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Nesticus henderickxi (Araneae, Nesticidae), a new blind troglobitic spider from Crete

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Summary

Nesticus henderickxi sp. n., an eyeless troglobitic spider species discovered in a limestone cave in Crete, is described as new. The possible affinities of the new species are discussed, and the possible causes of the development of extreme adaptations to cave life in troglobitic arthropods, such as complete loss of eyes, are commented upon.

Introduction

In July 1996, H. Henderickx searched the “Kournas cave” (Fig. 1), a limestone cave in NW Crete, for invertebrates. Two adult specimens of an undescribed species of *Nesticus* Thorell, 1869 (Nesticidae) were collected. The new species is completely eyeless (Figs. 2, 7) and devoid of pigment, characters typical of true troglobionts.

Material and methods

Specimens were studied under a binocular microscope, using incident light. In order to make a detailed drawing of the internal female genitalia, the vulva preparation was dissected free, cleared in methyl salicylate and photographed under a compound microscope under transmitted light. Photographs were electronically enhanced with an “unsharp masking” technique, using the computer programme Pictor vl.2 (Schollaerts & Houben, 1994). Terminology of male and female reproductive organs follows Huber (1993), unless stated otherwise.

Type specimens are deposited in the Royal Belgian Institute for Natural Sciences, Brussels (RBINS 28.476).

Abbreviations used in figures and text: ad=anterior diverticulum of vulval pocket; co=copulatory orifice; ef=epigastric furrow; efs=epigastric furrow sclerite; fd=fertilisation duct; Fe=femur; id=insemination duct; Mt=metatarsus; Pa=patella; sp=spermatheca; Ta=tarsus; Ti=tibia; Tm=distance between tibia/metatarsus junction and base of metatarsal trichobothrium, divided by metatarsus length; To=distance between metatarsus/tarsus junction and tarsal organ, divided by tarsus length; vf=ventral fold in female vulva; vpl=vulval pocket, lateral part; vpm=vulval pocket, medial part. Measurements are in mm, except for Tm and To, which are ratios.

Nesticus henderickxi, sp. n. (Figs. 2–8)

Type material: Male holotype, Crete, Kournas cave (35°19'00"N, 24°17'13"E), altitude 250 m, hand captured in limestone cave, 7 July 1996, Hans Henderickx leg. Paratype: one female, same data.

Etymology: The species is named after Hans Henderickx, who collected the type specimens.

Diagnosis: The male can be distinguished by the shape of the paracymbium and its cavity and by

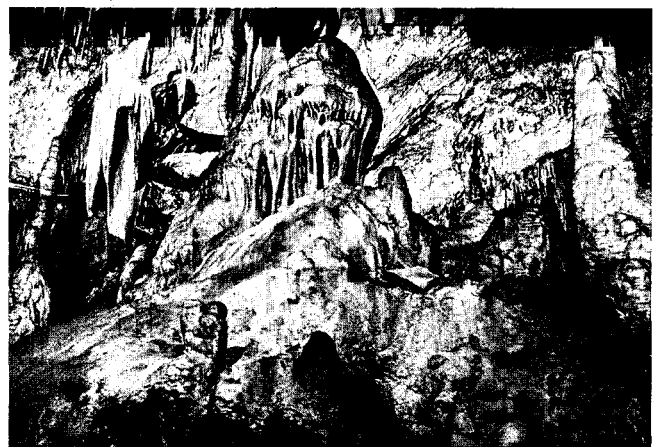


Fig. 1: Inside view of the type locality (Kournas cave, Crete).

the material compensation theory, which attributes a selective advantage to eye reduction in an environment with a low and erratic food supply such as a cave, because, as a result of the regression, no energy is wasted on developing a useless structure. A far more refined version of this theory has been supported by substantial evidence for blind mole rats. In *Spalax ehrenbergi* the brain volume that would normally be used for visuo-motor integration and for form and motion perception is entirely devoted to somatosensory processing. Only vestigial subcutaneous eyes and the central nervous system sections devoted to photoperiodic synchronisation have been retained (Cooper *et al.*, 1993; Diamond, 1996). While it must be admitted that the visual system is far more complex in mammals than in web-building spiders such as the Nesticidae, the fact remains that a large part of a spider's dorsal ganglionic mass is normally devoted to visual functions (Foelix, 1979). Devoting this processing power to more useful sensory functions would be of selective advantage to a cave arthropod.

While some species of cave organisms may have evolved through gradual accumulation of changes (Venanzetti *et al.*, 1993), the profound genomic reorganisation encountered in true troglobites has evolved, at least in a number of cases, in relatively short periods of time (Peck & Finston, 1993). In the case of *N. henderickxi*, the speciation event most probably occurred during the Pleistocene ice ages. After extinction of the epigeic population, as has apparently happened in the case of *N. henderickxi* on Crete, interaction of severe selection and genetic drift in the small populations usually encountered in caves (Gnaspini, 1996; Pinto-da-Rocha, 1996), can lead to fast allopatric speciation (Price, 1996). Whether or not chromosomal rearrangements (King, 1993) are involved in fast speciation of cave arthropods, as they are in mammals living in small populations (Wilson *et al.*, 1975; Nevo *et al.*, 1994; Vassart *et al.*, 1995), remains open to debate.

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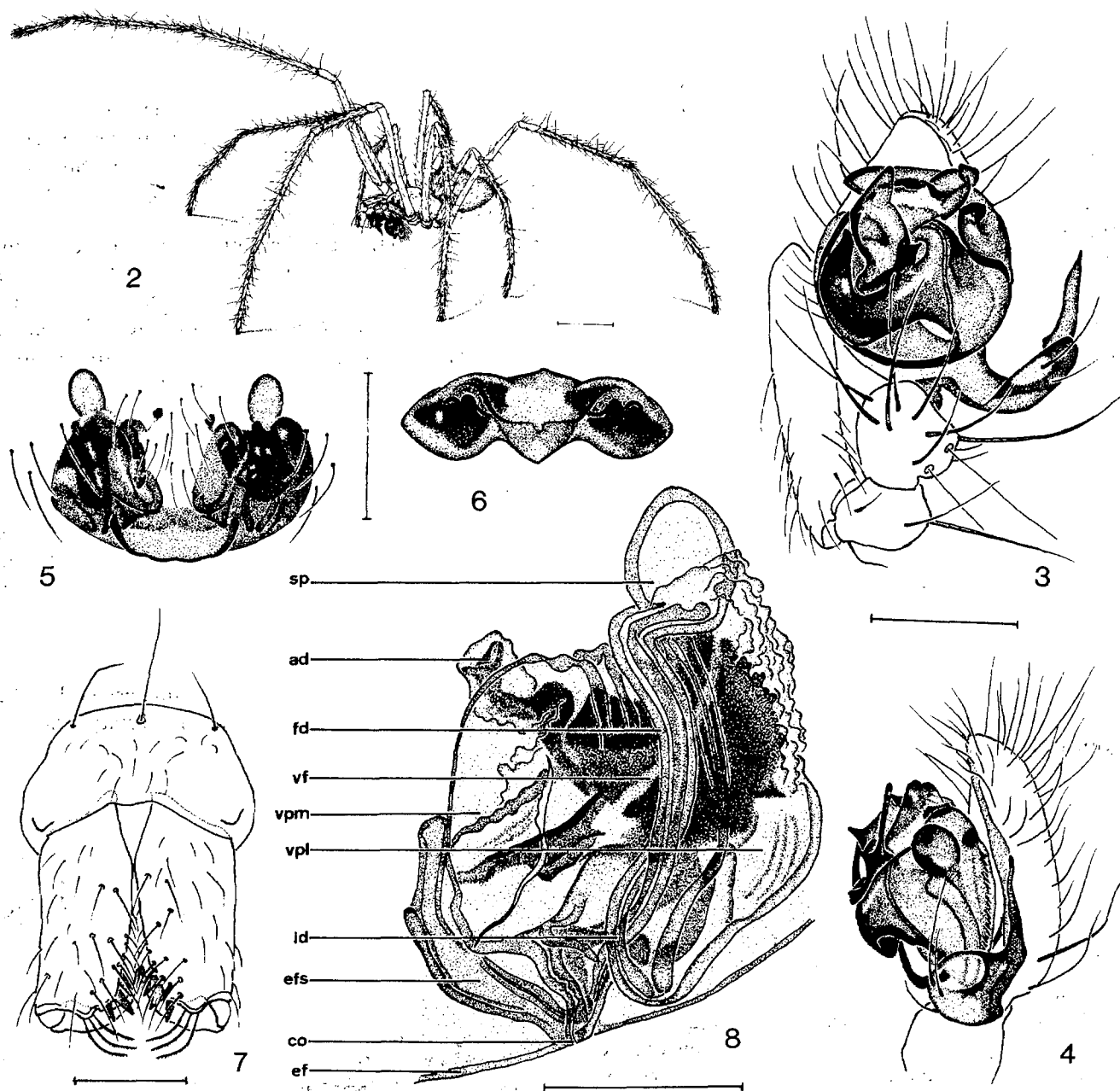
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the shape of the conductor and tegular apophysis of the male palp (Figs. 3, 4). The female can be distinguished by the shape of the scape of the epigyne (Fig. 5), the shape and position of the spermatheca, the connected ducts and the anterior diverticulum of the vulval pocket and by the distance between the medial parts of the vulval pockets (Fig. 8). Both sexes can be distinguished from most other *Nesticus* species by the absence of eyes. The new species shows some resemblance to *N. eremita* Simon, 1879 and is most closely related to *N. beshkovi* Deltshv, 1979. Further details of differences can be found in the discussion.

Male holotype (Fig. 2): Total length 2.13. Carapace length 1.00, width 0.95. Abdomen length 1.13, width 0.97. Sternum length 0.57, width 0.57. Carapace pale white, flattened, cephalic region bearing some erect, stiff, dark grey hairs. Eyes absent (Fig. 2). No trace of anterior or posterior median eyes; at places where lateral eyes would be expected, very shallow colourless dimples can be discerned under oblique light, using high magnification. Sternum white, smooth and shiny, sparsely covered with erect, stiff, dark grey hairs. Chelicerae light grey, promargin armed with three pale reddish brown teeth and bearing three stiff, comb-shaped setae on a bulge near base of fang; fang pale



Figs. 2-8: *Nesticus henderickxi*, sp. n. 2 Male holotype, habitus; 3 Male holotype, left palp, ventral view; 4 Ditto, retrolateral view; 5 Female paratype, epigyne, ventral view; 6 Ditto, posterior view; 7 Female paratype, cephalic region and chelicerae, frontal view; 8 Female paratype, cleared vulva, right-half, ventral view (for abbreviations see text). Scale lines = 1.0 mm (2), 0.25 mm (3-7), 0.1 mm (8).

reddish brown, sickle-shaped. Legs pale yellow, very slender, rather densely covered with long, thin, mostly straight hairs. No trichobothrium on metatarsus IV. Measurements:

	Fe	Pa	Ti	Mt	Ta	Total	Tm	To
I	3.56	0.49	3.86	3.51	1.27	12.69	0.54	0.74
II	2.48	0.43	2.48	2.30	0.97	8.66	0.45	0.67
III	1.76	0.38	1.46	1.49	0.73	5.82	0.44	0.56
IV	2.70	0.43	2.35	2.21	0.86	8.55	–	0.56

Abdomen pale yellowish grey, sparsely covered with thin, greyish, flexible hairs. Colulus very small, with two setae. Palp (Figs. 3, 4): ejaculatory duct almost straight, tegular apophysis rather large, hook-shaped. Paracymbial cavity cup-shaped, translucent.

Female paratype: Total length 2.97. Carapace length 1.22, width 1.03. Abdomen length 1.81, width 1.30. Sternum length 0.73, width 0.68. No trace of anterior or posterior median eyes; lateral eyes reduced to very shallow colourless dimples, as in male (Fig. 7). Other somatic characters also identical to those of male. Leg measurements:

	Fe	Pa	Ti	Mt	Ta	Total	Tm	To
I	3.70	0.49	3.75	3.38	1.30	12.62	0.58	0.77
II	2.70	0.46	2.40	2.13	1.00	8.69	0.49	0.70
III	1.86	0.38	1.35	1.40	0.78	5.77	0.35	0.52
IV	2.97	0.46	2.30	2.08	0.92	8.73	–	0.53

Epigyne and vulva: Figs. 5, 6, 8.

Distribution: Known only from the type locality.

Discussion

Although *N. eremita* is rare in Greece (Brignoli, 1979b), a detailed comparison has to be made between this widespread Mediterranean cavernicolous nesticid and the newly described species. The male of *N. henderickxi* differs from that of *N. eremita* in the following respects: the tip of the palpal paracymbium is thin and sharply pointed instead of wide and rounded, the conductor is smaller, less protruding and with a bipartite instead of a tripartite distal part, and the tegular apophysis ("median apophysis" of Dumitrescu (1979, 1980), Weiss (1981), Eskov & Marusik (1992) and Huber (1993)) is wide, hook-shaped and tapering to a blunt point distally, instead of suddenly narrowed into a semicircular, sickle-shaped and sharply pointed process, as in *N. eremita*. The female of *N. henderickxi* has an epigyne with two oval depressions and a wide, boat-shaped posterior scape, all different from the epigyne of *N. eremita*, which has two semi-oval grooves and a posterior scape which quickly tapers into a relatively narrow, rod-shaped extension flanked by two inflated processes. Good illustrations of the genitalia of *N. eremita* can be found in Kratochvil (1933), Wiehle (1963), Brignoli (1971) and Thaler (1981). Moreover, although eye development and pigmentation can vary widely in *N. eremita* (Dresco & Hubert, 1967; Kratochvil, 1978), no specimen with almost total eye loss, comparable to *N. henderickxi*, has ever been described.

The new species is closest to *N. beshkovi*, which was described from two females collected in the Trapezas cave, E. Crete (Deltshev, 1979). *N. beshkovi* resembles the present species in size and in being totally eyeless and devoid of pigment. However, the female of *N. henderickxi* can be easily distinguished from *N. beshkovi* by the relative position and shape of the spermatheca and its attached ducts. In *N. henderickxi*, the long axis of the egg-shaped spermatheca runs parallel to the vulval symmetry axis. The insemination and fertilisation ducts, which run parallel to each other for most of their length, originate at the wide, posterior end of the spermatheca and immediately make a sharp bend inwards, towards the vulval symmetry axis (Fig. 8). The ducts run perpendicular to the vulval symmetry axis for a distance of 0.05 mm and then turn at 90°, taking a course parallel to the vulval symmetry axis, leading towards the posterior end of the vulval pockets. In *N. beshkovi*, the long axis of the oval spermatheca makes an oblique angle with the vulval symmetry axis. The ducts originate at the innermost end of the spermatheca, closest to the vulval symmetry axis, make a shallow bend outwards and, halfway along their total length, make a second shallow bend in order to continue their course parallel to the vulval symmetry axis (Deltshev, 1979: fig. 5). Moreover; the medial parts of the vulval pockets are touching in *N. beshkovi*, while they are rather widely separated in *N. henderickxi*. The Trapezas cave, from which *N. beshkovi* was described, is situated at 1000 m above sea level at the border of the Lasithiou plateau, more than 100 km east of the Kournas cave and separated from it by the Psiloritis mountain range. Also, both Cretan *Nesticus* species show extreme adaptations to cave life and are obviously obligate troglobionts, so they can be considered geographically completely isolated.

N. henderickxi also appears related to the genus *Carpathonesticus* Lehtinen & Saaristo, 1980. Many of the male and female genital characteristics of the new species conform to the diagnostic criteria which Lehtinen & Saaristo (1980) cite for *Carpathonesticus*: paracymbium of the male palp with a simple, pointed tip, with a rounded basal modification and centrally toothed (barbed in some species); terminal apophysis ("radix" in Weiss (1981), Wunderlich (1986) and Eskov & Marusik (1992)) of the male palp compact; distal part of the conductor bipartite, ejaculatory duct almost straight; scape of the epigyne anteriorly wide; "receptacula" (vulval pockets) subglobular. However, the tegular apophysis of *N. henderickxi* is relatively large (Fig. 3), whereas in *Carpathonesticus* it should be reduced to a small hook.

Additionally, the genus *Carpathonesticus* was delimited in a confusing way by Lehtinen & Saaristo (1980). On one hand, they proposed the *C. fodinarum* group, a very homogeneous group of species from the Carpathian area. It is certainly defensible to consider this group as a genus, separate from *Nesticus*. If one includes the transfers made by Weiss & Heimer (1982), 17 species have been attributed to this group to date (Lehtinen & Saaristo, 1980; Weiss, 1983; Wunderlich, 1986; Platnick, 1989, 1993; Marusik, 1987; Eskov &

Marusik, 1992; Evtushenko, 1993), all described from the Carpathians or the Caucasus. It is clear from the illustrations and descriptions published by Dumitrescu (1979, 1980) that *N. ionescui*, *N. wiehlei*, *N. carpaticus*, *N. diaconui*, *N. orghidani* and *N. plesai* should also be transferred to this group.

On the other hand, Lehtinen & Saaristo (1980) also included a heterogeneous group of three species in the new genus, composed of *C. borutzkyi* (Reimoser), *C. parvus* (Kulczynski) and *C. menozzii* (Caporiacco). Not only is the distribution area of the genus greatly expanded in this way, now reaching from the Caucasus to the Ligurian Apennines in northern Italy, but the inclusion of at least one of the these species, *C. menozzii*, seems difficult to defend. The male palpal paracymbium of this species, as depicted by Caporiacco (1934), is totally unlike the paracymbium of typical *Carpathonesticus* species, and the epigynal scape is not wider anteriorly (Dresco, 1966). *C. menozzii*, a species with reduced eyes, seems related to two other Italian cavernicolous nesticid species with reduced eyes, *N. morisii* Brignoli, 1975 and *N. sbordonii* Brignoli, 1979, as can be deduced from the published descriptions (Brignoli, 1975, 1979a). These three species may in turn be related to *Typhlonesticus absoloni* (Kratochvil, 1933), as suggested by Brignoli (1979) and Thaler (1981). It is also possible that *C. menozzii* holds a rather separate position within *Nesticus sensu lato* (Cesaroni *et al.*, 1981).

In order not to add to this confusion, it is probably better to refrain from attributing any additional nesticid species from outside the Carpathian and Caucasian areas to *Carpathonesticus* at present. Such a move would require a revision of all European species belonging to *Nesticus sensu lato*, which is outside the scope of the present paper.

However, it is not unlikely that a large, eastern Mediterranean, *Carpathonesticus*-like complex of cavernicolous and troglophilous nesticid species exists and will eventually be described and delimited. Such a complex could include the *Nesticus* species described by Spassky (1932), Charitonov (1947), Pichka (1965) and Deltshv (1979), as well as the present species and probably additional species awaiting discovery in the caves of Turkey (Wiehle, 1963) and northern Cyprus.

Wunderlich (1986) states that *Carpathonesticus* is closely related to the fossil Eocene genus *Eopopino* Petrunkevitch, 1942, a conviction which is shared by Eskov & Marusik (1992) and by the present author. *Eopopino*, known from several closely related species preserved in Baltic amber, may be very similar to the ancestral stock from which the *Carpathonesticus* species group evolved. The shape of the male palpal paracymbium is similar in both genera, as are the compact terminal apophysis and rather straight ejaculatory duct of the male palp. Whether the *Eopopino* species were troglophilic (Wunderlich, 1986) or not (Eskov & Marusik, 1992) is at present impossible to decide, but most probably they were dependent on the high ambient humidity which must have prevailed in large parts of the subtropical Baltic amber forest (Mägdefrau, 1968). One can envision a scenario according to which the gradual

cooling of the central European climate during the Miocene epoch may have pushed the distribution area of an *Eopopino*-like *Carpathonesticus* ancestral stock further southward, towards the Mediterranean. Afterwards, catastrophic climatic changes, probably starting with the drying out of the Mediterranean at the end of the Miocene (Hsü, 1972) and culminating in the Pleistocene ice ages (Hewitt, 1996), may have wiped out most of the epigeic populations, of *Carpathonesticus*-like species, leaving behind isolated, sheltered cave populations which may have gone through rapid genetic changes resulting in allopatric speciation (Barr, 1967, 1968). However, judging by their rarity in the fossil record, representatives of the *Eopopino* species themselves may also have lived in small populations allowing fast speciation (Wunderlich, 1986). Eskov & Marusik (1992) consider the tempo of evolutionary change in the family Nesticidae to have been very high for spiders, and such intrinsically high speciation rates can help in explaining the large number of closely related species we find today in *Carpathonesticus* and allied species.

Most *Nesticus* and *Carpathonesticus* species are troglophiles: only a few species are found outside caves between limestone boulders. Nevertheless, far-reaching adaptations to cave life, such as increase in leg length (Merrett & Ashmole, 1989) and loss of eyes and pigment (Goodnight & Goodnight, 1960) are not the rule among species of *Nesticus sensu lato*. Among the 16 European species belonging to *Nesticus s.l.* described by Kratochvil (1933), only three are eyeless. Among the 41 North and Central American *Nesticus* species described by Gertsch (1984), seven are eyeless and eight have reduced eyes. The recently described cavernicolous *N. luquei* Ribera & Guerao, 1995 from northern Spain has only slightly reduced eyes (Ribera & Guerao, 1995), but the equally cavernicolous *Canarionesticus quadridentatus* Wunderlich, 1992 from Tenerife is completely eyeless (Wunderlich, 1992). All the nesticid species described by Spassky (1932), Charitonov (1947), Pichka (1965), Dumitrescu (1979, 1980), Weiss (1981, 1983), Weiss & Heimer (1982) and Marusik (1987) have normal eyes.

In the eastern Mediterranean, *C. parvus* and the two species described from Crete are the only known obligate troglolithes totally lacking eyes and pigment. The possible causes of this type of regressive evolution in cave animals have been the subject of considerable debate (Barr, 1968). Apart from the well-known Neolamarckian theories (Jeannel, 1943), several other explanations have been proposed, especially for the striking feature of eye loss. According to neutral mutation theory (Culver, 1982), any mutation leading to deterioration of eye structure and function is selectively neutral for an animal living permanently in a dark environment. Such a mutation can be fixed rapidly by genetic drift when population size is very small (Nachman & Searle, 1995; Price, 1996). Barr (1968) explains eye reduction by selection for pleiotropic alleles, which would combine a deleterious effect on eye development with characteristics of positive adaptive value in a cave environment. Barr (1968) also mentions