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1 Editorial overview: Social insects

2 **Beyond eusocial insects: Studying the *other* social insects to better understand**
3 **social evolution.**

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9 **Fascinating social insects**

10 When one thinks about social insects, the first reaction is generally to acknowledge the
11 fascinating eusocial organization present in bees, ants, termites and wasps. This
12 fascination generally comes from their complex societies in which up to several
13 thousands of workers cooperate to build sophisticated nest architecture, to find large
14 and distant food sources, as well as to defend each other against predators and
15 pathogens [1]. Moreover, these societies often rely on a unique system of division of
16 labor, in which very few individuals have access to reproduction (queens and kings),
17 whereas the vast majority of colony members is specialized in non-reproductive tasks
18 such as nursing, nest defense and foraging [1]. These fascinating social properties
19 have driven the interests of biologists for centuries and generated results of
20 fundamental importance in different fields of biology. For instance, they shed light on
21 the genetic and epigenetic parameters shaping extreme forms of altruism, on the
22 resolution of social conflicts that are inherent to group living, on the evolution of
23 sophisticated communication systems and on the emergence of collective defenses
24 against parasites and pathogens.

25 However, eusociality is but one form of social life in insects (it is present in only
26 2% of insect species [2]). For instance, caterpillars of many Lepidoptera species exhibit
27 a social life, in which dozens of individuals gather and use sophisticated
28 communication systems to express collective foraging activities and defenses against
29 predators [3]. Similarly, temporary family life is another, non-eusocial form of social life
30 [4] in which parents and juveniles exhibit frequent and tight social interactions reflecting
31 forms of cooperation (e.g. parental care), as well as competition and conflict (e.g.
32 sibling rivalry and sexual conflicts). This family life occurs, for instance, in earwigs and
33 burying beetles [3]. Even in bees and wasps, eusociality is but one type of social

34 system. The vast majority of bee and wasp species are indeed solitary, whereas the
35 rest exhibit social systems ranging from communal to semisocial [5,6]. Somewhat
36 surprisingly, other findings also question the omnipresence of eusociality in ants. In
37 colonies of the clonal raider ant *Cerapachys biroi*, for instance, there is no reproductive
38 caste and all “workers” reproduce simultaneously and show communal breeding [7].
39 This lack of a reproductive division of labor does not fit with the definition(s) of
40 eusociality [8] and underlines that unexpected fundamental variation in social systems
41 can occur even within well-known biological social models such as ants.

42 **The historical neglect of the *other* social insects**

43 While insects encompass one of the greatest diversities of social systems across
44 animal taxa [3], the term “social insects” has long been used – and is still used - as a
45 synonymous for “eusocial insects” in the literature. This misleading and erroneous
46 synonymy is a major issue, because it suggests that the ‘other’, non-eusocial insect
47 societies are not social and are thus not pertinent to improve our general
48 understanding of social evolution. However, only focusing on eusocial species to study
49 social evolution also comes with major limitations. Eusocial species indeed exhibit
50 highly derived and peculiar social traits (e.g. colony members have lost their capability
51 to live alone and have evolved secondary traits to cope with their obligatory and
52 permanent social life), which could make them of limited relevance to address
53 fundamental questions such as why and how social life i) has originally emerged from
54 a solitary state, ii) is maintained in a primitive form and/or evolve into different social
55 systems, as well as why and how social life iii) can be lost and/or exhibit variable levels
56 of complexity between sister species.

57 In 2006, a book written by James Costa and entitled “The other insect societies”
58 [3] provided a first remarkable overview of the *other* social insects. Based on a
59 comprehensive survey of the literature, this seminal book shed light on the broad
60 diversity of forms of group living and social organization present across insects, as well
61 as compiled the - sometimes very limited, sometimes relatively abundant - works
62 conducted in these species. The main conclusion of this book was that the *other* social
63 insects open scope for novel and promising research in social evolution (and in many
64 aspects of social life), which thus call for more studies on these species. Twelve years
65 later, did we follow the recommendation of this book? Are the *other* social insects still
66 neglected compared to eusocial species? Did studies on the *other* social insects
67 provide novel and important insights into our general understanding of social life and
68 its evolution?

69 **Recent advances in our understanding of social insects**

70 The main goal of this issue of *Current Opinion in Insect Science* is to provide an up-to-
71 date appraisal of the recent research conducted across all social insects and stress
72 how recent studies in the *other* social insects have provided key information for our
73 general understanding of social life and its evolution. The reviews presented here
74 survey recent advances in the study of insect social life in terms of genomics, behaviors
75 and physiology.

76 The genomic aspects of social life are discussed in two reviews. The first one
77 by **Kronauer and Libbrecht**, discusses how the genomic data currently available
78 supports (or not) alternative trajectories in eusocial evolution and explains how studies
79 investigating the molecular bases of brood care and nest defense in the *other* social
80 insects would provide novel and unique opportunities of functional analyses. The

81 second review by Taylor et al makes the case that the broad diversity of social systems
82 present in Vespid wasps provides a unique opportunity for testing hypotheses about
83 the molecular mechanisms underlying the different evolutionary transitions from
84 solitary to eusocial life.

85 The behavioral (in its broad sense) aspects of social life are discussed in four
86 reviews. The first review by Smiseth and Royle presents how recent works in the *other*
87 social insects changed our current view on the nature and outcomes of social
88 interactions between family members and call for a major shift from the traditional
89 emphasis on conflict to a greater emphasis on the balance between conflict and
90 cooperation. The second review by Van Meyel et al emphasizes how and why social
91 defenses against pathogen infections can and/or have emerged in almost all forms of
92 social life in insects and argue that these defenses could have played a central role in
93 the early evolutionary transition from solitary to group living. In the third review by
94 Onchuru et al, the authors survey the different mechanisms of transmission of
95 symbiotic microbes (gut microbiota) across all social insects and emphasize that social
96 transmissions could be of key importance to promote the evolution of social behaviors
97 and insect eusociality. Finally, the fourth review by Nehring and Steiger explores the
98 link between social and communication system complexities and argue that further
99 studies on the communication system of the *other* social insects are required to fill
100 some of our current gaps in the conceptual and empirical understanding of this link.

101 The physiological aspects of social life are discussed in two reviews. The first
102 review by Trumbo investigates whether the link between juvenile hormones and
103 parental care reported in subsocial insects could provide major insights into a
104 key assumption of social evolution, which is that the mechanisms regulating
105 reproductive versus non-reproductive phases of the life cycle of solitary ancestors are

106 key drivers of reproductive division of labor in eusocial species. The second review by
107 **Lihoreau et al** focuses on insect nutrition and argues that conceptual advances used
108 to study nutrition in solitary and gregarious insects provide a robust framework to
109 explore the role of food constraints in the evolution of insect social life.

110 Finally, the review by **James Costa** takes a broader perspective on the *other*
111 social insects. In this review, the author discusses ongoing issues with the
112 terminologies of social life, provides a brief and up-to-date overview of the main traits
113 of interest in the *other* social insects and finally presents emerging fields of inquiry that
114 derived from recent studies in these species.

115 **Future directions**

116 Even if the number of studies on the *other* social insects has increased over the last
117 decade, this number is still low. Yet, the reviews presented here emphasize that these
118 few studies provided major improvements in multiple fields of social evolution including
119 behavioral ecology, physiology, genomics and chemical ecology. So how can we
120 further promote the study of these *other* social insects in a near future? One simple
121 option would be to abandon the synonymy between “social” and “eusocial” insects both
122 in the literature and in the mind of social insect researchers and instead, to consider
123 as “social insect” every insect species exhibiting a form of social life. Disrupting the
124 dichotomy between eusocial and the *other* social insects would enforce researchers
125 interested in different forms of social life to unify their frameworks (e.g. in terms of
126 terminologies, theory and model assumptions) and ultimately promote the
127 development of novel, comprehensive and robust paradigms in social evolution. Such
128 a unification will be difficult, as terminologies can be dramatically different even within
129 eusocial species [9]. But it has already started – notably with the book “Comparative

130 social evolution” which proposed a unified approach to compare eusocial vertebrates
131 and invertebrates [2], and thus needs to be continued and strengthened further.
132 Moreover, considering social insects in their broad diversity would allow us to put aside
133 the question of their social classification when not essential (such as: is this species
134 gregarious, subsocial, semi-social, quasi-social, primitive eusocial or true eusocial?),
135 and instead allow focusing on the knowledge a work can provide to our general
136 understanding of social life. Hence, this simple change in social terminology – which
137 has been already called for at different degrees [10–12] - should profoundly strengthen
138 our current understanding of social evolution, as well as provide novel and unexpected
139 avenues for its further development. It is thus time for such a change.

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