

THE ECOLOGY OF THE ROCK-BORING CLAM

Penitella penita (Conrad 1837)

by

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A THESIS

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and the Graduate School of the University of Oregon
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Evans, John W., and David C. Fisher. 1966. A new species of Penitella from Coos Bay, Oregon. The Veliger, 8 (4): 222-224

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An Abstract of the Thesis of

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Title: The Ecology of the Rock-Boring Clam Penitella penita

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Penitella penita is a rock-boring clam found along the Pacific coast of North America.

The clams were sampled in substrates of differing hardness. Some experimental work on growth rate was done by planting animals in artificial burrows but in natural sites, in both their native and other rock types.

Observations made by Turner (1954-1955) on the effect of rock hardness on valve morphology were confirmed and extended.

Burrow shape appears controlled by a number of factors: erosion, substrate hardness, crowding and others.

Estimates of growth rates were arrived at by a number of methods, including valve size analysis of young animals from rocks exposed for a known length of time, analysis of size increase of animals replanted for an 11-1/2 month period. When the duration of time between deposition of successive growth bands was estimated, growth rate could also be estimated by analysis of growth band counts.

The growth rate of animals transplanted to softer than native rock was unexpectedly high whereas, in the converse case, growth rate was lower than normal. This suggests the possible existence of ecotypes in this species.

INTRODUCTION

The group of animals which live buried in hard marine substrates is known as the endolithic community (Kühnelt 1951). Rock-boring bivalves are primarily responsible for initiating and maintaining the community because they excavate most of the burrows into which the other members will move after the borers' death. In areas where no rock-borers exist, this community is necessarily absent.

Yonge (1963) states that seven groups of bivalves have independently taken to rock-boring. Hiatella (Saxicava) (Hunter 1940), Tridacna (Yonge 1936), Botula and Lithophaga (Yonge 1955) are all attached, at least initially, by byssus threads. Yonge (1955) claims that in these animals the habit of boring was preceded by that of nestling. The animals attach themselves in crevices which they may enlarge by movements of the valves.

Petricola (Duval 1963a and Yonge 1958), Platydon cancellatus (Yonge 1951) and the family Pholadidae have, according to Yonge (1961), evolved from forms that were originally deep burrowers in soft substrates. The pholads are the most efficient rock-borers in that they can penetrate rock far harder than can the other mechanical borers. They are also the most highly modified morphologically.

Most of the literature on marine borers before 1954 was compiled and annotated by Clapp and Kenk (1963). Most of their extensive volume (1136 pp.) is devoted to the economically

important wood-borers, notably the shipworms, Teredinidae, and the wood-boring isopod Limnoria. Studies on rock-boring clams of the family Pholadidae have been mainly concerned with their morphology, taxonomy and methods of boring. Very little detailed work has been done on the ecology of these animals.

The most extensive work to date on the Pholadidae is by Turner (1954, 1955); she discussed the morphology, systematics, distribution and ecology of members of this family that occur in the western Atlantic and eastern Pacific. Gomoiu and Müller (1962) studied in detail a benthic association dominated by Barnea candida in the Black Sea. Numbers and biomass measurements of 56 species were made and the roles of the more important members were discussed. Duval (1963) described some of the ecological conditions that control the distribution of Petricola pholadiformis, and other aspects of its natural history.

Penitella penita (Conrad 1837), often incorrectly referred to in the literature as Pholadidea penita, is the most common and best known of the pholads in the eastern Pacific (Turner 1955). The geographical distribution of P. penita, according to Turner (1955), is from Bering Island, Siberia, south as far as Bahia San Bartolome, Baja California. Ricketts and Calvin (3rd ed., p.232) place the southern end of the range at Ecuador.

The vertical distribution of P. penita is also broad. In the area of Coos Bay, Oregon, it is found as high as + 3 feet in the intertidal zone and extends down into the subtidal zone. Kofoid (1927) reported that Pholadidea penita (Penitella penita)

were dredged in rocks at a depth of 50 fathoms in San Francisco Bay.

Another factor influencing distribution is the presence of a suitable substrate, i.e., rock of suitable hardness and homogeneous texture. According to Lloyd (1897) P. penita does poorly in clay, preferring shale and sandstone of the open coast. Granites, conglomerates, and other very hard rocks are not bored.

During the summer of 1962 a preliminary examination was made of rocks heavily bored by P. penita. Observations on the effects of crowding posed a number of problems about the ecology and behavior of the animal. What kind of sensory mechanism enables it to avoid breaking into neighboring burrows? What is the effect of crowding on succession and subsequent settlement in the area?

Correlations between valve size and burrow length indicated that the surface rock was being eroded at a rate fast enough to affect the life span of the individual animal. This raised two questions. What is the rate of erosion in the area, and what is the relative importance of physical and biological causes of erosion?

As research progressed, the scope of the study came to include the following topics: (1) an analysis of the factors controlling valve and burrow morphology; (2) an analysis of growth and burrowing rates in rocks of different hardness; (3) a description of the sexual cycle, larval life and settlement; and (4) a discussion of the general ecology of the endolithic community.

MATERIALS AND METHODS

The tools required to carry out this work were on the whole very simple. Much of the field work involved quarrying pholad-infested rock with a sledge-hammer and cold chisels. The rocks or specimens were then removed to the laboratory where more careful dissection could be done. Most measurements were made with a vernier caliper.

The following measurements were made on the valves. (1) "Length" was measured from the tip of the beak to the most posterior point of the valve, not including the siphonoplax or callum. (2) "Depth" was measured as a straight line from the dorsal to the ventral extremities of the umbonal ventral sulcus. (3) "Growth band" counts were made by drawing a line from the umbone down the ventral sulcus on the outside surface of the shell, this line was divided into 1 cm-long sections, and the number of growth bands were counted between each mark, starting from the umbone. In most cases part of the umbonal reflection had to be removed, because it obscured the dorsal part of the sulcus.

In order to assess the effect of rock hardness on valve and burrow morphology it was necessary to determine the hardness of rock samples from the three areas. A method was devised which would measure relative hardness. A drill press was set at low speed, about 575 rpm. The drill had a constant downward thrust of 15 lbs maintained by a pulley and weight arrangement attached to the vertical feed lever. A constant drilling time of 2 seconds

was obtained with the aid of a photographic timer; the actual time was slightly longer since the drill slowed down and stopped while the pressure was still on. A 1/4-inch "Cyclotwist" tungsten carbide masonry bit was used to drill the holes.

The shape of the burrow of P. penita was studied by casting a plastic mold of its cavity. The base of the burrow was opened and the enclosed clam removed, measured, and preserved. The burrow was then cleaned, and the entrance opening blocked with wax. Liquid casting resin was then poured into the open base of the burrow. When the resin had hardened the rock was broken away from the plastic. From the mold the following measurements were taken: (1) total length, (2) minimum diameter (the diameter at the entrance of the burrow), (3) maximum diameter, (4) effective length (measured from minimum diameter to maximum diameter), (5) diameter halfway between maximum and minimum diameter (Fig. 15).

The sexual cycle of P. penita was studied over a 2-year period. The visceral masses of 295 adult and 90 actively boring animals were fixed in either Gilson's or F.A.A. fixative. The sections were stained in buffered azure eosin stain.

During the first half of August 1962, the edge of the lower bench at Fossil Point (see Study Areas) was cleared of pholad-infested rock by splitting off the superficial 15 to 30 cm of rock. An area 50 ft long and about 2 ft deep was cleared at the 0-ft tide level.

The purpose of this was threefold: to establish the period of the year during which settlement takes place, to examine factors affecting settling density, and to follow the growth rate of P. penita.

To establish the season at which maximum settling takes place, freshly exposed rock was collected at bi-monthly intervals from August 1963 to June 1964, from August to November 1964, and from June to August 1965. The surface area of the rock sample was estimated and then all pholads that could be located were extracted and measured.

The growth rate was studied by collecting samples of rock exposed for progressively longer periods of time. Samples of rock originally exposed on August 10, 1963 were collected 2-1/2, 4-1/2, 6-1/2, 8, 10, 12, 16, and 21 months later. The surface area was estimated, all animals were measured, and where possible, separated according to species.

Because of the large number of young animals processed, and because length could be measured much more quickly and accurately than depth, length measurements were used primarily in these studies. Because of the small deviation of the length to depth ratio at any particular size, it appears to make little difference which parameter is used in measuring active animals.

Data on factors affecting settling density were collected incidentally to the growth rate study. Density was related to the condition and orientation of the rock surface.

Growth rate and behavior of individual animals were studied by the replant method. Active animals were removed from the rock, their length and depth were measured and they were replaced in cylindrical holes of known diameter and length. The entrance of the hole was plugged with a polyethylene collar (Fig. 1). The size of the entrance could be set at 3, 6, 12, or 18 mm in diameter. The animals were collected about 11-1/2 months later, and the growth rate was analyzed.

FIGURE 1

Penitella penita in South Jetty rock. Replanted August 9, 1964; collected July 13, 1965. Dot indicates valve size when planted.

Note - Rock was split to make the burrow visible, the polyethylene plug has been cut to show 6 mm entrance. The straight sided burrow was drilled by a star drill. Rounded base was enlarged by the clam.



A method for growing P. penita in unconfined conditions was also devised. Young active P. penita were suspended inside test tubes by mono-filament lines which extended from the polyethylene plugs to the sides of the valves. These test tubes were in turn sunk into holes in the rock at Fossil Point and the animals were left to grow.

Standard statistical procedures were used for the most part. Procedures involving analysis of variance and covariance were used extensively.

STUDY AREAS AND SUBSTRATES

Penitella penita was collected at approximately zero tide level from three areas on the Oregon Coast: the north side of Cape Blanco, the south side of South Jetty at Coos Bay, Oregon (Fig. 2), at Fossil Point in Coos Bay (Fig. 3). [Fossil Point is misplaced 1/4 mile to the N.E. on the Empire, Oregon Topographic Sheet, 1944. Because of this, the writer has inadvertently referred to this misplaced area as Fossil Point. Some residents call the writer's area "Pigeon Point."] The first two sites are protected outer coast areas, whereas the latter area is in a bay protected from surf action.

Penitella penita was the only pholad found at South Jetty and Cape Blanco. At Fossil Point on the other hand Penitella gabbi, Zirfaea pilsbryi, and Penitella turnerae (Evans, Fisher 1966) are found quite commonly. Together, these three species make up about 10 per cent of the living pholads in the lower bench at Fossil Point. Another species, Nettastomella rostrata is found, but only rarely.

At Fossil Point, which was the principal work area, there are two flat intertidal benches. The horizontal surface of the upper bench is 5 to 6 ft above datum level. The western edge of the upper bench, adjoins the lower bench, the surface of which is between the + 1- and 0-ft level. Further north and west the edge of the lower bench drops off rapidly to the sandy bottom. Most of the work was done on the steep edges of these two benches.

South Jetty is a jetty protecting the mouth of Coos Bay. It extends in a westerly direction about a half mile into the sea from Coos Head.

FIGURE 2

South Jetty (oblique view)

Arrow indicates approximate position of rocks where
animals were collected and replanted.

Approximate scale 10 m to 1 cm.

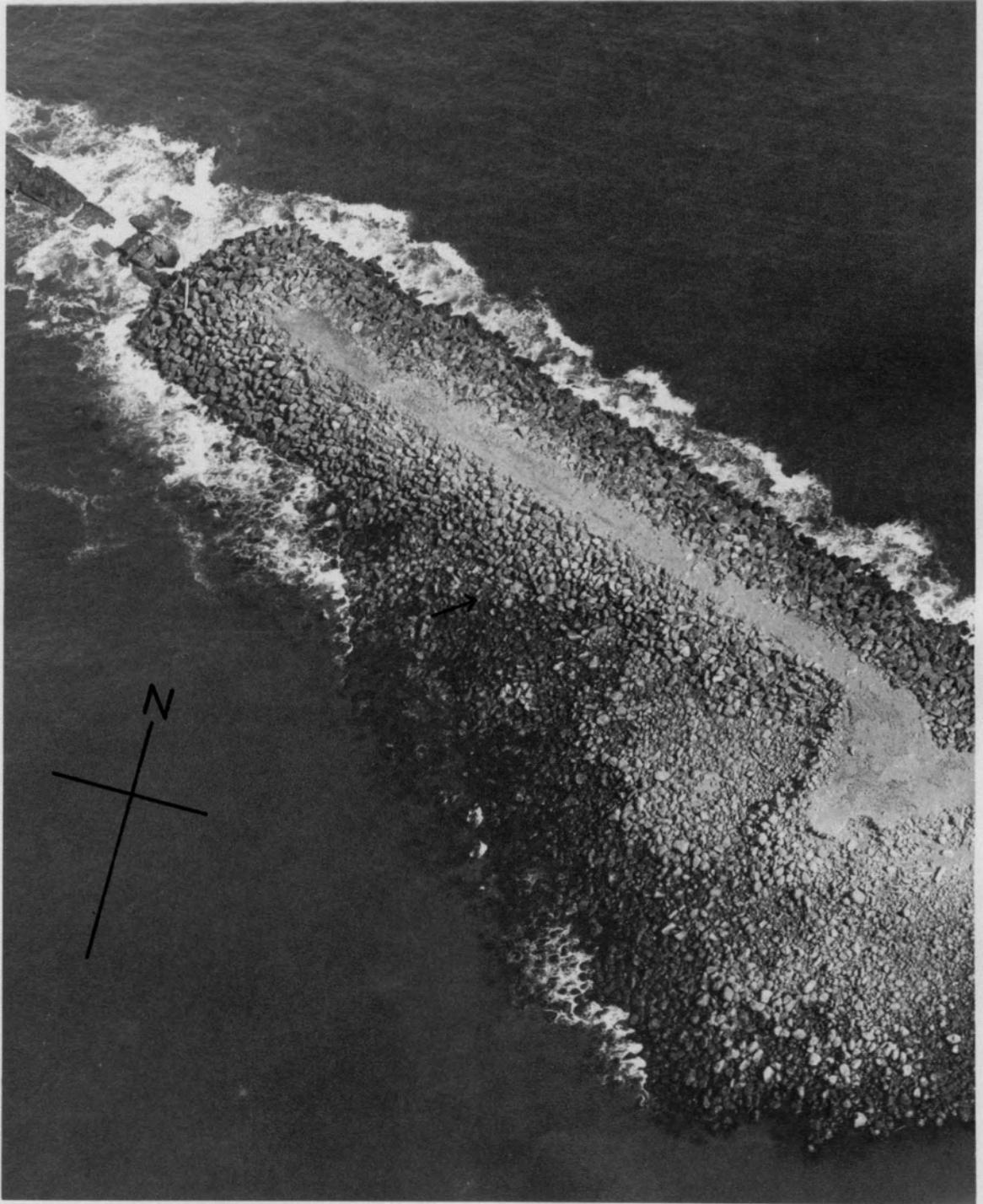


FIGURE 3

Fossil Point

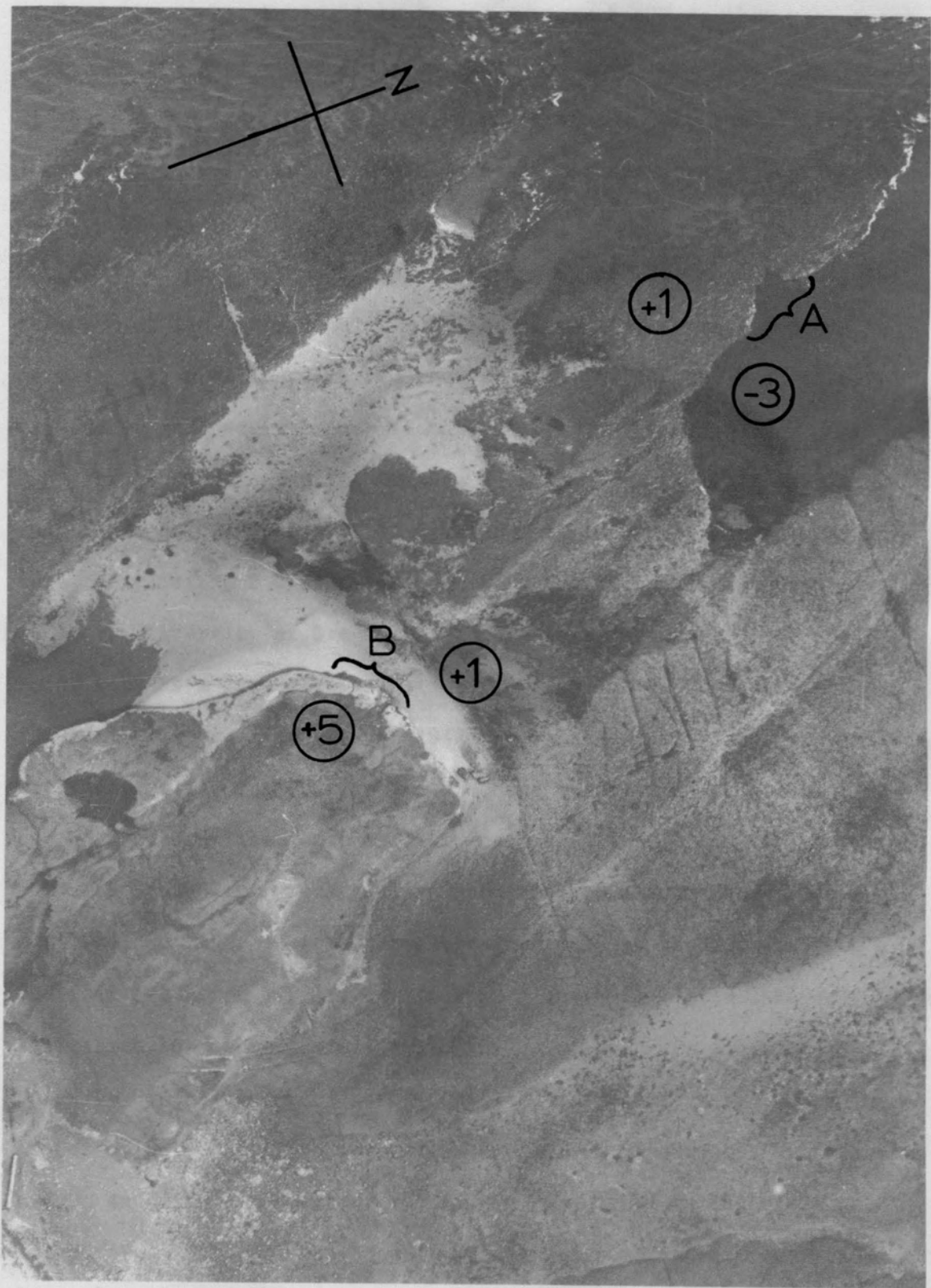
A - Part of lower bench used for settlement,
growth rate and replant studies.

B - Part of Upper Bench used for replant study.

① - Height of surface in intertidal in feet.

Scale 6.8 m to 1 cm.

The jetty has been repaired several times. The position of the



has taken place. There is a hard, rocky rock

The jetty has been rebuilt several times. The population of clams studied there were boring into Tyee sandstone boulders that were transported to the area about 40 years ago. How long they have been exposed at their present level could not be ascertained. The animals from this location were collected from a moderately exposed area at about 0-ft level.

Cape Blanco, the westernmost promontory of the Oregon coast, was the site of the third population. The clams there were found boring into very hard sedimentary bed rock at about 0-ft tide level in very exposed to moderately exposed conditions.

The rocks of these three areas were examined as whole specimens and thin sections by Dr. L. R. Kittleman of the Museum of Natural History, University of Oregon, and Dr. B. B. Van Diver of the Department of Geology, University of Oregon. All three are sandstone. The Fossil Point rock is a graywacke sandstone from the Empire Formation, of early to middle Pliocene age (Weaver 1942). It is very soft and fine-grained, with an argillaceous (clayey) matrix, there is little or no chlorite and no recrystallization or silicification.

The South Jetty rock is Tyee Sandstone of middle Eocene Age (Baldwin 1964, p. 25). It is a coarse-grained arkosic sandstone with a moderate amount of argillaceous matrix. There is little chlorite and no silicification or recrystallization.

The Cape Blanco rock is of Jurassic or Cretaceous age according to Dott (1962). It is a metagraywacke. Grain size ranges from fine to medium in different parts of the rock. The matrix is chloritic and silicified. The rock has been brecciated and recemented, recrystallization has taken place. This is a hard, brittle rock.

The grains of these rocks are mostly quartz, chert, and feldspar, which have a hardness on the Mohs scale of between 6 and 7. Since pholads apparently bore solely by a rasping mechanical action, their aragonite teeth, with a hardness of about 3.5, could not be expected to wear down the particles themselves but rather to dislodge them from the softer matrix. Ease of boring depends not on the mineral hardness of the particles but on friability, that is the firmness with which the particles are held together by the matrix; this will be called hardness in this paper.

Geologists apparently have developed no standard methods for measuring the hardness of sedimentary rocks. Several investigators working with other rock borers have improvised methods for measuring relative rock hardness. Kofoid (1927) mentions a crushing method of testing the quality of cement bored by P. penita. Hunter (1949) measured the hardness of rocks bored by two species of Hiatella by grinding them on a lapidary wheel (Comparative ease of abrasion=volume of rock abraded/unit time). Duval (1963) developed a method for measuring hardness of the soft rocks bored by Petricola pholadiformis which involved the repeated and uniform scraping of a weighted steel bar across the rock sample and measuring the depth of the groove after a certain number of abrasions.

In this study the relative hardness was determined by measuring the depth of holes drilled under conditions of constant time and force. The results are tabulated in Table 1.

TABLE 1

Hardness of rocks.

	No. of holes	Average depth (mm)	SE (mm)	Derived hardness scale	Adjusted hardness scale
Fossil Point	15	12.1	0.4	1	1
South Jetty	15	7.2	0.5	1.7	2
Cape Blanco	15	3.2	0.3	3.8	4

A hardness scale was established from the results of the drilling experiments. The Fossil Point rock was assigned a hardness of 1. The scale consists of a ratio: depth of penetration for Fossil Point rock to depth of penetration in other rock. South Jetty rock has a derived hardness of 1.7 and Cape Blanco rock a hardness of 3.8.

The test overestimates the hardness of the softest rock because as the hole depth increases the drilling efficiency decreases from interference by the powdered rock around the drill. This becomes especially noticeable in holes deeper than 10 mm. For this reason, and for simplicity, the hardness scale has been adjusted, making South Jetty rock twice as hard, and Cape Blanco rock four times as hard as Fossil Point rock.

The Cape Blanco rock apparently owes its hardness to the chloritic and siliceous matrix which binds the particles firmly together. The reason the South Jetty sandstone is harder than Fossil Point rock is not obvious from its lithology.

ORIENTATION AND LITERATURE REVIEW

This chapter is designed to serve as an introduction to the specialized morphology, behavior and general ecology of the group.

Morphology

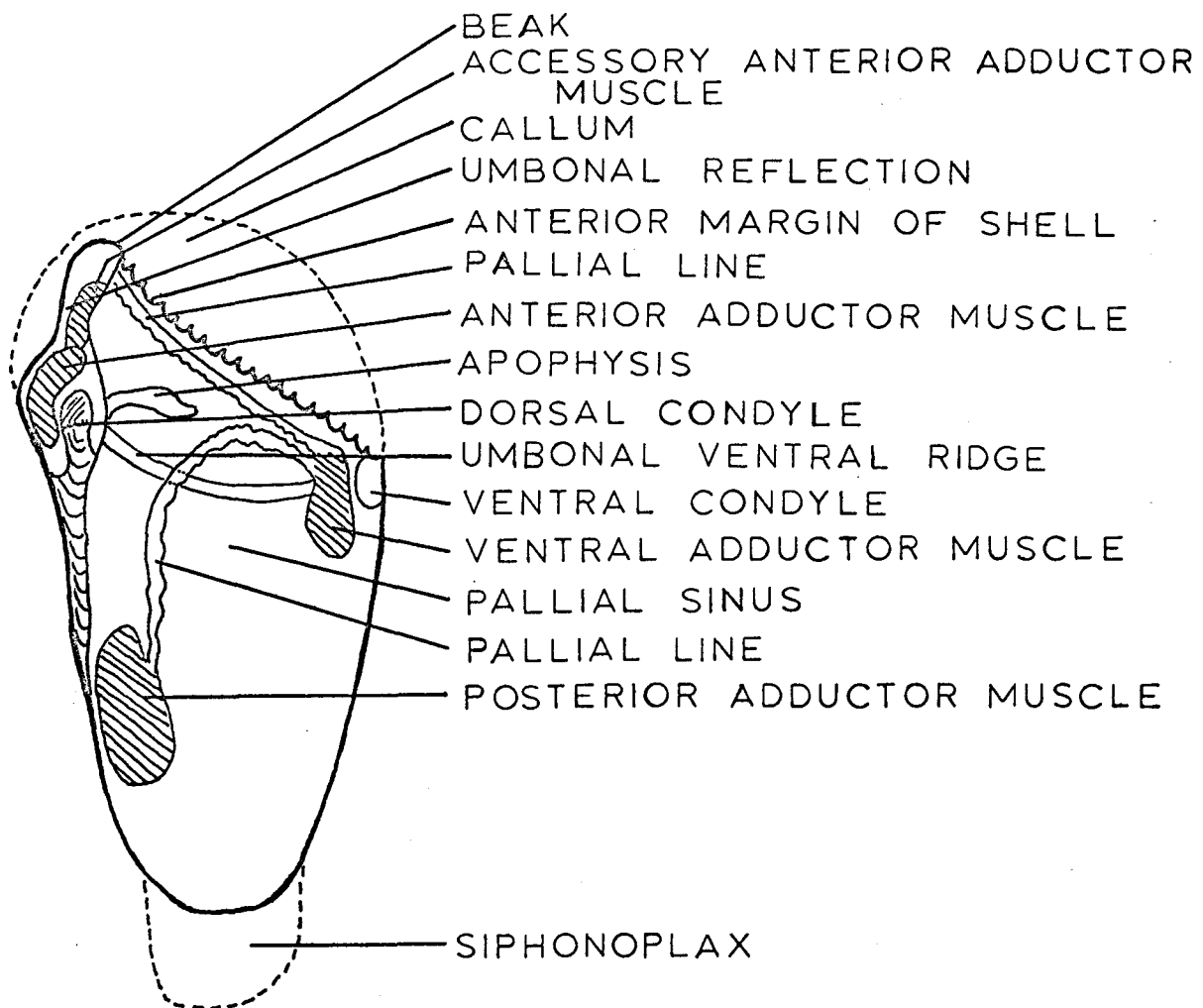
The morphology of the Pholadidae has been treated many times in the scientific literature. Turner (1954, 1955) has described in detail the morphology of western Atlantic and eastern Pacific pholads. Purchon (1955) described the functional morphology of several of the British Pholadidae.

Certain modifications of the basic bivalve plan adapt pholads to the rock boring habit. These modifications are especially well-developed in those pholads like Penitella penita that are able to bore into hard rock (Lloyd 1897, Purchon 1955).

The most significant modification is the elimination of the ligament and the rearrangement of the adductor muscles (Fig 4). In most other bivalves, contraction of the adductor muscles serves only to close the valves upon each other. This movement is opposed by the elasticity of the ligament or resilium which serves to open the valves when the adductors relax. In pholads the ligament has been wholly eliminated in those species adapted for boring in hard substrate and is only a vestigial structure in others (Purchon 1955). Comparatively complicated movements of the valves are controlled solely by muscular activity. There are two antagonistic muscle pairs: the posterior adductor opposes the accessory anterior adductor with the dorsal and ventral condyles acting as fulcra, the

FIGURE 4

Diagrammatic drawing of interior of left valve of Penitella penita. Dotted structures present only in nonbearing adult.



anterior adductor opposes the ventral adductor with the dorsal condyle acting as the fulcrum. The anterior adductor muscle is able to open the valves because it has moved to an external position. The mantle, which extends dorsally between the anterior part of the two valves and out over the outside, lays down a layer of nacreous shell upon which the anterior adductors insert. This flap of shell is the "umbonal reflection."

The foot is large, cylindrical and quite muscular. The principal point of insertion of the foot muscle is on the apophysis, a special rib-like extension of the valve which curves down under the umbo (Fig 5). The foot extends anteriorly and ventrally through a large pedal gape, and adheres to the rounded base of the burrow with a suction grip. On the anterior ventral edge of the valves, sharp, toothlike projections are deposited periodically, a new set with each period of shell deposition. These rasp the bottom of the burrow and are the main boring tool. The foot serves to push or pull the animal a short distance up and down the burrow, and also to rotate it. MacGinitie (1935) observed the boring movements of Zirfaea by placing them in test tubes or jars of clay in the laboratory. He observed that the rasping teeth are pressed against the burrow during the down stroke. This action is accomplished by contraction of two large muscles, the anterior adductor which spreads the ventral edge of the valves and the posterior adductor which spreads the beaks (Fig 5 upper). During the upward movement the valve edges are removed from contact with the sides of the burrow by contraction of the small accessory anterior adductor and the small ventral adductor (Fig 5 lower). Ross (1859) made essentially the same observations on the boring activity of Pholas.

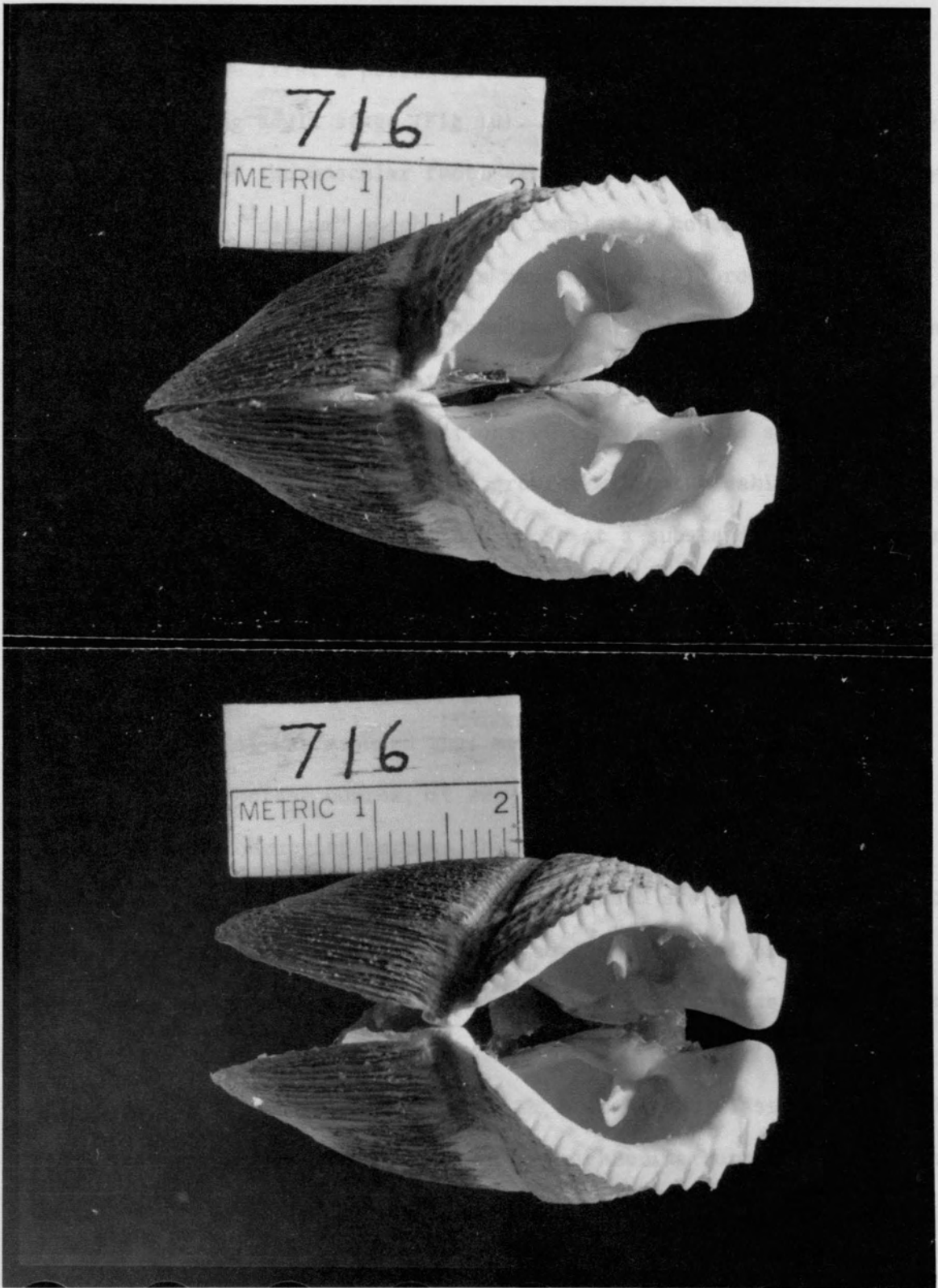
FIGURE 5

Upper

Ventral view of valves showing position when
posterior adductor muscle is contracted.

Lower

Ventral view of valves showing position when
accessory anterior adductor muscle is contracted.



716
METRIC 1 2

716
METRIC 1 2

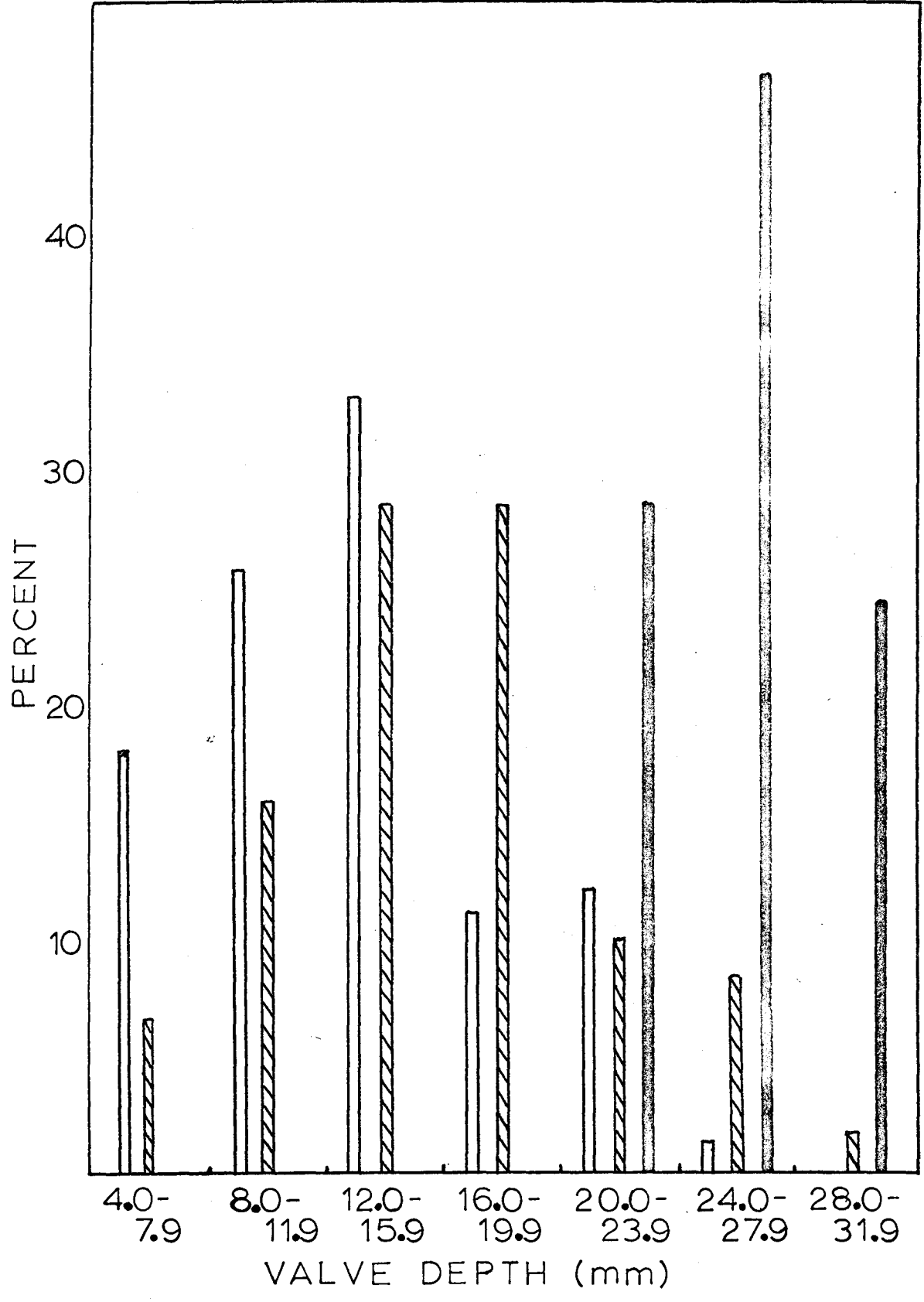
The life cycle of P. penita after settlement is divided into two distinct stages: first a period of active boring (Fig 5, 12) followed by the non-boring adult stage (Fig 10). The metamorphosis involves (1) the resorption of the muscular foot, (2) the deposition of an accessory shell plate, the "callum" which almost completely covers the anterior gape and the dorsal extension of the mantle, and (3) production of a pair of chitinous flaps, the "siphonoplax", on the posterior ends of the valves. Animals which reach mature size and metamorphose spontaneously are called "adults". Under conditions of crowding it is sometimes impossible for the animal to continue growing without breaking into neighboring burrows; these animals metamorphose at a substandard size and are known as "stenomorphs" (Bartsch 1923).

Two criteria were used to differentiate adult clams from stenomorphs. If the base of the burrow of a metamorphosed animal was within 1 mm of another burrow, it was assumed that metamorphosis was induced by the proximity of the other burrow, it was therefore classified as a stenomorph. Animals occupying burrows the bases of which are further than 1 mm from other burrows, and which have metamorphosed are assumed to have done so spontaneously and are classified as adults. A total of 180 animals from Fossil Point were classified in this way and the size distribution of actives, stenomorphs and adults were plotted on a percentage basis (Fig 6). The largest stenomorphs should probably be classified as adults since the proximity of their burrows to neighboring burrows may be coincidental.

FIGURE 6

Size distribution of Penitella penita from old undisturbed rock at Fossil Point.

- Active
- ▨ Stenomorph
- Adult



If only the valves are available for study, it is assumed that any metamorphosed animal above 25 mm in depth is adult and that those below 20 mm in depth are stenomorphs.

Substrates inhabited by Pholadidae

The members of the family Pholadidae are all obligatory borers. Different members of the family have definite preferences for certain types of substrate. Martesia and Xylophaga are restricted mainly to wood. Zirfaea prefers salt marsh peat and stiff mud, whereas Penitella and Parapholas bore into much harder shales and sandstones (Turner 1954). Rock borers prefer homogeneous substrates and avoid conglomerates containing hard fragments (Amemiya and Ohsima 1933; Kofoid 1927; Hunter 1949).

General description of burrow

Pholad burrows are conical in shape with a small entrance and a rounded bottom (Fig 14, 15). The burrow is relatively straight in uncrowded situations, but crowding may cause it to twist considerably (Fig 32). Settling occurs on both horizontal and vertical surfaces. The burrows orient more or less perpendicularly to the surface, with some tendency to slope downwards in horizontal burrows.

Sexual cycle

Sexual activity within the family Pholadidae is extremely variable. Larviparous and oviparous forms are known (Bouchard-Chantreaux 1879, Duval 1963b). Dioecious, protandric hermaphrodites and alternating hermaphrodites have been described by Nagabhushanam (1962a), Ganapati and Nagabhushanam (1953, 1955), Moore (1947), Pelseneer (1926), Sigerfoos (1895) and Duval (1963b). Spawning may occur throughout most of the

year or at specific times of rising or falling water temperatures (Duval 1963b, Ganapati and Nagabhushanam 1955, Moore 1947).

Period of maximum settlement

Nothing seems to be known concerning the settlement season of P. penita or any other pholad except M. striata, which settles throughout the year in Indian waters, with a maximum from March to June and a minimum in October (Nagabhushanam 1962b).

Factors affecting settlement

Thorson (1946) observed that Zirfaea crispata larvae are able to delay metamorphosis if a proper substratum is not available. Nagabhushanam, in a series of studies on factors influencing settling in Martesia striata, Teredo and Bankia, has shown: (1) Martesia shows a gregarious behavior since it settles three times more densely on previously settled boards than on controls (Nagabhushanam 1959a), (2) Martesia and Teredo settle 10 times more densely on wood blocks covered with a primary film (undefined) than on blocks lacking this film (Nagabhushanam 1959b), (3) settlement of Teredo, Bankia and Martesia was inhibited by the accumulation of fouling material. Infestation was 10 times heavier on panels that were kept scraped clean (Nagabhushanam 1960), (4) Martesia settled in all light ranges except total darkness. It preferred to settle on the underside of horizontal surfaces and less on more vertical surfaces (Nagabhushanam 1959c).

Growth rate

Only two studies have been made on the growth rates of rock-boring pholads. MacGinitie and MacGinitie (1949) calculated (method unknown) that P. penita could bore a burrow 1 inch in diameter and 5 to 6 inches deep in 5 or 6 years, and Prié (1884) claimed that Pholas dactylus can bore at the rate of about 4 inches in 5-1/2 years. These observations are relatively meaningless because no measure of substrate hardness is given. Turner (1954) states that the growth rate in pholads varies greatly and depends largely upon hardness of the substrate and the amount of crowding.

OBSERVATIONS AND RESULTS

Morphological variations as related to age

Numerous variations in morphological and dimensional features of the valves can be related to changes in age and variations in certain environmental factors, the chief of which appears to be rock hardness.

Change in ratio: length to depth as size increases

Huxley (1932, p. 4) gives $\log Y = \log b + K \log X$ as the formula for allometry. Any variables conforming to this formula will fall along a straight line if plotted on a double logarithmic grid.

The lengths and depths of valves of 150 active P. penita from Fossil Point were plotted on a double logarithmic grid (Fig 7).

A test for linearity suggests that the allometric relationship holds as a first approximation ($P < 0.05$). However, from the data, the hypothesis that a straight line adequately represents the relation between the variables must be rejected if a criterion of significance greater than 95% is applied. The valves of newly settled animals (Fig 21) are nearly round, while large P. penita from Fossil Point (Fig 12, top) are slightly more than twice as long as they are deep. Most young animals approach this latter shape rather earlier than they would if the change in shape was truly allometric.

Change in ratio: valve length to depth with metamorphosis

When active animals stop boring and metamorphose, the ratio: valve length to depth increases owing to an elongation of the posterior end of the valve.

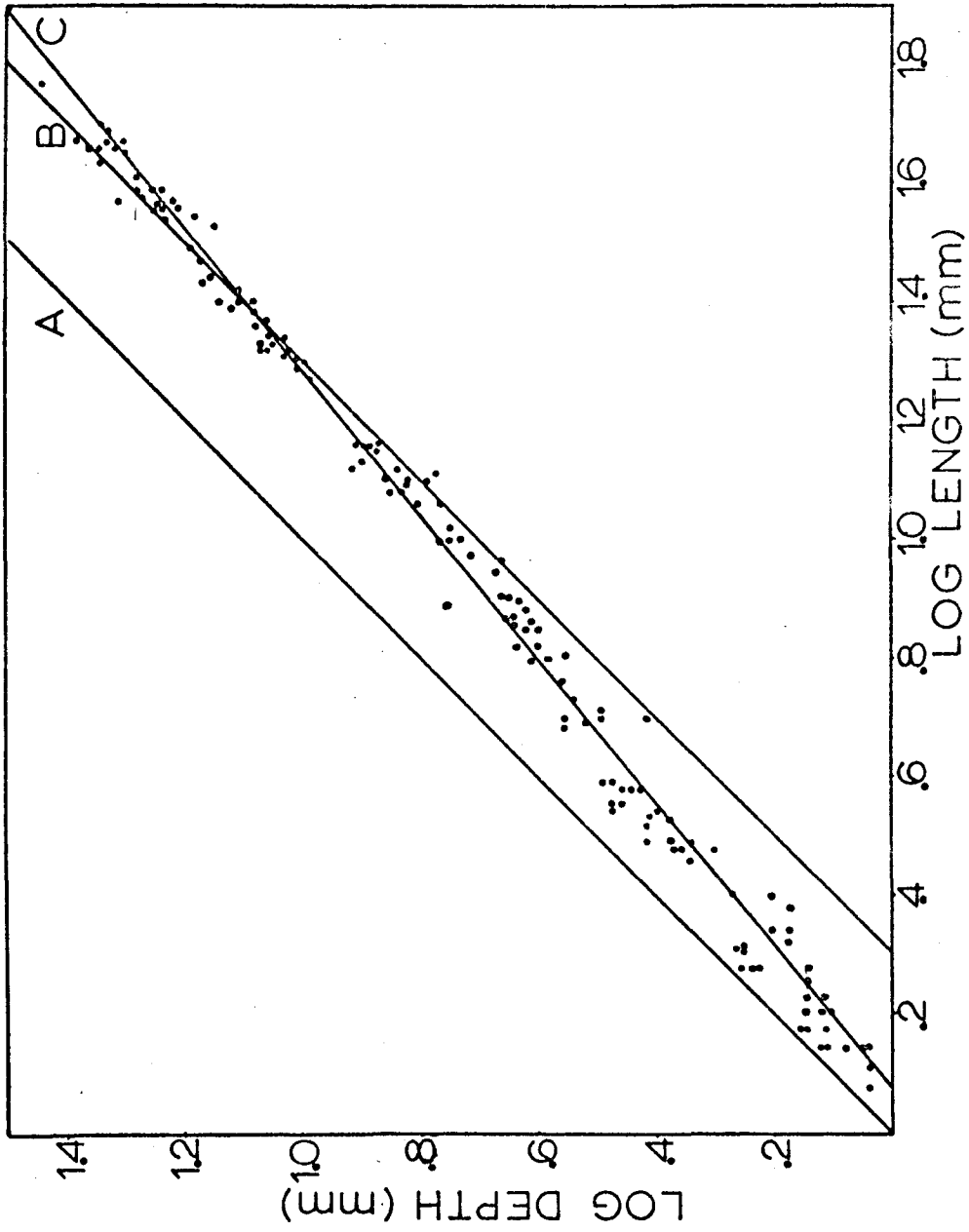
FIGURE 7

Valve depth and length of active Penitella penita
from Fossil Point plotted to show allometric change in
valve shape with growth.

Line A = 1:1 ratio

Line B = 2:1 ratio

Line C = Regression line



Valve length and depth in populations of actives, adults, and stenomorphs from Fossil Point were compared by analysis of covariance. This showed that one line is insufficient for all observations ($P < 0.01$). The slopes, however, are not significantly different (Fig 8). Thus valve shape varies significantly between these groups, active animals being shorter for a given depth.

Shell deposition during adult period

Clapp (1925) stated that stenomorphic teredos which cannot grow because of crowding continue to lay down denticulated ridges and increase valve thickness. This observation raised the question of whether shell deposition in pholads continues after metamorphosis.

Three hypotheses must be considered before the question can be answered: first, that metamorphosis is irreversible and that once the animal becomes adult it cannot grow or bore further into the rock; second, that burrow shape is fairly constant in any particular rock type; and third, that erosion is wearing away the surface rock at a rate fast enough to shorten significantly the burrow of an animal during its adult life. Evidence for these hypotheses will be presented later. If they are true, the relative age of an adult can be estimated by comparing the size of the animal with the length of its burrow. The smaller this ratio, the greater the amount of erosion which has taken place and therefore the longer the animal has been a nonboring adult.

FIGURE 8

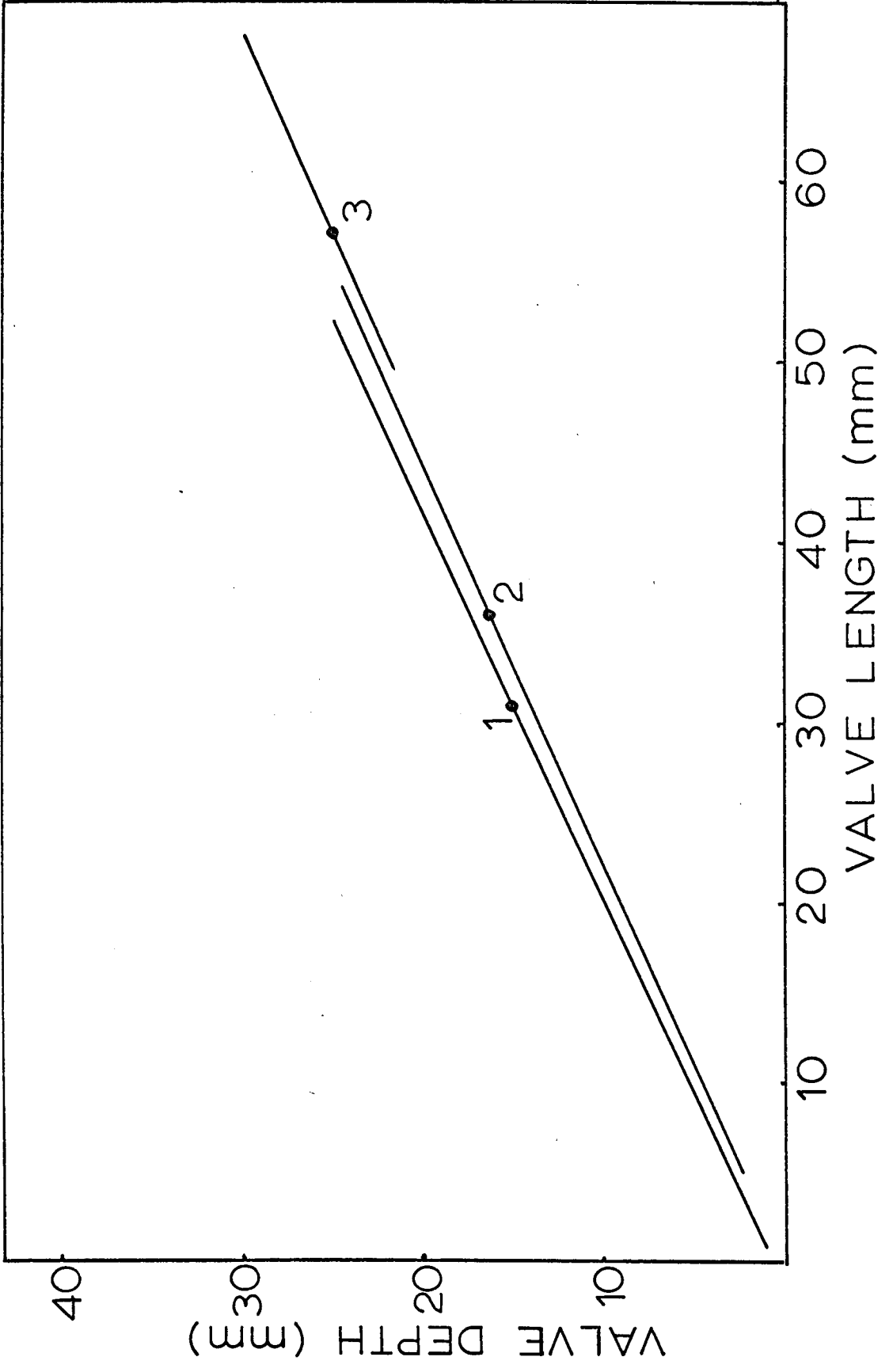
Change of valve shape of Penitella penita from
Fossil Point as related to condition of animal.

Regression line 1 = Active

Regression line 2 = Stenomorph

Regression line 3 = Adult

—●— indicates mean value of each ratio, the length of
the line indicates approximately the size range of each
class.



A population of 55 adult animals, all measuring more than 50 mm in length, was divided into three categories according to burrow length. Sixteen animals had short burrows with a ratio:burrow length to valve depth between 2.5 and 3.99, twenty-five had medium length burrows with a ratio:4.0 to 5.49, and fourteen had long burrows with a ratio:5.5 to 6.99.

If shell deposition continues after metamorphosis, then the valve weight of animals with short burrows should be greater than the valve weight of animals of equivalent size with long burrows.

Valve depth and valve weight of animals with long and short burrows were compared by analysis of covariance (Fig 9). One regression line was inadequate ($P < 0.05$). Since older animals from short burrows are significantly heavier than younger animals from long burrows, it follows that CaCO_3 is deposited during the adult period.

Morphological variations induced by substrate differences

Johnston (1850) observed that Pholas dactylus from soft sandstone have thin valves whereas those from hard rock have thick irregular valves. Purchon (1955) indicated that those species of Pholadidae that bore in hard rock develop more robust valves than those inhabiting soft rock.

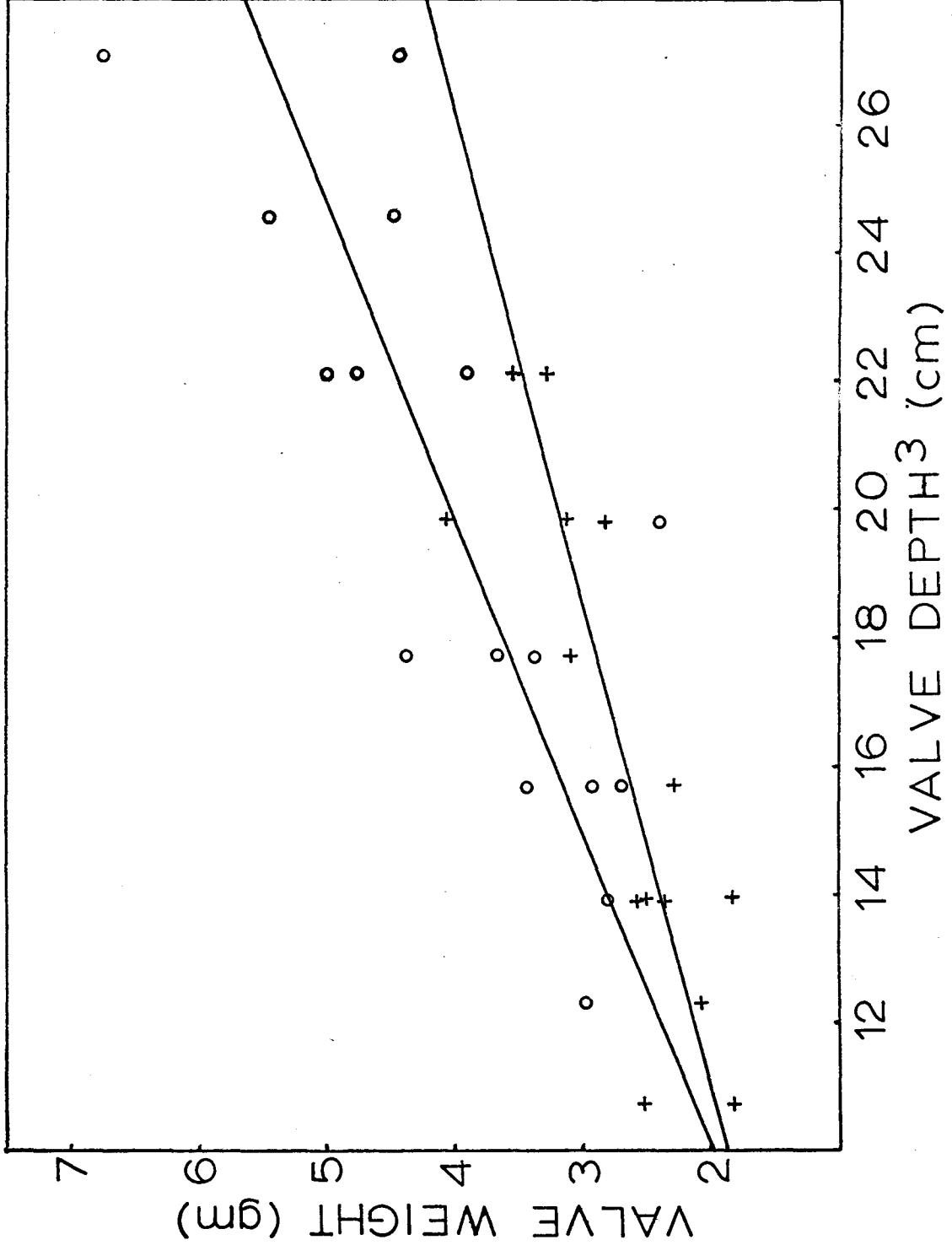
Duval (1963) in her study of Petricola pholadiformis concluded that greater variation in the ratio of valve length to breadth occurred among animals taken from the least suitable habitats, i.e. rock too hard (chalk) or too soft (like plasticine).

Turner (1954, 1955) noted the relationship between substrate hardness and valve morphology and growth rate. In the cases of Penitella

FIGURE 9

Shell deposition during adult period.

Valve weight and valve depth of adult Penitella
penita are plotted to compare those from long burrows +++
(burrow length : valve depth = 5.5 to 6.9) and those from
short burrows ooo (burrow length : valve depth =
2.5 to 3.99).



penita and Zirfaea crispata, she noted that the valves of animals from softer substrates are thinner, more elongate, and show evidence of more rapid growth (wider spacing of the growth bands) than those of animals from hard substrates.

In this study populations of P. penita were collected from three different locations, and the morphological variations were analyzed. Although environmental differences may exist between these three areas, it is theorized that the morphological differences observed are principally induced by differences in rock hardness (Table 1).

Kofoed (1927) studied Teredo from three areas in San Francisco Bay and attempted to relate the morphological variations to observed environmental differences such as salinity and temperature variations. Although certain morphological variations could be related to these environmental differences, he found that, for the population as a whole, the variations within groups were greater than the variations between groups. Significant differences in salinity, and temperature variations did not cause significant differences in Teredo morphology. I took no measurements of temperature or salinity variations, but have assumed, rightly or wrongly, that their effect on valve morphology is insignificant.

Valve size of adults as related to rock hardness

Populations of adult P. penita from Fossil Point, South Jetty and Cape Blanco were compared by analysis of variance. The means of valve depth were different in the three populations ($P < 0.01$). P. penita spontaneously becomes adult at a small size in the softest rock at Fossil

Point and at progressively larger sizes in South Jetty and Cape Blanco rock. (Table 2, Fig 10).

Valve shape as related to rock hardness

The relationships of valve length to depth in active animals from the three areas were compared by analysis of covariance (Fig 11). Animals more than 15 mm in length were used, so that the picture would not be confused by the allometric shape changes that were seen in smaller animals. P. penita from the soft Fossil Point rock were longer ($P < 0.01$) at any given depth than animals from the harder rock of South Jetty and these in turn were longer than those from the hardest rock from Cape Blanco (Fig 12). For example, active animals from Fossil Point, South Jetty and Cape Blanco, each with a depth of 20 mm, will have an average length of 42 mm, 35 mm, and 29 mm, respectively. It is also of interest that the slopes of the three lines were different ($P < 0.01$).

Valve weight as related to rock hardness

The relationships between valve size and weight in active animals from the three areas were compared by analysis of covariance. Because shape changes so radically in different rocks, valve profile (length x depth) was used as an indication of animal size rather than valve depth or length.

Animals from the soft Fossil Point rock were lighter in weight ($P < 0.01$) than those from South Jetty, which were in turn lighter than those from Cape Blanco. The slopes of these three lines were different ($P < 0.01$) (Fig 13).

TABLE 2

Relation between rock hardness and adult size

Area	Fossil Point	South Jetty	Cape Blanco
Relative rock hardness	1	2	4
Mean valve depth of adult <u>P. penita</u>	25.5mm	32.5mm	40.0mm
SE	0.368mm	0.579mm	0.766mm
N	48	48	30

FIGURE 10

Shows average sized adult Penitella penita from
Fossil Point, South Jetty, Cape Blanco. (Top to bottom)
scale 1.6 x.

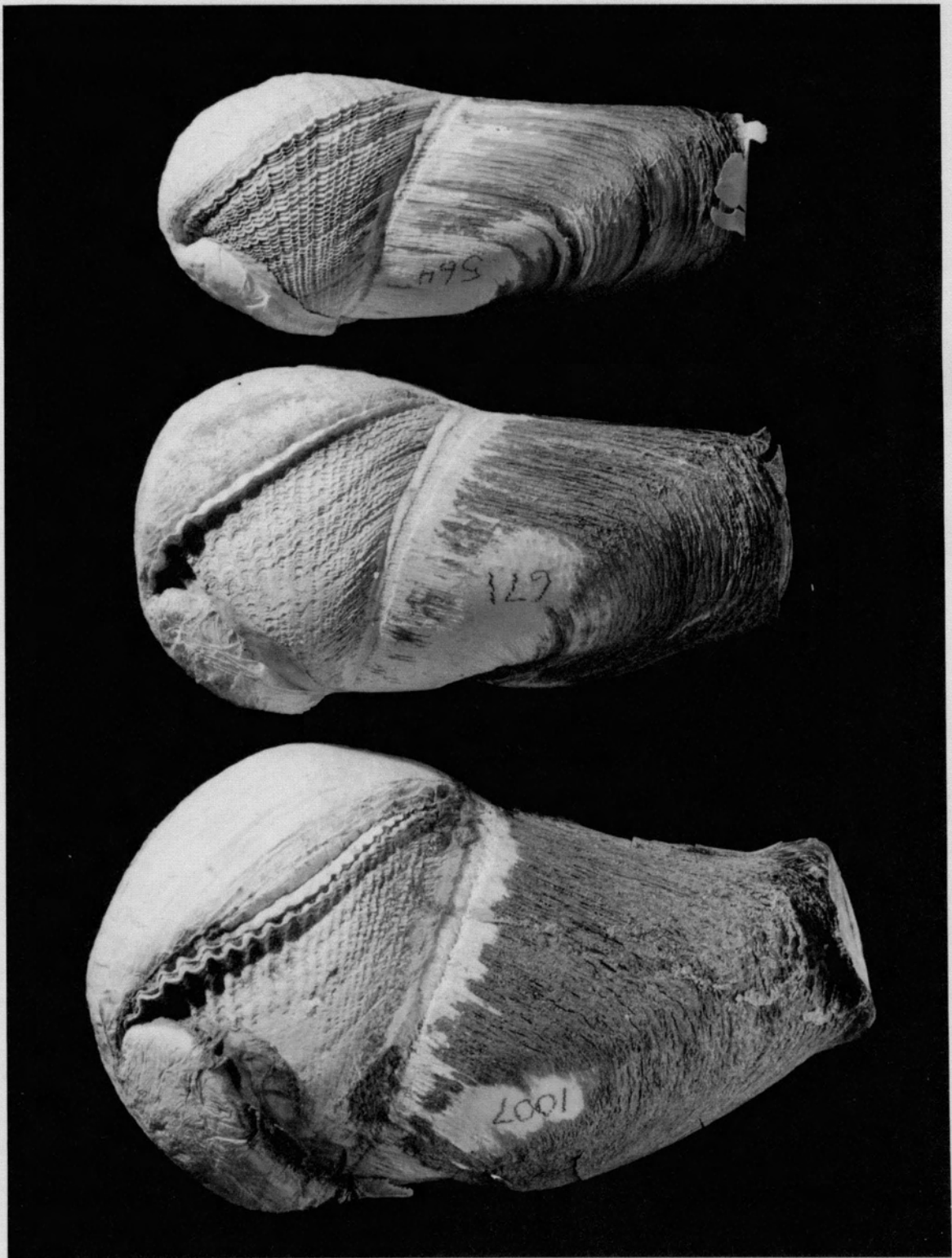


FIGURE 11

Relationship of valve length to valve depth of
active animals from different areas.

Fossil Point (. . . . regression line 1)

South Jetty (+ + + + regression line 2)

Cape Blanco (o o o o regression line 3)

⊕ indicates mean values.

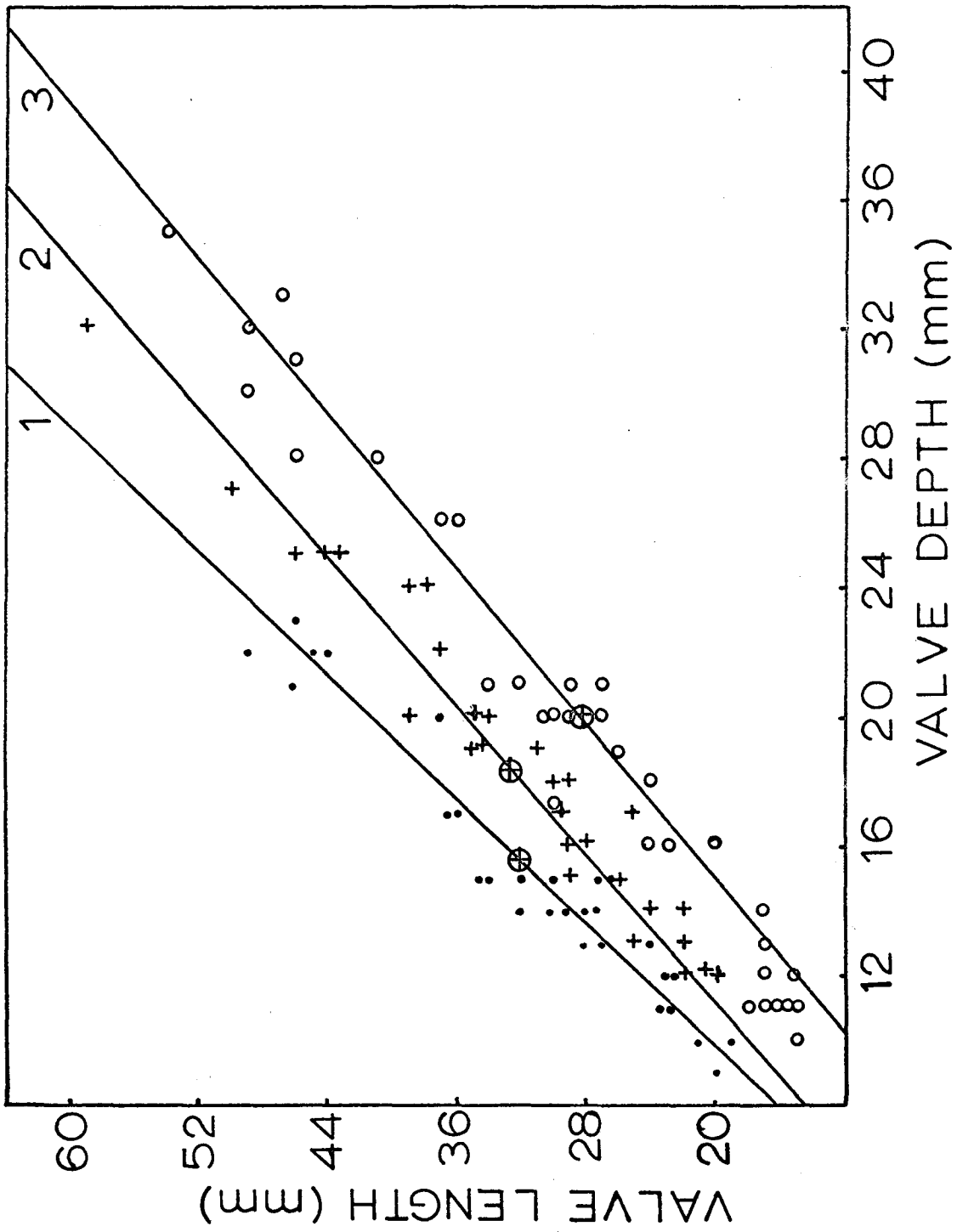


FIGURE 12

Valves of active Penitella penita.

Top - Fossil Point animal

Middle - South Jetty animal

Bottom - Cape Blanco animal

Compare shape and width of growth lines.

Scale 2.5 x

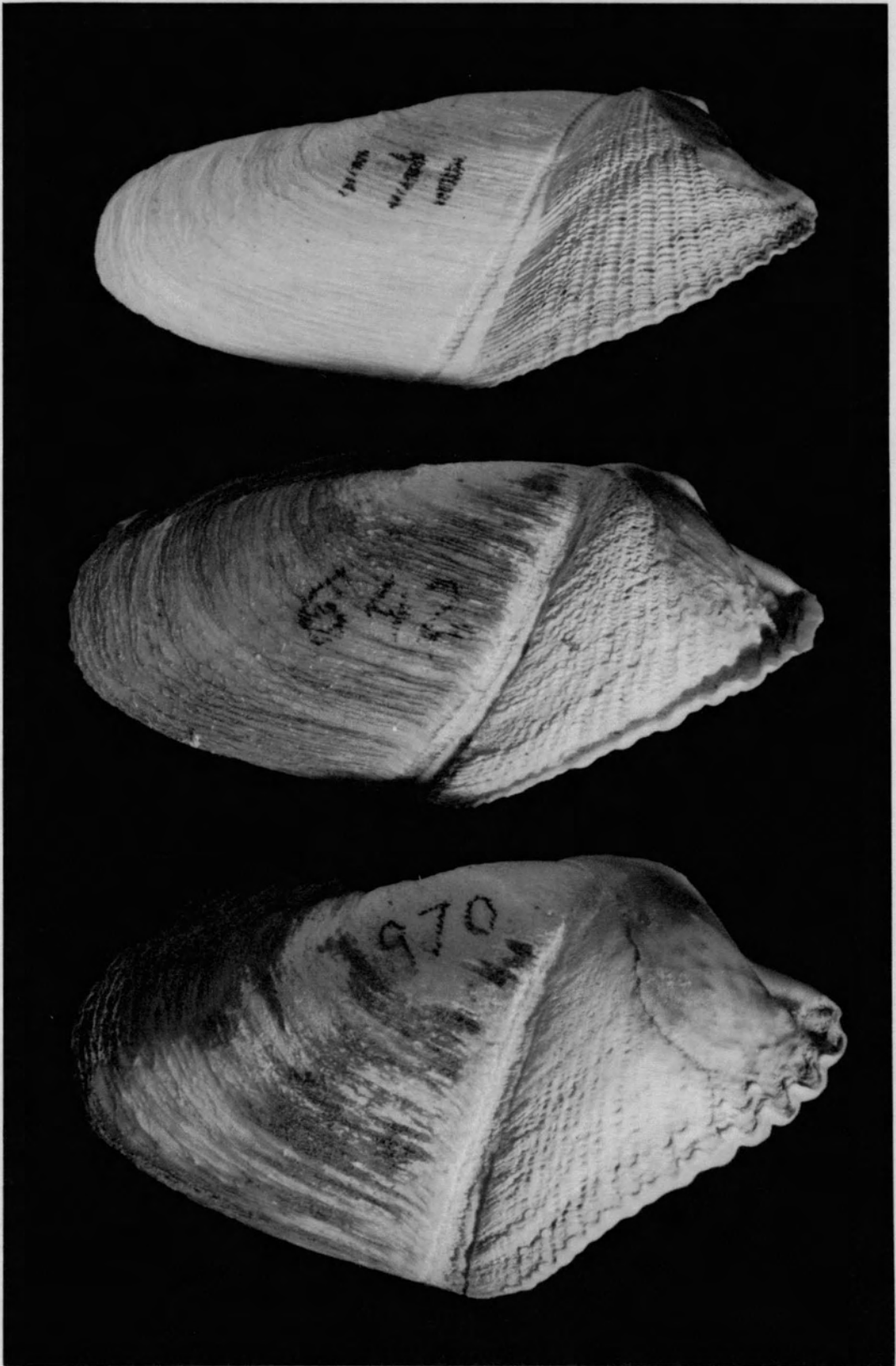


FIGURE 13

Relationship between weight of the valves and rock hardness. All animals are active Penitella penita.

.. Animals from Cape Blanco relative rock

hardness = 4

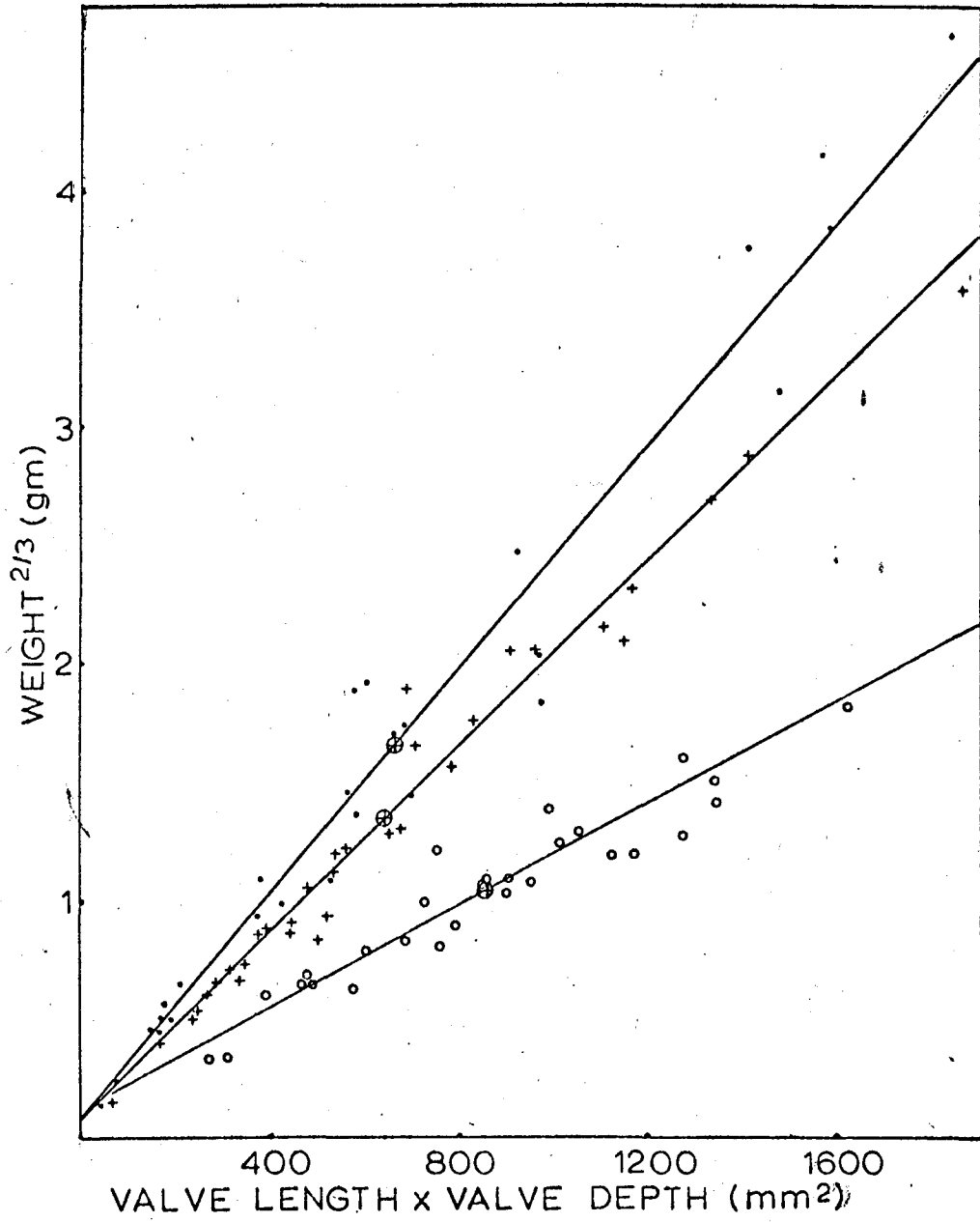
++ Animals from South Jetty relative rock

hardness = 2

oo Animals from Fossil Point relative rock

hardness = 1

⊕ Average values



Analysis of burrow shape

As Penitella penita bores into the rock it leaves behind a record of its movements. From an analysis of the shape of a number of burrows in the three major areas of study, certain inferences can be drawn about the factors that influence burrow shape and about the activity of the enclosed animal.

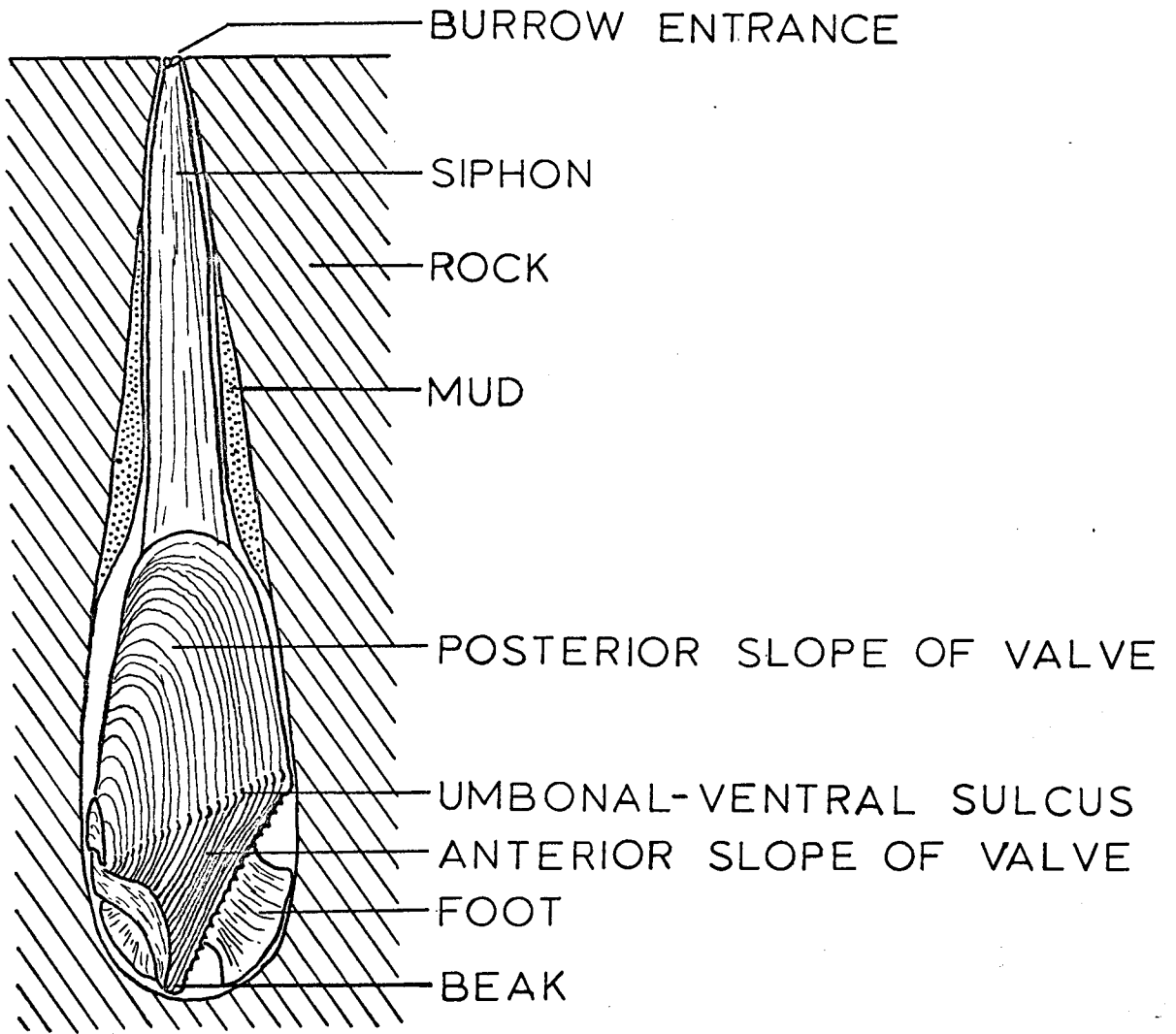
The method of constructing accurate molds of the burrows, and the measurements taken from these molds have already been described. It should be noted that the shape of a burrow occupied by the living animal differs from that of the burrow that was bored by the animal. This difference is due to mud being deposited along the wall of the burrow, mostly in the region just posterior to the valves (Fig 14). This mud appears to be plastered to the wall of the burrow by mucus from the siphon. It was cleaned out by pouring sodium hypochlorite solution into the freshly opened burrow. This dissolved the adhesive mucus, allowing the mud to fall away from the burrow wall.

Although the burrows may twist, they are essentially conical in shape, with a small entrance and large rounded bottom. The shape of this cone can best be described by calculating the apex angle. For more precision the angles of the upper and lower half were computed separately. Comparison of these two measurements was useful in clarifying some of the processes controlling burrow shape.

The angle of the apex cone is calculated by the formula $\tan \theta = (\text{maximum diameter} - \text{minimum diameter}) / (2 \times \text{length})$. The angle equals $1/2$ the apex angle of the cone. By taking the middle diameter, $\tan \theta$

FIGURE 14

Diagram of Penitella penita in burrow, showing mud which is plastered onto the walls just posterior to the valves.



can be calculated for the upper and lower half of the burrow. (Within the ranges used, there is a sufficiently linear relationship between ϕ and $\tan \phi$ that $\tan \phi$ will not be transformed to ϕ).

Basic burrow shape

The basic burrow is that resulting from a young active animal boring into uncrowded rock. This shape depends to a large extent on the hardness of the substrate. Erosion, crowding and action of the siphon impose secondary modifications on this basic shape.

At the beginning of this study, I postulated that the basic burrow had a perfectly conical shape (Fig 15a). This means that the ratio of $\tan \phi$ lower half of burrow to $\tan \phi$ upper half of burrow equals 1. The actual basic burrow of Fossil Point animals was described from a study of burrows of 18 young active animals (19 months maximum) growing in uncrowded conditions. The ratio of $\tan \phi$ lower half of burrow to $\tan \phi$ upper half of burrow was 0.737, SE = 0.0477. This difference from the expected value is due to two departures from the perfect cone: the angle decreases near the base of the burrow, and the angle, in burrows of young animals, is excessive in the first centimeter (Fig 15b). The larger angle at the entrance appears related to the shorter more tumid shape of the very small animals (Fig 21).

Effect of substrate hardness on burrow angle

The $\tan \phi$ of burrows from the three study areas were compared by analysis of variance (Table 3). The means of the three populations were different ($P < 0.01$). In harder rock the angle is larger (Fig 16). The

FIGURE 15

- A. Theoretical burrow showing measurements made on burrow molds.
- B. Actual shape of a burrow occupied by a young active animal in uncrowded rock.

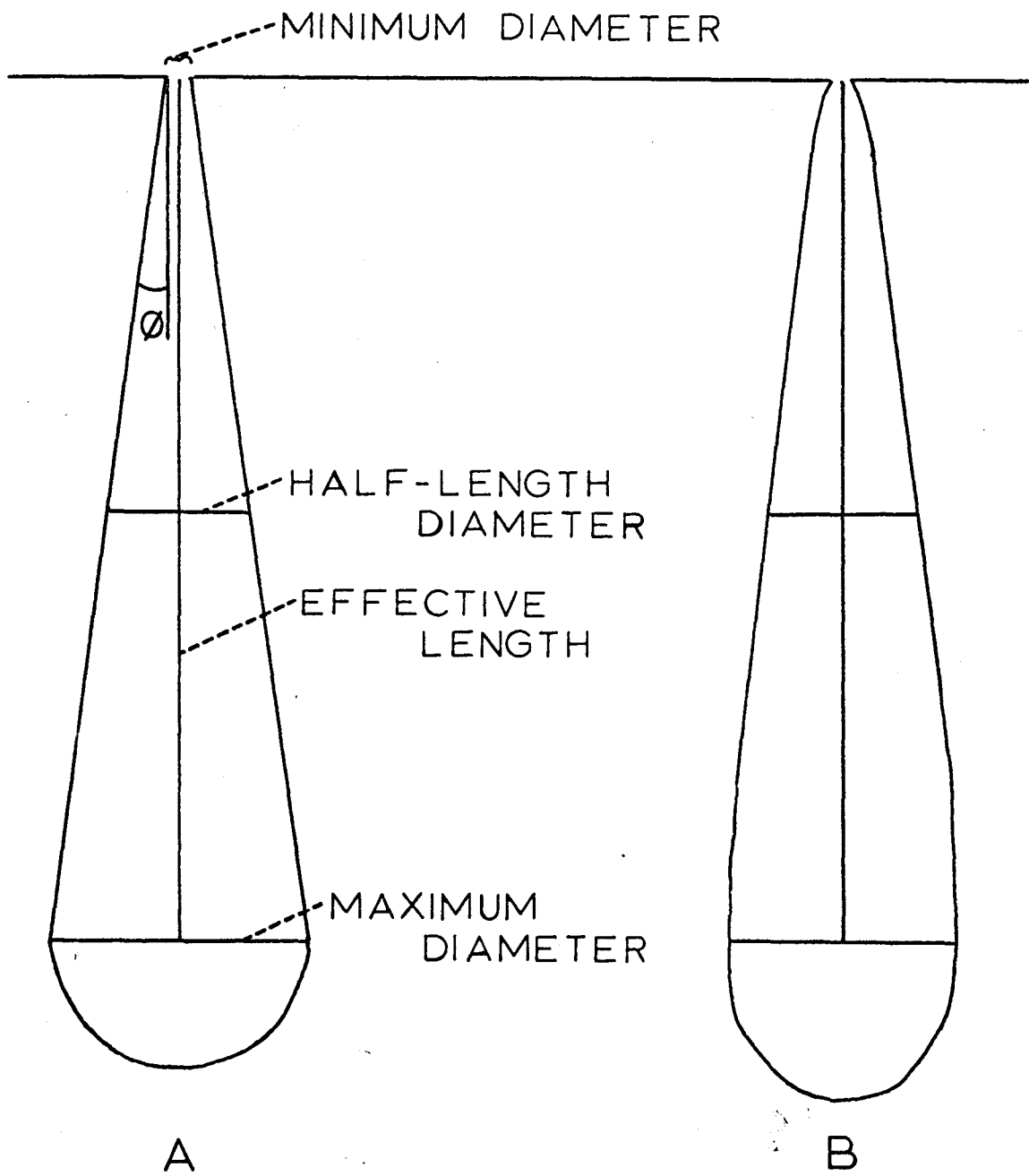


TABLE 3

Relation between rock hardness and burrow angle

	Crowded	Fossil Point 19-month animals	South Jetty	Cape Blanco
Rock Hardness adjusted scale	1	1	2	4
Average $\tan \phi$	0.091	0.098	0.148	0.207
SE	0.012	0.0035	0.020	0.021
N	51	17	18	17

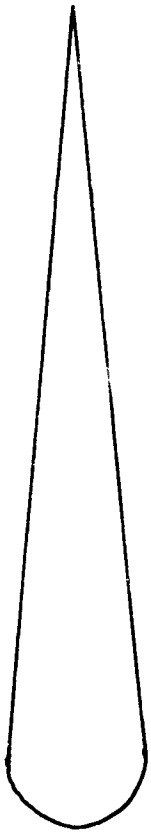
FIGURE 16

Model burrows. $\tan \phi$ same as in table 3.

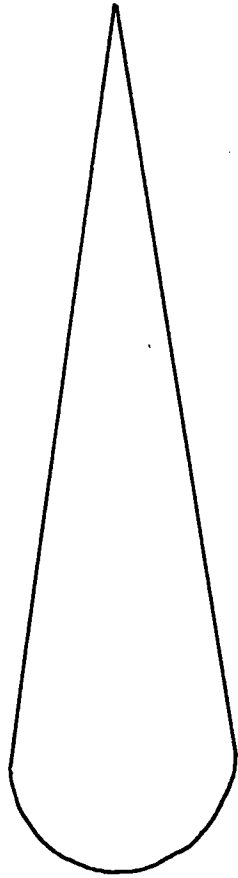
A = Fossil Point

B = South Jetty

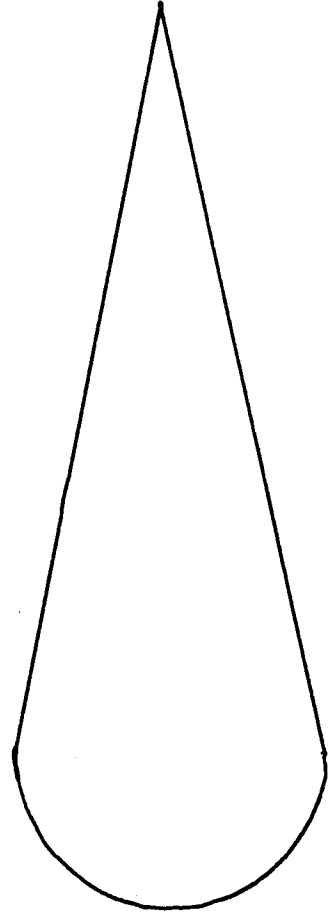
C = Cape Blanco



A



B



C

reason for this is not completely understood, but appears to be related to the shorter more tumid shape of animals in harder rock.

Effect of crowding on burrow shape

Because of their ability to avoid obstructing burrows, animals in crowded situations usually have twisted burrows. It sometimes happens that an animal is hemmed in by parallel burrows, and in these cases the burrow may elongate without increase in diameter, thus decreasing $\tan \phi$ in this part of the burrow. Evidence for this was obtained when the ratio: effective burrow length to valve depth was compared from crowded and uncrowded Fossil Point rock (Table 4). This shows that for equivalent-sized active animals, the burrows in crowded rock are, on the average, longer than those from uncrowded rock. Notice also that the SE is twice as great in the crowded rock, which points out the fact that for any given animal in crowded rock, conditions might be either cramped or uncrowded. As a result a random sample of burrows from crowded rock in Table 4 gives a lower average ratio than could be obtained by choosing only animals from cramped conditions. In extreme crowding, the animals are hemmed in from all sides and no further boring is possible without their breaking into another burrow. This causes metamorphosis regardless of animal size. This is the cause of stenomorph formation.

Enlargement of the entrance diameter with growth and age

The entrance diameter of the burrow of a pholad must be enlarged as the animal grows, so that there is sufficient room for the siphon to emerge. The opening must be large enough to allow the clam to circulate sufficient sea water for survival and growth.

TABLE 4

Burrow shape of active animals

	Crowded	Fossil Point 19-month animals	South Jetty	Cape Blanco
Mean valve depth	14.5	12.2		
Mean ratio: Effec- tive burrow length/ valve depth	4.5	4.1	3.6	1.9
SE of ratio	.31	.15	.21	.09
N	16	17	7	6

The fact that the entrance does enlarge with age is easily established. The original entrance diameter measures about 0.5 mm, the diameter of the newly settled clam. The average entrance diameter of 17 pholads, not more than 19 months old, was 2.8 mm (SE = 0.15 mm).

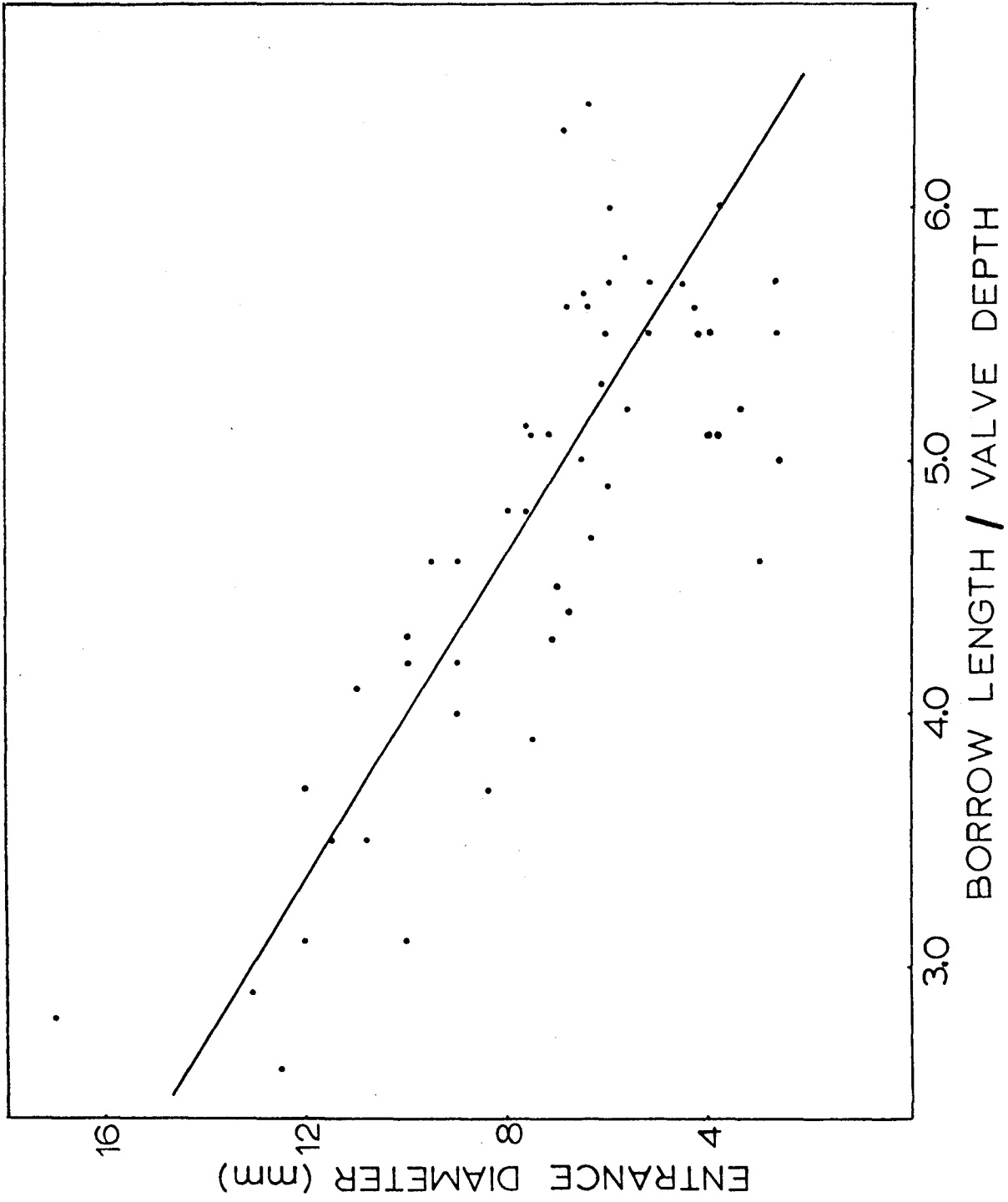
Russell and Yonge (1936) suggested that the entrances of pholad burrows are enlarged by some chemical activity of the siphon. It is unlikely that the animals at Fossil Point enlarge their entrance in this way because of the argillaceous nature of the matrix. Two other processes appear to account for entrance enlargement: mechanical abrasion by the siphon and the shortening of the burrow by erosion.

Erosion, by removing surface rock, truncates the burrow and thereby enlarges the entrance diameter. This is illustrated graphically by plotting entrance diameter of adult animals against the ratio of valve depth to burrow length. A negative regression line results (Fig 17). Animals with relatively long burrows have smaller burrow entrances than those with relatively short burrows.

The effect of mechanical abrasion by the siphon would be to enlarge the entrance diameter without concurrent shortening of the burrow. As noted previously during the first 19 months of life in the rock the opening of the burrow increased in diameter by about 2.3 mm. The approximate rate of surface erosion of the surrounding rock, due to physical factors, can be estimated. Stainless steel screws were placed in the rock, flush with the surface, at the time that the rock was originally exposed in August 1963. Two years later, the height that the screws were raised above the surface was measured. The average amount of erosion

FIGURE 17

Relationship between the relative burrow length of adult Penitella penita from Fossil Point and the burrow entrance diameter.



was 1.00 mm (SE = 0.24 mm, N = 19). This means that erosion by truncating the burrows cannot account for the increase in size of the burrow openings. Most of this increase must be due to the mechanical abrasive action of the siphon.

Relationship of size and condition of animal to burrow length

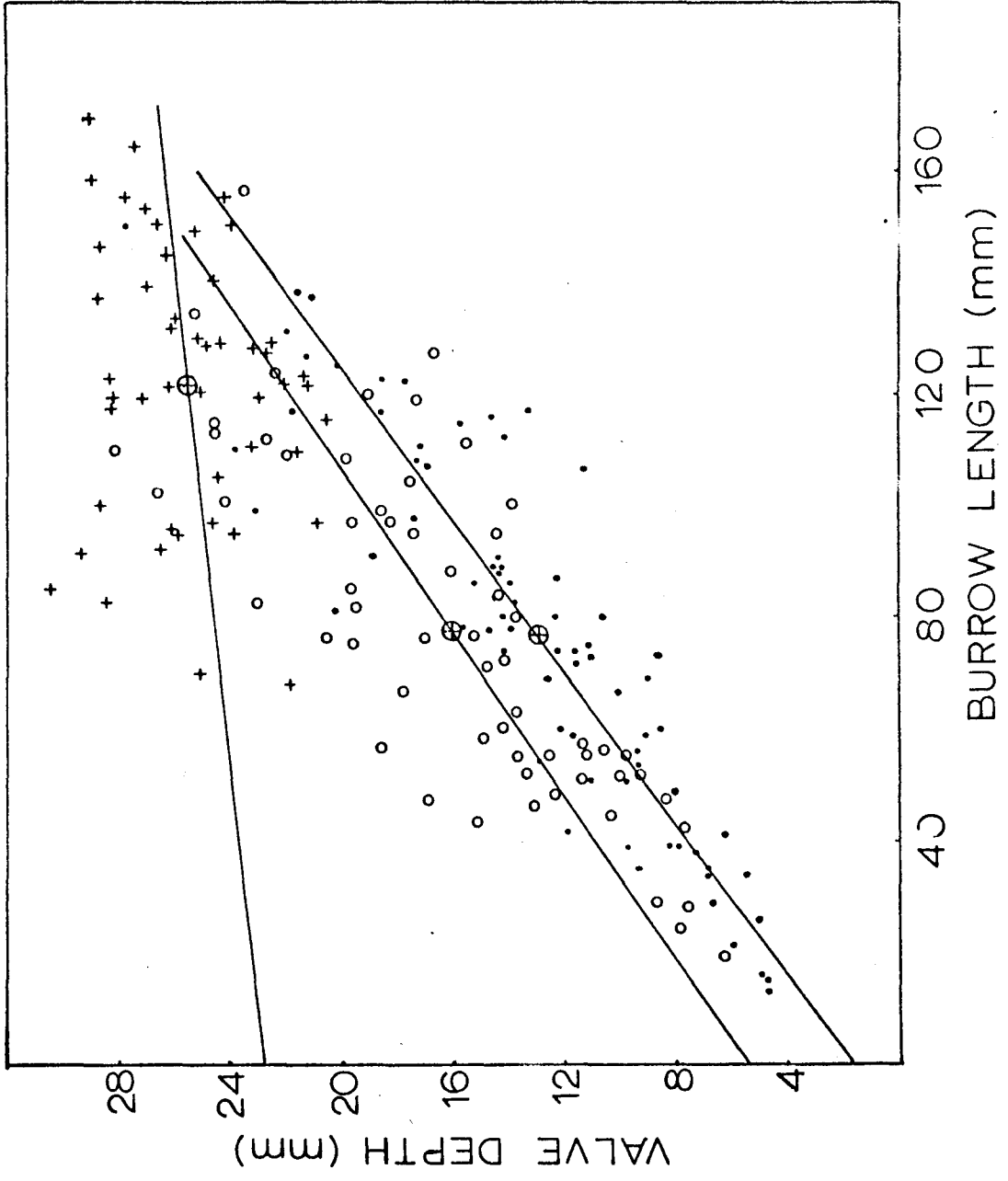
When valve depth is plotted against total burrow length (Fig 18), an interesting difference between the regression lines for actives, stenomorphs and adults, becomes apparent. Active animals, since they must bore deeper into the rock in order to grow, show a close direct correlation between valve depth and burrow length. By contrast, no such relationship holds for the adults. The burrows of these animals are shorter than expected in active animals of the same size, and there is considerable variation in burrow length for any particular size; the slope of the regression line is almost zero. This reduction in burrow length is due to various erosive forces which wear away the surface rock, thus shortening the burrow. Although erosion acts to shorten all of the burrows, its effect is most noticeable in non-boring adults because the burrow is not simultaneously being elongated. Old adults are more likely to have short burrows than young adults. The fact that the valves of adults in short burrows are heavier than those of adults in long burrows (Fig 9) also supports the contention that the former are older.

The life expectancy of adult pholads is not known. It is limited by the time it will take for erosion to shorten the burrow to such an extent that it becomes untenable. Animals probably become more subject to predation as the burrow becomes progressively shorter. Very few

FIGURE 18

Relationship between burrow length and size and condition of the animal. All Penitella penita from Fossil Point.

- Active animal
- + Stenomorphs
- Adults



animals at Fossil Point have burrows shorter than three times the valve depth. However, at Coos Head, live, adult animals can be found whose valves are protruding from the surface of the rock. Starfish, which are common in the former but not the latter area, may prey on pholads with shortened burrows, though they have never been observed to do so.

The burrows of stenomorphs are also shorter than could be expected in active animals. A correlation does exist between burrow length and valve depth, but it is not as precise as with active animals. The regression line nearly parallels that of the actives. It should be noted that these animals were defined as stenomorphs because of the proximity of their burrow base to another burrow. It is more than likely that most of the stenomorphs 24 mm or larger changed spontaneously and therefore should be classified as adults.

Growth studies

Knowledge of the growth rate and the factors controlling growth rate is basic to the understanding of the autecology of any organism. Haskin (1954) described three standard methods of estimating growth rate of mollusks; interpretation of growth interruption lines on the valves, size frequency analysis for year classes, and release and recovery of marked individuals.

The first method was not useful initially, in the case of P. penita, because the time interval between growth interruption lines was not known. However, the replant studies and growth band counts of 1-year-old animals gave some indication of the time factor, and rough calculations

of the time interval required to reach mature size were made on animals from the three areas (Table 6).

Year classes cannot be identified because the growth rate of individuals is variable, being controlled by crowding and rock hardness, and because the settlement period is very extended.

A modified mark and recapture procedure, the "replant method," was developed for calculating the growth rate of individuals under specific conditions (replant experiments).

Most of the aging and growth rate studies on marine wood boring mollusks have relied on the use of test boards exposed for known periods of time, after which the boards were collected and the animals removed and measured. Instead of boards, freshly cleared areas of rock on the edge of the lower bench at Fossil Point were used. Analysis of the size distribution of populations of young clams collected from these rock surfaces yielded data on growth rates. The advantages of this method are that conditions are close to natural, the complicating effect of crowding is not important, and growth rates of early stages can be calculated.

The problems of estimating growth rates of borers by this method were discussed by Kofoid (1927) in his work on Teredo. I quote from page 231.

The average individual rate of boring under a given set of conditions is difficult to determine because of the practical impossibility of knowing accurately the time at which any specimen had entered the wood. As attachment of larvae occurs over a considerable period of time, individuals of varying sizes and ages occur together in the same timber. To include the smaller specimens in the calculations involves the error of the differential time element; while to consider only the largest specimens does not give a fair average.

In this study, each age sample was divided into five subgroups with respect to size. The mean for each quintile was calculated and a family of curves was plotted (Fig 19). Bias is introduced here because a greater proportion of large than of small animals is recovered. The upper quintile, containing the largest animals, is assumed to be made up of animals which settled soon after August 10, 1963, the date of the original exposure. The lowest curve probably represents recent settling. The three intermediate quintiles represent a mixture in varying proportions, of animals that settled soon after the original exposure and those that settled subsequently. The upper limits of the growth rate curve are obtained from the first quintile. However, the lower limits are obscured by subsequent settlement. It appears that the growth rate starts to decrease after 10 months. The low value observed between 10 and 12 months is probably due to a combination of decreased growth rate during this period and sampling error from variability of the settling sites.

If growth rate remains relatively constant, the age at which animals reach adult size at Fossil Point can be calculated by extrapolating from results during the first 21 months for the upper quintile. On this basis, animals reach adult size after 34 to 40 months of growth.

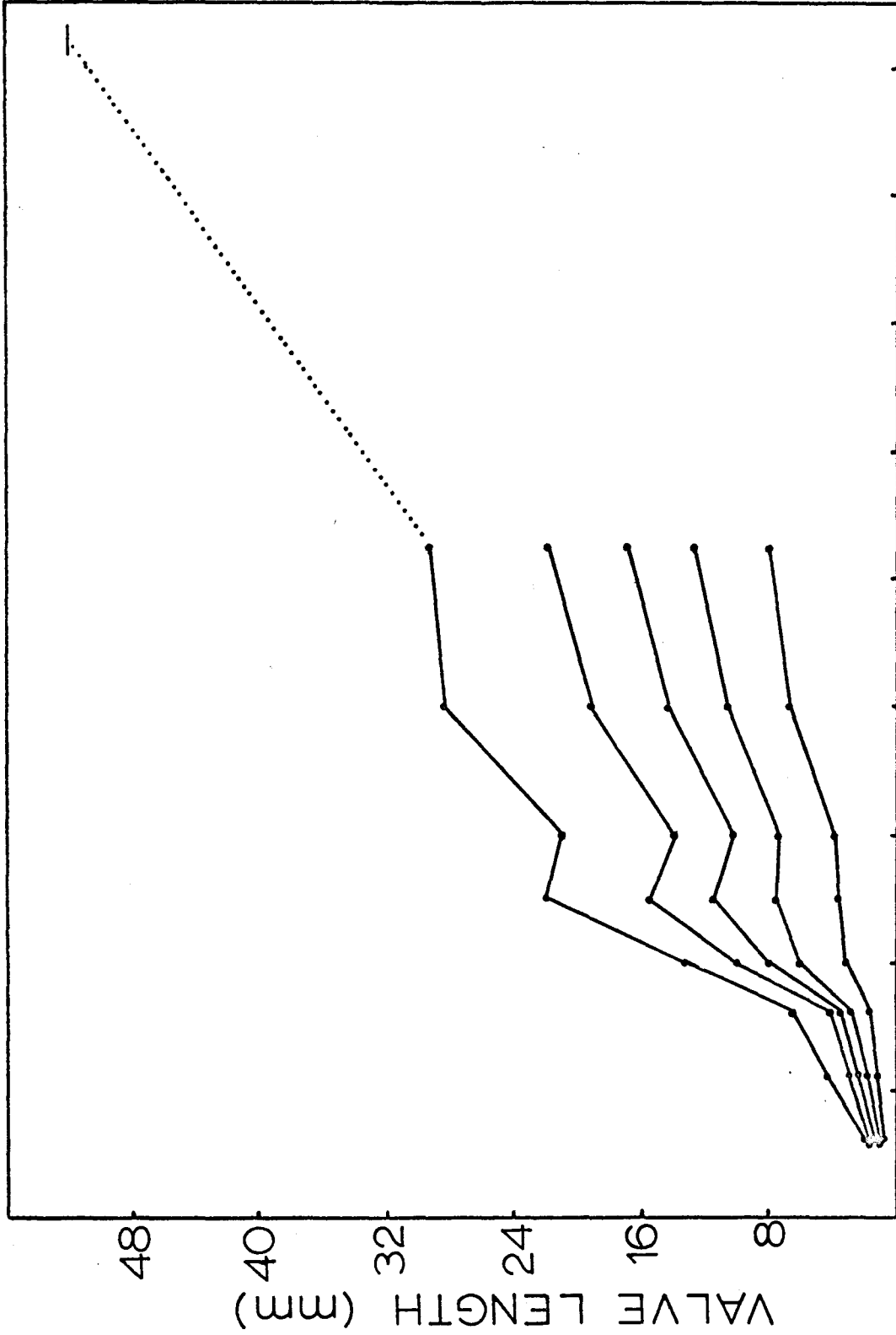
Calculations based on growth band counts (Table 6) give results somewhat less than this (average 30 months). Extrapolations of data from the replant experiments indicate that Fossil Point P. penita may become adult in as little as 28 months, but on the average within 36 months.

FIGURE 19

Growth rate of young Penitella penita at Fossil Point.

Each sample was divided according to size, into five equal quintiles, the mean value of each quintile is plotted.

The dotted line is an approximate extrapolation of the upper quintile to show expected age at adult size.



4 12 20 28 36
MONTHS EXPOSURE (STARTING AUG. 10 1963)

Growth bands

Growth interruption lines represent periods of growth stoppage preceded and followed by periods of growth. Haskin (1954) discussed the use of growth interruption lines for estimating growth rate. He stated that this was an unreliable method unless the interval between growth interruption lines was established by analysis of growth rates of marked animals. He also claims that growth checks can be caused by a number of normal and abnormal environmental factors. Only if the growth checks occur at regular intervals, can growth interruption lines be used for ageing or for calculation of growth rates. In this study the term "growth band" will be used to indicate the layer of shell between two growth interruption lines. In the Pholadidae a growth band probably represents a cyclic period of shell deposition followed by active boring. During the period of shell deposition, the mantle extends beyond the margins of the valves and deposits a new layer of shell. In the region of the pedal gape it extends laterally to deposit the sharp grinding teeth. During this time there is probably no boring activity. This period of quiescence is followed by a period of active boring; there is probably no shell deposition during this time. Nothing is known about the relative length of the active and quiescent periods.

Effect of animal size on width of growth bands

The number of growth bands per cm of umbonal ventral sulcus varies with the size of the animal when the bands were deposited. The number of growth bands in the first cm averaged almost twice as many as those

in the fourth cm (Table 5). In any one animal there are places where growth bands are wide, followed by areas where they are narrow. No regular pattern could be observed that would indicate yearly cycles.

Duration of growth cycle

Lindsay (1913) suggested that the formation of growth lines on the valves of rock-boring mollusks may have some relation to tidal or lunar periods, thus affording a means of ascertaining the age of animals and the speed of boring. Some of the data collected during this study supported this hypothesis, whereas other data did not.

The total number of growth bands of 10 young animals, close to but not exceeding 1 year of age, were counted. The mean value was 59.3, SE = 2.19, indicating that a new growth band is deposited on the average, every 6.2 days during the first year.

A count of the growth bands of a 2.5 month animal (Fig 21) indicates that the maximum interval between deposition of growth bands is 7.5 days.

The number of growth bands deposited per year decreases with increased age. Under good conditions active animals between 1 and 2 years of age deposited between 18 and 28 (mean 21) growth bands when replanted for nearly a year at both Fossil Point and South Jetty (Fig 29). One Penitella turnerae hung in a test tube at Fossil Point for 8 weeks deposited 4 growth bands. Older animals therefore can deposit a growth band every 14 days, possibly corresponding to a lunar period. Under disturbed or unfavorable conditions the formation of growth bands is inhibited for short or extended periods of time. Evidence for this was obtained from the results of the replant experiments. Animals in row 7 of the

TABLE 5

Counts of growth bands of specimens from three rock types (only the first 4 cm of umbonal ventral sulcus are considered)

Area		1st cm	2nd cm	3rd cm	4th cm	Total of first 4 cm
Fossil Pt.	Average no. of Growth Bands	35.8	26.6	18.5	14.2	95.2
(N = 13)	SE	1.09	1.02	1.10	0.57	2.55
South Jetty	Average no. of Growth Bands	34.8	39.1	32.0	22.9	128.7
(N = 14)	SE	1.67	1.54	1.11	0.62	3.12
Cape Blanco	Average no. of Growth Bands	120.6	92.6	81.7	70.0	364.3
(N = 7)	SE	7.93	8.43	13.46	11.02	37.24

upper bench survived 5 months of sand burial, but deposited no new growth bands during the burial period. The few animals (over 18 mm depth) which survived replanting in burrows with 3 mm entrance diameters grew little (Fig 28) and deposited few growth bands (Fig 29).

Effect of substrate hardness on width of growth bands and growth rates

The growth rate of P. penita, which inhabits snug burrows of its own manufacture, is intimately related to its boring rate, since only by enlargement of the burrow during the period of active boring can it increase the size of the valve. The question arises, is the growth rate limited primarily by the animal's ability to enlarge its burrow or by other factors? In order to answer this question, we must know the width of growth bands deposited by animals when they were not under confinement and compare this value with the width of growth bands deposited by animals under natural conditions.

Width of growth bands deposited under unconfined conditions

The average width of 16 growth bands which were deposited by 4 P. penita while they were suspended in test tubes at Fossil Point was 0.93 mm SE 0.043.

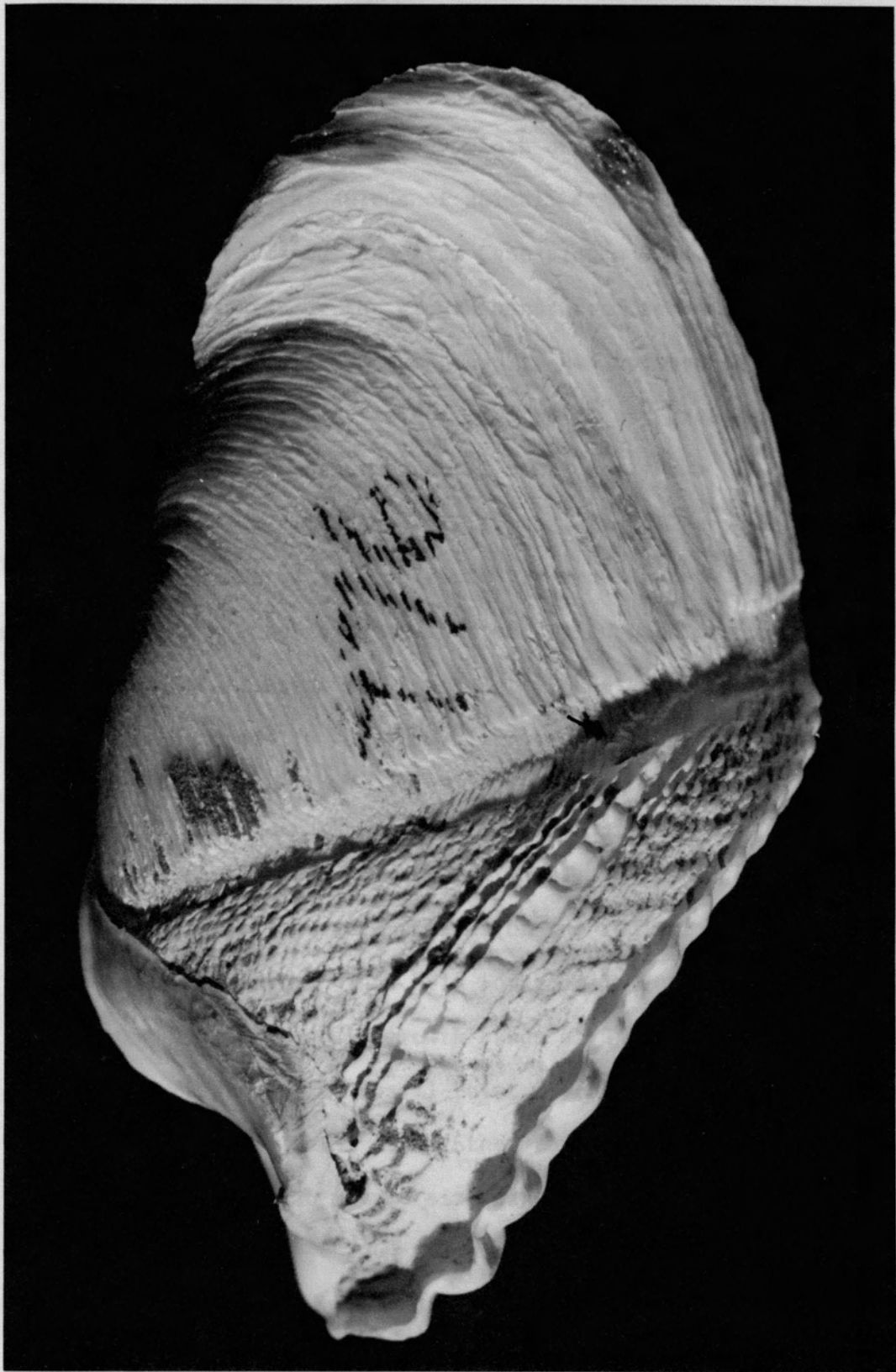
Some of the South Jetty animals were replanted in too large artificial burrows. The growth bands deposited immediately after replanting were abnormally wide, averaging about 1 mm in width. When the animal again filled its burrow, the width of the growth bands fell to normal (Fig 20). The width of the growth bands deposited under unconfined conditions depends on unmeasured and unknown factors.

Growth Band width measured in ventral umbonal sulcus.

FIGURE 20

Penitella penita replant animal from South Jetty. The wide growth bands were deposited immediately after the animal was planted in its artificial burrow which was too large for it. Once the animal grew to fill its burrow the width of the bands fell to normal.

Scale 6.8 x



Width of growth bands deposited under natural conditions

The number of growth bands in the first four cm of the umbonal ventral sulcus of animals from the three areas differed significantly ($P < 0.01$) (Table 5). The average width of the growth bands in the 4th cm of the umbonal ventral sulcus of animals from Fossil Point is 0.7 mm, from South Jetty 0.4 mm, and from Cape Blanco 0.14 mm.

When the widths of the growth bands from the naturally confined and unconfined animals are compared, it can be seen that in the soft Fossil Point rock, growth is not limited to any great extent by the boring rate. On the other hand, at South Jetty the growth rate is probably slowed down considerably (2 to 3 times) because of an inability to enlarge the burrow at a sufficiently rapid rate. On the assumption that the growth rate in unconfined conditions at Cape Blanco is about the same as at Fossil Point and South Jetty, the growth rate at Cape Blanco is greatly retarded (6 to 7 times) by the rock hardness.

Estimation of time required to reach adult size

As previously reported, approximately 26 growth bands were deposited in a year under the best conditions of the replant experiment at Fossil Point and South Jetty. This held for animals 10 mm in depth or larger. Very young animals deposit growth bands at a faster rate, averaging 60 during the first year at Fossil Point. If it is theorized that these values hold for all three areas, the growth rate and the time required for an animal to reach mature size can be calculated by the equation: (Total growth bands - 60/26 = N-1 years) (Table 6).

The average number of years required to reach maturity at Fossil Point according to this estimate (30 months) is somewhat lower than other

TABLE 6

Years required to reach adult stage calculated by
 (Total no. growth bands - 60 growth bands)/26 = N - 1 years

Fossil Point			South Jetty			Cape Blanco		
Valve Depth mm	Total Growth Bands	Years to Become Adult	Valve Depth mm	Total Growth Bands	Years to Become Adult	Valve Depth mm	Total Growth Bands	Years to Become Adult
28.7	119	3.3	28.1	141	4.1	41.2	488	17.5
29.5	115	3.1	32.8	186	5.8	32.7	457	16.3
26.9	91	2.2	37.4	136	3.9	45.4	443	15.7
28.6	95	2.3	31.8	170	5.2	36.5	397	14.0
26.3	88	2.1	34.5	147	4.3	41.9	430	15.2
24.6	85	2.0	40.7	200	6.4	36.3	790	29.1
28.7	97	2.4	32.9	158	4.8	28.6	522	18.8
29.1	93	2.3	33.2	173	5.3			
26.1	111	3.0	28.9	153	4.6			
29.0	102	2.6	32.3	159	4.8			
25.7	98	2.5	28.8	133	3.8			
31.1	94	2.3	31.0	159	4.8			
			34.2	168	5.2			
			32.2	177	5.5			
Average valve depth = 27.8 mm			Average valve depth = 32.8			Average valve depth = 37.5		
Average no. years to become adult = 2.5 years			Average no. years to become adult = 4.9 years			Average no. years to become adult = 18.0 years		

estimates (i.e., from young animals and replant studies, 34 to 40 months). According to this estimate, animals reach adult size at South Jetty and Cape Blanco in 4.5 and 18 years respectively. The greater amount of time required to reach adulthood is partly explained by the larger size of adults in harder rock, but mostly by the narrower growth bands.

Comparison of growth rates

If it is assumed that the interval between deposition of growth bands is constant in the three areas, the relative growth rate of medium-sized active animals can be estimated. The average numbers of growth bands in the 3rd and 4th cm of the umbonal ventral sulcus, the portion of the valve deposited by the medium to large active animals, may be compared (Table 7). On this assumption, South Jetty animals grow 0.6 times as fast as Fossil Point animals whereas Cape Blanco animals grow only 0.2 times as fast.

Sexual cycle

Over a period of two years the visceral masses of a total of 297 adult and 91 active animals were collected and prepared for histological examination (Appendix 2).

Fossil Point was the most intensively studied area. There was good correspondence between the 1963-64 sexual cycle and the 1964-65 cycle. Likewise at any particular time of year there was good correspondence between the sexual condition of adults from Fossil Point and those from other areas along the coast.

Active animals, throughout the season, were either completely immature (i.e., although gonad tubules were found, no gametes were present)

TABLE 7

Estimation of relative growth rate

Area	Fossil Point	South Jetty	Cape Blanco
Average no. growth bands in 3rd and 4th cm of umbonal ventral sulcus	33	55	152
Relative growth rate	$33/33 = 1.0$	$33/55 = 0.6$	$33/152 = 0.2$
N	13	14	7

or partially mature (i.e., although gonad tubules with active looking gametes were present they were never abundant and were widely scattered through the visceral mass). Larger active animals are more likely to have scattered gonadal tubules than small ones.

Animals in metamorphosis were usually in a partially mature condition. With few exceptions, adult animals, regardless of size, were in a fully mature condition (i.e., many large tubules filled with mature-looking gametes) from about June through November. In December, there is some evidence that spawning is taking place. Some of the females seem to be partially spawned out. Many of the males have tubules filled with degenerating sperm. By January some of the females have spawned out tubules whereas eggs in the others are irregular in shape and there is considerable cellular debris between them, indicating that they are beginning to degenerate. By February most of the animals are completely spawned out, or the unspawned gametes have been resorbed and the males are showing early signs of regeneration. In March, the gonads of adult animals are beginning to regenerate. They are about half regenerated in April and the gonads are fully regenerated by June. There is some evidence that there was partial spawning in early July 1964, since the gonads of nine animals collected on July 23 were partly regenerated.

Penitella penita is dioecious. In all of the animals examined there was no evidence of change of sex. There are significantly more males (60%) than females ($P < 0.01$).

Larval period

In a personal communication, K. W. Ockelmann, of the Marine Biological Laboratory, Helsingor, Denmark, states that he has no precise

data on the length of the pelagic larval life of pholads, but that it may be rather long. Moore (1947) states that Matesia striata in Australian waters spends about one month as a plankter. If further study bears out the observation that spawning of P. penita occurs in December and January and that most settling occurs from June through August, a 6- to 8-month larval period would be indicated.

Season of maximum settlement

Rock samples exposed for 2-month periods at various times during the year were examined for newly settled pholads. The data (Table 8) are incomplete and possibly unreliable because it was very difficult to locate the newly settled animals (Fig 21), which average less than 0.5 mm in length and are buried in algae-coated rock. Further variability was introduced because exact duplication of settling site conditions could not be achieved.

At almost any time of year some settlement can be demonstrated; however, the peak period of settlement is apparently June, July, and August. The smallest newly settled animals measured approximately 0.3 mm in length and depth. These animals have already partially buried themselves in the rock surface. No animals were found unburied on the rock surface, probably because of the washing treatment that the rocks were subjected to before they were examined.

It seems probable that August marks the end of a major settlement period. Rocks exposed between August 10 and October 4, 1964, received no larval settlement. However, rocks exposed between August 13 and November 2, 1963, received the largest observed settlement. It is of

TABLE 8

Intensity of larval settling

Period of exposure begins	Period of exposure ends	Duration of exposure	Approximate surface area of rock cm ²	Total no. of animals	No. of animals per 100 cm ²	Mean length
8/10/63	11/2/63	2 1/2	1,500	105	8	1.51 mm
11/2/63	12/29/63	2	1,500	5	0.3	.68 mm
12/29/63	2/23/64	2	1,520	0	0	-----
2/23/64	4/16/64	2	2,000	20	1	0.58 mm
4/16/64	6/10/64	2	450	15	3.3	-----
8/10/64	10/4/64	2	1,000	0	0	-----
6/27/65	8/4/65	1 1/4	450	15	3.3	0.65 mm

FIGURE 21

Young Penitella penita in Fossil Point rock. Maximum age 2-1/2 months. Length of valve approximately 1.5 mm.

Note that approximately 15 growth bands can be counted on the shell. The animal was probably about 0.33 mm long at the time of settlement. Therefore 5 of the bands were deposited prior to, and 10 after, settlement. Hence, the maximum interval between deposition of growth bands is 7.5 days.

interest that the average size of this population was considerably greater than the average size of other 2 south samples (Table 2). This can be



interest that the average size of this population was considerably greater than the average size of other 2-month samples (Table 8). This can be partly explained by the somewhat longer exposure period, by assuming that most of the settlement occurred soon after the initial exposure, and because larvae settling towards the end of a settling period are probably larger than those settling early in the settlement period (Bayne 1965).

Thorson (1946) states that success of larval settlement of sessile marine bottom animals is notably irregular. It is possible that in August 1963, settlement of P. penita was particularly heavy. It may be pertinent to note that settlement of the purple sea urchin, Strongylocentrotus purpuratus, was particularly successful in nearby Sunset Bay during the summer of 1963.

Factors affecting settling density

During the collection of samples for the study of growth rates, it was noticed that the density of animals per unit area varied considerably. Even on virtually uniform surfaces, density differences occurred. No tests were made to determine if the distribution was random or clumped.

One environmental variable that seemed to be related to settlement density is light. Settlement on surfaces facing approximately southeast was compared with those facing northeast (Table 9). The former surfaces quickly developed a heavy algal coating, presumably from the greater exposure to light, whereas the latter surfaces remained relatively free of algae but supported a heavy population of Balanus crenatus. The density of P. penita was greater on the northeast barnacle-encrusted surfaces than on the algae-coated surfaces.

TABLE 9

Settlement density as related to surface direction

Area (cm ²)	N	Southeast face algae covered	Northeast face barnacle covered	Exposure time (mo.)	Animals per 100 cm ²
50	44		x	2 1/2	88.0
70	3	x		2 1/2	4.3
190	21		x	6 1/2	11.0
350	16	x		6 1/2	4.6
800	353		x	8	44.1
800	157	x		8	19.6

This indicates that conditions required by settling pholads are similar to those suitable for B. crenatus settlement. It also seems likely that either algal cover or high light intensity inhibits settlement of both barnacles and pholads. (See Nagabhushanam 1960, 1959c, Isham et al. 1951 on taxis of marine larvae.)

Interference between barnacles and newly settled pholads

A certain amount of interference occurs during, and for a short time after settling, between young pholads and barnacles. If a pholad settles close to newly settled barnacles, it runs a risk of having its entrance occluded by the laterally expanding base of the barnacle. The pholad siphon, however, appears to be able to dissolve the edge of the barnacle and thus distort its symmetry (Fig 22).

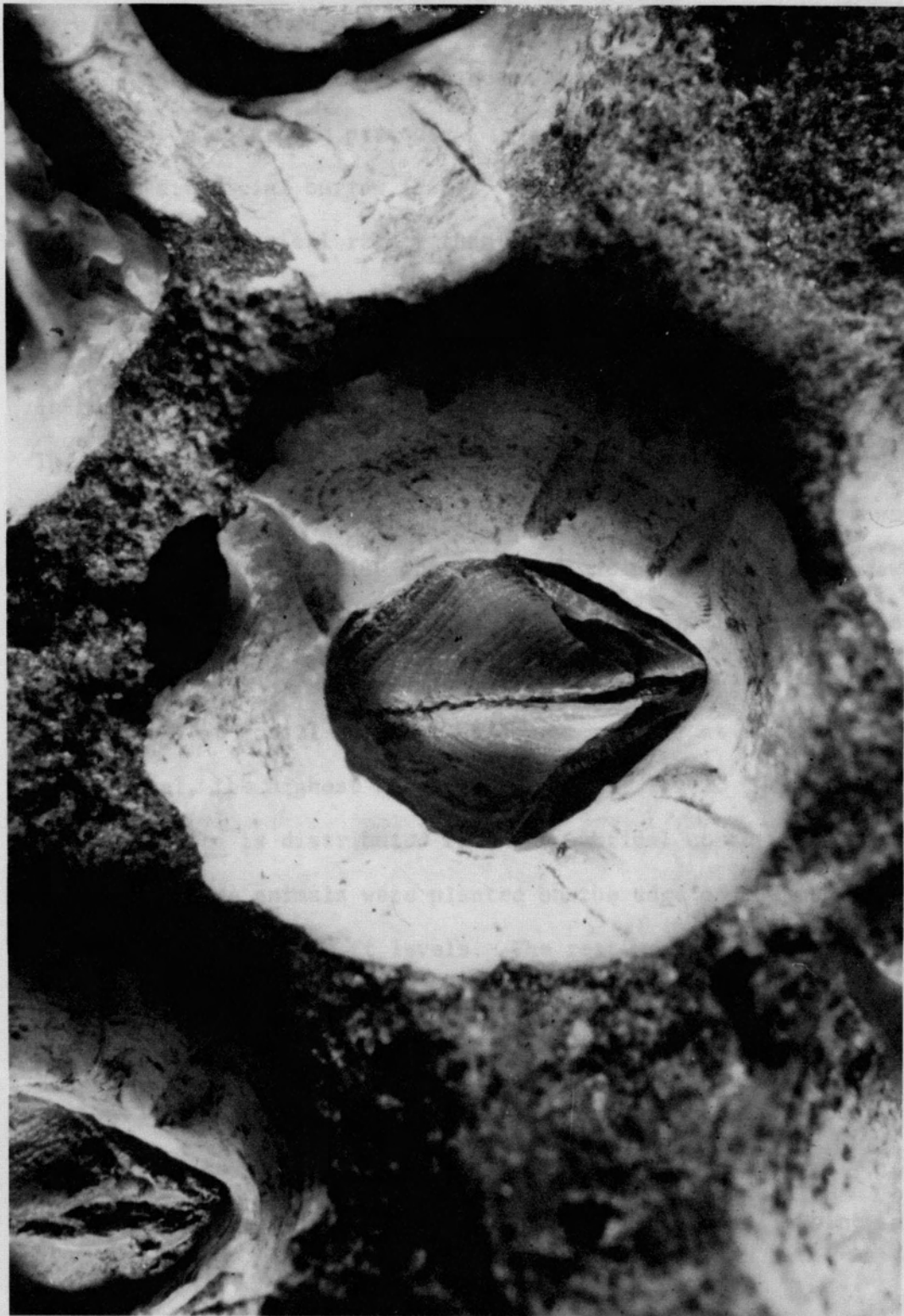
Examples of barnacles completely occluding burrow entrances were also found. The enclosed pholad was of course dead. It is not known whether the barnacle covered the entrance hole before or after the death of the clam.

Replant experiments

The replant experiments were designed primarily to provide data on growth rates of older animals. Individual growth rates were calculated by measuring animals before they were placed in and after they had been removed from artificial burrows which the animals occupied for a period of about 11 1/2 months. A number of experimental variables such as entrance diameter, height in intertidal, and substrate hardness were introduced while setting up the experiment; others (e.g., sand burial)

FIGURE 22

The distorted edge of the top central barnacle is caused by the young pholad siphon which emerged from the hole at the right. The siphon may have the ability to dissolve CaCO_3 .



were accidentally added during its course. Analysis of these variables yielded data on such varied subjects as morphogenesis, growth, survival, and duration of growth periods.

The artificial burrow (Fig 1) differs from the natural burrow in that it is cylindrical rather than conical and that the outer end is blocked by a rather sharply sloping polyethylene plug which has a fixed entrance diameter. How do the animals react to these abnormal conditions? In general, it appears that they adapt themselves very well and rapidly. The polyethylene plugs do not prevent the siphons from extending to the surface except in some cases of large animals inhabiting burrows with 3 mm entrances. Initially the shape of the burrow base is somewhat abnormal but this is quickly adjusted when the animal begins to bore.

A total of 180 Fossil Point animals were replanted in 10 horizontal rows at Fossil Point. The lowest row was at about the -2- ft tidal level, the highest at about the +4- ft level. Normally in this area P. penita is distributed from the subtidal up to the +2- ft level.

Sixty-nine animals were planted on the edge of the upper bench in the +1-, +2-, +3-, +4- ft levels. The rest were planted in the lower bench at or below the 0- ft level. For a number of reasons the results of replant experiments from the two areas will be treated separately.

At South Jetty, 11 South Jetty animals and 6 Fossil Point animals were replanted in a rock at about the 0-ft level. Conversely, 6 South Jetty animals were replanted in the lower bench, Fossil Point, at the 0-ft level.

Maximum growth rate of replants at Fossil Point

In the lower bench at Fossil Point the greatest size increase was found among animals that were originally 15.5 to 17.5 mm in depth and that were planted in burrows with 6 mm diameter entrances (Fig 24). In 11 1/2 months valves of these animals (still active) had increased in depth between 7.7 and 9.4 mm, about 50% increase.

From these data certain inferences can be drawn about the number of months required for P. penita to reach adult size at Fossil Point. When the above animals were originally planted, they were probably less than 2 years old. Animals of this size were commonly found in the 21 month exposed rock (Fig 19). The final depth of these animals ranged from 23 to 27 mm, which is well within the size range at which P. penita becomes adult spontaneously at Fossil Point. This suggests that P. penita can easily reach adult size within 3 years. It is conceivable that a rapidly growing individual could reach adult size in as little as 27 months. Since some 16-month-old animals measure up to 18 mm in depth. These time periods are in close agreement with growth rate estimates calculated from both growth band counts (Table 6) and from extrapolation of growth rates of populations of young animals of known maximum age (Fig 19).

Effect of entrance diameter on growth rate

When the Fossil Point animals, which were replanted in the lower bench, are separated into three groups according to the diameter of the entrance (3, 6, or 12 mm), some conclusions can be drawn as to the effect of entrance diameter on growth rate and survival.

Three mm entrance diameter (Fig 23). The total mortality in this group was 50%, mostly among the larger animals with depths of 19 to 24 mm. Most of these animals probably died of suffocation or starvation soon after being replanted. No growth took place in these animals. The few surviving large animals remained active or became adult, but in either case grew very little. Most of the few medium-sized animals (original valve depth 16.5 to 18.5 mm) survived and grew moderately before becoming adult. Most of the small animals (original valve depth 11 to 13 mm) survived and grew, increasing in depth about 7 mm during the 11 1/2 month period.

Six mm entrance diameter (Fig 24). The mortality among animals with 6 mm burrow entrances was only 8.5%. At least one of the three dead P. penita probably died as a result of predation by the flatworm Stylochus. All animals originally larger than 17 mm in valve depth became adult during the experimental period, after growing an average of 3 mm in depth. Most of the smaller animals (original valve depth 15 to 17 mm) remained active and grew an average of 8.5 mm.

Twelve mm entrance diameter (Fig 25). Originally, all of these animals had a valve depth of over 17 mm, and all that survived became adult during the 11 1/2 month period. The mortality of the group was 15%.

From these observations it is concluded that under replant conditions a 3 mm entrance diameter is just adequate until the animal reaches about 18 mm in valve depth, after which the siphon is so constricted that insufficient water is circulated to provide enough food and oxygen for growth and survival. A 6 mm entrance is large enough for any size of animal in the Fossil Point area. The question of whether mortality from

FIGURE 23

Growth and survival of P. penita replanted for about
11-1/2 months in Fossil Point rock. Entrance diameter 3 mm.

- | | | | |
|---|--------------|---|--------------------------------|
| • | Active alive | } | condition at end of experiment |
| ○ | Active dead | | |
| + | Adult alive | | |

P.g. Penitella gabbi

Try to combine Fig 23, 24, 25

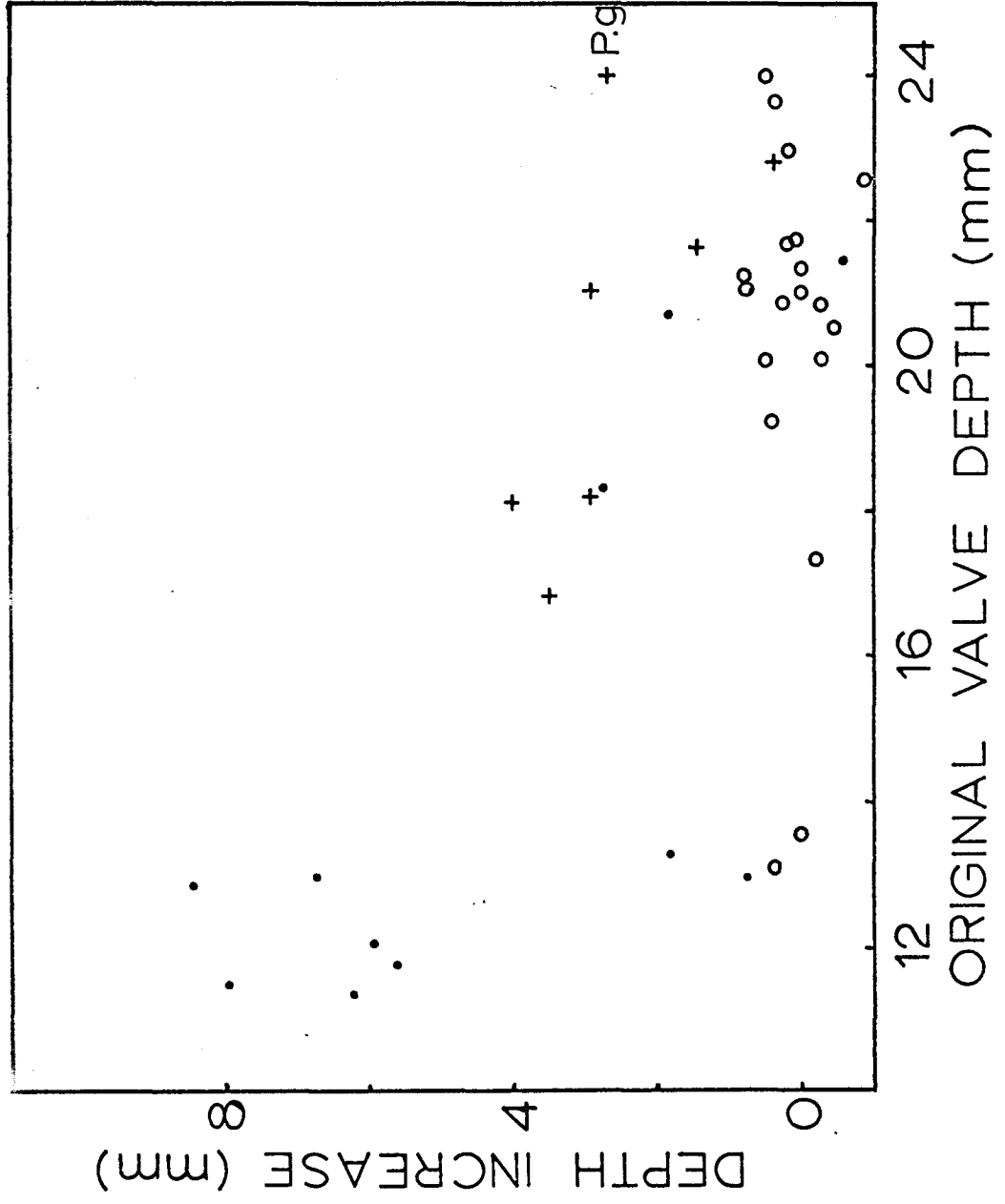


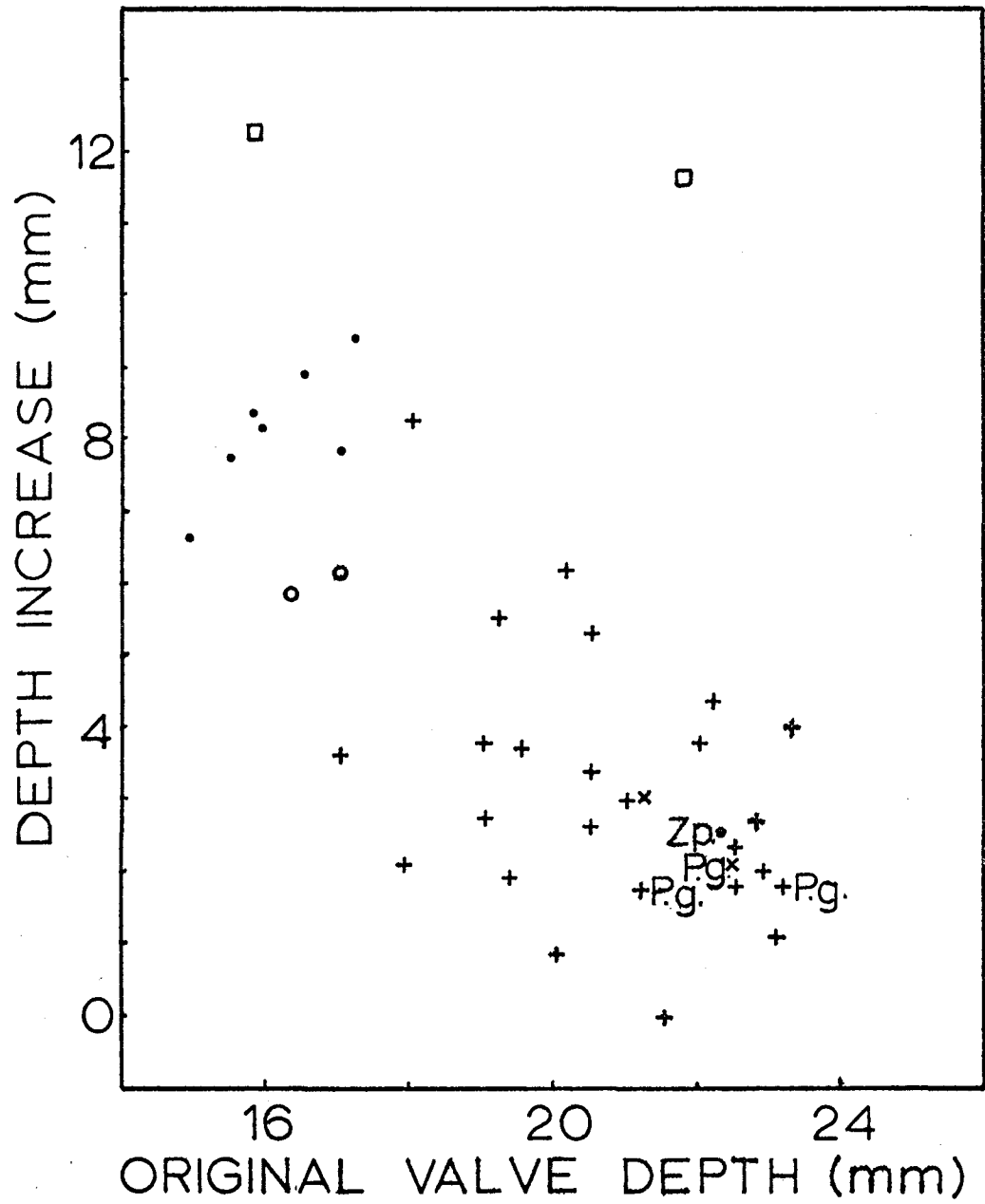
FIGURE 24

Growth and survival of P. penita replanted for about
11-1/2 months in Fossil Point rock. Entrance diameter 6 mm.

- Active alive
 - Active dead
 - + Adult alive
 - × Adult dead
 - Changing alive
- } condition at end of experiment

P.g. = Penitella gabbi

Z.p. = Zirfaea pilsbryi



Explain extra large charging animals.

FIGURE 25

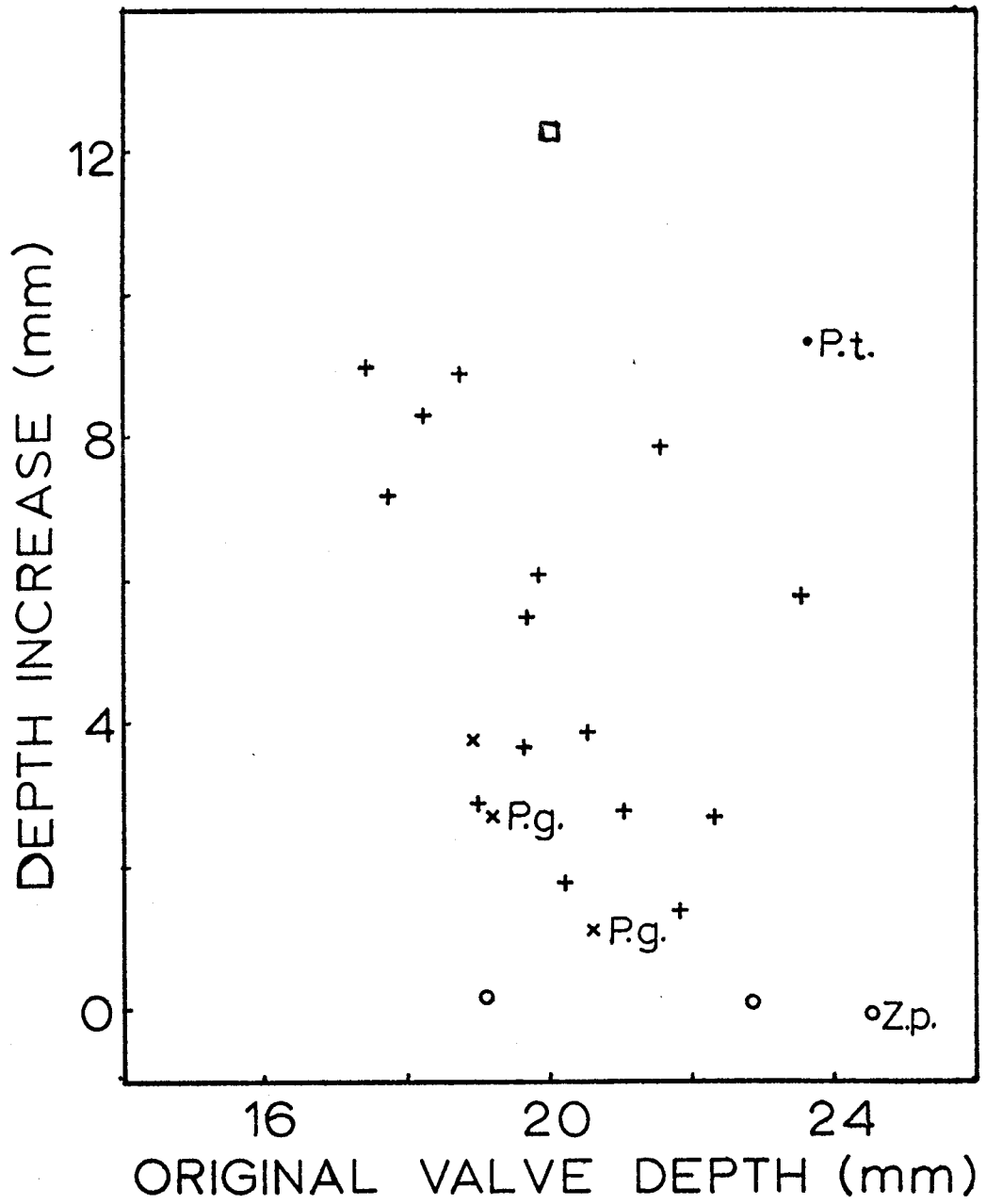
Growth and survival of P. penita replanted for about 11-1/2 months in Fossil Point rock, entrance diameter 12 mm.

- Active alive
 - Active dead
 - + Adult alive
 - x Adult dead
 - Changing alive
- } condition at end of experiment

P.g. = Penitella gabbi

P.t. = Penitella turnerae

Z.p. = Zirfaea pilsbryi



predation is greater in burrows with larger entrances cannot be answered at this time.

Factors inducing animals to metamorphose

Under uncrowded conditions P. penita became adult spontaneously within a specific size range that depends on the area in which they live (Table 2). Whether these differences are due to genetic factors, substrate hardness, or other environmental factors is not known. The size at which an individual becomes adult in any particular area is controlled to a certain extent by the diameter of the burrow entrance. Evidence for this comes from two sources; natural populations and replant animals.

The burrows of 53 mature adult P. penita from Fossil Point were examined. Four had entrance diameters 3 mm or smaller. The valve depths of the animals inhabiting these burrows (21 to 23 mm) were well below the average size for mature adults (25.5 mm). Since the animals were apparently not forced to metamorphose by crowding, it is probable that the substandard size is due to the narrowness of the entrance.

All Fossil Point animals replanted in burrows with 6 or 12 mm entrances became adult after 11 1/2 months if their original depth exceeded 18 mm. The amount of growth that takes place before the animal metamorphoses is highly variable. However, there is a slight tendency for the smaller animals to grow more than the larger. Animals in burrows with a 12 mm entrance diameter grow more before becoming adult than those in burrows with 6 mm entrances ($P < 0.01$). This may be due to the fact that food gathering is more efficient in animals with larger burrow entrances.

In the replant experiments, poor conditions, such as insufficiently large entrance diameter, sand burial and anaerobic conditions, inhibit growth but do not induce animals smaller than 20 mm to metamorphose. Crowding is the only known factor which will cause stenomorphs to form. Stenomorphs, whether complete or only in the process of changing, could not be induced to become active and bore again by replacing them in fresh uncrowded rock. Apparently once metamorphosis has begun, it is an irreversible process.

Morphology of the replanted animals

Animals which resumed active boring and remained active throughout the replant period maintained their normal shape except for a slight enlargement of the posterior ventral edges. Larger animals, which became adult without enlarging the artificial burrow, developed abnormally (Fig 26a). During the final period of lateral shell deposition (while the animal is metamorphosing) the margins of the valves are extended so as to fill the available space. As a result, in abnormal straight-sided burrows, the posterior ventral edges of the valves are extended more than usual, giving the animal a cylindrical rather than conical shape. Yonge (1951), in his study of the California mudstone borer, Platyodon cancellatus, observed that the greatest amount of growth occurs in the direction of least resistance.

Results of replant experiment in the upper bench

These replants were originally intended to complement those of the lower bench and to test the effect on growth rate of higher placement in the intertidal zone. Unfortunately the bottom half of this experimental

FIGURE 26

Modified morphology of some of the replants. Adult animals assume the shape of the burrow they inhabit.

- a) 535 Did not enlarge burrow after replanting
- b) 510 Enlarged burrow after replanting
- c) 563 Normal animal.

Scale 2 x

area was covered with sand by the middle of February. Records were kept



area was covered with sand by the middle of February. Records were kept of the approximate state of the sand at monthly intervals. It appears that row 7 was buried at least 5 months and row 8 at least 3 months; row 9 was partly buried up to 3 months and row 10 was never buried. Conditions in row 7 appeared anaerobic (the rock surface was black with sulfides and foul smelling) when the sand was shovelled away on July 15th. Barnacles on the rock surface survived some sand burial, but those below row 8 were all dead. The growth data for the four rows (Fig 27) indicate the following: (1) that animals can survive for a year in row 10, 2 ft above the normal vertical distribution. The growth rate, however, is much less than in similar animals planted in the lower bench or even in those that have been buried up to 3 months in rows 9 and 8. (2) Animals can survive sand burial for at least 5 months and anaerobic conditions for unknown periods of time. Growth during these periods however was inhibited.

Effect of substrate hardness on growth rate

The growth rates were compared in four classes of animals that had remained alive and active during 11 1/2 months of the replant period. The four classes are (1) Fossil Point animals in the lower bench of Fossil Point; (2) South Jetty animals in South Jetty rock; (3) Fossil Point animals in South Jetty rock; (4) South Jetty animals in the lower bench of Fossil Point. The data were kept separate for animals in burrows with 3 mm and 6 mm entrances (Fig 28). Growth bands were recorded (Fig 29). The different growth rates can be clearly seen in Figure 30.

Although the number of animals involved is rather low, the results seem to be clear. In the 6 mm entrance diameter group, South Jetty

FIGURE 27

Growth data from replant experiment in the upper bench
of Fossil Point.

<u>Row</u>	<u>Intertidal level</u>	<u>Sand burial</u>
10	+ 4 ft	none
9	+ 3 ft	mid March - June partial cover
8	+ 2 ft	mid March to June
7	+ 1 ft	mid Feb. - July 15th

-
- Alive Active
 - + Alive Adult
 - ± Alive Adult, but changing or changed
when replanted
 - x Changing
 - ⊙ Dead Active
 - ⊕ Dead Adult

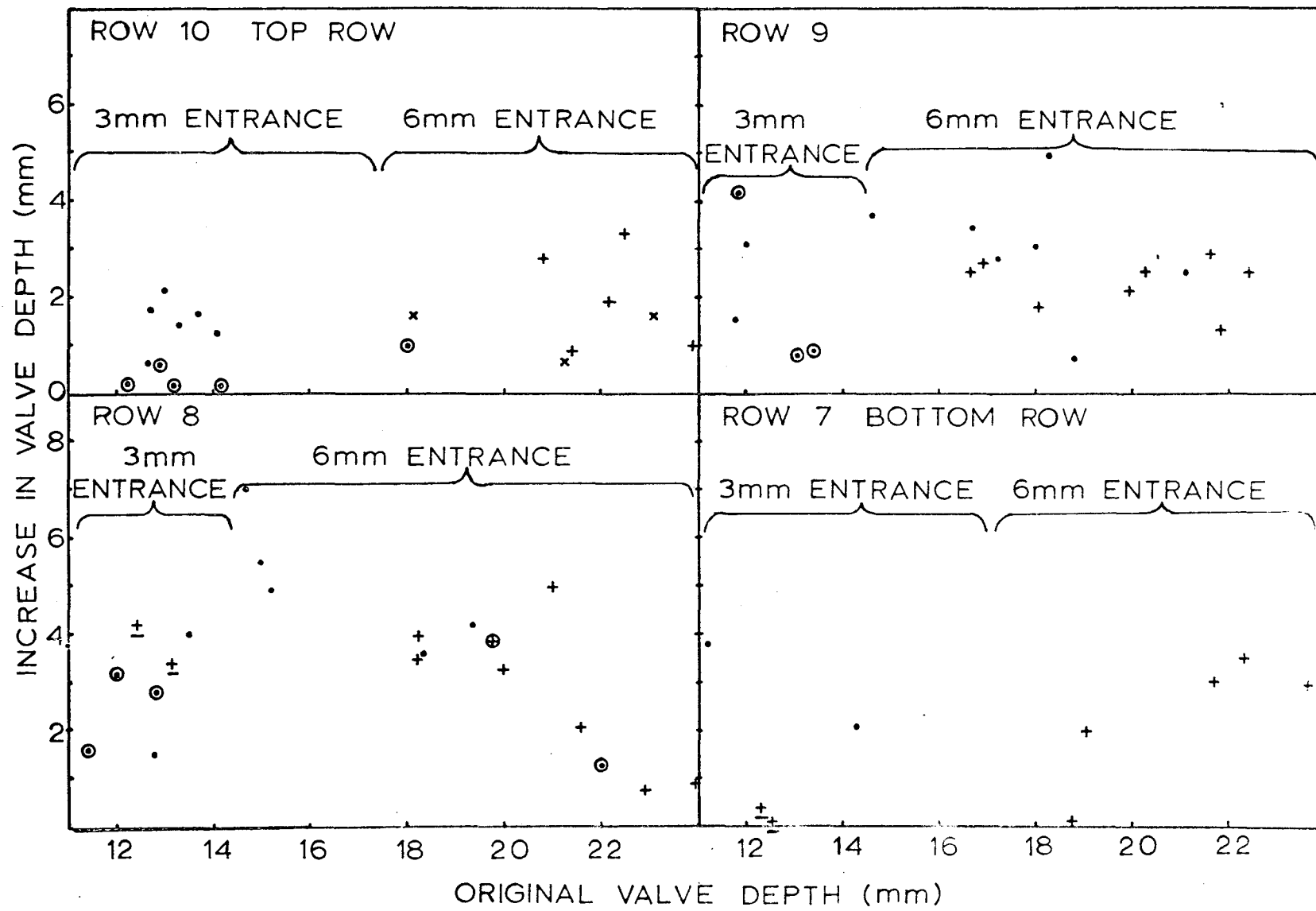


FIGURE 28

Growth rate of replant animals as related to rock hardness and original location in which the animal was growing.

- Fossil Point animal in Fossil Point rock.
- + South Jetty animal in South Jetty rock.
- ⊙ Fossil Point animal in South Jetty rock.
- ⊕ South Jetty animal in Fossil Point rock.

LP = Entrance plug lost during experiment.

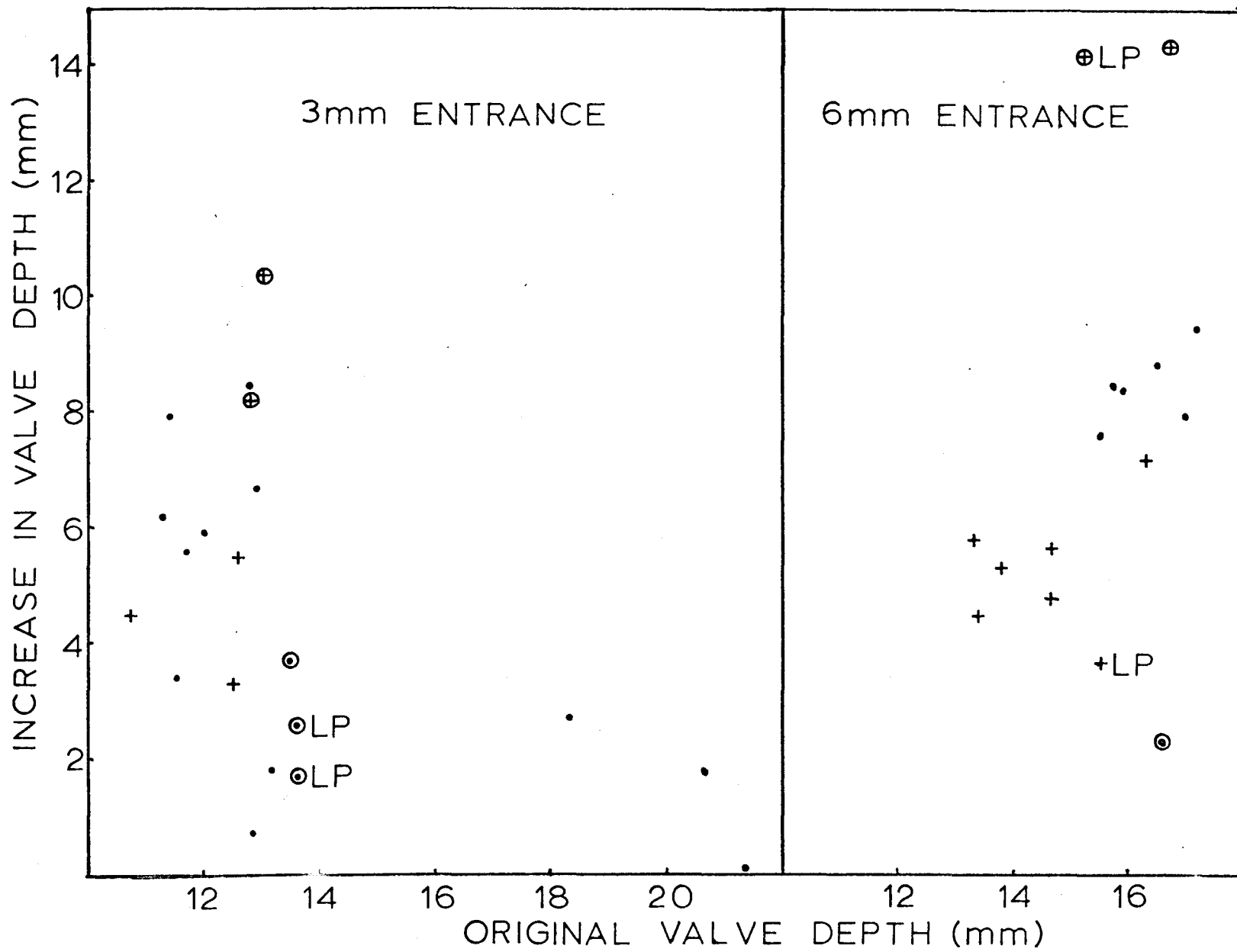


FIGURE 29

Number of growth bands deposited during 11-1/2 month experimental period as related to substrate hardness and area of origin.

- Fossil Point animal in Fossil Point rock.
- + South Jetty animal in South Jetty rock.
- ⊙ Fossil Point animal in South Jetty rock.
- ⊕ South Jetty animal in Fossil Point rock.

LP = Entrance plug lost during experiment.

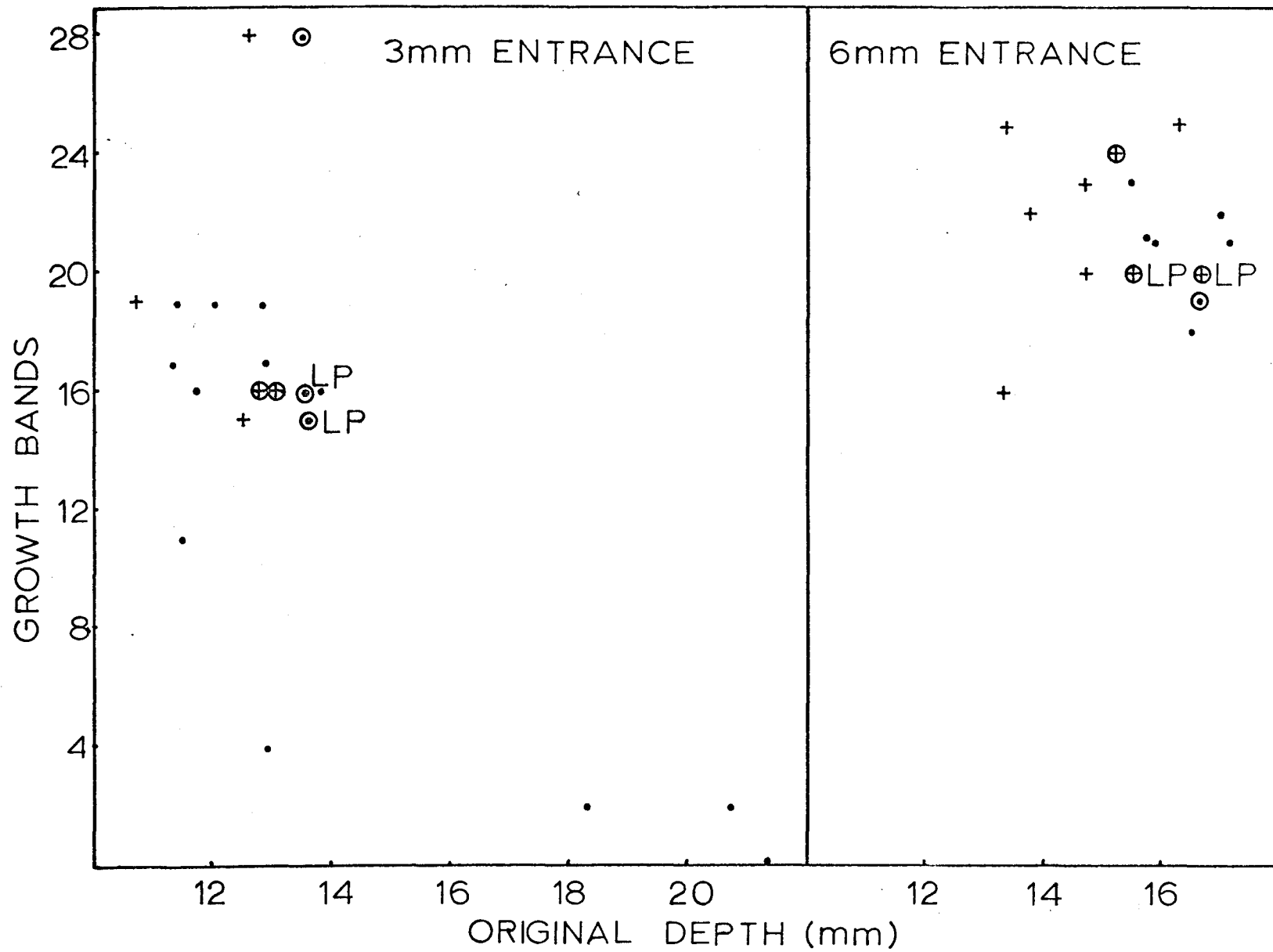
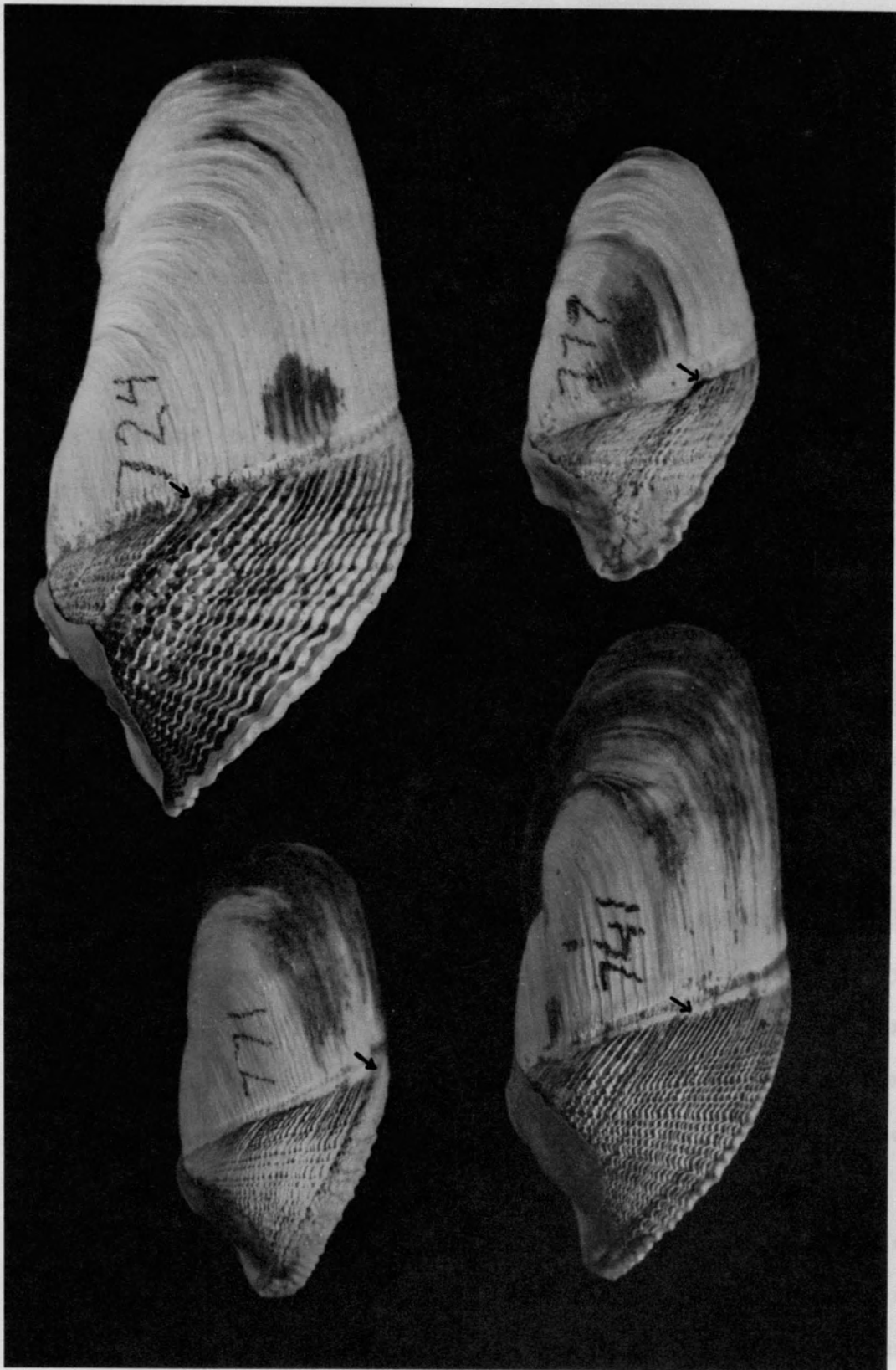


FIGURE 30

Effect of substrate hardness on growth of Penitella
penita replanted for about 11-1/2 months. Arrows indicate
size when experiment began.

- # 777 South Jetty animal replanted in South Jetty
rock
- # 741 Fossil Point animal replanted in Fossil Point
rock
- # 724 South Jetty animal replanted in Fossil Point
rock
- # 771 Fossil Point animal replanted in South Jetty
rock

Scale 2 x



mental/basis. In the first case, the two positions are considered as

animals in their native rock grow on an average 0.63 times as fast as Fossil Point animals in their native rock. This is close to the relative growth rate value (0.6) estimated by comparing the number of growth bands in the 3rd and 4th cm of the umbonal ventral sulcus (Table 7). In all four categories the average number of growth bands is about the same (21.0 at Fossil Point and 21.6 at South Jetty) for the 11 1/2 month period (Fig 29).

The very few animals that were successfully transplanted to a different rock type present an interesting contrast. Thin-shelled Fossil Point animals transplanted to hard South Jetty rock grew with less than half the speed of normal South Jetty animals. That part of the valve deposited during the replant period was thicker than the original valve. The number of growth bands was, however, about the same (19).

South Jetty animals transplanted to Fossil Point rock grew very rapidly, 1.7 times as fast as normal Fossil Point animals. Again, the average number of growth bands (22) was about the same.

The results of animals with 3 mm entrance diameter (Fig 29,30) are similar. The growth rates of most of the groups are considerably lower than those of animals in burrows with 6 mm entrances. The numbers of growth bands in general are somewhat lower also. This depression of growth rate and number of growth bands is probably due to the small size of the entrance.

The overcompensation of growth rate, as observed in South Jetty animals transplanted to Fossil Point rock, and the slow growth in the reverse experiment can be explained on either a genetic or an environmental basis. In the first case, the two populations are considered to

be genetically different, the South Jetty morph inherently having a heavier shell and greater boring powers than the Fossil Point morph. The other possibility is that the two populations are genetically identical, differences in morphology and boring powers being acquired characteristics.

The larval period of P. penita is probably quite long, allowing for a thorough mixing of larval populations from the various areas. The fact that no South Jetty morphs are found at Fossil Point, where their greater strength would give them an advantage over native Fossil Point animals, speaks against a genetic difference between the populations. The fact that the new shell deposited by South Jetty animals at Fossil Point was thinner than normal, and that deposited by Fossil Point animals at South Jetty was thicker than normal, suggests that the morphological differences are acquired due to environmental differences. The sustained overcompensation of growth exhibited by the South Jetty animals in Fossil Point rock on the other hand, suggests that South Jetty animals are inherently more vigorous borers than Fossil Point animals. The possibility that this is an effect of its early milieu seems remote considering the small size at which the animals were transplanted.

The role of *Penitella penita* in the Pacific coast endolithic community

Kuhnelt (1951) suggested the following terminology to describe the fauna of hard marine bottoms: animals living on the surface of rock occupy the epilithion, those partially embedded occupy the mesolithion, and those wholly embedded occupy the endolithion. The endolithic community is that of animals inhabiting the endolithion.

Penitella penita is the most numerous and most widely distributed rock borer along the eastern Pacific coast (Coan 1964; Turner 1955). It is found both subtidally and intertidally, on exposed coasts and protected bays wherever rock of suitable hardness is available. The boring activity of P. penita is primarily responsible for developing the endolithion as a possible habitat. The conical holes drilled by this animal form dwellings for a large number of nestling animals which move into the empty burrows after the pholads' death.

There appears to be little interaction between the organisms of the epilithion and P. penita except at the time of settling, when surface encrustations can inhibit settlement. Pholads, being filter feeders, derive their food from the overlying water. Botula californiensis, inhabiting the mesolithion, interferes with P. penita by settling in its burrow entrances or boring laterally into burrows. The interference caused is sometimes enough to kill P. penita.

The only animal that has been observed to prey on P. penita at both Fossil Point and South Jetty is the flatworm Stylochus sp. Pearse and Wharton (1938) report that S. inimicus is a predator of oysters. Stylochus can enter remarkably narrow holes. For example, a flatworm about 32 mm by 16 mm was found inside a burrow, the entrance of which was only 1.8 mm in diameter. Stylochus consumes the flesh of Penitella and leaves the valves in place. It often lays eggs on the inside of the burrow and valves.

The empty burrows left after the death of pholads are filled by a number of nestling animals, which make up the remainder of the endolithic community.

At Fossil Point the empty burrows eventually become filled with sand and mud, vertical burrows filling more quickly than horizontal burrows. Most of the silt-filled burrows are occupied by a terebellid worm, Thelepus sp., and its commensal scale worm, Halosydna brevisetosa. Thelepus appears to extract CaCO_3 from the pholad valves and desposit at least part of it as a chalky layer on the inside of its parchment burrow. The valves of the dead pholad are gradually dissolved completely.

Dead replant animals which were placed horizontally in vertical faces collected little silt during the 11 1/2 months of exposure. Usually these burrows were unoccupied but occasionally they contained nereid worms. The valves showed some, but not extensive, dissolution.

Occasionally bivalves such as Schizothaerus nuttallii, Petricola carditoides, Macoma nasuta and Irus lamellifer are found nestling in pholad burrows at Fossil Point. Addicott (1963) found fossil Tresus nuttallii (Schizothaerus nuttallii) nestling in P. penita burrows in rock of late Pleistocene age.

Just as the epifauna on exposed rocky shores is richer and more varied than in the muddy bays, so too the endolithic community in rocks exposed to the open ocean is more diverse. No attempt was made to compile a comprehensive list of organisms occupying this habitat, but the obvious forms were collected and identified (Table 10). On the open coast, 26 taxa were observed as compared with 9 at Fossil Point.

Pholads as agents of coastal erosion

Coastal erosive factors fall into two categories, biological and physical. The physical factors, which include wave action, sand scouring and solution, vary in their erosive power according to exposure and to

TABLE 10

Nestlers inhabiting vacated pholad burrows

Open coast	Fossil Point	Major taxa	Species
X		Coelenterata	Anthopleura artemisia
	X		Diadumene (Sagartia) leucolena
X	X	Annelida	Thelepus sp.
X	X		Halosydna brevisetosa
X			Serpula sp.
X			Eupolymnia heterobranchia
X			Ramex sp.
X			Pista elongata
X			Schizobranchia sp.
X			Distylia rugosa
X			Idanthersus sp.
X			Demonax medius
X		Sipunculoidea	Phascolosoma agassizii
X			Dendrostomum pyroides
X		Crustacea	Pachycheles rudis
X			Oedignathus inermis
X			Spirontocaris palpator
X			Betaeus harfordi
X		Mollusca	Crepidula nummaria
	X		Irus lamellifer
X			Trimusculus (Gadinia) reticulatus
	X		Schizothaerus nuttallii
	X		Petricola carditoides
X	X		Macoma nasuta
X			Protothaca staminea
X			Entodesma saxicola
X	X		Saxicava sp.
X			Kellia suborbicularis
	X		Botula californiensis
X		Urochordata	Pyura haustor

the chemical nature of the coast line. Chalk and limestone are more subject to solution than graywacke and granites. The biological factors include organisms like gastropods (Emery 1941) and chitons, which rasp algae from rock surfaces, a variety of chemical borers which attack carbonate rocks and mechanical borers which, like pholads, can attack both carbonate and noncarbonate rocks.

Because of the protected nature of the area and the chemical composition of the rock, I believe that at Fossil Point biological factors are much more important in erosion than the physical factors. One source of evidence for this belief is the slow rate of erosion due to physical factors acting by themselves. Rock around stainless steel screws placed in freshly exposed rock at the zero ft tide level in August 1963 was only eroded an average of 1 mm 2 years later.

Reid (1907) estimated that chalky, subtidal benches off the Norfolk coast were subsiding at a rate of 1 inch per year because of erosion caused by boring organisms. Jehu (1918) estimated erosion in the same area at about 1/2 inch per year. The rate of erosion at Fossil Point caused by borers cannot be estimated at this time. However, indirect evidence indicates that the bench must be eroding much faster than the 0.5 mm per year rate caused by physical factors alone. The burrows of some living, adult animals appear to have been shortened by as much as 8 cm, and it is inconceivable that these animals could live 160 years.

The upper bench at Fossil Point clearly shows the comparative effect of biological and physical factors working together and physical factors working alone. Pholads inhabit only the lower half of the bench, (up to

the +2 ft tidal level). The lower half is undercut, leaving the upper half jutting out (Fig 31). Hodgkin (1964) observed the same undercutting phenomenon on limestone benches but attributed it to the fact that the lower surface of the rock was exposed to the dissolving effect of sea water for more time than the upper portion.

At Fossil Point biological erosion can be ascribed to two bivalve families, Mytilidae and Pholadidae. The mytilid, Botula californiensis, probably has little erosive effect in this area, because of its relatively small size and low numbers. The Pholadidae, especially Penitella penita, the commonest form, are mainly responsible for rock destruction. The surface 7 to 10 cm are thoroughly riddled with burrows (Fig 32). This causes considerable weakening of the surface rock. The greatly weakened rock structure is probably crumbled by wave action and other physical factors. Erosion probably proceeds in a piecemeal fashion, rather than evenly over the whole surface.

Succession in the endolithic community

Hunter (1949) noted that bivalve boring is cyclic. An individual will only penetrate a relatively short distance into the rock. New borings will continue to be started until the outer layers of rock are honeycombed. A point will be reached where no further settlement or growth can take place without meeting interference from other burrows. If the greatly weakened surface rock were not removed by the mechanical action of the sea, the population numbers would with time decline towards extinction. However, erosion which probably proceeds in a piecemeal fashion, exposes fresh rock on which larvae can settle. An especially

FIGURE 31

Upper bench, Fossil Point, showing undercutting. Top of bench is at about +5 ft tidal level. Pholads bore actively up to about the +2 ft level.

Notice the rocks (foreground) which have broken off the flat face (center right) about 9 months previously.

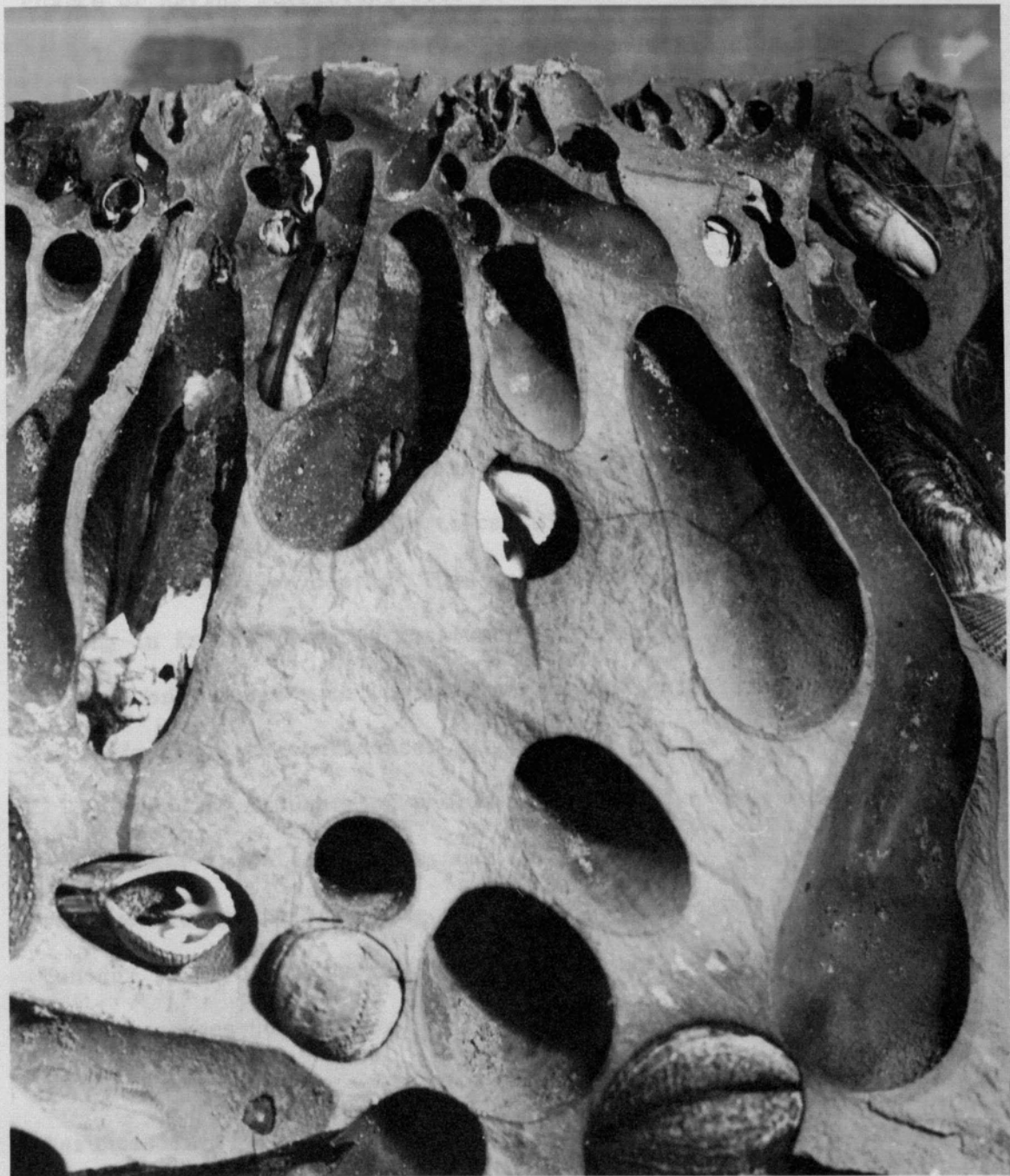


FIGURE 32

Photograph of a section of rock, collected near Newport, Oregon, to show crowded conditions. Rock from Fossil Point is crowded to a similar degree.

Scale Natural size

good site for new settlement is opened up when old large hollows are
shortened to such an extent that the openings are sealed off. In the
cup-shaped depression, several young shells can settle with a remarkable



good site for new settlement is opened up when old large burrows are shortened to such an extent that the nestlers are washed out. Into this cup-shaped depression, several young pholads can settle with a reasonable chance of having sufficient free rock for them to grow to maturity.

The primary limiting factor of the endolithic community appears to be space rather than food, which is available to some extent throughout the year.

Carrying capacity and utilization efficiency

Since pholads weaken the rock by their boring activity, it is of interest to know the proportion of rock that is actually removed at any depth. This can be estimated indirectly by counting and measuring the animals removed from a known area of rock. With a knowledge of the burrow shape, it is possible to calculate the area required by each animal at any given depth. This method only works with young animals boring in freshly exposed rock under reasonably uncrowded conditions because only under such conditions can the length and shape of the burrow be estimated with confidence.

The maximum number of pholads that can live in a square meter of rock, under these conditions, can be calculated. This value will be referred to as the "carrying capacity" of the rock. Because of the conical shape of the burrow, carrying capacity decreases as depth in the rock increases; also, since the angle of the cone increases in harder rock, the carrying capacity at any given depth decreases as substrate hardness increases.

Under hypothetical conditions of maximum utilization the burrows (all of one size) would have to be arranged in a honeycomb pattern. Each animal occupies a hexagonal area.

In order to calculate the area required by an animal at any particular depth it is first necessary to be able to estimate its valve depth. This can be done if the ratio of effective burrow length to valve depth of active animals is known. The value of this ratio varies with differences in substrate hardness and differences in the age and crowding condition in a given rock (Table 4).

Since the animal is somewhat loose in its burrow, valve depth is not a true measure of the diameter of the burrow. The valve depths of 17 active Fossil Point animals were compared with the maximum diameters of their burrows. The burrows averaged 0.9 mm larger than the depth of the valves (maximum 1.4 mm, minimum 0.4 mm). Also when calculating the area occupied by the animal one must take into account the fact that P. penita usually does not approach closer than 1 mm to a neighboring burrow. Therefore, 1 mm must be added to the burrow diameter to correct for wall thickness. The area required by an animal at any particular depth in the rock is therefore equal to a hexagon with an inscribed circle, the diameter of which equals the valve depth plus 1.9 mm to correct for space in the burrow and wall thickness. This diameter will be called the "effective diameter" of the animal.

The carrying capacity is obtained by dividing the area of the hexagon into one meter². The theoretical carrying capacity of different areas and depths is shown in Table 11.

TABLE 11
Theoretical Carrying Capacity

Rock depth (cm)	Crowded	Fossil Point		
		19-month animals	South Jetty	Cape Blanco
1	68,493	62,893	52,356	22,222
2	29,240	24,814	20,491	7,519
4	9,881	8,439	6,784	2,182
6	4,995	4,239	3,327	1,029
8	2,967	2,521	1,977	596
10	1,982	1,669	1,309	389
12	1,411	1,186	932	277*
14	1,071	891	694*	201
16	821*	690	539	156
18	658	550	429	124

* Maximum observed burrow length

Utilization efficiency

The efficiency with which the rock space is being utilized is determined by comparing the carrying capacity at a given depth with the actual number of animals that have reached or passed that depth.

The number of animals living at or below a given depth in the rock is assumed to be the number of animals that are equal to or larger than the mean theoretical size for that depth. This mean valve depth can be calculated for any particular burrow depth and substrate if the average ratio of effective burrow length to valve depth is known. For young animals (19 months maximum) at Fossil Point this ratio = 4.1.

The utilization efficiency of rock exposed for 12, 16, and 20 months at Fossil Point was calculated (Table 12). As expected, it increased at most depths with increased duration of rock exposure.

Boring behavior and probable sensory mechanism

Crowding is very common in pholad communities. Because the burrows increase in diameter as they become deeper, many more clams can settle at the surface than can live deep in the rock. An actively boring P. penita does not penetrate into neighboring burrows. When its base approaches within about 1 mm of a neighboring burrow, it will not bore further in that direction. Under such conditions it either turns to avoid the obstructing burrow, or, if there is no clear rock in another direction, ceases to bore entirely.

This ability to avoid neighboring burrows is a behavioral characteristic shared by most of the mechanically boring bivalves, including the Teredinidae, Pholadidae and others. However, exceptions to this rule

TABLE 12

Utilization efficiency using burrow shape of 19-month-old Fossil Point animal as standard. (ratio: effective burrow length to valve depth = 4.1)

A = Calculated effective burrow length cm = (Valve depth x 4.1)

B = Approximate carrying capacity at this depth in Fossil Point rock exposed 19 months.

C = Number animals/m² at or larger than given valve depth 12 month exposure

D = " " " " " " " " " " " 16 " "

E = " " " " " " " " " " " 20 " "

Valve depth cm	A	B	C	%utilization	D	%utilization	E	%utilization
.4	1.64	35000	2244	6.4	----	-----	3603	10.3
.6	2.46	16900	1333	7.9	2719	16.1	2897	17.1
.8	3.28	11400	815	7.1	1820	16.0	2164	19.0
1.0	4.10	8000	370	4.6	1180	14.8	1438	18.0
1.2	4.92	5800	133	2.3	683	11.8	890	15.3
1.4	5.74	4700	22	.5	401	8.5	432	9.2
1.6	6.56	3300			168	5.1	178	5.4
1.8	7.38	2900			53	1.8	41	1.4
2.0	8.20	2400			18	.8		

occasionally occur. Kofoid (1927) observed that occasionally one Teredo burrow passed directly through another. He suggests that the first animal was dead before the second entered its burrow, as otherwise it would doubtless have been able to protect itself by thickening its wall of nacre. Hunter (1949) observed that burrows of Hiatella occasionally intersect. Turner (1955) shows wood damaged by Martesia striata and Teredo. Apparently, M. striata makes no effort to avoid Teredo tubes. During my observations of many thousands of pholads and burrows, only one clear case of burrow intersection has been observed.

Botula californiensis, which sometimes nestles in the entrances of pholad burrows and sometimes bores actively, appears to make no effort to avoid other burrows. It has often been observed intruding into pholad burrows.

The sensory mechanism that enables borers to detect nearby burrows is not known, but one can hypothesize something of its nature from indirect evidence. The only sensory mechanisms that seem possible are either chemical, or vibratory. The latter seems more likely since P. penita avoids burrows regardless of their contents.

It is easy to imagine that the vibrations which result from the valves rasping the burrow walls during the boring movements could be monitored by the pholad. The intensity of these vibrations would increase as the thickness of the wall decreased. The actively boring P. penita turns to avoid a neighboring burrow when it approaches within about 1 mm; this implies that the sensory system is directional in nature. Proximity to a nearby burrow apparently inhibits boring activity when the animal has its ventral anterior side towards that burrow, but not when

its dorsal side is towards it. If a number of burrows surround the active animal, boring is inhibited completely because the ventral anterior side would receive strong feedback vibrations whichever way it turns. This complete inhibition of boring apparently triggers the start of metamorphosis, which results in a stenomorph.

DISCUSSION

In this study a number of aspects of the biology of Penitella penita have been examined. Interpretations of the individual analysis and experiments will be found in the main text. In this section, only the general ideas that have developed from this work and possibilities for future research will be discussed.

Differences in substrate hardness cause modifications in valve morphology and in growth rates. Animals from harder rock grow more slowly than those from soft rock. This has been observed before and is expected. However, the change in growth rate is not directly proportional to the difference in substrate hardness, animals from harder rock growing faster than would be expected. The heavier valves and proportionately larger muscles of animals in hard rock account for this increased boring vigor. Whether this difference in boring vigor is due to environmental conditioning or to genetic differences within the species cannot be decided at this time. With the methods for replanting well established, it should be possible to design experiments to answer this question.

Details of the boring behavior are not completely known. The relative duration of the periods of active boring and shell deposition of Penitella are presently being studied by Dr. Edmond Smith (personal communication). It would be of interest to know some of the factors that control the duration of the growth cycle.

The importance of Pholads as agents of erosion in areas of heavy infestation seems beyond question; however, no information is as yet available on (1) the relative importance of the physical and biological

eroders and how these factors interact, (2) how fast erosion proceeds in the heavily infested, undisturbed rock. If information were available on the latter point in any particular area, it would be possible to estimate roughly the age of adult animals and also to predict maximum life expectancy. Conversely, if the age of adult animals could be calculated, the rate of erosion in that area could then be estimated by measurement of burrow truncation. The fact that adult animals continue to deposit shell after becoming adult may be useful in this respect.

Growth in most mollusks may be indeterminate. However, growth of Penitella penita certainly terminates abruptly with the change from the active to the adult condition. Once the callum is deposited, boring movements are impossible and growth ceases. Normally sexual maturity in mollusks is reached quite early and reproduction continues throughout the remainder of the life span. In Penitella penita gonad maturation coincides with the end of the growth period. For the most part, active animals are sexually immature.

The factors that initiate metamorphosis are only partly understood. Crowding certainly induces stenomorph formation; if other environmental factors are involved, they are not known. The size at which larger animals metamorphose to adults is probably determined in part genetically and in part environmentally. In any area, adult size varies within a certain range. The size of an animal within this range appears directly related to the size of the burrow entrance diameter. Animals in burrows with small entrances are probably less efficient at gathering food than those with large entrances. Therefore, it is possible that within the adult size range metamorphosis is controlled by the food-gathering ability

of the animal. In different areas, the average adult size increases as the rock hardness increases. Whether this is a general phenomenon is not known.

Nothing is known of the physiological trigger that sets off the apparently irreversible metamorphosis. No detailed work has been done on the changes that take place at the histological level during metamorphosis. It may be of interest to follow the changes that take place in the cells of the dorsal extension of the mantle. Before adulthood, these cells secrete no CaCO_3 but start to deposit it at the onset of metamorphosis.

P. penita avoid boring into neighboring burrows by turning or by ceasing to bore altogether. This implies that they are equipped with a sensory system by which they can detect the presence and position of nearby burrows. I have hypothesized that this system is vibratory in nature, the animal monitors the reflection of its own boring noises. This sensory system has not been located. Knowledge of its morphology and physiology would make it possible to investigate in more detail the factors that cause stenomorph formation. This information could have practical application in the control of such economically important borers as Martesia striata and the Teredinidae.

Nothing definite is known about how the siphon of P. penita enlarges its burrow nor how it dissolves the edge of obstructing barnacles. The siphon of P. penita may dissolve CaCO_3 in a manner similar to the CaCO_3 dissolution observed in Lithophaga and the boring gastropod Urosalpinx cinerea.

Little is known about the relationship of P. penita to other members of the endo-, epi-, and mesolithic communities. The importance of various

predators and nestlers as causes of death and the sequence of organisms that inhabit the vacated burrow is not known.

Penitella penita, P. gabbi, P. turnerae and Zirfaea pilsbryi all inhabit a similar ecological niche in the same area. There may be competition between these forms for settlement space and space to grow. No attempt has been made to account for the broader distribution and greater abundance of P. penita.

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Appendix # 1

Mineral composition of the valve.

Penitella penita was found in substrates that differed considerably in hardness. P. gabbi, P. turnerae, Zirfaea pilsbryi were only found in the softest (Fossil Point) rock. In an attempt to provide an explanation for this different distribution it was hypothesized that the mineral composition of the valves might be different.

Necker (1839) claimed that the valves of Pholas crispata (Zirfaea crispata) consist of aragonite. Aragonite, the orthorhombic allomorph of CaCO_3 , is harder than calcite. Stenzel (1963) reported that the oyster shell is primarily composed of calcite with five small areas of aragonite located where the muscles insert and in the resilium. The mineral composition of valves of P. penita from Fossil Point, South Jetty and Cape Blanco and of P. turnerae, and Z. pilsbryi from Fossil Point were analysed by X-ray diffraction technique. The X-ray spectrographs were made by Mr. Wallace Johnson, Geology Department and analysed by Dr. L. R. Kittleman of the Museum of Natural History, both of the University of Oregon. All samples were composed almost entirely of aragonite.

Mineral composition, therefore, cannot be used to explain the different distributions of the Pholadidae.

APPENDIX 2b

Sexual Condition of Active P. penita

Date	Fossil Point			South Jetty			Other Areas			Sexual Condition	
	imm.	M.	F.	imm.	M.	F.	imm.	M.	F.		
63							Sunset Bay, Ore.			1	Scattered immature tubules
63	1										Scattered immature tubules.
63							Cape Blanco			1	Scattered tubules, mostly immature, a few with sperm
63	16	6	1								All very immature except two which have scattered tubules with mature sperm
63	4	4	1								All immature except one with scattered tubules containing mature eggs
63	10	2									Immature
64							Gold Beach			2 1	One immature male, one immature male with regeneration and sperm in scattered tubules, one regenerating female
64							Rocky Point			1	Immature
64				7	3	3					Immature or with moderately scattered tubules which contain mature gametes
64				11	3	5					Immature or with scattered tubules containing mature gametes. The larger actives are more likely to have gametes.
64				2	1						Immature or with gametes in scattered tubules
65	1			1		1					Immature or spawned out
65			1		1						Scattered tubules, male spawned out, female regenerating.
	32	12	3	21	8	9				2 3 1	Total number of actives - 91

APPENDIX 2a

Sexual Condition of Adult P. penita

Year	Fossil Point		South Jetty		Other areas		# M.	# F.	Sexual Condition of Most Animals
	# M.	# F.	# M.	# F.					
1963					Makah Bay, Wash.	1	1	Regenerating tubules.	
1963	51	34						All mature except 2 females which have scattered tubules with few eggs. 3 changing animals with immature tubules.	
1963	18	8						All mature except one female that looked spawned out.	
1963	5	6						Mature, except one changing female with scattered tubules.	
1963	8	7						Mature, except 2 females and one male which show few scattered tubules and rather immature development. 1 male looks spawned out.	
1964	5	8						All spawned out or partially so. One male with fairly full tubules filled with degenerating sperm.	
1964					Sunset Bay, Ore.	4	3	All but one female appear to be entirely or partly spawned out. The old sperm and eggs appear to be degenerating. Early regeneration of the tubule wall is taking place. No regional differences.	
1964					Windy Pt., Ore.	1	1		
1964					Gold Beach, Ore.	3	1		
1964					Rocky Pt., Ore.	2	3		
1964					Cape Blanco, Ore.		2		
1964	12	6						Middle regeneration.	
1964	6	4						Advanced regeneration.	
1964	6	3						Middle regeneration.	
1964					Cape Blanco, Ore.	1	4	Advanced regeneration, except 1 female immature, early regeneration.	
1964			11	10				All mature, crowded tubules, except 2 females with fewer scattered tubules.	
1964			3	3				2 males mature crowded, 1 with scattered tubules. 2 females mature crowded, 1 with scattered tubules.	
1964	4	4	4	4				The males from both areas have large tubules which are filled with broken down, degenerating sperm. The females are either fully mature or partially spawned out.	
1965	3	5	2	1				Females vary from spawned out to full tubules, eggs look somewhat degenerate. One male was spawned out, others had degenerating sperm in tubules.	
1965	3	2	3	3				Females were spawned out. Males - early regeneration, a few sperm in tubule, most of tubule in immature regenerating condition.	
1965	3	2	4	2				Females were in early regenerating condition. Males were mostly in early regeneration.	
1965	4	3						Both sexes were in early to middle regeneration.	
	128	92	27	23			12	15	Total Adults = 297

TYPED BY Mrs. Juma b. Sadi
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