

## Review of the cedar and oak forest-associated *Epuraea latipes* species group (Coleoptera: Nitidulidae, Epuraeinae), with description of a new species from southern Turkey

Sakine Serap Avgın, Donatella Magri, Gloria Antonini, Emiliano Mancini, Nicklas Jansson, Andrzej Lasoń, Andrew R. Cline & Paolo Audisio\*

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A new species of *Epuraea*, *Epuraea sutcuimamun* Avgın, Lasoń & Audisio **sp. n.**, from southern Turkey (Taurus Chain) was identified using morphological analyses. This species is a member of a circum-Mediterranean endemic group of sap beetles, the *Epuraea latipes* species group of the *Dadopora* lineage, which are mostly associated with cedar (*Cedrus* spp.) forests. Herein, the new species is described, the previously unknown association of the little-known *Epuraea subparallela* Grouvelle 1896 with meso-xerophilous oaks is reported, and some new records from southern Turkey (Taurus Chain) are listed for the latter species (previously only known from the Nur Mts. in SE Turkey, Osmaniye and Iskenderun provinces). An identification key to species of *Dadopora* lineage is also provided. Finally, the main palaeogeographic events affecting the Miocene to Holocene dispersal and evolution of species/populations of the *Dadopora* lineage on cedars and oaks, and the coincident distributional dynamics of Western Palaeartic *Cedrus* populations throughout the Mediterranean Basin, are discussed.

S.S. Avgın, Kahramanmaraş Sutcu Imam University, Faculty of Education, and Faculty of Arts and Science, Department of Biology, TR-46100 Kahramanmaraş, Turkey; E-mail: ssavgın@ksu.edu.tr; serapavgın@hotmail.com

D. Magri, Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Piazzale Aldo Moro 5, I-00185, Rome, Italy; E-mail: donatella.magri@uniroma1.it

G. Antonini, Dipartimento di Biologia e Biotecnologie “Charles Darwin”, Sapienza Università di Roma, Via Borelli 50, I-00161 Rome, Italy; E-mail: gloria.antonini@uniroma1.it

E. Mancini, Dipartimento di Scienze di Sanità Pubblica e Malattie Infettive, Sapienza Università di Roma, Piazzale Aldo Moro 5, I-00185, Rome, Italy; E-mail: emiliano.mancini@uniroma1.it

N. Jansson, Division of Ecology, Linköping University, 581 83 Linköping, Sweden; E-mail: nicja@ifm.liu.se

A. Lasoń, ul. Wiejska 4B/85, 15-352 Białystok, Poland; E-mail: haptors@interia.pl

A. R. Cline, Plant Pest Diagnostics Center, California Department of Food & Agriculture, 3294 Meadowview Road, Sacramento, CA 95832-1448, USA; E-mail: acline@cdfa.ca.gov

P. Audisio (\*corresponding author), Dipartimento di Biologia e Biotecnologie "Charles Darwin", Sapienza Università di Roma, Via Borelli 50, I-00161 Rome, Italy; E-mail: paolo.audisio@uniroma1.it

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## 1. Introduction

*Epuraea* Erichson 1843 comprises more than 300 species worldwide (Grouvelle 1913, Reitter 1919, Sjöberg 1939, Audisio 1993, Kirejtshuk 1998, Jelínek & Audisio 2007), and is the most speciose genus within Nitidulidae. Within this likely paraphyletic genus, different authors have recognized several monophyletic derived species-groups and/or subgenera, or described closely related genera whose taxonomy needs to be disentangled (see Kirejtshuk 1998). A preliminary re-examination of the genus-level taxonomy of the subfamily Epuraeinae, based on morphological and molecular data, is in preparation (Audisio, unpublished data). The subgenus *Dadopora* Thomson, 1859 (type species: *Nitidula guttata* Olivier, 1811) has been recognized as a distinct taxon by Kirejtshuk (1998), but, pending for new phylogenetic analyses, more recently it was tentatively considered a synonym of *Epuraea* s. str. by Jelínek and Audisio (2007). Following further analyses, this subgenus represents a likely distinct and monophyletic lineage formally including only two closely related species distributed in the Western Palaearctic [i.e. *E. guttata* (Olivier, 1811) and *E. fuscicollis* (Stephens, 1832)], both widespread in Europe and the Near East.

However, this lineage certainly also contains the related *E. latipes* Grouvelle, 1896 clade (Audisio 1983, 1993). Both groups are characterized (Figs. 1–2) by many shared characters, including peculiarly wide, robust and triangular protibiae (especially males); robust and markedly convex (in transverse section) mesotibiae; mesotibiae 2.8–3.3 times as long as wide; absent or markedly reduced sexual dimorphism in male mesotibiae; characteristically wide male pro-tarsal plates; lateral edges of pronotum and elytra

fringed by a single dense series of relatively short but markedly distinct and non-recumbent golden setae; simple (never toothed) tarsal claws; a transverse rather than convex body shape; very narrowly flattened sides of pronotum and elytra; regularly and shallowly arcuately emarginated anterior edge of pronotum; weakly impressed and posteriorly slightly delimited antennal grooves on ventral side of head; space between mesocoxal cavities narrower than space between procoxal cavities; relatively short antennae; and meta-ventrite with a broadly V-shaped posterior edge. All known species are mycetophagous sap-feeders (typically as larvae and adults), and are associated with old-growth oak or cedar forests in mostly xerophilous or mesoxerophilous vegetation zones.

The *Epuraea latipes* Grouvelle, 1896 species group of the *Dadopora* lineage, previously treated by Audisio (1983, 1993), comprises three species, in addition to the new species described below, that were believed to be all associated with cedar forests: *E. latipes* (northern Morocco and Algeria), *E. rifensis* Audisio, 1983 (northern Algeria and Morocco, with relictual populations in southern Spain), and *E. subparallela* Grouvelle, 1896 (Nur Mts. in SE Turkey) (see discussion below).

The recent discovery of a fourth species of this clade in SW Turkey, which appears closely related to *E. latipes* from western North Africa and was tentatively attributed to the true *E. latipes* by Lasoń (2007), and the rediscovery of *E. subparallela* Grouvelle, 1896 in southern Turkey caused us to reconsider the entire *Dadopora* lineage. The goal of this paper is to describe the new species, compare it with known members of the *Epuraea latipes* species-group, and construct a feasible scenario for the evolution of the *Dadopora* clade in the context of the known palae-

geographic, palaeoecological, and molecular data of the distribution and evolution of *Cedrus* (Pinaceae) throughout the Mediterranean Basin.

## 2. Material and methods

Part of the studied material from southern Turkey (Taurus Chain) was collected by the first author using vinegar-baited pitfall traps during a series of entomological studies on the saproxylic insect fauna (see Waage 1985, Niemelä 1998, Lemieux & Lindgren 1999, Koivula *et al.* 2003, and Brandmayr *et al.* 2005 for details of this trapping method). The fieldwork in an old-growth cedar forest (*Cedrus libani* A. Rich), in the proximity of Erdemli (Mersin province), was completed in the summer of 2010 by the first author. Pitfall traps were placed near and around trees, or in tree holes in cedar forests, and checked weekly during 20.VII.–13.VIII.2010. The material collected from the pitfall traps was immediately sorted and preserved in 80% ethanol and retained for morphological analyses (CAK, CAR, NMPC, ARCC and CLB, see below for definitions of acronyms). Some specimens were preserved in pure acetone for molecular analyses (CAR). Important additional material was also collected by N. J. together with Turkish colleagues, using window traps (30x50 cm sitting on the tree trunk) in southern Turkey (Mersin and Isparta provinces), during a research on saproxylic beetle communities associated with oaks (*Quercus* spp.; Jansson & Coskun 2008). This material is now preserved in CAR, EMDI, and CJL.

Museum specimens coincide mostly with those analyzed by Audisio (1983), and are found in CAR, NMPC, MNHN, BMNH, and CLB. Other material sources for the new species include specimens collected by R. Dobosz and R. Królik in S. Turkey [specimens from 20.VII.2004 and 9.–12.VI.2000 at light, others by swiping method] during entomological expeditions to Anatolia (years 2000–2006) by the Upper Silesian Museum (Bytom) and associated Polish entomologists.

The digital image of the dorsal habitus of the holotype (Fig. 1) of *Epuraea sutcuimamun* Avgin, Lasoń & Audisio, *sp. n.*, was taken using a Nikon DS-L1 camera mounted on a Leika

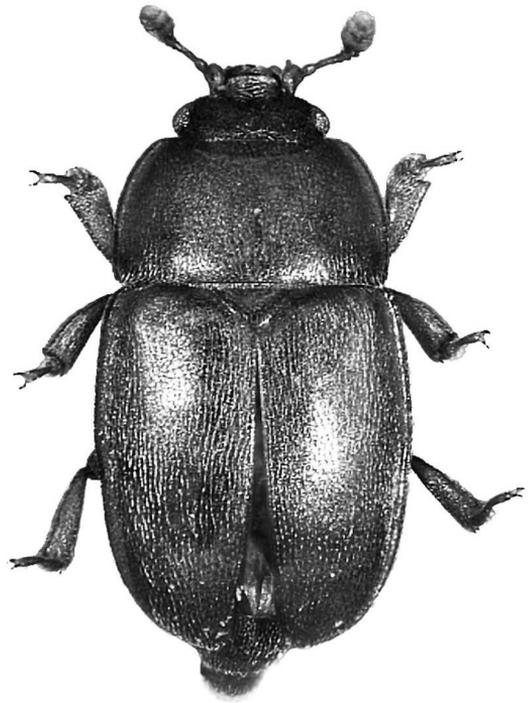


Fig. 1. *Epuraea sutcuimamun* *sp. n.*, male holotype from Turkey, Mersin province, near Aydinlar village, CAK. Length 2.4 mm. Scale bar = 1.0 mm.

MZ12.5 stereoscopic microscope and processed by Auto-Montage Pro, version 5.03.0096.

Acronyms of insect collections are:

- BMNH: The Natural History Museum, London, UK
- CAR: P. Audisio's collection, Dipartimento di Biologia e Biotechnologie "C. Darwin", Sapienza Università di Roma, Italy
- ARCC: A. R. Cline's collection, currently housed at the Plant Pest Diagnostics Center in Sacramento, California
- CAK: S. S. Avgin's collection, Department of Biology, Kahramanmaraş Sutcu Imam University, Turkey
- CLB: A. Lasoń's private collection, Białyystok, Poland
- CJL: Nicklas Jansson's private collection, Linköping, Sweden
- EMDI: Entomological Museum at Forest Faculty, Suleyman Demirel University in Isparta, Turkey

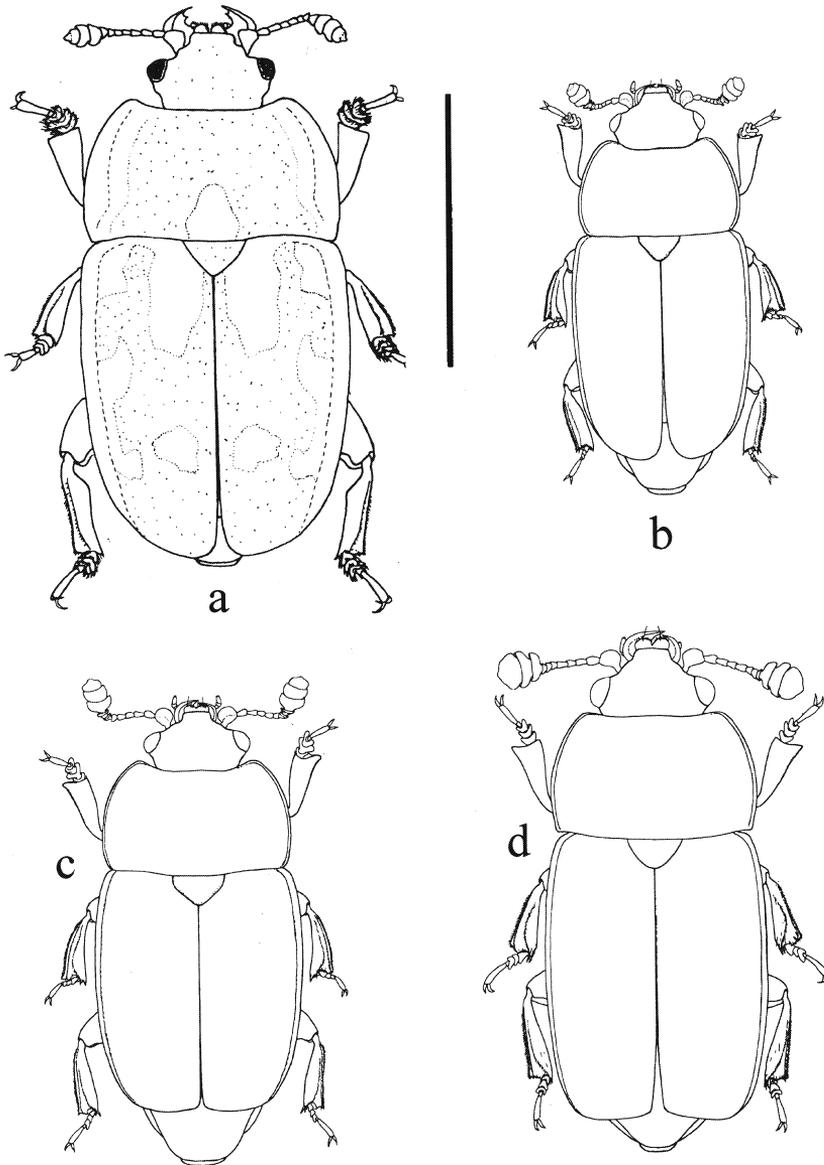


Fig. 2. – a. Male habitus outline of *Epuraea guttata* from Italy, Tuscany, Florence. – b. Male habitus outline of *Epuraea latipes* from Morocco, Rif, Bab-Besen, CAR. – c. Male habitus outline of *Epuraea rifensis* from Morocco, Rif, Bab-Besen, CAR. – d. Male habitus outline of *Epuraea subparallela*, male holotype from Turkey, Nur Mts. (above Akbez; = “Syria, Akbès”, in the original label), MNHN. Scale bar = 2.0 mm.

- MNHN: Muséum National d’Histoire Naturelle, Paris, France
- NMPC: National Museum (Natural History), Prague, Czech Republic
- NMW: Naturhistorisches Museum Wien, Austria
- RKK: Roman Królik’s private collection (Kluczbork, Poland)
- USMB: Upper Silesian Museum, Bytom, Poland

### 3. *Epuraea sutcuimamun* Avgin, Lasoń & Audisio, sp. n. (Figs. 1; 3d–f)

*Type material.* Holotype ♂ (CAK): Turkey, Mersin province, road Erdemli to Güzeloluk, nearly 30 km NE of Erdemli, Kargagedigi, near Aydinlar village, 1,350 m a.s.l., 36°44’51”N, 34°07’51”E, vinegar-baited pitfall traps in ancient cedar forest, 20.–29.VII.2010, S. S. Avgin leg. (CAK).

Paratypes: same data as holotype, vinegar-baited pitfall traps in ancient cedar forest,

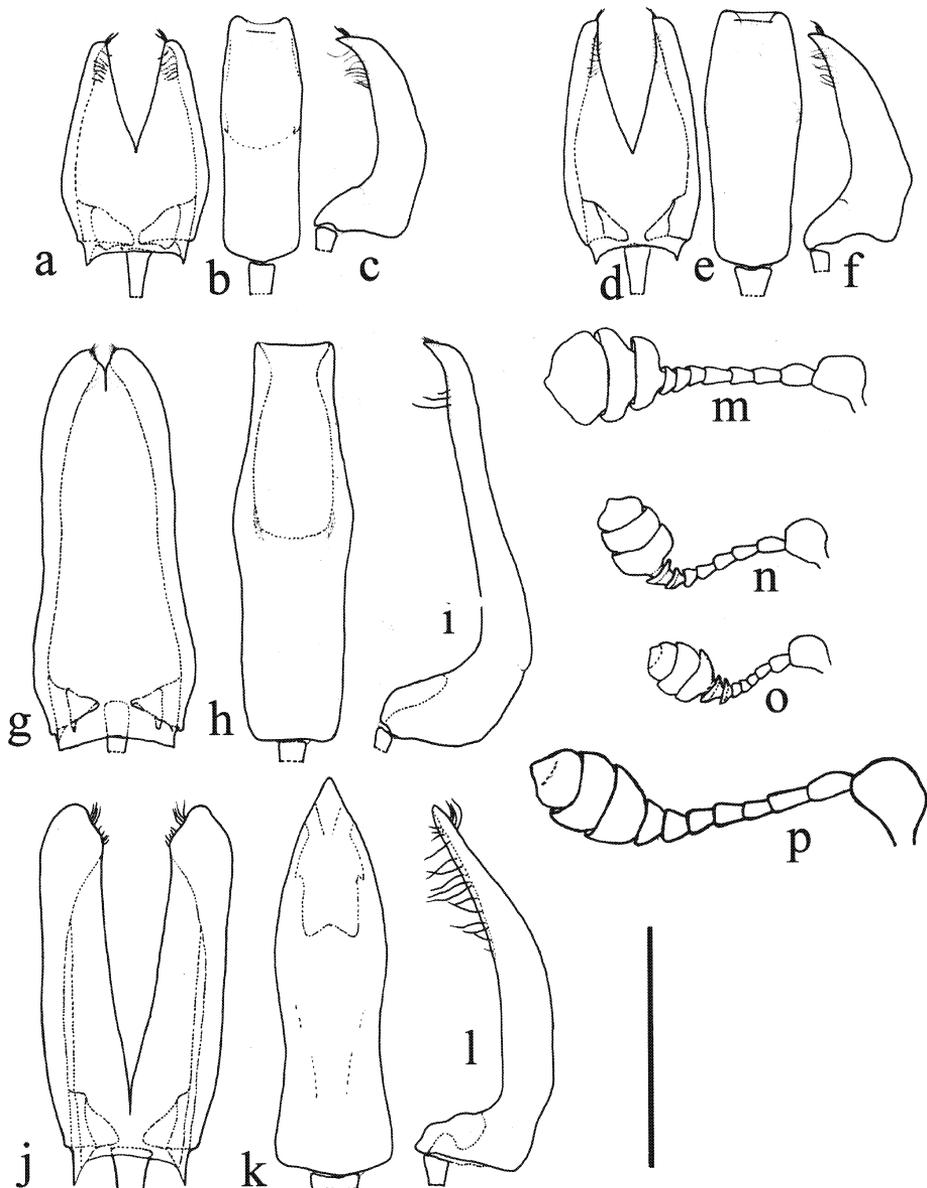


Fig. 3. – a. Paramera, dorsal view, *Epuraea latipes*, male from Morocco, Rif, Bab-Besen, CAR. – b. Median lobe of aedeagus, dorsal view (same). – c. Paramera, lateral view (same). – d. Paramera, dorsal view, *Epuraea sutcuimamun* **sp. n.**, male holotype from Turkey, Mersin province, near Aydinlar village, CAK. – e. Median lobe of aedeagus, dorsal view (same). – f. Paramera, lateral view (same). – g. Paramera, dorsal view, *Epuraea rifensis*, male paratype from Morocco, Rif, Bab-Besen, CAR. – h. Median lobe of aedeagus, dorsal view (same). – i. Paramera, lateral view (same). – j. Paramera, dorsal view, *Epuraea subparallela*, male holotype from Turkey, Nur Mts., above Akbez (= "Syria, Akbès", in the original label), MNHN. – k. Median lobe of aedeagus, dorsal view (same). – l. Paramera, lateral view (same). – m. Left antenna, *E. subparallela*, male holotype from Turkey, Nur Mts., MNHN. – n. Left antenna, *E. rifensis*, male paratype from Morocco, Rif, Bab-Besen, CAR. – o. Left antenna, *E. latipes*, male from Morocco, Rif, Bab-Besen, CAR. – p. Left antenna, *Epuraea guttata*, male from Italy, Tuscany, Florence, CAR. Scale bar = 0.4 mm (Figs. 3a–l), = 0.5 mm (Figs. 3m–p).

20.VII.–13.VIII.2010, S. S. Avgın leg., 28 specimens (CAR, NMPC, CAK, NMW, ARCC, CLB); 1 ♂, Turkey, Mersin province, road Erdemli to Güzeloluk, 25 km NE of Erdemli, 36°48'N, 34°10'E, 350 m a.s.l., 9–12.VI.2000, R. Królik leg. (NMPC); 1 ♂ 2 ♀♀ Turkey, Mersin province, 1.5 km S of Aydinlar, 1,395 m a.s.l., 36°45'N, 34°08'E, 20.VII.2004, at light, R. Dobosz leg. (USMB); 23 ♂♂ 17 ♀♀, ibidem, 31.VII.–2.VIII.2006, R. Dobosz leg. (USMB, CLB, RKK); 1 ♂ near Aydinlar, 9.–12.VI.2000, at light, R. Dobosz leg. (USMB); 1 ♂ 1 ♀, ibidem, 19.VII.2004, R. Dobosz leg. (USMB); 7 ♂♂ 6 ♀♀ Turkey, Mersin province, Darıpınarı, 420 m a.s.l., 37°09'N/34°44'E, 28.–31.VII.2006, R. Dobosz leg. (USMB, CLB); 1 ♂ Turkey, Isparta province, Yukangökdere near Eğridir, Kasnak Forest, 1,100–1,500 m a.s.l., 37°42'58"N, 30°49'54"E, 19.VII.2007, window traps, N. Jansson & M. Avci leg. (EMDI).

*Additional material.* Ten additional specimens collected at the type locality, preserved in pure acetone, awaiting molecular analyses.

*Differential diagnosis.* The new species is similar in external shape, color, and size (Fig. 1) to the closely related *Eपुरaea latipes* Grouvelle 1896 from western North Africa, which was redescribed by Audisio (1983, 1993). The species differs from *E. latipes* and other members of the species complex in the markedly longer and narrower paramera of the male genitalia (Figs. 3a–f) (see also the identification key below).

*Description.* 2.2–2.6 mm long (Fig. 1). Head, pronotum and elytra yellowish to light brown, discal area of elytra in some specimens slightly darker, reddish brown. Antennae and legs pale reddish brown. Almost identical to *Eपुरaea latipes* Grouvelle 1896 from western North Africa (Audisio 1983, 1993) in all other external characters. A detailed external description of the new species is then to be considered uninformative and unnecessary. See Audisio (1993, p. 322) for a recent and thorough description of *E. latipes*.

Male genitalia as figured (Figs 3d–f). Tegmen 1.80–1.85× longer than wide, with narrow paramera when observed in dorsal view (Fig. 3d), distinctly narrower and longer than in *E. latipes*, the latter exhibiting a tegmen only 1.50–1.55× longer than wide (Fig. 3a); tegmen scarcely curved

distad in lateral view (Fig. 3f), less curved than in *E. latipes* (Fig. 3c).

Female ovipositor. Similar to that of *E. latipes* (see identification key below).

*Distribution.* *Eपुरaea sutcuimamun* sp. n., despite being presently known only from the few localities listed above, likely has a more widespread Taurian distribution, and probably occurs at least in the southern side of the Taurus and the Antitaurus Chain in southern Turkey, which coincides with the present-day distribution of cedar forests dominated by *Cedrus libani* A. Rich. (see discussion below).

*Etymology.* The specific epithet is a derivation of the Kahramanmaraş Sutcu İmam University, Turkey, the species being dedicated to the Rector, Prof. Fatih Karaaslan, who kindly supported the entomological research of the first author in Turkey.

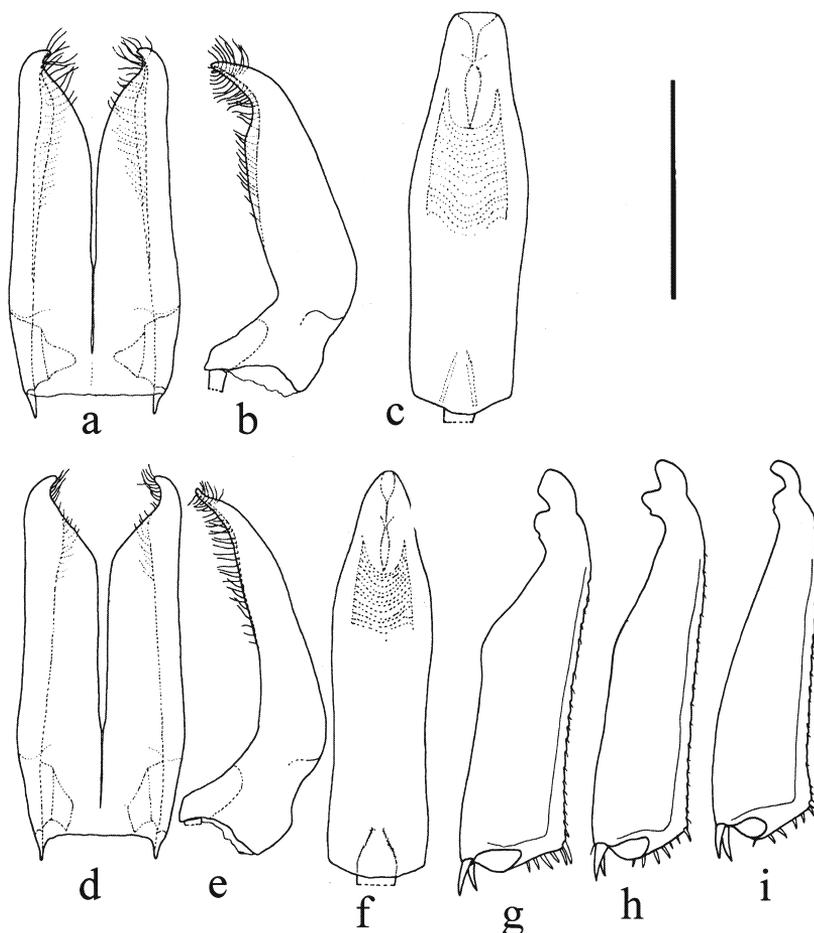
#### 4. *Eपुरaea subparallela* Grouvelle, 1896

The type material of *Eपुरaea subparallela* Grouvelle was collected in southeast Turkey in a montane area above Osmaniye (Nur Mts., formerly known as Amanus Mts.: Grouvelle 1896) where relictual cedar forests occur (Audisio 1983, 1993, Hajar *et al.* 2010; see discussion below). The species was believed to be likely associated with cedars, despite recent (VI. 2002) trapping on Nur Mts. in a small cedar forest near the village of Yarpuz (Audisio unpublished data), which was unsuccessful in providing additional specimens. However, *Eपुरaea* material recently collected by N.J. in southern Turkey yielded a small series of specimens belonging to this taxon, as indicated below.

##### 4.1. Examined material

1 ♂, 2 ♀♀ Turkey, Isparta province, Yukangökdere near Eğridir, Kasnak Forest, 1,100–1,500 m a.s.l., 37°42'58"N, 30°49'54"E, 17.V. 2007, window traps, hollow Quercus, N. Jansson & M. Avci leg. (CAR, EMDI, CJL); 1 ♀ Turkey, Mersin province, 40 km N of Gülnar, Köseçobanlı/Tasdüstü, 1,500 m a.s.l., 36°30'

Fig. 4. – a. Paramera, dorsal view, *Epuraea guttata*, male from Italy, Tuscany, Florence, CAR. – b. Median lobe of aedeagus, dorsal view (same). – c. Paramera, lateral view (same). – d. Paramera, dorsal view, *Epuraea fuscicollis* male from Italy, Latium, Circeo National Park. – e. Median lobe of aedeagus, dorsal view (same). – f. Paramera, lateral view (same). – g. Metatibia, dorsal view, *E. guttata*, male from Italy, Tuscany, Florence, CAR. – h. Metatibia, dorsal view, *E. guttata*, female from Italy, Tuscany, Florence, CAR. – i. Metatibia, dorsal view, *E. fuscicollis*, male from Italy, Latium, Circeo National Park, CAR. Scale bar = 0.4 mm.



22°N, 33°07'43"E, 24.V.2006, window traps, hollow Quercus, N. Jansson & M. Coskun leg. (ARCC); 1 ♀ ibidem, 26.VII.2006 (CAR); 1 ♀ ibidem, 26.VIII.2006 (EMDI).

#### 4.2. Variation

The species was previously known from two specimens, the single male holotype (MHNP) and one additional female probably from the same original locality (CAR; see Audisio 1983). The currently available small series from southern Turkey enables a greater appreciation of the rather unusual variation in size (body length: 2.8–4.5 mm) and general body shape of the species includes a variable proportion between elytral length and elytral width (ratio elytral length/elytral width = 1.18–1.25).

#### 4.3. Ecological data

Specimens of the recently collected series were obtained using flight intercept window traps positioned on a tree trunk, surrounded by hollow oak trees (*Quercus* spp.), in a largely grazed area that is being heavily transformed by local farmers (Köseçobanlı/Tasdüstü; oak species where the window traps were mounted: *Quercus ithaburensis* Decaisne, 1835, and *Q. cerris* Linnaeus, 1753). Other recently collected specimens were obtained from a nature reserve with free growing oaks in a grazed environment with several oaks in a more forested condition (Kasnak Forest; oak species where the window traps were mounted: *Quercus libani* G.Olivier, 1801 and *Q. x szechenyana* Borbas, 1886 (= *Q. vulcanica* Borzi, 1805 [hybrid between *Q. pubescens* Willd. and *Q. frainetto* Ten.]), in a mixture of other tree species

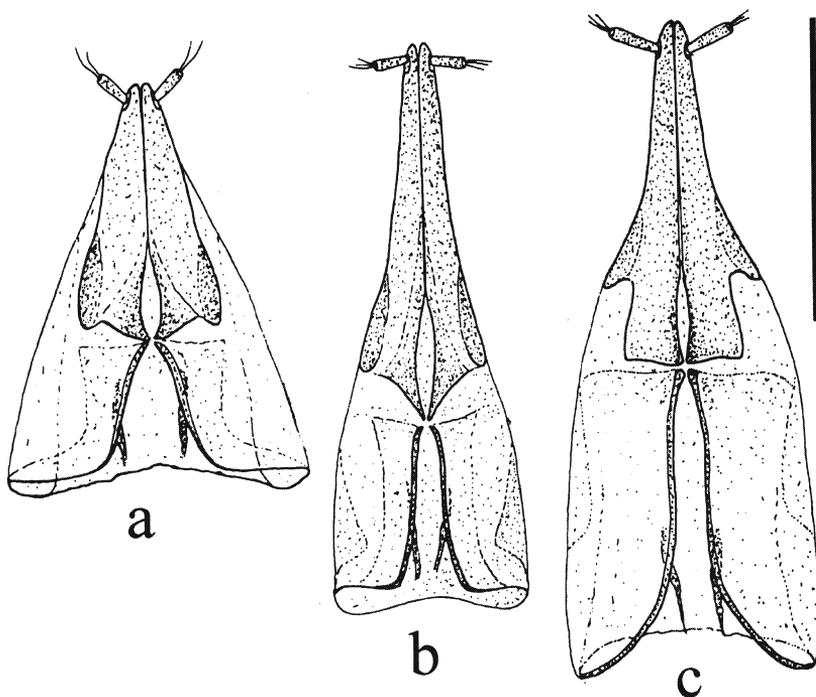


Fig. 5. – a. Ovipositor, ventral view, *Epuraea latipes*, female from Morocco, Rif, Bab-Besen, CAR. – b. Ovipositor, ventral view, *Epuraea rifensis*, female paratype from Morocco, Rif, Bab-Besen, CAR. – c. Ovipositor, ventral view, *Epuraea subparallela*, female from Turkey, Nur Mts., CAR. Scale bar = 0.3 mm.

like *Cedrus libani* A. Rich., *Pinus* spp., *Juniperus* spp., *Acer* spp., and *Fraxinus* spp.

### 5. Identification key to species of *Dadopora* lineage

1. Elytra broadly and separately rounded distad (Figs. 1, 2a–b). 2
- Elytra broadly truncate distad (Figs. 2c–d). 5
2. Antennae markedly shorter, 0.75–0.80× as long as head width (Figs. 1, 2b), with antennomere 5 nearly as long as wide (Fig. 3o). Space between mesocoxal cavities only slightly narrower than space between procoxal cavities. Dorsal surface uniformly ochreous, reddish or testaceous, without lighter yellowish spots on elytra and pronotum (Fig. 1) well-defined. On average, body smaller (length: 2.0–3.0 mm) and slender (Figs. 1, 2b). Male genitalia as in Figs. 3a–f. 3
- Antennae markedly longer, 0.90–0.95× as long as head width (Fig. 2a), chiefly with antennomere 5 much longer than wide (Fig. 3p). Space between mesocoxal cavities more distinctly narrower than space between procoxal cavities. Dorsal surface typically

nut-brown to pale brown, with several lighter yellowish spots on elytra and pronotum (Fig. 2a) rarely well-defined. On average, body larger (length: 2.2–4.4 mm) and wider (Fig. 2a). Male genitalia as in Figs. 4a–f. 4

3. Male genitalia short, tegmen 1.50–1.55× longer than wide, paramera wider in dorsal view and more curved distad in lateral view (Figs. 3a–c). Western North Africa (Morocco, N Algeria). *Epuraea latipes* Grouvelle, 1896
- Male genitalia long, tegmen 1.80–1.85× longer than wide, paramera narrower and thinner in dorsal view and less curved distad in lateral view (Figs. 3d–f). Southern Turkey (Taurus Chain). *Epuraea sutcuimamun* sp. n.
4. Inner margin of male metatibiae with prominent obtuse projection at proximal third (Fig. 4g), less prominent but distinct in females (Fig. 4h). Male genitalia as in Figs. 4a–c. Europe, Caucasus. *Epuraea guttata* (Olivier, 1811)
- Inner margin of metatibiae simple in both sexes (Fig. 4i). Male genitalia as in Figs. 4d–f. Europe, Caucasus, N Iran, North Africa. *Epuraea fuscicollis* (Stephens, 1832)
5. Third joint of antennal club smaller than second (Fig. 3n). Body relatively oval and

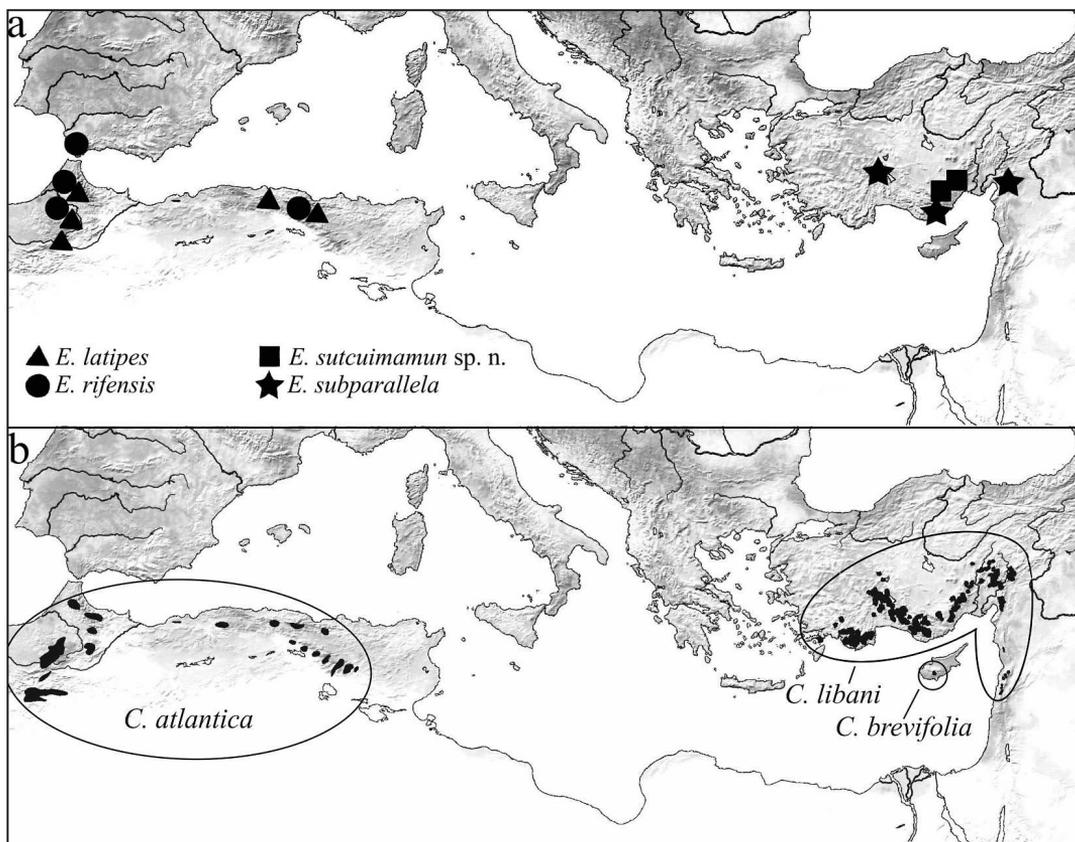


Fig. 6. – a. Distribution map of *Epuraea* spp. of the *E. latipes* group. – b. Distribution map of *Cedrus* spp. in the Mediterranean areas of Morocco and Algeria, Cyprus, as well as Turkey, Syria and Lebanon (redrawn from Quézel 1980, Hajar *et al.* 2010).

smaller, with shorter elytra (body length: 2.5–3.3 mm). Habitus as in Fig. 2c. Male genitalia as in Figs. 3g–i. Ovipositor as in Fig. 5b. Western North Africa (Morocco, N Algeria) and S Spain. *Epuraea rifensis* Audisio, 1983 – Third joint of antennal club nearly as large as preceding two combined (Fig. 3m). Body more parallel-sided, larger (body length: 2.8–4.5 mm). Habitus as in Fig. 2d. Male genitalia as in Figs. 3j–l. Ovipositor as in Fig. 5c. S Turkey.

*Epuraea subparallela* Grouvelle, 1896

## 6. Discussion

As discussed by Peyerimhoff (1926), *Epuraea latipes* Grouvelle from western North Africa is strictly associated in northern Algeria with old-growth cedar forests (*Cedrus atlantica* (Endl.)

Manetti ex Carrière; Pinaceae). There this species is a specialized saproxylic element on the phytoparasitic fungus *Clavaria cedretorum* R. Maire (Fungi, Clavariaceae), which grows on rotting cedar trees (Peyerimhoff 1926, Méquignon 1945). The same ecology is shared in North Africa (Morocco and Algeria) by the frequently sympatric *E. rifensis* Audisio. However, in extreme southern Spain (i.e. mountainous areas of the Cadiz province) this species was surprisingly collected in forests dominated by xerophilous oaks in areas where cedars are now absent (Audisio 1983, 1993 and unpublished data; Figs. 6a–b). *Epuraea subparallela* Grouvelle, was collected in southeastern Turkey in a montane area above Osmaniye (Nur Mts., formerly known as Amanus Mts.). Relictual cedar forests occur there (Audisio 1983, 1993, Hajar *et al.* 2010; Figs. 6a–b), and the species was believed to be probably associated with cedars. A recent (VI/2002) un-

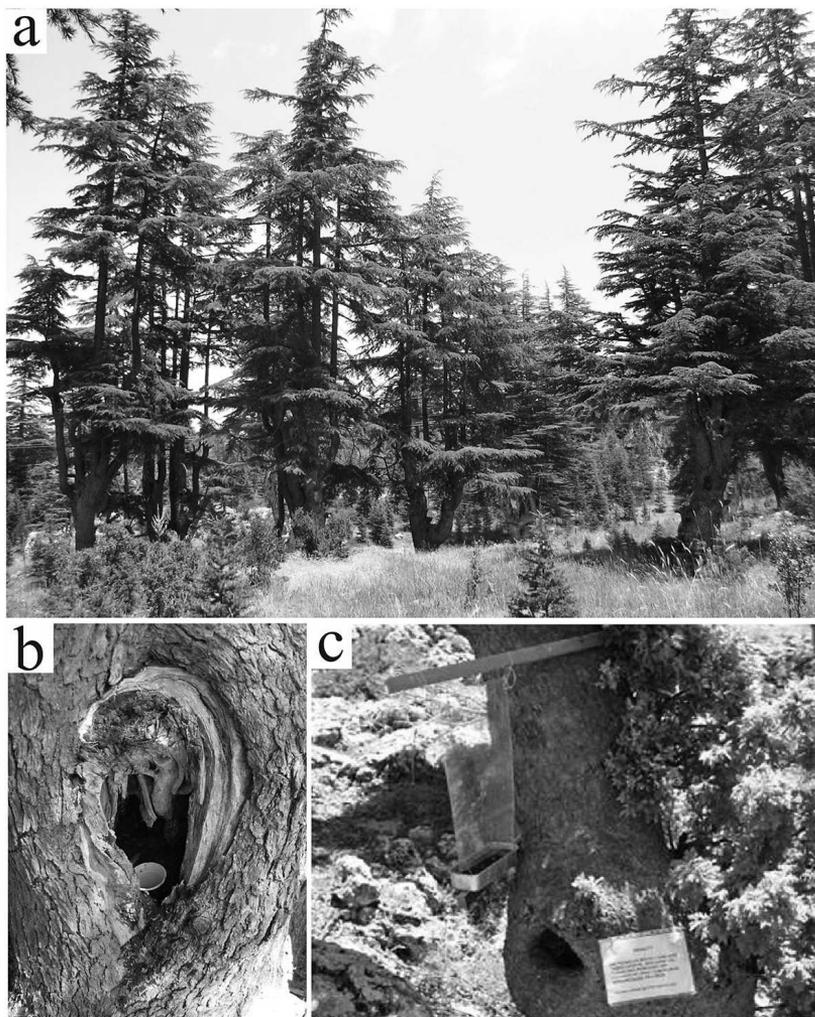


Fig. 7. – a. The Karga-gedigi old-growth cedar forest, near Aydinlar village, Turkey, type locality of *Epuraea sutcuimamun* **sp. n.** (photo: P. Audisio). – b. Hollow tree with a pitfall trap at the same locality (photo: S. S. Avgin). – c. Window trap in an hollow oak (*Quercus cerris*) in southern Turkey (photo: N. Jansson).

successful collecting event in cedar forests on Nur Mts near the village of Yarpuz (Audisio, unpublished data), and the above cited new records on hollow oaks in Isparta and Mersin provinces, clearly suggest its actual association with oak forests. The relationships of most members of the *Epuraea latipes* species group with cedars appears rather strict, suggesting parallel biogeographic tracks between these specialized sap beetles, the clavariaceae fungus, and cedar trees throughout the Mediterranean region (Fig. 6). However, as reported above, the *E. latipes* group is closely related to both recognized members of the *Dadopora* lineage, i.e. *E. fuscicollis* (Stephens, 1832) and *E. guttata* (Olivier, 1811) from central and southern Europe and the Near East. “*Dadopora*” members are saproxylic elements

strictly associated with fermenting sap produced by oaks following attacks by xylophagous insect larvae (Ratti 1978, Audisio 1993), and frequently inhabit old-growth forests and hollow trees (Figs. 7a–c).

*Cedrus* (true cedar) comprises four species with a highly disjunct distribution in circum-Mediterranean (Fig. 6b) and western Himalayas regions, i.e. *Cedrus deodara* (Roxb.) G. Don in the Hindu Kush, Karakorum and Indian Himalayan areas, *Cedrus libani* A. Rich in Turkey, Lebanon and Syria, *Cedrus brevifolia* (Hook. f.) Henry in Cyprus, and *Cedrus atlantica* (Endl.) Manetti ex Carrière in North Africa (northern Algeria and Morocco) (Quézel 1980, Qiao *et al.* 2007). Combined molecular, palaeogeographical and palaeoecological studies indicate that *Cedrus*

could have originated in the high latitude areas of Eurasia in the Paleogene, and its present distribution may be due to vicariance of southerly migrated populations during the Neogene, with further fragmentation and dispersal of these populations during Quaternary climatic oscillations (Qiao *et al.* 2007, Dagher-Kharrat *et al.* 2007).

Fossil data indicate that during the Middle Miocene (16–11 Ma) *Cedrus* was present in Turkey (Yavuz-Işık 2007), Bulgaria (Ivanov *et al.* 2002), and Austria (Jiménez-Moreno *et al.* 2008). During the Messinian (7.2–5.3 Ma), *Cedrus* was present in the Italian peninsula (Bertini & Martinetto 2011), where it persisted until the end of the early Pleistocene (ca. 0.8 Ma) and possibly later (Corrado & Magri 2011). In the Pliocene (5.3–2.6 Ma), *Cedrus* was found in southern France (Fauquette *et al.* 1999) and northern Spain (Suc & Cravatte 1982). By the Early Pleistocene it was not locally present in southern France (2 Ma: Leroy & Roiron 1996) or northern Spain (ca. 1.5 Ma: Leroy 1997) any longer. In continental Iberian pollen records south of 41°N latitude, only discontinuous occurrences of *Cedrus* pollen are documented from the Miocene to Pleistocene (Jiménez-Moreno & Suc 2007, Barrón *et al.* 2010). Similar sporadic occurrences, due to long-distance pollen transportation, appear in Holocene records from central Mediterranean regions (Magri & Parra 2002). Although Postigo-Mijarra *et al.* (2010) suggest that *Cedrus* may have been present in the Iberian peninsula during the Quaternary, continuous and appreciable records (2–6%) of *Cedrus* pollen are documented only from Upper Paleolithic-Epipaleolithic sediments (34–7 ka BP) in a coastal cave near Malaga (Cortés-Sánchez *et al.* 2008). These finds indicate a recent occurrence of *Cedrus* in the southernmost areas of Spain.

Only sparse fossil data are available from North Africa. However, regular occurrences of *Cedrus* pollen are recorded in Messinian sediments from western Morocco, suggesting that cedar was present in the Middle Atlas mountains (Feddi *et al.* 2011). A few cores from the Alboran Sea, which should be considered with a caution due to the over-representation of *Cedrus* in marine sediments, indicate its persistence during the Pliocene and Pleistocene (Feddi *et al.* 2011, Joannin *et al.* 2011). A marine core from the Me-

diterranean Sea off the coast of Libya spanning the last 245 ka does not record *Cedrus* pollen (Cheddadi 1988). Therefore, the fossil data suggest that *Cedrus* did not expand into the Iberian Peninsula south of 41°N, except along restricted coastal areas of southern Spain during the last glacial period. The cedar populations presently occurring in Morocco most likely descend from Upper Miocene populations that persisted in North Africa. By contrast, the European populations progressively disappeared during the early and middle Pleistocene (Tzedakis *et al.* 2006, Corrado & Magri 2011).

We hypothesize from preliminary results of morphological phylogenetic studies on Holarctic Epuraeinae (Audisio, unpublished data) that the current species of the *E. latipes* clade originated from an ancestral *Epuraea* species previously associated with boreal coniferous forests, most likely related to the present-day eastern Siberian *Epuraea quadrangula* Motschulsky, 1860. This ancestor then shifted to *Cedrus* during the first appearance of their present-day Mediterranean location (~20–15 Ma ago), following a much older separation of the Himalayan *Cedrus deodara* from the lineage including the three Mediterranean species (Qiao *et al.* 2007). Along the same ancestral stem, another early cladogenetic event likely occurred, probably during the Early-Middle Miocene in Near East, in concurrence with an early shift onto oaks, involving the origin of *E. subparallela* (the morphologically more isolated species of the *E. latipes* group) and the common ancestor of both *E. guttata* and *E. fuscicollis*. In a sister clade including the strictly cedar-associated species, *Epuraea rifensis* could be interpreted as the product of a more ancient range expansion of cedars and associated saproxylic beetle communities within North Africa, and further expanded its range with the subsequent local speciation of *Cedrus atlantica* (~18–10 Ma) (Qiao *et al.* 2007).

The present-day occurrence of *E. rifensis* in southern Spain would be more parsimoniously attributed to a diffusion of both beetles and cedars onto the Iberian Peninsula prior to the reopening of the Gibraltar Strait at the end of the Messinian salinity crisis (~5 Ma). However, this scenario is not supported by palynological data, which suggests absence of cedars in southern Spain (Barrón

*et al.* 2010) and the northwestern coast of Morocco (Feddi *et al.* 2011) during the Messinian. At that time *Cedrus* was known from the Rabat area in central-western Morocco (Feddi *et al.* 2011). However, cedars may have marginally reached Spain via the Gibraltar Strait from northern Morocco during one of the last glacial periods at a time with markedly lower sea levels, thereby allowing a limited Würmian presence of *C. atlantica* in extreme southern Spain (Cortés-Sánchez *et al.* 2008, Terrab *et al.* 2008). The presence of coastal cedar forests in northern Morocco and northern Algeria during the last glacial maximum has been demonstrated (Cheddadi *et al.* 2009), and was followed by postglacial local extinction of low altitude cedar populations. The present-day occurrence of *E. rifensis* in xerophilous oak forests of southern Spain may then be interpreted as an extreme “ecological relict” of this limited Würmian presence of *C. atlantica* forests along the southern coast of the Iberian Peninsula.

Similar patterns of relatively long term survival of *Epuraea* populations that are strictly associated with coniferous trees in modern day deciduous tree forests have been documented. In the Palaearctic, *Epuraea marseuli* Reitter 1872, which is typically associated with *Pinus*, *Abies* and *Picea* forests, is also known to occur in relictual pockets in northern Sicily at the edge of *Fagus* and *Quercus* forests where previous Holocene populations of *Abies* have been documented (Audisio *et al.* 1985).

Finally, the common ancestor of *E. sutcuimamun* **sp. n.** and *E. latipes* likely originated in the Near East on *Cedrus libani*, and expanded to North Africa during the Pleistocene at a time with markedly lower sea levels. This event possibly followed a documented presence of cedar forests in the Balkan and Italian peninsulas and Sicily, where *Cedrus* was present until at least the Early/Middle Pleistocene (~0.8 Ma). Fossil data indicate the absence of *Cedrus* in northeastern Africa, including northern Libya and northern Egypt, during the Middle and Late Pleistocene (Cheddadi 1988) at a time when sporadic pollen grains are apparent in the Italian records (Magri & Parra 2002). Under this scenario, *E. latipes* is

likely a more recent and only moderately differentiated Maghrebinian element of a widespread eastern Mediterranean species, associated with *Cedrus libani*, that migrated west and southward during an Early/Middle Pleistocene glacial period, eventually reaching North African *C. atlantica* forests, whose range had been recently fragmented (Cheddadi *et al.* 2009).

Molecular data are currently unavailable for many *Epuraea* species from both northern African species and *E. subparallela*. Further field research in Morocco, southern Spain, and in the recently discovered new localities in southern Turkey is planned to provide fresh specimens for molecular sequencing. These molecular data will test the palaeoecological and evolutionary hypothesis introduced herein for the entire clade. One component of the molecular analyses will be to investigate isolated, and relict populations (like those discovered in southern Spain) of *Epuraea* of the *latipes* clade potentially occurring on the Italian and Hellenic peninsulae, where, as discussed above, relatively large forests of *Cedrus* species were present before their Middle Pleistocene decline.

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