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Notes on *Cataglyphis* Foerster, 1850 of the *bicolor* species-group in Israel, with description of a new species (Hymenoptera: Formicidae)

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ABSTRACT

Five species of *Cataglyphis* belonging to the *bicolor* species-group are recorded from Israel, including a new species, *C. israelensis* n. sp. The relationships of the new species with other *bicolor* group species in the region, and relationships among species in the *niger* species-complex are discussed. The identification of isolated specimens belonging to the five Israeli species by morphological characters is investigated.

KEYWORDS: Hymenoptera, Formicidae, *Cataglyphis*, ants, Middle East, morphometry, new species.

INTRODUCTION

The classification and nomenclature of ants in the genus *Cataglyphis* is notoriously challenging due mainly to a high intraspecific variability among local populations (Knaden *et al.* 2012). At the beginning of the 20th century A. Forel and F. Santschi recognized several 'superspecies', which they divided into many geographical 'races'/'stirpes' and local varieties, in order to cope with this variability, but with limited success. For example, from Jerusalem, in addition to *Myrmecocystus viaticus* F. subsp. *niger* André (Forel 1910), was recorded a variety of *M. viaticus* F. r. *desertorum* Forel 'transitory' to r. *niger* (Forel 1904) as well as a form of *Cataglyphis bicolor* F. st. *nodus* Brullé v. *drusa* Santschi 'making the passage' to var. *assyria* Santschi (Santschi 1934), with *drusa* itself being a split-off of *nigra* that was described as 'making the passage' between *C. bicolor nodus* v. *desertorum* and *C. bicolor* st. *nodus* (Santschi 1929). Because *C. bicolor nodus* v. *drusa* Santschi and *C. bicolor nodus assyria* Santschi are unavailable names in the *nodus* species-complex (Agosti 1990) they will be referred to hereinafter as '*drusa*' and '*assyria*', respectively.

In modern reviews, based primarily on the morphology of males (Agosti 1990; Radchenko 1997) and workers (Radchenko 2001), the genus is divided into the informal categories of 'species-group' and 'species-complex', with the latter including previously described taxa that may or may not designate biological species. There is good agreement at species-groups level between classifications based on morphology and recent comprehensive molecular phylogenies of *Cataglyphis*

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(Knaden *et al*. 2012; Aron *et al.* 2016); the species-complexes, however, are split into distinct, statistically well-supported clusters.

In the last published checklist of ants of Israel, Vonshak and Ionescu (2010) listed six *Cataglyphis* species in the *bicolor* species-group: *C. holgerseni*, *C. isis*, *C. niger*, *C. savignyi*, *Cataglyphis* sp. IL02 and *Cataglyphis* sp. IL04. Following the diagnosis of species-complexes by Agosti (1990), and previous taxonomic work (Kugler 1988), it was suggested that the unnamed *C*. sp. IL02 belongs to the *nodus* species-complex, while *C*. sp. IL04, together with *C. niger* and *C. savignyi* belong to the *niger* species-complex. However, further chemical and genetic characterization of species in this group (Zeltzer 2013; Eyer unpubl. data) and studies of population structure (Saar *et al*. 2014; T. Reiner Brodetzki, pers. comm., 2016) later indicated that the identification of the Israeli ants using modern identification keys (e.g., Collingwood & Agosti 1996; Radchenko 1998) may be unreliable. The '*niger*' morph was distributed across distinct genetic clusters and *C.* sp. IL04 was split between *C.* sp. IL02 and *C. savignyi*.

Similar taxonomic issues regarding the *bicolor*-group were also highlighted by Knaden *et al*. (2012) and Aron *et al*. (2016). For example, *C. savignyi* in Aron *et al*. (2016) and *C. niger* in Knaden *et al*. (2012), both from the northern Negev in Israel, are genetically similar and close to *C. abyssinica* (Forel) from Egypt, but diverge from *C. niger* of the Coastal Plain of Israel, and are even more distant from *C. niger* of Jordan and *C. abyssinica* (Forel) of Yemen (Aron *et al*. 2016). *C. savignyi* from North Africa forms completely different clusters (Knaden *et al*. 2012; Aron *et al*. 2016), and while *C. savignyi* from Tunisia is similar to Tunisian *C. oasium* Menozzi (Wehner *et al*. 1994), it significantly differs from *C. oasium* of Iran (Knaden *et al*. 2012).

The incongruences between morphological and molecular classifications at the species-complex/species level in the *bicolor* species-group strongly suggest that the previous identifications (Vonshak & Ionescu-Hirsch 2010) require revision. Since there seem to be at least three genetically different species reported in the literature as *C. savignyi* (Knaden *et al*. 2012; Aron *et al*. 2016), *C. savignyi*, including part of *Cataglyphis* sp. IL04, will hereinafter be referred to as *C.* cf. *savignyi*.

Furthermore, *Cataglyphis* sp. IL02 and part of *Cataglyphis* sp. IL04 specimens are described as a new species and its relationships with other *bicolor* species from the Middle East are discussed. We investigate the identification of the Israeli species based on morphology and discuss relationships within the *niger* species-complex.

MATERIALS AND METHODS

The synonymy and nomenclature follows Bolton *et al*. (2006) and Bolton (2016). The original spelling of taxa names is used throughout in the text.

Names of localities and regions in Israel conform to their transliterated names in Kadmon (1997) and CBS (2015). The map of geographic regions of Israel (Fig. 1) is modified from Theodor (1975).

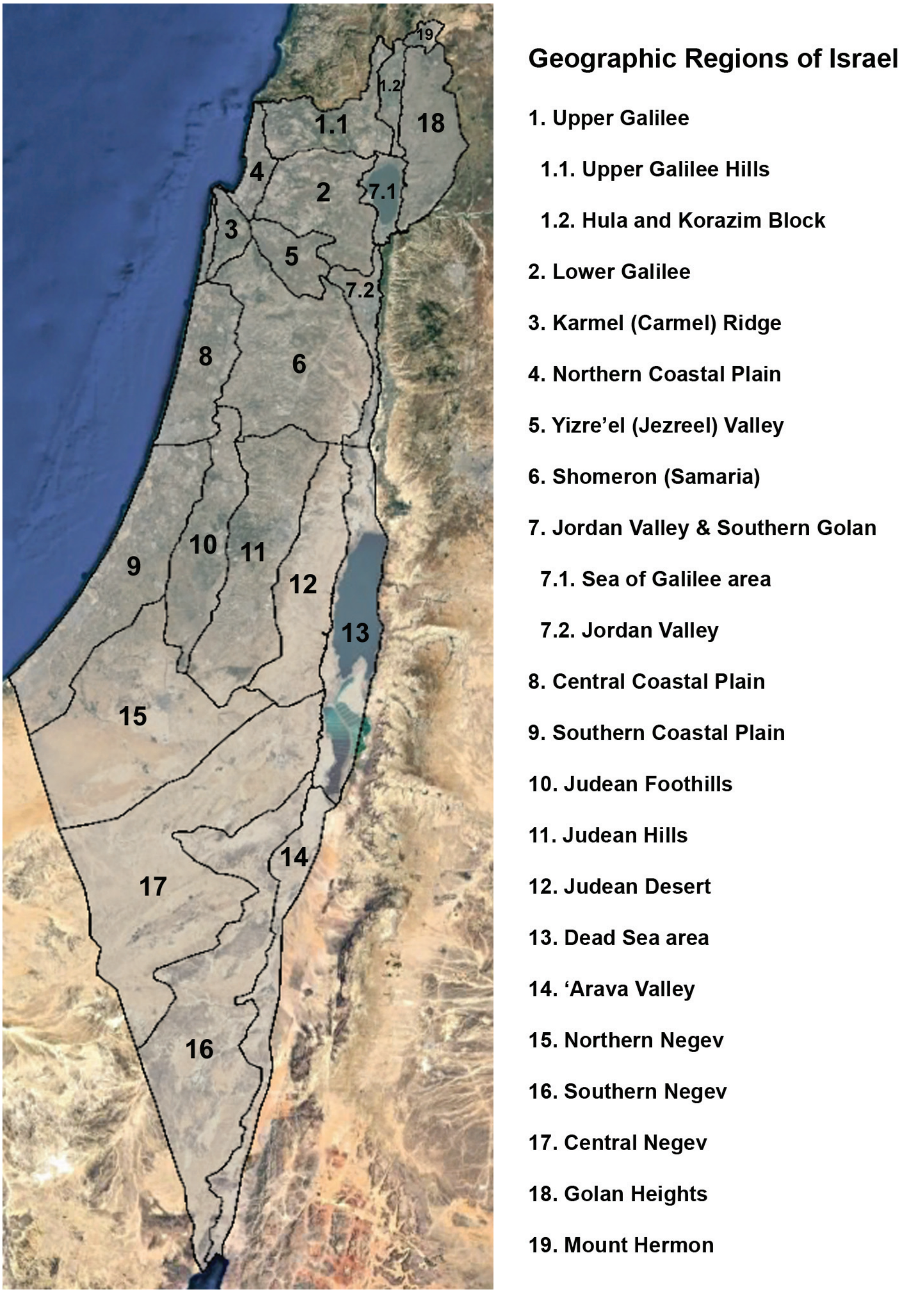


Fig. 1. Map of the geographic regions of Israel.

Measurements (in mm) were taken using a stereomicroscope LEICA MZ 8, fitted with an ocular micrometer. Abbreviations for measurements are as following:

TL (Total Length) – total outstretched length of a specimen, from mandibular apex to gastral apex.

HL (Head Length) – length of head, excluding mandibles, measured in a straight line from anteriormost point of median clypeal margin to midpoint of occipital margin in full-face view.

HW (Head Width) – width of head, below eyes, measured in full-face view.

EL (Eye Length) – maximum diameter of eye.

iOD (inter-Ocular Distance) – minimum distance between eyes, measured in full-face view (Fig. 2).

OcClD (Ocellus-Clypeal Distance) – shortest distance from anterior margin of median ocellus to frontoclypeal suture, measured in-full face view (Fig. 2).

SL (Scape Length) – straight-line length of antennal scape excluding condylar bulb.

F1L (Funiculus segment I Length) – length of 1st funiculus segment (Fig. 3).

F2L (Funiculus segment II Length) – length of 2nd funiculus segment (Fig. 3).

ML (Mesosoma Length) – diagonal length of mesosoma in lateral view from the point at which pronotum meets cervical shield to posterodorsal extremity of mesosoma (as in Fig. 4).

MW (Mesosoma Width) – maximum width of mesosoma in dorsal view.

PrL (Propodeum Length) – diagonal length of propodeum in lateral view from metanotal groove to posterodorsal extremity of propodeum (Fig. 4).

PrH (Propodeum Height) – maximum height measured perpendicularly from propodeum dorsum to imaginary line connecting metanotal groove with posterior margin of propodeum, in lateral view (Fig. 4).

PNL (Petiole Node Length) – length of petiolar node, in lateral view, without anterior and posterior peduncle of petiole, at level of petiole peduncles' dorsal surfaces (Fig. 5).

PNW (Petiole Node Width) – maximum width of petiole node, in dorsal view.

PNH (Petiole Node Height) – maximum height of petiole node measured perpendicular from imaginary line passing at level of petiole peduncles' dorsal surfaces to the highest point of petiole node dorsum, in lateral view (Fig. 5).

PNA (Petiole Node Angle) – angle between anterodorsal surface of petiole node and imaginary line connecting anteriormost and posteriormost points of petiole node in lateral view, measured as tangent (Fig. 5).

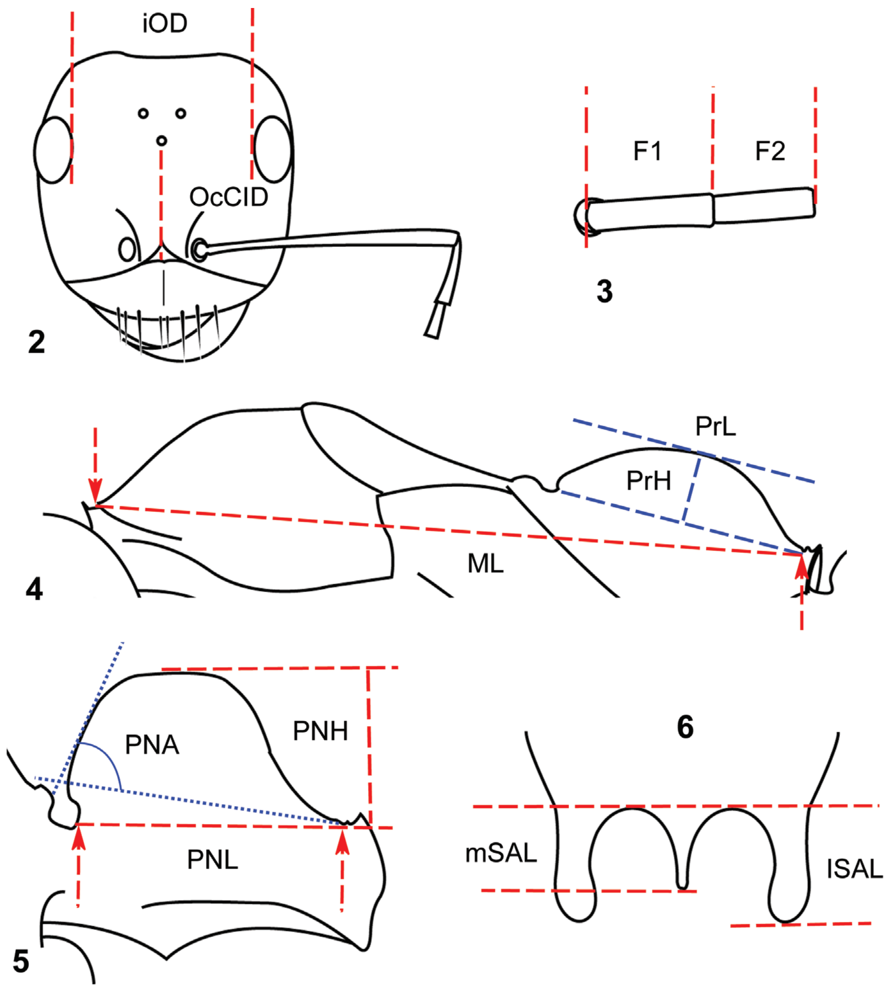
mFmL (mid Femur Length) – maximum length of mid femur in lateral view.

hTbL (hind Tibia Length) – maximum length of hind tibia in lateral view, with tibia at right angle to femur.

GL (Gaster Length) – length of gaster in lateral view, measured from point of articulation with petiole to posteriormost point of gaster.

mSAL (median Subgenital plate Appendage Length) – length of median appendage of subgenital plate, measured in ventral view (Fig. 6).

lSAL (lateral Subgenital plate Appendage Length) – length of lateral appendage of subgenital plate, measured in ventral view (Fig. 6).



Figs 2–6. Measurements for ant descriptions: (2) head of large worker in full-face view; (3) first (F1) and second (F2) funiculus segments of *C. isis* worker; (4) *C. israelensis* large worker, mesosoma outline in lateral view, pilosity omitted; (5) petiole node outline of large worker in lateral view, pilosity omitted; (6) male subgenital plate outline in ventral view. Abbreviations: iOD – inter-Ocular Distance, ML – Mesosoma Length, OcClD – Ocellus-Clypeal Distance, PrH – Propodeum Height, PrL – Propodeum Length, PNA – Petiole Node Angle, PNH – Petiole Node Height, PNL – Petiole Node Length, lSAL – lateral Subgenital Plate Appendage Length, mSAL – median Subgenital Plate Appendage Length.

The drawings were made with Adobe Illustrator 9.0 from photos taken with a digital camera through a ZEISS Discovery.V20 microscope.

Statistical analyses were done with the STATISTICA 13 package. Since sample sizes per nest series were small, measurements of ants from one locality and belonging to one species were combined.

Least square means and 95 % confidence intervals were calculated in the analysis of variance and covariance for the measurements per locality, geographical region or species over the entire data set.

In order to assess the individual variability of ants, linear regression coefficients per locality were averaged and the residuals to the common regression line were calculated. These transformed data were used in principal component/discriminant function analyses.

Diagnoses of the varieties *niger*, *savignyi*, *oasium* and *desertorum* by Santschi (1929) are based largely on color variation and body size. Santschi (1929) considered ants with TL=10 mm (7<TL<10 mm) of medium size and TL<7 mm as small, conventionally adopted thereafter. Because TL and GL are especially hard to measure in mounted specimens, MW is used as estimates of size.

The size of ants in the present study was estimated as following. Among the examined specimens, 27 of *C. niger* and 34 of *C.* cf. *savignyi* individuls had apparently intact gaster, i.e., not shrunken/expanded or otherwise damaged, and TL was estimated by summing HL, ML, PNL and GL. A further set of measurements was obtained from 66 ants randomly collected in alcohol in Tel-Aviv and by directly measuring their outstretched length; after mounting, the widely used proxies for overall size MW, HW, mFmL and hTbL were measured. These ants are not part of the specimens referred to in the 'Material examined' section. The two sets of measurements were similar for MW: for TL=10, MW=1.5 and for TL=7, MW=1.0; HW related non-linearly to TL; mFmL and hTbL differed significantly between *C. niger* and *C.* cf. *savignyi*.

Measurements of specimens belonging to the new species and the *niger* species-complex originating in areas of overlap among species were limited to voucher specimens provided by T. Reiner Brodetzki and R. Zeltzer, and to specimens collected by the authors in localities from which the ants were identified genetically. Codes like 'AT912' or '#3' appearing on data labels refer to different nests where the material was collected.

All specimens listed in the 'Material examined' section are housed in The Steinhardt Museum of Natural History, Tel Aviv University.

TAXONOMY

Cataglyphis israelensis n. sp.

(Figs 4, 7–13, 23–25)

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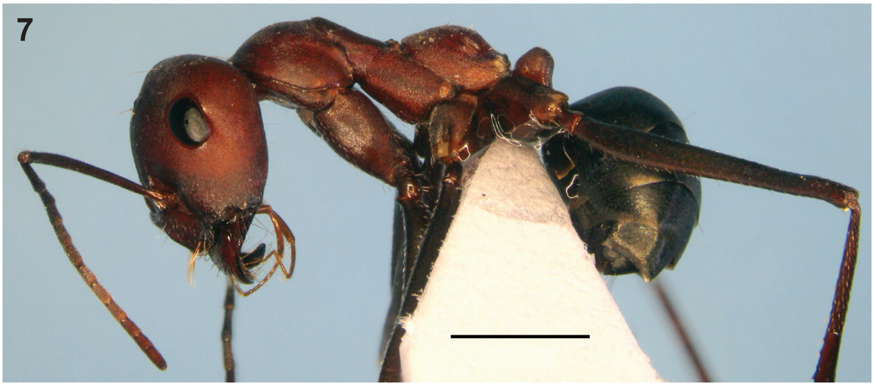
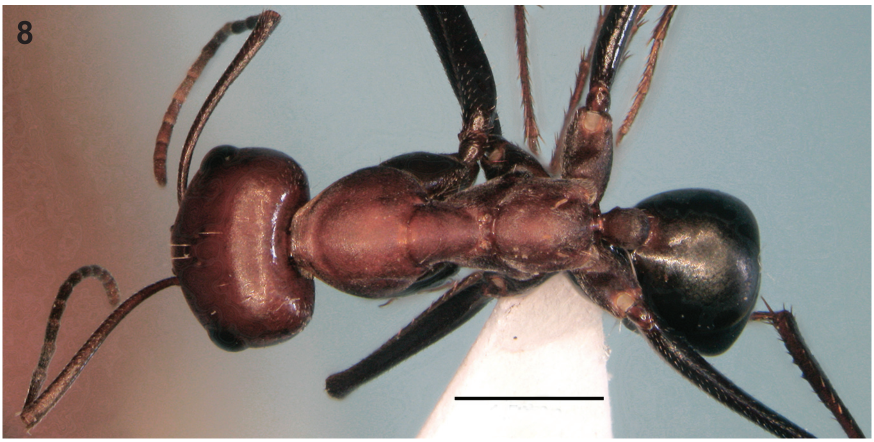


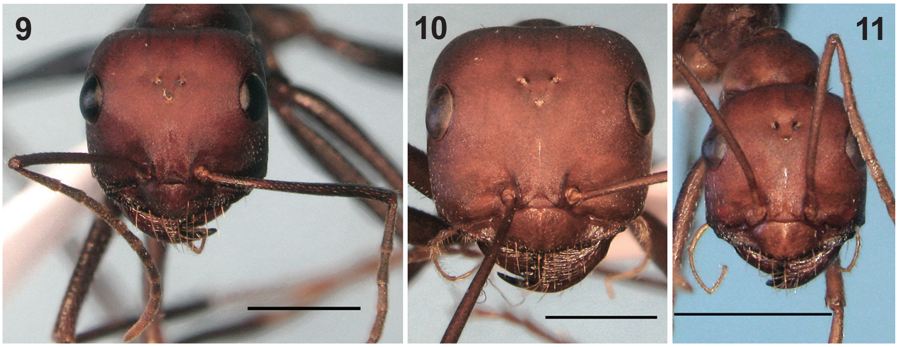


Figs 7, 8. *C. israelensis* holotype worker in lateral (7) and dorsal (8) views. Scale bars, 1.5 mm.

Etymology: This species is named after Israel, its known distribution area.

Description: Worker: *Head*. Head of large worker subquadrate with emarginated occipital margin, and slightly convex lateral margins converging apically (Fig. 10); head of minor worker (Fig. 11) distinctly elongate, with rounded occipital margin posterior to eye and parallel lateral margins, HW/HL=0.86–0.99; head width shows accelerating growth rate with head length; head width with ocellus-clypeal distance, and interocular distance with head length show isometrical growth; scape long (SL/HW=0.98–1.37), shows decelerating growth rate with head width; scape length variable among localities, shortest in ants from northern Coastal Plain, longest in ants from Judean Desert (Table 2); F1L/F2L=1.64–2.02.

Mesosoma. Mesonotum in lateral view distinctly raised over pronotum (Figs 4, 7) in 96 of 108 specimens; outline of propodeum dorsum smoothly arched in lateral view (Figs 4, 7, 12, 13); propodeum height variable, highest in ants from



Figs 9–11. *C. israelensis* worker, head in full-face view: (9) holotype, (10) large paratype, (11) small paratype. Scale bars, 1.5 mm.

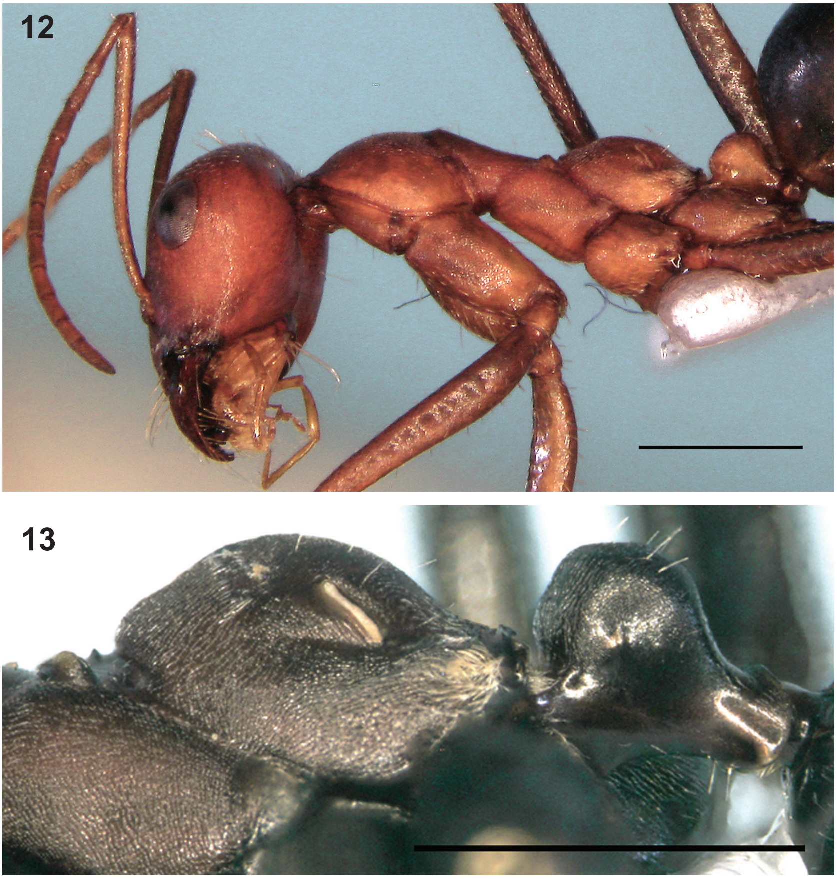
northern Coastal Plain (Fig. 13), lowest in ants from Judean Desert (Table 2); petiole node of largest workers high, dorsally slightly rounded (Figs 7, 13), petiole node of medium-small workers lower, more elongate (Fig. 12); petiole node angle variable, largest in ants from northern Coastal Plain (Table 2; Fig. 13); hindtibia 1.2–1.4 times longer than midfemur.

Sculpture. Entire body with piligerous pits; head, mesosoma and gaster dorsally and laterally reticulate/shagreened, matte; seashore populations with more accentuated sculpture, but part of specimens with laterally shiny gaster; mandible, leg and ventral surface of head and gaster finely striate/carinulate, shiny.

Pilosity. Pilosity white to yellowish brown: clypeus, frons, vertex, mesosoma, petiole node dorsum and gaster segments with sparse, erect, hairs; dorsum of promesonotum with 1–14 hairs, number not correlated with size; propodeum dorsum, from metanotal groove to propodeal spiracle, with 1–4 hairs (in 37/109 specimens); ventral surface of head, mandible, coxa and petiole node with erect to decumbent setae, on latter occasionally lacking; hind tibia with two rows of decumbent bristles on ventral surface; body covered with very short, appressed, white pubescence, more abundant on head and propodeum; convex face of scape with dense, appressed to subappressed pubescence on distal ⅓–½ of length.

Color. Highly variable: head, mesosoma and petiole bright red to ochraceous-orange, leg brownish to black, gaster black (Figs 7, 12) in populations from Lower Galilee, Yizre'el Valley, Sea of Galilee area and Upper Jordan Valley; head, mesosoma and petiole dark red to dark reddish brown, leg concolorous, gaster black in populations from Upper Galilee, Lower Hermon, Golan Heights and from Carmel Ridge to Judean Hills; and uniformly black in populations from northern Coastal Plain ('Atlit, Hof haBonim) and Judean Desert (Allon, Ma'ale Adummim); in bicolored nest series medium workers (MW=1.0–1.5) always lighter colored than larger specimens, smallest workers black.

Measurements: TL=6.4–13.3, HL=1.48–3.20, HW=1.37–3.07, EL=0.49–0.86, iOD=1.05–2.30, OcClD=0.80–1.43, SL=1.73–3.26, F1L=0.43–0.85, F2L=0.24–



Figs 12, 13. *C. israelensis*, propodeum and petiole node in lateral view: (12) small paratype worker, (13) worker from Hof haBonim. Scale bars, 1.5 mm.

0.49, ML=2.59–4.45, MW=0.94–2.01, PrL=0.89–1.54, PrH=0.19–0.45, PNL=0.49–0.84, PNW=0.29–0.63, PNH=0.28–0.53, PNA=65–84°, mFmL=1.95–3.91, hTbL=2.54–4.94 (n=110).

Differential diagnosis: *C. israelensis* is a large species of the *bicolor* species-group with habitus and color pattern similar to '*drusa*' and '*assyria*' (AntWeb CASENT0912219 and CASENT0912218). It has symmetrically and smoothly arched propodeum outline in lateral view (Figs 7, 13), similar to '*drusa*' and *C. nodus* (AntWeb CASENT0911115 and CASENT0911116), differing from higher and steeply rounded outline in *C. niger* (Fig. 16), *C.* cf. *savignyi* (Fig. 17) and *C. holgerseni* (Fig. 14), but higher and less flattened than in *C. isis* (Fig. 15; Table 1); populations from 'Atlit and Hof haBonim have high propodeum (Fig. 13), similar to neighboring *C.* cf. *savignyi* populations from northern and central Coastal Plain

(Table 2). *C. israelensis* has midfemur length similar to *C. niger* (Table 1) and to *C.* cf. *savignyi* from northern and central Coastal Plain (Table 2), but distinctly shorter than in *C.* cf. *savignyi* from Negev and 'Arava Valley (Table 2), and from *C. holgerseni* and *C. isis* (Table 1). *C. israelensis* has petiole node angle larger than the other species from Israel with flattened anterior surface of petiole (Table 1); this specific difference especially marked between populations from northern and central Coastal Plain (cf. Figs 13 vs. 16; Table 2). *C. israelensis* differs from *C. nodus* by raised mesonotum over pronotum in 89% (n=108) vs. 12% (n=48) of workers, respectively, character state intermediate in *C. niger* and *C.* cf. *savignyi*. It has scarce pilosity on propodeum dorsum, similar to *C. niger* and *C.* cf. *savignyi* vs. abundant pilosity in most examined *C. nodus* (1–19 setae), and all *C. isis*. Pilosity on propodeum dorsum and petiole node is less abundant than in the type of '*drusa*', but never completely absent as in the type of '*assyria*'. Pubescence of ventral surface of hindtibia fine and appressed, similar to other Israeli species vs. coarse in *C. nigripes* Arnol'di. In bicolored worker series, small to medium specimens (MW=1.0–1.5) have coxae and petiole concolorous with mesosoma pleura (Figs 7, 12), or to some extent darker, as opposed to black in *C.* cf. *savignyi* (Fig. 17). Light colored specimens of *C. israelensis* differ from similarly colored *C. viatica* (Fabricius) by matte gaster, seldom laterally shiny, vs. completely shiny gaster in *viatica*.

Material examined: *C. israelensis*: Holotype ☿, **Israel:** Daverat [32°39'14.2"N 35°22'39.7"E], 6.v.2016, P.-A. Eyer. Paratypes: same collection data as holotype (6☿); Montfort, 6.v.2016, P.-A. Eyer (7☿); Dishon, 17.v.1973, J. Kugler (3☿); Nahal Senir, 26.iv.1984, J. Kugler (2☿); Merom Golan, 15.vi.1971, J. Kugler (1♂); Tel Dan, 17.vi.1971, H. Bytinski-Salz (1☿, 1♀, 2♂); Panyas (Banyas), 12.v.1971, H. Bytinski-Salz (2☿); Agmon haHula #1, 2012, R. Zeltzer (3☿), #3, 2012, R. Zeltzer (4☿); Hula, 17.vii.2010, C. Drees (2☿); 'Ammi'ad #2, 2012, R. Zeltzer (1☿), #3, 2012, R. Zeltzer (1☿), #4, 2012, R. Zeltzer (1☿), #5, 2012, R. Zeltzer (5☿); Teverya [Tiberias], 12.v.19xx, H. Bytinski-Salz (1☿, 1♀, 2♂); Nahal Kanaf, 28.xi.1981, W. Ferguson (2☿); Tel Qazir, iv.1955, J. Wahrman (3♂); Hefzi Bah, 8.ix.2005, M. Vonshak (1☿); 'Atlit AT888, 12.iv.2016, T. Reiner-Brodetzki (1☿), AT889, 12.iv.2016, T. Reiner-Brodetzki (3☿), AT900, 12.iv.2016, T. Reiner-Brodetzki (3☿), AT901, 12.iv.2016, T. Reiner-Brodetzki (3☿), AT902, 12.iv.2016, T. Reiner-Brodetzki (3☿), AT910, 12.iv.2016, T. Reiner-Brodetzki (3☿), AT912, 12.iv.2016, T. Reiner-Brodetzki (8☿, 5♀), AT916, 12.iv.2016, T. Reiner-Brodetzki (6☿, 12♂); Hof haBonim HB884, 12.iv.2016, T. Reiner-Brodetzki (8☿), HB888, 12.iv.2016, T. Reiner-Brodetzki (4☿), HB890, 12.iv.2016, T. Reiner-Brodetzki (3☿), HB894, 12.iv.2016, T. Reiner-Brodetzki (2☿); Qedumim, 15.vi.2016, A.L.L. Friedman (1☿); Yerushalayim [Jerusalem], 12.vi.1941, H. Bytinski-Salz (3☿, 1♀, 1♂); Allon, 20.iii.2011, R. Zeltzer (6☿), #3, 20.iii.2011, R. Zeltzer (1☿), #4, 20.iii.2011, R. Zeltzer (7☿), #5, 20.iii.2011, R. Zeltzer (8☿); Ma'ale Adummim, 20.iii.1979, J. Kugler (5☿).

C. nodus: **Serbia:** Belgrade, 13.vii.1928, F.S. Bodenheimer (2☿); 4.ix.1928, F.S. Bodenheimer (2☿). **Montenegro:** Budua, 21.iii.1923 (1☿). **Greece:** Saloniki, 12.v.1972, Poldi (1☿); Marathon, 18.iv.1962, H. Bytinski-Salz (9☿); Nauplion, 13.vii.1928, H. Bytinski-Salz (3☿); Samos, 22.iv.1962, H. Bytinski-Salz (1☿). **Turkey:** Edirne [Adrianopel], C. Menozzi (1☿); Istanbul, Saudiye, 4.viii.1929, F.S. Bodenheimer (4☿), 11.iv.1972, H. Bytinski-Salz (7☿); Ankara, 28.iv.1939, F.S. Bodenheimer (6☿); 12.v.1939, F.S. Bodenheimer (3☿); 18.v.1972, H. Bytinski-Salz (3☿); Sardes, 1973, A. Shor (2☿); Sivrice, 15.viii.1939, F.S. Bodenheimer (3☿); Plage Sigirak, 25.v.1939, F.S. Bodenheimer (1☿); Diyarbakır, 17.v.1972, H. Bytinski-Salz (6☿); Slovia, 2.vii.1921, (1☿). **Iran:** Fars, Akabad-Kamin, 27.vii.1969, C. Felton (1☿).

C. viatica (Fabricius): **Morroco:** Oued Zate, 14.iv.1966 (1☿). **Algeria:** Sidi bel Abbes (1☿).

Notes: Ants from Israel were compared by Kugler (pers. comm., 2005) with types of '*drusa*' and '*assyria*' in the Santschi collection, and with types of *Myrmeco-*

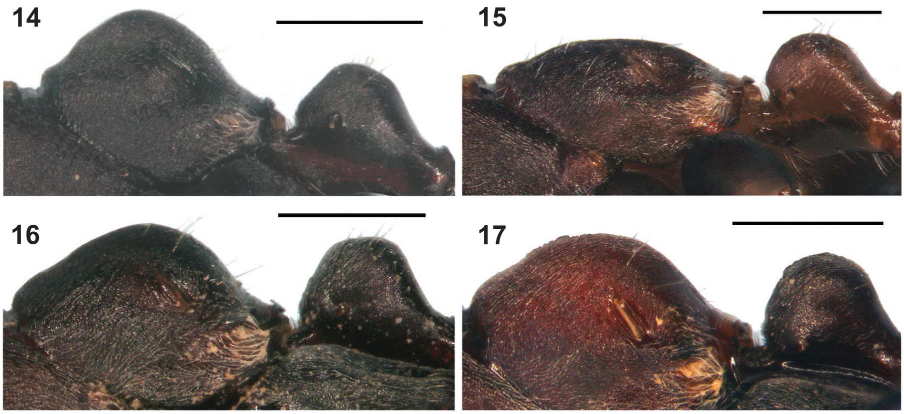
cystus viaticus var. *orientalis* Fore (junior synonym of *nodus*) in the Forel collection (there is is a specimen from Jerusalem among Forel's syntypes of *orientalis*). Specimens from northern Israel have the shape of the petiole, pilosity and color intermediate between the examined types, in accordance with Santschi (1929, 1934). Consequently, *C.* sp. IL02 (part) and *C.* sp. IL04 (part) were considered by Kugler as closely related to '*drusa*', and published as *C.* n. sp. near *nodus* (Kugler 1988). '*C. druzus*' together with *C. bicolor* (Fabricius) were reported as widely distributed in Lebanon by Tohmé (1969) and Tohmé & Tohmé (2014), whereas Knaden *et al*. (2012) reported *C. bicolor* and *C. viatica* from the Beqaa Valley (Lebanon). However, the relationship of these species to *C.* sp. IL02 is unknown, and according to D. Agosti (pers. comm., 1994) all reports of '*drusa*' or *C. nodus* from Israel are misidentifications. Furthermore, samples from the Beqaa Valley that were collected less than 5 km from the type locality of '*drusa*' by Knaden *et al*. (2012) cluster with *C. nodus*, at a distance from the Israeli species (Eyer unpubl. data).

Males and gyne of *C. nodus* were not available for this study; however, the species diagnosis based on the male and gyne morphology proposed by Agosti (1994) indicates for males SL/HW<1.70 in *C. nodus* vs. SL/HW>1.70 in *C. savignyi* and for gyne HW/HL<0.95 in *C. nodus* vs. HW/HL>0.95 in *C. savignyi*; in both species gyne with the red head and mesosoma. The present study found for males SL/HW=1.57–1.74 (n=21) in *C. israelensis*, similar to *C.* cf. *savignyi* from Israel (SL/HW=1.62–1.77, n=14) and *C. niger* (SL/HW=1.61–1.73, n=10); *C.* cf. *savignyi* from Sinai have SL/HW=1.71–1.85 (n=4). For gyne, in contrast to Agosti (1994), HW/HL=0.96–0.98 (n=8) in *C. israelensis* and HW/HL=0.91–0.99 (n=5) in *C.* cf. *savignyi*, in both species color variable, similar to associated workers. According to Agosti (1990) the apical appendages of the subgenital plate are of similar length in *C. nodus* (Agosti 1990, fig. 23), whereas in *C. israelensis* the median appendage of the subgenital plate is shorter than the lateral appendages (mSAL/lSAL=0.52–0.71, n=7) (Figs 23, 24), similar to *C. niger* (0.55–0.73, n=8) and to *C.* cf. *savignyi* (0.59–0.63, n=7) (Figs 26, 27, 29, 30). Likewise, in *C. israelensis* the stipites in the lateral view (Fig. 25) are similar to *C.* cf. *savignyi* (Fig. 31), intermediate between, but closer to *C. niger* (Fig. 28) than to *C. nodus* as illustrated in Agosti (1990, figs 45, 46). Therefore, contrary to the proposed affinity between *C.* sp. IL02 and *C. nodus* in Vonshak and Ionescu-Hirsch (2010), *C. israelensis* cannot be included in the *nodus* species-complex as diagnosed by Agosti (1990). It is possible that the diagnosis of the *nodus* species-complex is too restrictive, thus not accounting for the variation in this widely distributed group (see Emery 1906, figs 28–30; Knaden *et al*. 2012, fig. 4).

Cataglyphis israelensis is distributed uniformly in northern and north-eastern Israel, parapatric with *C.* cf. *savignyi*, and over most of its range the ants are bicolored, thus identifiable straightforwardly by their color pattern and the shape of the propodeum. However, in areas of the overlap between species containing black morphs, as in the northern Coastal Plain, Jerusalem and the Judean Desert, identification of individual ants is problematic. The first discriminant analysis on residuals of measurements on all specimens in four groups—'*holgerseni*', '*isis*', '*israelensis*' and '*niger* complex'—revealed 100 % correct classification of the unproblematic *C. holgerseni* and *C. isis*, 81 % correct classification of *C. israelensis* and 94 % correct classification of ants in the *niger* species-complex. The second analysis was limited to three groups comprising 73 *C. israelensis* (19 of them bicolored), 39 *C. niger* and 102 *C.* cf. *savignyi* specimens from localities sampled for molecular analyses. The discriminant analysis (Wilks' Lambda: 0.366 approx. $F(16,408)=16.675$, $p<0.001$) resulted in 86 % correct classification of ants belonging to *C. israelensis*, 84 % correct classification of *C.* cf. *savignyi* and only 45 % correct classification of *C. niger*. The scrutiny of the results showed that accounting for color increased the correct classification rate of *C. israelensis*: only four were misidentified as *C.* cf. *savignyi* and one as *C. niger*; and eight *C.* cf. *savignyi* and two *C. niger* were misidentified as *C. israelensis*. A direct comparison of 54 black *C. israelensis* and 49 *C.* cf. *savignyi* collected on the Coastal Plain was carried out by recalculating the average regression lines between the two groups for PrH, PNL, PNH and PNA. For *C. israelensis*, a low propodeum, short petiole node, high petiole node and large petiole node angle relative to average, and raised mesonotum over pronotum were considered characteristic. Forty-nine *C. israelensis* and 37 *C.* cf. *savignyi* displayed the characteristic condition in at least three variables, an 8 % rate of misclassification vs. 50 % in a random choice. Consequently, appropriate sample size and number of samples may support a reasonably high correct identification rate (*sensu* Seifert 2014) of *C. israelensis* by morphology, despite a high intraspecific variability within nest series and among local populations.

Cataglyphis holgerseni Collingwood & Agosti, 1996
(Figs 14, 18, 19)

Recognition: This is a large species (worker TL>10, MW>1.45) of the *urens* species-complex (Agosti 1990). Male has subgenital plate with short, triangular median process and two lateral distally divergent appendages (Fig. 18) similar to *C. urens* Collingwood (Agosti 1990, fig. 18) vs. parallel appendages in other Israeli species (Figs 21, 24, 27, 30). Stipes distinctly curved apically in lateral view (Fig. 19) vs. nearly straight in other Israeli species (Figs 22, 25, 28, 31). *C. holgerseni* worker has shortest and narrowest head relative to mesosoma width as compared to the other investigated species (Table 1). It has raised mesonotum over pronotum in all 50 examined specimens; *C. holgerseni* has high propodeum with nearly straight dorsum and declivity that form a rounded right-angle in lateral view (Fig. 14), similar to *C. urens*, differing from lower propodeum in sympatric *C. isis* and *C.* cf. *savignyi* (Tables 1, 2). Scape and leg distinctly longer than in *C.* cf. *savignyi* (Table 1), e.g. for MW=1.54, hTbL=4.56 (4.52–4.60) in 29 *C. holgerseni* vs. hTbL=3.99 (3.94–4.04) in 22 *C.* cf. *savignyi* from Hazeva; hTbL/mFmL=1.19–1.28, n=28,



Figs 14–17. Worker, propodeum and petiole node in lateral view: (14) *C. holgerseni*; (15) *C. isis*; (16) *C. niger*, Yafo; (17) *C.* cf. *savignyi*, Tel 'Arad. Scale bars: 1 mm in Fig. 14, 0.5 mm in Fig. 15, 0.8 mm in Figs 16, 17.

intermediate between *C. isis* and *C.* cf. *savignyi*. *Cataglyphis holgerseni* has propodeal dorsum from metanotal groove to propodeal spiracle without erect setae as opposed to profuse pilosity in *C. isis*. Usually entirely black, some specimens of *C. holgerseni* have dark red frons and, rarely, dark brown head and mesosoma. *C. holgerseni* differs from *C. urens* by more massive petiole node with average PNH=0.37 vs. 0.30 for PNL=0.71 and PNA=62–71° vs. 55–63°, respectively.

Measurements: TL=6.8–13.2, HL=1.70–2.87, HW=1.46–2.70, EL=0.47–0.76, iOD=1.05–1.95, OcClD=0.80–1.37, SL=2.19–3.63, F1L=0.51–0.86, F2L=0.29–0.51, ML=2.83–4.49, MW=1.05–1.91, PrL=0.94–1.52, PrH=0.33–0.62, PNL=0.56–0.97, PNW=0.37–0.70, PNH=0.27–0.55, PNA=62–71°, mFmL=2.38–4.45, hTbL=3.69–5.52 (n=30).

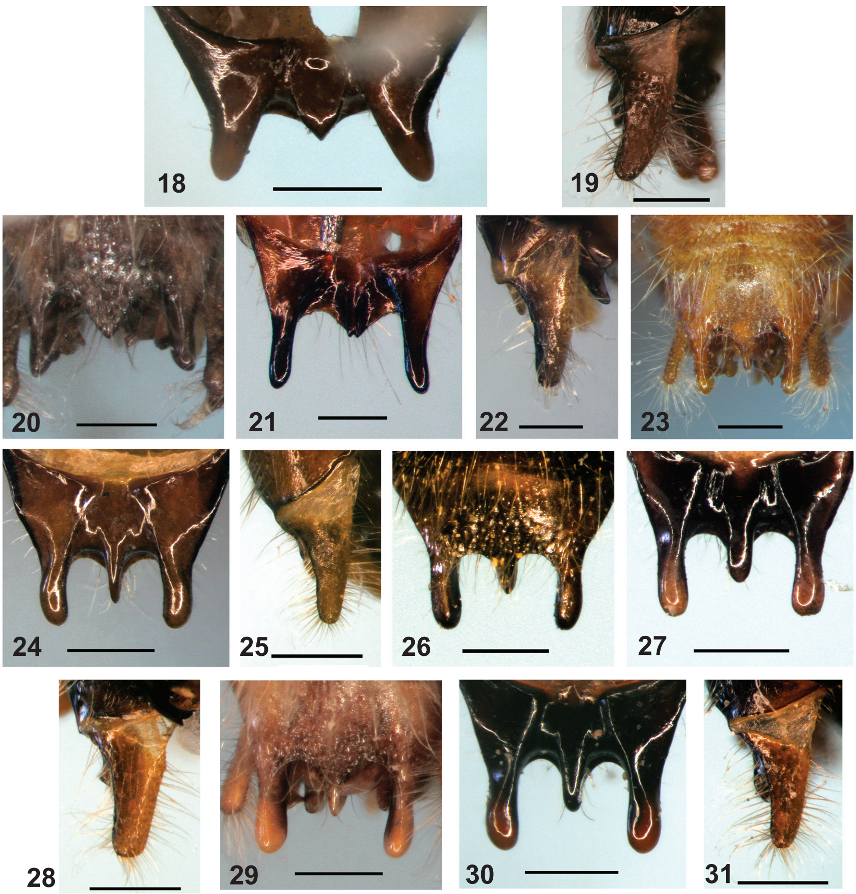
Material examined: *Cataglyphis holgerseni*: **Israel:** Hazeva Field School, 20.vii.1992, A. Hefetz (2☿), 16.ii.1994, Shapira (6☿); 22.iii.1994, A. Ionescu (2☿); 2012, R. Zeltzer (3☿); Hazeva, 2012, R. Zeltzer (7☿); Nahal Shezaf, 15.i.1994, Shapira (2☿); Nahal Shahaq, 15.i.1994, Shapira (2☿), 17.viii.1999, I. Yarom (14☿); Ein Yahav, 25.ii.2009, A. Ionescu (3☿); Elat, 5.v.1976, B. Shalmon (4☿, 1♀, 1♂), 2012, R. Zeltzer (6☿). **Jordan:** Aqaba, xi.1942, Feiga (3☿).

C. urens: **Saudi Arabia:** Wadi Shugub Turabah, 6.iv.1980, W. Buttiker (1☿); Riyadh, 1.vi.1980, Dr. Dishl (1☿); Sulaiel desert, 11.iv.1980, C.A. Collingwood (1☿).

Distribution: *C. holgerseni* is distributed in Israel in the 'Arava Valley (Fig. 1), in Egypt (Sinai), Jordan and the Arabian Peninsula (Collingwood & Agosti 1996).

Cataglyphis isis (Forel, 1913)
(Figs 15, 20–22)

Recognition: This is a medium-sized species (worker TL<10, MW<1.45) that belongs to the *diehlii* species-complex (Agosti 1990). Male has subgenital plate posteriorly with parallel lateral appendages, and large (mSAL/lSAL=0.56) triangular median process in one examined specimen (Fig. 20) or short (mSAL/lSAL= 0.31) bifid median process in another male from the same nest series (Fig. 21); the median process of the subgenital plate is long, digitiform in *C. israelensis*, *C. niger* and *C.* cf. *savignyi* (Figs 24, 27, 30). Stipes (Fig. 22) has a similar shape as in males of the *niger*-complex (Figs 25, 28, 31). *C. isis* worker has broadest head relative to the mesosoma width vs. sympatric *C. holgerseni* and *C.* cf. *savignyi* (Table 1);



Figs 18–31. Males, subgenital plate (SgP) and right stipes (St): (18, 19) *C. holgerseni*, SgP in dorsal view (18) and St in lateral view (19); (20–22) *C. isis* SgP in ventral (20) and dorsal (21) views and St in lateral view (22); (23) *C. israelensis*, Nahal Kanaf, SgP in ventral view; (24, 25) *C. israelensis*, Hof haBonim, SgP in dorsal view (24) and St in lateral view (25); (26) *C. niger*, Tel Aviv, SgP in ventral view; (27, 28) *C. niger*, Tel Barukh, SgP in dorsal view (27) and St in lateral view (28); (29) *C.* cf. *savignyi*, Nir Yizhaq, SgP in ventral view; (30, 31) *C.* cf. *savignyi*, Bezet, SgP in dorsal view (30) and St in lateral view (31). Scale bars: 0.5 mm in Figs 18, 19, 23–31 and 0.25 mm in Figs 20–22.

the head is slightly longer than wide (HW/HL=0.86–0.98), similar to sympatric *C. holgerseni* and *C.* cf. *savignyi* and related *C. diehlii* (Forel), vs. HW/HL>1 in a large *C. adenensis bugnioni* Santschi worker. The first funiculus segment of worker is short relative to the second segment, F1L/F2l=1.26–1.42, n=18 (Fig. 3), similar to *C. adenensis bugnioni* and *C. diehlii* vs. F1L/F2L=1.64–2.00, n=53 in the other Israeli species of the *bicolor* species-group (Figs 9, 11). The ratio hTbL/mFmL=1.17–1.26, n=30, is lower than in *C. holgerseni* and *C.* cf. *savignyi*. *Cataglyphis isis* has high petiole node (Table 1), with rounded anterior and dorsal surface (Fig. 15), similar to *C. adenensis bugnioni* vs. somewhat flattened anterior surface in the other Israeli species (Figs 13, 14, 16, 17) and *C. diehlii*. *Cataglyphis isis* has gaster slightly shiny, dorsally matte vs. completely shiny in *C. adenensis bugnioni* and *C. diehlii*. *Cataglyphis isis* has abundant pilosity in all 65 examined specimens; scape with occasional decumbent to erect hairs that lack in related *C. adenensis bugnioni* and *C. diehlii*; it is the sole Israeli species in this group with statistically significant positive correlation between number of erect hairs on mesosoma dorsum and mesosoma length; it has 1–16 setae on propodeum dorsum. Color of workers is highly variable among localities: from black (Paran and Nahal Ovil), sometimes with a bright red spot on frons (Elat), to uniformly dark brown (Fig. 15; 'Ein Hajla), and to light ochraceous-brown with black gaster in ants from Qualya, Hazeva and Mizpe Ramon.

Measurements: TL=5.0–9.6, HL=1.37–2.40, HW=1.04–2.30, EL=0.41–0.63, iOD=0.90–1.76, OcClD=0.65–1.13, SL=1.90–2.83, F1L=0.37–0.57, F2L=0.27–0.41, ML=2.25–3.55, MW=0.70–1.43, PrL=0.75–1.22, PrH=0.13–0.28, PNL=0.37–0.61, PNW=0.23–0.47, PNH=0.19–0.41, mFmL=1.93–3.65, hTbL=2.36–4.47 (n=30).

Material examined: *Cataglyphis isis*: **Israel:** 'Ein Hajla, 17.iii.2011, A. Ionescu (9☿, 1♀); Qalya, 5 km S, 15.xii.1944, H. Bytinski-Salz (9☿); Mizpe Ramon, 27.iv.2015, T. Rozenberg (3☿); Hazeva, 22.iii.1994, A. Ionescu (1☿); Paran, 15.iii.2016, P.-A. Eyer & A. Hefetz (6☿); Nahal Ovil, Rt. 40, 15.iii.2016, P.-A. Eyer & A. Hefetz (8☿); Be'er Menuha, 15.iii.2016, P.-A. Eyer & A. Hefetz (4☿); Elat, 19.i.1978, B. Shalmon (4☿, 1♀), 21.iv.1982, J. Kugler (20☿, 2♀, 2♂). **Egypt:** Sinai, Wadi Girafi, 30.viii.196[?], J. Kugler (1☿).

C. adenensis bugnioni: **Egypt**: Sinai, Nabek, 23.iii.1981, J. Kugler (2☿), A. Freidberg (2☿); Sharm el Sheik, 13.iii.1982, J. Kugler (3☿).

C. diehlii (Forel): **Tunisia:** Metlaoui Moulares, 28.v.1985, R. Wehner (2☿).

Distribution: *C. isis* is distributed in Israel in the Dead Sea area, central and southern Negev, and 'Arava Valley (Fig. 1). It was reported from Egypt (type locality) throughout Sinai and the Arabian peninsula to the Middle East (Radchenko 1997).

Cataglyphis niger (André, 1881)

(Figs 16, 26–28)

Recognition: *C. niger* is characterized by black color with a grayish tint due to abundant silvery pubescence on head and mesosoma and accentuated microsculpture, but out of the 70 medium/large examined specimens (MW>1.13), five with dark wine-red frons or head, and four also with similarly colored spots on mesonotum. Gaster matte except venter. *C. niger* has scarce pilosity on propodeum dorsum, 1–3 setae in 26/68 ants. It has more flattened propodeum (Figs 16, 17), and on average shorter scape and legs than *C.* cf. *savignyi* from most sampled localities (Table 2). It has raised mesonotum over pronotum in 44% (n=68) of examined specimens, a lower frequency than in *C. israelensis* and *C.* cf. *savignyi*.

Measurements: TL=5.6–13.0, HL=1.56–3.24, HW=1.37–3.23, EL=0.44–0.89, iOD=0.98–2.54, OcClD=0.72–1.55, SL=1.76–3.37, F1L=0.45–0.76, F2L=0.24–0.45, ML=2.20–4.47, MW=0.96–2.11, PrL=0.85–1.66, PrH=0.18–0.51, PNL=0.45–0.91, PNW=0.28–0.72, PNH=0.21–0.55, PNA=63–77°, mFmL=1.98–3.87, hTbL= 2.46–4.80 (n=73).

Material examined: Israel: Tel Aviv, Tel Barukh, 242, 2012, R. Zeltzer (12☿), 15.iii.2014, T. Reiner-Brodetzki (2☿, 1♂); Tel Aviv, Tel Barukh, dunes, 11.iv.2016, A. Ionescu (12☿); Tel Aviv, 10.vi.1962, H. Bytinski-Salz (1♂), 2.iv.1970, H. Bytinski-Salz (3☿, 1♀, 2♂), 8.v.1973, J. Kugler (2♂); 9.v.1982, Y. Zvik (1♂), 10.v.1988, O. Soussan (1♂); Yafo, 1.iv.2016, P.-A. Eyer & A. Hefetz (7☿), 26.v.2016, A. Ionescu (36☿); Holon, 29.v.1959, H. Bytinski-Salz (1♂); Ziqim West, #1, 2012, R. Zeltzer (6☿), #3, 2012, R. Zeltzer (4☿), #4, 2012, R. Zeltzer (3☿), #5, 2012, R. Zeltzer (8☿).

Distribution: The known distribution of *C. niger* in Israel is in the central and southern Coastal Plain. The species was reported as widely distributed from Egypt (Mohamed *et al*. 2001) throughout the Middle East to Iran (Radchenko 1998; Paknia *et al.* 2008).

Notes: Santschi (1929) defined *C. bicolor* st. *nigra* by its black color, gaster matte dorsally and laterally vs. shiny at least laterally in var. *savignyi* and var. *desertorum*; petiole node as high or higher than long and rounded (Santschi 1929, fig. 4) vs. lower and more elongate posteriorly in var. *savignyi*, and longer than high in st. *abyssinica*; st. *nigra* has sparse pilosity as compared to var. *isis* (Santschi 1929). In Collingwood and Agosti (1996) the diagnostic character that distinguishes *C. niger* from *C. savignyi* is a lower propodeum with a flatter curvature in *niger* (Collingwood & Agosti 1996, fig. 43).

The use of Santschi's (1929) identification key, which is based largely on color, leads to misidentification of all black specimens of *C. israelensis* and *C.* cf. *savignyi*, although the misidentification of *C. israelensis* and *C.* cf. *savignyi* from the northern and central Coastal Plain will be doubtful because the gaster in some of these ants is laterally shiny. Following Collingwood and Agosti (1996), black *C.* cf. *savignyi* with the high propodeum from Mishor Yamin and Holot 'Agur would be correctly identified, but the previous uncertain identifications from the northern and central Coastal Plain would become certain misidentifications.

Cataglyphis niger distribution in Israel seems to be restricted to the central and southern Coastal Plain, sympatric with *C.* cf. *savignyi*; but only a wider genetic characterization of ants from northern Africa and the Middle East may reveal its complete distribution range and provide a deeper understanding of the relationships between the different ant populations inhabiting this broad geographic region.

Table 1: Least square means ±95 % confidence interval at covariate mean, and sample size for 17 variables per taxon; see 'Materials and Methods' for full names of variables.

Variable covar. mean	*C. israelensis*	*C. niger*	*C.* cf. *savignyi*	*C. holgerseni*	*C. isis*
HL MW=1.54	2.48±0.01 n=105	2.43±0.02 n=48	2.45±0.01 n=184	2.35±0.02 n=26	2.51±0.02 n=26
HW MW=1.54	2.29±0.01 n=110	2.26±0.01 n=73	2.26±0.01 n=200	2.14±0.02 n=30	2.41±0.02 n=30
EL HL=2.80	0.68±0.02 n=61	0.67±0.03 n=47	0.70±0.02 n=55	0.67±0.05 n=12	0.53±0.04 n=26
iOD MW=1.55	1.71±0.01 n=94	1.70±0.02 n=54	1.69±0.01 n=165	1.53±0.03 n=11	1.82±0.02 n=26
OcClD MW=1.55	1.14±0.01 n=95	1.13±0.01 n=48	1.12±0.01 n=164	1.11±0.02 n=12	1.15±0.01 n=26
SL Ln(HW)=0.74	2.54±0.02 n=82	2.52±0.02 n=63	2.58±0.01 n=158	2.92±0.04 n=18	2.71±0.03 n=25
F1L MW=1.47	0.62±0.04 n=30	0.67±0.06 n=12	0.74±0.04 n=31	0.70±0.05 n=14	0.54±0.05 n=18
F2L F1L=0.66	0.36±0.01 n=30	0.37±0.01 n=12	0.36±0.01 n=31	0.38±0.01 n=14	0.46±0.01 n=18
ML MW=1.55	3.63±0.02 n=90	3.64±0.03 n=49	3.66±0.02 n=173	3.81±0.06 n=11	3.74±0.04 n=26
PrL MW=1.55	1.27±0.01 n=100	1.27±0.01 n=67	1.26±0.01 n=162	1.29±0.02 n=14	1.30±0.02 n=24
PrH PrL=1.27	0.31±0.01 n=100	0.35±0.01 n=67	0.35±0.01 n=161	0.48±0.02 n=14	0.28±0.01 n=24
PNL MW=1.55	0.70±0.01 n=83	0.71±0.01 n=49	0.72±0.01 n=143	0.80±0.02 n=12	0.66±0.01 n=21
PNW MW=1.54	0.48±0.01 n=93	0.47±0.01 n=51	0.47±0.01 n=164	0.53±0.01 n=28	0.49±0.01 n=25
PNH PNL=0.71	0.43±0.01 n=81	0.40±0.01 n=47	0.40±0.01 n=132	0.37±0.02 n=12	0.43±0.01 n=21
PNA PNL=0.73	76° ±1° n=75	71° ±1° n=46	71° ±1° n=119	65° ±2° n=12	– –
mFmL MW=1.54	3.05±0.02 n=109	3.02±0.02 n=73	3.11±0.01 n=199	3.66±0.04 n=29	3.72±0.04 n=30
hTbL MW=1.545	3.93±0.02 n=110	3.85±0.03 n=70	3.97±0.02 n=197	4.56±0.05 n=29	4.58±0.05 n=30

Cataglyphis cf. *savignyi* (Dufour, 1862)
(Figs 17, 29–31)

Recognition: *Cataglyphis* cf. *savignyi* is similar to *C. niger*, but in ten out of 20 sampled localities all medium and large specimens display the typical '*savignyi*' color pattern. In other localities most ants are black: in the Hazeva samples four out of 22 ants have red head, of the 49 ants from the northern Coastal Plain only two have brownish-red head and mesosoma, while the 31 ants from Mikhmoret and Palmahim and 23 ants from the central Negev are completely black. All 51 examined specimens from 11 localities in Egypt have red head. This species has raised mesonotum over pronotum in 74% (n=182) of examined specimens, a higher frequency than in *C. niger* and the ants from Egypt (37%, n=51). *C.* cf. *savignyi* shows a wide range of inter-population variability for most of the investigated characters. Scape and midfemur length of Israeli ants in most of the sampled localities is similar to that in *C.* cf. *savignyi* from Tunisia and the Nile region in Egypt, but is significantly longer in ants from Nir Yizhaq, Mishor Yamin and Sinai (Table 2). Likewise, the propodeum of ants from Nir Yizhaq, Mishor Yamin and Sinai is significantly higher than in other places (Table 2). Sculpture in most Israeli ants is similar to *C. niger* and *C.* cf. *savignyi* from Sinai, but gaster is laterally shiny in samples from the northern Coastal Plain, Mikhmoret and Modi'in, and in *C.* cf. *savignyi* from Tunisia and the Nile region in Egypt. Pilosity is variable among localities. For example, the pubescence on the convex face of scape is appressed to subappressed on distal ⅓ of length in ants from central Negev, similar to *C.* cf. *savignyi* from Tunisia, the Nile Delta and SE Sinai, but subappressed to decumbent, with occasional 1–2 erect hairs on distal ⅔ of length in ants from Tel 'Arad, although the erect hairs are fewer than in *C. isis*, and shorter than in *C. nigripes*. In *C.* cf. *savignyi* from Israel 48 out of 176 examined specimens display 1–4 setae on propodeum dorsum, but the frequency of ants with setae on propodeum dorsum is higher in Palmahim, Modi'in and Tel 'Arad (25/54) than in the northern Coastal Plain and central Negev (5/62), and Egypt (2/51). Overall, ants from the southern Coastal Plain seem similar to ants from northern Sinai and the Nile region, while ants from the central Negev resemble ants from central and SE Sinai.

Measurements: TL=5.3–12.8, HL=1.50–3.22, HW=1.31–3.16, EL=0.43–0.88, iOD=0.94–2.42, OcClD=0.71–1.51, SL=1.74–3.36, F1L=0.49–0.91, F2L=0.25–0.51, ML=2.38–4.61, MW=0.92–2.05, PrL=0.82–1.68, PrH=0.22–0.55, PNL=0.46–0.96, PNW=0.29–0.70, PNH=0.25–0.57, PNA=63–81°, mFmL=1.95–4.22, hTbL=2.44–5.22 (n=200).

Material examined: Israel: Bezet, 525, 15.iii.2014, T. Reiner-Brodetzki (10☿, 1♂); Nahariyya, 2012, R. Zeltzer (11☿); Bustan HaGalil, 2012, R. Zeltzer (17☿); 'Akko, 3.xi.2010, R. Zeltzer (8☿); Mikhmoret, 2012, R. Zeltzer (20☿); Ra'ananna, 10.v.1944, H. Bytinski-Salz (1♀, 2♂); Palmahim, 2012, M. Saar (20☿); Modi'in, 3.iii.2011, R. Zeltzer (21☿); Suseya, 15.iv. 2016, A.L.L. Friedman (1☿); Tel 'Arad, 26.ii.2009, A. Ionescu (3☿), 10.iv.2011, R. Zeltzer (4☿), #1, 10.iv.2011, R. Zeltzer (4☿), #2, 10.iv.2011, R. Zeltzer (4☿), #3, 10.iv.2011, R. Zeltzer (1☿), #4, 10.iv.2011, R. Zeltzer (4☿),

Table 2: Least square means ±95% confidence interval at covariate mean, and sample size for four variables per sampling localities grouped by taxon and geographic region; see 'Materials and Methods' for full names of variables and Fig. 1 for numbers and names of geographic regions.

Locality, no. of geogr. region	SL ln(HW)=0.74	PrH PrL=1.12	PNH PNL=0.71	PNA PNL=0.73	mFmL MW=1.54
Montfort & Daverat, **1**, **5**	2.47±0.03, 22	0.30±0.01, 17	0.42±0.02, 10	71.4±2.4°, 8	3.06±0.04, 22
Hula & 'Ammi'ad, **1b**, **2**	2.49±0.04, 14	0.32±0.01, 13	0.42±0.02, 13	72.4±2.1°, 11	3.03±0.04, 14
'Atlit, **4**	2.54±0.03, 18	0.33±0.01, 29	0.43±0.01, 29	77.3±1.4°, 27	3.03±0.03, 30
Hof haBonim, **4**	2.54±0.04, 12	0.35±0.01, 17	0.44±0.01, 15	78.1±1.8°, 15	3.01±0.04, 17
Allon, **12**	2.63±0.03, 21	0.29±0.01, 24	0.43±0.02, 14	74.4±1.9°, 14	3.07±0.03, 26
Tel Barukh, **8**	2.51±0.04, 11	0.34±0.01, 12	0.41±0.02, 12	71.6±2.1°, 12	2.99±0.05, 12
Yafo, **8**	2.52±0.02, 39	0.36±0.01, 42	0.40±0.01, 22	71.0±1.5°, 22	3.02±0.03, 43
Ziqim West, **9**	2.53±0.04, 13	0.35±0.01, 13	0.37±0.02, 13	69.9±2.1°, 12	3.03±0.04, 18
Nahariyya, **4**	2.52±0.04, 11	0.35±0.01, 11	0.38±0.02, 8	67.0±2.4°, 6	3.01±0.04, 14
'Akko, **4**	2.46±0.03, 22	0.35±0.01, 15	0.39±0.02, 10	70.4±2.9°, 8	3.01±0.03, 25
Mikhmoret, **8**	2.59±0.03, 17	0.35±0.01, 22	0.42±0.01, 18	72.3±1.8°, 15	3.02±0.04, 22
Palmahim, **9**	2.58±0.03, 19	0.35±0.01, 11	0.42±0.02, 10	71.0±2.3°, 10	3.12±0.04, 20
Ziqim East, **9**	2.58±0.04, 10	0.33±0.02, 10	0.37±0.02, 9	70.1±2.5°, 8	3.06±0.05, 10
Nir Yizhaq, **9**	2.67±0.04, 9	0.38±0.01, 11	0.40±0.02, 8	68.7±2.5°, 8	3.24±0.05, 12
Modi'in, **10**	2.56±0.04, 10	0.34±0.01, 14	0.39±0.02, 9	70.1±2.4°, 9	3.07±0.04, 21
Tel 'Arad, **15**	2.58±0.03, 15	0.35±0.01, 22	0.42±0.01, 19	71.2±1.7°, 18	3.20±0.03, 25
Hazerim, **15**	2.57±0.04, 11	0.36±0.02, 8	0.38±0.02, 5	71.3±4.1°, 3	3.13±0.05, 13
Mishor Yamin, **17**	2.70±0.03, 15	0.38±0.01, 15	0.39±0.02, 14	70.3±2.1°, 12	3.24±0.04, 16
Hazeva, **14**	2.73±0.03, 16	0.33±0.01, 22	0.39±0.01, 22	70.8±1.5°, 22	3.15±0.04, 21
Nile reg., Egypt	2.53±0.04, 11	0.37±0.01, 18	0.39±0.02, 14	72.0±2.0°, 13	3.12±0.04, 20
Sinai, Egypt	2.71±0.04, 11	0.39±0.01, 24	0.38±0.01, 16	69.9±1.6°, 20	3.23±0.03, 30

#5, 10.iv.2011, R. Zeltzer (6☿); Ziqim East, #1, 2012, R. Zeltzer (3☿), #2, 2012, R. Zeltzer (3☿), #3, 2012, R. Zeltzer (2☿), #4, 2012, R. Zeltzer (2☿); Horbat Mamshit, 28.iv.19[??], H. Bytinski-Salz (1♀, 3♂); Hazerim, 3.iv.2011, R. Zeltzer (3☿), #1, 3.iv.2011, R. Zeltzer (1☿), #2, 3.iv.2011, R. Zeltzer (4☿), #3, 3.iv.2011, R. Zeltzer (5☿); Bor Mashash, 20.iv.2005, G. Kunikov (1☿, 2♂); Holot Mashash, 14.iv.2003, A. Mozer (3☿, 2♂); Sede Boqer, 20.vi.1974, B. Mordechai (3☿, 1♀), 16.v.1974, J. Morad (1♂); Nir Yizhaq, 3.iv.2011, R. Zeltzer (12☿,1♂); Yeroham, 11.iv.19[??], H. Bytinski-Salz (1♂); Mishor Rotem, 26.ii.2009, A. Ionescu (3☿); Mishor Yamin, 10.iv.2011, R. Zeltzer (16☿); Qadesh Barnea', 29.v.1970, H. Bytinski-Salz (1☿); Holot 'Agur, 3.iii.2016, I. Renan (4☿); Hazeva, 25.v.1992, A. Ionescu (1☿, 1♀, 1♂), 15.i.1994, Shapira (4☿), 25.i.1994, Shapira (8☿), 6.ii.1994, Shapira (8☿), 22.iii.1994, A. Ionescu (2☿, 1♀, 1♂). **Egypt:** Quassasin, 16.xii.1945 (5☿); Saqqara (Sakkara), 12.ii.1981, J. Kugler (1☿); Dendera, 15.ii.1981, J. Kugler (2☿); Rafiah, 26.vi.1973, B. Shalmon (2☿) (*desertorum sensu* Santschi); W. Garandel, 28.iii.1969, J. Kugler (6☿); Mitla, 25.v.1971, H. Bytinski-

Salz (3☿), 13.iv.1973, D. Furth (4♂); Abu Ageilah, 6.iv.1968, Ch. Saudler (3☿); Oasis Feran, 25.v.1971, H. Bytinski-Salz (1☿); Djebel Katarina, 6.iv.1968, Ch. Saudler (3☿); Nabq, 4.iv.1968, Ch. Saudler (5☿); Ein Khadidja [En Chadjiah] (70 km SSW Nabq), 23.iv.1968, H. Schweiger (4☿).

C. cf. *savignyi* from northern Africa: **Tunisia:** Kairouan, Dr. Santschi (2☿), identified by Santschi as var. *desertorum* Forel (junior synonym of *savignyi*).

C. oasium (*sensu* Santschi): **Egypt:** Alexandria, 10.xi.1937 (3☿); Assiut, 14.ii.1981, J. Kugler (5☿); Komombo, 15.ii.1981, J. Kugler (2☿); Wadi Feran, 18.v.1970, H. Bytinski-Salz (2☿). **Iran:** Shiraz Env., 16–21.v.1972, H. Bytinski-Salz (2☿).

C. nigripes: **Iran:** Shiraz Env., 16–21.v.1972, H. Bytinski-Salz (19☿, 3♂).

C. abyssinica (*sensu* Santschi): **Senegal:** '309' (1☿).

Distribution: The species was reported as widely distributed from the northern fringe of the Sahara desert, from the Atlantic to northern Sinai and the Arabian Peninsula (Collingwood & Agosti 1996).

Notes: The Santschi's (1929) key for the bicolored specimens of *C.* cf. *savignyi* from Israel will identify them as '*savignyi*', with the exception of the samples from Tel 'Arad that key out to *C.* st. *saharae* Santschi. The ants from Egypt will split into '*savignyi*' and '*oasium*' (the samples from Alexandria, Assiut, Komombo and Wadi Feran); however, using this key, all identifications of ants from Israel and Sinai will be dubious, except for the ants from Modi'in, because of the accentuated gaster sculpture. Using the identification key of Collingwood and Agosti (1996) all *C.* cf. *savignyi* specimens from Israel and Egypt with bright-red mesosoma and/or low propodeum (Fig. 17) and petiole will key out to *C. abyssinicus* or *C. saharae* (*sensu* Collingwood in Sharaf *et al*. 2015).

A particular difficulty in defining the *niger* species-complex stems from the uncertainty related to the identity of *C. savignyi*. The description of *Formica savignyi* by Dufour (1862) is based on two illustrations of a worker and a male from Egypt by J. Savigny, and on specimens in the Dufour's collection considered by him as similar to the illustrations. The described workers were collected in the region of the Pyramids (Egypt) and in Algeria; and the single male was collected in Oran (Algeria). Santschi (1929) assumed that Dufour's types had been lost and designated new types from Egypt and Libya (AntWeb CASENT0912229) that best fit the original description, and provided a new diagnosis. However, Agosti (1990) retrieved two workers from 'Gizeh' and one worker and one male from 'North Africa' labeled *savignyi* in Dufour's collection in the Muséum National d'Histoire Naturelle, Paris. The workers belong to the *mauritanicus* species-complex (AntWeb CASENT0915501) and the male to the *niger* species-complex, the latter being selected as the lectotype of *C. savignyi* (Agosti 1990).

It is probable that the lectotype of *C. savignyi* is related to the *bicolor* group populations from northern Africa that were thoroughly investigated by morphometric, biochemical and molecular means by Wehner *et al*. (1994) and Knaden *et al*. (2005). These populations are genetically distinct from the Israeli *C.* cf. *savignyi*, and in the molecular phylogenies reconstructed in Knaden *et al*. (2012) and Aron *et al*. (2016) *C. savignyi* is paraphyletic. Because the name *C. savignyi* should be reserved for populations from which the type was selected, it seems that *C.* cf. *savignyi* from Israel needs renaming. *C.* cf. *savignyi* from Israel, *C.*

abyssinica from Egypt and *C*. *niger* are part of the same clade, but the taxonomic importance of the genetic divergence between *C*. *niger* and these other populations (Aron *et al*. 2016) is yet unknown; and, therefore, a nomenclatural change under the present state of knowledge of these ants seems inadvisable.

We will refer to *C*. *niger* and *C*. cf. *savignyi* from Israel collectively as the *C*. *niger*-complex because of the following: (i) *C*. *niger* cannot be reliably distinguished from black *C*. cf. *savignyi* from the Coastal Plain region; (ii) there are too few samples of *C*. cf. *savignyi* from NE Africa and the Middle East, that have been investigated by molecular means for confident assessment of the phylogenetic relationships between these ants; (iii) it is unclear, which ant population the name *C*. *savignyi* should be attributed to.

Discernment of species using traditional identification keys or morphometrics within the *niger* species-complex is very difficult for ants from Israel, if indeed there is more than one species. The primary cause of the inability to produce an identification key based on binary characters for use in faunistic studies, etc., which discriminates between *niger* and *savignyi*, is the bewildering variability of morphological characters of individuals within and among populations of *C*. cf. *savignyi*. This difficulty extends also to discrimination between *C*. cf. *savignyi* and other species, e.g. dark colored *C. israelensis* in the contingency areas between the species, or *C*. *abyssinicus* from Egypt (Knaden *et al*. 2014). Nevertheless, since *C*. cf. *savignyi* and *C*. *israelensis* are parapatric in Israel, the following key characters in conjunction with the known geographical distribution can be useful.

Key to *Cataglyphis bicolor*-group species of Israel

1 High propodeum with nearly straight dorsum and declivity that form a rounded right-angle in lateral view (Fig. 14) ('Arava Valley)...................... *C. holgerseni*
– Low propodeum with more arched dorsum in lateral view (Figs 13, 15–17) 2

2 First funiculus segment of worker is short relative to second segment, F1L/F2l<1.5 (Fig. 3) (Dead Sea area, central and southern Negev, 'Arava Valley).... ....*C. isis*
– First funiculus segment of worker is longer relative to second segment, F1L/F2l>1.5 (Fig. 11) 3

3 Symmetrically and smoothly arched propodeum outline in lateral view (Figs 7, 13); in bicolored worker coxae and petiole concolorous with mesosoma pleura (Fig. 7), or darker to some extent, medium workers (MW=1.0–1.5) always lighter than larger specimens (Figs 7, 12) (Hermon, Golan Heights, Galilee, Sea of Galilee area and Jordan Valley, Karmel Ridge, Yizre'el Valley, Shomeron, Judean Hills, Judean Desert, Dead Sea area) .... *C. israelensis*
– Propodeum higher and with steeply rounded outline in lateral view (Figs 16, 17); coxae and petiole distinctly darker than mesosoma pleura, usually black (Fig. 17), medium workers (MW=1.0–1.5) always darker than larger specimens (Coastal Plain, Judean Foothills, Negev, 'Arava Valley) ....*C. niger*-complex

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