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A report on the bees (Hymenoptera: Apoidea: Anthophila) of Cambodia

John S. ASCHER^{1,*}, HEANG Phallin², KHEAM Sokha², LY Kang², LORN Sokchan², CHUI Shao Xiong¹, Stéphane De GREEF³, Gerard CHARTIER⁴ & PHAUK Sophany²

¹ Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, 117543, Singapore.

² Cambodian Entomology Initiatives, Department of Biology, Faculty of Science, Royal University of Phnom Penh, 12101, Cambodia.

³ 24 Avenue De Gaulle, Siem Reap, 17252, Cambodia.

⁴ Rainbow Lodge, Tatai Commune, Koh Kong Province, Cambodia.

* Corresponding author. Email dbsajs@nus.edu.sg

Paper submitted 6 April 2016, revised manuscript accepted 17 May 2016.

មូលន័យសង្ខេប

មុននឹងមានការសិក្សានេះ ការប្រមូលសំណាកសត្វឃ្មុំត្រូវបានគេឃើញមាននៅកន្លែងស្រាវជ្រាវមួយចំនួនក្នុងប្រទេសកម្ពុជា ហើយឯកសារដ៏តិចតួចស្តីពីសត្វឃ្មុំក៏មិនធ្លាប់ត្រូវបានពិនិត្យឡើងវិញដែរ។ របាយការណ៍ជាបឋមនេះបានប្រមូលផ្តុំទិន្នន័យដែលមានស្តីពី នានាភាពឃ្មុំកម្ពុជា ដោយផ្អែកលើឯកសារកំណត់ត្រា សំណាកប្រមូលដោយក្រុមស្រាវជ្រាវសត្វឃ្មុំកម្ពុជា (Cambodian Entomology Initiatives) ជាមួយដៃគូសហការបរទេស និងទិន្នន័យរូបភាពប្រមូលបានដោយសារអ្នកវិទ្យាសាស្ត្រក្នុងស្រុក។ សរុបមានសត្វឃ្មុំ៨២ប្រភេទ ស្ថិតក្នុង២៧ពួក និង៤៤អំបូរ ត្រូវបានធ្វើកំណត់ត្រាសម្រាប់ប្រទេសកម្ពុជា។ ពួកមួយចំនួន (*Hylaeus*, *Eupetersia* និង *Pseudoanthidium*) និងប្រភេទមួយភាគធំជាកំណត់ត្រាថ្មីសម្រាប់កម្ពុជា វាឆ្លុះបញ្ចាំងពីភាពមានកម្រិតនៃការប្រមូលសំណាក និងការសំយោគឯកសារក្នុងតំបន់។ ប្រភេទមួយចំនួនត្រូវបានគេគិតថាជាប្រភេទថ្មី រួមមានសំណាកនៃពួក *Nomia* (*Maculonomia*) និង *Anthidiellum* (*Ranthidiellum*) ដែលត្រូវបានរកឃើញក្នុងដំណើរការស្រាវជ្រាវក្នុងខែកុម្ភៈ ឆ្នាំ២០១៦ ក្នុងតំបន់ព្រៃការពារសីម៉ា។ ព័ត៌មានប្លែកៗស្តីពីជីវិតក្នុងធម្មជាតិក៏ត្រូវបានប្រទះនៅទីនោះ ដូចជាភាពអាចនឹងមានទំនាក់ទំនងរវាងជួរ *Lasioglossum* (*Homalictus*) និងបាវ៉ាស៊ីត *Nomada* cleptoparasite។ រូបថតមួយចំនួនត្រូវបានបញ្ចូលដើម្បីបង្ហាញពីនានាភាពនៃសត្វឃ្មុំដែលទើបតែស្គាល់។ ការបោះពុម្ពនេះធ្វើអត្ថាធិប្បាយសង្ខេបលើចំណែកថ្នាក់ និងរបាយប្រភេទក្នុងតំបន់ ព្រមទាំងកែតម្រូវកំហុសមួយចំនួនដែលមានក្នុងឯកសារបោះពុម្ពស្តីពីកំណត់ត្រាសត្វឃ្មុំក្នុងប្រទេស។ នានាភាពនៃឃ្មុំកម្ពុជាត្រូវបានពិភាក្សា និងប្រៀបធៀបជាមួយនឹងប្រទេសជិតខាងដូចជា ឡាវ ថៃ និងវៀតណាម។

Abstract

Prior to this study, few historical collections were made of bees in Cambodia and the sparse literature had never been reviewed. This preliminary report assembles available data on Cambodian bee diversity based on literature records, specimens collected recently by the Cambodian Entomology Initiatives team and foreign collaborators, and image databases assembled by resident citizen scientists. In total, 82 bee species and morphospecies in 27 genera and four families are recorded for the country. Some of the genera (e.g., *Hylaeus*, *Eupetersia* and *Pseudoanthidium*) and a large proportion of the species and morphospecies are new for the country, reflecting limited historical collecting and a lack

CITATION: Ascher, J.S., Heang P., Kheam S., Ly K., Lorn S., Chui S.X., de Greef, S., Chartier, G. & Phauk S. (2016) A report on the bees (Hymenoptera: Apoidea: Anthophila) of Cambodia. *Cambodian Journal of Natural History*, **2016**, 23–39.

of comprehensive regional revisions. Several species are believed to be new to science, including specimens of *Nomia* (*Maculonomia*) and *Anthidiellum* (*Ranthidiellum*) discovered on an expedition in February 2016 to Seima Wildlife Sanctuary. Novel life history information was also obtained there, including a probable host-parasite association between a tiny *Nomada* cleptoparasite and its presumed *Lasioglossum* (*Homalictus*) host. Photographs document some of the newly detected bee diversity. This paper briefly comments on the taxonomy and distribution of regional species and corrects some erroneous country records in the literature. Cambodian bee diversity is discussed and compared to the neighbouring countries of Laos, Thailand, and Vietnam.

Keywords

Biodiversity, biogeography, insect, pollinators, Southeast Asia.

Introduction

Bees (Apoidea: Anthophila) are important pollinators and play a crucial role in plant reproduction in natural and agricultural ecosystems. Their populations must be maintained to ensure food security and because bees are also of very great value as a source of honey and hive products (McNaughton & Sotha, 2009). In Cambodia in particular, bees provide a source of protein through consumption of their larvae. Although Cambodia is known to have high diversity in other taxa such as birds (Goes, 2013), knowledge of its bees other than the relatively well-studied highly eusocial hive bees (Apini and Meliponini) remains very limited and inaccessible. Documentation of the Southeast Asian bee fauna is generally poor, and many groups lack modern revisions. However, many species descriptions have been made from countries such as Thailand, Peninsular Malaysia, and Indonesia, and recent studies have improved knowledge of regional bee ecology and distribution (Kato *et al.*, 2008; Tadauchi and Tasen, 2009; see also references in Corlett *et al.*, 2004). Among Southeast Asian countries, Cambodia and Laos are the least well known because the relatively little melittological research that occurred in French Indochina seems to have been concentrated in Tonkin, now North Vietnam (e.g., Blüthgen, 1926). While the bees of Indochina received little attention in the past, some of the larger or otherwise more conspicuous bee species were described from elsewhere in Asia as long ago as the 18th century (Linnaeus, 1758; Drury, 1773; Fabricius, 1775, 1787, 1793) and the mid-19th century (e.g., Lepeletier de Saint Fargeau, 1841; Smith, 1853, 1857). Recent taxonomic studies on the Indochinese fauna have focused largely on stingless bees (Sakagami, 1975, 1978), whereas ecological studies have focused on plant-pollinator interactions rather than taxonomic diversity (e.g., Kato *et al.*, 2008, for the Vientiane Plain in Laos). The review of the conservation and management of pollinators for sustainable agriculture in Laos (Vandame, 2006 and references therein) is also relevant to Cambodia.

Documentation of the bee fauna of Thailand has been more extensive and includes a series of publications by T.D.A. Cockerell (e.g., 1929a,b,c) documenting the results of a collecting expedition during 1928–1929 when he, his wife W.P. Cockerell and A. Mackie collected type specimens of many new species some of which are recorded herein from Cambodia. More recently, a large-scale survey conducted from 2006–2009 by the Thailand Inventory Group for Entomological Research (TIGER, <http://sharkeylab.org/tiger/>) yielded large samples of bees from national parks across Thailand, many of which have been identified by specialists and sequenced for COI as a contribution to the global Bee Barcode of Life project led by L. Packer. Results of the TIGER project for apoid wasps are a major advance in knowledge of this group (Lohrmann *et al.*, 2012), with 22 new genera recorded for Thailand. Additional results now being compiled should also greatly advance knowledge of the regional bee fauna.

The few notable studies of bee diversity in Cambodia in the 20th century were mostly undertaken by Japanese researchers in the late 1950s. Professors T. Sato and T. Takayama, members of the 1957 Hyogo University of Agriculture Expedition to Cambodia, collected bees in Stung Treng Province and a few other places, as reported by Sakagami (1960). Soon after, Cambodia was included among destinations visited for collecting and biological studies by the Osaka City University Biological Expedition to Southeast Asia from November 1957 to March 1958 (Sakagami & Yoshikawa, 1961). Cambodian bees obtained by this expedition were evidently few overall, and Hirashima's (1962) report does not mention any, but Cambodian samples of stingless and other bees obtained in 1958 by K. Yoshikawa in Kampong Cham Province on 20 February and Oudong, Kampong Speu Province, on 28 February were included in Sakagami's (1978) review of *Tetragonula* stingless bees of continental Asia. A few Cambodian records for other bee taxa are also mentioned incidentally, without details, in extra-limital taxonomic publications (e.g., Matsumura & Sakagami, 1971).

Reflecting a lack of historical studies of bees in Cambodia, no currently valid species was described from Cambodia until Pauly (2009) described three Nomiinae species from Siem Reap Province (localities are included in Fig. 1, and nomiine and other bees are illustrated in Fig. 2) in a revision of Oriental Nomiinae: *Lipotriches* (*Macronomia*) *angkorensis* (Pauly) from Angkor, Preah (as “Preadh”) Khan Temple; and two species from Angkor (as “Angor”) Thom: *Lipotriches* (*Maynenomia*) *indochinensis* (Pauly) and *Nomia* (*Gnathonomia*) *cambodiana* (Pauly). The latter taxon is the only bee species currently considered to be endemic to Cambodia, as the other two nomiines with Cambodian type localities are more widely distributed (Appendix 1). The three holotypes from Cambodia are held in the Institut Royal des Sciences Naturelles de Belgique (IRSNB), where additional Cambodian material can be found (A. Pauly, pers. comm.). All three were collected between June to December 2003: *L. angkorensis* by F. Goes and the other two by D.R. Jump.

While this paper was in the proof stage we learned of an accepted manuscript on the diversity of stingless bees in Cambodia and Laos (Lee *et al.*, 2016, accepted version). This provided occurrence records and behavioural data for Cambodian species, but the accepted version available online was found to have a large number of errors. On examination of the figures provided, reports of new species for the country proved to be misidentifications, but we were fortunately able to confer with the authors to ensure these problems were addressed. Putative new country records for Cambodia, including erroneous reports of *Pariotrigona pendleburyi* (Schwarz) and *Tetragonula sirindhornae* (Michener and Boongird, 2004) were reported in a poster abstract (Duwal & Lee, 2014) and images of nest entrances reported by Lee *et al.* (2016) should also be interpreted with caution as some are inconsistent with verified nests of the taxa in question.

A milestone in the development of entomological capacity in Cambodia has been the establishment of the Cambodian Entomology Initiatives (CEI) based at the Royal University Phnom Penh (RUPP). Goals of this multi-faceted initiative include establishment of the first national entomology collection, field expeditions to document the Cambodian fauna, training of the first generation of Cambodian entomology students and public outreach. The initial taxonomic focus has been on crop pests in the Hemiptera, especially Homoptera such as leafhoppers (Cicadellidae), treehoppers (Membracidae) and allies. Since 2013, efforts have also been made to document beneficial insects including bee pollinators and wasp predators and parasitoids. The first CEI field trips to focus on Hymenoptera have already yielded

several new species for the country and have discovered potential new taxa for science which we report below.

Methods

This study consists of a summary of records compiled from the following sources: 1) the sparse literature on bees pertinent to Cambodia (summarized above), with emphasis on taxonomic and distributional studies of non-*Apis* species; 2) bee samples collected to date by the CEI team and studied by JSA during visits to RUPP; 3) bee images taken by SDG, GC and other photographers resident in Cambodia and identified by JSA; 4) preliminary results of a CEI–National University of Singapore (NUS) collecting expedition to Monduliri Province in February 2016; 5) specimens of Indochinese bees sent to JSA for study from two Austrian collections (Oberösterreichisches Landesmuseum in Linz and the private collection of Maximilian Schwarz); and 6) a limited number of additional records gleaned from publicly available databases.

The first Hymenoptera collecting expedition to Seima Wildlife Sanctuary (WS) in Monduliri Province (Fig. 1) was conducted in February 2016 by the CEI team from RUPP led by PS, a team of NUS bee researchers led by JSA and including CSX, Gabriel Low and Adeline Seah. These researchers and additional students also collected bees on the RUPP campus in Phnom Penh during a workshop held prior to the expedition.

Concurrent with these collecting efforts, there has been a rapid development of citizen science efforts in Cambodia. Leading the research on Cambodian arthropods, SDG built and administrates the Facebook group Natural Cambodia (<http://www.facebook.com/groups/naturalcambodia>), which invites Cambodian residents and visitors to photograph biodiversity (including arthropods) and share their findings. Since 2011, a large amount of data, including photos, dates and locations of sightings, have been gathered from the public and images of arthropods shared have been identified by various experts, leading to dozens of new species distribution records across the country. For example, GC has documented the occurrence and behaviour of bees in Koh Kong Province. SDG has also documented Cambodian arthropods through macrophotography in the Angkor Archaeological Park and its immediate surroundings since 2007. From 2012, SDG has followed the protocol developed by the Meet Your Neighbours project, an international effort using high-quality photography of arthropod species on a white background to advance research and raise awareness.

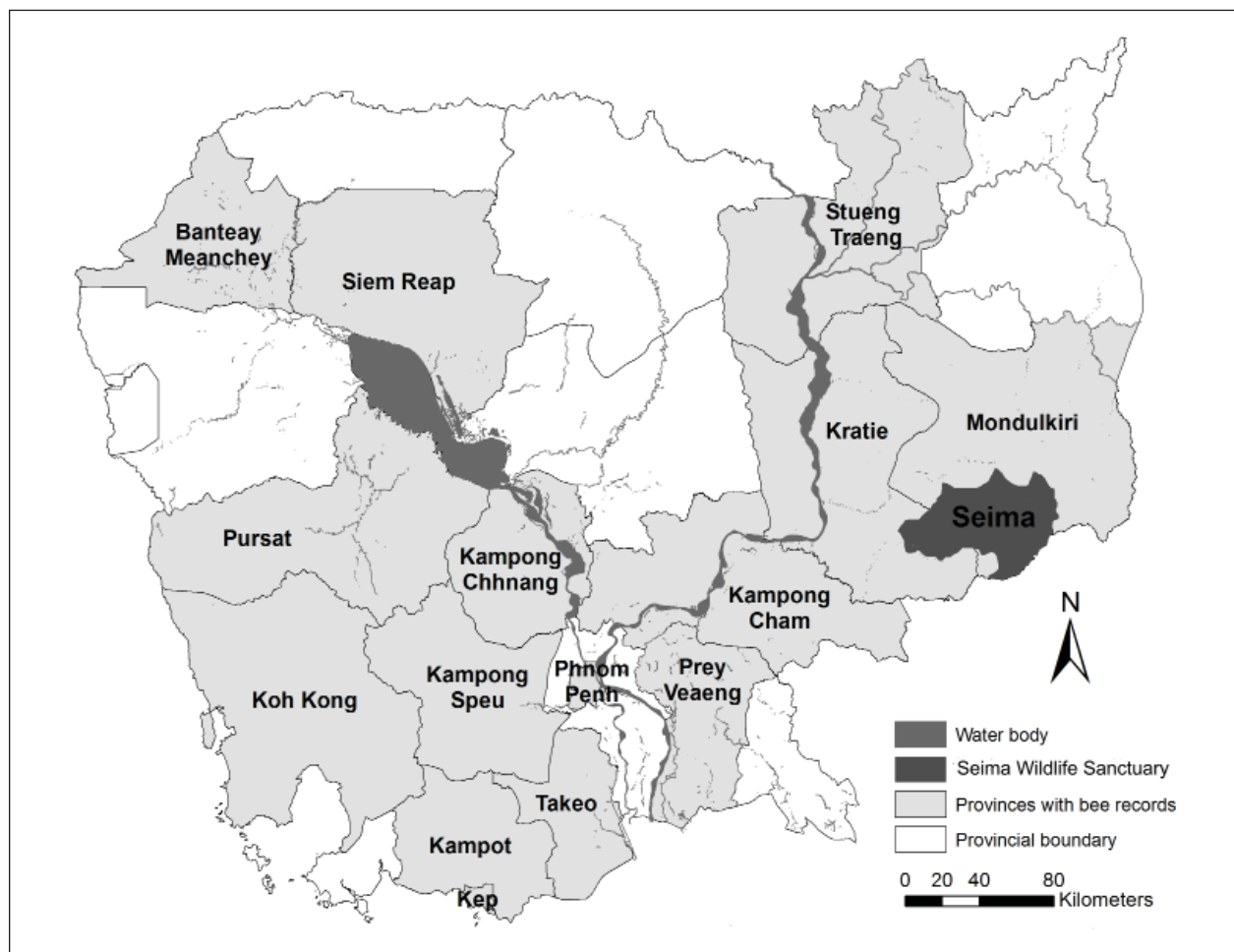


Fig. 1 Location of bee collection and survey areas in Cambodia.

Results

Records from Seima WS and RUPP campus

Notable findings of the 2016 expedition to Seima WS include the discovery of what are likely undescribed species of *Nomia* (*Maculonomia*) and *Anthidiellum* (*Ranthidiellum*). In addition, several genera were confirmed to occur in Cambodia for the first time including *Hylaeus* (Colletidae, a first country record for the family), the megachilid genera *Lithurgus*, *Anthidiellum*, *Pseudoanthidium*, *Heriades* and *Coelioxys*, and the apid genera *Braunsapis* and *Nomada*. At the subgeneric rank, notable findings included *Nomia* (*Maculonomia*) (three species), a *Lasioglossum* (*Homalictus*) species that appears to be the host of the small-bodied *Nomada*, and two species of *Ceratina* (*Xanthoceratina*). This expedition also documented the nest sites and nest entrances of many stingless bee species (tribe Meliponini) in evergreen forest and a total

of 48 bee species and morphospecies are now known from Mondul Kiri Province (Appendix 1).

Collections on the RUPP campus have confirmed the presence of *Pseudapis* (*Pseudapis*) *siamensis* (Cockerell, 1929b) in Phnom Penh, a new country record of a species first described from Thailand and now known to be widespread in the region. We have also established the presence of various other urban-adapted bee species including nests of stingless honey bees *Tetragonula fusco-balteata* (Cameron) and of *Megachile* (*Callomegachile*) aff. *umbripennis* Smith, inspected by *Coelioxys cleptoparasites* (Appendix 1).

Citizen science records

Photographs of bees taken for the Meet Your Neighbours project (Fig. 2) are of great scientific interest because they provide new provincial records for many well-known species and the first documentation of additional obscure

species including some potentially new to science, such as an unidentified species of *Lipotriches* (*Maynenomia*) (Fig. 2d). Subgenera and species new for Cambodia well-illustrated by these photographs include *Megachile* (*Lophanthedon*) *dimidiata* Smith (Fig. 2e) (this subgenus was recently described by Gonzalez & Engel, 2002) and *Amegilla* (*Glossamegilla*) *fimbriata* (Smith) (Fig. 2b), an attractive species recently redescribed and reported from Thailand by Attasopa & Warrit (2012). In addition to their scientific value, photographs of Cambodian bees are also of great utility for education and outreach.

Overview of the known bee fauna of Cambodia

Eusocial hive bees:

Apis honey bees are relatively well documented in Cambodia because their nests are of great economic importance as sources of honey, larvae consumed as food, and other hive products (McNaughton & Sotha, 2009); these are also the only bees that pose a serious danger to humans. Three species are very widely distributed in Cambodia and adjacent countries: the cavity-nesting Asian honey bee *Apis* (*Apis*) *cerana* F., the twig-nesting dwarf honey bee *A. (Micrapis)* *floreana* F., and the giant honey bee *A. (Megapis)* *dorsata dorsata* F. which is migratory and seasonally builds very large nests under the high branches of dipterocarps and other tall trees. It also occupies manmade structures in open areas such as water towers, and nests are sometimes induced in rafters to facilitate harvesting of honey (Waring & Jump, 2004). A fourth species, the black dwarf honey bee *A. (Micrapis)* *andreniformis* Smith, is less well known because it may be more or less restricted to humid evergreen forest and has been overlooked historically due to its similarity to the more common *A. floreana* (see review of the Asian species of *Apis* by Radloff *et al.*, 2011). Maa's (1953) revision of the Apini did not cite Cambodian records, but Otis (1996) included a few Cambodian records for *A. floreana* and stated that *A. andreniformis* "almost certainly" occurs, a conclusion corroborated here.

Stingless honey bees (tribe Meliponini) are of great importance as pollinators (Heard, 1999) and as producers of honey and hive products that can be more valuable on a per-unit basis than those of *Apis*. Elsewhere in Southeast Asia, notably Malaysia, a rapidly growing meliponiculture (stingless bee keeping) industry has developed (Jalil & Shuib, 2014) with the goal of sustainably maintaining commercially viable populations of many species and, among researchers and hobbyists, maintaining demonstration hives of most others. A few small-bodied *Tetragonula* species (reviewed by Sakagami, 1978) such as *T. fuscobalteata* (Cameron) and *T. pagdeni* (Schwarz),

are widespread in open areas, with the former nesting in green spaces within Phnom Penh such the RUPP campus. However, a larger-bodied species of *Tetragonula*, *T. geissleri* (Cockerell), and other meliponine species — including the exceptionally large *Geniotrigona thoracica* (Smith), and other larger species such as *Homotrigona fimbriata* (Smith) *sensu lato* (see Sakagami, 1975; Rasmussen, 2008) and *Tetrigona apicalis* (Smith) — are associated with mature evergreen forests, in particular those with large dipterocarp trees that are used as nesting sites and sources of resin for nest construction. Such forest-dependent stingless bees may be of conservation concern when their habitat is heavily logged or fragmented, as shown by the failure of larger-bodied stingless bees to survive in urban and scrub habitat in Singapore (JSA and CSX, unpublished data). Certain minute stingless bees such as the three species of *Lisotrigona* species found at Seima WS, two recently described by Engel (2000) including the distinctive *L. carpenteri* (Fig. 3b), are rarely observed on flowers and are instead more often detected when they are attracted to the sweat of field workers. The nest entrances of the various stingless bee genera and species are typically affixed to the trunk of a large dipterocarp tree and are distinctive, with each taxon having a characteristic form (Sakagami *et al.*, 1983). For example, a long slender tube in *Tetragonilla collina* (Smith, 1857) as opposed to a shorter tube shaped like a trumpet bell in both Cambodian species of *Lepidotrigona*.

The taxonomy and distribution of Southeast Asian stingless bees is relatively well known (Schwarz, 1939; Sakagami, 1975, 1978; Rasmussen, 2008), but many difficulties remain, especially regarding recognition of medium-sized *Tetragonula* species such as *T. pagdeni* (Schwarz) and *T. laeviceps* (Smith). The former is expected to be widespread in Indochina, but is likely under-recorded due to identification problems, whereas the latter, while reported from Cambodia (e.g., by Rasmussen, 2008, under the name *T. valdezi*, which we consider a junior synonym, cf. Sakagami, 1978), is better known in Sundaland (the neotype locality is Singapore, as established by Rasmussen & Michener, 2010), and its status in Indochina requires further verification. A large-bodied Cambodian *Tetragonula* recorded with various spellings by Lee *et al.* (2016, accepted version) as *T. iridipennis* (Smith), an Indian species, is likely *T. geissleri* (Cockerell).

Rasmussen's (2008) catalogue of regional Meliponini cited several species for Cambodia on the basis of records correctly attributable to Thailand. For example, the localities "Kum Puang Creek", "Nan" and "Pahtoop Mountain", are not in Cambodia but in Nan Province of Thailand. Records of *Heterotrigona bakeri* (Cockerell) for "Tung Nui" and "Satul" in Cambodia by Rasmus-

sen (2008; and for Cambodia by Lee *et al.*, 2016, accepted version) were probably a misplacement of Ban Thung Nui in Satun Province of southern Thailand: a more plausible locality for a species described from Penang in North-west Peninsular Malaysia. Likewise, Rasmussen's (2008) record of *Tetrigona peninsularis* (Cockerell) from "Patalung" should be attributed to Phatthalung Province of southern Thailand. This species, like *H. bakeri*, is restricted to the Malay Peninsula (with verified records extending north only to the Phatthalung and Saraburi provinces). Rasmussen also miscited "Tung Nui" and "Satul" for Cambodian localities in his entry for *Tetragonula biroi* (Friese, 1898). He correctly noted that the records in question were misidentified, but the inclusion of records from mainland Southeast Asian records under the heading for a species actually restricted to New Guinea and the Philippines has led to confusion (e.g., citation of *T. biroi* for Cambodia by Lee *et al.*, 2016, accepted version). Another source of confusion is the recognition at species rank by Rasmussen (2008) of described forms of uncertain and sometimes doubtful validity. While this is convenient for the purposes of cataloguing all literature citations, it may lead some authors to conclude that the more conservative classification of Sakagami (1975, 1978) has received comprehensive taxonomic review and been supplanted, when this is not actually the case. We concur with Sakagami that variation in size, colour and other characters among species (or superspecies) such as *Homotrigona fimbriata* (Smith), *Lepidotrigona ventralis* (Smith), and *Tetragonula laeviceps* (Smith) (*sensu lato*) is complex and not sufficiently congruent with well-corroborated biogeographic patterns to permit ready subdivision of these and other variable taxa into reliably identifiable taxa. Pending revisionary studies and availability of molecular diagnostics across their ranges, we prefer to recognize such species in a broad sense following Sakagami (1975, 1978), while noting the observed variation. We therefore cite ranges separately for the two colour forms of *Homotrigona fimbriata* [the flavinic *aliceae* (Cockerell) in western Cambodia and the melanic *anamitica* (Friese) in eastern Cambodia] and cite *flavibasis* in synonymy as the name available for Cambodian *Lepidotrigona ventralis* (Smith) *sensu lato* if considered a distinct species (Appendix 1).

Solitary and primitively eusocial bees:

Colletidae are rather poorly represented in Southeast Asia, with *Colletes* (Colletinae) having only recently been reported from mainland Southeast Asia based on recent description of *C. packeri* Kuhlmann 2015 (Kuhlmann & Proshchalykin, 2015) from Thailand and Laos. This genus may be restricted to highlands in the region, but *Hylaeus* (Hylaeinae) is more widespread. However, discovery and description of regional *Hylaeus* species and

their placement to subgenus requires much additional work (see Dathe, 2011, who described a new Asian subgenus which likely occurs in Cambodia but has yet to be recorded). An undetermined *Hylaeus* (*Paraprosopis*) species was found on the expedition to Seima WS, and a female *Hylaeus* species with three subequal facial markings resembling *H. (Nesoprosopis) penangensis* (Cockerell, 1920) was recorded in the Koh Kong and Mondulhiri provinces. [Images of the type specimen of *H. (Nesoprosopis) penangensis* are available through the Smithsonian collections database]. A similar bee has also been found in Singapore (J.S. Ascher, unpublished data).

Halictidae are well represented in Cambodia and elsewhere in Southeast Asia, especially the subfamily Nomiinae. Pauly's (2009) revision of Oriental nomiines included descriptions of three new species from Cambodia (see above). Our work has confirmed the presence of additional widespread species and what is apparently a new taxon related to *Nomia (Maculonomia) sanguinea* (Pauly) (Fig. 4d) (see discussion of a potential new subspecies in Pauly, 2009) and additional potential new species of *Nomia (Maculonomia)* (Figs 4b, 4c) and *Lipotriches (Maynemonia)* (Fig. 2d). Including unnamed morphospecies, 10 Nomiinae species are now known from Cambodia (Fig. 4). Whereas few identification resources exist for Cambodian bees other than the sparse primary literature, described species of Nomiinae can in most cases be readily identified by referring to well-illustrated species pages at the Atlas Hymenoptera website (<http://www.atlashymenoptera.net>). However, further taxonomic review is required and some widely distributed species as delimited by Pauly (2009) are in our view composite taxa. For example, such as *Nomia (Maculonomia) apicalis* Smith *sensu lato*, the Cambodian representatives of which we assign to a separate species: *Nomia (Maculonomia) niti-data* Strand (new status).

Halictinae are as yet poorly known in Cambodia but certainly include multiple species of *Lasioglossum* (*Ctenonomia*), including the widely distributed *L. albescens* (Smith) (Matsumura & Sakagami, 1971) and *L. vagans* (Smith), and at least one *Lasioglossum* (*Homalictus*) species belonging to the *Indohalictus* group (Pauly, 1980). An unidentified species of *Patellapis* (*Pachyhalictus*) was also recorded in Seima WS (see review of this taxon as *Pachyhalictus* by Pauly, 2007; and the review of the Chinese species by Pesenko & Wu, 1997). An important discovery from one of the first CEI collecting trips focusing on bees was the first Cambodian records of *Eupetersia* (*Nesoeupetersia*) *yanegai* Pauly, a parasitic halictine recently described from Thailand (Pauly, 2012) based in part on material collected during the TIGER project and now also known from mangroves in Singapore (J.S.

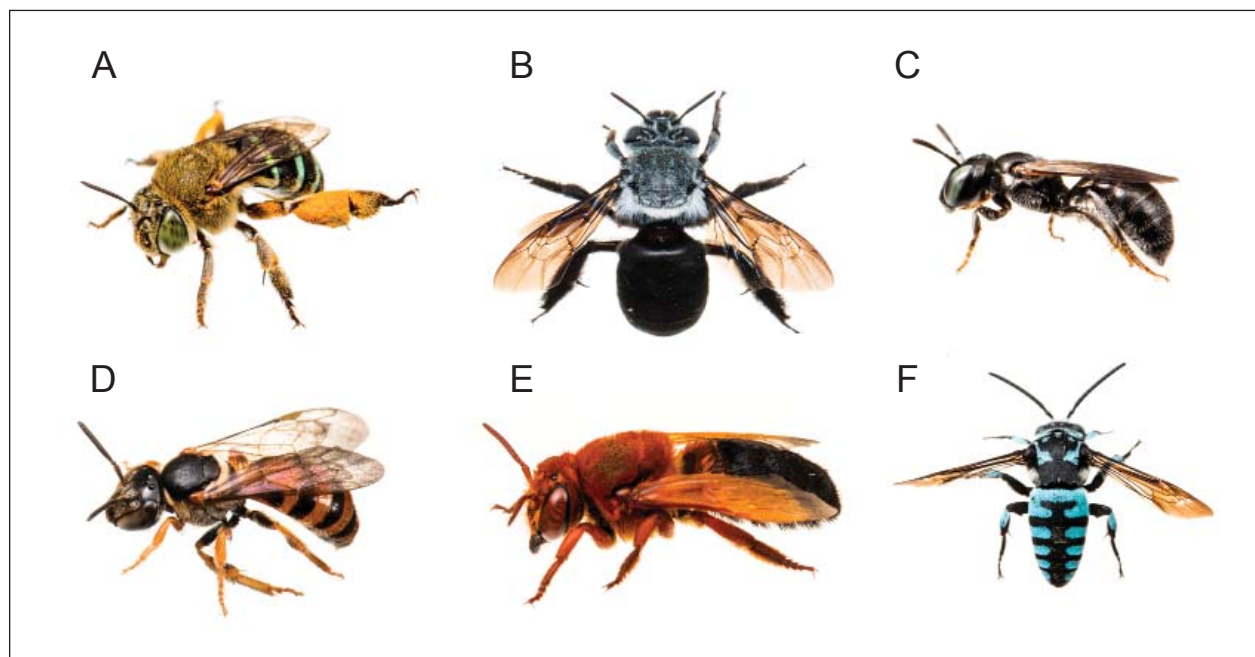


Fig. 2 Bees photographed at Angkor Archaeological Park: A) *Amegilla* (*Zonamegillia*) sp., ♀; B) *Amegilla* (*Glossamegilla*) *fimbriata* Smith, ♀; C) *Ceratina* (*Neoceratina*) *dentipes* Friese, ♀; D) *Lipotriches* (*Maynenomia*) sp., ♀; E) *Megachile* (*Lophanthedon*) *dimidiata* Smith, ♀; F) *Thyreus himalayensis* Radoszkowski, ♂ (© Stéphane De Greef).

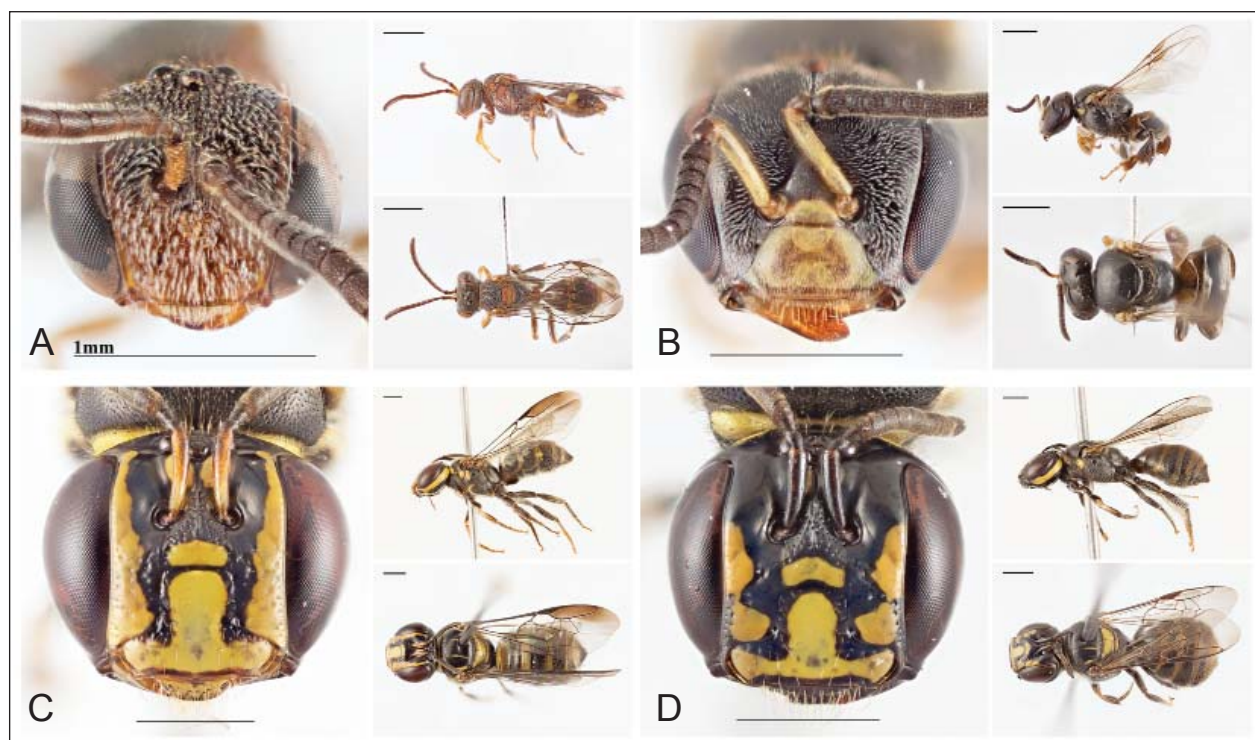


Fig. 3 General habitus plate of apid bees: A) *Nomada* sp., ♀; B) *Lisotrigona carpenteri*, ♀; C) *Ceratina* (*Xanthoceratina*) aff. *fuliginosa*, ♀; D) *Ceratina* (*Xanthoceratina*) aff. *humilior*, ♀ (© Chui Shao Xiong).

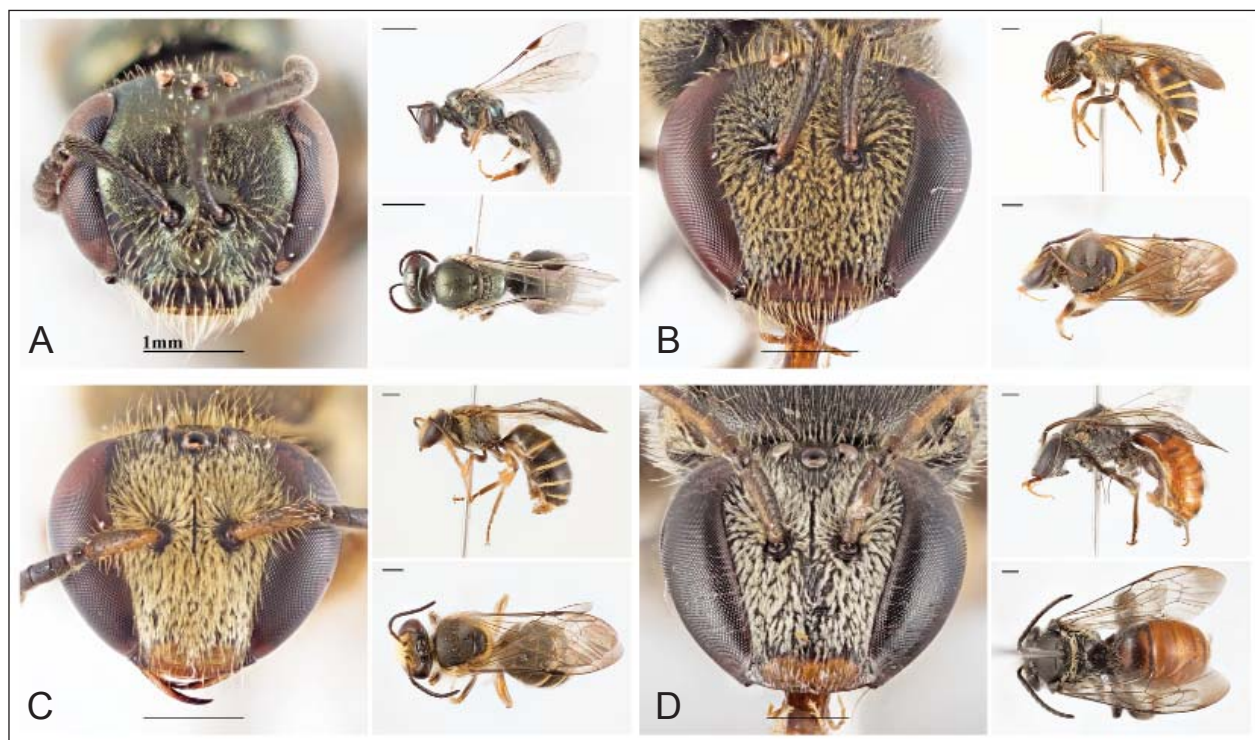


Fig. 4 General habitus plate of halictid bees: A) *Lasioglossum* (*Homalictus*) sp., ♀; *Nomia* (*Maculonomia*) n. sp., B) ♀ & C) ♂; D) *Nomia* (*Maculonomia*) *sanguinea*, ♂ (© Chui Shao Xiong).

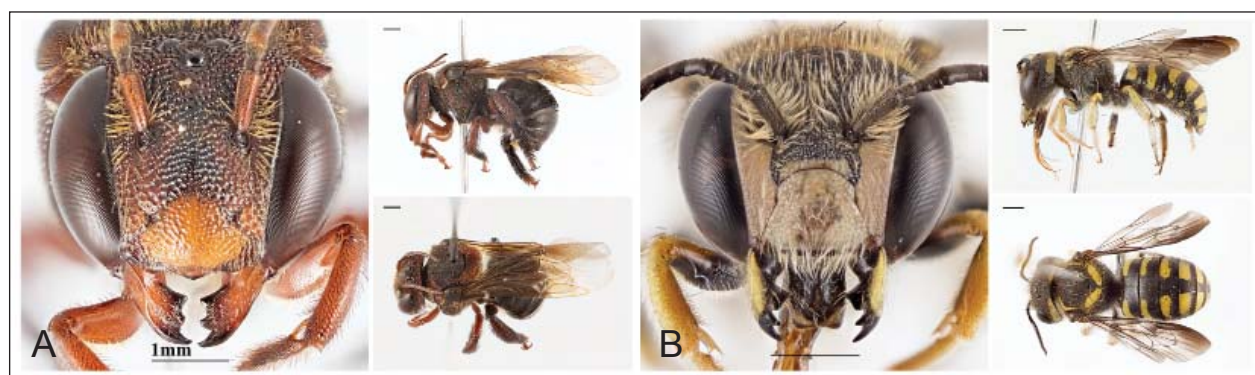


Fig. 5 General habitus plate of megachilid bees: A) *Anthidiellum* (*Ranthidiellum*) aff. *meliponiforme*, ♂; B) *Pseudoanthidium* (*Pseudoanthidium*) *orientale*, ♂ (© Chui Shao Xiong).

Ascher, unpublished data). The limited known distribution of *Eupetersia* (*Nesoeupetersia*) in tropical and subtropical Southeast Asia suggests a possible association with *Patellapis* (*Pachyhalictus*), but this remains to be demonstrated.

Megachilidae are diverse in Cambodia but like other families are under-recorded and many recorded taxa have not yet been identified to species (Fig. 5). Only four

identified *Megachile* species and six additional morphospecies have been confirmed, but many more surely exist in numerous subgenera, including both leaf-cutter and resin bees. These are parasitized by *Coelioxys* bees (also Megachilini) including a *Coelioxys* (*Allocoelioxys*) found at Seima WS and what is likely a different species observed on the RUPP campus (not included in Table 1 due to lack of a voucher specimen). In addition to Megachilini, the tribe Osmiini is represented by *Heriades* (*Michenerella*)

othonis Friese, 1914 (a new country record for the genus from Seima WS—species identification is tentative in the absence of a revision treating potentially similar or synonymous forms such as *Heriades laosella* Cockerell, 1929c, described despite its name, from Nan Province in Thailand). The Anthidiini tribe is represented by *Pseudoanthidium* (*Pseudoanthidium*) *orientale* (Bingham, 1897) (Fig. 5b) (new country record for the genus from the streambed below Bou Sra Waterfall; see revision by Pasteels, 1972, and photograph of a Thai specimen by Tadauchi & Tasen, 2009), and what may prove to be a new species of *Anthidiellum* (*Ranthidiellum*) (Fig. 5a) (new country record for the genus from Seima WS; see Engel, 2009). In addition to Megachilinae, the subfamily Lithurginae is represented in Seima WS by the wood-nesting *Lithurgus collieri* Cockerell, a species described from Thailand (Cockerell, 1929a).

Large carpenter bees in the genus *Xylocopa* (Xylocopinae: Xylocopini) are relatively diverse and numerous in Cambodia. These are large and conspicuous bees that attract attention through their burrows which can damage structural wood, but the regional fauna is relatively poorly known. Some *Xylocopa* subgenera are treated in a monograph by Hurd & Moure (1963; see also Maa, 1940a,b, 1946; Lieftinck, 1964) but definitive identification of all regional species of the *Koptortosoma* subgenus will require additional taxonomic revision and likely the use of molecular diagnostics given the difficulty of associating the sexes of certain species. Lieftinck (1964) recorded both *Xylocopa* (*K.*) *bryorum* (Fabricius) and *X.* (*K.*) *minor* Maidl from Cambodia. Blue-haired species belonging to the *Cyaneoderes* group of *Koptortosoma sensu lato* (synonymy of Michener, 2007) occur in Cambodia, of which we have identified only *X.* (*K.*) *caerulea* (Fabricius). However, the taxonomy of regional species has only recently been reviewed (Mawdsley, 2016) and additional species may be detected. Bamboo-nesting species of *Xylocopa* (*Biluna*) are commonly found even in Phnom Penh. Two (or more) species of *Xylocopa* (*Platynopoda*) are the largest bees found in Cambodia. The subgenus *Platynopoda* has been considered a junior synonym of *Mesotrichia* (Michener, 2007), but we agree with its reinstatement by Mawdsley (2015; endorsing the classification of Hurd and Moure, 1963). The smaller-bodied *Xylocopa* (*Zonohirsuta*) *dejeanii* Lepeletier (= *X. collaris* Lepeletier, 1841, pre-occupied) also occurs, females of which can be readily identified by the pale collar on the anterior of the thorax. This species is represented in French Indochina by the subspecies *yangweiella* Maa, recorded from Laos and Vietnam (Maa, 1940), and our Cambodian records likely pertain to this form, but its taxonomic validity and status in Cambodia both require further verification.

Small carpenter bees belonging to the *Ceratina* genus (Xylocopinae: Ceratinini) are also well-represented in Southeast Asia (Shiokawa & Sakagami, 1969; Shiokawa, 2009, 2015; Warrit *et al.*, 2012) and Cambodia. The expedition to Seima WS recorded four species in the *Ceratinidia* subgenus, three of which were new for the country (*C. lieftincki* was cited for Siem Reap by Warrit, 2007). A review of the species in Thailand is useful for Cambodia as well (Warrit *et al.*, 2012; see also Warrit, 2007). The two regionally common species in the *Pithitis* subgenus (Hirashima, 1969; Shiokawa & Sakagami, 1969; Baker, 1997) also occur in Cambodia: *C. (P.) unimaculata* being represented by the green form *palmerii* Cameron, 1908, rather than the blue form *nanensis* Cockerell, described from Thailand (as *C. simanensis nanensis* Cockerell, 1929b). Two species of the forest-associated subgenus *Xanthoceratina* were recorded in Seima WS, a larger species aff. *fuliginosa* Cockerell (Fig. 3c), and a smaller one aff. *humilior* Cockerell (Fig. 3d). Finally, the smallest-bodied regional taxon *Ceratina* (subgenus *Neoceratina*), is represented by the widely distributed *C. (Neoceratina)* *dentipes* Friese (Fig. 2c) and a second, smaller species with a shinier, less punctate thorax and redder front legs.

The Xylocopinae subfamily is further represented by the *Braunsapis* genus of which three widely distributed species regionally (see revision by Reyes, 1991) are newly recorded for Cambodia from Seima WS. The genus occurs more widely in Cambodia as documented by photographs. The Nomadinae subfamily (Apidae) is represented only by a minute species of *Nomada* (*Nomadini*) (Fig. 3a) found in Seima WS in association with an earth bank visited by slightly larger females of *Lasioglossum* (*Homalictus*) (Fig. 4a) that we infer to be the hosts.

The bee genus *Amegilla* is widely distributed in Cambodia but species identification remains problematic in Indochina as historical research was concentrated in Sundaland and to a lesser extent Thailand (cf. Lieftinck, 1956). One visually distinctive species, *Amegilla* (*Glossamegilla*) *fimbriata* (Smith, 1879) (Attasopa & Warrit, 2012), has recently been photographed in Siem Reap Province (Fig. 2a) and Ratanakiri Province. A female of another species of *Amegilla* (*Glossamegilla*) with orange hair found in Ratanakiri Province is identified tentatively as *A. himalajensis* (Radoszkowski), based in part on the orange rather than black background colour of the clypeus. A female and a sleeping male of what appears to be the same species have been photographed by GC in Koh Kong Province. Smaller-bodied species in the *Zonamegilla* subgenus are abundant in Cambodia, and at least three species occur in Seima WS alone. This subgenus is taxonomically difficult (see Engel & Baker, 2006) and prevents reliable identification of all species at present, but

we have been able to identify some taxa to species or morphospecies by referring to an unpublished thesis by K. Attasopa (supervised by N. Warrit). These *Zonamegilla* are parasitized by species of *Thyreus*, of which the widespread *T. himalayensis* (Radoszkowski, 1893) (Fig. 2f) was recorded in the taxonomic revision by Lieftinck (1962).

Discussion

The present work summarizes the known bee diversity of Cambodia to the extent currently feasible based the scant historical literature and initial reports of ongoing explorations by scientists and citizen scientists. Both the November 1957–1958 expedition by the Osaka City University (Sakagami & Yoshikawa, 1960) and the authors expedition in 2016 were conducted during the dry season, an unfavourable time for bee collecting due to scarcity of flowers, so both expeditions likely overlooked many species that could be collected under more favourable conditions, i.e. when more diverse and abundant flowers are in bloom. With thorough collections, additional genera will undoubtedly be found in Cambodia. These will certainly include the following genera widespread in tropical Southeast Asia: *Ceylalictus* (Halictidae: Nomiodini), *Sphcodes* (Halictidae: Halictinae), and *Euaspis* (Megachilidae: Anthidiini; see Pasteels, 1980; Baker, 1995). *Ctenoplectra* (Apidae: Apinae: Ctenoplectrini) should be detected if collections can be made from oil-producing cucurbitaceous host plants. Several additional bee genera favouring temperate climates such as *Andrena* (mining bees) and *Bombus* (bumble bees) have been recorded from the mountains of neighbouring Southeast Asian countries and may also be found in Cambodia when its higher mountains are properly surveyed, although these may prove to be too low in elevation and too far south to support other genera with temperate affinities.

Many dozens of bee species unquestionably remain to be discovered in Cambodia and many of these will prove to be new to science (including enigmatic species reported and illustrated in this study). The 82 species and morphospecies recorded here from Cambodia, while a very incomplete account of the total fauna, still represent a major advance in documentation for the country's bees. Species recorded to date include many abundant and conspicuous pollinators and those of greatest economic importance and much additional taxonomic work will be required to describe potential new taxa to science already discovered and to verify preliminary species identifications. This will require study of type material which is

mostly housed in European collections and benefit from integrative taxonomy incorporating molecular diagnostic markers such as DNA barcodes.

Too little is known about the Southeast Asian bee fauna in general and that of Indochina and the other monsoonal countries in particular to definitively compare the Cambodian bee fauna with that of neighbouring countries. Despite the discoveries reported here, Cambodia still has the smallest known bee fauna of the countries considered, with the 82 species and morphospecies reported here being far fewer than the 222 described species now known to occur in Thailand, and also fewer than the 83 and 86 described species now known from Vietnam and Laos respectively. If more extensive morphospecies totals were available for countries in the region alongside Cambodia, these would increase the discrepancy in known taxonomic richness, as many unnamed morphospecies are documented by DNA barcodes and images within the Barcode of Life Database for bees (L. Packer, pers. comm.). In comparison to neighbouring countries, Cambodia shares the highest number of shared species and morphospecies with Thailand (57) and the second highest total (44) and highest percentage of shared species with Laos. Since a high proportion of species in the better known highly eusocial taxa such as *Apis* and the Meliponini are shared among countries, we also expect additional faunal overlap will be documented among solitary species as these become better known.

Acknowledgements

The authors would like to thank the Forestry Administration for permission to access field sites in Monduliri, where the Wildlife Conservation Society generously supported our stay at Seima WS headquarters and arranged for forest guides. We thank Dr. Adeline Seah for leading the molecular portion of our Hymenoptera workshop, planning the fieldwork, collecting noteworthy bees and commenting on the manuscript. Gabriel Low of NUS also assisted our fieldwork in Monduliri. Korrawat Attasopa and Natapot Warrit shared an unpublished manuscript on the *Amegilla* of Thailand arising from the former's thesis. Martin Schwarz and Max Schwarz of Austria made Southeast Asian material from their collections available for study, some previously identified by Stephan Risch, which proved invaluable for understanding the regional fauna. Claus Rasmussen shared useful bibliographic files prepared in part for an FAO report organized by Barbara Gemmill-Herren and Laurence Packer provided helpful comments on the manuscript.

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About the Authors

JOHN S. ASCHER is an American biologist working as an Assistant Professor in the Department of Biology, National University of Singapore. He is a research associate of the Lee Kong Chian Natural History Museum and also the American Museum of Natural History in New York City where he worked for several years developing collaborative bee databases. He maintains an online compilation of the taxonomy and distribution of world bees and publishes research with his students and other collaborators on the systematics, biogeography, ecology, behavior, and conservation of bees and related wasps.

HEANG PHALLIN is a Cambodian research assistant and curator at the Cambodian Entomology Initiatives (CEI). She has assisted entomological research in Cambodia since 2014 with the CEI and is currently studying an Masters in Biodiversity Conservation at the Royal University of Phnom Penh (RUPP). She is interested in taxonomy and is currently developing a database to support her thesis on the diversity of Cambodian bee pollinators.

KHEAM SOKHA is a Cambodian biologist who currently works at the Department of Biology, RUPP. He is a co-founder of the CEI and has undertaken research on Hemiptera (Membracoidea) and Hymenoptera in Cambodia since 2013. He also teaches biological science at the RUPP and is currently conducting a study on the diversity of ants in Phnom Penh.

LY KANG is a Cambodian research assistant and entomological curator at the CEI and has an interest in Membracoidea (leaf-hoppers and tree-hoppers). He is currently assisting CEI to develop databases for the Membracoidea and other Cambodian insects.

LORN SOKCHAN is a Cambodian research assistant at the CEI and has assisted laboratory work and insect collecting activities since 2015. He is currently studying Biological Sciences at the RUPP and has an interest in

rice insect pests (Cicadellidae and Delphacidae) in Cambodia.

CHUI SHAO XIONG is a research assistant in the Insect Diversity Lab, Department of Biological Sciences, National University of Singapore, where he also did his undergraduate research on the pollination ecology and conservation of stingless bees (Meliponini). His roles in the lab include the collection, curation, imaging, databasing, and mapping of Hymenoptera in Singapore and Southeast Asia.

STÉPHANE DE GREEF is a Belgian environmental engineer who has lived in Cambodia since 2002. Since 2007, he has independently documented the arthropods of Siem Reap province, building a photographic database

of all insects and arachnid species encountered in the Angkor Archaeological Park. He recently described the predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia.

GERARD CHARTIER is an amateur naturalist living in the foothills of the Cardamom Mountains in Southwest Cambodia. He has studied the wildlife there for the past seven years.

PHAUK SOPHANY is a Cambodian entomologist and co-founder of the CEI at the Department of Biology, RUPP. He has been involved in capacity building and raising awareness of Cambodian insect fauna since 2013. He teaches entomology at RUPP and has an interest in insect ecology and the taxonomy of Membracoidea.

Appendix 1 Checklist of the Bees of Cambodia

The following list compiles data from the literature on bees in Cambodia, bee sampling collected to date by CEI team, image databases of SDG and other photographers resident in Cambodia and preliminary results of CEI-NUS collections in Monduliri Province in 2016. Species records for Thailand, Laos and Vietnam are taken from Ascher & Pickering (2016) with reference to the literature and studies of collections including those mentioned above.

Note: KP – Kep; KC – Kampong Cham; KG – Kampong Chhnang; KH – Kratie; KK – Koh Kong; KS – Kampong Speu; KT – Kampot; MK – Monduliri; PH – Preah Vihear; PO – Pursat; PP – Phnom Penh; RO – Ratanakiri; SI – Siem Reap; ST – Stung Treng; TA – Takeo.

No.	Taxon (Apoidea)	Cambodia	Thailand	Laos	Vietnam
COLLETIDAE					
Colletinae					
1	<i>Hylaeus</i> sp. [cf. <i>H. (Nesoprosopis) penangensis</i> (Cockerell, 1920)]	KK, MK	-	-	-
2	<i>Hylaeus (Paraprosopis)</i> sp.	MK	-	-	-
HALICTIDAE					
Nomiinae: Nomiini					
3	<i>Lipotriches (Austronomia) laminatrochanter</i> (Pauly, 2009)	KS	*	-	*
4	<i>Lipotriches (Macronomia) angkorensis</i> (Pauly, 2009)	SI	*	*	*
5	<i>Lipotriches (Maynenomia) indochinensis</i> (Pauly, 2009)	SI	*	*	*
6	<i>Lipotriches (Maynenomia)</i> n. sp. (Fig. 2d)	KK, SI	-	-	-
7	<i>Nomia (Acunomia) iridescens</i> Smith, 1857	SI	*	-	*
8	<i>Nomia (Acunomia) strigata</i> (Fabricius, 1793)	SI	*	*	-
9	<i>Nomia (Maculonomia) nitidata</i> Strand, 1913, new status	MK	-	*	*
10	<i>Nomia (Maculonomia) sanguinea</i> (Pauly, 2009) [new subspecies?]	SI	*	*	-

Appendix 1 (cont'd)

No.	Taxon (Apoidea)	Cambodia	Thailand	Laos	Vietnam
11	<i>Nomia</i> (<i>Maculonomia</i>) aff. <i>penangensis</i> Cockerell, 1920	MK	*	*	-
12	<i>Nomia</i> (<i>Maculonomia</i>) n. sp. (Figs. 4b,c)	MK	-	-	-
13	<i>Nomia</i> (<i>Gnathonomia</i>) <i>aurata</i> Bingham, 1897	PP	*	*	-
14	<i>Nomia</i> (<i>Gnathonomia</i>) <i>cambodiana</i> (Pauly, 2009)	SI	*	*	*
15	<i>Nomia</i> (<i>Gnathonomia</i>) <i>thoracica</i> Smith, 1875	SI	*	*	*
16	<i>Nomia</i> (<i>Hoplonomia</i>) <i>elliottii</i> Smith, 1875	MK	*	-	-
17	<i>Pseudapis</i> (<i>Pseudapis</i>) <i>siamensis</i> (Cockerell, 1929)	KS, PP	*	-	-
Halictinae: Halictini					
18	<i>Eupetersia</i> (<i>Nesoeupetersia</i>) <i>yanegai</i> Pauly, 2012	KK, MK	*	-	-
19	<i>Lasioglossum</i> (<i>Ctenonomia</i>) <i>albescens</i> (Smith, 1853)	MK	*	*	*
20	<i>Lasioglossum</i> (<i>Ctenonomia</i>) <i>deliense</i> (Strand, 1910)	KS	-	-	-
21	<i>Lasioglossum</i> (<i>Ctenonomia</i>) <i>vagans</i> (Smith, 1857)	MK	*	-	-
22	<i>Lasioglossum</i> (<i>Homalictus</i>) sp. [<i>Indohalictus</i> group] (Fig. 4a)	MK	-	-	-
23	<i>Patellapis</i> (<i>Pachyhalictus</i>) sp.	MK	-	-	-
MEGACHILIDAE					
Lithurginae: Lithurgini					
24	<i>Lithurgus</i> <i>collieri</i> Cockerell, 1929	MK	*	-	-
Megachilinae:					
Anthidiini					
25	<i>Anthidiellum</i> (<i>Ranthidiellum</i>) aff. <i>meliponiforme</i> (Cockerell, 1919)	MK	-	-	-
26	<i>Pseudoanthidium</i> (<i>P.</i>) <i>orientale</i> (Bingham, 1897) (Fig. 5b)	MK	*	-	-
Megachilini					
27	<i>Heriades</i> (<i>Michenerella</i>) <i>othonis</i> Friese, 1914	MK	-	*	-
28	<i>Megachile</i> (<i>Callomegachile</i>) aff. <i>disjuncta</i> (Fabricius, 1781)	RO	-	-	-
29	<i>Megachile</i> (<i>Callomegachile</i>) aff. <i>faceta/facetula</i>	RO	-	-	-
30	<i>Megachile</i> (<i>Callomegachile</i>) aff. <i>umbripennis</i> Smith, 1853	PP	-	-	-
31	<i>Megachile</i> (<i>Chelostomoda</i>) <i>aureocincta</i> Cockerell, 1927	MK	*	*	-
32	<i>Megachile</i> (<i>Chelostomoda</i>) sp. [tergal hair bands white]	SI	-	-	-
33	<i>Megachile</i> (<i>Lophanthedon</i>) <i>dimidiata</i> Smith, 1853 (Fig. 2e)	SI	-	-	*
34	<i>Megachile</i> (<i>Amegachile</i>) <i>bicolor</i> (Fabricius, 1781)	KS	*	-	-
35	<i>Megachile</i> (<i>Paracella</i>) <i>tricincta</i> Bingham, 1897	KK	*	*	-
36	<i>Megachile</i> (<i>Paracella</i>) sp. [not <i>tricincta</i>]	MK	-	-	-
37	<i>Megachile</i> sp. [resembles <i>M. atrata</i> Smith, 1853, nests in sand]	SI	-	-	-
38	<i>Coelioxys</i> (<i>Allocoelioxys</i>) sp.	MK	-	-	-
APIDAE					
Xylocopinae: Xylocopini					
39	<i>Xylocopa</i> (<i>Koptortosoma</i>) <i>bryorum</i> (Fabricius, 1775)	PP	*	-	*

Appendix 1 (*cont'd*)

No.	Taxon (Apoidea)	Cambodia	Thailand	Laos	Vietnam
40	<i>Xylocopa (Koptortosoma) caerulea</i> (Fabricius, 1804)	KA, KK	*	*	-
41	<i>Xylocopa (Koptortosoma) minor</i> Maidl, 1912	widespread ¹	*	*	*
42	<i>Xylocopa (Zonohirsuta) dejeanii</i> Lepeletier, 1841 [for ssp. see text]	KK, SI	*	*	*
43	<i>Xylocopa (Platynopoda) latipes</i> (Drury, 1773)	KK, KP	*	*	*
44	<i>Xylocopa (Biluna) nasalis</i> Westwood, 1838	PP, SI	*	*	-
45	<i>Xylocopa (Platynopoda) tenuiscapa</i> Westwood, 1840	SI	*	*	-
Ceratinini					
46	<i>Ceratina (Ceratinidia) bryanti</i> Cockerell, 1919	MK	*	-	-
47	<i>Ceratina (Ceratinidia) collusor</i> Cockerell, 1919	MK	*	*	-
48	<i>Ceratina (Ceratinidia) lieftincki</i> van der Vecht, 1952	MK, SI	*	*	-
49	<i>Ceratina (Ceratinidia) nigrolateralis</i> Cockerell, 1916	MK	*	*	*
50	<i>Ceratina (Neoceratina) dentipes</i> Friese, 1914 (Fig. 2c)	MK, SI	*	-	-
51	<i>Ceratina (Neoceratina) sp. 1</i> [smaller than <i>dentipes</i>]	MK	-	-	-
52	<i>Ceratina (Pithitis) smaragdula</i> (Fabricius, 1787)	widespread ¹	*	*	*
53	<i>Ceratina (Pithitis) unimaculata</i> Smith, 1879	MK	*	*	*
54	<i>Ceratina (Xanthoceratina) aff. fuliginosa</i> Cockerell, 1916 (Fig. 3c)	MK	-	-	-
55	<i>Ceratina (Xanthoceratina) aff. humilior</i> Cockerell, 1916 (Fig. 3d)	MK	*	-	-
Allodapini					
56	<i>Braunsapis clarihirta</i> Reyes, 1991	MK	*	-	*
57	<i>Braunsapis hewitti</i> (Cameron, 1908)	MK	*	*	*
58	<i>Braunsapis philippinensis</i> (Ashmead, 1904)	MK	*	*	*
Nomadinae: Nomadini					
59	<i>Nomada</i> sp. [small, with <i>Lasioglossum (Homalictus)</i>] (Fig. 3a)	MK	-	-	-
Apinae: Anthophorini					
60	<i>Amegilla (Zonamegilla) anakawarna</i> Engel, 2007	MK	*	-	-
61	<i>Amegilla (Glossamegilla) fimbriata</i> (Smith, 1879) (Fig. 2b)	KK, SI	*	-	-
62	<i>Amegilla (Glossamegilla) himalajensis</i> (Radoszkowski, 1882)	KK, RO	-	*	*
63	<i>Amegilla (Zonamegilla) parhypate</i> Lieftinck, 1975	MK	*	-	-
64	<i>Amegilla (Zonamegilla) cf. sp. 2</i> of Attasopa and Warrit, unpub.]	MK	*	-	-
65	<i>Thyreus himalayensis</i> (Radoszkowski, 1893) (Fig. 2f)	PO, SI	*	*	*
Apini					
66	<i>Apis (Apis) cerana</i> Fabricius, 1793	widespread ²	*	*	*
67	<i>Apis (Megapis) dorsata dorsata</i> Fabricius, 1793	widespread ²	*	*	*
68	<i>Apis (Micrapis) andreniformis</i> Smith, 1857	KK, MK	*	*	*
69	<i>Apis (Micrapis) florea</i> Fabricius, 1787	widespread ²	*	*	*
Meliponini					
70	<i>Geniotrigona thoracica</i> (Smith, 1857)	KP	*	*	*

Appendix 1 (cont'd)

No.	Taxon (Apoidea)	Cambodia	Thailand	Laos	Vietnam
71a	<i>Homotrigona fimbriata</i> (Smith, 1857) [<i>aliceae</i> (Cockerell, 1929)]	widespread ³	*	-	-
71b	<i>Homotrigona fimbriata</i> (Smith, 1857) [<i>anamitica</i> (Friese, 1908)]	MK ³	-	*	*
72	<i>Lepidotrigona terminata</i> (Smith, 1878)	widespread ⁴	*	*	*
73	<i>Lepidotrigona ventralis</i> (Smith, 1857) [= <i>flavibasis</i> (Cockerell)]	MK	*	*	*
74	<i>Lisotrigona cacciae</i> (Nurse, 1907)	MK, SI	*	*	*
75	<i>Lisotrigona carpenteri</i> Engel, 2000 (Fig. 3b)	MK	-		*
76	<i>Lisotrigona furva</i> Engel, 2000	MK	*	*	-
77	<i>Tetragonilla collina</i> (Smith, 1857)	widespread ⁵	*	*	*
78	<i>Tetragonula fuscobalteata</i> (Cameron, 1908)	widespread ⁶	*	*	*
79	<i>Tetragonula geissleri</i> (Cockerell, 1918)	KK, MK	*	*	-
80	<i>Tetragonula</i> sp. [cf. <i>laeviceps</i> (Smith, 1857)]	PP?, SI?, ST?	*	*	*
81	<i>Tetragonula pagdeni</i> (Schwarz, 1939)	KC, KK, PP ⁷	*	*	*
82	<i>Tetrigona apicalis</i> (Smith, 1857)	MK, ST	*	*	*
Total Species [For Cambodia and shared with Cambodia (including morphospecies) and, in parentheses, total known described species (not including all known morphospecies)]		82	57 (222)	44 (86)	36 (83)

¹ Subsocial bee species recorded from four provinces, *X. minor*: KC, KP, PP & SI; *C. smaragdula*: KK, KP, MK & RO.

² Expected to occur in all provinces and recorded from the following: *A. cerana*: KC, KK, KS, MK, PO, PP, SI & ST; *A. dorsata dorsata*: KK, KS, KT, MK, PP, SI & ST; *A. florea*: KC, KG, KK, KS, MK, PP, SI & TA.

³ Among stingless bees, two colour forms of *Homotrigona fimbriata sensu lato* recognized as valid species are listed separately but counted as a single species in the species totals. The form *aliceae* was recorded by us from KC & SI, and by Lee *et al.* (2016, accepted version) from MK, PH & SR, whereas our specimens from MK represent the *anamitica* (Friese) form.

⁴ Recorded by us from four provinces: KH, MK, SI & ST.

⁵ Recorded by us from MK, OM, SI & ST, and by Lee *et al.* (2016, accepted version) from PO & SI.

⁶ Recorded by us from KK & PP, and by Lee *et al.* (2016, accepted version) from PO, PH & SI.

⁷ Recorded by us from KK & PP, and by Lee *et al.* (2016, accepted version) from KK.

Cambodian Journal of Natural History

The preparation and printing of this volume was generously supported by:

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The present issue was also supported by a major foundation that chooses to remain anonymous.

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The Editors are grateful to our reviewers for their kind assistance with the production of this issue.

Cambodian Journal of Natural History

Volume 2016, Number 1

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71 Recent literature from Cambodia, *Neil M. Furey.*

74 Instructions for Authors.

