

Domestic and non-domestic cockroaches: facts versus received ideas

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SUMMARY

Cockroaches are very diverse but poorly known. Most of 4000 described species are not domestic and only occur in tropical regions. Cockroaches are not especially archaic, old, adaptable and unspecialised insects contrary to recurrent received ideas. All ubiquitous domestic species are small to medium-sized, oviparous, gregarious, nocturnal, resistant to water deprivation, they escape by running, and they shelter in confined spaces. These characteristics, probably in combination, can have permitted some cockroaches to remain domestic. The suppression of domestic cockroaches will come of age when the key-conditions relevant to cockroach survival are actually modified in human dwellings.

KEY-WORDS: Cockroaches. – Domestic. – Origin. – Control.

As for any group of living organisms, the general knowledge of cockroaches is a mosaic of old versus recent and reliable versus questionable information. The quality of this knowledge directly depends on the number of species that have been used to generalise the findings. It also depends on the way old and perhaps obsolete conceptions have been re-examined recently. This general knowledge of cockroaches is especially useful because a few species are very important to man being either ubiquitous domestic pests or laboratory model organisms. Thus, our ability to

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RÉSUMÉ

Blattes domestiques et sauvages: les faits face aux idées reçues. – Les blattes sont un groupe d'insectes à la fois très divers et très mal connu. La plupart des 4000 espèces décrites ne sont pas domestiques et peuplent uniquement les régions tropicales. Contrairement à une idée reçue très tenace, les blattes ne sont pas des insectes particulièrement archaïques, anciens, adaptables ou généralistes. Les espèces domestiques ubiquistes ont les caractéristiques suivantes; tailles petites à moyennes, ovipares, grégaires, nocturnes, résistantes au manque d'eau, capables de courir pour s'échapper, cherchant un abri dans des espaces confinés. Ces caractéristiques, probablement combinées, peuvent leur avoir permis de demeurer domestiques. En tous les cas, il n'y aura pas d'élimination durable et véritable des blattes domestiques tant que l'on n'aura pas agi sur de réels facteurs-clés de la survie des blattes dans les constructions humaines.

MOIS-CLÉS: Blattes. – Domestiques. – Origine. – Élimination.

control cockroaches as domestic pests or to interpret the scientific results obtained from cockroaches as laboratory model organisms mostly depends on a scientific background of knowledge which should be updated and examined repeatedly. This background is not so easy to bring up to date in the case of cockroaches. There are thousands of cockroach species, showing complex and diverse social and reproductive behaviours, distributed on all continents and in all biological regions. Most published studies deal with a few model species and the level of general knowledge

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is thus very low. Moreover, most observations in the field or most data on the general biology of feral species are ancient and anecdotal.

I present two examples which show how outdated notions could have detrimental consequences in both fields of pest control and scientific research. Then, I contrast domestic and feral cockroaches in the framework of the general knowledge. Finally, I emphasise on several received ideas which are recurrent in the scientific literature and should be rejected definitely.

OUTDATED NOTIONS AS PITFALLS IN THE KNOWLEDGE: TWO EXAMPLES

Sex pheromones and sex

A large body of evidence supported the idea that the reproduction of cockroaches is mostly mediated by sex pheromones emitted by one of the sexes only, most of time the females [3, 7, 22]. A well-known deviation to this rule was however found in the particular African subfamily Oxyhaloinae where only males produce sex pheromones [21, 25]. Domestic cockroaches do not belong to the subfamily Oxyhaloinae, except *Rhyparobia* (= *Leucophaea*) *maderae* and *Nauphoeta cinerea* (which in addition are not important ubiquitous pests). It was thus currently assumed that domestic cockroaches mate according to the following behavioural sequence: a female emits a sex pheromone active at long range – this pheromone attracts the male(s) which perform(s) courting behaviour and produces aphrodisiacs – the female takes the aphrodisiacs and the copulation *sensu stricto* is initiated by the male. This sequence is very useful to whom it may concern in the field of pest control. The general behaviour of a domestic species can be interpreted in this framework, helping to devise many appropriate control strategies. As a most obvious example, sex pheromones can be used as lures.

However, Abed *et al.* [1] have recently demonstrated that not only females but also males of *Blatta orientalis* emit sex pheromones. *Blatta orientalis* is a very well-known pest and laboratory animal whose mating behaviour was investigated several times [2, 22]. This new and recent finding not only revises the previous conceptions of *B. orientalis* behaviour but also the generalisation of knowledge of the mating behaviour in cockroaches. It should warn us about the possibility of other deviations to the generalised sequence of mating behaviour.

Social behaviour in cockroaches and in termites : analogy or homology?

Cockroaches, termites and mantids have long been recognized as closely related groups. Many cockroaches are gregarious or even subsocial (adults caring their larvae) while termites are all eusocial. For this reason, and because their morphology looks less specialised, cockroaches were often assumed to represent living ancestors of social termites [8]. A cockroach genus, *Cryptocercus*, was especially considered a living ancestor because it is xylophagous and harbours flagellate symbionts in his digestive track, like the so-called «lower termites» [6, 17]. These traditional conceptions have influenced famous writings about the evolution of social behaviour in termites [26].

Recently, both morphological and molecular phylogenetic studies [9, 11, 14] have shown that *Cryptocercus* was not a relict taxon dating back to the paleozoic roots of cockroaches and termites but a very modern one belonging to the family Polyphagidae, and having close relatives among other well-known modern genera. The characteristics of *Cryptocercus* were convergently acquired and its flagellates were captured and not inherited from a common ancestor with termites.

The new phylogenetic relationships of *Cryptocercus* bear important consequences for the understanding of termite evolution. In particular, it is no more possible to validate evolutionary models on the basis of a grade-like perspective progressing from the cockroach *Cryptocercus* to eusocial termites [14].

Both these examples demonstrate that well-known and general conceptions present in scientific literature are not always reliable. Cockroaches are diverse and poorly known. We urge researchers working in the field of medicine or applied entomology to consider that any general notion concerning cockroaches which is basic to their research should be carefully checked. It should be made clear that the more current a general opinion, the more questionable.

CONTRASTING DOMESTIC AND FERAL COCKROACHES IN THE FRAMEWORK OF PHYLOGENETICS

There are about 4000 described species of cockroaches [18]. No more than ten cockroach species can be considered as important pests, and only four species, namely *Blattella germanica*, *Supella longipalpa*, *Periplaneta americana* and *Blatta*

orientalis are actually ubiquitous and present in any human setting [7, 8, 12, 24]. A phylogenetic tree analysing the relationships between cockroach families has been recently proposed [11] and is presently used as a basis for understanding where domestic cockroaches take place, what is their possible origin, how they can be characterised relative to feral species. This tree shows that cockroaches become domestic by convergence in different and not closely related groups (fig. 1). Domestic species are found in four among six large extent families and the four ubiquitous domestic species belong to three different families.

A list of characteristics which maximally contrast domestic versus feral cockroaches has been implemented (table I). Domestic cockroaches are less diverse in most characteristics when they are compared to all other cockroaches. It can be hypothesized that the characteristics lacking in domestic cockroaches permitted them to become pests, and conversely, that their presence in other cockroaches prevented these latter ones to become pests. No characteristics are however totally exclusive either of domestic or of feral cockroaches. For example, all ubiquitous pests are oviparous but there are also many feral oviparous species. For this reason, we must consider that

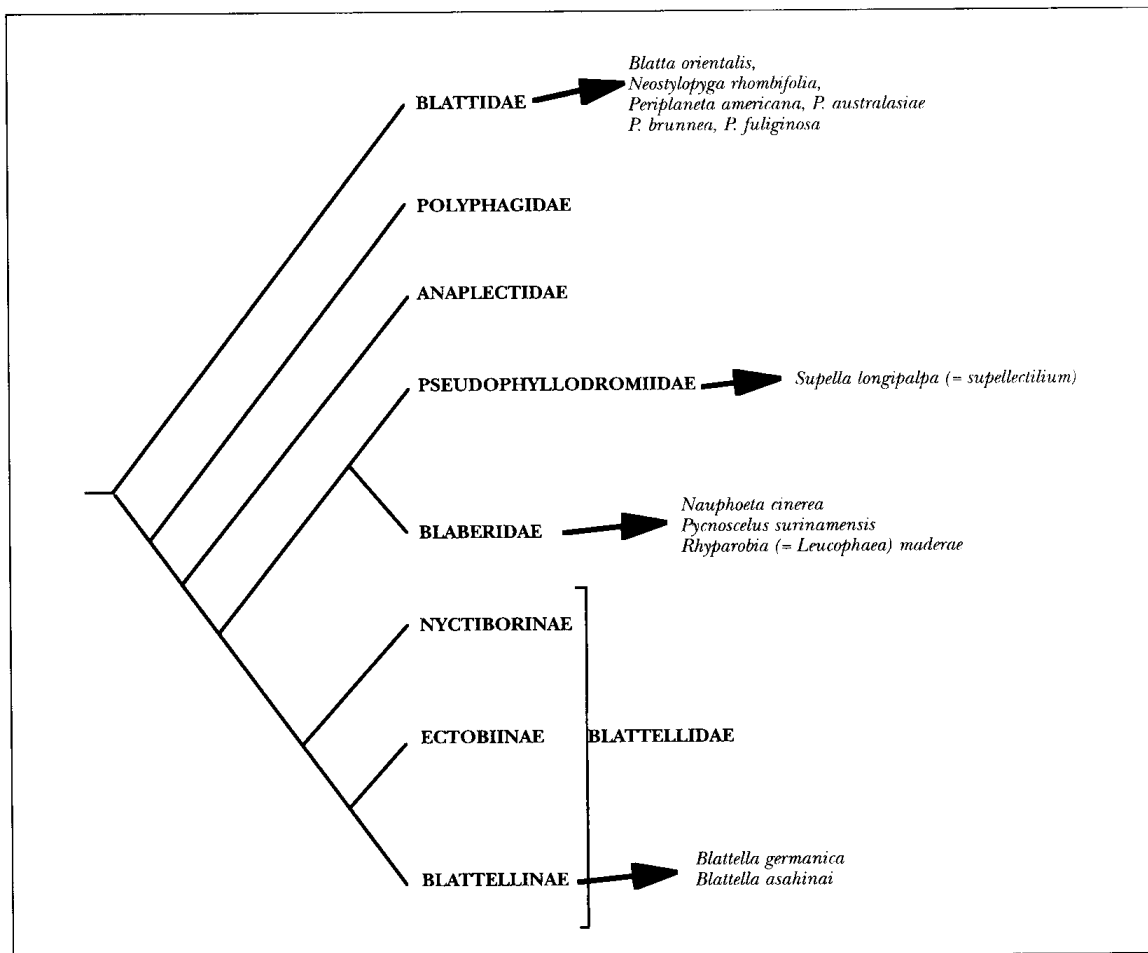


Fig. 1. - Phylogenetic position of 12 domestic species according to the free of Grandcolas (1996) [11].

TABLE I. – Contrasted characteristics of ubiquitous domestic (*Blatta orientalis*, *Blattella germanica*, *Periplaneta spp.*, *Supella longipalpa*) versus other cockroaches (partly taken from Grandcolas [12]). Information additional to a characteristic is provided between brackets. Water deprivation is characterised for oothecae, larvae and adults altogether.

<i>Characteristic</i>	<i>Domestic</i>	<i>Feral</i>
Size (range)	small to medium (1-6 cm)	very small to giant (0.4-14 cm)
Reproduction mode	oviparous (ovoviviparous)	ovi-, ovovivi-, viviparous
Fecundity	high	low to high
Development duration	short to medium (1-12 months)	short to long (1-84 months)
Circadian rhythm	nocturnal	nocturnal/diurnal
Social behaviour	gregarious	solitary/gregarious/subsocial
Habitat preference	confined space	confined/open space
Moving	running	running/walking
Escape behaviour (behavioural releaser)	running (air puff)	running (air puff) flying (air puff) freezing (vibration/contact) burrowing (vibration/contact)
Water deprivation	resistant	sensitive resistant

only a combination of several characteristics has permitted some cockroaches to become ubiquitous pests.

Some likely ad hoc explanations can be proposed to account for these differences. Too large species could have too special requirements for food consumption or thermoregulation to fit human environment. In the same way, species which take too long a time to develop would be disadvantaged for colonisation of a domestic environment. Both characteristics could be connected (the larger the species, the longer the development). A higher fecundity can be beneficial for colonisation (all other things being equal, e.g., larvae and adult survival). Social behaviour and habitat preference can be considered together: human environment is highly patchy and favourable niches are limited so that being gregarious in a confined (i.e. hidden, protected) place is probably the safest strategy. In the same way, being nocturnal and running after disturbance may permit to better escape human predators. Finally, the human environment is most often very dry by comparison with a natural environment: to resist successfully to water deprivation is thus highly advantageous.

It should be reminded that contrasting domestic and feral cockroaches can explain why some cockroaches remain domestic but it does not necessarily explain how and why they historically

became domestic. Recent cases of colonisation at a large scale (e.g., *Supella longipalpa* and *Blattella asahinai* in North America) do not provide us with many indications in this respect [4, 8]. Two important facts are however patent: large scale dispersal is mainly man-mediated and small scale dispersal is related to the species survival ability in the human environment. Two rules can be derived from these indications: the human large scale-transport facilities fit domestic species and the micro-environmental conditions of the human environment fit them too.

THE MOST COMMON RECEIVED IDEAS

Probably the most recurrent attributes of cockroaches in the mind of both scientists and lay people are antiquity, resistance and adaptability, according to the words of Garfield [10]: «The cockroach [...] ancient, seemingly indestructible pest».

Antiquity

The question of their antiquity can be addressed at two levels, respectively biological and human. From the point of view of the biological

age, the most traditional estimations date back to the paleozoic period [8]. Many old fossil remains (mostly wings and thorax fragments) were identified as belonging to fossil cockroaches. Some strange cockroaches with ovipositors were also described from the paleozoic era (reviewed by Roth) [20]. According to this fossil record, cockroaches were thus considered to be very ancient and to have evolved from paleozoic egg-laying with an ovipositor to producing ootheca and to becoming ovoviviparous in more recent periods [19, 20]. However, these paleozoic fossils are very poorly authenticated. Indeed, the only character which is obvious in these fossils – the ovipositor – is inconsistent with an hypothesis of relationship with Dictyoptera and Isoptera, all groups having reduced ovipositors [11, 15]. At the very least, cockroaches with ovipositors are not clear and unambiguous fossil cockroaches. Other small fossil remains cannot be identified reliably. Consequently, cockroaches cannot be dated back to the paleozoic period with reasonable confidence but only to the mesozoic period, just like most insect orders.

From the point of view of their relationship with mankind, antique writings already cited cockroaches as pests [16]. Cockroaches seem therefore to be associated with man since a long time. However, it is not possible to validate the assumption of Chopard [5] who hypothesized that the origin of domestic cockroaches occurred in prehistoric caves. No prehistoric records are known for domestic cockroaches, even if there are many prehistoric drawings of epigeal insects and cave insects.

Resistance and adaptability

The resistance and adaptability of domestic cockroaches to adverse conditions have been exaggerated. Their biological characteristics stand within the range of general cockroach characteristics (table 1). The potential for variation in life habits, in life history and in physiology which can be recorded for domestic cockroaches in classical textbooks is not much higher than for some feral cockroaches [8, 23]. In fact, man provides cockroaches with so ideal life conditions and he transports them so efficiently that they are forced to develop and establish. From the beginning, domestic cockroaches are small, nocturnal, rapid, gregarious, prolific and resistant to water deprivation. This is very sufficient to explain their success in a favourable human environment. In this perspective, they appear preadapted to the life in human environment. If some populations evolved

resistance to a few pesticides, this remains comparable to many other insect species which evolved when they faced adverse conditions. This is not evidence for an especially high adaptability. The real invading ability of cockroaches is very low, as shown for example for the peridomestic *Pycnoscelus surinamensis* [13]. Cockroaches are not necessarily able to move by themselves far from their colony and to invade a new territory. Most of time, they are transported. We are simply reluctant to acknowledge that we provide cockroaches with so ideal conditions that they have simply not to adapt in most cases [12].

WHY IS THIS SO DIFFICULT TO SUPPRESS COCKROACHES ?

One could wonder why cockroaches are so difficult to eliminate if they are not really adaptable. Actually, we have not changed the key-conditions which are favourable to cockroaches in our environment. There is a good and recent example of such an efficient but fortuitous change. *Blatta orientalis* was a very common domestic cockroach in European flats and houses until the last decades. Then, its prevalence decreased because of the introduction of central heating in these places, as experienced lately by the United Kingdom according to Cornwell [8]. Slightly modifying the temperature of dwellings has been very efficient to strongly repel this species. The effect on *Blattella germanica*, a species requiring hotter places (among many other differences), was just the opposite. We can use pesticides, traps and any other means to kill cockroaches. However, because they are small and hard to eliminate totally, because we import them from place to place anyway, and because they are prolific, they can develop colonies again and again [12]. To really improve the situation, we must find in human dwellings the particular parameter which is very relevant to domestic cockroaches survival and we must modify it.

In conclusion, cockroaches are paradoxical from the point of view of the knowledge. Most people believe that they are well-known, ancient, highly adaptable and that they are all very similar. Actually, they are poorly known, modern, not especially adaptable and very diverse. As for any living group, we need to know more about their diversity. This knowledge would undoubtedly help us to improve the control of domestic cockroaches and it would also teach us invaluable facts about evolutionary trends.

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