Doktori (PhD) értekezés

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Palearktikus pattanóbogarak taxonómiája

(Coleoptera: Elateridae)

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Az iskolavezető jóváhagyása A témavezető jóváhagyása

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1. ELŐZMÉNYEK ÉS CÉLKITŰZÉS

1.1. Előzmények

Jelen doktori értekezés célja a közel 20 éve tartó entomológiai kutatásaim folytatása, a doktori képzés előtt megkezdett, hasonló témakörben végzett taxonómiai és faunisztikai eredmények további, folyamatos közlése. A több elemből összeállított doktori értekezés a pattanóbogár-rendszertan és osztályozás témakörén belül különféle résztémákat fed le.

A pattanóbogarak az egyik legnagyobb fajszámú bogárcsalád, világszerte nagyjából 10000 fajuk ismert. Számos csoportjuk gazdasági, fejlődéstörténeti és ökológiai szempontból is jelentős. Változatos megjelenésű és életmódú fajaik közt előfordulnak haszonnövények gyökerét károsítók, érintetlen erdőkben fejlődő szaproxilofágok vagy például szárazföldi csigákat ragadozók is, benépesítve az esőerdei, sivatagi és magashegyi élőhelyeket is (BOUCHARD et al. 2017). Jelentőségük mind világszinten, mind pedig hazánkban természetvédelmi szempontból is számottevő. Idős erdőállományokhoz kötődő, élőhelyspecialista fajaik fontos erdőállapotjelzők, jelenlétük egyes mikrohabitatokban kulcsfontosságú (ECKELT et al. 2017). Ugyanakkor a legtöbb esetben nem ismerjük pontos ökológiai szükségleteiket, élőhelyigényeiket, pl. a holtfában fejlődő fajok számára szükséges holtfa minőségét, fajösszetételét, az adott terület klimatikus viszonyait stb. Palearktikus fajaik kutatottsága világszinten elfogadható, jelenleg azonban tucatnyi, még aktív specialista dolgozik csupán a csoporton. Kutatottságuk ellenére rendszer- és nevezéktanuk nem tisztázott, folyamatosan változik, egyes fajcsoportjaik tekintetében csak régi irodalmakra hagyatkozhatunk (STIBICK 1979). A nemzetközi szakirodalomban folyamatosan megjelenő publikációk ugyan részben tisztázzák számos csoport, genusz vagy faj rendszertani helyzetét (MUONA 1995, LAWRENCE et al. 2007), ám ez korántsem jelenti azt, hogy ne lenne feladata a jelen és jövő taxonómusainak.

A taxonómia a rendszerezés egységeivel, kategóriáival, a rendszerezés műveleteivel és szabályaival foglalkozó, alapvetően összehasonlító és analitikus szemléletű, leíró-rendszerező tudomány. Több száz éves múltú tudományterület, mely folyamatosan fejlődik, változik, ezzel egyre pontosabb képet adva a körülöttünk előforduló állat-, ezen belül bogárfajok rendszeréről. Taxonómiai alapok nélkül olyan tudományterületek, mint az ökológia, biogeográfia vagy a filogenetika nem állhat erős lábakon (LÖBL et al. 2023). Jelenlegi helyzete ugyanakkor – különféle társadalmi, tudományfinanszírozási és szemléletmódváltás-beli okok miatt – elismertség és jövőkép tekintetében korántsem pozitív (PÁLL-GERGELY et al. 2024). A zootaxonómiai cikkek többek közt lehetnek fajleírások (PROSVIROV 2016), fajcsoportokat, genuszokat érintő revíziók (MERTLIK et al. 2017) vagy katalógusok (KUNDRATA et al. 2019). A morfológia, azaz alaktan révén egységes, lényegretörő nyelvezettel megírt szöveggel és gyakran szemléltető ábrákkal segíti a taxonómiai leírások eredményeinek közérthetőségét. Ezek a cikkek gyakran további információt közölnek az említett fajok előfordulásáról, esetleges természetvédelmi vonatkozásaikról, illetve életmódjáról.

Rovartani kutatómunkám egyik célterülete a levantei régió, mely történelmi földrajzi terület, a Közel-Kelet egy része, az itt tárgyalt tanulmányok célfajai jellemzően itt fordulnak elő. Az elnevezés alatt Szíria, Libanon, Izrael, Palesztina és Jordánia határain belül elterülő területeket valamint a Földközi-tenger peremvidékeit és Törökország egyes részeit értjük. CSUZDI et al. (2007) szerint ez a terület egy nagyjából 150 km széles szakasz a Földközi-tenger és a szír-arab sivatagok közé ékelődve, északon a Taurosz-hegység, míg délen a Szuezi-csatorna határolja. Ez unikális régió, melynél a palearktikus, az orientális és az afrotrópusi fauna találkozik, úgynevezett biogeográfiai forró pont (MÉDAIL & QUÉZEL 1997, MYERS et al. 2000). Kutathatóságát nagyban nehezíti a régió geopolitikai helyzete, az évtizedek óta tartó háborús viszonyok, ezért az innen származó természetrajzi anyagok jelentősége felbecsülhetetlen.

Dolgozatom a fentiek tükrében általános taxonómiai kérdésekre is választ adhat. Ezek az alábbiak lehetnek:

Számíthatunk-e tudományra új, eddig nem ismert fajok előkerülésére kevéssé kutatott területekről?

Léteznek-e olyan területek, melyek hosszú éveken át tartó kutatására érdemes berendezkedni, és ha igen, akkor milyen tudományos eredmények születhetnek egy ilyen, hosszútávú kutatómunka során?

A jelen és jövő kutatói számára érdemes-e – és ha igen mi módon – összegyűjteni és közzétenni minden korábban publikált ismeretet egy adott fajról, fajcsoportról, kiegészítve azt a friss ismeretekkel?

1.2 Az első tanulmány (*Elathous*-katalógus) koncepciói és célkitűzései

Az *Elathous* Reitter, 1890 genusz ismert fajainak katalógusa és revíziója, különös tekintettel a nyugat-palearktikus fajokra. A nearktikus és a palearktikus régióban előforduló, a világ természetrajzi gyűjteményeiben ritkán reprezentált, kevésbé kutatott, zavaros rendszertanú fajok, leginkább levantei előfordulással. A genusz fajairól összefoglaló munka ezidáig nem született, főként különálló fajleírások voltak ismertek róluk. Korábbi cikkemben (NÉMETH 2019), mely Libanon pattanóbogárfaunáját mutatja be, leírtam egy tudományra új *Elathous*-fajt. A leírás során kiderítettem, hol találhatóak a típuspéldányok, milyen ismereteink vannak az ide tartozó fajokról, illetve felkutattam a megjelent szakirodalmakat, így alapvető ismereteket szereztem a tárgyalt genuszról. Ebben a tanulmányban célom volt egységes információt szolgáltani a jelen és jövő kutatói számára az ismert fajok irodalmi említéseiről, szinonímjairól, a fajok típuspéldányainak fellelhetőségéről, elterjedéséről, valamint első alkalommal színes ábrákon szemléltetni azokat.

1.3 A második tanulmány (*Elathous nemeri* sp. n.) koncepciói és célkitűzései

Egy, a tudomány számára ismeretlen *Elathous*-faj leírása Libanonból. 2015 és 2018 közötti libanoni gyűjtőútjaim eredményeként több tudományra új pattanóbogárfajt írtam le (NÉMETH 2019), valamint ebben az időszakban a környék, azaz a levantei régió pattanóbogárfaunáját is volt lehetőségem tanulmányozni (NÉMETH et al. 2020a, NÉMETH et al. 2020b). E kutatás során került elő egy, a tudomány számára máig nem ismert pattanóbogár, célom pedig ennek a fajnak a leírása volt.

1.4 A harmadik tanulmány (*Plastocerus angulosus*) koncepciói és célkitűzései

A *Plastocerus angulosus* (Germar, 1844) rendszertana, morfológiája és elterjedése. A rendszertanilag sokáig vitatott helyzetű, emblematikus bogárfaj komplex morfológia leírása, pontos elterjedésének közlése és nem ismert nőstényének modern taxonómiai leírása, valamint minden irodalmi említésének közlése volt a cél. A tanulmány továbbá célul tűzte ki, hogy a faj sokáig zavaros rendszertani helyzetét tisztázza, tételesen levezetve annak minden korábbi változását.

1.5 A negyedik tanulmány (*Elathous*-lárvaleírások) koncepciói és célkitűzései

Az *Elathous agilis* Németh, 2019 és *Elathous brucki* (Candéze, 1878) lárváinak összehasonlító morfológiai elemzése. E pattanóbogárfajoknak sem fejlődésmenetét, sem lárvaalakjának morfológiáját nem ismeri a tudomány. A genuszba tartozó rokon fajok lárvaleírásai több évtizeddel ezelőtt születtek, így a 2015–2018 közti libanoni, valamint a 2013-as és a 2015-ös görög kutatómunka során előkerült lárvák hosszú idő óta az első olyan példányok, melyek lehetővé teszik e ritka bogárcsoport lárváinak tanulmányozását és megismerését. E tanulmány célja tehát a fent említett fajok lárváinak modern taxonómiai módszerekkel történő leírása, mely fényt deríthet az alcsalád (Elateridae: Dendrometrinae) rokonsági kapcsolataira, segíthet jobban megismerni a pattanóbogarak egyes csoportjainak egymással való fejlődéstörténeti viszonyát.

1.6 Az ötödik tanulmány (*Lacon*-lárvaleírások) koncepciói és célkitűzései

Az Európában előforduló, három, veszélyeztetett szaproxilofág pikkelyespattanó-faj (*Lacon lepidopterus, L. punctatus & L. querceus* – utóbbi védett hazánkban) lárvájának morfológiai összehasonlítása. A tanulmány célja lehetővé tenni a három faj lárvaalakban történő határozását, továbbá minden ismert elterjedésbeli és ökológiai információt közölni róluk.

2. ANYAGOK ÉS MÓDSZEREK

A doktori értekezés tanulmányainak megvalósításához a klasszikus, modern taxonómiai cikkek készítéséhez szükséges módszertant alkalmaztam. A kikölcsönzött példányok tanulmányozása mikroszkóp alatt, boncolásuk illetve ivarszervpreparátumuk elkészítése 10%-os KOH oldatos fürdő után történt. Az ivarszerveket glicerinben fényképeztem, ehhez és a preparált imágók fényképezéséhez egy Nikon D5200-as digitális fényképezőgépet, valamint egy ehhez rögzített Mitutoyo M Plan Apo 5X mikroszkópobjektívet használtam. A fényképek rétegfotós eljárással, a Zerene Stacker szoftver segítségével készültek. A terepen készült fényképekhez Fuji Finepix HS25 EXR kamerát és Raynox 150/250 előtétlencséket használtam. A nevelt példányok esetében a terepről hazaszállított lárvákat műanyag dobozban neveltem, esetenként 2 éven keresztül. Az egyes példányok testhosszát a fej elülső szegélyétől a szárnyfedők végéig, míg testszélességét a szárnyfedő legszélesebb pontján mértem. Tudományra új faj esetén a leírás alapjául szolgáló példányt közgyűjteményben, a Magyar Nemzeti Múzeum Közgyűjteményi Központ Magyar Természettudományi Múzeumának Állattárában helyeztem el. A leírások alaktani terminológiája GLEN (1950), COSTA et al. (2010) és ROSA et al. (2019) munkáit követi. A katalógus esetében KUBACZKOVA & KUNDRATA (2017) cikkét követjük.

A különféle európai köz- és magángyűjteményekből hozzávetőlegesen 180 példányt kölcsönöztem ki. Ezek a gyűjtemények az alábbiak voltak:

Natural History Museum, London, United Kingdom; California Academy of Sciences, San Francisco, USA; coll. of Centre de Recherche Forestière, Rabat, Morocco; Florida State Coll. of Arthropods, Museum of Entomology, Gainesville, Florida, USA; Hayek Mirzayans Insect Museum, Tehran, Iran; Hungarian Natural History Musuem, Budapest, Hungary; Hacettepe University Zoology Museum, Ankara, Turkey; Museo Civico di Storia Naturale, Genova, Italy; Museo Civico di Storia Naturale, Verona, Italy; Museum of Comparative Zoology, Harvard University, USA; Museo Nacional de Ciencias Naturales, Madrid, Spain; Museum National d'Histoire Naturelle, Paris, France; National Museum, Prague, Czech Republic, National Museum of Nature and Science, Tokyo, Japan; coll. of A. Guglielmi, Verona, Italy; coll. of C. Wurst, Heilbronn, Germany; coll. of G. Kakiopoulos, Athens, Greece; coll. of G. Murzov, Stara Zagora, Bulgaria; coll. of G. Platia, Gatteo, Italy; coll. of H. Brustel, Toulouse, France; coll. of José Sáez Bolaño, Badajoz, Spain; coll. of Josef Mertlik, Opatovice nad Labem, Czech Republic; coll. of J. L. Zapata de la Vega, Madrid, Spain; coll. of N. Jansson, Linköping University, Sweden; coll. of N. Nemer, Tannourine, Lebanon; coll. of R. Preiss, Wimborne, Great Britain, coll of D. Szalóki, Budapest, Hungary; coll. of Georgios Gastouniotis, Nemea, Greece; coll. of George Kakiopoulos, Athens, Greece; collection of Martin Samek, Skalice, Czech Republic; coll. of Per Kristian Solevåg, Tranby, Norway; coll. of Petr Zahradník, Jesenice u Prahy, Czech Republic; coll. of Robin Kundrata, Olomouc, Czech Republic; coll. of Savvas Zafeiriou, Pirgoi Thermis, Lesvos, Greece; voucher collection of the laboratory of Biodiversity and Molecular Evolution, Palacky University, Olomouc, Czech Republic; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv University, Israel.

A tanulmányokban vizsgált további példányok jelentős részben saját, 2013 és 2023 közötti gyűjtőútjaimról, Albániából, Görögországból, Horvátországból, Macedóniából, Libanonból, Magyarországról és Szíriából származó anyagokból kerültek ki.

3. EREDMÉNYEK

3.1. Az első tanulmány (*Elathous*-katalógus) eredményei

Elkészítettük az ismert *Elathous*-fajok világkatalógusát, továbbá minden ismeretet közöltünk a fellelhető típuspéldányokról, korábbi szinonímokról, elterjedésükről és irodalmi említéseikről. A világ számos pontjáról kikölcsönzött – nagyjából 80 példány – típusanyag segítségével egy 35 oldalas, a jövő kutatói számára használható, fényképekkel is illusztrált, összegző munka született, az alábbi tartalommal:

Minden fajról fénykép, elsősorban típuspéldányokról; típuspéldányok lelőhelye; elterjedés; szinonímok; típuspéldányok elhelyezésének helye; elterjedés; minden irodalmi említés.

3.2. A második tanulmány (*Elathous nemeri* sp. n.) eredményei

A tanulmányban egy Északnyugat-Libanonból előkerült új pattanóbogárfajt írtam le *Elathous nemeri* Németh, 2021 néven. Az országból ismert pattanóbogarakat tárgyaló cikk (NÉMETH 2019) és a 2015. májusi, 2016. júniusi, 2017. májusi és a 2018. júliusi és augusztusi gyűjtőutak eredményei vezettek oda, hogy a területen előforduló fajokat alaposan megismerhessem, és a korábban félrehatározott példányról kiderüljön, hogy egy önáló, eddig még ismeretlen faj képviselője. Az új faj a regióban előforduló rokonaitól könnyen elkülöníthető a csápízek és az előtor formája, valamint a hímivarszerv felépítése alapján: a csáp egyértelműen túlnyúlik az előtor hátulsó szögletén; az előtor hosszabb, mint széles, legszélesebb annak középvonalánál; a paramérák határozottan keskenyednek a csúcs felé, oldalról íveltek, külső szegélyük határozottan széttart.

3.3. A harmadik tanulmány (*Plastocerus angulosus*) eredményei

A *Plastocerus* genusz rendszertani helyzete sokat változott az elmúlt idők során. A szerzők hol önálló családként (SCHWARZ 1907), hol pedig a pattanóbogarak egy genuszaként (MERTLIK & PLATIA 2008) tartották számon. Nőstényei az utóbbi időkig nem voltak ismertek, egyes szerzők azt feltételezték, hogy lágy testű, fejletlen szárnyfedelű alakok (CROWSON 1972). 2023-ban megjelent cikkünk áttekinti a faj morfológiáját, fajon belüli és ivari változatosságát, rendszertani helyzetét és elterjedését. Több mint 80 db, 1845 és 2017 közt gyűjtött, köz- és magángyűjteményből származó példányt tanulmányoztunk, s a vizsgálat eredményeként az alábbi következtetéseket vontuk le:

Fajon belüli változatosság: A vizsgált példányok változatosságot mutattak színezetben és több testrészük tekintetében. Az előtor pontozásában és a hímivarszerv felépítésében szignifikáns különbségeket mértünk. Nem találtunk összefüggést a földrajzi elterjedés és a mérések eredményeiből fakadó alaktani különbségek közt.

Elterjedés: Az irodalmi adatok alapján Görögországban, Izraelben, Törökországban és Szíriában előforduló fajt elsőként közöltük Libanonból, az ország faunájára új bogárfajként.

3.4. A negyedik tanulmány (*Elathous*-lárvaleírások) eredményei

Tanulmányunkban elsőként írjuk le az *Elathous agilis* Németh, 2019 és az *E. brucki* (Candéze, 1878) lárváját modern vizsgálati módszerek alkalmazásával. Részletesen tanulmányoztuk és közöltük minden fontos alaktani bélyegüket, nem csupán egymással, de közeli rokonaikkal is összehasonlítva a két fajt. Számos alaktani különbséget találtunk a vizsgált lárvák közt, melyek az alábbiak: a tori hátlemezek pontjainak mérete és sűrűsége, a fej oldalszegélye, a homlok hátulsó szegélyének formája, a potroh mélyedésein megfigyelhető keresztirányú ráncok hossza és a potroh 9. hátlemezének részletei. Az ismert leírások alapján megállapítottuk, hogy az *E. brucki* a homlok lekerekített hátsó része és a 9. hátlemez trapéz formájú benyomata alapján jelentősen különbözik a genusz ismert fajaitól, továbbá az *E. agilis* lárvája minden ismert fajtól különbözik abban, hogy a 9. hátlemez felszíne határozottan szegélyezett, de nem peremes, illetve egy pár benyomat található rajta.

3.5. Az ötödik tanulmány (*Lacon*-lárvaleírások) eredményei

A három, Európában előforduló pikkelyespattanó-faj, a *Lacon lepidopterus* (Panzer, 1801), *L. punctatus* (Herbst, 1779) és *L. querceus* (Herbst, 1784) lárvájának összehasonlító morfológiai elemzését közöljük tanulmányunkban, melyet az ismert irodalmak és saját megfigyeléseink alapján készítettük el. Elkülönítésük nemcsak természetvédelmi szempontból fontos feladat – hiszen a *L. querceus* hazánkban védett, emblematikus szaproxilofág faj –, de fontos mérföldkő is e kevéssé kutatott fajcsoport esetében. Megállapítottuk, hogy a korábbi leírások által tárgyalt faji bélyegek részben megfelelnek a valóságnak: A *L. querceus* lárvája valóban jelentősen eltér a másik két tárgyalt fajtól a fej oldalsó részén található hosszirányú élek alapján. Ugyanakkor a TARNAWSKI (2000) által említett határozóbélyegek ellenőrzése közben nem észleltünk különbséget a szklerotizált alapú nazális fogak felépítésében a vizsgált fajok közt. Terepi tapasztalataink és az elérhető tudományos publikációk alapján összegeztük életmódjukkal kapcsolatos információkat, különös tekintettel a három faj tápnövényeire, társfajaira, elterjedésére és fejlődésére.

4. KÖVETKEZTETÉSEK ÉS JAVASLATOK

A doktori képzés során megjelent publikációk jellemzően kevéssé ismert bogárfajokkal foglalkoznak (MERTLIK & DUŠÁNEK 2006). Ezek a fajok ritkák a közgyűjteményekben, kutatók szeme elé nem gyakran kerülnek, kivétel nélkül rejtett életmódot folytatnak (PLATIA et al. 2018). Fontos erdőállapotjelzők (ECKELT et al. 2017), akár maradvány- vagy zászlósfajok is lehetnek, de – ahogyan a fenti eredmények mutatják – a tudomány számára ismeretlen fajok is előfordulhatnak köztük. A közölt tanulmányokban összegyűjtöttünk minden fellehető információt, és kiegészítettük azokat több évtizedes muzeológiai és terepi tapasztalatunkkal, így új tudásanyaggal is szolgáltunk velük kapcsolatban. Ennek ellenére minden faj esetében megállapítható, hogy a korlátozott számú tanulmányozható példányon túl további anyagra van szükség, ahhoz, hogy megértsük az egyes fajok, fajcsoportok határait, rokonsági kapcsolatukat és jobbára ismeretlen ökológiájukat, jelentőségüket a biológiai rendszerekben. Célunk volt a jelen és a jövő kutatói számára tudományos ismereteket nyújtani ezekről a bogárcsoportokról, fejlődésmenetükről és elterjedésükről, valamint kifejlett és lárva állapotú morfológiájukról.

Mind az öt tanulmányban szerepel olyan faj, amely a levantei régióban fordul elő. A térség jelenlegi politikai és társadalmi helyzete miatt nehezen kutatható, ennek ellenére jelentek meg az utóbbi évtizedekben fajleírások (PREISS 2003, MERTLIK & DUŠANEK 2006) és katalógusok (MERTLIK & PLATIA 2008) a régióból. Másfél évtizede tartó kutatómunkám során számos bogárcsoporttal foglalkoztam, melyek alapjául szíriai és libanoni utakon gyűjtött anyag szolgált (DANILEVSKY & NÉMETH 2017, HÁVA & NÉMETH 2016, KUNDRATA et al. 2016, MÁRKUS & NÉMETH 2016, NÉMETH 2019, NÉMETH et al. 2019, 2020a, 2020b, PLATIA & NÉMETH 2011, SZÉNÁSI & NÉMETH 2019, SZÉNÁSI et al. 2019). Ez a munka azonban még korántsem teljes. Ezért különösen fontos volna a jövőben a világ köz- és magángyűjteményben tárolt bogáranyagok revíziója, elsősorban olyan bogárcsaládok példányainak vizsgálata révén, melyek a levantei régióból származnak. Ezekhez nélkülözhetetlen a nemzetközi együttműködés, a folyamatos konzultáció és a tudományos munkát támogató programok, mint például a Tempus államközi ösztöndíj, vagy a kutatóintézetek és múzeumok közti Synthesys program, melyek jelentős outputtal bírnak (KUNDRATA & NÉMETH 2019).

A pattanóbogarak lárvastádiumainak ismerete nemcsak ökológiai szempontból fontos (ROSA et al. 2020), hanem az egyes fajok rendszertani helyzetének megértéséhez is nagyban hozzájárul (SCHIMMEL & TARNAWSKI 2012). Ritka alkalom, hogy rejtett életmódot folytató bogárfajok esetében rendelkezésre álljon tanulmányozható, megbízhatóan határozott anyag. A két, lárvákkal foglalkozó publikáció az egyes alcsaládok közti, illetve genuszon belüli kapcsolatok ismereteit (ÔHIRA 1962, 1989) új információkkal támasztja alá. Frissen gyűjtött anyagok tanulmányozása (ROSA et al. 2019) segítheti azt, hogy egyre tisztább képet kapjunk az egyes alcsaládok rokonsági kapcsolatairól. Ezek az ismeretek genetikai eredményekkel megtámogatva sok esetben új koncepciókhoz, rendszertani elméletek megalkotásához vezethetnek. Távlati cél lehet egy komplex munka, melyet az összes pattanóbogár alcsaládból származó lárva és a hozzá tartozó imágó genetikai vizsgálata valamint morfológiai leírása tenne teljessé.

A levantei régió pikkelyespattanó-fajairól szóló újabb munkák (MERTLIK & NÉMETH 2014, KUNDRATA et al. 2019, NÉMETH et al. 2020b) ugyan bőséges ismeretanyagot közölnek, ám ezek a cikkek is jórészt a kifejlett bogarakkal foglalkoznak, lárváikkal nem. Az itt előforduló fajok lárváiról szinte semmi ismeretünk nincs, így a jövő entomológusai számára fontos, hogy tanulmányozható anyag álljon rendelkezésre az ilyen típusú munkákhoz. Ez egyrészt további terepi munka, másrészt gyűjteményi anyagok tanulmányozása révén érhető el, mindkét esetben segítve azt, hogy megérthessük a tárgyalt fajok életmódját és elterjedését, és esetleges természetvédelmi jelentőségüket is. Ehhez, és általánosságban véve taxonómiai munkák születéséhez megfelelő képzésekre, lelkes fiatal kutatókra, jó kézben lévő gyűjteményekre és összességében a taxonómiai munka elismerésére lenne szükség. A nemzetközi taxonómia (LÖBL et al. 2023), csakúgy, mint a hazai (PÁLL-GERGELY et al. 2024), sajnos hanyatlik, pedig „…minden értelmetlen a biológiában, amennyiben a tanulmányozott szervezetek nincsenek elnevezve és meghatározva” (DUBOIS et al. 2003).

5. ÚJ TUDOMÁNYOS EREDMÉNYEK

5.1. Az *Elathous*-genusz világkatalógusa

Szerzőtársaimmal publikáltuk az *Elathous* Reitter, 1890 genusz (Coleoptera: Elateridae: Dendrometrinae) fajainak világkatalógusát. A genusz 48 fajt tartalmaz, melyből hat a nearktikumból, 40 Marokkótól Iránig a nyugat-palearktikumból, kettő pedig Japánból ismert. Minden fajnál felsoroltuk az ismert szinonímeket, megadtuk a fellehető típusanyagot, összefoglaltuk elterjedésüket, valamint listáztuk irodalmi említéseiket. A kikölcsönzött típusokról és az eredeti típuscédulákról fényképeket közöltünk. A vizsgált fajok alaktani különbségei alapján feltételezhető, hogy két fajcsoport létezik a genuszon belül. Mivel a kevés rendelkezésünkre álló adat alapján úgy tűnik, ezek életmódban is eltérnek egymástól, ezért nem kizárt, hogy a jövőben szisztematikai és nevezéktani helyzetük változni fog. További kutatómunkával elkészítendő komplex genuszrevízió segíthetne abban, hogy átlássuk és megértsük ennek a csoportnak az evolúcióját és rendszertanát.

5.2. Új *Elathous*-faj leírása (Coleoptera: Elateridae) Libanonból

A tanulmányban egy Északnyugat-Libanonból előkerült pattanóbogárfajt írtam le *Elathous nemeri* Németh, 2021 néven. A területről publikált tudományra új faj rávilágít a levantei régió biodiverzitása megismerésének fontosságára, az ismert *Elathous*-fajok számát 49-re növelve. Az országból ismert pattanóbogarakat tárgyaló korábbi cikkem (NÉMETH 2019) és több éven át tartó gyűjtőutaim eredményei vezettek oda, hogy a területen előforduló fajokat alaposan megismerhessem, és a korábban félrehatározott példányról kiderüljön, hogy egy önálló, eddig még ismeretlen faj képvisel.

5.3. A *Plastocerus angulosus* (Germar, 1844) (Coleoptera: Elateridae) morfológiája, fajon belüli, genetikai és ivari változatossága, rendszertana, irodalmi említései és elterjedése

A több mint 80 db, 1845 és 2017 között gyűjtött, köz- és magángyűjteményekből származó példány tanulmányozása során vizsgáltuk a faj alaktani és nemek közti változatosságát. Megállapítottuk, hogy az egyes területekről származó egyedek eltérést mutatnak az előtor pontozásában, a színezetben és a hímivarszerv tekintetében. Továbbá ismertetjük elterjedését és elsőként közöljük Libanonból. Összeállítottuk a faj korábbi, változásokkal teli nevezéktani előéletének teljes áttekintését, valamint részletes leírással és azt ezt támogató ábraanyaggal szemléltettük a faj alaktani felépítését.

5.4. Az *Elathous agilis* Németh, 2019 és *E. brucki* (Candèze, 1878) lárváinak leírása és összehasonlító morfológiai elemzése

Munkánk során tanulmányoztuk a korábbi szerzők által alkalmazott diagnosztikai bélyegeket. A lárvák modern módszertannal történt leírása alapján megállapítható, hogy az *E. brucki* morfológiailag alapvetően különbözik minden ismert fajtól, az *E. agilis* pedig több stabil karakter alapján különíthető el az ismert fajoktól.

Kiegészítve a genusz fajainak fejlődésmenetével kapcsolatos kevés korábban publikált adatot, információt közöltünk a vizsgált fajok lárváinak ökológiájáról, jelezve, hogy a két faj szaproxilofág, azaz fejlődésük holtfához köthető.

5.5. Az európai pikkelyespattanók (Coleoptera: Elateridae: *Lacon* spp.) lárvái és életmódja

A pikkelyespattanók lárváinak összehasonlító morfológiai elemzése során kiegészítettük az eddig publikált eredményeket saját tapasztalatainkkal, ezzel lehetővé téve a három faj lárvájának elkülönítését. Megállapítottuk, hogy a korábbi szerzők által használt elkülönítő bélyegek csak részben alkalmazhatók a három faj elkülönítésére. Összegeztünk minden eddig ismert információt és általunk újonnan szerzett tapasztalatot, ezzel komplex képet adva a fajok ökológiai igényeiről, táplálkozásukról, tápnövényeikről, velük együtt előforduló bogárfajokról.

6. IRODALOMJEGYZÉK

BOUCHARD P., SMITH A. B. T., DOUGLAS H. B., GIMMEL M. L., BRUNKE A. J. & KANDA K. (2017): Biodiversity of Coleoptera. 337–417. p. In: FOOTTIT R. G., ADLER P. H., (Szerk.): *Insect Biodiversity: Science and Society, 2nd ed.* UK, West Sussex: John Wiley and Sons Ltd., 1007 p.

CSUZDI CS., PAVLÍČEK T. & MISIRLIOĞLU M. (2007): Earthworms (Oligochaeta: Lumbricidae, Criodrilidae and Acanthodrilidae) of Hatay province, Turkey, with description of three new lumbricids. In: *Acta Zoologica Academiae Scientiarum Hungaricae,* 53 347–361.

COSTA C., LAWRENCE J. F. & ROSA S. P. (2010): Elateridae Leach, 1815. 75–103 p. In: LESCHEN R. A. B., BEUTEL R. G., LAWRENCE, J. F. (Szerk.): *Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim).* Berlin/New York: Walter de Gruyter GmbH & Co. KG, 799 p.

CROWSON R. A. (1972): A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families Cneoglossidae and Omethidae. In: *Revista de la Universidad de Madrid,* 21 (82) 35–77.

DANILEVSKY M. & NÉMETH T. (2017): A new subspecies of Cortodera colchica (Faldermann, 1836) from Lebanon (Coleoptera, Cerambycidae). In: *Humanity space International almanac,* 6 (5) 837–842.

DUBOIS A., CROCHET P.-A., DICKINSON E. C., NEMÉSIO A., AESCHT E., BAUER A. M., BLAGODEROV V., BOUR R., DE CARVALHO M. R. & DESUTTER-GRANDCOLAS L. (2013): Nomenclatural and taxonomic problems related to the electronic publication of new nomina and nomenclatural acts in zoology, with brief comments on optical discs and on the situation in botany. In: *Zootaxa,* 3735 1–94.

ECKELT A., MÜLLER J., BENSE U., BRUSTEL H., BUSSLER H., CHITTARO Y., CIZEK L., FREI A., HOLZER E., KADEJ M., KAHLEN M., KÖHLER F., MÖLLER G., MÜHLE H., SANCHEZ A., SCHAFFRATH U., SCHMIDL J., SMOLIS A., SZALLIES A., NÉMETH T., WURST C., THORN S., BOJENSEN CHRISTENSEN H. R. & SEIBOLD S. (2017): Primeval forest relict beetles of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. In *Journal of Insect Conservation*, 22 15–28.

GLEN R. (1950): Larvae of the elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae). In: *Smithsonian Miscallenaous Collections,* 111 (11) 1–246.

HÁVA J. & NÉMETH T. (2016): Contribution to the occurrence of Dermestidae (Coleoptera) in Lebanon. In: *Folia Entomologica Hungarica,* 77 17–21.

IKEDA H., NISHIKAWA M. & SOTA T. (2012): Loss of flight promotes beetle diversification. In: *Nature Communications*, 3 (648).

KUBACZKOVA M. & KUNDRATA R. (2017): Annotated catalogue of the click-beetle subfamily Tetralobinae (Coleoptera: Elateridae). In: *Zootaxa*, 4323 151–184.

KUNDRATA R., KUBACZKOVA M., PROSVIROV A. S., DOUGLAS H. B., FOJTIKOVA A., COSTA C., BOUSQUET Y., ALONSO ZARAZAGA M. A. & BOUCHARD P. (2019): World catalogue of the genus-group names in Elateridae (Insecta, Coleoptera). Part I: Agrypninae, Campyloxeninae, Hemiopinae, Lissominae, Oestodinae, Parablacinae, Physodactylinae, Pityobiinae, Subprotelaterinae, Tetralobinae. In: *ZooKeys,* 839 83–154.

KUNDRATA R., MERTLIK J. & NÉMETH T. (2019): Unexpected diversity of Lacon Laporte, 1838 (Coleoptera: Elateridae: Agrypninae) in the Levant: revised species concepts, new species, and an identification key. In: *Zootaxa,* 4679 (3) 401–449.

KUNDRATA R. & NÉMETH T. (2019): Description of Penia mantillerii sp. nov. (Coleoptera: Elateridae: Dimini), with a key to Penia species from Vietnam and nearby areas. In: *Zootaxa,* 4612 (2) 275–281.

LAWRENCE J. F., MUONA J., TERAVAINEN M., STAHLS G. & VAHTERA V. (2007): Anischia, Perothops and the phylogeny of Elateroidea (Coleoptera: Elateriformia). In: *Insect Systematics and Evolution,* 38 205–239.

LÖBL I., KLAUSNITZER B., HARTMANN M. & KRELL F-T. (2023): The silent extinction of species and taxonomists an appeal to science policymakers and legislators. In: *Diversity,* 151053.

MÁRKUS A. & NÉMETH T. (2016): A new species of Alosterna Mulsant, 1863 from Lebanon, and notes on other species (Coleoptera: Cerambycidae). In: *Folia Entomologica Hungarica,* 77 23–32.

MERTLIK J. & DUŠÁNEK V. (2006): Description of five new species of click–beetles (Coleoptera, Elateridae) from the Palaearcticregion with remarks about the distributions 22 additional species. In: *Folia Heyrovskyana,* 13 (4) 145–162.

MERTLIK J. & NÉMETH T. (2014): Distributional notes on Lacon nadaii and L. unicolor (Coleoptera: Elateridae). In *Elateridarium,* 8 61–66.

MERTLIK J., NÉMETH T. & KUNDRATA R. (2017): Revision of the flightless click-beetle genus Dima Charpentier, 1825 (Coleoptera: Elateridae: Dimini) in the Balkan Peninsula. In: *Zootaxa,* 4220 (1) 001–063.

MERTLIK J. & PLATIA G. (2008): Catalogue of the family Cebrionidae, Elateridae, Lissomidae, Melasidae and Throscidae (Coleoptera) from Turkey. In: *Elateridarium,* 2 1–40.

MÉDAIL F. & QUÉZEL P. (1997): Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. In: *Annals of the Missouri Botanical Garden,* 84 112–127.

MUONA J. (1995): The phylogeny of Elateroidea (Coleoptera), or which tree is the best today? In: *Cladistics,* 11 317–341.

MYERS N., MITTERMEIER R. A., MITTERMEIER C. G., DA FONSECA G. A. B. & KENT J. (2000): Biodiversity hotspots for conservation priorities. In: *Nature,* 403 853–858.

NÉMETH T. (2019): Elateridae (Coleoptera) of Lebanon. In: *Zootaxa,* 4614 (1) 127–159.

NÉMETH T., PROSVIROV A. S. & KUNDRATA R. (2020): Two new species of Elathous Reitter, 1890 (Coleoptera: Elateridae) from Syria. In: *Zoology in the Middle East,* 66 (2) 167–177.

NÉMETH T., BRŮHA P. & KUNDRATA R. (2020): Discovery of a new species of Lacon Laporte (Coleoptera: Elateridae: Agrypninae) endemic to Cyprus, with a modified tarsal morphology. In: *Zootaxa,* 4780 (3) 554–562.

NÉMETH T., SZÉKELY K., KOTÁN A., MÁRKUS A., YAMMINE W., TANIOS C. & NEMER N. (2019): Notes on the longhorn beetles (Coleoptera: Cerambycidae) of Lebanon. In: *Folia Entomologica Hungarica,* 80 13–38.

ÔHIRA H. (1962): Morphological and Taxonomic Study on the Larvae of Elateridae in Japan (Coleoptera). Okazaki: Entomological Laboratory, Aichi Gakugei University. 179 p.

ÔHIRA H. (1989): Note on the larva of Tetrigus lewisi. In: *Coleoptera News,* 87 (88) 13.

PÁLL-GERGELY, B., KRELL F.-T., ÁBRAHÁM L., BAJOMI B., BALOG L. E., BODA P., CSUZDI CS., DÁNYI L., FEHÉR Z., HORNOK S., HORVÁTH A., KÓBOR P., KOCZOR S., KONTSCHÁN J., KOVÁCS P., KOVÁCS T., LUKÁTSI, M., MAJOROS G., MURÁNYI D., NÉMETH T., PERNECKER B., PUSKÁS G., RÓZSA L., SOLTÉSZ Z., SZITA É., SZŰTS T., TÓTH B., TŐKE A., VAS Z., ZSUGA K., ZSUPOS V., CSABAI Z. & MÓRA A. (2024): Identification crisis: A fauna-wide estimate of biodiversity expertise shows massive decline in a Central European country. In: *Biodiversity and Conservation*, 33 3871–3903.

PLATIA G., JANSSON N., SÜRGÜT H., TÜVEN A., AVCI M. & VARLI S. V. (2018): Click beetles (Coleoptera, Elateridae) from two areas with hollow oaks and plane trees in Turkey. In: *Boletín de la Sociedad Entomológica Aragonesa,* 63 253–257.

PLATIA G. & NÉMETH T. (2011): On some Palaearctic click beetles deposited in the Hungarian Natural History Museum (Coleoptera: Elateridae). – In: *Annales historico-naturales Musei nationalis hungarici,* 103 65–105.

PREIS R. (2003): A new Elathous Reitter, 1890, from Syria (Coleoptera: Elateridae). In: *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen,* 55 55–57.

PROSVIROV A. (2016): New and little-known species of the genus Lacon Laporte, 1838 (Coleoptera: Elateridae) of Afghanistan and adjacent countries. In: *Zootaxa,* 4168 (2) 279–296.

ROSA S. P., MARIANO R. D. R., VIVIANI V. R. & COSTA C. (2020): Morphology of immature stages of Pyrearinus pumilus (Candèze, 1863) (Coleoptera: Elateridae: Pyrophorini): the click beetle responsible for the luminous canga caves in the state of Pará, Brazil. In: *Zootaxa,* 4778 (3) 561–570.

ROSA S. P., NÉMETH T. & KUNDRATA R. (2019): Comparative morphology of immature stages of Ludioctenus cyprius (Baudi di Selve, 1871) (Coleoptera: Elateridae: Agrypninae), with discussion on the monophyly of Hemirhipini. In: *Zoologischer Anzeiger,* 283 33–39.

SCHIMMEL R. & TARNAWSKI D. (2012): Monograph of the monophylum Tetrigusina (Insecta: Coleoptera, Elateridae, Agypninae). In: *Polish Entomological Monographs*, 8 1–288.

SCHWARZ O. (1907): Coleoptera. Fam. Plastoceridae. 1–10. p, In: Wytsman P. (Szerk.): *Genera Insectorum. Fascicule 50.*, Bruxelles: V. Verteneuil & L. Desmet.

STIBICK J. N. L. (1979): Classification of the Elateridae (Coleoptera): relationships and classification of the subfamilies and tribes. In: *Pacific Insects,* 20 145–186.

SZÉNÁSI V. & NÉMETH T. (2019): Description of a new species of the subgenus Hippomias Yunakov, 2006 in the genus Brachysomus Schoenherr, 1823 (Coleoptera: Curculionidae: Entiminae) from Lebanon. In: *Zootaxa,* 4658 (2) 389–395.

SZÉNÁSI V., NÉMETH T. & NEMER N. (2019): Notes on snout beetles (Coleoptera: Curculionoidea, without Scolytinae and Platypodinae) of Lebanon. In: *Folia Entomologica Hungarica,* 80 39–72.

TARNAWSKI D. (2000): Elateridae, Sprężykowate Część I (Insecta: Coleoptera). Warsaw: Polskie Towarzystwo Entomologiczne. 722 p.

7. AZ ÉRTEKEZÉS TÉMÁJÁHOZ KAPCSOLÓDÓ PUBLIKÁCIÓK

7.1 Az értekezés témakörében készült publikációk

KUNDRATA, R., NÉMETH T., PROSVIROV A. S. & HOFFMANNOVA J. (2021): Annotated catalogue of the click-beetle genus Elathous Reitter, 1890 (Coleoptera: Elateridae: Dendrometrinae), including habitus photographs for all species. In: *Zootaxa,* 4995 (2) 231–265.

NÉMETH T. (2021): A new species of Elathous Reitter, 1890 (Coleoptera: Elateridae) from Lebanon. In: *Zoology in the Middle East,* 67 (4) 344–349.

NÉMETH T., HOFFMANNOVA J., KAKIOPOULOS G., KRAMP K. & KUNDRATA R. (2023): Plastocerus angulosus (Germar, 1844) (Coleoptera: Elateridae: Dendrometrinae): an enigmatic click beetle with a convoluted taxonomic history. In: *Zootaxa,* 5284 (2) 271–290.

NÉMETH T., ROSA S. P. & KUNDRATA R. (2024): Comparative morphology of larvae of Elathous agilis Németh, 2019 and Elathous brucki (Candèze, 1878) (Coleoptera: Elateridae: Dendrometrinae), with notes on their biology and ecology. In: *Zoologischer Anzeiger,* 308 25–34.

NÉMETH T., ROSA S. P., JETELINA D., SÁROSPATAKI M. & KUNDRATA R. (2025): Emblematic European saproxylic Lacon click beetles (Coleoptera: Elateridae): what do we know about their immature stages? – *Scientific Reports*, in press.

7.2. Az értekezés témájához kevésbé szorosan kapcsolódó, entomológiai témájú publikációk

BOROWSKY J. & NÉMETH T. (2024): Description of a male and redescription of a female of Bruchoptinus schatzmayeri (Pic, 1934) (Coleoptera: Ptinidae). In: *Zootaxa,* 5538 (3) 297–300.

MERKL O., SZÉNÁSI V., PINTÉR B. & NÉMETH T. (2022): Új bogárfajok a Naszályról. In: *Állattani Közlemények,* 107 1–17.

NÉMETH T. (2023): The mysterious Anelastes barbarus P. H. Lucas, 1846 from Montenegro (Coleoptera: Eucnemidae). In: *Folia Entomologica Hungarica,* 84 31–33.

NÉMETH T. (2024): Species of the genus Agriotes Eschscholtz, 1829 occurring in Hungary (Coleoptera: Elateridae). In: *Folia Entomologica Hungarica,* 85 137–146.

PÁLL-GERGELY, B., KRELL F.-T., ÁBRAHÁM L., BAJOMI B., BALOG L. E., BODA P., CSUZDI CS., DÁNYI L., FEHÉR Z., HORNOK S., HORVÁTH A., KÓBOR P., KOCZOR S., KONTSCHÁN J., KOVÁCS P., KOVÁCS T., LUKÁTSI, M., MAJOROS G., MURÁNYI D**.,** NÉMETH T., PERNECKER B., PUSKÁS G., RÓZSA L., SOLTÉSZ Z., SZITA É., SZŰTS T., TÓTH B., TŐKE A., VAS Z., ZSUGA K., ZSUPOS V., CSABAI Z. & MÓRA A. (2024): Identification crisis: A fauna-wide estimate of biodiversity expertise shows massive decline in a Central European country. In: *Biodiversity and Conservation*, 33 3871–3903.

SOMAY L. & NÉMETH T**.** (2022): Two parasitoid beetle species new to the fauna of Hungary (Coleoptera: Meloidae, Ripiphoridae). In: *Folia Entomologica Hungarica,* 83 13–19.

SZABÓ M., KUNDRATA R., HOFFMANNOVA J., NÉMETH T., BODOR E., SZENTI I., PROSVIROV A. S., KUKOVECZ Á. & ŐSI A. (2022): Ajkaelater merkli The first mainland European Mesozoic click-beetle (Coleoptera: Elateridae) revealed by X-ray micro-computed tomography scanning of an Upper Cretaceous amber from Hungary. In: *Scientific Reports,* 12 (1) 24.

8. KÖSZÖNETNYILVÁNÍTÁS

Hálás vagyok témavezetőmnek, Sárospataki Miklósnak, és társ-témavezetőmnek, Robin Kundratának (Csehország) jelen értekezés elkészítésében nyújtott önzetlen szakmai és emberi segítségért. Korábbi munkahelyem, a Magyar Természettudományi Múzeum munkatársainak, nevezetesen Grabant Arankának és néhai mesteremnek, Merkl Ottónak azért, hogy bogarászati munkámat a kezdetektől fogva lehetővé tették, támogatták és elismerték. Köszönettel tartozom továbbá Rédei Dávidnak, aki minden rovar- és nevezéktannal, szövegszerkesztéssel kapcsolatos kérdésemre precíz és minden részletre kitérő választ adott amióta ismerjük egymást. Hálás vagyok külföldi pattanóbogár-specialista kollegáimnak, Josef Mertliknek (Csehország) és Giuseppe Platiának (Olaszország), hogy pályám során folyamatosan fordulhattam hozzájuk kérdéseimmel.

9. MELLÉKLETEK

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Annotated catalogue of the click-beetle genus *Elathous* Reitter, 1890 (Coleoptera: Elateridae: Dendrometrinae), including habitus photographs for all species

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Abstract

An annotated catalogue of the genus *Elathous* Reitter, 1890 (Coleoptera: Elateridae: Dendrometrinae) is presented. There are 48 species classified in the genus, of which seven are from the Nearctic realm, 39 from the West Palearctic from Morocco to Iran, and two from Japan. For each taxon we provide synonyms, information on type material, type locality, distribution, and bibliography.

Key words: Elateroidea, diversity, *Leptoschema*, Nearctic realm, Palearctic realm, systematics

Introduction

Genus *Elathous* Reitter, 1890 (Elateridae: Dendrometrinae) contains 48 described species (Cate 2007, Etzler 2019). The center of diversity of this genus lies in the West Palearctic in the area from Morocco to Iran but some species also occur in North America and Japan (Cate 2007, Kabalak *et al*. 2013, Nasserzadeh *et al*. 2018, Németh 2019, Németh *et al*. 2020). The early history of the genus was rather complicated. *Elathous* was first established in 1890 (Reitter 1890) as a distinct genus but was later synonymized with *Leptoschema* Horn, 1885 by Schwarz (1903). In that study, he kept the name *Elathous* although *Leptoschema* was older, but it was later corrected (Schwarz 1906). The concept of Schwarz (1906) was followed by some subsequent authors (e.g., Blatchley 1910, Jakobson 1913, Buysson 1925, Schenkling 1927, Dolin 1964a, 1964b, Gurjeva 1965), but others considered *Elathous* a separate genus (e.g., Van Dyke 1932, Fall 1934, Stibick 1970, Lane & Lanchester 1971, Becker 1974). What is more, many species currently classified in *Elathous* were formerly placed in *Athous* Eschscholtz, 1829, *Limonius* Eschscholtz, 1829, *Elathouina* Reitter, 1905, and *Melanathous* Reitter, 1905, which makes the history of systematics of this genus even more chaotic.

While all North American species were described before 1935 (Say 1839, LeConte 1853, Van Dyke 1932, Fall 1934), most West Palearctic species were described in the 21st century (e.g., Preiss 2003, Mertlik & Dušánek 2006, Platia 2010, Platia *et al*. 2011, Zapata de la Vega & Sánchez-Ruiz 2012a, Kabalak *et al*. 2013, Németh *et al*. 2015, Nasserzadeh *et al*. 2018, Németh 2019, Németh *et al*. 2020). Most studies on *Elathous* were either catalogues or isolated species descriptions (e.g., Platia & Schimmel 1991, Platia 2010, Németh 2019), and the most comprehensive study is the review of Turkish fauna by Kabalak *et al*. (2013). Recently, Etzler (2019) revised the genera near to *Limonius* sensu Candèze, including *Elathous*. He defined *Elathous* by the unique combination of characters including the head with a triangular depression on the frons and well-developed frontal margin, prosternal sutures excavate and grooved anteriorly, hypomeron with posterior edge nearly straight and not emarginate, tarsi lacking membranous lobes, male genitalia usually wedge-shaped with parameres lacking apical hooks, and female internal genitalia

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with a pear-shaped uterus and an inverted pear-shaped bursa copulatrix bearing three apical accessary glands and subtle sclerotizations. However, his study was based on limited material, and a comprehensive taxonomic revision is necessary to better understand the limits and diversity of this genus.

In this study, we provide an up-to-date annotated catalogue of the *Elathous* species including information on the type material, synonyms, distribution, and bibliography for each species currently classified in this genus.

Material and methods

This study is based primarily on detailed literature examination but the type specimens of most species were also examined by the authors, either personally or from photographs. We present here the photographs of dorsal habitus and label data of primary types (i.e., holotype, syntype or lectotype) for most species (Figs 1–8). The photograph of the primary type label data was not available for *E. melanarius* Platia & Kakiopoulos, 2014. For *E. chiarae* Guglielmi & Platia, 1985, *E. graecus* Platia, 2008, *E. murzovi* Platia, 2010 and *E. zagrosensis* Nasserzadeh & Platia in Nasserzadeh *et al*., 2018, we show the paratypes. Type specimens of *E. discalceatus* (Say, 1839), *E. cyprius* (Baudi di Selve, 1871), *E. impressifrons* (Hampe, 1866), *E. perrisii* (Desbrochers des Loges, 1873) and *E. rufobasalis* Wurst, 1994 were not available, so we show reliably identified non-type specimens. We follow the general style used by Kubaczkova & Kundrata (2017), i.e., for each species we provide all synonyms, information on the type series and type depositories, type localities, distribution, and relevant bibliography. Additional information and original geographic names are put in square brackets. The year and page given for the incorrect subsequent spellings are the first year and page in which they are used. Incorrect subsequent spellings not in prevailing usage are unavailable (ICZN 1999, Art. 33.3). The generic definition of *Elathous* follows Etzler (2019). The following collection abbreviations are used:

BMNH	Natural History Museum, London, The United Kingdom
CAS	California Academy of Sciences, San Francisco, USA
CCRF	collection of Centre de Recherche Forestière, Rabat, Morocco
FSCA	Florida State Collection of Arthropods, The Museum of Entomology, Gainesville, Florida, USA
HMIM	Hayek Mirzayans Insect Museum, Tehran, Iran
HNHM	Hungarian Natural History Musuem, Budapest, Hungary
HUZOM	Hacettepe University Zoology Museum, Ankara, Turkey
MCNG	Museo Civico di Storia Naturale, Genova, Italy
MCSN	Museo Civico di Storia Naturale, Verona, Italy
MCZ	Museum of Comparative Zoology, Harvard University, USA
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Museum National d'Histoire Naturelle, Paris, France
NMNS	National Museum of Nature and Science, Tokyo, Japan
PCAG	collection of A. Guglielmi, Verona, Italy
PCCW	collection of C. Wurst, Heilbronn, Germany
PCGK	collection of G. Kakiopoulos, Athens, Greece
PCGM	collection of G. Murzov, Stara Zagora, Bulgaria
PCGP	collection of G. Platia, Gatteo, Italy
PCHB	collection of H. Brustel, Toulouse, France
PCJB	collection of José Sáez Bolaño, Badajoz, Spain
PCJM	collection of Josef Mertlik, Opatovice nad Labem, Czech Republic
PCJZ	collection of J. L. Zapata de la Vega, Madrid, Spain
PCNJ	collection of N. Jansson, Linköping University, Sweden
PCNN	collection of N. Nemer, Tannourine, Lebanon
PCRP	collection of R. Preiss, Wimborne, Great Britain
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SMNH	Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv University, Israel

Catalogue

Family Elateridae Leach, 1815

Subfamily Dendrometrinae Gistel, 1848

Tribe Dendrometrini Gistel, 1848

Genus *Elathous* Reitter, 1890

Elathous Reitter, 1890: 247. Type species. *Elathous buyssoni* Reitter, 1890; by subsequent designation (Hyslop 1921: 644).
Elathouina Reitter, 1905: 12, 19; synonymized with *Leptoschema* Horn, 1885 by Cobos (1969: 15) [this synonymy is not valid anymore since *Leptoschema* is a separate genus], later synonymized with *Elathous* by Platia (1994: 105). Type species. *Athous revelieri* Mulsant & Rey, 1875 [synonym of *Athous perrisii* Desbrochers des Loges, 1873]; by monotypy.
Athouinus Reitter, 1905: 114 [unavailable name, incorrect original spelling of *Elathouina* Reitter, 1905 (see Sánchez-Ruiz 1996: 107) (ICZN 1999, Art. 19.3); First Reviser (ICZN 1999, Art. 24.2): Schwarz (1906: 197)].
Melanathous Reitter, 1905: 24; synonymized with *Elathous* by Platia & Gudenzi (1996: 141). Type species. *Melanathous sequensi* Reitter, 1905 [synonym of *Athous brucki* Candèze, 1878]; by monotypy.
Malanathous: Reitter, 1905: 115 [unavailable name, incorrect original spelling of *Melanathous* Reitter, 1905 (see Sánchez-Ruiz 1996: 107) (ICZN 1999, Art. 19.3); First Reviser (ICZN 1999, Art. 24.2): Reitter (1906: 399)].
Athoina Reitter, 1906: 399 [unavailable name, incorrect subsequent spelling not in prevailing usage (see Sánchez-Ruiz 1996: 107)].

Literature. Dejean (1836: 102): catalogue [as *Limonius*]; Say (1839: 169): species description [as *Elater*]; LeConte (1853: 427): species description [as *Athous*]; Melsheimer (1853: 69): catalogue; Candèze (1860: 379): key, species description [as *Limonius*] and redescription [as *Athous*]; Marseul (1863: 143): catalogue [as *Limonius*]; Stierlin (1864: 192): key [as *Simonius* sic!]; Hampe (1866: 373): species description [as *Athous*]; LeConte (1867: 48): catalogue [as *Athous*]; Stein (1868: 66): catalogue [as *Athous*, *Limonius*]; Gemminger & Harold (1869: 1563): catalogue [as *Athous*, *Limonius*]; Baudi di Selve (1871: 54): species description [as *Athous*]; Baudi di Selve (1873: 99): review [as *Athous*]; Crotch (1873: 71): catalogue [as *Athous*]; Desbrochers des Loges (1873: 366): species description [as *Athous*]; Marseul (1873: 354): species redescription [as *Athous*]; Mulsant & Rey (1875a: 416): species description [as *Athous*]; Mulsant & Rey (1875b: 81): species redescription [as *Athous*]; Perris (1875: 4): species description [as *Athous*]; Stein & Weise (1877: 94): catalogue [as *Athous*, *Limonius*]; Candèze (1878: clxviii): species description [as *Athous*]; Henshaw (1885: 70): catalogue; Horn (1885: 51): taxonomic note [as *Leptoschema*]; Jäger (1883: 338): catalogue; Marseul (1887: 259): catalogue [as *Athous*, *Limonius*]; Reitter (1890: 247): original description of *Elathous*; Candèze (1891: 149): catalogue; Reitter (1891: 208): catalogue; Schwarz (1893: 191): species description; Schwarz (1897: 130): species description; Reitter (1898: 346): species description; Buysson (1902a: 275): taxonomic notes; Buysson (1902b: 15): catalogue [as *Athous*]; Dury (1902: 143): distributional note [as *Leptoschema*]; Schwarz (1903: 207): species description; Ulke (1903: 21): distributional note [as *Leptoschema*]; Bertolini (1904: 68): catalogue; Reitter (1905: 12): review, catalogue, description of *Elathouina*, genera *Athouinus*, *Leptoschema*, *Melanathous*; Reitter (1906: 399): catalogue, genera *Athoina*, *Elathous* [as *Leptoschema*], *Melanathous*; Schwarz (1906: 196): catalogue, genera *Elathous* [as *Leptoschema*], *Elathouina*, *Melanathous*; Blatchley (1910: 738): generic key, catalogue [as *Leptoschema*]; Schaufuss (1911: 657): catalogue [as *Elathouina*]; Jakobson (1913: 757): catalogue, genera *Elathous* [as *Leptoschema*], *Elathouina*, *Melanathous*; Buysson (1914: 86): generic key, genera *Elathous* [as *Leptoschema*], *Elathouina*, *Melanathous*; Sainte-Claire-Deville (1914: 290): catalogue [as *Athous*]; Pliginsky (1916: 123): catalogue [as *Leptoschema*]; Leng (1920: 168): catalogue, *Elathous* [as *Leptoschema*]; Hyslop (1921: 630): generic names; Hatch (1924: 569): distributional note [as *Leptoschema*]; Buysson (1925: 598): catalogue, genera *Leptoschema*, *Elathouina*, *Melanathous*; Buysson (1926: 163): remark [as *Leptoschema*]; Schenkling (1927: 292): catalogue, genera *Elathous* [as *Leptoschema*], *Elathouina*, *Melanathous*; Porta (1929: 357): generic key, catalogue, genera *Elathouina*, *Leptoschema*; Fuente (1930: 60): catalogue, *Elathous* [as *Leptoschema*]; Van Dyke (1932: 345): review of North American species, key, species descriptions [as *Limonius* and *Elathous*]; Leng & Mutchler (1933: 83): catalogue [as *Limonius* and *Elathous*]; Fall (1934: 30): species description; Miwa (1934: 104): key, catalogue; Mitsuhashi (1936: 440): remark [as *L. brunnea* (sic!)]; Blackwelder (1939: 39): catalogue; Seabra (1939: 226): catalogue [as *Leptoschema*]; Thomas (1941: 241): distributional note; Seabra

(1943: 60): catalogue [as *Leptoschema*]; Dietrich (1945: 7): generic and species key, distributional note, review; Glen (1950: 167): description and figures of larva; Lane (1952: 66): distributional note; Arnett (1955: 603): taxonomic note [as *Athoina*]; Kocher (1956: 100): catalogue, genera *Leptoschema*, *Elathouina*; Dolin (1960: 193): description of larva [as *Leptoschema*]; Becker (1961: 161): review; Arnett (1962: 502): generic key, remark; Dolin (1964a: 73): larval key, description of larva [as *Leptoschema*]; Dolin (1964b: 388): larval key, description of larva [as *Leptoschema*]; Gurjeva (1965: 269): generic key [as *Leptoschema*]; Inaizumi (1965: 32): distributional note [as *Leptoschema*]; Cobos (1969: 11): species description [as *Leptoschema*]; Gaedike (1969: 182): bibliography [as *Leptoschema*]; Ôhira (1970: 24): review [as *Limonius*]; Ruette (1970: 49): type depository; Stibick (1970: 154): generic key, taxonomic note; Agaev (1971: 38): distributional record [as *Leptoschema*]; Arnett (1971: 502): generic key, remark; Lane & Lanchester (1971: 19): generic key, distributional note, review; Leseigneur (1972: 172): generic key, catalogue, revision [as *Elathouina*]; Becker (1974: 714): taxonomic notes; Blackwelder (1974: 27): catalogue [as *Elathous* and *Leptoschema*]; Smith & Enns (1977: 439): generic key; Dolin (1978: 25): larval key; Becker (1979: 571): taxonomic notes; Agaev (1980: 17): key; Dolin (1982: 136): generic key, review; Guglielmi & Platia (1985: 185): species description; Kishii (1985: 9): taxonomic note; Ôhira (1985: 5): taxonomic notes; Agaev (1986: 16): remark; Pesarini (1986: 14): catalogue, generic key, review [as *Elathouina*]; Kishii (1987: 79): generic key, catalogue; Mardzhanyan (1987: 65): generic key, review; Suzuki (1987: 2): taxonomic note; Watanabe (1987: 20): distributional notes [as *Limonius*]; Agaev (1988a: 540): distributional note; Agaev (1988b: 15): generic key for larva and imago, review; Keaster *et al*. (1988: 10): bibliography [as *Elathous* and *Leptoschema*]; Watanabe (1990: 8): distributional notes; Agaev & Dolin (1991: 309): taxonomic note; Bousquet (1991: 177): distributional note; Platia & Schimmel (1991: 131): species description, key; Schimmel & Platia (1991: 880): remark; Ôhira (1992: 350): distributional note [as *Harminathous*]; Platia & Schimmel (1992: 92): species description; Bousquet (1993: 9): bibliography; Johnson (1993: 5): larval key; Kishii (1993: 18): distributional note; Platia & Schimmel (1993: 52): new species description and figures, comparison with other species; Suzuki (1993: 4): distributional note; Platia (1994: 102): generic key, review; Wurst (1994: 62): species description; Gobbi & Platia (1995: 4): catalogue; Ôhira (1995: 189): species description; Platia & Gudenzi (1996: 140): taxonomic note; Sánchez-Ruiz (1996: 106): catalogue; Kishii (1999: 26): catalogue; Suzuki (2001: 50): distributional note; Johnson (2002: 164): generic key, review; Platia & Serrano (2002: 312): distributional note; Pyshkin *et al*. (2002: 104): distributional note; Preiss (2003: 55): species description; Preiss & Platia (2003: 104): distributional note; Mertlik (2005: 168): species description; Platia & Gudenzi (2005: 113): species description; Kesdek *et al*. (2006: 421): distributional record; Mertlik & Dušánek (2006: 148): species description; Cate (2007: 164): catalogue; Thomas (2007: 24): bionomics; Toyoshima (2007: 43): distributional note; Zapata de la Vega & Sánchez-Ruiz (2007: 221): species description; Dušánek (2008: 149): distributional note, bionomics; Löbl & Smetana (2008: 24): taxonomic note; Majka & Johnson (2008: 7): distributional note; Mertlik & Platia (2008: 32): distributional note; Platia (2008: 141): species description; Al Dhafer (2009: 210): species description, key [as *Limonius*]; Arimoto (2010: 11): distributional note; Gülperçin & Tezcan (2010: 33): catalogue; Platia (2010: 27): species description; Tezcan *et al*. (2010: 66): distributional note; Hiramatsu (2011: 43): distributional note; Majka *et al*. (2011: 139): distributional note; Platia (2011: 834): distributional notes; Platia *et al*. (2011: 207): species description; Sert & Kabalak (2011: 505, 506): distributional note; Atay *et al*. (2012: 110): distributional note, bionomics; Tsutsumiuchi (2012: 5): distributional note; Webster *et al*. (2012: 96): distributional note; Zapata de la Vega & Sánchez-Ruiz (2012a: 108): species description; Zapata de la Vega & Sánchez-Ruiz (2012b: 166): catalogue, distributional map; Bousquet *et al*. (2013: 183): distributional note; Jarzabek-Müller (2013: 78): distributional note; Kabalak *et al*. (2013: 85): species description, distributional note, species key; Kamezawa (2013: 4): remark; Zapata de la Vega & Sánchez-Ruiz (2013: 165): catalogue, distributional map; Leseigneur (2014: 431): catalogue; Platia & Kakiopoulos (2014: 102): species; Platia *et al*. (2014: 44): species description; Sáez Bolaño *et al*. (2014: 136): distributional note; Zapata de la Vega & Sánchez-Ruiz (2014: 138): catalogue, distributional map; Delnatte *et al*. (2015: 43): distributional note, taxonomic note; Németh *et al*. (2015: 92): species description; Zapata de la Vega & Sánchez-Ruiz (2015: 165): catalogue, distributional map; Benyahia *et al*. (2016: 8): checklist; Gülperçin & Tezcan (2016: 134): bionomics, distributional notes; Rousette & Delnatte (2016: 175): bionomics; Zapata de la Vega & Sánchez-Ruiz (2016: 200): catalogue; Zapata de la Vega & Sánchez-Ruiz (2017: 279): catalogue; Kabalak & Özbek (2018: 147): distributional and taxonomic notes; Nasserzadeh *et al*. (2018: 528): species description; Platia *et al*. (2018: 254): distributional note, bionomics; Tarnawski *et al*. (2018: 116): catalogue; Zapata de la Vega & Sánchez-Ruiz (2018: 21): catalogue, distributional map; Etzler (2019: 304): generic key, review, checklist; Németh (2019: 136): species description; Zapata de la Vega & Sánchez-Ruiz (2019: 56): catalogue, distributional map; Németh *et al*. (2020: 168): species descriptions.

Species from the Nearctic realm

Elathous bicolor (LeConte)

(Fig. 1A,B)

Athous bicolor LeConte, 1853: 428.
Leptoschema bicolor: Horn, 1885: 51.
Elathous oberndorfferi Schwarz, 1903: 207; synonymized by Becker (1961: 166). Note that *E. oberndorfferi* was synonymized with *E. discalceatus* (Say, 1839) by Van Dyke (1932). However, Becker (1961) studied the type material and provided strong evidence that the Van Dyke's synonymization was erroneous and *E. oberndorfferi* should be a synonym of *E. bicolor*. Etzler (2019) omitted Becker's paper in his study and erroneously listed *E. oberndorfferi* as a synonym of *E. discalceatus*, following the earlier study by Van Dyke (1932).
Leptoschema oberndorfferi: Reitter, 1905: 22.
Leptoschema oberndorferi: Schwarz,1906: 197 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathous bicolor: Van Dyke, 1932: 358.
Limonius kondratieffi Al Dhafer, 2009: 299; synonymized with *Athous bicolor* LeConte, 1853 by Etzler (2019: 306).

Type depositories. *Athous bicolor*. Holotype, female (MCZ). *Elathous oberndorfferi*: Lectotype, female (SDEI). *Limonius kondratieffi*. Holotype, male (FSCA?); 1 paratype, male (FSCA?); should be in FSCA according to the original description, however, no type material of this species has been found there (Etzler 2019: 307).

Type localities. *Athous bicolor*. USA: New York. *Elathous oberndorfferi*. USA: New York, Buffalo. *Limonius kondratieffi*. USA: Ohio, Knox Co., Mt. Logan.

Distribution. Eastern parts of Canada and USA.

Literature. LeConte (1853: 428): original description of *Athous bicolor*; Candèze (1860: 486): redescription [as *Athous*]; LeConte (1867: 48): catalogue [as *Athous*]; Gemminger & Harold (1869: 1564): catalogue [as *Athous*]; Crotch (1873: 71): catalogue [as *Athous*]; Henshaw (1885: 70): catalogue; Horn (1885: 51): taxonomic note [as *Leptoschema*]; Candèze (1891: 201): catalogue [as *Leptoschema*]; Dury (1902: 143): distributional note [as *Leptoschema*]; Schwarz (1903: 207): original description of *E. oberndorfferi*; Ulke (1903: 21): distributional note [as *Leptoschema*]; Reitter (1905: 20, 22): key, review, remark [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Blatchley (1910: 761): catalogue, review [as *Leptoschema*]; Leng (1920: 168): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Leng (1928: 344): distributional note [as *Leptoschema*]; Van Dyke (1932: 356, 358, 360): key, bibliography; Leng & Mutchler (1933: 84): catalogue; Thomas (1941: 241): distributional note; Dietrich (1945: 16): species key, distributional note, review; Glen (1950: 167, 217, 239): description of larva, figures of larval characters; Becker (1961: 161, 166): review, synonymization of *E. oberndorfferi* with *E. bicolor*, comparison with other species, bibliography, figure of bursa copulatrix; Becker (1979: 612): remark; Blackwelder (1974: 27): catalogue; Al Dhafer (2009: 211, 214, 218, 227, 300, 307): original description and figures of *Limonius kondratieffi*, species key, comparison with other species, remarks; Bousquet *et al*. (2013: 183): distributional note; Etzler (2019: 306): checklist [*E. oberndorfferi* under the synonymy of *E. discalceatus*, see comment above].

Elathous brevicornis Fall

(Fig. 1C)

Elathous brevicornis Fall, 1934: 30.

Type depository. Holotype, male (MCZ).

Type locality. USA: California, San Bernardino Mts.

Distribution. USA (California).

Literature. Fall (1934: 30): original description; Blackwelder (1939: 39): catalogue; Blackwelder (1974: 27): catalogue; Etzler (2019: 306): checklist.

***Elathous brunnellus* Fall**
(Fig. 1D)

Elathous brunnellus Fall, 1934: 31.
Elathous brunelIus: Etzler, 2019: 306 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Holotype, male (MCZ).

Type locality. USA: California, Sierra Madre Mountains, 7000 feet, Pine Flats [presumably Pine Flat Lake (reservoir) east of Fresno].

Distribution. USA (California).

Literature. Fall (1934: 31): original description; Blackwelder (1939: 39): catalogue; Blackwelder (1974: 27): catalogue; Etzler (2019: 306): checklist.

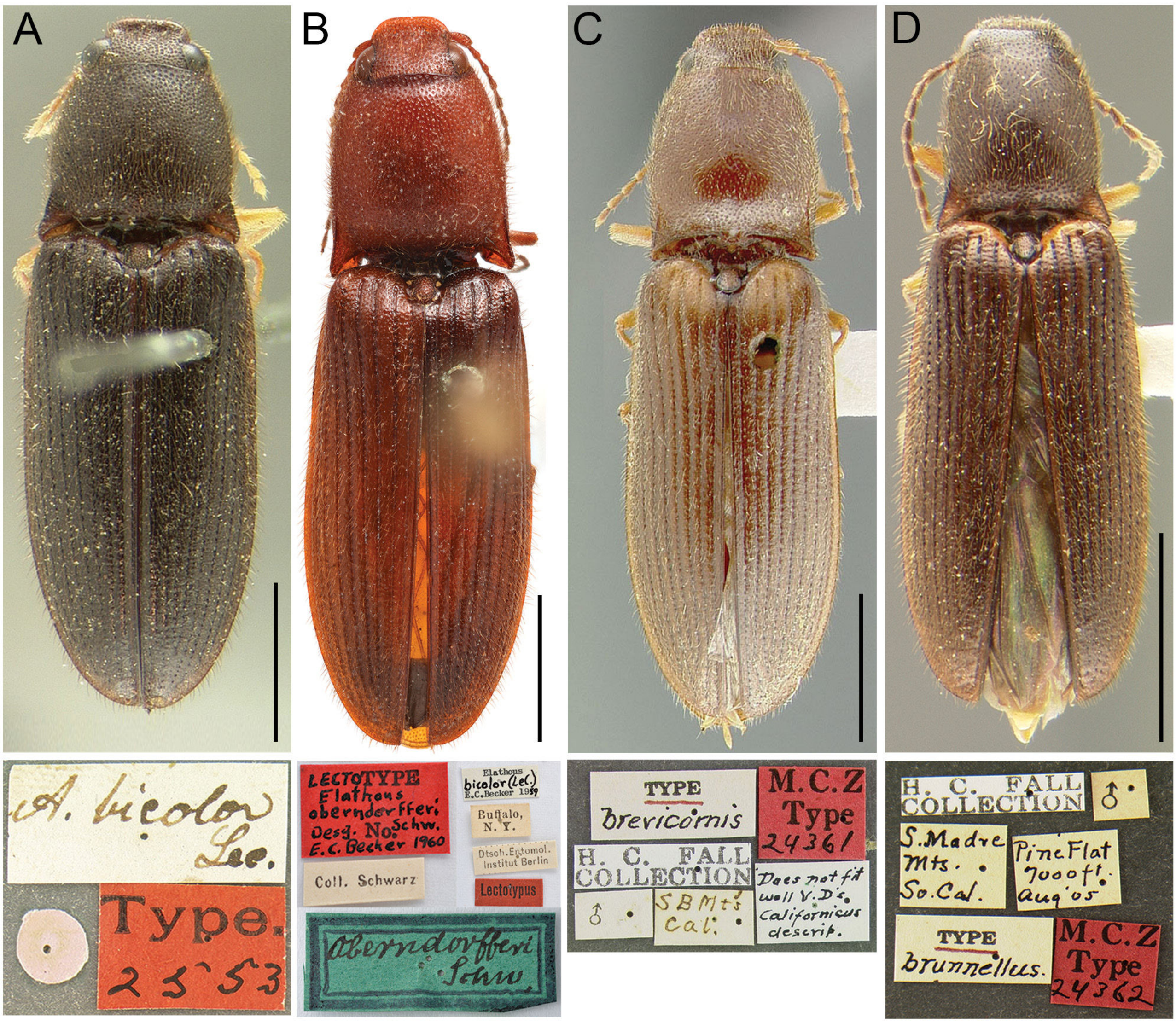

FIGURE 1. Nearctic species of genus *Elathous*. A, *E. bicolor* (LeConte, 1853), holotype, female; B, *E. oberndorfferi* Schwarz, 1903, lectotype, female; C, *E. brevicornis* Fall, 1934, holotype, male; D, *E. brunnellus* Fall, 1934, holotype, male. Photographs A & C provided by C. A. Maier (MCZ). Scale bars: 2.0 mm. Labels not to scale.

***Elathous californicus* Van Dyke**
(Fig. 2A)

Elathous californicus Van Dyke, 1932: 359.
Type depository. Holotype, male (CAS); allotype, female (CAS), 3 paratypes, females (CAS).

Type locality. USA: California, El Dorado Co., Strawberry Valley.

Distribution. Western parts of Canada and USA.

Literature. Van Dyke (1932: 359): original description; Leng & Mutchler (1933: 84): catalogue; Fall (1934: 31): comparison with other species; Blackwelder (1974: 27): catalogue; Bousquet (1991: 177): distributional note; Bousquet *et al*. (2013: 183): distributional note; Etzler (2019: 306): checklist.

***Elathous discalceatus* (Say)**
(Fig. 2B)

Elater discalceatus Say, 1839: 169.
Athous discalceatus: Melsheimer, 1853: 69.
Leptoschema discalceatum: Horn, 1885: 51.
Leptoschema discalceatus: Reitter 1905: 20.
Elathous discalceatus: Van Dyke, 1932: 360.
Elathous discalceatum: Thomas, 1941: 242.

Type depository. *Elater discalceatus*. Syntype, female (MCZ?); should be in the collection of Dr. Harris (now in MCZ) (LeConte 1853: 427), however, no such specimen has been found there (C. Maier, MCZ, personal communication).

Type locality. *Elater discalceatus*. USA: New Hampshire.

Distribution. Eastern parts of Canada and USA.

Literature. Say (1839: 169): original description of *Elater discalceatu*s; LeConte (1853: 427): redescription; Melsheimer (1853: 69): catalogue; Candèze (1860: 421, 455): key, redescription [as *Athous*]; LeConte (1867: 48): catalogue [as *Athous*]; Gemminger & Harold (1869: 1566): catalogue [as *Athous*]; Crotch (1873: 71): catalogue [as *Athous discalceatus* Lec. (sic!)]; Desbrochers des Loges (1873: 366): comparison with other species [as *Athous*]; Perris (1875: 4): comparison with other species [as *Athous*]; Henshaw (1885: 70): catalogue; Horn (1885: 51): taxonomic note [as *Leptoschema*]; Candèze (1891: 201): catalogue [as *Leptoschema*]; Reitter (1905: 20, 24): review, key, remark [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Blatchley (1910: 761): catalogue, review [as *Leptoschema*]; Leng (1920: 168): catalogue [as *Leptoschema*]; Hatch (1924: 569): distributional note [as *Leptoschema*]; Schenkling (1927: 304): catalogue [as *Leptoschema*]; Leng (1928: 344): distributional note [as *Leptoschema*]; Champlain & Knull (1932: 255): bionomics, distributional note [as *Leptoschema*]; Van Dyke (1932: 356, 358, 360): key, [erroneous] synonymization of *E. oberndorfferi* with *E. discalceatus*, bibliography; Thomas (1941: 242): distributional note; Dietrich (1945: 16): species key, distributional note, review; Becker, (1961: 161, 168): comparison with other species, taxonomic note; Blackwelder (1974: 27): catalogue; Bousquet (1991: 177): distributional note; Bousquet (1993: 9): bibliography; Thomas (2007: 24, 41, 66, 120, 165, 169): bionomics; Majka & Johnson (2008: 7): distributional note; Majka *et al*. (2011: 139): distributional note; Webster *et al*. (2012: 96, 99): distributional note; Bousquet *et al*. (2013: 183): distributional note; Etzler (2019: 306): checklist.

***Elathous huguenini* (Van Dyke)**
(Fig. 2C)

Limonius huguenini Van Dyke, 1932: 346.
Limonius hyguenini: Blackwelder, 1974: 26 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathous huguenini: Etzler (2019: 306).

Type depository. Holotype, female (CAS).

Type locality. USA: California, Plumas Co.

Distribution. USA (California).

Literature. Van Dyke (1932: 346): original description [as *Limonius*]; Leng & Mutchler (1933: 83): catalogue [as *Limonius*]; Blackwelder (1974: 26): catalogue [as *Limonius*]; Al Dhafer (2009: 210, 214, 219, 226, 296, 307): redescription, species key, comparison with other species, remarks, figure of aedeagus [as *Limonius*]; Etzler (2019: 306): checklist.

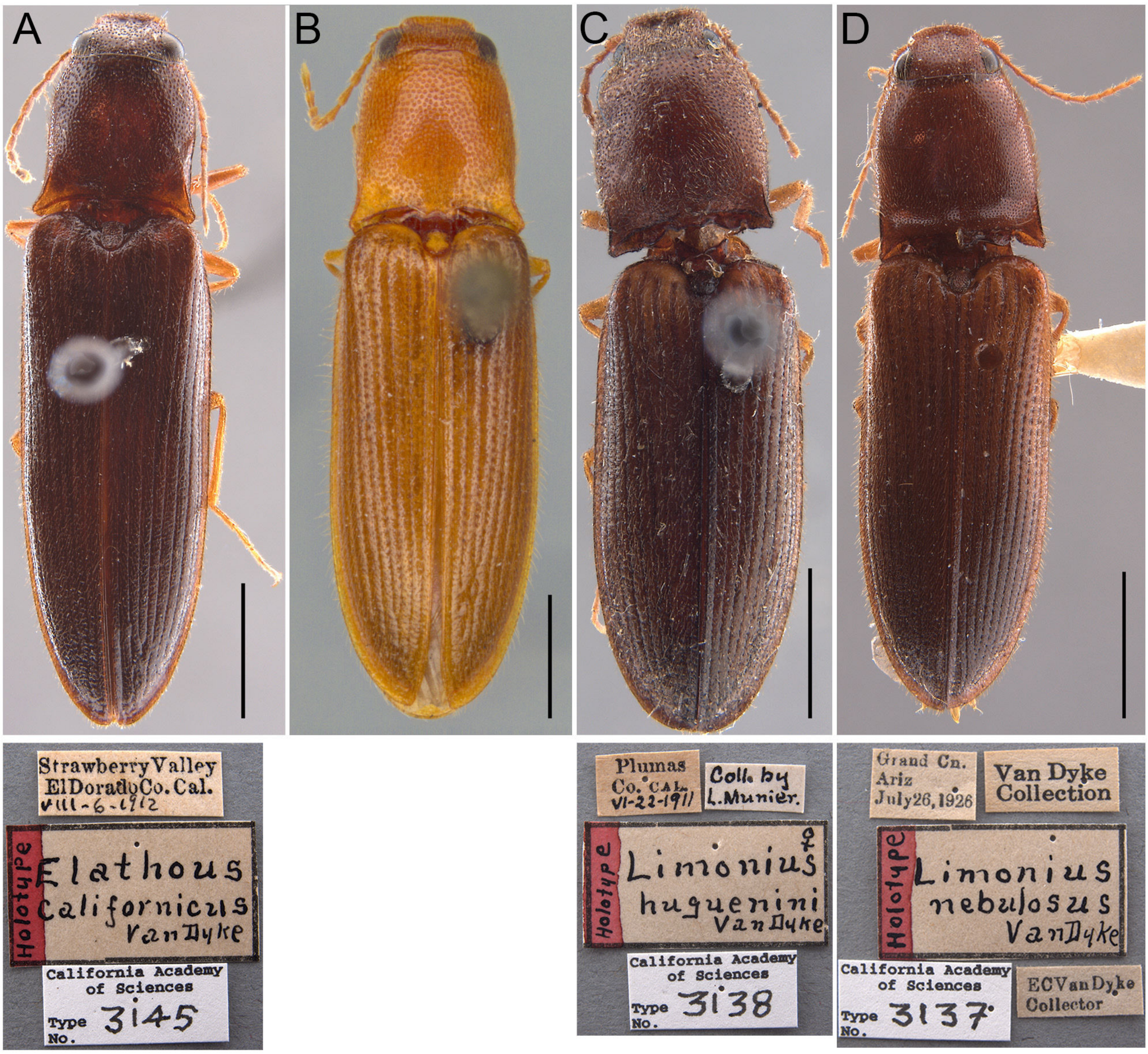

FIGURE 2. Nearctic species of genus *Elathous*. A, *E. californicus* Van Dyke, 1932, holotype, male; B, *E discalceatus* (Say, 1839), non-type specimen from Canada, sex unknown; C, *E. huguenini* (Van Dyke, 1932), holotype, female; D, *E. nebulosus* (Van Dyke, 1932), holotype, male. Photograph A provided by C. A. Maier (MCZ), B–D provided by R. Diaz-Bastin & C. Grinter (CAS). Scale bars: 2.0 mm. Labels not to scale.

Elathous nebulosus **(Van Dyke)**
(Fig. 2D)

Limonius nebulosus Van Dyke, 1932: 345.
Elathous nebulosus: Lane, 1952: 66.

Type depository. Holotype, male (CAS); 2 paratypes, sex undetermined (CAS). Although both paratypes should be deposited in the CAS collection (coll. of E. C. Van Dyke and coll. of R. Hopping; Van Dyke 1932: 345), only one paratype has been located there (C. Grinter, CAS, personal communication).

Type locality. USA: Arizona, El Tovar, Grand Canyon.

Distribution. Western parts of Canada and USA.

Literature. Van Dyke (1932: 345): original description [as *Limonius*]; Leng & Mutchler (1933: 83): catalogue [as *Limonius*]; Lane (1952: 66): distributional note; Ruette (1970: 49): type depository; Lane & Lanchester (1971: 21): distributional note, review; Blackwelder (1974: 26): catalogue [as *Limonius*]; Bousquet (1991: 177): distributional note; Al Dhafer (2009: 211, 214, 219, 229, 297, 300, 306): redescription, species key, comparison with other species, remarks, figure of aedeagus [as *Limonius*]; Bousquet *et al*. (2013: 183): distributional note; Etzler (2019: 306, 308): checklist, figures of imago morphology.

Species from the Palearctic realm

Elathous agilis Németh

(Fig. 3A)

Elathous agilis Németh, 2019: 136.

Type depositories. Holotype, male (HNHM); 55 paratypes, 30 males, 25 females (all but one female HNHM, one female PCNN).

Type locality. Lebanon: Northern gov., Ehden, Horsh Ehden Natural Reserve, 34°18'25"N, 35°59'6"E.

Distribution. Lebanon.

Literature. Németh (2019: 136, 152): original description and figures; Németh *et al*. (2020: 168, 172): comparison with other species.

Elathous brucki (Candèze)

(Fig. 3B)

Athous brucki Candèze, 1878: CLXVIII.
Melanathous sequensi Reitter, 1905: 25; synonymized by Platia & Gudenzi (1996: 141).
Malanathous sequensi: Reitter, 1905: 115 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Leptoschema brucki: Reitter, 1906: 399.
Elathous brucki: Guglielmi & Platia, 1985: 192.

Type depositories. *Athous brucki*: Syntype, sex unknown [without abdomen] (RBINS). *Melanathous sequensi*: Syntype [designated as the holotype by the former HNHM curator], male (HNHM).

Type localities. *Athous brucki*: Greece: Peloponnese, Mt. Taygetos. *Melanathous sequensi*: Greece: Peloponnese, Mt. Taygetos.

Distribution. Greece.

Literature. Candèze (1878: CLXVIII): original description [as *Athous*]; Oertzen (1886: 248): catalogue [as *Athous*]; Marseul (1887: 261): catalogue [as *Athous*]; Candèze (1891: 152): catalogue [as *Athous*]; Reitter (1891: 207): catalogue [as *Athous*]; Reitter (1905: 24): review, key, possible synonymy with *E. niger* Schwarz, 1897 [as *Athous*], original description of *Melanathous sequensi*; Reitter (1906: 399): catalogue [as *Leptoschema; E. brucki* as a possible synonym of *E. niger*; as *Melanathous*]; Schwarz (1906: 198): catalogue [as *Melanathous*]; Jakobson (1913: 757): catalogue [as *Leptoschema* [as a possible synonym *of L. nig*rum]*, Melanath*ous]; Buysson (1914: 87): catalogue [as *Melanathous*]; Hyslop (1921: 655): generic names [*Melanathous*]; Buysson (1925: 598): catalogue [as *Leptoschema*, *Melanathous*]; Schenkling (1927: 303): catalogue [as *Leptoschema*, *Melanathous*]; Guglielmi & Platia (1985: 192): distributional note; Platia & Schimmel (1991: 132, 141): comparison with other species, key, figures of imago morphology; Platia & Gudenzi (1996: 140): synonymization of *Melanathous sequensi* and *E. brucki*; Mertlik (2005: 171): comparison with other species; Cate (2007: 164): catalogue; Platia (2008: 144): comparison with other species; Platia & Kakiopoulos (2014: 102): comparison with other species; Etzler (2019: 306): checklist; Németh (2019: 137): comparison with other species.

Elathous brunneus (Lewis)

(Fig. 3C)

Limonius brunneus Lewis, 1894: 195.
Elathous brunneus: Suzuki, 1987: 2.
Limonius brunnea: Mitsuhashi, 1936: 440.

Type depository. Two syntypes, male and ?female (BMNH).

Type locality. Japan: Honshu, Tochigi Prefecture, Nikkō.

Distribution. Japan.

Literature. Lewis (1894: 195): original description [as *Limonius*]; Schwarz (1906: 194): catalogue [as *Limonius*]; Jakobson (1913: 757): catalogue [as *Limonius*]; Buysson (1925: 598): catalogue [as *Limonius*]; Schenkling (1927: 292): catalogue [as *Limonius*]; Miwa (1934: 104, 106): key, catalogue; Mitsuhashi (1936: 440): remark [as *L. brunnea* (sic!)]; Inaizumi (1965: 32): distributional note [as *L. brunnea* (sic!)]; Ôhira (1970: 24): review, taxonomic note [as *Limonius*]; Kishii (1985: 9): taxonomic note; Ôhira (1985: 5): taxonomic notes, figure of type specimen; Kishii (1987: 80): catalogue; Suzuki (1987: 1): taxonomic note, figures of imago morphology; Watanabe (1987: 20): distributional notes, figures of habitus and morphology of imago [as *Limonius*]; Watanabe (1990: 8): distributional notes; Ôhira (1992: 350): distributional note, figure of habitus of imago [as *Harminathous suturalis* (nec Candèze, 1873)]; Kishii (1993: 18): distributional note; Suzuki (1993: 4): distributional note; Ôhira (1995: 190): comparison with other species; Kishii (1999: 26): catalogue; Suzuki (2001: 50): distributional note, figure of habitus of imago; Cate (2007: 164): catalogue; Arimoto (2010: 11): distributional note, figures of habitus of imago; Tsutsumiuchi (2012: 5): distributional note, figures of habitus of imago; Kamezawa (2013: 4): remark; Etzler (2019: 306): checklist.

Elathous buyssoni Reitter

(Fig. 3D)

Elathous buyssoni Reitter, 1890: 248.
Leptoschema buyssoni: Reitter, 1905: 20.

Type depository. Syntype [erroneously labelled as holotype by the former HNHM curator], male (HNHM); 2 syntypes, males (HNHM), 1 syntype, male (SDEI).

Type locality. Azerbaijan: Nakchivan, Araxesthal [valley of Arax river], Ordubad.

Distribution. Armenia [needs to be confirmed], Azerbaijan (Nakchivan), Turkey.

Literature. Reitter (1890: 248): original description; Candèze (1891: 149): catalogue; Reitter (1891: 308): catalogue; Schwarz (1893: 191): comparison with other species; Reitter (1898: 346): comparison with other species; Buysson (1902a: 275): comparison with other species; Reitter (1905: 20, 115): review, key, catalogue [as *Leptoschema*]; Reitter (1906: 399): catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Hyslop (1921: 644): generic names, remark; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Mardzhanyan (1987: 67): review; Agaev (1988a: 540): distributional note; Agaev (1988b: 15, 51): key, review; Cate (2007: 164): catalogue; Mertlik & Platia (2008: 32): distributional note; Gülperçin & Tezcan (2010: 33): catalogue; Sert & Kabalak (2011: 505): distributional note; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Tarnawski *et al*. (2018: 116): catalogue; Etzler (2019: 306): checklist; Németh *et al*. (2020: 168, 172): comparison with other species.

Elathous candezei Reitter

(Fig. 3E,F)

Elathous candezei Reitter, 1890: 248.
Leptoschema candezei: Reitter, 1905: 20.

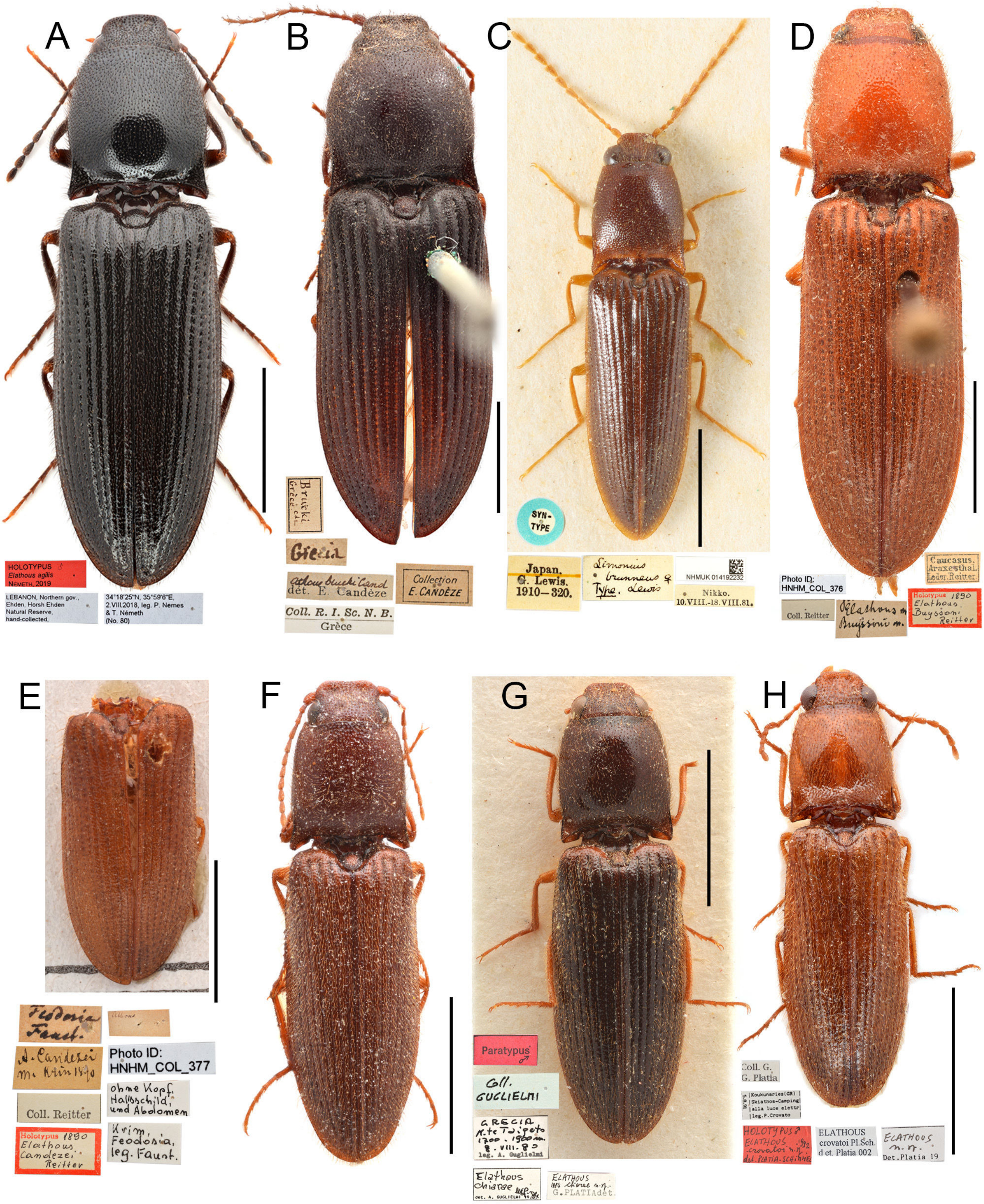

FIGURE 3. Palearctic species of genus *Elathous*. A, *E. agilis* Németh, 2019, holotype, male; B, *E. brucki* (Candèze, 1878), syntype, sex unknown; C, *E. brunneus* (Lewis, 1894), syntype, ?female; D, *E. buyssoni* Reitter, 1890, syntype [erroneously labelled as holotype by the former HNHM curator], male; E, *E. candezei* Reitter, 1890, syntype [erroneously labelled as holotype by the former HNHM curator], without abdomen; F, *E. candezei* Reitter, 1890, non-type specimen from Crimea, male; G, *E. chiarae* Guglielmi & Platia, 1985, paratype, male; H, *E. crovatoi* Platia & Schimmel, 1993, holotype, male. Photograph C provided by K. Matsumoto (BMNH). Scale bars: 3.0 mm. Labels not to scale.

Type depository. Syntype [erroneously labelled as holotype by the former HNHM curator], sex unknown (HNHM).

Type locality. Crimea: Theodosia.

Distribution. Russia/Ukraine (Crimea).

Literature. Reitter (1890: 248): original description; Candèze (1891: 149): catalogue; Reitter (1891: 308): catalogue; Schwarz (1893: 191): comparison with other species; Reitter (1905: 20, 22, 115): review, key, catalogue [as *Leptoschema*]; Reitter (1906: 399): catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Pliginsky (1916: 123): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Dolin (1960: 193): redescription of imago, description of larva, figures of larval characters [as *Leptoschema*]; Dolin (1964a: 79): description of larva, figures of larval characters [as *Leptoschema*]; Dolin (1964b: 387): description of larva, figures of larval characters [as *Leptoschema*]; Gurjeva (1965: 277): key to the species [as *Leptoschema*]; Gaedike (1969: 182, 195, 262): bibliography [as *Leptoschema*]; Dolin (1978: 49): larval key, figures of larval characters; Dolin (1982: 156): redescription of imago and larva, figures of larval and imaginal characters; Keaster *et al*. (1988: 53): bibliography [as *Leptoschema*]; Pyshkin *et al*. (2002: 104): distributional note; Cate (2007: 164): catalogue; Dušánek (2008: 149, 153): distributional note, bionomics, figure of habitus of imago; Etzler (2019: 306): checklist.

Elathous chiarae **Guglielmi & Platia**
(Fig. 3G)

Elathous chiarae Guglielmi & Platia, 1985: 192.

Type depository. Holotype, male (PCAG?); paratype, male (MCSN).

Type locality. Greece: Peloponnese, Mt. Taygetos, 1700–1900 m.

Distribution. Greece.

Literature. Guglielmi & Platia (1985: 185, 192, 213): original description and figures; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist.

Remark. According to the original description (Guglielmi & Platia 1985), the holotype of *E. chiarae* should be deposited in MCSN, Verona, Italy, and the paratype in the collection of the collector and co-author of this species, Alfredo Guglielmi (Verona, Italy). However, only the paratype is deposited in the MCSN (Roberta Salmaso, personal communication), and therefore, we assume that the holotype is in the collection of A. Guglielmi.

Elathous crovatoi **Platia & Schimmel**
(Fig. 3H)

Elathous crovatoi Platia & Schimmel, 1993: 52.

Type depository. Holotype, male (PCGP).

Type locality. Greece: Skiathos, Koukounaries [Koukunaries, Skiathos-Camping].

Distribution. Greece.

Literature. Platia & Schimmel (1993: 52): original description and figures; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist.

Elathous cyprius **(Baudi di Selve)**
(Fig. 4A)

Athous cyprius Baudi di Selve, 1871: 54.
Athous cypricus: Marseul, 1887: 261 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathous cyprius: Preiss & Platia (2003: 104).

Type depository. Described probably based on a single specimen; type depository unknown.

Type locality. Cyprus.

Distribution. Cyprus.

Literature. Baudi di Selve (1871: 54): original description [as *Athous*]; Baudi di Selve (1873: 99): review [as *Athous*]; Marseul (1873: 380): redescription [as *Athous*]; Marseul (1887: 261): catalogue [as *Athous*]; Candèze (1891: 153): catalogue [as *Athous*]; Reitter (1905: 114, 119): review, catalogue [as *Athous*]; Schenkling (1927: 341): catalogue [as *Athous incertae sedis*]; Preiss & Platia (2003: 104): catalogue, distributional note, habitus figure; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist; Németh (2019: 137): comparison with other species.

Elathous depressus Platia & Schimmel

(Fig. 4B)

Elathous depressus Platia & Schimmel, 1991: 131.

Type depository. Holotype, male (PCGP).

Type locality. Turkey: Adıyaman, Mt. Nemrut.

Distribution. Turkey.

Literature. Platia & Schimmel (1991: 131, 141): original description and figures; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 33): catalogue; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Tarnawski *et al*. (2018: 116): catalogue; Etzler (2019: 306): checklist.

Elathous ekaterinae Preiss

(Fig. 4C)

Elathous ekaterinae Preiss, 2003: 55.

Type depositories. Holotype, male (BMNH); 4 paratypes, males (3 PCRP, 1 SMNH).

Type locality. Syria: Golan Heights, Quneitra (Area of Separation, Charlie Gate), 950 m.

Distribution. Israel, Syria.

Literature. Preiss (2003: 55): original description and figures; Mertlik & Dušánek (2006: 153): comparison with other species; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist; Németh *et al*. (2020: 168, 172): comparison with other species, figures of imago.

Elathous emgei Schwarz

(Fig. 4D)

Elathous emgei Schwarz, 1893: 191.
Leptoschema emgei: Reitter, 1905: 22.

Type depository. Holotype, male (SDEI).

Type locality. Greece: Thessaloniki [„Salonichi"].

Distribution. Greece.

Literature. Schwarz (1893: 191): original description; Reitter (1905: 22, 115): review, key, catalogue [as *Leptoschema*]; Reitter (1906: 399): catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Guglielmi & Platia (1985: 192): comparison with other species; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist.

Elathous emrei Platia
(Fig. 4E)

Elathous emrei Platia in Platia *et al*., 2011: 208.

Type depositories. Holotype, male (PCGP); 10 paratypes: 2 males, 8 females (PCGP, PCNJ).

Type locality. Turkey: Mersin, 40 km N of Gülnar, Koseçobanli-Tasdustu.

Distribution. Turkey.

Literature. Platia *et al*. (2011: 208, 211, 213): original description and figures; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Gülperçin & Tezcan (2016: 134, 138, 141): bionomics, distributional notes; Kabalak & Özbek (2018: 147, 157): distributional note; Platia *et al*. (2018: 254): distributional note, bionomics; Tarnawski *et al*. (2018: 117): catalogue; Etzler (2019: 306): checklist.

Elathous graecus Platia
(Fig. 4F)

Elathous graecus Platia, 2008: 143.

Type depositories. Holotype, male (RBINS); 12 paratypes: 9 males, 3 females (RBINS, PCGP).

Type locality. Greece: Parnassos, Koukouvitza, 900 m.

Distribution. Greece.

Literature. Platia (2008: 141, 143, 145, 147): original description and figures; Etzler (2019: 306): checklist; Németh (2019: 137): comparison with other species.

Remark. Although the holotype should be deposited in RBINS according to the original description (Platia 2008: 143), it has not been located there (Jérôme Constant, personal communication).

Elathous impressifrons (Hampe)
(Fig. 4G)

Athous impressifrons Hampe, 1866: 373.
Elathous impressifrons: Buysson, 1902a: 275.
Leptoschema impressifrons: Reitter, 1905: 24.

Type depository. According to the original description (Hampe 1866), there should be more female syntypes. Hampe's specimens should be deposited in NHMW; however, no specimens of this species have been located there (H. Schillhammer, personal communication).

Type locality. Croatia: Zagreb [Agram].

Distribution. Croatia. Bertolini (1904: 68) recorded this species from France (Corsica) but this record was not confirmed in subsequent studies.

Literature. Hampe (1866: 373): original description [as *Athous*]; Stein (1868: 66): catalogue [as *Athous*]; Marseul (1873: 354): redescription [as *Athous*]; Stein & Weise (1877: 94): catalogue [as *Athous*]; Marseul (1887: 259): catalogue [as *Athous*]; Candèze (1891: 150): catalogue [as *Athous*]; Reitter (1891: 206): catalogue [as *Athous*]; Bertolini (1904: 68): catalogue; Reitter (1905: 24, 115): review, key, catalogue [as *Leptoschema*]; Reitter (1906: 399): catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1914: 87): catalogue [as *Leptoschema*]; Hyslop (1921: 652): taxonomic note [as *Athous*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Porta (1929: 359): catalogue, distributional note [as *Leptoschema*]; Mertlik (2005: 171): comparison with other species; Cate (2007: 164): catalogue; Etzler (2019: 306): checklist; Németh (2019: 137): comparison with other species.

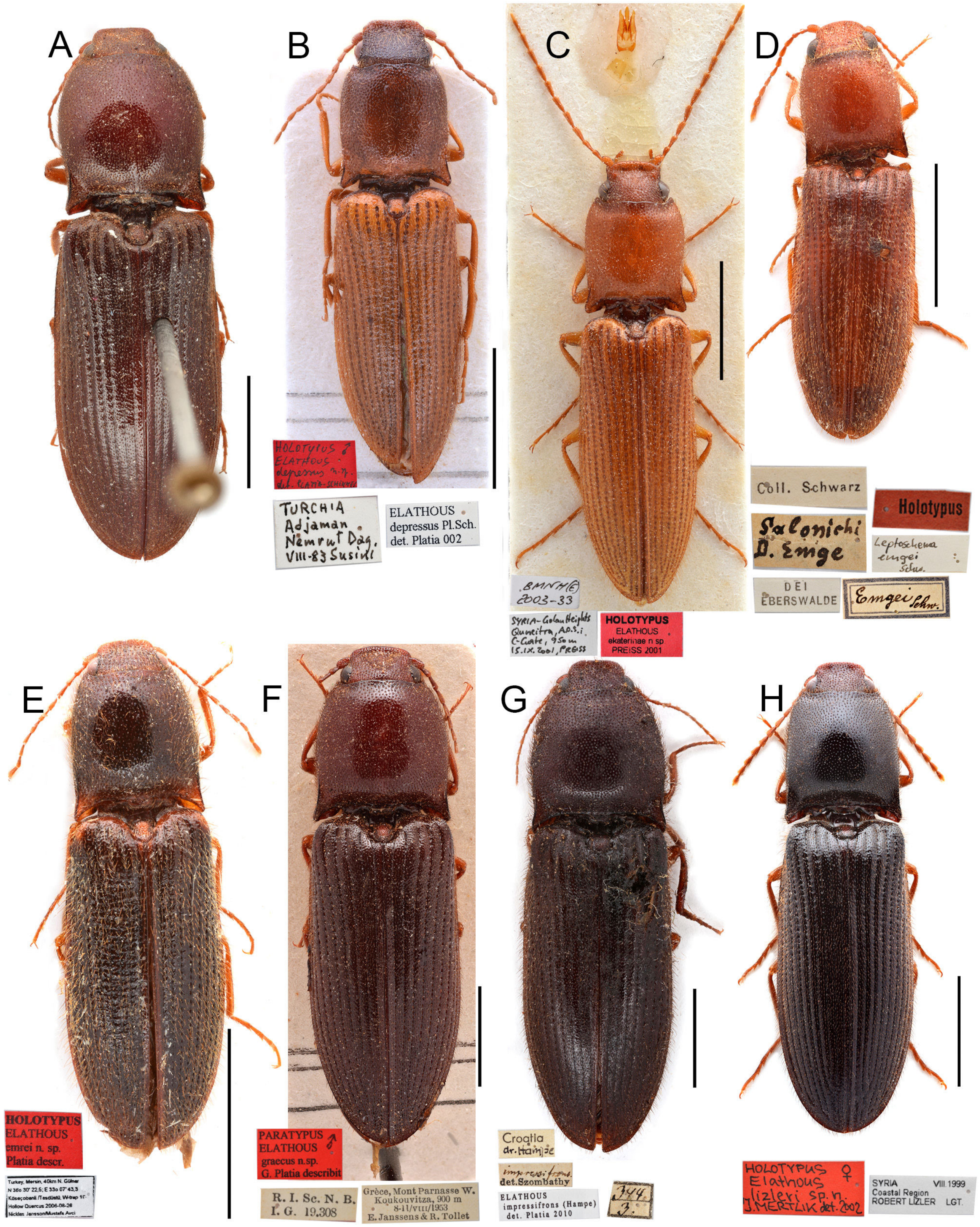

FIGURE 4. Palearctic species of genus *Elathous*. A, *E. cyprius* (Baudi di Selve, 1871), non-type specimen from Cyprus, male; B, *E. depressus* Platia & Schimmel, 1991, holotype, male; C, *E. ekaterinae* Preiss, 2003, holotype, male; D, *E. emgei* Schwarz, 1893, holotype, male; E, *E. emrei* Platia in Platia *et al*., 2011, holotype, male; F, *E. graecus* Platia, 2008, paratype, male; G, *E. impressifrons* (Hampe, 1866), non-type specimen from Croatia, female; I, *E. lizleri* Mertlik, 2005, holotype, female. Scale bars: 3.0 mm. Labels not to scale.

***Elathous lizleri* Mertlik**
(Fig. 4H)

Elathous lizleri Mertlik, 2005: 170.

Type depository. Holotype, female (PCJM); 1 paratype, female (PCJM).

Type locality. Syria: Coastal region.

Distribution. Syria.

Literature. Mertlik (2005: 168): original description and figures; Etzler (2019: 306): checklist; Németh (2019: 137): comparison with other species, figures of characters of holotype; Németh *et al*. (2020: 168, 172): comparison with other species.

***Elathous lizlerwerneri* Mertlik & Dušánek**
(Fig. 5A)

Elathous lizlerwerneri Mertlik & Dušánek, 2006: 152.

Type depository. Holotype, male (PCJM); allotype, female (PCJM).

Type locality. Turkey: Antalya Province, 24 km NE of Alanya, Köprülü env., 800 m.

Distribution. Turkey.

Literature. Mertlik & Dušánek (2006: 148, 151): original description and figures; Gülperçin & Tezcan (2010: 33): catalogue; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Platia *et al*. (2014: 44): comparison with other species; Nasserzadeh *et al*. (2018: 529): comparison with other species; Tarnawski *et al*. (2018: 117): catalogue; Etzler (2019: 306): checklist.

***Elathous maestrei* Zapata de la Vega & Sánchez-Ruiz**
(Fig. 5B)

Elathous maestrei Zapata de la Vega & Sánchez-Ruiz, 2012a: 108.

Type depository. Holotype, male (PCJZ).

Type locality. Spain: Teruel Province, Bronchales.

Distribution. Spain.

Literature. Zapata de la Vega & Sánchez-Ruiz (2012a: 108, 110): original description and figures; Zapata de la Vega & Sánchez-Ruiz (2013: 165, 184): catalogue, distributional map; Zapata de la Vega & Sánchez-Ruiz (2014: 160): catalogue; Zapata de la Vega & Sánchez-Ruiz (2015: 189): catalogue; Zapata de la Vega & Sánchez-Ruiz (2016: 200): catalogue; Zapata de la Vega & Sánchez-Ruiz (2017: 279): catalogue; Zapata de la Vega & Sánchez-Ruiz (2018: 35): catalogue; Etzler (2019: 306): checklist; Zapata de la Vega & Sánchez-Ruiz (2019: 77): catalogue.

***Elathous malatyanus* Etzler**
(Fig. 5C)

Elathous bicolor Platia, 2010: 27. Preoccupied by *Elathous bicolor* (LeConte, 1853: 428).
Elathous malatyanus Etzler, 2019: 306. Replacement name for *Elathous bicolor* Platia, 2010.

Type depository. Holotype, male (PCGP).

Type locality. Turkey: Malatya, Darende, 1570 m.

Distribution. Turkey.

Literature. Platia (2010: 27, 42, 46, 48): original description and figures; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Tarnawski *et al*. (2018: 116): catalogue; Etzler (2019: 306): checklist.

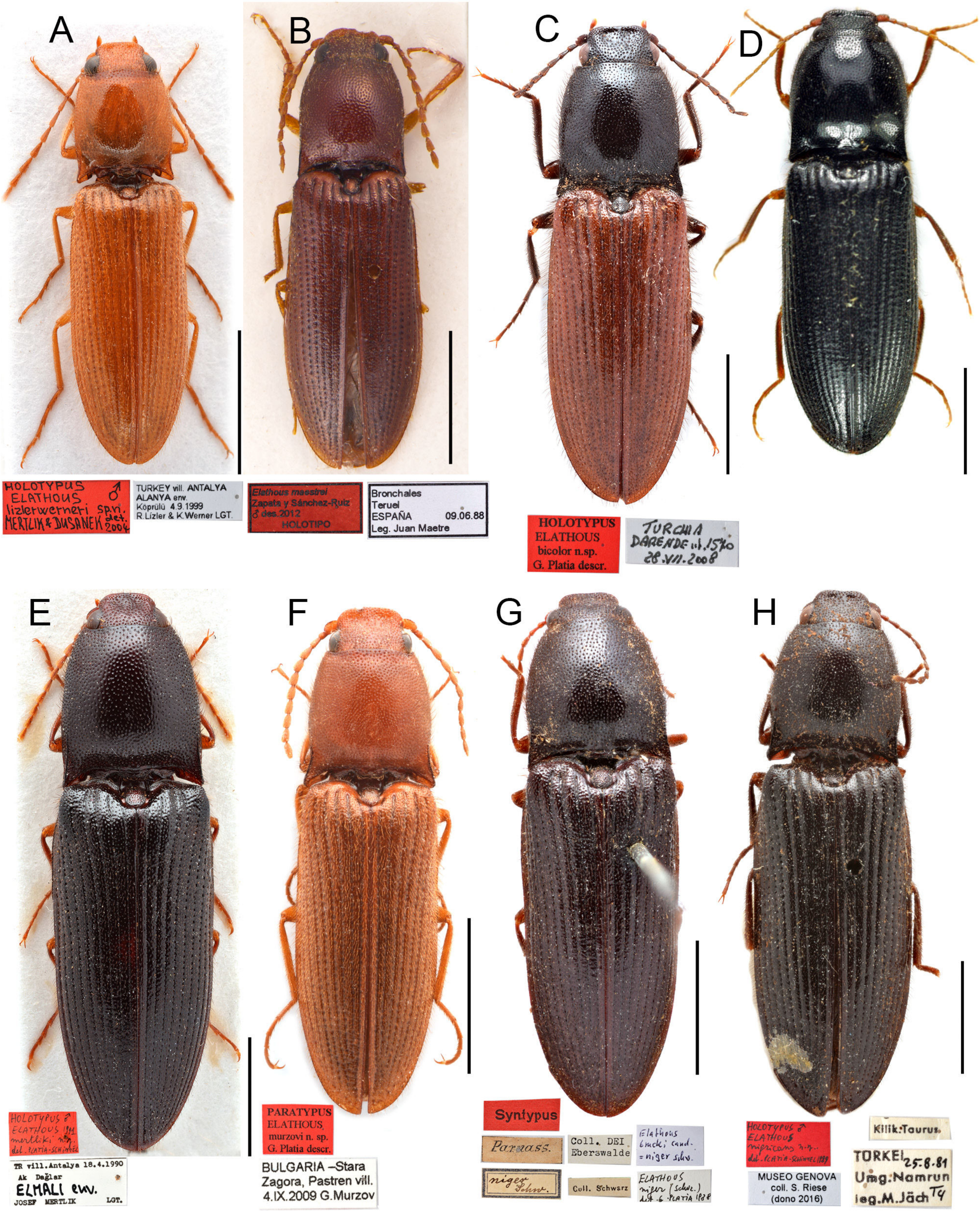

FIGURE 5. Palearctic species of genus *Elathous*. A, *E. lizlerwerneri* Mertlik & Dušánek, 2006, holotype, male; B, *E. maestrei* Zapata de la Vega & Sánchez-Ruiz, 2012, holotype, male; C, *E. malatyanus* Etzler, 2019 (replacement name for *E. bicolor* Platia, 2010), holotype, male; D, *E. melanarius* Platia & Kakiopoulos, 2014, holotype, male; E, *E. mertliki* Platia & Schimmel, 1992, holotype, male; F, *E. murzovi* Platia, 2010, paratype, male; G, *E. niger* Schwarz, 1897, syntype, male; H, *E. nigricans* Platia & Schimmel, 1991, holotype, male. Photograph B provided by M. París (MNCN), photograph D provided by G. Platia (Italy). Scale bars: 3.0 mm. Labels not to scale.

***Elathous melanarius* Platia & Kakiopoulos**
(Fig. 5D)

Elathous melanarius Platia & Kakiopoulos, 2014: 102.

Type depository. Holotype, male (PCGK).

Type locality. Greece: Attica, Mount Geraneia, 850 m.

Distribution. Greece.

Literature. Platia & Kakiopoulos (2014: 102, 104): original description and figures; Etzler (2019: 307): checklist; Németh (2019: 137): comparison with other species.

***Elathous mertliki* Platia & Schimmel**
(Fig. 5E)

Elathous mertliki Platia & Schimmel, 1992: 93.

Type depository. Holotype, male (PCJM).

Type locality. Turkey: Antalya Province, Elmalı, Ak Dağlar.

Distribution. Greece, Turkey.

Literature. Platia & Schimmel (1992: 92): original description and figures; Mertlik (2005: 171): comparison with other species; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 33): catalogue; Jarzabek-Müller (2013: 78): distributional note, figures of imago morphology; Kabalak *et al*. (2013: 88): distributional note, key, bionomics; Tarnawski *et al*. (2018: 117): catalogue; Etzler (2019: 307): checklist; Németh (2019: 137): comparison with other species.

***Elathous murzovi* Platia**
(Fig. 5F)

Elathous murzovi Platia, 2010: 27.

Type depository. Holotype, male (PCGM); 3 paratypes, males (PCGM, PCGP).

Type locality. Bulgaria: Pastren vill., Stara Zagora.

Distribution. Bulgaria.

Literature. Platia (2010: 27, 42, 46, 48): original description and figures; Etzler (2019: 307): checklist.

***Elathous niger* Schwarz**
(Fig. 5G)

Elathous niger Schwarz, 1897: 130.
Leptoschema nigra: Reitter, 1905: 24.
Leptoschema nigrum: Reitter, 1906: 399.
Elathous nigrum: Dolin, 1978: 51.

Type depository. Syntype, male (SDEI).

Type locality. Greece: Parnassos.

Distribution. Azerbaijan [dubious], Greece.

Literature. Schwarz (1897: 130): original description; Reitter (1905: 24, 115): review, key, catalogue [as *Leptoschema,* as possible syn. of *Athous brucki*]; Reitter (1906: 399): catalogue [as *Leptoschema,* as possible synonym of *Athous brucki*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1914: 87): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*, syn.

of *L. brucki* Candèze, 1878]; Schenkling (1927: 303): catalogue [as *Leptoschema*, syn. of *L. brucki*]; Agaev (1971: 38, 41): distributional record [as *Leptoschema*]; Dolin (1978: 49): larval key, figures of larval characters; Agaev (1980: 17, 20): key for larva and imago; Agaev (1986: 16): remark; Agaev (1988a: 543): distributional note; Agaev (1988b: 51): key, review; Platia & Schimmel (1991: 132): comparison with other species, key; Mertlik (2005: 171): comparison with other species; Cate (2007: 164): catalogue; Etzler (2019: 307): checklist; Németh (2019: 137): comparison with other species.

***Elathous nigricans* Platia & Schimmel**
(Fig. 5H)

Elathous nigricans Platia & Schimmel, 1991: 132.

Type depository. Holotype, male (MCNG); 6 paratypes: 5 males, 1 female (1 male: BMNH, 1 female: MCNG, 2 males: PCGP, 1 male PCPC; 1 male from Crete has not been located in any of the collections mentioned in the original description nor in the collections checked by authors).

Type locality. Turkey: Mersin prov., Çamlıyayla, Lampron castle (=Namrun Kalesi) env. [Umg. Namrun].

Distribution. Greece (Crete) [needs to be confirmed], Turkey.

Literature. Platia & Schimmel (1991: 132, 141): original description, key, figures; Mertlik (2005: 171): comparison with other species; Kesdek *et al*. (2006: 421): distributional record; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 34): catalogue; Sert & Kabalak (2011: 505): distributional note; Kabalak *et al*. (2013: 88): distributional note, key, bionomics; Gülperçin & Tezcan (2016: 134, 136, 138, 141): bionomics, distributional notes; Kabalak & Özbek (2018: 147): distributional note; Tarnawski *et al*. (2018: 117): catalogue; Etzler (2019: 307): checklist; Németh (2019: 137): comparison with other species.

***Elathous nurayae* Platia**
(Fig. 6A)

Elathous nurayae Platia in Platia *et al*., 2011: 207.

Type depositories. Holotype, male (PCGP); 2 paratypes, males (PCGP, PCNJ).

Type locality. Turkey: Egirdir, Yukangökdere, Kasnak forest.

Distribution. Turkey.

Literature. Platia *et al*. (2011: 207, 211, 213): original description and figures; Kabalak *et al*. (2013: 88): distributional note, key, bionomics; Gülperçin & Tezcan (2016: 134, 138, 141): bionomics, distributional notes; Kabalak & Özbek (2018: 147, 158): distributional note; Platia *et al*. (2018: 254): distributional note, bionomics; Tarnawski *et al*. (2018: 118): catalogue; Etzler (2019: 307): checklist.

***Elathous pavesii* Platia & Schimmel**
(Fig. 6B)

Elathous pavesii Platia & Schimmel, 1992: 94.

Type depository. Holotype, male (PCGP).

Type locality. Turkey: Mersin [Içel] Province, Çamlıyayla, 1200 m.

Distribution. Turkey.

Literature. Platia & Schimmel (1992: 94): original description; Platia & Schimmel (1993: 52): comparison with other species; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 34): catalogue; Kabalak *et al*. (2013: 87): distributional map, key, comparison with other species, figure of aedeagus; Tarnawski *et al*. (2018: 118): catalogue; Etzler (2019: 307): checklist.

***Elathous perrisii* (Desbrochers des Loges)**
(Fig. 6C)

Athous perrisii Desbrochers des Loges, 1873: 366.
Athous amicus Perris, 1875: 4; synonymized with *Athous revelieri* Mulsant & Rey, 1875 by Reitter (1905: 20).
Athous revelieri Mulsant & Rey, 1875: 416; synonymized with *Athous perrisii* Desbrochers des Loges, 1873 by Reitter (1905: 20).
Athous perrisi: Marseul, 1887: 261 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathouina revelierei: Reitter, 1905: 20 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Athouinus [sic!] *amictus*: Reitter, 1905: 114 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Athouinus [sic!] *perrisi*: Reitter, 1905: 114 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Athouinus [sic!] *revelieri*: Reitter, 1905: 114.
Athoina [sic!] *amica*: Reitter, 1906: 399.
Athoina [sic!] *perrisi*: Reitter, 1906: 399 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Athoina [sic!] *revelierei* [sic!]: Reitter, 1906: 399 [unavailable name, incorrect subsequent spelling not in prevailing usage]..
Elathouina perrisi: Jakobson, 1913: 757 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathouina revelieri: Jakobson, 1913: 757.
Elathouina amica: Jakobson, 1913: 757.
Leptoschema perrisi: Cobos, 1969: 12 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Leptoschema revelieri: Cobos, 1969: 12.
Elathous perrisii: Cate, 2007: 164.
Elathous perrisi: Zapata de la Vega & Sánchez-Ruiz, 2007: 222 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathous perisii: Löbl & Smetana, 2008: 24 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. *Elathous perrisii*. Type, male (MNHN?). *Athous amicus*. Unknown number and sex (MNHN?). *Athous revelieri*. Unknown number of female syntypes (MNHN?).

Type locality. *Elathous perrisii*. France: Corsica. *Athous amicus*. France: Corsica. *Athous revelieri*. France: Corsica.

Distribution. France (Corsica), Italy (Sardinia).

Literature. Desbrochers des Loges (1873: 366): original description of *A. perrisii*; Perris (1875: 4): original description of *A. amicus*; Mulsant & Rey (1875a: 416): original description of *A. revelieri*; Mulsant & Rey (1875b: 81): redescription [as description] of *A. revelieri*; Marseul (1887: 261): catalogue [as *Athous*]; Stein & Weise (1877: 95): catalogue [as *Athous*]; Candèze (1891: 153, 155): catalogue [as *Athous*]; Reitter (1891: 207): catalogue [as *Athous*]; Buysson (1902b: 15): catalogue [as *Athou*s]; Bertolini (1904: 68): catalogue [as *Athous*]; Reitter (1905: 20, 114): review, catalogue [as *Elathouina* and *Athouinus*]; Reitter (1906: 399): catalogue [as *Athoina*]; Schwarz (1906: 197): catalogue [as *Elathouina*]; Jakobson (1913: 757): catalogue [as *Elathouina*]; Sainte-Claire-Deville (1914: 290): catalogue [as *Athous*]; Hyslop (1921: 644): remark [as *Elathouina*]; Buysson (1925: 598): catalogue [as *Elathouina*]; Schenkling (1927: 304): catalogue [as *Elathouina*]; Luigioni (1929: 561): catalogue [as *Elathouina*]; Porta (1929: 359): catalogue [as *Elathouina*]; Sainte-Claire-Deville (1935: 220): catalogue [as *Elathouina*]; Kocher (1956: 100): catalogue [doubtful identification] [as *Elathouina*]; Cobos (1969: 12, 14): figures of characters of imago, key, comparison with other species [as *Leptoschema*]; Leseigneur (1972: 173, 183): catalogue, figures of aedeagus [as *Elathouina*]; Pesarini (1986: 26, 40): catalogue, review, figure of habitus of imago [as *Elathouina*]; Platia (1994: 106): review, figures of characters of imago; Gobbi & Platia (1995: 4): catalogue; Cate (2007: 164): catalogue; Zapata de la Vega & Sánchez-Ruiz (2007: 223): comparison with other species, figures of characters of imago; Löbl & Smetana (2008: 24): taxonomic note; Platia (2011: 834): distributional notes; Leseigneur (2014: 431): catalogue; Delnatte *et al*. (2015: 43): distributional and taxonomic notes; Rousette & Delnatte (2016: 175): bionomics; Etzler (2019: 307): checklist.

***Elathous platiai* Zapata de la Vega & Sánchez-Ruiz**
(Fig. 6D)

Elathous platiai Zapata de la Vega & Sánchez-Ruiz, 2007: 221.

Type depositories. Holotype, male (PCJZ); 35 paratypes: 6 males (PCJZ), 5 males (PCJB), 12 males (PCGP), 5 males (BMNH), 5 males, 1 female (MNCN), 1 male (HNHM).

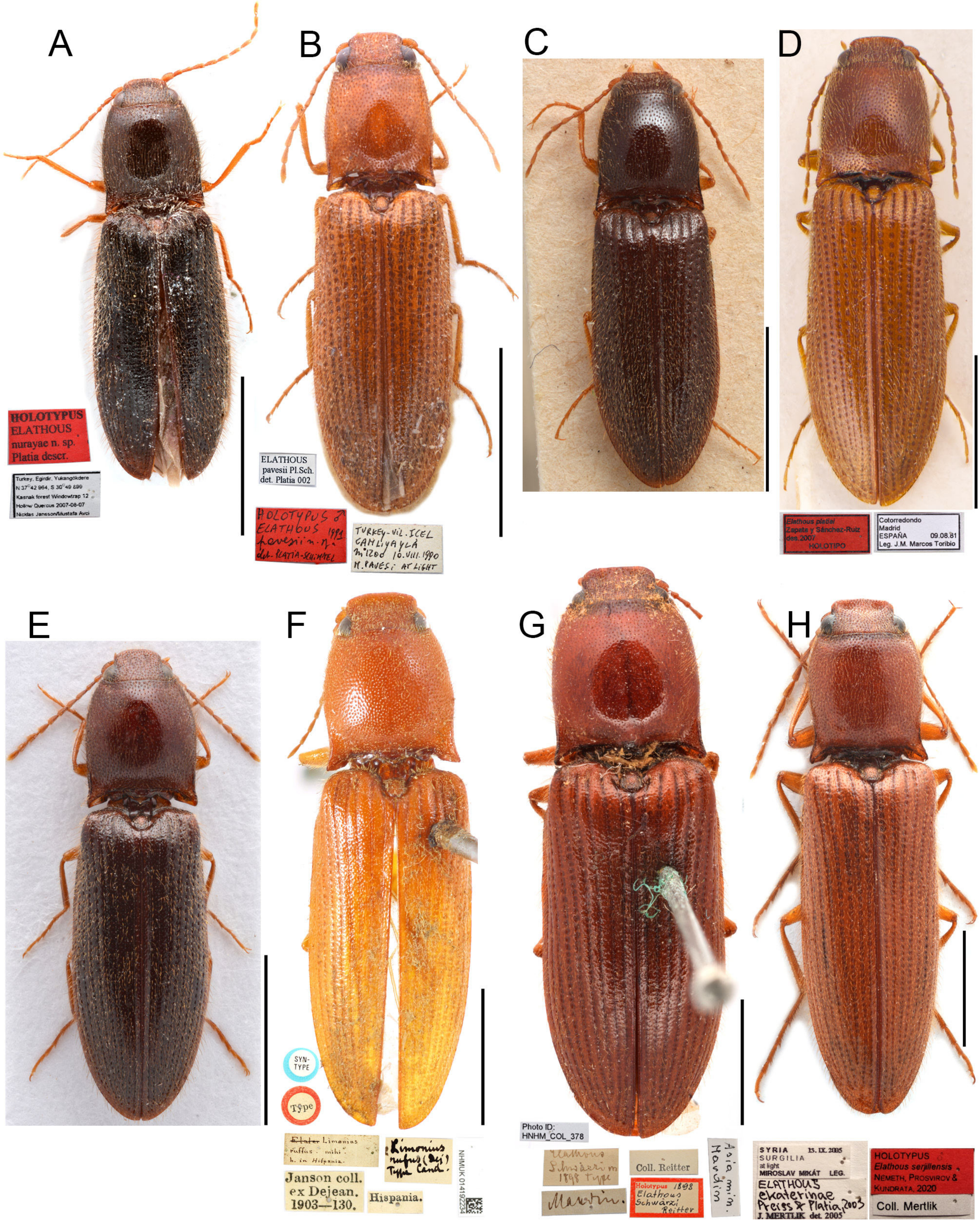

FIGURE 6. Palearctic species of genus *Elathous*. A, *E. nurayae* Platia in Platia *et al*., 2011, holotype, male; B, *E. pavesii* Platia & Schimmel, 1992, holotype, male; C, *E. perrisii* (Desbrochers des Loges, 1873), non-type specimen, male; D, *E. platiai* Zapata de la Vega & Sánchez-Ruiz, 2007, holotype, male; E, *E. rufobasalis* Wurst, 1994, non-type specimen from Turkey, female; F, *E. rufus* (Candèze, 1860), syntype, male; G, *E. schwarzi* Reitter, 1898, syntype [erroneously labelled as holotype by the former HNHM curator], male; H, *E. serjillensis* Németh, Prosvirov & Kundrata, 2020, holotype, male. Photograph D provided by M. París (MNCN), photograph F provided by K. Matsumoto (BMNH). Scale bars: 3.0 mm. Labels not to scale.

Type locality. Spain: Madrid, Cotorredondo.

Distribution. Spain.

Literature. Zapata de la Vega & Sánchez-Ruiz (2007: 221): original description; Zapata de la Vega & Sánchez-Ruiz (2012a: 108): comparison with other species, figures of characters of imago; Zapata de la Vega & Sánchez-Ruiz (2012b: 166, 260): catalogue, distributional map; Zapata de la Vega & Sánchez-Ruiz (2013: 184): catalogue; Sáez Bolaño *et al*. (2014: 136): distributional note, distributional map; Zapata de la Vega & Sánchez-Ruiz (2014: 160): catalogue; Zapata de la Vega & Sánchez-Ruiz (2015: 165, 189): catalogue, distributional map; Zapata de la Vega & Sánchez-Ruiz (2016: 200): catalogue; Zapata de la Vega & Sánchez-Ruiz (2017: 279): catalogue; Zapata de la Vega & Sánchez-Ruiz (2018: 21, 35): catalogue, distributional map; Etzler (2019: 307): checklist; Zapata de la Vega & Sánchez-Ruiz (2019: 56, 77): catalogue, distributional map.

Elathous rufobasalis **Wurst**

(Fig. 6E)

Elathous rufobasalis Wurst, 1994: 62.

Type depository. Holotype, male (PCCW).

Type locality. Turkey: Isparta Province, ca. 50 km N Eğirdir [misspelled as Eğridir], Kovada Hes, 1100 m.

Distribution. Turkey.

Literature. Wurst (1994: 62): original description; Mertlik (2005: 171): comparison with other species; Platia & Gudenzi (2005: 114): comparison with other species; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 34): catalogue; Platia *et al*. (2011: 207): comparison with other species; Atay *et al*. (2012: 110): distributional note, bionomics; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Gülperçin & Tezcan (2016: 134, 138, 141): bionomics, distributional notes; Kabalak & Özbek (2018: 147, 159, 165): distributional note, taxonomic note, figures of characters of imago; Tarnawski *et al*. (2018: 118): catalogue; Etzler (2019: 307): checklist.

Elathous rufus **(Candèze)**

(Fig. 6F)

Limonius russus Dejean, 1836: 102 [unavailable name, published without description, ICZN (1999); as a synonym of *L. rufus* Candèze, 1860 in Gemminger & Harold (1869: 1563)]
Limonius rufus Candèze, 1860: 384.
Simonius [sic!] *rufus* Dej.: Stierlin, 1864: 192.
Elathous rufus: Buysson, 1902a: 275.
Leptoschema rufa: Reitter, 1905: 23.
Elathous barrosi Reitter, 1905: 23 [unavailable name; in litteris].
Leptoschema rufum: Reitter, 1906: 399.

Type depository. Syntype, male (BMNH).

Type locality. Spain.

Distribution. Portugal, Spain.

Literature. Dejean (1836: 102): catalogue [as *Limonius*; unavailable name]; Candèze (1860: 379, 384): key, original description [as *Limonius*]; Marseul (1863: 143): catalogue [as *Limonius*]; Stierlin (1864: 192): key [as *Simonius* (sic!)]; Stein (1868: 66): catalogue [as *Limonius*]; Gemminger & Harold (1869: 1563): catalogue [as *Limonius*]; Stein & Weise (1877: 94): catalogue [as *Limonius*]; Jäger (1883: 338): catalogue; Marseul (1887: 259): catalogue [as *Limonius*]; Candèze (1891: 146): catalogue [as *Limonius*]; Reitter (1891: 206): catalogue [as *Limonius*]; Oliveira (1893: 193): catalogue [as *Limonius*]; Buysson (1902a: 275): taxonomic note, comparison with other species; Reitter (1905: 23, 115): review, key, catalogue [as *Leptoschema*]; Reitter (1906: 399): catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1914: 87): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Buysson (1926: 163): remark [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Fuente (1930: 60): catalogue [as *Leptoschema*]; Seabra (1939: 226): catalogue [as *Leptoschema*]; Seabra (1943: 60): catalogue [as *Leptoschema*];

Cobos (1969: 14): key [as *Leptoschema*]; Sánchez-Ruiz (1996: 107, 197): catalogue; Platia & Serrano (2002: 312, 321): distributional note, figures of imaginal characters; Cate (2007: 164): catalogue; Zapata de la Vega & Sánchez-Ruiz (2007: 223): distributional note, comparison with other species, figures of characters of imago; Zapata de la Vega & Sánchez-Ruiz (2012a: 108): comparison with other species, figures of characters of imago; Zapata de la Vega & Sánchez-Ruiz (2012b: 166, 260): catalogue, distributional map; Zapata de la Vega & Sánchez-Ruiz (2013: 184): catalogue; Zapata de la Vega & Sánchez-Ruiz (2014: 138, 160): catalogue, distributional map; Zapata de la Vega & Sánchez-Ruiz (2015: 189): catalogue; Zapata de la Vega & Sánchez-Ruiz (2016: 200): catalogue; Zapata de la Vega & Sánchez-Ruiz (2017: 279): catalogue; Zapata de la Vega & Sánchez-Ruiz (2018: 21, 35): catalogue, distributional map; Etzler (2019: 307): checklist; Zapata de la Vega & Sánchez-Ruiz (2019: 56, 77): catalogue, distributional map.

Elathous schwarzi **Reitter**
(Fig. 6G)

Elathous schwarzi Reitter, 1898: 346.
Leptoschema schwarzi: Reitter, 1905: 22.

Type depositories. Syntype [erroneously labelled as holotype by the former HNHM curator], male (HNHM); syntype, male (SDEI).

Type locality. Turkey: Mardin.

Distribution. Turkey.

Literature. Reitter (1898: 346): original description; Reitter (1905: 22, 115): review, key, catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 34): catalogue; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Tarnawski *et al*. (2018: 118): catalogue; Etzler (2019: 307): checklist; Németh *et al*. (2020: 168, 172): comparison with other species.

Elathous serjillensis **Németh, Prosvirov & Kundrata**
(Fig. 6H)

Elathous serjillensis Németh, Prosvirov & Kundrata, 2020: 168.

Type depository. Holotype, male (PCJM); paratype, male (PCJM).

Type locality. Syria: Surgilia [Serjilla, 35°40’17”N, 36°34’59”E].

Distribution. Syria.

Literature. Németh *et al*. (2020: 168): original description and figures.

Elathous serti **Kabalak, Avcı & Platia**
(Fig. 7A)

Elathous serti Kabalak, Avcı & Platia in Kabalak *et al*., 2013: 86.

Type depositories. Holotype, male (HUZOM); 17 paratypes: 7 males, 9 females (HUZOM), 1 male (PCGP).

Type locality. Turkey: Isparta Province, Aşağıgökdere village.

Distribution. Turkey.

Literature. Kabalak *et al*. (2013: 86): original description, bionomics; Tarnawski *et al*. (2018: 119): catalogue; Etzler (2019: 307): checklist.

Elathous smyrnensis Schwarz
(Fig. 7B)

Elathous smyrnensis Schwarz, 1903: 207.
Leptoschema smyrnensis: Reitter, 1905: 23.
Leptoschema smyrnense: Jakobson, 1913: 757.

Type depository. Syntype, female (SDEI).

Type locality. Turkey: Izmir [Smyrna].

Distribution. Turkey.

Literature. Schwarz (1903: 207): original description; Reitter (1905: 23, 115): review, key, catalogue [as *Leptoschema*]; Schwarz (1906: 197): catalogue [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Wurst (1994: 62): comparison with other species; Cate (2007: 164): catalogue; Gülperçin & Tezcan (2010: 34): catalogue; Tezcan *et al*. (2010: 66): distributional note; Kabalak *et al*. (2013: 88): distributional map, key, bionomics; Tarnawski *et al*. (2018: 119): catalogue; Etzler (2019: 307): checklist.

Elathous syriacus Schwarz
(Fig. 7C)

Elathous syriacus Schwarz, 1903: 208.
Leptoschema syriaca: Reitter, 1905: 23.
Leptoschema syriacum: Jakobson, 1913: 757.

Type depository. Lectotype, male (SDEI).

Type locality. Lebanon [Syria]: Beirut.

Distribution. Lebanon, Syria [needs to be confirmed].

Literature. Schwarz (1903: 208): original description; Reitter (1905: 23, 115): review, key, catalogue [as *Leptoschema*]; Schwarz (1906: 197, pl. 5): catalogue, figure of habitus of imago [as *Leptoschema*]; Jakobson (1913: 757): catalogue [as *Leptoschema*]; Buysson (1925: 598): catalogue [as *Leptoschema*]; Schenkling (1927: 303): catalogue [as *Leptoschema*]; Platia & Schimmel (1992: 94): comparison with other species; Cate (2007: 164): catalogue; Platia (2010: 27) comparison with other species; Etzler (2019: 307): checklist; Németh (2019: 136, 146): distributional record, figure of habitus of imago; Németh *et al*. (2020: 168, 172): comparison with other species.

Elathous talassemtani Németh & Platia
(Fig. 7D)

Elathous talassemtani Németh & Platia in Németh *et al*., 2015: 92.

Type depositories. Holotype, male (HNHM); 8 paratypes: 1 male, 2 females (HNHM), 2 males (CCRF), 2 males (PCHB), 1 male (PCGP).

Type locality. Morocco: 12 km SE of Chefchaouen, NP Talassemtane, N35°7’59”, W5°8’22”.

Distribution. Morocco.

Literature. Németh *et al*. (2015: 92, 95): original description; Benyahia *et al*. (2016: 8): checklist; Etzler (2019: 307): checklist.

Elathous tezcani Platia
(Fig. 7E)

Elathous tezcani Platia in Platia *et al*., 2014: 44.

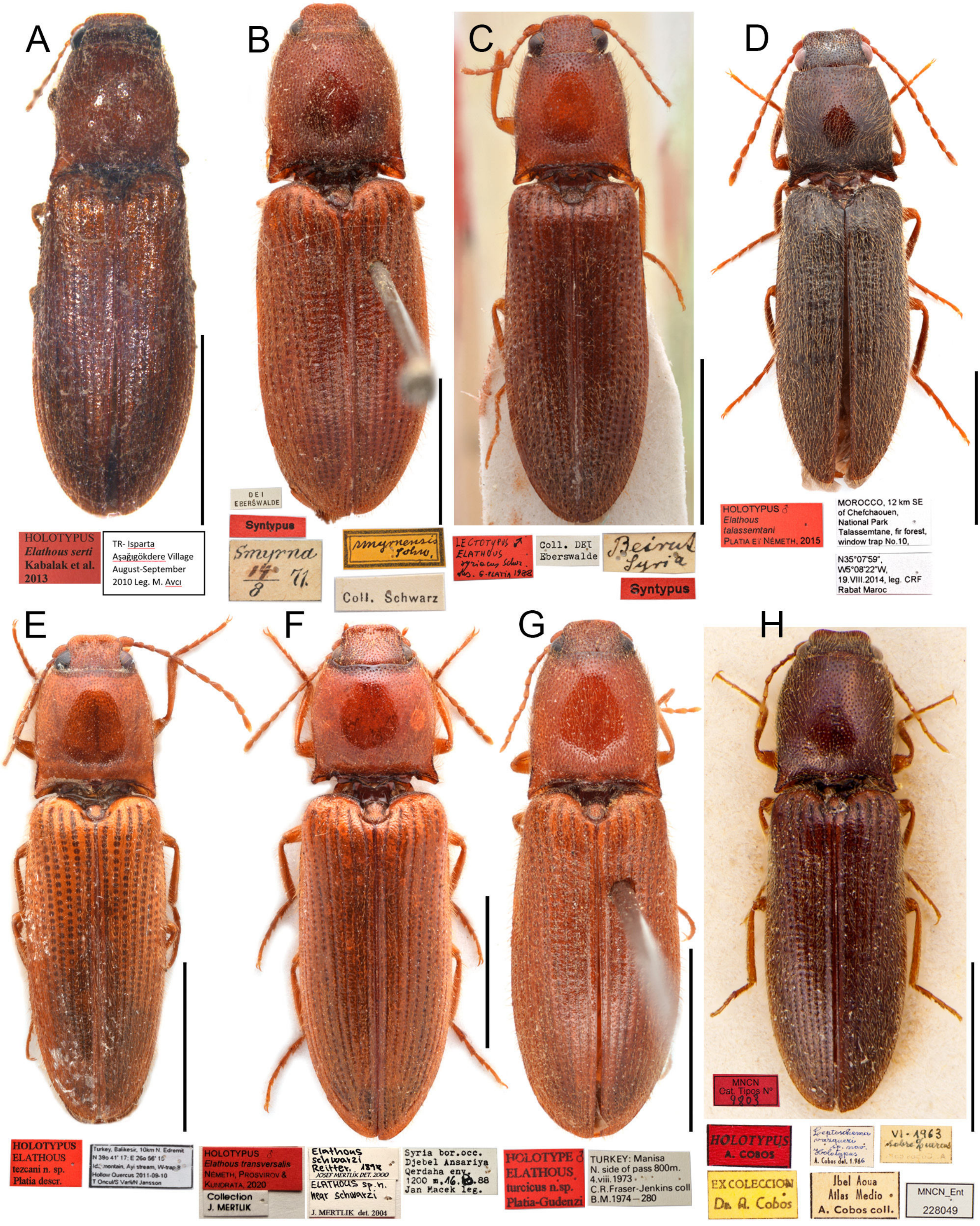

FIGURE 7. Palearctic species of genus *Elathous*. A, *E. serti* Kabalak, Avcı & Platia in Kabalak *et al*., 2013, holotype, male; B, *E. smyrnensis* Schwarz, 1903, syntype, female; C, *E. syriacus* Schwarz, 1903, lectotype, male; D, *E. talassemtani* Németh & Platia in Németh *et al*., 2015, holotype, male; E, *E. tezcani* Platia in Platia *et al*., 2014, holotype, male; F, *E. transversalis* Németh, Prosvirov & Kundrata, 2020, holotype, male; G, *E. turcicus* Platia & Gudenzi, 2005, holotype, male; H, *E. vazquezi* (Cobos, 1969), holotype, male. Photograph A provided by M. Kabalak (Turkey), photograph H provided by M. París (MNCN). Scale bars: 3.0 mm. Labels not to scale.

Type depository. Holotype, male (PCGP).

Type locality. Turkey: Balikesir, 10 km N Edremit, 39°41’17”N, 26°56’15”E.

Distribution. Turkey.

Literature. Platia *et al*. (2014: 44, 47): original description; Tarnawski *et al*. (2018: 119): catalogue; Etzler (2019: 307): checklist.

Elathous transversalis Németh, Prosvirov & Kundrata
(Fig. 7F)

Elathous transversalis Németh, Prosvirov & Kundrata, 2020: 171.

Type depository. Holotype, male (PCJM).

Type locality. Syria: Djebel Ansariya, Qerdaha [Jebel Ansariya, Qardaha] env.

Distribution. Syria.

Literature. Németh *et al*. (2020: 171): original description and figures.

Elathous turcicus Platia & Gudenzi
(Fig. 7G)

Elathous turcicus Platia & Gudenzi, 2005: 114.

Type depository. Holotype, male (PCGP).

Type locality. Turkey: Manisa, N side of pass, 800 m.

Distribution. Turkey.

Literature. Platia & Gudenzi (2005: 113, 117): original description and figures; Gülperçin & Tezcan (2010: 34): catalogue; Kabalak *et al*. (2013: 87): distributional map, key, comparison with other species, figure of aedeagus, bionomics; Tarnawski *et al*. (2018: 119): catalogue; Etzler (2019: 307): checklist.

Elathous vazquezi (Cobos)
(Fig. 7H)

Leptoschema boiteli Kocher, 1956: 100 [unavailable name; attributed to Buysson, in litteris].
Leptoschema vazquezi Cobos, 1969: 11.
Elathous vasquezi: Cate, 2007: 164 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Elathous vazquezi: Zapata de la Vega & Sánchez-Ruiz (2007: 222).

Type depository. Holotype, male (MNCN).

Type locality. Morocco: Moyen Atlas, J’bel Aoua.

Distribution. Morocco.

Literature. Cobos (1969: 11): original description, key [as *Leptoschema*]; Cate (2007: 164): catalogue; Zapata de la Vega & Sánchez-Ruiz (2007: 223): comparison with other species, figures; Németh *et al*. (2015: 93, 95): comparison with other species, figures; Etzler (2019: 307): checklist.

Elathous yamamotoi Ôhira
(Fig. 8A)

Elathous yamamotoi Ôhira, 1995: 189.

Type depository. Holotype, female (NMNS).

Type locality. Japan: Honshu, Wakayama Pref., Mt. Gomanodan.

Distribution. Japan.

Literature. Ôhira (1995: 189): original description; Kishii (1999: 26): catalogue; Cate (2007: 164): catalogue; Toyoshima (2007: 43): distributional note, figure of habitus of imago; Hiramatsu (2011: 43): distributional note, figure of habitus of imago; Etzler (2019: 307): checklist.

Elathous zagrosensis Nasserzadeh & Platia
(Fig. 8B)

Elathous zagrosensis Nasserzadeh & Platia in Nasserzadeh *et al*., 2018: 528.

Type depository. Holotype, male (HMIM); 2 paratypes, males (HMIM, PCGP).

Type locality. Iran: Ilam Province, 40 km NW of Ilam city, Ghallajeh.

Distribution. Iran.

Literature. Nasserzadeh *et al*. (2018: 528): original description.

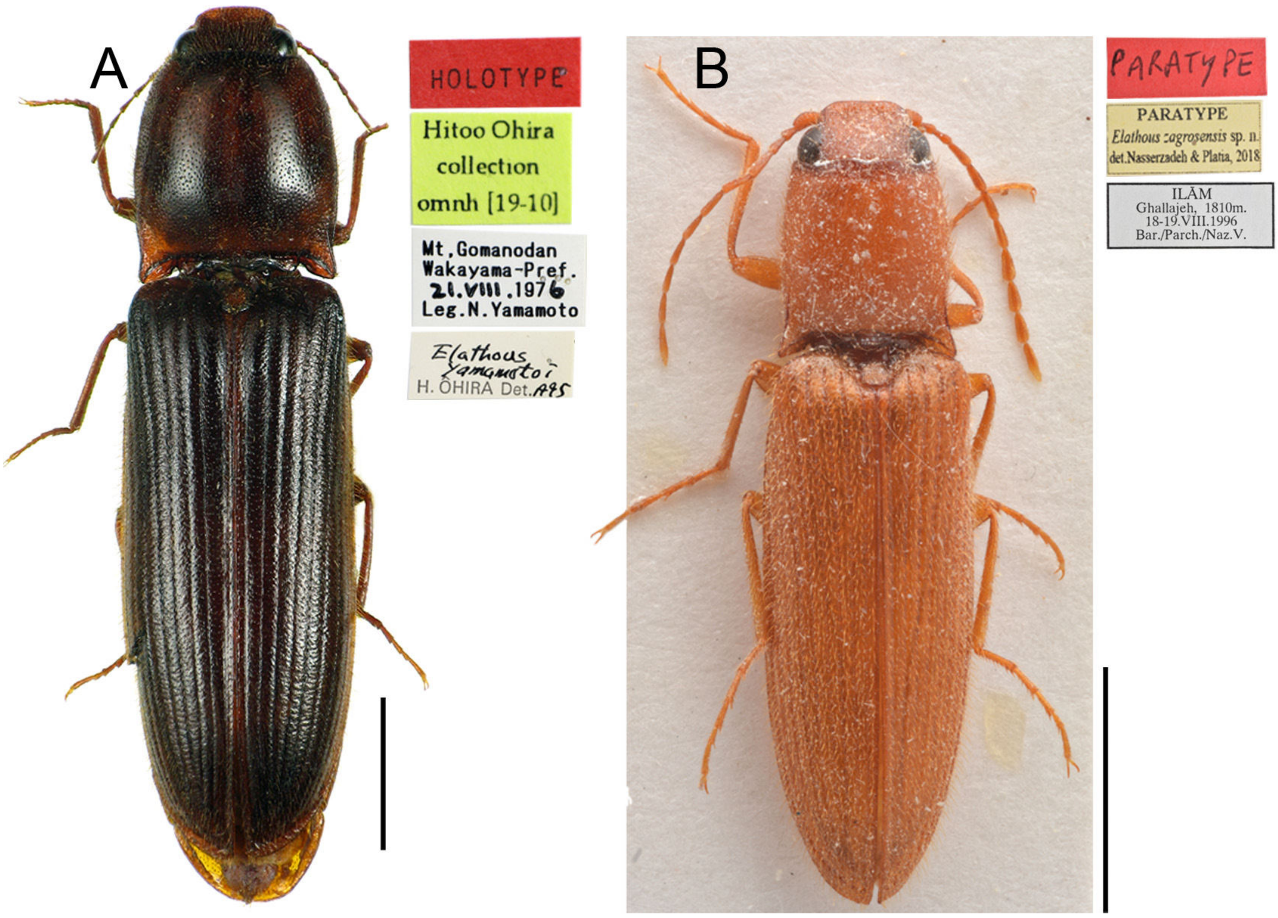

FIGURE 8. Type specimens of Palearctic *Elathous* species. A, *E. yamamotoi* Ôhira, 1995, holotype, female; B, *E. zagrosensis* Nasserzadeh & Platia in Nasserzadeh *et al*., 2018, paratype, male. Photograph A provided by H. Arimoto (Japan). Scale bars: 3.0 mm. Labels not to scale.

Discussion

We present here the first comprehensive catalogue of the genus *Elathous*. Although this genus had a rather chaotic history of its limits and classification, it is now relatively well-defined and settled in the system (e.g., Kabalak *et al*. 2013, Etzler 2019). However, all studies on this genus so far were based on the limited material with regard to the geographic sampling, and therefore, a comprehensive alpha-taxonomic revision is needed to confirm the limits of this genus. There are three geographically distinct groups of species, i.e., North American, Japanese and Mediterranean. The North American species were all described quite early, in the 19th and the first half of the 20th century, and after the revision and a key by Van Dyke (1932), species of North American *Elathous* were treated only occasionally (Fall 1934, Becker 1961, Etzler 2019). Two Japanese species are currently under revisionary study by H. Arimoto (personal communication). The Mediterranean is the center of diversity of the genus, and recently many new species were described (e.g., Platia *et al*. 2011, Kabalak *et al*. 2013, Nasserzadeh *et al*. 2018, Németh *et al*. 2020), although there are many single-specimen or single-population descriptions which might be problematic when much more material from all species and the Mediterranean subregions are examined for a revision. It is necessary to understand the intra- and interspecific variability in *Elathous* in order to establish a natural classification. Furthermore, based on the general habitus and shape of male genitalia, there are at least two large species groups in the Mediterranean *Elathous* (Etzler 2019; personal observations of authors). From all above mentioned remarks it is clear that a revision of *Elathous* is the next step to improve the systematics of the genus and closely related taxa.

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References

Agaev, B.I. (1971) Materialy k izucheniyu zhukov-shchelkunov (Coleoptera, Elateridae) yugo-vostochnoy chasti Azerbaydzhana [On click-beetles (Coleoptera, Elateridae) of southeastern Azerbaijan]. *Scientific reports of Azerbaijan State University, Biological Sciences Series*, 4, 38–42. [in Russian]

Agaev, B.I. (1980) *Faunistichesky sostav zhukov-shchelkunov Vostochnogo Azerbaydzhana* [Fauna of click-beetles of eastern Azerbaijan]. Azerbaijan research institute of scientific and technical information and techno-economic research of Gosplan of Azerbaijan SSR. Agriculture series, Baku, 32 pp. [in Russian]

Agaev, B.I. (1986) K voprosu o genezise elateridofauny (Coleoptera, Elateridae) Kavkaza [On the origin of fauna of click-beetles (Coleoptera, Elateridae) of Caucasus]. *In*: Terteryan, A.E. & Martinyan, T.K. (Eds.), *First Transcaucasian Entomological Conference (Erevan, 17–19 November 1986): abstracts*. Academy of Sciences of Armenian SSR Publishing House, Yerevan, pp. 15–16. [in Russian]

Agaev, B.I. (1988a) Zoogeographic analysis of click beetles (Coleoptera, Elateridae) from the East Transcaucasus. *Zoologichesky zhurnal*, 67 (4), 539–547. [in Russian]

Agaev, B.I. (1988b) *Zhestkokrylye-shchelkuny v biotsenozah Azerbaydzhana* [Click-beetles in biocenosis of Azerbaijan]. Azerbaijan state publishing house, Baku, 120 pp. [in Russian]

Agaev, B.I. & Dolin, V.G. (1991) Zhachenie lichinochnyh form v sistematike triby Athoini (Coleoptera, Elateridae) [Significance of larval characters in systematics of the tribe Athoini (Coleoptera, Elateridae)]. *In*: Dolin, V.G. (Ed.), *12th International Symposium on the Entomofauna of Central Europe. Kiev, 25–30 September 1988. Abstracts*. Naukova Dumka, Kiev, pp. 306–310.

Al Dhafer, H.M. (2009) Revision of the North American species of *Limonius* (Coleoptera: Elateridae). *Transactions of the American Entomological Society*, 135 (3), 209–352.
https://doi.org/10.3157/061.135.0301

Arimoto, H. (2010) [Record of *Elathous brunneus* from Tokyo]. *Coleopterists' News*, 169, 11. [in Japanese]

Arnett, R.H., Jr. (1955) Supplement and corrections to J. A. Hyslop's genotypes of the elaterid beetles of the world. *Proceedings*

of the United States National Museum, 103 (3336), 599–619.
https://doi.org/10.5479/si.00963801.3336.599

Arnett, R.H., Jr. (1962) Elateridae Leach, 1815. The click beetles. *In*: Arnett, R.H.Jr. (Ed.), *The beetles of the United States (a manual for identification). Pt. 3. Fasc. 46*. The Catholic University of America Press, Washington, D.C., pp. 497–512.

Arnett, R.H., Jr. (1971) Elateridae (Leach, 1815). The click beetles. *In*: Arnett, R.H.Jr. (Ed.), *The beetles of the United States (a manual for identification). Pt. 3. Fasc. 46*. The American Entmological Institute, Ann Arbor, Michigan, pp. 497–512.

Atay, E., Jansson, N. & Gürkan, T. (2012) Saproxylic beetles on old hollow oaks (*Quercus* spp.) in a small isolated area in southern Turkey. *Zoology in the Middle East*, 57, 105–114.
https://doi.org/10.1080/09397140.2012.10648969

Baudi di Selve, F. (1871) Coleopterorum messis in insula Cypro et Asia minore ab Eugenio Truqui congregatae recensitio: de Europaeis notis quibusdam additis. Pars quarta. *Berliner entomologische Zeitschrift*, 15, 49–71.
https://doi.org/10.1002/mmnd.18710150113

Baudi di Selve, F. (1873) Rassegna entomologica. *Bullettino della Società entomologica italiana*, 5 (2), 98–123.

Becker, E.C. (1961) The North American elaterid types of Otto Schwarz, with a revision of *Ctenicera bivittata* (Melsheimer) and allies (Coleoptera). *The Canadian Entomologist*, 93 (3), 161–181.
https://doi.org/10.4039/Ent93161-3

Becker, E.C. (1974) Revision of the nearctic species of *Athous* (Coleoptera: Elateridae) east of the Rocky Mountains. *The Canadian Entomologist*, 106 (7), 711–758.
https://doi.org/10.4039/Ent106711-7

Becker, E.C. (1979) Review of the western nearctic species of *Athous* (Coleoptera: Elateridae), with a key to the species north of Panama. *The Canadian Entomologist*, 111 (5), 569–614.
https://doi.org/10.4039/Ent111569-5

Benyahia, Y., Brustel, H., El Antry, S., Courtin, O., Maatouf, N., Valladares, L. & Rohi, L. (2016) Preliminary list of Coleoptera heritage species of the Talassemtane National Park, Morocco. *Journal of Insect Biodiversity*, 4 (13), 1–30.
https://doi.org/10.12976/jib/2015.4.13

Bertolini, S. (1904) *Catalogo dei Coleotteri d'Italia compilato dal Dr. Stefano Bartolini edito dalla "Rivista Italiana di Scienze naturali"*. Tipografia e Litografia Sordo-Muti di L. Lazzeri, Siena, 144 pp. [1899–1904]

Blackwelder, R.E. (1939) *Fourth supplement 1933 to 1938 (inclusive) to the Leng Catalogue of Coleoptera of America, north of Mexico*. John D. Sherman, Jr., Mount Vernon, New York, 146 pp.

Blackwelder, R.E. (1974) *Checklist of the Elateridae of Canada, United States, Mexico, Central America and the West Indies. North American Beetle Fauna Project. Family no. 46. Complete. Red Version*. Biological Research Institute of America, Inc., New York, 55 pp.

Blatchley, W.S. (1910) *An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhyncophora) known to occur in Indiana*. The Nature Publishing Co, Indianapolis, Indiana, 1386 pp.
https://doi.org/10.5962/bhl.title.56580

Bousquet, Y. (1991) Family Elateridae: click beetles. *In*: Bousquet, Y. (Ed.), *Checklist of Beetles of Canada and Alaska*. Agriculture Canada, Ottawa, Ontario, pp. 175–185.

Bousquet, Y. (1993) On Thomas Say's entomological publications printed in New Harmony, Indiana. *Entomological news*, 104 (1), 1–14.

Bousquet, Y., Bouchard, P., Davies, A.E. & Sikes, D.S. (2013) *Checklist of beetles (Coleoptera) of Canada and Alaska. Second edition*. Pensoft, Sofia, 402 pp.
https://doi.org/10.3897/zookeys.360.4742

Buysson, H. (1902a) Coléoptères. T. 5. *In*: Fauvel, C.A.A., Faune gallo-rhénane ou species des Insectes qui habitent la France, la Belgique, la Hollande, le Luxembourg, la Prusse Rhénane, le Nassau & le Valais. Avec tableaux synoptiques et planchees gravèes. *Revue d'Entomologie*, 21, 265–336.

Buysson, H. (1902b) Catalogus coleopterorum Galliae et Corsicae. *Miscellanea Entomologica*, 10 (1), 9–15.

Buysson, H. (1914) Tableaux analytiques des Coléoptères de la faune Franco-Rhénane (France, Hollande, Belgique, Région rhénane, Valais). Familie LII. Elateridae. *Miscellanea entomologica*, 22, 81–96.

Buysson, H. (1925) Elateridae. *In*: Winkler, A. (Ed.), *Catalogus Coleopterorum Regionis Palaearcticae. Pars 5*. Albert Winkler, Wien, pp. 578–616.

Buysson, H. (1926) Tableaux analytiques des Coléoptères de la faune Franco-Rhénane (France, Hollande, Belgique, Région rhénane, Valais). Familie LII. Elateridae. *Miscellanea entomologica*, 29, 161–208.

Candèze, E.C.A. (1860) Monographie des élatérides. III. *Mémoires de la Société Royale des Sciences de Liége*, 15, 1–512.

Candèze, E.C.A. (1878) Élatérides nouveaux. II. *Annales de la Société entomologique de Belgique*, 21, li–lxi + lxxv–lxxxv + cxxxv–cxliii + clxi–clxxii + clxxxix–cxcix.

Candèze, E.C.A. (1891) *Catalogue méthodique de Élatérides connus en 1890*. Vaillant-Carmanne, H., Liège, 246 pp.
https://doi.org/10.5962/bhl.title.47119

Cate, P.C. (2007) Elateridae. *In*: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 4. Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea, Cucujoidea*. Apollo Books, Stenstrup, pp. 89–209.

Champlain, A.B. & Knull, J.N. (1932) Fermenting baits traps for trapping Elateridae and Cerambycidae (Coleop.). *Entomological News*, 43 (10), 253–257.

Cobos, A. (1969) Tercer viaje entomológico a Marruecos. Coleópteros Sternoxia. *Archivos del Instituto de Aclimatación de Almería*, 14, 5–20.
Crotch, G.R. (1873) *Check list of the Coleoptera of America, north of Mexico*. Naturalists' Agency, Salem, Massachusetts, 136 pp.
https://doi.org/10.5962/bhl.title.38811
Dejean, P.F.M.A. (1836) *Catalogue des Coléoptères de la Collection de M. le Comte Dejean. Troisième édition, revue, corrigée et augmentée*. *Livraisons 1–4*. Méquignon-Marvis père et fils, Paris, pp. 1–384.
https://doi.org/10.5962/t.173109
Delnatte, J., Soldati, F. & Parmain, G. (2015) Nouvelles localités pour *Isidus moreli* Mulsant & Rey, 1874 sur le littoral français (Coleoptera Elateridae Elaterinae). *L'Entomologiste*, 71 (1), 41–46.
Desbrochers des Loges, J. (1873) [new taxa]. *In*: Marseul, S.A. (Ed.), Répertoire des Coléoptères d'Europe décrits isolément depuis 1863. Deuxième partie. Tome III. *L'Abeille*, 9, 1–448. [1872–1873]
Dietrich, H. (1945) *The Elateridae of New York State: Memoir 269*. Cornell University, Agricultural Experiment Station, Ithaca, New York, 79 pp.
Dolin, V.G. (1960) Neue und wenig bekannte Elateriden aus der Ukraine (Coleoptera: Elateridae). *Beiträge zur Entomologie*, 10 (1/2), 189–201.
Dolin, V.G. (1964a) *Lichinki zhukov-shchelkunov (provolochniki) Evropeyskoy chasti SSSR [Wireworms of the European part of the USSR]*. Urozhai, Kiev, 206 pp. [in Russian]
Dolin, V.G. (1964b) Podsemeystvo Lepturoidinae [subfamily Lepturoidinae]. *In*: Gilyarov, M.S. (Ed.), *Key to the larvae of insects inhabiting in the soil*. Nauka, Moscow, pp. 382–393. [in Russian]
Dolin, V.G. (1978) *Opredelitel lichinok zhukov-shchelkunov fauny SSSR [Key to wireworms of the fauna of the USSR]*. Urozhai, Kiev, 124 pp. [in Russian]
Dolin, V.G. (1982) *Zhuki-kovaliki. Agrypnini, negastriini, dimini, atoini, oestodini* [Click-beetles. Subfamilies Agrypninae, Negastriinae, Diminae, Athoinae, and Oestodinae]. *Fauna of the Ukraine. Vol. 19. Beetles. Issue 3*. Naukova Dumka, Kiev, 288 pp. [in Ukrainian]
Dury, C. (1902) A revised list of the Coleoptera observed near Cincinnati, Ohio, with notes on localities, bibliographical references and description of new species. *Journal of the Cincinnati Society of Natural History*, 20, 107–196. [1901–1906]
Dušánek, V. (2008) Putování za endemity Krymu (Coleoptera, Elateridae). In search for endemic species of the Crimea peninsula (Coleoptera, Elateridae). *Elateridarium*, 2, 138–155.
Etzler, F.E. (2019) Generic reclassification of *Limonius* Eschscholtz, 1829 (Elateridae: Dendrometrinae) sensu Candèze 1860 of the world. *Zootaxa*, 4683 (3), 301–335.
https://doi.org/10.11646/zootaxa.4683.3.1
Fall, H.C. (1934) On certain North American Elateridae, new and old. *Journal of the New York Entomological Society*, 47 (1), 7–36.
Fuente, J.M. (1930) Catálogo sistemático-geográfico de los Coleópteros observados en la Península Ibérica, Pirineos propiamente dichos y Baleares. Elateridae. *Boletín de la Sociedad Española de Entomología*, 13, 22–37 + 44–75.
Gaedike, R. (1969) Bibliographie der Elateridenlarven–Literatur der Welt. *Beiträge zur Entomologie*, 19 (1/2), 159–266.
Gemminger, M. & Harold, B. (1869) *Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tom V. Buprestidae, Trixagidae, Monommidae, Eucnemidae, Elateridae, Cebrionidae*. E. H. Gummi, Monachii, Paris/London, pp. 1347–1608.
https://doi.org/10.5962/bhl.title.9089
Glen, R. (1950) Larvae of the Elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae). *Smithsonian Miscellaneous Collections*, 111 (11), 1–246.
Gobbi, G. & Platia, G. (1995) Coleoptera Elateroidea, Buprestoidea. *In*: Minelli, A., Ruffo, S. & La Posta, S. (Eds.), *Checklist delle specie della fauna italiana*. Calderini, Bologna, pp. 1–18.
Guglielmi, A. & Platia, G. (1985) Contributo alla conoscenza degli Elateridi di Grecia e Turchia (Coleoptera). *Fragmenta Entomologica*, 18 (1), 169–224.
Gülperçin, N. & Tezcan, S. (2010) *Distributional catalogue of Turkish Elateridae (Insecta: Coleoptera) fauna*. Ege Üniversitesi, İzmir, 63 pp. [in Turkish]
Gülperçin, N. & Tezcan, S. (2016) Türkiye Orman Ekosistemlerinin Elateridae (Insecta: Coleoptera) Faunası Üzerinde Bir Değerlendirme. *Journal of Bartın Faculty of Forestry*, 18 (1), 132–144. [in Turkish]
Gurjeva, E.L. (1965) Sem. Elateridae-shchelkuny [Elateridae – click-beetles]. *In*: Bey-Bienko, G.G. (Ed.), *Keys to the insects of the European part of the USSR. Vol. 2*. Nauka, Moscow-Leningrad, pp. 266–280. [in Russian]
Hampe, C. (1866) Beschreibung einiger neuen Käfer. *Berliner entomologische Zeitschrift*, 10 (4), 371–375.
https://doi.org/10.1002/mmnd.18660100407
Hatch, M.H. (1924) A list of Coleoptera from Charlevoix County, Michigan. *Papers of the Michigan Academy of Science, Arts and Letters*, 4 (1), 543–586.
Henshaw, S. (1885) *List of the Coleoptera of America, North of Mexico*. American Entomological Society, Philadelphia, Pennsylvania, 161 pp.
https://doi.org/10.5962/bhl.title.13151
Hiramatsu, H. (2011) [New record of *Elathous yamamotoi* from Shikoku]. *Gekkan-Mushi*, 482, 43. [in Japanese]

Horn, G.H. (1885) A study of some genera of Elateridae. *Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Natural Sciences*, 12, 33–52.
https://doi.org/10.2307/25076448
Hyslop, J.A. (1921) Genotypes of the Elaterid beetles of the world. *Proceedings of the United States National Museum*, 58, 621–673.
https://doi.org/10.5479/si.00963801.2353.621
Inaizumi, M. (1965) A list of the Elateridae (Coleoptera) in Tochigi Prefecture. *Bulletin of the College of Agriculture, Utsunomiya University*, 6 (1), 19–50.
Jäger, G. (1883) *C. G. Calwers Käferbuch: Naturgeschichte der Käfer Europas zum Handgebrauche für Sammler*. *Vierte Auflage*. Julius Hoffmann, K. Thienemanns Verlag, Stuttgart, 667 pp.
Jakobson, G.G. (1913) *Zhuki Rossii i Zapadnoy Evropy. Rukovodstvo k opredeleniyu zhukov [Beetles of Russia and Western Europe. Manual for identification of beetles]. Fasc. 10*. A.F. Devrien's Publishing House, St. Petersburg, pp. 721–864. [in Russian]
Jarzabek-Müller, A. (2013) First records for eight click-beetles (Coleoptera, Elateridae) in Greece. *Elateridarium*, 7, 77–83.
Johnson, P.J. (1993) Immature insects. Vol. 2. Notes and errata to Elateridae and Throscidae. *Mola*, 2, 5–6.
Johnson, P.J. (2002) Elateridae Leach, 1815. *In*: Arnett, R.H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida, pp. 160–173.
Kabalak, M., Avci, M. & Platia, G. (2013) A new species of *Elathous* Reitter (Coleoptera: Elateridae) from Turkey. *Zootaxa*, 3737 (1), 85–91.
https://doi.org/10.11646/zootaxa.3737.1.7
Kabalak, M. & Özbek, H. (2018) Research on the family Elateridae (Coleoptera) of Turkey: new distributional data, female descriptions and distributional evaluation. *Transactions of the American Entomological Society*, 144 (1), 143–166.
https://doi.org/10.3157/061.144.0112
Kamezawa, H. (2013) An essay on "dry hollow" as a habitat of beetles. *Sayabane*, New Series, 11, 4–14. [in Japanese]
Keaster, A.J., Jackson, M.A., Ward, S.S. & Krause, G.F. (1988) *A worldwide bibliography of Elateridae*. *Special Report No. 378*. Missouri Agricultural Experiment Station, University of Missouri, Columbia, 294 pp.
Kesdek, M., Platia, G. & Yıldırım, E. (2006) Contribution to the knowledge of click-beetles (Coleoptera: Elateridae) fauna of Turkey. *Entomofauna*, 27 (35), 417–432.
Kishii, T. (1985) Notes on Elateridae from Japan and adjacent area (4). *Gekkan-mushi*, 175, 8–10.
Kishii, T. (1987) *A taxonomic study of the Japanese Elateridae (Coleoptera), with the keys to the subfamilies, tribes and genera*. T. Kishii, Kyoto, 262 pp.
Kishii, T. (1993) Notes on Elateridae from Japan and its adjacent area (12). *Bulletin of the Heian High School*, 37, 1–19.
Kishii, T. (1999) A check-list of the family Elateridae from Japan (Coleoptera). *Bulletin of the Heian High School*, 42, 1–144.
Kocher, L. (1956) Catalogue commenté des Coléoptères du Maroc. Fascicule III. Malacodermes-Serricornes. *Travaux de l'Institut Scientifique Chérifien*, Série Zoologie, 8, 1–153.
Kubaczkova, M. & Kundrata, R. (2017) Annotated catalogue of the click-beetle subfamily Tetralobinae (Coleoptera: Elateridae). *Zootaxa*, 4323, 151–184.
Lane, M.C. (1952) List of Elateridae of British Columbia. *Proceedings of the Entomological Society of British Columbia*, 48, 65–67.
Lane, M.C. & Lanchester, H.P. (1971) Family Elateridae. *In*: Hatch, M.H. (Ed.), *The Beetles of the Pacific Northwest. Part V. Rhipiceroidea, Sternoxi, Phytophaga, Rhyncophora and Lamellicornia. University of Washington publications in biology. Vol. 16*. University of Washington Press, Seattle, Washington and London, pp. 6–48.
LeConte, J.L. (1853) Revision of the Elateridæ of the United States. *Transactions of the American Philosophical Society*, New York, 10, 405–508.
https://doi.org/10.2307/1005288
LeConte, J.L. (1867) List of the Coleoptera of North America. Part 1. *Smithsonian Miscellaneous Collections*, 6 (140), 1–78.
Leng, C.W. (1920) *Catalogue of the Coleoptera of America, north of Mexico*. John D. Sherman, Jr., Mount Vernon, New York, 470 pp.
https://doi.org/10.5962/bhl.title.8777
Leng, C.W. (1928) Order Coleoptera. *In*: Leonard, M.D. (Ed.), *A list of the insects of New York with a list of the spiders and certain other allied groups: Memoir 101*. Cornell University Agricultural Experiment Station, Ithaca, New York, pp. 203–520.
Leng, C.W. & Mutchler, A.J. (1933) *Second and third supplements 1925 to 1932 (inclusive) to Catalogue of the Coleoptera of America, north of Mexico*. John D. Sherman, Jr., Mount Vernon, New York, 112 pp.
Leseigneur, L. (1972) Coléoptères Elateridae de la faune de France continentale et de Corse. *Supplément au Bulletin mensuel de la Societe Linneenne de Lyon*, 41, 1–379.
https://doi.org/10.3406/linly.1972.10023
Leseigneur, L. (2014) Elateridae Leach, 1815. *In*: Tronquet, M. (Ed.), *Catalogue des Coléoptères de France*. Association roussillonnaise d'entomologie, Perpignan, pp. 423–437.
Lewis, G. (1894) On the Elateridae of Japan. *Annals and Magazine of Natural History*, Series 6, 13 (74), 182–201.
https://doi.org/10.1080/00222939408677683

Löbl, I. & Smetana, A. (2008) Errata for Volume 4. *In*: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea*. Apollo Books, Stenstrup, pp. 22–27.
https://doi.org/10.1163/9789004260900

Luigioni, P. (1929) I Coleotteri d'Italia. Catalogo sinonimico-topografico-bibliografico. *Memorie della Pontificia Accademia delle Scienze I Nuovi Lincei*, Serie 2, 13, 1–1160.

Majka, C.G., Chandler, D.S. & Donahue, C.P. (2011) *Checklist of the beetles of Maine, USA*. Empty Mirrors Press, Halifax, 328 pp.

Majka, C.G. & Johnson, P.J. (2008) The Elateridae (Coleoptera) of the Maritime provinces of Canada: faunal composition, new records, and taxonomic changes. *Zootaxa*, 1811 (1), 1–33.
https://doi.org/10.11646/zootaxa.1811.1.1

Mardzhanyan, M.A. (1987) *Shchelkuny (Elateridae)* [Click-beetles (Elateridae)]. *Fauna of the Armenian SSR. Insecta: Coleoptera*. Academy of Sciences of Armenian SSR Publishing House, Erevan, 204 pp. [in Russian]

Marseul, S.A. (1863) *Catalogue des Coléoptères d'Europe et du Bassin de la Méditerranée en Afrique et en Asie. 2nd Edition*. Marseul, M.S.A.de, Deyrolle, A., Paris, 300 pp.

Marseul, S.A. (1873) Répertoire des Coléoptères d'Europe décrits isolément depuis 1863. Deuxième partie. Tome III. *L'Abeille*, 9, 1–448. [1872–1873]

Marseul, S.A. (1887) Catalogue des Coléoptères de l'Ancien-Monde. Quatrième série. Tome VI. *L'Abeille*, 24 [1886–1887], 193–360.

Melsheimer, F.E. (1853) *Catalogue of the described Coleoptera of the United States*. Smithsonian Institution, Washington, 174 pp.

Mertlik, J. (2005) Description of three new species of family Elateridae (Coleoptera) from Syria and Turkey. *Folia Heyrovskyana*, 12 (4), 167–173.

Mertlik, J. & Dušánek, V. (2006) Description of five new species of click–beetles (Coleoptera, Elateridae) from the Palaearctic region with remarks about the distributions 22 additional species. *Folia Heyrovskyana*, 13 (4), 145–162.

Mertlik, J. & Platia, G. (2008) Catalogue of the family Cebrionidae, Elateridae, Lissomidae, Melasidae and Throscidae (Coleoptera) from Turkey. *Elateridarium*, 2, 1–40.

Mitsuhashi, S. (1936) [Insects of Nikko]. *In*: Nikko Toshogu Shrine (Ed.), *Plants and Animals in Nikko*. Yokendo, Tokyo, pp. 355–476. [in Japanese]

Miwa, Y. (1934) The fauna of Elateridae in the Japanese Empire. *Report of the Department of Agriculture Government Research Institute, Formosa*, 65, 1–289.

Mulsant, E. & Rey, C. (1875a) Description d'une espèce nouvelle d'Élatéride. *Annales de la Société linnéenne de Lyon*, New Series, 21, 416–418.
https://doi.org/10.3406/linly.1875.1875

Mulsant, E. & Rey, C. (1875b) Description d'une espèce nouvelle d'Élatéride. *Opuscules entomologiques*, 16, 81–83.

Nasserzadeh, H., Platia, G., Parsi, F. & Serri, S. (2018) Three new species, *Elathous zagrosensis* sp. n., *Zorochros dilatatus* sp. n., and *Dicronychus iranicus* sp. n., and noteworthy records of click beetles from western Iran (Coleoptera: Elateridae). *Zootaxa*, 4394 (4), 517–536.
https://doi.org/10.11646/zootaxa.4394.4.3

Németh, T. (2019) Elateridae (Coleoptera) of Lebanon. *Zootaxa*, 4614 (1), 127–159.
https://doi.org/10.11646/zootaxa.4614.1.6

Németh, T., Platia, G. & Benyahia, Y. (2015) Click beetles from the Talassemtane National Park, Morocco, with description of a new species of *Elathous* and new distributional data (Coleoptera: Elateridae). *Folia Entomologica Hungarica*, 76, 89–98.
https://doi.org/10.17112/FoliaEntHung.2015.76.89

Németh, T., Prosvirov, A.S. & Kundrata, R. (2020) Two new species of *Elathous* Reitter, 1890 (Coleoptera: Elateridae) from Syria. *Zoology in the Middle East*, 66 (2), 167–177.
https://doi.org/10.1080/09397140.2020.1757909

Oertzen, E. (1886) Verzeichniss der Coleopteren Griechenlands und Cretas, nebst einigen Bemerkungen über ihre geographische Verbreitung und 4 die Zeit des Vorkommens einiger Arten betreffenden Sammelberichten. *Berliner Entomologische Zeitschrift*, 30 (1–2), 189–293.
https://doi.org/10.1002/mmnd.47918860211

Ôhira, H. (1970) [Elateridae in Japan (V)]. *Kontyû to Shizen [Nature and Insects]*, 5 (7), 19–24. [in Japanese]

Ôhira, H. (1985) [Notes on *Limonius brunneus* Lewis]. *Coleopterists' News*, 70, 5. [in Japanese]

Ôhira, H. (1992) [Elaterid beetles of Misakubo-chô in Shizuoka Prefecture]. *Mikawa no kontyu*, 39, 350–351. [in Japanese]

Ôhira, H. (1995) New or little-known Elateridae (Coleoptera) from Japan, XXXIII. *Elytra*, 23 (2), 187–193.

Oliveira, M.P. (1893) *Catalogue des insectes du Portugal. Coleoptères*. Imprensa da Universidade, Coimbra, 393 pp.

Perris, E. (1875) Descriptions de quelques insectes jugés nouveaux. *L'Abeille, Journal d'entomologiue*, 13, 1–14. [1875]

Pesarini, C. (1986) Insetti della Fauna Italiana. Coleotteri Elateridi. Guide di Sistematica del Museo di Storia Naturale di Milano. *Natura*, 77 (1–2), 1–44.

Pliginsky, V.G. (1916) Zhuki Kryma. IV [Beetles of Crimea. IV]. *Bulletin de la Société des naturalistes et des amis de la nature en Crimée*, 5, 115–144.

Platia, G. (1994) *Fauna d'Italia, Coleoptera Elateridae*. Calderini, Bologna, 429 pp.

Platia, G. (2008) New species and chorological data of click-beetles from western and southern Palearctic region (Coleoptera, Elateridae). *Biocosme Mésogéen*, 25 (3), 137–150.

Platia, G. (2010) New species and chorological notes of click beetles from Palearctic region, especially from the Middle East (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa*, 46, 23–49.

Platia, G. (2011) Coleoptera, Elateridae. *In*: Nardi, G., Whitmore, D., Bardiani, M., Birtele, D., Mason, F., Spada, L. & Cerretti, P. (Eds.), *Biodiversity of Marganai and Montimannu (Sardinia). Research in the framework of the ICP Forests network. Conservazione Habitat Invertebrati. Vol. 5*. Cierre, Sommacampagna, pp. 832–835.

Platia, G., Abacigil, T.Ö., Jansson, N., Kayis, T., Coskun, M. & Varli, S.V. (2014) Click-beetles (Coleoptera, Elateridae) from two oak forests in Turkey. *Boletín de la Sociedad Entomológica Aragonesa*, 55, 41–48.

Platia, G. & Gudenzi, I. (1996) Descrizione di tre nuove specie di Elateridi di Grecia, Turchia ed Isola di Cipro con note geonemiche e sinonimiche (Coleoptera, Elateridae). *Bollettino del Museo regionale di Scienze naturali Torino*, 14 (1), 139–150.

Platia, G. & Gudenzi, I. (2005) Description of eleven new species of click-beetles of the Palearctic region, a case of legs teratology and new records of some species of the Italian fauna (Insecta Coleoptera Elateridae). *Quaderno di Studi e Notizie di Storia Naturale della Romagna*, 21, 109–127.

Platia, G., Jansson, N., Avcı, M., Sarıkaya, O., Coşkun, M. & Kayış, T. (2011) New species of click beetles from Turkey (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa*, 48, 207–215.

Platia, G., Jansson, N., Sürgüt, H., Tüven, A., Avci, M. & Varli, S.V. (2018) Click beetles (Coleoptera, Elateridae) from two areas with hollow oaks and plane trees in Turkey. *Boletín de la Sociedad Entomológica Aragonesa*, 63, 253–257.

Platia, G. & Kakiopoulos, G. (2014) Description of four new species of click beetles from Greece with interesting new records (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa*, 55, 101–105.

Platia, G. & Schimmel, R. (1991) Descrizione di nuove specie di Elateridi di Grecia e Turchia con chiave per due gruppi di specie (Coleoptera Elateridae). *Società Veneziana di Scienze Naturali*, 16, 131–142.

Platia, G. & Schimmel, R. (1992) Descrizione di nuove specie di elateridi di Grecia e Turchia. (Coleoptera, Elateridae). *Società Veneziana di Scienze Naturali*, 17, 87–95.

Platia, G. & Schimmel, R. (1993) Descrizione di nuove specie di Elateridi di Grecia e Turchia con note su alcuni *Agriotes* Eschscholtz (Coleoptera, Elateridae). *Lavori Società Veneziana di Scienze Naturali*, 18, 51–57.

Platia, G. & Serrano, A.R.M. (2002) Contribution to the knowledge of the click-beetles of Portugal (Coleoptera, Elateridae). *Boletim da Sociedade Portuguesa de Entomologia*, VII-26, 309–326.

Porta, A. (1929) Elateridae. *In*: Porta, A. (Ed.), *Fauna Coleopterorum Italica. Vol. III*. Stabilimento Tipografico Piacentino, Piacenza, pp. 321–373.

Preiss, R. (2003) A new *Elathous* Reitter, 1890, from Syria (Coleoptera: Elateridae). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, 55, 55–57.

Preiss, R. & Platia, G. (2003) The click beetles of Cyprus with descriptions of two new species and notes on species of the genus *Haterumelater* Ôhira, 1968 (Coleoptera: Elateridae). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, 55, 97–123.

Pyshkin, V.B., Kobechinskaya, V.G., Gromenko, V.M. & Tarasov, Y.E. (2002) Analiz fauny zhukov-shchelkunov (Coleoptera, Elateridae) Kryma [Faunistic analysis of click-beetles (Coleoptera, Elateridae) of Crimea]. *In*: *Ecosystems of Crimea, their regulation and protection. Vol. 12.* Tavrida National V.I. Vernadsky University, Simferopol, pp. 103–108. [in Russian]

Reitter, E. (1890) Eine neue mit *Athous* verwandte Elateriden-Gattung aus russisch Armenien: *Elathous* n. g. *Entomologische Nachrichten*, 16 (16), 247–248.

Reitter, E. (1891) Elateridae. *In*: Heyden, L., Reitter, E. & Weise, J. (Eds.), *Catalogus Coleopterorum Europae, Caucasi et Armeniae Rossicae*. E. Friedländer, Berlin; Edmund Reitter, Modling and Revue d'Entomologie, Caen, pp. 202–210.

Reitter, E. (1898) Neue Coleopteren aus Europa und den angrenzenden Ländern. *Deutsche Entomologische Zeitschrift*, 1898 (2), 337–360.
https://doi.org/10.1002/mmnd.48018980222

Reitter, E. (1905) Bestimmungs-Tabelle der palaearctischen, mit *Athous* verwandten Elateriden (Subtribus Athouina), mit einer Übersicht der verwandten Coleopteren-Familien: Sternoxia und mit einem Bestimmungsschlüssel der Gattungen der Elateriden. *Verhandlungen des Naturforschenden Vereins in Brünn*, 43, 1–122.

Reitter, E. (1906) Elateridae. *In*: Heyden, L., Reitter, E. & Weise, J. (Eds.), *Catalogus Coleopterorum Europae, Caucasi et Armeniae Rossicae. Editio secunda*. R. Friedländer & Sohn, Berlin,; Edmund Reitter, Pascau; Revue d'Entomologie, Caen, pp. 386–404.

Ruette, R. (1970) A catalogue of types of Coleoptera in the Canadian National Collection of insects. *Memoirs of the Entomolocical Society Of Canada*, 72, 1–134.
https://doi.org/10.4039/entm10272fv

Rousset, J. & Delnatte, J. (2016) Observations de quelques espèces rares d'Elateridae dans les Alpes-Maritimes, notamment *Campylomorphus homalisinus* (Illiger, 1807) et *Lacon lepidopterus* (Panzer, 1800) (Coleoptera, Elateridae). *Le Coléoptériste*, 19 (3), 175–178.

Sáez Bolaño, J., Zapata de la Vega, J.L., Lencina Gutiérrez, J.L. & Sánchez-Ruiz, A. (2014) Nuevos registros de elatéridos (Coleoptera: Elateridae) de la Península Ibérica. *Arquivos Entomolóxicos*, 12, 129–144.

Sainte-Claire Deville, J. (1914) *Catalogue critique des Coléoptères de la Corse*. Imprimerie Adeline, G. Poisson et Cie, Successeurs, Caen, 573 pp.
https://doi.org/10.5962/bhl.title.102399

Sainte-Claire Deville, J. (1935) Catalogue raisonné des Coléoptères de France. *L'Abeille*, 36 (2), 161–264.
Sánchez-Ruiz, A. (1996) Catálogo bibliográfico de las especies de la familia Elateridae (Coleoptera) de la Península Ibérica e Islas Baleares. *In*: Ramos, M.A. (Ed.), *Documentos Fauna Ibérica. Vol. 2*. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Cientificas, Madrid, pp. 1–265.
Say, T. (1839) Descriptions of new North American insects, and observations on some already described. *Transactions of the American Philosophical Society*, New Series, 6, 155–190.
https://doi.org/10.2307/1005320
Schaufuss, C. (1911) Elateridae. *In*: Calwer, C.G. (Ed.), *Käferbuch, Naturgeschichte der Kafer Europas. Vol. 6*. Sprösser & Nägele, Stuttgart, pp. 622–668.
Schenkling, S. (1927) Elateridae II. *In*: Junk, W. & Schenkling, S. (Eds.), *Coleopterorum Catalogus. Vol. XI. Pars 88*. W. Junk, Berlin, pp. 265–636.
Schimmel, R. & Platia, G. (1991) Die Arten der Gattung *Neoathousius* n. gen. aus Nordindien, Pakistan und Afghanistan (Coleoptera: Elateridae). *Revue suisse de Zoologie*, 98 (4), 879–895.
https://doi.org/10.5962/bhl.part.79816
Schwarz, O. (1893) Eine neue europäische Art der Elateriden-Gattung *Elathous* Reitter. *Deutsche Entomologische Zeitschrift*, 1893 (1), 191.
https://doi.org/10.1002/mmnd.48018930119
Schwarz, O. (1897) Neue palaearctischen Elateriden-Arten. *Wiener Entomologische Zeitung*, 16 (4–5), 128–136.
Schwarz, O. (1903) Drei neue *Elathous*-Arten. *Wiener Entomologische Zeitung*, 22 (7–8), 207–208.
https://doi.org/10.5962/bhl.part.9741
Schwarz, O. (1906) Coleoptera Fam. Elateridae. *In*: Wytsman, P. (Ed.), *Genera Insectorum. Fascicule 46*. P. Wytsman, Bruxelles, pp. 1–370.
Seabra, A.F. (1939) Contribução para a historia da Entomologia em Portugal. Coleoptera. *Publicações. Direcção Geral dos Serviços Florestais e Aquicolas*, 6, 206–257.
Seabra, A.F. (1943) Contribuïções para o inventário da fauna lusitânica. Insecta. Coleoptera. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, Série 1, 142 (i–xx), 1–153.
Sert, O. & Kabalak, M. (2011) Faunistic, ecological and zoogeographical evaluations on the click-beetles (Coleoptera: Elateridae) of middle part of the Blacksea region of Turkey. *Annales de la Société Entomologique de France*, 47 (3–4), 501–509.
https://doi.org/10.1080/00379271.2011.10697741
Smith, J.W. & Enns, W.R. (1977) The click beetle subfamilies Agrypninae, Pyrophorinae, and Melanotinae (Coleoptera: Elateridae) in Missouri – part I. *Journal of the Kansas Entomological Society*, 50 (3), 436–468.
Stein, J.P.E.F. (1868) *Catalogus Coleopterorum Europae*. F. Nicolai (A. Effert & L. Lindtner), Berlin, 149 pp.
Stein, J.P.E.F. & Weise, J. (1877) *Catalogi Coleopterorum Europae. Editio secunda*. Libraria Nicolai (R. Stricker), Berlin; E. Janson, London and L. Buquet, Paris, 209 pp.
Stibick, J.N.L. (1970) A revision of the genus *Leptoschema* of California with a key to related genera (Coleoptera: Elateridae). *The Pan-Pacific Entomologist*, 46 (3), 153–166.
Stierlin, G. (1864) Uebersicht der in Europa und den angränzenden Ländern einheimischen Arten der Gattung *Simonius* [sic!]. Aus Candez Monographie der Elateriden ausgezogan und ins Deutsche überragen. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 1 (6), 192.
Suzuki, W. (1987) Taxonomic notes on the Far Eastern Elateridae (Coleoptera) (I). *Coleopterists' News*, 75, 1–8.
Suzuki, W. (1993) [Record of *Elathous brunneus* from Fukushima Prefecture]. *Coleopterists' news*, 101, 4–5. [in Japanese]
Suzuki, W. (2001) [Record of *Elathous brunneus* (Lewis) collected from beech tree hollow]. *Gekkan-Mushi*, 365, 50. [in Japanese]
Tarnawski, D., Platia, G. & Mertlik, J. (2018) *Catalogue of the family Elateridae (Coleoptera) from Turkey. Polish Entomological Monographs. Vol. 17*. Polish Entomological Society, Poznań, 287 pp.
Tezcan, S., Tezcan, F. & Gülperçin, N. (2010) *İzmir'den 4000 Böcek Türü. 4000 insect*
species from İzmir, Turkey. Ege Üniversitesi İzmir Araştırma ve Uygulama Merkezi Yayını, Egetan Basım Ltd. Şti., İzmir, 253 pp.
Thomas, C.A. (1941) The Elateridæ of Pennsylvania. *Journal of the New York Entomological Society*, 49 (3), 233–263.
Thomas, S.L. (2007) *Effects of forest management on click beetle (Coleoptera: Elateridae) assemblages in the Acadian forect of Maine*. PhD Thesis, University of Maine, Orono, Maine, 174 pp.
Toyoshima, K. (2007) [On *Elathous yamamotoi* Ôhira collected from Gifu Prefecture]. *Gekkan-Mushi*, 432, 43. [in Japanese]
Tsutsumiuchi, Y. (2012) [New record of *Elathous brunneus* (Lewis) from Kyushu]. *Gekkan-Mushi*, 502, 5. [in Japanese]
Ulke, H. (1903) A list of the beetles of the District of Columbia. *Proceedings of the United States National Museum*, 25 (1275), 1–57.
https://doi.org/10.5479/si.00963801.1275
Van Dyke, E.C. (1932) Miscellaneous studies in the Elateridae and related families of Coleoptera. *Proceedings of the California Academy of Science, fourth series*, 20 (9), 291–465.
https://doi.org/10.2307/3475385
Watanabe, A. (1987) Record of *Limonius brunneus* Lewis, 1894 for the first time in 105 years (Coloptera, Elateridae). *Gekkan-Mushi*, 195, 20–21. [in Japanese]

Watanabe, A. (1990) [Elaterid beetles of Okayama Prefecture, Supplement IV]. *Suzumushi*, 124, 8–10. [in Japanese]
Webster, R.P., Sweeney, J.D. & DeMerchant, I. (2012) New Coleoptera records from New Brunswick, Canada: Elateridae. *ZooKeys*, 179, 93–113.
https://doi.org/10.3897/zookeys.179.2603
Wurst, C. (1994) Neue Schnellkäfer der Unterfamilie Athoinae aus dem Taurusgebirge, Südtürkei (Coleoptera: Elateridae). *Mitteilungen Entomologischer Verein*, 29, 59–66.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2007) Nueva especie de *Elathous* Reitter, 1890 de la Península Ibérica (Coleoptera: Elateridae, Dendrometrinae). *Boletín de la Sociedad Entomológica Aragonesa*, 40, 221–225.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2012a) *Elathous maestrei*, nueva especie de elatérido de la Península Ibérica (Coleoptera: Elateridae, Dendrometrinae, Dendrometrini). *Arquivos entomolóxicos*, 7, 107–110.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2012b) Catálogo actualizado de los Elatéridos de la Península Ibérica e Islas Baleares (Coleoptera: Elateridae). *Arquivos entomolóxicos*, 6, 115–271.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2013) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, I. *Arquivos entomolóxicos*, 8, 159–190.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2014) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, II. *Arquivos entomolóxicos*, 10, 129–166.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2015) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, III. *Arquivos entomolóxicos*, 13, 153–194.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2016) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, IV. *Arquivos entomolóxicos*, 15, 175–205.
Zapata de la Vega, J.L & Sánchez-Ruiz, A. (2017) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, V. *Arquivos entomolóxicos*, 17, 243–284.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2018) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, VI. *Arquivos entomolóxicos*, 19, 11–40.
Zapata de la Vega, J.L. & Sánchez-Ruiz, A. (2019) Nuevas aportaciones al catálogo de la familia Elateridae (Coleoptera) en la Península Ibérica e Islas Baleares, VII. *Arquivos entomolóxicos*, 21, 43–82.

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A new species of *Elathous* Reitter, 1890 (Coleoptera: Elateridae) from Lebanon

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A new species of the genus *Elathous* Reitter, 1890 from Lebanon is described and illustrated. *Elathous nemeri* sp. nov. is similar to other Levantine species, but can be easily recognised from its congeners by its elongated pronotum as well as by the shape of the male genitalia.

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Keywords: Click-beetles; distribution; diversity; Levant

Introduction

The genus *Elathous* Reitter, 1890 is a relatively small click-beetle lineage which contains seven species from North America and 41 species from the Palaearctic region (e.g., Cate, 2007, Nasserzadeh et al. 2018, Etzler, 2019, Kundrata et al., 2021). Although the phylogenetic position of this genus was not assessed in any of the recent molecular analyses (e.g., Bi et al., 2019, Kundrata et al., 2019a, Douglas et al., 2021), its morphology suggests the close relationship with the genus *Limonius* Eschscholtz, 1829 and its relatives within the subfamily Dendrometrinae (Etzler, 2019). Several new species were described in the last decades (e.g., Mertlik & Dušánek, 2006; Platia, 2010; Kabalak et al., 2013; Nasserzadeh et al., 2018). Recently, Etzler (2019) provided an updated diagnosis for the genus, and Kundrata et al. (2021) provided an annotated catalogue containing all described species. The Levantine region is one of the most important hot-spots for the click-beetle diversity in the Mediterranean region (Kundrata et al., 2014, Kundrata et al., 2019b, Németh, 2019, Németh et al., 2020). Six species were recorded, i.e., *E. syriacus* Schwarz, 1903, *E. ekaterinae* Preiss, 2003, *E. lizleri* Mertlik, 2005, *E. agilis* Németh, 2019, *E. serjillensis* Németh, Prosvirov & Kundrata, 2020 and *E. transversalis* Németh, Prosvirov & Kundrata, 2020. Here, I report a new species of *Elathous* found in northwestern Lebanon.

The discovery of the new species was preceded by the recent checklist of the click-beetles of Lebanon (Németh, 2019), and my field work in North Lebanon (in May 2015, June 2016, May 2017, and July and August 2018) during which I also studied the material of the Tannourine Nature Reserve Entomological Collection. A specimen of *Elathous* in this collection, which I assumed to be a member of *E. syriacus,* was listed as such in the checklist (Németh, 2019: 136). Later, we took photographs of type specimens for the catalogue of *Elathous* species of the World (Kundrata et al., 2021), and after publication of the catalogue, I re-examined some specimens of *Elathous* from the

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Mediterranean, including the specimen from the northwestern Lebanon which I first had misidentified as *E. syriacus* (Németh, 2019). However, the comparison with the type specimen of *E. syriacus* revealed that the examined specimen clearly represents a new species, which is described here.

Material and Methods

The study is based on the morphology of adults. The genitalia were dissected after a short treatment in hot 10% KOH. Main diagnostic characters were photographed using a Nikon D5200 and Nikon AF Micro Nikkor 60 mm lens and Mitutoyo M Plan Apo 5X microscope lens. Multiple exposures were stacked in Zerene Stacker, subsequent image work was done with Photoshop CS5. The measurements were taken with an eyepiece graticule. Body length was measured from the anterior margin of head to the apex of the elytra, body width at about middle of elytra, pronotal length at midline, pronotal width at the posterior angles, scutellar shield length at midline, and scutellar shield width at middle. I follow the definition of *Elathous* by Kabalak et al. (2013) and Etzler (2019). Morphological terminology follows Németh (2019) and Kundrata et al. (2018). The newly described species were compared to their congeners from the Levant, deposited at the Natural History Museum, London, The United Kingdom (NHMUK), Hungarian Natural History Musuem, Budapest, Hungary (HNHM), Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI), and the collections of Robin Kundrata, Olomouc, Czech Republic (PCRK), Giuseppe Platia, Gatteo, Italy (PCGP) and Josef Mertlik, Opatovice nad Labem, Czech Republic (PCJM).

Taxonomy

Elathous Reitter, 1890

Elathous nemeri **sp. nov.** (Figure 1)

Material. Holotype, male, “LE Tannourine 2016-08-20, Nabil Nemer.” (HNHM).

Differential diagnosis. *Elathous nemeri* sp. nov. is distinguished from its congeners by the following combination of characters: body elongated, medium sized (9.5 mm long), yellowish-brown; antenna long, surpassing posterior pronotal angles by about two antennomeres; pronotum widest at middle, with sides convex medially and slightly narrowed at posterior third; only slightly divergent posterior angles; and outer edges of parameres slightly concave. *Elathous syriacus* from Syria and Lebanon (Cate, 2007; Németh, 2019) has pronotum strongly narrowed from middle anteriorly and antennae shorter than pronotum. Two recently described species from Syria have a similar body colouration as *E. nemeri* sp. nov. (Németh et al., 2020): *Elathous serjillensis* has larger and elongated body and pronotum with convex sides, only slightly longer than wide and *E. transversalis* has pronotum 1.15 times wider than long and antenna about reaching posterior angles, parameres with wider, widely rounded anterior part. *Elathous ekaterinae* described from Syria has pronotal sides almost parellel and parameres of aedeagus with straight outer edges. Additionally, *E. lizleri* from Syria and *E. agilis* from Lebanon clearly differ from *E. nemeri* sp. nov. in the blackish body colouration, shorter antenna (not surpassing posterior angles), shorter legs, and the latter also by the strongly convex outer edges of parameres and the body size (both *E. lizleri* and *E. agilis* are usually more than 11 mm long).

Elathous nemeri sp. nov. can also be distinguished from its congeners in the region by easily observable characters on antenna, pronotum and aedeagus. Antenna is long, clearly surpassing the posterior angle of pronotum; the pronotum is longer than wide and widest medially; and parameres are distinctly narrowed apically, curved laterally, and with outer edges gradually roundly emarginate. *Elathous lizlerwerneri* Mertlik &

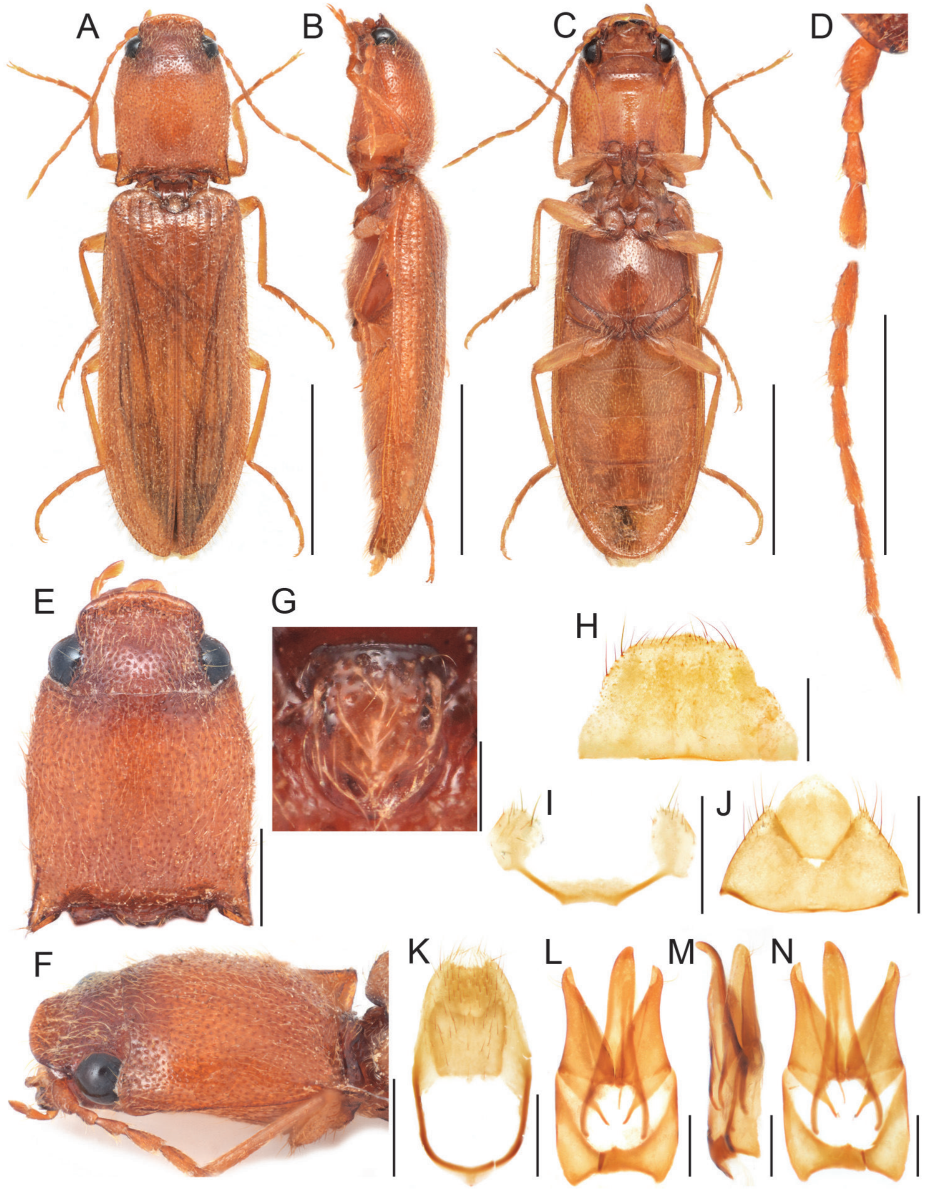

Figure 1. *Elathous nemeri* sp. nov. Holotype, male. A–C. Habitus, dorsal, lateral and ventral view, respectively. D. Antenna. E. Pronotum in dorsal view. F. Pronotum in dorso-lateral view. G. Scutellar shield. H–N. Abdominal pregenital segments and genitalia. H. Abdominal tergite VIII. I. Abdominal sternite VIII. J. Abdominal tergites IX–X. K. Abdominal sternites IX–X. L. Aedeagus in dorsal view. M. Aedeagus in lateral view. N. Aedeagus in ventral view. Scale bars = 0.2 mm (G), 0.5 mm (H–N), 1.0 mm (D–F), 3.0 mm (A–C).

Dušánek, 2006 is very similar in body size and shape, but the pronotum is as long as wide (longer than wide in *E. nemeri* sp. nov.) and parameres of aedegus are with parallel sides at base (curved in *E. nemeri* sp. nov.). *Elathous pavesii* Platia & Schimmel, 1992 has pronotum widest at first third, antennae shorter, and parameres with much more concave sides. Another three species, *Elathous depressus* Platia & Schimmel, 1991, *Elathous emrei* Platia, 2011 and *Elathous nurayae* Platia, 2011, have antenna shorter and pronotum with almost parallel sides. *Elathous rufobasalis* Wurst, 1994 differs in its typical body colouration. It has dark reddish-brown body, with shorter and convex pronotum, and shorter antenna. *Elathous serti* Kabalak, Avcı & Platia, 2013 has pronotum as long as wide, and antenna shorter than pronotum. *Elathous smyrnensis* Schwarz, 1903 has antenna shorter than pronotum and aedeagus with almost parallel sided parameres. *Elathous tezcani* Platia in Platia et al., 2014 has antenna not reaching the posterior end of pronotum, and pronotum with almost parallel sides from base to anterior third, and from there clearly narrowed. *Elathous turcicus* Platia & Gudenzi, 2005 has antenna shorter than pronotum and pronotum almost parallel sided from base to anterior third, and from there clearly narrowed.

Description. Male (Figure 1). Body elongate, moderately convex; 9.50 mm long, 2.75 mm wide; yellowish-brown, with head slightly darker; pubescence yellowish-golden, semi-erect, slightly curved. – *Head* (Figure 1E, F) including eyes 0.80 times as wide as pronotum; frons with a pair of shallow depressions latero-apically, apically slightly overhanging base of labrum; frontal carina distinct, sharp, slightly curved from from both dorsal and apical view. Labrum transverse, convex, frontally clearly rounded, roughly covered with large shallow punctures, with sparse, long, erect setae. Head surface with shallow punctures, punctation dense, punctures separated usually more than about half of their diameter; pubescence on head sparse, moderately long, semi-erect, more or less directed forwards. Mandible robust, rather broad, with sparse short erect setae. Maxillary palpus slender, pale brown, with apical palpomere twice as long as wide. Antenna (Figure 1D) slender, surpassing posterior pronotal angles by about length of two antennomeres, antennomeres III and IV slightly serrate, V to XI with almost parallel sides. Scape moderately wide, antennomeres II–X elongate, from II to V each gradually slightly widened apically, antennomeres II and III subequal in length, antennomere IV and following ones about 1.4 times longer than each of antennomeres II and III, antennomeres IV–X subequal in length; about three times as long as wide; ultimate antennomere narrow, elongate, slightly longer than penultimate antennomere, wirh almost parallel sides.

Pronotum (Figure 1E, F) moderately convex, widest at middle (but at posterior angles only slightly narrower than at middle), longer than wide (2.14 mm long and 2.00 mm wide, length-width ratio: 1.07). Anterior margin widely concave, gradually emarginate medially; anterior angles short and rounded; lateral sides rounded, with widest place at middle, then almost parallel toward posterior angles; posterior angles moderately long, sharp, only slightly divergent, with both outer and inner margins almost straight. Lateral carina distinct, sinuate, not visible in dorsal view. Sublateral carina short, distinct, located near lateral carina, meeting with lateral carina at apex of posterior angle. Disc shiny, sparsely punctate; punctures moderately large, rounded, usually of equal size, separated usually about 1.0–3.0 times of their diameter, interstices smooth; surface with pubescence moderately dense and long, thin, semi-erect, directed forwards. Hypomeron shiny, with punctation as on pronotal disc. Pronotosternal sutures almost straight, shortly opened anteriorly. Prosternum (Figure 1C) elongate, including prosternal process about 1.85 times as long as wide, in front of coxal cavities (i.e., excluding prosternal process) about 1.65 times as long as wide, with punctures as on hypomeron. Prosternal lobe with anterior margin widely rounded, with punctures as on prosternal disc. Prosternal process (Figures 1B, C) rather short, about 0.5 times as long as prosternum in front of procoxal cavities, with surface punctated as on prosternal disc; from dorsal view with almost parallel sides, widely rounded at apex; from lateral view

straight dorsally and sharply bent toward body ventrally, narrowed toward apex. Scutellar shield (Figure 1G) convex at anterior third, then flattened, about 1.18 times as long as wide; anterior margin slightly convex, sharp; lateral margins gradually sinuate; posterior margin rounded; surface almost smooth, shiny, covered with small and shallow punctures, and sparse long, semi-erect pubescence. Mesoventrite (Figure 1C) transverse, surface almost smooth, shiny, frontal margin medially slightly produced forward; sides distinctly sinuate, posterior process short, with apex almost straight; procoxal rests distinct, moderately deep; mesoventral cavity large, wide, with walls more developed posteriorly. Metaventrite large, wider than long, with punctures as on prosternum; discrimen distinct, long. Metacoxal plate (Figure 1C) with basal portion distinct, sinuate anteriorly, at about first third obliquely narrowed towards body edge. Elytra (Figure 1A, B), elongate, slightly convex, together 2.5 times as long as wide (6.5 mm long, 2.6 mm wide) and 2.9 times as long as pronotum, widest at about middle; disc slightly flattened, with striae with shallow punctures, separated usually about their diameter; interstriae rugose, slightly convex, with very sparse punctures which are slightly smaller than those on striae; pubescence sparse, semi-erect, moderately long, oriented backwards. Hind wing fully developed. Leg slender; each tibia elongate, narrow, with paired tibial spurs; all tarsi slightly longer than tibiae; tarsomere I longest, shorter than tarsomeres II and III combined, tarsomere II elongate, longer than tarsomere III, tarsomere III elongate, longer than tarsomere IV, tarsomere IV shortest, longer than wide, tarsomeres I–IV widened ventroapically, ventrally with combination of thick thorn-like setae and fine hair-like setae, apical tarsomere elongate, slender, only sparsely covered with fine hair-like setae; pretarsal claw elongate, narrow, gradually curved. – *Abdomen* (Figure 1C) with ventrites very finely puncate and covered with short, curved, and longer, straight semi-erect pubescence; apical ventrite rounded apically. Tergite VIII (Figure 1H) transverse, sclerotized, apically sparsely covered with short setae; sternite VIII (Figure 1I) transverse, apico-medially membranous, sparsely covered with short setae. Tergite IX wider than long, apico-medially deeply emarginate, connected by membrane to tergite X (1J); sternite X small, longer than wide, apically roundedm connected by membrane to sternite IX (Figure 1K) apically widely rounded, apical half covered with combination of short and moderately long setae. Aedeagus (Figure 1L–N) robust, about twice as long as wide. Median lobe rather robust, surpassing tip of parameres, without basal struts slightly longer than phallobase, basal third (without struts) about 2.5 times wider than apical third, sides abruptly narrowed after basal third, then subparallel toward apex; apex clearly curved from lateral view (Figure 1M), narrowly rounded; basal struts long, forming about third of median lobe length. Paramere robust, wide basally, distinctly narrowed apically, curved laterally, with outer edge gradually roundly emarginate; apical portion narrowed and slightly curved. Phallobase robust, wider than long, basally distinctly emarginate, with sides subparallel, only basally abruptly narrowed.
Female and immature stages unknown.

Etymology. The specific epithet is a patronym in honor of Dr. Nabil Nemer (Lebanon), who collected the type specimen.

Distribution. Known only from the type locality in northwestern Lebanon.

Remark. In the study on the Lebanese fauna, Németh (2019: 136) erroneously treated this species as *Elathous syriacus* Schwarz, 1903. However, after the study of the type material of *E. syriacus*, it became clear that the here studied specimen represents a new species.

Disclosure Statement

No potential conflict of interest was reported by the authors.

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References

Bi, W.-X., He, J.-W., Chen, C-C., Kundrata, R., & Li, X.-Y. (2019). Sinopyrophorinae, a new subfamily of Elateridae (Coleoptera, Elateroidea), with the first record of a luminous click beetle in Asia and evidence for multiple origins of bioluminescence in Elateridae. *ZooKeys, 864*, 79–97.

Cate, P. C. (2007). Family Elateridae Leach, 1815 (Cebrioninae, Lissominae, Subprotelaterinae). Pp. 94–207. In: I. Löbl & A. Smetana (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 4.* Stenstrup: Apollo Books.

Douglas, H. B., Kundrata, R., Brunke, A. J., Escalona, H. E., Chapados, J. T., Eyres, J., Richter, genomics, evolution and systematics of Elateridae: Are all bioluminescent Elateroidea derived click beetles? *Biology*, *10*, 451.

Etzler, F. E. (2019). Generic reclassification of *Limonius* Eschscholtz, 1829 (Elateridae: Dendrometrinae) sensu Candèze 1860 of the world. *Zootaxa, 4683*, 301–335.

Kabalak, M., Avci, M., & Platia, G. (2013). A new species of Elathous Reitter (Coleoptera: Elateridae) from Turkey. *Zootaxa, 3737*, 85–91.

Kundrata, R., Kobieluszova, L. & Bocak, L. (2014). A review of Drilini (Coleoptera: Elateridae: Agrypninae) of the Northern Levant, with description of a new species from Syria and a key to Levantine species. *Zootaxa, 3755*, 457–469.

Kundrata, R., Mertlik, J. & Németh, T. (2019b). Unexpected diversity of *Lacon* Laporte, 1838 (Coleoptera: Elateridae: Agrypninae) in the Levant: revised species concepts, new species, and an identification key. *Zootaxa, 4679*, 401–449.

Kundrata, R., Németh, T., Prosvirov, A. P. & Hoffmannova, J. (2021). Annotated catalogue of the click-beetle genus *Elathous* Reitter, 1890 (Coleoptera: Elateridae: Dendrometrinae), including habitus photographs for all species. *Zootaxa, 4995*, 231–265.

Kundrata, R., Prosvirov, A. S., Vondracek, D. & Sormova, E. (2019a). Congruence between molecular data and morphology: phylogenetic position of Senodoniini (Coleoptera: Elateridae). *Insects, 10*, 231 (17 pp.).

Kundrata, R., Sormova, E., & Prosvirov, A. S. (2018). Revisiting the diversity of *Ludioctenus* Fairmaire (Elateridae: Agrypninae), with description of a new species from Afghanistan, and discussion on the systematic position of Tetrigusina. *Zootaxa, 4455*, 377–388.

Mertlik, J. & Dušánek, V. (2006). Description of five new species of click-beetles (Coleoptera, Elateridae) from the Palaearctic region with remarks about the distributions 22 additional species. *Folia Heyrovskyana, 13*, 145–162.

Nasserzadeh, H., Platia, G., Parsi, F. & Serri, S. (2018). Three new species, *Elathous zagrosensis* sp. n., *Zorochros dilatatus* sp. n., and *Dicronychus iranicus* sp. n., and noteworthy records of click beetles from western Iran (Coleoptera: Elateridae). *Zootaxa, 4394*, 517–536.

Németh, T. (2019). Elateridae (Coleoptera) of Lebanon. *Zootaxa, 4614*, 127–159.

Németh, T., Prosvirov, A. S., & Kundrata, R. (2020). Two new species of *Elathous* Reitter, 1890 (Elateridae: Dendrometrinae) from Syria. *Zoology in the Middle East, 66*, 167–177.

Platia, G. (2010). New species and chorological notes of click beetles from Palearctic region, especially from the Middle East (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa, 46,* 23–49.

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Plastocerus angulosus (Germar, 1844) (Coleoptera: Elateridae: Dendrometrinae): an enigmatic click beetle with a convoluted taxonomic history

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Abstract

Plastocerus angulosus (Germar, 1844) is one of the only two species of genus *Plastocerus* Schaum, 1852 within the monogeneric click beetle tribe Plastocerini. It is distributed in the area comprising Greece, Turkey, Syria, Israel, and Lebanon (first record for Lebanon published here). Due to the slightly modified morphology of *P. angulosus*, this taxon has a convoluted taxonomic history and was earlier classified in various families and even superfamilies. However, recent phylogenies place it in Elateridae: Dendrometrinae. In this study, we review the morphology, intraspecific morphological and genetic variability, sexual dimorphism, systematics, bibliography, and distribution of *P. angulosus*. Our results show rather low morphological and relatively high genetic variability in this species. Females, which are larger than males and differ mainly in the antennae and abdominal ventrites, are not so rare as previously thought. Further field research should focus on the discovery of immature stages to describe their morphology and understand their biology and ecology.

Key words: Asia Minor, classification, diversity, Elateroidea, Greece, Levant

Introduction

The elateroid genus *Plastocerus* Schaum, 1852 has a convoluted taxonomic history (Crowson 1972, Branham 2010, Hájek *et al.* 2020). Although it was usually classified in Elateridae (e.g., Lacordaire 1857, Candèze 1863, Reitter 1891, Hyslop 1921, Fleutiaux 1941, Mertlik & Platia 2008), some authors placed it to a separate family Plastoceridae, either sensu LeConte (1861; Schwarz 1907, Schenkling 1927) or Crowson (1972; Lawrence 1988, Lawrence & Newton 1995, Branham 2010). Due to the visible protrochantins, more freely articulated abdominal ventrites, ventrite 1 lacking intercoxal process, and female presumably with shortened elytra (which is, however, not true), Crowson (1972) included Plastoceridae to the soft-bodied Cantharoidea rather than to the clicking and well-sclerotized Elateroidea. Modern concept of Elateroidea also includes soft-bodied lineages previously classified in Cantharoidea (Lawrence 1988), and molecular analyses suggested multiple origins of the less-sclerotized lineages (Bocakova *et al.* 2007, Kundrata & Bocak 2011, McKenna *et al.* 2015, Douglas *et al.* 2021). Based on the molecular data, *Plastocerus* is currently classified again in Elateridae (Bocak *et al.* 2018, Kusy *et al.* 2018, Douglas *et al.* 2021). Currently, *Plastocerus* contains two species; *P. angulosus* (Germar, 1844) is known from Greece, Asia Minor, and Levant, and *P. thoracicus* Fleutiaux, 1918 is known from East and South East Asia (Branham 2010, Lin & Yang 2012, Hájek *et al.* 2020).

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Schaum (1852) erected a new genus *Plastocerus* in "Cebrionites" for an earlier described *Callirhipis angulosa* from Turkey (Germar 1844). Unfortunately, subsequent authors thought that Schaum's taxonomic act was invalid and that the new genus name was a nomen nudum, and so the authorship of the genus *Plastocerus* was usually attributed to LeConte (1853), who described an elaterid species *P. schaumii* LeConte, 1853 from the USA, California. This lead to the long-term confusion about the status and limits of *Plastocerus*. LeConte's broader concept included Palaearctic *P. angulosus* along with several Nearctic taxa (LeConte 1861). Although some authors continued to classify *Plastocerus* in Cebrionidae (Marseul 1857, Redtenbacher 1857), others placed them in Elateridae (e.g., Lacordaire 1857, LeConte 1861, Candèze 1863, Harold 1869). Heyden in Heyden *et al.* (1883) proposed a new generic name *Ceroplastus* Heyden, 1883 for *P. angulosus*, probably considering Nearctic species as true *Plastocerus*. This was followed by subsequent authors (e.g., Seidlitz 1888, Reitter 1891, Schwarz 1907, Hyslop 1923, Schenkling 1927, Fleutiaux 1941). It should be noted that Heyden *et al.* (1883) and Reitter (1891) placed *P. angulosus* (as *Ceroplastus*) to Elateridae: Denticollini (currently Dendrometrini).

Reitter (1896) described new genus *Pseudophyllocerus* Reitter, 1896 based on a single species, *Ps. atricolor* Reitter, 1896, from Turkey. Schwarz (1897) immediately recognized that it was in fact a female of *P. angulosus*, and hence synonymized *Ps. atricolor* with *P. angulosus.* Schwarz (1902) erroneously attributed *Plastocerus* to Candèze (1863), and because he was aware that Palaearctic and Nearctic *Plastocerus* sensu LeConte are not congeneric, he proposed a replacement generic name *Cladocerus* Schwarz, 1902 for the Palaearctic *Plastocerus*. However, Heyden (1902) immediately pointed out that his name *Ceroplastus* has priority over *Cladocerus*. For more details on the complicated nomenclatural history of *Plastocerus*, see Hájek *et al.* (2020).

Broader concept of plastocerids (in various taxonomic ranks) sensu LeConte (1861) and Schwarz (1907), with *Plastocerus* considered a New World genus and *Ceroplastus* an Old World genus, lasted until Crowson (1972) redefined the group. He treated plastocerids as a separate family in Cantharoidea, and corrected the usage of *Plastocerus*. He recognized the Old World genus *Plastocerus* Schaum (with *Ceroplastus* as a junior synonym) and followed Arnett (1962) in using the name *Octinodes* Candèze, 1863 for all New World *Plastocerus* LeConte. Although Lawrence (1988) formally merged Cantharoidea with Elateroidea, he pointed out that Plastoceridae should belong to the cantharoids despite their elateroid-like features. Some authors then continued to classify *Plastocerus* in Plastoceridae (Lawrence 1991, Lawrence & Newton 1995, Bocak 2007, Branham 2010, Bouchard *et al.* 2011); however, elaterid experts recognized *P. angulosus* is a click-beetle and classified it again in Elateridae (e.g., Mertlik & Platia 2008, Gülperçin & Tezcan 2010, Platia & Németh 2011). This was repeatedly confirmed using molecular phylogenetic and phylogenomic approaches (Bocak *et al.* 2018, Kusy *et al.* 2018, Douglas *et al.* 2021).

In the 21st century, there is a great progress not only in our understanding the phylogenetic relationships of *P. angulosus* but also in improving our knowledge on its morphology and distribution. In the Handbook of Zoology, Branham (2010) reviewed knowledge of that time about Plastoceridae, providing two images of *P. angulosus*, but he erroneously stated that females of this group are unknown. Bocak *et al.* (2018) provided some images of body details of both sexes of *P. angulosus*; however, they focused on its phylogenetic placement and did not redescribe it fully. Lawrence *et al.* (2021) provided the image and description of hind wing venation. Regarding the distribution, *P. angulosus* was long known mainly from western and southern Turkey. Although Oertzen (1886) reported *P. angulosus* from the mainland Greece, and Reitter (1910) reported it from "Palestina", those records were omitted in later works (Schwarz 1907, Bocak 2007). Recently, *P. angulosus* was found in Israel, Samos Island, and Syria (Platia 2010, Platia & Németh 2011, Platia & Kakiopoulos 2014). In this study, we review our knowledge on morphology, intraspecific variability, sexual dimorphism, systematics, and distribution of *P. angulosus*, and for the first time, we report it from Lebanon.

Material and methods

Morphological part

The study is based on the morphology of adults. We examined four males and three females from Greece, two males from Lebanon, 68 males and 12 females from Turkey, and a single male from Syria. Additionally, we examined several specimens from Greece and Turkey based on the photographs. The genitalia were dissected after a short treatment in hot 10% KOH. Main diagnostic characters were photographed using a Nikon D5200 camera attached to a Mitutoyo M Plan Apo 5X microscope lens. The measurements were taken with an eyepiece graticule. Body length was measured from the anterior margin of head to the apex of the elytra, body width at the widest place across elytra, pronotal length at midline, and, if not specified, pronotal width at the posterior angles. Morphological terminology follows Branham (2010), Costa *et al.* (2010), and Lawrence *et al.* (2010, 2021). The locality labels are cited verbatim. The material listed in this study is deposited in the following collections:

BMNH	Natural History Museum, London, The United Kingdom
HNHM	Hungarian Natural History Musuem, Budapest, Hungary
MNHN	Museum National d'Histoire Naturelle, Paris, France
NHMW	Naturhistorisches Museum, Vienna, Austria
NMPC	National museum, Prague, Czech Republic
PCDS	collection of Dezső Szalóki, Budapest, Hungary
PCGG	collection of Georgios Gastouniotis, Nemea, Greece
PCGK	collection of George Kakiopoulos, Athens, Greece
PCGP	collection of Giuseppe Platia, Gatteo, Italy
PCJM	collection of Josef Mertlik, Opatovice nad Labem, Czech Republic
PCMS	collection of Martin Samek, Skalice, Czech Republic
PCPS	collection of Per Kristian Solevåg, Tranby, Norway
PCPZ	collection of Petr Zahradník, Jesenice u Prahy, Czech Republic
PCRK	collection of Robin Kundrata, Olomouc, Czech Republic
PCSZ	collection of Savvas Zafeiriou, Pirgoi Thermis, Lesvos, Greece
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SMNH	The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel
UPOL	voucher collection of the Laboratory of Biodiversity and Molecular Evolution, CATRIN-CRH, Palacky University, Olomouc, Czech Republic

Molecular part

We sequenced the specimen of *P. angulosus* from Greece, Peloponnese, Parnon Mts. (voucher number RK1245; for more details see "Material examined"). The voucher specimen has been stored in pure ethanol and is deposited in PCRK. Whole genomic DNA was extracted using the E.Z.N.A Tissue Kit (Omega Bio-tek Inc. Norcross, USA) according to the manufacturer protocol for tissue DNA. Elution was performed twice with 100µl Elution buffer each. Two fragments of the mitochondrial genome were sequenced, i.e., *cox1-3*' (723 bp) and *rrnL* (453 bp). For *cox1-3*', we used primers TL2-N-3014 (Pat) and C1-J-2183 (Jerry) originally reported by Simon *et al.* (1994) and modified as in Sormova *et al.* (2018). For *rrnL*, we used primers AR-L and BR-H (Palumbi *et al.* 1991). Amplifications were performed in 15µl reactions containing 7.5µl 2x Qiagen Multiplex PCR Plus Master Mix (Qiagen, Hilden, Germany), 0.3µM of each primer, RNase-free water and 0.5µl template DNA. Amplification conditions were as follows: initial PCR activation step at 95°C 5 min, 38 cycles of 30 s denaturing at 95°C, 90 s annealing (47°C for *cox1-3*', 45°C for *rrnL*), 90 s extension at 72°C, followed by a final extension of 30 min at 68°C. The PCR products were visualized on a 1.4% agarose gel stained with Gel Red (0.1, Biotium, Hayward, USA), purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany), and sequenced on an ABI3730XL sequencer using Big Dye v. 3.1 Terminator Kit (Thermo Fisher Scientific, Darmstadt, Germany) by Macrogen, Netherlands.

The newly generated sequences were assembled, manually checked and edited using Sequencher 5.4.6 (Gene Codes Corporation, Ann Arbor, MI USA; www.genecodes.com) and deposited in GenBank with accession numbers OQ745741 (*cox1-3*') and OQ745740 (*rrnL*). We compared the newly sequenced specimen RK1245 (Greece) with the specimen UPOL A01544 (Turkey) reported by Bocak *et al.* (2018). The *cox1-3*' and *rrnL* sequences of the latter are publicly available from GenBank under the accession numbers KX648446 and KX648440, respectively. We aligned sequences of both specimens using default Geneious algorithm in Geneious Prime 2022.2.2 (Biomatters Ltd. Auckland, New Zealand; www.geneious.com; Kearse *et al.* 2012). Basic statistics and the maximum uncorrected pairwise genetic distances (p-distances) between both specimens were calculated using MEGA 11 (Tamura *et al.* 2021).

Results

Family Elateridae Leach, 1815

Subfamily Dendrometrinae Gistel, 1848

Tribe Plastocerini Crowson, 1972 [nec LeConte, 1861; an application should be submitted to the International Commission of Zoological Nomenclature to suppress LeConte's name to conserve Crowson's name as valid (ICZN 1999); for more information see Bouchard *et al.* (2011) and Hájek *et al.* (2020)]

Composition and distribution

Only a single genus *Plastocerus* with two species is included in this tribe. *Plastocerus angulosus* is known from Greece, Asia Minor, and Levant, and *P. thoracicus* is known from East and South East Asia (Branham 2010, Lin & Yang 2012, Hájek *et al.* 2020). *Pseudophyllocerus atricolor* was considered a separate species by Reitter (1896, 1910) but other authors followed Schwarz (1897) who synonymized it with *P. angulosus*. Recently, *Binhon atrum* Pic, 1922 was synonymized with *P. thoracicus* by Hájek *et al.* (2020).

Genus *Plastocerus* Schaum, 1852

Plastocerus Schaum, 1852: 49. Type species. *Callirhipis angulosa* Germar, 1844: plate 5; by monotypy.
Ceroplastus Heyden in Heyden, Reitter & Weise, 1883: 111. Unnecessary replacement name for *Plastocerus* Schaum, 1852, nec LeConte, 1853.
Pseudophyllocerus Reitter, 1896: 234. Type species. *Pseudophyllocerus atricolor* Reitter, 1896: 234; by monotypy. Synonymized with *Plastocerus* Schaum, 1852 by Schwarz (1897: 64).
Pseudophillocerus: Reitter, 1902: 93 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Cladocerus Schwarz, 1902: 200. Unnecessary replacement name for *Plastocerus* sensu Candèze (1863), i.e., *Plastocerus* Schaum, 1852, nec LeConte, 1853.
Binhon Pic, 1922: 29. Type species. *Binhon atrum* Pic, 1922: 29; by monotypy. Synonymized with *Plastocerus* Schaum, 1852 by Hájek *et al.* (2020: 392).
Ceroplatus: Branham & Wenzel, 2001: 580 [unavailable name, incorrect subsequent spelling not in prevailing usage].
Pseudophylocerus: Bocak, 2007: 209 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Plastocerus angulosus (Germar, 1844)

(Figs 1–3)

Callirhipis angulosa Germar, 1844: plate 5.
Campylus orientalis Frivaldszky, 1845: 177 [unavailable name, nomen nudum, published without description; see Bálint & Abadjiev 2006].
Plastocerus angulosus: Schaum, 1852: 49.
Phyllocerus angulosus: Marseul, 1857: 99; see Candèze (1863: 486).
Ceroplastus angulosus: Heyden *et al.*, 1883: 111.
Pseudophyllocerus atricolor Reitter, 1896: 234; synonymized with *P. angulosus* by Schwarz (1897: 64).
Cladocerus angulosus: Schwarz, 1902: 200.
Ceroplastus atricolor: Reitter, 1910: 178.

Type localities

Callirhipis angulosa: Turkey: "Smyrna" [Izmir]. *Pseudophyllocerus atricolor*: Turkey: "Adalia" [Antalya].

Type material

Callirhipis angulosa: Described based on an unknown number of male specimens; probably a single specimen (collection unknown). Not found in any European museum so far, including the Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (MFNB) and BMNH. *Pseudophyllocerus atricolor*: Holotype, female (collection unknown). Not found in any European museum so far, including HNHM and NHMW.

Material examined

GREECE. 1 male, "Taygetos" (MNHN); 1 male, "Greece, SE Peloponnesus, Parnon Mts, near Tsitalia village, alt ~ 600 m, 27/VII/2017, George Kakiopoulos lgt., RK1245" (PCRK); 1 male, "Peloponnesos, Messenia, near Langada vill., 450 m, 5.VIII.1990, G. Kakiopoulos, on grass (PCGK); 1 male, "NW Peloponnesos, Achaia, near Kato Lousi vill., 650 m, 10.VIII.2009, G. Kakiopoulos (PCGK); 1 female, "Olympia, 6. 1965, leg. Wewalka" (NHMW); 1 female, "Greece, 30. 7. 1991, Mykeny, J. Slabý lgt., Peloponésos [on underside of label], *Plastocerus* ♀ *angulosus* (Germ.), Det. Platia 1982" (PCJM); 1 female, "Peloponnesus, Nemea, inside the town, 20.VII.2021, unique individual, escaped prey from swallows nest, legit G. Gastouniotis" (PCGK). **LEBANON**. 1 male, "Appl. 1878 I., Beirut" (NHMW); 1 male, "Lebanon: Aley. 2,700 feet. vii–viii. 1945. (A. Sandison)., Middle East Biological Studies Scheme, G. H. Q. M. E. F., B. M. 1947-393., *Ceroplastus* sp. det. R. A. Crowson" (BMNH). **TURKEY**. 2 males, 1 female, "Mann 1863, Brussa [Bursa], *Plastocerus angulosus*" (NHMW); 2 males, 1 female, "collect. Türk" (NHMW); 1 female, "Türk" (NHMW); 2 males, "Brussa [Bursa], coll. E. Friv., *C. angulosus* Germ., coll. E. Frivaldszky" (HNHM); 1 female, "Taurus, As. min., coll. Käufel, *Plastocerus angulosus* ♀" (MNHN); 1 male, "Akbes 94, *Pl. angulosus* ♂" (MNHN); 1 male, "Akbes (Delagrange)" (MNHN); 2 males, no label data (MNHN); 1 male, "Kusadasi Törökország [Turkey], 1977.VI.3. leg. A. Podlussány, *Plastocerus angulosus* det. Platia, 2010" (HNHM); 1 male, "Syrie, Akbés [Turkey: Hatay province], Ch. Delagrange, Eté 1890 231" (NHMW); 1 male, "Turkey, Kemer env., 12.7.2009, Vítězslav Tomášek lgt." (PCRK); 2 males, "Besika Bay [Çanakkale: Beşik Bay], G. C. Champion, BMNH (E) 1927-409" (BMNH); 1 male, "Besika Bay [Çanakkale: Beşik Bay], 94-58" (BMNH); 1 male, "Sharp Coll. 1905-313" (BMNH); 1 male, "Besika Bay [Çanakkale: Beşik Bay], *Plastocerus*, Sharp Coll. 1905-313" (BMNH); 2 males, "Turkey, Janson coll. 1903-130" (BMNH); 1 male, "Turcia, Janson coll. ex Dejean 1903-130, *Plastocerus angulosus* Germar ♂, *Orientalis* (Friv.), Turcia ♂♀ Friv." (BMNH); 1 male, "Asia Minor, Janson coll. 1903-130, *Plastocerus angulosus* Germ., Schaum, Cand. ♂" (BMNH); 1 male, "Brussa [Bursa], Janson coll. 1903-130, *Plastocerus angulosus* Germ., Schaum, Cand. ♂" (BMNH); 1 male, "Turkey, 206, *Campylus orientalis* Friv., Bosphorus, *Plastocerus angulosus* Germ. (Det. W. Janson)" (BMNH); 1 female, "Brussa [Bursa], Janson coll. 1903-130, *Plastocerus angulosus* Germ., Schaum, Cand. ♀" (BMNH); 1 female, "Besika Bay [Çanakkale: Beşik Bay], G. C. Champion, BMNH (E) 1927-409" (BMNH); 1 female, "Turcia, Janson coll. ex Dejean 1903-130, Friv., *P. angulos*. ♀" (BMNH); 1 female, "Turkey - vill. Izmir, Zeytindağ, 19. 6. 2002, Martin Samek lgt." (PCJM, ex. PCMS); 3 males, "Turcia, Coll. Kraatz" (SDEI); 1 male, "Anatolien, Ak-Chehir, coll. Künnemann, *Ceroplastus angulosus* Germ." (SDEI); 3 males, 1 female, "Brussa [Bursa], Coll. Kraatz" (SDEI); 1 female, "Brussa [Bursa], Coll. Kraatz, *Plastocerus* ♀" (SDEI); 2 males, "TR. Bahramkale [Behramkale] (Assos), 19.–24. 7. 91, Vít Kubáň leg. [one with an additional label: *Plastocerus* ♂ *angulosus* Germ., Det. Platia 1982]" (PCJM); 3 males, "S Turkey 15km W of Mersin, 1–5.vii.1992, leg. D. Hauck" (PCJM); 8 males, "TR vill. Adana, 10.–12. 7. 1997, Pozanti env., Ak Daği, Josef Mertlik lgt." (PCJM); 1 male, "TR vil. Isparta, 12.–13. 7. 2000, Davraz Daği, Yukarigökdere env., R. Lizler & K. Werner lgt." (PCJM); 1 male, "Turkiye b. - occ., Porsuk Baraji Lake, Eskisehir env., 7. 7. 1993, A. Šlachta lgt." (PCJM); 4 males, "Turkey m. (Antalya), Beldibi p. Kemer, 1.–15. 7. 1998, Bey Dagl., P. Bulirsch lgt." (PCJM); 1 male, "Turkei, 30. 6. 97, Adana, Cinarli, lgt. Jiří Hájek" (PCJM); 1 male, "Turkei, 5. 7. 96, Alpu, lgt. Jiří Hájek" (PCJM); 1 male, "TR - vil. Bursa, 4. 7. 2006, Uludağ. 20 km S of Bursa, Çaybaşi env., Josef Mertlik lgt." (PCJM); 2 males. 1 female, "Turkey occ., Osmaniye, Karatepe, 3.–7. VII. 1994, leg. P. Kabátek" (PCJM); 2 males, "Turkey, Turk. 2001 Expedition, Adana vil. (45km N); 24.–25. VI. 2001, 1 km Boztahta (river, springs), 37°23'N, 35°12'E; 330 m, M. Fikáček, J. Hájek & J. Straka lgt." (NMPC); 1 male, "Anatolien, Ak-Chehir, 1900. Korb." (NMPC); 1 male, "Turcia, *Plastocerus angulosus*, (Germar, 1844), Jiří Hájek det. 2011" (NMPC); 1 male, "Turkey, Nurdağ Pass (Hasanbeyli env.), ex coll. S. Kadlec, National Museum Prague, Czech Republic" (NMPC); 1 male, "Anatolien, Ak-Chehir, 1900. Korb., *Ceroplastus angulosus*, Det. Dr Obenberger" (NMPC); 1 male, "Nurdag, Tyr + Var., ex coll. S. Kadlec, National Museum Prague, Czech Republic" (NMPC); 1 male, "Turkey m., Nurdag Pass (Hasanbeyli env.), 24. 6. 1995, Tyrner & Voříšek lgt., Collectio – Coleoptera, Stanislav Kadlec, Czech Republic, ex coll. S. Kadlec, National Museum Prague, Czech Republic, *Plastocerus angulosus* (Germ), L. Bocák det. 2007" (NMPC); 1 male, "Turcia, *Ceroplastus angulosus*" (NMPC); 1 male, "Turkey NW, vil. Bursa, Çagliyan env. (near Bursa), 20.–23.vii.1998, J. Bezděk lgt., ex coll. V. Kubáň, National Museum Prague, Czech Republic" (NMPC); 1 male, "Turkey S, vil. Adana, Çiçekli env. (25 km N from Adana), 50 m, 3.–5.vii.1998, M. Říha lgt., ex coll. V. Kubáň, National Museum Prague, Czech Republic" (NMPC); 1 male, "TR. Bahramkale (Assos) 19.–24.7.91, Vít Kubáň leg, ex coll. V. Kubáň, National Museum Prague, Czech Republic, *Plastocerus angulosus* Germ., Josef Mertlik det. 1992" (NMPC); 1 male, "Syrie, Akbes, C.D. 1891, Coll. Delagrange., *Plastocerus angulosus* Germ., Syrie - Akbés" (NMPC); 1 female, "Turkey, Nurdağ Pass (Hasanbeyli env.), ex coll. S. Kadlec, National Museum Prague, Czech Republic" (NMPC). **SYRIA**. 1 male, "Syria, muh. Hama, Al Ghab, Shatha al Dardar, 35°32.195'N, 36°15.076E, 180 m, 26.VI.2006, D. Szalóki" (PCDS).

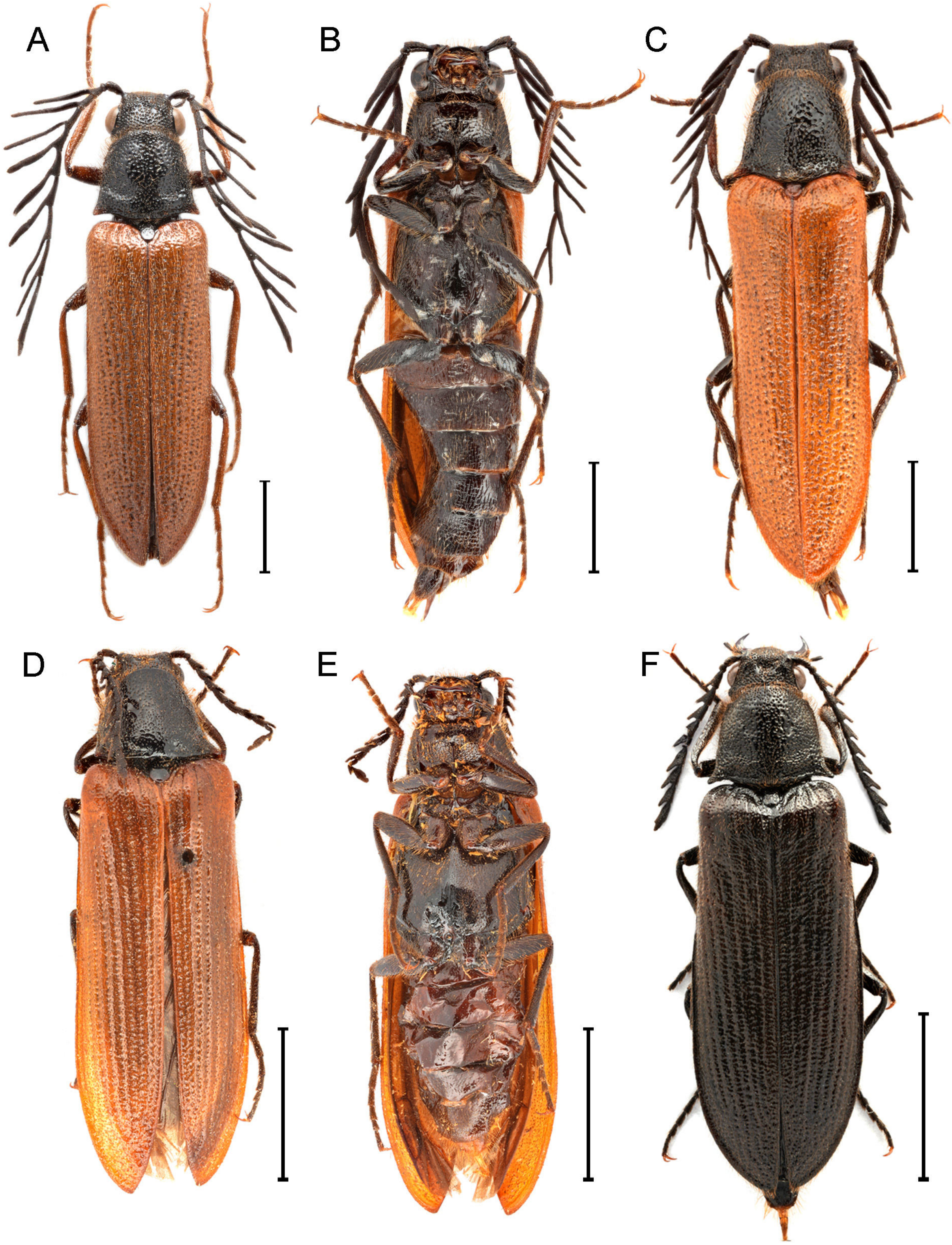

FIGURE 1. Morphology of *Plastocerus angulosus* (Germar, 1844). Male habitus. **A.** Turkey, Kemer, dorsal view; **B.** Turkey, Kusadasi, ventral view; **C.** Turkey, Kusadasi, dorsal view. Female habitus. **D.** Turkey, Taurus, dorsal view; **E.** Turkey, Taurus, ventral view; **F.** Turkey, Zeytindağ, dorsal view. Scale bars: 2.0 mm (A–C), 5.00 mm (D–F).

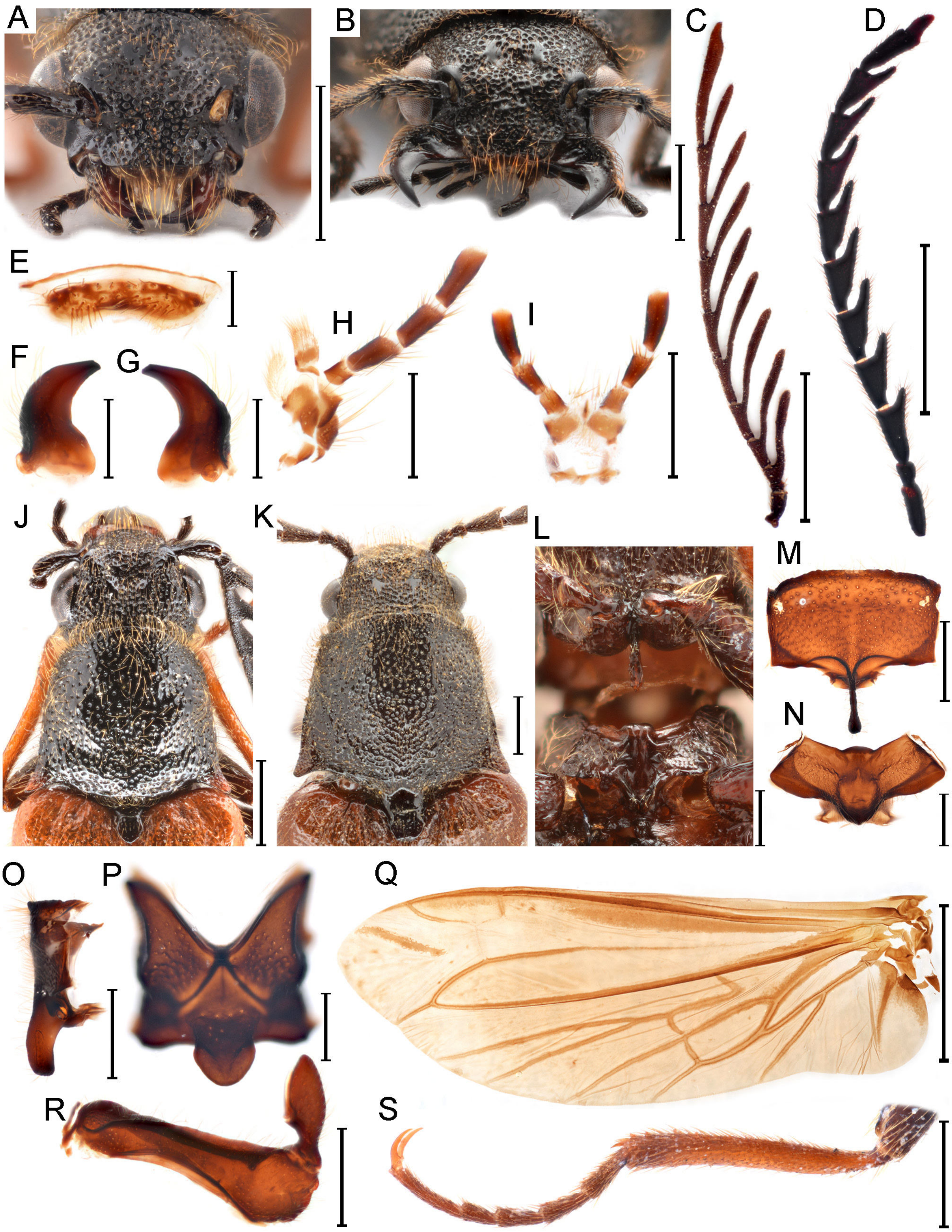

FIGURE 2. Morphology of *Plastocerus angulosus* (Germar, 1844). **A.** male head, frontal view; **B.** female head, frontal view; **C.** male antenna; **D.** female antenna; **E.** male labrum; **F.** male left mandible; **G.** male right mandible; **H.** male maxilla; **I.** male labium; **J.** male pronotum, dorsal view; **K.** female pronotum, dorsal view; **L.** male prosternal process and mesoventrite; **M.** male prosternum; **N.** male mesoventrite; **O.** male scutellum, lateral view; **P.** male scutellum, dorsal view; **Q.** male hind wing; **R.** male metacoxal plate; **S.** male fore tibia and tarsus. Scale bars: 2.0 mm (C,D,Q), 1.0 mm (A,B,J,K,M,R,S), 0.5 mm (F–H,I,N,O,P,R), 0.2 mm (E).

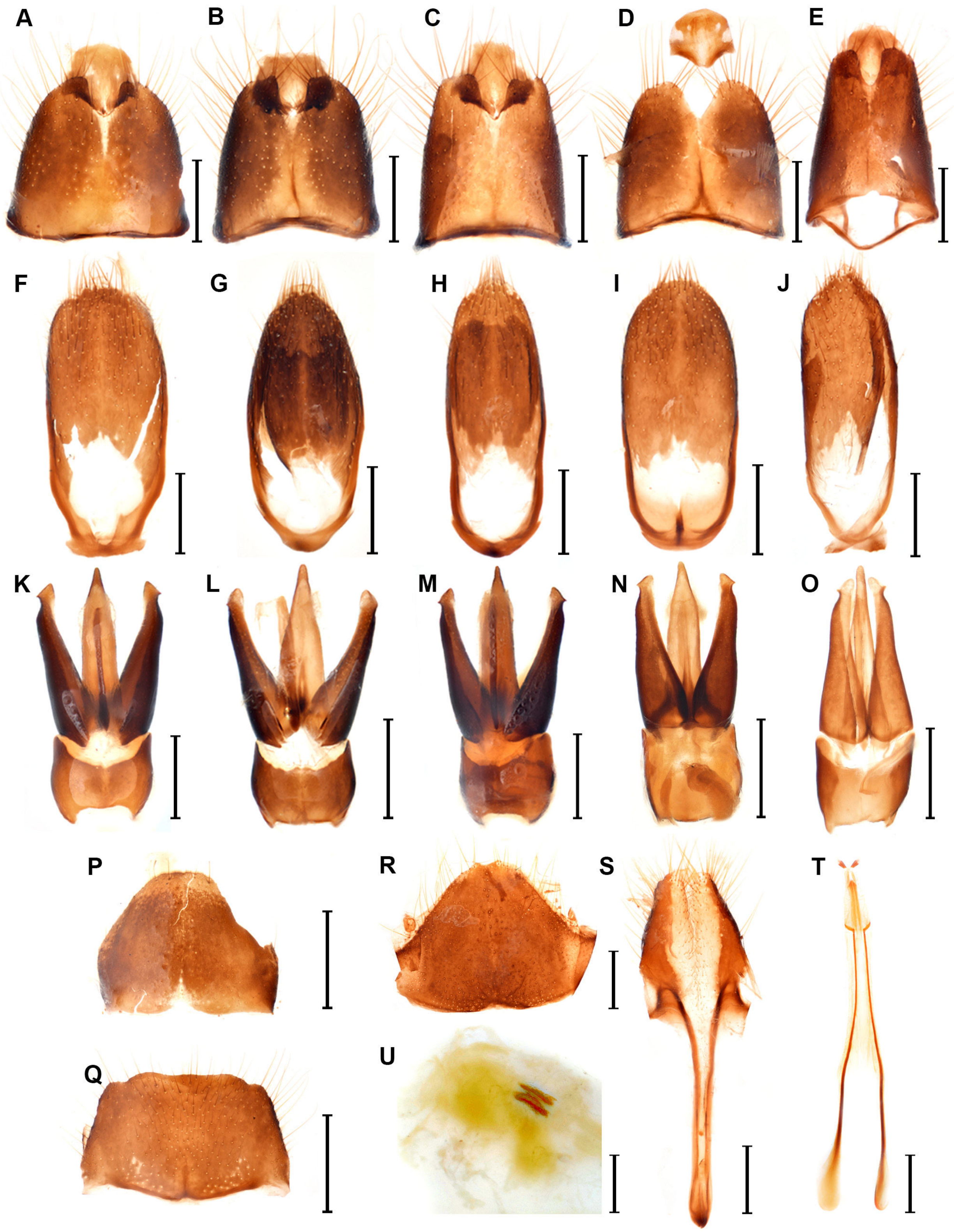

FIGURE 3. Morphology of *Plastocerus angulosus* (Germar, 1844), abdominal pregenital segments and genitalia. Male. **A–E,** abdominal tergites IX–X. **A.** Lebanon, Beirut; **B.** Turkey, Kusadasi; **C.** Syria, Shatha al Dardar; **D.** Greece, Taygetos Mts.; **E.** Turkey, Bursa; **F–J.** abdominal sternite IX; **F.** Lebanon, Beirut; **G.** Turkey, Kusadasi; **H.** Syria, Shatha al Dardar; **I.** Greece, Taygetos Mts.; **J.** Turkey, Bursa; **K–M.** aedeagus, ventral view; **K.** Lebanon, Beirut; **L.** Turkey, Kusadasi; **M.** Syria, Shatha al Dardar; **N–O.** aedeagus, dorsal view; **N.** Greece, Taygetos Mts.; **O.** Turkey, Bursa; **P.** abdominal tergite VIII; **Q.** abdominal sternite VIII. Female. **R.** abdominal tergite VIII; **S.** abdominal sternite VIII; **T.** ovipositor; **U.** inner sclerites of bursa copulatrix. Scale bars: 0.5 mm.

Material examined from the photographs

GREECE. 1 male, "SE Peloponnesos, 10 km S Leonidion, nr. Tsitalia vill., 550 m, 28.VII.2014, G. Kakiopoulos" (PCGP); 1 male, "Samos Is., 1990, A. Kullberg" (PCGP); 1 male, 1 female, "Peloponnese, Nemea Korinthias, 15–28/7/2017, Leg Georgios Gastouniotis" (PCGG); 7 ex. (only one male photograph examined by the authors), "Hellas [Greece], Messinia: Kardamili [36°53'18.95"N, 22°14'20.26"E; P. K. Solevåg, pers. comm.], 1. VII. 2009, Leg PK Solevåg" (PCPS); 1 male, "Greece, Lesvos, 39°11'22.6"N 26°26'44.4"E, collected by hand from grasses (Poaceae) in olive grove, 08/07/2020, Savvas Zafeiriou lgt." (PCSZ). **TURKEY**. 1 male, "Namrun, 26.VII.1985, Niehuis" (PCGP); 1 male, "Isparta, Davraz Dag, 25.V.2001, M. Snizek" (PCGP); 1 male, "Adana Prov., Hasanbeyli vill., 950 m, 18–19.VII.2006, R. Krolik" (PCGP).

Published data on *P. angulosus* not examined in our study

TURKEY. Frivaldszky (1845: 177) reported a specimen of *Campylus orientalis* (=*P. angulosus*) from Bithynian Olympus (currently Uludağ in Bursa Province). Mertlik & Platia (2008: 34) reported two male specimens from the collection of Giuseppe Platia (PCGP) with the following data: "Turkey, prov. Isparta, Isparta, Davraz Dağ, 25.v.2001, M. Snížek leg." and "Turkey, prov. Içel (Mersin), Namrun, 26.vii.1985, Niehuis leg.", respectively. Additionally, they reported two male specimens from the collection of Petr Zahradník (PCPZ) with the following data: "Turkey, prov. Zonguldag, Karabük, 20 km E, 22.–23.vi.1996, P. Zahradník leg., J. Vávra det. 2006". These specimens could not be located by P. Zahradník (pers. comm., 2022). Bocak *et al.* (2018: 2) reported a male specimen with the following data: "Turkey, Çanakkale province, Ayvacık, Behramkale env., 20 m a. s. l., 3 Jul. 2015, 39°29'N, 26°20'E" (UPOL). **GREECE**. Platia & Kakiopoulos (2014: 118) reported specimens from "Peloponnesos, Arcadia, near Leonidion town, 8.–9.VIII.1992, 0–600 m, on various plants". Those specimens included approximately 40 males which were not collected but only observed by G. Kakiopoulos. **ISRAEL**. Platia (2010: 41) reported a single male specimen from Israel (first country record) with the following data: "Israel: Beit Guvriot, 16.VI.1964, leg. Kugler" (SMNH). A century ago, Reitter (1910: 178) reported a single female from "Palestina".

Diagnosis

Diagnostic characters for both sexes. Head (Fig. 2A,B) prognathous; mandible (Fig. 2F,G) unidentate. Pronotum (Fig. 2J,K) with short divergent posterior angles, without sublateral carinae; lateral carina separating pronotal disk and hypomeron short, incomplete anteriorly. Prosternum (Fig. 2L,M) wider than long, anteriorly truncate, without chin-piece; prosternal process (Fig. 2M) very narrow, blade-like. Trochantins exposed. Elytra (Fig. 1A,C,D,F) punctate-striate, with punctures more or less organized to vaguely defined puncture rows. Hind wing (Fig. 2Q) with wedge cell well developed. Tarsomeres (Fig. 2S) simple; pretarsal claws (Fig. 2S) simple.

Additional diagnostic characters specific for males. Antenna (Fig. 2C) reaching 2/3 of elytral length, strongly pectinate, with rami of antennomeres III–X distinctly longer than their respective stems; antennomeres IV–X gradually longer toward apex. Abdomen (Fig. 1B) with seven visible sternites (III–IX), the first three of which are connate.

Additional diagnostic characters specific for females. Antenna (Fig. 2D) reaching just after humeri, shortly pectinate, with rami of antennomeres III–X shorter or about as long as their respective stems; antennomeres IV–X about subequal in length. Abdomen (Fig. 2E) with six free visible sternites (III–VIII). Ovipositor (Fig. 3T) with paraprocts 4.0–4.5 times as long as gonocoxites; styli short and subapically attached to gonocoxites. Bursa copulatrix (Fig. 3U) with two elongate small inner sclerites.

Diagnostic redescription

Male (Figs. 1A–C; 2A,C,E–J,L–S; 3A–Q). Body (Fig. 1A–C) 8.9–12.5 mm long and 2.6–3.3 mm wide, 3.4–4.0 times as long as wide. Body elongate, more or less parallel-sided. Body coloration dark brown to black, femora usually lighter, dark brown, and apices of pronotal posterior angles, tibiae, tarsi, and elytra usually light brown to reddish brown or brown (see Intraspecific variability section below); dorsal body pubescence yellowish to light brown.

Head (Fig. 2A) prognathous, including eyes 1.0–1.1 times as wide as anterior margin of pronotum; its surface rough, covered with large punctures, mostly contiguous but irregular, with smooth interstices which are mostly reduced to wrinkles but are larger dorso-medially; each puncture with moderately long seta which is oriented forwards. Frontoclypeal region (Fig. 2A) more or less strongly declined, with anterior margin well defined, sharp, more or less straight to slightly rounded. Eyes (Fig. 2A,J) moderately large and strongly protuberant, their minimum frontal separation 1.55–1.90 times maximum eye diameter. Antennal insertions (Fig. 2A) widely separated, slightly raised. Labrum (Fig. 2E) not visible from dorsal view, hidden under anterior margin of frontoclypeus, strongly transverse, free, well-sclerotized, anteriorly slighly emarginate, with surface sparsely covered with large punctures and with several long stiff setae. Mandible (Fig. 2F,G) robust, unidentate, basally broader and with long setae, apically strongly curved, shiny; mola and prostheca absent. Maxilla (Fig. 2H) partly reduced, with galea and lacinia short, lightly sclerotized and setose, palpus 4-segmented, with basal palpomere shortest, only slightly longer than wide, palpomeres 2 and 3 elongate, subequal in length, apical palpomere longest, rather flattened and slightly securiform. Labium (Fig. 2I) partly reduced and membranous, with ligula highly reduced; palpus 3-segmented, basal palpomere shortest, apical palpomere longest, rather flattened and slightly securiform. Antenna (Fig. 2C) with 11 antennomeres, slender, long, reaching 2/3 of elytral length, pectinate from antennomere III. Length ratio of antennomeres I–XI = 3.4–3.7 : 1.0 : 1.6–2.2 : 2.7–3.3 : 3.6–4.1 : 4.0–5.0 : 4.1–5.3 : 4.6–6.0 : 4.7–6.1 : 4.9–6.7 : 10.3–14.3. Scape elongate, slightly curved, widened apically; pedicel minute, short, about as long as wide, apically widened; antennomeres III–X pectinate, with rami extending from distal portions of their respective stems, slender, flattened, distinctly longer than their respective stems; antennomere III short, distinctly shorter than antennomere IV, antennomeres IV–X elongate, each gradually longer towards apex; ultimate antennomere longest, 2.0–2.2 times as long as preceding antennomere, simple, slightly widened toward apex, subapically abruptly narrowed at one side, slightly emarginate or obliguely cut, apex narrowly rounded.

Pronotum (Figs. 1A,C; 2J) 1.15–1.25 times as wide as long, moderately convex, gradually narrowed toward anterior margin, widest at posterior angles. Anterior margin somewhat rounded; anterior angles inconspicuous, not produced forward; lateral sides very slightly rounded or almost straight; posterior margin trisinuate, posterior angles short, prominent, divergent, apically subacute to narrowly rounded. Lateral carina slightly explanate posteriorly, obsolete at anterior half. Disk rather smooth or only slightly rugose, sparsely and coarsely punctured; punctures semi-circular to circular, usually larger medially and smaller near margins, usually separated by about 1–3 puncture diameters, denser mainly near posterior margin; each puncture with moderately long semi-erect seta which is oriented forwards except for posterior angles where setae are usually oriented dorsolaterally. Hypomeron (Fig. 1B) moderately densely punctate, pronotosternal sutures short, curved, anteriorly divergent, closed. Prosternum (Fig. 2M) including prosternal process (Fig. 2L) slightly wider than long, in front of coxae about twice as wide as long, anteriorly truncate, without chin-piece; punctures usually small, sparser and larger in anterior part. Prosternal process (Fig. 2L,M) very narrow, parallel-sided in most of its length, blade-like, slightly shorter than portion of prosternum in front of procoxae, apically slightly widened. Procoxae transverse, with trochantins broadly exposed. Procoxal cavities transverse, narrowly separated, broadly open. Scutellar shield (Fig. 2O,P) almost flat, tongue-shaped, longer than wide, roughly on same plane as anterior portion of scutellum; sides strongly sinuate, posterior margin more or less narrowly rounded; surface smooth, with several punctures and short pubescence. Elytra (Fig. 1A,C) 2.35–2.90 times as long as their combined width, and 3.50–4.05 times as long as pronotum, punctate-striate, with punctures more or less organized to vaguely defined puncture rows; apico-lateral margins strenghtened, apices almost conjointly rounded; elytral pubescence shorter than that on head and pronotum, usually straigh, semi-erect, oriented backwards. Epipleura very narrow, wider at base. Mesoventrite (Fig. 2L,N) with anterior edge roughly on same plane as metaventrite, procoxal rests shallow, mesoventral cavity small, shallow, with less defined walls; surface of mesoventrite covered with small punctures and long setae. Mesocoxae (Fig. 1B) projecting, very narrowly separated, with exposed trochantins; mesocoxal cavity (Fig. 1B) open to both mesepimeron and mesanepisternum. Metaventrite (Fig. 1B) slightly convex, with long discrimen, sparsely punctate and covered with long semi-erect setae. Metanepisternum (Fig. 1B) narrow, slightly wider basally, gradually narrowed toward apex. Metacoxae (Fig. 1B) contiguous, extending laterally to meet elytra; metacoxal plates (Fig. 2R) narrow. Hind wing (Fig. 2Q) well developed, elongate, 2.7–2.8 times as long as wide, with very short apical field containing a single oblique support sclerite; radial cell elongate; cross-vein r3 almost horizontal; RP very long; medial field with five free veins; wedge cell well developed, almost three times as long wide, apically truncate; ano-jugal with only a single vein (AP3+4), without distinct anal embayment. Leg (Fig. 2S) relatively long, tibia elongate, simple, with paired tibial spurs, tarsus elongate, tarsomeres simple, apical tarsomere distinctly longest; pretarsal claws simple, slightly curved.

Abdomen (Fig. 1B) with seven visible sternites (III–IX), the first three of which are connate; surface very finely puncate and covered with moderately long semi-erect setae. Abdominal sternite III (ventrite 1) without intercoxal process, anteromedially only slightly raised; sternite VI (ventrite 4) free but connected to preceding sternite by only short membrane; sternite VII (ventrite 5) with posterior margin widely rounded, apically slightly protruded, connected to preceding sternite by longer membrane; sternite VIII (Fig. 3Q) partly retracted to sternite VII, transverse, approximately 1.7 times as wide as long, slightly narrowed apicad, sclerotized, sparsely covered with moderately long setae; sternite IX (Fig. 3F–J) elongate, 2.3–2.7 times as long as wide, lateral sides subparallel to slightly rounded, apically rounded, basal third membranous, apical two thirds covered with micropunctures and short setae, which are denser and longer apically. Abdominal tergite VIII (Fig. 3P) slightly wider than long, sclerotized, apically sparsely covered with short setae; Tergite IX (Fig. 3A–E) usually slightly wider than long, in some cases approximately as wide as long (sometimes lateral sides are bent ventrally so it appears that tergite IX is longer than wide; see Fig. 3D,E), apico-medially deeply emarginate, connected by membrane to tergite X; tergite X (Fig. 3A–E) small, slightly longer than wide, apically widely rounded. Aedeagus (Fig. 3K–O) robust, 2.4–2.7 times as long as wide. Median lobe rather robust, slightly surpassing tip of parameres, subparallel-sided to gradually narrowed toward apex for most of its length, more abruptly narrowed toward apex at about 3/5 or 4/5 of its length, apex narrowly rounded; basal struts short. Paramere robust, elongate, wide basally, distinctly narrowed subapically, with outer edge bisinuate; apical portion after subapical emargination short, with minute outward hooks. Phallobase slightly wider than long if length measured from anterior to posterior angle, about twice as wide as long if length measured medially, basally distinctly widely emarginate, with sides roughly rounded.

Female (Figs. 1D–F; 2B,D,K; 3R–U). Resembles male in most aspects, except following characters. Body (Fig. 1D–F) 14.0–18.0 mm long and 4.0–5.5 mm wide, 3.2–3.7 times as long as wide. Head (Fig. 2B) including eyes 0.8–1.0 times as wide as anterior margin of pronotum. Eyes with their minimum frontal separation 1.90–2.30 times maximum eye diameter. Antenna (Fig. 2D) reaching just after humeri, shortly pectinate, with rami of antennomeres III–X shorter or about as long as their respective stems. Length ratio of antennomeres I–XI = 2.1–2.3 : 1.0 : 2.4 : 2.1–2.3 : 2.1–2.3 : 2.1–2.3 : 2.1–2.3 : 2.1–2.3 : 2.1–2.3 : 2.1–2.3 : 3.6–3.9. Antennomere III slightly longer or about as long as antennomere IV; ultimate antennomere 1.7–1.8 times as long as preceding antennomere. Pronotum (Fig. 2K) with surface usually rough, punctation variably dense, usually separated by half to one puncture diameter but sometimes posteriorly denser, almost contiguous, or generally sparser. Scutellar shield (Fig. 2K) only slightly longer than wide, posteriorly widely rounded or very slightly emarginate. Elytra (Fig. 1D,F) 2.55–2.80 times as long as their combined width, and 4.05–4.20 times as long as pronotum. Leg (Fig. 1D,F) moderately long. Abdomen (Fig. 1E) with six free visible sternites (III–VIII) which are connected by short membranes. Abdominal tergite VIII (Fig. 3R) widely subtriangular, 1.3–1.4 times as wide as long, sparsely covered with fine micropunctures and short setae, which are denser at margins and apex; abdominal sternite VIII (Fig. 3S) roughly triangular, 1.3–1.4 times as long as wide, apically more or less narrowly rounded, apically and medially membranous, relatively densely covered with fine punctures and long setae; spiculum ventrale relatively short and stout, 1.0–1.5 times sternite length. Ovipositor (Fig. 3T) relatively long; paraprocts 4.0–4.5 times as long as gonocoxites; styli present, short, subapically attached to gonocoxites. Bursa copulatrix (Fig. 3U) membranous, sac-like, with two elongate small inner sclerites.

Immature stages. Unknown.

Sexual dimorphism

Crowson (1972) stated that the female of *P. angulosus* reminds that of *Omalisus* Geoffroy, 1762 (a genus in Elateridae: Omalisinae, which is a soft-bodied and morphologically modified group of neotenic click-beetles) in being larger than male, wingless, and with the elytra much shorter than the abdomen. Although females of *P. angulosus* are usually really larger than their male counterparts, they are not wingless and elytra fully cover their abdomen (Fig. 1D–F). Bocak *et al.* (2018) studied two female specimens from BMNH, and found out that the sexual dimorphism in *P. angulosus* includes the shape of antennae, terminal abdominal ventrites, and slightly wider pronotum in female. Our results show that females are larger than males, being 14.0–18.0 mm long (8.9–12.5 mm in males; Fig. 1A–F), have shorter antennae which are reaching just after humeri (up to 2/3 of elytral length in males; Fig. 1D–F), less pectinate antennae, with the rami of antennomeres III–X shorter or about as long as their respective stems (distinctly longer than their respective stems in males; Fig. 2C,D), relatively longer antennomere III which is slightly longer or about as long as antennomere IV (distinctly shorter than antennomere IV in males), antennomeres IV–X about subequal in length (gradually longer toward apex in males), ultimate antennomere 1.7–1.8 times as long as preceding antennomere (2.0–2.2 times in males), relatively wider scutellar shield with widely rounded or slightly emarginate posterior margin (narrowly rounded in males; Fig. 2J,K), more robust and relatively shorter legs (Fig. 1A–F), abdomen with six free visible sternites (with seven visible sternites, the first three of which are connate in males), and abdominal sternite VII (ventrite 5) subtriangular, with posterior margin rounded (more transverse, with posterior margin more widely rounded in males). Additional differences are less apparent. Females have head including eyes 0.8–1.0 times as wide as anterior margin of pronotum (1.0–1.1 times in males), eyes relatively smaller, with their minimum frontal separation 1.90–2.30 times maximum eye diameter (1.55–1.90 times in males), and elytra 4.05–4.20 times as long as pronotum (3.50–4.05 times in males). For some differences in coloration, see the Intraspecific variability section below.

Intraspecific variability

Coloration and morphology

There are usually only slight differences in body coloration in *P. angulosus*. In males, elytral coloration ranges from light brown to reddish brown or brown. Females have a tendency to have more or less darker elytra than males, and have greater variability in elytral coloration than males. Two females from Turkey are completely dark brown to black; the first one was described as *Pseudophyllocerus atricolor* by Reitter (1896), and the second one (Fig. 1F) was collected in 2002 by the Czech amateur entomologist Martin Samek (currently deposited in PCJM). Posterior angles of pronotum in males and most females are lighter than pronotal disk; however, some specimens have them less distinctly lighter, and some females have them dark brown to black, i.e., of the same color as pronotal disk. Scutellar shield in males is usually brown to black but some specimens have it distinctly lighter, of the same color as elytra. All available females have their scutellar shield dark brown to black. In males, femora are always darker than tibiae and tarsi; in some cases, tibiae (at least partly) are even lighter than tarsi. In females, legs are usually uniformly dark brown to black (brown in a single specimen); in one specimen tibiae are partly lighter, reddish brown to brown. Body size varies between 8.9 and 12.5 mm in males, and between 14.0 and 18.0 mm in females. The pronotum in males is usually rather smooth and with punctures which are separated by about 1–2 (in some parts 3) puncture diameters, with punctures being denser at margins, mainly at posterior margin. However, some specimens have pronotal surface quite rough and punctures denser, separated by about a half of puncture diameter at least in some parts of pronotum. The pronotum in females is usually rough and with punctures which are separated by about 0.5–1.0 puncture diameters; only one available female has pronotum rather smooth and with sparser punctation. The abdominal sternite IX (Fig. 3F–J) is usually 2.3–2.5 times as long as wide, with lateral sides subparallel for most of their length (e.g., 3H); however, some specimens have this sternite relatively narrower, up to 2.7 times as long as wide (e.g., 3I), and in some other specimens, the sides are somewhat rounded (e.g., 3G). There are also some differences in male genitalia among the studied specimens, mainly in the shape of the median lobe (Fig. 3K–O). The median lobe is in its basal 3/5 or 4/5 usually somewhat subparallel-sided; however, some specimens has that part of the median lobe gradually narowed toward apex. There are also slight differences in the shape of the apical portion of median lobe (Fig. 3K–O).

DNA

The uncorrected pairwise distances between the specimens from Turkey, Behramkale and Greece, Peloponnese, were 7.33% (*cox1*) and 2.43% (*rrnL*).

Biology and ecology

There is almost no information on the biology and ecology of *P. angulosus*. Adults can be found since the end of May till August; however, most specimens with known data were collected or observed in June and July. Adults were usually swept from the vegetation (Fig. 4A, B).

Distribution

Turkey (Germar 1844), Greece (Oertzen 1886), Israel (Platia 2010), Syria (Platia & Németh 2011). The first record from "Palestina" was published by Reitter (1910). New record for Lebanon (Fig. 4C).

Comparison

Plastocerus angulosus differs from its only congener, *P. thoracicus*, in having the pronotum widest posteriorly (widest anteriorly in *P. thoracicus*), the pronotal sides non-explanate (sides explanate in *P. thoracicus*), the aedeagal parameres narrower, with inner side distinctly sinuate (parameres broader, with inner sides only weakly sinuate in *P. thoracicus*), and the apices of parameres more strongly and narrowly protruded (shortly and roundly protruded in

P. thoracicus). Furthermore, all known males and most females of *P. angulosus* have elytra light brown to reddish brown or brown, being distinctly lighter than the head and prothorax (Fig. 1A–E) while all known specimens of *P. thoracicus* are uniformly blackish (Hájek *et al.* 2020). However, some females of *P. angulosus* also have elytra darker, dark brown to black (Fig. 1F).

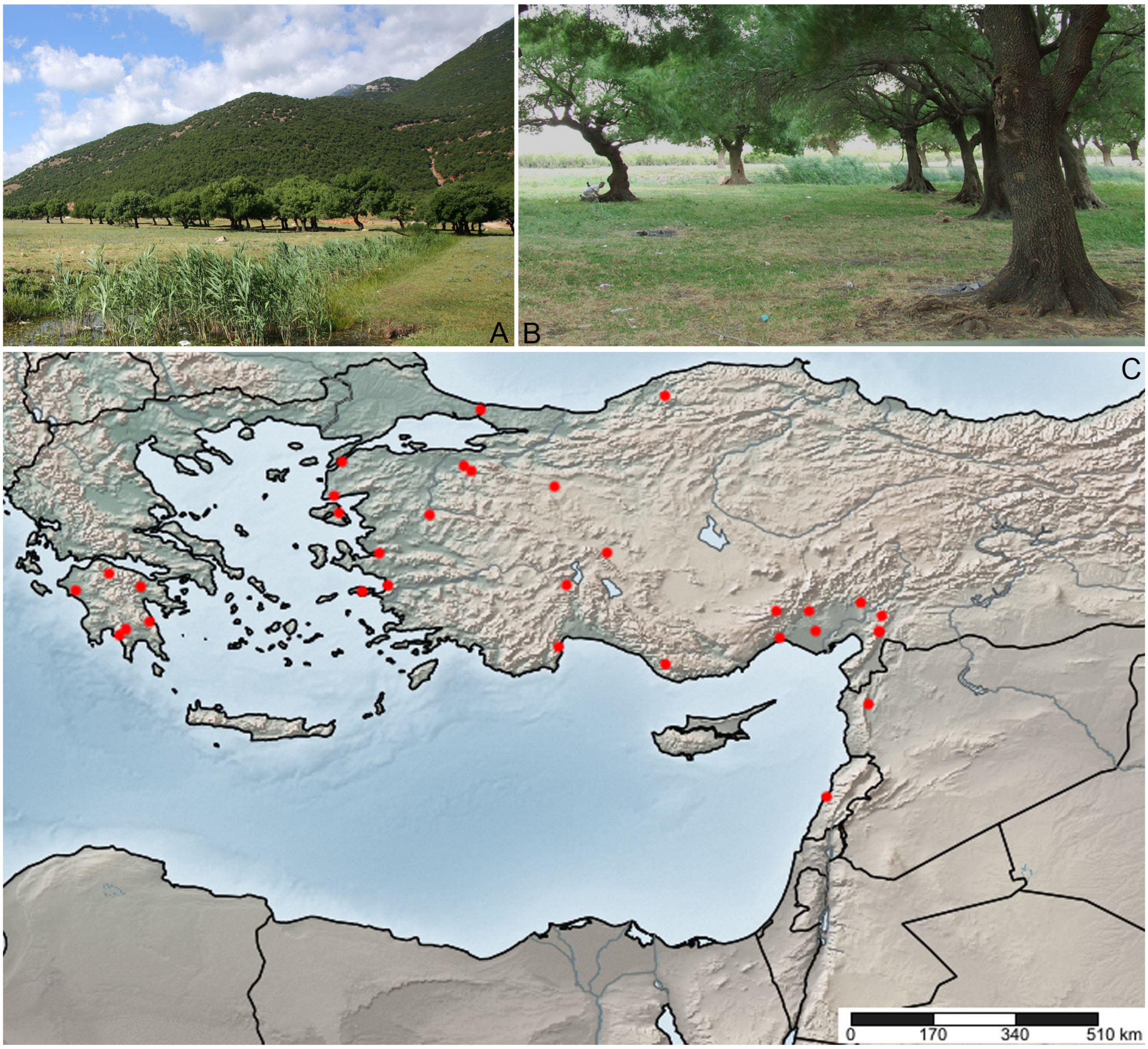

FIGURE 4. Habitat and distributional map of *Plastocerus angulosus* (Germar, 1844). **A–B.** habitat in Syria, Al Ghab, Shatha al Dardar; **C.** distributional map.

Systematics and phylogeny

The classification of *P. angulosus* is full of changes and different opinions by different authors. Early authors placed it usually in Cebrionidae or Elateridae (incl. Cebrioninae) (e.g., Schaum 1852, LeConte 1853, Lacordaire 1857, Marseul 1857, Candèze 1863). LeConte (1861) erected the tribe Plastocerini in Elateridae, with two subgroups, Aphrici for the genus *Aphricus* LeConte, 1853, and Plastoceri for the genera *Plastocerus* sensu LeConte and *Euthysanius* LeConte, 1853.

Schwarz (1907) treated Plastoceridae as a separate family and classified there 11 genera, including *Ceroplastus* (= *Plastocerus* Schaum), *Plastocerus* LeConte (currently *Octinodes*), *Aphricus*, *Aplastus* LeConte, 1859, *Cephalodendron* Latreille, 1834, *Diplophoenicus* Candèze, 1895, *Dodecacius* Schwarz, 1902, *Eniconyx* Horn, 1884, *Euplastius* Schwarz, 1903, *Euthysanius*, and *Phyllocerus* Lepeletier & Serville, 1828. Genera except *Ceroplastus* (= *Plastocerus* Schaum) are currently classified in various elaterid subfamilies such as Cardiophorinae, Morostominae, Elaterinae (tribe Aplastini), and also in the family Eucnemidae (e.g., Muona 1993; Dolin 2000; Johnson 2002, 2017;

Kundrata & Bocak 2011, Douglas *et al.* 2018). It is worth mentioning that none of them is classified in Cebrionini as reported by Bocak *et al.* (2018). The presence of the eucnemid *Phyllocerus* in Plastoceridae of that time was probably the reason why *Plastocerus* was in some cases classified in Phylloceridae or Elateridae: Phyllocerinae (e.g., Reitter 1905, Jakobson 1913, Winkler 1925, Fleutiaux 1941).

Crowson (1972) redefined Plastoceridae to include only *Plastocerus* Schaum but not the New World *Plastocerus* sensu LeConte (i.e., *Octinodes*), and classified it in the superfamily Cantharoidea together with Drilidae, Omalisidae (both currently also in Elateridae), Cantharidae, Lampyridae, Lycidae, Omethidae, Phengodidae, and Telegeusidae (currently in Omethidae). His concept of a separate monogeneric family was followed by some authors even after Cantharoidea were merged with Elateroidea (e.g., Lawrence 1988, 1991; Lawrence & Newton 1995; Branham & Wenzel 2001, 2003; Bocak 2007; Branham 2010; Bouchard *et al.* 2011). Lawrence (1988) hypothesized that *Plastocerus* is sister to all remaining cantharoids, and this view was adopted by Branham & Wenzel (2001, 2003).

On the other hand, the affinities of *Plastocerus* to Elateridae were again recognized by recent elaterid taxonomists (Mertlik & Platia 2008, Gülperçin & Tezcan 2010, Platia & Németh 2011) and confirmed by molecular analyses (e.g., Bocak *et al.* 2018; Kusy *et al.* 2018, 2021a, 2021b; Douglas *et al.* 2021). In vast majority of those studies, plastocerids were considered a separate subfamily Plastocerinae. In the analyses by Bocak *et al.* (2018), *Plastocerus* formed a clade with *Oxynopterus* Hope, 1842 or with *Oxynoperus* and *Pectocera* Hope, 1842, depending on the dataset analyzed (with or without *Pectocera*). Kusy *et al.* (2018, 2021a) did not include *Oxynopterus* in their analyses, and *Plastocerus* formed a clade with *Pectocera*. Kusy *et al.* (2021b) included only a limited number of elaterids in their analyses, without any Oxynopterini, and *Plastocerus* was recovered in Dendrometrinae, sister to *Anostirus* Thomson, 1859.

Douglas *et al.* (2021) provided so far the largest phylogenomic analysis for Elateridae, and found *P. angulosus* within the subfamily Dendrometrinae, hence lowering status of Plastocerinae to a tribal level. *Plastocerus* was sister to *Oxynopterus* in a clade with Dimini (Douglas *et al.* 2021). It is worth mentioning that already Heyden *et al.* (1883) and Reitter (1891) placed *P. angulosus* in Denticollini (currently a synonym of Dendrometrinae).

Literature

Germar (1844: 5): habitus drawing of *Callirhipis angulosa*; Frivaldszky (1845: 177): distributional note [as *Campylus orientalis*]; Schaum (1845: 207): remarks on species published by Germar (1844); Schaum (1852: 49): transfer of *Callirhipis angulosus* to the new genus *Plastocerus* [in "Cebrionites"]; LeConte (1853: 502): taxonomic remarks [*Plastocerus* LeConte, nec Schaum; currently *Octinodes*; in Elaterides: Cebrionites]; Lacordaire (1857: 232): catalogue [as *Callirhipis angulosa*; in Élatérides: Campylides]; Marseul (1857: 99): catalogue [as *Phyllocerus angulosus*; in Cebrionidae]; Redtenbacher (1857: 516): catalogue [in Cebrionides]; Jacquelin du Val (1859: 129): catalogue, drawings of male habitus and tarsus [in Élatérides: Ludiites]; LeConte (1861: 174): catalogue, identification key, tribe Plastocerini based on the American concept of the genus (now *Octinodes*) [only genus name mentioned]; Candèze (1863: 485): catalogue, redescription; drawings of female habitus, and male and female antenna [in Élatérides: Campylides]; Harold (1869: 1601): catalogue [in Elateridae]; Redtenbacher (1872: 557): catalogue [in Elaterides]; Heyden *et al.* (1883: 111): catalogue, *Ceroplastus* for the first time as a replacement name for *Plastocerus* [in Elateridae: Denticollini]; Oertzen (1886): distributional record from Greece; Marseul (1887: 265): catalogue [in Elateridae]; Seidlitz (1888: 41): identification key [as *Ceroplastus*; in Campylini]; Reitter (1891: 210): catalogue [as *Ceroplastus*; in Elateridae: Denticollini]; Reitter (1896: 234): original descriptions of *Pseudophyllocerus* and *Ps. atricolor*, habitus drawing of *Ps. atricolor*; Schwarz (1897: 64): synonymy of *Pseudophyllocerus atricolor* with *Plastocerus angulosus*; Heyden (1902: 152): nomenclatural note on *Plastocerus* vs. *Cladocerus* vs. *Ceroplastus*; Reitter (1902: 93): notes on a generic name for *Plastocerus angulosus* [also as *Pseudophillocerus* [sic!] *atricolor*]; Schwarz (1902: 199): taxonomic/nomenclatural problem *Plastocerus* LeConte vs *Octinodes* Candèze, replacement name *Cladocerus* for *Plastocerus* sensu Candèze (1863); Reitter (1905: 4): identification key [only genus name *Ceroplastus*, in Phylloceridae]; Schwarz (1907: 5): catalogue, drawings of male and female habitus [as *Ceroplastus angulosus*; in Plastoceridae]; Heyne & Taschenberg (1908: 166): catalogue [only genus name mentioned; as *Ceroplastus*, in Elateridae: Plastocerini]; Reitter (1910: 178): systematic notes on *Ceroplastus atricolor* and *C. angulosus*; Jakobson (1913: 765): catalogue [as *Ceroplastus*; in Phylloceridae (Plastoceridae)]; Hyslop (1921: 634, 635): catalogue of genus-group names, *Callirhipis angulosus* as the type species for both *Ceroplastus* and *Cladocerus* [in Rhipiceridae]; Hyslop (1923: 157): status of Plastoceridae [as *P. angulosa* [sic!]; in Elateridae: Cebrioninae]; Winkler (1925: 578): catalogue [as *Ceroplastus*; in Phylloceridae]; Schenkling (1927: 5): catalogue [as *Ceroplastus*;

in Plastoceridae]; Fleutiaux (1941: 36): remark [as *Ceroplastus*; in Elateridae: Phyllocerinae]; Crowson (1972: 44): new family Plastoceridae in Cantharoidea for *Plastocerus* Schaum, taxonomical remarks on *Plastocerus* vs. *Ceroplastus* vs. *Octinodes* problem, drawings of prothorax, metendosternite, and aedeagus; Stibick (1979: 175): remark, notes on classification [in Elateridae: Aplastinae: Aplastini]; Lawrence (1988: 15): phylogeny [only genus name mentioned; in Plastoceridae]; Lawrence (1991: 422): remarks [in Plastoceridae]; Lawrence & Newton (1995: 855): catalogue, taxonomic remarks [in Plastoceridae]; Branham & Wenzel (2001: 580): morphology-based phylogeny [also as *Ceroplatus* [sic!]; in Plastoceridae]; Branham & Wenzel (2003: 5): morphology-based phylogeny [also as *Ceroplatus* [sic!]; in Plastoceridae]; Bocak (2007: 209): catalogue [also as *Pseudophylocerus* [sic!]; in Plastoceridae]; Mertlik & Platia (2008: 27, 34): catalogue [in Elateridae: Plastocerinae]; Branham (2010: 103): review of Plastoceridae (distribution, biology, ecology, morphology, phylogeny, classification), photographs of male habitus and prothorax, ventral view [in Plastoceridae]; Gülperçin & Tezcan (2010: 52): catalogue, distribution [in Elateridae: Plastocerinae]; Platia (2010: 41): distributional record (first record from Israel) [in Elateridae: Aplastini]; Hájek (2011: 57): remark [in Plastoceridae]; Bouchard *et al.* (2011: 320): catalogue of family-group names, ICZN problem [only genus name mentioned; in Plastoceridae]; Platia & Németh (2011: 104): distributional records (first record from Syria) [in Elateridae: Aplastini]; Platia & Kakiopoulos (2014: 118): distributional record (first record from the continental Greece), photographs of male habitus and genitalia [in Plastoceridae]; Bocak *et al.* (2018: 2): molecular phylogeny, morphology, photographs of male and female habitus, and details of body parts including genitalia [in Elateridae: Plastocerinae]; Kusy *et al.* (2018: 4): genome-based phylogeny, remarks, photograph of female habitus [in Elateridae: Plastocerinae]; Hájek *et al.* (2020: 392): remarks, comparison with another species [in Elateridae: Plastocerinae]; Kusy *et al.* (2021a: 115): genome-based phylogeny, *Plastocerus* [only genus name mentioned; *P. angulosus* in Supplements; in Elateridae]; Kusy *et al.* (2021b: 3): mitogenome-based phylogeny [in Elateridae: Plastocerinae or Dendrometrinae], Douglas *et al.* (2021: 10): molecular phylogeny, *Plastocerus* [only genus name mentioned; in Elateridae: Dendrometrinae: Plastocerini]; Lawrence *et al.* (2021: 592): hind wing venation description and photograph [in Elateridae].

Discussion

Plastocerus has always been an enigmatic and interesting beetle lineage from the systematic, morphological, and evolutionary point of view. Although some mysteries and questions about *Plastocerus* have been, at least partly, solved, others remain to be fully understood.

The systematic placement of *Plastocerus* in Elateridae seems to be no longer a question anymore. Higher number of free abdominal ventrites, which was one of the characters used for the definition of Plastoceridae, can be found in some other morphologically modified Elateridae, such as Elaterinae: Cebrionini, Agrypninae: Drilini, and Omalisinae (Kundrata & Bocak 2019). It should be noted, that although some (male) or all (female) abdominal ventrites of *P. angulosus* are free, they are clearly much more sclerotized than in the soft-bodied elateroids like e.g., fireflies (Lampyridae), net-winged beetles (Lycidae) or soldier-beetles (Cantharidae). Recent molecular phylogenetic and phylogenomic studies suggest close relationships of *Plastocerus* and Oxynopterini (Bocak *et al.* 2018, Douglas *et al.* 2021). Douglas *et al.* (2021) considered the clade "Dimini + (Plastocerini + Oxynopterini)" as a part of the widely delimited Dendrometrinae; however, further analyses with much denser sampling are needed to better understand their relationships. If that clade is indeed sister to all remaining dendrometrines, than it is a matter of opinion if one consider the above-listed three groups as tribes in Dendrometrinae or three separate subfamilies.

There is also an interesting question whether all known populations of *P. angulosus* represent a single species. Reitter (1896) described a unicolor dark female as a separate genus and species (i.e., *Pseudophyllocerus atricolor*), and although it was immediately synonymized with *P. angulosus* by Schwarz (1897), Reitter (1910) later recognized it at least as a separate species of *Ceroplastus* (=*Plastocerus*) due to its different body coloration. Here, we examined by far the most specimens of *P.angulosus* ever studied in a single study (over 70 specimens from various collections, ranging from historical specimens to freshly collected materials), and we found some variability in the body size, coloration, protonal punctation, and the shape of pregenital segments and genitalia (Fig. 3). None of the variable characters is correlated with geographic distribution, and there is no indication that there is some cryptic species within *P. angulosus*. Dark brown to black female specimens are indeed just color morphs of *P. angulosus* and do not represent a different species, as already suggested by Schwarz (1897). Such variability in the body coloration can be found in various other Palaearctic Elateridae, such as *Denticollis linearis* (Linneaus, 1758), *Hypoganus* *inunctus* (Panzer, 1795), *Calambus bipustulatus* (Linnaeus, 1767), and *Elater ferrugineus* Linneaus, 1758 (pers. observ. of authors). For the first time, we also compared widely used *cox1* mitochondrial genetic marker between two populations of *P. angulosus*. Relatively high genetic difference in the *cox1* fragments (7.33%) between the specimens from Turkey, Behramkale and Greece, Peloponnese, indicates that the intraspecific genetic variability within *P. angulosus* may be even higher when we take into account geographically much more distant populations, e.g., from the Levant. Such divergence greatly surpasses the previously widely accepted 3% threshold indicating separate species in many insect groups (Hebert *et al.* 2003) but even higher intraspecific genetic distances were reported for various beetle groups (e.g., Hendrich *et al.* 2015, Kundrata *et al.* 2015). Higher genetic differentiation can often be found in lineages with limited dispersal propensity rather than in good dispersers (Ikeda *et al.* 2012). Both sexes of *P. angulosus* are fully winged but we have no data how good fliers they are.

There were some confusing and misleading statements about the females of *P. angulosus* in the past. The female of this species was clearly known to elaterid specialists already in the 19th century. Candèze (1863) provided description and illustrations for a female of *P. angulosus*. The female was generally similar to male but was more robust and had less pectinate antennae. Additionally, Schwarz (1897) pointed out that *Pseudophyllocerus atricolor* described by Reitter (1896) from Turkey is in fact a female specimen of *P. angulosus*. Our current research on *Plastocerus* shows that there is quite a number of historical female specimens present in various European museums. Having this in mind, it is rather surprising that Crowson (1972) stated that female of *P. angulosus* resembles that of *Omalisus* in having no wings and the elytra much shorter than the abdomen. This was repeated by Branham & Wenzel (2001). What is more, Branham (2010) stated that the female of *Plastocerus* was unknown. However, it has been known for more than 150 years; it is similar to male and with fully developed hind wings and elytra (Fig. 1D–E).

The immature stages of *P. angulosus* still remain to be discovered and described. Crowson (1972) speculated that the yet undescribed larva of *Plastocerus* would be expected to resemble that of *Omalisus* but this was probably based on his wrong assumption that *Plastocerus* is closely related to omalisids, and that also its females resemble those of *Omalisus*. Because adults are often collected by sweeping in grassy areas, we can hypothesize that larvae live in soil as many other Palaearctic dendrometrine click-beetles, such as *Athous* Eschscholtz, 1829, *Cidnopus* Thomson, 1859, and *Selatosomus* Stephens, 1830. (T. Németh, pers. observ.).

We hope that our study will motivate our colleagues to collect more materials of this enigmatic click-beetle species, and that the remaining above-mentioned questions about *P. angulosus* will soon be answered.

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References

Arnett, R.H. (1962) *The beetles of the United States (a manual for identification). Part III Suborder Polyphaga (cont.) series Staphyliniformia (concl.) Histeroidea, Series Scarabaeiformia Scarabaeoidea, Dascilloidea, Series Elateriformia Byrrhoidea, Dryopoidea, Buprestoidea, Elateroidea*. Catholic University of America Press, Washington, D.C., pp. 369–526.

Bálint, Z. & Abadjiev, S. (2006) An annotated list of Imre Frivaldszky's publications and the species-group and infraspecies names proposed by him for plants and animals (Regnum Plantare and Animale). *Annales Historico-Naturales Musei Nationalis Hungarici*, 98, 185–280.

Bocak, L. (2007) Plastoceridae Crowson, 1972. *In*: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 4. Elateroidea Derodontoidea Bostrichoidea Limexyloidea Cleroidea Cucujoidea*. Apollo Books, Stenstrup, pp. 209.

Bocak, L., Motyka, M., Bocek, M. & Bocakova, M. (2018) Incomplete sclerotization and phylogeny: The phylogenetic classification of *Plastocerus* (Coleoptera: Elateroidea). *PLoS One*, 13 (3), e0194026.
https://doi.org/10.1371/journal.pone.0194026

Bocakova, M., Bocak, L., Hunt, T., Teraväinen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics*, 23 (5), 477–496.
https://doi.org/10.1111/j.1096-0031.2007.00164.x

Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A. & Smith, A.B.T. (2011) Family-group names in Coleoptera (Insecta). *ZooKeys*, 88, 1–972.
https://doi.org/10.3897/zookeys.88.807

Branham, M.A. (2010) 4.8. Plastoceridae Crowson, 1972. *In*: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds.), *Coleoptera, Beetles. Vol. 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. *In*: Kristensen, N.P. & Beutel, R.G. (Eds.), *Handbook of Zoology, Arthropoda: Insecta*. Walter de Gruyter GmbH and Co. KG, Berlin/New York, pp. 103–104.
https://doi.org/10.1515/9783110911213.103

Branham, M.A. & Wenzel, J.W. (2001) The Evolution of bioluminescence in Cantharoids (Coleoptera: Elateroidea). *The Florida Entomologist*, 84 (4), 565–586.
https://doi.org/10.2307/3496389

Branham, M.A. & Wenzel, J.W. (2003) The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics*, 19 (1), 1–22.
https://doi.org/10.1111/j.1096-0031.2003.tb00404.x

Costa, C., Lawrence, J.F. & Rosa, S.P. (2010) 4.7. Elateridae Leach, 1815. *In*: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds.), *Coleoptera, Beetles. Vol. 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. *In*: Kristensen, N.P. & Beutel, R.G. (Eds.), *Handbook of Zoology, Arthropoda: Insecta*. Walter de Gruyter GmbH and Co. KG, Berlin/New York, pp. 75–103.
https://doi.org/10.1515/9783110911213.75

Candèze, E.C.A. (1863) Monographie des Élatérides. Tome quatriéme. *Mémoires de la Société Royale des Sciences de Liége*, 17, 1–534.

Crowson, R.A. (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid*, 21 (82), 35–77.

Dolin, V.G. (2000) Znachenie lichinochnykh priznakov i zhilkovaniya krylev v sistematike Elateroidea (Coleoptera). Doklad na pyat'desyat vtorom ezhegodnom chtenii pamyati N A Kholodkskogo 1 aprelya 1999 g. [A role of larval and wing venation characters in the systematics of Elateroidea (Coleoptera). Meetings in memory of N.A. Chlodkovsky. Lecture at the 52nd annual meeting, 1 April 1999]. Zoologicheskiy Institut, St. Petersburg, 50 pp. [in Russian]

Douglas, H., Kundrata, R., Janosikova, D. & Bocak, L. (2018) Molecular and morphological evidence for new genera in the click-beetle subfamily Cardiophorinae (Coleoptera: Elateridae). *Entomological Science*, 21 (3), 292–305.
https://doi.org/10.1111/ens.12306

Douglas, H., Kundrata, R., Brunke, A.J., Escalona, H.E., Chapados, J.T., Eyres, J., Richter, R., Savard, K., Ślipiński, A., McKenna, D. & Dettman, J.R. (2021) Anchored phylogenomics, evolution and systematics of Elateridae: Are all bioluminescent Elateroidea derived click beetles? *Biology*, 10, 451.
https://doi.org/10.3390/biology10060451

Fleutiaux, E. (1941) Les Élatérides de l'Indo-Chine Française. *Bulletin de la Société Entomologique de France*, CIX, 19–40.

Frivaldszky, I. (1845) Rövid Áttekintese Egy Természetrajzi Utazásnak, Az Európai Törökbirodalomban, Egyszersmind Nehány A Közben Újdonnat Fölfedezett Állatnak Leirása*. A Királyi Magyar Természettudományi Társulat Évkönyvei*, 1, 163–187.

Germar, E.F. (1844) *Fauna Insectorum Europae. Fasciculus XXIII*. C. A. Kümmelii, Halae, 25 pls.

Gülperçin, N. & Tezcan, S. (2010) *Distributional catalogue of Turkish Elateridae (Insecta: Coleoptera) fauna*. Meta Basým, Izmir, 64 pp.

Hájek, J. (2011) World catalogue of the family Callirhipidae (Coleoptera: Elateriformia), with nomenclatural notes. *Zootaxa*, 2914 (1), 1–66.
https://doi.org/10.11646/zootaxa.2914.1.1

Hájek, J., Ivie, M.A. & Lawrence, J.F. (2020) *Binhon atrum* Pic – a junior synonym of *Plastocerus thoracicus*, with nomenclatural notes on *Plastocerus* (Coleoptera: Elateridae: Plastocerinae). *Acta Entomologica Musei Nationalis Pragae*, 60 (2), 391–396.
https://doi.org/10.37520/aemnp.2020.23

Harold, B. (1869) Familia XXXVIII. Elateridae. *In*: Gemminger, M. & Harold, B. (Eds.), *Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. V. Buprestidae, Trixagidae, Monommidae, Eucnemidae, Elateridae, Cebrionidae*. E. H. Gummi, Monarchii, Paris and London, pp. 1487–1604.

Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society London B*, 270 (1512), 313–321. https://doi.org/10.1098/rspb.2002.2218

Hendrich, L., Morinière, J., Haszprunar, G., Hebert, P.D.N., Hausmann, A., Köhler, F. & Balke, M. (2015) A comprehensive DNA barcode database for Central European beetles with a focus on Germany: adding more than 3500 identified species to BOLD. *Molecular Ecology Resources*, 15 (4), 795–818. https://doi.org/10.1111/1755-0998.12354

Heyden, L. von, Reitter, E. & Weise, J. (1883) *Catalogus coleopterorum Europae et Caucasi*. *Editio tertia*. Edw. Janson, Londini/Libraria Nicolai, Berolini/Luc. Buquet, Parisiis, 228 pp. https://doi.org/10.5962/bhl.title.8788

Heyden, L. von (1902) Bemerkung zu der Arbeit des Herrn O. Schwarz über die Elateriden-Gattungen *Plastocerus* Leconte und Candèze. *Deutsche Entomologische Zeitschrift*, 1902 [46] (1), 152.

Heyne, A. & Taschenberg, O. (1908) *Die Exotischen Käfer in Wort und Bild*. J.F. Schreiber, Esslingen und München, 262 pp., 39 pls.

Hyslop, J.A. (1921) Genotypes of the Elaterid beetles of the world. *Proceedings of the United States National Museum*, 58 (2353), 621–673. https://doi.org/10.5479/si.00963801.2353.621

Hyslop, J.A. (1923) The present status of the coleopterous family Plastoceridae. *Proceedings of the Entomological Society of Washington*, 25 (7–8), 156–160.

ICZN [International Commission on Zoological Nomenclature] (1999) *International Code of Zoological Nomenclature. 4th Edition*. The International Trust for Zoological Nomenclature, London, 306 pp.

Ikeda, H., Nishikawa, M. & Sota, T. (2012) Loss of flight promotes beetle diversification. *Nature Communications*, 3, 648. https://doi.org/10.1038/ncomms1659

Jacquelin du Val, C. (1859) Famille des Élatérides. *In*: Jacquelin du Val, C. (Ed.), *Manuel entomologique. Généra des Coléoptères d'Europe comprenant leur classification en familles naturelles, la description de tous les genres, des tableaux synoptiques destinés à faciliter l'étude, le catalogue de toutes les espèces, de nombreux dessins au trait de charactères et plus de quinze cents types représentant un ou plusieurs insectes de chaque genre dessinés et peints d'après nature avec le plus grand soin par M. Jules Migneaux. Tome troisième*. Chez A. Deyrolle, Paris, pp. 123–141.

Jakobson, G.G. (1913) *Zhuki Rossii i Zapadnoy Evropy. Fasc. 10*. Izdaniye A. Devriena, St. Petersburg, pp. 721–864.

Johnson, P.J. (2002) Elateridae Leach 1815. *In*: Arnett, R.H., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2*. *Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, pp. 160–173.

Johnson, P.J. (2017) A new species of *Dodecacius* Schwarz (Coleoptera: Elateridae) from Madre de Dios, Peru. *Revista Peruana de Biología*, 24 (3), 243–248. https://doi.org/10.15381/rpb.v24i3.13903

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12), 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kundrata, R., Baalbergen, E., Bocak, L. & Schilthuizen, M. (2015) The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Systematics and Biodiversity*, 13 (1), 52–75. https://doi.org/10.1080/14772000.2014.968236

Kundrata, R. & Bocak, L. (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta*, 40 (4), 364–378. https://doi.org/10.1111/j.1463-6409.2011.00476.x

Kundrata, R. & Bocak, L. (2019) Molecular phylogeny reveals the gradual evolutionary transition to soft-bodiedness in click-beetles and identifies sub-Saharan Africa as a cradle of diversity for Drilini (Coleoptera: Elateridae). *Zoological Journal of the Linnean Society*, 187 (2), 413–452. https://doi.org/10.1093/zoolinnean/zlz033

Kusy, D., Motyka, M., Bocek, M., Vogler, A.P. & Bocak, L. (2018) Genome sequences identify three families of Coleoptera as morphologically derived click beetles (Elateridae). *Scientific Reports*, 8, 17084. https://doi.org/10.1038/s41598-018-35328-0

Kusy, D., He, J.-W., Bybee, S.M., Motyka, M., Bi, W.-X., Podsiadlowski, L., Li, X.-Y. & Bocak, L. (2021a) Phylogenomic relationships of bioluminescent elateroids define the 'lampyroid' clade with clicking Sinopyrophoridae as its earliest member. *Systematic Entomology*, 46 (1), 111–123. https://doi.org/10.1111/syen.12451

Kusy, D., Motyka, M. & Bocak, L. (2021b) Click beetle mitogenomics with the definition of a new subfamily Hapatesinae from Australasia (Coleoptera: Elateridae). *Insects*, 12 (1), 17. https://doi.org/10.3390/insects12010017

Lacordaire, J.T. (1857) *Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome quatrième. Contenant les familles des Buprestides, Throscides, Eucnémides, Élatérides, Cébrionides, Cérophytides, Rhipicérides, Dascyllides, Malacodermes, Clérides, Lyméxylones, Cupésides, Ptiniores, Bostrichides et Cissides*. Librairie Encyclopédique de Roret, Paris, 579 pp.

Lawrence, J.F. (1988) Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. *Invertebrate Taxonomy*, 2, 1–53.
https://doi.org/10.1071/IT9880001

Lawrence, J.F. (1991) Plastoceridae (Cantharoidea). *In*: Stehr, F.W. (Ed.), *Immature Insects. Vol. 2*. Kendall/Hunt Publishing, Dubuque, pp. 422.

Lawrence, J.F., Beutel, R.G., Leschen, R.A.B., Ślipiński, A. (2010) Glossary of morphological terms. *In*: Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (Eds.), *Coleoptera, Beetles; Vol. 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. *In*: Kristensen, N.P. & Beutel, R.G. (Eds.), *Handbook of Zoology, Arthropoda: Insecta*. Walter de Gruyter GmbH and Co. KG, Berlin/New York, pp. 9–20.
https://doi.org/10.1515/9783110911213.9

Lawrence, J.F. & Newton, A.F. (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). *In*: Pakaluk, J. & Ślipiński, S.A. (Eds.), *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson. Volume 2*. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 779–1083.

Lawrence, J.F., Zhou, Y.-L., Lemann, C., Sinclair, B. & Ślipiński, A. (2021) The hind wing of Coleoptera (Insecta): Morphology, nomenclature and phylogenetic significance. Part 1. General discussion and Archostemata–Elateroidea. *Annales Zoologici*, 71 (3), 421–606.
https://doi.org/10.3161/00034541ANZ2021.71.3.001

LeConte, J.L. (1853) Revision of the Elateridae of the United States. *Transactions of the American Philosophical Society*, 10, 405–508.
https://doi.org/10.2307/1005288

LeConte, J.L. (1861) *Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution, Part I. Smithsonian Miscellaneous Collections*. The Smithsonian Institution, Washington, 286 pp.

Lin, M.-Y. & Yang, X.-K. (2012) Acanthocnemidae and Plastoceridae newly recorded from China (Coleoptera). *Acta Zootaxonomica Sinica*, 37 (2), 447–449.

Marseul, S.A. de (1857) *Catalogue des Coléoptères d'Europe*. S. A. de Marseul, Paris, xvi + 200 pp.
https://doi.org/10.5962/bhl.title.66031

Marseul, S.A. de (1887) Catalogue des Coléoptères de l'Ancien-Monde: Clavicornes (suite). *L'Abeille: Journal D'Entomologie*, XXIV (VI), 193–213.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R. & Farrell, B.D. (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, 40 (4), 835–880.
https://doi.org/10.1111/syen.12132

Mertlik, J. & Platia, G. (2008) Catalogue of the family Cebrionidae, Elateridae, Lissomidae, Melasidae and Throscidae (Coleoptera) from Turkey. *Elateridarium*, 2, 1–40.

Muona, J. (1993) Review of the phylogeny, classification and biology of the family Eucnemidae (Coleoptera). *Entomologica Scandinavica* , 44 (Supplement), 1–133.

Oertzen, E. von (1886) Verzeichniss der Coleopteren Griechenlands und Cretas, nebst` einigen Bemerkungen über ihre geographische Verbreitung und 4 die Zeit des Vorkommens einiger Arten betreffenden Sammelberichten. *Berliner Entomologische Zeitschrift*, 30 (2), 189–293.
https://doi.org/10.1002/mmnd.47918860211

Palumbi, S.R., Martin, A.P., Romano, S.L., McMillan, W.O., Stice, L. & Grabowski, G. (1991) The simple Fool's Guide to PCR. Department of Zoology, University of Hawaii, Honolulu, 45 pp.

Pic, M. (1922) Nouveautés diverses. *Mélanges Exotico-Entomologiques*, 36, 1–32.

Platia, G. (2010) New species and chorological notes of click beetles from Palearctic Region, especially from the Middle East (Coleoptera, Elateridae). *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)*, 46, 23–49.

Platia, G. & Kakiopoulos, G. (2014) Interesting records of beetles from Greece, with description of a new species (Coleoptera, Elateridae and Plastoceridae). *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)*, 54, 117–120.

Platia, G. & Németh, T. (2011) On some Palearctic click beetles deposited in the Hungarian Natural History Museum (Coleoptera: Elateridae). *Annales Historico-Naturales Musei Nationalis Hungarici*, 103, 65–106.

Redtenbacher, L. (1857) *Fauna Austriaca. Die Käfer. Nach der analytischen Methode bearbeitet. Zweite, gänzlich umgearbeitete, mit mehreren Hunderten von Arten und mit der Charakteristik sämmtlicher europäischen Käfergattungen vermehrte Auflage. Mit zwei Kupfertafeln*. Carl Gerold's Sohn, Wien , 1017 pp. [1856–1858]

Redtenbacher, L. (1872) *Fauna Austriaca. Die Käfer. Nach der analytischen Methode bearbeitet. Dritte, gänzlich umgearbeitete und bedeutend vermehrte Auflage. Erster Band. Mit zwei Kupfertafeln*. Carl Gerold's Sohn, Wien , 564 pp. [1871–1874]

Reitter, E. (1891) Elateridae. *In*: Reitter, E. (Ed.), *Catalogus Coleopterorum Europae. Caucasi et Armeniae rossicae. Auctoribus Dr. L. v. Heyden, E. Reitter & J. Weise cum aliis sociis coleopterologicis*. R. Friedländer & Sohn, Berlin and Edmund Reitter, Mödling, Caen, pp. 202–210.

Reitter, E. (1896) Abbildungen mit Beschreibungen zehn neuer Coleopteren aus der palaearctischen Fauna (Hierzu Tafel III.).

Wiener Entomologische Zeitung, XV (VIII), 233–240.
https://doi.org/10.5962/bhl.part.13881
Reitter, E. (1902) Coleopterologische Notizen. *Wiener Entomologische Zeitung*, XXI (IV), 92–93.
Reitter, E. (1905) *Bestimmungs-Tabelle der europäischen Coleopteren. LVI. Heft (56.). Enthaltend: Elateridae. 1 Theil. Elaterini, Subtribus: Athouina, aus der palaearctischen Fauna. Mit einer Uebersicht der Familiengruppe der Sternoxia und der Gattungen der Familie der Elateridae*. Verlag von Edmund Reitter—Druck von W. Burkart, Brünn, 122 pp.
Reitter, E. (1910) Beschreibungen neuer Coleopteren aus der Familie der Elateriden und Bemerkungen über bekannte Arten. *Wiener Entomologische Zeitung*, XXIX (V & VI), 165–178.
https://doi.org/10.5962/bhl.part.23347
Schaum, H.R. (1845) Germar Fauna Insectorum Europae fasc. XXIII. *Entomologische Zeitung Stettin*, 6, 207–208.
Schaum, H.R. (1852) *Catalogus Coleopterorum Europae. Herausgegeben vom entomologischen Verein in Stettin. Vierte Auflage*. Trowitzsch und Sohn, Berlin, v + 96 + 12 pp.
Schenkling, S. (1927) Plastoceridae, Dicronychidae. *In*: Junk, W. & Schenkling, S. (Eds.), *Coleopterorum Catalogus. Pars 93*. W. Junk, Berlin, pp. 3–10.
Schwarz, O. (1897) *Pseudophyllocerus atricolor* Reitt. = *Plastocerus angulosus* Germ. ♀. *Deutsche Entomologische Zeitschrift*, 1897 [41] (1), 64.
https://doi.org/10.1002/mmnd.48018970114
Schwarz, O. (1902) Ueber die Elateriden-Gattungen *Plastocerus* Le Conte und *Octinodes* Cand. *Deutsche Entomologische Zeitschrift*, 1901 [45] (2), 199–201.
Schwarz, O. (1907) Coleoptera. Fam. Plastoceridae. *In*: Wytsman, P. (Ed.), *Genera Insectorum. Fascicule 50*. V. Verteneuil & L. Desmet, Bruxelles, pp. 1–10, 1 pl.
Seidlitz, G.C.M. von (1888) *Fauna Baltica. Die Kaefer der Ostseeprovinzen Russlands. Zweite neu bearbeitete Auflage. II. Lieferung*. Hartungsche Verlagsdruckerei, Königsberg, 224 pp.
Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651–701.
https://doi.org/10.1093/aesa/87.6.651
Stibick, J.N.L. (1979) Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. *Pacific Insects*, 20 (2–3), 145–186.
Sormova, E., Kramp, K. & Kundrata, R. (2018) Diversity and phylogenetic relationships of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Cyprus. *Zoologischer Anzeiger*, 275, 1–12.
https://doi.org/10.1016/j.jcz.2018.04.001
Tamura, K., Stecher, G. & Kumar, S. (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*, 38 (7), 3022–3027.
https://doi.org/10.1093/molbev/msab120
Winkler, A. (1925) *Catalogus Coleopterorum regionis palaearcticae. I. A. Caraboidea, B. Palpicornia, Staphylinoidea, C. Diversicornia. Pars 5*. Albert Winkler, Wien, pp. 497–624.

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Research paper

Comparative morphology of larvae of *Elathous agilis* Németh, 2019 and *Elathous brucki* (Candèze, 1878) (Coleoptera: Elateridae: Dendrometrinae), with notes on their biology and ecology

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ABSTRACT

The click-beetle genus *Elathous* Reitter, 1890 (Elateridae: Dendrometrinae) contains almost 50 species distributed in the Palaearctic and Nearctic realms. Specimens of this genus are rare in collections, partly due to their largely unknown biology and ecology. Until now, larvae were known only for three species, all of them described decades ago. Due to the intensive fieldwork research by the first author, who found larvae of *Elathous agilis* Németh, 2019 in Lebanon and *Elathous brucki* (Candèze, 1878) in Greece, we have an opportunity to describe their morphology for the first time. We compare them with each other and the remaining known larvae of *Elathous* and related genera. Although we are able to differentiate larvae of all known *Elathous* species, our limited knowledge on dendrometrine immature stages as well as the genus-level systematics is insufficient to propose a reliable generic diagnosis for *Elathous* based on the larval morphology. Additionally, we provide updated information on biology and ecology of *Elathous* species.

1. Introduction

Immature stages of click-beetles (Coleoptera: Elateridae) play an important role in understanding not only the ecology and biology of the given species but also their systematic placement and phylogenetic relationships (e.g., Hyslop 1917; Glen 1950; Ôhira 1962; Zacharuk 1962; Dolin 1978). Regarding click-beetles, most of the approximately 11,000 described species lack information on their immature stages. What is more, knowledge on click-beetle larvae is biased towards the Palaearctic realm, mainly due to the efforts of Ôhira (1962) and Dolin (e.g., 1960a, 1960b, 1964a, 1964b, 1978), and the Neotropical realm, mainly due to the excellent works of the Brazilian authors (e.g., Costa 1992; Costa et al., 1992; Casari & Bellusci 1996; Casari & Costa 1998; Casari 2002; Casari & Biffi 2012; Rosa et al., 2015; 2019; 2020; Marinho et al., 2023).

The genus *Elathous* Reitter, 1890 (Elateridae: Dendrometrinae) contains 49 described species known mostly from the West Palaearctic (from Morocco to Iran) but also some species from North America and Japan (Kundrata et al., 2021; Németh 2021). Specimens of this genus are rare in collections, most probably due to their unknown biology and ecology. Larvae are known only for three species, all of them described decades ago. Glen (1950) described the larva of the eastern North American *Elathous bicolor* (LeConte, 1853). Dolin (1960b, 1964a, 1964b, 1978, 1982) provided description and illustrations of the larva of *Elathous candezei* Reitter, 1890, and Dolin (1978) and Agaev (1980) provided the same for larva identified as *Elathous niger* Schwarz, 1897. *Elathous* larva was also included in the generic identification keys by Agaev (1988) and Johnson (1993).

The intensive fieldwork focused on the Elateridae species of the Balkans by Czech and Hungarian expeditions between 2009 and 2019 led to many interesting discoveries, including descriptions of new species (Mertlik et al., 2017; 2018) and new faunistic records for many taxa (Kovács et al., 2012; Németh et al., 2014; 2017; 2019). Collecting trips in Lebanon, organized by the Hungarian Natural History Museum with the cooperation of Holy Spirit University of Kaslik and The Committee of Cedar Forest Friends between 2015 and 2018, aimed to increase knowledge on the entomofauna of the country and resulted in discoveries of new species (Márkus & Németh 2016; Szénási & Németh 2019) and interesting faunistic data (Háva & Németh 2016; Németh et al., 2019; Szénási et al., 2019). They also resulted in a huge amount of valuable materials deposited in the collections.

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The first author, who participated in all the above-mentioned expeditions, discovered *Elathous* larvae in Greece and Lebanon. In Greece, he found several larvae in two expeditions to Mt. Timfristos (2013, 2015), with some of them reared in the laboratory to adults allowing their identification as *Elathous brucki* (Candèze, 1878). In Lebanon, similar larvae were collected during the first field trip (2015) to the ancient forest of Horsh Arz el-Rab. These larvae were also reared in laboratory conditions and four adults of, at that time, an unknown *Elathous* species emerged during the summer of 2015. The following field trips in Lebanon between 2016 and 2018 resulted in further specimens of both larvae and adults. Based on the adults, Németh (2019) described a new species, *Elathous agilis* Németh 2019; however, the larvae remained unstudied in detail.

The *Elathous* larval specimens collected during the extensive fieldwork by the first author allow us to describe larval morphology of *E. brucki* and *E. agilis* for the first time and compare those species with each other, their known congeners, and other related genera.

2. Material and methods

This study was based on the larval specimens of *E. agilis* from Lebanon (Figs. 1, 2 and 5A, E) and *E. brucki* from Greece (Figs. 3 and 4). For *E. agilis*, 13 larvae were collected in the field (Fig. 5A, C–E): 10 of them were reared to adults (Fig. 5B) in plastic boxes (capacity 1L) with rotten wood at room temperature and checked every two weeks, two were kept in absolute ethanol (one dissected; Figs. 1 and 2), and one was kept dry, mounted on cardboard. For *E. brucki*, nine larvae were collected in the field (Fig. 5G): five of them were reared to adults using the same conditions as described above (Fig. 5F), two were kept in absolute ethanol (one dissected; Figs. 3 and 4), and two were kept dry and later mounted on a cardboard. For more details, see Material examined under respective species. Several other larval specimens of both species were observed in the field, collected, but were not successfully reared. One larva of each species was first photographed and then dissected after a short treatment in hot 10 % KOH. Dissected parts of the head were transferred to glycerol. Diagnostic characters were photographed using a Mitutoyo M Plan Apo 5X microscope lens and Nikon AF Micro Nikkor 60 mm lens attached to a Nikon D5200 camera. Photographs

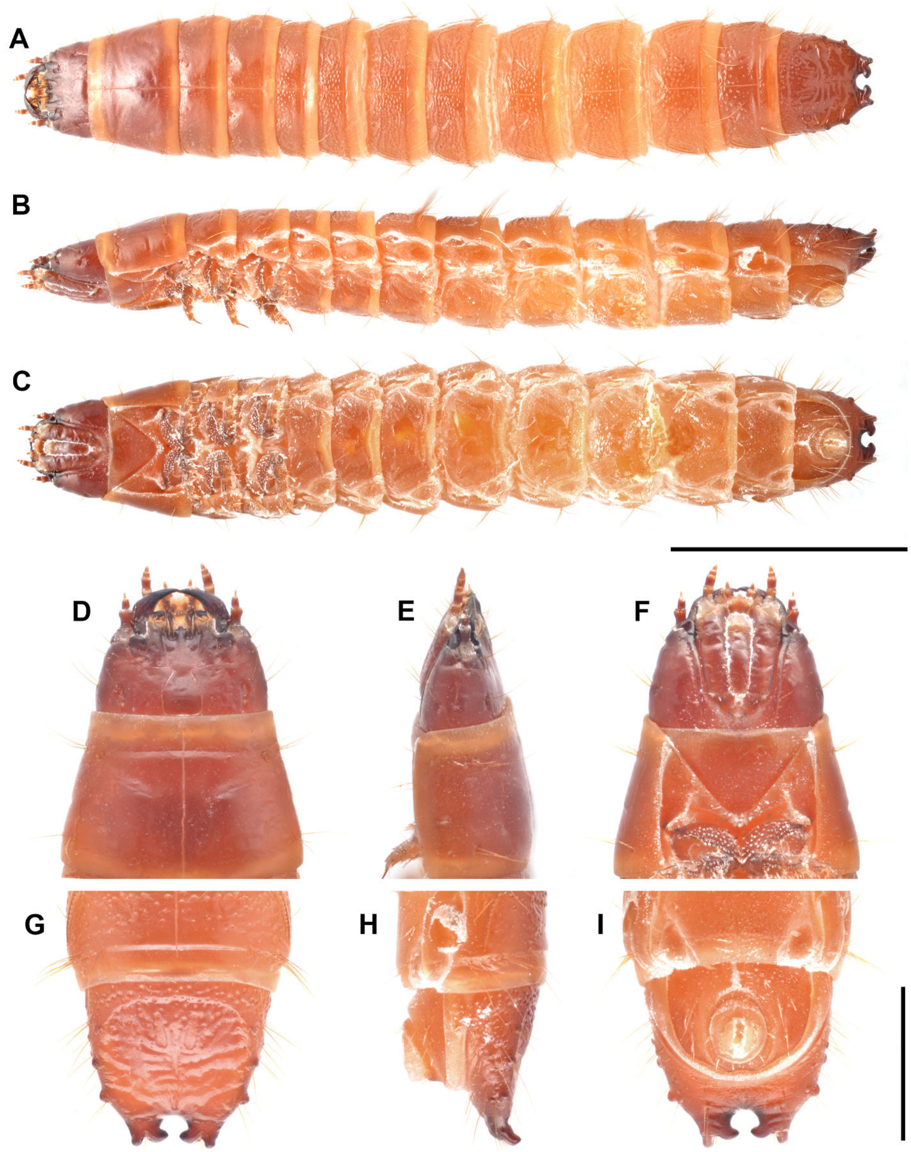

Fig. 1. *Elathous agilis* Németh, 2019, larval morphology. Habitus: (A) dorsal view; (B) lateral view; (C) ventral view. Head and prothorax: (D) dorsal view; (E) lateral view; (F) ventral view. Terminal abdominal segments: (G) dorsal view; (H) lateral view; (I) ventral view. Scale bars: A–C = 5 mm, D–I = 2 mm.

Fig. 2. *Elathous agilis* Németh, 2019, larval morphology. Maxillo-labial complex: (A) dorsal view; (B) ventral view. Antenna: (C) dorsal view; (D) ventral view. Mandible: (E) dorsal view; (F) ventral view. Metathoracic leg: (G) dorsal view. Scale bars: A–B, G = 0.5 mm, C–D = 0.2 mm, E–F = 0.3 mm.

were combined with the Zerene Stacker image stacking software. Measurements were taken with a scale bar in an eyepiece. Photographs of habitats and living specimens were taken with a Fuji Finepix HS25 EXR camera and Raynox 150 and 250 lens. Morphological terminology for larval descriptions follows Glen (1950), Costa et al. (2010), and Rosa et al. (2019). The dorsal plate of segment IX was measured as follows: length at midline from anterior edge of carina or declivity to posterior notch, and width at widest part between lateral edges of carina or declivity, excluding teeth. The lyre-shaped frontal arms of the species examined here (as well as in Elateridae in general) are constricted at approximately midlength, forming two areas with very different shapes and widths, with the anterior part being about three times wider than the posterior part (see e.g., Lawrence et al., 1999). Here we describe differences among *Elathous* species in the shape of the posterior part of frons, which we define as the region from the abrupt constriction between frontal arms up to its base where the frontal arms meet. The locality labels are cited verbatim. The material examined in this study is deposited in the Coleoptera Collection of the Hungarian Natural History Museum, Budapest, Hungary (HNHM).

3. Results

Family Elateridae Leach, 1815.
Subfamily Dendrometrinae Gistel, 1848
Tribe Dendrometrini Gistel, 1848
Genus *Elathous* Reitter, 1890.

Elathous Reitter, 1890: 247. Type species: *Elathous buyssoni* Reitter, 1890; by subsequent designation (Hyslop, 1921: 644).

For the synonyms and more information see the annotated catalogue by Kundrata et al. (2021).

3.1. *Elathous agilis* Németh, 2019

(Figs. 1, 2, 5A–E)

3.1.1. Material examined

One larval specimen in absolute ethanol (dissected; Figs. 1 and 2), with the following label data: "Lebanon, Northern gov., 2 km N Harissa, Tannourine Cedars Nat. Reserve, from rotten *Cedrus libani* log, 34°12′34"N, 35°55′45"E, 1750 m, 24.VII.2018, leg. T. Németh". One larval specimen in absolute ethanol, with the following label data: "Lebanon, Northern gov., Bcharre env., Quadisha Valley, from rotten *Juglans*, 34°14′57"N, 35°58′34"E, 970 m, 5.V.2017, leg. T. Németh". One larval specimen dry, glued to cardboard, with the following data: "Lebanon, Northern gov., Tannourine env., 2 km N Harissa, Tannourine Cedars Nat. Reserve, from rotten Cedar log, 34°12′34.56"N, 35°55′45.15"E, 1750 m, 23.V.2015., leg. T. Németh."

Ten larvae from the following localities were successfully reared to adults: 1 male, "Lebanon, Northern gov., Tannourine env., 2 km N Harissa, Tannourine Cedars Nat. Reserve, reared from hollow oak, 34°12′34"N, 35°55′45″E, 1750 m, 6.V.–VII.2017, leg. A. Kotán, P. Nemes & T. Németh" (Fig. 5A); 1 male, 2 females, "Lebanon, Northern gov.,

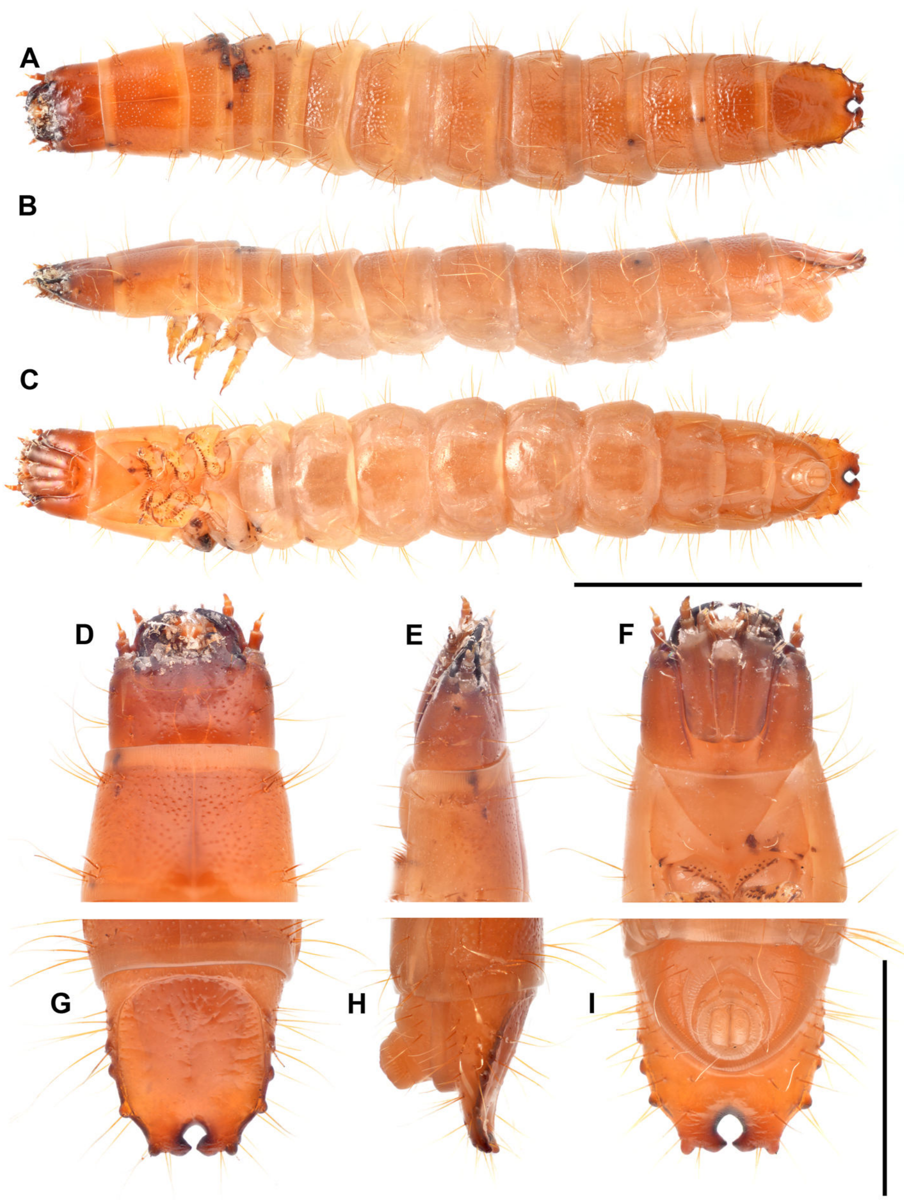

Fig. 3. *Elathous brucki* (Candéze, 1878), larval morphology. Habitus: (A) dorsal view; (B) lateral view; (C) ventral view. Head and prothorax: (D) dorsal view; (E) lateral view; (F) ventral view. Terminal abdominal segments: (G) dorsal view; (H) lateral view; (I) ventral view. Scale bars: A–C = 5 mm, D–I = 2 mm.

Bcharre env., 1 km E Ariz, Horsh Arz el-Rab, ancient *Cedrus* forest, larva from *Cedrus* log, 34°14′33"N, 36°2′59″E, 1900 m, 20.V.–25.VII.2015, leg. A. Márkus & T. Németh"; 1 female, "Lebanon, Northern gov., Tannourine env., 2 km N Harissa, Tannourine Cedars Nat. Reserve, reared from rotten *Cedrus* log, 34°12′34"N, 35°55′45″E, 1750 m, 1.V.2017, leg. A. Kotán, P. Nemes & T. Németh"; 2 males, 3 females, "Lebanon Northern gov., Bcharre env., 1 km E Ariz, Horsh Arz el-Rab, ancient *Cedrus* forest, pupa from rotten *Cedrus* log, 34°14′33"N, 36°2′59″E, 1900 m, 24.VI.2016, leg. A. Kotán, P. Nemes & T. Németh".

The photographs of live larval specimen of *E. agilis* were published by Németh (2019: 152) and can also be found in Fig. 5A, E.

3.1.2. Diagnosis

The mature larva of *E. agilis* can be distinguished from its known congeners by the following combination of characters: head with sides slightly rounded in dorsal view, stemmata absent, head and thoracic mediotergites with punctures narrower than thoracic mid-dorsal suture, separated by a distance of 6–10 puncture diameters; posterior part of frons with sides divergent on anterior half, subparallel on posterior half; abdominal mediotergites with transverse branches reaching 2/3 of the lateral half of mediotergite width, and a transverse row of short 14–16 setae near posterior margin, with longest setae about 2/3 of segment length; dorsal plate of segment IX bordered by declivous edge, with three lateral teeth, a pair of paramedian impressions, a median longitudinal groove and several transverse grooves; apical notch semicircular.

3.1.3. Description

Mature larva. Body (Fig. 1A–C, 5A, E): about 14.2–18.7 mm long, subcylindrical, parallel-sided. Tegument yellow, head and tergite IX dark brown; pronotum and anterior part of mesonotum and metanotum light brown, each anterolateral region of abdominal mediotergites I–VIII with prominent impression extending mesally at approximately a 90-degree angle forming longitudinal and transverse branches; transverse branches of impressions reaching about 3/4 of distance from longitudinal branches to mid-dorsal suture; claws and spine-like setae on legs brown. Vestiture consisting of sparse, light brown setae of various length. Live specimens slightly darker than those preserved in ethanol.

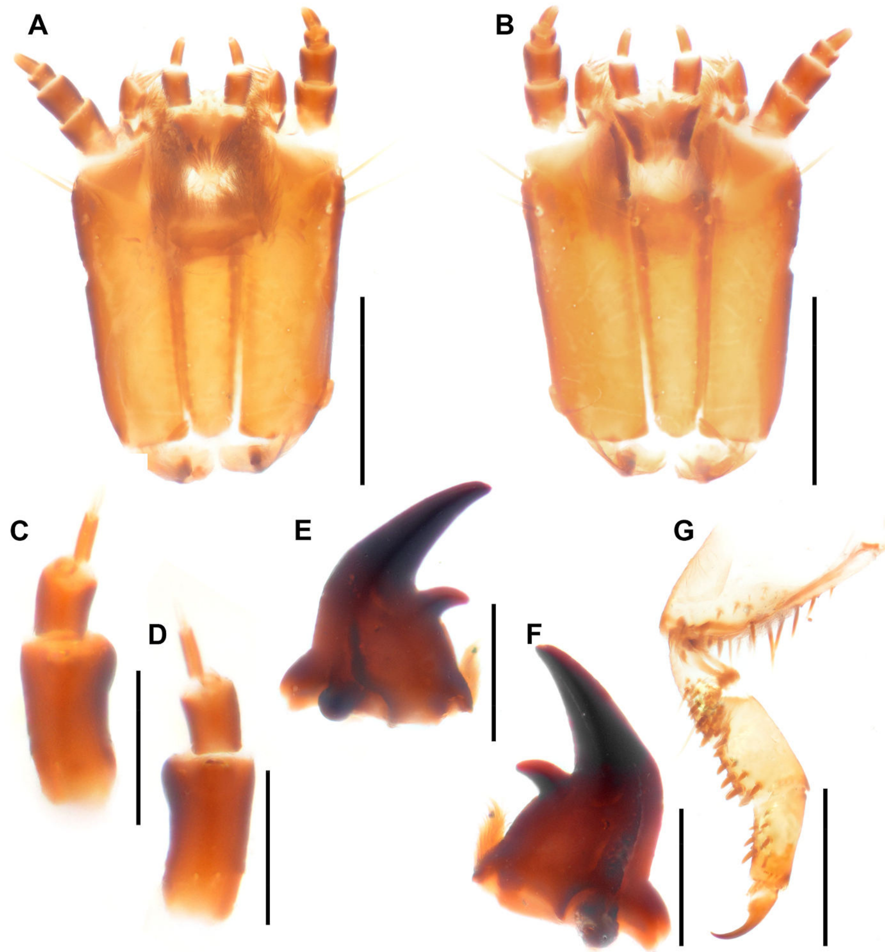

Fig. 4. *Elathous brucki* (Candéze, 1878), larval morphology. Maxillo-labial complex: (A) dorsal view; (B) ventral view. Antenna: (C) dorsal view; (D) ventral view. Mandible: (E) dorsal view; (F) ventral view. Metathoracic leg: (G) dorsal view. Scale bars: A–B, G = 0.5 mm, C–D = 0.2 mm, E–F = 0.3 mm.

Head (Fig. 1D–F): excluding mouthparts, 1.8 times wider than long, with sides slightly rounded in dorsal view, depressed, sparsely punctate, punctures fine, each side with one lateral seta at antennifer base, one dorsal seta posterior to antennifer (at anterior third), one long lateral seta at posterior third, longitudinal dorsal row of three large punctures, most anterior one with long seta, two posterior ones with smaller setae; dorsal epicranial ridges and stemmata absent; coronal suture and endocarina absent. Frontal arms (Fig. 1D) lyre-shaped, frons with sparse punctures mainly distributed at anterolateral margins, anterior corners rounded, four setae along edge of nasal and adnasalia; posterior part of frons with sides divergent at anterior half, parallel at posterior half; nasale produced, tridentate, as long as wide; adnasalia twice as long as nasale, separated by distance 0.5 times as wide as each adnasalium width (measured at base); ventral surface (Fig. 1F) smooth except for one long seta on posterolateral margin and row of shorter setae along outer edge of ventral ridges.

Mandible (Fig. 2E and F) about 1.3 times as long as wide (width measured at base), unidentate; incisor edge with retinaculum, lateral surface of basal half concave, penicillus as long as retinaculum, two setae dorsolaterally. Maxilla (Fig. 2A and B) with stipites about four times as long as wide, subparallel-sided, widely separated at base (distance between stipites 1.2 times as wide as each stipes width at base), anterior margin narrowed and membranous; lateral margin with sparse punctures, few long setae at anterior corner; maxillary palpus four-segmented, elongate, sparsely setose, relative length of palpomeres as follows: I as long as II, III 0.4–0.5 times as long as II, IV as long as III; galea palpiform, two-segmented, with stiff setae at apex; lacinia reduced to densely setose area; cardines somewhat triangular, wider than long. Labium (Fig. 2A and B) with prementum 1.2 times wider than long, with two pairs of setae near anterior margin, parasagittal one longer and thicker, ligula produced, with 2 setae; postmentum 3.6 times as long as wide, sides weakly convergent posteriorly, membranous anteriorly; one pair of long setae anteriorly, few smaller punctures irregularly distributed along lateral margins, apex with pair of long thick setae; basal palpomere 1.4 times longer than apical palpomere. Antenna (Fig. 2C and D) with basal antennomere glabrous, with few campaniform sensilla, 1.6 times as long as median antennomere; second antennomere glabrous, 2.5 times as long as apical antennomere, with conical sensorium lateroventrally; third antennomere with two setae apically.

Thorax (Fig. 1A–F): tergites with fine punctures (0.3–0.5 times as wide as mid-dorsal suture), punctures weakly impressed, mostly separated by distance of 6–10 puncture diameters; prothorax 1.5 times as wide as long, about twice as long as mesothorax, anterior corner with 2 setae laterodorsally and 4 longer setae laterally, posterior corner with 3 setae; prosternum with one seta at each anterior angle, pair of setae apically; mesothorax and metathorax subequal in size, each with 2–3 setae laterally, one seta dorsolaterally at midlength, and two setae dorsolaterally near posterior margin. Leg (Fig. 2G) with lateral surfaces with strongly sclerotized, short, spine-like setae (with rounded sides), longer and acuter on ventral borders (up to three times longer on coxa), densely distributed (distance between setae smaller than seta width); ventrally with few long fine setae; claw with one seta on each basal side.

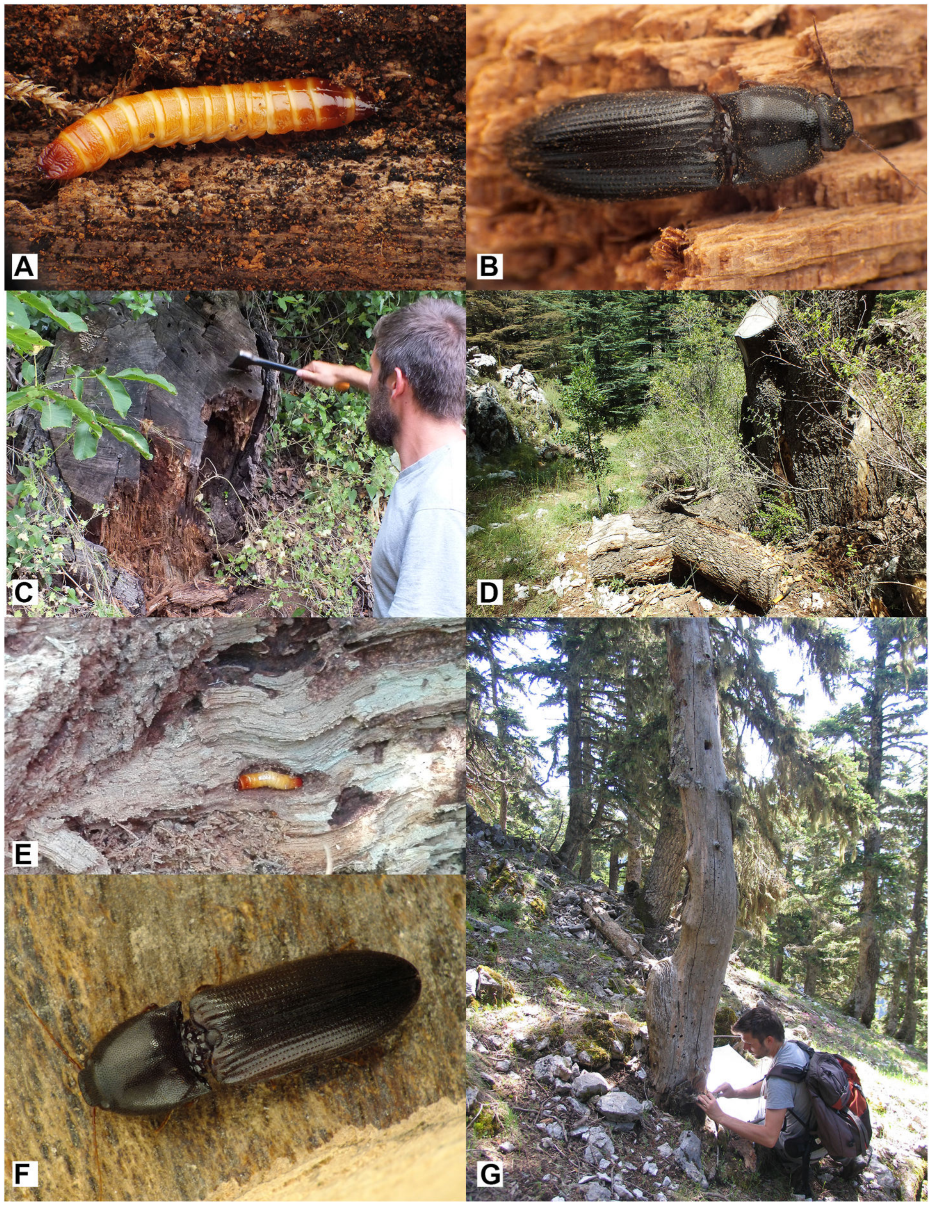

Fig. 5. *Elathous* species and their habitats. (A) Larva of *E. agilis* Németh, 2019, live specimen collected in 2017 in the Tannourine Nature Reserve, Lebanon. (B) Adult female of *E. agilis*, live specimen, reared from a larva collected in 2015 in Bcharre, Lebanon. (C) Collecting *Elathous* larvae from rotten *Juglans regia* in 2015 in Quadisha Valley, Bcharre, Lebanon. (D) Habitat of *E. agilis* in the Tannourine Nature Reserve, Lebanon (2016). (E) Larva of *E. agilis*, live specimen in situ at Tannourine Nature Reserve, Lebanon (2017). (F) Adult female of *E. brucki* (Candéze, 1878), live specimen reared from a larva collected in 2013 in Mt. Timfristos, Greece. (G) Collecting *Elathous* larvae from rotten *Abies* sp. in Mt. Timfristos, Greece.

Abdomen (Fig. 1A–C): mediotergites I–VIII with punctures about 10 times larger than those of metathorax, mostly separated by distance 0.1–0.3 puncture diameter, each side near midlength with 1 seta laterally, transverse row of 14–16 short setae near posterior margin; laterotergite I with two setae posteriorly; pleura with one seta; sternite with lateral pair of setae anteriorly, two lateral pairs of setae posteriorly; segment IX (Fig. 1G–I) with dorsal plate 1.3 times as wide as long, bounded anterolaterally by raised edge, median surface with punctures about 10 times smaller and sparser than those of mediotergite VIII, with well impressed mediodorsal groove and several lateral transverse grooves, anteriorly with pair of paramedian impressions; lateral sides with three blunt teeth, each of them bearing one seta; apex with semicircular notch forming two urogomphi; each urogomphus with two prongs, outer prong directed dorsad, longer than inner prong, inner prong directed medially; lateral and ventral surfaces with long setae; segment X (Fig. 1G–I) tubular, ventral, with long setae anteriorly at base and shorter setae along anal opening; anal hook absent.

3.2. *Elathous brucki* (Candèze, 1878)

(Figs. 3, 4, 5F–G)

Athous brucki Candèze, 1878: clxviii; transferred to *Elathous* by Guglielmi & Platia (1985: 192).

= *Melanathous sequensi* Reitter, 1905: 25; synonymized by Platia & Gudenzi (1996: 141).

3.2.1. Material examined

Four larval specimens: two in absolute ethanol (one dissected; Figs. 3 and 4), two dry glued to cardboard, all with the following label data: "Greece, Central Gr., distr. Evrytania, Mt. Timfristos, 1,5 km NE Karpenissi, fir-forest, 38°55′25.07"N; 21°48′33.45"E, 1451 m, from rotten *Abies*, 11.V.2013., leg. T. Németh". Four larvae from the same locality as well as one larva from the locality with the following label data "Greece, distr. Evritanía, Timfristos Mts., Karpeníssi env., *Abies* forest, 38°55′23.98″N, 21°48′36.43″E, 1420 m, 9.VI.2015., leg. P. Brůha, J. Mertlik, T. Németh & B. Zbuzek" were successfully reared to adults. Four specimens collected in 11.V.2013 emerged in 15.VII.2013, and a single specimen collected in 9.VI.2015 emerged in 9.VII.2015.

3.2.2. Diagnosis

The mature larva of *E. brucki* can be distinguished from known congeners by the following combination of characters: head parallel-sided, with a pair of stemmata, head and thoracic mediotergites with punctures as wide as or wider than thoracic mid-dorsal suture, separated by distance 2–3 puncture diameter; posterior part of frons with sides rounded; abdominal mediotergites with transverse branches reaching the mid-dorsal suture, and transverse row of 8–9 relatively long setae near posterior margin, with longest setae as long as the segment; dorsal plate of segment IX bordered by steep carina, with four lateral teeth and five longitudinal grooves, apical notch lozenge-shaped.

3.2.3. Description

Mature larva. Body (Fig. 3A–C): about 12.0–14.5 mm long, subcylindrical, subparallel-sided, with slighly widened abdominal segments II to VI. Tegument brown, paler ventrally, head and tergite IX darker; each anterolateral region of abdominal mediotergites I–VIII with prominent pigmented impression extending mesally at approximately 90-degree angle forming longitudinal and transverse branches; transverse branches reaching median dorsal suture; claws and spine-like setae on legs brown. Vestiture consisting of sparse light brown setae of various lengths. Alive specimens are slightly darker than those preserved in ethanol.

Head (Fig. 3D–F): excluding mouthparts, 1.8 times wider than long, with sides subparallel, depressed, with well-impressed punctures, each side with one lateral seta at antennifer base, one dorsal seta posterior to antennifer (in anterior third), two long lateral setae in posterior third, longitudinal dorsal row of three large punctures, most anterior one with long seta and flanked by smaller puncture with smaller seta, two posterior ones with smaller setae; stemmata present; coronal suture and endocarina absent. Frontal arms (Fig. 3D) lyre-shaped, frons with sparse punctures mainly in anterolateral margins, anterior corners rounded, four setae along edge of nasal and adnasalia; posterior part of frons with sides rounded, widest at midlength; nasale produced, tridentate, as long as wide; adnasalia twice as long as nasale, separated by distance 0.5 times as wide as each adnasalium width (measured at base); ventral surface (Fig. 3F) smooth except for one long setae on posterolateral margin and row of shorter setae along outer edge of ventral ridges.

Mandible (Fig. 4E and F) about 1.3 times as long as wide, unidentate, incisor edge with retinaculum, lateral surface of basal half concave, penicillus as long as retinaculum; two setae dorsolaterally. Maxilla (Fig. 4A and B) with stipites about four times as long as wide, subparallel-sided, widely separated at base (distance between stipites 1.2 times as wide as each stipes width at base), anterior margin narrowed and membranous; lateral margin with sparse punctures, few long setae in anterior corner; maxillary palpus four-segmented, elongate, sparsely setose, relative length of palpomeres: I as long as II, III 0.5 times as long as II, IV 1.4 times as long as III; galea palpiform, two segmented, with stiff setae at apex; lacinia reduced to densely setose area; cardines somewhat triangular, wider than long. Labium (Fig. 4A and B) with prementum 1.2 times as wide as long, two pairs of setae near anterior margin, parasagittal one longer and thicker, ligula produced, with two setae; postmentum 3.6 times as long as wide, sides weakly convergent posterad, membranous anteriorly; one pair of long setae anteriorly, few smaller punctures irregularly distributed along lateral margins, apex with pair of long thick setae; basal palpomere 1.3 times as long as apical palpomere. Antenna (Fig. 4C and D) with basal antennomere glabrous, with few campaniform sensilla, about twice as long as median antennomere; second antennomere glabrous, 1.6 times as long as apical antennomere, with conical sensorium lateroventrally; third antennomere with two setae apically.

Thorax (Fig. 3A–F): tergites with large punctures (1.0–1.2 times as wide as mid-dorsal suture), mostly separated by distance 2–3 puncture diameter. Prothorax 1.3 times as wide as long, about twice as long as mesothorax, anterior corner with two setae laterodorsally, 4–5 longer setae laterally, posterior corner with 4–5 setae; prosternum with one seta in anterior angle, pair of setae apically; mesothorax and metathorax subequal in size, each with three setae laterally, two setae dorsolaterally near anterior margin, and four setae dorsolaterally near posterior margin. Leg (Fig. 4G) with lateral surfaces with strongly sclerotized, short, spine-like setae (with sides rounded), longer and sharper on ventral margins (up to three times longer on coxa), sparsely distributed (distance between setae as long as or longer than seta width) ventrally with few long fine setae, claw with one seta on each basal side.

Abdomen (Fig. 3A–C): mediotergites I–VIII with punctures about 1.2–1.5 times as large as those of metathorax, mostly separated by distance 0.3–0.5 puncture diameter, each side near midlength with one seta laterally, transverse row of 8–9 relatively long setae near posterior margin; laterotergite I with two setae posteriorly; pleura with 2–3 setae, sternite with lateral pair of setae anteriorly, two lateral pairs of setae posteriorly; segment IX (Fig. 3G–I) with dorsal plate as wide as long, bounded anteriorly and laterally by steeply declivous carina, dorsal surface mostly smooth, with few punctures about 3–5 times smaller than those on mediotergite VIII, with five grooves: one pair anteriorly, convergent posterad, one mediodorsal, and one pair laterally; lateral sides of carina with four blunt teeth, each one bearing one seta; apex with a lozenge-shaped notch forming two urogomphi; each urogomphus with prongs, outer prong directed posterad, as long as inner prong, inner prong directed medially; lateral and ventral surfaces with long setae; segment X (Fig. 3G–I) tubular, ventral, with long setae anteriorly at base and shorter setae along anal opening; anal hook absent.

3.3. Biology and ecology of *Elathous*

There is only limited information on the biology and ecology of *Elathous*. Adult specimens in collections were usually collected at light, rarely using pitfall traps and window traps. Specimens of smaller, yellowish-brownish *Elathous* species were often collected at open areas without deadwood, while larger, blackish species usually occur in forests or groves. Regarding immature stages, Glen (1950) wrote that the larvae of North American *E. bicolor* were collected from the decaying wood; however, he did not provide any other details.

Both species examined here are clearly saproxylic and their larvae probably feed not only on the rotten part of the logs, but very possibly on smaller insect larvae, as observed in some other dendrometrines (T. Németh, pers. observ.). When describing *E. agilis* ffrom Lebanon (Németh 2019) wrote that the larvae develop in different kinds of rotten wood for at least two years. Immature stages of *E. agilis* were found in red-rotten wood of hollow oaks as well as in dry, white-rotten trunks infected with fungus and in dry portions of an opened cavity of Lebanese cedar (*C. libani* A. Rich., 1823). Further, *E. agilis* was found in a rotten portion of a hollow in *Juglans regia* L., 1753 (Fig. 5C), together with larvae of *Pittonotus* sp. and *Haterumelater fulvago* (Marseul, 1838) (both Elateridae: Elaterinae; T. Németh, pers. observ.). Adults were collected during the day from underneath stones near fallen cedar trunks or flying around vegetation among solitary *Pinus* trees (Németh 2019). It should be noted that the oak in which the larvae of *E. agilis* had been found in Lebanon, was originally identified as *Quercus pinnatifida* Gmelin, 1826 (Németh 2019). However, the taxonomic and nomenclatural situation of *Quercus* species in the region is rather complex, and the correct name for the oak species with associated *Elathous* larvae is *Quercus kotschyana* O. Schwarz, 1935 (Stephan & Teeny 2017).

In Greece, the larvae of *E. brucki* were found in a red-rot in the cavity in *Abies* sp.; under the dead bark of the same tree there were some other saproxylic beetles like *Peltis grossa* (Linnaeus, 1758) (Trogossitidae) and

Allonyx quadrimaculatus (Schaller, 1783) (Cleridae; T. Németh, pers. observ.).

Based on the personal observations by the Elateridae specialist Josef Mertlik (Czech Republic), the larvae of *Elathous nigricans* Platia & Schimmel, 1991 in Turkey were found in the fallen trunk of *Pinus* sp., those of *Elathous mertliki* Platia & Schimmel, 1992 from Turkey were found in tree stump of *Pinus* sp. and in an opened cavity of Oriental thuja (*Platycladus orientalis* (L.) Franco, 1949), and those of *Elathous* sp. from Bulgaria were found in the fallen trunk of a chestnut tree (*Castanea sativa* Mill., 1768).

4. Discussion

In our study, for the first time we report, describe and provide photographic evidence of the larvae of *E. agilis* from Lebanon and *E. brucki* from Greece. We examined in detail their morphology, including all characters which were considered diagnostic by previous authors (e.g., Glen 1950; Dolin 1960b; 1978), and compared them not only with each other but also with their known congeners and related genera. Larvae of *E. agilis* and *E. brucki* can be differentiated by several features (Table 1). The most conspicuous are the size and density of punctation on thoracic tergites (punctures larger and denser in *E. brucki*), the sides of head (slightly rounded in *E. agilis*; parallel in *E. brucki*), the shape of the posterior part of frons (with straight sides, divergent anteriorly and parallel posteriorly in *E. agilis*; with rounded sides in *E. brucki*), the length of the transverse branches of abdominal impressions (shorter in *E. agilis*), and several details on the dorsal plate of abdominal tergite IX (uncarinate, with one longitudinal groove, three lateral teeth and a pair of paramedian impressions in *E. agilis*; carinate, with five longitudinal grooves, four lateral teeth and without paramedian impressions in *E. brucki*).

Some of the variable, species-specific, features found in those two species have also been described and/or illustrated for *E. bicolor* (Glen 1950), *E. candezei* (Dolin 1960b; 1978), and *E. niger* (Dolin 1978) (Table 1). Based on the available information, *E. brucki* is unique among its congeners in having rounded sides on the posterior part of the frons and a lozenge-shaped notch on tergite IX (that notch is semicircular in remaining species). *E. agilis* can be separated from all other known

Table 1
Comparison of larval features among known larvae of *Elathous*. Question marks indicate characters not described or illustrated in the literature.[1] - based on Glen (1950),[2] - based on Dolin (1960b),[3] - based on Dolin (1978).

Characters	*Elathous agilis*	*E. brucki*	*E. bicolor*[1]	*E. candezei*[2,3]	*E. niger*[3]
Head shape	sides slightly rounded	sides subparallel	?	?	?
Stemmata	absent	present	present	?	?
Mandible - number of teeth	1	1	1	1	1
Head/thoracic mediotergites - size of punctation	fine (narrower than mid-dorsal suture)	large (as wide as or wider than mid-dorsal suture)	fine (?)	fine (?)	?
Head/thoracic mediotergites - density of punctation	separated by distance 6–10 puncture diameter	separated by distance 2–3 puncture diameter	sparse (?)	sparse (?)	?
Head, epicranium - anterior seta of dorsosulcal setae	unpaired	paired by smaller setae	?	?	?
Head, epicranium - number of lateral setae on posterior third	1	2	2	?	?
Frons – shape of posterior part	sides divergent in anterior half, subparallel in posterior half	sides rounded	?	sides divergent in anterior half, subparallel in posterior half	sides divergent in anterior half, subparallel in posterior half
Leg - density of spine-like setae	dense (distance between setae shorter than seta width)	sparse (distance between setae as long as or longer than seta width)	?	?	?
Abdominal mediotergites - size of punctation	ca. 10 times larger than those on metathorax	1.2–1.5 times larger than those on metathorax	?	?	?
Abdominal mediotergites - density of punctation	dense (spaced by 0.1–0.3 puncture diameter)	dense (spaced by 0.3–0.5 puncture diameter)		sparse (spaced by 2–4 puncture diameter)	sparse (spaced by 2–4 puncture diameter)
Abdominal mediotergites - transverse branches of impressions/lateral half of mediotergite width	reaching 2/3	reaching median suture	reaching 3/4	reaching median suture	reaching median suture
Abdominal mediotergites - transverse row of setae near posterior margin (number, length)	14–16, short	8–9, long	?	?	?
Abdominal pleura - number of setae	1	2–3	3	3	3
Segment IX – dorsal plate ratio	1.3 times as wide as long	1.0 times as wide as long	1.2 times as wide as long	1.1 times as wide as long	1.0 times as wide as long
Tergite IX – delimitation of dorsal plate	declivous, not carinate	steep carina	steep carina	steep carina	steep carina
Tergite IX – grooves on dorsal plate	1 medially, several lateral transverse grooves	1 pair anteriorly, convergent posterad; 1 mediodorsal; 1 pair lateral.	1 long mediodorsal	1 pair anteriorly, convergent posterad; 1 mediodorsal; 1 pair lateral.	1 pair anteriorly, convergent posterad; 1 mediodorsal; 1 pair lateral.
Tergite IX - paramedian impressions on dorsal plate	present	absent	absent	absent	absent
Tergite IX – number of lateral teeth of dorsal plate	3	4	3	4	4
Tergite IX - shape of apical notch	semicircular, wider than long	lozenge-shaped	semicircular	semicircular	semicircular
Tergite IX - outer prong of urogomphus projecting	dorsad	posterad	dorsad and forward	dorsad	dorsad
Tergite IX - outer prong length/ inner prong length	longer	equal	subequal–shorter	subequal–longer	subequal
Tergite IX - outer prong tip	blunt	blunt	acute	blunt	blunt

Elathous larvae by the dorsal plate of tergite IX with borders raised but not carinate, and a pair of paramedian impressions. It should be noted, that the pair of paramedian impressions is also present in other dendrometrine species like e.g., *Selatosomus destructor* (Brown, 1935), *S. pruininus* (Horn, 1873), and *Limonius dubitans* LeConte, 1853 (Glen, 1950: F. 7, 15, 32, labelled there as "pim").

While all those larval features provided in Table 1 are useful to differentiate known species of *Elathous*, they are insufficient to propose a generic diagnosis, which could support the monophyly of *Elathous* when compared to the morphologically similar, historically associated genera like *Athous* Eschscholtz, 1829 and *Limonius* Eschscholtz, 1829 (Candèze 1860; Etzler 2019; Kundrata et al., 2021). Most Dendrometrinae larvae, and mainly those of *Athous* (e.g., Dolin 1978; 1960a; 1964a; 1964b; 1982; Glen 1950; Penev 2005), show high variability in the features listed in Table 1. Dolin (1960b) mentioned that the larva of *E. candezei* differs from *Athous* larvae in having the most lateral pair of setae on the anterior margin of frons reduced while *Athous* species have it well developed. However, some *Athous* larvae have also much smaller setae, while *E. niger* has lateral setae almost as long as the inner setae. The dorsal plate of tergite IX in *Athous* varies from smooth to densely punctate, but it is always glabrous as in *Elathous*; the outer prong of urogomphus varies from short and blunt (like in *Limonius* larvae) to long and acute, and the grooves are quite variable, with a median groove and a lateral region with longitudinal or transverse grooves in different combinations, including similar patterns as in *Limonius* spp. (two parallel pairs; e.g., *Athous haemorrhoidalis* Fabricius, 1801 and *Athous rosinae* Reitter, 1899), in *E. brucki* (one pair anteriorly which is convergent posterad, one mediodorsal, and one pair lateral; e.g., *Athous circassicus* Reitter, 1888 and *A. jejunus* Kiesenwetter, 1858) or *E. agilis* (several transverse grooves laterally; e.g., *Athous lomnickii* Reitter, 1905 and *A. pliginskyi* Reitter, 1910, the latter currently being a synonym of *A. dilaticornis* Reitter, 1905; see Cate, 2007). In *Athous* larvae, the transverse branches of impressions on the abdominal mediotergites can be almost straight (e.g., *A. hirtus* (Herbst, 1784)) to strongly sinuous (e.g., *A. mollis* Reitter, 1889), reaching either the median dorsal suture or 3/4 of the lateral half of the mediotergite width, which represents a similar variability as in *Elathous* (Table 1). Additionally, the shape of the posterior part of the frons in *Athous* can have rounded or straight lateral sides, as in most *Elathous* larvae. Glen (1950) separated *E. bicolor* from *Athous* species by a combination of small caudal notch and the outer urogomphal prong being not longer than the inner prong. However, in *Athous*, the caudal notch can be small (as wide as or narrower than base of the urogomphus) or large (at least twice as wide as the urogomphus), and some species of *Athous* (and *Hemicrepidius* Germar, 1839, to which many *Athous* species were transferred after Glen 1950), have the outer prong about as long or even shorter than the inner prong (e.g., *Hemicrepidius inornatus* Lewis, 1894 and *A. rosinae*). Additionally, *Elathous* species have a mediodorsal groove, while in *Athous* and *Hemicrepidius* the mediodorsal groove may be either present or absent.

Based on morphology, *Elathous* belongs to the *Limonius* group of genera, which additionally comprises *Gambrinus* LeConte, 1853, *Limonius*, *Pheletes* Kiesenwetter, 1858, and Tetralimonius Etzler, 2019. (Candèze, 1860; Etzler, 2019). Known larvae of *Gambrinus* differ from *Elathous* by the combination of abdominal mediotergites with 5–6 long setae near posterior margin, and the dorsal plate which is rounded, without grooves, and with small lateral teeth, while in *Elathous*, the abdominal mediotergites have 8–16 setae, and the dorsal plate has less rounded sides, with at least a median groove and relatively longer lateral teeth (Ôhira 1962; Dolin 1978). *Elathous* larvae can be separated from typical *Limonius* larvae (i.e., excluding the possibly mis-associated one; see Etzler 2019) by the combination of a prominent outer prong of urogomphus and the presence of a dorsal median groove on tergite X. Instead, *Limonius* larvae have a small but not prominent outer prong, which is tubercle-like, and tergite IX without a median groove, which seems to be a unique combination of features among Dendrometrinae (Glen 1950; Etzler 2019). Within the group, *Pheletes* larvae possess unique mandibles with three apical teeth and the abdominal mediotergites with transverse branches of impressions short, extending less than 1/2 distance from longitudinal branches to median dorsal suture (Glen 1950). *Tetralimonius* larva is unknown. The complex taxonomic history and lack of phylogenetic studies on *Elathous*, *Athous*, and other related genera in Dendrometrini hamper the proposal of diagnoses for genera based on larval characters. It should be noted that *Elathous* has not been included in any molecular phylogenetic study (e.g., Kundrata et al., 2019; Douglas et al., 2021; Qiu 2023). Nevertheless, due to numerous variable characters and potential phylogenetic information the larval characters should be considered in future studies on Dendrometrinae.

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Data availability

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References

Agaev, B.I., 1980. Faunistichesky sostav zhukov-shchelkunov Vostochnogo Azerbaydzhana [Fauna of click-beetles of eastern Azerbaijan]. Azerbaijan research institute of scientific and technical information and techno-economic research of Gosplan of Azerbaijan SSR. Agriculture series, Baku, p. 32 ([in Russian]).

Agaev, B.I., 1988. Zhestkokrylye-shchelkuny v biotsenozah Azerbaydzhana [Click-beetles in biocenosis of Azerbaijan]. Azerbaijan state publishing house, Baku, p. 120 ([in Russian]).

Candèze, E.C.A., 1860. Monographie des Élatérides. Tome troisième. Mem. Soc. R. Sci. Liege 15, 1–512.

Candèze, E.C.A., 1878. Élatérides nouveaux. II. Ann. Soc. entomol. Belg. 21, li–lxi + lxxv–lxxxv + cxxxv–cxliii + clxi–clxxii + clxxxix–cxcix.

Casari, S.A., Biffi, G., 2012. Immatures of *Dicrepidius* Eschscholtz, 1829 and *Dipropus* Germar, 1839 (Elateridae, Elaterinae, Ampedini, Dicrepidiina). Zootaxa 3587, 65–77. https://doi.org/10.11646/zootaxa.3587.1.3.

Casari, S.A., 2002. Larvae of *Alaus myops, A. oculatus, Chalcolepidius porcatus, Hemirhipus apicalis* and generic larval characterization (Elateridae, Agrypninae, Hemirhipini). Iheringia Ser. Zool. 92, 93–110. https://doi.org/10.1590/S0073-47212002000200009.

Casari, S.A., Bellusci, S., 1996. Larvae of Neotropical Coleoptera XXV. *Pherhimius dejeani* (Candèze, 1857) and *P. fascicularis* (Fabricius, 1787) (Elateridae, Pyrophorinae, Hemirhipini). Iheringia Ser. Zool. 80, 55–63.

Casari, S.A., Costa, C., 1998. Description of larva and pupa of *Paracalais prosectus* (Candèze) (Elateridae, Agrypninae, Hemirhipini). Rev. Bras. Zool. 15, 703–708. https://doi.org/10.1590/S0101-81751998000300015.

Cate, P.C., 2007. Elateridae. In: Löbl, I., Smetana, A. (Eds.), Catalogue of Palaearctic Coleoptera, 4. Apollo Books, Stenstrup, pp. 89–209.

Costa, C., 1992. Larva and pupa of *Thoramus laevithorax* (White, 1846) and the systematic position of the genus *Thoramus* Sharp, 1877 (Coleoptera, Elateridae, Pyrophorinae). Rev. Bras. Entomol. 36 (1), 223–227.

Costa, C., Casari-Chen, S.A., Vanin, S.A., 1992. On the larvae of Tetralobini (Coleoptera, Elateridae). Rev. Bras. Entomol. 36 (4), 879–888.

Costa, C., Lawrence, J.F., Rosa, S.P., 2010. Elateridae Leach, 1815. In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim). Walter de Gruyter GmbH & Co. KG, Berlin/New York, pp. 75–103.

Dolin, V.G., 1960a. Ličinki ščelkunov roda *Athous* esch. (Coleoptera, Elateridae) Ukrainskoj SSR. Zool. Zh. 39 (8), 1156–1168.

Dolin, V.G., 1960b. Neue und wenig bekannte Elateriden aus der Ukraine (Coleoptera: Elateridae). Beitr. Entomol. 10 (1/2), 189–201.

Dolin, V.G., 1964a. Lichinki Zhukov-Shchelkunov (Provolochniki) Evropeyskoy Chasti SSSR [Wireworms of the European Part of the USSR]. Urozhai, Kiev, p. 206 (pp. [in Russian]).

Dolin, V.G., 1964b. Podsemeystvo Lepturoidinae [subfamily Lepturoidinae]. In: Gilyarov, M.S. (Ed.), Key to the Larvae of Insects Inhabiting in the Soil. Nauka, Moscow, pp. 382–393 ([in Russian]).

Dolin, V.G., 1978. Opredelitel Lichinok Zhukov-Shchelkunov Fauny SSSR [Key to Wireworms of the Fauna of the USSR]. Urozhai, Kiev, p. 124 (pp. [in Russian]).

Dolin, V.G., 1982. Zhuki-kovaliki. Agrypnini, Negastriini, Dimini, Atoini, Oestodini [Click-beetles. Agrypninae, Negastriinae, Diminae, Athoinae, Oestodinae]. Beetles. Issue 3. In: Fauna of the Ukraine, 19. Naukova Dumka, Kiev, p. 288 (pp. [in Ukrainian]).

Douglas, H.B., Kundrata, R., Brunke, A.J., Escalona, H.E., Chapados, J.T., Eyres, J., Richter, R., Savard, K., Ślipiński, A., McKenna, D., Dettman, J.R., 2021. Anchored phylogenomics, evolution and systematics of Elateridae: are all bioluminescent Elateroidea derived click beetles? Biology 10, 451. https://doi.org/10.3390/biology10060451.

Etzler, F.E., 2019. Generic reclassification of *Limonius* Eschscholtz, 1829 (Elateridae: Dendrometrinae) sensu Candèze 1860 of the world. Zootaxa 4683 (3), 301–335. https://doi.org/10.11646/zootaxa.4683.3.1.

Glen, R., 1950. Larvae of the elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae). Smithsonian Misc. Collect. 111 (11), 1–246.

Guglielmi, A., Platia, G., 1985. Contributo alla conoscenza degli Elateridi di Grecia e Turchia (Coleoptera). Fragm. Entomol. 18 (1), 169–224.

Háva, J., Németh, T., 2016. Contribution to the occurrence of Dermestidae (Coleoptera) in Lebanon. Folia Entomol. Hung. 77, 17–21. https://doi.org/10.17112/FoliaEntHung.2016.77.17.

Hyslop, J.A., 1917. The phylogeny of the Elateridae based on larval characters. Ann. Entomol. Soc. Am. 10, 241–263. https://doi.org/10.1093/aesa/10.3.241.

Hyslop, J.A., 1921. Genotypes of the elaterid beetles of the world. Proc. U. S. Natl. Mus. 58, 621–673. https://doi.org/10.5479/si.00963801.2353.621.

Johnson, P.J., 1993. Immature insects. Notes and errata to Elateridae and Throscidae. Mola 2, 5–6, 2.

Kovács, T., Németh, T., Merkl, O., 2012. Beetles new to Albania, Croatia and Serbia (Coleoptera: Elateridae, Cucujidae, Melandryidae, Cerambycidae). Folia hist.-nat. Mus. Matra. 36, 43–44.

Kundrata, R., Németh, T., Prosvirov, A.S., Hoffmannova, J., 2021. Annotated catalogue of the click-beetle genus *Elathous* Reitter, 1890 (Coleoptera: Elateridae: Dendrometrinae), including habitus photographs for all species. Zootaxa 4995 (2), 231–265. https://doi.org/10.11646/zootaxa.4995.2.2.

Kundrata, R., Prosvirov, A.S., Vondracek, D., Sormova, E., 2019. Congruence between molecular data and morphology: phylogenetic position of Senodoniini (Coleoptera: Elateridae). Insects 10, 231. https://doi.org/10.3390/insects10080231.

Lawrence, J.F., Hastings, A.M., Dallwitz, M.J., Paine, T.A., Zurcher, E.J., 1999. Beetle larvae of the World: Descriptions, illustrations, identification, and information retrieval for families and subfamilies. CD-ROM, Version 1.1 for MS-Windows. CSIRO Publishing, Melbourne.

Marinho, T.A.S., Casari, S.A., Prosvirov, A.S., Rosa, S.P., 2023. Description of immature stages and redescription of adults of *Monocrepidius fuscofasciatus* (Eschscholtz, 1829) (Elateridae, Agrypninae, Oophorini). Zootaxa 5271, 329–344. https://doi.org/10.11646/zootaxa.5271.2.7.

Márkus, A., Németh, T., 2016. A new species of *Alosterna* Mulsant, 1863 from Lebanon, and notes on other species (Coleoptera: Cerambycidae). Folia Entomol. Hung. 77, 23–32. https://doi.org/10.17112/FoliaEntHung.2016.77.23.

Mertlik, J., Németh, T., Kundrata, R., 2017. Revision of the flightless click-beetle genus *Dima* Charpentier, 1825 (Coleoptera: Elateridae: Dimini) in the Balkan Peninsula. Zootaxa 4220 (1), 1–63. https://doi.org/10.11646/zootaxa.4220.1.1.

Mertlik, J., Németh, T., Kundrata, R., 2018. Additions to the revision of *Dima* Charpentier, 1825 (Coleoptera: Elateridae: Dimini) in the Balkan Peninsula, with the descriptions of five new species. Zootaxa 4433 (2), 325–351. https://doi.org/10.11646/zootaxa.4433.2.5.

Németh, T., 2019. Elateridae (Coleoptera) of Lebanon. Zootaxa 4614 (1), 127–159. https://doi.org/10.11646/zootaxa.4614.1.6.

Németh, T., 2021. A new species of *Elathous* Reitter, 1890 (Coleoptera: Elateridae) from Lebanon. Zool. Middle East 67 (4), 344–349. https://doi.org/10.1080/09397140.2021.1980968.

Németh, T., Dušánek, V., Mertlik, J., Kundrata, R., 2014. New distributional data on Elateroidea (Coleoptera: Elateridae, Eucnemidae and Omalisidae) for Albania, Montenegro and Macedonia. Elateridarium 8, 112–117.

Németh, T., Lauš, B., Tallósi, B., 2017. New distributional data on Elateroidea (Elateridae and Eucnemidae) for Albania, Bulgaria, Croatia, Greece, Macedonia, Montenegro and Serbia. Folia Entomol. Hung. 78, 47–56. https://doi.org/10.17112/FoliaEntHung.2017.78.47.

Németh, T., Székely, K., Kotán, A., Márkus, A., Yammine, W., Tanios, C., Nemer, N., 2019. Notes on the longhorn beetles (Coleoptera: Cerambycidae) of Lebanon. Folia Entomol. Hung. 80, 13–38. https://doi.org/10.17112/FoliaEntHung.2019.80.13.

Ôhira, H., 1962. Morphological and taxonomic study on the larvae of Elateridae in Japan (Coleoptera). University Okazaki, Okazaki, p. 179.

Penev, L., 2005. Description of the larva of *Athous monilicornis* (Coleoptera, Elateridae) with notes on the species distribution. Vestn. Zool. 39 (1), 55–58.

Platia, G., Gudenzi, I., 1996. Descrizione di tre nuove specie di Elateridi di Grecia, Turchia ed Isola di Cipro con note geonemiche e sinonimiche (Coleoptera, Elateridae). Boll. Mus. Reg. Sci. Nat. Torino 14 (1), 139–150.

Qiu, L., 2023. Complete mitochondrial genomes of two click-beetles, *Sinelater perroti* and *Sternocampsus coriaceus* (Coleoptera: Elateroidea: Elateridae), and their phylogenetic implications. J. Asia Pac. Entomol. 26, 102059 https://doi.org/10.1016/j.aspen.2023.102059.

Reitter, E., 1890. Eine neue mit *Athous* verwandte Elateriden-Gattung aus russisch Armenien: *Elathous* n. g. Ent. Nachr. 16 (16), 247–248.

Reitter, E., 1905. Bestimmungs-Tabelle der europäischen Coleopteren. Heft 56. Elateridae. 1 Theil. Elaterini, Subtribus: Athouina, aus der palaearctischen Fauna. Mit einer Uebersicht der Familiengruppe der Sternoxia und der Gattungen der Familie der Elateridae. Bd. 43. Verhandlungen des naturforschenden Vereins in Brünn, p. 122.

Rosa, S.P., Németh, T., Kundrata, R., 2019. Comparative morphology of immature stages of *Ludioctenus cyprius* (Baudi di Selve, 1871) (Coleoptera: Elateridae: Agrypninae), with discussion on the monophyly of Hemirhipini. Zool. Anz. 283, 33–39. https://doi.org/10.1016/j.jcz.2019.08.002.

Rosa, S.P., Mariano, R.R., Viviani, V.R., Costa, C., 2020. Morphology of immature stages of *Pyrearinus pumilus* (Candèze, 1863) (Coleoptera: Elateridae: Pyrophorini): the click beetle responsible for the luminous canga caves in the state of Pará, Brazil. Zootaxa 4778, 561–570. https://doi.org/10.11646/zootaxa.4778.3.7.

Rosa, S.P., Albertoni, F.F., Bená, D.C., 2015. Description of the immature stages of *Platycrepidius dewynteri* Chassain (Coleoptera, Elateridae, Agrypninae, Platycrepidiini) from Brazil with a synopsis of the larval characters of Agrypninae tribes. Zootaxa 3914, 318–330. https://doi.org/10.11646/zootaxa.3914.3.5.

Stephan, J., Teeny, P., 2017. Revealing the taxonomy of an endemic oak of Lebanon. Plant Sociol 54, 97–100. https://doi.org/10.7338/pls2017542S1/09.

Szénási, V., Németh, T., 2019. Description of a new species of the subgenus *Hippomias* Yunakov, 2006 in the genus *Brachysomus* Schoenherr, 1823 (Coleoptera: Curculionidae: Entiminae) from Lebanon. Zootaxa 4658 (2), 389–395. https://doi.org/10.11646/zootaxa.4658.2.13.

Szénási, V., Nemer, N., Németh, T., 2019. Notes on snout beetles (Coleoptera: Curculionoidea, without Scolytinae and Platypodinae) of Lebanon. Folia Entomol. Hung. 80, 39–72. https://doi.org/10.17112/FoliaEntHung.2019.80.39.

Zacharuk, R.Y., 1962. Sense organs of the head of larvae of some Elateridae (Coleoptera): their distribution, structures and innervation. J. Morphol. 111, 1–33. https://doi.org/10.1002/jmor.1051110102.

Emblematic European saproxylic *Lacon* click beetles (Coleoptera: Elateridae) and what we know about their immature stages

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Abstract

The saproxylic beetles play an important role in forest ecosystems; however, many of them are nowadays rare and threatened. Since they often serve as umbrella species for forest conservation or indicators of forest biodiversity, we should have an accurate and up-to-date information about their morphology, biology, and distribution. Unfortunately, we often lack detailed information on larvae of saproxylic beetles although they represent the longest stage of ontogenetic development and therefore usually play more important ecological roles than adults. Here, we focused on larvae of European saproxylic species of the click-beetle genus *Lacon* Laporte, 1838 which develop in decayed wood and are predators of other saproxylic insects. Larvae are only known for *L. lepidopterus* (Panzer, 1801), *L. punctatus* (Herbst, 1779) and *L. querceus* (Herbst, 1784), which are all considered primeval forest relicts. We provided updated information on their morphology, biology and ecology including host trees, and compared their diagnostic characters with all other known Holarctic congeners. Further, we updated the larval diagnosis of *Lacon*, and compared the morphology of this genus with other Agrypnini. Future research should focus on descriptions and biology of larvae of other *Lacon* species as well as on the morphology of different instars.

Keywords: Agrypninae - Elateroidea - distribution - forest relicts - larva - morphology

Introduction

Beetles, with almost 450,000 described and even more undescribed species, constitute the largest insect order[1,2]. During their early evolution in the Carboniferous and the Permian, the first beetle lineages likely occupied habitats associated with wood and bark[3], and a significant proportion of beetle groups is saproxylic even today[4]. Saproxylic beetles are dependent on dead and decaying wood for at least part of their life cycle and therefore are involved in decomposition processes and the recycling of nutrients in natural ecosystems, playing important ecological roles mostly in forest habitats[5–7]. They are of various feeding types like e.g., xylophagy, mycophagy, saprophagy or predatory, being associated with wood either for whole their lives or only in some ontogenetic stages, typically larvae, and are adapted to various succession stages of wood decomposition, and to various microhabitats from the bark to the interior of a dead log[4,5]. Saproxylic beetles are generally popular because they provide reliable data on the preservation of the environment and are often used as umbrella species or indicators of forest biodiversity[5,8]. Saproxylic beetles belong to numerous families, including Cerambycidae, Staphylinidae, Curculionidae, Buprestidae, Elateridae, Eucnemidae, Ptinidae, and Tenebrionidae, among others[4,5,9].

Elateridae, commonly known as click beetles, is a worldwide group of more than 10,000 species[10,11] well known for their jumping ability due to the presence of pro-mesothoracic clicking mechanism[12]. They have a long evolutionary history[13], and at least some click-beetle fossils, dated back to Mesozoic, were hypothesized to be associated with decaying wood[14]. Today, although some click-beetles develop in soil and can be severe agricultural pests[15], many others develop in wood[16]. In Europe, saproxylic Elateridae contain many emblematic species like, for example, *Elater ferrugineus* Linnaeus, 1758, *Limoniscus violaceus* (Müller, 1821) (currently in *Gambrinus* LeConte, 1853 by some authors), and species of *Ampedus* Dejean, 1833 and *Lacon* Laporte, 1838[5,7,9].

In this study, we focused on the European *Lacon* species, with an emphasis on their immature stages. *Lacon* is a morphologically rather diverse and geographically widespread genus belonging to the subfamily Agrypninae, traditionally classified in the tribe Agrypnini[17,18] although some authors place it to the separate tribe Laconini[19]. This genus was previously mixed up with *Adelocera* Latreille, 1829[20]. The genus *Lacon* currently contains approximately 150 described species, of which more than 50 species are known from the Palearctic realm[17,20–25]. Only six species are known from Europe if we do not count Cyprus which is geographically a part of Asia. While *Lacon lepidopterus* (Panzer, 1801), *L. punctatus* (Herbst, 1779), and *L. querceus* (Herbst, 1784) are widely distributed in Europe (although being rare; see below), *L. gillerforsi* Platia & Schimmel, 1994, *L. graecus* (Candèze, 1857), and *L. ladae* Mertlik & Dušánek, 2006 are known only from Greece (all three are additionally known from Türkiye, *L. gillerforsi* from Cyprus, and *L. ladae* from Syria)[17,23]. It should be noted that *Lacon conspersus* (Gyllenhal, 1808) and *L. fasciatus* (Linnaeus, 1758), classified in *Lacon* in older literature[26,27], are currently in a separate genus *Danosoma* Thomson, 1859[18], and *L. kapleri* Platia & Schimmel, 1994, described from Greece, was recently synonymized with *L. graecus*[23].

Larvae are known only for three European species: *L. lepidopterus*, *L. punctatus*, and *L. querceus* (Figs. 1–7, S1). All three species are considered saproxylic primeval forest relict beetles which are the species that require primeval habitat features and continuous habitat availability, have high requirements with regard to dead wood quality and quantity (Figs. S2–S4), and became extinct or were severely diminished in forests managed for timber production[9]. All three species are in the list of 168 Central European umbrella primeval forest relict species of saproxylic beetles compiled in 2016 to help protect the European primeval forest remnants[9]. Not surprisingly, rather rare *L. lepidopterus* and *L. querceus* are in the first of two categories - primeval forest relict species *sensu stricto*, *i.e*., restricted today to a few remnants of natural forests. All three species are therefore considered threatened in many European countries[28–30], and are also listed in the European Red List of saproxylic beetles by the International Union for Conservation of Nature (IUCN)[5,7,30].

Larvae are insufficiently known in Elateridae despite the fact that they may bear important diagnostic morphological characters useful for the separation of taxa on various levels as well as for the phylogenetic reconstructions[26,31,32]. For example, two large subfamilies of Elateridae, i.e., Elaterinae and Dendrometrinae (=Denticollinae), are difficult to separate based on adult morphology but are easily distinguishable based on larval characters[10]. Comparison of characters of mature larvae on a tribal level within the subfamily Agrypninae was carried out by Rosa et al.[32]. In this study, we provide updated information on the morphology, biology and ecology of larvae of European species of *Lacon*, compare their diagnostic characters with all other known congeneric larvae from Asia and North America, update the larval diagnosis of *Lacon*, and compare the morphology of this genus with other Agrypnini.

Results

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Elateroidea Leach, 1815
Family Elateridae Leach, 1815
Subfamily Agrypninae Candèze, 1857
Tribe Agrypnini Candèze, 1857

Genus *Lacon* Laporte, 1838

Lacon Laporte, 1838. Type species: *Elater atomarius* Fabricius, 1798 (=*Elater punctatus* Herbst, 1784). For a list of synonyms and other details see Hayek[20], Cate[17], and Kundrata et al.[18].

Larval diagnosis. Body (Figs. 1A, C, E; 2A–C, 4A–C, 6A–C; S2A–B, S4A–B) flattened, cream-white or yellow with head, pronotum and dorsal surface of segment IX strongly sclerotized; head (Figs. 2D–E, 4D–E, 6D–E, S1A–C) with dorsal surface medially depressed, laterally gradually elevated or with subparallel keels; epicranial stem and coronal suture absent; posterior part (lobe) of frontoclypeal plate 2.7–4.0 times longer than anterior part, abruptly or gradually narrowed at apical third; nasale about 3 times wider than long, tridentate, adnasalia moderately to widely separated (distance between them 1.0–1.5 times adnasalium width when measured at base); thoracic and abdominal segments with several fine setae; abdominal spiracles I–VIII large, well visible in lateral view; legs (Figs. 3G–I, 5G–I, 7G–I) with strongly sclerotized elliptic setae, denser and forming a row on anterior edge; segment IX (Figs. 3J–L, 5J–L, 7J–L, S1D–F) strongly sclerotized, with dorsal surface medially depressed, with parasagittal grooves, covered with 50–160 nodule-like tubercles, 1–2 pairs of larger tubercles with long setae; lateral margins with acute teeth, urogomphus with two prongs, outer prong bent dorsad; anal hooks robust, as long as pygopod.

Remark. This diagnosis is based on all currently known *Lacon* larvae, i.e., *L. altaicus* (Candèze, 1882), *L. discoideus* (Weber, 1801), *L. funebris* (Solsky, 1881), *L. lepidopterus*, *L. marmoratus* (Fabricius, 1801), *L. parallelus* (Lewis, 1894), *L. punctatus*, and *L. querceus*[26,31,33,34], and may be further updated after the future descriptions of larvae of additional species. See Table 1 for the comparison between all known *Lacon* larvae.

Lacon species from Europe

Lacon gillerforsi Platia & Schimmel, 1994

Larva. Unknown.

Biology and ecology. Unknown.

Distribution. Europe: Greece; Asia: Cyprus, Türkiye.

Lacon graecus (Candèze, 1857)

Larva. Unknown.

Biology and ecology. In Greece, adults of this species were collected under the bark of oaks or in bark cracks near the ground, or were collected under stones in an area with macchia and *Euphorbia* bushes[23].

Distribution. Europe: Greece; Asia: Türkiye.

Lacon ladae Mertlik & Dušánek, 2006

Larva. Unknown.

Biology and ecology. This species probably develops in oaks and plane trees[35,36]. One specimen from Turkey was collected from the larval tunnels of *Dorcus peyronis* Reiche & Saulcy, 1856 (Lucanidae) in a hollow oak[23].

Distribution. Europe: Greece; Asia: Syria, Türkiye.

Lacon lepidopterus (Panzer, 1801)

(Figs. 1A–B; 2–3; S1A, D; S2)

Material examined. Nine specimens: Czech Republic, Moravia, Salajka, ex *Abies alba*, VI. 2019, Procházka lgt. (1 ex.; MZM); Czech Republic, NP České Švýcarsko, Havraní skála, VI. 2022, Procházka lgt. (1 ex.; MZM); Hungary, Somogy county, Ságvár, Kastély-tető, ex *Pinus*, 46°47'41.52"N, 18° 3'26.27"E, 23.IV.2019, leg. P. Farkas, A. Kotán, T. Németh & V. Szénási (2 ex.; HNHM); Hungary, Somogy county, Ságvár, Kastély-tető, ex *Pinus*, 46°47'41.52"N, 18° 3'26.27"E, 02.XI.2023, leg. T. Németh (5 ex.; HNHM).

Diagnosis of mature larva. Dorsal surface of head sublaterally with slight longitudinal subparalell elevations (Fig. 2B, D); posterior part (lobe) of frontoclypeal plate abruptly narrowed after the widened place, apically finger-like, U-shaped (Figs. 2D, S1A); postmentum 2.5–2.6 times longer than wide (Figs. 2F, 3A–B); dorsal surface of segment IX with about 90–130 nodule-like tubercles, medially with two pairs of distinct long setae set in tubercles (Figs. 3J–K, S1D); urogomphus 1.2–1.4 times as long as wide; notch between urogomphi about 0.3 times as long as whole segment IX and 1.90–2.25 times as wide as urogomphus when urogomphus width is measured at half and notch width at the widest place, notch always posterior to fourth lateral tooth. For the overview of diagnostic characters, see Table 1.

Biology and ecology. This species typically develops in old dead wood (e.g., veteran trees) of conifers, i.e., pine (*Pinus brutia* Ten., 1816, etc.), fir (e.g., *Abies alba* Mill., 1768, *Abies cephalonica* Loudon, 1838), spruce, and larch[37–44]. However, they can live in deciduous trees like oak (*Quercus robur* L., 1753, etc.), beech and birch, even though these findings are generally rarer[27,38–40,42,45]. Larvae live in trunks, branches and stumps usually of larger diameter, which are already inhabited by other saproxylic insects, on which they prey. Larvae of *L. lepidopterus* can be found in the same tree together with e.g., *Ampedus praeustus* (Fabricius, 1792) (Elateridae), *Helops caeruleus* (Linnaeus, 1758), *Uloma rufa* (Piller & Mitterpacher, 1783), *Prionychus ater* (Fabricius, 1775), *P. fairmairei* (Reiche, 1860), *Tenebrio opacus* Duftschmid, 1812 (all Tenebrionidae), *Gnorimus variabilis* (Linnaeus, 1758) (Scarabaeidae), *Peltis ferruginea* (Linnaeus, 1758), *P. grossa* (Linnaeus, 1758), *Tenebroides mauritanicus* (Linnaeus, 1758), *Thymalus limbatus* (Fabricius, 1787) (all Trogossitidae), *Eurythyrea quercus* (Herbst, 1780) (Buprestidae), *Dryophthorus corticalis* (Paykull, 1792) (Dryophthoridae), *Bothrideres interstitialis* Heyden, 1870 (Bothrideridae), *Rhyncolus ater* (Linnaeus, 1758), *R. elongatus* (Gyllenhal, 1827) (both Curculionidae), *Ipidia binotata* Reitter, 1875 (Nitidulidae), *Aesalus scarabaeoides* (Panzer, 1794) (Lucanidae), and *Prostomis* *mandibularis* (Fabricius, 1801) (Prostomidae)[39,42,46] (incl. pers. observ. by T. Németh). It is noteworthy that in France, *L. lepidopterus* was found in the same fir tree together with *L. querceus* and 13 other beetle species, i.e., *Rhysodes sulcatus* (Fabricius, 1787) (Carabidae), *Ampedus elegantulus* (Schönherr, 1817), *A. melanurus* Mulsant & Guillebeau, 1855 (both Elateridae), *Xylophilus corticalis* (Paykull, 1800) (Eucnemidae), *Rhyncolus ater*, *Treptoplatypus oxyurus* (Dufour, 1843) (Curculionidae), *Plegaderus* sp. (Histeridae), *Mycetophagus quadripustulatus* (Linnaeus, 1761) (Mycetophagidae), *Diaperis boleti* (Linnaeus, 1758), *Corticeus unicolor* Piller & Mitterpacher, 1783 (both Tenebrionidae), (Tenebrionidae), *Hallomenus binotatus* (Quensel, 1790) (Tetratomidae), *Peltis ferruginea*, *P. grossa* (both Trogossitidae), and also with ants (*Lasius* sp.) and the polypore fungus *Pycnoporellus fulgens* (Fr.) Donk, 1971[43]. For examples of typical habitats of *L. lepidopterus* see Fig. S2C–F. The development cycle lasts at least three years. In natural conditions, pupation usually occurs between July and August[42]. Adults (Fig. 1B) overwinter in pupal chambers or in cracks and under bark, and are usually active in May and June, although they can be found throughout the whole year.

Distribution. Europe: Austria, Belarus, Bulgaria, Croatia, Czech Republic, Denmark (?), Finland, France, Germany, Hungary, Greece, Italy, Latvia, Poland, Romania, Russia, Slovakia, Slovenia, Spain, Sweden (?), Switzerland, Ukraine; Asia: Georgia, Iran, Türkiye. According to the IUCN[30], this species is extinct in Denmark, Sweden, and Germany (but for the latter, see Lorenz[47]).

***Lacon punctatus* (Herbst, 1779)**
(Figs. 1C–D; 4–5; S1B, E; S3)

Material examined. 11 specimens: Croatia, 4km SE Drage, 43.867708°, 15.576883°, 11.IX.2021, leg. T. Németh (2 ex.; HNHM); Hungary, Bács-Kiskun county, Kunfehértó, 46.356, 19.391, from rotten *Pinus nigra*, 20.06.2019, leg. T. Németh (1 ex.; HNHM); Montenegro, Bar distr., Mt. Vrsouta, Sutorman, mixed forest, from rotten log, 42°9'18.32"N, 19°5'52.81"E, 2.VI.2014, leg. T. Németh et al. (1 ex.; HNHM); Albania, Vlorë county, S of Himarë, grazed Mediterranean oak forest, 100–190 m, N40.0814°, E19.7767°, 18.06.2017, from hollow of *Q. macrolepis*, T. Kovács, G. Puskás, G. Szövényi (1 ex.; MM); Greece, Peloponnese, Zacharo env., 1.V.2013 (2 ex.); Greece, Peloponnese, distr. Arkadhia, Dirrahi, macchia-oak grove, 37°12'42.57"N; 22°11'26.43"E, 752 m, 14.V.2013, leg. Kotán, P. Nemes, Gy. Németh, T. Németh & V. Szénási (1 ex.; HNHM); Greece, Peloponnese, distr. Lakonia, Mt. Taigetos, 1 km NW, Georgitsi, beech forest, 37°11'14.15"N; 22°17'7.68"E, 756 m, from red rotten oak, 14.V.2013, leg. A. Kotán, P. Nemes, Gy. Németh, T. Németh & V. Szénási (2 ex.; HNHM); Macedonia, Southeastern region, Plavuš hills, Valandovo, Manastir Sv. Gjorgi, N41°19.555’, E22°32.935’, 305 m, 20.02.2014, from hollow of *Platanus orientalis*, D. Angyal, L. Dányi, T. Kovács, D. Murányi (1 ex.; MM).

Diagnosis of mature larva. Dorsal surface of head sublaterally with slight longitudinal subparalell elevations (Fig. 4B, D); posterior part (lobe) of frontoclypeal plate abruptly narrowed after the widened place, apically finger-like, U-shaped (Figs. 4D, S1B); postmentum 2.4–2.7 times longer than wide (Figs. 4F, 5A–B); dorsal surface of segment IX with about 120–150 nodule-like tubercles, medially with two pairs of distinct long setae set in tubercles (Figs. 5J–K, S1E); urogomphus 1.0–1.2 times as long as wide; notch between urogomphi about 0.2 times as long as whole segment IX and 1.05–1.25 times as wide as urogomphus when urogomphus width is measured at half and notch width at the widest place; notch always clearly posterior to fourth lateral tooth. For the overview of diagnostic characters, see Table 1.

Biology and ecology. The larvae live in decayed wood of trunks, stumps and under the bark of both coniferous and deciduous trees, where they feed on larvae and pupae of other saproxylic insects which are often associated with dead, fungus-infested wood[38]. They are often attracted to dead trees after wildfires (Fig. S3F). The prey of *L. punctatus* includes e.g., *Dorcus parallelipipedus* (Linnaeus, 1758) (Lucanidae) but especially Cerambycidae, for example *Stictoleptura rubra* (Linnaeus, 1758), *Clytus* sp., and *Morimus funereus* Mulsant, 1863[34,48–50]. *Lacon punctatus* develops in a variety of trees, including coniferous cedar (e.g., *Cedrus libani* A. Rich., 1823), fir (*Abies nordmanniana* Spach, 1841) and pine (e.g., *Pinus brutia*, *P. halepensis* Mill., 1768, *P. nigra* J. F. Arnold, 1785, *P. pinaster* Aiton, 1785), and deciduous alder (*Alnus orientalis* Decne., 1835), almond (*Prunus dulcis* (Mill.) D. A. Webb, 1967), ash (*Fraxinus angustifolia* Vahl, 1804), beech (*Fagus orientalis* Lipsky, 1898, *F. sylvatica*), birch (e.g., *Betula aetnensis* Raf. ex J. Presl & C. Presl, 1822), black locust (*Robinia pseudoacacia* L., 1753), Christ's thorn (*Paliurus* sp.), elm (*Ulmus* sp.), hackberry (*Celtis* sp.), hawthorn (*Crataegus* sp.), oak (e.g., *Quercus cerris* L., 1753, *Q. faginea* Lam., 1785, *Q. frainetto* Ten., 1813, *Q. ilex* L., 1753, *Q. ithaburensis* Lecne., 1835, *Q. pubescens* Willd., 1796, *Q. pyrenaica* Willd., 1805, *Q. robur* L., 1753, *Q. suber* L., 1753), olive (*Olea* *europaea* L., 1753), pear (*Pyrus communis* L., 1753), plane tree (*Platanus orientalis* L., 1753), poplar (*Populus alba* L., 1753), sweet chestnut (*Castanea sativa* Mill., 1768), wild cherry (*Prunus (Cerasus) avium* (L.) L., 1753), and willow[25,36,38–41,49,51–58]. In Cyprus, they can be found even in evergreen *Eucalyptus* trees[25]. In France, they were found in a beech together with *L. querceus*[39], and in Cyprus, they occur sympatrically with the recently described *L. cyprius* Németh et al., 2020[25]. Specimens of *L. punctatus* can be found in the same tree with e.g., *Aesalus scarabaeoides* (Lucanidae), *Uloma rufa*, *Tenebroides maroccanus* Reitter, 1884 (Trogossitidae), *Osmoderma barnabita* Motschulsky, 1845 (Scarabaeidae), and *Rhaesus serricollis* (Motschulsky, 1838) (Cerambycidae)[39,59] (incl. pers. observ. by T. Németh). For examples of typical habitats of *L. punctatus* see Fig. S3A–F. Depending on the geographic location, pupation usually occurs in either August, September or October, adults (Fig. 1D) overwinter in pupal chambers or under the bark, and usually emerge either in April, May or June[34,38,44,60], and in warm autumns even in October (T. Németh, pers. observ.).

Distribution. Europe: Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Malta, Montenegro, North Macedonia, Portugal, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Switzerland, Ukraine; Asia: Armenia, Azerbaijan, Cyprus, Georgia, Iran, Israel, Jordan, Lebanon, Syria, Türkiye; Africa: Algeria, Moroco, Tunisia. Records from Pakistan probably represent different species[22].

***Lacon querceus* (Herbst, 1784)**

(Figs. 1E–F; 6–7; S1C, F; S2E, S3A, S4)

Material examined. 16 specimens: Czech Republic, Moravia, Nové Mlýny, Křivé jezero, 31. 3. 2019, lgt. Trnka (2 ex.; PCFT); Czech Republic, Moravia, Tovačov, April 2019 (2 ex.; PCFT); Hungary, Pest county, Nagymaros, Rigó-hegy, 15.III.2020, from red rotten *Quercus*, leg. T. Németh (10 ex.; HNHM); Hungary, Pest county, Perőcsény, Godóvár, 15.VI.2021, 47.983, 18.891, leg. T. Németh (2 ex.; HNHM).

Diagnosis of mature larva. Dorsal surface of head sublaterally with distinct longitudinal subparalell keels (Fig. 6B, D); posterior part (lobe) of frontoclypeal plate after the widened place gradually narrowed and almost V-shaped (Figs. 6D, S1C); postmentum 3.1–3.4 times longer than wide (Fig. 6F, 7A–B); dorsal surface of segment IX with about 50–90 nodule-like tubercles, medially with one or two pairs of distinct long setae and several short setae set in tubercles (one or both pairs of long setae may be asymmetrical; Figs. 7J–K, S1F); urogomphus 1.1–1.2 times as long as wide; notch between urogomphi about 0.3 times as long as whole segment IX and 1.80–2.15 times as wide as urogomphus when urogomphus width is measured at half and notch width at the widest place; notch about at level of fourth lateral tooth or even slightly deeper. For the overview of diagnostic characters, see Table 1.

Biology and ecology. This species typically inhabits cavities, hollows, logs and stumps of old oaks (e.g., *Quercus petraea* (Matt.) Liebl., 1784, *Q. robur*) with red rot[27,38,39,54,61,62], but it can also develop in beech (*Fagus sylvatica* L., 1753; found there together with *L. punctatus*), maple (*Acer campestre* L., 1753, *A. pseudoplatanus* L., 1753, etc.), sweet chestnut (*Castanea sativa* Mill., 1768), wild cherry (*Prunus (Cerasus) avium* (L.) L., 1753), birch[38,39,44,54,62], and surprisingly also in the coniferous fir, where it was found together with *L. lepidopterus*[43]. One adult was found on almond (*Prunus amygdalus* Batsch, 1801)[39]. Larvae live in rotting wood infested with fungus *Laetiporus sulphureus* (Bull.) Murrill, 1920 which serves as food for invertebrates on which *Lacon* larvae prey[61,63]. Larvae of *L. querceus* were reported to prey on the larvae and pupae of other beetles like e.g., *Mycetophagus piceus* (Fabricius, 1777), *M. quadriguttatus* Müller, 1821 (Fig. S4B) (both Mycetophagidae), *Pentaphyllus testaceus* (Hellwig, 1792) (Tenebrionidae), *Euglenes pygmaeus* (DeGeer, 1775) (Aderidae), *Xestobium rufovillosum* (De Geer, 1774), *Dorcatoma flavicornis* (Fabricius, 1792), and *D. dresdensis* Herbst, 1792 (all Ptinidae)[34,61,63,64]. According to some authors, they also could prey on ants (*Lasius* sp.)[38,44]. Additionally, larvae of *L. querceus* were found in the same oak trees together with *Ampedus cardinalis* (Schiødte, 1865) (Elateridae), *Cerambyx cerdo* Linnaeus, 1758 (Cerambycidae), *Anitys rubens* (Hoffmann, 1803) (Ptinidae), *Gnorimus variabilis* (Linnaeus, 1758) (Scarabaeidae), *Trox scaber* (Linnaeus, 1767) (Trogidae), *Tenebrio opacus* Duftschmid, 1812 (Tenebrionidae), and *Dendroleon pantherinus* (Fabricius, 1787) (Neuroptera: Myrmeleonidae), and in the same beech tree with *Aesalus scarabaeoides* (Lucanidae)[39,54,62]. In France, *L. querceus* was found in the same fir tree together with *L. lepidopterus* and 13 other beetle species (see above under the latter)[43]. In some rare cases, either larvae or adults can be found in high numbers within the same log[62] (Fig. S4D). For examples of typical habitats of *L. querceus* see Figs. S2E, S3A, S4E–F. Pupation usually occurs between August and September/October. Adults (Figs. 1F, S4C–D) overwinter in pupal chambers or in cracks and under bark, and emerge in May and are usually active until August but in warm autumns even longer[38,44,48] (incl. pers. observ. by T. Németh).

Distribution. Europe: Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Great Britain, Greece, Hungary, Italy, Lithuania (dubious; D. Telnov and V. Tamutis, pers. comm.), Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland, Ukraine.

General description of mature larvae of *Lacon* species from Europe

Body (Figs. 1A, C, E; 2A–C; 4A–C; 6A–C; S2A–B, S4B) length up to 35 mm; thorax and abdomen slightly flattened dorsoventrally. Dorsal surface pale yellow, except for brown head, pronotum, anterior part of mesonotum, and posterior 2/3 of tergite IX; ventral surface mostly pale yellow, except for brown prothorax and abdominal sternite IX; claws, elliptic setae on legs and anal hooks dark brown. Vestiture consisting of sparse fine setae.

Head (Figs. 2D–F, 4D–F, 6D–F) prognathous, heavily sclerotized, epicranium with punctures usually separated by 2–3 puncture diameters; frontoclypeal plate (Figs. 2D, 4D, 6D, S1A–C) with punctures finer and sparser; dorsal surface medially depressed, gradually declivous anterad, gradually or strongly sloping to lateral region forming a pair of longitudinal subparalell elevations or keels. Epicranium dorsally with two long setae at midlength and row of three larger punctures with short setae near posterior margin; dorsolaterally with row of 5–7 setae at base of antennifer, laterally with one seta near antennifer, two setae at midlength. Stemmata and coronal suture absent. Frontal arms lyriform, posterior part (lobe) of frontoclypeal plate about 3.3–3.8 times longer than anterior part, with apical third either abruptly narrowed and finger-like or gradually narrowed and almost V-shaped; nasale tridentate, teeth subequal in size or median tooth slightly larger than the lateral ones, two or three setae between each lateral and median teeth. Adnasalia surpassing anterad the median nasal tooth, widely separated (distance between them 1.00–1.35 times adnasalium width measured at base), densely fringed by setae. Ventral surface of head mostly glabrous except lateroventral margins with one long seta at base of antennifer, one smaller seta on anterior 1/5, two long setae at midlength, and few setae along outer edge of ventral ridges. Antenna (Figs. 3C–D, 5C–D, 7C–D) with few setae; basal antennomere as long as median one; median antennomere 2.3–2.7 times longer than apical one; apex of median antennomere with conical sensorium lateroventrally; apical antennomere with few very small setae and one thick seta twice longer than antennomere itself. Mandible (Figs. 3E–F, 5E–F, 7E–F) 1.9–2.3 times longer than wide, unidentate, incisor edge smooth, concave, penicillus minuscule; one seta dorsolaterally at midlength, one dorsal seta near base. Maxilla (Figs. 3A–B, 5A–B, 7A–B) with stipes about 3.0 times longer than wide, weakly narrowed posteriorly, anterior edge abruptly narrowed and membranous, lateral margin with sparse setae, longer and thicker on anterior corner; maxillary palp 0.5 times as long as stipes, with few setae, apical palpomere with minuscule basiconic sensilla; galea 2-segmented, palpiform, apical segment with short thick setae; lacinia reduced, densely setose. Cardines fused to each other. Labium (Figs. 3A–B, 5A–B, 7A–B) with prementum about twice as wide as long, two lateral long setae near anterior edge; postmentum triangular, 2.5–3.2 times as long as wide, anterior edge membranous; one pair of long setae anteriorly, one pair of long setae at apex; palp 0.3 times as long as prementum, apical palpomere 0.4 times as long as basal palpomere; ligula absent.

Prothorax (Figs. 2A–C, 4A–C, 6A–C) strongly sclerotized, 1.7 times as long as mesothorax, mesothorax 0.9 times as long as metathorax; pronotum finely punctate (punctures narrower in diameter than mid-dorsal suture), each side with few setae. Prosternum with two pairs of lateral setae near anterior margin, one pair of setae and other few unpaired setae on apex. Each side of meso- and metanotum with one anterior pair of dorsolateral setae, one posterior pair of dorsolateral setae; lateral margin with several short to long setae; mesopleura with large biforous spiracle anteriorly. Leg (Figs. 3G–I, 5G–I, 7G–I) stout, short, with sparse fine setae; strongly sclerotized elliptic setae along edges of trochanter, femur and tibia, denser on anterior edge; pretarsus with two setae at inner base.

Abdominal segments I–VIII (Figs. 2A–C, 4A–C, 6A–C) with spiracles large, well visible in lateral view; mediotergites with each side with longitudinal row of 5–7 setae laterally (last one more dorsal) and two setae dorsoposteriorly, laterotergites with four setae, pleurae with two setae; sterna with a pair of setae anterolaterally, two pairs of setae posterolaterally. Segment IX (Figs. 3J–L, 5J–L, 7J–L, S1D–F) well sclerotized, with dorsal surface medially depressed, with pair of parasagittal grooves, covered with 50–150 small nodule-like tubercles, one or two pairs of larger tubercles with longer setae, in some cases with several short setae; lateroventrally with few short and several longer setae; four lateral acute teeth, increasing in size posteriorly with seta at base; each urogomphus 1.0–1.4 times as long as wide, with two prongs subequal in length, outer prong bent dorsad; notch between urogomphi 0.2–0.3 times as long as whole segment IX and 1.05–2.25 times as wide as urogomphus when urogomphus width is measured at half and notch width at the widest place; anterior edge of notch variably deep, posterior to slightly anterior to fourth lateral tooth. Segment X (Figs. 3K–L, 5K–L, 7K–L) tubular, ventral, with few setae along apicolateral margin and near anal opening, with pair of strongly sclerotized anal hooks; anal hooks as long as pygopod.

Discussion

The *Lacon* species are mostly saproxylic; however, larvae of *L. funebris* from central Asia, for example, develop in soil, often in arable lands[26,65]. Adults of some Mediterranean species with unknown larvae were collected from under the stones in places without large trees[23]; however, numerous adult specimens of clearly saproxylic species like e.g. *L. punctatus* or *L. graceus* were also found under the stones[23,41,53]. Larvae of the North American species are usually associated with conifers; *L. discoideus* was found in decaying wood of pine but also in hackberry and oak, *L. marmoratus* in soft maple and black gum (tupelo; *Nyssa sylvatica* Marsh., 1785) *L. rorulentus* (LeConte, 1859) in the Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco, 1950), *L. auroratus* (Say, 1839) in the pitch pine (*Pinus rigida* Mill., 1768), *L. avitus* (Say, 1839) in dead hickory trees, and an unspecified *Lacon* species in the Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson, 1836)[33,66,67] (incl. pers. comm. by Paul J. Johnson). Larvae of the species identified as *L. modestus* (Boisduval, 1835) from Myanmar develop in teak (*Tectona grandis* L. f., 1782)[68]. Larvae of *L. altaicus* from central Asia usually develop in rotten wood of coniferous trees, mainly pines[69]. Chinese *Lacon* species were also found in decaying wood[70] but there is no available information on the immature stages of this genus from there (L. Qiu, pers. comm.). The Levantine *L. candezei* (Desbrochers des Loges, 1875) and *L. cyprius* from Cyprus are both associated with the kermes oak (*Quercus coccifera* L., 1753), and the latter also with the East Mediterranean pine (*Pinus brutia*)[23,25].

Larvae of European *Lacon* develop in the decayed wood of both coniferous and deciduous trees. The Mediterranean *L. graecus* and *L. ladae* are both associated with oaks, and the latter also with the plane trees[23]. Although *L. lepidopterus* is usually found in the coniferous trees (usually fir, pine and spruce[38,40,42]) and *L. querceus* in deciduous trees (usually oak[38–40,62]), they can live in both types of trees[38,42,43], and *L. punctatus* inhabits even much wider range of trees (beech, birch, cedar, chestnut, hawthorn, oak, pine, plane tree, poplar, elm, willow, and others)[36,38–40,52,53] (see the respective parts under each species above). It seems that the type and stage of the decayed fungus-infested wood (usually red rot) is more important for them than the tree species[43].

The *Lacon* larvae usually feed on immature stages of other insects which are usually wood-boring and/or associated with the decaying wood infested by fungus, like e.g., Ptinidae, Scolytinae, and Cerambycidae[48,61,63,66,71] (also pers. observ. by authors and colleagues; Fig. S4B). The predatory behavior is typical for Agrypninae, which feed not only on other arthropods[72,73] but also on snails[74,75] or even the sea turtle eggs[76]. It should be noted that even larvae of some *Agrypnus*, which live in soil and are considered agriculture pests, are carnivorous/omnivorous[10,15]. In the Holarctic saproxylic *Lacon* species, pupation usually occurs between July and September/October; adults overwinter in pupal chambers or in cracks or under the bark, and emerge from April to June depending on the species and location[33,38,42]. This kind of information is basically missing for all other *Lacon* species.

Larvae were at least partly described and/or illustrated for only eight out of approximately 150 *Lacon* species, including the West Palaearctic *L. punctatus*[26,27,34,77–79], *L. querceus*[26,27,34,80] and *L. lepidopterus*[26,27,34], the North American *L. discoideus* (Weber, 1801) and *L. marmoratus* (Fabricius, 1801)[33,81], the Japanese *L. parallelus* (Lewis, 1894)[31], and the central Asian *L. altaicus* (Candèze, 1882) and *L. funebris* (Solsky, 1881)[26,65]. Most of those descriptions and drawings were focused on the frontoclypeal plate and the abdominal segment IX while other characters like the details of chaetotaxy are hardly comparable with the specimens we examined here (Table 1). Regarding the Palaearctic species, larvae of *Lacon funebris* and *L. parallelus* differ from all other known *Lacon* larvae (including the Nearctic ones) by their short and wide urogomphi which are much wider than the apical notch on abdominal segment IX, and with the apical notch being only about 1/10 as long as the segment IX[26,31]. *Lacon altaicus* has the most elongate urogomphi which are about 1.8 times as long as wide (up to 1.4 times in other species)[26].

Regarding European species, Dolin[26,27] and Tarnawski[34] constructed the identification keys to separate *L. lepidopterus*, *L. punctatus*, and *L. querceus*, and provided the drawings of the frontoclypeal plate and the abdominal tergite IX for each of them. The most recent key by Tarnawski[34] separated the European species by the shape of the posterior lobe of the frontoclypeal plate, the sclerotization of the nasal teeth, the size of the apical notch on abdominal segment IX, and the presence of short setae on small tubercles on dorsal surface of abdominal segment IX. Here, we tested the characters used in earlier keys and added more details. It should be noted that all mentioned features are consistent among the species (Table 1) but we avoid using the sclerotization of nasal teeth in the species diagnoses. Tarnawski[34] wrote that "denticles of nasale [are] with a narrowly sclerified base" in *L. punctatus*, while they are "with no sclerified base" in remaining two species. We cannot exclude the possibility that this is a valid diagnostic character but at the moment we are not sure if the presence of a more sclerotized part between individual nasal teeth is connected with the specific species or with the size of the body, as we observed the sclerotized part between the nasal teeth also in larger larvae of *L. lepidopterus*. We keep this open to further investigation.

Lacon querceus is generally smaller than the remaining species and is easily distinguishable from them by having the dorsal surface of head sublaterally with distinct longitudinal subparalell keels (Fig. 6B, D), the posterior part of the frontoclypeal plate after the widened place gradually narrowed and almost V-shaped (Figs. 6D, S1C), the postmentum more elongate, being more than three times longer than wide (Fig. 7A–B), the dorsal surface of segment IX medially not only with one or two pairs of distinct long setae (of which some can be asymmetrical) but also with several short setae set in tubercles (Figs. 7J, S1F), and the apical notch between urogomphi about at the level of the fourth lateral tooth. Some of these characters are unique among all known *Lacon* larvae (Table 1).

Lacon lepidopterus and *L. punctatus* are more similar to each other, and in many aspects also to the most of other known *Lacon* larvae (Table 1). They share the dorsal surface of head sublaterally with longitudinal subparalell elevations without any distinct keels (Figs. 2B, D; 4B, D), the posterior part of the frontoclypeal plate after the widened place abruptly narrowed, finger-like (Figs. 2D, 4D, S1A–B), the postmentum up to 2.7 times as long as wide (Figs. 3A–B, 5A–B), the dorsal surface of segment IX medially only with two pairs of distinct long setae (Figs. 3J, 5J, S1D–E), and the apical notch between urogomphi always posterior to the level of the fourth lateral tooth. It should be noted that although the latter character was absolutely clear and consistent in all our studied specimens (i.e., the apical notch never reached the level of the fourth lateral tooth), Dolin[26] made his drawing of the apical notch of *L. lepidopterus* that it was deeper, reaching the level of the fourth lateral tooth. This drawing was later also used by Tarnawski[34]. Here, we corrected it (Fig. S1D). *Lacon punctatus* can be easily distinguished from both *L. lepidopterus* and *L. querceus* by its relatively narrower apical notch between urogomphi. While it has the notch maximally 1.25 times as wide as urogomphus when urogomphus width is measured at half and notch width at the widest place (Figs. 5J, L; S1E), the notch of both *L. lepidopterus* and *L. querceus* is usually about twice as wide as urogomphus (Table 1; Figs. 3J, L; 7J, L; S1D, F). *Lacon punctatus* has also relatively larger tubercles on the abdominal tergite IX (Figs. 3J, 5J, 7J, S1D–F). While examining the diagnostic characters between the *Lacon* species, we thought that the number of nodule-like tubercles medially on abdominal tergite IX could also be used to separate *L. querceus* from both *L. lepidopterus* and *L. punctatus*. In most specimens of *L. querceus*, there were about 50–80 tubercles, while in *L. lepidopterus* and *L. punctatus* usually more than 100. However, we found one *L. querceus* and one *L. lepidopterus* which had roughly around 90 tubercles. Hence, although this character may help to diagnose these species using most examined specimens, there is some variability (Table 1). Further research should answer the question if this character is of taxonomic importance for European *Lacon* species or if the larger larvae mostly have more tubercles regardless the species.

It is undisputable that the worldwide research on *Lacon* larvae should be improved. So far, the descriptions and drawings were usually based on a limited number of specimens, and also the identity of some larvae should be confirmed by the DNA-based approach. It is advisable, that, similar as in our study, the descriptions of important diagnostic characters are improved, supplemented or edited in all other species based on the examination of higher numbers of specimens from different populations. For example, Ôhira[31] described *L. parallelus* based on a larva found with adults in the same log, but did not rear them to adult stage. He provided excellent drawings and description in which, however, he did not mention the depressed area with parallel elevations on the head which is typical for other *Lacon* species (Table 1). This character should be re-examined for *L. parallelus* and also for *L. marmoratus* in future.

Within the tribe Agrypnini, larvae are only described for several genera other than *Lacon*, including *Agraeus* Candèze, 1857, *Agrypnus* Eschscholtz, 1829, *Candanius* Hayek, 1973, *Compsolacon* Reitter, 1905, *Danosoma*, *Dilobitarsus* Latreille, 1834, and *Meristhus* Candèze, 1857[26,31,32,82–84]. Based on the available larval features found in *Lacon* compared to the known larvae of other genera in Agrypnini, we proposed a unique combination of characters to distinguish this genus (see the generic larval diagnosis above). It seems that the most striking characters of *Lacon* larvae are the dorsal surface of head which is laterally gradually elevated or with subparallel keels (Figs. 2B, D; 4B, D; 6B, D), numerous nodule-like tubercles on the dorsal surface of abdominal segment IX (Figs. 3J, 5J, 7J, S1D–F), and large anal hooks on segment X (Figs. 3K, 5K, 7K). The most similar larvae to *Lacon* species are those of the genera *Danosoma*, earlier classified in *Lacon*[26], and *Candanius*. All other known larvae of Agrypnini differ from *Lacon* in lacking the lateral elevations on dorsal head, and having the posterior part of the frontoclypeal plate usually up to about twice as long as the anterior part (except 2.4–2.5 times in *Dilobitarsus* and 2.8 times in *Meristhus*; in *Lacon* spp. 2.7–4.0 times; Table 1), and very small anal hooks, usually about 1/10 of the pygopod length (about as long as pygopod in *Lacon* spp.). *Danosoma* shares with *Lacon* the parallel elevations on dorsal head and the large anal hooks[26,34] but differs in the combination of the different shape of the posterior part of the frontoclypeal plate (2.3–2.4 times longer than anterior part and gradually narrowed apically, being roughly similar only to *L. parallelus*; Table 1), the dorsal surface of abdominal segment IX without or with at most 20 nodule-like tubercles, and the apical notch between urogomphi very small (up to 0.1 times as long as whole segment IX, being similar only to *L. funebris* and *L. parallelus*; Table 1). The larva of Chilean *Candanius lueri* Pineda, 2020 (described based on the last larval exuvia) is even more similar to those of *Lacon*[84]. Both genera share the shape of the posterior part of the frontoclypeal plate (in *Candanius* 3.5 times longer than anterior part, with apical third rather abruptly narrowed), the depressed dorsal surface of head gradually elevated laterad, the shape of prongs, and the size of anal hooks. *Candanius* differs in having the median antennomere twice longer than the basal one (both subequal in *Lacon*; Figs. 3C–D, 5C–D, 7C–D), the distance between adnasalia up to 0.8 times the width of adnasalium (1.0–1.5 times in *Lacon*), and the anterior margin of adnasalium rounded (more or less pointed in *Lacon*; Figs. 2D, 4D, 6D, S1A–C), and in the lack of the tubercles on the abdominal tergite IX[84]. Hayek[20] mentioned that the diagnostic characters separating *Lacon* and *Candanius* based on adults are mostly of any importance at the generic level in Agrypnini, and that future research may show that they should belong to a single genus. The larval characters are helpful in separating *Candanius* from *Lacon*; however, larvae of more species of the latter should be described and studied in order to see the real infrageneric variability in principal diagnostic characters. Larvae of *Lacon*, *Danosoma* and *Candanius* are mostly saproxylic[26,84], while known larvae of other Agrypnini live in soil, leaf litter, under bark or stones, or even in termite mounds and bromeliads[26,31,32,82,83].

The European *Lacon* species are not only worthy of study from the systematic point of view but they are very important for the nature protection initiatives since they can serve as focal and umbrella species for forest conservation[5,7,9]. Eckelt et al.[9] considered all three species of Central European *Lacon* are the umbrella primeval forest relict species, placing *L. lepidopterus* and *L. querceus* to the first category and *L. punctatus* to the second one. *Lacon lepidopterus* and *L. querceus* are both assessed as Near Threatened regarding the European regional assessment of the IUCN Red List of Threatened Species, or even Endangered (*L. lepidopterus*) and Vulnerable (*L. querceus*) regarding the EU 27 regional assessment[30]. Both species are dependent upon veteran trees and their populations are decreasing[30]. On the other hand, *L. punctatus* is assessed as Least Concerned due to its wide distribution and ability to develop in a variety of host trees. Although its population trend is officially unknown[30], based on the observations of some colleagues, the populations of this species are decreasing at least in some places of Europe. *Lacon ladae* is assessed as Least Concern in the Mediterranean assessment, and *L. gillerforsi* and *L. graecus* currently fall within the category Data deficient[30]. It should be noted that although saproxylic *Lacon* species are generally considered rare and threatened, they appear only in several national Red Lists in Europe and are legally protected only in some countries.

Although we here summarized information on *Lacon* larval morphology, biology and ecology, including the improvements of diagnoses of the whole genus as well as of the European species, and the lists of the known host trees for all species, still there are many important questions to be solved. Future research should focus on the number of instars and the morphological differences between them, as well as on the morphology of pupae which have not yet been properly described. Findings of immature stages of other species and more populations of the already known species as well as findings of the larvae of Agrypnini genera for which they have not yet been described will help to test the diagnoses on both species and genus level.

Material and methods

This study was based on the larval specimens of *L. lepidopterus* (nine ex., 18–27 mm long; Figs. 2, 3) from the Czech Republic and Hungary, *L. punctatus* (11 ex., 19–35 mm long; Figs. 4, 5) from Albania, Croatia, Greece, Hungary, Macedonia, and Montenegro, and *L. querceus* (16 ex., 11–18 mm long; Figs. 6, 7) from the Czech Republic and Hungary. All specimens but those from Albania, Czech Republic and Macedonia were collected during the field trips of the first author between 2013 and 2023. They were collected in the field into 96% ethanol, then photographed and some of them dissected after a short treatment in hot 10% KOH. Dissected parts of head were transferred to glycerol. Diagnostic characters were photographed using the Mitutoyo M Plan Apo 5X microscope lens and Nikon AF Micro Nikkor 60mm lens attached to a Nikon D5200 camera. Photographs were combined with the Zerene Stacker image stacking software. The measurements were taken directly from specimens with a scale bar in an eyepiece and from photographs and illustrations using a ruler tool in Adobe Photoshop CC 2019. For the measurements of main diagnostic characters we refer to Fig. S1G,H. The material examined in this study is deposited in the Coleoptera Collection of the Hungarian Natural History Museum (HNHM), Budapest, Hungary, except for two specimens of *L. punctatus* from Albania and Macedonia, which were collected during the expeditions by T. Kovács and are deposited in Mátra Museum (MM), Hungary, four specimens of *L. querceus* from the Czech Republic, which were collected during the entomological surveys under the Nature Conservation Agency of the Czech Republic and are deposited in the collection of Filip Trnka, Tršice, Czech Republic (PCFT), and two specimens of *L. lepidopterus* from the Czech Republic, which were collected by Jiří Procházka during the official entomological surveys (under the official permits by the administrations of the

Protected Landscape Area Beskydy and the České Švýcarsko National Park, respectively), and are deposited in the Moravian museum, Brno, Czech Republic (MZM). All photographs in Figs. 1 and S2–S4 were taken by the first author except for Figs. S3F and S4F, which were taken by Boris Lauš (Croatia; used with written permission from the author). Photographs of live specimens (Fig. 1B, D, F; S2A–B; S4A–D) were taken with Fuji Finepix HS25 EXR camera and Raynox 150 and 250 lens. Morphological terminology for larval descriptions follows partly Glen[85], Tarnawski[34], Costa et al.[11], and Rosa et al.[73]. Distribution data were taken from Cate[17], IUCN[30], and numerous taxonomic and faunistic studies, and were consulted with colleagues (see Acknowledgements). Collecting permits for Hungary, Greece, and Croatia were issued by the Budapest Government Office (PE-KTFO/329-16/2019; 2019–2028), the Ministry of Environment and Energy (171978/1594; 2013), and the Ministry of Environmental Protection and Energy (Class: UP/I-612-07/20-48/39; URBROJ: 517-05-1-1-20-4; 2020–2024), respectively.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper. The high resolution photographs of the examined specimens are available from the corresponding author upon reasonable request.

References

1. Stork, N. E., McBroom, J., Gely, C. & Hamilton, A. J. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 7519–7523 (2015).
2. Goczał, J., Beutel, R. G., Gimmel, M. L. & Kundrata, R. When a key innovation becomes redundant: Patterns, drivers and consequences of elytral reduction in Coleoptera. *Syst. Entomol.* **49**, 193–220 (2024).
3. Beutel, R. G. et al. The evolutionary history of Coleoptera (Insecta) in the late Palaeozoic and the Mesozoic. *Syst. Entomol.* **49**, 355–388 (2024).
4. Gimmel, M. L. & Ferro, M. L. General overview of saproxylic Coleoptera in *Saproxylic Insects: Diversity, Ecology and Conservation* (ed. Ulyshen, M. D.) 51–128 (Springer International Publishing, 2018).

5. Nieto, A. & Alexander, K. N. A. *European red list of saproxylic beetles* (Publications Office of the European Union, IUCN, Luxembourg, 2010).
6. Stokland, J. N., Siitonen, J. & Jonsson, B. G. *Biodiversity in dead wood* (Cambridge University Press, 2012).
7. Cálix, M. et al. European red list of saproxylic beetles. Brussels, Belgium: IUCN. Available at: https://portals.iucn.org/library/node/47296 (2018).
8. Parisi, F. et al. Diversity patterns of Coleoptera and saproxylic communities in unmanaged forests of Mediterranean mountains. *Ecol. Indic.* **110**, 105873 (2020).
9. Eckelt, A. et al. Primeval forest relict beetles of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *J. Insect Conserv*. **22**, 15–28 (2018).
10. Calder, A. A. Click beetles: Genera of the Australian Elateridae (Coleoptera). *Monographs on Invertebrate Taxonomy, Vol. 2* (CSIRO Publishing, 1996).
11. Costa, C., Lawrence, J. F. & Rosa, S. P. Elateridae Leach, 1815 in *Coleoptera, Beetles; Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (eds. Leschen, R. A. B., Beutel, R. G. & Lawrence, J. F.) in *Handbook of Zoology, Arthropoda: Insecta* (eds. Kristensen, N. P. & Beutel, R. G.) 75–103 (Berlin/New York: Walter de Gruyter GmbH & Co, 2010).
12. Ruan, Y. et al. Functional morphology of the thorax of the click beetle *Campsosternus auratus* (Coleoptera, Elateridae), with an emphasis on its jumping mechanism. *Insects* **13**, 248 (2022).
13. Kundrata, R., Packova, G., Prosvirov, A. S. & Hoffmannova, J. The fossil record of Elateridae (Coleoptera: Elateroidea): described species, current problems and future prospects. *Insects* **12**, 286 (2021).
14. Szabó, M. et al. The frst mainland European Mesozoic click-beetle (Coleoptera: Elateridae) revealed by X-ray micro-computed tomography scanning of an Upper Cretaceous amber from Hungary. *Sci. Rep.* **12**, 24 (2022).
15. Traugott, M., Benefer, C. M., Blackshaw, R. P., Herk, van W. G. & Vernon, R. S. Biology, ecology, and control of elaterid beetles in agricultural land. *Annu. Rev. Entomol.* **60**, 313–334 (2015).
16. Douglas, H. B., Etzler, F. E., Johnson, P. J. & Hammond, H. E. J. Matrix-based key to the click beetle genera of Canada and USA with a summary of habitat use (Coleoptera, Elateridae). *ZooKeys* **1200**, 75–144 (2024).

17. Cate, P. C., Sánchez-Ruiz, A., Löbl, I. & Smetana, A. Family Elateridae Leach, 1815 in *Catalogue of Palaearctic Coleoptera vol. 4. Elateroidea – Derontoidea – Bostrichoidea – Lymexyloidea – Cleroidea – Cucujoidea* (eds. Löbl, I. & Smetana, A.) 89–209 (Apollo Books, Stenstrup, 2007).

18. Kundrata, R. et al. World catalogue of the genus-group names in Elateridae (Insecta, Coleoptera). Part I: Agrypninae, Campyloxeninae, Hemiopinae, Lissominae, Oestodinae, Parablacinae, Physodactylinae, Pityobiinae, Subprotelaterinae, Tetralobinae. *ZooKeys* **839**, 83–154 (2019).

19. Girard, C. Catalogue commenté des Coléoptères Elateridae d´Afrique subsaharienne (Cardiophorinae exclus). *Soc. Entomol. Fr.* **10**, 1–404 (2017).

20. Hayek von, C. M. F. A reclassification of the subfamily Agrypninae (Coleoptera: Elateridae). *Bull. Br. Mus. Nat. (Natural History) Entomology* **20**, 1−309 (1973).

21. Prosvirov, A. S. New and little-known species of the genus *Lacon* Laporte, 1838 (Coleoptera: Elateridae) of China. *Zootaxa* **4132**, 373–382 (2016).

22. Prosvirov, A. S. New and little-known species of the genus *Lacon* Laporte, 1838 (Coleoptera: Elateridae) of Afghanistan and adjacent countries. *Zootaxa* **4168**, 279–296 (2016).

23. Kundrata, R., Mertlik, J. & Németh, T. Unexpected diversity of *Lacon* Laporte, 1838 (Coleoptera: Elateridae: Agrypninae) in the Levant: revised species concepts, new species, and an identification key. *Zootaxa* **4679**, 401–449 (2019).

24. Kundrata, R., Németh, T. & Jarzabek-Müller, A. Description of *Lacon mertliki* sp. nov. (Coleoptera: Elateridae: Agrypninae) from the Hyrcanian forest ecoregion, with a key to the *Lacon* species of Iran. *Eur. J. Taxon.* **535**, 1–13 (2019).

25. Németh, T., Brůha, P. & Kundrata, R. Discovery of a new species of *Lacon* Laporte (Coleoptera: Elateridae: Agrypninae) endemic to Cyprus, with a modified tarsal morphology. *Zootaxa* **4780**, 554–562 (2020).

26. Dolin, V. G. *Opredelitel lichinok zhukov-shchelkunov fauny SSSR* [Key to wireworms of the fauna of the USSR] (Urozhai, Kiev, 1978).

27. Dolin, V. G. *Click-beetles (Agrypninae, Negastriinae, Diminae, Athoinae, Oestodinae).* Fauna Ukraini, 19 (Akademia Nauk Ukranian SSR, Kiev, 1982).

28. Hejda, R., Farkač, J. & Chobot, K. *Červený seznam ohrožených druhů České republiky. Bezobratlí. Red list of threatened species of the Czech Republic. Invertebrates* (Agentura ochrany přírody a krajiny ČR, 2017).

29. Buchholz, L. *Lacon lepidopterus* (Panzer, 1801). Polska czerwona księga zwierząt, Bezkręgowce. Available at: https://www.iop.krakow.pl/pckz (2024).
30. IUCN. The IUCN red list of threatened species. Version 2024-2. Available at www.iucnredlist.org (2024).
31. Ôhira, H. *Morphological and taxonomic study on the larvae of Elateridae of Japan (Coleoptera)* (Entomological Laboratory Aichi Gakugei University, 1962).
32. Rosa, S. P., Albertoni, F. F. & Bená, D. C. Description of the immature stages of *Platycrepidius dewynteri* Chassain (Coleoptera, Elateridae, Agrypninae, Platycrepidiini) from Brazil with a synopsis of the larval characters of Agrypninae tribes. *Zootaxa* **3914**, 318–330 (2015).
33. Jewett, H. H. Identification of some larval Elateridae found in Kentucky. *Bull. Ky. Agric. Exp. Stn*. **489**, 1–40 (1946).
34. Tarnawski, D. *Elateridae, Sprężykowate Część I (Insecta: Coleoptera)* (Polskie Towarzystwo Entomologiczne, 2000).
35. Jarzabek-Müller, A. First records for eight click-beetles (Coleoptera, Elateridae) in Greece. *Elateridarium* **7**, 77–83 (2013).
36. Gülperçin, N. & Tezcan, S. Türkiye Orman Ekosistemlerinin Elateridae (Insecta: Coleoptera) Faunası Üzerinde Bir Değerlendirme. *Bartın orman fak. derg.* **18**, 132–144 (2016).
37. Binaghi, G. Note di caccia (Coleoptera). IV. *Ann. Mus. Civ. Stor. Nat. Giacomo Doria*. **76**, 307–318 (1967).
38. Leseigneur, L. Coléoptères Elateridae de la fauna de France continentale et de Corse. *Bull. Mens. Soc. Linn. Lyon* **41**, 3–382 (1972).
39. Brustel, H. & Meer, C. Sur quelques éléments remarquablesde l'entomofaune saproxylique pyrénéenne et des régions voisines (Coleoptera). *Bull. Soc. entomol. Fr.* **104**, 231–240 (1999).
40. Laibner, S. *Elateridae of the Czech and Slovak Republics* (Kabourek, 2000).
41. Kesdek, M., Platia, G. & Yildirim, E. Contribution to the knowledge of click-beetles fauna of Turkey (Coleoptera: Elateridae). *Entomol. Z.* **27**, 417–432 (2006).
42. Delnatte, J. Nouvelle observation de *Lacon lepidopterus* (Panzer, 1801) dans les Alpes-Maritimes (Coleoptera Elateridae). *L'Entomologiste* **64**, 143–146 (2008).
43. Grancher, C., Chekir, L. & Lefebvre, V. Observation étonnante de *Lacon querceus* (Herbst, 1784) dans les Pyrénées-Atlantiques (Coleoptera Elateridae). *Bull. Soc. linn. Bordx.* **148**, 403–406 (2013).

44. Chatenet du, G. *Phytophagous beetles of Europe. Buprestidae, Elateridae, Cleridae, Cerambycidae. Volume 1* (N.A.P. Editions, 2017).
45. Holzer, E. Erstnachweise und Wiederfunde für die Käferfauna der Steiermark (XVIII) (Coleoptera). *Joannea Zoologie* **18**, 195–208 (2020).
46. Moncoutier, B. Contribution à la connaissance de la Faune des Pyrénées Occidentales. Découverte d'une espèce nouvelle pour la France et redécouverte d'une espèce mythique (Col. Elateridae et Rhizophagidae). *L'Entomologiste* **51**, 133–138 (1995).
47. Lorenz, J. „Urwaldrelikt"-Käferarten in Sachsen (Coleoptera). *Sächsische Entomologische Zeitschrift* **5**, 69–98 (2010).
48. Burakowski, B., Mroczkowski, M. & Stefańska, J. Chrząszcze. Coleoptera. Buprestoidea, Elateroidea i Cantharoidea in *Katalog Fauny Polski 23 (10)* (ed. Nowakowski, E.) 1–401 (Państwowe Wydawnictwo Naukowe, 1985).
49. Akkuzu, E. *Hendek Orman İşletme Müdürlüğü ormanlarında entomolojik problemler [Entomological problems in the forests of Hendek State Forest Enterprise]*. PhD Thesis, 1–202 (İstanbul Üniversitesi, Fen Bilimleri Enstitüsü, 2004).
50. Özdikmen, H. The predators of longhorned beetle species of Turkey. *Mun. Ent. Zool.* **18**, 1656–1660 (2023).
51. Dolin, V. G. *On the issue on the trophic preferences of the larvae of click beetles (wireworms). Materials for the study of fauna and ecology of insects in the central regions of the forest-steppe of Ukraine*, 116–147 (Kiev University Publishers, 1963).
52. Mardzhanyan, M. A. *Shchelkuny (Elateridae) [Click-beetles (Elateridae)]. Fauna of the Armenian SSR. Insecta: Coleoptera* 204 (Academy of Sciences of Armenian SSR, 1987)
53. Gülperçin, N. & Tezcan, S. Faunistic notes on the species of Elateridae (Coleoptera) in İzmir province of Turkey. *Mun. Ent. Zool.* **4**, 519–526 (2009).
54. Németh, T. & Merkl, O. Rare saproxylic click beetles in Hungary: distributional records and notes on life history (Coleoptera: Elateridae). *Folia Ent. Hung.* **70**, 95–137 (2009).
55. Kovács, T., Németh, T. & Merkl, O. Beetles new to Albania and Macedonia (Coleoptera: Elateridae, Cleridae, Endomychidae, Tenebrionidae, Cerambycidae). *Folia Hist.-Nat. Mus. Matraensis* **38**, 83–86 (2014).
56. Rocca, F. D., Stefanelli, S. & Bogliani, G. *Robinia pseudoacacia* as a surrogate for native tree species for saproxylic beetles inhabiting the riparian mixed forests of northern Italy. *Agric. For. Entomol.* **18**, 250–259 (2016).

57. Baviera, C. & Platia, G. The Elateridae (Coleoptera: Elateroidea) excl. Cebrionini and Drilini of Sicily: recent records and updated checklist. *Atti Accad. Peloritana dei Pericolanti Cl. Sci. Fis. Mat. Nat.* **96**, 1–33 (2018).
58. Yalçın, M., Akçay, C., Taşçıoğlu, C. & Yüksel, B. Insect species damaging industrial wood in western Black Sea region of Turkey. *Drv. Ind.* **70**, 183–191 (2019).
59. Kovács, T. & Merkl, O. Beetles from Albania, Macedonia and Montenegro, with new country records (Coleoptera). *Folia Hist.-Nat. Mus. Matraensis* **37**, 89–92 (2013).
60. Orlov, V. N. Family Elateridae in *Coleopterous insects (Insecta, Coleoptera) of Republic of Adygheya (Annotated catalogue of species), Fauna conspecta of Adygheya, No. 1* (eds. Zamotajlov, A. S. & Nikitsky, N. B.) 130–141 (Adyghea State University, 2010).
61. Alexander, K. N. A. The invertebrates of living and decaying timber in Britain & Ireland, A provisional annotated checklist. *Eng. Nat. Res. Rep.* **467**, 1–142 (2002).
62. Kovács, T. & Németh, T. Ritka szaproxilofág álpattanóbogarak, pattanóbogarak és lárváik a Mátra és a Bükk területérõl (Coleoptera: Cerophytidae, Elateridae). *Folia Hist.-Nat. Mus. Matraensis* **36**, 19–28 (2012).
63. Burakowski, B. Uwagi i spostrzeżenia dotyczące chrząszczy [Coleoptera] żyjących w próchnowiskach. *Wiad. Entomol.* **4**, 197–206 (1997).
64. Beiko, V. B. & Kompantseva, T. V. New, rare and need be protected insects from Tellerman Forest. *Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol.* **102**, 26–30 (1997).
65. Dolin, V. G. & Atamuradov, K. I. *Zhuki-shchelkuny (Elateridae) Turkmenistana [Click-beetles (Elateridae) of Turkmenistan]* (Institut Zoologii NAN Ukrainy, Kiev, 1994).
66. Kirk, H. B. Biological notes on Elateridae and Melasidae (Col.). *Entomol. News* **33**, 236–240 (1922).
67. Lane, M. C. Elateridae [excl. Cardiophorinae] in *The Beetles of the Pacific Northwest. Part V: Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia* (ed. Hatch, M. H.) 6–34 (University of Washington Press, Seattle, 1971).
68. Stebbing, E. P. *Indian forest insects of economic importance: Coleoptera* (Eyre & Spottiswoode, London, 1914).
69. Tscherepanov, A. I. *Provolčiki Zapadnoj Sibiri [Wireworms of Western Siberia]* (Nauka, Moscow, 1965).
70. Qiu, L. & Prosvirov, A. S. On the little-known click-beetle genus *Rostricephalus* (Coleoptera: Elateridae: Lissominae), with description of a new species from China. *Ann. Soc. Entomol. Fr.* **59**, 91–100 (2023).

71. Vitali, F. *Atlas of the Insects of the Grand-Duchy of Luxembourg: Coleoptera, Cerambycidae*. *Ferrantia 79* (Musée national d'histoire naturelle, Luxembourg, 2018).
72. Costa, C. & Vanin, S. A. Coleoptera larval fauna associated with termite nests (Isoptera) with emphasis on the "Bioluminescent termite nests" from Central Brazil. *Psyche* **2010**, 723947 (2010).
73. Rosa, S. P., Németh, T. & Kundrata, R. Comparative morphology of immature stages of *Ludioctenus cyprius* (Baudi di Selve, 1871) (Coleoptera: Elateridae: Agrypninae), with discussion on the monophyly of Hemirhipini. *Zool. Anz.* **283**, 33–39 (2019).
74. Kundrata, R., Baalbergen, E., Bocak, L. & Schilthuizen, M. The origin and diversity of *Drilus* Olivier, 1790 (Elateridae: Agrypninae: Drilini) in Crete based on mitochondrial phylogeny. *Syst. Biodivers.* **13**, 52–75 (2015).
75. Sato, N., Okamiya, H. & Yamada, A. Ambush hunter attacks land snails in its burrow: Unique larval stage of the click beetle *Anthracalaus sakaguchii*. *Ecology* **105**, e4245 (2024).
76. Donlan, E. M., Townsend, J. H. & Golden, E. A. Predation of *Caretta caretta* (Testudines: Cheloniidae) eggs by larvae of *Lanelater sallei* (Coleoptera: Elateridae) on Key Biscayne, Florida. *Caribb. J. Sci.* **40**, 415–420 (2004).
77. Lucas, M. H. Remarques sur les metamorphoses observées chez lez Élatérides et description de la larve de l'*Agrypnus atomarius Fabr. Ann. Soc. Entomol. Fr.* **10**, 261–274 (1852).
78. Perris, E. Histoire des insectes du Pin maritime. *Ann. Soc. Entomol. Fr.* **3**, 85–160 (1854).
79. Schiødte, J. C. De metamorphosi eleutheratorum observationes: bidrag til insekternes udviklingshistoire. *Naturhist. Tidsskr.* **6**, 467–530 (1870).
80. Blisson, M. J. F. J. Description des larves du *Steatoderus ferrugineus*, Fabr., de l'*Agrypnus varius* Fabr., et du *Silpha obscura* Fabr. *Ann. Soc. Entomol. Fr.* **2**, 65–741 (1846).
81. Dogger, J. R. The Elateridae of Wisconsin. I. A list of the species found in Wisconsin and keys to the identification of genera of adults and larvae. *Wis. Acad. Sci. Arts Letters* **48**, 103–120 (1959).
82. Costa, C. & Casari-Chen, S. A. Larvae of Neotropical Coleoptera VIII.: Elateridae, Agrypninae, Elaterinae and Physorhininae. *Rev. Bras. Entomol.* **28**, 315–328 (1984).
83. Dolin, V. G. Die Bedeutung der Larven-Merkmale und Flugelgeader in der Systematik Elateroidea (Coleoptera). *Entomol. Basil.* **22**, 179–183 (2000).
84. Pineda, C. Notas sobre *Candanius* von Hayek (Coleoptera: Elateridae), con descripción de una nueva especie de Chile. *Rev. Chil. Entomol.* **46**, 255–262 (2020).

85. Glen, R. *Larvae of the elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae).* (Smithsonian Institution, Washington, 1950).

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Author contributions

R.K. and T.N. conceived and designed the study. T.N. dissected specimens, made photographs, and created figure plates with help of R.K. S.P.R. (lead), R.K. and T.N. carried out the morphological investigation. T.N., D.J., R.K., S.P.R. and G.P. performed the literature search. R.K. (lead), T.N. and S.P.R. wrote the initial manuscript with help of D.J. All authors discussed the results, and edited, reviewed and approved the manuscript.

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Supplementary Information

The online version contains supplementary material available at https://xxxxxxxxxxx

Figure S1. Drawings of larval morphology of *Lacon lepidopterus*, *L. punctatus*, and *L. querceus*.

Figure S1. Larval and habitat images of *Lacon lepidopterus*.

Figure S2. Habitat images of *Lacon punctatus*.

Figure S3. Larval, adult and habitat images of *Lacon querceus*.

Competing interests

The authors declare no competing interests.

Figure captions

Figure 1. Larvae and adults of three European *Lacon* species. A–B) *L. lepidopterus*, Hungary: Ságvár. C–D) *L. punctatus*, Hungary: Ásotthalom. E–F) *L. querceus*, Hungary: Nagymaros. Not to scale.

Figure 2. Larva of *Lacon lepidopterus*, Hungary. A) Habitus, dorsal view. B) Habitus, lateral view. C) Habitus, ventral view. D) Head, dorsal view. E) Head, lateral view. F) Head, ventral view. Scale bars: 5.0 mm (A–C), 1.0 mm (D–F).

Figure 3. Larva of *Lacon lepidopterus*, Hungary. A) Maxillolabial complex, dorsal view. B) Maxillolabial complex, ventral view. C–D) Antenna, different views. E–F) Mandible, different views. G–I) Pro-, meso- and metathoracic leg, different views. J) Abdominal segment IX, dorsal view. K) Abdominal segments IX and X, lateral view. L) Abdominal segment IX, ventral view. Scale bars: 1.0 mm (A–B, J–L), 0.2 mm (C–D), 0.5 mm (E–I).

Figure 4. Larva of *Lacon punctatus*, Hungary. A) Habitus, dorsal view. B) Habitus, lateral view. C) Habitus, ventral view. D) Head, dorsal view. E) Head, lateral view. F) Head, ventral view. Scale bars: 5.0 mm (A–C), 1.0 mm (D–F).

Figure 5. Larva of *Lacon punctatus*, Hungary. A) Maxillolabial complex, dorsal view. B) Maxillolabial complex, ventral view. C–D) Antenna, different views. E–F) Mandible, different views. G–I) Pro-, meso- and metathoracic leg, different views. J) Abdominal segment IX, dorsal view. K) Abdominal segments IX and X, lateral view. L) Abdominal segment IX, ventral view. Scale bars: 0.5 mm (A–B, E–I), 0.2 mm (C–D), 1.0 mm (J–L).

Figure 6. Larva of *Lacon querceus*, Hungary. A) Habitus, dorsal view. B) Habitus, lateral view. C) Habitus, ventral view. D) Head, dorsal view. E) Head, lateral view. F) Head, ventral view. Scale bars: 2.5 mm (A–C), 0.5 mm (D–F).

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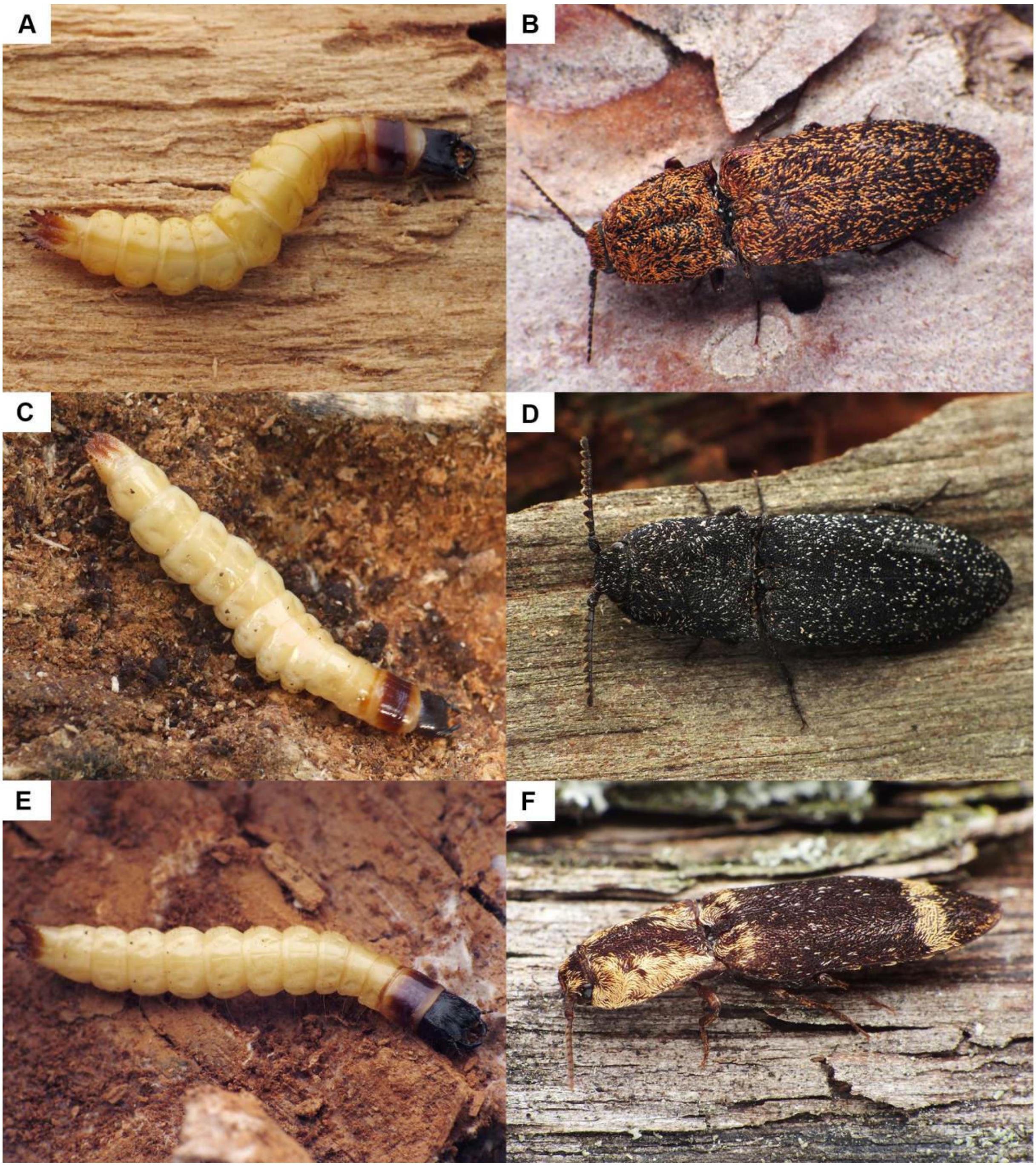
Table 1. Comparative morphology of known larvae of *Lacon* species. Characters of non-European species were taken from the literature. Question marks indicate characters not described or illustrated in the literature.

Species	***L. lepidopterus***	***L. punctatus***	***L. querceus***	***L. altaicus***	***L. funebris***	***L. parallelus***	***L. discoideus***	***L. marmoratus***
Geographic distribution	West Palaearctic	West Palaearctic	West Palaearctic	central Asia	central Asia	East Palaearctic	Nearctic	Nearctic
Head, depressed area in relation to lateral edges	graduallly sloping	gradually sloping	strongly sloping, forming keel	gradually sloping	gradually sloping	?	gradually sloping	?
Frontoclypeal plate, posterior part (lobe) length/ anterior part length	3.6–3.8	2.9–3.0	3.3–3.4	4.0	3.7	2.7	3.3	?
Frontoclypeal plate, shape of apical third of posterior part (lobe)	abruptly narrowed	abruptly narrowed	gradually narrowed	?	abruptly narrowed	gradually narrowed	abruptly narrowed	abruptly narrowed
Segment IX, number of distinct long setae on median dorsal surface	2 pairs	2 pairs	1–2 pairs	2 pairs	2 pairs	2 pairs	1 pair	2 pairs
Segment IX, short setae on small tubercles on median dorsal surface	absent	absent	present	absent	absent	absent	absent	?
Segment IX, approximate number of nodule-like tubercles on dorsal surface	90–130	120–150	50–90	100	50	80	160	160
Segment IX, apical notch length/segment IX length	0.30–0.35	0.20–0.25	0.30	0.30	0.10	0.10	0.15	0.15
Segment IX, apical notch width/urogomphus width	1.90–2.25	1.05–1.25	1.80–2.15	2.25	0.50	0.65	1.45	1.35
Segment IX, notch in relation to last lateral tooth	posterior	posterior	at the level or anterior	posterior	posterior	posterior	posterior	posterior



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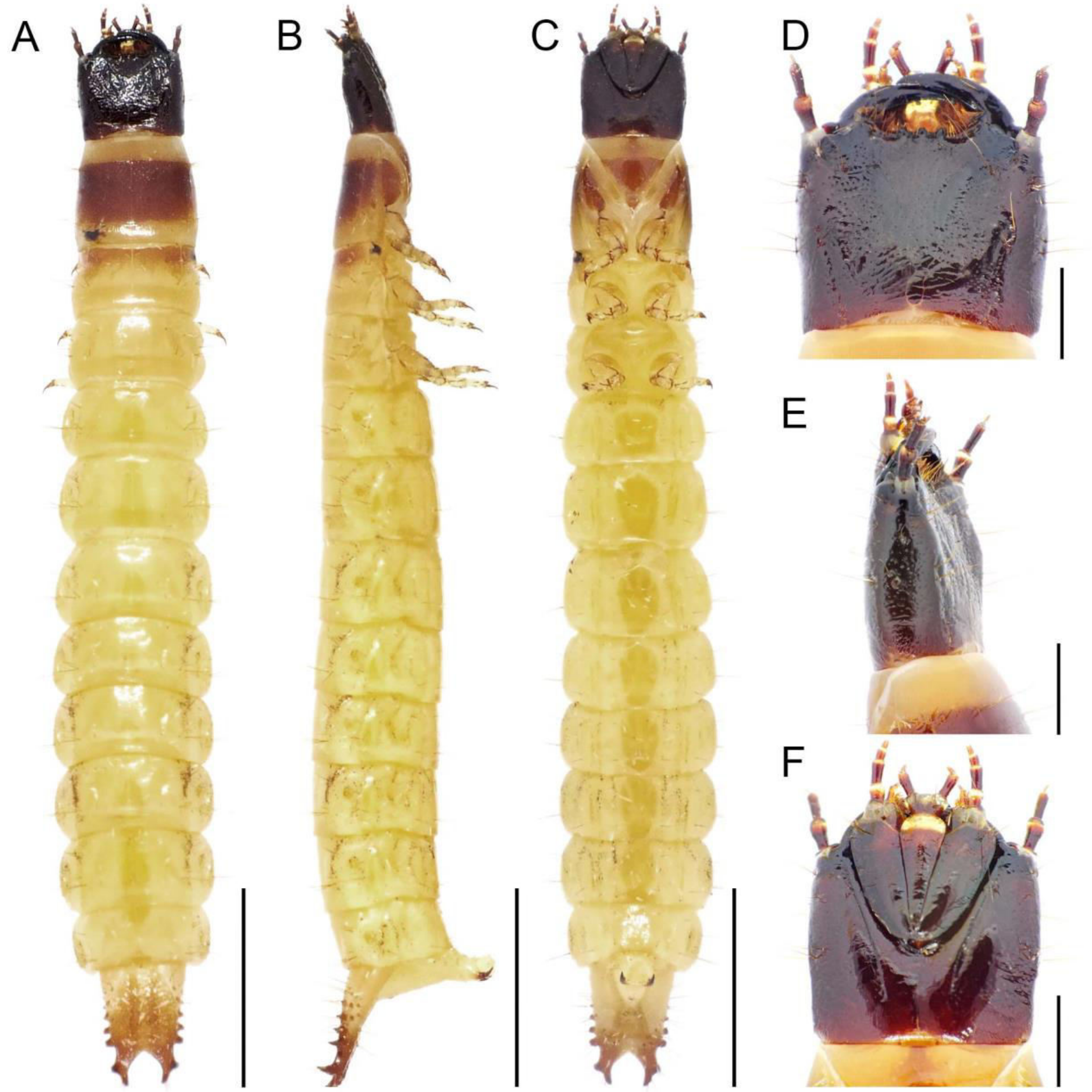

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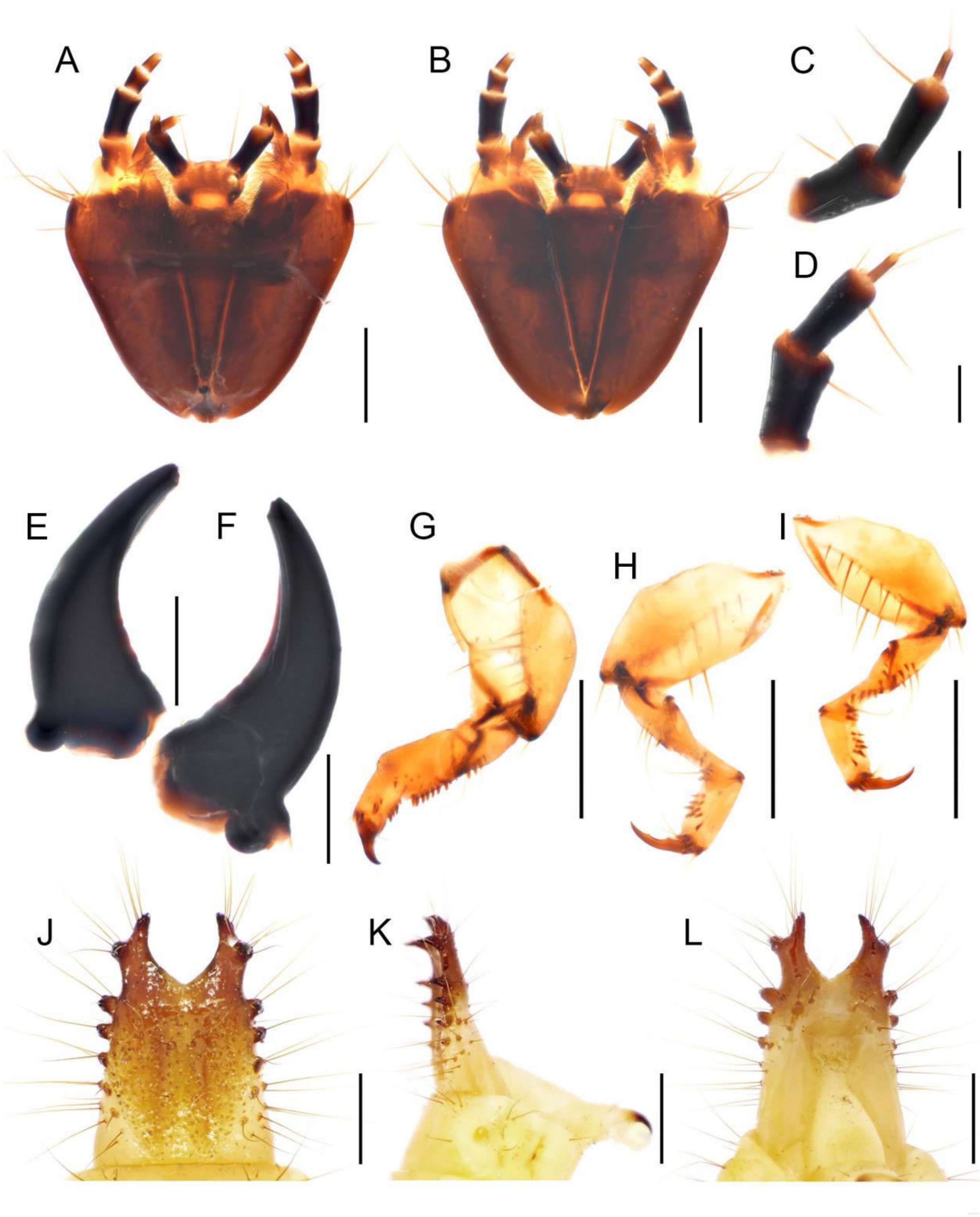

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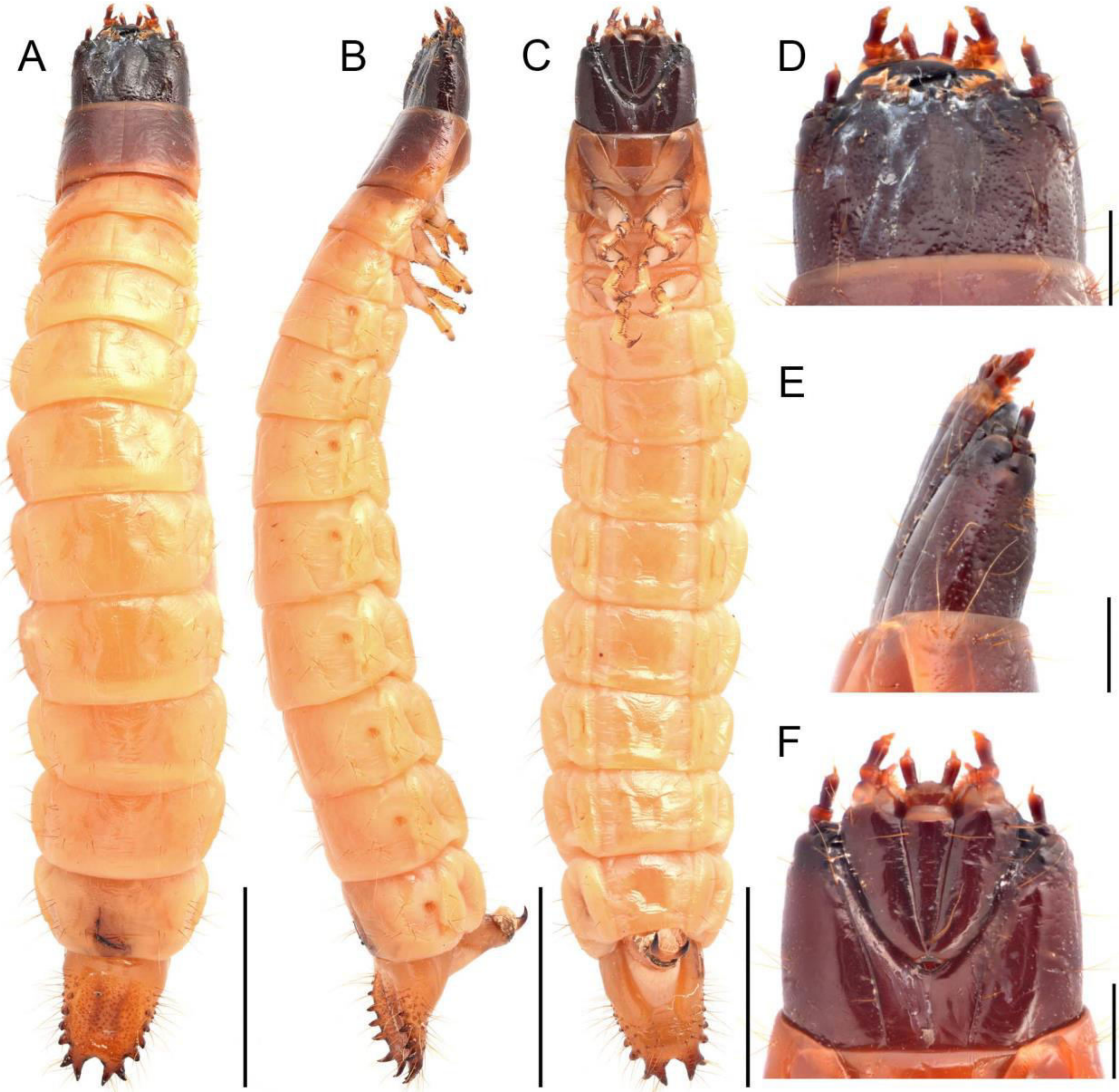

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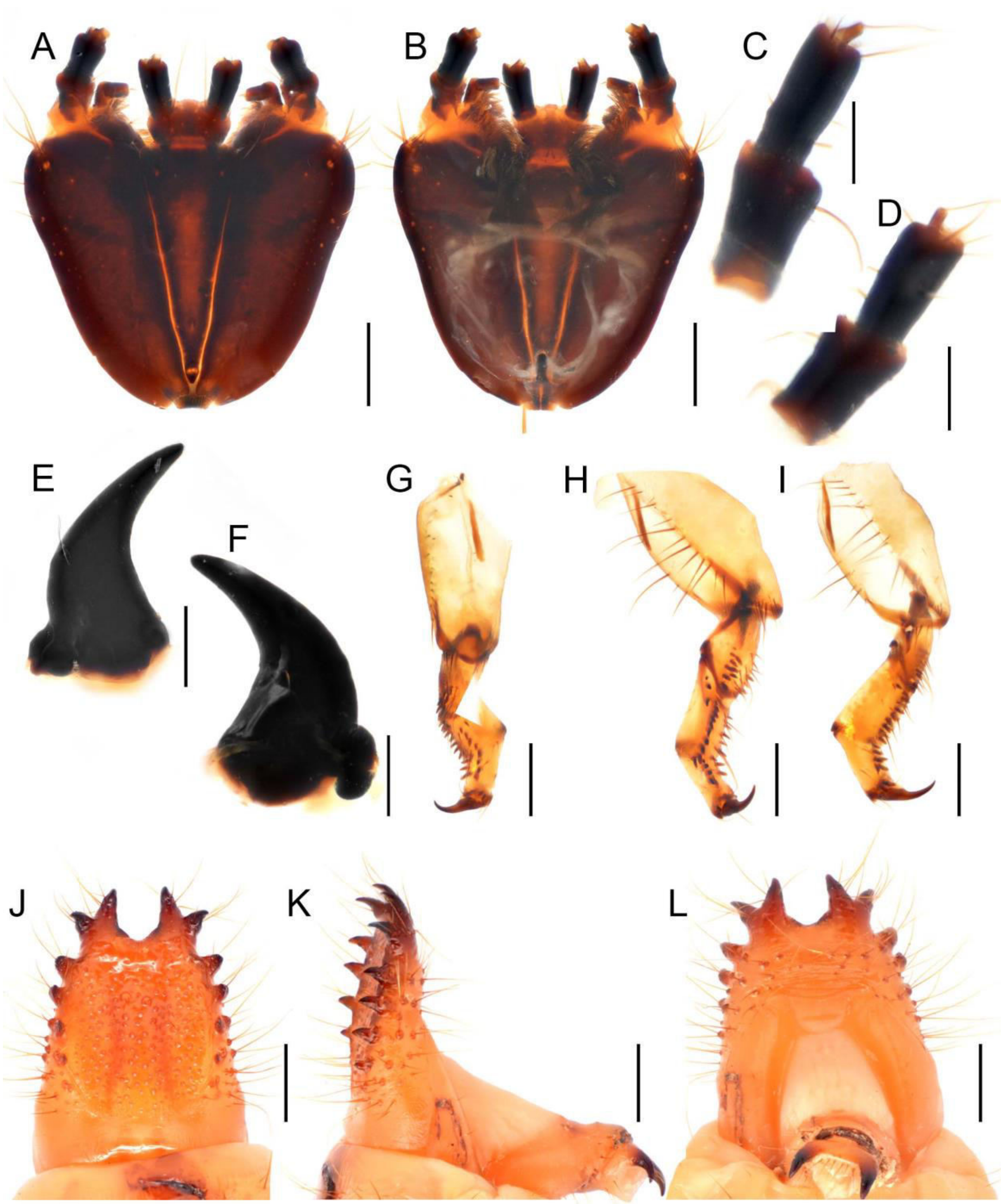

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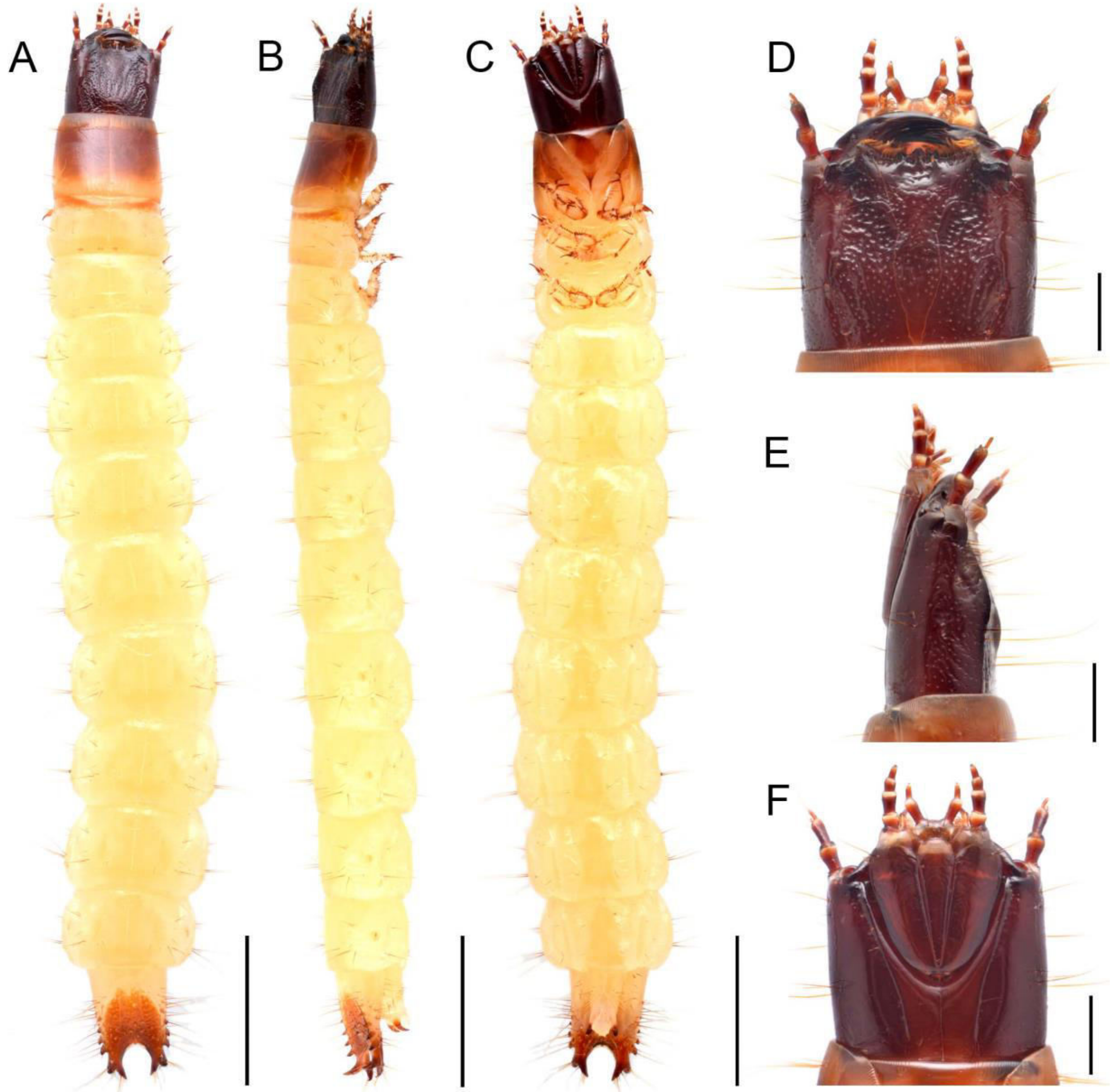

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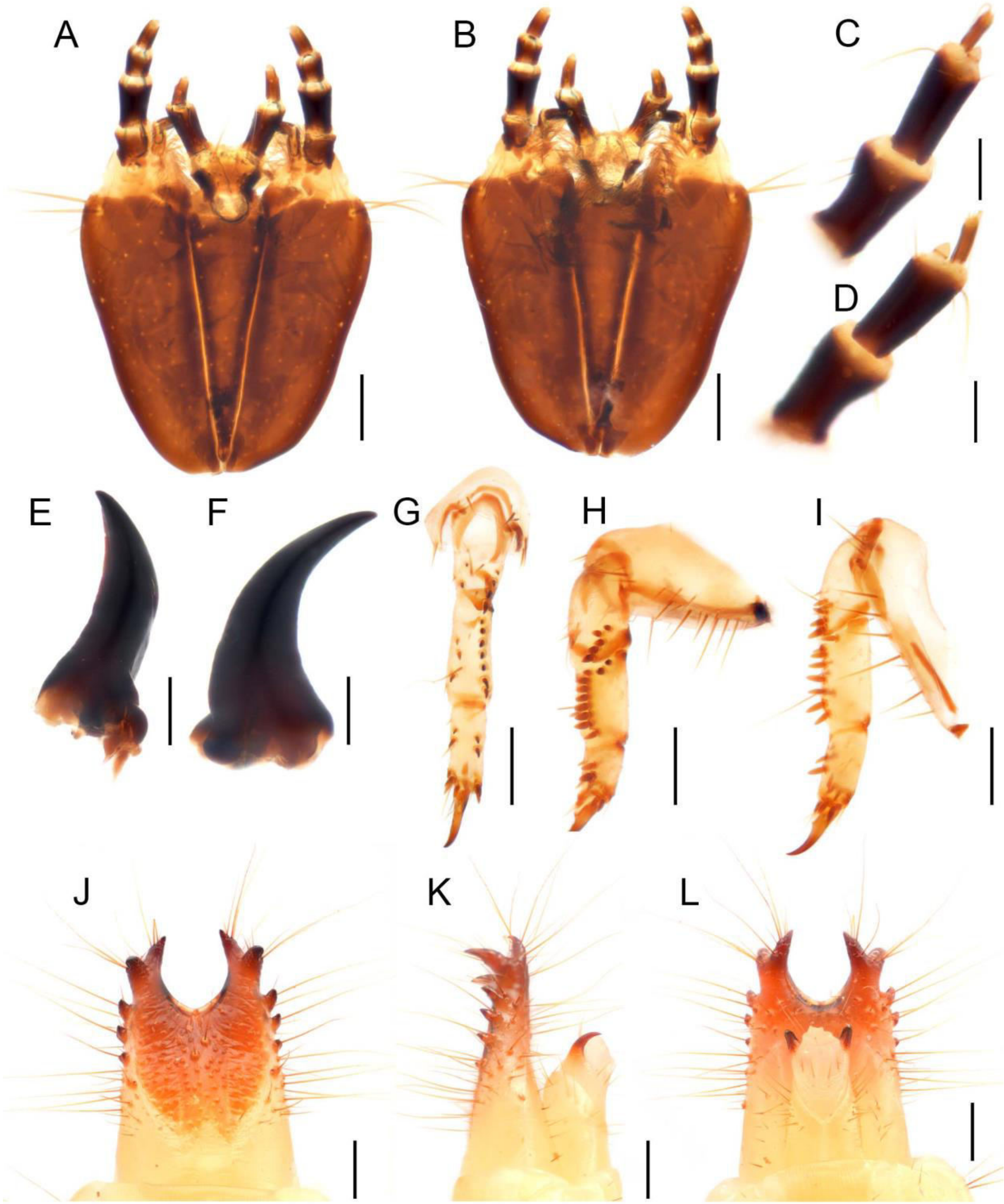

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SUPPLEMENTARY INFORMATION

Emblematic European saproxylic *Lacon* click beetles (Coleoptera: Elateridae): what do we know about their immature stages?

Tamás Németh, Simone Policena Rosa, David Jetelina, Miklós Sárospataki, Gabriela Packova & Robin Kundrata

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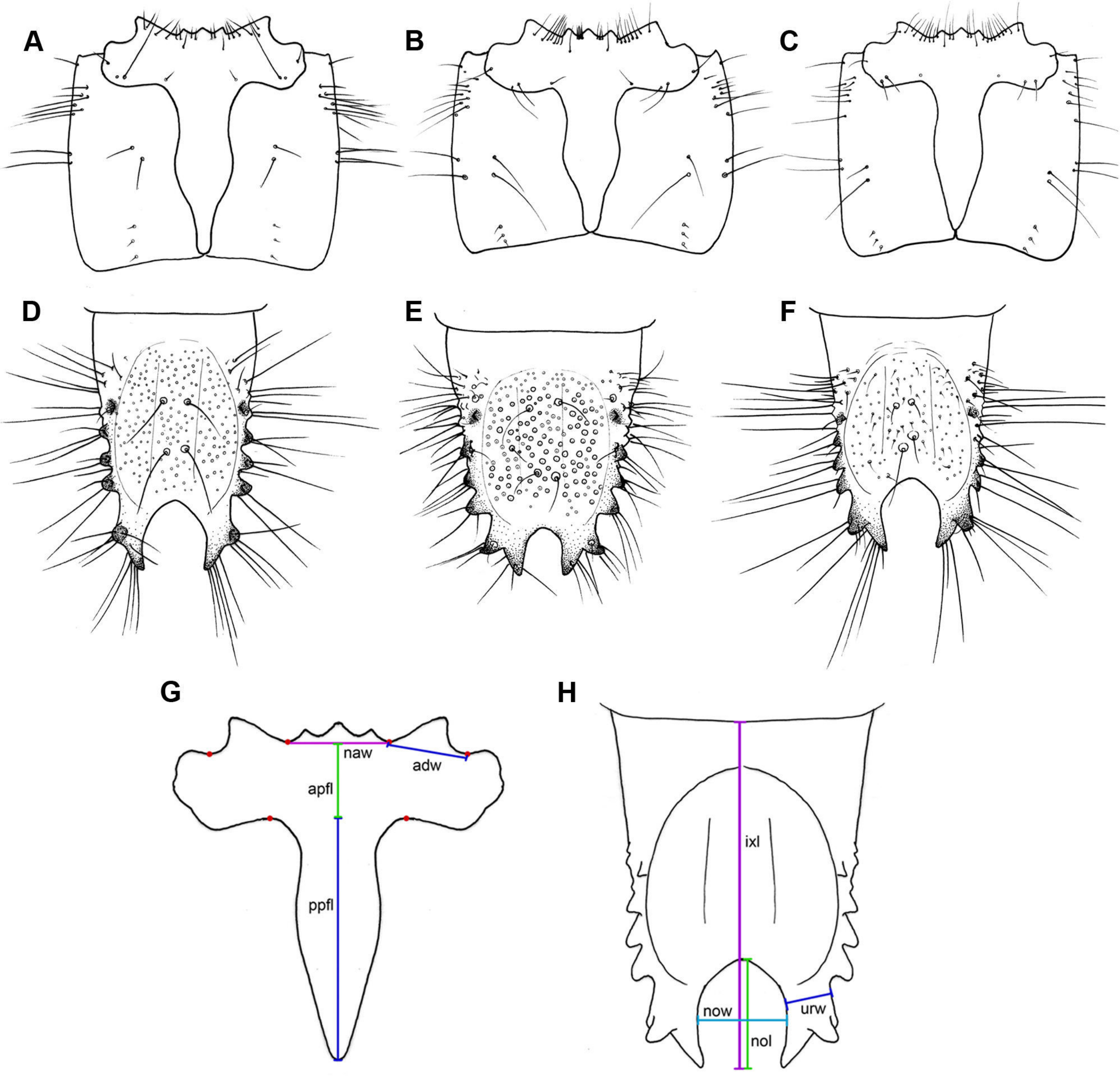
Figure S3. Habitat images of *Lacon punctatus*. A) Mt. Ossa, Greece (also habitat of *L. querceus*). B) Tikveš, Croatia. C) Llogara Pass, Albania. D) Mt. Vrsouta, Montenegro. E) Kerkyra, Greece. F) Nature Park Biokovo, Croatia; credit: Boris Lauš (used with permission from the author). Unless stated otherwise, all photographs: T. Németh.

Figure S4. Larval, adult and habitat images of *Lacon querceus*. A) Praepupa in pupal chamber in red rotten oak. B) Mature larva feeding on larvae of *Mycetophagus quadriguttatus*. C) Adult specimens in copula. D) 23 adult specimens found in a single red rotten oak, Börzsöny Mts., Hungary. E) Habitat in Vértes Mts., Hungary. F) Habitat in Stupnički lug, Zagreb, Croatia; credit: Boris Lauš (used with permission from the author). Unless stated otherwise, all photographs: T. Németh.



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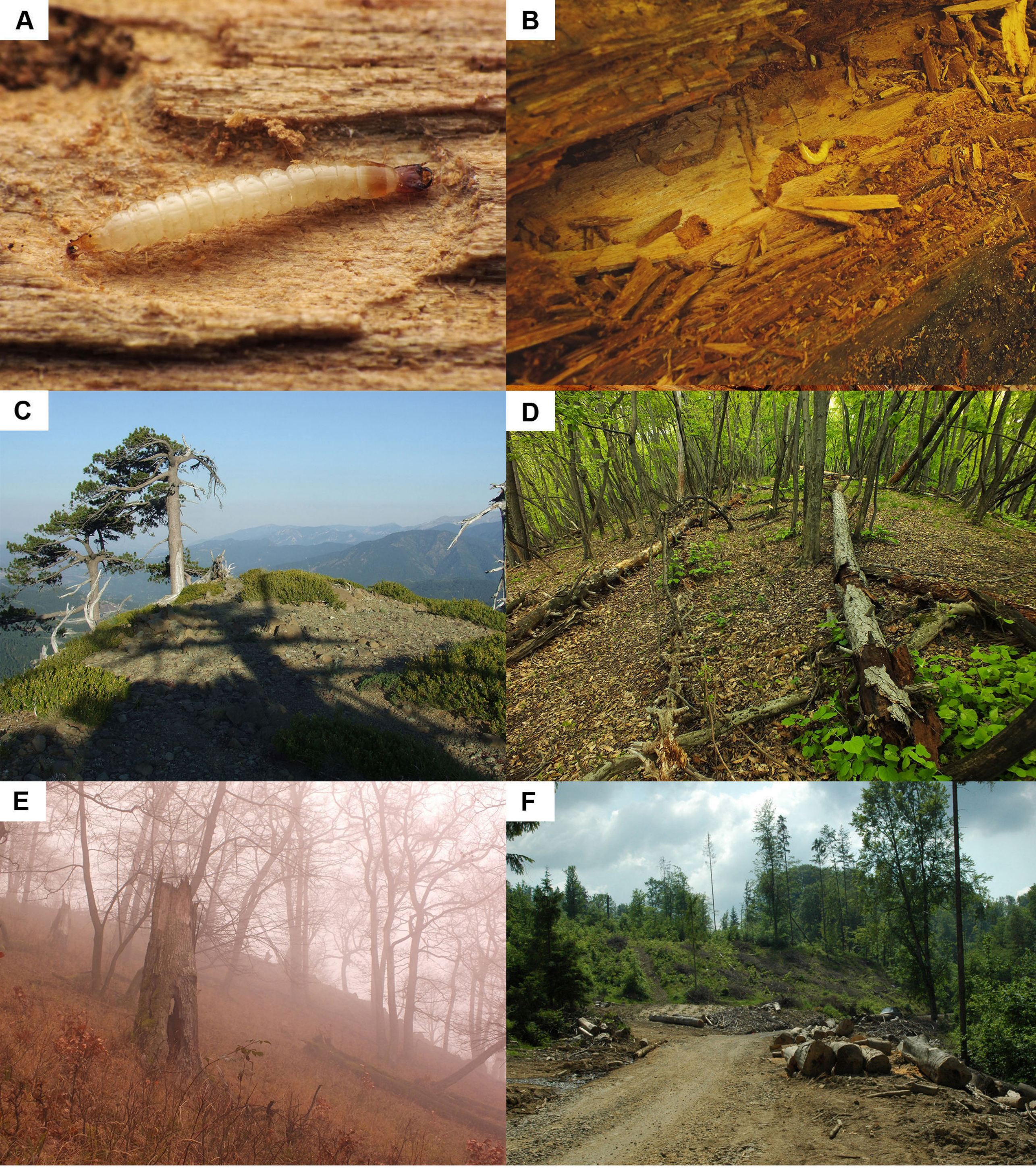

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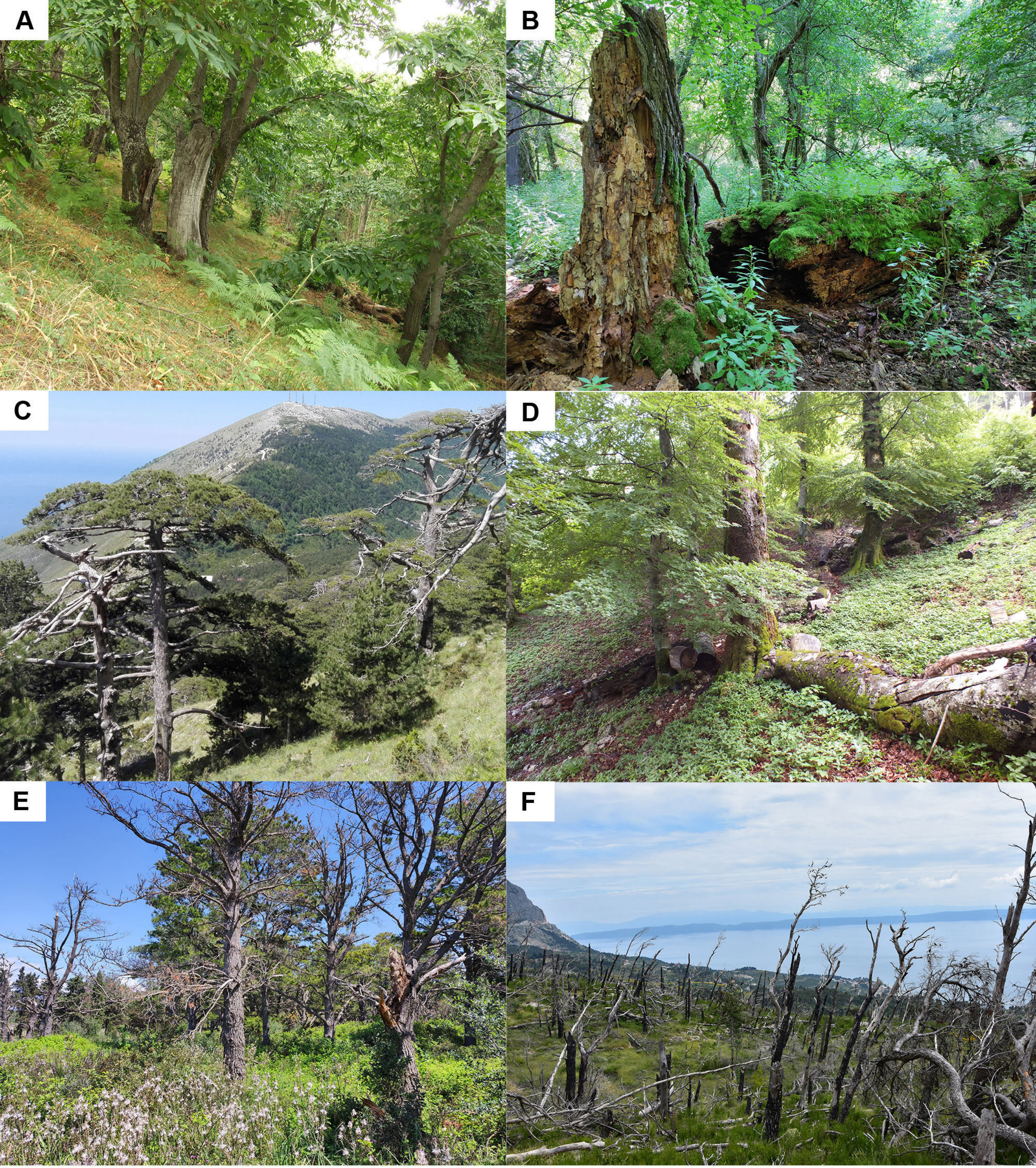

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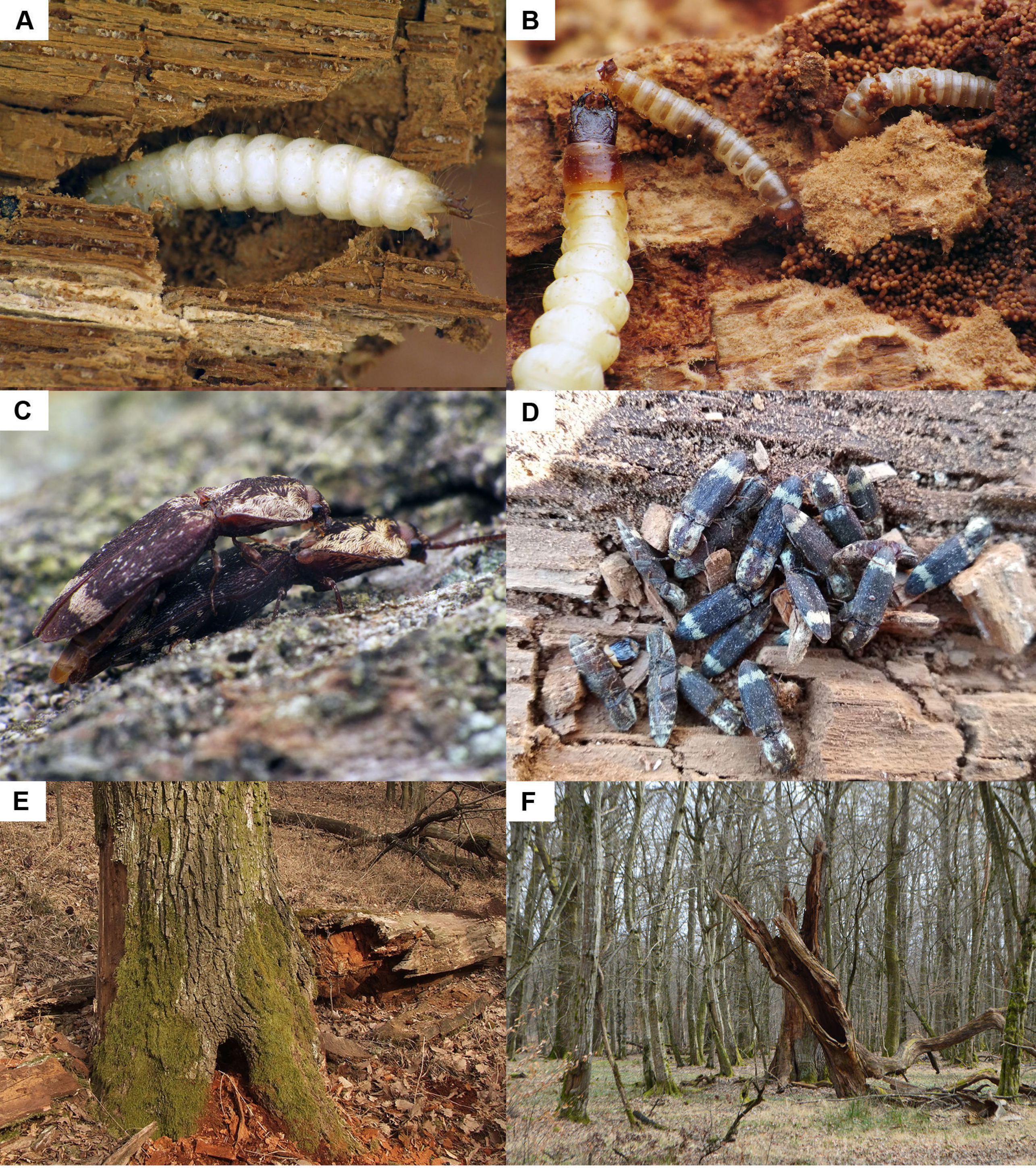

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