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3 The distribution of *Apis laboriosa* revisited:
4 range extensions and biogeographic affinities
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31 **Abstract**

32

33 *Apis laboriosa*, the Himalayan giant honeybee, inhabits the foothills of the Himalaya and
34 neighboring mountainous regions. Here we revise its distribution in light of recent reports and
35 discoveries. The range now extends from longitude 105.9°E in Cao Bang, Vietnam, in the east to
36 74.4°E in the Pir Panjal Range of western Himalaya, a linear distance of 3300 km, with the most
37 notable new localities in northeastern Vietnam, central Myanmar, northern Thailand, and AJK-
38 Pakistan. The species generally occurs at lower elevations in the eastern part of its range than in
39 Nepal, northern India, and the border region between India and Pakistan. Most but not all of the
40 new localities are within the range predicted by species distribution modelling. We discuss the
41 new localities that fall outside of the predicted range, the biotic characteristics of the terrestrial
42 ecoregions in which the species occurs, and the remaining regions that may harbor this
43 spectacular honey bee species.

44

45 **Key Words:** *Apis laboriosa*, *Megapis*, Pakistan, Myanmar, Thailand, ecoregion, range map

46 **Short title:** Distribution of *Apis laboriosa*

47

48 1. Introduction

49 “*Distribution maps are among the most fundamental and historically informative*
50 *data of any biogeographic study.*”

51 Parenti and Ebach (2009), Comparative Biogeography

52
53 The Himalayan giant honey bee, *Apis laboriosa* Smith, 1871, has been documented in
54 mountainous regions of Asia, from northern India to northern Vietnam (Kitnya et al., 2020;
55 Huang et al., 2022). It is a significant pollinator and a major source of honey in high-elevation
56 regions of Asia (Batra, 1996; Gupta, 2014; Gogoi et al., 2017). The species was first collected
57 and described from Yunnan, China (Moore et al., 1871), following which it was largely ignored
58 until Maa (1953) resurrected it as a species, *Megapis laboriosa*, and provided a taxonomic
59 description and key for identification. It again faded into obscurity until Sakagami et al. (1980)
60 provided details for a number of distinct characters that clearly distinguish it from its sister
61 species of mainland Asia, *Apis dorsata* F., 1793 (e.g., in workers, the colour of thoracic hairs and
62 gastral tergites, size of ocelli, ocellar platform, ocellocular distance, malar length, and number of
63 sting barbs; see Fig. 1a, b). Recently, genetic and morphometric analyses from several sites of
64 sympatry in Arunachal Pradesh, India, confirmed that *A. laboriosa* and *A. dorsata* are distinct
65 species (Kitnya et al., 2022). Classical morphological taxonomy (Kitnya et al., submitted) and
66 recent genetic analyses (e.g., Arias and Sheppard, 2005; Raffiudin and Crozier, 2007; Lo et al.,
67 2010; Kitnya et al., 2022; Bhatta et al., submitted) also differentiate all populations of these two
68 species.

69 Gradually, through accumulation of specimens, increasing amounts of research, and
70 observations by naturalists, the distribution of *A. laboriosa* has been elucidated. Maa (1953)

71 described its range as limited to “India (Sikkim; Assam); China (W. Yunnan). Probably also
72 occurring in N. Burma.” Sakagami et al. (1980) created the first range maps for *A. laboriosa*,
73 depicting it as a resident from central Nepal to Yunnan, China. Batra (1996) reported it from
74 mountain valleys of Uttarakhand, India, ca. 600 km northwest of where it was known to occur in
75 Nepal. Its distribution was further extended northward to Sichuan Province, China, and eastward
76 to northern Laos (Otis, 1996) and at about the same time even further eastward to northwestern
77 Vietnam (Trung et al., 1996). Gogoi et al. (2017) provided a generalized range map that showed
78 it extending southward in the mountains near the border between northeastern India and western
79 Myanmar. An updated distribution map that integrated information from the literature,
80 iNaturalist reports, museum collections, and the authors’ personal observations added numerous
81 localities in Bhutan, northeastern India, and northern Vietnam, and confirmed that it occurs in
82 the Naga Hills of northeastern India and Chin Hills of west central Myanmar (Kitnya et al.,
83 2020). Most recently, Huang et al. (2022) added several localities in China and Myanmar.

84 Kitnya et al. (2020) used rainfall and elevation patterns to suggest a number of regions
85 where *A. laboriosa* was likely to occur but had not been documented: the Pir Panjal Range at the
86 border between India and Pakistan; western Nepal; eastern Myanmar, and possibly as far south
87 as Thailand; and along river valleys that extend into the eastern edge of the Hengduan Mountains
88 of China. Subsequently, a species distribution model was generated for *A. laboriosa* by Huang et
89 al. (2022). Species distribution modelling (SDM; also referred to by other names such as
90 ecological niche modelling) allows one to predict the complete range of a species based on the
91 environmental characteristics of sites where it has been documented to occur (Guisan et al.,
92 2017). The range estimated by Huang et al. (2022) echoed most of the same regions predicted by
93 Kitnya et al. (2020), as well as sites in northeastern Vietnam and a region on the Tibetan Plateau.

94 Here, we report several new discoveries that significantly extend the range of *Apis*
95 *laboriosa* further to the east, south, and west. New discoveries in Xizang, China, provide hints
96 about its possible migrations along river valleys. Evaluation of the biotic characteristics of the
97 ecoregions (Olson et al., 2001; Dinerstein et al., 2017) and the climatic zones (Geiger, 1961;
98 Kottek et al. 2006) it inhabits may be instructive in predicting other locations where this species
99 does and does not occur.

100 2 Methods

101

102 To create our revised range map for *Apis laboriosa*, we began with a base map of Asia from
103 OpenStreetMap-Boundaries (OSMBoundaries, 2024). Then, using QGIS (Version 3.32.2-Lima),
104 we mapped locality records we obtained from various sources onto the base map. The lowermost
105 layer consists of the records with coordinates reported in the supplementary data file to Kitnya et
106 al. (2020). We have eliminated several of their records that lacked a source or for which the
107 geographic coordinates had previously been approximated, resulting in 339 records, and we
108 corrected one site in SE Nepal that previously had been entered incorrectly. We then added a
109 layer showing the localities used by Huang et al. (2022) for species distribution modeling,
110 excluding the records already reported by Kitnya et al. (2020) and those reported in GBIF (2023)
111 and iNaturalist (2023a, b) (explained below).

112 In the third layer we have presented records obtained from the Global Biodiversity
113 Information Facility (GBIF). GBIF (2023) reported occurrences of *A. laboriosa* in 8 datasets; we
114 reviewed all of those (up to 3 November, 2023). Because records with coordinates from the
115 Snow Entomological Museum, University of Kansas, and the US National Museum had been
116 included by Kitnya et al. (2020) and most other GBIF records either lack coordinates or

117 identifiable photos of the bees, we only obtained five new records from GBIF, all from the
118 citizen science database Observation.org (Observation, 2023). Following the example of Dorey
119 et al. (2023), we also checked the Symbiota Collections of Arthropods Network (SCAN, 2023);
120 it contained only the records for specimens housed in the Snow Entomological Museum which
121 already had been retrieved from the GBIF database. iDigBio (2023) lacked records for this
122 species. Data for specimens housed in the Natural History Museum London were included by
123 Kitnya et al. (2020). There were no specimens in the American Museum of Natural History, the
124 Chicago Field Museum, or the Bishop Museum (Hawaii).

125 In the fourth layer, we have presented records from three citizen-science databases that
126 contain identifiable images of bees in searches of *Apis laboriosa* or *Indicator xanthanotus* Blyth,
127 the yellow-rumped honeyguide that is intimately associated with nests of the bee: iNaturalist
128 (iNaturalist, 2023a, 2023b; all posted records for the species checked between 28–30 October,
129 2023), and the Bhutan Biodiversity Portal (BBP, 2023) and Macaulay Library (2023) (sightings
130 with photographs reported to eBird) (both reviewed on 7 November, 2023). Recent records that
131 show abandoned honeycombs without identifiable bees were excluded. One additional locality
132 was obtained from specimens housed in the insect collection of the Institute of Ecology and
133 Biological Resources, Hanoi, Vietnam. After removing the records previously extracted from
134 these websites and included by Kitnya et al. (2020), we found 61 verifiable postings.

135 We searched the Web of Science under the topic “*Apis laboriosa*” on 11 November, 2023
136 and retrieved several recently published papers. J.S. Xu (pers. comm.) confirmed the coordinates
137 of the two locations from which mtDNA genomes were sequenced (Tang et al., 2003). Cao et al.
138 (2023) reported five regions within Yunnan and Xizang, China, from which colonies were
139 sampled; we have included two of those with narrow ranges of latitude and longitude. Gautam et

140 al. (2022) studied pollination by honey bees at two sites in Uttarakhand, India. M. Kato (pers.
141 comm.) confirmed one site where he and his associates observed *laboriosa* in Laos (Site S4 of
142 Kato et al., 2020). Localities reported in Vietnam by Long et al. (2012) were not added because
143 it seems that their identifications of *A. laboriosa* and *A. dorsata* were likely confused. These
144 localities from literature sources were plotted in the fifth layer.

145 The 6th layer shows 39 new localities where *A. laboriosa* was observed by the authors or
146 it was reported to them by reliable sources (e.g., honey-hunters) who included videos or
147 photographs with identifiable images of bees.

148 Finally, we added the uppermost 7th layer with 16 observations that seem credible but are
149 not supported by specimens, photographs, or videos.

150 To better understand the communities inhabited by *A. laboriosa*, we reviewed the
151 ecoregions established by Olson et al. (2001) and Wikramanayake et al. (2002) and Köppen-
152 Geiger climatic zones (Geiger, 1961; Kottke et al., 2006, Karki et al., 2016) that are known to be
153 inhabited by *A. laboriosa*.

154 The geographical terminology of Liu et al. (2022) for the Pan-Tibetan Highland region
155 has been adopted.

156 3 Results

157 Figure 2 depicts the revised range of *Apis laboriosa*. It was created using data from refereed
158 research publications, museum specimens, records with identifiable images of bees in publicly
159 available databases, personal observations of the authors, and photos/videos and their
160 coordinates submitted to the authors by honey-hunters and beekeepers. This map extends the
161 distribution in three cardinal directions—east, south, and west—and fills in several previous
162 gaps.

163 In the east, in Vietnam and eastern Laos, the number of known localities was more than
164 doubled, with the most easterly nests documented to date in Cao Bang Province, Vietnam
165 (22.6°N, 105.9°E; Pham et al., 2023), nearly 200 km east of localities reported by Kitnya et al.
166 (2020). Interestingly, although most nests in Vietnam are aggregated on cliffs (Fig. 1D), in some
167 regions a higher proportion of nests are constructed on tree branches (Fig. 1E).

168 Across China, a number of new records add to the many already reported from there. Of
169 note are the observations along several river valleys that extend northward into Xizang and
170 Yunnan Provinces. For example, X. Zhou and his students recently collected specimens from
171 several sites in Jilong County, Xizang, near the border of Nepal, and within the Kirong Tsangpo
172 (called the Trishuli River in Nepal) drainage. Two nearly 50-year-old specimens in the National
173 Zoological Museum of China were also collected in this same region. Cao et al. (2023) collected
174 samples from several villages in Rikaze, Xizang, in the watershed of Phung Chu (the upper
175 reaches of the Arun River) that extends northward from eastern Nepal. Further to the east, Huang
176 et al. (2022) reported on specimens housed in the National Zoological Museum of China
177 collected in the upper regions the Brahmaputra River: one along the Yarlung Zangbo River (in
178 Motuozen, Medog County), and another near Bomé along the Palong Zhangbo River, a
179 tributary to the Yarlung Zhangbo, both in Nyingche Prefecture, Xizang. Cao et al. (2023)
180 analyzed specimens collected in the nearby watershed of the Palong Zhangbo River. In Yunnan,
181 Yang et al. (2015) reported the species from Deqin County (Shengpingzhen), near the Lancang
182 River (upper Mekong River; included in Huang et al., 2022). We did not learn of any recent
183 records from Sichuan Province.

184 In India, seven new records from Sikkim and West Bengal States (iNaturalist, 2023a, b)
185 confirm previous old specimens collected in 1924 and 1938 in that region (Kitnya et al., 2020).

186 We have confirmed *A. laboriosa* in four districts of Karnali Province in western Nepal.

187 We also learned from agricultural extension agents, honey sellers, and honey hunters of
188 additional three regions that we were unable to verify (e.g., Kalikot, Salyan and West Rukum
189 Districts, Karnali Prov.; Bajura District, Sudurpashchim Prov.); these have depicted with open
190 circles in Figure 2.

191 Several remarkable new records come from the southern and western edges of the range
192 of the species. In extreme northwestern Thailand, *A. laboriosa* was independently observed
193 foraging and nesting at the highest point in Doi Pha Hom Pok National Park, by nature
194 photographers (iNaturalist, 2023a) and park personnel (Vorahab et al., 2024). In central
195 Myanmar, bees collecting fluids from soil were photographed northwest of Taunggyi, in central
196 Myanmar (21.1°N, 96.8°E), near mountains that exceed 2000 m in elevation at the western edge
197 of the Shan Plateau. Y.Q. Peng collected the species above 3000 m on Mt. Victoria (Natma
198 Taung), Chin State, western Myanmar (21.2°N, 93.9°E) (Huang et al., 2022).

199 Most surprisingly, we have confirmed that *A. laboriosa* inhabits the Neelum Valley, a
200 region in northern Azad Jammu and Kashmir, Pakistan (AJK-P) dominated by coniferous trees
201 (latitude 34.8°N). Active colonies were observed in Taobat at 2750 m elevation and foragers
202 were observed on red and white clover (*Trifolium* spp.) in both Taobat and Arang Kel.
203 Aggregations of nests or foragers that were likely but not confirmed to be *A. laboriosa* were
204 observed in Leepa; along the Neelum Jhelum River, and in Tolipir National Park. The giant
205 honey bees reported by Khan et al. (2014) from Murree, Pakistan, at ca. 2000 m, were likely *A.*
206 *laboriosa* that were incorrectly reported as *A. dorsata*. We have included these probable
207 localities as open circles on Figure 2 (see also Supplementary Data File).

208 Our review of the ecoregions of Asia (Wikramanayake et al., 2002) indicates that *A.*
209 *laboriosa* predominantly inhabits the Tropical and Subtropical Moist Broadleaf Forests Biome in
210 several ecoregions (Northern Indochina Subtropical Forests, Chin Hills-Arakan Yoma Montane
211 Rain Forests, Meghalaya Subtropical Forests, Eastern Himalayan Broadleaf Forests, Himalayan
212 Subtropical Broadleaf Forests, Western Himalayan Broadleaf Forests). All of these ecoregions
213 exhibit strong Himalayan biogeographic affinities (e.g., a predominance of oaks and numerous
214 rhododendrons) and have moist to wet climates. Additionally, some localities in the western part
215 of its range lie within the Himalayan Subtropical Pine Forests ecoregion and possibly Western
216 Himalayan Subalpine Conifer Forests (e.g., at Rara Lake, Nepal and the Neelum Valley, AJK-
217 Pakistan).

218 Over most of its range, from Yunnan, China, to Uttarakhand, India, and southward along
219 the Arakan Mountains, *A. laboriosa* inhabits the Cwb (warm temperate, winter dry, warm
220 summer) climate zone (Kottek et al., 2006). In contrast, in northern Vietnam and Laos the
221 occupied climate zone is Cwa (warm temperate, dry winter, hot summer) and Cfa (warm
222 temperate, fully humid, hot summer). In most parts of AJK-Pakistan, the inhabited regions are
223 classified as Cfb (warm temperate, fully humid, warm summer), but the Neelum Valley is
224 classified as Dfb (snow, fully humid, warm summer) (Geiger, 1961). These classifications are
225 averages for the regions inhabited by the bee; in mountainous areas, microclimates can differ
226 considerably over short distances due to local differences in elevation and rainfall.

227 4 Discussion

228 Our compilation of records provides the most up-to-date and comprehensive database for
229 occurrences of *Apis laboriosa* (Supplementary Data File). We have indicated the categories of
230 the sources of information, should others want to exclude some types of data from future

231 analyses. The new observational records are conservative, in that for us to include them they
232 were either made by one of the authors who is familiar with the species or were accompanied by
233 a photo or video with identifiable bees, specimens, or publicly accessible DNA sequences.

234 We report here many new localities for *A. laboriosa* in northern Vietnam and Laos, more
235 than one quarter of which were at elevations <1000 m, including what appears to be a combless
236 wintering swarm (Fig. 1c; see Underwood, 1990), (Fig. 2). This species is widespread in the
237 highlands of northern Vietnam, where we report for the first time that solitary nests are regularly
238 constructed on tree branches, sometimes more frequently than on cliffs (C.H. Phung,
239 unpublished data; Fig. 1e). Laos remains poorly sampled. The new records we report coupled
240 with predictions from species distribution modelling (Huang et al., 2022) suggest that this
241 species is likely much more widely distributed in northern Laos than has been documented. The
242 mountains of northern Vietnam and Laos are the southeasternmost extension of the Himalaya
243 Range (Sterling et al., 2006) and exhibit considerable Himalayan biogeographic affinities (e.g.,
244 Spitzer et al., 1993; Bain and Truong, 2004; Sterling et al., 2006; Bakalin et al., 2018, 2023) that
245 undoubtedly influence the success of the bee there. In contrast, further south in the Central
246 Highland region of Vietnam, despite some Himalayan influences in the flora (e.g., Vuong and
247 Sridith, 2016; Wu et al., 2023), several searches by C.H. Phung and his colleagues for *A.*
248 *laboriosa* in the region south of 15.5°N latitude and at elevations >1000 m have failed to detect
249 this species. This may be a consequence of the habitats having unsuitable flora and/or climate, or
250 a lack of connectivity with populations in the northern highlands resulting from the broad region
251 between 16.5°–18.7°N latitude where elevations do not exceed 700 m.

252 We have now confirmed the species from several sites in western Nepal. An apparent gap
253 in its distribution in that part of Nepal was discussed by Kitnya et al. (2020). Considering the

254 new records (both confirmed and tentative), that gap likely represented a lack of scientific
255 exploration in that remote part of the country. It is likely that this species occurs along the entire
256 southern edge of the Himalaya in Nepal in a band of subtropical broadleaf forests
257 (Wikramanayake et al., 2002) with Cwb climate (Karki et al., 2016), with extensions into
258 landscapes dominated by conifers. The relatively dry environment of western Nepal may cause
259 its occurrence there to be patchy (Karki et al., 2016). Additional confirmations through well
260 documented observations and collections are warranted.

261 Both Kitnya et al. (2020) and Huang et al. (2022) predicted the occurrence of *A.*
262 *laboriosa* along river valleys that extend into the Tibetan Plateau and Hengduan Mountains of
263 China. This prediction is supported by observations of bees in the upper watersheds of the
264 Trishuli River/Kirong Tsangpo, Arun River/Phung Chu, Brahmaputra River/Yarlung
265 Zangbo/Tsangpo, and the Mekong River/Lancang. Despite being surrounded by high mountains,
266 valleys, lower elevations along these rivers experience a subtropical climate dominated by
267 broadleaf forests (Ni, 2000). *A. laboriosa* likely also occurs along the Salween River/Nu Jiang,
268 the Nu River/Jinsha Jiang (the western tributary of the Yangtze River), and possibly more
269 easterly tributaries of the Yangtze (i.e., Dadu, Min, and Jialing). It is not clear if it is a permanent
270 inhabitant of these river valleys or if swarms migrate into them seasonally, as suggested by
271 Underwood (1990) and Kitnya et al. (2020). Research on seasonal altitudinal migrations of this
272 species is long overdue.

273 In Myanmar, *A. laboriosa* occurs near the summit of Natma Taung (Mt. Victoria), within
274 the Chin Hills-Arakan Yoma Montane Rain Forests ecoregion (Wikramanayake et al., 2002).
275 Cloud forests above 2000 m on the mountain are dominated by Himalayan tree taxa and have a
276 distinctly Palearctic temperate flora (Wikramanayake et al., 2002). The Purvanchal and Arakan

277 mountain ranges extend continuously from the Himalaya southward through northeastern India
278 and western Myanmar, providing contiguous habitat and a corridor for bee dispersal along the
279 N/S axis of the mountains. Considering all these factors, the presence of *A. laboriosa* on Natma
280 Taung was anticipated.

281 Discoveries of *A. laboriosa* in central Myanmar and northwestern Thailand extend its
282 distribution southward. These localities are far (ca. 350 km and 240 km respectively) from the
283 closest known populations in Yunnan, China. It was predicted that the species may occur on Doi
284 Pha Hom Pok, Thailand (Kitnya et al., 2020; Huang et al., 2022), as has now been confirmed
285 (iNaturalist 2023a; Voraphab et al., in press). On the Shan Plateau of eastern Myanmar,
286 relatively large areas exceed 1000 m in elevation (see map provided by Evers and Taft 2016), the
287 approximate elevation at which the species was photographed in Pindaya Township, Shan State,
288 and where the climate is classified as “temperate, dry winter, hot summer” (Cwa) (Geiger 1961;
289 Kotttek et al. 2006). Scattered over this region at higher elevations, the climatic zone is
290 “temperate, dry winter, warm summer (Cwb) and more suitable for the bee. *Apis laboriosa* likely
291 inhabits many of these high elevation sites on the Shan Plateau, some of the more southerly of
292 which were not predicted by Huang et al. 2022. It may even occur as far south as Nattaung
293 (latitude 18.8°N), the highest mountain (2623 m) of the Karen Hills, and the high elevation
294 region surrounding that mountain.

295 The most exciting new discoveries are located in the Pir Panjal Range, in regions
296 administered by Pakistan, ca. 530–630 km northwest of the closest known populations of *A.*
297 *laboriosa* in Uttarakhand, India. Visual observations in four different regions of AJK-Pakistan
298 were made by U.A.A. Sheik and A.H. Faiz who are very familiar with *Apis dorsata*, the species
299 with which it would most likely be confused. They identified *A. laboriosa* at four sites in the

300 Neelum Valley, Leepa Valley, and along the Jhelum River on the basis of coloration of bees that
301 were observed both foraging on flowers and nesting on rock cliffs. In the Neelum Valley they
302 were observed in September at high elevations (e.g., >2500 m). Unfortunately, specimens and
303 photographs that support these observations are currently lacking. The climate in the sites the
304 bees have been reported from spans zones Cfb (Temperate, no dry season, warm summer), Dfb
305 (cold, no dry season, warm summer), and Dsb (cold, dry summer, warm summer) in the upper
306 Neelum Valley; Geiger 1961). Interestingly, some of these sites are dominated by conifers (e.g.,
307 Ecoregion 31: Himalayan subtropical pine forests) rather than broadleaf evergreen forests
308 (Wikramanayake et al., 2002), suggestive that the niche of the species is broader than indicated
309 by the predominantly broadleaf forests it usually inhabits elsewhere. Kitnya et al. (2020)
310 predicted its occurrence in AJK-Pakistan. In contrast, although Huang et al. (2022) indicated it
311 may occur near Srinigar, India, their species distribution modeling results did not include regions
312 administered by Pakistan. Earlier reports of *Apis dorsata* at three sites at ca. 2000 m elevation
313 near Murree, Pakistan, were likely of *A. laboriosa* (Khan et al., 2014; specimens not retained,
314 K.A. Khan, pers. comm.). We have depicted unconfirmed sites with open circles on our revised
315 distribution map (Fig. 2) in the hope that others will be stimulated to confirm the occurrence of
316 this disjunct population and study its biology in the Pir Panjal Mountain Range.

317 Species distribution modelling predicted most of the new sites in which *A. laboriosa* has
318 now been documented, showing the general utility of this research tool. However, it failed to
319 detect the Central Myanmar and AJK-Pakistan localities. Conversely, it did predict its
320 occurrence on the southwestern Tibetan Plateau (between ca. 81.0–85.3°E longitude; Huang et
321 al., 2022), for example in the upper basin of the Yarlung Zangbo River in Zhongba and Saga
322 Counties, Xizang. This is a semi-arid region dominated by grasslands, with mean annual

323 temperature <0°C (Wang et al., 2020). The climate over most of this region has been classified
324 as “Polar, tundra” (ET), with small portions of the region classified as “Snow, winter dry, warm
325 summer (Dwb)” and “Snow, winter dry, cool summer” (Dwc) (Kottek et al., 2006). As discussed
326 above, the species has been documented along the Yarlung Zangbo River, but much further to
327 the east (Medog County, Nyingche/Linzhi) which, along with many other parts of Yunnan, has
328 broadleaf forests and climate classified as “Warm temperate, winter dry, warm summer” (Cwb)
329 (Kottek et al. 2006). The high elevation (>4000 m), cold climate, and alpine meadow vegetation
330 of the Tibetan Plateau north of Himalaya (Li et al. 2010), as well as the lack of river valleys that
331 could serve as migration corridors to warmer sites within migration distance on the southern
332 edge of the mountains, make it questionable that *A. laboriosa* inhabits this region. Two sites on
333 the Tibetan Plateau reported by Kitnya et al. (2020), the geographic coordinates of which were
334 estimated from a general description of their location, have been removed from the current data
335 (Supplementary Data). The environmental conditions at those sites may have influenced the
336 species distribution modelling of Huang et al. (2022). The questionable existence of this species
337 in this part of southwestern Xizang should be checked through field work.

338 Our analysis shows that *Apis laboriosa* occurs from northeastern Vietnam to AJK-
339 Pakistan, an linear east-west distance of ca. 3300 km, and from Sichuan, China, in the north to
340 northern Thailand in the south. It is a regular inhabitant of high elevation, moist evergreen
341 broadleaf forests with strong Himalayan floral influences. In the western portion of its range it
342 extends into coniferous forests. We anticipate that *A. laboriosa* will eventually be confirmed in
343 appropriate habitats/climates of: (1) the mountains of Himachal Pradesh and (2) Jammu in
344 regions administered by India; (3) the sites we have provisionally shown, as well as the Murree
345 Hills and the Galis in regions administered by Pakistan; (4) additional sites in an elevational

346 band with appropriate climate and habitat across western Nepal; (5) at numerous sites in northern
347 Laos, particularly in the northeast; and (6) scattered over the Shan Hills of eastern Myanmar,
348 potentially as far southward as the Karen Hills. We hope that this reassessment of the range of
349 *Apis laboriosa*, coupled with hints of ecological differences over this large region, will inspire
350 more detailed studies of its ecology, population genetics, migratory behavior along river systems,
351 and role as a pollinator within agroecosystems (e.g., Gautam et al., 2022) and natural
352 communities (e.g., Kato et al., 2020).

DRAFT

353 [Data Availability](#)

354 All locality information used to generate the distribution map (Fig. 2) is presented in the
355 Supplementary Data.

356

357 [Ethics Statement](#)

358 Ethics review and approval were not required for this study. *Apis laboriosa* is not endangered,
359 nor is it listed under CITES.

360

361 [Author Contributions](#)

362 GWO and NK: conceptualization; MJH, YQP, UAAS, AHF, CHP, NW, XZ, HMO, NA: field
363 work and contacting honey hunters and beekeepers; GWO: searching websites and literature for
364 locality data; NK: creation of the distribution map; GWO: photos of the worker and drone; CHP:
365 photo of tree nest; GWO: writing manuscript drafts. All authors edited and approved the
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367

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389

390 Conflict of Interest

391 The authors declare that the research was conducted in the absence of any commercial, financial,
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393

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545 Figure Legend

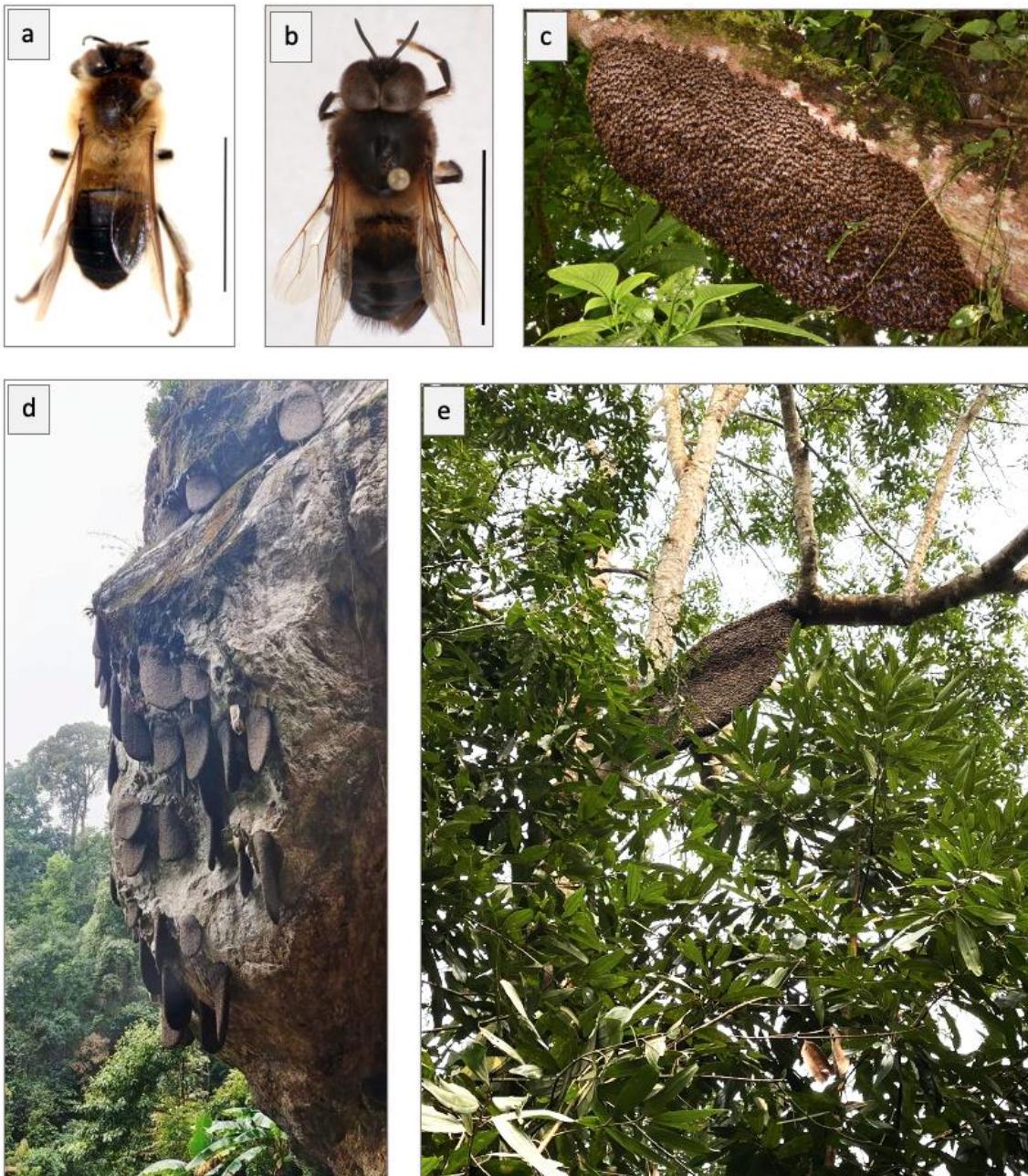
546

547 Figure 1. Habitus of worker (a) and drone (b) of *Apis laboriosa*; scale bar: 1 cm; specimens
548 collected by B.A. Underwood, Kaski District, Nepal, 1675 m elevation (specimens in the Cornell
549 University Insect Collection). (c) Wintering swarm (bivouac) on a tree branch 2–3 m above
550 ground in Yen Bai Province, Vietnam, at 1200 m elevation; photo taken on 20 November 2022
551 by Eugene Popov. (d) Typical aggregation of nests on a cliff in Dien Bien Province, Vietnam;
552 photo taken by Lo Van Anh of Son La Province. (e) *Apis laboriosa* nest constructed on a tree
553 branch in Van Ban District, Lao Cai Province; photo taken by C. H. Phung.

554

555 Figure 2. Revised distribution of *Apis laboriosa*. The colors of the dots reflect the source of
556 locality information as indicated in the key at the lower left. Solid circles depict confirmed
557 localities; open circles indicate probable localities based on credible reports that lack confirming
558 photos, videos, or specimens.

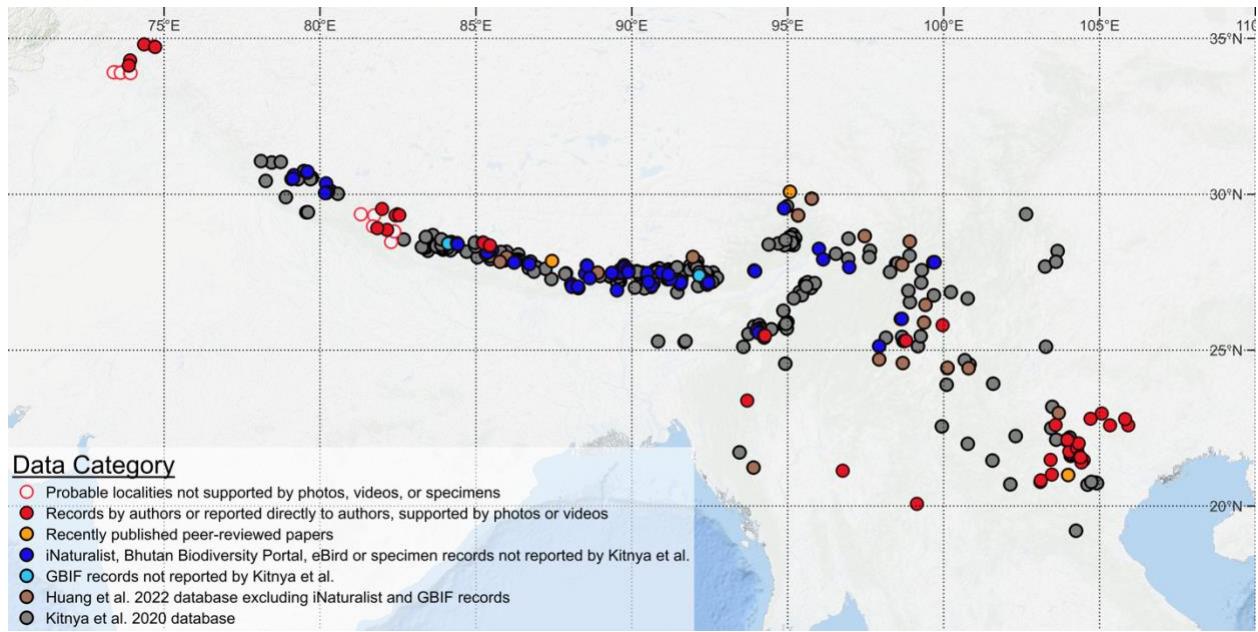
559 Figure 1.



560

561 Figure 2.

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