EVOLUTION OF SUBSTRATUM PREFERENCE IN BIVALVES (MOLLUSCA)

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ABSTRACT—The occurrence of abundant *Lampsilis radiata siliquoidea* (Unionidae), a filter-feeding bivalve living on muddy substrata in the western basin of Lake Erie, has led to the evaluation of extrinsic environmental factors that affect the realized adaptive potential of the bivalve form. Comparison of substratum specificity of marine and freshwater bivalves shows that niche width is broader in freshwater forms because of such factors as reduced competition and predation pressure. The identification of these selective pressures which led to the evolution of substratum preference in bivalves strongly suggests that knowledge of the life habits of modern marine invertebrates is not sufficient to reconstruct the paleoecology of fossil forms. Any conclusions regarding paleoecology of a fossil group must also take into account selective pressures that may be reflected in such factors as the life position, orientation, and lithological associations of the fossils.

INTRODUCTION

THE TAXONOMIC diversity of suspension-feeding organisms is usually low on soft muddy substrata where the surface sediment is easily resuspended (Rhoads, 1970; Rhoads and Young, 1970; Aller and Dodge, 1974). Although suspension–feeders do not completely eschew muddy environments, they are mainly found in areas of these environments where the activities of various biological agents (e.g., tube-building polychaetes) locally stabilize the substratum (Rhoads and Young, 1971; Young and Rhoads, 1971).

Moreover, the sediment distribution of filter-feeding bivalves in the marine realm shows that with few exceptions they are usually found on bottoms where turbidity is low (see summary of Steele-Petrović, 1975). It is of interest, therefore, to report finding abundant *Lampsilis radiata siliquoidea* (Barnes, 1823) (Unionidae), a filter-feeding bivalve, living in soft, easily resuspended muds in the western basin of Lake Erie.

One purpose of this paper is to compare and contrast the substratum specificity of marine and freshwater bivalves. Differences in substratum preference may be due to some special morphological or behavioral adaptation or to some differences in environmental factors influencing distribution and abundance (e.g., predation) in these two realms.

We will examine the adaptations of the abundant and widely distributed *L. r. siliquoidea* to life on soft substrata, and in addi-

tion, summarize pertinent literature on the substratum preferences of bivalves. We hope not only to provide an explanation of the evolution of substratum preference in bivalves, but also to provide a further assessment of the adaptive range of the typical bivalve form, particularly as to how niche width is expanded or limited by extrinsic environmental factors.

LIFE HABITS

Methods.—Lampsilis r. siliquoidea (Text-fig. 1; see also morphological description by Clarke, 1973) and associated sediments (median grain size 3–4 μ) were collected by divers from depths of 7–9 m in the western basin of Lake Erie and were transported to temperature-regulated aquaria containing native western basin sediment and filtered Lake Erie water maintained at 19°C. Life habits described here are based on laboratory observations.

Biometric measurements follow the manner of Stanley (1970), as does terminology regarding burrowing, life position and calculation of burrowing rate indices (B.R.I.'s). Anastrophic burial techniques and terminology follow those of Kranz (1974). Radiographic equipment used in studying life position included a Continental GR-A radiography unit and Kodak X-Omat MA2 film.

Burrowing period and life position.—The manner of burrowing of this species is similar to that described by Trueman (1966, 1968a, b) and by Trueman et al. (1966) for marine bi-

valves and the freshwater bivalve *Margaritifera*. The burrowing period for the observed individuals encompassed at least several hours and occasionally took a day to complete. Burrowing rate indices calculated for this species show a mean of 0.06 (n = 4, with an average of 19 burrowing sequences). These values are representative of a very slow burrower.

Most of the animals burrowed until the posterior tip of the shell was flush with the sediment surface (Text-fig. 2). Because the sediments were cohesive, the bivalves formed small depressions in the general surface in achieving life position. Thus, while the shell posterior was flush with a local surface, it was actually located on the bottom of a depression 1–3 cm below the general interface. These burrowing activities often formed in the sediments a semi-permanent vent for water pressurized by valve adduction. Final life orientation of the angle of the antero-posterior axis with respect to the substratum surface, as determined by radiography, ranged from 55° to 75°, with a mean of 65° (n = 5).

Anastrophic burial.—The minimal escape potential of *L. r. siliquoidea* was determined by placing it on its native sediments, allowing it to achieve life position, and then burying it under 10 cm of sediment. This depth represents a generous estimate of the maximum depth of a sediment layer that could be deposited by any single natural event (most likely a storm) in western Lake Erie. In this way, it was found that the escape potential of this species is >10 cm. The time involved for escape was usually about 48 hours (cf. Imlay, 1972).

In other experiments, individuals were covered by a thin layer of sediment 1–2 cm deep. The animals cleared the sediment away from their apertural areas by ejecting water from the mantle cavity through these apertures, and not by burrowing. The normal sequence consisted of an interval of up to 5–10 minutes when the bivalves were inactive after this shallow inundation, followed by a burst of water that locally resuspended the sediments 7–8 cm into the overlying water. If the sediments were not sufficiently cleared away, one or two more jets of water were ejected within the next few minutes.

Water intake and ciliation.—Highly turbid mixtures of water and sediment introduced by pipette to the region around the inhalant ap-
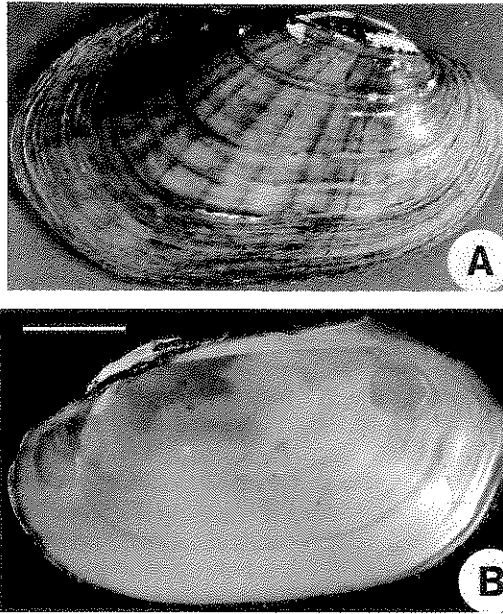

TEXT-FIG. *1*—Exterior (*A*) and interior (*B*) views of a right valve of *L. r. siliquoidea* collected from western Lake Erie. Scale = 2 cm.

erture were routinely drawn into the mantle cavity. Frequently, sedimentary aggregates >2 mm in diameter passed through the fringe of tentacles lining the inside of the aperture. Study of the mantle cavity with one valve and corresponding mantle lobe removed showed a gill ciliary pattern like that described by Atkins (1937) for other unionids, and by Tevesz (1975) for *Neotrigonia*. The predominantly posteriorly and ventrally directed pedal and mantle ciliation were likewise not unusual with respect to most other bivalve groups.

FUNCTIONAL MORPHOLOGY

The moderately inflated form of *L. r. siliquoidea* (average obesity = 1.5; n = 6) may enhance its bouyancy and help preclude its sinking into soft sediments. Living *L. r. siliquoidea*, whether extended from or retracted into their shells, did not naturally sink below the sediment surface. Also, this inflation allows for spacious lateral mantle cavities that permit retention of enough water between the valves to blow away a shallow covering of sediments from the inhalant and exhalant areas.

Behaviorally, the escape potential of >10 cm is obviously adaptive to its shallow-water environment where sediment may be easily
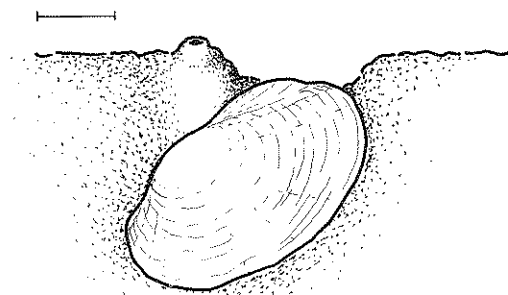
TEXT-FIG. 2—Life position of *L. r. siliquoidea* in soft mud substrata (median grain diameter = 3–4 μ) from western Lake Erie. Scale = 2 cm.

resuspended then redeposited by frequent storms. In this respect, the relatively large size of the collected individuals (average length = 6.3 cm; n = 6) compared to some marine forms found on similar substrata (e.g., see Levinton and Bambach, 1970) may be advantageous (see Kranz, 1974). Furthermore, the ability to survive at least two days completely buried in the sediment and the apparent tolerance to turbidity are also important adaptations to the muddy habitat. Interestingly, while the animal takes in copious quantities of sediment without apparent harm, there do not appear to be special ciliary tracts or other obvious internal structures designed specifically to cope with large amounts of ingested sediments.

The form and environmental preference of this bivalve do not seem consistent with its low rate of burrowing. Based on its somewhat streamlined, prosogyrous form, it might be expected to burrow more rapidly (Stanley, 1970, 1975). Since this form lives in sediments that may be easily eroded by currents (Fukuda, 1978), rapid reburrowing ability could be advantageous to the animal. By comparison, many marine bivalves living in unstable substrata are more rapid burrowers (Stanley, 1970).

While *L. r. siliquoidea* seems well adapted to its environment, from the standpoint of shell form and life orientation there is little to distinguish this species from a great variety of prosogyrous, equivalve, shallow-burrowing, moderate sized, infaunal filter-feeding marine bivalves. Some of these forms also have comparable escape potentials (Kranz, 1974). Curiously, such forms are almost invariably absent

from comparably muddy sediments in marine environments (see, for example, Rhoads, 1974).

SUBSTRATUM PREFERENCE OF MARINE AND FRESHWATER BIVALVES

Unionidae.—It is of interest to see if the substratum preference of *L. r. siliquoidea* in the collection area is typical with respect to its substratum distribution not only in other areas of the lake, but also in other parts of its geographical range. Also, it is of interest to see if the substratum preference of this species is unusual with respect to that of other freshwater bivalves, particularly Unionidae.

Within the western basin of Lake Erie, Wood (1953) showed that this species has an abundance peak on sediments of phi median of 7.3 (fine silt). Nevertheless, he also stated that this species occurred on most other substratum types as well. Brown, Clark, and Gleissner (1938) additionally reported this species (called by them *L. siliquoidea*) on bottoms varying from large rubble to sand to silt.

Lampsilis r. siliquoidea occurs widely outside Lake Erie. It is found from New York to Minnesota and as far north as the region near Great Slave Lake, occurring in both rivers and lakes (Clarke, 1973). Throughout this range, it has been reported from all kinds of substrata. In the Canadian Interior Basin, for example, Clarke (1973) found *L. r. siliquoidea* on all bottom types—clay, mud, sand, or gravel. Wittine (1969) reported its occurrence on bottoms ranging from predominantly mud to gravel in Hinkley Creek, Ohio. Interestingly, the bivalve preferred a sand bottom in this creek. Observations on the distribution of 158 *L. r. siliquoidea* from the Vermilion River, Ohio, confirm these published accounts regarding its wide substratum tolerance (Tevesz and Fisher, unpublished data).

This wide substratum tolerance and predilection for mud bottoms seem to be the rule rather than the exception among unionids and other freshwater bivalves. Cvancara (1970) reported *L. radiata luteola* and *L. ventricosa* occurring in large numbers in soft mud along the Red River, North Dakota. Wittine (1969) found *Anodonta grandis* occurring only on mud bottoms in Hinkley Creek, Ohio. Eighteen of the twenty-two unionid species from the western basin of Lake Erie described by Wood (1953) occurred on all bottom types

from silt-clay to sand and gravel, with maximum abundance on silt-clay bottoms. Clarke (1973) showed that eleven of the sixteen total unionid species inhabiting the Canadian Interior Basin occurred on muddy substrata. Moreover, at least fourteen of these sixteen species (representing nine genera) were found on a variety of substratum types. Clarke's Charts 1–9 illustrate in a particularly detailed manner this substratum non-specificity for *Anodonta* species.

Johnson (1970) gave a detailed account of the substratum distribution of 39 species of unionid bivalves (representing eleven genera) from the southern Atlantic slope region of the United States. Seventeen of these species (eight genera) were found to occur on mud bottoms (three of these species reported from "sandy mud"). Another two species were reported from nearly "every kind of substratum," thus likely including mud. Additionally, 24 species (nine genera) were reported from more than one substratum type.

Additional information confirming the frequent occurrence of diverse unionids on mud and of individual species on a variety of substrata are found in several papers, including Harman (1970) and Baker (1922, 1928).

Reference has also been made to wide substratum preference in other freshwater bivalves, including the corbiculacean *Rangea* (Davies, 1972). Also, many sphaeriid species, including *Sphaerium striatinum* from the Vermilion River, Ohio, are found on a variety of substratum types (Tevesz, personal obs.; see also Baker, 1928; Clarke, 1973).

Marine bivalves.—Marked contrasts exist between the sediment distributions of freshwater bivalves referred to above and the sediment distribution of most filter-feeding marine forms. For example, selecting from information concerning bivalve distribution compiled by Ford (1923) off Plymouth, England, it is possible to look at the taxonomic distribution of bivalves on at least three "pure" substratum categories: 1) gravels, 2) clean sand, and 3) black mud. Of the 46 total bivalve species he reported from these bottoms, only three species were found on all three kinds of substrata. Moreover, only ten were found on more than one kind of bottom.

Consolidating Jones' (1951) sediment categories into four main groups (gravel, fine sand, muddy sand, and mud), it is seen that of the 36 bivalve species reported off the south Isle of Man, only one species was found on all four sediment types; only two species were found on three of the four sediment types; and eight species were restricted to a single sediment type.

More examples of this substratum specificity of marine bivalves are shown by the data of Jones (1952) from a study of the bottom fauna off the Cumberland coast of England. Jones identified fifteen species of bivalves occurring on one or more of the following kinds of bottoms: fine sand, muddy sand, and mud. Of these fifteen species, only one was found on all types of bottoms, and six were restricted to a single substratum type.

Concerning the benthic communities of the ocean bottom off Accra, Ghana, Buchanan (1958) made the following comment: "In fact there are very few species which are common to two or more different communities, and in the cases where this happens, the species in common are generally important in one community but insignificant in the other communities in which they are present." Significantly, each of Buchanan's five communities was associated with a particular dominant sediment type (medium-fine sand; very fine sand; silty sand; sandy silt; coarse sand). Only one of the 34 bivalve species he mentioned was listed as occurring in more than one community.

In all these studies, the lowest species richness of bivalves occurred on muddy bottoms. Moreover, many of the forms mentioned as occurring on these bottoms were small deposit-feeding forms (see also Rhoads, 1974).

THE EVOLUTION OF SUBSTRATUM PREFERENCE

General.—The central purpose of this study is to explain the difference in habitat (substratum) selection displayed by the two groups of bivalves. That is, why are niche widths of freshwater unionids broader than marine filter-feeding bivalves? While we speak of "niche width," we are examining only one aspect of the bivalve niche (habitat use). As this approach is not without precedent (see MacArthur, 1972; Pielou, 1972; Levins, 1968; Colwell and Futuyma, 1971), and as the consideration of this dimension has yielded valuable results for a number of animal

groups, we retain both the terminology and the method here.

Unionids have apparently evolved no obvious, unique morphologic adaptations for life in soft substrata, so our explanation of the evolution of bivalve substratum preference will center on factors extrinsic to individual populations. In particular, we will explore the phenomenon of ecologic release and examine the role of climatic stability in determining niche widths.

Ecological release.—In the absence of competition or predation, an expansion of the species niche commonly results. This phenomenon has been termed ecological release, and has been described primarily for land birds in mainland-island comparisons (Crowell, 1962; Grant, 1966; Diamond, 1970; MacArthur et al., 1972, 1973; Cox and Ricklefs, 1977), mountaintop-lowland comparisons (Vuilleumeir, 1970; Brown, 1971, for mammals), and summer-winter comparisons (Cody, 1974).

Vermeij (1977) summarized the major groups of Recent aquatic molluscivores. Of the fourteen groups described by him, only three (Teleostei, Aves, decapod crustaceans) are potentially important freshwater predators. Freshwater lungfishes (Dipnoi) have a very restricted distribution and are probably not important predators today. Vermeij ignores the Mammalia, which contain both marine and freshwater predators, but these are important in freshwater environments only in shallow water (Call, 1898). Likewise, certain Turbellaria (flatworms) and Hirudinea (leeches) may be mollusc predators in both environments, but their importance has not yet been assessed to our knowledge. At any rate, important bivalve predators in marine environments— echinoderms, decapod crustaceans, and drilling gastropods—are relatively rare or absent in freshwater environments. In addition, the diversity and abundance of surface deposit-feeding invertebrates which graze juvenile molluscs are reduced in freshwater environments.

Many unionids possess morphologic and life history adaptations well suited to life on soft bottom environments. These include thin shells for lower bulk density, delayed maturity and slow growth to large size in a periodically unfavorable environment. These characteristics are not selected for where predation is intense. Echinoderms and decapods will devour both small and large bivalves (Coe, 1972; Christensen, 1970), and gastropods can more easily bore through thin than thick shells. Also, surface deposit–feeders will clear mud bottoms of slow-growing juveniles or metamorphosing larvae (Thorson, 1966; Muus, 1973). It is worth noting that unionids settle to the bottom as post-metamorphic juveniles (Coker et al., 1921) and, because of increased size and shell thickness compared to the larval state, partially avoid the problem of digestion by surface deposit-or filter-feeders.

Although it has been reported that filter-feeding bivalves are often absent from soft bottoms because they are not able to feed and respire effectively in turbid waters (Bretsky et al., 1969; Steele-Petrović, 1975), the evidence is not conclusive. Most experiments demonstrate increased mortality of filter–feeders only at unnaturally high turbidities of unnaturally long duration (Loosanoff, 1962; Davis et al., 1969; Ellis, 1936). In addition, experimental particle size distributions frequently do not reflect natural particle size distributions of solids resuspended from pelletized bottoms. The absence of suspension–feeders on soft bottoms may be more closely related to frequent burial of juveniles on these bottoms (Rhoads and Young, 1970). When suspension–feeders are provided with a firm footing *and* protection from predators, growth rates in turbid environments can increase (Rhoads, 1973; Rhoads et al., 1975). More experiments are required, but we suggest a synergism between substratum instability, predation, and grazing action to keep bivalves from fine-grained, soft substrata in marine environments.

Competitive interactions among molluscs on mud and sand bottoms have not been studied much. Eisenberg (1966) and Lassen (1975) noted the importance of competition in governing the distribution of freshwater gastropod species. Fenchel (1975a, b) documented ecological release and character displacement due to competition in marine deposit-feeding gastropods. Food limitation and the importance of competition have been postulated for marine deposit-feeding bivalves by Levinton (1972). Hylleberg and Gallucci (1975) demonstrated the adaptive advantage (enhanced growth) of resource specialization in the deposit-feeding bivalve *Macoma nasuta*. Among filter-feeding bivalves the situation is different. While there is anecdotal evidence for re-

source limitation and specialization (Solokova, 1959; Jørgensen, 1966; Loosanoff and Davis, 1963), the evidence for competition among the filter-feeding bivalves of mud and sand sediment is poor. In its absence, biotic control of bivalve distribution has been attributed to predation (Jackson, 1973, 1974; Stanley, 1973).

Climatic stability.—If resources undergo large seasonal fluctuations or are unpredictable in time, species cannot afford to specialize on them. Widely distributed generalist species with large populations are less liable to extinction and are selected for in unstable environments (Pianka, 1970; MacArthur and Wilson, 1967; Gadgil and Solbrig, 1972; Grassle, 1972; Cody, 1974; Southwood et al., 1974, among others). If resources are predictable and present throughout the year, then specialist species, because they are efficient in the use of those resources, will be selected for.

Although statements indicating the instability of shallow freshwater environments are easy to find (e.g., Patrick, 1970), it is difficult to make precise comparisons of the effects of climatic stability in marine and freshwater environments. On the basis of climatic (temperature and rainfall) patterns (Hutchinson, 1967; MacArthur, 1972), comparisons of zooplankton community structure (Allan, 1976) and molluscan diversity in river-lake systems and marine environments, it may be said that stability in most shallow freshwater environments is less than in marine open water (outer continental shelf and slope) environments and somewhere in between estuarine and normal marine inshore benthic environments. In addition, river basins and lakes are relatively isolated environments and chances for local extinction in these fluctuating aquatic environments are large compared, say, to oceans (Hesse, Allee and Schmidt, 1951). While a variety of estuarine benthos exhibit less substratum selection than deeper water benthos (Jackson, 1974; Fenchel, 1975a, b), filter-feeding bivalves remain uncommon on soft substrata in all these environments. It is only when predation or competition or both are reduced that mud bottoms are colonized.

The distribution of filter-feeding bivalves inhabiting both marine and brackish waters is instructive. The bivalves *Mya arenaria, Mya truncata, Mytilus edulis, Macoma balthica,* and *Cardium edule* are found primarily on fine sand bottoms in normal marine environments, but occur abundantly on soft mud bottoms in brackish waters (Remane, 1971). Remane attributes both this phenomenon and a tenfold increase in depth range of the *Macoma balthica* and parts of the *Abra alba* community to reduced competition and an absence of predators in brackish waters. Gage (1974) found a similar expansion of habitat use in brackish water by a variety of sea-loch benthos. Thus it is concluded that while some of the niche width differences between freshwater and marine filter-feeding bivalves are perhaps due to differences in climatic stability, this factor alone is inadequate to account for the observed patterns of distribution.

Other factors.—As the resource productivity of an environment decreases, niche width should increase, other factors being equal (see MacArthur and Pianka, 1966; MacArthur, 1972; Pianka, 1976, and contained references). Where food is scarce, an animal cannot afford to be selective about food items. Beggars, as they say, cannot be choosers. However, since freshwater bivalves appear to have broad niches in both productive and nonproductive rivers and lakes while marine bivalves have relatively narrow niches in variably productive environments, it is clear that productivity is not the major determinant of niche width in this case.

Species niches may differ along more than one dimension. Food resources and habitat utilization are two commonly contrasted dimensions. Species which have similar food requirements may use different habitats; similar species living in the same habitat may use different food resources. For example, Schoener (1968, 1974) and Pianka and Pianka (1976) demonstrated an inverse relationship of food resource and habitat utilization overlap among pairs of lizard species. Thus, it might be argued that the observed difference in niche breadth between marine and freshwater bivalves is the result of food resource specialization in freshwater bivalves relative to marine bivalves. The biology of suspension–feeding in both groups is still poorly understood, but given the opportunistic and seasonal nature of freshwater plankton, it is likely that food resource specialization in freshwater bivalves is poorly developed and possible only among long-lived individuals. This requirement of long life brings us back full circle to the ulti-

mate importance of the difference in predation levels in the two environments.

PALEOECOLOGICAL SIGNIFICANCE

The observations that niche width expands when marine species invade brackish water, and that freshwater bivalves have generally broader niches than comparably equipped marine varieties, both suggest that the adaptive potential of the bivalve form may be strongly influenced by extrinsic environmental factors such as competition, predation, and climatic stability. This means that caution must be exercised in using ecological information concerning living marine bivalves to infer the paleoecology of fossil forms. For example, Vermeij (1977) has presented data which suggest that predation pressure on marine molluscs has greatly increased since the late Paleozoic. It is thus reasonable to infer that significant molluscan niche shifts may have occurred over this time period.

In addition to habitat utilization, such important life habit information as ecological tolerance and life position could be erroneously reconstructed if the reconstruction were based solely on the life habits of similarly shaped Recent species. An example contrasting morphologically analagous freshwater (broad niche) and marine (narrow niche) bivalves demonstrates this point. Examination of the life position of 158 *L. r. siliquoidea* in the Vermilion River, Ohio, shows that this bivalve may typically assume either an infaunal or semi-infaunal posture on soft sediments and will nestle in or crawl over rocky bottoms. Yet marine forms capable of burrowing that are roughly similar in terms of shell form (i.e., prosogyrous, equivalve species such as most Veneroida) are in general typically infaunal.

This strongly suggests that observations of modern marine organisms do not always provide sufficient information for determining the paleoecology of similar fossil forms. It should therefore be emphasized that field data such as life position, orientation, and associated lithology must be integral parts of all paleoecological reconstructions.

CONCLUSIONS

We have emphasized the role of extrinsic environmental factors in influencing the evolution of substratum preference of marine and freshwater bivalves. We have given the example that under a certain selective regime

(reduced competition, or predation or both), large filter-feeding bivalves may occur in abundance on soft muddy bottoms. Given the reality of shifts in selective pressure over geologic time, generalizations derived from the study of Recent marine environments must be applied with caution to the fossil record. Information concerning life position, orientation, and lithological associations of fossils must be used in conjunction with life habit information derived from analagous Recent forms to accurately determine the paleoecology of fossil taxa. Freshwater environments may provide a valuable natural laboratory for deciphering the evolutionary paleoecology of animal groups held in common with marine environments.

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