observations are: (i) what is the extent and distribution of the CO_2-rich fluid and hydrate within the JADE field in relation to those of hydrothermal vents, (ii) what is the effect on the geochemical and biological processes associated with hydrothermal venting, (iii) do they occur at other submarine arc and backarc volcanoes, and (iv) is the carbon flux from these submarine volcanoes important relative to the global carbon flux?

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15. The gas samples were shaken, on board the tendership *Natsushima*, successively with 1 M Zn-acetate solution and a saturated $Ba(OH)_2$ solution and the volume changes were ascribed to formation of H_2S and CO_2, respectively. The residual gas was combusted with CuO at 800°C. The CO_2 produced was used to estimate CH_4 in the residual gas. The ZnS, $BaCO_3$, and CO_2 that formed during these procedures were used to measure the stable isotopic ratios of H_2S, CO_2, and CH_4, respectively. The He isotopic ratios were measured on the residual gases (*16*).
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18. We thank all the scientists, pilots, and operation team members of "Shinkai 2000" who were involved in this project and the captain and crew of the tendership *Natsushima*. We also thank K. Marumo and M. Kimura, who first found the bubbling phenomena and gave us detailed information on it, and H. Hotta. Technical assistance by K. Hasegawa and N. Sueda is greatly appreciated. This study was supported in part by the Grant in Aid for Scientific Study from the Ministry of Education, Sciences and Culture, Nos. 60430010 and 01549468, to H.S. and T.G.

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Chemosynthetic Mussels at a Brine-Filled Pockmark in the Northern Gulf of Mexico

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A large (540 square meters) bed of *Bathymodiolus* n. sp. (Mytilidae: Bivalvia) rings a pool of hypersaline (121.35 practical salinity units) brine at a water depth of 650 meters on the continental slope south of Louisiana. The anoxic brine (dissolved oxygen ≤0.17 milliliters per liter) contains high concentrations of methane, which nourishes methanotrophic symbionts in the mussels. The brine, which originates from a salt-cored diapir that penetrates to within 500 meters of the sea floor, fills a depression that was evidently excavated by escaping gas. The spatial continuity of the mussel bed indicates that the brine level has remained fairly constant; however, demographic differences between the inner and outer parts of the bed record small fluctuations.

THE VIOLENT ESCAPE OF GAS through surface sediment often forms sea floor pockmarks (*1*) or craters (*2*). During a submarine survey of the continental slope, northern Gulf of Mexico, we found pockmarks that were filled with hypersaline brine. These features are evidently a consequence of salt tectonism in a hydrocarbon province. One of the pockmarks, brine pool NR-1, was ringed by a large bed of *Bathymodiolus* n. sp., a mussel (*3*) that possesses methanotrophic symbionts (*4*). This discovery signals that the potential habitat for *Bathymodiolus* n. sp. on the slope may be greater than previously thought and demonstrates that chemosynthetic fauna, already known for their tolerance of toxic sulfides (*5*) and aromatic compounds (*6*), also tolerate hypersaline conditions.

Tectonic deformation of the Louann Salt, a Jurassic evaporite deposit, has created much structural complexity in the northern Gulf of Mexico (*7*); common features include salt diapirs and growth faults. The faults provide a conduit for natural hydrocarbon seepage (*8–10*), which is recognized as a widespread phenomenon on the Louisiana slope (*11*). Large chemosynthetic communities, which have been reported at oil and gas seeps in water depths of 500 to 900 m (*12*), are biological consequences of hydrocarbon seepage.

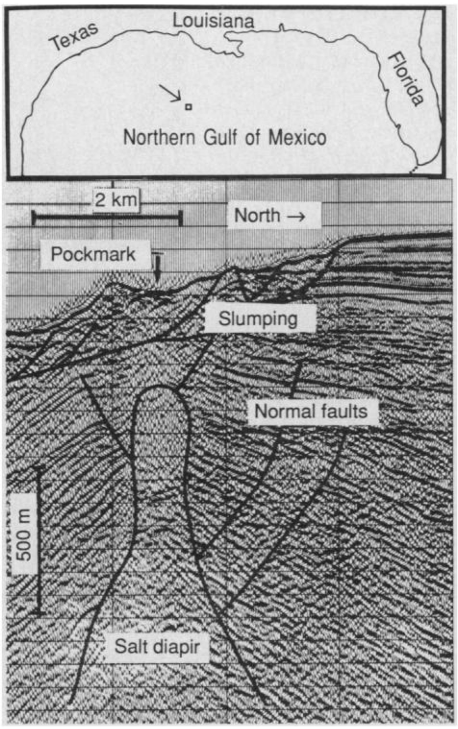

Fig. 1. Two dimensionally processed, common-depth-point (CDP) seismic data showing a north-south transect of the pockmark. Inset map shows its general location in the northern Gulf of Mexico. [Data provided courtesy of Halliburton Geophysical Services, Inc.]

Because many salt diapirs penetrate recent sedimentary strata, sea floor brine seepage is also thought to be a common phenomenon in the Gulf of Mexico (*7*), but only a few actual seeps have been documented. Brine that originates from the Louann Salt has been found in a shallow (~25 cm deep) pool on the Texas shelf (*13*) and in a large (90 km^2) basin (*14*) on the lower Louisiana slope; both features are filled from the side by drainage from salt deposits located above. Brine that originates from saline aquifers in the Florida-Bahama platform saturates surface sediments at the abyssal base of the Florida escarpment (*15*). Reduced compounds associated with this brine nourish chemosynthetic communities that include a second species of mussel (*16, 17*).

Brine pool NR-1 was found (*18*) approximately 285 km southwest of the Mississippi Delta (27°43′24″N, 91°16′30″W) near the

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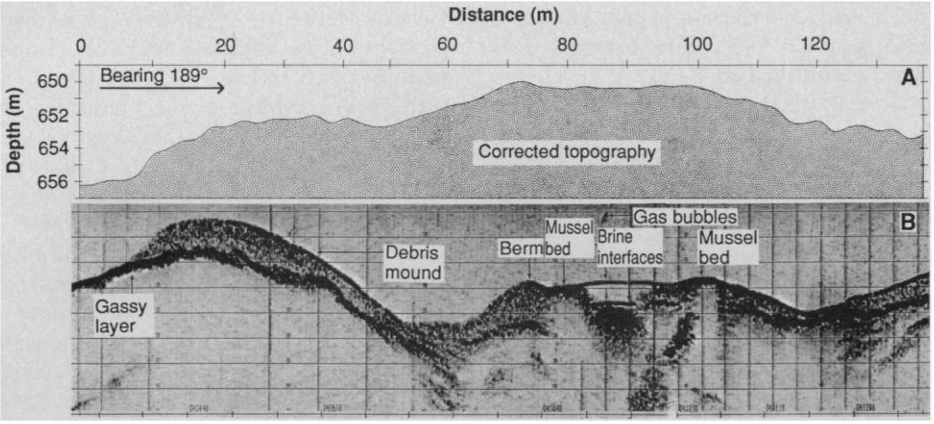

Fig. 2. A north-south transect of pockmark and brine pool recorded by Submarine *NR-1*. (**A**) Corrected topographic profile and (**B**) subbottom profile (25 kHz) at same horizontal and vertical scale. The apparent differences between the corrected topography and subbottom profile are an artifact of changes in the submarine's altitude along the transect. The horizontal axis is proportional to transit time so that distance on the figure is a function of the submarine's speed.

location where Anderson *et al.* collected sediment cores that contained crude oil (*8*). The pool lies at a water depth of 650 m among a series of recent slump terraces at the head of a broad, trough-like graben that deepens to the southeast (*10*). A salt diapir, the top of which is ~500 m below the sediment-seawater interface, is evident in seismic profiles across this site as a seismic anomaly and hyperbolic reflector (Fig. 1). Normal faults generated by salt uplift extend from the diapir and terminate against the base of the slump block. Shallow gas saturation in the near-surface sediments is indicated by a high-amplitude feature at the sediment surface and signal attenuation beneath the pockmark.

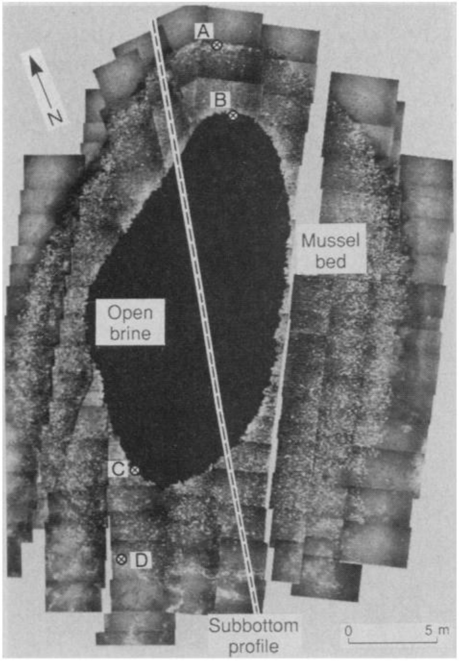

Fig. 3. A mosaic of 231 video photographs showing the brine-filled pockmark and surrounding mussel bed. The photographs were recorded on half-inch tape and digitally reduced to a constant scale. Inner "shoreline" of mussel bed was manually traced, and open brine was imaged with a constant gray tone. The irregular southern edge of the mussel bed is due to lateral seepage of brine from the low (southern) side of the pockmark. Approximate locations in mussel bed where mussels were collected for measurement are labeled as follows: (A) northern outer, (B) northern inner, (C) southern inner, and (D) southern outer.

As shown in a 25-kHz profile, brine fills a 22-m-long, 11-m-wide, elliptical crater that is situated atop a mound with a height of about 6 m and a basal diameter of about 130 m (Fig. 2A). In nongassy sediments, such profiles typically show sedimentary strata to depths of ~20 m below the ocean bottom. On the periphery of the pool, the seismic signal was attenuated by highly reflective layers <2 m below the bottom. Judging from gas fractures and hydrates in piston cores we collected in nearby areas, these layers suggest that gas-rich sediments and possibly diffuse hydrates occur near the mudline at this site (Fig. 2B). Streams of fine bubbles were seen rising from the center of the pool and appear as a slight trace in the 25-kHz record. No bubbles were observed at the pool edges or in the mussel bed.

A debris lobe on the north side of the pool suggests that vigorous expulsion and down-slope slumping of sediment occurred when the pool formed. The subbottom profiles of the near-surface strata and direct observations gave no indication of a rocky substratum. We infer that the mound is composed of fine-grained and poorly consolidated sedimentary material that has been disrupted by upwardly migrating gas.

A berm, approximately 0.5 m high, encloses the mussel bed and the pool to the east, north, and west, but is reduced or absent to the south (Fig. 2A). Open brine in the pool can be readily distinguished in subbottom profiles by its sharp, flat density interface (Fig. 2B). A second horizontal reflector 1.5 m beneath the interface appears to indicate the maximum depth of the brine. However, when we attempted to plant a 3.5-m pole upright in the center of the pool, it sank straight down and disappeared. Therefore, the second reflector is probably also a density interface. The edges of the pool are well defined by the subbottom profiler, where layers of mussel shells provide an intense seismic reflector (Fig. 2B).

Brine was collected (*19*) from the upper density layer near the center of the pool. Although its salinity (121.35 practical salinity units, ~3.5 times seawater salinity) was less than saturation, it is likely that the density layer below contains more saline brine. The temperature of the upper layer (8.7°C) exceeded the ambient seawater temperature by 1.6°C. The brine was nearly anoxic (dissolved O_2 = 0.17 ml/liter); mea-

Fig. 4. Living *Bathymodiolus* n. sp. (Mytilidae: Bivalvia) partly submerged in anoxic brine at the edge of the brine-filled pockmark. Blackened shells of dead mussels can be seen completely submerged in brine at the lower edge of the frame. The anoxic-oxic interface at the surface of the brine is evident in the abrupt change in color from dark blue (reduced) to orange (oxidized) over 'the lengths of the mussels shells. The shaggy coatings visible on some mussels are silt-fouled byssus. The larger mussels are approximately 120 mm long.

sured dissolved oxygen may have resulted from contamination during collection. Odor of H_2S was strong in the dive chamber when brine samples were collected. Vigorous effervescence during collection indicated that some dissolved gases were at saturation with respect to an ambient pressure of 1 atm.

Bubbles collected in a bell jar over the center of the pool were predominantly CH_4 (76.3%), with trace quantities of C_2H_6 (452 ppm) and C_3H_8 (145 ppm). The carbon isotope ratio of the CH_4 ($\delta^{13}C = -63.8$ per mil) and the low proportion of higher hydrocarbons indicate that the CH_4 in the bubbles was primarily microbial in origin (*20*). Biodegraded oil recovered in surface sediments on the periphery the pockmark indicated the presence of thermogenic hydrocarbons in the area.

Chemosynthetic mussels surrounded the open brine in a continuous band, approximately 3 m wide on the narrowest side, the northwest edge, and 7 m wide on the southeast edge (Fig. 3). The mussel bed was elevated only a matter of centimeters above the brine-seawater interface; its total area was ~540 m^2 whereas the area of the open brine was ~190 m^2. Transition from the mussel bed to bare sediment was abrupt on the north, west, and east, but more gradual to the south, where the berm was reduced or absent. To the south, gaps of stained sediments appeared as the continuous bed gave way to curvilinear stringers, intermingled with patches of disarticulated mussel shells (which were mostly broken and pitted) and filamentous colonies of white bacteria. Shells continued to dot the sediments 20 m south of the bed. There was no sign of a brine-outflow channel through the bed. We infer that the irregular southern edge of the mussel bed results from lateral percolation of brine through surface sediments.

A diverse and abundant biological community was associated with the mussel bed. Chemosynthetic tube worms, *Lamellibrachia* n. sp., which are abundant at other Louisiana slope oil seeps (*12*), were represented here by a few solitary individuals. Demersal fishes included *Chaunax pictus*, seen resting on the bottom outside the bed, the eel *Synaphobranchus* sp., and the hag fish *Eptatretus* sp. We collected a severely disoriented fish, *Nezumia* sp., as it swam in circles upside down just above the open brine, possibly affected by hydrogen sulfide toxicity. Our operations over the brine created internal waves, which lifted well-preserved dead fish from the bottom of the pool and into view around its edges. Epifaunal crustaceans observed among the mussels included a large magid crab, *Rochinia crassa*, as well as numerous shrimp, *Alvinocaris stactophila*, and galatheid crabs, *Munidopsis* sp., which browsed the interstices of the mussel bed. An unidentified paranoid polycheate formed a dense mat beneath the bed.

Several differences were evident between the outer edges of the mussel bed and the inner margin adjacent to the open brine. Mussels on the outer edge rested flat on the sediments or were loosely shingled one on another, whereas those on the inner edge stood vertically, with their anterior ends down, firmly bound by their byssus into a dense mat. Mussels on the inner edge adjacent to the open brine were partly submerged in brine; the interface between oxic seawater and anoxic brine was distinctly visible here because their upper (posterior) ends were rust-colored whereas their lower (anterior) ends were black (Fig. 4). The innermost bed was formed from completely submerged, dead individuals, whose valves, heavily blackened by mineral deposits, were still articulated and in many cases contained poorly preserved remains of the soft tissues.

Bathymodiolus n. sp. require adequate supplies of dissolved methane and free oxygen for growth (*4*). Because the brine supplies dissolved methane to the mussels at this site whereas oxygen is obtained from ambient seawater, the spatial distribution and demography of the mussels record the local extent of the oxic-anoxic interface and may indicate subtle fluctuations in brine level. Mussels collected from the outer edge (*21*) apparently all belonged to a single settlement class of intermediate length, whereas inner-edge mussels formed four apparent settlement classes (*22*) that ranged from recently settled spat to the largest specimens collected from the site (Fig. 5). Individuals of the intermediate-length settlement class that was prevalent on the outer edge were rare on the inner edge.

Spat of chemosynthetic mussels from the Gulf of Mexico evidently settle or survive preferentially on substrata where brine supplies dissolved methane (*15, 16, 23*); this preference is evident in the prevalence of spat and juveniles on the inner edge of the bed. The mussels tolerate partial submergence in the anoxic brine; however, complete submergence would undoubtedly be lethal. A rise in brine level of a few centimeters would therefore kill many of the mussels on the inner edge but would also broaden the distribution of methane-rich brine and promote settlement on the outer edge. Settlement would cease on the outer edges with subsequent lowering of the brine level and would resume on the inner edges.

Lack of recent settlement on the outer edges, the broad size range of mussels on the inner edges, and the accumulation of dead individuals in the pool all indicate that these mussels exist at an equilibrium between an adequate concentration of nutritive methane and an oversupply of anoxic brine. Despite evident fluctuations, the overall spatial continuity of the mussel bed is striking. Compared with the patchy fine-scale distribution of chemosynthetic fauna in communities reported from elsewhere (*5, 12, 16, 23, 24*), this mussel bed maintains a relatively uniform density over a significantly larger area. The density of the brine traps methane beneath a distinct interface with oxic seawater, and the morphology of the pockmark edges provides a stable substratum beneath a thin layer of brine. Such conditions are clearly favorable for methanotrophic symbiosis.

We have also found brine-filled pockmarks at two other locations on the Louisiana slope (*25*). They occurred on low mounds, had raised rims, and contained a dense, light-refractive fluid from which bubbles were escaping. One of these was evidently in active formation because its steep

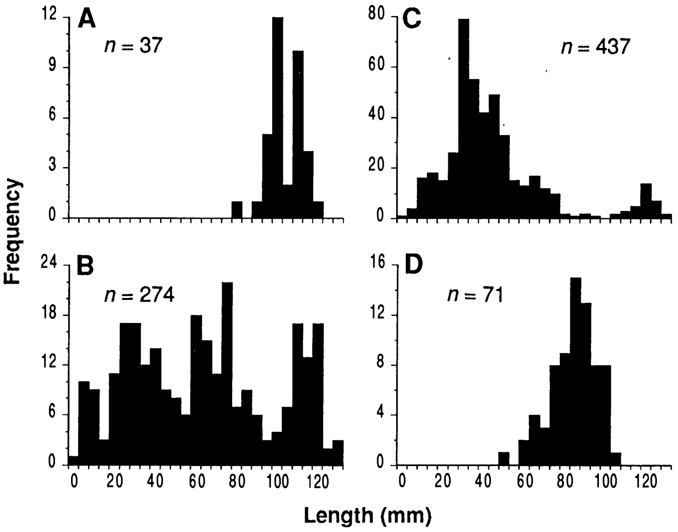

Fig. 5. Length frequency histograms of mussels collected from the mussel bed surrounding the brine-filled pockmark. Collection locations (**A**–**D**) refer to the description in Fig. 3. Mean lengths (±1 SD) for the samples are as follows: (A) 104 ± 8.7 mm, (B) 63 ± 35.3 mm, (C) 45 ± 26.6 mm, (D) 84 ± 11.5 mm.

(~80°) rim was seen collapsing into the pool while plumes of fine sediment were ejected by vigorous bubble discharges. Despite apparent concentrations of methane, neither feature had been colonized by mussels. Either the unstable substrata on the rims impeded settlement of mussels, or the features were so recent that colonization had not yet occurred.

Doming of the sea floor under pressure from upwardly migrating gas, followed by eruption, will excavate a pockmark with raised rims (*1, 2*). If hypersaline pore fluids are present, as they are in the vicinity of brine pool NR-1 (*10*), lateral seepage through the pockmark walls will fill the depression with brine. Sediments suspended at the bottom of the pool may continue to be excavated by bubble discharge after the initial eruption. Anoxic conditions may also inhibit microbial oxidation of methane and prevent the formation of authigenic carbonates, which are common at North Sea pockmarks (*5*) and Gulf of Mexico gas seeps (*10, 11*). Although these features may be relatively small, a careful examination of seismic records should reveal additional brine-filled pockmarks on the continental slope of the northern Gulf of Mexico. Their potential as habitats for chemosynthetic communities is evident.

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18. The site was discovered in May 1989 by scientists on board the U.S. Navy Submarine *NR-1*, which acquired video and emulsion photographs, side-scan sonar records, and 25-kHz subbottom profiles. It was revisited in September 1989 with the submersible Johnson *Sea-Link I*, which took additional photographs and collected samples of the brine, escaping gas, and over 1000 living mussels.
19. The mechanical arm of the Johnson *Sea Link I* was lowered about 1 m below the density interface. Brine was collected at 1 atm inside the dive chamber via a hose that ran from the end of the arm. Temperature was measured by a Sea Bird conductivity and temperature detector (CTD) held by the arm. Salinity was measured with a conductive salinometer after weight dilution to near seawater conductance. Dissolved oxygen was measured by Winkler titration. Gaseous hydrocarbons were determined by flame-ionized gas chromatography. Carbon isotope ratios are reported as per mil deviations from a PDB standard: $\delta^{13}C$ (per mil) = $10^3 \times (^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{PDB} - 1)$.
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21. Mussels were collected at discrete locations with a mechanical scoop and placed in a closed container. Water and sediment from the container were sieved through a 1-mm mesh, and all recovered specimens were measured with a calipers. Some of these specimens were maintained alive for up to 5 months with methane gas as their sole source of food.
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25. Near 27°26'30"N, 91°40'30"W at 662-m depth, and near 27°35'59"N, 92°55'58"W at 590-m depth.

26. We thank the captains and crews of the U.S. Navy Submarine *NR-1* and the Johnson *Sea-Link I* for enabling our submersible operations. R. A. Burke, Jr., supervised gaseous hydrocarbon analyses. Ship time was funded by Office of Naval Research and National Oceanic and Atmospheric Administration–National Undersea Research Program. Additional support was from the Texas A&M University and Louisiana State University Sea Grant Programs. We thank Exxon Corporation, U.S.A., and Ensearch Exploration, Inc., for support and suggesting dive sites for study.

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Upper Eocene Gilled Mushroom from the Dominican Republic

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***Coprinites dominicana* gen.nov., spec.nov. (Coprinaceae) found in amber from the Dominican Republic is the earliest known gilled mushroom, the first fossil fleshy agaric determinable, and the only known fossil "mushroom" (Agaricales) from the tropics. This find is of significance with respect to the evolutionary development of the Basidiomycetes. Because the appearance of this fossil is quite modern, it suggests that mushrooms as a group probably arose much earlier than the early to mid-Tertiary.**

THE RELATIVELY RECENT EXTRACTION of fossiliferous amber in the Dominican Republic has led to the discovery of many new taxa of invertebrates as well as vertebrates (*1*). Up to the present, however, there has been no report on the occurrence of higher fungi in Dominican amber. In fact, fossil Agaricales (Polyporaceae, Paxillaceae, Gomphidiaceae, Boletaceae, and "Agaricaceae") in general are extremely rare.

A nearly complete fossil representative of the "Agaricaceae" recently found in amber from the Dominican Republic consisted of a complete pileus (cap) containing spore-bearing lamellae and the top portion of the stipe. Part of the broken bottom portion of the stipe lay adjacent to the pileus.

The fossil specimen originated from the La Toca mine, located between Santiago and Puerto Plata in the Cordillera Septentrional of the northern portion of the Dominican Republic. The mine is in the Altimira facies of the El Mamey Formation (upper Eocene), which is shale-sandstone interspersed with a conglomerate of well-rounded pebbles (*2*). Differences in the magnitudes of absorption peaks in nuclear magnetic resonance spectra of the exo-methylene group of amber (*3*) from different mines in the Dominican Republic were used to calibrate the ages of the various mines, with the age (20 million to 23 million years) (based on foraminifera counts) of the Palo Alto mine used as a standard (*4*). The ages of various specimens of Dominican amber ranged from 15 million to 40 million years; that from the La Toca mine was the oldest, some 35 million to 40 million years old (lower Oligocene to upper Eocene).

The amber containing the fossil has all the visual characteristics of natural Dominican amber. A series of chemical and physical tests (*5*) performed on a small portion of the amber piece verified that it was authentic. The piece of yellow transparent amber containing the mushroom weighed 0.5 g and

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