



Comparative analysis of the odorants of cilantro (*Coriandrum sativum* L.) and culantro (*Eryngium foetidum* L.) as aromatic crop mimics of family: *Apiaceae*

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ABSTRACT

Purpose: Fresh leaves of cilantro (*Coriandrum sativum* L.), and culantro (*Eryngium foetidum* L.) are used interchangeably based on similar odor, aroma and flavor and considered culinary substitutes. Cilantro is ethnically called “false coriander” and a mixed method approach to determine the possibility of crop mimicry was reviewed. Critical analysis was done on botanical, phylogenetic traits and trees, dendrogram, molecular, and phytochemical similarities of the odorants. **Findings:** The study indicated that *C. sativum* and *E. foetidum*, belonged to two different subfamilies of *Apiaceae*, appeared morphologically divergent, but phytochemically similar in aroma and odorants indicating a classical example of convergent evolution in the plant kingdom. Five odor clusters with over 20 similar phytochemicals with the co-elution of *E*-2-alkenals and *E*-2-alken-1-ols were identified. Greater levels *E*-2-dodecenal in *E. foetidum* (63.5%) compared to *C. sativum*, (26.0%) accounted for dominant odor which is found in crop mimics due to selective agricultural practices and the evolution of agricultural races of weeds. Multiple mechanisms explained how plant mimic evolved from “de-domestication” and hybridization. Evolutionary origins and genetic diversity characterized genomics of *E. foetidum* as an aggressive aromatic pungent weed, and *C. sativum* as a fragrant herb. **Limitations:** There are no limitations in this review. **Directions for future research:** Organoleptic preference for the essential oils of coriander seeds and a clearer understanding of the phytochemical relationships between *C. sativum* and *E. foetidum* are required.

INTRODUCTION

Eryngium foetidum L. (Umbelliferae–Apiaceae) is a pungent aromatic herb known by several common names, such as “Mexican coriander, spirit weed, fit weed, culantro, bhandhanian and shado beni” (Ramcharan, 1999). The plant is indigenous to Tropical America and the West Indies (Seaforth et al., 2008). It was introduced and became naturalized across South Asia, the Pacific islands, Tropical Africa and the warmer southern parts of Europe (Paul et al., 2011). The indigenous people of Northeast India have domesticated the plants in their kitchen gardens and orchards. The plant is often mistaken and misnamed for *Coriandrum sativum* (L.) commonly called cilantro or coriander. Ganesan (2013) found that *C. sativum* is more popular and widely used as a dried-seed spice as coriander instead of the leaves. The fresh leaves are rich in bioactive compounds. Seaforth et al. (1983) reported that the leaves of both plants have high contents of essential oils which are common in curry and fresh seasonings in ethnic cooking, but are more widely utilized as a spread or garnish and in the production of chutneys.

The early East Indian indentured laborers (1860’s) who migrated to the Caribbean worked in the sugar and cocoa plantations. They manually brush-cut the fields early in the morning as part of their task. Historical evidence indicated that when they swiped the bushes and weeds early in the morning, the released volatiles were scented similar to coriander [dhanian], and on closer examination, it was discovered as the broadleaf weed which they were acquainted to in India. This familiar odor encouraged them to substitute the weed as the “new coriander”, but since it was not real (bhan = false), they called it the false coriander [bhan-dhanian] (Mohammed, Pers Comm., 2020). However, emigrants from Northeast India who were previously exposed to the plant adopted it in their traditional cooking.

The herb was later introduced around the 1880’s into South East Asia by the Chinese, who were early inhabitants to the West Indies (Paul et al., 2011). They used it as a substitute condiment for the coriander (*C. sativum* L.) possibly due to its similar pungent odor (Shavandi, 2012). While the appearance of both plants is morphologically different, the leaf aromas are similar, although *E. foetidum* L. is more pungent. It is this similarity in aroma that promoted the wide spread interchangeable use of the leaves in many food preparations, and the one major reason for the misnaming of one herb for the other. Due to its apparent similarity and its ease as a culinary substitute, this review attempts to conduct a comparative analysis of the odorants of cilantro (*Coriandrum sativum* L.), and culantro (*Eryngium foetidum* L.) which may be crop mimics of the *Apiaceae* family.

Ramcharan (1999) reported that false coriander or culantro is extensively used in cooking, and has ethno-culturally derived names based on the country eg. *Awa-phadigom* in Manipuri, *Bahkhawr* in Mizo, *Ban dhanian* in Hindi, *Naga*; *Dhanian* in Assamese and Nepali or *Bhutia dhanian* in Nepali and *Bilati Dhaney* in Bengali. Regionally, it is called *Andu kola* in Sri Lanka, *Shado beni* in Trinidad, *Chadron benee* in Dominica, *Fitweed* in Guyana, *Coulante* in Haiti, *Recao* in Puerto Rico, *Langer coriander*; Germani, *Walangan* in Indonesia, *Pak chi farang* in Thai, *Ngo ngai* in Vietnamese.

Extensive research has been conducted and reported on the agronomy and production of *C. sativum* L. and *E. foetidum* L., including the botany, utilization, recipes, ethno-medicinal and post-harvest and processing (Puente, 2019; Mohammed & Wickham, 1995; Sankat & Maharaj, 1991). Bijaya et al. (2016) compared the extraction and chemical analysis of the essential oils and oleoresins of both plants, and also the economics. This review focused on a hybrid approach using both qualitative and quantitative methodologies. The evidence is based on analytical chemistry and quantitative published research, and triangulating the findings

with the authors and experts in the field, including reviews of graduate students' theses on the chemistry of both crops.

The paper attempts to explore the hypothesis that if the plants are compatible and equivalent substitutes, then the term "false coriander" for *E. foetidum* L. (Apiaceae) is applicable and relevant. Further, the extensive literature available is used to propose and test the hypothesis of the similarities of the odorants making them "crop mimics" of *C. sativum* L., and *E. foetidum* L.

DISCUSSION

Phylogeny analysis

The phylogeny of plants within a family demonstrates an evolutionary relationship and is usually depicted as a phylogenetic tree. These relationships are determined by comparisons of the botanical and ecological characteristics, and also anatomical and genetic similarities. More recently, molecular relational phylogeny has been conducted based on the DNA and protein structure. The higher level relationships within the *Apiaceae* (Umbelliferae) subfamily *Apioideae* was found to be limiting and controversial, with no widely acceptable modern classification available (Downie et al., 2000). Based on that premise, in this study phylogenetic analysis is supported by phytochemical analysis of the essential oils of both plants.

In the phylogenetic analysis for the commonality of odorants between *C. sativum* L., and *E. foetidum* L., the approach was to determine the botanical and taxonomic similarities, and expand these into the agro ecological conditions under which the plants evolved and the conditions in which they are cultivated. Further comparative analysis was undertaken based on the phylogeny tree, dendrogram and molecular phylogeny.

Uses

Both plants are commonly used as herbs and spices and are linked chemically, based on their physiological effects on human's taste and smell. They have no caloric value but are more popular for their ethno-medicinal uses (Paul et al., 2011). Herbs or spices are used in small quantities, to enhance the characteristic flavors or odors when added to food. This is as a result of the essential oils or odorants which are easily recognized and detected by human scent and taste receptors. The odorants are produced in specialized glands, and secreted when the plant is damaged or cut. These chemicals serve as inhibitors from insects and other herbivores feeding on them (Paul et al., 2011).

The essential oil has economic value in the perfumery and cosmetic industries, traditional teas (Chicaiza, 2019), and demonstrated pharmacological properties (Cardozo et al., 2004). However, the evolving demand and use in the Western hemisphere is for the fresh leaves to be used as a condiment and seasoning in Caribbean and Latin American cuisines. Popular chefs in the USA have demonstrated its culinary versatility as a garnish that out-classed the common use of cilantro (Mohammed Pers Comm., 2020).

The fresh leaves *C. sativum* are widely used in all classes of cooking, but the seeds are more valuable as coriander seeds. The essential oils of the leaves are rich in many bioactive compounds (polyphenols, alkaloids and flavonoids) and used in herbal medicines due to its multiple bioactive functions (antioxidant, anticancer, antimicrobial antidiabetic and hepatoprotective) (Nadeem et al., 2013). International chefs are referring to *E. foetidum* L. as the neo-spice/herb or culantro which is widely used for garnishing, marinating, flavoring and seasoning of foods, apart for its ethno-medicinal role (Sankat & Maharaj., 1991; Ganesan et al., 2013). It is replacing cilantro in the food industry. Pharmacological investigations have

demonstrated anthelmintic, anti-inflammatory, analgesic, anti-convulsant, anti-clastogenic, anti-carcinogenic, anti-diabetic and anti-bacterial properties (Garcia et al., 1999).

Table 1. The botanical classification of *C. sativum* L. and *E. foetidum*

| Scientific classification | Botanical nomenclature | |
|---------------------------|----------------------------------|----------------------------------|
| | <i>Coriandrum sativum</i> L. | <i>Eryngium foetidum</i> L. |
| Kingdom: | Plantae | Plantae |
| Subkingdom | Tracheobionta – Vascular plants | Tracheobionta – Vascular plants |
| Superdivision | Spermatophyta – Seed plants | Spermatophyta – Seed plants |
| Division | Magnoliophyta – Flowering plants | Magnoliophyta – Flowering plants |
| Class | Magnoliopsida – Dicotyledons | Magnoliopsida – Dicotyledons |
| Subclass | Rosidae | Rosidae |
| Clade: | Angiosperms | Angiosperms |
| Clade: | Eudicots | Eudicots |
| Clade: | Asterids | Asterids |
| Higher classification | Coriandrum | Eryngos |
| Order: | Apiales | Apiales |
| Family: | Apiaceae | Apiaceae |
| Genus: | <i>Coriandrum</i> | <i>Eryngium</i> |
| Species: | <i>C. sativum</i> | <i>E. foetidum</i> |

Table 2. Comparison of the leaf shape and morphology between both *E. foetidum* and *C. sativum*

| Leaf Character | Character states | |
|-----------------------------|---|---|
| | <i>C. sativum</i> | <i>E. Foetidum</i> |
| Lamina | <ul style="list-style-type: none"> • Simple • Pinnatifid • Pinnatipartite • Decompound | <ul style="list-style-type: none"> • long and broad • Simple |
| Shape | <ul style="list-style-type: none"> • Ovate • Lanceolate • Oblanceolate to spatulate ovate | <ul style="list-style-type: none"> • Elongate • Oblanceolated • Spatulate • Non-Palm Foliage |
| Shape ultimate leaf segment | <ul style="list-style-type: none"> • Oblong to lanceolate • Linear lanceolate to linear • Deltoid rhomboid | <ul style="list-style-type: none"> • Variable in shape • Lobed at the base • Slender and feathery higher on stems. • Oblanceolate-spatulate • Fecundate at the base. |
| Nature | <ul style="list-style-type: none"> • Cauline throughout • Cauline at base radical in the upper region | <ul style="list-style-type: none"> • Fleshy waxy leaves • Spirally around stem to form a basal rosette |
| Leaf-let tip | <ul style="list-style-type: none"> • Acute to acuminate • Rounded | <ul style="list-style-type: none"> • Obtuse with spinous-toothed • rounded tips, tapered base |
| Margin | <ul style="list-style-type: none"> • Entire • Serrate-spinulose • Glabrous to hispid • Serrate undulate | <ul style="list-style-type: none"> • Serrated toothed • Small yellow spine • Glabrous and strongly scented |

Botany

The Apiaceae family includes crops such as parsley, mint, and dill. There about 228 species of the genus *Eryngium* Linnaeus of *Apiaceae* as compared to *C. sativum*. The species *E. foetidum* Linnaeus is domesticated, cultivated and used extensively (Ramcharan, 1999). *E. foetidum* L. (Apiaceae) is a neo-tropical herbal crop indigenous to the New World and often mistaken for *C. sativum*. The latter is traded internationally as dried seeds of spice as coriander. *C. sativum* which is a soft plant growing (50 cm height) while the latter is an annual rosette herb (Ramcharan, 1999).

Both species are dicotyledonous vascular flowering plants that are reproduced by seeds, but the plant has shown that it can be propagated by shoot cuttings (Table 1). Botanically, they are very similar as they belong to the same sub-class (*Rosidae*), and Caldes (*Eudicots and Asterids*). The genus *Coriandrum* and *Eryngium* both belong to the Order: *Apiales* and the Family: *Apiaceous* (Rodrigues et al., 2020). Taxonomically, this is the first evidence of similarity between both plants (Table 1).

Leaf morphology

There are many differences in the leaf shape and morphology between both *E. foetidum* and *C. sativum*, which are not influenced by the various ecosystems under which the plants have evolved or cultivated (Table 2). *E. foetidum* is a spiny herb with fleshy waxy leaves with a deep tap-root and belongs to *Eryngium* which comprises over 200 tropical and temperate species (Willis, 1960). The leaves (30 cm long and 4 cm wide) are arranged spirally around the thickened stem to form a basal rosette. The leaf margin is serrated, each tooth of the margin containing a small yellow spine (Seaforth et al., 1983). *E. foetidum* is described as a short perennial herb (25-40 cm) with a highly aromatic tuberous root system with branched dichotomous stem (Seaforth et al., 2008). The plant has simple elongated leaves (lamina 5-10 cm x 0.6-2.5 cm) which are oblanceolate-spathulate and cuneate at the base. The apex is obtuse and spinous-toothed.

C. sativum is an annual herb (0.20 and 1.40 m) which has an epigeal germination developing into a plant with a deep tap root, and an erect and sympodial, monochasial-branched stem at the basal node. *C. sativum* leaves are alternate gathered in a rosette with the basal leaf blade either undivided with three lobes or tripinnatifid. The older leaves of the nodes following are to a higher degree pinnatifid. The upper leaves are narrow lanceolate or even filiform-shaped blades and appear dark or light green with the underside waxy. However, the leaves turn red or violet during the flowering period (Maroufi et al., 2010).

Phylogenetic trees

The phylogenic analysis is based on phylogenetic trees which are used to develop and illustrate relationships among taxa or a group of biological entities at any level in the taxonomic hierarchy (Huelsenbeck et al., 1996). It is based on the relative order of speciation events. These trees are computed on the morphological characteristics of plants and can identify congruency, similar to that of molecular determination. It is more reliable than visual morphology which uses taxonomic characterization and ambiguity in tracing phylogeny. Based on this advantage, this approach was used in tracing phylogeny between *C. sativum* L. and *E. foetidum*.

It was already evident that both *C. sativum* L. and *E. foetidum* belonged to the *Apioidae*. Simple leaves are common in *Saniculoideae*, which have ancestral relationship of the tribes of both *Steganotaenieae* and *Saniculeae* with nonpalmate leaves (Das, 2020). This is a plesiomorphic feature also present in the ancestors of subfamily *Saniculoideae*, the ancestor

of *Apioideae* (Das, 2020). The simple leaf is presumed as a primitive condition, which evolved and progressed with gradual increase into a marginal pinnately dissected pinnatifid ultimately to decompose leaves with narrow linear segments (Fig. 1). In a same manner, ovate-lanceolate cotyledonary leaves may be considered to represent the primitive characteristic which will evolve into narrow linear cotyledonary leaves (Das, 2020).

This argument was used to advance the similarity of *E. foetidum* (which included in the subfamily *Saniculoideae*) which represented the ancestral stock of having pinnatifid, pinnatifid to pinnatisect-decompose leaves with narrow linear segments (Das, 2020). This has evolved into *C. sativum* L. which is supposed to be a probable descendent (not immediate) from long coriander or Culantro (Fig. 1). Two evolutionary trends are easily recognizable from *C. sativum* L., as celery, parsley, and fennel. *E. foetidum* has shown a wide divergence from all the other members like coriander and celery (Fig. 1). Using molecular phylogeny, Downie et al. (2000) in a study involving a large number of taxa reflected on the overall phylogeny in *Apioideae* thereby providing the missing links (Diederichsen & Hammer, 2003).

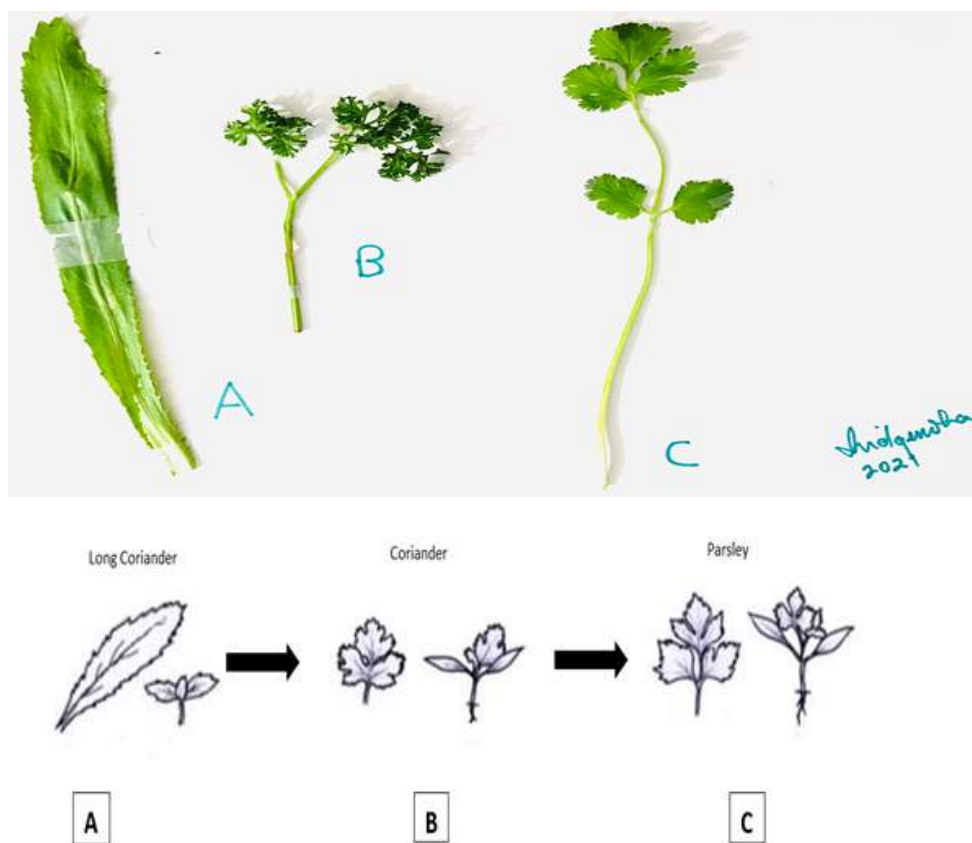


Fig. 1. Line drawing and photographs of the leaf morphology of *C. sativum* L., and [A] *E. foetidum*, [B] *C. sativum* and [C] *Petroselinum crispum*.

Dendrogram

Apart from phylogenetic trees, dendrograms are computed from morphological features which appear to be more supportive to the derived putative trend. Dendrograms are used to group leaf margin patterns, seedling morphology along with other morphological features (Das, 2020). These morphological parameters are significant enough to minimize the variations between different phylogenetic interpretations. Along with molecular parameters, it could be proved promising to derive phylogeny in *Apiaceae* especially in subfamily *Apiioideae*. A comprehensive analysis of the family *Apiaceae* Lindl. (*Umbelliferae* Juss.) Has been known to comprise between 300–455 genera and more than 3000–3750 species (Das, 2020). Included amongst the family are many acquainted vegetables which are used as flavorings or garnishes eg. Angelica, anise (aniseed), caraway, celery, chervil, coriander (cilantro), cumin, dill, fennel, and parsley. A phylogenetic tree (Fig. 2), demonstrated the similarity index of *C. sativum* L., and *E. foetidum* (Alp & Geboluglu, 2017). It showed that *E. foetidum* or Long coriander was more closely related to carrot and parsley, and also coriander. It is interesting to note, that *E. foetidum* when cultivated in deep sandy soils was reported to produce long radish-like tap roots, similar to carrots (Mohammed, Pers Comm., 2020).

Molecular profiles

The phylogeny analysis of the *Apiaceae* especially subfamily *Apiioideae* was more efficient compared to molecular systematics but this was not conclusive. The phylogeny method on the *Apiaceae* was also used based on chloroplast DNA *rpl16* and *rpoC1* intron sequences and a suprageneric classification of subfamily *Apiioideae*. The results of that analysis were more consistent, but considerably less resolved than relationships derived from these ITS regions (Das, 2020). That study affirmed that the application of ITS sequences was more useful for phylogenetic inference among related members of *Apiioideae*. However, due to the high rates of nucleotide substitution, it was less useful in resolving relationships among the more ancestral nodes of the phylogeny. The inconclusiveness in the molecular systematics was established on the fact that there is limited support for any existing system of classification of that subfamily, which was previously based largely on morphological and anatomical features of the plants (Das, 2020).

It was assumed that the higher level relationships within *Apiaceae* (*Umbelliferae*) subfamily *Apiioideae* were controversial, with no widely acceptable modern classification available (Downie et al., 2000). This was after the researchers used comparative sequencing of the intron in chloroplast ribosomal protein gene *rpl16* to examine evolutionary relationships among 119 species (99 genera) of subfamily *Apiioideae* and 28 species from *Apiaceae* subfamilies *Saniculoideae* and *Hydrocotyloideae*, and putatively allied families *Araliaceae* and *Pittosporaceae*.

It was also reported that *Apiaceae* particularly in the subfamily *Apiioideae*, molecular data provided little support for interpretation on phylogeny (Das, 2020). Further, the application of phytochemical components as individual character or character state was rare in taxonomy, not evidenced in *Apiaceae* (Diederichsen & Hammer, 2003).

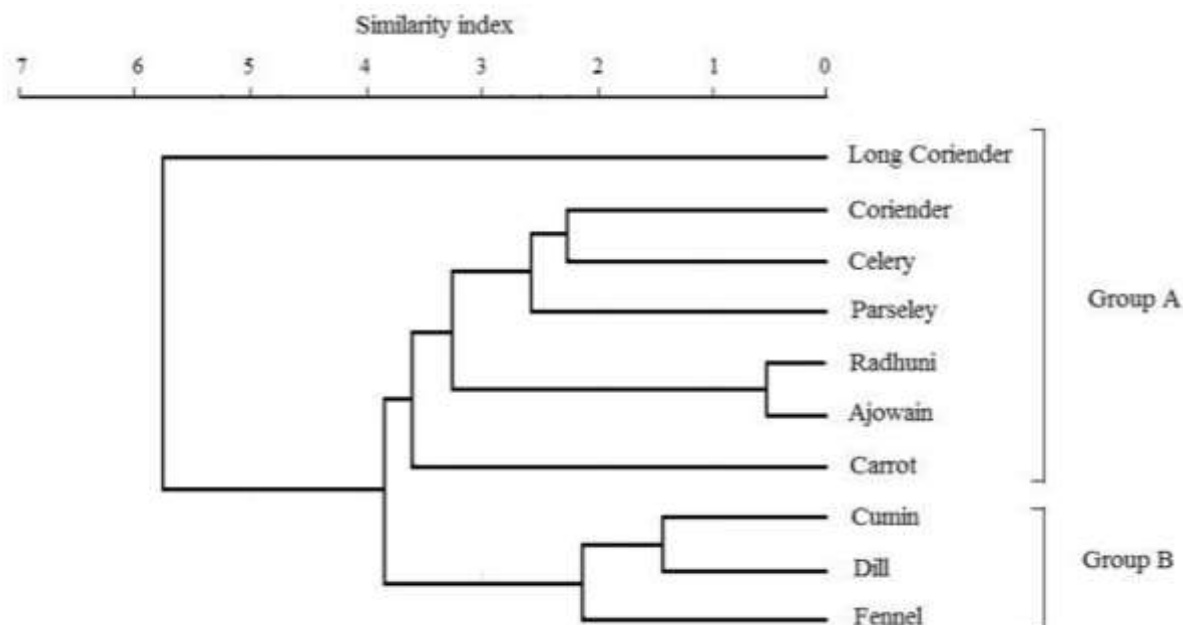


Fig. 2. Dendrogram computed from pairing affinity values on morphological features of (*C. sativum* L.), and *E. foetidum* L. (Adapted After Das, 2020).

Phytochemistry

However, using the phytochemical analysis along with plant morphology, the relative closeness among ten selected members of *Apiaceae* was conducted. The results indicated that *C. sativum* and *E. foetidum*, while they belong to two different subfamilies of *Apiaceae* appeared morphologically quite divergent, but phytochemically much alike having similar aroma and odorants indicating a classical example of convergent evolution in the plant kingdom.

The phytochemical commonality approach used in this study involved chemical screening. This is an effective method which utilized the previous findings of other scientists to characterize the phytochemicals by group functionality. The bioactive profile *C. sativum* and *E. foetidum* indicated many chemicals of therapeutic importance such as alkaloids, tannins, saponins, phenols, flavonoids and terpenoids were already quantitatively identified. Generally, all the researchers used aqueous and/or organic extracts of plant samples which were then analyzed for the presence of these secondary metabolites using simple separation techniques such as thin-layer chromatography (TLC), HPLC, GC, GC-O, GC/MS and H-NMR (Wong et al., 1994; Diederichsen & Hammer, 2003).

The phytochemicals from the leaves of the plants *C. sativum* and *E. foetidum* after they were critically analyzed and assessed for commonality and functionality revealed that there were a total of 10 major groups of chemicals (IPUCA). The major chemicals included alcohols, aldehydes, alkenes, alkanes, cyclic ethers, esters, fatty acids, fatty alcohols, unsaturated fatty acids, and a group called any-others or miscellaneous groups. These compounds which are known for their role in flavor and fragrance were further investigated for its functions as mimics and chemical /aroma similarity in the plant odorants.

Table 3. The presence of the alcohol group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC]* | E.F | C.S |
|-------------------|-------------------------------|-----|-----|
| Alcohol | 5-methylnonan-5-ol | - | + |
| Aliphatic diol | decane-1,10-diol | - | + |
| Aromatic alcohol | 2-(4-methylphenyl)propan-2-ol | + | - |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

* The International Union of Pure and Applied Chemistry (IUPAC). - = absent; + = present.

Alcohol group

There were 3 alcohol compounds that were extracted and identified, with 2 present in *C. sativum* and 1 in *E. foetidum* (Table 3). These compounds are known for their role in flavor and fragrance, but none were common in both plants, and may not have contributed to their similarity in odor or aroma. It was found that generally alcohols facilitate the inter-conversion between alcohols and aldehydes or ketones with the reduction of nicotinamide adenine dinucleotide (NAD⁺) to NADH (An et al., 2019). Most plants, utilized alcohol dehydrogenases to catalyze the opposite reaction as part of fermentation or anaerobiosis to ensure a constant supply of NAD (Bridgemohan et al., 2020). Generally, plant metabolizes alcohols through the enzyme alcohol dehydrogenase into an aldehyde or ketone by removing hydrogen from the alcohol. This may account for the high level of aldehydes in both plants.

Aldehyde group

In the aldehyde group, there were 6 chemical compounds that were extracted and identified of which 4 were medium chain and 2 long chain fatty acids. In both plants, 5 aldehydes were common, except the aromatic aldehyde (2,4,6-trimethylbenzaldehyde) which was present in only *E. foetidum* (Table 4). It was confirmed that the aliphatic aldehydes and aromatic compounds (E-2-dodecenal, 5-dodecene, tetradecanal, tetradecenal) and aromatic (2,3,5-trimethylbenzaldehyde, trimethylphenol) were high and constituted the major essential oils from the Colombian sources of *E. foetidum* and that the aliphatic aldehydes were the more predominant phytochemicals (Jaramillo et al., 2011).

High levels of decanal (19.09%) were observed in *C. sativum* leaves (Potter & Fagerson, 1990). In plants, fatty aldehyde and alcohol metabolism are essential for epidermal differentiation (Rizzo, 2014). These long-chain aldehydes are produced by the catabolic reaction of lipids (including fatty alcohols and certain aliphatic lipids) through α - or ω -oxidation. The medium-to long-chain aliphatic aldehydes (Table 4) and alcohols (Table 3) exist as metabolic products of other precursor lipids. The fatty aldehydes and alcohols are generally structurally diverse and depending on the metabolism of corresponding fatty acids.

The aromatic aldehyde (2,4,6-trimethylbenzaldehyde) which was present only in the essential oils of *E. foetidum*, is suggested to be the main compound that differentiated both plants and may be the cue for the high odorant character in *E. foetidum*. That aromatic aldehyde is a benzaldehyde and is used as an intermediate compound in agricultural and pharmaceutical products, and for flavor and fragrance in cooking.

C. sativum is described as having an unpleasant soapy or even metallic taste. This is based on the chemical composition of the essential oils which comprised around 40 different organic compounds, with 82% of these being aldehydes, and 17% alcohols (Eriksson et al., 2012). It is reported that the aldehydes which is responsible for the aroma of the leaves is perceived to have a soapy taste with slight repulsive side effects.

Alkene group

Of the alkene group, 5 compounds were extracted and identified of which 4 were present in *C. sativum* and only 1 was found in *E. foetidum* (Table 5). There were no similar phytochemicals in this group that were common to both plants.

Alkane group

Similarly, in the alkanes group, 3 such phytochemicals were found present, but only in the *C. sativum* leaves (Table 6). It was found that both alkanals and alkenals embodied the main chemical category in the leaf oil, while (E)-2-dodecenal as the most abundant component (59.72%). There were no traces of aromatic and terpene aldehydes, but 2,3,6-trimethylbenzaldehyde (37.55%) and 2-formyl-1,1,5-trimethylcyclohexa-2,4-dien-6-ol (19.82%), were found present mainly in the roots (Wong et al., 1994).

Table 4. The presence of the aldehyde group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | MW (g/mol) | E.F | C.S |
|---------------------------|-----------------------------|------------|-----|-----|
| Aldehyde | (E)-undec-2-enal | 168.28 | + | + |
| Aromatic aldehyde | 2,4,6-trimethylbenzaldehyde | 148.2 | + | - |
| Fatty Aldehyde | undecanal | 170.29 | + | + |
| | decanal | 156.26 | + | + |
| long-chain fatty aldehyde | <i>E</i> -dodec-5-en-1-ol | 184.32 | + | + |
| | tetradecanal | 212.37 | + | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 5. The presence of the alkene group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | MW (g/mol) | E.F | C.S |
|--------------------|--------------------------------------|------------|-----|-----|
| Alkene | 2,4 dimethylheptane | 128.25 | - | + |
| Alkene | pentadec-1-ene | 210.4 | - | + |
| Cyclic alkene | 1-methyl-4-prop-1-en-2-ylcyclohexene | 136.23 | + | - |
| Aromatic | 1-methyl-2-propan-2-ylbenzene | 134.22 | - | + |
| Unstaurated cyclic | ethylidenecyclooctane | 138.25 | - | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 6. The presence of the alkane group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | MW (g/mol) | E.F | C.S |
|-----------------------|--|------------|-----|-----|
| Cyclic alkane | Cyclododecane | 168.32 | - | + |
| Cyclic alkane alcohol | Cyclooctyl alcohol | 128.21 | - | + |
| Double cyclic alkane | 1,2,3,3a,4,5,6,7,8,8a-decahydroazulene | 138.25 | - | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 7. The presence of the cyclic ether group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | MW (g/mol) | E.F | C.S |
|-------------------|---|------------|-----|-----|
| Cyclic ether | 1,3,3-trimethyl-2-oxabicyclo[2.2.2]octane | 154.25 | + | + |
| Cyclic ether | 2-tetradecyloxirane | 240.42 | - | + |
| Cyclic ether | 2-octyloxirane | 156.26 | - | + |
| Cyclic ether | 2-decyloxirane | 184.32 | + | - |

Cyclic ether

The cyclic ether group had 4 chemicals of which 3 were present in *C. sativum* and in *E. foetidum* (Table 7). However, there was one cyclic ether phytochemical common in both *C. sativum* and *E. foetidum* which is 1,3,3-trimethyl-2-oxabicyclo (2.2.2) octane also referred to as eucalyptol (C₁₀H₁₈O / MW: 154.25) (Seaforth et al., 2008; Paul et al., 2011). These groups of saturated cyclic ethers is also present in tropical and semi-tropical crops in abundance, and are found in numerous biologically active natural products and as the active ingredient in many pharmaceutical products (Lu et al., 2019). The essential oil of fresh *E. foetidum* L leaves consisted mainly of fatty aldehyde ((E)-2-dodecenal 61.8–62.2%, n-dodecanal (10.9–15.5%)), and cyclic ether ((E)-2-tetradecenal (6.7–7.6%) and 1-tetradecene (3.6–5.7%)) (Banout et al., 2010).

Ester group

Like the alkanes group, there were 2 other chemicals found in the ester group. However, these were only present *C. sativum*, and do not share phytochemical commonality with *E. foetidum* (Table 8). These organic compounds are formed when an acid and an alcohol combine. They are volatile with characteristic and pleasant aromas which create the fragrances and flavors in leaves (Wong et al., 1994). This may partially explain the pleasant odor difference between *C. sativum* and the offensive *E. foetidum*. Esters are generally used in the food flavorings industry, and hence there are more applications of *C. sativum* in food processing compared to *E. foetidum* (Mohammed & Wickham, 1995).

Fatty acid

There were 6 phytochemicals identified in the fatty acid group, and all were present in both *C. sativum* and *E. foetidum* (Table 9). Fatty acids (FAs) are long unbranched hydrophobic chains, with hydrophilic carboxylic acid groups at one end (Kachroo & Kachroo, 2009). They are essential components of membrane lipids and serve as reserve energy. Fatty acids metabolism in plant have a major role in their defense against pathogens, insects and herbivore defense and are the biosynthetic precursors for cuticular components of phytohormones such as jasmonic acid. These fatty acids breakdown products have demonstrated a more direct role in inducing various modes of plant defenses. This mechanism is possibly the explanation for the high odor which evolved when the *E. foetidum* plants were cut during harvesting or weed control.

Fatty alcohol group

In the fatty acid group, 6 phytochemicals were found present in *E. foetidum* and two in *C. sativum*, but there was no chemical commonality between the plants or within the chemical group (Table 10). This group of chemicals is different from the unsaturated fatty acid (Table 11).

Unsaturated fatty acids

The unsaturated fatty acid group of chemicals was the largest with 7 phytochemicals distilled in the essential oils and identified, with 6 being common to both plants (Table 11). The exception is (E)-dodec-2-enal which was found only in *E. foetidum*. The analysis of coriander leaf volatiles showed several unsaturated fatty acids (Potter & Fagerson, 1990), including decanal (19.09%), trans-2-decenal (17.54%), 2-decen-1-ol (12.33%) and cyclodecane (12.15%), cis-2-dodecena (10.72%), dodecanal (4.1%), and dodecan-1-ol (3.13%).

Table 8. The presence of the ester group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | E.F | C.S |
|-------------------|---------------------------------|-----|-----|
| Ester | (4-prop-2enylphenyl) acetate | - | + |
| Ether | 1-methoxy-4-prop-2-enoxybenzene | - | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 9. The presence of the fatty acid group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | E.F | C.S |
|-------------------|--------------------|-----|-----|
| Fatty acid | decanoic acid | + | + |
| Fatty acid | nonanoic acid | + | + |
| Fatty acid | octanoic acid | + | + |
| Fatty acid | undecanoic acid | + | + |
| Fatty acid | tridecanoic acid | + | + |
| Fatty acid | Undecanoic acid | + | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 10. The presence of the fatty alcohol group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | E.F | C.S |
|------------------------------|---------------------|-----|-----|
| Fatty alcohol/Aliphatic diol | Decane-1,2-diol | - | + |
| Fatty alcohol | Hexadecan-1-ol | + | - |
| Fatty alcohol | (E)-dec-2enoic acid | - | + |
| Fatty alcohol | nonan-1-ol | + | - |
| Fatty alcohol | undecan-1-ol | + | - |
| Fatty alcohol | Decane-1,2-diol | + | - |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 11. The presence of the unsaturated fatty acid group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | E.F | C.S |
|----------------------------|---------------------------|-----|-----|
| Unsaturated Fatty Acid | undec-10-enoic acid | + | + |
| Unsaturated Fatty alcohol | (E)-dodec-5-en-1-ol | + | + |
| Unsaturated Fatty aldehyde | (E)-dodec-2-enal | + | + |
| Unsaturated Fatty aldehyde | (E)-tridec-2-enal | + | + |
| Unsaturated fatty aldehyde | (E)-dodec-2-enal | + | - |
| Unsaturated fatty aldehyde | tridec-2-enal | + | + |
| Unsaturated fatty acid | (E)-tetradec-2-enoic acid | + | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

A review of *Eryngium foetidum* L. as an ethno-medicinal herb, revealed that the chemical evaluation of the leaves consisted of a combination flavonoid, tannins, a saponins and several triterpenoids; but no alkaloids were reported (Paul et al., 2011). It was found that the main essential oil of the plant is *E*-2-dodecenal ("eryngial"), with isomers of trimethylbenzaldehyde. The authors concluded that the composition of essential oil was variable and is possibly dependent on the geographic location and agro-ecological conditions.

It was observed that the volatile oils *E. foetidum* L. had (*E*)-2-dodecenal which have a fruity, sweet and sour odor. This was attributed to the presence of aliphatic aldehyde reductase and aldehyde dehydrogenase. This accounted for the formation of alcohols and acids from their corresponding aldehydes into a volatile concentrate, possibly due to the observed enzymatic activities prevalent and further observed that it affected the overall odor of the herb (Shahwar et al., 2012).

Several other phytochemicals were identified as coriander leaves essential oil (CLEO) (Shahwar et al., 2012). Among the volatile compounds were included (*E*)-2-decenal (32.23%), linalool (13.97%), (*E*)-2-dodecenal (7.51%), (*E*)-2-tetradecenal (6.56%), 2-decen-1-ol (5.45%), (*E*)-2-undecenal (4.31%), dodecanal (4.07%), (*E*)-2-tridecenal (3.00%), (*E*)-2-

hexadecenal (2.94%), pentadecenal (2.47%), and α -pinene (1.9%). Furthermore, several scientists (Shahwar et al., 2012) found similar CLEO's including decanal (7.645 and 7.74 %), decanol < n- > (25.12 and 39.35 %), undecanal (1.20 and 1.75 %), dodecanal (7.07 and 2.61 %), tridecen-1-al < 2E > (6.67 and 1.21 %), dodecen-1-ol < 2E- > (16.68 and 8.05 %), 13-tetradecenal (9.53 and 8.60 %), tetradecanal (5.61 and 4.35 %) and 1-octadecanol (1.25 and 3.67 %).

The analysis has shown that the unsaturated fatty acid group had the highest number phytochemicals present in both plants. Plants grown under harsh environmental conditions are subjected to severe stresses which affect both plant health and productivity. The biotic (viruses, bacteria, fungi, nematodes, and arthropods), and the abiotic stressors (temperature extremes, water (deficit or excess), ultraviolet rays, salt, and heavy metals) are known to induce the plants to produce allelochemicals (Cohen et al., 1991; Bridgemohan et al., 2020).

It was observed that any activity that resulted in changes in the plant osmotic pressure or oxidative damage whether mechanical damage or insect / herbivore activity, induced leakage of the phytochemicals would give rise to the particular odor of these plants (Mei He & Nai-Zheng, 2020). Octanoic, decanoic, dodecanoic, tetradecanoic, hexadecanoic, octadecanoic and 9-octadecenoic acids are metabolized into the saturated and unsaturated fatty acids of lipids in the leaves. These compounds act as precursors of oleic, linoleic and linolenic acids and enable resistance in plants. All of these fatty acids also have industrial and/or pharmaceutical applications.

Linolenic acid (Ln) released from chloroplast membrane galactolipids is a precursor of the phytohormone jasmonic acid (JA). The involvement of this hormone in different plant biological processes is observed under responses to biotic stress conditions (Mata-Pérez et al., 2015). It was observed that stress acclimating plants respond to abiotic and biotic stress by remodeling membrane fluidity and by releasing α membrane lipid (Upchurch, 2008). The high level of the presence of the unsaturated fatty acid group of phytochemicals in *C. sativum* and *E. foetidum* suggest that they are both phytochemically related and this is manifested in their odor especially under stress conditions.

Other chemicals

In this group, termed other chemicals, 6 phytochemicals were identified, 3 in *E. foetidum* and 2 in *C. sativum*, and one common to both. The common chemical in the leaves in both plants was dodecanoic acid, decanoic acid also known as capric acid, or decylic acid, and is a saturated fatty acid.

Table 12. The presence of other chemicals compounds group of phytochemicals in *C. sativum* and *E. foetidum*

| Functional groups | Compounds [IUPAC] | E.F | C.S |
|-----------------------------------|--|-----|-----|
| Fatty Amine | benzene-1,3-diamine | - | + |
| FURAN, THIOL | 5-hexyloxolane-2-thione | + | - |
| Mono-unsaturated fatty acid | (Z)-octadec-9-enoic acid | - | + |
| Phenol | 3,4,5-trimethylphenol | + | - |
| Saturated medium-chain fatty acid | dodecanoic acid | + | + |
| Terpene | (1Z,4Z,8Z)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene | + | + |

(Adapted after Wong et al., 1994; Jaramillo et al., 2011; Shahwar et al., 2012; Eyres et al., 2005; Ganesan et al., 2013).

Table 13. Similar phytochemicals odorants present in *C. sativum* and *E. foetidum*

| | Compounds [IUPAC] | E.F | C.S |
|------------------------|--|-----|-----|
| Aldehyde | (E)-undec-2-enal | + | + |
| | undecanal | + | + |
| | decanal | + | + |
| | <i>E</i> -dodec-5-en-1-ol | + | + |
| | tetradecanal | + | + |
| Cyclic ether | 1,3,3-trimethyl-2-oxabicyclo[2.2.2]octane | + | + |
| Fatty acid | decanoic acid | + | + |
| | nonanoic acid | + | + |
| | octanoic acid | + | + |
| | undecanoic acid | + | + |
| | tridecanoic acid | + | + |
| | undecanoic acid | + | + |
| Unsaturated Fatty Acid | undec-10-enoic acid | + | + |
| | <i>E</i> -dodec-5-en-1-ol | + | + |
| | <i>E</i> -dodec-2-enal | + | + |
| | <i>E</i> -tridec-2-enal | + | + |
| | tridec-2-enal | + | + |
| | <i>E</i> -tetradec-2-enoic acid | + | + |
| Saturated fatty acid | dodecanoic acid | + | + |
| Others | (1Z,4Z,8Z)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene | + | + |

Odorants

Further comparison for phytochemical similarity of odors has shown that there were 5 clusters of functional groups which had 20 similar phytochemicals interspersed within the clusters (Table 12). The term ‘odor-clusters’ was developed in the characterization of the essential oil and aroma profiles of coriander leaves of *C. sativum* and *E. foetidum*, using comprehensive two-dimensional gas chromatography (GC×GC) combined with time-of-flight mass spectrometry (TOFMS) (Eyres et al., 2005). It was found that during the GCO analysis, the co-elution of *E*-2-alkenals and *E*-2-alken-1-ols resulted in the perception of ‘odor-clusters’.

Further analysis of the odorants in *C. sativum* revealed a combination of *Z*-2-decenal, a co-eluting odor-cluster (*E*-2-dodecenal, *E*-2-dodecen-1-ol, and 1-dodecanol), β-ionone, eugenol, and *E*-2-decenal. Additionally, *E*-2-decen-1-ol was the most abundant compound in *C. sativum* (26.0% TIC), but only contributed 0.39% of the total odor activity (Table 13).

On the other hand, *E. foetidum* was more aromatic and had more *E*-2-dodecenal (63.5% TIC) compared to *C. sativum*, and which accounted for the most odor activity (52.9%). The other important odorants identified were either eugenol or a trimethylbenzaldehyde isomer, β-ionone, *Z*-4-dodecenal, dodecanal, and *E*-2-tetradecenal. GC×GC–TOFMS allowed the identification of 42 and 20 compounds not previously reported in the literature for *C. sativum* and *E. foetidum*, respectively. In particular, β-ionone was determined to be an important odorant in both samples but could not be identified with GC–qMS (Eyres et al., 2005).

However, using the phytochemical analysis along with plant morphology, the relative closeness among ten selected members of Apiaceae was conducted. The results indicated that *C. sativum* and *E. foetidum*, while they belonged to two different subfamilies of Apiaceae appeared morphologically quite divergent, but were phytochemically much alike having similar aroma and odorants indicating a classical example of convergent evolution in the plant kingdom (Das, 2020).

Linolenic acid (Ln) released from chloroplast membrane galactolipids is a precursor of the phytohormone jasmonic acid (JA). The involvement of this hormone in different plant biological processes, such as responses to biotic stress conditions (Mata-Pérez et al., 2015). It was found that stress acclimating plants respond to abiotic and biotic stresses by remodeling membrane fluidity and by releasing α -membrane lipids (Upchurch, 2008). The high level of the presence of the unsaturated fatty acid group of phytochemicals in *C. sativum* and *E. foetidum* suggested that they are both phytochemically related and this is manifested in their odor especially under stress conditions.

CONCLUSION

This mixed method study explored the possibility that the term “false coriander” for *E. foetidum* L. (Apiaceae) as a culinary substitute for *C. sativum* L., could be as a result of crop mimicry. The evidence provided by analysis phylogenetic traits and phytochemical similarities have shown that the aromas of the odorants made them “crop mimics”.

The study indicated that *C. sativum* and *E. foetidum*, both belonged to two different subfamilies of Apiaceae which appeared morphologically quite divergent. However, phytochemically they had similar aroma and odorants, which is alluded to their convergent evolution. The phytochemical similarity into ‘odor-clusters’ have identified 5 clusters with over 20 similar phytochemicals with the co-elution of *E*-2-alkenals and *E*-2-alken-1-ols. There was more *E*-2-dodecenal in *E. foetidum* (63.5%) compared to *C. sativum*, (26.0%) which accounted for the most odor activity.

This similarity is found in crop mimics, and is not uncommon as the selective activities in agricultural practices can result in the evolution of agricultural races of weeds or agro ecotypes. There are many agro ecotypes and biotypes found in weed species which resembles the crop at specific stages. Biotypes of corn grass (*Rottboellia cochinchinensis*), and red rice (*O. rufipogon*), and jungle rice (*E. crus-galli* var. *oryzicola*) are examples of morphological and phenological resemblance that can be found in the cultivated maize (*Zea mays*) and rice (*Oryza sativa* L.), respectively, (Bridgemohan et al., 2020).

Multiple mechanisms have been proposed to explain how plant mimic have evolved including “de-domestication” and hybridization into new phenotypes. ‘Crop mimics’, usually share some domestication traits with the crop, although they display genetic diversity but are closely related taxonomically. Evolutionary origins and genetic diversity characterized the evolutionary genomics of *E. foetidum* as an aggressive aromatically pungent weed, and *C. sativum* as the fragrant delicate herb. Human preference over the taste for the essential oils of coriander seeds may have induced ‘Vavilovian mimicry’ which has been hypothesized to be driven by unintentional human selection (Shavandi et al., 2012; Singh et al., 2014).

Conflict of interest

The authors have no conflict of interest.

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