American strain of H. petaloides to attack nematodes in this study, since only one species of nematode was used.

More species of gilled fungi capable of attacking nematodes will likely be discovered. The distribution and importance of these carnivorous fungi in nature and their ecological relation to other microbial inhabitants of their environments remain to be determined. Shigo (8)has reported a succession of microorganisms during the process of tree decay. In areas of advanced decay he found a variety of organisms in addition to the primary wood-rotting fungi (Hymenomycetes), including bacteria, nematodes, and other fungi. Blanchette and Shaw (15) reported that the presence of bacteria and yeasts significantly increased wood decay by the three Hymenomycetes tested.

Whatever their direct roles in nitrification and decay, bacteria are an important food source for free-living nematodes, and it would not be surprising if substantial populations of nematodes, as indicated by Shigo (8), were present in the decayed cores of standing trees. However, quantitative data on nematode populations in such habitats are scarce. We had the opportunity to analyze a sample collected from the rotting core (5 to 10 cm in diameter) of a standing maple (60 cm in diameter) within 6 hours of felling, and 912 nematodes per 100 ml of decayed wood were recovered after a 24hour extraction with the use of a Baermann funnel.

In habitats such as rotting wood where nitrogen is limiting because of scarcity or intense microbial competition, the ability of fungi to feed on nematodes may be a significant advantage. Gilled fungi which supplement their carbohydrates obtained by the breakdown of wood with a diet of captured nematodes are analogous in principle to the carnivorous higher plants which supplement their photosynthetic energy with protein from captured insects.

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Late Triassic Naticid Drillholes: Carnivorous Gastropods Gain a Major Adaptation but Fail to Radiate

Abstract. Infaunal and reclining bivalves of the Late Triassic Cassian Formation of northern Italy contain drillholes that closely resemble those produced by modern naticid gastropods. The oldest drillholes previously reported are from the late Early Cretaceous; this suggests that the drilling adaptation was lost soon after its appearance in the Late Triassic and originated independently in another naticid clade 120 million years later. The perceived selective value of such an adaptation may thus not always be a good predictor of its long-term survival, which is ultimately governed by factors that affect the speciation and extinction rates of the clade that carries it.

Drillholes produced by certain carnivorous gastropods, which penetrate the shells of their prey, are among the most readily recognized traces of predation in the fossil record. Analysis of fossil faunas for drillhole frequencies, positions, and preferred prey provides a direct means of assessing the evolution of predation and its ecologic impact on marine communities (1, 2). Occurrence of apparent naticid drillholes in Late Triassic bivalves, 120 million years older than the oldest previously known drillholes in the late Early Cretaceous, suggests that drilling capability evolved at least twice in the Naticidae. The innovation was apparently lost at the end of the Triassic, presumably because of extinction of the clade in which it originated, and reappeared in an Early Cretaceous species.

The Late Triassic (Carnian) Cassian Formation of the Southern Alps contains several benthic associations dominated by mollusks that inhabited fine-grained substrata in protected shallow-water environments (3). At least two kinds of borings occur in the shells of Cassian bivalves. One is a cylindrical tube 0.2 to 1.3 mm in diameter that penetrates the shell at various angles; borings of this type are difficult to attribute to any particular predator or sessile shell-borer. The second type of boring closely resembles holes drilled by naticid gastropods. These holes occur in the infaunal deposit-feeder *Palaeonucula* and the reclining suspension-feeder Cassianella (exclu-

sively in the lower, buried valve) and less commonly in other infaunal bivalves such as *Palaeocardita* and *Prosoleptus*; thus an infaunal or semi-infaunal habit is indicated for the producer of the drillholes. The borings are circular to slightly oval in plan view (outside diameter, 0.65 to 1.3 mm; mean, 1.07; N = 39) and exihibit the typical parabolic cross section of modern naticid drillholes (1-6) (Fig. 1A). Many of the borings are incomplete, which is unusual but not unknown in assemblages of naticid-drilled shells (1, 2), and incomplete holes exhibit the central boss typical of naticid holes-a result of the characteristic holecenter to hole-margin radular movements when drilling (4, 6). The drillholes are only present in articulated shells, as would be expected if the driller were an infaunal predator. Some shells contain four or five incomplete drillholes, but invariably only a single complete hole is present, further supporting the predator interpretation. Stereotypy of prey-handling behavior similar to that observed in naticids (1, 4-7) is suggested by the concentration of drillholes in the center of the lower valve of Cassianella and near the umbo in Palaeonucula; as observed by Kitchell et al. (1) in experiments with living naticids, multiple drilling sites on a single shell are adjacent to, or overlap, one another.

Naticid gastropods that could have been responsible for the drillholes are abundant in the Cassian Formation, notably Ampullina sanctaecrucis, A. paludinaris, and A. subhydridica (8). These species range in diameter from 5.0 to 10.0 mm; therefore, the relation between the size of the hypothesized driller and drill holes is in the range reported by Wiltse (9) for modern naticids (although the upper size limit of drillholes is larger) and is close to a line extrapolated from the data of Kitchell *et al.* (1).

These Late Triassic perforations, then, closely resemble drillholes of Cretaceous to Recent naticid gastropods in morphology, position, and chosen prey; they are readily distinguished from holes produced by other mollusks including muricid, capulid, cassid, cymatiid, and nudibranch gastropods and octopodid cephalopods (4-6, 10). Reports of Paleozoic gastropod drillholes have been generally discredited (11-13) [but see (14)], suggesting that the Late Triassic drillholes represent the initiation of the drilling habit in naticids, or perhaps in any gastropod. However, no comparable drillholes have been reported in the extensively studied molluscan faunas of the Jurassic. The oldest post-Triassic naticid drillholes are from the late Early Cretaceous (Albian) of England (11), followed soon thereafter by several occurrences in the early Late Cenomanian (12, 13). Sohl (13) relates the Cretaceous records to the first appearance of the naticid subfamily Polinicinae, and concludes that the pre-Albian naticids, primarily members of the subfamily Ampullospirinae, did not drill. Our data suggest that at least one ampullospirine species did in fact drill. The bearer or bearers of this innovation apparently became extinct, however, without giving rise to the kind of diversification that is generally regarded as the inevitable consequence of a major expansion of niche dimensions in the presence of few competitors (that is, exploitation of shelly, infaunal prey) (15).

Contrary to a purely deterministic view of macroevolution, the fate of a key innovation depends not only on its immediate adaptive value (and such innovations have surely triggered adaptive radiations in the past) but also on the speciation and extinction rates of the clade that carries it. Over geological time scales, these rates are governed by factors that may be unrelated to the innovation itself-in marine benthic naticids, for example, by larval dispersal capability, geographic range, and adult environmental tolerance (16). As Gould (17) pointed out, "Many features must come to prominence through their fortuitous phyletic link with high speciation rates.' 6 APRIL 1984

Conversely, many features must vanish not because they are maladaptive but because they originated in clades with low speciation rates or high extinction rates, or are lost through chance events early in the history of a clade when total number of constituent species is low (18). Unlike the ill-fated, innovative maxillary joint of the bolyerine snakes, lost with the extinction of the small island population in which it arose (19), the drilling habit in naticid gastropods appears to have originated a second time, probably in a different subfamily, some 120 million years after its initial appearance. The habit has persisted, with its bearers participating in the general diversification of durophagous predators that characterized the late Mesozoic (12, 20). Even if our familial assignment is incorrect, the fact remains that the predatory drilling niche was briefly occupied in the Late Triassic, then virtually unexploited until the mid-Cretaceous.

Our proposal that the drilling habit was lost by the naticids at the end of the Triassic can be readily refuted by the discovery of naticid drillholes in Jurassic fossils. Marine Jurassic sediments are more extensive, represent a greater range of environments, and have been more intensively sampled than those of Triassic age (21), so that the lack of recorded Jurassic drillholes suggests that drilling predators were indeed absent, or at least extremely localized or rare, during that period. At any rate, the widespread occurrence of drilling predation



Fig. 1. Naticid drillholes in Late Triassic (Carnian) bivalves from the Cassian Formation, northern Italy. (A) Complete and incomplete drillholes in *Cassianella ampezzana*; note central boss in incomplete hole. (B and C) Complete and incomplete drillholes in *Palaeonucula strigilata*; note placement of drillhole near (damaged) umbo in (B) and central boss of incomplete hole in (C).

was delayed until the mid-Cretaceous and thus cannot be linked simply to the presumed adaptive value of the drilling habit

The apparent reinvention of the drilling habit in naticids, or other instances of parallel or iterative evolution within a single clade, fits well with some interpretations of the role of development in the evolution of morphological novelties. In a hierarchically organized developmental system, recurrence of certain morphologies is to be expected because (i) developmental constraints limit and channel the spectrum of available innovations, and (ii) major phenotypic effects can be the result of relatively few or small changes in regulatory genes (22). We are not claiming that enzymes, radula, and other features of Triassic drilling naticids were identical to those of Cretaceous drilling naticids, or that the drilling habit arose each time in a single evolutionary step, but that ancestors of both the Triassic and Cretaceous forms possessed similar anatomies [and thus similar preadaptations (23)] and similar developmental programs that would tend to respond to genetic modifications and subsequent selection in similar ways (24). With regard to the naticids, then, the more difficult problem may be why there is a gap of 120 million years between the two origination events (25).

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rarely the most abundant taxa in subtidal benrarely the most abundant taxa in subtidal ben-thic communities, it is possible that the Triassic naticids were taking soft-bodied prey as well. Furthermore, undoubted drilling naticids are known to reach high abundances, and even dominate, in some Cretaceous and Cenozoic molluscan associations [N. F. Sohl, U.S. Geol. Surv. Prof. Pap. 331-A (1960), table 1; R. J. Stanton, Jr., E. N. Powell, P. C. Nelson, Mala-cologia 20, 251 (1981)]. W. I. Wiltse, J. Exp. Mar. Biol. Ecol. 42, 187 (1980).

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 Or, more strictly, potential exaptations [S. J. Gould and E. S. Vrba, Paleobiology 8, 4 (1982)].
 A second, and no less spectacular, example of parallel evolution in carnivorous gastropods is
- parallel evolution in carnivorous gastropods is parallel evolution in carnivorous gastropous is the apparently independent derivation in two turrid subfamilies of the true toxoglossan, hypo-dermic radula. This hollow, barbed, dartlike tooth allows rapid capture and envenomation of active prey [R. L. Shimek and A. J. Kohn, *Malacologia* 20, 423 (1981)].
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- 26 Taty, for the loan of the bulk of the investigated material and M. R. Carriker, S. M. Kidwell, J. A. Kitchell, N. F. Sohl, and two anonymous reviewers for comments. Supported in part by NSF grant EAR 81-21212 (D.J.).
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An Unusual Phycoerythrin from a Marine Cyanobacterium

Abstract. Phycoerythrin conjugates are reagents for cell sorting and analyses in which the argon-ion laser line at 488 nanometers is used for excitation. Many marine Synechococcus strains contain phycoerythrins with absorption maxima at approximately 490 and 550 nanometers; these maxima indicate the presence of phycourobilin and phycoerythrobilin prosthetic groups in the protein. Phycoerythrins of red algae contain both groups, but those of freshwater and soil cyanobacteria contain only phycoerythrobilin. Phycoerythrin purified from Synechococcus WH8103 has molecular properties typical of red algal phycoerythrins, but its phycourobilin content is higher than that of other phycoerythrins. The protein has absorption maxima at 492 and 543 nanometers and corresponding molar extinction coefficients of 2.78 and 1.14×10^6 ; it fluoresces maximally at 565 nanometers with a quantum yield of 0.5. Conjugates of Synechococcus WH8103 phycoerythrin could increase the sensitivity of cell analysis techniques to almost twice that possible with other phycoerythrin conjugates.

Phycoerythrins form a part of the photosynthetic light-harvesting antennae of cyanobacteria and red algae (1). In red algae, the visible absorption spectra of these proteins show peaks at about 566 nm and peaks or shoulders at about 540 and 500 nm with varying relative intensities (2). Red algal phycoerythrins carry two types of covalently attached tetrapyrrole prosthetic groups, phycoerythrobilin (PEB) and phycourobilin (PUB) (3). The PEB groups give rise to the 566- and 540-nm peaks, and the PUB's give rise to the 500-nm peak. In contrast, phycoerythrins purified from cyanobacteria isolated from soil or fresh water contain only PEB groups and do not exhibit the 500-

nm peak. The cyanobacterium Gloeobacter violaceus does contain a phycoerythrin with both PEB and PUB chromophores (4), but this organism is atypical in other respects as well (5). The difference in the bilin composition of red algal and cyanobacterial phycoerythrins may be related to the changing nature of solar radiation as it penetrates seawater. Marine algae are exposed to maximum transmission of light at approximately 500 nm (6), and the presence in these organisms of a photosynthetic accessory pigment (PUB) that absorbs maximally at this wavelength appears to be more than coincidental.

Unicellular cyanobacteria containing