

Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 81 (2008)

Heft: 3-4

Artikel: Revision of the complex of *Nebria* (s. str.) *taygetana* Rottenberg, 1874 from the Peloponnesian peninsula (Greece) (Coleoptera, Carabidae)

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DOI: <https://doi.org/10.5169/seals-402968>

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Revision of the complex of *Nebria* (s. str.) *taygetana* Rottenberg, 1874 from the Peloponnesian peninsula (Greece) (Coleoptera, Carabidae)

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Nebria (s. str.) *taygetana* Rottenberg, 1874 from the Peloponnesian peninsula (Greece) is revised. *N. taygetana* turns out to be a polytypic complex separable in two distinct groups with different body shapes. *N. t. chelmosensis* Mařan, 1944 comprises populations with a slender body shape from the Chelmos, Erimanthos and Panahaikó Mts. This taxon is upgraded to a valid species. *N. t. taygetana* comprises populations with a wide body shape from the Taygetos, Kyllini, Elikon and Parnon Mts. Two new subspecies are described: *N. t. hermes* n. ssp. from the Kyllini and Elikon Mts., and *N. t. paon* n. ssp. from the Parnon Mt.

Keywords. Carabidae, *Nebria*, *taygetana*, *chelmosensis*, taxonomy, new subspecies, Peloponnesus, Greece.

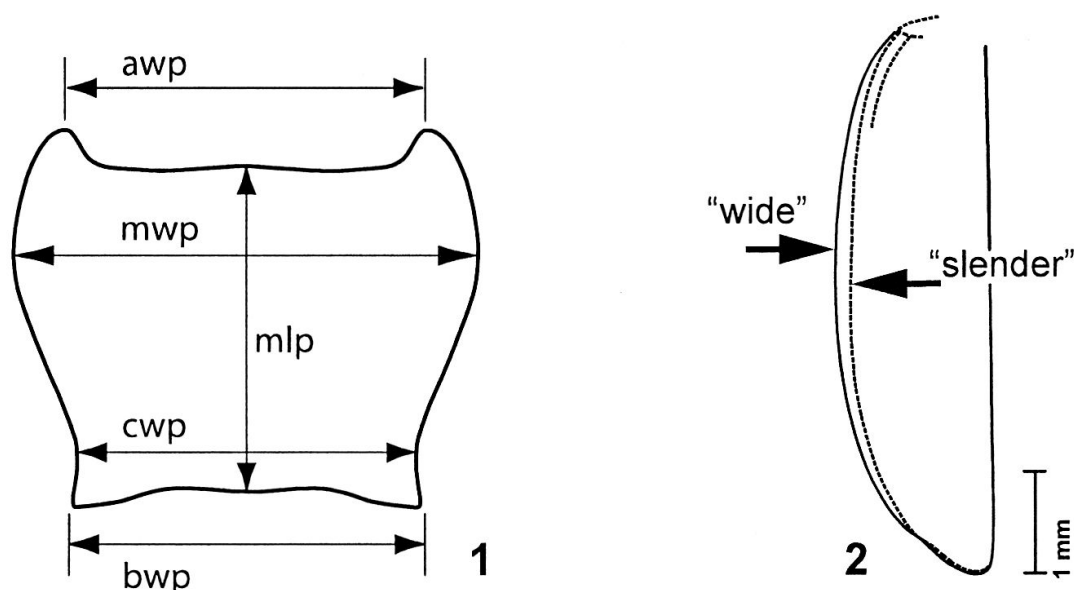
INTRODUCTION

Nebria (s. str.) *taygetana* Rottenberg, 1874 was known from isolated subalpine and alpine populations living in the Taygetos Mt., the Chelmos Mt. (Aroánia Ori) and the Kyllini Mts. on the Peloponnesian peninsula (Greece) (Apfelbeck 1904, Mařan 1938), until Mařan (1944) separated the population from the Chelmos Mt. as subspecies *N. taygetana chelmosensis*. The population from the Kyllini Mts. was attributed to the nominal form (Mařan 1938, Ledoux & Roux 1992). Recently Ledoux & Roux (2005) listed the Kyllini population as an element of *N. t. chelmosensis* without giving any reasons for this displacement.

The present-day distribution area of *N. t. taygetana* covers the Taygetos Mt. and Parnon Mt. in the southern part of the peninsula (Ledoux & Roux 2005). The subspecies *N. t. chelmosensis* covers the northern part including Chelmos Mt., Kyllini Mts. and Erimanthos Mt. The subspecies *N. t. chelmosensis* is smaller than the nominal form and differs furthermore in the slender and more flattened elytra, in the parallel shape of the elytra, and in the protruding posterior angles of the pronotum (Ledoux & Roux 2005).

The systematic position of the Kyllini population is uncertain and has to be clarified. The above mentioned characters do not apply to the Kyllini specimens. Therefore a lot of material of *N. taygetana* of different isolated Peloponnesian mountains has been studied to revise this complex.

N. vseteckai Mařan, 1938 from the Parnass Mt. (Greek mainland) is considered as a species by Ledoux & Roux (2005), whereas Farkač & Janata (2003) clas-



Figs 1–2: — Fig. 1. Measurements taken of the pronotum: awp = anterior width, bwp = basal width, cwp = constriction width, mlp = median length, mwp = maximal width. — Fig. 2. Shape of elytra: «wide» shape of populations from the Taygetos, Parnon and Kyllini Mts., and the «slender» shape of populations from Chelmos, Erimanthos and Panahaikó Mts.

sify it as a subspecies of *N. taygetana*. *N. vseteckai* is easily recognizable by its bisetose basal antennomere. We agree with Ledoux & Roux (2005) and do not include *N. vseteckai* in the present analysis.

MATERIAL AND METHODS

295 specimens of *N. taygetana* of private and museum collections were studied from the following isolated areas (Fig. 9): Taygetos Mt. (2100–2300 m), Parnon Mt. (1380–1900 m), Kyllini Mts. (1900–2200 m), Elikon Mt., Chelmos Mt. (2100–2300 m), Erimanthos Mt. (2100 m) and Panahaikó Mt. (1325–1550 m). The syntype series of *N. taygetana* was also examined.

Abbreviations of the investigated collections:

DEI	Deutsches Entomologisches Institut Greifswald, Germany
NHMW	Naturhistorisches Museum Wien, Austria
NMBE	Naturhistorisches Museum Bern, Switzerland
cME	collection Manfred Egger, Wattens, Austria
cPMG	collection Pier Mauro Giachino, San Martino Canavese, Italy
cWH	collection Walter Heinz, Schwanfeld, Germany
cWM	collection Werner Marggi, Thun, Switzerland

The following measurements were taken (Fig. 1):

- head width (wh, distance between the eyes)
- anterior width of the pronotum (awp)
- maximal width of the pronotum (mwp)

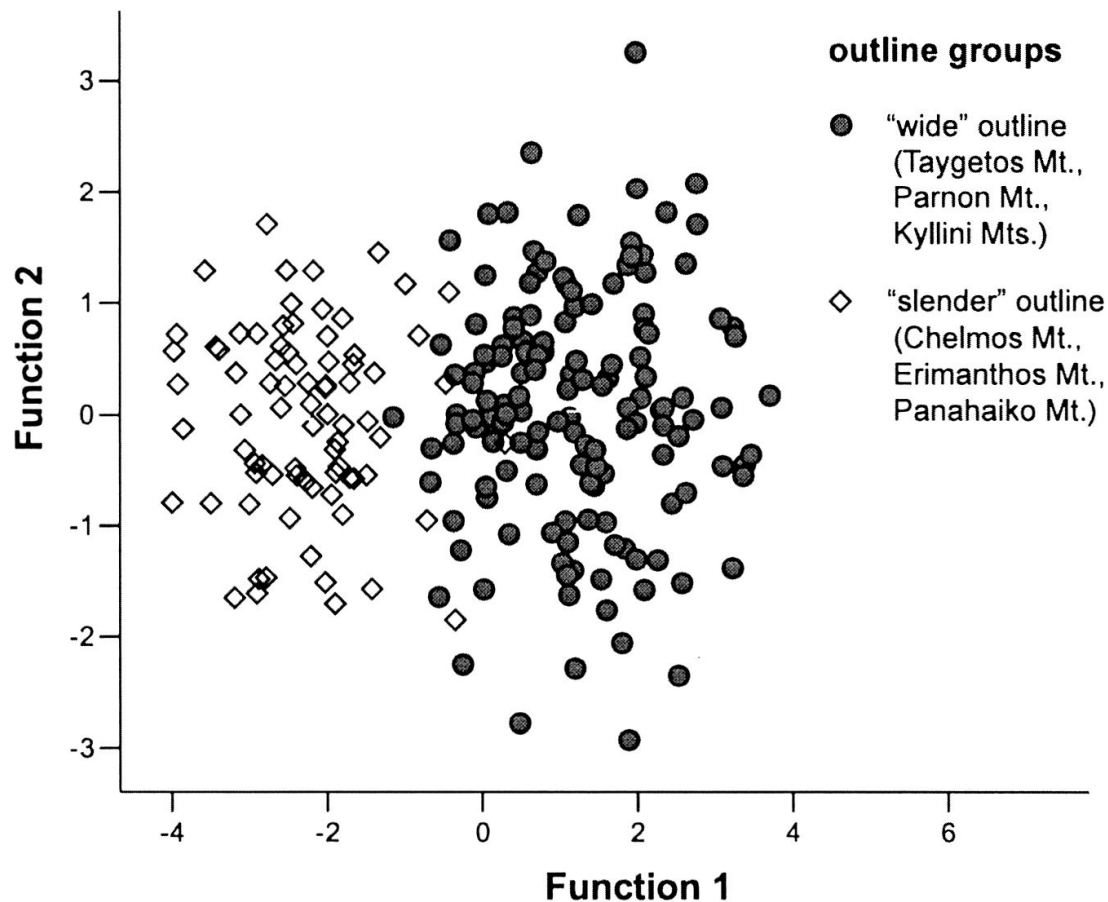


Fig. 3: Canonical discriminant analysis separating the *N. taygetana* populations into a group with a slender body shape and a group with a wide body shape. Used characters: outline slenderness SL, elytral slenderness ESL and anterior narrowing of the pronotum ANP (definitions see text).

- constriction width of the pronotum (cwp)
- basal width of the pronotum (bwp)
- median length of the pronotum (mlp, pl)
- humeral width of the elytra (hwe, distance between the humeral teeth)
- maximal width of the elytra (mwe)

Six morphometrical ratios were used as parameters independent of sex and height:

- anterior narrowing of the pronotum ANP (mwp/awp)
- constriction of the pronotum CP (mwp/cwp)
- basal extension of the pronotum BEP (bwp/cwp)
- form of the pronotum FP (mwp/mlp)
- outline slenderness SL (hwe/wh)
- elytral slenderness ESL (mwe/hwe).

228 specimens were used for the statistical analysis (principal components analysis and discriminant analysis) on SPSS 15.0 for Windows. Analyses of sex-linked variables as the body size were made separately.

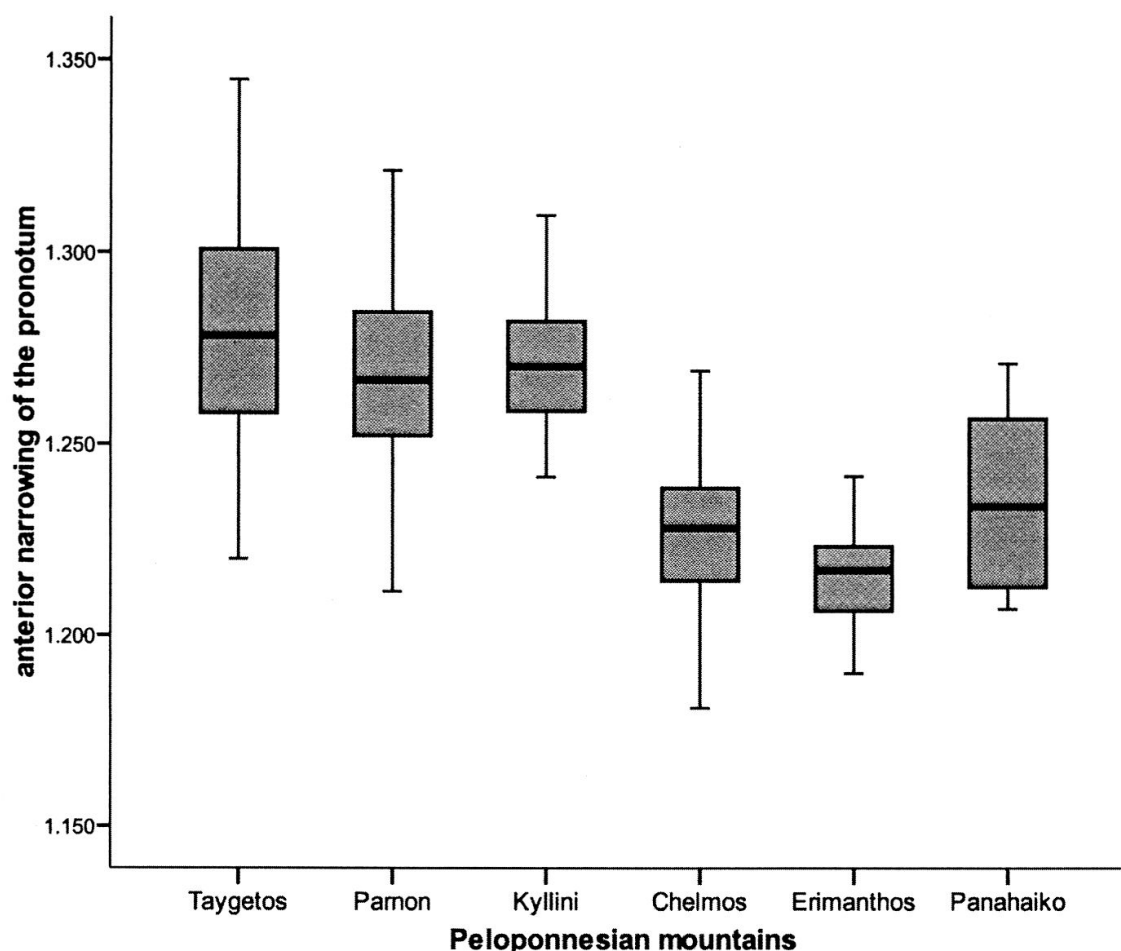


Fig. 4: Anterior narrowing of the pronotum ANP (definition see text) of the *Nebria taygetana* complex. The pronota are weakly narrowed in the group with a slender body shape (Chelmos, Erimanthos, Panahaikó Mts.), strongly narrowed in the group with a wide body shape (Taygetos, Parnon, Kyllini Mts.).

SYSTEMATICS

Differentiation of the taxa *taygetana* and *chelmosensis*

The morphological characters indicated by Ledoux & Roux (2005) to separate the two subspecies *N. t. taygetana* and *N. t. chelmosensis* were examined on material from the loci typici. The following morphometrical characters are used (Fig. 1): The basal pronotal extension (BEP) representing the protruding posterior angles of the pronotum, the ratio of shoulder width/head width (SL) representing the outline slenderness, and the head width representing the size. In the discriminant analysis 98.1 % (males) and 99.2 % (females) of the selected cases were correctly classified. *N. t. chelmosensis* Mařan, 1944 is evidently separable from the nominal taxon *N. t. taygetana* by the characters mentioned by Ledoux & Roux (2005).

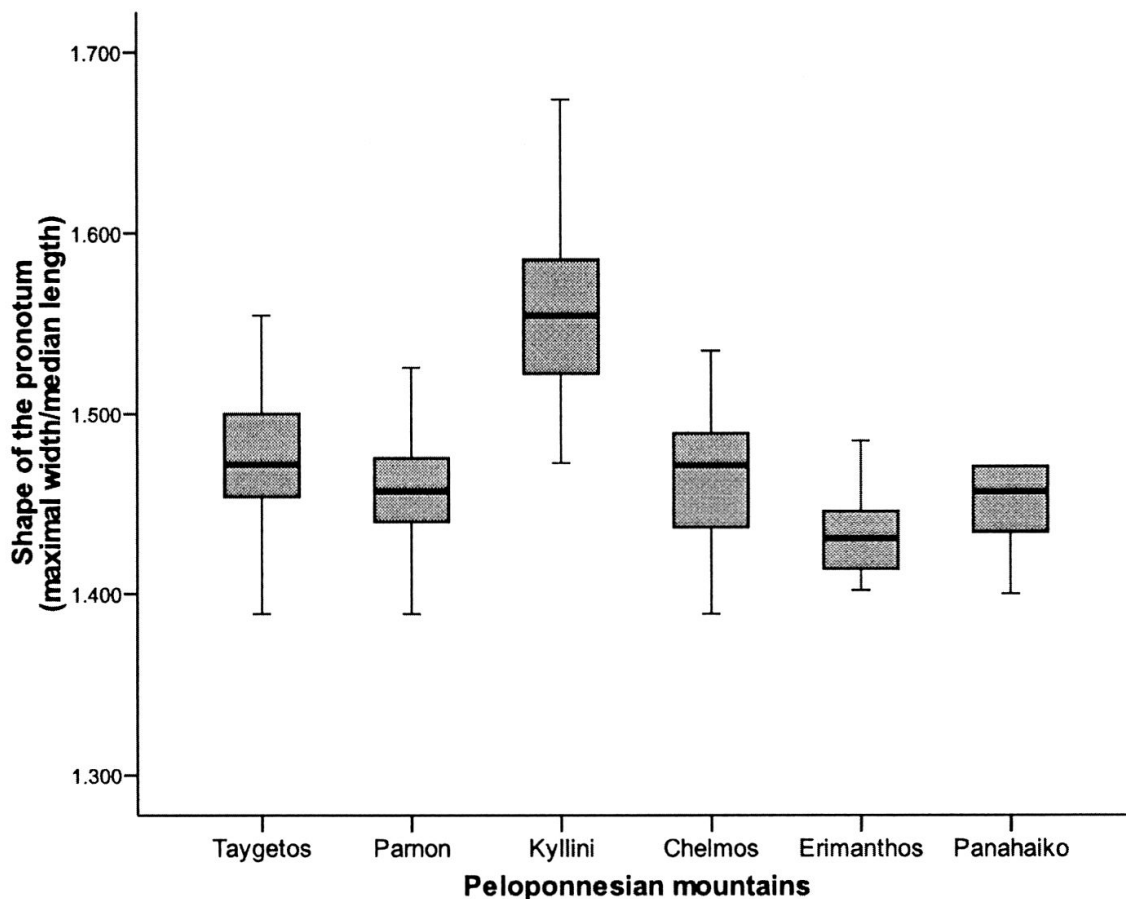


Fig. 5: Shape of the pronotum of *Nebria chelmosensis* (Chelmos, Erimanthos, Panahaikó Mts.) and *N. taygetana* (Taygetos, Parnon, Kyllini Mts.).

The examined material from the loci typici, Taygetos Mt. and Chelmos Mt. respectively, shows that the taxa differ significantly in three size characters, which are the width of the head, the width of the shoulder and the width of the elytra. *N. t. chelmosensis* is significantly smaller than the nominal form (Ledoux & Roux, 2005).

Isolated populations from several Peloponnesian mountains were examined for three morphometrical characters representing the slenderness of the body shape: The outline slenderness SL, the elytral slenderness ESL and the anterior narrowing of the pronotum ANP representing the pronotal slenderness. In the discriminant analysis 95.6 % of the selected cases are correctly classified and are separated in two distinct groups (Figs 2, 3). The group with a wide body shape includes the populations from Taygetos Mt., Parnon Mt., Kyllini Mts. and Elikon Mt. The group with a slender body shape includes the populations from Chelmos Mt., Erimanthos Mt. and Panahaikó Mt. (Fig. 9).

Additionally the Kyllini population differs significantly in its transverse shape of the pronotum from all Peloponnesian populations (Fig. 5). Obviously the Kyllini population does not belong to the group with a slender body shape including the Chelmos populations as asserted by Ledoux & Roux (2005). The Kyllini popula-

tion has to be removed from *chelmosensis* and has to be placed into the group with a wide body shape, which is near to the nominal form *N. t. taygetana* as it was suggested by Mařan (1938) and Ledoux & Roux (1992). The systematic position proposed by Ledoux & Roux (2005) is incorrect.

The separation of two groups with different body shape is additionally confirmed by morphological characters of the anterior and posterior angles of the pronotum: In the group with a wide body shape the anterior angles of the pronotum are wide and the lateral margins of the pronotum are strongly curved towards the apex (Fig. 7a–c), whereas in the group with a slender body shape the anterior angles are more acute and slender and the lateral margins are less curved towards the apex (Fig. 7d–e) causing a weaker anterior narrowing of the pronotum (Fig. 4). The posterior angles are acute and strongly protruding outwards and posteriorly in the «slender» group indicating a distinct basal extension of the pronotum (Ledoux & Roux 2005). Additionally the elytral striae are distinctly punctate in the «slender» group, whereas in the «wide» group the striae are weakly punctate or even impunctate.

The group with a slender body shape (*chelmosensis* group)

The isolated populations with a slender body shape from the Chelmos, Erimanthos and Panahaikó Mts. are not separable either morphologically or statistically. They are all attributed to the taxon *chelmosensis* which is upgraded to a species due to the evident differences compared to *N. taygetana*.

***Nebria (Nebria) chelmosensis* Mařan, 1944, stat. nov.**

Material examined: 20 specimens Chelmos Mt., 22. 5. 2001, 2000 m, leg. Huber & Marggi, NMBE. 33 specimens Kalavritá, Chelmos Mt., 20. 5. 1997, leg. Egger Manfred. cME. 12 specimens same data, NMBE. 5 specimens Chelmos Mt., 4. 6. 1994, 1950 m, cPMG. 3 specimens Panahaikó Mt./Ano Kastritsi/Peloponnes, 30. 3. 2000, 1550 m, gefrorenes Gras, Schneefeld, leg. L. Behne, DEI. 2 specimens Panahaikó Mt./Avriokambpos/Peloponnes, 1. 4. 2000, 1550 m, gefrorenes Gras, Schneefeld, leg. Zerche & Behne, NMBE. 1 specimen Klokou Keruneias/Pteri/Peloponnes, 29. 3. 2000, 1325m, Abies-Wald, Schneefeld, leg. Zerche & Behne, DEI. 8 specimens Erimanthos Mt./Peloponnes, 2000 m, 20. 5. 2001, leg. Huber & Marggi, NMBE.

Measurements. Size: 9–11 mm. Ratio width/length of the pronotum = 1.46 ± 0.04 (1.39–1.58).

Genitalia. Median lobe as in Fig. 8d–e.

Distribution. The species is restricted to the Chelmos, Erimanthos and Panahaikó Mts. on the northern and north-western Peloponnesus (Fig. 9). The records from Kyllini Mts. so far attributed to *N. t. chelmosensis* refer to the subspecies *N. t. hermes* n. ssp. (see below).

The group with a wide body shape (*taygetana* group)

Within the «wide» group the populations of the Kyllini and Elikon Mts. are recognizable by their smallness and their transverse shape of the pronotum (Fig. 5).

In the discriminant analysis to separate the Kyllini populations, 94.8 % (males)

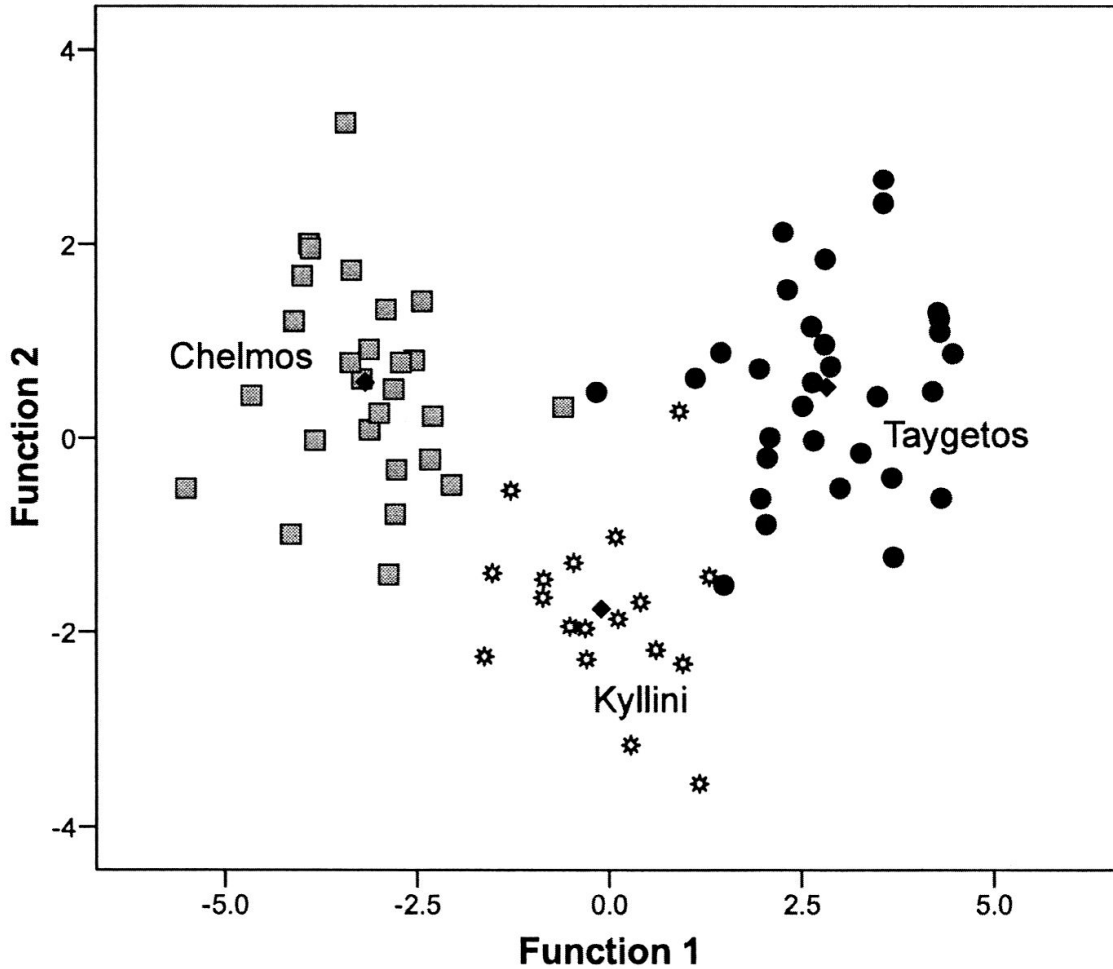


Fig. 6: Canonical discriminant analysis of isolated populations of the *Nebria taygetana* group (males) indicating that the population of the Kyllini Mts. (*N. t. hermes* n. ssp.) is separable from the populations of the Taygetos Mt. (*N. t. taygetana*) and the Chelmos Mt. (*N. chelmosensis*) respectively.

and 98.9 % (females) of the selected cases are correctly classified (Fig. 6). To separate *chelmosensis* and *taygetana* the three morphological characters used by Ledoux & Roux (2005) (size, slenderness, protruding of the posterior pronotal angles) and the pronotal shape character were compared. The Kyllini populations are herein described as a new subspecies of *N. taygetana*.

The population of the Parnon Mt. is also described as a new subspecies of *N. taygetana* due to different morphological characters and the significant difference in male size between the Parnon population and the nominal Taygetos population. A subspecific separation of the Parnon population was already discussed by Ledoux & Roux (2005).

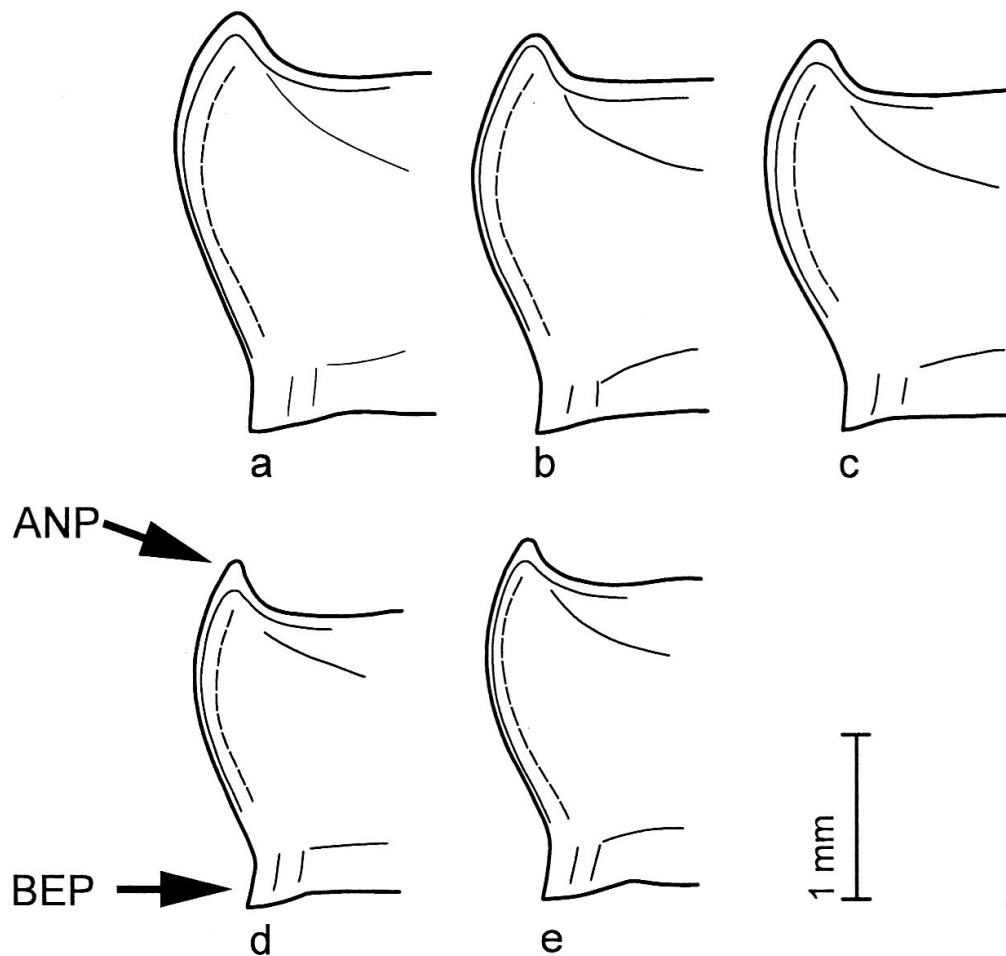


Fig. 7: — 7a–c: Pronota of *Nebria taygetana taygetana* (Taygetos Mt., a), *N. t. paon* n. ssp. (Parnon Mt., b) and *N. t. hermes* n. ssp. (Kyllini Mts., c) representing the group with a wide body shape.— 7d–e: Pronota of *Nebria chelmosensis* from the Chelmos Mt. (d) and the Erimanthos Mt. (e) representing the group with a slender body shape.

***Nebria (Nebria) taygetana taygetana* Rottenberg, 1874**

Material examined: 3 syntype specimens Taygetos, leg. Raymond, DEI. 22 specimens Anavryti, Taygetos, Peloponnes, 28.4.1961, NHMW. 22 specimens Mar-marokastro, Taygetos, Peloponnes, 30.4.1961, NHMW. 23 specimens Profitis Ilias, Taygetos, Peloponnes, 24. 5. 2001, leg. Huber & Marggi, NMBE.

Measurements. Size: 10.5–13 mm. Ratio width/length of the pronotum = 1.47 ± 0.04 (1.39–1.57).

Pronotum. Anterior angles strongly curved to the apex (Fig. 5a).

Genitalia. Median lobe as in Fig. 8a.

Distribution. The nominal form of *N. taygetana* is restricted to the Taygetos Mt. on Southern Peloponnesus (Fig. 9).

***Nebria (Nebria) taygetana hermes* n. ssp.**

Type material. Holotype ♂, Kyllini Mts., 1900–2100 m, Peloponnes, Greece, N 37° 56,9' E 22° 25', 19. 5. 2001, leg. Huber & Marggi, NMBE.

Paratypes: 15 ♂♂, 15 ♀♀, same data, NMBE, 11 ♂♂, 16 ♀♀, same data, cWM.

Additional material examined: 1 ♂, 2 ♀♀ Oros Elikon, Elikonas, 750 m, cPMG.

Measurements. Rather small-sized: Size: 9–11 mm. Ratio width/length of the pronotum = 1.56 ± 0.04 (1.47–1.67).

Colour. Head, pronotum and elytra brown to dark brown. Vertex of the head with a lighter brownish spot. The appendages of the head and the legs lightened reddish brown. Sutural interval of the elytra lightened brown.

Head. Smooth. Head behind the eyes cylindrical. Eyes slightly prominent, temples weak and oblique. 1 supraorbital seta. Antennae slender, extending to mid-length of the elytra. Antennal scape stout, basally narrowed, cylindrical apically, with 1 long dorsal seta. 2nd antennomere with 1 long ventroapical seta; sometimes (26%) with 1 additional short apico-posterior seta which is shorter than the diameter of the antennomere, but without any dorsal seta. Antennomeres 3–4 with 6–7 apical setae, antennomeres 5–11 pubescent. Microreticulation of the head isodiametric. Submentum with 3 setae on each side.

Pronotum. Cordate, moderately convex, distinctly transverse, widest in the anterior third. The transverse shape of the pronotum differs significantly from the pronotal forms of all other *taygetana* (and *chelmosensis*) populations (Fig. 5). Lateral margin strongly curved anteriorly and sharply sinuate before the posterior angles; the latter subrectangular with parallel sides, rarely slightly projecting outwards (Fig. 7c). Anterior angles triangular and strongly protruding (Fig. 7c). Lateral gutter flat, moderately broadened anteriorly. Basolateral seta present; midlateral seta in the apical half of the pronotum. Basal foveae deep. Pronotum basally (foveae and transverse impression) and laterally punctate. Diskal microreticulation isodiametric, the distinct longitudinal impression is shortened anteriorly and is almost reaching the base.

Elytra. Apterous. Elytral shape ovoid-elongate, flattened, sides evenly curved, without parallel sides as in *N. t. chelmosensis*; less slender than latter. Elytra widest a little behind the middle. Striae weak, weakly punctate, reaching the apex. Intervals flat. Interval 3 with 2–3 pores near striae 3. Humeral teeth present. Humeral edge developed. Marginal gutter narrow, interval 9 near the humeral tooth often flattened, giving the impression of an enlarged marginal gutter and a shallow depression. Apical carena not developed. Scutellar setae present. Microreticulation isodiametric.

Legs. Protarsi of male with 3 dilated tarsomeres. Metatarsi slender, the apical end of tarsomere 4 of the metatarsi straight or sometimes a little oblique, without a tooth-like projection on the bottom side (usually with a tooth in *N. t. taygetana*). Metacoxa with 1 subbasal and 1 subapical seta.

Lower surface. Intercoxal process of the prosternum margined, sometimes weakly margined at the apex; without a longitudinal bulge. Sterna 3–5 each with 1

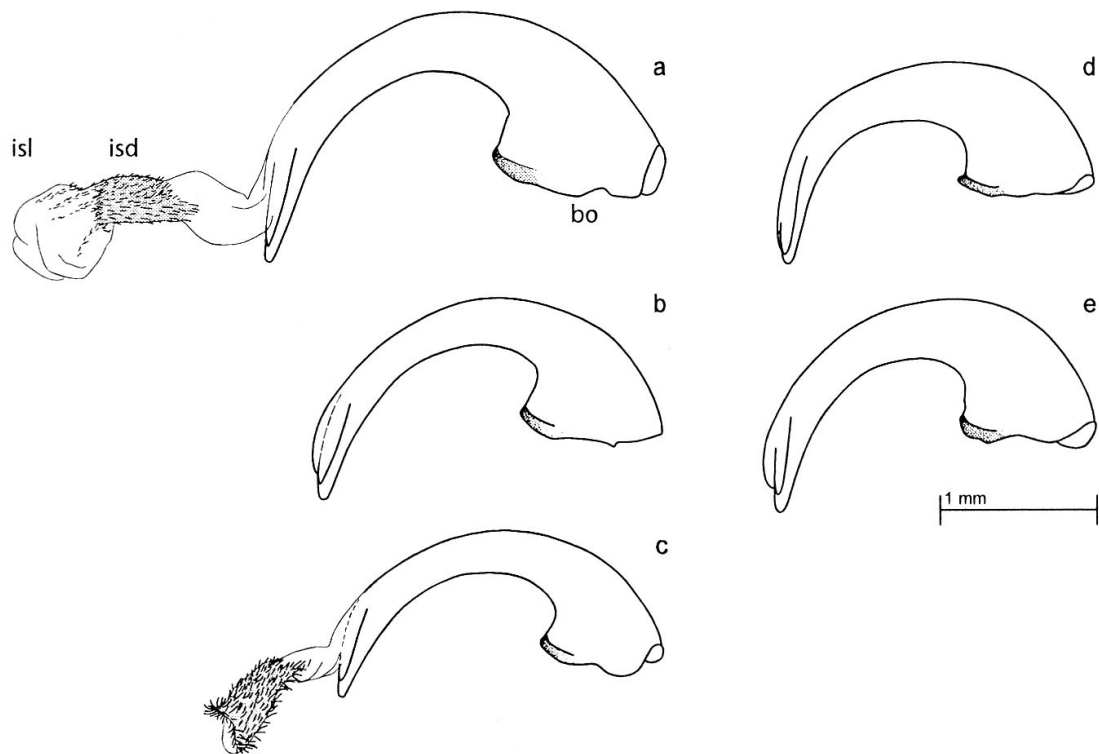


Fig. 8: Right lateral aspect of the male genitalia of *Nebria taygetana taygetana* (a), *N. t. paon* n. ssp. (b), *N. t. hermes* n. ssp. (c), *N. t. chelmosensis* of the Chelmos population (d) and of the Erimanthos population (e). bo = basal orifice, isd = duct of the everted internal sac, isl = end lobe of the internal sac.

posterior seta on each side. Sternum 6 with 1 pair of apical setae in the male, 2 pairs in the female.

Genitalia. Median lobe (Fig. 8c) much smaller and more slender than in the nominal form, regularly curved towards apex. Basal orifice relatively narrow. Apex deflected to the left. The everted internal sac with a short shaft. Basal third of the shaft smooth, the apical two thirds tightly covered with fine and short setae. End lobe of the internal sac smooth.

Distribution. The new subspecies is known from the Kyllini Mts. on the north-eastern Peloponnese and from the Elikon Mt. (south of Livadia) on the Greek mainland north of the Gulf of Corinth (Fig. 9).

Etymology. The name (noun in apposition) refers to Hermes, the son of Zeus and Maia in the Greek mythology, and the god of shepherds, land travel, merchants, weights and measures, oratory, literature, athletics and thieves. Hermes was born in a cave on the Kyllini Mts.

Differential diagnosis. *N. t. hermes* n. ssp. differs significantly from *N. chelmosensis* and from the other taxa of *N. taygetana* in the distinctly transverse shape of the pronotum. Elytra flatter than in the nominal form. Humeral teeth and humeral edges less prominent than in the nominal form.

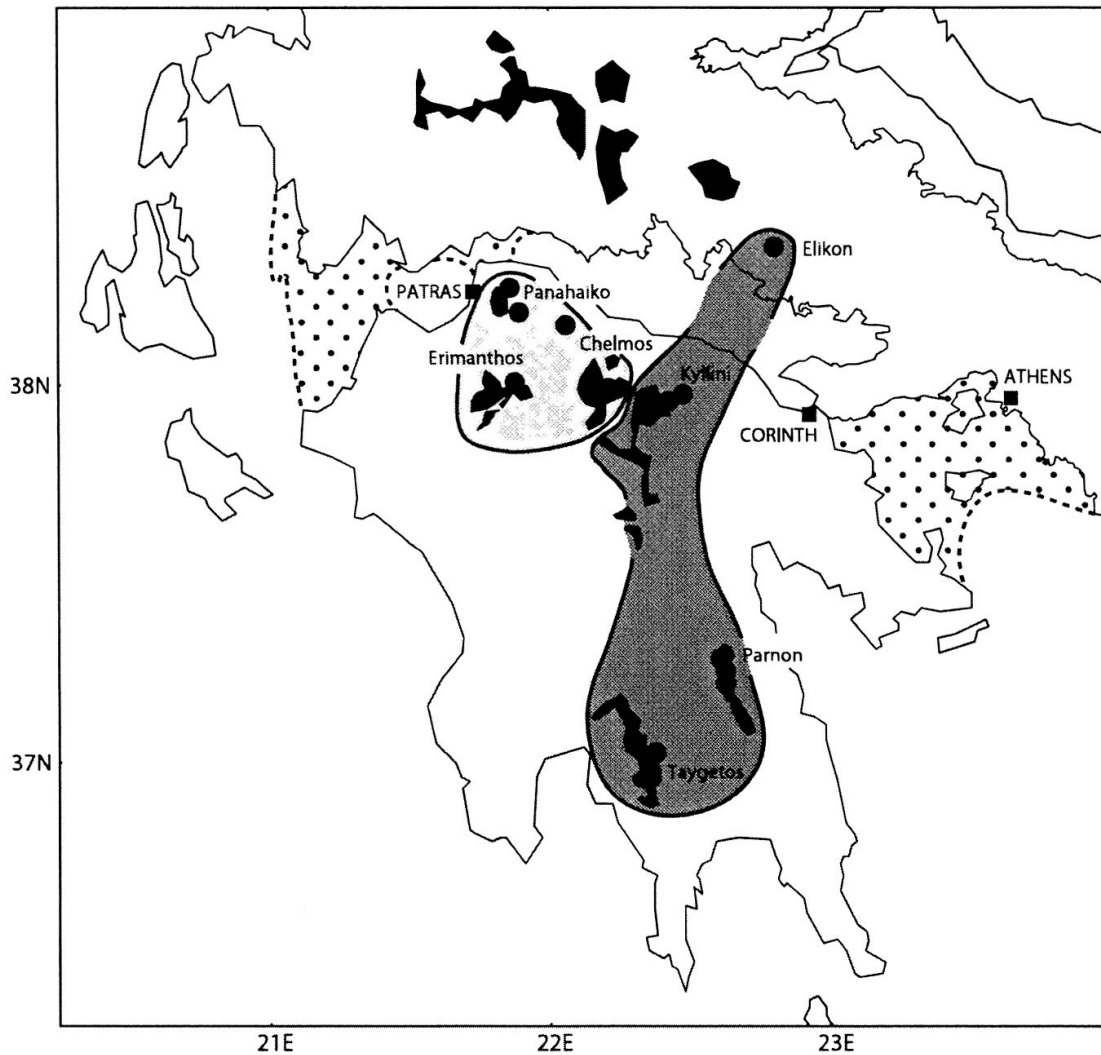


Fig. 9: Distribution area of *Nebria chelmosensis* (light grey, solid line) and *Nebria taygetana* (medium grey, solid line) including *N. t. taygetana* (Taygetos Mt.), *N. t. paon* n. ssp. (Parnon Mt.) and *N. t. hermes* n. ssp. (Kyllini and Elikon Mts.). Mountains higher than 1600 m above sea level are in dark grey. Land connections (dotted areas, dotted line) between the mainland and the Peloponnese in the Late Pleistocene, after Perissoratis & Conispoliatis (2003).

***Nebria (Nebria) taygetana paon* n. ssp.**

Type material: Holotype ♂, Parnon, Gipfel, Schneerand, 3. 4. 1970, Griechenland, leg. Kühnelt, NHMW.

Paratypes: 13 ♂♂, 3 ♀♀, same data, NHMW. 2 ♂♂, 2 ♀♀, same data, NMBE. 2 ♂♂, 3 ♀♀, Parnon, 5. 4. 1971, cWH. 1 ♀, Kastanitsa/Parnon/Peloponnes, 18. 4. 1998, 1380 m, Kiefern-, Tannenwald, leg. Zerche, DEI. 5 ♂♂, 4 ♀♀, Parnon Mt., Megalo Tourla/Peloponnes, 19. 4. 1999, 1645 m, Abies-Wald, leg. Zerche & Behne, DEI. 3 ♂♂, 3 ♀♀, Parnon Mt., Megalo Tourla/Agios Petros/Peloponnes, 21. 4. 2000, 1680 m, einzelne Abies, Hochebene, leg. Zerche & Behne, DEI.

Measurements. Smaller sized than the nominal form, especially the males. Size: 9.5–11.5 mm. Ratio width/length of the pronotum = 1.46 ± 0.03 (1.39–1.53).

Colour. Head, pronotum and elytra brown to dark brown. Vertex of the head with a lightened brownish spot. Appendages of the head lightened reddish brown. Legs yellow to brown, always brighter than the antennae. Femur not darkened. Sutural interval of the elytra lightened brown.

Head. Smooth. Head behind the eyes cylindrical. Eyes slightly prominent, temples weak and oblique. 1 supraorbital seta placed somewhat before the level of posterior margin of the eye. Antennae slim, reaching midlength of the elytra. Basal antennomere stout, subcylindrical, basally narrowed, with 1 dorsal seta. 2nd antennomere generally bi- to quadrisetose; additionally to the long ventral seta always with a supplementary short apico-posterior seta, and mostly (in 63 % of the cases) with 1–2 additional short dorsal setae; all the non-ventral setae of the 2nd antennomere are shorter than its diameter. Antennomeres 3–4 with 6–7 apical setae, antennomeres 5–11 pubescent. Microreticulation of the head isodiametric. Submentum with 3 setae on each side.

Pronotum. Cordate, moderately convex, transverse, widest in the anterior third. Lateral margin curved anteriorly and sharply sinuate before the posterior angles, the latter acute and clearly projecting outwards (Fig. 7b). Anterior angles triangular and strongly protruding. Lateral gutter flat, moderately broadened anteriorly. Basolateral seta present; midlateral seta in the apical half of the pronotum. Basal foveae deep. The foveae and the posterior transverse impression distinctly punctate, even the lateral gutter and usually the anterior transverse impression. Diskal microreticulation isodiametric, the distinct longitudinal impression is shortened anteriorly and is almost reaching the base.

Elytra. Apterous. Elytral shape ovoid-elongate, sides evenly curved, more flattened than in the nominal form. Elytra widest a little behind the middle. Striae weak, weakly punctate or even impunctate, reaching the apex. Intervals flat. Interval 3 with usually 2–3 pores near striae 3. Humeral teeth present. Humeral edge developed. Marginal gutter narrow. Apical carena not developed. Scutellar setae present. Microreticulation isodiametric.

Legs. Protarsi of male with 3 dilated tarsomeres. Metatarsi slender, the apical end of the tarsomere 4 straight or sometimes weakly oblique, without a ventral tooth-like projection. Metacoxa with 1 subbasal and 1 subapical seta.

Lower surface. Intercoxal process of the prosternum margined at most laterally; the apex not or only weakly margined. Prosternal apex variable, flattened or with a bulge. Sterna 3–5 each with 1 posterior seta on each side. Sternum 6 with 1 pair of apical setae in the male, 2 pairs in the female.

Genitalia: Median lobe (Fig. 8b) much smaller and more slender than in the nominal form, regularly curved towards apex. Apex deflected to the left. The everted internal sac with a short shaft. Basal third of the shaft smooth, the apical two thirds tightly covered with fine and short setae. End lobe of the internal sac smooth.

Distribution. The new subspecies is restricted to the Parnon Mt. (1380–1900 m) on the south-eastern Peloponnesus (Fig. 9).

Etymology. The name (noun in apposition, in ancient Greek spelling) refers to Pan, the god of shepherds and flocks in the Greek mythology. Pan was a son of Hermes (see taxon above).

Differential diagnosis. 2nd antennomere with a supplementary apico-posterior seta (in all cases) and 1–2 additional dorsal setae (in 63 % of the cases). Legs always lighter brownish or yellowish, brighter than the appendages of the head, and brighter than in *N. taygetana hermes* n. ssp. as well as in the nominal form where the femora are darkened. The marginal gutter of the pronotum only moderately broadened anteriorly, whereas it is distinctly broadened in the nominal form. Pronotum distinctly punctate, whereas it is sparsely punctate in the nominal form; anterior transverse impression impunctate. Humeral tooth and humeral edge less prominent than in the nominal form. The males are significantly smaller than in the nominal form.

KEY

- 1 Slender. Anterior angles of the pronotum slender and acute (Fig. 7d–e). Elytra subparallel, striae punctate. On mountains of north-western Peloponnesus (Chelmos, Erimanthos, Panahaikó) *chelmosensis* Mařan, 1944
- Robust. Anterior angles of the pronotum broad and rounded (Fig. 7a–c). Elytral shape more curved, wide, not subparallel; striae weakly punctate or impunctate 2
- 2 Pronotum distinctly transverse (ratio width/length = 1.56 ± 0.04). Restricted to the Kyllini Mts. in north-eastern Peloponnesus and to the Elikon Mt. south of Livadia on the Greek mainland *taygetana hermes* n. ssp.
- Pronotum less transverse (ratio width/length = 1.46 ± 0.04) 3
- 3 2nd antennomere generally bi- to quadrisetose. Pronotum distinctly punctate. Restricted to the Parnon Mt. on south-eastern Peloponnesus *taygetana paon* n. ssp.
- 2nd antennomere generally unisetose with 1 long ventroapical seta. Pronotum sparsely punctate. Restricted to the Taygetos Mt. on southern Peloponnesus *taygetana taygetana* Rottenberg, 1874

DISCUSSION

The isolated population of *N. t. hermes* n. ssp. from the Elikon Mt. on the Greek mainland north of the Gulf of Corinth points to a formerly contiguous distribution area of *N. taygetana* during the ice age and indicates a phylogenetic relationship to the alpine species of the mainland *N. aetolica* Apfelbeck, 1901 from the Pindos Mt. and *N. vseteckai* Mařan, 1938 from the Parnass Mt. respectively. The present-day isolation dates from the latest Pleistocene period.

In the last glacial period (Wurm, isotopic stage 2) 21500 yr BP (years before present) the lowest sea level was –120 m. Large submarine areas were subaerially exposed such as the continental shelf area west of Patras in the Ionian Sea, which interrupted the offshore connection of the gulfs of Patras and Corinth respectively (Perissoratis & Conispoliatis 2003). Both gulfs were lakes, separated by the present-day submarine barrier of –62 m at the Rion Straits east of Patras. During the extreme low sea level during Wurm stage 2, the entire Gulf of Patras was subaerially exposed (Chronis *et al.* 1991). The Rion Straits have no Late Pleistocene sedi-

ment but only Early Pleistocene or Pliocene strata.

This resulted in three land connections from the mainland to the Peloponnese (Fig. 9): the subaerial shelf area west of Patras as the western connection, an eastern connection via the Perahora peninsula (Geránia Mt., 1069 m) between Corinth and Athens, and in between the connection at Rion Straits. About 18000 yr BP the sea level started rising rapidly flooding the western land connection and opened the Gulf of Patras to the Kefallinia Basin of the Ionian Sea. 11500 yr BP the narrow land connection at Rion was flooded (sea level at –60 m), and the Gulf of Corinth was opened to the west. Since that time the Isthmus of Corinth is the only land bridge to the Peloponnese.

The land connection at Rion Straits seems to have been the «easiest» way for *Nebria* specimens to cross the Gulf of Corinth southwards. The mountains north and south of Rion (Nafpaktias Mt. and Panahaiko Mt. respectively) belong to the same mesozoic Pindos-Olonos nappe regime (Jacobshagen 1986), and moreover, these two subalpine habitats were a small distance apart.

Probably *N. taygetana* was formerly distributed around the Gulf of Corinth leaving a relict population at Elikon Mt. *N. chelmosensis* could have been separated early from *N. taygetana* or could have crossed the land bridge at Rion Straits southwards autonomously. Suitable subalpine habitats for *Nebria* species can probably be found also in the mountains north of the Gulf of Corinth, as the Kithairon Mt. (1409 m) and Geránia Mt. in the eastern row, or the Lidorikiou Mt. (1911 m), Trikorpha Mt. (1545 m) and Nafpaktias Mt. (1472 m) in the western row, leading to the former land connection at Rion Straits. However the *Nebria* species of these peaks have not been examined so far.

ACKNOWLEDGEMENTS

For the loan of material we are very grateful to Manfred Egger, Wattens A, Pier Mauro Giachino, San Martino Canavese I, Walter Heinz, Schwanfeld D, Heinrich Schönmann, Naturhistorisches Museum, Wien A, and Lothar Zerche, Deutsches Entomologisches Institut, Eberswalde D. We gratefully acknowledge the help of Margret Gosteli and Elsa Obrecht (both NMBE) with the manuscript and of Hannes Baur (NMBE) with statistics.

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(received July 17, 2008; accepted September 22, 2008)