

Species diversity, chorology, and biogeography of the Steninae MacLeay, 1825 of Iran, with comparative notes on *Scopaeus* Erichson, 1839 (Coleoptera, Staphylinidae)

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Abstract

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The species diversity, chorology, and biogeography of the Steninae MacLeay, 1825 (Coleoptera: Staphylinidae) in Iran is described. A total of 68 species of *Stenus* Latreille, 1797 and one species of *Dianous* Leach, 1819 is recorded for this Middle Eastern country. *Dianous coerulescens korgei* Puthz, 2002, *Stenus bicornis* Puthz, 1972, *S. butrintensis* Smetana, 1959, *S. cindeloides* Schaller, 1783, *S. comma comma* Le Conte, 1863, and *S. hospes* Erichson, 1840 are recorded for the Iranian fauna for the first time. Records of *S. cordatoides* Puthz, 1972, *S. guttula* P. Müller 1821, *S. melanarius melanarius* Stephens, 1833, *S. planifrons planifrons* Rey, 1884, *S. pusillus* Stephens, 1833, and *S. umbricus* Baudi di Selve, 1870 for Iran are, however, implausible or proved erroneous. Based on literature records and recent collecting data since 2004, the distribution of the stenine species in Iran is mapped, and their biogeographical relationships are discussed. As far as possible, the species are attributed to the commonly accepted distribution types in the Palaearctic Region after the theory of Pleistocene refuges of the arboreal biota. With the example of the Steninae and *Scopaeus* Erichson, 1839 (Staphylinidae: Paederinae), a cluster analysis is performed to examine the similarity of commonly accepted geographical units of Iran. The similar biogeographic pattern of the Steninae and *Scopaeus* reveal the high impact of Mediterranean elements on the fauna of Iran. The Hyrcanian subregion of the Caspian refuge is identified as the most significant center of origin of *Stenus* in Iran.

Introduction

The Steninae MacLeay, 1825 constitute a monophyletic group (Clarke and Grebennikov 2009: 354, 355; McKenna et al. 2014: 17) which is well characterized by bulging eyes and abdominal glands, which secrete a multifunctional hydrophobic substance for locomotion on the surface of water (Schierling et al. 2012). Steninae preferably dwell in humid or wet places such as banks of both running and standing waters, swamps, bogs, and wet grasslands (Schierling et al. 2012: 45). The subfamily presently comprises *Stenus* Latreille, 1797 with a world-

wide distribution and 2674 named species including fossil taxa (Puthz, unpublished) and the less speciose sister group *Dianous* Leach, 1819. *Stenus* is characterized by the eversible labium of the adults (Betz 1996: 15). It is protrusible for prey capture and allows the beetle to catch even prey which is able to escape rapidly such as Collembola, a frequent diet of *Stenus*. Kastcheev and Puthz (2011: 454) defined two morpho-ecological forms of *Stenus* species: “stratobionts” with a more compact body and short legs, which live in dense layers of vegetation litter, and “open-living species”, which prefer the banks of sandy, loamy or clayey shallows with sedges or bulrush.

Though the taxonomic diversity of the *Stenus* of Iran was relatively well known, the biogeography of the Iranian species still was to be investigated. Most of our knowledge on the *Stenus* species of Iran we owe to Puthz (e.g. 1972a, 1979), who described nine species from Iran mainly based on the samples of A. Senglet at the Muséum d'histoire naturelle, Geneva, which were collected between 1973 and 1975 in many provinces of Iran. Most of these species are endemics of the Hyrcanian subregion in the South Caspian mountain ranges and members of the *S. ochropus-ludyi-coarcticollis* group, which is the most speciose of the 26 species groups of *Stenus* reported from Iran. Recently, Puthz (2009) added two more endemics from this region from the same species group. Up to now, a total of 69 species of Steninae is confirmed to be distributed in Iran.

Iran is situated in the western Iranian Plateau and constitutes one of the largest countries of the Middle East. Some 47% of Iran is covered by natural grasslands, 31% by a variety of semiarid and arid environments, 14% by arable land, and 8% by woodlands (Yale et al. 2001: 24). The great variety of habitats includes salt marshes, deserts, and bare-rock mountains. The central plateau of Iran at an elevation of about 1000–1500 m above sea level receives 100–400 mm annual precipitation only, because it is surrounded by high mountain ranges. Two vast deserts, Dasht-e Kavir and Dasht-e Lut, occupy most of the northeast and east of the plateau, where the summer temperature exceeds 55 °C. Though most of Iran is arid, the green woodlands between the Caspian Sea and the northern slopes of the Elburz Mountains receive significantly more rain, some 1300–2000 mm or more per year. The average annual precipitation sums up to about 500–1000 mm in the Zagros Mountains, in the northwest of which the lowest winter temperature, -30 °C, was measured (Hangay et al. 2005: 1).

Due to its geographic location within the Middle Eastern transitional zone of the Palaearctic, the Oriental, and the Afrotropical Regions and its diverse geology and topography, Iran shows a significant biogeographic variety. Though the country is located in the Palaearctic Region, the fauna of southern Iran is significantly influenced by Afrotropical and Oriental faunal elements. Although the leading biogeographical concepts of Iran are based on phytogeography (e.g. Hedge and Wendelbo 1978, Parsa 1978, Zohary 1973), they also reflect the distribution pattern of animals. These concepts include three major phytogeographic regions in Iran: the Hyrcano-Euxine or Euxino-Hyrcanian Province of the Euro-Siberian Region, which includes the Elburz and Talish Mountains in the north of Iran, the southern Caucasus and the northern slopes of the Pontus Mountains in northeastern Turkey, the Irano-Turanian Region, a part of the Asian steppe zone, which occupies more than two-thirds of Iran, and the Saharo-Sindian Region in the south of Iran. According to many biogeographers, e.g. Naumann (1987), Afrotropical and Oriental faunal elements dispersed into this southern region of Iran.

A commonly accepted concept of the zoogeographical units of Iran has not yet been published. De Lattin (1949,

1951, 1957, 1967), however, identified glacial refuges of the arboreal and eremial faunas as the result of an analysis of the distribution pattern of Lepidoptera. He established the long accepted hypothesis that the postglacial dispersal events started at these refuges, which thus constitute the centres of origin for recent biogeographical patterns. Accordingly, he proposed distribution types for the arboreal and eremial faunas, which go back to the glacial refuges. Among the arboreal refuges proposed by de Lattin, the Caspian, Iranian, Sindian, Syrian, and Turkestanian refuges and the Mediterranean refuge have a great influence on the present distributional pattern of the fauna of the Middle East.

Despite of the unique geographical features of the country, we have insufficient information about the specific zoogeographical pattern and the degree of endemism of the Iranian fauna (Zehzad et al. 2002: 9). Nevertheless, a high degree of endemism is expected particularly in the isolated mountains within the steppes and deserts, where the gradual desiccation and aridization of the Iranian plateau in the Neogene with its maximum at the end of the Pleistocene (Ganji 1978: 154) led to the allopatric speciation of riparian species in relict freshwater systems (Frisch 2008: 285). We already know from many publications (e.g. Frisch 2006a, 2006b, 2008; Ganji 1978) that the South Caspian mountain ranges, the Zagros Mountains, and the high elevations in the central Iranian Plateau constitute centers of origin of many Iranian endemics.

In this contribution, we present the results of a research project of the first author on the diversity and biogeography of the Steninae in Iran. The aim of the study was to identify zoogeographical patterns of the stenine fauna of Iran and to compare them with the zoogeographical patterns of the strictly riparian staphylinid genus *Scopaeus* Erichson, 1839, research subject of the second author, to test whether they follow the same distributional patterns.

We compile the data on the distribution of the 68 *Stenus* species and one species of *Dianous* known from Iran so far, which include both previously unpublished, mostly recent records and plausible literature records, most of which were published in the last 44 years only. Finally, a cluster analysis with paired groups using Dice Similarity Coefficient was performed to gain a concept of the similarity of the *Stenus* fauna of defined geographical regions of Iran. It was compared with a cladogram for the *Scopaeus* species of Iran provided by the same method.

Material and methods

This study is mainly based on the results of recent field work of the authors from 2004 to 2011. The chorological data are compiled in the MS Excel 2007 supplementary file (supplementary material 1; 967 records). In this compilation, the locality labels of the specimens usually are not cited verbatim, but standardized and completed by adding the province name. Missing GPS – coordinates were subsequently taken from Taseo.com and are indicat-

ed by rectangular brackets to distinguish them from those measured at the exact collecting site.

The samples were identified by the first author and in difficult cases confirmed by Volker Puthz, the leading specialist of Steninae. Literature records were considered only if they were confirmed by examination of the reference specimens or are plausible, because they were published by well-known *Stenus* specialists. The dubious records of 19 species for Iran by Hadian et al. (2011: 3–4), Ghahari et al. (2009a: 1954, 2009b: 1964, 2009c: 661), Sakenin et al. (2008, 2010), and Samin et al. (2011a: 2–3, 2011b: 140–142, 2011c: 1238) we could not confirm, because our repeated attempts to contact the authors were unsuccessful.

The specimens referred to in this contribution are stored in Hayk Mirzayans Insect Museum, Tehran, except otherwise stated. Specimens collected by A. Senglet are kept in the Muséum d'histoire naturelle, Geneva and the private collection of Volker Puthz. The collections are abbreviated as follows (in alphabetical order):

APCE = Andreas Pütz private collection, Eisenhüttenstadt; HNHM = Hungarian Natural History Museum, Budapest; HMIM = Hayk Mirzayans Insect Museum, Tehran; LHCP = Lubomír Hromádka private collection, Prague; MNHB = Museum für Naturkunde Berlin; MHNG = Muséum d'histoire naturelle Geneva; MHNP = Muséum national d'histoire naturelle Paris; MZMC = Zoological Museum of the Moscow Lomonosov State University; NHMW = Naturhistorisches Museum Wien; NMEC = Naturkundemuseum Erfurt; NMPC = Národní Muzeum, Prague; SMNS = Staatliches Museum für Naturkunde Stuttgart; USNM = National Museum of Natural History, Smithsonian Institution, Washington; UZMH = Finnish Museum of Natural History, Helsinki; VPCS = Volker Puthz private collection, Schlitz; ZICP = Zoological Museum of the Zoological Institute of the Academy of Sciences, St. Petersburg.

The general information on the distribution of the species in the results section is taken from Schülke and Smetana (2015: 798–847) unless otherwise stated. The terminology of the Pleistocene glacial refuges follows de Lattin (1949, 1951, 1957, 1967). The dubious species reported by Hadian et al. (2011: 3–4), Ghahari et al. (2009a: 1954, 2009b: 1964, 2009c: 661), Sakenin et al. (2008, 2010), and Samin et al. (2011a: 2–3, b: 140–142, c: 1238) are discussed separately.

The subgeneric classification of *Stenus* has been subject to controversial discussions. According to Ryvkin (2011: 59), a comprehensive phylogenetic analysis is necessary to identify the monophyletic lineages within *Stenus*, which are blurred by a high amount of parallelism and do not reflect the phylogenetic relationships. In the first edition of the Catalogue of Palaearctic Coleoptera, Smetana (2004: 540–564) still followed the traditional subgeneric concept and distinguished *Hemistenus* Motschulsky, 1860, *Hypostenus* Rey, 1884, *Stenus* Latreille, 1797, *Metastenus* Ádám, 1987 (replacement name: *Metatesnus* Ádám, 2001), and *Tesnus* Rey, 1884 as valid subgenera of *Stenus*. Puthz (2008: 141–147) recently

replaced that artificial classification by 157 monophyletic species groups according to apomorphic characters of the aedeagus, spermatheca, and terminal abdominal sclerites. In the current edition of the Catalogue of Palaearctic Coleoptera, Schülke and Smetana (2015: 798–847) followed Puthz (2008: 141–147) and rejected the traditional subgenera. In this contribution, we follow this concept.

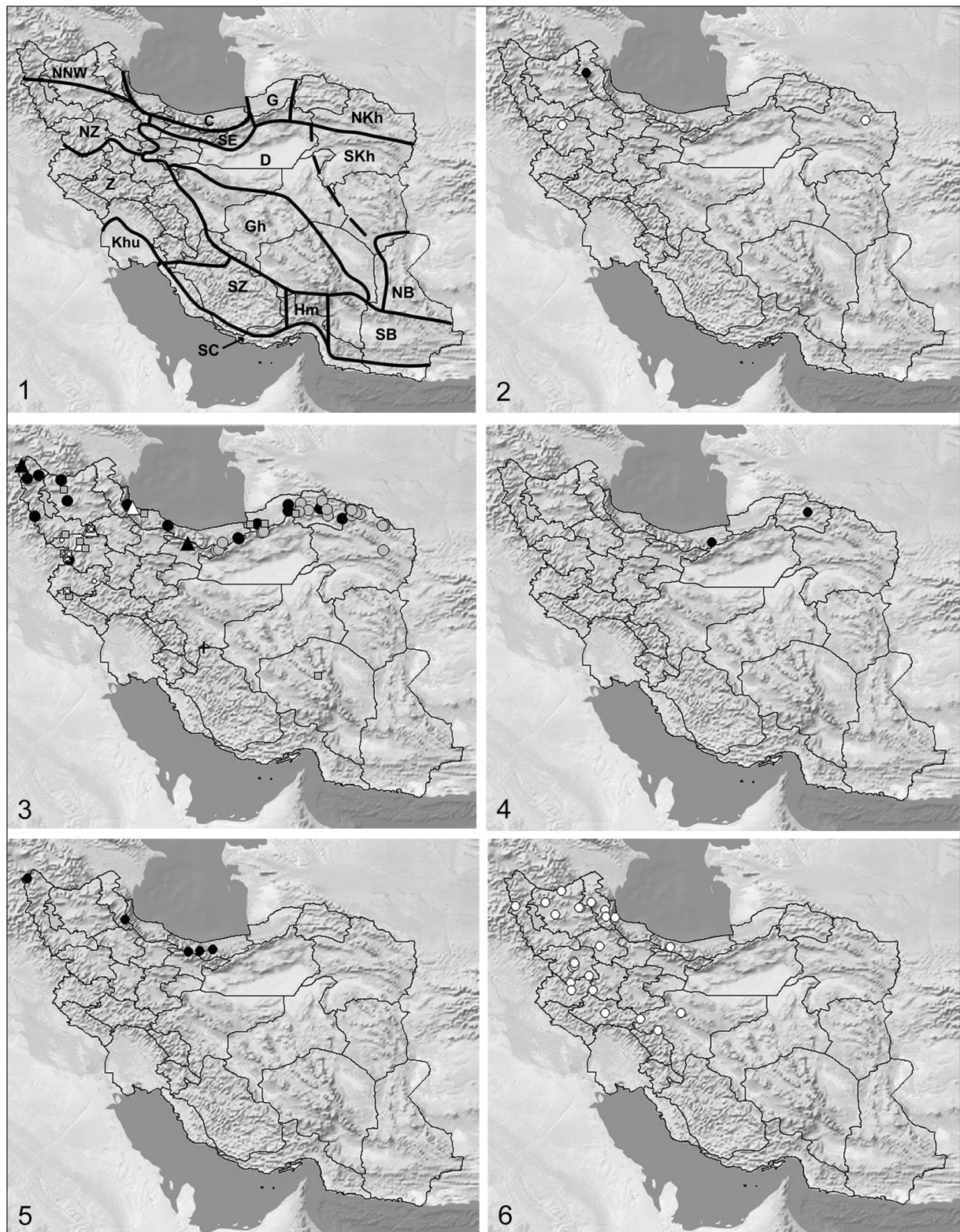
The distribution maps were prepared using the biodiversity software BIOOFFICE and do not include dubious literature records. The distributional patterns of all members of a particular species group are combined in one map.

The biogeographical cluster analysis was carried out using NTSYS (2.02) (Rohlf 1998). The qualitative input data are coded 1 for presence and 0 for absence of a species in a geographical unit. The complete distributional information for the Steninae analysis is presented in this contribution. The analyzed data of the genus *Scopaeus* were previously published by Frisch (2006a, 2006b, 2007a, 2007b, 2008, 2009, 2010, 2014) and Anlaş and Frisch (2014).

The underlying geographical subdivisions mainly follow Petrov (1955: 140–179), who distinguished the following seven “natural regions” of Iran: 1) North Iranian mountain region (Northwest Iran, South Caspian mountains, Turkmeno-Khorasanian mountains), 2) Caspian wet forest region, 3) Southwest Iranian mountain region (Poshte-Kuh or Kabir-Kuh Mountains, Zagros Mountains, Karun Plain, 4) Central Iranian mountain region (Ghohrud Mountains, Benan Mountains, Gavkhoni swamp), 5) South Iranian mountain region (east of Karun to Pakistan), 6) East Iranian mountain region (Jam and Kayen Mountains, Palangan mountain ranges, Serhed Plain), 7) highlands of Iranian Plateau (Kavir Desert, Lut Desert, Hamun-e Sistan salt marshes). Some geographical units of Petrov (1955) were, however, modified as follows based on significant differences of their stenine fauna: The northwestern part of the Northern Iranian mountain region is divided in two parts, Golestan is separated from the Caspian wet forest region, the Karun subregion of the Southwest Iranian mountain region, the North Baluchestan subregion of the East Iranian mountain region, and each of the subdivisions of the South Iranian mountain region are considered as separate regions.

The geographical subdivisions of Iran used in the biogeographical cluster analysis are illustrated in Fig. 1 and abbreviated as follows: C - Caspian wet forest region, D - deserts and salt marshes, G - Golestan region, Gh - Ghohrud Mountains, Hm - mountains of Hormozgan, Khu - Khuzestan Plain, NB - North Baluchestan Mountains, NKH - North Khorasan Mountains, NNW - northern part of North Zagros Mountains, NZ - North Zagros Mountains, SB - South Baluchestan Mountains, SC - coast of Persian Gulf and Oman Sea, SE - southern slopes of Elburz Mountains, SKh - southern Khorasan Mountains, SZ - southern Zagros Mountains in Fars, Z - Zagros Mountains.

Our expeditions between 2004 and 2011 covered most of Iran. While our samples from northern and western



Figures 1–6. Distribution of Steninae in Iran. **1.** Geographical subdivision of Iran modified after Petrov (1955) and **2–6** distribution data of Steninae: **2.** *Dianous* and the *Stenus alpicola* species group: ● *D. coeruleus korgei*, ○ *S. proprius*; **3.** *S. ater* species group: + *S. affaber*, ● *S. ater*, △ *S. hypoproditor*, ■ *S. intricatus zoufali*, ● *S. mongolicus*, ○ *S. nodipes*, ▲ *S. skoraszewskyi*; **4.** *S. brunnipes* species group: ● *S. b. brunnipes*; **5.** *S. canaliculatus* species group: ● *S. canaliculatus*; **6.** *S. cautus* species group: ○ *S. cautus*. Abbreviations: C - Caspian wet forest region, D - deserts and salt marshes, G - Golestan region, Gh - Ghohrud Mountains, Hm - mountains of Hormozgan, Khu - Khuzestan Plain, NB - North Baluchestan Mountains, NKh - North Khorasan Mountains, NNW - northern part of North Zagros Mountains, NZ - North Zagros Mountains, SB - South Baluchestan Mountains, SC - coast of Persian Gulf and Oman Sea, SE - southern slopes of Elburz Mountains, SKh - southern Khorasan Mountains, SZ - southern Zagros Mountains in Fars, Z - Zagros Mountains.

Iran must be looked upon as quite representative for these regions, the results from the mountains of southern Khorasan are poor and preliminary, because in this region we had a short collecting chance only. In view of the niche preferences of the *Steninae* species, however, we don't expect the existence of a rich *Stenus* fauna in the dry, salty lowlands of the coastal regions of the Persian Gulf and the Oman Sea.

Results

1. Species list, chorology and biogeographical characterization of the *Steninae* of Iran

In the following species chapters, we discuss the biogeography of the 69 species of *Steninae* known from Iran against the background of the Pleistocene glacial refuges (De Lattin 1949, 1951, 1957, 1967) based on the distributional data compiled in the supplementary file 1. This species list includes the first records of five species of *Stenus* and the genus *Dianous* for the Iranian fauna. The species are listed alphabetically in the species groups defined by Puthz (2008: 141–143), which are listed in alphabetical order as well. The distribution of the species is mapped in Figs 2–24.

Dianous Leach, 1819

Dianous coerulescens korgei Puthz, 2002

Fig. 2, Suppl. material 1

Chorology. *Dianous coerulescens*, widely distributed in the temperate West Palaearctic, is recorded as far east as Kazakhstan (Kastcheev and Puthz 2011: 438) and western Siberia (Schülke and Smetana 2015: 799). Judging from the distribution in the Caucasus and Turkey (Schülke and Smetana 2015: 799), the occurrence in northern Iran was expected. One male of *D. coerulescens*, which was collected in moss at a small waterfall in the northern slope of Mount Sabalan, represents the first record of both the genus and the species in Iran (Fig. 2). This southernmost finding of the polytypical species at 38°19'N belongs to *D. coerulescens korgei* Puthz, 2002, which was hitherto known only from the type locality near Trabzon, Northeast Turkey.

Biogeographical characterization. *Dianous coerulescens* cannot be assigned to any of de Lattin's (1951, 1957, 1967) southern Palaearctic glacial refuges.

Stenus Latreille, 1797

Stenus alpicola species group

Stenus proprius L. Benick, 1921

Fig. 2, Suppl. material 1

Chorology. *Stenus proprius* is recorded from Greece (Schülke and Smetana 2015: 837), northeastern Iran

(Puthz 2003: 93), and Central Asia (Kastcheev and Puthz 2011: 450). A second Iranian locality was recently discovered in the northwestern Zagros Mountains (Kordestan). Judging from the findings in the very northwest and northeast of Iran (Fig. 2), *S. proprius* is most probably distributed across the north of the country.

Biogeographical characterization. Although the species was found in Greece and is expected to occur in Anatolia, its main distribution in Central Asia concurs with the Turkestanian glacial refuge. Thus, *Stenus proprius* can be regarded as an expansive Turkestanian faunal element. Kastcheev and Puthz (2011: 454) described this species as Kazakhstan-Turanian. Hitherto, *S. proprius* is the only representative of the *S. alpicola* species group in Iran.

Stenus ater species group

Stenus affaber Baudi di Selve, 1848

Fig. 3, Suppl. material 1

Chorology. *Stenus affaber* is previously published for Lebanon, Syria, Turkey, Iran, and Kazakhstan. It is collected in the eastern Zagros Mountains, northern Fars (Fig. 3). The record from Kazakhstan is, however, dubious, because it is based on a female only identified as *S. cf. affaber* (Kastcheev and Puthz 2011: 439). The lack of records between Southwest Iran and Kazakhstan moreover does not support a Central Asian distribution.

Biogeographical characterization. Kastcheev and Puthz (2011: 454) consider *Stenus affaber* to be a species of Mediterranean origin. Judging from the distribution west (Levant), north (Anatolia), and east (Zagros Mountains) of the Mesopotamian plain, however, we assign this rarely collected species to the Syrian faunal element.

Stenus ater Mannerheim, 1830

Fig. 3, Suppl. material 1

Chorology. *Stenus ater* is widespread in the West Palaearctic and recorded as far east as European Russia, Azerbaijan, and North Iran, where it reaches its eastern limit of distribution in the Turkmeno-Khorasanian Mountains at about 58°06'E (Fig. 3). Records from Kazakhstan (Smetana 2004: 554), which were adopted by Schülke and Smetana (2015: 806), mainly refer to other species and are not reliable (Kastcheev and Puthz 2011: 454). In Iran, *S. ater* is the most widespread member of the *S. ater* group. Towards the east, it is replaced by its close relative *S. mongolicus*. The two species occur sympatrically in the eastern Elburz and the Turkmeno-Khorasanian Mountains (Fig. 3). Ghahari et al. (2009b: 1964) recently published *S. ater* for Behshahr, Mazandaran, a record which is in accord with the distribution pattern of the species.

Biogeographical characterization. Judging from the vast distribution in the Mediterranean, we consider *Stenus ater* to be an expansive Holomediterranean faunal element.

***Stenus hypoproditor* Puthz, 1965**

Fig. 3, Suppl. material 1

Chorology. *Stenus hypoproditor* is distributed from the northeastern Mediterranean, Southeast Europe, Turkey, and Iran as far east as Kazakhstan, Uzbekistan, and Kyrgyzstan. In Iran, it is known from the northwest (Fig. 3) only. The find in the northwestern Zagros Mountains at about 36°59'N constitutes the southernmost record of this species. Further to the south, *S. hypoproditor* is replaced by the allopatric relative *S. nodipes*.

Biogeographical characterization. Kastcheev and Puthz (2011: 454) consider *Stenus hypoproditor* to be a Mediterranean species. According to the Pleistocene refuge theory, it can be regarded as an expansive Pontomediterranean faunal element.

***Stenus intricatus zoufali* Fleischer, 1909**

Fig. 3, Suppl. material 1

Chorology. *Stenus intricatus zoufali* is distributed from southeastern Central Europe and the Balkans across Anatolia, Transcaucasia, and Iran as far east as Central Asia and Afghanistan (Kastcheev and Puthz 2011: 445). In Iran, the species is distributed in the north, but the record in the southeast at about 30°17'N (Kerman), the southernmost collecting site of the *S. ater* group, suggests the distribution in most of the country (Fig. 3).

Biogeographical characterization. Kastcheev and Puthz (2011: 454) describe *Stenus intricatus zoufali* as a Mediterranean species. Judging from the distribution in the southeastern Mediterranean, we consider it to be an expansive Pontomediterranean faunal element.

***Stenus mongolicus* Eppelsheim, 1889**

Fig. 3, Suppl. material 1

Chorology. *Stenus mongolicus* is widely distributed in Asia and the Middle East from China, Mongolia, and East Siberia as far south as Indian Kashmir, Pakistan, Afghanistan, and Iran and westwards to Anatolia and Caucasia. In Iran, the species is restricted to the Elburz and Turkmeno-Khorasanian Mountains in the northeast and recorded as far south as 35°42'N in Razavi Khorasan (Fig. 3). Recent records from the lowlands of Ivanaky, Semnan Province (Hadian et al. 2011: 4), and from rice fields and grassland in Lahijan, Gilan (Ghahari et al. 2009c: 661) need confirmation.

Biogeographical characterization. Kastcheev and Puthz (2011: 454) consider *Stenus mongolicus* as a Kazakhstan-Turanian species. Judging from its Central Asian distribution centre, *S. mongolicus* can be regarded as a Turkestanian faunal element, which expanded westward.

***Stenus nodipes* Puthz, 1972**

Fig. 3, Suppl. material 1

Chorology. Described from Bulgaria (Puthz 1972b: 250), *Stenus nodipes* is common from the Balkans throughout Turkey and Syria eastwards to Armenia and Iran (Puthz 2009: 34). In Iran, the species is known only from a comparatively small area in the northwestern Zagros Mountains between southern West Azarbaijan and northern Ilam (Fig. 3).

Biogeographical characterization. Due to its distribution in Southeast Europe, Anatolia, and the Caucasus region, we consider *Stenus nodipes* to be an expansive Pontomediterranean species.

***Stenus skoraszewskyi* Korge, 1971**

Fig. 3, Suppl. material 1

Chorology. *Stenus skoraszewskyi* was described from Kars, northeastern Turkey (Korge 1971: 21), and also recorded for Armenia and Iran, where it was found in the very northwest of West Azarbaijan and in the Central Elburz near Tehran, the southeasternmost record of the rare species at about 36°N 51°E (Fig. 3).

Biogeographical characterization. These few, scattered localities in the Irano-Anatolian highlands and the Elburz do not sufficiently describe the distribution pattern of *Stenus skoraszewskyi*, which is why we preliminarily term it as an Irano-Anatolian species.

Stenus brunnipes* species group**Stenus brunnipes brunnipes* Stephens, 1833**

Fig. 4, Suppl. material 1

Chorology. The nominotypical subspecies of *Stenus brunnipes* is widely distributed in the West Palaearctic eastwards to Iran and Turkmenistan. In Iran, the subspecies seems to be restricted to the northern mountain ranges, where it was found in the eastern Elburz and the Turkmeno-Khorasanian mountains (Fig. 4).

Biogeographical characterization. Puthz (2012a: 288) considers *Stenus b. brunnipes* to be Holomediterranean and we follow this hypothesis.

Stenus canaliculatus* species group**Stenus canaliculatus* Gyllenhal, 1827**

Fig. 5, Suppl. material 1

Chorology. The Holarctic *Stenus canaliculatus* is widely distributed across the temperate and northern Palaearctic as far east as Russian Far East and China. In Iran, the species is confined to the temperate north (West Azarbaijan, Ardabil, Mazandaran; Fig. 5). Thus, the record from Fars (Samin et al. 2011a: 2, 2011c: 1238), far south of the confirmed distribution, is implausible.

Biogeographical characterization. *Stenus canaliculatus*, a faunal element of the temperate Holarctic, cannot be assigned to any of de Lattin's (1951, 1957, 1967) southern Palaearctic glacial refuges.

Stenus cautus species group

Stenus cautus Erichson, 1839

Fig. 6, Suppl. material 1

Chorology. *Stenus cautus* is widely distributed across the temperate and northern Palaearctic from France to the Russian Far East. The first record for Iran was published by Puthz (2012a: 304). As far as known presently, the species reaches its southern limit of distribution in the northwest of Iran (Fig. 6), where it was found as far south as Chadegan (Esfahan Province).

Biogeographical characterization. No biogeographical assigning is possible for this trans-Palaearctic species.

Stenus circularis species group

Stenus planifrons robustus L. Benick, 1914

Fig. 7, Suppl. material 1

Chorology. The distribution of the polytypical *Stenus planifrons* reaches from Germany and Switzerland over the Balkans, Anatolia, the Levant, and the Ukraine eastwards to South Russia, Caucasia, Iran, and Turkmenistan. In Iran, the species is represented by the southeastern subspecies *S. p. robustus*, which is distributed in Cyprus, Lebanon, Israel, Syria, Anatolia, Iraq, and northern Iran as far east as Turkmenistan.

Biogeographical characterization. Due to this arched areal north, west, and east of the Mesopotamian plain, the evolutionary origin of the subspecies goes back to the Syrian Pleistocene refuge. In Iran, *Stenus p. robustus* reaches its southern and eastern distribution limit in the southern Zagros Mountains (29°40'N) and the Turkmeno-Khorasanian mountain ranges (59°54'E) (Fig. 7).

Bionomics. This cold resistant taxon was found in altitudes up to 3250 m.

Stenus clavicornis species group

Stenus caspius Puthz, 1972

Fig. 8, Suppl. material 1

Chorology. Described from the Talish Mountains (Puthz 1972d: 127), *Stenus caspius* has its main distribution in Transcaucasia and the South Caspian mountain ranges from Georgia as far east as the Turkmeno-Khorasanian mountains. It apparently is the most common *Stenus* in the Hyrcanian zone in the northern slopes of the Talish and Elburz Mountains, but it was also found outside of this biogeographical unit in West Azarbaijan, the northern Zagros Mountains, and south of the Elburz (Fig. 8).

Biogeographical characterization. Judging from this distribution pattern, *Stenus caspius* is a typical expansive Caspian faunal element.

Stenus providus providus Erichson, 1839

Fig. 8, Suppl. material 1

Chorology. The nominotypical subspecies of *Stenus providus* is widespread in the West Palaearctic as far east as Kazakhstan (Kastcheev and Puthz 2011: 450). The first record for Iran in this work is missing in the current Catalogue of Palaearctic Coleoptera (Schülke and Smetana 2015: 837). In Iran, *S. p. providus* is distributed in the South Caspian mountains and the very north of the Zagros Mountains (Fig. 8). In the Hyrcanian zone, the species is replaced by its close, allopatric relative *S. caspius*, but in high elevations of the northern slopes of the Elburz Mountains there is a narrow zone of sympatry.

Biogeographical characterization. Judging from the distribution in all of the arboreal Mediterranean, *Stenus providus* is to be attributed to the Holomediterranean distribution type. Kastcheev and Puthz (2011: 454) already described it as a Mediterranean species.

Stenus comma species group

Stenus aereus Solsky, 1871

Fig. 9, Suppl. material 1

Chorology. *Stenus aereus* is distributed in Caucasia, the Middle East, Central Asia, and West Siberia. In Iran, it apparently is a rare species, which we did not succeed to collect. The record from West Azarbaijan published by Samin et al. (2011b: 140) is plausible in view of the record from East Azarbaijan (Fig. 9), but needs confirmation.

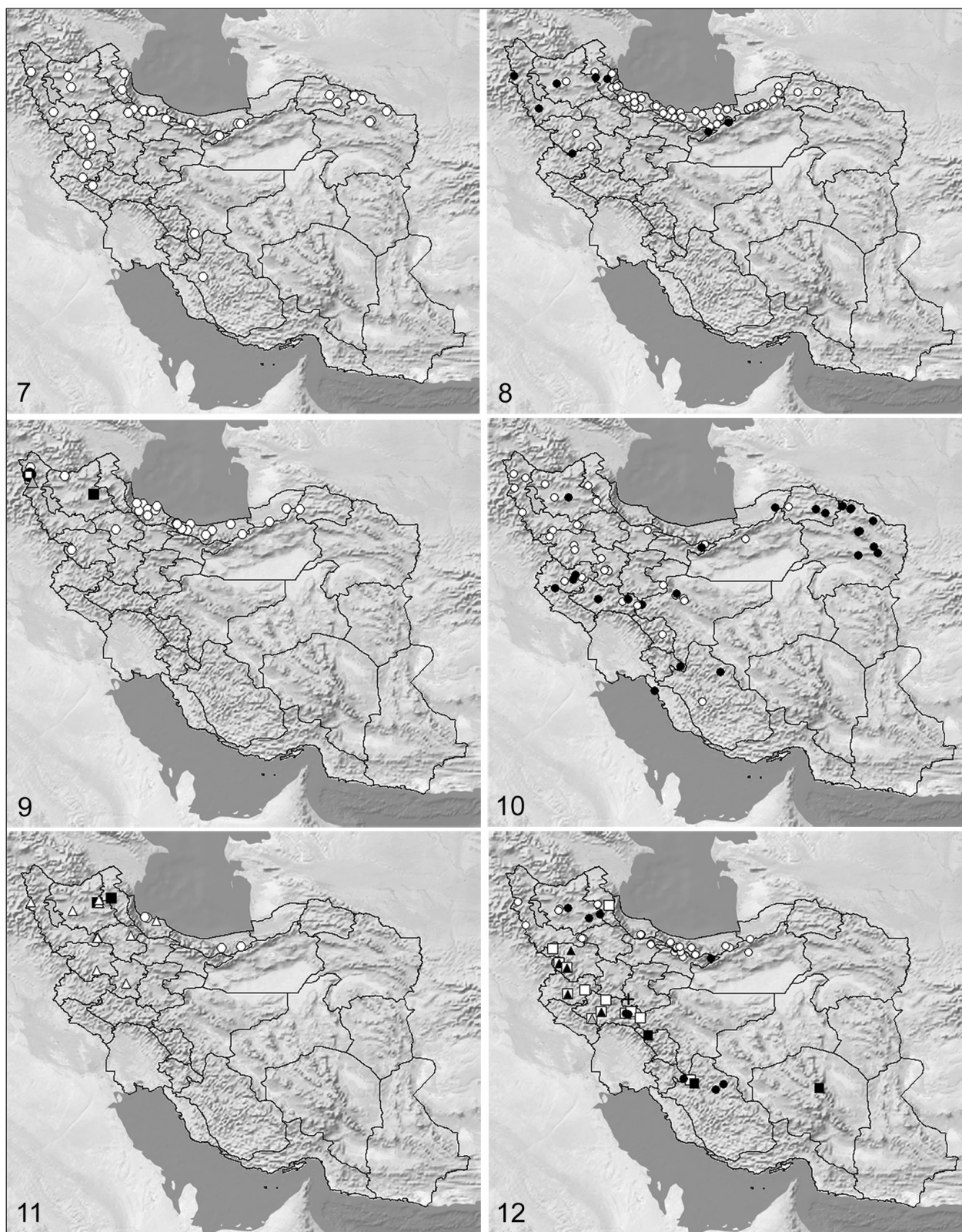
Biogeographical characterization. Kastcheev and Puthz (2011: 454) term *Stenus aereus* a Kazakhstan-Turanian species. According to the hypothesis of Pleistocene refuges, we consider it to be an expansive Turkestanian faunal element, which dispersed towards the Mediterranean.

Stenus asiaticus Bernhauer, 1940

Fig. 9, Suppl. material 1

Chorology. The Middle Eastern *Stenus asiaticus* is recorded for Georgia, Turkey, Syria, Iraq, Iran, and Turkmenistan. In Iran, it is the most widespread member of the *S. comma* species group and distributed in the South Caspian mountains and the northern Zagros Mountains (Fig. 9).

Biogeographical characterization. It is difficult, to assign *Stenus asiaticus* to a particular distribution type judging from the total distribution. In view of the high abundance of records in the Hyrcanian zone in the northern slopes of the Elburz Mountains and the distribution in Transcaucasia, the regions which constitute the Caspian refuge, we consider *S. asiaticus* to be an expansive Caspian faunal element.



Figures 7–12. Distribution of Steninae in Iran. **7.** *Stenus circularis* species group: ○ *S. planifrons robustus*; **8.** *Stenus clavicornis* species group: ○ *S. caspius*, ● *S. p. providus*; **9.** *Stenus comma* species group: ■ *S. aereus*, ○ *S. asiaticus*, ● *S. bicornis*, ▲ *S. biguttatus*, □ *S. c. comma*; **10.** *Stenus cordatus* species group: ○ *S. araxis*, ● *S. turk*; **11.** *Stenus crassus* and *S. fornicatus* species groups: ■ *S. crassus*, △ *S. formicetorum*, ○ *S. fornicatus*; **12.** *Stenus glacialis* species group: + *S. armeniacus*, ▲ *S. hospes*, ■ *S. limicola*, ○ *S. medus*, ▲ *S. parciur*, □ *S. persicus*, ● *S. schah*.

***Stenus bicornis* Puthz, 1972**

Fig. 9, Suppl. material 1

Chorology. Described from Macedonia and Turkey (Puthz 1972c: 170), *Stenus bicornis* is distributed in the Balkans and Anatolia. The recent records in the very northwest of Iran (Fig. 9) are the first for the Iranian fauna and represent the easternmost known localities of this species.

Biogeographical characterization. Due to its distribution in the northeastern Mediterranean, *Stenus bicornis* can be regarded as a Pontomediterranean species.

***Stenus biguttatus* (Linnaeus, 1758)**

Fig. 9, Suppl. material 1

Chorology. *Stenus biguttatus* is widely distributed across the northern Palaearctic eastwards to Russian Far East and Japan (Kastcheev and Puthz 2011: 440). In Iran, the species seems to be rare and restricted to the northwest, where we collected it just once (Fig. 9). The dubious records from Rasht and Fouman published by Samin et al. (2011a: 2, 2011c: 1238) were not adopted by Schülke and Smetana (2015: 808).

Biogeographical characterization. The enormous area of distribution of *Stenus biguttatus* cannot be attributed to a particular Pleistocene refuge and distribution type, respectively.

***Stenus comma comma* Le Conte, 1863**

Fig. 9, Suppl. material 1

Chorology. The Holarctic *Stenus comma* is widespread across the temperate and northern Palaearctic as far east as Russian Far East, China, and Japan. In Iran, the northern species seems to be confined to the temperate northwest. Our find in West Azarbaijan constitutes the first country record of *S. c. comma* for Iran (Fig. 9).

Biogeographical characterization. The wide distribution of this species cannot be explained by the Pleistocene refuge theory.

Stenus cordatus* species group**Stenus araxis* Ryvkin, 1990**

Fig. 10, Suppl. material 1

Chorology. *Stenus araxis* was described from Armenia (Ryvkin 1990: 213) and already recorded for Iran (Schülke and Smetana 2015: 805), where it is distributed from the northwest throughout the Iranian highlands as far east as 53°13'E in North Khorasan and as far south as 29°06'N in Central Fars (Fig. 10). Particularly in the Zagros Mountain, we usually collected *S. araxis* in high abundance.

Biogeographical characterization. The distribution pattern of *Stenus araxis* definitely matches the Iranian glacial refuge.

***Stenus turk* Puthz, 1972**

Fig. 10, Suppl. material 1

Chorology. *Stenus turk* is recorded from Azerbaijan, Georgia, Ukraine, Turkey, Iran, and Central Asia. Both Iranian representatives of the *S. cordatus* species group, *S. araxis* and *S. turk*, reach their southern distributional limit in Iran and occur sympatrically in the Zagros and Elburz Mountains (Fig. 10). Recent Iranian records of *S. turk* were mostly collected in the Khorasan provinces in the northeast, which concurs with the wide distribution of this species in Central Asia.

Biogeographical characterization. Kastcheev and Puthz (2011: 454) described *Stenus turk* as Kazakhstan-Turanian species. Judging from its distribution pattern in Central Asia, this species represents the Turkestanian faunal element.

Stenus crassus* species group**Stenus crassus* Stephens, 1833**

Fig. 11, Suppl. material 1

Chorology. *Stenus crassus* is widely distributed across the temperate and northern West Palaearctic eastwards to Russia, Kazakhstan, and Mongolia (Kastcheev and Puthz 2011: 443). The species reaches its southernmost limit of distribution in the very north of western Iran (Fig. 11). In view of this distribution pattern, the record by Ghahari et al. (2009a: 1954) from Kaleybar in East Azarbaijan, which is the first record for Iran, can be correct.

Biogeographical characterization. The distribution pattern of *Stenus crassus* cannot be explained by the theory of Pleistocene refuges.

***Stenus formicetorum* Mannerheim, 1843**

Fig. 11, Suppl. material 1

Chorology. The Holarctic *Stenus formicetorum* is widely distributed in the temperate and northern Palaearctic as far east as Russian Far East and as far south as Afghanistan and northwestern Iran (Fig. 11).

Biogeographical characterization. The wide distribution in the northern and temperate Palaearctic cannot be attributed to a particular Pleistocene refuge.

Stenus fornicatus* species group**Stenus fornicatus* Stephens, 1833**

Fig. 11, Suppl. material 1

Chorology. Unlike other members of the *Stenus fornicatus* species group which are endemic to the eastern parts of the Palaearctic, *S. fornicatus* is widely distributed in the West Palaearctic including the Mediterranean and reaches East Siberia. In Iran, the species is hitherto

known from the Hyrcanian zone of the northern slopes of the South Caspian mountain ranges only (Fig. 11).

Biogeographical characterization. Due to the wide distribution of this species in the Mediterranean, Puthz (2012a: 288) considered *Stenus fornicatus* to be a Holo-mediterranean species. Here we follow this interpretation.

Stenus glacialis species group

Stenus armeniacus Puthz, 1967

Fig. 12, Suppl. material 1

Chorology. *Stenus armeniacus* was described from Yerevan, Armenia (Puthz 1967: 248), and later recorded from the Kopet Dag in Turkmenistan and the eastern Zagros Mountains (Arak) in Iran (Puthz 1973: 292). Only recently, Puthz (2012b: 153) published first records of this species from southern Turkey and revealed that the record from Turkmenistan is based on a misidentification. The record from Arak represents the southernmost collection site (Fig. 12). This species is rare and we didn't succeed in collecting it.

Biogeographical characterization. In view of the widely scattered localities in the Irano-Anatolian highlands we propose an Irano-Anatolian type of distribution for *Stenus armeniacus*.

Stenus hospes Erichson, 1840

Fig. 12, Suppl. material 1

Chorology. *Stenus hospes* is widely distributed in the Mediterranean Region from France and Italy across the Balkans as far east as Anatolia, the Levant, and Caucasia. The recent records from the Zagros Mountains (Fig. 12) constitute the first for the Iranian fauna and considerably extend the known distribution to the southeast.

Biogeographical characterization. Judging from its distribution pattern, *Stenus hospes* can be regarded as a Pontomediterranean species.

Stenus limicola Korge, 1967

Fig. 12, Suppl. material 1

Chorology. Described from the Erzincan Province in the east of Turkey (Korge 1967: 251), *Stenus limicola* was later recorded for Iran (Smetana 2004: 544) and the north of Iraq (Puthz 2010: 61). We collected *S. limicola* in the Zagros Mountains and Kerman (Fig. 12). The gap of records between eastern Turkey (Tunceli Province; Anlaş 2009: 280) and the Central Zagros Mountains most probably is a collecting artifact.

Biogeographical characterization. Owing to the sparse records of *Stenus limicola*, it is not possible to explain its Irano-Anatolian distribution pattern with de Latini's hypothesis.

Bionomics. Because descriptions of many species of the *Stenus glacialis* group were based on single specimens and the species never collected again, Assing (2003:711)

assumed they inhabit unknown subterranean habitats and are found only by chance. *Stenus limicola* seems to be restricted to high elevations. In Iran, we collected it between 2860 and 3000 m.

Stenus medus Puthz, 1981

Fig. 12, Suppl. material 1

Chorology. *Stenus medus*, described from Armenia, Azerbaijan, and northern Iran (Puthz 1981: 702), is widely distributed in Transcaucasia, Turkey, and northern and northwestern Iran between 44°00'E (Orumieh) and 53°00'E (Shahmirzad) (Fig. 12).

Biogeographical characterization. Due to its distribution in Transcaucasia and its high abundance in the Hyrcanian zone in the northern slopes of the Elburz Mountains, *Stenus medus* is a typical expansive Caspian faunal element.

Stenus parciior Bernhauer, 1929

Fig. 12, Suppl. material 1

Chorology. Unlike the other representatives of the *Stenus glacialis* species group in Iran, *S. parciior* is widely distributed throughout the Balkans, Anatolia, Cyprus, Lebanon, and Iran as far east as Uzbekistan. The record from Pol-e Dokhtar in the southwestern Zagros Mountains (Puthz 2008: 171) at less than 1000 m elevation constitutes the easternmost record of this species (Fig. 12).

Biogeographical characterization. The distribution of *Stenus parciior* in the eastern Mediterranean and the Middle East corresponds to the expansive Pontomediterranean faunal element.

Stenus persicus Puthz, 1981

Fig. 12, Suppl. material 1

Chorology. *Stenus persicus* seems to be endemic to Azerbaijan and western Iran (Fig. 12). Besides a find in the Ardabil Province, we repeatedly collected it in the Zagros Mountains from Kordestan southwards to northern Fars, usually in higher elevations and sympatrically with relatives of the *S. glacialis* species group such as *S. hospes* and *S. schah*.

Biogeographical characterization. Judging from the distribution pattern in the Zagros Mountains and Northwest Iran (Ardabil Province), *Stenus persicus* can be regarded as an Iranian faunal element.

Stenus schah Puthz, 1981

Fig. 12, Suppl. material 1

Chorology. As far as known presently, *Stenus schah* is endemic to Iran. The new records, which are the first after the description, revealed its wider distribution in the Zagros Mountains.

Biogeographical characterization. The distribution pattern in both the Zagros and Elburz Mountains (Fig. 12) exactly correspond to the Iranian glacial refuge, which is why *Stenus schah* is an Iranian faunal element.

Stenus guttula species group

Stenus erythrocnemus Eppelsheim, 1884

Fig. 13, Suppl. material 1

Chorology. *Stenus erythrocnemus* is a Middle Eastern species, which is distributed from Anatolia and Caucasica across the Iranian Plateau eastwards to Kyrgyzstan, Tadzhikistan, Afghanistan, and Pakistan. *Stenus erythrocnemus* has a vast distribution in the mountain ranges of Iran (Fig. 13).

Biogeographical characterization. Because the majority of records originated from the highlands of Iran (Assing 2005: 307), we consider *Stenus erythrocnemus* to be an expansive Iranian faunal element, which dispersed northwestwards to Anatolia and Caucasica and eastwards to Central Asia and the Hindu Kush.

Stenus maculiger Weise, 1875

Fig. 13, Suppl. material 1

Chorology. *Stenus maculiger* is widely distributed in the Northeast Mediterranean and eastern Europe eastwards to South Russia and Iran. The first records for Iran were published from Ghaemshahr in Mazandaran (Ghahari et al. 2009b: 1964) and Jangal-e Abr in the Semnan Province (Hadian et al. 2011: 4). However, we doubt these records, because we were unable to find this species in the South Caspian mountains. Our collections in Northwest Iran must be regarded as the first confirmed country records (Fig. 13). The locality in the Ardabil Province moreover constitutes the easternmost collecting site of the species.

Biogeographical characterization. Judging from the distribution pattern, *Stenus maculiger* belongs to the expansive Pontomediterranean faunal element.

Stenus hopffgarteni species group

Stenus fuscicornis Erichson, 1840

Fig. 14, Suppl. material 1

Chorology. *Stenus fuscicornis* is widely distributed throughout most of Europe and the Mediterranean including the Maghreb countries and Turkey. The first record for Iran was published by Puthz (2012a: 312). In Iran, we discovered the species in a relatively small area in the western Elburz and the Talish Mountains (Fig. 14). Unlike most members of the *S. hopffgarteni* species group which are European endemics, *S. fuscicornis* is the only representative of the species group in the Middle East.

In Iran, the species obviously reaches its eastern limit of distribution.

Biogeographical characterization. *Stenus fuscicornis* is a Holomediterranean species according to Puthz (2012a: 312).

Stenus humilis species group

Stenus callidus Baudi di Selve, 1848

Fig. 15, Suppl. material 1

Chorology. *Stenus callidus* exists in the Balkans, Caucasica, and the Middle East. According to Puthz (2008: 157), the record for Kyrgyzstan in Smetana (2004: 555), which was adopted by Schülke and Smetana (2015: 810), is based on a misidentification and probably refers to *S. cephalenicus*. *Stenus callidus* is the second widespread species of the genus (Fig. 15) in Iran. It was recorded in all of the northwest, in the northern Qohrud Range, and in the Elburz as far east as 53°38'E in eastern Mazandaran. Most frequently, however, it was collected in the Zagros Mountains. The records from southeastern Iran at about 56°E in the provinces of Hormozgan and Kerman considerably extend the range of this species towards east.

Biogeographical characterization. Due to its vast distribution in the eastern Mediterranean, Anatolia (Puthz 2008: 153), and Iran, *Stenus callidus* can be considered as an expansive Pontomediterranean species.

Stenus impressus species group

Stenus heinzianus Puthz, 1970

Fig. 16, Suppl. material 1

Chorology. *Stenus heinzianus* was described from Damash in Gilan, Iran (Puthz 1970a: 223), and subsequently recorded from Azerbaijan and Afghanistan. In Iran, it is abundant in the entire Hyrcanian zone from northern Gilan as far east as Golestan (Fig. 16).

Biogeographical characterization. Judging from this distribution pattern, *Stenus heinzianus* is an expansive Caspian faunal element.

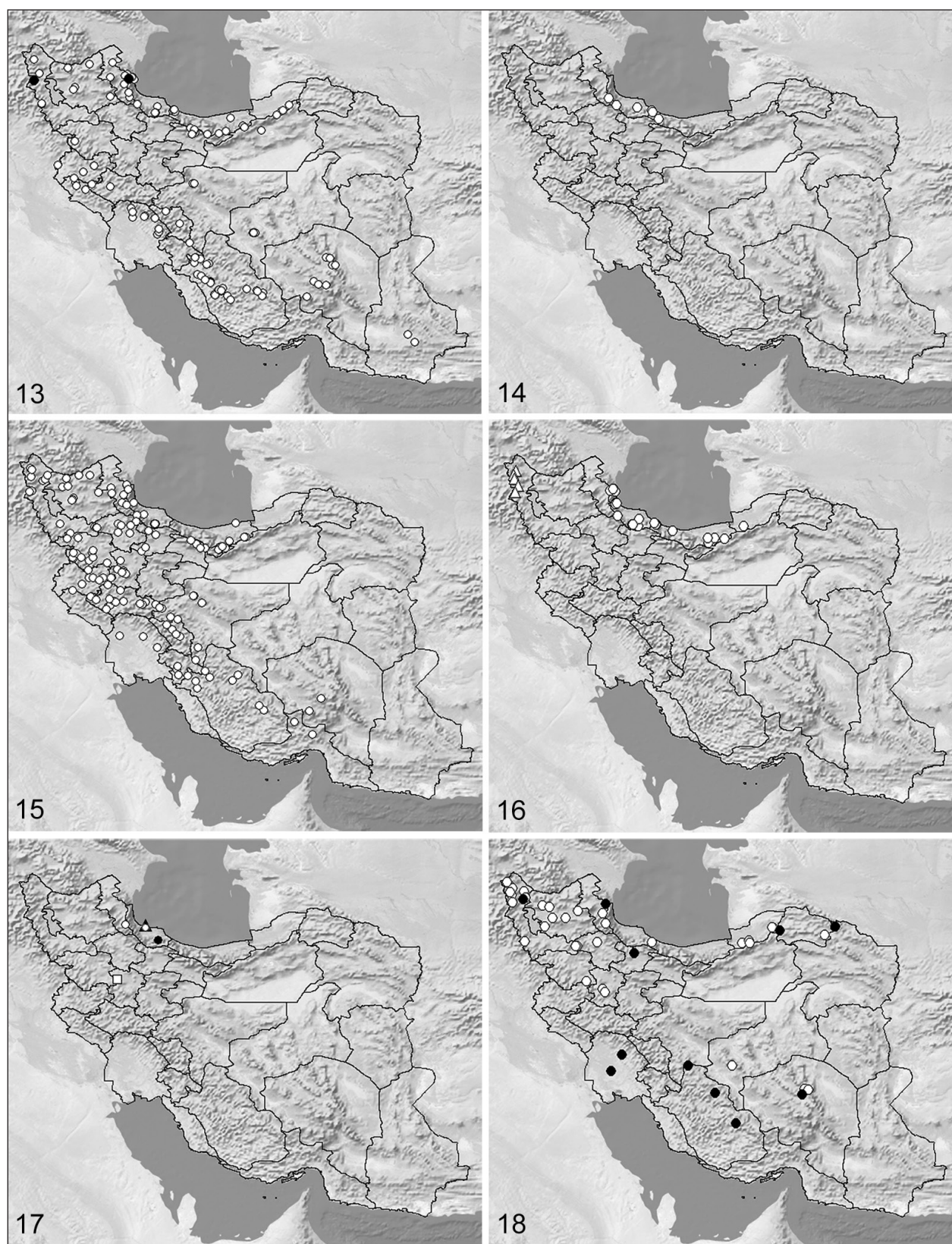
Stenus incanus species group

Stenus taurus Serri & Frisch, 2013

Fig. 16, Suppl. material 1

Chorology. *Stenus taurus* was described only recently from westerly facing slopes of mountain ranges close to the Turkish border in West Azarbaijan (Serri and Frisch 2013: 99–103; Fig. 16).

Biogeographical characterization. It is difficult to assign *Stenus taurus* to a particular distribution type, because its total distribution is still unknown. However, we expect it to be endemic to the Irano-Anatolian highlands.



Figures 13–18. Distribution of Steninae in Iran. **13.** *Stenus guttula* species group: ○ *S. erythrocnemus*, ● *S. maculiger*; **14.** *Stenus hopffgarteni* species group: ○ *S. fuscicornis*; **15.** *Stenus humilis* species group: ○ *S. callidus*; **16.** *Stenus impressus* and *S. incanus* species groups: ○ *S. heinzianus*, △ *S. taurus*; **17.** *Stenus latifrons* and *S. melanarius* species groups: ▲ *S. latifrons*, ○ *S. incrassatus*, ■ *S. morio*, ● *S. peripherus*; **18.** *Stenus melanopus* species group: ○ *S. atratulus*, ● *S. piscator*.

Stenus latifrons species group

The *Stenus latifrons* species group is here proposed for *S. latifrons* based on the deviant morphology of the paraglossae following a recommendation of V. Puthz (pers. comm., 2015).

Stenus latifrons Erichson, 1839

Fig. 17, Suppl. material 1

Chorology. *Stenus latifrons* is widely distributed across Europe from the Balkans and Italy northwards to Scandinavia. Towards the east, the species reaches Turkey, Caucasasia, and Iran. A recent record from Kazakhstan (Kastcheev and Puthz 2011: 447) is based on a single female. In Iran, the species is known from the Caspian plain in Gilan (Fig. 17).

Biogeographical characterization. Kastcheev and Puthz (2011: 454) consider *Stenus latifrons* to be a Mediterranean species. In view of the absence in the western Mediterranean, we follow Puthz (2012a: 287) and attribute the species to the Pontomediterranean type of distribution.

Stenus melanarius species group

Stenus incrassatus Erichson, 1839

Fig. 17, Suppl. material 1

Chorology. *Stenus incrassatus* is widely distributed in the northern and temperate Palaearctic from Ireland to China and Russian Far East. In Iran, we collected *S. incrassatus* only in the Talish Mountains (Fig. 17) from sea level up to 1850 m.

Biogeographical characterization. The vast range of the trans-Palaearctic species cannot be attributed to a particular Pleistocene refuge in the West Palaearctic and Middle East, respectively.

Stenus morio Gravenhorst, 1806

Fig. 17, Suppl. material 1

Chorology. *Stenus morio* is a Holarctic species with a trans-Palaearctic distribution. The first records for Iran (West and East Azarbaijan) were published only recently by Ghahari et al. (2009b: 1964). However, we were not given the opportunity to see the underlying specimens. Like other members of the *S. melanarius* group, *S. morio* seems to be rare in Iran and restricted to the northwest of the country, because we collected it in the northern Zagros (Hamedan Province) only (Fig. 17).

Biogeographical characterization. The trans-Palaearctic distribution of *Stenus morio* can not be explained by particular Pleistocene refuges.

Stenus peripherus Korge, 1971

Fig. 17, Suppl. material 1

Chorology. *Stenus peripherus* was described as a subspecies of *S. melanarius* from Turkey (Korge 1971: 24), but only recently raised to species rank by Puthz (2008: 149). The species is distributed in eastern Turkey, Armenia, and Iran, where it reaches its southernmost known limit of distribution in the southern Talish at 36°54'N, 49°59'E (Fig. 17).

Biogeographical characterization. The few localities hitherto known suggest an expanded Caspian distribution for *Stenus peripherus*.

Stenus melanopus species group

Stenus atratulus Erichson, 1839

Fig. 18, Suppl. material 1

Chorology. The West Palaearctic *Stenus atratulus* is widely distributed throughout Europe, the Mediterranean including the Maghreb countries Algeria and Tunisia, and Turkey eastwards to Iran, where it is most abundant in the northwest (Fig. 18), from where it dispersed across the South Caspian mountains as far east as the Koppeh Dag at about 58°E in North Khorasan, the easternmost confirmed locality of the species. Interestingly, *S. atratulus* was not found in the Zagros Mountains south of Hamedan Province, but it occurs in the dryer Qohrud Range, where we recorded it at Shir Kuh and in the mountains of Kerman (Fig. 18).

Biogeographical characterization. Due to its Mediterranean distribution centre, we classify *Stenus atratulus* as a Holomediterranean species following Puthz (2012a: 78).

Stenus piscator Saulcy, 1864

Fig. 18, Suppl. material 1

Chorology. *Stenus piscator* is distributed from the eastern Mediterranean (Turkey, Cyprus, Levant) across Anatolia and northern Mesopotamia as far north as Transcaucasia and eastwards to Iran and Turkmenistan. In Iran, the species has a disjunct distribution pattern (Fig. 18) and is recorded for the Talish, the Turkmeno-Khorasanian mountains, the southern Zagros, the plain of Khuzestan, and Kerman. *Stenus piscator* reaches its easternmost known locality in the Koppeh Dag at about 58°30'E.

Biogeographical characterization. The arched distribution pattern west, north, and east of Mesopotamia characterizes *Stenus piscator* as an expansive Syrian faunal element.

Stenus mendicus* species group**Stenus alienigenus* Puthz, 1964**

Fig. 19, Suppl. material 1

Chorology. Described as a subspecies of *Stenus mendicus* from Israel (Puthz 1964: 229), *S. alienigenus* is distributed in the Levant (Lebanon, Israel and Syria) and Iran, where it seems to be restricted to the northern Zagros Mountains (Fig. 19).

Biogeographical characterization. Due to its distribution in the arboreal regions west and east of the Mesopotamian plain, we consider *Stenus alienigenus* as a Syrian faunal element.

***Stenus ignotus* Eppelsheim, 1890**

Fig. 19, Suppl. material 1

Chorology. *Stenus ignotus* was described from the Talish Mountains near Lenkoran, Azerbaijan (Eppelsheim 1890: 226). Its area of distribution reaches from Italy and the Balkans over Anatolia, Syria, Iraq, Caucasia, and Iran eastwards to Central Asia. In Iran, *S. ignotus* is distributed in the very northwest, the northern Zagros Mountains, and the South Caspian mountains, where we recorded it as far east as about 53°30'E in eastern Mazandaran (Fig. 19).

Biogeographical characterization. Judging from the wide distribution in the northeastern Mediterranean, *Stenus ignotus* belongs to the Pontomediterranean type of distribution.

***Stenus orientis* Puthz, 1967**

Fig. 19, Suppl. material 1

Chorology. *Stenus orientis* is restricted to the Levant, Iraq, and western Iran, where it is recorded in the South Caspian mountains as far east as about 53°30'E (eastern Mazandaran) and in the Zagros Mountains southwards to 29°24'N (Central Fars) (Fig. 19).

Biogeographical characterization. Due to this arched distribution around the northern Mesopotamian plain, we consider *Stenus orientis* as a Syrian faunal element.

***Stenus ochropus-ludyi-coarcticollis* species group**

Biogeographical characterization. Except for *Stenus ochropus*, the Iranian species of the *S. ochropus – ludyi – coarcticollis* species group are endemic to the Hyrcanian forest zone, the South Caspian subunit of the Caspian glacial refuge (Fig. 20). Their vertical distribution concurs with that forest zone, where they were found from the Caspian plain up to about 1500 m in the mountains. Thus, these species represent the Hyrcanian faunal element within the Caspian type of distribution sensu De Lattin (1951: 208–210, 1957: 388, 1967: 322).

***Stenus barbarae* Hromadka, 1979**

Fig. 20, Suppl. material 1

Chorology. *Stenus barbarae* was described from the Talish Mountains in Gilan, Iran (Hromadka 1979: 183). The new record close to the type locality is the first after the description. As far as known presently, *S. barbarae* is endemic to some north-facing valleys in the southern Talish at about 37°N, 49°E (Fig. 20).

***Stenus confrater* Eppelsheim, 1890**

Fig. 20, Suppl. material 1

Chorology. *Stenus confrater* is endemic to the northern Talish Mountains in Iran and Azerbaijan (Fig. 20). In Gilan, it was collected at an elevation of 30 m only in the foothills of the Talish Mountains. In higher elevations, the species seems to be replaced by its close relatives *S. barbarae* and *S. darius*.

***Stenus darius* Puthz, 2009**

Fig. 20, Suppl. material 1

Chorology. As far as known presently, *Stenus darius* is endemic to the northeast-facing freshwater system of the Masuleh Valley in the southern Talish Mountains at about 37°N, 49°E (Fig. 20).

***Stenus derwisch* Puthz, 1981**

Fig. 20, Suppl. material 1

Chorology. *Stenus derwisch* is a Hyrcanian endemic, which is comparatively widespread in the South Caspian mountains (Fig. 20). The species is hitherto recorded from the very north of Gilan at 38°13'N, 48°53'E (As-tara) eastwards to Central Mazandaran at about 52°20'E (Amol).

***Stenus guilanensis* Puthz, 1979**

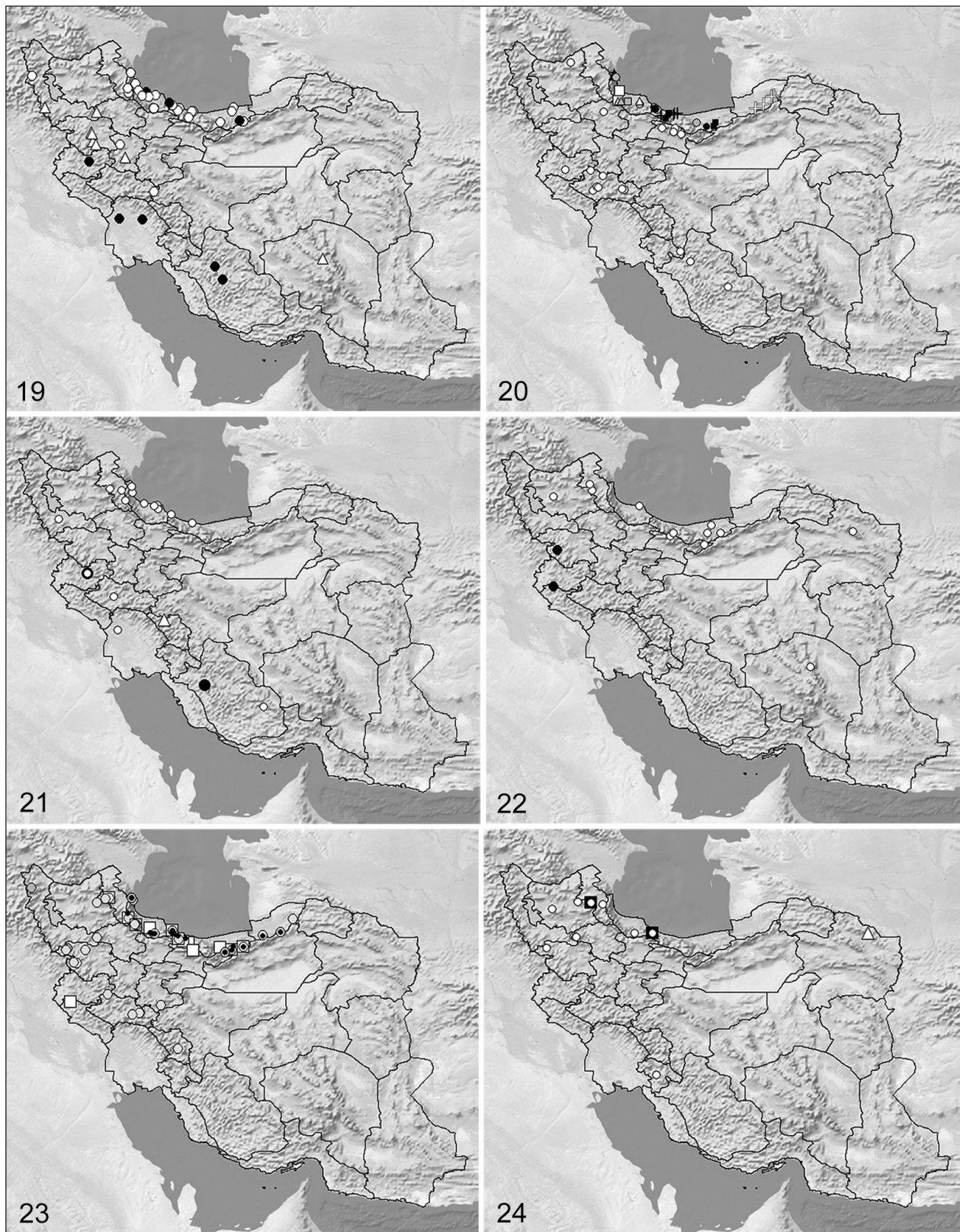
Fig. 20, Suppl. material 1

Chorology. *Stenus guilanensis* was described from Lahijan, Gilan (Puthz 1979: 57). The Hyrcanian endemic is hitherto known only from the type locality in the north-westernmost foothills of the Elburz (Fig. 20).

***Stenus kambyes* Puthz, 2009**

Fig. 20, Suppl. material 1

Chorology. *Stenus kambyes* is presently known only from the type locality in the southernmost Talish Mountains, Gilan (Fig. 20), and certainly endemic to the Hyrcanian district.



Figures 19–24. Distribution of Steninae in Iran. **19.** *Stenus mendicus* species group: \triangle *S. alienigenus*, \circ *S. ignotus*, \bullet *S. orientis*; **20.** *Stenus ochropus-ludyi-coarcticollis* species group: \blacksquare *S. barbarae*, \blacktriangle *S. confrater*, \triangle *S. darius*, \bullet *S. derwisch*, \triangle *S. guilanensis*, \blacksquare *S. kambyes*, \bullet *S. martensi*, \circ *S. ochropus*, \blacksquare *S. pieperi*, $+$ *S. resili*, \oplus *S. wittmeri*; **21.** *Stenus pallitarsis* species group: \bullet *S. arabicus*, \triangle *S. butrintensis*, \circ *S. claritarsis*; **22.** *Stenus picipes* species group: \circ *S. ganglbaueri*, \bullet *S. picipes*; **23.** *Stenus pusillus* species group: \blacksquare *S. lenkoranus*, \bullet *S. machulkai*, \bullet *S. viti*; **24.** *Stenus similis* species group: \triangle *S. bernhauerianus*, \blacksquare *S. cicindeloides*, \circ *S. similis*.

***Stenus martensi* Puthz, 1983**

Fig. 20, Suppl. material 1

Chorology. Including the new records from western Mazandaran, the first after the description, *Stenus martensi* is endemic to the Hyrcanian forest zone of the Elburz, where it was collected between 50°34'E (Ram-sar) and 52°49'E (Alasht) in altitudes up to 1450 m (Fig. 20).

***Stenus ochropus* Kiesenwetter, 1858**

Fig. 20, Suppl. material 1

Chorology. *Stenus ochropus* is the most widespread member of the *ochropus-ludyi-coarcticollis* species group. The West Palaearctic species is distributed from Europe, except for the Iberian Peninsula, as far east as Central Asia including Anatolia, the Levant, Caucasasia, and Iran, where it is recorded from the northwest as far east as Tehran and southwards to 29°09'N in Fars (Fig. 20).

Biogeographical characterization. Judging from its wide distribution in the northeastern Mediterranean, we follow Puthz (2012a: 313), who classified *Stenus ochropus* as an expansive Pontomediterranean species.

***Stenus pieperi* Puthz, 1983**

Fig. 20, Suppl. material 1

Chorology. *Stenus pieperi* was described from Alamdeh, West Mazandaran (Puthz 1983: 353). Our recent records further east, which are the first after the description, indicate that the species is endemic to the Hyrcanian forest zone of the Elburz Mountains from about 50°30'E eastwards to about 53°10'E (Fig. 20).

***Stenus resslı* Puthz, 1979**

Fig. 20, Suppl. material 1

Chorology. *Stenus resslı* was described from the northern foothills of the Elburz in the Caspian plain south and east of Chalus (Puthz 1979: 54). We rediscovered it somewhat further to the west south of Tonekabon. Seemingly, *S. resslı* is endemic to a small area in the Hyrcanian forest belt of western Mazandaran (Fig. 20).

***Stenus wittmeri* Puthz, 1972**

Fig. 20, Suppl. material 1

Chorology. *Stenus wittmeri*, described from Minudasht, Golestan (Puthz 1972a: 123), is the easternmost representative of the *S. ochropus-ludyi-coarcticollis* species group in Iran. The species is endemic to the Hyrcanian forest belt of the eastern Elburz (Fig. 20).

Stenus pallitarsis* species group**Stenus arabicus* Sauley, 1864**

Fig. 21, Suppl. material 1

Chorology. The Middle Eastern *Stenus arabicus* is recorded from Lebanon, Israel, Jordan, Syria, Turkey, and Iran as far north as Armenia. The record from China in Smetana (2004: 552), which was repeated by Schülke and Smetana (2015: 805), is a lapsus (V. Puthz, pers. comm.). We collected the species in two widely separate localities in the Zagros Mountains (Fig. 21).

Biogeographical characterization. Due to its arched distribution in arboreal regions around northern Mesopotamia, *Stenus arabicus* can be considered as a Syrian faunal element.

***Stenus butrintensis* Smetana, 1959**

Fig. 21, Suppl. material 1

Chorology. The West Palaearctic *Stenus butrintensis* was previously known from western Europe as far east as Turkey. The record for Spain in Smetana (2004: 552), adopted by Schülke and Smetana (2015: 810), is a lapsus (Puthz 2012a: 310). The first record of *S. butrintensis* for Iran in the Central Zagros considerably extends the known limit of distribution to the southeast (Fig. 21).

Biogeographical characterization. Due to its wide distribution in the northeastern Mediterranean, we adopt Puthz' (2012a: 310) classification as a Pontomediterranean species.

***Stenus claritarsis* Puthz, 1971**

Fig. 21, Suppl. material 1

Chorology. Described from Lenkoran, Azerbaijan (Puthz 1971: 100), *Stenus claritarsis* is distributed from eastern Europe (Austria, northern Balkans, Ukraine, South Russia) across Caucasasia and Iran eastwards to Central Asia. In Iran, the species is widespread in the South Caspian mountains, where we collected it as far east as 51°29'E in western Mazandaran and in the Zagros Mountains southwards to 28°45'N in southeastern Fars. It was also found in the plain of Khuzestan (Fig. 21).

Biogeographical characterization. Puthz (2012a: 312) proposed a Ponto-Mediterranean distribution for *Stenus claritarsis*, which is unlikely in view of the lack of records in all of the eastern Mediterranean. The distribution across Transcausasia and the South Caspian mountains points to an expansive Caspian faunal element.

Stenus picipes* species group**Stenus ganglbaueri* Bernhauer, 1905**

Fig. 22, Suppl. material 1

Chorology. *Stenus ganglbaueri* is distributed from Italy and the Balkans across Ukraine, Anatolia, the Levant, Syria, Caucasus, and Iran eastwards to Turkmenistan. The species is widespread in northern Iran as far east as the Binalud Mountains (Fig. 22), but a find in Kerman Province, which considerably extends the known range of *S. ganglbaueri* to the south, suggests a much wider distribution in the western Iranian Plateau.

Biogeographical characterization. Due to its distribution in the southeastern Mediterranean, we consider *Stenus ganglbaueri* to be a Pontomediterranean faunal element.

***Stenus picipes* Stephens, 1833**

Fig. 22, Suppl. material 1

Chorology. *Stenus picipes* is widespread in the temperate West Palaearctic as far east as western Russia, Anatolia, the Levant (Lebanon, Jordan, Syria), and Iran. The records from the northwestern Zagros Mountains (Puthz 2010: 61), the first for Iran, mark the southeastern distributional limit of this species (Fig. 22). The specimens from Iran belong to the type form *S. p. picipes*, which differs from *S. p. brevipennis* Thomson, 1851 by broader elytra with well developed humeral angels. These sympatric morphs are formally treated as subspecies in recent catalogues (Schülke and Smetana 2015: 835, 836) and key books (Puthz 2012a: 309).

Biogeographical characterization. The wide area of distribution of *Stenus picipes* can not be attributed to particular Pleistocene refugia of the arboreal, which is why no biogeographical assigning is possible for this West Palaearctic species.

Stenus pusillus* species group**Stenus lenkoranus* Puthz, 1970**

Fig. 23, Suppl. material 1

Chorology. *Stenus lenkoranus* was described as a subspecies of *S. nanus* Stephens, 1833 (Puthz 1970b: 211), but later raised to species rank (Ryvkin 1990: 158). The species is hitherto known from Azerbaijan and Iran only. The first records for Iran originate from the South Caspian mountains, Mt Sabalan in West Azarbaijan, and the northwestern Zagros in Ilam (Fig. 23).

Biogeographical characterization. We propose an expansive Caspian distribution for *Stenus lenkoranus*.

***Stenus machulkai* Hromadka, 1977**

Fig. 23, Suppl. material 1

Chorology. *Stenus machulkai*, described from the Araxes Valley (Hromadka 1977: 4), is known from Caucasus (Azerbaijan, Armenia, Georgia), Lebanon, Turkey, and Iran. The species is widely distributed in the northwest of the country, the northern and central Zagros, and the South Caspian mountains, where it is recorded as far east as 55°46'E (Fig. 23).

Biogeographical characterization. Judging from its existence in the northeastern Mediterranean, *Stenus machulkai* can be attributed to the Pontomediterranean type of distribution.

***Stenus viti* Puthz, 1977**

Fig. 23, Suppl. material 1

Chorology. *Stenus viti*, endemic to the northern slopes of the South Caspian mountains and presently known from Iran only, is recorded from northern Gilan at 48°49'E (Astara) throughout Mazandaran eastwards to Golestan at 55°14'E (Ramian) (Fig. 23).

Biogeographical characterization. This species is a Hyrcanian faunal element sensu De Lattin (1951: 208–210, 1957: 388, 1967: 322).

Stenus similis* species group**Stenus bernhauerianus* Jakobson, 1909**

Fig. 24, Suppl. material 1

Chorology. Described from Aulie Ata (Taraz) in southern Kazakhstan, the Central Asian *Stenus bernhauerianus* was also recorded from Kyrgyzstan and the Koppeh-Dagh (Fig. 24) in the northeast of Iran (Puthz 2010: 60).

Biogeographical characterization. Due to its distribution pattern, this rare species can be regarded as a Turkestanian faunal element.

***Stenus cicindeloides* Schaller, 1783**

Fig. 24, Suppl. material 1

Chorology. The Euro-Siberian *Stenus cicindeloides* has a trans-Palaearctic distribution from the British Isles east to Japan. The species is here for the first time reported for Iran from Ardabil and Mazandaran in the northwest of the country (Fig. 24).

Biogeographical characterization. It is not possible to assign the distribution pattern of *Stenus cicindeloides* to any of de Lattin's (1951, 1957, 1967) southern Palaearctic glacial refuges.

Stenus similis Herbst, 1784

Fig. 24, Suppl. material 1

Chorology. *Stenus similis* is widely distributed throughout the West Palaearctic eastwards to Kazakhstan and Mongolia. The species exists in northwestern Iran and was recorded as far south as 30°44'N in the Zagros Mountains (Fig. 24).

Biogeographical characterization. Judging from the existence in all of the arboreal Mediterranean, *Stenus similis* belongs to the Holomediterranean type of distribution.

Dubious and erroneous records of *Stenus* species from Iran

The following *Stenus* species were for the first time reported for Iran by Ghahari et al. (2009 a, b, c), Hadian et al. (2011), Sakenin et al. (2008, 2010), and Samin et al. (2011a, b, c). Below we discuss the plausibility of these records, because we were not given the opportunity to examine the reference specimens. Therefore we don't accept these species as members of the Iranian fauna and did not include them in the biogeographical analysis below. All of these dubious records require confirmation by the examination of the reference specimens considering the obvious misidentifications of Iranian *Scopaeus* species in these works (see Anlaş and Frisch 2014: 159, 160, 164, 165; Frisch 2010: 184, 194, 199).

Stenus aceris Stephens, 1833

Records. East Azarbaijan: Arasbaran, 8.2005 (Samin et al. 2011a: 2). **West Azarbaijan:** Maku, 9.2007 (Samin et al. 2011c: 1238).

Remarks. The distribution of the widespread Holomediterranean *Stenus aceris* is confirmed as far east as Cyprus, Lebanon, and Turkey. The existence in northwestern Iran is doubtful.

Stenus assequens assequens Rey, 1884

Record. Gilan (Samin et al. 2011 b: 140).

Remarks. The Palaearctic distribution of the Holarctic *Stenus a. assequens* reaches from Western Europe and the arboreal North Africa eastwards to the Russian Far East and China. Puthz (1977: 111) wrote that he received a single female from Nav Valley, Gilan, but this record was not adopted by Schülke and Smetana (2015: 806). Owing to the existence of *S. a. assequens* in Caucasus, Turkey, and Central Asia, the above record for Gilan could be correct.

Stenus binotatus Ljungh, 1804

Records. West Azarbaijan: Mahabad, 9.2003 (Ghahari et al. 2009a: 3). **Semnan:** Jangal-e Abr, 4.-5.2011 (Hadian et al. 2011: 3).

Remarks. *Stenus binotatus* is widely distributed across the Palaearctic from the British Isles to East Sibe-

ria. According to Kastscheev and Puthz (2011: 440), the record for Kazakhstan in Smetana (2004: 552), which was not repeated by Schülke and Smetana (2015: 808), is based on a misidentification. In view of the distribution in Caucasus and Turkey, the existence of *S. binotatus* in Iran is conceivable.

Stenus circularis Gravenhorst, 1802

Records. Golestan: Kordkoy, 6.2005 (Ghahari et al. 2009b: 1964). **Semnan:** Shahrud, 4.2009 (Hadian et al. 2011: 4).

Remarks. *Stenus circularis* is widely distributed throughout Europe and western Asia as far east as Turkey, Caucasus, West Siberia, and Central Asia. In view of this West Palaearctic distribution pattern the above records could be correct.

Stenus cordatoides Puthz, 1972

Remarks. Samin et al. (2011b: 141) erroneously misinterpreted Puthz (1972a: 125, 1972b: 280), who mentioned "*Stenus cordatoides* variant A" from Esfahan Province, which the same author later described as *S. turk* (Puthz 1972: 178). Therefore the Pontomediterranean *S. cordatoides*, which is distributed in the Balkans, Turkey, and the Levant, does not belong to the Iranian fauna. Schülke and Smetana (2015: 813) do not cite the species for Iran.

Stenus cyaneus Baudi di Selve, 1848

Record. East Azarbaijan: Arasbaran (Sakenin et al. 2008).

Remarks. *Stenus cyaneus* is distributed in Lebanon, Israel, Jordan, Syria, and Turkey. Sakenin et al. (2008) recorded the species for Iran as *S. glacialis cyaneus*, because until recently it was considered as a subspecies of the Central and Southeast European *S. glacialis* Heer, 1839. The existence of *S. cyaneus* in Iran is conceivable.

Stenus guttula P. Müller 1821

Record. Sistan & Baluchestan (Samin et al. 2011b: 141).

Remarks. This record was adopted from Scheerpeltz (1961: 4), though it already turned out to be based on a misidentification (Herman 2001: 2208). Consequently, the Holomediterranean *S. guttula*, which is widely distributed in Europe and the Mediterranean, but also recorded for Egypt (Sinai) and Yemen, does not exist in Iran.

Stenus melanarius melanarius Stephens, 1833

Remarks. Samin et al. (2011b: 141) cited *Stenus m. melanarius* for Iran referring to the catalogues of Herman (2001: 2276) and Smetana (2004: 559). The underlying specimens represent *S. peripherus* Korge, 1971 (Puthz, pers. comm.). Thus, the trans-Palaearctic *S. melanarius* is not yet recorded for the fauna of Iran. This erroneous record is, however, cited by Schülke and Smetana (2015: 828) again.

***Stenus melanopus* Marsham, 1802**

Records. **Razavi Khorasan:** Mashad, 3.2006 (Samin et al. 2011c: 1238). **South Khorasan:** Birjand, 6.2001 (Samin et al. 2011a: 3).

Remarks. The Holarctic *Stenus melanopus* is widely distributed throughout the western Palaearctic eastwards to China. The cited records from Northeast Iran are dubious as well as an old record from “Perse méridionale” (Fauvel 1873: 256), because, except for Turkey, the species is unknown from the Middle East and Central Asia.

***Stenus paludicola* Kiesenwetter, 1858**

Records. **Ardabil:** Ardabil, 6.2004 (Ghahari et al. 2009a: 1954). **Semnan:** Shahrud, 11.2010 (Hadian et al. 2011: 4).

Remarks. The area of distribution of the Pontomediterranean *Stenus paludicola* stretches over the Balkans, Anatolia, and the Levant. The existence in northwestern Iran is imaginable.

***Stenus pallitarsis* Stephens, 1833**

Records. **Gilan:** Rasht (Jarrige 1971: 498; cited by Samin et al. 2011b: 142).

Remarks. The area of distribution of *Stenus pallitarsis* stretches over the arboreal Palaearctic eastwards to East Siberia and China. In view of the distribution in Caucasia, Turkey, and Central Asia, the existence in Iran is conceivable.

***Stenus picipennis* Erichson, 1840**

Record. **Iran** (Schülke and Smetana 2015: 835).

Remarks. *Stenus picipennis* is widely distributed in Europe and the Mediterranean, but unknown from Turkey, the Levant, and Caucasia. In view of this distribution pattern the record for Iran in the current edition of the Catalogue of Palaearctic Coleoptera far east of the area of distribution of *S. picipennis* appears doubtful. The underlying reference for this country record, which was not yet cited in the first edition of the catalogue (Smetana 2004: 552), is unknown to us.

***Stenus planifrons planifrons* Rey, 1884**

Record. **Semnan** (Sakenin et al. 2010: 13).

Remarks. The nominotypical form of *Stenus planifrons* has a Pontomediterranean distribution in south-eastern Europe and Turkey. Considering the allopatry of subspecies, the record from Semnan is implausible, because the collecting site is situated deeply within the area of distribution of *S. planifrons robustus* in northwestern Iran and the South Caspian mountains (Fig. 7).

***Stenus pseudofossulatus* Scheerpeltz, 1960**

Record. **East Azarbaijan:** Arasbaran (Sakenin et al. 2008).

Remarks. This species was described from Afghanistan (Scheerpeltz 1960: 74) and since then never recorded again. Its existence in East Azarbaijan is doubtful.

***Stenus pusillus* Stephens, 1833**

Records. **Esfahan:** Lenjan, 8.2000 (Ghahari et al. 2009b: 1964). **Semnan:** Garmsar, 3.2011 (Hadian et al. 2011: 4).

Remarks. *Stenus pusillus* is widely distributed across Europe and the arboreal North Africa (Morocco). As the species was never recorded for western Asia and the Middle East, respectively, the presence in Iran is implausible.

***Stenus solutus* Erichson, 1840**

Records. **Fars:** Kazerun, 10.2002 (Samin et al. 2011a: 3); Shiraz, 5.2008 (Samin et al. 2011c: 1238).

Remarks. The area of distribution of the West Palaearctic *Stenus solutus* stretches from the British Isles as far east as Anatolia and Azerbaijan. Its existence in South Iran is doubtful.

***Stenus stigmula* Erichson, 1840**

Records. **East Azarbaijan:** Kaleybar, 8.2006 (Ghahari et al. 2009a: 1954). **Semnan:** Jangal-e Abr, 4.2011 (Hadian et al. 2011).

Remarks. In view of the confirmed distribution of the Pontomediterranean *Stenus stigmula* in Turkey and Transcaucasia, the records from northwestern Iran are plausible.

***Stenus subaeneus* Erichson, 1840**

Records. **Ardabil:** Meshkinshahr, 6.2007 (Samin et al. 2011c: 1238). **East Azarbaijan:** Arasbaran, 8.2005 (Samin et al. 2011a: 3).

Remarks. *Stenus subaeneus* is widely distributed throughout the arboreal Mediterranean and Europe as far east as Lebanon, Syria, and Turkey. The records from northwestern Iran are questionable.

***Stenus turbulentus* Bondroit, 1912**

Records. **Semnan** (Sakenin et al. 2010).

Remarks. *Stenus turbulentus* has a restricted distribution in Greece, Turkey, Cyprus, and Israel. The existence of this species in North Iran is doubtful.

***Stenus umbricus* Baudi di Selve, 1870**

Records. **Khuzestan:** Ahvaz, 4.2007 (Samin et al. 2011c: 1238); Dezful, 5.2003 (Samin et al. 2011a: 3).

Remarks: In view of the restricted distribution of *Stenus umbricus* in France (Corse), Switzerland, and Italy, the record from Khuzestan is certainly based on a misidentification and here rejected.

Table 1. Faunal elements of the subfamily Steninae and genus *Scopaeus* in Iran with species numbers and percentage of species in each group.

Steninae			Scopaeus		
faunal element	species number	%	faunal element	species number	%
Pontomediterranean	14	20.29	Iranian	10	33.33
Hyrcanian	11	15.94	Irano-Anatolian	5	16.67
Caspian	7	10.14	Syrian	3	10
Holomediterranean	6	8.69	Holomediterranean	2	6.67
Syrian	6	8.69	Pontomediterranean	2	6.67
Trans-Palaeartic	5	7.25	Caspian	2	6.67
Turkestanian	5	7.25	Hyrcanian	2	6.67
Iranian	4	5.80	Trans-Palaeartic	1	3.33
Holarctic	4	5.80	Palaeotropic	1	3.33
Irano-Anatolian	4	5.80	South Iranian	1	3.33
West Palaeartic	3	4.35	Sindian	1	3.33
Palaeotropic	0	0	West Palaeartic	0	0
Sindian	0	0	Holarctic	0	0
South Iranian	0	0	Turkestanian	0	0
Species number	69	100	Species number	30	100

2. Biogeographical analysis of the *Stenus* and *Scopaeus* fauna of Iran

As a result of this study, a total of 69 species of Steninae is recorded for Iran, the following of which represent new country records: *Dianous coerulescens korgei*, *Stenus bicornis*, *S. butrintensis*, *S. cicindeloides*, *S. c. comma*, and *S. hospes*.

As shown in Table 1, the distribution of 76.8% of the Iranian Steninae species can be interpreted by the glacial refuge hypothesis (28.98% faunal elements of polycentric Holomediterranean glacial refuge, 26.08% of Caspian refuge including Hyrcanian subregion, 8.7% of Syrian refuge, 7.25% of Turkestanian refuge and 5.8% of Iranian refuge). The Irano-Anatolian type of distribution comprises 5.8% of the species. About 17.4% of the Steninae of Iran are more widely distributed and show West Palaeartic, trans-Palaeartic, and Holarctic distribution pattern. Almost the same percentage (73%) of the *Scopaeus* species in Iran shows a distribution pattern which is in accord with the glacial refuge theory: 33% are faunal elements of the Iranian glacial refuge, 13% elements of the Holomediterranean refuge, 13% Caspian elements, 10% Syrian elements and 3.3% Sindian faunal elements. The distribution pattern of 26% of the *Scopaeus* known to occur in Iran cannot be interpreted by the glacial refuge hypothesis, 17% of which are endemic to restricted areas within the Irano-Anatolian highlands.

The results obtained from the biogeographical analysis of the distributional pattern of the subfamily Steninae in Iran are shown in Tables 2, 3 and Fig. 25. No records of *Stenus* were available from the arid plains of the Iranian highlands and North Baluchestan. From the 69 species included in the data matrix, 40 species (57.97%) occur in the Caspian wet forest region. This area in the Caspian

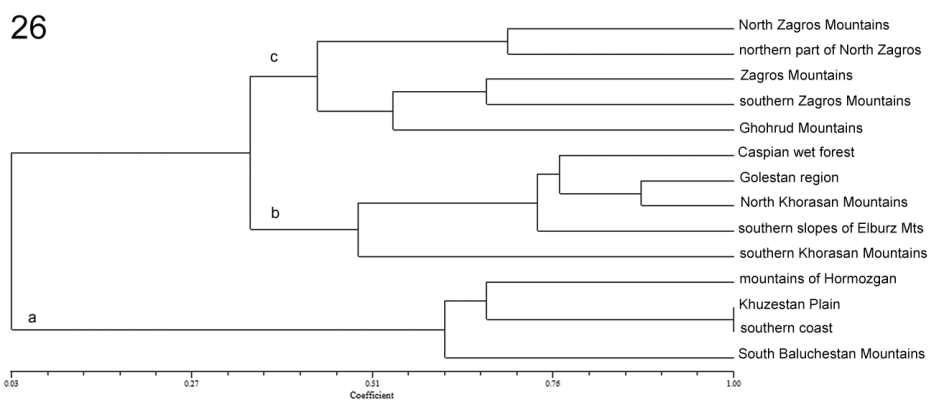
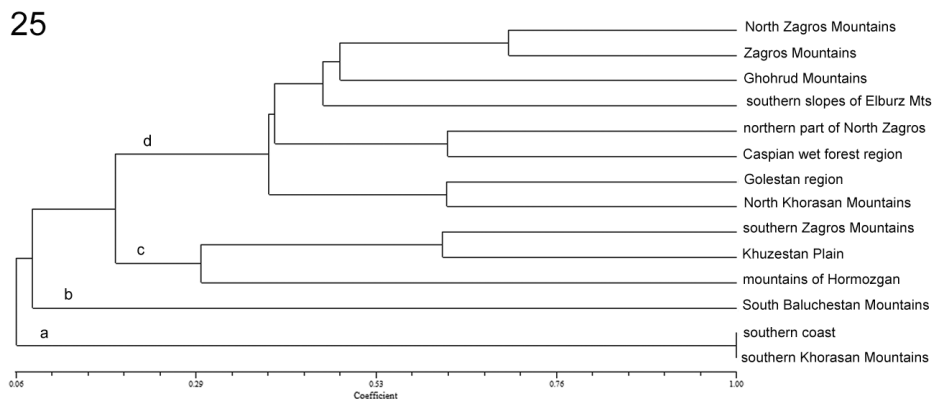
plain and the adjacent forest zone of the northern slopes of the Elburz and Talish Mountains, which is known as the Hyrcanian district of the Hyrcano-Euxine subregion of the Euro-Siberian temperate forest belt, bears the highest diversity of *Stenus* species in Iran including eleven endemics. De Lattin (1951: 208–211, 1957: 388, 1967: 322) considered this region as the eastern part of the Caspian glacial refuge in the Pleistocene. With 35 species, the northern part of the Northwest Iranian mountain region (NNW) is the second speciose region (Table 2). This area mainly matches the Iranian part of the Lesser Caucasus. The valleys and northeastern mountain slopes in this area constitute the Caucasian part of the Caspian glacial refuge proposed by de Lattin (1951, 1957). The least speciose region is the coast of the Persian Gulf and the Oman Sea in South Iran. As shown in Fig. 25, the low similarity among the northern and southern regions suggests the relative isolation and independency of their faunas. The analysis yields four different biogeographical clades (Fig. 25).

The clade a “southern Coast + South Khorasan region” is, however, likely to be an artifact, because the close similarity between these regions is caused by only one common species, *S. turk*, and not by a joint biogeographical history or habitat resemblance.

South Baluchestan, clade b, comprises *S. erythronemus* only. It is an outlier to the clusters with higher species numbers. Considering the arid character of this region, the existence of a rich *Stenus* fauna in South Baluchestan is not probable. Obviously, the diversity of the Steninae in Iran decreases considerably towards the eremial south and southeast owing to the increase of aridity and salinity of freshwater ecosystems.

The clade c comprises the mountains of Hormozgan, the southern Zagros Mountains in Fars, and the Khuzestan Plain with a total of nine species (13%). Southern Zagros Mountains and Khuzestan Plain show a high similarity (about 60%) with Hormozgan as an outlier with less similarity to them. It seems that appropriate habitats for *Stenus* species diminish towards the east and south, because the number of permanent water bodies decreases and their salinity rises.

The northern clade, d, constitutes the largest cluster of biogeographical regions of Iran. It comprises the northern, western, and central parts of the country, which reveal the least similarity with the southern clusters. It is made up of two sister clades. The first consists of Golestan and North Khorasan with 20 species and about 60% similarity. The next comprises the central and northern Zagros (37 species) with the Ghohrud Mountains and the southern Elburz as outliers with 40 species and is the sister clade to the other, which includes the Hyrcanian (Caspian) wet forest region of the Talish and the Elburz Mountains and the northwestern part of the Iranian mountain ranges with 52 species (about 75% of the Iranian Steninae). This significantly higher diversity impressively reflects the strong impact of the Pleistocene refuges proposed for these regions by de Lattin (1957, 1967). Before we conducted the cluster analysis, we suspected that the species composition of the



Figures 25–26. Cladograms of Dice similarity values between geographical subdivisions of Iran. An average linkage cluster analysis (UPGMA) was used to test cluster similarities. Different clades are indicated by small letters. **25.** Steninae fauna; **26.** *Scopaeus* fauna.

Table 2. Qualitative listing of Steninae species collected in Iran. See Material and methods section for abbreviations of the geographical subdivisions.

Species/ Regions	NZ	NNW	C	G	SE	NKh	Z	SZ	Gh	Hm	SB	Khu	SC	SKh
<i>Stenus aereus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. affaber</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. alienigenus</i>	1	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>S. arabicus</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>S. araxis</i>	1	1	0	1	1	1	1	1	1	0	0	0	0	0
<i>S. armeniacus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. asiaticus</i>	1	1	1	1	0	1	0	0	0	0	0	0	0	0
<i>S. ater</i>	1	1	1	1	0	1	0	0	0	0	0	0	0	0
<i>S. atratulus</i>	1	1	1	1	0	1	1	0	1	0	0	0	0	0
<i>S. barbarae</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. bernhauerianus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>S. bicornis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. biguttatus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. brunnipes</i>	0	0	1	1	0	1	0	0	0	0	0	0	0	0
<i>S. butrintensis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. callidus</i>	1	1	1	0	1	0	1	1	1	1	0	1	0	0
<i>S. canaliculatus</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. caspius</i>	1	1	1	1	0	1	0	0	0	0	0	0	0	0
<i>S. cautus</i>	1	1	1	0	0	0	1	0	1	0	0	0	0	0
<i>S. cicindeloides</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. claritarsis</i>	1	1	1	0	0	0	1	1	0	0	0	1	0	0

Species/ Regions	NZ	NNW	C	G	SE	NKh	Z	SZ	Gh	Hm	SB	Khu	SC	SKh
<i>S. comma comma</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. confrater</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. crassus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. darius</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. derwisch</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. erythrocnemus</i>	1	1	1	1	1	0	1	1	1	0	1	0	0	0
<i>S. formicetorum</i>	1	1	1	0	0	0	1	0	0	0	0	0	0	0
<i>S. formicatus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. fuscicornis</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. ganglbaueri</i>	0	1	1	0	1	1	0	0	1	0	0	0	0	0
<i>S. guilanensis</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. heinzianus</i>	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>S. hospes</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. hypoproditor</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. ignotus</i>	0	1	1	0	0	0	1	0	0	0	0	0	0	0
<i>S. incrassatus</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. intricatus zoufali</i>	1	1	1	1	0	1	1	0	1	0	0	0	0	0
<i>S. kambyes</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. latifrons</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. lenkoranus</i>	0	1	1	0	1	0	1	0	0	0	0	0	0	0
<i>S. limicola</i>	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>S. machulkai</i>	1	1	1	1	0	0	1	0	0	0	0	0	0	0
<i>S. maculiger</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. martensi</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. medus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>S. mongolicus</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	0
<i>S. morio</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. nodipes</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. ochropus</i>	1	1	0	0	1	0	1	1	0	0	0	0	0	0
<i>S. orientis</i>	0	0	1	0	0	0	1	1	0	0	0	1	0	0
<i>S. parciar</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. peripherus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. persicus</i>	1	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. picipes</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. pieperi</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. piscator</i>	1	0	0	0	1	1	1	1	1	0	0	1	0	0
<i>S. planifrons robustus</i>	1	1	1	0	1	1	1	1	0	0	0	0	0	0
<i>S. proprius</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>S. providus providus</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>S. resslis</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. schah</i>	1	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>S. similis</i>	1	1	1	0	0	0	1	0	0	0	0	0	0	0
<i>S. skoraszewskii</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>S. taurus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. turk</i>	1	0	0	1	1	1	1	0	1	0	0	0	1	1
<i>S. viti</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>S. wittmeri</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Dianous coerulescens</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Species number	27	35	40	15	14	14	30	9	11	1	1	4	1	1
Percentage	39.13	50.72	57.97	21.74	20.29	20.29	43.49	13.04	15.94	1.45	1.45	5.80	1.45	1.45

Golestan region would be similar to that of the Caspian region as the Caspian wet forest reaches Gorgan, though it gradually becomes dryer there towards the east. Surprisingly, these geographical units appear in two different biogeographical clades, which reflect the low faunal similarity of less than 40%. Golestan is grouped with North Khorasan, while the Caspian region and the Northwest Iranian

mountains (similarity 60%) constitute a cluster with the southern slope of the Elburz, the northern and Central Zagros and the Ghohrud Mountains (similarity <45%). Thus, the composition of the stenine fauna of Iranian Caucasia is very similar to that of the northern slopes of the Elburz Mountains. This result strongly supports the Caspian glacial refuge of de Lattin (1951: 208–210, 1957: 388).

Table 3. Number of Steninae faunal elements in each geographical unit. See Material and methods section for abbreviations of the geographical subdivisions.

	NZ	NNW	C	G	SE	NKh	Z	SZ	Gh	Hm	SB	Khu	Sc	SKh
Pontomediterranean	7	8	7	2	3	2	9	2	3	1	0	1	0	0
Hyrceanian	0	0	10	2	0	0	0	0	0	0	0	0	0	0
Caspian	4	6	7	4	3	2	2	1	0	0	0	1	0	0
Holomediterranean	3	4	6	3	1	3	1	0	1	0	0	0	0	0
Turkestanian	2	1	1	2	2	4	1	0	1	0	0	0	1	1
Trans-Palaeartic	2	5	4	0	0	0	2	0	1	0	0	0	0	0
Syrian	3	1	2	0	2	2	6	4	2	0	0	2	0	0
Iranian	4	3	1	2	3	1	4	2	2	0	1	0	0	0
Holarctic	1	3	2	0	0	0	2	0	0	0	0	0	0	0
West Palaearctic	1	2	0	0	0	0	1	0	0	0	0	0	0	0
Irano-Anatolian	0	2	0	0	0	0	2	0	1	0	0	0	0	0
Species number	27	35	40	15	14	14	30	9	11	1	1	4	1	1

Table 4. Qualitative listing of *Scopaeus* species collected in Iran. See Material and methods section for abbreviations of the geographical subdivisions.

Species/ Regions	NZ	NNW	C	G	SE	NKh	Z	SZ	Gh	Hm	SB	Khu	SC	SKh
<i>Scopaeus alborzensis</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	0
<i>S. azerbaijani</i>	0	0	1	1	0	1	0	0	0	0	0	0	0	0
<i>S. borumandi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. cameroni</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. chalcodactylus</i>	1	1	1	1	1	1	1	0	1	0	0	0	0	0
<i>S. debilis</i>	1	1	0	1	1	1	1	1	1	0	0	0	0	1
<i>S. ebneri</i>	1	1	0	0	1	0	1	1	1	0	0	0	0	0
<i>S. farsensis</i>	0	0	0	0	0	0	1	1	1	0	0	0	0	0
<i>S. femursetosus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. filiformis</i>	0	0	0	0	0	0	0	1	0	1	1	1	1	0
<i>S. gracilis</i>	1	1	1	1	1	1	1	1	1	0	0	0	0	1
<i>S. hyrcanus</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>S. iranensis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. kermanensis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. khnזורiani</i>	1	1	0	0	0	0	1	1	0	0	0	0	0	0
<i>S. kurdistanus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. laevigatus</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	1
<i>S. mariae</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. minimus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. mutatus</i>	0	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>S. pakistanensis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>S. persicus</i>	1	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>S. qohrudensis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. schillhammeri</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>S. serriae</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>S. signifer</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>S. similis minor</i>	0	0	1	1	1	1	0	0	0	0	0	0	0	1
<i>S. stramineus</i>	0	0	0	0	0	0	0	1	1	1	0	0	0	0
<i>S. ulughdaghensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. zagrosensis</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Species number	12	11	9	8	8	8	11	10	8	2	2	1	1	4
Percentage	40	36.67	30	26.67	26.67	26.67	36.67	33.33	36.67	6.67	6.67	3.33	3.33	13.33

The results of the cluster analysis of the Iranian species of *Scopaeus* are provided in Table 5 and Fig. 26. Like in *Stenus*, no species were found in the central Deserts and North Baluchestan. While the riparian species are not expected to occur in the deserts, the lack of records from

North Baluchestan is a collecting artifact. The most speciose region is North Zagros with 12 species (40% of Iranian *Scopaeus*), which belong to the Mediterranean type of distribution or are Irano-Anatolian endemics. Like in *Stenus*, the clades a and b + c represent the southern and

Table 5. Number of *Scopaeus* faunal elements in each geographical unit. See Material and methods section for abbreviations of the geographical subdivisions.

	NZ	NNW	C	G	SE	NKh	Z	SZ	Gh	Hm	SB	Khu	Sc	SKh
Iranian	1	0	2	2	2	2	6	3	3	0	0	0	0	1
Irano-Anatolian	4	3	1	0	1	0	1	1	0	0	0	0	0	0
Syrian	2	2	0	0	1	0	1	2	1	0	0	0	0	0
Caspian	1	2	2	2	2	2	1	0	1	0	0	0	0	0
Hyrceanian	0	0	2	2	0	1	0	0	0	0	0	0	0	0
Holomediterranean	2	2	1	2	2	2	2	2	2	0	0	0	0	2
Pontomediterranean	2	1	1	0	0	0	0	0	0	0	0	0	0	0
Sindian	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Paleotropic	0	0	0	0	0	0	0	1	0	1	1	1	1	0
Trans-Palaeartic	0	1	0	0	0	1	0	0	0	0	0	0	0	1
South Iran and Oman	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Species number	12	11	9	8	8	8	11	10	8	2	2	1	1	4

northern regions of Iran with well separated *Scopaeus* species spectra. The southern cluster (a) of consists of Hormozgan, Khuzestan Plain, and southern Coast with South Baluchestan as outlier. Though the close affinity between Khuzestan Plain and southern Coast is expected, we believe that more collecting activity will bring new insights to their actual biogeographical relationships. These southern regions are the least speciose areas. As in *Stenus*, the *Scopaeus* fauna shows a gradient of decreasing species diversity towards the increasingly eremial east and south – a fact which can be easily explained by the strong adaptation of both genera to humid and riparian habitats.

The northern cluster, b + c, with 25 species the most speciose clade in the *Scopaeus* cladogram, is composed of two major subgroups.

The first (clade b) comprises the South Caspian and Turkmeno-Khorasanian mountain ranges. South Khorasan constitutes the outlier of the remaining geographical units of this clade. The southern Elburz is the outlier of the Caspian or Hyrcanian Region, Golestan, and North Khorasan. The two latter units reveal a significant faunal similarity (>85%), which is even higher than the considerable similarity of 60% in the Steninae.

The second subgroup (clade c) comprises Northwest Iran, the Zagros, and the Qohrud Mountains. It is made up of two sister clades with significant faunal similarity, a northern one comprising the Northwest and the adjacent North Zagros and a southern one with the Central and South Zagros and their outlier Ghohrud Mountains. The *Scopaeus* fauna shows a higher similarity between the northern, central, and southern parts of the Zagros compared to the *Stenus* fauna with a high similarity of the South Zagros and the southern regions of Khuzestan and Hormozgan.

Discussion

The present study confirms previous findings (e.g. Aiydov and Frisch 2014: 75; de Lattin 1949, 1951; Frisch 2010:

189–196; Naumann 1987) and contributes additional evidence that the distributional pattern of many species in Iran can be interpreted by the Pleistocene refugial centers in the West Palaeartic. As shown in Table 1, about 78% of the Steninae and 73% of the *Scopaeus* species of Iran are endemic to these refuges or dispersed out of them after the last glacial period.

The results reveal that the composition of the Steninae fauna in Iran is most strongly influenced by faunal elements of the Mediterranean refuge (Table 3). Like the tropics, the Mediterranean Basin is considered as one of the world's biodiversity hotspots (Ribera et al. 2004: 179). Most of the Mediterranean *Stenus* species in Iran dispersed from the Pontomediterranean subrefuge in the northeastern Mediterranean. Mediterranean species are distributed in most of the investigated geographical units of Iran and have the strongest influence on the fauna of the Zagros Mountains. The northwest-southeast trending Zagros chains, a part of the Alpine-Himalayan orogenic system (Mouthereau 2011: 728) and the Irano-Anatolian mountain barrier, extend from the East Anatolian fault in eastern Turkey to southern Iran and prevent the dispersal of many Steninae species towards the east both as a barrier and owing to their Mediterranean climate. The Mediterranean influence on the Iranian fauna of *Scopaeus* is lower compared to the Steninae, but nevertheless the pervasive effect of Mediterranean species cannot be denied in most geographical units. The *Scopaeus* fauna of Iran is rather characterized by a high percentage of endemics, which are restricted to particular mountain ranges mainly in the Zagros Mountains. Like in *Scopaeus*, Mediterranean faunal elements notably influenced the stenine fauna of the Hyrcanian region and northern Khorasan (Table 3, 4). The similarity of the species composition of the Steninae fauna of the Zagros, the Ghohrud Mountains, and the southern slopes of the Elburz (see Fig. 25) is mainly caused by Mediterranean and Iranian faunal elements. Likewise, the similarity of the *Scopaeus* fauna of the central and southern Zagros Mountains and the Ghohrud Mountains is caused by the same Mediterranean species,

though the latter mountain range also includes *Scopaeus* species with an endemic Iranian distribution.

The second most frequent biogeographical element of the Iranian Steninae is the Caspian faunal element with a percentage of about 27%. Compared to the more widespread Holo-Caspian species (10.14%), which dispersed from the Caspian refuge from the Crimea to the southern shore of the Caspian Sea, however, the Hyrcanian faunal element with about 16% of the species has a greater impact on the stenine fauna of Iran. The Hyrcanian faunal elements originate from the Hyrcanian forest zone in the South Caspian plain and the northern slopes of the South Caspian mountains, the eastern subunit of the Caspian refuge. According to Frisch (2006: 262), the Hyrcanian subregion is a unique speciation center judging from the high numbers of endemics. Our results actually prove that it moreover constitutes the most significant center of origin for *Stenus* in Iran. The Caspian faunal elements constitute the main causative factor for the high similarity between Iranian Caucasia and the Hyrcanian region (more than 60%), and moreover strongly affect the *Stenus* fauna of the Golestan region and the northern Zagros Mountains. Although the Caspian *Scopaeus* have a considerably lower impact on the species diversity of the Iranian fauna (about 13%) compared to *Stenus*, some of them are relatively widespread and dispersed over geographical units of Iran adjacent to the Hyrcanian zone. *Scopaeus chalcodactylus* Kolenati even spread southwards to the mountains of Kerman.

Besides the Mediterranean and Caspian species, the widespread Holarctic, trans-Palaearctic, and West Palaearctic species (about 18% of the Iranian fauna) also have a great impact on the composition of the Steninae fauna of Iran, mostly in the more humid, temperate north and northwest of the country due to suitable habitats. On the contrary, the percentage of trans-Palaearctic species is much lower in the Iranian *Scopaeus* fauna (Table 1).

The Syrian and Iranian refuges have their greatest influence on the Steninae fauna in the central, southern, and northern Zagros Mountains and almost the same effect on the *Scopaeus* fauna of these regions.

We employed the geographical units of Iran after Petrov (1955) for our biogeographical analysis in order to have a tested base to compare our results with those of other recent works, which are based on the same subdivisions (e.g. Dubatolov and Zahiri 2005, Matov et al. 2008). We did without comparing our results, however, to cladistic biogeographical contributions which employed different geographical subdivisions of Iran, e.g. Burckhardt and Lauterer (1993). Although the studies of Dubatolov and Zahiri (2005) and Matov et al. (2008) were carried out on Lepidoptera, the results were not compatible with each other in many aspects probably due to the different habitat and niche preferences of the studied insects. Our results correspond with each of those studies in some aspects. For example, the heliothine faunas in the southern Caucasus and the Hyrcanian region show high resemblance (Matov et al. 2008: 32), a result

which matches the close affinity between the Steninae faunas of Iranian Caucasia and the Hyrcanian region in our study, both of which are subdivisions of the Caspian glacial refuge sensu de Lattin (1967: 322).

As the results obtained by Dubatolov and Zahiri (2005: 509), our cluster analysis yields a high similarity (more than 50%) between the faunal composition of Gorgan and North Khorasan, which seems to be caused by a similar composition of Mediterranean, Caspian, Turkestanian, and Iranian species.

The distribution patterns of the stenine fauna of Iran as well as their zoogeographical relationships and degree of endemism were unknown prior to this study. With the example of these riparian rove beetles we demonstrated, that the Mediterranean Pleistocene refuge performs a huge influence on the recent fauna of this country – a result we did not expect in view of the geographical position of Iran within the Middle East and at the interface of the Palaearctic, Afrotropical, and Oriental zoogeographical regions. Our interesting results significantly contribute to a better knowledge of the biogeography of Iran and highlight the great importance of the Mediterranean for the understanding of the biogeography of the entire Middle East and beyond.

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Supplementary material 1

Distribution data of Steninae species from Iran.

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Data type: Excel

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