Geographische Parthenogenese bei der Schabe *Phyllodromica subaptera* (Blattoptera, Blattellidae, Ectobiinae) und Revision des *subaptera*-Artenkomplexes

Dissertation
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Vorgelegt von
Thomas Knebelsberger

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1. Berichterstatter: Prof. em. Horst Bohn
2. Berichterstatter: Prof. Gerhard Haszprunar

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Inhaltsverzeichnis

Artikel I

Knebelsberger, T. & Bohn, H. (2003) Geographic parthenogenesis in the *subaptera*-group of *Phyllodromica* (Blattoptera, Blattellidae, Ectobiinae). *Insect Syst. and Evol.* 34: 427-452.

Artikel II

Knebelsberger, T. & Miller, M. A. (2007) Revision and phylogeny of the *subaptera*-group of *Phyllodromica* (Blattoptera: Blattellidae: Ectobiinae), including a parthenogenetic species and the evaluation of COI sequences for species identification (DNA barcoding). *Zootaxa* 1522: 1-68.

1. Einleitung

Die Ectobiinae, eine Unterfamilie der Schaben, sind in Eurasien und Afrika verbreitet. Innerhalb der Ectobiinae werden in der Hauptsache zwei Gattungen unterschieden, *Phyllodromica* und *Ectobius*. Diese sind durch ein auffälliges Merkmal gut charakterisierbar: die Arten der Gattung *Phyllodromica* haben stark verkürzte Flügel, wohingegen diejenigen der Gattung *Ectobius* gut ausgebildet sind und meist über das Ende des Abdomens hinausragen.

Viele Arten der Gattung *Phyllodromica* sind auf der iberischen Halbinsel verbreitet. Dazu gehört auch die Art *Phyllodromica subaptera* (Rambur 1838), die sich von ihren nächsten Verwandten aus der *carpetana*- und *nana*-Gruppe morphologisch gut unterscheiden lässt. Im Gegensatz zu den beiden zuletzt genannten Artengruppen, deren Verbreitung auf die iberische Halbinsel beschränkt ist, gibt es für *P. subaptera* auch eine ganzen Reihe von Nachweisen außerhalb der iberischen Halbinsel. Sehr erstaunlich ist in diesem Zusammenhang die Tatsache, dass an diesen Fundplätzen stets nur weibliche Exemplare gesammelt werden konnten; alle Nachweise für männliche Vertreter der Spezies blieben auf die iberische Halbinsel beschränkt. Die wahrscheinlichste Erklärung für dieses Phänomen ist, dass sich *P. subaptera* außerhalb der iberischen Halbinsel durch Parthenogenese (Jungfernzeugung) vermehrt.

Im Rahmen seiner langjährigen Arbeit an der spanischen Schabenfauna führte Horst Bohn erste morphologische Analysen bei *P. subaptera* durch und bemerkte, dass die Männchen je nach Fundort deutliche morphologische Unterschiede aufweisen können. Möglicherweise verbergen sich hinter dem Namen *P. subaptera* verschiedene Arten. Im Gegensatz zu den Männchen unterscheiden sich die Weibchen kaum voneinander. Dieses Phänomen ist bei Schaben weit verbreitet und beispielsweise auch bei den Arten der *carpetana*-Gruppe zu beobachten.

Die Aufgabe meiner Dissertation bestand nun einerseits in einer Untersuchung des Phänomens der Parthenogenese und andererseits in der Klärung der taxonomischen Verhältnisse bei der Art *P. subaptera*.

Die Ergebnisse meiner Doktorarbeit wurden bereits in Form zweier Publikationen in international anerkannten Fachzeitschriften veröffentlicht (Knebelsberger & Bohn 2003, Knebelsberger & Miller 2007) und bilden den Hauptteil meiner Dissertationsschrift. Im folgenden Text sind die wichtigsten Resultate kurz zusammengefasst.

2. Allgemeine äußere Merkmale von *P. subaptera*

Abb. 1 zeigt einen typischen männlichen (A) und weiblichen (B) Vertreter von *P. subaptera.*

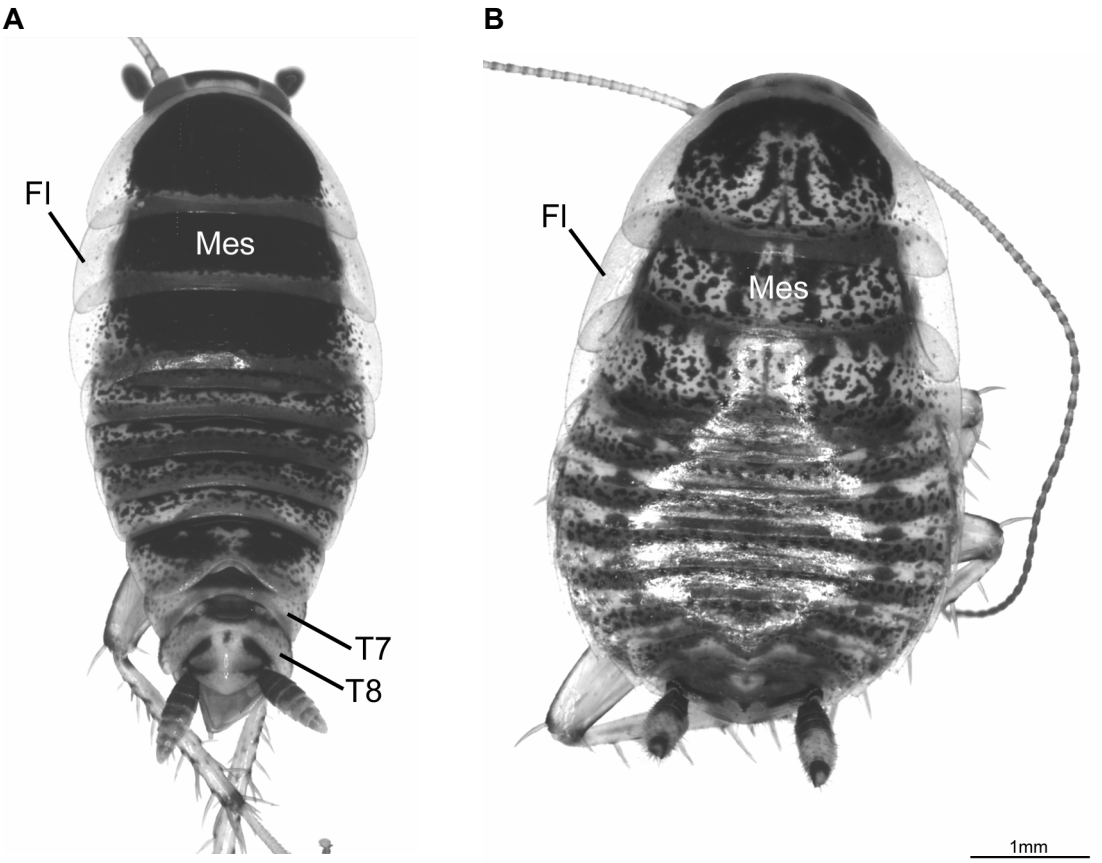

Abb. 1. Männchen (**A**) und Weibchen (**B**) in Dorsalansicht, das anteriore Ende ist nach oben ausgerichtet. Abkürzungen: **Mes** Mesonotum, **Fl** Flügel, **T7** Tergit 7, **T8** Tergit 8.

Die Vorderflügel sind bei beiden Geschlechtern stark reduziert. Sie erreichen mit ihrem posterioren Ende gerade den hinteren Rand des Mesonotums, an dessen vorderen Rand sie seitlich angebracht sind. Die Hinterflügel sind vollständig reduziert. Die Männchen von *P. subaptera* sind überwiegend dunkel gefärbt, ihr Körper ist relativ schmal. Die Körper der Weibchen hingegen sind breiter und erscheinen insgesamt heller.

3. Verbreitung von *P. subaptera*

Ältere Fundnachweise

Die meisten Exemplare von *P. subaptera* wurden auf der iberischen Halbinsel gefunden. Darüber hinaus gibt es aber auch Beschreibungen von Funden aus Frankreich, Korsika, Sizilien, dem früheren Jugoslawien, Bulgarien, Griechenland und Tunesien (Princis 1971). In

den meisten Fällen konnten allerdings nur einzelne oder wenige Individuen nachgewiesen werden und viele dieser Nachweise sind zudem unsicher, da kein Belegmaterial vorhanden ist. Nur aus Frankreich und von der kroatischen Insel Korčula sind größere Aufsammlungen bekannt. Erstaunlich ist, dass außerhalb der iberischen Halbinsel nur Weibchen gefunden wurden. Dies scheint bei Einzelfunden nicht sehr außergewöhnlich zu sein, aber beispielsweise fand Bucchich vor über 100 Jahren auf der Insel Korčula circa 150 Weibchen und kein einziges Männchen (Bucchich 1885).

Männchen von *P. subaptera* wurden bisher nur auf der iberischen Halbinsel nachgewiesen. Sie scheinen allerdings viel seltener zu sein als die Weibchen: Fernandes berichtete in seiner Revision der iberischen Ectobiinae, dass er in den wichtigsten Sammlungen Spaniens und Portugals unter 135 Individuen von *P. subaptera* nur 17 Männchen fand (Fernandes 1962). Harz entdeckte kein einziges Männchen in den Sammlungen, die er untersuchte (Harz 1976).

Aktuelle Aufsammlungen

Der im letzten Absatz dargestellte Befund führt zu der Frage, warum bislang so wenig Männchen von *P. subaptera* auf der iberischen Halbinsel gefunden werden konnten. Eine mögliche Erklärung dafür ist die kürzere Lebensspanne der Männchen, die sich auf das Frühjahr (März-Mai) beschränkt. Die Weibchen leben wesentlich länger und sind unter Umständen noch bis in den Herbst hinein zu finden. Um nun das Vorkommen der Männchen möglichst genau beschreiben zu können, wurden Aufsammlungen von Horst Bohn (seit den 1980er Jahren) und eigene Sammelreisen gezielt in der Zeitspanne von März bis April durchgeführt. An zahlreichen Fundplätzen konnten dabei *P. subaptera*-Männchen auf der iberischen Halbinsel nachgewiesen werden. Trotzdem gab es auch dort weiterhin viele Fundorte, an denen ausschließlich Weibchen vorkamen.

Auch außerhalb der iberischen Halbinsel konnten bei zahlreichen Sammelreisen, die ebenfalls im Frühjahr durchgeführt wurden, über das westliche Mittelmeergebiet verteilt viele neue Vorkommen von *P. subaptera* nachgewiesen werden (Spanien, Balearen: 10 Fundorte, Frankreich: 27 Fundorte, Schweiz: 7 Fundorte, Italien, Festland: ein Fundort, Italien, Sizilien: 13 Fundorte, Kroatien: 8 Fundorte, Marokko: 7 Fundorte, Algerien: 2 Fundorte und Tunesien: 4 Fundorte). Obgleich an vielen dieser Fundstellen eine Vielzahl von Tieren gesammelt wurde, handelte es sich ausschließlich um Weibchen.

4. Nachweis für Parthenogenese bei *P. subaptera*

Das Auftreten von *P. subaptera*-Populationen, die ausschließlich aus Weibchen bestehen, läßt sich nur durch eine parthenogenetische Vermehrung erklären. Zum tatsächlichen Nachweis der Parthenogenese wurden folgende Untersuchungen (I-III) durchgeführt:

(I) In einigen Fällen von Parthenogenese ist bekannt, dass bei den parthenogenetischen Weibchen die Spermatheken, die der Aufbewahrung von männlichen Spermien dienen, reduziert sind. So trifft dies beispielsweise für die Diplopodenart *Nemasoma varicorne* zu (Enghoff 1976a). Im Fall von *P. subaptera* erbrachte die Untersuchung der Spermatheken allerdings keine Unterschiede zwischen mutmaßlich parthenogenetischen und bisexuellen Weibchen.

(II) Die direkteste Methode zum Nachweis von Parthenogenese ist die Aufzucht von Nachkommen. Parthenogenetische *P. subaptera* Weibchen sollten ausschließlich weiblichen Nachwuchs produzieren.

Für die Aufzuchtexperimente wurden Weibchen aus ein- und zweigeschlechtlichen Populationen gesammelt (beprobt wurden 7 eingeschlechtliche Populationen außerhalb der iberischen Halbinsel und aus Spanien 6 zwei- und 12 eingeschlechtliche Populationen) und lebend ins Labor nach München gebracht. Nach einiger Zeit legten die Weibchen ihre Ootheken ab, die bis zum Schlüpfen der Larven in feuchten Kammern aufbewahrt wurden. Die frisch geschlüpften Larven – meist 10-12 Tiere pro Oothek – wurden bald nach der Aushärtung präpariert. Die Geschlechtsbestimmung der Larven erfolgte durch die Analyse der Subgenitalplatte, die bei den weiblichen Larven in der Mitte eingekerbt (schwarzer Pfeil in Abb. 2A), bei den männlichen Larven glatt erscheint (schwarzer Pfeil in Abb. 2B).

Die Aufzuchtexperimente ergaben, dass Weibchen aus eingeschlechtlichen Populationen ausschließlich weibliche Larven produzierten, wohingegen Weibchen aus zweigeschlechtlichen Populationen männliche und weibliche Nachkommen in einem meist sehr ausgewogenen Verhältnis erzeugten. Die Weibchen aus den eingeschlechtlichen Populationen von *P. subaptera* pflanzen sich also durch eine Form von Parthenogenese fort, die als Thelytokie bezeichnet wird. Aus unbefruchteten diploiden Eiern entwickeln sich hierbei ausschließlich Weibchen. Die Thelytokie ist die häufigste Form der Parthenogenese.

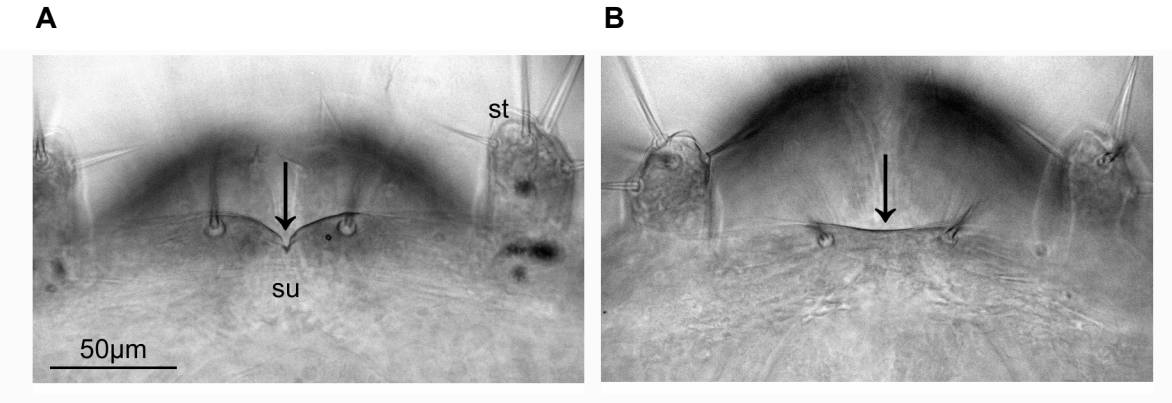

Abb. 2. Ventralansicht der abdominalen Enden zweier *P. subaptera*-Larven des ersten Larvalstadiums.
(**A**) weibliche, **(B)** männliche Larve. Die schwarzen Pfeile deuten jeweils auf die Mitte des posterioren Endes der Subgenitalplatte, die bei den Weibchen (A) eingekerbt, bei den Männchen (B) glatt erscheint.
Abkürzungen: **st** Stylus, **su** Subgenitalplatte.

(III) Parthenogenetische und bisexuelle Weibchen können auch durch eine Untersuchung des Inhalts der Spermatheken bestimmt werden. Dazu wurden fixierte Tiere aus der Sammlung von Horst Bohn verwendet.

Die Untersuchungen zeigten, dass in Populationen mit ausgewogenem Männchen- und Weibchenvorkommen die Spermatheken aller Weibchen Spermien enthalten (Abb. 3A). Bei den untersuchten Populationen mit reinen Weibchenvorkommen waren die Spermatheken erwartungsgemäß leer (Abb. 3B).

Bei einigen Populationen wies ein Teil der analysierten Weibchen trotz des Vorkommens von Männchen leere Spermatheken auf. Bisexuelle und parthenogenetische Weibchen kommen dort offensichtlich sympatrisch vor.

Mit diesem Ergebnis wurde der Nachweis erbracht, dass es sich im Fall von *P. subaptera* um eine obligatorische Parthenogenese handeln muss; die parthenogenetischen Weibchen verpaaren sich nicht mehr mit den Männchen, die Spermatheken bleiben leer.

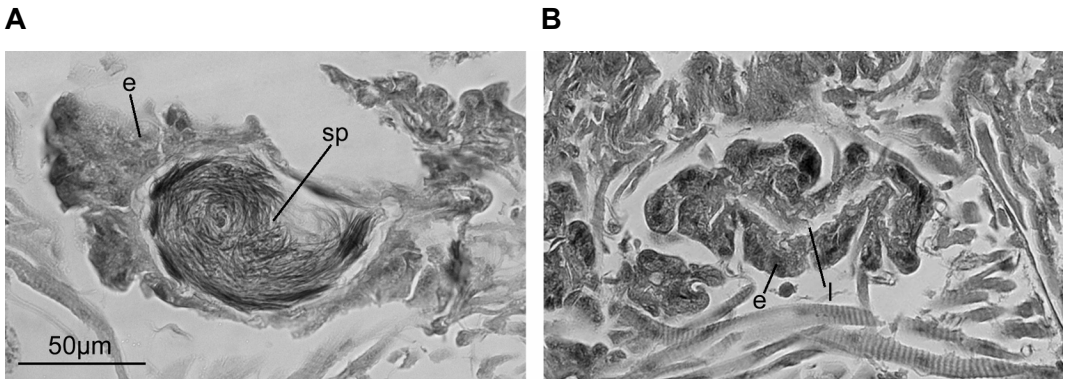

Abb. 3. Histologische Schnitte durch die Spermathek eines bisexuellen Weibchens gefüllt mit Spermien (**A**) und die eines parthenogenetischen Weibchens ohne Spermien (**B**).
Abkürzungen: **e** Epithelium, **l** Lumen der Spermathek, **sp** Spermien.

Die Fähigkeit zur parthenogenetischen Vermehrung konnte bereits bei einigen anderen Schabenarten nachgewiesen werden (Roth & Willis 1956). Dabei handelte es sich allerdings meist um eine fakultative Form von Parthenogenese. Nur bei der Spezies *Pycnoscelus surinamensis* liegt ebenfalls eine obligatorische Parthenogenese vor (Roth 1967). Die Art ist somit sexuell vollständig isoliert von ihrem zweigeschlechtlichen Vorfahren *Pycnoscelus indicus*.

Bei *P. subaptera* gelang der zweite Nachweis obligatorischer thelytoker Parthenogenese innerhalb der Schaben. Trotzdem ist nicht auszuschließen, dass im Gebiet der zweigeschlechtlichen Form auch fakultative Parthenogenese vorkommen kann. Außerhalb der bisexuellen Zone besteht allerdings kein Zweifel daran, dass die Parthenogenese obligatorisch ist.

Geographische Parthenogenese

Aus der umfangreichen Analyse der Spermatheken – auf der iberischen Halbinsel wurden über 100 Populationen untersucht – und den Ergebnissen aus den Larvenaufzuchtexperimenten ergab sich ein detailliertes Verbreitungsbild der bisexuellen und der parthenogenetischen Form von *P. subaptera*: Abb. 4 zeigt die Verbreitung der beiden Formen auf der iberischen Halbinsel: Im Süden und Nordosten dominiert die parthenogenetische Form. Im übrigen Verbreitungsgebiet ist die bisexuelle Form vorherrschend, die Nachweise von parthenogenetischen Weibchen sind dort relativ selten. An einigen Fundorten kommen die beiden Formen jedoch auch sympatrisch vor.

Außerhalb der iberischen Halbinsel ist nur die parthenogenetische Form anzutreffen.

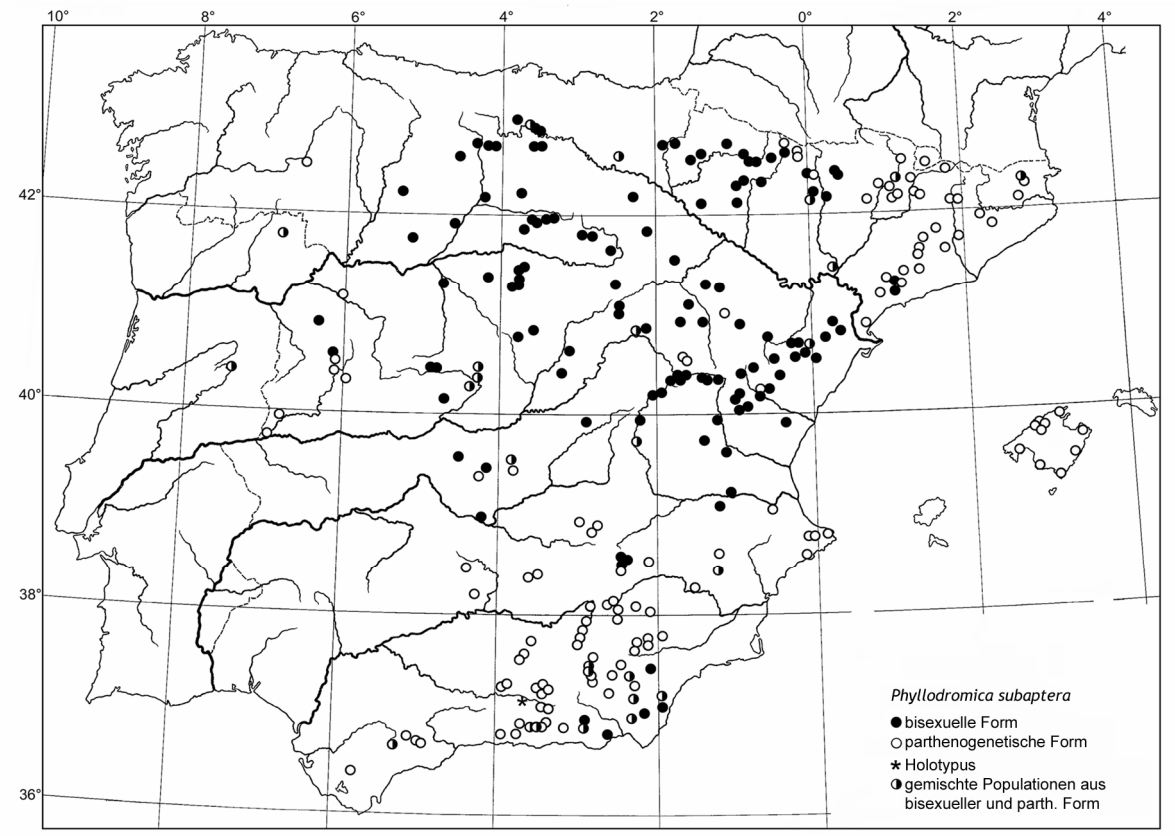

Abb. 4. Verbreitung der parthenogenetischen und der bisexuellen Form von *P. subaptera* auf der iberischen Halbinsel.

Das Verbreitungsmuster der beiden Sexualrassen von *P. subaptera* kann sehr gut mit dem Begriff der "geographischen Parthenogenese" charakterisiert werden. Dieser Terminus beschreibt jenes Verbreitungsmuster von parthenogenetischen Individuen und ihren nächsten bisexuellen Verwandten bei dem die zuletzt genannten ein relativ kleines zentrales Gebiet besetzen, umgeben von den Parthenogeneten, die über ein wesentlich größeres Gebiet verbreitet sind (Vandel 1928). Die beiden Fortpflanzungsformen kommen dabei größtenteils allopatrisch vor, Sympatrie gibt es gar nicht oder nur dort, wo sich die Verbreitungsgebiete berühren.

Geographische Parthenogenese wurde bei einer Vielzahl von Tieren beobachtet und wird oft als Ergebnis glazialer oder postglazialer Ereignisse angesehen (Seiler 1961, Suomalainen 1969). Mit dem Rückzug großer Eismassen am Ende einer Eiszeit können sich Arten wieder neu ausbreiten, wobei parthenogenetische Organismen generell die besseren Kolonisten darstellen. Zum einen sind sie nicht abhängig von der Anwesenheit eines andersgeschlechtlichen Partners und können zum anderen ihren Reproduktionserfolg verdoppeln, da sie keine Männchen produzieren.

Ferner wurde beobachtet, dass Parthenogeneten häufig besser an unvorteilhafte Umweltbedingungen angepasst sind (Vandel 1940, Lindroth 1954).

Das scheint auch für *P. subaptera* zuzutreffen: Die Überlegenheit der parthenogenetischen Form hinsichtlich ihrer Ausbreitung könnte damit zusammenhängen, dass die Männchen der bisexuellen Form weniger gut an trockene Bedingungen angepasst sind wie die Weibchen. Im Labor schienen die kleineren und kurzlebigeren Männchen sensitiver gegenüber Austrocknung zu sein als die Weibchen. Ähnliche Beobachtungen wurden bei der Schabenart *Pycnoscelus indicus* (Parker & Niklasson 1995) und dem Diplopoden *Nemasoma varicorne* (Enghoff 1976b) gemacht.

Das relativ seltene Auftreten parthenogenetischer *P. subaptera*-Populationen innerhalb des zentralen Verbreitungsgebiets der bisexuellen Form in Spanien könnte darauf hindeuten, dass bisexuelle Individuen dort erfolgreich gegen parthenogenetische Individuen konkurrieren und diese verdrängen.

Die aktuelle Verbreitung der bisexuellen Form, die endemisch auf der iberischen Halbinsel vorkommt, deutet auf einen iberischen Ursprung der parthenogenetischen Form hin, die sich dann von dort aus über das Mittelmeergebiet ausgebreitet haben muß.

Trotz der Tatsache, dass die Parthenogeneten eine sehr große Verbreitung aufweisen, obwohl sie nicht flugfähig sind, ist die Entstehung der Parthenogenese wahrscheinlich ein relativ junges Ereignis, da zwischen den parthenogenetischen Weibchen und den Weibchen der bisexuellen Form (mit Ausnahme derjenigen aus Südspanien) noch keine morphologischen Unterschiede sichtbar sind. Auch die Spermatheken der Parthenogeneten sind noch vollständig entwickelt, obwohl sie keine Aufgabe mehr erfüllen. Das trifft auch für andere Fälle von Parthenogenese bei Arthropoden zu (*Trichoniscus*, *Bacillus*, *Otiorrhynchus, Solenobia*) wohingegen wie bereits erwähnt bei dem Myriapoden *Nemasoma varicorne* (Enghoff 1976a) die Spermatheken der Parthenogeneten bereits reduziert sind.

Entstehung von obligatorischer Parthenogenese

Im Normalfall kommt es bei bisexuell reproduzierenden, mehrzelligen Tieren während der Oogenese zu einer Reduktionsteilung. Dadurch werden haploide befruchtungsfähige Eizellen gebildet. Durch die Verschmelzung einer haploiden Eizelle mit einer haploiden Samenzelle wird der diploide Zustand wieder hergestellt und der entscheidende Impuls für die Entwicklung der Zygote ist gegeben.

Bei *P. subaptera* hat die Analyse der Chromosomenzahlen (siehe Kapitel 7) gezeigt, dass sowohl bisexuelle als auch parthenogenetische Individuen ein diploides Genom aufweisen. Da bei einer parthenogenetischen Vermehrung keine Besamung stattfindet, muss ein Mechanismus vorhanden sein, der den diploiden Zustand der unbefruchteten Eizelle

gewährleistet und somit die Entwicklung des unbesamten Eis ermöglicht. Allgemein werden die folgenden zwei Mechanismen unterschieden:

Im 1. Fall, der Apomixis, findet keine Meiose statt. Dies entspricht einer klonalen Produktion von Nachkommen über ein Eizellenstadium wobei der Heterozygotiegrad der Elterngeneration stets erhalten bleibt.

Im 2. Fall, der Automixis, kommt es zunächst zu einer normal verlaufenden meiotischen Chromosomenreduktion. Der diploide Zustand wird durch die Fusion zweier Meioseprodukte wiederhergestellt. Die Automixis entspricht demnach einer Selbstbefruchtung. Je nachdem, wie sich die Chromosomen bei der Segregation verteilt haben und welche der haploiden Meioseprodukte anschließend wieder miteinander verschmelzen, sind die Nachkommen mehr oder weniger homozygot.

Um eine obligatorische Parthenogenese zu etablieren, müssen die Vorgänge, wie sie im Fall 1 und 2 geschildert wurden, genetisch fixiert sein.

Die Apomixis kommt weitaus häufiger als die Automixis und wurde auch bei der obligatorisch parthenogenetischen Schabe *Pycnuscelus surinamensis* nachgewiesen (Matthey 1945). Ob bei *P. subaptera* Apomixis oder Automixis vorliegt, ist derzeit noch nicht geklärt.

Neben den soeben beschriebenen zytologischen Mechanismen, die den Erhalt der Diploidie auch ohne Befruchtung der Eizelle gewährleisten, müssen bestimmte äußere Umstände gegeben sein, die zur Entstehung von obligatorischen parthenogenetischen Linien führen. Im Falle von *P. subaptera* sind die beiden folgenden Möglichkeiten für die Entstehung der Parthenogenese denkbar.

(1) Obligatorische Parthenogenese kann aus einer zufällig erfolgten fakultativen Parthenogenese entstehen. Letztere tritt zum Beispiel in Gebieten auf, in denen, bedingt durch eine geringe Populationsdichte, bisexuelle Weibchen unbegattet bleiben. Die obligatorisch parthenogenetische Schabenart *Pycnuscelus surinamensis* ist wahrscheinlich auf diese Weise entstanden.

(2) Daneben kann es auch durch Hybridisierung nah verwandter bisexueller Arten zur Entstehung einer diploiden Nachkommenschaft kommen, die sich durch obligatorische Parthenogenese vermehrt.

Die beiden soeben genannten Fälle gehen in der Natur häufig mit einer Polyploidisierung, das heißt mit einer Vervielfachung des Genoms einher. Im ersten Fall kann es durch Rückkreuzungen parthenogenetischer Individuen mit der bisexuellen Ausgangsform zur Entstehung polyploider Linien kommen. So entstanden die triploiden Parthenogeneten von

Pycnuscelus surinamensis möglicherweise durch Kreuzungen der zweigeschlechtlichen Art *Pycnuscelus indicus* mit diploiden parthenogenetischen Linien (Parker et al. 1977).
Im zweiten Fall können Rückkreuzungen der diploiden Parthenogeneten mit einer der beiden Ursprungsarten zu einer Polyploidisierung der Nachkommenschaft führen. Dieses Phänomen kann beispielsweise bei vielen parthenogenetischen Orthopterenarten, die durch Hybridisierung entstanden sind, beobachtet werden (Bullini & Nascetti 1987).
Bei *P. subaptera* wurden bislang keine polyploiden parthenogenetischen Linien gefunden. Momentan kann auch noch keine klare Aussage darüber getroffen werden, welche der beiden dargestellten Möglichkeiten zur Entstehung der parthenogenetischen Form führte.

5. Die zweigeschlechtliche Form von *P. subaptera*

Taxonomie – morphologische Analysen

Die Männchen besitzen an den Tergiten 7 und 8 des Abdomens charakteristisch geformte Drüsengruben, die bei der Paarung eine wesentliche Rolle spielen. Die Drüsengruben sind am unpräparierten Tier, wie in Abb. 1A dargestellt, nicht zu erkennen. Sie werden vom Hinterrand des jeweils vorhergehenden Tergits verdeckt und mussten zu einer genaueren Untersuchung präpariert werden. Je nach Fundort traten erhebliche morphologische Unterschiede auf, die eventuell auf das Vorhandensein verschiedener Arten hinweisen.
Eine umfangreiche Analyse ergab, dass die unterschiedlichen Ausprägungen der Drüsengrubenstrukturen nicht in Form eines morphologischen Gradienten mit fließenden Übergängen auftreten, sondern eine Unterteilung in 4 distinkte Morphen ermöglichen.
Im ersten Fall, bei Morph #1, sind die Drüsengrubenstrukturen an den Tergiten 7 und 8 am deutlichsten ausgebildet. Bei beiden Tergiten ist in der Mitte eine hügelartige Erhebung (**m**) (Abb. 5A, B) ausgebildet; an der anterioren Flanke der Erhebung befinden sich am 7. Tergit zwei ovale, aneinander angrenzende Vertiefungen, die sogenannten Borstenfelder (**bf**); davor (anterior) liegt eine transversal verlaufende Rinne (**tr**), deren vordere Begrenzung sehr steil ansteigt und schließlich den anterioren Tergitrand bildet. Am 8. Tergit ist die hügelartige Erhebung anterior durch eine scharfe, transversal verlaufende Kante begrenzt (**te**) (Abb. 5 B). Daran schließen sich drei Fortsätze an (anterior), wovon der mittlere konusartig geformt ist (**cp**). Die beiden anderen sind einfach ausgeprägt (**ap**).
Im zweiten Fall, bei Morph #2, sind die gleichen Strukturen vorhanden, erscheinen aber wesentlich kleiner und weniger stark ausgebildet (Abb. 5C, D).

Morph #3 ähnelt Morph #2, wobei der konusartige Fortsatz (**cp**) bei Morph #3 nur noch als sehr kleines membranöses Bläschen ausgeprägt ist (Abb. 5E, F).
Im letzten Fall, bei Morph #4, sind die Tergite relativ flach. Der konusartige Fortsatz (**cp**) am 8. Tergit fehlt vollständig.

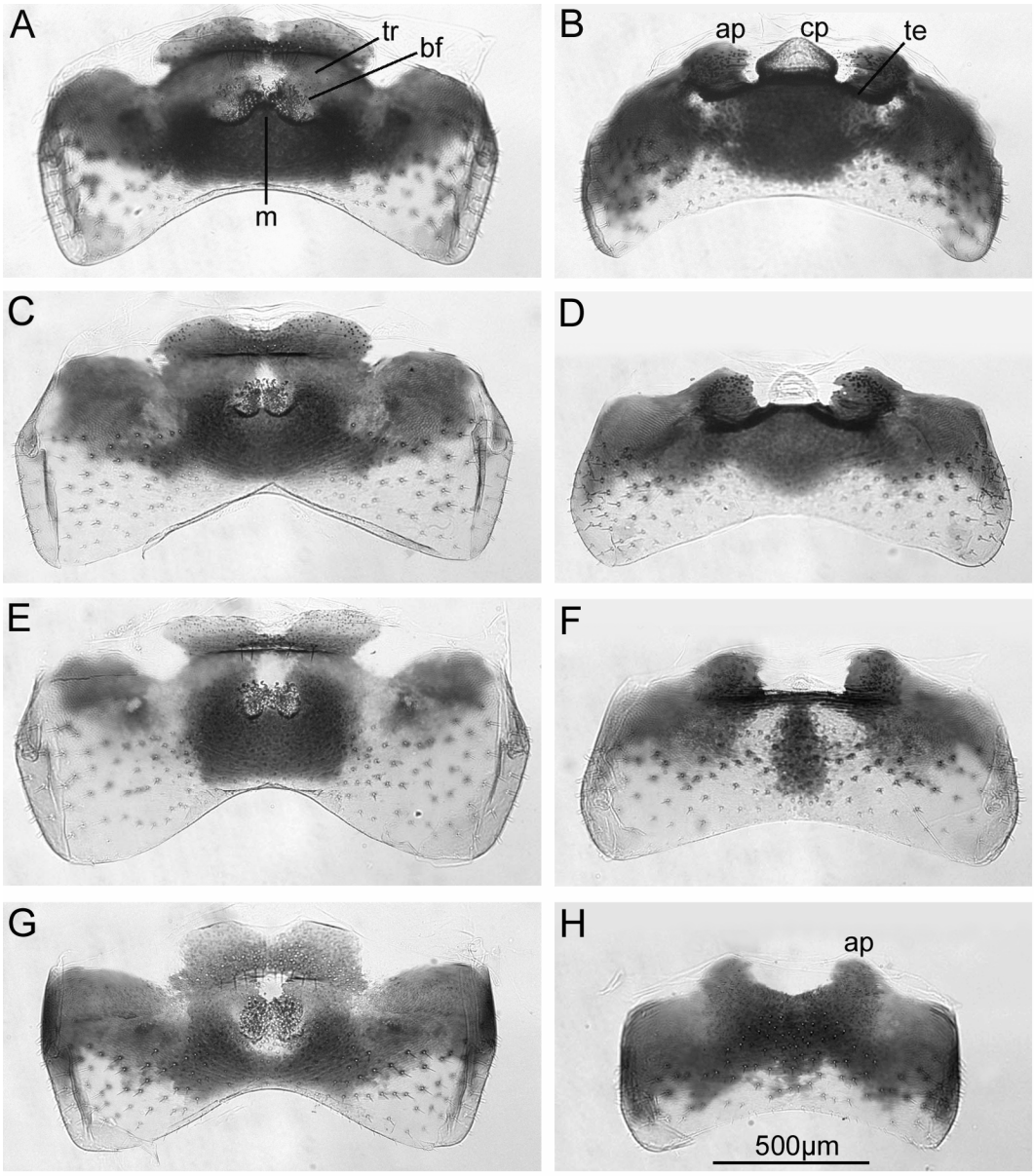

Abb. 5. Abdominale Tergite 7 (links) und 8 (rechts) von *P. subaptera* Männchen, Morph #1 (**A**, **B**), Morph #2 (**C**, **D**), Morph #3 (**E**, **F**) und Morph #4 (**G**, **H**).
Abkürzungen: **ap** anteriorer Fortsatz, **bf** Borstenfeld, **cp** konusartiger Fortsatz, **m** hügelartige Erhebung, **te** transversale Kante, **tr** transversale Rinne.

Neben den Drüsengrubenstrukturen unterscheiden sich die Morphen auch noch in anderen Merkmalen. Die Männchen von Morph #2 weisen am 6. Tergit eine wulstartige mit Borsten besetzte Erhebung auf. Ähnliche Strukturen sind auch in manchen Populationen von Morph #3 zu finden, bei den Morphen #1 und #4 wurden derartige Strukturen bislang nicht gefunden.

Die Männchen von Morph #4 unterscheiden sich von den Männchen der Morphen #1-3 in der Zahl der Tibia-Dornen an den Extremitäten. Die Weibchen von Morph #4 lassen sich anhand der Färbung des Pronotums und der Ausbildung des Genitalapparates eindeutig identifizieren. Die 4 Morphen unterscheiden sich auch in ihrer Verbreitung voneinander. Sie weisen spezifische, teilweise überlappende Verbreitungsgebiete auf (Abb. 6).

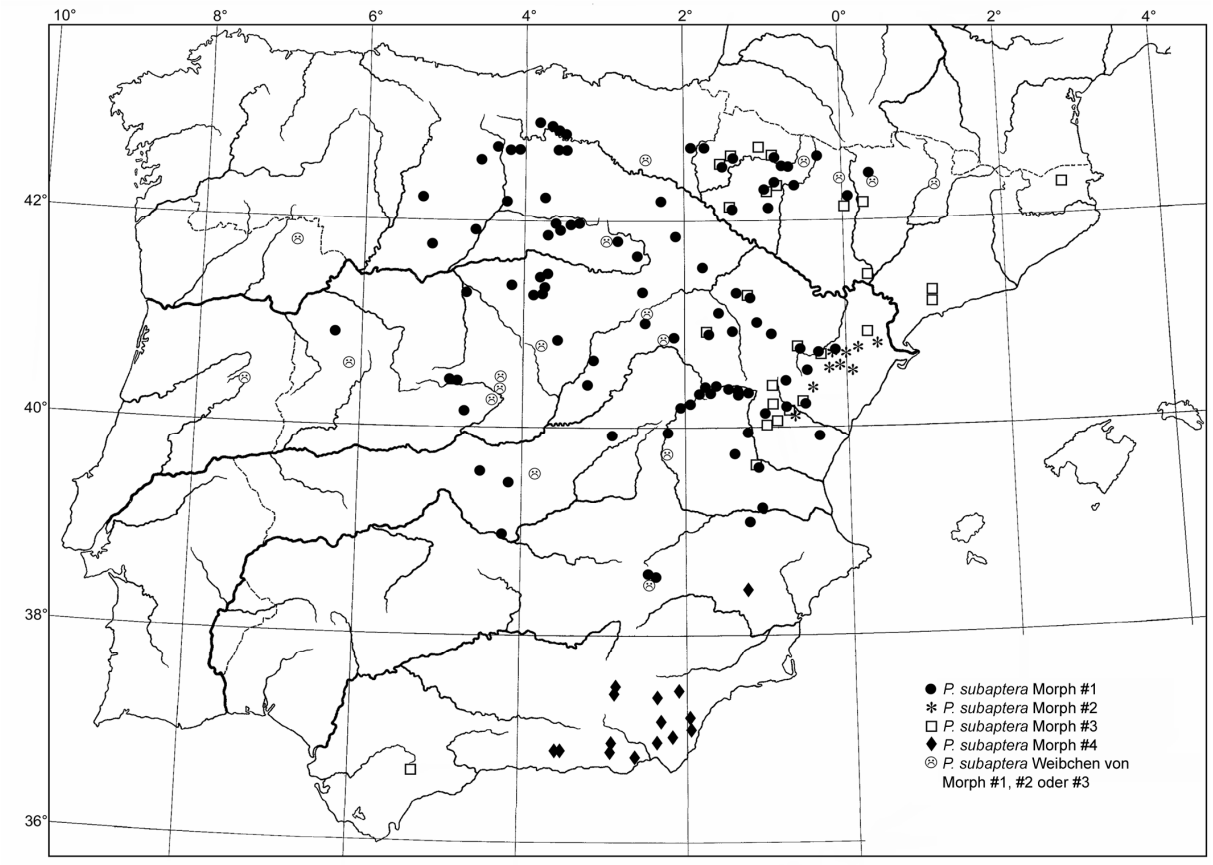

Abb. 6. Verbreitung der bisexuellen Morphen #1-4 von *P. subaptera* auf der iberischen Halbinsel. Fundorte, an denen zwei verschiedene Morphen gefunden wurden, sind durch sich überlappende Symbole dargestellt.
An einigen Stellen konnten keine Männchen gefunden werden ("sad face"-Symbol); aber die weiblichen Spermatheken enthielten entweder Spermien und/oder es schlüpften aus den abgelegten Ootheken männliche und weibliche Nachkommen. Beides weist auf die Anwesenheit der bisexuellen Form hin.

Es stellt sich die Frage, ob es sich bei den 4 Morphen um 4 separate Arten handelt. Im Fall von Morph #4 sprechen viele Anzeichen dafür: Morph #4 weist eine ganze Reihe morphologischer Autapomorphien auf, die nicht nur die Drüsengrubenstrukturen der Tergite 7 und 8 betreffen, sondern wie bereits erwähnt auch andere Strukturen, wie zum Beispiel die Zahl der Dornen an den Extremitäten, ein Merkmal, das dieser Form schließlich ihren Namen als neu beschriebene Art *P. quadracantha* gab. Auch die Weibchen von *P. quadracantha* lassen sich anhand mehrerer autapomorpher Merkmale eindeutig bestimmen.

Anders verhält es sich bei den Morphen #1-3. Diese unterscheiden sich zwar anhand der Ausprägung der Drüsengrubenstrukturen der Männchen, daneben gibt es allerdings keine morphologischen Merkmale, die für eine klare Aufteilung in eigene Arten sprechen würden.

Die wulstartige mit Borsten besetzte Erhebung am 6. Tergit wie sie bei Morph #2 und in ähnlicher Ausprägung auch in manchen Populationen von Morph #3 auftritt, deutet eher auf eine partielle Hybridisierung dieser beiden Morphen hin und spricht somit gegen eine Aufspaltung in separate Arten.
Bei den Weibchen lassen sich keine morphologischen Unterschiede zwischen den Morphen #1-3 feststellen, die auf das Vorhandensein verschiedener Arten hindeuten würden.

Taxonomie – genetische Distanzen

Die Frage nach dem taxonomischen Status aller bisexuellen Morphen von *P. subaptera* lässt sich allein mit morphologischen Unterscheidungsmerkmalen nicht klären. Darum wurden zusätzlich genetische Daten erhoben. Die Entscheidung fiel dabei auf die Analyse der DNA-Sequenz des mitochondriellen Gens Cytochrom c Oxidase Untereinheit I (COI) mit einer Länge von 1570 Basenpaaren. Die Sequenzen kleinerer Fragmente dieses Gens werden mittlerweile weltweit als Referenz zur Charakterisierung und Unterscheidung von Arten innerhalb der Zoologie verwendet (DNA-Barcoding). Neben den bisexuellen Formen wurde auch die parthenogenetische Form in die genetische Analyse mit eingeschlossen.
Im Falle der neu beschriebene Art *P. quadracantha* wird das Ergebnis der morphologischen Analyse durch die genetischen Daten bestätigt. *P. quadracantha* weist zu den bisexuellen Morphen #1-3 und zur parthenogenetischen Form genetische Distanzen von ca. 9 % auf. Genetische Distanzen derselben Größenordnung wurden bereits zwischen vielen anderen congenerischen Insektenarten nachgewiesen: Hebert et al. beispielsweise fanden in ihrer breit angelegten Studie zwischen mehreren tausend congenerischen Arten aus verschiedenen Insektenordnungen durchschnittliche Sequenzdivergenzen von 9-10% (Hebert et al. 2003a).
Die parthenogenetische Form zeigt ca. 1,8% genetische Distanz zu den bisexuellen Morphen #1-3. Diese Distanzwerte sind relativ niedrig im Vergleich zu denjenigen von *P. quadracantha*, doch auch Hebert et al. fanden in ihrer oben genannten Studie immer wieder Artenpaare mit relativ geringen Distanzen. Bei der Untersuchung von 200 Lepidopterenarten ergaben sich für 4 congenerische Artenpaare ebenfalls Distanzwerte unterhalb von 2% (Hebert et al. 2003b). Die Autoren vermuten, dass diese niedrigen Werte auf einen relativ jungen Ursprung dieser Arten hinweisen könnten. Für die parthenogenetische Form kann höchstwahrscheinlich ebenfalls ein junger Ursprung angenommen werden. Dafür spricht auch, dass die parthenogenetischen Weibchen zu den Weibchen der Morphen #1-3 noch keine morphologischen Unterschiede aufweisen.
Sexuell ist die parthenogenetische Form durch ihre obligatorisch parthenogenetische Vermehrungsweise eindeutig von den Morphen #1-3 isoliert. Aufgrund dieser Tatsache

erscheint es trotz der relativ geringen genetischen Distanzen gerechtfertigt, die parthenogenetische Form von den bisexuellen Formen taxonomisch abzutrennen.
Für die Namensgebung war entscheidend, dass der Holotypus von *P. subaptera* ein Weibchen ist, das aus einer Region im Süden Spaniens stammt, in der neben *P. quadracantha* nur parthenogenetische Weibchen vorkommen. Da die Weibchen von *P. quadracantha* morphologisch eindeutig von den parthenogenetischen Weibchen unterschieden werden können, handelt es sich bei dem Holotypenexemplar höchstwahrscheinlich um ein parthenogenetisches Weibchen. Die parthenogenetische Form erhält somit den Namen *P. subaptera.*
Zwischen den Morphen #1-3 sind die genetischen Distanzen sehr gering und liegen maximal bei 0,7%. Diese Werte befinden sich damit im Bereich der intraspezifischen Variabilität (Hebert et al. 2003b). Die Morphen #1-3 wurden daher zu einem Taxon zusammengefasst und als neue Art *P. iberica* definiert.

6. Phylogenetische Analyse

Zur Untersuchung der phylogenetischen Beziehungen zwischen den Taxa *P. quadracantha*, *P. subaptera* und *P. iberica* wurden sowohl die morphologischen Merkmale als auch die DNA-Sequenzdaten des COI-Gens verwendet.

Phylogenetische Analyse mittels morphologischer Merkmale

Zur Durchführung einer kladistischen Analyse wurden 24 variable, morphologische Merkmale in einer Matrix zusammengestellt. Neben den Taxa *P. quadracantha* und *P. iberica* wurden auch die am nächsten verwandten Gruppen (*carpetana*-, *nana*-, und *panteli*-Gruppe) in die Analyse miteinbezogen und als Außengruppen definiert. Die parthenogenetische Art *P. subaptera* konnte nicht in die Analyse miteinbezogen werden, da keine männlichen Merkmale verfügbar sind und die Weibchen selbst nur sehr wenige unterschiedliche Merkmale aufweisen. Das aus der Matrix resultierende Kladogramm ist in Abb. 7 dargestellt.

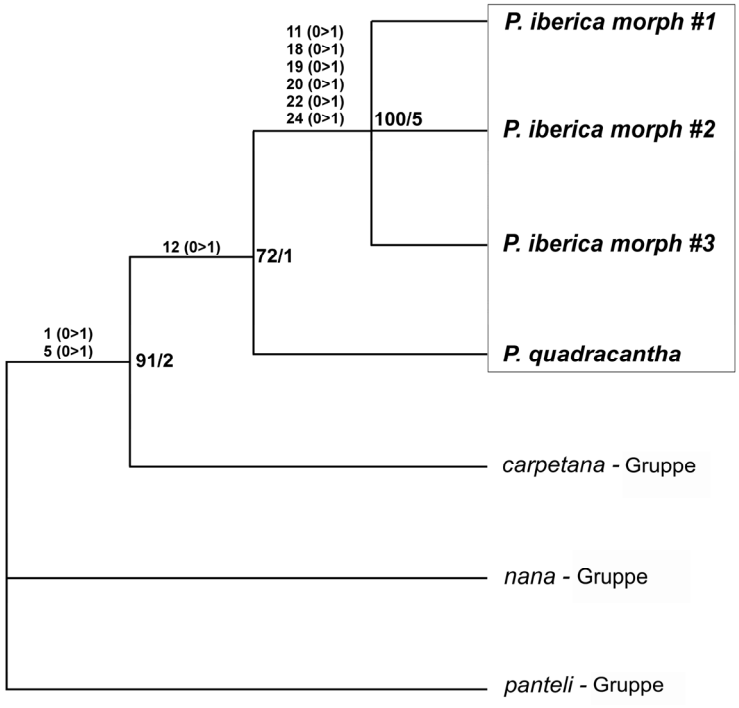

Abb. 7. Ergebnis der kladistischen Analyse der morphologischen Datenmatrix. Konsensusbaum aus den drei "sparsamsten" Kladogrammen (Baumlänge: 38 Schritte) einer Maximum Parsimonie Analyse. Die Anzahl informativer Merkmalsänderungen ist oberhalb der Äste angegeben. An den Knotenpunkten sind die Werte für die Bootstrap-Unterstützung über 50% (bei 10 000 Replikaten), gefolgt von den Werten für die Bremer-Unterstützung, angegeben.

Im Kladogramm erscheinen die Taxa *P. iberica* und *P. quadracantha* monophyletisch und als Schwestergruppe der *carpetana*–Gruppe. Die Anordnung der Taxa *P. iberica* und *P. quadracantha* könnte darauf hinweisen, dass eine schrittweise Evolution der Drüsengrubenstrukturen am 7. und 8. Tergit stattfand, die ihren Ausgangspunkt bei *P. quadracantha* (Abb. 5G, H) mit der schwächsten Merkmalsausprägung hat und über *P. iberica* Morph #3 (Abb. 5E, F) und Morph #2 (Abb. 5C, D) bis zu Morph #1 (Abb. 5A, B) mit der stärksten Merkmalsausbildung fortschreitet.

Es gibt jedoch auch Argumente, die gegen diese Entwicklungsrichtung sprechen und den umgekehrten Prozess, eine schrittweise Reduktion von Drüsengrubenstrukturen, unterstützen.

Das überzeugendste Argument bezieht sich dabei auf die Ausprägung der Strukturen am 8. Tergit. Wie bei *P. iberica* sind auch bei *P. quadracantha* am Vorderrand zwei Fortsätze (**ap**) ausgebildet (Abb. 5B, H). Zwischen den Fortsätzen befindet sich im Fall von *P. quadracantha* ein membranöser Abschnitt (Abb. 5H) genau an der Stelle, an der sich bei den verschiedenen Morphen von *P. iberica* ein konusartiger Fortsatz (**cp**) befindet, der bei Morph #1 (Abb. 5B) sehr stark ausgebildet ist und bei Morph #3 (Abb. 5F) nur noch als membranartige Ausstülpung auftritt. Dies könnte man als eine schrittweise Reduktion der Strukturen am 8. Tergit, die bei *P. iberica* Morph #1 beginnt und bei *P. quadracantha* mit deren vollständiger

Reduktion endet, interpretieren. Im umgekehrten Fall, mit *P. quadracantha* als Ausgangspunkt, hätte sich der membranöse Abschnitt zwischen den beiden Fortsätzen (**ap**) als neue Struktur herausbilden müssen (Abb. 5H). Aus biologischer Sicht scheint dies jedoch wenig sinnvoll, da diese Struktur keine erkennbare Aufgabe erfüllt und auch bei anderen *Phyllodromica*-Arten nicht vorhanden ist. Plausibler ist es, diese Struktur als das Endstadium einer Reduktionsreihe anzusehen.

Die Hypothese einer schrittweisen Reduktion der Drüsengrubenstrukturen wird durch einen Blick auf die nächstverwandten Gruppen unterstützt, denn sowohl in der *nana*- als auch in der *carpetana*-Gruppe treten sekundäre Reduktionen von Drüsengrubenstrukturen am 8. Tergit auf.

Obwohl die soeben dargestellte Argumentation sehr plausibel erscheint, zeigt die kladistische Analyse eindeutig ein anderes Bild. Wäre *P. quadracantha* der Endpunkt einer Reduktionsreihe, dann wären *P. iberica* Morph #3 und *P. quadracantha* Schwestertaxa und *P. iberica* wäre somit paraphyletisch. In der kladistischen Analyse ist aber die Monophylie von *P. iberica* durch eine ganze Reihe von Autapomorphien sehr gut unterstützt (Abb. 7), die nicht die Drüsengrubenstrukturen betreffen. Zum Beispiel besitzen die Weibchen von *P. iberica* (und auch die von *P. subaptera*) ein zusätzliches Genitalsklerit, das den Weibchen von *P. quadracantha* und auch den untersuchten Außengruppen fehlt. Bei den Männchen von *P. iberica* ist beispielsweise die Ausbildung des rechten Paraprocts und des Helm-Sklerits als abgeleitet anzusehen. In der Summe ergibt sich daraus eine starke Unterstützung für die Monophylie von *P. iberica.*

Phylogenetische Analyse mittels DNA-Sequenzen

Um das Ergebnis der kladistischen Analyse zu testen, wurde zusätzlich eine phylogenetische Analyse basierend auf COI-Sequenzdaten, durchgeführt. Als Beispiel ist das Ergebnis einer Maximum Parsimonie Analyse in Abb. 8 dargestellt, Maximum Likelihood- und MrBayes-Analysen lieferten nahezu identische Ergebnisse. Als Außengruppe wurde *Blattella germanica* definiert.

Die molekulare Phylogenie zeigt eindeutig, dass *P. iberica* ein monophyletisches Taxon darstellt und unterstützt somit das Ergebnis der kladistischen Analyse. *P. quadracantha* liegt demnach unzweifelhaft an der Basis der "*subaptera*-Gruppe" und hat sich höchstwahrscheinlich als erstes von einem gemeinsamen Vorfahren abgespalten.

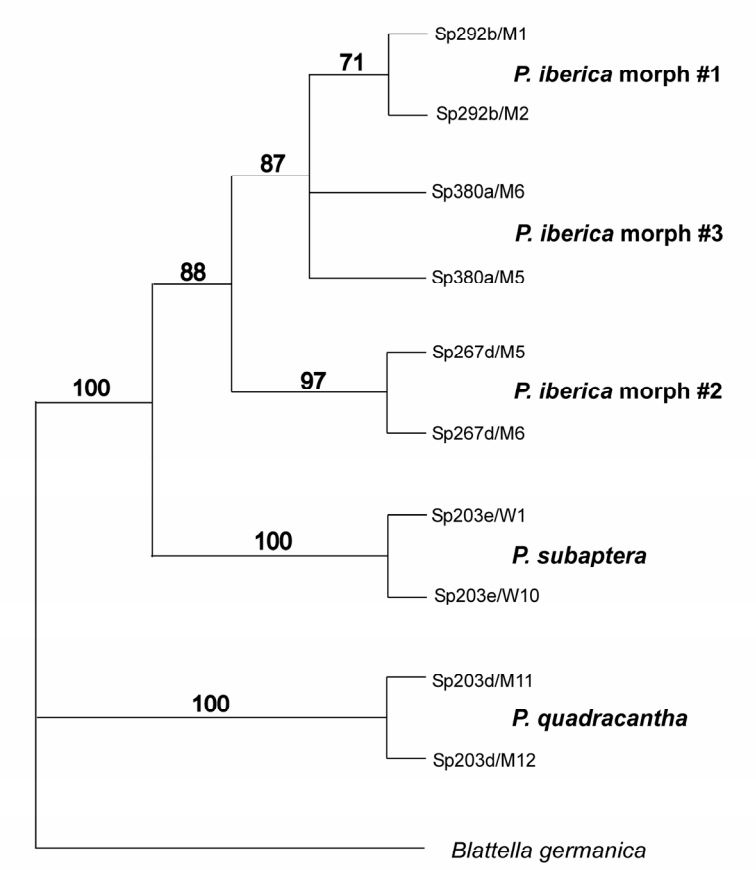

Abb. 8. Strikter Konsensus Baum (Länge 374 Schritte) einer Maximum Parsimonie Analyse. Oberhalb der Äste stehen die Bootstrap-Werte > 50 % (bei 2000 Bootstrap-Replikaten).

P. iberica Morph #1 und Morph #2 sind jeweils monophyletisch, Morph #3 ist paraphyletisch. Zwischen den Morphen #2 und #3 scheint eine engere Verwandtschaft zu bestehen. Diese Ergebnisse sind allerdings als vorläufig anzusehen. Es müssten wesentlich mehr Populationen von *P. iberica* in die Analyse miteinbezogen werden, um ein genaues Bild der Beziehungen zwischen den drei Morphen zu erhalten.

Der große Vorteil der genetischen Analyse ist, dass auch die parthenogenetische Art *P. subaptera* miteinbezogen werden konnte. Die beiden hier analysierten Individuen stammen vom selben Fundort, zeigen aber eine beachtliche Sequenzdivergenz. Das könnte bedeuten, dass an dieser Lokalität mindestens zwei parthenogenetische Linien sympatrisch vorkommen. Andererseits erscheinen die beiden Individuen monophyletisch und zeigen auf Sequenzebene einige Synapomorphien. Höchstwahrscheinlich entstanden die Sequenzunterschiede durch die Akkumulation von spontanen Mutationen in den einzelnen Linien und nicht durch eine multiple Abstammung von bisexuellen Vorfahren.

P. subaptera ist eindeutig als Schwestergruppe von *P. iberica* anzusehen. Somit könnte die Frage nach dem Ursprung der parthenogenetischen Form geklärt sein. Die sehr klare Trennung von *P. iberica* und *P. subaptera* zeigt, dass *P. subaptera* höchstwahrscheinlich von

einem gemeinsamen Vorfahren abstammt und nicht etwa von einer der drei Morphen von *P. iberica*. Die Frage, ob die parthenogenetische Form mehrmals oder nur einmal entstanden ist, kann im Moment nicht beantwortet werden, da dazu Populationen aus dem gesamten Verbreitungsgebiet von *P. subaptera* untersucht werden müssten.

Bei der parthenogenetischen Schabe *Pycnoscelus surinamensis* wird beispielsweise ein multipler Ursprung angenommen (Parker et al. 1977, Roth & Cohen 1968), da dort ebenfalls eine hohe genetische Diversität festgestellt wurde.

7. Analyse der Chromosomenzahlen

Die Bestimmung der Chromosomenzahlen wurde primär durchgeführt um zu untersuchen, ob *P. subaptera* ein polyploides Genom aufweist. Im vierten Kapitel wurde bereits darauf hingewiesen, dass parthenogenetische Tiere sehr häufig ein polyploides Genom besitzen. Darüber hinaus können durch den Vergleich von Chromosomenzahlen eventuell zusätzliche Aussagen über phylogenetische Zusammenhänge getroffen werden.

Bei Schaben wurden bereits umfangreiche Analysen der Chromosomenzahlen durchgeführt (Cohen & Roth 1970). Für die Unterfamilie der Ectobiinae wurden dabei 21/22 (♂/♀) Chromosomen nachgewiesen. Dies scheint die basale Chromosomenzahl innerhalb der Ectobiinae zu sein.

Für die vorliegende Arbeit wurden die Chromosomensätze von mehr als 200 Individuen der *subaptera*-Gruppe analysiert (ein kleiner Teil der Ergebnisse ist bereits publiziert).

Es konnte gezeigt werden, dass die parthenogenetische Spezies *P. subaptera* kein polyploides Genom aufweist. Die meisten der parthenogenetischen Weibchen hatten 12 Chromosomen (Abb. 10A). An einzelnen Lokalitäten aus Spanien wurden allerdings auch Weibchen mit 13 und 16 Chromosomen (Abb. 10B, C) gefunden.

P. quadracantha und *P. iberica* Morph #2 zeigten stets ein Genom von 21/22 Chromosomen. *P. globososacculata,* eine Spezies aus der *carpetana*-Gruppe, weist die gleiche Anzahl von Chromosomen auf (Abb. 9).

Variable Chromosomenzahlen wurden bei *P. iberica* Morph #1 gefunden, es können dort sowohl 21/22 als auch 11/12 Chromosomen vorkommen. *P. iberica* Morph #3 wies stets nur 11/12 Chromosomen auf.

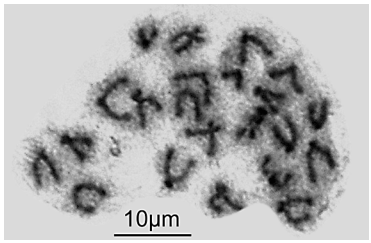

Abb. 9. Chromosomen in der Metaphase eines Weibchens von *P. globososacculata*. Anzahl der Chromosomen: 22.

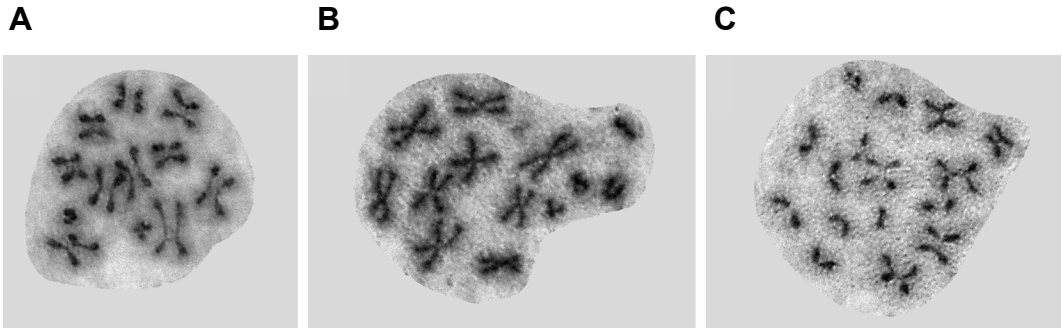

Abb. 10. Chromosomen in der Metaphase bei *P. subaptera*. Anzahl der Chromosomen: (A) 12, (B) 13 und (C) 16.

Die Chromosomenzahl 11/12 ist bislang die niedrigste, die jemals bei Schaben beschrieben wurde. Die Reduktion der ursprünglichen Anzahl von 22 (♀) auf 12 (♀) Chromosomen ist höchstwahrscheinlich durch paarweise Fusion von ursprünglich 20 akrozentrischen Chromosomen, wie sie bei *P. iberica* zu finden sind, zu 10 metazentrischen Chromosomen zustande gekommen. Daraus resultierende Genome bestehen aus 12 (♀) Chromosomen, davon treten mindestens 10 metazentrisch in Erscheinung. Das Phänomen der Chromosomenfusion in Verbindung mit einer Reduktion des Chromosomensatzes wurde bei Schaben bereits mehrfach beobachtet (Cohen & Roth 1970, Luykx 1983, Kambhampati et al. 1996, Burnside et al. 2000).

Aus den vorliegenden Ergebnissen lässt sich allerdings nicht schließen, ob die Chromosomenzahl 12 (♀) nur einmal oder mehrfach entstanden ist. Ebenso gibt es keine eindeutige Erklärung für die Entstehung der Chromosomenzahlen 13 (♀) und 16 (♀), wie sie bei *P. subaptera* gefunden wurden. Sie könnten sowohl durch Fusion einiger Chromosomen aus Individuen mit ursprünglich 22 (♀) Chromosomen entstanden sein, als auch aus Individuen mit ursprünglich 12 (♀) Chromosomen durch eine sekundäre Trennung einzelner Chromosomen.

Da sowohl *P. quadracantha* als auch *P. iberica* teilweise oder ausschließlich die für die Ectobiinae basale und somit plesiomorphe Chromosomenzahl 21/22 (♂/♀) aufweisen, können daraus keine phylogenetischen Schlussfolgerungen gezogen werden. Es ist nicht

auszuschließen, dass die niedrigeren Chromosomenzahlen 11/12 (♂/♀) auch bei *P. quadracantha* und *P. iberica* Morph #2 auftreten können.

Eine Aussage darüber, ob die parthenogenetische Spezies *P. subaptera* einfachen Ursprungs ist oder ob sie sich aus mehrfach parallel entstandenen Linien zusammensetzt, lässt sich aus den bislang gewonnenen Ergebnissen nicht ableiten. Es treten zwar, wie bereits erwähnt, neben der Zahl 12 auch noch höhere Chromosomenzahlen auf, die sich aber auch aus *P. subaptera* Individuen mit 12 Chromosomen durch eine sekundäre Trennung von Chromosomen ableiten lassen und nicht als Beweis für einen multiplen Ursprung der Parthenogenese interpretiert werden können.

Um die Fragen zum Ursprung der Parthenogenese und zur Ausbreitungsgeschichte von *P. subaptera* über das Mittelmeergebiet beantworten zu können, müssen genetische Analysen auf einer breiten Basis durchgeführt werden. Hierzu sollen zunächst die DNA-Sequenzen des COI-Gens von einer Vielzahl von Tieren aus möglichst vielen Populationen, die das gesamte Verbreitungsgebiet abdecken, analysiert werden. Reicht die Auflösung der Sequenzinformation nicht aus, können einzelne Fragestellungen durch Mikrosatelliten oder Fragmentanalyse-Techniken geklärt werden.

8. Zusammenfassung

Innerhalb der *subaptera*-Gruppe der Gattung *Phyllodromica* wurde ein neuer Fall von obligatorischer thelytoker Parthenogenese nachgewiesen. Parthenogenetische und bisexuelle Weibchen können nach morphologischen Merkmalen nicht unterschieden werden. Die Verbreitung der beiden Sexualrassen wurde somit durch eine Geschlechtsanalyse der Nachkommen und eine Untersuchung des Spermathekeninhalts vorgenommen. Parthenogenetische Weibchen produzieren nur weibliche Nachkommen, ihre Spermatheken sind stets leer, während bisexuelle Weibchen Nachkommen im Geschlechtsverhältnis 1:1 erzeugen und – nach der Begattung – mit Spermien gefüllte Spermatheken aufweisen.

Die Verbreitungsareale der beiden Sexualrassen sind unterschiedlich: Die zweigeschlechtliche Form ist auf die iberische Halbinsel beschränkt, wohingegen die parthenogenetischen Weibchen über einen Großteil des Mittelmeergebiets verbreitet sind. Allgemein lässt sich dieses Verbreitungsmuster sehr gut mit dem Begriff der geographischen Parthenogenese bezeichnen.

Parthenogenetische Linien sind häufig polyploid. Im Falle der *subaptera*-Gruppe trifft das nicht zu. Die Vielzahl der parthenogenetischen Weibchen und ein Teil der bisexuellen Individuen weisen die geringste Anzahl an Chromosomen auf, die jemals bei Schaben gefunden wurde.

Die Männchen der bisexuellen Form der *subaptera*-Gruppe zeigen je nach Fundort beachtliche morphologische Unterschiede, vor allem an den Drüsengrubenstrukturen am Vorderrand des 7. und 8. Tergits. Eine umfassende Revision der *subaptera*-Gruppe mit morphologischen und molekularen Markern führte zur Beschreibung zweier neuer bisexueller Arten, *P. quadracantha* und *P. iberica*. Letztere besteht ihrerseits aus drei eindeutig unterscheidbaren Morphen, die möglicherweise noch nicht vollständig genetisch separiert sind. Beim Holotypus von *P. subaptera* handelt es sich höchstwahrscheinlich um ein parthenogenetisches Weibchen, darum wird der Name *P. subaptera* zukünftig für die parthenogenetische Form verwendet.

Die phylogenetische Analyse der molekularen Marker – DNA-Sequenzen des COI-Gens – zeigten, dass *P. subaptera* und *P. iberica* Schwestergruppen darstellen. Der Ursprung der parthenogenetischen Form scheint somit geklärt zu sein. *P. subaptera* stammt höchstwahrscheinlich von einem gemeinsamen Vorfahren der beiden Arten ab und nicht von einem oder mehreren der Vorfahren der einzelnen *P. iberica*-Morphen. Obwohl die parthenogenetischen Weibchen genetische Diversität aufweisen, kann die Frage, ob die Parthenogenese einmal oder mehrmals unabhängig voneinander entstanden ist, nicht eindeutig

beantwortet werden. Dazu wäre eine breit angelegte molekulare Studie, die parthenogenetische Populationen aus dem gesamten Verbreitungsgebiet beinhaltet, notwendig. Die Frage nach der Ausbreitungsgeschichte von *P. subaptera* ausgehend von Spanien über einen großen Teil des Mittelmeergebiets, sollte damit ebenfalls beantwortet werden können.

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Lebenslauf

Persönliche Daten

Name Thomas Knebelsberger

Geburtstag 27.01.1971

Schullaufbahn

1977 – 1981 Grundschule Moosburg a. d. Albinstrasse

1981 – 1991 Karl – Ritter – von – Frisch – Gymnasium Moosburg

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Zivildienst

1992 – 1993 Malteser Hilfsdienst, Dienststelle Moosburg, Tätigkeit: Altenpflege und Fahrdienst.

Universitätsstudium

1993 – 1999 Biologiestudium an der Ludwig – Maximilians – Universität München.

Thema der Diplomarbeit: Geographische Parthenogenese bei der im Mittelmeerraum beheimateten Schabe *Phyllodromica subaptera* (Rambur, 1838) (Blattellidae, Ectobiinae).

Betreuer: Prof. Dr. Horst Bohn

Note der Diplomarbeit: **1,0**

Gesamtnote im Diplom: **1,1**

Promotion

1999 – 2008 Promotion an der Fakultät für Biologie der Ludwig – Maximilians – Universität München (LMU).

Betreuer: Prof. Dr. Horst Bohn

Auslandspraktika

1996 Rumänien für 3 Monate

Ziel: Bewertung unterschiedlicher Feuchthabitate in Rumänien als Voraussetzung für die Wiedereinbürgerung des Bibers.

Das Praktikum absolvierte ich im Rahmen meines Nebenfachs Wildbiologie bei Prof. Dr. Wolfgang Schröder.

1997 Ecuador, Südamerika für 6 Monate

Ziel: Charakterisierung verschiedener Lebensräume (Bäche, Höhlen und Waldhänge) im Gebirgsregenwald von Huacamayos (SO von Quito) anhand der dort vorkommenden Arthropodenfauna.

Dieses Praktikum konnte ich bei der Organisation PROBONA unter der Leitung von Dr. Xavier Izko durchführen. Das "Programa Regional de Conservación de Bosques Nativos Andinos" (PROBONA) ist Teil des IUCN Programms (The World Conservation Union).

Weitere Freilandforschung im Ausland

1999 – 2003 Jährliche Aufenthalte in Spanien, jeweils 3 – 5 Wochen

2001 Aufenthalt in Kroatien für 2 Wochen

2002 Aufenthalt in der Schweiz und in Südfrankreich für 1 Woche

2007 Sammelreise auf die Kapverden für 3 Wochen

Berufserfahrung

1996 – 2002 Zahlreiche Tätigkeiten als wissenschaftliche Hilfskraft, z. B. Bestimmung von Insekten am Lehrstuhl für Landnutzungsplanung und Naturschutz der LMU-München.

2000 Lehrtätigkeit an der LMU: Durchführung des Kurses "Vergleichende Morphologie der Insekten und Myriapoden" (Vorlesung und praktische Anleitung der Studierenden) zusammen mit Prof. Dr. Horst Bohn.

2000 und 2001

Lehrtätigkeit an der LMU: Durchführung des Kurses "Morphologie der Tiere" (Vorlesung und praktische Anleitung der Studierenden) zusammen mit Prof. Dr. Horst Bohn u. a.

September 2003 – September 2004

Wissenschaftlicher Angestellter (BAT 2a 1/2) an der Zoologischen Staatssammlung in München im Rahmen des GBIF (Global Biodiversity Information Facility) Projekts (Knoten "Evertebrata II", Teilprojekt MOTYMUNHACIS: Mollusken-Typenerfassung).

Oktober 2004

Gründung der Firma kmbioservices.

Oktober 2004 - September 2005

Bewilligung eines Förderantrages im Rahmen der EXIST SEED Gründerförderung des BMBF: Wissenschaftlicher Angestellter am Department I der LMU München (BAT 2a 1/2).

Januar 2006 – Dezember 2006

Bewilligung eines Förderantrages im Rahmen der FLÜGGE-Gründerförderung des Bayerischen Staatsministeriums für Wissenschaft, Forschung und Kunst: Wissenschaftlicher Angestellter an der Zoologischen Staatssammlung München (ZSM) (BAT 2a 1/2).

seit Januar 2007

Ausübung der selbstständigen Tätigkeit in der Firma kmbioservices.

Einwerbung einer Förderung zur Produktentwicklung durch das BayTOU-Programm des Bayerischen Staatsministeriums für Wirtschaft, Infrastruktur, Verkehr und Technologie.

seit Juni 2007

Wissenschaftlicher Angestellter an der Zoologischen Staatssammlung München (ZSM) in einem von der DFG geförderten Projekt zum "Aufbau eines DNA-Bank-Netzwerkes als Serviceeinrichtung für die wissenschaftliche Forschung in Deutschland".

Geographic parthenogenesis in the *subaptera*-group of *Phyllodromica* (Blattoptera, Blattellidae, Ectobiinae)

THOMAS KNEBELSBERGER and HORST BOHN

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A new case of obligatory thelytokous parthenogenesis in Blattoptera is reported in the Mediterranean species *Phyllodromica subaptera* (Rambur, 1838) (Blattellidae: Ectobiinae). The females of the parthenogenetic and bisexual forms cannot be distinguished by external features; their distribution was studied by analysis of the sex of the offspring and the contents of spermathecae. The parthenogenetic strain is spread over most of the Mediterranean countries, the bisexual forms are restricted to the Iberian peninsula, a distribution which is in keeping with the term "geographic parthenogenesis".
Chromosomal counts were made in order to analyse the ploidy-level of the parthenogens. The number of chromosomes in the parthenogenetic strain is mostly 12, exceptionally also 13 or 16; the bisexual forms have 12 or 22 chromosomes (♀, 2n). The parthenogens are certainly not polyploid. Therefore, polyploidy as a reason for the development of parthenogenesis can be excluded. The males show considerable variation in the structures of tergites 6-8 indicating that they might represent several species (*subaptera*-group). There is strong evidence that the type specimen of *P. subaptera* belongs to the parthenogenetic strain. The origin of the parthenogens and their spreading are discussed.

Thomas Knebelsberger (knebelsberger@zi.biologie.uni-muenchen.de), Horst Bohn (author for correspondence, bohn@zi.biologie.uni-muenchen.de). University of Munich, Department Biologie II, Luisenstrasse 14, D 80 333 München, Germany.

Introduction

Phyllodromica subaptera (Rambur, 1838) is a species with mainly Mediterranean distribution. According to Princis' catalogue (1971) the species had been found on the Iberian peninsula, in France, Corsica, Sicily, the former Yugoslavia, Bulgaria, Greece, and in Tunesia. Own collectings have revealed its occurrence also in Switzerland, on the peninsula Italy, in Morocco, and in Algeria. In the past, males of this species have rarely been found. Bucchich (1885) reported from Korcula that he had collected no fewer than 150 females, but not a single male. Fernandes (1962), for his revision of the Iberian Ectobiinae, had studied the material of the main insect collections of Spain and Portugal; among the 135 specimens of *P. subaptera* he only found 17 males. Harz (1976) did not see any male in the collections he studied.

One reason for the rareness of males certainly is their short life span in early spring. Females, on the contrary, are longer-lived and may be found from spring to autumn. During extended collectings over the last years males had been found at many localities in Spain. However, there was a large number of Iberian localities where, in spite of thorough searching at a time when a proportion of the animals was still in nymphal stage, only females or female nymphs were collected. Similarly, no male has ever been found outside the Iberian peninsula. The suspicion that parthenogenesis might occur in *P. subaptera* was confirmed by rearing experiments: the offspring of females from selected maleless regions were exclusively of female sex.

In this paper – in the chapter "Parthenogenesis" – a thorough analysis of the distribution of the parthenogenetic strain in and outside the Iberian peninsula is presented mainly based on the deter-

mination of the sex of offspring of the females and on the study of the contents of the female spermathecae. Moreover, chromosomal counts were made in order to determine the ploidy-level of the parthenogens. In the chapter "Systematic aspects" the *subaptera*-group will be introduced by a short treatment of its phylogenetic position and a description of the main characteristics with emphasis on the structure of the male tergal glands on tergits 7 and 8, not yet described in detail.

Methods and materials

Preparations of cuticular structures. – The respective parts of the body were treated overnight at room temperature (dried or alcohol fixed specimens) or at 40°C (formol fixed specimens) with 10% KOH to remove the soft tissues, then washed in water, dehydrated and finally mounted in Canada Balsam on microscope slides. Observations were made under a Zeiss Universal Microscope and photographs taken with a Zeiss Ikon camera.

Scanning electron microscopy. – The preparations of cuticular structures for SEM were similar as for light microscopy. The washed preparations were transferred to acetone, dried with the critical point method, mounted on aluminum stubs with adhesive carbon tubs, sputtered with gold in a BioRad SEM coating system, and inspected and photographed under a Philips XL 20 SEM.

Histological sections of spermathecae. – Genital atrium and genital chamber of females were opened ventrally by a longitudinal cut through the subgentital plate. Then the dorsal wall of the genital chamber with adhering spermathecaes was cut out leaving the sclerites of the basivalvula intact. When freshly killed animals were available the dissected tissues were fixed in Kahle's fixative (alcohol-formol-acetic acid); in most cases, however, the tissues had to be taken out from animals which, as a whole, had been fixed in formol. The tissues were then washed in alcohol, dehydrated, embedded in paraffin and sectioned (5 µm thick) on a Jung Table Microtome. The sections were mounted with a protein-glycerol mixture on microscope slides, deparaffinized and stained with Eosin-Haematoxilin and embedded in Eukitt. The stained sections were examined for the presence of sperms within the spermathecae (Fig. 4 A - F).

Rearing of nymphs and determination of sex. – Oothecae after their deposition were put into a moist chamber and kept at room temperature till the juveniles hatched. The first nymphal stages were fixed and embedded in Canada Balsam; sometimes only exuviae were available which were directly embedded in Eukitt. The sex of the nymphs could be determined by examining the subgenital plate. In females the posterior border of the subgenital plate has a median indentation, which is missing in males (Fig. 3 F, G).

Determination of the number of chromosomes. – The method used was that described by Cohen & Roth (1970). Nymphs or adults were injected with a tiny drop of a solution containing 0.05% colchicine; after about 18 hrs the tissues were dissected out, fixed, squashed, stained with orcein, mounted in Eukitt and observed under phase-contrast optics. Because of the small size and the young age of the animals – often quite young nymphs had to be used – mitoses could not be studied in the gonads as done by Cohen & Roth (1970); instead, gut tissue was used which contained mitoses in sufficient quantities at any stage of nymphal development.

List of localities. – Localities from which specimens were examined are shown figs 5 and 7 and are listed in Appendix 1 at the end of the paper.

Systematical aspects

In the series of revisions of the species of the genus *Phyllodromica* started by one of the authors (H.B.), the *subaptera*-group has not yet been treated. This paper, mainly dealing with parthenogenesis and the parthenogenetic strain, presents only a short introduction into the main characteristics of the group and their variability sufficient to allow a clear identification of the members of this group. A more complete description of all species and their features will be given in a following taxonomical revision which is in progress.

Phylogenetic position of the subaptera*-group*

The phylogenetic relationship of the *subaptera*-group had been discussed recently (Bohn 1999). It is considered as sister group of the *carpetana*-group with which it shares two characteristics concerning the bristles of the glandular structures on T7: the bristles are highly specialized (Fig. 3 C, D) with strongly broadened and irregularly curved distal ends, and they are crowded in dense bristle fields at the posterior part of the glandular pit.

Another related group is the *nana*-group. All three groups have in common the presence of glandular specializations on T7 and T8, the presence of extended membrane glands in the intersegmental regions of T4/5 and T5/6 (also found in the *panteli*-group) and the shortened sclerotization on the hook shaft of the phallomeres.

Representatives of the *subaptera*-group may be confused with those of the *nana*-group because of very similar wings and a similar colouration. Distinguishing features are listed in the following key. The species of the *nana*-group have not yet been described.

Key to distinguish the subaptera- *and* nana-*group*

- *subaptera*-group

  Male: T6 with posterior border sinusoid brought about by a deep median emargination and the broadly rounded posteriolateral edges (Fig. 3 A); glandular specialization of T7 forming a laterally open transverse trough, bristles strongly modified, arranged in two very dense bristle fields (Fig. 3 C, D).

  Female: Genital sclerites with additional sclerite anterior to the intercalary sclerite (Fig. 1 I); if missing (bisexual forms of southeastern Spain, morph #4, Fig. 1 K) pronotal disk without larger dark areas, mottled throughout (Fig. 1 H).

  Distribution: Bisexual species: Iberian peninsula; parthenogenetic strain: most Mediterranean countries and Switzerland.

- *nana*-group

  Male: T6 with only weakly concave posterior border, lateroposterior edges less broadly rounded (Fig. 3 B); glandular specialization of T7 forming a shallow transversely oval pit, bristles less strongly modified, disperse.

  Female: Genitalia without additional sclerite, pronotal disk for the most part dark.

  Distribution: restricted to the northern part of the Iberian peninsula, mainly in and near the Pyrenees.

Characteristics of the subaptera-*group*

The structures of legs, genitalia and terminal abdominal segments are very similar to those of the closely related *carpetana*-group (Bohn 1999); see there for a description.

Wings: Forewings reduced to small widely separated scalelike structures scarcely surpassing the posterior border of the mesonotum, very narrow, with almost parallel borders, broadest near the base. Hindwings missing.

Wing size and shape are almost identical in the *nana*-group; in other groups having similarly shortened wings (*panteli*-group; *carpetana*-group, partly; subgenus *Lobolampra*, partly) these are less narrow, ± egg-shaped with curved interior border, broadest at about the middle.

Male abdominal tergites (6-8): These three tergites are considerably longer than the preceding and following tergites. *Glandular specializations* are found on the surface of T7 and T8 (glandular pits) and in the membraneous intersegmental region of T4/5 and T5/6 (membrane glands). Posterior part of tergites with dispersed rather long and strong *bristles*.

Tergite 6 (Fig. 3 A) rather long; anterior border laterally with large rounded excisions at the site of the membrane glands; posterior border strongly sinusoidal brought about by a deep median emargination and the broadly rounded lateroposterior corners.

Tergite 7 (Fig. 2 A): Anterior border trilobed by two narrow but relatively deep membraneous excisions (which means that the sclerotized parts are replaced by a soft colourless membrane), the broader median lobe somewhat produced and by a slight median excision in itself bilobed; posterior border relatively strongly concave, lateroposterior corners angularly rounded. *Glandular "pit"* developed as a short transversal trough immediately behind the median lobe of the anterior tergite margin. The anterior limitation of the trough is a ± steep wall declining from the median lobe; the posterior limitation is less well marked by a mound ascending from the bottom of the trough and declining again towards the posterior border of the tergite. The trough has no lateral limitation, its bottom is at the same level as the adjacent tergit surface. The *bristle fields* (Fig. 3 C) are arranged on the anterior slope of the mound forming two small longitudinally oval shallow grooves lying close together. Medially the bottoms of the grooves elevate to a longitudinal ridge separating the grooves. Posteriorly the grooves are well demarcated, but fading away towards anteriorly. At the edge formed by the median lobe and the anterior wall of the trough there is a row of rather long and strong bristles pointing posteriorly. There

is considerable variation in the length of the median lobe, in the deepness of the trough, in the size of the mound, and in the size and shape of the bristle fields (Figs 2 C, E, G; 3 D).

Tergite 8: The cuticular differentiations on T8 vary between the following extremes: In the simplest construction (Fig. 2 H) the median part of the anterior border is broadly produced, in the middle with a broad and deep membranous excision leaving two more or less tonguelike sclerotized anterior processes; the surface of the tergite is without any sculpturing. In the other extreme (Fig. 2 B) the tergite is strongly sculptured, with an elevation on the surface, anteriorly declining in a sinusoidal transversal edge and with a conelike process between the two anterior processes. The conelike process is dorsoventrally flattened, unsclerotized and densely covered by microvilli-like processes (Fig. 3 E).

The variations in the structure of tergites 7 and 8 are not arbitrary; there seems to be a strict correlation between the structures of the two succeeding segments: a strongly sculptured tergite 7 is always combined with a similarly strong sculpturing on tergite 8, and reversely. Moreover, the variations are not forming a gradually changing continuum, but rather distinct classes ("morphs"). At least 4 different "morphs" may be distinguished: morph #1 (Fig. 2 A, B) with the strongest, morph #4 (Fig. 2 G, H) with the weakest sculpturing on tergites 7 and 8; morph #2 (Fig. 2 C, D) and morph #3 (Fig. 2 E, F) are in between. Most likely, the morphs represent different species, each with a specific, but often mutually overlapping distribution (Fig. 6). Two or more of the morphs may occur together at a specific locality without obvious crossing.

An extended analysis of the species complex is in progress and will be published elsewhere.

Colouration. – Male: Head dark with whitish transversal band in the posterior interocular space. Thoracal nota with dark disk and broad (as broad as the wings) whitish-transparent margins. Abdominal tergites (1-8): anterior part dark, posterior part lightly (yellowish or whitish) coloured, with dark, anteriorly often clustered spots each having a central bristle. *Female:* Similarly though usually lighter coloured than the male. Dark central areas on the thoracal nota posteriorly broken up into dark spots; at the anterior border of the pronotal disk usually remaining a crescent-shaped dark area (Fig. 1 A - G). The bisexual population in southeastern Spain (morph #4) is characterized by a regularly mottled pronotum disk without a dark crescent (Fig. 1 H).

Apart from morph #4, bisexual and parthenogenetic females cannot be distinguished by external features; even the spremathecae are equally well developed in both forms.

In both sexes the dark colour on the pronotum may be replaced by a red-orange colour, as can also be observed in other species of *Phyllodromica* (*P. marginata, P. carpetana*).

The type specimen of P. subaptera *(Rambur 1838)*

P. subaptera was described first by Rambur 1838 after a female collected in southern Spain in or near Granada. The type specimen is preserved in the Natural History Museum, London. Unfortunately, the abdomen of the animal is completely missing. Therefore, a direct determination of its belonging to the parthenogenetic or bisexual strain by looking for sperms in the spermathecae was not possible. There is, however, strong indirect evidence indicating that it is a representative of the parthenogenetic strain: the locality of the type specimen (* in Fig. 6) is situated within an area where only parthenogenetic animals had been found. The only bisexual forms occurring in the further surroundings are those of morph #4; the type specimen, however, does not show the colour pattern of this morph on its pronotum (Fig. 1 G, H).

Parthenogenesis

The recognition of the parthenogenetic females

The most reliable and direct method to identify the parthenogenetic females is to follow their reproduction; the offspring of a parthenogenetic female in cockroaches should all be of female sex (thelytokous parthenogenesis). The sex of the 1. stage nymphs could be determined via the structure of the last abdominal sternite (subgenital plate, see p. 4 and Fig. 3 F, G). But living females, necessary for this kind of analysis, could only be collected in some of the localities; in most cases only formol or alcohol fixed animals were available.

In the fixed animals, the kind of reproduction could be analysed by examining the contents of the spermathecae, which are equally well developed in both bisexual and parthenogenetic females. The analysis was made with serially dis-

sected spermathecae. The spermathecae of bisexual females should contain sperms (Fig. 4 A - C), those of parthenogenetic females should be empty (Fig. 4 D - F). But an empty spermatheca could also mean that a bisexual female did not (yet) find a male or was not yet ready for copulation. The certainty with which a parthenogenetic population can be identified by this method increases with the number of females analysed and with the age of a female: the older the animal the higher the possibility that it could have met males if there were any.

On the other hand, a fairly clear decision about the state of a population was also possible when the animals were collected very early in the year. When at a locality some females were found together with only female nymphs there was little doubt that they belonged to the parthenogenetic strain. As long as nymphs were found it was not to be expected that the short-lived males had already died and disappeared.

The most difficult task, of course, was the identification of parthenogenetic females within a mixed population. The examination of a pure bisexual population has shown that the females had filled spermathecae in almost 100% of the cases. Therefore, when in a population a considerable number of the females had empty spermathecae this indicated the presence of parthenogenetic females. The parthenogenetic females, however, can hardly be recognized when they are much fewer in number than the bisexual forms. The low incidence of parthenogenetic females within the zone of the bisexual strain (Fig. 6) may at least be partly due to the inability to recognize sporadic parthenogenetic females among a bisexual population.

The distribution of the parthenogenetic and bisexual forms

(Figs 5 - 8)

The localities where *P. subaptera* had been found are listed in the following. Because of the difficulties mentioned above, a clear decision about the kind of reproduction was not possible in every case; the doubtful cases are provided with a question mark. Localities, where both forms have been found are set off by bold printing. The localities are represented only by their code; for the geographic parameters see Appendix 1.

Bisexual forms

Spain: Sp 4, 5a, 12b, 13a, b, 14a, 84b, 85, **88** ,**89**, **90**, **91**, **94**, a, 95a, 96a, b, 97, a, b, c, 98, a, 99a, b, 100, a, b, **108**, 112, 116, 119, b, 134, 135, 136, 137, a, 170, **186**, a, b, 189, **191**, a, **195**, **203**, a, b, c, d, **207**, a, 265, a, 266, a, 267, a, b, c, d, 268, a, 269a, 270, a, b, c, 271, 272, 273, 274, 276, 292, a, 294, 295, 296, 300, 302, 307, 324, 330, 331, 332, **333**, 334, 335, 336, 337, 360, a, 361, a, 363, 364, **365**, a, 366, a, 367, 368, 371, 372, 375, 376, 378a, 379, 380, a, **381**a, 382, a, 384, 386, a, 387, a, 388, a, 389, a, 390, 391, **393**, 394, **395**, 418, **419**, 420, 421, 422, 423, 426, 427, 428, 431, 432, 433, 434, 435, 436, 437, 438, 439, 440, 441, 442, 443, 444, 446, a, 447, a, 448, a, 449, a, 450, 451, 453, 455, 459, a, b, 460, 463, 464, a, b, 467, a, 471a, **472**, a, b, **473**, a, 492, a, b, **493**, **495**, 497, **498**, 499, 500, 501, 502, **504**, a, 506, 507, a, 509, 510, 511, 512, a. Museum material: I, II. – **Portugal**: Po **19**, **24**.

Parthenogenetic forms

Spain: Sp 10a, 11a, 17, 18a, 19a, 24a, 61, b, c, 62, 63, 65, 68, 71, a, b, 72, 73, 76, 78, b, 79, c, 80 (?), **88**, **89**, **90**, **91**, 92, 93, **94**, 101 (?), 105, a, 107, **108**a, b, 109, a, 114a, 139, 140, a, b, 141, 142, 143, 148, a, 149 (?), 169, 172, 173a, 174a, **186**b, 188a, **191**a, **195**, 196, 197, 198, 199, 200, 201, 202, **203**, a, b, c, d, 204, 205, 205a, 206, **207**, a, 208, 209, 210, 214, 229, 230, 253, 254, 256, 258, 262 (?), 263, 264, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289, 290, 293, 320, **333**, 339, 340, 342, a, 343, a, 345, 354, a, 355, a, 356, 357, 358, 359 (?), 362, **365**, 377, **381**, a, 383, **393**, **395**, 396, 397, a, b, **419**, 454, 456, 469, 470, **472**, a, b, **473**, a, 474, a, 475, 476, 480, 481, 483, 484, **493**, 494, **495**, 496, **498**, 503, **504**, a, 505, 508. – **Baleares**: Ba 8, 15, 17, 19, 21, 23, 24, 25, 26, 27. – **Portugal**: Po **19**, **24**. – **France**: F 2, 3, 4, 5, 8, 11, 12, 13, 13a, 15, 15a, 17, 18, 19, 20, 21, 22, 25, 26a, 34, 39, 41, 42, 48, 63, 79, 91, 99, a, 100. – **Switzerland**: He 1, a, 4, a, 5, a, 6, 26, a, 27, 31. – **Italy**: It 90. – **Sicily**: Sz 11a, 25, 26, 27, 41, 53, 54, 57, 60, 62, 64, 67, 69. – **Croatia**: Hr 14, 15, 20, 24, 26, 27, 28, 29. – **Morocco**: Ma 14a, 176a, 258, 259, 264, 273, 288. – **Algeria**: Al 14, 16. – **Tunesia**: Tu 5, 8, 9, 10.

The bisexual forms only occur on the Iberian peninsula (Figs 5, 6). They are mainly distributed in the northeastern quarter of the peninsula, but also reach – though only with few localities – Portugal and southern Andalusia.

The parthenogenetic strain is distributed over most of the Mediterranean countries (Fig. 7) including Portugal, Spain, France, Italy, Croatia, Morocco, Algeria, Tunesia, and – quite far from the Mediterrenean Sea – Switzerland (Wallis). It is also occurring on part of the Mediterranean islands such as Baleares, Sicily and the Adriatic islands Korčula and Hvar. *P. subaptera* is also reported from Bosnia-Herzegovina and Macedonia (Us & Matjevev 1967), Bulgaria (Drenski 1939, Buresch & Peschev 1957), Greece (Burr & al. 1923, Werner 1927) and from Corsica (Brunner 1882), but we did not see representatives from there. The records of *P. subaptera* in Switzerland, continental Italy, Morocco and Algeria are new to science. On the Iberian peninsula, within the main area of the bisexual forms, localities with parthenogenetic females are relatively rare; but they become more frequent in the adjacent areas in the Northeast (east of 1°E) and in the South (south of 38° 30'N) (Fig. 6).

There are several localities in which both, bisexual and parthenogenetic females, were found together. Such mixed populations were studied in more detail in southeastern Spain (near Baza) where the differently reproducing females can easily be distinguished thanks to a very characteristic colour pattern on the pronotum of the bisexual form (morph #4, Fig. 1 H). The area is situated near Baza adjacent to a highway. Within the area, localities could be found with either pure bisexual, or pure parthenogenetic or mixed populations (Fig. 8). At a suitable position – where the area was more or less regularly covered with larger bushes of *Quercus sp.* under which the animals were found – animals were collected along a transect of about 1 km length along one side of the highway at distances of 40 to 50 m. The transect started in an area with pure parthenogenetic populations (in the Southwest) and ended in an area with pure parthenogenetic populations (in the Northeast). The localities in between had mixed populations mediating between the extremes by a more or less gradual change in the relative frequences of the two forms. The localities (bushes) were marked with a permanent label in order to allow the registration of changes in the relative frequences of the two forms over the following years.

In the parthenogenetic cockroach *Pycnoscelus surinamensis* males are produced as a rare event

Table 1. Chromosomal numbers in *P. subaptera* and related species. [1] not determined, deduced from the female numbers. [2] From Cohen & Roth 1970.

Species	Locality		Number of chromosomes (2n) ♂	♀	Shape of chromosomes	Number of specimens examined ♂	♀	Number of metaphases counted ♂	♀
Phyllodromica subaptera (Rambur)									
bisexual forms morph #1	Spain	Sp 492b	21	22	almost all acrocentric	3	5	14	20
		Sp 511	11	12	almost all metacentric	2	3	8	12
morph #2		Sp 267d	21	22	almost all acrocentric	3	3	7	16
morph #3		Sp 459b	11	12	almost all metacentric	3	3	18	7
morph #4		Sp 203a	21[1]	22	9 acrocentric, 13 metacentric		1		10
parthenogenetic form		Sp 203a		12	almost all metacentric		1		2
		Sp 473		12	almost all metacentric		1		14
		Sp 474		13	9 meta-, remainder acro- or submetac.		1		27
		Sp 397		16	6 meta- , remainder acrocentric		1		10
	France	F 15a		12	almost all metacentric		1		5
		F 99a		12	almost all metacentric		1		4
		F 100		12	almost all metacentric		1		7
	Switzerland	He 1a		12	almost all metacentric		2		9
		He 26a		12	almost all metacentric		2		10
	Morocco	Ma 259		12	almost all metacentric		1		1
Phyllodromica globososacculata Bohn	Spain	Sp 370a	21	22	5 submeta-, remainder acrocentric	3	1	34	6
Ectobius pallidus (Olivier) [2]			21	22	all submetacentric				

(Matthey 1945, Roth & Cohen 1968). Their formation is presumably caused by a non-disjunction of the x-chromosomes; they are not functional. In *P. subaptera* there is no indication of the formation of such rare males: outside the Iberian peninsula no male had ever been found.

Chromosomal numbers

Very often parthenogenetic animals are polyploid. The presence or absence of polyploidy may give an indication about why and how parthenogenesis has developed. Therefore, the number of chromosomes was determined in nymphs and adults of the bisexual and parthenogenetic forms of *P. subaptera* from various localities in Spain, France, Switzerland and Morocco; for comparison, chromosomal counts were also made in *P. globososacculata*, representative of the *carpetana*-group, the presumed sister-group of *P. subaptera* (Table 1, Fig. 9).

The number of chromosomes in *P. globososacculata* is 21 in males and 22 in females; the same numbers have also been found in most of the bisexual morphs of *P. subaptera*: in morph #2, morph #4 and part of morph #1. On the other hand, morph #3, part of morph #1 and the parthenogens from Switzerland, France, Morocco and from two localities in Spain only have 12 chromosomes; the parthenogenetic females from two other Spanish localities have 13 and 16 chromosomes, respectively. *Ectobius pallidus*, another representative of the subfamily Ectobiinae studied by Cohen & Roth (1970), also has 21/22 chromosomes.

The basic diploid number in females of Ectobiinae seems to be 22, from which the lower numbers have to be derived. In *P. subaptera*, in the sets with 22 chromosomes most of the chromosomes are acrocentric (except in morph #4); in those with 12 at least 10 of them are metacentric. Obviously, the reduction of the chromsome numbers from 22 to 12 has been brought about by a pairwise centric fusion of 10 of the acrocentric chromosomes (yielding haploid 5, diploid 10 metacentric chromosomes). Whether the reduction of the chromosomal numbers from 22 to 12 has happened only once or several times independently during the evolution of the *subaptera*-group remains to be clarified. Similarly, the origin of the two populations of parthenogens with 13 or 16 chromosomes cannot be traced with certainty. They may either have descended from bisexuals with 22 chromosomes by chromosomal fusion, or from bisexuals or parthenogens with 12 chromosomes by chromosomal fission. The odd number (13) could either be explained by the fission of just one member of a pair of metacentric homologues in parthenogens with 12 chromosomes, or by non-disjunction of one chromosomal pair.

The finding of populations with various numbers of chromosomes in the parthenogens and in morph #1 makes it desirable to extend the analysis to more localities within and outside the Iberian pensinsula.

The comparison of chromosomal numbers of bisexual and parthenogenetic forms clearly show that the latter are certainly not polyploid; their numbers are the lowest found in cockroaches. Cohen & Roth (1970) have analysed the chromosomal numbers in more than a hundred species of Blattoptera covering all of the higher categories of the system. They found numbers between 16 and 80, the most frequent being 38. They also report a case with strong differences in chromosome numbers within a genus most likely due to centric fusion: *Lophoblatta brevis* has 32 mostly acrocentric chromosomes, another species of the same genus, *L. fissa*, has 16 mostly metacentric chromosomes. Similarly, the various chromosomal numbers in the American species of *Cryptocercus* ranging from 38 to 48 were also assumed to be caused by centric fusions (Luykx 1983, Kambhampati & al. 1996, Burnside & al. 2000).

Discussion

Parthenogenesis in cockroaches

Facultative parthenogenesis has been observed in several species of cockroaches: *Periplaneta americana, Blatta orientalis, Polyphaga saussurei, Blattella germanica, Supella longipalpa, Nauphoeta cinerea* (Roth & Willis 1956, Corley et al. 1999). Virgin females of these species may lay eggs which show some development and even hatching of nymphs. The offspring were always of female sex (thelytokous parthenogenesis). In *P. americana* parthenogenesis was carried out through two filial generations. But the fitness of the parthenogens is considerably lower than in offspring of fertilized females and there is little chance of their survival under natural conditions in competition with the bisexual forms.

So far, only one case of *obligatory parthenogenesis* was known in cockroaches: *Pycnoscelus surinamensis* which seems to be sexually isolated

from its presumable bisexual parental species *Pycnoscelus indicus* (Roth 1967). Various chromosome numbers are observed in the bisexual (♀ 2n: 34, 36, 38) as well in the parthenogenetic species (34, 35, 37, 39, 53, 54) (Roth & Cohen 1968); the strains with 53 or 54 chromosomes presumably are triploid or almost so (Roth & Cohen 1968, White 1976). The chromosome number in the parthenogenetic species is preserved by apomixis, both maturation divisions during oogenesis are mitotic (Matthey 1945).

The native country of both species is the Indo-Malayan region, but the exact distribution there is not known. *Pycnoscelus surinamensis* is now distributed circumtropically, mainly spread by man. The occurrence of *Pycnoscelus indicus* on Hawaii also points to a spread of this species by man's activity.

Geographic parthenogenesis

The parthenogenesis of *P. subaptera* is the second case of obligatory thelytokous parthenogenesis being observed in cockroaches. Though it cannot be excluded that facultative parthenogenesis might occur in the bisexual form possibly generating part of the parthenogenetic females found within the area of the bisexual form, there cannot be any doubt that parthenogenesis is obligatory outside this area.

The geographical distribution of the parthenogenetic and bisexual form of *P. subaptera* very well fits the pattern designated as *geographical parthenogenesis* by Vandel (1928): The two forms, as a result of a quite recent species splitting, show a largely allopatric distribution with only little or no overlapping; the bisexual form usually occupies a rather small central area surrounded by the much more extended area inhabited by the parthenogenetic form. Geographical parthenogenesis had first been reported from Europe for a variety of animals (Vandel 1928: Crustacea – *Trichoniscus*; Matthey 1941: Orthoptera – *Saga*; Seiler 1961: Lepidoptera – *Solenobia*; Suomalainen 1969: Coleoptera – *Otiorrhynchus*; Enghoff 1976 a: Myriapoda – *Nemasoma*), but meanwhile examples are also known from North America (Sweeney & Vannote 1987: Ephemeroptera; Sandoval & al. 1998: Phasmatodea – *Timema*), South America (Normak 1996: Coleoptera – Curculionidae), and even Australia (White 1980: Orthoptera – *Warramaba*).

The pattern is often considered as a consequence of glacial and postglacial climatic events (Seiler 1961, Suomalainen 1969; for alternative explanations see following chapter). It is assumed that the area occupied by the bisexual form represents the glacial refugium of the species during the last glaciation period. The later retreat of the ice allowed a renewed expansion of the species during which parthenogenetic forms – eventually appearing along the borders of the distribution area – were especially successful. According to Vandel (1940) and Lindroth (1954) the parthenogens usually occupy the areas with less favourable conditions to which they appear better adapted than the bisexual form. A further reason for the – at least temporary – success of the parthenogenetic forms certainly is their assumed better colonizing ability since they are not dependent on the presence of individuals of the other sex for reproduction. Moreover, provided they produce the same number of eggs, their reproductive success is twice that of the bisexual form since they need not produce "useless" males.

In *P. subaptera* the parthenogenetic form also has – as compared with the bisexuals – a much more extended distribution, mainly towards the East. Outside the Iberian peninsula the parthenogens inhabit rather low altitudes, in the respective geographic region usually connected with a hot and arid climate. The superiority of the parthenogens may at least partly be due to a better adaptation to more arid conditions. Under laboratory conditions the short-lived and smaller males appear to be more sensitive to dessication than females. Similar observations have also been made in *Pycnoscelus indicus* (Parker & Niklasson 1977) and in the diplopode, *Nemasoma varicorne* (Enghoff 1976 b). On the other hand, in some of the countries the parthenogenetic form of *P. subaptera* does not appear to be that successful: it is seldom found in North Africa, in Italy and in the Balkans.

The relatively rare occurrence of parthenogens within the central area of distribution of the bisexual form in Spain could indicate that the latter successfully compete with the former in this area. But the scattered localities of the bisexual form outside the central area in the South could also be considered as remnants of a formerly more extended area from which they were displaced by the expanding, possibly superior parthenogenetic form.

Parthenogenesis and polyploidy

Parthenogenesis in animals and plants is very often accompanied by polyploidy (Vandel 1928, Stebbins 1950); in the weevil genus *Otiorrhynchus* nearly all parthenogenetic races appear to be polyploid (Suomalainen & al. 1976). There is, however, no agreement about the interdependence of the two phenomena and the sequence of their appearing during evolution. In this connection mainly three alternatives are discussed: 1. Obligatory parthenogenesis arises from facultative parthenogensis in areas with low population densities; the resulting parthenogens are diploid. Polyploidy is later established by crossings of the diploid parthenogens with the bisexual form (Seiler 1961). 2. Development of parthenogenesis and polyploidy is caused by hybridization of closely related species. The hybrids reproduce by parthenogenesis; they may first be diploid and later become, possibly by new incrossings, polyploid (Bullini 1985, Bullini & Nascetti 1987, Scali & Marescalchi 1987, Saura & al. 1993). 3. Polyploidy develops as an adaptation to specific environmental conditions; accordingly, the development of parthengenesis is merely seen a consequence of polyploidy (Vandel 1940, Suomalainen 1969, Bierzychudek 1985, Beaton & Hebert 1988). Most likely there is no unique mechanism which could explain all cases of parthenogenesis and polyploidy in animals and plants; any of the three possibilities may be realized somewhere depending on the geographic region and its recent geological history as well as on the taxon in question.

The 3rd hypothesis as an explanation for the generation of parthenogenesis in *P. subaptera* can be excluded, since the parthenogens are not polyploid. Diploid parthenogens, however, are to be expected in the first phase of events according to the two remaining hypotheses. Favorable conditions may have been present for both: 1. Facultative parthenogenesis (at least deposition of oothecae) in virgin females does not seem to be a rare event in cockroaches; in view of this fact it appears rather astonishing that obligatory parthenogenesis had not developed more often. 2. The prerequisites of hybridisation also seem to be realized in *P. subaptera*, at least at present: there are several closely related species or races which are distributed in adjacent or overlapping areas. A decision between the two hypothesis is not possible at the moment, but molecular and/or genetic analyses of parthenogens and the various bisexual morphs finally should allow recognition of, for example, a possible hybrid origin of the parthenogens. In the case of *Pycnoscelus surinamensis* there are indications, that parthenogenesis and polyploidy have evolved according to the 1st of the hypothesis mentioned above. The results of a genetic analysis suggest that triploid parthenogenetic strains developed from crossings of bisexual with diploid parthenogenetic strains (Parker et al. 1977).

Origin and spreading of the parthenogenetic form in P. subaptera

The present distribution of the bisexual species of the *subaptera*-group and its relatives (*nana*- and *carpetana*-group), which are all endemic to the Iberian peninsula, suggest an Iberian origin of the group and of the parthenogenetic strain subsequently invading most of the Mediterranean countries.

In spite of the fact that the parthenogens – though they cannot fly – have a very wide distribution, the development of parthenogenesis should have been a rather recent event: the parthenogenetic females have not yet developed any remarkable morphological differences to their bisexual forerunners. Even the spermathecae (receptacles), which are without function in parthenogens, are as well developed as in the bisexual forms. The same has been observed in many other cases of parthenogenesis in arthropods (*Trichoniscus*, *Bacillus*, *Otiorrhynchus, Solenobia,* for references see Vandel 1928), whereas in the myriapod *Nemasoma* (Enghoff 1976a) the parthenogens have reduced receptacles.

The question, which of the bisexual morphs might be considered as parental species of the parthenogenetic form, cannot be answered right now. The results of the chromosomal countings are ambiguous since numbers of 12 are found in morph #1 as well as in morph #3. The morphological studies also don't allow a clear decision since the females of most of the bisexual morphs cannot be distinguished from the parthenogenetic females. It is, therefore, tempting to look for rare male parthenogenones (s. p. 432f) as have been found in *Pycnoscelus surinamensis* (Matthey 1945, Roth 1967, Roth & Cohen 1968). But the chance of a success in this matter might be very low: The ability to produce male parthenogenones

seems to be restricted to specific strains. The phenomenon of rare male parthenogenones has also been observed in *Trichoniscus* (Vandel 1934) and, though extremely rarely, in *Sago* (Matthey 1941); it is quite common in Phasmatodea (Cappe de Baillon & al. 1938, White 1976). But the males of the latter have a female chromosomal constitution (XX), overruled by some masculinizing environmental conditions. Similar mechanisms are not expected to work in cockroaches.

The question for the parental species or race of the parthenogens is strongly connected with the question whether the parthenogens have a mono- or polyphyletic origin. The occurrence of various chromosomal numbers (2n = 12, 13, 16) in parthenogens does not necessarily imply a polyphyletic origin. The higher numbers could also be explained by a secondary fission of chromosomes in parthenogens with 12 chromosomes, or simply by non-disjunctiuon. The distribution pattern – a central bisexual population followed in the north and south by parthenogenetic populations – could suggest that parthenogenesis had arisen independently at the two borders and that the parthenogens have spread from there towards the East. The study of several clones in the parthenogenetic *Pycnoscelus surinamensis* has revealed a very high genetical diversity which was attributed to a multiple origin of parthenogenesis (Parker & al. 1977), which was also suspected by Roth & Cohen (1968). A polyphyletic origin of parthenogenesis is also assumed for *Solenobia* (Seiler 1961, 1967, Lokki & al. 1975), but is controversially discussed for *Otiorrhynchus* (Smith 1971, Suomalainen & al. 1976, Tomiuk & Loeschke 1992). In the milliped *Nemosema* (Jensen et al. 2002), however, the thelytokous strain is assumed to have evolved only once from the bisexual strain, though the present distribution of the two strains – with the bisexuals in the center, surrounded by the parthenogens – could suggest a polyphyletic origin of the parthenogens. The molecular analysis argues for a migration of both, bisexuals and parthenogens, from the presumable site of their separation in central Europe to northern Europe.

At the moment, no statements are possible about how the parthenogens in *P. subaptera* have spread and over which routes they have reached the remote countries and islands of the Mediterranean Sea.

Prospect

In the above discussion a series of still unsolved problems has been pointed out: The composition of the species complex of *P. subaptera*, the relationships of the bisexual species among themselves and with the parthenogens, how and how often the parthenogens have developed, and how they have spread over such a vast area. Extended investigations using a combination of morphological, cytological, and molecular methods are in progress in order to get satisfying answers to the questions put forward.

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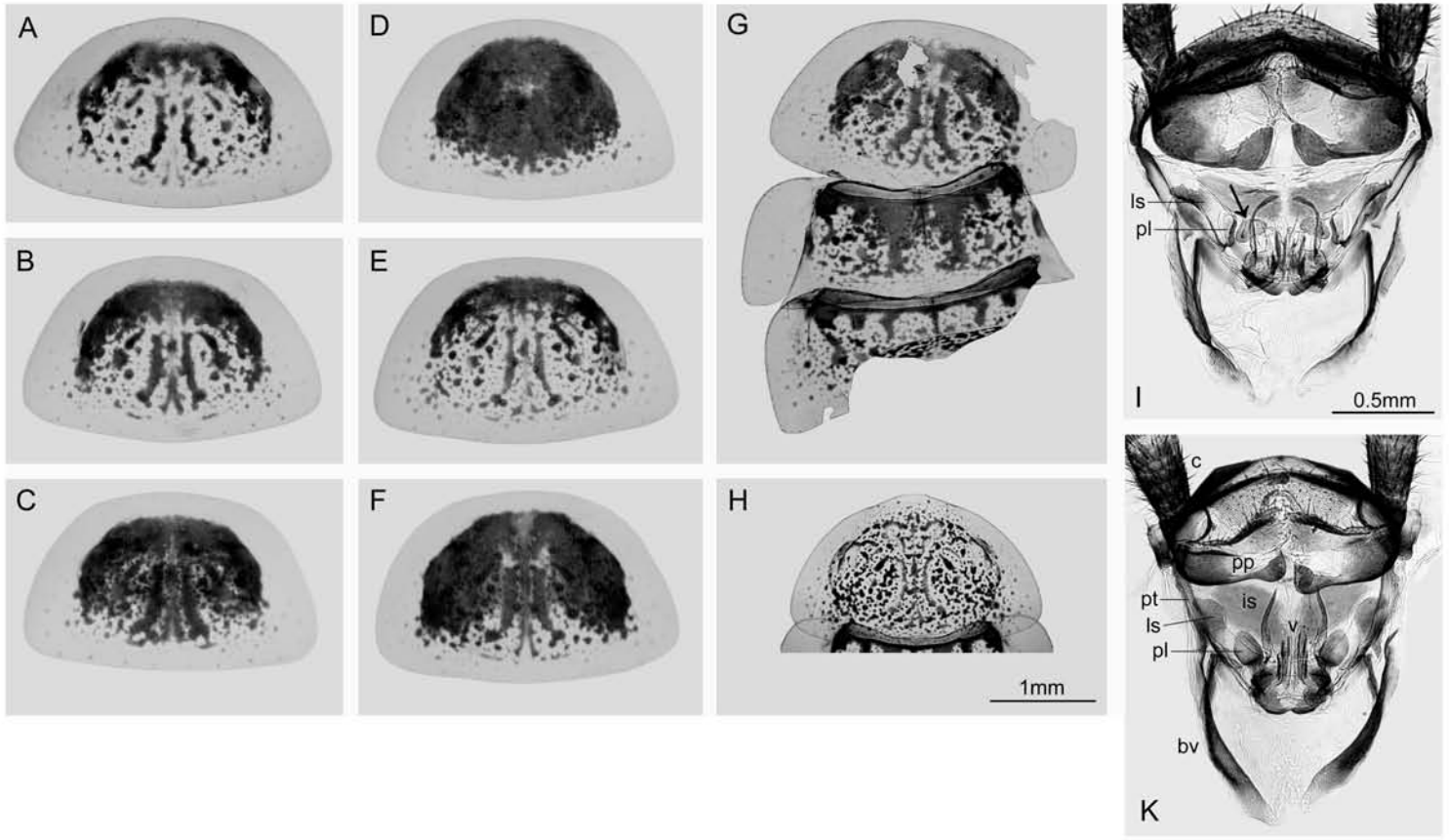

Fig. 1. **A-H** Colour pattern of the pronotum in females of *P. subaptera*. A-F Parthenogens from Spain (A-D), Switzerland (E), and Morocco (F); (G) thoracic nota of the holotype of *P. subaptera* from Granada, partly damaged; (H) bisexual female of morph #4. **I, K** Female genital sclerites of *P. subaptera*, dorsal complex. Ventral view, posterior end on top. (I) Parthenogen from France, with additional sclerite (arrow); (K) bisexual, morph #4, without additional sclerite but with a larger **pl**. **c** cercus, **bv** basivalvular sclerites, **is** intercalary sclerite, **ls** laterosternite IX, **pl** posterior lobe of valvifer II, **pp** paraproct, **pt** paratergites, **v** valves. Same scale for (A-H) and for (I, K).
Localities: (A-D) Sp 203c, (E) He 26, (F) Ma 258, (H, K) Sp 203d, (I) F 100.

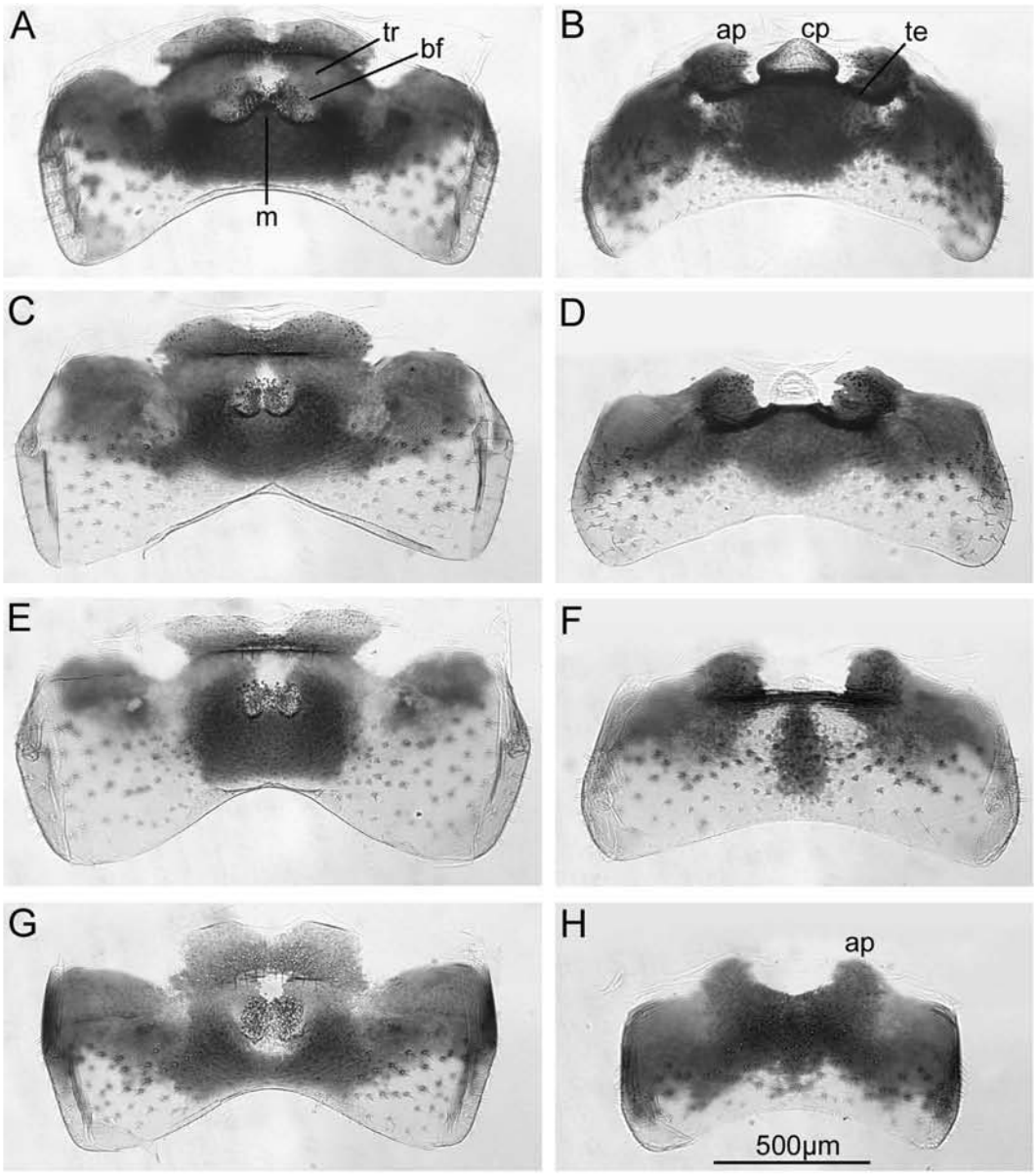

Fig. 2. Abdominal tergites 7 (left) and 8 (right) of males of *P. subaptera*, morph #1 (**A**, **B**), #2 (**C**, **D**), #3 (**E**, **F**), and #4 (**G**, **H**). **ap** anterior process, **bf** bristle field, **cp** conelike process, **m** mound, **te** transversal edge, **tr** trough.
Same scale for (A - H).
Localities: (A, B) Sp 510, (C, D) Sp 267, (E, F) Sp 380, (G, H) Sp 203.

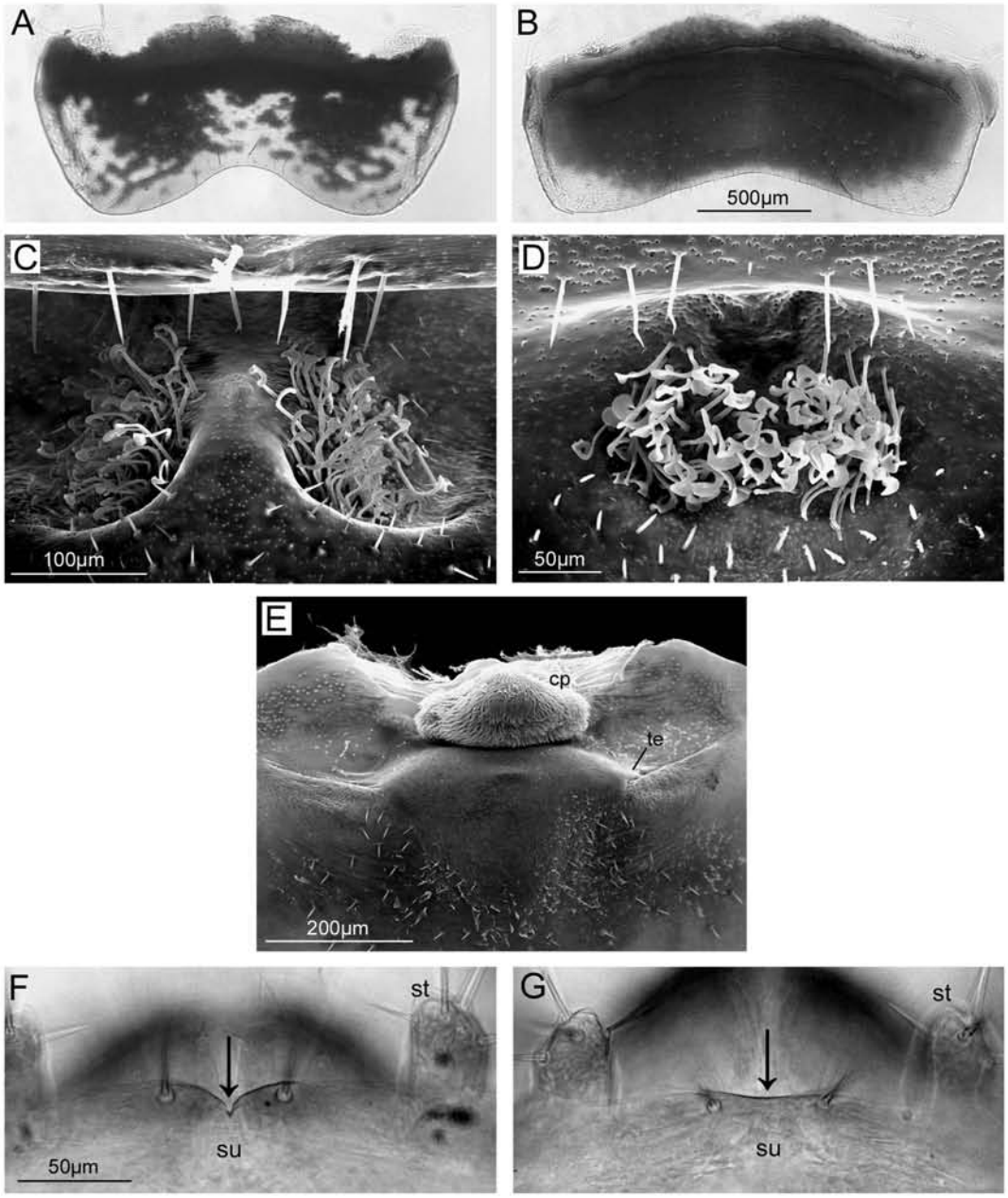

Fig. 3. **A**, **B** Tergite 6 of *P. subaptera*, morph #1 (A) and of a representative of the *nana*-group (B). **C**, **D**, **E** SEM pictures of tergite structures. Bristle fields of tergite 7 of morph 1# (C) and #4 (D) with specialized bristles having broadened tips; hairy conelike process on tergite 8 of morph #4 (E). **F, G** Posterior end of 1. stage nymphal from ventral. Female nymphs have a median excision (arrow) at the posterior border of the subgenital plate (F), which is missing in the male (G). **cp** conelike process**, st** stylus, **su** subgenital plate (sternite 9), **te** transversal edge.
Same scale for (A, B) and for (F, G).
Localities: (A) Sp 510, (B) Sp 387a, (C) Sp 85, (D) Sp 473a, (E) Sp 450, (F, G) Sp 364.

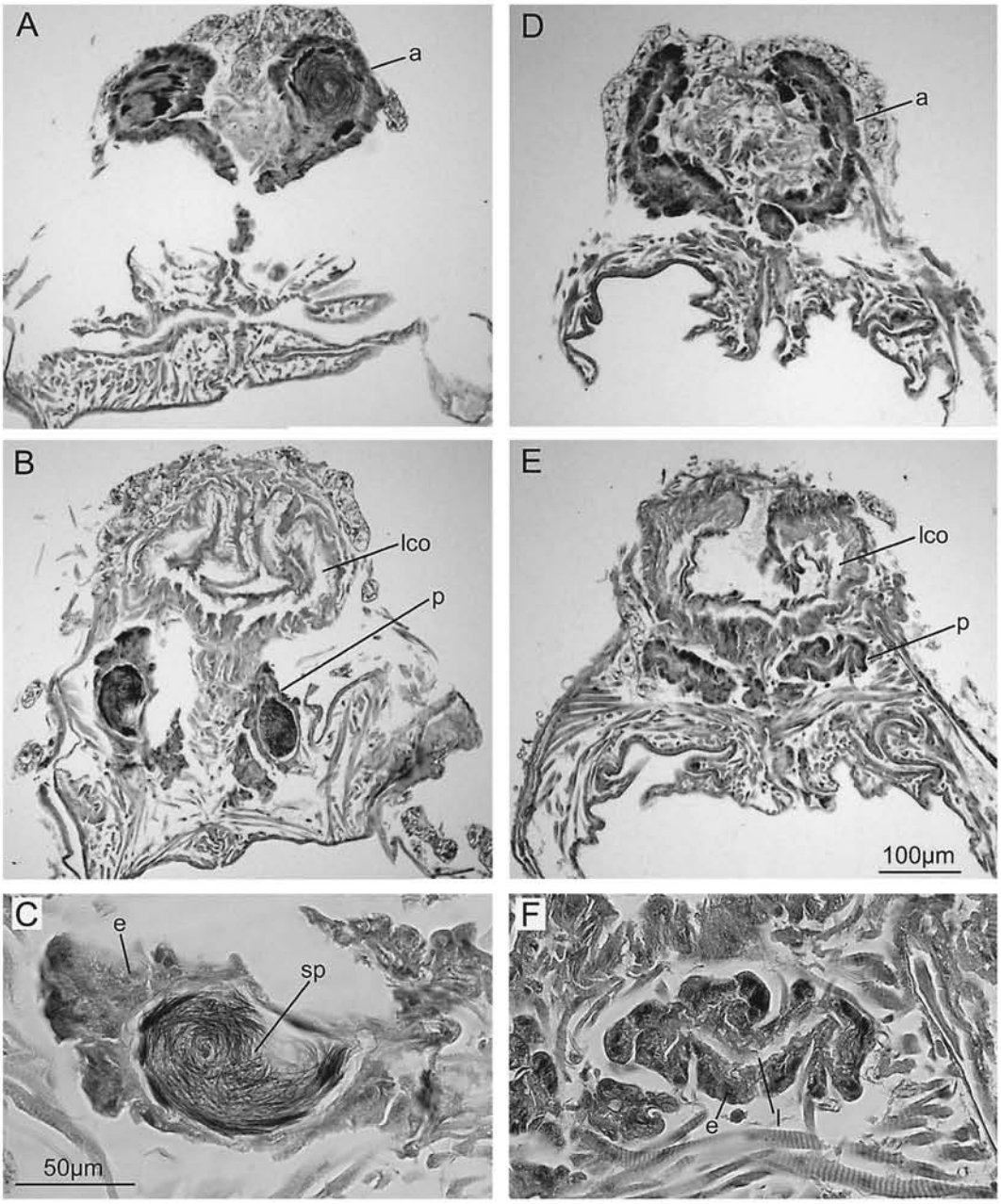

Fig. 4. Histological sections of spermathecae of a bisexual female (**A - C**, containing sperms), and of a parthenogenetic female (**D - F**, without sperms). (A, D) anterior pair of spermathecs, (B, E) posterior pair, (C, F) enlargement of the latter. **a** anterior/**p** posterior pair of spermathecae, **e** epithelium/**l** lumen of the spermathecae, **lco** lumen of common oviduct, **sp** sperms. Same scale for (A, B, D, E) and (C, F). Localities: (A - C) Sp 191, (D - F) Sp 79.

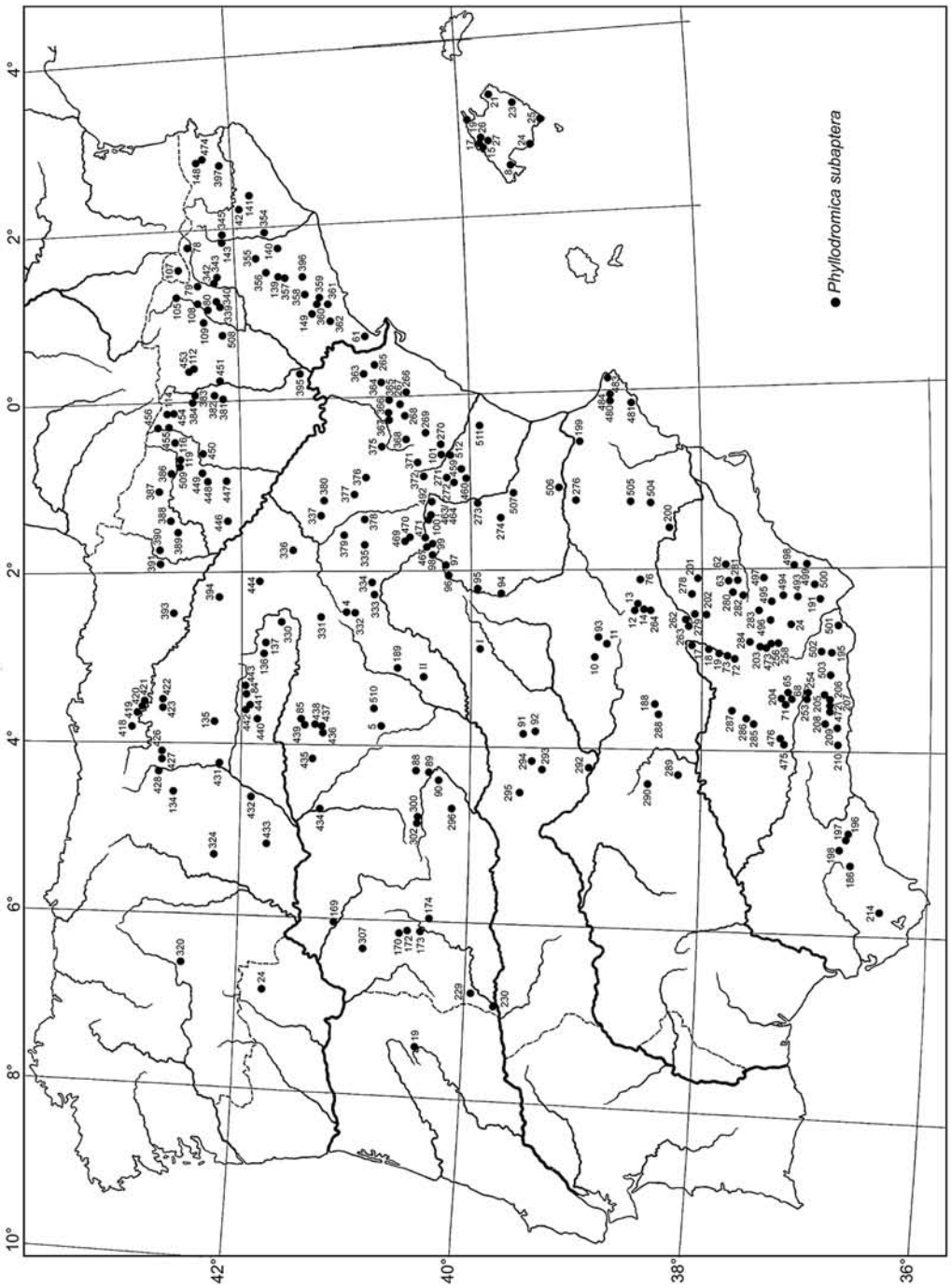

Fig. 5. Map with the localities of *P. subaptera* on the Iberian peninsula. The numbers refer to the list of localities presented under "Appendix 1". Spain, Portugal and the Baleares have separate numbering systems.

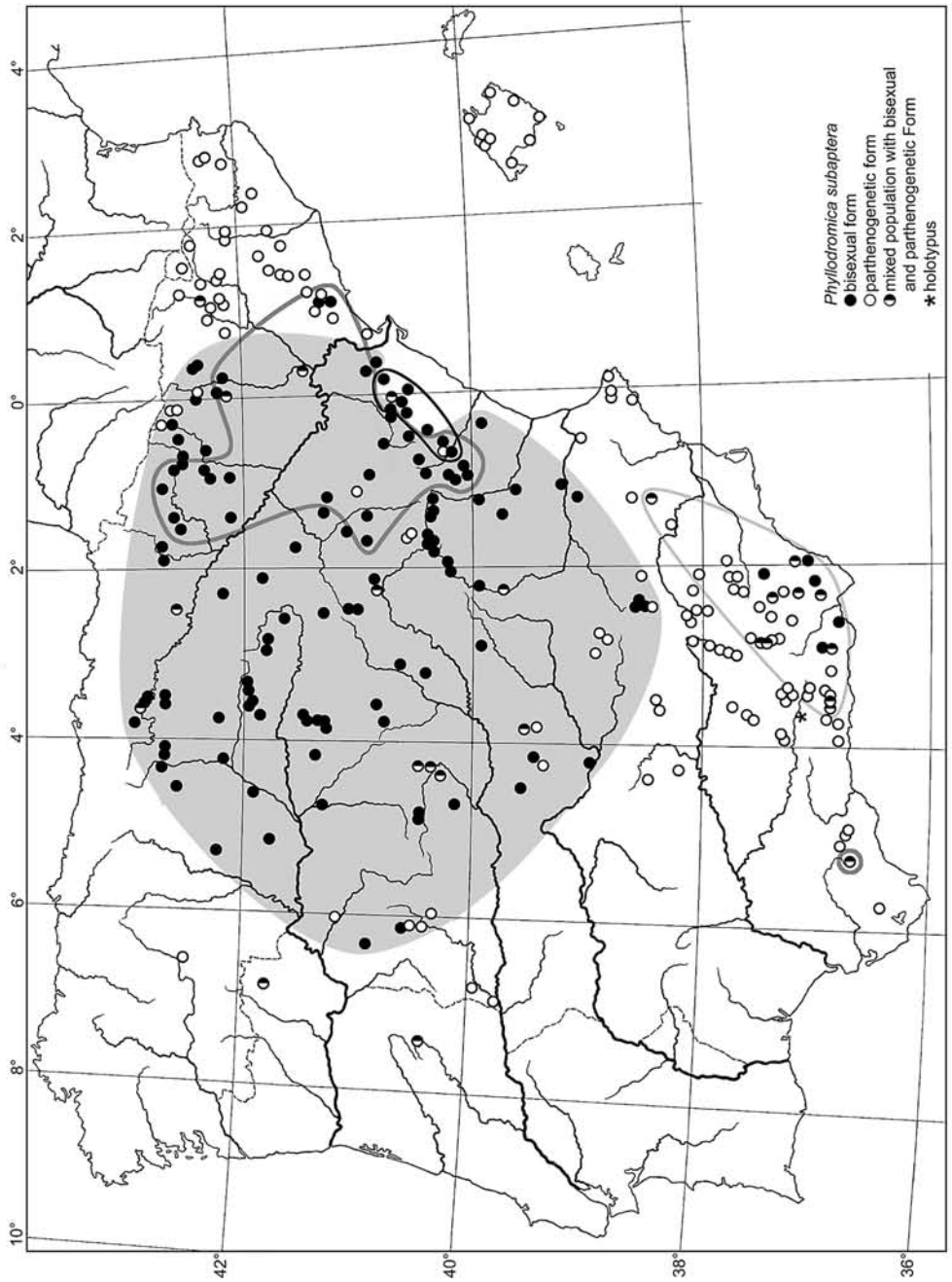

Fig. 6. Distribution of the parthenogenetic and bisexual forms of *P. subaptera* on the Iberian peninsula. Among the bisexuals four different morphs can be distinguished with partly overlapping distributions: morph #1 (gray area), morph #2 (black borderline), morph #3 (thick gray borderline; see also isolated locality in the South), morph #4 (thin gray borderline).The bisexual forms from three localities (Po 19, 24 and Sp 108 in NE Spain) could not be attributed to any of the morphs since no males had been found there, but fertilized females.

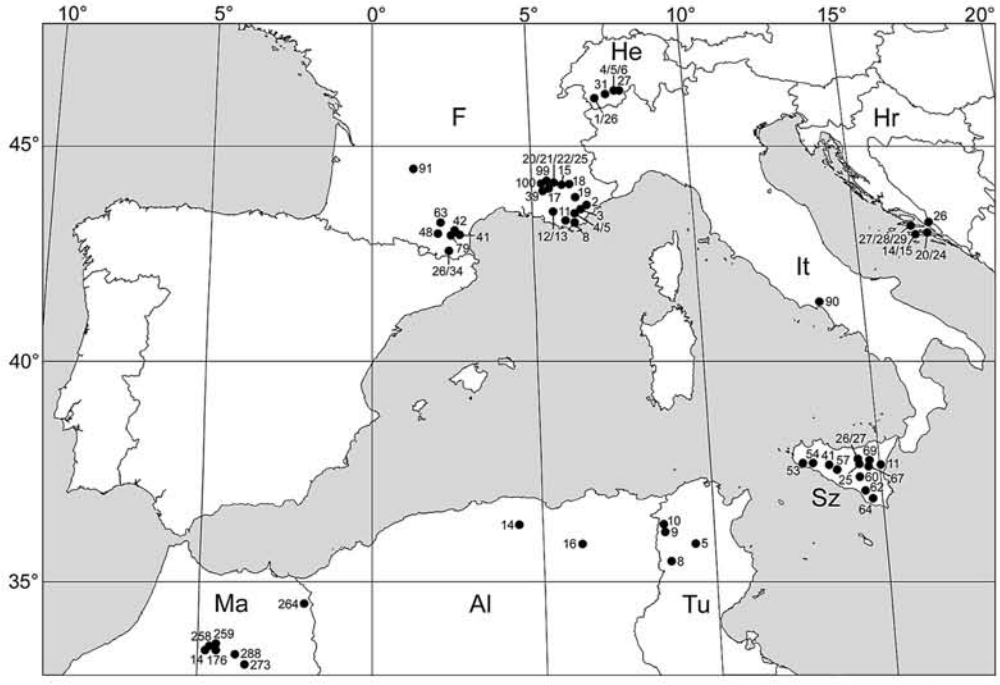

Fig. 7. Distribution of *P. subaptera* outside the Iberian penisula, where only the parthenogenetic form occurs. Material collected by the authors. The species is also reported from Corsica, Bulgaria, and Greece.

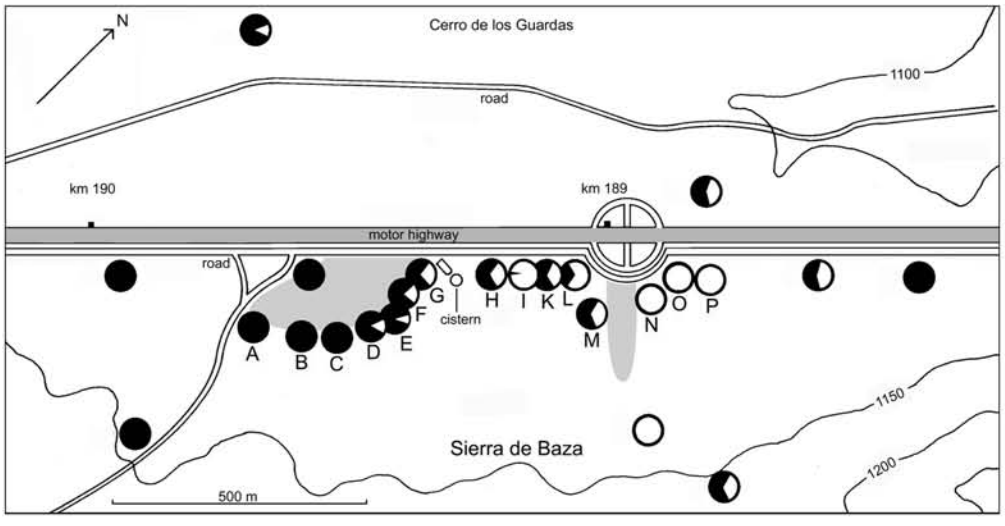

Fig. 8. Detailed map from a locality (Sp 203, southern Spain, near Baza) where bisexual (morph #4) and parthenogenetic forms occur together. Sampling was done at short distances (about 40-50 m) over a transect of about 1 km length along a highway, from sites with pure parthenogenetic (A-C) to sites with pure bisexual populations (N-P). The circles at the sites of sampling show the relative frequences of parthenogenetic (black) and bisexual forms (white).The gray areas below the highway are fields.
Number of animals collected: A 28, B 13, C 24, D 13, E 11, F 22, G 15, H 13, I 18, K 3, L 9, M 14, N 8, O 9, P 8.

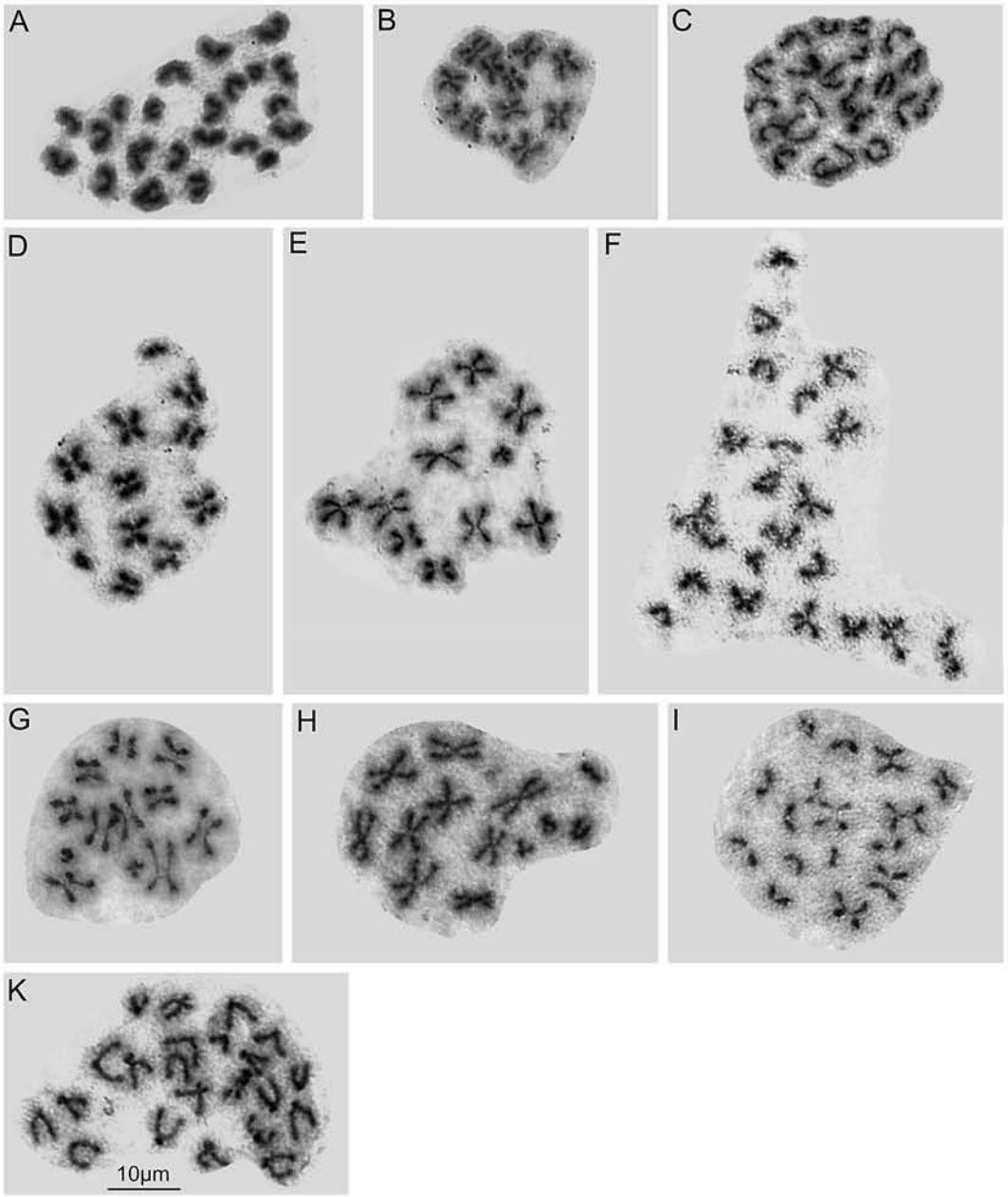

Fig. 9. Metaphase plates, females except in E (male). **A - F** *P. subaptera*, bisexual forms. (A) morph #1: 22 (number of chromosomes); (B) morph #1: 12; (C) morph #2: 22; (D) morph #3, female: 12; (E) morph #3, male: 11; (F) morph #4: 22. **G - I** *P. subaptera*, parthenogenetic forms with 12 (G), 13 (H) and 16 chromosomes (I). **K** *P. globososaccu-lata*: 22.
Same scale in all pictures.
Localities: (A) Sp 492b, (B) Sp 511, (C) Sp 267d, (D, E) Sp 459b, (F) Sp 203a, (G) He 4a, (H) Sp 474, (I) Sp 397a, (K) Sp 370a.

Appendix 1. List of localities

If not stated otherwise the collectors at the localities listed below were B. & H. Bohn.

The localities of each country (and of larger islands) are numbered consecutively. When a locality was visited more than once the later collectings are indicated by a small letter following the number of the locality.

In the above text the localities are represented by their code consisting of an abbreviation of the country or island and the respective number of the locality.

Spain (Sp)

4 Prov. Soria, Pto. Esteras (S Medinaceli), 1000 m, 12.VIII.1983
5a Prov. Madrid, 2 km NE Miraflores de la Sierra (N Madrid), 1200 m, 1.VI.1985
10a Prov. Ciudad Real, Pantano de Peñarroya (E Manzanares), 750 m, 2.VI.1985
11a Prov. Ciudad Real, Campo de Montiel, 10 km NNE Villahermosa, 900 m, 3.VI.1985
12b Prov. Albacete, Sa. de Alcaraz, ca. 2 km NNW Pto. del Barrancazo, 1200 m, 6.IV.1999, leg. T. Knebelsberger
13a Prov. Albacete, Sa. de Alcaraz, ca. 4 km ESE Pto. del Barrancazo, 1200 m, 3.VI.1985 / 13b: 8.IV.1999, leg. T. Knebelsberger
14a Prov. Albacete, Sa. de Alcaraz, Pto. de las Crucetillas, 1450 m, 17.VI.1991
17 Prov. Jaén, Sa. de Cazorla, Emb. del Tranco, near Bujaraiza, 700 m, 19.VIII.1983
18a Prov. Jaén, Sa. de Cazorla, Pto. de las Palomas (NE Cazorla), 1300 m, 18.VI.1984
19a Prov. Jaén, Sa. de Cazorla, 5 km S Puente de las Herrerías, 1300 m, 18.VI.1984
24a Prov. Almería, Sa. de los Filabres, 5 km SW Observatorio del Calar Alto, 2000 m, 12.VI.1984
61 Prov. Tarragona, 3 km WNW Perelló (near Tortosa), 200 m, 10.VI.1984 / 61b: 3.VI.1991 / 61c: 13.III.2001, leg. T. Knebelsberger
62 Prov. Murcia, Sa. del Pericay, near Emb. de Valdeinfierno, 900 m, 10.VI.1984
63 Prov. Almería, S slope of Mt. Gabar (NW Vélez Rubio), 1000 m, 11.VI.1984
65 Prov. Granada, Sierra Nevada, 2 km NE Tocón (NE Granada), 1300 m, 13.VI.1984
68 Prov. Granada, Sierra Nevada, btw. Tocón & Pto. de la Mora (NE Granada), 1400 m, 14.VI.1984
71 Prov. Granada, Sierra Nevada, Pto. de la Mora (NE Granada), 1390 m, 17.VI.1984 / 71a: 9.VI.1989 / 71b: 17.IV.1992
72 Prov. Jaén, Sa. de Pozo, 4 km SSE Tiscar, 1200 m, 17.VI.1984
73 Prov. Jaén, Sa. de Pozo, 2 km S slope of Mt. Cabañas, 1700 m, 18.VI.1984
76 Prov. Albacete, Sa. de Alcaraz, 3 km S Royo Odrea (ca. 20 km NW Elche de la Sierra), 800 m, 20.VI.1984
78 Prov. Lérida, above (N) Bellver de Cerdanya (E Seo de Urgel), 1100 m, 28.V.1985 / 78b: 10.IV.1995
79 Prov. Lérida, 1-4 km W Parroquia de Orto (SW Seo de Urgel), 1100 m, 28.V.1985 / 79c: 20.IV.1999, leg. T. Knebelsberger
80 Prov. Lérida, Desfiladero de Callegats, ca. 7 km NE La Pobla de Segur, 700 m, 28.V.1985
84b Prov. Burgos, 2 km E Santo Domingo de Silos, 1000 m, 13.V.1996
85 Prov. Segovia, Carabias (30 km S Aranda de Duero), 1000 m, 31.V.1985
88 Prov. Madrid, 4 km SSW Robledo de Chavela (NE S. Martín de Valdeiglesias), 900 m, 1.VI.1985
89 Prov. Madrid, San Juan (W S. Martín de Valdeiglesias), 500 m, 1.VI.1985
90 Prov. Madrid/Toledo, 9 km SE San Martín de Valdeiglesias, 700 m, 2.VI.1985
91 Prov. Toledo, Sa. de los Yébenes, Molino (near Los Yébenes), 800 m, 2.VI.1985
92 Prov. Toledo, 2 km N Estacion de Urda (20 km W Consuegra), 700 m, 2.VI.1985
93 Prov. Albacete/Ciudad Real, Campo de Montiel, El Sabinar (ca. 10 km S Ossa d. M.), 900 m, 3.VI.1985
94 Prov. Cuenca, Embalse de Alarcón, 3 km NW Villaverde y Pasaconsol, 820 m, 4.VI.1985 / 94a: 9.IV.1999, leg. T. Knebelsberger
95a Prov. Cuenca, 20 km SW Cuenca (Carret. N 420), 900 m, 9.IV.1999, leg. T. Knebelsberger
96a Prov. Cuenca, Serranía de Cuenca, 2 km NNW La Ciudad Encantada, 1300 m, 3.V.1998 / 96b: 9.IV.1999, leg. T. Knebelsberger
97 Prov. Cuenca, Serranía de Cuenca, Embalse de la Toba, 1100 m, 5.VI.1985 / 97a: 3.V.1998 / 97 b: 9.IV.1999, leg. T. Knebelsberge / 97c: 19.III.2001, leg. T. Knebelsberger
98 Prov. Cuenca, Serranía de Cuenca, 8 km WSW Pto. de El Cubillo, 1400 m, 5.VI.1985 / 98a: 4.V.1998
99a Prov. Teruel, Montes Universales, 5 km W Frías de Albarracín, 1600 m, 2 VI.1997 / 99b: 4.V.1998
100 Prov. Teruel, 10 km SE Albarracín, 1400 m, 6.VI.1985 / 100a: 12.IV.1999, leg. T. Knebelsberger / 100b: 17.III.2001, leg. T. Knebelsberger
101 Prov. Teruel, btw. Mora de Rubielos & Rubielos de Mora (WSW Teruel), 1000 m, 6.VI.1985
105 Prov. Lerida, 3 km NE Llavorsí, (12 km N Sort), 950 m, 19.V.1986 / 105a: 11.IV.1995
107 Andorra, Anyos (near Andorra la Vella), 1300 m, 21.V.1986
108 Prov. Lerida, 3 km N Gerri de la Sal, (12 km S Sort), 700 m, 22.V.1986 / 108a: 20.IV.1999, leg. T. Knebelsberger / 108b: 11.IV.2001, leg. T. Knebelsberger
109 Prov. Lerida, 4 km S Senterada (20 km N Tremp), 800 m, 22.V.1986 / 109a: 21.IV.1999, leg. T. Knebelsberger
112 Prov. Huesca, 5 km SE Foradada (ca. 25 km E Ainsa), 800 m, 22.V.1986
114a Prov. Huesca, btw. Broto & Torla (near P.N. de Ordesa), 1000 m, 17.V.1996
116 Prov. Huesca, 6 km E Jaca, 850 m, 23.V.1986
119 Prov. Huesca, Santa Cruz de la Serós (near Jaca), 900 m, 24.V.1986 /119b: 9.IV.2001, leg. T. Knebelsberger
134 Prov. Palencia, 5 km ENE Villaeles de Valdavia (40 km N Carrión d. los Condes), 900 m, 27.V.1986
135 Prov. Burgos, 3 km E Sarracín (S Burgos), 900 m, 28.V.1986
136 Prov. Soria, 10 km W Abejar (30 km W Soria), 1100 m, 28.V.1986

137 Prov. Soria, 2 km E Abejar (30 km W Soria), 1100 m, 28.V.1986 / 137a: 14.V.1996
139 Prov. Barcelona, La Panadella (25 km W Igualada), 750 m, 29.V.1986
140 Prov. Barcelona, Sa. de Montserrat, ca. 5 km N El Bruc, 650 m, 29.V.1986 / 140a: 14.IV.1995 / 140b: 23.IV.1999, leg. T. Knebelsberger
141 Prov. Barcelona, Sa. de Montseny, Viladrau, 800 m, 30.V.1986
142 Prov. Barcelona, 9 km WNW Vic, 700 m, 30.V.1986
143 Prov. Barcelona, 5 km N Berga, 800 m, 30.V.1986
148 Prov. Gerona, Sant Martí Sesseres (25 km W Figueres), 400 m, 25.IV.1987 / 148a: 24.IV.1999, leg. T. Knebelsberger
149 Prov. Tarragona, Sa. La Llena, 4 km N Prades (near Montblanc), 1000 m, 7.VI.1987
169 Prov. Salamanca, 3 km NNW Ledesma (NW Salamanca), 750 m, 13.VI.1987
170 Prov. Salamanca, Sa. de la Peña de Francia, surr. of El Cabaco, 900-1100 m, 13.VI.1987
172 Prov. Salamanca, Sa. de la Peña de Francia, El Portillo (near La Alberta), 1150 m, 14.VI.1987
173aProv. Salamanca/Cáceres, 9 km NW Vegas de Coria (near Emb. de Gabriel y Galán), 400 m, 25.IV.1992
174aProv. Salamanca, Lagunilla (SW Béjar), 900 m, 25.IV.1992
186 Prov. Málaga, Serranía de Ronda, Cortijo de Montero (10 km SSW Ronda), 1000 m, 27.III.1988 / 186a: 5.IV.1990 / 186b: 23.III.2000, leg. T. Knebelsberger
188aProv. Jaén, Pto. de los Jardines (20 km NE La Carolina), 870 m, 19.IV.1992
189 Prov. Guadalajara, Taracena (near Guadalajara), 750 m, 9.IV.1988
191 Prov. Almería, Sierra Alhamilla, btw. Mts. Colativí & Sa. Alhamilla, ca. 1200 m, 15.V.1989 / 191a: 5./6.IV.2000, leg. T. Knebelsberger
195 Prov. Almería, Sa. de Gádor, NE Castala (near Berja), ca. 1500 m, 3.V.1990
196 Prov. Málaga, Serranía de Ronda, Alozaina (NW Coín), 400 m, 3.V.1990
197 Prov. Málaga, Serranía de Ronda, Pto. de las Abejas (E Ronda), 820 m, 3.V.1990
198 Prov. Málaga, Serranía de Ronda, Pto. del Viento (NE Ronda), 1190 m, 4.V.1990
199 Prov. Valencia, 6 km NW Játiva (ca. 55 km SSW Valencia), 180 m, 4.IV.1991
200 Prov. Murcia, Sa. de la Cabeza del Asno, Casa de Raton (ca. 15 km NW Cieza), 200 m, 4.IV.1991
201 Prov. Murcia, Sa. de Mojantes (SW Caravaca), 1000 m, 4.IV.1991
202 Prov. Granada, Sa. de la Sagra, btw. Puebla de Don Fadrique & Cortijos Nuevos de la Sierra, 1300 m, 5.IV.1991
203 Prov. Granada, Sa. de Baza, ca. 15 km WSW Baza, 1100 m, 5.IV.1991 / 203a: 2.V.1998 / 203b: 2.-6.IV.1999, leg. H. Bohn & T. Knebelsberger / 203c: 26.III.-1.IV.2000, leg. T. Knebelsberger / 203d: 20.-23.III.2001, leg. T. Knebelsberger
204 Prov. Granada, Ventas del Molinillo (btw. Guadix & Granada), 1300 m, 5.IV.1991
205 Prov. Granada, Sierra Nevada, above (NE) Soport-újar, 1500 m, 6.IV.1991 / 205a: 2.V.1998
206 Prov. Granada, Sierra Nevada, Bayacas (N Orgiva), 700 m, 6.IV.1991
207 Prov. Granada, Sierra Nevada, Lanjarón, 700 m, 6.IV.1991 / 207a: 2.V.1998
208 Prov. Granada, Sa. de Albuñuelas, Mt. Herrero, 1400 m, 6.IV.1991
209 Prov. Granada, Sa. del Chaparral, Venta de Cabramontés (NW Otívar), 1000 m, 7.IV.1991
210 Prov. Málaga, Sa. de Almijara, btw. Cómpeta & Cortijo del Daire, 800 m, 7.IV.1991
214 Prov. Cádiz, 4 km NE Alcalá de los Gazules (NW Algeciras), 100 m, 9.IV.1991
229 Prov. Cáceres, Sa. de la Garrapata (W Coria), 12 km NE Zarza la Mayor, 400 m, 24.IV.1991
230 Prov. Cáceres, Alcántara, 300 m, 24.IV.1991
253 Prov. Granada, Sierra Nevada, Loma Cunas de los Cuartos (ESE Guejar - Sierra), 1800 m, 14.VI.1991
254 Prov. Granada, Sierra Nevada, Barranco La Solana (ENE Guejar - Sierra), 1800-1900 m, 14./15.VI. 1991
256 Prov. Granada, Sa. de Baza, N slope of Mt. Sta. Bárbara, ca. 1800 m, 15.VI.1991
258 Prov. Granada, Sa. de Baza, Rio Gallego, 1700 m, 15.VI.1991
262 Prov. Jaén, Sa. de Segura: Sa. de Almorchón, 4 km WNW Santiago de la Espada, 1700 m, 16.VI.1991
263 Prov. Jaén, Sa. de Segura: Sa. de Almorchón, 4 km ESE Pontones, 1600 m, 16.VI.1991
264 Prov. Albacete, Sa. de Alcaraz, Pto. del Arenal, 1150 m, 17.VI.1991
265 Prov. Tarragona, surr. of Los Puertos (ca. 20 km W Tortosa), 750-1400 m, 11.IV.1992 / 265a: 14.IV.1999, leg. T. Knebelsberger
266 Prov. Castellón, Pto. de Querol (50 km W Vinarós), 1030 m, 11.IV.1992 / 266a: 13.IV.1999, leg. T. Knebelsberger
267 Prov. Castellón, 3 km SW Morella, ca. 1000 m, 12.IV.1992 / 267a: 13.IV.1999, leg. T. Knebelsberger / 267b: 13./14.IV.2000, leg. T. Knebelsberger / 267c:16.III.2001, leg. T. Knebelsberger / 267d: 4.IV.2002, leg. T. Knebelsberger
268 Prov. Castellón, btw. Cinctorres & Portell de Morella (SW Morella), 1200 m, 12.IV.1992 / 268a:13.IV.1999, leg. T. Knebelsberger
269aProv. Teruel, Sa. del Rayo, btw. Cantavieja & Mosqueruela, 1500 m, 17.IV.1995
270 Prov. Teruel, Sa. de Nogueruelas, 16 km NNE Rubielos de Mora, 1600 m, 12.IV.1992 / 270a: 12.IV.1999, leg. T. Knebelsberger / 270b: 12.IV.2000, leg. T. Knebelsberger / 270c: 4.IV.2001, leg. T. Knebelsberger
271 Prov. Teruel, 4 km SW La Puebla de Valverde (23 km SE Teruel), 1200 m, 12.IV.1992
272 Prov. Teruel, Sa. de Javalambre, btw. Collado de El Gavilán & Mt. Javalambre, 1600 m, 13.IV.1992
273 Prov. Cuenca, 3 km N Sta. Cruz de Moya (60 km S Teruel), 750 m, 13.IV.1992
274 Prov. Cuenca, Sa. de Mira, Mt. Rebollo, 1250 m, 13.IV.1992
276 Prov. Valencía, Mt. Palomeras (W Ayora), 1000-1200 m, 14. IV.1992
278 Prov. Murcia, Sa. de Taibilla, Mt. Revolcadores, 1450-1550 m, 15.IV.1992
279 Prov. Granada, Sa. de la Hoya del Espina, Pto. del Pinar, 1500-1600 m, 15.IV.1992
280 Prov. Almería, btw. Casablanca & María (NW Vélez Rubio), 1200 m, 15.IV.1992
281 Prov. Almería, near Vélez Blanco (NW Vélez

Rubio), 1000 m, 16.IV.1992
282 Prov. Almería, S. de Maria, ca. 4 km N Chirivel (W Vélez Rubio), 1400 m, 16.IV.1992
283 Prov. Granada/Almería, Sa. de Lucar, btw. Oria & Cúllar Baza, 1200 m, 16.IV.1992
284 Prov. Granada, Mt. Jabalcón (N Baza), 1000-1400 m, 16./17.IV.1992
285 Prov. Jaén, Sa.de Alta Coloma, Mt. Cerro Quemado, 1150-1450 m, 17.IV.1992
286 Prov. Jaén, Sa.de Alta Coloma, Pto. de las Palomas, 1350 m, 18.IV.1992
287 Prov. Jaén, Sa. Almadén, btw. Mancha Real & Mt. El Almadén, 1300-1550 m, 18.IV.1992
288 Prov. Jaén, near Miranda del Rey (N La Carolina), 800 m, 19.IV.1992
289 Prov. Córdoba, 2 km S Venta del Charco (ca. 30 km N Villa del Río), 650 m, 19.IV.1992
290 Prov. Ciudad Real, Sa. de la Garganta, 3 km S Pto. Valderrepisa (SW Puertollano), 850 m, 20.IV.1992
292 Prov. Ciudad Real, btw. Los Pozuelos de Calatrava & Piedrabuena (W Ciudad Real), 700 m, 21.IV.1992 / 292a: 27.III.2001, leg. T. Knebelsberger
293 Prov. Ciudad Real, Mtes. del Toledo, btw. El Bullaque & Emb. Torre de Abraham, 600 m, 21.IV.1992
294 Prov. Ciudad Real, Mtes. del Toledo, Sa. de los Torneros, Mt. Becerra, 1300 m, 21.IV.1992
295 Prov. Toledo, Mtes. de Toledo, Mt. Corral de Cantos (10 km S Navahermosa), 1000 m, 22.IV.1992
296 Prov. Toledo, Sa. de San Vicente (NE Talavera), 2 km N El Real de San Vicente, 900 m, 22.IV.1992
300 Prov. Ávila, Sa. de la Paramera, btw. Burgohondo & Navalmoral, 950 m, 23.IV.1992
302 Prov. Ávila, Sa. de la Paramera, btw. Navarredondilla & Navalacruz, 1100 m, 24.IV.1992
307 Prov. Salamanca, btw. El Cubo de Don Sancho & Traguntía (W Salamanca), 800 m, 26.IV.1992
320 Prov. León, btw. Molinaseca & Riego de Ambros (E Ponferrada), 750-850 m, 4.V.1992
324 Prov. León, btw. Mantanza & Mayorga (SE Valencía de Don Juán), 750 m, 4.V.1992
330 Prov. Soria, near Lubia (15 km S Soria), 1050-1100 m, 6.V.1992
331 Prov. Soria, 4 km S Adradas (23 km N Medinaceli), 1100 m, 6.V.1992
332 Prov. Guadalajara, btw. Alcolea del Pinar & Luzaga (S Medinaceli), 1200 m, 6.V.1992
333 Prov. Guadalajara, btw. Huertahernando & Olmeda de Cobeta (ca 30 km W Molina d. A.), 1200 m, 7.V.1992
334 Prov. Guadalajara, 6 km E Cobeta (ca. 20 km W Molina de Aragon), 1225 m, 7.V.1992
335 Prov. Guadalajara, btw. Embid & Eta. de Sto. Domingo (SW Daroca), 1125 m, 7.V.1992
336 Prov. Zaragoza, Sa. de la Virgen (NW Calatayua), S Santuario, 1050-1250 m, 8.V.1992
337 Prov. Zaragoza, Sa. de la Algairén (N Daroca), btw. Pto. de Codos & Mt. Valdemadera, 1050-1270 m, 8.V.1992
339 Prov. Lérida, 4 km NE Isona (19 km E Tremp), ca. 800 m, 12.IV.1995
340 Prov. Lérida, Collado de Faidella, 1250 m, 12.IV.1995
342 Prov. Lérida, El Palau (btw. Organyá & Alinyá, S Seo de Urgel), 600 m, 12.IV.1995 / 342a: 20.IV.1999, leg. T. Knebelsberger
343 Prov. Lérida, above Cambrils (S Seo de Urgel), ca. 1100 m, 12.IV.1995 / 343a: 20.IV.1999, leg. T. Knebelsberger
345 Prov. Barcelona, Emb. de la Baélls, btw. Berga & Vilada, ca. 600 m, 12.IV.1995
354 Prov. Barcelona, 3 km SE Navarcles (8 km NE Manresa), ca. 350 m, 14.IV.1995 / 354a: 17.IV.1999, leg. T. Knebelsberger
355 Prov. Barcelona, Sa. de Castelltallat (NW Manresa), btw. San Mateu d. B. & La Molsosa, 900 m, 15.IV.1995 / 355a: 18.IV.1999, leg. T.Knebelsberger
356 Prov. Barcelona, 2 km E Calaf (30 km W Manresa), ca. 700 m, 15.IV.1995
357 Prov. Lérida, 2 km S Belmunt (ca. 30 km W Igualada), ca. 700 m, 15.IV.1995
358 Prov. Tarragona, ca. 3 km NE L'Illa (btw. Valls & Montblanc), 600-750 m, 15.IV.1995
359 Prov. Tarragona, btw. Montreal & Alcover (N Reus), ca. 700 m, 15.IV.1995
360 Prov. Tarragona, 1 km NE Montreal (N Reus), ca. 800 m, 16.IV.1995 / 360a: 5.V.1998
361 Prov. Tarragona, btw. L'Albiol & La Mussara (N Reus), ca. 1000 m, 16.IV.1995 / 361a: 5.V.1998
362 Prov. Tarragona, 1 km SW Pto. de la Teixeta (22 km W Reus), ca. 600 m, 16.IV.1995
363 Prov. Tarragona, ca. 4 km NE Arnés (NW Tortosa), ca. 500 m, 16.IV.1995
364 Prov. Teruel, Ptos. de Beseit, SE Emb. de Peña, ca. 700 m, 16./17.IV.1995
365 Prov. Castellón, 2 km E Pto. de Torre Miró (11 km N Morella), 1200 m, 17.IV.1995 / 365a: 14.IV.1999, leg. T. Knebelsberger
366 Prov. Teruel, btw. Villores & Luco de Bordón (NW Morella), ca. 900 m, 17.IV.1995 / 366a: 13./14.IV. 2000, leg. T. Knebelsberger
367 Prov. Teruel, btw. Luco de Bordón & Bordón (NW Morella), ca. 800 m, 17.IV.1995
368 Prov. Teruel, Pto. de Cuarto Pelado (89 km NE Teruel), 1600 m, 18.IV.1995
371 Prov. Teruel, 2 km NE Monteagudo del Castillo (ca. 40 km NE Teruel), ca. 1500 m, 18.IV.1995
372 Prov. Teruel, Pto. de Cabigordo (27 km NE Teruel), 1550 m, 18.IV.1995
375 Prov. Teruel, Pto. de Majalinos (90 km NE Teruel), 1450 m, 19.IV.1995
376 Prov. Teruel, 2 km S Seguro de los Baños (52 km SE Daroca), ca. 1100 m, 19.IV.1995
377 Prov. Teruel, Pto. de Fonfría (ca. 30 km SE Daroca), 1470 m, 19.IV.1995
378aProv. Teruel, btw. Calamocha & Tornos (S Daroca), 1100 m, 5.IV.2001, leg. T. Knebelsberger
379 Prov. Zaragoza, Sa. de Sta. Cruz (W Daroca), Pto. de Used, 1200 m, 20.IV.1995
380 Prov. Zaragoza, 2 km E Pto. de Paniza (10 km S Cariñena), 900 m, 20.IV.1995 / 380a: 5.IV.2001, leg. T. Knebelsberger
381 Prov. Huesca, 2 km NE Adahuesca (20 km NW Barbastro), ca. 600 m, 20.IV.1995 / 381a: 5./6.IV.2001, leg. T. Knebelsberger
382 Prov. Huesca, Coll. de San Caprasio (ca. 30 km NW Barbastro), ca. 800 m, 21.IV.1995 / 382a: 5.IV.2001, leg. T. Knebelsberger
383 Prov. Huesca, 2.5 km S Latorrecilla (SW Ainsa),

ca. 600 m, 21.IV.1995
384 Prov. Huesca, near Campodarte (btw. Pto. de Sarrablo & Bollaño, W Ainsa), 1100 m, 21.IV.1995
386 Prov. Huesca, 3 km ESE Berdím (40 km W Jaca), ca. 600 m, 22.IV.1995 / 386a: 6.IV.2001, leg. T. Knebelsberger
387 Prov. Navarra, Pto. Las Coronas (N Mon. de Leyre), 950 m, 22.IV.1995 / 387a: 7.IV.2001, leg. T. Knebelsberger
388 Prov. Navarra, near Pto. Olaz (15 km NW Sanguesa), 700 m, 22.IV.1995 / 388a: 7./8.IV.2001, leg. T. Knebelsberger
389 Prov. Navarra, Alto Lerga (15 km NE Olite), 750 m, 23.IV.1995 / 389a: 7./8.IV.2001, leg. T. Knebelsberger
390 Prov. Navarra, btw. Pto. del Perdon & Mt. Perdon, 700-1000 m, 23.IV.1995
391 Prov. Navarra, Pto. de Guirguillano (10 km NW Puenta la Reina), 725 m, 23.IV.1995
393 Prov. Navarra, near Lapoblación (ca. 12 km N Logrаño), 900 m, 23.IV.1995
394 Prov. La Rioja, Caserlo las Bargas (ca. 20 km SW Arnedo), 750 m, 24.IV.1995
395 Prov. Huesca, Vall de Carreras, 3 km SSW Torrente de Cinca (30 km SW Lérida), ca. 200 m, 25.IV.1995
396 Prov. Tarragona, Mt. Montagut (NE Mon. Santes Creus), Coll de la Torreta, 700 m, 25.IV.1995
397 Prov. Gerona, near Pujarnol (6 km SW Banyoles), ca. 400 m, 26.IV.1995 / 397a: 5.V.1998 / 397b: 14.III.2001, leg. T. Knebelsberger
418 Prov. Burgos, 2 km SE Sancillo (ca. 75 km S Santander), 940 m, 9.V.1996
419 Prov. Burgos, btw. Valdenoceda & Incinillas (ca. 70 km N Burgos), 600 m, 9.V.1996
420 Prov. Burgos, Igl. San Pedro de Tejada (near Quecedo, ca. 70 km N Burgos), 600 m, 9.V.1996
421 Prov. Burgos, near Panizares (10 km NW Oña), 620 m, 9.V.1996
422 Prov. Burgos, 1 km W Cornudilla (18 km NW Briviesca), 670 m, 9.V.1996
423 Prov. Burgos, 3.5 km W Poza de la Sal (23 km NW Briviesca), 950 m, 9.V.1996
426 Prov. Burgos, btw. La Riba d.V. & Humada (ca. 20 km SE Aguilar d. C.), 1000 m, 10.V.1996
427 Prov. Burgos, 2 km W Rebolledo de Traspeña (SE Aguilar d. C.), 1000 m, 10.V.1996
428 Prov. Palencia, 12 km NW Villela (15 km S Aguilar d. C.), 950 m, 10.V.1996
431 Prov. Palencia, near San Cebrián de Buena Madre (20 km SE Fromista), 850 m, 11.V.1996
432 Prov. Palencia, btw. Dueñas & Sta. Cecilia del Acor (SW Palencia), 850 m, 11.V.1996
433 Prov. Valladolid, 6 km NE Urueña (ca. 44 km NNW Valladolid), 850 m, 12.V.1996
434 Prov. Valladolid, 4 km W Olmedo (43 km S Valladolid), 775 m, 12.V.1996
435 Prov. Segovía, 2 km NW Hontalbilla (17 km SE Cuéllar), 900 m, 12.V.1996
436 Prov. Segovía, btw. Sebúlcor & Villar de Sobrepeña (near Sepúlveda), 900 m, 12.V.1996
437 Prov. Segovía, 1 km W Sepúlveda, 1000 m, 12.V.1996
438 Prov. Segovía, btw. Sta. Cruz & Urueñas (N Sepúlveda), 1050 m, 13.V.1996
439 Prov. Segovía, btw. Navares d. l. C. & Aldeanueva d.l.S. (S Aranda d.D.), 1150 m, 13.V.1996
440 Prov. Burgos, 3 km NE Oquillas (ca. 20 km N Aranda d.D.), 950 m, 13.V.1996
441 Prov. Burgos, 3.5 km S Tejada (W Sto. Domingo d. S.), 1075 m, 13.V.1996
442 Prov. Burgos, Pico de la Sierra (W Sto. Domingo d.S.), 1300 m, 13.V.1996
443 Prov. Burgos, btw. Carazo & Hacinas (Esto. Domingo d. S.), 1050 m, 14.V.1996
444 Prov. Soria, 2 km N Pto. del Madero (btw. Soria & Tarazona), 1220 m, 14.V.1996
446 Prov. Narvarra/Zaragoza, Portillo de Sta. Margarita (30 km NE Tudela), 450 m, 15.V.1996 / 446a: 9./10.IV.2001, leg. T. Knebelsberger
447 Prov. Zaragoza, Santuario de Na. Sa. de Monlora (ca. 20 km E Ejea d. l. C.), 600 m, 15.V.1996 / 447a: 9.IV.2001, leg. T. Knebelsberger
448 Prov. Zaragoza, 4 km N El Frago (NE Ejea d. l. C.), ca. 600 m, 15.V.1996 / 448a: 10.IV.2001, leg. T. Knebelsberger
449 Prov. Zaragoza/Huesca, Pto. Sierra Mayor (ca. 20 km NW Ayerbe), 900 m, 15.V.1996 / 449a: 10.IV.2001, leg. T. Knebelsberger
450 Prov. Huesca, above Castillo de Loarre (NW Huesca), 1150-1400 m, 16.V.1996
451 Prov. Huesca, near La Puebla de Castro (ca. 20 km NE Barbastro), 670 m, 16.V.1996
453 Prov. Huesca, Coll. de Foradada (ca. 24 km E Ainsa), 1020 m, 16.V.1996
454 Prov. Huesca, btw. Sarvisé & Breto (S Valle de Ordesa), 950 m, 16.V.1996
455 Prov. Huesca, near Biescas (15 km N Sabiñánigo), 980 m, 17.V.1996
456 Prov. Huesca, near Escarilla (17 km SE Pto. del Portalet), 1120 m, 17.V.1996
459 Prov. Teruel, Sa. de Javalambre, 3 km NNE Manzanera, 1150 m, 1.VI.1997 / 459a:4.IV.2001, leg. T. Knebelsberger / 459b: 14.IV.2002, leg. T. Knebelsberger
460 Prov. Teruel, Sa. de Javalambre, near Torrijas, 1400-1500 m, 1.VI.1997
463 Prov. Teruel, Montes Universales, Mt. Carbonera (SE Albarracín), 1500 m, 1.VI.1997
464 Prov. Teruel, Montes Universales, below (S) Mt. Carbonera, (SE Albarracín), 1300 m, 1.VI.1997 / 464a:12.IV.1999, leg. T. Knebelsberger / 464b: 19.III.2001, leg. T. Knebelsberger
467 Prov. Teruel, Montes Universales, El Portillo (SW Guadalaviar), 1700 m, 2.VI.1997 / 467a: 4.V.1998
469 Prov. Teruel, Montes Universales, 2 km E Orihuela del Tremedal, 1400 m, 2.VI.1997
470 Prov. Teruel, Montes Universales, Pto. de Bronchales (NE Bronchales), 1500 m, 2.VI.1997
471a Prov. Teruel, Montes Universales, 2 km SW Tramacastilla, 1500 m, 11.IV.1999, leg. T. Knebelsberger
472 Prov. Granada, Sierra Nevada, 3 km W Lanjarón, 600-650 m, 1.V.1998 / 472a: 3.IV.1999, leg. H. Bohn & T. Knebelsberger / 472b: 25.III.2001, leg. T. Knebelsberger
473 Prov. Granada, Sa. de Baza, 3km SE Autovia exit Sa. de Baza, 3.V.1998 / 473a: 2.IV.1999, leg. H. Bohn & T. Knebelsberger
474 Prov. Gerona, 3 km NW Cabanelles (12 km WSW Figueras), 5.V.1998 / 474a : 15.IV.2000, leg. T. Knebelsberger

475 Prov. Granada, Mte. Parapanda, (near Montefrío), 1550 m, 1.IV.1999, leg. H.Bohn & T. Knebelsberger
476 Prov. Granada, Mte. Parapanda (near Montefrío), N slope, 1300 m, 1.IV.1999, leg. H. Bohn & T. Knebelsberger
480 Prov. Alicante, Benimaurell (ca. 30 km WSW Denia), 24.IV.2000, leg. T.M.Saks
481 Prov. Alicante, Mt. Campana (NW Benidorm), 26.IV.2000, leg. T.M.Saks
483 Prov. Alicante, Denia - Cap de Sant Antoni, 1.V.2000, leg. T.M.Saks
484 Prov. Alicante, btw. Orba & Alcalalí (NW Benissa), 2.V.2000, leg. T.M.Saks
492 Prov. Teruel, 1,5 km SW San Blas (ca. 6 km W Teruel), 1050 m, 12.IV.1999, leg. T. Knebelsberger / 492a: 18.III.2001, leg. T. Knebelsberger / 492b: 14.IV.2002, leg. T. Knebelsberger
493 Prov. Almería, Sra. de los Filabres, ca. 6 km E Senés, ca. 1000 m, 6.IV.2000, leg. T. Knebelsberger
494 Prov. Almería, Sra. de los Filabres, ca. 10 km S Oluola del Río, 1000 m, 6.IV.2000, leg. T. Knebelsberger
495 Prov. Almería, Sra. de Lúcar, 2,5 km ESE Urracal, 875m, 7.IV.2000, leg. T. Knebelsberger
496 Prov. Almería, Sra. de Lúcar, 2,5 km NW Hígueral, 925 m, 7.IV.2000, leg. T. Knebelsberger
497 Prov. Almería, Sra. de las Estancias, 1 km N Taberno, 800 m, 7.IV.2000, leg. T. Knebelsberger
498 Prov. Almería, Sra. de Bédar, 2 km NW Bédar, ca. 500 m, 7.IV.2000, leg. T. Knebelsberger
499 Prov. Almería, Sra. Cabrera, 4 km NE Gafarillos, 550 m, 7.IV.2000, leg. T. Knebelsberger
500 Prov. Almería, Sra. de Alhamilla, 9 km NE Nijar, 550 m, 23.III.2001, leg. T. Knebelsberger
501 Prov. Almería, Sra. de Gador, ca. 6 km E Félix, 550 m, 8.IV.2000, leg. T. Knebelsberger
502 Prov. Almería, Sra. de Gador, ca. 4 km S Laujar de Andarax, 1050 m, 8.IV.2000, leg. T. Knebelsberger
503 Prov. Granada, Sra. de Contraviesa, ca. 6 km N Murtas, 1050 m, 8.IV.2000, leg. T. Knebelsberger
504 Prov. Murcia, Sra. de Sopalmo, 11 km SE Jumilla, 650 m, 10.IV.2000, leg. T. Knebelsberger / 504a: 1.IV.2001, leg. T. Knebelsberger
505 Prov. Murcia, 10 km WSW Yecla (near Puerto de Jumilla), 950 m 10.IV.2000, leg. T. Knebelsberger
506 Prov. Valencía, Sra. de Martes, ca. 4 km N Confrentes, 600 m, 11.IV.2000, leg. T. Knebelsberger
507 Prov. Valencía, Sra. de Utiel, btw. Villar de Tejas & Casas de Medina, 1200 m, 11.IV.2000, leg. T. Knebelsberger / 507a: 17.III.2001, leg. T. Knebelsberger
508 Prov. Lerida, ca. 18 km E Tremp, 1000 m, 11.IV.2001, leg. T. Knebelsberger
509 Prov. Huesca, 3 km N Alastuey (ca. 26 km E Jaca), 650 m, 9.IV.2001, leg. T. Knebelsberger
510 Prov. Madrid, 4 km NE Torrelaguna (ca. 70 km N Madrid), 1050 m, 30.III.2001, leg. T. Knebelsberger
511 Prov. Castellón, Sra. de Espadán, ca. 2 km SW Ahín (21 km ENE Segorbe), 780m, 10.IV.2002, leg. T. Knebelsberger
512 Prov. Teruel, 8 km - 13 km SW Rubielos de Mora, 890-990 m, 12.IV.2000, leg. T. Knebelsberger / 512a: 4.IV.2001, leg. T. Knebelsberger

Spain, Baleares (Ba)

8 Mallorca, Coll d'es Vent, E side (6 km W Palma), 150 m, 17.IV.1987
15 Mallorca, above Fornalutx (near Soller), 400 m, 19.IV.1987
17 Mallorca, btw. Casas de la Calobra & Cala Turent (N Puig Mayor), 200 m, 19.IV.1987
19 Mallorca, Pto. de Pollença (near Pollença), 30 m, 20.IV.1987
21 Mallorca, Mt. Moleta de Ley (7 km N Arta), 200 m, 21.IV.1987
23 Mallorca, Mt. Llodra (7 km SE Manacor), 200 m, 21.IV.1987
24 Mallorca, Punta Llobera (near Cabo Blanco), 100 m, 22.IV.1987
25 Mallorca, Cabo Salinas, 10 m, 22.IV.1987
26 Mallorca, Caimari (N Inca), 200 m, 23.IV.1987
27 Mallorca, btw. Lloseta & Alaró (W Inca), 300 m, 23.IV.1987

Portugal (Po)

19 Distr. de Guarda, Serra da Estrela, 8 km E Manteigas, 600 m, 22.IV.1991
24 Distr. de Bragança, Serra de Nogueira, N slope of Mt. Nogueira, 1000-1300 m, 27./28.IV.1992

France (F)

2 Dept. Var, Callian (ca. 22 km SW Grasse), 400 m, 1.VI.1982
3 Dept. Var, Bois de Palayson, (5 km E Le Muy), 80 m, 1.VI.1982
4 Dept. Var, Val de l'Argent, near Le Thoronet (ca.10 km N Le Luc), 100 m, 2.VI.1982
5 Dept. Var, Forêt de la Darboussière (ca. 15 km NW Le Luc), 250 m, 2.VI.1982
8 Dept. Var, 6 km WSW La Môle (18 km SW St.Tropez), 70 m, 4.VI.1982
11 Dept. Var, La Guiranne (4 km NNW Solliès-Pont), 120 m, 6.VI. 1982
12 Dept. Bouches-du-Rhône, Montagne Ste.Victoire, 2 km W Puyloubier, 400 m, 6.VI.1982
13 Dept. Var/Bouches-du-Rhône, Montagne Ste.Victoire, 6 km NE Puyloubier, 450 m, 6.VI.1982 / 13a: 28.V.1998
15 Dept. Basses-Alpes, above Les Mées (25 km WSW Digne), 750 m, 7.VI.1982 / 15a: 29.V.1998
17 Dept. Basses-Alpes, Carniol (W Forcalquier), 600 m, 8.VI.1982
18 Dept. Basses-Alpes, near Châteauredon (12 km S Digne), 600 m, 10.VI.1982
19 Dept. Basses-Alpes, Grand Canyon du Verdon, La Maline, 550-700 m, 10.VI.1982
20 Dept. Basses-Alpes, Montagne de Lure, btw. Cruis & Mallefougasse-Augès, 720 m, 11.VI.1982
21 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 840 m, 11.VI.1982
22 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 1640 m, 11.VI.1982
25 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 1000 m, 11.VI.1982
26a Dept. Pyrénées-Orientales, near Fillols (S Prades), 650 m, 26.V.1985
34 Dept. Pyrénées-Orientales, near Castell (2.5 km S Vernet-les-Bains), 800 m, 26.V.1985

39 Dept. Vaucluse, near Apt, ca. 300 m, VI.1992, leg. K. Klass
41 Dept. Pyrénées-Orientales, near Vingrau (ca. 20 km NW Perpignan), 250 m, 8.IV.1995
42 Dept. Aude, Montagne de Tauch, E slope, 400-600 m, 8.IV.1995
48 Dept. Aude, near Quillan, 350 m, 9.IV.1995
63 Dept. Aude, 2 km NE Malviès (ca. 25 km SW Carcassonne), 200 m, 29.IV.1995
79 Dept. Aude, near Chateau de Quéribus (ca. 30 km NW Perpignan), 600 m, 20.V.1996
91 Dept. Cahors, btw. Pern & St.Paul-de-Loubressac (10 km NE Castelnau-Montratier), 270 m, 3.VIII.1996
99 Depts. Drome - Basses-Alpes, Col de Pigiere (3 km SE Séderon), 970 m, 29.V.1998 / 99a: 12.VII.2002, leg. T. Knebelsberger
100 Dept. Vaucluse, 2,5 km ESE Col N.D. des Abeilles (near Sault), 980 m, 29.V.1998

Switzerland (He)

1 Kanton Wallis, Saillon, 500 m, 25.V.1996 / 1a: 27.V.1998
4 Kanton Wallis, Hohtenn, 650 m, 26.V.1996 / 4a: 27.V.1998
5 Kanton Wallis, Hohtenn, 900 m, 26.V.1996 / 5a: 7.VIII.1996
6 Kanton Wallis, Hohtenn, 1100 m, 26.V.1996
26 Kanton Wallis, Mont du Rosel (bei Martigny), 450 m, 26.V.1998 / 26a: 12.VII.2002, leg. T. Knebelsberger
27 Kanton Wallis, Eggerberg (bei Visp), 1500 m, 27.V.1998
31 Kanton Wallis, 1 km WSW Chermignon d'en Bas (bei Sierre), 840 m, 14.VI.2001

Italy (It)

90 Lazio, Monti Aurunci, 4.5 km NW Maranola (near Formia), 750 m, 11.IV.1999

Italy, Sicily (Sz)

11a Monte Etna, Monti Rossi (near Nicolosi), 800 m, 29.IV.1999
25 btw. Leonforte & Assaro (near Enna), 6oo m, 17.IV.1999
26 Monti Erei, 1 km E Portella Creta (near Enna), 800 m, 17.IV.1999
27 Monti Erei, Bosco di Sperlinga (W Nicosia), 850 m, 18.IV.1999
41 1 km SE Santo Stefano, 900 m, 21.IV.1999
53 Granitola-Torretta (10 km SE Mazara del Vallo), 10 m, 24.IV.1999
54 1 km SW Portella Misilbesi (16 km NNW Sciacca), 300 m, 24.IV.1999
57 Monte Campanella (near Milena, NNE Agrigento), 570 m, 25.IV.1999
60 Monte Navone (Mazzarino - Piazza-Armerina), ca. 500 m, 25.IV.1999
62 3 km N Alcate (9 km NW Vittoria), 140 m, 26.IV.1999
64 10 km W Santa Croce Camerina (SW Ragusa), 250 m, 26.IV.1999
67 1 km NE Catenanuova, 170 m, 27.IV.1999
69 below Castello di Spanò (ca. 20 km SE Troina), 350 m, 28.IV.1999

Croatia (Hr)

14 I. Korčula, plain W Mt. Klupca, 450 m, 13.-15.V.2001, leg. Bohn, Knebelsberger & Saks
15 I. Korčula, Zavalatica, 50 m, 14.V.2001, leg. Bohn, Knebelsberger & Saks
20 Pelješac, Gornji Nakovanj, 300 m, 15.V.2001, leg. Bohn, Knebelsberger & Saks
24 Pelješac, 3 km WNW Kasarni Do, 400 m, 16.V.2001, leg. Bohn, Knebelsberger & Saks
26 Rilić Mts., S slope of Sokolić, ca. 2 km N Drvenik, 150 m, 16.-17.V.2001, leg. Bohn, Knebelsberger & Saks
27 I. Hvar, Mt. Ublina, 5 km W Sućuraj, 200 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks
28 I. Hvar, E slope of Mt. Hum, ca. 500 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks
29 I. Hvar, Mt. Odzdrin (E Brusje), 400 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks

Morocco (Ma)

14a Moyen Atlas, Dayèt Iffer (NE Ifrane), 1600 m, 26./27.IV.1998
176a Moyen Atlas, btw. Aghrame-Amelall & El-Aderj (ca. 65 km NE Boulemane), 1100-1200 m, 27./28.IV.1998
258 Moyen Atlas, Jbel Cherbana (near Tazouta, SE Sefrou), 1600 m, 27.IV.1998
259 Moyen Atlas, Tizi-n'Tilrhemine (17.5 km S Ribat-el-Kheir, SE El-Menzel), 1100 m, 28.IV.1998
264 Jbel Mahssor (S Oujda), Oude-El-Heimer, 950 m, 21.II.1999
273 Haut Atlas (NE slope), Missour - Bouânane, 9 km NW Talsinnt, 1500 m, 24.II.1999
288 Moyen Atlas, Jbel Gaberaal, near Tirnest (NW Outat-Oulad-El-Haj), 1800 - 2000 m, 30.III.2000

Algeria (Al)

14 Chaîne des Biban, Hammam-El-Biban, 450 m, 27.IV.1990
16 Monts de Belzma, Seriana, 1100-1300 m, 27.IV.1990

Tunesia (Tu)

5 Forêt de Kesra (E Makthar), 800-1000 m, 13.IV.1990
8 Montes de Tébessa, J. Azered, ca. 20 km SW Thala, 850 m, 15.IV.1990
9 ca. 20 km WSW Le Kef, 500 m, 16.IV.1990
10 btw. Sakiet Sidi Youssef & Touiret (NW Le Kef), 16.IV.1990

Material from Museum collections

I 1♂ [Spain, Prov. Cuenca] Uclés, Père Pantel dedit, coll. A.Finot (MNHN)
II 1♂ [Spain] Nuevo Baztán, [Prov.] Madrid, 10.V.1928 (MNMS)

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Artikel II

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Revision and phylogeny of the *subaptera*-group of *Phyllodromica* (Blattoptera: Blattellidae: Ectobiinae), including a parthenogenetic species and the evaluation of COI sequences for species identification (DNA barcoding)

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THOMAS KNEBELSBERGER[1,3] & MICHAEL A. MILLER[2]

Zoologische Staatssammlung München, Münchhausenstrasse 21, 81247 Munich, Germany.
E-mail: [1]knebelsberger@zi.biologie.uni-muenchen.de; [2]miller@zsm.mwn.de
[3]Corresponding author

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Abstract

Until recently the *subaptera*-group of *Phyllodromica* contained only one species. The revision of the *subaptera*-group herein consists of the two newly described bisexual species, *P. iberica* and *P. quadracantha*, endemic to the Iberian Peninsula and a parthenogenetic species, *P. subaptera* (Rambur, 1838), which is widely distributed over most of the Mediterranean countries and islands. Within *P. iberica* three conspecific morphotypes are distinguished. The morphological characteristics of the *subaptera*-group are described. The species and their distributions are described and depicted. A key for the morphological determination of *P. quadracantha* and the morphotypes of *P. iberica* is given. DNA sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene are included in the species descriptions. The sequence data are suitable for species identification (DNA barcodes). A cladistic analysis of the morphological data and a phylogenetic analysis of the DNA sequences were performed to infer the phylogenetic relationships between the species of the *subaptera*-group.

Key words: Blattoptera, Blattellidae, Ectobiinae, *Phyllodromica*, new species, thelytoky, geographic parthenogenesis, mtDNA, COI, DNA sequences, DNA barcodes, molecular phylogeny

Introduction

The phenomenon of parthenogenesis has been observed in several cockroach species (Roth & Willis 1956, Corley *et al.* 1999). Obligatory parthenogenesis was only known in *Pycnoscelus surinamensis* which is assumed to be sexually isolated from its presumed bisexual ancestor *Pycnoscelus indicus* (Roth 1967). The parthenogenesis of the *subaptera*-group of *Phyllodromica* (Blatellidae: Ectobiinae) is the second case of obligatory thelytokous parthenogenesis observed in cockroaches (Knebelsberger & Bohn 2003).

This paper presents a revision of the *subaptera*-group and provides new information on the origin and evolution of parthenogenesis in Blattoptera.

The bisexual and the parthenogenetic forms of the *subaptera*-group exhibit different geographical distributions. The bisexual forms are endemic to the Iberian peninsula, whereas the parthenogens can be found in most of the Mediterranean countries and islands (Knebelsberger & Bohn 2003). This distribution pattern is consistent with the term "geographic parthenogenesis" first proposed by Vandel (1928). Morphological investigations have shown that males of the *subaptera*-group exhibit remarkable morphological variation mainly in the glandular structures of tergites 7 and 8 (Knebelsberger & Bohn 2003). Four morphotypes ('morphs') with partially overlapping distributions were distinguished. In contrast to the males, the bisexual and the parthenogenetic females for the most part cannot be distinguished by their external features.

To investigate the taxonomical state of the identified 'morphs' an extended morphological analysis was performed based on the material in the collection of Horst Bohn and T. K., and as a whole covered most of the mountain regions of the Iberian Peninsula.

Analysis of DNA sequence data provided information about the degree of the separation of the morphs which may possibly even represent new species. In cockroaches the investigation of DNA sequence variation was already used to detect new species and species boundaries. Kambhampati *et al.* (1996) investigated the sequence variation of two mitochondrial rRNA genes to obtain evidence for newly detected sibling species of *Cryptocercus punctulatus*. Based on this study Nalepa *et al*. (1997) and Burnside *et al*. (2000) described new species of *Cryptocercus* and the latter included sequence data (12S rRNA and 16S rRNA) in the descriptions of new species.

In this paper two new bisexual species are described. The parthenogenetic strain (species) retains the name *Phyllodromica subaptera* (Rambur 1838) because the holotype specimen is most likely a parthenogenetic female. The complete sequences of the mitochondrial COI gene are included in the description of each species. One important aim of the genetic characterisation of the species is to support the potential use of the sequence information as a taxonomic tool for subsequent species re-identification as recommended by Tautz

et al. (2003). The COI gene has already been proven its usefulness for DNA taxonomy purposes in many studies (e.g. Hebert *et al*. 2003a/b).

Although the area encompassed by the sampling locations and reflected in the distribution areas of the species in the *subaptera*-group are large there are, nevertheless, still some regions which are inadequately investigated.

Material and methods

Insect material

The material in the collection of H. Bohn was fixed in 5% formaldehyde and used only for preparations of cuticular structures. The specimens collected by T. Knebelsberger (1998 to 2003) were preserved in 98% ethanol and thus also suitable for DNA sequencing.

Prepared specimens are identfied by the code of the collection locality (see below) followed by an abbreviation of the sex ('M' for male and 'W' for female) and an individual number, for instance Sp 203a/M1, M2, and Sp 203a/W1, W2. Specimens prepared by H. Bohn bear only the locality code and an individual number, for instance Sp 203/1, 2.

Sample localities

The localities mentioned in the text are represented only by their code; geographic parameters, date of collection, and name of the collector can be found in Appendix 1. If no collector is denoted, the material was collected by Barbara & Horst Bohn.

Preparations of cuticular structures

The respective parts of the body were treated overnight at 40° C (material fixed in formol) or at room temperature (unfixed or alcohol treated material) with 10% KOH to remove the soft tissues, then washed in water, dehydrated, and mounted in Canada balsam on microscope slides.

Light microscopy (LM)

Observations were made and photos taken under a Olympus SZX 12 binocular microscope with a Jenoptik ProgRes C12 Plus digital camera and under a Leica DMR Microscope with a Visitron Systems Spot Insight Color digital camera.

Scanning electron microscopy (SEM)

The preparation of cuticular structures for SEM was similar as for light microscopy except that after washing the pieces were transferred to acetone. After drying with the critical point method the specimens were mounted on alumium stubs with adhesive carbon tabs, sputtered with gold in a BioRad SEM coating system, and examined with a Philips XL 20 SEM.

Interpretation of the pictures of sclerotized and membraneous cuticle structures (under LM and SEM)

In the SEM images the differentiation between sclerotized cuticle and membraneous structures is not possible. In the LM images of tergite 7, for instance, the anterior border of the tergite appears trilobed by two narrow, but relatively deep, membraneous incisions (Fig. 6 D) which cannot be identified in the SEM images (Fig. 7 D). On the anterior border of tergite 8 two sclerotized anterior processes appear in the LM images with a membraneous structure in between (Fig. 12 E) whereas in the SEM images the anterior processes and the membraneous structure cannot be distinguished (Fig. 13 B).

Figures

If not stated otherwise, the position of the structures in the figures is in dorsal view with the anterior end on the top.

Measurements

For measurements of the length of pronota of the different taxa (see species descriptions) more than 20 specimens from various localities dispersed over the whole distribution area were used for each sex.

Characters

A total of 24 morphological characters (Appendix 2) were analysed in the *subaptera*-group taxa and in the outgroups (*nana*-, *carpetana*- and *panteli*-group) which represent the closest relatives of the *subaptera*-group (Bohn 1999).

The results of the character analysis were used for the compilation of a data matrix (Appendix 3). If characters could not be homologized with the structures found in the outgroup taxa they were coded by a dash (-). If characters appear in 2 states within a single taxon, both states were coded. All characters were weighted equally and not ordered.

Cladistic analysis

The data matrix of the morpological characters was used for the cladistic analysis of the interrelationships between the members of *subaptera*-group and the outgroup taxa. The parthenogenetic species *P. subaptera* is not included in the analysis because it cannot be distinguished from the females of *P. iberica*.

Maximum parsimony analysis (MP) was performed using PAUP* (Phylogenetic Analysis Using Parsimony ver. 4.0 β 10; Swofford 2003). We used the heuristic search option with branch swapping by tree bisection and reconnection (TBR) on 10,000 starting trees with random stepwise addition sequences. No outgroups were declared in the PAUP calculation because many of the characters found in the ingroups cannot be homologized with the structures found in the outgroups (see above). After MP calculation the trees were rooted with the *panteli*-group which presumably is the most basal group used in this analysis (Bohn 1999). To test the robustness of the topology found by the MP analysis 10,000 bootstrap replications (and 25 random addition sequence replicates for each bootstrap replicate) were performed. Bremer support values (Bremer 1994) were calculated using TreeRot.v2 (Sorenson 1999).

DNA sequencing

A DNA fragment including the complete mitochondrial cytochrome oxidase subunit I (COI) gene was sequenced in two paratypes of each of the two bisexual species (in case of *P. iberica* four additional specimens were analysed) and in two specimens of the parthenogenetic *P. subaptera* (see descriptions of species).
Abdominal tissues were used for proteinase K procedure with DNeasy tissue kit (Quiagen), following the manufacturer's protocol for animal tissues with slight modifications. Digestion was performed for 12 hours. DNA was then eluted with molecular biology grade water (Eppendorf). Prior to sequencing, the DNA concentration was measured using a fluorometer (BioRad, VersaFluor™) and adjusted to 50 ng/µl with molecular biology grade water. The COI gene was amplified with PCR in a PTC 220 DYAD thermocycler (MJ Research) using protocols and primers especially designed or as described in Simon et al. (1994). Direct sequencing of dye labelled templates was carried out using an ABI 377 automated sequencer (Applied Biosystems). Up to 10 single sequences per individual were assembled and aligned to the COI sequence of *Blattella germanica* (Blattoptera, Blattellidae, Blattellinae; EBI accession number AY176057) visually in BioEdit (Hall 1999).

The new sequences are deposited at EBI (European Bioinformatics Institute) / NCBI (National Center for Biotechnology Information) respectively. The accession numbers are given in the species descriptions.

Analysis of the sequence data

For the different analyses 1570 basepairs of the mitochondrial DNA sequences of the 10 *subaptera*-group specimens were used (Appendix 4). In *Blattella germanica*, which is used as outgroup, the positions 1537–1570 were coded as gaps with the "gapmode = missing". The pairwise genetic distances were calculated using PAUP*.

To infer the phylogenetic relationships among the taxa, three different analytical methods were used: **Maximum parsimony** (MP), **Maximum likelihood** (ML) and **Bayesian analysis**. MP was conducted using the heuristic search option with branch swapping by tree bisection and reconnection (TBR) on 10,000 starting trees with random stepwise addition sequences. Ten replicates were performed within each heuristic search. The ML analysis requires a specific model of sequence evolution to be specified *a priori*. In order to select the substitution model that best describes our data, sequences were analysed with Modeltest v.3.7 (Posada & Crandall 1998).

ML was performed with the heuristic search option, branch swapping by tree bisection and reconnection (TBR) and random stepwise addition sequences using the optimal model defined by Modeltest.

MP and ML trees based on the COI sequence data were constructed by defining *Blattella germanica* as outgroup. To assess the robustness of relationships, 2,000 bootstrap replications (and 25 random addition sequence replicates for each bootstrap replicate) were performed for MP. Due to prohibitive computer time, the bootstrapping method was not used in the ML analysis.

Bayesian analysis was performed with MrBayes version 3.1 (Ronquist & Huelsenbeck 2003). The evolutionary model was set to the GTR model with gamma-distributed rate variation across sites and a proportion of invariable sites. Two runs were performed starting from different random trees and the default value of four Markov chains per run was used. The "temperature" parameter was set to 0.2. The number of generations (Monte Carlo Markov chain length) was set to 1 billion and trees were sampled every 1,000 generations. It was not necessary to continue the analysis beyond 1 billion generations because the average standard deviation of split frequencies was far below 0.01 after the run. Sample parameter values were summarized, the first 25 % were discarded. For the construction of the cladogram with the posterior probabilities for each split and the phylogram with the mean branch lengths the trees were also summarized by discarding the first 25 %.

Abbreviations of Museums

BMNH British Museum of Natural History, London; **MNHN** Muséum National d'Histoire Naturelle, Paris; **MNMS** Museo Nacional de Ciencias Naturales, Madrid; **ZSM** Zoologische Staatssammlung München.

Results and discussion

Characteristics of the *subaptera*-group

Wings

Tegmina (forewings) (**tm**) reduced to small widely separated scalelike structures scarcely surpassing the posterior border of the mesonotum, very narrow, with almost parallel borders, broadest near the base (Figs 1 A, B, 8 F). **Alae** (hindwings) missing.

Male

Thoracal nota (Fig. 3 A). Pronotum (**pro**) semicircular in outline, with broadly rounded latero-posterior edges; mesonotum (**mes**) with the tegmina laterally set off, latero-posterior corners acute; lateral borders of metanotum (**met**) straight, posterior border slightly concave, latero-posterior edges scarcely produced, angularly rounded.

Abdominal tergites

Glandular structures are found on the surface of tergites 7 and 8 (glandular pits) (Fig. 3 D, E) and in the membraneous intersegmental region of tergite 4/5 and tergite 5/6 (membrane glands, **mg** see black arrows in Fig. 3 B, C and Figs 5 C, 14 A). Additionally, glandular pores may be present at various sites, especially on tergites 6–8 (Fig. 4 H).

A well developed transversal ridge (**tr**) (Figs 3 B, 7 A) dividing the tergite surface into a narrower anterior and a wider posterior part is present on tergites 1–6; in tergite 7 it is present only laterally (Figs 12 D, 14 F) or missing (Fig. 3 D); it is always missing in tergites 8–10.

Posterior part of tergites with dispersed rather long and strong bristles (Fig. 7 A, B).

Tergite 5 (Fig. 3 B). Anterior border laterally at the sites of the membrane glands with ± shallow, but extended concavities (the sclerite is replaced there by membraneous glands), in the middle often with a small membraneous indentation; posterior border as in preceding tergites weakly concave.

Tergites 6–8 considerably longer than other tergites.

Tergite 6 (Fig. 3 C)**.** Anterior border laterally at the sites of the membrane glands with large membraneous incisions, in the middle with a small membraneous indentation; posterior border strongly sinusoidal brought about by a deep median emargination and the broadly rounded latero-posterior edges.

Tergite 7 (Figs 3 D, 4 A–C, G). Anterior border trilobed by two narrow but relatively deep membraneous incisions (only visible in light microscopy images), the broader median lobe (**ml**) somewhat produced and in itself bilobed by a slight median incision (Fig. 3 D); posterior border relatively strongly concave, latero-posterior corners angularly rounded.

The strongest sculpturation of cuticule and glandular structures on the tergite 7 are found in *P. iberica* morph #1: **Glandular pit** developed as a transversal trough (**tt**) immediately behind the median lobe of the anterior tergite margin (Figs. 3 D, 4 B, C). The anterior limitation of the trough is a steep wall declining from the median lobe; wall on both sides slightly hollowed out anteriorly (Fig. 4 A, white arrows). The posterior limitation of the trough is less well marked by a high and large mound (**m**) occupying about one third of the tergite breadth, ascending from the bottom of the trough and declining again towards the posterior border of the tergite (Fig. 4 A, B). The trough has no lateral limitation.

Posterior part of the glandular pit densely covered with bristles, forming two **bristle fields** (**bf**) (Figs 3 D, 4 B, C). They are arranged on the anterior slope of the mound forming two longitudinally oval grooves. Medially the walls of the grooves elevate to a broad longitudinal bristleless ridge (**r**) separating the grooves, in dorsal view appearing as a broad nose-like structure (Fig. 4 C). Posteriorly, the grooves are on both sides of the ridge deepened to shallow pouches beneath the mound (appearing as a crescent-shaped black shadow posteriorly of each of the two bristle fields; white arrow heads in Fig. 3 D), but fading away towards anteriorly. On the crest formed by the median lobe and the anterior wall of the trough there is a row of rather long and strong bristles pointing posteriorly (Figs 4 B, C).

P. iberica morph #2 and #3 and *P. quadracantha* show variable reductions concerning the length of the median lobe, the deepness of the trough, the size of the mound, and the size and shape of the bristle fields; the ridge separating the bristle fields may be absent.

Tergite 8. *P. iberica* morph #1 also exhibits the strongest sculpturation of cuticule structures on tergite 8 (Figs 3 E, 4 D–F, H, I): Surface of the tergite with a high and broad central mound (**cm**), anteriorly declining to a sinusoidal transversal edge (**se**) (Figs 3 E, 4 D). Mound densely covered with glandular pores (Fig. 4 H) but without bristles, causing a median emargination in the distribution of the bristles (white arrow heads in Fig. 4 D). Transversal edge laterally with concavities continuing down to the anterior tergite border forming shallow pits (**sp**) opening antero-dorsally (Figs 3 E, 4 D, E). The median part of the anterior tergite border is membraneous in the middle, leaving two lateral ± tonguelike sclerotized anterior processes (**ap**) (Fig. 3 E) (only visible in light microscopy images; see Methods and Material). Between the anterior processes with a well developed conelike process (**cp**), which is dorso-ventrally flattened, unsclerotized and densely covered with tiny soft villi (Figs 3 E, 4 D–F, I); cone elevating in antero-dorsal direction (Fig. 7 H).

In *P. iberica* morph #2 and morph #3 the various sculpturations are variously reduced mainly regarding the height and breadth of the mound, the expression of the sinusoidal edge and the dimension of the conelike process. In *P. quadracantha* (Figs 12 E, 13 B) the surface of the tergite is almost without any sculpturing.

The formation of the structures on tergites 7 and 8 seems to be intercorrelated: a strongly sculptured tergite 7 is always combined with a similarly strong sculpturing on tergite 8.

Tergite 9 and tergite 10 in the longitudinal midline slightly elevated to a weakly rooflike structure.

Tergite 9. Anterior border in the middle with an angular membraneous incision, posterior border trilobed. Broad posterior median lobe (**pml**) rounded triangular (Figs 3 F, 6 F, 9 F), in *P. quadracantha* broadly rounded (Fig. 12 F). The narrower lateral lobes, mainly composed of the paratergites, are curved ventrad along the longitudinal axis, their surfaces pointing laterally.

Tergite 10 (Fig. 6 G). Supraanal plate (**sa**) anteriorly slightly emarginated (Fig. 6 G), posterior lobe behind insertion of cerci rounded triangular (Figs 3 G, 6 G, 9 G) or more transverse and broadly rounded (Fig. 12 G). **Cerci** (**c**) (Fig. 3 G) relatively short and stout, in outline lanceolate.

Abdominal sternites

Subgenital plate (sternite 9, **sub**) (Fig. 9 I). Posterior (sclerotized) lobe rounded triangular, slightly asymmetrical, with one (left) unspecialized short **stylus** (**s**); anteriorly with two very long apodemal processes (**a**) of unequal length.

Genital sclerites

Left phallomere (Fig. 9 H, I) with hook and a spatular endophallic apodeme (**ea**). **Hook** (Fig. 9 H) with a long straight shaft (**sh**) bearing at its apical part a sclerotized shallow trough measuring about 2/3 of the length of the shaft; shaft apically tapering to a short stalk (**st**) followed by an angularly bent claw (**cl**); claw on one side with a broad membraneous process, the velum (**v**). **Right phallomere** (Fig. 9 I) consisting of the cleft sclerite (**cs**) and a weakly developed **R3** apodeme. Between the phallomeres with a **helmet sclerite** (**hs**) (Figs 8 E, 14 D) which in *P. quadracantha*—similar to those found in closely related groups (*carpetana-*, *nana*-group)—has the shape of a short handled spoon, with a broadly rounded "frontal" part (**fr**) and a relatively long acuminate process in the "rear" (**re**) (Fig. 14 D). In *P. iberica* the helmet sclerite appears reduced at both ends (Fig. 8 E). The terms "frontal" and "rear" are not correlated with the position of the sclerite within the animal.

Paraprocts (Figs 3 G, 5 D)**.** Right paraproct (**rp**) with a spinelike process (**sp**) and a medio-anteriorly directed process (**mp**). The medio-anterior process of *P. quadracantha* is unique in having a bulge (**b**) at the base (Figs 12 G, 14 B).

Colouration

Head (**h**) (Fig. 1 A) dark, ocelli and a narrow transversal band in the posterior interocular space whitish. Antennae brownish, lighter at the base; maxillar and labial palps dark.

Thorax. Pronotum (Figs 1 A, 3 A) disk dark, semicircular to transversely oval, surrounded by a whitish-transparent margin which is laterally broader than anteriorly and posteriorly. In all species individuals may be found having a red-orange disk. Light margin near disk at least in the latero-posterior corners with variously sized dark spots. **Mesonotum** (Figs 1 A, 3 A) mainly dark, with a moderately broad whitish posterior margin bearing dispersed dark dots. **Tegmina** (Figs 1 A, 3 A) transparent, slightly darkened along the medial margin, with dispersed dots except in the costal region. **Metanotum** (Figs 1 A, 3 A) dark with broad lateral and narrower whitish posterior margin. Dark area in the latero-posterior corners broken up into larger and smaller spots reaching for some part into the light margins.

Legs. Basal sclerites dark, legs variously coloured from nearly completely dark (Fig. 8 I) to nearly completely light, but mostly in between (Fig. 8 H); light areas in the coxa-trochanter region whitish, in other parts

yellowish. In dark legs only the distal part of coxa plus trochanter and basal parts of the tarsus lightly coloured; in light legs at least the proximal parts of the coxae, parts of the dorsal and ventral surface of the femora, small proximal and distal parts of the tibia, the insertion area of the tibial spines, and the distal parts of the tarsi are dark. Tibial spines reddish.

Abdomen

Tergites. Abdominal tergites 1–8 with dark anterior and lighter coloured (yellowish or whitish) posterior part, the latter with dark spots.

Tergites 2–5 (tergites 2–4: Fig. 1 A; tergite 5: Fig. 3 B). Anterior parts including the transversal ridge dark. The dark areas extending for some part also beyond the ridge sometimes not as continuous front but broken up into variously shaped posterior extensions.

Posterior part of tergite light with dark spots becoming smaller and less dense towards the posterior border. Each spot with a bristle in the middle. In the transition region between dark and spotted area the spots are quite dense and often clustered.

Light ground colour in the transition region yellowish, becoming whitish towards posteriorly. Laterally, just anteriorly of the transversal ridge, often with a wedge-shaped light patch (Fig. 12 B).

Tergite 6. Dark area posteriorly reaching the posterior border of the tergite (region of the deep median posterior emargination) (Fig. 12 C) or leaving a variously broad light margin (Fig. 6 C); in some species dark area often variously lightened along the longitudinal midline and along a transversal line shortly behind the median ridge (Figs 3 C, 8 A–D); in few cases dark area behind the ridge reduced to clusters of dark spots (Fig. 5 A). Latero-posterior parts of the tergite always lightly coloured with dark spots.

Tergite 7 (Fig. 3 D). Dark area not uniformly dark; central area (mound area) darker than the remaining parts. Trough in the middle always with a whitish patch. Latero-posterior parts of the tergite always lightly coloured with dark spots (similar to T6).

Tergite 8 (Fig. 3 E) variously coloured, posterior part usually light with dark spots. Dark area medially and medio-laterally often with posterior extensions (Fig. 6 E).

Tergites 9–10 (Figs 1 A, 9 F, 12 F) mainly dark, posterior part whitish, often with a median anterior extension, with indistinct dark spots. The median anterior extension may reach the anterior border of the tergite (Fig. 3 F).

Sternites 2–8 mostly dark, latero-posterior corners whitish with some dark spots.

Sternite 9 (subgenital plate) (Fig. 3 I). Posterior lobe mainly dark, subapically on both sides with a small indistinct lightening.

Female

Thoracal nota as in male, **abdominal tergites** without glandular structures.

Genitalia. Not much differing from the usual Ectobiinae pattern. **Dorsal complex** (Fig. 2 D). Latero-dorsal sclerites of the basivalvula (**bd**) converging anteriorly, but not fused, tapering towards anteriorly; accompanying latero-ventral sclerites (**bv**) considerably broader and longer. In the angle between the intercalary sclerite (**is**) and the posterior lobe (**pl**) of valvifer II in *P. subaptera* and *P. iberica* with an additional, sigmoidally shaped sclerotization (**as**) (Figs 2 D, E) which is missing in *P. quadracantha* (Fig. 13 G). It is possibly derived from the posterior lobe of valvifer II since the latter is broad in *P. quadracantha* and slender in the remaining species. **Ventral complex** (Figs 2 F, 13 H) consisting of the laterosternal shelf (**l**) with a central rounded part including the vestibular sclerite and two short posteriorly diverging arms; between the arms with intersternal folds (**i**). **Subgenital plate** (Sternite 7) (Figs 2 C, 13 F) undivided, anteriorly with two short apodemal processes (**a**), posteriorly broadly rounded.

Ootheca (Fig. 1 D) short, containing about 10-12 eggs, surface smooth, without longitudinal ridges, rotated 90° prior to deposition as in almost all Ectobiinae (keel at the right).

Colouration

Females usually lighter coloured than males.

Head (Fig. 1 B, C)**.** Usually dark, area above the insertion of the antenna and a transversal band in the posterior interocular space whitish. Often more areas lightened: genae and postgenae, clypeolabrum, and sometimes even the whole face yellowish. Antennae brownish, basal part yellowish; palps with at least distal segments dark.

Thorax. Pronotum with a semicircular to transversely oval disk, surrounded by a whitish-transparent margin, laterally broader than anteriorly and posteriorly.

In *P. subaptera* and *P. iberica* disk of pronotum anteriorly dark, forming a dark crescent, posteriorly lightly coloured, mottled with larger and smaller dark spots, in the middle often arranged to a lyrate pattern (Figs 2 A, 5 F, 8 F, 10 G). Dark anterior area variously extended, sometimes disk nearly completely dark (Figs 2 A, 5 H). Light margins near the disk at least in the latero-posterior corners with dark spots. In *P. quadracantha* pronotum disk always regularly mottled, without dark crescent (Fig. 13D). Except in *P. quadracantha* individuals may be found which have reddish instead of dark markings, except in *P. quadracantha*. **Meso-** and **metanotum** (Figs 1 B, 5 F) with light margins as in males, but margins less well defined since the spotted areas may nearly reach the notal borders. Central area between margins never completely dark, posteriorly to a various degree broken up into larger and smaller spots. Dark anterior area usually with 6 or 7 irregular posterior extensions. Dark area on mesonotum usually more extended than on metanotum.

Tegmina coloured as in male (Figs 1 B, 8 F). **Legs** (Fig. 1 C)**.** Basal sclerites usually dark, legs mainly lightly coloured. Light areas of coxa whitish, the more distal parts yellowish. In a relatively dark leg proximal half of coxa, dorsal and ventral surface of femur, ventro-posterior surface and distal part of the tibia and most of the tarsus dark; in the other extreme dark areas restricted to a narrow basal part of the coxa, the dorsal surface of the femur, and a small distal part of tibia and tarsal segments.

Abdomen.

Tergites 2–6 (Fig. 5 G, I)**.** Anterior part, anteriorly of the transversal ridge, dark, laterally with a lightly coloured edge often extending towards the middle as a narrow, partly interrupted yellowish transversal stripe completely or partly separating the anterior dark area from the narrow dark stripe accompanying the transversal ridge (Fig. 13 E). Posteriorly along the ridge with 5 dark patches, largest in the center, less regularly followed on each side by two smaller patches. Remaining posterior part of the tergite whitish with dark spots becoming smaller towards the posterior border.

Cerci (Figs 1 B, 2 D). Ventral surface dark, dorsal surface dark at the base and tip, yellowish in between.

Sternites 2 and 3 mostly dark, with lateral lightenings.

Sternites 4–6 anterior part dark, with three broad ± triangular extensions behind the transversal ridge. Remaining parts whitish, with dark spots.

Sternite 7 (subgenital plate) (Fig. 2 C) mostly dark, anteriorly, behind the apodemal processes with two variously sized and shaped yellowish patches, along the posterior margin with several (usually 4) whitish patches.

Distinction of the *subaptera*-group from other closely related groups

The *subaptera*-group is considered as sister group of the *carpetana*-group (Bohn 1999). Specimens of both groups can easily be distinguished by shape and colouration of the tegmina. In the *carpetana*-group the tegmina are broadest in the middle and, except at the costal area, scattered with dark spots which at the base fuse to a larger patch. In the *subaptera*-group the tegmina are broadest near the base and have only few dispersed dots along the medial margin.

Confusion may occur between specimens of *subaptera*- and *nana*-group due to their very similarly shaped wings (broadest near the base) and a similar colouration of the body. A key to distinguish between *subaptera*- and *nana*-group specimens is given in Knebelsberger & Bohn (2003).

Key for the morphological determination of the bisexual species of the *subaptera*-group

1. Eight visible sternites; last (sternite 9) with very narrow visible part, triangular (Fig. 3 I); tergite 7 always with a glandular pit (Fig. 3 D). .....male 2
- Six visible sternites; last (sternite 7) very broad and large, semicircular (Fig. 2 C); tergite 7 always without pit. ..... female 5
2. Distal end of mid tibia with 4 spines (Fig. 14 C); medio-anterior process of right paraproct with bulge (Fig. 14 B); tergite 8 always without prominent sculpturing (Figs 12 E, 13 B). ....*P. quadracantha* **spec. nov.**
- Distal end of mid tibia with 5 spines (Fig. 5 E); medio-anterior process of right paraproct without bulge (Fig. 5 D); tergite 8 strongly sculptured, with a conelike process at the anterior margin and a sinusoidal transversal edge behind that (Figs 3 E, 4 D-F, 6 E, 7 F-H, 9 E, 10 B-D, F). .....*P. iberica* **spec. nov.**
Determination of *P. iberica* morphotypes..... 3
3. Tergite 8 without a central mound, bristles on the tergite surface in the middle reaching far anteriorly near to the conelike process (white arrows in Fig. 10 B, F), the latter forming a kind of bubble of different sizes.....*P. iberica* morph #3
- Tergite 8 with a central mound bearing pores displacing the bristles on the tergite surface in the middle towards posteriorly (white arrow heads in Figs 4 D, 7 F). 4
4. Tergite 6 posteriorly of the transversal ridge with a transversal torus bearing bristles (Fig. 7 A–C); tergite 7 with smaller and lower mound, bristle fields very small and immediately adjacent to each other (Figs 6 D, 7 D, E); tergite 8 central mound about as broad as shallow pit (Figs 6 E, 7 F, G). ...*P. iberica* morph #2
- Tergite 6 posteriorly of the transversal ridge without a transversal torus (Fig. 3 C); tergite 7 with a large and high mound, bristle fields large, separated by a broad rounded ridge (Figs 3 D, 4 A–C); tergite 8 central mound broader than shallow pit (Figs 3 E, 4 D, E).....*P. iberica* morph #1
5. Disk of pronotum at least with a dark crescent along the anterior margin, dark area often still more extended (Figs 1 B, 2 A, 5 F, H); genital sclerites near the intercalary sclerites with an additional sclerotization (Fig. 2 D, E); distal end of mid tibia always with 5 spines..... *P. subaptera, P. iberica*
The females of the two species cannot be distinguished by morphological features or colouration. The females of *P. subaptera* may be recognized by their parthenogenetic reproduction (Knebelsberger & Bohn 2003).
- Disk of pronotum never with larger dark area but regularly spotted throughout (Fig. 13 D); genital sclerites without an additional sclerotization near the intercalary sclerite (Fig. 13 G); distal end of mid tibia mostly with 4 but sometimes also with 5 spines.....*P. quadracantha*

Description of the species of the *subaptera*-group

The parthenogenetic species *P. subaptera* and the females of *P. iberica* cannot be distinguished by external features. In the following species descriptions the females of *P. iberica* will not be described. The description of *P. subaptera* and the description of the females in the section "Characteristics of the *subaptera*-group" can be seen also as representative for the females of *P. iberica*.

***Phyllodromica subaptera* (Rambur, 1838)**
(Figs 2 A–F, 16)

Blatta subaptera Rambur, 1838. —Faune entom. Andalousie 2: 14.
Polyzosteria subaptera.—Fischer 1853, Orth. Europ., Lipsiae: 94.

Aphlebia subaptera.—Brunner v. W. 1865, Nouv. Syst. Blatt., Wien: 73.
Hololampra subaptera.—Kirby 1904, Syn. Cat. Orth. 1: 70.
Hololampra (Lobolampra) subaptera. —Houlbert 1927, Thysan., Derm. et Orth. France 2, Paris: 24.
Dziriblatta subaptera. —Chopard 1936, Bull. Soc. Sci. nat. Maroc 16 (2): 153, 154.
Phyllodromica (*Lobolampra*) *subaptera*. —Princis 1971, In: Beier (Ed.): Orthopterorum Catalogus 14, s' Gravenhage: 1113; Harz 1976, In: Harz & Kaltenbach: Die Orthopteren Europas. 3, The Hague: 305, figs 904, 905.

Holotype: ♀, Spain, Prov.Granada enviroment of "Grenade" (Granada); BMNH.

Additional material. Numerous specimens from the following localities: **Spain**: Sp 10a, 11a, 17, 18a, 19a, 24a, 61, b, c, 62, 63, 65, 68, 71, a, b, 72, 73, 76, 78, b, 79, c, 80 (?), 88, 89, 90, 91, 92, 93, 94, 101 (?), 105, a, 107, 108a, b, 109a, 114a, 139, 140a, b, 141, 142, 143, 148, a, b, 149 (?), 169, 172, 173a, 174a, 186b, 188a, 191a, 195, 196, 197, 198, 199, 200, 201, 202, 203, a, b, c, d, 204, 205, 205a, 206, 207, a, 208, 209, 210, 214, 229, 230, 253, 254, 256, 258, 262 (?), 263, 264, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289, 290, 293, 320, 333, 339, 340, 342, a, 343, a, 345, 354, a, 355, a, 356, 357, 358, 359 (?), 362, 365, 377, 381, a, 383, 393, 395, 396, 397, a, b, 419, 454, 456, 469, 470, 472, a, b, 473, a, 474, a, 475, 476, 480, 481, 483, 484, 493, 494, 495, 496, 498, 503, 504, a, 505, 508. - **Baleares**: Ba 8, 15, 17, 19, 21, 23, 24, 25, 26, 27. - **Portugal**: Po 19, 24. - **France**: F 2, 3, 4, 5, 8, 11, 12, 13, 13a, 15, 15a, 17, 18, 19, 20, 21, 22, 25, 26a, 34, 39, 41, 42, 48, 63, 79, 91, 99, a, 100. - **Corsica**: 12a, 54a. - **Switzerland**: He 1, a, 4, a, 5, a, 6, 26, a, 27, 31. - **Italy**: It 90, It 250. - **Sicily**: Sz 11a, 25, 26, 27, 41, 53, 54, 57, 60, 62, 64, 67, 69. - **Croatia**: Hr 14, 15, 20, 24, 26, 27, 28, 29. - **Morocco**: Ma 14a, 176a, 258, 259, 264, 273, 288. - **Algeria**: Al 14, 16. - **Tunesia**: Tu 5, 8, 9, 10.

Due to the difficulties in distinguishing the females of *P. subaptera* and *P. iberica* there are some doubtful localities which are indicated by a question mark.

Identification of the holotype specimen as parthenogenetic female. Unfortunately, the abdomen of the holotype specimen is completely missing. There is, however, strong indirect evidence indicating that it is a representative of the parthenogenetic strain: the locality of the type specimen is situated within an area where only parthenogenetic animals have been found (Fig. 16). The only bisexual species occurring in the surroundings is *Phyllodromica quadracantha* of which the females show a completely different colour pattern on the pronotum.

Description. Size. Length of pronotum: ♀ 1,68–2,00 (mean 1,89) mm.

Legs. Distal end of mid tibia with 5 spines: 4 long ones and 1 shorter in ventro-posterior position.

Genitalia. With an additional sclerite in the angle between the intercalary sclerite and the posterior lobe of valvifer II (Fig. 2 D, E).

Colouration. Pro-, meso- and metanotum similarly coloured as in *P. iberica* for detailed description see corresponding parts of the section "Characteristics of the *subaptera*-group".

Genetic Data. 1597 basepairs of the mitochondrial genome including the complete cytochrome c oxidase subunit I (COI) gene were analysed in two specimens from the holotype region (Sp 203e/W1, Sp 203e/W10). The sequences of *Phyllodromica subaptera*_Sp 203e/W1_1597bp and *Phyllodromica subaptera*_Sp 203e/W10_1597bp differ in 9 positions (Appendix 5). The complete sequences are shown in Appendix 4.
DNA and associated parts of body are stored in the DNATAX collection of ZSM (Zoologische Staatssammlung München; Munich, Germany) under storage numbers DNATAX02861 (Sp 203e/W10) and DNATAX02862 (Sp 203e/W1). The sequences were submitted to GenBank under the accession numbers: AM600684 (DNATAX02861) and AM600683 (DNATAX02862).

Geographical distribution (Fig. 16). The parthenogenetic species is distributed in most of the Mediterranean countries including Portugal, Spain, France, Italy, Croatia, Morocco, Algeria, Tunesia, and - quite far from the Mediterrenean Sea - Switzerland (in the Wallis region). It also occurs in part of the Mediterranean islands such as Baleares, Sicily, Corsica, and the Adriatic islands Korcula and Hvar.

P. subaptera is also reported from Bosnia-Herzegovina and Macedonia (Us & Matjevev 1967), Bulgaria

(Drenski 1939, Buresch & Peschev 1957) and Greece (Burr et al. 1923, Werner 1927), but we did not see representatives from there.

Other species of the *subaptera*-group found. Bisexual females of unknown specificity: Po 19, 24; Sp 88, 89, 90, 91, 94, 108, 333, 393; *P. iberica*: morph #1: Sp 419; morph #2: Sp 365; morph #3: Sp148, 186, 381, 395; *P. quadracantha*: Sp 191, 195, 203, 207, 472, 473, 493, 495, 498, 504.

Phyllodromica iberica, spec. nov.

(Figs 1 A–C, 3 A–I, 4 A–I, 5 A–I, 6 A–I, 7 A–H, 8 A–I, 9 A–I, 10 A–H, 11 A–L, 17)

Phyllodromica subaptera, morph #1, #2 and #3. —Knebelsberger & Bohn, 2003.

Holotype: ♂, Spain, Prov. Ciudad Real, btw. Los Pozuelos de Calatrava & Piedrabuena (W Ciudad Real), 700 m, 21.IV.2003, leg. T. Knebelsberger (on two slides, Sp 292b/M3); deposited in ZSM.

Paratypes: 5 ♂, same data as holotype. Sp 292b/M1 (frozen DNA; parts of body in 98 % ethanol); Sp 292b/M2 (frozen DNA; parts of body in 98 % ethanol); Sp 292b/M4 (on two slides); Sp 292b/M5 (on two slides), Sp 292b/M6 (on two slides).

Paratype DNA and associated parts of body are stored in the DNATAX collection of ZSM under storage numbers DNATAX02859 (Paratype Sp 292b/M2) and DNATAX02860 (Paratype Sp 292b/M1). The sequences were submitted to GenBank under the accession numbers: AM600686 (DNATAX02859) and AM600685 (DNATAX02860). The remaining 3 paratypes (Sp 292b/M4-6) are deposited in the private collection of T. Knebelsberger.

Etymology: The name of the species refers to its distribution covering a large area of the Iberian peninsula.

Remarks: Within *P. iberica* three morphotypes (morphs) can be distinguished and will be described in detail. The holotype and paratype specimens of *P. iberica* were selected from morph #1 which has the widest distribution.

The females of *P. iberica* cannot be distinguished by external features. At the localities Po 19, 24; Sp 4, 5a, 14a, 88, 89, 90, 91, 94, a, 108, 112, 116, 136, 170, 333, 384 and 393 bisexual females were found, but not the appertaining males; their specificity remains to be clarified.

Phyllodromica iberica morph #1

(Figs 1 A–C, 3 A–I, 4 A–I, 5 A–I, 8 H, 17)

Phyllodromica subaptera morph #1.—Knebelsberger & Bohn, 2003.

Material. Numerous specimens from the following localities: Spain. Sp 12b, 13a, b, 84b, 85, 95a, 96a, b, 97, a, b, c, 98, a, 99a, b, 100, a, b, 119, b, 134, 135, 137, a, 189, 270, a, b, c, 272, 273, 274, 276, 292, a,b, 294, 295, 296, 300, 302, 307, 324, 330, 331, 332, 334, 335, 336, 337, 366, 366a, 367, 368, 371, 375, 376, 378a, 379, 380a, 382, a, 386, a, 388, a, 389, a, 390, 391, 394, 418, 419, 420, 421, 422, 423, 426, 427, 428, 431, 432, 433, 434, 435, 436, 437, 438, 439, 440, 441, 442, 443, 444, 446, a, 447, a, 448a, 449, 450, 453, 455, 463, 464, a, b, 467, a, 471a, 492, a, b, 506, 507, a, 509, 510, 511, 512, a. Material from museum collections: I: 1 ♂ [Spain, Prov. Cuenca] Uclés, Père Pantel dedit, coll. A. Finot (MNHN). II: 1 ♂ [Spain] Nuevo Baztán, [Prov.] Madrid, 10.V.1928 (MNMS).

Description. Size. Length of pronotum: ♂ 1.34–1.6 (mean 1.5) mm; ♀ 1.81–1.95 (mean 1.89) mm.

Legs. Distal end of mid tibia with 5 spines (Fig. 5 E).

Male

Tergites. —Tergite 6. Emargination of the posterior border relatively broad, without a transversal torus behind the median ridge (Figs 3 C, 5 A). **Tergites 7 and 8**. Cuticule and glandular structures of *Phyllodromica*

iberica morph #1 strongly sculptured as already described in detail in the section "The characteristics of the *subaptera*-group". Median lobe of T7 short, shorter than distance between bristle fields and the posterior border of the tergite, almost without glandular pores (Fig. 3 D). **Tergite 10**, Supraanal plate triangularely rounded (Fig. 3 G).

Sternites. —Paraproct. Medio-anterior process of the right paraproct without a bulge (Figs 3 G, 5 D).

Genitalia. —Helmet sclerite. "Frontal" part and in the "rear" reduced (see section "The characteristics of the *subaptera*-group").

Colouration.—**Tergites 2–5**. Posterior extensions of the dark anterior area usually weakly developed or missing (Fig. 3 B). **Tergite 6**. Dark area may reach near to the posterior border of the tergite leaving at least a narrow light margin, often lightened to various extents along the longitudinal midline and along a transversal line shortly behind the ridge (Fig. 3 C), sometimes reduced to two relatively small clusters of dark spots behind the ridge (Fig. 5 A). **Tergite 7**. Posterior and lateral slopes of the mound very dark (brown), remaining parts of the dark area much lighter coloured, at the bottom of the trough in the middle with a whitish patch (Fig. 3 D). **Tergite 8**. Median dark extension broad, laterally often bordered by anterior projections of the light posterior area sometimes reaching the transversal edge (Fig. 5 B), or at the same position near the edge with a pair of light patches (Fig. 3 E). Mediolateral extensions usually indistinct. Conical process as a rule lightly coloured (Fig. 5 B).

Female (Fig. 5 F–I).

For description of legs, genitalia and colouration see description of *P. subaptera*.

Genetic Data. 1597 basepairs of the mitochondrial genome including the complete cytochrome c oxidase subunit I (COI) gene were analysed in two paratype specimens (see above). *Phyllodromica iberica*_Paratype Sp 292b/M1_1597bp and *Phyllodromica iberica*_Paratype Sp 292b/M2_1597bp share the same sequence. The complete sequences are shown in Appendix 4.

Geographical distribution (Fig. 16). Widely distributed in Spain, except in the northeastern and northwestern corners and the south, presumably also occurring in Portugal (females at localities Po 19 and 24, Figs 15, 17).

Other species of the *subaptera*-group found. *P. subaptera*: Sp 419.

Other morphs of *P. iberica* found. Morph #2: Sp 366, 512; morph #3: Sp 270, 335, 367, 375, 380, 386, 388, 389, 446, 448, 449, 507, 512.

Phyllodromica iberica morph #2

(Figs 6 A–I, 7 A–H, 8 A–G, 17)

Phyllodromica subaptera morph #2. —Knebelsberger & Bohn, 2003.

Material. Numerous specimens from the following localities: Spain. Sp 265, a, 266, a, 267, a, b, c, d, 268, a, 269a, 364, 365, a, 366, 512, a.

Description. Size. Length of pronotum: ♂ 1.46–1.59 (mean 1.53) mm; ♀ 1.76–1.93 (mean 1.83) mm.

Legs. Distal end of mid tibia with 5 spines.

Male

Tergites. —Tergite 6. Emargination of the posterior border narrower than in all other representatives of the group and deeper than in morph #1 (Figs 6 C, 8 A–D). Immediately behind the transversal ridge cuticle elevated to a narrow torus running in parallel to the transversal ridge (Fig. 7 A–C). The torus is interrupted in the middle and fades away laterally, shortly before the ridge disappears. Along the torus the bristles are arranged in an extraordinary density. Posteriorly the torus declines medio-laterally to two shallow longitudinal depressions (white arrows in Fig. 7 A). **Tergite 7**. Median lobe somewhat longer than in morph #1, but shorter than distance between bristle fields and the posterior border of the tergite, almost without glandular pores (Fig. 6 D). Trough (Figs 6 D, 7 D) less deep than in morph #1, anterior wall scarcely hollowed out anteriorly,

medially relatively steep. Mound low and small, less broad than the median lobe (Fig. 6 D). Bristle fields small, longitudinally oval, immediately adjacent, rarely separated by a very narrow bristleless ridge (Fig. 6 D). The bristle fields are on both sides of the ridge deepened to shallow grooves with relative strongly declining posterior wall, appearing as a crescent-shaped black shadow posteriorly of each of the two bristle fields (white arrow heads in Fig. 6 D), but less deep than in morph #1. **Tergite 8**. Similar as in morph #1, but central mound lower, sinusoidal edge anteriorly less steeply declining, mound not broader than the lateral pits, with a smaller conelike process; median gap of bristles smaller (Figs 7 F–H). **Tergite 10**, supraanal plate triangular, more rounded than in morph #1 (Fig. 6 G).

Sternites. —Paraproct. Medio-anterior process of right paraproct without bulge (Fig. 6 G).

Colouration. —**Tergites 2–5**. Posterior extensions of the dark area usually weakly developed (Fig. 6 B) or missing. **Tergite 6**. Dark area not reaching the posterior border of the tergite leaving a light margin (Fig. 6 C), often with small lightenings forming a central **Y**- or **v**-shaped figure (Fig. 8 A, C) occasionally with prolonged transversal arms along the tori (Fig. 8 B, D). **Tergite 7** (Fig. 6 D). Very similar to morph #1, but very dark (brown) colouration posteriorly and laterally of the mound, often extended latero-posteriorly. **Tergite 8** (Fig. 6 E). Very similar to morph #1, but dark area posteriorly less extended with median and mediolateral extensions. Conical process lighter coloured than in morph #1.

Female (Fig. 8 F, G)

For description of legs, genitalia and colouration see description of *P. subaptera.*

Genetic Data. 1597 basepairs of the mitochondrial genome including the complete cytochrome c oxidase subunit I (COI) gene were analysed in two specimens (Sp 267d/M5, Sp 267d/M6). DNA and associated parts of body are stored in the DNATAX collection of the ZSM under storage numbers DNATAX02863 (Sp 267d/M5) and DNATAX02864 (Sp 267d/M6). The sequences were submitted to GenBank under the accession numbers:AM600687 (DNATAX02863) and AM600688 (DNATAX02864).

The sequences of *P. iberica* morph #2_ Sp 267d/M5_1597bp and *P. iberica* morph #2 Sp 267d/M6_1597bp differ in one position (Appendix 5). The complete sequences are shown in Appendix 4.

Geographical distribution (Fig. 17). Small distribution area in eastern Spain, running ± parallel to the coast between Rio Ebro and Rio Túria.

Other species of the *subaptera*-group found. *P subaptera*: Sp 365.

Other morphs of *P. iberica* found. Morph #1: Sp 366, 512; morph #3: Sp 512.

Phyllodromica iberica morph #3

(Figs 9 A–I, 10 A–H, 11 A–L, 17)

Phyllodromica subaptera morph #3. —Knebelsberger & Bohn, 2003.

Material. Numerous specimens from the following localities: Spain. Sp 148b, 186, a, b, 270, a, b, c, 271, 335, 360, a, 361, a, 363, 367, 372, 375, 380, a, 381a, 386, a, 387, a, 388, a, 389, a, 395, 446, a, 448, 449a, 451, 459, a, b, 460, 507a, 512.

Description. Size. Length of pronotum: ♂ 1.44–1.64 (mean 1.56) mm; ♀ 1.78–2.05 (mean 1.91) mm.

Legs. Distal end of mid tibia with 5 spines.

Male

Tergites. —**Tergite 6**. Emargination of the posterior border similar as in morph #1 (Figs 9 C, 11 B, D, E, F, I). Behind the transversal ridge sometimes with structures similar to morph #2: A variably enhanced density of bristles in a line (Fig. 11 D) was found at the following localities: Sp 363 (in 1of 1 specimen), Sp 375 (in 1 of 2 specimens), Sp 395 (in 2 of 2 specimens), Sp 449b (in 1 of 1 specimen), Sp 451 (in 1 of 1 specimen) and Sp 460 (in 1 of 2 specimens). A line of bristles on a kind of torus (Fig. 11 B, C) was found at the localities Sp 148b (in 1of 1 specimen), Sp 270c (in 5 of 6 specimens), Sp 449a (in 3 of 3 specimens), Sp 459a (in 1 of 1 specimen) and Sp 512 (in 2 of 7 specimens). The structures were never as strongly developed as in morph #2.

Tergite 7. Median lobe longer than in the other morphs but shorter than distance between bristle fields and the posterior border of the tergite, almost without glandular pores. Trough, mound and bristle fields similar as in morph #2: anterior wall of trough scarcely hollowed out anteriorly, medially relatively steep (Fig. 9 D). Mound lower and smaller than in morph #2. Bristle fields small and longitudinally oval, mostly somewhat smaller and with fewer bristles than in morph #2. Anteriorly, bristle fields immediately adjacent, rarely separated by a very narrow bristleless ridge (Fig. 10 A). Posteriorly, bristle fields separated by a bristleless ridge appearing as a small noselike structure as in morph #1 but considerably smaller. Bristle fields laterally limited by a bulge-like cuticular structure (white arrow heads in Fig. 10 A). **Tergite 8**. Surface scarcely elevated, with only a slight slope towards the anterior border; cone forming a variously sized membraneous bubble, sometimes relatively large (Fig. 10 B) but in most cases rather small and often partly invaginated (due to preparation for scanning electrone microscopy?) (Fig.10 F, C, D). Distance between anterior processes small (Figs 9 E, 11 A, H, L). Without a median gap in the distribution of the bristles in the mound region (Fig. 10 B, F). **Tergite 10**. Supraanal plate triangular, similarly rounded as in morph #2 (Fig. 9 G).

Sternites. —Paraproct. Medio-anterior process of right paraproct without bulge (Fig. 9 G).

Colouration. —**Tergites 2–5**. Posterior extensions of dark area weakly developed or missing (Fig. 9 B). **Tergite 6**. Dark area variously extended, almostly reaching to the posterior border of the tergite, but always leaving at least a narrow light margin (Fig. 9 C), without or with lightenings especially along the longitudinal midline (Fig. 11 D) and in a transversal line behind the ridge (Fig. 11 E, F, I); in some cases dark area appearing as two transversely oval clusters of dark spots just behind the transversal ridge (Fig. 11 E), similar as in some specimens of morph #1. **Tergite 7**. Similar to morph #2 (Fig. 11 K), in some cases lateral parts of the dark area less dark (Fig. 9 D). **Tergite 8**. Dark area with light anterior projections which are much closer together than in morph #1 and enclosing a dark band (Figs 9 E, 11 L) or a completely isolated dark patch; sometimes the median dark marking is missing completely and the light anterior projections combine to a broad tongue (Fig. 11 A).

Female (Fig. 10 G, H)

For description of legs, genitalia and colouration see description of *P. subaptera*.

Genetic Data. 1597 basepairs of the mitochondrial genome including the complete cytochrome c oxidase subunit I (COI) gene were analysed in two specimens (Sp 380a/M5, Sp 380a/M6). DNA and associated parts of body are stored in the DNATAX collection of ZSM under storage numbers DNATAX02865 (Sp 380a/M5) and DNATAX02866 (Sp 380a/M6). The sequences were submitted to GenBank under the accession numbers: AM600689 (DNATAX02865) and AM600690 (DNATAX02866). The sequences of *P. iberica* morph #3_Sp 380a/M5_1597bp and *P. iberica* morph #3_Paratype Sp 380a/M6_1597bp differ in 6 positions (Appendix 5). The complete sequences are shown in Appendix 4.

Geographical distribution (Fig. 17). Morph #3 is found in two distinct areas, one covering nearly the whole north eastern part of Spain, the other covering only a very small area in the south in the western Serranìa de Ronda. The absence of this morph in areas between is certainly not a sampling artefact since there are numerous localities in-between where other morphs had been found (Figs 16 and 17).

Other species of *subaptera*-group found. *P. subaptera*: Sp148, 186, 381, 395.

Other morphs of *P. iberica* found. Morph #1: Sp 270, 335, 367, 375, 380, 386, 388, 389, 446, 448, 449, 507, 512; morph #2: Sp 512.

Remarks. At several localities remarkable variations in tergites 7 and 8 of the males have been found: At the localities Sp 186b, 270c, 459b and 512 (Fig. 17, morph #3 symbols labeled with an arrow) the bulge-like cuticule limitation of the bristle field on tergite 7 of some of the males appears more extended laterally (white arrows in Fig. 11 G). In these cases the colouration of the tergite also differs: the lateral parts of the darkly coloured area appear scarcely lighter than the mound region (Fig. 11 G). These structures and the colouration of tergite 7 were always combined with a mostly darkly coloured tergite 8 (except for a light posterior margin) (Fig. 11 H).

At locality 335 (Fig. 17, morph #3 symbol labeled with an "+") all the males have been found with bristle fields which appear slightly larger than in the remaining specimens of morph #3 and of morph #2. The trough and the mound are well expressed. The posterior wall of the bristle fields appears more strongly hollowed out posteriorly (appearing as a crescent-shaped black shadow posteriorly of each of the two bristle fields, white arrows in Fig. 11 K), and are more pronounced than in the remaining specimens of morph #3 and of morph #2. This formation of the structures on tergite 7 was always combined with a relatively large cone on T8 (Fig. 11 L).

Inspite of the remarkable morphological intraspecific variability morph #3 can always be clearly distinguished from morph #2.

***Phyllodromica quadracantha*, spec. nov.**
(Figs 8 I, 12 A–I, 13 A–H, 17)

Phyllodromica subaptera morph #4. —Knebelsberger & Bohn, 2003.

Holotype: ♂, Spain, Prov. Granada, Sa. de Baza, ca. 15 km WSW Baza, 1100 m, 20.–23.III.2001, leg. T. Knebelsberger (on two slides, Sp203d/M1); deposited in ZSM.

Paratypes: 5 ♂, same data as holotype. Sp 203d/M11 (frozen DNA; parts of body in 98 % ethanol); Sp 203d/M12 (frozen DNA; parts of body in 98 % ethanol); Sp 203d/M2 (on two slides); Sp 203d/M3 (on two slides); Sp 203d/M9 (on two slides).

Paratype DNA and associated parts of body are stored in the DNATAX collection of ZSM under storage numbers DNATAX02867 (Paratype Sp 203d/M11) and DNATAX02868 (Paratype Sp 203d/M12). The sequences were submitted to GenBank under the accession numbers: AM600691 (DNATAX02867) and AM600692 (DNATAX02868). The remaining 3 paratypes (Sp 203d/M2, 3, 9) are deposited in the private collection of T. Knebelsberger.

Additional material. Numerous specimens from the following localities: Spain. Sp 191, a, 195, 203, a, b, c, d, 207, a, 472, a, b, 473, a, 493, 495, 497, 498, 499, 500, 501, 502, 504, a.

Etymology. The name of the species refers to the presence of only 4 distal tibia spines on the second pair of legs in males.

Description. Size. Length of pronotum: ♂ 1.35–1.56 (mean 1.45) mm; ♀ 1.71–1.90 (mean 1.81) mm.

Legs. Distal end of mid tibia with only 4 spines (Fig. 14 C), females rarely 5.

Male

Tergites. —Tergite 6. Emargination of the posterior border relatively broad and less deep than in the other species, without torus behind the transversal ridge (Fig. 12 C). **Tergite 7**. Median lobe long, at least as long as the distance between the bristle fields and the posterior border of the tergite, covered with numerous glandular pores (Figs 12 D, 13 A). Trough very shallow, almost in the plane of the tergite surface. Mound flat, mainly elevated behind the bristle fields. Bristle fields moderately large, in outline broadly oval to circular, immediately adjacent, rarely separated by a very narrow bristleless ridge, posteriorly appearing deepened by the elevating surface of the mound; bristle fields with indistinct borders (Fig. 13 A). The male from locality Sp 504a (Fig. 14 E–G) differs slightly in the morphology of the bristle fields: the bristle fields are somewhat larger and slightly separated by a bristleless ridgelike structure (Fig. 14 F). **Tergite 8**. Without any sculpturing on the surface, rarely with weak depressions at the base of the anterior processes; membraneous incision between the anterior processes narrow (Figs 12 E). Note: The membraneous incision between the anterior processes appears relatively broad due to an unnatural stretching of the tergite during preparation (Fig. 14 G). Cone completely missing (Fig. 13 C); without median gap in the distribution of the bristles (Fig. 13 B). **Tergite 10**. Supraanal plate broadly rounded (Fig. 12 G).

Sternites. —Paraproct. Medio-anterior process of the right parapoct with a bulge (**bu**) at the base (Fig. 14 B).

Genitalia. —Helmet sclerite. "Frontal" part (**fr**) broadly rounded, in the "rear" (**re**) with a relatively long acuminate process (Fig. 14 D) (in *P. iberica* the anterior part and the acuminate process of the helmet sclerite are reduced (Fig. 8 E)).

Colouration. —Tergites 2–5. Dark anterior area often with short posterior extensions (Fig. 12 B). **Tergite 6**. Dark area broadly reaching the posterior tergite border, behind the transversal ridge often with small lightenings medially and/or along a transversal line at some distance from the ridge (Figs 12 C, 14 E). **Tergite 7.** As in tergite 6 with dark area broadly reaching the posterior border, central and posterior part darker than the remainder, bristle fields and immediate surroundings not seldom lightly coloured, trough in the middle with a whitish patch (Fig. 12 D) as in the other species. **Tergite 8**. Dark posterior extensions medio-laterally usually not strongly pronounced, median extension often well developed (Fig. 12 E).

Female

Legs. Distal end of mid tibia usually with only 4 long spines, rarely with a fifth short spine in ventro-posterior position.

Genitalia. No additional sclerotization in the angle between intercalary sclerite and the posterior lobe of valvifere II, the latter very broad, egg-shaped (Fig. 13 G).

Colouration. Disk of pronotum regularly mottled with variously shaped dark spots; anterior border never with a dark crescent (Fig. 13 D). Transparent margin of the pronotum not well set off, especially anteriorly and in the latero-posterior region with numerous small dots. Meso- and metanotum with dark anterior part ending shortly behind the transversal ridge, from there with 6 to 7 bar-shaped posterior projections, remaining surface quite regularly mottled.

Genetic Data. 1597 basepairs of the mitochondrial genome including the complete cytochrome c oxidase subunit I (COI) gene were analysed. in two paratype specimens (Sp203d/M11, Sp203d/M12). The sequences of *Phyllodromica quadracantha*_Paratype Sp203d/M11_1585bp and *Phyllodromica quadracantha*_Paratype Sp203d/M12_1585bp differ in 19 positions (Appendix 5). The complete sequences are shown in Appendix 4.

Geographical distribution (Fig. 17). Relatively small distribution area in the southeast of Spain separated from other bisexual species. One isolated population (Sp 504) has been found further northeast.

Other species of the *subaptera*-group found. *P. subaptera*: Sp 191, 195, 203, 207, 472, 473, 493, 495, 498, 504.

Remarks. At the locality Sp504 only one male (and some females) has been found. It shows remarkable differences in the structures of tergite 7, which might indicate a taxonomic separation. More material is necessary to clarify the situation.

Species separation

Morphological differences

As already noted in the species descriptions, *P. iberica* and *P. quadracantha* can be clearly identified and separated from one another using the morphological differences in the males and females.

Within the males of *P. iberica* three morphs can be distinguished. Morph #1 can be clearly separated from morph #2 and #3. The males of the latter two morphs exhibit one structure which possibly indicates recent genetic exchange between them: In morph #2 on tergite 6, immediately behind the transversal ridge, the cuticle is elevated to a narrow torus (Fig. 7 A–C). It is interrupted in the middle and fades away laterally. The bristles along the torus are extraordinarily dense. At several collecting localities of morph #3, specimens have also been found with an enhanced density of bristles sometimes even combined with a torus-like structure (see species description of *P. iberica* morph #3: T6). As in morph #2, the structures are located immediately behind the transversal ridge of tergite 6 (Fig. 11 B, C) but they are never as strongly developed as in morph

#2. The suspicion may arise that the structures in morph #3 are the result of recent hybridisation with morph #2. If hybridisation occurs one would expect the strongest expression of the features on tergite 6 in specimens of morph #3 exclusively or more frequently at localities where these morphs live in sympatry or in close neighbourhood. At the only locality where morph #2 and morph #3 were found in sympatry (Figs 15, 17; locality Sp 512) specimens of morph #3 with an enhanced density of bristles combined with a toruslike structure have actually been found. Morph #3 have also been found at two other localities in close neighbourhood (Figs 15, 17; localities Sp 270 and 459) where morph #2 does not occur. But specimens of morph #3 with similarly strongly expressed structures on tergite 6 were collected at two localities in the Pyrenees near the French border (Figs 15, 17; localities Sp 148 and 449) far away from the next known occurrence of morph #2 . At these localities hybridisation between these *P. iberica* morphs could not have been possible over a long period of time. This fact may indicate the independent occurrence of the structures on tergite 6 by spontaneous mutations and not by hybridization with morph #2.

Despite the clear morphological separation of the males of the three morphs of *P. iberica* they are not described as separate species in this work. The results of the morphological investigation possibly indicate recent genetic exchange between morph #2 and #3 which means that the sexual isolation is not yet completed.

DNA sequence divergence

Additional evidence indicating the degree of separation of the *subaptera*-group species (and the three morphs of *P. iberica*) is shown by comparing the inter- and intraspecific genetic differences (Appendices 6 and 7).

(1) Interspecific genetic differences

As expected, the outgroup taxon *Blattella germanica* has a rather large and constant genetic distance to the species of the *subaptera*-group ranging between **15.31 %** and **16.07 %** (Appendix 7).

The highest value of interspecific sequence divergence within the *subaptera*-group has been found between *P. quadracantha* and the remaining two species *P. subaptera* and *P. iberica* ranging from **8.86 %** to **9.11 %**. This result is in concordance with the results of the morphological analysis where *P. quadracantha* exhibits the highest number of species distinguishing features. *P. quadracantha* is obviously completely separated from the other species; it holds 114 species identifying sequence positions within the species of the *subaptera-group* (Appendix 4). The values we found are well within the range of interspecific genetic differences between closely related animal species as for instance reported by Hebert *et al.* (2003b).

Morphologically, the parthenogenetic species *P. subaptera* cannot be distinguished from the females of *P. iberica*, but remarkable differences are present at the DNA sequence level. In *P. subaptera* 8 species identifying sequence positions have been found (positions 105, 198, 312, 552, 789, 864, 1029, 1047, 1131 and 1146, Appendix 4) within the *subaptera* - group and 7 in *P. iberica* (positions 39, 237, 498, 1015, 1290, 1299 and 1488, Appendix 4) which allow clear separation. The genetic distances between *P. subaptera* and *P. iberica* range from **1.75 %** to **1.85 %**. These values are relatively low, but Hebert et al. (2003b) also found in nearly 2% of the investigated species pairs sequence divergances below 2%. Very few or even no sequence divergances were for instance reported between putatively recently diverged species of the genus *Elachista* (Lepidoptera: Gelechioidea: Elachistidae) (Kaila & Stahls, 2006).

P. subaptera reproduces through obligatory thelytokous parthenogenesis and does not interbreed with *P. iberica* which is sexually completely isolated from *P. subaptera*. This was confirmed by the genetic distances found between the two taxa.

(2) Intraspecific variability

Within *P. iberica* morph #2 exhibits 4 identifying sequence positions (positions 138, 387, 678 and 996, Appendix 4) whereas morph #1 only has one (position 1559, Appendix 4) and morph #3 no species identifying sequence position. The genetic distances between the three morphs are: **0.73 %** between morph #2 and

morph #3; **0.61 %** between morph #1 and morph #2 and **0.32 %** between morph #1 and morph #3 (Appendix 7). The value between morph #1 and morph #3 is within the range of intraspecific differences reported for instance by Hebert et *al*. (2003a) in Lepidoptera. The genetic distances for morph #2 may indicate that it is a separate species with a very recent origin. But as mentioned in the section "Morphological differences" the morphological data might indicate genetic exchange between morph #2 and morph #3. The taxonomic state of morph #2 remains to be clarified.

The sequence divergence between the two specimens of each morph of *P. iberica* is very different: the two specimens of morph #1 share the same sequence and the divergence between the morph #2 specimens is only **0.06 %** (only one basepair difference) whereas the genetic distance between the two specimens of morph #3 reaches **0.38 %**. The genetic distance between the morph #3 and morph #1 specimens are 0,26 % and 0,38 % respectively (Appendix 6). This means that the sequence divergence between morph #1 and the two specimens of morph #3 is in one case equal to the sequence divergence between the two specimens of morph #3 and in the other case even smaller. This result may indicate an incomplete separation of these two morphs because one would usually expect values of genetic variability within a morph being lower than the variability between morphs, especially when the analysed specimens of a morph were collected at the same locality. It should be noted that the direct distance between the sampled localities of morph #1 und #3 is about 400 kilometers (Fig. 15, localities Sp 292 and Sp 380)while the two specimens of morph #3 were collected on the same tuft of grass.

In *P. quadracantha* the genetic distance between the two specimens is **1.21 %** (Appendix 7) which is considerably more than the genetic distances between the three morphs of *P. iberica* (see above). The high intraspecific variability may indicate either a considerably higher age or an accelerated evolution of *P. quadracantha*. High levels of intraspecific variability are also described by Memon *et al.* (2006) who found a great overlap between intra- and interspecific genetic variability for congeneric Hemiptera COI sequences. Such results point to the problem of a exclusively DNA based species-level taxonomy which was for instance suggested by Tautz *et al*. (2003).

The intraspecific genetic distance in the parthenogenetic species *P. subaptera* is **0.57 %** which is larger than the variability found within each of the three *P. iberica* morphs. Nevertheless the two females examined here are monophyletic and share 8 synapomorphic mutations (see above).

The two examined females of *P. subaptera* have different coloured pronotal disks. In one case it is nearly completely dark (similar to Fig. 5 H), in the other case the dark colouration is less extended (similar to Fig. 5 F). Investigations of the chromosome numbers (unpublished data) have shown that parthenogenetic females with the same colouration of the pronotal disk have the same number of chromosomes which is always different to the chromosome number of parthenogenetic females with other colour patterns. Most likely the parthenogenetic species consists of different clonal strains which occur also in sympatry. The fact that the two genetically investigated strains share 8 synapomorphic sequence mutations may indicate that clonal diversity arose due to spontaneous mutations within the parthenogens and not due to a multiple origin of different clonal strains from bisexual ancestors.

(3) DNA barcoding

One aim of the inclusion of the DNA sequences in this study was to get additional information for the description of new species and to evaluate the possibility to use the sequences as DNA barcodes for species identification.

P. quadracantha specimens are easily identifiable by analysing the DNA sequences. But adult males and females may be more rapidly identified by morphology even without a deeper taxonomical knowledge of the *subaptera*-group.

Due to the 7 species identifying sequence positions within the *subaptera*-group a genetic identification of *P. iberica* specimens is possible. It is also possible to distinguish between females of *P. iberica* and the parthe-

nogenetic *P. subaptera* which do not have morphological distinguishing features. In contrast to the females, the males of *P. iberica* may be more easily identifiable by the morphological features but only if they are adults.

On the basis of DNA barcodes *P. subaptera* individuals can also be clearly identified and distinguished from the females of *P. iberica*. *P. subaptera* has 8 species identifying sequence positions within the *subaptera*-group (see above). DNA barcoding can be a helpful tool in investigating the phenomenon of parthenogenesis within the *subaptera*-group. Mainly in cases of sympatry the ratio of sexual and parthenogenetic females can be analysed relative quickly (without keeping the females alive over weeks and cultivating the oothecae until the offspring hatch and their sex analysed). Fluctuations of the frequencies can be investigated over time which may give us some details about the relative fitness of the two reproductive forms and the evolution of parthenogenesis in general.

Cladistic analysis of morphological data

A total of 24 morphological characters, 22 for males and 2 for females, was used in this study (Appendix 2). The morphology of the male glandular structures and the variation in cuticular structures on the tergites 7 and 8 in males provide the majority of variable characters (Appendix 2, characters 3–17). Of the 24 characters, 14 were coded into binary states, the remaining 10 (characters 2, 3, 6, 9, 10, 13, 14, 15, 16, 19) into multistates. Some characters appear in 2 states within a single taxon, in these cases both states were coded (e.g. "0+1" for character 11 in *nana* – group in Appendix 3). All characters were weighted equally and not ordered.

The data matrix (Appendix 3) shows that most of the characters cannot be homologized with the structures found in the outgroup taxa (Appendix 3, characters 3, 4, 6, 8, 9, 13–17), in these cases they were coded by a dash (-).

To clarify the phylogenetic relationships a cladistic analysis of morphological characters including the bisexual taxa of *subaptera*-group and the nearest related groups was performed. The MP analysis of the data matrix (Appendix 3) of the 24 distingishing characters (Appendix 2) resulted in 3 most parsimonious cladograms (length = 38 steps, consistancy index (CI) = 1.0 and retention index (RI) = 1.0). The strict consensus tree is shown in Fig. 18. Of the 24 characters, 9 (1, 5, 11, 12, 18, 19, 20, 22, 24) were parsimony informative which means they occur in 2 or more states in at least 2 terminal taxa. The states of the remaining 15 characters are autapomorphic conditions which means they do not have any influence on the internal phylogenetic relationships. The bootstrap values range between 72 % and 100 %, Bremer's support values between 1 and 5.

In the cladogram the *subaptera*-group appears monophyletic (bootstrap value of 72 %, Bremer's support = 1) supported by one synapomorphic character (Appendix 2, character 12), namely the presence of two anterior processes on tergite 8. The sistergroup relationship between *carpetana*- and *subaptera*-group is supported by 2 synapomorphic characters (Appendix 2, characters 1 and 5; bootstrap value of 91 %, Bremer's support = 2). Both groups show strongly expressed excavations in the region of the intersegmental membrane glands on tergites 5 and 6; the bristle fields of the glandular structures on tergite 7 are in both cases strongly deepened at the posterior border.

Within the *subaptera*-group the three morphs of *P. iberica* appear monophyletic supported by 6 synapomorphies (bootstrap value of 100 %, Bremer's support = 5):

1. The medio-anterior process of the right paraproct (Appendix 2, character 18) does not have a bulge at the base.

2 & 3. Both ends of the helmet sclerite are reduced (Appendix 2, characters 19 and 20).

4. The supraanal plate is triangularly rounded (Appendix 2, character 22).

5. The female genitalia show an additional sigmoidal sclerotization (Appendix 2, character 24).

6. All three taxa have glandular structures on tergite 8 (Appendix 2, character 11).

The phylogenetic relationship between the three morphs could not be resolved by the cladistic analysis of the morphological data. This indicates a recent origin of the morphs which most likely have not yet evolved to well separated taxa.

Within the *subaptera*-group the shape of the structures on tergite 7 and 8 is obviously correlated. Well developed glandular structures on tergite 7 are always combined with well developed structures on tergite 8.

In *P. iberica* morph #1 the central mound on tergite 7 (Fig. 3 D) as well as the conelike process on tergite 8 (Fig. 3 E), for instance, appear well developed. In morph #2 and #3 the central mound of tergite 7 (Figs 6 D, 9 D) as well as the conelike process on tergite 8 (Figs 7 F, 10 F) appear smaller. In *P. quadracantha* the central mound of tergite 7 (Fig. 12 D) is even smaller and the conelike process (Fig. 13 B) is completely missing.

The arrangement of the taxa of *subaptera-group* found by the MP analysis may suggest a step by step evolution of glandular structures and cuticular structures on tergites 7 and 8 from *P. quadracantha,* which shows the weakest expression to that in *P. iberica* morph #3 and morph #2 up to morph #1 with the most strongly expressed structures on both tergites. This process which is here called "**formation-hypothesis**" postulates a common ancestor of the *subaptera*-group with weakly expressed structures on tergite 7 and without glandular structures on tergite 8. This basal state of the characters is still more or less present in *P. quadracantha*.

But there are also arguments which contradict the "formation-hypothesis" and support the reverse evolutionary process - a step by step reduction of the structures on tergites 7 and 8. In this "**reduction-hypothesis**" *P. iberica* morph #1 represents the most basal character state with well developed cuticular structures and glandular structures on both tergites which were stepwise reduced in *P. iberica* morph #2 and morph #3 down to *P. quadracantha*.

The most important argument to support the "reduction-hypothesis" is the presence of the two anterior processes and a membraneous part between them which can be found on tergite 8 of *P. quadracantha* (Fig. 12 E). The shape of these structures, especially the membraneous part between the anterior processes, can more likely be explained as the relict of stepwise reduced structures between the processes. In the "formation-hypothesis" where *P. quadracantha* represents the basal state of characters the presence of these structure cannot be easily explained because they have no obvious biological function.

Additionally, the distance between the anterior processes on tergit 8 is connected with the state of reduction of the structures between them. In *P. iberica* morph #1 the distance is rather large (Fig. 3 E) and becomes smaller in morph #2 (Fig. 6 E) and morph #3 (Fig. 9 E). In *P. quadracantha* (Fig. 12 E), where the central mound and the conelike process are completely reduced, the distance between the anterior processes is smallest. In *P. iberica* morph #2, morph #3 and *P. quadracantha* the glandular structures and the cuticular structures, which are located in the central parts of the tergite, obviously undergo a step by step reduction and the lateral parts of the tergite shift towards the middle.

The "reduction-hypothesis" gets additional support by an examination of the closest relatives of the *subaptera*-group: In the *nana*- and *carpetana*-group secondary reductions of glandular structures on tergite 8 have also been assumed. Glandular structures on tergite 8 are presumably not an autapomorphy within *subaptera*-group but a synapomorphy of *nana*-, *carpetana*- and *subaptera*-group (Bohn 1999). It seems to be unlikely that the structures were reduced first in the common ancestor of *subaptera*-group and than secondarily evolved again up to *P. iberica* morph #1. If the "reduction-hypothesis" is true *P. quadracantha* and *P. iberica* morph #3 have to be seen as sistertaxa which means that the *P. iberica*–group is paraphyletic.

The "formation-hypothesis" seems to be the more likely postulate because the monophyly of the morphs of *P. iberica* is very well supported by 6 autapomorphic characters (see above). Even if character 11 (Appendix 2) dealing with the presence and absence of glandular structures on tergite 8 has to be treated with special care (discussed in detail above), there are 5 remaining characters, where tergites 7 & 8 are not involved, which demonstrate that *P. quadracantha* most likely represents the plesiomorphic character states and has to be seen as sister taxon of *P. iberica*:

1. The medio-anterior process of the right paraproct has a bulge at the base (Fig. 14 B) (Appendix 2, character 18) which can also be found in all of the outgroup taxa but not in *P. iberica* (Fig. 5 D).

2. & 3. The helmet sclerite is normally formed (Fig. 14 D) (Appendix 2, characters 19 and 20) as in the two closest relative groups, the *nana*- and the *carpetana*-group and not reduced as in *P. iberica* (Fig. 8 E).

4. The supraanal-plate is broadly rounded (Fig. 12 G) (Appendix 2, character 22) which can also be found in all outgroup taxa; in *P. iberica* the supraanal plate is triangularly rounded (e. g. Fig. 9 G). Although a triangularely rounded supraanal plate can also sometimes be found in the *carpetana*-group the broadly rounded one is presumably the plesiomorphic alternative.

5. The female genitalia show no additional sigmoidal sclerotization (Fig. 13 G) (Appendix 2, character 24) which is also missing in the outgroup taxa and only developed in *P. iberica* as well as in parthenogenetic *P. subaptera* (Fig. 2 D, E). In a few specimens of *P. carpetana* an additional sclerotization has been found; but it differs in shape and position from the sclerotization found in *P. iberica* and cannot be easily considered as homologous structure.

Due to the relatively weak support of the sistergroup relationship between *P. iberica* and *P. quadracantha* there may still be the possibility that the *subaptera*-group is paraphyletic and *P. quadracantha* is the sister taxon of *carpetana*-group.

Phylogenetic analyses of DNA sequences

To test the phylogeny based on the morphological characters and the two hypotheses of the direction of the evolution of the glandular structures on tergites 7 and 8 – the ”reduction hypothesis” and the “formation-hypothesis” (see above) - phylogenetic analyses of the molecular data were performed. The great advantage of the molecular analysis over the cladistic analysis of the morphological data is that the parthenogenetic species can also be included in the phylogenetic reconstruction. The sequences of 2 specimens of *P. subaptera*, *P. quadracantha* and each of the *P. iberica* morphs and the sequence of *Blattella germanica* were involved in the different calculations.

COI sequence data.

The sequences analysed show the typical A/T bias known for insect sequences (base frequencies: 0.31 A, 0.16 C, 0.15 G, 0.38 T). Within the complete dataset, including *Blattella germanica*, 325 variable positions could be detected (parsimony-informative positions: 154). Within the *subaptera*-group 173 positions were variable (parsimony-informative positions: 146). The species determining positions have already been mentioned in the section “DNA sequence divergence”.

Phylogenetic analysis.

The MP analysis resulted in 2 equally most parsimonious trees (length = 374 steps, CI = 0.94, RI = 0.90). The two trees only differ in the arrangement of the two *P. iberica* morph #3 specimens. In one case they are monophyletic, in the other paraphyletic. The strict consensus tree is shown in Figure 19.

The best fit ML model (GTR+I) contained the nucleotide substitution rate parameters: [A-C] = 0.2014, [A-G] = 12.7427, [A-T] = 7.9342, [C-G] = 0.0000, [C-T] = 44.9768, [G-T] = 1.0000. The estimated nucleotide frequencies were A = 0.3119, C = 0.1569, G = 0.1541 and T = 0.3771. The proportion of invariable sites (I) was 0.6665. This model of sequence evolution supports one best tree (-lnL = 3767.4592), shown in Figure 20.

The ML tree was identical in topology with one of the two MP trees. The consensus tree resulting from the Bayesian analysis including the posterior probabilities (pp) of each clade is shown in Figure 21. The tree has also the same topology as the ML tree.

P. iberica appears monophyletic in every calculation (Fig. 19, MP bootstrap value = 88 %; Fig. 21, pp = 99 %). *P. iberica* morph #1 as well as morph #2 show also monophyly (Fig. 19, MP bootstrap values of 71 % / 97 %; Fig. 21, pp = 100 %). Morph #3 appears monophyletic in one of the two MP trees and paraphyletic in the other calculations.

The monophyly of *P. iberica* was also very well supported in the analysis of the morphological characters (Fig. 18) but there was no information on the phylogenetic relationships between the three morphs. The molecular analysis found sister group relationship between morph #1 and morph #3 (Fig. 19, MP bootsrap value of 87 %; Fig. 21, pp = 54 %). But if morph #2 and morph #3 show hybridization as discussed in the section "species separation" they should be more closely related than morph #1 and morph #3 where none of the morphological features indicate recent genetic exchange. The molecular results suggest that morph #3 didn't have genetic exchange with other morphs. But these results have to be seen as preleminary. A more extended sampling at the level of populations–as performed in the analysis of the morphological characters–is necessary to elucidate the phylogenetic relationships and the degree of separation between the three morphs of *P. iberica*. Sequence data of ribosomal genes (e. g. 28s rRNA) should also be included in the further analyses.

The parthenogenetic species *P. subaptera* is also monophyletic (Figs 19–21, MP bootstrap support of 100 %, pp = 99 %) although the two specimens analysed most likely represent two different parthenogenetic strains. Highest support was obtained for the sistergroup relationship between *P. subaptera* and *P. iberica* (MP bootstrap support of 100 %, pp = 100 %). The question on the bisexual ancestor of the parthenogenetic species *P. subaptera* seems to be answered. The clear separation of *P. subaptera* as sister taxon of *P. iberica* indicates an evolution of these parthenogens from a common ancestor and not from one of the three bisexual morphs of *P. iberica*. But the question of the origin (multiple or unique) and the spreading of the parthenogens can only be answered by a broader scaled analysis on the level of populations.

Finally, the monophyletic *P. quadracantha* (MP bootstrap support of 100 %, pp = 100 %) is undoubtly located at the base of *subaptera*-group (Figs 19–21) and may have split first from the common ancestor of the species group. But our dataset does not indicate monophyly of the whole *subaptera*-group; there was no support for a sister-group relationship between *P. quadracantha* and the remaining species. This may be due to the selection of the outgroup. The results may be different when closer related groups (*nana*- and *carpetana*-group) are included. In the analysis of the morphological characters where the closest relatives are involved the *subaptera*-group is monophyletic (Fig. 18).

The arrangement of *P. quadracantha, P. subaptera* and the three morphs of *P. iberica* is only compatible with the "formation-hypothesis" of the glandular structures within *subaptera*-group which is also supported by the phylogeny based on the morphological data.

Chromosomal numbers

Additional evidence of the phylogenetic relationships may be derived from the analysis of the chromosmal numbers of the s*ubaptera*-group species which was performed in an earlier study (Knebelsberger & Bohn 2003).

P. quadracantha and *P. iberica* morph #2 have in the female sex 22 chromosomes (21 in the male). Morph #3 has 12 (11 in the male) and in morph #1 both numbers, 12 and 22, are found. The parthenogenetic *P. subaptera* exhibits various numbers, 12, 13 and 16.

The basic diploid chromosome number in females of Ectobiinae seems to be 22 (21 in the males) which has been found in *Ectobius pallidus* by Cohen and Roth (1970) and also in *P. globososacculata*, a species of the *carpetana*-group (Knebelsberger & Bohn 2003). The lower numbers can be explained by the fusion of acrocentric chromosomes.

In this study only a few species from a few localities have been investigated; since *P. quadracantha* as

well as *P. iberica* morph #1 exhibit, partly or exclusively, the plesiomorphic number of chromosomes the data cannot contribute to the phylogenetic discussion.

Considering the low number of sampled localities it cannot be excluded that lower chromosome numbers also occurring in *P. iberica* morph #2 and *P. quadracantha*.

Conclusions

P. quadracantha represents morphologically as well as genetically a well separated species with a basal position within the *subaptera*-group. This supports the "formation hypothesis" of the evolution of the glandular structures on tergites 7 and 8 starting from *P. quadracantha* which represents the basal state of the characters up to *P. iberica* morph #1 with the most derived state of characters within this species-group.

The sequence divergence between specimens of the different *P. iberica* morphs is below 1% possibly indicating recent origin and incomplete separation. Nevertheless there is still weak support for a closer relationship between morph #1 and morph #3.

Due to the accumulation of autapomorphic morphological characters the *P. iberica* morphs can be clearly distinguished from each other. The partly sympatric occurrence of all 3 morphs may on the one hand indicate their status as separate species - no intermediate forms of the glandular structures on tergite 7 and 8 indicating hybridization between two morphs had ever been found. On the other hand the morphological structures on tergite 6 indicate rare genetic exchange between morph #2 and morph #3. But since the genetic analysis argues for a closer relationship between morph #1 and morph #3 hybridization between morph #2 and morph #3 seems to be unlikely. Following the genomic integrity species definition, introduced for butterfly species by Sperling (2003), "species are defined as populations that maintain their genomic integrity when they contact each other, even though they may occasionally exchange genes". This means in our case that the *P. iberica* morphs can be seen as individual species even though hybridization may rarely occur, but the species genome for at least a central core of it remains stable and cohesive (genomic integrity). At the moment, it is premature to raise the different morphs to species rank. This may be done as a consequence of a broader scaled molecular analysis using different molecular marker systems.

Crossbreeding experiments were performed years ago by one of the authors (T. K.), but the breeding conditions in the laboratory did not allow successful reproduction. To test the degree of the separation of the *P. iberica* morphs a replication of the crossbreeding experiments with an incubator system imitating the optimal environmental conditions should be undertaken. But even if hybrids are obtained in the laboratory this would not be absolute evidence that hybridization occurs in nature.

The genetic data have clearly shown a sister group relationship of the parthenogenetic species *P. subaptera* with *P. iberica*. This indicates the evolution of the parthenogenetic species from a common ancestor. The two *P. subaptera* specimens analysed (from the same locality) show a remarkably high sequence divergence. This indicates that *P. subaptera* consists of at least two different clonal races. The occurance of several synapomorphies on sequence level suggests that the two races most likely have been originated through the accumulation of spontaneous mutations in single strains and not through multiple origin from bisexual ancestors. The question of the origin in addition tothe reconstruction of the spreading of the parthenogenetic forms over nearly the whole Mediterranean region will be one main focus of further investigations.

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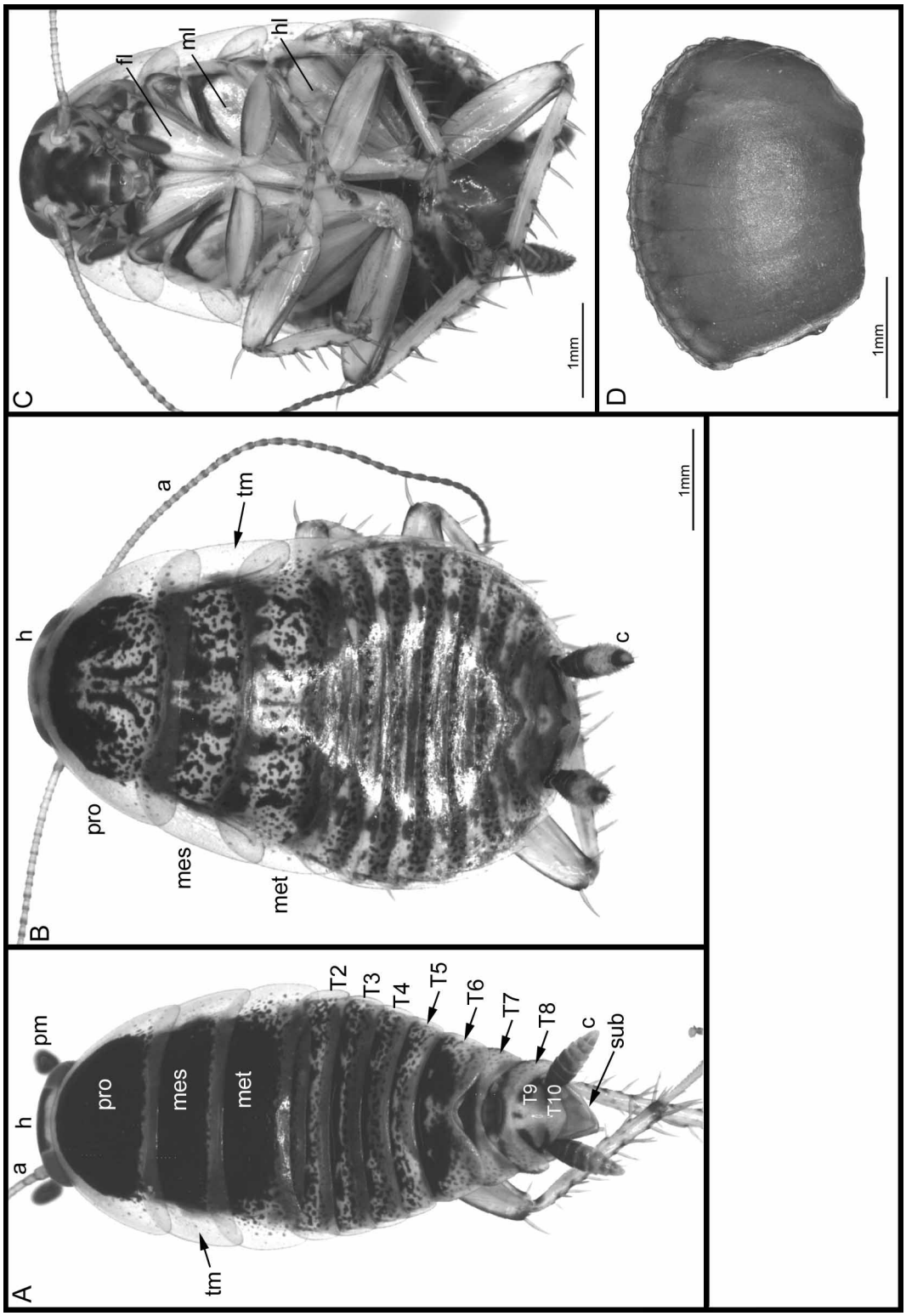


FIGURE 1. A–C *P. iberica* morph #1, habitus. (A) Male in dorsal view; (B) female in dorsal and (C) ventral view. **D** Oothek of *P. quadracantha* (lateral view). Abbreviations: **a** antenna, **c** cercus, **fl** coxa of foreleg, **h** head, **hl** coxa of hindleg, **mes** mesonotum, **met** metanotum, **ml** coxa of midleg, **pm** palpus maxillaris, **pro** pronotum, **sub** subgenital plate, **T2–T10** tergites 2–10, **tm** tegmen. Same scale in A and B. Localities: (A–C) Sp 449a, (D) Sp 500.

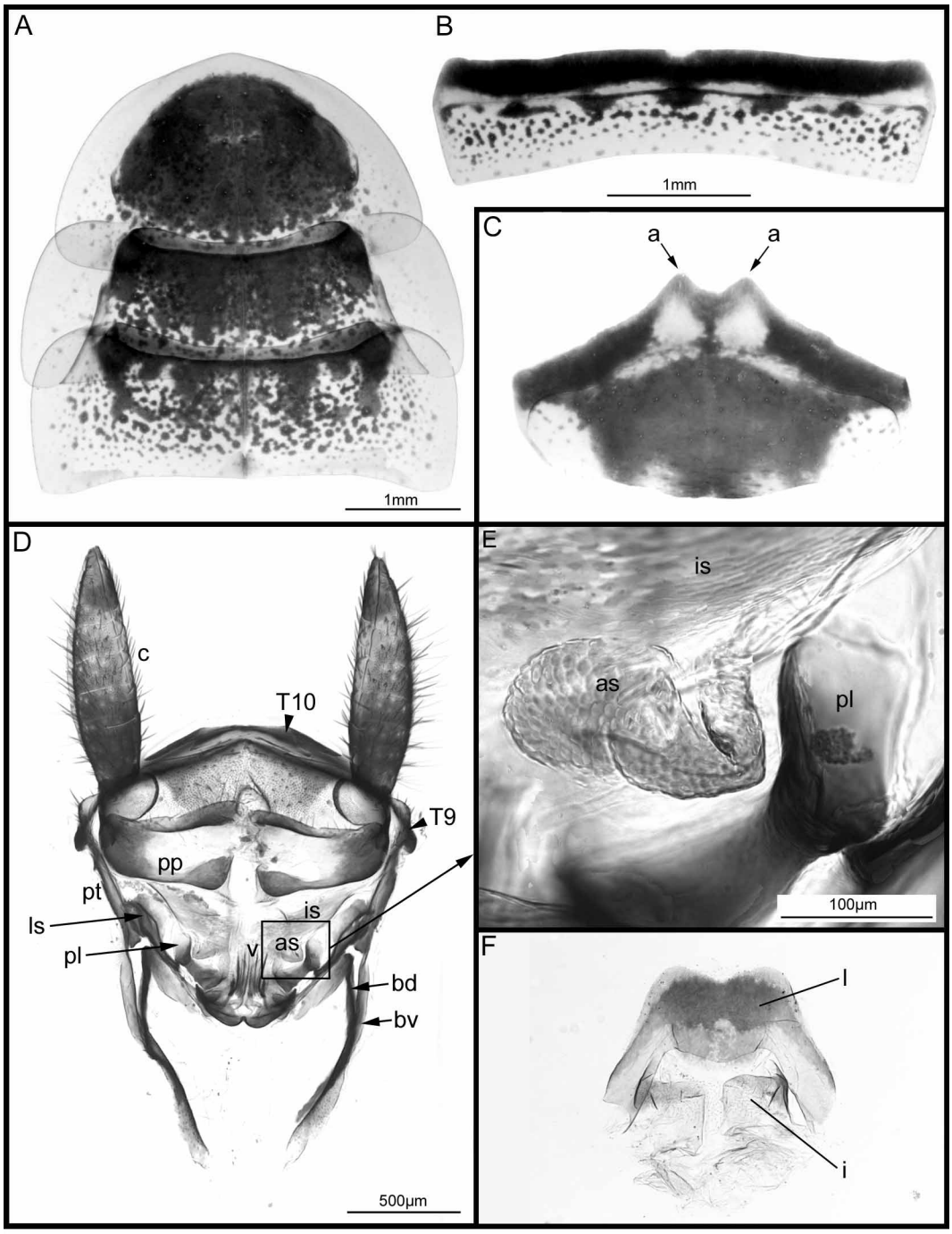


FIGURE 2. *Phyllodromica subaptera* (female). **A** Thoracal nota. **B** Abdominal tergite 5. **C** Subgenital plate with two apodemal processes (**a**). **D** Dorsal complex of genitalia with additional sclerite (**as**): ventral view, posterior end on top. **E** Additional sclerite in higher enlargement (equivalent to "black frame" in D). **F** Ventral complex of genitalia: laterosternal shelf with intersternal folds between the arms. Abbreviations: **as** additional sclerite, **a** apodemal process, **bd** dorsal sclerite of basivalvula, **bv** ventral sclerite of basivalvula, **c** cercus, **i** intersternal fold, **is** intercalary sclerite, **l** laterosternal shelf, **ls** laterosternite IX, **pl** posterior lobe of valvifer II, **pp** paraproct, **pt** paratergites, **T9** tergite 9, **T10** tergite 10, **v** valves. Same scale for (B, C) and (D, F). Identification: Sp 203c/W4.

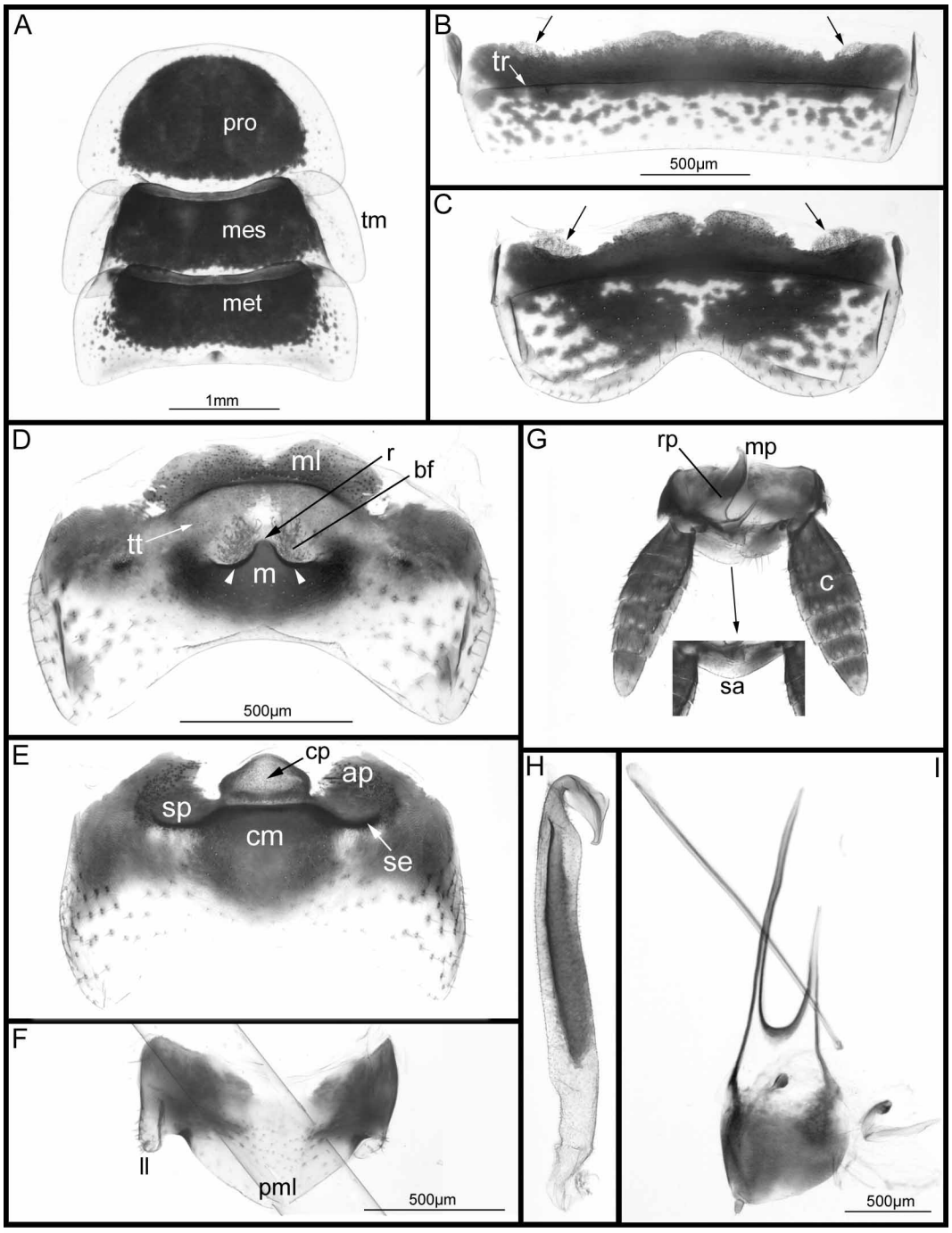


FIGURE 3. *Phyllodromica iberica* morph #1, male (holotype). **A** Thoracal nota. **B**–**F** Abdominal tergites 5–9. (B) Tergite 5 and (C) tergite 6 with membranous glands in the lateral region of the anterior margin of tergites (black arrows); (D) tergite 7, white arrow heads point to the shallow pouches appearing as crescent–shaped black shadows; (E) tergite 8; (F) tergite 9 on glass rod. **G** Terminalia with tergite 10 (**sa**), cerci and paraprocts. **H** Hook of left phallomere with the posterior end on the top. **I** Subgenital plate with remaining genital sclerites (without hook). Abbreviations: **ap** anterior process, **bf** bristle field, **c** cercus, **cm** central mound, **cp** conelike process, **ll** lateral lobe, **m** mound, **mes** mesonotum, **met** metanotum, **ml** median lobe, **mp** medio-anterior process, **pml** posterior median lobe, **pro** pronotum, **r** ridge between bristle fields, **rp** right paraproct, **sa** supraanal plate, **se** sinusoidal edge, **sp** shallow pits, **tm** tegmen, **tr** transversal ridge, **tt** transversal trough. Same scale for (B, C, G) and (D, E, H). Identification: Sp 292b/M3 (holotype).

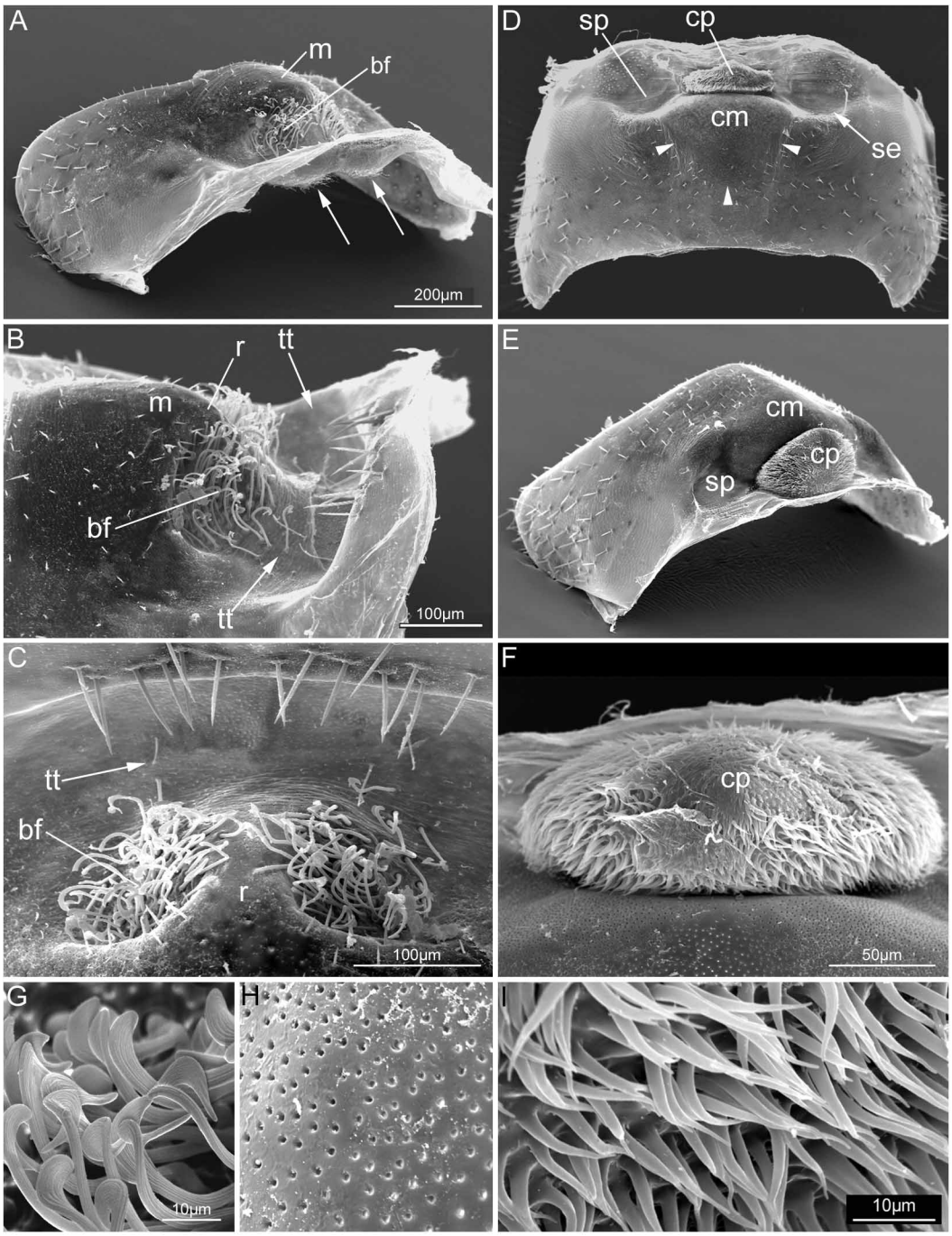


FIGURE 4. *Phyllodromica iberica* morph #1, male, SEM pictures of tergal glandular structures. **A**–**C, G** Tergite 7. (A) Latero-frontal view from slightly above, anterior wall of trough slightly hollowed out anteriorly (white arrows); (B) lateral view of the glandular region from slightly above; (C) glandular region in dorsal view; (G) bristles of bristle field. **D**–**F, H, I** Tergite 8. (D) Dorsal view of the whole tergite, median emargination in the distribution of the bristles (white arrow heads); (E) latero-frontal view from slightly above; (F) dorsal view of the conelike process; (H) porous surface of the central mound; (I) soft villi on the surface of the conelike process. Abbreviations: **bf** bristle field, **cm** central mound, **cp** conelike process, **m** mound, **r** ridge, **se** sinusoidal edge, **sp** shallow pit, **tt** transversal trough. Identification: (A–C, E–I) Sp 270a/M4, (D) Sp 85/11.

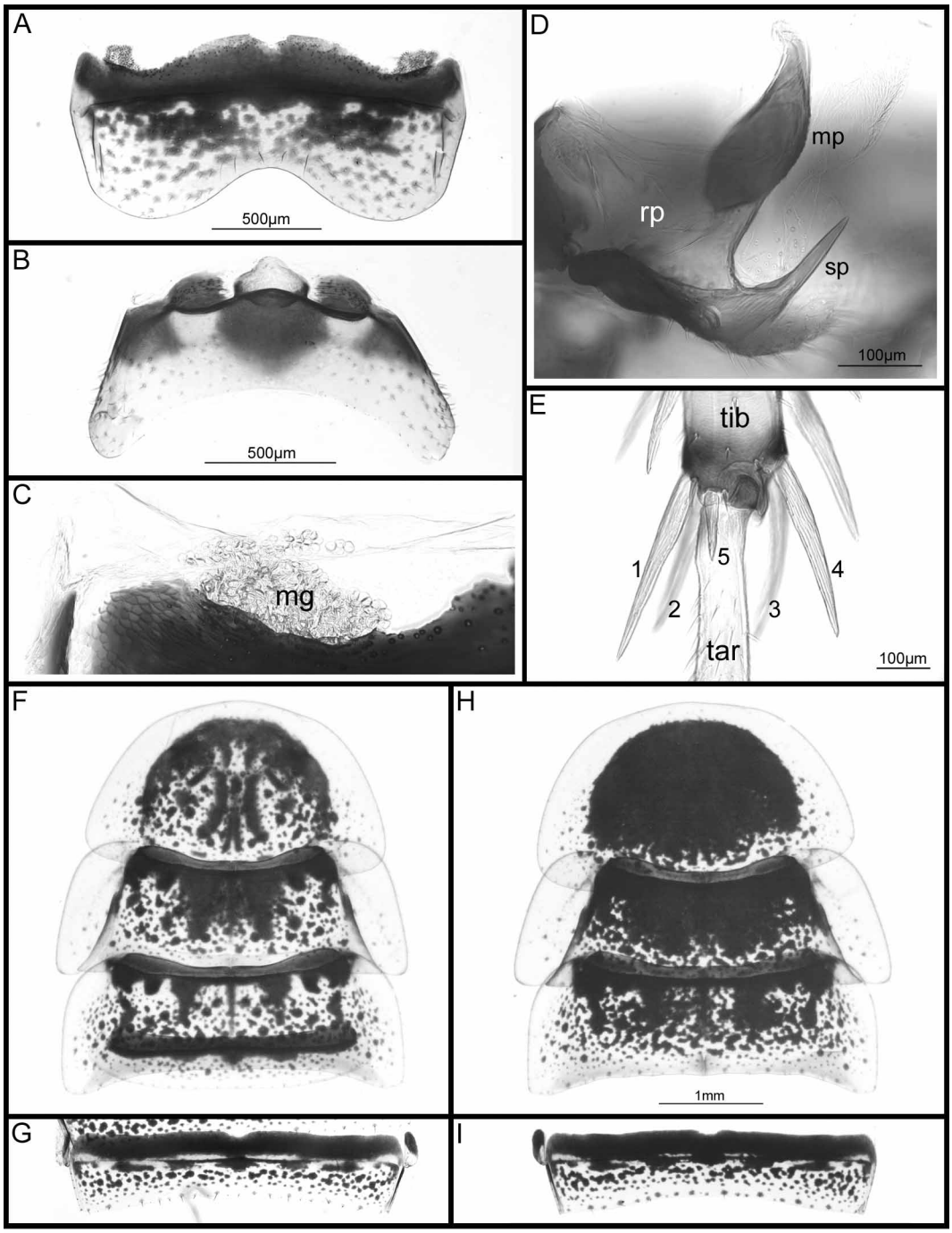


FIGURE 5. *Phyllodromica iberica* morph #1, **A**–**E**, male. (A) Tergite 7 and (B) tergite 8 of a male specimen differing from the holotype in its colouration; (C) membrane glands of the left lateral region on the anterior border of tergite 6; (D) right paraproct; (E) distal end of tibia of the right mid leg (bearing 5 distal spines) in posterior view. **F**–**I**, female. (F, H) Different colour pattern of pronotum; (G, I) tergite 5. Abbreviations: **mg** membrane glands, **mp** medio-anterior process of right paraproct, **rp** right paraproct, **sp** spinelike process of right paraproct, **tar** tarsus, **tib** tibia. Same scale for (C, D) and (F–I). Identification: (A, B) Sp 330/3, (C, D) Sp 292b/M3 (holotype), (E) Sp 510/M1, (F, G) Sp 292b/W1, (H, I) Sp 292b/W2.

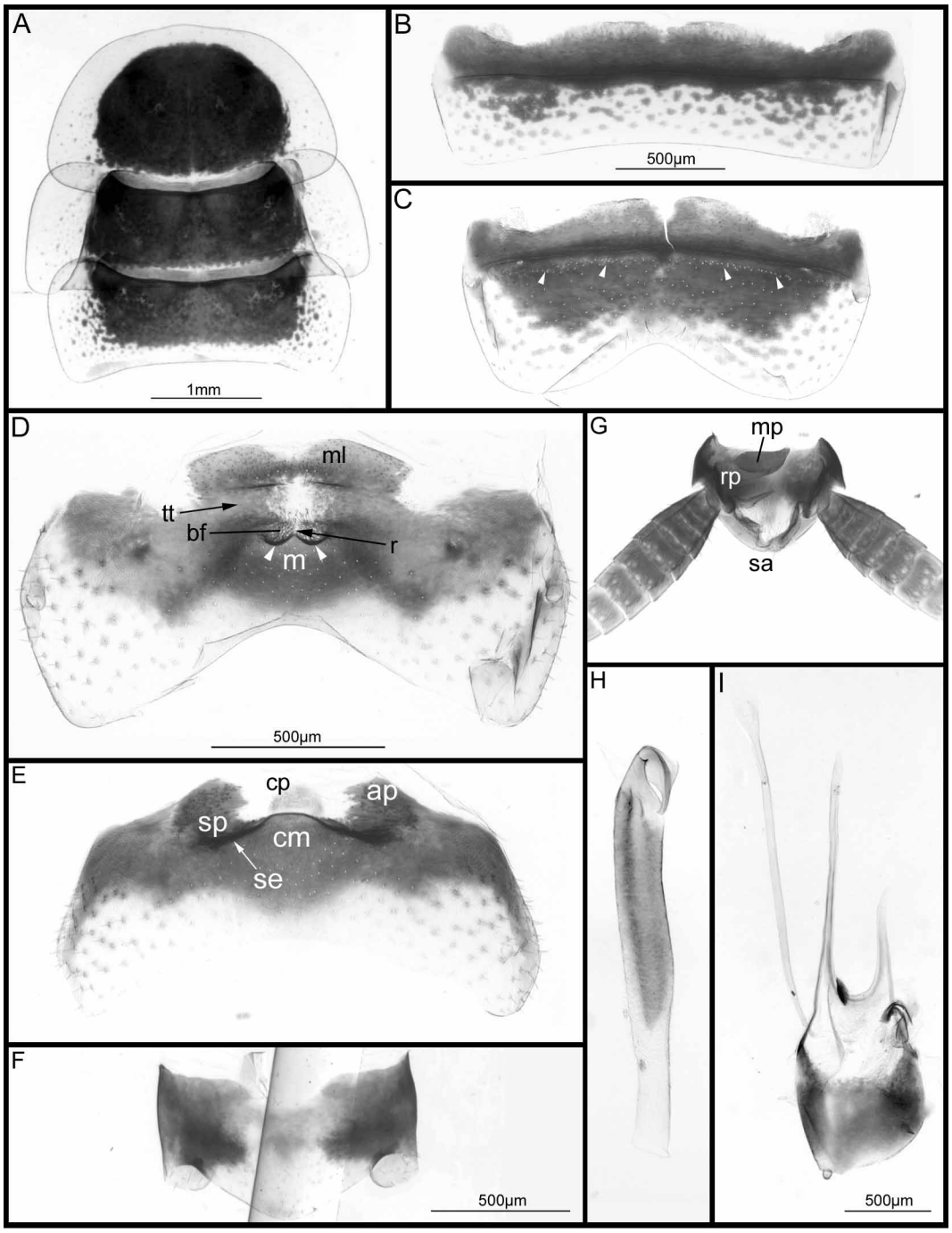


FIGURE 6. *Phyllodromica iberica* morph #2, male. **A** Thoracal nota. **B–F** Abdominal tergites 5–9. (B) Tergite 5; (C) tergite 6 with a narrow transversal torus (white arrow heads) bearing bristles (white spots) in extraordinary density; (D) tergite 7, white arrow heads point to the shallow pouches appearing as crescent–shaped black shadows; (E) tergite 8; (F) tergite 9 on glass rod. **G** Terminalia with tergite 10 (**sa**), cerci and paraprocts. **H** Hook of left phallomere with the posterior end on the top. **I** Subgenital plate with remaining genital sclerites (without hook). Abbreviations: **ap** anterior process, **bf** bristle field **cm** central mound, **cp** conelike process, **m** mound, **ml** median lobe, **mp** medio-anterior process of right paraproct, **r** ridge between bristle fields, **rp** right paraproct, **sa** supraanal plate, **se** sinusoidal edge, **sp** shallow pit, **tt** transversal trough. Same scale for (B, C, G) and (D, E, H). Identification: Sp 267c/M2.

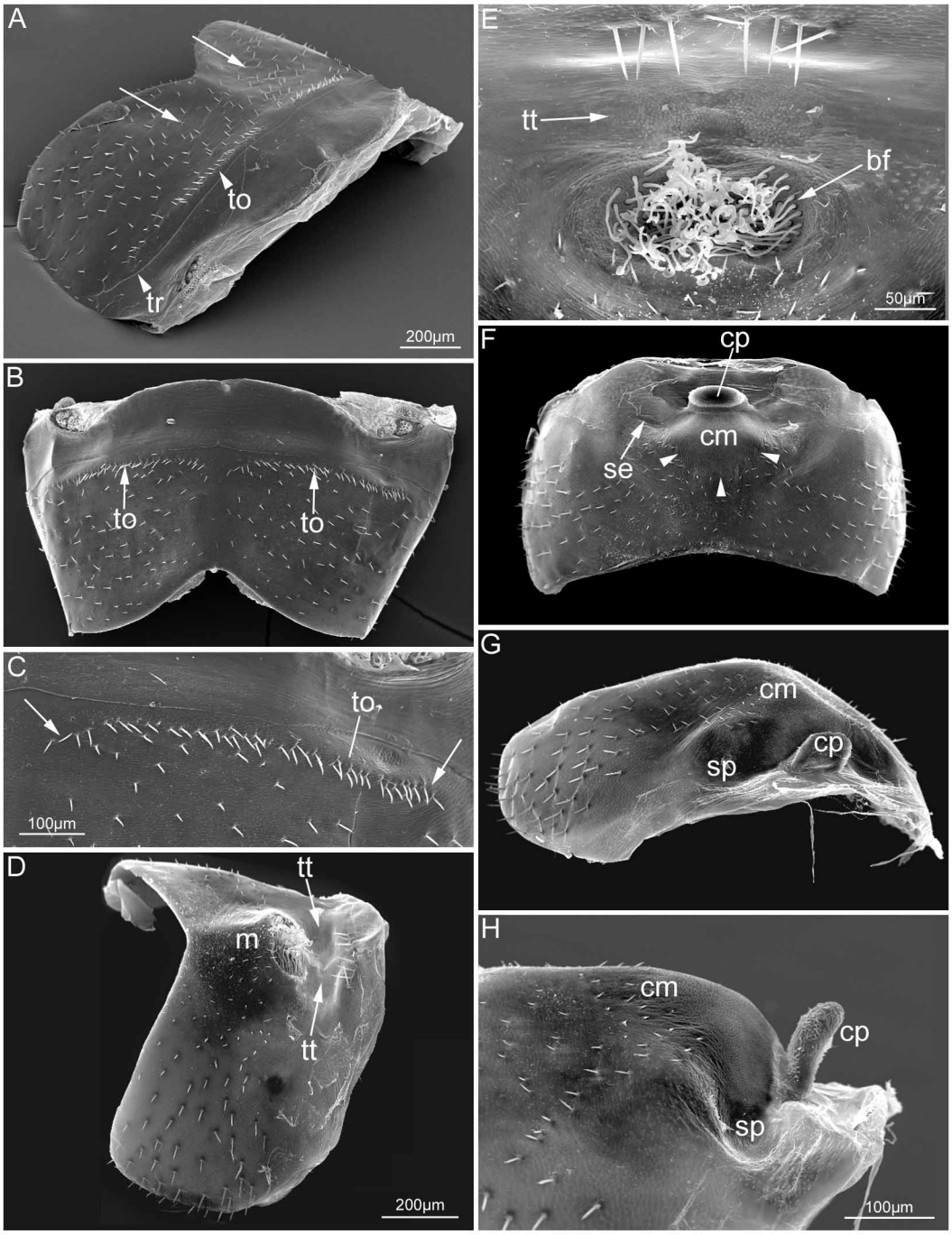


FIGURE 7. *Phyllodromica iberica* morph #2, male, SEM pictures of tergite 6 and the tergal glandular structures. **A–C** Tergite 6. (A) Latero-frontal view from slightly above, white arrows point to two shallow longitudinal depressions posteriorly of the torus (**to**); (B) dorsal view of the whole tergite; (C) transversal torus with bristles (between arrows) of the right half of the tergite. As a result of the preparation procedure for SEM the posterior margin of the tergite and its emargination in the middle (in B) appear narrower than under natural conditions. **D, E** Tergite 7. (D) Lateral view of tergite from slightly above; (E) glandular region in dorsal view. **F–H** Tergite 8. (F) Dorsal view of the whole tergite with median emargination in the distribution of the bristles (white arrow heads); (G) latero-frontal view from slightly above; (H) lateral view of the anterior part of the tergite. Abbreviations: **bf** bristle field, **cm** central mound, **cp** conelike process, **m** mound, **se** sinusoidal edge, **sp** shallow pit, **to** transversal torus, **tr** transversal ridge, **tt** transversal trough. Same scale for (A, B) and (D, F, G). Identification: (A–C) Sp 267b/M6, (D–H) Sp 267b/M4.

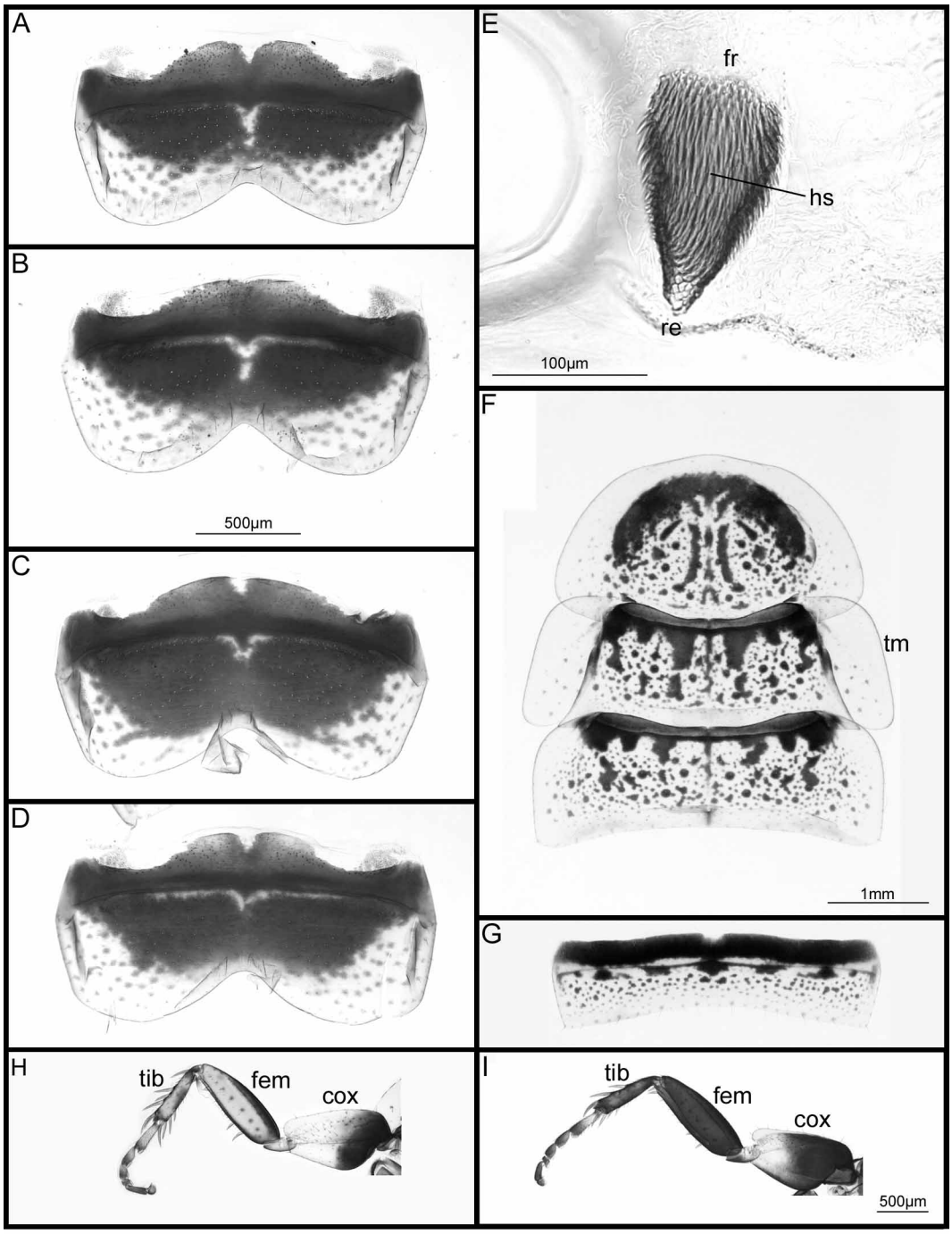


FIGURE 8. A–E *Phyllodromica iberica* morph #2, male. (A–D) Different colour patterns of tergite 6; (E) helmet sclerite. **F, G** *Phyllodromica iberica* morph #2, female. (F) Thoracal nota; (G) abdominal tergite 5. **H** Right front leg of *Phyllodromica iberica* morph #1, male in frontal view. **I** Right front leg of *Phyllodromica quadracantha*, male in frontal view. Abbreviations: **fr** "frontal" part of helmet sclerite, **cox** coxa, **fem** femur, **hs** helmet sclerite **re** "rear" of helmet sclerite, **tib** tibia, **tm** tegmen. Same scale for (A–D), (F, G) and (H, I). Identification: (A) Sp 266/2, (B) Sp 365/3, (C) Sp 365a/M14, (D) Sp 365a/M8, (E) Sp 267c/M1, (F, G) Sp 267c/W2, (H) Sp 510/M11, (I) Sp 203d/M1 (holotype)..

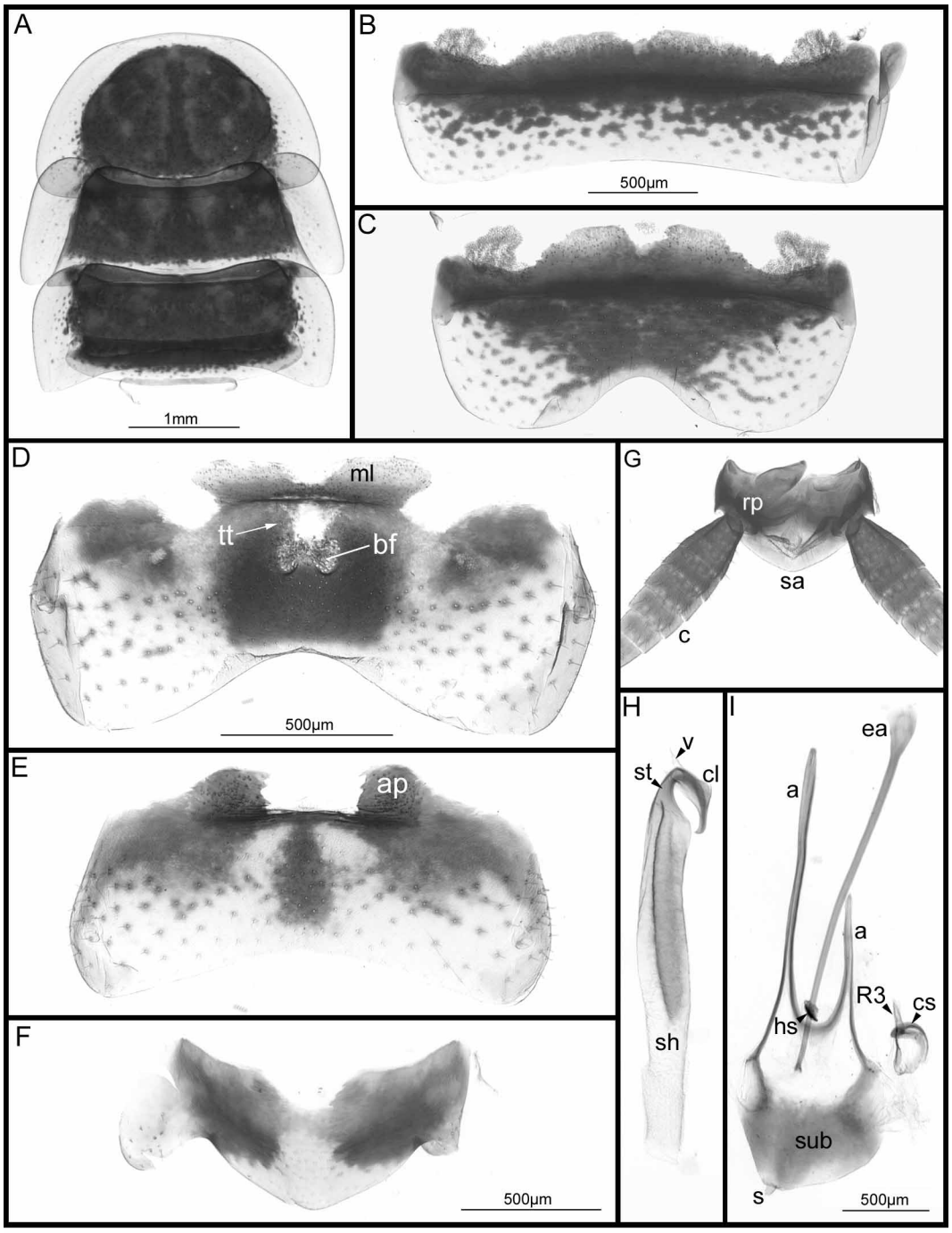


FIGURE 9. *Phyllodromica iberica* morph #3, male. **A** Thoracal nota. **B–F** Abdominal tergites 5–9. (B) Tergite 5; (C) tergite 6; (D) tergite 7 and (E) tergite 8 with glandular structures in the anterior part of the tergites; (F) tergite 9. **G** Terminalia with tergite 10 (**sa**), cerci and paraprocts. **H** Hook of left phallomere with the posterior end on the top. **I** Subgenital plate with remaining genital sclerites (without hook). Abbreviations: **a** apodemes of subgenital plate, **ap** anterior process, **bf** bristle field, **c** cercus, **cl** claw of hook, **cs** cleft sclerite, **ea** endophallic apodeme, **hs** helmet sclerite, **ml** median lobe, **rp** right paraproct, **R3** sclerite of the right phallomere, **s** stylus, **sa** supraanal plate, **sh** shaft, **st** stalk, **sub** subgenital plate, **tt** transversal trough, **v** velum. Same scale for (B, C, G) and (D, E, H). Identification: Sp 380/M2.

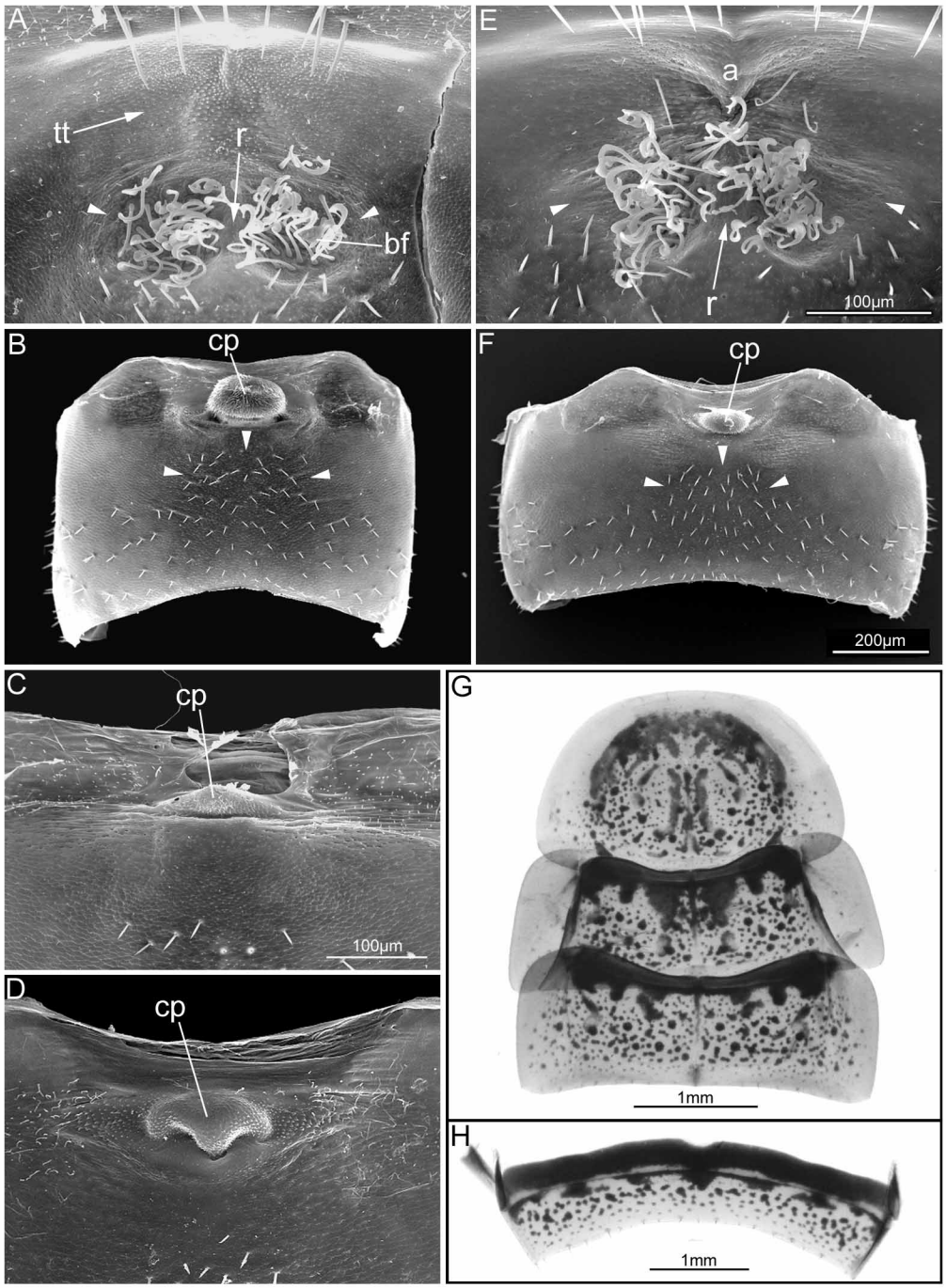


FIGURE 10. *Phyllodromica iberica* morph #3. **A**–**F** male, SEM pictures of different tergal glandular structures in dorsal view. (A, B), (E, F) Two different forms of glandular structures of tergites 7 and 8 of two specimens; white arrow heads in A point to the bulge-like cuticule limitations of the antero-lateral borders of the bristle fields which is absent in the other form (white arrow heads in E); on tergite 8 bristles are also present in the central region of the tergite (white arrow heads in B, F); (C, D) Medio-anterior part of tergite 8 of two further specimens showing variously developed conelike processes. The unnatural shape of the tergite in B (compared with F) is due to an mounting artefact. **G**, **H** female. (G) Thoracal nota; (H) abdominal tergite 5. Abbreviations: **a** artificial structures (originated during SEM preparation procedure), **bf** bristle field, **cp** conelike process**, r** ridge between bristle fields, **tt** transversal trough. Same scale for (A, E), (B, F) and (C, D). Identification: (A, B) Sp 388/M1, (E, F) Sp 512/M1, (C) Sp 186/M7, (D) Sp 361/M2, (G, H) Sp 380/W1.

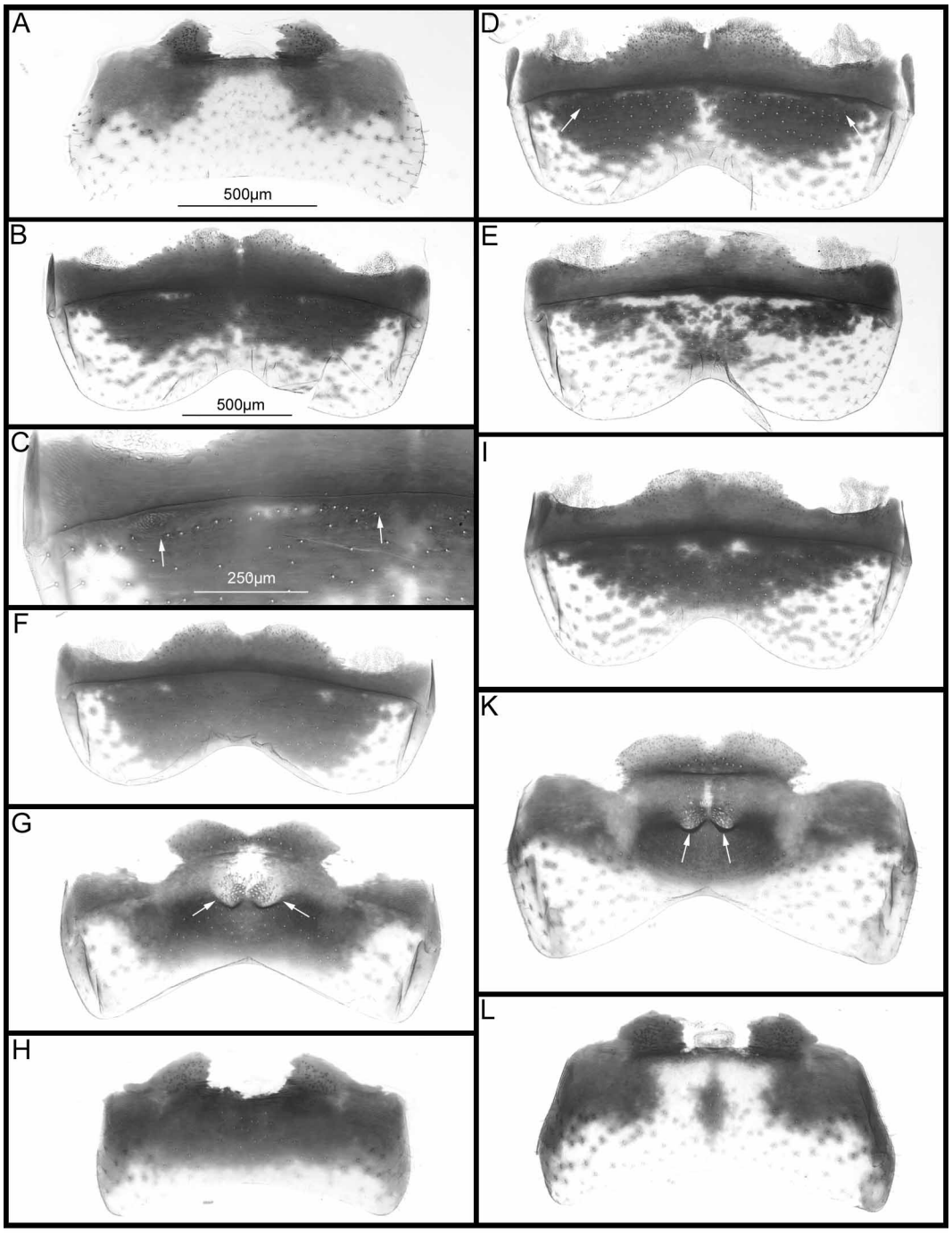


FIGURE 11. *Phyllodromica iberica* morph #3, male. **A** Tergite 8; **B-E** Tergite 6; in C, enlargement of the left half of the tergite depicted in B with narrow transversal torus-like structure (between white arrows) bearing bristles (white spots) in enhanced density; in D, lack of torus-like structure, only bristles (white spots) in enhanced density. D, E Tergite 6, two examples of different tergite colouration. **F**–**H** Abdominal tergites 6–8 of one specimen. (F) Tergite 6; (G) tergite 7, bristle fields antero-lateral without bulge-like cuticule limitations (white arrows); (H) tergite 8, conelike process nearly completely missing. **I**–**L** Abdominal tergites 6–8 of one specimen. (I) Tergite 6; (K) tergite 7, white arrows point to the shallow pouches appearing as crescent–shaped black shadows; (L) tergite 8, well developed conelike process. Same scale for (A, G, H, K, L) and (B, D, E, F, I). Identification: (A) Sp 395/M1, (B, C) Sp 148b/M1, (D) Sp 460/M1, (E) Sp 387a/M1, (F, G, H) Sp 270a/M1, (I, K, L) Sp 335/5.

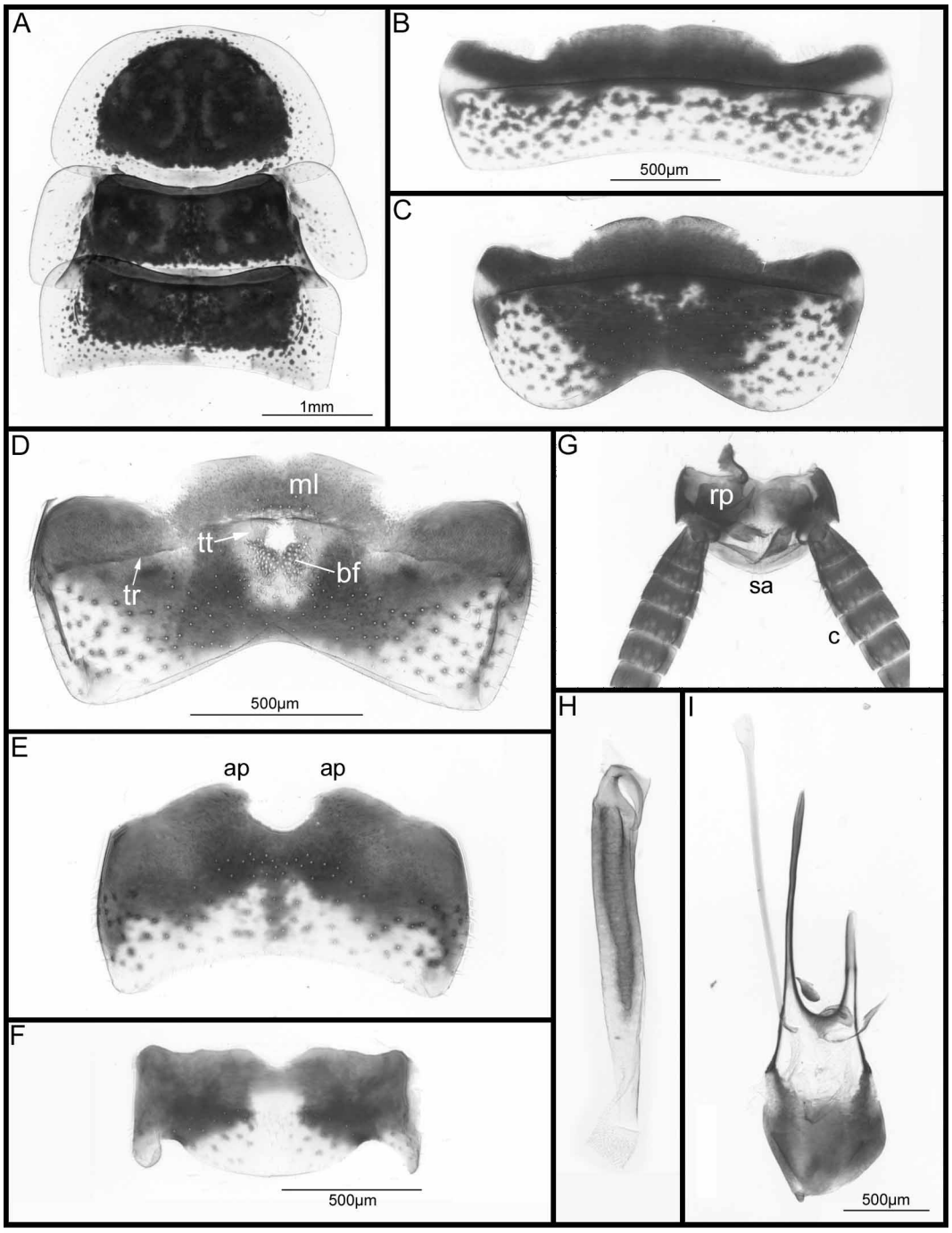


FIGURE 12. *Phyllodromica quadracantha*, male (holotype). **A** Thoracal nota. **B**–**F** Abdominal tergites 5–9. (B) Tergite 5; (C) tergite 6; (D) tergite 7 and (E) tergite 8 with glandular structures in the anterior part of the tergites; (F) tergite 9. **G** Terminalia with tergite 10 (**sa**), cerci and paraprocts. **H** Hook of left phallomere with the posterior end on the top. **I** Subgenital plate with remaining genital sclerites (without hook). Abbreviations: **ap** anterior process, **bf** bristle field, **c** cercus**,** **ml** median lobe, **rp** right paraproct, **sa** supraanal plate, **tr** transversal ridge, **tt** transversal trough. Same scale for (B, C, G) and (D, E, H). Identification: Sp 203d/M1 (holotype).

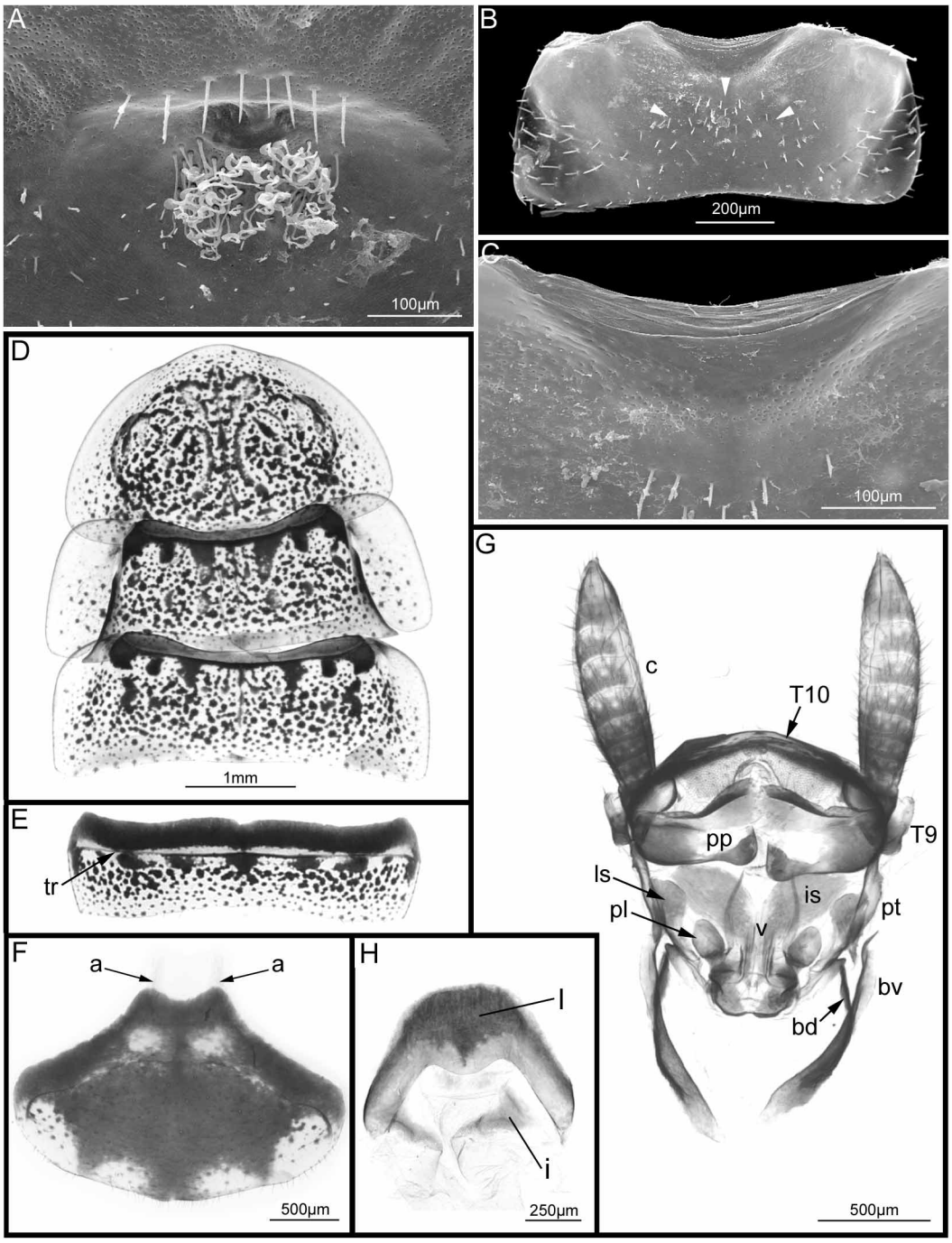


FIGURE 13 *Phyllodromica quadracantha*. **A–C** male, SEM pictures of glandular structures of tergites 7 and 8 in dorsal view. (A) Tergite 7; (B) tergite 8, bristles are present also in the median tergite region (white arrow heads); (C) anterior-median region of tergite 8, no conelike process present. **D–H** female. (D) Thoracal nota; (E) Tergite 5; (F) Subgenital plate; (G) dorsal complex of genitalia in ventral view, posterior end on top, without additional sclerite between **pl** and **is** (compare Fig. 2 D, E); (H) ventral komplex of genitalia: laterosternal shelf with intersternal folds between the arms. Abbreviations: **a** apodemal process, **bd** dorsal sclerite of basivalvula, **bv** ventral sclerite of basivalvula, **c** cercus, **i** intersternal fold, **is** intercalary sclerite, **l** laterosternal shelf, **ls** laterosternite IX, **pl** posterior lobe of valvifer II, **pp** paraproct, **pt** paratergites, **tr** transversal ridge, **T9** tergite 9, **T10** tergite 10, **v** valves. Same scale for (D, E). Identification: (A–D) Sp 499/M1, (E–I) Sp 203d/W1.

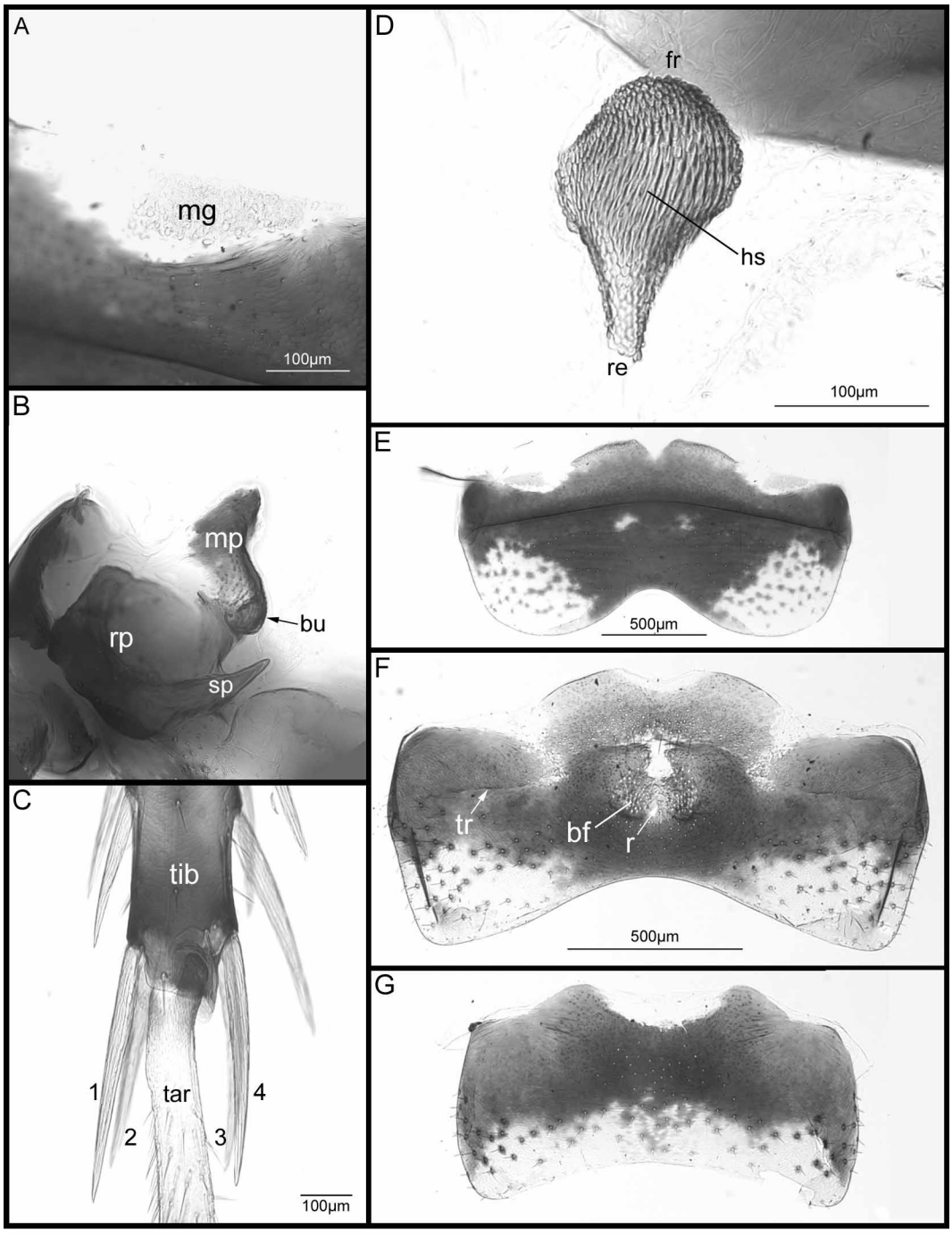


FIGURE 14 *Phyllodromica quadracantha*, male. **A** membrane glands of the right lateral region of the anterior border of tergite 6. **B** right paraproct with bulge on the medio-anterior process (compare Fig. 5 D). **C** distal end of tibia from the right mid leg (bearing 4 distal tibia spines; compare Fig. 5 E) in posterior view. **D** helmet sclerite, the nomenclature "**fr**" and "**re**" do not indicate the orientation of the sclerite within the animal. **E–G** tergites 6 (E), 7 (F) and 8 (G) of specimen with slightly different tergal structures on tergite 7. Due to unnatural squeezing of the tergite 8 (G) during the mounting procedure the distance between the anterior processes appears broader than under natural conditions. Abbreviations: **fr** "frontal" part of helmet sclerite, **bf** bristle field, **bu** bulge, **hs** helmet sclerite, **mg** membrane glands, **mp** medio-anterior process of right paraproct, **re** "rear" of helmet sclerite, **r** ridge, **rp** right paraproct, **sp** spinelike process, **tar** tarsus, **tib** tibia, **tr** transversal trough. Same scale for (A–D) and (F–G). Identification: (A, E–G) Sp 504a/M1, (B, C) Sp 203d/M1(holotype). (D) Sp 203b/M7.

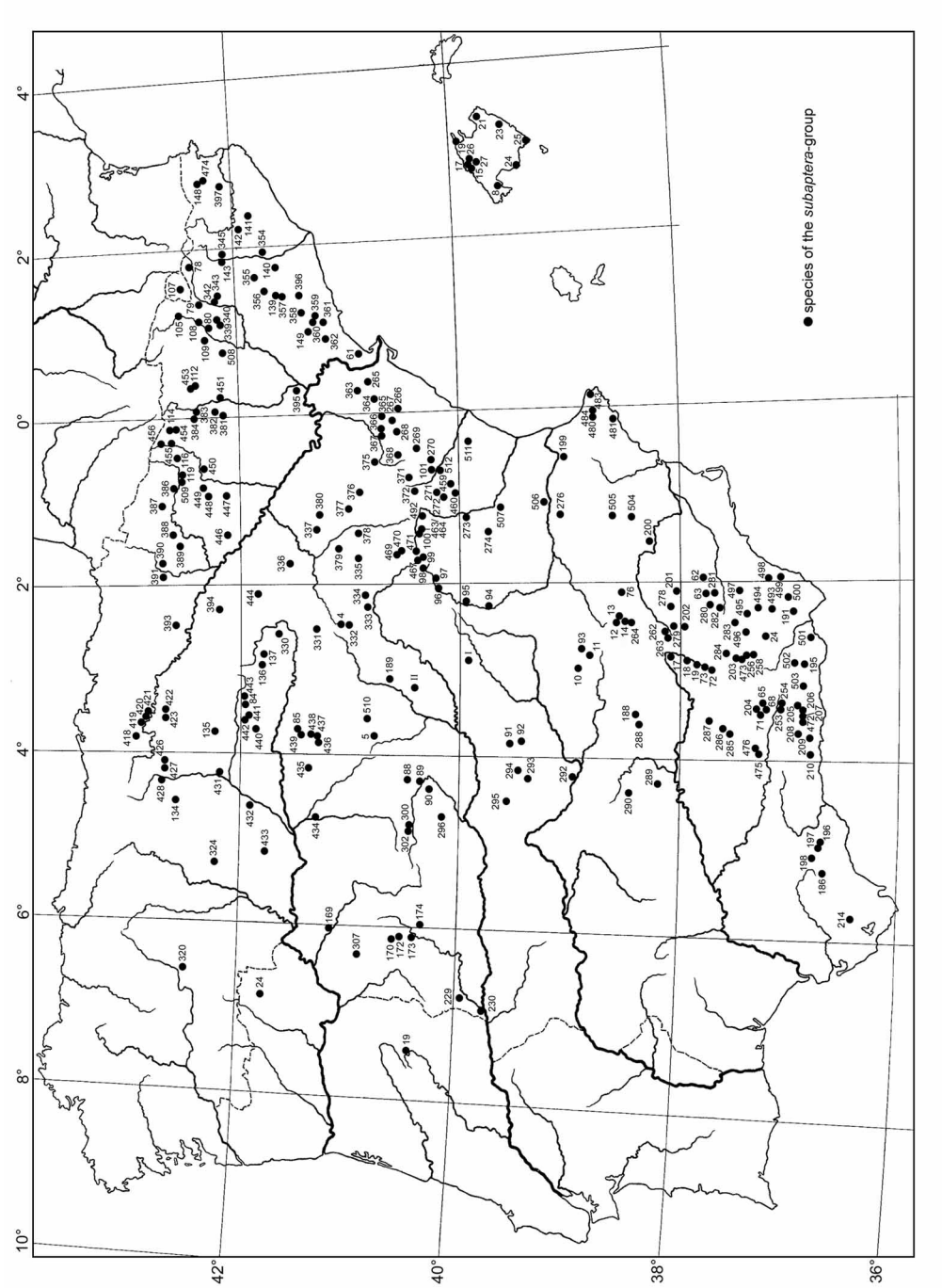


FIGURE 15. Map with the localities of the species of the *subaptera*-group on the Iberian peninsula. The numbers refer to the list of localities presented under "Appendix 1". Spain, Portugal and the Baleares have different numbering systems.

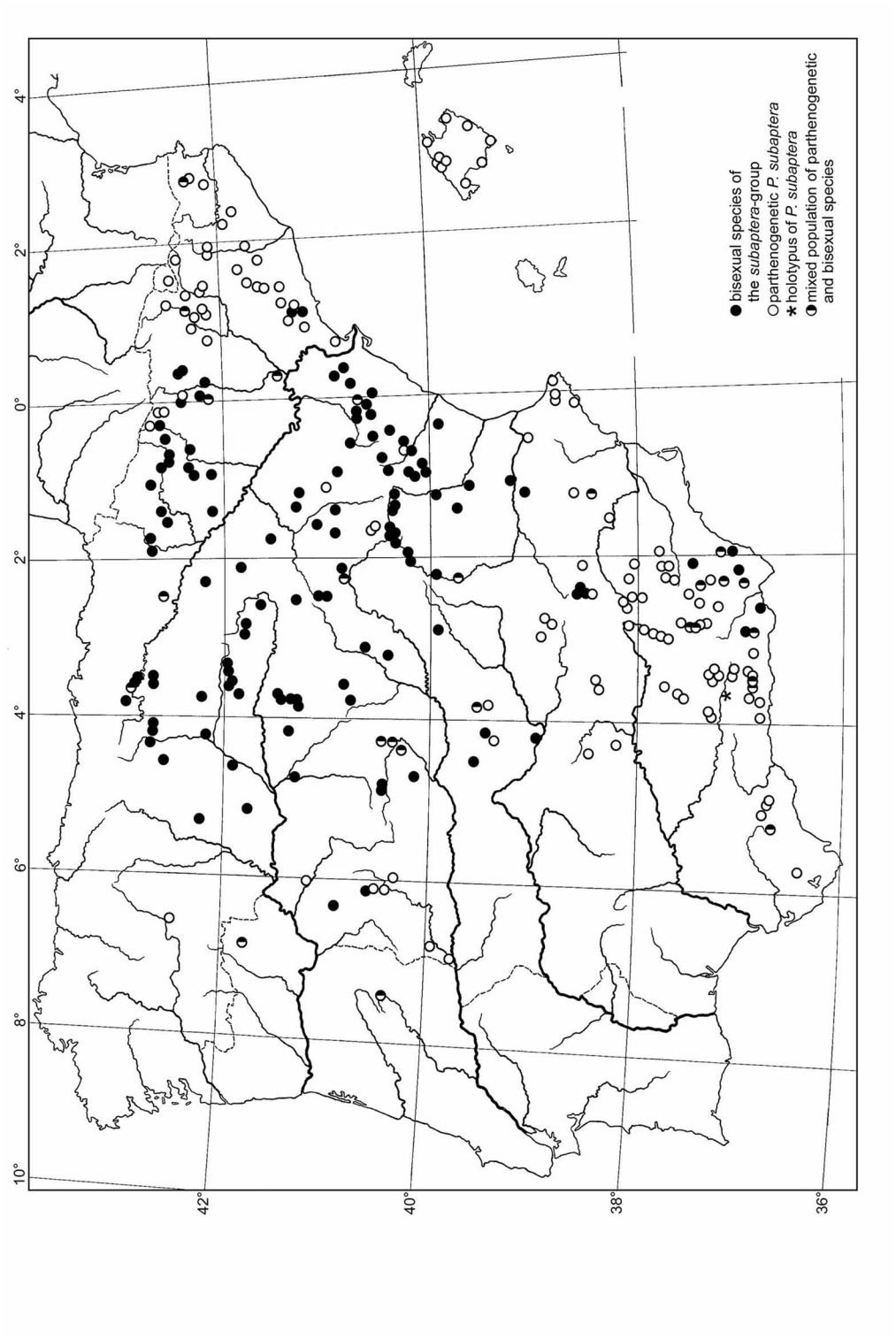


FIGURE 16. Distribution of bisexual species of the *subaptera*-group and the parthenogenetic species *P. subaptera* on the Iberian peninsula.

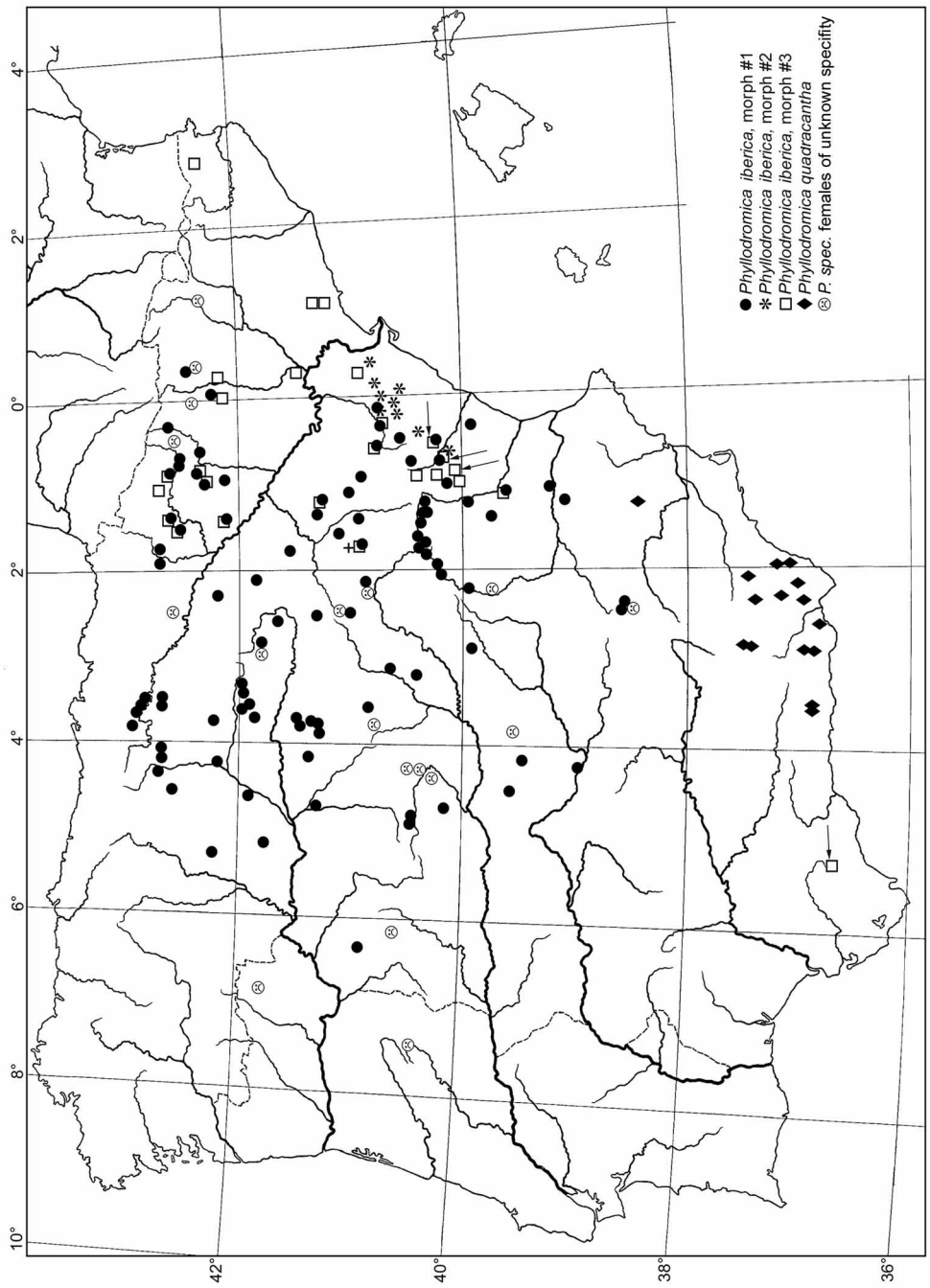


FIGURE 17. Distribution of the bisexual species of the *subaptera*-group: *Phyllodromica iberica* morph #1, #2 and #3, and *P. quadracantha;* these species only occur on the Iberian Peninsula. In cases where two different symbols partly overlap, two *P. iberica* morphs are found at the same locality; in one case all three morphs occur together (Fig. 15, Sp 510 ca. 1° W, 40° N). *P. iberica* morph #3 symbols labeled with a "+" (Fig. 15, Sp 335) or an "←" (Fig. 15, Sp 186, 270, 469 and 512) indicate the presence of morphological variations. At some localities no males have been found ("sad face" symbol) but females with spermathecae containing sperms and/or with oothecae containing male and female offspring. Both facts indicate the presence of a bisexual species of unknown specifity.

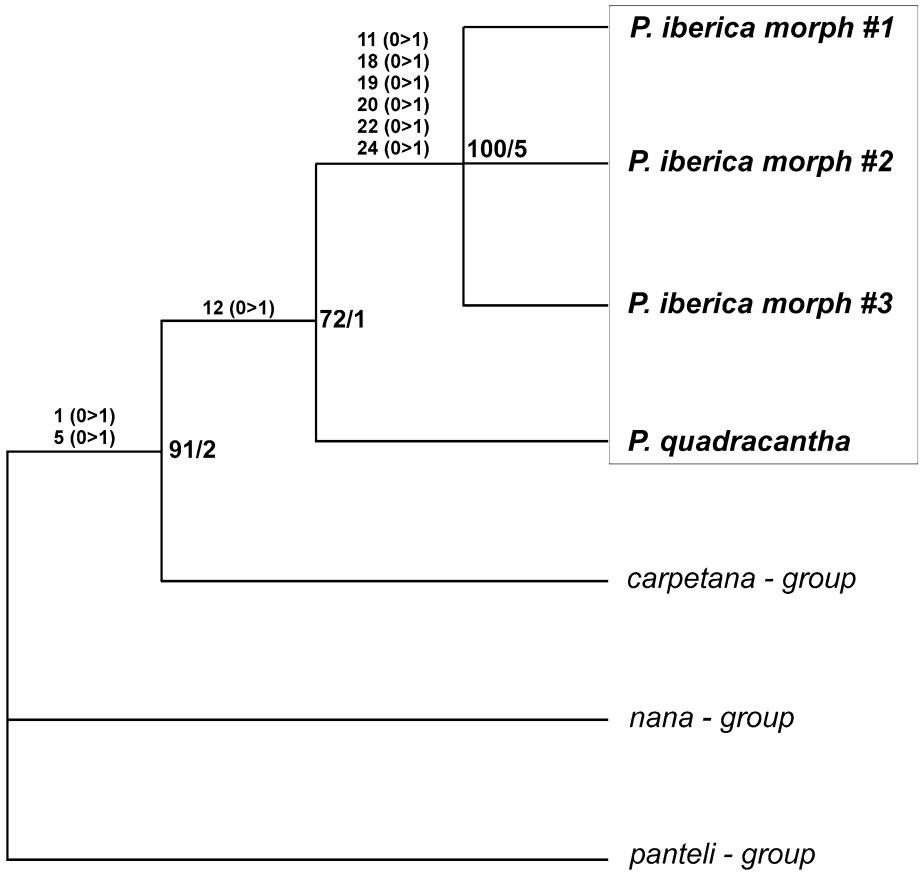


FIGURE 18. Cladistic analysis of the morpological data matrix (Appendix 3). Strict consensus tree of three most parsimonious cladograms (length 38 steps, CI 1.00, RI 1.00) derived from a maximum parsimony analysis. Parsimony-informative character changes are shown above branches, bootstrap support values > 50 % (10 000 replications) at nodes followed by Bremer's support. The analysis includes the bisexual taxa of *subaptera*-group (black frame) and three outgroup taxa.

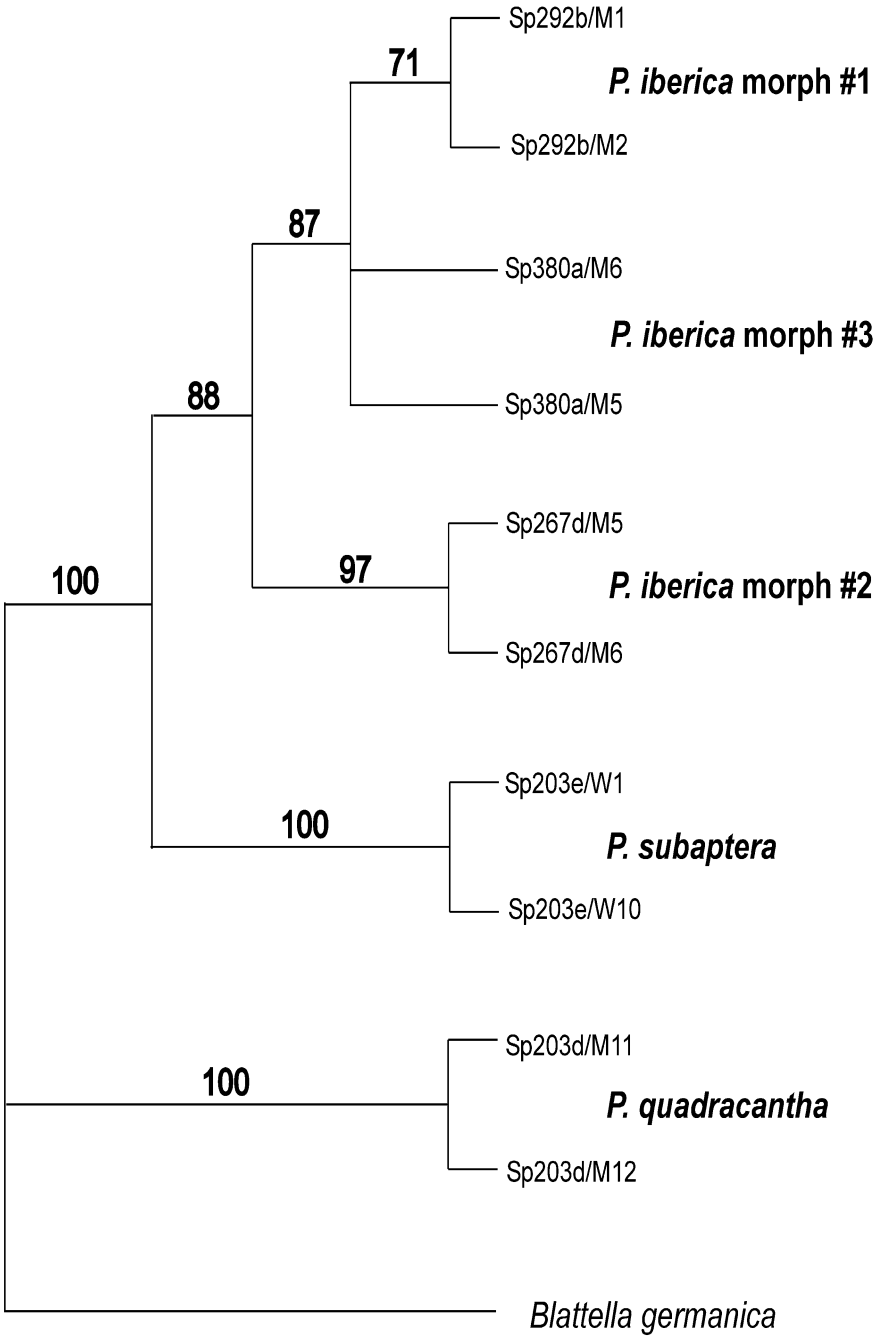


FIGURE 19. Strict consensus tree (length 374 steps, CI 0.94, RI 0.90) of a maximum parsimony analysis of the DNA sequence data (Appendix 4). Maximum parsimony bootstrap values > 50 % are shown above branches (2000 replications). The analysis includes the *subaptera* – group taxa and one outgroup.

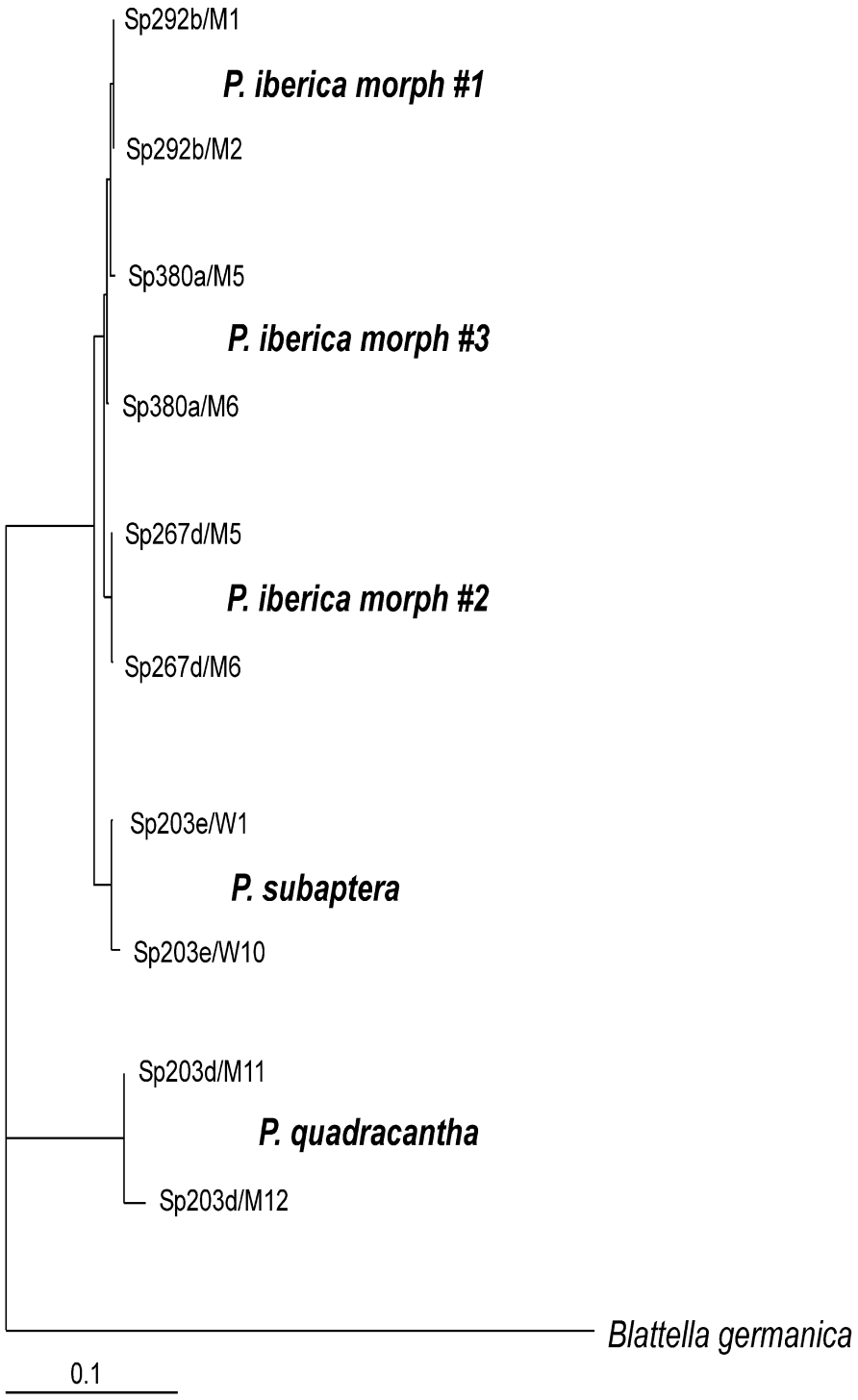


FIGURE 20. Phylogram of a maximum likelihood analysis of the DNA sequence data (Appendix 4) using the general time reversible model. The analysis includes the *subaptera* – group taxa and one outgroup.

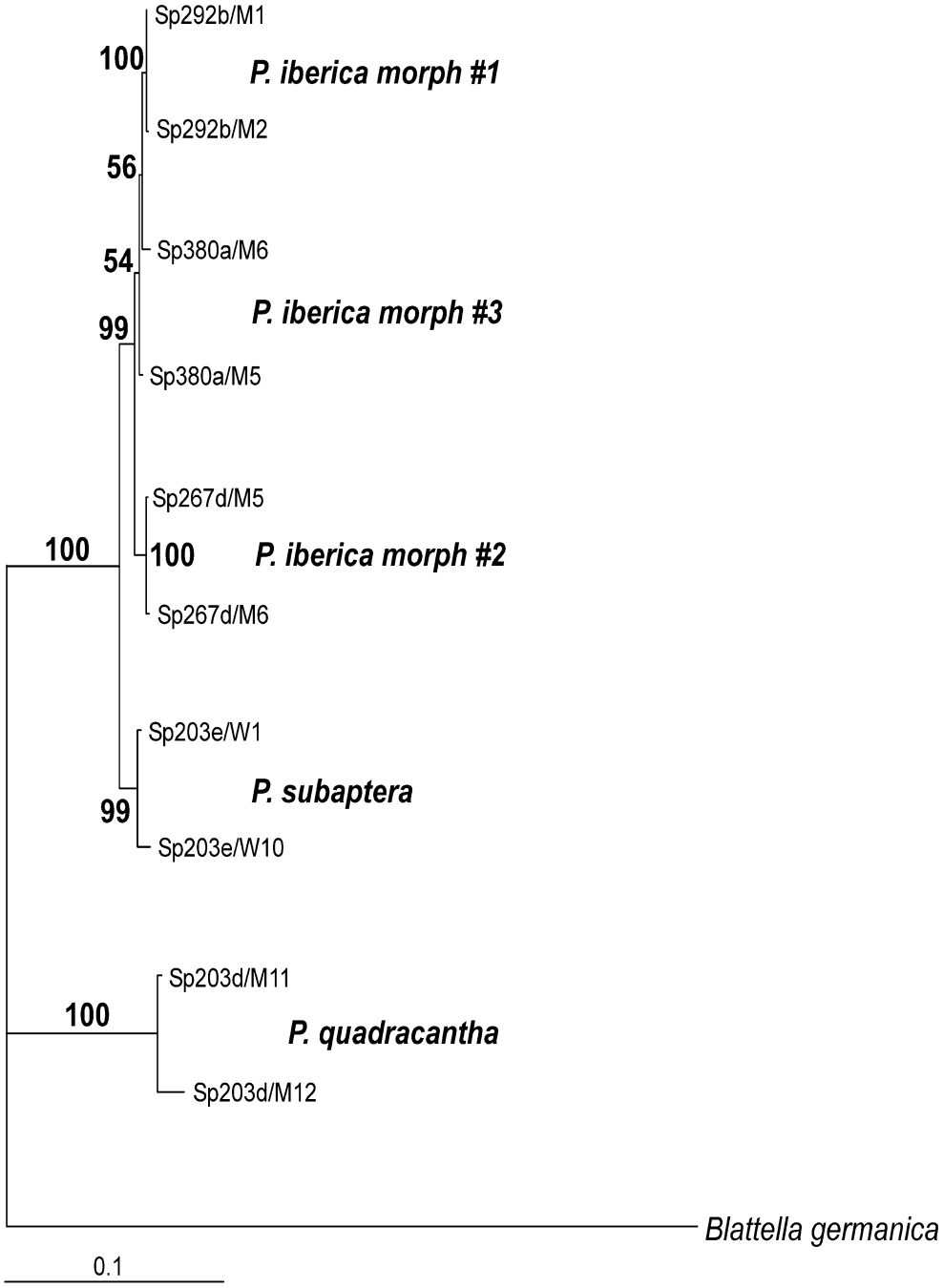


FIGURE 21. Consensus tree (50 % majority rule) of a Bayesian analysis of the DNA sequence data (Appendix 4). Values at nodes represent the posterior probability of each clade. The analysis includes the *subaptera* – group taxa and one outgroup taxon.

Appendix 1. List of localities

If not stated otherwise the collectors at the localities listed below were B. & H. Bohn.

The localities of each country (and of larger islands) are numbered consecutively. When a locality was visited more than once the later collectings are indicated by a small letter following the number of the locality.

In the above text the localities are represented by their code consisting of an abbreviation of the country or island and the respective number of the locality.

Spain (Sp)

4 Prov. Soria, Pto. Esteras (S Medinaceli), 1000 m, 12.VIII.1983
5a Prov. Madrid, 2 km NE Miraflores de la Sierra (N Madrid), 1200 m, 1.VI.1985
10a Prov. Ciudad Real, Pantano de Peñarroya (E Manzanares), 750 m, 2.VI.1985
11a Prov. Ciudad Real, Campo de Montiel, 10 km NNE Villahermosa, 900 m, 3.VI.1985
12b Prov. Albacete, Sa. de Alcaraz,ca. 2 km NNW Pto. del Barrancazo, 1200 m, 6.IV.1999, leg. T. Knebelsberger
13a Prov. Albacete, Sa. de Alcaraz, ca. 4 km ESE Pto. del Barrancazo, 1200 m, 3.VI.1985 / 13b: 8.IV.1999, leg. T. Knebelsberger
14a Prov. Albacete, Sa. de Alcaraz, Pto. de las Crucetillas, 1450 m, 17.VI.1991
17 Prov. Jaén, Sa. de Cazorla, Emb. del Tranco, near Bujaraiza, 700 m, 19.VIII.1983
18a Prov. Jaén, Sa. de Cazorla, Pto. de las Palomas (NE Cazorla), 1300 m, 18.VI.1984
19a Prov. Jaén, Sa. de Cazorla, 5 km S Puente de las Herrerías, 1300 m, 18.VI.1984
24a Prov. Almería, Sa. de los Filabres, 5 km SW Observatorio del Calar Alto, 2000 m, 12.VI.1984
61 Prov. Tarragona, 3 km WNW Perelló (near Tortosa), 200 m, 10.VI.1984 / 61b: 3.VI.1991 / 61c: 13.III.2001, leg. T. Knebelsberger
62 Prov. Murcia, Sa. del Pericay, near Emb. de Valdeinfierno, 900 m, 10.VI.1984
63 Prov. Almería, S slope of Mt. Gabar (NW Vélez Rubio), 1000 m, 11.VI.1984
65 Prov. Granada, Sierra Nevada, 2 km NE Tocón (NE Granada), 1300 m, 13.VI.1984
68 Prov. Granada, Sierra Nevada, btw. Tocón & Pto. de la Mora (NE Granada), 1400 m, 14.VI.1984
71 Prov. Granada, Sierra Nevada, Pto. de la Mora (NE Granada), 1390 m, 17.VI.1984 / 71a: 9.VI.1989 / 71b: 17.IV.1992
72 Prov. Jaén, Sa. de Pozo, 4 km SSE Tiscar, 1200 m, 17.VI.1984
73 Prov. Jaén, Sa. de Pozo, 2 km S slope of Mt. Cabañas, 1700 m, 18.VI.1984
76 Prov. Albacete, Sa. de Alcaraz, 3 km S Royo Odrea (ca. 20 km NW Elche de la Sierra), 800 m, 20.VI.1984
78 Prov. Lérida, above (N) Bellver de Cerdanya (E Seo de Urgel), 1100 m, 28.V.1985 / 78b: 10.IV.1995
79 Prov. Lérida, 1-4 km W Parroquia de Orto (SW Seo de Urgel), 1100 m, 28.V.1985 / 79c: 20.IV.1999, leg. T. Knebelsberger
80 Prov. Lérida, Desfiladero de Callegats, ca. 7 km NE La Pobla de Segur, 700 m, 28.V.1985
84b Prov. Burgos, 2 km E Santo Domingo de Silos, 1000 m, 13.V.1996
85 Prov. Segovia, Carabias (30 km S Aranda de Duero), 1000 m, 31.V.1985
88 Prov. Madrid, 4 km SSW Robledo de Chavela (NE S. Martín de Valdeiglesias), 900 m, 1.VI.1985
89 Prov. Madrid, San Juan (W S. Martín de Valdeiglesias), 500 m, 1.VI.1985
90 Prov. Madrid/Toledo, 9 km SE San Martín de Valdeiglesias, 700 m, 2.VI.1985
91 Prov. Toledo, Sa. de los Yébenes, Molino (near Los Yébenes), 800 m, 2.VI.1985
92 Prov. Toledo, 2 km N Estacion de Urda (20 km W Consuegra), 700 m, 2.VI.1985
93 Prov. Albacete/Ciudad Real, Campo de Montiel, El Sabinar (ca. 10 km S Ossa d. M.), 900 m, 3.VI.1985
94 Prov. Cuenca, Embalse de Alarcón, 3 km NW Villaverde y Pasaconsol, 820 m, 4.VI.1985 / 94a: 9.IV.1999, leg. T. Knebelsberger
95a Prov. Cuenca, 20 km SW Cuenca (Carret. N 420), 900 m, 9.IV.1999, leg. T. Knebelsberger
96a Prov. Cuenca, Serranía de Cuenca, 2 km NNW La Ciudad Encantada, 1300 m, 3.V.1998 / 96b: 9.IV.1999, leg. T. Knebelsberger
97 Prov. Cuenca, Serranía de Cuenca, Embalse de la Toba, 1100 m, 5.VI.1985 / 97a: 3.V.1998 / 97 b: 9.IV.1999, leg. T. Knebelsberge / 97c: 19.III.2001, leg. T. Knebelsberger
98 Prov. Cuenca, Serranía de Cuenca, 8 km WSW Pto. de El Cubillo, 1400 m, 5.VI.1985 / 98a: 4.V.1998
99a Prov. Teruel, Montes Universales, 5 km W Frías de Albarracín, 1600 m, 2 VI.1997 / 99b: 4.V.1998
100 Prov. Teruel, 10 km SE Albarracín, 1400 m, 6.VI.1985 / 100a: 12.IV.1999, leg. T. Knebelsberger / 100b: 17.III.2001, leg. T. Knebelsberger
101 Prov. Teruel, btw. Mora de Rubielos & Rubielos de Mora (WSW Teruel), 1000 m, 6.VI.1985
105 Prov. Lerida, 3 km NE Llavorsí, (12 km N Sort), 950 m, 19.V.1986 / 105a: 11.IV.1995
107 Andorra, Anyos (near Andorra la Vella), 1300 m, 21.V.1986

108 Prov. Lerida, 3 km N Gerri de la Sal, (12 km S Sort), 700 m, 22.V.1986 / 108a: 20.IV.1999, leg. T. Knebelsberger / 108b: 11.IV.2001, leg. T. Knebelsberger
109 Prov. Lerida, 4 km S Senterada (20 km N Tremp), 800 m, 22.V.1986 / 109a: 21.IV.1999, leg. T. Knebelsberger
112 Prov. Huesca, 5 km SE Foradada (ca. 25 km E Ainsa), 800 m, 22.V.1986
114a Prov. Huesca, btw. Broto & Torla (near P.N. de Ordesa), 1000 m, 17.V.1996
116 Prov. Huesca, 6 km E Jaca, 850 m, 23.V.1986
119 Prov. Huesca, Santa Cruz de la Serós (near Jaca), 900 m, 24.V.1986 /119b: 9.IV.2001, leg. T. Knebelsberger
134 Prov. Palencia, 5 km ENE Villaeles de Valdavia (40 km N Carrión d. los Condes), 900 m, 27.V.1986
135 Prov. Burgos, 3 km E Sarracín (S Burgos), 900 m, 28.V.1986
136 Prov. Soria, 10 km W Abejar (30 km W Soria), 1100 m, 28.V.1986
137 Prov. Soria, 2 km E Abejar (30 km W Soria), 1100 m, 28.V.1986 / 137a: 14.V.1996
139 Prov. Barcelona, La Panadella (25 km W Igualada), 750 m, 29.V.1986
140 Prov. Barcelona, Sa. de Montserrat, ca. 5 km N El Bruc, 650 m, 29.V.1986 / 140a: 14.IV.1995 / 140b: 23.IV.1999, leg. T. Knebelsberger
141 Prov. Barcelona, Sa. de Montseny, Viladrau, 800 m, 30.V.1986
142 Prov. Barcelona, 9 km WNW Vic, 700 m, 30.V.1986
143 Prov. Barcelona, 5 km N Berga, 800 m, 30.V.1986
148 Prov. Gerona, Sant Martí Sesseres (25 km W Figueres), 400 m, 25.IV.1987 / 148a: 24.IV.1999, leg. T. Knebelsberger / 148b: 15.IV.2003, leg. T. Knebelsberger
149 Prov. Tarragona, Sa. La Llena, 4 km N Prades (near Montblanc), 1000 m, 7.VI.1987
169 Prov. Salamanca, 3 km NNW Ledesma (NW Salamanca), 750 m, 13.VI.1987
170 Prov. Salamanca, Sa. de la Peña de Francia, surr. of El Cabaco, 900-1100 m, 13.VI.1987
172 Prov. Salamanca, Sa. de la Peña de Francia, El Portillo (near La Alberta), 1150 m, 14.VI.1987
173a Prov. Salamanca/Cáceres, 9 km NW Vegas de Coria (near Emb. de Gabriel y Galán), 400 m, 25.IV.1992
174a Prov. Salamanca, Lagunilla (SW Béar), 900 m, 25.IV.1992
186 Prov. Málaga, Serranía de Ronda, Cortijo de Montero (10 km SSW Ronda), 1000 m, 27.III.1988 / 186a: 5.IV.1990 / 186b: 23.III.2000, leg. T. Knebelsberger
188a Prov. Jaén, Pto. de los Jardines (20 km NE La Carolina), 870 m, 19.IV.1992
189 Prov. Guadalajara, Taracena (near Guadalajara), 750 m, 9.IV.1988
191 Prov. Almería, Sierra Alhamilla, btw. Mts. Colativí & Sa. Alhamilla, ca. 1200 m, 15.V.1989 / 191a: 5./6.IV.2000, leg. T. Knebelsberger
195 Prov. Almería, Sa. de Gádor, NE Castala (near Berja), ca. 1500 m, 3.V.1990
196 Prov. Málaga, Serranía de Ronda, Alozaina (NW Coín), 400 m, 3.V.1990
197 Prov. Málaga, Serranía de Ronda, Pto. de las Abejas (E Ronda), 820 m, 3.V.1990
198 Prov. Málaga, Serranía de Ronda, Pto. del Viento (NE Ronda), 1190 m, 4.V.1990
199 Prov. Valencia, 6 km NW Játiva (ca. 55 km SSW Valencia), 180 m, 4.IV.1991
200 Prov. Murcia, Sa. de la Cabeza del Asno, Casa de Raton (ca. 15 km NW Cieza), 200 m, 4.IV.1991
201 Prov. Murcia, Sa. de Mojantes (SW Caravaca), 1000 m, 4.IV.1991
202 Prov. Granada, Sa. de la Sagra, btw. Puebla de Don Fadrique & Cortijos Nuevos de la Sierra, 1300 m, 5.IV.1991
203 Prov. Granada, Sa. de Baza, ca. 15 km WSW Baza, 1100 m, 5.IV.1991 / 203a: 2.V.1998 / 203b: 2.-6.IV.1999, leg. H. Bohn & T. Knebelsberger / 203c: 26.III.-1.IV.2000, leg. T. Knebelsberger / 203d: 20.-23.III.2001, leg. T. Knebelsberger / 203e: 19.IV.2003, leg. T. Knebelsberger
204 Prov. Granada, Ventas del Molinillo (btw. Guadix & Granada), 1300 m, 5.IV.1991
205 Prov. Granada, Sierra Nevada, above (NE) Soportújar, 1500 m, 6.IV.1991 / 205a: 2.V.1998
206 Prov. Granada, Sierra Nevada, Bayacas (N Orgiva), 700 m, 6.IV.1991
207 Prov. Granada, Sierra Nevada, Lanjarón, 700 m, 6.IV.1991 / 207a: 2.V.1998
208 Prov. Granada, Sa. de Albuñuelas, Mt. Herrero, 1400 m, 6.IV.1991
209 Prov. Granada, Sa. del Chaparral, Venta de Cabramontés (NW Otívar), 1000 m, 7.IV.1991
210 Prov. Málaga, Sa. de Almijara, btw. Cómpeta & Cortijo del Daire, 800 m, 7.IV.1991
214 Prov. Cádiz, 4 km NE Alcalá de los Gazules (NW Algeciras), 100 m, 9.IV.1991
229 Prov. Cáceres, Sa. de la Garrapata (W Coria), 12 km NE Zarza la Mayor, 400 m, 24.IV.1991
230 Prov. Cáceres, Alcántara, 300 m, 24.IV.1991
253 Prov. Granada, Sierra Nevada, Loma Cunas de los Cuartos (ESE Guejar - Sierra), 1800 m, 14.VI.1991
254 Prov. Granada, Sierra Nevada, Barranco La Solana (ENE Guejar - Sierra), 1800-1900 m, 14./15.VI.1991
256 Prov. Granada, Sa. de Baza, N slope of Mt. Sta. Bárbara, ca. 1800 m, 15.VI.1991
258 Prov. Granada, Sa. de Baza, Rio Gallego, 1700 m, 15.VI.1991
262 Prov. Jaén, Sa. de Segura: Sa. de Almorchón, 4 km WNW Santiago de la Espada, 1700 m, 16.VI.1991
263 Prov. Jaén, Sa. de Segura: Sa. de Almorchón, 4 km ESE Pontones, 1600 m, 16.VI.1991

264 Prov. Albacete, Sa. de Alcaraz, Pto. del Arenal, 1150 m, 17.VI.1991
265 Prov. Tarragona, surr. of Los Puertos (ca. 20 km W Tortosa), 750-1400 m, 11.IV.1992 / 265a: 14.IV.1999, leg. T. Knebelsberger
266 Prov. Castellón, Pto. de Querol (50 km W Vinarós), 1030 m, 11.IV.1992 / 266a: 13.IV.1999, leg. T. Knebelsberger
267 Prov. Castellón, 3 km SW Morella, ca. 1000 m, 12.IV.1992 / 267a: 13.IV.1999, leg. T. Knebelsberger / 267b: 13./14.IV.2000, leg. T. Knebelsberger / 267c:16.III.2001, leg. T. Knebelsberger / 267d: 4.IV.2002, leg. T. Knebelsberger
268 Prov. Castellón, btw. Cinctorres & Portell de Morella (SW Morella), 1200 m, 12.IV.1992 / 268a:13.IV.1999, leg. T. Knebelsberger
269a Prov. Teruel, Sa. del Rayo, btw. Cantavieja & Mosqueruela, 1500 m, 17.IV.1995
270 Prov. Teruel, Sa. de Nogueruelas, 16 km NNE Rubielos de Mora, 1600 m, 12.IV.1992 / 270a: 12.IV.1999, leg. T. Knebelsberger / 270b: 12.IV.2000, leg. T. Knebelsberger / 270c: 4.IV.2001, leg. T. Knebelsberger
271 Prov. Teruel, 4 km SW La Puebla de Valverde (23 km SE Teruel), 1200 m, 12.IV.1992
272 Prov. Teruel, Sa. de Javalambre, btw. Collado de El Gavilán & Mt. Javalambre, 1600 m, 13.IV.1992
273 Prov. Cuenca, 3 km N Sta. Cruz de Moya (60 km S Teruel), 750 m, 13.IV.1992
274 Prov. Cuenca, Sa. de Mira, Mt. Rebollo, 1250 m, 13.IV.1992
276 Prov. Valencía, Mt. Palomeras (W Ayora), 1000-1200 m, 14. IV.1992
278 Prov. Murcia, Sa. de Taibilla, Mt. Revolcadores, 1450-1550 m, 15.IV.1992
279 Prov. Granada, Sa. de la Hoya del Espina, Pto. del Pinar, 1500-1600 m, 15.IV.1992
280 Prov. Almería, btw. Casablanca & María (NW Vélez Rubio), 1200 m, 15.IV.1992
281 Prov. Almería, near Vélez Blanco (NW Vélez Rubio), 1000 m, 16.IV.1992
282 Prov. Almería, S. de Maria, ca. 4 km N Chirivel (W Véez Rubio), 1400 m, 16.IV.1992
283 Prov. Granada/Almería, Sa. de Lucar, btw. Oria & Cúllar Baza, 1200 m, 16.IV.1992
284 Prov. Granada, Mt. Jabalcón (N Baza), 1000-1400 m, 16./17.IV.1992
285 Prov. Jaén, Sa.de Alta Coloma, Mt. Cerro Quemado, 1150-1450 m, 17.IV.1992
286 Prov. Jaén, Sa.de Alta Coloma, Pto. de las Palomas, 1350 m, 18.IV.1992
287 Prov. Jaén, Sa. Almadén, btw. Mancha Real & Mt. El Almadén, 1300-1550 m, 18.IV.1992
288 Prov. Jaén, near Miranda del Rey (N La Carolina), 800 m, 19.IV.1992
289 Prov. Córdoba, 2 km S Venta del Charco (ca. 30 km N Villa del Río), 650 m, 19.IV.1992
290 Prov. Ciudad Real, Sa. de la Garganta, 3 km S Pto. Valderrepisa (SW Puertollano), 850 m, 20.IV.1992
292 Prov. Ciudad Real, btw. Los Pozuelos de Calatrava & Piedrabuena (W Ciudad Real), 700 m, 21.IV.1992 / 292a: 27.III.2001, leg. T. Knebelsberger / 292b: 21.IV.2003, leg. T. Knebelsberger
293 Prov. Ciudad Real, Mtes. del Toledo, btw. El Bullaque & Emb. Torre de Abraham, 600 m, 21.IV.1992
294 Prov. Ciudad Real, Mtes. del Toledo, Sa. de los Torneros, Mt. Becerra, 1300 m, 21.IV.1992
295 Prov. Toledo, Mtes. de Toledo, Mt. Corral de Cantos (10 km S Navahermosa), 1000 m, 22.IV.1992
296 Prov. Toledo, Sa. de San Vicente (NE Talavera), 2 km N El Real de San Vicente, 900 m, 22.IV.1992
300 Prov. Ávila, Sa. de la Paramera, btw. Burgohondo & Navalmoral, 950 m, 23.IV.1992
302 Prov. Ávila, Sa. de la Paramera, btw. Navarredondilla & Navalacruz, 1100 m, 24.IV.1992
307 Prov. Salamanca, btw. El Cubo de Don Sancho & Traguntía (W Salamanca), 800 m, 26.IV.1992
320 Prov. León, btw. Molinaseca & Riego de Ambros (E Ponferrada), 750-850 m, 4.V.1992
324 Prov. León, btw. Mantanza & Mayorga (SE Valencía de Don Juán), 750 m, 4.V.1992
330 Prov. Soria, near Lubia (15 km S Soria), 1050-1100 m, 6.V.1992
331 Prov. Soria, 4 km S Adradas (23 km N Medinaceli), 1100 m, 6.V.1992
332 Prov. Guadalajara, btw. Alcolea del Pinar & Luzaga (S Medinaceli), 1200 m, 6.V.1992
333 Prov. Guadalajara, btw. Huertahernando & Olmeda de Cobeta (ca 30 km W Molina d. A.), 1200 m, 7.V.1992
334 Prov. Guadalajara, 6 km E Cobeta (ca. 20 km W Molina de Aragon), 1225 m, 7.V.1992
335 Prov. Guadalajara, btw. Embid & Eta. de Sto. Domingo (SW Daroca), 1125 m, 7.V.1992
336 Prov. Zaragoza, Sa. de la Virgen (NW Calatayua), S Santuario, 1050-1250 m, 8.V.1992
337 Prov. Zaragoza, Sa. de la Algairén (N Daroca), btw. Pto. de Codos & Mt. Valdemadera, 1050-1270 m, 8.V.1992
339 Prov. Lérida, 4 km NE Isona (19 km E Tremp), ca. 800 m, 12.IV.1995
340 Prov. Lérida, Collado de Faidella, 1250 m, 12.IV.1995
342 Prov. Lérida, El Palau (btw. Organyá & Alinyá, S Seo de Urgel), 600 m, 12.IV.1995 / 342a: 20.IV.1999, leg. T. Knebelsberger
343 Prov. Lérida, above Cambrils (S Seo de Urgel), ca. 1100 m, 12.IV.1995 / 343a: 20.IV.1999, leg. T. Knebelsberger
345 Prov. Barcelona, Emb. de la Baélls, btw. Berga & Vilada, ca. 600 m, 12.IV.1995
354 Prov. Barcelona, 3 km SE Navarcles (8 km NE Manresa), ca. 350 m, 14.IV.1995 / 354a: 17.IV.1999, leg. T. Knebelsberger
355 Prov. Barcelona, Sa. de Castelltallat (NW Manresa), btw. San Mateu d. B. & La Molsosa, 900 m, 15.IV.1995 /

355a: 18.IV.1999, leg. T.Knebelsberger
356 Prov. Barcelona, 2 km E Calaf (30 km W Manresa), ca. 700 m, 15.IV.1995
357 Prov. Lérida, 2 km S Belmunt (ca. 30 km W Igualada), ca. 700 m, 15.IV.1995
358 Prov. Tarragona, ca. 3 km NE L'Illa (btw. Valls & Montblanc), 600-750 m, 15.IV.1995
359 Prov. Tarragona, btw. Montreal & Alcover (N Reus), ca. 700 m, 15.IV.1995
360 Prov. Tarragona, 1 km NE Montreal (N Reus), ca. 800 m, 16.IV.1995 / 360a: 5.V.1998
361 Prov. Tarragona, btw. L'Albiol & La Mussara (N Reus), ca. 1000 m, 16.IV.1995 / 361a: 5.V.1998
362 Prov. Tarragona, 1 km SW Pto. de la Teixeta (22 km W Reus), ca. 600 m, 16.IV.1995
363 Prov. Tarragona, ca. 4 km NE Arnés (NW Tortosa), ca. 500 m, 16.IV.1995
364 Prov. Teruel, Ptos. de Beseit, SE Emb. de Peña, ca. 700 m, 16./17.IV.1995
365 Prov. Castellón, 2 km E Pto. de Torre Miró (11 km N Morella), 1200 m, 17.IV.1995 / 365a: 14.IV.1999, leg. T. Knebelsberger
366 Prov. Teruel, btw. Villores & Luco de Bordón (NW Morella), ca. 900 m, 17.IV.1995 / 366a: 13./14.IV.2000, leg. T. Knebelsberger
367 Prov. Teruel, btw. Luco de Bordón & Bordón (NW Morella), ca. 800 m, 17.IV.1995
368 Prov. Teruel, Pto. de Cuarto Pelado (89 km NE Teruel), 1600 m, 18.IV.1995
371 Prov. Teruel, 2 km NE Monteagudo del Castillo (ca. 40 km NE Teruel), ca. 1500 m, 18.IV.1995
372 Prov. Teruel, Pto. de Cabigordo (27 km NE Teruel), 1550 m, 18.IV.1995
375 Prov. Teruel, Pto. de Majalinos (90 km NE Teruel), 1450 m, 19.IV.1995
376 Prov. Teruel, 2 km S Seguro de los Baños (52 km SE Daroca), ca. 1100 m, 19.IV.1995
377 Prov. Teruel, Pto. de Fonfría (ca. 30 km SE Daroca), 1470 m, 19.IV.1995
378a Prov. Teruel, btw. Calamocha & Tornos (S Daroca), 1100 m, 5.IV.2001, leg. T. Knebelsberger
379 Prov. Zaragoza, Sa. de Sta. Cruz (W Daroca), Pto. de Used, 1200 m, 20.IV.1995
380 Prov. Zaragoza, 2 km E Pto. de Paniza (10 km S Cariñena), 900 m, 20.IV.1995 / 380a: 5.IV.2001, leg. T. Knebelsberger
381 Prov. Huesca, 2 km NE Adahuesca (20 km NW Barbastro), ca. 600 m, 20.IV.1995 / 381a: 5./6.IV.2001, leg. T. Knebelsberger
382 Prov. Huesca, Coll. de San Caprasio (ca. 30 km NW Barbastro), ca. 800 m, 21.IV.1995 / 382a: 5.IV.2001, leg. T. Knebelsberger
383 Prov. Huesca, 2.5 km S Latorrecilla (SW Ainsa), ca. 600 m, 21.IV.1995
384 Prov. Huesca, near Campodarte (btw. Pto. de Sarrablo & Bollaño, W Ainsa), 1100 m, 21.IV.1995
386 Prov. Huesca, 3 km ESE Berdím (40 km W Jaca), ca. 600 m, 22.IV.1995 / 386a: 6.IV.2001, leg. T. Knebelsberger
387 Prov. Navarra, Pto. Las Coronas (N Mon. de Leyre), 950 m, 22.IV.1995 / 387a: 7.IV.2001, leg. T. Knebelsberger
388 Prov. Navarra, near Pto. Olaz (15 km NW Sanguesa), 700 m, 22.IV.1995 / 388a: 7./8.IV.2001, leg. T. Knebelsberger
389 Prov. Navarra, Alto Lerga (15 km NE Olite), 750 m, 23.IV.1995 / 389a: 7./8.IV.2001, leg. T. Knebelsberger
390 Prov. Navarra, btw. Pto. del Perdon & Mt. Perdon, 700-1000 m, 23.IV.1995
391 Prov. Navarra, Pto. de Guirguillano (10 km NW Puenta la Reina), 725 m, 23.IV.1995
393 Prov. Navarra, near Lapoblación (ca. 12 km N Lograño), 900 m, 23.IV.1995
394 Prov. La Rioja, Caserlo las Bargas (ca. 20 km SW Arnedo), 750 m, 24.IV.1995
395 Prov. Huesca, Vall de Carreras, 3 km SSW Torrente de Cinca (30 km SW Lérida), ca. 200 m, 25.IV.1995
396 Prov. Tarragona, Mt. Montagut (NE Mon. Santes Creus), Coll de la Torreta, 700 m, 25.IV.1995
397 Prov. Gerona, near Pujarnol (6 km SW Banyoles), ca. 400 m, 26.IV.1995 / 397a: 5.V.1998 / 397b: 14.III.2001, leg. T. Knebelsberger
418 Prov. Burgos, 2 km SE Sancillo (ca. 75 km S Santander), 940 m, 9.V.1996
419 Prov. Burgos, btw. Valdenoceda & Incinillas (ca. 70 km N Burgos), 600 m, 9.V.1996
420 Prov. Burgos, Igl. San Pedro de Tejada (near Quecedo, ca. 70 km N Burgos), 600 m, 9.V.1996
421 Prov. Burgos, near Panizares (10 km NW Oña), 620 m, 9.V.1996
422 Prov. Burgos, 1 km W Cornudilla (18 km NW Briviesca), 670 m, 9.V.1996
423 Prov. Burgos, 3.5 km W Poza de la Sal (23 km NW Briviesca), 950 m, 9.V.1996
426 Prov. Burgos, btw. La Riba d.V. & Humada (ca. 20 km SE Aguilar d. C.), 1000 m, 10.V.1996
427 Prov. Burgos, 2 km W Rebolledo de Traspeña (SE Aguilar d. C.), 1000 m, 10.V.1996
428 Prov. Palencia, 12 km NW Villela (15 km S Aguilar d. C.), 950 m, 10.V.1996
431 Prov. Palencia, near San Cebrián de Buena Madre (20 km SE Fromista), 850 m, 11.V.1996
432 Prov. Palencia, btw. Dueñas & Sta. Cecilia del Acor (SW Palencia), 850 m, 11.V.1996
433 Prov. Valladolid, 6 km NE Urueña (ca. 44 km NNW Valladolid), 850 m, 12.V.1996
434 Prov. Valladolid, 4 km W Olmedo (43 km S Valladolid), 775 m, 12.V.1996
435 Prov. Segovía, 2 km NW Hontalbilla (17 km SE Cuéllar), 900 m, 12.V.1996

436 Prov. Segovía, btw. Sebúlcor & Villar de Sobrepeña (near Sepúlveda), 900 m, 12.V.1996
437 Prov. Segovía, 1 km W Sepúlveda, 1000 m, 12.V.1996
438 Prov. Segovía, btw. Sta. Cruz & Urueñas (N Sepúlveda), 1050 m, 13.V.1996
439 Prov. Segovía, btw. Navares d. l. C. & Aldeanueva d.l.S. (S Aranda d.D.), 1150 m, 13.V.1996
440 Prov. Burgos, 3 km NE Oquillas (ca. 20 km N Aranda d.D.), 950 m, 13.V.1996
441 Prov. Burgos, 3.5 km S Tejada (W Sto. Domingo d. S.), 1075 m, 13.V.1996
442 Prov. Burgos, Pico de la Sierra (W Sto. Domingo d.S.), 1300 m, 13.V.1996
443 Prov. Burgos, btw. Carazo & Hacinas (Esto. Domingo d. S.), 1050 m, 14.V.1996
444 Prov. Soria, 2 km N Pto. del Madero (btw. Soria & Tarazona), 1220 m, 14.V.1996
446 Prov. Narvarra/Zaragoza, Portillo de Sta. Margarita (30 km NE Tudela), 450 m, 15.V.1996 / 446a: 9./10.IV.2001, leg. T. Knebelsberger
447 Prov. Zaragoza, Santuario de Na. Sa. de Monlora (ca. 20 km E Ejea d. l. C.), 600 m, 15.V.1996 / 447a: 9.IV.2001, leg. T. Knebelsberger
448 Prov. Zaragoza, 4 km N El Frago (NE Ejea d. l. C.), ca. 600 m, 15.V.1996 / 448a: 10.IV.2001, leg. T. Knebelsberger
449 Prov. Zaragoza/Huesca, Pto. Sierra Mayor (ca. 20 km NW Ayerbe), 900 m, 15.V.1996 / 449a: 10.IV.2001, leg. T. Knebelsberger
450 Prov. Huesca, above Castillo de Loarre (NW Huesca), 1150-1400 m, 16.V.1996
451 Prov. Huesca, near La Puebla de Castro (ca. 20 km NE Barbastro), 670 m, 16.V.1996
453 Prov. Huesca, Coll. de Foradada (ca. 24 km E Ainsa), 1020 m, 16.V.1996
454 Prov. Huesca, btw. Sarvisé & Breto (S Valle de Ordesa), 950 m, 16.V.1996
455 Prov. Huesca, near Biescas (15 km N Sabiñánigo), 980 m, 17.V.1996
456 Prov. Huesca, near Escarilla (17 km SE Pto. del Portalet), 1120 m, 17.V.1996
459 Prov. Teruel, Sa. de Javalambre, 3 km NNE Manzanera, 1150 m, 1.VI.1997 / 459a:4.IV.2001, leg. T. Knebelsberger / 459b: 14.IV.2002, leg. T. Knebelsberger
460 Prov. Teruel, Sa. de Javalambre, near Torrijas, 1400-1500 m, 1.VI.1997
463 Prov. Teruel, Montes Universales, Mt. Carbonera (SE Albarracín), 1500 m, 1.VI.1997
464 Prov. Teruel, Montes Universales, below (S) Mt. Carbonera, (SE Albarracín), 1300 m, 1.VI.1997 / 464a:12.IV.1999, leg. T. Knebelsberger / 464b: 19.III.2001, leg. T. Knebelsberger
467 Prov. Teruel, Montes Universales, El Portillo (SW Guadalaviar), 1700 m, 2.VI.1997 / 467a: 4.V.1998
469 Prov. Teruel, Montes Universales, 2 km E Orihuela del Tremedal, 1400 m, 2.VI.1997
470 Prov. Teruel, Montes Universales, Pto. de Bronchales (NE Bronchales), 1500 m, 2.VI.1997
471a Prov. Teruel, Montes Universales, 2 km SW Tramacastilla, 1500 m, 11.IV.1999, leg. T. Knebelsberger
472 Prov. Granada, Sierra Nevada, 3 km W Lanjarón, 600-650 m, 1.V.1998 / 472a: 3.IV.1999, leg. H. Bohn & T. Knebelsberger / 472b: 25.III.2001, leg. T. Knebelsberger
473 Prov. Granada, Sa. de Baza, 3km SE Autovia exit Sa. de Baza, 3.V.1998 / 473a: 2.IV.1999, leg. H. Bohn & T. Knebelsberger
474 Prov. Gerona, 3 km NW Cabanelles (12 km WSW Figueras), 5.V.1998 / 474a : 15.IV.2000, leg. T. Knebelsberger
475 Prov. Granada, Mte. Parapanda, (near Montefrío), 1550 m, 1.IV.1999, leg. H. Bohn & T. Knebelsberger
476 Prov. Granada, Mte. Parapanda (near Montefrío), N slope, 1300 m, 1.IV.1999, leg. H. Bohn & T. Knebelsberger
480 Prov. Alicante, Benimaurell (ca. 30 km WSW Denia), 24.IV.2000, leg. T.M. Saks
481 Prov. Alicante, Mt. Campana (NW Benidorm), 26.IV.2000, leg. T.M. Saks
483 Prov. Alicante, Denia - Cap de Sant Antoni, 1.V.2000, leg. T.M. Saks
484 Prov. Alicante, btw. Orba & Alcalalí (NW Benissa), 2.V.2000, leg. T.M. Saks
492 Prov. Teruel, 1,5 km SW San Blas (ca. 6 km W Teruel), 1050 m, 12.IV.1999, leg. T. Knebelsberger / 492a: 18.III.2001, leg. T. Knebelsberger / 492b: 14.IV.2002, leg. T. Knebelsberger
493 Prov. Almería, Sra. de los Filabres, ca. 6 km E Senés, ca. 1000 m, 6.IV.2000, leg. T. Knebelsberger
494 Prov. Almería, Sra. de los Filabres, ca. 10 km S Oluola del Río, 1000 m, 6.IV.2000, leg. T. Knebelsberger
495 Prov. Almería, Sra. de Lúcar, 2,5 km ESE Urracal, 875m, 7.IV.2000, leg. T. Knebelsberger
496 Prov. Almería, Sra. de Lúcar, 2,5 km NW Hígueral, 925 m, 7.IV.2000, leg. T. Knebelsberger
497 Prov. Almería, Sra. de las Estancias, 1 km N Taberno, 800 m, 7.IV.2000, leg. T. Knebelsberger
498 Prov. Almería, Sra. de Bédar, 2 km NW Bédar, ca. 500 m, 7.IV.2000, leg. T. Knebelsberger
499 Prov. Almería, Sra. Cabrera, 4 km NE Gafarillos, 550 m, 7.IV.2000, leg. T. Knebelsberger
500 Prov. Almería, Sra. de Alhamilla, 9 km NE Nijar, 550 m, 23.III.2001, leg. T. Knebelsberger
501 Prov. Almería, Sra. de Gador, ca. 6 km E Félix, 550 m, 8.IV.2000, leg. T. Knebelsberger
502 Prov. Almería, Sra. de Gador, ca. 4 km S Laujar de Andarax, 1050 m, 8.IV.2000, leg. T. Knebelsberger
503 Prov. Granada, Sra. de Contraviesa, ca. 6 km N Murtas, 1050 m, 8.IV.2000, leg. T. Knebelsberger

504 Prov. Murcia, Sra. de Sopalmo, 11 km SE Jumilla, 650 m, 10.IV.2000, leg. T. Knebelsberger / 504a: 1.IV.2001, leg. T. Knebelsberger
505 Prov. Murcia, 10 km WSW Yecla (near Puerto de Jumilla), 950 m 10.IV.2000, leg. T. Knebelsberger
506 Prov. Valencía, Sra. de Martes, ca. 4 km N Confrentes, 600 m, 11.IV.2000, leg. T. Knebelsberger
507 Prov. Valencía, Sra. de Utiel, btw. Villar de Tejas & Casas de Medina, 1200 m, 11.IV.2000, leg. T. Knebelsberger / 507a: 17.III.2001, leg. T. Knebelsberger
508 Prov. Lerida, ca. 18 km E Tremp, 1000 m, 11.IV.2001, leg. T. Knebelsberger
509 Prov. Huesca, 3 km N Alastuey (ca. 26 km E Jaca), 650 m, 9.IV.2001, leg. T. Knebelsberger
510 Prov. Madrid, 4 km NE Torrelaguna (ca. 70 km N Madrid), 1050 m, 30.III.2001, leg. T. Knebelsberger
511 Prov. Castellón, Sra. de Espadún, ca. 2 km SW Ahín (21 km ENE Segorbe), 780m, 10.IV.2002, leg. T. Knebelsberger
512 Prov. Teruel, 8 km - 13 km SW Rubielos de Mora, 890-990 m, 12.IV.2000, leg. T. Knebelsberger / 512a: 4.IV.2001, leg. T. Knebelsberger

Spain, Baleares (Ba)
8 Mallorca, Coll d'es Vent, E side (6 km W Palma), 150 m, 17.IV.1987
15 Mallorca, above Fornalutx (near Soller), 400 m, 19.IV.1987
17 Mallorca, btw. Casas de la Calobra & Cala Turent (N Puig Mayor), 200 m, 19.IV.1987
19 Mallorca, Pto. de Pollença (near Pollença), 30 m, 20.IV.1987
21 Mallorca, Mt. Moleta de Ley (7 km N Arta), 200 m, 21.IV.1987
23 Mallorca, Mt. Llodra (7 km SE Manacor), 200 m, 21.IV.1987
24 Mallorca, Punta Llobera (near Cabo Blanco), 100 m, 22.IV.1987
25 Mallorca, Cabo Salinas, 10 m, 22.IV.1987
26 Mallorca, Caimari (N Inca), 200 m, 23.IV.1987
27 Mallorca, btw. Lloseta & Alaró (W Inca), 300 m, 23.IV.1987

Portugal (Po)
19 Distr. de Guarda, Serra da Estrela, 8 km E Manteigas, 600 m, 22.IV.1991
24 Distr. de Bragança, Serra de Nogueira, N slope of Mt. Nogueira, 1000-1300 m, 27./28.IV.1992

France (F)
2 Dept. Var, Callian (ca. 22 km SW Grasse), 400 m, 1.VI.1982
3 Dept. Var, Bois de Palayson, (5 km E Le Muy), 80 m, 1.VI.1982
4 Dept. Var, Val de l'Argent, near Le Thoronet (ca.10 km N Le Luc), 100 m, 2.VI.1982
5 Dept. Var, Forêt de la Darboussière (ca. 15 km NW Le Luc), 250 m, 2.VI.1982
8 Dept. Var, 6 km WSW La Môle (18 km SW St.Tropez), 70 m, 4.VI.1982
11 Dept. Var, La Guiranne (4 km NNW Solliès-Pont), 120 m, 6.VI. 1982
12 Dept. Bouches-du-Rhône, Montagne Ste.Victoire, 2 km W Puyloubier, 400 m, 6.VI.1982
13 Dept. Var/Bouches-du-Rhône, Montagne Ste.Victoire, 6 km NE Puyloubier, 450 m, 6.VI.1982 / 13a: 28.V.1998
15 Dept. Basses-Alpes, above Les Mées (25 km WSW Digne), 750 m, 7.VI.1982 / 15a: 29.V.1998
17 Dept. Basses-Alpes, Carniol (W Forcalquier), 600 m, 8.VI.1982
18 Dept. Basses-Alpes, near Chateauredon (12 km S Digne), 600 m, 10.VI.1982
19 Dept. Basses-Alpes, Grand Canyon du Verdon, La Maline, 550-700 m, 10.VI.1982
20 Dept. Basses-Alpes, Montagne de Lure, btw. Cruis & Mallefougasse-Augès, 720 m, 11.VI.1982
21 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 840 m, 11.VI.1982
22 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 1640 m, 11.VI.1982
25 Dept. Basses-Alpes, Montagne de Lure, Sommet - St. Étienne-les-Orgues, 1000 m, 11.VI.1982
26a Dept. Pyrénées-Orientales, near Fillols (S Prades), 650 m, 26.V.1985
34 Dept. Pyrénées-Orientales, near Castell (2.5 km S Vernet-les-Bains), 800 m, 26.V.1985
39 Dept. Vaucluse, near Apt, ca. 300 m, VI.1992, leg. K. Klaß
41 Dept. Pyrénées-Orientales, near Vingrau (ca. 20 km NW Perpignan), 250 m, 8.IV.1995
42 Dept. Aude, Montagne de Tauch, E slope, 400-600 m, 8.IV.1995
48 Dept. Aude, near Quillan, 350 m, 9.IV.1995
63 Dept. Aude, 2 km NE Malviès (ca. 25 km SW Carcassonne), 200 m, 29.IV.1995
79 Dept. Aude, near Chateau de Quéribus (ca. 30 km NW Perpignan), 600 m, 20.V.1996
91 Dept. Cahors, btw. Pern & St.Paul-de-Loubressac (10 km NE Castelnau-Montratier), 270 m, 3.VIII.1996
99 Depts. Drome - Basses-Alpes, Col de Pigiere (3 km SE Séderon), 970 m, 29.V.1998 / 99a: 12.VII.2002, leg. T. Knebelsberger

100 Dept. Vaucluse, 2,5 km ESE Col N.D. des Abeilles (near Sault), 980 m, 29.V.1998

France, Corsica (Co)
12a Dolmen de Fontanaccia (18 km SSW Sartène), 100 m, 28./29.V.2003
54a Cavo/Ghisoni, 700 m, 31.V.2003

Switzerland (He)
1 Kanton Wallis, Saillon, 500 m, 25.V.1996 / 1a: 27.V.1998
4 Kanton Wallis, Hohtenn, 650 m, 26.V.1996 / 4a: 27.V.1998
5 Kanton Wallis, Hohtenn, 900 m, 26.V.1996 / 5a: 7.VIII.1996
6 Kanton Wallis, Hohtenn, 1100 m, 26.V.1996
26 Kanton Wallis, Mont du Rosel (bei Martigny), 450 m, 26.V.1998 / 26a: 12.VII.2002, leg. T. Knebelsberger
27 Kanton Wallis, Eggerberg (bei Visp), 1500 m, 27.V.1998
31 Kanton Wallis, 1 km WSW Chermignon d'en Bas (bei Sierre), 840 m, 14.VI.2001

Italy (It)
90 Lazio, Monti Aurunci, 4.5 km NW Maranola (near Formia), 750 m, 11.IV.1999
250 Giglio, surrounding of Campes, early in IV.2005, leg. M. Unsöld

Italy, Sicily (Sz)
11a Monte Etna, Monti Rossi (near Nicolosi), 800 m, 29.IV.1999
25 btw. Leonforte & Assaro (near Enna), 6oo m, 17.IV.1999
26 Monti Erei, 1 km E Portella Creta (near Enna), 800 m, 17.IV.1999
27 Monti Erei, Bosco di Sperlinga (W Nicosia), 850 m, 18.IV.1999
41 1 km SE Santo Stefano, 900 m, 21.IV.1999
53 Granitola-Torretta (10 km SE Mazara del Vallo), 10 m, 24.IV.1999
54 1 km SW Portella Misilbesi (16 km NNW Sciacca), 300 m, 24.IV.1999
57 Monte Campanella (near Milena, NNE Agrigento), 570 m, 25.IV.1999
60 Monte Navone (Mazzarino - Piazza-Armerina), ca. 500 m, 25.IV.1999
62 3 km N Alcate (9 km NW Vittoria), 140 m, 26.IV.1999
64 10 km W Santa Croce Camerina (SW Ragusa), 250 m, 26.IV.1999
67 1 km NE Catenanuova, 170 m, 27.IV.1999
69 below Castello di Spanò (ca. 20 km SE Troina), 350 m, 28.IV.1999

Croatia (Hr)
14 I. Korčula, plain W Mt. Klupca, 450 m, 13.-15.V.2001, leg. Bohn, Knebelsberger & Saks
15 I. Korčula, Zavalatica, 50 m, 14.V.2001, leg. Bohn, Knebelsberger & Saks
20 Pelješac, Gornji Nakovanj, 300 m, 15.V.2001, leg. Bohn, Knebelsberger & Saks
24 Pelješac, 3 km WNW Kasarni Do, 400 m, 16.V.2001, leg. Bohn, Knebelsberger & Saks
26 Rilić Mts., S slope of Sokolić, ca. 2 km N Drvenik, 150 m, 16.-17.V.2001, leg. Bohn, Knebelsberger & Saks
27 I. Hvar, Mt. Ublina, 5 km W Sućuraj, 200 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks
28 I. Hvar, E slope of Mt. Hum, ca. 500 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks
29 I. Hvar, Mt. Odzdrin (E Brusje), 400 m, 17.V.2001, leg. Bohn, Knebelsberger & Saks

Morocco (Ma)
14a Moyen Atlas, Dayèt Iffer (NE Ifrane), 1600 m, 26./27.IV.1998
176a Moyen Atlas, btw. Aghrame-Amelall & El-Aderj (ca. 65 km NE Boulemane), 1100-1200 m, 27./28.IV.1998
258 Moyen Atlas, Jbel Cherbana (near Tazouta, SE Sefrou), 1600 m, 27.IV.1998
259 Moyen Atlas, Tizi-n'Tilrhemine (17,5 km S Ribat-el-Kheir, SE El-Menzel), 1100 m, 28.IV.1998
264 Jbel Mahssor (S Oujda), Oude-El-Heimer, 950 m, 21.II.1999
273 Haut Atlas (NE slope), Missour - Bouanane, 9 km NW Talsinnt, 1500 m, 24.II.1999
288 Moyen Atlas, Jbel Gaberaal, near Tirnest (NW Outat-Oulad-El-Haj), 1800 - 2000 m, 30.III.2000

Algeria (Al)
14 Chaîne des Biban, Hammam-El-Biban, 450 m, 27.IV.1990
16 Monts de Belzma, Seriana, 1100-1300 m, 27.IV.1990

Tunesia (Tu)
5 Forêt de Kesra (E Makthar), 800-1000 m, 13.IV.1990

8 Montes de Tébessa, J. Azered, ca. 20 km SW Thala, 850 m, 15.IV.1990
9 ca. 20 km WSW Le Kef, 500 m, 16.IV.1990
10 btw. Sakiet Sidi Youssef & Touiret (NW Le Kef), 16.IV.1990

Appendix 2. List of characters (1–24) used in the cladistic analysis of the *subaptera*-group

1. Male: T5 and T6: excavations of membrane glands at the anterior border of the segments:
0. weak
1. strong

2. Male: T6 transversal torus with bristles:
0. always present and well developed
1. only sometimes present and weaker developed
2. absent

3. Male: T7 glandular structures: transversal trough:
0. deep
1. less deep
2. very shallow

4. Male: T7 glandular structures: anterior wall of trough:
0. slightly hollowed out anteriorly
1. nearly upright

5. Male: T7 glandular structures: bristle fields:
0. not deepened into grooves
1. strongly deepened forming two longitudinally oval grooves

6. Male: T7 glandular structures: bristle fields:
0. large
1. moderately large
2. small

7. Male: T7 glandular structures: shape of bristles:
0. modified
1. strongly modified

8. Male: T7 glandular structures: median ridge:
0. high and broadly rounded
1. low and obtuse angled

9. Male: T7 glandular structures: mound:
0. high and broad
1. less high, small
2. very shallow and small

10. Male: T7 glandular structures: median lobe:
0. very short
1. short
2. long

11. Male: T8 glandular structures:
0. absent
1. present

12. Male: T8 anterior processes:
0. absent
1. present

13. Male: T8 space beween anterior processes:
0. broad
1. less broad

2. narrow
3. very narrow

14. Male: T8 glandular structures: conelike process:
0. well developed
1. small
2. forming a membraneous bubble
3. absent

15. Male: T8 glandular structures: sinusoidal edge:
0. well developed, steep and broad
1. less steep and broad
2. edge only slightly present and not sinusoidal
3. absent

16. Male: T8 glandular structures: central mound:
0. high and broad
1. lower and less broad
2. strongly reduced
3. absent

17. Male: T8 glandular structures: glandular pores on surface of the central mound:
0. present
1. absent

18. Male: medio-anterior process of right paraproct:
0. with a bulge at the base
1. without bulge

19. Male: helmet sclerite:
0. with relatively long acuminate process in the "rear"
1. acuminate process in the "rear" reduced
2. acuminate process in the "rear"completely missing

20. Male: helmet sclerite:
0. "frontal" part opposite to the process normally formed
1. "frontal" part opposite to the process shortened

21. Male: distal end of mid tibia:
0. with 5 spines
1. with 4 spines

22. Male: supraanal plate (T10):
0. broadly rounded
1. triangularly rounded

23. Female: disc of pronotum:
0. with variously extended dark area
1. throughout regularly mottled

24. Female: genitalia:
0. without additional sigmoidal sclerotization
1. with additional sigmoidal sclerotization

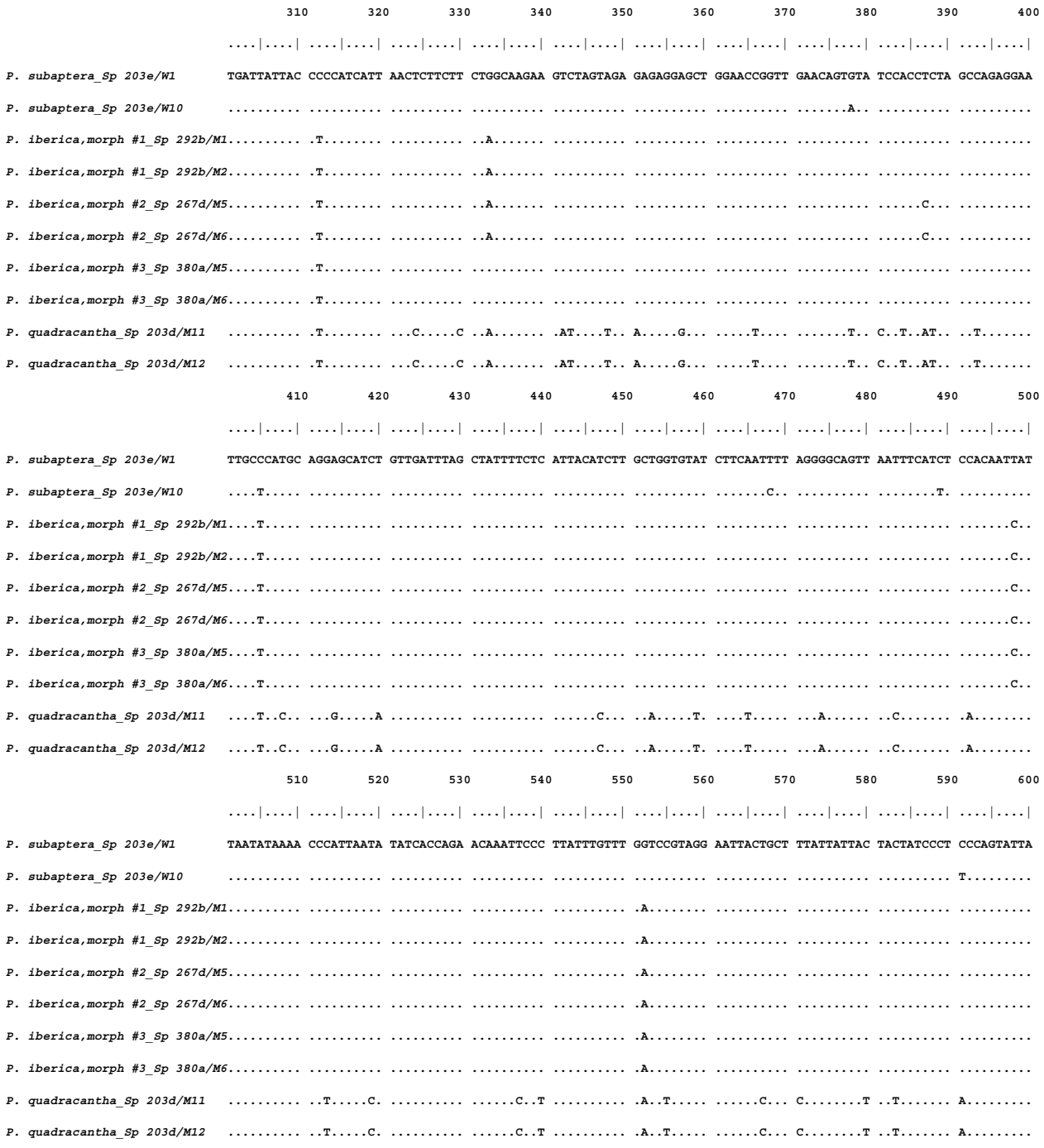
Appendix 3. Distribution of 24 characters in chosen taxa for cladistic analysis of *subaptera*-group. Inapplicable states are shown as "-".

character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
outgroup taxa																								
nana-group	0	2	-	-	0	-	0	-	-	0	0+1	0	-	-	-	-	-	0	0	0	0	0	0	0
carpetana-group	1	2	-	-	1	-	1	-	-	-	0+1	0	-	-	-	-	-	0	0	0	0	0+1	0	0
panteli-group	0	2	-	-	0	-	-	-	-	-	0	0	-	-	-	-	-	0	2	0	0	0	-	0
ingroup taxa																								
P. iberica morph #1	1	2	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	1	0	1
P. iberica morph #2	1	0	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1
P. iberica morph #3	1	1	1	1	1	1+2	1	1	2	1	1	1	2	2	2	2	1	1	1	1	0	1	0	1
P. quadracantha	1	2	2	1	1	1	1	1	2	2	0	1	3	3	3	3	-	0	0	0	1	0	1	0

Appendix 4. Sequence data

Mitochondrial DNA sequences including the whole sequence of the mitochondrial cytochrome c oxidase subunit I gene (COI) of the analysed specimenses of *subaptera*-group. Within the 10 taxa the first 1570 bp include 173 variable positions.

```
                                    10         20         30         40         50         60         70         80         90        100
                                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1             CTGAAGCGAT GATTATTTTC AACCAATCAT AAGGACATTG GCACTTTGTA CTTTATTTTT GGTGCCTGAT CAGGAATAGT AGGCACTTCT TTAAGTATAT
P. subaptera_Sp 203e/W10            .......... .......... .......... .....T.... .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M1                  .......... ........C. .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M2.......... .......... .......... ........C. .......... .......... .......... .......... .......... ..........
P. iberica,morph #2_Sp 267d/M5.......... .......... .......... ........C. .......... .......... .......... .......... .......... ..........
P. iberica,morph #2_Sp 267d/M6.......... .......... .......... ........C. .......... .......... .......... ........A. .......... ..........
P. iberica,morph #3_Sp 380a/M5.......... .......... .......... ........C. .......... .......... .......... .......... .........C ..........
P. iberica,morph #3_Sp 380a/M6.......... .......... .......... ........C. .......... .......... .......... .......... .......... ..........
P. quadracantha_Sp 203d/M11   .....A.... ....G..... ......C... .......... .......A.. .......... .......... ..A....G.. ......A... .........C
P. quadracantha_Sp 203d/M12   .....A.... ....G..... .......... .......... .......A.. .......... .......... ..A....G.. ......A... .........C
                                   110        120        130        140        150        160        170        180        190        200
                                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1             TAATCCGCAC TGAATTAAAT CAACCGGGTT CATTAATTGG TGATGATCAA ATTTATAATG TTATTGTTAC AGCTCATGCA TTTATTATAA TTTTCTTCAT
P. subaptera_Sp 203e/W10            .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M1....T..... .......... .......... .......... .......... .......... .......... .......... .......... .......T..
P. iberica,morph #1_Sp 292b/M2....T..... .......... .......... .......... .......... .......... .......... .......... .......... .......T..
P. iberica,morph #2_Sp 267d/M5....T..... .......... .......... .......C.. .......... .......... .......... .......... .......... .......T..
P. iberica,morph #2_Sp 267d/M6....T..... .......... .......... .......C.. .......... .......... .......... .......... .......... .......T..
P. iberica,morph #3_Sp 380a/M5....T..... .......... .......... .......... .......... .......... .......... .......... .......... .......T..
P. iberica,morph #3_Sp 380a/M6....T..... .......... .......... .......... .......... .......... .......... .......... .......... .......T..
P. quadracantha_Sp 203d/M11   ....T..T.. .......... .....A.... .......... A.....C... ..C....... .......C.. ...C...... .......... .......T..
P. quadracantha_Sp 203d/M12   ....T..T.. .......... .....A.... .......... A.....C... ..C....... .......C.. ...C...... .......... .......T..
                                   210        220        230        240        250        260        270        280        290        300
                                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1             AGTTATACCA ATTTTAATTG GAGGATTTGG AAATTGATTA GTACCTTTAA TATTAGGAGC ACCGGATATA GCATTTCCAC GAATAAATAA TATAAGATTC
P. subaptera_Sp 203e/W10            .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M1.......... .......... .......... ......G... .......... .......... .......... .....C.... .......... ..........
P. iberica,morph #1_Sp 292b/M2.......... .......... .......... ......G... .......... .......... .......... .....C.... .......... ..........
P. iberica,morph #2_Sp 267d/M5.......... .......... .......... ......G... .......... .......... .......... .......... .......... ..........
P. iberica,morph #2_Sp 267d/M6.......... .......... .......... ......G... .......... .......... .......... .......... .......... ..........
P. iberica,morph #3_Sp 380a/M5.......... .......... .......... ......G... .......... .......... .......... .....C.... .......... ..........
P. iberica,morph #3_Sp 380a/M6.......... .......... .......... ......G... .......... .......... ...T...... .....C.... .......... ..........
P. quadracantha_Sp 203d/M11   .......... ..C....... ....T..... .......... ..T..A.... .......G.. ...T.....G ..C..C.... .......... ......C..T
P. quadracantha_Sp 203d/M12   .......... ..C....... ....T..... .......... ..T..A.... .......G.. ...T.....G ..C..C.... .......... ......C..T
```


310 320 330 340 350 360 370 380 390 400
P. subaptera_Sp 203e/W1 TGATTATTAC CCCCATCATT AACTCTTCTT CTGGCAAGAA GTCTAGTAGA GAGAGGAGCT GGAACCGGTT GAACAGTGTA TCCACCTCTA GCCAGAGGAA
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12
410 420 430 440 450 460 470 480 490 500
P. subaptera_Sp 203e/W1 TTGCCCATGC AGGAGCATCT GTTGATTTAG CTATTTTCTC ATTACATCTT GCTGGTGTAT CTTCAATTTT AGGGGCAGTT AATTTCATCT CCACAATTAT
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12
510 520 530 540 550 560 570 580 590 600
P. subaptera_Sp 203e/W1 TAATATAAAA CCCATTAATA TATCACCAGA ACAAATTCCC TTATTTGTTT GGTCCGTAGG AATTACTGCT TTATTATTAC TACTATCCCT CCCAGTATTA
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12

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                                610        620        630        640        650        660        670        680        690        700
                               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1        GCTGGTGCAA TTACTATATT ATTAACTGAT CGAAATCTTA ATACTTCTTT TTTTGATCCA GCAGGAGGGG GTGACCCTAT TTTATATCAA CATCTATTTT
P. subaptera_Sp 203e/W10       .......... .......... .......... .......... .......... .......... .......... ....T..... .......... ..........
P. iberica,morph #1_Sp 292b/M1.......... .......... .......... .......... .......... ......C... .......... ....T..... C......... ..........
P. iberica,morph #1_Sp 292b/M2.......... .......... .......... .......... .......... ......C... .......... ....T..... C......... ..........
P. iberica,morph #2_Sp 267d/M5.......... .......... .......... .......... .......... .......... .......... ....T..C.. .......... ..........
P. iberica,morph #2_Sp 267d/M6.......... .......... .......... .......... .......... .......... .......... ....T..C.. .......... ..........
P. iberica,morph #3_Sp 380a/M5.......... .......... .......... .......... .......... ......C... .......... ....T..... C......... ..........
P. iberica,morph #3_Sp 380a/M6.......... .......... .......... .......... .......... ......C... .......... ....T..... .......... ..........
P. quadracantha_Sp 203d/M11    .......... .......... .......... ........C. .......... .........G ........A. .A........ ...G...... ..C.......
P. quadracantha_Sp 203d/M12    .......... .......... .......... ........C. .......... .........G ........A. .A........ ...G...... ..C.......
                                710        720        730        740        750        760        770        780        790        800
                               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1        GATTCTTTGG ACATCCAGAA GTTTATATTT TAATTCTACC AGGATTTGGT ATAATCTCTC ATATTATTTG TCATGAAAGA GGTAAAAAGG AAGCATTCGG
P. subaptera_Sp 203e/W10       .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M1.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. iberica,morph #1_Sp 292b/M2.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. iberica,morph #2_Sp 267d/M5.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. iberica,morph #2_Sp 267d/M6.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. iberica,morph #3_Sp 380a/M5.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. iberica,morph #3_Sp 380a/M6.......... .......... .......... .......... .......... .......... .......... .......... ........A. ..........
P. quadracantha_Sp 203d/M11    ....T..C.. .......... ..C....... .....T.... .......... ........A. .......... .........T ..G.....A. ..........
P. quadracantha_Sp 203d/M12    ....T..C.. .......... ..C....... .....T.... .......... ........A. .......... .........T ..G.....A. ..........
                                810        820        830        840        850        860        870        880        890        900
                               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
P. subaptera_Sp 203e/W1        AAACCTAGGA ATAATTTTTG CTATATTAGC AATTGGTTTA TTAGGATTTG TAGTTTGAGC TCACCATATA TTTACTGTAG GAATAGATGT AGATACCCGA
P. subaptera_Sp 203e/W10       .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M1.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. iberica,morph #1_Sp 292b/M2.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. iberica,morph #2_Sp 267d/M5.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. iberica,morph #2_Sp 267d/M6.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. iberica,morph #3_Sp 380a/M5.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. iberica,morph #3_Sp 380a/M6.......... .......... .......... .......... .......... .......... ...T...... .......... .......... ..........
P. quadracantha_Sp 203d/M11    ...TT.G..T .......... .......... ......A... .......... .G........ ...T...... .....A.... .......... ..........
P. quadracantha_Sp 203d/M12    ...TT.G..T .......... .......... ......A... .......... .G..A..... ...T.....G .....A.... .......... ..........
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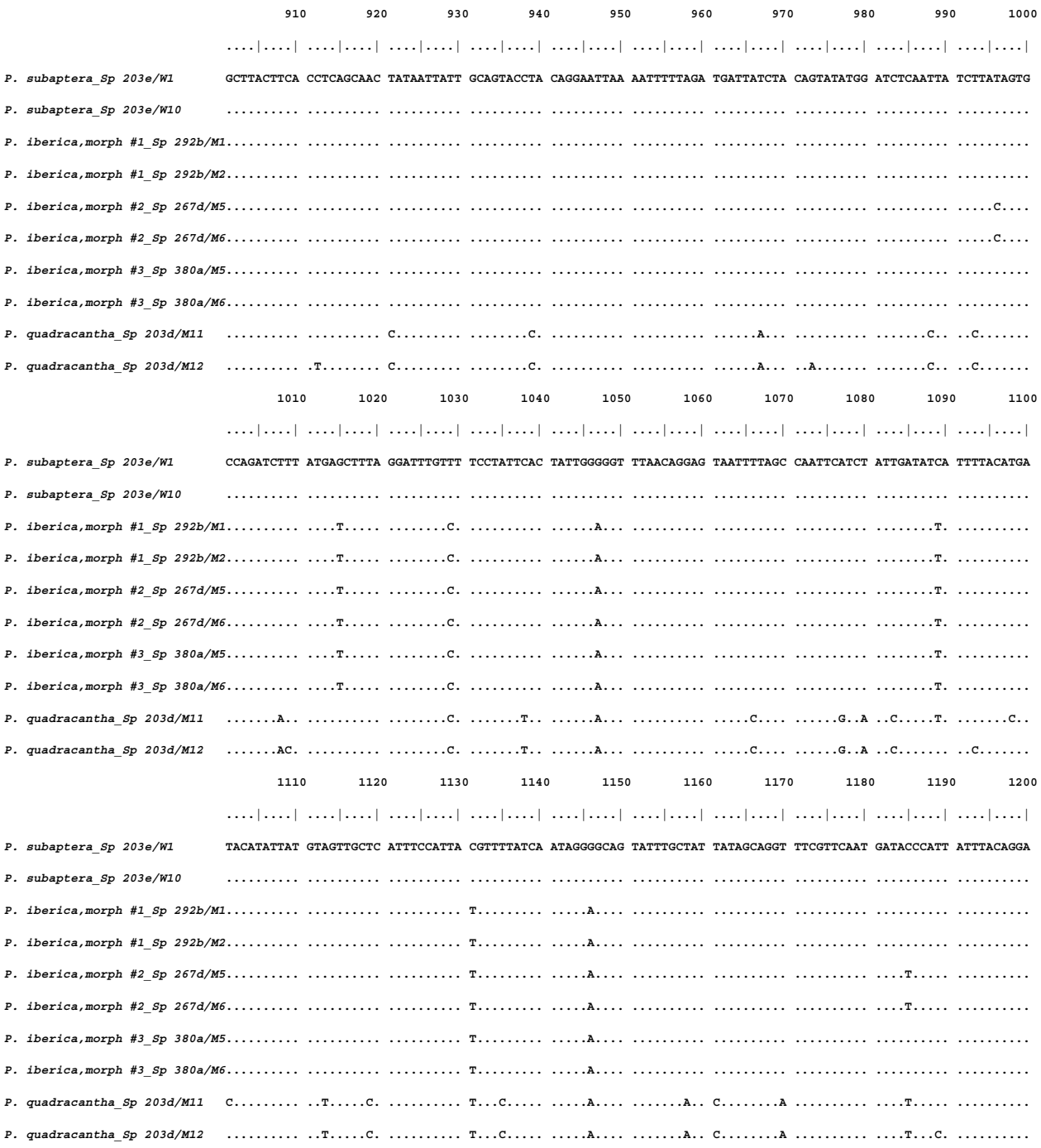
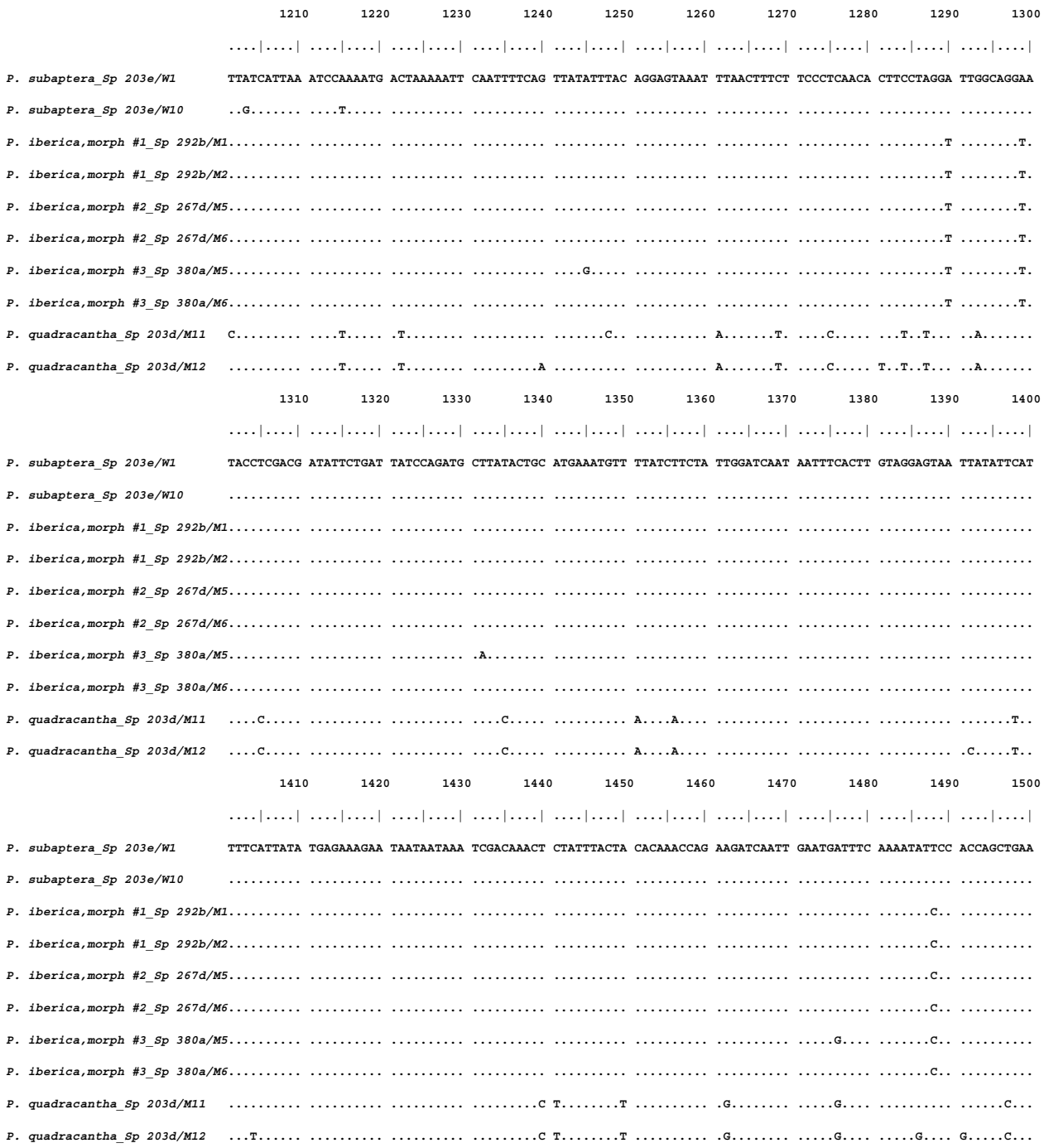

910 920 930 940 950 960 970 980 990 1000
P. subaptera_Sp 203e/W1 GCTTACTTCA CCTCAGCAAC TATAATTATT GCAGTACCTA CAGGAATTAA AATTTTTAGA TGATTATCTA CAGTATATGG ATCTCAATTA TCTTATAGTG
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12
1010 1020 1030 1040 1050 1060 1070 1080 1090 1100
P. subaptera_Sp 203e/W1 CCAGATCTTT ATGAGCTTTA GGATTTGTTT TCCTATTCAC TATTGGGGGT TTAACAGGAG TAATTTTAGC CAATTCATCT ATTGATATCA TTTTACATGA
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12
1110 1120 1130 1140 1150 1160 1170 1180 1190 1200
P. subaptera_Sp 203e/W1 TACATATTAT GTAGTTGCTC ATTTCCATTA CGTTTTATCA ATAGGGGCAG TATTTGCTAT TATAGCAGGT TTCGTTCAAT GATACCCATT ATTTACAGGA
P. subaptera_Sp 203e/W10
P. iberica,morph #1_Sp 292b/M1
P. iberica,morph #1_Sp 292b/M2
P. iberica,morph #2_Sp 267d/M5
P. iberica,morph #2_Sp 267d/M6
P. iberica,morph #3_Sp 380a/M5
P. iberica,morph #3_Sp 380a/M6
P. quadracantha_Sp 203d/M11
P. quadracantha_Sp 203d/M12


1210 1220 1230 1240 1250 1260 1270 1280 1290 1300
P. subaptera_Sp 203e/W1 TTATCATTAA ATCCAAAATG ACTAAAAATT CAATTTTCAG TTATATTTAC AGGAGTAAAT TTAACTTTCT TCCCTCAACA CTTCCTAGGA TTGGCAGGAA
P. subaptera_Sp 203e/W10 ..G..... ....T..... .....
P. iberica,morph #1_Sp 292b/M1 .....T .....T.
P. iberica,morph #1_Sp 292b/M2 .....T .....T.
P. iberica,morph #2_Sp 267d/M5 .....T .....T.
P. iberica,morph #2_Sp 267d/M6 .....T .....T.
P. iberica,morph #3_Sp 380a/M5 ....G..... .....T .....T.
P. iberica,morph #3_Sp 380a/M6 .....T .....T.
P. quadracantha_Sp 203d/M11 C..... ....T..... .T..... .....C.. ..... A.....T. ....C..... ...T..T... ..A.....
P. quadracantha_Sp 203d/M12 ....T..... .T..... .....A .... A.....T. ....C..... T..T..T... ..A.....
1310 1320 1330 1340 1350 1360 1370 1380 1390 1400
P. subaptera_Sp 203e/W1 TACCTCGACG ATATTCTGAT TATCCAGATG CTTATACTGC ATGAAATGTT TTATCTTCTA TTGGATCAAT AATTTCACTT GTAGGAGTAA TTATATTCAT
P. subaptera_Sp 203e/W10 .....
P. iberica,morph #1_Sp 292b/M1 .....
P. iberica,morph #1_Sp 292b/M2 .....
P. iberica,morph #2_Sp 267d/M5 .....
P. iberica,morph #2_Sp 267d/M6 .....
P. iberica,morph #3_Sp 380a/M5 .....A..... .....
P. iberica,morph #3_Sp 380a/M6 .....
P. quadracantha_Sp 203d/M11 ....C..... ....C..... ..... A....A.... ....T..
P. quadracantha_Sp 203d/M12 ....C..... ....C..... ..... A....A.... ....C.....T..
1410 1420 1430 1440 1450 1460 1470 1480 1490 1500
P. subaptera_Sp 203e/W1 TTTCATTATA TGAGAAAGAA TAATAATAAA TCGACAAACT CTATTTACTA CACAAACCAG AAGATCAATT GAATGATTTC AAAATATTCC ACCAGCTGAA
P. subaptera_Sp 203e/W10 .....
P. iberica,morph #1_Sp 292b/M1 .....C.. .....
P. iberica,morph #1_Sp 292b/M2 .....C.. .....
P. iberica,morph #2_Sp 267d/M5 .....C.. .....
P. iberica,morph #2_Sp 267d/M6 .....C.. .....
P. iberica,morph #3_Sp 380a/M5 .....G.... .....C.. .....
P. iberica,morph #3_Sp 380a/M6 .....C.. .....
P. quadracantha_Sp 203d/M11 .....C T.....T ..... .G..... .....G.... ....C...
P. quadracantha_Sp 203d/M12 ...T..... ....C T.....T ..... .G..... .....G.... .....G.... G.....C...

```
                                    1510       1520       1530       1540       1550       1560       1570       1580       1590
                                   ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|..
P. subaptera_Sp 203e/W1            CATAGTTATT CAGAATTACC AACAATTTTA AATTATCTAA TATGGCAGAT AAGTGCAGTG GATTTAAGCT CCACATATAA AGTTTTTACT TTTATTA
P. subaptera_Sp 203e/W10           .......... .......... .......... .......... .......... .......... .......... .......... .......... .......
P. iberica,morph #1_Sp 292b/M1..... .......... .......... .......... .......... .......... ........A. .......... .......... .......... .......
P. iberica,morph #1_Sp 292b/M2..... .......... .......... .......... .......... .......... ........A. .......... .......... .......... .......
P. iberica,morph #2_Sp 267d/M5..... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......
P. iberica,morph #2_Sp 267d/M6..... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......
P. iberica,morph #3_Sp 380a/M5..... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......
P. iberica,morph #3_Sp 380a/M6..... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......
P. quadracantha_Sp 203d/M11   .....A.... .C..... .......... .......... .......... .......... .......A.. A......... .......... .....
P. quadracantha_Sp 203d/M12   .....A.... .C..... .......... .......... .......... .......... .......A.. A.........
```

Appendix 5: Variable positions of COI sequences of *subaptera*-group

Variable positions of *Phyllodromica subaptera*

positions:	36	378	405	468	489	591	675	1203	1215
*Phyllodromica subaptera*_Sp 203e/W1	C	G	C	T	C	C	C	A	A
*Phyllodromica subaptera*_Sp 203e/W10	T	A	T	C	T	T	T	G	T

Variable position of *Phyllodromica iberica* morph #2

position:	79
P. iberica morph #2_Sp 267d/M5	G
P. iberica morph #2_Sp 267d/M6	A

Variable positions of *Phyllodromica iberica* morph #3.

positions:	90	264	681	1245	1332	1476
P. iberica morph #3_Sp380a/M5	C	G	C	G	A	G
P. iberica morph #3_Sp380a/M6	T	T	T	A	T	A

Variable positions of *Phyllodromica quadracantha*.

positions:	27	855	870	912	973	1009
*P. quadracantha*_Paratype Sp 203d/M11	C	T	A	C	G	T
*P. quadracantha*_Paratype Sp 203d/M12	T	A	G	T	A	C

1089	1093	1098	1101	1189	1201	1240	1248	1281	1392	1404	1486	1491
T	T	C	C	T	C	G	C	C	T	C	A	A
C	C	T	T	C	T	A	T	T	C	T	G	G

Appendix 6. Pairwise sequence distance matrix of analysed *subaptera*-group specimens and *Blattella germanica* from GenBank. 1570 base pairs of the mitochondrial DNA sequences shown in Appendix 4 were used in this calculation. In *Blattella germanica* the positions 1537–1570 were coded as gaps. Below diagonal: uncorrected ("p") distances in percent. Above diagonal: total character differences mean character differences.

		1	2	3	4	5	6	7	8	9	10	11
1	*P. subaptera_Sp 203e/W1*	-	9	25	25	26	27	27	23	138	145	240
2	*P. subaptera_Sp 203e/W10*	0.57	-	30	30	31	32	32	28	141	148	238
3	*P. iberica,morph #1_Sp 292b/M1*	1.59	1.91	-	0	9	10	6	4	135	144	237
4	*P. iberica,morph #1_Sp 292b/M2*	1.59	1.91	0.00	-	9	10	6	4	135	144	237
5	*P. iberica,morph #2_Sp 267d/M5*	1.66	1.98	0.57	0.57	-	1	13	9	135	144	235
6	*P. iberica,morph #2_Sp 267d/M6*	1.72	2.04	0.64	0.64	0.06	-	14	10	136	145	236
7	*P. iberica,morph #3_Sp 380a/M5*	1.72	2.04	0.38	0.38	0.83	0.89	-	6	137	146	242
8	*P. iberica,morph #3_Sp 380a/M6*	1.47	1.78	0.26	0.26	0.57	0.64	0.38	-	133	142	236
9	*P. quadracantha_Sp 203d/M11*	8.79	8.98	8.60	8.60	8.60	8.66	8.73	8.47	-	19	249
10	*P. quadracantha_Sp 203d/M12*	9.24	9.43	9.17	9.17	9.17	9.24	9.30	9.05	1.21	-	245
11	*Blattella germanica*	15.60	15.48	15.41	15.41	15.28	15.34	15.74	15.34	16.20	15.94	-

Appendix 7. Means of values from specimens genetic distances of *subaptera*-group taxa and *Blattella germanica* derived from the data shown in Appendix 6.

distances within taxa		distances between taxa				
		P. iberica morph #1	*P. iberica* morph #2	*P. iberica* morph #3	*P. quadracantha*	*B. germanica*
0.57 (9)	*P. subaptera*	**1.75** (27.5)	**1.85** (29)	**1.75** (27.5)	**9.11** (143)	**15.54** (239)
0.00 (0)	*P. iberica* morph #1		**0.61** (9.5)	**0.32** (5)	**8.86** (139.5)	**15.41** (237)
0.06 (1)	*P. iberica* morph #2			**0.73** (11.5)	**8.92** (140)	**15.31** (235.5)
0.38 (6)	*P. iberica* morph #3				**8.89** (139,5)	**15.54** (239)
1.21 (19)	*P. quadracantha*					**16.07** (247)

Bold values: mean uncorrected “p” distances in percent. Values in parentheses: mean basepair differences.