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The Appearance of Xylophagy in Cockroaches: Two Case Studies with Reference to Phylogeny

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ABSTRACT.—Xylophagy in cockroaches has been considered a rare attribute, inherited from a common ancestor with termites. This point of view is discussed in a phylogenetic perspective for two independent tropical cockroach lineages: the subfamily Polyphaginae and the group (Zetoborinae + Blaberinae + Gyninae + Diplopterinae). A phylogeny was constructed for each of these two lineages. Xylophagy occurs in *Cryptocercus* in the subfamily Polyphaginae and has recently been discovered in *Parasphaeria* (subfamily Zetoborinae). This allows one to propose, in reference to phylogenies, that xylophagy is recently derived, that slow development is a correlate of xylophagy rather than a prerequisite, and that xylophagy appearance preceded the conquest of temperate areas at least once.

INTRODUCTION

Xylophagy and flagellate symbionts usually have been viewed as ancestral traits in Dictyoptera (Cleveland *et al.* 1934, Grassé and Noirot 1959, Nalepa 1984) as well as in Isoptera (Grassé and Noirot 1959, Noirot 1992, Wilson 1971). This assumption was made in reference to the so-called "primitive nature" of the xylophagous taxa (the cockroach *Cryptocercus* Scudder, 1862, and "lower" termites), which were supposed to show numerous relictual features inherited from some very ancient ancestors. More recently, the evolution of xylophagy in Dictyoptera was studied relative to an independent phylogeny (Hennig 1981, Deleporte 1988). This allows one to consider the evolution of xylophagy with less *a priori* arguments and to avoid reconstructing a history consistent with previous ideas about the "primitive xylophagous taxon" concept. The evolutionary scenario of xylophagy in Dictyoptera and Isoptera depended heavily on the phylogenetic position of the xylophagous cockroach, *Cryptocercus*. This last taxon was until recently considered the sister-group of all other cockroaches (Deleporte 1988, Thorne and Carpenter 1992). For this reason, xylophagy and the presence of symbionts were for a time thought to be present in a common ancestor of *Cryptocercus* and some termites. Some authors favored different hypotheses, including a possible convergence and a transfer of flagellates between *Cryptocercus* and some termites (Emerson 1935, Boudreaux 1979, Thorne 1990). But they based their hypotheses on the old phylogenetic position of *Cryptocercus*, and even recently, Thorne (1990) considered xylophagy and the function of symbionts as very ancient and having occurred in "roachoid and termitoid lines", "millions of years ago".

Recently, Grandcolas and Deleporte (1992) and Grandcolas (in press) showed that treating *Cryptocercus* as the sister group to all other cockroaches was due to a lack of discovered synapomorphies and to a biased sampling of other cockroach families. A new phylogenetic position was proposed after the discovery of numerous synapomorphies and leads to a new hypothesis on the evolution of xylophagy.

Xylophagy was decidedly misrepresented in cockroaches and its origin is still not well understood; but it is also more common than previously considered. It was previously known in *Cryptocercus* and also in several genera of the subfamily Panesthiinae (Chopard 1938, Roth and Willis 1960). But recently two other cases of xylophagy were recently discovered in the subfamilies Nyctiborinae and Zetoborinae (Grandcolas 1993c, Grandcolas, Desutter-Grandcolas, in prep.).

New phylogenetic studies and a comparison of several different cases could enhance our understanding of xylophagy in cock-

roaches. Using a phylogenetic framework, I here study the evolution of xylophagy in two lineages, the subfamilies Polyphaginae and Zetoborinae. I test whether xylophagy is ancestral or derived, whether peculiar life histories are correlates or prerequisites for xylophagy evolution, and whether xylophagy followed or preceded the conquest of temperate areas. A climatic analysis of distributional patterns is also performed in xylophagous taxa and in their common ancestors.

MATERIAL AND METHODS

Studied lineages

(Zetoborinae + Blaberinae + Gyninae + Diplopterinae) is a tropical worldwide monophyletic group, prevalent in forested regions (Grandcolas 1993d) and belonging to the family Blaberidae. The first two subfamilies are Neotropical, whereas the last two ones are African and Australasian, respectively. Phylogeny at the generic level is based on Grandcolas (1993d). In this lineage, one genus, *Parasphaeria* Brunner v. W., 1865, comprises xylophagous species in the austral part of South America (Grandcolas, Desutter-Grandcolas, in prep.).

The subfamily Polyphaginae is also a worldwide tropical group (Grandcolas and Deleporte 1992, Grandcolas 1994) in the family Polyphagidae. It is present in the deserts of all continents (excluding those of Australia) (Grandcolas in prep., *contra* Mackerras 1968) and in dry forests and rainforests of Africa and Asia. Its phylogeny at the generic level is obtained from Grandcolas (1994). Only the genus *Cryptocercus* in this subfamily contains xylophagous species (Cleveland *et al.* 1934, Bey-Bienko 1950).

Ecological attributes

Ecological attributes are features in which *a priori* homology and polarization are so hazardous that one prefers to make these operations in relation to an independent phylogeny (Grandcolas 1991). Each attribute may display several possible states and is coded in a non-additive way (Farris 1988). Unknown states are indicated with a question mark. When an attribute in a genus presents several states in different species, it is coded as polymorphic. When it consists of several states in the same species, it is coded as another and supplementary state. Ecological attributes are based either on my own field and laboratory observations (in French Guiana, Gabon, Saudi Arabia) or on literature records. The state of an attribute in a genus is considered as known if at least one species has been observed. This assumption appears reasonable, because 17% of genera are monospecific and 31% of the genera have several or all species with known and similar life habits. Two attributes are studied in relation to phylogeny in addition to

xylophagy, namely the occupation of a particular biome (Grandcolas 1993b), and life-history characteristics (development duration). Xylophagy consists of two states: non-xylophagous and xylophagous. Occupancy of a particular biome is defined after distribution reports which are then compared with vegetation maps (Cochrane 1963, Unesco 1981, White 1986, Whitmore 1984, Ying 1983). Biome occupancy is defined as follows: for the first lineage, occupation of tropical rainforest (including both montane and lowland rainforests), dry and open woodlands (including *Acacia* bush, cerrado, carab xerophytic forest), savanna, temperate forest, (Grandcolas 1993b), and for the second lineage: tropical forest (including both rain and dry forests), temperate forest, desert, and desert and temperate forest together. Development duration is arbitrarily defined as comprising two states: short development (less than 400 days from hatching to adult) versus long development (more than 400 days from hatching to adult). Laboratory rearing under standard conditions provide some estimates (Grandcolas 1993a, pers. obs., and literature, cf *infra*).

Inference of evolutionary scenarios

Evolutionary scenarios of attributes are inferred from the phylogeny. Biological attributes and phylogenetic characters are then two independent data sets. The method, called "character optimization" (Farris 1970), is applied to attributes using strict parsimony, as recommended by Brooks and McLennan (1991). The attribute states are mapped on the existing phylogeny and the most parsimonious evolutionary scenario(s) among all those possible is chosen: it consists of placing each state of an attribute at the root of the tree and then computing the subsequent number of changes necessary to obtain the present state distribution in existing taxa. The scenario(s) requiring the smallest number of evolutionary changes of attribute states is (are) kept as the best estimate of the course of evolution. The value of phylogenetic hypotheses, including associated scenarios, lies only in the evidence of its

smallest number of steps relative to others, notwithstanding testing statistics and random models with unrealistic covering assumptions (Carpenter 1992). The most parsimonious scenario is taken as the more likely hypothesis. Alternative scenarios simply need more data to be reexamined.

Climatic analysis

The distributional patterns of cockroaches are compared to the climatic maps of North and South America and of Asia (UNESCO, WMO 1975, 1979, 1981). The localities were taken from the literature and from my personal data. Only annual mean temperature and annual total rainfall are considered. The isohyet nearest to the border of the distribution areas is considered as a tentative climatic limit.

RESULTS

Xylophagy was suspected by Grandcolas (1991) in the genus *Parasphaeria* which belongs to the subfamily Zetoborinae in the group Zetoborinae + Blaberinae + Gyninae + Diplopterinae. This was recently confirmed by field and laboratory observations (Grandcolas, Desutter-Grandcolas, in prep). Xylophagy has been known for a long time in *Cryptocercus* (Cleveland *et al.* 1934) of the subfamily Polyphaginae. The most parsimonious scenario about xylophagy indicates that it appeared once in each lineage — in the ancestor of *Parasphaeria* for the first lineage, and in the ancestor of *Cryptocercus* for the second lineage (Figs. 1, 2). This scenario implies for each lineage a single step. A converse and less parsimonious scenario requires five steps under the hypothesis of an ancestral inheritance followed by several losses.

The length of development was observed to vary in different groups, ranging from two months to several years (Table 1). When total development time was not known, a minimal estimate was computed on the basis of five times the mean instar duration. The smallest number of instars known for ovoviviparous species is

Table 1. Mean durations of development (days \pm SE) in taxa belonging to (Zetoborinae + Blaberinae + Gyninae + Diplopterinae) and to Polyphaginae, with the origin of data (mean duration of one instar, when total duration not known).

Taxon	Duration of Development	Source
<i>Blaberus craniifer</i>	245	Lefevre (1963)
<i>Byrsotria fumigata</i>	276	Lefevre (1969)
<i>Diploptera punctata</i>	46	Schal <i>et al.</i> (1984)
<i>Gyna</i> sp.	about 100	Pers. obs.
<i>Hyporhnicoda litomorpha</i>	307	Lefevre (1969)
<i>Lanxoblatta emarginata</i>	349 \pm 3	Grandcolas (1993e)
<i>Parasphaeria</i> sp.	more than 150 for any instar	Pers. obs.
<i>Paradicta rotunda</i>	about 360	Pers. obs.
<i>Phortioeca nimbata</i>	188.5 \pm 2.5	Grandcolas (1993e)
<i>Schultesia lampyridiformis</i>	77.2 \pm 19.5	Grandcolas (1993e)
<i>Thanatophyllum akinetum</i>	335 \pm 26.4	Grandcolas (1993e)
<i>Arenivaga tonkowa</i>	about 150	Cochran (1979)
<i>Cryptocercus punctulatus</i>	more than 2000	Cleveland <i>et al.</i> (1934); Nalepa (1984)
<i>Ergaula capensis</i>	less than 30 for any instar	Pers. obs.
<i>Heterogamisca chopardi</i>	less than 30 for any instar	Pers. obs.
<i>Polyphaga aegyptiaca</i>	less than 30 for any instar	Pers. obs.
<i>Therea petiveriana</i>	less than 300	Pers. obs.

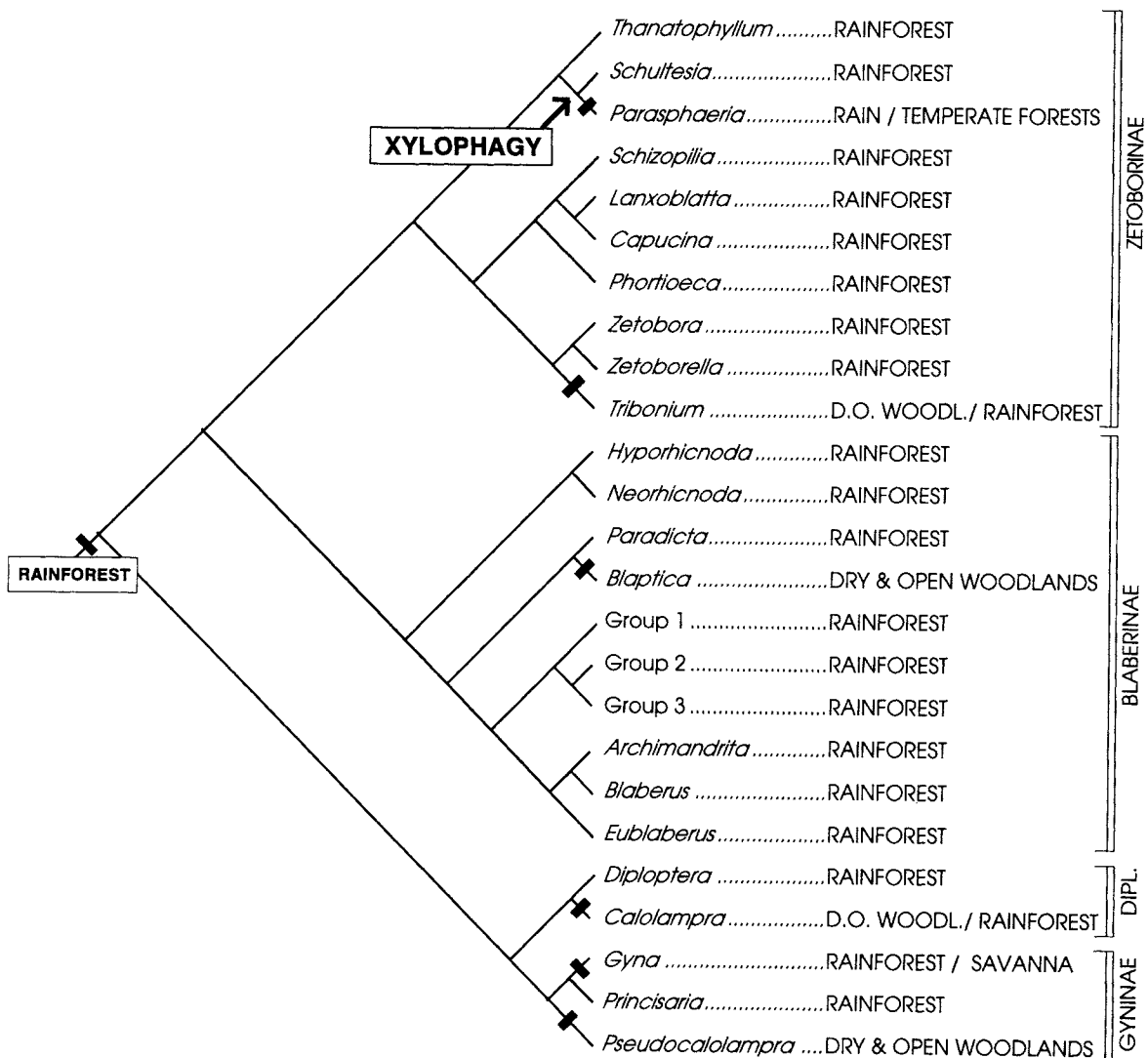


Fig. 1. Character optimization of biome occupancy upon the phylogeny of (Zetoborinae + Blaberinae + Gyninae + Diplopterinae). A change of biome occupancy is shown with a thick line. The ancestral state is inferred "rainforest". The inferred appearance of xylophagy is indicated by a label.

five (e.g., Lefeuvre 1969, Schal *et al.* 1984). Nevertheless, most development times were equal to or less than 400 days, and only the two xylophagous taxa had development times of more than 400 days. In reference to the phylogenies, the long development appears to have evolved independently for *Parasphaeria* and *Cryptocercus* and therefore requires one step each time (Figs. 3, 4). The converse scenario, taking long development as an ancestral state, supposes five steps each time.

Biome occupancy was already analysed in Grandcolas (1993b) for the group (Zetoborinae + Blaberinae + Gyninae + Diplopterinae) and occupancy of "rainforest" was hypothesized to be ancestral, implying only six steps against twelve steps for the second most parsimonious scenario (Fig. 2). Biome occupancies for the subfamily Polyphaginae are shown in Figure 1. Five different biomes were occupied and five genera occupied two different biomes. The most parsimonious scenario implies that desert occupancy is ancestral and that four changes subsequently occurred. In these scenarios, the occupation of temperate biomes (temperate forest) appeared secondarily in some species of *Parasphaeria* and all species of *Cryptocercus*.

Distribution of xylophagous taxa and of their nearest ances-

tors are depicted on maps in which some annual climatic isohyets are shown (Figs. 5, 6). The occupation of temperate forests corresponds in xylophagous taxa of both lineages to spreading respectively beyond the 5°C and 10°C isotherms. The xylophagous taxa contrary to their nearest parents do not spread beyond the isohyet 1200 mm.

An estimate of the relative timing of all these evolutionary events may be obtained when the three evolutionary scenarios are combined. Xylophagy appeared first, together with long developmental time; in one case the spread to temperate forests occurred secondarily.

DISCUSSION

Xylophagy appears to have evolved independently in the subfamilies Polyphaginae and Zetoborinae. This invalidates the classical scenario of ancestral xylophagy involving *Cryptocercus* (Cleveland *et al.* 1934, Grassé and Noiro 1959, Nalepa 1984), as already noted by Grandcolas and Deleporte (1992). It is probable then that xylophagy and flagellate symbionts evolved independently in *Cryptocercus*, by convergence and transfer, respectively,

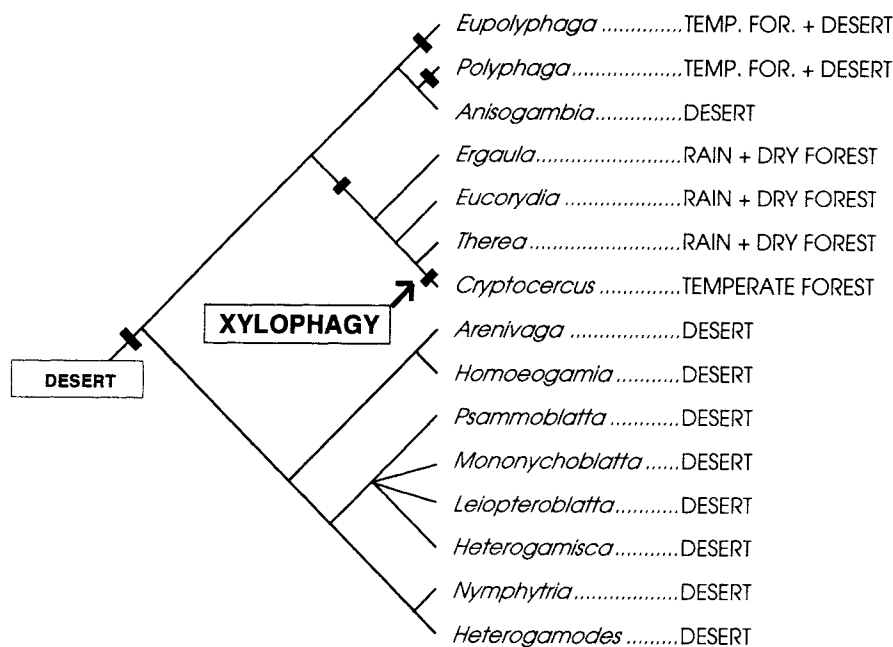


Fig. 2. Character optimization of biome occupancy upon the phylogeny of subfamily Polyphaginae. A change of biome occupancy is shown with a thick line. The ancestral state is inferred "desert". The inferred appearance of xylophagy is indicated by a label.

and that the similarity with mastotermitid termites and other wood-eating Isoptera is due to convergence. Another scenario was proposed by several workers (Emerson 1935, Boudreaux 1979, Thorne 1990) was the unsupported hypothesis of an ancient but independent appearance of xylophagy in *Cryptocercus*. This last scenario is also improbable, since it is based on the now discredited older phylogenetic position of *Cryptocercus*. The new phylogenetic position does not allow one to consider *Cryptocercus* as a relictual taxon which would have inherited a very ancient xylophagy from an ancestor shared with the early termites. *Cryptocercus* has many closely related ancestors, and geographical vicariations among all these taxa do not allow one to consider that the ancestor of *Cryptocercus* to be so ancient (Grandcolas 1994). One may consider that Hennig (1981) was probably correct, when he hypothesized on the probable recent origin of xylophagy in *Cryptocercus*.

Xylophagy has many life-history correlates (Haack and Slansky 1987). A wood diet generally leads to a dearth of available nitrogen, even if xylophagous species have symbionts or endocellulases which digest cellulose (Cleveland *et al.* 1934, Scrivener *et al.* 1989). A nitrogen scarcity has been hypothesized to slow down development (Haack and Slansky 1987; Nalepa 1988, 1990), a prediction which seems to be verified in the two cockroach lineages under study: xylophagous taxa have very long development times while related but nonxylophagous taxa have shorter ones.

One could, however, argue that xylophagous taxa develop slowly, because they inhabit temperate regions. In a seasonal and cold environment, two life-history strategies could occur: a) maximizing the development rate within the favorable season or b) maximizing nutrient uptake within several seasonal cycles (Denno and Dingle 1981). It is then necessary to compare the three scenarios to see if long development was acquired together with xylophagy before a shift into temperate areas. The diversification in biome occupation was different in the two lineages. In (Zetoborinae + Blaberinae + Gyninae + Diplopterinae), the ancestor probably

inhabited the rainforest and several changes led to occupation of other biomes, except deserts. These changes did not involve many groups within the lineage. Polyphagines originally occupied the desert biomes, and the lineage is still prevalent there. Repeated changes occurred in one part of the lineage, leading to the successive conquest of both dry forests and rainforests, and then of temperate forests. The transition to temperate forests occurred in both lineages in the ancestors of extant xylophagous taxa. The phylogenetic pattern shows that in *Parasphaeria* slow development should be hypothesized to appear before a spread into temperate areas. A consideration of all the evolutionary scenarios does not allow one to fully resolve the question: in only one case a xylophagous taxon seems to have acquired slow development before it spread in a temperate biome. In the other case, the three evolutionary events appear simultaneously and the comparison of scenarios does not provide information.

Why do xylophagous species have such peculiar climatic distributions and sometimes inhabit temperate areas, especially when these areas are cold and humid? Slow development, if it preceded the occupation of temperate zones, could have provided a selective advantage against seasonality and coldness. Sexual maturity could be attained within several seasons. Conversely, with a short development maturity could be attained at the end of the first season, but adults may be unable to reproduce before the following unfavorable season. This hypothesis, however, presupposes that slow developing species are cold-resistant to pass through cold period, that this has been proved only in the species *Cryptocercus punctulatus* Scudder (Hamilton *et al.* 1985). Another possibility is the appearance of a diapause for adults, larvae, or eggs in rapidly developing species. But the prevalence of diapause occurrence is unknown in cockroaches, apart from the family Blattellidae (Brown 1980). A long development time in the present hypothetical context would appear to be an *exaptive* attribute (Gould and Vrba 1982), *i.e.*, it could have been selected in a nutritional context but have a selective value in a climatic context.

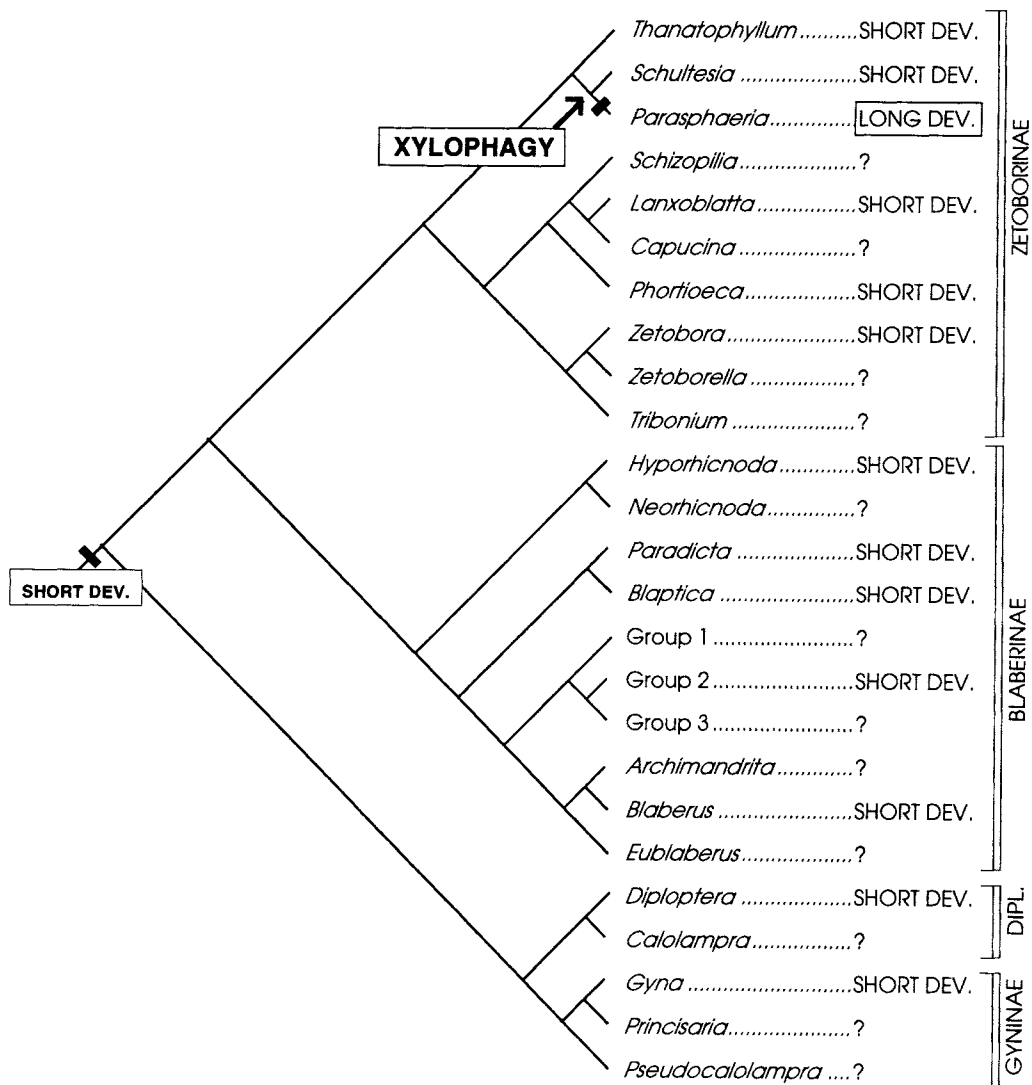


Fig. 3. Character optimization of short versus long development upon the phylogeny of subfamily (Zetoborinae + Blaberinae + Gyninae + Diplopterinae). A change of state is shown with a thick line. The ancestral state is inferred "short development".

This context does not explain why xylophagous species of both studied lineages are limited to especially humid areas. Wood quality is known to vary with its moisture content (Haack and Slansky 1987), and it should be tested in the future to see if these xylophagous cockroaches require wood with an especially high moisture content. Such a requirement could explain why xylophagous species are limited to very humid areas.

This study is only a preliminary work for clarifying the study of xylophagy in cockroaches. More data are needed to examine in detail the attributes and the evolutionary scenarios. More case studies are also necessary to test the hypotheses emerging from these scenarios. The study of xylophagy has until now suffered from the poor knowledge regarding the phylogeny of the involved xylophagous taxa and from *a priori* ideas concerning these taxa.

Three facts are very important in my opinion to enhance this study. Firstly, *a priori* ideas about evolutionary scenarios should be abandoned, especially those involving the concept of "primitive taxon". This concept is particularly misleading because it

leads to dependent and circular reasoning (Dawkins 1987) and has no place in phylogenetic studies (Nelson 1989). Secondly, evolutionary scenarios gain credence only with reference to a phylogeny: this allows one to study the polarity, number, and relative position of evolutionary events and to minimize *a priori* statements (Carpenter 1989, Coddington 1988, Deleporte 1988, Grandcolas 1991). Thirdly, workers should not focus solely on *Cryptocercus*; but they should try to consider other xylophagous taxa (e.g., Matsumoto 1987, 1988). They could consider, therefore, not only homology when using the phylogenetic reference but also analogy, when comparing several independent case studies: the comparison of several independent and then analogous scenarios is a way to test the generality of evolutionary hypotheses (Grandcolas 1991).

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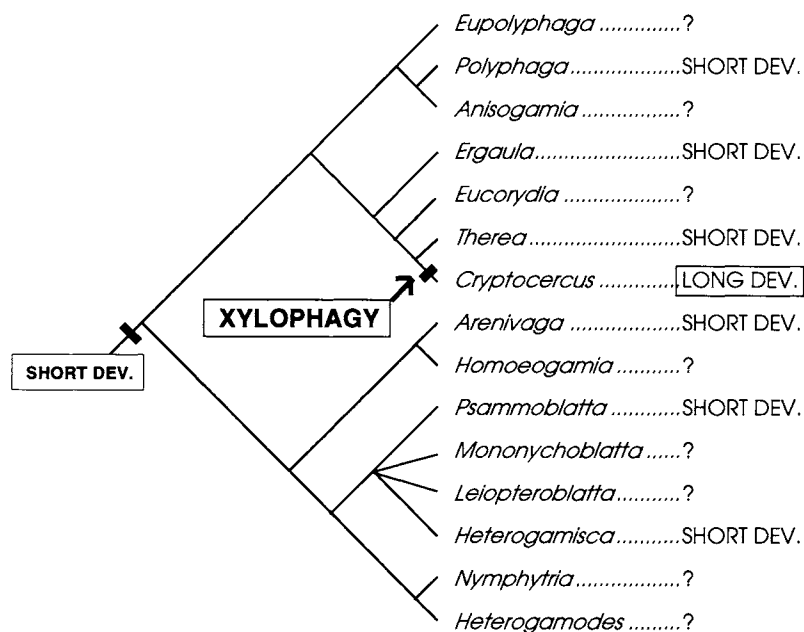


Fig. 4. Character optimization of short versus long development upon the phylogeny of subfamily Polyphaginae. A change of state is shown with a thick line. The ancestral state is inferred "short development".

comments on the phylogenetic studies on which is based the present study. Field work was made possible with Action spécifique de Museum de Paris and program SOFT of Ministère de l'environnement (French Guiana), the NWRC guest researcher program (Saudi Arabia), and IRET assistance (Gabon). I thank the curators of institutions which loan to me some specimens. The work has been supported by URA CNRS 373 in Laboratoire de Primatologie-Biologie évolutive and I have had access to the national insect collections in Paris Museum.

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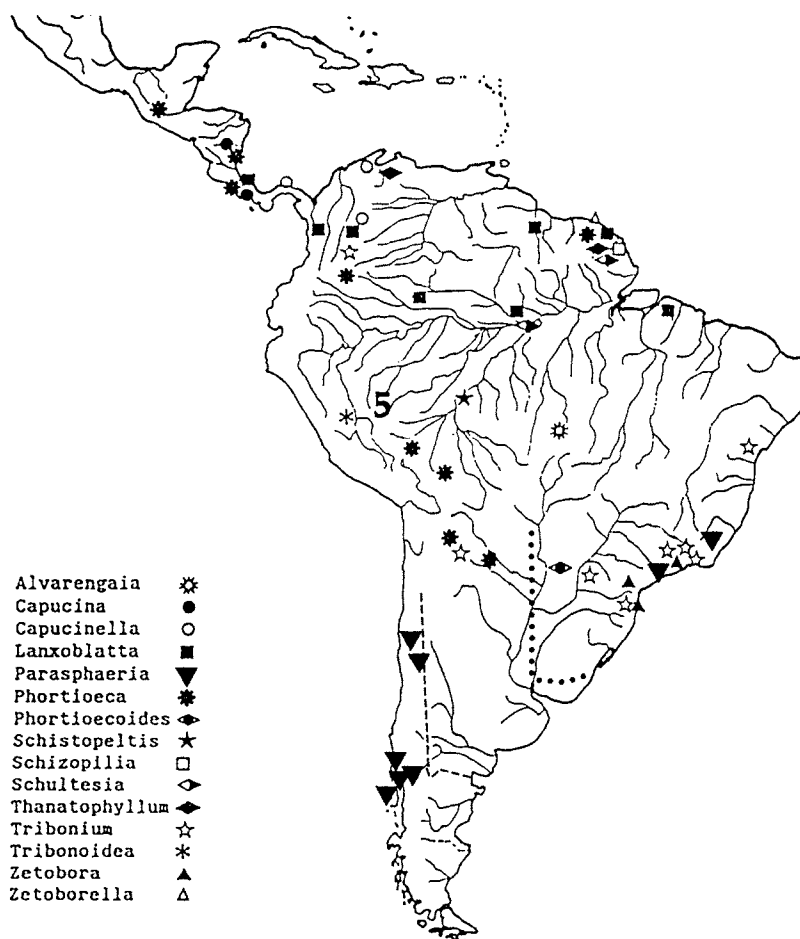


Fig. 5. Distribution map of the genera of the subfamily Zetoborinae in South and Central America. The isohyets which indicate respectively annual means of 10°C (dashed line) and 1200 mm (dotted line) are placed on the map.

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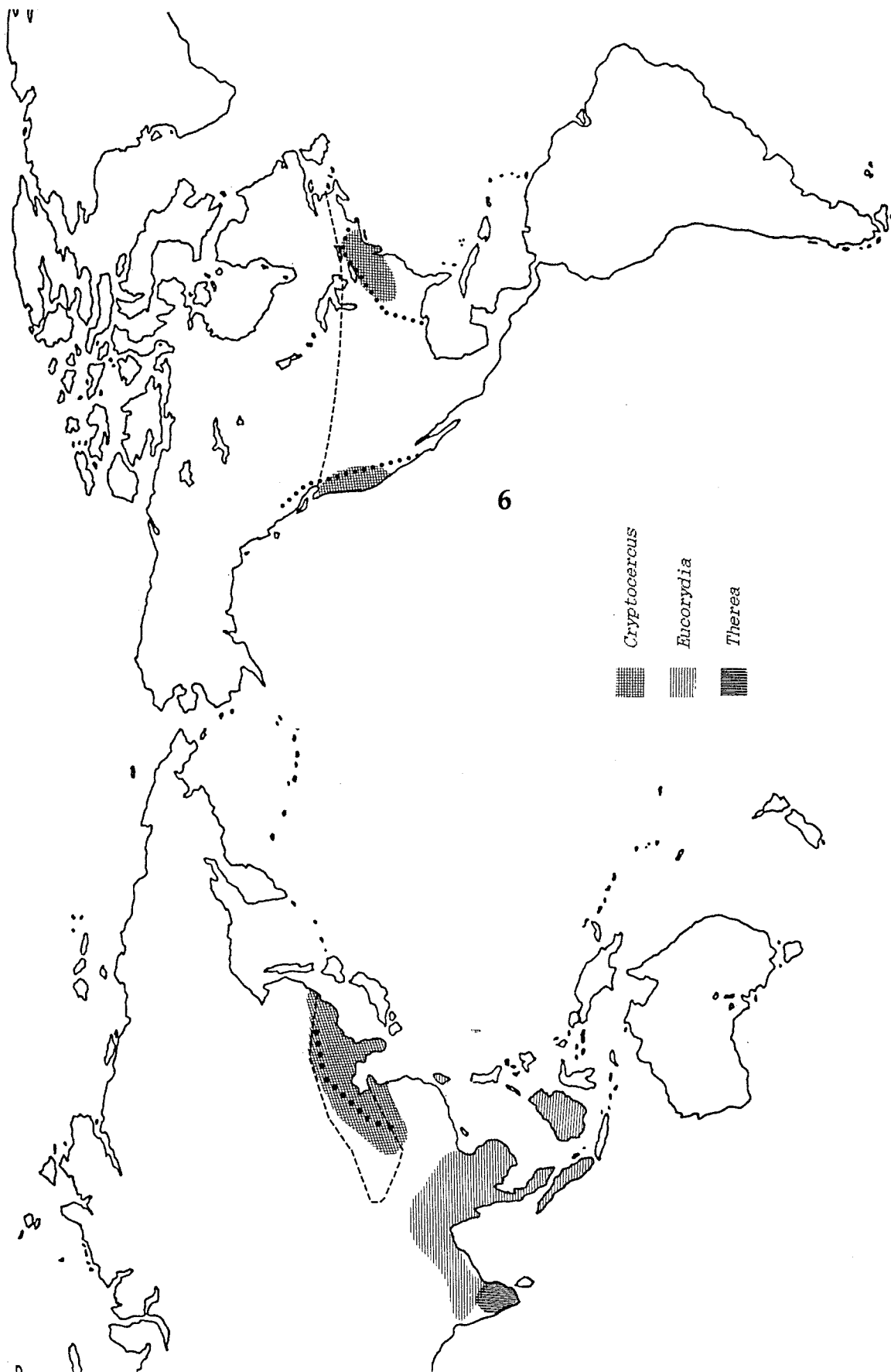


Fig. 6. Distribution of the genera *Cryptocercus*, *Eucorydia*, and *Therea* of the subfamily Polyphaginae in Southeast Asia and in North America. The isohyetes which indicate respectively annual means of 5°C (dashed line) and 1200 mm (dotted line) are placed on the map.