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A redescription of the Mediterranean endemic cladoceran *Daphnia chevreuxi* Richard, 1896 (Cladocera: Daphniidae)

ALEXEY A. KOTOV[1*], PETR G. GARIBIAN[1,3], ANNA N. NERETINA[1,4] & FEDERICO MARRONE[2]
[1]*A.N. Severtsov Institute of Ecology and Evolution, Leninsky Prospect 33, Moscow 119071, Russia.*
[2]*Department of Biological, Chemical and Pharmaceutical Sciences and Technologies, University of Palermo, via Archirafi 18, 90123, Italy. federico.marrone@unipa.it; https://orcid.org/0000-0002-4730-0452*
[3] *petr.garibyan21@mail.ru; https://orcid.org/0000-0003-4505-3133*
[4] *neretina-anna@yandex.ru; https://orcid.org/0000-0002-6876-079X*
[*]*Corresponding author. alexey-a-kotov@yandex.ru; https://orcid.org/0000-0002-8863-6438*

Abstract

The Mediterranean area is a biodiversity and endemism hotspot. "Circum-Mediterranean" taxa are known among different hydrobionts, including the water fleas. Some Mediterranean endemic cladoceran taxa have been described or redescribed according to modern taxonomical standards, but accurate drawings are missing for others. Here we redescribe the Mediterranean endemic *Daphnia chevreuxi* Richard, 1896 (Crustacea: Cladocera) and briefly review available data on its distribution and ecology. The species is confirmed to be a typical inhabitant of the temporary ponds of the central Mediterranean area, whereas its populations from the eastern Balkans and the Middle East should be studied in order to check for their actual identity. We conclude that the Mediterranean area is an example of a well-studied region as Cladocera are concerned, but the study of other regions is necessary in order to understand better the cladoceran diversity and distribution patterns in Eurasia.

Key words: Cladocera, taxonomy, morphology, description, Mediterranean area

Introduction

Several parts of the Palearctic biogeographical region are biodiversity hotspots, and the Mediterranean area is among these (Myers *et al.* 2000; Ramos *et al.* 2001; Cuttelod *et al.* 2009). It is known that the biodiversity hotspots are not always congruent with the endemism hotspots (Orme *et al.* 2005), but the Mediterranean area is an exception from this rule, and it is also a well-known endemism zone for terrestrial and inland water species (Ramos *et al.* 2001; Reyjol *et al.* 2007; Cheikh Albassatneh *et al.* 2021); this is possibly due to its role as a refuge for European terrestrial and freshwater fauna during the coldest phases of the Pleistocene (Hewitt 2001; Stewart & Lister 2001). In fact, in spite of the semi-arid climate currently characterizing most of the area, which could be suggestive of a poorly differentiated inland water fauna, circum-Mediterranean endemic taxa (sensu Bănărescu 1990) are frequent among different hydrobionts (Bănărescu 1990; Blondel *et al.* 2010; Hermoso & Clavero 2011; Tierno de Figueroa *et al.* 2013; Marrone *et al.* 2014; Marrone *et al.* 2017).

Cladocera (Crustacea: Branchiopoda) biodiversity is relatively well-studied there as its investigation has been carried out since the 19th century (Lucas 1849; Richard 1887; Guerne & Richard 1986; Gurney 1909; Gauthier 1928; Parenzan 1932; Parenzan 1933). In several countries, the cladoceran fauna has also been intensively studied in the last decades; this is the case of Spain (Alonso 1985; Alonso 1990; Alonso 1991; Alonso 1996; Alonso 1998), mainland Italy (Margaritora 1983; Margaritora 1985; Margaritora 2005) and large Tyrrhenian islands (Margaritora 1970; Margaritora & Ferrara 1974; Margaritora *et al.* 1975; Marrone *et al.*, 2005; Marrone *et al.* 2006), Turkey (Margaritora *et al.* 1977; Güher 2014; Bozkurt & Aktaş 2016), Israel (Bromley 1993), Algeria and Tunisia (Dumont 1979; Dumont *et al.* 1979; Samraoui 2002; Ghaouaci *et al.* 2018); conversely, recent synoptical data are lacking for other countries and regions. Useful synopses of the available data, bibliography and distribution for the circum-Mediterranean countries are those provided by Mouelhi *et al.* (2000) and Błędzki & Rybak (2016).

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Several endemic cladoceran taxa from the Mediterranean area (including the Balkans) are adequately described or redescribed according to the current standards of morphological taxonomy (Alonso 1996; Alonso & Pretus 1989; Brancelj 1990; Sinev *et al.* 2012; Alonso *et al.* 2021), but accurate morphological characterizations are missing for others.

The circum-Mediterranean species of the genus *Daphnia* O.F. Müller (Anomopoda: Daphniidae) were a subject of special interest for the cladocerologists at the end of the 20th century (Alonso 1985; Alonso 1996; Glagolev & Alonso 1990), but such a program of morphological studies apparently came to an end, while some molecular investigations were done recently in frames of wide-range phylogenetic (Petrusek *et al.* 2008; Petrusek *et al.* 2009; Adamowicz *et al.* 2009) and phylogeographic (De Gelas & Meester 2005; Crease *et al.* 2012) investigations, or to check the identity of local populations belonging to cryptic species complex or invasive taxa (Marková *et al.* 2015; Vecchioni *et al.* 2021).

Among the daphniids of the Mediterranean area, *Daphnia chevreuxi* Richard, 1896 is a remarkable species typical of poorly mineralized temporary water ponds (Benzie 2005; Błędzki & Rybak 2016). After the species description from Algeria (Richard 1896), it was found in the whole Maghreb (Gurney 1909; Gauthier 1928; Ramdani 1988), in continental Mediterranean Europe including the Balkans (Stephanides 1948; Petkovski 1970; Flössner 1980; Negrea 1983; Naidenow 1994), in different large and small islands in the Mediterranean Sea (Stephanides 1948; Margaritora 1983; Margaritora *et al.* 1975; Błędzki & Rybak 2016; Marrone *et al.* 2019a), and in Israel (Bromley 1993), while in the Iberian Peninsula it is replaced by the closely-related *Daphnia hispanica* Glagolev & Alonso, 1990 (Alonso 1991; Alonso 1998). However, to date, just a few drawings of *Daphnia chevreuxi* are available (Richard 1896; Stephanides 1948; Glagolev 1995; Margaritora 1985; Benzie 2005), and these do not fulfil the modern standards of cladoceran morphological taxonomy.

The aim of this paper is, therefore, to redescribe the morphology of *D. chevreuxi*, i.e. based on numerous samples of J. Richard kept at the Smithsonian National Museum of Natural History, USA (Kotov & Ferrari 2010) and novel samples from Italy and North Macedonia, and review data on its distribution and ecology.

Material and methods

Most samples studied here were collected by FM by means of a 125-μm mesh-sized hand net, paying attention to sample in each microhabitat present in each site, and fixed in situ in 95% ethanol; some additional samples were obtained from our colleagues. Samples were initially examined under a stereoscopic dissecting microscope Leica MZ7.5. For morphological analysis, samples were placed in small Petri dishes; specimens were picked from them by pipettes, placed on slides in drops of glycerol, covered by coverslips and examined under a high-power microscope Olympus CX41. Ten parthenogenetic females, five adult males and two juvenile males (if present) and females from each sample were dissected for analysis of appendages. Drawings were made using *camera lucida*. Some specimens were lyophilised, attached to aluminum stubs, coated with gold in a S150A Sputter Coater, and studied under a Tescan Vega TS5130MM scanning electron microscope.

Abbreviations in illustrations and text: ejh = ejector hooks on limb I; epp = epipodite; ext = exopodite; idl = inner distal lobe of limb I; odl = outer distal lobe of limb I; pep = preepipodite.

Abbreviations for collections: DGF = Collection of David G. Frey, Smithsonian National Museum of Natural History, Museum Support Center in Suitland, Maryland, U.S.A. GLAG = personal collection of S.M. Glagolev gifted to the Laboratory of aquatic ecology and biological invasions of A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (IEE), Moscow, Russia. AAK = personal collection of A.A. Kotov stored at IEE.

Results

Order Anomopoda Sars, 1865

Family Daphniidae Straus, 1820

Genus *Daphnia* O.F. Müller, 1776

Subgenus *Daphnia* (*Ctenodaphnia*) Dybowski & Grochowski, 1895

***Daphnia* (*Ctenodaphnia*) *chevreuxi* Richard, 1896**
(Figs. 1–14)

Daphnia chevreuxi Richard, 1896: P. 206–209, Pl. 20, Figs. 10–11; Pl. 21, Fig. 4; Pl. 23, Fig. 18; Pl. 24, Fig. 4. Gauthier, 1928: P. 44–45, Fig. 15A–H. Petkovski, 1970: P. 139–142, Figs. 1–7. Flössner, 1980: P. 65–67, Fig. 3. Negrea, 1983: P. 104. Margaritora, 1983: P. 58–62, Fig. 37. Margaritora, 1985: P. 116–119, Figs. 49A–H. Glagolev and Alonso, 1990: P. 159–162. Glagolev, 1995: P. 53, Pl. 41, Figs. 1–5. Benzie, 2005: P. 125–128, Figs. 343–352. Kotov *et al*. 2010: P. 201, Fig. 117: 5–9. Korovchinsky *et al*., 2021: P. 138–140, Fig. 41: 10–14.
Daphnia psittacea Baird, 1850 in Stephanides 1948: P. 7–8, Pl. 9, Fig. 9–13.
? *Daphnia byzantina* Muckle, 1951: P. 373–374, Fig. 2a–g.

Type locality. «Algérie: Environs de Bòne (Guerrah El M'Krada, bord du lac Fetzara, marais des Kharézas, et abreuvoirs des environs de Bòne)» (Richard 1896).

Type material. Syntypes. Many parthenogenetic, ephippial females and males in samples DGF 730 and DGF 767, "Environs de Bòne, Abreuvoir"; DGF 779, "Environs de Bòne. Dans une abreuvoir", DGF 783; "Environs de Bòne"; DGF 761, "Guerrah el M'Krada. Eau legerement salee"; DGF 797 "Au bord du Guerrah el M'Krada", all from Algeria.

Other material studied here. Italy: Sicily. Many males, ephippial and parthenogenetic females from a swamp (37.85847°N, 12.92082°E), Margio di Gallitello (Calatafimi), coll. by F. Marrone in 02.03.2014, AAK M-5314. Parthenogenetic females from the same locality, coll. by Marrone in 30.11.2018, AAK M-6906. Many males, ephippial and parthenogenetic females from a pond (37.87225°N, 14.67638°E), Stagno di C. da Buffali (Nebrodi, Cesarò), coll. by F. Marrone in 16.05.2018, AAK M-6932. Many males, ephippial and parthenogenetic females from the same locality, coll. by F. Marrone on 19.05.2021, AAK M-6941. Few juvenile females from Gorgo di Gaetanello (37.88559°N, 13.36919°E), coll. by F. Marrone in 08.03.2009, AAK M-5317. Parthenogenetic females from a pond (37.97351°N, 13.4936°E), Pozze di Bosco Tumminia (Bolognetta), coll. by F. Marrone in 09.11.2018, AAK M-6938. Many males, ephippial and parthenogenetic females from a pond (38.02833°N, 13.32666°E), Gorgo di Rebuttone (Altofonte), coll. by F. Marrone in 19.02.2021, AAK M-6943. Parthenogenetic females from a pond (38.10313°N, 12.67736°E), Gorgo di Baglio Cofano (Monte Cofano), coll. by F. Marrone in 19.12.2019, AAK M-6928. Parthenogenetic females from the same locality, coll. by F. Marrone in 11.12.2019, AAK M-6946. **North Macedonia.** Many males, ephippial and parthenogenetic females from Slavej (41.3°N, 21.4°E) coll. by T. Petkovski in 25.05.1985, GLAG040.

Diagnosis. Adult parthenogenetic female with body high for the subgenus (body height/length without shell spine = 0.56–0.62). Head shield with projected, angled-rounded fornices, a median anterior projection of carapace especially short for the subgenus, it penetrates only to about 1/5–1/6 of length of the head shield. Postabdomen obviously tapering distally. Numerous small anal teeth of subequal size located on anal portion, this row continues more laterally on preanal portion where it is accompanied by groups of smaller spinules. The first (proximal) and second pectens on outer face of postabdominal claw consisting of relatively strong teeth (the longest ones approximately as long as claw diameter); the third pecten consisting of somewhat shorter spines. Antenna I as a minute conical tubercle with nine terminal aesthetascs; tips of aesthetascs not projected beyond tip of rostrum. Limb I with accessory seta; outer distal lobe bearing a long seta distally armed with short setules, and a short second seta; inner distal lobe with a single, long anterior seta 1 armed distally with short setules. Limb II with inner-distal lobe bearing a thin, stiff anterior seta with length 3/4 of soft seta length, armed with minute setules distally. Limb V with exopod supplied with two distal setae and a large lateral seta.

Ephippium dark brown, elongated, bean-like; two eggs with axes located at a very acute angle or almost parallel to the dorsal margin; anterior processes present, postero-dorsal portion of valves (with shell spine) initially incorporated into ephippium. Sculpture of ephippium as a network of small protuberances having smooth tips oriented somewhat posteriorly.

Adult male with head having anteriormost extremity completely occupied with a very large optic vesicle; a shallow post-ocular depression present. Abdomen with a shallow mound on basal segment, other segments without projections. Postabdomen tapering distally, its distal portion bent, ventral margin convex; gonopore opens subdistally, any genital papilla absent. Few anal teeth present only in basal portion of anal margin. Antenna I long, somewhat bent; length of flagellum less than half body antenna I length; distal segment of flagellum covered with short setules. Limb I with inner distal lobe bearing a single long seta (1) and a rudimentary seta 1'. Limb II inner distal portion with seta 1 remarkably stronger as in female, slightly bent and asymmetrically setulated, with a blunt tip. Limb V as in female.

Size of parthenogenetic females 0.9–3.8 mm, adult males 1.1–2.4 mm.

Redescription. Adult parthenogenetic female. *General.* Body almost transparent, high for the subgenus (body height/length without shell spine = 0.56–0.62), subovoid in lateral view, with maximum height in middle of valves (Figs. 1A, 2A–B, 3A–B). Dorsal margin slightly convex. Postero-dorsal angle with a moderately developed to long caudal spine projected posteriorly and somewhat dorsally (Figs. 1A, 2A–B, 3A–B, 4A), ventral margin regularly convex.

Head with a short, rounded rostrum (Figs. 1B, 2C–D, 3C–D); posterior margin of head slightly concave, without a projection, pre-rostral fold not expressed; antero-ventral margin usually almost straight, but rarely slightly concave; maximum body anterior extremity lies somewhat dorsally to body longitudinal midline. Head without any pre-ocular and post-ocular depressions, a very shallow depression present in posterior head portion, but this is not a border between head and valves. Any helmet fully absent in the adults. Compound eye relatively small, ocellus minute. Head shield with projected, angled-rounded fornices; the median anterior projection of carapace especially short for the subgenus since it penetrates only to about 1/5–1/6 of length of the head shield (Fig. 2E–F). Labrum as a fleshy lobe with a large distal plate (Fig. 5A).

Carapace in general semi-ovoid, the free edge uniformly convex. A group of relatively long setae in middle of its ventral margin (Fig. 4A–C); short setae at postero-ventral and posterior margin, with setules between them (Fig. 4D–F).

Abdomen with the first (proximalmost) abdominal segment with a relatively short (but longer than postabdominal claw) process, slightly bent anteriorly; the second segment with a long process (also longer than postabdominal claw) bent posteriorly; the third segment with a massive process; the fourth process small. All processes covered by rows of minute setules (Figs. 1C–D, 4G–I).

Postabdomen elongated, obviously tapering distally. Postanal margin straight, preanal and postanal angle smooth. Numerous small anal teeth of subequal size located on anal portion, this row continues more laterally on preanal portion where it is accompanied by groups of smaller spinules (Figs. 1C, E, 4G-H). Postabdominal seta as long as preanal margin, its distal segment somewhat shorter than proximal segment. Postabdominal claw regularly bent, with a pointed tip. On its outer side, along the dorsal margin there are three pectens: the first (proximal) and second pectens consisting of relatively strong teeth, the longest ones about as long as the diameter of the claw base; the third pecten consisting of somewhat shorter spines, not reaching tip of claw (Figs 1E, 4J).

Antenna I as a minute conical tubercle with nine terminal aesthetascs; tips of aesthetascs not projected beyond tip of rostrum; antennular sensory setae small, arising from base of mound of antenna I and projecting beyond the mound (Fig. 5A–B).

Antenna II relatively long (Fig. 5C–D); coxal portion with two short setae (Fig. 5E-F); basal segment distally with a short anterior spine (Fig. 5D: arrow) and a longer posterior seta (Fig. 5G: arrow). A spine on second exopod segment short (Fig. 5D: arrow). Antennal formula: setae 1–1–3/0–0–1–3. Length of apical setae approximately equal to the length of the branches.

Maxilla I as a projection bearing three longer and a single shorter seta (Fig. 6A).

Limb I with accessory seta (Fig. 6C: acs). Outer distal lobe (Figs 1F, 6B–D: odl) cylindrical, with a long seta distally armed with short setules, and a short second seta. Endite 5 = inner distal lobe (Fig. 6C: idl) with a single, long anterior seta 1 armed distally with short setules. Endite 4 with a long anterior seta (Fig. 6C: 2) and two posterior setae (a–b). Endite 3 with a long anterior seta (Fig. 6C: 3) and two posterior setae (c–d). Endite 2 with a relatively short anterior seta (Fig. 6C: 4) and four posterior setae (e–h). Endite 1 = gnathobase fully absent. Two ejector hooks of different length (Fig. 6C: ejh).

Limb II with exopodite as an elongated lobe (Fig. 6E: ext) bearing a soft distal seta, and a large, soft, lateral seta of same size with the former. Inner-distal lobe bearing five setae: four posterior setae (Fig. 6E: a–d) and a thin, stiff anterior seta (1) with length 3/4 of soft seta length, armed with minute setulae distally. Gnathobase (Fig. 1G) with two rows of setae: four anterior setae (Fig. 6F: 1'–4'), and numerous posterior setae of gnathobasic filter plate.

FIGURE 1. *Daphnia chevreuxi*, adult parthenogenetic female from "Environs de Bòne", Algeria, sample DGF 0783 (A–B) and Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy (C–G): A, large adult female. B, its head. C, postabdomen. D, abdomen. E, distal portion of postabdomen. F, limb I. G, gnathobase of limb II. H, limb V. Scale bars: 1 mm A; 0.1 mm for B–H.

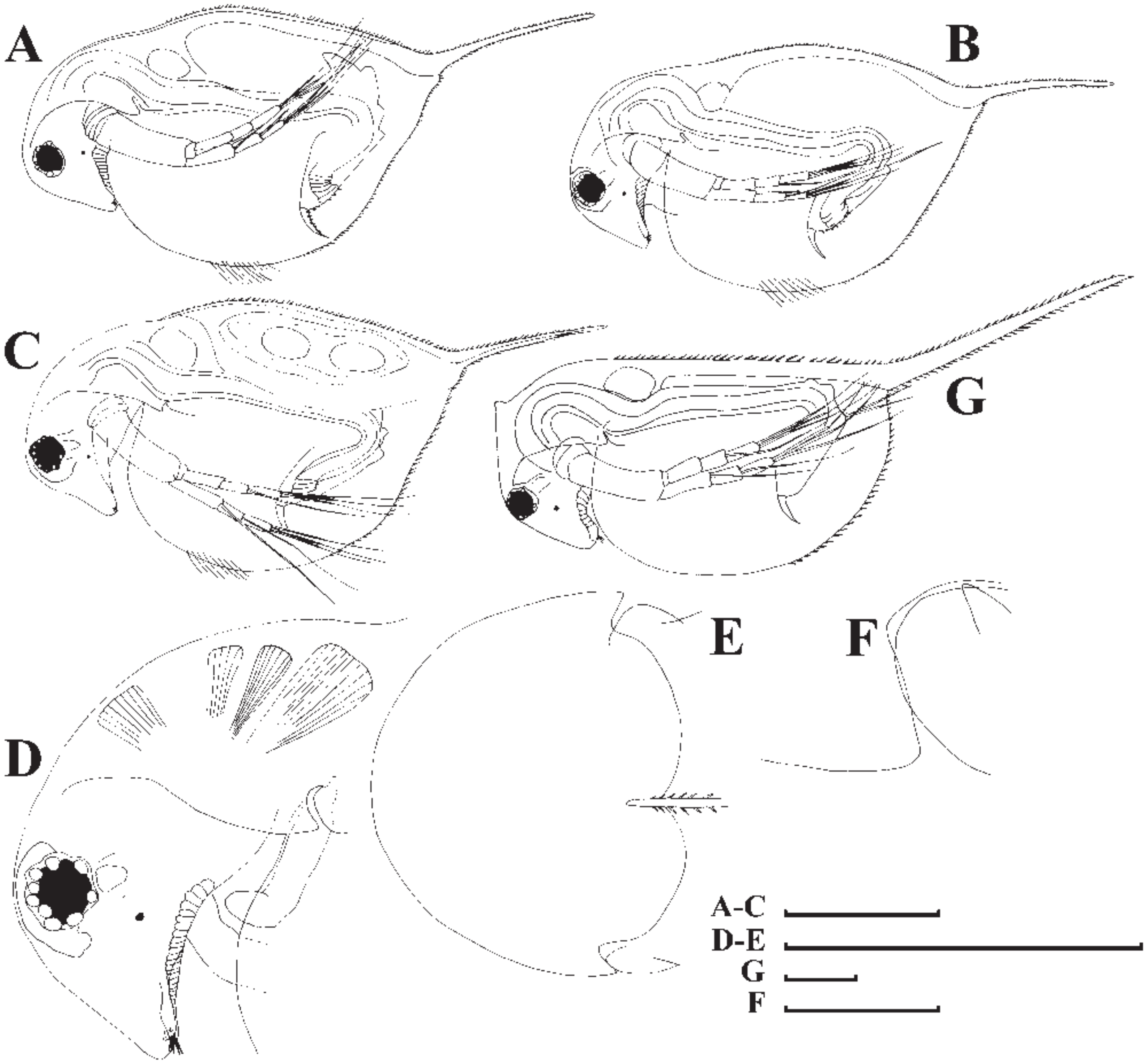

FIGURE 2. *Daphnia chevreuxi*, female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy: A–B, adult parthenogenetic female. C, ephippial female. D, head, lateral view. E, head shield, dorsal view. F, fornix. G, juvenile female. Scale bars: 1 mm A–E; 0.1 mm for F–G.

Limb III with a large, setulated pre-epipodite (Fig. 7A: pep), ovoid epipodite (epp) and a flat exopodite (ext) bearing four distal setae (Fig. 7A: 1–4), among them seta 2 longest, distally with short setules (Fig. 7B), and two lateral setae (Fig. 7A: 5–6). Inner-distal portion of limb with endite 5 bearing a single, large anterior seta (Fig. 7C: 1), armed distally with short setulae and a large posterior seta, bearing long setulae (Fig. 7C: a); endite 4 with a single setulated anterior seta (2) and a single setulated posterior seta (b) somewhat shorter than anterior seta; endite 3 with a large anterior seta (Fig. 7C: 3) and two posterior setae; endite 2 with a large anterior seta (Fig. 7C: 4) and four posterior setae. The rest of the limb inner-distal portion as a singular large lobe, modified gnathobase, bearing numerous posterior soft setae, an anterior seta in its distal corner (Fig. 7C: 1') and two very short setae in middle of filter plate (Fig. 7D: 2' and 3').

Limb IV with a large, setulated pre-epipodite (pep), ovoid epipodite (epp) and a wide, flat exopodite (ext), bearing four distal (Fig. 7E: 1–4) and two lateral (Fig. 7E: 5–6) setae. Inner-distal portion of this limb with completely fused endites, distally with two setae of unclear homology (Fig. 7F: 1 and 2); the most part of limb inner margin is a gnathobase filter plate consisting of numerous posterior setae.

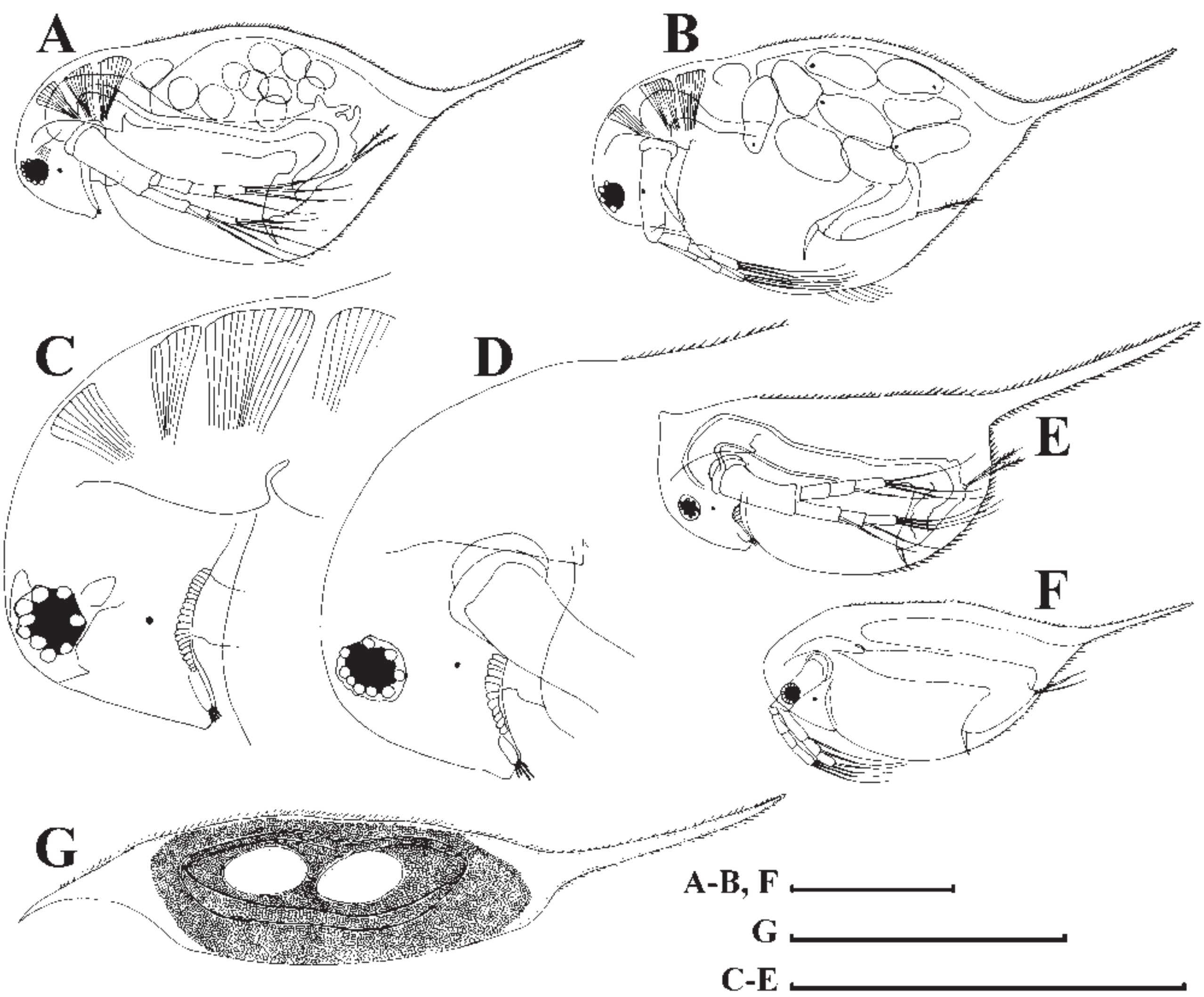

FIGURE 3. *Daphnia chevreuxi* from «Environs de Bòne», sample DGF 0783 (A–F) and «Environs du Bòne, Abreuvoir», sample DGF 0730 (D), Algeria: A–B, large adult parthenogenetic female. C–D, head, lateral view. E, juvenile female, instar I. F, juvenile female. G, ephippium. Scale bars 1 mm.

Limb V with a large, subovoid epipodite (epp), triangular exopodite (ext) supplied with two distal setae (Fig. 1H, 7G–H: 1–2), and a large, slightly curved lateral seta (3). Inner limb portion as an ovoid flat lobe, with setulated inner margin and a single, large seta.

Juvenile female. Body more elongated, dorsal margin almost straight, caudal spine longer (Figs 2G, 3E–F, 8A). Head relatively large as in adult female, with a rounded rostrum (Fig. 8B–C), sometimes with a small pointed helmet (Figs 2G, 3E). In instar I, head shield according to *Ctenodaphnia*-type: median anterior projection from carapace somewhat widened anteriorly, almost touching dorsal organ (Fig. 8D–E), instead of *Daphnia*-type with solely located dorsal organ and absent anterior projection of valves (Kotov & Boikova 2001).

Ephippial female. Only dorsal carapace portion modified in ephippial female (Fig. 2C). Ephippium dark brown, elongated, bean-like (Figs 2C, 3G); two eggs with axes located at a very acute angle or almost parallel to dorsal margin; anterior processes present; postero-dorsal portion of valves (with shell spine) initially incorporated into ephippium. Dorsal margin of carapace specially re-enforced (Fig. 9A–C). Sculpture of ephippium as a network of small protuberances having smooth tips oriented somewhat posteriorly (Fig. 9B–D).

Preephippial female. A female transits from parthenogenesis to gamogenesis after two moults. Preephippial (after first such moult) female has an ephippium forming covers of its carapace. As a result, sculpture of future ephippium partly seen through its covers (Fig. 10A–F).

Adult male. *General.* Body elongated, body height/length (without shell spine) about 0.45–0.5; dorsal margin of valves almost straight, elevated above head; no distinct depression between head and valves; postero-dorsal angle distinct, with a relatively long caudal spine (Figs. 11A–C, 12A).

Head with a very short, rounded rostrum; its posterior margin straight; ventral margin straight or slightly concave, anteriormost extremity completely occupied with a very large optic vesicle (Figs 11D, 12B); a shallow post-ocular depression present. Compound eye especially large, ocellus minute. A short anterior projection from valves (Fig. 12D). Fornices well-developed, their tips smooth (Figs 11D, 12C–E).

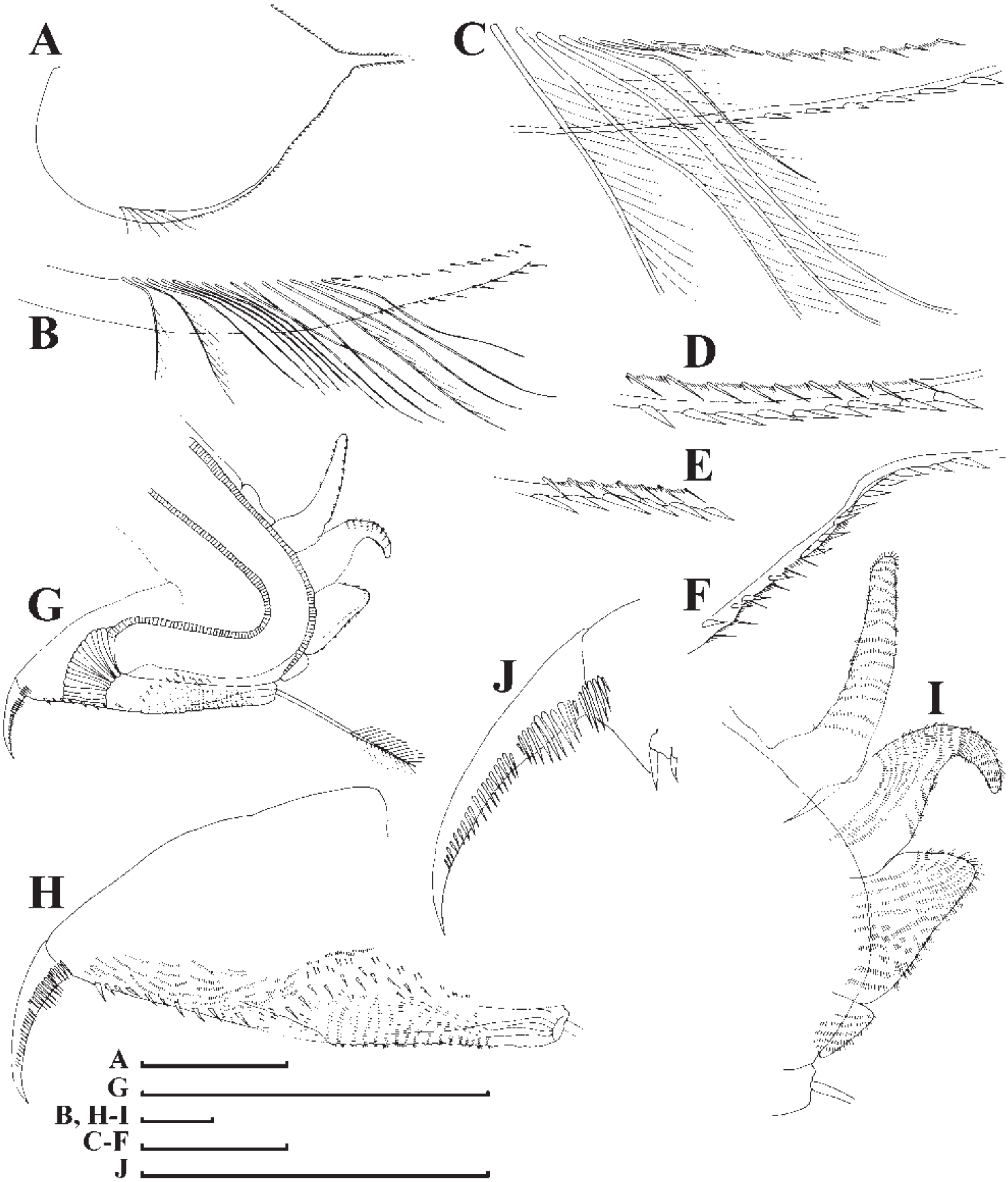

FIGURE 4. *Daphnia chevreuxi*, adult parthenogenetic female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy; A, valve. B–C, ventral margin. D–F, postero-ventral margin. G, postabdomen. H, its distal portion. I, abdomen. J, postabdominal claw. Scale bars: 1 mm A, G; 0.1 mm for B–F, I–J.

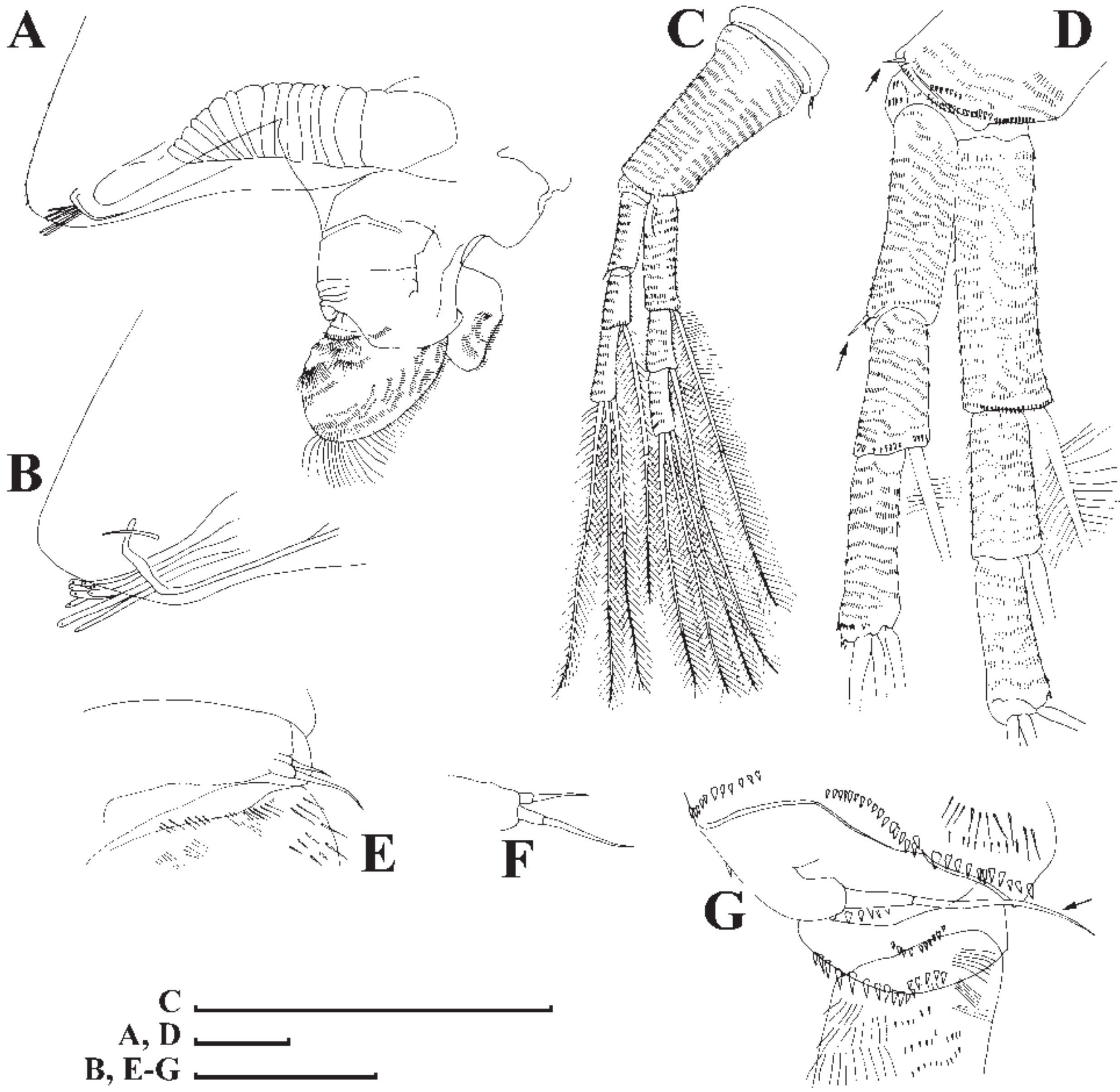

FIGURE 5. *Daphnia chevreuxi*, adult parthenogenetic female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy: A–B, rostrum and antenna I. C–D, antenna II. E–F, coxal portion. G, distal portion of basal segment. Scale bars: 1 mm C; 0.1 mm for A–B, D–G.

Valve with anterior margin slightly convex, supplied with exactly marginal, relatively short setae (Fig. 13A–B); antero-ventral angle prominent anteriorly, supplied with long setae; whole ventral margin with numerous setae located submarginally on inner face of valve. Postero-ventral portion of valve with marginal denticles and short setae located submarginally on inner face of valve; short setules between these setae (Fig. 13C–D).

Abdomen with a shallow mound on basal segment, other segments without projections (Figs 11E, 14A).

Postabdomen tapering distally, its distal portion bent (Figs 11E, 14A); ventral margin convex; preanal margin straight; anal margin depressed; gonopore opens subdistally (Fig. 11F, 14B); genital papilla absent. Few anal teeth present only in basal portion of anal margin (Figs. 11F, 14B). On outer side of postabdominal claw, the first and second (proximal) pectens consisting of relatively strong teeth; longest teeth shorter than the diameter of the claw base; third pecten consisting of numerous fine setulae not reaching the tip of claw.

Antenna I long, regularly curved (Figs 11D, 12B, 13E). Nine short aesthetascs; antennular sensory seta very short, located distally. Length of flagellum less than half body length of the antenna I. The distal segment of flagellum covered with short setules (Figs. 11G, 13E).

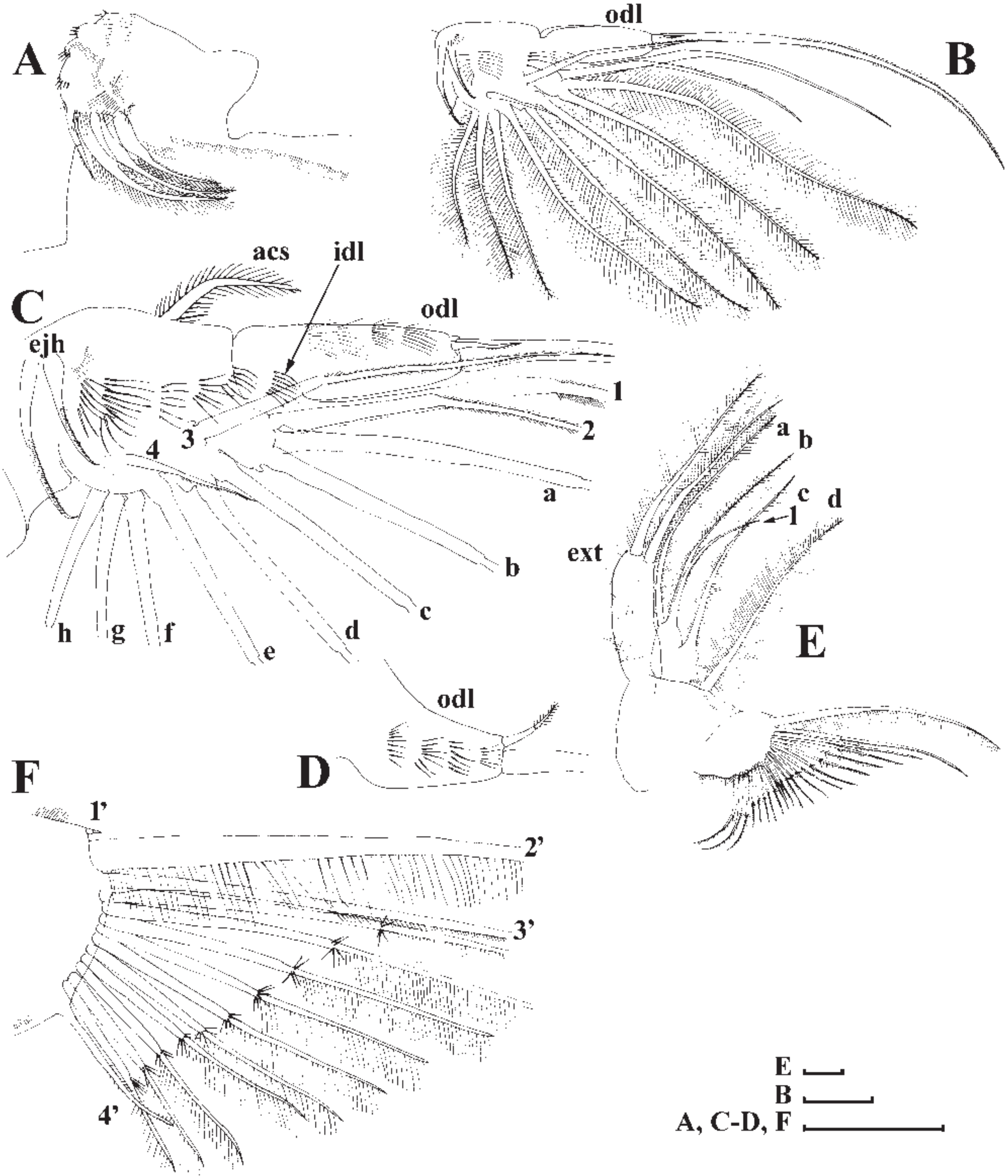

FIGURE 6. *Daphnia chevreuxi*, head and thoracic limbs of adult parthenogenetic female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy: A, maxilla I. B–C, limb I. D, its outer distal lobe. E, limb II. F, its gnathobase. Scale bars 0.1 mm.

Antenna II (Figs 12A, 13F) relatively larger as compared to female.

Limb I. Outer distal lobe (Fig. 14C–E: odl) large, bearing a rudimentary seta, a small hillock and a very large seta. Inner distal lobe (idl) with a bent copulatory hook, a single long seta (Fig. 14 E: 1) and a rudimentary seta (Fig. 14 E: 1’). Additional seta on endite 4 (Fig. 14 D: 2’) anterior seta shorter than in female and supplied with longer setules (Fig. 14 D: 3) while anterior seta longer than in female (Fig. 14 D: 4).

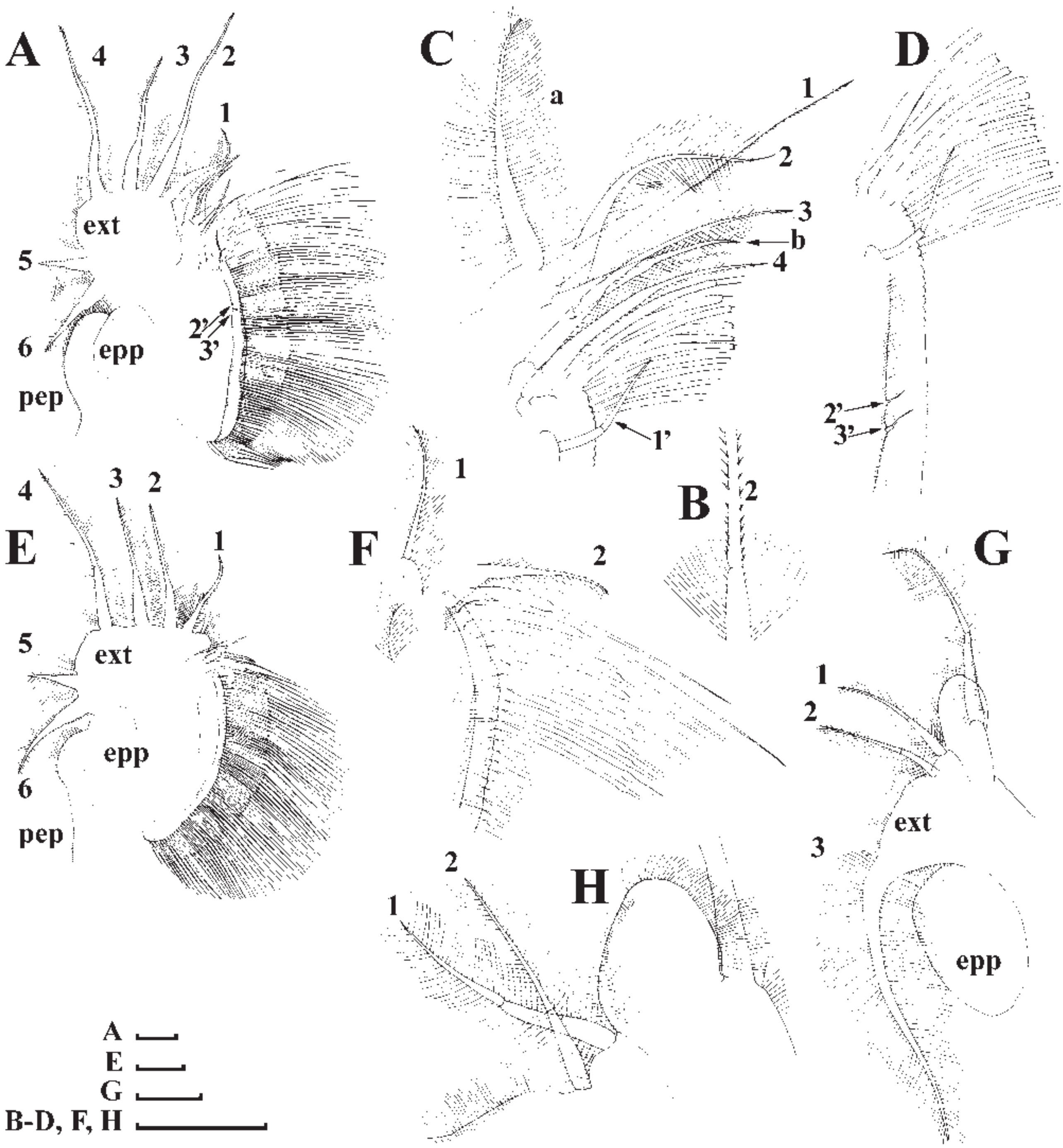

FIGURE 7. *Daphnia chevreuxi*, thoracic limbs of adult parthenogenetic female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy: A, limb III. B. seta 2 of its exopodite. C–D, its inner-distal portion. E, limb IV. F, its inner-distal portion. G, limb V. H, its distal portion. Scale bars 0.1 mm.

Limb II. Distalmost endite with seta 1 remarkably stronger than in female, slightly bent and asymmetrically setulated, with a blunt tip (Figs 11H: arrows, 14F: 1). Limb V as in female (Fig. 14G).

Juvenile male II. Body elongated, eye capsule less developed as compared to adult male, posterior incision more protected anteriorly, fornices small; no setules at antero-ventral valve portion, antenna I shorter that in adult male, with shorter flagellum (Fig. 12F–G).

Size. Parthenogenetic females 0.9–3.8 mm in our material (2.4–3.8 mm according to Benzie, 2005); adult males 1.1–2.4 mm in our material (1.3–1.6 mm according to Benzie, 2005).

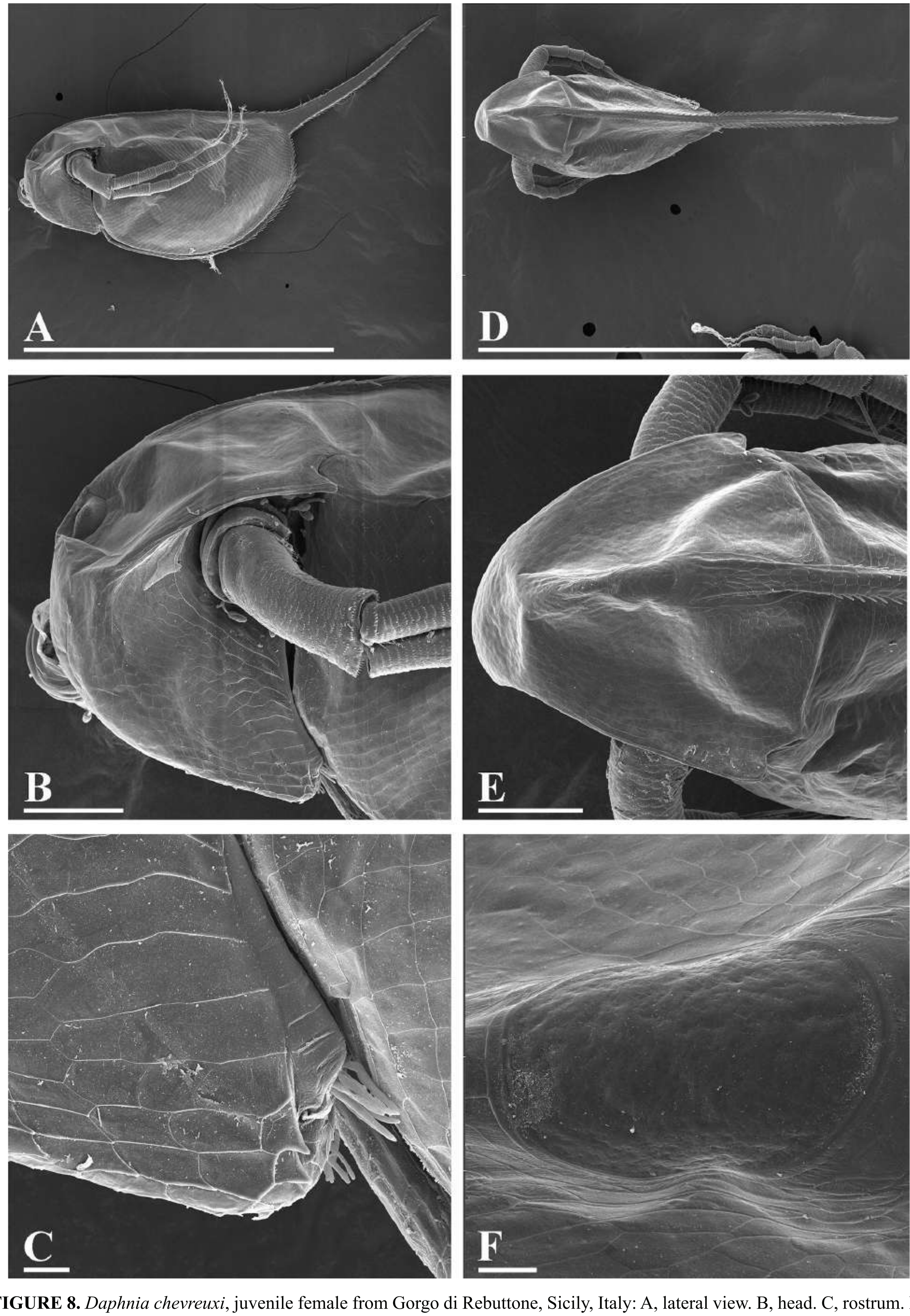

FIGURE 8. *Daphnia chevreuxi*, juvenile female from Gorgo di Rebuttone, Sicily, Italy: A, lateral view. B, head. C, rostrum. D, dorsal view. E, head, dorsal view. F, dorsal organ. Scale bars: 1 mm for A, B; 0.1 mm for B, E; 0.01 mm for C, F.

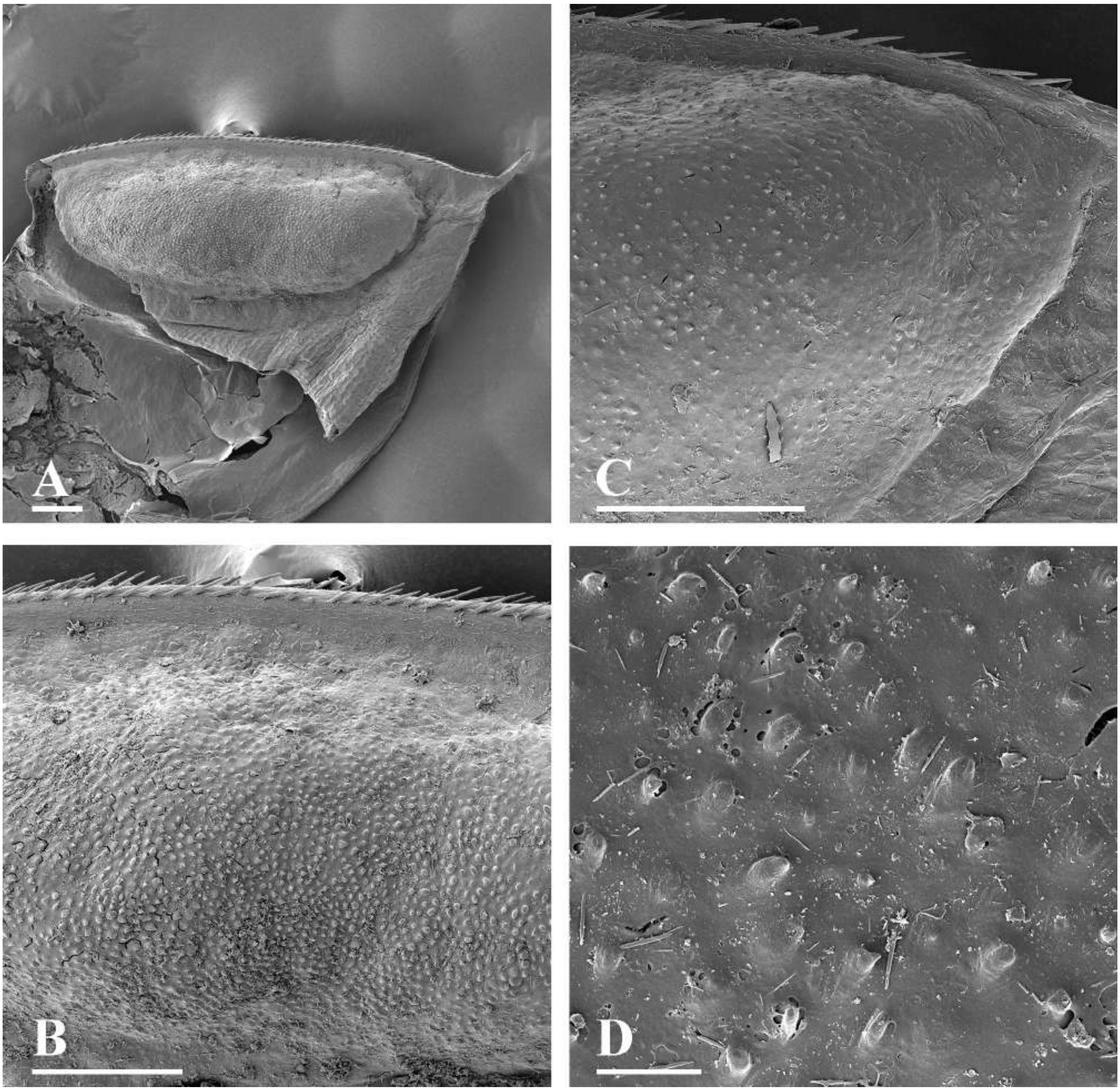

FIGURE 9. *Daphnia chevreuxi*, ephippial female from «Environs de Bòne. Abreuvoir», sample DGF 0767, Algeria: A, carapace with ephippium. B–D, ephippium sculpture. Scale bars: 0.1 mm for A–C; 0.01 mm for D.

Differential diagnosis. Main characteristic traits of this taxon are (1) strongly reduced (almost undiscernible) body of antenna I and (2) a very short median anterior projection of the carapace (its length less than 0.2 of head shield length) (Glagolev & Alonso 1990; Glagolev 1995; Benzie 2005; Korovchinsky *et al.* 2021). Among Eurasian species of the subgenus, only *D.* (*C.*) *chevreuxi* and *D.* (*C.*) *hispanica* have an accessory seta on limb I (Glagolev & Alonso 1990). Moreover juveniles of *D.* (*C.*) *chevreuxi* sometimes bear a small triangular helmet not characteristic of other Eurasian ctenodaphniids.

D. chevreuxi has no: lateral keels on the head shield as *D.* (*C.*) *magna*; sharp elongated fornices as *D.* (*C.*) *lumholtzi*; dorsal head plate as *D.* (*C.*) *atkinsoni*-group; sharp dorsal keel as *D.* (*C.*) *hispanica.* The most problematic is differentiation between *D.* (*C.*) *chevreuxi* and *D.* (*C.*) *similis*-group, first of all, the former and *D.* (*C.*) *similis* s.str. which is common in southern half of Europe. Female of *D.* (*C.*) *chevrexi* has: (1) more curved dorsal margin; (2) more reduced (almost undiscernible) body of antenna I; (3) longer seta 1' on gnathobase III (lengh c.a. 0.5 length of seta 4); (4) two well-developed distal setae on exopodite V (while one of them reduced in size or completely absent in in *D. similis* group). Male has: (1) strongly reduced postanal teeth, (2) regularly curved antenna I; (3) two well-developed distal setae on exopodite V.

Distribution and ecology. We have analysed *D.* (*C.*) *chevreuxi* specimens from Algeria, Sicily and North Macedonia. In North Macedonia, the species was found in former clay pits (Petkovski 1970), but such populations could have been introduced due to human activities, and their native status is questionable.

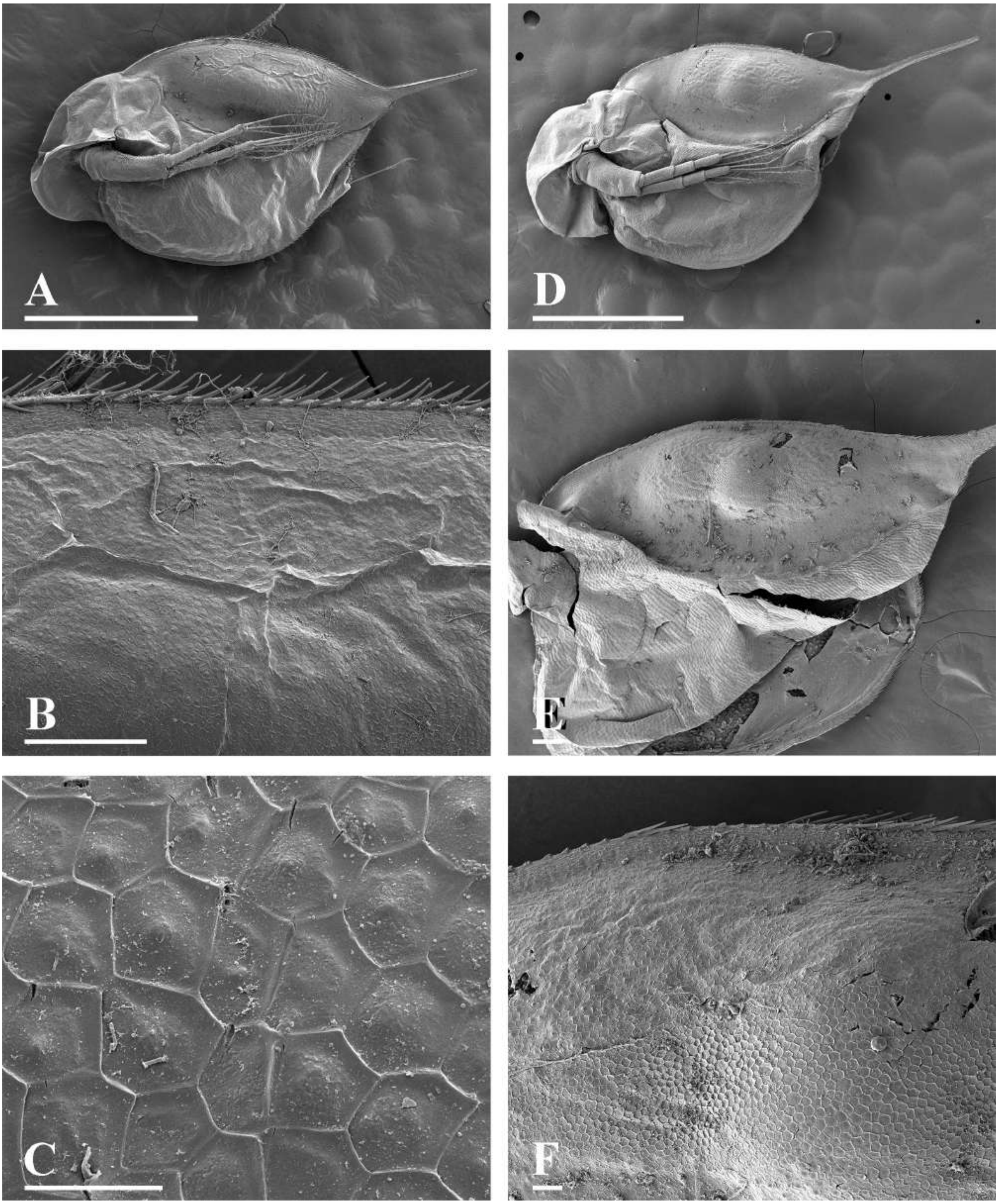

FIGURE 10. *Daphnia chevreuxi*, pre-ephippial female from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy (A–C) and Slavej, North Macedonia (D–F): A, lateral view. B–C, sculpture of carapace. D, lateral view. E, carapace. F, its sculpture. Scale bars: 1 mm for A, D; 0.1 mm for B, E; 0.01 mm for C, F.

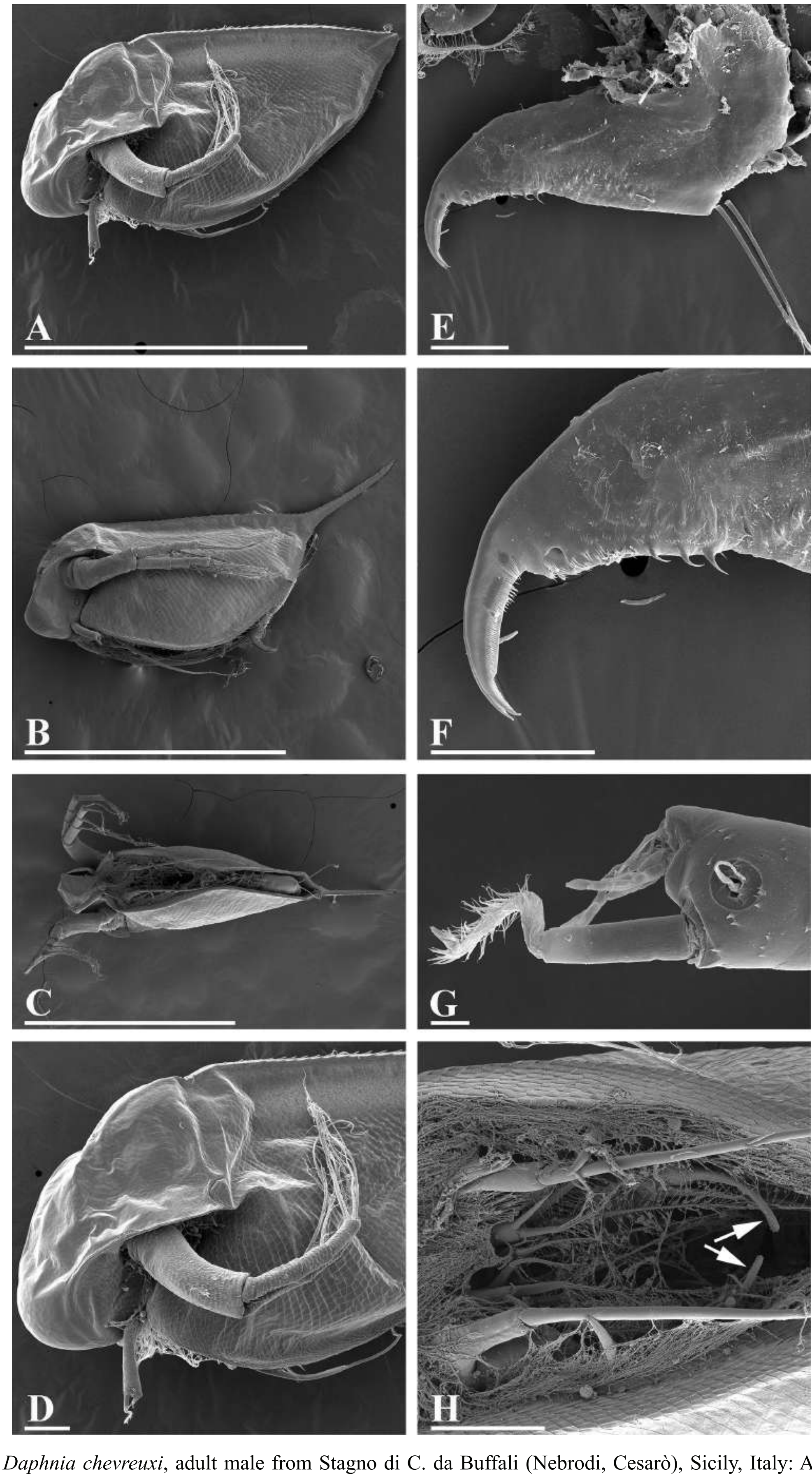

FIGURE 11. *Daphnia chevreuxi*, adult male from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy: A–B, lateral and latero-ventral view. C. ventral view. D. head. E, postabdomen. F, its distal portion. G, distal portion of antenna I. H, central portion of body, ventral view. Scale bars: 1 mm for A–C; 0.1 mm for D–F, H; 0.01 mm for G.

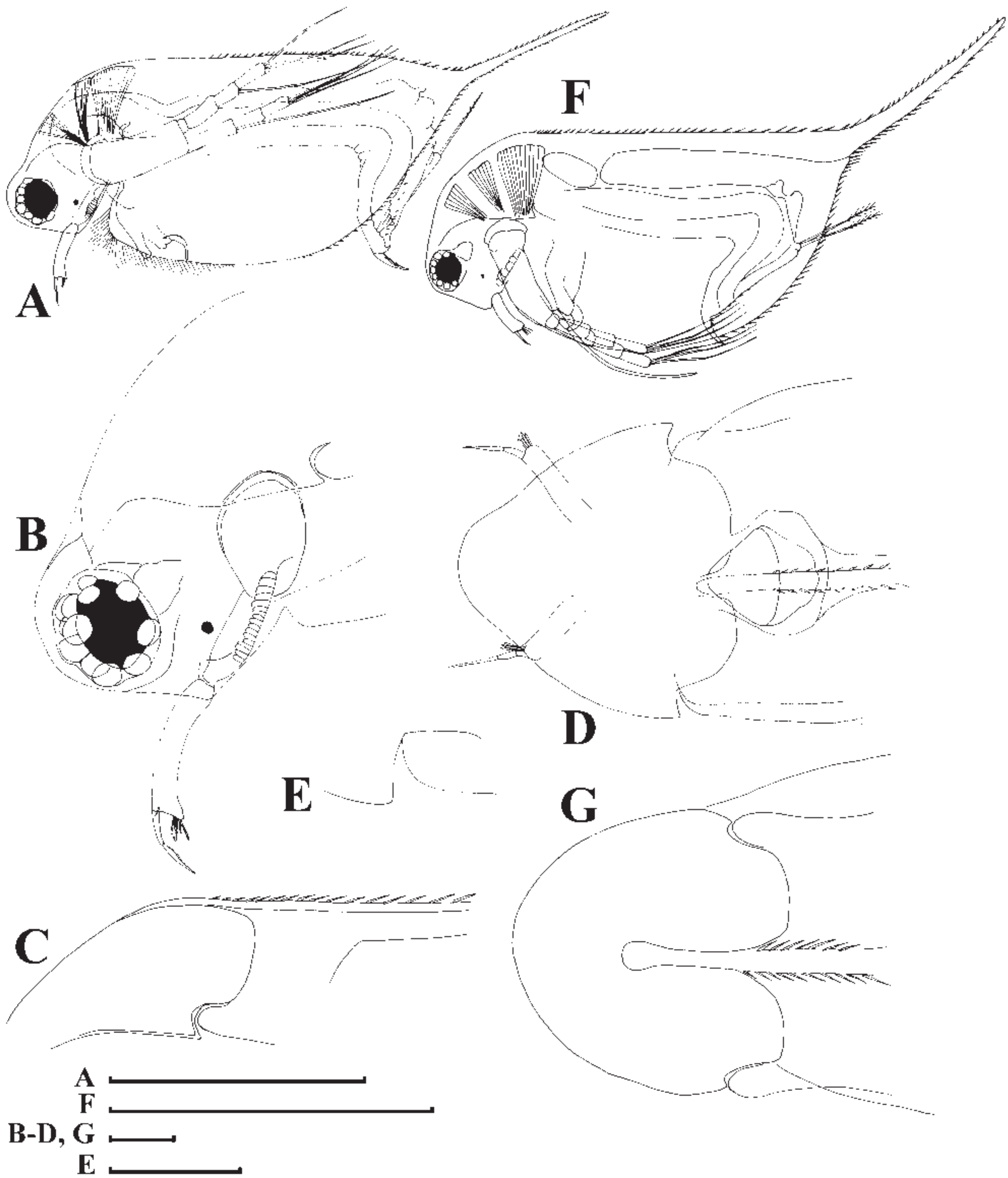

FIGURE 12. *Daphnia chevreuxi*, male from Stagno di C. da Buffali (Nebrodi, Cesarò), Sicily, Italy (A–B, D–E) and "Environs de Bòne", Algeria, sample DGF 0783 (C, F–G): A, adult male, lateral view. B, head. C, dorsal portion of head, lateral view. D, head, dorsal view. E, fornix. F, juvenile male of instar II. G, head, dorsal view. Scale bars: 1 mm for A, F; 0.1 mm for B–E, G.

The taxon was also recorded from mainland Italy (Margaritora 1983; Margaritora 1985), mainland Greece (Stephanides 1948; Marrone *et al.* 2019b), Romania (Negrea 1983), Bulgaria (Flössner 1980; Naidenow 1994), Corfu (Stephanides 1948), Corsica and Sardinia (Margaritora 1985; Margaritora *et al.* 1975), Crete (Marrone *et al.* 2019b), and the Maghreb (Dumont 1979; Mouelhi *et al.* 2000), but no samples from these regions have been analysed in the frame of present work. This species is also reported from Israel, although the actual conspecificity of

Israeli populations with *D. chevreuxi* s.str. should be investigated with molecular tools (Adamowicz *et al.* 2009). In reality, the taxon could be represented by a series of close species as it is demonstrated for some other Mediterranean endemics (e.g. Marrone *et al.* 2010).

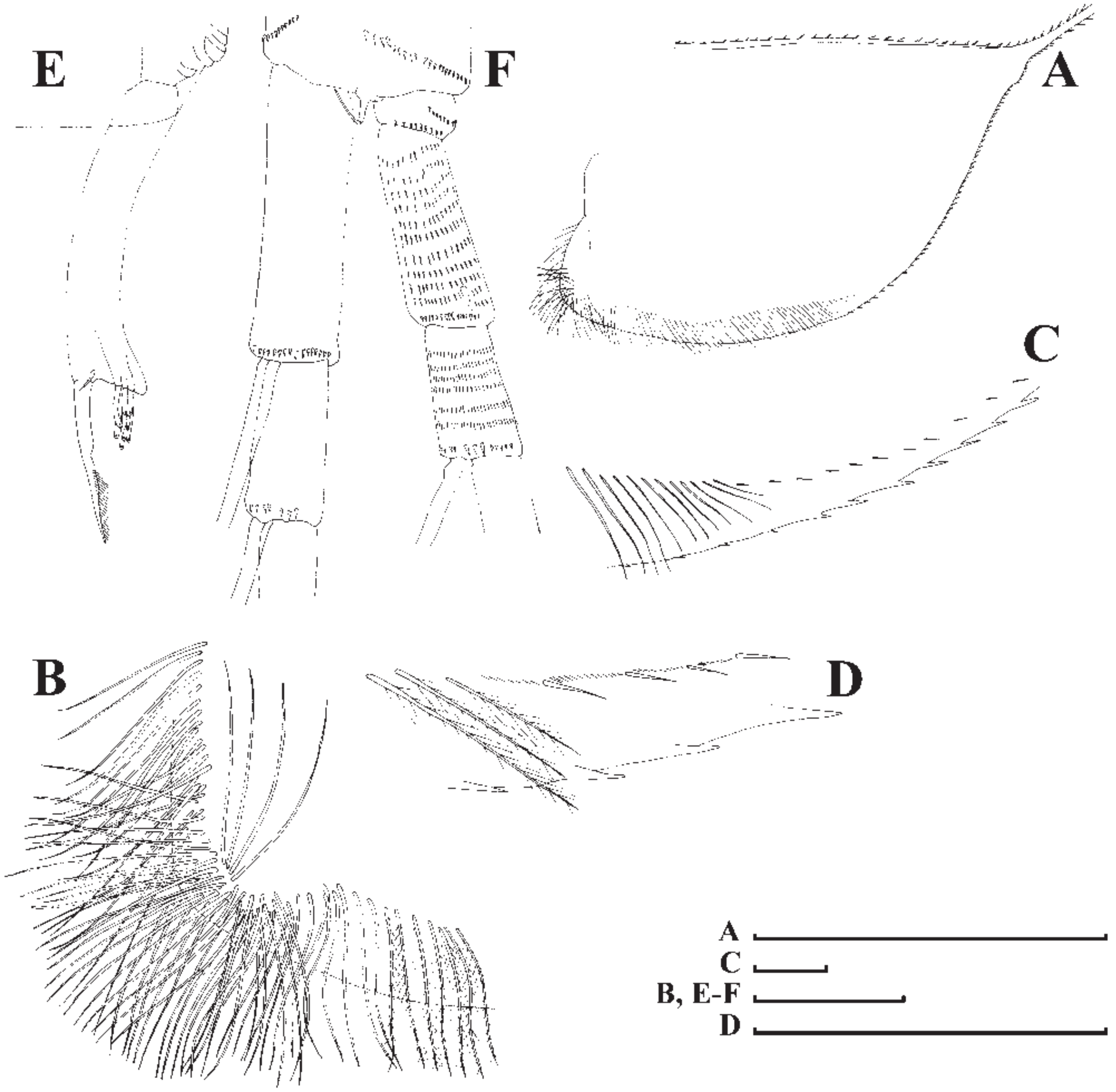

FIGURE 13. *Daphnia chevreuxi*, adult male from Gorgo di Rebuttone (Altofonte), Sicily, Italy: A, valve. B, its anterior portion. C–D, its postero-ventral portion. E, antenna I. F, antenna II. Scale bars: 1 mm for A; 0.1 mm for B–F.

Actual occurrence of the species in Morocco (Mouelhi *et al.* 2000; Ramdani 1988) and Romania (Negrea 1983) needs to be verified. *D. chevreuxi* is considered a "circum-Mediterranean" taxon (Benzie 2005), but its verified distribution ranges from the Maghreb through Italian Peninsula and Tyrrhenian islands to the Balkans, whereas it is absent from Iberian Peninsula (Alonso 1996), France (Amoros 1984), Libya, Egypt (Dumont 1979) and Turkey (Güher 2014). Moreover *D. byzantina* Muckle, 1951 described from Turkey (Muckle 1951) is most probably a junior synonym of *D. chevreuxi*, or a member of the *chevreuxi* group possibly conspecific with the aforementioned taxon from Israel.

The species is linked with long-lasting and poorly mineralized temporary ponds, located from the sea level up to 1500 m.a.s.l. (Gauthier 1928; Stephanides 1948; Margaritora 1985; Ghaouaci *et al.* 2018; Marrone & Vecchioni 2021), in areas characterized by a typical Mediterranean climate (Peel *et al.* 2007).

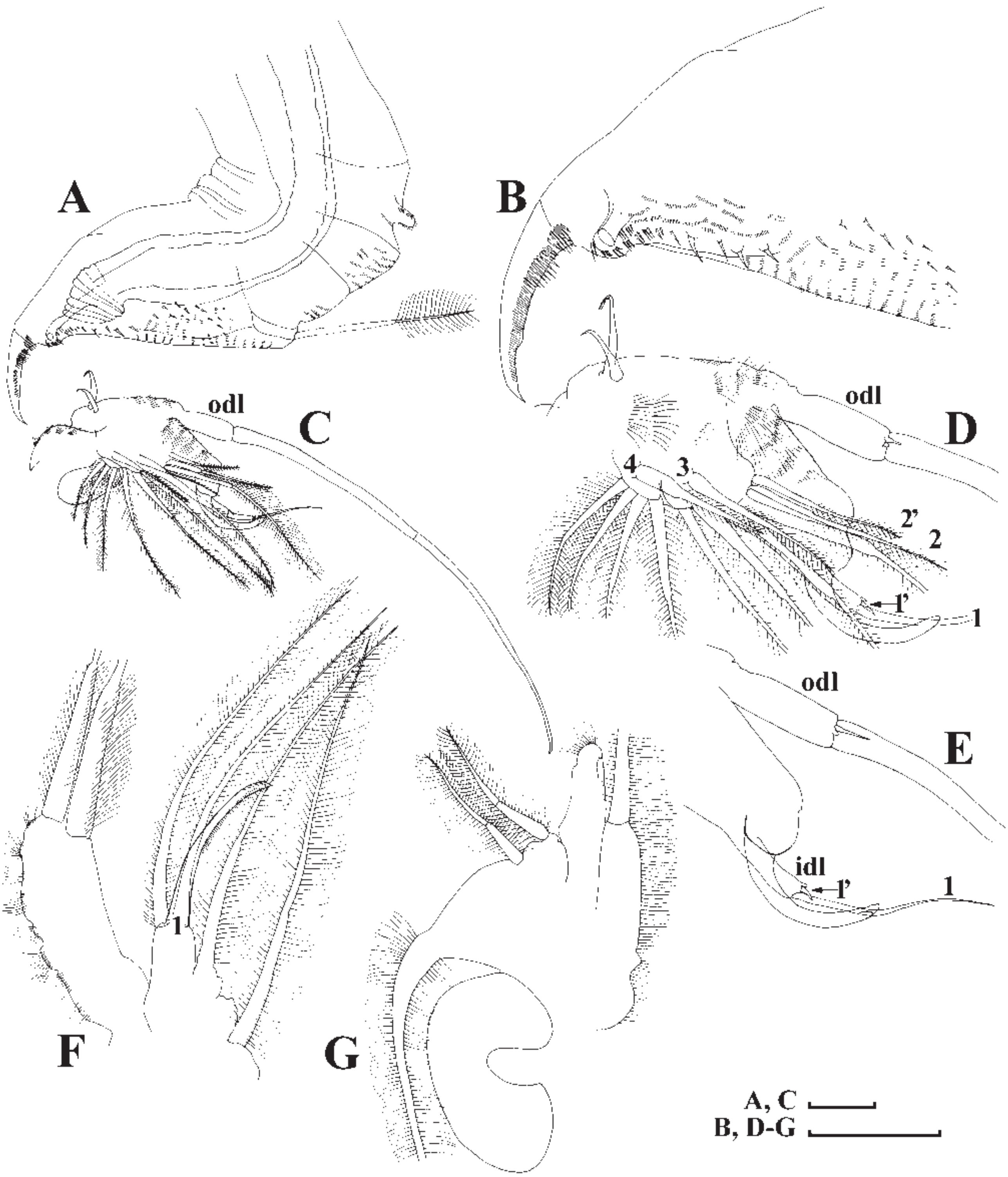

FIGURE 14. *Daphnia chevreuxi*, adult male from a pond, Gorgo di Rebuttone (Altofonte), Sicily, Italy: A, postabdomen. B, its distal portion. C–D, limb I. E, its inner distal lobe. F, distal portion of limb II. G, limb V. Scale bars 0.1 mm.

Discussion

The genus *Daphnia* is relatively well characterized in the Mediterranean area: *D.* (*Ctenodaphnia*) *chevreuxi* was the last endemic species of the subgenus *D.* (*Ctenodaphnia*) which was inadequately described to date. In addition to *D.* (*C.*) *chevreuxi*, two other Mediterranean endemic species of this subgenus are well-described, namely *D.* (*C.*)

mediterranea Alonso, 1985 and *D.* (*C.*) *hispanica* Glagolev & Alonso, 1990; the latter is the sister species of *D. chevreuxi* (Adamowicz *et al.* 2009). Moreover, several cryptic lineages with presumably endemic Mediterranean distribution are known within *D. atkinsoni* group (Petrusek *et al.* 2009).

Daphnia chevreuxi is currently associated with areas which were only marginally influenced by the drastic climate changes, including strong aridification and cooling phases, which took place during coldest Pleistocene phases (Hewitt 2001; Stewart & Lister 2001). According to Korovchinsky (2006), the subtropics and adjacent regions with warm climate represent zones currently inhabited by pre-Quaternary relicts which could survive in situ during Plio-Pleistocene climatic fluctuations (Marrone *et al.* 2010; Reniers *et al.* 2013; Marrone *et al.* 2017; Kappas *et al.* 2017). In this frame, *Daphnia chevreuxi* represents both a biogeographical relictual taxon and a strongly diverging species within the subgenus *D.* (*Ctenodaphnia*) as it is distributed in regions known as important Pleistocene refugia, and it belongs to an earlier derived branch of this subgenus (Adamowicz *et al.* 2009).

To date, no Mediterranean endemic species are known for the subgenus *Daphnia* (*Daphnia*). Such a pattern is possibly to be ascribed to the occurrence of a latitudinal diversity pattern differently affecting the two *Daphnia* subgenera in Eurasia (Benzie 2005). Within the genus *Daphnia*, the highest diversity of *Daphnia* (*Daphnia*) is located at temperate and higher latitudes of the Palaearctic region, and that of *D.* (*Ctenodaphnia*) is located at lower latitudes and in warmer climates. In this way, *D*. (*Ctenodaphnia*) could be considered the most typical *Daphnia* subgenus of the Mediterranean area, and its pattern of endemicity seems consistent with it.

Moreover, representatives of the subgenus *D.* (*Ctenodaphnia*) are, with few exceptions, typical inhabitants of temporary and ephemeral waters, which are often regarded as "ecological refugia" (Davis *et al.* 2013), hosting an ancient and very peculiar crustacean biota (Sahuquillo & Miracle 2013); conversely, the vast majority of the species belonging to *Daphnia* (*Daphnia*) prefers larger and permanent water bodies, although they can be present in temporary waters as well (Benzie 2005). The paradox of temporary pools being "probably the most permanent of all freshwater habitats" (Fryer 1985) is well-known, and temporary pools are also inhabited by other "living fossils", including large branchiopods (Dumont & Negrea 2002). Stability of such communities during millions of years are confirmed by fossil records (Gueriau *et al.* 2016; Zharov *et al.* 2020); unfortunately, temporary water bodies and their biota are nowadays threatened by human activities and human-induced climate change, which is predicted to have a significant impact on the inland waters of the Mediterranean area (Markovic *et al.* 2017). In this framework, the realization of a complete and precise inventory of the biological diversity of the inland waters of the Mediterranean area is urgent and necessary to understand, and possibly face, the risks it currently faces.

Temporary waters of Eurasia are also inhabited by the representatives of *Daphnia* (*Daphnia*) *pulex* and *D*. (*D*.) *obtusa* species complexes (Benzie 2005), which coexist with the ctenodaphniids. The former are awaiting detailed revisions and there are only preliminary ideas about their distribution in Eurasia (Crease et al. 2012). However there is a well-studied group of *D.* (*Daphnia*) inhabiting temporary waters with a contrast pattern to *D*. (*Ctenodaphnia*), namely the *D. (D.) curvirostris* complex. In Southern Europe it is represented by a single taxon, *D. curvirostris* Eylmann, 1887, and only in the Tatras there are few relict populations of the closely related *D. hrbaceki* Juračka, Kořínek & Petrusek, 2010. In contrast, along the Pacific coast of Eurasia temporary water bodies are populated by many endemic taxa of the *D.* (*D.*) *curvirostris* species complex, which differentiated in early-middle Caenozoic (Kotov *et al.* 2021), whereas temporary water bodies are inhabited only by a single ctenodaphniid species, *D.* (*C.*) *sinensis* Gu, Xu, Li, Dumont & Han, 2013 (Xiang *et al.* 2015; Garibian *et al.* 2020). Therefore, we observe contrasting patterns at the two ends of Eurasia: several species of *D.* (*Ctenodaphnia*) and only one species of the *D.* (*D.*) *curvirostris* complex in the West, and a single *D.* (*Ctenodaphnia*) with several *curvirostris*-like species in the East.

Subtropics and closest territories of the Pacific coast of Eurasia represent another relict endemism zone predicted by Korovchinsky (2006). Many endemic species and locally distributed clades have been found there recently based on morphology, molecular methods and their combination (Kotov *et al.* 2021; Korovchinsky 2013; Maruoka *et al.* 2018; Neretina *et al.* 2021) similarly to the Mediterranean region. To date, the two ends of Eurasia are well-studied, while the subtropics and adjacent territories in the central portion of continent are significantly less studied, and studies of the Pontocaspian region and Middle Asia are missing.

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