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COENAGRION LINDENII ZERNYI (SCHMIDT): AN EAST MEDITERRANEAN TAXON THREATENED WITH EXTINCTION BY INTROGRESSION FROM THE WEST (ZYGOPTERA: COENAGRIONIDAE)

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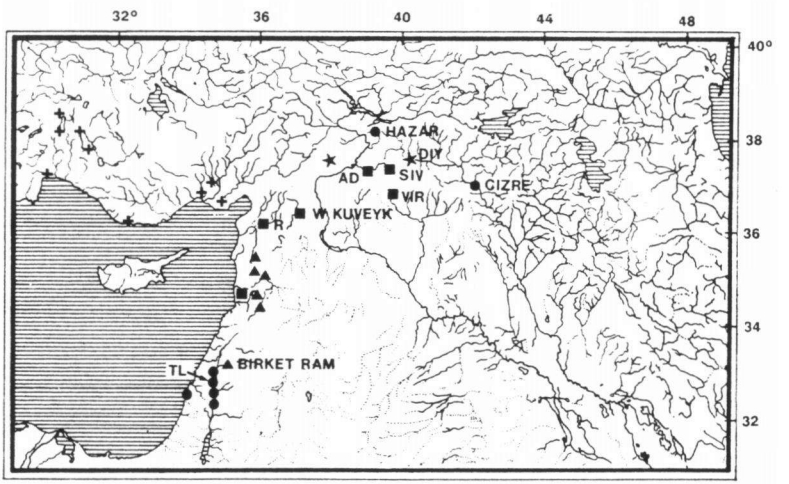
S and E of the Bay of Iskenderun in Turkey, *C. lindenii* (Sél.) changes from the nominal subspecies to spp. *zernyi* Schmidt in an introgressive manner with the formation of genetic 'islands' rather than a stable cline. In populations in E Anatolia, imagos emerging early in the season are close to *lindenii* (i.e. large and dark), while those emerging later in summer, are *zernyi*. Thus, a different time of development and eclosion of the larvae restricts the gene flow between the 2 taxa, and slows down introgression.

INTRODUCTION

Among West-Palaearctic dragonflies, there are numerous examples of postglacial expansion from East to West, such as *Epallage fatime, Caliaeschna microstigma*, etc. There are also cases, especially in Anatolia, where the westward expansion of a taxon seems to involve introgression with preexistent taxa, to the extent that the less expansive taxon becomes genetically extinct by incorporation of its genome into that of the expansive taxon (which, in the act, broadens its gene pool, and sometimes, though not always, its variation width). Such cases seem to be rather common in *Calopteryx*, where e.g. *C. splendens waterstoni* seems - at least on the century scale - on the brink of extinction in its small range along the north-eastern Black Sea coast of Anatolia. Similarly, expansion of *C. s. intermedia* towards the South along the East Mediterranean coast causes hybridization with *C. s. hyalina* (SCHNEIDER, 1986). These hybrids have been named *C. s. pseudosyriaca* by BUCHHOLTZ (1955).

There are far fewer cases of eastward expansion of a western taxon, with introgressive absorption of an eastern vicariant. The present paper explores such a case, in the coenagrionid damselfly *Coenagrion lindenii*, of which two subspecies *C. l. lindenii* (Sélys, 1840) (the western taxon) and *C. l. zernyi* (Schmidt, 1939) (the eastern taxon) have been described. The nominal subspecies, although originally described from Belgium, is a widespread thermophilic form, common in the Maghreb and on the Iberian peninsula, as well as in France, Italy, the Adriatic countries, Greece, and Anatolia. It reaches its limit of north-western extent in South and SW Germany, with outlying populations in Poland and Austria (map in ASKEW, 1988). All across this vast range, it shows remarkably little variation.

The subspecies *zernyi*, described by SCHMIDT (1939) from the Jordan Valley,



Map 1. Distribution of *C. lindenii* in the Near East. – Symbols: ● *C.l. zernyi* (T.L. = type locality); – ▲ intermediate hydrids; – ▮ hybrids with a strong phenotypic prevalence of *C.l. lindenii*; – + *C.l. lindenii*; – ✻ localities with spring animals phenotypically *C.l. lindenii*, but summer animals predominantly *C.l. zernyi* (note: at the scale of the map, a dot may represent several adjacent populations). – [Other abbreviations: Ad: Adiyaman; – Siv: Siverek; – Vir: Viranşehir; – R: Reyhanli]

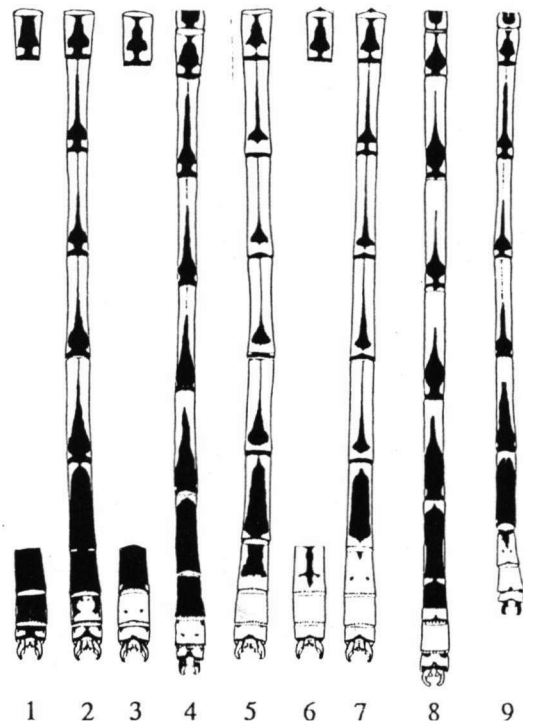
and believed until recently to be endemic of that area (DUMONT, 1991), has recently been found to be far more widespread, both to the North and the East (see further). However, nowhere does it seem to cover a coherent range; rather it occurs in more or less isolated populations, surrounded and/or invaded by the nominal subspecies.

Here, we analyse this introgressive hybridization, using populations from Israel, Syria, and East Anatolia.

We use the generic name *Coenagrion* for this species for convenience only, being aware of (but expressing no opinion on) alternative classifications, e.g. in *Cercion* or *Erythromma* (HEIDEMANN & SEIDENBUSCH, 1993).

MATERIAL EXAMINED

ISRAEL: 'En Te'o, VI-1972, ♂, ♀; – Bet She'an, VI-1972, 2 ♂ (see DUMONT, 1991). – JORDAN: Jisr Banat Ya'qub, 20-IV-1945, BM London, 3 ♂, 6 ♀. – SYRIA: Ain Zhaqà, 25/27-III-1979, ♂; – River Orontes (Asi) at Tall al-'Asharina, 17-VIII-1980, ♂; – as-Safsafiya, 11-VIII-1978, ♂; – River Orontes at Shaizar, 17-VIII-1980, 24 ♂, 8♀; – Nahr al-Abrash, 29-III-1980, ♂, and 22-VIII-1980, 2 ♂; – Wadi al-Mizrab, 11-VIII-1980, 22 ♂, 3 ♀ (see SCHNEIDER, 1981, 1986). – GOLAN HEIGHTS: Birket Ram, 12-VI-1972, 10 ♂, 8 ♀ (see DUMONT, 1991). – ANATOLIA (TURKEY): Wadi-Kuveyk (Halep Çayi) at intersection with road Kilis-Elbeyli, 15-V-1988, 9 ♂, 7 ♀; – Viranşehir, stream, 18-V-1988, 20 ♂, 7 ♀; – 5 km W. Siverek, 19-V-1988, 12 ♂, 6 ♀ (for locs 1-3, see DUMONT et al., 1988); – Içel: Anamur, 20-VIII-1987, ♀ (MP); – Adana, Sakarcali, Ceyhan nehri, 24-V-1994, ♀ (MP); – Urfa, Karabahçe, 24-VI-1993, ♂, ♀ (MP); – Hazar Gölü (Lake Hazar), 12-VIII-1980, 2 ♂, 2 ♀ (MP); – Mardin, 5 km SW Cizre, 20-VIII-1988 (MP), 3 ♂, ♀; – Adiyaman, Kalburcu Çayi (25 km E Adiyaman), 12-VIII-1988 (MP), 3 ♂, ♀; – 4 km E Adiyaman, 3-VI-1994, ♂; – Diyarbakir, Arpaçay 2-VI-1994, 17 ♂, 4 ♀ (MP); – same locality, 14-VIII-1988 (MP), 4 ♂; same locality, 24-VI-1993, 8 ♂; – Diyarbakir, Kirmasirt Cayi, 7-VII-1992, 6 ♂ (MP); same locality, 25-VIII-1989, 14 ♂, 7 ♀ (MP) [MP = collected by M. Pavesi]; – Reyhanli, former tributary of Amik Gölü, 21-IX-1982, 1 ♂ (SCHNEIDER, 1985).

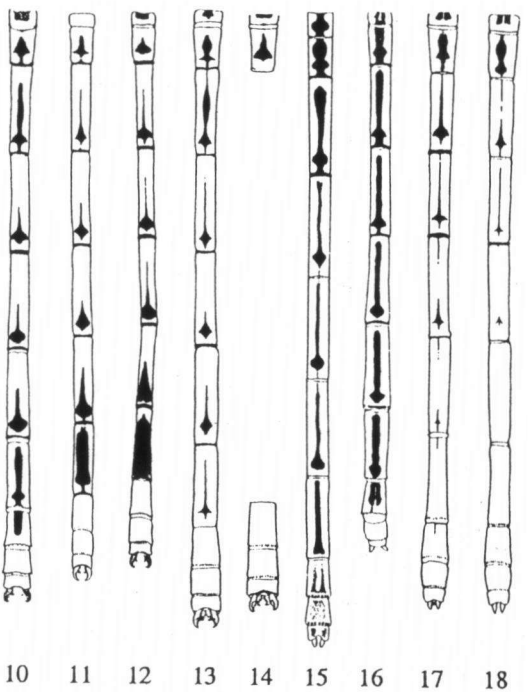


Figs 1-9. *Coenagrion lindenii* s.l., abdomen, males: (1-3) Wadi Kuveyk, TR, 15-V-1988; – (4) Nahr al Abrash, Syria, 29-III-1980; – (5) Arpaçay, TR, 2-VI-1994; – (6) Arpaçay, TR, 24-VI-1993; – (7) Kirmasirt, Tl, 25-VIII-1989; – (8) Birket Ram, Golan Heights, 12-VI-1972; – (9) Reyhanli, TR, 21-IX-1982. – [1-4: "typical" *lindenii*; – 5-9: various phases of transition towards *zernyi*, suggesting multiple hybridisation; drawings not exactly to same scale]

RESULTS

C. l. lindenii can be morphologically defined as a robust coenagrionid, with males heavily marked with black on a blue background, such that modally only the dorsum of abdominal segment 9 (and partly 10) is blue. The dorsum of the head is also heavily marked with black, leaving only room for an occipital blue bar and two almost linear postocular spots (cf. Fig. 25). *C. l. zernyi* is smaller, more delicate, with the black markings on the body reduced and, no black (or only a tiny central black stripe) on the 8th abdominal segment (S8).

In females, the background colour is olive to brown, marked with black. This results, in typical *lindenii*, in a pair of small postocular spots, while the dorsum of the abdomen is completely (up to S10) marked with black. In *zernyi*, the postocular spots are wide, and tend to become confluent, while the black on the abdomen recedes, from S10 forwards.



Figs 10-18. *Coenagrion lindenii* s.l., abdomen: (Figs 10-14: males; Figs 15-18: females): (10) Shaizar, Orontes, Syria, 17-VIII-1980; – (11) Bet She'an, Israel, 16-VI-1972; – (12) Betania, Israel, 15-V--1931; – (13) Hazar Gölü, 12-VIII-1990; – (14) Haral Gölü, 15-VII-1986. [10: almost "pure" *zernyi*, – 11-14: pure *zernyi*, but showing progressive reduction in black markings]. – (15) Birket Ram, Golan Heights, 12-VI-1972; – (16) Shaizar, Syria, 17-VIII-1980; – (17-18) Hazar Gölü, TR, 15-VII-1986 and 12-VIII-1980; – [15-16: hybrids transitory to *zernyi*, – 17-18: typical *zernyi*; drawings not exactly to same scale]

We consider a specimen of either sex to be classifiable as *zernyi* if (1) the postocular spots become confluent and (2) if S8 is (almost completely) devoid of black.

On these grounds, we found all Anatolian populations as far East as the lower Ceyhan River to be typical *lindenii* (Map 1) (DUMONT, 1977; DEMIRSOY, 1982). However, further South and East the situation becomes complicated. Populations in the Orontes catchment, and on some short coastal rivers in Syria (e.g. the An--Nahr al Kabir South) were either intermediate between *lindenii* and *zernyi*, or with a predominance of *lindenii*-phenotypes (SCHNEIDER, 1985, 1986). The *zernyi* phenotypes only were found in the Jordan valley (there is, as yet, no information on populations from the Litani valley), although a population on the Golan Heigths again showed intermediate features. Moving East from the NE tip of the Mediterranean, at ca 37°30 N (see DUMONT et al., 1988), one hits a series of populations (both in the Tigris and Euphrates catchments) that are either intermediate with a prevalence of *lindenii* phenotypes, or *lindenii*-dominated in spring, but *zernyi*-dominated in summer, or pure *zernyi* (as far as known, because it was not sampled across the summer). It should be added that these latter populations (Hazar Gölü or Lake Hazar, and Cizre, Map 1) stand out by the fact that they contain phenotypes which have a more extreme expression of *zernyi* characters than in its type area, the Jordan valley, (Figs 13, 14, 17, 18 for abdomens, and Figs 29-30 for heads).

Variability is inherent to all populations sampled. The most extreme *zernyi*-phenotypes seen were in the Kirmasirt population (Diyarbakir) on 25-VIII-1989, where some females had lost all dorsal markings on segments 5-10, and males on segments 7-10. On the female's head, the black dorsal markings had become broken up in patches. But even in that sample, there were specimens with slight transitions towards *lindenii*-phenotypes, i.e. two males out of 14 showed slight black stripes on the carina of S8 (cf. Figs 6-7, 9-10).

It should be noted that the decrease in blackening on abdomen and head, although on average occurring simultaneously, was not systematical, i.e. specimens with the clearest abdomen did not necessarily have the clearest head, and vice versa.

Conversely, some spring populations with a predominance of *lindenii* phenotypes (like Arpaçay 2-VI-1994 and 24-VI-1993), contained few specimens transistory to *zernyi* (Figs 6-7, 9-10).

Even spring populations further to the Southwest, with strong *lindenii* phenotypes, like the Wadi Kuveyk population (Figs 1-3) show strong variation, from the hyper-*lindenii* phenotype of Figure 1 (even S9 black), to the individuals in which S10 and S9 progressively become lighter, with only two black dots left on S9 (Figs 1-3, 19-23). In such specimens, there is correlative variation in the surface area covered by the black markings on S1 and S2. This population looks very close to the adjacent one of Nahr al Abrash, Syria (Fig 4).

Because a difference in size between the two taxa was visually obvious, the opportunity of repeated sampling (spring and summer) from the two populations that

had phenotypes changing with season was taken to quantitatively examine this character. Abdomen length (without appendages) was used as a criterion of size. Table I summarizes the five samples that were used.

Table I

Difference in mean abdominal length in the populations with a seasonal phenotype variation

	Group 1 (n=29)			Group 2 (n=20)	
	Arpaçay I(1)	Arpaçay II(2)	Arpaçay III(3)	Kirmasirt I(4)	Kirmasirt II(5)
Date	14-VIII-1988	24-VI-1993	2-VI-1994	25-VIII-1989	7-VII-1992
Nr of specimens	4	8	17	14	6
Mean abdominal length (mm)	22.00	25.12	25.50	21.75	23.42
Standard deviation (mm)	0.91	1.06	0.66	0.51	0.49

We first tested the pooled data (49 observations from two localities = groups) for homogeneity of variances. Because they were found to be heterogeneous, a Kruskal--Wallis (non-parametric) one-way analysis of variance was used to test the null--hypothesis that all were drawn from a single pool:

Group:	Count:	Rank Sum:
Arapaçay	29	962.0
Kirmasirt	20	263.0

The significance of the rank sums, tested by Mann-Whitney U-test was $P<0.000$, indicating that the five samples constituted a heterogeneous mix.

Next, we repeated the analysis within groups. At Kirmasirt, the Kruskall-Wallis ranking was:

Group:	Count:	Rank Sum:
Kirmasirt 1 (25-VIII-1989)	14	106.0
Kirmasirt 2 (07-VII-1992)	6	104.0

which (Mann-Whitney, U-test) is still highly significant at $P = 0.001$.

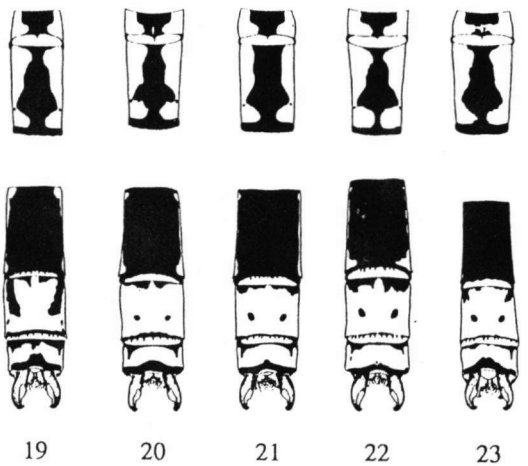
At Arpaçay, an analysis of variance revealed, again, strong differences between samples:

	ANOVA				
source of variation	Sum of squares	DF	mean square	F	probability
between groups	40.159	2	20.080	30.047	0.000
within groups	17.375	26	0.668		

Finally, a Tukey test of multiple comparisons on the three component series of group 1 was conducted. The matrix of pairwise comparisons, with their probability, is given hereunder:

	1	2	3
1	1.000		
2	0.000	1.000	
3	0.000	0.541	1.000

It leads to the conclusion that (1) is significantly different (smaller) from (2) and (3), but (2) and (3) are drawn from the same (a larger-sized) population. All this confirms that both spatial size differences (between localities), and seasonal size differences (at single localities) occur. Both are neatly correlated with relative extent of black markings on the body.

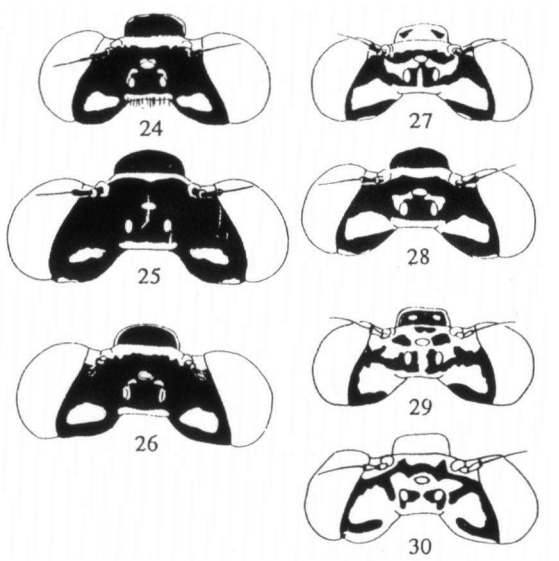


Figs 19-23. Variation in first and terminal abdominal segments in *C. lindenii* (with normal facies) from a spring (May) population on Wadi Kuveyk, TR.

DISCUSSION

It does not seem likely that the observed differences can be explained by environmental influences only. We rather favour a model that interpretes the variation seen in Syria and East Anatolia as the result of an inflow of genes from the West into a pre-existing gene pool, capable of readily absorbing them. Without recourse to molecular methods and a comprehensive survey of the entire *C. lindenii* range, it is not possible to state whether this gene migration started in the western Mediterranean, or is of local (e.g. Aegean or West Anatolian) origin. Likewise, it is impossible to specify an age for the phenomenon (e.g. whether it started shortly after the end of the Würm III glaciation, or it is of a more recent date). However, the extensive introgression revealed by the numerous hybrid populations suggests that the two taxa have correctly been assigned to the subspecific status. The expansion of one (*lindenii*) appears well underway to obliterate the other (*zernyi*).

With respect to the seasonal differences evidenced at single sites, suggesting the presence of two temporally segregated populations, larval development in ssp. *lindenii* seems to proceed at lower temperatures (i.e. requires less degree-days), in spite of the fact that this subspecies is the more robust of the two. Perhaps the



Figs 24-30. Markings on dorsum of head in *C. lindenii* s.l.: (24) ♂, Reyhanli, Turkey; – (25) ♂, Nahr al-Abrash, Syria; – (26) ♂, Betania, Israel; – (27) ♂, Shaizar, Syria; – (28) ♀, Shaizar, Syria; – (29) ♂, Hazar Gölü, TR; – (30) ♀, Hazar Gölü, TR. – [25 is almost as in typical *lindenii*; although this is a hybrid specimen, reduction of black on the head is suspected to be slower than on the abdomen]

larvae of *lindenii* also have a lower upper temperature tolerance than those of *zernyi*, resulting in the occurrence of the latter in the "warm" Jordan valley, but hybrid populations on the Golan Heights. Such a physiological difference can slow down the pace of introgression considerably, but evidently does not eliminate it, as seen in the presence of *zernyi*-like animals in spring populations, and *lindenii*-like animals in *zernyi* populations in East Anatolia. In fact, viewed against this background, it can be stated that the Jordan Valley *zernyi* are already mildly invaded by *lindenii*--genes, since the Hazar and Kirmasirt populations, situated further East, are more purely *zernyi* than those in the type area.

SCHMIDT (1954) reported a couple of *zernyi* from south-central Iran (Siwand), a considerable eastward expansion of the subspecies' range. However, the east Anatolian populations here documented narrow this apparent disjunction considerably, and suggest the existence of populations in the gap. These should be expected to show a gradient of increasing *zernyi*-facies, at least in the South, since in more northerly - hence cold-water-areas, *C. l. lindenii* may already have expanded further East via the Black Sea coast, and have reached the Caspian depression. It has been found in Georgia (SHENGELIA, 1975), and in Armenia it has occurred in the Araks valley at Aralich in June (AKRAMOWSKI, 1948). Further eastward extensions into northern Iran are still undocumented.

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