

ORIGINAL ARTICLE

Phylogenetic analysis of social behavior evolution in [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] cockroaches: an update with the study of endemic radiations from the Atlantic forest

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Abstract

We updated the phylogenetic analysis of the evolution of habitat choice and social habits in the cockroach group of [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] (Dictyoptera: Blaberidae) elaborated by Grandcolas (1998b). The original phylogenetic matrix was updated with new data obtained in the Brazilian Atlantic forest for the genera *Parasphaeria* and *Zetobora* (Zetoborinae), *Monastria*, *Petasodes* (Blaberinae) and *Pycnoscelus* (Pycnoscelinae) (one outgroup). These new data did not change the tree topology but showed that the fauna of the Atlantic forest has a complex evolutionary origin with several different radiations, one of which is local, and behavioral convergences or originalities.

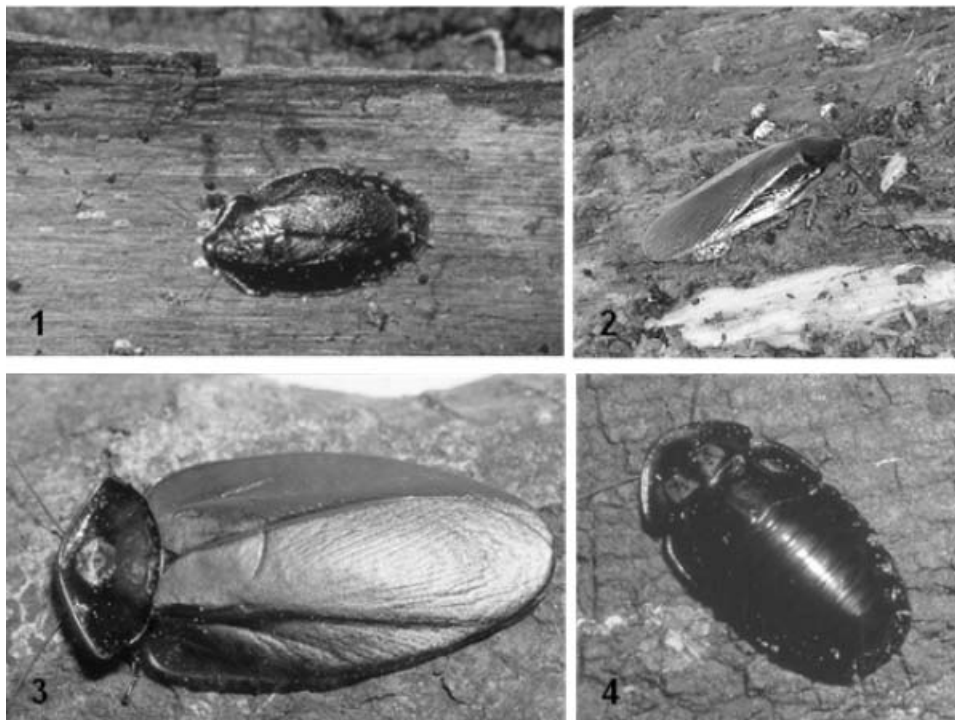
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Introduction

The evolution of social behavior and habitat choice in cockroaches has been studied very rarely in the field, except for domestic species (Schal et al., 1984; Grandcolas, 1998a; Roth, 2003). A particular mention can, however, be made concerning the large cockroaches belonging to the Neotropical groups, the subfamilies Blaberinae and Zetoborinae which comprise the well-known genera *Blaberus* Serville, 1831 or *Eublaberus* Hebard, 1920. These groups have been studied from a phylogenetic and comparative perspective (Grandcolas, 1993a, 1997a, 1998b) because they were the only ones for which previously existed a number of field and laboratory studies that provided a beginning and an impetus for further and wider comparative researches (e.g. Roth & Willis, 1960; Schal et al., 1984; Wendelken & Barth, 1987; Gautier et al., 1988).

Subsequently, a phylogenetic hypothesis based on morphology has been proposed for the Neotropical subfamilies Blaberinae and Zetoborinae, and the

Paleotropical subfamilies Gyninae and Diplopterinae (Grandcolas, 1993a). This morphological hypothesis has been partly tested and validated by recent molecular studies (Pellens et al., 2006). A series of behavioral field studies carried out both in French Guiana and in Africa brought new data about the natural history of these groups (Grandcolas, 1993b, 1994, 1995, 1997b; Van Baaren et al., 2002a). With respect to both the new behavioral data collected and the phylogenetic trees inferred, some general hypotheses of evolution were derived for these subfamilies (Grandcolas, 1993c, 1997a, 1998b). Some recent works have also been done independently, such as the discovery of luminescence in the genus *Hormetica* Burmeister, 1838, which led to the description of the new genus *Lucihormetica* Zompro & Fritzsche, 1999 and the study of its life habits (Zompro & Fritzsche, 1999; Fritzsche, 2003). Later, more detailed behavioral studies have been performed in the laboratory to assess the differences among gregarious and solitary species (Van Baaren & Deleporte, 2001, 2003; Van



Figures 1–4. (1) *Zetobora* sp., adult female. (2) *Parasphaeria boleiriana*, adult male. (3) *Petasodes dominicana*, adult male. (4) *Monastria biguttata*, adult female. All specimens in the field from Atlantic forest in Espirito Santo, Brazil.

Baaren et al., 2002b, 2003). Regarding the Neotropical subfamilies, all these studies focused on Amazonian taxa, because the behavior of several taxa was poorly known or even completely unknown outside this region.

Recently, the first author conducted a general study to describe the systematics and the ecology of cockroach communities in the Brazilian Atlantic forest and she observed subsequently the behavior of several species belonging to the subfamilies Zetoborinae and Blaberinae. These observations involved the finding of new social behaviors and habitats for species of these groups, including rare and interesting wood-eating habits and subsocial behavior (Pellens & Grandcolas, 2002, 2003; Pellens et al., 2002; Grandcolas & Pellens, 2006). The present paper deals with the re-examination and the update of previous studies of social behavior evolution with reference to the phylogeny in the light of these new findings. Such an update is possible with comparative phylogenetic studies, since they are opened to addition of new data and to successive revisions with regard to the evolution of knowledge (McLennan, 1993; Grandcolas et al., 2001; Brooks & McLennan, 2002).

Materials and methods

Both the matrix including the outgroups and the phylogenetic tree of [Zetoborinae + Blaberinae +

Gyninae + Diplopterinae] were taken from Grandcolas (1993b). Two kinds of natural history data were considered: habitat and social habits (Grandcolas, 1993c, 1998b). They were updated for the genera *Zetobora* Burmeister, 1838 and *Parasphaeria* Brunner von Wattenwyl, 1865 of the subfamily Zetoborinae (Figures 1, 2), *Petasodes* Saussure, 1864 and *Monastria* Saussure, 1864 of the family Blaberinae (Figures 3, 4), and *Pycnoscelus* Scudder, 1862 of the family Pycnoscelinae (out-group), according to the following publications (Pellens, 2002; Pellens & Grandcolas, 2002, 2003; Pellens et al., 2002; Fritzsche, 2003; Grandcolas & Pellens, 2006).

Phylogenetic analysis was first performed with morphological characters. In a second step, behavioral data (habitat choice and social habits) were added to morphological characters. Parsimony analyses (RAS + TBR) and optimizations of the behavioral traits were performed with the software Nona 2.0 and WinClada 1.00.08 (Goloboff, 1999; Nixon, 1999–2002). The tree was rooted with the genus *Panesthia* Serville, 1831 (subfamily Panesthiinae). To test the monophyly, several taxa not belonging to the ingroup were also included, namely *Pycnoscelus* Scudder, 1862 (subfamily Pycnoscelinae), *Ateloblatta* Saussure, 1891 and *Oxyhaloa* Brunner von Wattenwyl, 1865 (subfamily Oxyhaloinae), *Derocalymma* Burmeister, 1838 (subfamily Perisphaeriinae), *Epilampra* Burmeister,

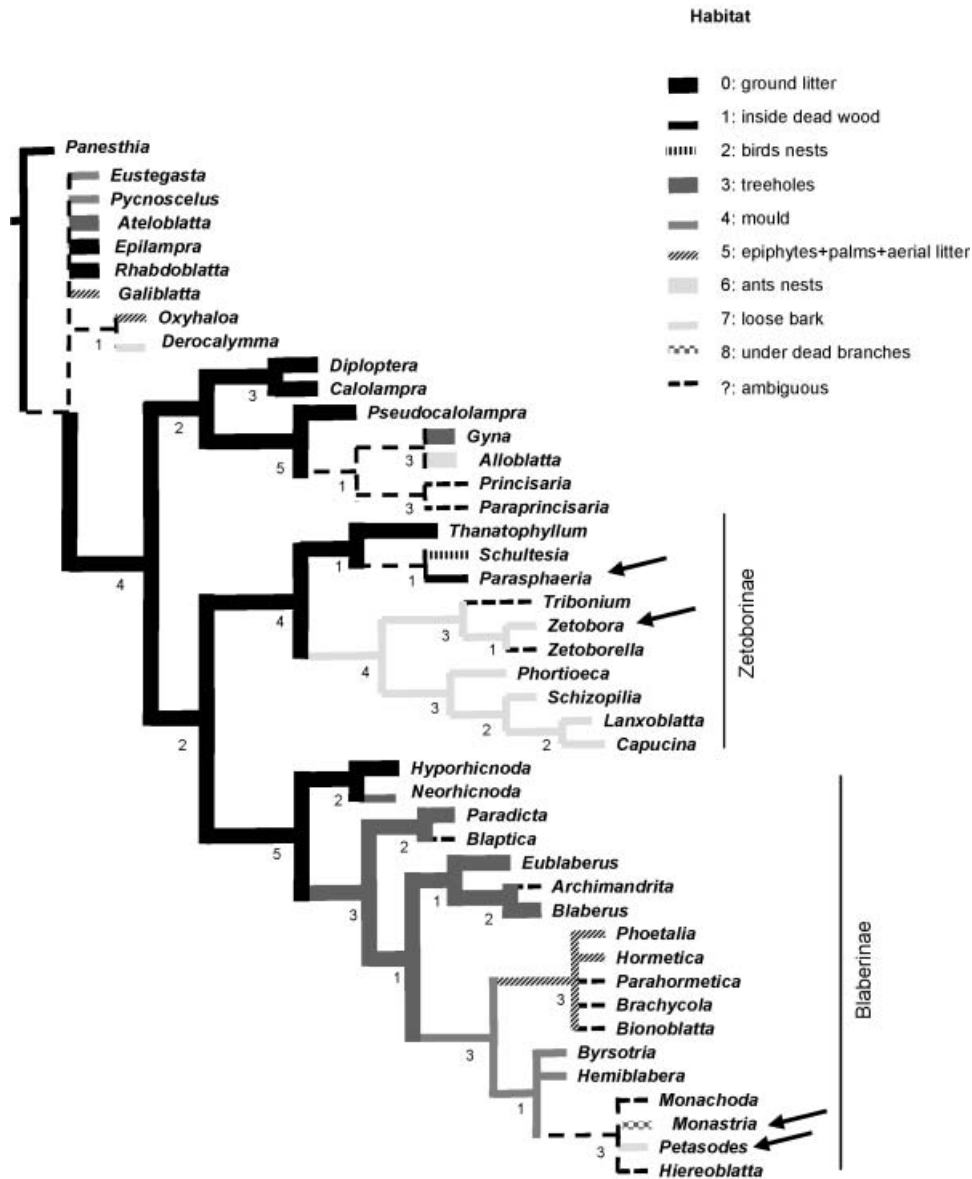


Figure 5. Phylogenetic tree of the group of four subfamilies [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] with the optimization of habitat choice. This topology is a strict consensus of 100 equally parsimonious trees (length=112; CI=0.78; RI=0.94) obtained after the analysis of a matrix of 44 taxa and 80 characters with the software WinClada and Nona (multiple TBR, 100 replications). Bremer branch supports (steps) is given below the branches. Habitat choice (nine character states) included in the analysis is mapped on the tree (unambiguous changes only, 15 steps). Arrows indicate new observations in taxa from the Brazilian Atlantic forest.

1838, *Galiblatta* Hebard, 1926 and *Rhabdoblatta* Kirby, 1903 (subfamily Epilamprinae), *Eustegasta* Gerstaecker, 1883 (*incertae sedis* within the Family Blaberidae). The resulting unambiguous phylogenetic patterns (resulting from the combination of *ACCTRAN* and *DELTRAN* optimizations) are detailed and discussed for each trait.

Results

The analysis of the original matrix of 78 morphological characters resulted in one most parsimonious

tree with several large polytomies within the outgroups and in some parts of the subfamily Blaberinae, retrieving the tree (length=88; CI=0.88; RI=0.97) illustrated in Grandcolas (1993a, 1998b). When the behavioral characters “habitat choice” and “social habits” were added to the matrix, therefore making a total of 80 characters, 100 equally parsimonious trees were obtained and the strict consensus is shown in Figures 5 and 6 (length=112; CI=0.78; RI=0.94). The topology of the tree remained the same.

The phylogenetic tree obtained with the reconstruction of the evolution of habitat choice is

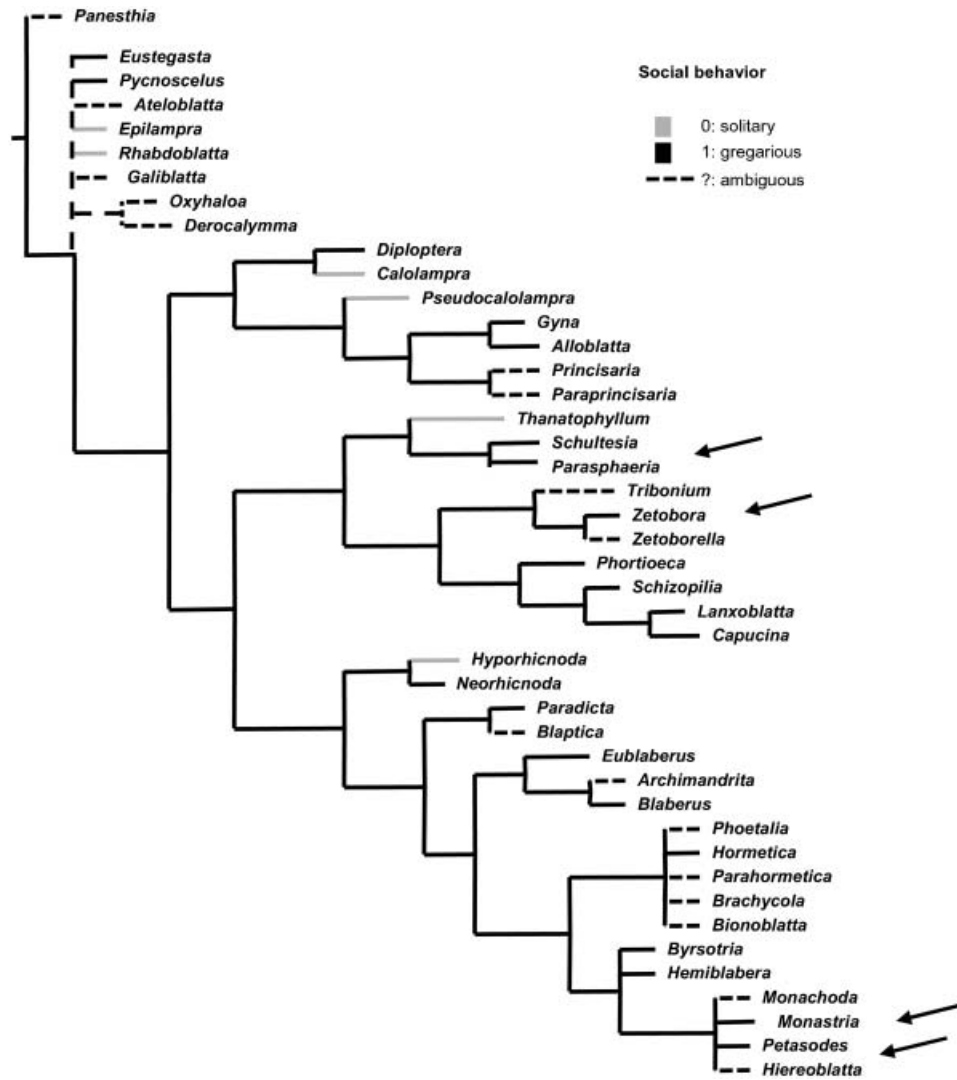


Figure 6. Phylogenetic tree of the group of four subfamilies [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] with the optimization of social behavior. This topology is a strict consensus of 100 equally parsimonious trees (length=112; CI=0.78; RI=0.94) obtained after the analysis of a matrix of 44 taxa and 80 characters with the software WinClada and Nona (multiple TBR, 100 replications). Social behavior (two character states) included in the analysis is mapped on the tree (unambiguous changes only, six steps). Arrows indicate new observations in taxa from the Brazilian Atlantic forest.

presented in Figure 5. As a whole, it did not change with respect to the previous ones (Grandcolas, 1993b, 1998b). Nine different habitats were found and the shortest pattern for this character has 15 steps, therefore showing a much higher amount of homoplasy than most morphological characters (CI=0.53). New data allowed documentation of several different evolutionary events that were unknown or poorly documented until now. The first was the addition of one more taxon in a radiation linked with a particular habitat. Two species of the genus *Zetobora* (Figure 1) are now known with details for living under loose bark (Pellens, 2002) as do related species from the genera *Capucina* Saussure, 1893, *Lanxoblatta* Hebard, 1931, *Phortioeca* Saussure, 1862 and *Schizopilia* Saussure,

1864 from other Neotropical regions. A second situation is represented by two cases of addition of new habitats to the list of habitats within the clade. The first case concerns *Parasphaeria boleiriana* Grandcolas & Pellens, 2002 (Figure 2) whose individuals live inside of and feed on dead wood (Grandcolas & Pellens, 2002; Pellens et al., 2002). The second case is *Monastria biguttata* (Thunberg, 1826) (Figure 4) which lives on the bark or wood on the underside of dead trunks and branches (Pellens & Grandcolas, 2003). Similarly to wood-feeding, this habitat choice had not been registered before to the clade and was not yet known in South America. A third evolutionary event inferred by these analyses is a convergence to the habitat “under loose bark”, between the subfamily Zetoborinae (the radiation

mentioned just before) and the subfamily Blaberinae with the genus *Petasodes*. This genus has a flattened shape with lateral pronotal, tergal and alar expansions. It was studied in the Atlantic forest with the species *P. dominicana* (Burmeister, 1838) (Figure 3) which was found only beneath loose bark of dead and living trees. According to the phylogenetic tree, this genus evolved toward this habitat convergently with Zetoborinae.

The phylogenetic tree with the reconstruction of the evolution of social behavior is presented in Figure 6. Two different social habits were found, respectively solitary and gregarious behavior, as already documented in Grandcolas (1998b). Subsocial behavior (i.e. brood care by parents) could be superimposed on this analysis but it has been poorly studied, being only clearly documented in *Byrsotria fumigata* Guérin-Méneville, 1837 (Liechti & Bell, 1975), *Parasphaeria boleiriana* (Pellens et al., 2002) and *Monastria biguttata* (Pellens & Grandcolas, 2003). Such an optimization would lead to three independent origins of subsociality (three autapomorphies). Mapping this character with two states (solitary and gregarious) on the tree resulted in a pattern of six steps (CI=0.16) with four reversals toward solitary habits in the ingroup, as already found in Grandcolas (1998b). New data brought by the present study only resulted in nesting more gregarious species within parts of the clade where species are all gregarious. The resulting tree excludes any solitary species from the Atlantic forest where only gregarious ones are known. So far, solitary species of these subfamilies have been observed only in Amazonia and in Central America.

Discussion

Bringing new natural history data from the Brazilian Atlantic forest has allowed the reconstitution of behavioral evolution in the clade [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] to be updated. As a whole, the patterns have remained similar and only additional apical character changes have been documented. This justifies retrospectively that comparative studies can be carried out with reasonable taxon and character samples, resulting in robust phylogenetic evolutionary reconstructions that will not become necessarily outdated, but simply more accurate when more data are available (Brooks & McLennan, 2002).

From the evolutionary point of view, the two behavioral characters studied—habitat choice and social behavior—appeared quite homoplasious and that did not substantiate the optimistic empirical claims that behavior has usually standard levels of homoplasy when compared with morphology or molecules (de Queiroz & Wimberger, 1993). This

does not mean that these more-than-usual homoplasious characters become misleading regarding phylogenetic reconstruction, as argued by de Queiroz (1996). Actually, these characters can be informative at some levels and convergent at others, therefore providing useful information for phylogenetic reconstruction (Eldredge & Cracraft, 1980; Grandcolas et al., 2001). This is exemplified by some new large-level convergences detected in the present phylogenetic update. Habitat choice both supported the monophyly of a group of Zetoborinae cockroaches living under loose bark (Figure 1) and provided an autapomorphy for the Blaberinae genus *Petasodes* (Figure 3). Conversely, a lack of convergence concerning living in ground litter is not necessarily informative since it is relatively plesiomorphic for most taxa and groups within the clade under study. We must especially consider that the amount of homoplasy or congruence among morphology, molecules and behavior is not a criterion for estimating the validity of a phylogenetic reconstruction. Homoplasy is not necessarily noise (Källersjö et al., 1999; Wenzel & Siddall, 1999), and incongruence among arbitrarily separated data sets does not necessarily indicate different evolutionary signals but differently nested homoplasies (Grant & Kluge, 2003). The only true scientific criterion is the stability of the phylogenetic reconstruction and the derived evolutionary patterns for some characters facing addition of data (taxa and characters).

The new behavioral data gathered and used therein allowed some of the evolutionary characteristics of the cockroach fauna from the Atlantic forest to be figured out. We documented that the fauna had several different evolutionary components, namely parts of Neotropical behavioral radiations (loose bark Zetoborinae), behavioral autapomorphies (e.g. Blaberinae living under branches), and behavioral convergences with other related Neotropical groups (e.g. loose bark Blaberinae). From this point of view, the subfamily Blaberinae would be especially worthwhile studying in the future with a local diversification involving the genera *Hiereoblatta* Rehn, 1937, *Monastria* Saussure, 1864, *Monachoda* Burmeister, 1838 and *Petasodes* Saussure, 1864. It must be noted that the genus *Monachoda*, which has a similar morphology to *Petasodes*, in the future could be found in a similar habitat (under loose bark), but probably in the upper layers of the forest canopy, as suggested by past captures by light traps. The case of wood-feeding and living inside dead trunks of *Parasphaeria* Brunner von Wattenwyl, 1865 is more particular since this genus has a southern and both temperate and tropical distribution by vicariance with the Amazonian *Schultesia* Roth, 1973. This later genus,

which lives only in *Cacicus* pendulous nests (Grandcolas, 1993c; Van Baaren et al., 2002a), has been searched for unsuccessfully in Espirito Santo, which corroborates its absence according to previous studies of the Brazilian fauna (Grandcolas & Pellens, 2006). Finally, the discovery of luminescence in a species previously classified in the genus *Hormetica* and presently in the genus *Lucihormetica* (subfamily Blaberinae) also opened interesting avenues for behavioral and evolutionary studies (Zompro & Fritzsche, 1999; Fritzsche, 2003).

As ever, the Atlantic forest appeared not only as a biogeographical crossroad (Oliveira-Filho & Fontes, 2000) but also as a center of diversification which accumulated biodiversity by different evolutionary events, geographical vicariance either with behavioral inertia or with behavioral evolutionary convergence. The relationships between habitat and social behavior have been amply analyzed by Grandcolas (1998b) and remained unchanged according to the present analysis: reversals toward a solitary way of life occurred with an ancestral habitat, the ground litter, which could be part of an anti-predator strategy in the particular context of mass predation by Army ants (Grandcolas & Deleporte, 1994).

In conclusion, this study reaffirms the interest of behavioral comparative studies based on phylogenetic analysis. They allow general evolutionary conclusions to be made which draw attention to critical results, here with respect to the Brazilian Atlantic forest. They also indicate which areas (taxa or characters) are particularly in need of study. By their capacity of being updated, they are also truly scientific, allowing hypotheses to be re-evaluated in the light of additional data. In this respect, the present study shows that the update does not invalidate previous conclusions but brings more details to our knowledge.

As Greene (2005) repeatedly and justly argued, it also suggests that systematists and ecologists should give more attention to natural history data, even if they look modest or isolated, for they can contribute to building these general comparative pictures.

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