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Research article

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First record of the planthopper tribe Adenissini (Hemiptera: Caliscelidae) from Socotra Island, with description of a new genus and two new species

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Abstract. The planthopper family Caliscelidae (Hemiptera: Auchenorrhyncha: Fulgoromorpha) and the tribe Adenissini are recorded here for the first time from the Socotra Archipelago (Yemen). A new genus, *Oceatra* gen. nov., is described for two new species from Socotra Island – *Oceatra litoralis* gen. et sp. nov. (type species) from coastal sand dunes and salt marshes, and *O. scandens* gen. et sp. nov. from evergreen montane woodland and shrub communities of the Hagher mountains. *Oceatra* gen. nov. is similar to *Perissana* Metcalf, 1952 but differs in the structure of the male style and phallobase. A key to distinguish the genera of the subtribe Adenissina is provided.

Keywords. Auchenorrhyncha, Fulgoromorpha, Afrotropical Region, Arabian Peninsula, morphology, taxonomy.

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Introduction

Planthoppers (Hemiptera: Auchenorrhyncha: Fulgoromorpha) are a morphologically and ecologically diverse group of mostly phytophagous, rarely mycetophagous insects (O'Brien 2002; Bartlett *et al.* 2014, 2018). Planthoppers are currently classified into 21 extant families with more than 13 500 described species (Bourgoin 2023). One of the smaller families is the Caliscelidae Amyot & Audinet-Serville, 1843 with 78 genera and 245 species (Gnezdilov 2013; Bourgoin 2023). Caliscelidae have a worldwide distribution (excluding Oceania) and are divided into Ommatidiotinae Fieber, 1875, currently limited by the Old World, and Caliscelinae Amyot & Audinet-Serville, 1843, found in both the Old and New Worlds

(Gnezdilov 2013; Bartlett *et al.* 2014, 2018; Bourgoin *et al*. 2016). The Ommatidiotinae are further divided into three tribes, one of which is Adenissini Dlabola, 1980, originally distinguished by Dlabola (1980) for two genera within Issidae Spinola, 1839. Gnezdilov (2003) pointed out that the similarity of Adenissini to Issidae was only superficial and placed the tribe in Caliscelidae. Currently, the Adenissini comprise four subtribes (Gnezdilov & Wilson 2006; Gnezdilov 2013), of which the nominotypical subtribe Adenissina Dlabola, 1980 includes three genera: *Perissana* Metcalf, 1952, with four species, *Adenissus* Linnavuori, 1973, with eight species, and *Raunolina* Gnezdilov & Wilson, 2006, with four species. These taxa are known from Azerbaijan (Nakhchivan), northern Iraq (Dahuk Province), Iran, the Arabian Peninsula, Egypt, and Sudan (Puton 1890; Linnavuori 1973; Dlabola 1980, 1985; Gnezdilov & Wilson 2006, 2011; Gnezdilov 2013, 2017a, 2017b, 2020; Gnezdilov & Mozaffarian 2023). All taxa of Adenissina occur in arid or semiarid areas, such as deserts and coastal sand dunes. Although most other Caliscelidae feed on graminoids (Emeljanov 1969; Catanach 2013; Bartlett *et al.* 2014, 2018; Chen *et al*. 2014), Adenissini are known to be associated with *Calligonum* L. (Fabaceae), *Limonium* Mill. (Plumbaginaceae) (Gnezdilov & Wilson 2006, 2011), and *Ephedra* spp. (Gymnospermae: Ephedraceae) (Emeljanov 1999; Gnezdilov & Mozaffarian 2023); *Perissana bispinata* (Dlabola, 1980) was swept from oaks (*Quercus* sp.) (Dlabola 1980). Adenissina are more or less short-winged and their dispersal ability is probably limited. To date, Adenissina have never been recorded on islands.

In 2012, two new species of an undescribed caliscelid genus belonging to Adenissina were collected by the second author in coastal habitats and mountains of Socotra Island in the northwestern part of the Indian Ocean. With an area of ca 3600 km^2, Socotra Island is the largest island of the Socotra Archipelago, one of the governorates of Yemen. Currently, Socotra Island is located 350 km south of Ras Fartak in southern Yemen, and 233 km east of Cape Guardafui in Somalia (Culek 2014). The island is continental in origin and was joined to the Arabian plate before the rifting of the Gulf of Aden, about 20–17 Ma ago (Leroy *et al.* 2012; Culek 2014). The long geographic isolation of Socotra is responsible for the high degree of endemism in both the local flora (Miller & Morris 2004; Banfield *et al.* 2011; Brown & Mies 2012) and fauna (Wranik 2003; Batelka 2012; Fasola *et al.* 2020; Purchart *et al.* 2020). This also seems to be true for the fauna of planthoppers on Socotra, although the latter is still poorly known and requires further taxonomic work. Apart from the recently introduced *Ommatissus lybicus* de Bergevin, 1930 (Tropiduchidae Stål, 1866), an invasive pest of date palms (Witt *et al.* 2020), and a species of Lophopidae Stål, 1866, originally described by Kirkaldy (1899, 1903) as *Elasmoscelis iram* Kirkaldy, 1899 from Socotra, but later synonymized by Distant (1910) with *Elasmoscelis trimaculata* Walker, 1851 which is widespread in sub-Saharan Africa (Bourgoin 2023), all species and genera of Flatidae Spinola, 1839 previously recorded from Socotra are known only from that island (Melichar 1902, 1923; Świerzewski *et al.* 2014, 2017, 2018; Stroiński *et al.* 2016, 2018).

Here, we provide the formal descriptions of the taxa of Caliscelidae from Socotra, as another step towards a better knowledge of the taxonomy of Adenissina and the planthopper fauna of this remarkable biodiversity hotspot and UNESCO World Heritage Site.

Material and methods

Morphological terminology follows Anufriev & Emeljanov (1988) for most structures and Gnezdilov & Wilson (2006) for the male genitalia.

Male genital segments were macerated for one minute in boiling 10% KOH solution. Drawings were made from dissected parts temporarily mounted in glycerine jelly using a Leica MZ9.5 light microscope with a camera lucida attachment. Photos were taken using a Leica Z16 APOA with a Leica DFC 490 camera. Images were produced using the Leica Application Suite ver. 4.5, Helicon Focus ver. 6.7.1 and Adobe Photoshop CS5 software. The map was created in ArcGIS ver. 10.8.2.

Geographical names of localities in Socotra are spelled according to Bezděk *et al.* (2012). Plant nomenclature follows the WFO Plant List (2022).

The type specimens of the species described below are deposited in the Moravian Museum, Brno, Czech Republic (MMBC) and the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZIN).

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Auchenorrhyncha Duméril, 1806
Infraorder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1807
Family Caliscelidae Amyot & Audinet-Serville, 1843
Subfamily Ommatidiotinae Fieber, 1875
Tribe Adenissini Dlabola, 1980

Subtribe **Adenissina** Dlabola, 1980

Key to genera of Adenissina

1. Forewings with many transverse veins (Fig. 4). Gonoplacs, in lateral view, rounded, short, with dorso-caudal angle not protruding beyond the apex of anal tube (Figs 2D, 7B) 2
– Forewings with only longitudinal veins distinctly visible. Gonoplacs, in lateral view, angular, long, with dorso-caudal angle clearly protruding beyond the apex of anal tube (Gnezdilov 2017a: figs 10, 12) .....***Raunolina*** Gnezdilov & Wilson, 2006

2. Male pygofer with a spine- or tooth-like process on each side of its dorso-caudal margins (Gnezdilov & Wilson 2011: figs 7, 12, 18). Suspensorium with horn-shaped process (Gnezdilov & Wilson 2011: figs 1, 8, 16; Gnezdilov 2017b: fig. 9a). Aedeagus without ventral hooks ....***Adenissus*** Linnavuori, 1973
– Male pygofer and suspensorium without processes. Aedeagus with pair of ventral hooks (Figs 6F, 8A, vh) 3

3. Style with small capitulum on short neck. Each dorso-lateral phallobase lobe with broadly rounded (not mushroom-shaped) outgrowth above ventral lobe. Ventral phallobase lobe wide (Gnezdilov & Wilson 2006: figs 20–22) .....***Perissana*** Metcalf, 1952
– Style with massive, curved capitulum, without neck (Figs 6D–E, 8E–F). Each dorso-lateral phallobase lobe with mushroom-shaped outgrowth above ventral lobe (Figs 6F, 8A, mot). Ventral phallobase lobe narrow (Figs 6G, 8C, vl) .....***Oceatra*** gen. nov.

Genus ***Oceatra*** gen. nov.
urn:lsid:zoobank.org:act:C9107B76-69A3-4304-AA05-43D5542E6ADF

Type species

Oceatra litoralis gen. et sp. nov., designated here.

Diagnosis

Metope with median and sublateral carinae; median carina running to clypeus, but far not reaching upper margin of metope. Forewings with hypocostal plate and reticulate venation (with many transverse veins). Cubitus posterior (CuP) of forewings indistinct. Phallobase with ventral lobe narrow, without denticles, and dorso-lateral lobes each with mushroom-shaped outgrowth above ventral lobe. Style

with large, curved capitulum, without neck, bearing small lateral tooth or lacking it. Gonoplacs short, rounded, with dorso-caudal angle not protruding beyond the apex of anal tube (in lateral view).

Etymology

The name of the genus is a combination from the Latin noun '*oceanus*' (= 'ocean', 'sea', 'large body of water') and Socotra, referring to the geographical isolation of the newly described planthopper taxa on Socotra Island in the Indian Ocean. Gender feminine.

Key to species of *Oceatra*

1. Body coloration mostly light ochreous, dark pattern on forewings restricted to clavus outer margin and cells in apical half of corium (Figs 1A–B, 2A). Metope and coryphe relatively narrow: metope about as long at midline as wide below eyes (Figs 1C, 2B, 5B), coryphe nearly twice wider than long medially (Figs 1A, 2A, 5A). Male anal tube, in dorsal view, slightly widening apically (Fig. 6C). Style with hind margin straight (Fig. 6A, D). Phallobase apex, in dorsal view, with strongly convex margin (Fig. 6H–I). Each apical process of aedeagus with one long spiny and several small teeth apically (Fig. 6F, aep) ..... ***O. litoralis*** gen. et sp. nov.
– Body coloration mostly dark brown, forewings dark brown, each with three light patches: basally, medially and subapically (Fig. 3A–B). Metope and coryphe relatively broad: metope 0.8 times as long as wide at midline below the eyes (Figs 3C, 5E), coryphe 2.5 times as wide as long medially (Figs 3A, 5D). Male anal tube, in dorsal view, parallel-sided (Fig. 8B). Style with hind margin convex (Fig. 8A, E). Phallobase apex, in dorsal view, with notched margin (Fig. 8D). Each apical process of aedeagus with two long spiny teeth (Fig. 8A, aep) ..... ***O. scandens*** gen. et sp. nov.

Oceatra litoralis gen. et sp. nov.
urn:lsid:zoobank.org:act:C3F31EA9-7579-425A-BA43-C2A916A36F78
Figs 1–2, 4B–C, 5A–C, 6–7

Diagnosis

See the identification key to species of *Oceatra* gen. nov. above.

Etymology

From the Latin adjective '*litoralis*' (= 'of the seashore', 'littoral'), referring to the habitat of the new species in the coastal salt marshes.

Type material

Holotype

YEMEN • ♂; Socotra Island, ca 3 km NE of Shuab; 12°34.1′ N, 53°23.9′ E; 3 m a.s.l.; 20–21 Jun. 2012; I. Malenovský, P. Kment, J. Bezděk, J. Hájek, V. Hula, J. Niedobová and L. Purchart leg.; sweeping and suction sampling in *Avicennia marina* mangrove, salt marsh and sand dunes; MMBC.

Paratypes

YEMEN – **Socotra Island** • 1 ♀; same collection data as for holotype; MMBC • 1 ♂, 1 ♀; same collection data as for holotype; ZIN.

Description

Measurements. Total body length: males – 3.0 mm, females – 4.0 mm.

Coloration. Male (Fig. 1). General coloration light ochreous. Upper half of metope dark brown to black, carinae light ochreous (Fig. 1C). Postclypeus with dark brown dots and spots laterally. Anteclypeus dark

brown. Rostrum dark brown ventrally, black apically. Pedicel brown to dark brown. Coryphe with dark brown dots (Fig. 1A). Preocular fields dark brown. Paranotal lobes of pronotum with dark brown dots. Mesonotum with dark brown spot in each anterior angle. Forewing with dark brown pattern concentrated along outer clavus margin between CuP and Pcu and in cells of corium in its apical half (Fig. 1B). Hind coxae brown posteriorly. Femora and tibiae with dark brown bands. Third tarsomeres with dark brown apical halves. Claws and dorso-lateral plates of pretarsus dark brown. Apices of spines on legs black. Each laterotergite with large dark brown to black spot. Style light yellow, with dark brown capitulum. Penis dark brown (Fig. 1D). Female (Fig. 2) similar to male. Forewing with dark brown cells along outer clavus margin and in posterior half of corium (Fig. 2A) or only with sparse dark brown spots scattered across whole wing. Visible abdominal tergites VI–VIII with dark brown spots. Gonoplacs

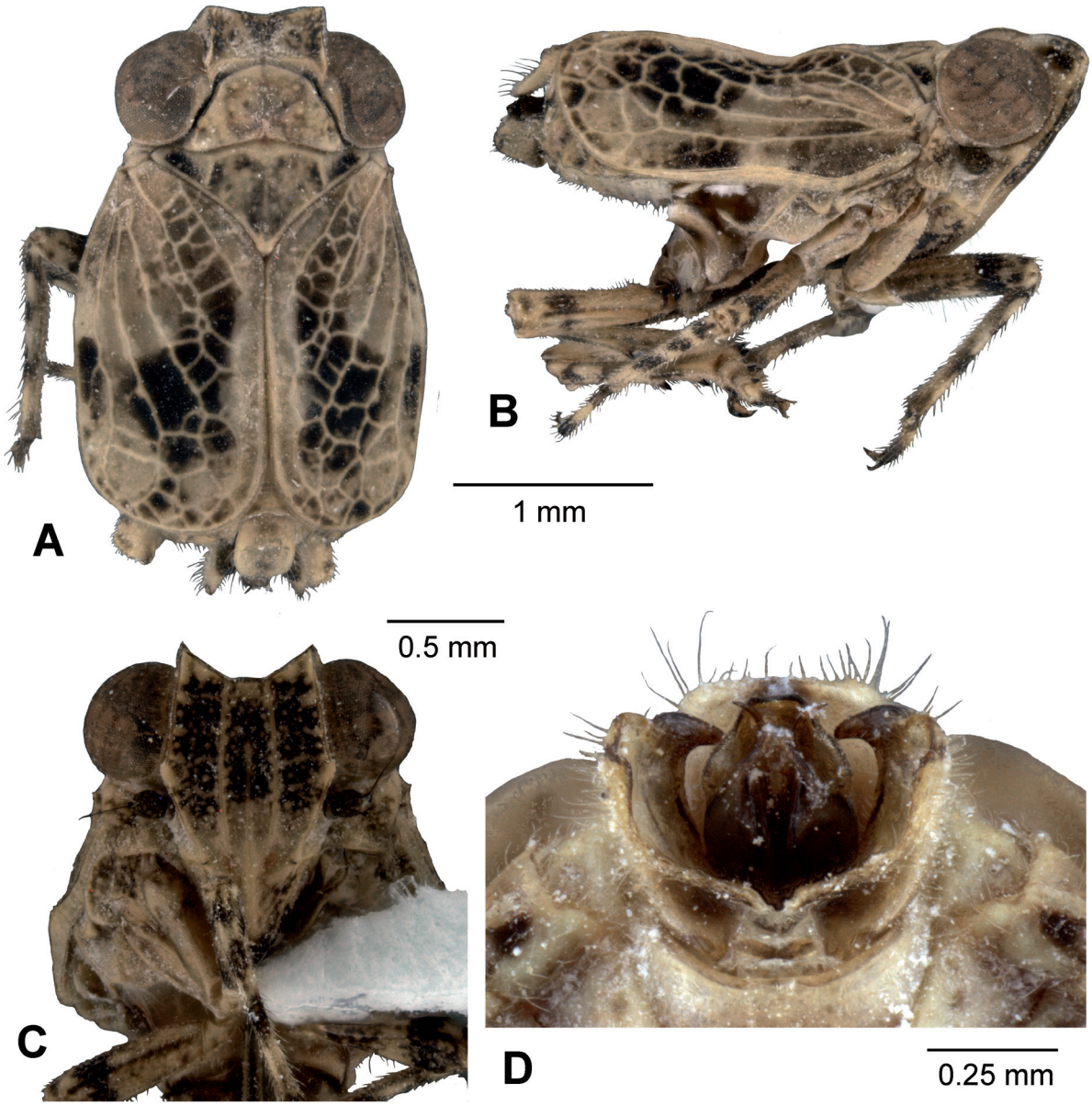

Fig. 1. *Oceatra litoralis* gen. et sp. nov., holotype, ♂ (MMBC). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view. **D**. Genital block, caudal view.

brown (Fig. 2C–D). Anal tube with black median stripe running and expanding from paraproct to its hind margin.

External structure. Metope (Figs 1C, 2B, 5B) about as wide as long, with lateral margins obtusely angular below eyes; upper margin sharply trapezoidal, concave. Median carina distinct from the level of eye middle through whole postclypeus, interrupted by metopoclypeal suture; sublateral carinae extending from upper margin of metope almost to metopoclypeal suture. Metopoclypeal suture distinct. Coryphe transverse, nearly twice as wide as long medially (Fig. 5A). Ocelli absent. Pedicel globular. Rostrum long, reaching sternite VI, not narrowing apically; second segment 0.25 times as long as third one (Fig. 5C). Pronotum wide, depressed in the middle, without carinae or with very short median carina at its hind margin (Fig. 5A). Paradiscal fields of pronotum very narrow, not visible behind eyes. Paranotal lobes nearly rectangular. Mesonotum as long as pronotum medially, with median and lateral

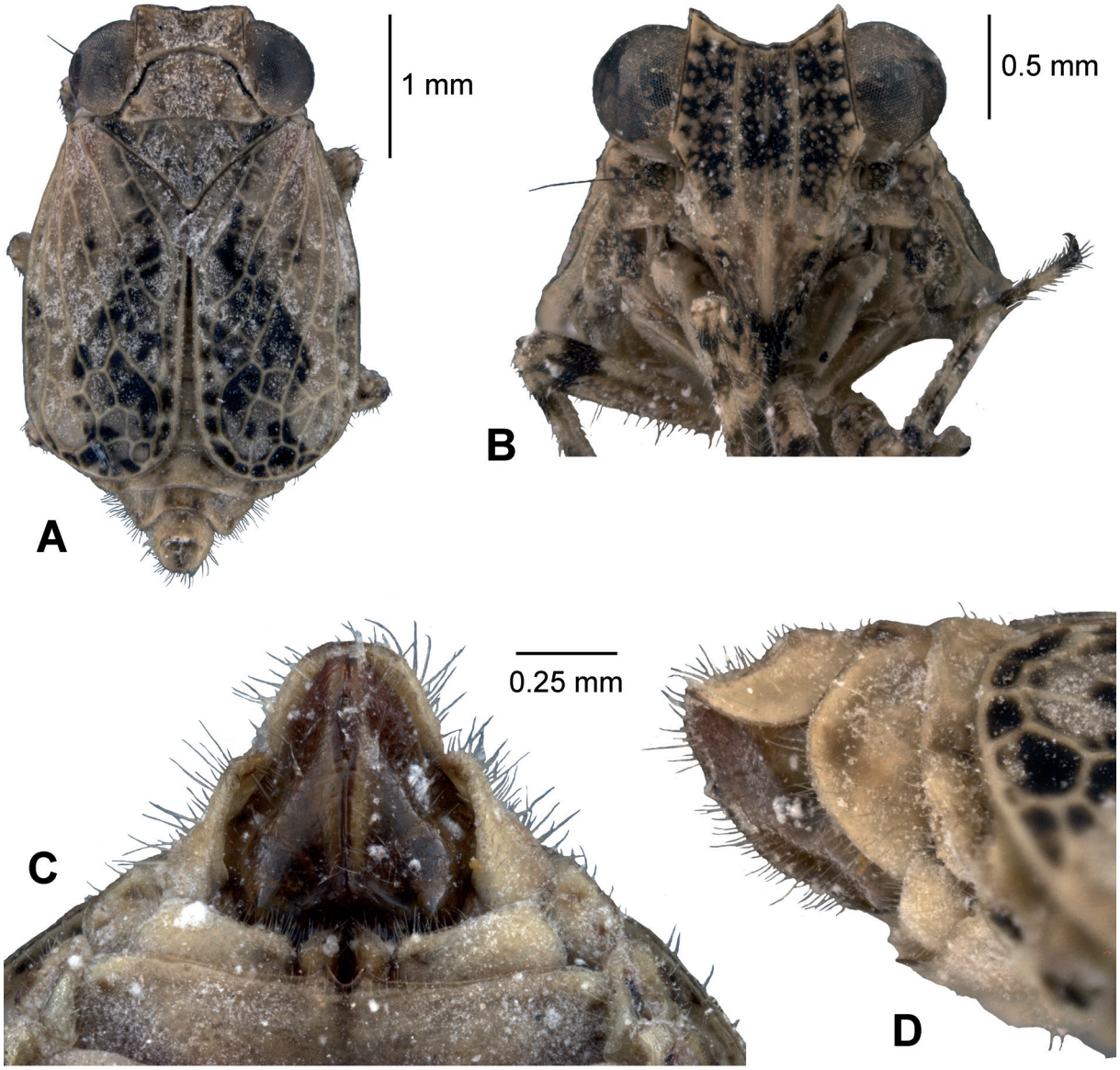

Fig. 2. *Oceatra litoralis* gen. et sp. nov., paratype, ♀ (MMBC). **A**. Dorsal view. **B**. Frontal view. **C**. Terminalia, ventral view. **D**. Terminalia, lateral view.

carinae. Forewing (Fig. 4B–C) widely truncate apically, reaching hind margin of pygofer in male and surpassing hind margin of tergite VII in female. Hypocostal plate relatively wide and long, extending along three quarters of wing length. Radius and median veins running from basal cell in one short stem. R, M, CuA, and Pcu furcating apically. Hind tibia with two lateral spines in apical half and seven apical spines. First metatarsomere 1.5 times as long as second one, with two latero-apical and five intermediate spines arranged in arc. Second metatarsomere with only two latero-apical spines. Claws, in dorsal view, nearly twice as long as arolium of pretarsus, each with a single long seta. Dorso-lateral plates of pretarsus narrow.

Male terminalia (Figs 1D, 6). Anal tube, in dorsal view, wide, 0.7 times as wide as long at midline, slightly widening apically, with slightly obtusely angulate anterior margin (Fig. 6C). Anal column short and wide. Pygofer, in lateral view, narrow, with hind margins strongly convex in upper half (Fig. 6A–B). Anal tube and phallobase with well-sclerotised connection (Fig. 6F). Phallobase, in lateral view, wide, slightly enlarged apically (Fig. 6A, F). Dorso-lateral lobes of phallobase fused dorsally in one lobe with strongly convex margin (Fig. 6I); each dorso-lateral lobe with mushroom-shaped outgrowth above ventral phallobase lobe (Fig. 6F, mot). Ventral phallobase lobe short and narrow, narrowing apically (Fig. 6G, vl). Apical processes of aedeagus extending beyond phallobase margin, long and wide, each with one long spiny and several small teeth apically (Fig. 6F, aep). Ventral aedeagal hooks arising at aedeagal apex, almost as long as aedeagus, directed basally, acute apically (Fig. 6F–G, vh). Connective with large, widely opened cup. Style massive, with large curved capitulum without neck, hind margin of style straight, caudal angle rounded (Fig. 6D). Capitulum, in dorsal view, with small apical tooth and weak lateral tooth (Fig. 6E).

Female terminalia (Figs 2C–D, 7). Hind margin of sternite VII with two short teeth medially (Fig. 7C). Anal tube, in dorsal view, as wide as long, with hind margin concave (Fig. 7A); in lateral view, ventral part of anal tube convex (Fig. 7B). Anal column short and wide.

Distribution and ecology

So far only known from the western coast of Socotra Island, close to the cape and village of Shuab (Fig. 9). The type series was collected in coastal sand dunes and salt marshes in vegetation dominated by the semi-succulent plant species *Limonium sokotranum* (Vierh.) Radcl.-Sm. (Plumbaginaceae), *Arthrocnemum macrostachyum* (Moric.) K. Koch (Amaranthaceae) and *Zygophyllum qatarense* Hadidi (Zygophyllaceae) (Fig. 10A). Most specimens were swept from *L. sokotranum* which might be a host plant for *O. litoralis* gen. et sp. nov. Another planthopper species, *Haloflata arthrocnemi* Świerczewski, Malenovský & Stroiński, 2017 from the family of Flatidae, co-occurred at the site (see Świerczewski *et al.* 2017 for details).

Oceatra scandens gen. et sp. nov.
urn:lsid:zoobank.org:act:1A305662-5F2E-4191-BE76-45A01CC1B2F3
Figs 3, 5D–E, 8

Diagnosis

See the identification key to species of *Oceatra* gen. nov. above.

Etymology

Derived from the present participle of the Latin verb '*scandō*' (= 'to climb', 'ascend', 'mount'), referring to the type locality of the new species close to the top of the highest peak of Socotra Island, Mt Scand.

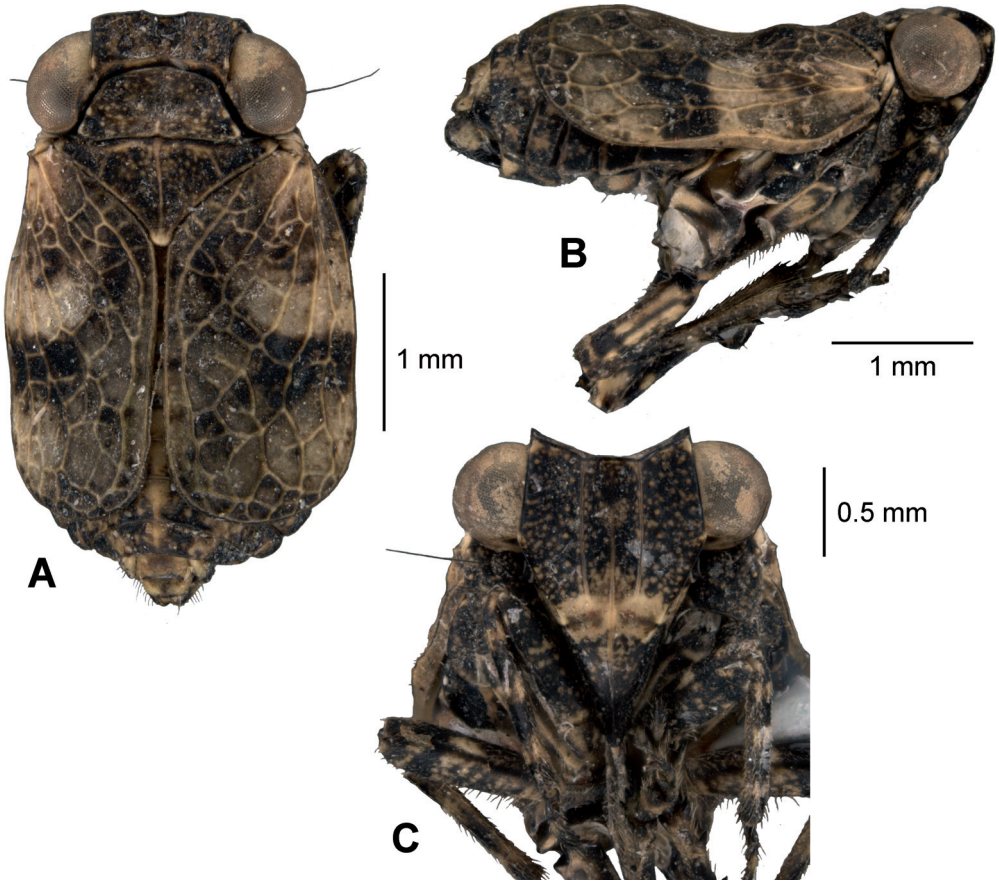

Fig. 3. *Oceatra scandens* gen. et sp. nov., holotype, ♂ (MMBC). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view.

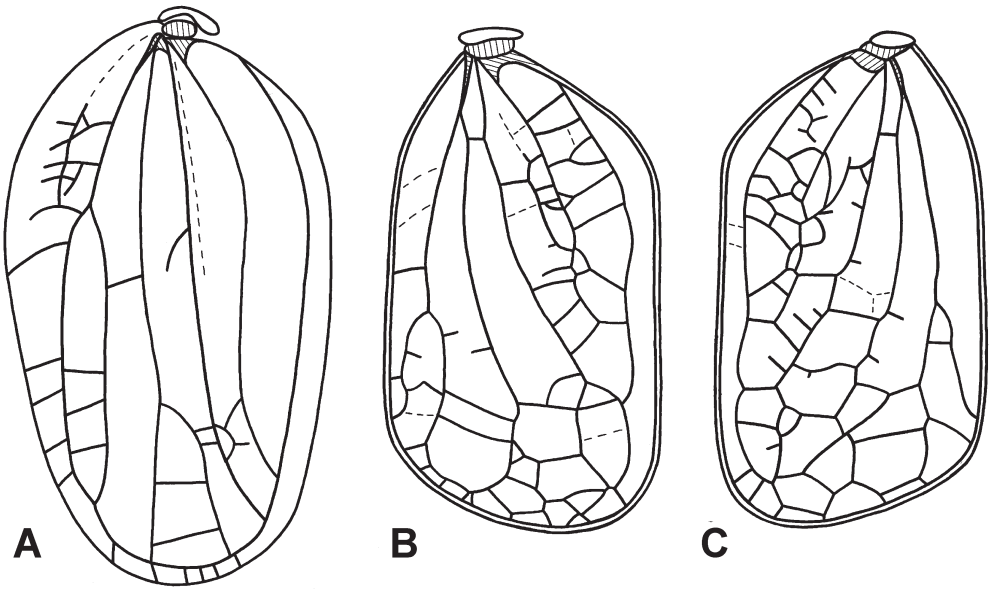

Fig. 4. Adenissina Dlabola, 1980, forewings. **A**. *Perissana dlabolai* Gnezdilov & Wilson, 2006, ♂. **B–C**. *Oceatra litoralis* gen. et sp. nov., paratype, ♂ (ZIN). **B**. Left wing. **C**. Right wing. Not to scale.

Type material

Holotype

YEMEN • ♂; Socotra Island, Hagher Mountains, Mt Scand env.; 12°34.6′ N, 54°01.5′ E; 1450 m a.s.l.; 16–18 Jun. 2012; I. Malenovský, P. Kment, J. Bezděk, J. Hájek, V. Hula, J. Niedobová and L. Purchart leg.; sweeping and suction sampling in montane evergreen woodland; MMBC.

Description

Measurements. Total body length: male – 3.8 mm.

Coloration (Fig. 3). General coloration dark brown. Metope, genae and postclypeus dark brown to black, with light ochreous transverse band above metopoclypeal suture and light ochreous dots and pustules (traces of larval sensory pits) between lateral margins and sublateral carinae, genae with light ochreous spot above each pedicel; median carina light ochreous, sublateral carinae brown (Fig. 3C). Anteclypeus dark brown to black including median carina. Rostrum dark brown, black apically. Scapus and pedicel black. Preocular fields dark brown to black, each with two light ochreous spots at anterior angles (Fig. 3B). Coryphe and pronotum with paranotal lobes dark brown, with light ochreous dots (Fig. 3A). Mesonotum dark brown, with light ochreous dots and carinae. Scutellum and tegulae light ochreous.

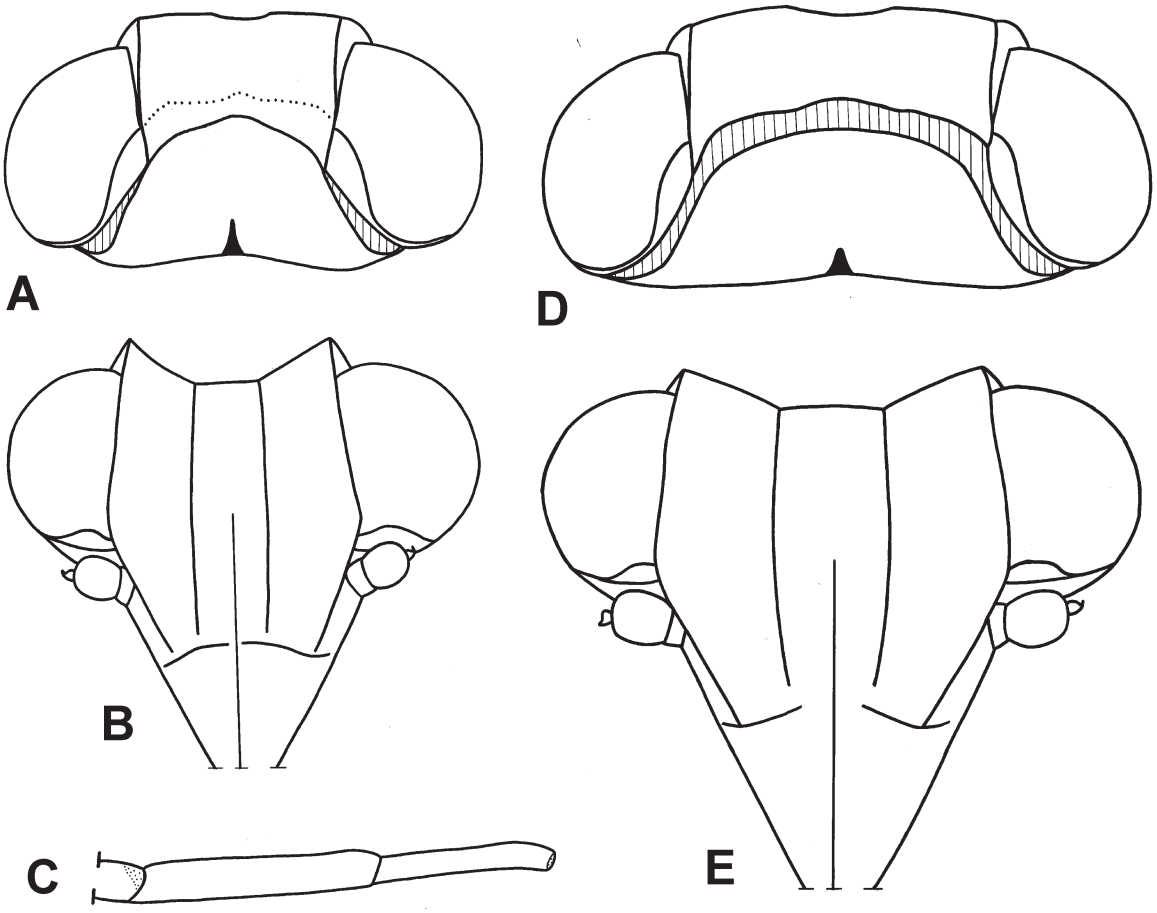

Fig. 5. A–C. *Oceatra litoralis* gen. et sp. nov., holotype, ♂ (MMBC). **D–E**. *Oceatra scandens* gen. et sp. nov., holotype, ♂ (MMBC). **A, D**. Head and pronotum, dorsal view. **B, E**. Head, frontal view. **C**. Rostrum, lateral view. Not to scale.

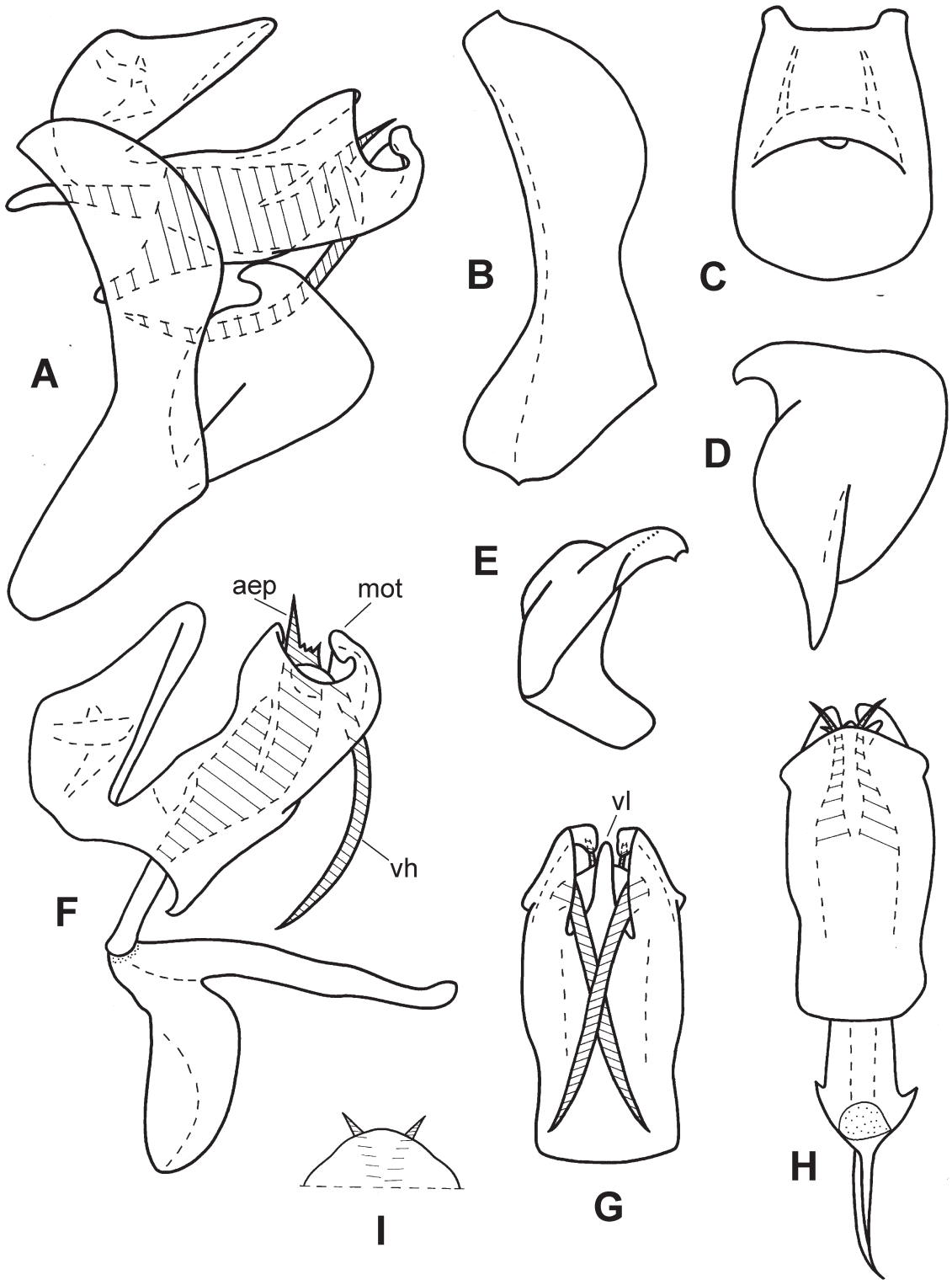

Fig. 6. *Oceatra litoralis* gen. et sp. nov., holotype, ♂ (MMBC), terminalia. **A**. Genital block, lateral view. **B**. Pygofer, lateral view. **C**. Anal tube, dorsal view. **D**. Style, lateral view. **E**. Style, dorsal view. **F**. Penis, connective, and anal tube, lateral view. **G**. Penis, ventral view. **H**. Penis and connective, dorsal view. **I**. Apex of penis, dorsal view. Abbreviations: aep = apical aedeagal process; mot = mushroom-shaped outgrowth of phallobase; vh = ventral aedeagal hooks; vl = ventral phallobase lobe. Not to scale.

Forewings brown to dark brown, each with three large light areas: basally, around basal cell and basal portions of main veins; a band in the middle across of corium; a subapical patch in apical fourth of wing at wing margin (Fig. 3A–B). Veins and hypocostal plate light brownish. Episternae and epimerae black. Fore and middle coxae light ochreous, with brown areas. Legs largely dark brown to black, with light ochreous bands. Abdominal tergites black, with ochreous spots and stripe along midline. Laterotergites black. Abdominal sternites dark brown to black, with light ochreous hind margins; sternites III–VI each with pair of large brown ochreous lateral patches. Fore and middle legs with second tarsomeres light ochreous dorsally; third tarsomeres and claws black. First metatarsomere black basally and apically, light ochreous medially; third metatarsomere light ochreous basally and black apically. Apices of spines on legs black. Anal tube light ochreous. Pygofer dark brown to black, except light ochreous near anal tube and ventral edge. Styles dark brown to black, with large light yellow patch on the plate.

External structure. Generally similar to *O. litoralis* gen. et sp. nov. Metope 0.8 times as long as wide at midline below the eyes (Figs 3C, 5E). Coryphe 2.5 times as wide as long medially (Figs 3A, 5D). Pronotum depressed in the middle, with very short median carina at hind margin (Fig. 5D). Forewing reaching middle of tergite VI. First metatarsomere with two latero-apical and six intermediate spines arranged in arc. Claws, in dorsal view, 0.3 times as long as arolium of pretarsus. Arolium of pretarsus, in dorsal view, with straight hind margin. Dorso-lateral plates of pretarsus narrow.

Male terminalia (Fig. 8). In general as described for *O. litoralis* gen. et sp. nov. Anal tube, in dorsal view, 0.8 times as wide as long medially, parallel-sided, anterior margin rounded (Fig. 8B). Style with hind margin convex, caudal angle obtuse (Fig. 8E); in dorsal view, style with distinct pointed lateral tooth (Fig. 8F, lt). Phallobase with dorso-lateral lobes fused dorsally in one lobe with notched margin (Fig. 8D). Aedeagus with each apical process with two long spiny teeth (Fig. 8A, aep).

Distribution and ecology

So far only known from the highest elevations of the Hagher mountains in the central part of the Socotra Island (Fig. 9). The holotype was collected by sweeping on low shrubs in quite open, montane evergreen woodland (Fig. 10B). The local low shrub plant community was dominated by *Hypericum scopulorum* Balf.f. (Hypericaceae), *Leucas hagghierensis* Al-Gifri & Cortés-Burns (Lamiaceae), and *Euryops*

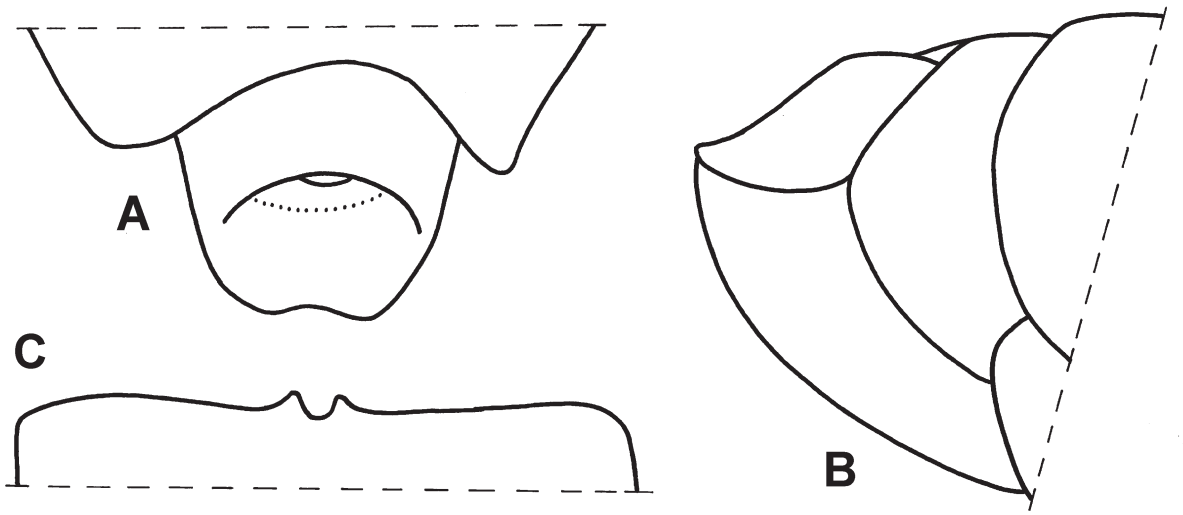

Fig. 7. *Oceatra litoralis* gen. et sp. nov., paratype, ♀ (MMBC), terminalia. **A**. Pygofer and anal tube, dorsal view. **B**. Genital block, lateral view. **C**. Sternite VII, ventral view. Not to scale.

arabicus Steud. ex Jaub. & Spach. (Asteraceae). *Oceatra scandens* gen. et sp. nov. was found syntopic with the flatid planthoppers *Socoflata aurolineata* Stroiński, Malenovský & Świerczewski, 2018, *S. histrionica* Stroiński, Malenovský & Świerczewski, 2018, and *Kirkamflata socotrana* Świerczewski, Malenovský & Stroiński, 2014 (see Świerczewski *et al.* 2014 and Stroiński *et al.* 2018 for more details including a more explicit description of the habitat).

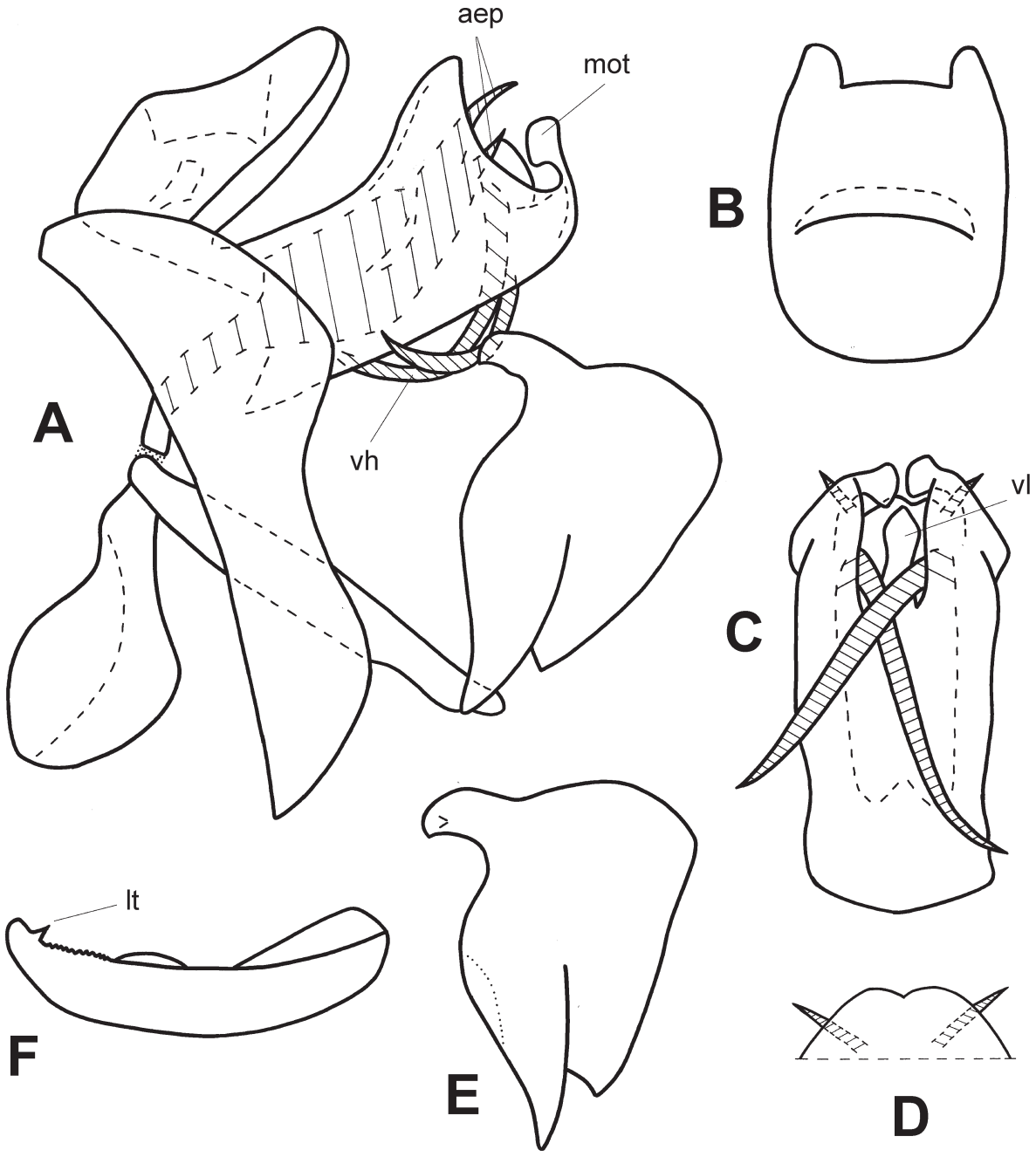

Fig. 8. *Oceatra scandens* gen. et sp. nov., holotype, ♂ (MMBC), terminalia. **A**. Genital block, lateral view. **B**. Anal tube, dorsal view. **C**. Penis, ventral view. **D**. Apex of penis, dorsal view. **E**. Style, lateral view. **F**. Style, dorsal view. Abbreviations: aep = apical aedeagal process; lt = lateral tooth; mot = mushroom-shaped outgrowth of phallobase; vh = ventral aedeagal hooks; vl = ventral phallobase lobe. Not to scale.

Discussion

Oceatra gen. nov. resembles *Adenissus* in a massive male style, with a large, curved capitulum without neck. However, the presence of well-developed ventral aedeagal hooks and the absence of probable autapomorphies of *Adenissus*, such as the spine-like process on the dorso-caudal margin of the male pygofer and the horn-like process of the suspensorium, may make *Oceatra* more closely related to *Perissana* and *Raunolina*. On the other hand, unlike *Oceatra* the latter two genera share a male style with a small capitulum with three teeth on a short neck. Thus, *Oceatra* could be a sister taxon to *Perissana* + *Raunolina*. However, a more detailed phylogenetic analysis, including other morphological and/or molecular characters, is needed to clarify the relationships of *Oceatra* within Adenissina.

The centre of diversification of Adenissina is probably in the Middle East as most species of *Adenissus*, *Perissana* and *Raunolina* are known from Iran and the Arabian Peninsula, while only one species of *Raunolina* has been described from northeastern Sudan in continental Africa (Gnezdilov 2017a). The presence of probably endemic taxa of Adenissina on Socotra raises the question of dispersal possibility across oceanic barriers for brachypterous insects. The geological history of the Socotra Archipelago is quite complex and still incompletely known, but periods of lower sea level or ocean currents may have facilitated dispersal from Arabia or continental Africa even after Socotra's complete separation from the mainland (Culek 2014). Both species of *Oceatra* gen. nov. are likely closely related based on their very similar morphology and may have descended from a common ancestor isolated on Socotra by a vicariant or single colonisation event. Remarkably, the two species of *Oceatra* occupy different habitats at the extremes of the altitudinal gradient on Socotra, namely the coastal arid zone and the highest mountain peaks, considered wet refugia (Banfield *et al.* 2011; Brown & Mies 2012; De Sanctis *et al*. 2013), suggesting ecological speciation of a common ancestor of *Oceatra* spp., perhaps through macrospatial habitat isolation (Coyne & Orr 2004). Analogous cases of sister species with very similar morphology but separated by distribution and habitat preferences even within the relatively small island of Socotra are known from other plant and animal taxa, such as reptiles (Fasola *et al.* 2020). Other planthopper taxa on Socotra, namely various species of Flatidae, are also known to occupy distinct habitat and altitudinal niches (Świerzewski *et al.* 2014, 2017, 2018; Stroiński *et al.* 2016, 2018), generally reflecting the rather

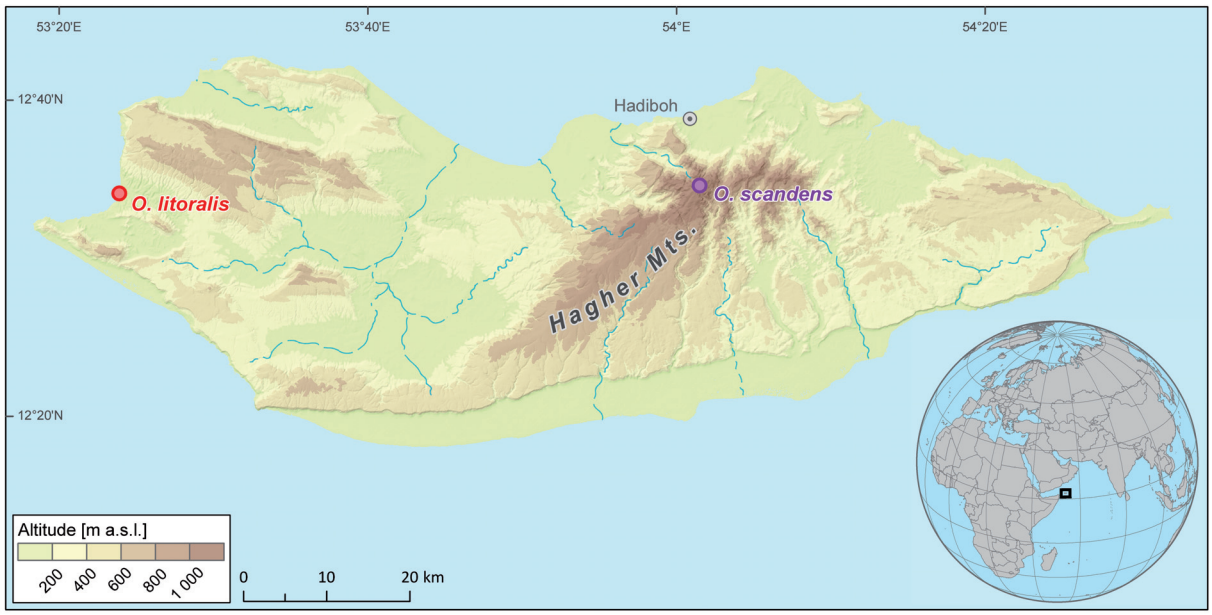

Fig. 9. Distribution of *Oceatra* spp. in Socotra Island.

sharp zonation of the vegetation along the elevation and moisture gradient (Brown & Mies 2012; De Sanctis *et al.* 2013). Socotran planthoppers could therefore represent an interesting model group for future studies to explain the origins and evolution of insular biodiversity, ideally within a phylogenetic framework.

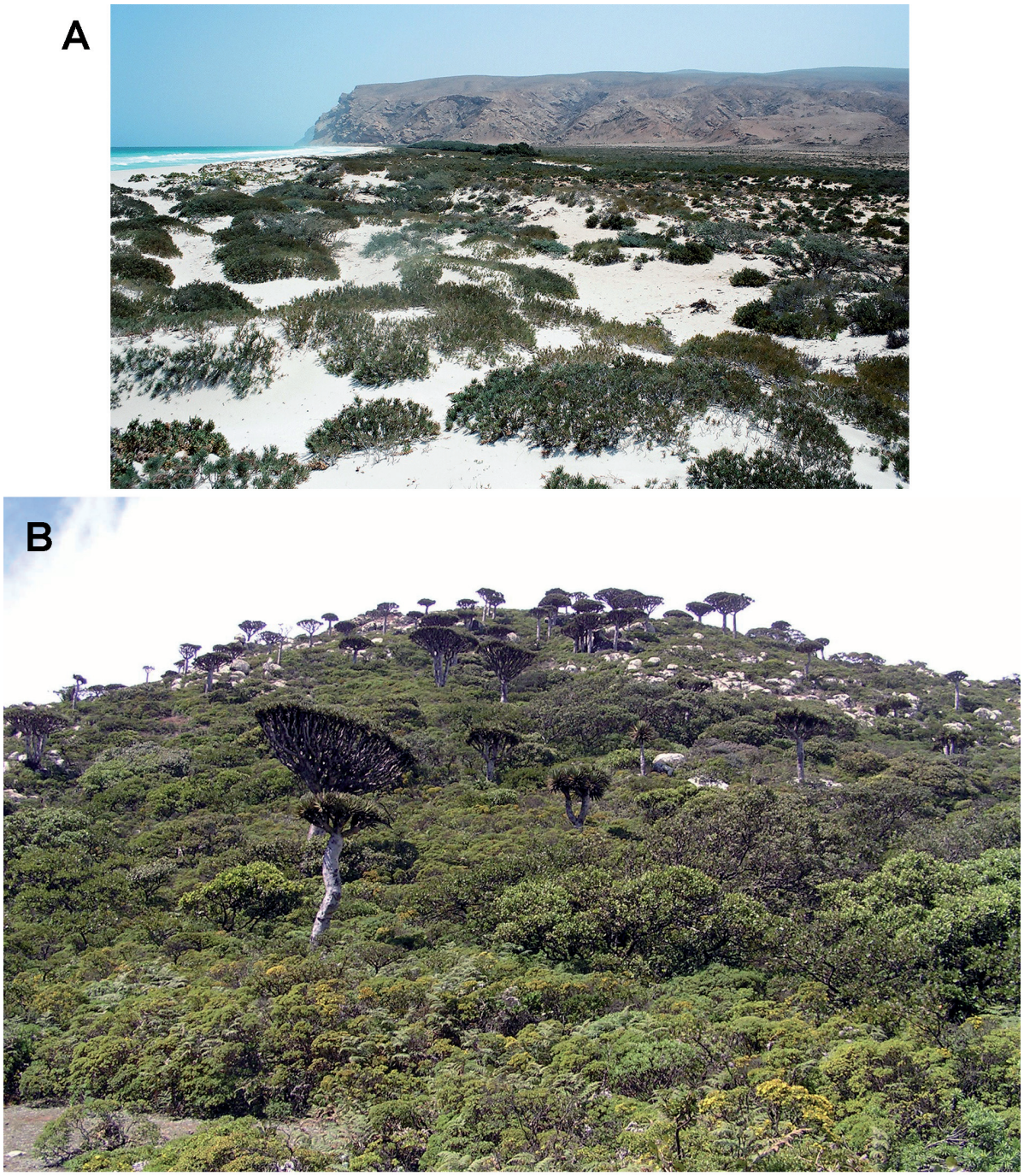

Fig. 10. Habitats of *Oceatra* spp. in Socotra Island. **A**. Type locality of *O. litoralis* gen. et sp. nov., coastal sand dunes and salt marshes near Shuab (photograph by I. Malenovský, 20 Jun. 2012). **B**. Type locality of *O. scandens* gen. et sp. nov., open montane woodland and low shrub communities on slopes of Mt Scand in the Hagher Mountains (photograph by L. Purchart, 1 Feb. 2010).

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