Bonn zoological Bulletin 69 (2): 309–366
2020 · Steenis J. van et al.
https://doi.org/10.20363/BZB-2020.69.2.309

ISSN 2190–7307
http://www.zoologicalbulletin.de

Research article

urn:lsid:zoobank.org:pub:34A9FC4A-EBEC-4617-A91B-C3D767E24A11

Faunistical overview of the European species of the genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 (Diptera: Syrphidae)

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Received: 03.08.2020
Accepted: 15.10.2020

Corresponding editor: X. Mengual
Published: 27.10.2020

Abstract. The European fauna of the genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 is reviewed. The distribution and phenology based on extensive literature and database research are provided. The biology of adults as well as larval habitats are treated. An illustrated key is presented for easy identification of the adults, including three species known from adjacent Mediterranean countries. A key to the larvae, based on the available literature, is also provided. The data originate from a study of available literature, from several databases and from the private collections of the authors. The data are compiled into one large dataset in which all the available information is gathered together with the source of the data. Based on the biology and trend analysis for each species it is indicated whether they show stable, fluctuating or extremely fluctuating populations. The habitat preferences of the adults and larvae are used to discuss possible threats to each of the species for future survival. Finally, the main habitat of all species is discussed from a conservation point of view.

Key words. Distribution, biology, habitat threats, trend analysis, identification key, larvae.

INTRODUCTION

The genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 are found in the Holarctic and Oriental realms with 44 species of *Brachyopa* and five species of *Hammerschmidtia* currently described (Stackelberg 1952; Chu 1994; Van Steenis 2015; Skevington et al. 2019). In Europe, 20 species of *Brachyopa* and two species of *Hammerschmidtia* are known to occur (Speight 2020). Except for one species known from the Oriental realm, the occurrence of both genera is concentrated in the Nearctic subrealm and in the Mediterranean and Circumboreal region, and in the Caucasian and Manchurian provinces within the Palearctic subrealm. All these biogeographical areas are characterized by the occurrence of coniferous and deciduous, broadleaved forest (Udvardy 1975; Reemer et al. 2009; Van Steenis 2015; Skevington et al. 2019). Central Europe, as part of the Circumboreal and Mediterranean regions, harbours a high number of species and several of them are endemic to this region (Kaplan & Thompson 1981; Kassebeer 2000a, 2000c, 2001, 2002; Doczkal & Dziock 2004; Van Steenis & Van Steenis 2014; Pérez-Bañón et al. 2016).

Adults of *Brachyopa* and *Hammerschmidtia* superficially resemble dung-flies (Scatophagidae) and some Anthomyiidae and Muscidae (Torp 1994; Rotheray 1996). They can be separated from other Syrphidae by the following combination of characters: small to medium sized (4–12 mm), rather broad, mainly brown, brown-red or black coloured flies with relatively small heads and a yellow face; postpronotum pilose; eyes bare; basoflagellomere round to oval, third antennal segment often with clearly visible sensory pit; arista subbasal, bare to long plumose; vein R_{4+5} straight; crossvein rm before middle of discal cell; vein M_1 oblique to vein R_{4+5} (Meigen 1822; Schummel 1834; Thompson & Rotheray 1998).

Larvae occur in a diverse array of microhabitats associated with tree sap runs in or within dead or living trees. Some of the species are generalists and can be found in broadleaved as well as coniferous trees, while other species seem to have a more restricted tree preference (Lundbeck 1916; Hartley 1961; McLean & Stubbs 1990; Rotheray 1991, 1996; Sivova et al. 1999; Krivosheina 2005; Dussaix 2013; Ricarte et al. 2013). Adults, and especially the males, are regularly found patrolling damaged live or dead trees with sap runs or accumulations of sap, but also on trees, tree trunks or tree logs with no visible sap runs or any other visible damage. Flower visiting is observed regularly in most *Brachyopa* species at plants with abundant, "open" and generally white coloured flowers, such as species within the families Apiaceae and Rosaceae. The flight period is from March until July (Torp 1994; Bartsch et al. 2009; Reemer et al. 2009; Bot & Van de Meutter 2019). It is not unusual to find several species of *Brachyopa* simultaneously on the same flower or around trees with supposed sap runs (e.g., Wakkie et al. 2011; Van Steenis & Van Steenis 2014; Mutin et al. 2016).

Larvae can be separated from other Syrphidae by the following characters: dorso-ventrally flattened; gradually elongating projections along lateral margin; posterior respiratory process dark, longer than broad and marked with pits and striations, four groups of sensilla anterior to anal opening (Krivosheina & Mamaev 1967; Rotheray 1996; Rotheray & Gilbert 1999; Krivosheina 2005, 2019; Pérez-Bañón et al. 2016).

Brachyopa larvae are slow-moving, possibly to avoid being detected by predators such as birds, carabid beetles and the larvae of other Diptera such as *Phaonia subventa* (Harris, 1780) (Muscidae) and *Systenus pallipes* (Von Roser, 1840) (Dolichopodidae) (Rotheray 1996). The larvae are disguised by being coated with dried sap, especially on the posterior part of the body. This sap hides the larvae from detection in the existing sap run by crypsis and possibly also by the virtual absence of gustatory and movement cues (Rotheray 1996). In general appearance they are similar to larvae of *Fannia* spp. (Fanniidae) and *Nosodendron fasciculare* (Olivier, 1790) (Coleoptera: Nosodendridae) with which they often share microhabitat. Some species can be very abundant in sap runs, with 100 larvae present in one sap-run, and some can tolerate desiccation better than others with survival after desiccation of 65% in *Brachyopa pilosa* Collin, 1939 against 95% for *Brachyopa insensilis* Collin, 1939 (Rotheray 1996).

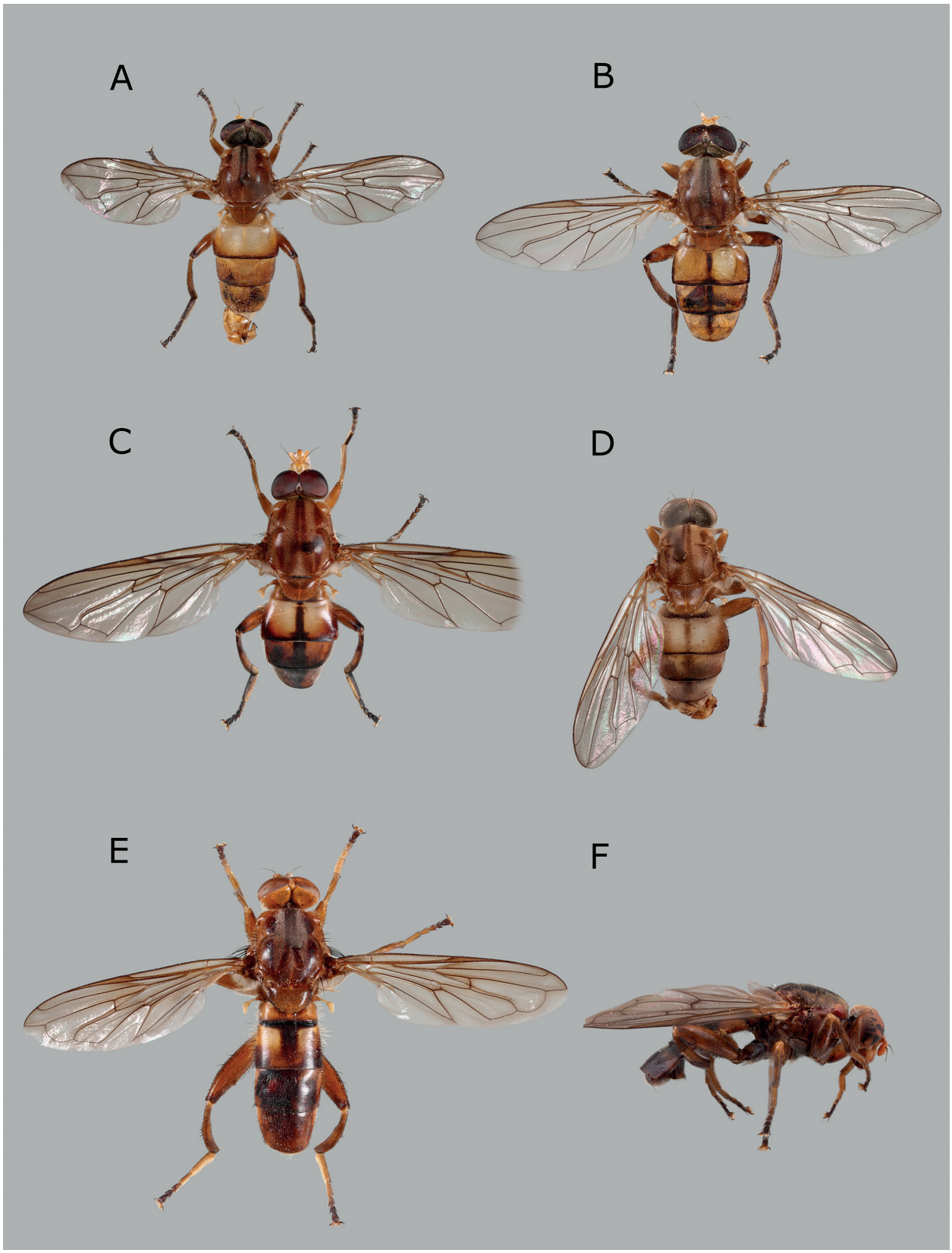

Fig. 1. Adult habitus, **A**–**E** dorsal view, **F** lateral view. **A**. *Brachyopa obscura*, male, Olloy-s-Viroin, Belgium. **B**. *B. testacea*, male, Engsbergen, Belgium. **C**. *B. vittata*, male, Eupen, Belgium. **D**. *B. zhelochovtsevi*, male, Tumnin, Russian Far East. **E**. *Hammerschmidtia ferruginea*, male, Fiby urskog, Sweden. **F**. *H. ingrica*, male, Bychika, Russian Far East.

Some authors have posed the question as to whether *Hammerschmidtia* is merely a subgenus of *Brachyopa* (Vockeroth & Thompson 1987; Speight 2020). Based on recent molecular studies (Skevington et al. 2019) these genera are clearly separated and this opinion is followed here. One species, *Brachyopa* (*Trichobrachyopa*) *tristis* Kassebeer, 2001, has been placed in a different subgenus (Kassebeer 2001) but no phylogenetic studies are available to support this classification.

The European species of the genus *Brachyopa* can be separated into two subgroups based on larval morphology and ecology. One subgroup (which includes *Brachyopa dorsata* Zetterstedt, 1837, *B. panzeri* Goffe, 1945 and *B. vittata* Zetterstedt, 1843) comprises larvae with a strongly developed anal segment living in the tunnels made by other animals, mainly Coleoptera (Lymexylidae). The other subgroup has larvae with a poorly developed anal segment which live in sap-runs or accumulations of sap under bark (Krivosheina 2005).

Adults can be separated morphologically into three subgroups based on the colour of the scutum, the length of the aristal pile and the presence of an antennal pit (Zetterstedt 1837; Kassebeer 2000a; Doczkal & Dziock 2004). The first subgroup comprises all species with red-brown scutum, plumose arista and large antennal pit: *Brachyopa obscura* Thompson & Torp, 1982, *B. testacea* (Fallén, 1817), *B. vittata* and *B. zhelochovtsevi* Mutin, 1998, with possibly *B. dorsata* and *B. panzeri* also belonging to this subgroup, or maybe forming their own group. Members of the second subgroup have a grey pollinose scutum, short pilose arista and a clearly visible and sometimes very large antennal pit: *Brachyopa pilosa***,** *B. plena* Collin, 1939 and *B. scutellaris* Robineau-Desvoidy, 1844. The species of the third and most species-rich subgroup have a grey pollinose scutum, bare arista and, at most, a small and weakly visible antennal pit: *Brachyopa atlantea* Kassebeer, 2001, *B. bicolor* (Fallén, 1817), *B. bimaculosa* Doczkal & Dziock, 2004, *B. cinerea* Wahlberg, 1844, *B. grunewaldensis* Kassebeer, 2000, *B. insensilis*, *B. maculipennis* Thompson, 1980, *B. minima* Vujić & Pérez-Bañón in Pérez-Bañón et al., 2016, *B. quadrimaculosa* Thompson in Kaplan & Thompson, 1981, *B. silviae* Doczkal & Dziock, 2004 and *B. vernalis* Van Steenis & Van Steenis, 2014. This last subgroup has previously been referred to as the *B. bicolor* group or, alternatively, the *B. quadrimaculosa* group (Kassebeer 2002; Doczkal & Dziock 2004; Pérez-Bañón et al. 2016). Further research is needed to establish monophyly of these morphological groups.

The starting point of this paper was the initiation of the IUCN European Syrphidae Red List and the first workshop held in Novi Sad, Serbia in April 2019. For this workshop preliminary distributional data, habitat preferences and possible threats were presented as basis for further evaluation of the species. This paper gives literature as well as original, new information on distribution, phenology and habitat preferences for the species of the genera *Brachyopa* and *Hammerschmidtia*. A short introduction is presented about population dynamics of some of the species. A literature review on habitat changes and threats is presented too. A key is presented for the known larvae and adults of the species. The key is based on literature and own observations on the adults. Each species is presented based on a fixed format with information from literature and own observations and discussion. This could be used for a final Red List assessment as required by the IUCN.

MATERIAL AND METHODS

The data presented here result from a merging of information from literature sources, online and offline databases, visits to museum collections as well as the acquisition of new data from private collections.

The terminology used and the way the specimens are measured is based on the comprehensive morphology list in Skevington et al. (2019).

For countries having a centralised database including faunistic data (e.g., Reemer et al. 2009), the data are incorporated in the central database of this study. Other resources are accessible online of which the following ones have been used for this study: Artportalen Sweden (https://www.artportalen.se/), Artsobservasjoner Norway (https://www.artsobservasjoner.no/), Diptera.info (https://diptera.info/forum/index.php), the Finnish Biodiversity Information Facility (https://laji.fi/en), Global Biodiversity Information Facility (https://www.gbif.org/, https://doi.org/10.15468/dl.7l1aax), Observation.org (https://observation.org/) including Waarneming (https://waarneming.nl/, https://waarneming.be/), National Biodiversity Network UK (https://species.nbnatlas.org/) and the National Biodiversity Data Centre Ireland (https://maps.biodiversityireland.ie/Dataset/159). The authors of this article have provided additional data from other resources that are not published or online, such as private collections, e.g., indicated as PJSA (private collection Jeroen van Steenis Amersfoort) and preliminary national checklists (e.g., Austria and Switzerland). Much additional data from literature sources is incorporated for which details are provided in the datafile rather than in the manuscript. All the literature consulted is listed in the reference section.

The following collections were visited and their records are incorporated in the database with reference to the relevant depository: FSUNS, University of Novi Sad, Faculty of Science, Department of Biology and Ecology, Novi Sad, Serbia; MEB, Museum of East Bohemia, Hradec Králové, Czech Republic; MMB, Moravian Museum, Brno, Czech Republic; MWBP, Museum of West Bohemia, Plzeň, Czech Republic; MZH, Zoological Museum Helsinki, Helsinki, Finland; NBC, Naturalis Biodiversity

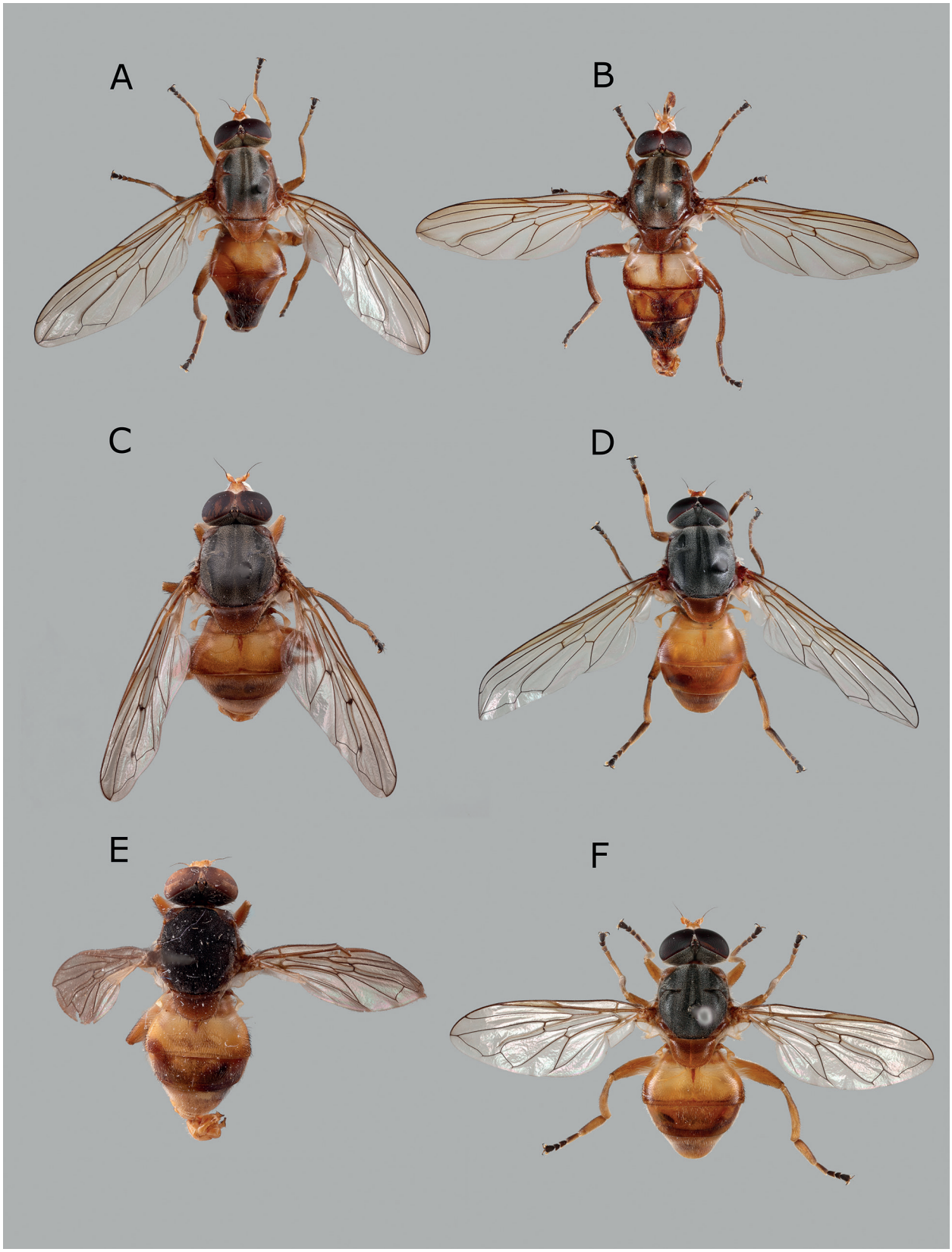

Fig. 2. Adult habitus, dorsal view. **A**. *Brachyopa dorsata*, male, Hessen, Germany. **B**. *B. panzeri*, male, Hestreux, Belgium. **C**. *B. maculipennis*, male, Fruška Gora, Serbia. **D**. *B. pilosa*, male, Drentsche Aa, the Netherlands. **E**. *B. plena*, male, Ioannina, Greece. **F**. *B. scutellaris*, male, Savelsbos, the Netherlands.

Center, Leiden, The Netherlands; NHM, Natural History Museum, London, UK; NRC, Nature Research Center, Vilnius, Lithuania; NMP, National Museum, Prague, Czech Republic; UMO, Oxford University Museum of Natural History, Oxford, UK; ZISP, Zoological Institute of the Russian Academy of sciences, Saint Petersburg, Russia; ZMSU, Zoological Museum of the Moscow State University, Moscow, Russia; ZMUC, Zoological Museum University, Copenhagen, Denmark.

The validity of several of the old literature records and some of the records from websites has not been verified by the authors. Due to name changes (Thompson 1980) and recently split species (Kassebeer 2000a; Doczkal & Dziock 2004; Van Steenis & Van Steenis 2014) several old records applied the wrong names such as *Brachyopa insensilis* and *B. bicolor* for *B. grunewaldensis* (Ricarte et al. 2013) or *B. insensilis* identified as *B. bicolor* (e.g., Claussen 1984; Kassebeer 1993). The name *B. conica* (Panzer, 1798) has been used for many species (Thompson 1980) and made the separation of *B. obscura* from *B. testacea* a puzzle (Torp 1979) until Thompson & Torp (1982) clarified this when describing *B. obscura*. The distinction of some species, especially between *B. dorsata* and *B. panzeri*, has been problematic (e.g., Reemer et al. 2007) particularly when based on photographs alone. These difficult identifications will possibly have affected some of the species distribution patterns. However, the most likely effect will be that it overestimates the common species while underestimating the rare species. This should be taken into account while reading the discussion under each species. In addition, several national Red Lists have been published and these have been discussed under each species, where relevant.

The information for each species is presented is a fixed format. The Distribution section lists the known worldwide distribution in general and the more specific European distribution. The European distribution is based on literature and own observations and we indicate if the species is here recorded as new country record. In the Biology section the information about the adult and larval biology is given. The information about biology from the literature is listed first, with all used references given, and new information is listed after. The flight period and altitudinal range are both taken from the species database and consists of information from literature and new observations. The section Population fluctuations are interpretations based on the literature, own observations and the known or suspected habitat preferences and, as such, it is a novelty of this work. The Remarks are used to highlight specific information about identification, taxonomy, explanation for its distribution or other noteworthy comments; most of this information has not been published before. The Red List section gives an overview of the published Red List status of the species in several European countries followed by a novel discussion on the possible threats for this species in Europe as a whole.

The habitat and habits of the species are taken from literature and extended by personal observations and by notes in the consulted online and offline databases. For each species the published information is given first with references, followed by the unpublished information without reference, which is referred to the main database (see below).

The names of the food plants are taken from the literature and the current name and authorship for each taxon is in line with the Plant List (WFO 2019).

Illustrations

The illustrations of pinned specimens were made using a digital SLR camera. The camera setup consisted of a Canon 6D, Canon MPE-65 macro lens, a transmitter directing two flashes and a macro rail. Helicon Focus 7.6.1 stacking software was used and photos were edited in Adobe Photoshop® 20.0.4. For the composition of the illustrations of the basoflagellomere, a similar setup was used with the addition of a Canon Extender EF 2x III and a Yongnuo YN14EX macro ring lite as light source. With the aid of a Cognisys StackShot rail, multiple pictures were taken which were stacked with Zerene Stacker 1.03. The illustrations of immature stages are taken from the literature, as acknowledged under each figure. All illustrations were further edited and assembled into the figures with GNU Image Manipulation Program 2.8.22.0.

Databasing and distribution maps

The diverse datasets available from online databases, collections, literature citations, institutional and private databases and data sheets were converted to a standardized database format designed to provide distribution maps and flight activity diagrams for this paper (refered as database hereafter).

The different coordinate systems were converted to geodetic WGS84 coordinates. If no coordinates were available in the dataset, on specimen labels or literature citations, the locality information on the label / dataset / citation was used to search Google Earth® (www.google.nl/intl/nl/earth) and GeoNames (www.geonames.org) for coordinates. In uncertain cases this was verified by searching for the coordinates through the Google search engine (www.google.com).

Some records are based on province lists. In this case, the coordinates of the centre of the province are used. Outliers on the maps were checked carefully, whether the given coordinates correlate with the label/record information.

Using records from different sources has a risk of duplicates with (slightly) different coordinates, for instance coordinates of the precise location and coordinates of the centre of the province. For the distribution maps it does not matter that much as long as duplicate records have

approximately the same coordinates, especially for areas with a high number of records. For species with fewer than 100 records, the records were checked manually: same date, observer and location description was used as an indication of a duplicate. If all information in other fields of these records supports this evidence, the derivative record was marked as a duplicate of the first record. This was also done in areas with only a few records: the Mediterranean, Ireland, Fenno-Scandia North of the Polar circle and Russia.

For the flight activity diagrams the database was queried for records of adults with a single observation datum (start date = end date). This was summed per week starting January 1st and plotted as moving average of two weeks. Outliers were checked manually and corrected or rejected when information in other fields of the record provided evidence to do so.

Altitude information from labels, literature records, databases and datasheets were used to give an altitudinal range per species. Elevations in feet were transferred to metres and all subsequent elevations are expressed in metres above sea level.

All data are included in the distribution maps, except for those marked as duplicates. The distribution maps are made in QGIS 3.10.6 with Natural EarthII (@naturalearthdata.com) as background. The country borders in the maps are from ©EuroGeographics for the administrative boundaries. Records are placed in the distribution maps in order of year of observation, with the most recent observation on top of older ones. Records with no given date are represented with a cross; records before 1950 are represented with an open symbol (white), records between 1950 and 1999 are represented with an open symbol with a central dot, and records from 2000 onwards are represented as filled symbols. Records with doubtful locality data are represented with an open symbol with a question mark.

RESULTS

Population dynamics

Only few published papers deal with the temporal dynamics of populations of the genera *Brachyopa* or *Hammerschmidtia* (Nilsson et al. 2007, 2012; Rotheray et al. 2008, 2014). Based on these papers and the known or suspected larval habitat, deductions can be made on the fluctuation in the number of populations and their density.

In the Scottish Highlands several populations of *Hammerschmidtia ferruginea* (Fallén, 1817) have been investigated and the number of populations and population sizes varied greatly over the years (Rotheray et al. 2008). In that work, authors discussed the decline and rise in number of populations from as many as 13 down to 5, and back up to 8 over a period of 16 years. These fluctuations were caused by randomly occurring storms and coincided with the number of fallen trees, with an increase in populations after a delay of 2–5 years, each of which then lasts for 1–3 years (Rotheray & MacGowan 2000; Rotheray et al. 2014). These population fluctuations are likely to be more extreme in areas with scattered forest patches of small size, because only one locality in Scotland was found to hold stable populations when monitored from 1990 onwards (Rotheray & MacGowan 2000; Rotheray et al. 2008). The size of the forest patches with stable populations from 1990 to 2008 was between 5 and 25 ha, and the overall mean dispersal distance was measured to be 1 km, with a maximum of 5 km (Rotheray et al. 2014). A single forest with a size of more than 15 ha seems to be the lower limit for continuous survival. The number of logs is crucial for survival, and although one single fallen log can produce as many as one thousand hatched adults, the number of usable trees each year should be 3–4 at a minimum (Rotheray et al. 2008).

Similar population fluctuations have been observed for both *Brachyopa* and *Hammerschmidtia* at Stenbrohult, Djäknabygd, Sweden as well (Nilsson et al. 2007, 2012). At this 17-ha site with 7 ha of forest, *Hammerschmidtia ferruginea* and seven species of *Brachyopa* were found in large numbers between 2007 and 2010 after a storm in 2005 created suitable larval habitat. This was especially so for the species supposedly dependent upon wet decay in fallen logs or in standing dead trees, such as *Brachyopa obscura* and *Hammerschmidtia ferruginea*, both of which showed remarkably high numbers of individuals present compared to other sites in Sweden.

Species depending on sap runs on living trees (e.g., *Brachyopa bicolor*, *B. insensilis* and *B. minima*) are most likely to exhibit extreme fluctuations dependent upon the availability of suitable old trees (Sjuts 2004; Pérez-Bañón et al. 2016). In Great Britain *Brachyopa insensilis* suffered from loss of suitable larval habitat (slime fluxes on *Ulmus* spp.) due to the Dutch Elm disease causing most trees to die (Stubbs & Falk 1996). On the island of Lesvos, *B. minima* was only found on one single sap run on a *Populus nigra* L. between the years 2005 and 2011: by 2013 the tree was almost completely healed (Pérez-Bañón et al. 2016) with only a few larvae found by that time.

Another group of *Brachyopa* species (e.g., *B. dorsata*, *B. testacea* and *B. vittata*), which develop in trees with tunnels of various saproxylic insects and in tree stumps with wet decay, have a more long lived larval habitat and seem less dependent on infrequent natural storms (Löhr 1992; Krivosheina 2005). However, they are likely to benefit from the regular felling of trees during forest management, as is the case for *Blera fallax* (Linnaeus, 1758) (Rotheray & MacGowan 2015).

Some species, e.g., *Brachyopa bicolor*, have benefited strongly from massive planting of fast-growing poplars

along roads. Such trees are often pruned and inhabited by goat moth caterpillars (*Cossus cossus* Linnaeus, 1758), resulting in the frequent presence of sap runs and suitable conditions for dispersion.

Besides storms and forest management, diseases causing damage to trees can be a major factor influencing population fluctuations, as in the case of the oak dieback causing acute oak decline, Dutch Elm disease and, more recently, the bleeding canker of Horse-Chestnuts (Clouston & Stansfield 1979; Führer 1998; Thomas 2008; de Keijzer et al. 2012; Denman et al. 2014; Denman et al. 2018).

Habitat changes and threats

The species of the genera *Brachyopa* and *Hammerschmidtia* are highly dependent on a very specific larval habitat, namely senescent trees with sap runs or recently fallen tree trunks and stumps with a buildup of decaying sap. The adults are often found near the larval habitat and feed on various flowering herbs, shrubs and trees. The population size will probably be restricted by the availability of suitable larval habitat, but perhaps the availability of a nearby adult food source may also play a role in maintaining healthy populations (Fayt et al. 2006). Several species are known to visit flowers frequently and are likely be able to fly long distances.

Both the quality and quantity of resources, e.g., the number of senescent trees and the surface of the forested area, are probably the most important factor influencing the population size of the species. The changes in European forest dynamics and de- or re-forestation have been thoroughly investigated (Kaplan et al. 2009; Taff et al. 2009; Hughes et al. 2012). Forest cover has changed considerably over time, leading to a net decrease of ancient forest throughout Europe. Broadleaved floodplain forests, swamp forests of different kinds and some Macaronesian and Mediterranean forests are most severely threatened. The central European alluvial and swamp forests have been lost due to the regulation of rivers and changes in hydrology, with possibly only 5% preserved in small remnants (Hughes et al. 2012; Potapov et al. 2012; Birks et al. 2016; European Commission 2016; Zanon et al. 2018). In some West-European countries, however, the forested area is recovering and forest management has changed in ways that favour Syrphidae (Reemer 2005; Fuller et al. 2013).

In Europe, small areas with primaeval forest remain in Fennoscandia, Poland, Portugal and the alpine countries, while in South-Eastern Europe larger areas still have untouched forest (Sabatini et al. 2018; Jaroszewicz et al. 2019). Many of these forest remnants are not protected, and even those that are protected are threatened by logging activities and large infrastructure development (Jaroszewicz et al. 2019; McGrath 2019). Meanwhile, in Eastern Europe there are reports of reforestation due to changing land use. People are moving from the countryside to cities and the abandoned fields eventually become overgrown with trees. However, the intensive management of the forest has also ceased in many places, influencing the forest composition and possibly in some cases causing a deterioration of adult (loss of flowering plants due to abandoning fields) and even the larval habitat (Alix-Garcia et al. 2016; Gutman & Radelof 2017; Prokopová 2018). Commercial forests tend to have a monoculture of tree species with few flowering herbs and shrubs as potential adult food sources. In more open agricultural landscapes, these flowering plants are still available but solitary old trees are being removed in an increasingly way. These two effects result in a spatial mismatch between larval and adult habitat, likely to lead to a decrease in population size and eventually also in the number of populations (de Foresta et al. 2013; Scherber et al. 2014; Felton et al. 2016; Liu et al. 2018).

Traditionally oak (*Quercus* sp.) has been widely managed and used for a variety of purposes, such as bark for tanning, wood for construction and mining, glass production and forest pasture for livestock. In the absence of traditional forestry practices, such as coppicing with standards, most oak and oak-hornbeam forest undergoes a natural succession to beech-dominated forest in which ancient oak trees with sap runs disappear. This loss can be exacerbated by modern forestry practices in which all trees are harvested at the same time (Bobiec et al. 2018; Mölder et al. 2019). However, it has also been suggested that the natural succession to beech could possibly be suppressed by diseases causing a (recent) decline in beech populations (Jung 2009).

Other threats to the forest come from deposition of nitrogen, carbon dioxide and pesticides (Bleeker & Erisman 1998; Wamelink et al. 2009; van Dobben & de Vries 2017; Zou & Knops 2018) disturbing the natural balance within the forest and causing multifaceted effects. The effects have not been studied in detail for Syrphidae, but it seems that nitrogen and carbon dioxide influence floral growth rate in such a way that trees tend to age faster (Erisman et al. 2014; Vogels et al. 2017; Wallis de Vries & Bobbink 2017; EEA 2018). This could, temporarily, increase the larval habitat. A recent study, however, showed a negative impact on pollinators as a response to increased deposition of nitrogen (Carvalheiro et al. 2020). Insecticides and fungicides on the other hand have a strong negative influence on larval development and adult fecundity in aphidophagous Syrphidae (Colignon et al. 2003). It is highly likely these pesticides will also have a negative influence on saproxylic species like in the genera *Brachyopa* and *Hammerschmidtia*.

Finally, global climate change has a great impact on the natural world and forest composition, which in turn will have a great effect on its fauna (Ramsfield et al. 2016; Morin et al. 2018; Pureswaran et al. 2018; Jactel et al. 2019; Jandel et al. 2019). These effects are even more

complex than those from nitrogen or pesticide deposition and are increasingly being investigated for Syrphidae. These studies (Radenković et al. 2017; Miličić et al. 2018; Milić et al. 2019) show that different species have different responses, ranging from extensions in range, to declines and even extinction. The dispersal capability of each species and especially the dispersion of the habitat of that species are factors not easily accounted for and thus range extension is not only related to climate change per se, but mostly to habitat change (Warren et al. 2001; Schweiger et al. 2012; Fourcade et al. 2017; Milić et al. 2019). The most remarkable conclusion was that this could lead to a decrease in lowland species richness (Roth et al. 2014; Miličić et al. 2018; Milić et al. 2019), which in turn could lead to an increased decline of already rare species due to possible increased competition from commoner species (Warren et al. 2001).

It is clear that the forests and woodlands of Europe are threatened in many ways and that protective measures are needed to ensure their future survival and the flora and fauna dependent upon them. The EU (2016) list of threatened habitats is a good example of what is needed for this protection. Under each Syrphidae species the threat category of the habitat, given in the codes of the EUNIS (EUropean Nature Information System) habitat classifications of Woodlands, is discussed based on the information from this Red List.

Key to the adults of the European and circum Mediterranean species of *Brachyopa* and *Hammerschmidtia*

1 Vein M_1 perpendicular to vein R_{4+5} and abdomen straight, almost parallel-sided (Fig. 1E); all femora enlarged, clearly thicker than 2.2 times the width of tibiae; metatibia with short stout black setae posteromedially (Fig. 16G); male with tuberculate face (Figs 8E, 8F) …***Hammerschmidtia*** Schummel

– Vein M_1 ending oblique to vein R_{4+5} and abdomen conical, widest at posterior part of tergum II, gradually and clearly narrowing towards posterior tip of abdomen (see Figs 1A–C); femora only slightly enlarged and not much wider than 1.5 times the width of tibiae; metatibia with only normal short pile; male and female without facial tubercle (see Figs 8A–D) .....***Brachyopa*** Meigen

***Hammerschmidtia* key**

1 Arista plumose (Fig. 19E); katepisternum with dorsal and ventral pile patch, in female dorsal patch consisting of very few pili; postero-ventral part of katepisternum with long, strong, black setae; apex of profemur anteriorly with 1–4 strong, long yellow or black setae (Fig. 16F); apex of mesofemur posteriorly with 3 long and very strong, black setae, more than 3 times longer than other black setae; large species 11–15 mm ….....
.....***Hammerschmidtia ferruginea*** (Fallén, 1817)

– Arista short pilose and pile no longer than 3 times the diameter of arista at base (Fig. 19F); katepisternum with ventral pile patch and sometimes some white pile on postero-dorsal corner; postero-ventral part of katepisternum only with normal white pile; apex of profemur anteriorly without strong, long yellow or black setae; apex of mesofemur posteriorly with 3 rather long and strong, black setae, at most 2 times longer than other black setae; smaller species 8–11 mm ….....***Hammerschmidtia ingrica*** Stackelberg, 1952

***Brachyopa* key**

Not all species were available and the key is adjusted based on the studied material and the following literature: Kassebeer (2000a, b, 2001, 2002), Doczkal & Dziock (2004), and Pérez-Bañón et al. (2016). All the species from the circum Mediterranean region including North Africa and Turkey are incorporated here as well since they could occur in Europe too. The genitalia of several species o*f Brachyopa* have been illustrated by Pellmann (1998), for each of these species this is indicated by "*GP" indicating the * sign as remark and GP as genitalia Pellmann (1998). Most of the missing species in Pellmann (1998) have been illustrated in the papers in which the species were published for the first time (e.g., Thompson & Torp 1982; Mutin 1998; Kassebeer 2001; Van Steenis & Van Steenis 2014).

1 Frons bulging, clearly visible above the eyes in lateral view; face very wide; subscutellar pile fringe well developed; proepimeron pilose; length 12.7 mm ….***Brachyopa* (*Trichobrachyopa*) *tristis*** Kassebeer, 2001 (Only known from its type locality in Algeria)

– Frons flat, hardly visible above the eyes; face narrow; subscutellar fringe at most poorly developed; proepimeron at most with a few pili; smaller species ….....2 (***Brachyopa*** sensu stricto)

2 Arista pilose to bare, length of pile at most 1,5 times longer than width of basal part of arista (Figs 20 –21); scutum and pleura blueish-grey with black ground colour (see Figs 2C–F) or brown-reddish (Figs 2A, 2B) 6

– Arista plumose, length of pile at least 2 times longer than width of basal part of arista (Figs 19A–D); scutum and pleura almost entirely brown-reddish (see Figs 1A–D) 3

3 Arista long plumose, pile more than 3 times longer than width of basal part of arista (Fig. 19C); katepisternum with dorsal and ventral pile patch;

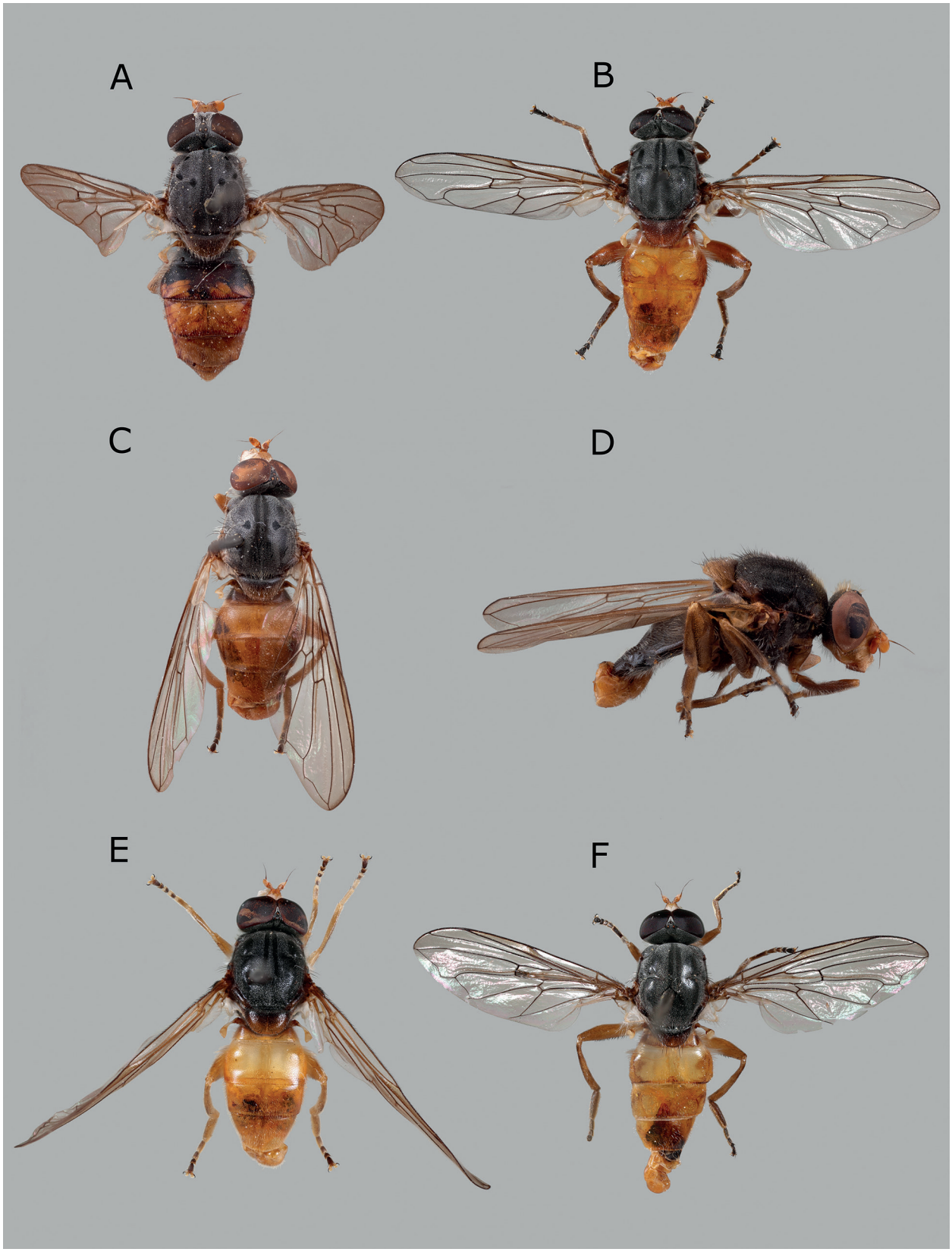

Fig. 3. Adult habitus, A-C, E, F dorsal view; D lateral view. **A**. *Brachyopa atlantea*, female, Granada, Spain. **B**. *B. bicolor*, male, Engsbergen, Belgium. **C**. *B. bimaculosa*, male, Bolgenachtal, Germany. **D**. *B. cinerea*, male, Komsomolsk-na-Amur, Russian Far East. **E**. *B. grunewaldensis*, male, Arkadia, Greece. **F**. *B. insensilis*, male, Diest, Belgium.

face strongly produced antero-ventrally; posterior anepisternum with 4–10 long strong black setae; post-alar callus with long and strong black setae-like pile mixed with light-yellow pile, black pile almost twice as long as pile on scutum; length 8–11 mm .... ***Brachyopa vittata*** Zetterstedt, 1843 *GP

– Arista short plumose, pile at most 3 times longer than width of basal part of arista (Figs 19A, 19B, 19D); katepisternum with ventral pile patch only; face weakly to slightly produced antero-ventrally; posterior anepisternum with at most 3–5 rather long, black setae; post-alar callus with yellow or mixed yellow and black pile, black pile only slightly longer and stronger than pile on scutum 4

4 Face rather strongly produced antero-ventrally (Fig. 8D); katepisternum and meron brown-reddish, same colour as rest of pleura; sensory pit narrow, longer than wide, tapering towards ventral margin; arista rather long pilose, pile 2–3 times larger than diameter of arista at base (Fig. 19D); length 6.0–7.5 mm ..... ***Brachyopa zhelochovtsevi*** Mutin, 1998

– Face only slightly produced antero-ventrally (Figs 8A, 8B); in males at least ventral half of katepisternum and meron dark-brown to black, contrasting with brown-reddish rest of pleura; sensory pit small and circular; arista long or short pilose (Figs 19A, 19B) 5

5 Abdomen with medial black vitta on terga II–IV (Fig. 1B); face produced antero-ventrally (Fig. 8B); arista longer pilose, pile almost 3 times longer than width of arista basally (Fig. 19B); length 6.5–8.0 mm ..... ***Brachyopa testacea*** (Fallén, 1817) *GP

– Abdomen without medial black vitta on terga II–IV (Fig. 1A); face weakly produced antero-ventrally (Fig. 8A); arista rather short pilose, pile about 2 times longer than basal width of arista (Fig. 19A); length 5–7 mm .... ***Brachyopa obscura*** Thompson & Torp, 1982

6 Arista virtually bare and sensory pit on basoflagellomere at most weakly developed small and round (Figs 20C, 21) 11

– Arista pilose, pile at least as long as width of arista and sensory pit on basoflagellomere clearly developed, round or oval to large kidney shaped (Figs 20A–B, 20D–F) 7

7 Scutum and pleura greyish, blue-grey pollinose with weaker pollinose pattern (Figs 2C–D) 9

– Scutum and pleura reddish-brown, brownish pollinose with extensive shiny pattern (Figs 2A, 2B) 8

8 Posterior margin of scutellum with long black bristles, 2–4 times longer than pile in the middle of scutellum; scutellar disc extensively pollinose medially and anteriorly; sensory pit as small as diameter of arista at base (Fig. 20A); postero-dorsal corner of anepisternum with some black setae; length 6–9 mm .... ***Brachyopa dorsata*** Zetterstedt, 1837 *GP

– Posterior margin of scutellum without long black bristles; scutellum only anterior margin narrowly pollinose; sensory pit large, more than 2,5 diameter of arista at base (Fig. 20B); anepisternum with only white pile; length 6–9 mm .... ***Brachyopa panzeri*** Goffe, 1945 *GP

9 Postpronotum and post-alar callus blackish, same colour as scutum and tergum II with at most a few black pili on posterolateral margin (Fig. 2D); frons in male more narrowly pollinose (Fig. 13C); length 6–8 mm ..... ***Brachyopa pilosa*** Collin, 1939 *GP

– Postpronotum and post-alar callus orange-brownish, lighter than scutum and tergum II extensively black pilose postero-lateral margin (Figs 2E, 2F); frons in male broadly pollinose (Figs 13D, 13E) 10

10 Sensory pit on basoflagellomere small, rounded (Fig. 20E); scutellar disc rather long pilose, pile length about half as long as posterior scutellar setae; length 7–8 mm ..... ***Brachyopa plena*** Collin, 1939

– Sensory pit on basoflagellomere large, kidney-shaped (Fig. 20F); scutellar disc rather short pilose, pile length at most 1/3 as long as posterior scutellar setae; length 6–8 mm ..... ***Brachyopa scutellaris*** Robineau-Desvoidy, 1844 *GP

11 Abdomen shiny black, antennae, face, scutellum and male genitalia orange-yellow (Fig. 3D); length 6–8 mm ..... ***Brachyopa cinerea*** Wahlberg, 1844

– Abdomen reddish, often with dark-brown to black markings, scutellum and genitalia greyish (Figs 3A–C, 3E–F, 4) 12

12 Wing with two small black maculae and postpronotum dark-orange, lighter than rest of scutum (Fig. 2C); length 7.0–9.5 mm .... ***Brachyopa maculipennis*** Thompson, 1980 *GP

– Wing hyaline and postpronotum dark brown, greyish pollinose, same colour as rest of scutum (Figs 3A, 3B, 3E, 3F, 4) 13

13 Notopleural sulcus at most weakly developed; scutellum with a distinct transverse depression and with distinct patch of microtrichia at base; protarsus entirely black; metafemur enlarged; basoflagellomere with distinct sensory pit (Fig. 21B); length 6–9 mm ..... ***Brachyopa bicolor*** (Fallén, 1817) *GP

– Notopleural sulcus well developed; scutellum without transverse depression; protarsus mixed black and yellow coloured; mesofemur less clearly

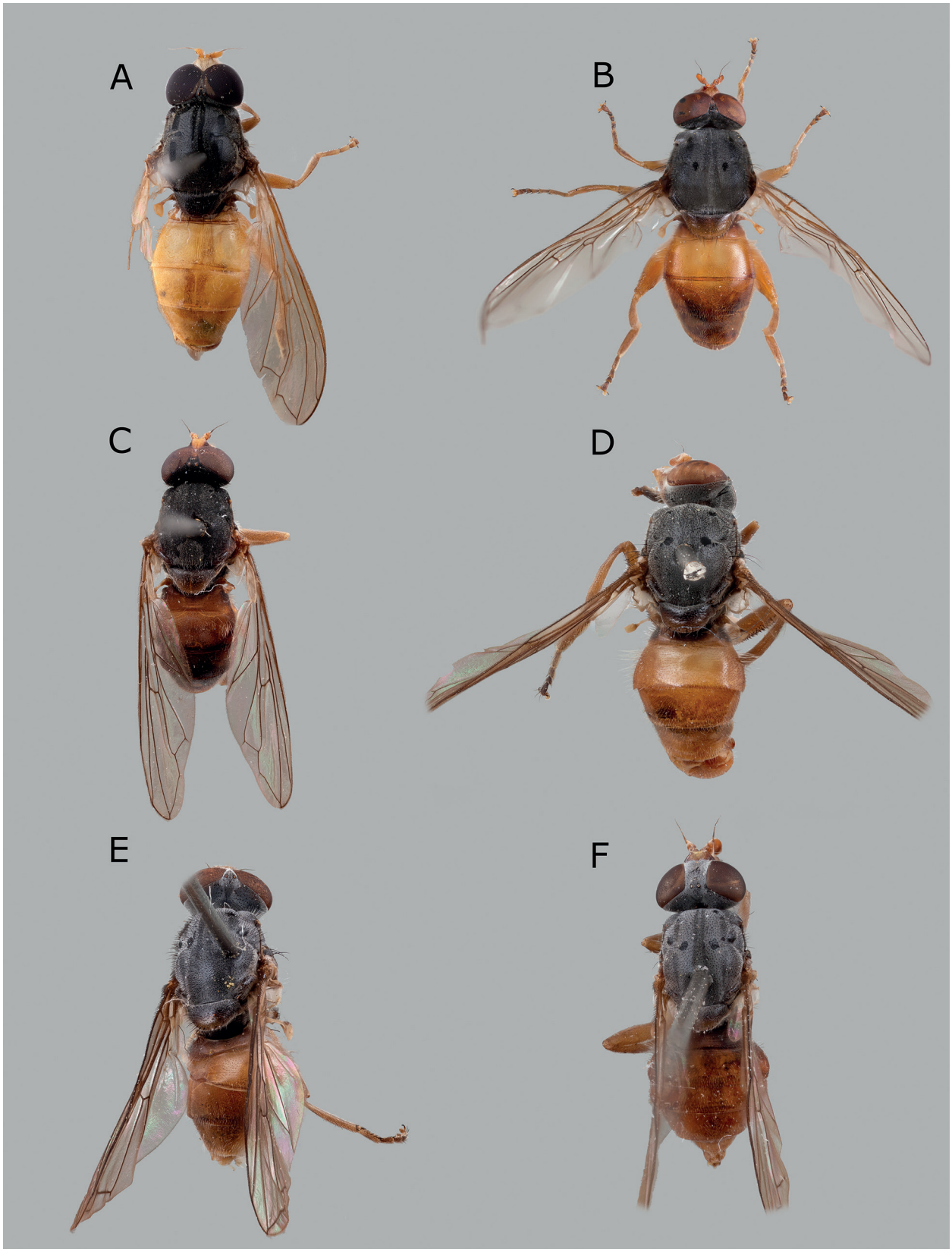

Fig. 4. Adult habitus, dorsal view. **A**. *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B**. *B. silviae*, male, Bringhausen, Germany. **C**. *B. minima*, male, Lesvos, Greece. **D**. *B. vernalis*, male paratype, Crete, Greece. **E**. *B. quadrimaculosa*, male, Samos, Greece. **F**. *B. quadrimaculosa*, female, Samos, Greece.

enlarged; basoflagellomere with at most a weak sensory pit (Figs 21A, 21C, 21E, 21F) 14

14 Scutum (Fig. 4A) and vertical triangle (Fig. 15A) extensively shiny, black with weak coverage of blue-greyish microtrichia; length 6–7 mm ..... ***Brachyopa cruriscutum*** Van Steenis & Van Steenis, 2014
– Scutum and vertical triangle almost entirely to entirely covered with blue-greyish microtrichia (Figs 4B–F, 14, 15B–D) 15

15 Scutum microtrichose except for 2 or more clear black shiny maculae, bare of microtrichia (Figs 3A, 3C, 4B, 4D–F); postalar callus entirely microtrichose or with medial part bare and shiny 17
– Scutum entirely covered with microtrichia (Figs 3E, 3F); postalar callus microtrichose, with medial part bare and shiny 16

16 Protarsus almost entirely dark-brown to black coloured (Fig. 3F); ocellar triangle entirely greyish pollinose (Fig. 14E); mouth-edge rather strongly protruding (Fig. 10F); length 6.0–8.5 mm ..... ***Brachyopa insensilis*** Collin, 1939 *GP
– Protarsus with tarsomeres bicoloured, basal part yellow apical part dark-brownish (Fig. 3E); ocellar triangle weakly pollinose, with shiny black pattern (Fig. 14D); mouth-edge only weakly protruding (Fig. 10E); length 7.0–8.5 mm ..... ***Brachyopa grunewaldensis*** Kassebeer, 2000

17 Halter entirely yellow 19
– Halter yellow except for capitulum which is partly dark-greyish (see Fig. 4D) 18

18 Face yellow with black triangular fascia between eyes and antennae (vaguely visible in Fig. 11D); proleg with tarsomere 1 yellow, tarsomeres 2–3 dark-brown with broad yellow apical margin, and tarsomeres 4–5 entirely dark-brown; posteroventral corner of anterior anepisternum nearly entirely microtrichose, at most a tiny bare macula; length 5.5–7.5 mm ..... ***Brachyopa vernalis*** Van Steenis & Van Steenis, 2014
– Face yellow, mouth edge narrowly black (Figs 11E, 11F); proleg with tarsomeres 1–5 entirely dark-brown; posteroventral corner of anterior anepisternum with shiny macula, bare of microtrichia; length 6–8 ..... ***Brachyopa quadrimaculosa*** Thompson, 1981

19 Postalar callus with medial part bare and shiny ... 21
– Postalar callus entirely microtrichose 20

20 Scutum with one pair of round bare shiny maculae at the transverse suture (Fig. 3C); hypostomal bridge yellow (Fig. 10C); ocellar triangle densely covered with microtrichia, not shiny (Fig. 14B); ventral scutellar fringe absent; sterna entirely pollinose; length 6–8 mm .... ***Brachyopa bimaculosa*** Doczkal & Dziock, 2004
– Scutum with one pair of triangular bare shiny maculae at the transverse suture (Fig. 4B); hypostomal bridge blackish (Fig. 11B); at least centre of ocellar triangle bare of microtrichia, shiny black; ventral scutellar fringe present; more than half of the surface of sterna 3 and 4 non-pollinose; length 7–8 mm ..... ***Brachyopa silviae*** Doczkal & Dziok, 2004

21 Wing with dark-brown macula on vein r-m; medial end of transverse suture with brownish pollinose macula; scutellum entirely orange-brown; length 6.5 mm ..... ***Brachyopa tabarkensis*** Kassebeer, 2002
– Wing hyaline (Figs 3A, 4C); medial end of transverse suture with non-pollinose, shiny black macula (Fig. 3A) or grey pollinose like the other pollinosity of the scutum; scutellum orange-brown with dark-brown anterior margin 22

22 Medial end of transverse suture with non-pollinose, shiny black macula (Fig. 3A); length 6–8 mm ..... ***Brachyopa atlantea*** Kassebeer, 2000
– Medial end of transverse suture pollinose; length 6–7 mm ..... ***Brachyopa minima*** Vujić & Pérez-Bañón, 2016

Key to the known third-instar larvae of the European species of *Brachyopa* and *Hammerschmidtia*

(Based on Krivosheina & Mamaev 1967; Rotheray 1996; Rotheray & Gilbert 1999; Kassebeer 2000a; Krivosheina 2003; Krivosheina 2005, 2019; Pérez-Bañón et al. 2016)

1 Posterior respiratory process (prp) relatively short, protruding only slightly beyond last pair of anal lappets (Fig. 5C); anal lappets of nearly equal length; dorsal part of abdomen evenly coated in setae, not forming "transverse rows"; abdominal segments 2–6 with oblique furrow, separating the medial from the dorsal sensilla ..... ***Hammerschmidtia*** Schummel
– PRP relatively long, protruding strongly beyond last pair of anal lappets (Fig. 5A); anal lappets of unequal length, becoming increasingly shorter posteriorly; dorsal part of abdomen with either transverse rows of setae or coated in blotches; abdominal terga 2–6 without oblique furrow, the medial and dorsal sensilla not separated from each other ..... ***Brachyopa*** Meigen

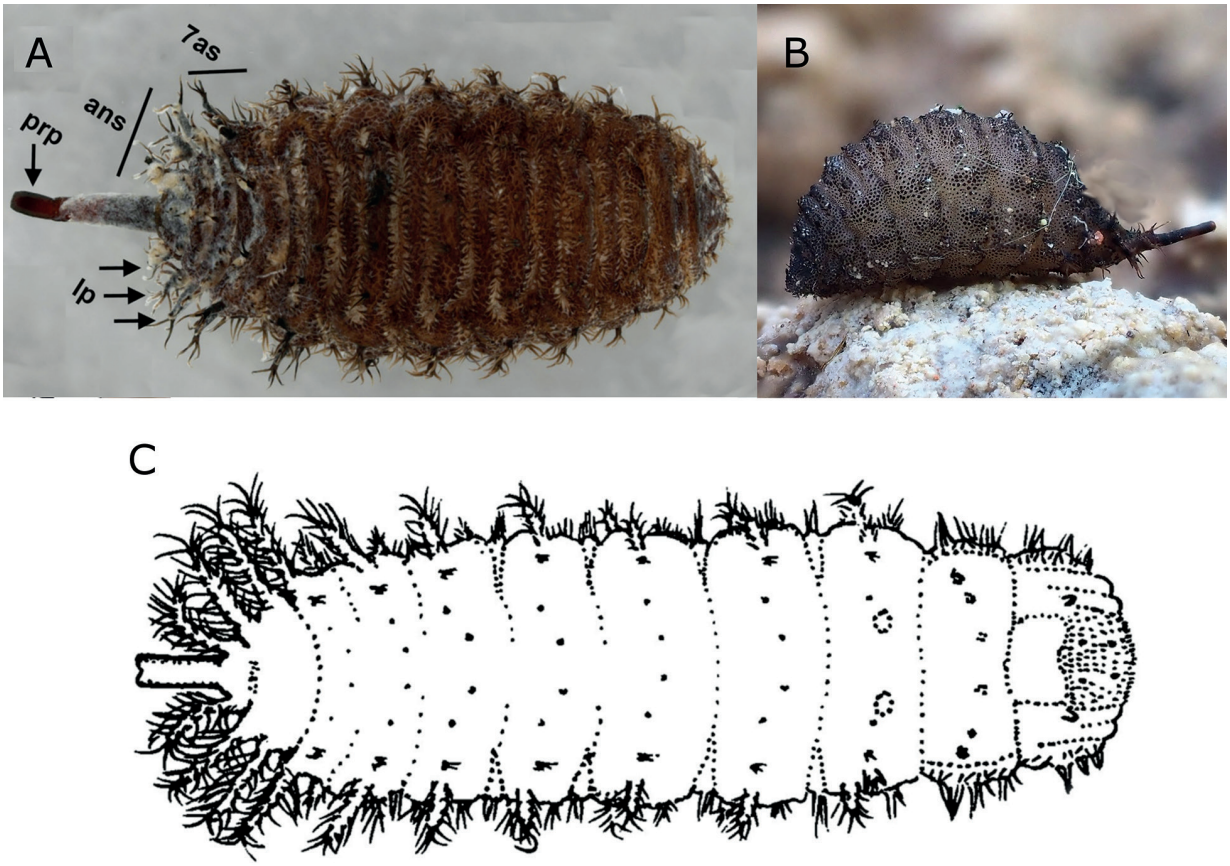

Fig. 5. Third instar larva and pupa. **A**. *Brachyopa bicolor*, larva, after Pérez-Bañón et al. 2016. **B**. *Brachyopa insensilis*, pupa, Brussels, Belgium, photo B. Wakkie. **C**. *Hammerschmidtia ingrica*, larva, after Krivosheina 2003. Abbreviations: 7as = 7th abdominal segment; ans = anal segment; lp = lappets; prp = posterior respiratory process.

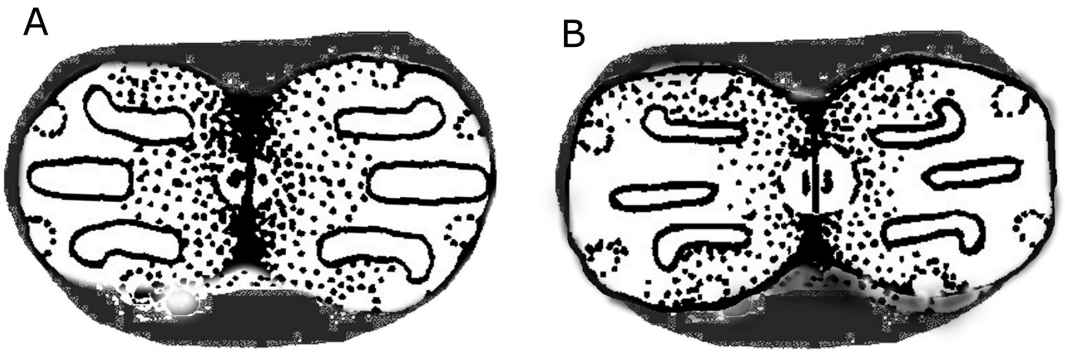

Fig. 6. Posterior respiratory process, after Krivosheina 2003. **A**. *Hammerschmidtia ferruginea*. **B**. *Hammerschmidtia ingrica*.

Key to the larvae of the European species of *Hammerschmidtia*

1 Posterior respiratory process (prp) with three pairs of spiracular openings, length about half the width of the prp, the lateral pairs strongly bent, the medial pair ending close to the lateral margin of the prp (Fig. 6A) .... ***Hammerschmidtia ferruginea*** (Fallén)

– PRP with openings shorter, about 1/3 of the width of the prp, lateral respiratory opening more straight, the medial pair further away from the lateral margin (Fig. 6B) .... ***Hammerschmidtia ingrica*** Stackelberg

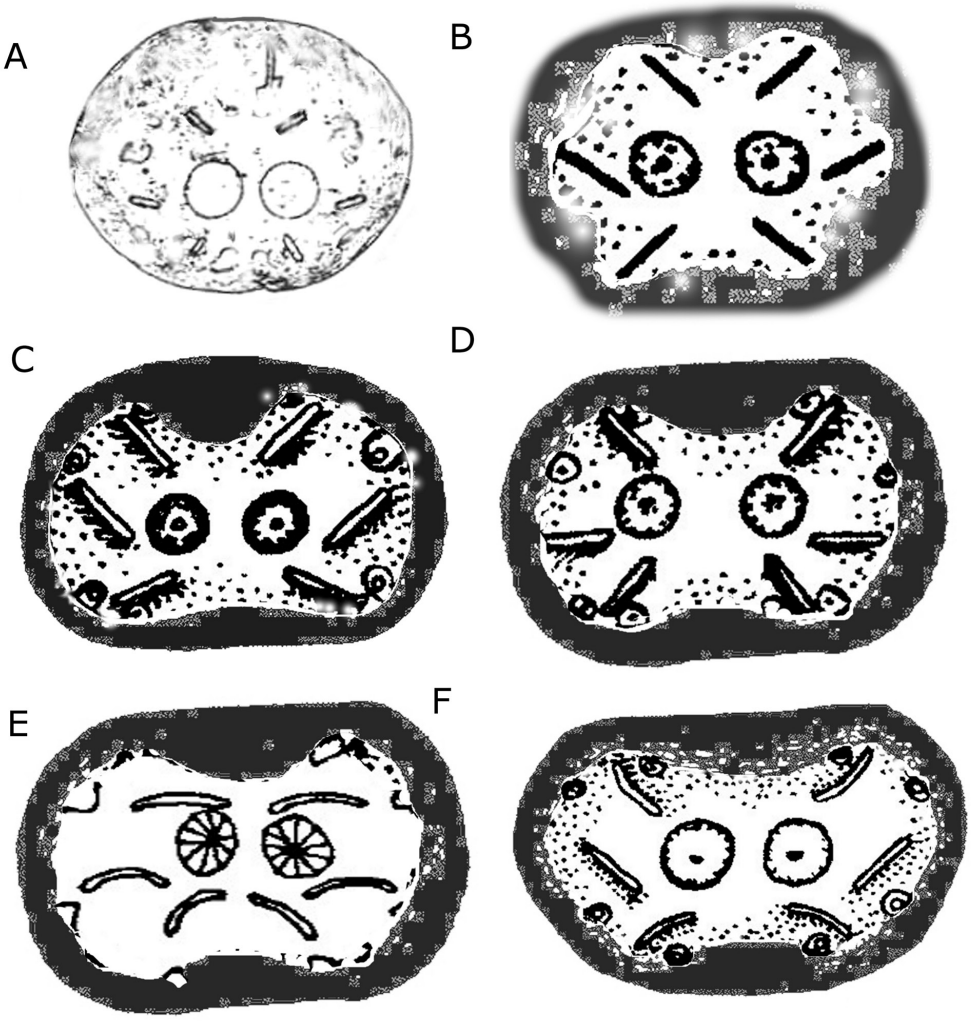

Fig. 7. Posterior respiratory process, **A** after Kassebeer 2000c, **B–D, F** after Krivosheina 2005, **E** after Rotheray 1996. **A**. *Brachyopa atlantea*. **B**. *Brachyopa bicolor*. **C**. *Brachyopa dorsata*. **D**. *Brachyopa pilosa*. **E**. *Brachyopa scutellaris*. **F**. *Brachyopa vittata*.

Key to the known larvae of the European species of *Brachyopa*

Note: larvae of ***B****rachyopa obscura, B. testacea, B. zhelochovtsevi, B. plena, B. bimaculosa, B. cinerea, B. grunewaldensis, B. maculipennis, B. quadrimaculosa, B. silviae, B. vernalis* and *B. tristis* are not known.

1 Body with dense spinae; posterior end of abdomen oval, usually darker than rest of the body 2
– Body at most with scattered spinae; posterior end of abdomen conical, same colour as rest of the abdomen 4

2 Lateral papillae on posterior segments small, tuberculate; posterior segments with several tubercles, without rows of spinae ..... ***Brachyopa vittata*** Zetterstedt
– At least 3 or 4 lateral papillae on posterior segments well developed, large; posterior segments with several tubercles, with clear rows of spinae 3

3 Lateral papillae on posterior segment unequally sized, 5th and 6th as long as wide, 7th about 1.5 times longer than wide; 3rd and 4th pair of papillae short, with short lateral appendages and 2 longer apical appendages ..... ***Brachyopa panzeri*** Goffe
– Lateral papillae 5–7 on posterior segments equally sized, about 1.5 times longer than wide; all papillae with long curved appendages, some longer than papilla ..... ***Brachyopa dorsata*** Zetterstedt

4 Abdomen without transverse rows of setae, some isolated stump like setae may be present; body coated in dark coloured blotches of various sizes .. 5
– Abdomen with rows of setae; body with blotches inconspicuous and pale, or entirely absent..... 6

5 A large tubercle present between the first pair of sensilla on tergum VII; setae of last three pairs of anal lappets directed apically ....***B. minima*** Vujić & Pérez-Bañón
– Area between the first pair of sensilla flat; setae of last three pairs of anal lappets directed laterally and apically ..... ***B. insensilis*** Collin

6 Rows of setae on abdomen strictly aligned; abdominal segments 1–6 with sensilla pairs 1 and 2 with 2 large and 2 small setae 7
– Rows of setae on abdomen not aligned; sensilla pairs 1 and 2 usually with more than 2 large setae 8

7 Spiracular opening on prp long and obliquely placed (Fig. 7B) ..... ***B. bicolor*** (Fallén)
– Spiracular openings on prp short and medial pairs almost horizontally placed (Fig. 3A) ....***B. atlantea*** Kassebeer

8 PRP > 1 mm long, as long as or longer than width of body; ventral surface of prp apically smooth, without pits .....***B. pilosa*** Collin
– PRP < 1 mm long, shorter than width of body; ventral surface of prp apically with pits ....***B. scutellaris*** Robineau-Desvoidy

The European species of the genus *Brachyopa* Meigen, 1822

***Brachyopa atlantea* Kassebeer, 2000**

Brachyopa atlantea Kassebeer, 2000c: 142; ♂ and ♀ types in private collection of C.F. Kassebeer (present condition or whereabouts unknown), not studied.
Figs 3A, 7A, 10A, 18A, 21A, 22

Distribution. Described from Morocco, based on five adult specimens and several puparia and larvae collected in Morocco. Only one European record from Spain (Van Steenis & Van Steenis 2014) is known. It is classified as an Ibero-Maghreb endemic species.

Biology. Adults, puparia and larvae have been found on external sap runs on *Populus* spp. in the Atlas Mountains. The species was collected at the same locality two years in a row (Kassebeer 2000c). The record from Europe was most likely from the South-Western part of the Sierra Nevada in an area with Mediterranean evergreen Oak (*Quercus ilex* Lour. and *Q. pyrenaica* Willd.) forest.

The flight period is not well known as only one adult was collected, on the 24th of March, in the field. All other records are from larvae and puparia, many of which were empty, between March 6th and April 16th (Kassebeer 2000c). The European specimen was collected on the 13th of April (Van Steenis & Van Steenis 2014).

The species has been collected at altitudes of 550 and 1000 m a.s.l.

Population fluctuations. In Morocco the species was collected at the same locality two years in a row. It is not known if the species disappeared after that or that the locality has not been visited after these years. Based on the larval habitat, external sap-runs, which tend to dry out in the course of several years (Pérez-Bañón et al. 2016) it is likely the population shows large fluctuations.

Remarks. The identification of the European specimen is based on the characters given in Kassebeer (2000b). The female specimen is listed in the database and, in the distribution map, the African distribution of this species is not shown.

Red List. Not present on any Red List. Due to its presumed relict occurrence in Europe and the small area of occupancy in Morocco this species has little flexibility of coping with threats. If major habitat threats are present, its future survival will be under severe pressure, however, the presumed forest type G2.1 is listed as "Least Concern" in the European Red List of habitats (European Commission 2016).

***Brachyopa bicolor* (Fallén, 1817)**

Rhingia bicolor Fallén, 1817: 33; ♂ lectotype and ♀ paralectotype, in NHRS, not studied.
Figs 3B, 5A, 7B, 10B, 14A, 18B, 21B, 23, 38A

Distribution. A widespread European species occurring from Southern Norway and Sweden to Spain and Greece and from Wales into the European part of Russia and Japan.

Biology. Its main habitat consists of different deciduous woodland and parkland forest types such as alluvial *Alnus-Quercus-Fraxinus*, thermophilous and xerophilous *Quercus-Ulmus-Fraxinus* forests (Reemer et al. 2009; Speight & Castella 2011; Ball & Morris 2014).

Larvae are known from a wide variety of trees, deciduous: *Aesculus hippocastanum* L., *Fagus sylvatica* L., *Platanus* spp., *Populus alba* L., *Pyrus* spp., *Quercus* spp. and *Ulmus* spp. as well as coniferous *Abies* spp., in accumulations of sap under bark of live trees or tree trunks and sap runs. Larvae are associated with sap runs caused by larvae of the caterpillar of *Cossus cossus* (Lepidoptera) and larvae of the beetles *Hylecoetus flabellicornis* (Schneider, 1791), *Trypodendron lineatum* (Olivier,

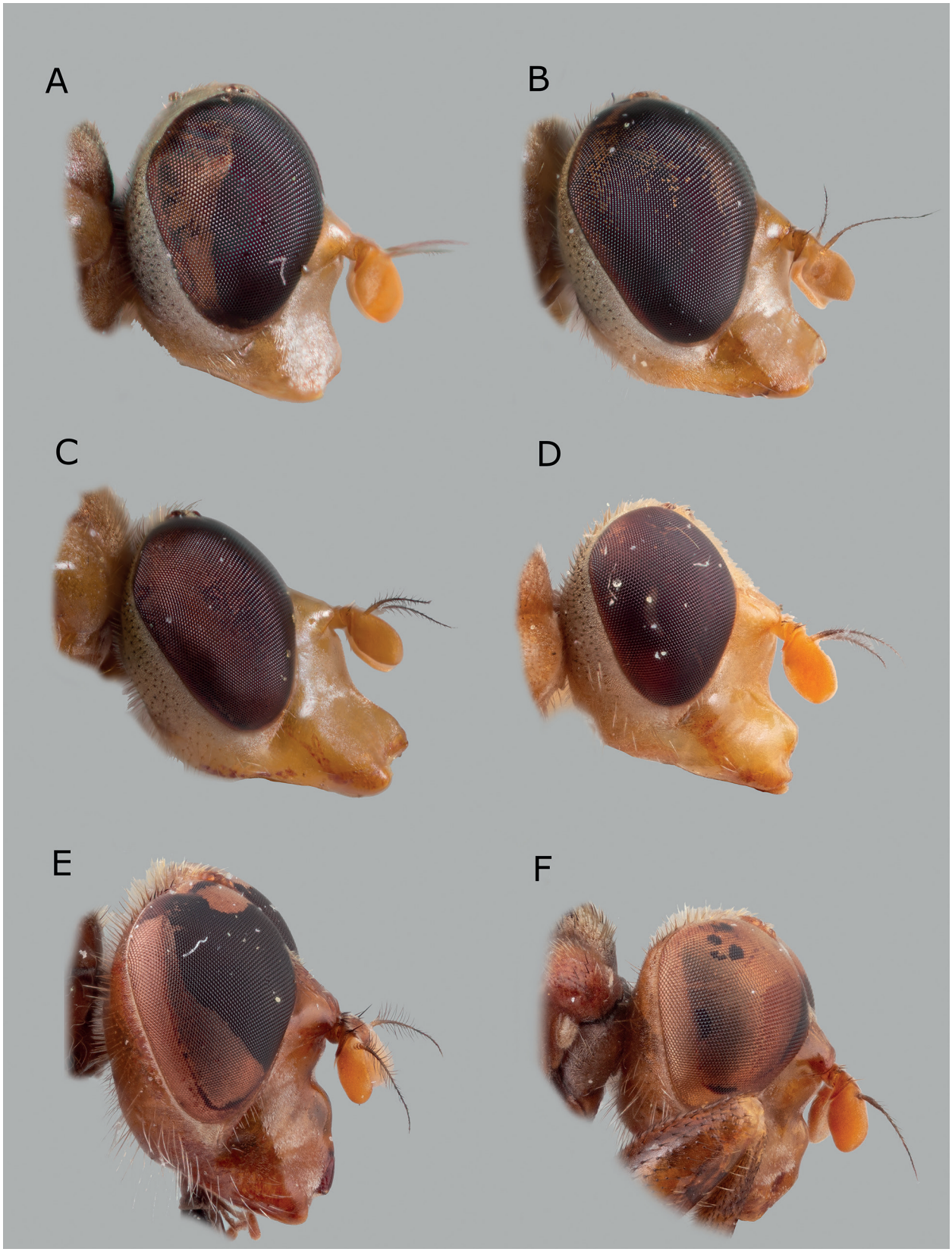

Fig. 8. Head male, lateral view. **A**. *Brachyopa obscura*, Olloy-s-Viroin Belgium. **B**. *B. testacea*, Elzetterbos, the Netherlands. **C**. *B. vittata*, Eupen, Belgium. **D**. *B. zhelochovtsevi*, Aktru, Altay, Russia. **E**. *Hammerschmidtia ferruginea*, Borjomi NP, Georgia. **F**. *H. ingrica*, Bychika, Russian Far East.

1795) and *T. signatum* (Fabricius, 1792) on *Abies* spp., *Populus tremula* L., *Quercus robur* L. and *Salix* spp. (Torp 1986; Rotheray 1991; Nielsen 2005; van Eck et al. 2016; Wolton & Luff 2016; Krivosheina 2019).

It is assumed that sap runs on *Quercus* spp. is the preferred larval habitat of this species (Ball & Morris 2014; Krivosheina 2019). One population on a single *Quercus robur* tree was monitored over a period of seven years after which the tree was storm felled. This tree had an age of 118 years and possibly over the last 20 years it suffered from drought stress and loss of hardwood creating suitable larval habitat (Wolton & Luff 2016). The larvae found in sap-runs on *Aesculus hippocastanum* and *Quercus robur* are prone to be parasitized by *Tetrastichus brachyopae* Graham, 1991 (Hymenoptera: Eulophidae), with up to 18 wasps hatching from one single puparium (Rotheray 1996; van Eck et al. 2016).

Adults were found visiting flowers of e.g. *Acer* spp., *Crataegus laevigata* (Poir.) DC., *Prunus padus* L., *P. serotina* Ehrh., *P. spinosa* L., *Valeriana* spp.(Stuke 1996; Bartsch et al. 2009; Nilsson et al. 2012), and *Platanus* spp. (database). They are more often found flying around trees such as *Acer pseudoplatanus* L., *Betula pendula* Roth, *Castanea sativa* Mill., *Populus* spp., *Salix alba* L. and the above mentioned trees with supposed sap-runs where they can fly high into the trees (Röder 1990; Torp 1994; Nilson et al. 2007; Reemer et al. 2009; Ricarte et al. 2014; van Steenis et al. 2019; Mielczarek et al. 2019) as well as *Carpinus betulus* L., *Fagus* spp. and *Tilia* spp. (database). The larvae overwinter, with puparial formation occurring from February to May; the duration of the puparial phase is 3.5 weeks (Dussaix 2013).

The overall flight period is from the beginning of April until the end of July with extreme dates of the 6th of March and the 15th of August (Fig. 38A). There is a range shift and shortening in flight period from south to north, so that the flight period in the boreal countries is from the end of April until the end of June. Collected at altitudes of 0–1620 m a.s.l. (Maibach et al. 1992; database). This species has many records from the 19th century in several countries, e.g., Austria, Germany and Sweden, but has only rather recently been found in the Netherlands and Norway, with the first records from 1966 and 1980 respectively. The number of observations in different time periods of 50 years differs greatly between and also within countries. Over the periods before 1900, from 1900 to 1950, from 1950 to 2000 and after 2000, in Austria there were respectively 6, 2, 0 and 6 records; in Serbia 0, 0, 6 and 7 records are known, while in Sweden 2, 2, 5 and 31 records are known.

Population fluctuations. This species is associated with external sap runs on *Quercus* spp. and several other trees, and as this type of microhabitat is known to fluctuate over time this species would be expected to be adapted to sucj fluctuations. In light of this, it is most likely this species shows large fluctuations, especially within marginal habitats and possibly even within large areas with suitable habitat. This conclusion can also be drawn from the fluctuating number of records as given above.

Remarks. Several of the old records of this species could actually belong to different species.

Red List. This species occurs on several regional Red Lists and is categorized from "Least Concern" to "Endangered" (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011; Ball & Morris 2014; Henriksen & Hilmo 2015; Artdatabanken 2019). Even within Germany large differences between the "Bundesländer" exist where it is classified from "Data Deficient" and "Vulnerable" to "Endangered" (Pellmann et al. 1996; Stuke et al. 1998; Doczkal et al. 2001; Dziock et al. 2001; von der Dunk et al. 2003; Dziock et al. 2004). These differences depend on several factors, such as being at the edge of its distributional range and thus being at a higher threat level, the availability of new records lowering the threat category and possibly also the use of different criteria.

Brachyopa bimaculosa Doczkal & Dziock, 2004

Brachyopa bimaculosa Doczkal & Dziock, 2004: 45; ♀ holotype in SMNM, not studied
Figs 3C, 10C, 14B, 18C, 21C, 24

Distribution. Single records are known from three localities around the Alps (Germany and Slovenia) and one in central Greece. A large population has been found on the Peloponnesos, Greece (van Steenis & van Steenis 2014). This species is regarded as a European endemic.

Biology. The species is recorded in sub-alpine forests dominated by *Abies alba* Mill. and *Fagus sylvatica* along small rivers in the shade of trees such as *Acer* spp., *Alnus* spp. and *Salix* spp. (Doczkal & Dziock 2004; van Steenis et al. 2013) and on open flower-rich limestone meadows within forests dominated by *Abies cephalonica* Loudon and *Pinus nigra* J.F. Arnold. No larval records are known and adults have only been found while visiting flowers of several different plant species such as *Acer* spp., *Aegopodium podagraria* L., *Bupleurum* cf. *rotundifolium*, *Prunus* spp. and *Salix aurita* L. (Doczkal & Dziock 2004; van Steenis et al. 2013; van Steenis & van Steenis 2014).

In the Alpine population the specimens were collected on the 3rd and 19th of June at altitudes of 970 and 1050 m a.s.l. respectively (Van Steenis & Van Steenis, 2014). In the Northern part of the Schwarzwald one specimen was collected on the 31st of March between 260 and 310 m a.s.l. (Doczkal & Dziock, 2004). In Greece the species was collected between 22nd of April and the 28th of May and had an altitudinal range of 980–1700 m a.s.l. (Van Steenis & Van Steenis, 2014, database). The first record

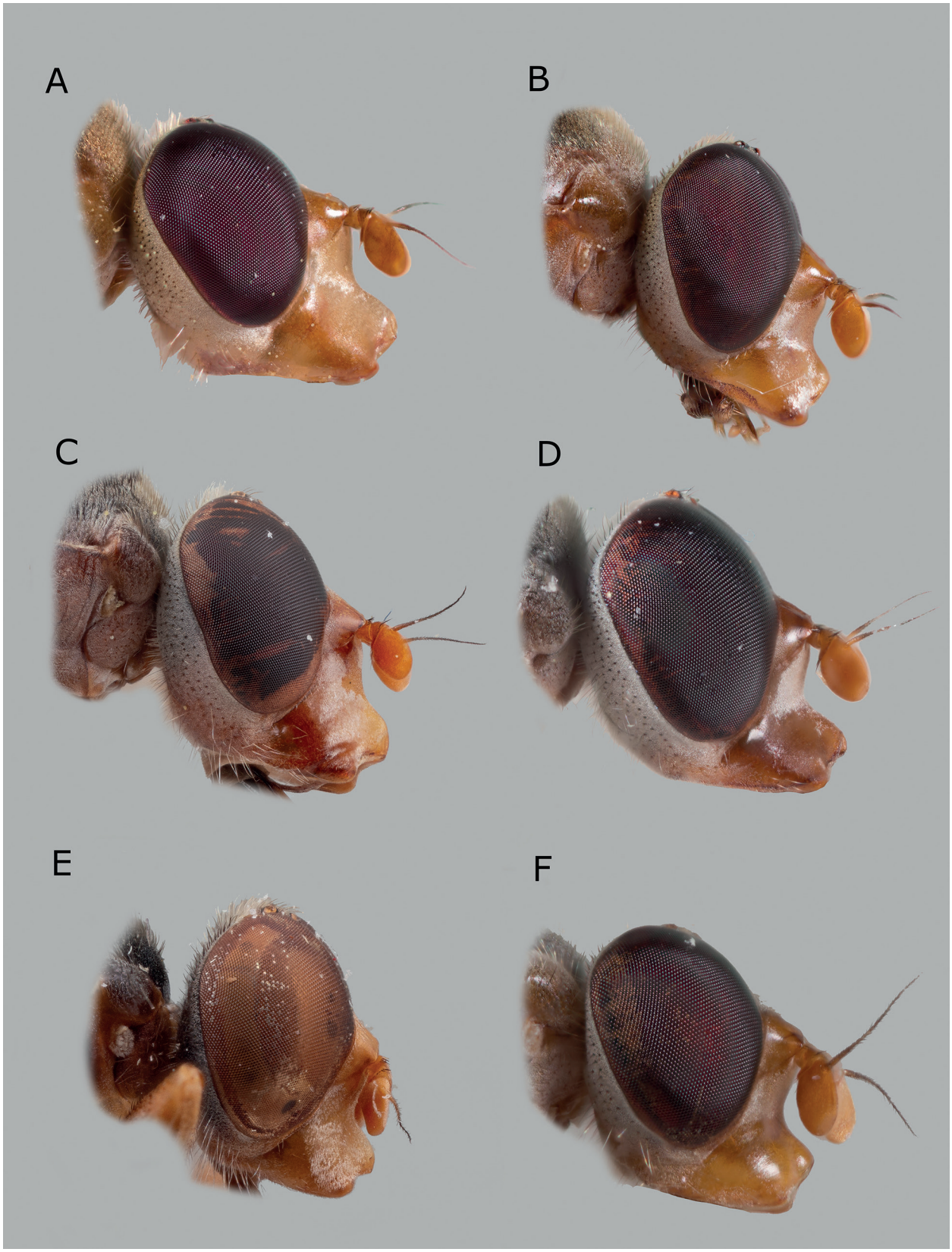

Fig. 9. Head male, lateral view. **A**. *Brachyopa dorsata*, Rocherath, Belgium. **B**. *B. panzeri*, Oudergem, Belgium. **C**. *B. maculipennis*, Fruška Gora, Serbia. **D**. *B. pilosa*, Drentsche Aa, the Netherlands. **E**. *B. plena*, Ioannina, Greece. **F**. *B. scutellaris*, Oudergem, Belgium.

dates back to 1990 and it has been seen regularly in the 21st century.

Population fluctuations. Only post 1990 records are available from very widely separated localities. It is possible this species has been recorded before 1990 but was not separated from similar species such as *B. insensilis*. No evidence was found that this species has an extreme fluctuation in populations or in population size.

Remarks. This species has a restricted range of occurrence and is only found in larger numbers on the Peloponnesos. The localities around the Alps are possibly relict populations and may not be viable for maintaining a steady population. The species distribution is severely fragmented and the seemingly large population on the Peloponnesos is not likely to colonize the Alpine localities. The larval habitats of the species of *Brachyopa* are all connected with sap-runs or accumulations of sap under bark and thus depending on natural forests with overmature trees. This habitat is under pressure in Greece and especially on the Peloponnesos and on many Mediterranean islands due to overgrazing and forest fires (WWF 2007; Caballero 2009; Kizos et al. 2013; Kalabokidis et al. 2013).

The male specimens from the Alps differ in several morphological characters from those collected on the Peloponnesos in such a way that two species could be involved. The male genitalia as well as molecular data do not show large variation between these two putative species and further study is needed to sort out the taxonomy of the species.

Red List. This species only occurs on one regional Red List. In Germany it is regarded as "Data Deficient" as only one record was known (Ssymank et al. 2011). The habitat where the species was found in the Alpine region could be classified as G4 and possibly G4.1 both of which are categorized as "Least Concern" (European Commission 2016); the Peloponnesian Black pine forests (G3.5) are "Least Concern" too (European Commission 2016). On Mt Taygetos, where part of the population was found, the negative effect of forest fires clearly pose a great threat to this type of forest (Sarris et al. 2014) despite its classification, and thus to this *Brachyopa* species.

In the light of the possible split of this species, it is advised to treat the Alpine populations separately from the Greek populations.

Brachyopa cinerea Wahlberg, 1844

Brachyopa cinerea Wahlberg, 1844: 65; types in NHRS, not studied.
Figs 3D, 10D, 14C, 18D, 21D, 24

Distribution. Found in the boreal parts of Norway, Sweden and Finland, and eastwards into the boreal zone of Siberia and Japan.

Biology. A relatively early flying subarctic species found in *Betula-Salix-Alnus* and mountain *Betula* forests visiting flowers of *Ribes rubrum* L. and *Salix glauca* L. (Nielsen 1992, 1998; Mutin 1998; Bartsch et al. 2009) and *Anthriscus sylvestris* L. (database). In the Russian Far East it is more widespread and 'with more specimens found together visiting *Prunus padus* and *Salix bebbiana* Sarg. (Mutin et al. 2016). No larval records are known.

The flight period of this species is from the beginning of May until the middle of July (database). Collected at altitudes between 25 and 1475 m a.s.l. (database). The number of records from the 21st century equals that of the period 1950-2000. The relatively many records from the period from 1900-1950 indicate a possible decline in populations.

Population fluctuations. This species has not been collected at the same locality in different years and as only single records are known from Europe it cannot be concluded that this species shows extreme fluctuations.

Remarks. A rare and very local species, which almost always occurs as single specimens at collecting sites. Very little is known about its biology. Due to the low numbers found in Europe, it could be argued that the species is at its western limit of occurrence, and hence vulnerable to habitat changes.

Red List. This species occurs on the Red List of Finland, Norway and Sweden, and it is classified from "Near Threatened" to "Vulnerable" (Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). These categories seem to be based on weak assessments since, given its distribution, there is likely to be considerable undersampling of this species. More research is required in order to make a well founded decision on its status in Europe. The main habitat for this species, forest type G1.5, is classified as "Vulnerable" (European Commission 2016).

Brachyopa dorsata Zetterstedt, 1837

Brachyopa dorsata Zetterstedt, 1837: 35; types in ZIL, not studied
Brachyopa sibirica Violovitsh, 1982: 58, type in ZISP, (syn by Mutin & Barkalov 1991), not studied.
Figs 2A, 7C, 9A, 13A, 17A, 20A, 25, 38B

Distribution. A widespread temperate and boreal (Finland, Norway and Sweden) species with its western distributional boundary from the western part of the French Pyrenees along the Alps and the Vosges into the eastern parts of Belgium and the Netherlands, eastwards through

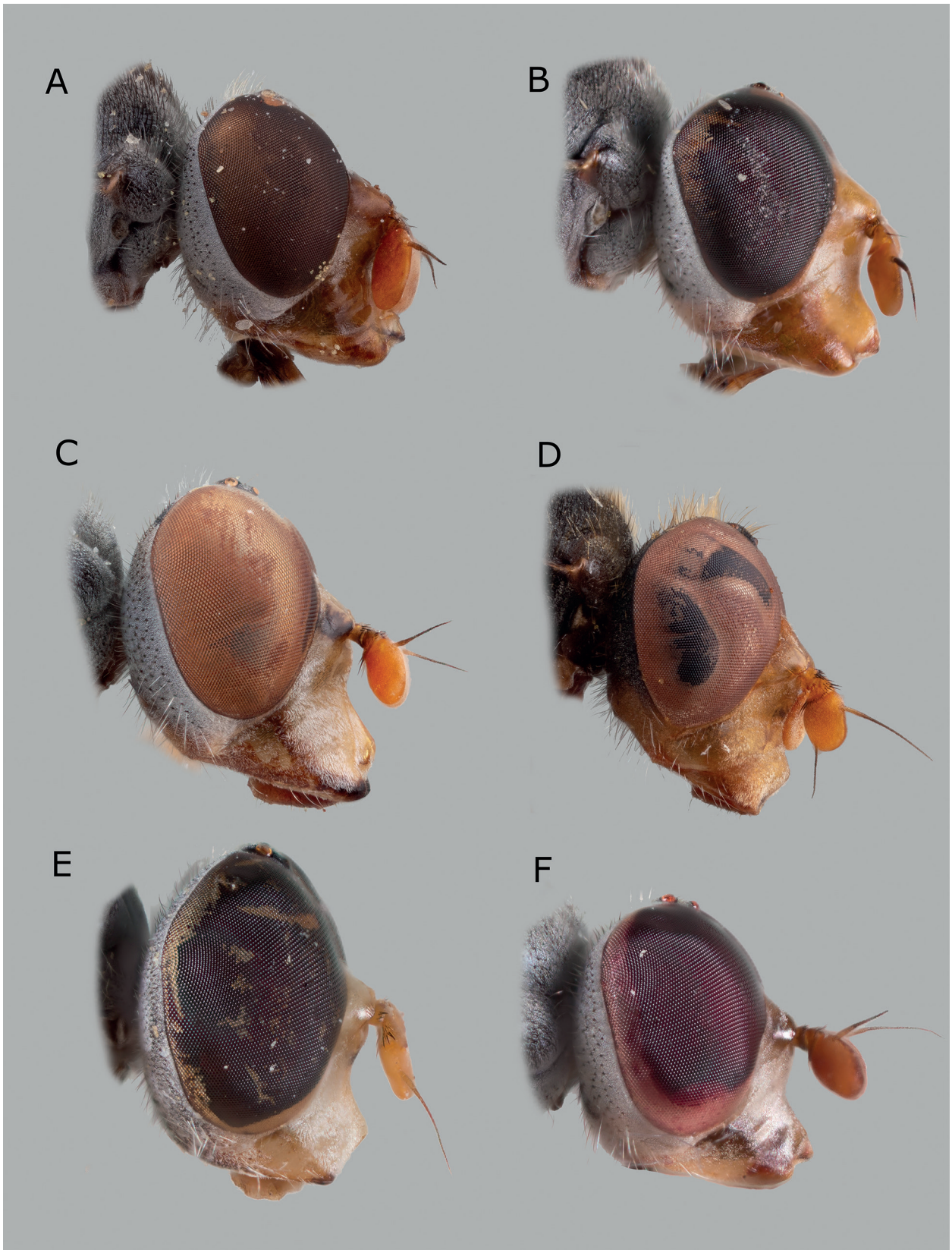

Fig. 10. Head, lateral view. **A**. *Brachyopa atlantea*, female, Granada, Spain. **B**. *B. bicolor*, male, Engsbergen, Belgium. **C**. *B. bimaculosa*, male, Arkadia, Greece. **D**. *B. cinerea*, male, Komsomolsk-na-Amur, Russian Far East. **E**. *B. grunewaldensis*, male, Zagreb, Croatia. **F**. *B. insensilis*, male, Engsbergen, Belgium.

Serbia and European Russia into the Russian Far East and Japan. No records are known from the Mediterranean area.

Biology. The adult habitat consists of lowland to subalpine mixed forest and of palsa- (see Zuidhoff & Kolstrup 2005; van Steenis & Zuidhoff 2013) and *Pinus-Betula*-bogs in Northern Scandinavia (Hippa et al. 1981; Nielsen 1992; Reemer et al. 2007; Bartsch et al. 2009).

Larvae are found in accumulations of sap under bark of trunks and stumps of *Betula* spp., *Populus tremula* and *Ulmus* spp. often together with other Diptera larvae: *Libnotes ladogensis* (Lackschewitz, 1940) and *Gnophomyia acheron* Alexander, 1950 (both Limoniidae), *Hammerschmidtia ingrica* Stackelberg, 1952 (Syrphidae), *Solva semota* Krivosheina, 1972 (Xylomyidae) and larvae of the beetle *Hylecoetus dermestoides* (Linnaeus, 1760) (Lymexylidae) (Mutin 1998; Krivosheina 2005, 2019).

Found on flowers of *Acer platanoides* L., *Caltha palustris* L., *Crataegus* spp., *Euphorbia cyparissias* L., *Malus sylvestris* (L.) Mill., *Prunus domestica* ssp. *insititia*, (L.) Bonnier & Layens, *P. padus*, *Rubus chamaemorus* L., *Salix* spp. (Hippa et al. 1981; Nilsson et al. 2007; Reemer et al. 2007; Bartsch et al. 2009; van Steenis 2011; Nilsson et al. 2012; Speight 2020), and also *Anthriscus sylvestris* (L.) Hoffm., *Geranium sylvatica* L., *Prunus avium* (L.) L., *Salix udensis* Trautv. & C.A. Mey. and *Spirea* spp. (database). Adults are more often found near trunks and stumps of *Betula* spp. and damaged coniferous trees or at sap runs on *Fagus* spp. and *Quercus* spp. (Röder 1990; Mutin et al. 2016; Mielczarek et al. 2019). In the Russian Far East, it is found near damaged coniferous trees together with several other *Brachyopa* species such as *B. panzeri*, *B. testacea* and *B. zhelochovtshevi* (Mutin et al. 2016). Larvae are found in tunnels created by Lymexylidae larvae from *Betula* and *Ulmus* (Krivosheina, 2005) and under bark of *Fagus*, *Picea*, *Populus* and *Quercus* trees (Mutin 1998; Dussaix, 2020).

This species has a main flight period (Fig. 38B) from the beginning of April until the end of July, with extreme dates of the 17th of March and the 5th of August. The altitude at which this species is collected range from 0–1503 m a.s.l. (database). It has been found in fluctuating numbers during different periods in Austria and Germany, with relatively many records from before 1900. In several other countries it has been recorded increasingly many times since 1980 (Sweden), 2007 (Netherlands) and 2009 (Belgium) indicating a possible extension of its distributional range.

Population fluctuations. No clear trends are published, but based on the larval habitat it seems likely this species will not exhibit strong population fluctuations. The larval habitat consists of trunks and stumps of a wide variety of tree species which form a natural and rather constant factor in European forests.

Remarks. This is a species that has been misidentified in many instances. References before 1980 should be treated with special care (cf. Reemer et al. 2007). The discriminating characters were first fully understood by Thompson (1980), but even since then, this species and *Brachyopa panzeri* have been mixed up (e.g. Stuke et al. 2000; Mielczarek et al. 2019). It seems that *B. dorsata* is the more northern and Alpine species, and has recently spread to the Netherlands and Belgium (Bot & Van de Meutter 2019).

Red List. This species is mentioned in four regional Red Lists and was either not evaluated or assumed to be of "Least Concern" (Bygebjerg 2004; Ssymank et al. 2011; Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019).

Brachyopa grunewaldensis Kassebeer 2000

Brachyopa grunewaldensis Kassebeer 2000a: 8; ♂ holotype in private collection of C.F. Kassebeer (present condition or whereabouts unknown), not studied.

Figs 3E, 10E, 14D, 21E, 26

Distribution. A temperate and southern European species with a very scattered distribution from Spain in the west, to Belgium and the eastern part of Germany in the north, and to Slovakia in the east. Also known from several countries on the Balkan Peninsula. This species is regarded as a European endemic.

Biology. Adults are found in Mediterranean acidophilus *Quercus-Fraxinus* forests, mixed thermophilus *Quercus-Carpinus* and *Fagus-Picea* forests, alluvial *Quercus-Populus* and *Carpinus* forest and riparian *Platanus* forest (Kassebeer 2000a; Doczkal & Dziock 2004; van Steenis et al. 2019; Speight 2020).

The larva is unknown but adults were collected in emergence traps on *Fraxinus angustifolia* Vahl, *Quercus faginea* Lam. and *Q. pyrenaica*, indicating the larvae live in rot-holes in at least these tree species (Ricarte et al. 2013).

It visits flowers of *Acer* spp., *Crataegus monogyna* Jacq., *Pyrus spinosa* Forssk., *Sorbus torminalis* (L.) Crantz and *Tamarix* spp. (Marcos-García 1987; van Steenis & van Steenis 2014; Mielczarek et al. 2019; Speight 2020) and flies close to trees with sap runs including *Aesculus hippocastanum*, *Carpinus betulus*, *Castanea sativa*, and *Quercus* spp. (Doczkal & Dziock 2004; Mielczarek et al. 2019; van Steenis et al. 2019; Speight 2020), and *Acer* spp. (database).

This widely distributed but very scattered species has been collected between the 8th of April and the 16th of June, with extreme dates of the 28th of February and the 16th of July. There are no indications of differences between southern and northern populations (Kassebeer

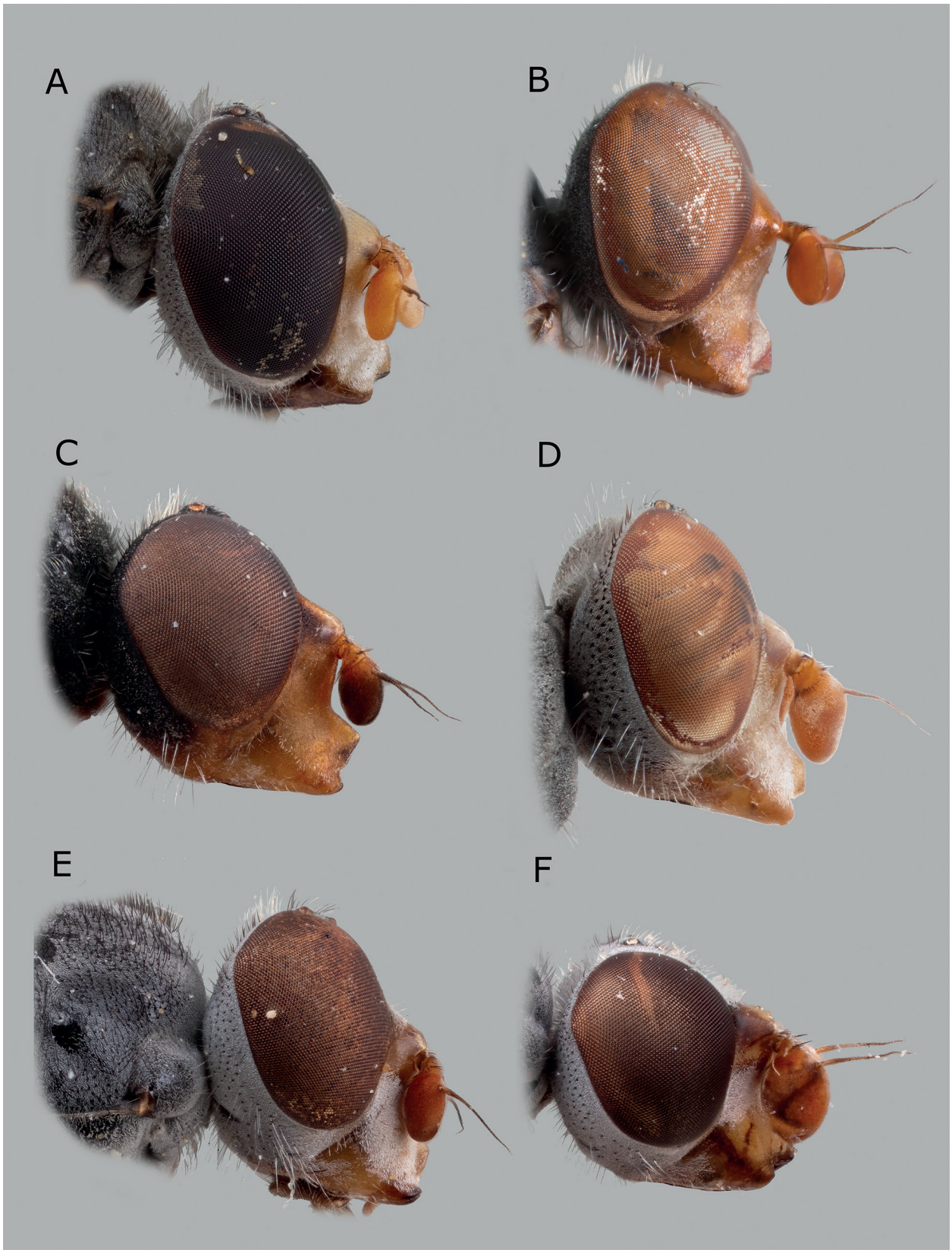

Fig. 11. Head, lateral view. **A**. *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B**. *B. silviae*, male, Bringhausen, Germany. **C**. *B. minima*, male, Lesvos, Greece. **D**. *B. vernalis*, male paratype, Crete, Greece. **E**. *B. quadrimaculosa*, male, Samos, Greece. **F**. *B. quadrimaculosa*, female, Samos, Greece.

2000; Doczkal & Dziock 2004, database). Collected at altitudes of 50–1700 m a.s.l. (database). The first record dates from 1969, and most of its records are from the 21st century. This is most likely due to the fact that more entomologists know this species and thus tend to collect it more often.

Population fluctuations. This species is only recently described and it seems to be a very rare but widespread species. The habitat preferences are not fully known and, as such, it is impossible to know whether this species might undergo population fluctuations.

Remarks. This is a recently described species confused with *B. bicolor* in the past and possibly more widespread than presently known. The habitat preferences are not well known and it might be a very specialized species with high demands on its habitat. This will make the species more vulnerable to habitat changes and thus its future survival more threatened.

Red List. It is only listed on the German Red List under category "Endangered" (Ssymank et al. 2011). The habitat of this species consists of a wide range of different forest types and each of these types is classified in a different threat category. The Mediterranean acidophilus forest (G1.8) is "Vulnerable" while the thermophilous forests (G1.7 and G4.6) are classified as "Least Concern". The alluvial forests (G1.1–G1.3) are categorized from "Near Threatened" to "Endangered" (European Commission 2016). The precise habitat preferences are not well known and due to its very scattered distribution and low population density nothing can be concluded about its main habitat. The combination of low population density, the very scattered occurrence and the supposed threat to several of its habitats indicates that this species is at risk. The database does not provide any evidence to estimate any overall population trend or possibility of fluctuating populations and so the exact threat category is unknown as this can only be estimated by applying the IUCN Red List criteria.

Brachyopa insensilis Collin, 1939

Brachyopa insensilis Collin, 1939: 105; ♂ lectotype, 4 ♂♂, 3 ♀♀ paralectotypes in UMO, studied.
Figs 3F, 5B, 10F, 14E, 18E, 21F, 27, 38C

Distribution. A widespread European species from southern Sweden south to Spain, Italy and Greece and from Ireland through central Europe into the European part of Russia. It is regarded as European endemic species.

Biology. Found in a wide variety of wooded habitats from tree-lined streets in cities to broadleaved and mixed forests and often found flying around sap runs on trees in these situations (e.g., Torp 1994; Bartsch et al. 2009; Reemer et al. 2009).

Larvae are found in a wide variety of external sap runs on broadleaved trees: *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Alnus glutinosa* (L.) Gaertn., *Betula* spp., *Cornus mas* L., *Fagus* spp., *Populus* spp., *Quercus* spp. and *Ulmus glabra* Huds. and also on coniferous trees: *Abies alba* and *Pinus nigra* (e.g. Trop 1979; Claussen 1985, Rotheray 1991, 1996; Schmid & Grossmann 1996; Stubbs & Falk 1996; Bygebjerg 2001; van Steenis et al. 2001; Dussaix 2013; Ricarte et al. 2014; van Steenis & van Steenis 2014; Krivosheina 2019).

The larvae are found together with larvae of the wood gnat *Mycetobia pallipes* Meigen, 1818 (Diptera: Anisopodidae) (Krivosheina 2019). Large and small larvae are present in the sap runs at the same time as the flight period of the adults indicating a life cycle of more than one year for the larvae (Rotheray 1996). Larvae, found on *Quercus robur*, were infested by *Tetrastichus brachyopae* (Hymenoptera: Eulophidae) (van Eck et al. 2016). Infestation with parasitoid wasps, possibly *T. brachyopae,* was also observed in reared larvae collected from *Pinus nigra* on the Peloponnesos, Greece (J. van Steenis, pers. obs.).

Several species of flowers are visited by adults such as *Aegopodium podagraria*, *Anthriscus sylvestris*, *Malus sylvestris*, *Photinia* spp., *Prunus padus* and *Sorbus* spp. (Torp 1973; Claussen 1985; de Buck 1990; Bygebjerg 2001; Bartsch et al. 2009; Speight 2020) and *Cornus mas*, *Prunus serotina*, *P. spinosa* and *Pyrus* spp. (database). In many instances adults were found flying around sap runs on these larval trees and also on the following trees: *Platanus* spp., *Salix alba* (Mielczarek et al. 2019; van Steenis et al. 2019), and *Acer campestre* L., *Betula* spp., *Carpinus* spp., *Fraxinus excelsior* L. and *Populus* spp. (database).

The main flight period (Fig. 38C) is from the beginning of April until the end of July with extreme dates of the 27th of March and the 30st of August. These early and late extremes were found in SE Europe only, but no clear differences in main flight period between other southern or northern populations has been found (database). Found from sea level up to 1760 m a.s.l. (database). The records of this species are not evenly distributed over different time periods in different countries. In several countries such as Denmark and Germany the species has many records from before 1920 and only few recent records. In other countries, such as Great Britain, Hungary, the Netherlands and Sweden, the first records date from around 1950 with most records from the 21st century, although in Sweden there are large gaps of three to eight years in which no records are available. The records from Austria, Belgium and France are mostly from the 21st century (database).

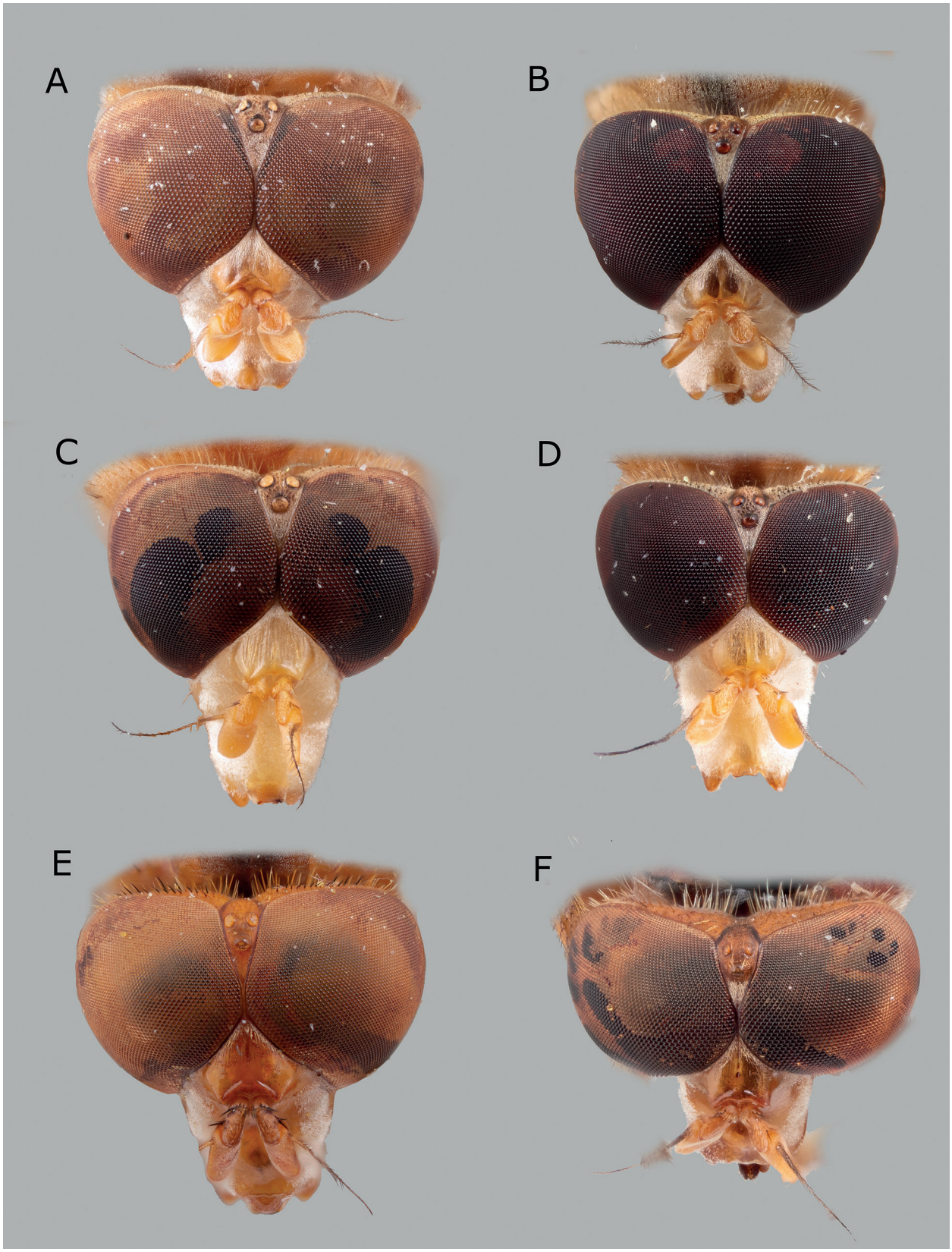

Fig. 12. Head male, dorsal view. **A**. *Brachyopa obscura*, Fiby urskog, Sweden. **B**. *B. testacea*, Elzetterbos, the Netherlands. **C**. *B. vittata*, Mångkarbo, Sweden. **D**. *B. zhelochovtsevi*, Aktru, Altay, Russia. **E**. *Hammerschmidtia ferruginea*, Riikanmaa, Finland. **F**. *H. ingrica*, Bychika, Russian Far East.

Population fluctuations. This species is very likely to have a strongly fluctuating population size and density since it is highly dependent upon external sap runs. These sap runs tend to dry out over a short period of time causing fluctuations in suitable larval habitat (e.g., Pérez-Bañón et al. 2016). The occurrence tends to follow several tree specific diseases (see more under remarks) causing large fluctuations in the availability of larval habitat. Population fluctuations could also be argued from the fluctuating records noted above.

Remarks. Previously in Great Britain this species was believed to be dependent on sap runs on *Ulmus* spp. (Robinson 1953; Stubbs & Falk 1996). This was probably influenced by Dutch Elm disease, a vasular wilt disease affecting leaves and causing death of the tree within several years, creating many damaged trees. This first "wave" of Dutch Elm disease entered England in 1927 and died out around 1940, and was a mild one causing delayed growth and only slightly damaging trees. A more aggressive form was first noticed around 1960 and by 1990 hardly any Elm trees were left (Clouston & Stansfield 1979; Holmes & Heybrook. 1990; Harris 2017). This century the available larval habitat has increased (Sjuts 2004) again since 2001–2002 throughout Western Europe due to the bleeding canker affecting *Aesculus hippocastanum* trees (e.g. de Keijzer et al. 2012; Laue 2014; Pirc et al. 2018). This increase in larval habitat will eventually decrease again due to recent discoveries of methods to stop this disease (de Keijzer et al. 2012), and there are also indications that trees naturally become more and more resistant to this bacteria (Pánkóva et al. 2015) thus decreasing the number of affected trees and hence suitable larval habitat.

Molecular data show two separate groups (J.H. Skevington, pers. comm.), one from the Peloponnesos and the other from the rest of Europe indicating some kind of gene flow barrier and possible speciation.

Red List. This species occurs on several regional Red Lists and is mostly classified as "Least Concern" (Bygebjerg 2004; Ssymank et al. 2011; Ball & Morris 2014; Artdatabanken 2019) but also "Vulnerable" (Farkač et al. 2005).

Brachyopa maculipennis Thompson, 1980

Brachyopa maculipennis Thompson, 1980: 211; new name for *Musca arcuata* Panzer, 1798: 15, primary homonym preoccupied by Linnaeus (1758); type in private collection of Panzer (presumably lost), not studied.

Brachyopa arcuata var. *lateralis* Oldenberg, 1916: 105; type in DEI, (syn by Peck 1988), not studied.

Figs 2C, 9C, 14F, 20C, 28, 38D

Distribution. This is a temperate European species with scattered records from Germany in the north to Italy in the south, eastwards to Ukraine. This species is endemic to Central Europe.

Biology. The main habitat consists of alluvial *Salix-Tilia-Populus* forest and to a lesser extent also humid broadleaved *Fagus* spp. forest with *Populus alba*, *Quercus petraea* (Matt.) Liebl. and some scattered *Pinus* spp. (Radenković et al. 2004; Mielczarek et al. 2019; van Steenis et al. 2019).

Adults have been found near external sap-runs on *Populus alba* and *Salix alba* (van Steenis et al. 2019) and on *Aesculus* spp. (database), and it is assumed that these sap-runs form the larval habitat of the species. In Poland oviposition was observed on senescent *Populus alba*. The oviposition took place about 15 cm away from the sap run (P. Trzciński, pers. comm.). Adults visit flowers of *Crataegus* spp., *Malus* spp., *Prunus padus* and *Frangula alnus* Mill. (as *Rhamnus frangula* L.) (Mielczarek et al. 2019; Speight 2020).

The species is collected between the 7th of April and 24th of June (Fig. 38D) at altitudes of 70–800 m a.s.l. The species seems to be collected relatively often in the 19th and 21st century, but with a strong decline in the first half of the 20th century. Many of the old records are from Croatia, Germany, Italy and Slovakia (database).

Population fluctuations. As with other species dependent on external sap-runs, such as *B. insensilis* and *B. minima*, it is very likely that this species also shows fluctuations in population size and densities over several decades. In Germany and Italy there are only old records and the species seems to be Critically Endangered in these countries although Germany does seem to have some post-2000 records (https://diptera.info/forum/viewthread.php?thread_id=6239) but the precise information was not available for this paper. In Serbia and especially the Czech Republic and Poland there are several recent records (Mielczarek et al. 2019; van Steenis et al. 2019) indicating there are still flourishing populations.

Remarks. The species is easy to identify and does not seem to be misidentified (e.g. Sommaggio 2007). Its occurrence is unlikely to have been overlooked in Austria, Germany or Italy in recent years, indicating that the evidence of decline is a true decline.

Red List. This species is listed as "decreasing" in the Balkan Peninsula (Vujić et al. 2001), "Endangered" in the Czech Republic (Farkač et al. 2005) and "Critically Endangered" in Germany (Ssymank et al. 2011). It is a very rare species with few and scattered records throughout its distributional range. Especially in the northern and western edge of its distribution there are mostly old records indicating a strong decline. The habitat from

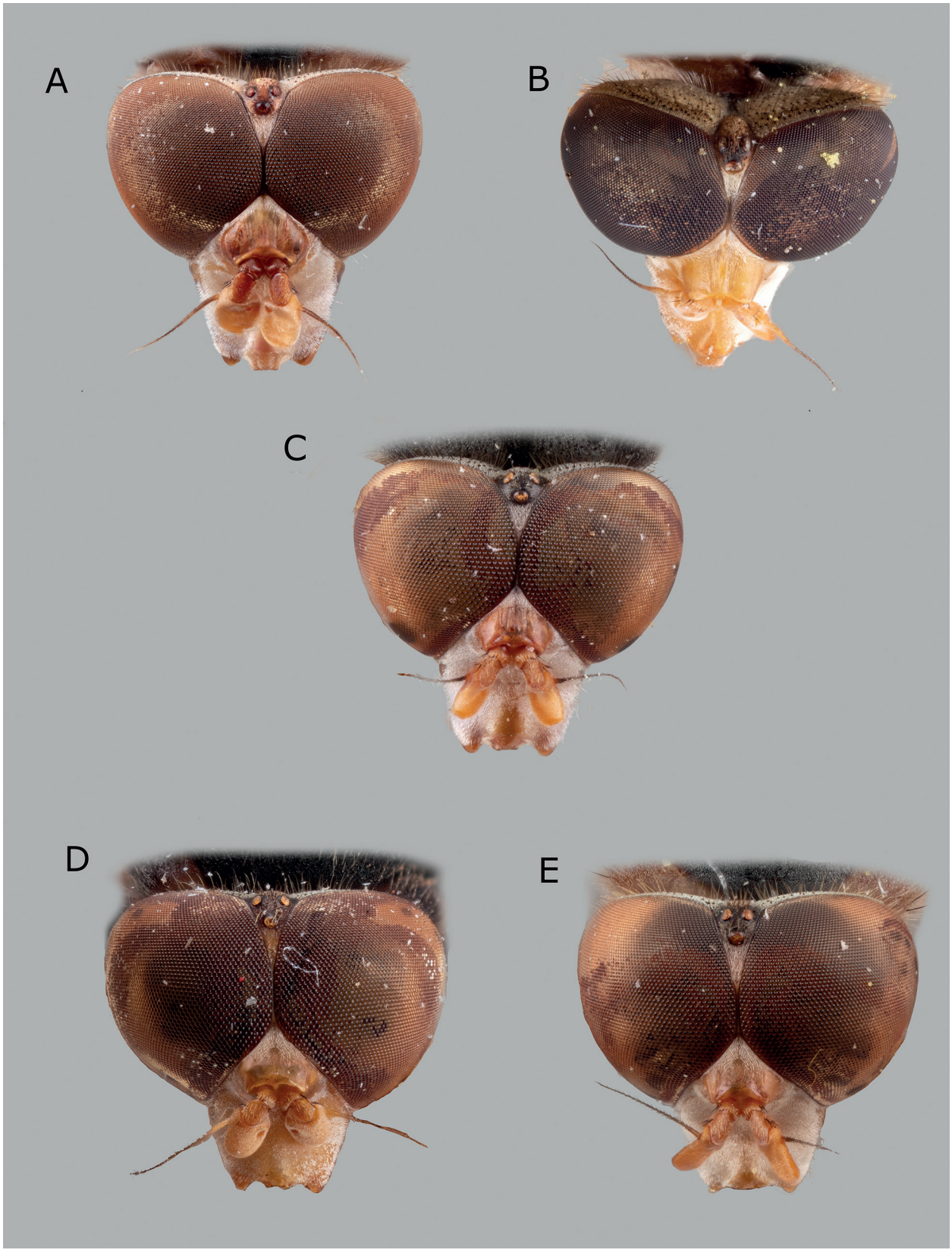

Fig. 13. Head male, dorsal view. **A**. *Brachyopa dorsata*, Den Treek, the Netherlands. **B**. *B. panzeri*, Beek (Gld), the Netherlands. **C**. *B. pilosa*, Hågadalen, Sweden. **D**. *B. plena*, male, Ioannina, Greece. **E**. *B. scutellaris*, Eure et Loire, France.

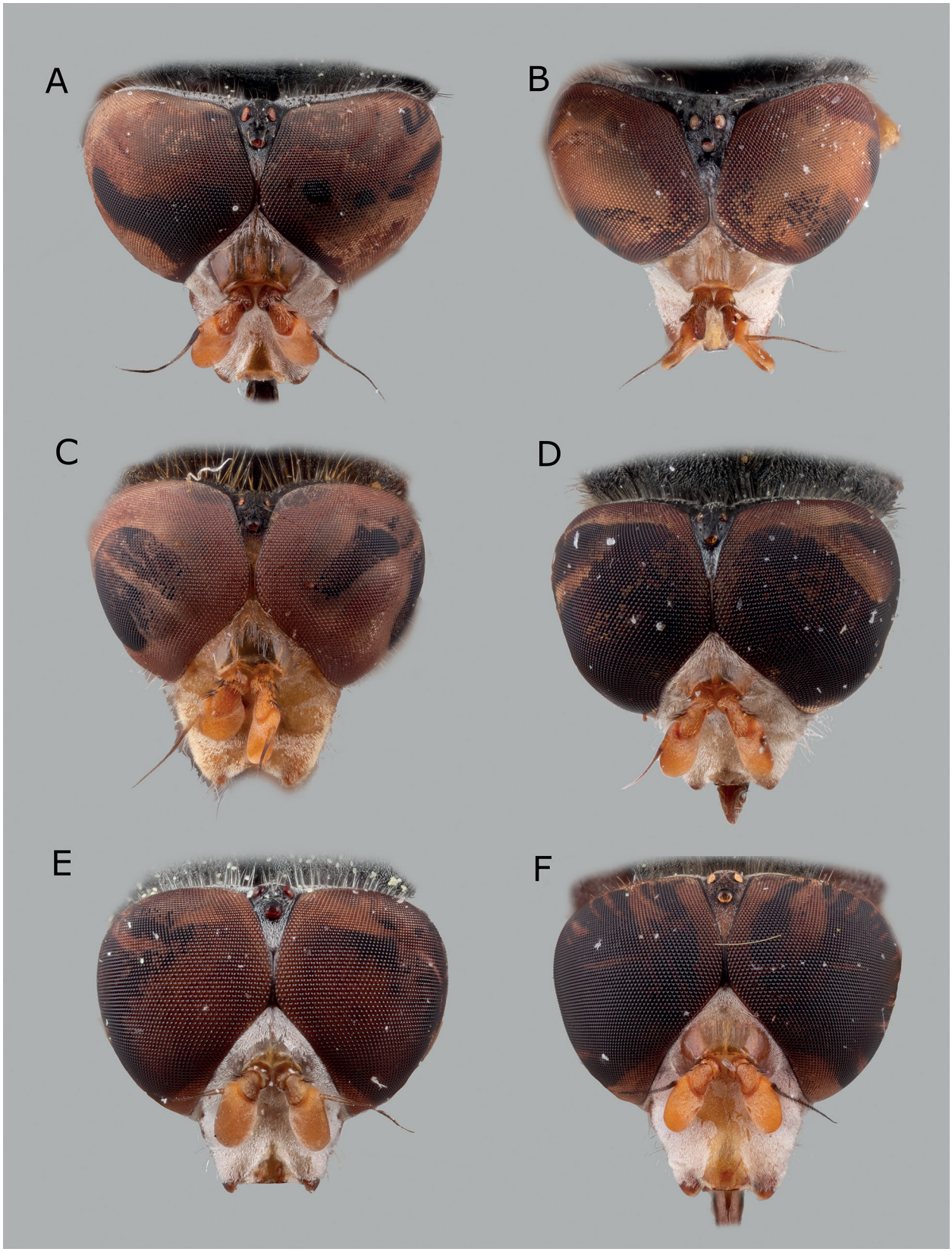

Fig. 14. Head male, dorsal view. **A**. *B. bicolor*, Novi Sad, Serbia. **B**. *B. bimaculosa*, Bolchenachtall, Germany. **C**. *B. cinerea*, Komsomolsk-na-Amur, Russian Far East. **D**. *B. grunewaldensis*, Arkadia, Greece. **E**. *B. insensilis*, Novi Sad, Sebia. **F**. *B. maculipennis*, Fruška Gora, Serbia.

which this species is known can be categorized as riparian forests under EUNIS classification G1.1 to G1.3 and G1.A. These forest classes are considered "Vulnerable" to "Endangered" on the Red List of European habitats (European Commission 2016). The area and quality of the alluvial forests in Europe are rapidly declining (Secerov & Nevenic 2004; Hughes et al. 2012) and, as such, this habitat and *Brachyopa maculipennis* could be classified as "Endangered" or even "Critically Endangered".

Brachyopa minima Vujić & Pérez-Bañón in Pérez-Bañón et al. 2016

Brachyopa minima Vujić & Pérez-Bañón in Pérez-Bañón et al. 2016: 220; ♂ holotype, 6 ♂♂, 3 ♀♀ paratypes in FSUNS and ♀ paratype in MZH, studied.
Figs 4C, 11C, 15B, 22

Distribution. Only known from two localities in Greece, on Lesvos Island from one single *Populus nigra* tree, and northern Greece (Vujić et al. 2020). It is assumed to be a European endemic.

Biology. Larvae were found from the 26th of April until the 3rd of May and on the 13th and the 28th of September. The adults and larvae were all found on a single *Populus nigra* tree with a large wound creating a slime-flux with different larval stages of several species present: *Brachyopa* aff *pilosa* and *B. quadrimaculosa*. The *B. minima* larvae survived desiccation for two years, as found in the similar *B. insensilis*. The tree was part of a small *Populus* stand along a small stream, otherwise surrounded by olive groves. The *Populus nigra* tree was the only one in a large area with a visible sap run (Pérez-Bañón et al. 2016).

Collected between the 12th of April and the 3rd of May at altitudes between 25 and 225 m a.s.l. (database).

Population fluctuations. It seems very likely this species shows extreme fluctuations in population size as it is highly dependent on naturally occurring external sap-runs on old *Populus* trees. These sap-runs are known to be scarce on the island of Lesbos and tend to heal over after relatively short periods of time (Pérez-Bañón et al. 2016), mostly no longer than 10 years.

This species seems to be at risk due to overgrazing, mainly by sheep (Kizos et al. 2013), and forest fires (Kalabokidis et al. 2013) which are major threats to the natural forests on Lesvos (Pérez-Bañón et al. 2016).

Remarks. This species belongs to a widespread species complex with possibly more undescribed Mediterranean species.

Red List. This species is not mentioned in any Red List as it has only very recently been described. Based on its restricted occurrence and the possible threat to the habitat, as outlined above, this species is severely threatened.

Brachyopa obscura Thompson & Torp, 1982

Brachyopa obscura Thompson & Torp, 1982: 441; ♂ holotype and 8 ♂♂ paratypes in ZISP, studied here.
Figs 1A, 8A, 12A, 16A, 19A, 29, 39A

Distribution. A widespread northern species with a disjunct distribution in other parts of central and south-eastern Europe. Its occurrence east of European Russia is unknown but likely.

Biology. It is associated with mixed boreal forests with overmature trees such as *Betula* spp., *Populus tremula* and *P. nigra* and other rich deciduous forests of the "*Alnion glutinosae*" and "*Alno-Ulmion*" classes (Nielsen 1992; Stuke 2001b; Bartsch et al. 2009; Wakkie et al. 2011; Pétremand et al. 2020). Unlike the very similar adults of *B. testacea*, it is very rare in coniferous dominated forests.

The larva is unknown but there is one record of an adult which hatched from the bark of a *Pyrus* spp. (Nielsen 2005), indicating the larvae live in accumulations of sap under bark or in internal sap-runs.

This species has been collected on flowering herbs and bushes such as *Acer platanoides*, *Aegopodium podagraria*, *Anthriscus sylvestris*, *Crataegus* spp., *Prunus padus*, *P. serotina*, *P. spinosa*, *Ribes alpinum* L. and *Salix* spp. (van Steenis 1998; Stuke 2001b; Haarto & Kerpolla 2007; Nilsson et al. 2007; Bartsch et al. 2009; van Steenis 2011; Nilsson et al. 2012; Mielczarek et al. 2019) and *Filipendula ulmaria* (L.) Maxim (database).

The overall flight period is from May to July (Fig. 39A) and the Northern populations have a flight period from the 2nd of May to the 2nd of July, with an extreme datum of 15th of July. The other scattered records throughout east and central Europe are from the 20th of April to the 21st of June. The altitudinal range is from 40–1560 m a.s.l. (database).

Population fluctuations. Population size increased strongly a few years after a large storm during which several *Populus tremula* trees were felled (Nilsson et al. 2007, 2012). Based on these observations in Sweden this species shows an extreme fluctuating population size.

Remarks. The records in central and south-eastern Europe could be interpreted as isolated populations. The extreme fluctuations in population size, in combination with the lack of suitable habitat, could account for the fact that *B. obscura* records are so scattered over this part of Europe.

Red List. This species is reported in the Fennoscandian Red Lists as of "Least Concern" to "Endangered" (Hen-

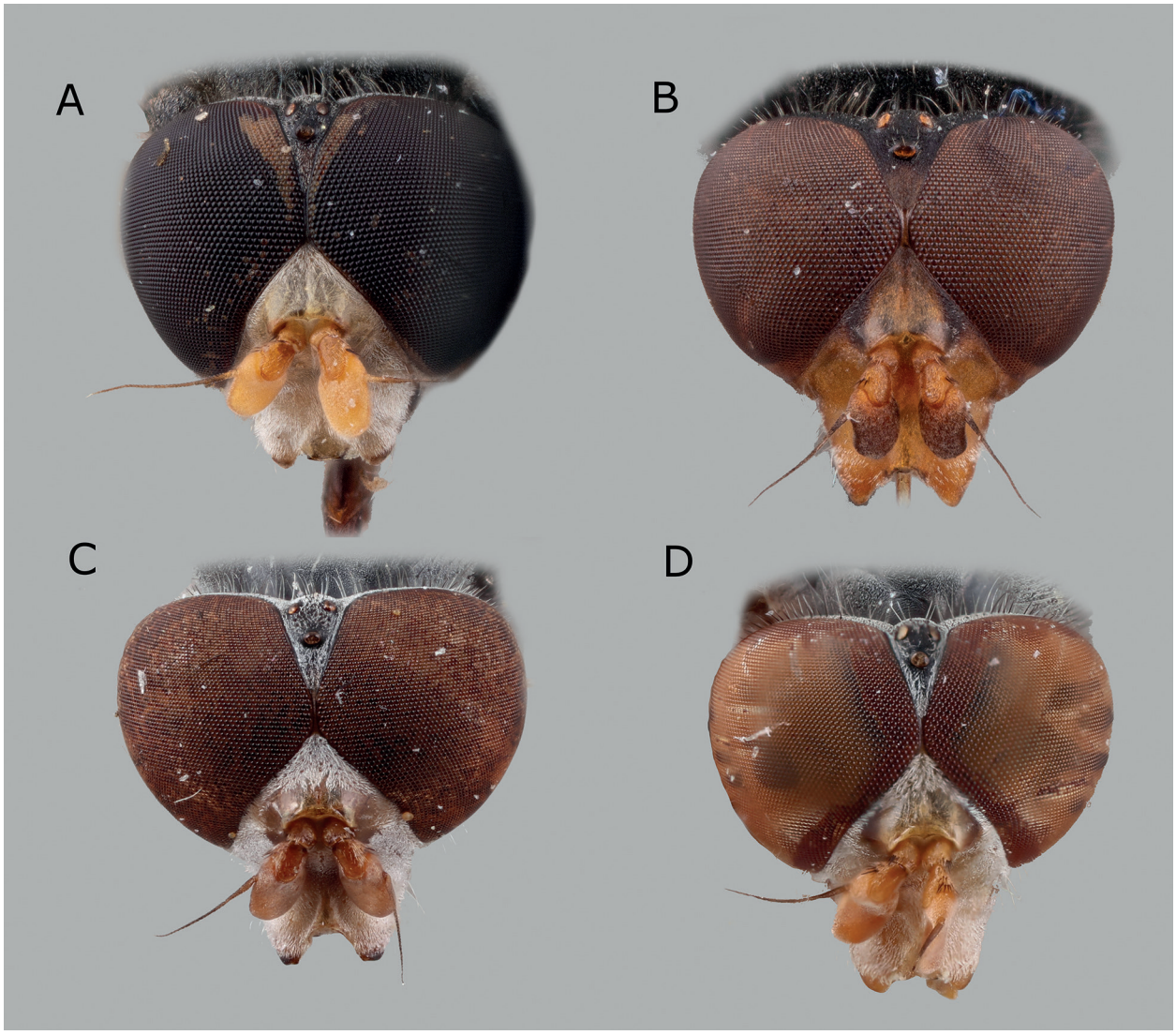

Fig. 15. Head male, dorsal view. **A**. *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B**. *B. minima*, male, Lesvos, Greece. **C**. *B. vernalis*, male paratype, Crete, Greece. **D**. *B. quadrimaculosa*, male, Samos, Greece.

riksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). In Germany it is very rare and not put into any Red List category (Ssymank et al. 2011). On the Balkan Peninsula it occurs in a very small and restricted area and is categorized as "Threatened" (Vujić et al., 2001).

It has a wide occurrence in Fennoscandia and a very disjunct distribution in other parts of Europe and regional differences in threat category are to be expected.

Brachyopa panzeri Goffe, 1945

Brachyopa panzeri Goffe, 1945: 278; new name for *conica* Panzer, 1798: 20, junior primary homonym, according to Thompson (1980) preoccupied by Gmelin (1790); type in private collection of Panzer or NWM (presumably lost), not studied.

Figs 2B, 9B, 13B, 17B, 20B, 30, 39B

Distribution. Widespread in northern and temperate Europe from southern Sweden to Spain and from central France eastwards through European Russia and into Siberia.

Biology. Mostly found in humid *Fagus* forests but also in alluvial *Populus* forest, mixed *Carpinus-Quercus-Pinus* forests and even in coniferous forests (Torp 1994; Lauterbach 2001, 2002; Reemer et al. 2009).

The larva has been found in a sap run on *Fagus sylvatic*a (Stuke & Schulz 2001) and maybe also in a *Picea* spp. stump in the larval tunnels of *Hylecoetus flabellicornis* (Coleoptera: Lymexylidae) (Krivosheina 2005). The larvae are found together with larvae of *Gnophomyia lugubris* (Zetterstedt, 1838) (Diptera: Limoniidae), *Mycetobia pallipes* (Diptera: Anisopodidae) and with *Brachyopa vittata* (Krivosheina 2019). The records from

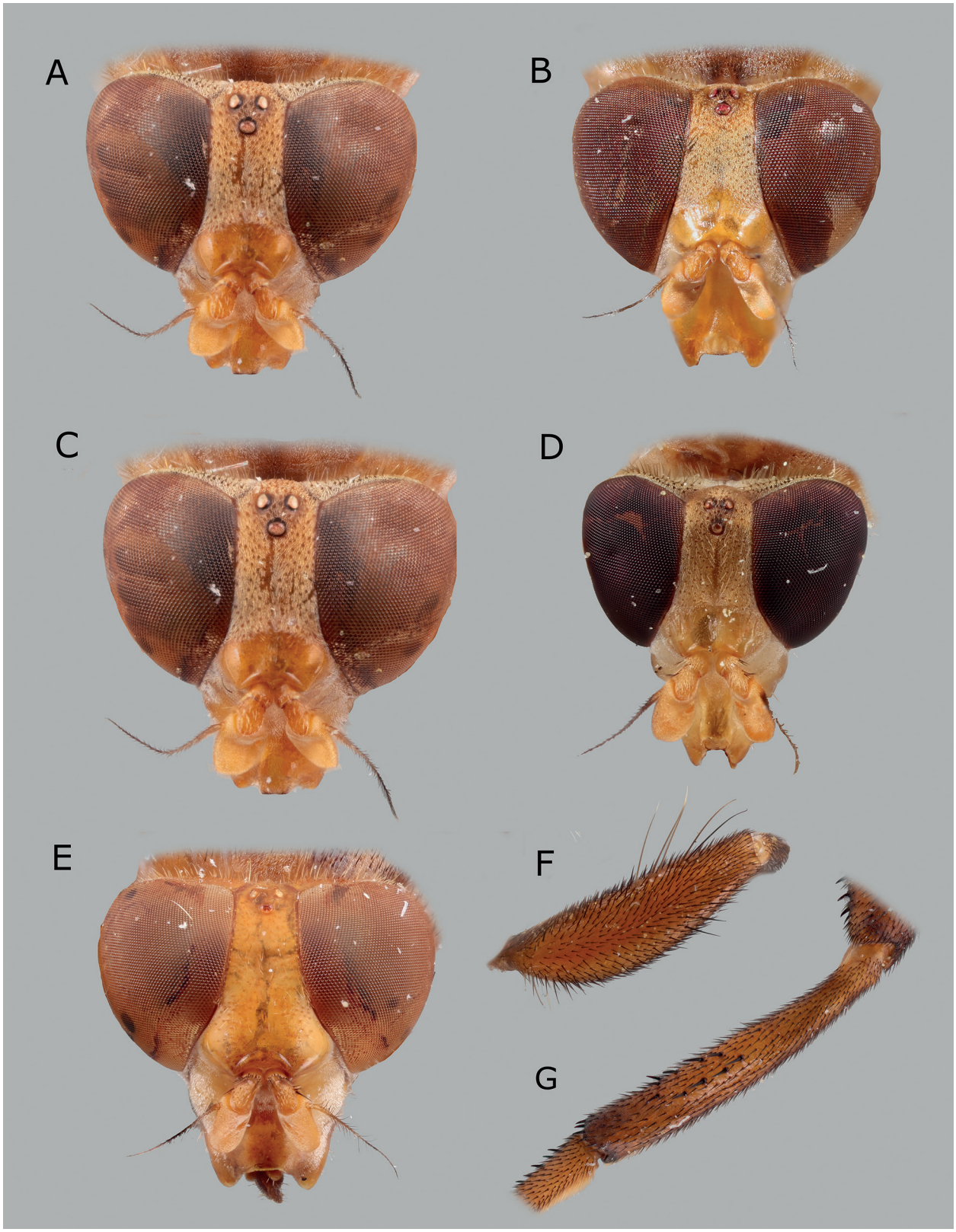

Fig. 16. *Brachyopa* and *Hammerschmidtia* species, **A–E** head female, dorsal view, **F** male profemur, dorsal view, **G** male metatibia, dorsal view. **A**. *Brachyopa obscura*, Fiby urskog, Sweden. **B**. *B. testacea*, Hautes-Fagnes, Belgium. **C**. *B. vittata*, Bolgenachtall, Germany. **D**. *B. zhelochovtsevi*, Aktru, Altay, Russian. **E**. *Hammerschmidtia ferruginea*, Fiby urskog, Sweden. **F**. *H. ferruginea*, Riikanmaa, Finland. **G**. *H. ferruginea*, Fiby urskog, Sweden.

Krivosheina (2005, 2019) are based on larvae only and it is not clear if these larvae really belong to *B. panzeri* as no adults were reared from these larvae (Speight 2020).

Adults have been seen visiting flowers of *Acer pseudoplatanus*, *Anthriscus sylvestris*, *Crataegus* spp., *Prunus padus*, *P. spinosa*, *Salix* spp., *Sambucus racemosa* L., (Barkemeyer, 1986; Röder 1990; Nilsson et al. 2007; Reemer et al. 2009) as well as on *Prunus cerasus* L. (database). Adults are more often found hovering around stumps or at sap runs on *Acer* spp., *Aesculus hippocastanum*, *Castanea sativa*, *Fagus* spp., *Pinu*s spp. and *Ulmus* spp. (Torp 1994; Lauterbach 2002; Bartsch et al. 2009; Merz 2009; Ricarte et al. 2014; Mutin et al. 2016).

The flight period (Fig. 39B) is from the beginning of April until the beginning of July, with the latest date of the 20th of July. It was collected at altitudes of 0–1375 m a.s.l. (Barkemeyer 1986; Maibach et al. 1992; Ricarte et al. 2014; database). In several countries pre 1900 records are available, but several other countries only have records after 1950 to 1970. In most countries there are no records over several consecutive years and the number of records seems to have increased during the 21st century.

Population fluctuations. This species seems to fluctuate over the years in the Netherlands and has not been found in consecutive years at the same locality. The larval habitat consists of trunks and stumps of a wide variety of tree species which form a natural and rather constant factor in European forests. Thus, based on the larval habitat, it is predicted that this species will not show strong population fluctuations.

Remarks. In Western Europe this species is supposedly connected with *Fagus* forests which have provided consistent forest cover for centuries and perhaps explains why this species does not seem to fluctuate much in the number of populations (database).

Red List. In most countries treated as "Near Threatened" or "Vulnerable", except in Germany where it is of "Least Concern". However, in several Bundes-Länder it is classified as "Vulnerable" (Pellmann et al. 1996; Doczkal et al. 2001; Bygebjerg 2004; Dziock et al. 2004; Farkač et al. 2005; Ssymank et al. 2011; Artdatabanken 2019). The habitat of this species is listed as "Least Concern" in the European Red List of habitats (European Commission 2016).

Brachyopa pilosa Collin, 1939

Brachyopa pilosa Collin, 1939: 107; 3 ♂♂ syntypes NHM and 2 ♂♂ syntype in UMO, studied here.
Figs 2D, 7D, 9D, 13C, 17C, 20D, 31, 39C

Distribution. A widespread European species, from northern Norway south to the Pyrenees and Italy, and from Ireland to European Russia in the east; also known from Georgia.

Biology. Found either in rich deciduous forests (preferably *Fagus*), alluvial forests with *Populus nigra*, humid *Picea* spp. forest or even city parks (Röder 1990; Reemer et al. 2009; Ball & Morris 2014).

Larvae are found under bark of *Betula* spp., *Fagus sylvatica*, *Populus tremula*, *Quercus* spp., and *Picea abies* trunks (McLean & Stubbs 1990; Rotheray 1991; Kassebeer 1993; Torp 1994; Lauterbach 2001; Krivosheina 2005; Mielczarek et al. 2019). The species is often accompanied by larvae of the following species: *Gnophomyia viridipennis* (Gimmerthal, 1847) (Diptera: Limoniidae), *Mycetobia pallipes*, *Sylvicola cinctus* (Fabricius,1787) (Diptera: Anisopodidae) and species of the family Sesiidae (Lepidoptera) and Ceratopogonidae (Diptera). In contrast to the known larvae of other *Brachyopa* species, there are no xylophagous larvae associated with *Brachyopa pilosa* (Krivosheina 2019). Larvae are known to be parasitized by *Tetrastichus* spp. (Hymenoptera: Eulophidae) (Kassebeer 1993). Several larvae found in a sap run on *Quercus robur* were infested by *Tetrastichus brachyopae* (van Eck et al. 2016).

Flowers visited include *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Aegopodium podagrica*, *Allium ursinum* L. *Anemone nemorosa* L., *Anthriscus sylvestris*, *Cardamine pratensis* L., *Crataegus* spp., *Heracleum pubescens* (Hoffm.) M. Bieb., *Malus sylvestris*, *Photinia* spp., *Prunus cerasifera* Ehrh., *P. padus*, *P. spinosa*, *Pyrus communis* L., *Salix* spp. and *Viburnum opulus* L. (Torp 1973, 1994; Claussen 1985; de Buck 1990, Kormann 1993; Bygebjerg 2001; Nilsson et al. 2007; van Steenis 2016; Speight 2020) as well as *Astilbe* spp., *Cornus* spp., *Prunus avium*, *P. serotina*, *Rhamnus cathartica* L., *Spirea* spp. and *Tilia* spp. (database). Adults are found on the tree trunks of *Betula* spp. *Populus tremula*, *Quercus rubra* or the logs of coniferous trees such as *Larix* spp. and *Picea* spp. They are seldomly seen around trees with sap runs (Reemer et al. 2009).

The main flight period (Fig. 39C) is from the end of March until the end of July, with extreme dates of the 21st of February and the 24th of July, from an altitudinal range from sea level up to 1582 m a.s.l. (Maibach et al. 1992; database). In many countries this species seems to have stable populations because the number of records does not show great fluctuations over the years. In Denmark the species seems to have declined although the map is somewhat misleading as many records are from 1990 to 1999 and thus rather recent.

Population fluctuations. This species can be found during many consecutive years at the same locality and it seems unlikely that this species shows strong population fluctuations. The larval habitat consists of trunks and

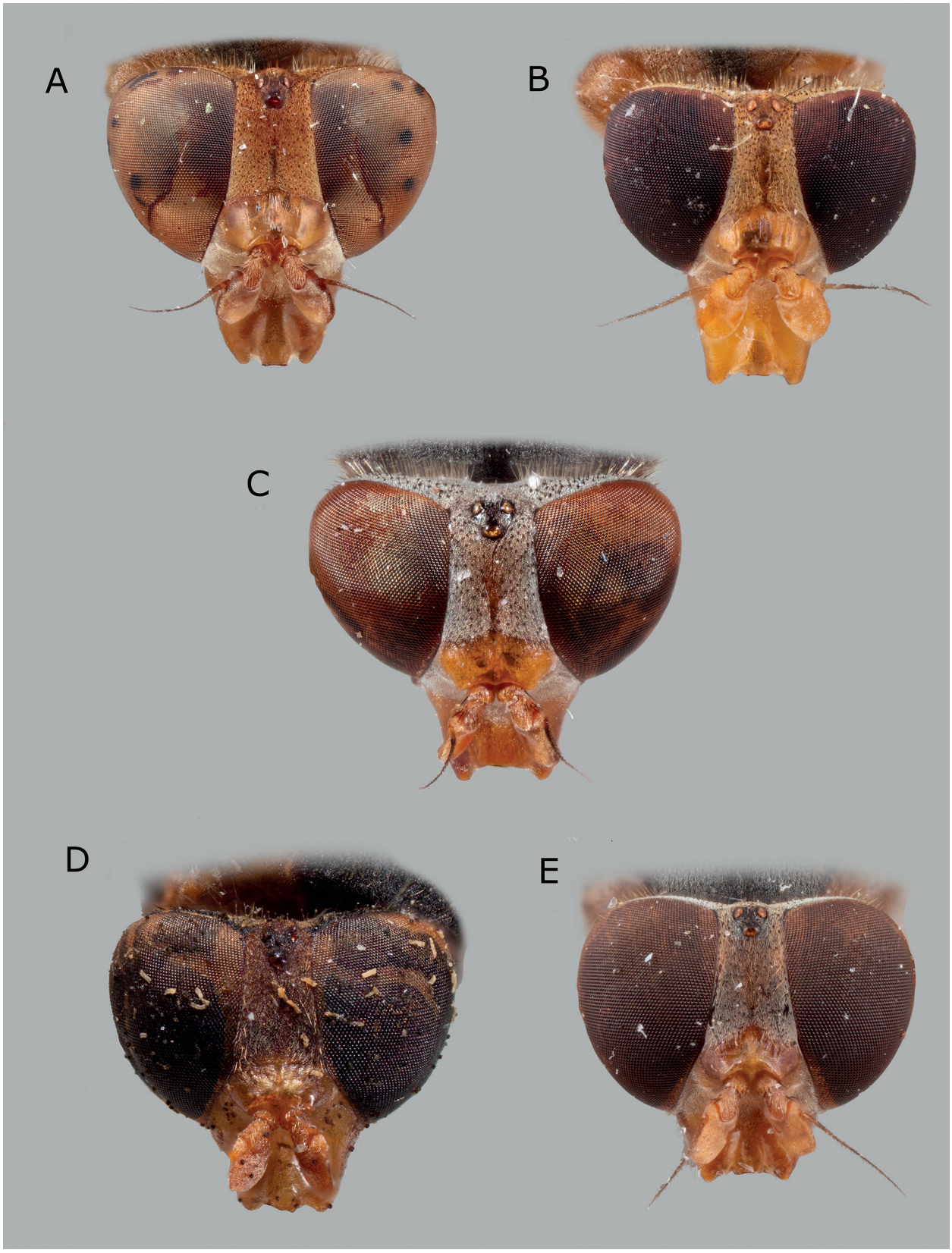

Fig. 17. Head female, dorsal view. **A**. *Brachyopa dorsata*, Fiby urskog, Sweden. **B**. *B. panzeri*, Tumnin, Russian Far East. **C**. *B. pilosa*, Fiby urskog, Sweden. **D**. *B. plena*, Zagreb, Croatia. **E**. *B. scutellaris*, Gronsveld, the Netherlands.

stumps of a wide variety of tree species which form a natural and rather constant factor in European forests.

Remarks. A widespread species possibly with good dispersal capacities because it has spread throughout the Netherlands within 50 years (Reemer et al. 2009), and colonized a small city park in an otherwise agriculture-dominated environment within some years of the felling of *Populus* spp. (J. and W. van Steenis, pers. obs.).

Red List. Mentioned in several European Red Lists and mainly categorized as "Least Concern" except in the Czech Republic ("Vulnerable") and Norway ("Endangered") (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011; Ball & Morris 2014; Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). In Norway the species reaches its northern distributional limit which makes it vulnerable. The habitat is listed as "Least Concern".

The wide distribution in many parts of Europe is the reason why this species is classified as "Least Concern" on other Red Lists.

Brachyopa plena Collin, 1939

Brachyopa plena Collin, 1939: 108; 2 ♂♂ syntypes in UMO, studied.
Figs 2E, 9E, 13D, 17D, 20E, 32

Distribution. A South-East European species with records from Germany (Kassebeer, 2000; Lauterbach 2002, see below) and further known from Austria, Czechia, Hungary, Slovakia and the Balkan Peninsula. This is a European endemic.

Biology. Found in Mediterranean oak forests and deciduous alluvial gallery forest within *Pinus brutia* Ten. forest (Speight 2020).

Flowers visited include *Acer campestre*, *Crataegus* spp., *Pyrus spinosa*, *Salix* spp. and *Sorbus torminalis* (Speight 2020). Adults are also seen flying around the base of *Quercus* spp. (database).

This species has been collected between the 4th of April and the 28th of May with an latest date of the 19th of July. The altitudinal range of this species is 113–1000 m a.s.l. (database). The number of records in the 21st century equals those of the 20th century and based on the strong increase in observers in the 21st century possibly indicating a slow decline.

Population fluctuations. There are no data supporting a strong fluctuation in population size or density. The larval habitat of this species is not well known. This makes it impossible to estimate if this species experiences strong population fluctuations.

Remarks. Almost identical with *B. scutellaris* that replaces this species in the western parts of Europe. The study of the type material of *B. plena* (J. van Steenis, pers. obs.) confirms the identity of the south-east European specimens as belonging to this species. The differences between these specimens and those of the western counterpart *B. scutellaris* are very small and further study is needed to see whether these species should be synonymized or kept as two separate species. Molecular data show a small difference between *B. plena* and *B. scutellaris* indicating there is some genetic variation between these species (J.H. Skevington, pers. comm.).

Red List. It is listed in Germany (Ssymank et al. 2011) as "data deficient" possibly based on the record by Lauterbach (2002). This record is very doubtful as no records of *B. scutellata*, much more common in Germany, were mentioned in Lauterbach's paper; therefore this record is not taken into account in the present paper.

Brachyopa quadrimaculosa Thompson in Kaplan & Thompson, 1981

Brachyopa quadrimaculosa Thompson in Kaplan & Thompson, 1981: 208, ♂ holotype and ♀ allotype in ECTAU and 11 ♂♂, 2 ♀♀, in CNC, ECTAU, NHM and USNM, not studied.
Figs 4E, 4F, 11E, 11F, 15C, 18F, 33

Fig. 18. (suggested).

Distribution. Originally described from Israel with a few additional records from North Greece, the islands of Lesvos and Samos, and a first record for Cyprus (database).

Biology. Adults were found in alluvial and *Platanus orientalis* L. forest within Mediterranean *Quercus frainetto* Ten. and *Q. pubescens* forest, alluvial *Populus* forest within *Pinus brutia* forest and Mediterranean maquis. Found visiting flowers of *Pyrus spinosa* and *Smyrnium olusatrum* L. (Kaplan & Thompson 1981; Speight 2020). Also collected in alluvial *Alnus orientalis* forest within mixed *Platanus orientalis* and *Pinus brutia* forest (collection A. van Eck).

The flight period is from the 31st of March until the 1st of May and the species is collected at altitudes of 25–550 m a.s.l. (database). The first European record dates back to 1988 and all other records are from 2007 or later.

Population fluctuations. Too little is known about the habitat preferences of this species to say anything about the population fluctuations.

Remarks. This species is most likely to have the same habitat preferences as *Brachyopa minima*, and is likely to be affected by the same habitat threats on Greek islands,

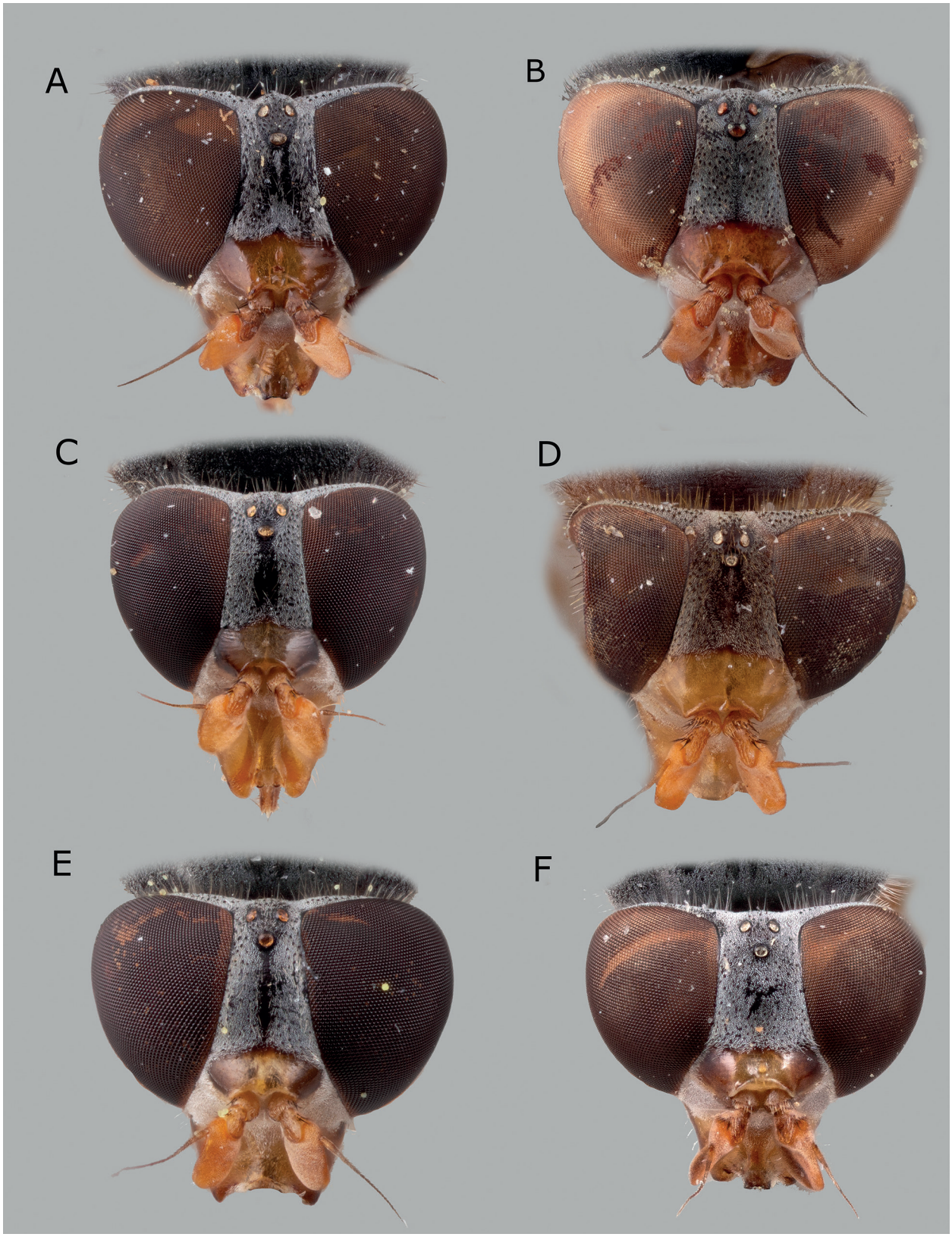

Fig. 18. Head female, dorsal view. **A**. *Brachyopa atlantea*, female, Granada, Spain. **B**. *B. bicolor*, Maarn, the Netherlands. **C**. *B. bimaculosa*, Arkadia, Greece. **D**. *B. cinerea*, Komsomolsk-na-Amur, Russian Far East. **E**. *B. insensilis*, Novi Sad, Serbia. **F**. *B. quadrimaculosa*, Samos, Greece.

namely sheep grazing (Kizos et al. 2013) and forest fires (Kalabokidis et al. 2013).

Red List. Not mentioned on any Red List. See further comment under *Brachyopa minima*.

Brachyopa scutellaris Robineau-Desvoidy, 1844

Brachyopa scutellaris Robineau-Desvoidy, 1844: 39; ♀ holotype in MNHNP, not studied.
Figs 2F, 7E, 9F, 13E, 17E, 20F, 32, 39D

Distribution. A west European species, regarded as European endemic.

Biology. Found in humid deciduous forests, most notably alluvial and swamp forests.

Larvae are found in sap runs on *Acer pseudoplatanus*, *Alnus* spp., *Fraxinus excelsior*, *Populus tremula*, *Taxus baccata* L. and *Ulmus glabra* (Seguy 1961; Rotheray 1996; Pellmann 1998; Reemer et al. 2009). In a sap run on *Fraxinus excelsior* in Bretagne, France, the larvae of this species were accompanied by larvae of *Ferdinandea cuprea* Scopoli and *Volucella inflata* Fabricius (Diptera: Syrphidae) (J. van Steenis, pers. obs.).

Visiting flowers of *Aegopodium podagraria*, *Anthriscus sylvestris*, *Cardamine pratensis*, *Cornus* spp. *Crataegus* spp., Heracleum *Malus* spp., *Photinia* spp., *Prunus padus*, *Rubus fruticosus*, *Sorbus* spp. and *Viburnum opulus* (de Buck 1990; Bygebjerg 2001; Reemer et al. 2009; Mielczarek et al. 2019), as well as *Acer* spp., *Chaerophyllum temulum* L., *Genista* spp. *Heracleum* spp., *Prunus serotina*, *Salix* spp. and *Smyrnium olusatrum* (database). Adults are more often found on tree trunks of *Fagus* spp., *Quercus* spp., and sap runs on *Betula* spp. or hovering around *Castanea sativa* (Ricarte et al. 2014), and around *Acer* spp. (database).

The flight period (Fig. 39D) is from the beginning of April until end of July with the extreme dates of the 20th of March and the 20th of August (database). A species found at altitudes of 0–1250 m a.s.l. (Maibach et al. 1992; Ricarte et al. 2014; database). In France and Great Britain this species shows large fluctuations in the number of records each year, while in several other countries the number of records seems to be more stable.

Population fluctuations. This species can be found in the same locality several years in a row, sometimes even in forests seemingly without suitable external sap-runs. The larvae are mostly associated with external sap-runs, a habitat showing extreme fluctuations over time. This makes this species will very likely also show strong population fluctuations.

Remarks. In Poland, large variation in the size and shape of the sensory pit was found (Mielczarek et al. 2019), which could indicate that *Brachyopa plena* is just a variant of *B. scutellaris* and not a separate species. There are also other scenarios possible and the area where these specimens were found would be the place to visit for further study, to see if there is overlap in the distinguishing characteristics between these two species.

Red List. Mentioned on several regional Red Lists under "Near Threatened", "Vulnerable" and even "Endangered" (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011). In Sweden it is listed as "not applicable" (Artdatabanken 2019) but the reason why is not very clear; its real threat category for Sweden could be "Near Threatened" to "Endangered". The corresponding habitat types in the EU list are, with the threat category in brackets G1.2a (LC), G1.2b (EN) and G1.4 (VU) (European Commission 2016).

Brachyopa silviae Doczkal & Dziock, 2004

Brachyopa silviae Doczkal & Dziock, 2004: 50; ♂ holotype in NMM, 2 ♂♂, 3 ♀♀ paratypes in private collections, not studied.
Figs 4B, 11B, 33

Distribution. Known from its type locality in Germany and recently reported from France and Serbia (Doczkal & Dziock 2004; Speight et al. 2013; van Steenis et al. 2019) and also known from Austria. It is an endemic species for Europe.

Biology. Found near sap runs on a trunk of a *Carpinus betulus* tree and in ancient *Quercus-Fagus* forests (van Steenis et al. 2019) as well as in thermophilous *Quercus* and mesophilous *Fagus* forests (Doczkal & Dziock 2004; Speight et al. 2013).

Visiting flowers of *Crataegus* spp. and *Pyrus spinosa* (Speight 2020) and *Acer pseudoplatanus* (database).

The species has been collected between the 3rd of April and the 12th of May at an altitude of 75–925 m a.s.l. (database). All 10 records are post 1999.

Population fluctuations. This species has only observed regularly in Germany. The records for Austria, France and Serbia were mostly single specimens on a single occasion. The German records are too few to see any sign of extreme fluctuations.

Remarks. This is a very rare species found in three widely separated locations. Only the German population can be considered to be stable. The localities are so far apart that there will not be any exchange between them and, as such, the distribution is extremely fragmented.

Red List. Only mentioned on the German Red List, classified as "data deficient" (Ssymank et al. 2011).

***Brachyopa testacea* (Fallén, 1817)**

Rhingia testacea Fallén, 1817: 34, types in NHRS, not studied.

Figs 1B, 8B, 12B, 16B, 19B, 34, 40A

Distribution. A widespread boreo-alpine species found from northern Norway south to the Pyrenees and Bulgaria and from Belgium east through the Alps and the Baltic states into European Russia. It is also widely distributed in the boreal zone of the Palaearctic region up to the Russian Far East.

Biology. The adult habitat consists of pine forests or pine-dominated mixed forests (Löhr 1992; Bartsch et al. 2009; Reemer et al. 2009). Adults are also observed in broadleaved dominated mixed forests, often while visiting flowers (database).

Larvae and puparia have been found under bark of *Picea* stumps in association with tunnels of Lymexylidae larvae (Coleoptera) (Nielsen 1992; Löhr 2002; Bartsch et al. 2009; Krivosheina 2019).

Adults are often found near damaged coniferous trees, especially stumps of *Picea abies* (Löhr 1992; Mutin et al. 2016) but also further away from coniferous trees in mixed forests foraging on flowering herbs and shrubs of *Prunus padus* and *Sorbus aucuparia* L. (J. van Steenis, pers. obs.). Other flowers visited are *Acer pseudoplatanus*, *Aegopodium podagraria*, *Anemone nemorosa*, *Angelica archangelica* L., *Angelica sylvestris* L., *Anthriscus sylvestris*, *Cardaminopsis arenosa* (L.) Lawalrée, *Crataegus* spp., *Malus* spp., *Meum* spp., *Myrrhis odorata* (L.) Scop. *Prunus avium* (as *Cerasus avium* in part of database), *P. spinosa*, *Ribes alpinum*, *Salix* spp., *Saxifraga granulata* L., *Scorzonera humilis* L., *Stellaria holostea* L., *Taraxacum* spp., *Valeriana* spp. and *Viburnum opulus* (Torp 1994; Bartsch et al. 2009; Speight 2020) and *Pimpinella major* (L.) Huds. and *Spirea* spp. (database).

The main flight period (Fig. 40A) is from the middle of April until the end of July with extreme dates of the 2nd of April and 21st of August. Found at altitudes from sea level up to1880 m a.s.l. (database). In all countries recorded extensively during the 21st century, but no recent records from Denmark (since 1999) and Switzerland (since 1996).

Population fluctuations. This species is dependent on pine forests. The larvae are dependent on rather freshly cut stumps. This habitat is heavily managed and will produce a constant amount of suitable larval habitat due to regular tree felling. It seems this species does not show strong population fluctuations.

Red List. This species is listed as "Least Concern" on all regional Red Lists and also its habitat does not seem to be threatened (Bygebjerg 2004; Ssymank et al. 2011; Henriksen & Hilmo 2015; European Commission 2016; Artdatabanken 2019; Hyvärinen et al. 2019).

***Brachyopa vernalis* Van Steenis & Van Steenis, 2014**

Brachyopa vernalis Van Steenis & Van Steenis, 2014: 13; ♂ holotype in NBC, 7 ♂♂ paratypes in NBC, PJSA, PMRL, PWSB, FSUNS, ZMUC, all types studied.

Figs 4D, 11D, 15D, 22

Distribution. Only known from three localities on Crete (Greece), based on material collected in 1997, 2008 (van Steenis & van Steenis 2014) and 2012, and hence a European endemic.

Biology. Found visiting flowers of *Crataegus* spp. and *Prunus* spp. in Mediterranean deciduous forests and in a forested part of a deep ravine.

This species was collected on the 28th of March, the 8th of April and the 8th of May at an altitudinal range of 350–900 m a.s.l. (database).

Population fluctuations. Nothing can be concluded based on the data we have here, but as seen for some other Mediterranean species of *Brachyopa*, its larvae are most likely living in sap runs and as such, prone to show large population fluctuations.

Remarks. Crete has been visited by renowned dipteran collectors (Jan Lucas, Claus Claussen, etc.) in the past and only recently nine specimens of this species have been collected, indicating it should be classified as an extremely rare species. It has been recorded at three localities in Crete, all in forested habitats. Only one locality is within a protected area. As in many Mediterranean areas this habitat is under threat due to overgrazing and forest fires. This in combination with the restricted range of occurrence makes this species very vulnerable to extinction.

Red List. Not mentioned on any Red List but, due to its restricted distribution and the threats to its habitat, a candidate to be listed in one of the IUCN threat categories.

***Brachyopa vittata* Zetterstedt, 1843**

Brachyopa vittata Zetterstedt, 1843: 687; type in ZIL, not studied.

Figs 1C, 7F, 8C, 12C, 16C, 19C, 35, 40B

Distribution. A widespread species found from northern Sweden south to the Pyrenees and northern Greece and from the Netherlands east into European Russia and further to the Russian Far East and Japan.

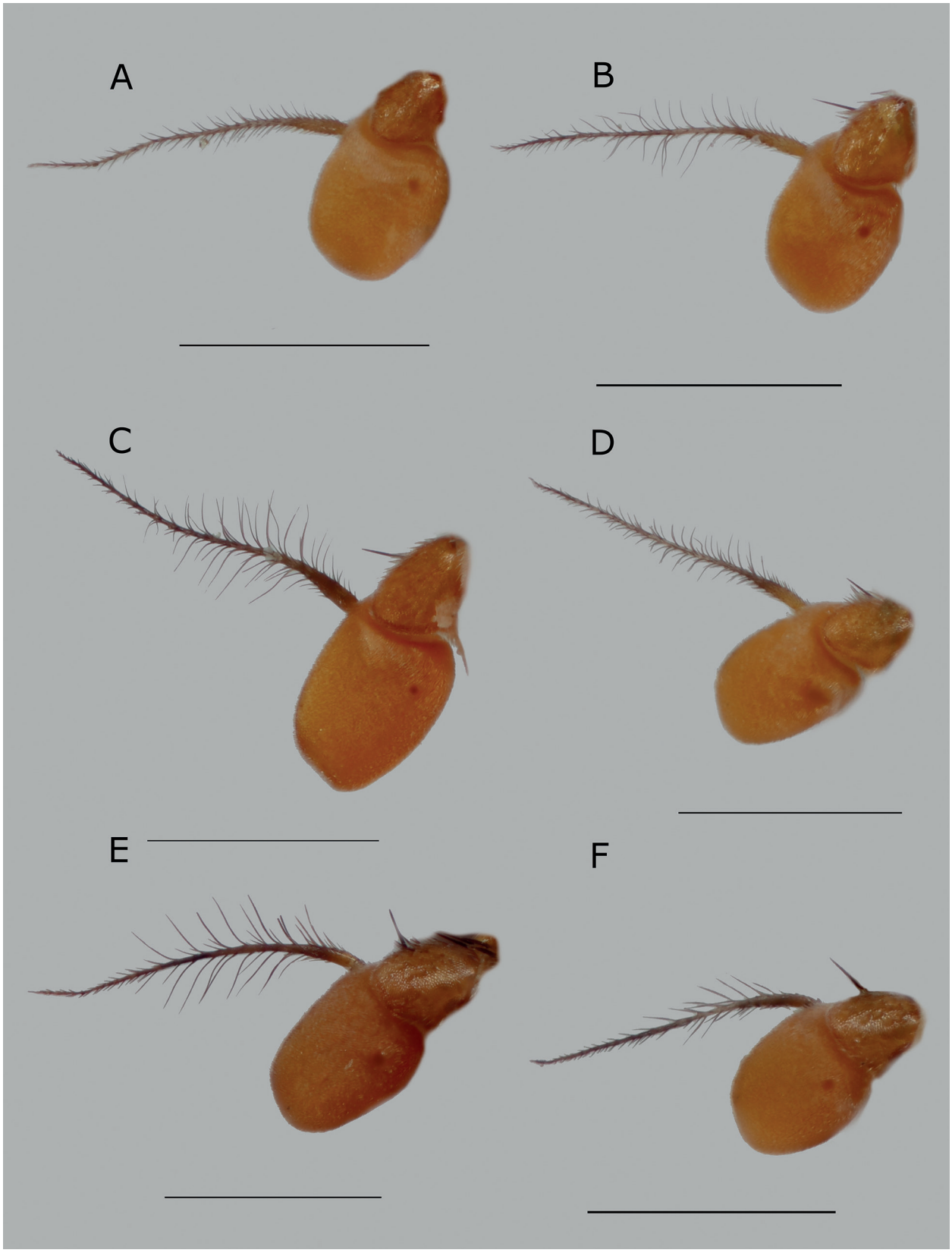

Fig. 19. Basoflagellomere male, medio-lateral view. **A**. *Brachyopa obscura*, Hågadalen, Sweden. **B**. *B. testacea*, Bolgenachtall, Germany. **C**. *B. vittata*, Belchen, Germany. **D**. *B. zhelochovtsevi*, Aktru, Altay, Russia. **E**. *Hammerschmidtia ferruginea*, Hinteralfeld, France. **F**. *H. ingrica*, Tuva, Russia.

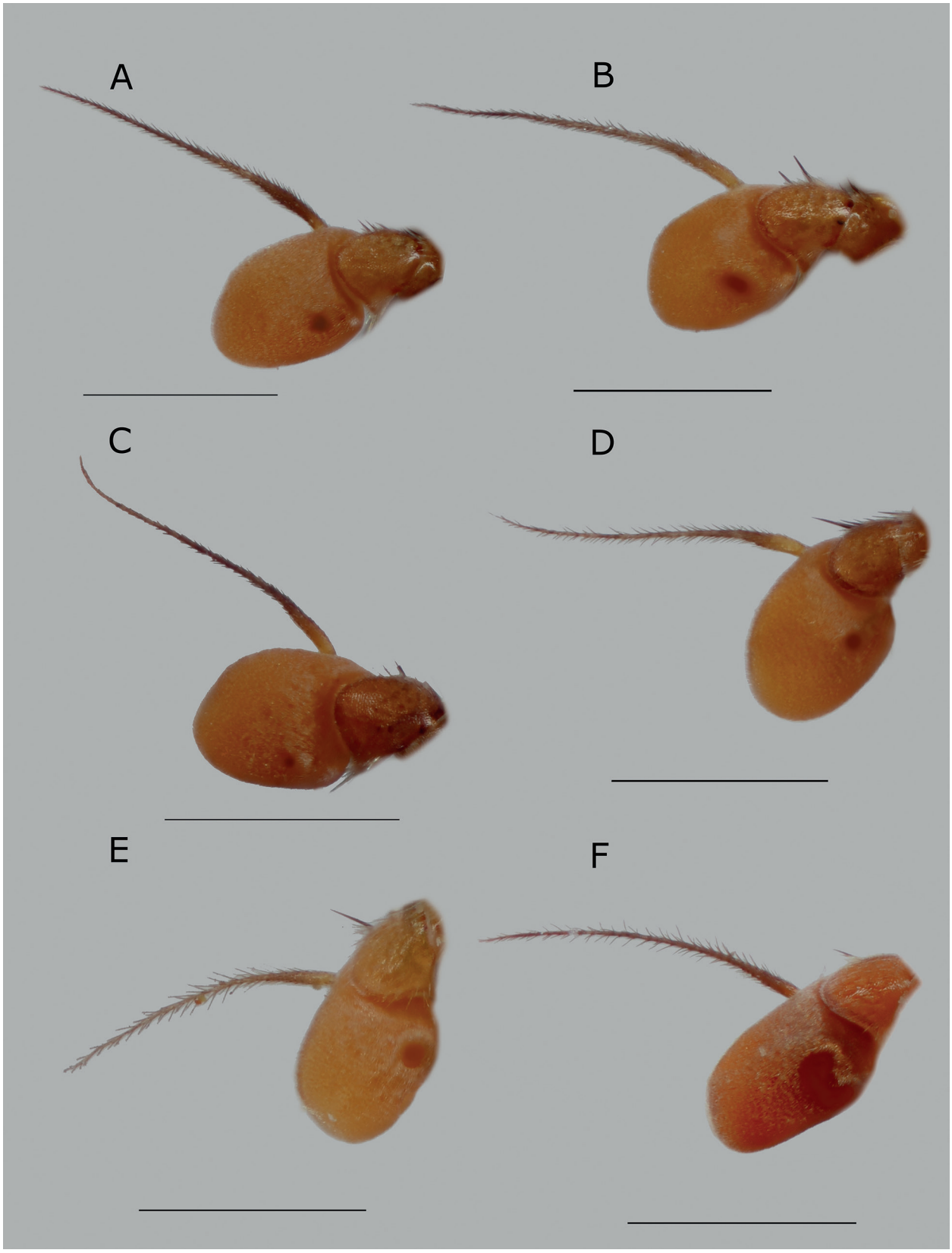

Fig. 20. Basoflagellomere male, medio-lateral view. **A**. *Brachyopa dorsata*, Belchen, Germany. **B**. *B. panzeri*, Dresden, Germany. **C**. *B. maculipennis*, Novi Sad, Serbia. **D**. *B. pilosa*, Valkenburg, the Netherlands. **E**. *B. plena*, Kalavryta, Greece. **F**. *B. scutellaris*, Cadier en Keer, the Netherlands.

Biology. Adult habitat is old growth *Picea* and *Pinus* forests but also found in mixed swamp forest (Löhr 1992; Bartsch et al. 2009; Reemer et al. 2009).

Larvae live in *Picea* spp. and *Larix* spp. stumps as well as in standing trunks and stumps of *Abies* spp. with tunnels of *Hylecoetus flabellicornis* (Coleoptera: Lymexylidae), *Trypodendron lineatum*, *Ips sexdentatus* (Boerner, 1767) (Coleoptera: Curculionidae) and *Zabrachia minutissima* (Zetterstedt, 1838) (Diptera: Stratiomyidae). They are also accompanied by the saprophagous larvae of *Sylvicola cinctus* (Diptera: Anisopodidae) (Krivosheina 2005, 2019).

Flowers visited include *Aegopodium podagraria*, *Anthriscus sylvestris*, *Caltha palustris*, *Crataegus laevigata*, *Crataegus monogyna*, *Prunus avium*, *P. padus*, *Salix* spp., *Sambucus nigra* L., *S. racemosa*, *Sorbus aucuparia* and *Viburnum* spp. (Séguy 1961; Barkemeyer 1986; de Buck 1990; Röder 1990; Nielsen 1992; van Steenis 2011; Speight 2020), as well as *Alliaria petiolata*, *Pimpinella major*, *Spirea* spp. and *Valeriana officinalis* L. (database). Adults are found on tree stumps and trunks of a wide range of coniferous trees.

The flight period (Fig. 40B) is from the middle of April until the middle of August (database). The altitudinal range of this species is 10–2270 m a.s.l. (Barkemeyer 1986; Maibach et al. 1992; database). This species has been recorded during all time periods in France and Germany and in many other countries regularly after its first discovery. Only in Sweden it was recorded around 1900 with the next records from 1999, 2009 and 2013, indicating strong population fluctuations.

Population fluctuations. As indicated for *Brachyopa testacea*, this is a species dependent upon pine forests and, as larvae, on rather freshly cut stumps. This habitat is heavily managed and will produce a constant amount of suitable larval habitat due to regular tree felling. It seems this species does not show strong population fluctuations in its central distributional range.

Remarks. This is a species of coniferous forests often found near trunks and stumps defending a territory.

Red List. This species is listed from "Least Concern" to "Endangered" on the regional Red Lists (Ssymank et al. 2011; Henriksen & Hilmo 2015; Artdatabanken 2019). In Finland it is listed as "data deficient" (Hyvärinen et al. 2019). These categories contrast strongly with one another because there are only very few records for each country and most of these are from recent times, except in Sweden where there are some very old records and some recent ones too, indicating a possible absence of many years. The species seems to be at its northern limits in these countries, so the threat category seems to depend on how important you judge the local populations. The species should either be categorized as "data deficient" in all three countries or in one of the threat categories "Vulnerable" to "Critically Endangered". In Central Europe the species seems to be widespread with stable populations, and its habitat is classified as "Least Concern" (European Commission 2016), so there seem to be significant differences in the threat category between Fennoscandia and the rest of Europe.

Brachyopa zhelochovtsevi Mutin, 1998

Brachyopa zhelochovtsevi Mutin, 1998: 4; ♂ holotype in ZMSU, studied.

Figs 1D, 8D, 12D, 16D, 19D, 33

Distribution. Only known in Europe from two Finnish records for this otherwise East-Palaearctic species, with some records from the Altai.

Biology. Found in an ancient forest with fallen logs of *Abies* spp., *Betula* spp. and *Populus tremula* (Haarto & Kerppola 2009). Adults found near damaged coniferous trees (Mutin et al. 2016). Flowers visited *Ledum palustre* L. (Speight 2020).

Collected on the 24th and the 29th of June and on the 13th of July. One old record from 1911 and the other two from 2008 (database).

Population fluctuations. Nothing can be concluded concerning fluctuations in population size.

Remarks. This species is very similar to both *B. obscura* and *B. testacea*, and is easily overlooked in the field, although *B. obscura* tends to be the more light-coloured and *B. zhelochovtsevi* the most dark-coloured species. The distribution of this species could be wider than currently known. As very little is known about its adult and larval habitat no conclusions can be drawn on possible threats.

Red List. For Finland the species is categorised as "data deficient" (Hyvärinen et al. 2019).

The European species of the genus *Hammerschmidtia*

Hammerschmidtia ferruginea (Fallén, 1817)

Rhingia ferruginea Fallén, 1817: 34; type in NHRS, not studied.

Hammerschmidtia vittata Schummel, 1834: 740; type in NMW, (syn by Peck 1988), not studied.

Figs 1E, 6A, 8E, 12E, 16E–G, 19E, 36, 40C

Distribution. A widespread species found from northern Norway south to the Pyrenees and from central France east through the Alps, the Balkan Peninsula and Poland to European Russia. Also known from Scotland and Georgia and further east to the Russian Far East. The re-

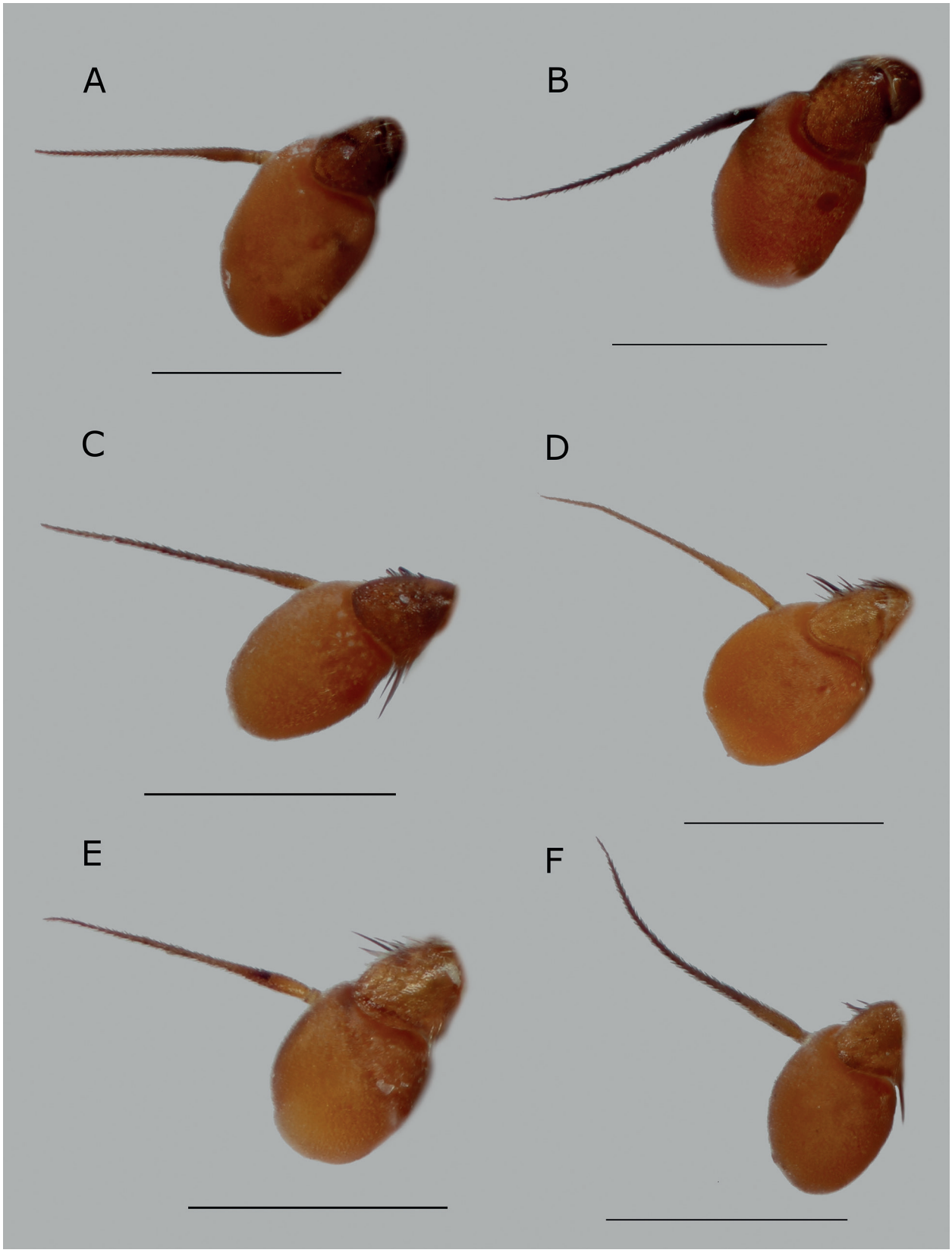

Fig. 21. Basoflagellomere, medio-lateral view **A**. *Brachyopa atlantea*, female, Granada, Spain. **B**. *B. bicolor*, male, Arkadia, Greece. **C**. *B. bimaculosa*, male, Arkadia, Greece. **D**. *B. cinerea*, female, Komsomolsk-na-Amur, Russian Far East. **E**. *B. grunewaldensis*, male, Arkadia, Greece. **F**. *B. insensilis*, male, Novi Sad, Serbia.

cord in NW France (Séguy, 1961) is a strange record and needs verification.

Biology. The adult habitat consists of pine and birch taiga in Scandinavia and Scotland, and mixed alpine forests up to 1200 m a.s.l. with large stands of *Populus tremula* (Nielsen 1992; Rotheray & McGowan 2000; Bartsch et al. 2009).

The larval habitat has been intensively studied in Scotland and consists of sap accumulations in fallen logs of *Populus tremula* or sap runs on the same tree (Rotheray 1991; Rotheray & McGowan 2000; Rotheray et al. 2009, 2014). The larvae live in recently fallen logs with sappy decay, which lasts for 2 to 3 years. From one such log almost 1000 specimens were collected in emergency traps (Rotheray et al. 2014). In other parts of the world larvae have been found in similar conditions (Krivosheina 2003).

Adults visit flowers of *Aegopodium podagraria*, *Angelica sylvestris*, *Anthriscus sylvestris*, *Conopodium majus* (Gouan) Loret, *Crataegus* spp., *Prunus padus*, *Pyrus communis*, *Ranunculus acris* L., *Rosa* spp., *Rubus fruticosus*, *Salix* spp., *Sorbus aucuparia*, *Syringa* spp. and *Valeriana* spp. (de Buck 1990; Röder 1990; Nielsen 1992; Stubbs & Falk 1996; Nilsson et al. 2007; Ball & Morris 2014; Speight 2020), as well as *Chaerophyllum temulum*, *Filipendula ulmaria*, *Heracleum sphondylium* L., *Malus sylvestris*, *Prunus laurocerasus* L., *Sambucus nigra*, *Spirea* spp. and *Viburnum opulus* (database).

Its flight period (Fig. 40C) is from the end of April until the beginning of August with extreme dates of the 2nd of April and the 19th of August. This species is found at altitudes of 20–1925 m a.s.l. (database).

Population fluctuations. Extreme fluctuations were found in the Scottish Highlands (Rotheray et al. 2008; Ball & Morris 2014) and based on its larval biology it is highly likely this species shows fluctuations over its entire distributional range.

Remarks.This is a very characteristic species which is unlikely to be overlooked in the field due to its size and preference for flowering Apiaceae as an adult food source.

Red List. In northern countries this species is listed as "Least Concern" (Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019), while it is "Endangered" to "Critically Endangered" in Germany and Great Britain (Ssymank et al. 2011; Ball & Morris 2014). In Scotland conservation actions are in place (Rotheray et al. 2008), and these actions will probably have a positive impact on its occurrence in Great Britain.

In other parts of Europe, the specific habitat of the species falls within EUNIS category G1.4 or possibly G1.9 and G4.8 of which G1.4 is considered "Vulnerable" (European Commission 2016). In light of this, *Hammerschmidtia ferruginea* could also be threatened and would possibly classify under the same category although the species is not considered threatened in the Balkan Peninsula (Vujić et al. 2001).

Hammerschmidtia ingrica Stackelberg, 1952

Hammerschmidtia ingrica Stackelberg, 1952: 37; ♂ holotype and 2 ♂♂, 1 ♀ paratypes in ZISP, studied.
Figs 1F, 5C, 6B, 8F, 12F, 19F, 37

Distribution. Described from European Russia with many records from the surroundings of St Petersburg and Moscow (Stackelberg 1952, database), and with a range extending eastwards to the Russian Far East. (Mutin et al. 2016). Recently recorded in Finland.

Biology. Adults are found in mixed boreal forests with overmature deciduous trees (Krivosheina 2003; Mutin et al. 2016).

The larvae are found in sap accumulations under the bark of *Juglans mandshurica* Maxim., *Populus tremula* and *Ulmus* spp. (Krivosheina 2003). Adults were collected in an emergence trap on a *Populus tremula* trunk (Polevoi et al. 2018).

In the Russian Far East, it was found visiting flowers of *Cornus alba* (as *Swida alba* in Mutin et al. 2016).

The flight period in Europe is from the 25th of April until the 30th of June at altitudes between 25 and 400 m a.s.l. (database).

Population fluctuations. The larvae seem to have similar habitat preferences to *Hammerschmidtia ferruginea*. It is likely that both *Hammerschmidtia* species show similar population fluctuations.

Remarks. The Finnish island where this species was found is a former Soviet Military base, and several plant species have been found there which originate from Russia. It is hypothesized that *H. ingrica* is an introduced species now maintaining a population on the island (Kerppola 2011). However, this is questionable because it occurs in the nearby European part of Russia, and similar habitats occur on both sides of the border.

It seems that the Nearctic *Hammerschmidtia rufa* Williston, 1882 and eastern-Palaearctic specimens of *H. ingrica* have identical DNA, and thus it is proposed that *H. ingrica* should be a junior synonym of the older name *H. rufa* (Skevington et al. 2019). This synonymy was proposed in a field guide without mentioning the descriptive authority, nor has the type of *H. ingrica* been studied, and so this change is not applied here.

Red List. As a supposed non-native species to Finland, it is listed as "not applicable" in the Red List of this country (Hyvärinen et al. 2019).

DISCUSSION

This discussion will focus on the results given under each species and summarize this in a generalized way. For ease of reading no references are given here. The discussion focuses on the current knowledge and especially gaps which need to be investigated more thoroughly to understand more fully the possible effects of changing habitat on population dynamics of the species.

The species of the genera *Brachyopa* and *Hammerschmidtia* are highly specialized in their larval habitat. In general, different kinds of tree sap accumulations form the larval habitat. This can be external sap runs caused by physical damage or other larvae, or internal accumulations of sap under bark of stumps or fallen logs. Most of these habitats are within living trees, but accumulations of sap on recently felled trees are also used by some species. This habitat is restricted by a variety of factors and its availability could fluctuate greatly over time. The amount of suitable larval habitat increases after storms, fires, infectious outbreaks causing damage to trees or felling activity by forestry. These fluctuations are mostly random and hard to predict, causing large fluctuations in population densities. Moreover, each year, the sap-runs tend to dry out in autumn, making survival of the larvae a challenging process. Consequently, adaptations have evolved in response to these uncertainties. The extensive longevity and high desiccation tolerance in the larval stage help to overcome the yearly fluctuations. The longevity can also span the period of tree recovery when little larval habitat is present. Other strategies involve the adults, and probably include high mobility and the ability to identify the larval habitat at great distances, especially in the females.

Within the genus *Brachyopa* there are basically two larval biotopes, and species tend to have a preference for either one. Some species are generalists, with larvae occurring in a wide range of deciduous and coniferous trees, whilst others tend to occur only in coniferous trees. The latter are mostly larvae living in sap accumulations under bark of stumps and trunks, perhaps a more stable habitat than sap runs on living trees. The sap-run-dependent species tend to have a wider range of host trees, including deciduous and coniferous trees, although it seems they do have some preference, for instance, *Quercus* spp. being preferred by *Brachyopa bicolor* and *Aesculus hippocastanum* by *B. insensilis*.

Most knowledge about larval habitat is gathered from field observations rather than through extensive ecological or behavioural studies. Only *Hammerschmidtia ferruginea*, a true specialist on accumulations of sap under bark of recently felled *Populus tremula* logs, has been investigated in great detail. These studies suggested the minimal forest area needed for survival as being at least 15 ha with large stands of *Populus tremula* in all life stages. All other species need to be investigated as thoroughly as *H. ferruginea* in order to establish what tree species are needed, how large the forest area should be and how near other forests need to be in order to ensure their future survival.

It seems that no species of *Brachyopa* or *Hammerschmidtia* have become extinct in Europe yet. Two very rare species in Europe (*Brachyopa atlantea* and *B. zhelochovtsevi*) could be relicts with a larger range in the past. Two other species (*Brachyopa testacea* and *B. vittata*) could have benefitted from the increasing area of coniferous plantations in Western Europe. Most of the species dependent upon deciduous forests have extended their ranges northwards since the last ice age, along with the reforestation of Europe in this period. The species thus seem to be able to adapt to a changing environment, but we do not know how quickly they are able to do this and whether they will be able to continue to thrive as habitat changes accelerate due to global warming and other human impacts.

In this paper we have compiled all information available to us and have provided data on distribution, habitat, ecology, habitat threats and possible population fluctuations. This could serve as a basis for compiling a nationwide or regional Red List and, most of all, to encourage biologists to do more research on the ecology of the species of these two genera.

Acknowledgements. We wish to thank the following persons for loan of material and for other valuable help: Gunilla Ståhls (Helsinki, Finland), Cyrille Dussaix (France), Xavier Lair (France), Jonathan Voise (France), Jean-David Chapelin Viscardi (Laboratoire d'Eco-Entomologie, France), Damien Hemeray (Réserve Naturelle de Saint Mesmin, France), Dieter Doczkal (Gaggenau, Germany), Úna FitzPatrick (National Biodiversity Data Centre, Waterford, Ireland), Pasquale Ciliberti (Leiden, the Netherlands), Ruud van der Weele (Zoelmond, the Netherlands), Snorre Henriksen (Artsdatabanken, Norway), Toril L. Moen (Artsdatabanken, Norway), Tore Nielsen (Sandnes, Norway), Arjen Leendertse (Oslo, Norway), Lennart Carlsson (Artportalen Sweden), Artur Larsson (The Species Fact System, Sweden), Sophia Ratcliffe (NBN Trust, UK) and Francis Gilbert (UK). The first author wishes to thank Olga Ovchinnikova and Nikolai Paramonov (St Petersburg, Russia) and Andrey Ozerov, Marina Krivosheina and Anatoly Shatalkin (Moscow, Russia) for their generosity while visiting their museums. The Dutch Uyttenboogaart-Eliasen foundation under numbers SUB.2014.12.16, SUB.2017.12.05 and SUB.2019.05.21 and the Royal Entomological Society Outreach fund 2018, provided funding for the visit of the the NHM, London; UMO, Oxford; the ZMSU, Moscow and the ZISP, Saint Petersburg, are acknowledged by the first author. The work of Jiří Hadrava was supported by GAUK 1030119/2019.

Fig. 22. Distribution map. *Brachyopa atlantea*, dot; *B. minima*, star; *B. vernalis*, square. (white <1950, white with black point ≥1950 <2000, black ≥2000).

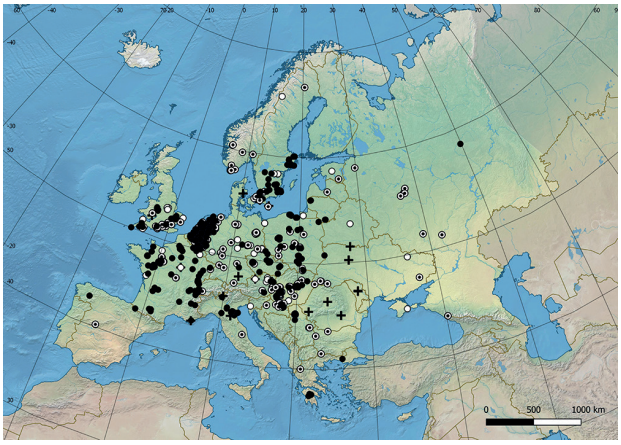

Fig. 23. Distribution map. *Brachyopa bicolor* (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

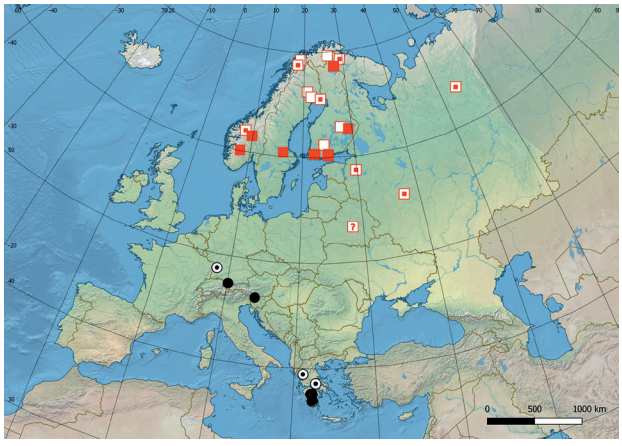

Fig. 24. Distribution map. *Brachyopa bimaculosa*, dot; *B. cinerea*, square. (white <1950, white with black point ≥1950 <2000, black ≥2000, **?** = uncertain record).

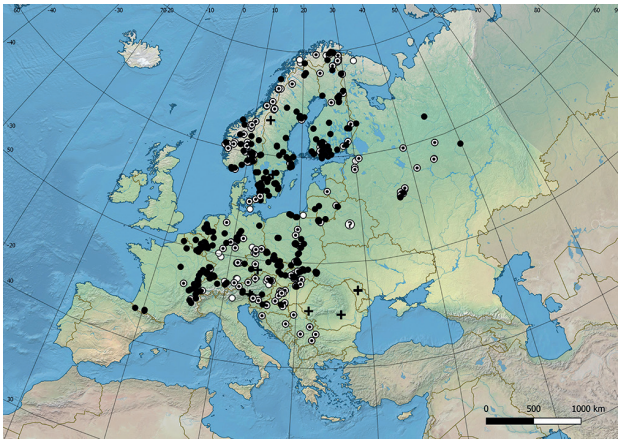

Fig. 25. Distribution map. *Brachyopa dorsata*. (white <1950, white with black point ≥1950 <2000, black ≥2000, **?** = uncertain record, + datum unknown).

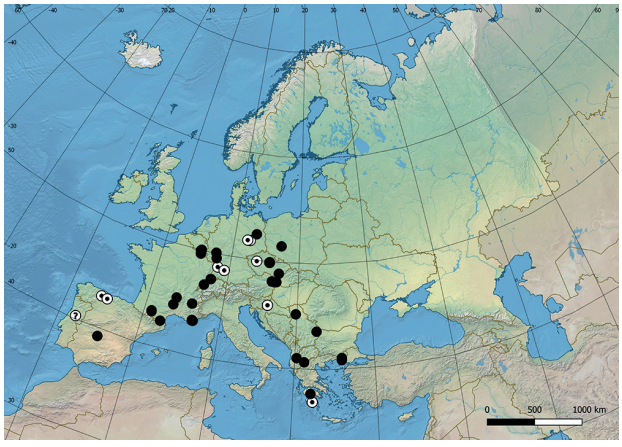

Fig. 26. Distribution map. *Brachyopa grunewaldensis*. (white <1950, white with black point ≥1950 <2000, black ≥2000, **?** = uncertain record).

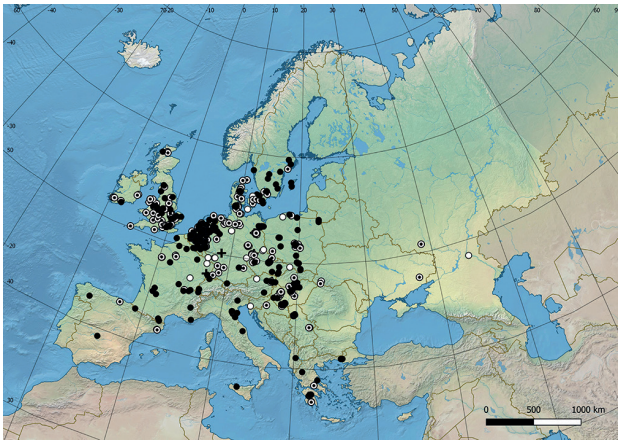

Fig. 27. Distribution map. *Brachyopa insensilis*. (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

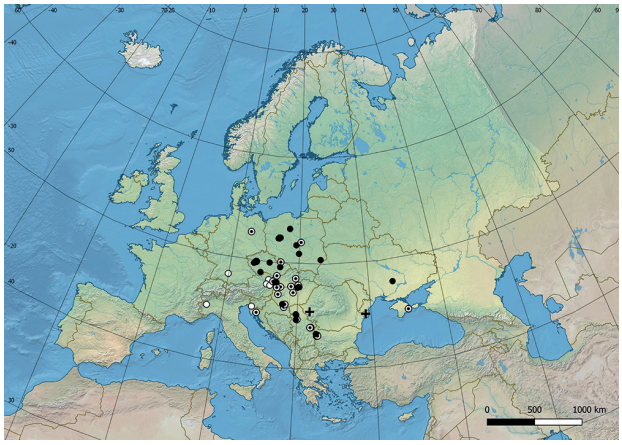

Fig. 28. Distribution map. *Brachyopa maculipennis*. (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

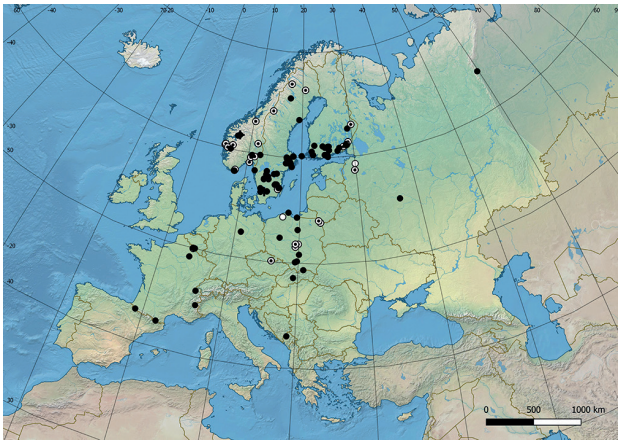

Fig. 29. Distribution map. *Brachyopa obscura*. (white <1950, white with black point ≥1950 <2000, black ≥2000).

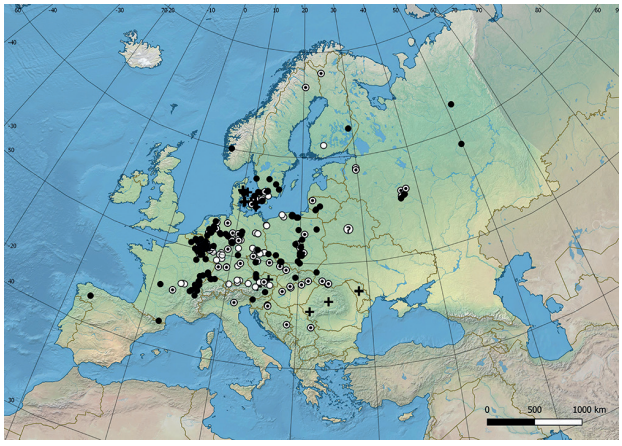

Fig. 30. Distribution map. *Brachyopa panzeri*. (white <1950, white with black point ≥1950 <2000, black ≥2000, ? = uncertain record, + datum unknown).

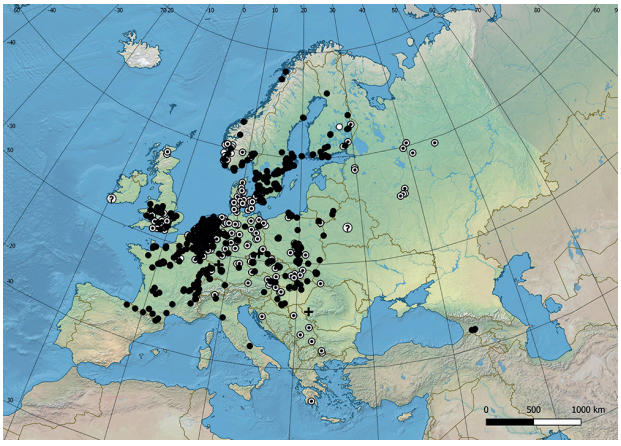

Fig. 31. Distribution map. *Brachyopa pilosa*. (white <1950, white with black point ≥1950 <2000, black ≥2000, ? = uncertain record, + datum unknown).

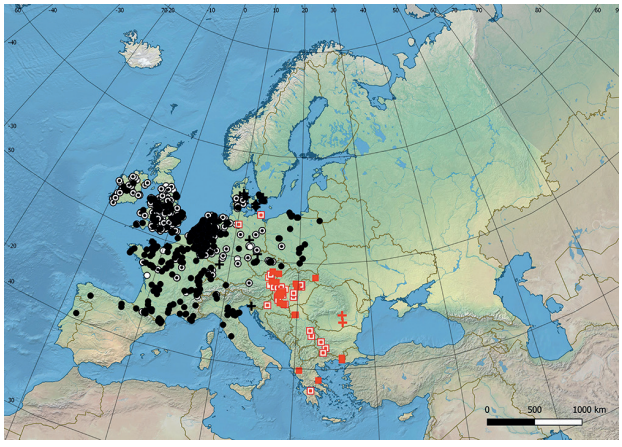

Fig. 32. Distribution map. *B. scutellaris*, black dot; *Brachyopa plena*, red square. (white <1950, white with black/red point ≥1950 <2000, black/red ≥2000, + datum unknown).

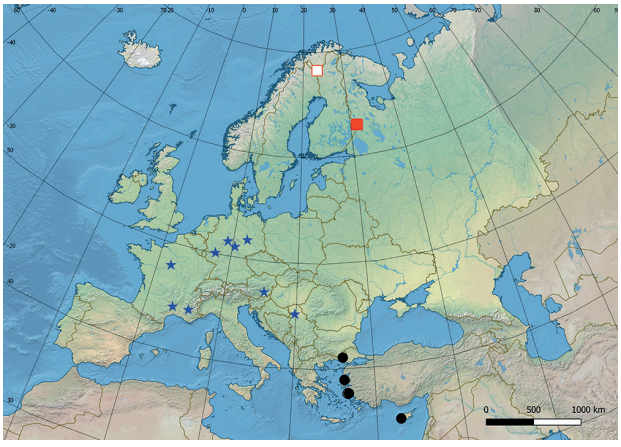

Fig. 33. Distribution map. *Brachyopa quadrimaculosa*, dot; *B. silviae*, stars; *B. zhelochovtsevi*, square. (white <1950, white with black point ≥1950 <2000, black ≥2000).

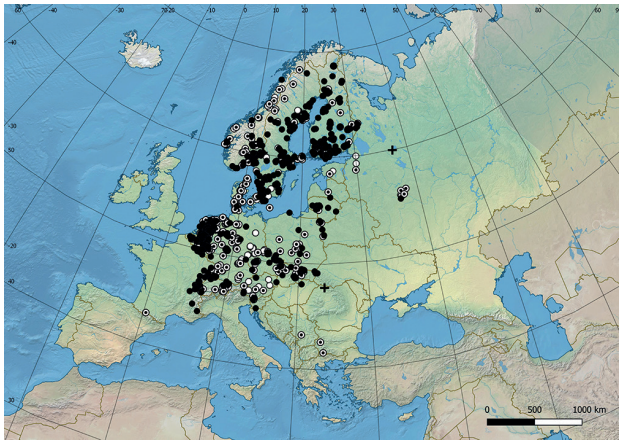

Fig. 34. Distribution map. *Brachyopa testacea*. (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

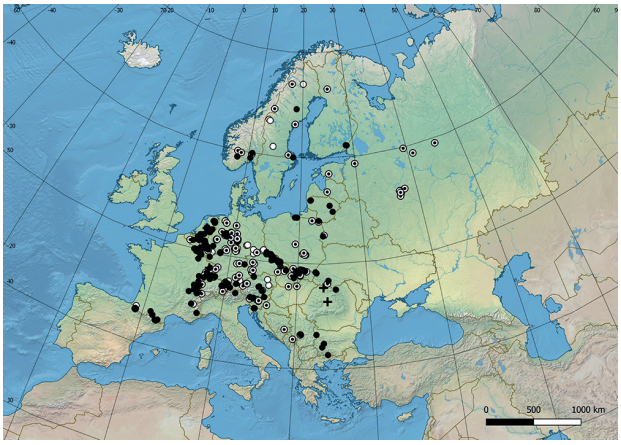

Fig. 35. Distribution map. *Brachyopa vittata*. (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

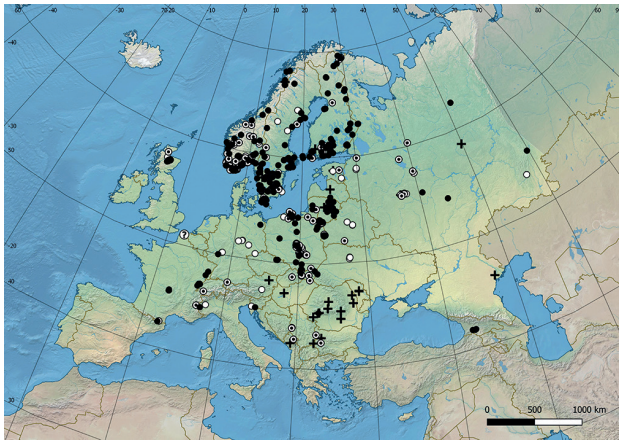

Fig. 36. Distribution map. *Hammerschmidtia ferruginea*. (white <1950, white with black point ≥1950 <2000, black ≥2000, **?** = uncertain record, + datum unknown).

Fig. 37. Distribution map. *Hammerschmidtia ingrica*. (white <1950, white with black point ≥1950 <2000, black ≥2000).

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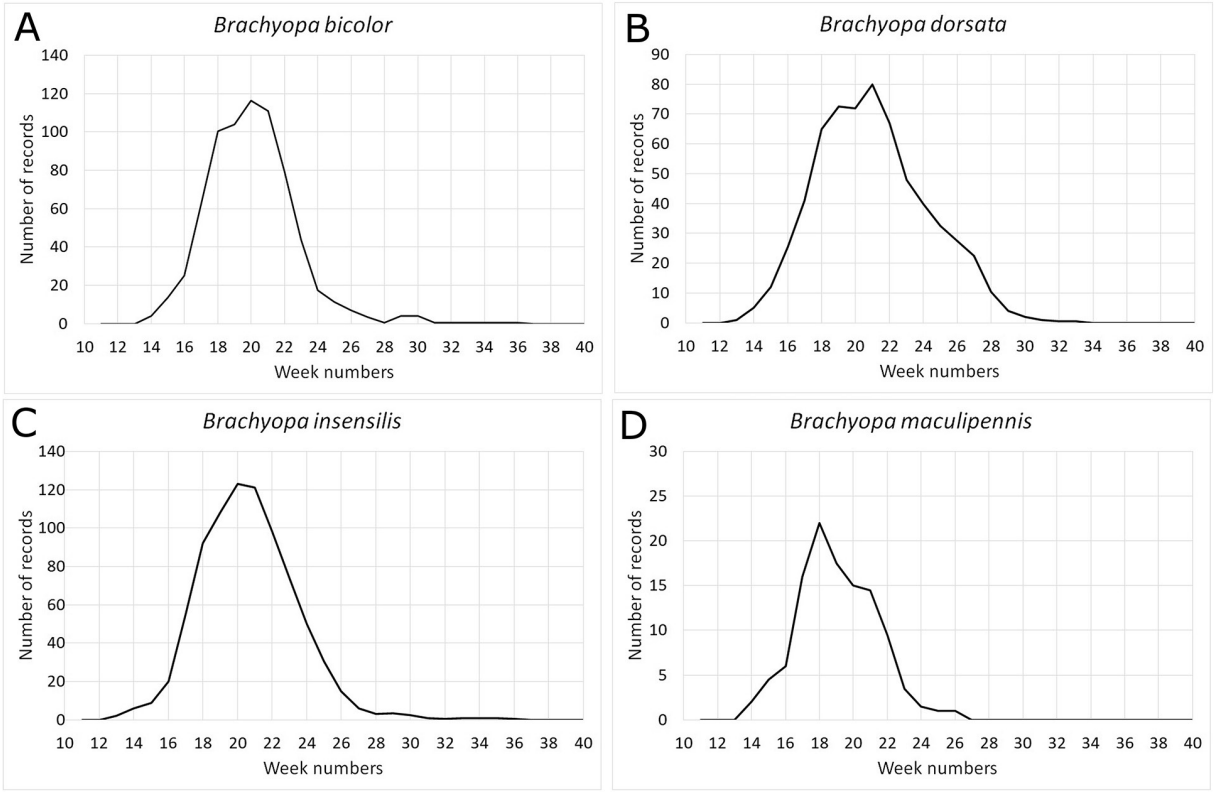

Fig. 38. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa bicolor*. **B.** *Brachyopa dorsata*. **C.** *Brachyopa insensilis*. **D.** *Brachyopa maculipennis*.

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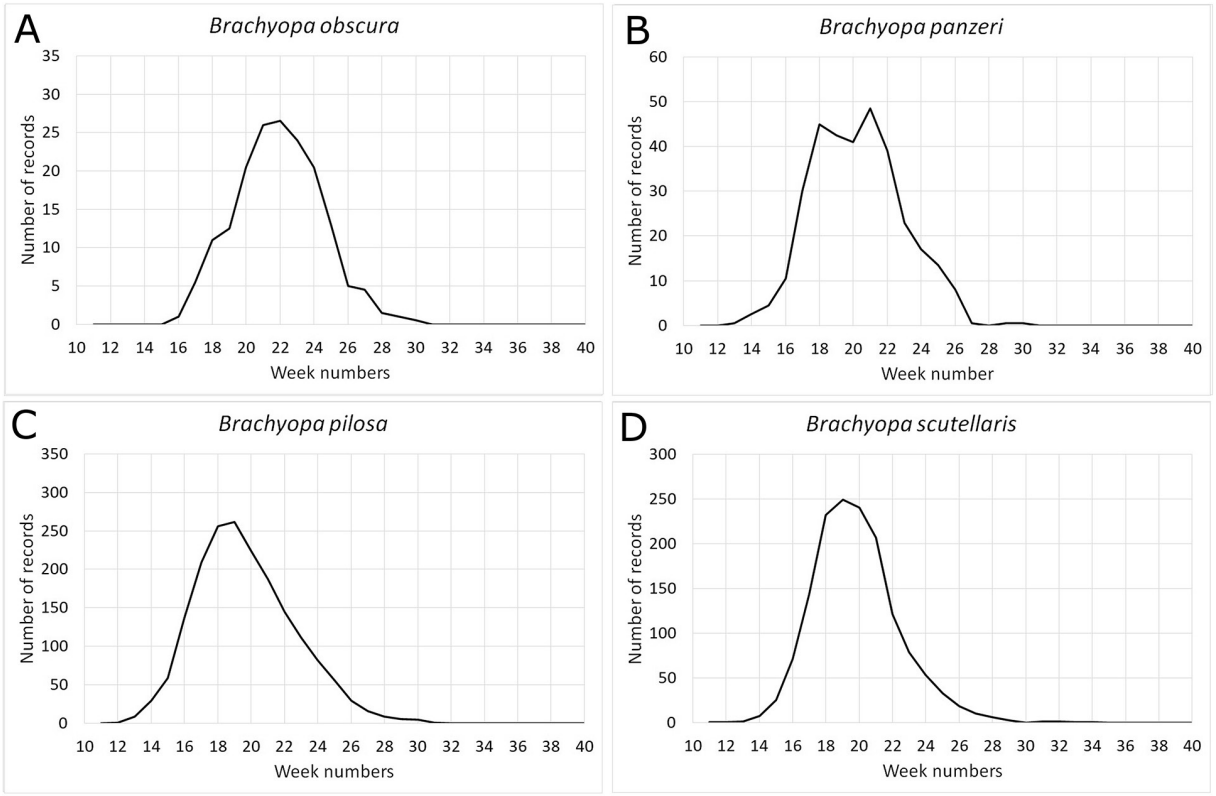

Fig. 39. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa obscura*. **B.** *Brachyopa panzeri*. **C.** *Brachyopa pilosa*. **D.** *Brachyopa scutellaris*.

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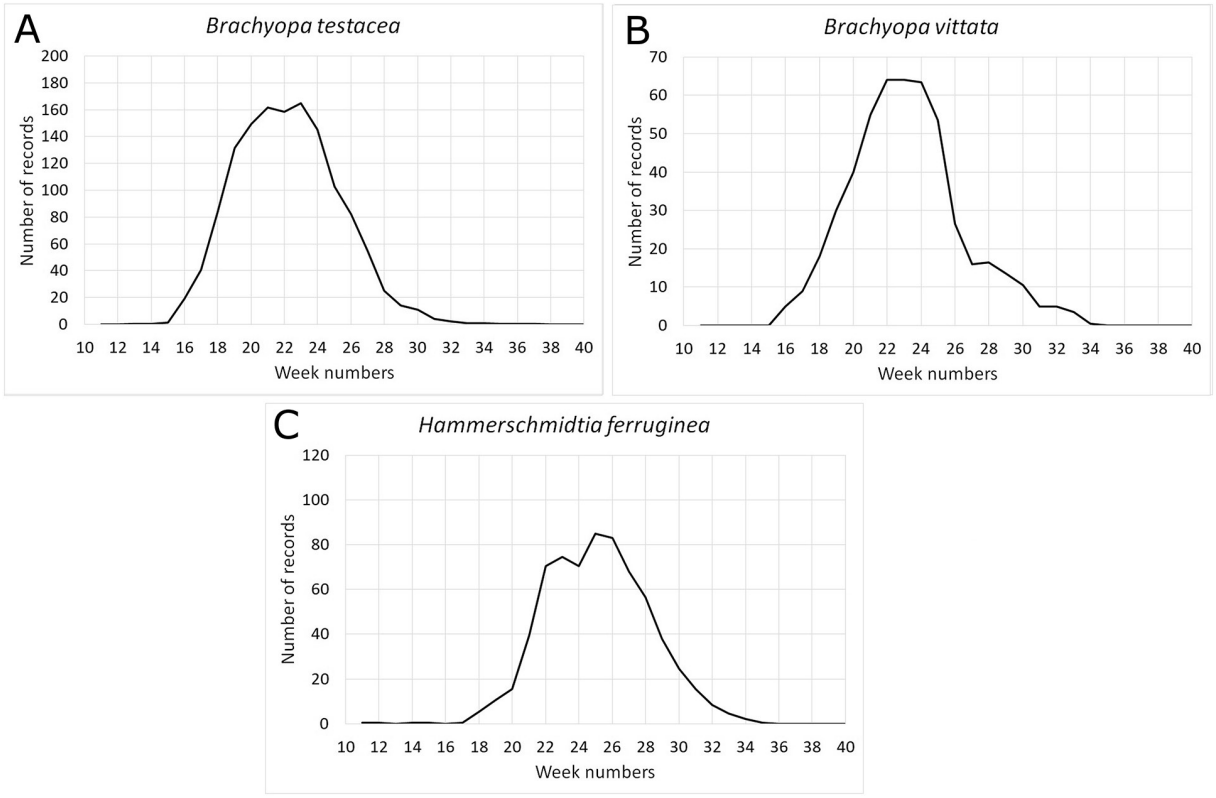

Fig. 40. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa testacea*. **B.** *Brachyopa vittata*. **C.** *Hammerschmidtia ferruginea*.

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