

The rhinoceros beetle *Cyphonistes tuberculifrons* Quedenfeldt 1884 attracted by quinones (Coleoptera Scarabaeidae Dynastinae): primary olfactory attraction of a saprophagous beetle by its source of food?

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The rhinoceros beetle *Cyphonistes tuberculifrons* Quedenfeldt 1884 (Coleoptera Scarabaeidae Dynastinae Oryctini) was attracted by different quinones in a gallery forest in northeastern Ivory Coast. Quinones are widespread in organic matter, e.g. in termite defensive secretions, fruit, rotting fruit, wood, and rotting wood. We consider the attraction to rotting wood, rotting fruit and perhaps attacked termite mounds to be the most probable function of the attractive effect of quinones on *C. tuberculifrons*.

KEY WORDS: chemical ecology, primary attraction, quinone, xylosaprophagy, frugivory, saprophagy, Scarabaeidae, Dynastinae, *Cyphonistes*, Côte d'Ivoire.

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INTRODUCTION

During experiments on the attraction of necrophagous dung beetles by quinones (KRELL et al. 1997, 1998) we sometimes found rhinoceros beetles of the species *Cyphonistes tuberculifrons* Quedenfeldt 1884 (Scarabaeidae Dynastinae Oryctini) in our pitfall traps. This observation prompted us to investigate in which context quinones are attractive to Dynastinae.

If a consumer uses host-produced volatile substances as kairomones (or apneumones, if they originate from a dead host; LANIER 1990) for host finding, this is called primary attraction. By contrast, secondary attraction is caused by other consumers through aggregation pheromones or other semiochemicals (TUNSET et al. 1993). Primary attraction of saprophagous or xylodetriticolous rhinoceros beetles (Coleoptera Scarabaeidae Dynastinae) has never been documented. The cues by which they find their hosts are unknown, despite the fact that these beetles are of economic importance (they attack palms (BEDFORD 1980) and other commercial plants) and thus have been studied intensively. We interpret that the attractive effect of quinones on *C. tuberculifrons* to be the first proven case of primary attraction of Dynastinae to their larvae's microhabitat or to resources essential for the adult beetles themselves.

MATERIAL AND METHODS

Study area. We conducted our experiments in the Parc National de la Comoé in north-eastern Ivory Coast (= Côte d'Ivoire, West Africa) near the research camp of Würzburg University (Lola-Camp; 3°48'58"W, 8°45'07"-14"N). The area is situated at the border between the Guinea and Subsoudan savanna; it is attributed by POREMSKI (1991) to the former and by e.g. POILECOT (1991) to the latter. All traps were set in the gallery forest of the Comoé River.

Traps. We used pitfall traps made of a transparent plastic funnel (about 10 cm diameter; polyethylene) placed on the top of a transparent plastic cup (polystyrol) without conservation fluid. The bait was placed beneath the funnel at the bottom of the cup.

Bait. The following substances were tested as attractants, sometimes dissolved in ethanol p.a. (Riedel de Haën, Germany, 32221) (see Table 1):

- 1,4-benzoquinone (2) [numbers refer to Fig. 1], > 98% (Fluka, Buchs, Switzerland, 12310; lot no. 358421/1 1296),
- 2,5-dihydroxy-1,4-benzoquinone (8), 98% (Sigma-Aldrich, Steinheim, Germany, 19,546-4; lot no. 10643-077),
- 2,3-dimethoxy-1,4-benzoquinone (5) (synthesized after SHARMA et al. 1985),
- 2,3-dimethoxy-5-methyl-1,4-benzoquinone (7), > 99% (Fluka, Buchs, Switzerland, 38775; lot no. 256800/1 896),
- 2-methoxy-3-methyl-1,4-benzoquinone (4) [synthesized after GODFREY et al. (1974) and LULY & RAPOPORT (1981)],
- 2-hydroxy-3-methyl-1,4-benzoquinone (3) + 2,6-dimethoxytoluene (synthesized according to the procedure proposed by ATTYGALLE et al. (1993) for 2-methoxy-3-methyl-1,4-benzoquinone, but the MS spectrum shows that our product was a mixture of the aforementioned substances),
- toluquinone (1), > 98% (2-methyl-1,4-benzoquinone; Fluka, Buchs, Switzerland, product number 89590; lot no. 358564/1 297),
- toluhydroquinone (6), > 98% (2-methyl-1,4-hydroquinone; Fluka, Buchs, Switzerland, 89600; lot no. 339925/1 595).

As dispenser for these substances we used white unperfumed toilet paper of Ivorian fabrication. In the control traps, toilet paper without quinones but sometimes with ethanol (see Table 1) was exposed.

Experiments. The traps with the bait were exposed on 8 days between May 6th and June 20th, 1997, and on 6 days between April 1st and April 17th, 1998 (see Table 1), from before dusk (04:00 to 06:00 p.m.) to after dusk (08:00 to 10:00 p.m.). Since these were preliminary experiments for another project, the number of traps and bait substances differed between days (see Table 1). Statistical tests were performed with xISTAT 3.4.

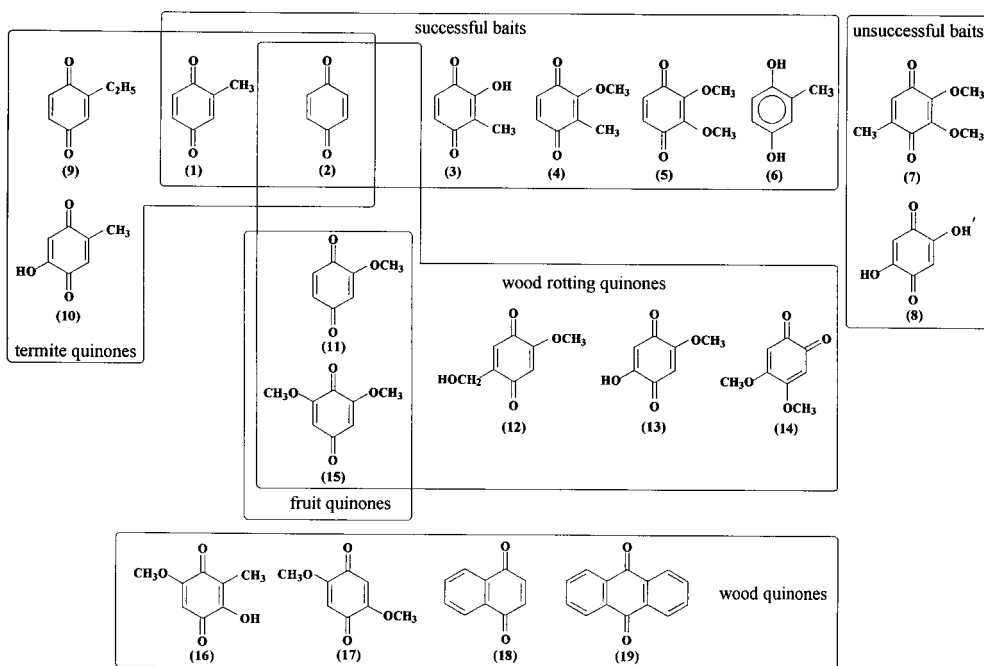


Fig. 1. — Quinones. (1)-(6): Quinones attractive for *Cyphonistes tuberculifrons* in our experiments. (1): 2-methyl-1,4-benzoquinone (toluquinone). (2): 1,4-benzoquinone. (3): 2-hydroxy-3-methyl-1,4-benzoquinone. (4): 2-methoxy-3-methyl-1,4-benzoquinone. (5): 2,3-dimethoxy-1,4-benzoquinone. (6): 2-methyl-1,4-dihydroquinone (toluhydroquinone). (7)-(8): Quinones not attractive for *Cyphonistes tuberculifrons* in our experiments. (7): 2,3-dimethoxy-5-methyl-1,4-benzoquinone. (8): 2,5-dihydroxy-1,4-benzoquinone. (1)-(2), (9)-(10): Quinones found in termite defensive secretions. (1), (2): see above. (9): 2-ethyl-1,4-benzoquinone. (10): 5-hydroxy-2-methyl-1,4-benzoquinone. (2), (11)-(15): Quinones found in rotting wood. (2): see above. (11): 2-methoxy-1,4-benzoquinone, (12): 5-hydroxy-methyl-2-methoxy-1,4-benzoquinone. (13): 5-hydroxy-2-methoxy-1,4-benzoquinone. (14): 4,5-dimethoxy-1,2-benzoquinone. (15): 2,6-dimethoxy-1,4-benzoquinone. (11), (15): Quinones found in fruit. (11), (15): see above. [(16)-(19): Quinones found in wood]. (16): 2-hydroxy-5-methoxy-3-methyl-1,4-benzoquinone. (17): 2,5-dimethoxy-1,4-benzoquinone (Thermophillin). (18): 1,4-naphthoquinone. (19): Anthraquinone. In wood and heartwood, substituted naphthoquinones and anthraquinones are present.

Species. *Cyphonistes* Burmeister 1847 is a genus comprising 17 species of rhinoceros beetles (Scarabaeidae Dynastinae) from tropical and South Africa. *Cyphonistes tuberculifrons* is distributed from Ivory Coast to Angola and Tanzania (ENDRÖDI 1985), but was rarely seen in the study area. Its flight activity starts after sunset and seems to reach its peak before 08:00 p.m. (BURGEON 1947: 301; F.-T. KRELL pers. obs.).

RESULTS

During 60 trap-nights we caught 16 specimens of *Cyphonistes tuberculifrons* with 14 baited traps, whereas during 22 trap-nights with control traps no specimen of the rare species was caught (Table 1). There was a significant difference between the attraction success of the two trap types ($P = 0.017$; two-sided Fisher's Exact Test). Because the beetles fly only during the first nights after rain (F.-T. KRELL pers. obs.), trapping was unsuccessful on some days. Since we tested whether *C. tuberculifrons* was attracted by quinones during its activity time rather than at all times, we did not include the unsuccessful, dry trap-nights in the statistical evaluation. However, also when all trap-nights were considered (82 baited, 14 successful; 25 control, none successful), the results of the bait and control experiments showed a significant difference in the number of attracted beetles ($P = 0.037$).

It is highly improbable that the 16 specimens of *C. tuberculifrons* went into the baited traps by chance, since not a single beetle went into an unbaited one.

DISCUSSION

Quinones or ethanol?

Different types of quinones seemed to be successful baits for attracting rhinoceros beetles of the species *Cyphonistes tuberculifrons*. Since we used ethanol as a solvent to increase the dispersion surface of the quinones, we had to check its possible attractive effect. Alone or in a mixture with other host volatiles, ethanol is known to attract xylophagous and also some associated predatory beetles of the families Cerambycidae, Curculionidae (including Scolytinae and Platypodinae), Nitidulidae, Melandryidae, Cleridae, and Monotomidae (= Rhizophagidae) (INSCOE 1982, CHÉNIER & PHILOGENE 1989, SCHROEDER & LINDELÖW 1989, JAFFÉ et al. 1993). They are supposed to locate fresh wounds of host plants or to determine their deterioration on the basis of an odour bouquet containing ethanol (JAFFÉ et al. 1993: 1717, TUNSET et al. 1993: 163), since ethanol emanates from fresh wounds of plants and from rotting plant products rich in carbohydrates, e.g. fruit.

There was no significant difference between the success of the traps with and without ethanol. Since traps with quinones, not dissolved in ethanol, were also attractive, and none of the control traps baited only with ethanol attracted any specimen, we can exclude any attractive or attraction-increasing effect of ethanol in our experiment. This was as expected because the ethanol had completely evaporated no later than 30 min after exposure and all traps were exposed more than 30 min before the flight activity of *C. tuberculifrons* began. Hence, without doubt the quinones were the attractants.

Table 1.

Results of trapping experiments with quinones in 1997 and 1998. The number of traps is given in parentheses. Since the beetles fly only after rains, some dry nights without any trapping success are not listed. The defensive secretions of *Pelmatojulus tigrinus* Hoffman & Mahsberg 1996 (Diplopoda: Spirobolida) consist of 2-methyl-1,4-benzoquinone (1) and 2-methoxy-3-methyl-1,4-benzoquinone (4) (KRELL et al. 1998). An asterisk indicates addition of ethanol as solvent or control substance.

Bait / date	6.V.97	7.V.97	22.V.97	1.VI.97	9.VI.97	1.IV.98	5.IV.98	10.IV.98	13.IV.98	17.IV.98	Σ
1,4-benzoquinone	1♀ (1*)	0 (1*)	1♀ (3*)	1♂ (6*)	1♀ (3*)	1♀ (3*)	0 (3*)	1♂, 1♀ (2*)	0 (1)	0 (1)	7 (24)
2-methyl-1,4-benzoquinone	0 (1*)	0 (1*)	—	—	—	—	—	1♂ (1, 2*)	0 (1)	0 (1)	1 (7)
2-methoxy-3-methyl-1,4-benzoquinone	—	—	—	—	—	—	—	0 (1)	0 (1)	1♂ (1)	1 (3)
2,5-dihydroxy-1,4-benzoquinone	—	—	—	—	—	—	—	—	0 (1)	0 (1)	0 (2)
2-methyl-1,4-benzoquinone + 2-methoxy-3-methyl-1,4-benzoquinone	—	—	—	—	—	—	—	2♂♂ (3)	0 (1)	1♂ (2)	3 (8)
Defensive secretions of <i>Pelmatojulus tigrinus</i>	—	—	—	—	—	0 (3)	—	—	—	—	0 (3)
2-methyl-1,4-hydroquinone	0 (1*)	1♂ (1*)	0 (3*)	—	—	—	—	—	0 (1)	0 (1)	1 (7)
2-hydroxy-3-methyl-1,4-benzoquinone + 2,6-dimethoxytoluene	1♀ (1*)	0 (1*)	—	—	—	—	—	—	—	—	1 (2)
2,3-dimethoxy-1,4-benzoquinone	2♀♀ (1*)	0 (1*)	—	—	—	—	—	—	—	—	2 (2)
2,3-dimethoxy-5-methyl-1,4-benzoquinone	0 (1*)	0 (1*)	—	—	—	—	—	—	—	—	0 (2)
Σ quinones	4 (6)	1 (6)	1 (6)	1 (6)	1 (3)	1 (6)	2 (6)	3 (7)	1 (7)	1 (7)	16 (60)
Control	0 (2)	0 (2)	0 (3)	0 (3)	0 (2)	0 (3)	0 (3*)	0 (1, 1*)	0 (1)	0 (1)	0 (22)

Known attractants for Oryctini

MARIAU (1968) assumed that plant wounds were attractive to adults of *Oryctes* Illiger 1798, but his experiments did not distinguish between primary and secondary attraction. To date, only a few substances have been identified as chemical attractants for Oryctini. Ethyl dihydrochrysanthemumate (BARBER et al. 1971) and ethyl chrysanthemumate (MADDISON et al. 1973, JULIA 1974) have been used as attractants for the biological control of the rhinoceros beetles *Oryctes rhinoceros* (L. 1758) and *O. monoceros* (Olivier 1789). VANDER MEER et al. (1979) found a further strong attractant: (\pm)-Des-N-morphinan, a phenanthrene. A few other chrysanthemumates, geraniol, curlure (4-(*p*-hydroxyphenyl)-2-butanone acetate), siglure (1-methylpropyl trans-6-methyl-3-cyclohexane), 2,5-dimethyl-2,4-hexadiene, isopentyl and phenethyl butyrate, trans-2-hexenal, butyl and pentyl hexanoate were much less attractive in field experiments (BARBER et al. 1971, VANDER MEER et al. 1979). Pheromones of Oryctini are known only from the above-mentioned two species: a male aggregation pheromone, ethyl-4-methyloctanoate, and a further attractive substance, ethyl-4-methylheptanoate (GRIES et al. 1994, HALLETT et al. 1995, MORIN et al. 1996, RENOUE et al. 1998). Recently, RENOUE et al. (1998) found olfactory receptor cells in the antennae of female *O. rhinoceros* for ethyl-4-methyloctanoate, phenyl ethanol, phenol, phellandrene, isoamyl acetate, Z3-hexenol, and ethyl chrysanthemumate.

Thus, quinones or quinone derivatives have never been recorded as being attractive to rhinoceros beetles, neither as pheromones nor as primary attractants of the host plants. Since the identification of phenol and phenyl ethanol as possible attractants by RENOUE et al. (1998) was published after our field experiments we were not able to test these substances.

Quinones and the feeding ecology of Oryctini

Quinones are repellents or deterrents for both vertebrates and invertebrates, often causing toxic effects. They are present in defensive secretions of Diplopoda (EISNER et al. 1978), Isoptera (see later), Orthoptera, Dermaptera, Dictyoptera, Thysanoptera, Coleoptera, and Opiliones (WHITMAN et al. 1990) as well as in termite resistant timbers (FLOYD et al. 1976, LEISTNER 1985). It seems strange that such effective repellents act as attractants for some insects. Recently, however, we found that necrophagous dung beetles of the genus *Onthophagus* Latreille 1802 (Scarabaeidae Coprinae) use the quinones of diplopod defensive secretions to locate fresh millipede carcasses; thus they can be the first and most effective users of this resource which is unattractive for most of their competitors (KRELL et al. 1997, 1998). It is not easy to find a connection between rhinoceros beetles and quinones since they do not feed on animals or animal remains containing defensive secretions.

The feeding habits of adult *Cyphonistes tuberculifrons* are virtually unknown, as are those of the other species of this genus. BURGEON (1947: 301) reported that, in the Congo, it was found in the soil under fallen fruit but did not indicate any feeding activity. NONVEILLER'S (1984: 37) affirmation of rhizophagy in *C. tuberculifrons* is based on pure speculation without any supporting facts (G. NONVEILLER in litt. 1998). According to PÉRINGUEY (1885) the southern African species *C. corniculatus* Burmeister 1847 was frequently found under termite mounds in the Cape region. Later he "ascertained that it feeds upon the material of which the more or less conical base of the termite nest is made" (PÉRINGUEY 1901-1902: 558; the "conical base" is likely to be the fungus garden, J. KORB pers. comm.).

In eastern Africa, EICHELBAUM (1913) found larvae of *Cyphonistes tuberculifrons* in rotting wood and reared them to pupal and adult stage. Although this is only one observation, we assume that the larvae are saproxylophagous, since larvae of Dynastinae generally do not move between different microhabitats. They stay in their substratum all their life.

In the view of these hints we are searching for connections between quinones and the presumed habit or substratum of *Cyphonistes tuberculifrons*, i.e. wood, dead wood, rotting fruit, and termite mounds.

Quinones as components of termite defensive secretions

Defensive secretions of some species of *Mastotermes* (Mastotermitidae), *Macrotermes*, *Microtermes*, *Hypotermes* and *Odontotermes* (Macrotermitidae) contain the quinones (1), (2), (9), and (10) (MASCHWITZ & THO 1974, HOWSE 1975, WOOD et al. 1975, OLAGBEMIRO et al. 1988), the first two of which were attractive in our experiments. The termite species include *Macrotermes bellicosus* (Smeathman 1781) which is common in the study area (KORB 1997). PÉRINGUEY (1885, 1901-1902) reported a possible termitophily of *Cyphonistes corniculatus* in South Africa.

If the adults of *Cyphonistes tuberculifrons* feeds on fungus gardens of termites, using termite defensive secretions to find termite mounds would be an economic strategy. Termites use their defensive secretions in large amounts directly at their mound in cases of attack by ants or vertebrates. These predators may kill or at least weaken the colony. Thus, *Cyphonistes* has easier access to the fungus gardens.

Quinones in rotting fruit

In more than half the orders of plants, phenolic compounds are present, mostly of the flavonoid type. These polyphenols can be found in different parts of the cormus, including fruit. The browning in plant tissues is caused by oxidation of the polyphenols to *o*-quinones. Browning is greatly hastened after mechanical injury (MATHEW & PARPIA 1971, ESPÍN et al. 1995). Hence, quinones are frequently formed in rotting fruit fallen to the ground. Moreover, in fruit of some species of at least six families occurring in the study region, various quinones were found even before rotting (THOMSON 1987, 1997); among them, but in a lower proportion, were simple substituted 1,4-benzoquinones [(11), (15)].

C. tuberculifrons has been found only once under rotting fruit (BURGEON 1947). They may have been attracted by the quinones present in the fruit or emerging from the rotting fruit. However, there is no indication that rotting fruit are used as a food resource by this species, even though other rhinoceros beetles are known to feed as adults on fruit (LÖSER 1991).

Quinones as wood components and products of rotting wood

Quinones are present in the wood, heartwood or stem bark of some species belonging to at least 18 families (LEISTNER 1985; THOMSON 1987, 1997) present in the study area (POILECOT 1991). The molecular structure of these quinones is mostly much more complex than those tested. Naphthoquinones (18), anthraquinones (19) and a few other substances found are polycyclic; obtusaquinones are quinoneme-

thides; only three "simple" benzoquinones, (15), (16), and (17), were found in wood or heartwood of five families (THOMSON 1971, 1997; LEISTNER 1985) occurring in the study area (POILECOT 1991). Since Dynastinae larvae prefer to inhabit rotting wood rather than live wood, we have to ascertain in which way the overall concentration of simple quinones develops during the rotting process.

Different quinones are obligatorily formed by white-rot and brown-rot fungi and other micro-organisms during lignin degradation. Therefore, rotting wood contains more quinones than living wood. The following rotting wood quinones have been detected: (2), (11), (12), (13), (14), (15), the corresponding hydroquinones, and two bicyclic quinones (BOLLAG et al. 1982; KIRK et al. 1986; SCHMIDT et al. 1989; SCHOEMAKER et al. 1989; WARIISHI et al. 1989, 1991; ERIKSSON et al. 1990: 309ff; TUOR et al. 1992). One of these quinones, 1,4-benzoquinone (2), was attractive to *C. tuberculifrons* in our experiments. The other monocyclic benzoquinones and hydroquinones are of relatively simple structure and resemble the quinones attractive in our experiments. Since rotting wood is the larval habitat of *Cyphonistes tubercoli-frons*, attraction of the adults by quinones could help them find a suitable substratum for reproduction.

CONCLUSION

We cannot conclude that the quinones most frequently present in some woods attract *C. tuberculifrons* because they are much more complex than the attractive quinones, are much less volatile and have a different steric configuration which will hardly fit receptors that respond to simple quinones. However, we did not test these complex quinones and, hence, do not know anything about their attractivity. Adult Oryctini though do not feed in massive wood or hardwood but only in softer parts of trees like buds. Indeed, the larvae of *C. tuberculifrons* feed on rotting wood and their parents have to look for rotting wood for their mating and oviposition.

We presume that the quinones originating from lignin degradation during the wood rotting process can attract *C. tuberculifrons* because they resemble or are the same quinones (1,4-benzoquinone (2)), that were attractive in our experiments. The few simple quinones found in undegraded wood may fit the unspecific receptors of *C. tuberculifrons* as well, possibly increasing the attractivity of rotting wood. Attraction by the quinones of termite defensive secretions, fruit or rotting fruit is another possible mechanism helping the adults to find sources of food for precopulatory, egg-ripening feeding, but not to find resources for reproduction. It is also possible that *C. tuberculifrons* has quinones as pheromones. However, the substances identified as pheromones in Dynastinae have nothing to do with quinones; so these results are not of much help for our discussion. However, in chafers, the subfamily Melolonthinae closely related to Dynastinae, phenolic compounds are used as pheromones (LEAL 1998). Since we attracted both males and females with quinones, it is improbable that they are sexual pheromones. Moreover, sexual pheromone reception is mostly specific; even chirality and stereoisomerism of the semiochemicals may be crucial for their effect and their efficacy (LEAL 1996, 1998). In our case, different quinones were attractive. They could, however, be less specific aggregation pheromones for both sexes, but it is not necessary to develop a costly aggregation pheromone mechanism based on a substance that is present in the aggregation place. Moreover, lesser specificity of semiochemical receptor cells indicates a kairomone or apneumone system rather than a pheromone system (MUSTAPARTA 1986: 266).

In summary, it is most probable that the attraction of *C. tuberculifrons* to quinones indicates a primary attraction of a saprophagous beetle to the substratum that serves for feeding or reproduction: termite fungus gardens, rotting fruit and/or rotting wood.

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REFERENCES

- ATTYGALLE A.B., XU S.-C., MEINWALD J. & EISNER T. 1993. Defense secretion of the millipede *Floridobolus penneri*. *Journal of Natural Products* 56: 1700-1706.
- BARBER I.A., MCGOVERN T.P., BEROZA M., HOYT C.P. & WALKER A. 1971. Attractant for the coconut rhinoceros beetle. *Journal of Economic Entomology* 64: 1041-1044.
- BEDFORD G.O. 1980. Biology, ecology, and control of palm rhinoceros beetles. *Annual Review of Entomology* 25: 309-339.
- BOLLAG J.-M., LIU S.-Y. & MINARD R.D. 1982. Enzymatic oligomerization of vanillic acid. *Soil Biology and Biochemistry* 14: 157-163.
- BURGEON L. 1947. Catalogues raisonnés de la faune entomologique du Congo Belge. Coléoptères: Dynastinae, Valginae, Melolonthinae p.p. *Annales du Musée du Congo Belge, (C, Zoologie), Série III (II) 5 (4): 277-340.*
- CHÉNIER J.V.R. & PHILOGENE B.J.R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. *Journal of Chemical Ecology* 15: 1729-1745.
- EICHELBAUM F. 1913. Käferlarven und Käferpuppen aus Deutsch-Ostafrika. *Zeitschrift für Wissenschaftliche Insektenbiologie* 9: 12-15.
- EISNER T., ALSOP D., HICKS K. & MEINWALD J. 1978. Defensive secretions of millipeds, pp. 41-72. In: Bettini S., Edit. Arthropod venoms. *Berlin: Springer*, XXXIII + 977 pp.
- ENDRÖDI S. 1985. The Dynastinae of the world. *Budapest: Akadémiai Kiadó*, 800 pp., 46 pls.
- ERIKSSON K.-E.L., BLANCHETTE R.A. & ANDER P. 1990. Microbial and enzymatic degradation of wood and wood components. *Berlin: Springer*, IX + 407 pp.
- ESPÍN J.C., MORALES M., VARON R., TUDELA J. & GARCÍA-CANOVÁS F. 1995. Monophenolase activity of polyphenol oxidase from Verdedoncella apple. *Journal of Agricultural and Food Chemistry* 43: 2807-2812.
- FLOYD M.A., EVANS D.A. & HOWSE P.E. 1976. Electrophysiological and behavioural studies on naturally occurring repellents to *Reticulitermes lucifugus*. *Journal of Insect Physiology* 22: 697-701.
- GODFREY I.M., SARGENET M.V. & ELIX J.A. 1974. Preparation of methoxyphenols by Baeyer-Villiger oxidation of methoxybenzaldehydes. *Journal of the Chemical Society Perkin Transactions (I): 1353-1354.*
- GRIES G., GRIES R., PEREZ A.L., OEHLISCHLAGER A.C., GONZALES L.M., PIERCE H.D., ZEBEYOU M. & KOUAME B. 1994. Aggregation pheromone of the African rhinoceros beetle, *Oryctes monoceros* (Olivier) (Coleoptera: Scarabaeidae). *Zeitschrift für Naturforschung* 49c: 363-366.
- HALLETT R.H., PEREZ A.L., GRIES G., GRIES R., PIERCE H.D., YUE J., OEHLISCHLAGER A.C., GONZALES L.M. & BORDEN J.H. 1995. Aggregation pheromone of coconut rhinoceros beetle, *Oryctes rhinoceros* (L.) (Coleoptera: Scarabaeidae). *Journal of Chemical Ecology* 21: 1549-1570.

- HOWSE P.E. 1975. Chemical defences of ants, termites and other insects: some outstanding questions, pp. 23-40. In: Noirot C. et al., Edits. Pheromones and defensive secretions in social insects. *Dijon: French Section of the International Union for the Study of Social Insects*, VII + 248 pp.
- INSCOE M.N. 1982. Insect attractants, attractant pheromones, and related compounds, pp. 201-295. In: Kydonieus A.F. & Beroza M., Edits. Insect suppression with controlled release pheromone systems, Vol. 2. *Boca Raton, Florida: CRC Press*, 312 pp.
- JAFFÉ K., SÁNCHEZ P., CERDA H., HERNÁNDEZ J.V., JAFFÉ R., URDANETA N., GUERRA G., MARTÍNEZ R. & MIRAS B. 1993. Chemical ecology of the palm weevil *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae): attraction to host plants and to a male-produced aggregation pheromone. *Journal of Chemical Ecology* 19: 1703-1720.
- JULIA J.G. 1974. Les ravageurs et maladies du palmier à huile et du cocotier. Piégage de l'*Oryctes* au chrysenthémate d'éthyle. *Oléagineux* 29: 79-80.
- KIRK T.K., TIEN M., KERSTEN P.J., MOZUCH M.D. & KALYANARAMAN B. 1986. Ligninase of *Phanerochaete chrysosporium*. Mechanism of its degradation of the non-phenolic arylglycerol β -aryl ether substructure of lignin. *Biochemical Journal* 236: 279-287.
- KORB J. 1997. Lokale und regionale Verbreitung von *Macrotermes bellicosus* (Isoptera; Macrotermitinae): Stochastik oder Deterministik? *Berlin: Wissenschaft & Technik Verlag*, 158 pp., 2 pls.
- KRELL F.-T., SCHMITT T., DEMBELE A. & LINSEMAIR K.E. 1998. Repellents as attractants - extreme specialization in afrotropical dung beetles (Coleoptera: Scarabaeoidea) as a competition avoiding strategy. *Zoology, Analysis of Complex Systems* 101, Supplement 1: 12.
- KRELL F.-T., SCHMITT T. & LINSEMAIR K.E. 1997. Diplopod defensive secretions as attractants for necrophagous scarab beetles (Diplopoda - Insecta: Coleoptera: Scarabaeidae). *Entomologica Scandinavica Supplementum* 51: 281-285.
- LANIER G.N. 1990. Principles of attraction-annihilation: mass trapping and other means, pp. 25-45. In: Ridgway R.L. et al., Edits. Behavior-modifying chemicals for insect management. Applications of pheromones and other attractants. *New York, Basel: Marcel Dekker*, XVI + 761 pp.
- LEAL W.S. 1996. Chemical communication in scarab beetles: reciprocal behavioral agonist-antagonist activities of chiral pheromones. *Proceedings of the National Academy of Sciences USA* 93: 12112-12115.
- LEAL W.S. 1998. Chemical ecology of phytophagous scarab beetles. *Annual Review of Entomology* 43: 39-61.
- LEISTNER E. 1985. Occurrence and biosynthesis of quinones in woody plants, pp. 273-290. In: Higuchi T., Edit. Biosynthesis and biodegradation of wood components. *Orlando: Academic Press*, 679 pp.
- LÖSER S. 1991. Exotische Insekten, Tausendfüßer und Spinnentiere. Eine Anleitung zur Haltung und Zucht. *Stuttgart: Ulmer*, 175 pp.
- LULY J.R. & RAPOPORT H. 1981. Amine addition to unsymmetrical benzoquinones. *Journal of Organic Chemistry* 46: 2745-2752.
- MADDISON P.A., BEROZA M & MCGOVERN T.P. 1973. Ethyl chrysanthemumate as an attractant for the coconut rhinoceros beetle. *Journal of Economic Entomology* 66: 591-592.
- MARIAU D. 1968. Biologie du comportement alimentaire de l'*Oryctes*. *Oléagineux* 23: 377-380.
- MASCHWITZ U. & THO Y.P. 1974. Chinone als Wehrsubstanzen bei einigen orientalische [sic!] Macrotermitinen. *Insectes Sociaux* 21: 231-234.
- MATHEW A.G. & PARPIA H.A.B. 1971. Food browning as a polyphenol reaction. *Advances in Food Research* 10: 75-145.
- MORIN J.-P., ROCHAT D., MALOSSE C., LETTERE M., DESMIER DE CHENON R., WIBWO H. & DESCOINS C. 1996. Le 4-méthylcatnoate d'éthyle, composant principal de la phéromone mâle de *Oryctes rhinoceros* (L.) (Coleoptera, Dynastinae). *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la Vie* 319: 595-602.
- MUSTAPARTA H. 1986. Allelochemical effects of pheromones: receptor responses, pp. 263-268. In: Payne T.L. et al., Edits. Mechanisms in insect olfaction. *Oxford: Clarendon Press*, XVI + 364 pp.

- NONVEILLER G. 1984. Catalogue commenté et illustré des insectes du Cameroun d'intérêt agricole (appartitions, répartition, importance). *Institut pour la Protection des Plantes, Beograd, Mémoires* 15: 1-210.
- OLAGBEMIRO T.O., LAJIDE L., SANI K.M. & STADDON B.W. 1988. 2-Hydroxy-5-methyl-1,4-benzoquinone from the salivary gland of the soldier termites *Odontotermes magdalenae*. *Experientia* 44: 1022-1024.
- PÉRINGUEY L. 1885. Insects injurious to forest trees in South Africa. *Transactions of the South African Philosophical Society* 4: 15-25.
- PÉRINGUEY L. 1901-1902. Descriptive catalogue of the Coleoptera of South Africa (Lucanidae and Scarabaeidae). *Transactions of the South African Philosophical Society* 12: 1-920, 12 pls.
- POILECOT P. (Edit.) 1991. Un écosystème de savane soudanienne: Le Parc National de la Comoé (Côte d'Ivoire). *Projet UNESCO/PNUD n°IVC/87/007, Note Technique* 2: 346 pp.
- POREMBSKI S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-83.
- RENOU M., TAUBAN D. & MORIN J.-P. 1998. Structure and function of antennal pore plate sensilla of *Oryctes rhinoceros* (L.) (Coleoptera: Dynastidae). *International Journal of Insect Morphology and Embryology* 27: 227-233.
- SCHMIDT H.W.H., HAEMMERLI S.D., SCHOEMAKER H.E. & LEISOLA M.S.A. 1989. Oxidative degradation of 3,4-dimethoxybenzyl alcohol and its methyl ether by the lignin peroxidase of *Phanerochaete chrysosporium*. *Biochemistry* 28: 1776-1783.
- SCHOEMAKER H.E., MEIJER E.M., LEISOLA M.S.A., HAEMMERLI S.D., WALDNER R., SANGLARD D. & SCHMIDT H.W.H. 1989. Oxidation and reduction in lignin biodegradation, pp. 454-471. In: Lewis N.G. & Paice M.G., Edits. *Plant cell wall polymers. Biogenesis and biodegradation*. ACS Symposium Series 399. Washington, DC: American Chemical Society, XII + 676 pp.
- SCHROEDER L.M. & LINDELÖW Å. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α -pinene and ethanol. *Journal of Chemical Ecology* 15: 807-817.
- SHARMA P.K., ROHATAGI B.K. & KHANNA R.N. 1985. Synthesis of antibacterial quinones. *Acta Chimica Hungarica* 120: 163-166.
- THOMSON R.H. 1971. Naturally occurring quinones. Second edition. London, New York: Academic Press, VII + 734 pp.
- THOMSON R.H. 1987. Naturally occurring quinones III. Recent advances. London, New York: Chapman and Hall, IX + 732 pp.
- THOMSON R.H. 1997. Naturally occurring quinones IV. Recent advances. London: Blackie Academic & Professional, VII + 746 pp.
- TUNSET K., NILSSEN A.C. & ANDERSEN J. 1993. Primary attraction in host recognition of coniferous bark beetles and bark weevils (Col., Scolytidae and Curculionidae). *Journal of Applied Entomology* 115: 155-169.
- TUOR U., WARIISHI H., SCHOEMAKER H.E. & GOLD M.H. 1992. Oxidation of phenolic arylglycerol β -aryl ether lignin model compounds by manganese peroxidase from *Phanerochaete chrysosporium*: oxidative cleavage of an α -carbonyl model compound. *Biochemistry* 31: 4986-4995.
- VANDER MEER R.K., GHATAK U.R., ALAM S.K. & CHAKRABORTI P.C. 1979. (\pm)-Des-N-morphinan: a unique bridged hydrocarbon attractant for the rhinoceros beetle, *Oryctes rhinoceros*; and development of an olfactometer. *Environmental Entomology* 8: 6-10.
- WARIISHI H., VALLI K. & GOLD M.H. 1989. Oxidative cleavage of a phenolic diarylpropane lignin model dimer by manganese peroxidase from *Phanerochaete chrysosporium*. *Biochemistry* 28: 6017-6023.
- WARIISHI H., VALLI K. & GOLD M.H. 1991. In vitro depolymerization of lignin by manganese peroxidase of *Phanerochaete chrysosporium*. *Biochemical and Biophysical Research Communications* 176: 269-275.
- WHITMAN D.W., BLUM M.S. & ALSOP D.W. 1990. Allomones: chemicals for defense, pp. 289-351. In: Evans D.L. & Schmidt J.O., Edits. *Insect defenses. adaptive mechanisms and strategies of prey and predators*. Albany: State University of New York Press, XV + 482 pp.
- WOOD W.F., TRUCKENBRODT W. & MEINWALD J. 1975. Chemistry of the defensive secretion from the African termite *Odontotermes badius*. *Annals of the Entomological Society of America* 68: 359-360.