REVIEW

Check for updates

The science of minerality

Hui-Chung Tai [ID] *[ab] and Evmorfia Kostaki [ID] [c]

Minerality in wine has been a subject of intense debate. The current perception of minerality in wine is mainly based on geological viewpoints and sensory studies, and the scientific understanding remains limited. We review interdisciplinary studies and integrate their key findings with physicochemical guidelines to unravel the fundamental principles of minerality. Minerality arises from the combinatorial activity of various sensory receptors stimulated by versatile minerals, promoting complexity and uniqueness. This comprehensive review will revolutionize how mineral sensation is perceived and will allow the creation of convincing marketing strategies. A great impact on the research of terroir, winemaking, and molecular mechanisms of mineral sensing is foreseen.

1 Introduction

In wine tasting, minerality has been a fashionable and highly regarded quality of wines for decades. Mineral tastes/aromas are often used to differentiate products and to command high prices.[1] The current understanding of minerality is mainly based on a geological perspective where rocks and stones have no taste and solid minerals do not easily evaporate into the air to be detected.[2] Furthermore, minuscule minerals in wine are usually considered to be present below human detection thresholds. This perceived minerality was proposed to originate
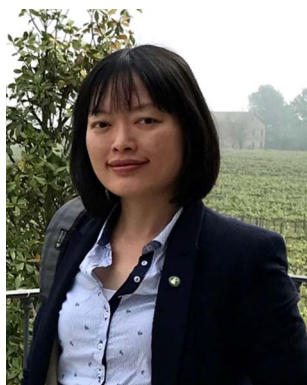
from organic compounds such as lipids rather than any minerals.[2,3] Hence, mineral related terms in wine tasting are often used with care among wine professionals. On the other hand, sensory study and statistical analysis of tasting notes are common approaches to investigate relationships between mineral descriptors and chemical compositions and flavors of wine.[4,5] Although this viewpoint provides important insights, the physicochemical origins and the associated chemical elements/pathways that give rise to minerality are largely unclear and elusive.[3]

The main difficulty of understanding minerality lies in the broad range of related wine descriptors. How to use these descriptors highly depends on personal wine knowledge and tasting experiences/sensitivity.[1,6,7] In addition, diverse metallic sensations and combinations of the involved receptors make it

aTipple Scientist, Institute of Biomedical Sciences, Academia Sinica, Taipei 115, Taiwan. E-mail: drtai@tipplescientist.com

bWeinakademie Österreich GmbH, Seehof, 7071 Rust, Austria

cKostaki Winery, Epameinonda Stamatiadi 4, Samos, Greece

Hui-Chung Tai

Hui-Chung Tai is the director and chief scientist of Tipple Scientist, a consultancy focused on tasting and understanding wines and spirits from scientific perspectives. She holds a PhD in chemistry from the University of Warwick, a diploma qualification in wines and spirits from the British Wine and Spirit Education Trust (WSET), and a Weinakademiker from the Austria Wine Academy and she has been a researcher at the Korean Institute of Advanced Study, Academia Sinica, and in the biotech sectors. Her research interests range from bioinorganic chemistry, computer-aided drug design, theoretical chemistry, and wine chemistry.

Evmorfia Kostaki

Evmorfia Kostaki is a founding partner of Kostaki Winery. After a obtaining a bachelor's degree in chemistry from the University of Athens, she left Greece to join Vinifera Euromaster and study Viticulture and Enology. Her studies led her to France, Italy and California, where she wrote her thesis while at UC Davis. At the same time she completed the WSET Diploma in Wines and Spirits. In 2020 she was accepted into the Institute of Masters of Wine, where she was awarded with three scholarships, and is now a Stage 2 Practical Only Student.

challenging to define and characterise metallic sensations.[6] Furthermore, mineral compounds in soils, vines, grapes, and wines are usually present in minute amounts and can constantly transform between different states (*e.g.* gas, liquid, solid) *via* oxidation/reduction and by interacting with various chemicals in the environment.[8,9] In particular, a significant number of minerals involve metal cations. Metal cations can exist in various oxidation states that can form a wide range of stable compounds by interacting with different negatively charged anions.[3,10] These compounds often show different chemical properties and reactivity. Therefore, it is challenging to track how these ions are transported. How and in what quantity the ions can be absorbed by vines and utilized for grape growing is regulated by various viticultural factors such as the soil conditions, water availability, rootstocks, and grape varieties.[2,3,11] Moreover, mineral content in growing environments can be increased by artificial chemicals used to tune the pH of the soil, the nutrients in the soil (*e.g.* $Ca(NO_3)_2$ as a nitrogen fertilizer) or to prevent vine diseases (*e.g.* $CuSO_4$ in Bordeaux mixture). In turn, mineral content can be decreased by heavy precipitation and loose soils. Mineral profiles in wine are further affected by winemaking processes like pressing, fermentation, fining, and filtration. Certain minerals are often removed as precipitates or by filtration, whereas some can be introduced *via* winemaking equipment, anti-microbial chemicals (*e.g.* sulfur dioxide, potassium bisulfite), and fining agents (*e.g.* bentonite, copper sulfate).[2,12,13] Most studies have shown no positive relationship between the intensity of perceived minerality and concentrations of related minerals in the wine and no clear connection between mineral profiles in soils and the wine.[3]

To gain a deeper understanding of minerality and to scientifically use the related descriptions in wine tasting and quality assessment, it is of prime importance to address the following questions: (1) does minerality arise from specific wine components as various aromas in wine? (2) do different descriptors for minerality in wine originate from distinct groups of wine components and what are the associated chemical pathways? (3) what factors can affect the intensity of perceived minerality in wine? and (4) how are different minerals recognized by human sensory receptors to trigger mineral perception?

In this work, we show that minerality can be broadly categorized into three main groups according to the physico-chemical source and the chemical reactions involved: metal, metal-catalyzed, and sulfur (Table 2). We explain how environmental factors can influence the intensity of perceived minerality and how they correlate with mineral concentrations in wines and illustrate how minerality can reflect part of the terroir of a wine. Moreover, we summarize recent research on how distinct minerals target different human olfactory/taste receptors to initiate cellular signaling for mineral perception and elucidate the fundamental principles of mineral-receptor recognition.

2 Scientific definition and principles of minerality

2.1 Minerals in wines can Be present above the sensory threshold

The perception thresholds of minerals given in previous studies are collected in Table 1. For comparison, concentration ranges of minerals that are frequently found in wine at higher levels are listed: sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), iron (Fe), copper (Cu), and volatile sulfur compounds.[2,3] Although the sensory thresholds of most metal-containing minerals are assessed in water rather than in wine, the numbers can serve as references. The perception thresholds and the corresponding ranges of concentrations in wine can overlap with each other and the estimations are subject to participants' individual sensitivity and how the tastings are performed.[8,14–17] In general, comparing the perception thresholds of various minerals with their concentration ranges in wines shows that minerality can remain within perceivable ranges.

2.2 Define and categorize minerality

To reduce confusing and misleading terms in wine tasting, it is important to scientifically define and categorize minerality. Minerals are inorganic compounds (typically they do not contain carbon atoms or carbon–carbon bonds) with an ordered atomic arrangement and thus can form a particular crystal shape (*e.g.* NaCl, FeS). According to their origin and the chemical reactions involved, minerality in wine can be generally classified into three main groups: metal, metal-catalyzed, and sulfur (Table 2). Some descriptors may come from organic sources. Based on current knowledge, the generation of the flavored/aromatic molecules in wine may not involve inorganic elements. Thus, they are organized into a separate organic category. Metal ions that directly induce the perceived flavors/aromas are in the metal group. Metal ions that do not directly account for flavors/aromas yet catalyze chemical reactions (mostly oxidation or reduction) to produce volatile compounds are in the metal-catalyzed group. The sulfur group mainly contains sulfur-containing compounds with distinctive aromas. The chemical elements/compounds listed in Table 2 are well-studied examples but not exhaustive.

2.2.1 Flavored/aromatic minerals.
Some inorganic compounds in the three main groups of minerals can be directly tasted or smelled. For example, NaCl and NaI in the metal group have salty tastes. H_2S and SO_2 in the sulfur group mostly create flinty/reductive aromas (Table 2). Magnesium/calcium salts in the metal group can be bitter or sour, but so are many other organic compounds such as benzaldehyde from bitter almonds and various acidic molecules. It is difficult to distinguish the subtle differences of bitter/sour taste from mineral and organic origins without further investigation. Volatile sulfur molecules include a wide range of compounds produced from fermentation and lees ageing or are generated/regenerated *via* chemical reactions involved copper during winemaking or bottle ageing. Thiols like methanethiol (MeSH) are organic compounds.

Table 1 Perception thresholds of minerals in water and wines as well as mineral concentration ranges in wines around the world. ND denotes not detected

	Perception threshold in water (mg L^{-1})	Perception threshold in wine (mg L^{-1})	Range in wine (mg L^{-1})
NaCl	140–1780 (ref. 14)	80–5060 (ref. 14)	2.94 (ref. 15)–310 (ref. 9)
	75.4–1270 (ref. 8)	ND	
MgCl$_2$	45–60 (ref. 16)	ND	7.80–718 (ref. 9)
CaCl$_2$	100–300 (ref. 16)	ND	3.5–241 (ref. 9)
FeSO$_4$	1.14–65.2 (ref. 17)	ND	0.001–10.7 (ref. 9)
FeCl$_2$	2.69–65.3 (ref. 17)	ND	
CuSO$_4$	0.511–8.68 (ref. 17)	ND	0.001 (ref. 9)–646 (ref. 15)
CuCl$_2$	0.457–5.04 (ref. 17)	ND	
H$_2$S	ND	0.001–0.002 (ref. 18)	ND–0.035 (ref. 18)
MeSH	ND	0.002–0.003 (ref. 18)	ND–0.008 (ref. 18)

Table 2 The three main categories of minerals perceived in wine according to their physicochemical sources and the chemical reactions involved. The organic group may not necessarily be associated with minerals. The listed compounds/elements are typical examples but are not exhaustive

	Minerality				Organic
Category	Metal		Sulfur	Metal-catalyzed	Organic
Perceived minerality	Salty	Bitter	Reductive, flinty, gunpowder, match	Wet stone, petrichor, metallic	Earthy
Flavored/aromatic compound	NaCl, NaI, KCl	MgCl$_2$, MgCO$_3$, CaCl$_2$, CaCO$_3$	H$_2$S, SO$_2$, MeSH, EtSH	1-Octen-3-one (derivative of fatty acids)	2-Methylisoborneol (derivative of terpenes)
Associated inorganic element	Na, K, Cl, I	Mg, Ca, Cl	S	Fe, Cu	Unknown

However, sulfur is highly reactive and inorganic and organic sulfur compounds can easily convert from one another with the assistance of yeasts.[9] Thus, the flinty/match aromas from thiols, particularly pronounced in reductive conditions with low levels of oxygen exposure during winemaking, can be associated with inorganic sulfur sources.[18]

2.2.2 Flavor/aroma stimulating minerals. The metal-catalyzed group includes metal ions that can accelerate the oxidation/reduction of organic molecules such as lipids to release volatile organic compounds (Table 2).[3] For instance, skin that has touched a metal coin can give off a metallic odor. Research has shown that reactive blood Fe^{2+} ions can reduce and decompose lipid peroxides on the surface of the skin to the odorous molecule 1-octen-3-one while simultaneously being oxidized to Fe^{3+}. 1-Octen-3-one is perceivable by humans at very low concentrations (20 ng L^{-1} in white wine).[19,20] The quantity of the volatile carbonyl compounds and the metallic odor increased in line with the quantity of Fe^{2+} ions in contact with the skin. Moreover, the addition of a blood-iron chelator suppressed the perceived metallic odor and greatly reduced the levels of 1-octen-3-one produced, indicating that Fe^{2+} ions play a key role in the chemical reaction of the aroma generation.[20] Likewise, aromas such as wet stone and petrichor can be produced *via* similar chemical pathways involving metal ions. These aromas often accompany the first rains after a warm sunny period.[21] The higher temperature facilitates the release and accumulation of various volatile lipids in the air. The

suddenly condensed moisture drives these organic compounds to interact with minerals on rock and stone. Theses metal ions can stimulate similar chemical reactions to release aromatic compounds. Wine often contains abundant fatty acids of various kinds along with different metal ions.[22,23] Aromatic molecules can be easily produced following the pathways illustrated above. In contrast, 2-methylisoborneol, a volatile organic molecule that often gives an earthy odor, can be produced by microorganisms or from other unknown pathways that may not necessarily involve metals. The chemical reactions associated with these odors need further investigation.[3,24] Based on current understanding, the organic group is used to differentiate the chemical sources and pathways from the three main categories of minerality.

2.3 Effects of environmental factors on intensity of perceived minerality

Environmental effects on mineral intensity are commonly observed. For example, wines from cooler climates tend to show more observable minerality because they usually undergo slower chemical reactions in lower temperatures compared to warmer climates. Reactive minerals or volatile compounds can be better preserved under such conditions. In addition, the lower pH values of wines from cooler climates help preserve more freely available SO$_2$, further reducing the levels of oxidation. Likewise, wines produced in reductive winemaking processes (*e.g.* with the use of stainless steel and screwcaps)

tend to undergo less oxidation. Subtle volatile compounds and reactive minerals are less likely to be lost during the processes. In particular, iron in the oxidation state Fe^{3+} often forms less soluble salts in water/wine that can precipitate and are not easy to recover. In the previous study, the intensity of the metallic odor showed a positive correlation with the quantity of 1-octen-3-one and Fe^{2+} ions in contact with the skin, suggesting that a positive relationship between concentrations of the associated minerals and intensity of the minerality in wine can be observed in a controlled experimental environment.[20] Recent research has shown that the intensity of flinty and reductive aromas is positively connected to concentrations of metal ions in wine. Sulfur has a high affinity with metals and the affinity can vary according to the various oxidation states of the metals and different oxygen exposure. Therefore, the minerality created can be influenced by the amounts of metal ions present and the free and metal-bound sulfur compounds as well as environmental factors and other chemicals competing to bind the metals.[9]

2.4 Mineral perception arises from combinatorial activity of diverse sensory receptors

The sense of smell and taste is initiated *via* the stimulation of sensory receptors by chemical compounds. Depending on their structural characteristics and flexibility, each sensory receptor can recognize a subset of chemicals and a single chemical can activate multiple receptors. The molecular mechanisms usually involve key conformational changes of receptors upon binding of specific chemicals to further trigger cellular signaling.[25] Hence, we focus on structure-based studies of human sensory receptors. Mineral perception is a combination of taste sensation by metal ions and thiols as well as olfactory/retronasal sensation *via* volatile sulfur-containing molecules and lipid oxidation catalyzed by metals. Human mineral sensory receptors mainly comprise ion channels and G protein-coupled receptors (GPCRs, the largest family of human membrane proteins with seven conserved transmembrane helices that transmit signals from extracellular stimuli, such as the binding of ions and odorants to the intracellular G proteins).[6,26] Humans have approximately 400 olfactory receptors (ORs), all in the GPCR family. The study of how odorants are recognized by ORs is still in its infancy but is rapidly evolving. The cryo-electron microscopy (cryo-EM) structures of the OR51 and OR52 families show the recognition of fatty acids, indicating their

association with mineral perception. In particular, the structure of OR51 shows a binding pocket composed of polar, hydrophobic (to accommodate hydrocarbon tails), and positively charged (to stabilize carboxylic acid odorants) residues.[25,27]

Current research has identified five main types of mineral taste receptors. Transient receptor potential (TRP) ankyrin subtype 1 (TRPA1) and vanilloid subtype 1 (TRPV1) and epithelial sodium channels (ENaC) are ion channels, whereas the sweet and umami taste receptor 1 type 3 (Tas1R3) as well as the bitter taste receptor 2 type 7 (Tas2R7) are GPCRs.[26] Table 3 lists the model structures of key mineral olfactory/taste receptors and their pairing minerals. Currently, no human structure is available for Tas2R7.[6] These structures provide important insights into the molecular mechanisms of mineral-receptor recognitions and the resulting signal transduction for mineral sensation.

In essence, metal selectivity in receptors is governed by the metal properties (net charge, ionic radius, charge-accepting ability), the properties of the binding residues (net charge, charge-donating/-accepting ability), the characteristics of the composite metal and binding residues (coordination number, coordination geometry), as well as the effects of the protein matrix (pore size, rigidity, dielectric constant).[28] ENaC is the major salty taste receptor, which selects Na^+ over K^+ *via* its narrow and rigid pore (ionic radii 1.02 and 1.30 Å for hexacoordinated Na^+ and K^+, respectively). Yet the smaller Li^+ revert can be accommodated. The noncharged selectivity filter (SF) motif of (G/S)xS favors monovalent over divalent cations.[29] TRPA1 is a tetrameric nonselective cation channel with a relatively wide yet rigid SF of LGD, binding to metals *via* the Leu and Gly backbone groups and the Asp^- side chain. The four negatively charged residues with a rigid protein matrix favor divalent over monovalent cations. Fe^{2+} is a dication that may be less favorable for TRPA1 binding as its spin state can change from high-spin for interacting with the Asp^- side chain (charge-donor with small metal d-orbital splitting) to low-spin for binding to the Leu and Gly backbone groups (charge-acceptor with large d-orbital spitting). The low-spin Fe^{2+} with a markedly decreased ionic radius may not fit well in the rigid channel. In addition, TRPA1 may bind to heavy metals and thiol groups using the cysteine-rich pocket.[6,30] TRPV1 ion channels share a similar tetramer scaffold with the TRPA1 family but have a distinct GMGD SF motif. Despite the presence of four acidic residues, the wide and flexible pore with better solvent accessibility can accommodate a wide range of

Table 3 Structures of the key receptors involved in mineral perception

Receptor family	Receptor	SF motif	Selective mineral	Model	PDB ID[a]
Olfactory GPCRs	OR51/52		1-Octen-3-one	Human	8F76
Taste GPCRs	Tas1R3		Ca^{2+}, Fe^{2+}	Human	9UT8
	Tas2R7		Mg^{2+}, Ca^{2+}, Cu^{2+}, Al^{3+}not monovalent ions	Heterologous	6BQG
Ion Channels	ENaC[b]	(G/S)xS	Na^+, Li^+	Human	6WTH
TRP Ion Channels	TRPA1	LGD	Thiols, Ca^{2+}, Cu^{2+}, Zn^{2+}, Cd^{2+}	Human	6PQP
	TRPV1	GMGD	Ca^{2+}, Fe^{2+}, Cu^{2+}, Zn^{2+}, Na^+, K^+	Human	9P6B

[a] Other structures of human sensory receptors may be available in the protein data bank. The listed PDB ID only serves as a model example. [b] No structure yet solved for the SF of ENaC.

metal ions.[31] Tas1R3 forms a heterodimer with Tas1R1 and Tas1R2 to constitute the umami and sweet taste receptors, respectively, and is essential for triggering umami and sweet sensation. Structural studies suggest that Tas1R3 may play a key role in the conformational transition of Tas1R2. Tas1R3 was shown to be activated by Ca^{2+} *in vitro*, and potentially by other dications. Solving the structure of Tas1R3 in the presence of metal ions is required to identify the exact metal-binding site and to explore its metal ion selectivity.[32] Among the 25 human bitter taste receptors, Tas2R7 was reported to respond to various divalent and trivalent cations but not to monovalent ions *in vitro*. Molecular modeling and docking identified an EHEE binding cavity with a high level of negative charge density that favors divalent/trivalent cations over monovalent cations.[33] This finding demonstrates that potassium chloride is little known for its bitterness.[6,26]

3 Applications and future outlook

This study disentangles the fundamental principles of minerality and will have great impact on how wines are tasted and analysed, the applied viticulture and winemaking for mineral wine styles, novel marketing strategies to promote distinctive wine styles, mineral perception mechanisms, the design of new cuisine and olfactory/taste modulators, and the engineering of sensory receptors with desirable properties. During the preparation of the manuscript, a thesis from the Institute of Masters of Wine reported a thorough statistical analysis of 20 678 tasting notes published in Decanter.[4] Stone, salty, metal, and smoke were concluded to be the highest positive predictors of minerality, supporting the main concepts in this work. Scientific and linguistic studies ultimately achieve the same conclusion. Importantly, this work shows that a broad knowledge of chemistry ranging from inorganic, theoretical, and wine chemistry to biochemistry and structural biology can not only advance the interdisciplinary research in agriculture, enology, food and drink science, and beverage marketing, but also provide scientific education to the general public. The main applications and future research are discussed as follows.

3.1 Petrol and kerosene in wines may be stimulated by metals

1,1,6-Trimethyl-1,2-dihydronapthalene (TDN) is well known to create aromas like petrol in white wines and kerosene in red wines. TDN is usually produced from the decomposition of nonvolatile compounds called carotenoids. The production pathways involve reduction/oxidation catalyzed by metal-containing enzymes (carotenoid cleavage dioxygenases), where metals have been reported to play key roles.[34,35] However, the overall mechanisms remain unclear. The chemical pathways and the resulting concentrations of TDN are known to be promoted by warm temperatures and sunlight.[36] Whether similar families of enzymes are present in wines or if metal ions, in addition to temperature and light, in wines can facilitate reduction/

oxidation for TDN decomposition from precursor compounds requires further investigation.

3.2 Mechanisms of mineral perception

Depending on its structural and physicochemical properties, an individual sensory receptor may accommodate different minerals and undergo distinct conformational changes to trigger specific signaling pathways. The intricate structure–activity relationships pose great challenges in understanding the mechanisms of mineral perception. Nonetheless, cryo-EM, quantum chemical calculations, and computer simulations have been shown to provide important structure and dynamic insights to reveal key molecular interactions governing mineral-receptor recognition.[25] A leap in how mineral-receptor pairing activates specific cellular signaling and the structure–perception relationships of minerals in the near future can be anticipated.

3.3 Connection between minerality and terroir

The concept of terroir emphasises how the growing environment can affect wine quality. Unique terroir is often used to promote wine quality and command high prices.[37] However, recent analysis of chemical compositions of soils, vines, berries, and wines showed no clear connection between soils and resulting wine products.[2,13,38,39] Indeed, the chemical profiles of soils through wines can be a powerful tool to quantify and analyse their main features and explore the corresponding relationships.[40] As numerous factors related to climate, soil conditions, and viticultural and vinification practices can all have great impacts on wine components and flavors, the direct comparison of the chemical compositions of wines cannot easily uncover their complicated correlations. A more logical analysis can be performed by regulating a few selected factors while maintaining others under the same conditions. For instance, by comparing samples of a specified varietal from a specific vineyard with identical viticultural and vinification processes yet produced in warm and cool vintages or in years with highest and lowest precipitation, the unique chemical profiles resulting from different growing temperatures or levels of rain can be effectively revealed. On the other hand, interpretation of correlation analysis for terroir and minerality is challenging as conclusions are highly dependent on the range of datasets, the conditions of the measurements, and the statistical models applied. Furthermore, the general concept of terroir cannot easily be translated into a simple variable required in the analysis and its relationship with minerality may not be monotonic.[41]

Versatile mineral compositions including various metals and other inorganic elements in wine can potentially provide distinct fingerprints and may reflect terroir.[38,42] Recent studies showed that elements frequently used in chemical agents for viticulture and vinification or easily forming precipitates (*e.g.* Mg, Ca, K, Cu) may need to be considered carefully.[38] In addition to minerals, some unique organic phenolic compounds in Malbec have been shown to be strongly related to terroir features in Mendoza, Argentina.[40]

The uptake of mineral ions from soils to vines is mainly regulated by the soil conditions, water, and the rootstocks. Slightly acidic soils (pH 6–7) tend to facilitate the absorption of most minerals, whereas alkaline soils lower the availability of transition metals such as iron and copper.[2] Microorganisms can improve soil texture and are more active in mildly acidic soils. Sufficient water is critical to dissolve minerals from soils to be absorbed by vines. Soils with a higher percentage of organic components (humus) and clay can help attract and hold metal cations.[2] Depending on nutrient availability and the preference of grape variety, suitable rootstocks can be selected to improve the absorption of minerals.

3.4 Winemaking skills to preserve or enhance minerality

Minerals have been shown to greatly influence the taste, aroma, and mouthfeel of wine by directly inducing the sensation or as a catalyst to stimulate the production of volatile molecules. The composition of minerals in wine is subject to change depending on the various winemaking approaches used.[10,38] Less human intervention in winemaking using less chemicals such as fining agents can help preserve the minerals from grapes. Reductive winemaking and storage can also maintain the concentrations of metal ions (*e.g.* copper, iron) as well as volatile sulfur minerals and lipids that are highly reactive to oxygen. On the other hand, the addition of anti-microbials/anti-oxidants such as SO_2 may increase the reductive odors.[9,12] Other approaches such as fining with bentonite and using rocks or vessels containing minerals (*e.g.* amphorae made of clay, metals) can also elevate mineral contents[2] and thus artificially promote minerality so long as the types of minerals can dissolve in wine at levels above the perception threshold. Theoretically, deliberately making mineral wine for the mass market could be possible.

3.5 Minerality as a marketing strategy

Mineral aromas/flavors have long been used in wine promotion despite the intense debate surrounding their interpretation. This study has provided a fundamental understanding of the origins and the chemical pathways involved in wine minerality, which can further create strengths and opportunities for marketing. The diverse mineral lexicon can be rationally used to describe different wines and to emphasise their high quality and unique style. These concepts can be used to create compelling stories linking distinctive geographies/climates and skilful winemaking to wines exhibiting specific mineral sensations typical of the wine regions as well as to inform consumers what exactly they are paying higher prices for. A market trend for premiumization of mineral wines could be developed. In addition, mineral compounds common in food means that mineral wine pairing is feasible in daily life. The incorporation of the science of minerality in wine education could attract high-involvement consumers, whereas its integration in wine tourism and fine dining can engage low-involvement customers.

4 Conclusions

This review integrates interdisciplinary studies with physico-chemical guidelines to unravel the fundamental principles of mineral perception as well as to highlight future directions of research and the wide applications of research into terroir, winemaking, and the molecular mechanisms of mineral flavour sensing. The unconventional perspectives on and key concepts of minerality are summarized as follows.

1. Broad knowledge of chemistry is indispensable to unravel the underlying principles and gain a comprehensive understanding of mineral perception.

2. Frequently encountered mineral perception can be classified into three main groups: metal, sulfur, and metal-catalyzed according to the chemical source and pathway which created the minerality. Metal ions that directly cause perceived flavours/aromas are found in the metal group. NaCl and KCl are common examples that give a salty sensation. Metal ions that do not directly account for flavours/aromas yet catalyze the chemical reactions to produce volatile compounds are in the metal-catalyzed group. Reactive blood Fe^{2+} ions that can reduce and decompose lipidperoxides on the surface of the skin to produce the odorous molecule 1-octen-3-one are a classic example. The sulfur group is composed of mainly aromatic sulfur-containing molecules. H_2S and MeSH with flinty/reductive aromas are typical examples of the wide range of sulfur compounds in wines.

3. Chemical components in wine can internally interact with one another to generate various compounds with different properties. Furthermore, these chemical reactions can be accelerated or decelerated by external environmental factors such as temperature and exposure to oxygen. Thus, a positive connection between mineral intensity and concentrations may not be observed in experiments.

4. Mineral perception is a combinatorial taste sensation caused by metal ions and thiols as well as olfactory/retronasal sensation *via* volatile sulfur-containing molecules and lipid oxidation catalyzed by metals. Current research has identified five types of human mineral taste receptors. TRPA1, TRPV1, and ENaC are ion channels, whereas Tas2R7 and Tas1R3 are GPCRs. The principles of metal selectivity in proteins provide important structure–perception relationships for minerals. The study of odorant and olfactory receptor (all GPCRs) pairing is still in its infancy. The cryo-EM structures of the OR51 and OR52 families reveal the recognition of fatty acids, indicating an association with mineral perception.

Author contributions

Hui-Chung Tai: conceptualization, methodology, analysis, writing, and review. Evmorfia Kostaki: conceptualization and review.

Conflicts of interest

No potential conflict of interest is reported by the authors.

Data availability

No primary research results, software or code have been included and no new data were generated as part of this review.

References

1 S. J. Evens, *Minerality in wine: What does it mean to you?*, https://www.decanter.com/premium/minerality-in-wine-what-does-it-mean-to-you-245668/, accessed 19 March 2025.

2 A. Maltman, *Vineyards, Rocks, and Soils the Wine Lover's Guide to Geology*, Oxford University Press, 2018.

3 W. Parr, A. Maltman, S. Easton and J. Ballester, *Beverages*, 2018, **4**, 77.

4 J. Martindale, Master of Wine Thesis, 2021.

5 A. J. Biss and R. H. Ellis, *Aust. J. Grape Wine Res.*, 2024, **2024**, 1–13.

6 M. J. Y. Ecarma and A. A. Nolden, *Chem Senses*, 2021, **46**, 1–8.

7 P. Deneulin, Y. Le Fur and F. Bavaud, *Food Res. Int.*, 2016, **90**, 288–297.

8 M. Z. Bekker, M. P. Day and P. A. Smith, *Molecules*, 2019, **24**, 1523.

9 N. Müller and D. Rauhut, *Fermentation*, 2018, **4**, 62.

10 A. C. Clark, *Metal Ion Speciation: Understanding its Role in Wine Development and Generating a Tool to Minimise Wine spoilage*, Charles Sturt University, 2018.

11 C. Van Leeuwen, J.-P. Roby and L. De Rességuier, *OENO One*, 2018, **52**, 173–188.

12 *Wine & Spirit Education Trust Level 4 Diploma in Wines: D1 Wine Production*, Wine & Spirit Education Trust, 2021.

13 Z. Temerdashev, A. Abakumov, A. Khalafyan, M. Bolshov, A. Lukyanov, A. Vasilyev and E. Gipich, *Molecules*, 2024, **29**, 2251.

14 L. C. de Loryn, P. R. Petrie, A. M. Hasted, T. E. Johnson, C. Collins and S. E. P. Bastian, *Am. J. Enol. Vitic.*, 2013, **65**, 124–133.

15 E. M. Epke and H. T. Lawless, *Physiol. Behav.*, 2007, **92**, 487–491.

16 V. Honig, P. Prochazka, M. Obergruber and H. Roubik, *Foods*, 2020, **9**, 1875.

17 The Australian Wine Research Institute, *Removal of volatile sulfur compounds*, https://www.awri.com.au/industry_support/winemaking_resources/storage-and-packaging/pre-packaging-preparation/removal-volatile-sulfur-compounds/, accessed 19 March 2025.

18 M. Z. Bekker, M. Taraji, V. Hysenaj and N. Lloyd, *Heliyon*, 2024, **10**, e28929.

19 M. C. Cravero, *Beverages*, 2020, **6**, 41.

20 D. Glindemann, A. Dietrich, H. J. Staerk and P. Kuschk, *Angew. Chem., Int. Ed.*, 2006, **45**, 7006–7009.

21 I. J. Bear and R. G. Thomas, *Nature*, 1964, **201**, 993–995.

22 C. Csutoras, N. Bakos-Barczi and B. Burkus, *Acta Aliment*, 2022, **51**, 33–42.

23 K. Yunoki, M. Tanji, Y. Murakami, Y. Yasui, S. Hirose and M. Ohnishi, *Biosci. Biotechnol. Biochem.*, 2004, **68**, 2623–2626.

24 K. C. Fugelsang and C. G. Edwards, *Wine Microbiology Practical Applications and Procedures*, Springer, 2007.

25 C. B. Billesbølle, C. A. De March, W. J. C. Van Der Velden, N. Ma, J. Tewari, C. L. Del Torrent, L. Li, B. Faust, N. Vaidehi, H. Matsunami and A. Manglik, *Nature*, 2023, **615**, 742–749.

26 S. Sood, L. Methven and Q. Cheng, *Crit. Rev. Food Sci. Nutr.*, 2025, **65**, 3444–3458.

27 C. Choi, J. Bae, S. Kim, S. Lee, H. Kang, J. Kim, I. Bang, K. Kim, W.-K. Huh, C. Seok, H. Park, W. Im and H.-J. Choi, *Nat. Commun.*, 2023, **14**, 8105.

28 T. Dudev and C. Lim, *Chem. Rev.*, 2014, **114**, 538–556.

29 C. Lim and T. Dudev, in *The Alkali Metal Ions: Their Role for Life*, ed. A. Sigel, H. Sigel and R. K. O. Sigel, Springer International Publishing, Cham, 2016325–347.

30 Y. Suo, Z. Wang, L. Zubcevic, A. L. Hsu, Q. He, M. J. Borgnia, R.-R. Ji and S.-Y. Lee, *Neuron*, 2020, **105**, 882–894.

31 A. Neuberger, M. Oda, Y. A. Nikolaev, K. D. Nadezhdin, E. O. Gracheva, S. N. Bagriantsev and A. I. Sobolevsky, *Nat. Commun.*, 2023, **14**, 2451.

32 Z. Juen, Z. Lu, R. Yu, A. N. Chang, B. Wang, A. W. P. Fitzpatrick and C. S. Zuker, *Cell*, 2025, **188**, 4141–4153.

33 Y. Wang, A. L. Zajac, W. Lei, C. M. Christensen, R. F. Margolskee, C. Bouysset, J. Golebiowski, H. Zhao, S. Fiorucci and P. Jiang, *Chem Senses*, 2019, **44**, 339–347.

34 A. Daruwalla, J. Zhang, H. J. Lee, N. Khadka, E. R. Farquhar, W. Shi, J. von Lintig and P. D. Kiser, *Proc. Natl. Acad. Sci. U. S. A.*, 2020, **117**, 19914–19925.

35 Y. J. Solano, M. P. Everett, K. S. Dang, J. Abueg and P. D. Kiser, *Nat. Chem. Biol.*, 2024, **20**, 779–788.

36 C. Black, L. Francis, P. Henschke, D. Capone, S. Anderson, M. Day, H. Holt, W. Pearson, M. Herderich and D. Johnson, *Wine & Viticulture Journal*, 2012, **27**, 20–26.

37 *Wine & Spirit Education Trust Level 4 Diploma in Wines: D2 Wine Business*, Wine & Spirit Education Trust, 2021.

38 S. Catarino, M. Madeira, F. Monteiro, I. Caldeira, R. Bruno de Sousa and A. Curvelo-Garcia, *Beverages*, 2018, **4**, 85.

39 A. Maltman, *J. Wine Res*, 2013, **24**, 169–181.

40 R. Urvieta, G. Jones, F. Buscema, R. Bottini and A. Fontana, *Sci. Rep.*, 2021, **11**, 2863.

41 P. Schober, C. Boer and L. A. Schwarte, *Anesth. Analg.*, 2018, **126**, 1763–1768.

42 S. Đurđić, M. Pantelić, J. Trifković, V. Vukojević, M. Natić, Ž. Tešić and J. Mutić, *RSC Adv.*, 2017, **7**, 2151–2162.