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30. For PHA and PMA induction, Jurkat cells were treated with 50 ng/ml of TPA and 250 ng/ml of calcium ionophore (Sigma C-9275) 10 hours before the cells were harvested.

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Role of the Gastropod Shell and Operculum in Inhibiting Predation by Fishes

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In contrast to the diets of other cottid fishes and most teleosts, the diet of *Asemichthys taylori* is dominated by gastropod mollusks. Access to this underused prey appears to be made possible by morphological specializations of the neurocranium that allow *Asemichthys* to puncture the shells of its prey during mastication. Unpunched, the shell and operculum act as a barrier to digestion; more than 40% of the unpunched gastropods emerged alive in the feces. *Asemichthys* adjusted its punching behavior in an apparently adaptive way; other prey lacking such barriers to digestion were rarely punched. The ability of some shelled invertebrates to avoid digestion may make them less desirable as prey for many fishes that cannot masticate this kind of prey. The ability of shelled mollusks to survive in the digestive tracts of vertebrates may provide a dispersal mechanism for otherwise sedentary species.

A MAJOR GOAL OF FUNCTIONAL MORPHOLOGY is the identification of the potential adaptive roles of morphological structures in organisms (*1*). Of equal interest, albeit more difficult in practice, is the identification of limits imposed by morphology on ecology and behavior. Predator-prey interactions involving gastropod mollusks have provided several clear insights into this relation between form and function. Abundant paleontological and neontological evidence documents the strong influence of predation on shell form (*2*). Experiments reveal the role of such gastropod shell features as thickness, spire height, surface ornamentation, and aperture size in thwarting predators such as crabs and fish (*3*). These features are believed to constrain the suite of potential predators on gastropods. Fish species that prey extensively on hard-shelled mollusks are rare among teleosts and usually show structural adaptations for crushing their prey (*4*). In contrast, a wide variety of teleosts with and without crushing morphologies feed successfully on other comparatively hard-shelled organisms such as crabs.

I present evidence that minor modifications of a general body plan can allow a teleostean predator (*Asemichthys taylori*) access to this underutilized prey resource (gastropods). Further, cases of unsuccessful predation by this species highlight the value of a key morphological feature of the prey that may inhibit wider exploitation by fishes.

Asemichthys taylori is a member of the Cottidae, a family of benthic teleostean fishes found primarily in the temperate and boreal Northern Hemisphere. The range of *Asemichthys* extends from southeastern Alaska to Puget Sound, Washington. Cottids are diverse and abundant in intertidal and near-shore subtidal habitats of the northeast Pacific where they are important predators of benthic invertebrates, primarily crustaceans (*5*). The diet of *Asemichthys* differs from that of other cottids (*6*). Gastropods predominate (40% of the diet by mass), with three prosobranch gastropod genera (*Alvinia*, *Margarites*, and *Lacuna*) being the most common (*7*). Predation on a secondary prey, gammarid amphipods (20% by mass), also reflects the strong influence of gastropods in that one gammarid species common in the diet of *Asemichthys* is a Batesian mimic of *Lacuna* and *Margarites* (*8*).

Most teleostean fishes swallow their prey intact with a minimum of mastication (*9*). Most prey in the stomachs of cottid fishes, including *Asemichthys*, are intact. However, most snail shells consumed by this species show a distinct pattern of damage, ranging from a major punch (Fig. 1A) to a row of small holes (Fig. 1B) at a single site on the shell. *Asemichthys* lacks the structural modifications (robust bones and molariform teeth) of the primary jaws or the pharyngeal jaws that allow molluscivorous teleosts to crush their prey. The key morphological innovations producing these holes are found on the vomer, the anteroventral element of the

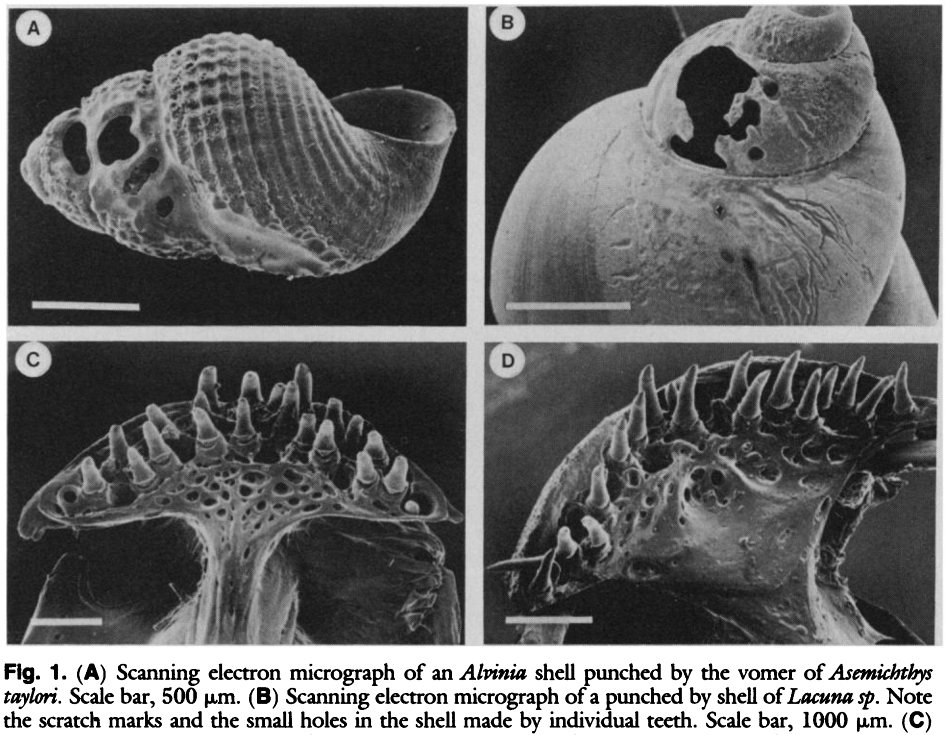

Fig. 1. (**A**) Scanning electron micrograph of an *Alvinia* shell punched by the vomer of *Asemichthys taylori*. Scale bar, 500 μm. (**B**) Scanning electron micrograph of a punched by shell of *Lacuna sp*. Note the scratch marks and the small holes in the shell made by individual teeth. Scale bar, 1000 μm. (**C**) Scanning electron micrograph of the anteroventral region of the neurocranium of a typical cottid, *Artedius harringtoni* (53-mm standard length). Scale bar, 250 μm. (**D**) Scanning electron micrograph of the anteroventral region of the neurocranium of *Asemichthys taylori* (48-mm standard length). Replacement teeth in the process of migrating anteriorly into the main row can be seen on the right side of the vomer. Scale bar, 250 μm.

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Table 1. Frequency of punched shells and number of survivors for the hard-shelled prey of *Asemichthys*. Gastropods were punched more often (*G* test, $G = 144$, $P < 0.001$, df = 2) and survived better when unpunched ($G = 97.78$, $P < 0.001$, df = 2) than did either bivalves or hermit crabs.

Taxon	Punched shells (%)	Unpunched shells (%)	Survivors (*n*)	Ingested shells (*n*)
Gastropods	76.5	23.5	23	238
Bivalves	7.0	93.0	2	72
Hermit crabs	9.1	90.9	0	22

Table 2. Frequency of punched shells and number of survivors for gastropods with operculi and for limpets that lack operculi (Crepidulidae and Acmeidae). The frequencies of punching (*G* test, $G = 2.069$, $P > 0.25$, df = 3) and survival ($G = 1.56$, $P > 0.50$, df = 3) were not significantly different among the taxa with operculi. However, these taxa were punched more often ($G = 42.42$, $P < 0.001$, df = 1) and unpunched individuals survived better ($G = 16.92$, $P < 0.001$, df = 1) than did limpets.

Taxon	Punched shells (%)	Unpunched shells (%)	Survivors (*n*)	Ingested shells (*n*)
Alvinia spp.	79.2	20.8	13	101
Lacuna spp.	86.1	13.9	7	72
Margarites spp.	77.4	22.6	3	31
Limpets	0	100	0	13

neurocranium. The vomer of a typical cottid is T-shaped when viewed ventrally and multiple rows of teeth extend onto the lateral wings, which are supported by the central shaft (Fig. 1C) (*10*). The vomer of *Asemichthys* is stout with a slight anteroventral curve, projecting into the buccal cavity. The short lateral wings are well supported by the central shaft and the teeth are arranged in a single row (Fig. 1D). Observations made during mastication show that strong dorsal movements of the hyoid drive the snail shell against the vomerine teeth, concentrating an impact load over a small area, leading to local failure of the shell (*11*). Punches in gastropod shells are comparable in size to the length of the vomerine tooth row.

Not all shelled prey are punched, and not all ingested prey die. In field samples, bivalves and shells inhabited by hermit crabs were rarely punched and the animals rarely survived (Table 1) (*12*). In contrast, more than 75% of the gastropod shells were punched, and more than 40% of the unpunched gastropods survived passage through the digestive tract. Examining the patterns of punching and survival among the gastropods reveals a compelling explanation for punching. Among the gastropods, the three most common genera had similar, high frequencies of punching and survival, but none of the limpets were punched or survived (Table 2). The key morphological difference between these two groups is that limpets lack an operculum (*13*). The operculum and shell combination of these prosobranch gastropods prevents digestion. Punching the shell circumvents the operculum and allows digestive enzymes access to the soft parts of the snail. The hard shell is the vulnerable element. Hermit crabs lack a structural analog to an operculum and require no special handling to promote digestion. Most of the bivalve species eaten by *Asemichthys* lack snug-fitting valves and are vulnerable to digestion (*14*).

The shells of bivalves have the potential to function as barriers to digestive enzymes. In laboratory feeding experiments that examined the ability of a bivalve with snug-fitting valves to survive ingestion by *Asemichthys*, four of ten unpunched *Transennella tantilla* were recovered alive in the feces, but none of the punched individuals survived (*G* test, $G = 6.39$, $P < 0.01$, df = 1) (*15*). *Asemichthys* can adjust its mastication when feeding on prey with this ability, punching 22 of 32 *T. tantilla* ingested in the laboratory experiments, a higher frequency than seen for other bivalve species recovered from the feces (*G* test, $G = 61.28$, $P < 0.001$, df = 1). The mechanism by which *Asemichthys* distinguishes "vulnerable" and "protected" bivalves is unknown.

Asemichthys does not punch all gastropods it eats, although the shells of these species do not appear to be too tough to punch. Shells from genera lacking sculpture were not punched more often than those from genera with sculpture, nor were smaller (thinner) shells punched more often than larger shells (*16*). Many unpunched shells show no evidence of mastication (scrapes, scratches, and so on). Perhaps the unpunched gastropods are the beneficiaries of overly vigorous strikes by *Asemichthys*. During suction feeding, the momentum of the high-speed suction jet may carry the prey directly into the stomach before an opportunity for buccal processing can occur.

The relation between *Asemichthys* and its molluscan prey has broad implications for fish-mollusk interactions. The role of the operculum and shell as a barrier to digestive enzymes provides a plausible explanation for the scarcity of prosobranch gastropods in the diet of most fishes without shell-crushing mastication. Why eat what you cannot digest? Gastropods that lack the operculum and shell combination often have other means of deterring predation (*17*). The ability of shelled mollusks to survive in the digestive systems of vertebrates could provide a dispersal mechanism for otherwise sedentary species (*18*).

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6. The diet of *Asemichthys* was determined by standard diet analysis techniques [E. J. Hyslop, *J. Fish Biol.* **17**, 411 (1980)] applied to the stomach contents of 105 individuals collected in fall 1982 and summer 1983 from subtidal habitats in the San Juan Islands of Washington. Gastropods constituted 40% of the prey by number and occurred in 35% of the individuals. Twenty-five percent of the prey individuals were gammarid amphipods; they were found in 20% of *Asemichthys* examined. Bivalves constituted 10% of the diet by mass.
7. *Lacuna* species in the diet include *L. variegata*, *L. vincta*, and *L. marmorata*. *Margarites* species include *M. helicinus* and *M. pupillus*. The taxonomy of small *Alvinia* is not well resolved.
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10. In most cottid fishes, including *Asemichthys*, villiform teeth cover the tooth plates of the upper and lower pharyngeal jaws and are arranged in rows along the dentary and the ascending process of the premaxilla. In all cottids examined, except *Asemichthys*, there are at least two complete rows of teeth on the vomer [S. F. Norton, unpublished observations; M. Yabe, *Mem. Fac. Fish. Hokkaido Univ.* **32**, 1 (1985)].
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12. To document the pattern of punching and survival of the hard-shelled prey of *Asemichthys*, 176 fish (mean ± SD; 42.3 ± 6.3 mm standard length) were collected in the field and placed in individual holding tanks. Fecal boli from each individual were collected over the next 48 hours and examined for the presence of punched shells and live prey. Hermit crab shells were identified by the presence of exoskelton at the aperture. Gastropods and bivalves were determined to have survived if they demonstrated closing behavior after disturbance. Three ostracods were also recovered alive in the feces. Live gastropods with well-developed operculi have been reported in the feces of an opisthobranch snail [R. T. Paine, *Veliger* **6**, 1 (1966)] and a starfish [A. M. Christensen, *Ophelia* **8**, 1 (1970)].
13. Among the subclasses of gastropods, a snug-fitting operculum is common only among the prosobranchs [L. Schmekel, in *The Mollusca*, E. R. Trueman and M. R. Clarke, Eds. (Academic Press, New York, 1985), vol. 10, pp. 221–267; A. Solem, S. Tillier, P. Mordan, *Veliger* **27**, 193 (1984)].
14. The bivalve species common in the feces, *Entodesma saxicola*, *Lyonasia californica*, and *Hiatella arctica*, lack snug-fitting valves, except *Clinocardium nuttalli*.
15. In the bivalve experiments six *T. tantilla* (1.1 to 3.2 mm in length) were presented to each of 15 *Asemichthys* in individual holding tanks. All uneaten bivalves were removed after 4 hours. Ingested bivalves were collected from the feces after 48 hours and examined for punching and survival.
16. The frequency of punching among *Lacuna* (no sculpture), *Margarites* (spiral sculpture), and *Alvinia* (spiral and axial sculpture) did not differ significantly (*G* test, $G = 1.75$, $P > 0.25$, df = 2). Nor were there significant differences in the size of punched versus unpunched shells in each genus (*Alvinia*, $t(91) = 1.60, P > 0.10$; *Margarites*, $t(30) = 0.228, P > 0.75$; *Lacuna*, $t(60) = 0.306, P > 0.75$).
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Technical Comments

Testing for Periodicity of Extinction

In several papers (*1–4*), we have argued that the extinction record of the past 250 million years (my) shows a 26-my periodicity. Stigler and Wagner (*5*) have challenged this conclusion on two grounds. First, they have found a 26-my periodicity embedded in the geologic time scale such that any random assignment of extinction events using that time scale has a nontrivial likelihood of showing a 26-my periodicity. Second, they have shown that the tendency for random series to exhibit the 26-my periodicity is enhanced by applying a certain kind of moving average filter (designed to simulate the Signor-Lipps effect).

We consider the challenges here in the order of their presentation by Stigler and Wagner. An interesting irony of the first challenge is that the Stigler and Wagner analysis actually strengthens the case for periodicity.

In our first paper (*1*), we wrote (p. 803): "the results could have been generated by periodic elements in the time scale itself rather than from the distribution of extinctions." This was a natural question to raise because the geologic time scale is based in large part on extinctions (*6*).

The basic geological chronology was developed in the 19th century before the discovery of radioactivity, and most of the named intervals were established on the basis of changes in fossil biotas. It is thus no accident that most of the mass extinctions fall at or near major boundaries in the time scale. The well-known Cretaceous-Tertiary (K-T) extinction at the end of the Cretaceous marks the boundary between two eras (Mesozoic and Cenozoic). The largest mass extinction of all is at or near the Paleozoic-Mesozoic boundary. The Jurassic-Cretaceous boundary is based on an extinction event in the Tithonian stage, and so on.

With the discovery of radioactivity in the 20th century, the fossil-based chronology was calibrated by a few radiometrically dated "tie-points," but the classification of geologic time was not altered by the calibration. Therefore, if extinctions carry some periodic signal, one would expect it to be reflected in the radiometric time scale to the extent that boundaries are located at times of extinction. This is not to say that all boundaries in the time scale are at major extinction events, because other criteria for defining boundaries have been and are used. But the historical connection between the time scale and extinction is incontrovertible.

Because times of extinction so pervade the geologic time scale, it has even been suggested that the best way to look for extinction periodicity is to analyze the placement of the time boundaries rather than to work with the raw data of extinction (*7*). Bayer (*8*) has carried this reasoning further by using an assumption of periodicity to refine the existing radiometric time scale.

A reasonable conclusion from the foregoing is that, *if* extinctions in the geologic

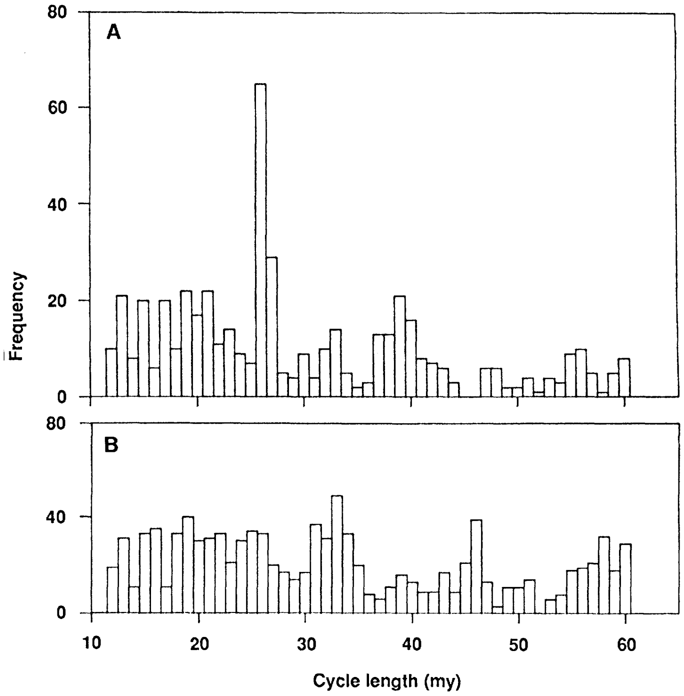

Fig. 1. The frequency distribution of the best fitting period for pseudorandom series (**A**) 500 simulations using the 40-interval Harland time scale for comparison with Stigler and Wagner's figure 4 (*5*). (**B**) One thousand simulations using the 51-interval time scale of Sepkoski (*4*). With the coarser Harland scale, a preference for the 26-my period is evident, but this preference is absent with the finer 51-interval scale.