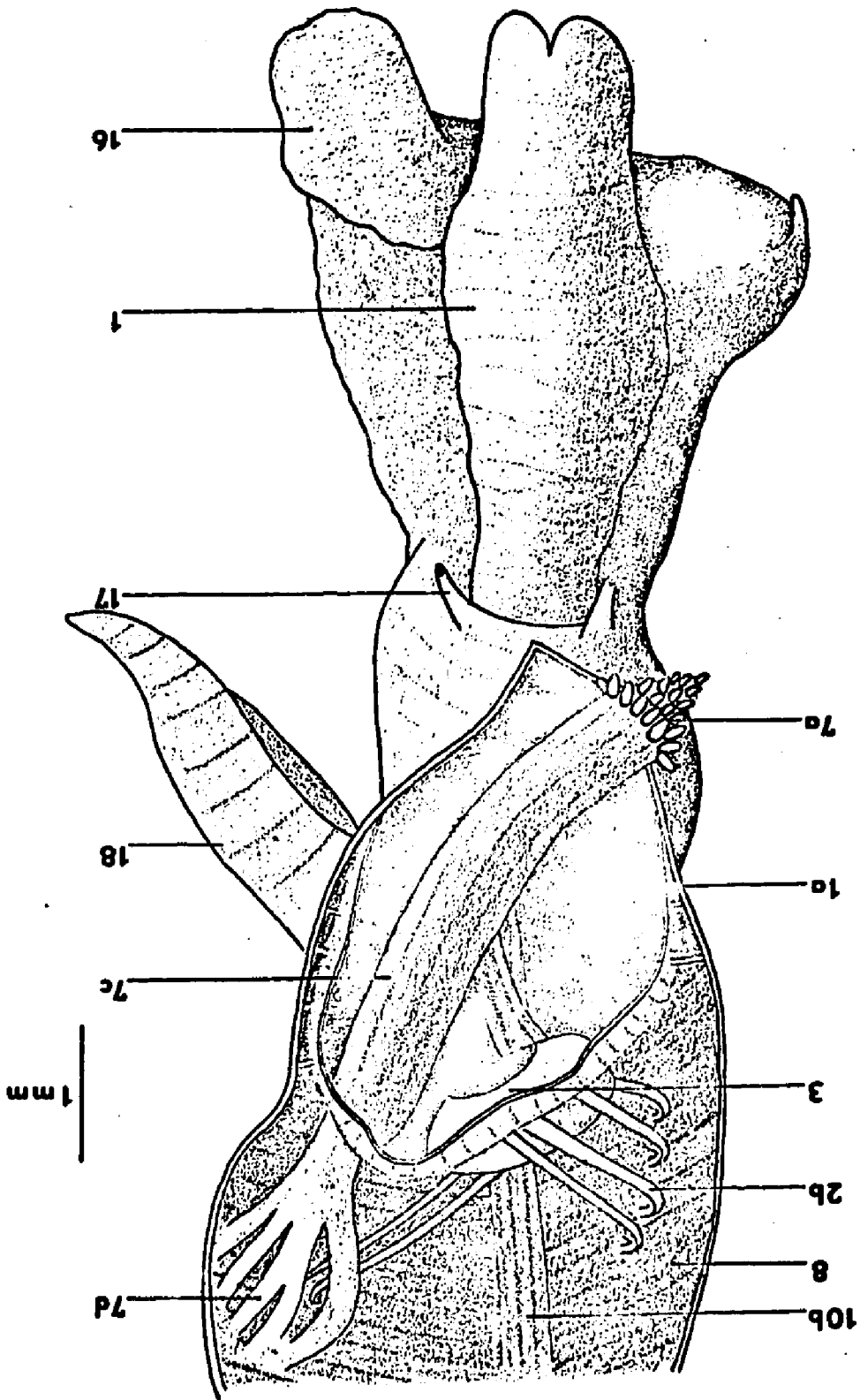
8.....cephalic hemocoel

10b....post-ganglionic esophagus

16.....foot

17.....eyestalk

18.....siphon



Gut analyses were performed on 104 T. affinis collected during the morning from a sand pocket 5 square meters in area located in the windward reef at Eniwetok Islet. Seven animals were found with freshly captured prey in the foregut, seven with prey remains in the upper intestine, and 12 with feces in the lower rectum. In species of other feeding types, the prey are undigested in the foregut and can usually be easily identified, but in T. affinis the prey in the foregut consisted of an amorphous bright red mass containing neither sand nor setae to aid in identification.

Feeding was not observed in the field or laboratory, but indirect evidence indicates the prey eaten by T. affinis. The freshly captured prey in the foregut was bright red in color, and a thorough sieving of the sand pocket through a $\frac{1}{4}$ inch mesh sieve revealed only one infaunal species of red-color. This was a small bright red cirratulid polychaete Cirriformia sp. present in densities of 200-400 individuals per square meter. This species lives shallowly buried in the sand or small holes in the coral rock, and extends a large number of long red tentacles over the surface of the substratum. As additional evidence, I have found T. affinis living in association with a cirratulid polychaete in Kaneohe Bay in Oahu and Kealakekua Bay in Hawaii, but gut analyses of 35 specimens revealed no prey in the foregut.

Assuming that Cirriformia sp. is the prey of T. affinis, how is feeding effected? As a working hypothesis based on indirect evidence, I propose the following explanation until further studies are completed. Terebra affinis emerges from the sand at night, crawls over the surface and probably contacts the cirratulid tentacles with the propodium of the foot. When feeding commences, the labial tube everts as in other terebrids, and the accessory feeding organ, swollen by hemostatic pressure, extends and passes out of the labial tube. I suggest that the accessory organ is used in one of two ways. The finger-like papillae located on the anterior cone are muscular, and extend and contract when the animal is living. It is possible that these papillae could be used to grasp the cirratulid tentacles, and the organ would then retract and transfer the tentacles to the buccal cavity. Absence of both sand and setae in the gut contents would indicate that the whole worm is not ingested. However, since no undigested remains were found in the foregut, it is probable that the organ primarily functions to produce an enzyme which partly digests the tentacles and body in situ, and then contracts to transfer the partly digested prey to the buccal cavity.

In some species (T. conspersa, T. flavofasciata) (Fig. 1 B & C) the accessory feeding organ is very small, and

could not possibly extend out of the labial tube. In this instance the organ is obviously not functional in prey capture. Feeding is probably facilitated by the labial tube alone, as in Type I terebrids, and the accessory organ is then used to assist in prey transfer from the labial tube to the buccal tube, or to provide some fluid utilized in digestion.

It is fairly certain that this type of accessory feeding organ, known only in the Type III terebrids, is utilized in a method of feeding previously undescribed for the proso-branchs. Further studies on other Type III species should clarify details of the feeding method, and will hopefully demonstrate the evolutionary relationship of Type III terebrids to the other members of the family.

SECTION IV

FACTORS EFFECTING THE DISTRIBUTION AND ABUNDANCE
OF TEREBRA GOULDI (TEREBRIDAE: GASTROPODA)
IN A HAWAIIAN SUBTIDAL SAND FLAT

Introduction

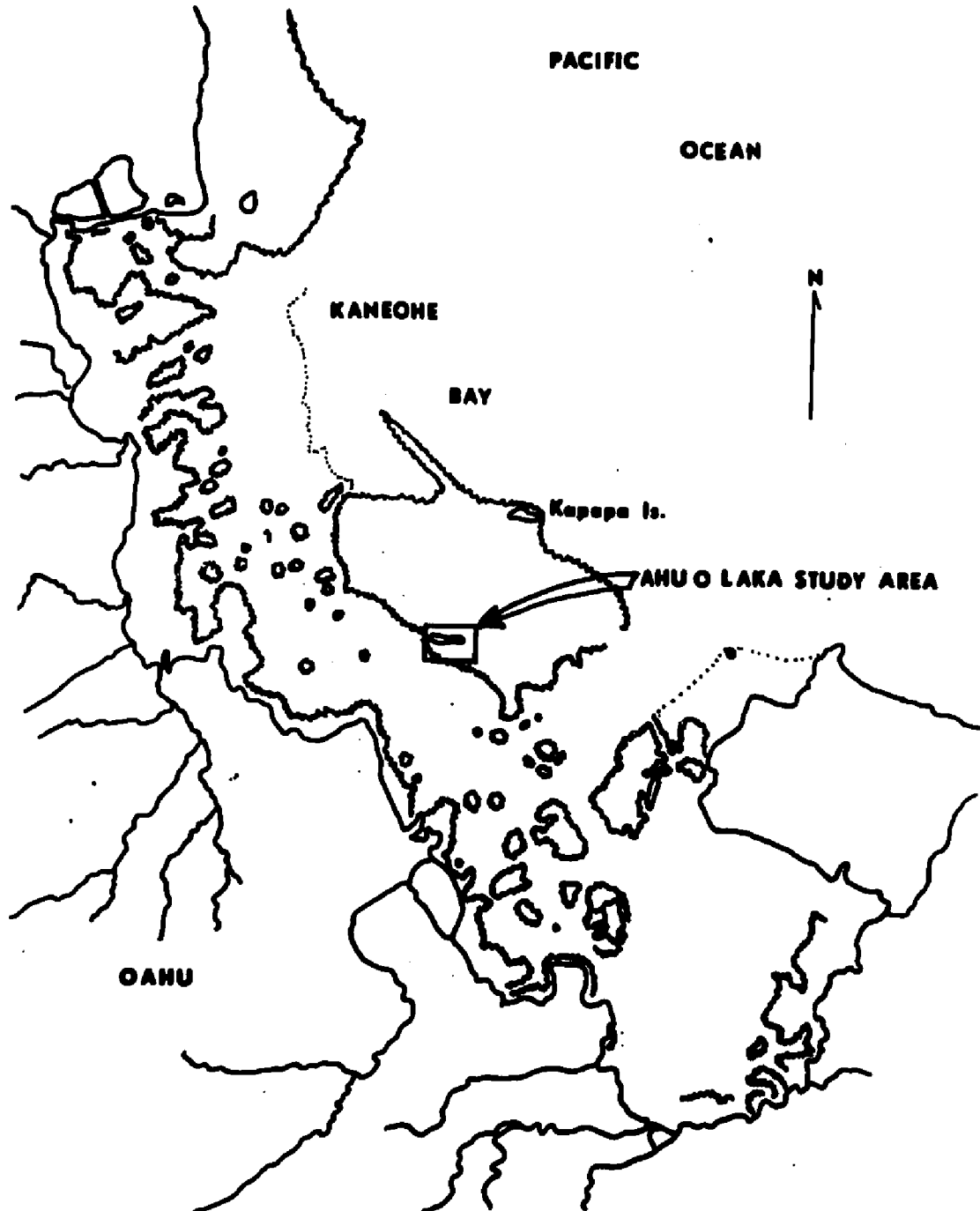
Little is known concerning the factors effecting distribution patterns of subtidal macroinfaunal species. Terebrid gastropods are important components of subtidal infaunal communities in the tropics, and as many as 20 species may be found living in close proximity to one another. The habitats are superficially uniform, but subtle environmental factors limit each species to a fairly well-defined population center. The nature of these factors in most cases is not readily determined. Because of the extensive size of most sand flats and the problems involved in sampling a subtidal habitat, the study site must necessarily be sheltered from strong waves and currents, and should be easily accessible throughout the year. Moreover, the species studied must be abundant, easily collected, and amenable to a life history study. Several terebrids are abundant in calm shallow waters around Oahu, but T. gouldi is the only species for which I have a detailed understanding

of the life history.

As shown in my work on the life history of T. gouldi, this species is a primary carnivore, preying exclusively on the enteropneust Ptychodera flava, a non-selective deposit feeder. The sexes are separate, eggs are layed in capsules attached to gravel, and there is no planktonic larval stage. Juveniles hatch through a perforation in the capsule from 30 to 40 days after development begins, and immediately burrow into the sand. Adults grow to a maximum size of seven centimeters, and appear to live for a maximum of from seven to ten years. Natural predation on adults results mainly from the sand crab Calappa hepatica and the gastropod Natica marochiensis.

I have found that the species is widely distributed throughout sandy subtidal environments in the Hawaiian Islands. Most of the populations occur in five to ten meters of water, but at several sites around Oahu T. gouldi is found in water less than one meter in depth. A concentrated population of the species is present on an extensive sand flat surrounding Ahu O Laka Island in Kaneohe Bay (Fig. 1). Ahu O Laka Island is located on the leeward edge of a shallow limestone platform extending from Kapapa Island on the windward coral reef fringing Kaneohe Bay southwestward to the deep channel in the center of the Bay.

Fig. 1. Map of Kaneohe Bay, Oahu, indicating the
Ahu O Laka Island study area.



Although the habitat is subtidal, it is readily accessible at low tide and free from strong wind and wave action.

This study is concerned with describing the distribution pattern of T. gouldi at Ahu O Laka Island, and determining those physical and biological factors influencing this distribution. The habitat, indicated by the enclosed area in Figure 1, was intensively studied for one year from June 1968 to June 1969. Observations and collections were made on an average of four times per week from June to December, and twice a week for the remainder of the study period. Data were gathered on the distribution and abundance of T. gouldi and associated macroinfauna, and on general topographical features, currents and wave action, tidal level, sediment composition, and distribution of H_2S .

General description of the habitat

Ahu O Laka Island is actually a sand bar completely covered by water at tidal heights above 0.3m and is approximately 300 meters long at LLWN (Figs. 2 & 3). It is bounded on the southwest by a channel 4-6 meters deep, while on the other sides it is surrounded by a subtidal sand flat lying in less than 0.2 meters of water at LLWN. The entire island is underlain by a limestone platform. Sand in the central area of the island is deep, covering the limestone platform

to a depth of 15-30 centimeters. This area is free from vegetation. On both sides of the island beyond this central area the depth of the sand decreases, and in some places the coral platform is exposed. To the south and east the algae Acanthophora specifera covers areas where the limestone platform extends through the sand to the surface, and where broken pieces of coral provide a stable substratum. Beyond these areas water depth increases rapidly, living coral appears, and the shelf drops steeply to a depth of 4-6 meters. To the north and west of the island, the sand continues for a short distance and is then covered by large patches of Halophila madagascariensis and several algal species. Further to the northwest the vegetation thins, and sand with coral heads predominates up to the ocean boundary of the reef.

A relatively constant current (Fig. 2) flows across the seaward reef throughout most of the year and at all stages of the tidal cycle (Bathen, 1968). The water approaches Ahu O Laka Island from the northeast, and at high tide passes in a southwest direction over the entire island. As the tide falls the island emerges, forming an effective barrier and dividing the water flow. The current on the windward side is then deflected and runs nearly parallel to the long axis of the island, while that to the leeward slows

Fig. 2. Detailed map of the Ahu O Laka study area
indicating general topographic features.

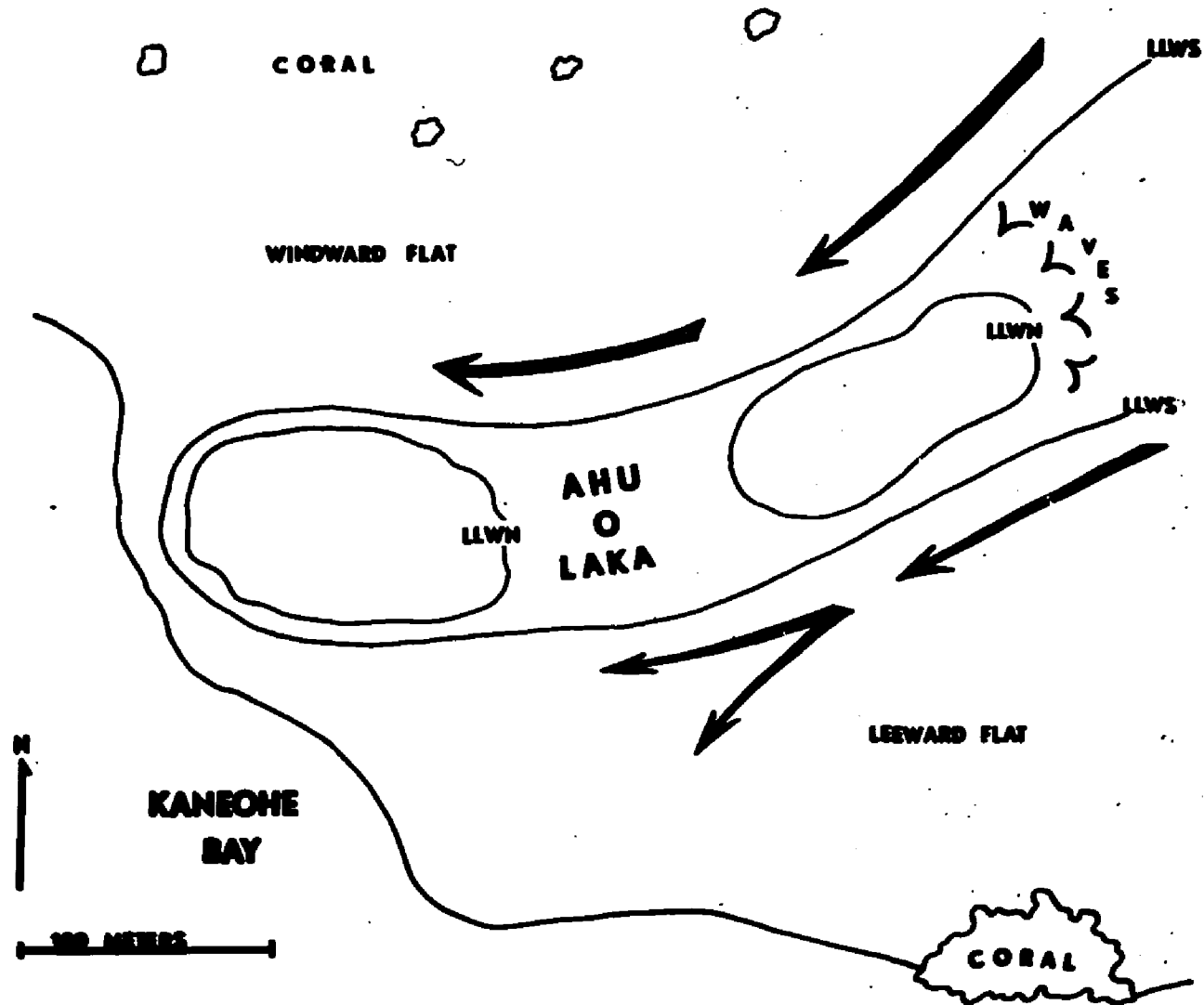


Fig. 3. The Ahu O Laka study area.

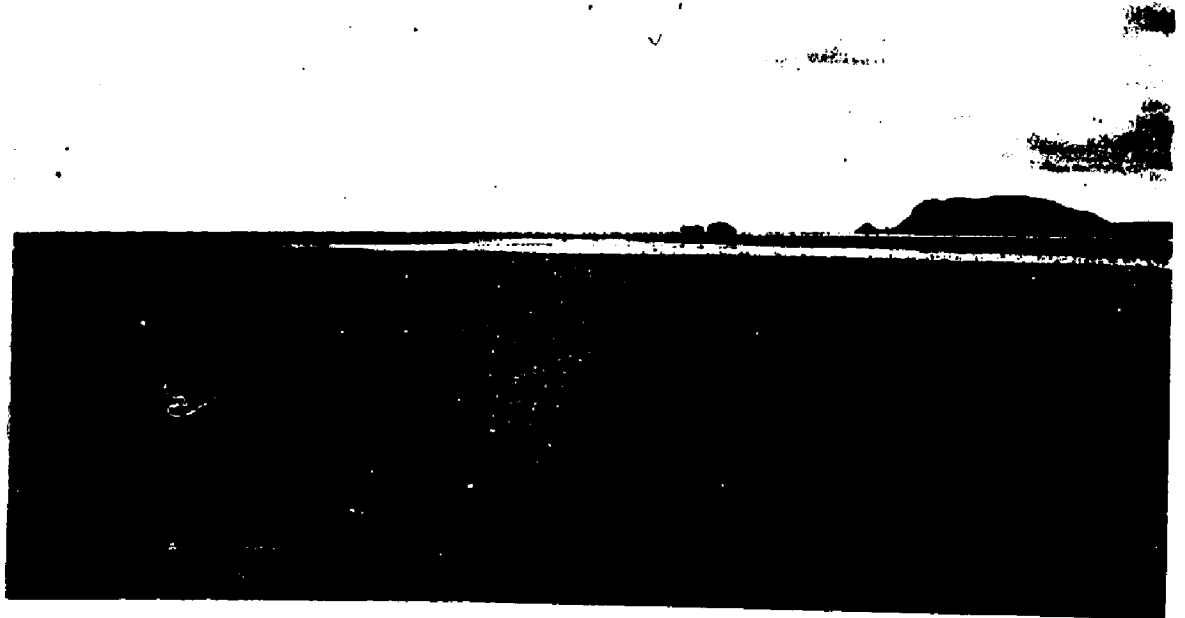
- A. View from the center of the island looking over Kaneohe Bay toward Oahu.
- B. View from the center of the island looking over the reef flat toward Kapapa Island
- C. View along the long axis of the island facing east.



A



B



C

and may become stationary at low tide.

Wave action does not appear to be significantly important at the Ahu O Laka habitat. Waves are generally small or absent during the summer months, but may reach a height of approximately 0.5 meters during the winter when large swells pass over the reef and break on the northeast shore of the island. Wave action is usually restricted to this portion of the reef flat, but small waves generated by local southwest winds or passing boats impinge on the shore around most of the island.

Biotic Factors

Methods .

The sampling design was set up to determine the distribution and abundance of T. gouldi and associated macroinfauna. Six transects were run perpendicular to the long axis of Ahu O Laka Island at 70 meter intervals across the entire sand flat, and samples were taken every ten meters along each transect line. A rectangular frame 33 x 50 centimeters on a side and 15 centimeters deep was forced into the sand to a depth of 10 centimeters. The sand was then removed and sieved through a screen two millimeters in mesh size. Living animals were identified, and their

densities recorded.

Terebra gouldi.

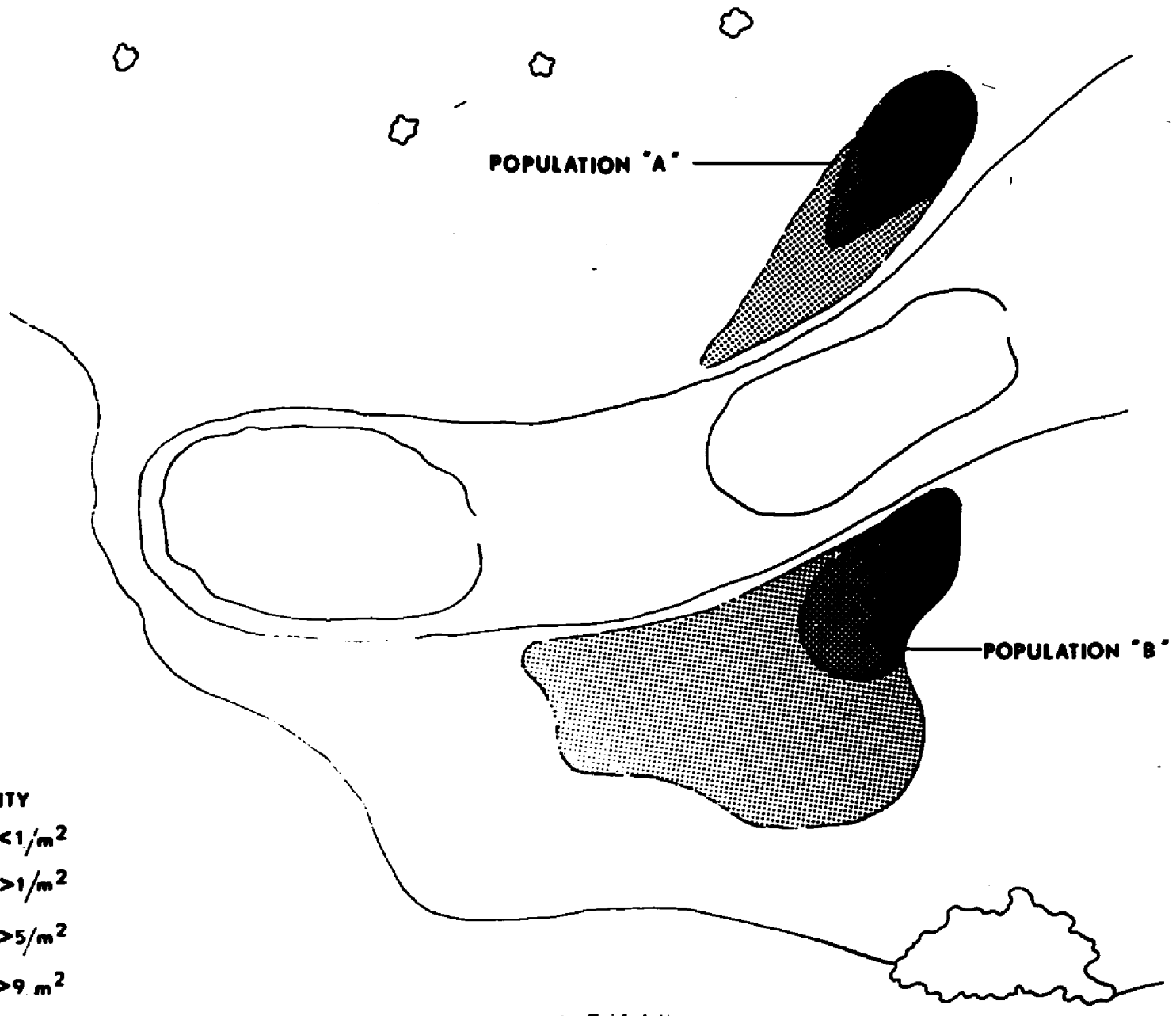
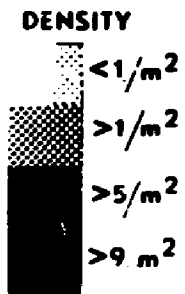
Terebra gouldi was not distributed around the entire Ahu O Laka sand habitat. Two distinct populations were identified, one located to the windward and one to the leeward of the island, inciated in Figure 4 as Populations A and B. Population A occupied an area of approximately 3000 square meters, while Population B occupied more than twice that area.

The animals in each population were not uniformly distributed but were concentrated in two relatively small epicenters where densities as high as 12 animals per square meter were recorded. Densities decreased with increasing distance from the epicenters, and were as low as 0.1 specimens per square meter around the periphery of each population. The average density for the species over the entire expanse of both areas was approximately one individual per square meter.

Associated macroinfauna.

The macroinfaunal community around Ahu O Laka Island contains over 40 species of animals which spend part or all of their lives buried in the sand. The most abundant species

Fig. 4. The distribution and abundance of Terebra
gouldi around Ahu O Laka Island.



are listed in Table 1. Molluscs form the largest component of the community in number of species. There are 15 gastropods, 14 of them predatory, and three pelecypods. At least six species of polychaetes are present in abundance. Most of the polychaetes are sedentary, and are primarily detritus feeders. With the exception of two predatory crustaceans and a flounder, the remainder of the species are particulate feeders. Observations in the field and laboratory indicate that three of the infaunal species directly affect the existence of T. gouldi.

Predators .

Natural predators appear to be of minor importance to adult T. gouldi (See Section III). The sand crab Calappa hepatica is occasionally successful in cracking the lip of a Terebra shell sufficiently to eat the animal, and Natica marochiensis successfully bores into the shell to feed. However, rates of predation appear to be low, and since both of the predators are distributed throughout the Ahu O Laka habitat, they would appear to have little effect on terebrid distribution. Nothing is known concerning predation of the egg capsules or juveniles. It is probable, however, that juveniles are ingested along with the sand by Ptychodera flava and other deposit feeders. Human predation

Table I. Maximum densities of common macroinfaunal species
at the Ahu O Laka Island (Maximum number/square meter)

| | |
|----------------------------------|----------|
| Coelenterata | |
| <u>Cerianthus</u> sp. | 35 |
| <u>Edwardsia</u> sp. | colonial |
| <u>Marcanthea</u> sp. | 8 |
| Annelida | |
| <u>Chaetopterus</u> sp. A | 2400 |
| <u>Chaetopterus</u> sp. B | 600 |
| <u>Chaetopterus</u> sp. C | 120 |
| <u>Cirratulus</u> sp. | 15 |
| <u>Dispio magna</u> | 33 |
| <u>Prinospio malmergrini</u> | 200 |
| Sipunculida | |
| sipunculid species | 50 |
| Mollusca | |
| <u>Natica marochiensis</u> | 1 |
| <u>Otopleura mitralis</u> | 2 |
| <u>Pyrimidella sulcata</u> | 1 |
| <u>Terebra affinis</u> | 1 |
| <u>Terebra crenulata</u> | 2 |
| <u>Terebra gouldi</u> | 15 |
| <u>Terebra textilis</u> | 14 |
| <u>Ctena bella</u> | 12 |
| <u>Macoma dispar</u> | 7 |
| <u>Pinquitellina robusta</u> | 30 |
| Crustacea | |
| <u>Calappa hepatica</u> | 5 |
| <u>Callianassa</u> sp. | 4 |
| <u>Emerita pacifica</u> | 5 |
| <u>Portunus sanguinolenta</u> | 3 |
| Holothuria | |
| <u>Chirodota rigida</u> | 160 |
| <u>Holothuria</u> sp. | 40 |
| Hemichordata | |
| <u>Ptychodera flava</u> | 150 |
| Cephalochordata | |
| <u>Epigonichthys maldivensis</u> | 2 |

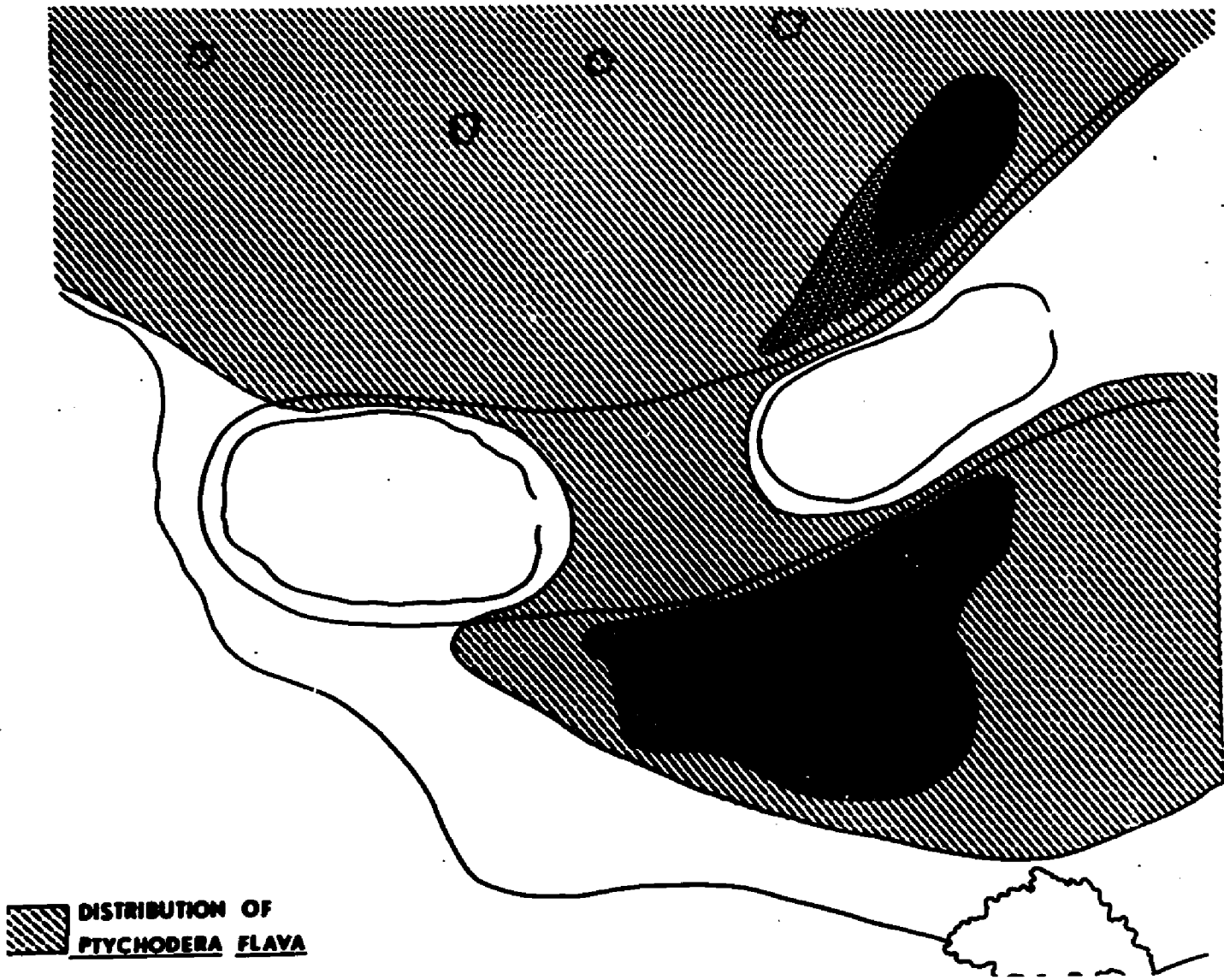
may be the primary cause of adult mortality, since large numbers of terebrids are collected by skin divers during the summer months. The effect of this collecting upon distribution and abundance, while probably significant, is difficult to evaluate.

Prey.

Since T. gouldi feeds exclusively on P. flava, it is reasonable to assume that there might be a correlation between the presence of the predator and the presence of the prey. Ptychodera flava is distributed over an extensive portion of the reef flat (Fig. 5). The species is rarely found above LLWN, but is abundant in the lower intertidal and subtidal zones where it is one of the most abundant deposit feeders in the sand community. Densities of 200 to 300 animals per square meter were common, and most stations sampled within the area occupied by P. flava contained a minimum of 25 individuals per square meter during the year. Some of the areas of lowest density were located around the population centers of T. gouldi.

As would be expected, T. gouldi is found only within the area occupied by its prey. However, large areas of the habitat where P. flava was common contained no T. gouldi, and in these areas factors other than prey availability

Fig. 5. The distribution of Ptychodera flava
around Ahu O Laka Island.



 DISTRIBUTION OF
PTYCHODERA FLAVA

must be examined to determine their importance in restricting distribution.

Physical factors

Substratum .

Many infaunal burrowers have a narrow tolerance of substratum variation. (Crocker, 1967; Southward, 1965; Wade, 1968). Since T. gouldi lies buried in the substratum during the day and crawls over the surface in the evening, the nature of the substratum might be an important limiting factor in determining the distribution of the species.

Three parameters of the substratum were investigated; 1) sediment particle size, 2) general nature of the terrain, such as sediment depth, consolidation, and presence of algae or coral rocks, and 3) presence of H_2S .

Sediment Particle Size.

Sediment samples were taken at each sampling station by forcing a metal cylinder three centimeters in diameter into the sediment to a maximum depth of seven centimeters, since preliminary observations indicated that T. gouldi and most associated macroinfauna were restricted to this depth. Samples were brought to the laboratory, washed, placed in a drying tray, and dried in an oven at 150° for 24 hours.

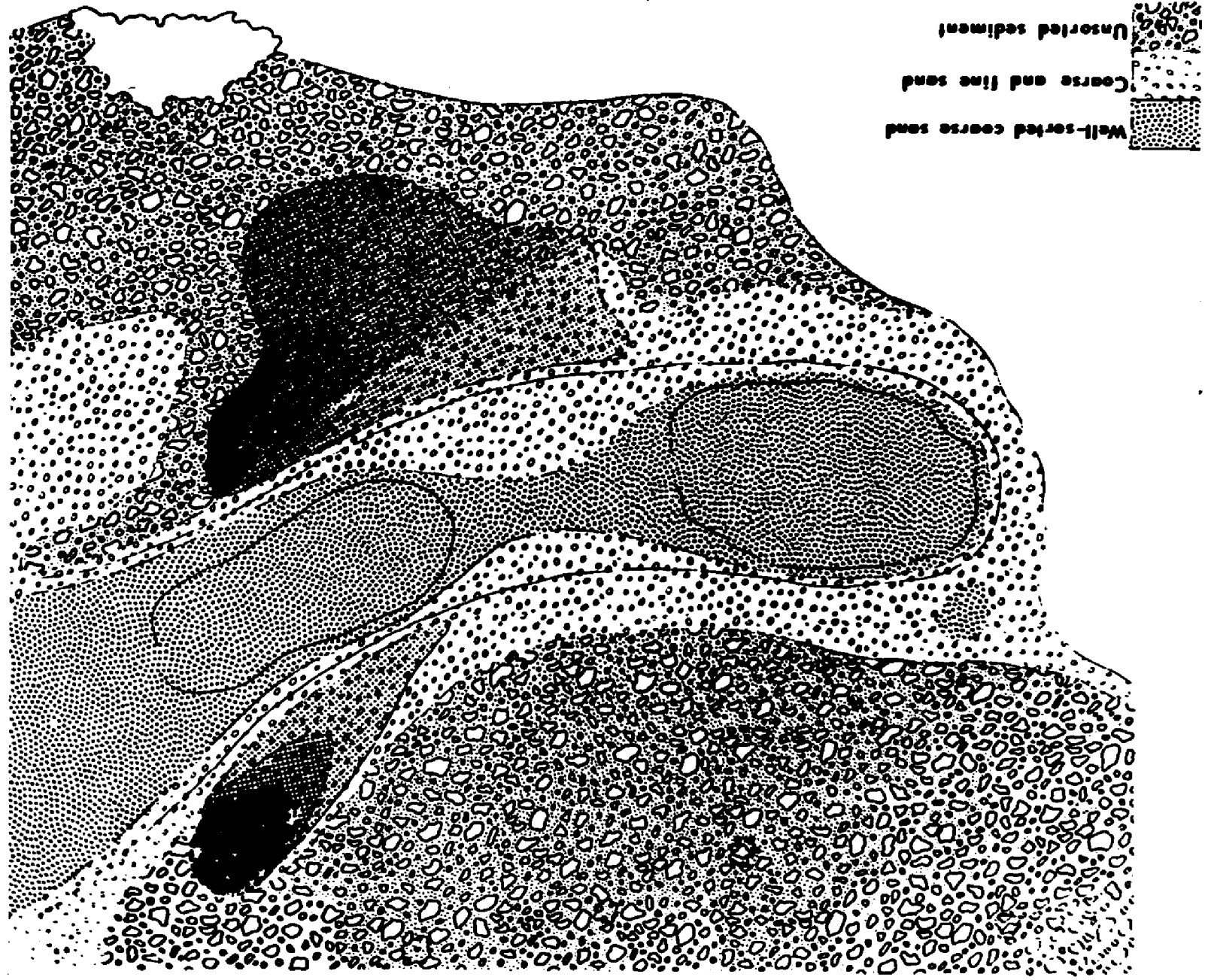
The sediment was then dry-sieved through a standard Wentworth sieve series (3.96, 2.0, 1.0, 0.5, 0.25, 0.125mm). Each fraction was weighed and the percent composition was determined. One hundred and twelve sand samples were collected and analysed.

In contrast to most Hawaiian inshore areas, the substratum at Ahu O Laka Island is mainly derived from marine organisms, and is composed primarily of calcium carbonate. Large amounts of sand and gravel in the form of broken coral, coralline algae, and shells are carried into the habitat from the reef edge during periods of strong northwest swells. In addition, a considerable portion of the sediment is composed of empty shells of common sand dwelling bivalves and gastropods, foraminiferans, and several species of crustaceans.

The nature of the sediment at any one location probably depends on local waves and current patterns. Most of the sediment is relatively unsorted, as would be expected in an area of limited wave action, but the degree of sorting increases rapidly as one enters the intertidal zone. My analysis indicated three characteristic substratum types (Fig. 6).

Intertidal areas of the reef flat are washed by small waves every day, and the fine sand and silt component is

Fig. 6. Sediment distribution at Ahu O Laka Island.



reduced or absent. The sediment is consequently well-sorted ($S_o=1.4$) with a median particle size of 1.0 millimeters. This coarse sand usually comprises 40 to 50% of the total by weight.

Subtidal areas immediately surrounding the island also have a median sand diameter of 1.0 millimeter, but in addition there is a considerable amount of fine and very fine sand that is not present intertidally, usually comprising 20-30% of the total by weight.

To the leeward of the island and in the dense vegetation mat to the windward, the substratum is rarely affected by wave action, and the sediment is unsorted ($S_o=2.9$). There is a fairly uniform distribution of particle size from gravel through fine sand and silt, and no component accounts for more than 20% of the total composition by weight. This substratum is generally very soft, and contains variable amounts of broken shells derived from sand-dwelling molluscs.

There is no evidence from Ahu O Laka Island to indicate any preference by T. gouldi for sand particle size or degree of sorting. Population A is found in partly sorted substratum that is composed primarily of coarse sand and gravel, while Population B is primarily found in unsorted sand with a high percentage of fine sand and silt. In both instances the sediment is unconsolidated. Collections of the species

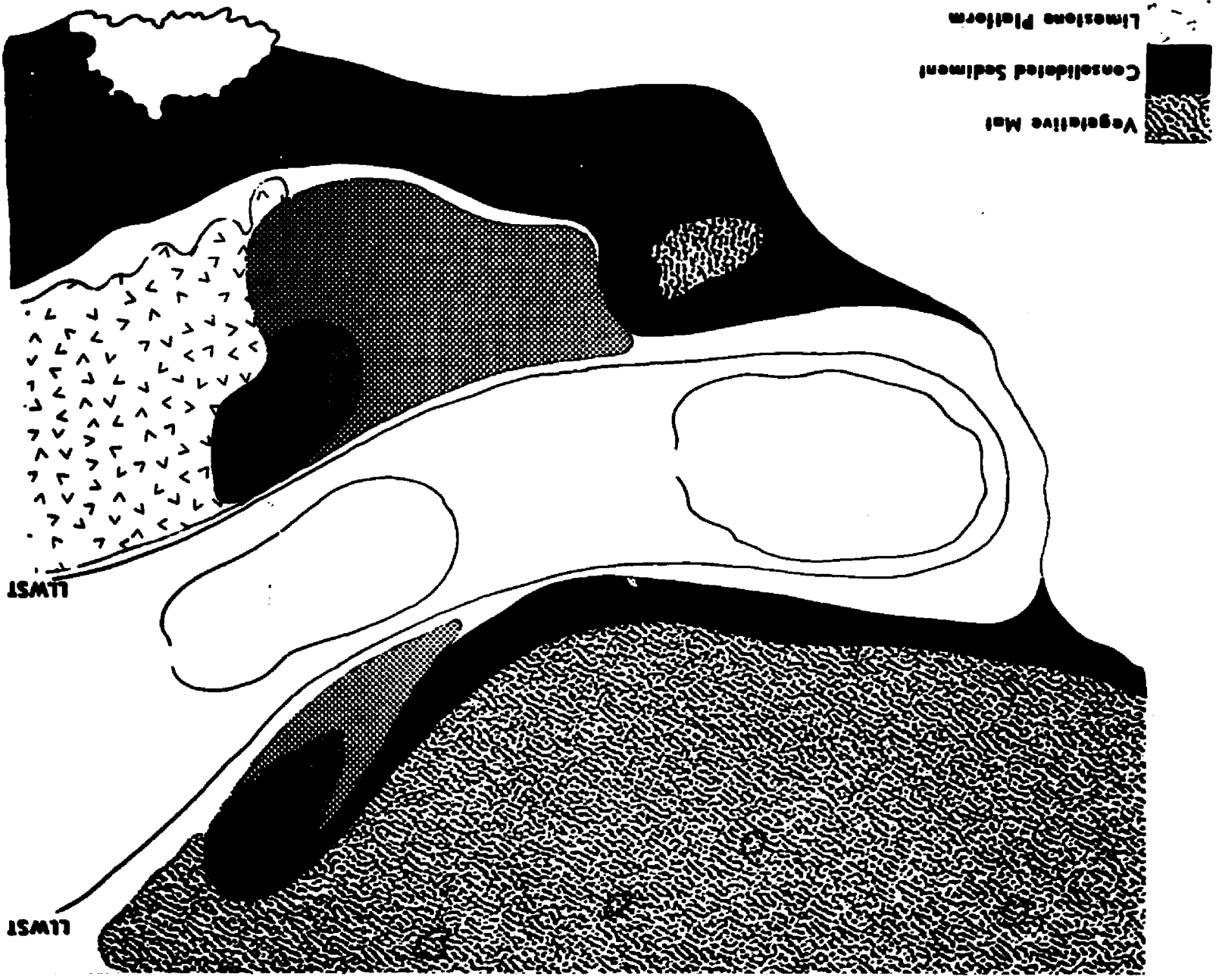
from other subtidal habitats around Oahu likewise indicate that large populations are found in a wide spectrum of substratum types. For example, at Wailupe on leeward Oahu the animals are found in a well-sorted coarse sand, and at Punaluu on the windward shore in well-sorted fine sand.

Terrain.

Although the particle size and degree of sorting of the sediment are not significant in effecting distribution patterns of T. gouldi, other attributes of the substratum are important. Prey availability does not necessarily indicate prey utilization, and large areas of the Ahu O Laka habitat containing prey in high abundance are unsuitable for habitation by T. gouldi through substratum limitations influencing locomotion and feeding. These areas contain substrata of three general types (Fig. 7).

An extensive vegetative mat extends from the windward side of Ahu O Laka Island northward toward the reef edge, with a small patch near the southwest portion of the island. The predominant species, Halophila madagascariensis is a halophyte with small leaves forming a dense cover over the substratum, and slender roots binding the fine sediment into a mat 3-4 centimeters thick. The alga Acanthophora specifera is commonly attached to Halophyla, as well as to coral and

Fig. 7. Distribution of substratum types at Ahu O
Laka Island.



Limestone Platform
Consolidated Sediment
Vegetative Mat

LSM17

LSM17

shells.

Two large areas of hard, consolidated sand stretch along both the windward and leeward sides of the island. Here the sand is very firm, contains few infaunal species, and is not overturned during stormy periods when less consolidated sand is shifted, causing ripple marks.

Several areas characterized by the presence of an exposed limestone platform with small pockets of sand and gravel are found on both sides of the island. The limestone generally supports a dense growth of Acanthophora specifera.

Terebra gouldi was not found in any of these habitat types, even though Ptychodera was abundant, and it appears that the subtidal limits of distribution are determined by these features of the substratum. To test the behavior of T. gouldi in these habitats, on two successive days 10 individuals were placed during daylight hours on each of the 3 substratum types, as well as on a control area in the animals' normal sand habitat. Observations were made each hour for 3 hours to determine the behavior of the animals. Results are shown in Table 2.

In the normal habitat, the usual daytime response to removal from the sand is rapid reburrowing. Sixteen of the 20 animals crawled over the sand surface for a short distance and were completely buried within 10 minutes. All of the

Table II. Reburrowing success of T. gouldi on different substrata

| Substratum type | No. | No. animals completely buried | | | |
|---------------------|-----|-------------------------------|---------------|---------------|-------|
| | | After 1 hour | After 2 hours | After 3 hours | Total |
| | 20 | | | | |
| Unconsolidated sand | 20 | 20 | - | - | 20 |
| Vegetative mat | 20 | 0 | 0 | 5 | 5 |
| Consolidated sand | 20 | 0 | 1 | 1 | 2 |
| Coral Platform | 20 | 0 | 0 | 0 | 0 |

animals were buried after one hour.

The vegetative mat does not present a barrier to burrowing forms such as Ptychodera, but T. gouldi is prevented from crawling on the surface by the leaves of Halophila, and from burrowing by the dense network of roots. Seven of the animals were partially successful in reburrowing after 2 hours, but none of the shells were fully covered. After 3 hours, only 5 animals were completely buried, and those animals that did not burrow showed limited locomotion. The species probably avoids this type of substratum completely, as do other Indo-Pacific terebrids (Miller, 1966).

Terebra gouldi is capable of locomotion over hard consolidated sand, but burrowing into this substratum is restricted. After 3 hours only 2 of the animals were partly buried. Probably few individuals in Population B enter these areas, for they are far from the population epicenter, and those in Population A that do presumably continue crawling until a substratum suitable for burying is located.

Burrowing is not possible in the area occupied by limestone platform, and locomotion is hindered by the attached Acanthophora. Although Ptychodera is present in the sand pockets, T. gouldi does not crawl into these areas, presumably for the same reasons it avoids the vegetative mat.

It is therefore apparent that the area suitable for

habitation by T. gouldi is small in relation to the total size of the sand habitat around Ahu O Laka Island, and that the nature of the substratum is important in limiting the dispersal of the population subtidally. In an unconsolidated sand environment T. gouldi can crawl on the surface of the sand and rapidly burrow. These activities are both necessary for successful feeding. In the area surrounding the observed population centers, feeding is limited either by the inability of the animals to crawl over the surface of the substratum in search for prey, or to burrow into the substratum to capture prey when it is located.

H₂S.

Initially a Hach Chemical Kit was used to determine the presence of H₂S, but it was soon apparent that suitable results could be obtained by visually observing the depths of the black reducing layer in the otherwise white carbonate sand. H₂S is found just below the surface in the consolidated sand patches on both sides of the island, in the windward vegetative mat, and around the extreme west end of the island where sand and detritus carried off the Ahu O Laka flat are continually deposited.

It is difficult to evaluate the effect of H₂S on the distribution of T. gouldi. The species is not found in

areas around Ahu O Laka where the black reducing layer is at or near the surface, but absence from these areas can also be explained by the absence of Ptychodera or by the presence of substratum unsuitable for feeding or locomotion.

Tidal levels.

Terebra gouldi was not found above LLWS at Ahu O Laka, although P. flava is abundant in the lower intertidal (Fig. 5), and there is no evidence to indicate that sediment differences or physical barriers are effective in preventing upward dispersal of the animals (Figs. 6 & 7).

Species of Terebra have not been collected intertidally in any sand habitat that I have studied throughout the Central Pacific, and they in general appear to avoid habitats subject to periodic reduction in salinity or continual wave action. None of the more than 40 species of terebrids living around the Hawaiian Islands have been found in brackish water, and I have found that T. gouldi and several other species will usually select sea water in preference to slightly brackish water in a choice test. It is therefore probable that one important factor prohibiting the distribution of T. gouldi into intertidal areas is the reduced salinity during heavy rains. This reduction in salinity is especially significant in Kaneohe Bay at low tides

during severe storms of the winter rainy season (Banner, 1968). In addition, T. gouldi responds to water agitation in the laboratory by rapid retraction into the shell, and the animals are probably adversely affected by small waves which constantly impinge on the island in the intertidal areas.

Intrapopulation distribution

The factors already discussed are important in preventing the dispersal of T. gouldi into intertidal areas, and in limiting distribution in the subtidal to two well-defined population centers. Within each of these populations, the individuals are not uniformly spaced, but the densities are highest immediately down-current from the locomotory barriers, as shown in Figure 4, and they progressively diminish in the down-current direction. I propose two explanations to explain these observed density gradients.

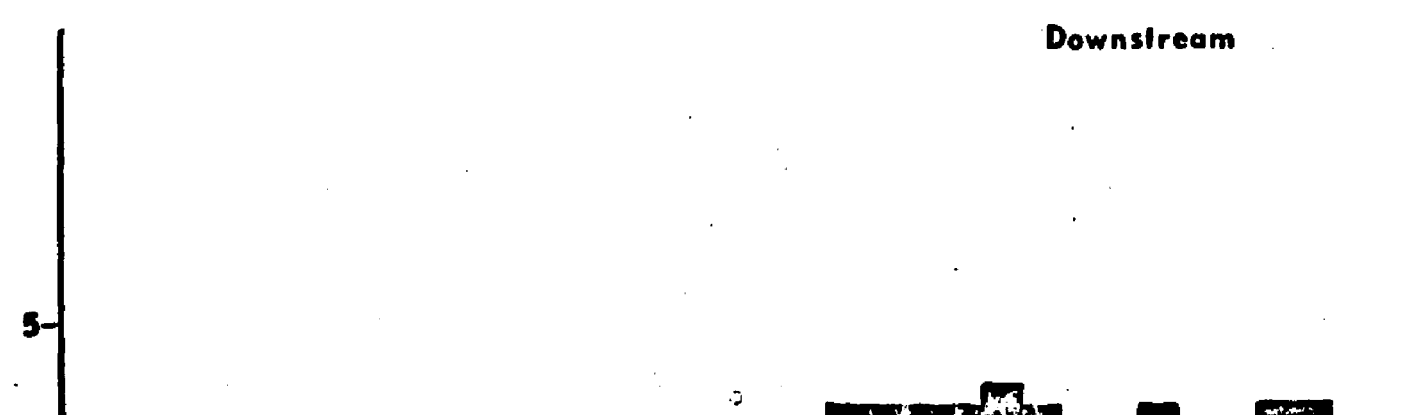
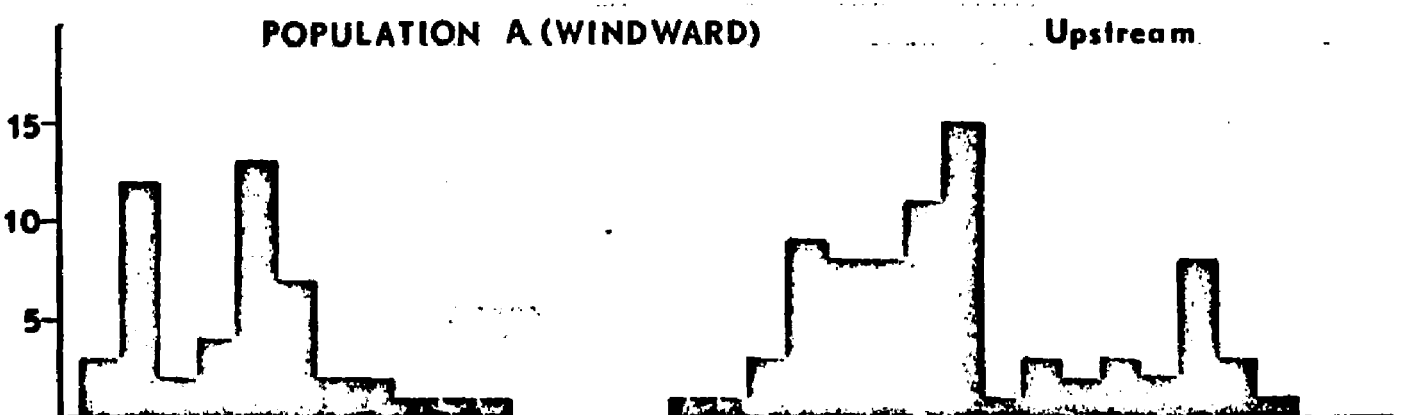
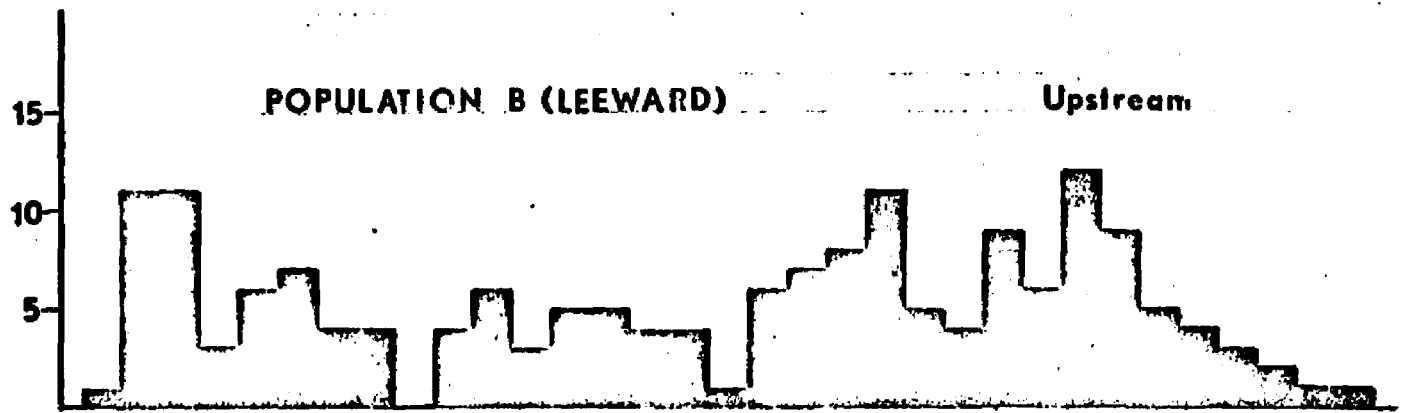
As discussed under the life history of T. gouldi, observations in the field and laboratory indicate that prey are initially detected through distance chemoreception by following some exocrine substance, possibly iodoform, released upstream by a prey specimen. It could be expected that T. gouldi would tend to move upstream into the prevailing

northeast current until they reached unsuitable conditions. This hypothesis is supported by the fact that the density of adult T. gouldi is up to three times greater in the upstream segment of each population than in the downstream segment.

Feeding considerations alone are not sufficient, however, to explain the high concentration of individuals in the upstream area. An examination of the size-frequency histograms from the high-density upstream segment of each population, and size-frequency histograms for the remainder of each population is instructive (Fig. 8). The most striking feature is the complete absence of young Terebra in the low density area, and the presence of a complete size distribution in the high density epicenters. I believe this distribution is based on several factors. As has been shown earlier, sexual encounters appear to depend on two separate responses. The male is probably initially attracted to the female by distance chemoreception and follows some yet undescribed sexual attractant upstream. When contact is made with the mucous trail produced by the female as she crawls along the sand surface, the male follows the trail until the female is overtaken, and mating commences. Since there are more sexually mature individuals in the high-density areas due to their aggregation upcurrent in search

Fig. 8. Length-frequency distribution of T. gouldi from the upstream and downstream portions of each population.

NUMBER



SHELL LENGTH (mm.)

of prey, sexual encounters would be more frequent. Egg capsule deposition takes place in the vicinity of mating, and since development occurs in the capsule and there is no planktonic veliger stage, the juveniles would hatch at the site of capsule deposition and immediately burrow into the substratum. In these areas the sand is soft, prey is abundant, and currents and wave action are negligible. Successful growth of the young should then be possible. As the animals mature they would tend to disperse somewhat from their original settlement area. With periodic reversals in the direction of current flow during extended periods of southwest winds in the winter months, the animals would gradually move away from the density centers, until the remainder of the habitat suitable for colonization was eventually occupied. Both of these explanations are probably important for determining the observed intrapopulation distribution of the species.

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