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A neuropteran insect with the relatively longest prothorax: the "giraffe" among insects is the larva of a *Necrophylus* species from Libya

(Neuroptera, Nemopteridae)

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The larvae of holometabolan insects often differ morphologically significantly from their corresponding adults. This is also true for lacewings (Neuroptera). Almost all lacewing larvae, such as ant lions and aphid lions, are fierce predators with rather unusual morphologies. Yet, the larvae of thread-winged lacewings (Crocinae) are special even among neuropteran larvae. While they share the basic body organisation with prominent piercing stylets with other neuropteran larvae, many of them differ by having very long neck regions. The most extreme neck elongations are known in larvae of *Necrophylus*. We report here a single specimen of a stage two larva that has the relatively longest functional neck region (neck + pronotum) among neuropteran larvae. Additionally, it closes a distinct gap in the biogeography of the specimen: the new specimen originates from Libya, where *Necrophylus* has so far been unknown, while it has been known to occur in the surrounding countries.

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Introduction

Most adult insects are easily identified as such, as the overall body organisation of most insects is more or less stereotypic. Larvae of holometabolan insects (but also of some other insects groups) seem more "creative" concerning their overall body organisation. Some of the more unusual morphologies can be found among the larvae of neuropteran insects, better known as lacewings.

Lacewing larvae are characterised by having piercing and sucking mouthparts, being mostly predators of other insects (e.g. Sole et. al. 2013). Piercing-sucking type mouthparts may not appear unusual, as we know them well from mosquitoes or bugs, yet the piercing-sucking mouthparts of lacewing larvae are different. While the mouthparts of mosquitoes and bugs form a single elongated mouth-cone, lacewing larvae have a pair of piercing-sucking stylets: each mandible interacts with an enditic protrusion of the maxillae ("galea") to form a tube (e. g. Beutel et al. 2010, their fig. 8). For indeed piercing, the stylets work against each other in larvae of most neuropteran ingroups; for doing so they are often inward curved.

Like many others, the larvae of the thread-winged lacewings, those of the group Crocinae, are "sit and wait" predators, or simpler, ambush predators. Normally these larvae can be found under rocks, in caves and similar arid habitats. Thread-winged lacewings occur with most species in the Afrotropical and Australasian regions, as well as in the Middle East (Kral & Devetak 2016). In general, the larvae of lacewings are still understudied (e. g. Gepp 1984), yet within Crocinae we have quite a good coverage: Crocinae is usually subdivided into 17 species groups ("genera"), and of twelve of these, larval forms are known for at least one species each (Monserrat 2008). On first sight, some larvae of thread-winged lacewings resemble those of their close relatives, the antlions, which already clearly represent a body organisation deviating from the more common insect appearance with their massive heads and prominent fierce stylets. Yet, some species of Crocinae are clearly more weird in appearance; their larvae possess an elongated neck. The cervix, a special sclerite between the head and first trunk segment present in all neuropteran larvae, is strongly elongated, as is the first trunk segment or prothorax. This is the case in larvae of species of the groups *Laurhervasia*, *Tjederia*, *Moramida*, *Amerocroce*, *Dielocroce* and *Necrophylus* (Monserrat 2008). In larvae of *Dielocroce* and *Necrophylus*, the elongation is more extreme than in the others.

The first larva with a long neck and prothorax was discovered by Roux (1833) in tombs in Egypt, and for this reason, it was named *Necrophylus arenarius*. Based on quite similar larvae with a long neck, Klug (1836), Withycombe (1923) and Pierre (1952) described additional species and named them *Nemoptera capillaris*, *Pterocroce storeyi* and *Pterocroce troglophilus*, respectively. However, Hölzel (1975) suggested that these four supposed species represent in fact the same species and therefore united them under the name *Pterocroce capillaris; N. arenarius*, *P. storeyi* and *P. troglophilus* should represent its synonyms (Monserrat 2008). More recently, after revising the nomenclatural history of *Necrophylus*, Monserrat (2008) re-established *Necrophylus arenarius* as the valid name for the species.

This species, with its larval stages possessing the very long neck, has been recorded in Morocco, Algeria, Tunisia, Chad, Egypt, Lebanon, Saudi Arabia and Iran (Aspöck et al. 2001). Here, we report for the first time *Necrophylus* from Libya. Concerning relative lengths, the specimen has the longest neck + prothorax length known within Neuroptera representing an "extreme" type of morphology (see Haug et al. 2016 for the term).

Material and methods

Material

The single specimen in the centre of this study is housed in the Zoologische Staatssammlung München (ZSM). Label data: "Larva: Libya SW, Akakus Geb. Serir-Fläche, Fels II, 12.4.2004 leg. Burmeister". The location where the larva was found lies in the Southwest of Libya in the Akakus Mountains, right on the border to Algeria near the city of Ghat. The Akakus Mountains are the eastern foothills of the Hoggar Mountains. The larva was found on a boulder under a flat stone, which was lined by drifting sand. The designation 'Rock II (Fels II in German)' indicates one of the valleys, which show numerous early rock paintings and carvings. The specimen is stored in 70 % ethanol.

Imaging methods

The specimen was documented in its original storage liquid, 70 % ethanol. For imaging, the specimen was placed in a petri dish and fixed with a cover-slip. Images were recorded on a Keyence BZ-9000 fluorescence microscope, exploiting the autofluorescence capacities of the cuticle, as well as on a Keyence VHX-6000 digital microscope. All images were recorded as composite images (e. g. Haug et al. 2011) overcoming the limitations of field of view by recording many adjacent image details and by overcoming limitation of depth of field by recording each image detail with several images differing in focal level. All images of one image detail differing in focal plane ("frames") were fused to a sharp image, either with the free software CombineZP or with the build-in software of the VHX-6000. Fused images were stitched to large panorama images in Adobe Photoshop CS3 or Elements 11, or with the built-in software of the VHX-6000. Optimisation (saturation, levels, sharpness, removal of background) was performed in Adobe Photoshop CS2. The antennae were additionally documented with an oil immersion objective with transmitted light and processed following Haug et al. (2009).

Digital drawings

Drawings of the investigated specimen and specimens from the literature were prepared in Adobe Illustrator CS2. Optimisation (filter effects, addition of smooth gradient) was performed in Adobe Photoshop CS2. The Google map included in this paper was made through Berkeley Mapper (http://berkeleymapper.berkeley.edu/).

Measurements

Drawings and images from the literature were used to take measurements of all available specimens interpreted as representatives of *Necrophylus* (Table 1). Measured structures include the length of cephalic capsule, head, neck (cervix), neck + pronotum and entire body length excluding appendages (Fig. 1).

Results

Description of the specimen

General. The specimen corresponds to a second instar larva of a species of Crocinae, as indicated by the long neck (Figs 2A,B, 3A). Most neuropteran species are known to develop through exactly three larval stages. The specimen is too far differentiated to represent a first instar. It is also unlikely to represent a third instar. The outer cuticle of the larva is transparent in most regions of the body, revealing the morphology of the next instar below (Figs 2B, 3F; see e.g. Saltin et al. 2016 for this phenomenon). The morphology of the inner cuticle is already differentiated, clearly indicating that the next instar will still possess a larval morphology. The specimen is therefore interpreted as a stage two larva.

Anterior body, head and neck. The body is organised distinctly into head and trunk. Head forming enclosed capsule. Head capsule triangular, or better trapezoidal in dorsal view, tip pointing backwards; slightly longer than width at anterior rim; anterior rim more than 3 × as wide as posterior rim. Along the anterior and posterior margins several distinct modified papillae (dolichaster) (Figs 3B,C). Paired

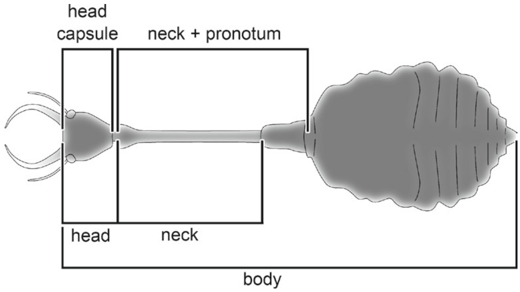

Fig. 1. Measured dimensions of the neuropteran larvae.

eyes with 6 ocelli on each side, far anteriorly. Head capsule dorsally with a deep y-shaped moulting suture (Fig. 3A). Antennae (appendages of post-ocular segment 1) arising dorso-anteriorly from the head capsule. Antenna with the first element tubular and centrally narrowed. Distally carrying flagellum with 9 flagellomeres. Distal flagellomere already with indication of future subdivision (Fig. 2C,D); first flagellomere almost as long as the rest; last flagellomere (9) longer than flagellomeres 2–8, with 3 setae on the apex (sensilla basiconica), one of the setae thicker than the other two (Fig. 2D).

Mandibles and maxillae (appendages of post-ocular segments 3 and 4) forming pair of functional stylets. Stylets inward curved, tapering distally, about as long as head capsule. Edges smooth, without teeth (Figs 2A,B, 3A). Stylets arising functionally anteriorly (prognath).

Appendages of post-ocular segments 5 conjoined to form labium. Distally, functionally anteriorly with paired palps. Each palp with three tubular elements.

Table 1. Measurements on all known specimens interpreted as representatives of *Necrophylus*. All dimensions in mm.

Source	figure	neck	head capsule	neck + pronotum	head	body length	refigured in Fig. 5
New specimen		3.4	1.1	4.2	1.2	8.07	A, C
Aspöck & Aspöck 1999	fig. 54	2.45	0.89	3.2	0.93	8.08	G
Badano 2018	fig. 1D	2.46	0.77	3.09	0.83	6.79	
Hölzel 1975	fig. 8	2.79	0.99	3.53	1.13	7.74	
Hölzel 1975	fig. 9	2.79	0.8	3.45	0.92	–	
Monserrat 1983	fig. 4	0.65	0.41	0.89	0.42	1.85	B
Monserrat 1983	fig. 5	2.88	1.03	3.74	1.18	8.29	E
Monserrat 2008	fig. 11L	2.89	1.04	3.73	1.16	8.11	
Monserrat 2008	fig. 9I	2.89	1	3.78	1.12	9.16	
Pierre 1952	fig. 24	2.79	0.92	3.47	1.06	7.52	F
Roux 1833	fig. 3	3.51	0.76	3.98	0.83	8.17	D
Withycombe 1923	fig. 2	2.28	0.93	3.15	1	–	
Withycombe 1923	fig. 3	2.7	0.77	3.37	0.86	–	
Withycombe 1923	fig. 4	2.7	0.79	3.39	0.88	–	

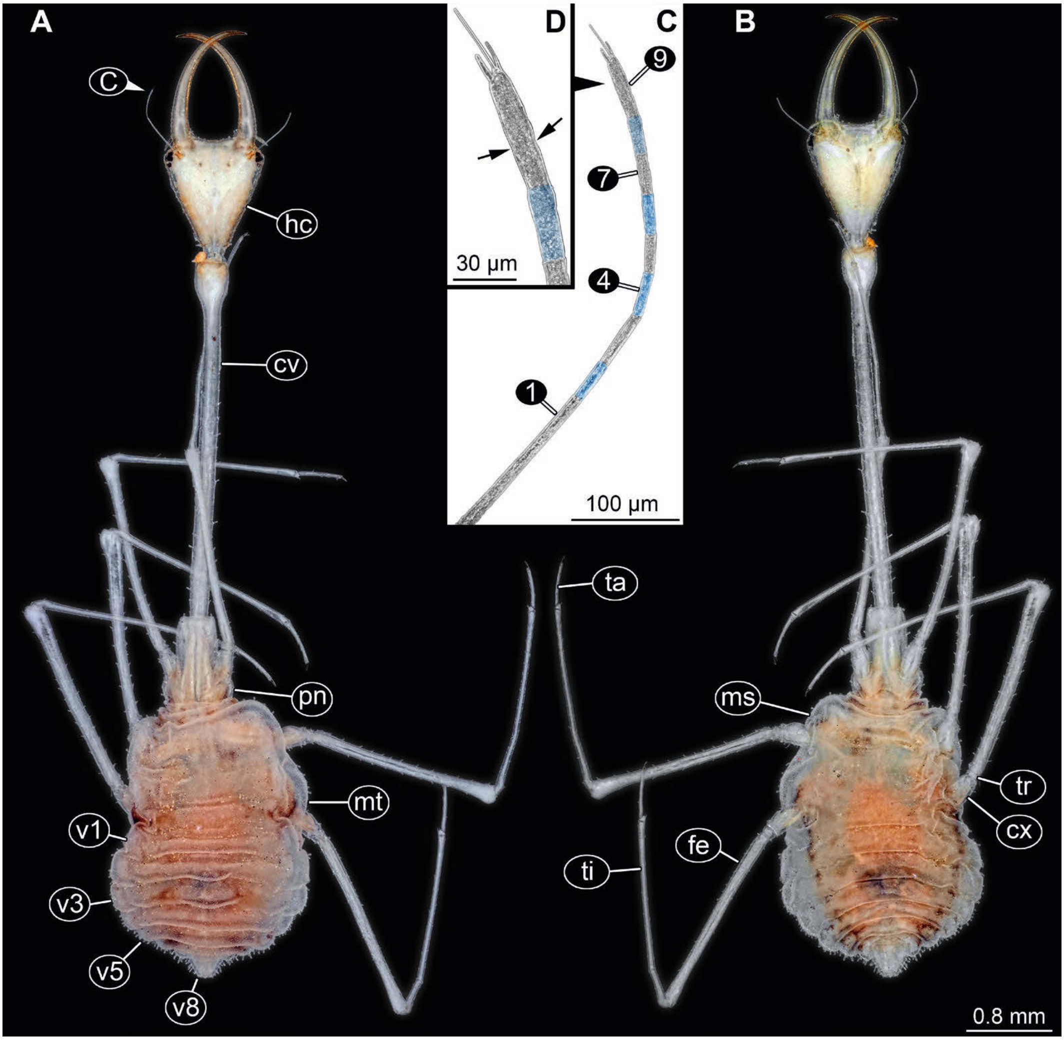

Fig. 2. *Necrophylus* sp. larva. **A, B.** Composite images under cross-polarised light. **A.** Dorsal view. **B.** Ventral view. **C, D.** Projections of details of the antennae following Haug et al. (2009). **C.** Subdivision into 9 elements (enhanced by colour-markings). **D.** Close-up on distal element; arrow marks future subdivision into two elements. Abbreviations: cv, cervix, neck; cx, coxa; fe, femur; hc, head capsule; ms, mesonotum; mt, metanotum; pn, pronotum; ta, tarsus; tr, trochanter; v1–8, visible abdominal segments 1–8.

Palp slightly thicker than antenna. Proximal element about 5 × as long as wide. Element two narrower and shorter, about 4 × as wide as long. Third element longer, almost as long as elements 1 + 2. First widening until 60 % of the entire length, then tapering.

Head jointed to elongate neck, cylindrical. Wider in the anterior part, in the posterior about as wide as the posterior rim of the head. In the anterior region almost 2 × as wide. Overall length more than 3 × as long as the head. Anterior region about as long as wide, then gently tapering. Lateral rims with numerous dolichaster-like structures. Neck articulating to the trunk.

Trunk. Trunk only weakly subdivided into segments and tagmata, only indicated by fold system, not by distinct sclerotisations (tergites, sternites). All trunk segments along the lateral rim with few dolichaster-like structures. Anterior tagma (thorax) with three segments.

First thorax segment (prothorax) anteriorly jointed with neck anteriorly and set off distinctly from succeeding segment by prominent folds and

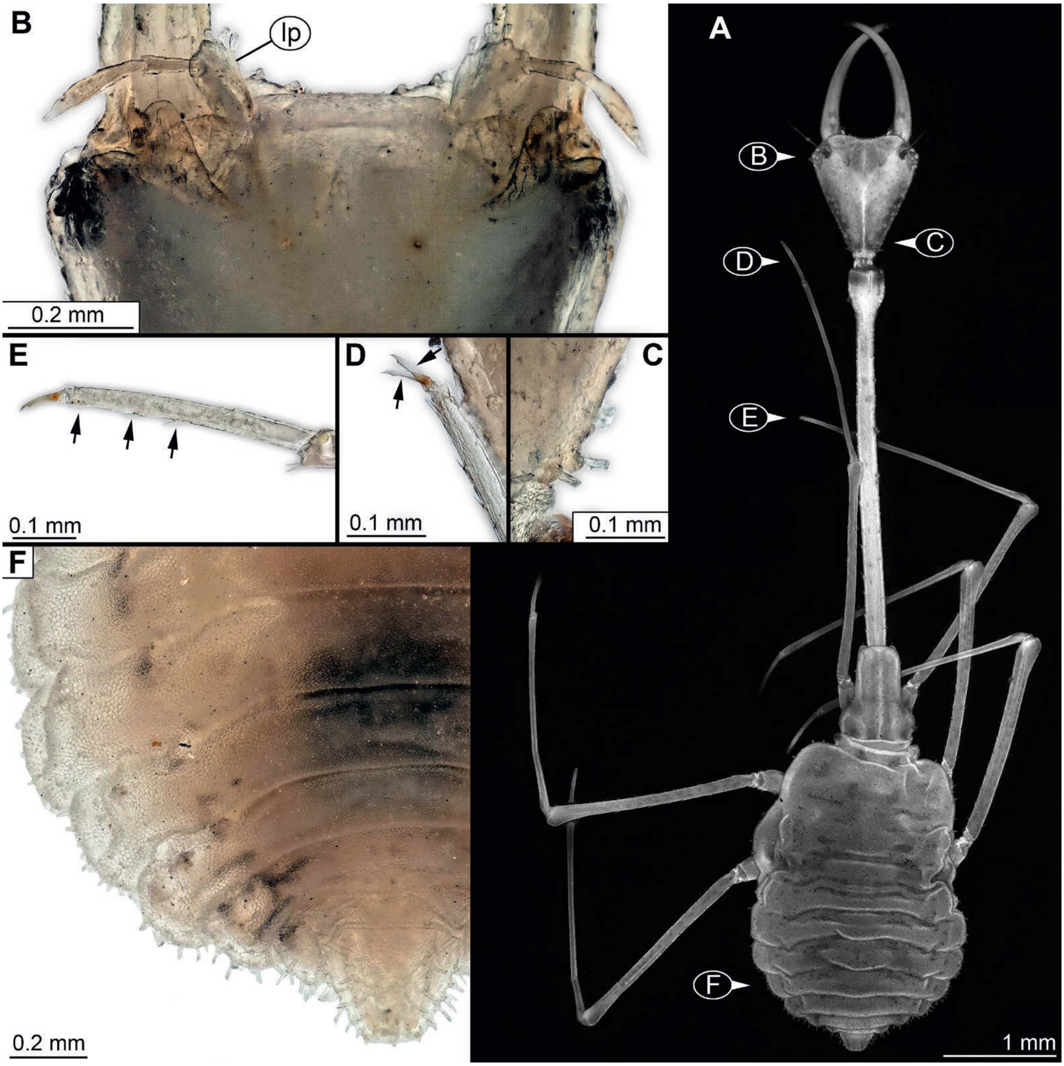

Fig. 3. *Necrophylus* sp. larva. **A.** Composite image under fluorescence light. **B–F.** Close-up images under cross-polarised light. **B.** Anterior head region with labial palps (lp) with three elements. **C.** Posterior head region with dolichaster-like structures. **D.** Distal tip of prothoracic appendage; arrows mark the two claws. **E.** Tarsus of prothoracic appendage, lacking subdivision; arrows mark prominent setae. **F.** Lateral edge of posterior abdominal segment with numerous dolichaster-like structures; note the outer and inner cuticle.

a change in width. Anterior rim about 2 × as wide as the neck, about 2.5 × as long as the anterior rim. Widening gently posteriorly until about 60 % of the entire length, then widening more abruptly to almost 2 × the width of the anterior rim. Dorsal region (pronotum) not strongly sclerotised, but weakly set off from ventral region by thin fold.

In this wider region ventrally a pair of appendages inserts. Insertion area directed forward. First thoracic appendage tubular, proximally slightly narrower in diameter than neck, but slightly longer. Appendage subdivided into 5 elements. Proximal element (coxa) about 3 × as long as wide. Element 2 (trochanter) shorter (about 40 % of the coxa length), slightly narrower, only indistinctly set off from element 3. Element 3 (femur) very long, about 6 × as long as coxa. Element 4 (tibia) more slender, but slightly shorter than femur. Tarsus shorter, about as long as coxa but much more slender, also more slender than tibia. Tarsus without any subdivisions (a single

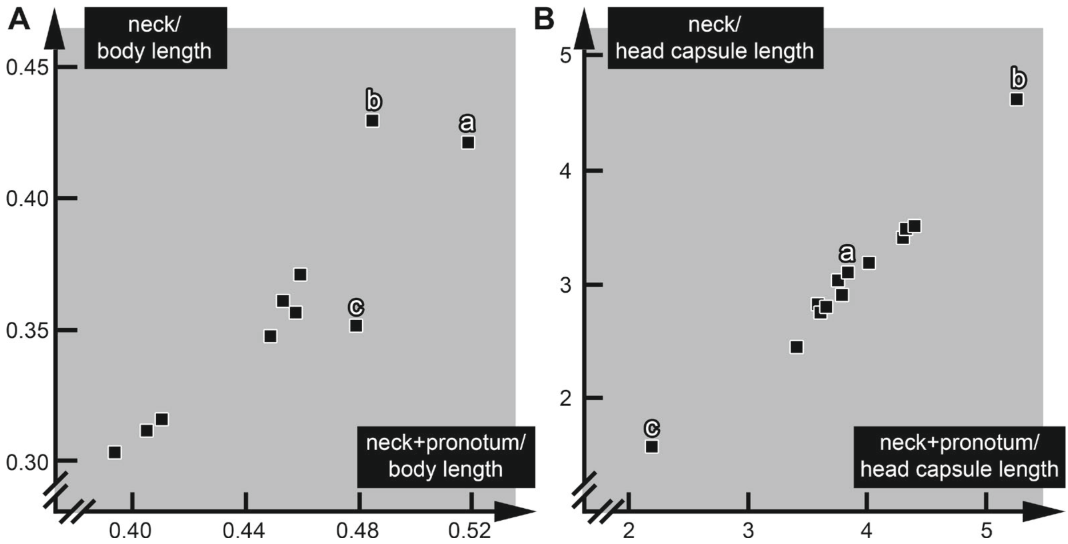

Fig. 4. Scatterplots of ratios measured from larvae of *Necrophylus*. **A.** Ratio of neck length and body length versus ratio of neck+pronotum length and body length. **B.** Ratio of neck length and head capsule length versus neck+pronotum length and head capsule length. Specimen references: a, new specimen; b, specimen from Roux (1833); c, neonate specimen from Monserrat (1983).

element) (Fig. 3E). Distally bearing two claws, less than 20 % of the length of the tarsus. Slightly curved inwards towards the apex and bearing a small preapical tooth (Fig. 3D).

Thorax segments 2 and 3 not well separated from each other with a more or less continuous dorsal (mesonotum + metanotum) and ventral surface. Roughly trapezoidal in dorsal view, widening slightly posteriorly, edges gently rounded. Anterior width about 2 × as wide as maximum width of pronotum. About 2 × as wide as long. Laterally with two pairs of appendages (thoracic appendages 2 and 3). These are roughly similar to thoracic appendage 1.

Further posterior trunk, abdomen, separated from thorax by fold and distinct constriction. Further subdivided into eight more or less well discernible units by folds. It is unclear how these exactly correspond to segments. The fold system is structured in a way that the fold between thorax and abdomen could represent only membrane or an entire segment. It is therefore unclear whether the first distinct unit is abdominal segment 1 or 2. Also posteriorly it remains unclear whether the terminal unit encompasses several segments. Reference is given in the following to the eight units as 'visible abdominal segments 1–8', yet, emphasizing here that it is unclear whether these are truly abdominal segments 1–8. Visible abdominal segment 1 anteriorly about as wide as metathorax, slightly widening posteriorly. Anterior-posterior dimensions about 25 % of the length of mesothroax + metathorax. Visible abdominal segment 2 wider than preceding segment, about the same length. Visible abdominal segment 3 roughly similar in dimensions to abdominal segment 2. Visible abdominal segment 4 narrower than preceding segment, about the same length, narrowing posteriorly. Visible abdominal segment 5 narrower than preceding segment, slightly shorter in length, narrowing significantly posteriorly. Visible abdominal segment 6 distinctly narrower than preceding segment, shorter in length, narrowing significantly posteriorly. Visible abdominal segment 7 distinctly narrower than preceding segment, shorter in length, narrowing significantly posteriorly. Visible abdominal segment 8 distinctly narrower than preceding segment, only about 60 %, narrowing posteriorly. Longer than preceding segments, about as long as visible abdominal segment 1. Ventrally visible abdominal segments 1–7 are posteriorly curved; towards the posterior progressively stronger curved.

All abdominal segments armed laterally with dolichaster-like structures along the rim. Surface with delicate net-like pattern. Overall the trunk and neck have the shape of a classical guitar.

Measurements

Measured dimensions are given in Table 1.

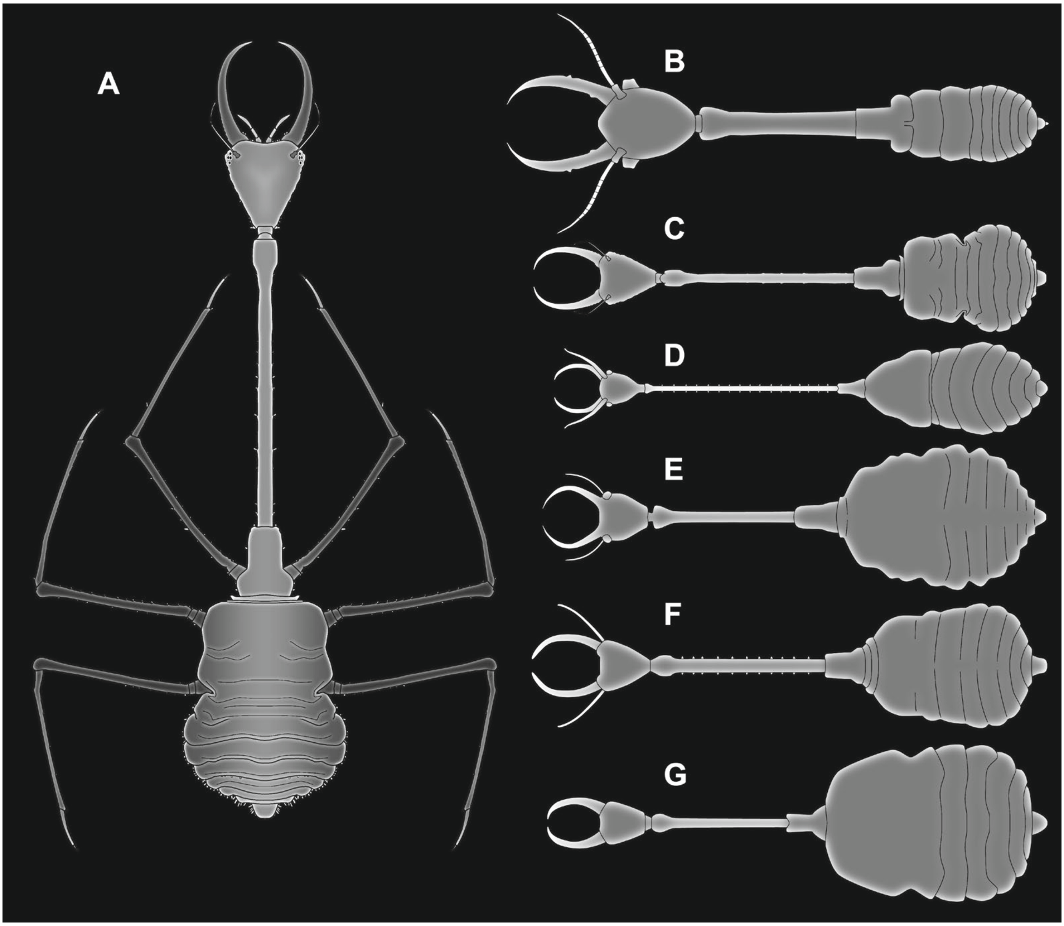

Fig. 5. Comparison of the new specimen to specimens from the literature. **A.** Restoration of new specimen of *Necrophylus* sp. **B–G.** Schematic representations of the central body, emphasising the relative neck lengths; not to scale. **B.** 1st instar larva ("*Pterocroce capillaris*") simplified from Monserrat (1983, his fig. 4); **C.** New specimen. **D.** Holotype specimen simplified from Roux (1833, his fig. 3); **E.** 3rd instar larva ("*Pterocroce capillaris*") redrawn from Hölzel (1999, his fig. 4); **F.** 3rd instar larva ("*Pterocroce troglophilus*") simplified from Pierre (1952, his fig. 24). **G.** 3rd instar larva ("*Pterocroce capillaris*") simplified from Aspöck & Aspöck (1999, their fig. 54).

Scatter plots

Plotting the ratio of neck length and body length versus the ratio of neck + pronotum length and body length reveals two more or less distinct clusters (Fig. 4A); the new specimen and that presented by Roux (1833) are resolved in extreme positions. Plotting the ratio of neck length and head capsule length versus the ratio of neck + pronotum length and head capsule length reveals one distinct cluster and two points as extremes (Fig. 4B). The lower left one is a stage 1 larva (all other specimens are stage 2 or 3), and the upper right one is the specimen of Roux (1833).

Discussion

Identity of the specimen

As pointed out above, larvae with very long neck regions are known in species of the group Crocinae, especially in the two species groups *Dielocroce* and *Necrophylus* (Fig. 5). Both *Dielocroce* and *Necrophylus* have a triangular head, a cup-shaped "neck", and the mandibles are relatively smooth and lack prominent teeth (Tjeder 1967). Yet, the neck in larvae of *Necrophylus* is even longer than that in larvae of *Dielocroce*, the relative neck length of our specimen being more similar to known larvae of *Necrophylus*.

So far *Necrophylus* comprises only one species, *Necrophylus arenarius*. One might therefore argue that the specimen should be a representative of this species. Yet, the case is more complicated. As pointed out, we can see the next layer of cuticle very well in some areas of the specimen. The morphology is strongly resembling the outer cuticle. Although this seems the general condition even in cases where the inner cuticle will change over time (Saltin et al. 2016), in this case, the inner cuticle appears already quite differentiated, indicating that there will be another stage with a rather similar morphology after this one. The specimen is, therefore, most likely a second stage larva.

Most of the known larvae of thread-winged lacewings are third stage larvae. The second stage larva of *N. arenarius* has not been described or illustrated in detail so far. The only mentioning by Monserrat (1983, page 114) is: "The second stage achieves practically the proportions achieved after the second and last change." This would indicate that it should resemble the third stage larva. Yet, there are some subtle differences of the specimen described here and the known third stage specimens of *N. arenarius*. Most apparent the shape of the head is more elongated in this specimen than in *N. arenarius*. Also, the base of the head is more concave in this larva, while it appears quite convex in larvae of *N. arenarius*.

Many other characters are not available as the specimen seems to have lost colour over time. The abdomen is very different and appears rather underdeveloped. Yet, this difference may be attributed to the fact that the larva is only in its second stage. Additionally, this impression might be more expressed if the larva had to starve for some time.

In summary, the larva seems most likely a representative of the group *Necrophylus*. It remains partly unclear whether it represents a larva of *N. arenarius*; it could be a larva of a yet to be described closely related species. Also the observed pattern when plotting the ratios of head to body for known larvae of *N. arenarius* relates to the same problem (Fig. 4). There are two rather distinct clusters, besides the more isolated position of the new specimen. The differences in the sample may be related to different degrees of feeding, the lower cluster being well-fed specimens which then possess a relatively shorter neck, as the abdomen will appear longer. This is supported by the plot of the ratio of the neck length and neck + pronotum length versus a less deformable part of the body, i. e. the head capsule (Fig. 4B). Here we see one distinct cluster of all known larvae (and the new specimen) with only the stage 1 larva and the larva described by Roux (1833) plotting separately. For improving the situation, a precise comparison of the variability of larvae of *N. arenarius* will be necessary, but will require a larger set of specimens from a single locality. For the moment, we will refer to the new larva as *Necrophylus* sp.

Biogeography

So far representatives of the group *Necrophylus* have been reported from along North Africa to Arabia. This includes in North Africa the countries Morocco, Algeria, Tunisia, Chad, Egypt, reaching further into the Arabian countries Lebanon, Saudi Arabia and Iran (Aspöck et al. 2001). This has left Libya somehow as a kind of "blind spot". Therefore it should have been well expected that the group is present in this area. Our find closes this gap and demonstrates the presence of the group *Necrophylus* in Libya (Fig. 6).

Extreme larvae

As pointed out, the larvae of thread-winged lacewing larvae are quite unusual compared to other neuropteran larvae, representing "extreme morphologies" with the extraordinary length of neck and pronotum. Aspöck & Aspöck (2007) have suggested that this is of advantage for their hunting strategies, but the exact functional morphological advantage is still unclear. Among the long-necked larvae of species of Crocinae those of *Necrophylus* and *Dielocroce* seem to be even more extreme. The larva described here tops them all.

The relative length of the functional elongated region, neck plus prothorax, is in relation to the overall body length (excluding stylets) the most extreme so far recorded. This seems to be due to the short length of the abdomen, which might have been slightly longer if the larva would have been better fed. Still it is quite astonishing.

Concerning the neck-only aspect the larva falls slightly short behind the holotype of *Necrophylus arenarius* Roux, 1833 (simplified here in Fig. 5D, compare with Fig. 5C), i. e. this specimen has the relatively longest neck (cervix). However, the correctness of the proportions of the original drawing from Roux (1833) have been doubted; although the drawing was reproduced by several authors (e. g. Westwood 1840, Sharp 1895), its proportions received criticism. Baron Ferussac (Roux 1833, page 76) in a footnote in Roux's (1833) paper states that the drawing leaves much to be desired, to the point that it was not possible to know based on the drawing if it was the larva of an insect. Eltringham (1923) mentions several imprecisions in the drawing (e. g. position of front legs incorrect, structures of the mandibles and antennae found in the drawing, but not in the specimens). Finally, Monserrat (2008) suggested that Roux (1833) incorrectly exaggerated neck length as the most striking element.

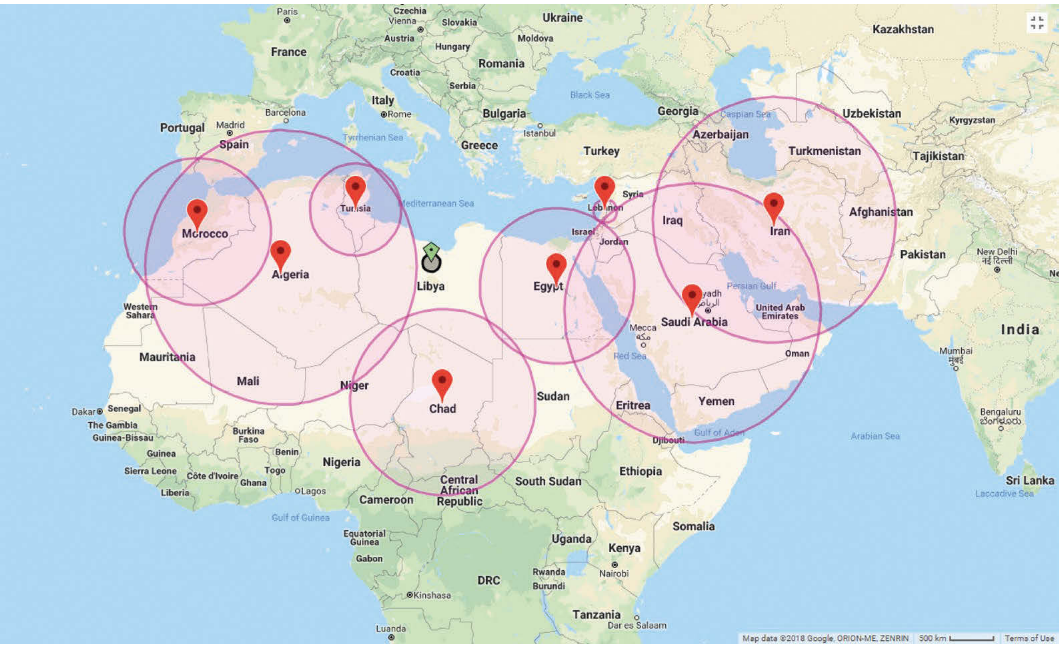

Fig. 6. Distribution of *Necrophylus*. In red so far known reports; in green the new report.

Also our plot of ratios of the neck versus the head capsule is interesting in this aspect. The specimen as depicted by Roux (1833) plots clearly outside the range of all the other specimens (Fig. 4B). This could indeed be read as an indication that some of the proportions in this drawing are incorrect.

Therefore, the new specimen has quite likely also the longest neck-only to overall body ratio so far found in Neuroptera. It seems likely that this is a general feature for stage 2 larvae of *Necrophylus*, but has to be supported by further finds. Extreme morphologies indicate what is possible from a functional morphological perspective. For sure the specimen represents an unusual morphology among insect larvae and demonstrates the evolutionary and functional-morphological possibilities of a seemingly stereotypic body organisation as supposed to be present in insects.

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