

The transition from table grapes (left) to wine grapes (right) by wild introgression resulted in smaller berries with thicker skins, less sugar, and larger seeds.

ously with a high degree of shared signatures of selection on the same genes. Recent evidence demonstrates that long-distance networks of human communication and exchange over this distance occurred in the Epipalaeolithic, 10 to 20 ka (7, 8). The findings of Dong *et al.* appear to show multiple emergences of domesticated forms occurring at a landscape level in which human communication would likely have been a key factor in promoting gene flow (9). To what extent the same domestication alleles might have been transported between different populations by humans or were present in the wild populations is a question that remains, and the answers will illuminate the role of human agency in grapevine domestication.

The South Caucasus domestication had limited spread and very little further influence, but the Near Eastern domestication came to dominate, establishing four major European cultivated grape clusters. Domestication is estimated to have occurred 11.5 ka, contemporaneous with the initial emergence of cereals, and the dates of the splits to form four European clusters match tantalizingly closely with the initial spread of the Neolithic into Europe. These dates are much earlier by several thousand years for both origin and spread than is expected from the archaeological evidence from domesticated seed morphology, which is distinct from wild seeds. The processes of selection that led to plant domestication can greatly predate the rise of morphological forms (10), so these earlier-than-expected dates may indicate exploitation of wild forms. Alternatively, although Dong *et al.* attempted to account for it, the long history of vegetative propagation (asexual reproduction) in grape cultivation (11) may be a confounding factor in divergence estimates by inflating generation time, which could explain the discrepancy with the archaeological record. To test between these alternatives will require direct investigation of the archaeological record using ancient DNA (archaeogenomics), as the authors also conclude.

The spread of domesticated plants from the Near East into new European environments is associated with a requirement for adaptation (12, 13). Unlike cereals, grapes had wild populations in Europe from which they could obtain local adaptations. Gene flow from wild populations into domesticated forms can be hard to avoid and supplies both locally adapted variation and a resurgence of wild traits. Such adaptive

introgression has also been noted in previous grape studies (5, 6) and was recently reported in flax, which also originates from the Near East and has wild populations distributed throughout Europe (14). In both cases, the adaptive introgression is associated with a change in use. In flax, wild flowering-time genes introgressed and enabled adaptation to changes in daylength at higher latitudes. This was at the cost of seed size and oil content but also generated an architecture that was suitable for fiber production and may well have driven the textile revolution in central Europe, around 6 ka. In grapes, adaptations to the environment have been acquired that are associated with water stress and disease resistance (1, 5). However, such introgressions also carried wild traits that compromise edibility. Compared with table grapes, wine grapes are smaller and thick skinned and have lower sugar content. These traits are more similar to those of wild grapes, which also makes them more suited for winemaking and less appealing for eating. That natural environmental adaptations under the transition to wine raises key questions about the drivers behind such usage changes and to what extent they were forced by natural selection rather than by humans.

The enormous dataset produced by Dong *et al.* will provide insight into the finer points of grape evolution for some time to come. The increased resolution has pinpointed the lightening of berry color to some unknown genes close to the previously implicated *MybA* locus (15) and has suggested that the ancient Muscat flavor is unexpectedly rare possibly because of a pleiotropic constraint that prevents fixation. This study does not stray into the effects of structural variation in the genome, whereby many regions have been lost across various cultivar lineages. This has been shown to be key to the functional changes seen in domesticated grapes relative to their wild ancestors (15). The next big step will be to integrate these data into a structural landscape. ■

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10.1126/science.adg6617

BIOACOUSTICS

Voices in the ocean

Toothed whales evolved a third way of making sounds similar to that of land mammals and birds

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The ability of humans to sing and speak requires precise neural control of the larynx and other organs to produce sounds. This neural control is limited in most mammals (1). For animals that create complex sounds, less is known about how peripheral anatomical structures enable vocal feats (2). On page 928 of this issue, Madsen *et al.* (3) demonstrate that toothed whales, such as dolphins and killer whales, have a distinct nasal structure that produces diverse sounds in a broad frequency range that spans >4 orders of magnitude.

The findings of Madsen *et al.* stem from two long-standing strands of research: cetacean (toothed whales and baleen whales) communication and human voice science. For decades, studies of cetacean communication have relied on evidence from sound recordings complemented by postmortem anatomical investigation. However, cetaceans are large and patchily inhabit the ocean, so sampling sounds from specific individuals can be difficult and the rare postmortem samples cannot elucidate what happens “in action.” As a result, finding the mechanism behind the sound production of toothed whales has proved elusive. In parallel, techniques have been developed to measure fine-grained dynamic parameters of the human vocal apparatus and map them to the sounds that are produced. Madsen *et al.* apply the methods used to study human voice to toothed whales to show that they blow air through their nasal passage and finely control it to produce diverse sounds.

This newly described voice production sys-

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tem in the nasal passage of toothed whales has a striking similarity to what is known about vocalization in humans, terrestrial mammals, frogs, and birds, for which sound production typically occurs in the larynx or syrinx. An exhalatory aerodynamic force sets the laryngeal vocal folds or syringeal membranes into self-sustained oscillation with no need for recurring muscular contractions. The ensuing oscillatory tissue motion introduces cyclic variation into the exhalatory airstream. The resulting air-pressure variations are transmitted through the oral, pharyngeal, and nasal cavities (the “vocal tract”) and are then emitted from the mouth and partly from the nose. This so-called myoelastic-aerodynamic (MEAD) principle (4) converts the exhalatory aerodynamic energy into sound.

Further parallels may exist between toothed whales and other mammals. The vocal sound generator in humans is a complex system of coupled subsystems (5), namely the oscillating tissue and its surrounding airspace (the trachea and vocal tract). Each of these physically interacting components produces its own set of biomechanically controlled resonance frequencies, which enables multiple types of oscillation for the sound generator (6). The distinct combinations of tissue vibratory modes that emerge establish different “voice registers.” Alpine yodels and “voice cracks” in pubescent boys exemplify different vocal registers within one single bout of phonation.

Three human voice registers (7) are physically analogous to those that Madsen *et al.* documented in toothed whales (see the figure). Mechanism M0, the “vocal fry,” can be

heard in “creaky voice,” which often occurs in speech at the onset or offset of phrases. M1, the “chest register,” is the stereotypical register in which humans speak. M2, the “falsetto register,” is sometimes used in speech and also for exclamations and emotional responses. Voice registers are well-documented in human speech and singing, but finding these sound production mechanisms in toothed whales is unexpected.

Humans and almost all mammals make sounds by means of a laryngeal, self-sustained MEAD mechanism. Birds have a larynx but use their syrinx—a recently evolved organ whose MEAD mechanics resemble those of the mammalian larynx—to produce sound (8). Madsen *et al.* now show another versatile mechanism that toothed whales use to make sounds according to the MEAD principle: their nasal passage, whose mechanics resemble those of the larynx and the syrinx. Toothed whales not only produce clicks in the vocal fry (M0) register to echolocate but also social vocalizations in the chest (M1) and falsetto (M2) registers. The same vocal organ produces both pitched sounds in social communication and rhythmicity in echolocation clicks. This raises questions about perception: as the repetition rate of sounds becomes faster, humans stop perceiving them as rhythmic and start hearing a pitch. At what point does this transition happen in the hearing of toothed whales?

How did the similarities between toothed whales and all other MEAD-users emerge? Similar evolutionary pressures on two species may lead to functionally similar traits even when their last common ancestor

lacked that trait. For example, doves and bats independently evolved wings; likewise, humans and toothed whales independently developed their main phonatory systems in the larynx and the nasal passage, piggybacking on different parts of the respiratory system. The physical mechanism of producing vocalizations through airflow-induced, self-sustained vibration of sound-generating tissue is so physically convenient that it keeps being repurposed, with at least three independent evolutionary strategies in mammals, birds, and toothed whales.

However, some mammals may also produce sounds without “normal” laryngeal phonation used by humans. For example, small koalas produce disproportionately “deep” sounds through a distinct vocal organ (9), but apparently also according to the MEAD principle. Conversely, cat purrs may arise through cyclic muscular contractions (10). Some seals haunt Antarctica with electronic-like vocalizations (11). *Indri indri* lemurs reach extreme sound intensities in their trumpet-like songs (12). The list continues with tongue-clicking bats (13) and whistling mice (14). Even more sound production mechanisms may be awaiting discovery.

Combined approaches are needed to understand the acoustic world around us. Mammalian bioacoustics excels at answering ethological questions, and songbird research has pinpointed the neural control mechanisms for song. Human voice research has described the physics and physiology of the sound production apparatus, thereby mapping potential pathologies and highlighting medical solutions. Singing voice research has described how the voice production system can be used artistically. The study of Madsen *et al.* adds to this important cross-fertilization of different scientific fields by revealing that toothed whales can display extraordinary vocal abilities while diving at 1000 meters and feasting on seafood. At least vocally, humans are not so special after all. ■

Vocal mechanisms in humans and toothed whales

Vocal folds in the human larynx perform self-sustained oscillations during exhalation, which alters air pressure through the vocal tract, allowing complex sound generation. This myoelastic-aerodynamic (MEAD) principle is also applicable to toothed whales, which generate sound by blowing air through phonic lips in the nose. This sets up pressure oscillations that are focused in the melon to create sound for echolocation and communication.

Humans

M0 “vocal fry”
(creaky voice)



M1 “chest”
(speech/singing)



M2 “falsetto”
(singing)

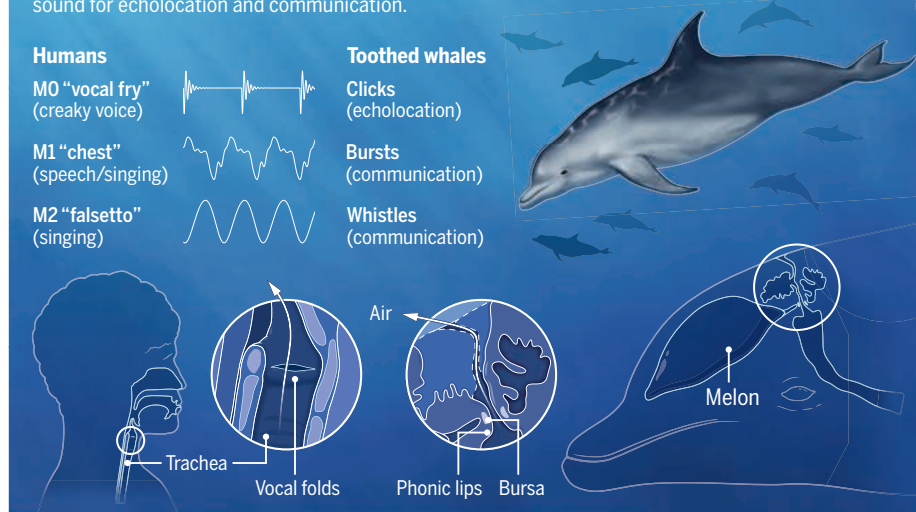


Toothed whales

Clicks
(echolocation)

Bursts
(communication)

Whistles
(communication)



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