

Catnip and the Catnip Response¹

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Fourteen chemical compounds from diverse biological sources elicit a unique pattern of behavior in most species of the family Felidae. These chemicals may be grouped into 7-methylcyclopentapyranones, 7-methyl-2-pyridines, and 4-methylbenzofuranones. They may function as either hallucinogens or cross-react with naturally occurring social odors.

Catnip (*Nepeta cataria* L., Lamiaceae) has been long known to elicit a unique sequence of responses in the domestic cat (*Felis catus*). Over 200 yr ago John Ray first noted that the animal was attracted to catnip when the plant was withered or bruised; this was later reported and confirmed by Philip Miller (1759). Until about 50 yr ago, these two observations remained the only published reports on catnip.

THE CATNIP RESPONSE

Todd (1962, 1963) described the response of the domestic cat to catnip as consisting of four components: (1) sniffing, (2) licking and chewing with head shaking, (3) chin and cheek rubbing, and (4) head-over rolling and body rubbing. He stated that, although none of these automatisms is unique to catnip, the sequence is almost invariable. Additional observed reactions are digging or pawing, scratching, salivating, and washing or grooming. The complete catnip response seldom exceeds 15 min and is accompanied by a 1-hr refractory period. The response is not elicited during the first 6 to 8 wk after birth, and it may not develop until 3 mo of age. Estrogen injections cause some immediate increase in the intensity of the catnip response among responding animals, but the response wanes as spontaneous courtship display reaches a peak. Palen and Goddard (1966) stated that the combination of body rolling and face rubbing in response to catnip is independent of sex or the presence of gonads. They further stated that catnip does not result in an increase in killing, fighting, or sexual mounting when cats are paired with live rats or with cat-size objects. Catnip does produce, however, an increased attention to stuffed objects and a decreased attention to rats; the increased attention appears to be similar to that shown by males to estrous females. The rolling pattern produced by catnip also appears to be similar to that pattern exhibited by estrous females, but catnip does not induce posturing (lordosis), treading, or tail deviation, and vocalization is rare (Palen and Goddard 1966; Todd 1963).

Hatch (1972) modified Todd's four-component sequence to include six phases in about 10 min when cats are presented with stuffed toys that have been sprayed

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with catnip extract. Hatch also noted additional responses of stretching, animated leaping, licking of the genital region, apparent hallucinations, sexual stimulation, euphoria, sleepiness, and/or eating. Environmental factors that qualitatively influenced the catnip response include environmental (sounds and routines of the habitat), physiological (early acute urinary infections, loss of smell, urination, defecation), and psychological factors (adjustment to habitat). The personality and emotional factors were found to be the most important: withdrawn cats react poorly while friendly, outgoing cats react best.

Genetics of the response

Todd (1962), in a study of the catnip response using a documented pedigree of Siamese cats, found that the response is inherited as an autosomal dominant gene. He also observed a random sample of 84 cats from the Boston area and found that one-third of the population did not respond to catnip (i.e., $q^2 = 0.31$ in the Hardy-Weinberg equilibrium).

Distribution of the response

Hayashi (1968), who tested a wide range of animals (dogs, rabbits, mice, rats, guinea pigs, fowls, and cats) with powders of *Actinidia polygama* and *N. cataria*, found that the catnip response is induced in cats alone. Todd (1963) tested 22 animals from nine genera (one to five individuals per genus) in four subfamilies from the Viverridae (*Arctictis*, *Atilax*, *Cryptoprocta*, *Genetta*, *Herpestes*, *Ichneumia*, *Nandinia*, *Paguma*, and *Viverra*) (Anderson and Jones 1967) and three individuals from one genus (probably *Crocuta*) of the Hyaenidae, but did not find the typical catnip response. Within the subfamily Pantherinae of the Felidae, Todd (1963) found the typical catnip response in: 16 lions (*Panthera leo*) (14 positive responders, 2 negative responders), 23 tigers (*Panthera tigris*) (8 incomplete responders, 13 negative responders, 2 inconclusive responders), 18 leopards (*Panthera pardus*) (14 positive responders, 4 negative responders), 8 jaguars (*Panthera onca*) (7 positive responders, 1 negative responder), 4 snow leopards (*Panthera uncia*) (4 positive responders), and 1 clouded leopard (*Neofelis* [*Panthera*] *nebulosa*). Within the subfamily Acynonychinae of the Felidae, he found that 3 cheetahs (*Acinonyx jubatus*) did not respond to catnip. Within the subfamily Felinae of the Felidae, he found the typical catnip response in the 2 bobcats (*Felis* [*Lynx*] *rufus*) (1 positive responder, 1 negative responder), 1 European lynx (*Felis* [*Lynx*] *lynx*), 5 pumas (*Felis* [*Puma*] *concolor*) (2 positive responders, 2 negative responders, 1 inconclusive responder), 1 Asiatic golden cat (*Felis* [*Profelis*] *temmincki*), 5 ocelots (*Felis* [*Leopardus*] *pardalis*) (4 positive responders, 1 negative responder), and 6 margay cats (*Felis* [*Leopardus*] *wiedii*) (4 positive responders, 2 negative responders); no catnip response was observed in 2 servals (*Felis* [*Lep-tailurus*] *serval*), 1 swamp cat or jungle cat (*Felis* *chaus*), 1 Pallas' cat (*Felis* [*Octocolobus*] *manul*), 1 leopard cat (*Felis* [*Prionailurus*] *bengalensis*), 1 African golden cat (*Felis* [*Profelis*] *aurata*), 2 fishing cats (*Felis* [*Prionailurus*] *viverrina*), 4 jaguarundis (*Felis* [*Herpailurus*] *yagouaroundi*), and 1 pampas cat (*Felis* [*Lyn-chailurus*] *pajeros*). Hill et al. (1976) found that lions (5 positive responders, 6 partial responders, 1 negative responder) and jaguars (3 positive responders) are extremely sensitive to catnip, while tigers (5 negative responders), pumas (4 neg-

ative responders), leopards (4 partial responders, 4 negative responders), and bobcats (2 negative responders) gave little or no response. They also found that both males and females of the same species test alike, while reproductive-age adults are more sensitive than either aged or immature animals.

CHEMISTRY

Nepeta cataria

Hixon (1922) first reported on the presence of a lactone and a sesquiterpene in catnip oil but did not characterize them further. McElvain et al. (1941, 1942) later described a compound named nepetalactone in catnip oil. Meinwald (1954a,b) verified the structure of nepetalactone (Fig. 1), and McElvain and Eisenbraun (1955) determined the *cis-trans* arrangement of the molecule. Later workers found the *cis-trans* isomer (nepetalactone or $4\alpha\alpha,7\alpha,7\alpha\alpha$ -nepetalactone) to be 70–99.9% and the *trans-cis* isomer (epinepentalactone, isonepentalactone, or $4\alpha\alpha,7\alpha7\alpha\beta$ -nepetalactone) to be 0.1–30% of the essential oil (Bates et al. 1958; Bates and Siegel 1963; McGurk 1968; Nelson 1968; Regnier et al. 1967a,b; Sakan et al. 1965). Also reported from *N. cataria* (Fig. 1) were dihydronepentalactone (Regnier et al. 1967a,b; Sakan et al. 1965), isodihyronepentalactone (Nelson 1968; Sakan et al. 1965), neonepentalactone (Regnier et al. 1967a), and 5,9-dehydronepentalactone (Sastry et al. 1972).

McElvain et al. (1942) showed that nepetalactone is the physiologically active component of catnip oil by testing 10 African lions with pledgets of cotton soaked with nepetalactone. The seven adult lions responded similarly to nepetalactone as to whole catnip; the three lion cubs did not respond. The activity of the *cis-trans* isomer (nepetalactone) was clearly demonstrated by Bates and Siegel (1963) on domestic cats, but the activity of the *trans-cis* isomer (epinepentalactone) could not be ascertained. Dihyronepentalactone, isodihyronepentalactone, and neonepentalactone were also shown to induce the catnip response in domestic cats (Sakan et al. 1965).

Other Nepeta Species

Nepetalactone, epinepentalactone, and dihydronepentalactone were reported to form 12.2% of the essential oil in *N. cataria* var. *citriodora* (Becker) Balb. (*N. citriodora* Becker) (Regnier et al. 1967b). One study of another cultivated species, *N. mussinii* Spreng. ex Henckel, showed nepetalactone forms 16.7% and epinepentalactone 70.0% of the essential oil (Regnier et al. 1967b), but later studies (Eisenbraun et al. 1974, 1980; McGurk 1968) found that the major isomer in this species is *cis-cis* ($4\alpha\beta,4\alpha,7\alpha\beta$ -nepetalactone) (Fig. 1) rather than *trans-cis* (epinepentalactone). *Nepeta nepetella* L. (*N. lanceolata* Lam.), another cultivated species reported to attract cats (Garnier et al. 1961), contains 76.5% nepetalactone, 1.6% dihydronepentalactone, 0.6% epinepentalactone, 0.4% neonepentalactone, and traces of 5,9-dehydronepentalactone (Bicchi et al. 1984). Thus it is no surprise that the hybrid of *N. mussinii* × *N. nepetella* (*N.* × *faassenii* Bergmans ex Stearn) elicits a similar response (Meikle 1963; Perry 1972; Stearn 1950). *Nepeta sibthorpii* Benth., a native of Greece, is known to excite cats (Niebuhr 1970), although no chemical studies have been done. Natives of India, *N. hindostana* Haines, with

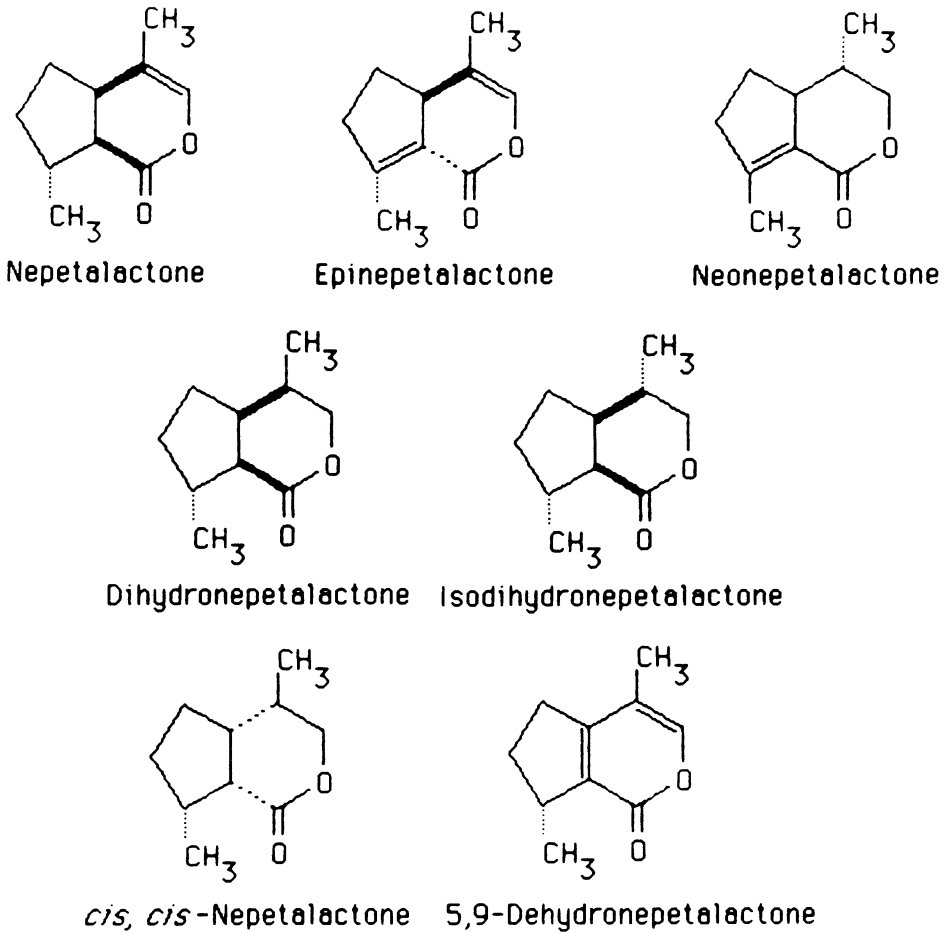


Fig. 1. Nepetalactone and its isomers isolated from *Nepeta* species. The isomers *cis,cis*-nepetalactone and 5,9-dehydronepetalactone have never been tested on cats, and the activity of epinepetalactone is questionable.

7.5% nepetalactone (Purohit and Nigam 1959), and *N. leucophylla* Benth., with 3% nepetalactone (Baslas 1970; Gupta et al. 1971), may also attract cats.

"RAISON D'ETRE" OF NEPETALACTONE

Eisner (1964) noted that nepetalactone is chemically related to certain other cyclopentanoid monoterpenes that have been isolated from insects (Cavill and Clark 1971; Plouvier and Favre-Bonvin 1971; Roth and Eisner 1962; Weatherston 1967; Weatherston and Percy 1970; Wilson 1963). Some of these compounds, nepetalactone included, can repel other insects (see, also, the discussion below of the defensive secretions of dolichoderine ants, a stick insect, rove beetles, and leaf beetles). Therefore, Eisner concluded that nepetalactone protects catnip against phytophagous insects.

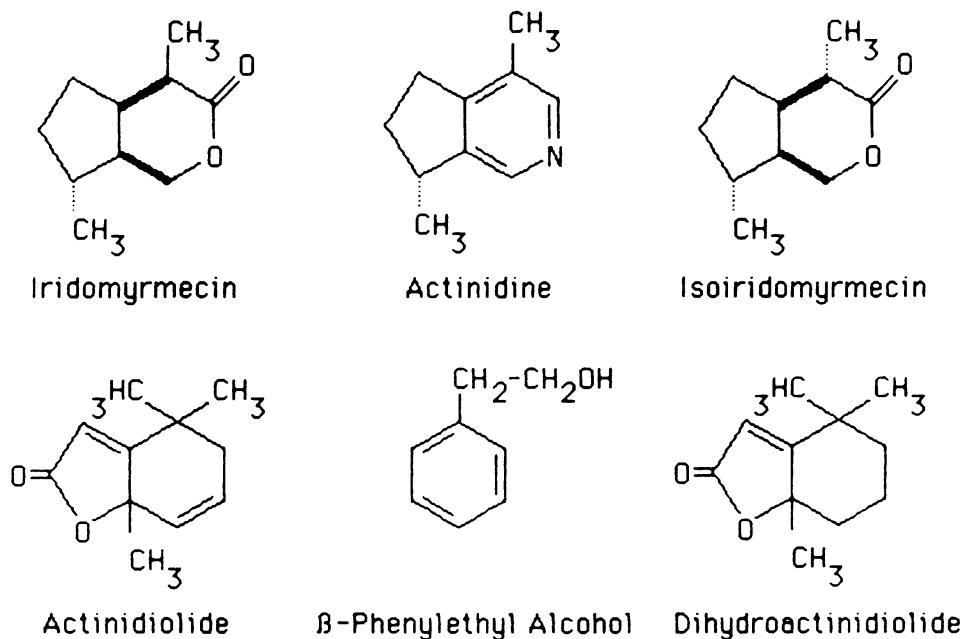


Fig. 2. Some of the physiologically active compounds isolated from *Actinidia polygama*.

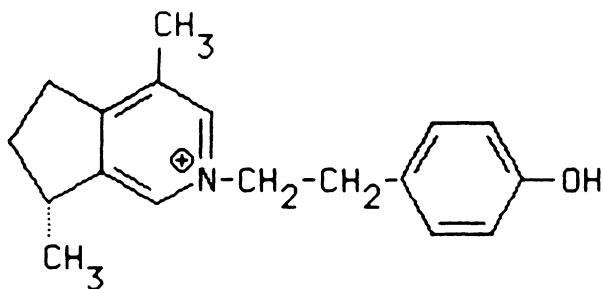
OTHER ORGANISMS

Actinidia species

Actinidia polygama (Sieb. & Zucc.) Maxim. (silver vine, mata-tabi) and *A. kolomikta* (Rupr. & Maxim.) Maxim. (miyama-mata-tabi) of the Actinidiaceae are deciduous scandent shrubs native to Japan and China (Liberty Hyde Bailey Hortorium 1976; Ohwi 1965). Horticulturists have repeatedly noticed that cats are attracted to these two species (Fairchild 1906; Hottes 1947; Slate 1954; Wilkinson 1946), and Hazama (Yoshii et al. 1963) described a "matatabi" reaction similar to the catnip response reported by Todd (1962). Hottes (1947) related the story that the Chinese disposed of surplus cats after attracting them with a stupefying smudge prepared from these plants.

Sakan et al. (1959a, 1960a) first identified actinidine (a monoterpenoid alkaloid), matatabilactone, and beta-phenylethyl alcohol (Fig. 2) from leaves and galls of *A. polygama*. The structure of actinidine (Fig. 2) was later confirmed by Fujino (1960) and Sakan et al. (1960b,c). Gross et al. (1972) also isolated actinidine from *A. arguta* (Sieb. & Zucc.) Maxim.

Matatabilactone, first thought to be a mixture of dihydronepetalactone and possibly isodihyronepetalactone (Sakan et al. 1959a), was later identified as a mixture of iridomyrmecin and isoiridomyrmecin (Murai 1960; Sakan 1967; Sakan et al. 1959b) (Fig. 2). However, dihydronepetalactone, isodihyronepetalactone, and neonepetalactone have since been isolated from *A. polygama* (Sakan 1967; Sakan et al. 1965) (Fig. 1), and Nelson (1968) confirmed the presence of all five compounds in the matatabilactone fraction. Actinidine and the five compounds of the matatabilactone fraction are physiologically active in cats (Sakan et al. 1959a, 1960a, 1965), while beta-phenylethyl alcohol induces salivation (Sakan et



N-(2-*p*-hydroxy-phenyl)ethyl-actinidine

Fig. 3. The alkaloid of Torssell-Wahlberg isolated from *Valeriana officinalis*.

al. 1960a). Interestingly, beta-phenylethyl alcohol is one of the most widely used perfume ingredients (Arctander 1969), and certain perfumes and cosmetics have long been known to attract cats (Buffon 1756).

The above lactones from *A. polygama* are all 7-methylcyclopentapyranones (i.e., with a 6-membered lactone ring). Sakan et al. (1967a) isolated two more compounds from *A. polygama* that attract cats but are 4-methylbenzofuranones (i.e., with a 5-membered lactone ring): actinidiolide and dihydroactinidiolide (Fig. 2). After synthesizing actinidiolide, Demole and Enggist (1968) verified its structure. Dihydroactinidiolide is frequently reported as a trace compound in other essential oils: black tea (*Camellia sinensis* (L.) Kuntze, Theaceae) (Bricout et al. 1967; Ina et al. 1968), cured tobacco (*Nicotiana tabacum* L., Solanaceae) (Bailey et al. 1968; Kaneko and Ijichi 1968), the floral absolute of cassie (*Acacia farnesiana* (L.) Willd., Mimosaceae) (Demole et al. 1969), a spikerush (*Eleocharis parvula* (Roem. & Schult.) Link ex Buffon & Fingerh., Cyperaceae) (Stevens and Merrill 1980), heated mango (*Mangifera indica* L., Anacardiaceae) (Sakho et al. 1985), and the red imported fire ant (*Solenopsis invicta*) (Glancey et al. 1984).

Valeriana species

Valeriana officinalis L. (common valerian, garden heliotrope) of the Valerianaceae is a herbaceous perennial native to Europe and Asia (Liberty Hyde Bailey Hortorium 1976; Ockendon 1976). Torssel and Wahlberg (1966, 1967) isolated N-(2-*p*-hydroxy-phenyl)ethyl-actinidine (Fig. 3) from dried valerian roots and stated that it yielded actinidine on pyrolysis. Gross et al. (1971) confirmed the presence of this alkaloid and, in addition, reported actinidine in their extract; Johnson and Waller (1971), Cionga et al. (1976), and Janot et al. (1979) also found actinidine. Thus, actinidine may be the chemical basis for the attraction of cats to valerian roots reported in popular works (e.g., Grieve 1967; Wilder 1936; Wood 1854). Grieve (1967) also stated that valerian roots are equally attractive to rats, and that the success of the Pied Piper of Hamelin should be attributed to *V. officinalis*. Valerian roots, in addition, are used to attract members of the family Canidae to traps (Bateman 1971).

Valeriana celtica L., a native of the Alps (Ockendon 1976), has 1.3% nepetalactone in its essential oil, and this species of *Valeriana* also attracts cats (Bicchi et al. 1983).

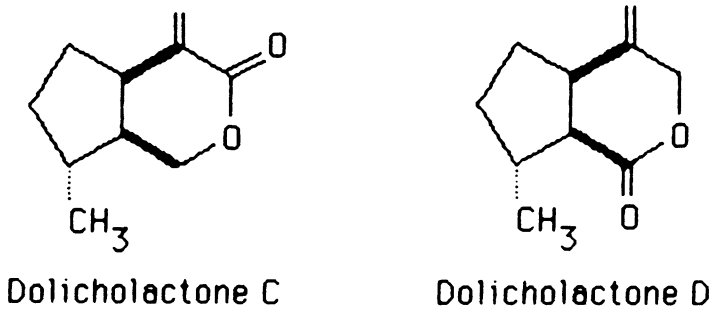


Fig. 4. The lactones isolated from *Teucrium marum*.

Teucrium marum

Teucrium marum L. (marum, cat thyme) of the Lamiaceae is a subshrub native to southern Spain, Southern France, Italy, and Yugoslavia (Tutin and Wood 1972). This species has long been known to attract cats (Farrer 1930; Gams 1927; Garnier et al. 1961; Loudon 1836). Pagnoni et al. (1976) and Beaupin et al. (1977, 1978, 1979) found two new 7-methylcyclopentapyranones in *T. marum* (Fig. 5): dolicholactone C (Fig. 4) was found to form 4% of the oil from Sardinian plants but only trace amounts of the oil from Corsican plants, whereas dolicholactone D (Fig. 4) was found to form 76% of the oil of Sardinian plants but only 17% of the oil from Corsican plants. Neither compound in its pure form has been tested on cats.

Boschniakia rossica

Boschniakia rossica (Cham. & Schlecht.) B. Fedtsch. in B. Fedtsch. & Flerow (oniku) of the Orobanchaceae, parasitic on the roots of *Alnus* spp. (especially *A. maximowiczii* Callier in Schneider), is native to northern Europe and Asia and northwestern North America (Kartesz and Kartesz 1980; Ohwi 1965; Rix and Webb 1972). Sakan et al. (1967b) isolated two compounds from this species that are attractive to cats: boschniakine and boschnialactone (Fig. 5). Sakan et al. (1969) also isolated onikulactone from *B. rossica* and found that it induced the catnip response in cats.

Menyanthes trifoliata

Menyanthes trifoliata L. (buckbean, bog myrtle, mitsu-gashiwa) of the Menyanthaceae is found in shallow water of bogs and ponds of the Northern Hemisphere (Kartesz and Kartesz 1980; Ohwi 1965; Tutin 1972). Sakan et al. (1969) isolated mitsugashiwalactone (Fig. 6) and found it also induced the catnip response in cats.

Tecoma and Campsis species

Tecoma stans (L.) Juss. ex Humb., Bonpl., et Kunth (*Stenolobium stans* Seem., yellowbells) of the Bignoniaceae is a small tree or shrub indigenous from Florida to the West Indies and South America (Pelton 1964). Dickinson and Jones (1969) and Dohnal (1976) isolated boschniakine and actinidine from *T. stans*. The attraction of cats to *T. stans* is unknown.

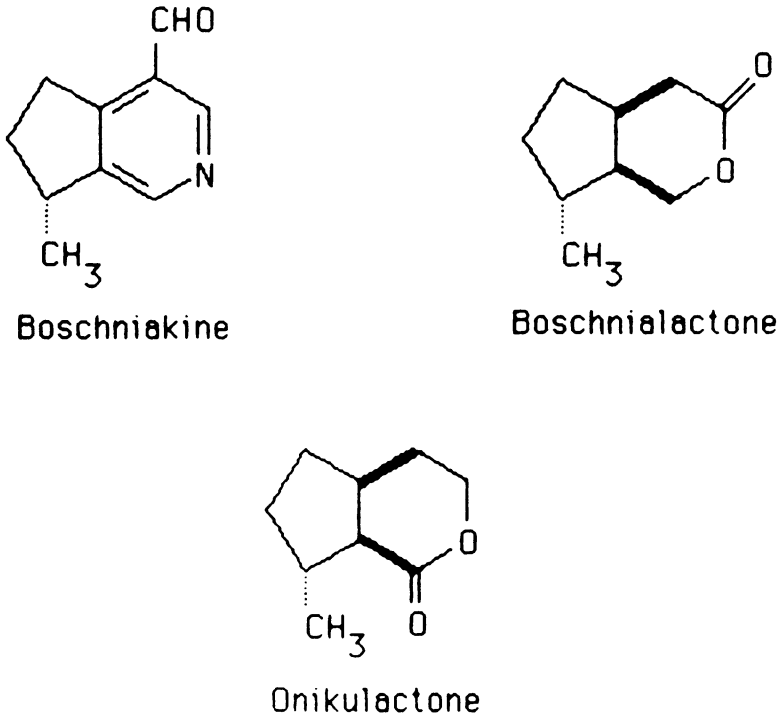


Fig. 5. The physiologically active compounds isolated from *Boschniokia rossica*.

Campsis radicans (L.) Seem. ex Bureau (*Tecoma radicans* (L.) Juss., trumpet creeper) is a vine of the Bignoniaceae indigenous to North America from Pennsylvania to Florida, west to Illinois and Texas (Liberty Hyde Bailey Hortorium 1976). Gross et al. (1972) isolated boschniakine from *C. radicans*. The attraction of cats to *C. radicans* is unknown.

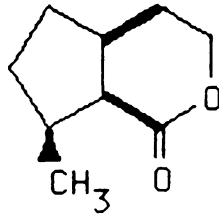
Myoporum desertii

Nepetalactone has also been reported from *Myoporum desertii* A. Cunn. ex Benth. of the Myoporaceae, a shrub widespread in dry inland areas of Australia (Sutherland and Park 1967). The attraction of cats to *M. desertii* is unknown.

Other plants

Nemophila menziesii Hook. et Arnott (*N. insignis* Douglas ex Benth.), or baby blue-eyes, of the Hydrophyllaceae is a procumbent annual native from California to Oregon (Constance 1941). Earle (1922), Finbert (1960), and Wilder (1936) reported that cats are partial to baby blue-eyes, but no further reports exist in the literature.

Additional plants that have been reported to attract cats include: *Origanum dictamnus* L., or dittany of Crete, of the Lamiaceae (Elliott 1966); *Valeriana phu* L. of the Valerianaceae (Loudon 1836); *Lippia javanica* (Burm. f.) Spreng. of the Verbenaceae (Schaller 1972); and *Viburnum opulus* L., or cranberry bush, of the Caprifoliaceae (Necker 1977).



Mitsugashiwalactone

Fig. 6. The physiologically active compound isolated from *Menyanthes trifoliata*.

Dolichoderine ants and other insects

Ants of the genera *Dolichoderus*, *Iridomyrmex*, and *Tapinoma*, subfamily Dolichoderinae (Formicidae) (Smith 1951, 1958, 1967) have yielded various compounds known to attract cats: *D. diceratoclinea scabridus*, an Australian ant, isoiridomyrmecin (Cavill 1960; Cavill and Hinterberger 1960) (Fig. 2); *I. humilis*, the cosmopolitan Argentine ant, iridomyrmecin (Cavill and Houghton 1974; Cavill et al. 1956a, b, 1976; Fusco et al. 1955) (Fig. 2); *I. nitidus*, an Australian ant, isoiridomyrmecin (Cavill and Clark 1967; Cavill and Locksley 1957; Cavill et al. 1956a,b) and isodihydronepetalactone (Cavill and Clark 1967) (Fig. 1); *I. pruinosus analis*, a North American ant, iridomyrmecin (McGurk et al., 1968); *I. purpureus*, the common meat ant, dihydronepetalactone (and/or isodihydronepetalactone) and iridomyrmecin (and/or isoiridomyrmecin) (Cavill et al. 1984); and *T. sessile*, the North American odorous house ant, isoiridomyrmecin (McGurk et al. 1968).

In addition to these ants, rove beetles of the genera *Cafius*, *Creophilus*, *Gabrius*, *Hesperus*, and *Philonthus*, family Staphylinidae, produce actinidine in their defensive secretions (Bellas et al. 1974; Dettner 1983; Jefson et al. 1983). *Creophilus maxilosus* also produces dihydronepetalactone in its defensive secretion (Jefson et al. 1983).

The defensive secretion of the coconut stick insect, *Graeffea crouani*, includes nepetalactone (Smith et al. 1979).

Defensive secretions of several species of chrysomelid (leaf beetle) larvae and adults yield plagiolactone, epiplagiolactone, and gastrolactone (Pasteels et al. 1982, 1984) and are structurally similar to iridomyrmecin/isoiridomyrmecin. These may induce the catnip response but have never been tested.

CHEMICAL CONSIDERATIONS

Fourteen compounds from those species that have been shown to elicit a unique behavioral pattern, known as the catnip response (or, alternatively, the matatabi reaction), in the Felidae have been listed. Each can be placed in one of three classes of chemical compounds. The 7-methylcyclopentapyranones (IUPAC, International Union of Pure and Applied Chemistry, name), also called methylcyclopentanoid monoterpenes or simple iridoids (Plouvier and Favre-Bonvin 1971), include nepetalactone, epinepetalactone, dihydronepetalactone, isodihydronepetalactone, neonepetalactone, iridomyrmecin, isoiridomyrmecin, boschnialactone,

onikulactone, and mitsugashiwalactone. The 7-methyl-2-pyridines (IUPAC name), also called monoterpenoid alkaloids (Plouvier and Favre-Bonvin 1971; Wildman et al. 1969), include actinidine and boschniakine. The 4-methylbenzofuranones (IUPAC name) include actinidiolide and dihydroactinidiolide. Beta-phenylethyl alcohol also induces salivation.

In addition to the above 14 compounds, 10 others that are structurally similar deserve further investigation if possible. Two 7-methyl-2-pyridines that should be investigated for physiological activity in cats are 4-noractinidine (Sakan et al. 1967b) and tecostidine (Hammouda and LeMen 1963) from *Tecoma stans*. The nepetalactone isomers 5,9-dehydronepetalactone from *N. cataria* and *N. nepetella* (Bicchi et al. 1984; Sastry et al. 1972) and *cis,cis*-nepetalactone from *N. mussinii* (Eisenbraun et al. 1974, 1980; McGurk 1968) should also be tested on cats. The activity of epinepetalactone was never ascertained (Bates and Siegel 1963). The two dolicholactones from *Teucrium marum* (Beaupin et al. 1977, 1978, 1979; Pagnoni et al. 1976) have never been tested on cats. Plagiolactone, epiplagiolactone, and gastrolactone from chrysomelid larvae and adults (Pasteels et al. 1982) would undoubtedly show activity but have never been tested.

The structural similarity of the 7-methylcyclopentapyranones and the 7-methyl-2-pyridines prompts the question of whether the indoles may behave physiologically in the same manner because of their structural similarity to 4-methylbenzofuranones. Beta-phenylethyl alcohol is also noted to be structurally similar to phenylpropenes. Literally a plethora of chemical compounds could be suggested for future research, but the above structural similarities are indicated because methylindoles, indole alkylamines, and phenylpropenes are recognized as hallucinogens (Farnsworth 1968, 1969; Hoffer and Osmond 1967; Schultes 1969a,b).

FUNCTION OF THE CATNIP RESPONSE

Thus the question arises of whether the compounds active in the catnip response function as hallucinogens (Carley 1969; Superweed n.d.). Actinidine, the matabilactone fraction, and beta-phenylethyl alcohol are cholinergic (Hano 1967; Yoshii et al. 1963) and hence can be classified as hallucinogens (Hoffer and Osmond 1967). If the above analogy between 4-methylbenzofuranones and indoles is correct, this cholinergic effect may not be surprising because many indoles are recognized as inhibitors of acetylcholinesterase (Hoffer and Osmond 1967). Jackson and Reed (1969) reported cases of human responses to the smoking of catnip. In these instances, catnip was used in cigarettes or pipes or a liquid extract from the plant was sprayed on tobacco to make "one appear happy, contented, and intoxicated." Catnip has also been reported to be employed as an antispasmodic in humans (Morton 1974).

An extract of *Actinidia polygama* apparently induces addictive behavior and continual stimulation may produce brain damage in cats (Leyhausen 1973). Intraperitoneal administration of catnip oil elicits effects of a depressant nature in mice and rats (Harney et al. 1978). Sherry and Hunter (1979), Sherry and Koontz (1979), and Sherry et al. (1981) found that catnip tea induces light sleep periods in young chicks but the activity is relatively weak, variable, and not dose-dependent. Hatch (1972) found that the catnip response in cats is prolonged by morphine, chlorpromazine, and histidine. Drugs that shorten the response include

atropine sulfate, physostigmine, neostigmine, pilocarpine, mecamylamine, methysergide, and pentobarbital. Those that abolish the response are hexamethonium, amphetamine, 5-hydroxytryptophan, atropine plus methysergide, and diphenhydantoin. Atropine methyl nitrate, N-(2-chloroethyl)dibenzylamine, propranolol, and chlorpheniramine do not affect the duration of the response. These results indicate, according to Hatch, peripheral nicotinic and central muscarinic cholinceptive and serotonergic facilitation of the catnip response, with a prominent voluntary component. Inhibition of the response seemingly involves central muscarinic and nicotinic cholinceptive mechanisms linked with an adrenoceptive component.

The restrictions of the catnip response to olfactory stimulation of cats, however, raises some questions as to the hallucinogenic nature of the physiologically active compounds. Smell—not taste or circulation—prompts the catnip response (Hayashi 1968; Todd 1963), and the vomeronasal organ is not involved (Hart and Leedy 1985). Oral administration of nepetalactone also apparently does not induce the catnip response (Waller et al. 1969), but the ventromedial nucleus of the hypothalamus (which is involved in regulation of eating) responds to olfactory stimulation by catnip and valerian (Campbell et al. 1969). The unilateral ablation of the amygdala (which affects sexual behavior) has no effect on the response of cats to *Actinidia polyama* (Katahira and Iwai 1975). Additional pharmacological studies involving injection or cerebral application of actinidine, the matatabilactone fraction, or beta-phenylethyl alcohol affect blood pressure, etc. (Hano 1967; Yoshii et al. 1963), but apparently these compounds do not induce the catnip response via these routes of administration. Caution is necessary in interpreting pharmacological studies because the responses elicited by hallucinogens may vary from animal to animal with the same species and from species to species, as well as by the dosage and means of administration (Hoffer and Osmond 1967).

Thus, because each automatism in the catnip response, when evaluated separately, is part of normal ingestive or sexual behavior (Leyhausen 1960, 1979; Todd 1962, 1963), the question arises whether these compounds cross-react with a naturally occurring social odor in the Felidae. Sources of social odors in the Felidae include anal glands, facial glands, interdigital glands, supracaudal glands, urine, and feces (Macdonald 1985).

Anal gland secretions, combined with urine, are commonly used for scent marking in carnivores (Eisenberg and Kleiman 1972; Ewer 1968, 1973; Macdonald 1985) and in the male domestic cat prior to sexual behavior (Kling et al. 1969; Macdonald 1985; Rosenblatt and Scheirla 1962). The anal glands of the domestic cat have been characterized as having apocrine and holocrine components and containing a mixture of fatty and serous materials and cellular debris (Greer 1966; McColl 1967). The chemistry of the anal glands of the domestic cat is unknown except for two aldehydes and 2-piperidone (Preti et al. 1976), but the anal glands of the lion contain abundant fatty acids, including *iso*-valeric acid (Albone et al. 1974; Albone and Grönneberg 1977). The odor of a male cat is sufficient to induce mating behavior in an estrous female cat (Michael 1961), and valeric acid induces mating behavior in anestrus cats but not in castrated female cats (Lissák 1962). Turning again to the Viverridae, a primitive (but diverse) family closely allied to the Felidae (Anderson and Jones 1967; Ewer 1973; Leyhausen 1965), the civet cats, or species of *Viverra*, secrete skatole (3-methylindole) and macrocyclic ke-

tones in their anal glands (Dorp et al. 1973; Lederer 1950). Utilizing an ether extract of urine from a tomcat, Todd (1963) was able to induce the catnip response in male and female cats. Todd did not state, however, how the urine was prepared without contamination from anal gland secretions.

The chemical composition of the facial glands, interdigital glands, supracaudal glands, and feces of the domestic cat has not been analyzed. Interestingly, though, in the Canidae, Albone (1975) isolated dihydroactinidiolide from the supracaudal gland of the red fox, *Vulpes vulpes*. The supracaudal gland, or dorsal Schwanzorgan, of domestic cats was described by Schaffer (1940) and further discussed by Macdonald (1985) as an elliptical mass of largely sebaceous tissue on the dorsal surface of the tail near to the root and sometimes reaching downwards on both sides of the tail in both males and females. Other than supplying a source of social odor, the function of the supracaudal gland is unknown.

In retrospect, then, although the compounds that elicit the catnip response may be shown to be hallucinogens under appropriate conditions, caution should be exercised against interpreting this property as their sole means of normal action in cats until additional research is performed on possible naturally occurring social odors in glandular secretions, urine, and feces. In particular, the supracaudal gland of the cat needs further investigation. Also in need of investigation is the atmospheric concentration of the various compounds necessary to elicit a catnip response. The compounds eliciting the catnip response may be supranormal stimuli that produce more intense reactions than those normally found (Hart 1974; Leyhausen 1979).

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