

Article

High Diversity in Urban Areas: How Comprehensive Sampling Reveals High Ant Species Richness within One of the Most Urbanized Regions of the World

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Abstract: The continuous increase in urbanization has been perceived as a major threat for biodiversity, particularly within tropical regions. Urban areas, however, may still provide opportunities for conservation. In this study focused on Macao (China), one of the most densely populated regions on Earth, we used a comprehensive approach, targeting all the vertical strata inhabited by ants, to document the diversity of both native and exotic species, and to produce an updated checklist. We then compared these results with 112 studies on urban ants to illustrate the dual roles of cities in sustaining ant diversity and supporting the spread of exotic species. Our study provides the first assessment on the vertical distribution of urban ant communities, allowing the detection of 55 new records in Macao, for a total of 155 ant species (11.5% being exotic); one of the highest species counts reported for a city globally. Overall, our results contrast with the dominant paradigm that urban landscapes have limited conservation value but supports the hypothesis that cities act as gateways for exotic species. Ultimately, we argue for a more comprehensive understanding of ants within cities around the world to understand native and exotic patterns of diversity.

Keywords: biological invasions; biodiversity; species checklist; urban ecology; conservation



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Citation: Brassard, F.; Leong, C.-M.; Chan, H.-H.; Guénard, B. High Diversity in Urban Areas: How Comprehensive Sampling Reveals High Ant Species Richness within One of the Most Urbanized Regions of the World. *Diversity* **2021**, *13*, 358. <https://doi.org/10.3390/d13080358>

Academic Editor: Michael Wink

Received: 2 July 2021

Accepted: 29 July 2021

Published: 4 August 2021

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1. Introduction

Over the past century, urbanization has increased drastically in most regions around the world [1–3]. This increase threatens biodiversity [4–6], with pollution [7–9], habitat loss [10], and the spread of invasive species [11] being major causes of local species extinction or population decline. As such, urban habitats have historically been considered as species-poor concrete jungles [12]. However, urban environments are not necessarily depauperate ecosystems, and may, in fact, have some degree of conservation value by harboring native species [13]. Recent studies suggest that urban habitats can harbor a high diversity of both native (including endemic species) and non-native species, and even, sometimes, surpass surrounding rural areas in terms of species richness [12–16]. The survey and monitoring of biodiversity within cities may thus allow the identification of novel habitats and species worthy of protection within urban matrices. In particular, urban habitats including large and high quality patches of green spaces and forest fragments may still support high species diversity [17–20]. How much biodiversity these areas can contain is still open for debate, but it is paramount to understand the potential conservation value of urban centers.

Beyond assessing the number of species in cities, another crucial component to consider is the composition and identity of the species present. Indeed, cities can facilitate invasions by non-native species in part due to their high level of disturbance, which provides ecological niches suitable for many exotic species [21–23]. Moreover, the constant flux of merchandise in and out of urban centers through airports, harbors, and train stations make them the ideal gateways for exotic species introductions with the common arrival of new propagules [24–26]. Consequently, surveying urban centers and their surroundings to detect new arrivals is essential to limit their spread and mitigate their potential impact on native biodiversity. This is especially true for coastal regions, which host the highest richness of exotic species [27], and, in the case of China, may represent a source of spread towards more inland regions [28].

To evaluate the biodiversity value of urban environments, surveying all flora and fauna would be ideal, but unrealistic, especially for tropical and subtropical regions where there is limited data and taxonomic knowledge. As such, ecological surveys must select a subset of taxa representing useful biodiversity proxies. For conservation monitoring purposes, ants represent an ideal taxon [29]. Indeed, their taxonomy is relatively well-resolved in comparison with most other diverse insect groups, and they can be sampled through the use of standardized and replicable protocols [30]. They are also ecologically and taxonomically diverse, abundant, and ubiquitous [31]. Moreover, they are adequate bioindicators [32,33], play key ecological roles as predators, scavengers, and herbivores [31,32,34,35], with some species acting as ecosystem engineers by modifying soil properties [34].

Ants also include some of the most damaging invasive species, impacting native ants [35–37], non-ant invertebrates [38], vertebrates [39], and plant communities [40], ultimately causing ecosystem disruptions [41]. Invasive ant species can also negatively impact human socioeconomic activities such as farming or education [42], whereas others are considered household pests [43,44], with some exotic species even acting as vectors of pathogens in hospitals [45,46]. Thus, surveying the ant fauna of urban regions and producing ant species checklists should be an important tool not only to evaluate the conservation value of cities, but also to record the worldwide spread of exotic species.

To date, the majority of studies have been limited to ecological studies (Table 1), limited in time and space, and using only a subset of sampling methods to characterize urban ant communities. However, establishing an exhaustive list of a region's ant fauna presents multiple concerns and challenges. For instance, within a specific habitat, and especially within tropical regions, distinct ant species are stratified along the vertical strata (i.e., from underground to the canopy) [47–51]. Generally, ants can be classified into three broad categories: arboreal, epigeic (i.e., ground surface-dwelling, including ants living in leaf litter), and hypogeic (i.e., subterranean). To perform a complete inventory of ants within a region, surveys should, thus, include the different dimensions of this vertical stratification by using methods targeting species from each microhabitat. Unfortunately, most studies in urban habitats use sampling methods focusing mainly or solely on epigeic ants [52], thereby potentially under-estimating the species richness and composition of local communities, as well as the magnitude of invasions. Additionally, this may misrepresent the diversity of hypogeic and arboreal ants within urban habitats and overlook the potential discovery of undescribed species [53–55].

Considering the current expansion of urban habitats [1], describing patterns in urban ant diversity is of great urgency. This is essential to foster biodiversity in cities, but also to gain a better understanding of which factors may facilitate the spread of exotic species. To the best of our knowledge, however, few cities have comprehensive ant species checklists, especially in tropical Asia (Figure 1, Table 1), which makes meaningful comparisons in urban biodiversity challenging at best. More biodiversity surveys and checklists are, thus, required to address this issue.

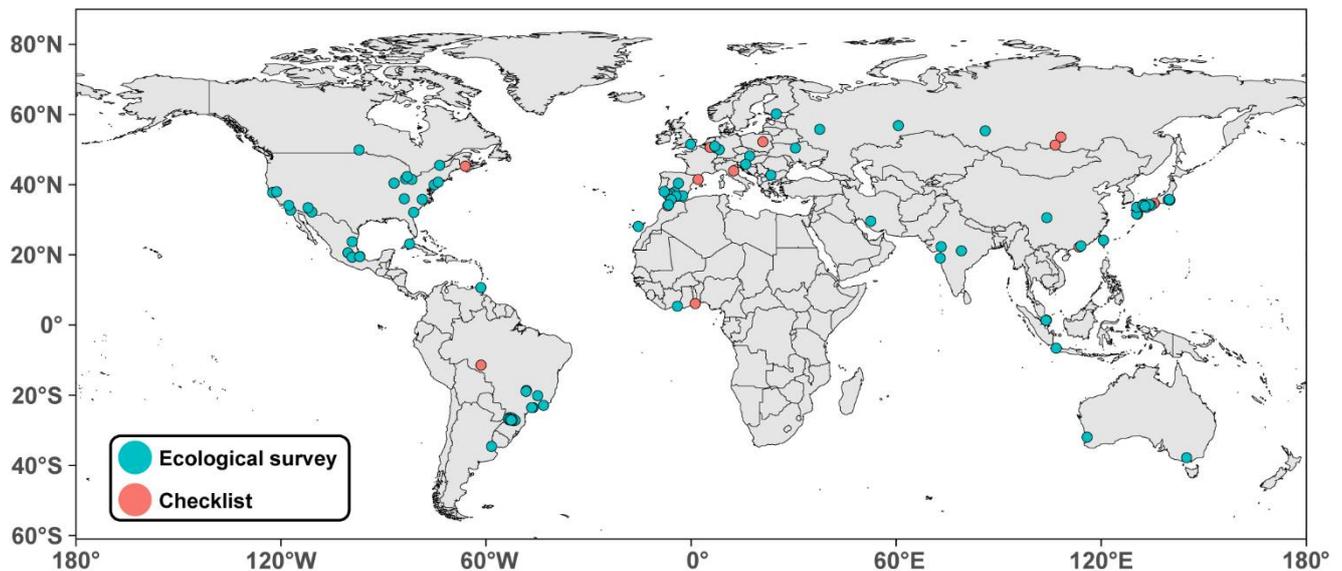


Figure 1. World map showcasing the locations of studies compiled in Table 1. Points show urban locations for which ant species richness estimates were available. Color indicates the type of study (i.e., ecological survey or checklist, see legend).

One such region is the Guangdong–Hong Kong–Macao Greater Bay Area, a major Asian megalopolis [56]. Located in subtropical China, it covers an area of 56,000 km² and has a combined population of 68 million people [56]. Within the Greater Bay Area, Macao can be distinguished by its human density, which exceeds 20,000 hab./km², making it the most densely populated region on the planet [57,58]. Macao also represents an historical global hotspot in its role within the global trade exchange, first within the Portuguese network and then within China [59,60], making it particularly vulnerable to biological invasions. Finally, the development of Macao has led to a complex matrix of habitats with various levels of disturbance. As such, Macao represents a unique opportunity to better understand how much biodiversity a city characterized by extreme urban development may contain and assess the role of cities as gateways for exotic species.

Following the publication of a preliminary checklist of the ant species of Macao [53] and the discovery of a new subterranean ant species [61], a new survey was conducted across Coloane Island, in the southern half of Macao. To our knowledge, our survey is the first to use an exhaustive sampling approach covering all vertical strata inhabited by ants within an urban area (i.e., arboreal, ground-dwelling, and subterranean). We hypothesized that this sampling coverage would uncover a substantial amount of new species records, give a fair representation of the ant species richness of Macao, and detect new introductions of exotic species. Moreover, we expected that this methodology, which could be replicated across cities around the world, would be particularly useful for finding cryptic and potentially undescribed species. Finally, we compare our results with previous published studies on urban ants to illustrate the potential that cities may represent for ant diversity, but also more broadly for other insect groups.

Table 1. Ecological and taxonomic studies that produced ant species richness values for a city. Studies are classified by a function of their study region and ranked by the function of the overall species richness retrieved. Studies not providing a complete species list or without enough information on habitats sampled were not included. (*) Complete list of species not provided in article, (**) a combination of 3 articles by the same author and in the same city, and (***), richness value is a combination of more than one urban region.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Africa (7)							
Kouakou et al. 2018 [62]	ecological survey	Abidjan, Ivory Coast	5.3	422	170	6	176
Yeo et al. 2016 [63]	ecological survey	Abidjan, Ivory Coast	5.3	422	83	8	91
Kassenev et al. 2019 [64]	checklist	Lomé (Togo)	6.1	99.1	41	2	43
Taheri et al. 2017 [65]	ecological survey	Tangier, Morocco	35.76	116	30	8	38
Bernard 1958 [66]	checklist	Rabat, Kenitra and Tangier, Morocco	34.3 to 35.8	905 (multiple cities included)	5 ***	11 ***	16 ***
Bernard 1974 [67]	ecological survey	Kenitra, Morocco	34.3	112	13	0	13
Reyes-Lopez and Carpintero 2014 [68]	ecological survey	Las Palmas, Canary Islands	28.2	100.6	6	6	12
Asia (42)							
Ito et al. 2001 [69]	checklist	Bogor, Java, Indonesia	−6.6	118.5	202	11	213
This study	checklist	Macao, SAR, China	22.2	32.9	137	18	155
Leong et al. 2017 [61]	checklist	Macao, SAR, China	22.2	32.9	88	10	98
Rizali et al. 2008 [70]	ecological survey	Bogor, West Java, Indonesia	−6.6	118.5	82	12	94
Terayama 2005a,b and 2014 [71–73]	ecological survey **	Tokyo, Japan	35.7	2194.1	54	0	54
Matsumura and Yamane 2012 [74]	ecological survey	Kagoshima City, Japan	31.6	547.6	48	3	51
Liu et al. 2019 [75]	ecological survey	Taichung City, Taiwan	24.2	2215	?	?	50 *
Natuhara 1998 [76]	checklist	Osaka City, Japan	34.7	225.2	44	5	49
Tan and Corlett 2012 [77]	ecological survey	Singapore	1.3	728.3	38	4	42
Harada et al. 2012 [78]	checklist	Isa City, Japan	32.1	392.4	40	0	40
Iwata, Eguchi and Yamane 2005 [79]	ecological survey	Kagoshima City, Japan	31.6	547.6	37	2	39
Yamaguchi 2004 [80]	ecological survey	Chiba, Japan	35.6	271.8	37	1	38
Park et al. 2014a [81]	ecological survey	Fukuoka City, Japan	33.6	343.4	35	3	38
Matsumura and Yamane 2012 [74]	ecological survey	Kagoshima City, Japan	31.6	547.6	36	2	38
Wang et al. 2012 [82]	ecological survey	Shenzhen, Guangdong, China	22.5	2050	29	6	35

Table 1. Cont.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Khot et al. 2014 [83]	ecological survey	Mumbai, Maharashtra, India	19.1	603	25	3	28
Yamaguchi 2004 [80]	ecological survey	Tokyo, Japan	35.7	2194.1	27	1	28
Hiroyuki 2012 [84]	checklist	Matsuyama, Japan	33.8	429.4	28	0	28
Harada et al. 2021 [85]	ecological survey	Kagoshima City, Japan	31.6	547.6	21	6	27
Miyake et al. 2002 [86]	ecological survey	Hatsukaichi City, Japan	34.4	489.4	22	4	26
Tan et al. 2009 [87]	ecological survey	Chengdu, Sichuan, China	30.7	885.6	24	2	26
Park et al. 2014b [88]	ecological survey	Hiroshima city, Japan	34.4	906.7	21	4	25
Touyama, Ogata and Sugiyama 2003 [89]	ecological survey	Hatsukaichi and Hiroshima city, Japan	34.4	1395 (multiple cities included)	23 ***	1 ***	24 ***
Harada and Yamashita, 2019 [90]	ecological survey	Tokushima, Japan	34.1	191	21	1	22
Yasuda and Koike 2009	ecological survey	Matsudo, Japan	35.8	61.4	?	?	22 *
Malozemova and Malozemov 1999 [91]	ecological survey	Yekaterinburg, Russia	56.8	495	20	1	21
Harada 2020 [92]	ecological survey	Hioki City, Japan	31.6	253.1	16	3	19
Roshanak et al. 2017 [93]	ecological survey	Shiraz, Iran	29.6	240	19	0	19
Hosoishi et al. 2019 [94]	ecological survey	Fukuoka City, Japan	33.6	343.4	17	1	18
Terayama et al. 2006 [95]	ecological survey	Iwakuni City, Japan	34.2	873.7	14	2	16
Putyatina et al. 2017 [96]	ecological survey	Moscow, Russia	55.8	2511	16	0	16
Kumar and Archana 2008 [97]	ecological survey	Vadodara, Gujarat, India	22.3	220	15	0	15
Harada and Yamashita, 2019 [90]	ecological survey	Kochi, Japan	33.6	309.2	15	0	15
Terayama et al. 2006 [95]	ecological survey	Iwakuni City, Japan	34.2	873.7	12	2	14
Antonov 2008 [98]	checklist	Irkutsk, Baikal, Russia	52.3	277	14	0	14
Harada and Yamashita, 2019 [90]	ecological survey	Takamatsu, Japan	34.4	375.4	14	0	14
Harada and Yamashita, 2019 [90]	ecological survey	Matsuyama City, Japan	33.8	429.4	12	1	13
Hosaka et al. 2019 [99]	ecological survey	Tokyo, Japan	35.7	2194.1	11	0	11
Antonov 2008 [98]	checklist	Gusinoozersk, Baikal, Russia	51.3	?	7	0	7
Blinova 2008 [100]	ecological survey	Kemerovo, Russia	55.4	282.3	7	0	7

Table 1. Cont.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Meshram et al. 2015 [101]	ecological survey	Nagpur, Maharashtra, India	21.2	393.5	25 (genera)	3	NA *
Yong et al. 2017 [102]	checklist	Pulau Aubin, Singapore	1.3	10.2	35 (genera)	2 (no total mentioned)	NA *
Australia (6)							
Ossola et al. 2015 [103]	ecological survey	Melbourne, Australia	−37.8	9993	59 *	1 *	60
Heterick et al. 2013 [104]	ecological survey	Perth, Australia	−32.0	6418	54	6	60
Majer and Brown 1986 [105]	ecological survey	Perth, Australia	−32.0	6418	45	2	47
Callan and Majer 2009 [106]	ecological survey	Perth, Australia	−32.0	6418	32	4	36
Heterick et al. 2000 [107]	ecological survey	Perth, Australia	−32.0	6418	19	8	27
May and Heterick 2000 [108]	ecological survey	Perth, Australia	−32.0	6418	18	8	26
Europe (28)							
Radchenko et al. 2019 [109]	checklist	Kyiv, Ukraine	50.5	839	55	4	59
Ordóñez-Urbano, Reyes-López and Carpintero-Ortega 2008 [110]	ecological survey	Córdoba, Sevilla, Málaga and Cádiz, Spain	36.5–37.9	>1800 (multiple cities included)	?	?	59 *,***
Antonova and Penev 2006 [111–113]	ecological survey	Sofia, Bulgaria	42.7	492	54	0	46
Dauber 1997 [114]	ecological survey	Mainz, Germany	50.0	97.7	49	0	49
Dauber and Eisenbeis [114]	ecological survey	Mainz, Germany	50.0	97.7	46	0	46
Reyes-Lopez and Carpintero 2014 [68]	ecological survey	Cordoba and Seville, Spain	37.4 and 37.9	1393 (multiple cities included)	39 ***	5 ***	44 ***
Pisarski and Czechowski 1978 [115]	checklist	Warsaw, Poland	52.2	517.2	36	1	37
Pisarski 1982 [116]	checklist	Warsaw, Poland	52.2	517.2	35	2	37
Ruiz Heras et al. 2011 [117]	ecological survey	Madrid, Spain	40.4	604.3	36	1	37
Klesniakova et al. 2016 [118]	ecological survey	Bratislava, Slovakia	48.1	367.6	?	1 *	36 *
Trigos-Peral et al. 2020 [119]	ecological survey	Warsaw, Poland	52.2	517.2	32	2	34
Reyes-Lopez and Carpintero 2014 [68]	ecological survey	Almeria, Cadiz, Huelva and Malaga, Spain	36.5 to 37.3	859.1 (multiple cities included)	24 ***	8 ***	32 ***
Ješovnik and Bujan 2021 [120]	ecological survey	Zagreb, Croatia	45.8	641	30	0	30
Behr, Lippke and Cölln 1996 [121]	ecological survey	Köln (Cologne), Germany	51.0	405.1	25	3	28

Table 1. Cont.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Ślipiński et al. 2012 [122]	ecological survey	Warsaw, Poland	52.2	517.2	27	0	27
Behr and Cölln 1993 [123]	checklist	Gönnersdorf, Germany	50.5	5.2	27	0	27
Rigato and Wetterer 2018 [124]	checklist	San Marino	43.9	61.2	23	0	23
Espadaler and López-Soria 1991 [125]	checklist	Sant Cugat, Barcelona, Spain	41.5	48.2	22	1	23
Vepsäläinen, Ikonen and Koivula 2008 [126]	ecological survey	Helsinki, Finland	60.2	213.8	17	2	19
Trigos Peral and Reyes Lopez 2018 [127]	ecological survey	Beja, Portugal	38.0	1146	17	0	17
Vepsäläinen, Ikonen and Koivula 2008 [126]	ecological survey	Helsinki, Finland	60.2	185	16	0	16
Stukalyuk 2017 [128]	ecological survey	Kyiv, Ukraine	50.5	839	16	0	16
Reyes López and Taheri 2018 [129]	checklist	Cádiz, Andalusia, Spain	36.5	12.1	6	9	15
Smith et al. 2006 [130]	ecological survey	London, UK	51.5	1572	6	0	6
Gaspar and Thirion 1978 [131]	checklist	Liege, Belgium	50.6	69.4	6	0	6
N. America (22)							
Guénard et al. 2015 [16]	ecological survey	Raleigh, NC, USA	35.8	380	77	12	89
Nuhn and Wright 1979 [132]	checklist	Raleigh, NC, USA	35.8	380	50	6	56
Baena et al. 2019 [133]	ecological survey	Coatepec, Mexico	19.5	255.8	51	4	55
Menke et al. 2011 [134]	ecological survey	Raleigh, NC, USA	35.8	380	49	5	54
Miguelena and Baker 2019 [135]	ecological survey	Tucson, AZ, USA	32.2	623.6	45	3	48
Rocha-Ortega and Castano-Meneses 2015 [136]	ecological survey	Santiago de Querétaro, Mexico	20.6	363	45	3	48
Toennisson et al. 2011 [137]	ecological survey	Knoxville, TN, USA	36.0	270	44	2	46
Suarez et al. 1998 [138]	ecological survey	San Diego, CA, USA	32.7	964.6	42	4	46
Gochnour et al. 2019 [139]	ecological survey	Garden City, Georgia, USA	32.1	37.6	32	13	45
Savage et al. 2015 [140]	ecological survey	New York, NY, USA	40.7	778	36	6	42
Baena et al. 2019 [133]	ecological survey	Xalapa, Mexico	19.5	124.4	36	4	40
Uno S. pers. Comm. In Friedrich and Philpott 2009 [141]	ecological survey	Toledo, USA	39.9	217.1	?	?	35 *
García-Martínez et al. 2019 [142]	ecological survey	Ciudad Victoria, Mexico	23.7	188	28	4	32
Fairweather et al. 2020 [143]	checklist	St-John, NB, Canada	45.3	316	30	0	30

Table 1. Cont.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Uno, Cotton and Philpott 2010 [144]	ecological survey	Toledo, USA	41.7	217.1	28	2	30
Ivanov and Keiper 2010 [145]	ecological survey	Cleveland, Oh, USA	41.5	201	28	1	29
Uno, Cotton and Philpott 2010 [144]	ecological survey	Detroit, USA	42.3	370.1	26	1	27
Lessard and Buddle 2005 [146]	ecological survey	Montreal, CAN	45.5	431.5	23	1	24
Clarke, Fisher and LeBuhn 2008 [147]	ecological survey	San Francisco, CAL, USA	37.8	600.6	18	3	21
Buczkowski and Richmond 2012 [10]	ecological survey	West Lafayette, Indiana, USA	40.4	35.8	19	1	20
King and Green 1995 [148]	ecological survey	Philadelphia, PA, USA	40.0	369.6	18	1	19
Staubus et al. 2015 [149]	ecological survey	Claremont, CAL, USA	34.1	34.9	12	6	18
Pećarević et al. 2010 [150]	ecological survey	New York, NY, USA	40.7	778	10	3	13
Thompson and McLachlan 2007 [151]	ecological survey	Winnipeg, Manitoba, Canada	49.8	464.1	10	0	10
Villar and Ríos-Casanova [152]	ecological survey	La Cantera Oriente, Mexico city, Mexico	19.3	0.1	8	2	10
Stahlschmidt and Johnson 2018 [153]	ecological survey	Stockton, CAL, USA	38.0	169	4	5	9
Marussich and Faeth 2009 [154]	ecological survey	Phoenix, AZ, USA	33.4	1341	7	1	8
S. and C. America (31)							
Pacheco and Vasconcelos 2007 [155]	ecological survey	Uberlândia, Brazil	−18.9	4116	137	6	143
Santos et al. 2019 [156]	ecological survey	Rio de Janeiro, Brazil	−22.9	1221	116	4	120
Santos-Silva et al. 2016 [157]	checklist	Cacoal, Rondônia, Brazil	−11.4	3793	98	4	102
De Souza et al. 2012 [158]	ecological survey	Mogi das Cruzes, Brazil	−23.5	713	91	1	92
Lutinski et al. 2013 [159]	ecological survey	Chapecó, Santa Catarina, Brazil	−27.1	624.3	89	2	91
Munhae et al. 2014 [160]	ecological survey	Alto Tietê region, São Paulo, Brazil	−23.5	1455 (multiple cities included)	82 ***	5 ***	87 ***
Lutinski et al. 2013 [159]	ecological survey	Palmitos, Santa Catarina, Brazil	−27.1	350.7	81	4	85
Lutinski et al. 2013 [159]	ecological survey	Campo Erê, Santa Catarina, Brazil	−26.4	478.7	82	3	85
Lutinski et al. 2013 [159]	ecological survey	Xanxerê, Santa Catarina, Brazil	−26.9	377.8	80	3	83
Lutinski et al. 2013 [159]	ecological survey	São Miguel do Oeste, Santa Catarina, Brazil	−26.7	234.4	81	2	83

Table 1. Cont.

References	Study Type	Locality	Latitude	Area (km ²)	Natives	Exotics	Total
Lutinski et al. 2013 [159]	ecological survey	Abelardo Luz, Santa Catarina, Brazil	−26.6	953.6	81	2	83
Lutinski et al. 2013 [159]	ecological survey	Concórdia, Santa Catarina, Brazil	−27.2	800	80	2	82
Lutinski et al. 2013 [159]	ecological survey	Pinhalzinho, Santa Catarina, Brazil	−26.8	128.3	76	4	80
Lutinski et al. 2013 [159]	ecological survey	Joaçaba, Santa Catarina, Brazil	−27.1	232.4	76	3	79
Morini et al. 2007 [161]	ecological survey	São Paulo, Brazil	−23.6	1521.1	76	3	79
Lutinski et al. 2013 [159]	ecological survey	Seara, Santa Catarina, Brazil	−27.1	312.5	75	3	78
Iop et al. 2009 [162]	checklist	Xanxerê, Santa Catarina, Brazil	−26.9	377.8	45	2	67
Caldart et al. 2012 [163]	ecological survey	Chapecó, Santa Catarina, Brazil	−27.1	624.3	63	3	66
Ilha et al. 2017 [164]	ecological survey	Chapecó, Santa Catarina, Brazil	−27.1	624.3	60	3	63
Josens et al. 2017 [165]	ecological survey	Buenos Aires, Argentina	−34.6	203	57	3	60
Kamura et al. 2007 [166]	ecological survey	Mogi das Cruzes, São Paulo, Brazil	−23.5	713	49	9	58
Santiago et al. 2018 [167]	ecological survey	Divinópolis, Minas Gerais, Brazil	−20.1	192	55	0	55
De Souza-Campana et al. 2016 [168]	checklist	São Paulo, Brazil	−23.6	1521	46	1	47
Piva and de Carvalho Campos 2012 [169]	ecological survey	São Paulo, Brazil	−23.6	1521	38	6	44
Simonetti, Brito and Luis 2010 [170]	ecological survey	Havana City, Cuba	23.1	728.3	?	?	37*
Ribeiro et al. 2012 [171]	ecological survey	São Paulo, Brazil	−23.6	1521	33	3	36
Lutinski and Mello Garcia 2005 [172]	ecological survey	Chapecó, Santa Catarina, Brazil	−27.1	624.3	32	0	32
Lange et al. 2015 [173]	ecological survey	Araguari, Minas Gerais, Brazil	−18.6	2730.6	21	2	23
Starr and Ballah 2017 [174]	ecological survey	Port of Spain, Trinidad	10.7	12	23	0	23
Soares et al. 2006 [175]	ecological survey	Uberlândia, Minas Gerais, Brazil	−18.9	4116	10	4	14

2. Materials and Methods

2.1. Geographic and Climatic Characteristics of Macao

Macao is a special administrative region on the southern coast of China. It is located 60 km south-west of the Hong Kong special administrative region, separated from it by the pearl river delta. Macao's climate is characterized by dry winters and hot summers [176], with an average daily temperature of 22.8 °C and an annual rainfall of 1967 mm [177].

In the 19th century, Macao's land surface was only 10.28 km² but, following numerous reclamation projects, it now covers around 32.9 km² [58,178]. Despite its high urbanization, Macao still retains several nature parks consisting of young secondary forests, most of which are on Coloane Island. Macao's government started managing these forest patches

in 1980, protecting them from wild-fires and establishing restoration plantations of *Pinus massoniana* and *Acacia confusa* [179].

2.2. Sampling Effort and Collection Methods

Most ant specimens examined were collected during a survey conducted in 2019, from March to October, across 21 plots in Coloane Island, Macao (Figures S1 and S2, Table S1). The survey focused on collecting ants within Coloane's nature parks, which consist of secondary forests, but also covered two golf courses and a mangrove site. To extensively sample the hypogeic, epigeic, and arboreal ants of Macao, we used a range of sampling methods during the 2019 survey. Across the 21 sites, we used 225 ground baits, hand collection, and 42 leaf litter extractions with Winkler bags. Half the Winkler extractions consisted of combining the leaf litter of $4 \times 1 \text{ m}^2$ quadrats taken at each corner of a plot of $20 \times 20 \text{ m}$ (i.e., standard area method), and half consisted of combining a few handfuls of leaf litter taken at 12 random locations within the same plot (i.e., species pool method). For a subset of 16 sites, we used 256 subterranean and 320 arboreal baits, and 1024 artificial nests. For more details on traps, baits, and nest design, see Brassard et al. (2020) [54]. Note that the nests were built following Booher et al. (2017) [180], and were mainly used to obtain sociometric data for the species collected (i.e., colony size and composition). The remainder of the specimens included are from collections made by hand or leaf litter extractions between 2015 and 2020 from different locations across Macao, with detailed collection information presented in the species accounts section.

2.3. Sample Processing

We processed samples by first sorting specimens to morphospecies, which we then stored in ethanol 70%. For each morphospecies, we point-mounted at least one individual and labeled it with a locality and collection label. All specimens are currently located in the Insect Biodiversity and Biogeography Laboratory (IBBL) at The University of Hong Kong.

2.4. Imaging

We used a Leica DFC450 camera mounted on a Leica M205 C dissecting microscope to image mounted specimens of each species and morphospecies. We used the Leica Application suite v. 4.5 to take, stack, and enhance image montages. When necessary, we used Adobe Photoshop Lightroom to make final color corrections and diminish ghosting effects.

2.5. Mapping Species Distributions and Urban Studies

We used *R* to produce all maps [181]. The maps shown at the south-east Asia scale use records at the country level, or the administration level for larger countries (e.g., China, India, and Japan). Following previous work [182,183], we used island boundaries instead of political boundaries for large islands. For maps centered on Macao, we used the GPS coordinates associated with each specimen to add their collection localities.

2.6. Analyses

We produced maps, bar graphs, heatmaps, species accumulation curves, and Venn diagrams using *ggplot2* [184], whereas we used Adobe Illustrator to assemble the species account figures (Figures A1–A158). We produced species accumulation curves and diversity estimates using the package *iNEXT* [185].

2.7. Literature Search

To compile studies that produced a species checklist for cities, we performed a Scopus search using the following formula on the 9th of February 2021: "formicidae" AND "checklist" AND "city" OR "urban". We then pruned the resulting dataset manually by reading the abstracts and only keeping the studies that produced a total number of species for a city. We further added appropriate studies known by authors that were not present within the Scopus search. In particular, we use the literature information combined

in GABI [186] to identify suitable articles on urban ants. We classified studies as either ecological or checklists. If a study was primarily hypotheses driven, with limited sampling efforts in time, habitats, or in the methods used, it was classified as ecological, whereas studies solely producing a species checklist, including records from previous published studies, were classified as checklists. Studies including other non-urban habitats outside the main city area, and for which detailed information did not allow to separate species composition and richness, were not considered.

2.8. Notes on Invasion Status

An understanding of the native and introduced ranges of species represents a fundamental step in the detection and management of biological invasions. However, for many species of ants, clear geographic boundaries between those ranges remain undetermined, either at global (e.g., uncertainty in the realm of origin) or regional scales (e.g., native vs. introduced range within a particular realm). Here, we thus distinguish three categories between native, exotic, and tramp species. For species that we could establish with some confidence whether or not they were introduced, we used the exotic and native status, respectively. We used the tramp status for species whose biogeographic origins were more uncertain in Macao or south China. Note that all species here labelled as tramps have been previously transported in other regions of the world and have established populations in non-native habitats. This demonstrates their potential to colonize new regions. Furthermore, these tramp species often occur within anthropogenic habitats. As such, tramp species, regardless of their potential non-native status, are important to consider from a management perspective, as they have the potential to invade non-native localities. The establishment of the native and exotic ranges for each species was based on the maps available on antmaps.org [186,187].

2.9. Notes on Records

Since the last publication of a species checklist for Macao [53], two studies with a focus on specific genera (i.e., *Polyrhachis* and *Strumigenys*) published new species records for the region [54,55]. Since all but one species record—*Polyrhachis tyrannica* [55]—are from specimens collected during our 2019 sampling, we here report these specimens, with the exception of *P. tyrannica*, as new records for Macao.

2.10. Notes on Taxonomy

To identify our specimens at species-level, we used the Insect Biodiversity and Biogeography Lab (IBBL) ant collection as a reference. For the especially challenging species, we relied on the taxonomic knowledge of Dr. Benoit Guénard. To verify our identification of the genera *Nylanderia* and *Carebara*, we shared stacked images with specialists familiar with their taxonomy, Dr. Jason L. Williams and Dr. Georg Fischer, respectively. When a species could not be identified at species level with certainty, we labelled it as “nr.” the morphologically closest known species (e.g., *Colobopsis* nr. *nipponica*). If the unknown species was morphologically distinct but not identifiable, we used the unique morphospecies code their collector used to label it (e.g., *Camponotus* sp.1 FB).

3. Results

Our 2019 survey collected a total of 112 species and morphospecies from 46 genera and nine subfamilies. Among these, 51 species (46%), 10 genera (22%), and one subfamily (11%) represented new records for Macao. We also found four additional species and one new genus record among the specimens opportunistically collected between 2017 and 2020. In total, the new records reported here include one subfamily, 11 genera, and 55 species and morphospecies (Figure 2, Table 2). The new genera reported for Macao are: *Brachymyrmex* (exotic), *Buniapone*, *Dilobocondyla*, *Gesomyrmex*, *Iridomyrmex*, *Mayriella*, *Probolomyrmex*, *Proceratium*, *Pseudolasius*, *Rotastruma* and *Vollenhovia*, while the Proceratiinae subfamily is here recorded for the first time. The overall number of ant species known

from Macao thus increases by 55%, from 100 to 155 species and morphospecies (Figure 2, Table 2), which represents the third highest urban ant diversity out of 123 entries (see Figure 1, Table 1). For images of these species and maps of their distribution in Macao and SE Asia, see Appendix A (Figures A1–A158).

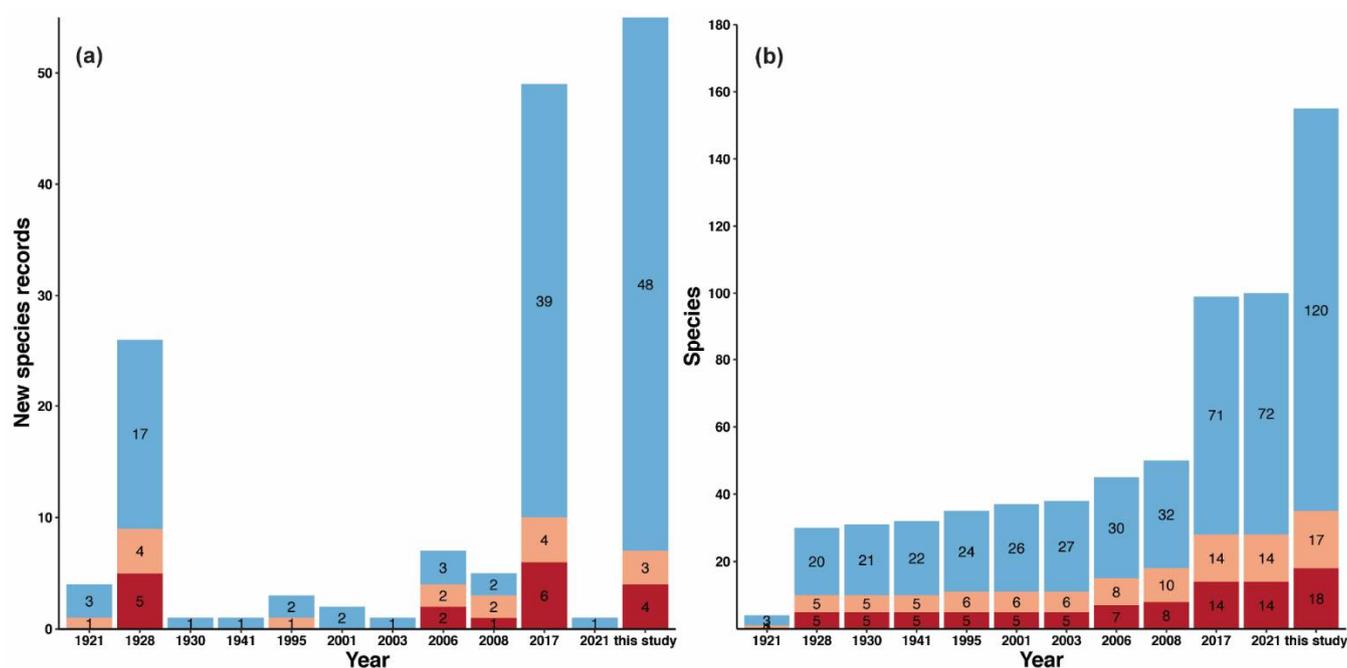


Figure 2. Number of new records per year in Macao. Bar plots showing (a) the number of new ant species record for Macao based on literature records and this study and (b) bar plots showing the accumulation of ant species found in Macao based on literature records and this study. The proportion of native species (blue), tramp species (light orange), and exotic species (dark red) are denoted within bar plots.

Table 2. Summary table of all new ant species records made in Macao over time with details on the number of reported ant species, subspecies, and morphospecies.

Studies	Species	Subspecies	Morphospecies	Total per Year	Cumulative Total
Wheeler 1921 [188]	4	0	0	4	4
Wheeler 1928 [189]	24	2	0	26	30
Wheeler 1930 [190]	1	0	0	1	31
Wu 1941 [191]	0	1	0	1	32
Tang et al. 1995 [192]	3	0	0	3	35
Zhou 2001 [193]	2	0	0	2	37
Xu 2003 [194]	1	0	0	1	38
Hua 2006 [195]	6	1	0	7	45
Eguchi 2008 [196]	5	0	0	5	50
Leong, Shaijo and Guénard 2017 [53]	41	1	7	49	99
Wong and Guénard 2021 [55]	1	0	0	1	100
This study	40	0	15	55	155

The sampling methods varied in their overlap for the species they collected (Figure 3). Of the 112 species collected during the 2019 survey, 10 species were only found in leaf litter extractions, five in ground baits, 10 in subterranean baits, 13 in hand collections, and eight in arboreal baits, whereas the other 66 were collected with more than one method. Artificial nests did not collect new species records nor unique species, but they did provide

sociometric data for 15 species from a total of 913 nests recovered, for a colonization rate of 3% (Table S2).



Figure 3. Heatmap showing the number of shared species between collection methods used in the 2019 survey. Color illustrates the strength of the correlation between sampling methods in the shared species they collect. The diagonal represents the total number of species collected for each method. Abbreviations are for hand collection (Hand. Col.), subterranean trap (Sub. Trap.), ground nest (G. Nest), ground bait (G. Bait), arboreal bait (Arb. Bait), leaf litter extraction with the species pool technique (LLSP), and leaf litter extraction with the standard area technique (LLSA).

We found few habitat generalists, with only seven species collected in all strata (Table 3, Figure 4)—*Monomorium intrudens*, *M. floricola*, *Nylanderia sharpii*, *Pheidole megacephala*, *P. tumida*, *Tapinoma indicum*, and *T. melanocephalum*—three of which (43%) are exotics. Ten species were only collected within the subterranean stratum and 14 species only in the arboreal stratum (Table 3, Figure 4). In contrast, most species were ground-dwelling ($n = 52$) or collected within two strata ($n = 36$). The highest proportion of new records found solely within one stratum were in the subterranean (9/10 species: 90%), arboreal (9/14 species: 64%), and then ground (25/52 species: 48%) strata (Figure 4).

Table 3. Summary checklist of the species recorded during previous studies and the current study in Macao. Status of species are mentioned as native, tramp, or exotic. The asterisk symbol (*) denotes new records. The dagger symbol (†) denotes morphospecies collected in 2019 that probably belong to previous records but could not be assigned a species name due to incomplete taxonomic descriptions (as such, they were not counted in the total number of species). The diesis symbol (‡) denotes a species collected previously, but with a mislabeled status. An “X” under the column Arboreal, Ground, or Subterranean indicates that this species was collected within this stratum during the 2019 survey. We left blanks for species not collected during the 2019 survey. For images of species and maps of their distribution in Macao and SE Asia, see Figures A1–A158. For detailed accounts of the material examined, see the species account section of the supplementary material.

Subfamily	Genus	Species	Status	Year of First Published Record	Arboreal	Ground	Subterranean	
AMBLYOPONINAE DOLICHODERINAE	<i>Stigmatomma</i>	nr. <i>rothneyi</i>	native	1928	-	X	-	
	<i>Chronoxenus</i>	<i>dalyi</i>	native	1928				
		<i>walshi</i>	native	2006				
		<i>wroughtonii</i>	native	1995				
		<i>wroughtonii formosensis</i>	native	2006				
		† morpho1	native	2021	-	X	X	
		† morpho2	native	2021	-	X	X	
		<i>Dolichoderus</i>	<i>taprobanae</i>	native	1928			
			nr. <i>sibiricus</i>	native	2017	X	-	-
		<i>Iridomyrmex</i>	sp. <i>anceps</i> cplx *	tramp	2021	-	X	-
		<i>Ochetellus</i>	<i>glaber</i>	tramp	1928	-	X	-
	<i>Tapinoma</i>	<i>indicum</i>	native	2017	X	X	X	
		<i>melanocephalum</i>	tramp	1921	X	X	X	
		sp. 1 FB *	native	2021	X	-	-	
	<i>Technomyrmex</i>	<i>brunneus</i>	tramp	1995	-	X	-	
		<i>horni</i> *	native	2021	-	X	-	
	DORYLINAE FORMICINAE	<i>Ooceraea</i>	<i>biroi</i>	exotic	2017	-	X	X
<i>Acropyga</i>		<i>acutiventris</i>	native	2017				
	<i>sauteri</i>	native	1928					
	sp. mo02	native	2017					
	<i>Anoplolepis</i>	<i>gracilipes</i>	exotic	1928	X	X	-	
		<i>patagonicus</i> *	exotic	2021	X	-	-	
	<i>Brachymyrmex</i> <i>Camponotus</i>	<i>albosparus</i>	native	1928				
		<i>carin</i> *	native	2021				
		<i>irritans</i> *	native	2021	-	X	-	
		<i>lighti</i>	native	2017				
		<i>mitis</i>	native	1928	X	X	-	
<i>nicobarensis</i>		native	2017	X	X	-		
<i>parius</i>		native	1921					
<i>vitiosus</i>		native	2017	X	-	-		
<i>variegatus</i>		tramp	2006					
<i>variegatus dulcis</i>		native	1928					
<i>variegatus proles</i>	native	1941						
sp. 1 FB *	native	2021	-	X	-			
<i>Colobopsis</i>	nr. <i>nipponica</i>	native	2017					
	nr. <i>vitrea</i>	native	2017	X	-	-		
<i>Gesomyrmex</i>	<i>howardi</i> *	native	2021					
<i>Lepisiota</i> <i>Nylanderia</i>	<i>rothneyi</i>	native	1921	-	X	-		
	<i>amia</i>	tramp	1928					
	<i>bourbonica</i>	tramp	2006	-	X	-		
		<i>indica</i>	native	1928	-	X	-	

Table 3. Cont.

Subfamily	Genus	Species	Status	Year of First Published Record	Arboreal	Ground	Subterranean
		<i>sharpii</i>	native	2021	X	X	X
		<i>taylori</i> *	native	2021	-	X	-
		<i>vividula</i>	exotic	2006			
		<i>yerburyi</i>	native	1928			
		sp. 3 BG *			-	X	-
		sp. 6 BG *	native	2021	-	X	-
	<i>Paraparatrechina</i>	<i>sauteri</i>	native	2006			
		sp.1 BG *	native	2021	-	X	X
	<i>Paratrechina</i>	<i>longicornis</i>	exotic	1928	-	X	X
	<i>Plagiolepis</i>	<i>alluaudi</i> *	exotic	2021	X	-	-
	<i>Polyrhachis</i>	<i>confusa</i> *	native	2021	-	X	-
		<i>demangei</i>	native	2017			
		<i>dives</i>	native	1995	X	-	-
		<i>illaudata</i>	native	2017	X	X	-
		<i>latona</i> *	native	2021	-	X	-
		<i>tyrannica</i>	native	2021			
	<i>Pseudolasius</i>	<i>risii</i> *	native	2021			
LEPTANILLINAE	<i>Leptanilla</i>	<i>macaoensis</i>	native	2017			
MYRMICINAE	<i>Cardiocondyla</i>	<i>minutior</i>	exotic	2017	-	X	-
		<i>wroughtonii</i> *	tramp	2021	X	-	-
	<i>Carebara</i>	<i>affinis</i> *	native	2021	-	X	X
		<i>capreola</i>	native	2003			
		<i>diversa</i>	native	1921	-	-	X
		<i>diversa laotina</i>	native	2017			
		<i>melasolena</i> *	native	2021	-	X	X
		<i>sangi</i> *	native	2021	-	-	X
		<i>zengchengensis</i>	native	2017	-	X	X
	<i>Crematogaster</i>	<i>binghamii</i> *	native	2021	-	X	-
		<i>biroi</i>	native	1928			
		<i>dohrni</i>	native	1928			
		<i>ferrarii</i>	native	2017	X	X	-
		<i>macaoensis</i>	native	1928			
		<i>quadriruga</i>	native	2017	-	X	-
		<i>rogenhoferi</i>	native	2017	X	-	-
	<i>Dilobocondyla</i>	<i>propotriangulata</i> *	native	2021	X	-	-
	<i>Mayriella</i>	<i>granulata</i> *	native	2021	-	X	-
	<i>Meranoplus</i>	sp. mo01 nr. <i>bicolor</i>	native	2017			
	<i>Monomorium</i>	<i>chinense</i> *	native	2021	X	X	X
		<i>intrudens</i> *	tramp	2021	X	X	-
		<i>floricola</i>	tramp	2017	X	X	X
		<i>pharaonis</i>	exotic	2017	-	X	X
		sp. psw-cn01	native	2021	-	X	-
	<i>Myrmecina</i>	<i>nomurai</i> *	native	2021	-	X	-
		<i>sinensis</i>	native	2017			
	<i>Pheidole</i>	<i>elongicephala</i> *	native	2021	-	-	X
		<i>fervens</i>	tramp	2008	-	X	X
		<i>hongkongensis</i>	native	2008	-	X	-
		<i>indica</i>	tramp	1928			

Table 3. Cont.

Subfamily	Genus	Species	Status	Year of First Published Record	Arboreal	Ground	Subterranean
		<i>megacephala</i>	exotic	2008	X	X	X
		<i>ochracea</i>	native	2017	-	X	X
		<i>parva</i>	tramp	2008	-	X	X
		<i>pieli</i> *	native	2021	-	X	X
		<i>taipoana</i>	native	2008	-	X	X
		<i>tumida</i>	native	2017	X	X	X
		<i>nodus</i>	tramp	2017	-	X	-
		<i>vulgaris</i> *	native	2021	-	X	-
		<i>zoceana</i> *	native	2021	-	X	-
		nr. <i>ryukyuensis</i> *	native	2021	-	-	X
	<i>Recurvidris</i>	<i>recurvoispinosa</i>	native	2017	-	X	-
	<i>Rotastruma</i>	<i>stenoceps</i> *	native	2021	-	X	-
	<i>Solenopsis</i>	<i>geminata</i>	exotic	1928			
		<i>invicta</i>	exotic	2006	-	X	-
		<i>jacoti</i>	native	2017	-	X	X
	<i>Strumigenys</i>	<i>emmae</i>	exotic	2017	-	X	-
		<i>elegantula</i>	native	2020	-	X	-
		<i>exilirhina</i>	native	2017	-	X	-
		<i>feae</i>	native	2020	-	X	-
		<i>membranifera</i>	exotic	1928	-	X	-
		<i>minutula</i>	native	2017	-	X	-
		<i>†nepalensis</i>	exotic	2017	-	X	-
		<i>sauteri</i>	native	2020	-	X	-
		<i>subterranea</i>	native	2020	-	-	X
	<i>Sylophopsis</i>	nr. <i>cryptobia</i> *	native	2021	-	-	X
		sp. mo01 nr <i>sechellensis</i>	native?	2017	-	X	X
		sp. 1 BMW *	native	2021	-	X	X
		sp. 2 BMW *	native	2021	-	X	-
	<i>Tetramorium</i>	<i>bicarinatum</i>	tramp	2017	X	X	-
		<i>indicum</i> *	native	2021	X	-	-
		<i>insolens</i> *	exotic	2021	-	X	-
		<i>kraepelini</i>	tramp	2017	-	X	X
		<i>lanuginosum</i>	exotic	1928	-	X	-
		<i>nipponense</i>	native	2017	X	X	-
		<i>parvispinum</i>	native	2017			
		<i>simillimum</i>	exotic	2017			
		<i>tonganum</i> *	exotic	2021	X	-	-
		<i>wroughtonii</i> *	native	2021	-	X	-
		nr. <i>elisabethae</i> *	native	2021	-	-	X
		sp.1 <i>obseum</i> gr.	native	2017	-	X	-
		sp. 2 JF *	native	2021	X	-	-
		sp. 9 JF *	native	2021	-	-	X
	<i>Vollenhovia</i>	sp.1 BG *	native	2021	-	X	-
		sp. 2 BG *	native	2021	-	X	-
PONERINAE	<i>Anochetus</i>	<i>risii</i>	native	2017	-	X	-
	<i>Bothroponera</i>	<i>rubiginosa</i>	native	1928			
	<i>Brachyponera</i>	<i>luteipes</i>	tramp	1928			
		<i>obscurans</i>	native	1928	-	X	X

Table 3. Cont.

Subfamily	Genus	Species	Status	Year of First Published Record	Arboreal	Ground	Subterranean
	<i>Buniapone</i>	<i>amblyops</i> *	native	2021	-	-	X
	<i>Diacamma</i>	sp. 1	native	2017	X	X	-
	<i>Ectomomyrmex</i>	<i>annamitus</i> *	native	2021	-	-	X
		<i>astutus</i>	native	2001			
	<i>Euponera</i>	<i>leeuwenhoecki</i>	native	2017	-	X	-
		<i>pilosior</i>	native	2017	-	-	X
		<i>sharpi</i>	native	1928			
	<i>Harpegnathos</i>	<i>venator</i>	native	2001	-	X	-
		<i>venator rugosus</i>	native	1928			
	<i>Hypoponera</i>	<i>exoecata</i>	native	2017	-	X	-
		sp. mo01	native	2017	X	X	-
	<i>Leptogenys</i>	<i>chinensis</i>	native	2017			
		<i>peuqueti</i>	native	1928	-	X	-
	<i>Odontoponera</i>	<i>denticulata</i>	native	2017	-	X	-
	<i>Pseudoneoponera</i>	<i>rufipes</i>	native	1930	-	X	-
PROCERATIINAE	<i>Probolomyrmex</i>	<i>dabermanii</i> *	native	2021			
	<i>Proceratium</i>	sp. cf. <i>bruelheidei</i> *	native	2021	-	X	-
PSEUDOMYR-MICINAE	<i>Tetraoponera</i>	<i>allaborans</i>	native	2017			
		<i>binghami</i> *	native	2021	X	X	-
		<i>nitida</i> *	native	2021	X	-	-

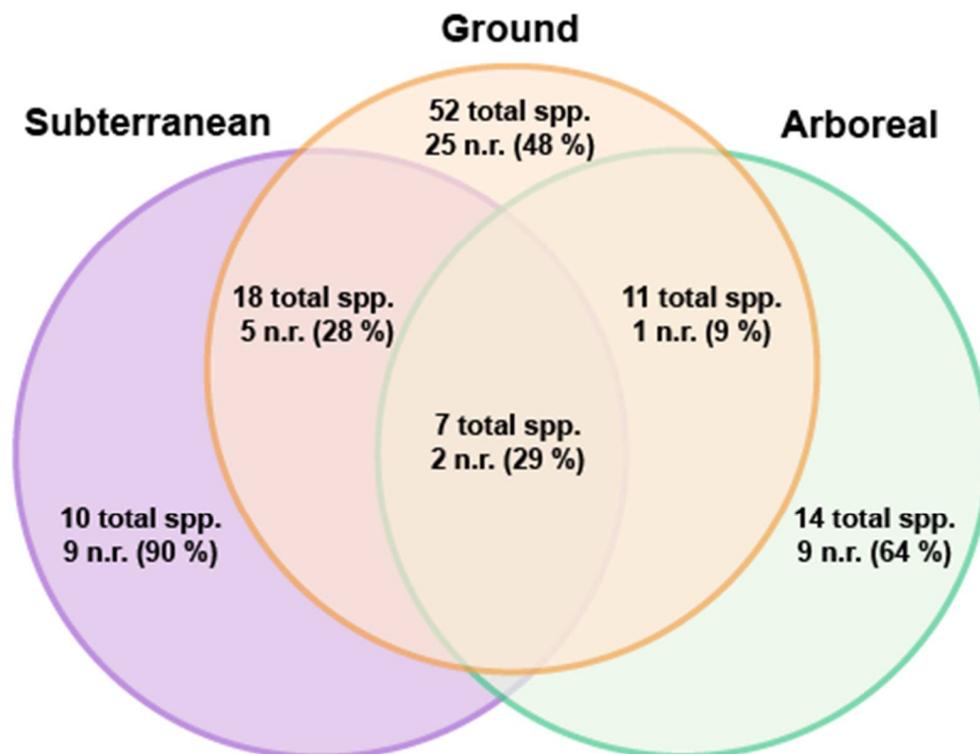


Figure 4. Venn diagram showing the total number of species (112 spp.) and new species records (51 n.r.) collected in each stratum during the 2019 survey. Numbers in parentheses represent the proportion of species collected within a stratum that are new records from the last 2017 checklist (Leong et al. 2017). Note that this figure does not include the four records added from specimens collected besides the main 2019 survey.

At least five of the species collected during our 2019 survey, which belong to the genera *Strumigenys*, *Sylophopsis*, *Tetramorium*, and *Vollenhovia*, were considered potentially novel to science at the time of collection. We found three of the undescribed species in subterranean traps (i.e., *Strumigenys subterranea*, *Sylophopsis* nr. *Cryptobia*, and *Tetramorium* sp. 9 JF), one in leaf litter samples (i.e., *Vollenhovia* sp. 2 BG), and one in arboreal traps (i.e., *Tetramorium* sp. 2 JF).

Several of the new records have rarely been reported in the literature and represent extensions of their known range. First, we found workers of *Dilobocondyla propotriangulata*, an arboreal species described from Vietnam [197], at two different sites in Macao, which represents the third and fourth records of the species worldwide. Second, we found workers and a queen of *Mayriella granulata*, also described from Vietnam [198], which represents the first record of this species in China. Lastly, we found a worker of *Probolomyrmex* (*P. dammermani*), a pantropical but rarely collected genus [199–201], which represents the first record of this species in China.

Before our survey, 14 tramp and 14 exotic species were known to occur in Macao. Here, we report four additional exotic species records: *Brachymyrmex patagonicus*, *Plagiolepis alluaudi*, *Tetramorium insolens*, and *T. tonganum*. We also report three additional tramp species records: *Cardiocondyla wroughtonii*, *Iridomyrmex* sp. *anceps* complex, and *Monomorium intrudens*. Moreover, we report new localities in Macao for several exotic species: *Anoplolepis gracilipes*, *Cardiocondyla minutior*, *Monomorium pharaonis*, *Ooceraea biroi*, *Paratrechina longicornis*, *Pheidole megacephala*, *Solenopsis invicta*, *Strumigenys emmae*, *S. membranifera*, *S. nepalensis*, and *Tetramorium lanuginosum*.

Nevertheless, despite achieving a high sampling coverage (i.e., between 80 to 98% depending on the method), species accumulation curves indicate that further sampling should uncover several more species on Coloane Island (Figure 5, Table 4). Indeed, estimates predict that each sampling method could collect from 2 to 25 additional species each.

Table 4. Summary of the species richness collected, the sampling completeness, and the richness estimates for each sampling method used during the sampling done in Coloane in 2019.

Sampling Method	Observed Richness	Sampling Completeness	Estimated Richness
Arboreal Bait	26	0.98	28.49
Ground Bait	42	0.95	49.17
Ground Nest	21	0.80	41.14
Leaf Litter Sampling (Standardized area)	59	0.93	64.70
Leaf Litter Sampling (Species pool)	64	0.86	88.80
Subterranean trap	35	0.88	56.25

We identified 112 studies, representing 109 cities, that focused on ants within urban environments (Figure 1, Table 1). Among those, 23 studies provided species checklists, while 88 represented ecological surveys. The studies were unevenly distributed across biogeographic regions. The highest numbers were from North America ($n = 41$), Asia ($n = 34$), Europe ($n = 24$), and Central and South America ($n = 21$), whereas Australia ($n = 6$) and Africa ($n = 5$) had the lowest number of studies. Although Asia had the second highest number of studies, most of these originated from temperate regions, with only eight studies (23.5%) conducted within tropical or subtropical regions.

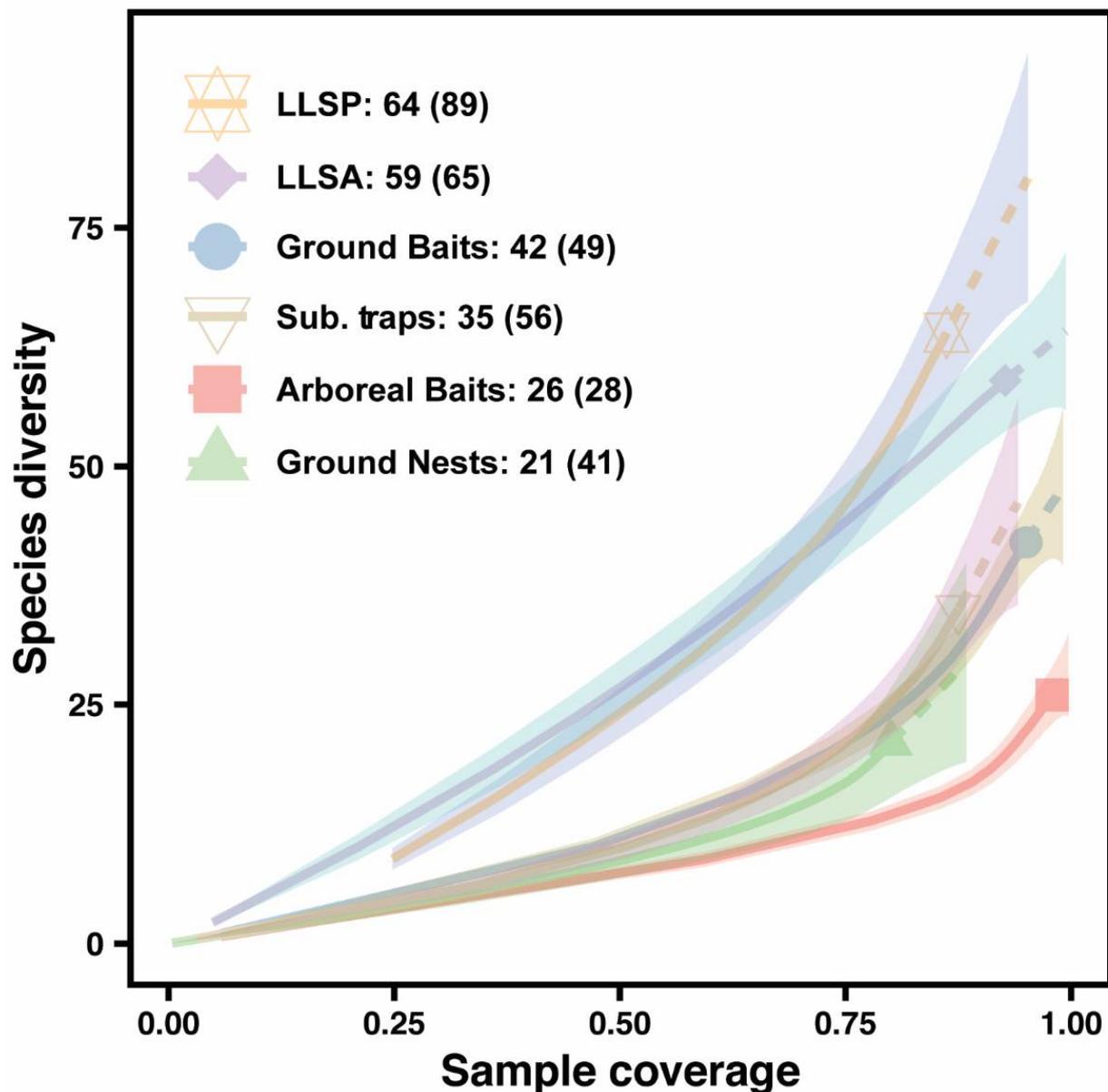


Figure 5. Species diversity in relation to sampling coverage for each standardized technique used in Macao in 2019. Values in the legend represent the number of species collected, and, in brackets, the estimated number of species that would be collected by this method if sampling coverage would reach 100% (asymptotic estimates of order $q = 0$ obtained using the function ChaoRichness in the package iNEXT). The dotted line shows the extrapolation for the predicted number of new records if sampling completeness would reach 100% (i.e., a value of 1.00 on the graph). Shaded areas represent the 95% confidence intervals of each curve. Calculation method used species incidence frequency. Leaf litter samples were considered as four units of 1 m^2 per Winkler sack (which pooled 4 m^2 of leaf litter). Abbreviations are (LLSP) leaf litter extraction with the species pool technique and (LLSA) leaf litter extraction with the standard area technique.

4. Discussion

A common perception of urban biodiversity is that it is characterized by low species richness and dominated by exotic species [12]. This perception may be induced by the excess of local scale studies (α diversity) compared to the limited number of studies at larger scale (γ diversity) encompassing the full diversity encountered within of a city (Table 1). Here, our results contrast with the former assumption but agree with the latter. Indeed, we found that Macao hosts a diverse ant fauna, but that a high number of that fauna consists of exotic and tramp species.

Macao's ant fauna presents one of the highest known ant richness reported for an urban region (Table 1). Our results indicate that, while there are few comprehensive studies for tropical regions—most studies on urban ants have been conducted within temperate regions where species diversity is usually much lower than in tropical and subtropical regions [202]—several cities, including Macao, offer potential conservation values for ants. For instance, a study limited to the botanical garden of Bogor (Java), a small green oasis within an urban area, captured 216 ant species [69]. Similarly, ecological studies in Abidjan (Ivory Coast, 176 species) and Uberlândia (Brazil, 143 species), among others, also presented high ant species richness [62,155]. Altogether, these results highlight the potential conservation value of urban habitats, but also their potential to increase the biogeographic and taxonomic knowledge on ants. Indeed, contrary to most natural habitats, urban habitats are characterized by their easy access, which facilitates continuous and thorough sampling. As for tropical forests, the vertical stratification of ants within cities does exist, and, as a result, researchers should consider diversifying their sampling approach to include subterranean and arboreal communities as well as epigeic ants.

Ant assemblages are known to be highly structured along a vertical gradient ranging from the top soil layer (first 50 cm) to the tree canopy [203,204], but such stratification had not been shown for urban environments prior to this study. Our results show that ignoring these strata may lead to an underestimation of species richness estimates. Indeed, although most of the new species records were collected within the ground stratum, we found several previously unrecorded arboreal and subterranean specialists. In particular, of the 35 species collected with our subterranean trapping, 10 were found only within that stratum, nine of which were new records, and three represented undescribed species. Remarkably, this parallels the results of previous surveys focusing on multiple strata but conducted within natural ecosystems [205]. For instance, in Ecuador, Wilkie and collaborators collected 47 species in subterranean probes, nine of which were exclusively subterranean, and two were undescribed [205]. It is also worth noting that 14 species collected during the 2019 survey were unique to the arboreal stratum, nine of which were new records, and one was an undescribed species. This shows the importance of using sampling methods targeting the ant communities of all vertical strata, instead of focusing solely on ants found within a single stratum as is commonly done in urban studies [52].

Other methods captured fewer novel records, but, nonetheless, provided ecological and biogeographic information for a wide range of species. For instance, ground baits often collected large series of workers, including multiple worker castes for polymorphic species, which is often essential for their identification. As for ground nests, they had the lowest rate of capture, but provided important and rarely collected sociometric data, including new colony size information for seven species (Guénard, unpublished). Since we still lack information on the sociometry of most ant species [206,207], ground nests proved especially useful in collecting this valuable data. However, it is worth noting that the colonization rate of the ground nests, with 3%, was neatly inferior to the rate observed in previous studies using similar devices (e.g., 8% in [180]), or from other urban areas [141]. While the type of nests may be suboptimal for the ant community present in Macao, it is surprising that they were not more heavily exploited by ants, especially because urban habitats are usually characterized by limited nesting resources [141]. Perhaps the subtropical conditions characterized by heavy rains prevented the establishment of ants. Indeed, several nests had their openings clogged with mud and some had their inner cavities filled with fungal growths. Just as with temperate regions [141], the testing and deployment of different artificial nest apparatuses may represent an interesting opportunity to census urban ants and their sociometric characteristics.

Even though we used an exhaustive sampling approach, and our results substantially increased our knowledge on Macanese ants, species accumulation curves indicate a substantial number of unrecorded species to be collected using a similar methodology (Figure 4). This is supported by the several species previously recorded within Macao, but not collected in this study (Table 2). Previous studies conducted within more natural or relatively undisturbed habitats showed that achieving an exhaustive sampling of local diversity represents a challenging task [125,208,209]. After two separate survey programs ([53], this study), our results confirm this is similar for urban areas. Furthermore, other sampling methods not used here could have been added, such as pitfall traps to collect larger ground-dwelling ants [210], canopy fogging to collect arboreal species [211], Malaise traps to collect alates [212], and multiple soil sampling methods to collect subterranean ants [50]. Thus, while our study contributes to a better understanding of ant species richness and composition in Macao, it represents a steppingstone and not a final outcome, with future sampling likely to provide additional new records, and potentially more undescribed species.

Despite the geographic limitations of our sampling, being restricted to Coloane island, this allowed us to considerably increase the list of Macanese ant species. These new records highlight the potential for urban forest fragments and other urban habitats to maintain a significant portion of ant diversity. Similar examples can be found in Asia, such as in Bogor and Singapore [69,102]. Likewise, Hong Kong harbors a high ant richness (Lee et al. in press, Guénard unpublished), with numerous new records and species recently reported (e.g., [55,192]). Additionally, comparative studies focusing on old growth and secondary forests in both cities also reported no significant difference in ant richness between the types of forests ([213,214], Nooten et al. submitted). As such, past studies and the current one should motivate the conservation of forest patches in and around urban matrices in Asia, whether they are primary or secondary.

Nevertheless, a key difference between disturbed and undisturbed habitats lies within their species composition instead of in the number of species they harbor, and a significant part of Macao's fauna consists of non-native species. The previous survey reported several new records of exotic species in Macao [53], which are here completed with the additions of four exotic and three tramp species (Figure 1), totaling in 18 exotic species and representing 11.5% of the Macanese ant fauna. The most notable newly reported exotic is *Brachymyrmex patagonicus*, a major pest in south-east USA [215]. This represents the second record of *B. patagonicus* in continental Asia, with the first report from Hong Kong [216]. Its presence in Macao is worrisome, and clear plans to determine the extent of its distribution, with programs to destroy established populations, should be developed quickly. We also report the spread of several alien and potentially harmful species. We found the three exotic species *Anoplolepis gracilipes*, *Monomorium pharaonis*, and *Paratrechina longicornis* in five, seven, and six forested sites, respectively. They can, thus, establish populations and persist in forested habitats, where their effects on native ants are unknown. Through our standardized sampling, we also found the notorious invasive species *Solenopsis invicta* and *Pheidole megacephala* but, interestingly, rarely found it in Coloane's forested sites. Despite finding several workers and queens of *S. invicta* through hand collection in open and urban habitats, we found this species in only one forested site near a hiking trail: one individual was found in a leaf litter sample and several workers colonized two ground baits at that site. This reflects previous findings that the distribution of *S. invicta* is mainly restricted to disturbed habitats [217–219]. Similarly, while we found a high abundance of workers of *P. megacephala* on one golf course, we collected only two individuals in forested sites. For both of these species, notorious for their destructive impacts on native communities [220–222], this would indicate that, for now, they are mainly restricted to more open and disturbed habitats. This suggests that forested habitats may help preserve local biodiversity while simultaneously limiting the distribution of some invasive ant species, reflecting results from Hong Kong and Hainan, where less disturbed habitats harbored relatively fewer exotic species than did more disturbed ones [223].

Nonetheless, the occurrence of exotic species in Macao is high. In comparison, the checklist of the ants of Yunnan reports that only 2% of its species are introduced [224], a proportion 5.75 times lower than in Macao. Based on current knowledge, Macao appears to have one of the highest numbers and proportions of exotic species encountered within cities (Table 1). Alas, we also report the presence of 17 tramp species, some of which may very well be introduced, as our biogeographic understanding and the region of origin for several species remains limited; thus, the overall number may be even higher. The high proportion of exotic and tramp species in Macao supports the hypothesis that coastal cities act as gateways for the introduction of exotic species through high propagule pressure [225]. In addition, since the occurrence of non-native species is an indicator of reduced ecological integrity [226], the high proportion of non-native species we found in Macao suggests these habitats have suffered substantial damage. It is, thus, crucial to make periodical biodiversity surveys in Macao and other cities to monitor their habitats' health through time, as well as to identify new arrivals of exotics and prevent their further spread.

An historic baseline is lacking for Macao's ant assemblages, but we suspect there may be substantial differences compared to the ant assemblages before urbanization. Indeed, several genera known to occur in southern China and within neighboring cities of the Greater Bay Area, such as Hong Kong, are missing from Macao. These include *Aenictus* and *Dorylus* army ants, *Discothyrea*, *Odontomachus*, *Ponera*, and weaver ants (*Oecophylla smaragdina*). The absence of army ants in Coloane (except *O. biroi*, an exotic species), such as species of *Aenictus* and *Dorylus*, may be explained by the morphology of the queen caste in these genera: they lack wings and, thus, cannot disperse by flight [227]. As such, if these ants disappeared from Coloane during a disturbance event, we may expect that it would be arduous for these species to recolonize the island. Of course, native army ant species may have been absent from Coloane throughout Macao's urbanization history due to its insularity or of its small size ([228], but see [229]). However, the presence of native army ants on several of Hong Kong' islands—for example, the *Aenictus* species found on Lamma Island (13.55 km², François Brassard pers. obs.)—suggests they could have been extirpated from Coloane Island and then failed to recolonize. More puzzling is the absence of genera such as *Discothyrea*, *Odontomachus*, *Oecophylla*, and *Ponera*. Small and relatively uncommon species of *Discothyrea* and *Ponera* may have escaped our sampling or may be especially sensitive to disturbance. However, for unknown reasons, large and conspicuous species such as *Odontomachus* and especially *Oecophylla*, frequently encountered on forest edges or in disturbed habitats within Hong Kong, are probably truly absent from the island.

5. Conclusions

In summary, this study highlights the importance of conducting holistic biodiversity surveys in cities to discover new records as well as potential new species for science, and to monitor the introduction of new exotic species. Our results suggest that forest patches in cities can harbor a diverse ant fauna and may have a significant conservation value. However, exhaustive ant diversity surveys in cities are rare, and are often based on incomplete sampling approaches. Thus, until the completion of several more surveys in cities around the world, particularly within tropical regions, a clear understanding of how urban environments may act as biodiversity refuges and gateways for exotic species will be lacking. As such, we advocate that conservation management practices should implement regular biodiversity surveys using an exhaustive sampling approach in urban regions worldwide. Whenever possible, we also recommend that urban biodiversity assessments be combined with surveys done in less urbanized habitats nearby to compare the diversity and composition of each habitat.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13080358/s1>. Figure S1: Map of Coloane showing the 21 sites sampled in the 2019 survey. White dots mark sites where the full protocol was done (i.e., standardized and species pool leaf litter extractions, ground baiting, ground nests, subterranean traps, and arboreal traps), whereas grey dots mark preliminary sites where only ground baiting and leaf litter extractions were done. Hand

collection was also opportunistically used at each site. Figure S2: Design of a 20 × 20 m sampling plot. Each of the 1 × 1 m quadrats where subterranean traps and leaf litter extraction (standardized area) was performed were placed at a corner of the plot. Black dots show the emplacement of nest bundles. For the species pool leaf litter extraction, 12 microhabitats were sampled within the light gray area. For the arboreal baiting protocol, four trees measuring a minimum of 5 m height were sampled within the grey area. Table S1: List of the localities of each sampling sites, their associated number, and their geolocation. The date refers to the first sampling event made at a site, which corresponded to the leaf litter extraction and placement of subterranean traps. Sampling protocols are defined as follows: the letter (P) signifies a partial sampling protocol (i.e., leaf litter extraction, ground baiting, and hand collection), whereas the letter (F) signifies a full protocol (i.e., leaf litter extraction, ground baiting, ground nests, subterranean traps, arboreal traps, and hand collection). Table S2: Sociometry data collected using ground nests. Macao species: material examined.

Author Contributions: Conceptualization, F.B. and B.G.; methodology, F.B. and B.G.; validation, F.B. and B.G.; formal analysis, F.B.; investigation, F.B.; resources, B.G., H.-H.C., and C.-M.L.; data curation, F.B. and B.G.; writing—original draft preparation, F.B.; writing—review and editing, F.B., B.G., C.-M.L., and H.-H.C.; visualization, F.B.; supervision, B.G.; project administration, B.G.; funding acquisition, B.G. All authors have read and agreed to the published version of the manuscript.

Funding: F.B. was supported by the Instituto para os Assuntos Municipais, Macao SAR, China, CML was supported by the Macao Foundation and the Direcção dos Serviços do Ensino Superior, Macao SAR, China, and CML and FB were supported by The University of Hong Kong, Hong Kong SAR, China.

Institutional Review Board Statement: Ethical review and approval were waived for this study, due to our work being conducted on invertebrates.

Data Availability Statement: The data presented in this study are available in tables within the main text and within the supplementary material section.

Acknowledgments: We thank Jason L. Williams and Georg Fischer for their help with the identification of species within the genera *Nylanderia* and *Carebara*, respectively. We acknowledge that the images we shared with these specialists are not optimal for identification and, as such, if some misidentifications are later revealed, these errors should be considered our own, not theirs. We thank Siu Yiu for her help conducting fieldwork, as well as with sorting, mounting, and imaging specimens. We thank Carly McGregor for her help conducting fieldwork. We thank Sabine Nooten for her help producing species accumulation curves. We also thank the Environmental Protection Bureau, Caesars Golf Macau, and the Macau Golf and Country Club for allowing us to sample on their premises.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

The appendix shows all species for which we had specimens within the IBBL collection. These are shown in lateral, dorsal, and face view. Within the figure, we include a map of south-east Asia showing the distribution of the species. We colored polygons according to whether a species was recorded as a native or exotic species, or unrecorded for a specific region. Note that we could not use the label tramp because most studies do not distinguish beyond native or exotic. We also include an inset map showing where the species was found in Macao. Black triangles indicate collection locations made during the 2019 survey, whereas white dots indicate collection locations not done during the survey.

Appendix A.1 AMBLYOPONINAE

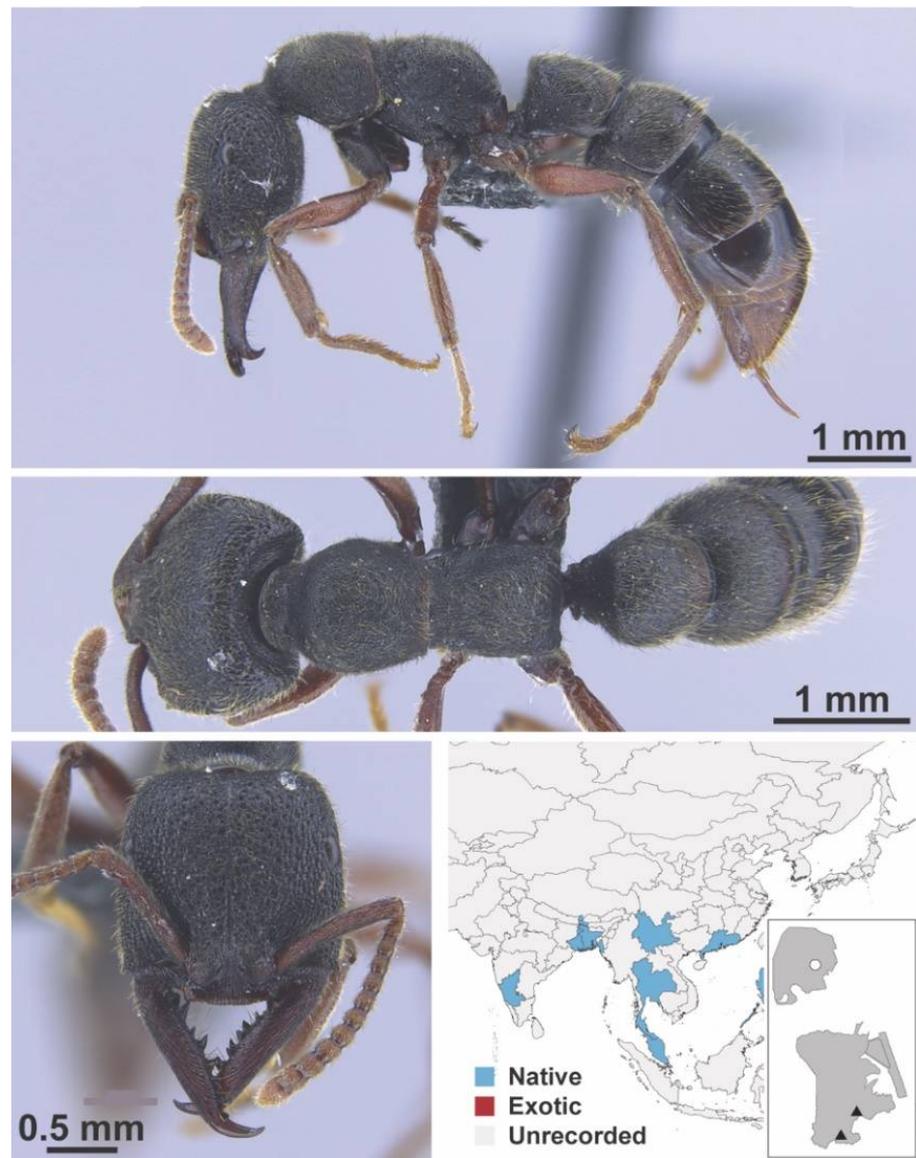


Figure A1. *Stigmatomma rothmeyeri* Forel, 1900 worker (MAC_S11_LLSA_Sp.2, IBBL).

Appendix A.2 DOLICHODERINAE

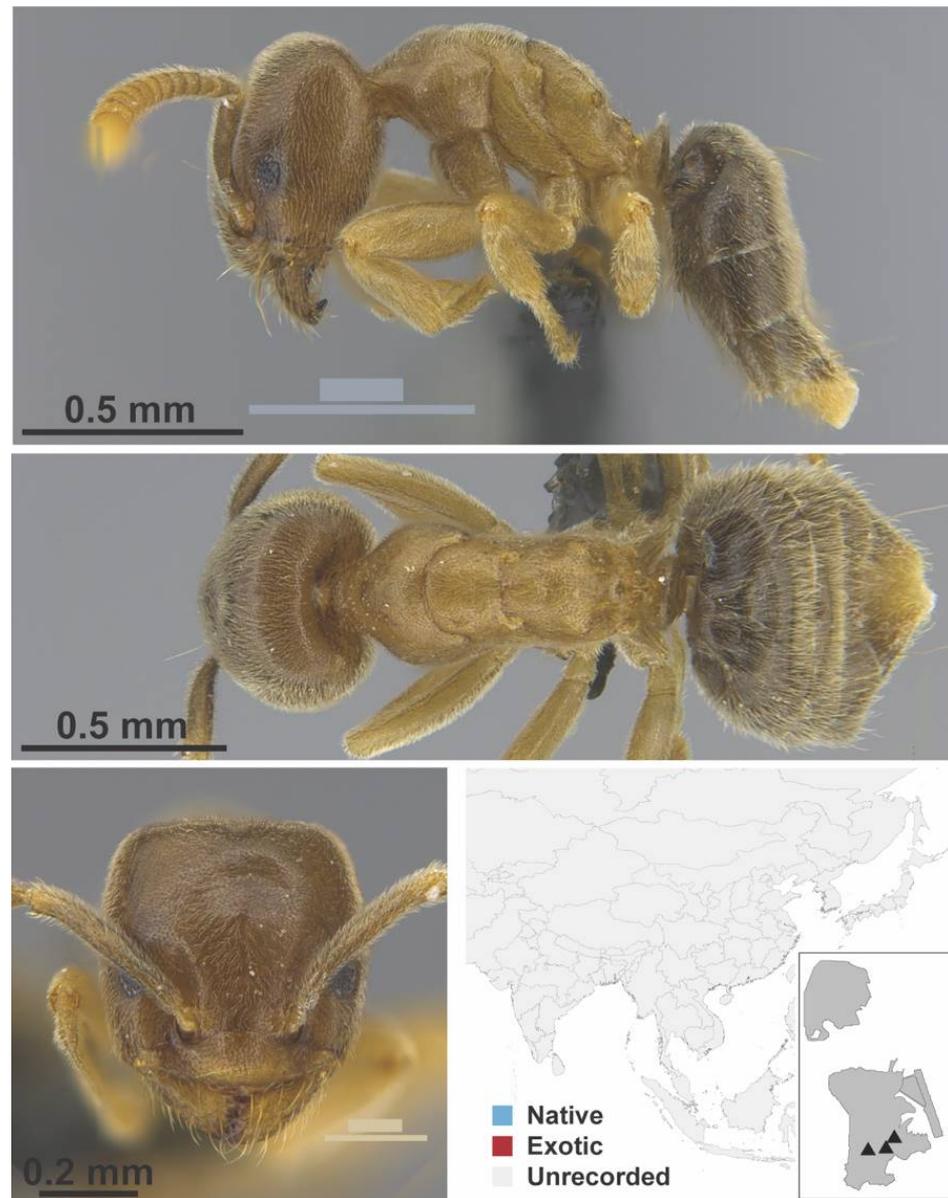


Figure A2. *Chronoxenus morpho 1* worker (MAC_S14_LLSP, IBBL).

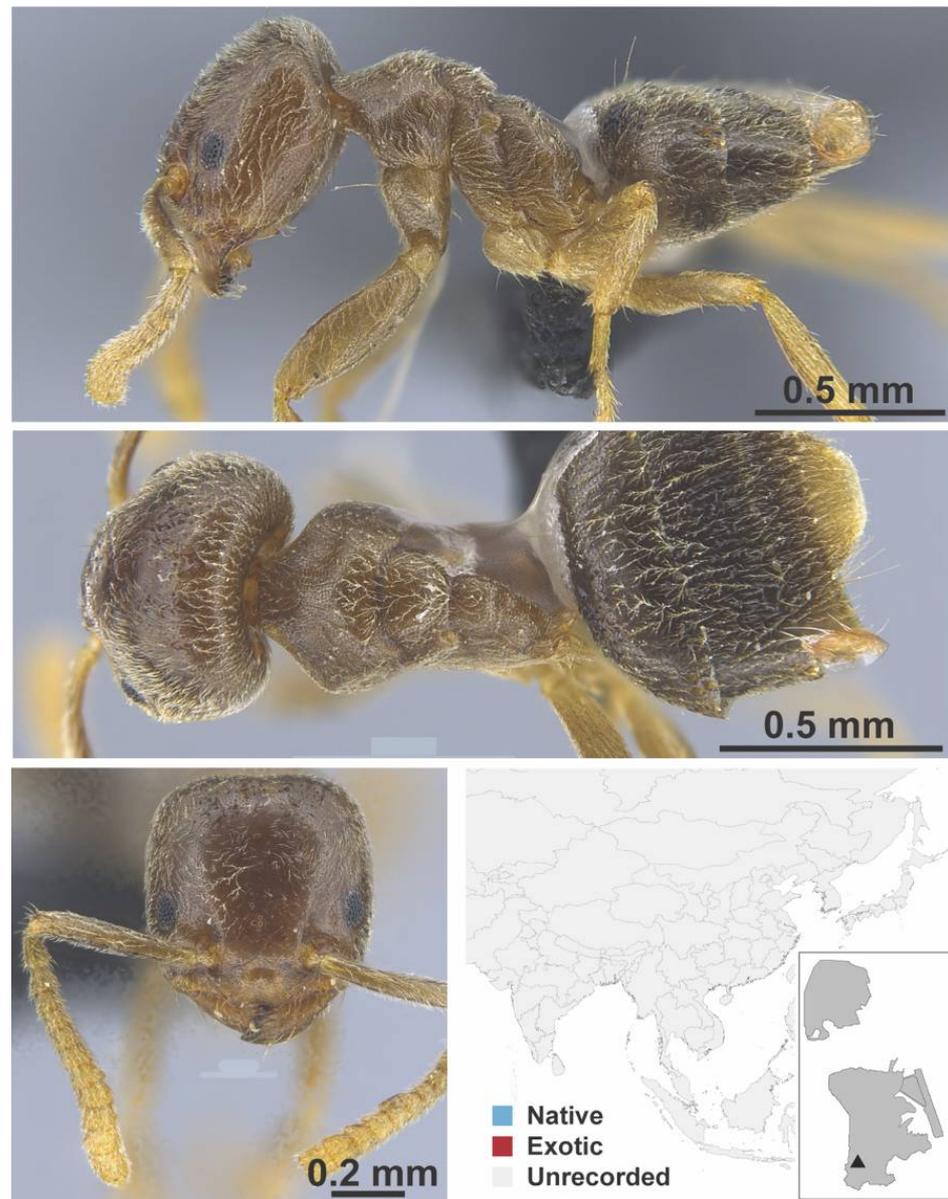


Figure A3. *Chronoxenus morpho* 2 worker (MAC_S21_q2_50_sp.2, IBBL).

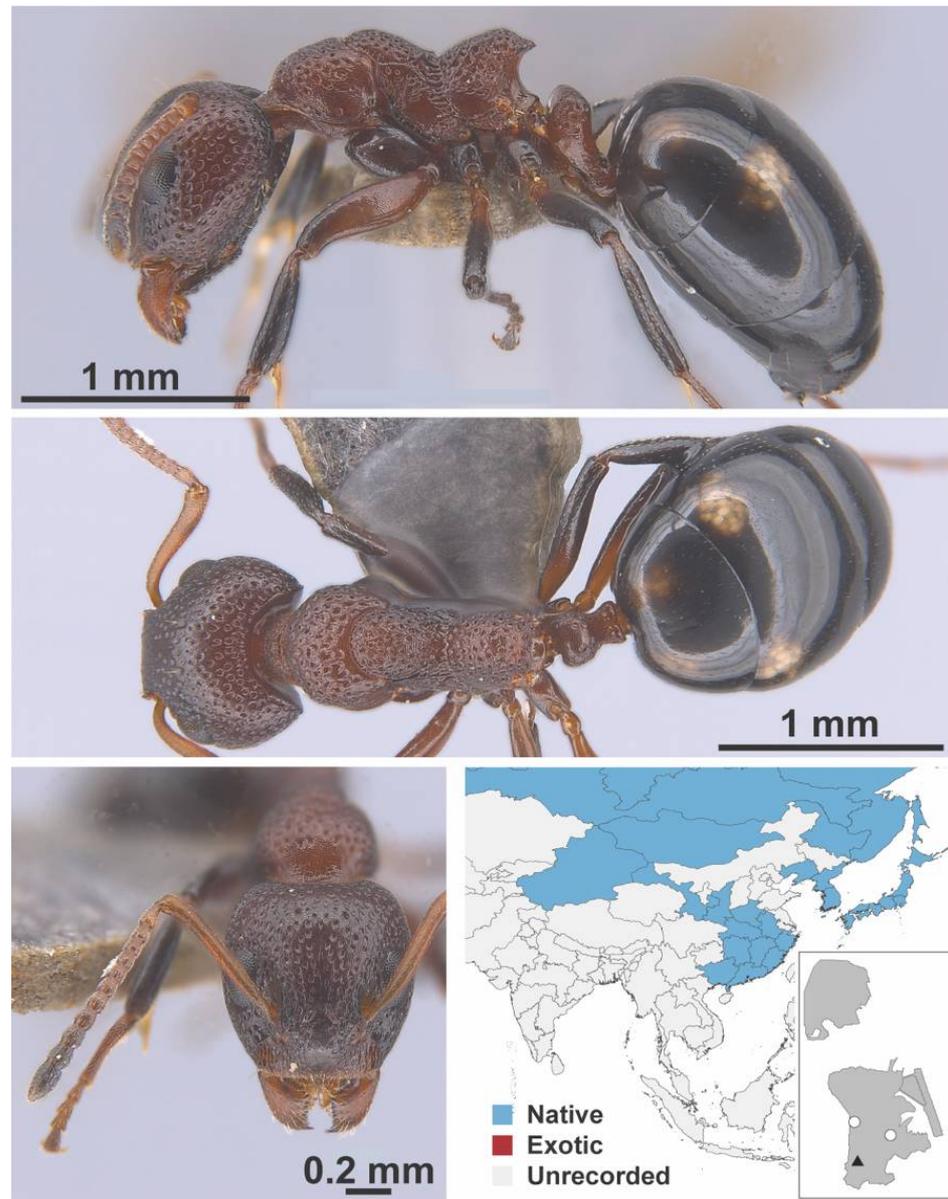


Figure A4. *Dolichoderus* nr. *sibiricus* Emery, 1889 worker (FB19279, IBBL).

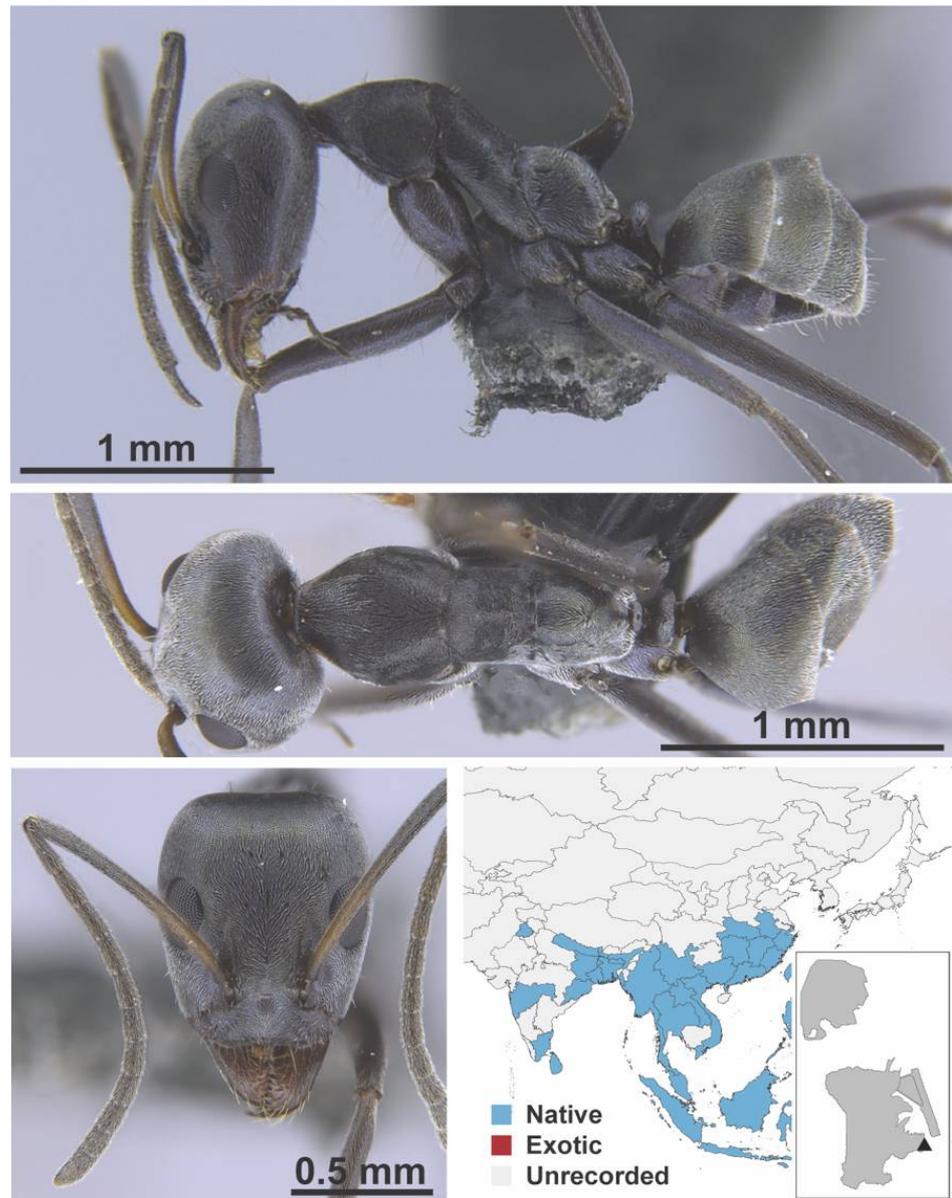


Figure A5. *Iridomyrmex anceps* grp. Roger, 1863 worker (FB19166, IBBL).

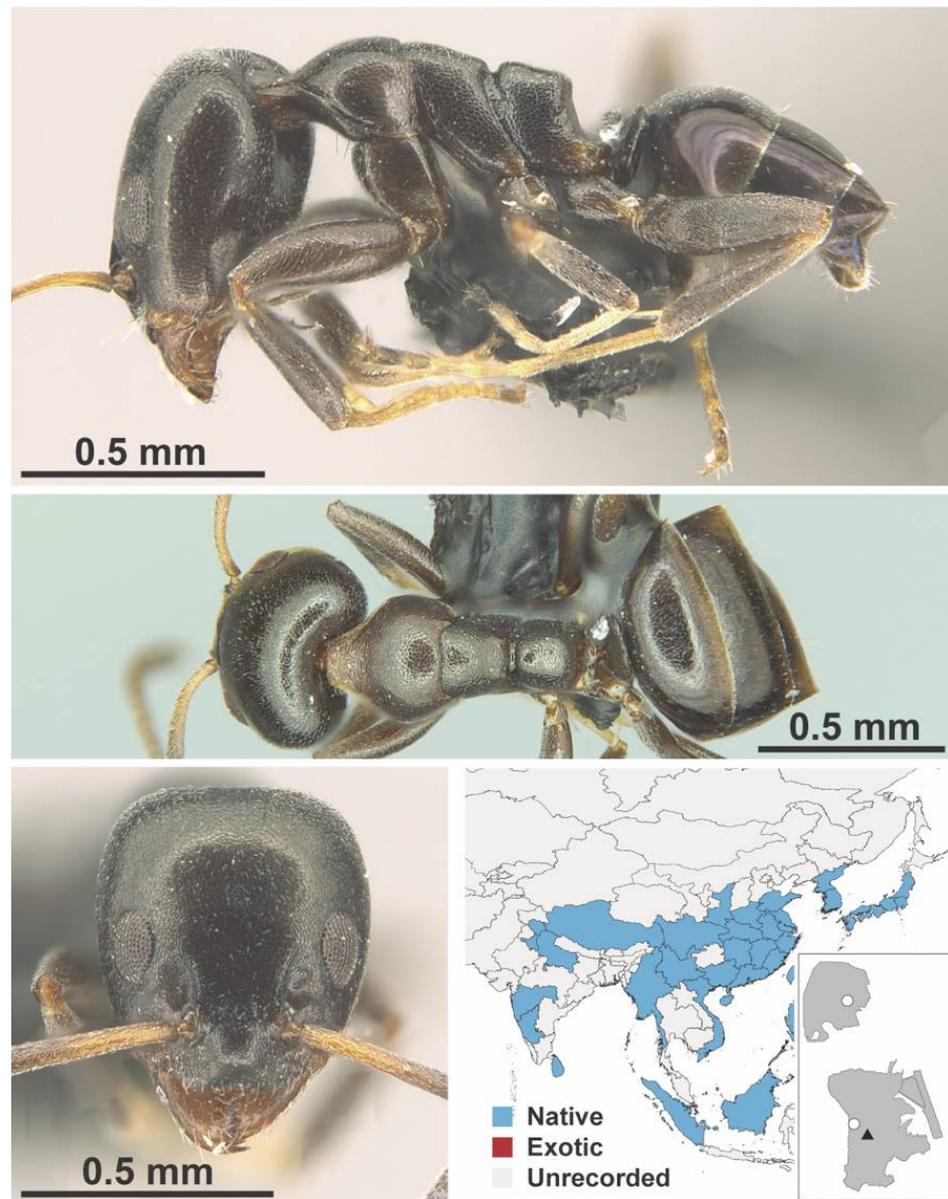


Figure A6. *Ochetellus glaber* Mayr, 1862 worker (MAC_S19_LLSP_sp.5, IBBL).

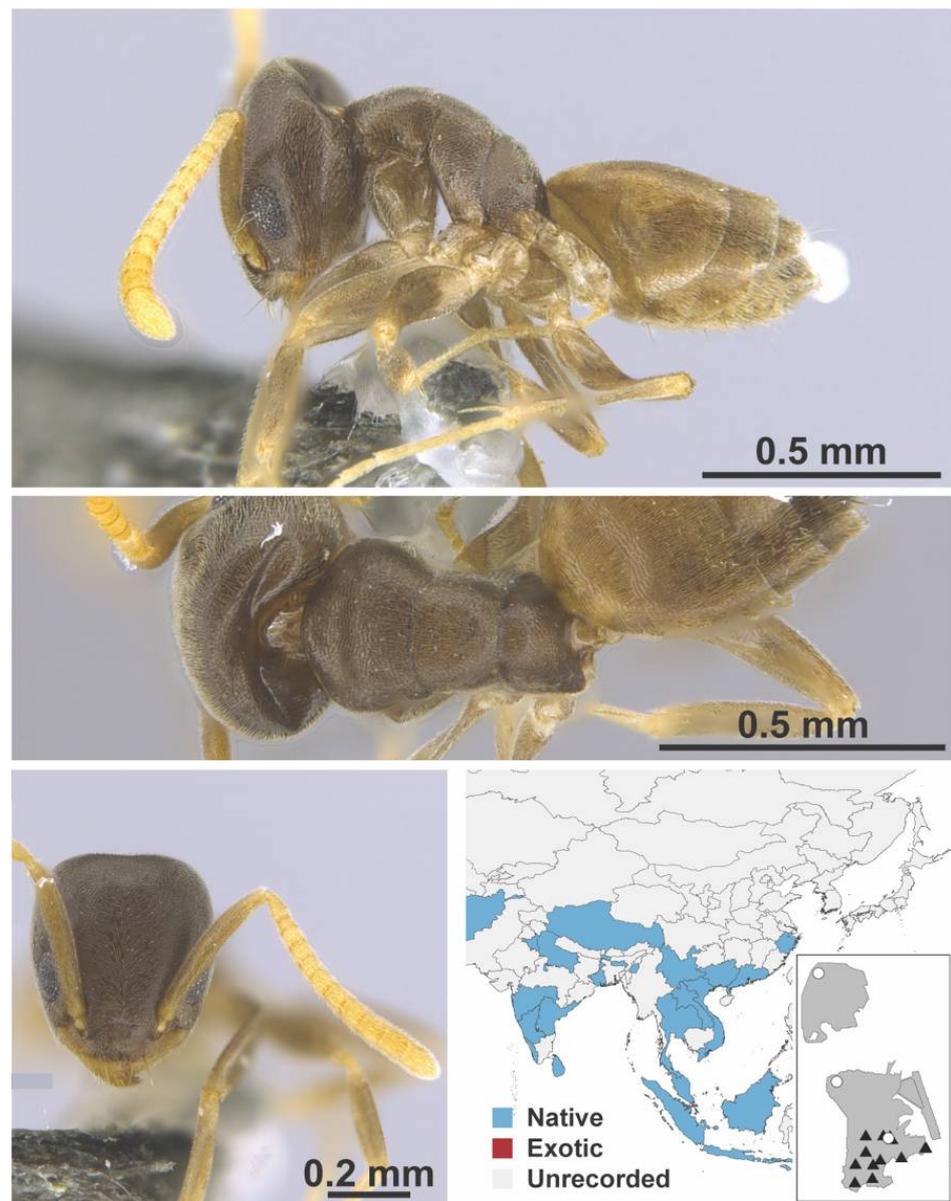


Figure A7. *Tapinoma indicum* Forel, 1895 worker (MAC_S01_LLSP_Sp.9, IBBL).

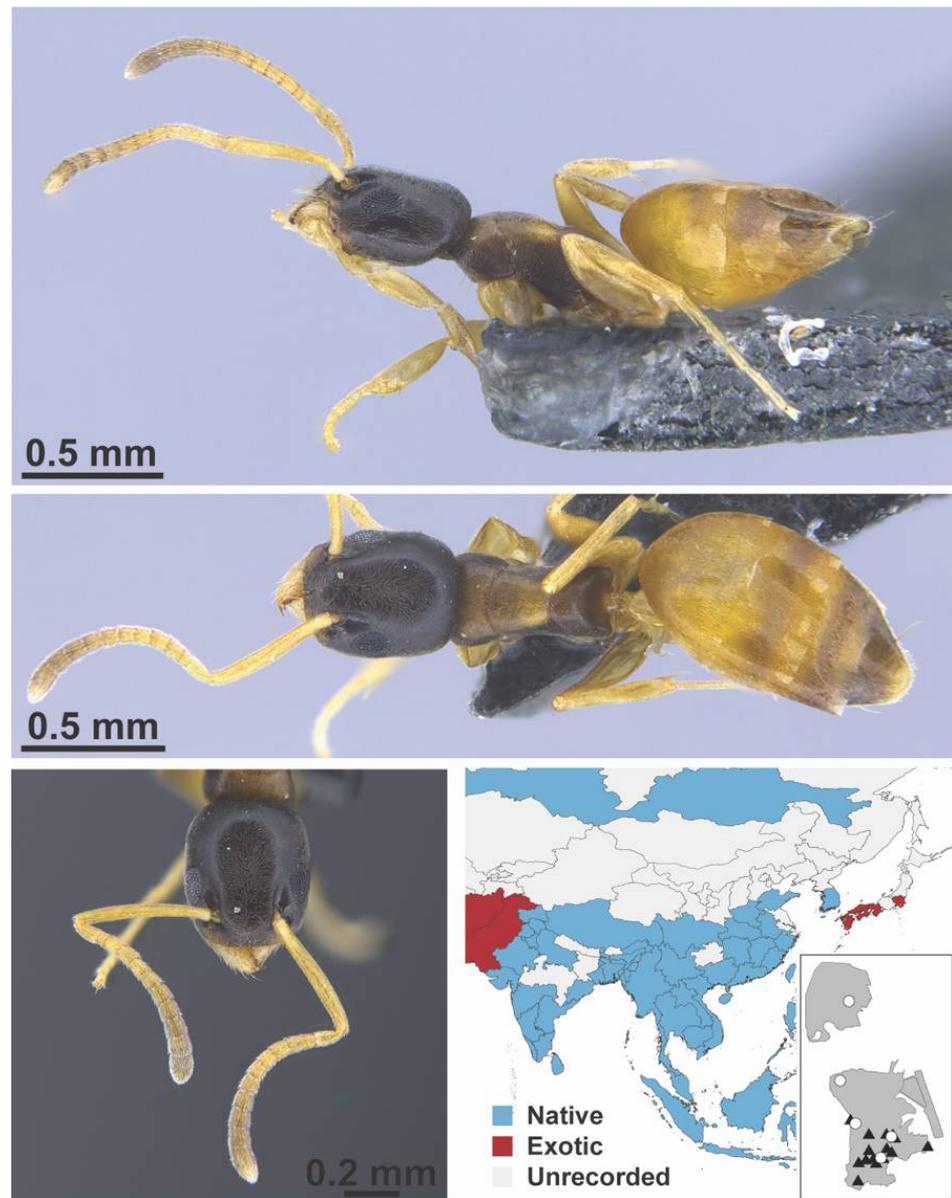


Figure A8. *Tapinoma melanocephalum* Fabricius, 1793 worker (MAC_S01_LLSP_Sp.6, IBBL).

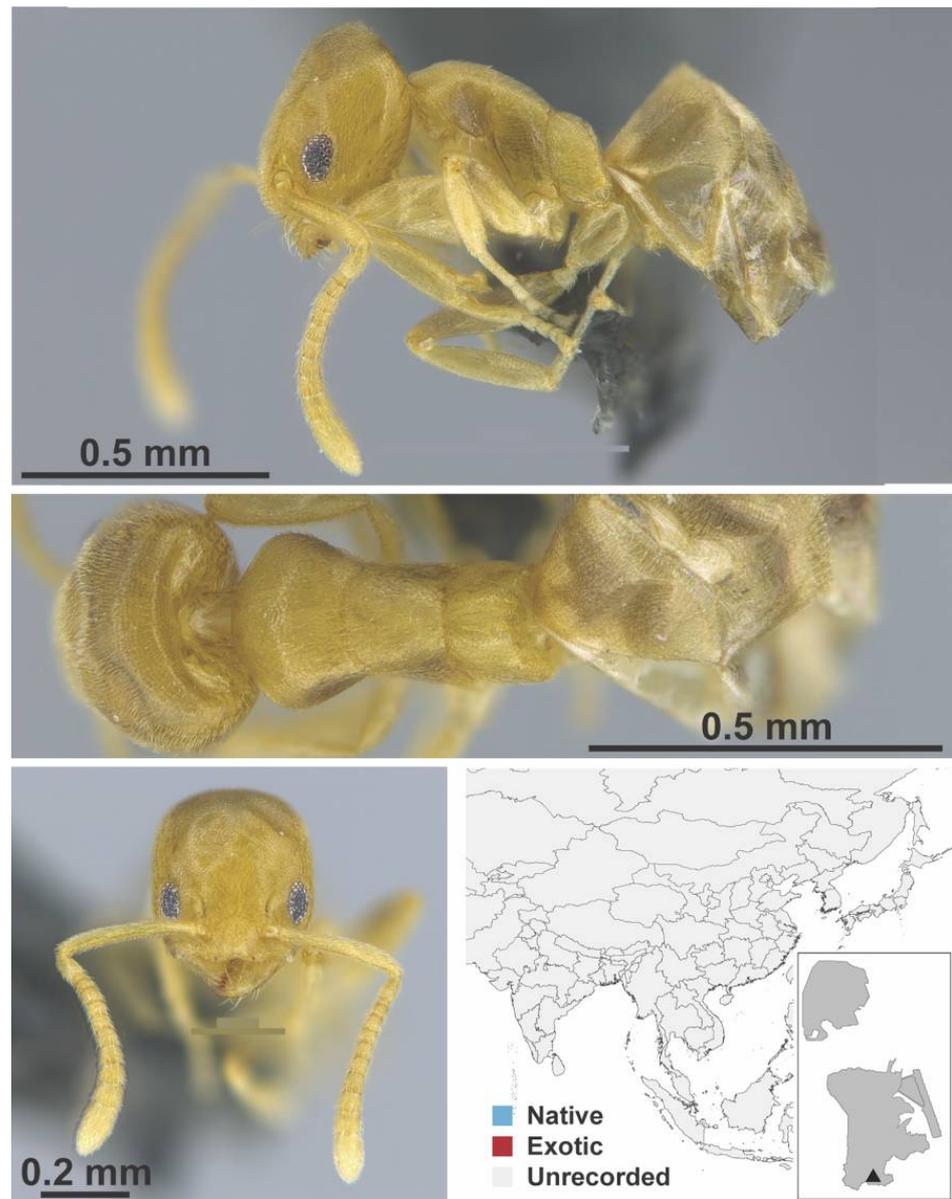


Figure A9. *Tapinoma* sp. 1 FB worker (MAC_S11_T4_1m_sp.2, IBBL).

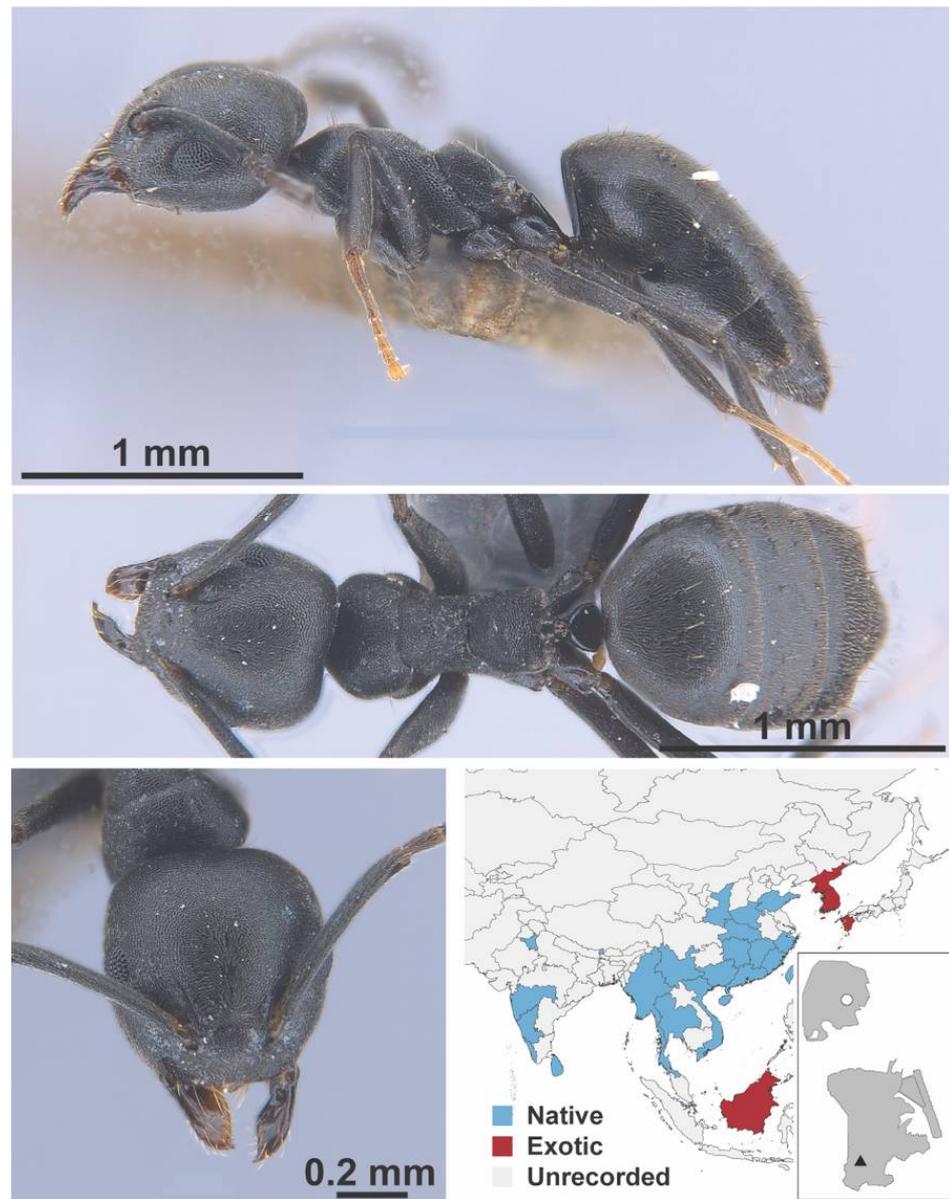


Figure A10. *Technomyrmex brunneus* Forel, 1895 worker (FB19281, IBBL).

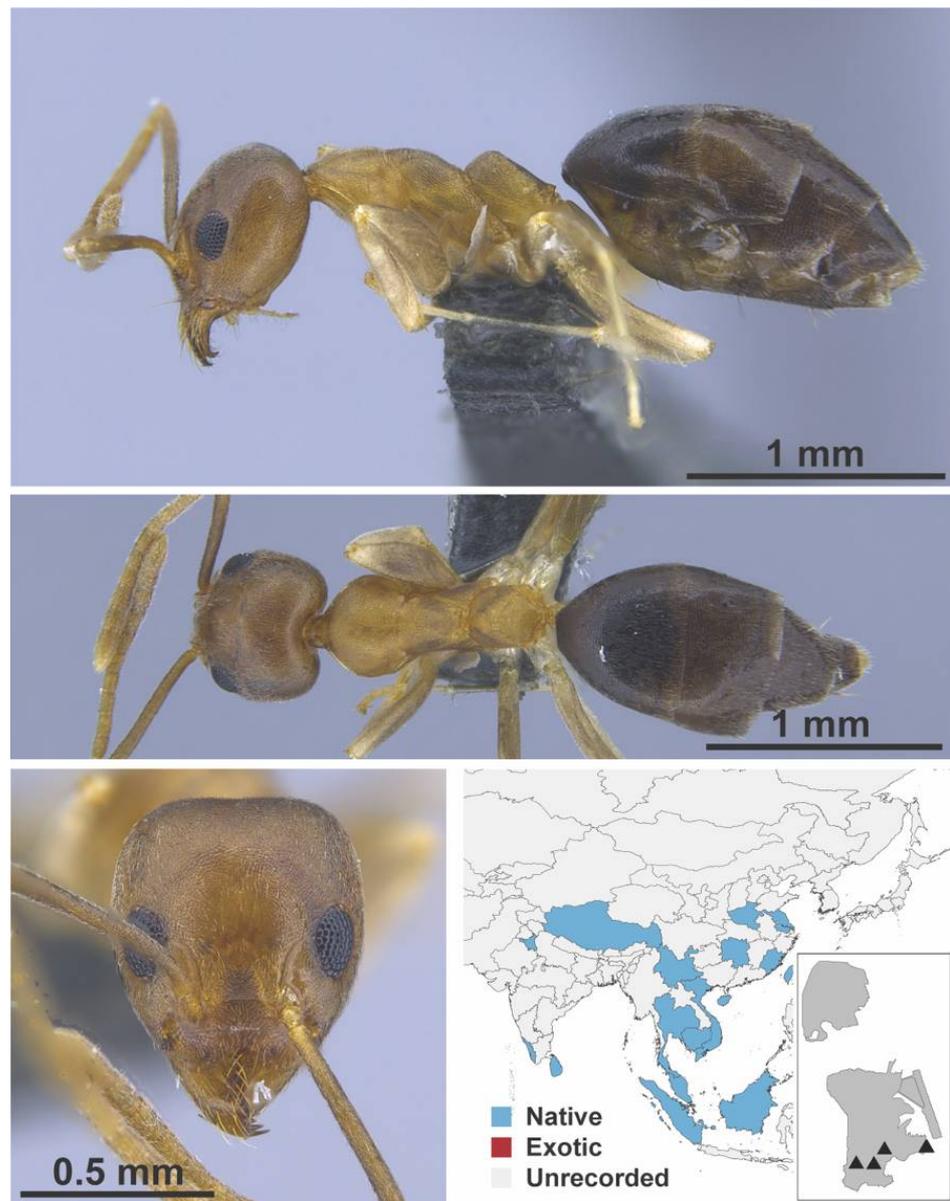


Figure A11. *Technomyrmex horni* Forel, 1912 worker (MAC_S01_LLSP_Sp.2, IBBL).

Appendix A.3 DORYLINAE

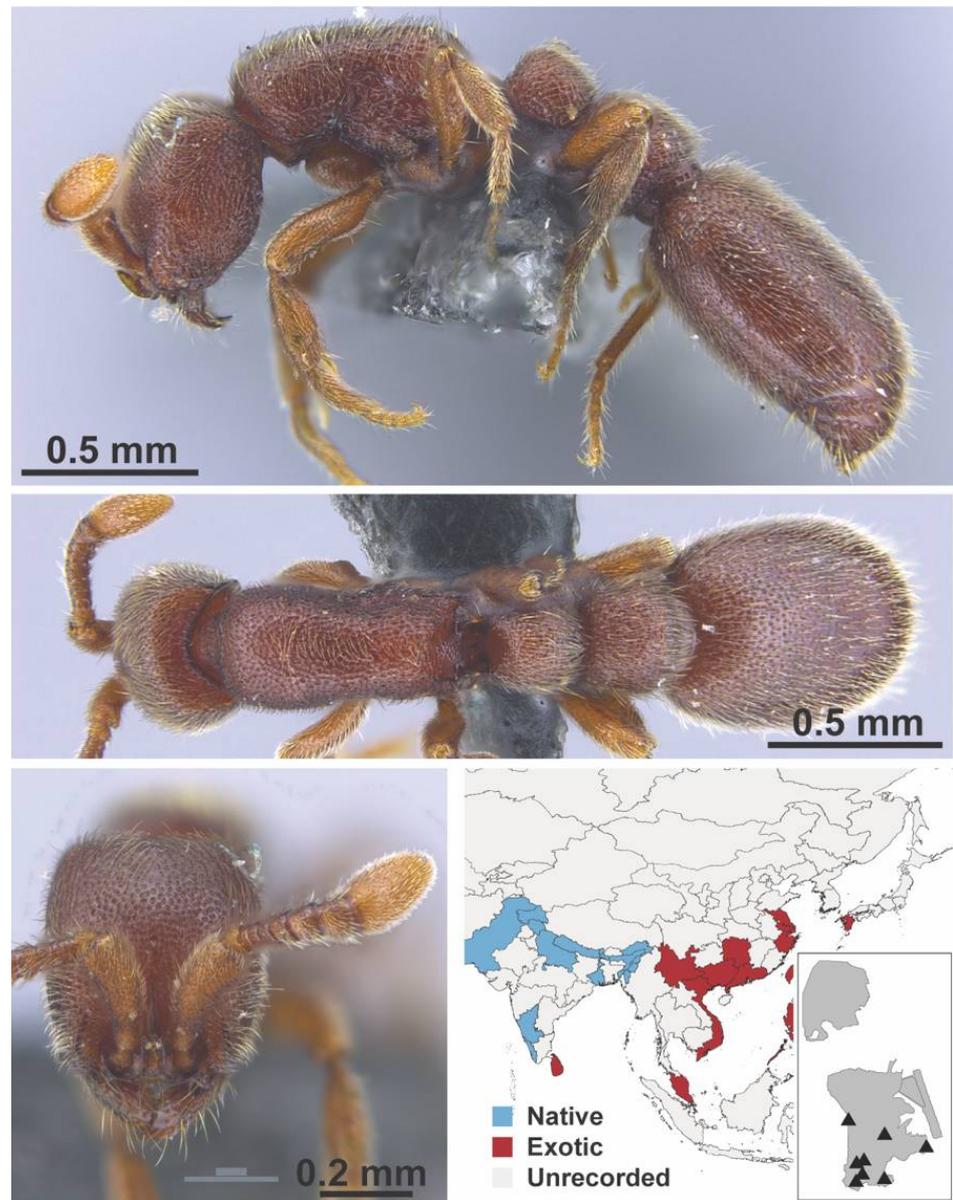


Figure A12. *Ooceraea biroi* Forel, 1907 worker (MAC_S02_LLSP_Sp.4, IBBL).

Appendix A.4 FORMICINAE

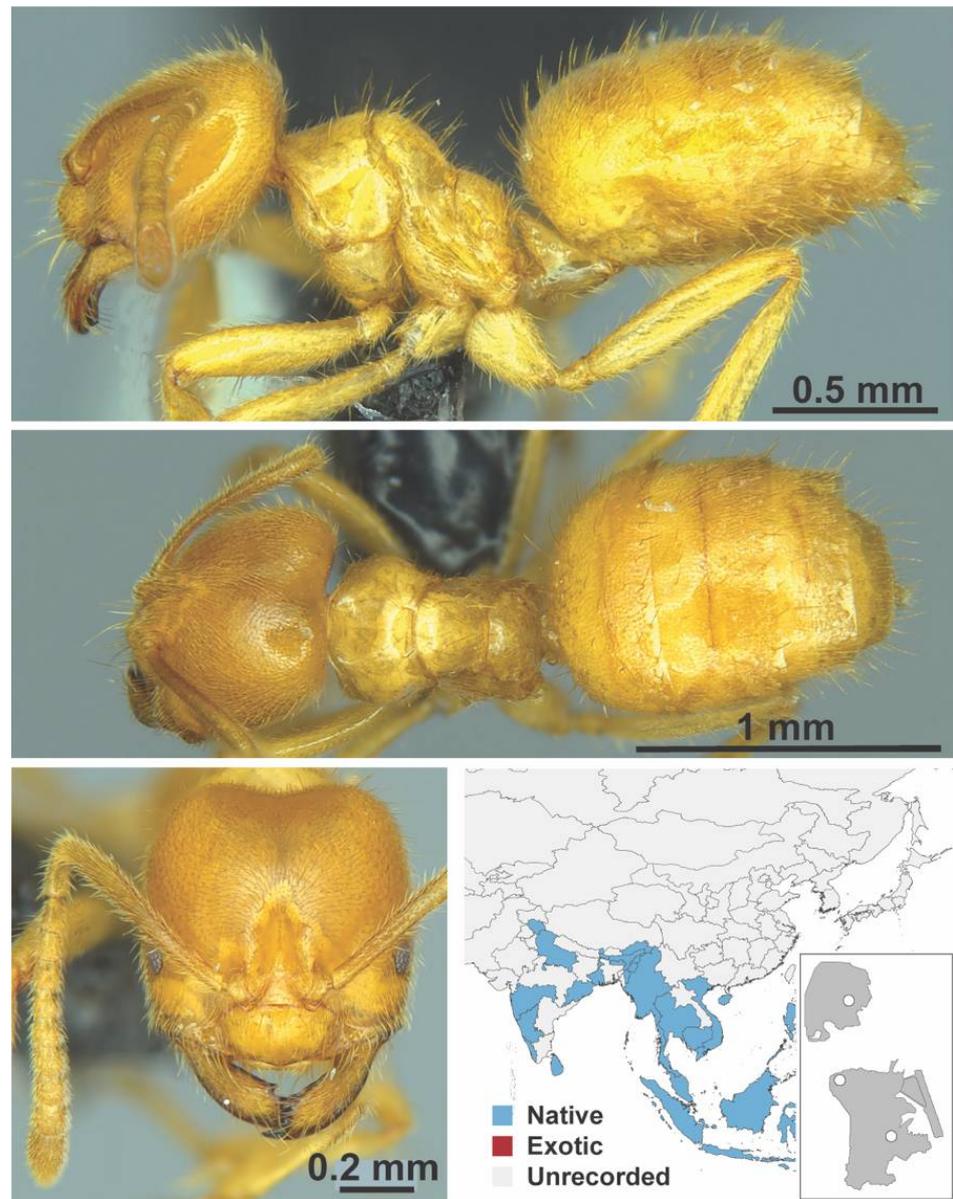


Figure A13. *Acropyga acutiventris* Roger, 1962 worker (*Acropyga acutiventris*, CML collection).

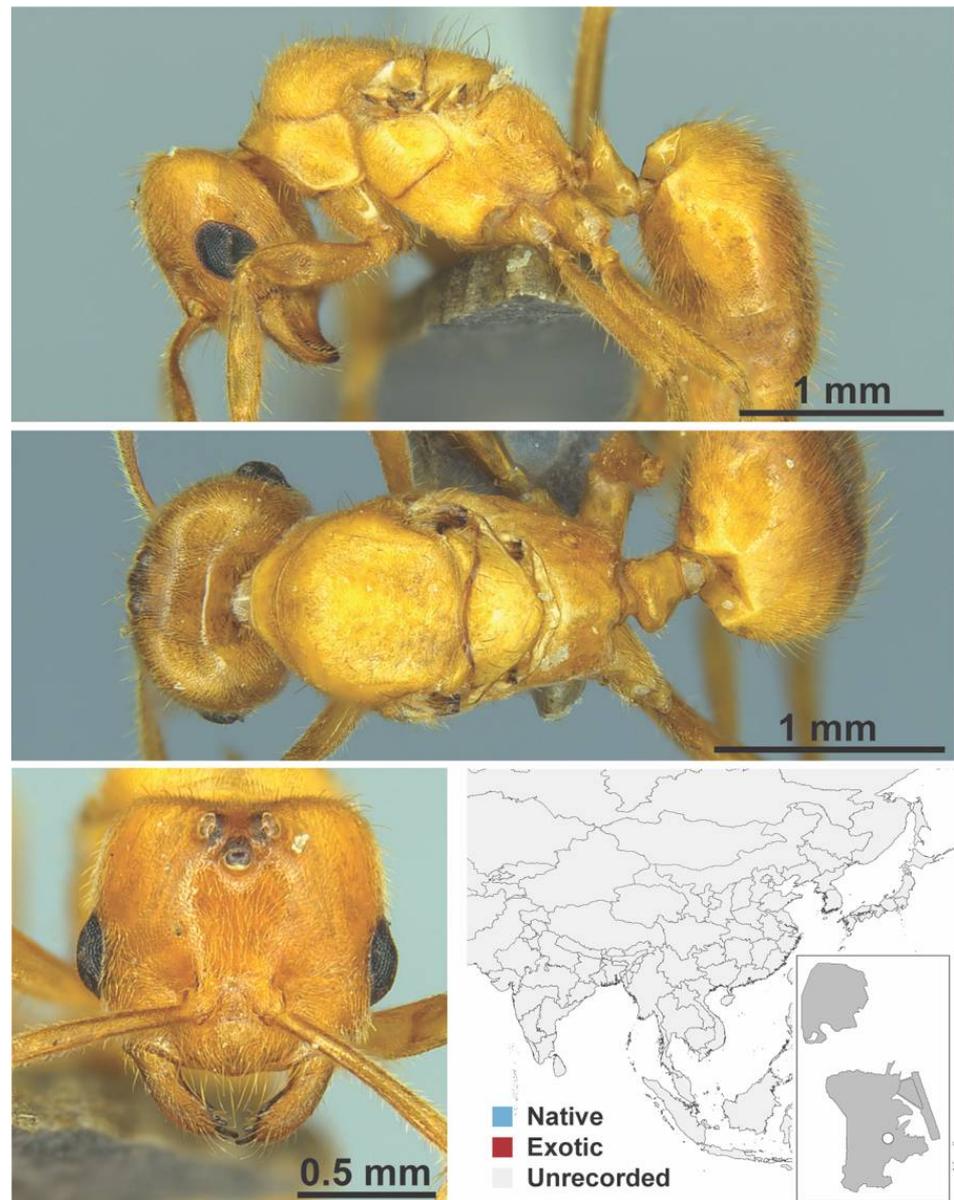


Figure A14. *Acropyga* sp. mo02 gyne (*Acropyga* sp. mo02, CML collection).

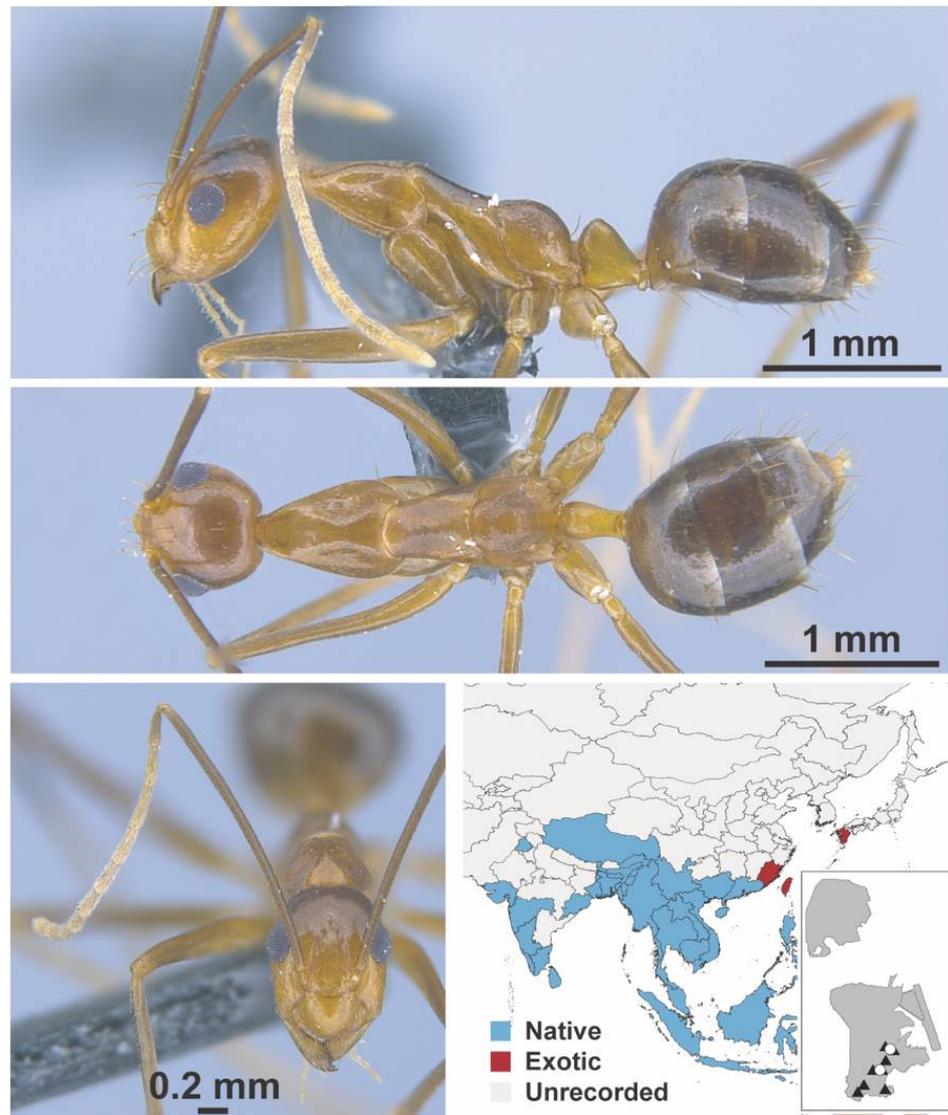


Figure A15. *Anoplolepis gracilipes* Smith, 1857 worker (MAC_S14_LLSA_Sp.14, IBBL).

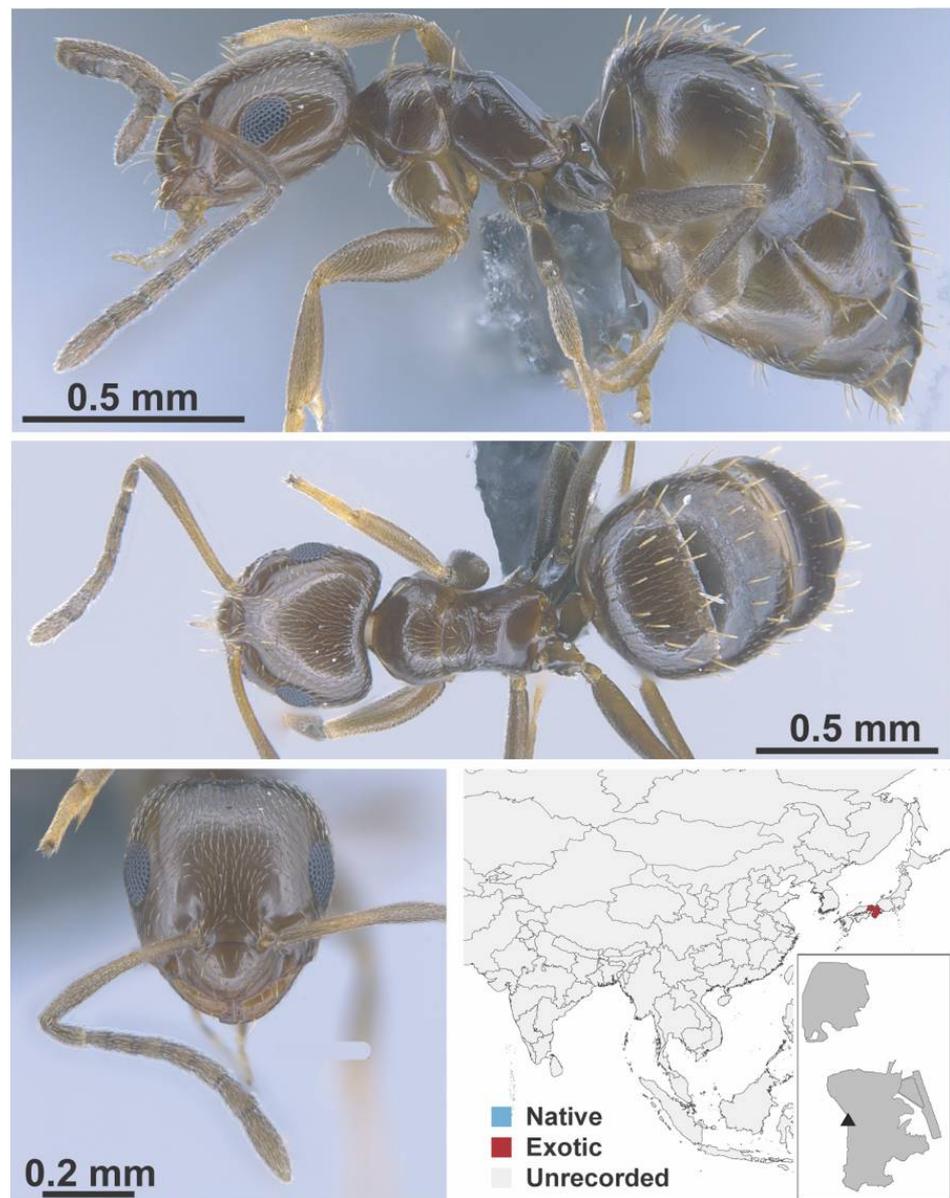


Figure A16. *Brachymyrmex patagonicus* Mayr, 1868 worker (FB19202, IBBL).

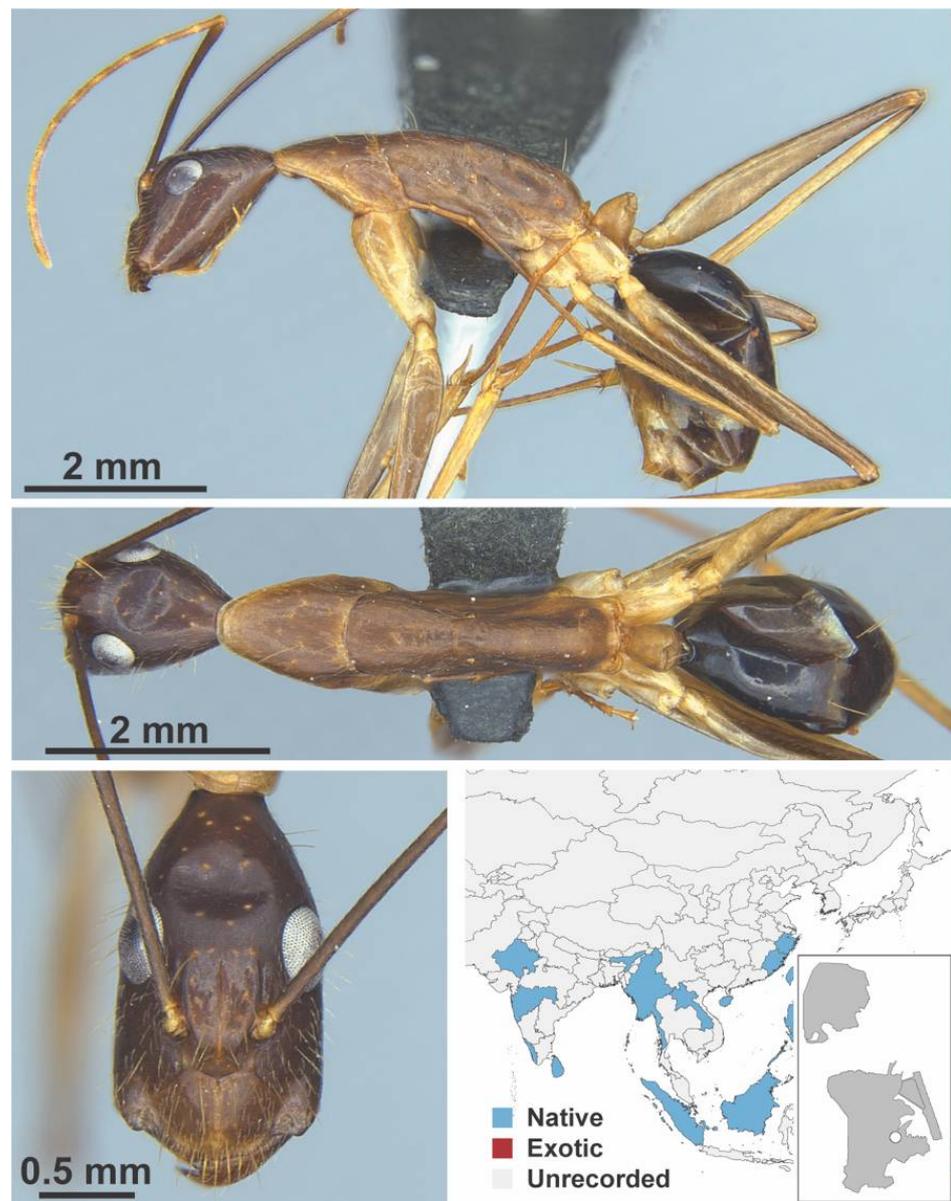


Figure A17. *Camponotus carin* Emery, 1889 worker (*Camponotus carin*, CML collection).

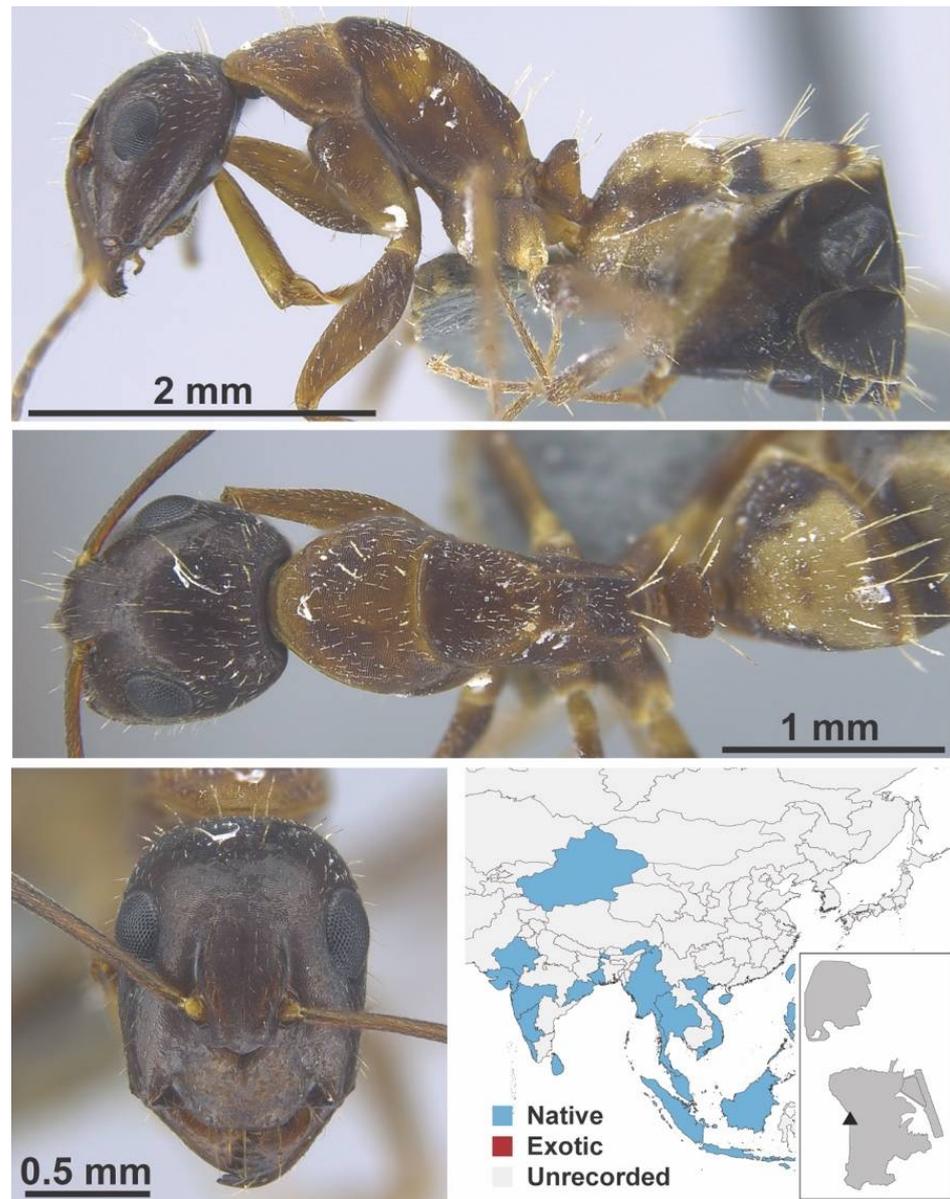


Figure A18. *Camponotus* nr. *irritans* Smith, F., 1857 worker (MAC_S20_B08, IBBL).

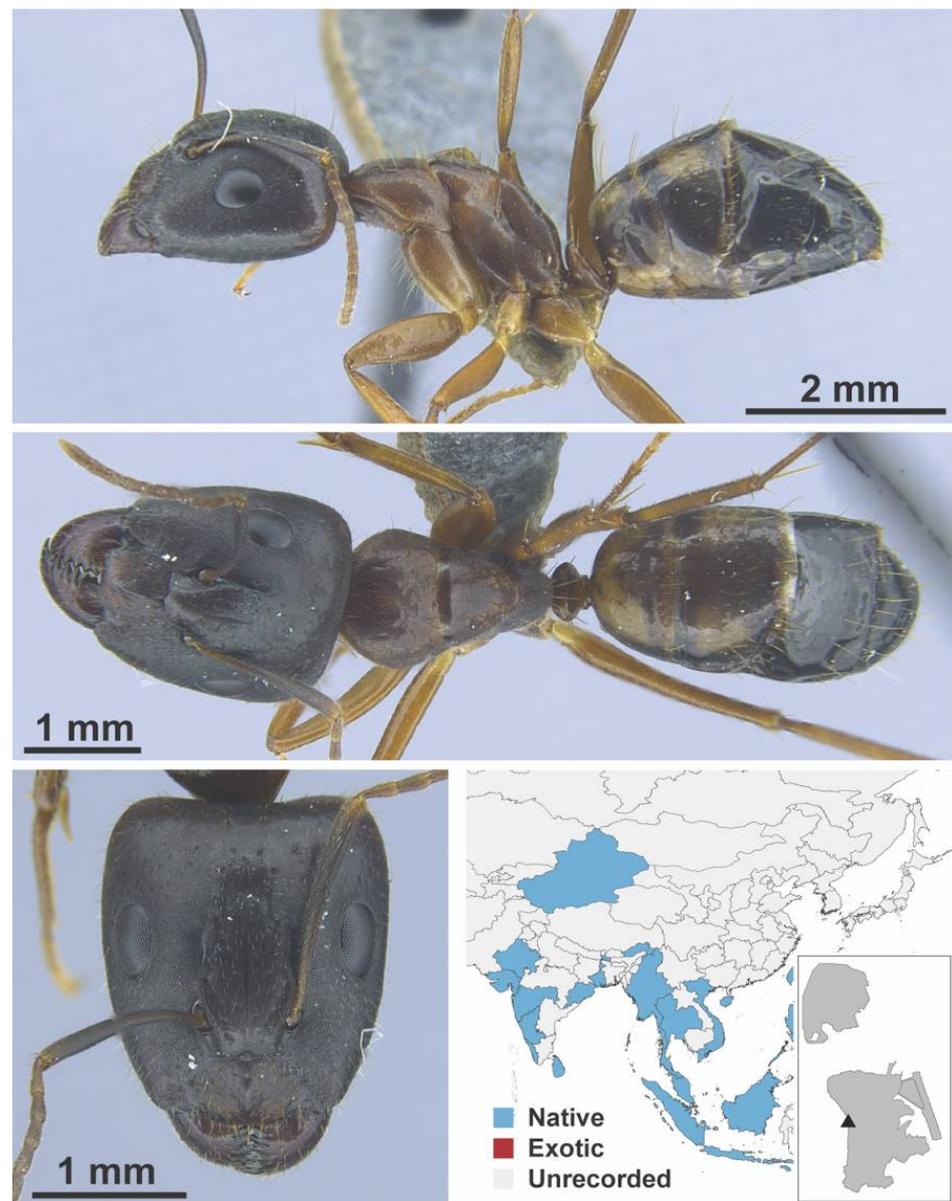


Figure A19. *Camponotus* nr. *irritans* Smith, F., 1857 major (MAC_S20_B08, IBBL).

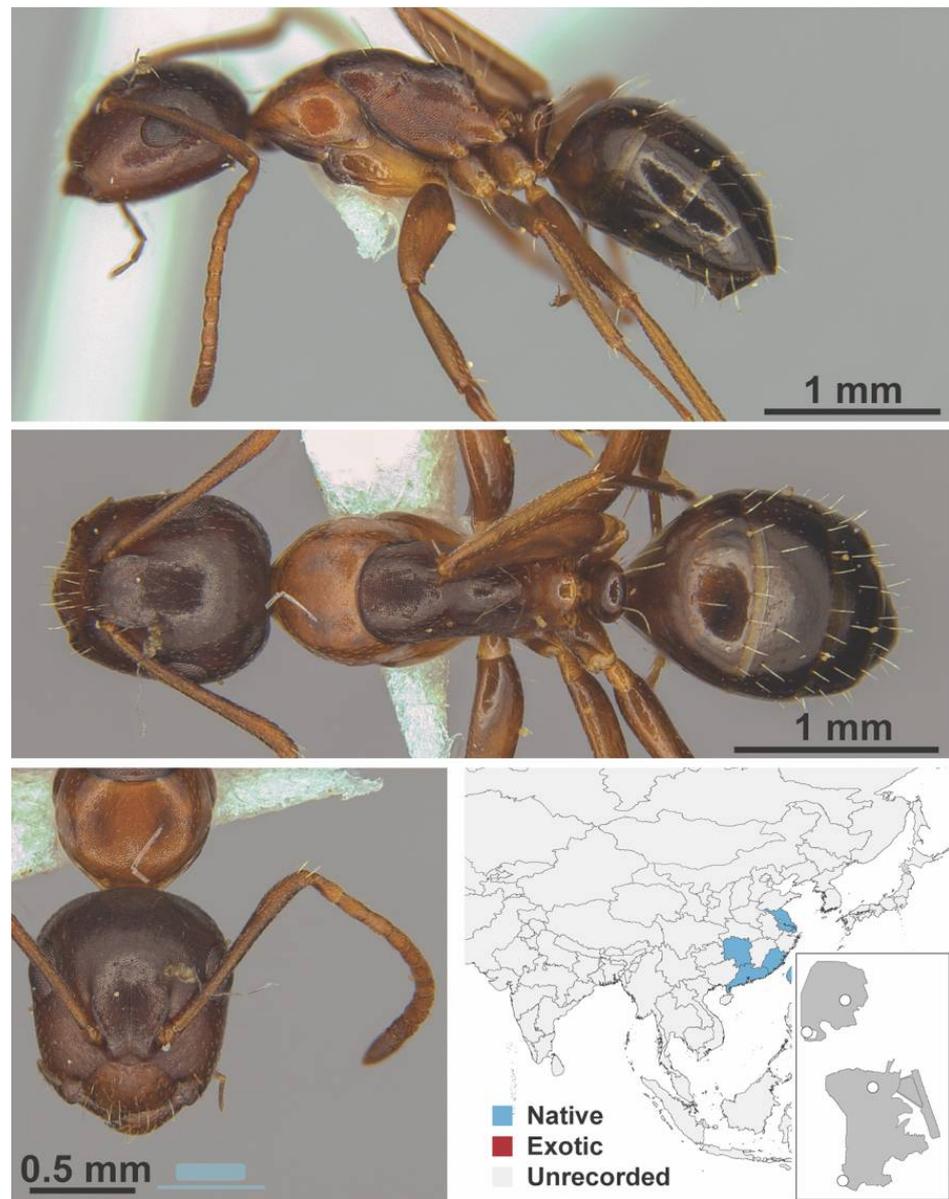


Figure A20. *Camponotus lighti* Wheeler, 1927 worker (*Camponotus lighti*, CML collection).

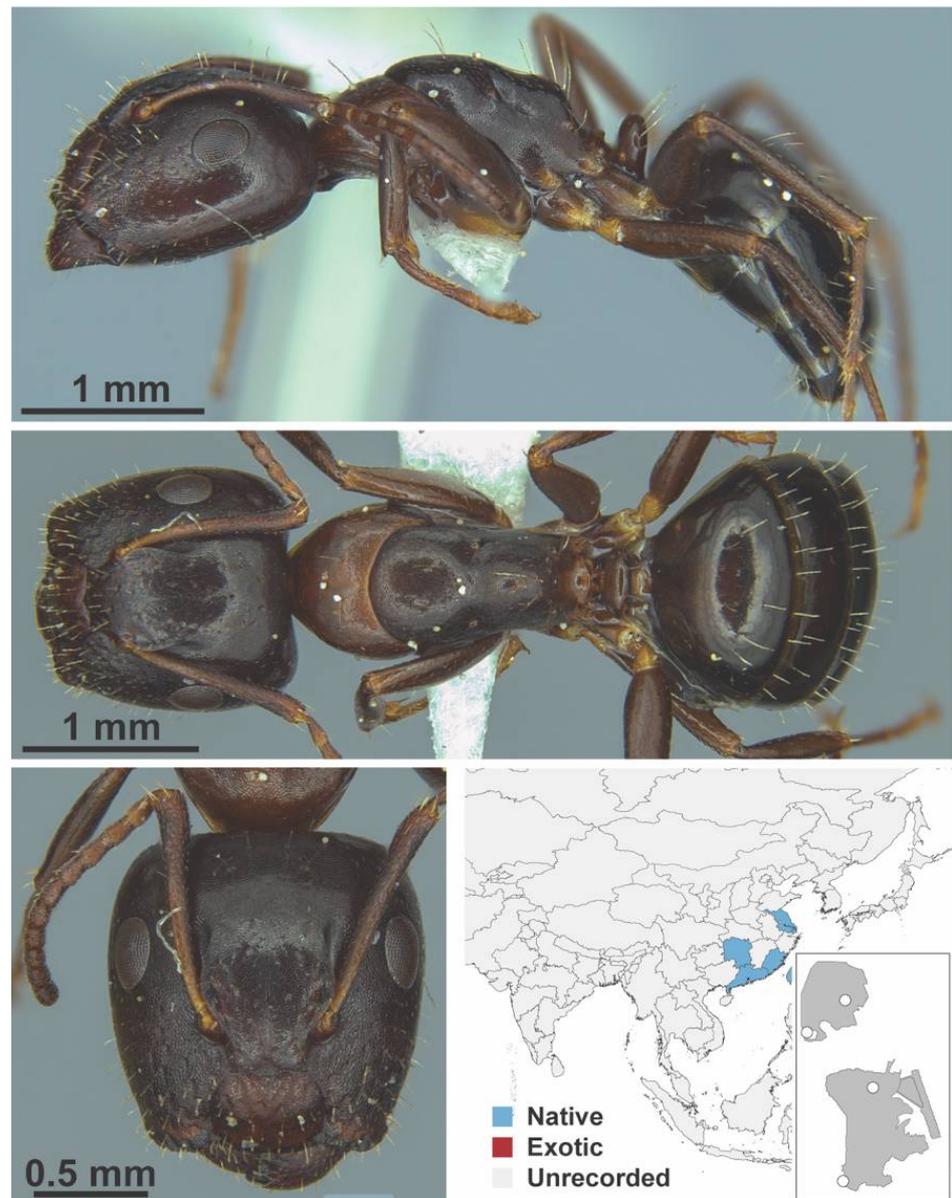


Figure A21. *Camponotus lighti* Wheeler, 1927 major (*Camponotus lighti*, CML collection).

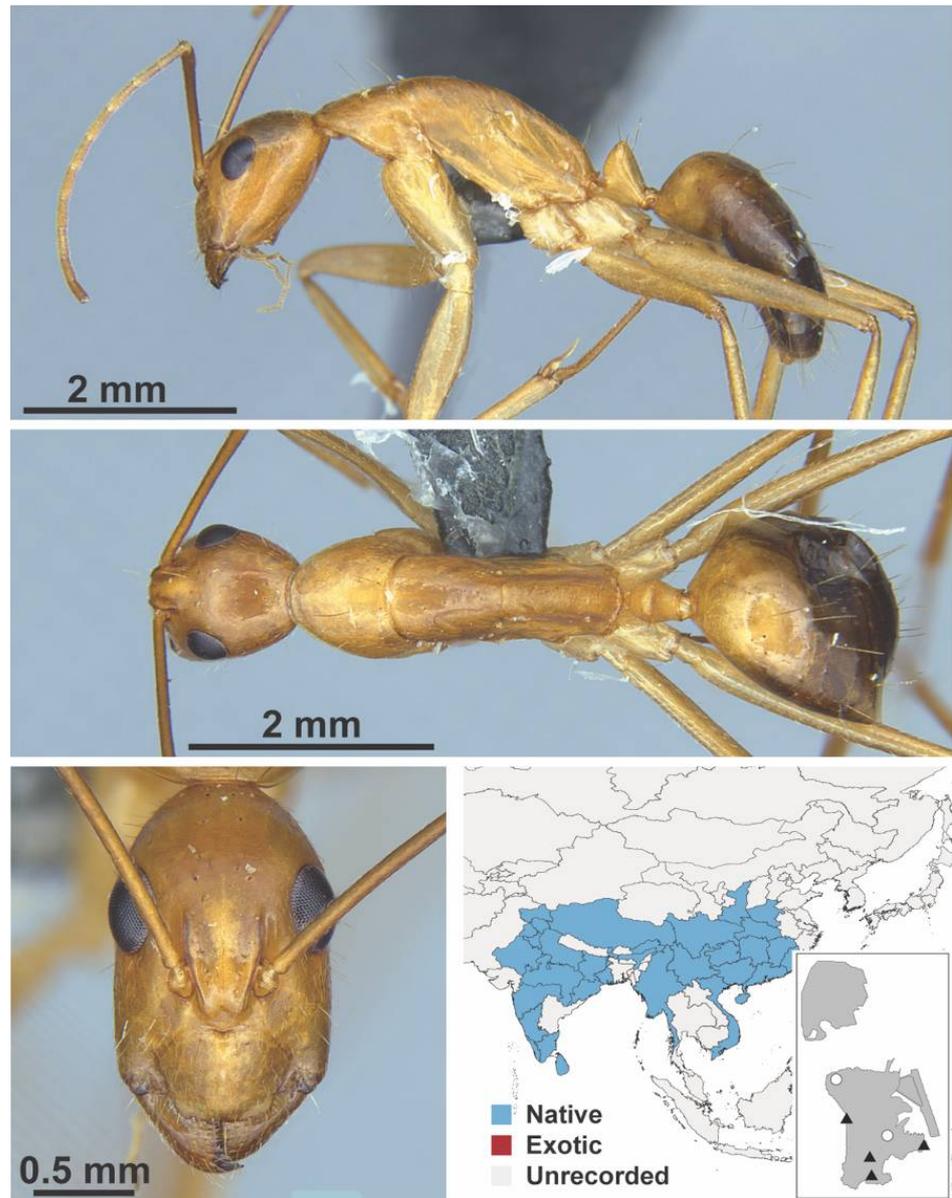


Figure A22. *Camponotus mitis* Smith, 1858 worker (MAC_S07_LLSA_sp.1, IBBL).

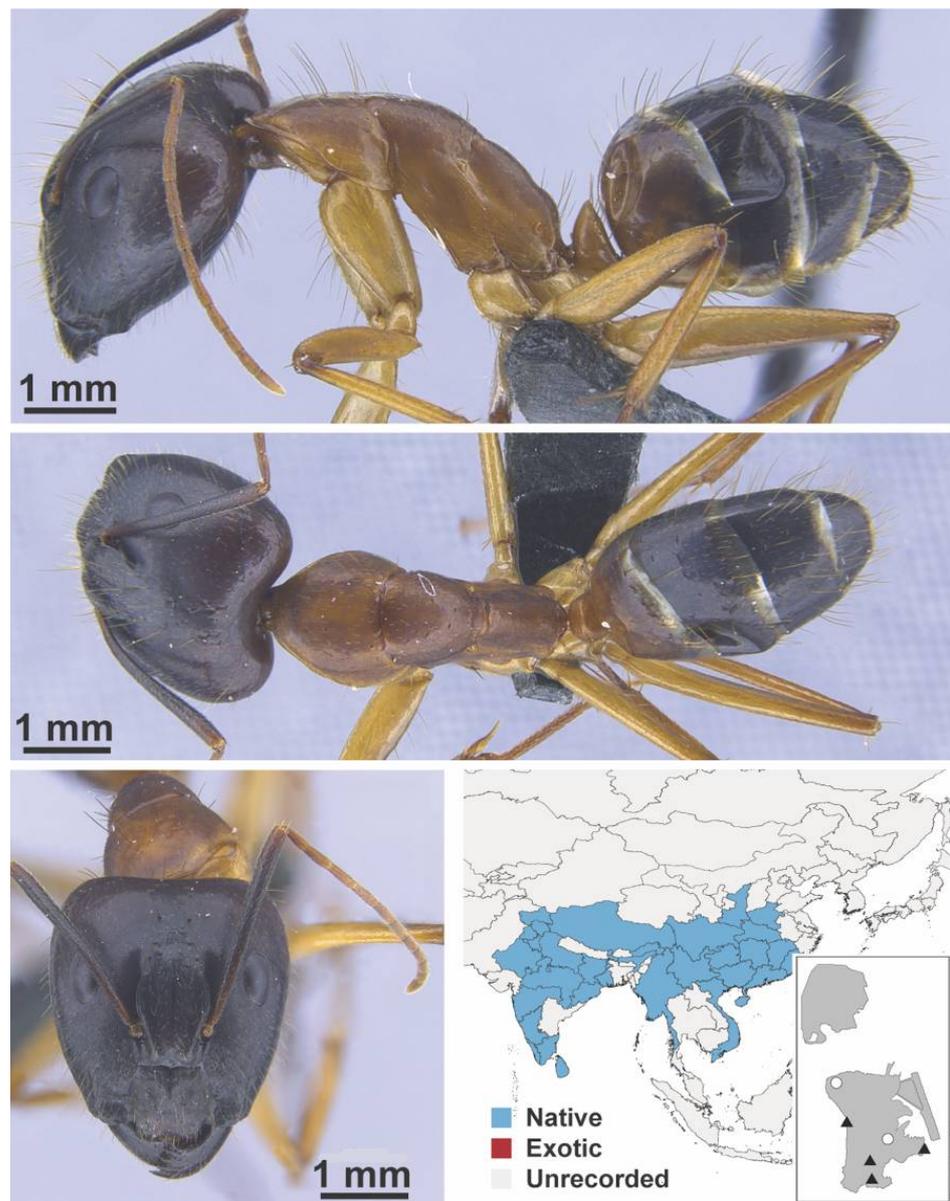


Figure A23. *Camponotus mitis* Smith, 1858 major (MAC_S11_LLSP_Sp.12, IBBL).

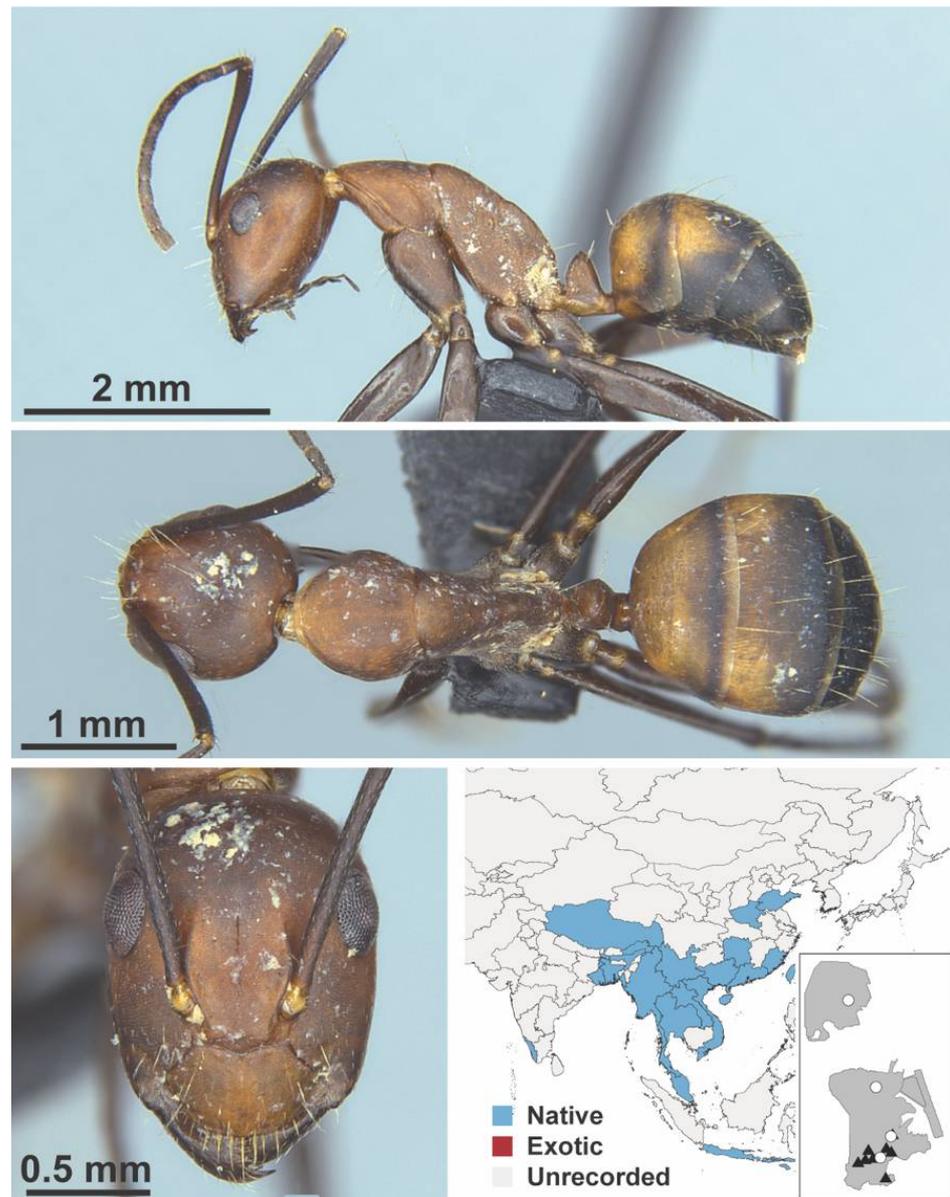


Figure A24. *Camponotus nicobarensis* Mayr, 1865 worker (MAC_S21_LLSP, IBBL).

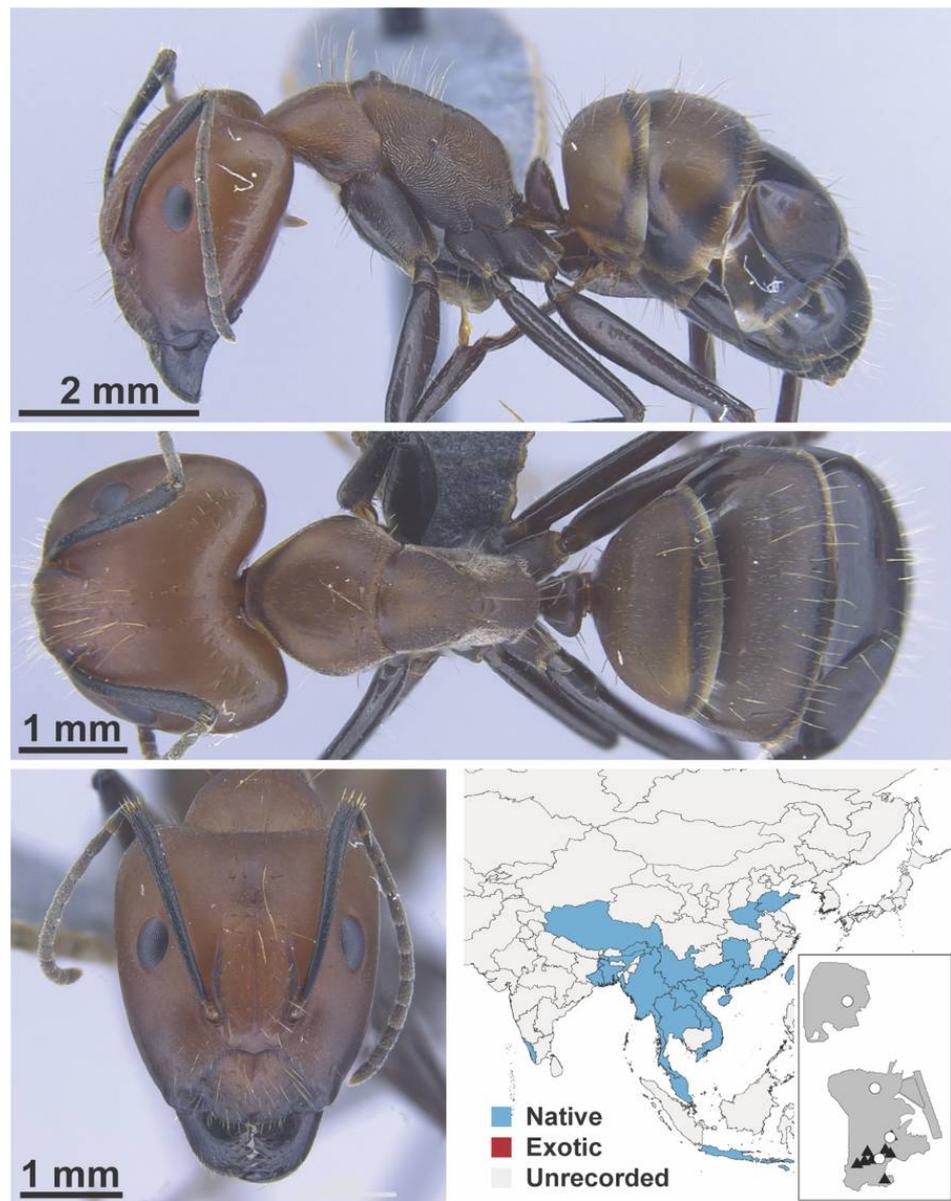


Figure A25. *Camponotus nicobarensis* Mayr, 1865 major (MAC_S16_T1_5m_sp.3, IBBL).

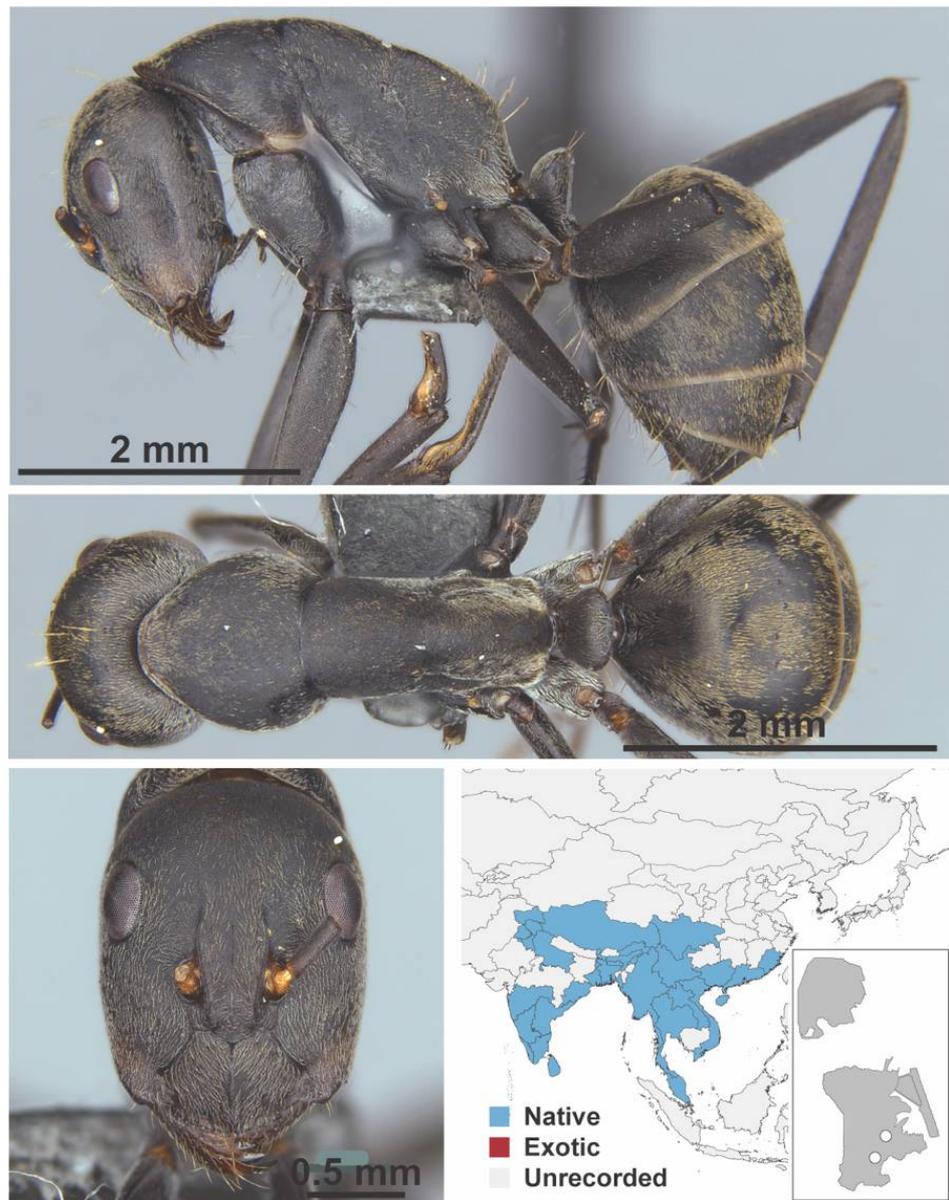


Figure A26. *Camponotus parius* Emery, 1889 worker (*Camponotus parius*, CML collection).

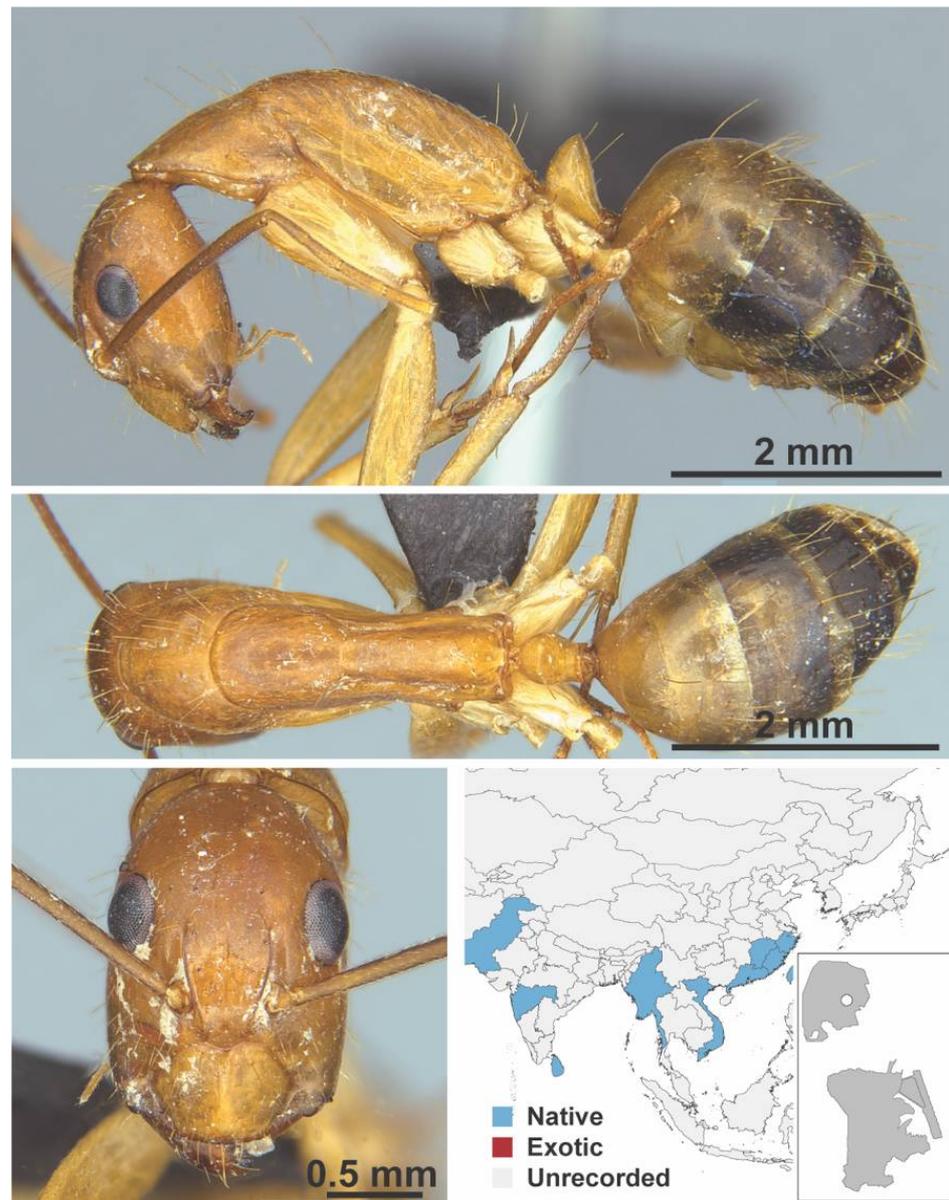


Figure A27. *Camponotus variegatus dulcis* Dalla Torre, 1893 worker (*Camponotus variegatus dulcis*, CML collection).

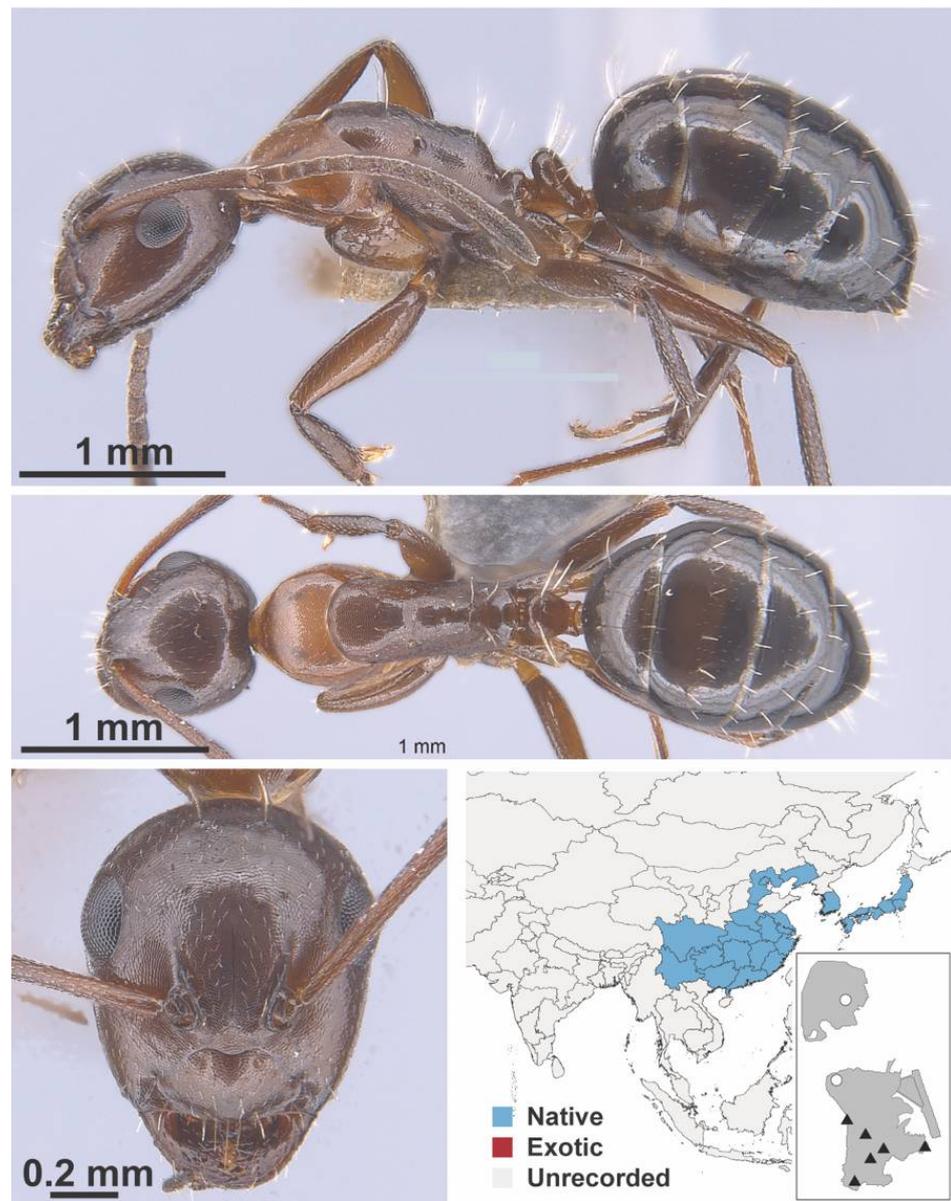


Figure A28. *Camponotus vitiosus* Smith, 1874 worker (MAC_S20_T4_2m_Sp.1, IBBL).

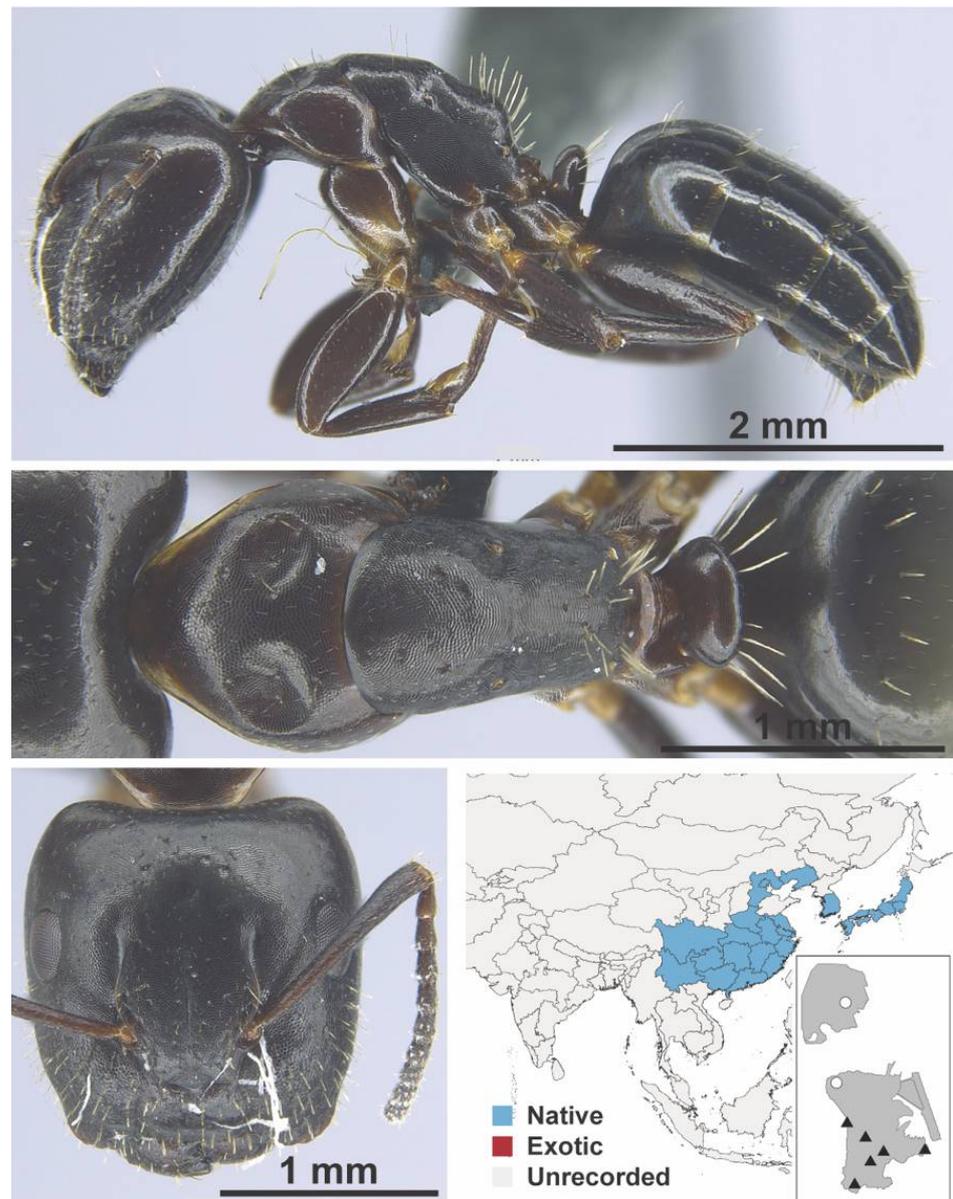


Figure A29. *Camponotus vitiosus* Smith, 1874 major (MAC_S14_T1_3m_Sp.1, IBBL).

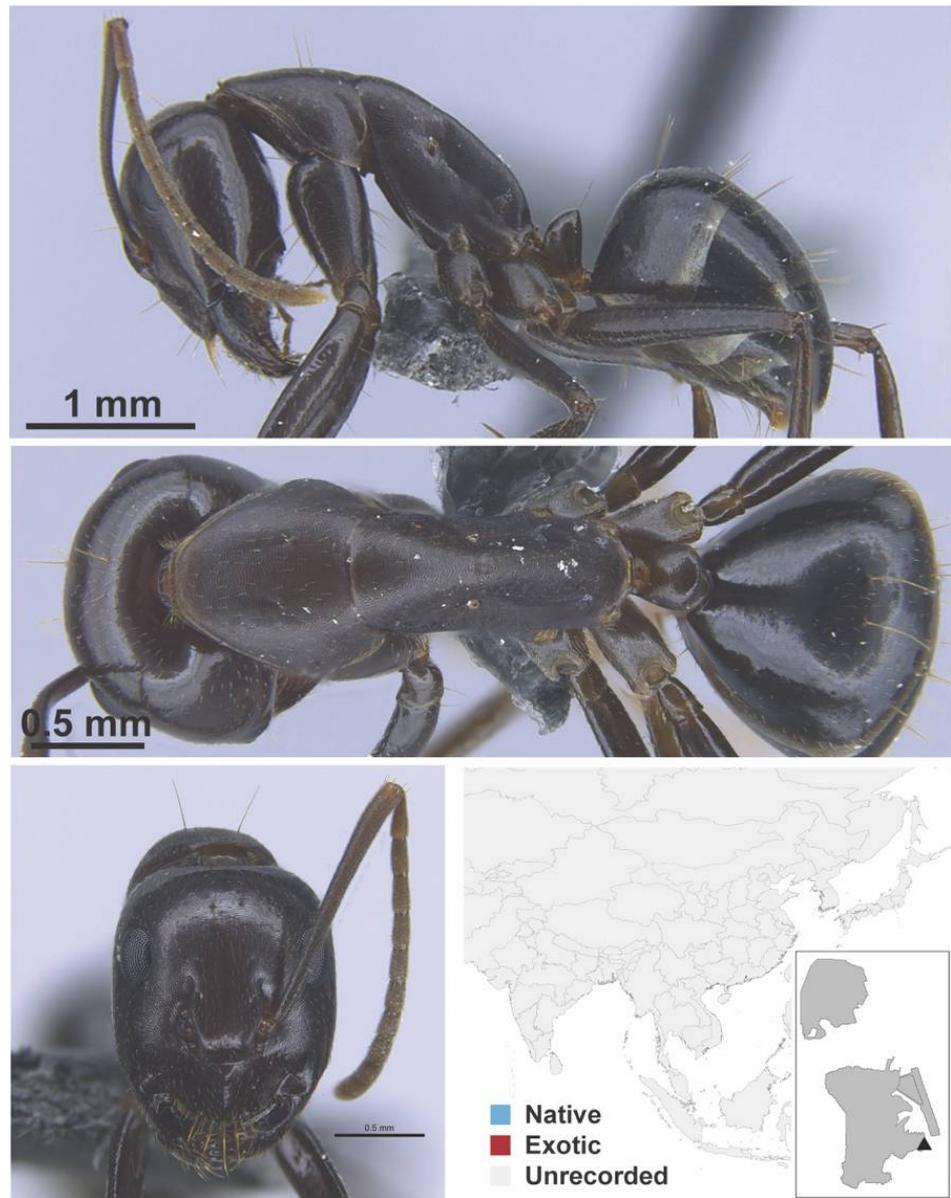


Figure A30. *Camponotus* sp.1 FB worker (MAC_FB19182, IBBL).

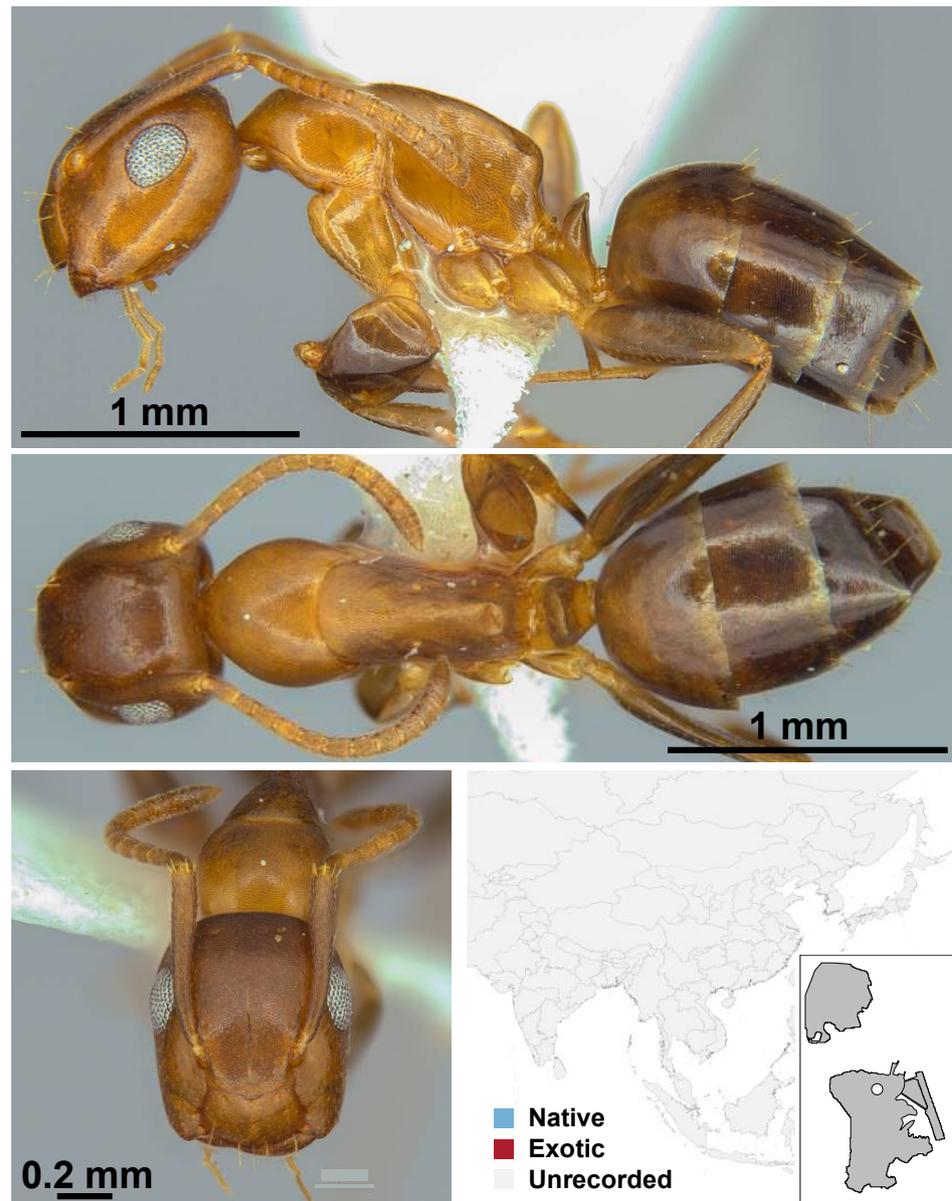


Figure A31. *Colobopsis nr. nipponica* Wheeler, 1928 worker (*Colobopsis nr. nipponica*, CML collection).

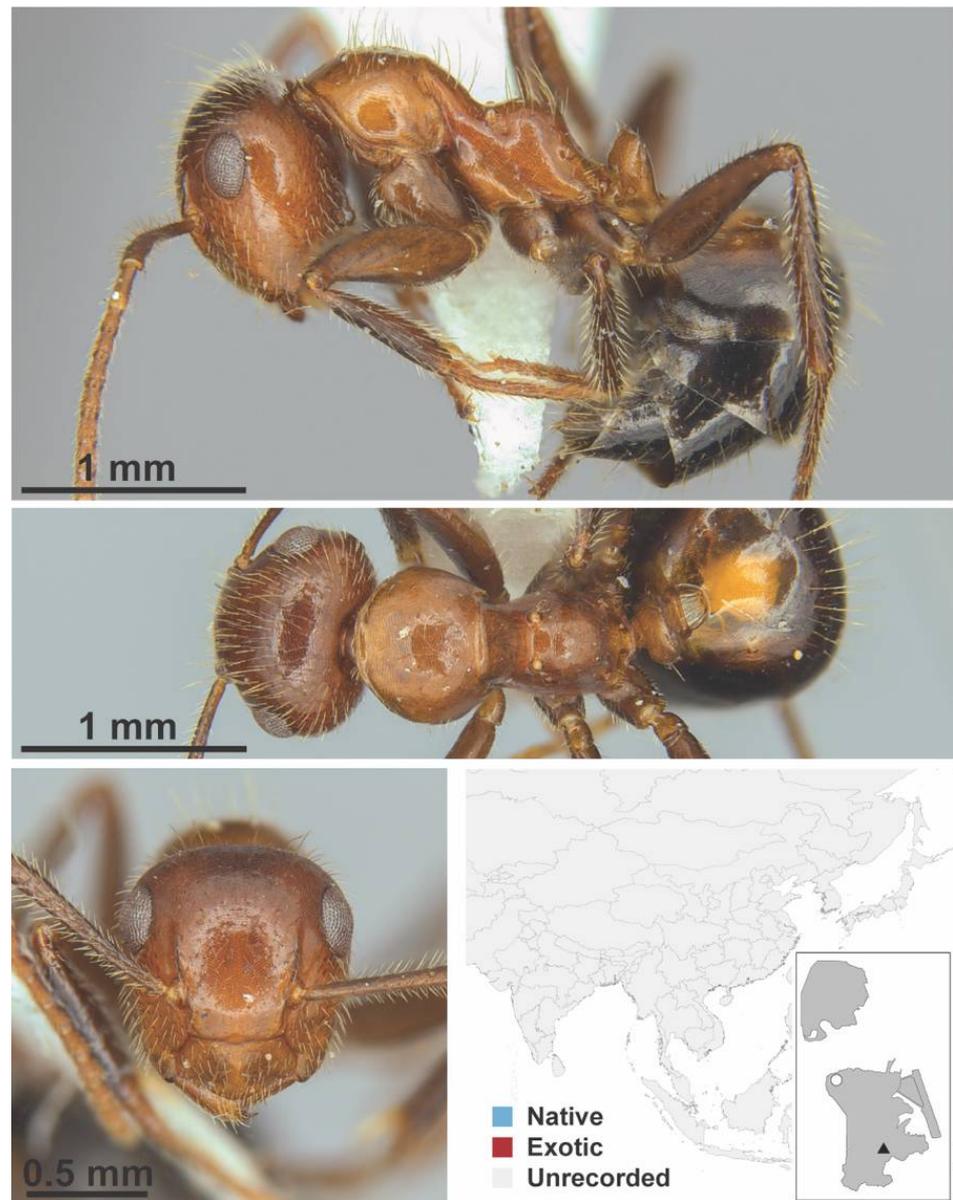


Figure A32. *Colobopsis nr. vitrea* Smith, 1860 worker (*Colobopsis nr. vitrea*, CML collection).

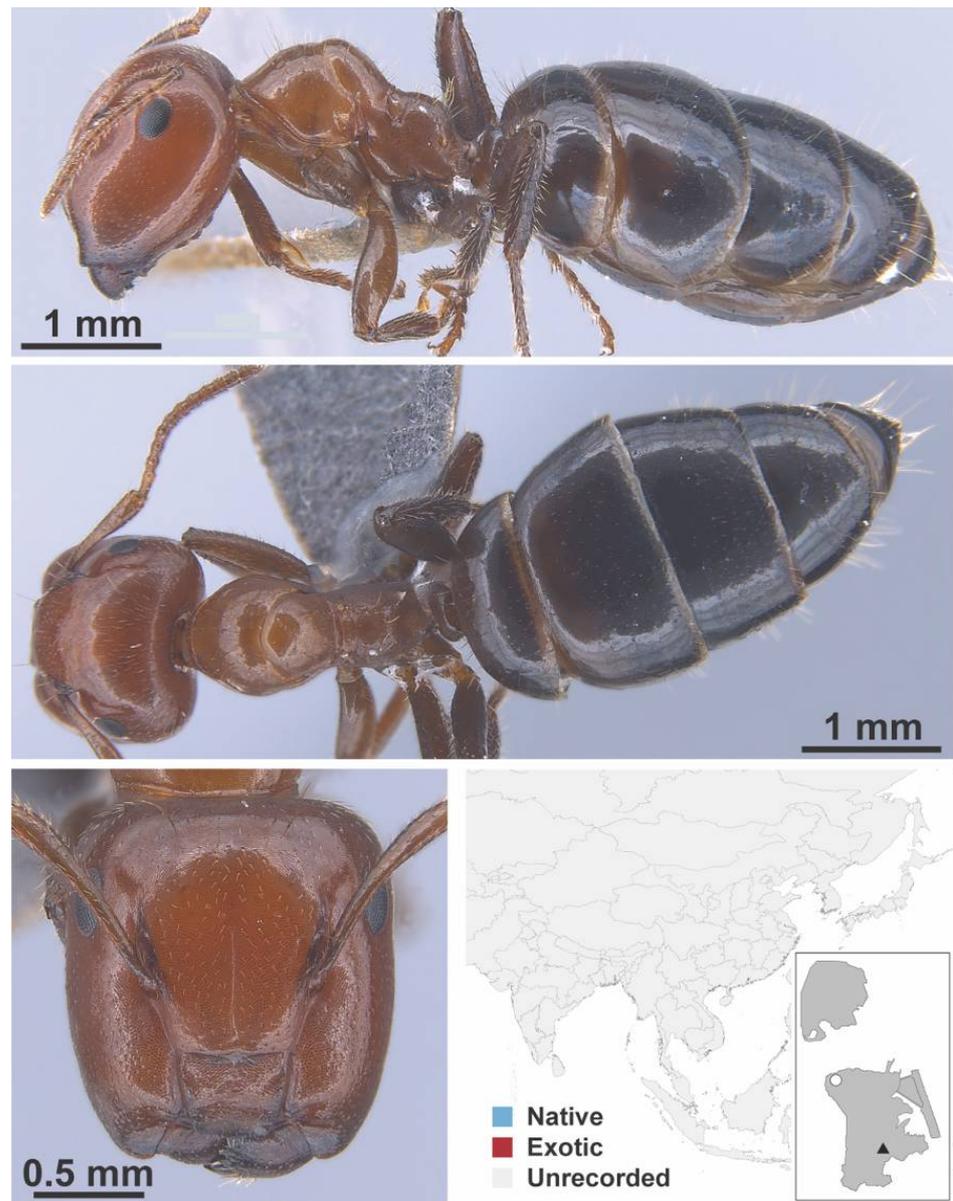


Figure A33. *Colobopsis nr. vitrea* Smith, 1860 major (FB19268, IBBL).

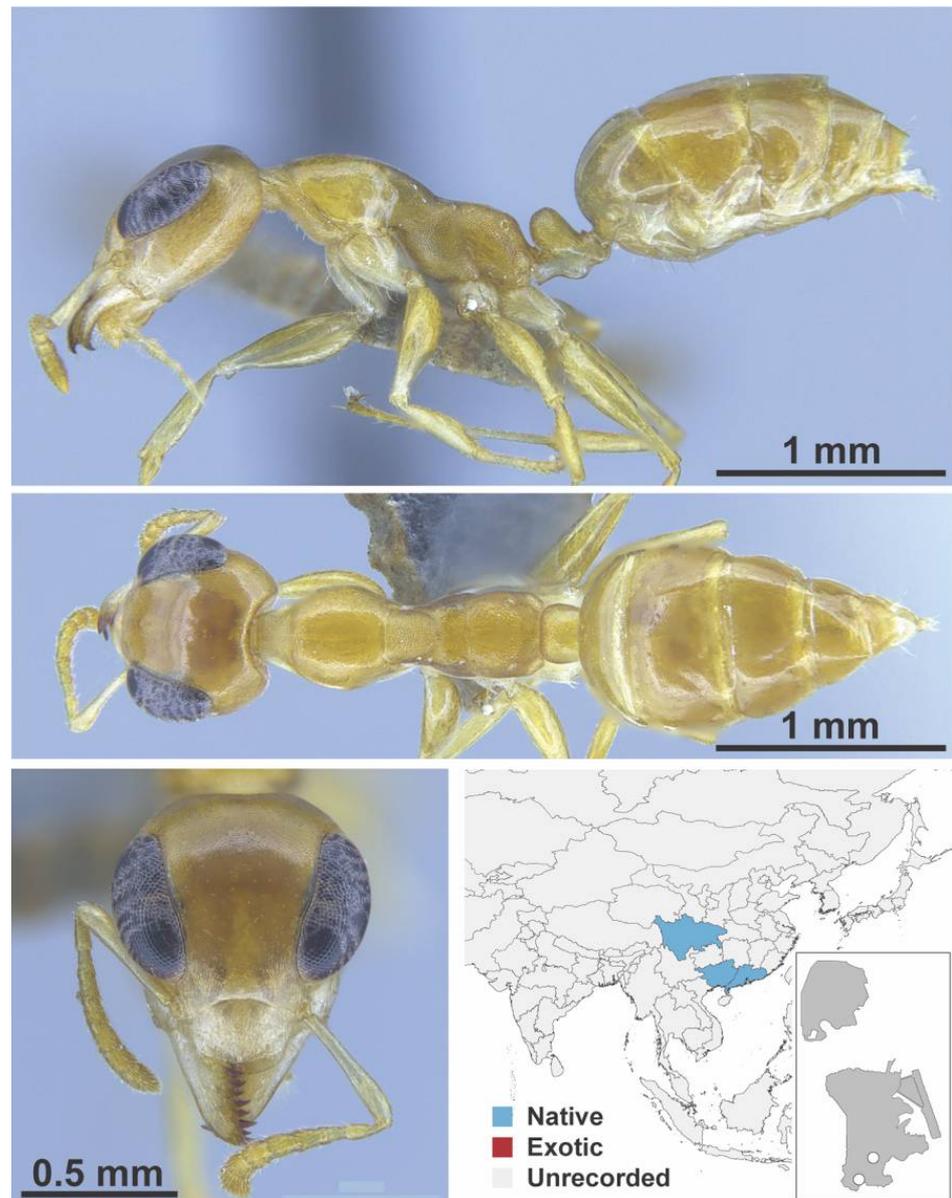


Figure A34. *Gesomyrmex howardi* Wheeler, W. M., 1921 worker (MWong_MaiPo_7viii2018, IBBL).

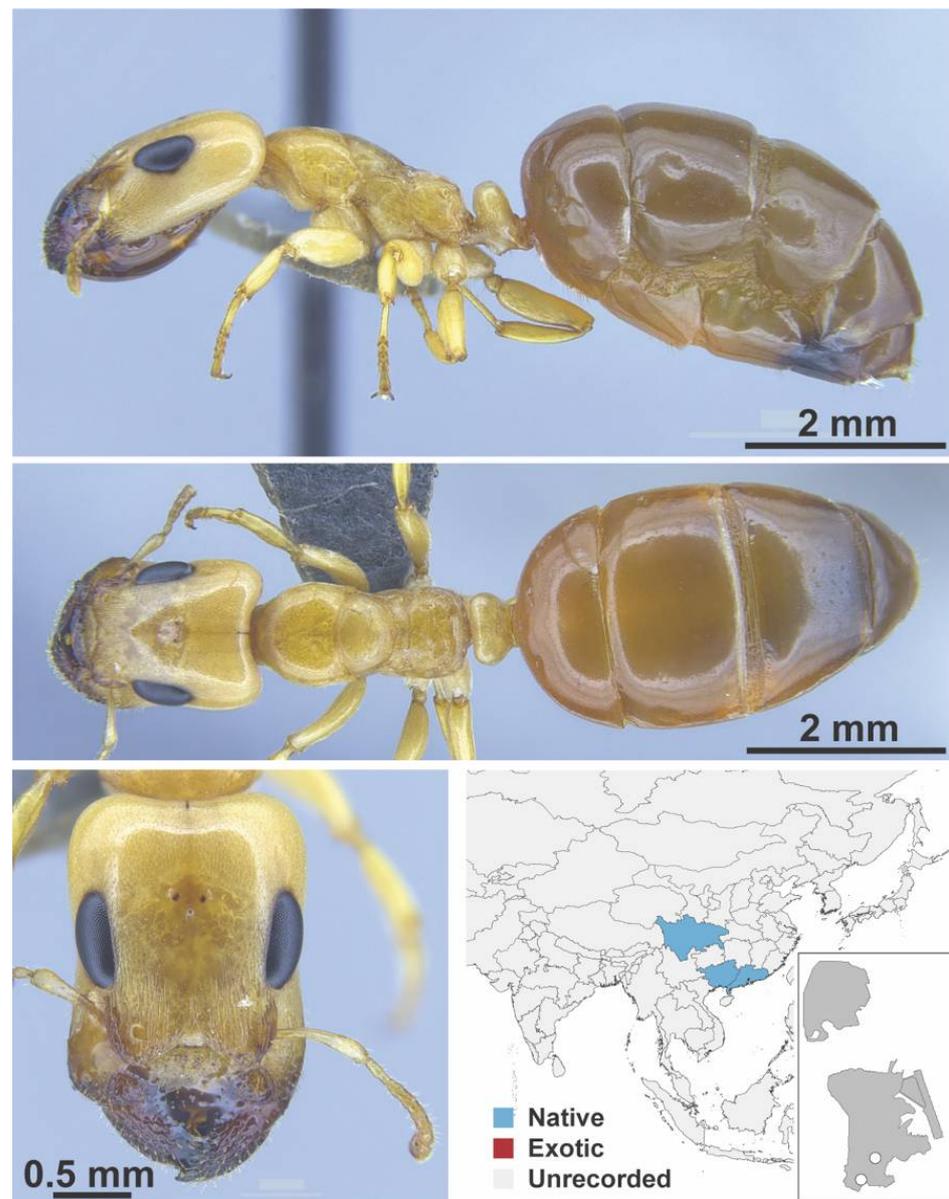


Figure A35. *Gesomyrmex howardi* Wheeler, W. M., 1921 supermajor (MWong_MaiPo_7viii2018_Colony4_6_2.6x12.5, IBBL).

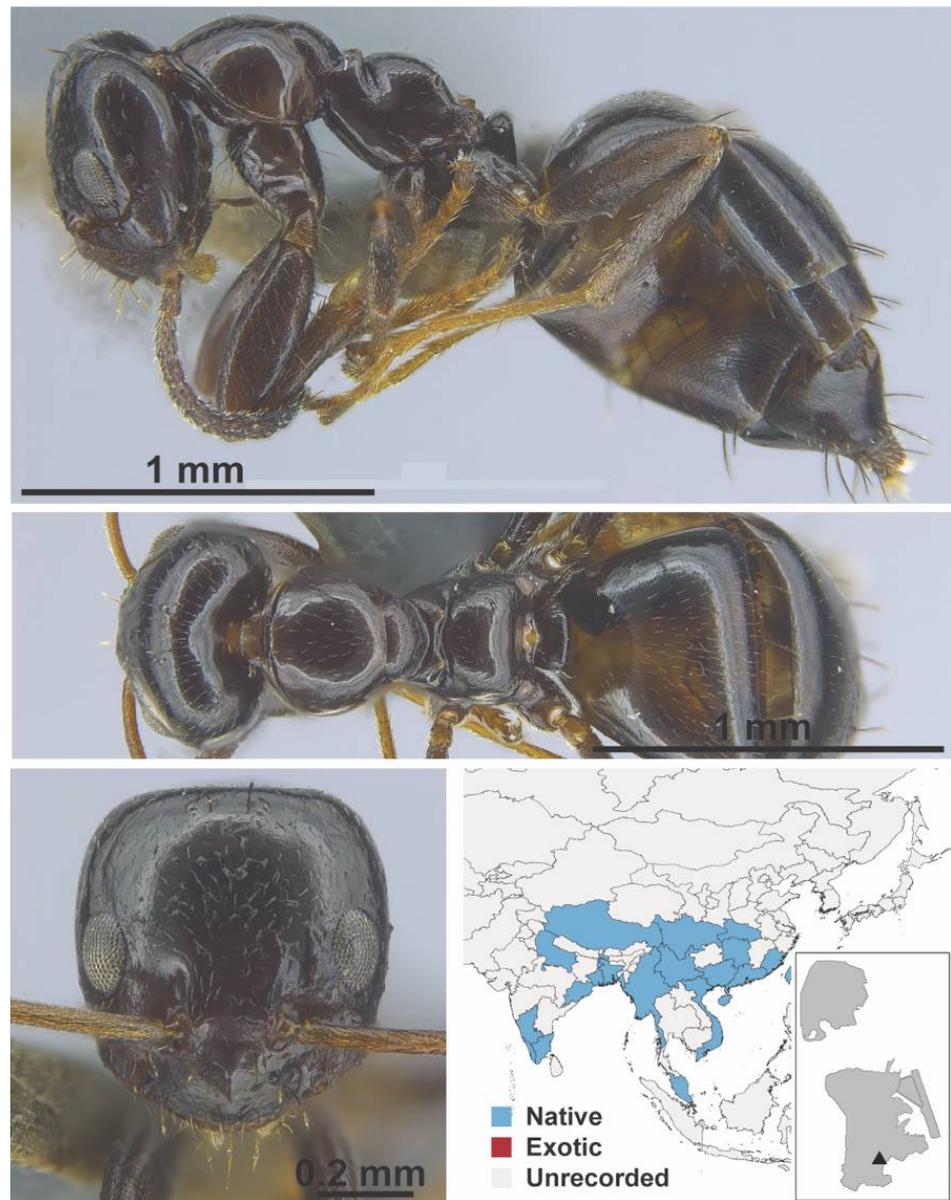


Figure A36. *Lepisiota rothneyi* Forel, 1894 worker (MAC_S06_B08_Sp.1_top, IBBL).

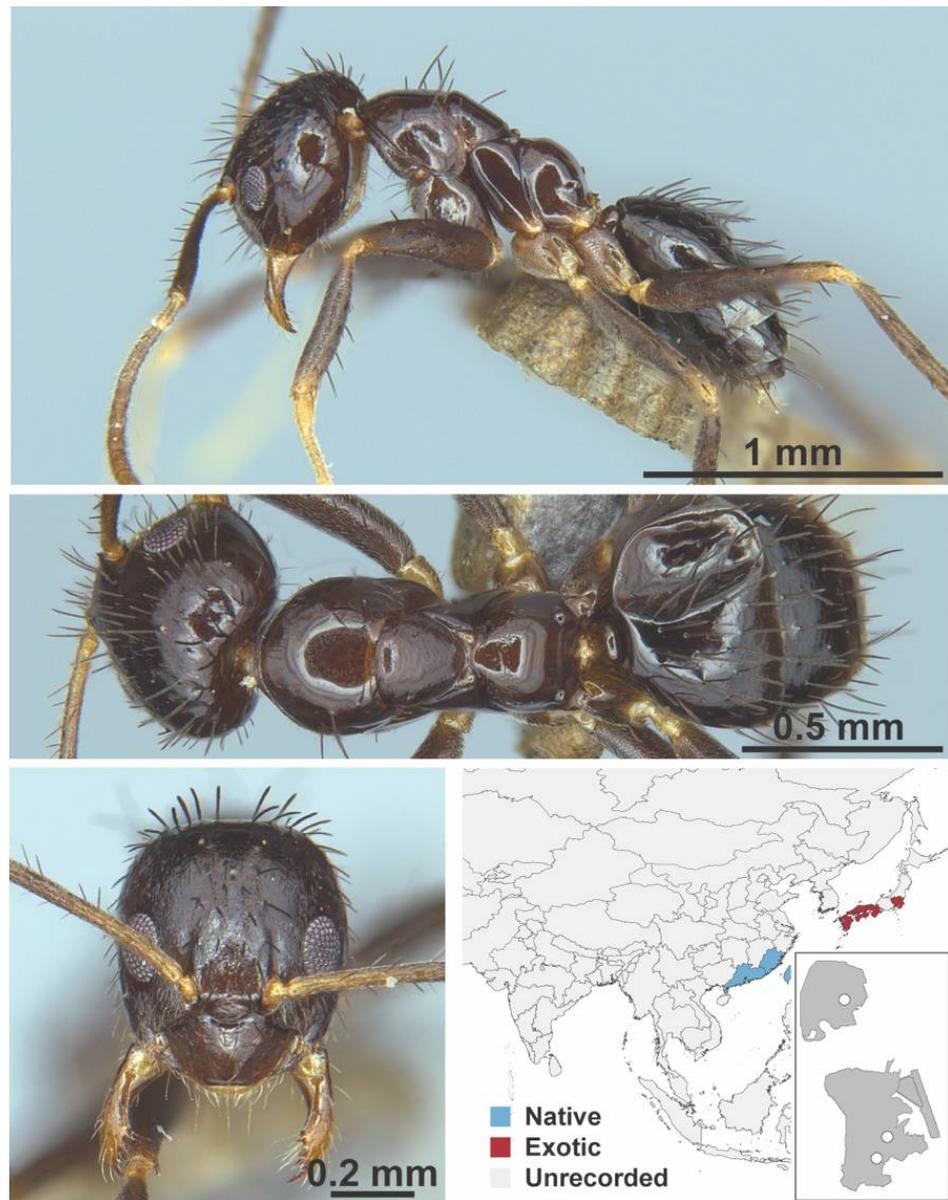


Figure A37. *Nylanderia amia* Forel, 1913 worker (ANTWEB1016677, IBBL).

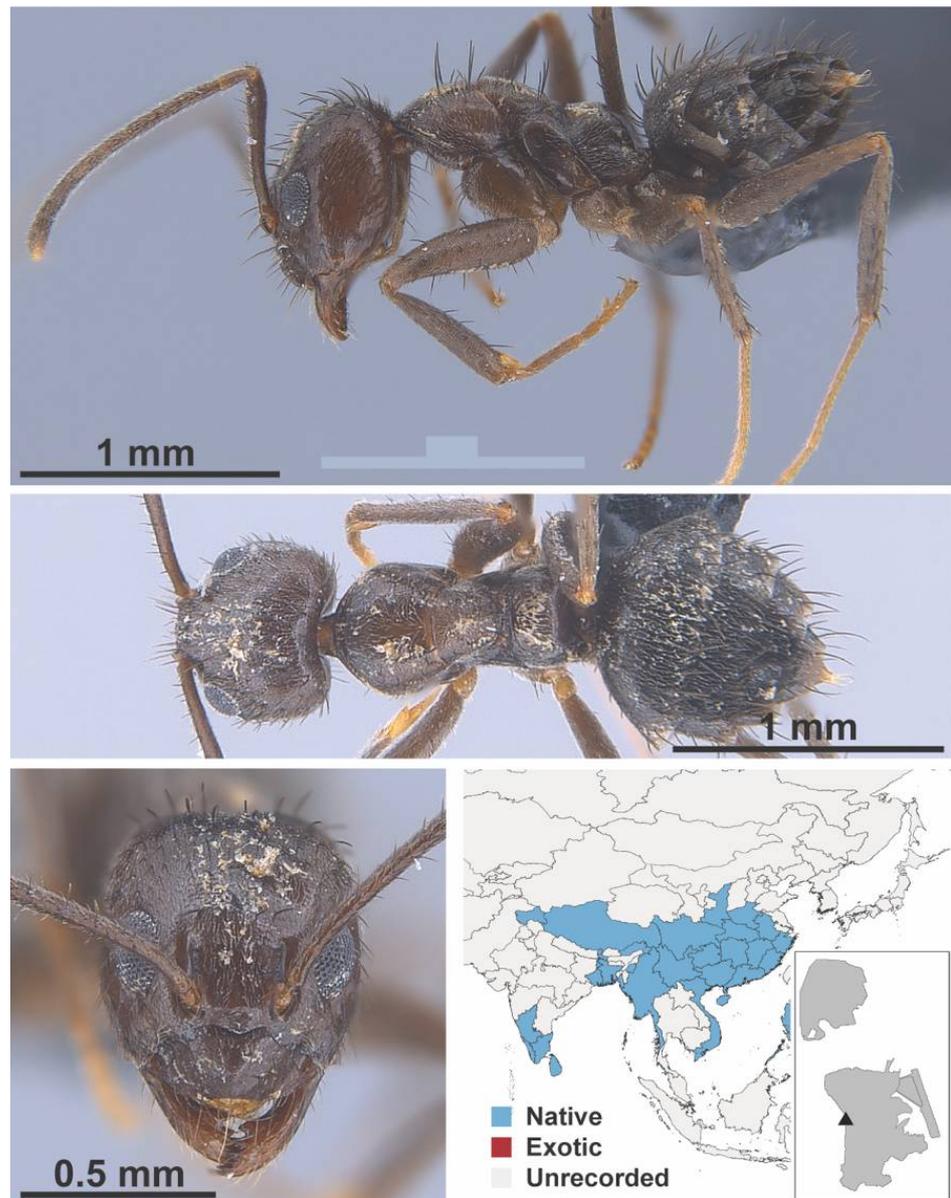


Figure A38. *Nylanderia bourbonica* Forel, 1886 worker (MAC_S20_LLSP_Sp.4, IBBL).

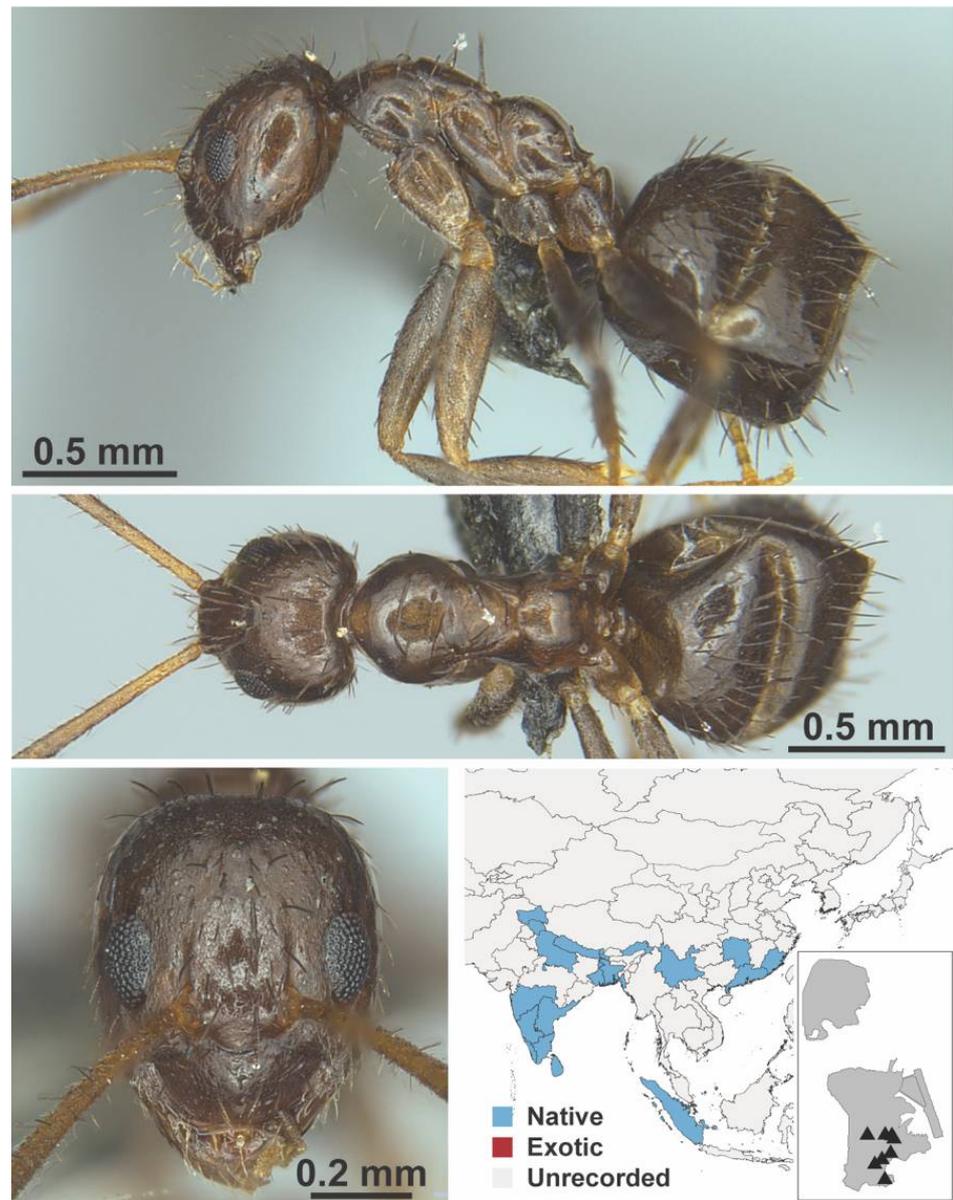


Figure A39. *Nylanderia indica* Forel, 1894 worker (MAC_S12_LLSP_sp.4, IBBL).

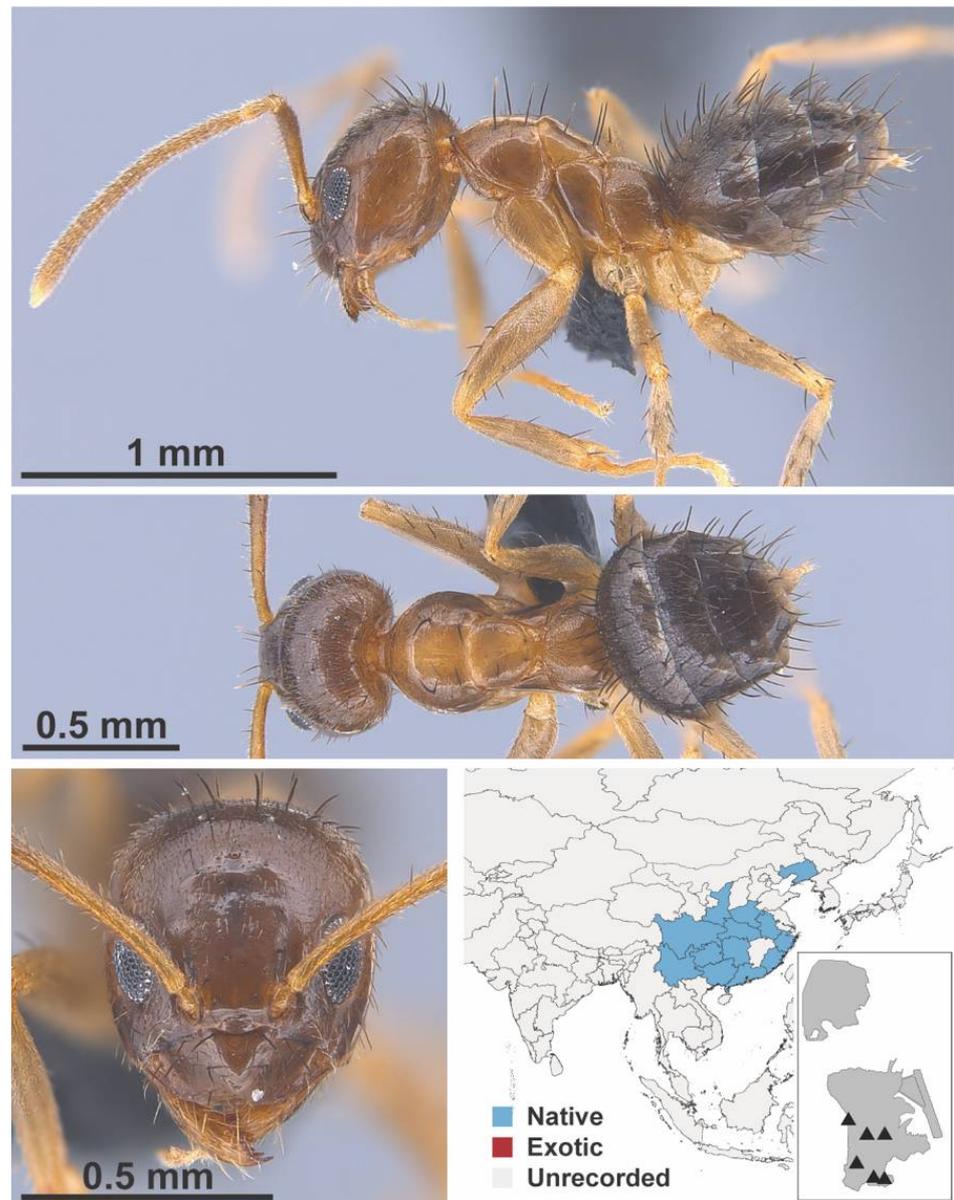


Figure A40. *Nylanderia sharpii* Forel, 1899 worker (MAC_S19_LLSA_Sp.5, IBBL).

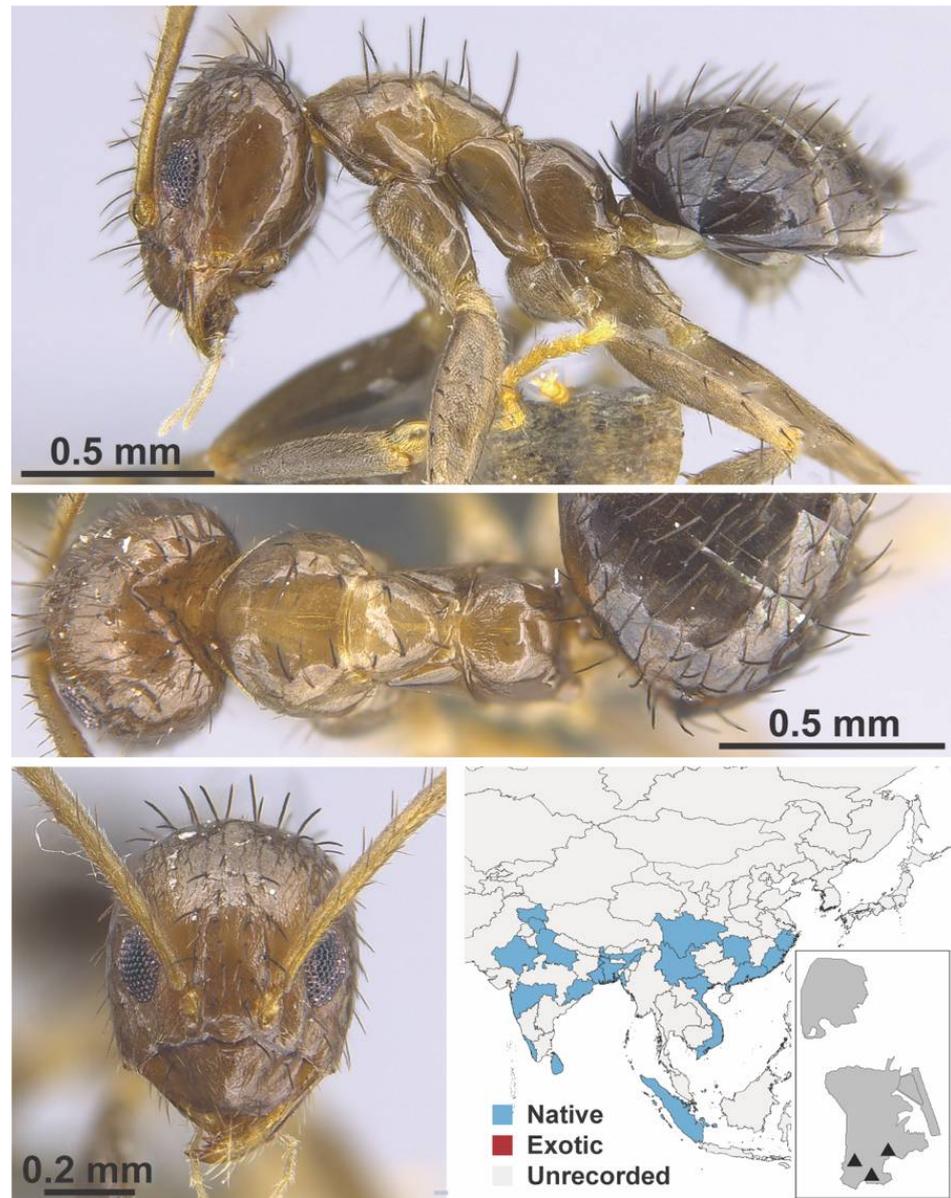


Figure A41. *Nylanderia taylori* Forel, 1894 worker (MAC_S21_GN1_H4_n1_bottom, IBBL).

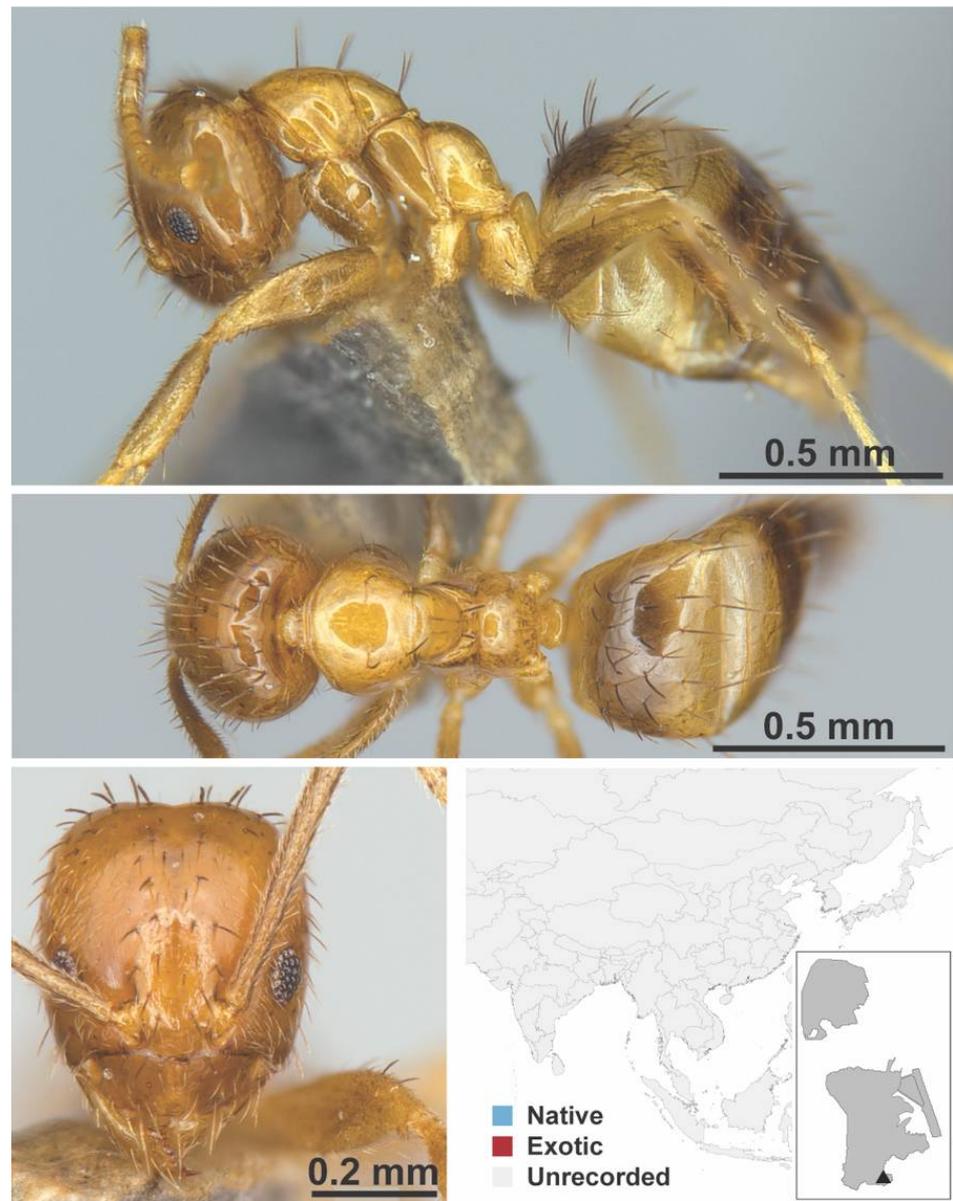


Figure A42. *Nylanderia* sp. 3 BG worker (MAC_S15_B03_sp.3, IBBL).

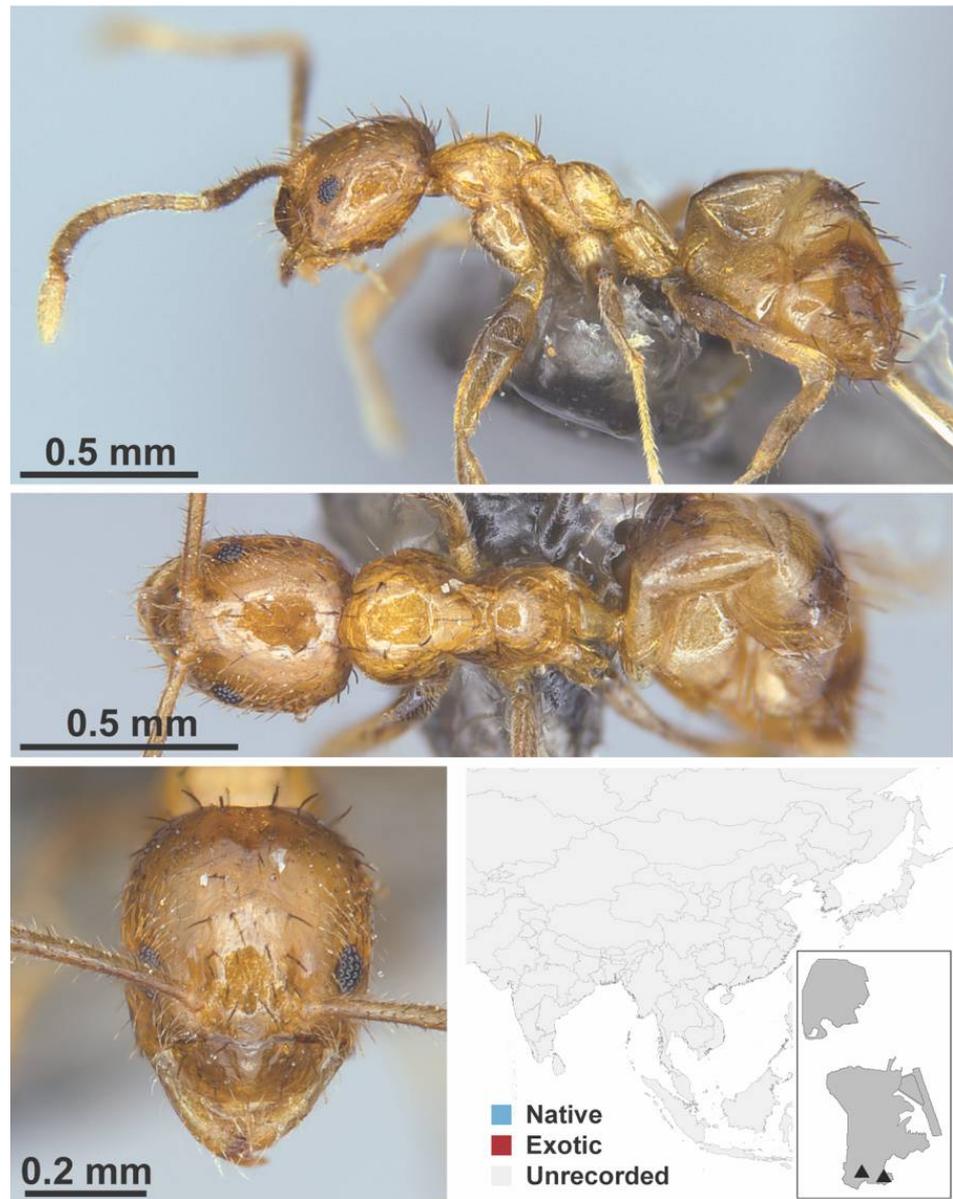


Figure A43. *Nylanderia* sp. 6 BG worker (MAC_S15_LLSP_sp.10, IBBL).

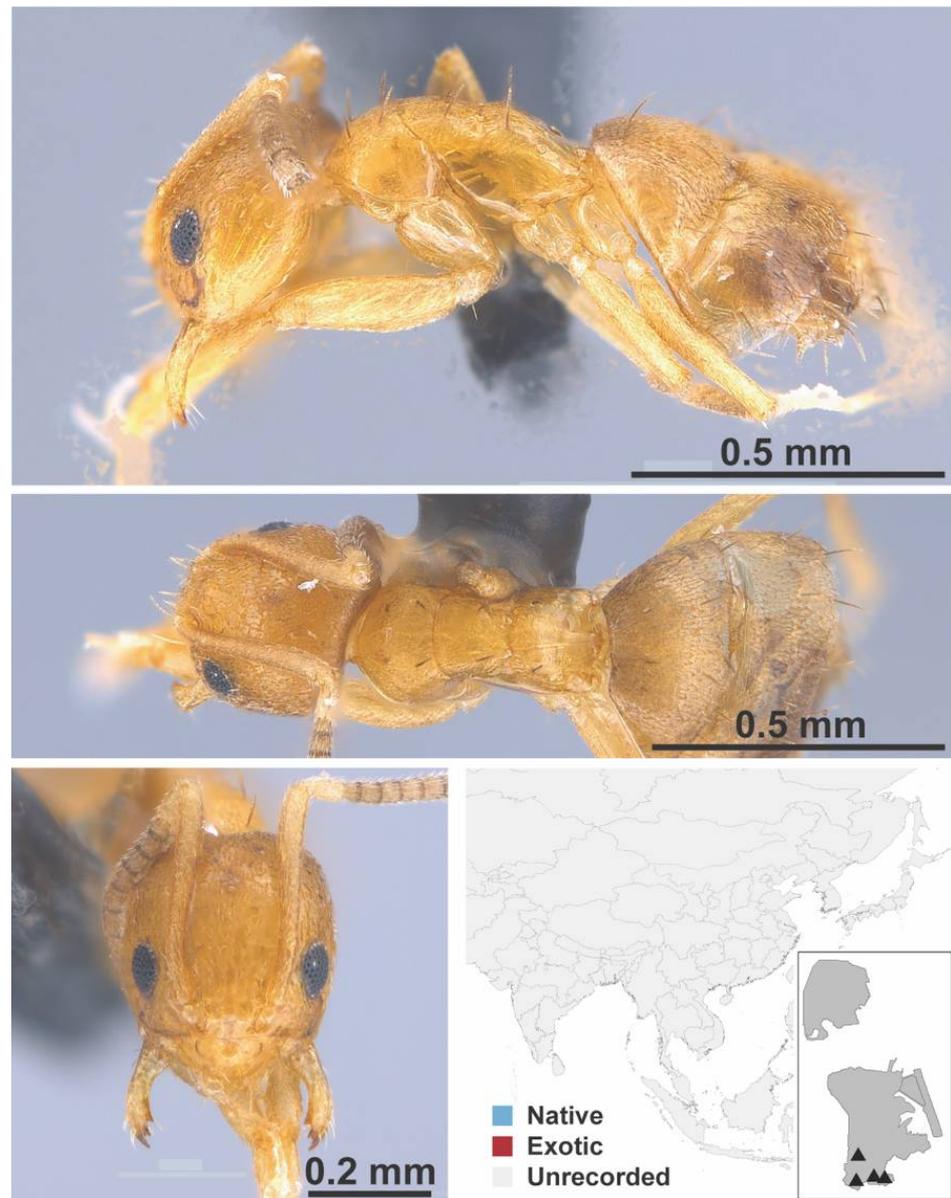


Figure A44. *Parapatrechina* sp.1 BG Forel, 1913 worker (MAC_S18_q2_37.5_Sp.2, IBBL).

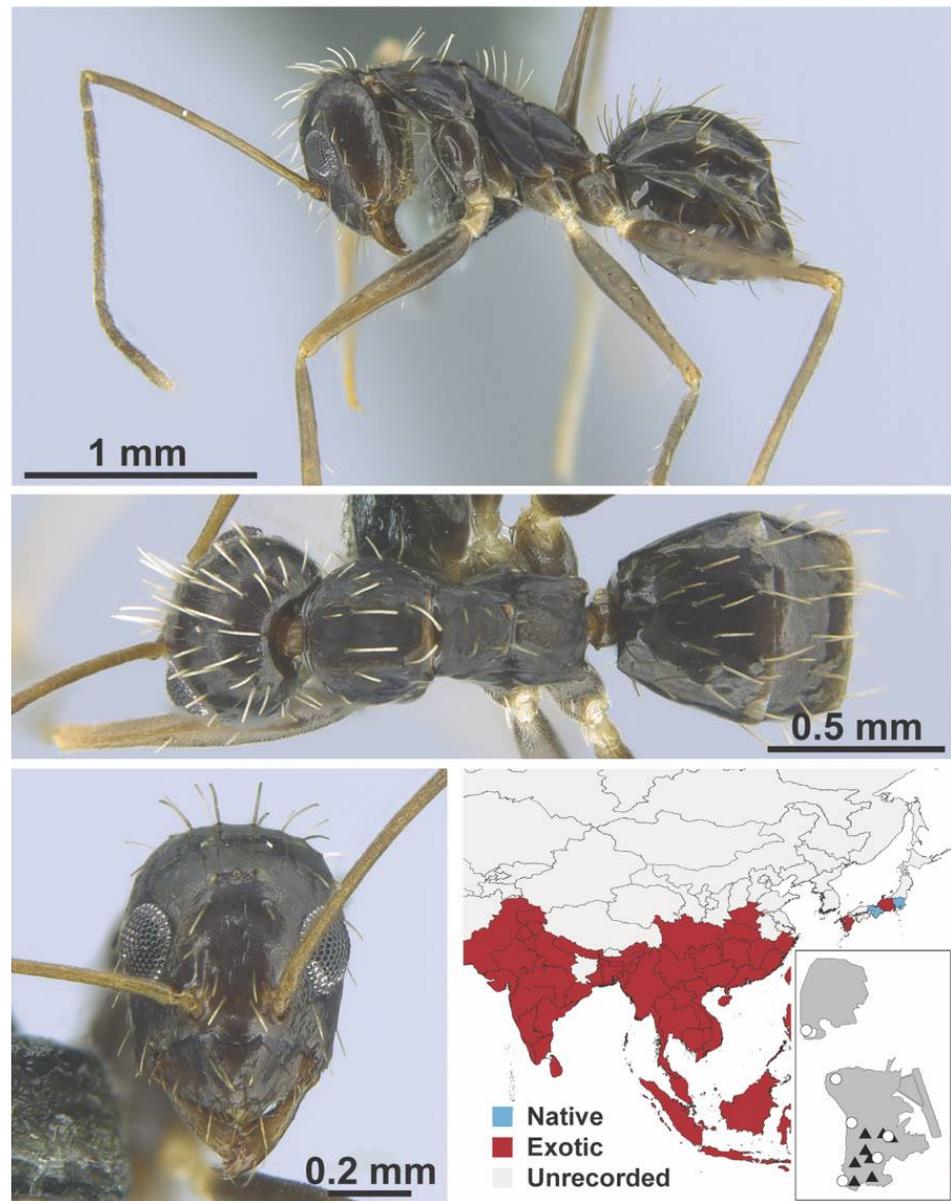


Figure A45. *Paratrechina longicornis* Latreille, 1802 worker (MAC_S11_LLSP_Sp.6, IBBL).

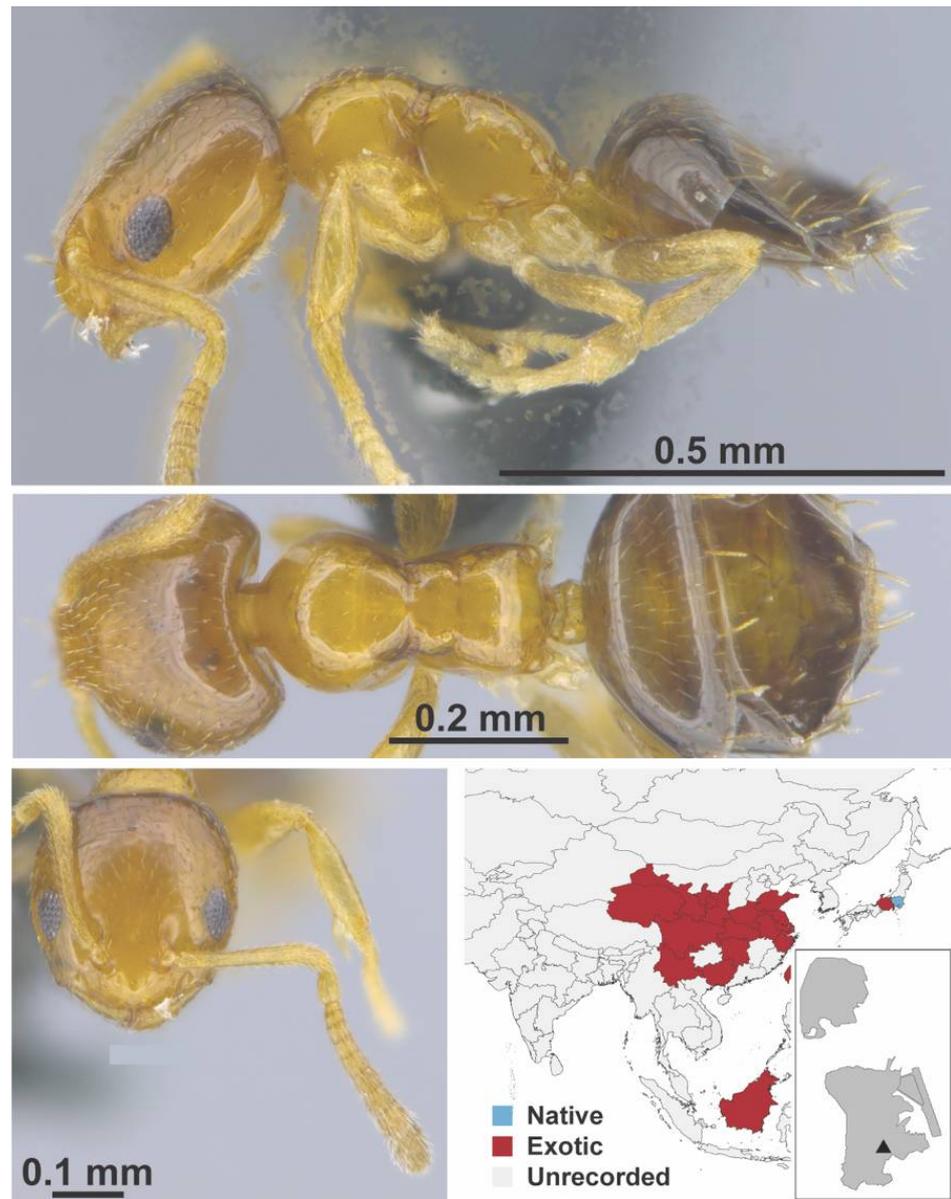


Figure A46. *Plagiolepis alluaudi* Emery, 1894 worker (MAC_S14_T2_2m_Sp.1, IBBL).

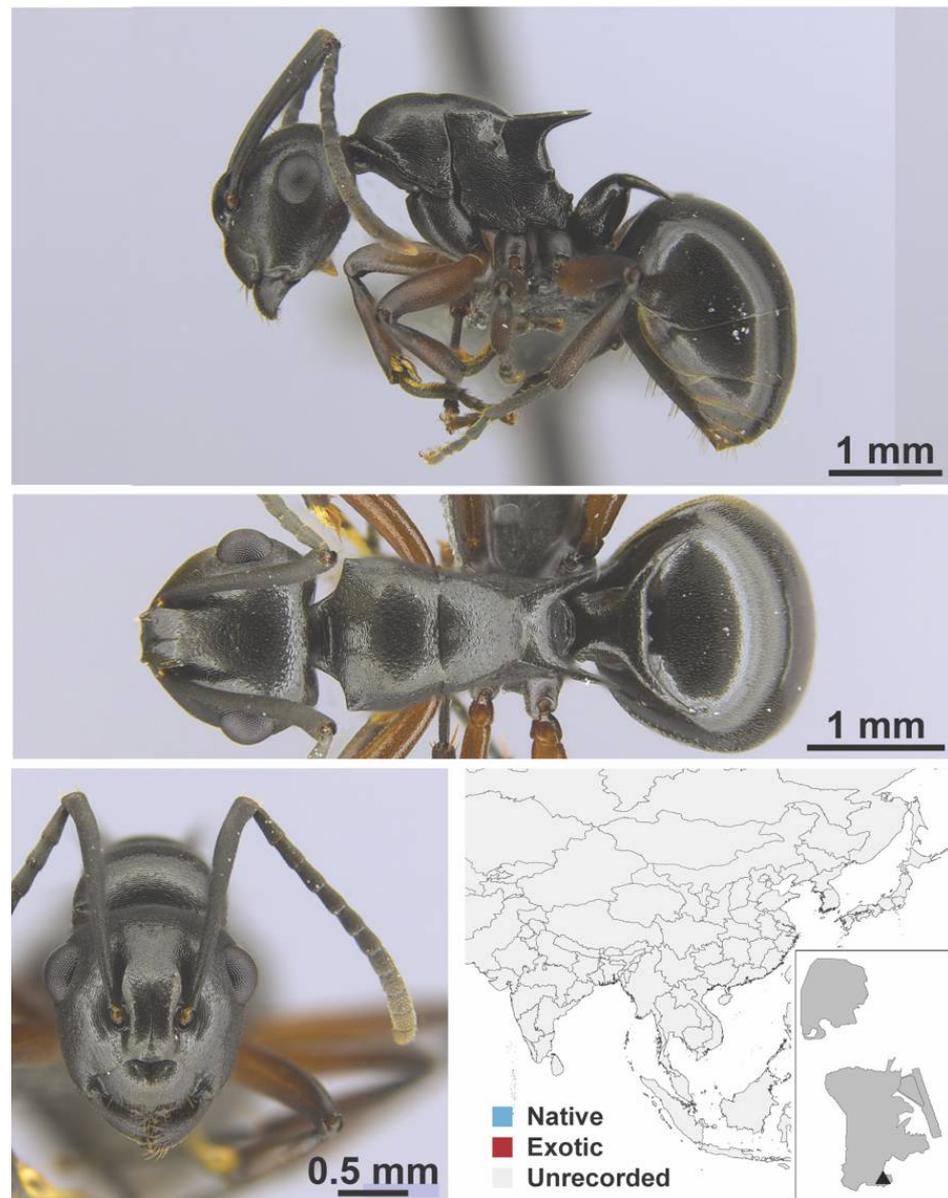


Figure A47. *Polyrhachis confusa* Emery, 1893 worker (FB19152, IBBL).

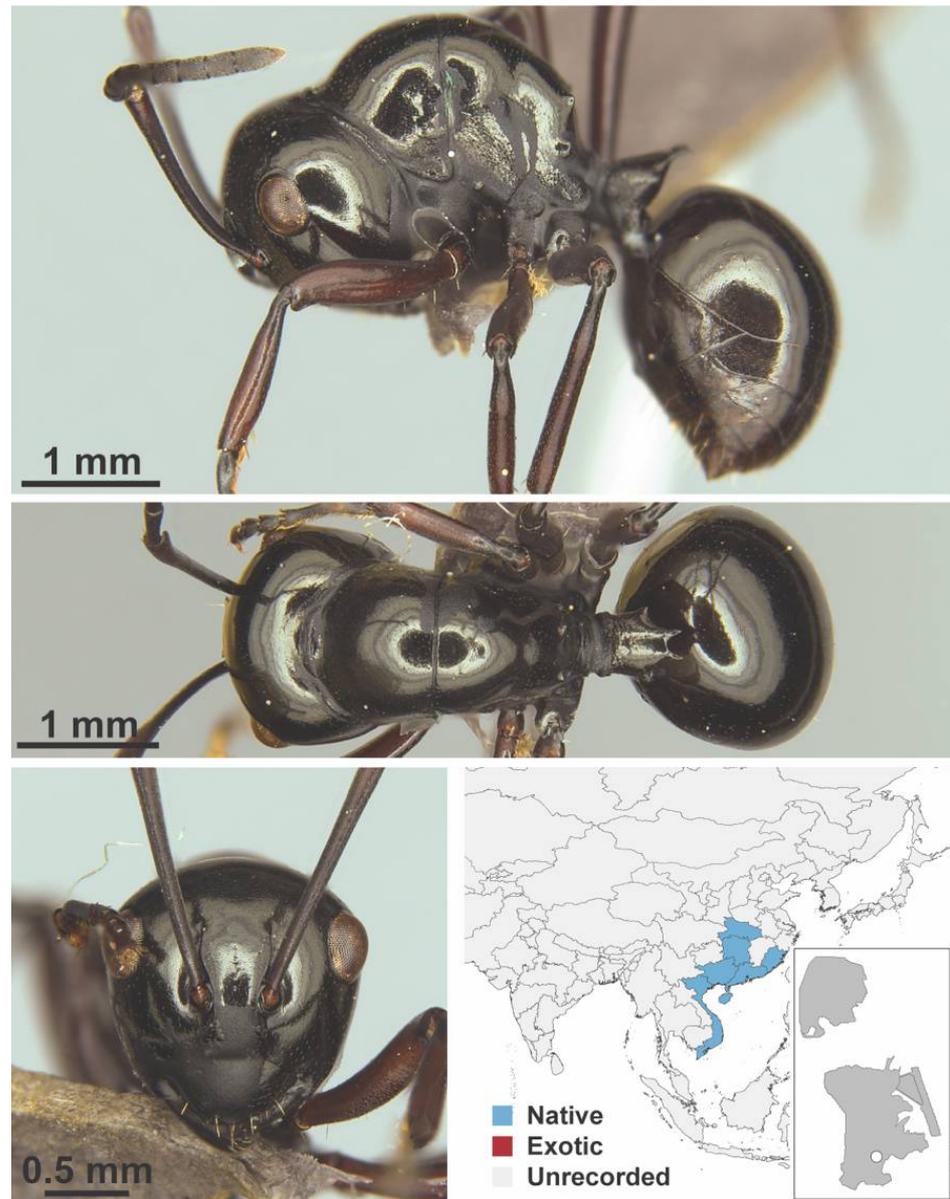


Figure A48. *Polyrhachis demangei* Santschi, 1910 worker (*Polyrhachis demangei*, CML collection).

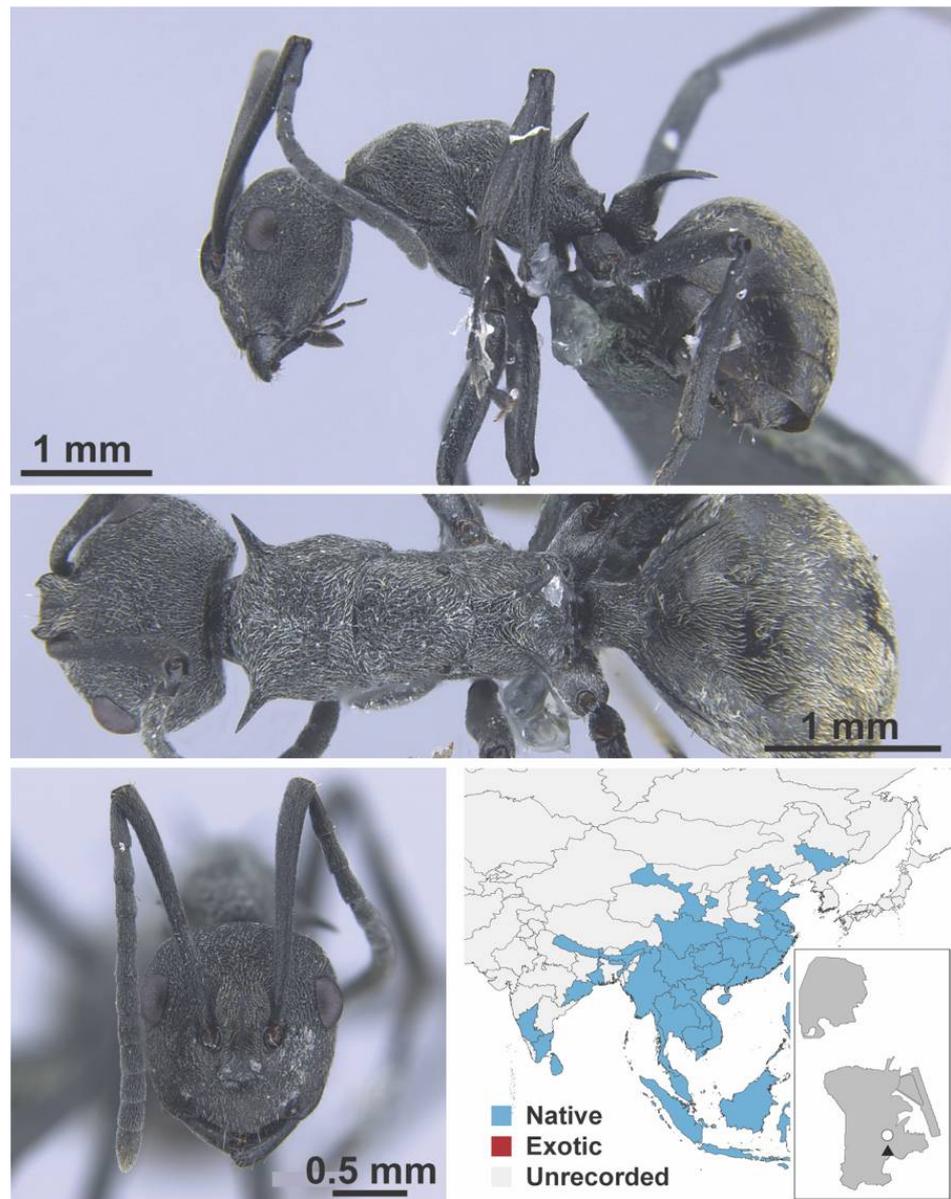


Figure A49. *Polyrhachis dives* Smith, 1857 worker (MAC_S03_HC_01_Sp.2, IBBL).

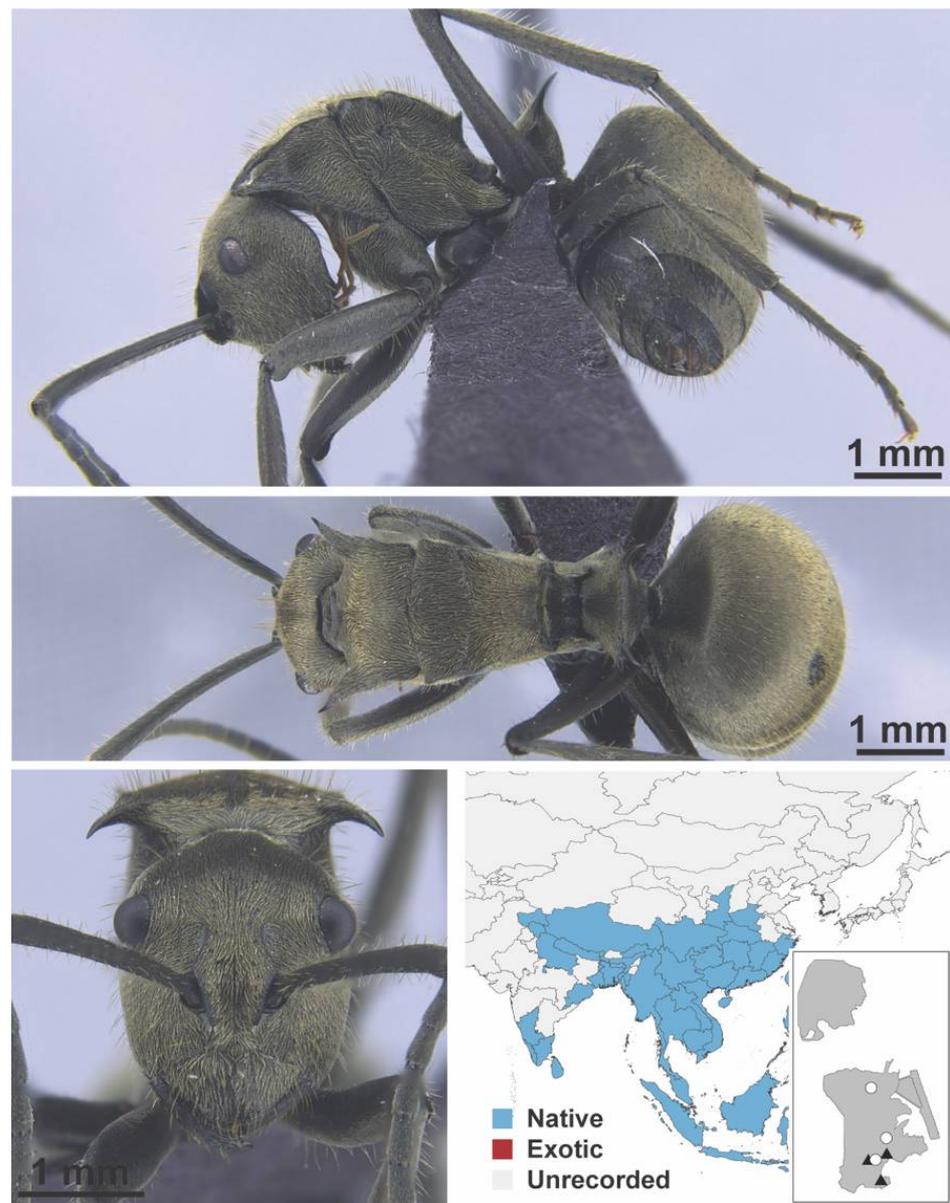


Figure A50. *Polyrhachis illaudata* Walker, 1859 worker (MAC_S03_HC_01_Sp.1, IBBL).

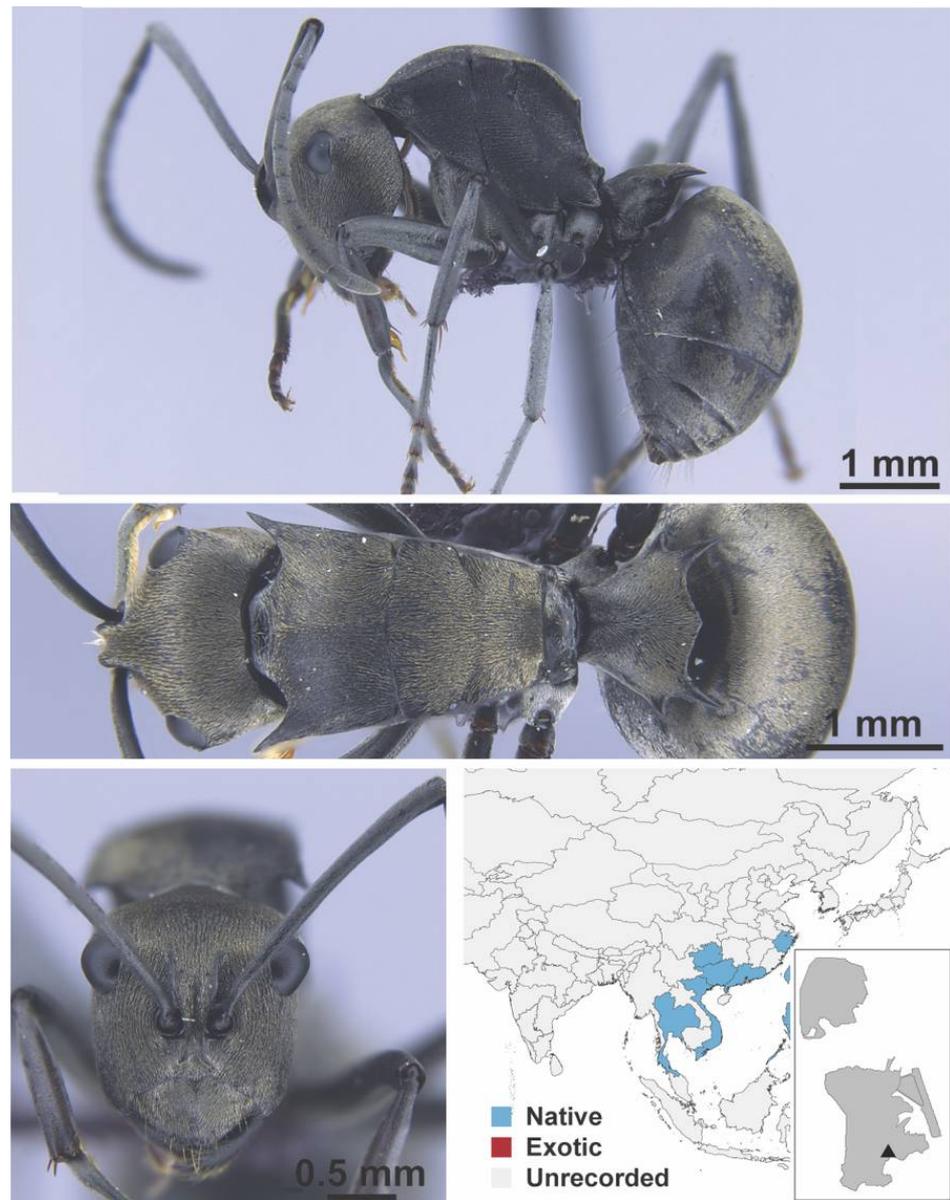


Figure A51. *Polyrhachis latona* Wheeler, 1909 worker (MAC_S03_LLSA_Sp.5, IBBL).

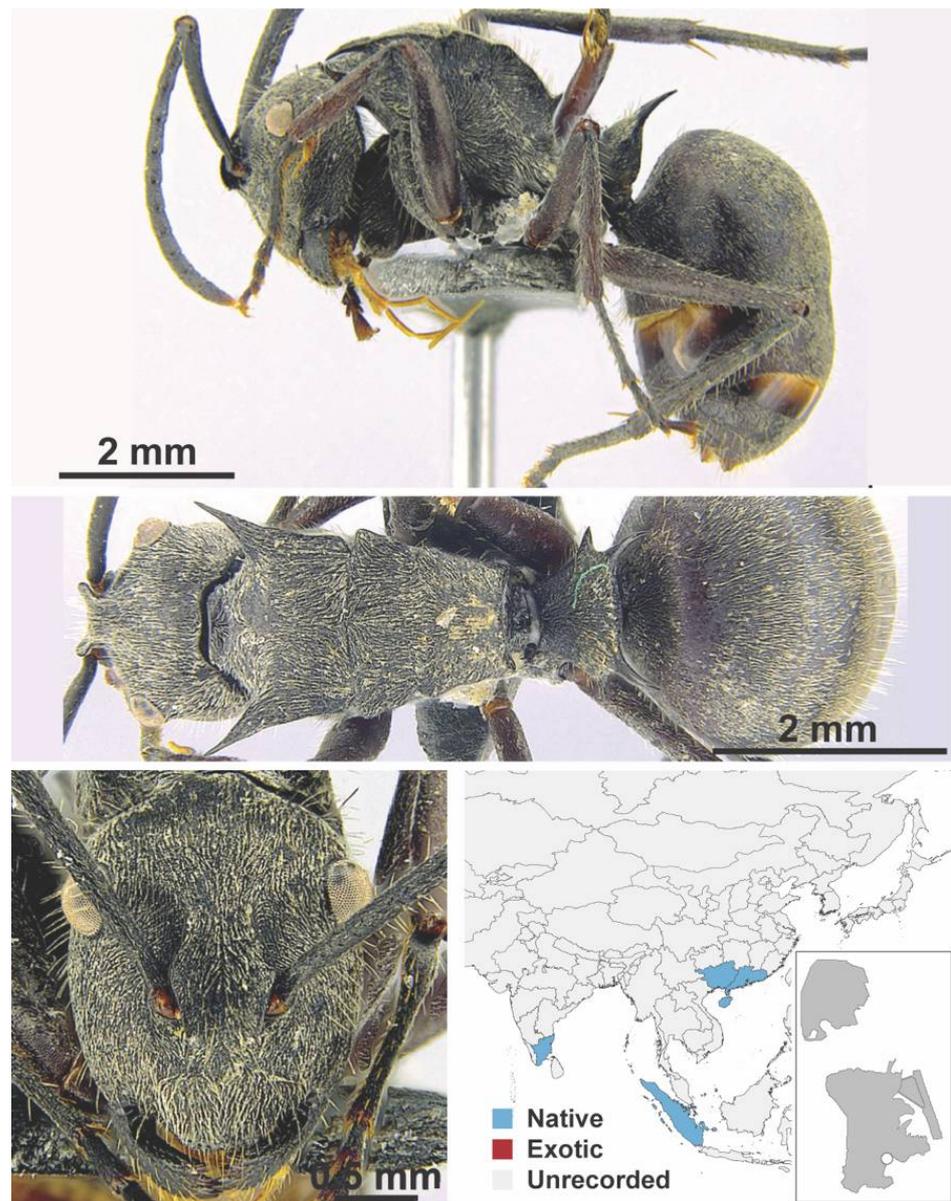


Figure A52. *Polyrhachis tyrannica* Smith, 1858 worker (K6558(2)). Species images taken from Wong and Guénard 2020 [55] with permission.

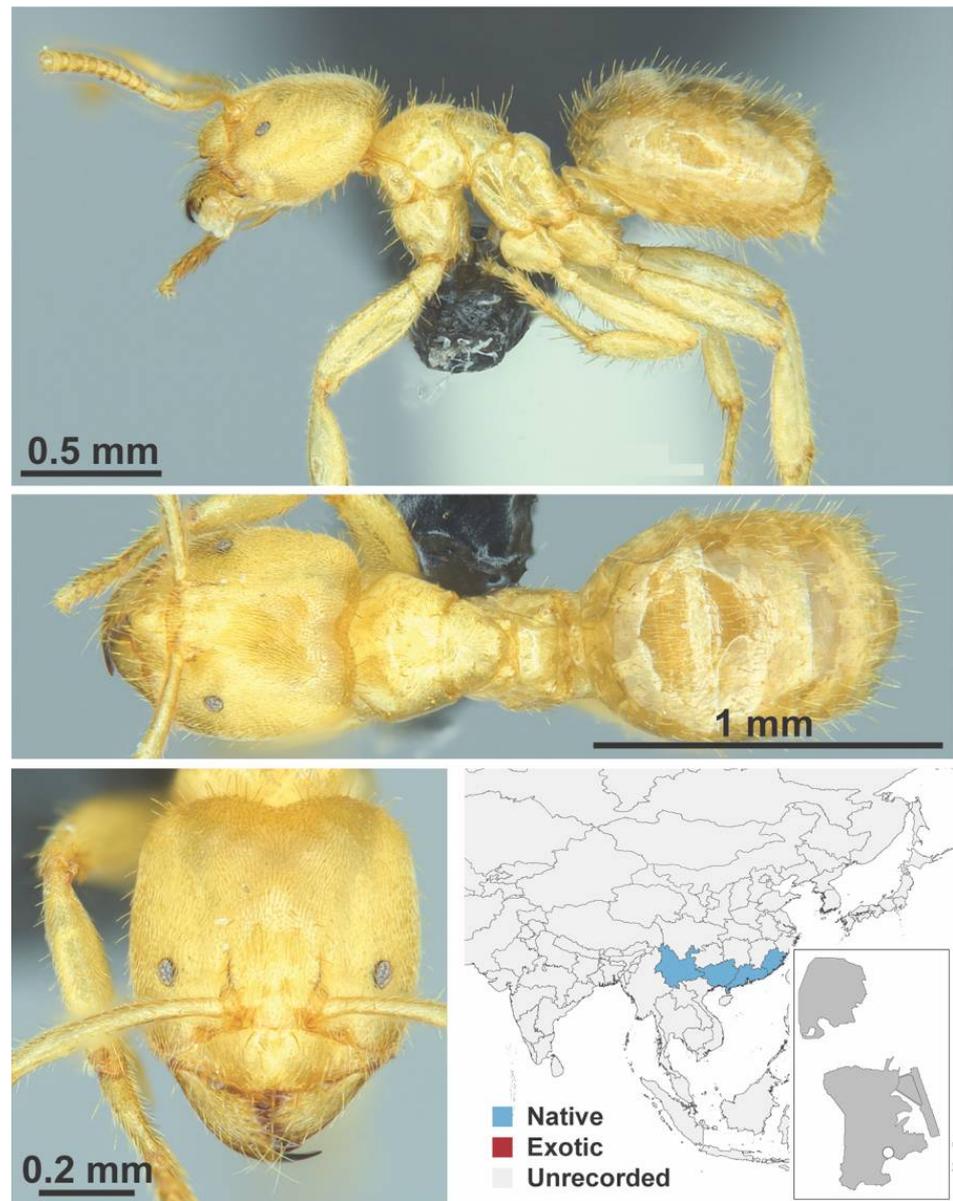


Figure A53. *Pseudolasius risii* Forel, 1894 worker (*Pseudolasius risii*, CML collection).

Appendix A.5 LEPTANILLINAE

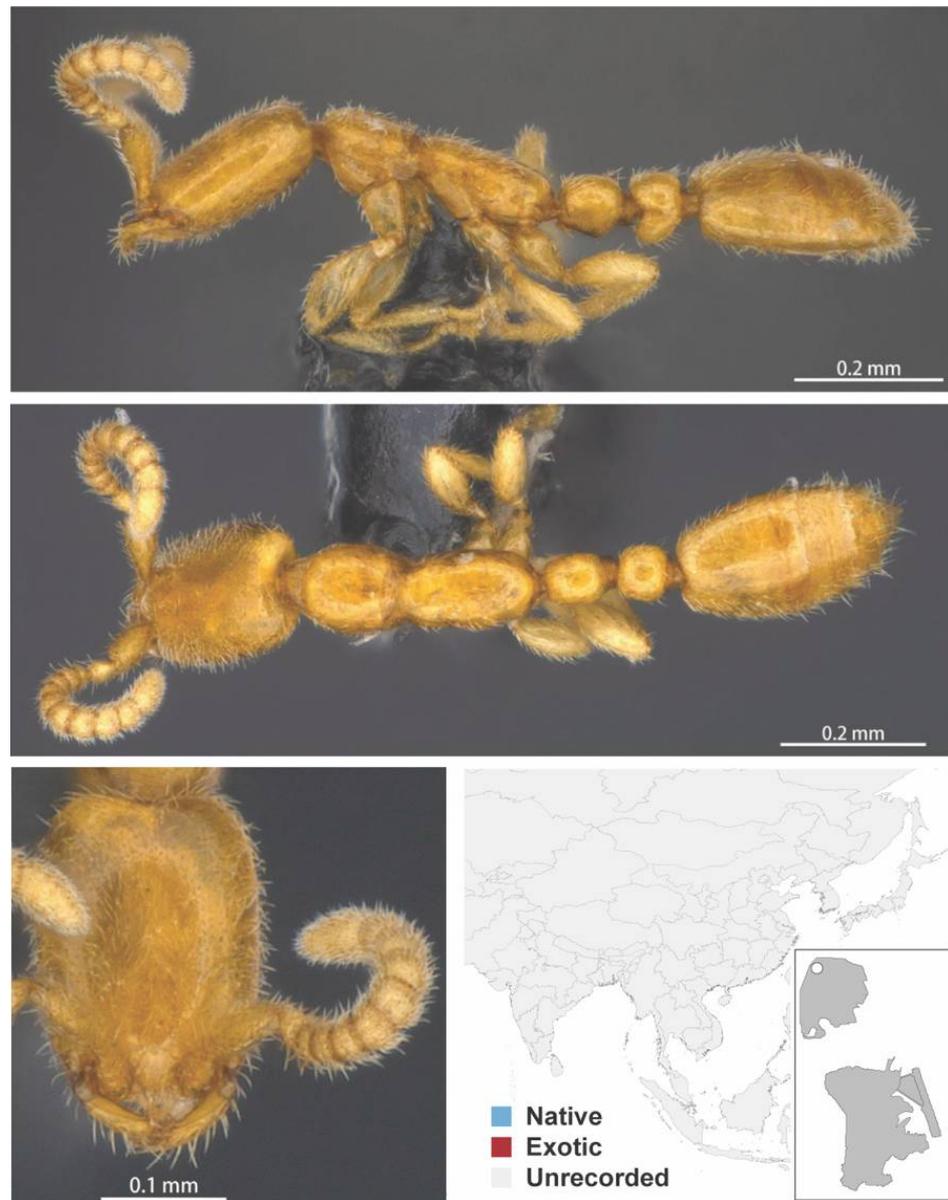


Figure A54. *Leptanilla macaoensis* Leong, Yamane & Guénard, 2018 worker (LCM00039, IBBL). Species images taken from Leong, Yamane & Guénard, 2018 [61] with permission.

Appendix A.6 MYRMICINAE

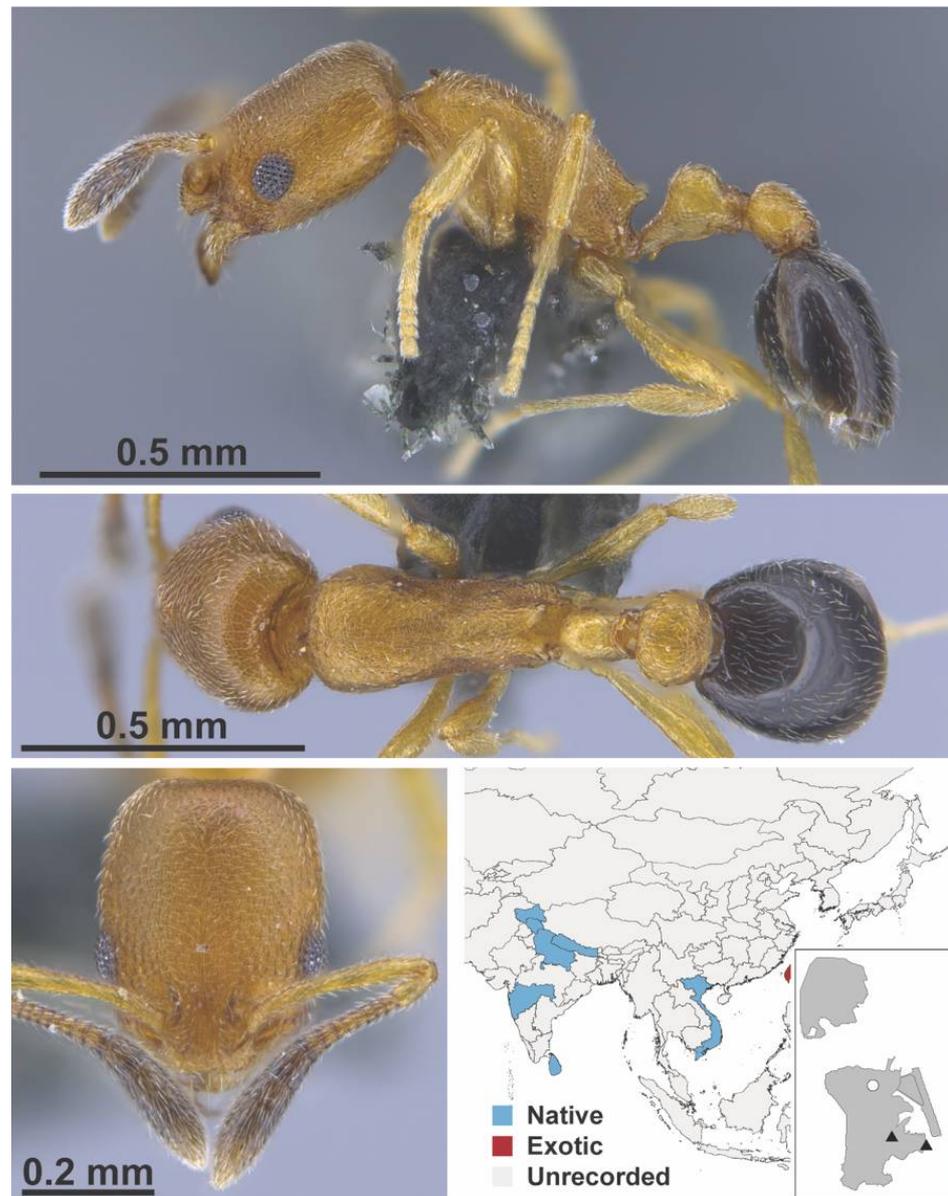


Figure A55. *Cardicondyla minutior* Forel, 1899 worker (MAC_S04_LLSP_sp.6, IBBL).

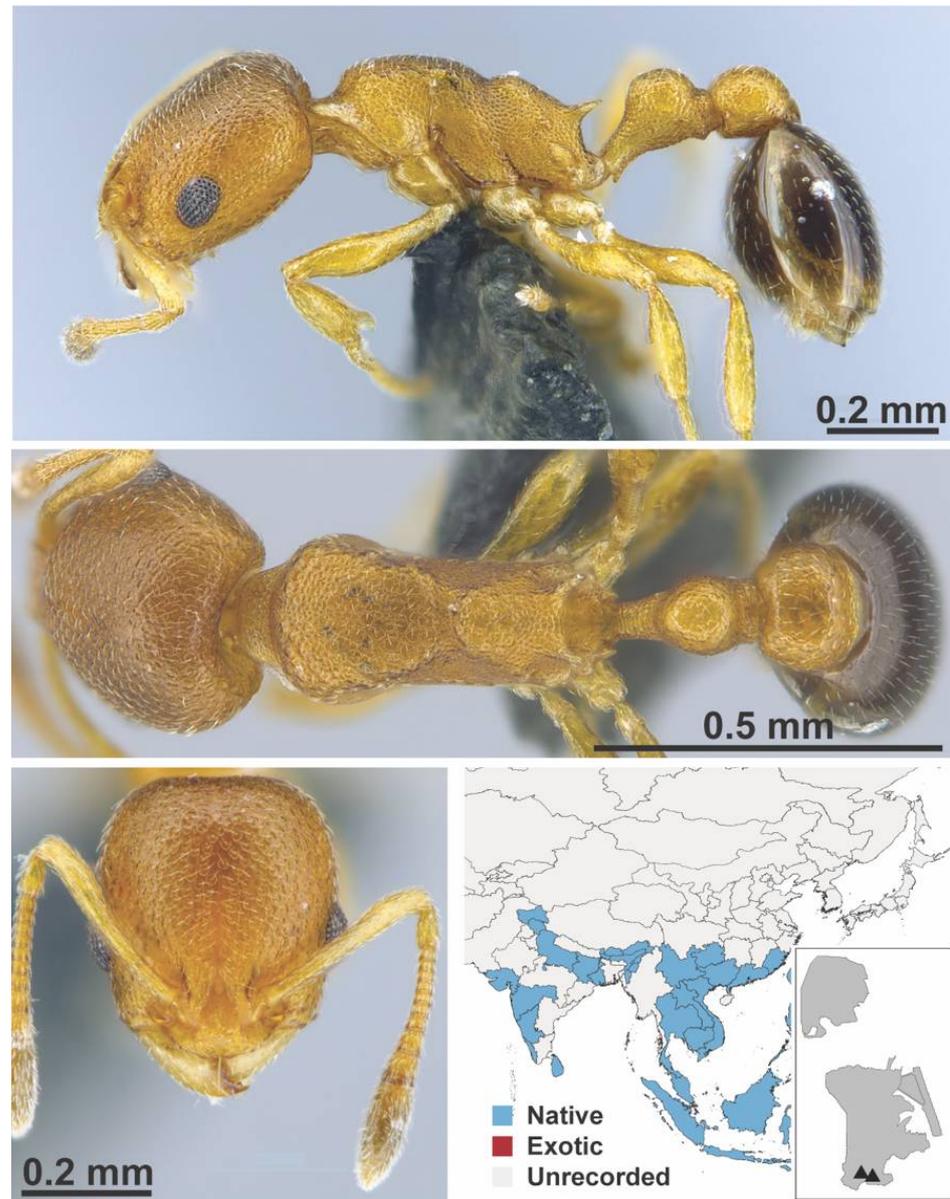


Figure A56. *Cardiocondyla wroughtonii* Forel, 1890 worker (MAC_S11_T3_3m_sp.4, IBBL).

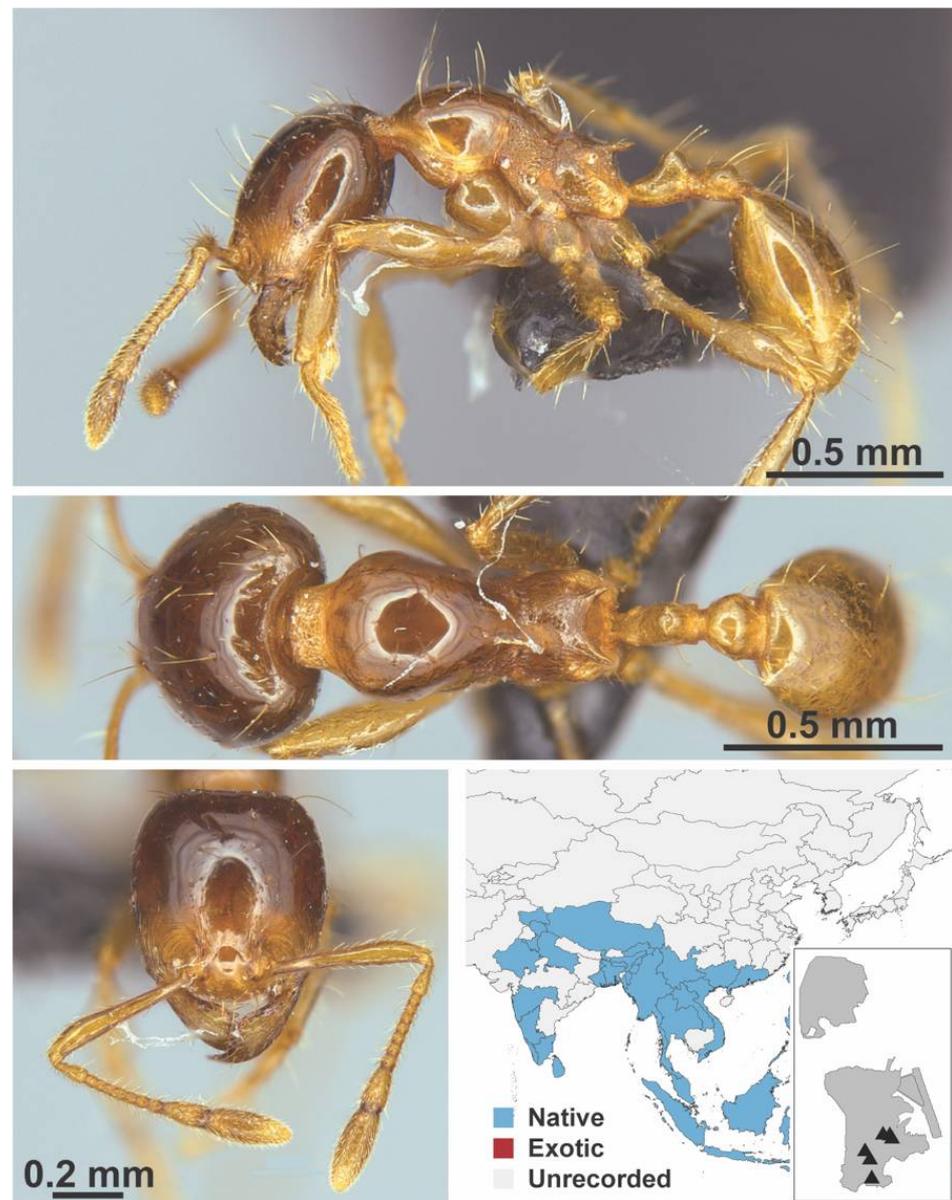


Figure A57. *Carebara affinis* Jerdon, 1851 worker (MAC_S9_37.5_q2_sp.1, IBBL).

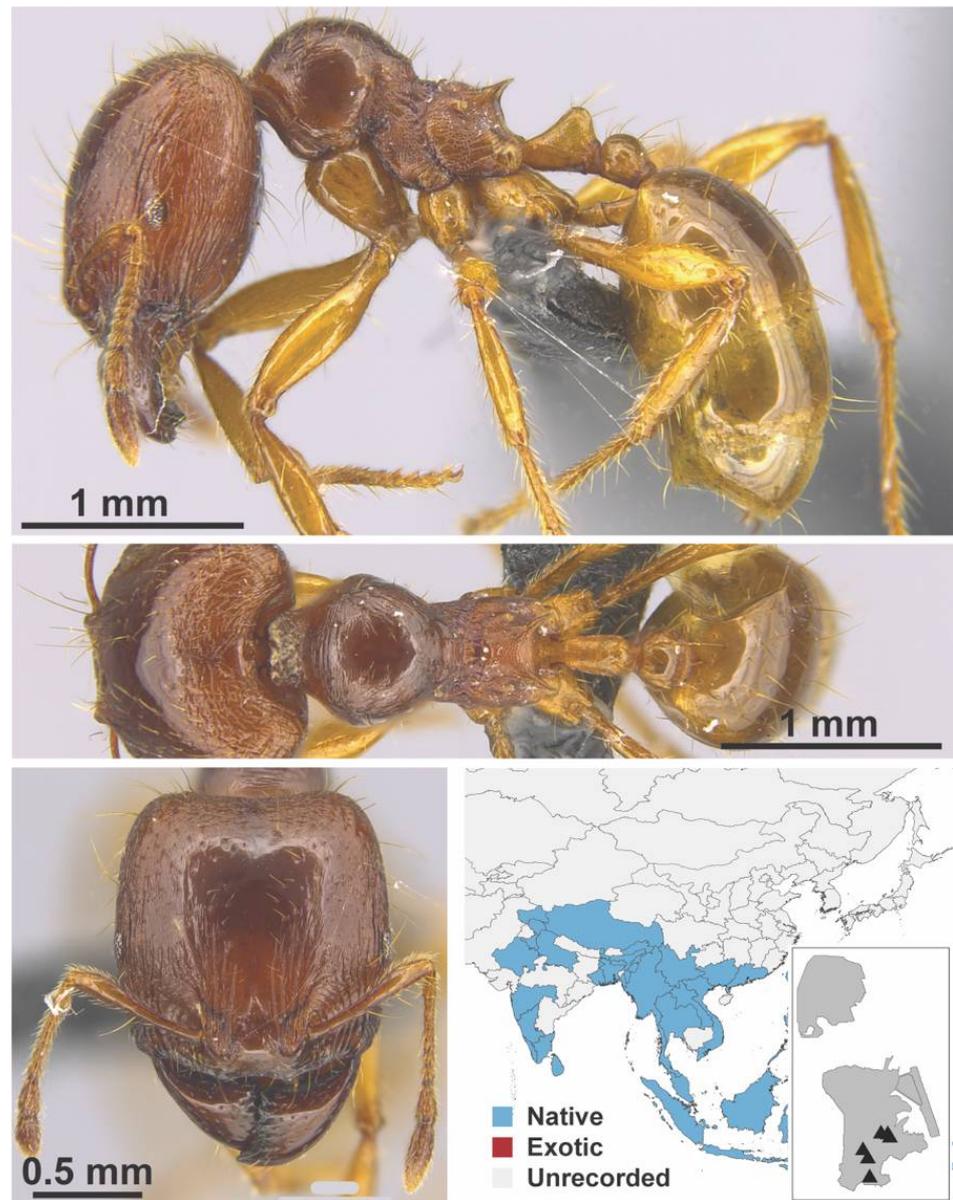


Figure A58. *Carebara affinis* Jerdon, 1851 major (MAC_S8_25_q1_sp.1, IBBL).

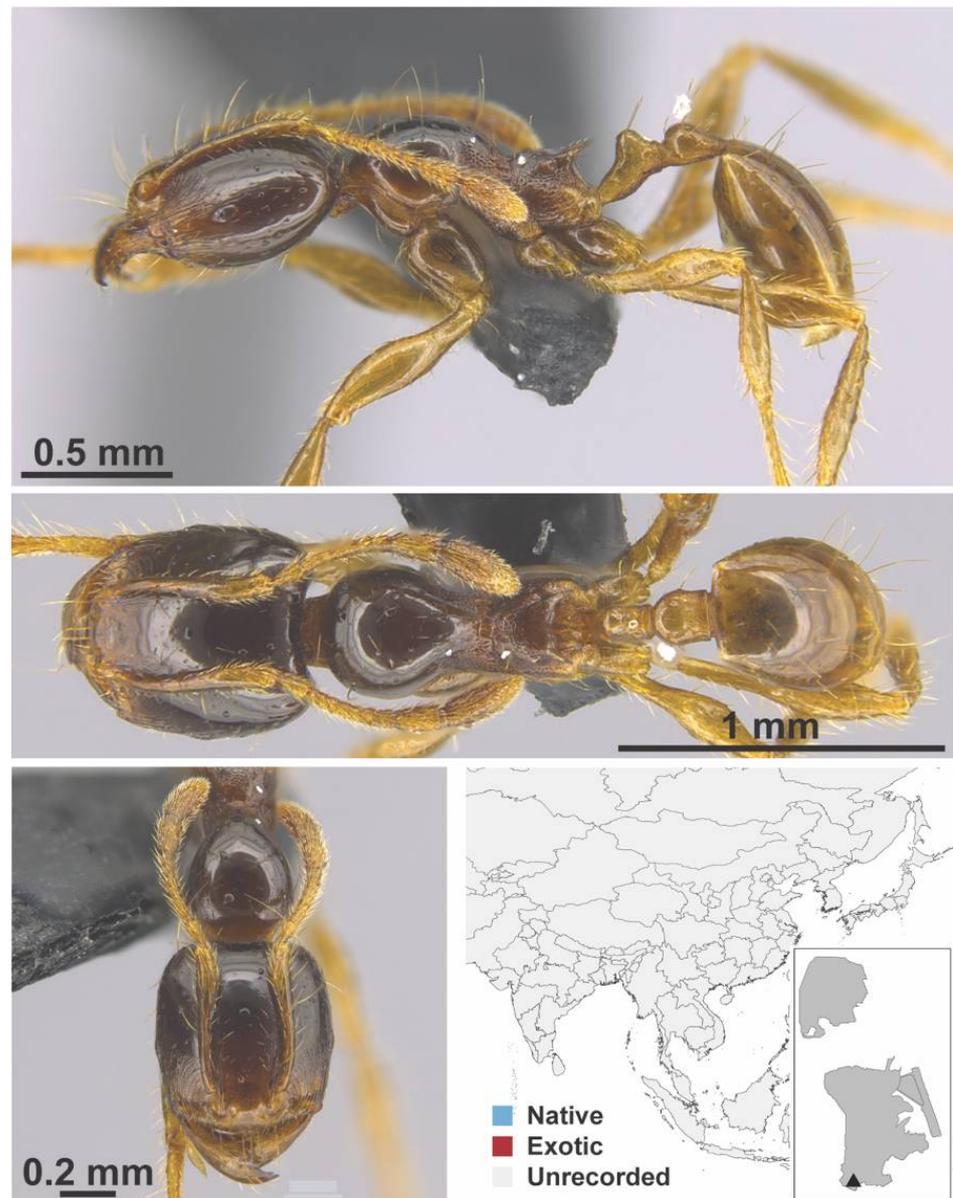


Figure A59. *Carebara* nr. *diversa* Jerdon, 1851 worker (MAC_S18_q2_37.5_sp.3, IBBL).

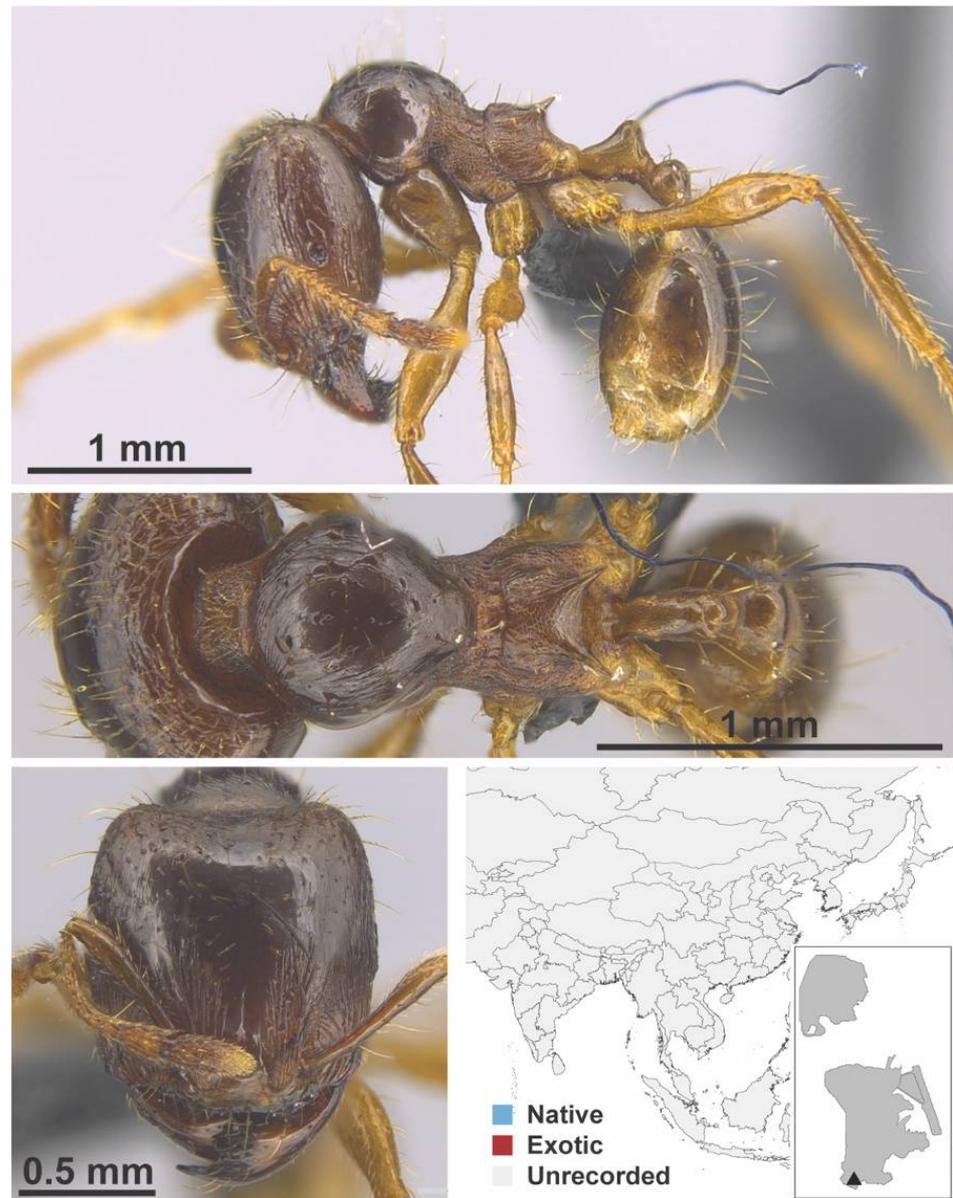


Figure A60. *Carebara* nr. *diversa* Jerdon, 1851 major (MAC_S18_q2_37.5_sp.3, IBBL).

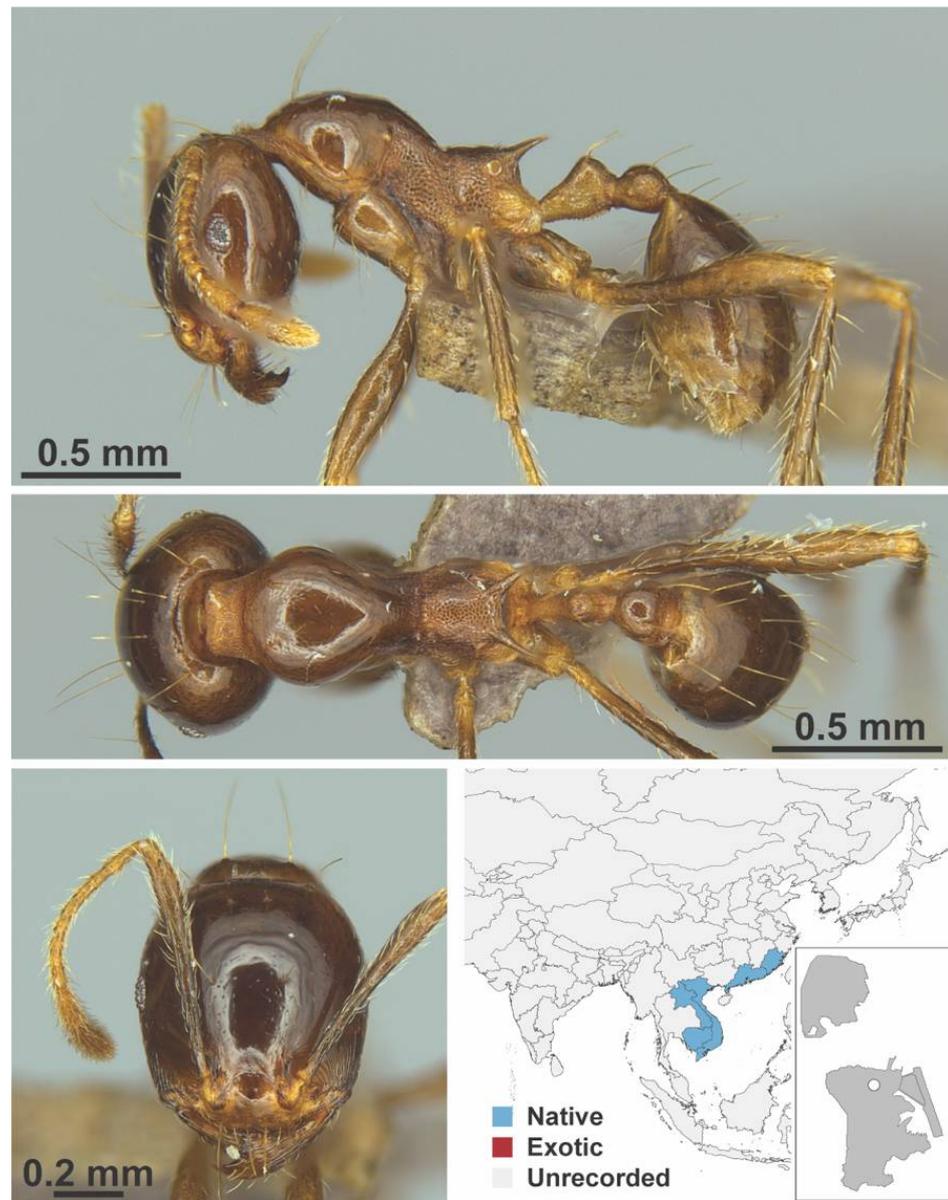


Figure A61. *Carebara diversa laotina*, Santschi, 1921 worker (*Carebara diversa laotina*, CML collection).

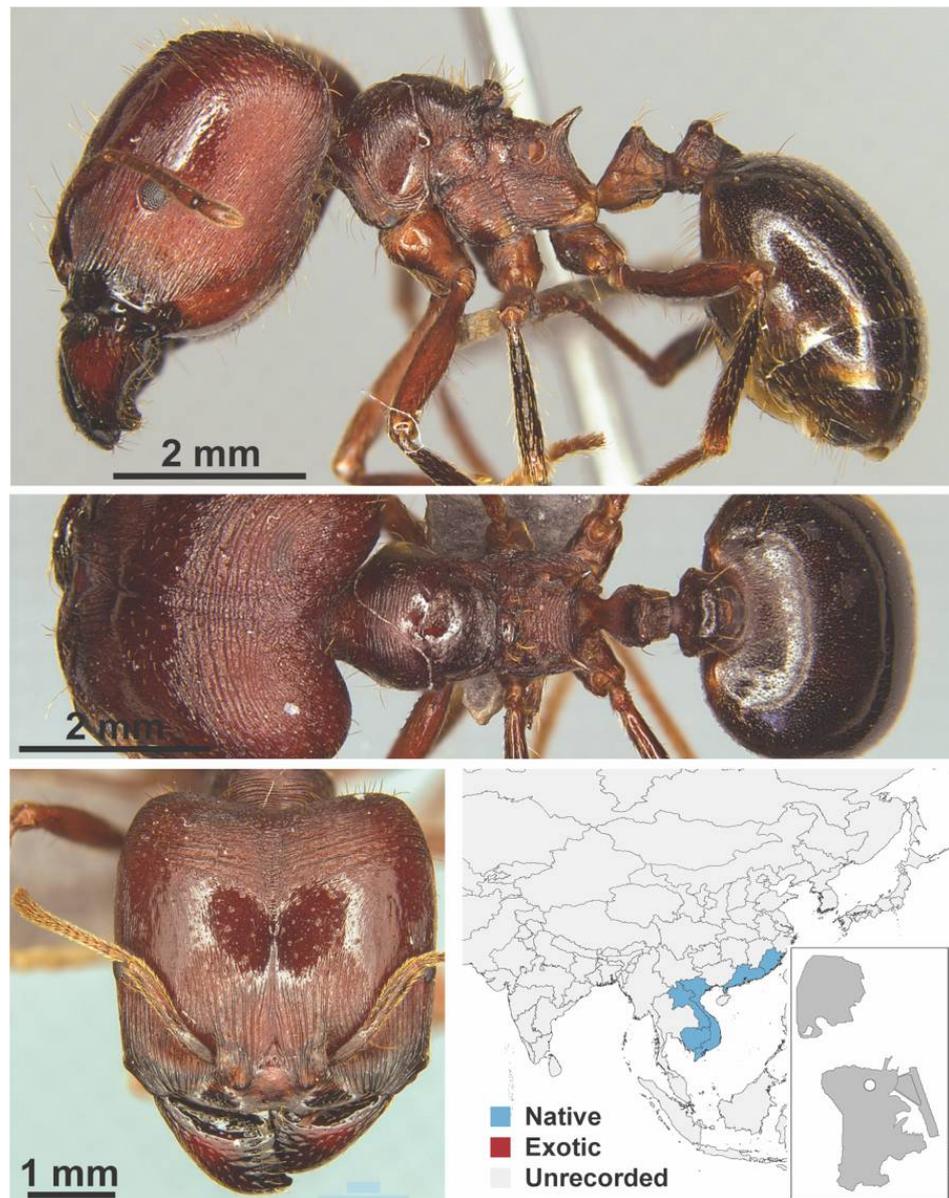


Figure A62. *Carebara diversa laotina*, Santschi, 1921 major (*Carebara diversa laotina*, CML collection).

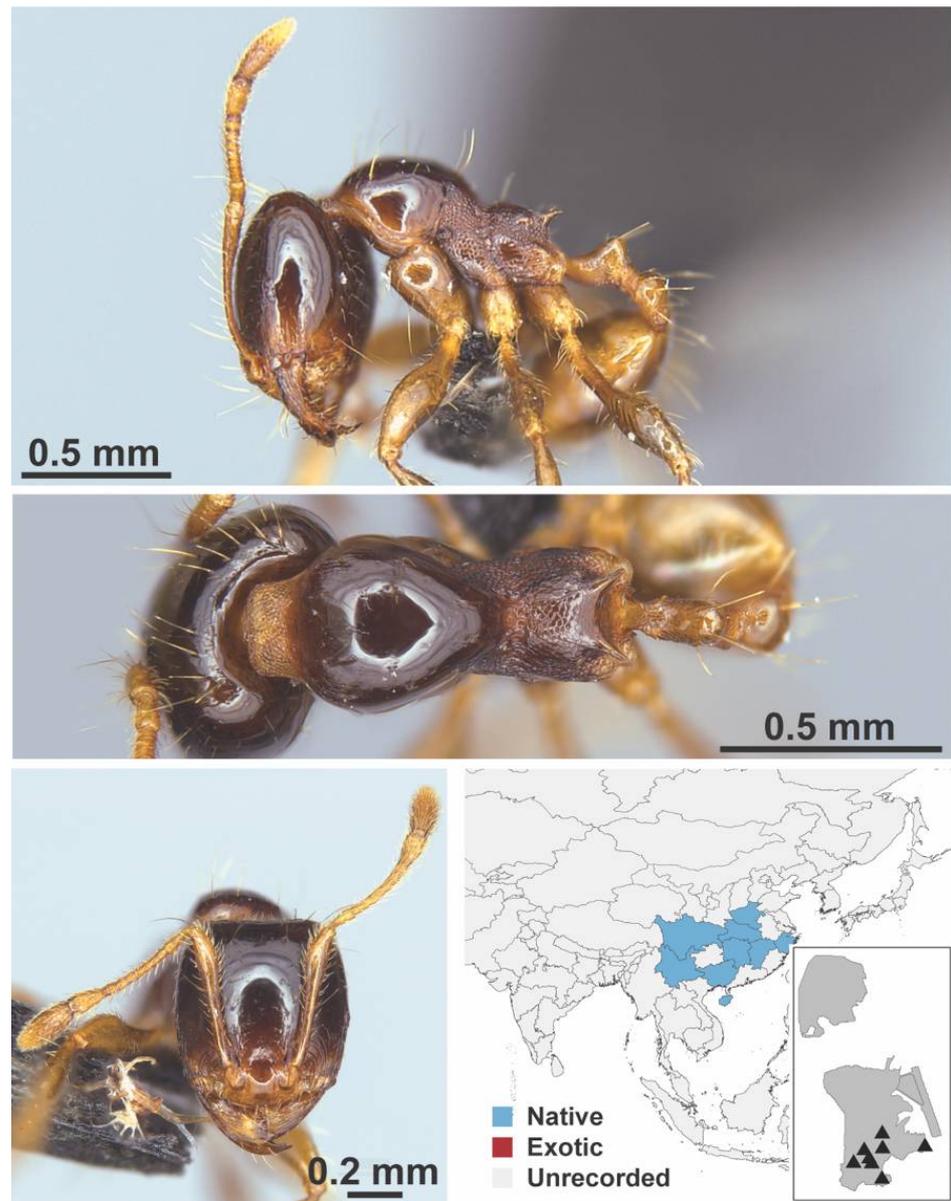


Figure A63. *Carebara melasolena* Zhou & Zheng, 1997 worker (MAC_S12_LLSA_sp.1, IBBL).

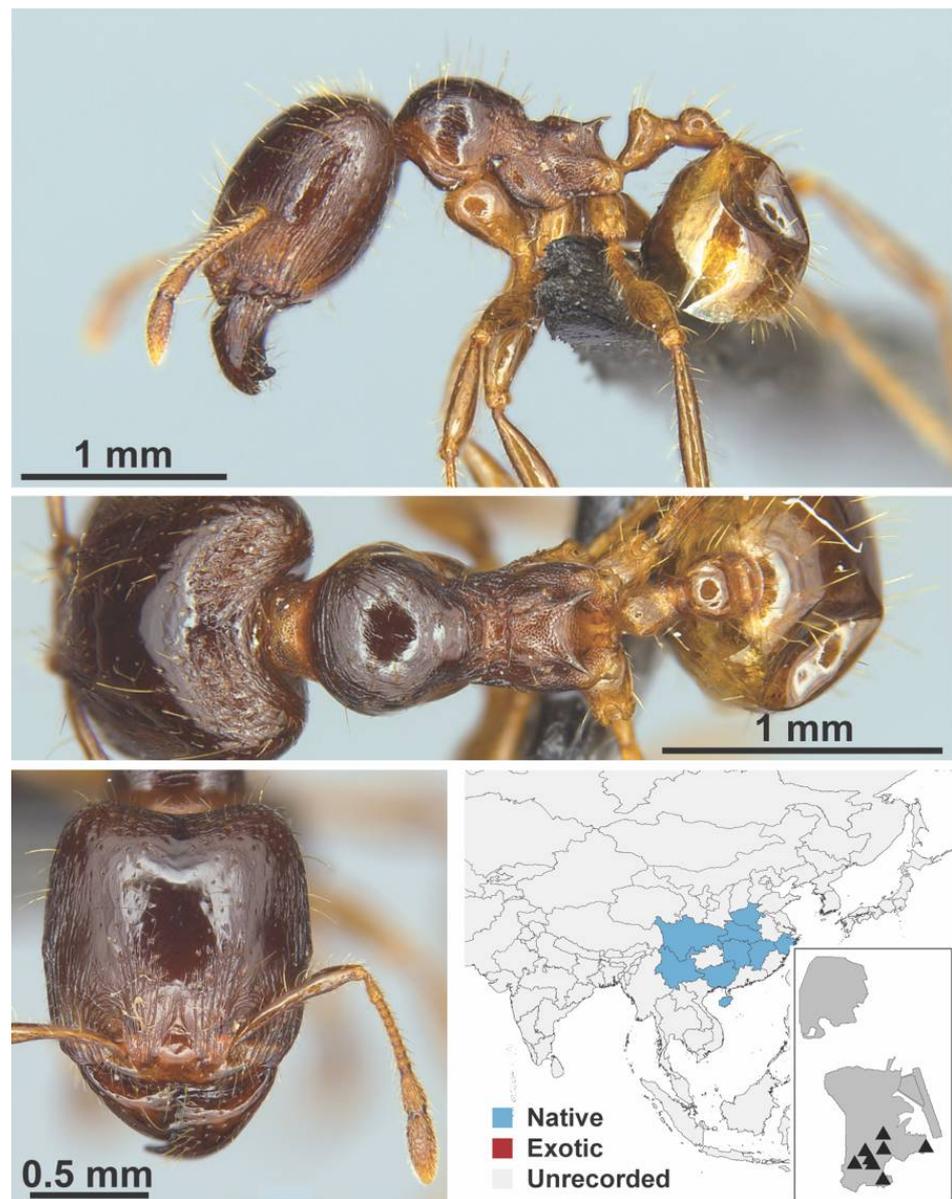


Figure A64. *Carebara melasolena* Zhou & Zheng, 1997 major (MAC_S12_LLSA_sp.1, IBBL).

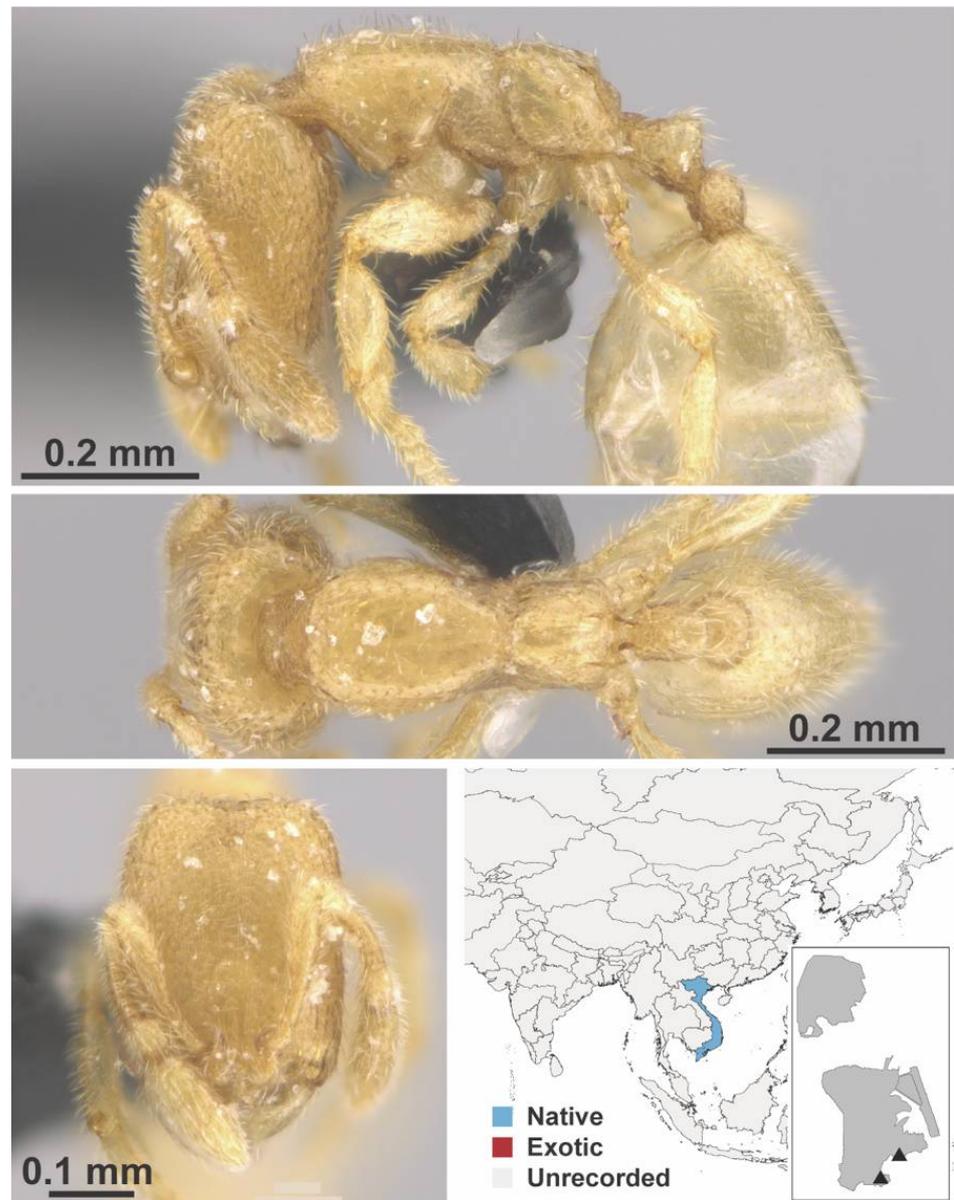


Figure A65. *Carebara sangi* Eguchi & Bui, 2007 worker (MAC_S13_q1_25_Sp.2, IBBL).

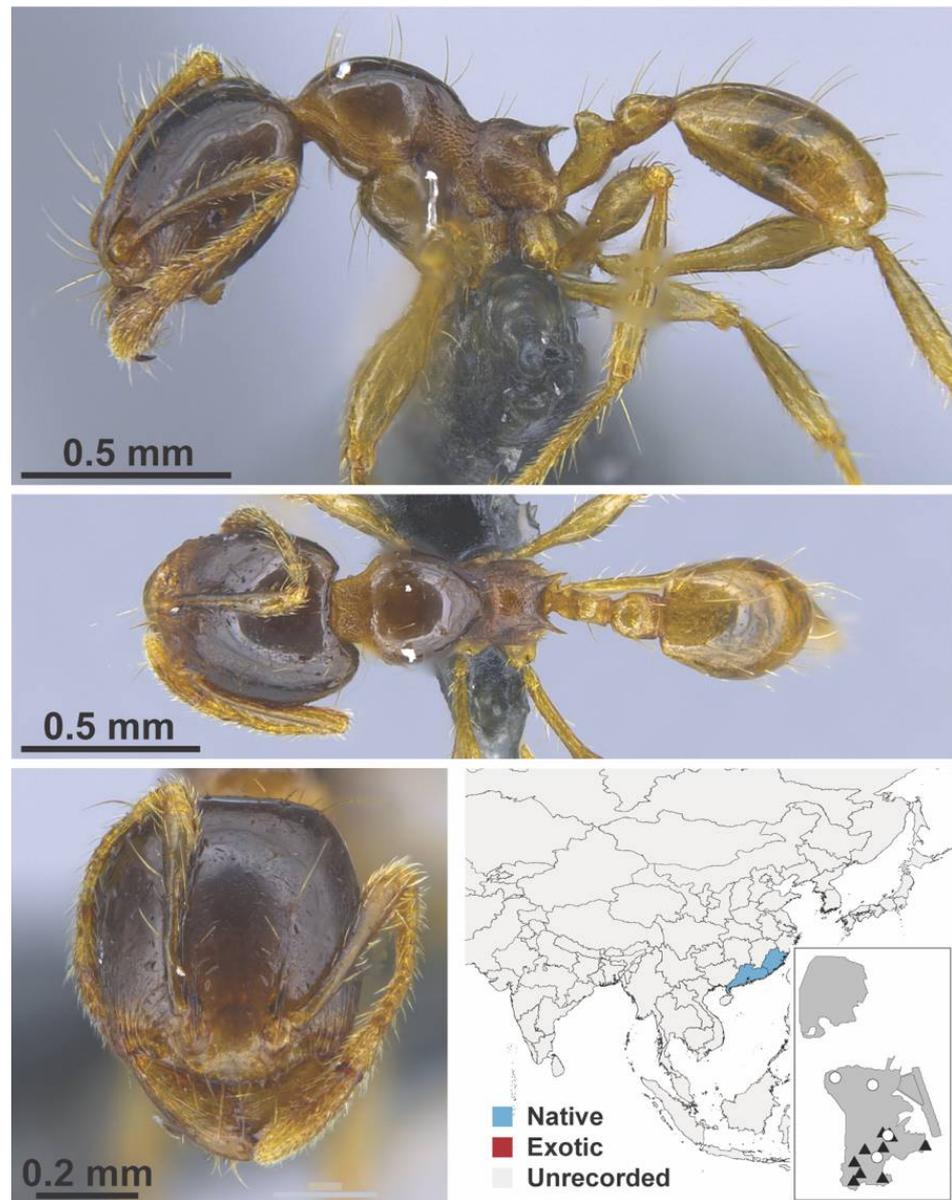


Figure A66. *Carebara zengchengensis* Zhou, Zhao & Jia, 2006 worker (MAC_S12_q3_37.5_Sp.4, IBBL).

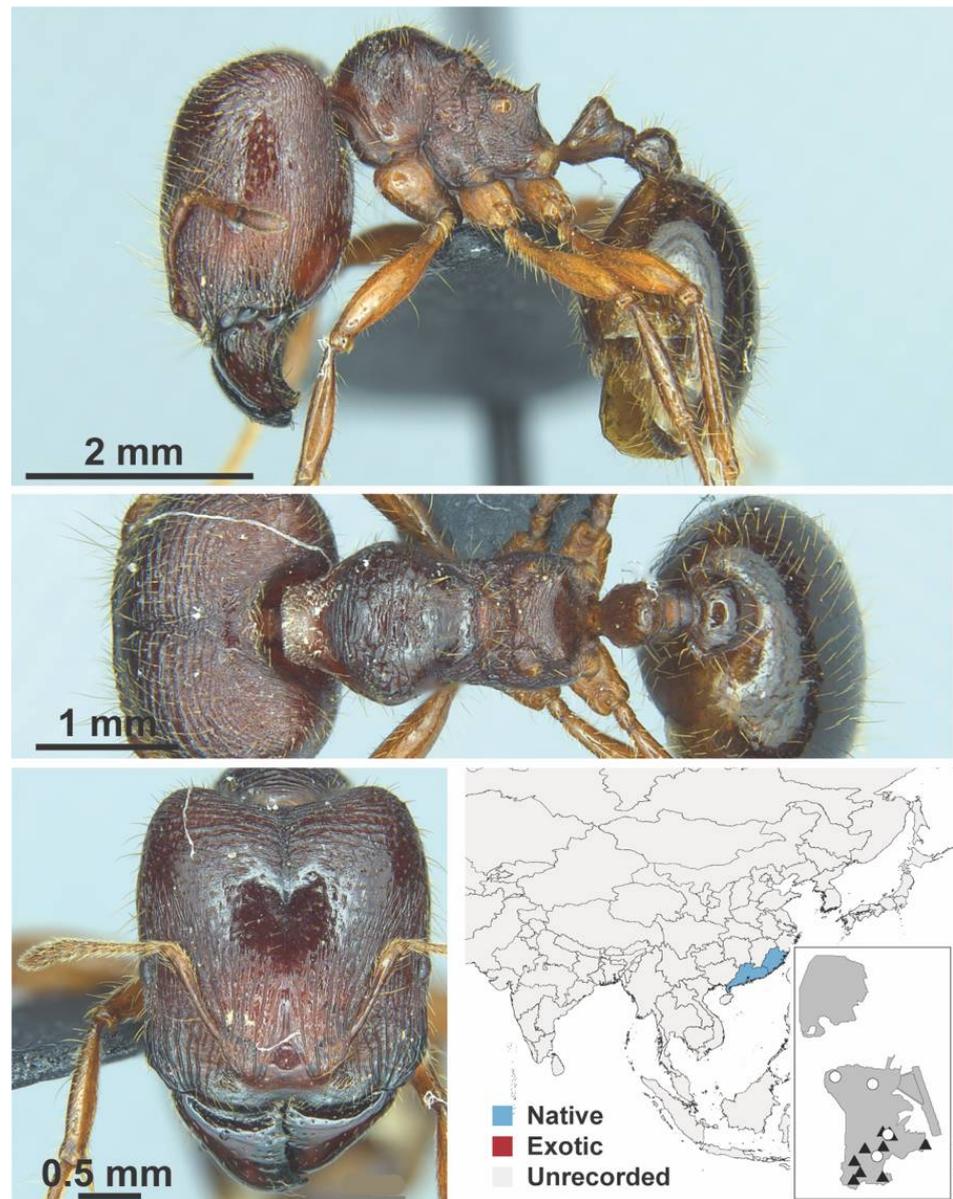


Figure A67. *Carebara zengchengensis* Zhou, Zhao & Jia, 2006 worker (MAC_S12_q3_37.5_Sp.4, IBBL).

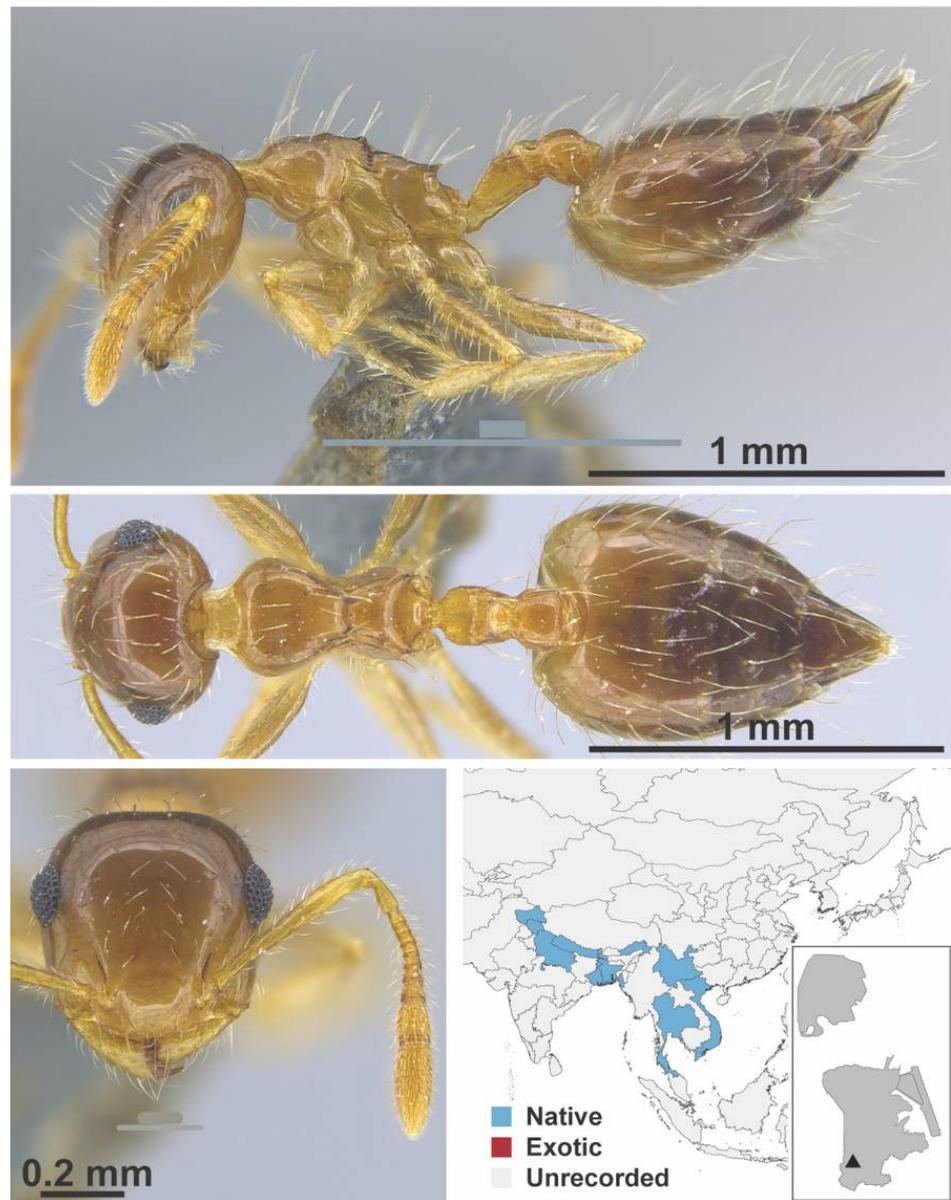


Figure A68. *Crematogaster binghamii* Forel, 1904 worker (MAC_S21_B08_sp.1, IBBL).

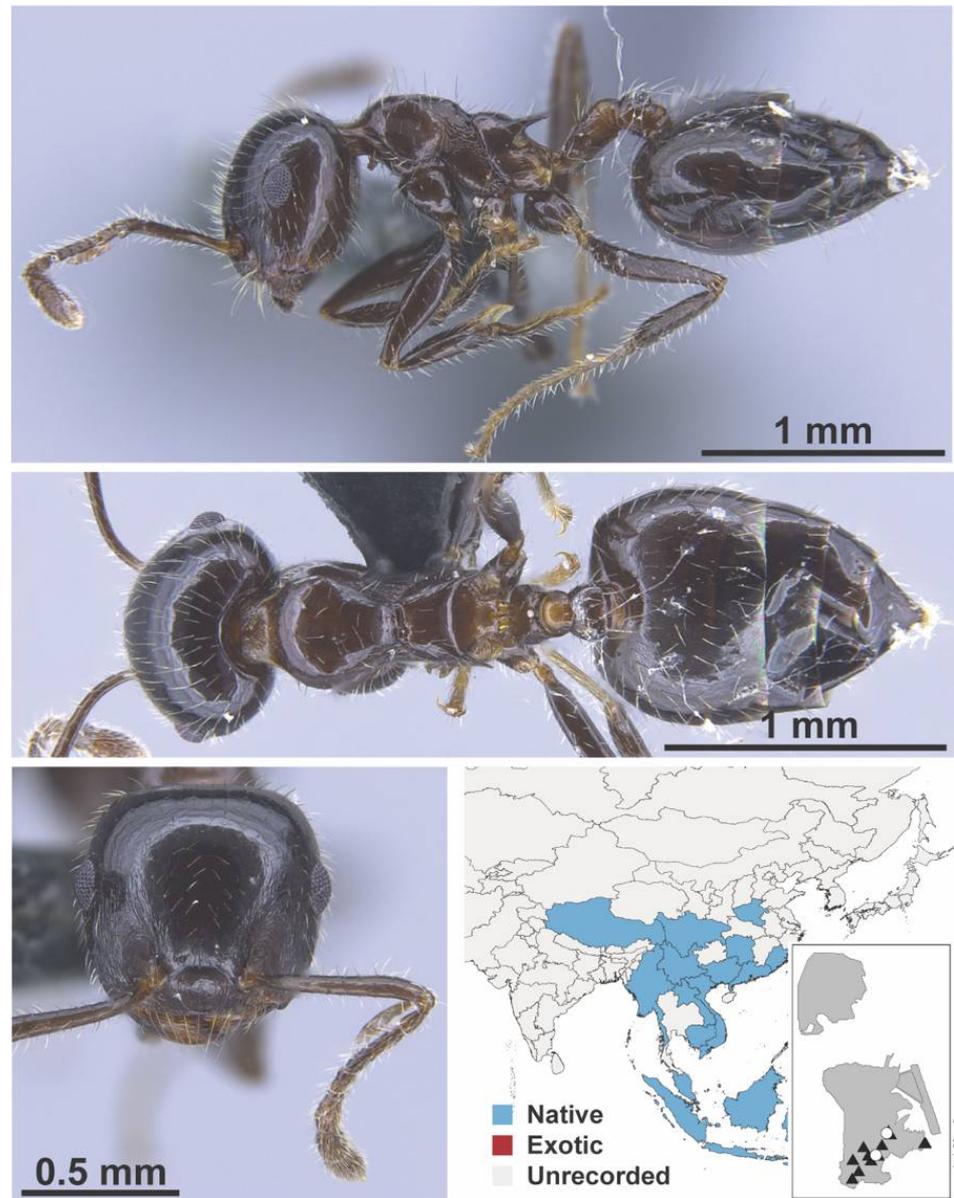


Figure A69. *Crematogaster ferrarii* Emery, 1888 worker (MAC_S01_LLSP_Sp.7, IBBL).

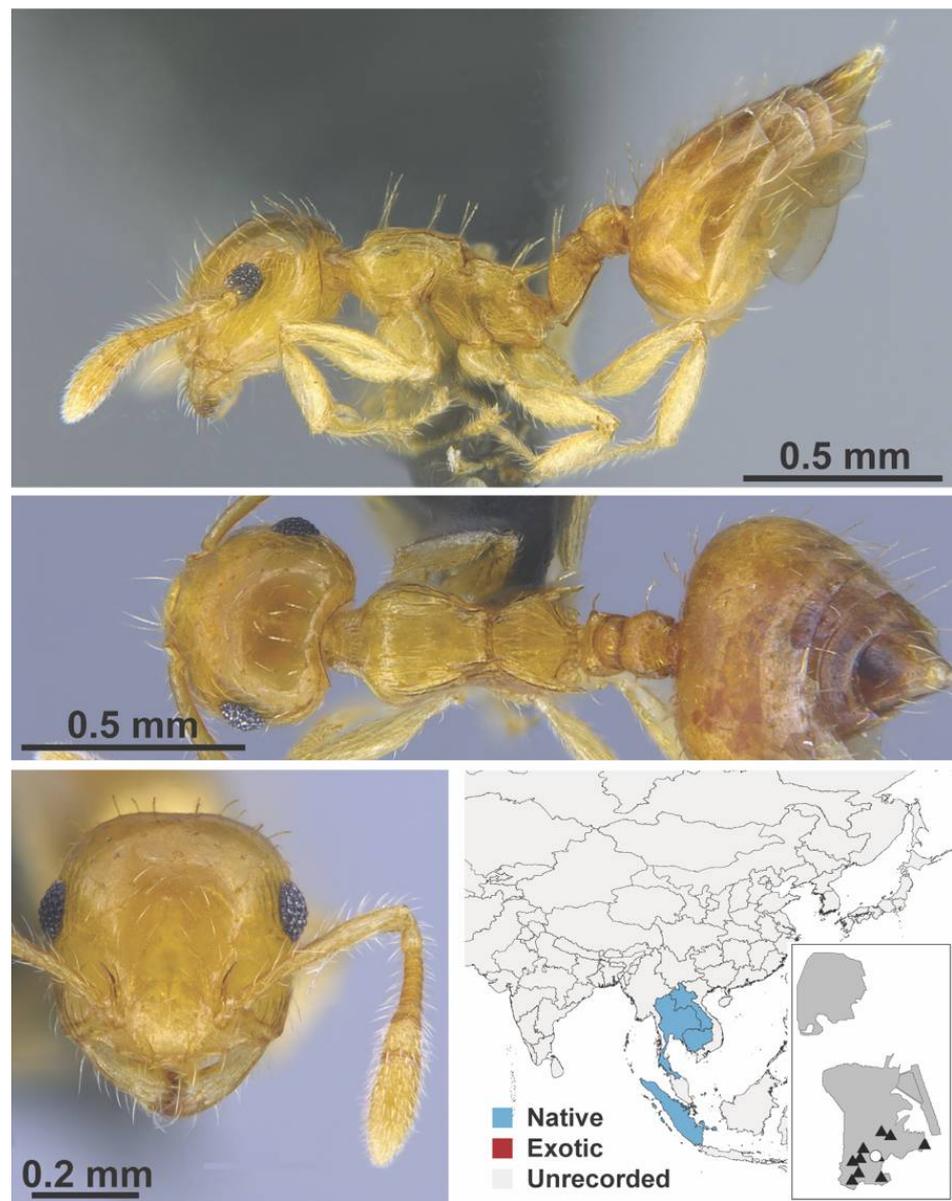


Figure A70. *Crematogaster quadriruga* Forel, 1911 worker (MAC_S06_LLSA_sp.1, IBBL).

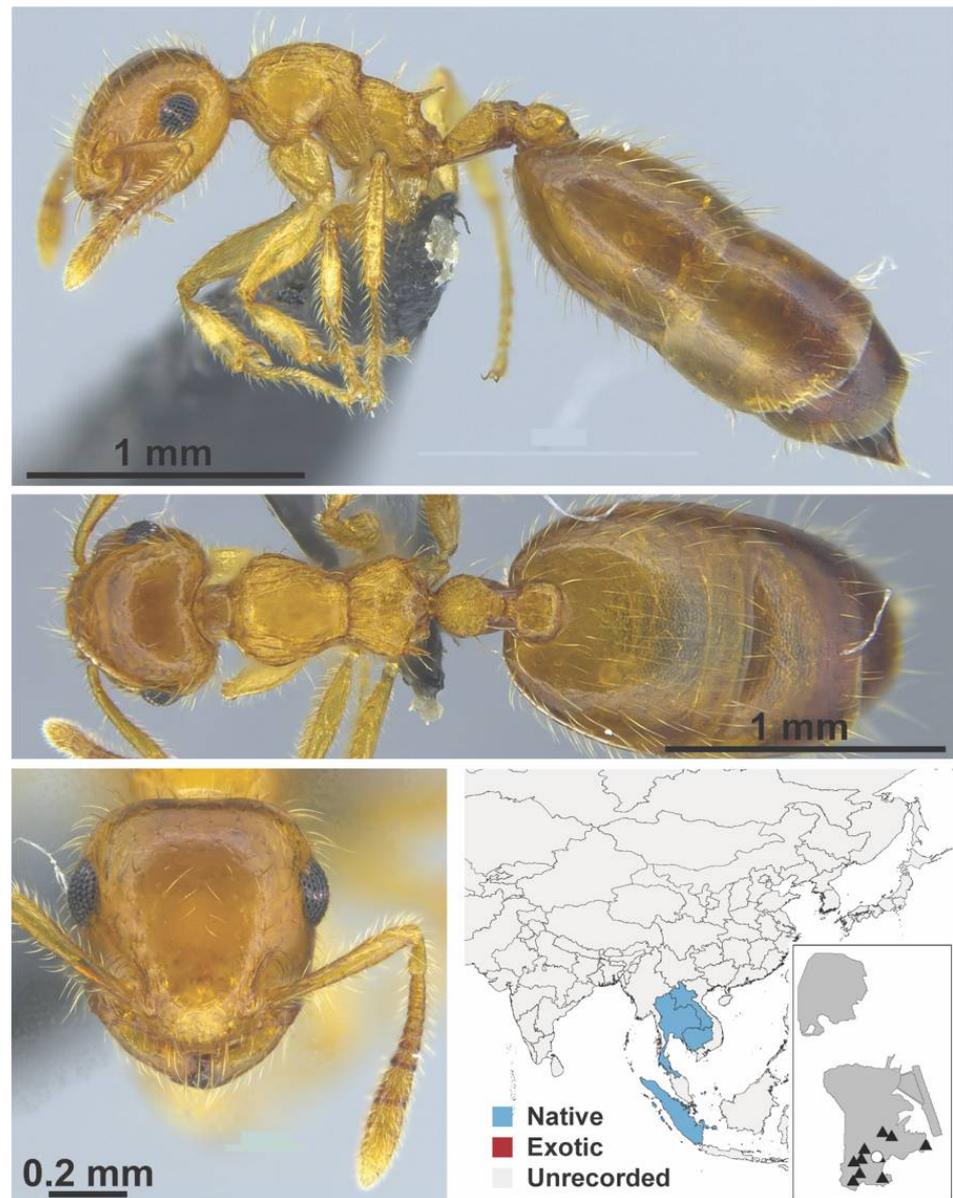


Figure A71. *Crematogaster quadriruga* Forel, 1911 intercaste (MAC_S17_LLSA_sp.3, IBBL).

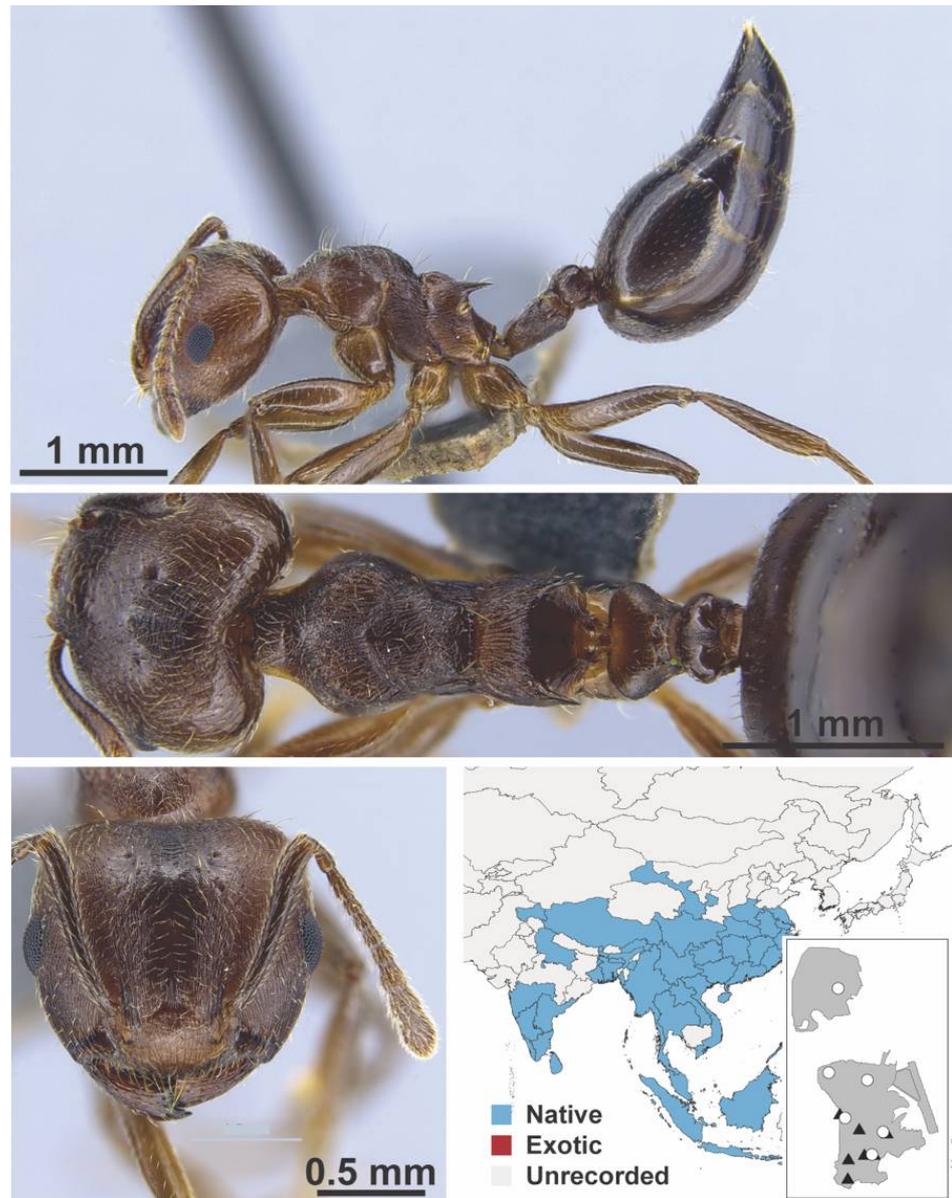


Figure A72. *Crematogaster rogenhoferi* Mayr, 1879 worker (MAC_S19_T4_1m_sp.1, IBBL).

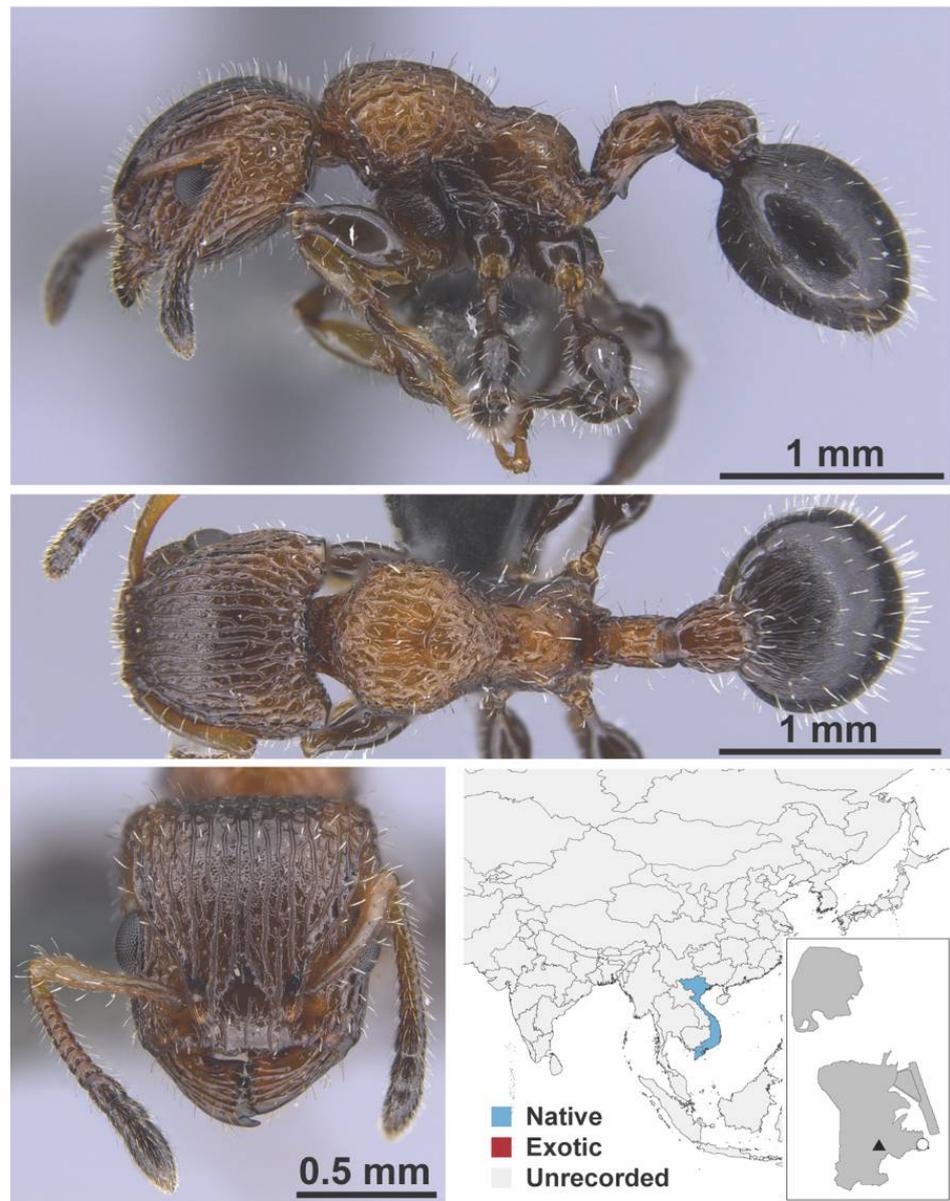


Figure A73. *Dilobocondyla propotriangulata*, Bharti & Kumar, 2013 worker (FB19145, IBBL).

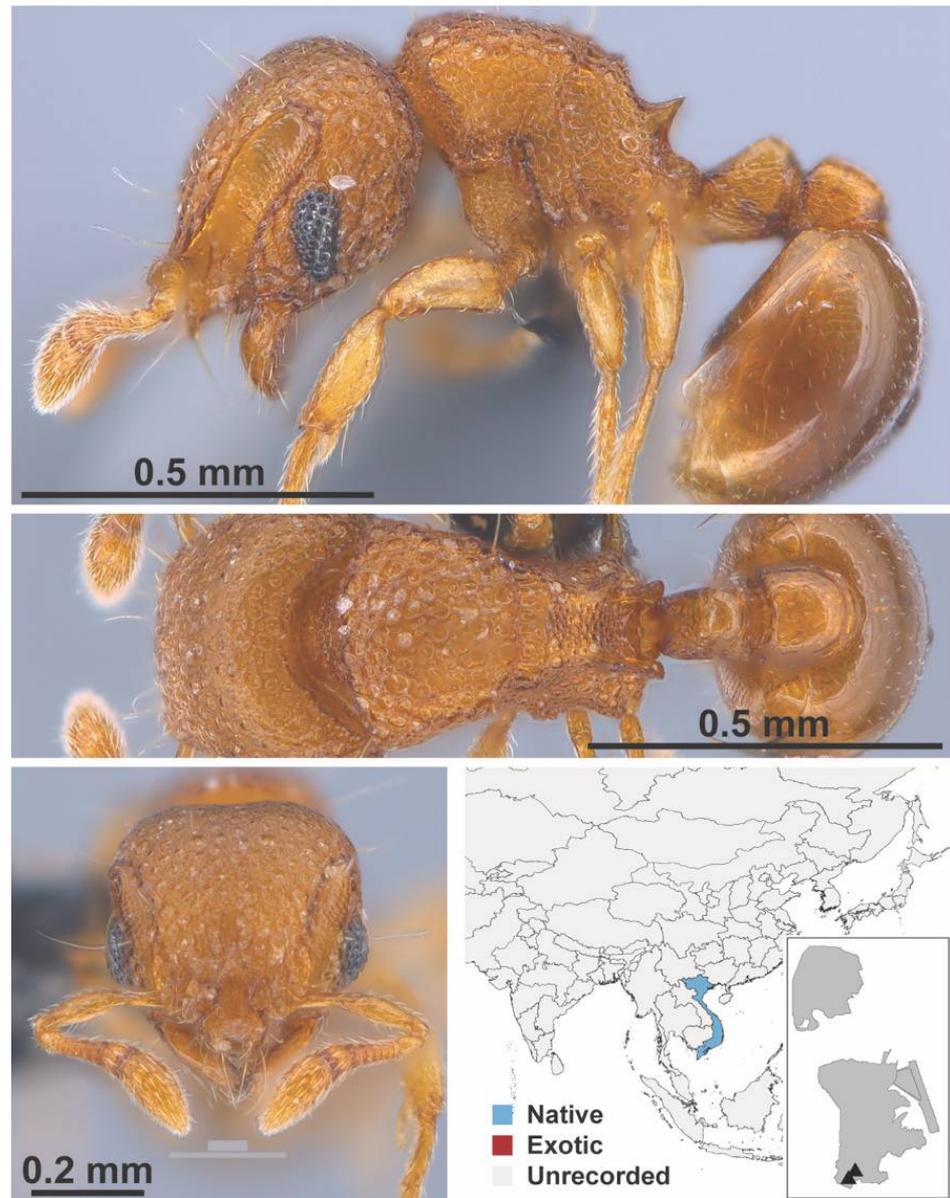


Figure A74. *Mayriella granulata*, Dlussky & Radchenko, 1990 worker (MAC_S18_LLSA_Sp.4, IBBL).

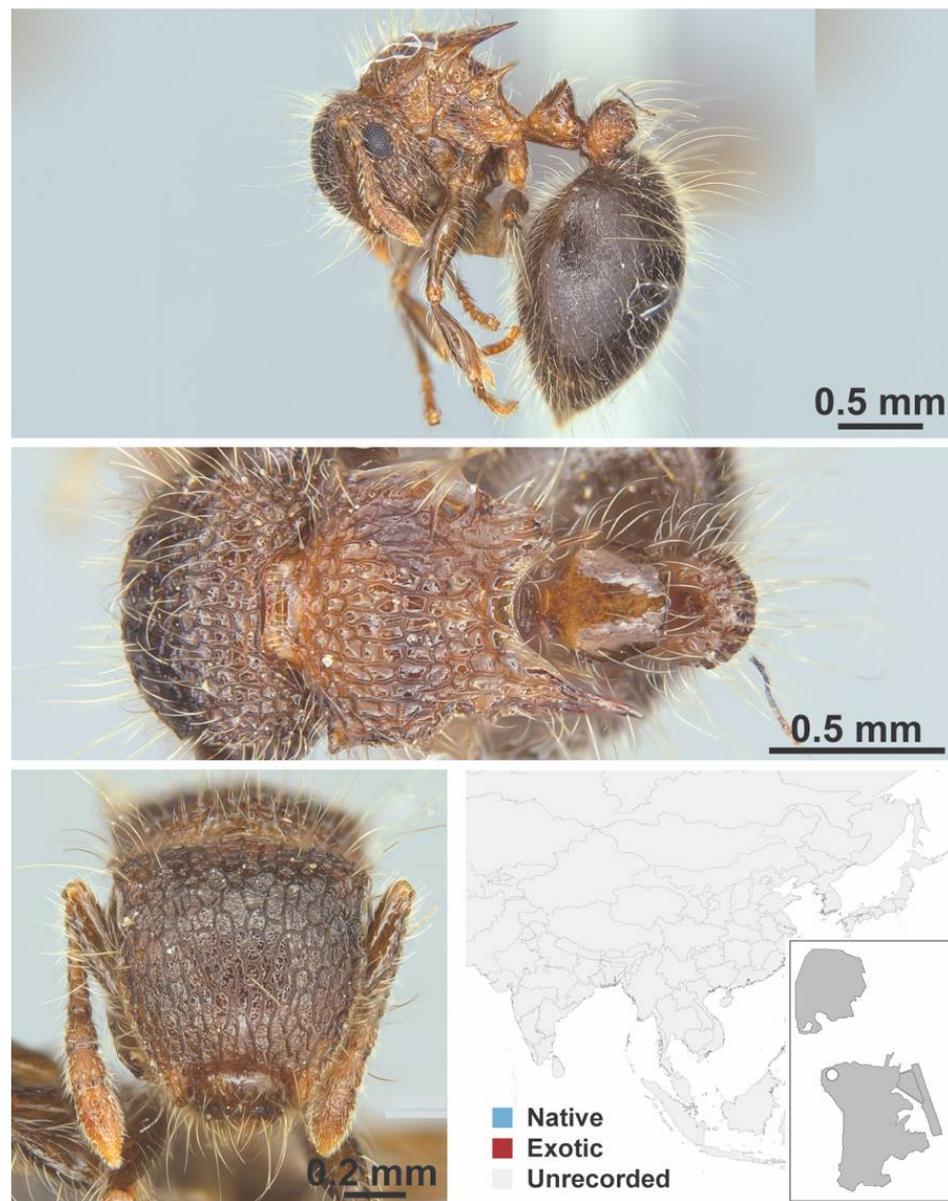


Figure A75. *Meranoplus* sp. mo01 nr. *bicolor* Guérin-Ménéville, 1844 worker (*Meranoplus* sp. mo01 nr. *Bicolor*, CML collection).

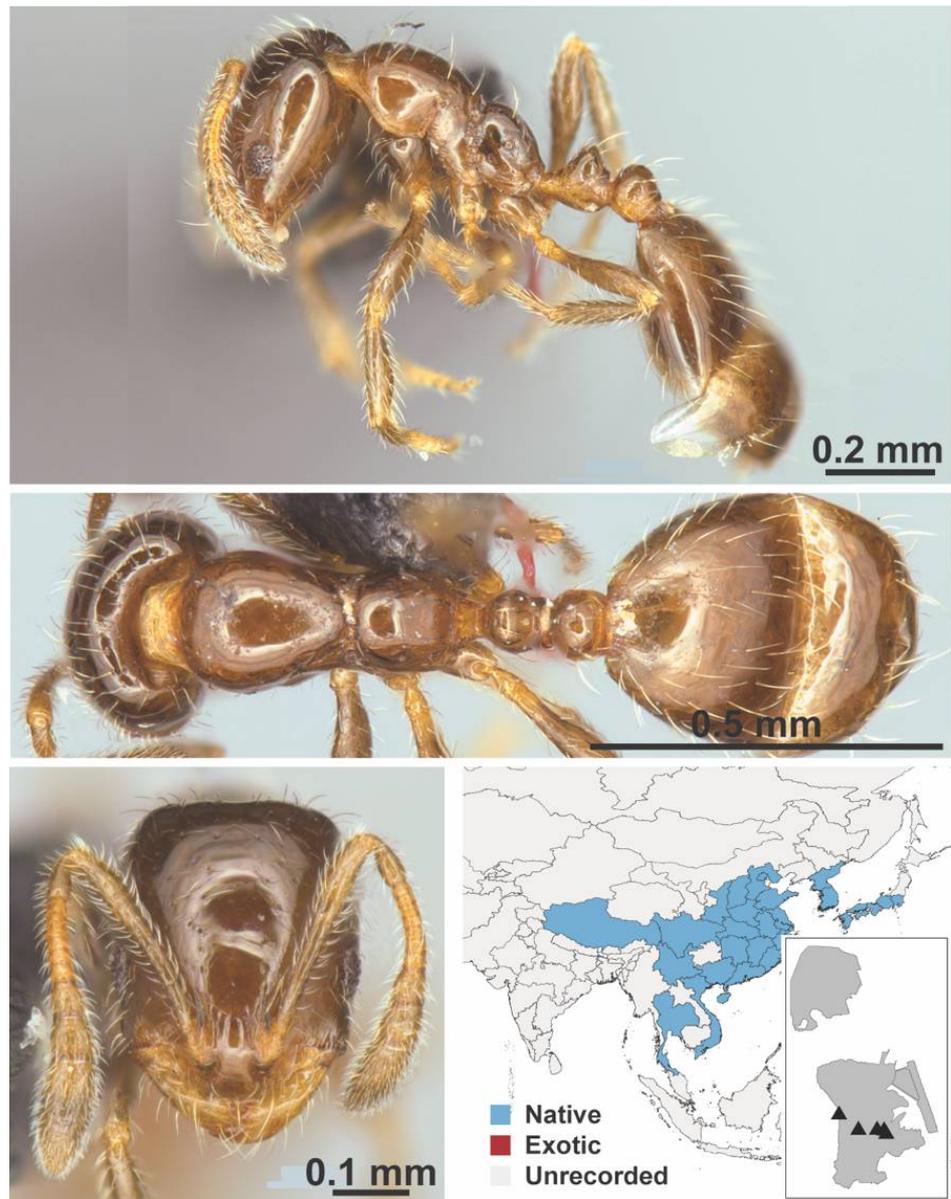


Figure A76. *Monomorium chinense* Santschi, 1925 worker (MAC_S20_LLSP_sp.12, IBBL).

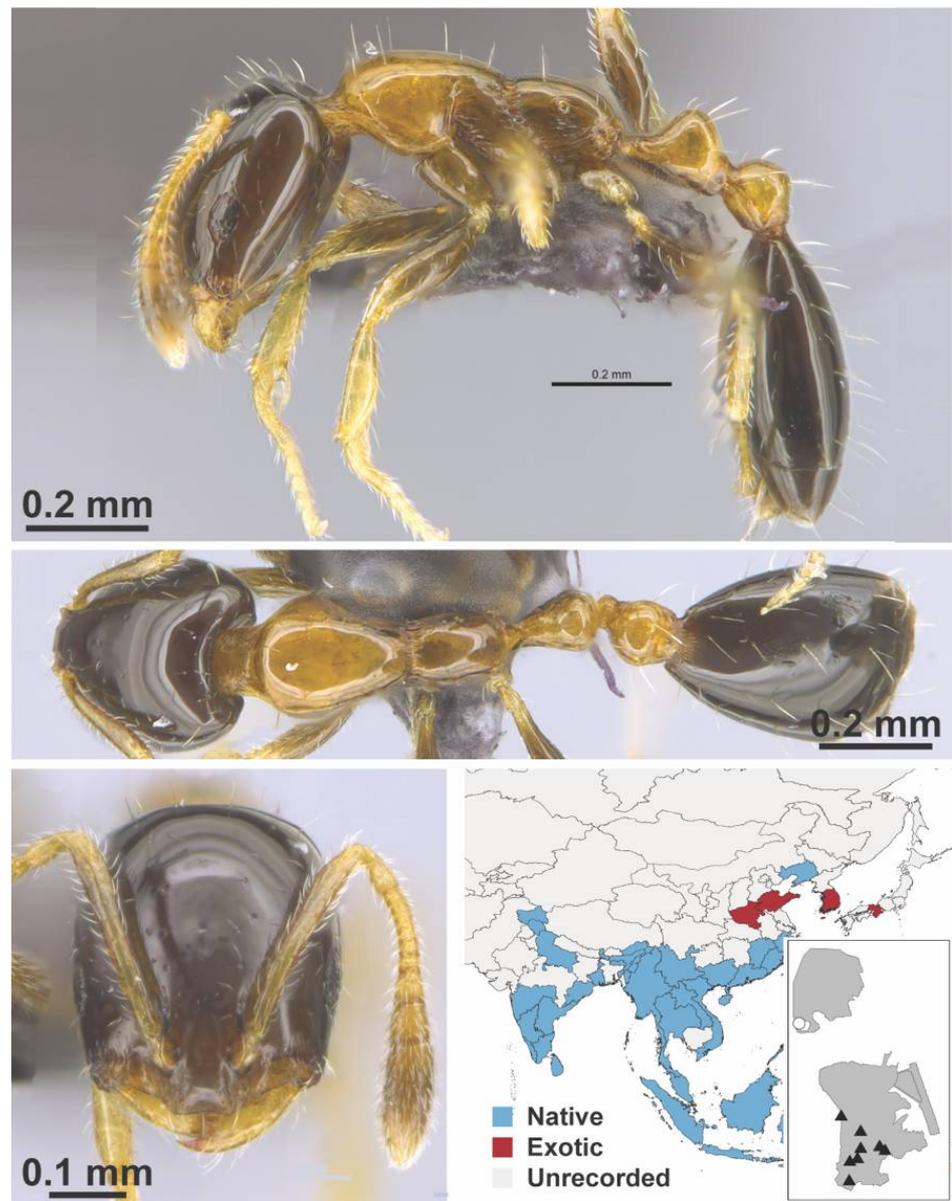


Figure A77. *Monomorium floricola* Jerdon, 1851 worker (MAC_S03_LLSA_Sp.8, IBBL).

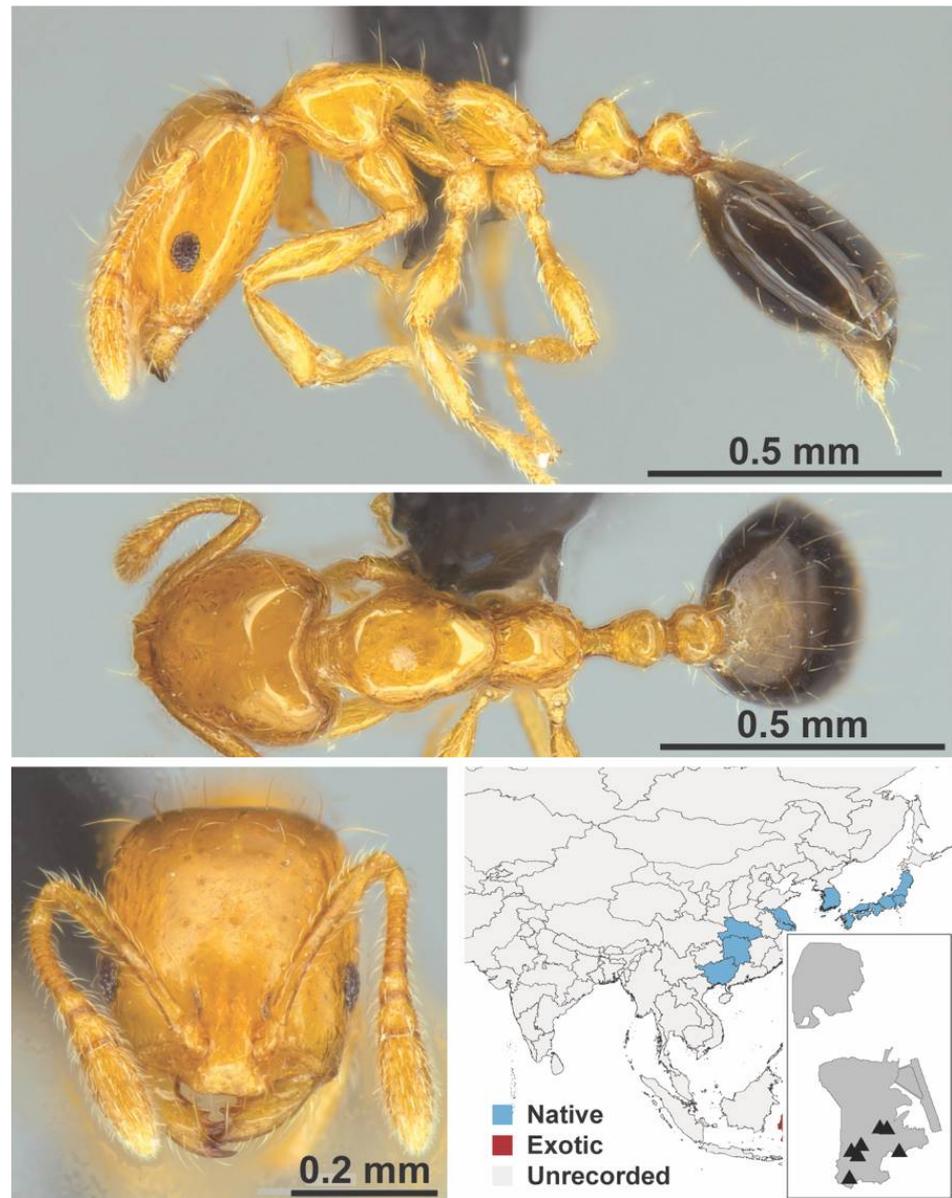


Figure A78. *Monomorium intrudens* Smith, 1874 worker (MAC_S18_LLSP_sp.3, IBBL).

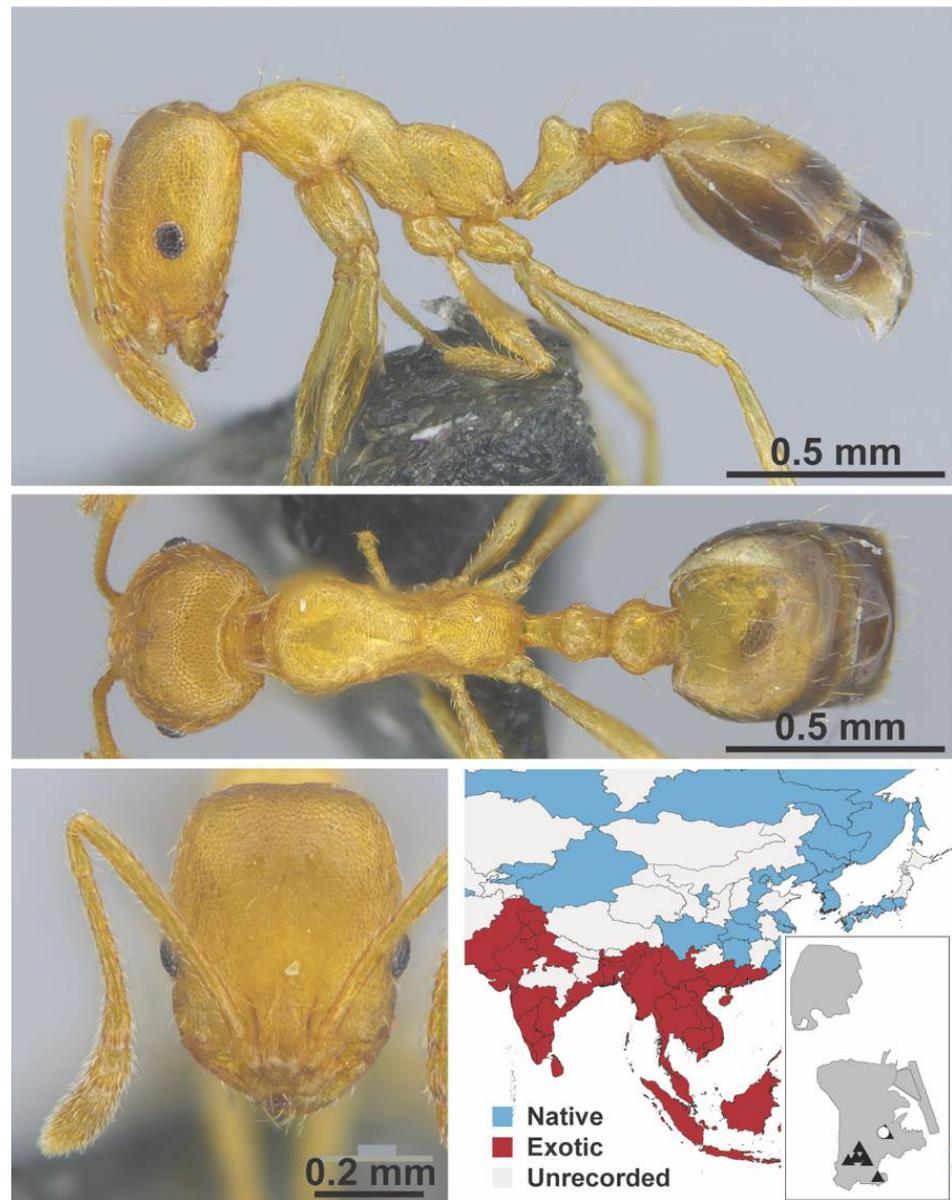


Figure A79. *Monomorium pharaonis* Linnaeus, 1758 worker (MAC_S09_LLSA_sp.9, IBBL).

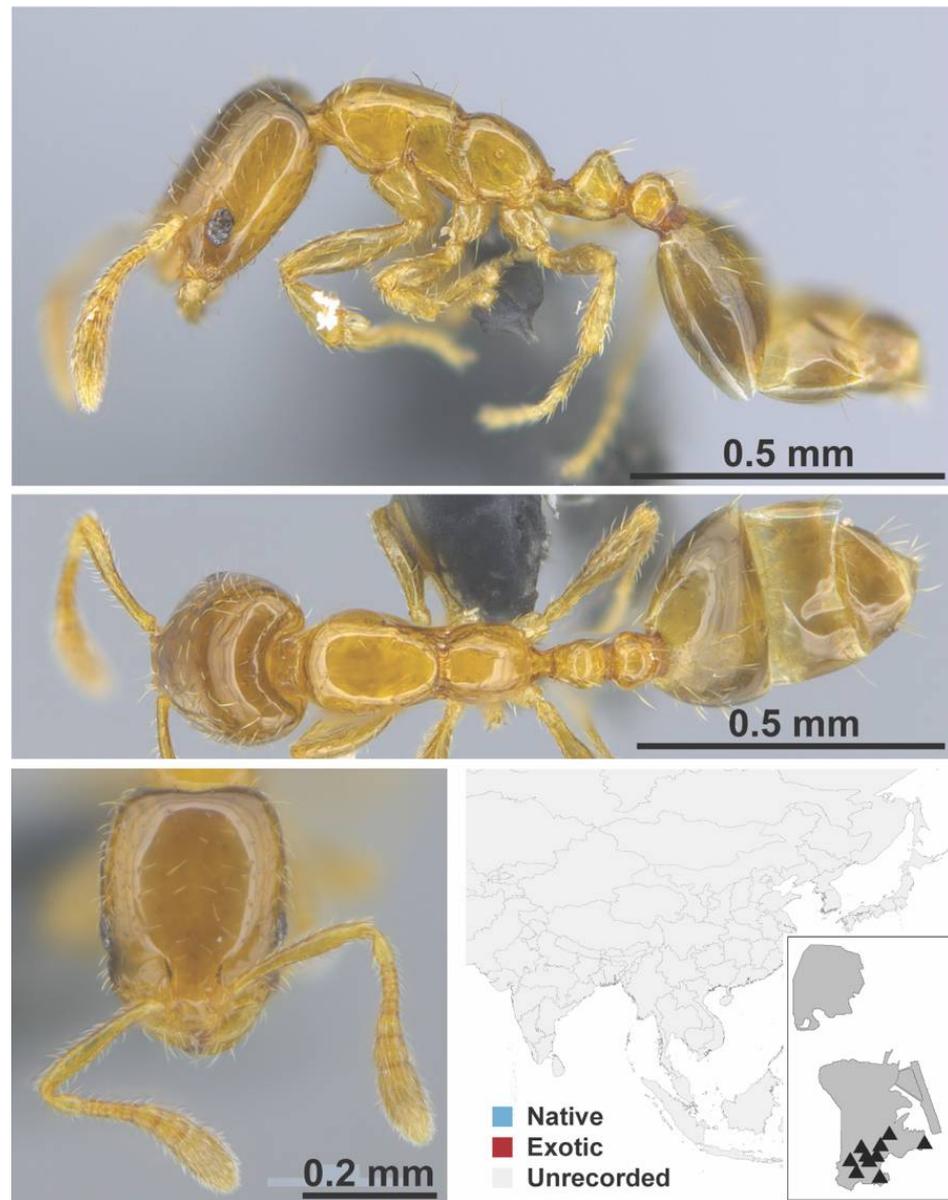


Figure A80. *Monomorium* sp. psw-cn01 worker (MAC_S21_LLSA_bottom_sp.2, IBBL).

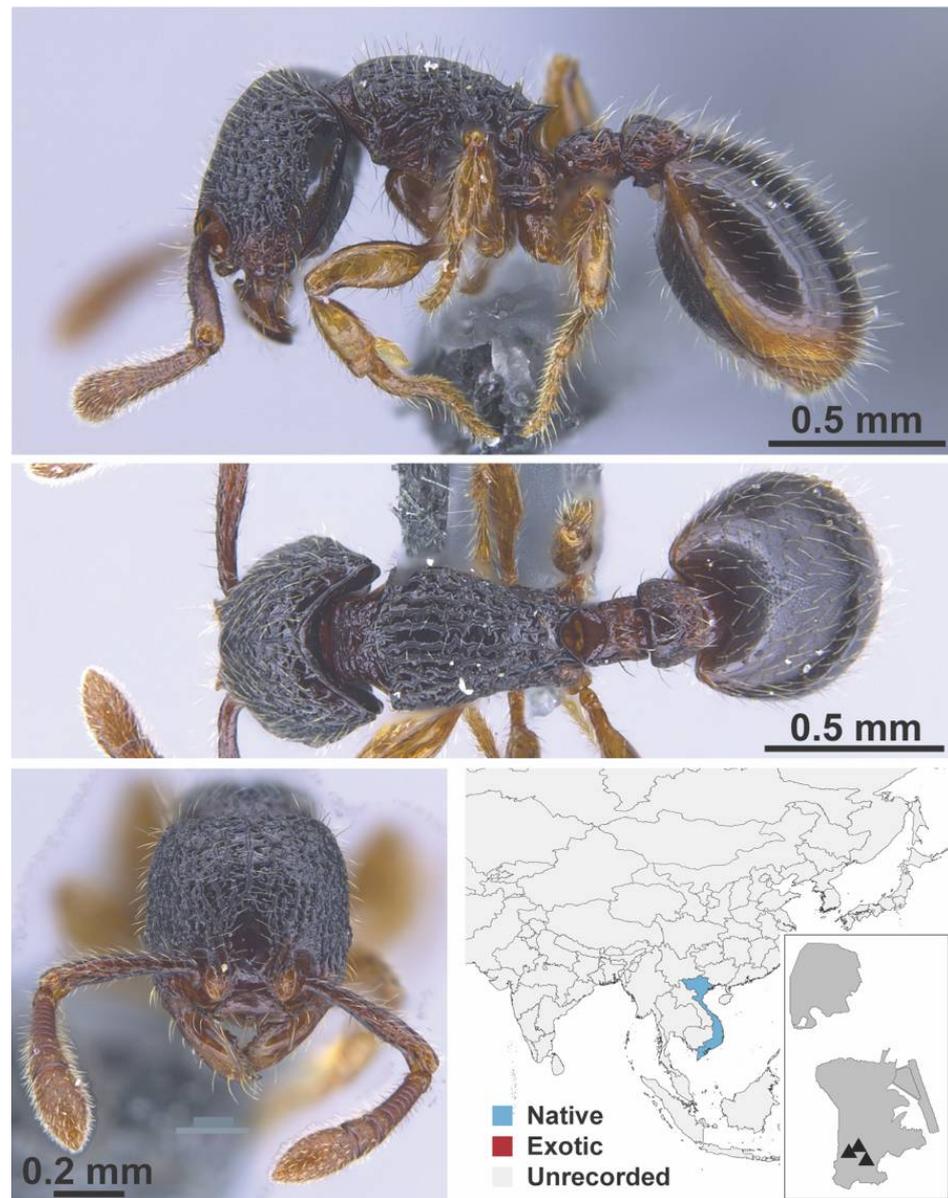


Figure A81. *Myrmecina nomurai* Okido, Ogata & Hosoishi, 2020 worker (MAC_S05_LLSA_Sp.1, IBBL).

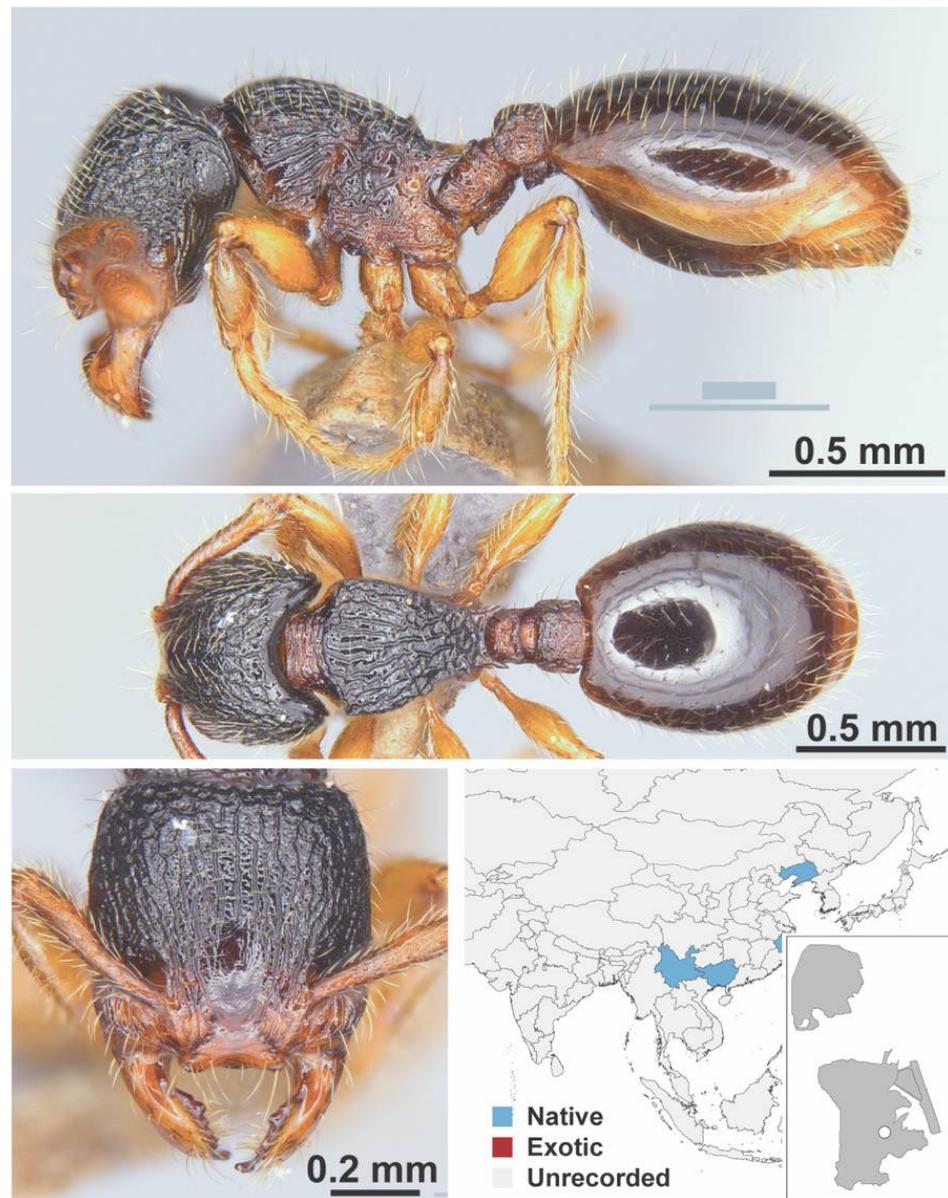


Figure A82. *Myrmecina sinensis* Wheeler, W. M., 1921 worker (*Myrmecina sinensis*, CML collection).

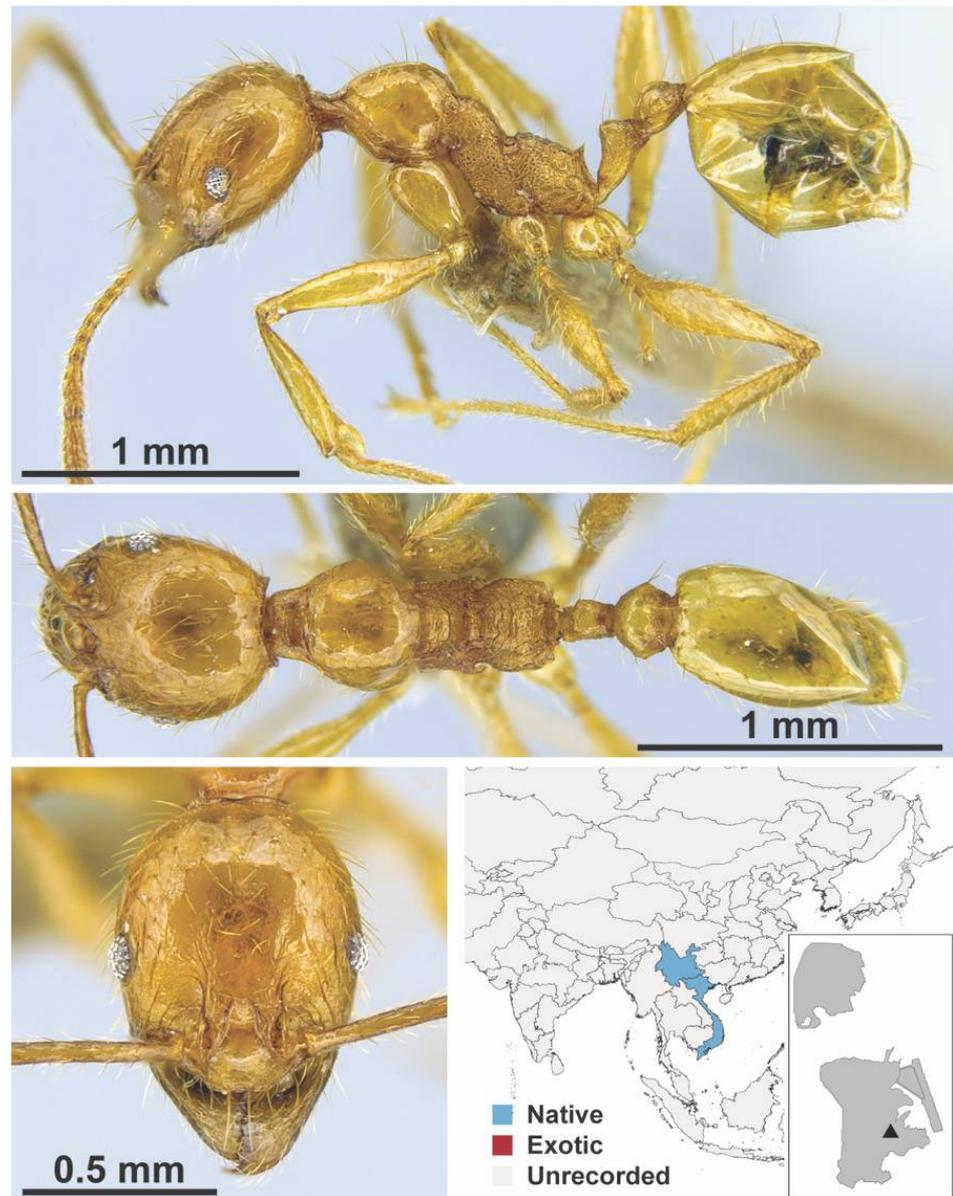


Figure A83. *Pheidole elongicephala* Eguchi, 2008 worker (MAC_S09_q2_25_sp.2, IBBL).

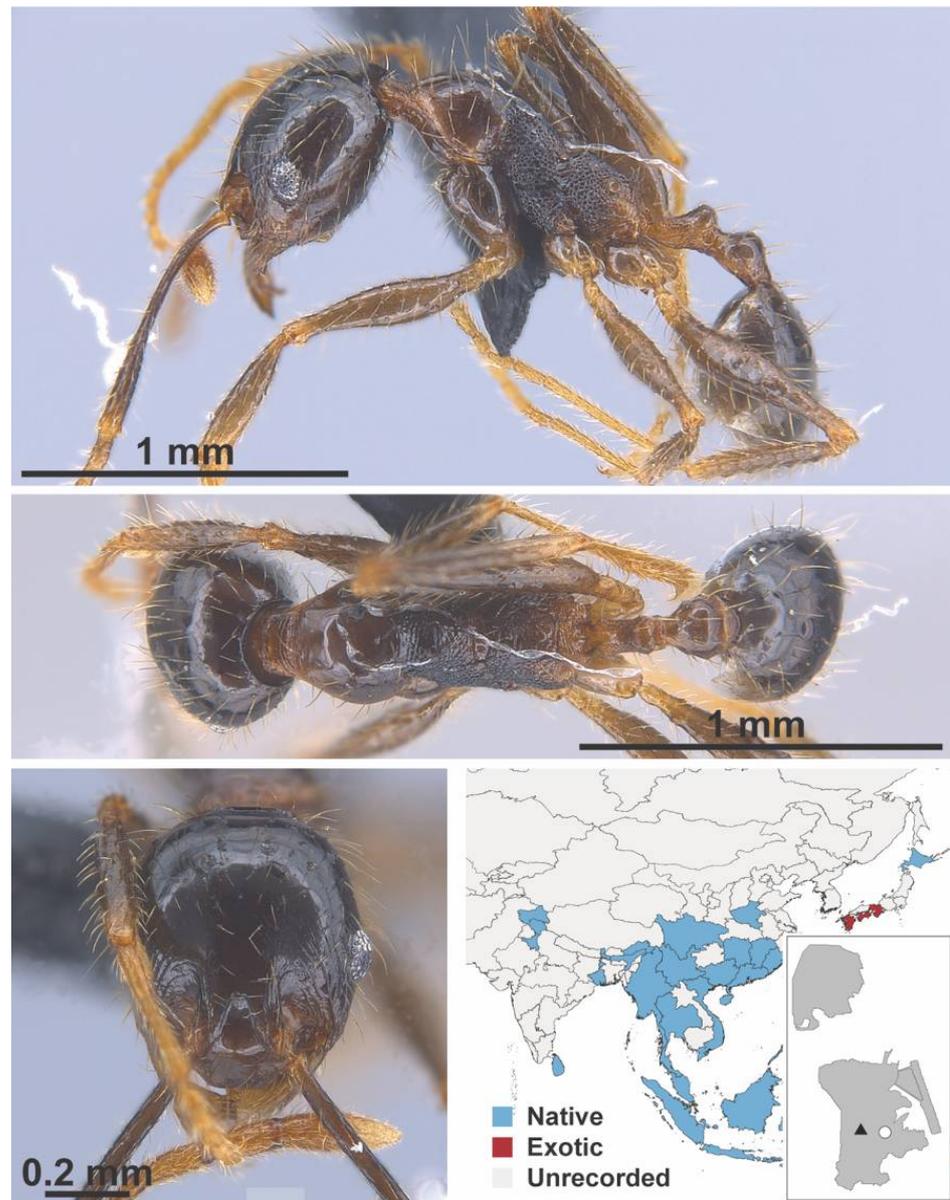


Figure A84. *Pheidole feroens* Smith, 1858 worker (MAC_S19_q4_GL_03_Sp.2, IBBL).

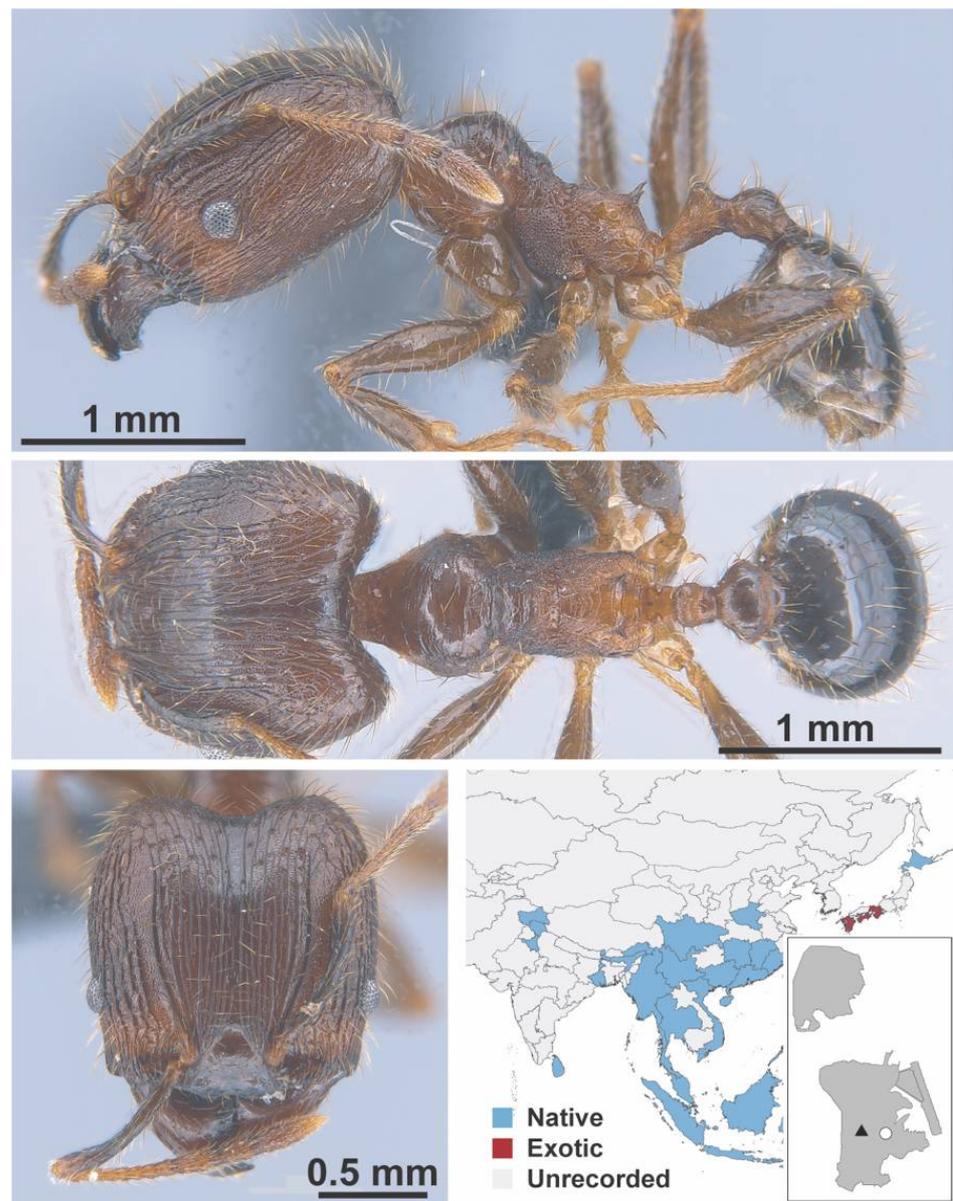


Figure A85. *Pheidole feroens* Smith, 1858 major (MAC_S19_q4_GL_03_Sp.2, IBBL).

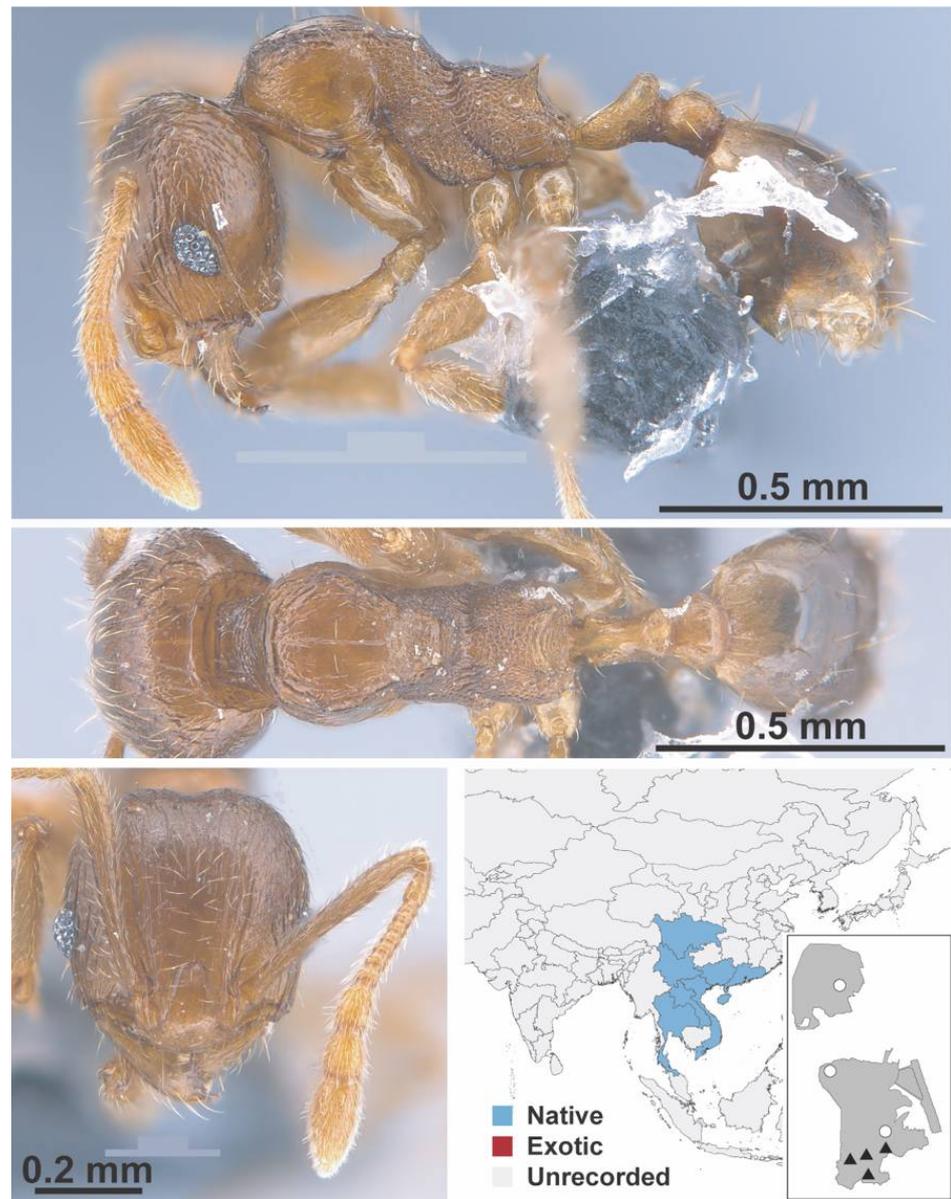


Figure A86. *Pheidole hongkongensis* Wheeler, 1928 worker (MAC_S21_LLSP_Sp.9, IBBL).

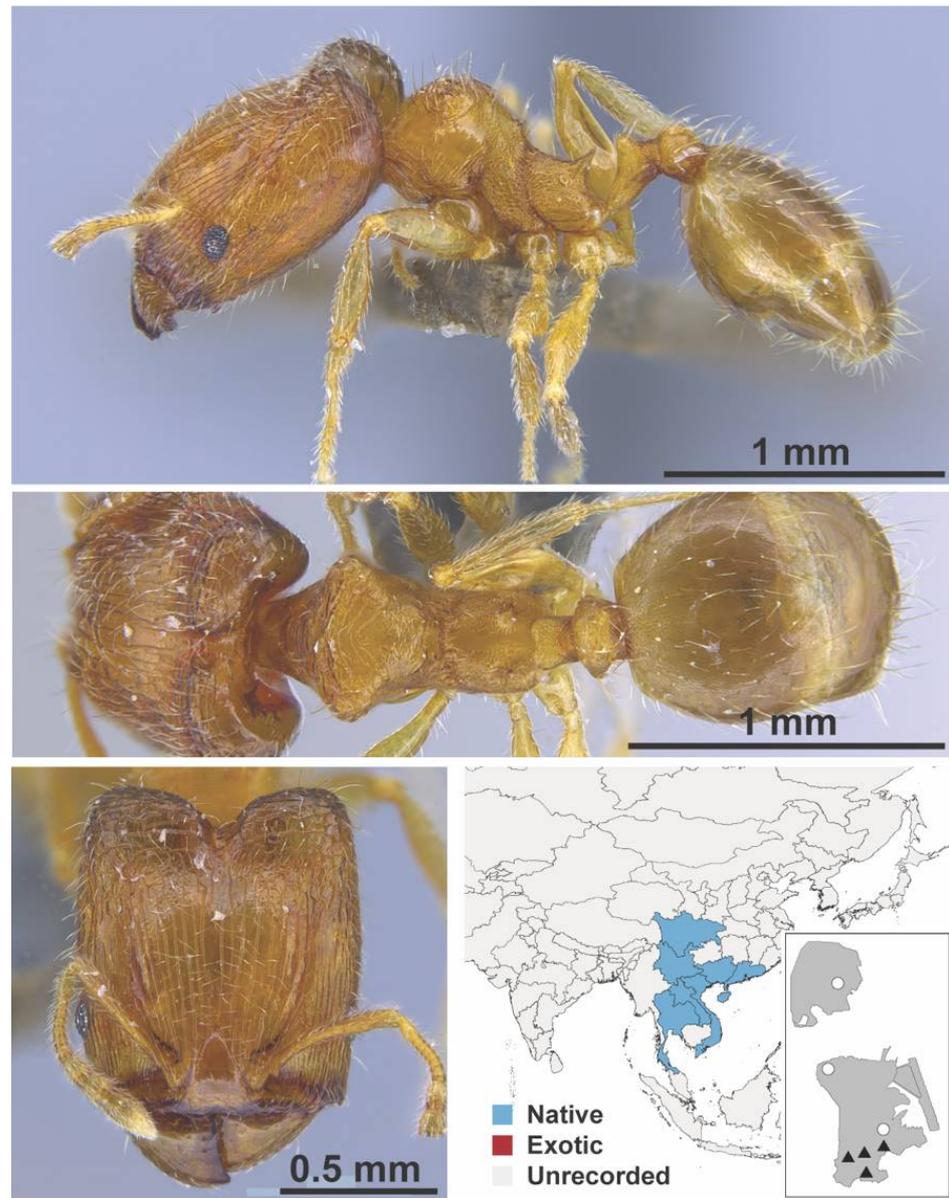


Figure A87. *Pheidole hongkongensis* Wheeler, 1928 major (MAC_S07_B08_sp.1, IBBL).

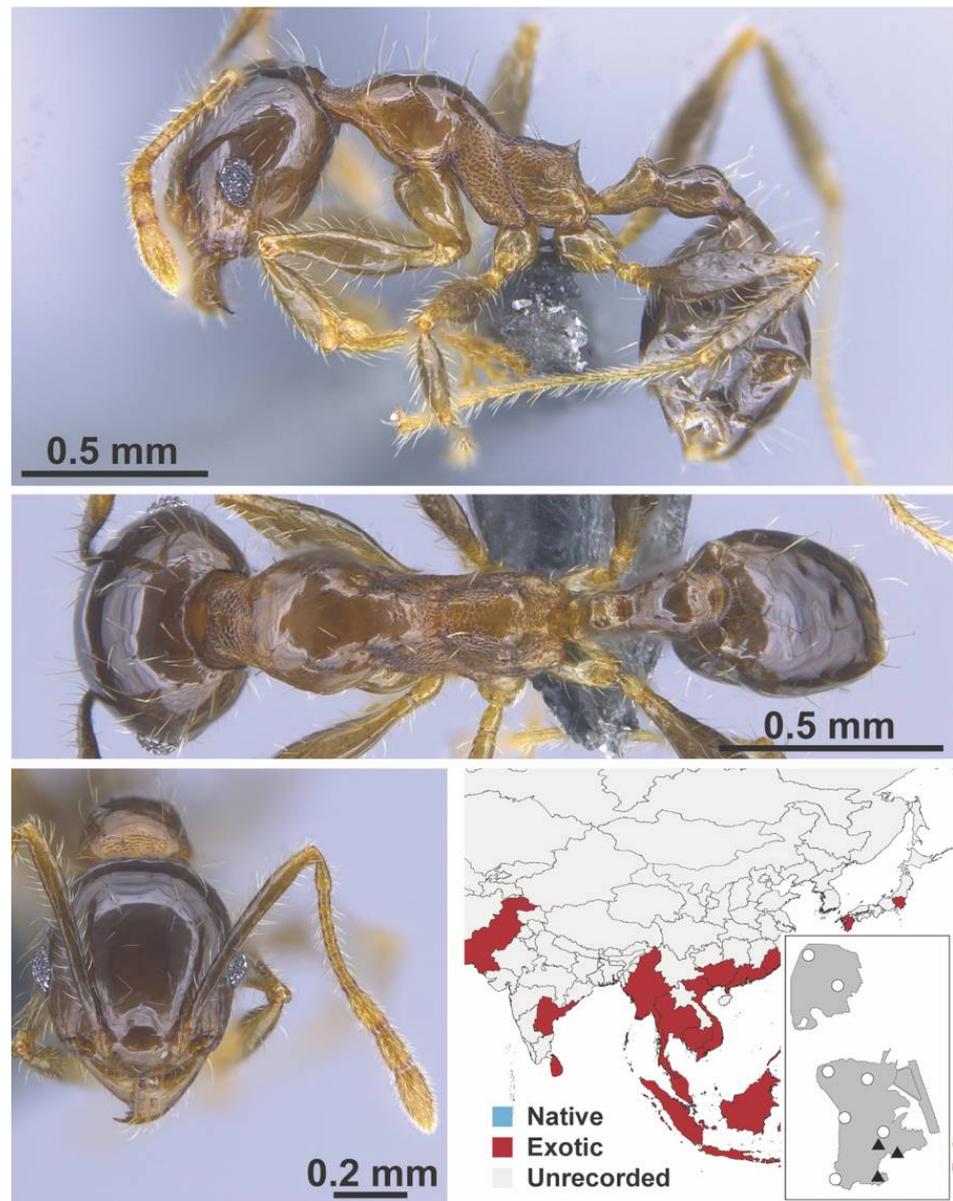


Figure A88. *Pheidole megacephala* Fabricius, 1793 worker (MAC_S13_LLSP_Sp.1, IBBL).

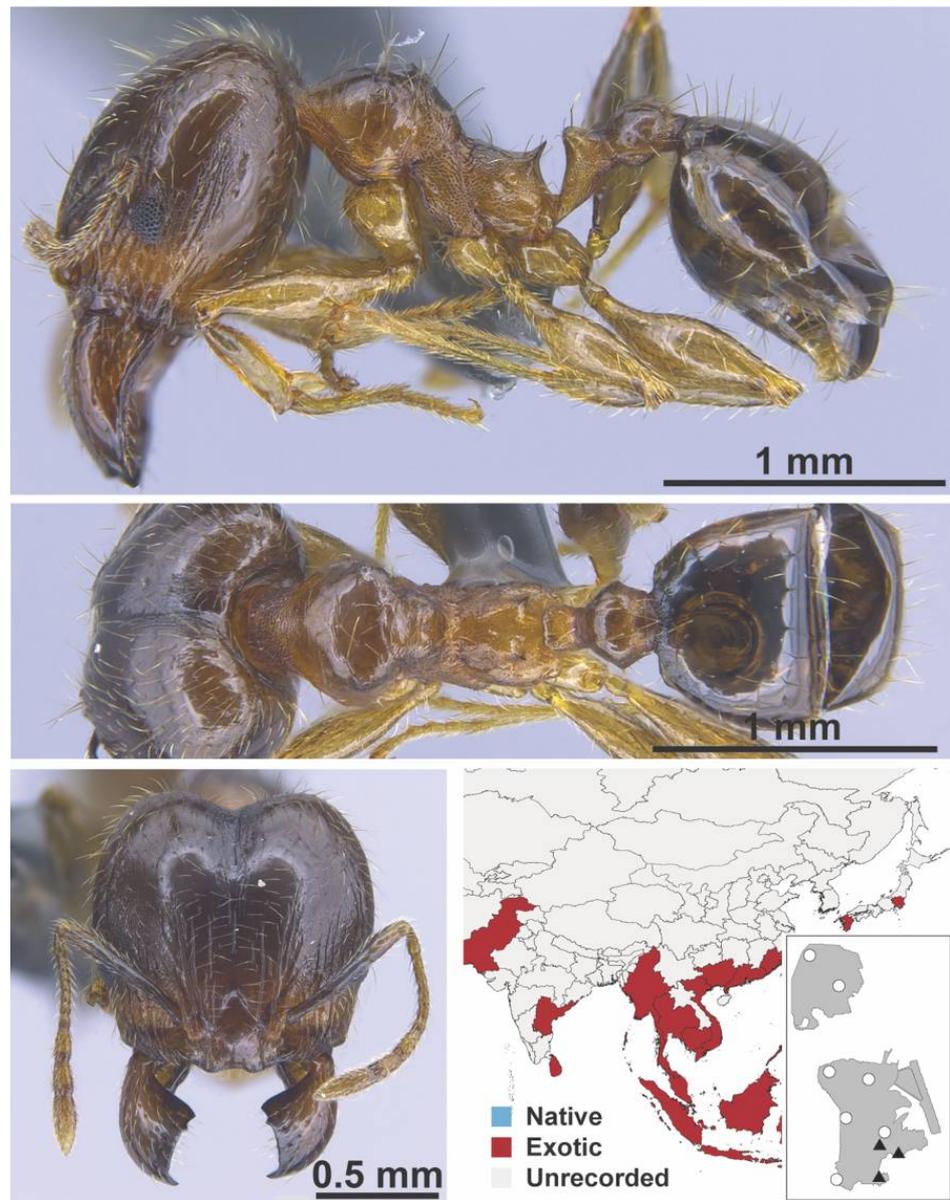


Figure A89. *Pheidole megacephala* Fabricius, 1793 major (MAC_S13_LLSP_Sp.1, IBBL).

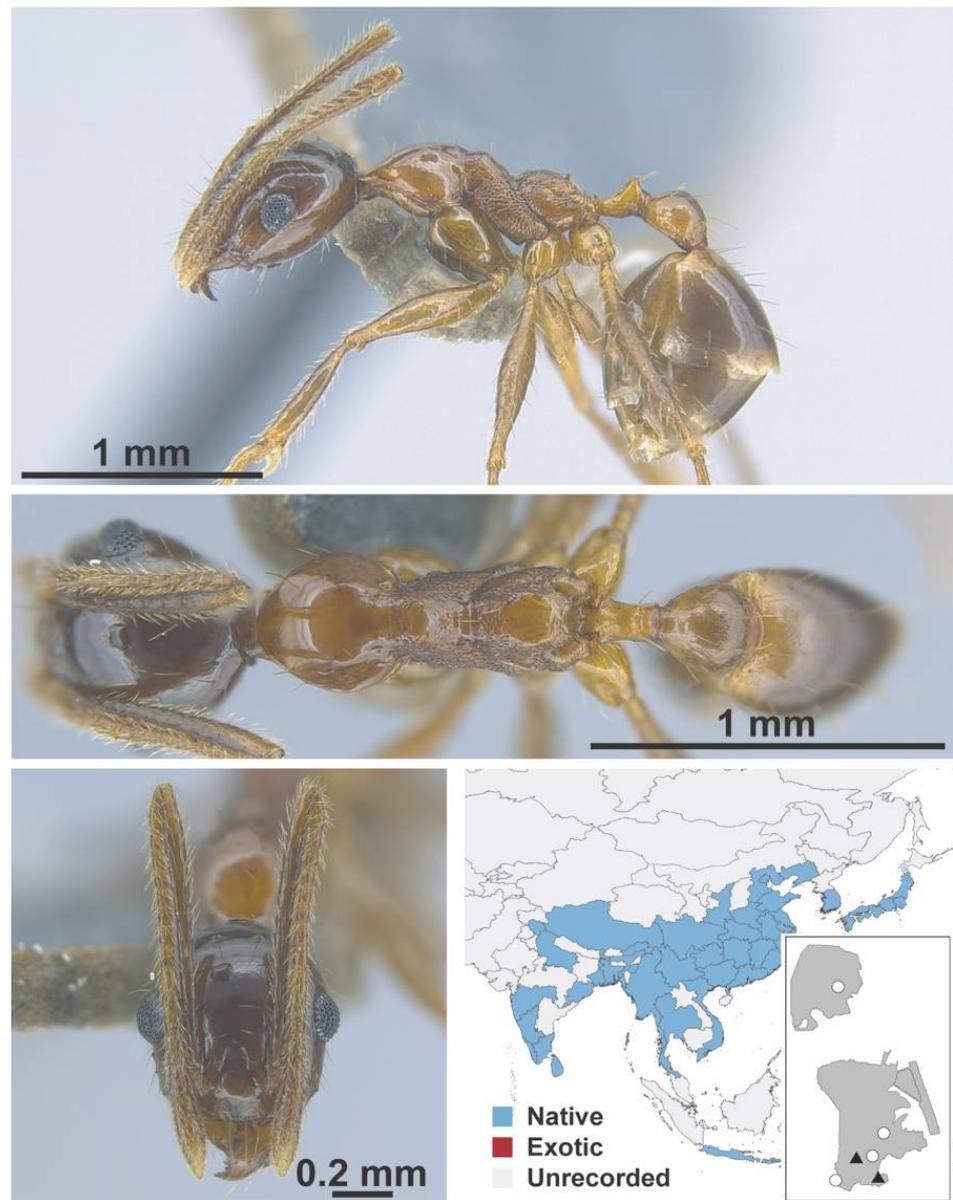


Figure A90. *Pheidole nodus* Smith, 1874 worker (MAC_S02_B09_sp.1_top, IBBL).

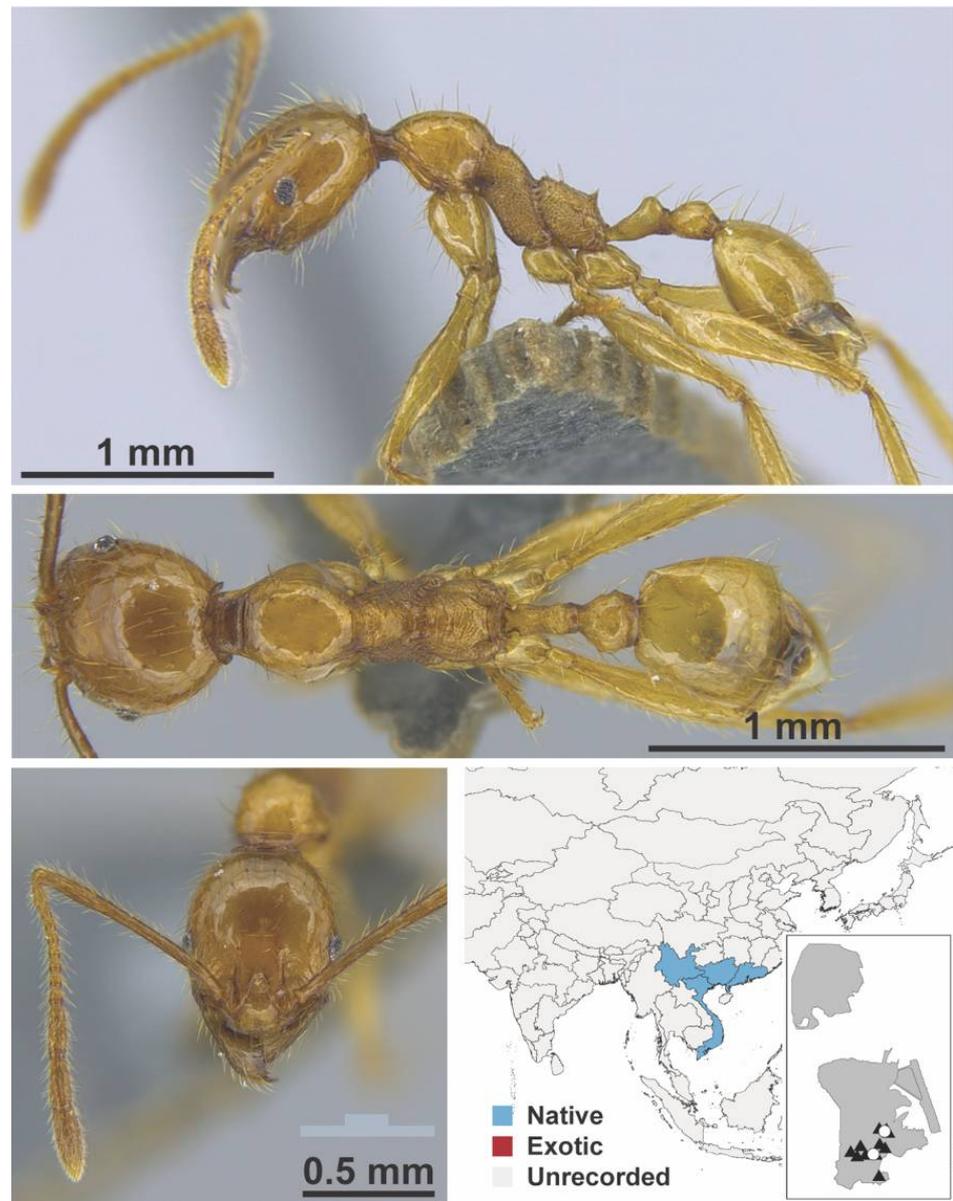


Figure A91. *Pheidole ochracea* Eguchi, 2008 worker (MAC_S03_B03_sp.1, IBBL).

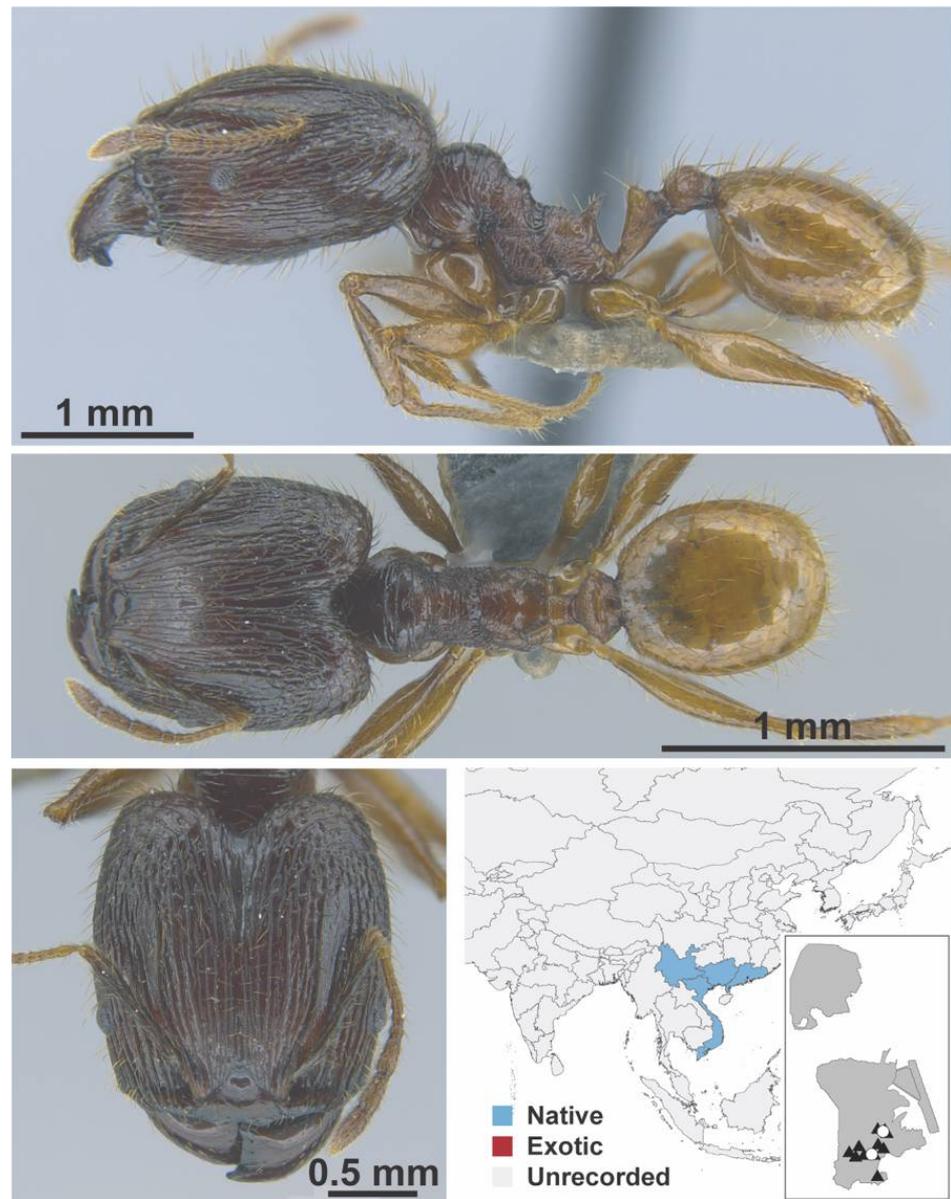


Figure A92. *Pheidole ochracea* Eguchi, 2008 major (MAC_S03_B03_sp.1, IBBL).

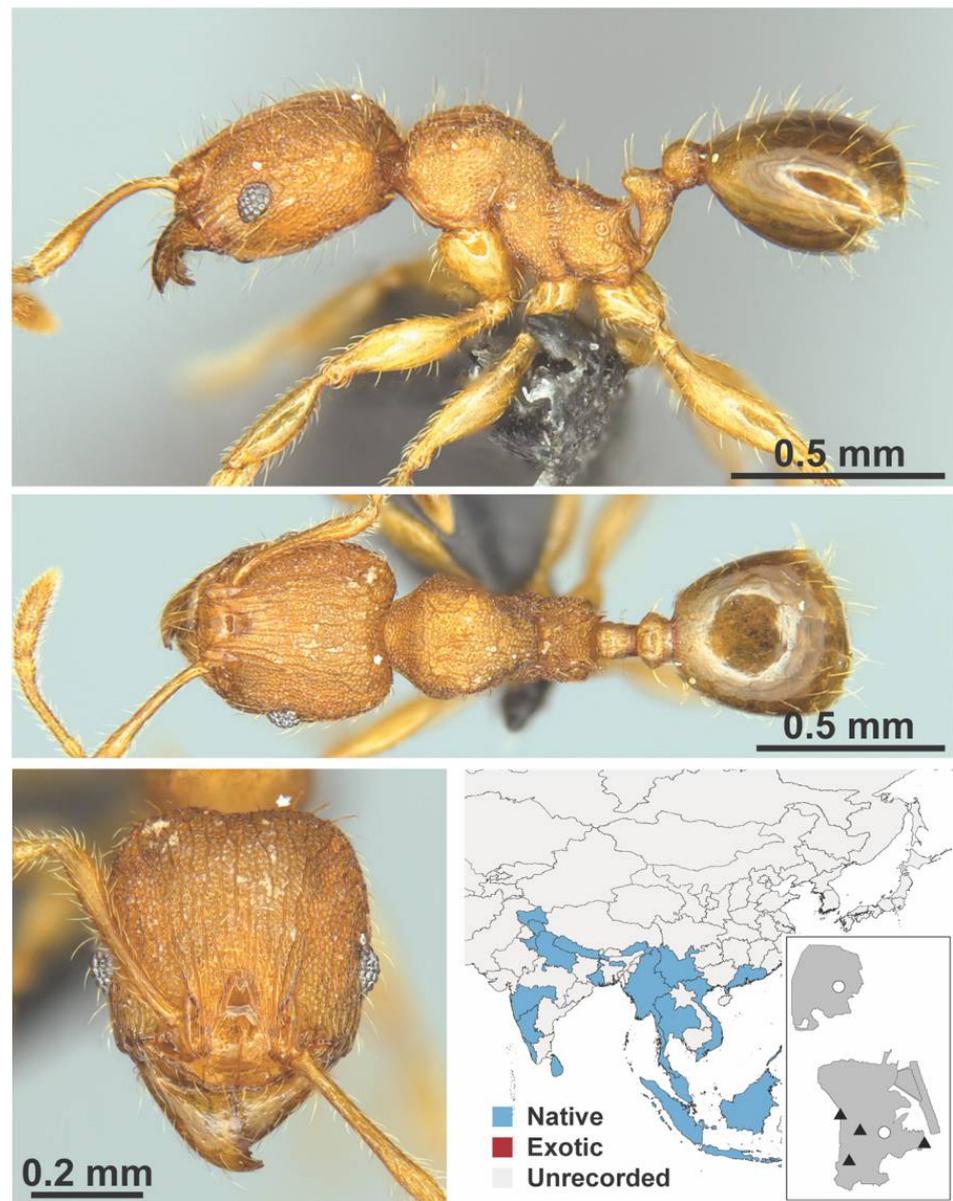


Figure A93. *Pheidole parva* Mayr, 1865 worker (MAC_S20_LLSA_sp.4, IBBL).

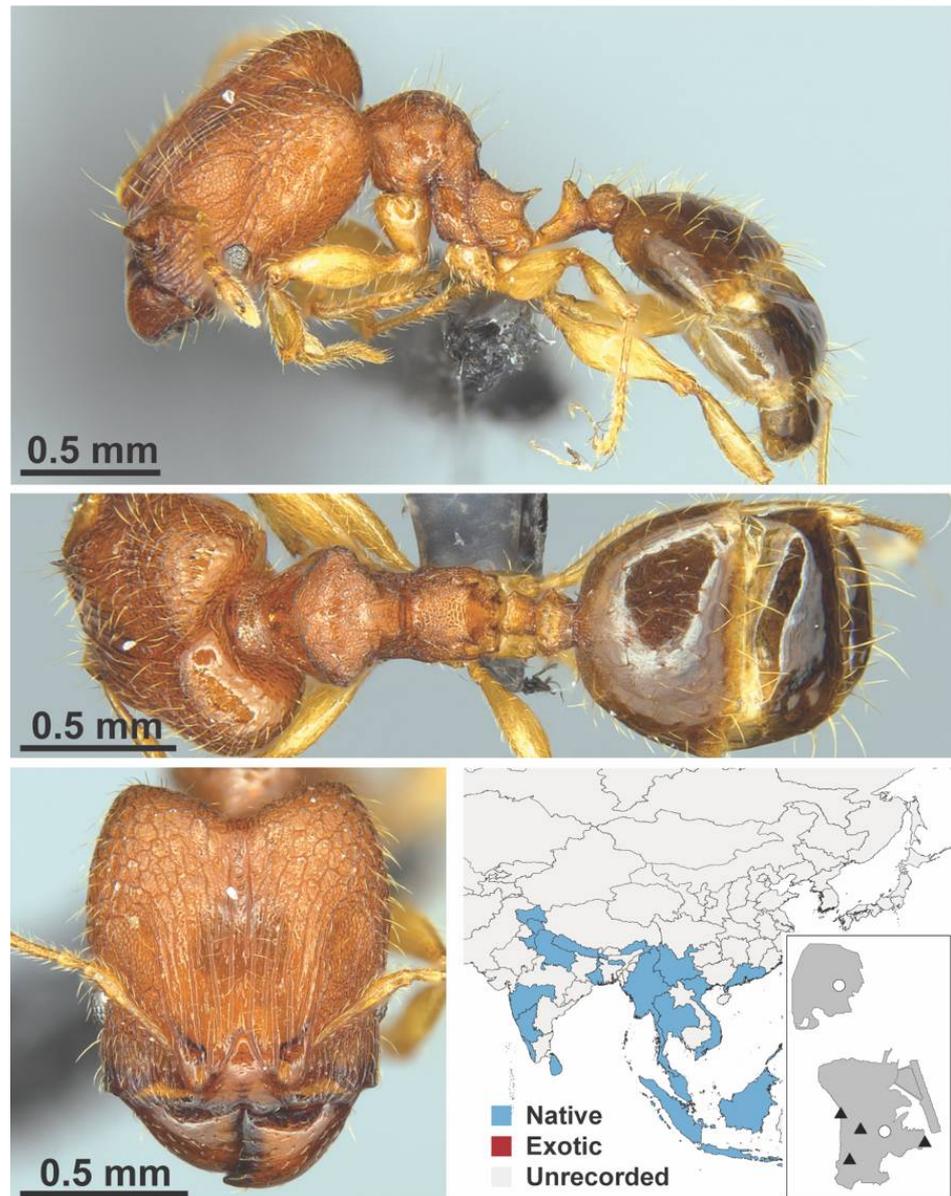


Figure A94. *Pheidole parva* Mayr, 1865 major (MAC_S20_LLSA_sp.4, IBBL).

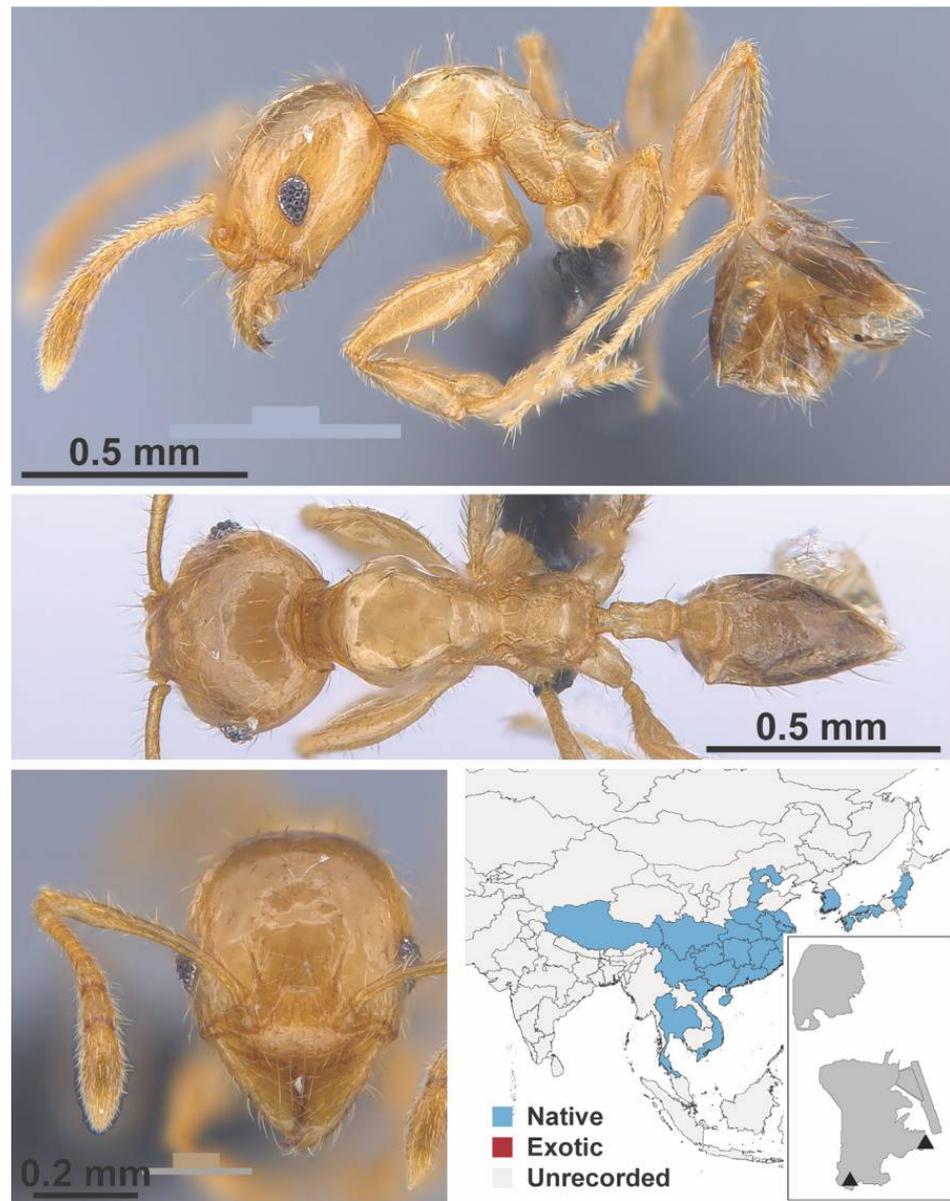


Figure A95. *Pheidole pieli* Santschi, 1925 worker (MAC_S17_LLSA_Sp.4, IBBL).

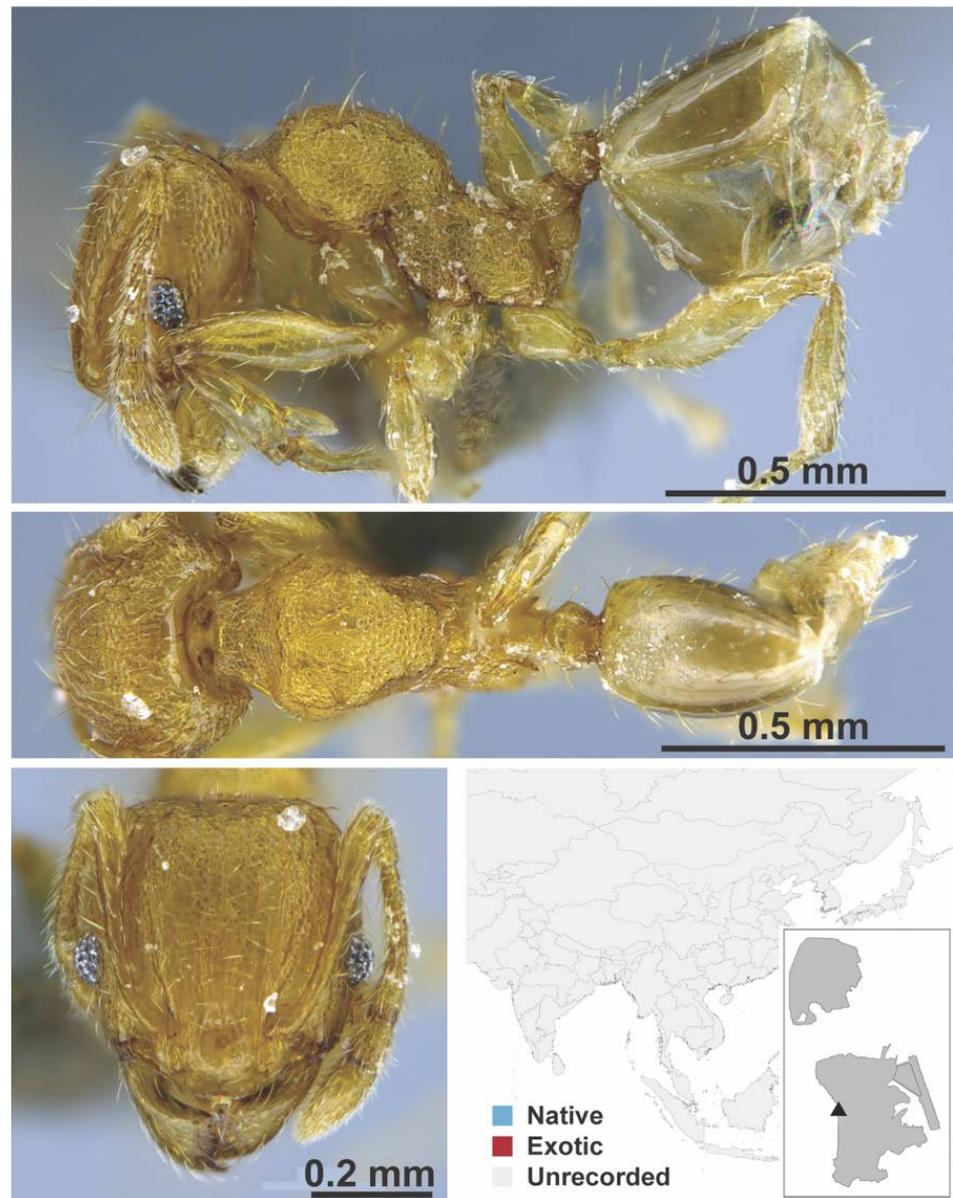


Figure A96. *Pheidole* nr. *ryukyuensis* Ogata, 1982 worker (MAC_S20_12.5_q4_sp.2, IBBL).

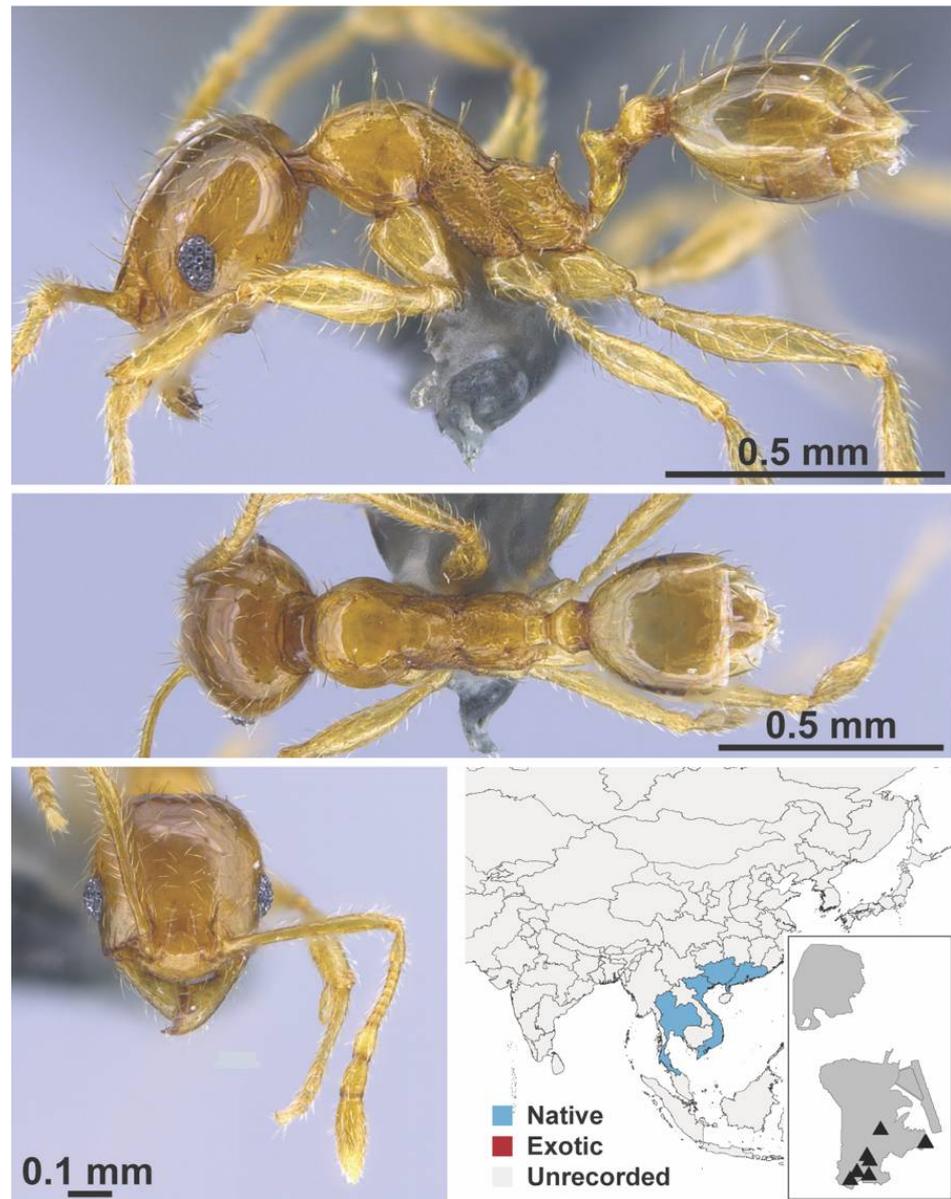


Figure A97. *Pheidole taipoana* Wheeler, 1928 worker (MAC_S04_LLSA_Sp.4, IBBL).

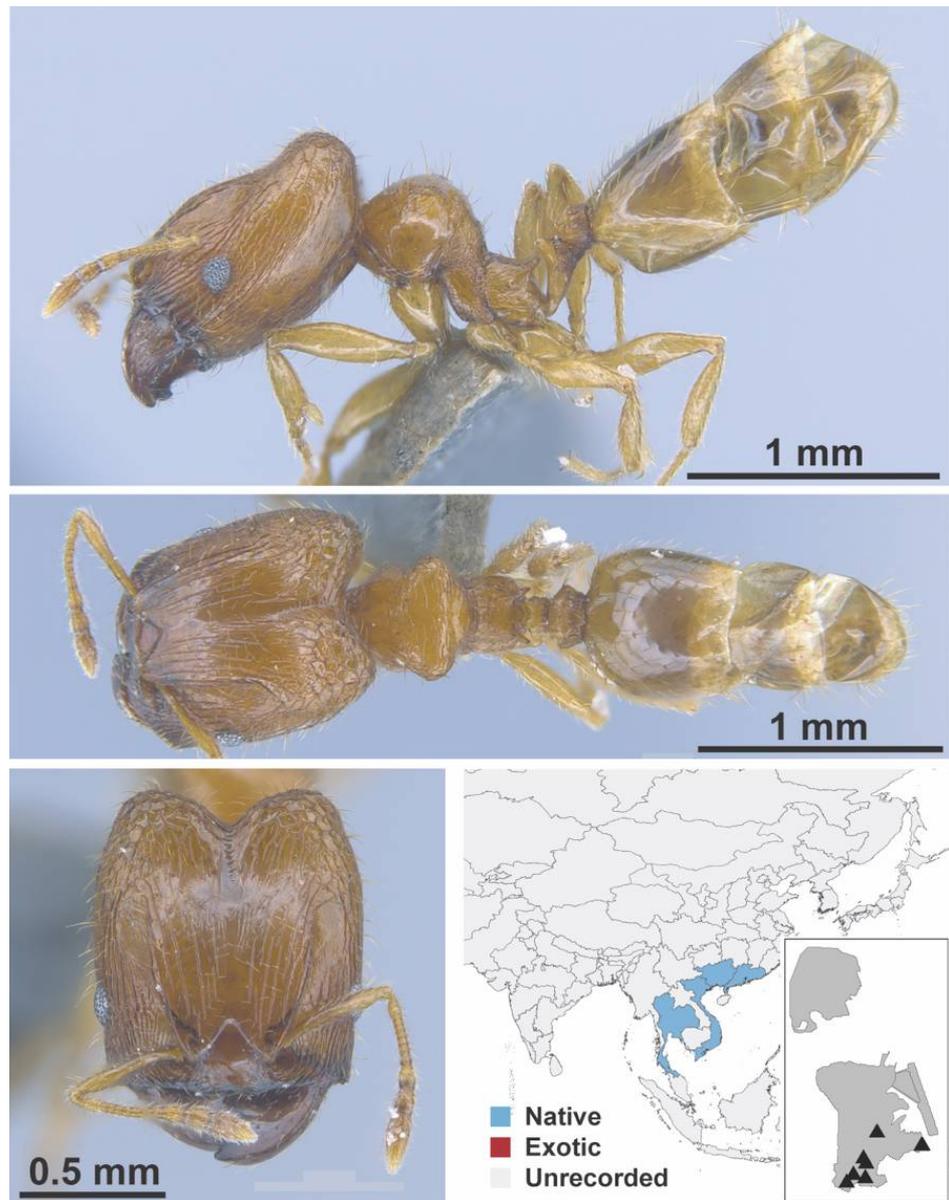


Figure A98. *Pheidole taipoana* Wheeler, 1928 major (MAC_S04_B07_sp.1_top, IBBL).

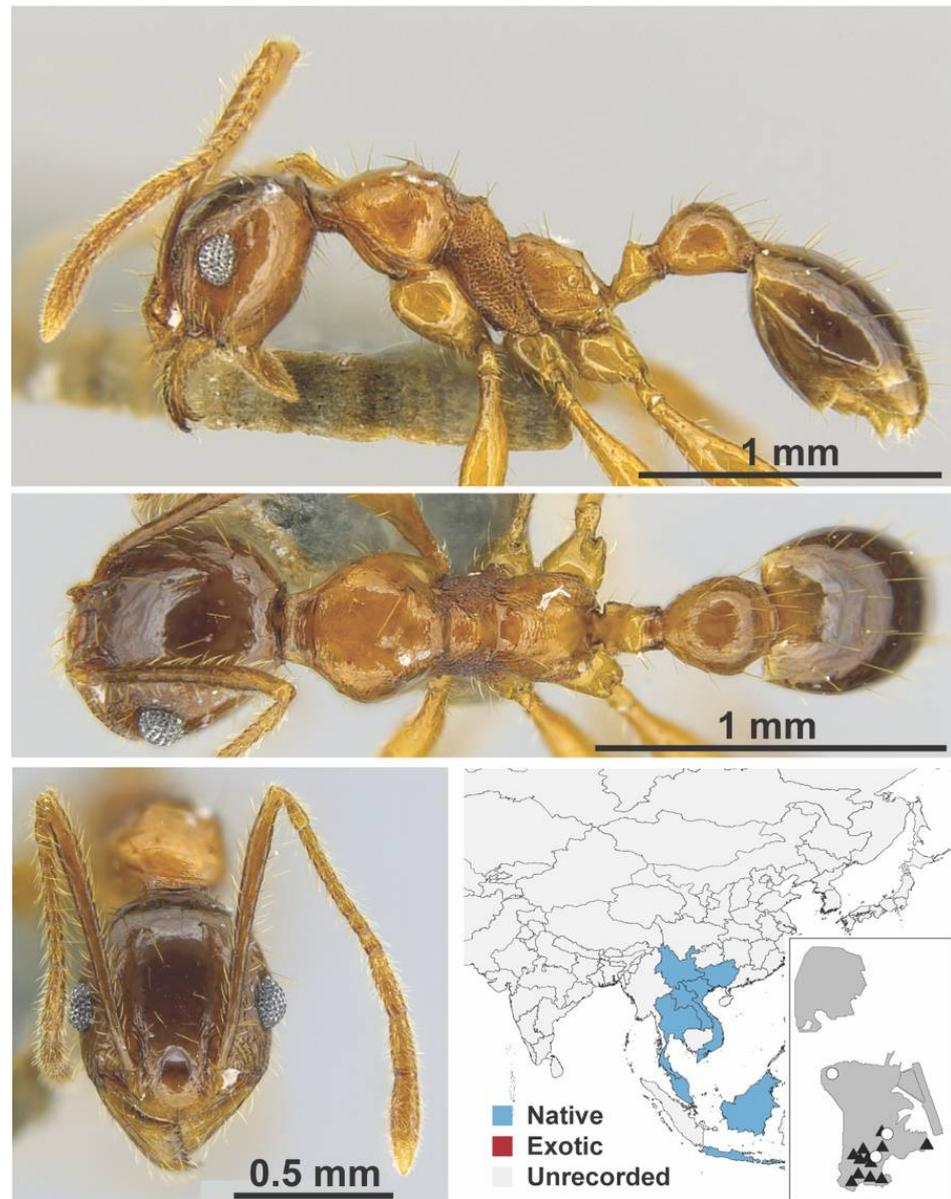


Figure A99. *Pheidole tumida* Eguchi, 2008 worker (MAC_S04_B06_sp.2_top, IBBL).

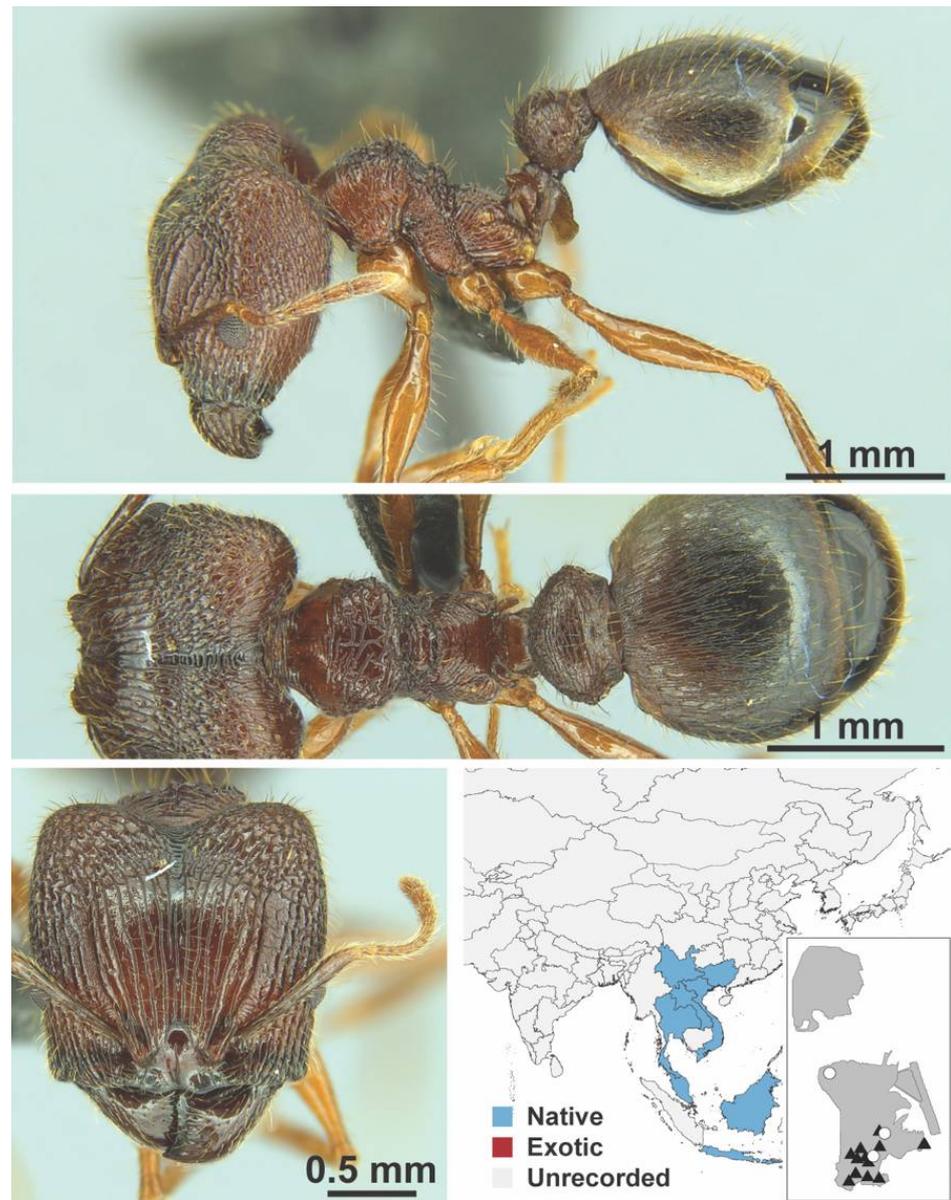


Figure A100. *Pheidole tumida* Eguchi, 2008 major (MAC_S7_GN1_H4_n1, IBBL).

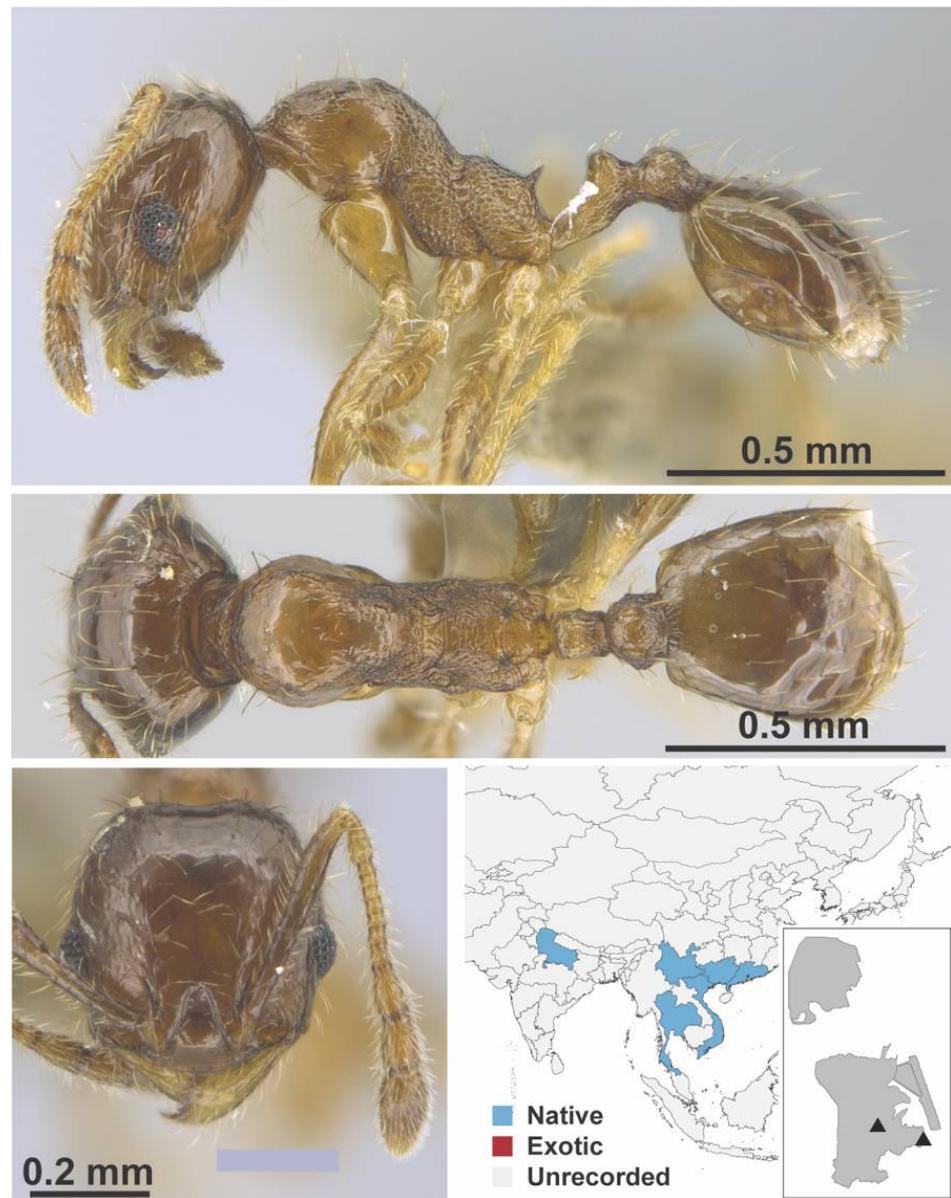


Figure A101. *Pheidole vulgaris* Eguchi, 2006 worker (MAC_S12_B04_sp.2_bottom, IBBL).

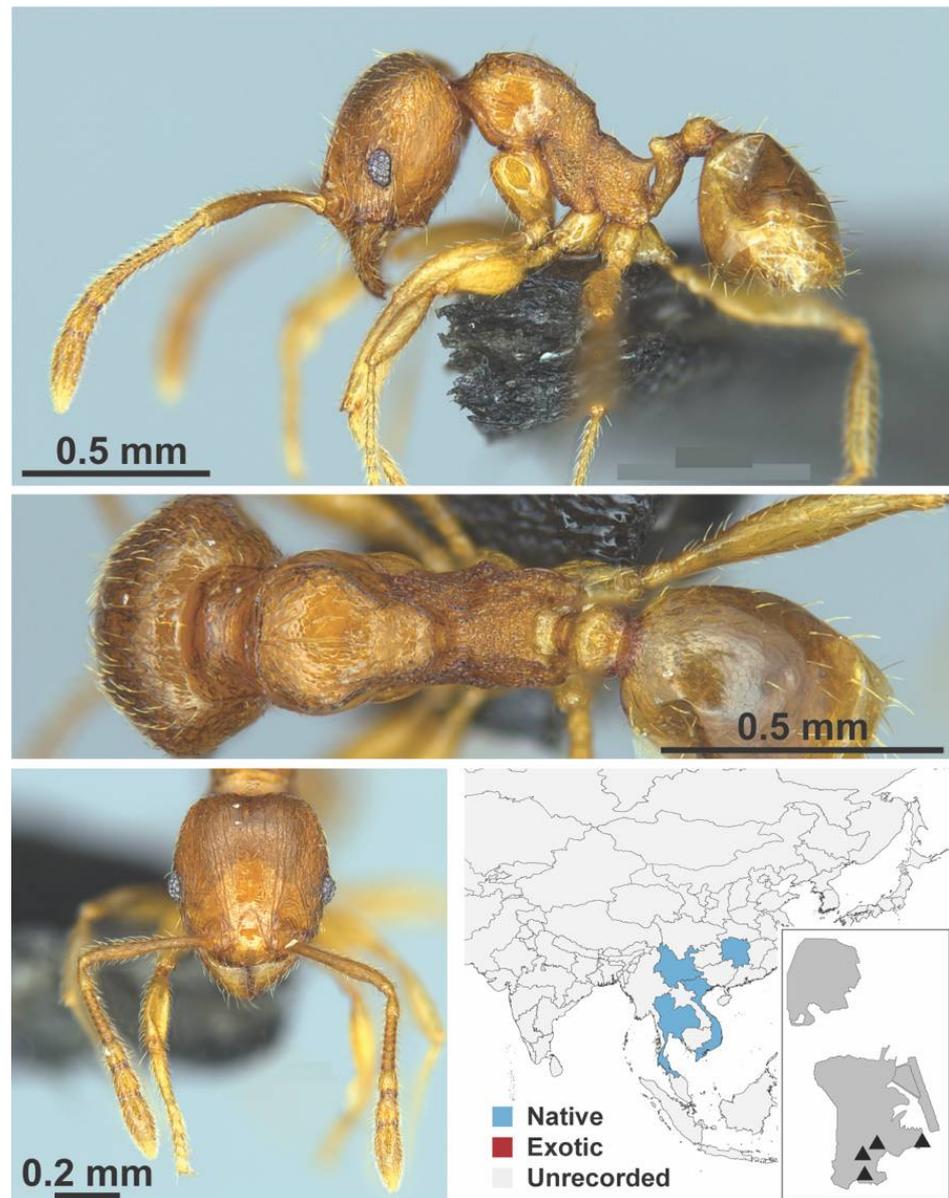


Figure A102. *Pheidole zoceana* Santschi, 1925 worker (MAC_S11_LLSA_sp.6, IBBL).

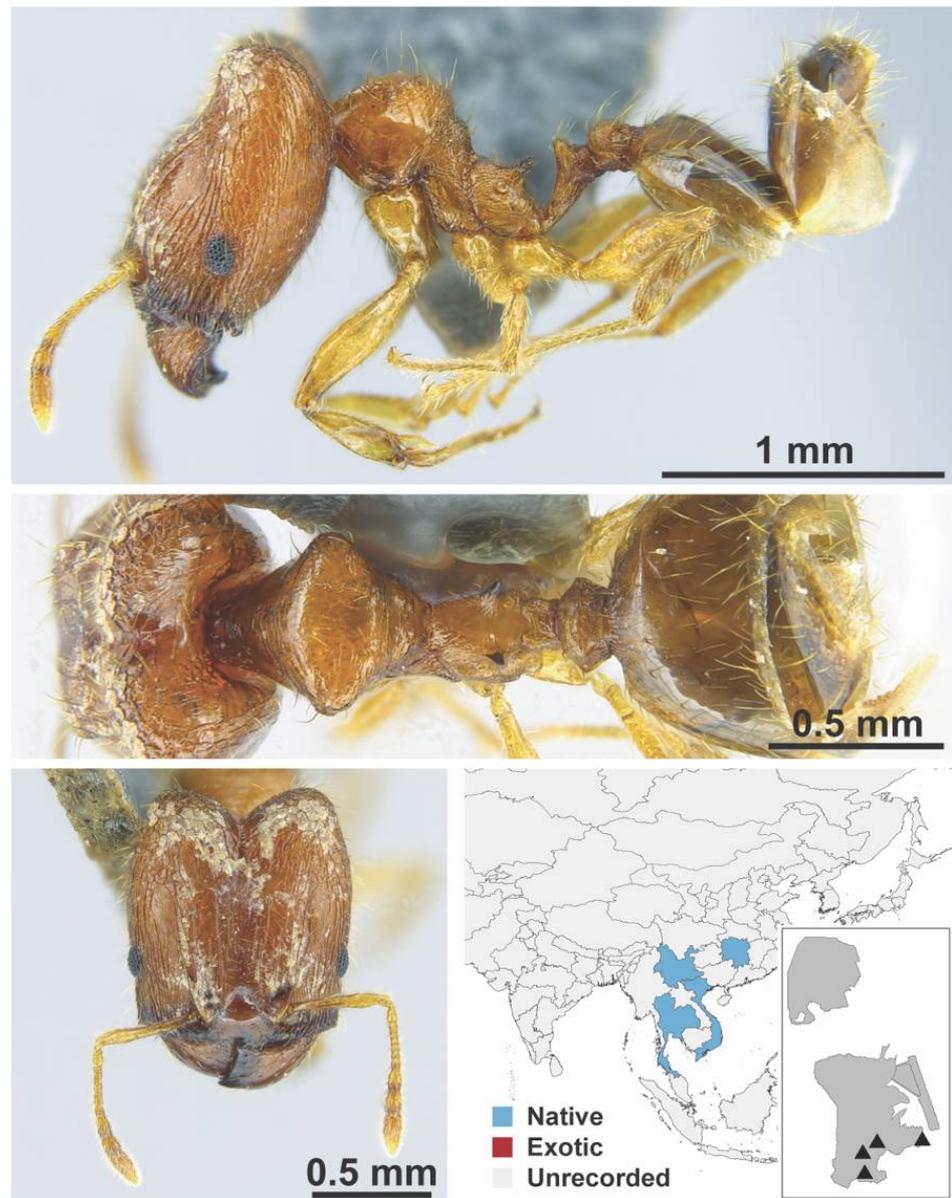


Figure A103. *Pheidole zoceana* Santschi, 1925 major (MAC_S17_LLSA_sp.1, IBBL).

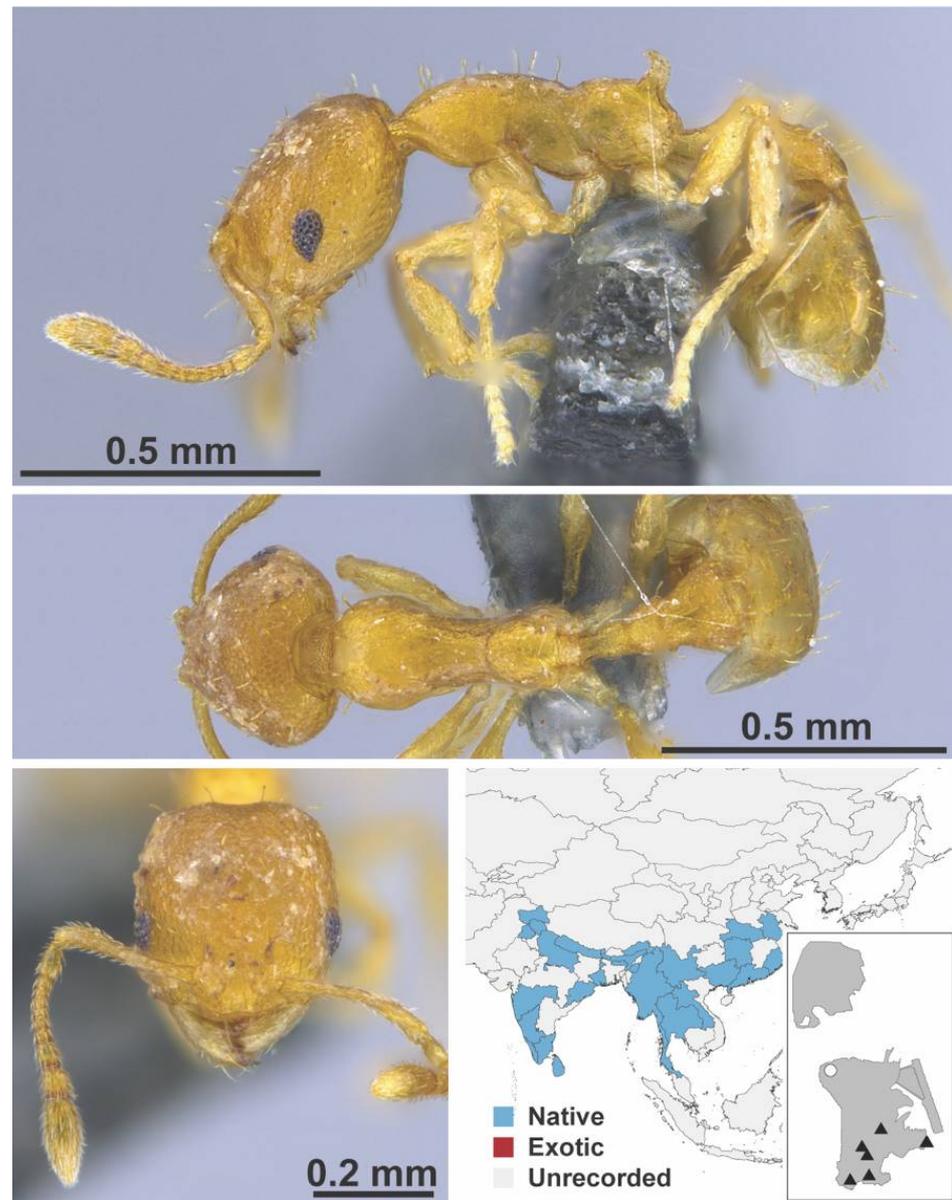


Figure A104. *Recurvidris recurvispinosa* Forel, 1890 (MAC_S12_LLSA_Sp.9, IBBL).

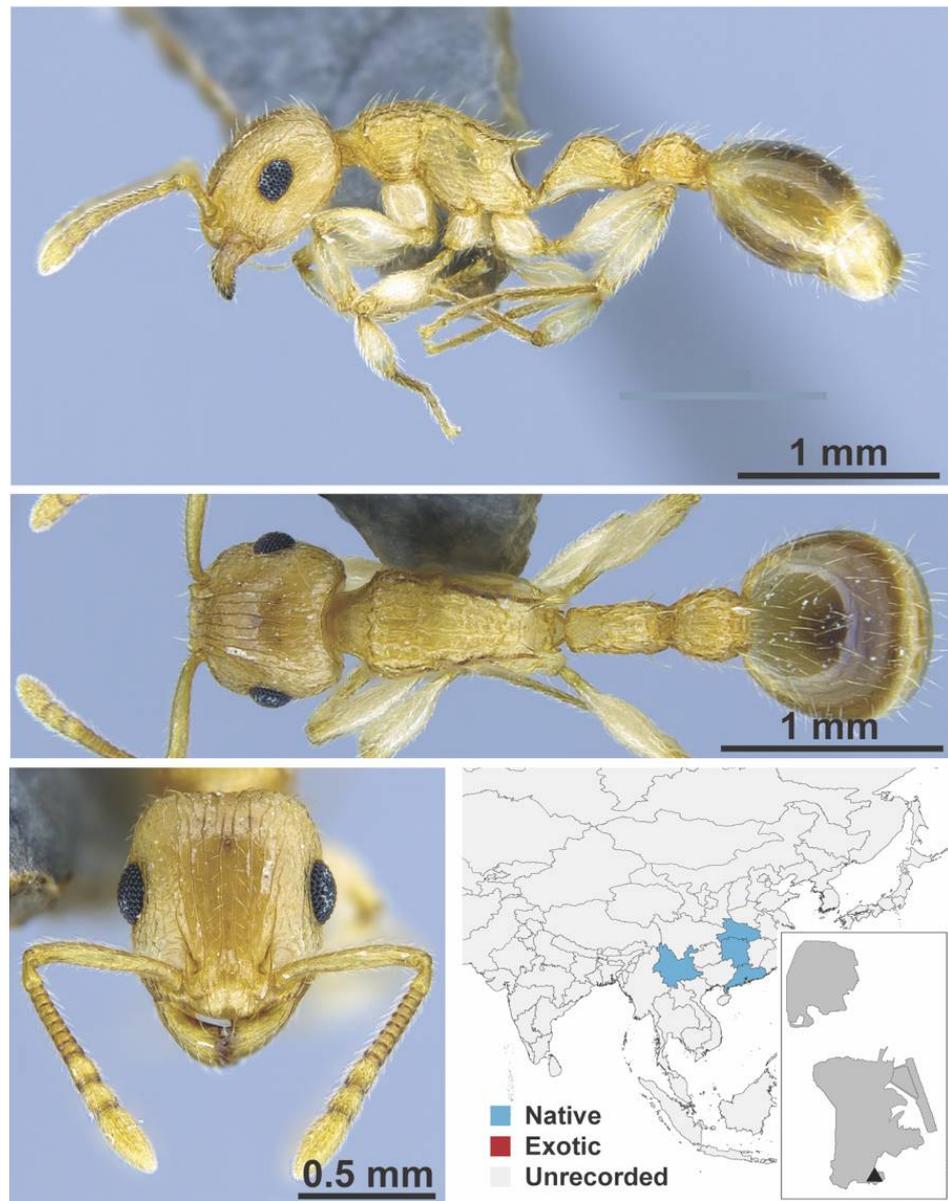


Figure A105. *Rotastruma stenoceps* Bolton, 1991 worker (MAC_S15_LLSA_sp.6, IBBL).

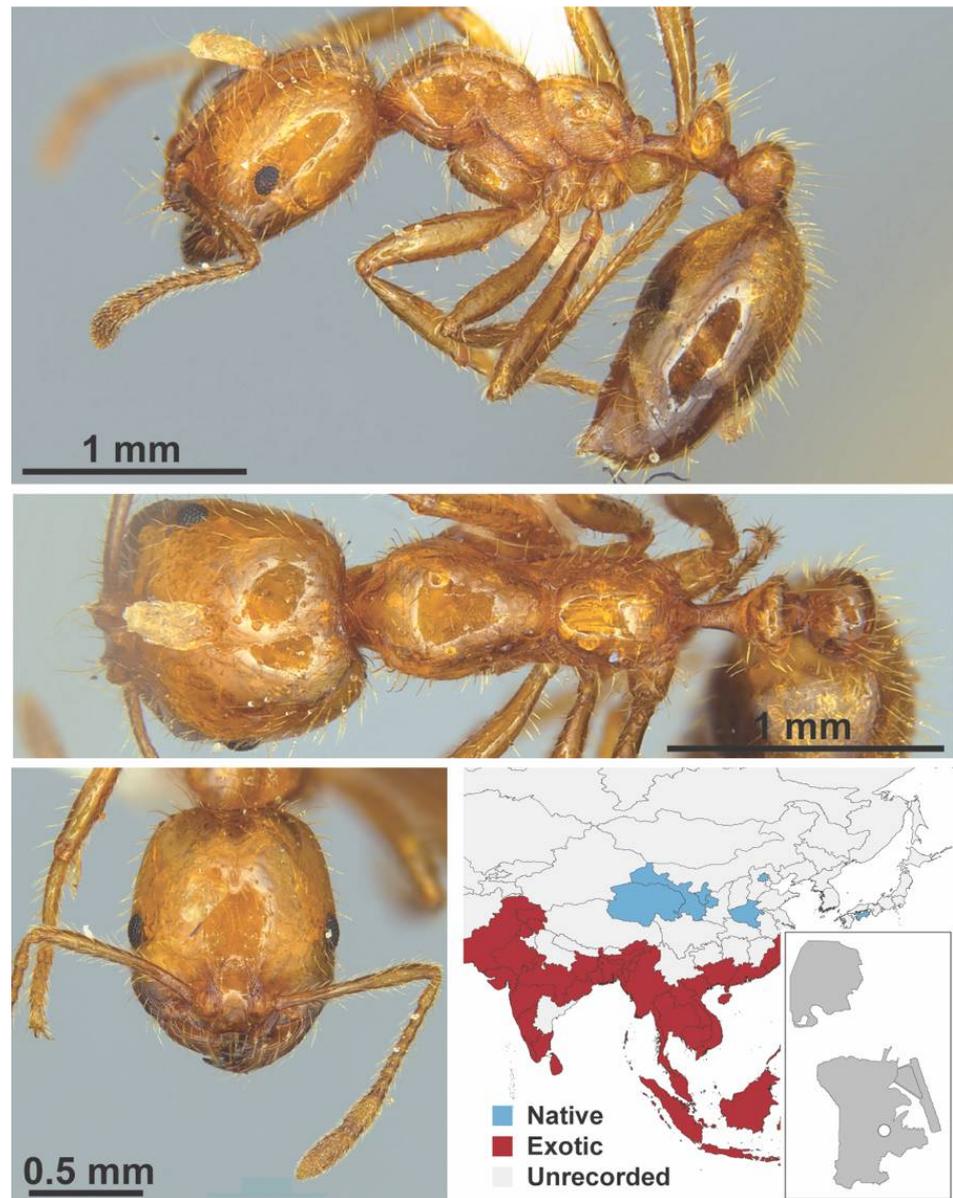


Figure A106. *Solenopsis geminata* Fabricius, 1804 worker (*Solenopsis geminata*, IBBL).

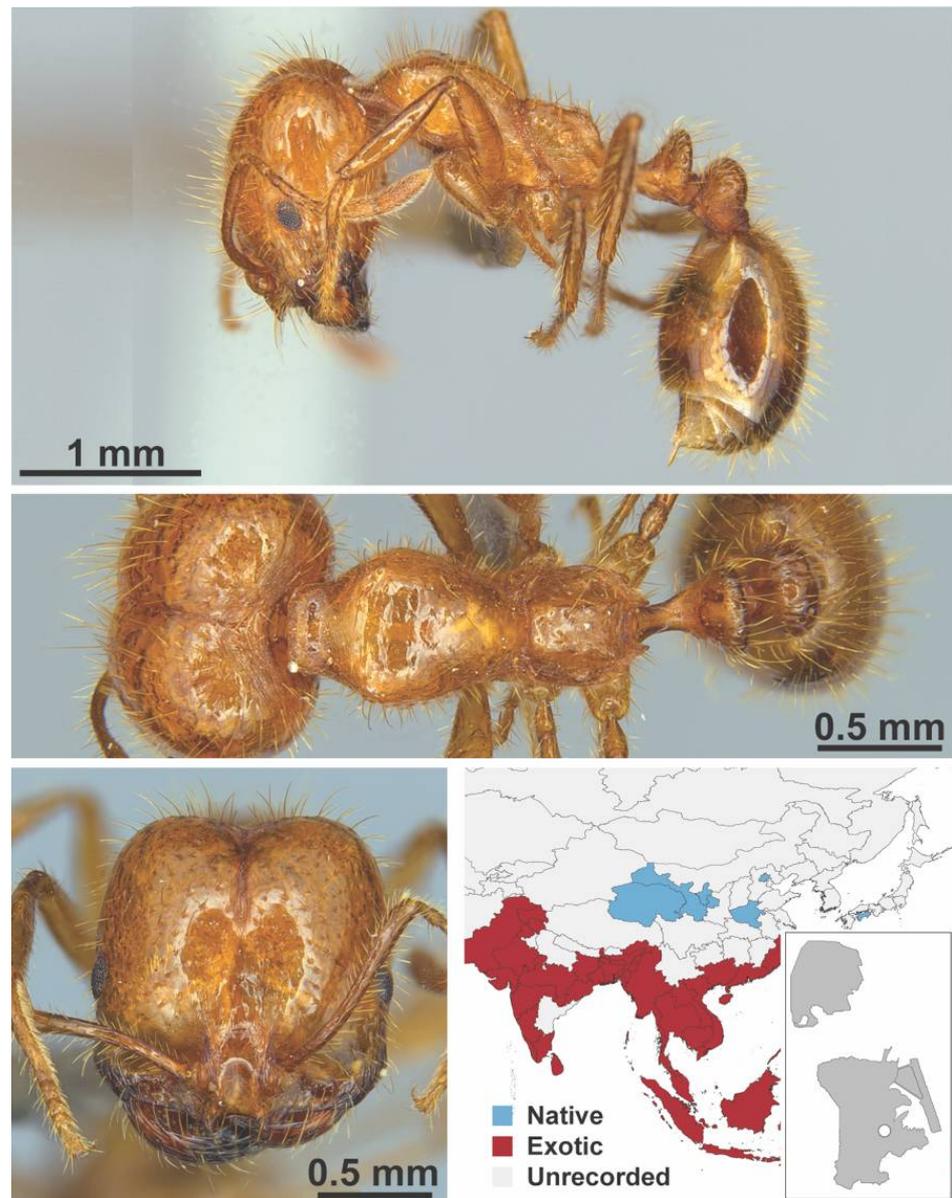


Figure A107. *Solenopsis geminata* Fabricius, 1804 major (*Solenopsis geminata*, IBBL).

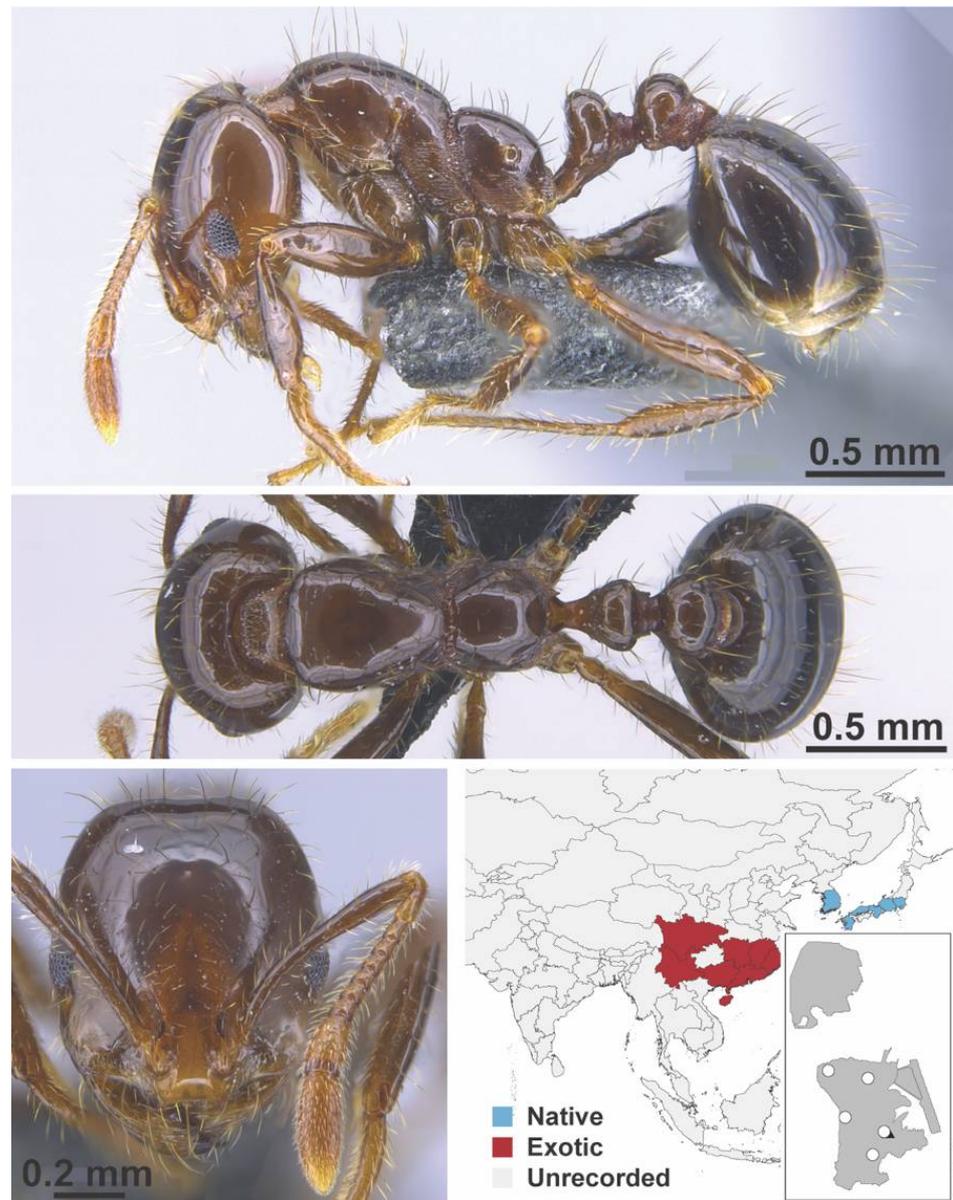


Figure A108. *Solenopsis invicta* Buren, 1972 worker (MAC_S09_LLSP_Sp.5, IBBL).

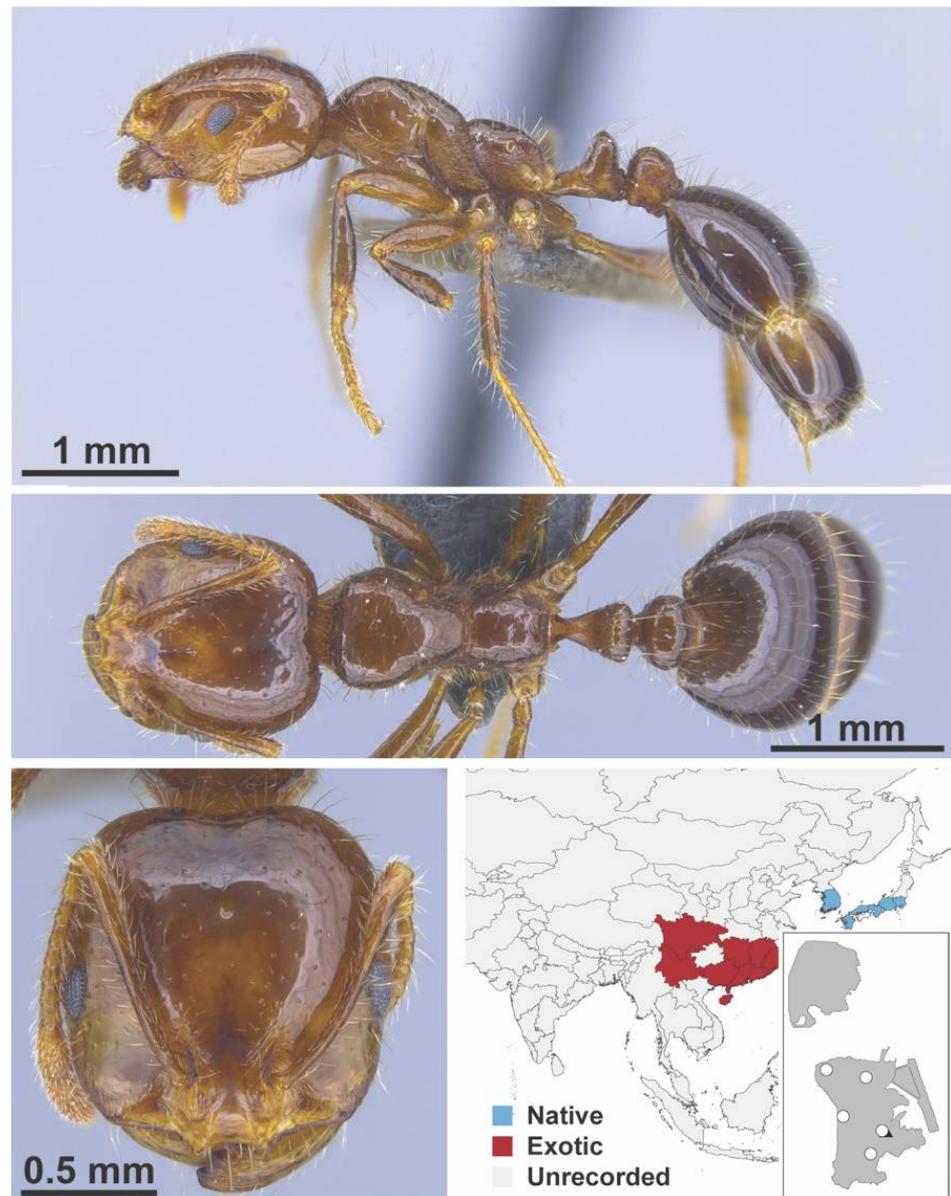


Figure A109. *Solenopsis invicta* Buren, 1972 major (MAC_S09_B05_sp.1_bottom, IBBL).

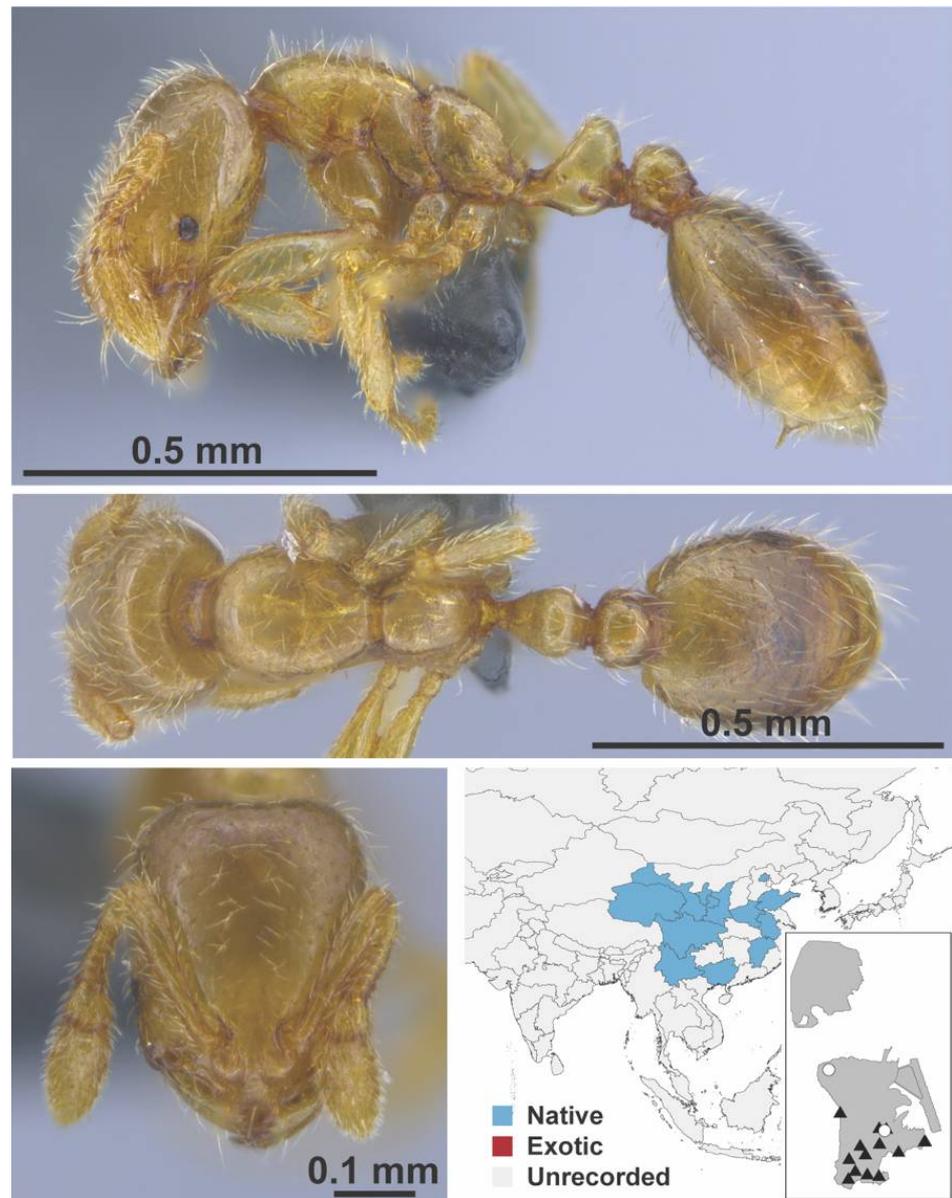


Figure A110. *Solenopsis jacoti* Wheeler, 1923 worker (MAC_S12_q3_37.5_sp.2_top, IBBL).

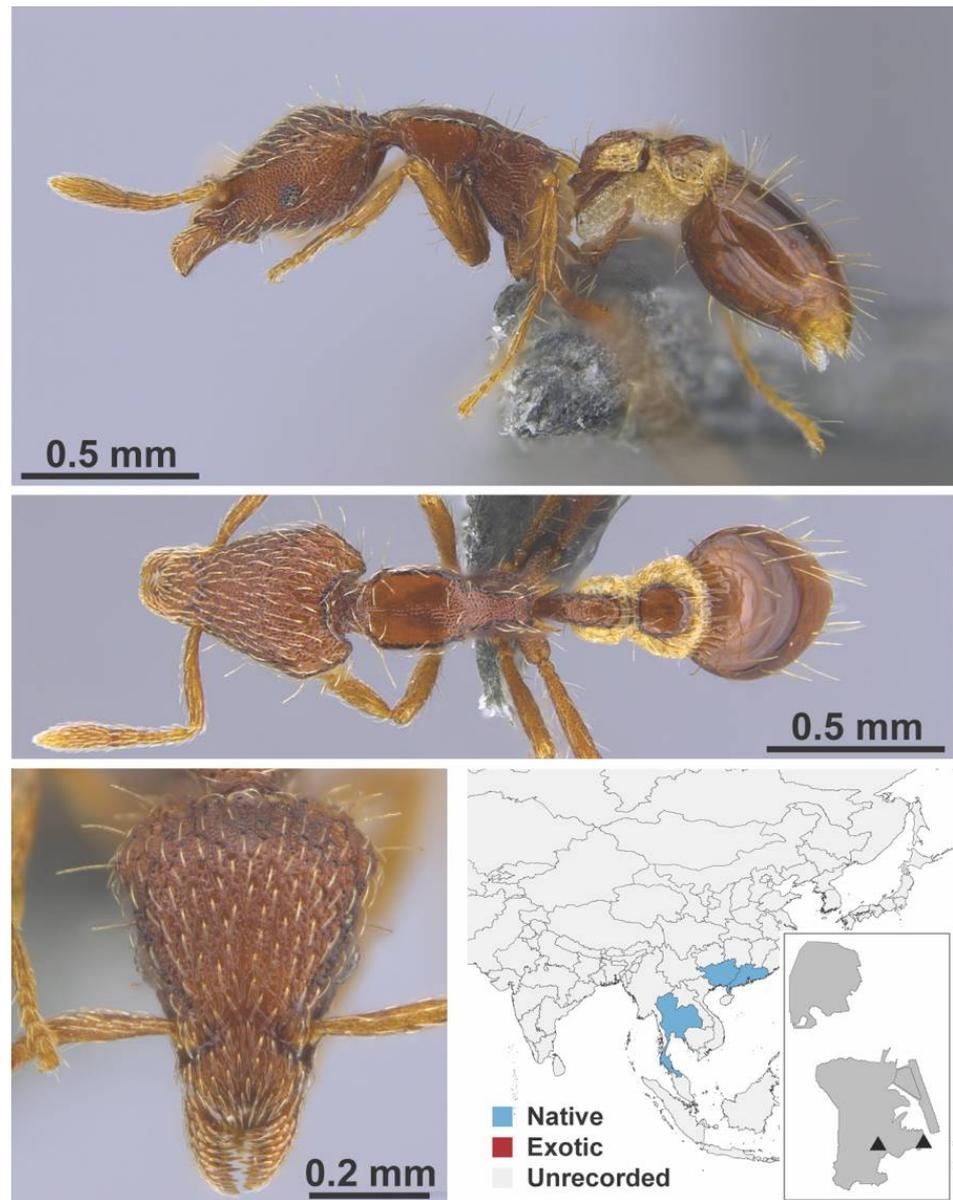


Figure A111. *Strumigenys elegantula* Terayama & Kubota, 1989 worker (MAC_S04_LLSP_sp.9, IBBL).

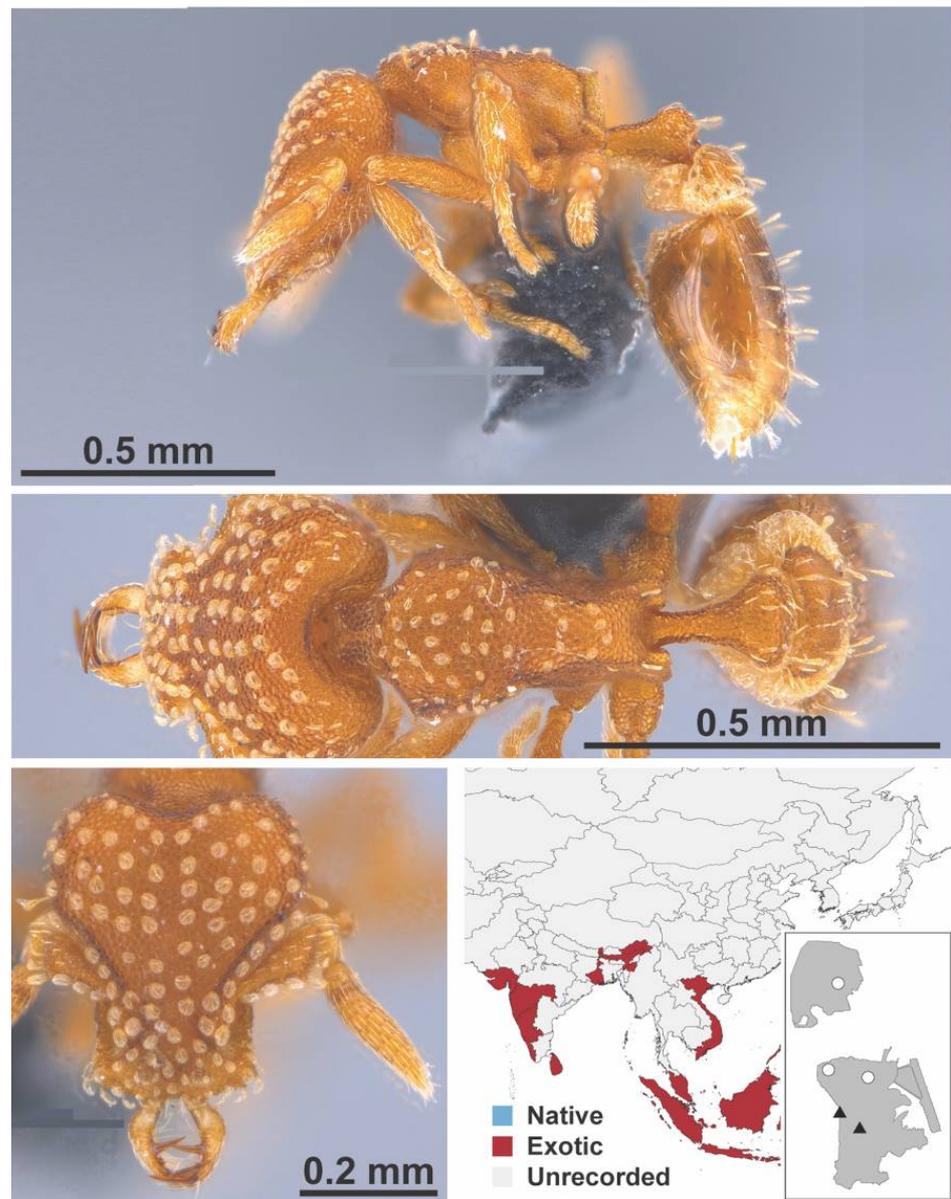


Figure A112. *Strumigenys emmae* Emery, 1890 worker (MAC_S20_LLSP_Sp.7, IBBL).

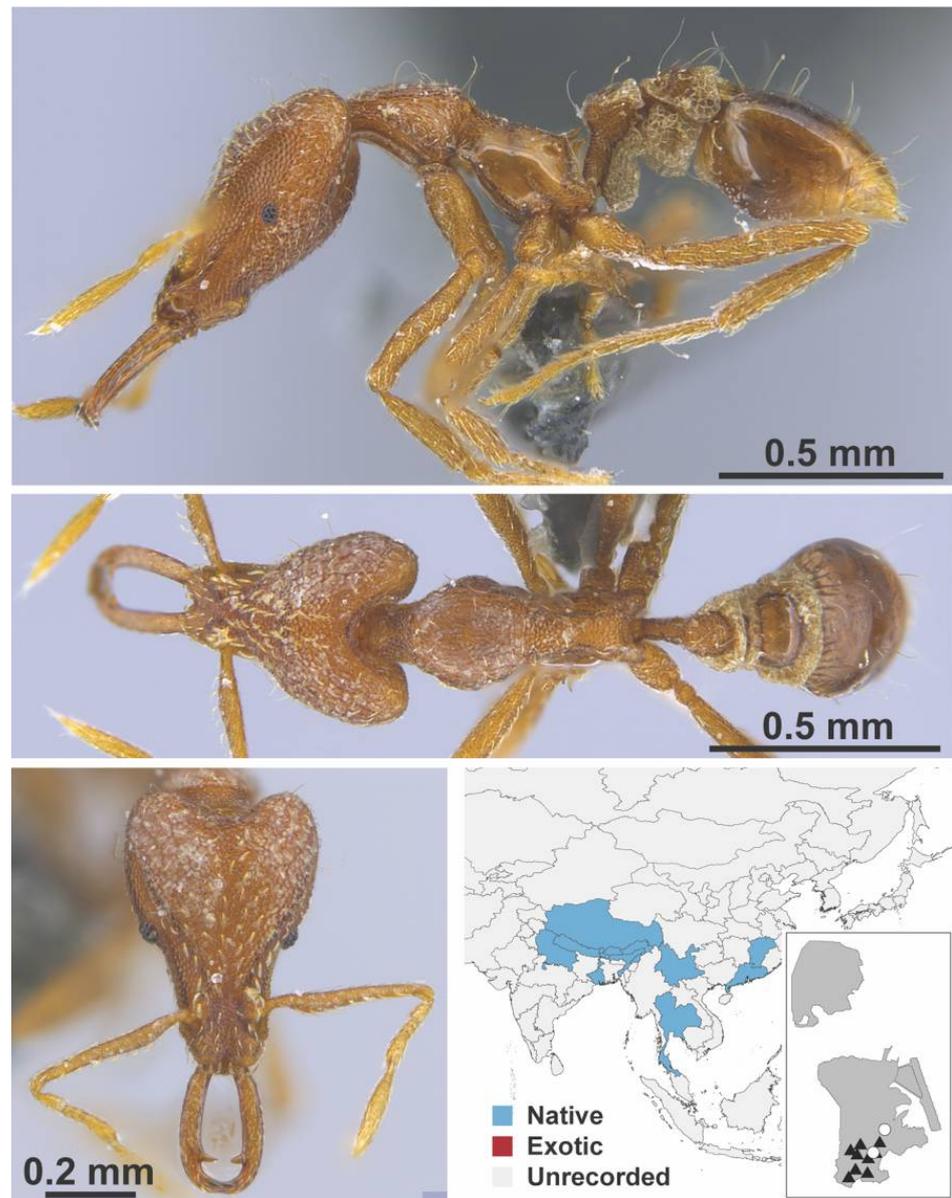


Figure A113. *Strumigenys exilirhina* Bolton, 2000 worker (MAC_S01_LLSA_Sp.3, IBBL).

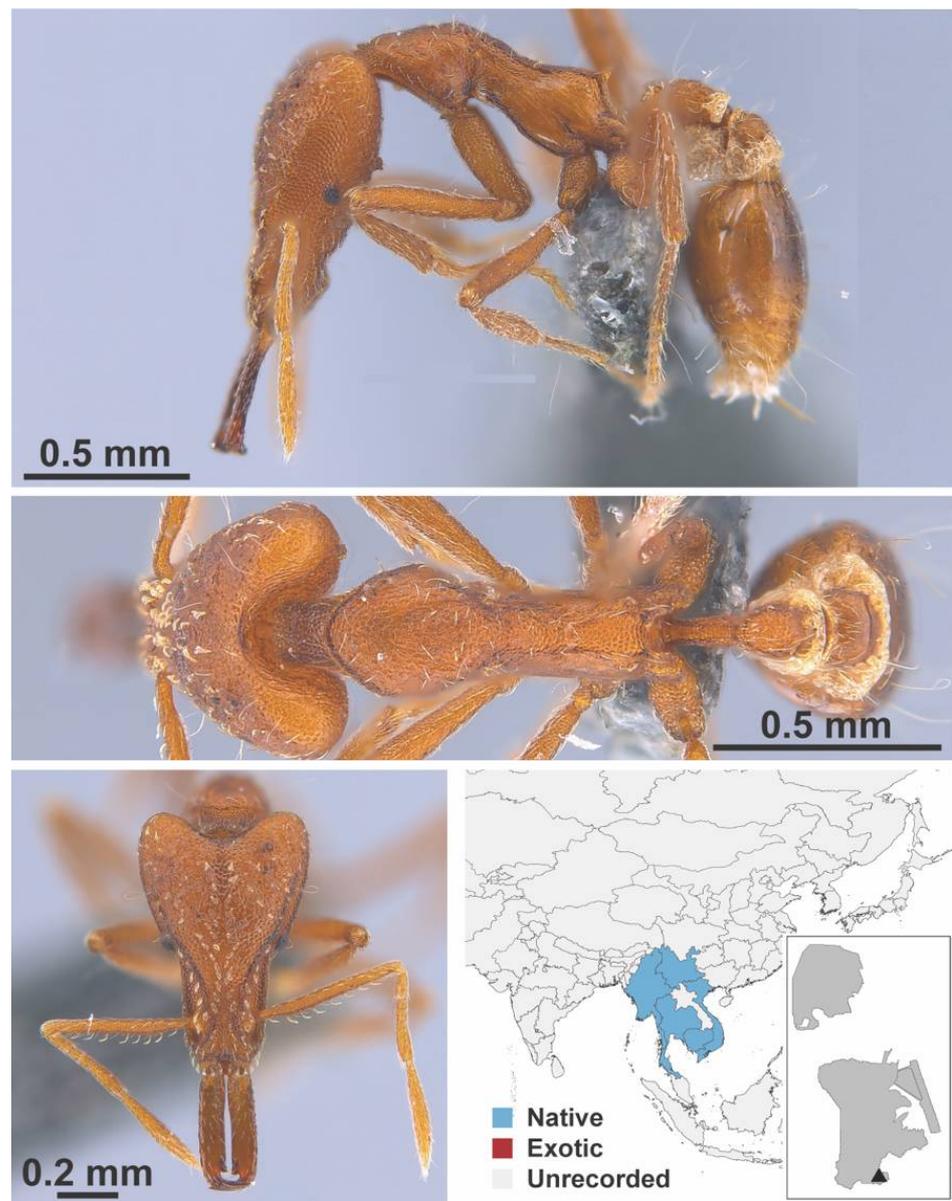


Figure A114. *Strumigenys feae* Emery, 1895 worker (MAC_S15_LLSP_Sp.8, IBBL).

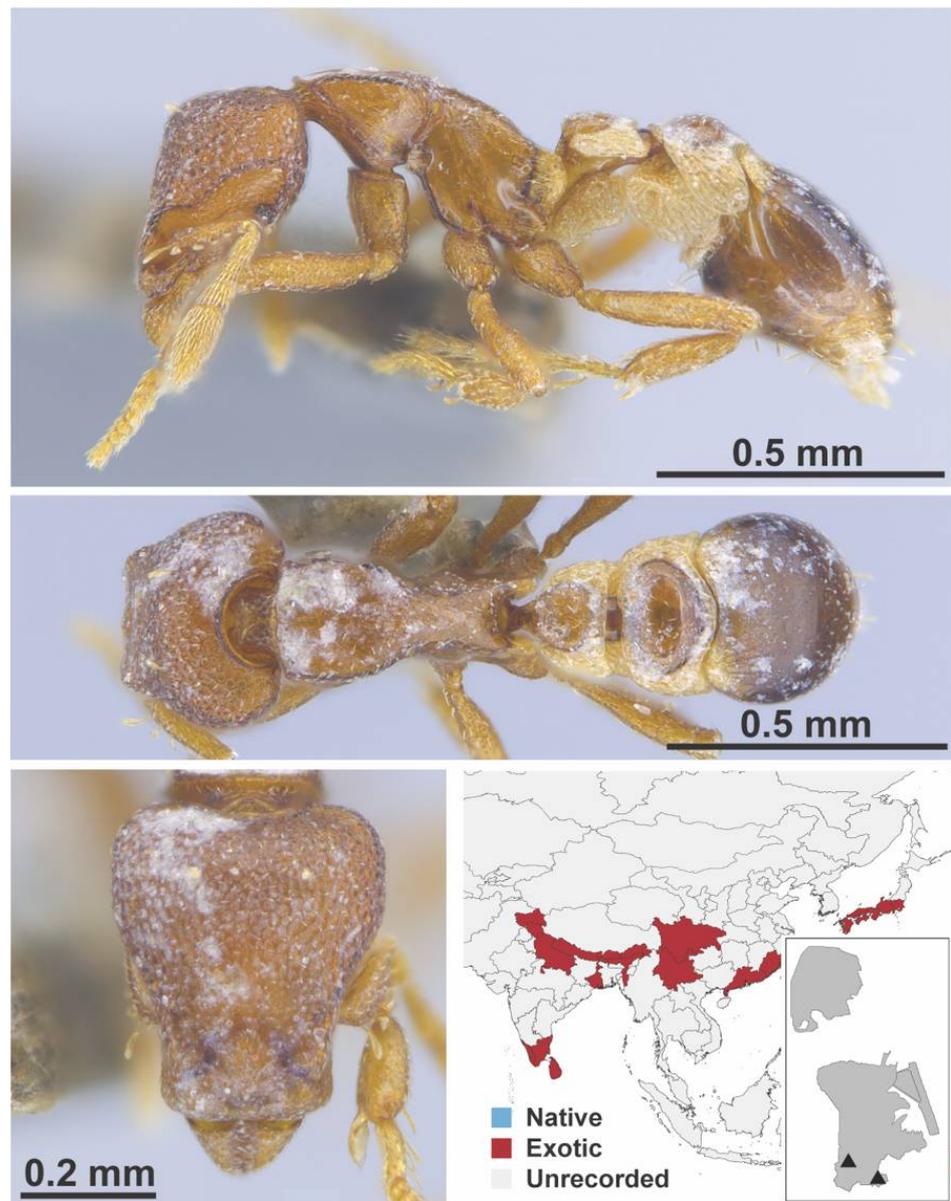


Figure A115. *Strumigenys membranifera* Emery, 1869 worker (MAC_S15_GN3_H3_n1_top, IBBL).

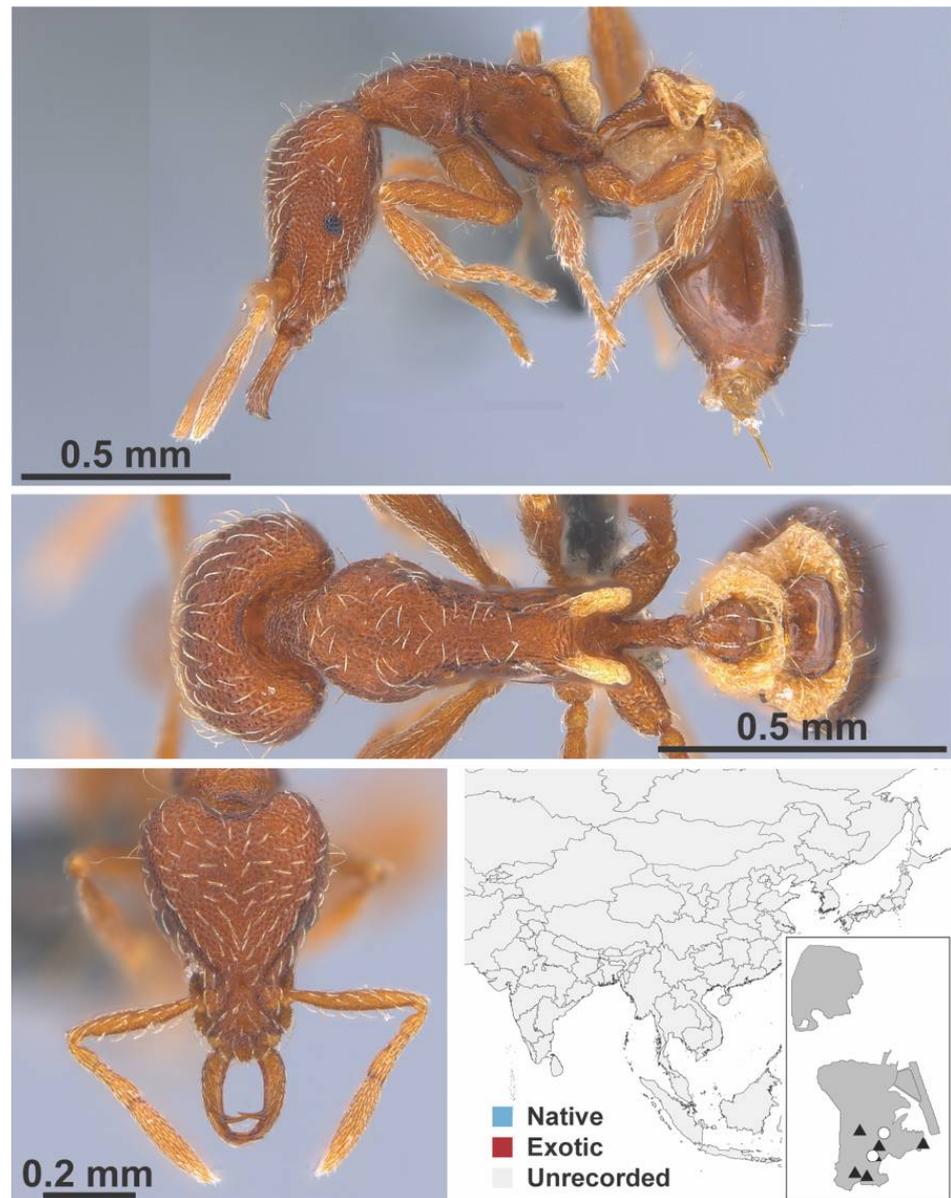


Figure A116. *Strumigenys minutula* Terayama & Kubota, 1989 worker (MAC_S14_LLSP_Sp.4, IBBL).

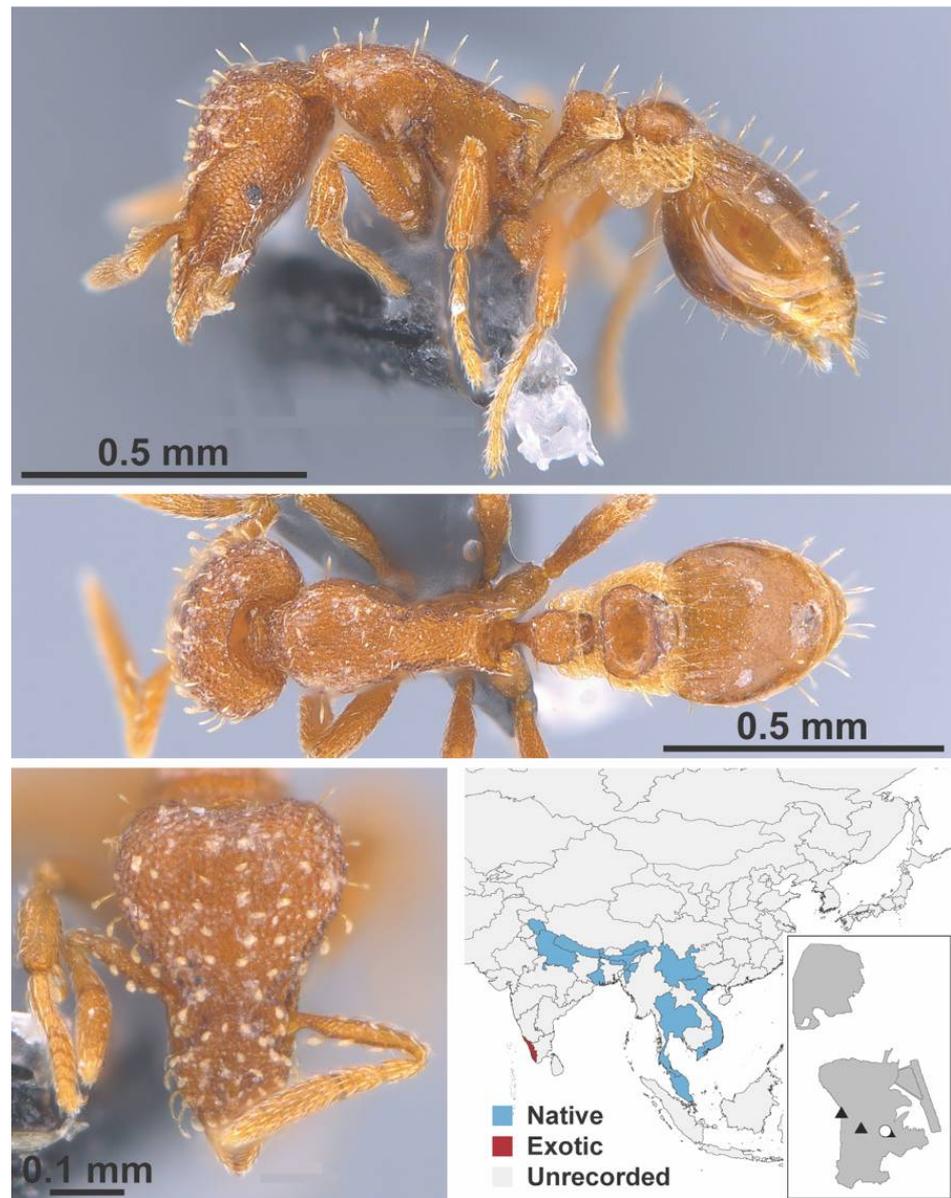


Figure A117. *Strumigenys nepalensis* Baroni Urbani & De Andrade, 1994 worker (MAC_S19_LLSP_Sp.3, IBBL).

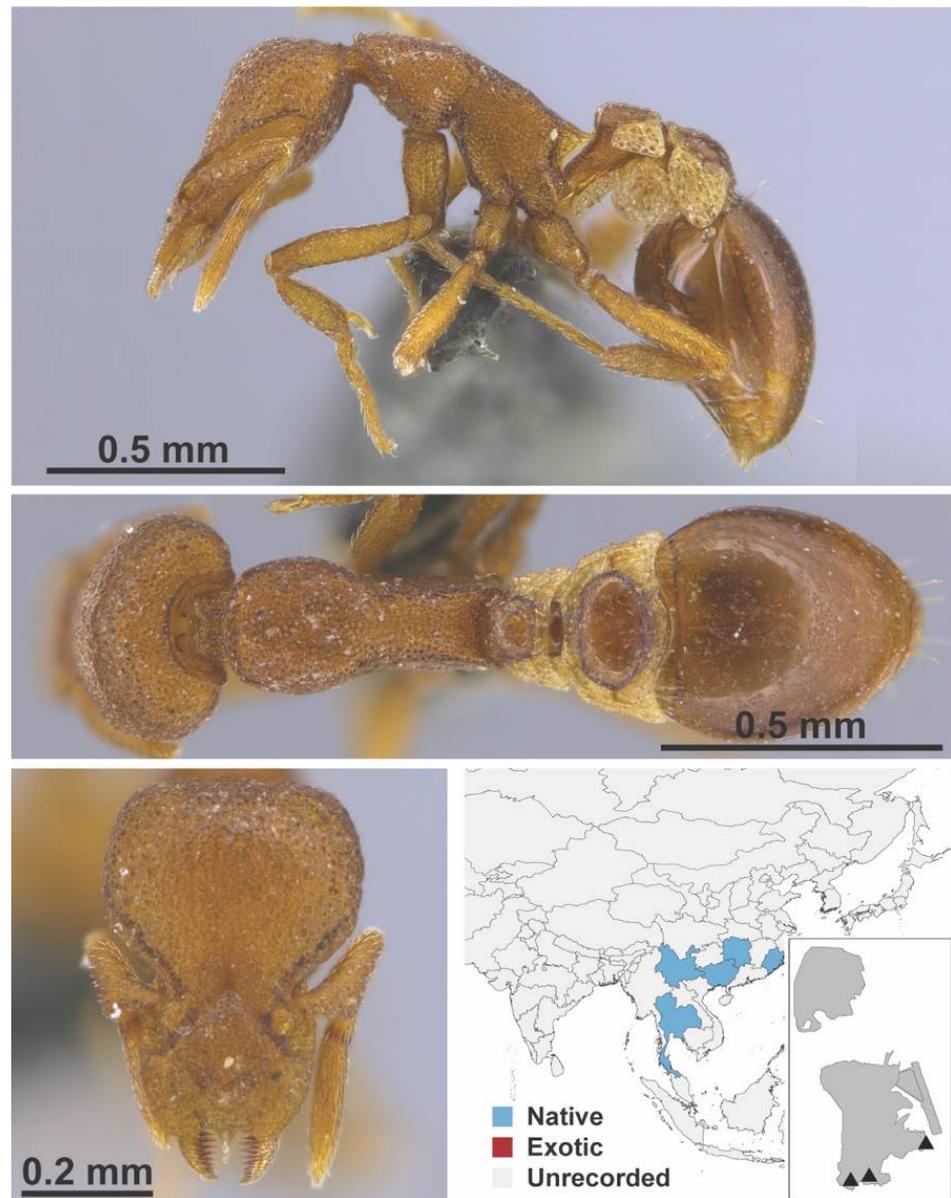


Figure A118. *Strumigenys sauteri* Forel, 1912 worker (MAC_S04_LLSP_sp.2, IBBL).

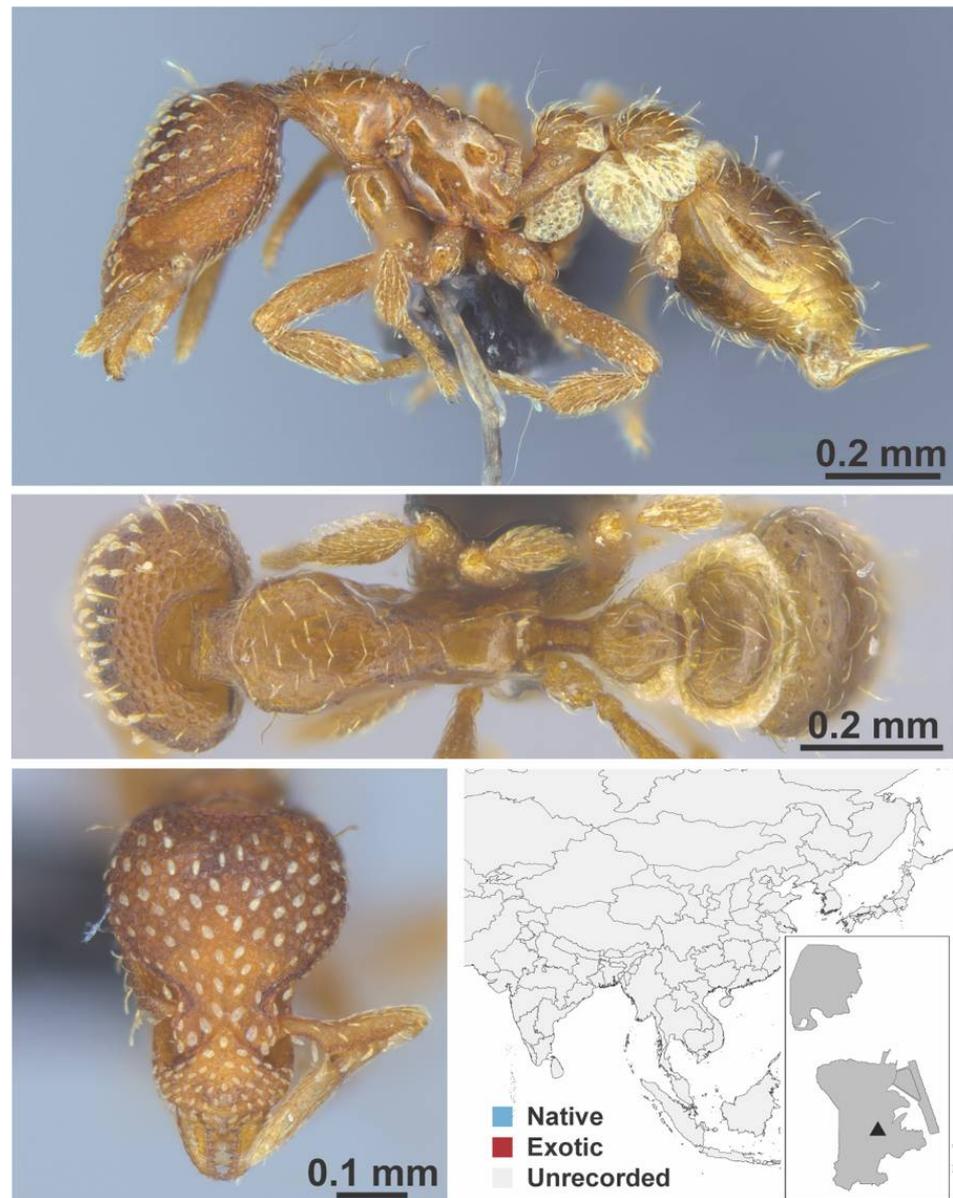


Figure A119. *Strumigenys subterranea* Brassard, Leong & Guénard, 2020 worker (MAC_S12_q4_12.5_sp.2, IBBL).

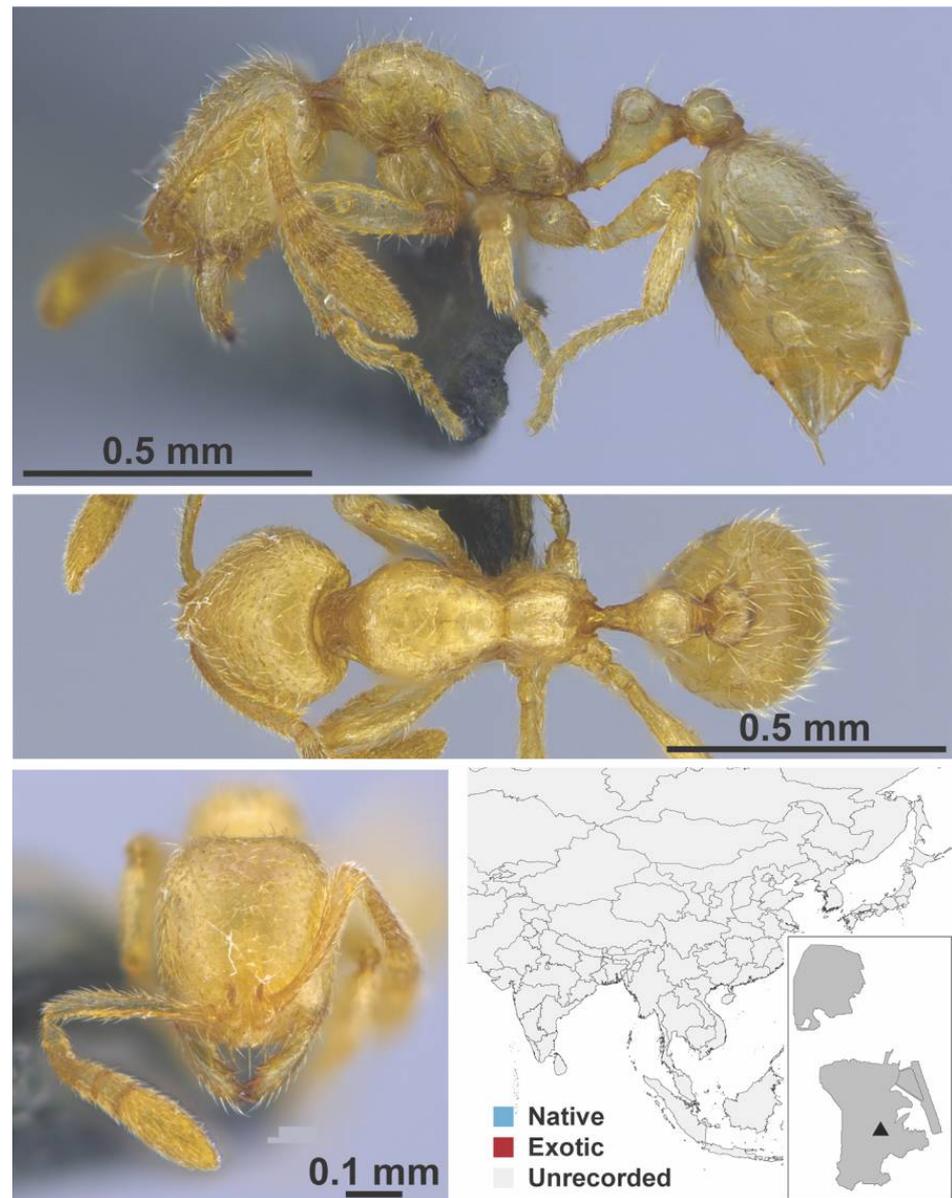


Figure A120. *Sylophopsis* nr. *cryptobia* worker (MAC_S12_q3_37.5_sp.3, IBBL).

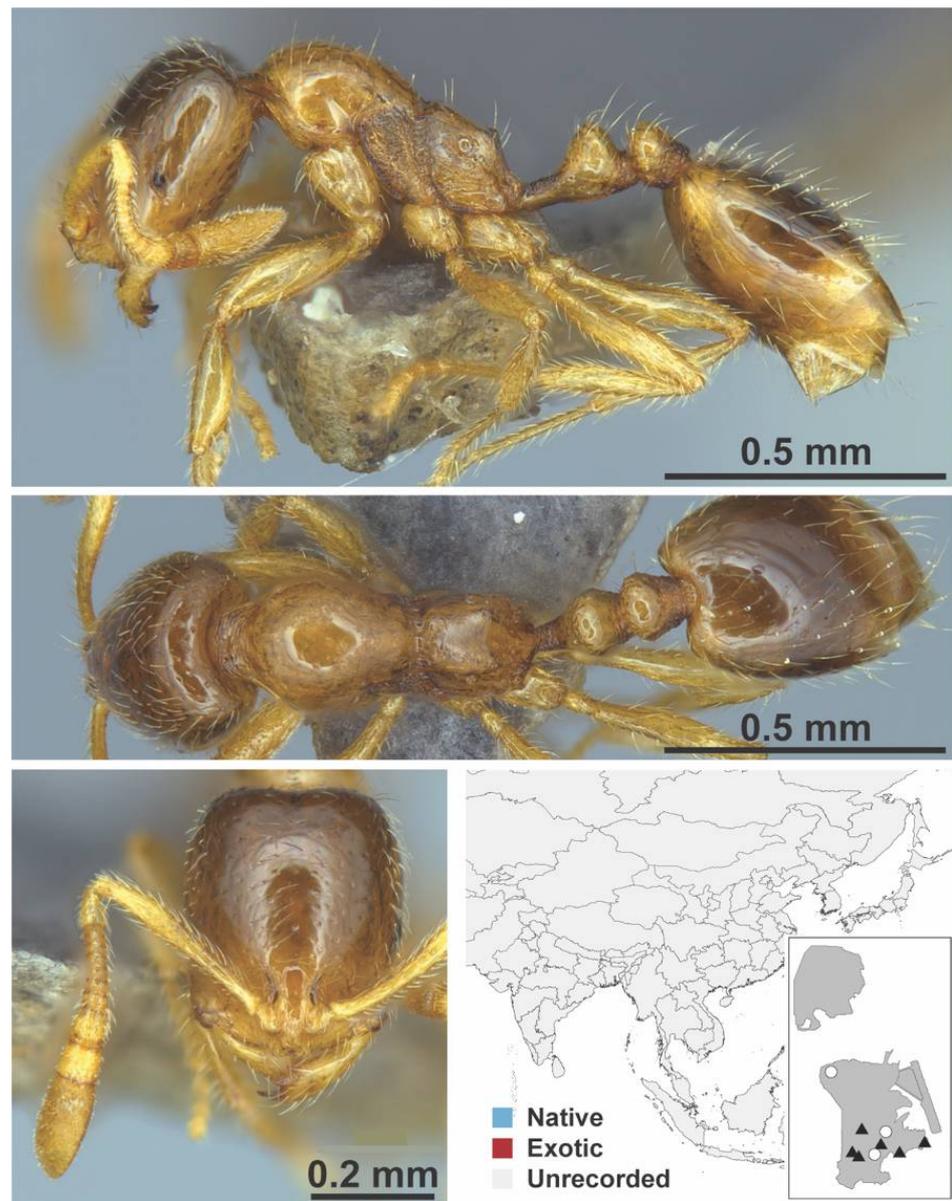


Figure A121. *Sylophopsis* sp. mo01 nr. *sechellensis* Emery, 1894 worker (*Sylophopsis* sp. mo01 nr. *Sechellensis*, CML collection).

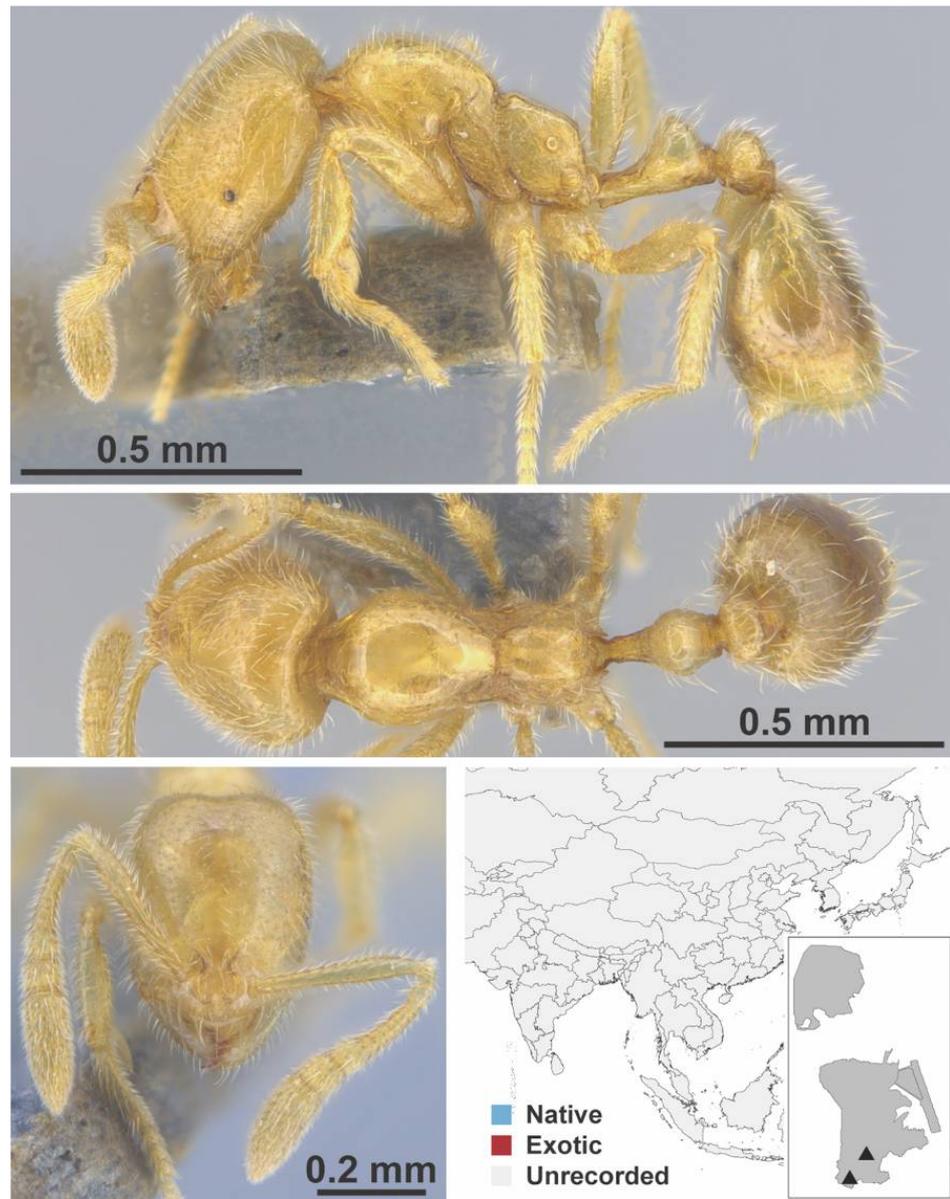


Figure A122. *Sylophopsis* sp. 1 FB worker (MAC_S18_q3_12.5_sp.4, IBBL).

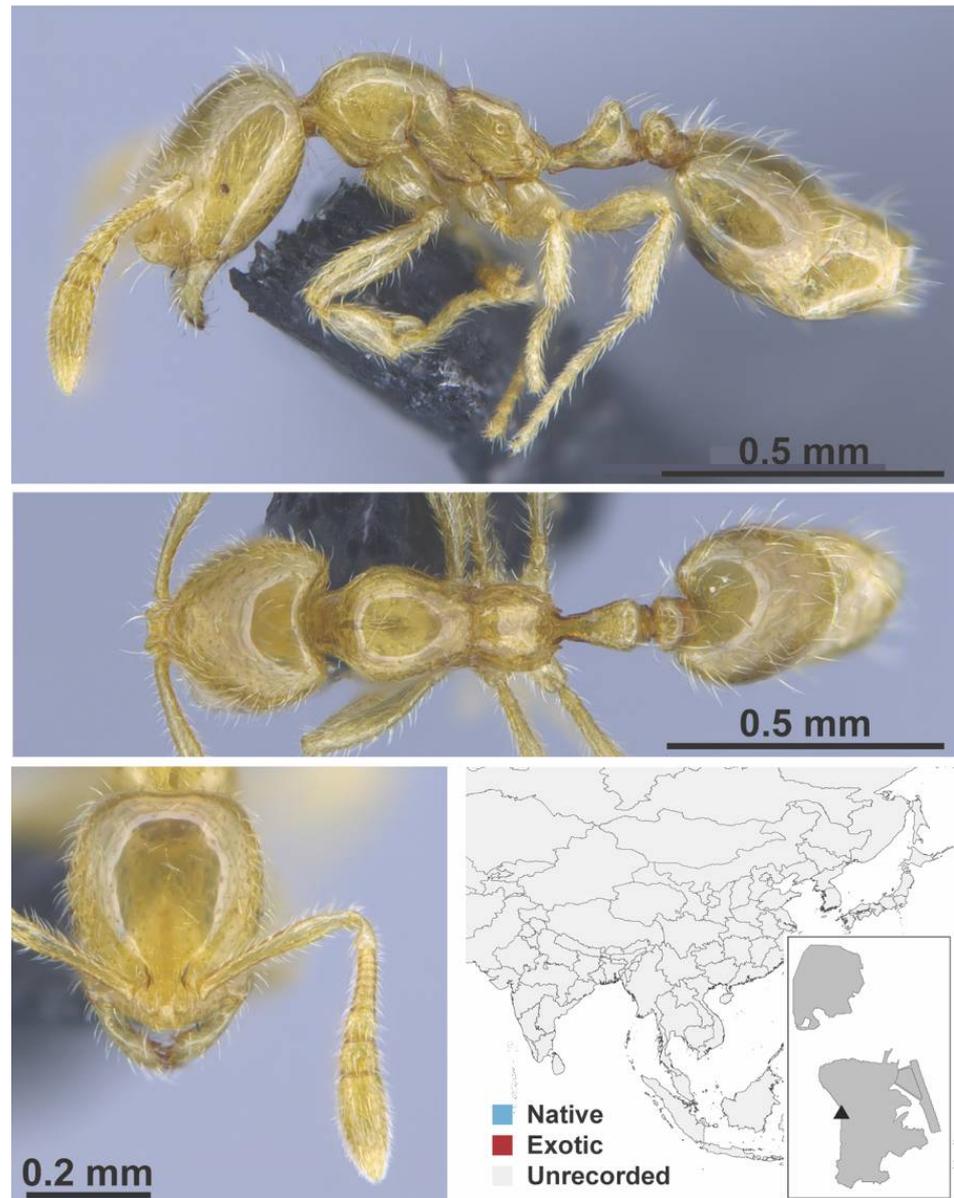


Figure A123. *Sylophopsis* sp. 2 FB worker (MAC_S20_LLSP_sp.10_top, IBBL).

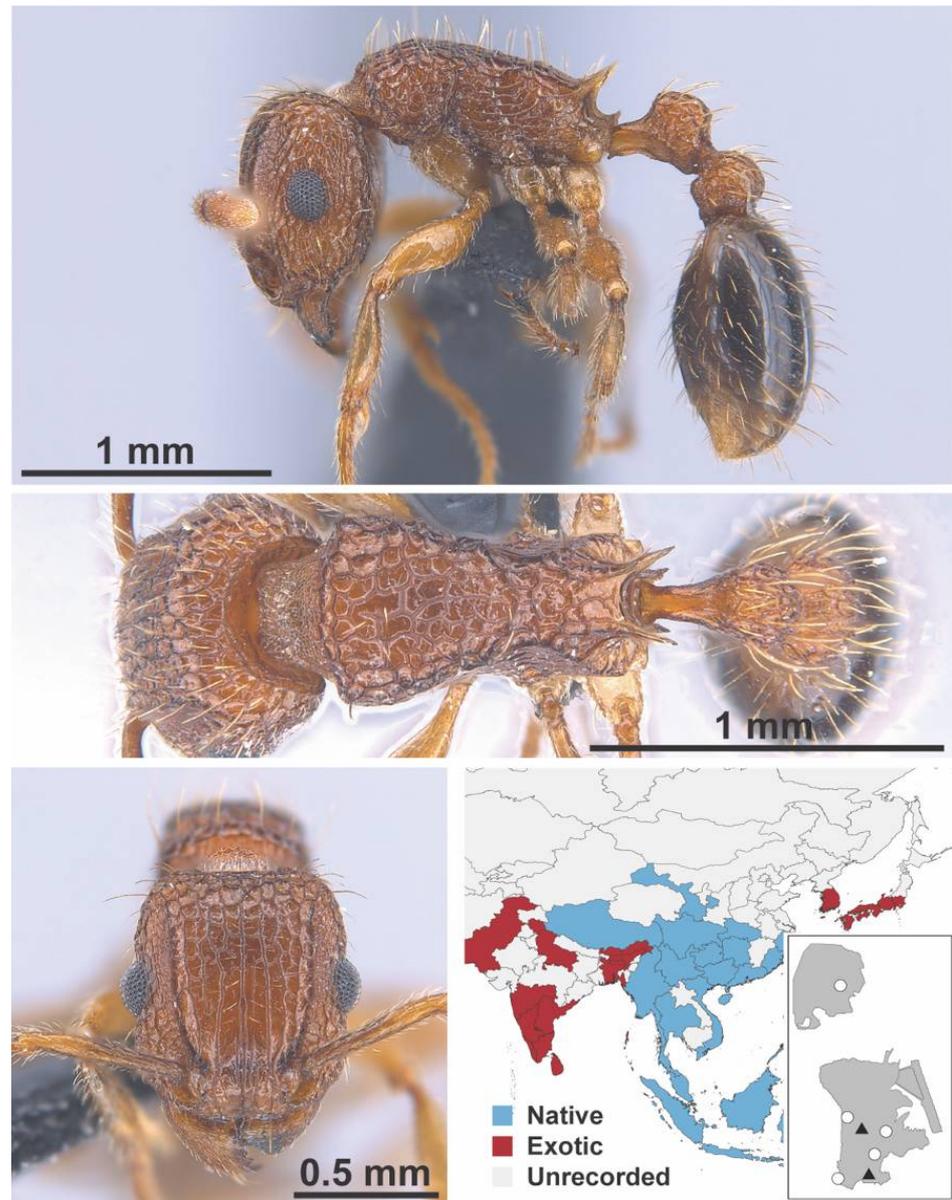


Figure A124. *Tetramorium bicarinatum* Nylander, 1846 worker (MAC_S19_LLSP_Sp.9, IBBL).

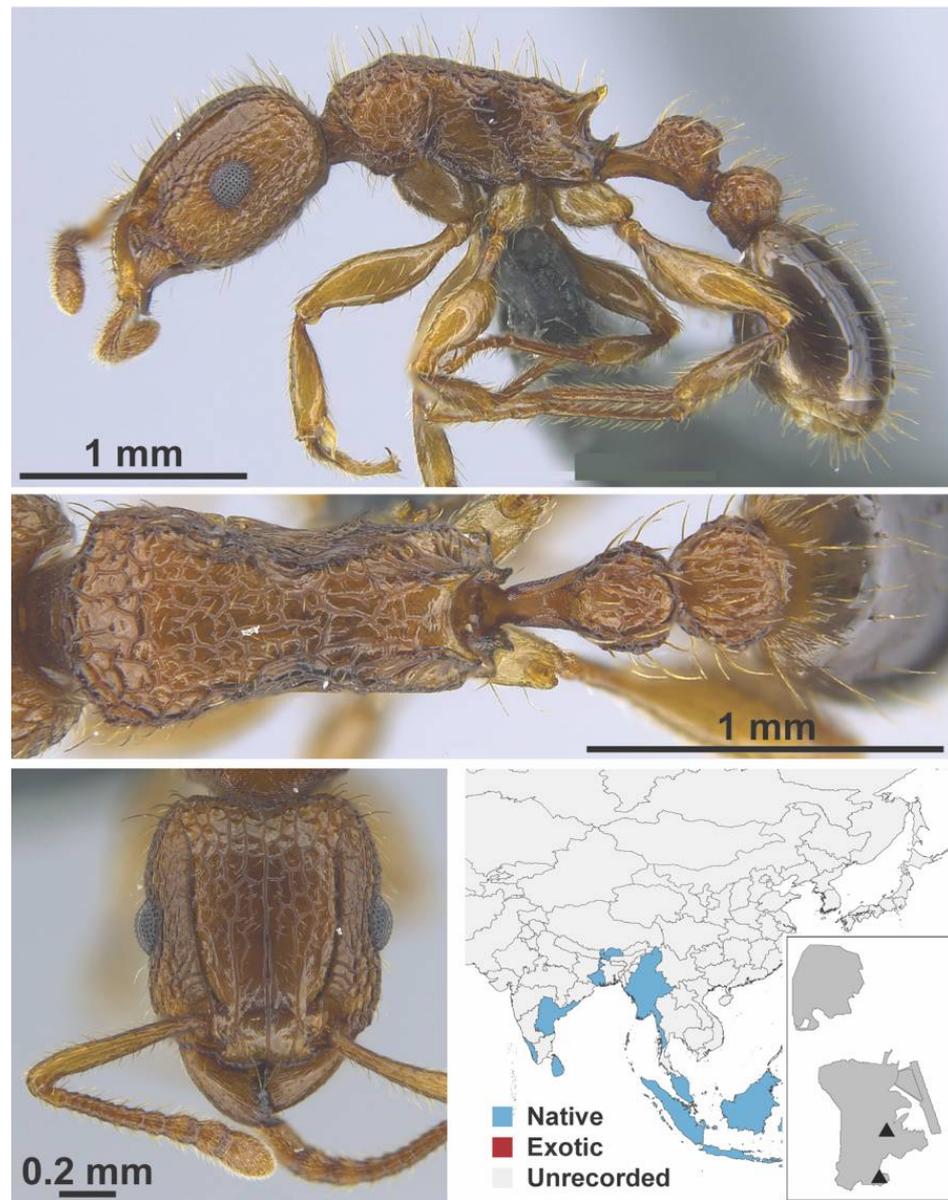


Figure A125. *Tetramorium indicum* Forel, 1913 worker (MAC_S08_T3_1m_sp.1, IBBL).

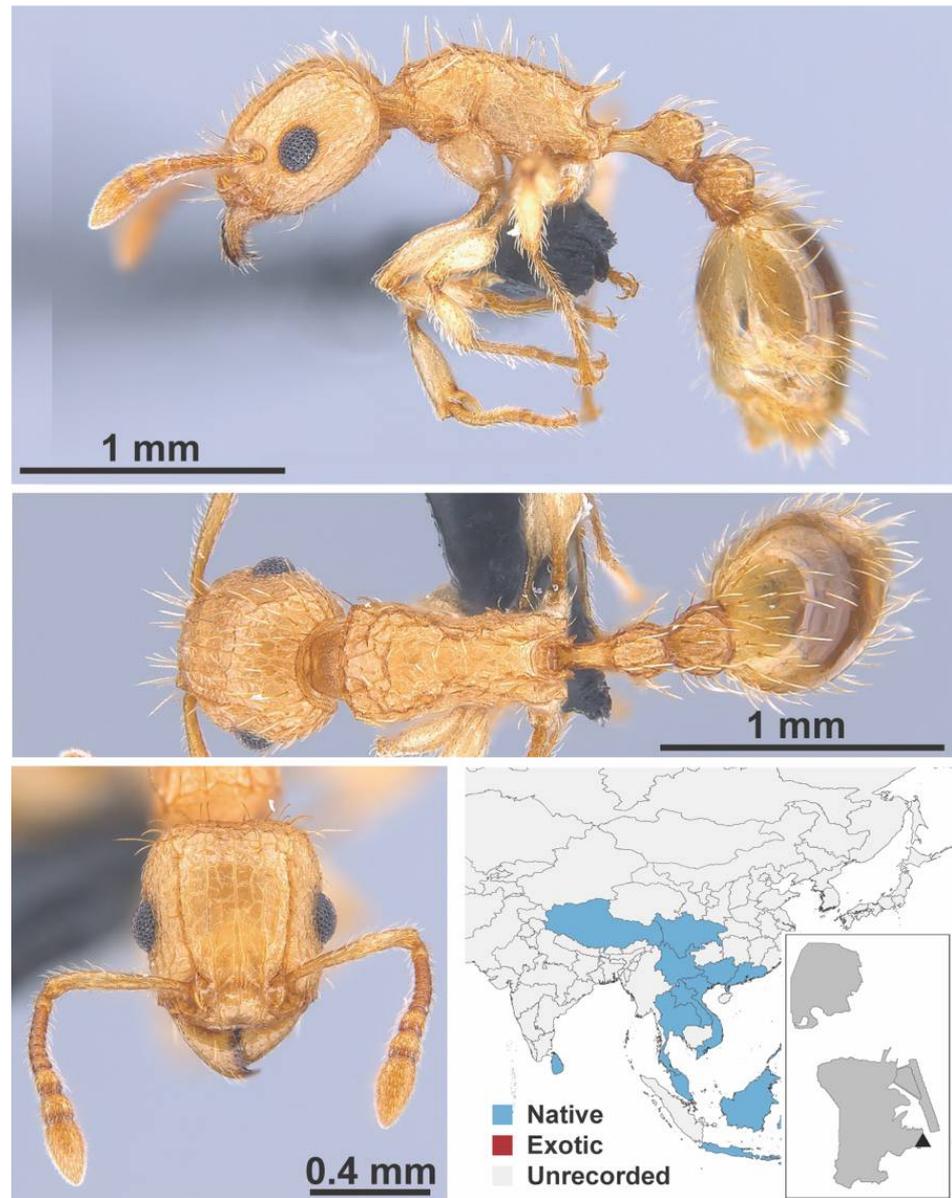


Figure A126. *Tetramorium insolens* Smith, 1861 worker (MAC_S17_LLSA_Sp.3, IBBL).

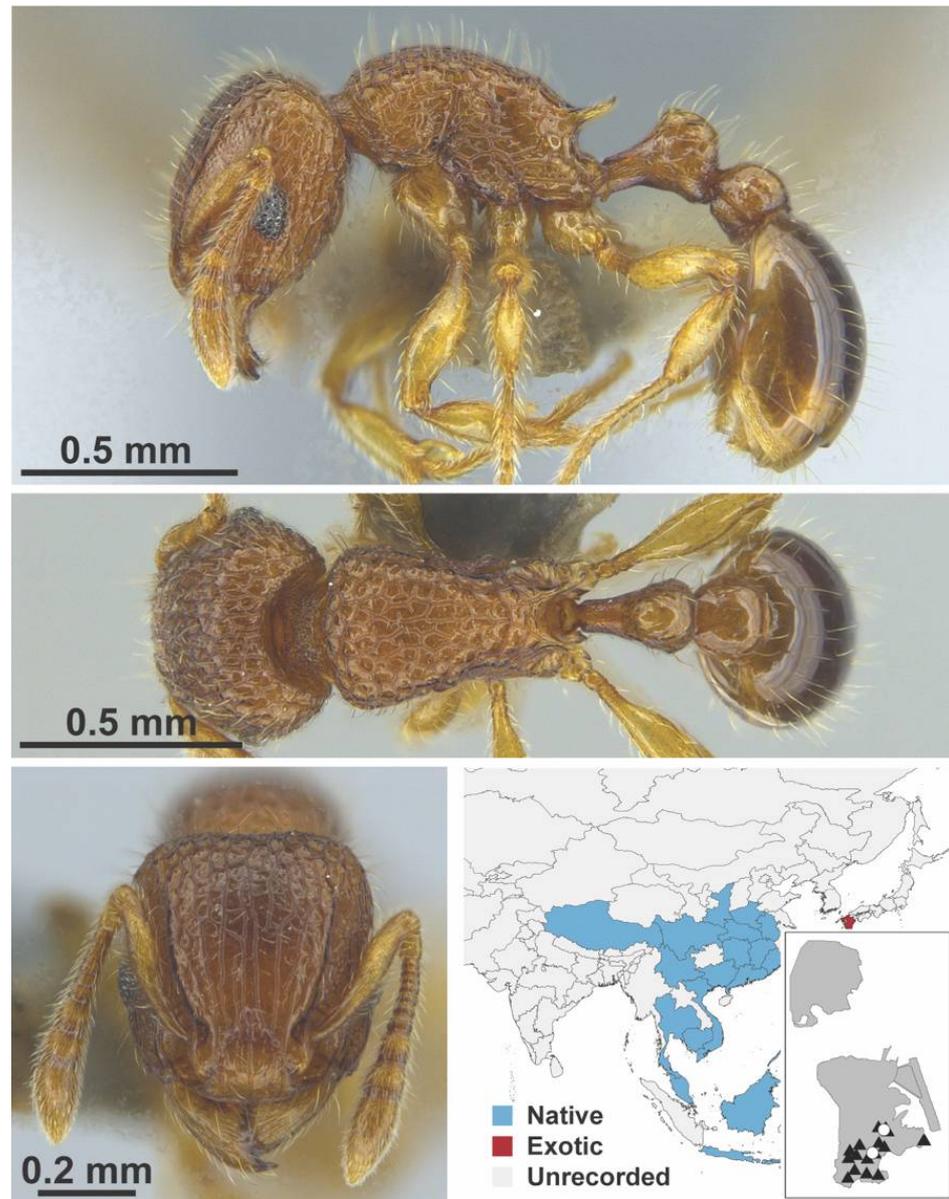


Figure A127. *Tetramorium kraepelini* Forel, 1905 worker (MAC_S8_GN1_H2_n1_sp.1, IBBL).

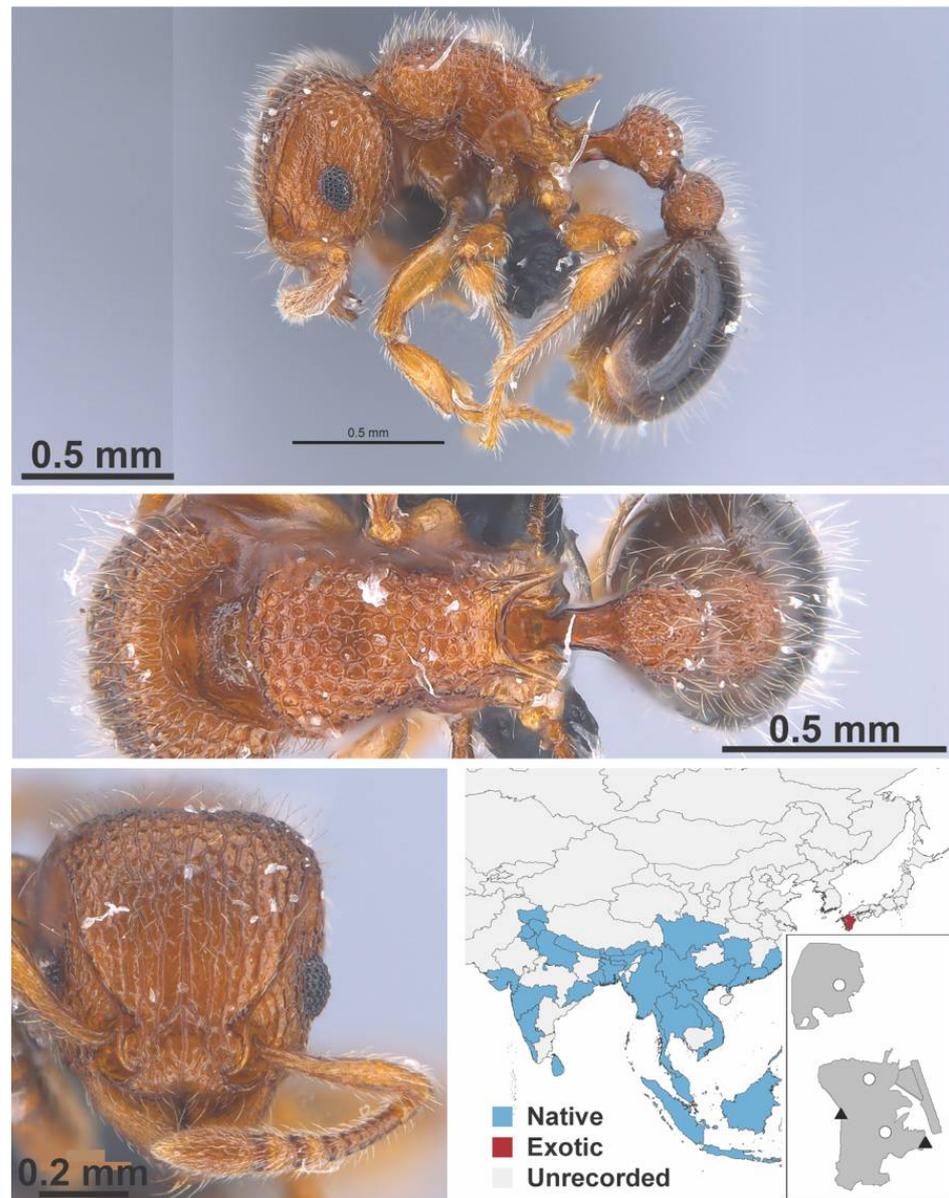


Figure A128. *Tetramorium lanuginosum* Mayr, 1870 worker (MAC_S17_LLSA_Sp.2, IBBL).

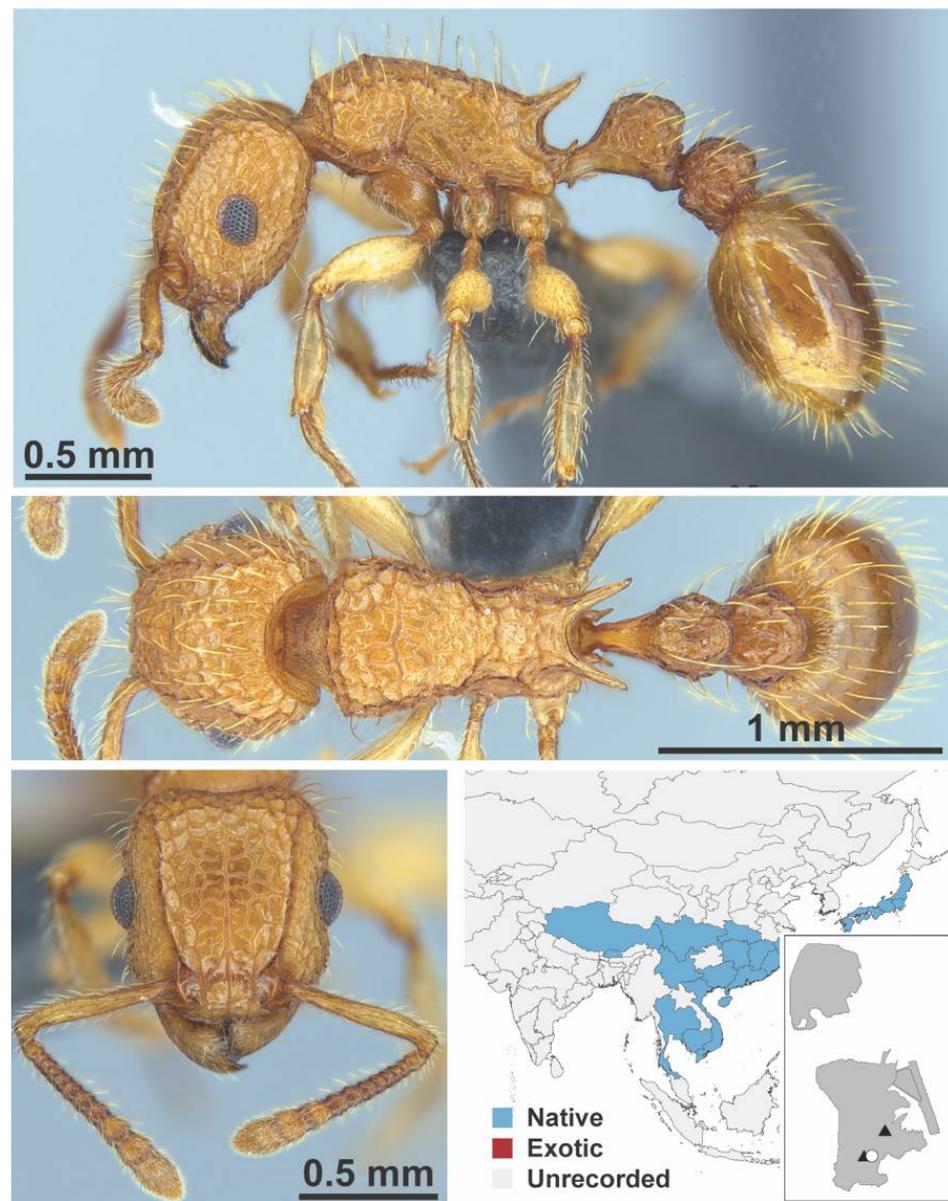


Figure A129. *Tetramorium nipponense* Wheeler, 1928 worker (MAC_S7_GN2_H4_n1, IBBL).

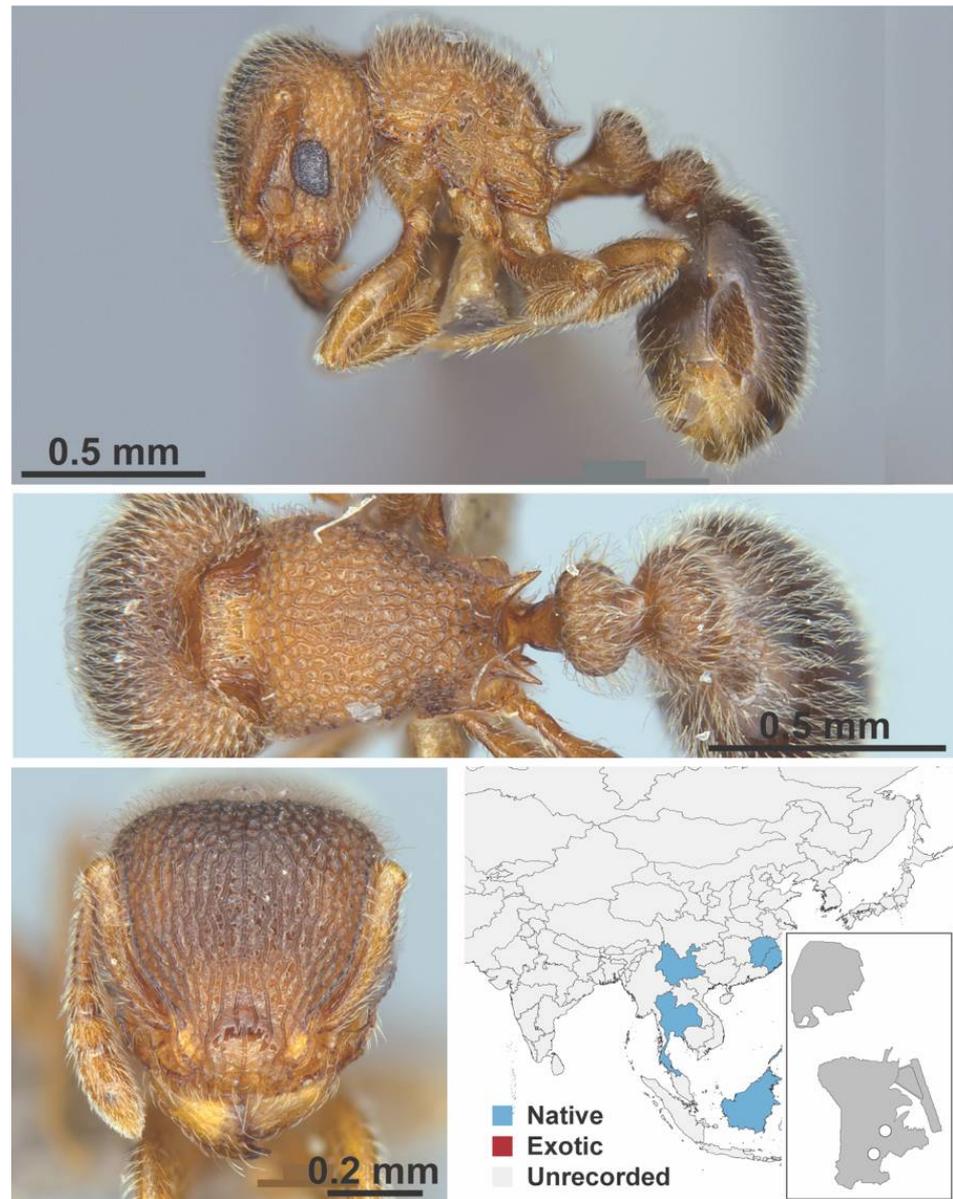


Figure A130. *Tetramorium parvispinum* Emery, 1893 worker (*Tetramorium parvispinum*, CML collection).

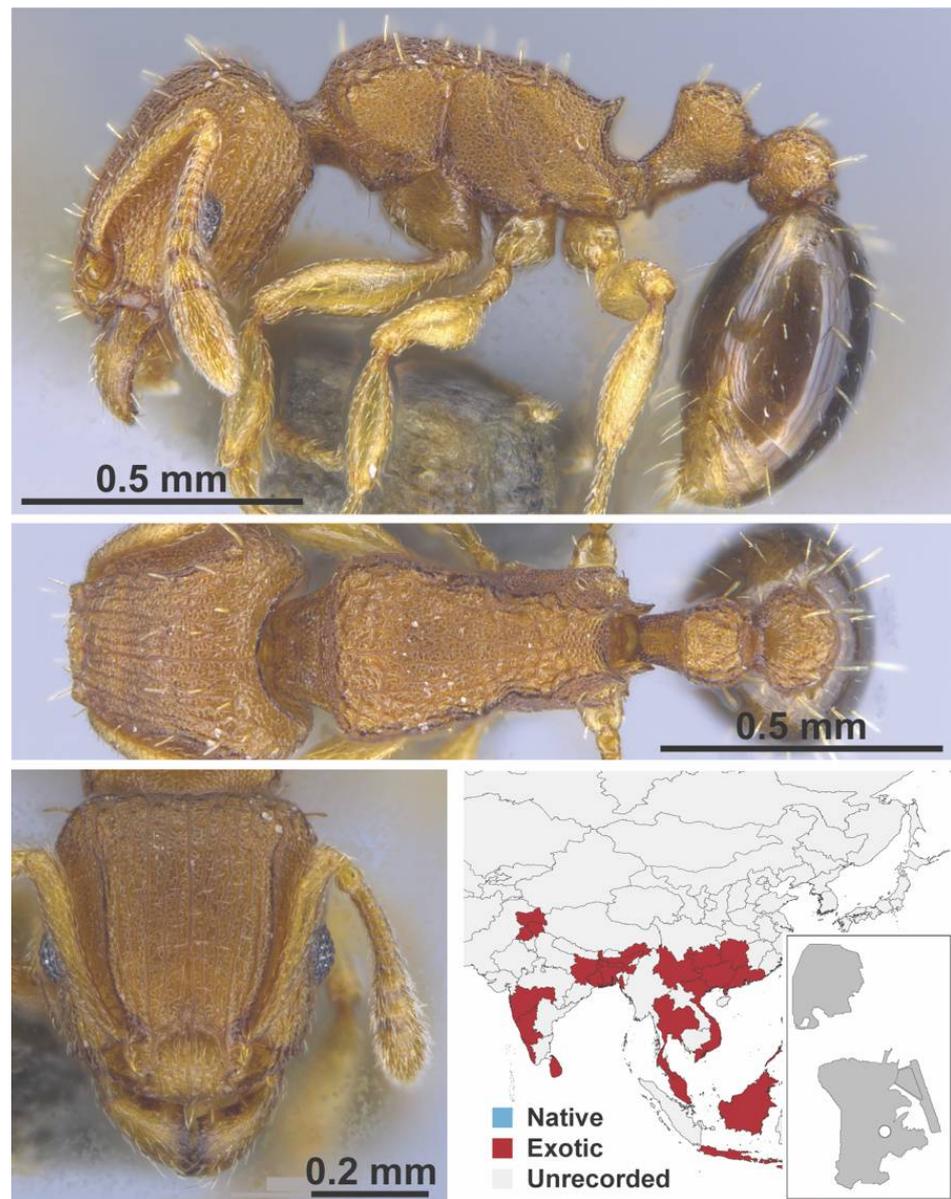


Figure A131. *Tetramorium simillinum* Smith, 1851 worker (*Tetramorium simillinum*, IBBL).

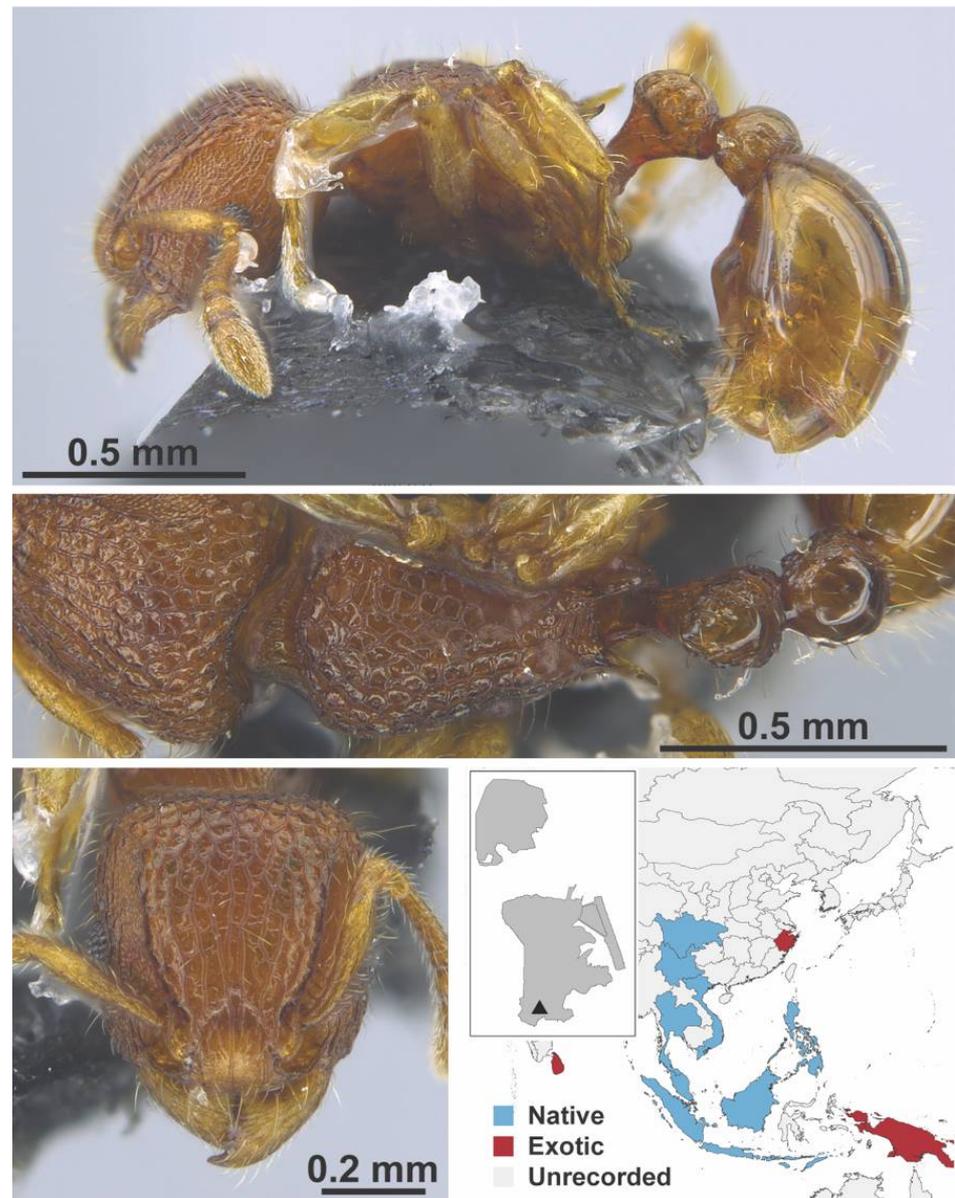


Figure A132. *Tetramorium tonganum* Mayr, 1870 worker (MAC_S10_T2_1m_sp.2, IBBL). Note that we changed the location of the map of Macao to show the localities where this species has been recorded as an exotic species in Southeast Asia.

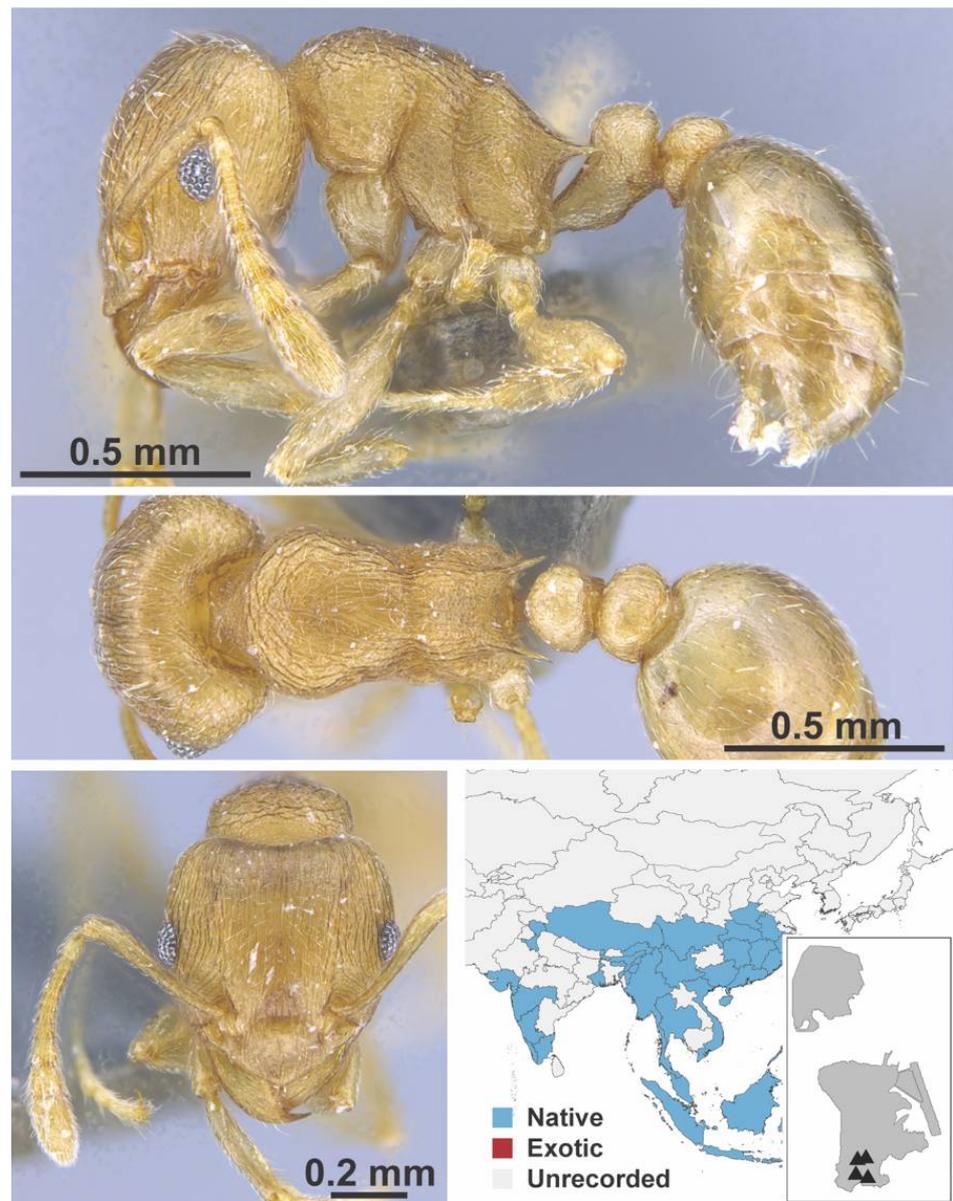


Figure A133. *Tetramorium wroughtonii* Forel, 1902 worker (MAC_S10_B03_sp.1_top, IBBL).

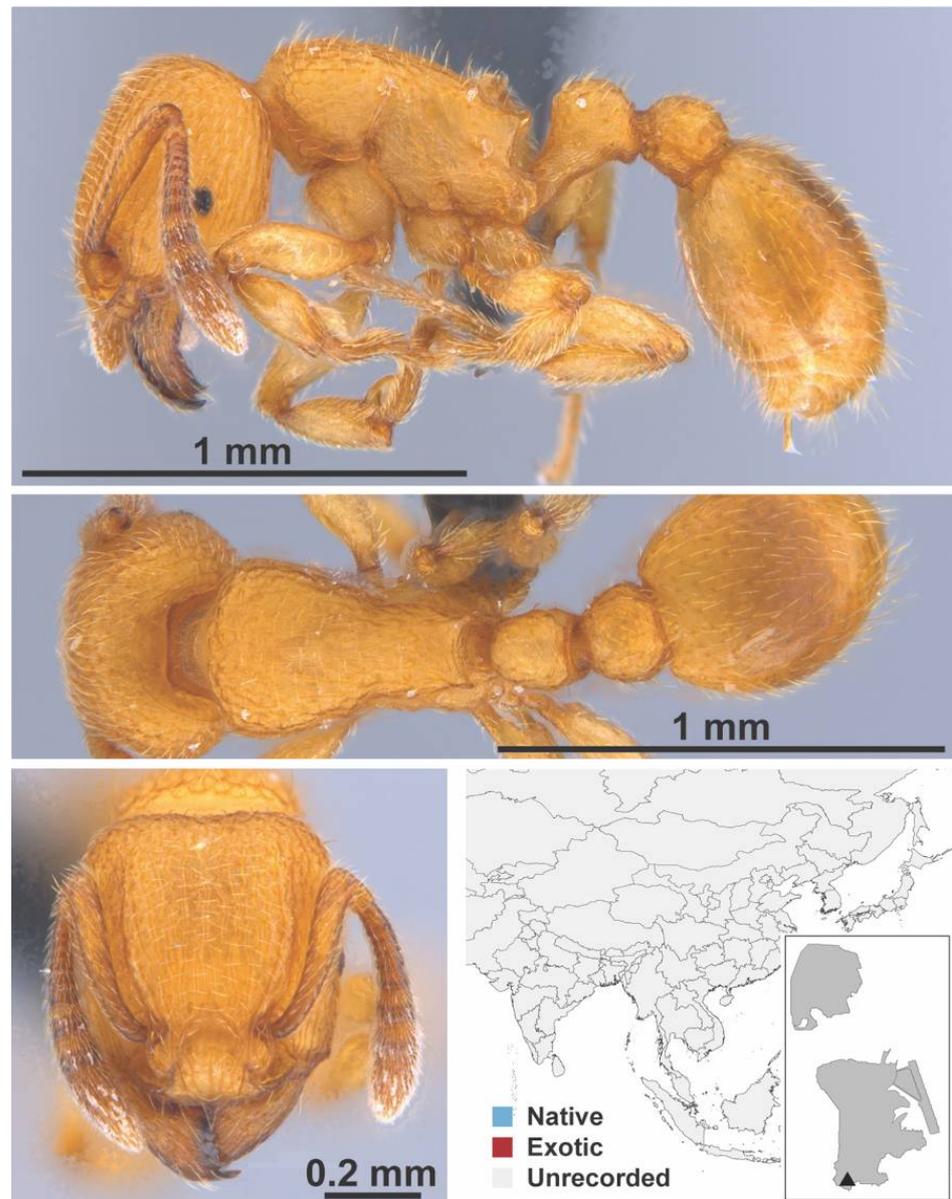


Figure A134. *Tetramorium* nr. *elisabethae* Forel, 1904 worker (MAC_S18_q1_25_Sp.2, IBBL).

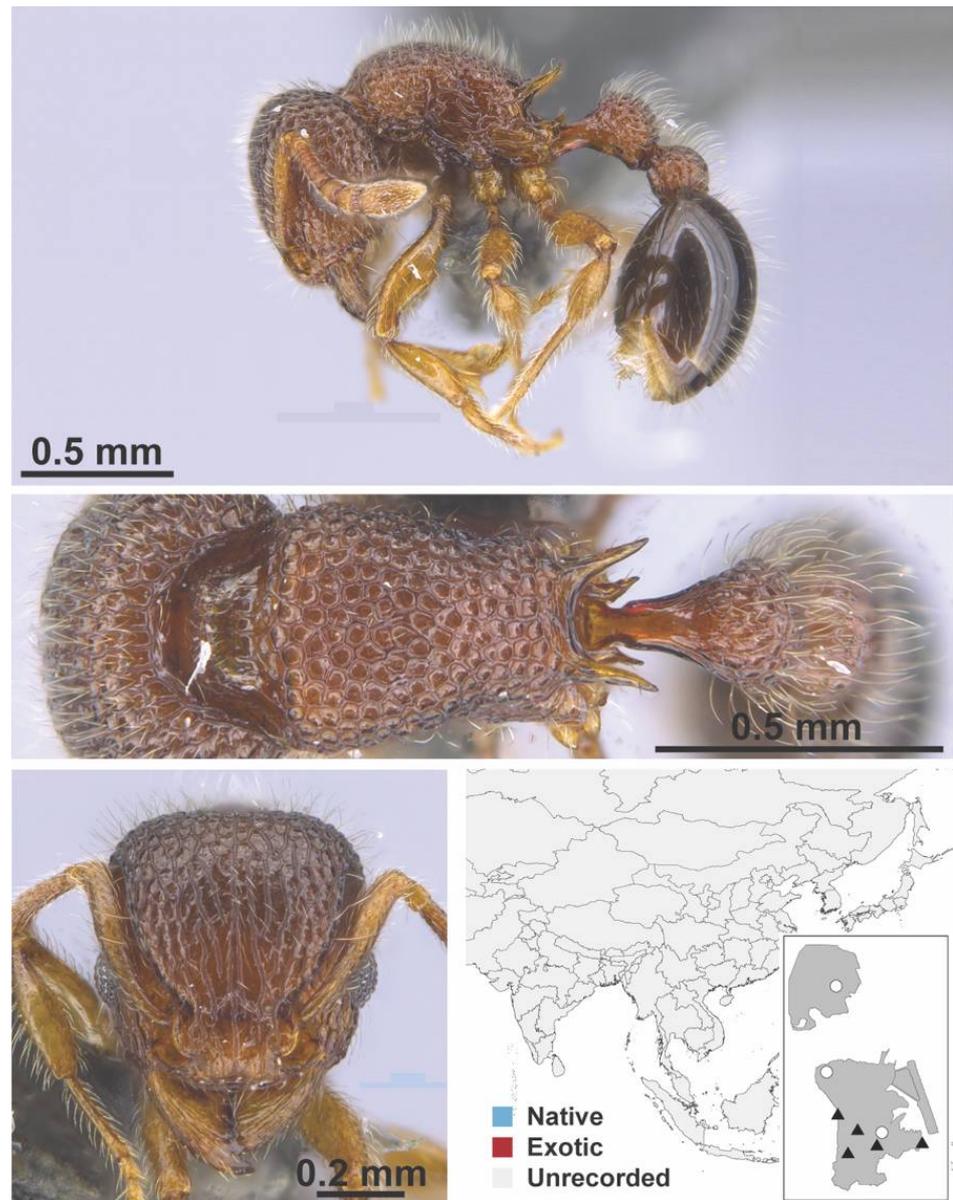


Figure A135. *Tetramorium* sp. 1 BG (*obesum* group Bolton, 1976) worker (MAC_S04_LLSP_Sp.3, IBBL).

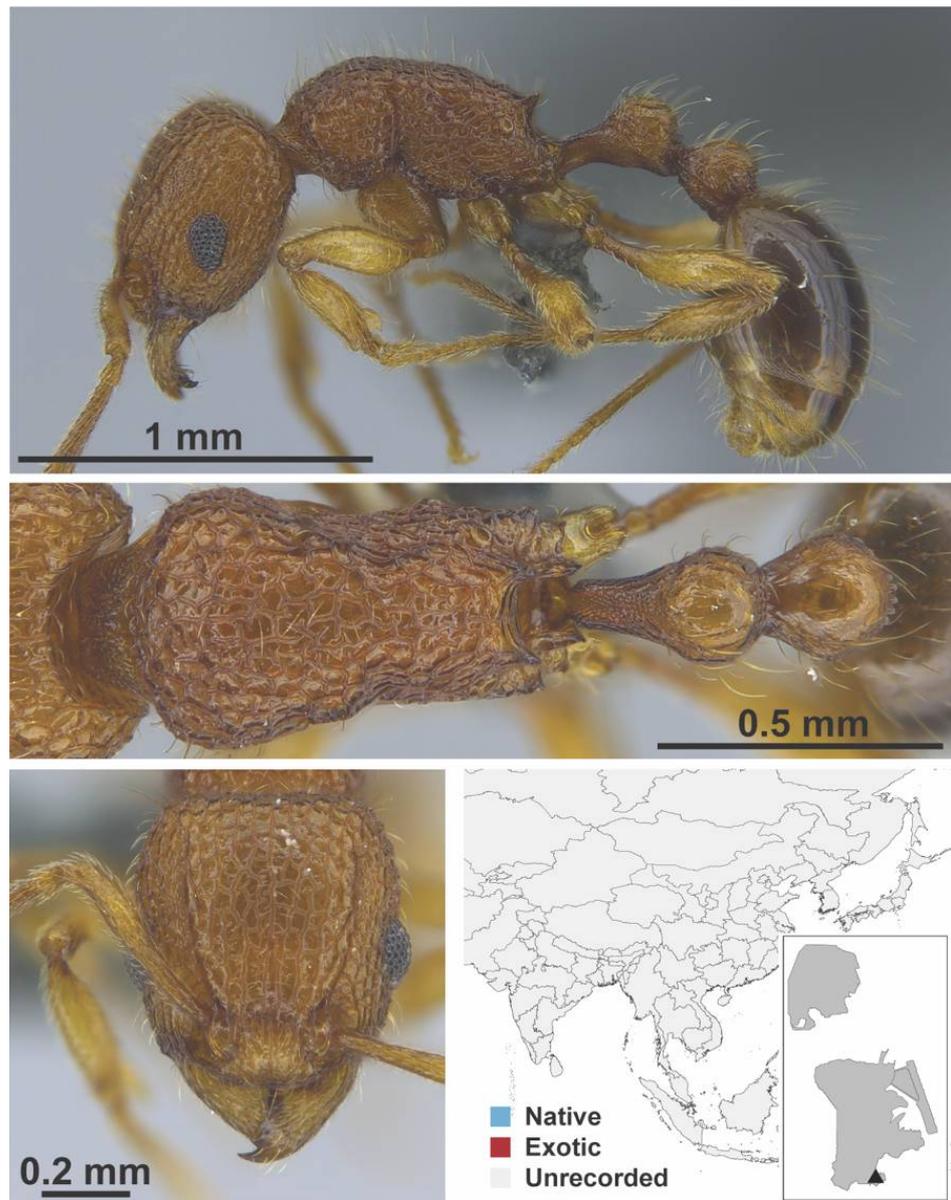


Figure A136. *Tetramorium* sp. 2 JF worker (MAC_S15_T1_3m_sp.2, IBBL).

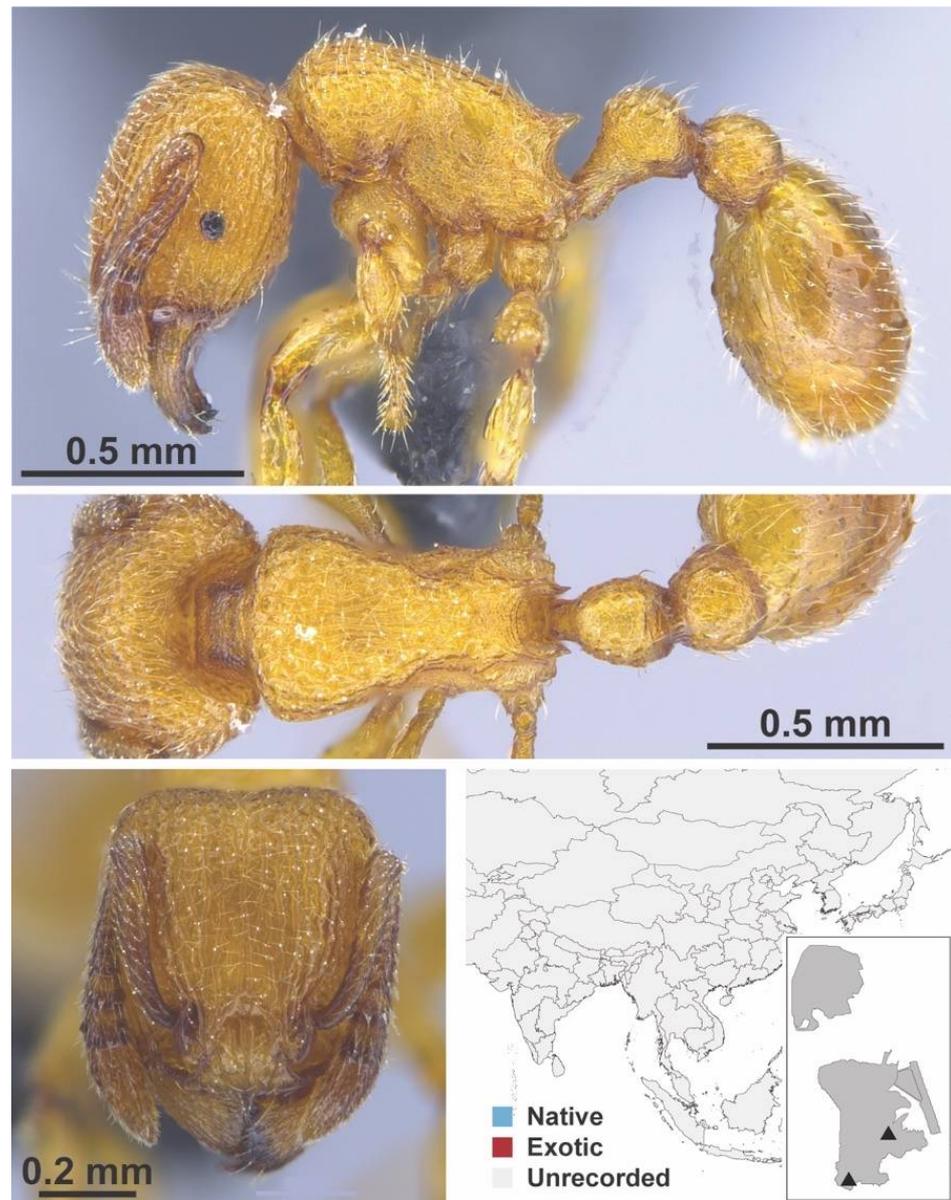


Figure A137. *Tetramorium* sp. 9 JF worker (MAC_S18_q2_25_sp.1, IBBL).

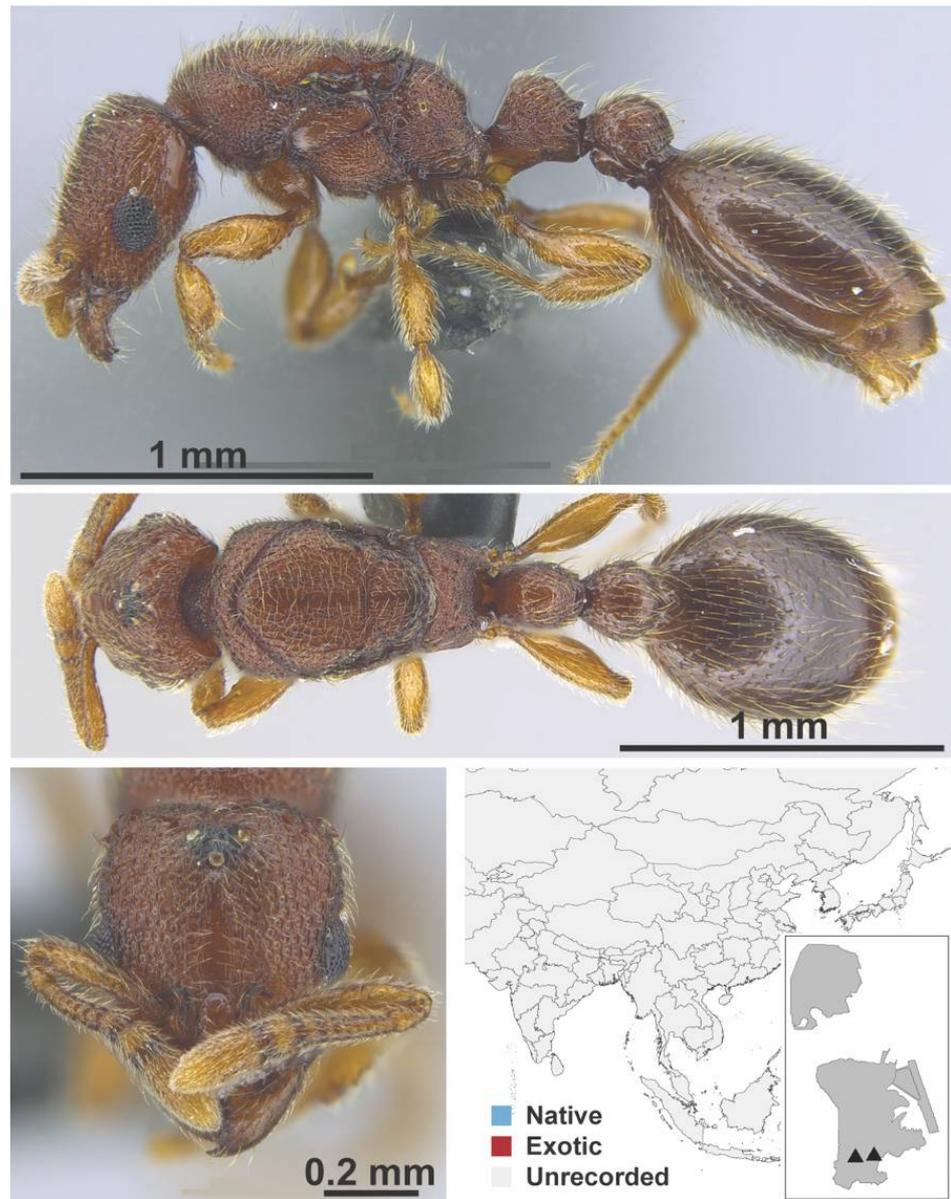


Figure A138. *Vollenhovia* sp. 1 BG queen (MAC_S06_GN3_H3_n1, IBBL).

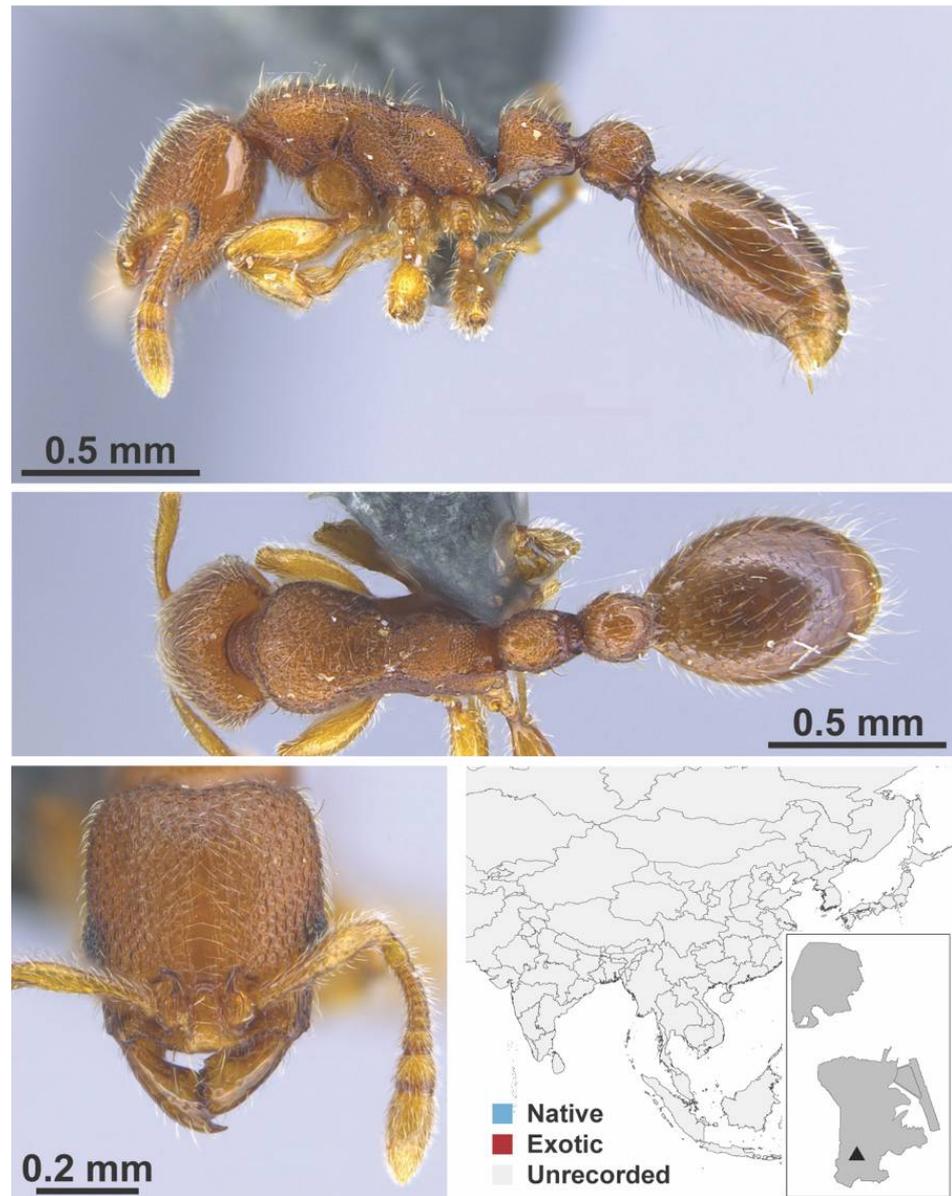


Figure A139. *Vollenhovia* sp. 2 BG worker (MAC_S02_LLSP_Sp.5, IBBL).

Appendix A.7 PONERINAE

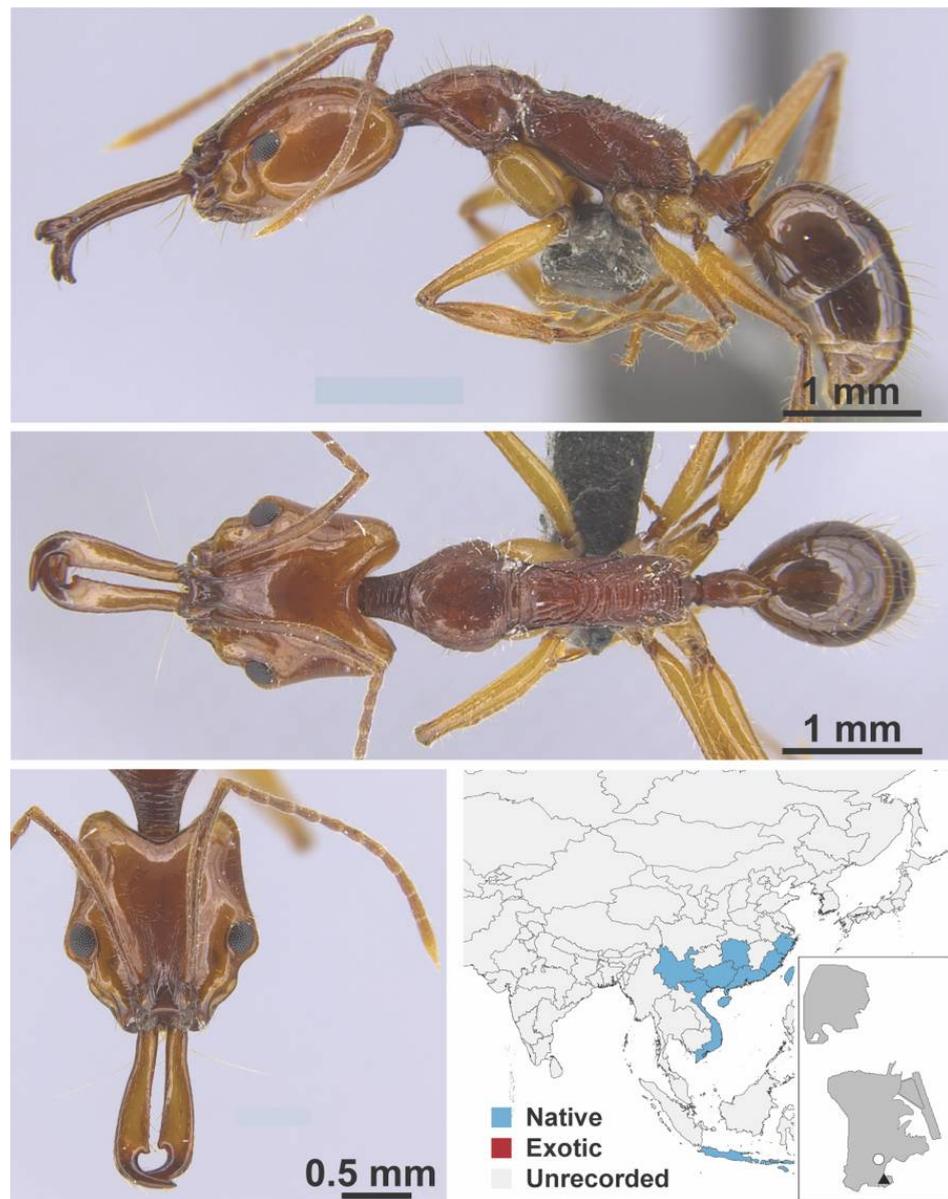


Figure A140. *Anochetus risii* Forel, 1900 worker (MAC_FB19180, IBBL).

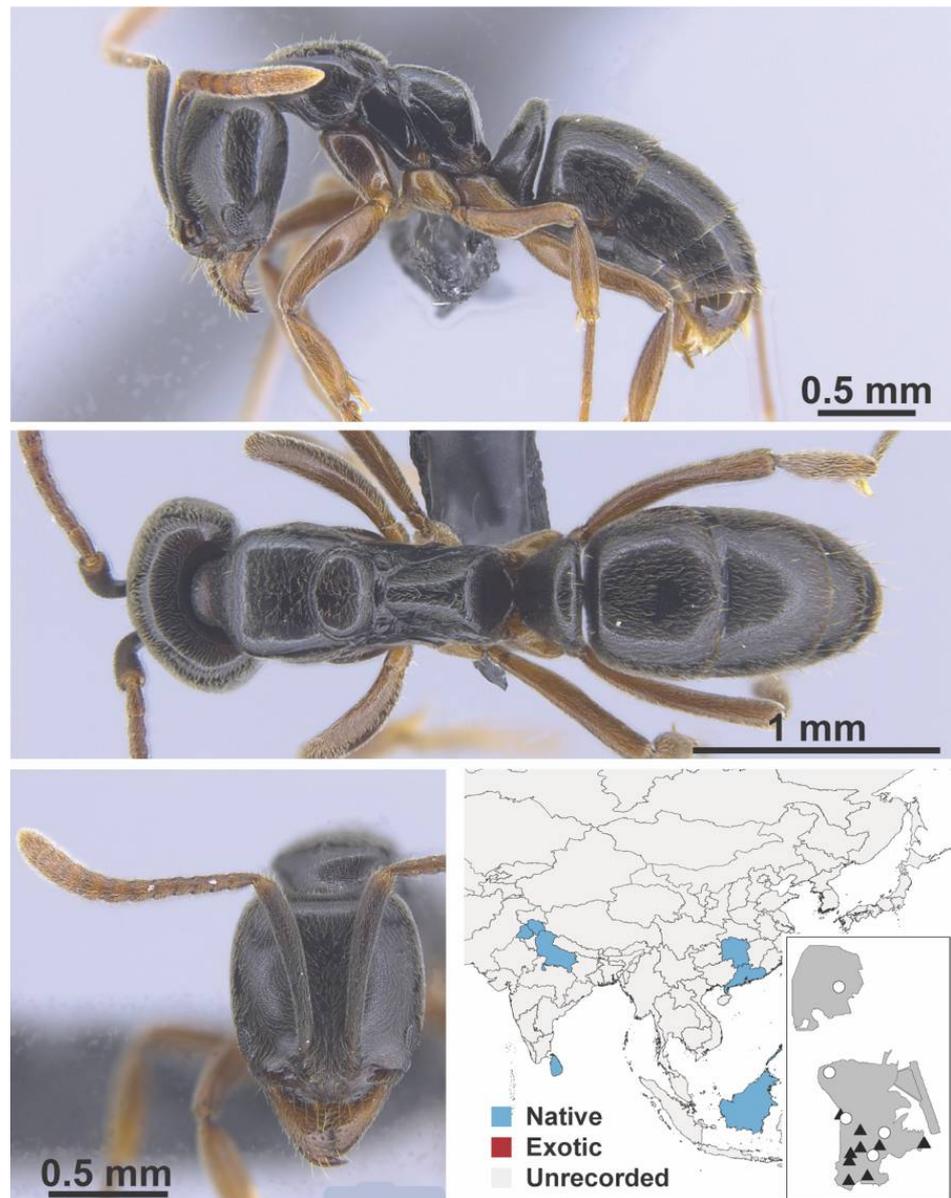


Figure A141. *Brachyponera obscurans* Mayr, 1862 worker (MAC_S19_LLSA, IBBL).

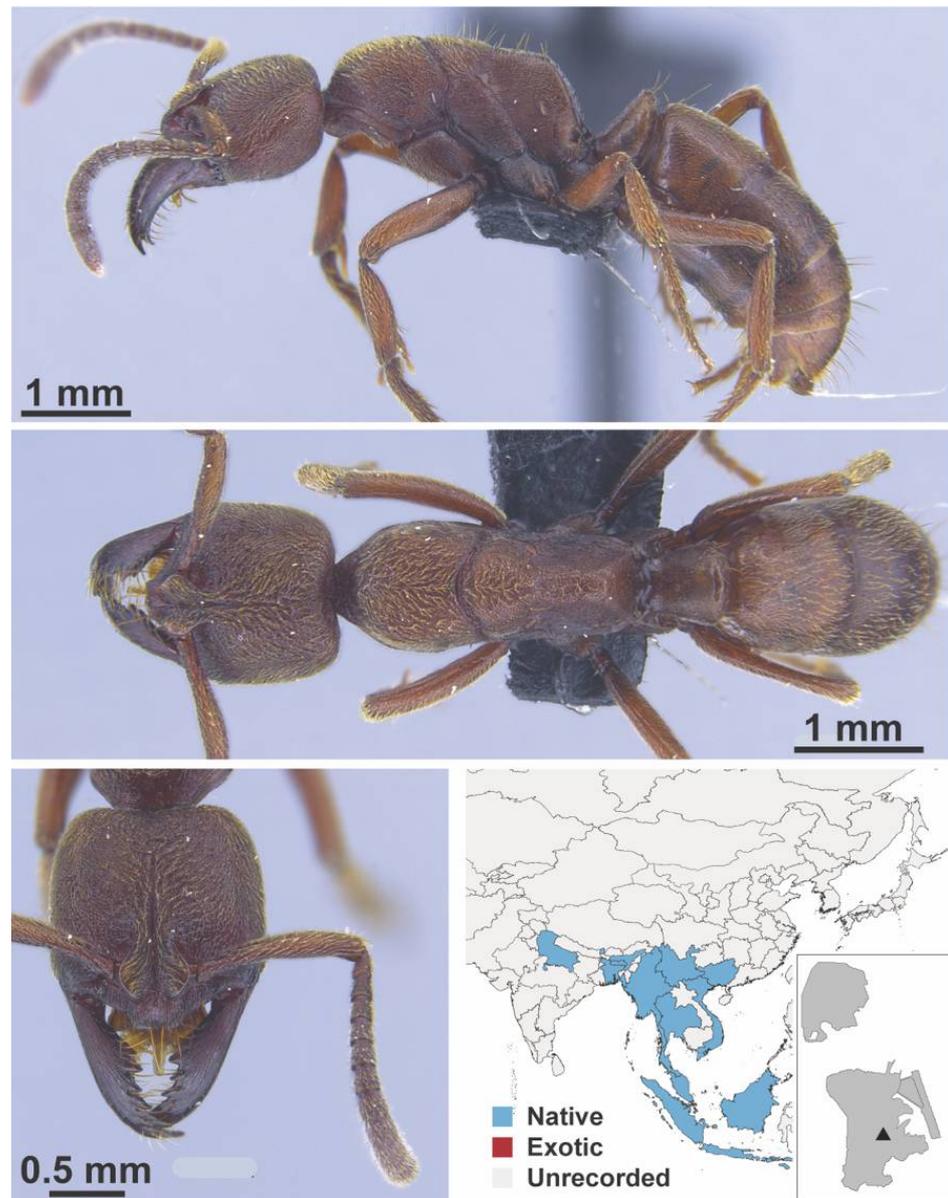


Figure A142. *Buniapone amblyops* Emery, 1887 worker (MAC_S12_q4_50_sp.2_top, IBBL).

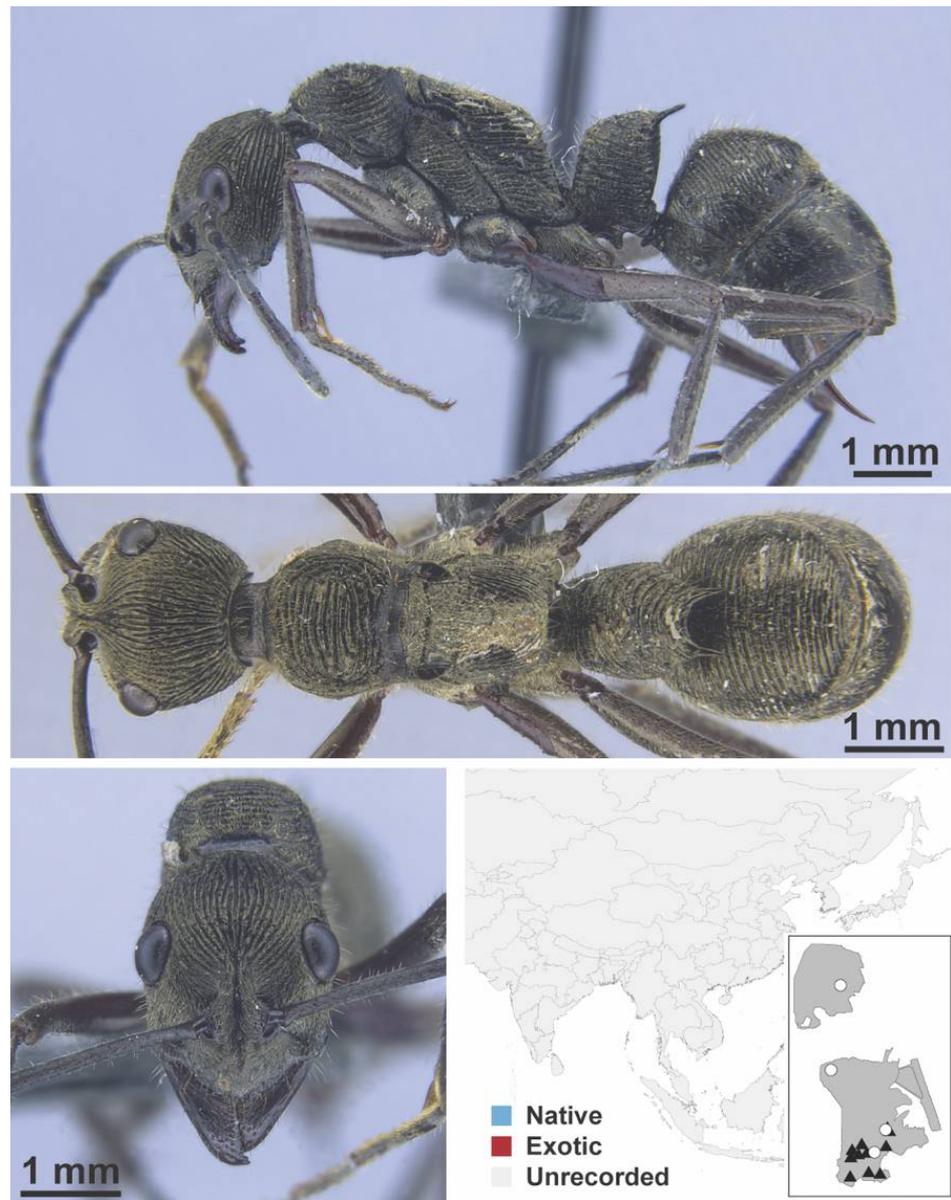


Figure A143. *Diacamma* sp. 1 worker (MAC_S15_LLSA_sp.1, IBBL).

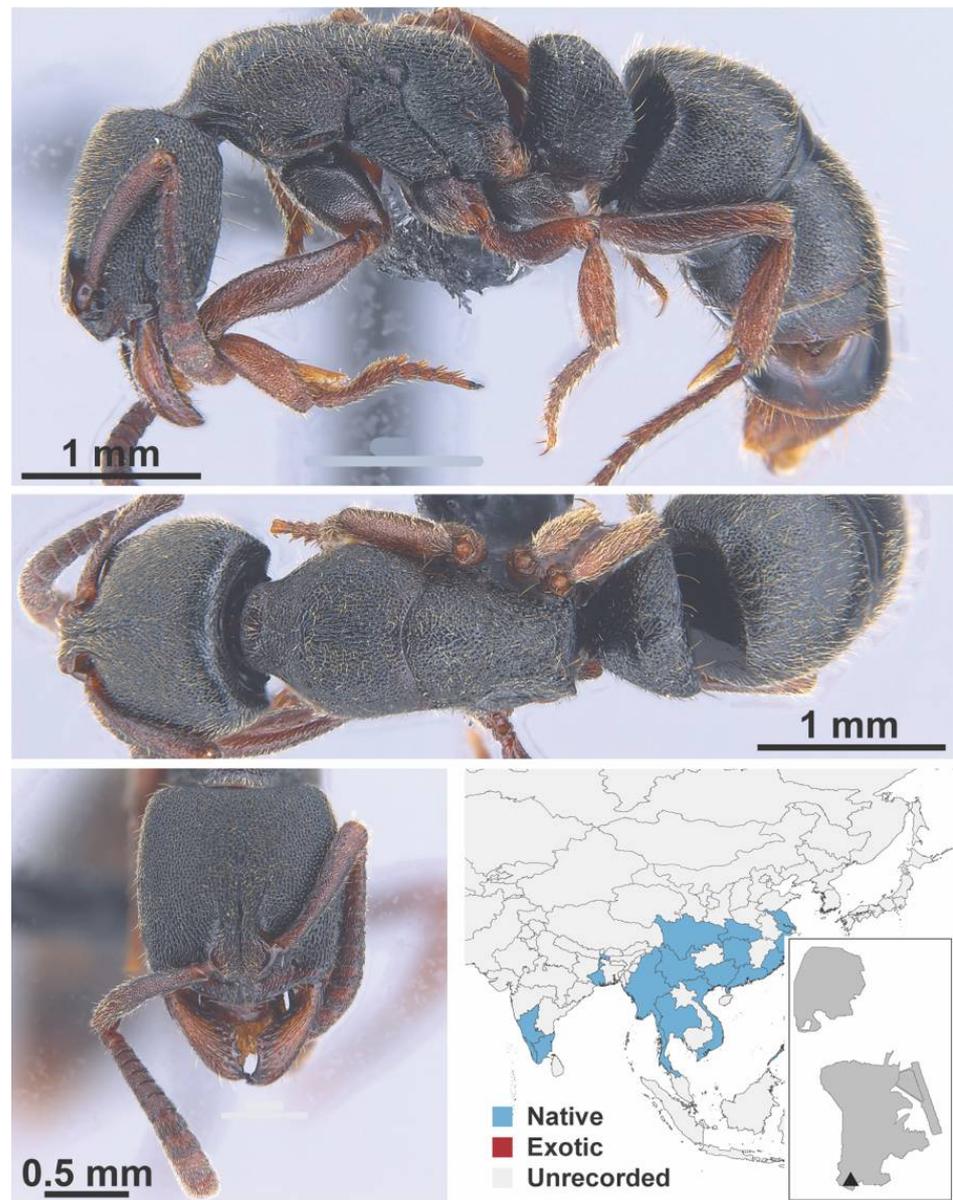


Figure A144. *Ectomyrmex annamitus* André, 1892 worker (MAC_S18_q2_37.5_Sp.4, IBBL).

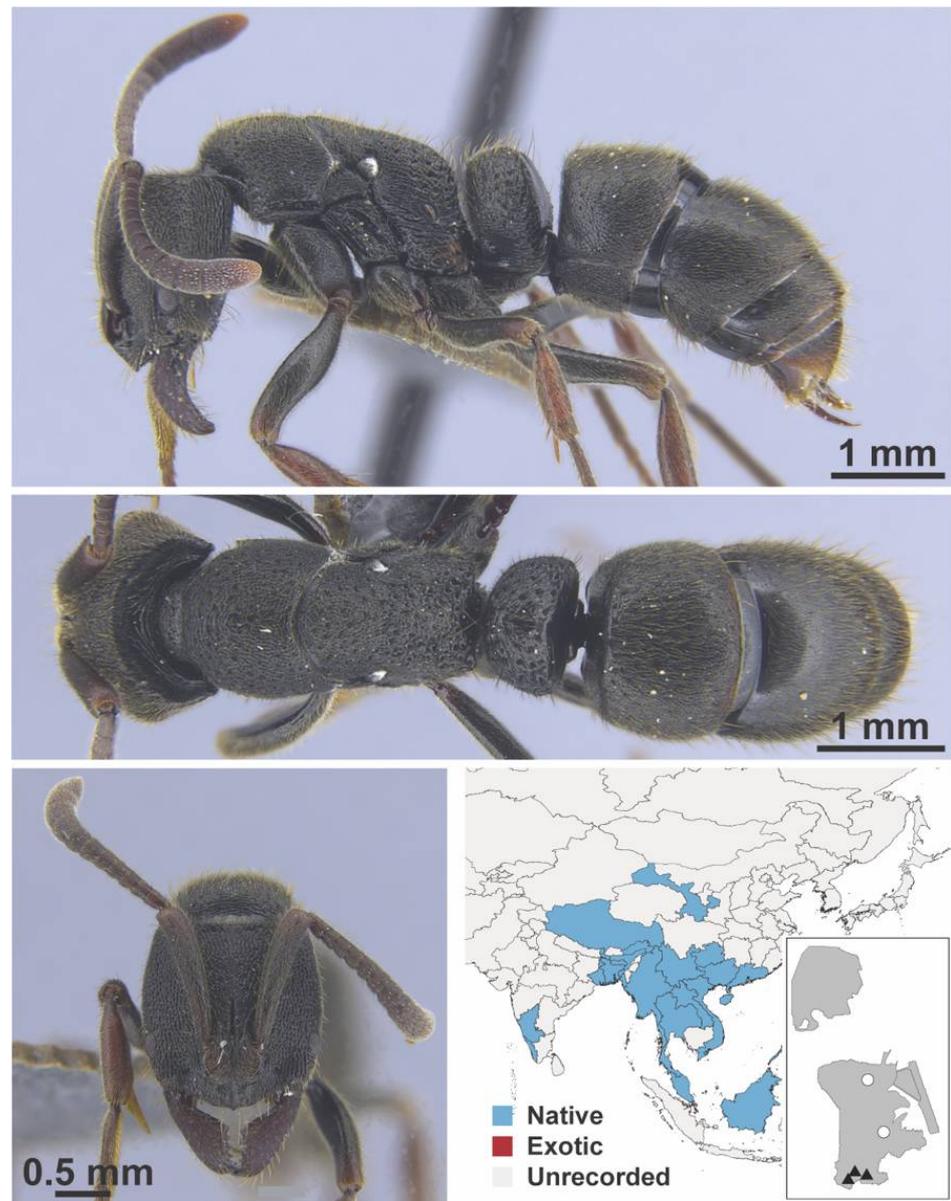


Figure A145. *Ectomyrmex leeuwenhoecki* Forel, 1886 worker (MAC_S18_GN5_H4_n1, IBBL).

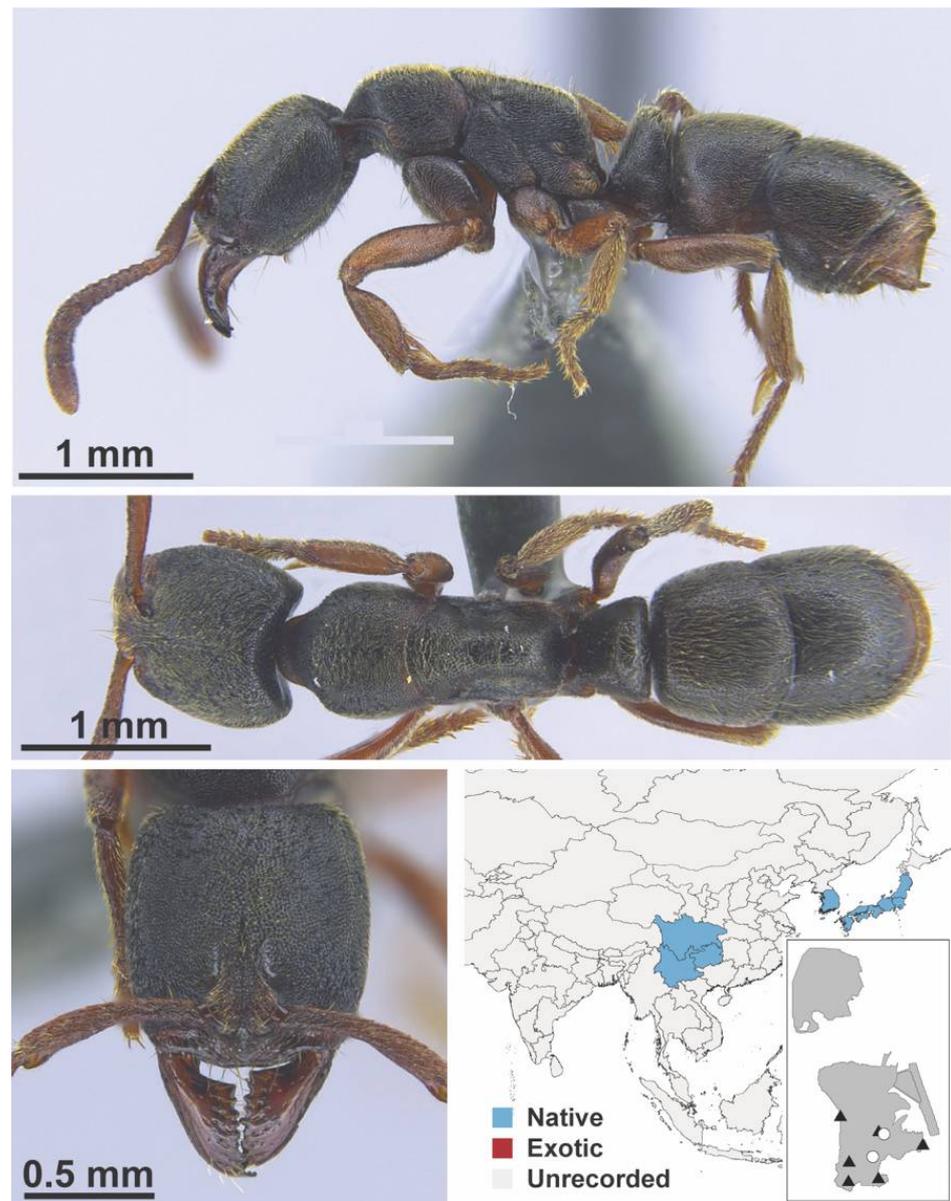


Figure A146. *Euponera pilosior* Wheeler, 1928 worker (MAC_S12_q3_50_Sp.1, IBBL).

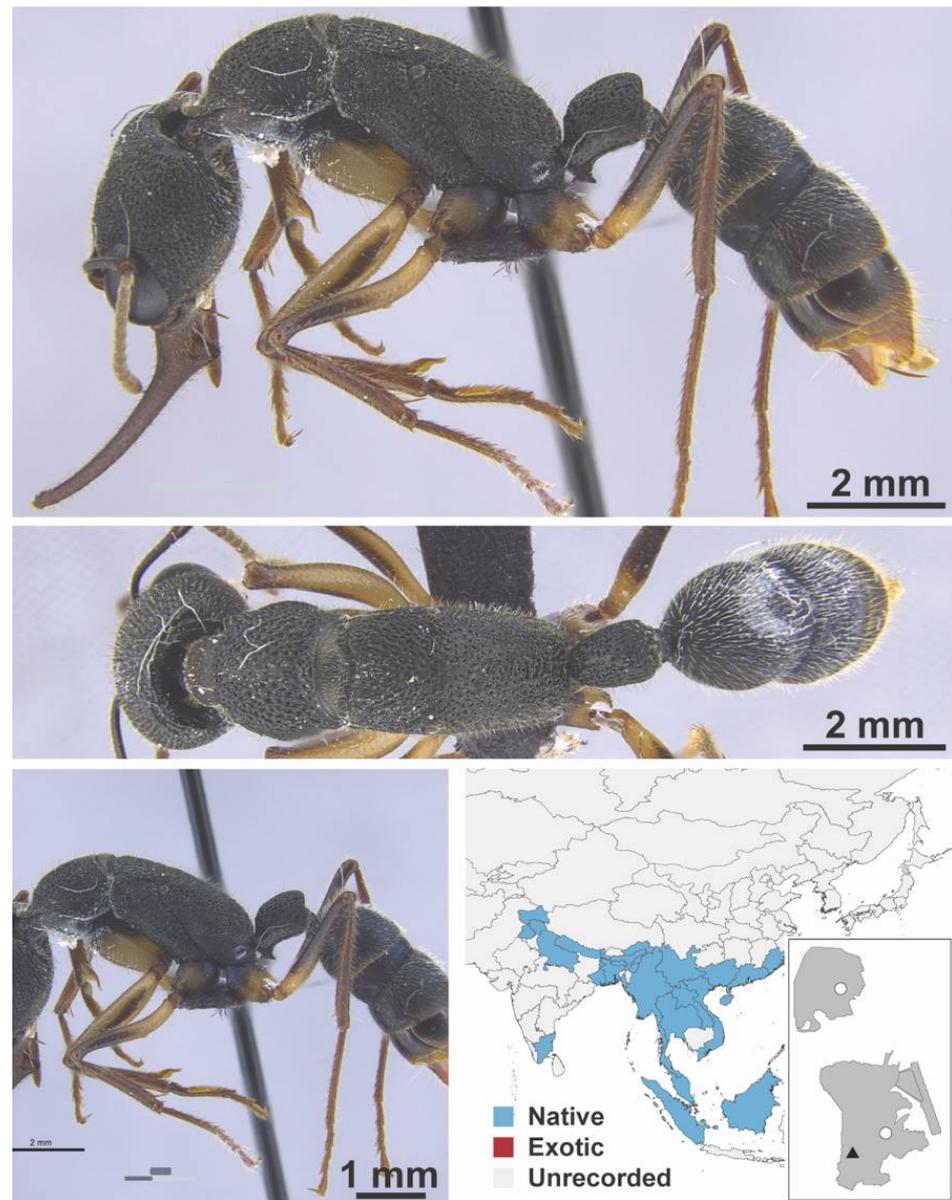


Figure A147. *Harpegnathos venator* Smith, 1858 worker (MAC_ZOO_HC07_Sp.1, IBBL).

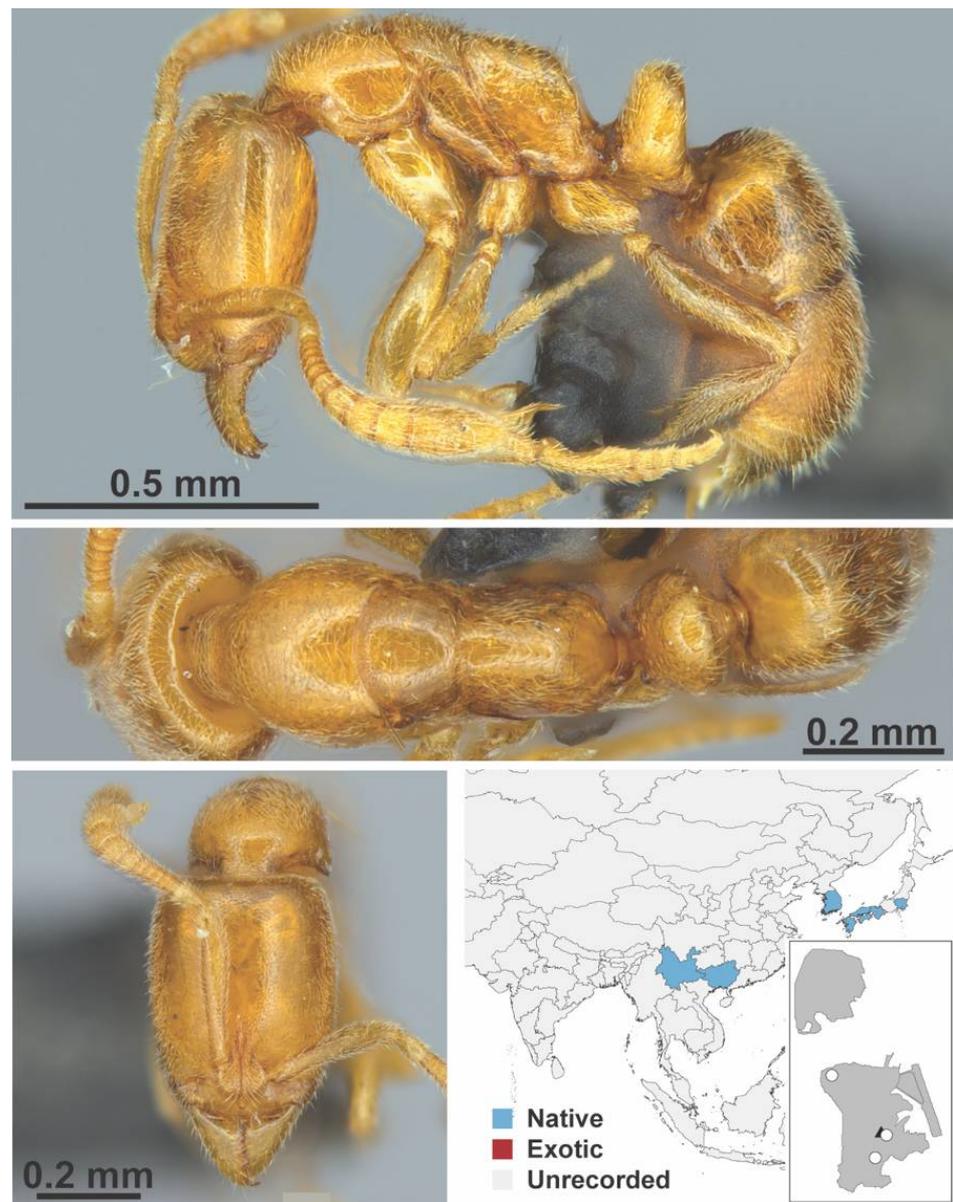


Figure A148. *Hypoponera exoecata* Wheeler, 1928 worker (*Hypoponera exoecata*, CML collection).

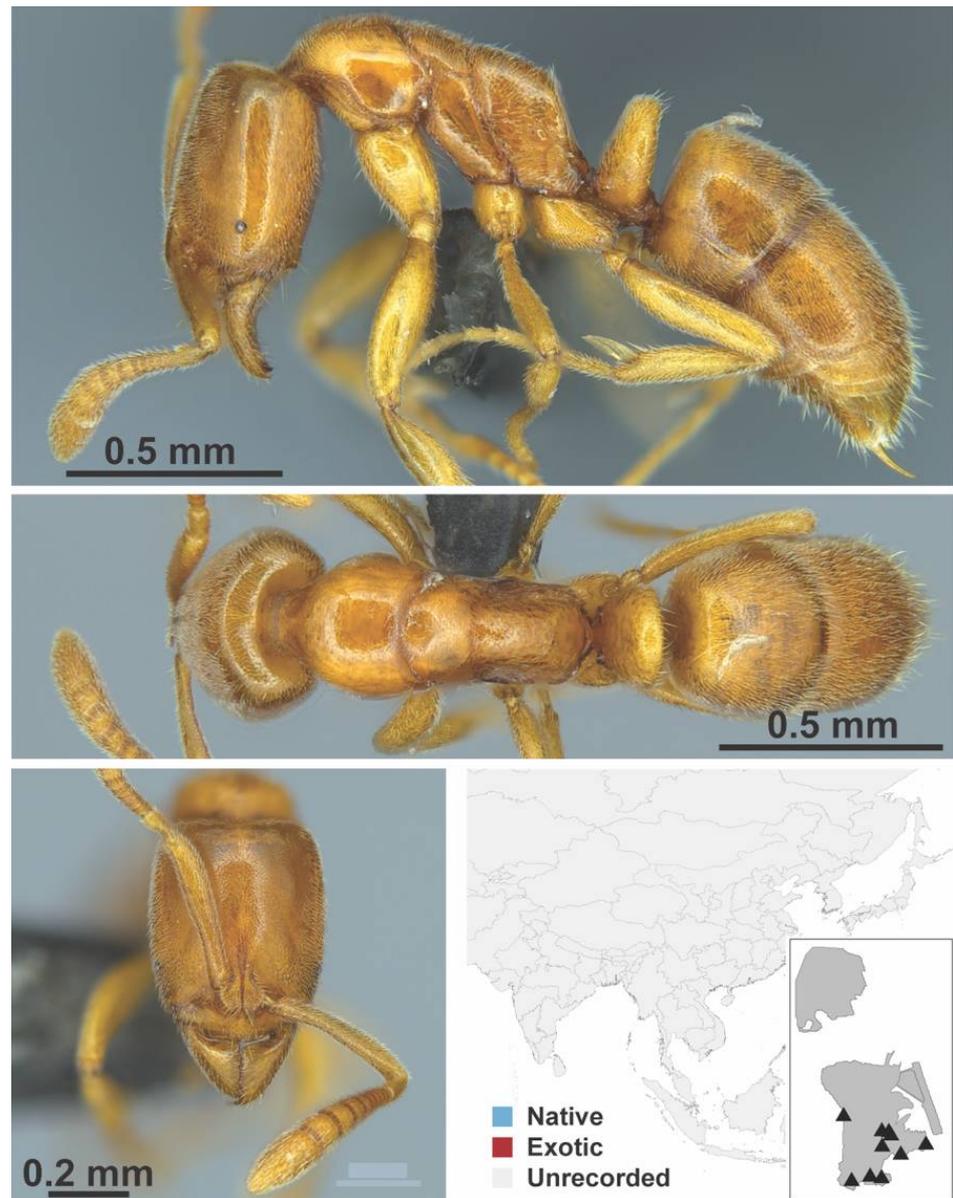


Figure A149. *Hypoponera* sp. psw-cn01 worker (*Hypoponera* sp. psw-cn01, CML collection).

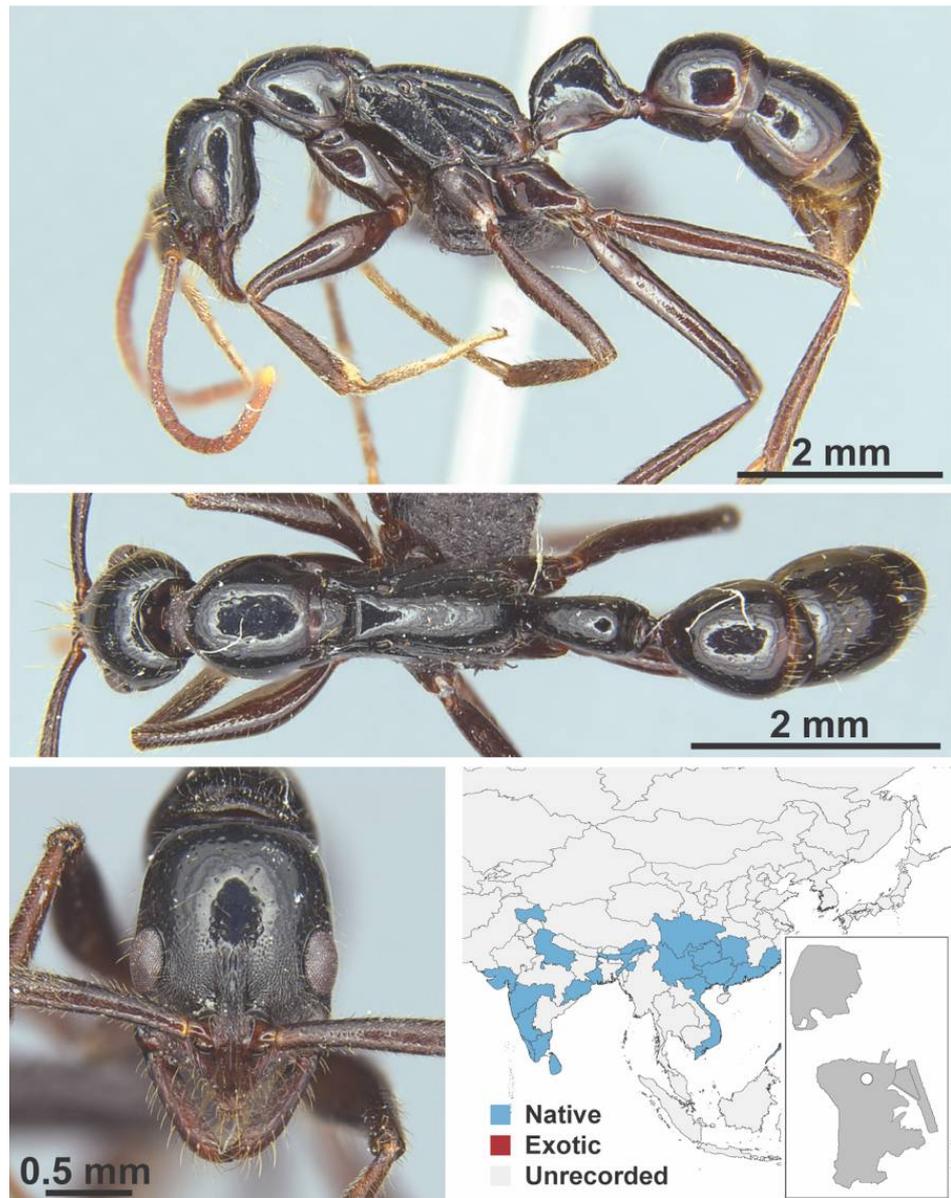


Figure A150. *Leptogenys chinensis* Mayr, 1870 worker (RHL00861, IBBL).

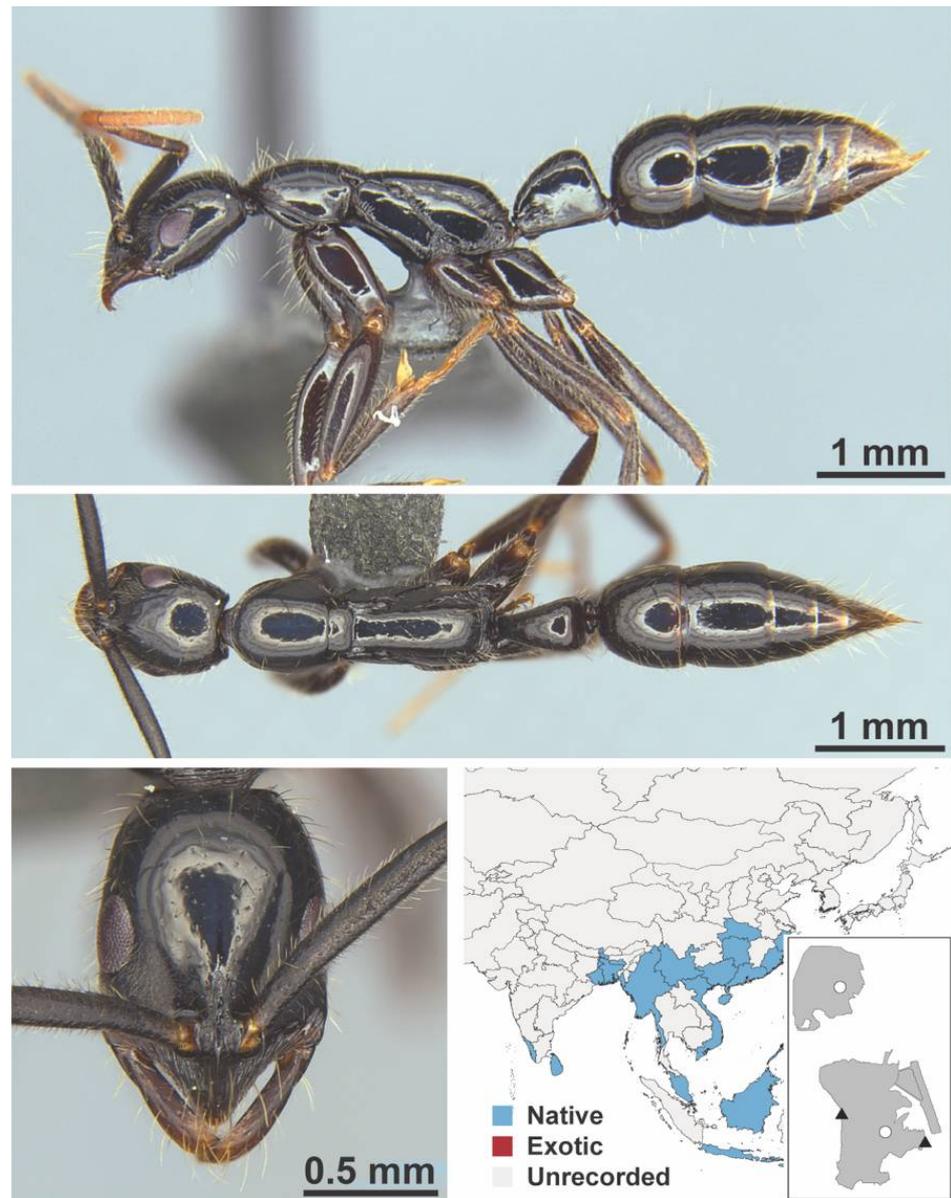


Figure A151. *Leptogenys peuqueti* André, 1887 worker (*Leptogenys peuqueti*, CML collection).

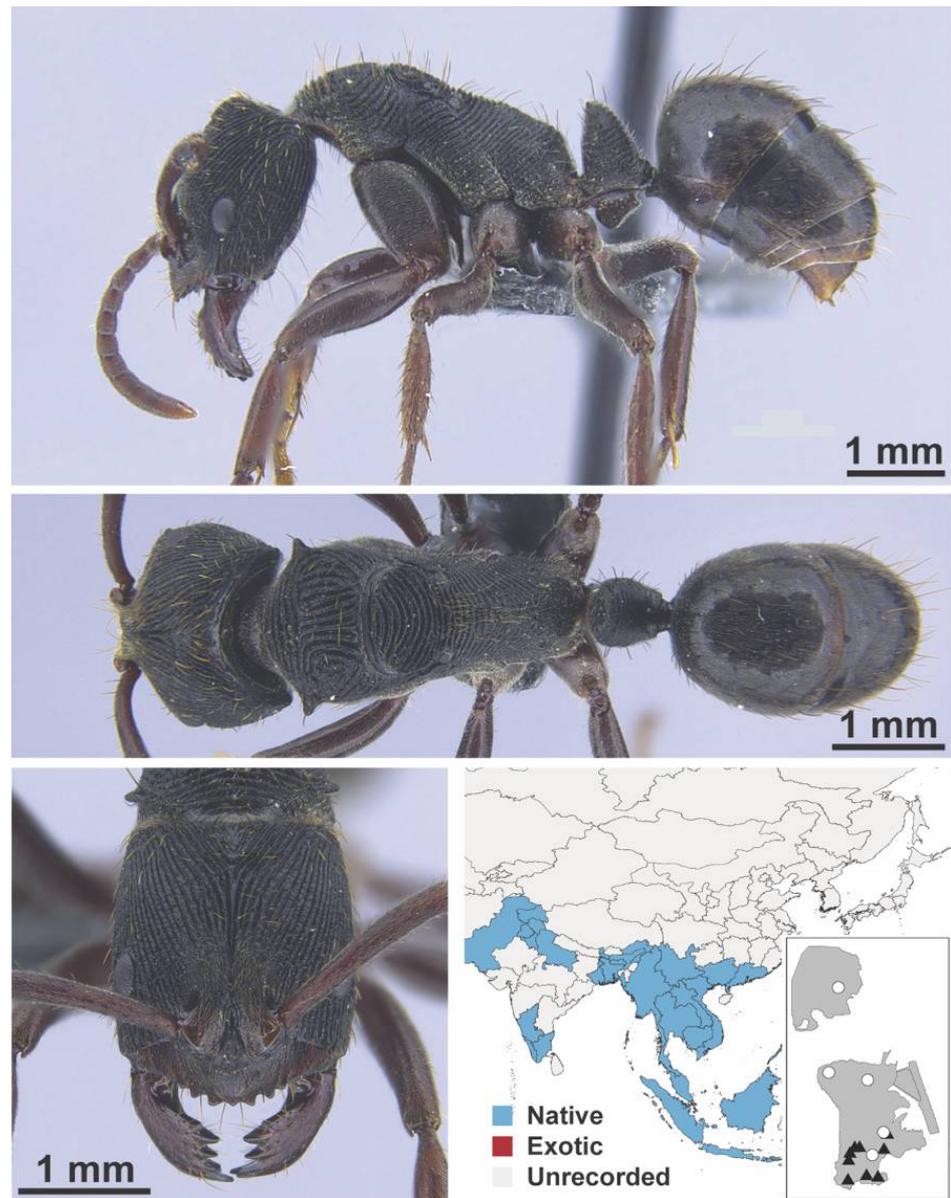


Figure A152. *Odontoponera denticulata* Smith, 1858 worker (MAC_S09_LLSA_Sp.3, IBBL).

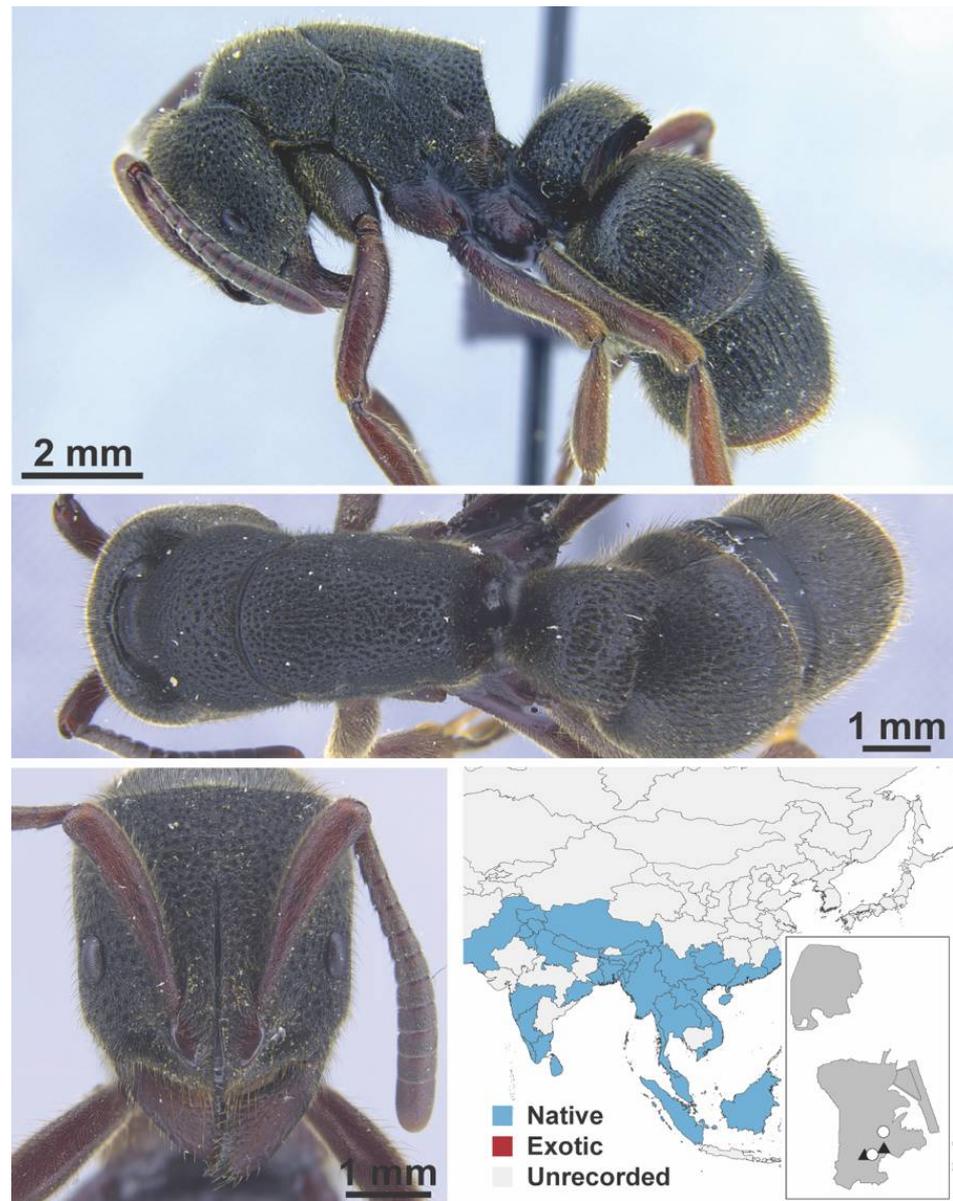


Figure A153. *Pseudoneoponera rufipes* Jerdon, 1851 worker (MAC_S03_LLSA_Sp.1, IBBL).

Appendix A.8 PROCERATIINAE

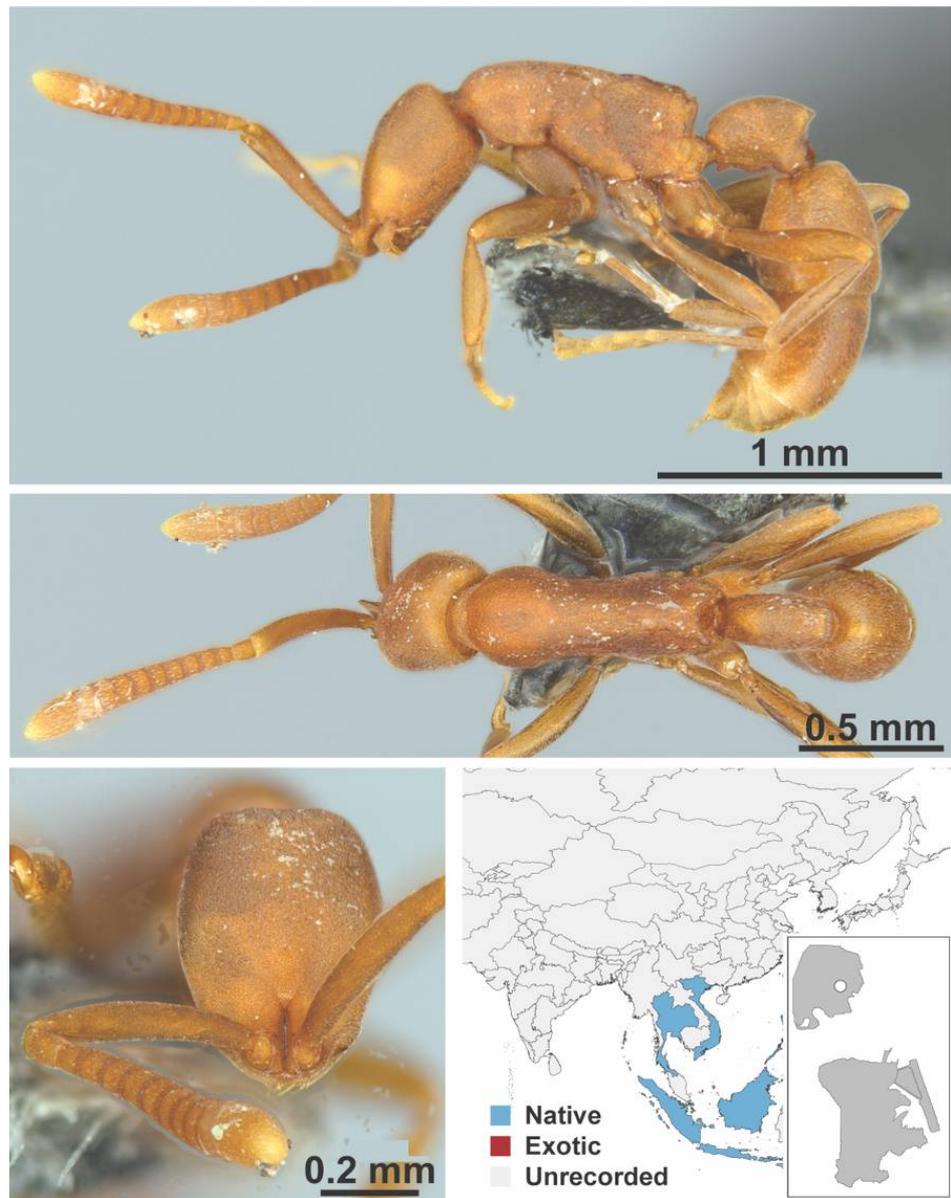


Figure A154. *Probolomyrmex dammermani* Wheeler, W. M., 1928 worker (*Probolomyrmex dammermani*, IBBL).

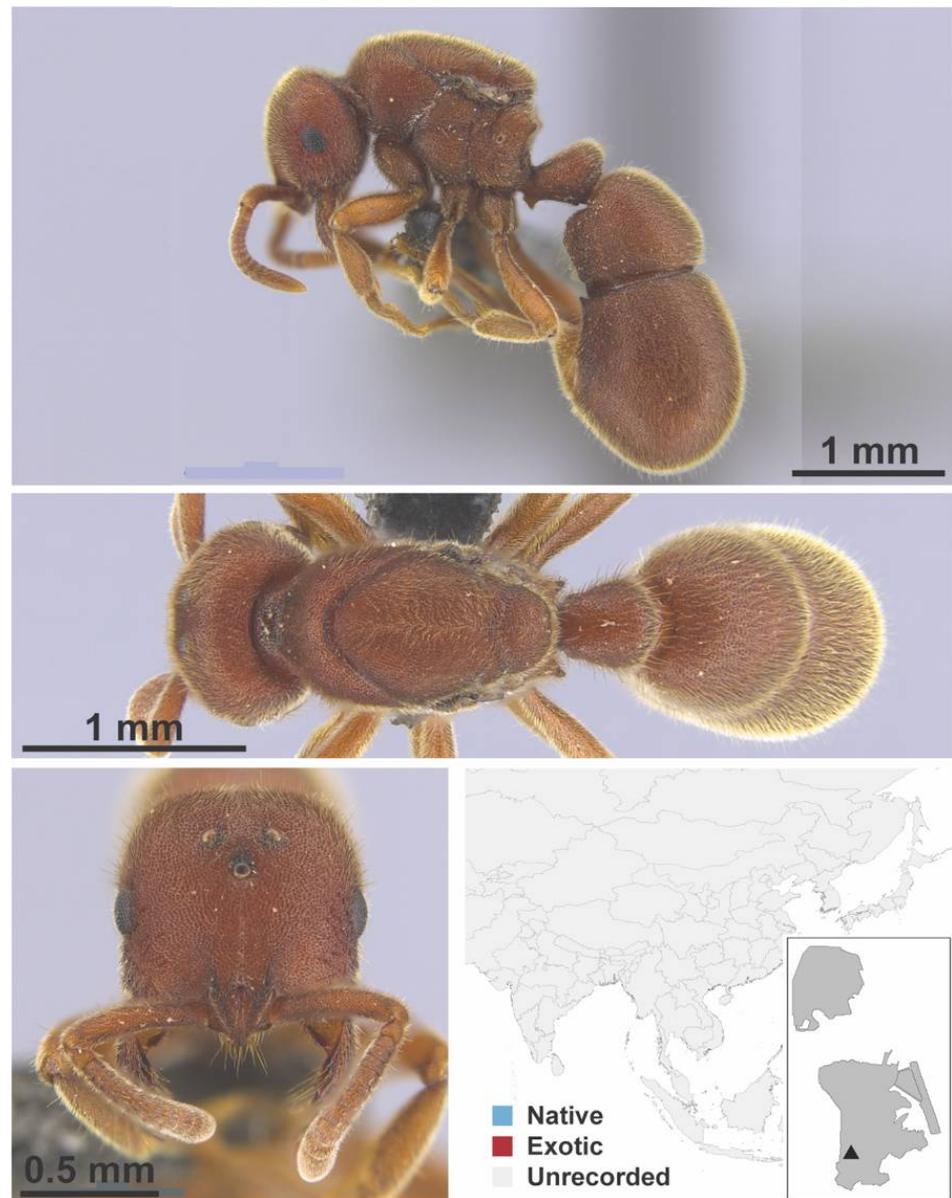


Figure A155. *Proceratium* sp. cf. *bruelheidei* Staab, Xu & Hita Garcia, 2018 queen (MAC_S05_LLSP_Sp.1, IBBL).

Appendix A.9 PSEUDOMYRMICINAE

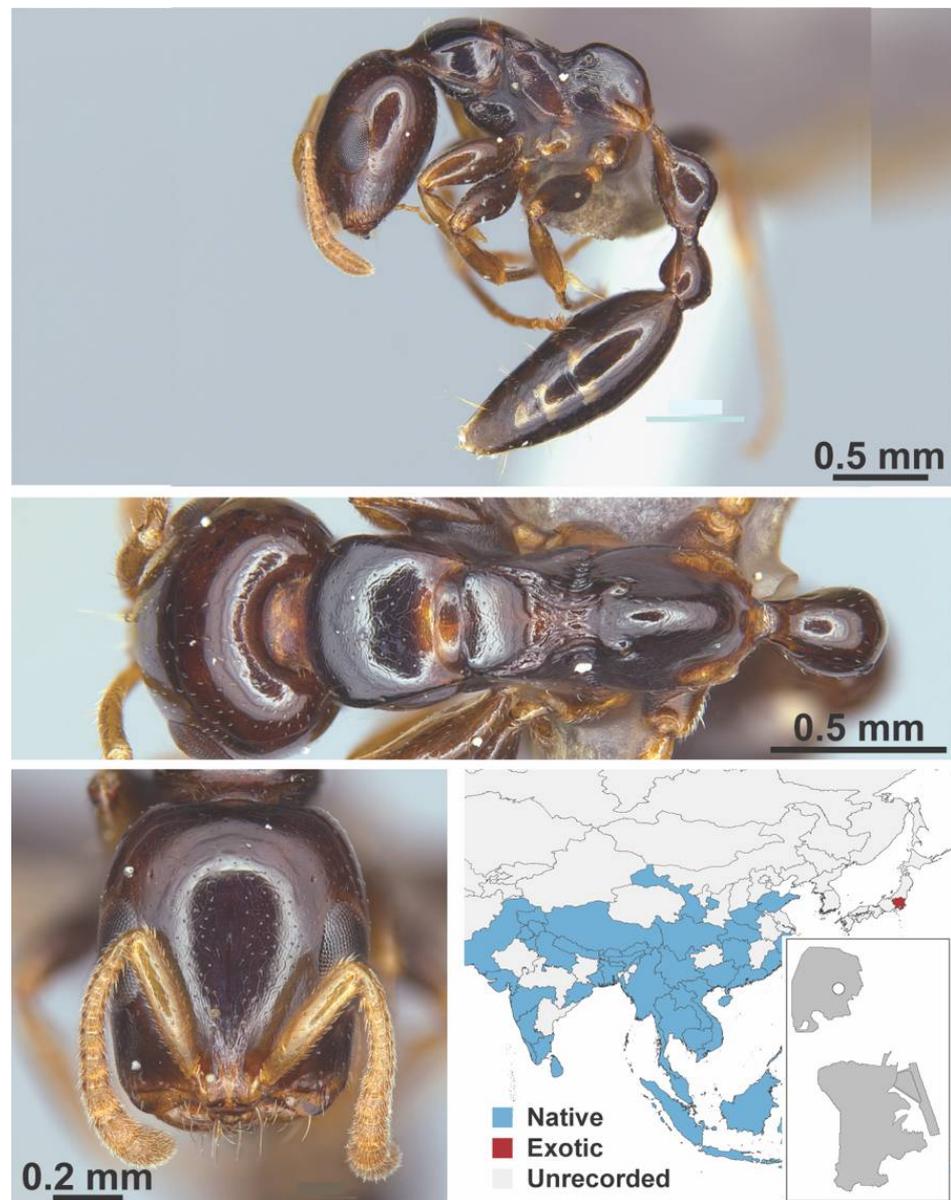


Figure A156. *Tetraponera allaborans* Walker, 1859 worker (*Tetraponera allaborans*, CML collection).

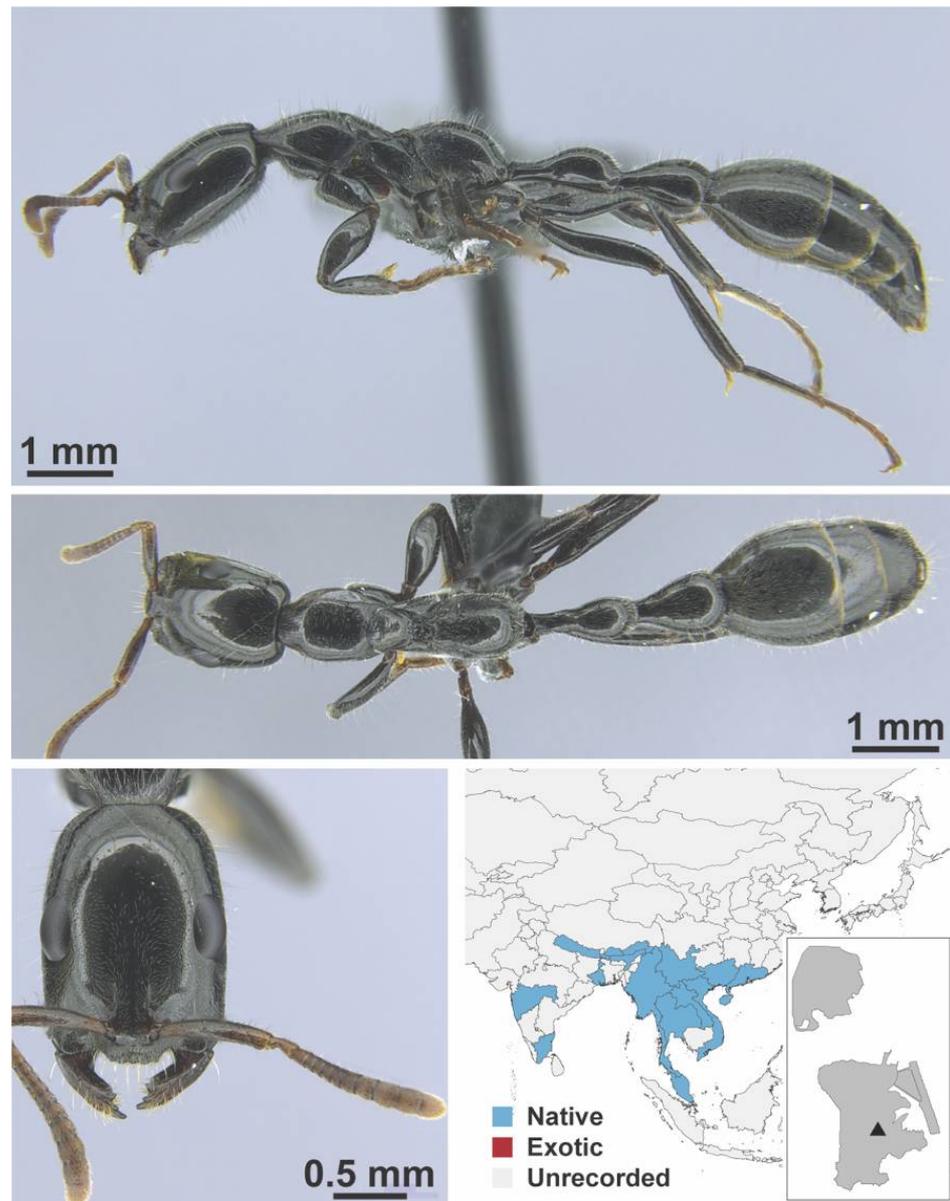


Figure A157. *Tetraponera binghami* Forel, 1902 worker (FB19140, IBBL).

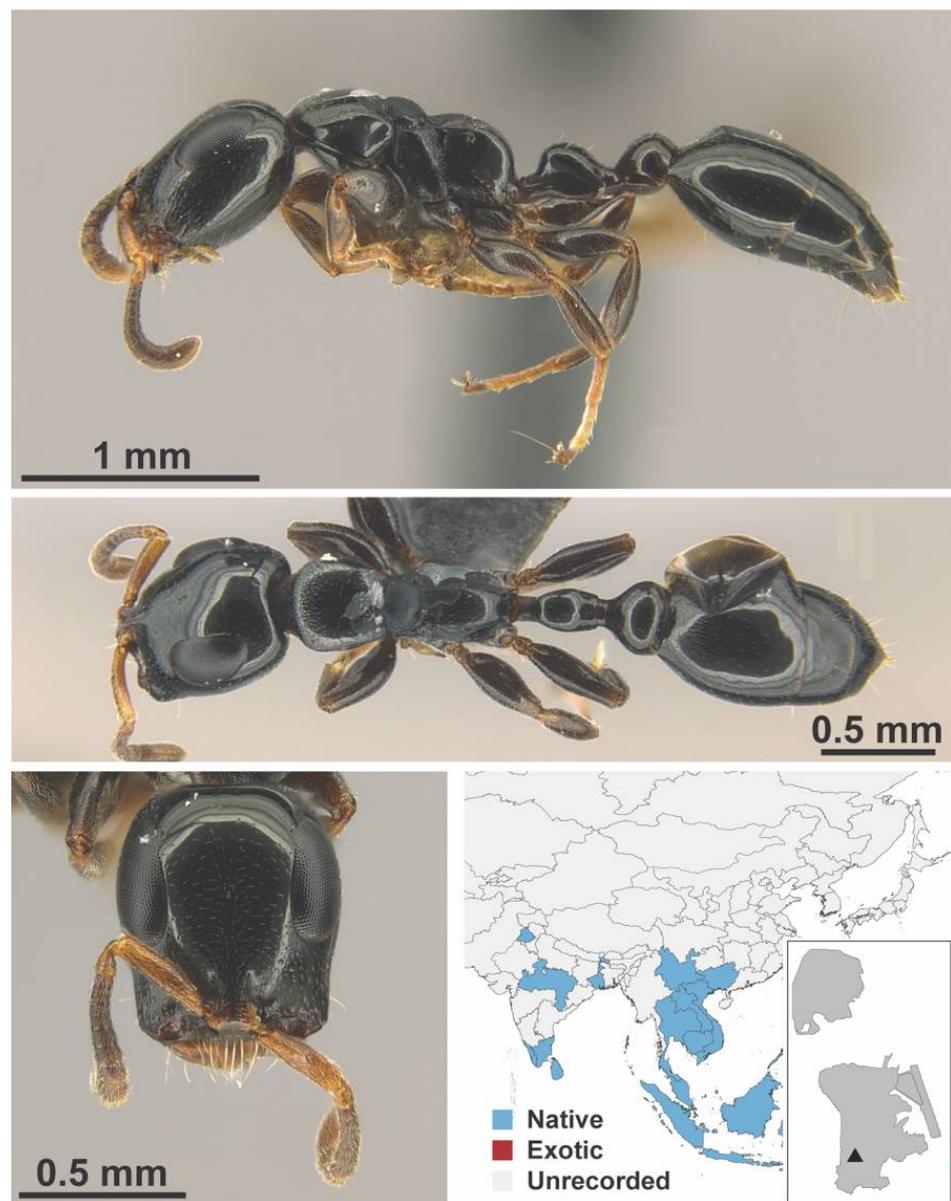


Figure A158. *Tetraponera nitida* Smith, 1860 worker (MAC_GOV_Workshop, IBBL).

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