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# A taxonomic revision of the genus *Hyoidea* (Hemiptera: Heteroptera: Miridae)

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**Abstract.** The Palaearctic orthotyline genus *Hyoidea* Reuter, 1876 (Heteroptera: Miridae: Orthotylinae: Orthotylini), comprising nine species, is revised. Diagnoses and detailed redescriptions, data on distribution and hosts are provided for the genus and all species and a key is presented to facilitate identification of species. Photos of the dorsal habitus, scanning electron micrographs and figures of genitalic structures are given. Two species, *Hyoidea horvathi* Montandon, 1890 and *Hyoidea kerzhneri* Hoberlandt, 1963, are reported for the first time from Tunisia and Turkmenistan, respectively.

**Key words.** Heteroptera, Miridae, Orthotylinae, key to species, diagnosis, review, systematics, host plant, *Ephedra*, Palaearctic Region

## Introduction

The genus *Hyoidea* was described from the Astrakhan Province of Russia by Reuter (1876) based on a single species, *H. notaticeps* Reuter, 1876. This species is currently known from Hungary and southern Slovakia in the west, through the Ukraine, southern European Russia, and Caucasus to Central Asia and northern China in the east. The second species added to the genus, *H. horvathi*, was described by Montandon (1890) from Algeria. The only revision of *Hyoidea* was made by Hoberlandt (1963) who added descriptions of two new species, *H. lindbergi* and *H. kerzhneri*. The former species is currently known from Morocco and Tunisia, while the distributional range of the latter species is similar to that of *H. notaticeps* and ranges from Crimea, Turkey and Israel to Central Asia and northern China. Five more species were described within the next forty years from different localities in the Mediterranean region. Linnavuori (1989) described *H. hermione* from Israel. *Hyoidea hannothiauxi* was described by Carapezza (1997) from a single specimen collected in Tunisia. Three species, *H. flavolimbata* Ribes & Ribes, 2000, *H. lopezcoloni* Baena & Günther, 2001, and *H. stehliki* Baena & Günther, 2001, were almost simultaneously described from several localities in Spain (Ribes & Ribes 2000, Baena & Günther 2001). Thus constituted the genus includes nine species, all of them apparent specialized feeders on the shrubs of the genus *Ephedra* (Gnetales: Ephedraceae) and known mainly from the Mediterranean region and Central Asia.

Although the genus is not apparently difficult taxonomically, a review of the genus is required as five species were described since the most current revision (Hoberlandt 1963). This study of *Hyoidea* was also necessary as a baseline for the description of a new monotypic genus from Central Asia, *Angulonotus* Knyshov & Konstantinov, 2012 (see Knyshov & Konstantinov 2012). The present paper therefore summarizes current knowledge about *Hyoidea* including species delimitation, distributional ranges, and host plant associations. As a consequence, a generic diagnosis and description, key to all nine species, and standardized species descriptions with detailed illustrations are provided. It was not possible to study specimens of *H. flavolimbata*; we have provided a diagnosis and included it in our key to species based on the original description (Ribes & Ribes 2000).

## Materials and methods

All examined specimens are retained in the following institutions and private collections. Their abbreviations are given as follows:

BMNH Natural History Museum, London, United Kingdom;
MNHN Museum National d'Histoire Naturelle, Paris, France;
NHMM Natural History Museum, Mainz, Germany;
NMPC National Museum, Prague, Czech Republic;
NMWC National Museum of Wales, Cardiff, Wales, United Kingdom;
ZISP Zoological Institute, Russian Academy of Science, St. Petersburg, Russia;
ZMUH Zoological Museum, University of Hamburg, Germany.

All 255 specimens examined during this study were assigned a unique specimen identifier (USI) with the contained information digitized in the Planetary Biodiversity Inventory locality database. USI is printed as a matrix code label with a prefix and numeric string (e.g. AMNH_PBI 00337188) and mounted on one pin with the insect. The associated information can be obtained from the website of the Planetary Biodiversity Inventory Project on Plant Bugs (http://research.amnh.org/pbi/heteropteraspeciespage/) and also accessed through the www.discoverlife.org website.

Georeferenced data for each locality were obtained from gazetteers, atlases, and other sources. The distributional maps were created using DIVA-GIS 7.5 software (http://www.diva-gis.org, accessed March, 24, 2012). The names of host plants are given according to the International Plant Names Index (http://www.ipni.org, accessed December, 21, 2012).

Habitus photographs were taken using a Nikon SMZ 1500 stereomicroscope equipped with Nikon D70 or D700 camera. Subsequent focus stacking was performed using CombineZP software (http://www.hadleyweb.pwp.blueyonder.co.uk/CZP/News.htm, accessed March, 06, 2012). Digital images of selected structures were taken with Leica DM 4000 equipped with digital camera. Scanning micrographs were taken with a Hitachi TM 3000 tabletop microscope.

All measurements are in millimeters. Measurements are shown in the Table 1 and include body length (measured from clypeus to apex of hemelytron in both sexes including submacropterous females), clypeus to cuneus length, head width, pronotum length and width, inter-ocular distance, length and width of antennal segment I, and length of antennal segment II. The body length given in descriptions of species was measured from clypeus to apex of

hemelytron in male and from clypeus to apex of abdomen in female. The terminology used for male genitalia follows Konstantinov (2003) and for females follows Schwartz (2011). All explanations of additional terms used in descriptions of the parameres and vesical spicules are given in the Figs 40–56.

## Results

### *Hyoidea* Reuter, 1876

*Hyoidea* Reuter, 1876: 34 (original description)

*Hyoidea*: Carvalho (1958: 7) (catalogue); Hoberlandt (1963: 261) (redescription, key to species); Kerzhner (1964: 971) (redescription); Wagner (1974: 138) (redescription); Schuh (1995: 123) (catalogue); Kerzhner & Josifov (1999: 249) (catalogue); Knyshov & Konstantinov (2012) (habitus illustration, figures of male and female genitalia, measurements, discussion).

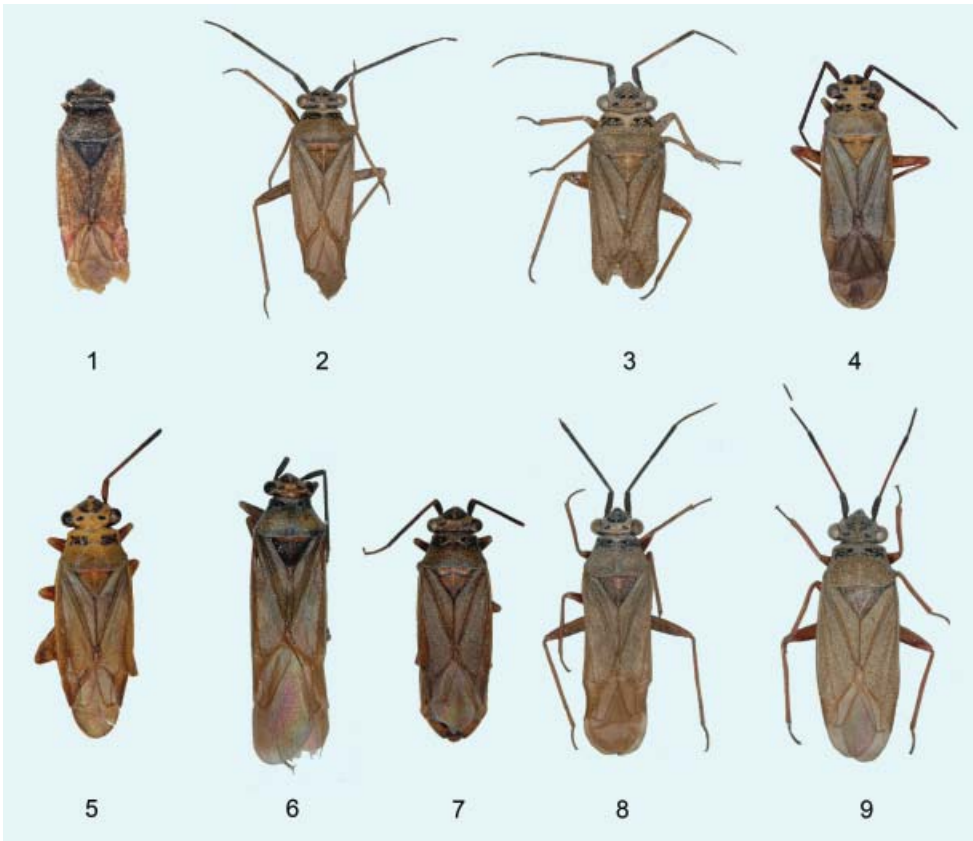
**Type species.** *Hyoidea notaticeps* Reuter, 1876 (by monotypy).

**Redescription.** ***Male*:** Macropterous, nearly parallel-sided, small to middle-sized, 3.7–5.6. COLOURATION (Figs 1–17): Dirty yellow to brown, dorsum in many species covered with minute dark spots. Head: Clypeus typically with dark medial spot at base and two dark longitudinal stripes at sides extending from base to middle or even to apex of clypeus; sometimes spots on clypeus large and confluent or clypeus entirely dark; frons with a series of large dark stripes radiating from midline and with small lateral dark spots; vertex with two large rounded spots near eyes, in *H. hannothiauxi* with large transverse dark stripe; antenna dark brown to black with uniformly coloured segments, sometimes segment II with somewhat darkened apical half; labium brown to dark brown with darkened apex of segment IV. Thorax: Pronotal collar pale, with darkened middle part or entirely darkened; pronotal disc dirty yellow to brown, usually with dense, minute, more or less round dark spots; calli pale to brown with black confluent spots or entirely black; two pits between calli always dark; exposed part of mesonotum pale to dark brown, sometimes with orange tinge; scutellum pale to dark brown, usually with more or less expressed pale midline; thoracic pleurites pale brown. Hemelytron: Dirty yellow to brown, usually with dense minute, round dark spots; hemelytron uniformly coloured in all species except *H. flavolimbata* with contrastingly yellow exocorium and *H. hannothiauxi* with reddish brown cuneus; membrane uniformly pale brown to brown, with somewhat darker veins. Legs: Femora pale brown, with dark spots on dorsal and ventral surfaces, uniformly brown in dark specimens; tibiae pale to dark brown, without spots at bases of tibial spines; tarsi uniformly pale to dark brown. Abdomen: Uniformly pale brown or dorsally darker than ventrally. SURFACE AND VESTITURE: Dorsum dull, finely rugose, scutellum and basal part of pronotum frequently with fine transverse wrinkles; pronotum always with two minute pits between calli; pronotum and clavus in some species with dense, shallow and darkened punctation; clothed with mixture of contrastingly short semiadpressed simple setae ranging in color from pale to black and small, oval, silvery scales (Figs 22–24, 26), in *H. horvathi* replaced with longer and moderately flattened, silvery scalelike setae; each anterior angle of pronotum with long dark stiff seta; tibial spines brown and short, located on inner surface of tibia, almost equal in length to width of tibia, absent at base, scarce and

usually arranged in two rows at middle and dense at apex of tibia; thoracic and abdominal venter with pale simple setae. STRUCTURE: Head: Eyes ovate in lateral view (Fig. 21), facets flat (Fig. 25); frons convex, vertex with two dark, round, distinctly sculptured spots (Figs 21–22); head posteriorly with more or less raised transverse carina (Figs 21, 23); labium reaching middle coxa. Thorax: Pronotum trapeziform, with straight or slightly concave lateral and posterior margins; anterolateral angles distinctly carinate (Figs 20–21, 23–24); pronotal collar thin, but distinct (Figs 20–21, 22–24); calli convex (Figs 21, 23); scutellum slightly convex, with weakly pointed apex; metepisternal scent gland evaporatory area relatively large, triangular, with abundant mushroom bodies, peritreme covered with microtrichia (Fig. 27). Hemelytron: Cuneus twice as long as broad at base; membrane of forewing relatively long, far extending beyond apex of abdomen. Legs: Femora somewhat flattened, tibiae cylindrical; third tarsal segment equal in length to first and second segments combined; pretarsus with long, smoothly curved claws and lamellate, apically convergent parempodia, pulvilli absent (Figs 28–29). GENITALIA: Genital capsule with distinct large tooth on left side of genital opening (Figs 30–32, 34–36) in all species except *H. hannothiauxi* (Fig. 33); genital opening located at apex of genital capsule; cuplike sclerite noticeably protruding posteriorly beyond margin of genital capsule; left paramere L-shaped, often with well-developed sensory lobe and additional caudal process (Figs 40–48); apical process of left paramere strongly curved at apex, hook-like; right paramere club-shaped, with curved and serrate apex (Figs 37–39); aedeagus with strongly sclerotized phallotheca and two spicules, with right spicule usually larger than left one and divided into two branches at extreme base (Figs 49–56).

***Female*:** Macropterous, small to middle-sized, 3.0–5.5. COLOURATION, SURFACE AND VESTITURE: Similar to male. STRUCTURE: Usually larger in body size than male, with larger interocular distance, less developed anterolateral angles of pronotum, shorter hemelytron and particularly cuneus, and relatively large, broader abdomen usually noticeably extending beyond apex of membrane. GENITALIA: Posterior wall with dorsally projecting interramal lobes and weakly sclerotized central area; interramal lobes varying in shape from weakly cleft to smoothly rounded (Figs 59–60); dorsal labiate plate membranous or partly sclerotized, with clearly ovate sclerotized rings (Figs 57–58); vestibular sclerites relatively simple, only slightly asymmetrical (Fig. 61); first gonapophysis apically widened ventrally (Figs 63, 65, 67); second gonapophysis apically arrow-shaped (Figs 62, 64, 66).

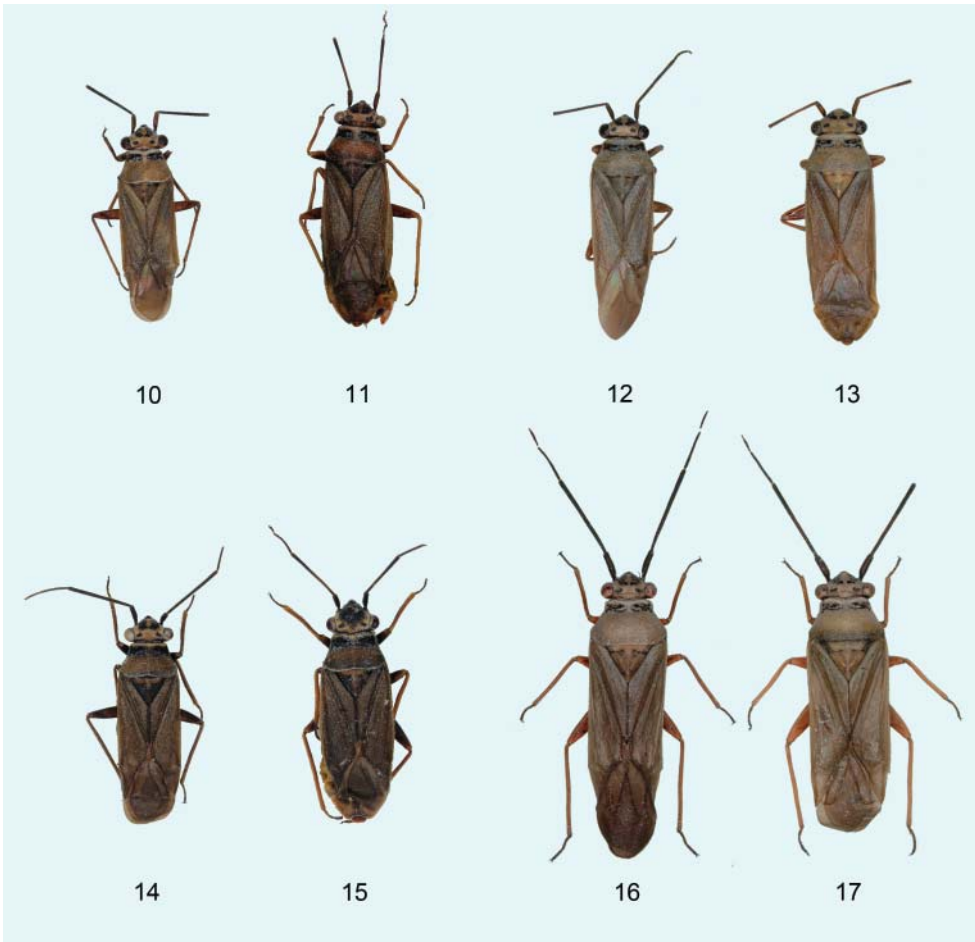
**Differential diagnosis.** Distinguished from other Palaearctic genera of *Orthotylus* group by the following combination of characters: lateroapical pronotal angles distinctly carinate and protruding (Figs 20–21, 23–24); pronotal collar thin, but distinct (Figs 20–21, 23–24); vertex with transverse posterior carina (Figs 21, 23); hemelytron in male relatively long, with base of cuneus far surpassing abdominal apex; vestiture represented by simple setae and oval, short scalelike setae (Figs 24, 26); vertex always with two dark rounded spots, sometimes merging into single dark stripe; left paramere L-shaped, with well-developed additional processes and serrations on sensory lobe and body of paramere (Figs 40–48); right paramere club-shaped, with curved and serrate apex (Figs 37–39); aedeagus with two large spicules, right spicule bifurcated at extreme base (Figs 49–56); sclerites encircling vulva asymmetrical (Fig. 61); first gonapophysis slightly widened apically (Figs 63, 65, 67); second gonapophysis apically arrow-shaped (Figs 62, 64, 66).




Figs 1–9. Dorsal habitus of *Hyoidea* species. 1 – *Hyoidea hannothiauxi* Carapezza, 1997, male. 2–3 – *Hyoidea hermione* Linnavuori, 1989: 2 – male; 3 – female. 4–5 – *Hyoidea horvathi* Montandon, 1890: 4 – male; 5 – female. 6–7 – *Hyoidea kerzhneri* Hoberlandt, 1963: 6 – male; 7 – female. 8–9 – *Hyoidea lindbergi* Hoberlandt, 1963: 8 – male; 9 – female.

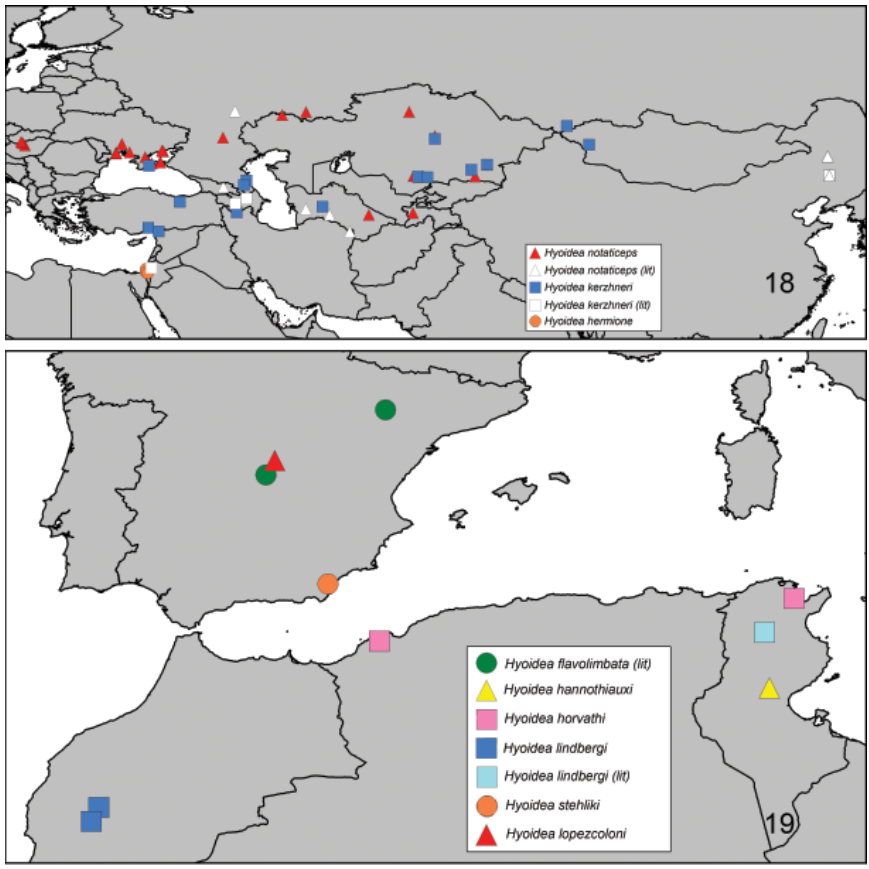
**Host associations.** Hosts are known for seven of the nine species currently recognized within this genus. Based on current evidence, *Hyoidea* is one of the two Palaearctic mirid genera that are exclusively associated with *Ephedra* spp. (Ephedraceae) (for review see Kment & Bryja 2007).

**Distribution.** *Hyoidea* is a Palaearctic genus, principally distributed in the Mediterranean region (Figs 18–19), with two species, *H. notaticeps* and *H. kerzhneri*, ranging Eastern Europe to Central Asia, and northern China. Distributional data on *Hyoidea* species are scarce, with only two species, *H. notaticeps* and *H. kerzhneri* sufficiently sampled. Two species, *Hyoidea horvathi* and *H. lindbergi*, were recorded from a few localities that are distant from localities of the remaining species (*H. flavolimbata*, *H. hannothiauxi*, *H. hermione*, *H. lopezcoloni*, and *H. stehliki*), which are known from the type localities only.




Figs 10–17. Dorsal habitus of *Hyoidea* species. 10–11 – *Hyoidea lopezcoloni* Baena & Günther, 2001: 10 – male; 11 – female. 12–15 – *Hyoidea notaticeps* Reuter, 1876: 12, 14 – males (12 – Iliyskiy on Ili River, Kazakhstan; 14 – Čenkov, Slovakia); 13, 15 – females (13 – Iliyskiy on Ili River, Kazakhstan; 15 – Čenkov, Slovakia). 16–17 – *Hyoidea stehliki* Baena & Günther, 2001: 16 – male; 17 – female.

**Discussion.** *Hyoidea* belongs to the *Orthotylus* group of genera (*sensu* Schuh 1974, see Knyshov & Konstantinov 2012 for details). The combination of several peculiar diagnostic features separates *Hyoidea* from all other orthotyline genera. It seems to be most similar to *Angulonotus*, and is putatively its sister-genus. Both genera share distinctly carinate antero-lateral angles of the pronotum, a thin but distinct pronotal collar, and several large dark spots on the frons and vertex. All *Hyoidea* species can be clearly distinguished from *Angulonotus* by the distinct mushroom bodies of the evaporatory area of the metathoracic scent gland, the short and broad scale-like setae on the dorsum, flat eye ommatidia, and the shape of the




Figs 18–19. 18 – Distribution map for *Hyoidea hermione* Linnavuori, 1989, *H. notaticeps* Reuter, 1876, and *H. kerzhneri* Hoberlandt, 1963. 19 – Distribution map for *H. flavolimbata* Ribes & Ribes, 2000, *H. hannothiauxi* Carapezza, 1997, *H. horvathi* Montandon, 1890, *H. lindbergi* Hoberlandt, 1963, *H. stehliki* Baena & Günther, 2001, and *H. lopezcoloni* Baena & Günther, 2001. Literature data are excerpted from the following sources: *H. notaticeps* (Kiritshenko 1918, 1951; Linnavuori & Modarres 1999; Putshkov & Putshkov 1989; Qi et al. 1995); *H. kerzhneri* (Gidayatov 1971, Linnavuori 1989, Qi et al. 1995); *H. flavolimbata* (Ribes & Ribes 2000); *H. lindbergi* (Carapezza 1997).

male and female genitalic structures (also see Knyshov & Konstantinov 2012 for further discussion).

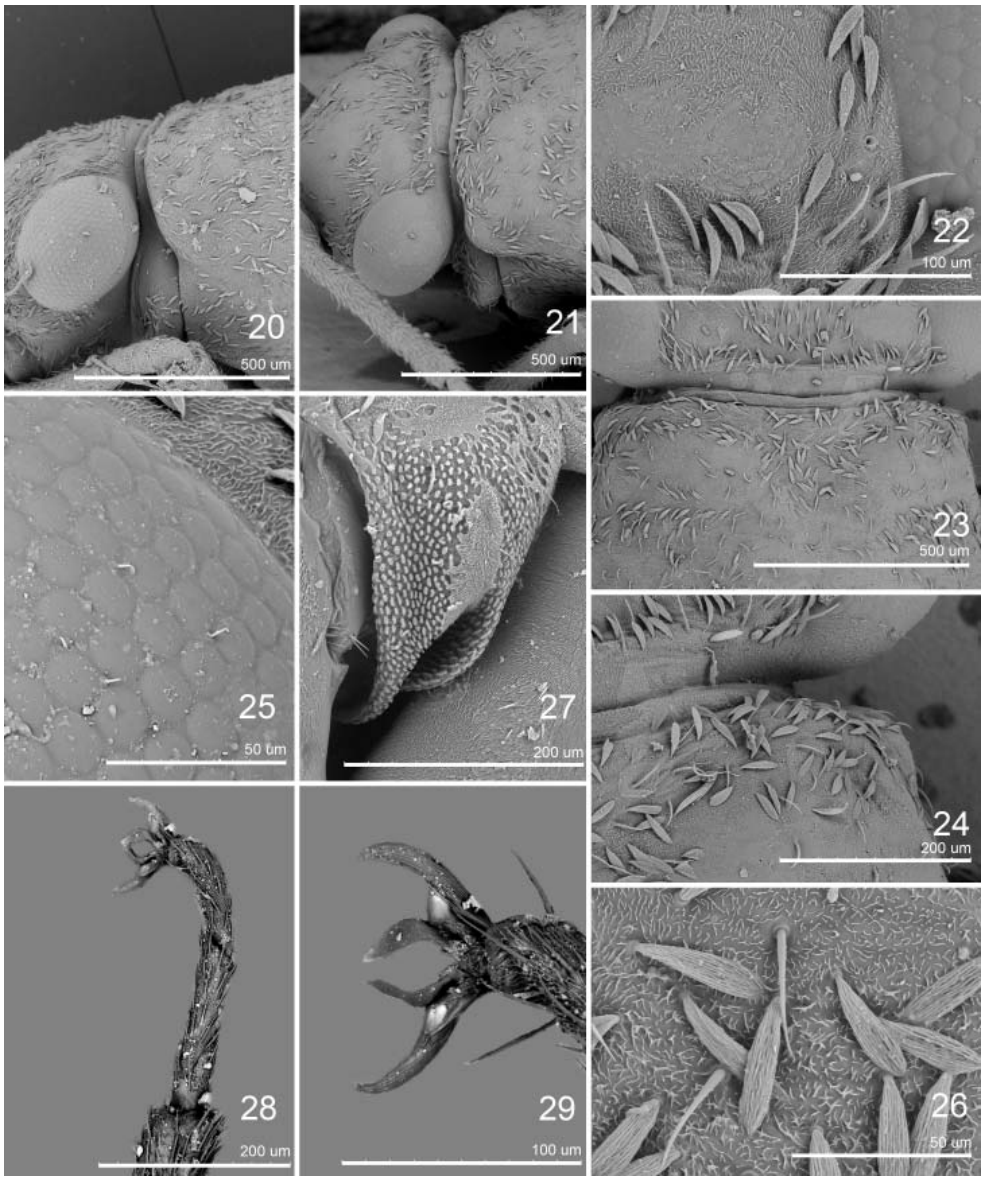
The nine species of *Hyoidea* currently are easily separated from each other by the structure of the male genitalia and, to a lesser extent, by the colouration, ratios and measurements. The genus can also be divided into several geographically defined groups of species. The first group includes *H. notaticeps* and *H. kerzhneri*, which are distributed in southeastern Europe and Asia, and *H. hermione*, which is restricted to Israel. The second group comprises those species restricted to the Iberian Peninsula, namely *H. flavolimbata*, *H. lopezcoloni*, and *H. stehliki*. *Hyoidea hannothiauxi*, *H. horvathi* and *H. lindbergi* comprise a third group, and

are known from proximate localities on the northwestern coast of Africa. Species in each group can be easily distinguished from each other, except *H. horvathi* and *H. lindbergi*, which are discussed in relevant sections.

Female genitalic structures of *Hyoidea* are not distinctive between species, and in some cases accurate identifications of females requires their association with conspecific males. Sclerotized rings of the dorsal labiate plate, interramal lobes as well as first and second gonapophysis vary only slightly in shape within *Hyoidea* and also do not differ from those of many other orthotyline taxa. Dissections of many female specimens of the largely sympatric *H. notaticeps* and *H. kerzhneri* revealed only slight intraspecific variability in genitalic structures, despite their strikingly different habitus.

## Key to species

1. Two black spots on vertex merged into black stripe (Fig. 1); genital capsule without tooth (Fig. 33). Tunisia. ..... ***H. hannothiauxi*** Carapezza, 1997
– Two black spots on vertex not confluent (Figs 2–17); genital capsule with large tooth on left side (Figs 30–32). ..... 2
2. Body uniformly dirty yellowish, with dense black minute spots (Figs 2–3, 8–9); disc and hemelytron with scale-like setae and black simple setae. ..... 3
– Body brown or dark brown, or black minute spots absent (Figs 4–7, 10–17); entire dorsum or at least head with pale simple setae in addition to scales. ..... 4
3. Vesical spicules smooth, without serrations (Fig. 55); body 4.3–4.8 mm in male, 4.2–5.1 mm in female. Morocco, Tunisia. ..... ***H. lindbergi*** Hoberlandt, 1963
– Vesical spicules apically serrate (Fig. 53); body 4.0–4.1 mm in male, 3.8–4.0 mm in female. Israel. ..... ***H. hermione*** Linnavuori, 1989
4. Left spicule of aedeagus apically rounded and enlarged, with lateral serration (Figs 51–52). ..... 5
– Left spicule of aedeagus apically not rounded (Figs 53–56), or if rounded, apically not enlarged (Fig. 50). ..... 6
5. Right spicule of aedeagus twice as long as left one (Fig. 52); sensory lobe of left paramere curved (Figs 47–48). Eastern Europe, Central Asia and northern China. ..... ..... ***H. notaticeps*** Reuter, 1876
– Both spicules equal in size (Fig. 51); sensory lobe of left paramere straight (Fig. 41). Spain. ..... ***H. lopezcoloni*** Baena & Günther, 2001
6. One branch of right vesical spicule with noticeable medial tooth (Fig. 54); colouration dark brown (Figs 6–7). ..... 7
– Vesical spicules without medial tooth (Figs 50, 56); colouration dirty yellowish (Figs 4–5, 16–17). ..... 8
7. Left paramere with caudal process; spicules of aedeagus equal in length, almost not serrate (see Figs 7–10 in Ribes & Ribes 2000). Spain. .... ***H. flavolimbata*** Ribes & Ribes, 2000
– Left paramere without caudal process (Fig. 45); left spicule of aedeagus shorter than right, right spicule distinctly serrate (Fig. 54). From Crimea, Turkey and Israel in the west to Altai, Mongolia and northern China in the east. ..... ***H. kerzhneri*** Hoberlandt, 1963




Figs 20–29. Scanning micrographs of selected structures (partly modified from Knyshov & Konstantinov 2012). 20 – *Hyoidea notaticeps* Reuter, 1876, head and pronotum. 21–26 – *H. kerzhneri* Hoberlandt, 1963: 21 – head and pronotum; 22 – vertex; 23 – pronotum; 24 – anterolateral angle of pronotum; 25 – eye facets; 26 – vestiture on hemelytron. 27 – *H. notaticeps*, scent gland evaporatory area. 28–29 – *H. lindbergi* Hoberlandt, 1963: 28 – tarsus, foreleg; 29 – pretarsus, foreleg.

8. Spicules of aedeagus long, nearly equal in length, right spicule with one wide and one narrow branch (Fig. 56); pronotal disc distinctly convex, entirely covered with black simple setae; pronotum 1.3–1.4× as wide as head in male, 1.2–1.3× in female. Spain. .....***H. stehliki*** Baena & Günther, 2001
– Left spicule of aedeagus shorter than right spicule, branches of right spicule relatively slender (Fig. 50); pronotal disc weakly convex, only basal part covered with black simple setae; pronotum 1.1× as wide as head in both sexes. Algeria, Tunisia. ..... ..... ***H. horvathi*** Montandon, 1890

### *Hyoidea flavolimbata* Ribes & Ribes, 2000
(Fig. 19)

*Hyoidea flavolimbata* Ribes & Ribes, 2000: 51 (original description)

**Type locality.** Spain, Zaragoza province (Aragon), Sierra de Alcubierre, Monegrillo.
**Type material.** Holotype: ♂, **SPAIN: Zaragoza province (Aragon):** Sierra de Alcubierre, Monegrillo. Paratypes: **SPAIN: Zaragoza province (Aragon):** Sierra de Alcubierre, Monegrillo, 1 May 1999, J. Blasco-Zumeta, 1 ♂ 1 ♀ (J. Ribes coll.). **Madrid province:** Aranjuez, 4 May 1990, U. Koschwitz, 1 ♀ (M. Baena coll.) (not examined).

**Differential diagnosis.** Distinguished by the following combination of characters: black spots on vertex and calli not confluent; cuneus concolorous with corium; left side of genital opening with distinct large tooth; sensory lobe of left paramere flattened, apically slightly widened and serrate, caudal process relatively short, with two teeth (see Figs 7–9 in Ribes & Ribes 2000); left spicule of aedeagus long, thin and curved, with medial tooth; both branches of right spicule long and thin. The species is most similar to *H. kerzhneri* in the general brown colouration, and in the presence of medial tooth on right vesical spicule, but differs in the contrastingly yellow exocorium, left paramere with caudal process, and smooth spicules of aedeagus (see Fig. 10 in Ribes & Ribes 2000).
**Host associations.** Ribes & Ribes (2000) lists the host plant as *Ephedra nebrodensis* Tineo.
**Distribution.** So far known from two close localities: Monegrillo (Sierra de Alcubierre, Zaragoza Prov.), and Aranjuez (Madrid Prov.), Spain (Fig. 19) (Ribes & Ribes 2000).
**Discussion.** The species was described from four specimens, with one female paratype sampled at a great distance apart, more than 300 km. Unfortunately we have not examined material of this species, and the diagnosis given above is based on the sufficiently detailed original description (Ribes & Ribes 2000). The species can be clearly distinguished from similar species (*H. kerzhneri* and *H. hannothiauxi*) as well as from other species known from Spain (*H. lopezcoloni* and *H. stehliki*) by the characters listed in the above diagnosis.

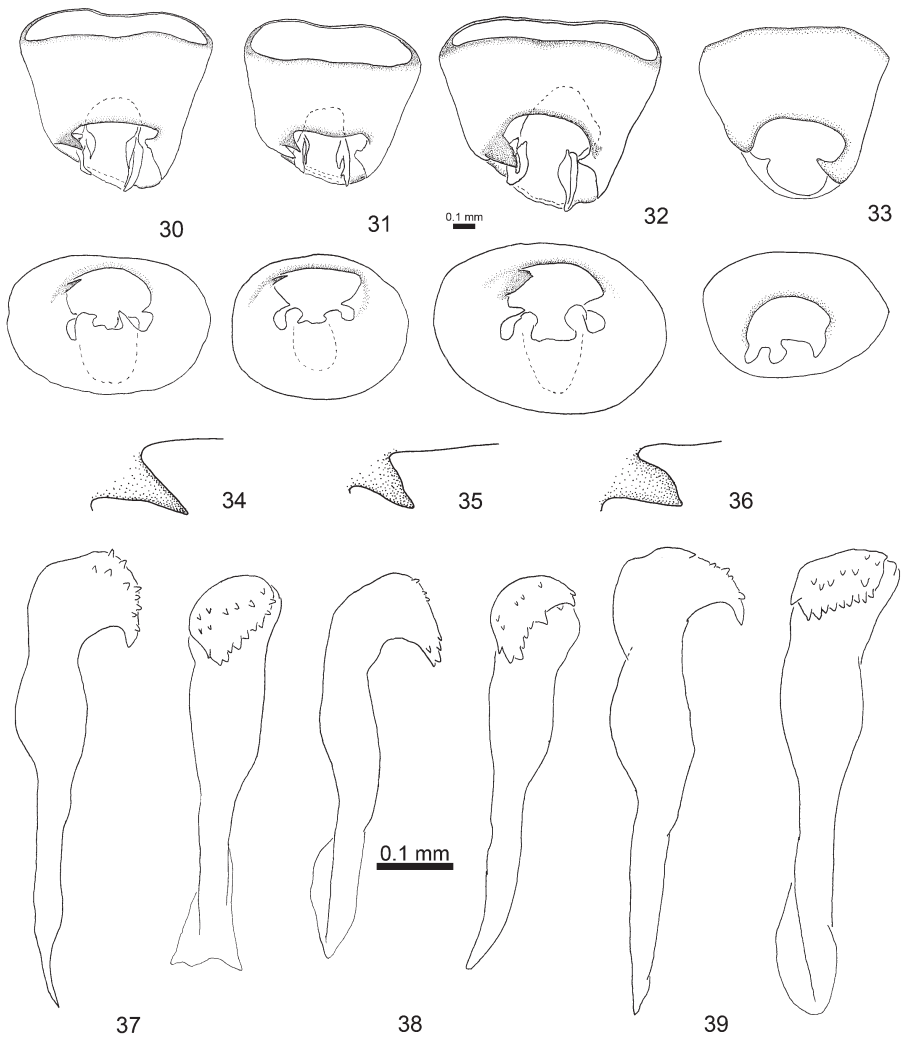
### *Hyoidea hannothiauxi* Carapezza, 1997
(Figs 1, 19, 33, 40, 49)

*Hyoidea hannothiauxi* Carapezza, 1997: 72 (original description)
*Hyoidea hannothiauxi*: Kerzhner & Josifov (1999: 249) (catalogue)

**Type locality.** Tunisia, Djebel Bou Hedma.
**Type material examined.** Holotype: ♂, **TUNISIA:** Djebel Bou Hedma, 34.46667°N 9.53333°E, no date provided, Hannothiaux Coll. (AMNH_PBI 00337189) (MNHN).

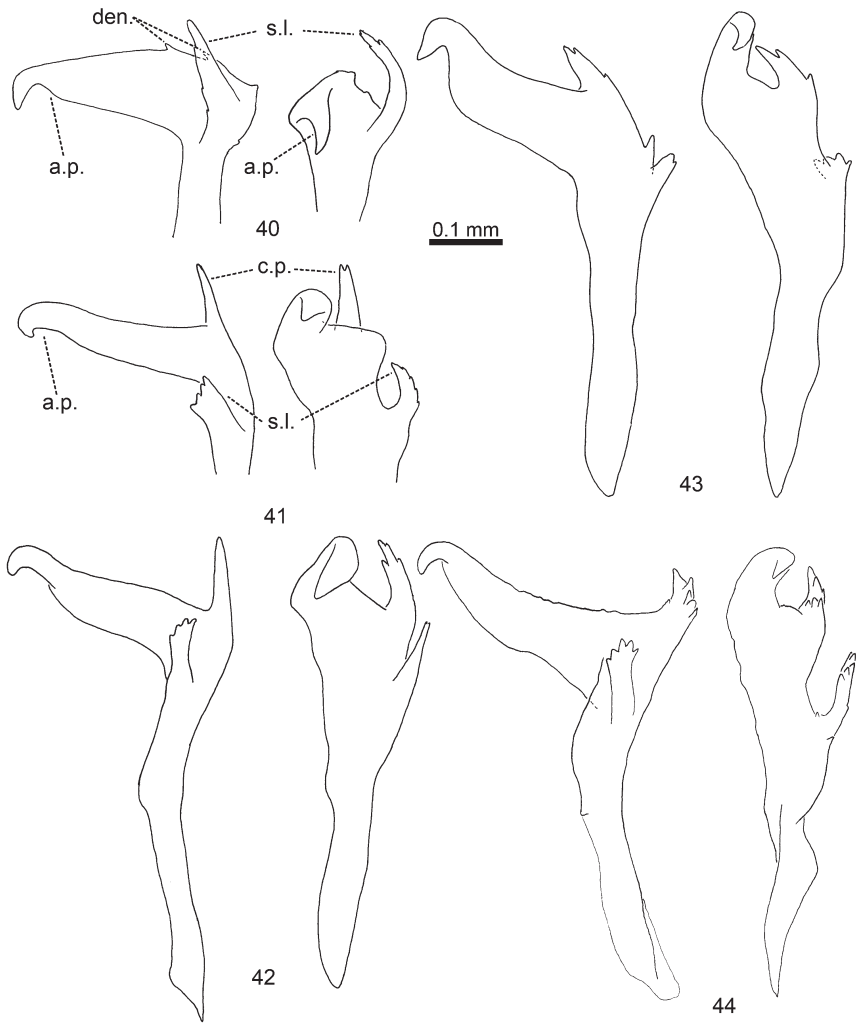
**Redescription. *Male*:** Small-sized, 4.1 mm. COLOURATION (Fig. 1): Dorsum brown, with conspicuous minute dark brown spots. Head: Clypeus pale brown, with narrow U-shaped macu-

la along edges; mandibular and maxillary plates with reverse V-shaped dark spot originating from antennal fossa; frons with black, not confluent, distinctly bordered stripes radiating from midline; vertex with two black spots merged into single transverse stripe; antennal segment I entirely black, segments II–IV missing; labium dark brown, apex of segment IV black. Thorax: Pronotal collar and anterior edge of pronotum darkened, calli entirely black, pronotum between calli also black forming wide black stripe, reminder of pronotum pale brown, with




Figs 30–36. Male genitalia (partly modified from Knyshov & Konstantinov 2012). 30–33 – Male genital capsule in dorsal and caudal views. 30 – *Hyoidea lindbergi* Hoberlandt, 1963; 31 – *H. notaticeps* Reuter, 1876; 32 – *H. stehliki* Baena & Günther, 2001; 33 – *H. hannothiauxi* Carapezza, 1997. 34–36 – *H. notaticeps*, tubercle of genital capsule. 37–39 – right paramere: 37 – *H. lindbergi*; 38 – *H. notaticeps*; 39 – *H. stehliki*.

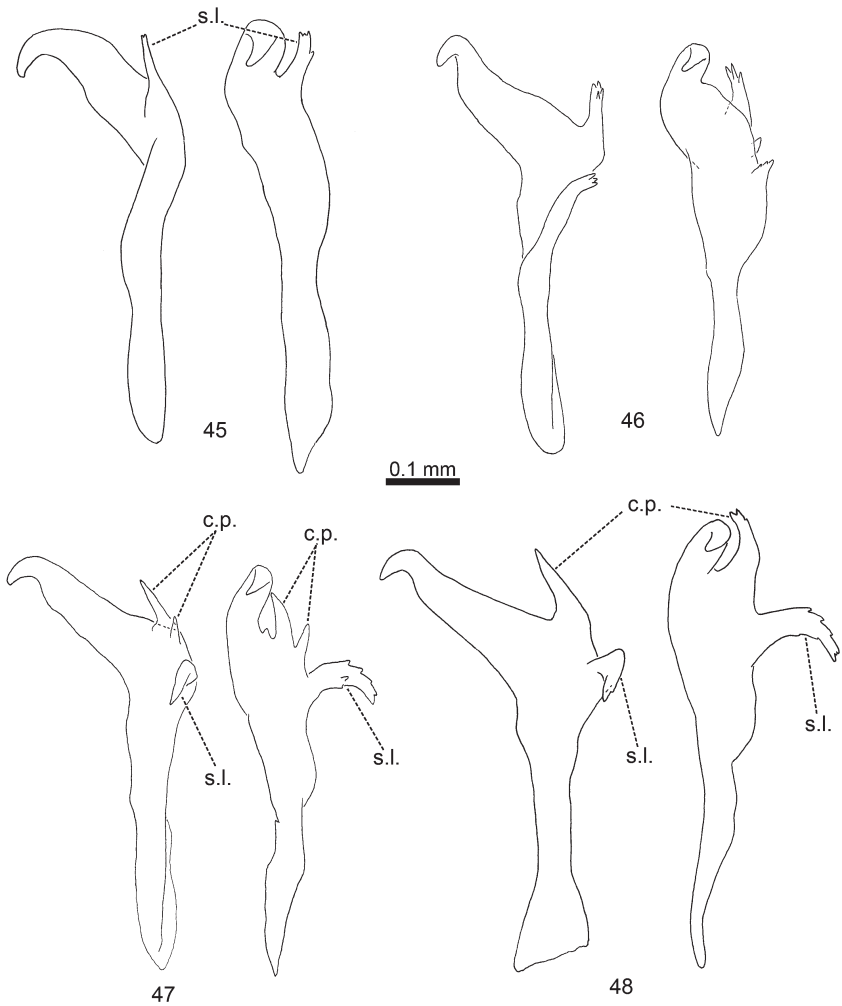
dense minute dark brown spots (Fig. 1); exposed part of mesonotum and scutellum black, the latter with two brown basal spots at sides; thoracic pleurites pale brown, narrowly darkened dorsally and ventrally. Hemelytron: pale brown, with dense minute dark brown spots, cuneus with reddish tinge along inner margin. Legs: Coxae dark, fore femur almost entirely black dorsally, brown ventrally, remaining legs missing. Abdomen: Dorsally dark brown, ventrally pale brown. SURFACE AND VESTITURE: Dorsum smooth, not punctured, disc finely rugose; simple setae on dorsum black, intermixed with oval silvery scales. STRUCTURE:




Figs 40–44. Left paramere. 40 – *Hyoidea hannothiauxi* Carapezza, 1997; 41 – *H. lopezcoloni* Baena & Günther, 2001; 42 – *H. hermione* Linnavuori, 1989; 43 – *H. horvathi* Montandon, 1890; 44 – *H. stehliki* Baena & Günther, 2001. Lettering: a.p. – apical process, s.l. – sensory lobe, c.p. – caudal process, den. – denticles.

Head: Vertex 2.1 × as wide as eye; antennal segment I relatively long, 0.5 × as long as width of head, remaining segments missing. Thorax: Pronotum 1.6 × as wide as long and 1.2 × as wide as head. GENITALIA: Genital capsule without tooth on left side of genital opening (Fig. 33); sensory lobe of left paramere long, gradually curved, with several denticles apically, caudal process absent, caudal margin of left paramere with two small denticles (Fig. 40); left spicule of aedeagus long and straight, gradually narrowing apically, without serrations; one branch of right spicule long, narrowing apically, similar in shape to left spicule, another branch distinctly shorter, wide, with weak apical serration (Fig. 49).

***Female***: Unknown.




Figs. 45–48. Left paramere. 45 – *Hyoidea kerzhneri* Hoberlandt, 1963; 46 – *H. lindbergi* Hoberlandt, 1963; 47–48 – *H. notaticeps* Reuter, 1876. Lettering: s.l. – sensory lobe, c.p. – caudal process.

**Differential diagnosis.** Distinguished by the following combination of characters: dorsum with conspicuous minute dark brown spots; two black spots on vertex merged into transverse stripe (Fig. 1); cuneus with reddish tinge; vestiture on dorsum composed of black simple setae and oval silvery scales; genital capsule without tooth on left side of genital opening (Fig. 33); sensory lobe of left paramere long, gradually curved, with several denticles apically, caudal process absent, caudal margin of left paramere with two small denticles (Fig. 40); left spicule of aedeagus long and narrowing apically (Fig. 49); one branch of right spicule long and narrowing apically, other branch distinctly shorter, wide, with weak apical serration (Fig. 49). Clearly distinguished from all congeners by the merged dark spots on vertex, relatively long antennal segment I, 0.5 × as long as width of head, and genital capsule without large tooth.
**Host associations.** Unknown.
**Distribution.** Known only from the type locality, Djebel Bou Hedma, Tunisia (Fig. 19) (Carapezza 1997).

### *Hyoidea hermione* Linnavuori, 1989

(Figs 2–3, 18, 42, 53, 57, 59, 61)

*Hyoidea hermione* Linnavuori, 1989: 50 (original description)
*Hyoidea hermione*: Schuh (1995: 123) (catalogue); Kerzhner & Josifov (1999: 249) (catalogue)

**Type locality.** Israel, Southern District, 17 km S of Be'er Sheva'.
**Type material examined.** Paratypes: **ISRAEL: HaDarom (Southern District):** 17 km S of Be'er Sheva' (Beersheba), 31.08°N 34.82°E, 27 Apr 1986, R. Linnavuori, 1 ♀ (AMNH_PBI 00337188) (NMWC). Ze'elim (S of Negev Desert), 31.2°N 34.5333°E, 23 Jul 1986, R. Linnavuori, 1 ♂ (AMNH_PBI 00337187) (NMWC).
**Additional material examined. ISRAEL: HaDarom (Southern District):** Ashqelon, dunes at seashore, 31.663°N 34.564°E, 12 Jun 1999, I. M. Kerzhner, 1 ♀ (AMNH_PBI 00312779) (ZISP). Ze'elim (S of Negev Desert), 31.2°N 34.5333°E, 23 Jul 1986, R. Linnavuori, 1 ♂ (AMNH_PBI 00312777), 1 ♀ (AMNH_PBI 00312778) (ZISP).

**Redescription. *Male*:** Small-sized, 4.0–4.1 mm. COLOURATION (Fig. 2): Dirty yellowish. Head: Clypeus pale brown with small black longitudinal spot at base and two black lateral stripes extending from base to middle of clypeus; mandibular plate entirely pale, maxillary plate darkened at apex; frons with radiating black not confluent stripes; vertex with two black, not confluent spots; antenna entirely dark brown to black, or segment II proximally brown, distally dark brown, segments III and IV somewhat paler; labium dark brown, apex of segment IV black. Thorax: Calli almost entirely covered with dense and largely confluent black spots; disc with dense brown minute spots; scutellum typically with more or less expressed brown minute spots and pale stripe along midline, rarely uniformly dirty yellow; thoracic pleurites pale, with darkened propleural suture. Hemelytron: Clavus, corium and cuneus with diffuse and sometimes indistinct brown minute spots. Legs: Dirty yellow to pale brown, sometimes with orange tinge, dorsal and ventral surfaces of all femora with a series of minute, partly confluent dark brown spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Pale brown. SURFACE AND VESTITURE: Smooth, disc and base of clavus with dense and very fine darkened punctation, scutellum typically with transverse wrinkles; vestiture composed of intermixed black simple setae and silvery scales. STRUCTURE: Head: Vertex 2.3–2.8 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal II segment 1.5 × as long as width of head and 1.2–1.3 × as long as

width of pronotum. Thorax: Pronotum 1.7 × as wide as long and 1.1–1.2 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere flattened, apically slightly widened and serrate, caudal process long and apically serrate (Fig. 42); left spicule of aedeagus with small denticles laterally; right spicule twice as long as left one, with both branches long and thin, with apical serration (Fig. 53).

***Female*:** Small-sized, 4.3 mm. COLOURATION (Fig. 3), SURFACE AND VESTITURE: As in male. STRUCTURE: More stumpy than male, with larger interocular distance and somewhat wider pronotum; vertex 2.7–3.1 × as wide as eye; antennal segment I 0.3–0.4 × as long as width of head; antennal segment II 1.1–1.2 × as long as width of head and 0.9–1.0 × as long as width of pronotum; pronotum 1.8–1.9 × as wide as long and 1.1–1.2 × as wide as head; abdomen larger and partly extending beyond apex of membrane; membrane reaching base of VIII tergite. GENITALIA: Dorsal labiate plate as in Fig. 57; interramal lobes of posterior wall as in Fig. 59; vestibular sclerites as in Fig. 61.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots usually well expressed on pronotal disc and hemelytron; two black spots on vertex not confluent (Figs 2–3); vestiture on dorsum composed of black simple setae and silvery scales; genital capsule with large tooth on left side; sensory lobe of left paramere flattened, apically slightly widened and serrate, caudal process long and apically serrate (Fig. 42); left spicule of aedeagus 0.5 × as long as right, with small subapical denticles (Fig. 53); both branches of right spicule long and not widened, with apical serration (Fig. 53). Most similar to *H. lindbergi* in the pale brown dorsum with dark minute spots, but differs in the smaller body size, and the shape of spicules of aedeagus.

**Host associations.** Linnavuori (1989) gives the host plant as *Ephedra campylopoda* C.A.Mey.

**Distribution.** This species is only known from the type locality, Southern District, Israel (Fig. 18) (Linnavuori 1989).

### *Hyoidea horvathi* Montandon, 1890

(Figs 4–5, 19, 43, 50)

*Hyoidea horvathi* Montandon, 1890: 178 (original description)

*Hyoidea horvathi*: Carvalho (1958: 76) (catalogue); Hoberlandt (1963: 270) (redescription); Wagner (1974: 142) (redescription); Schuh (1995: 123) (catalogue); Kerzhner & Josifov (1999: 249) (catalogue)

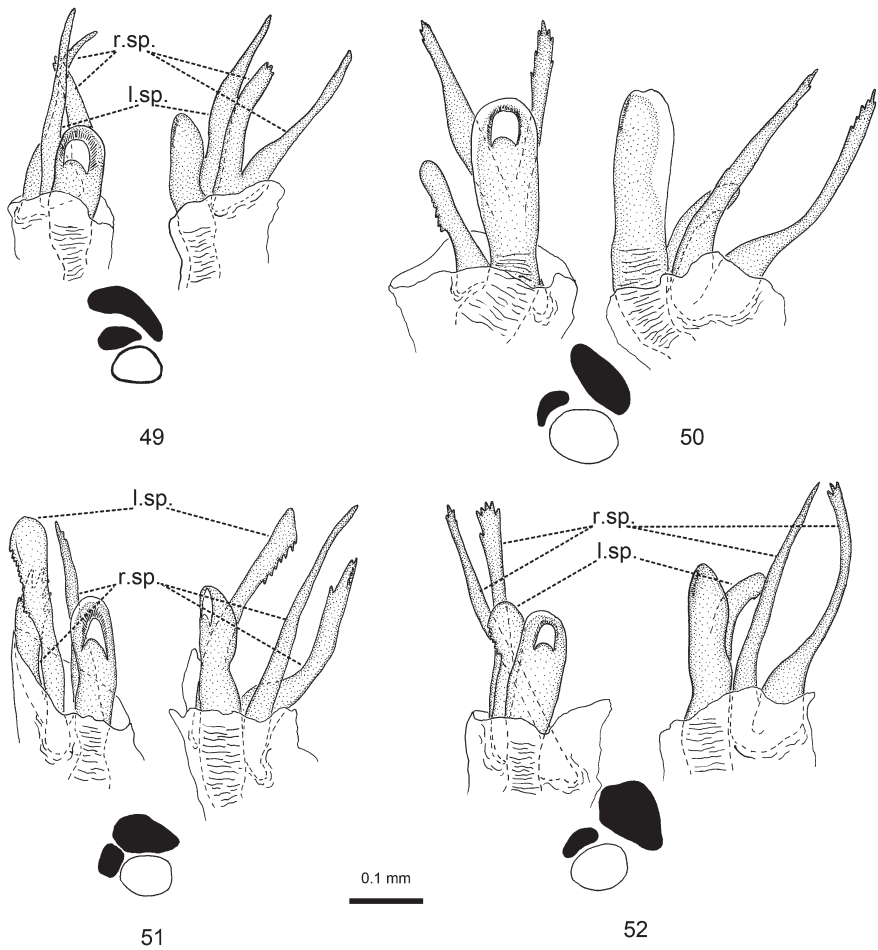
**Type locality.** Algeria, Oran.

**Type material examined.** Syntype: ♀, **ALGERIA: Oran:** Oran, 35.69111°N 0.64167°W, 111 m, L. Moisson (AMNH_PBI 00340429) (BMNH).

**Additional material examined. ALGERIA: Oran:** Oran, 35.69111°N 0.64167°W, 111 m, L. Moisson, 1 ♂ (AMNH_PBI 00340440), 1 ♀ (AMNH_PBI 00340430) (BMNH); Oran, 1887 – 1888, coll. A. Puton, 1 ♀ (AMNH_PBI 00340283) (ZMUH); Oran, 1893, P. Mathieu, 1 ♀ (AMNH_PBI 00340432) (BMNH). **TUNISIA:** Tunis, 36.8°N 10.18°E, no date provided, Vauloger, 1 ♀ (AMNH_PBI 00340431) (BMNH).

**Redescription. *Male*:** Middle-sized, 4.5 mm. COLOURATION (Fig. 4): Dirty yellowish. Head: Clypeus dirty yellow, with small black longitudinal spot at base and two black lateral stripes extending from base to middle of clypeus; mandibular plate entirely pale brown, maxillary plate dirty yellow with black apex; frons with black, not confluent stripes radiating

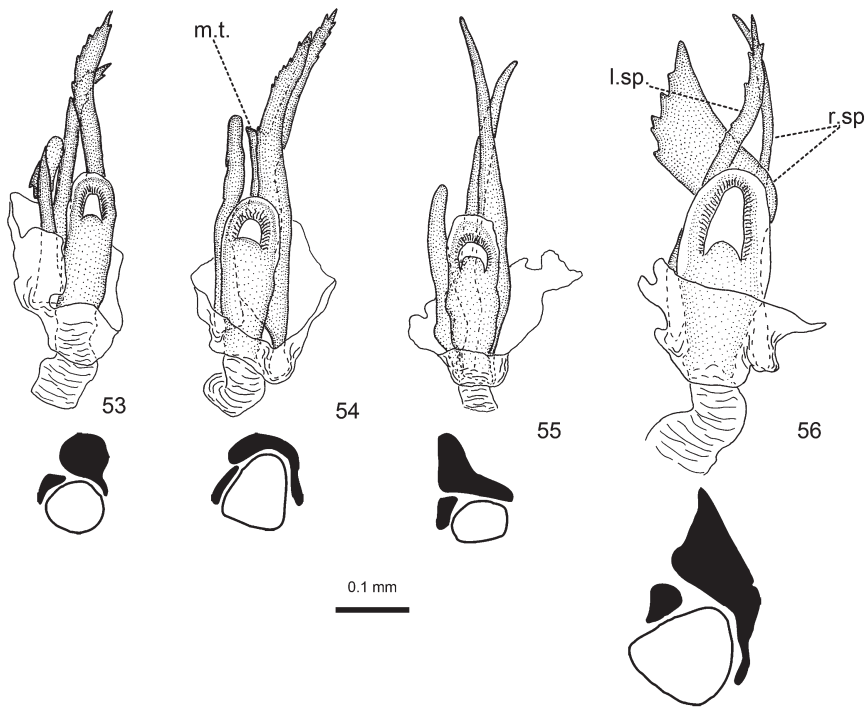
from midline and two small black spots near eyes; vertex with two large, black, not confluent spots; antenna entirely dark brown or segment II apically black; labium dark brown, apex of segment IV black. Thorax: Pronotal collar and anterior part of pronotum dirty yellow; calli almost entirely covered with dense and largely confluent black spots; disc pale brown, some specimens with sparse minute dark spots; mesonotum brown, scutellum brown with more or less expressed pale brown middle stripe; thoracic pleurites pale, with darkened propleural suture. Hemelytron: corium with sparse minute dark spots; claval fracture, claval commissure and medial fracture somewhat darkened; cuneus with slightly darkened apex. Legs: Pale brown with reddish tinge, dorsal and ventral surfaces of all femora with a series of minute, partly



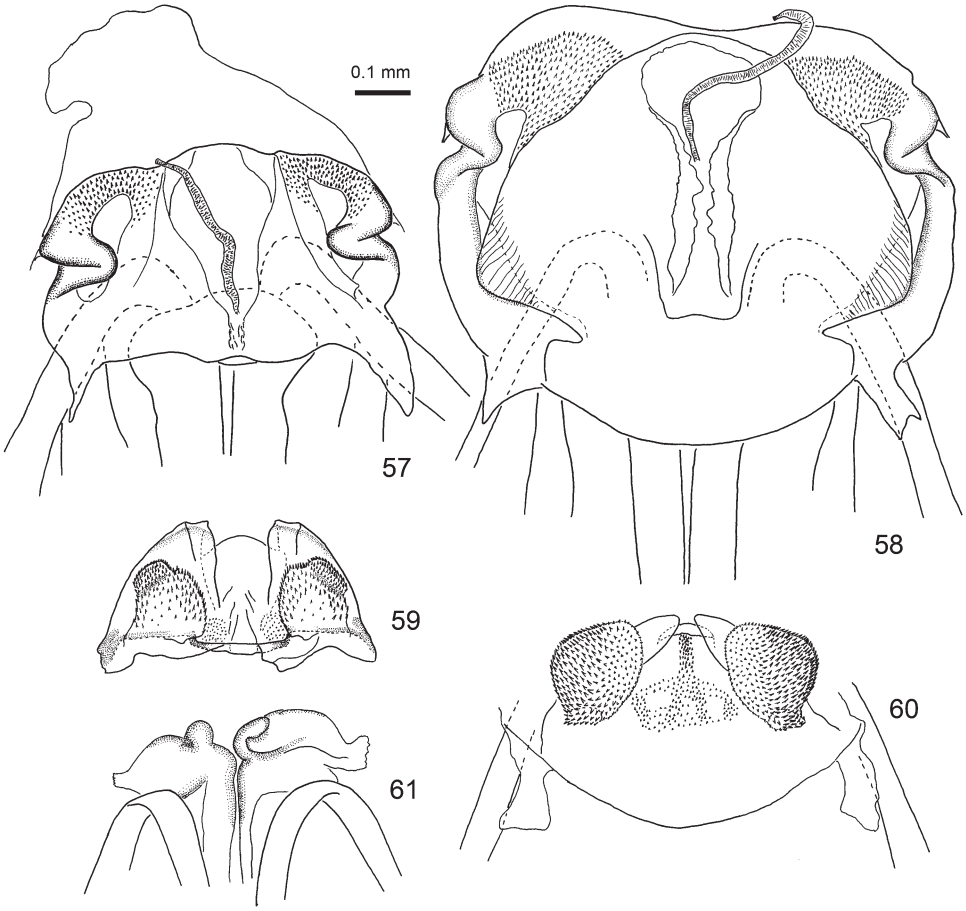

Figs 49–52. Aedeagus in ventral view, lateral view and in transverse section at base (phallotheca and phallobase removed). 49 – *Hyoidea hannothiauxi* Carapezza, 1997; 50 – *H. horvathi* Montandon, 1890; 51 – *H. lopezcoloni* Baena & Günther, 2001; 52 – *H. notaticeps* Reuter, 1876. Lettering: l.sp. – left spicule, r.sp. – right spicule.

confluent dark brown spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Pale brown. SURFACE AND VESTITURE: Smooth, disc at base with sparse, very fine, and darkened punctures, base of disc and scutellum typically with transverse wrinkles; vestiture composed of intermixed simple setae and long and moderately flattened silvery scalelike setae; simple setae pale on head and anterior part of pronotum, black on disc and hemelytron. STRUCTURE: Head: Vertex 2.4–2.5 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II 1.4–1.5 × as long as width of head and 1.2 × as long as width of pronotum. Thorax: Pronotum 1.6–1.7 × as wide as long and 1.1–1.2 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere short, flattened and serrate, caudal process relatively thick, bearing denticles and forming acute angle with apical process (Fig. 43); left spicule of aedeagus 0.5 × as long as right one, with small denticles at side; both branches of right spicule long and narrowing apically, with apical serration (Fig. 50).

***Female*:** Middle-sized, 4.2–4.9 mm. COLOURATION (Fig. 5), SURFACE AND VESTITURE: As in male. STRUCTURE: Larger than male, with larger interocular distance, vertex 2.9–3.2 × as wide as eye; antennal segment I 0.3–0.4 × as long as width of head; antennal



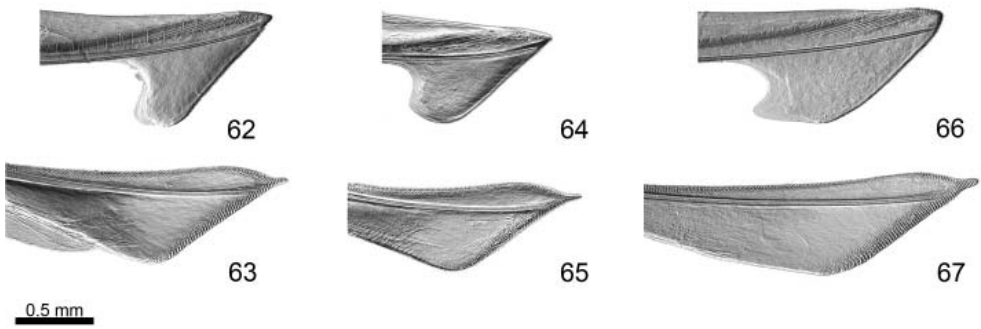

Figs 53–56 (modified from Knyshov & Konstantinov 2012). Aedeagus in ventral view and in transverse section at base (phallotheca and phallobase removed). 53 – *Hyoidea hermione* Linnavuori, 1989; 54 – *H. kerzhneri* Hoberlandt, 1963; 55 – *H. lindbergi* Hoberlandt, 1963; 56 – *H. stehliki* Baena & Günther, 2001. Lettering: l.sp. – left spicule, r.sp. – right spicule, m.t. – medial tooth.




Figs 57–61 (modified from Knyshov & Konstantinov 2012). Female genitalic structures. 57–58 – dorsal labiate plate: 57 – *Hyoidea hermione* Linnavuori, 1989; 58 – *H. kerzhneri* Hoberlandt, 1963. 59–60 – posterior wall: 59 – *H. hermione*; 60 – *H. kerzhneri*. 61 – *H. hermione*, vestibular sclerites encircling vulva.

segment II 1.2 × as long as width of head and 1.0–1.1 × as long as width of pronotum; pronotum somewhat wider than in male, 1.7–1.8 × as wide as long and 1.1–1.2 × as wide as head; abdomen larger than in male and partly extending beyond apex of membrane; membrane reaching base of tergite IX.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots indistinct, expressed only on basal part of disc and corium; two black spots on vertex not confluent; simple setae pale on head and anterior part of pronotum and black on disc and hemelytron; scales absent and replaced with moderately flattened silvery scale-like setae; genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere short, flattened and serrate, caudal process relatively thick, bearing denticles and forming acute




Figs 62–67 (modified from Knyshov & Konstantinov 2012). Apices of ovipositor. 62–63 – *Hyoidea notaticeps* Reuter, 1876: 62 – second gonapophysis; 63 – first gonapophysis. 64–65 – *H. kerzhneri* Hoberlandt, 1963: 64 – second gonapophysis; 65 – first gonapophysis. 66–67 – *H. lindbergi* Hoberlandt, 1963: 66 – second gonapophysis; 67 – first gonapophysis.

angle with apical process (Fig. 43); left spicule of aedeagus 0.5 × as long as right one, with small denticles at side (Fig. 50); both branches of right spicule long and narrowing apically, with apical serration (Fig. 50).

The species is easily distinguished from all *Hyoidea* representatives except *H. lindbergi*. Both *H. horvathi* and *H. lindbergi* are known from northwestern Africa and are similar in habitus and colouration. However, these species differ in the shape of the pronotum, which is abruptly widened at the level of the calli, with concave lateral margins in *H. horvathi*, and relatively narrow apically, with straight lateral margins in *H. lindbergi*. This character can be described as a ratio between the width of pronotum at base and at the level of the calli. According to our observations, this ratio is <1.4 in male and < 1.3 in female of *H. horvathi*, while in *H. lindbergi* the ratio is >1.5 in male and >1.4 in female. Dark minute spots in *H. horvathi* are almost absent or scarce, only the pronotal disc and corium are noticeably covered with spots, while the anterior part of the pronotum and vertex are never punctured. The dorsum of *H. lindbergi* is usually heavily covered with minute dark spots, rarely with scarce spots, but the vertex and anterior part of pronotum always have spots. Vestiture on the dorsum is always composed of dark simple setae and oval scales, while in *H. horvathi* simple setae are pale on the head and anterior part of pronotum and dark elsewhere, intermixed with moderately flattened, long and slender silvery setae. In addition, males differ in the structure of aedeagus (compare Figs 50 and 55).

**Host associations.** Unknown.

**Distribution.** Northwestern Africa (Fig. 19); known from Oran in Algeria (Montandon 1890) and Tunis in Tunisia (new record).

**Discussion.** The species was described by Montandon from several specimens from Oran, collected by Moisson (Montandon 1890). The type series is now dispersed over several European museums (Kerzhner & Josifov 1999), and we had an opportunity to examine only one syntype, female, deposited in BMNH. We also examined several male and female specimens with the same locality labels, but they were probably not studied by Montandon.

### *Hyoidea kerzhneri* Hoberlandt, 1963

(Figs 6–7, 18, 21–26, 45, 54, 58, 60, 64–65)

*Hyoidea kerzhneri* Hoberlandt, 1963: 264 (original description)

*Hyoidea kerzhneri*: Kerzhner (1964: 971) (diagnosis); Gidayatov (1971: 85) (record); Wagner (1974: 141) (redescription); Putshkov & Putshkov (1983: 17) (host); Linnavuori (1989: 51) (record); Qi et al. (1995: 59) (record); Schuh (1995: 123) (catalogue); Kerzhner & Josifov (1999: 249) (catalogue)

**Type locality.** Kazakhstan, Karaganda province, Samenj-Kum Sands, N Karakoin Lake, W Betpak-dala Desert.

**Type material examined.** Holotype: ♂, **KAZAKHSTAN: Karaganda Province:** Samenj-Kum Sands, N Karakoin Lake, W Betpak-dala Desert, 29 May 1962, I. M. Kerzhner, *Ephedra distachya* (Ephedraceae) (AMNH_PBI 00311256) (ZISP). Paratypes: **KAZAKHSTAN: Karaganda Province:** Samenj-Kum Sands, N Karakoin Lake, W Betpak-dala Desert, 29 May 1962, I. M. Kerzhner, *Ephedra distachya* (Ephedraceae), 7 ♂♂ (AMNH_PBI 00311257-AMNH_PBI 00311262, AMNH_PBI 00311270), 7 ♀♀ (AMNH_PBI 00311274–AMNH_PBI 00311280) (ZISP). **South Kazakhstan Province:** Karasay, Dzhagan-ata, Kara-tau, 43.46666°N 69.51666°E, 27 May 1936 – 29 May 1936, A.K. Lukyanovich, 3 ♀♀ (AMNH_PBI 00311282–AMNH_PBI 00311284) (ZISP). **Zhambul Province:** Muyunkum Sands, Kargaly-kol' Lake, 43.38333°N 70.7°E, 19 May 1910, A. N. Kiritshenko, 1 ♀ (AMNH_PBI 00311288) (ZISP). **RUSSIAN FEDERATION: Dagestan:** Tarku-Tau Mt. nr Makhachkala, 42.96666°N 47.5°E, 10 Jun 1945, Ryabov, 1 ♂ (AMNH_PBI 00311267) (ZISP). **UKRAINE: Crimea:** Sudak, 44.85°N 34.96666°E, 04 Jun 1915, A. N. Kiritshenko, 1 ♂ (AMNH_PBI 00311263) (ZISP).

**Additional material examined. ARMENIA:** Meghri on Araks River, 38.88333°N 46.25°E, 04 Jun 1957, Tryapitsin, 1 ♀ (AMNH_PBI 00311294) (ZISP). **KAZAKHSTAN: Almaty Province:** Sarytaukum Sands, 150 km NNE Almaty, 44.33333°N 76.33333°E, 06 May 1981, Reznik, 1 ♂ (AMNH_PBI 00311268) (ZISP). Taldyqorghan [= Taldykurgan], 45°N 78.36666°E, 23 May 1937, A. K. Lukyanovich, 2 ♀♀ (AMNH_PBI 00312715, AMNH_PBI 00312716) (ZISP). **Karaganda Province:** 40 km S of Atasu [= Zhana-Arka], 48.31666°N 71.66666°E, 29 Jun 1960, I. M. Kerzhner, *Ephedra distachya* (Ephedraceae), 1 ♂ (AMNH_PBI 00312659) (ZISP). **South Kazakhstan Province:** Karasay, Dzhagan-ata, Kara-tau, 43.46666°N 69.51666°E, 27 May 1936 – 29 May 1936, A.K. Lukyanovich, 2 ♀♀ (AMNH_PBI 00311285, AMNH_PBI 00311287) (ZISP). **Zhambul Province:** Muyunkum Sands, Kargaly-kol' Lake, 43.38333°N 70.7°E, 24 May 1910, A. N. Kiritshenko, 2 ♀♀ (AMNH_PBI 00311290, AMNH_PBI 00311289) (ZISP). **MONGOLIA: Hovd Aimak:** 15 km WNW of Dut, 47.555°N 91.445°E, 08 Jul 1980, I. M. Kerzhner, 1 ♂ (AMNH_PBI 00311269) (ZISP). **RUSSIAN FEDERATION: Altai Republic:** Kosh-Agach, 49.98333°N 88.63333°E, 26 Jun 1964, I. M. Kerzhner, *Ephedra distachya* (Ephedraceae), 1 ♂ (AMNH_PBI 00311266) (ZISP); 22 Jul 1964, I. M. Kerzhner, 1 ♀ (AMNH_PBI 00311293) (ZISP). **Dagestan:** Khadzhalmakhi, 42.4°N 47.16666°E, 25 Jun 1926, Ryabov, 2 ♀♀ (AMNH_PBI 00311291, AMNH_PBI 00311292) (ZISP). **TURKEY: Hatay:** Bakras Kalesi, 36.42689°N 36.22503°E, 10 May 2007, Kment P., 1 ♀, *Ephedra campylopoda* (Ephedraceae) (AMNH_PBI 00337230) (NMPC). **Mersin:** Tarsus, 36.9178°N 34.8917°E, 17 m, 19 Apr 1955 – 23 Apr 1955, Seidenstücker, 1 ♂ (AMNH_PBI 00340285) (ZMUH). **Ankara:** Ankara Baraj, 40.23333°N 38.91667°E, 02 May 1968 – 03 May 1968, Seidenstücker, 2 ♂♂ (AMNH_PBI 00340286, AMNH_PBI 00340287), 2 ♀♀ (AMNH_PBI 00340298, AMNH_PBI 00340299) (ZMUH). **TURKMENISTAN:** Garagum sands, Kirpili, 39.6°N 57.21666°E, 02 May 1965, Tokgaev, *Ephedra* sp. (Ephedraceae), 4 ♀♀ (AMNH_PBI 00311295) (ZISP). **UKRAINE: Crimea:** Sudak, 44.85°N 34.96666°E, 04 Jun 1915, A. N. Kiritshenko, 2 ♂♂ (AMNH_PBI 00311264, AMNH_PBI 00311265) (ZISP).

**Redescription. *Male*:** Relatively large, gracile, almost parallel-sided, 4.9–5.6 mm. COLOURATION (Fig. 6): Brown. Head: Clypeus dark brown, with big black longitudinal spot at base and two black lateral stripes extending from base to apex of clypeus, all spots largely confluent, and in most cases clypeus entirely black; mandibular plate entirely pale brown, maxillary plate pale brown with black apex; frons with black, not confluent stripes radiating from midline and several small black spots near eyes; vertex with two large, black, not confluent spots, in addition frons and vertex in some specimens with dark brown minute spots; antenna black; labium dark brown, apex of segment IV black. Thorax: Pronotal collar brown, medially darkened; anterior part of pronotum brown, calli almost entirely covered with largely confluent black spots, in many cases entirely black; pronotum between calli usually black,

rarely brown; mesonotum brown, scutellum brown to black; in some specimens pronotum and scutellum with dark brown minute spots; thoracic pleurites pale at margins, centrally darkened, with darkened propleural suture. Hemelytron: Clavus and cuneus uniformly brown; corium usually uniformly brown, rarely with dark brown minute spots. Legs: Brown to dark brown; femora apically darkened, with a series of minute, partly confluent dark brown to black spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Dorsally dark brown, ventrally pale brown. SURFACE AND VESTITURE: Smooth, disc at base in some specimens with dense and very fine darkened punctures, scutellum typically with transverse wrinkles; vestiture composed of intermixed simple setae and silvery scales; simple setae usually entirely pale; if dark brown spots expressed on dorsum, simple setae, originating from these spots, usually black. STRUCTURE: Head: Vertex 2.2–2.4 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II 1.4–1.7 × as long as width of head and 1.1–1.2 × as long as width of pronotum. Thorax: Pronotum 1.7–1.9 × as wide as long and 1.3–1.4 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere slender and apically serrate, caudal process absent (Figs 45); left spicule of aedeagus 0.5 × as long as right, medially bent and apically rounded (Fig. 54); one branch of right spicule with denticle at middle (Fig. 54).

***Female*:** Middle-sized, 4.4–4.6 mm. COLOURATION (Fig. 7): as in male, but dark minute spots on dorsum usually better expressed. SURFACE AND VESTITURE: Same as in male. STRUCTURE: Smaller but wider than male, with larger interocular distance, vertex 2.8–3.1 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II 1.1–1.2 × as long as width of head and 0.9–1.0 × as long as width of pronotum; pronotum 1.7–1.8 × as wide as long and 1.2 × as wide as head; abdomen larger and usually partly extending beyond apex of membrane; membrane at least reaching base of tergite IX, or reaching apex of abdomen. GENITALIA: Dorsal labiate plate as in Fig. 58; interramal lobes as in Fig. 60; first gonapophysis as in Fig. 65; second gonapophysis as in Fig. 64.

**Differential diagnosis.** Distinguished by the following combination of characters: two dark spots on vertex not confluent; vestiture on dorsum composed of pale or dark simple setae and silvery scales; genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere slender and apically serrate, caudal process absent (Fig. 45); left spicule of aedeagus noticeably shorter than right, medially bent and apically rounded (Fig. 54); one branch of right spicule with denticle at middle (Fig. 54). Differs from all other species by the combination of elongated parallel-sided body, brown ground colour, and relatively long antennal segment I, 0.4 × as long as width of head; males further differ in having left paramere without caudal process and medial tooth on the right spicule of aedeagus.

**Host associations and bionomics.** This species has been recorded from the following three congeneric species: *Ephedra distachya* L. (Hoberlandt 1963, Putshkov & Putshkov 1983), *Ephedra campylopoda* C.A.Mey. (Linnavuori 1989), *Ephedra major* Host (Putshkov & Putshkov 1983). Data on the bionomics of this species are available only for Azerbaijan (Gidayatov 1971): larvae occur in May, adults from May until June.

**Distribution.** Widely distributed in the steppe and semidesert zones of Palaearctic (Fig. 18), in the Crimea (Ukraine) (Hoberlandt 1963), Turkey (Hoberlandt 1963), Israel (Linnavuori 1989), Dagestan (Russia) (Hoberlandt 1963), Azerbaijan (Gidayatov 1971), Armenia (Putshkov & Putshkov 1983), Turkmenistan (new record), Kazakhstan (Hoberlandt 1963), Altai

(Russia) (Kerzhner & Josifov 1999), Mongolia (Kerzhner & Josifov 1999), and northern China (Inner Mongolia: Tongliao) (Qi et al., 1995).

### *Hyoidea lindbergi* Hoberlandt, 1963

(Figs 8–9, 19, 28–29, 30, 37, 46, 55, 66–67)

*Hyoidea lindbergi* Hoberlandt, 1963: 267 (original description)
*Hyoidea lindbergi*: Wagner (1974: 141) (redescription); Schuh (1995: 123) (catalogue); Carapezza (1997: 75) (record); Kerzhner & Josifov (1999: 249) (catalogue); Baena & Günther (2001: 89) (figure of pygophore).

**Type locality.** Morocco, Atlas Mts., Reraia Valley, near Asni.
**Type material examined.** Holotype: ♂, **MOROCCO:** Atlas Mai, Reraia, 29 May 1926 – 15 Jun 1926, Lindberg (AMNH_PBI 00337199) (NMPC). Paratypes: **MOROCCO:** Atlas Mai, Reraia, 29 May 1926 – 15 Jun 1926, Lindberg, 1 ♂ (AMNH_PBI 00337200), 2 ♀♀ (AMNH_PBI 00337201, AMNH_PBI 00337202) (NMPC).
**Additional material examined. MOROCCO:** Atlas Mai, Reraia, 29 May 1926 – 15 Jun 1926, Lindberg, 1 ♀ (AMNH_PBI 00337203) (NHMM), 2 ♀♀ (AMNH_PBI 00340300, AMNH_PBI 00340284), 1 ♂ (AMNH_PBI 00340282) (ZMUH). Atlas Mts, Ijoukak, 30.98333°N 8.15°W, 1209 m, 20 May 1973, Eckerlein, *Ephedra fragilis* (Ephedraceae), 1 ♂ (AMNH_PBI 00311351), 5 ♀♀ (AMNH_PBI 00311354–AMNH_PBI 00311356, AMNH_PBI 00311359, AMNH_PBI 00311273) (ZISP). Hoher Atlas, Tahanaote, 31.35°N 7.95°W, 10 May 1970, Eckerlein, *Ephedra fragilis* (Ephedraceae), 4 ♂♂ (AMNH_PBI 00311347–AMNH_PBI 00311350), 4 ♀♀ (AMNH_PBI 00311357, AMNH_PBI 00311358, AMNH_PBI 00311271, AMNH_PBI 00311272) (ZISP).

**Redescription.** ***Male*:** Middle-sized, 4.3–4.7 mm. COLOURATION (Fig. 8): Dirty yellowish. Head: Clypeus pale brown with small black longitudinal spot at base and two black lateral stripes extending from base to middle of clypeus; mandibular plate entirely pale, maxillary plate darkened at apex; mandibular and maxillary plates entirely pale brown; frons with large radiating black not confluent stripes at middle and several small black spots on each lateral side; vertex with two large black not confluent spots; frons and vertex with dark brown minute spots; antenna entirely dark brown to black, or segment II proximally pale brown, distally dark brown; labium brown, apex of segment IV dark brown to black. Thorax: Calli almost entirely covered with dense and largely confluent black spots; disc with dense minute dark spots; scutellum pale brown to brown with more or less expressed pale middle stripe; thoracic pleurites pale, with darkened propleural suture. Hemelytron: Clavus, corium and cuneus with diffuse and sometimes indistinct brown minute spots; membrane pale brown with brown veins. Legs: Pale brown to brown with reddish tinge, femora with a series of minute, partly confluent dark brown spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Pale brown. SURFACE AND VESTITURE: Smooth, disc and base of clavus with dense and very fine darkened punctation, scutellum typically with transverse wrinkles; vestiture composed of intermixed simple setae and silvery scales, simple setae on dorsum black. STRUCTURE: Head: Vertex 1.8–2.4 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II 1.5–1.6 × as long as width of head and 1.2–1.3 × as long as width of pronotum. Thorax: Pronotum 1.6–1.8 × as wide as long and 1.2–1.3 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening (Fig. 30); sensory lobe of left paramere short, flattened and serrate apically, caudal process slender and apically serrate (Fig. 46); right paramere as in Fig. 37; left spicule of aedeagus 0.5 × as long as right one, apically rounded; both branches of right spicule long and thin, without apical serration (Fig. 55).

***Female*:** Small to middle-sized, 4.7–5.0 mm. COLOURATION (Fig. 9), SURFACE AND VESTITURE: As in male. STRUCTURE: Almost of the same length as male or slightly larger, but noticeably wider, with larger interocular distance, vertex 2.9–3.3 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II 1.2–1.4 × as long as width of head and 1.0–1.1 × as long as width of pronotum; pronotum 1.6–1.9 × as wide as long and 1.2–1.4 × as wide as head; abdomen larger and usually partly extending beyond apex of membrane; membrane at least reaching base of VIII tergite, rarely cover abdomen wholly. GENITALIA: First gonapophysis as in Fig. 67; second gonapophysis as in Fig. 66.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots well expressed on head, disc and hemelytron; two black spots on vertex not confluent (Figs 8–9); vestiture on dorsum composed of black simple setae and silvery scales; genital capsule with large tooth on left side of genital opening (Fig. 30); sensory lobe of left paramere short, flattened and serrate apically, caudal process slender and apically serrate (Fig. 46); left spicule of aedeagus 0.5 × as long as right one, apically rounded; both branches of right spicule long and thin, without apical serration (Fig. 55). Most similar to *H. hermione* in having pale brown dorsum with dark brown minute spots (compare Figs 2–3 and 8–9), and to *H. horvathi* in the middle-sized body, and dirty yellowish ground colour, but differs in the larger body size from the former and in the shape of pronotum, as well as in surface and vestiture of head and pronotum from the latter (see also relevant section in *H. horvathi*). Male specimens of all species also clearly differ in the shape of spicules of aedeagus (compare Figs 50, 53, and 55).

**Host associations.** *Ephedra fragilis* Desf. (Hoberlandt 1963).

**Distribution.** Northwestern Africa, Morocco (Atlas Mountains) (Hoberlandt 1963) and Tunisia (Siliana) (Carapezza 1997) (Fig. 19).

### *Hyoidea lopezcoloni* Baena & Günther, 2001

(Figs 10–11, 19, 41, 51)

*Hyoidea lopezcoloni* Baena & Günther, 2001: 82 (original description)

**Type locality.** Spain, Madrid province, Rivas-Vaciamadrid, Cerro del Telegrafo.

**Type material examined.** Paratypes: **SPAIN: Madrid:** Torres de la Alameda, 40.408°N 3.364°W, 10 May 1997, L. Arnaiz and P. Bercedo, 1 ♀ (AMNH_PBI 00337185) (NHMM); 21 May 1997, L. Arnaiz and P. Bercedo, 1 ♂ (AMNH_PBI 00337184) (NHMM).

**Redescription. *Male*:** Small-sized, 3.6–4.0 mm (according to Baena & Günther 2001). COLOURATION (Fig. 10): Brown. Head: Clypeus brown, with big black longitudinal spot at base and two black lateral stripes extending from base to apex of clypeus, all spots largely confluent; mandibular and maxillary plates pale with darkened apices; frons with large, black, not confluent stripes radiating from midline and several small black spots near eyes; vertex with two large, black, not confluent spots; frons and vertex in some specimens with dark brown minute spots; antenna dark brown to black, or antennal segment II basally brown, apically black; labium brown to dark brown, apex of segment IV black. Thorax: Anterior part of pronotum dirty yellowish; calli densely covered with largely confluent black spots or entirely black; disc brown, basally somewhat darkened, with pale stripe along midline and basal edging; in some specimens disc at base with dark brown minute spots; scutellum with

more or less expressed pale midline; thoracic pleurites pale with reddish tinge, and darkened propleural suture. Hemelytron: Clavus, corium and cuneus uniformly pale brown. Legs: Brown with reddish tinge, femora with a series of minute, partly confluent dark brown spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Dorsally brown, ventrally pale brown. SURFACE AND VESTITURE: Smooth, without punctures; disc distinctly rugose; vestiture composed of intermixed simple setae and silvery scales; simple setae pale on head and pronotum, brown on hemelytron. STRUCTURE: Head: Vertex 2.6 × as wide as eye; antennal segment I 0.3 × as long as width of head; antennal segment II 1.2 × as long as width of head and 1.1 × as long as width of pronotum. Thorax: Pronotum 1.7 × as wide as long and 1.1 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere apically serrate and turned towards apical process, caudal process slender, with apical denticles (Fig. 41); left spicule and both branches of right spicule nearly equal in length; left spicule wide, with serrate margin; one branch of right spicule thin, another slightly widened apically, both with apical serration (Fig. 51).

***Female*:** Small-sized, 3.6–4.5 mm (according to Baena & Günther 2001). COLOURATION (Fig. 11), SURFACE AND VESTITURE: As in male. STRUCTURE: Larger than male, with larger interocular distance, vertex 3.3 × as wide as eye; antennal segment I 0.3 × as long as width of head; antennal segment II 1.0 × as long as width of head and 0.9 × as long as width of pronotum; pronotum 1.8 × as wide as long and 1.2 × as wide as head; abdomen larger than in male and usually partly extending beyond apex of membrane; membrane reaching at least base of segment IX.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots on dorsum absent; two black spots on vertex not confluent (Figs 10–11); simple setae pale on head and pronotum, somewhat darkened on hemelytron; silvery scales short and oval; genital capsule with large tooth on left side of genital opening; sensory lobe of left paramere apically serrate and turned towards apical process, caudal process slender, with apical denticles (Fig. 41); left spicule and both branches of right spicule equal in length; left spicule wide, with serrate lateral margin; one branch of right spicule thin, another slightly widened apically, both with apical serration (Fig. 51). Most similar to dark forms of *H. notaticeps* in the body size, length of the antennal segment I, and colouration, but differs in the shape of spicules of aedeagus and straight sensory lobe of the left paramere.

**Host associations.** Baena & Günther (2001) have reported the host plant is *Ephedra fragilis* Desf. as the host of this species.

**Distribution.** This species is only known from the type locality, Madrid Prov., Spain (Fig. 19) (Baena & Günther 2001).

### *Hyoidea notaticeps* Reuter, 1876

(Figs 12–15, 18, 20, 27, 31, 34–36, 38, 47–48, 52, 62–63)

*Hyoidea notaticeps* Reuter, 1876: 34 (original description)

*Hyoidea notaticeps*: Kiritshenko (1918: 152) (record); Kiritshenko (1951: 181) (diagnosis); Carvalho (1958: 76) (catalogue); Hoberlandt (1963: 273) (redescription); Kerzhner (1964: 971) (diagnosis); Putshkov & Putshkov (1983: 17) (host); Kaplin (1993: 166) (bionomics); Qi et al. (1995: 59) (record); Schuh (1995: 123) (catalogue); Kerzhner & Josifov (1999: 249) (catalogue); Linnavuori & Modarres (1999: 222) (record)

**Type locality.** Russian Federation, Volgograd prov., Sarepta [= Krasnoarmeysk district of Volgograd].
**Type material examined.** Lectotype: ♀ (designated by Hoberlandt (1963)), **RUSSIAN FEDERATION: Volgograd Province:** Sarepta [= Krasnoarmeysk distr. of Volgograd], 48.5°N 44.48333°E, V. Jakovlev coll. (AMNH_PBI 00312702) (ZISP).
**Additional material examined. HUNGARY:** Budapest, 47.5004°N 19.02679°E, 122 m, 1700, unknown collector, 1 ♀ (AMNH_PBI 00340446) (BMNH). R. Palota, 25 May 1885, G. Horváth, 1 ♂ (AMNH_PBI 00340445) (BMNH). **KAZAKHSTAN: Akmola Province:** Atbasar, 51.8°N 68.35°E, 30 Jul 1936, Rezvoy, 1 ♀ (AMNH_PBI 00312713) (ZISP). **Almaty Province:** Iliyskiy on Ili River, 43.52194°N 76.82972°E, 17 May 1937 – 18 May 1937, A. K. Lukyanovich, 10 ♂♂ (AMNH_PBI 00312728–AMNH_PBI 00312737), 27 ♀♀ (AMNH_PBI 00312721–AMNH_PBI 00312724, AMNH_PBI 00312751–AMNH_PBI 00312766, AMNH_PBI 00312769–AMNH_PBI 00312771, AMNH_PBI 00312773–AMNH_PBI 00312776) (ZISP); 17 Jun 1937 – 18 Jun 1937, A. K. Lukyanovich, 2 ♀♀ (AMNH_PBI 00312767, AMNH_PBI 00312772) (ZISP); 17 Sep 1937 – 18 Sep 1937, A. K. Lukyanovich, 1 ♀ (AMNH_PBI 00312768) (ZISP), 1 ♂ (AMNH_PBI 00340288), 4 ♀♀ (AMNH_PBI 00340302–AMNH_PBI 00340305) (ZMUH). Taldyqorghan [= Taldykurgan], 45°N 78.36666°E, 23 May 1937, A. K. Lukyanovich, 6 ♀♀ (AMNH_PBI 00308477, AMNH_PBI 00308478, AMNH_PBI 00312717–AMNH_PBI 00312720), 4 ♂♂ (AMNH_PBI 00308483, AMNH_PBI 00312655–AMNH_PBI 00312657) (ZISP). **Karaganda Province:** Atasu [= Zhana-Arka], 48.68333°N 71.65°E, 18 Jul 1960, A. F. Emeljanov, 1 ♀ (AMNH_PBI 00312712) (ZISP). **South Kazakhstan Province:** Karasay, Dzhagan-ata, Kara-tau, 43.46666°N 69.51666°E, 27 May 1936 – 29 May 1936, A. K. Lukyanovich, 1 ♀ (AMNH_PBI 00311286) (ZISP). **West Kazakhstan Province:** Spartak on Bykovka River, 51.4°N 52.08333°E, 28 May 1949, K. G. Romadina, 1 ♀ (AMNH_PBI 00312714) (ZISP). **Zhambul Province:** Achi-Say, Teresakan river, Karatau Mts Ridge, 43.55417°N 68.88889°E, 01 Jun 1936, A. K. Lukyanovich, 2 ♀♀ (AMNH_PBI 00312710, AMNH_PBI 00312711) (ZISP). **RUSSIAN FEDERATION: Orenburg Province:** Nr Orenburg, 51.76666°N 55.1°E, 06 Jun 1924, A. I. Ivanov, 3 ♀♀ (AMNH_PBI 00312705–AMNH_PBI 00312707) (ZISP). **Volgograd Province:** Sarepta [= Krasnoarmeysk], 48.5°N 44.48333°E, V. Jakovlev coll., 2 ♀♀ (AMNH_PBI 00312700, AMNH_PBI 00312701), 4 ♂♂ (AMNH_PBI 00312651–AMNH_PBI 00312654) (ZISP). **SLOVAKIA:** Čenkov, 47.95°N 18.53333°E, 07 Jun 1960, Exc. M. N. Pragae, *Ephedra distachya* (Ephedraceae), 1 ♂ (AMNH_PBI 00340447), 1 ♀ (AMNH_PBI 00340448) (BMNH); 05 Jun 1965, Štys, 1 ♂ (AMNH_PBI 00340289), 5 ♀♀ (AMNH_PBI 00340295–AMNH_PBI 00340297, AMNH_PBI 00340293, AMNH_PBI 00340294) (ZMUH); 08 Jun 1965, M. Kocourek, 5 ♂♂ (AMNH_PBI 00337218–AMNH_PBI 00337222), 5 ♀♀ (AMNH_PBI 00337223–AMNH_PBI 00337227) (NMPC). Štúrovo, 47.8°N 18.7333°E, 18 Jun 1991, H. Günther, 1 ♂ (AMNH_PBI 00337217), 1 ♀ (AMNH_PBI 00337229) (NHMM). **TAJIKISTAN:** Between Kvak and Kondara, Valley of Varzab River, 38.83°N 68.83°E, 17 May 1937 – 18 May 1937, A. K. Lukyanovich, 7 ♀♀ (AMNH_PBI 00312744–AMNH_PBI 00312750) (ZISP); 08 Jun 1943, A. N. Kiritshenko, 2 larvae (AMNH_PBI 00312741, AMNH_PBI 00312742), 1 ♀ (AMNH_PBI 00312743) (ZISP). **TURKMENISTAN:** Repetek, 38.58333°N 63.18333°E, 17 Apr 1905 – 18 Apr 1905, V. Oshanin coll., 1 ♀ (AMNH_PBI 00312703) (ZISP); 29 Apr 1972, Kaplin, *Ephedra strobilacea* (Ephedraceae), 1 ♂ (AMNH_PBI 00312658) (ZISP); 04 May 1972, Kaplin, *Ephedra strobilacea* (Ephedraceae), 1 ♀ (AMNH_PBI 00312709) (ZISP). **UKRAINE: Crimea:** Feodosiya distr., Karadag, 45.18°N 35.32°E, 07 May 1927, E. Kuznetsova and V. Kuznetsov, 1 ♀ (AMNH_PBI 00312708) (ZISP). Kerch, 45.33333°N 36.45°E, 30 May 1915, A. N. Kiritshenko, 4 ♀♀ (AMNH_PBI 00312670–AMNH_PBI 00312672, AMNH_PBI 00312699) (ZISP); 14 May 1917, A. N. Kiritshenko, 3 ♀♀ (AMNH_PBI 00312662–AMNH_PBI 00312664), 1 ♂ (AMNH_PBI 00312633) (ZISP); 17 May 1917, A. N. Kiritshenko, 2 ♂♂ (AMNH_PBI 00308486, AMNH_PBI 00312648), 2 ♀♀ (AMNH_PBI 00312665, AMNH_PBI 00312666) (ZISP); 19 May 1917, A. N. Kiritshenko, 1 ♀ (AMNH_PBI 00312667) (ZISP); 21 May 1917, A. N. Kiritshenko, 1 ♂ (AMNH_PBI 00312649) (ZISP); 23 May 1918, A. N. Kiritshenko, 1 ♂ (AMNH_PBI 00312650), 2 ♀♀ (AMNH_PBI 00312668, AMNH_PBI 00312669) (ZISP). Katerlez [= Voykovo] nr Kerch', 45.373°N 36.428°E, 09 May 1908, A. N. Kiritshenko, 2 ♀♀ (AMNH_PBI 00312660, AMNH_PBI 00312661) (ZISP). 18 km NE of Voznesensk, Yuzhnyi Bug river, 47.694°N 31.489°E, 09 Jun 1921, A. N. Kiritshenko, 1 ♂ (AMNH_PBI 00312738) (ZISP). Berdyansk N of Azov Sea Coast, 46.75°N 36.8°E, 15 May 1939, Topchiev, 1 ♂ (AMNH_PBI 00312726), 1 ♀ (AMNH_PBI 00312740) (ZISP). Chongar, Sivash Lake, 46°N 34.5°E, 07 Jun 1940, A. K. Lukyanovich, 1 ♀ (AMNH_PBI 00308481), 2 ♂♂ (AMNH_PBI 00308482, AMNH_PBI 00312725) (ZISP). Dal'niye Makarty nr Berdyansk, 46.81666°N 36.63333°E, 22 May 1939, Nikolaev, 1 ♀ (AMNH_PBI 00312739) (ZISP). Arnautka [= Kamyshany] nr Kherson, 46.61666°N 32.48333°E, 18 May 1939, Nikolaev, 1 ♂ (AMNH_PBI 00312727) (ZISP). Kryzhanovka, NE of Odessa, 46.55°N 30.78333°E, 18 Jun 1924, E. Kiritshenko, 1 ♀ (AMNH_PBI 00312644) (ZISP). Odessa, Khadzhib Liman, 46.46666°N 30.71666°E, 15 May 1921,

A. N. Kiritshenko, 8 ♀♀ (AMNH_PBI 00308479, AMNH_PBI 00312634–AMNH_PBI 00312637, AMNH_PBI 00312640–AMNH_PBI 00312642), 6 ♂♂ (AMNH_PBI 00308484, AMNH_PBI 00312621–AMNH_PBI 00312625) (ZISP); 28 May 1922, A. N. Kiritshenko, 3 ♀♀ (AMNH_PBI 00312638, AMNH_PBI 00312639, AMNH_PBI 00312643), 1 ♂ (AMNH_PBI 00312626) (ZISP). Odessa, Kuyalnitskiy Liman, 46.55°N 30.73333°E, 24 May 1923, A. N. Kiritshenko, 1 ♂ (AMNH_PBI 00312627) (ZISP). Odessa, Luzanovka, 46.46666°N 30.71666°E, 02 May 1920, A. N. Kiritshenko, 3 ♂♂ (AMNH_PBI 00308485, AMNH_PBI 00312628, AMNH_PBI 00312629), 2 ♀♀ (AMNH_PBI 00312645, AMNH_PBI 00312646) (ZISP); 04 May 1920, A. N. Kiritshenko, 2 ♀♀ (AMNH_PBI 00308480, AMNH_PBI 00312647), 3 ♂♂ (AMNH_PBI 00312630–AMNH_PBI 00312632) (ZISP).

**Redescription.** ***Male*****:** Small to middle-sized, 3.7–4.5 mm. COLOURATION (Figs 12, 14): Varies from dirty yellowish to brown. Head: Always pale brown; clypeus in pale specimens with black longitudinal spot at base and two black lateral stripes extending from base to middle of clypeus; in dark specimens clypeus entirely black; frons with black, confluent stripes radiating from midline, entirely merged in two large spots in dark specimens; vertex with two black, not confluent spots, in dark specimens with dark brown minute spots; antenna dark brown to black; labium brown to dark brown, apex of segment IV black. Thorax: Pronotal collar in pale specimens dirty yellowish with darkened central part, in dark specimens entirely brown; anterior part of pronotum dirty yellowish; calli covered with largely confluent black spots or entirely black; disc entirely yellowish in pale specimens, brown with more or less darkened base in dark specimens, sometimes with pale brown stripe along midline and pale basal edging; in some dark specimens disc at base with black minute spots; mesonotum pale brown to brown; scutellum dirty yellowish in pale specimens, dark brown to black with more or less expressed pale midline in dark specimens; thoracic pleurites dirty yellowish, sometimes with darkened central part; propleural suture black. Hemelytron: Clavus, corium and cuneus usually uniformly coloured, dirty yellow in pale specimens, brown in dark specimens, rarely corium in dark specimens with dark brown minute spots. Legs: In pale specimens, femora dirty yellow to pale brown, with a series of minute, partly confluent dark brown spots running along posterior margin at base and apically extending to anterior margin; in dark specimens fore femur additionally with large stripe along fore margin, middle femur with two large and partly confluent stripes along fore and hind margins, and hind femur almost uniformly brown to dark brown, with pale apex. Abdomen: Uniformly dirty yellowish in pale specimens, with more or less darkened tergites in dark specimens. SURFACE AND VESTITURE: Smooth, disc finely rugose in pale specimens and strongly rugose in dark specimens, with very fine punctures; scutellum typically with transverse wrinkles; vestiture composed of intermixed simple setae and silvery scales; simple setae uniformly pale in pale specimens, usually somewhat darker on hemelytron of dark specimens. STRUCTURE: Head: Vertex 2.4–2.8 × as wide as eye; antennal segment I 0.3–0.4 × as long as width of head; antennal segment II 1.1–1.5 × as long as width of head and 0.9–1.2 × as long as width of pronotum. Thorax: Pronotum 1.6–1.8 × as wide as long and 1.1–1.3 × as wide as head. GENITALIA: Genital capsule with large tooth on left side of genital opening (Figs 31, 34–36); sensory lobe of left paramere thick, curved and serrate (Figs 47–48), caudal process apically dentate (Fig. 48) or tooth-like, without denticles and with large claw-shaped additional process at base (Fig. 47); right paramere as in Fig. 38; left spicule of aedeagus 0.5 × as long as right one, with serrate lateral margin; both branches of right spicule long and thin, with apical serration (Fig. 52).

***Female*:** Small to middle-sized, 3.6–4.7 mm. COLOURATION (Figs 13, 15), SURFACE AND VESTITURE: As in male. STRUCTURE: Slightly larger than male, with larger interocular distance, vertex 3.0–3.6 × as wide as eye; antennal segment I 0.3 × as long as width of head; antennal segment II 0.9–1.1 × as long as width of head and 0.8–1.0 × as long as width of pronotum; pronotum 1.7–2.0 × as wide as long and 1.0–1.2 × as wide as head; abdomen larger and usually partly extending beyond apex of membrane; membrane reaching at least base of segment IX. GENITALIA: First gonapophysis as in Fig. 63; second gonapophysis as in Fig. 62.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots on dorsum absent; two black spots on vertex not confluent (Figs 12–15); simple setae on dorsum pale, rarely somewhat darkened on hemelytron; genital capsule with large tooth on left side of genital opening (Figs 31, 34–36); sensory lobe of left paramere thick, curved and serrate (Figs 47–48), caudal process of variable shape (Figs 47, 48); left spicule of aedeagus 0.5 × as long as right one, with serrate lateral margin; both branches of right spicule long and thin, with apical serration (Fig. 52). Most similar to *H. lopezcoloni* in the general colouration of dark forms and length of the antennal segment I, but differs in the shape of spicules of aedeagus and curved sensory lobe of left paramere.

**Host associations and bionomics.** According to Hoberlandt (1963) and Putshkov & Putshkov (1983), the host plants of this species are *Ephedra distachya* L., *E. strobilacea* Bunge, and *E. intermedia* Schrenk & C. A. Mey. The bionomics of *H. notaticeps* was carefully documented in the Repetek Nature Reserve, Turkmenistan (Kaplin 1993). The species was shown to be univoltine, larvae were collected from the end of March until the middle of May, adults – from April until May. According to Hoberlandt (1963), in Central European conditions, adults occur from the middle of May until June.

**Distribution.** Widely distributed in the steppe zone and xeric habitats of Palaearctic (Fig. 18), in Slovakia and Hungary (Hoberlandt 1963), in southern Ukraine (Hoberlandt 1963), in Volgograd (Reuter 1876, Kiritshenko 1951), Saratov (Kiritshenko 1951) and Orenburg provinces (Kiritshenko 1951) of Russia, in Georgia (Kiritshenko 1918), Iran (Linnavuori & Modarres 1999), Kazakhstan (Hoberlandt 1963), Tadzhikistan (Kiritshenko 1951), Turkmenistan (Putshkov & Putshkov 1983), and in northern China (Inner Mongolia: Tongliao and Hinggan) (Qi et al. 1995).

**Discussion.** The species shows considerable geographic variability in colouration and the structure of male genitalia. All specimens from the western part of its distributional range, particularly from Hungary and Slovakia are dark coloured, with largely confluent black stripes on the frons, and entirely black calli (Figs 14–15). All specimens from Kazakhstan are pale coloured, with non-confluent radiating stripes on the frons and calli with confluent dark spots but not entirely black (Figs 12–13). Both dark and pale morphs as well as specimens with intermediate colouration were found in the central part of the distributional area, i.e. in Ukraine and Volgograd province of Russia, with most specimens including the lectotype being pale.

In terms of male genitalia, the western populations of *H. notaticeps* differ somewhat in having a blunt tubercle on the genital capsule (Fig. 36), similar to that of *H. stehliki*, and a single, apically serrate caudal process of the left paramere (Fig. 48). In specimens from

Kazakhstan the large tooth of the genital capsule is spine-like (Fig. 34) while the left paramere is equipped with an additional claw-shaped process at the base of the edentate caudal process (Fig. 47). However, in both pale and dark specimens from southern Russia and Ukraine the shape of the large tooth of the genital capsule is somewhat intermediate (Fig. 35), while the left paramere bears a single caudal process. No differences in the aedeagus were revealed between western and eastern populations of *H. notaticeps.*

### *Hyoidea stehliki* Baena & Günther, 2001

(Figs 16–17, 19, 32, 39, 44, 56)

*Hyoidea stehliki* Baena & Günther, 2001: 86 (original description)
*Hyoidea stehliki*: Günther et al. (2007: 172) (record)

**Type locality.** Spain, Almeria Prov., Bédar.
**Material examined. SPAIN: Valenciana:** [Sierra de] Bédar, Prov. Almeria, 37.18333°N 1.98333°W, 100 m, 27 Apr 2001, H. Günther, 2 ♂♂ (AMNH_PBI 00337182, AMNH_PBI 00337183) (NHMM), 2 ♂♂ (AMNH_PBI 00334229, AMNH_PBI 00337441), 2 ♀♀ (AMNH_PBI 00334230, AMNH_PBI 00337442) (ZISP), 1 ♂ (AMNH_PBI 00340290), 1 ♀ (AMNH_PBI 00340291) (ZMUH).

**Redescription.** ***Male*:** Relatively large, 5.0–5.6 mm. COLOURATION (Fig. 16): Dorsum dirty yellowish to pale brown. Head: Clypeus with black longitudinal spot at base and two black lateral stripes extending from base to middle of clypeus; mandibular plate entirely pale, maxillary plate darkened at apex; frons with black, not confluent stripes radiating from midline; vertex with two black, not confluent spots, rarely also with brown minute spots; antenna dark brown to black, sometimes antennal segment I paler than others; labium brown, apex of segment IV black. Thorax: Pronotal collar darkened medially; calli covered with largely confluent black spots; disc entirely pale brown or pale brown apically and brown basally; scutellum pale brown to brown with pale brown midline, and sometimes with brown minute spots; thoracic pleurites dirty yellowish. Hemelytron: Clavus, corium and cuneus uniformly pale brown. Legs: Pale-brown with reddish tinge, femora with a series of minute, partly confluent dark brown spots running along posterior margin at base and apically extending to anterior margin. Abdomen: Dorsally brown, ventrally pale brown. SURFACE AND VESTITURE: Smooth, disc finely rugose, with shallow, sometimes indistinct, usually darkened punctures; scutellum with transverse wrinkles. Vestiture composed of intermixed simple setae and silvery scales; simple setae usually black and extremely short everywhere on dorsum, rarely pale on head. STRUCTURE: Head: Vertex 2.2–2.6 × as wide as eye; antennal segment I 0.4–0.5 × as long as width of head; antennal segment II 1.5–1.6 × as long as width of head and 1.1–1.2 × as long as width of pronotum. Thorax: Pronotum 1.6–1.8 × as wide as long and 1.3–1.4 × as wide as head; disc extremely convex. GENITALIA: Genital capsule with large tooth on left side of genital opening (Fig. 32); sensory lobe of left paramere flattened, apically widened and serrate, caudal process short, thick and serrate (Fig. 44); right paramere as in Fig. 39; left spicule of aedeagus long and thin, slightly curved, with denticles on the top; one of the branches of right spicule long and thin with apical serration and basal tooth, another branch broad and curved, with serrate apical margin (Fig. 56).

***Female*:** Relatively large, 5.2 mm. COLOURATION (Fig. 17): as in male, but dark minute spots on vertex usually better expressed. SURFACE AND VESTITURE: As in male. STRUCTURE: Almost of the same size as male, with larger interocular distance, vertex 2.7–2.9 × as wide as eye; antennal segment I 0.4 × as long as width of head; antennal segment II

Table 1. Measurements of species of *Hyoidea* Reuter, 1876. Abbreviations: TL – total length; Cl-Cu – length from clypeus to cuneus; PrL – pronotal length; HW – head width; PrAW – pronotal apex width; PrBW – pronotal base width; AS1L – length of antennal segment I; AS1W – width of AS1; AS2L – length of AS2; IOcDi – interocular distance.

| | | TL | Cl-Cu | PrL | HW | PrAW | PrBW | AS1L | AS1W | AS2L | IOcDi |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Hyoidea hannothiauxi*** | | | | | | | | | | | |
| Male | | 4.10 | 3.40 | 0.75 | 0.98 | 0.80 | 1.16 | 0.53 | 0.15 | – | 0.50 |
| ***Hyoidea hermione*** | | | | | | | | | | | |
| Males N = 2 | Minimum | 3.95 | 3.40 | 0.66 | 0.99 | 0.78 | 1.11 | 0.39 | 0.10 | 1.45 | 0.53 |
| | Maximum | 4.05 | 3.55 | 0.73 | 0.99 | 0.81 | 1.23 | 0.40 | 0.11 | 1.49 | 0.58 |
| Females N = 3 | Mean | 3.88 | 3.63 | 0.76 | 1.16 | 0.98 | 1.34 | 0.41 | 0.13 | 1.32 | 0.68 |
| | Minimum | 3.80 | 3.45 | 0.73 | 1.13 | 0.95 | 1.23 | 0.40 | 0.13 | 1.28 | 0.65 |
| | Maximum | 3.95 | 4.00 | 0.79 | 1.20 | 1.03 | 1.48 | 0.43 | 0.14 | 1.38 | 0.73 |
| ***Hyoidea horvathi*** | | | | | | | | | | | |
| Male | | 4.46 | 3.76 | 0.70 | 1.06 | 0.84 | 1.20 | 0.40 | 0.11 | 1.48 | 0.58 |
| Females N = 5 | Mean | 4.55 | 3.97 | 0.74 | 1.20 | – | 1.31 | 0.43 | – | 1.42 | 0.72 |
| | Standard Deviation | 0.28 | 0.17 | 0.02 | 0.03 | – | 0.03 | 0.01 | – | 0.05 | 0.02 |
| | Range | 0.68 | 0.48 | 0.06 | 0.06 | – | 0.06 | 0.02 | – | 0.12 | 0.04 |
| | Minimum | 4.22 | 3.72 | 0.72 | 1.16 | 1.03 | 1.26 | 0.42 | 0.14 | 1.34 | 0.70 |
| | Maximum | 4.90 | 4.20 | 0.78 | 1.22 | 1.03 | 1.32 | 0.44 | 0.14 | 1.46 | 0.74 |
| ***Hyoidea kerzhneri*** | | | | | | | | | | | |
| Males N = 5 | Mean | 5.19 | 4.24 | 0.76 | 1.01 | 0.82 | 1.34 | 0.43 | 0.10 | 1.52 | 0.54 |
| | Standard Deviation | 0.24 | 0.10 | 0.04 | 0.03 | 0.02 | 0.04 | 0.01 | 0.01 | 0.09 | 0.02 |
| | Range | 0.67 | 0.23 | 0.10 | 0.07 | 0.04 | 0.10 | 0.02 | 0.01 | 0.22 | 0.04 |
| | Minimum | 4.88 | 4.18 | 0.70 | 0.97 | 0.80 | 1.29 | 0.41 | 0.10 | 1.41 | 0.52 |
| | Maximum | 5.55 | 4.41 | 0.80 | 1.04 | 0.84 | 1.38 | 0.44 | 0.11 | 1.62 | 0.56 |
| Females N = 4 | Mean | 4.28 | 3.68 | 0.75 | 1.09 | 0.92 | 1.31 | 0.40 | 0.13 | 1.27 | 0.65 |
| | Standard Deviation | 0.17 | 0.31 | 0.02 | 0.03 | 0.03 | 0.02 | 0.01 | 0.01 | 0.05 | 0.02 |
| | Range | 0.38 | 0.70 | 0.05 | 0.07 | 0.04 | 0.05 | 0.02 | 0.01 | 0.12 | 0.05 |
| | Minimum | 4.15 | 3.25 | 0.73 | 1.04 | 0.90 | 1.29 | 0.39 | 0.13 | 1.21 | 0.63 |
| | Maximum | 4.53 | 3.95 | 0.78 | 1.12 | 0.94 | 1.33 | 0.41 | 0.14 | 1.33 | 0.68 |
| ***Hyoidea lindbergi*** | | | | | | | | | | | |
| Males N = 6 | Mean | 4.59 | 3.92 | 0.79 | 1.02 | 0.81 | 1.30 | 0.42 | 0.11 | 1.60 | 0.54 |
| | Standard Deviation | 0.19 | 0.11 | 0.04 | 0.03 | 0.04 | 0.04 | 0.01 | 0.01 | 0.06 | 0.04 |
| | Range | 0.52 | 0.34 | 0.09 | 0.07 | 0.10 | 0.08 | 0.03 | 0.01 | 0.17 | 0.12 |
| | Minimum | 4.30 | 3.72 | 0.75 | 0.99 | 0.75 | 1.26 | 0.41 | 0.10 | 1.53 | 0.47 |
| | Maximum | 4.82 | 4.06 | 0.84 | 1.06 | 0.85 | 1.34 | 0.44 | 0.11 | 1.70 | 0.59 |
| Females N = 7 | Mean | 4.62 | 4.08 | 0.81 | 1.17 | 0.96 | 1.42 | 0.43 | – | 1.45 | 0.70 |
| | Standard Deviation | 0.39 | 0.18 | 0.05 | 0.07 | 0.05 | 0.04 | 0.02 | – | 0.05 | 0.03 |
| | Range | 0.92 | 0.55 | 0.12 | 0.19 | 0.13 | 0.12 | 0.05 | – | 0.12 | 0.10 |
| | Minimum | 4.20 | 3.75 | 0.73 | 1.02 | 0.90 | 1.36 | 0.41 | 0.13 | 1.38 | 0.63 |
| | Maximum | 5.12 | 4.30 | 0.85 | 1.21 | 1.03 | 1.48 | 0.46 | 0.13 | 1.50 | 0.73 |
| ***Hyoidea lopezcoloni*** | | | | | | | | | | | |
| Male | | 3.85 | 3.25 | 0.63 | 0.98 | 0.73 | 1.08 | 0.31 | 0.09 | 1.13 | 0.55 |
| Female | | 4.15 | 3.60 | 0.70 | 1.05 | 0.86 | 1.24 | 0.28 | 0.10 | 1.09 | 0.65 |
| ***Hyoidea notaticeps*** | | | | | | | | | | | |
| Males N = 10 | Mean | 4.13 | 3.54 | 0.69 | 0.97 | 0.81 | 1.15 | 0.34 | 0.09 | 1.22 | 0.55 |
| | Standard Deviation | 0.25 | 0.21 | 0.03 | 0.03 | 0.03 | 0.05 | 0.02 | 0.01 | 0.11 | 0.02 |
| | Range | 0.83 | 0.72 | 0.11 | 0.10 | 0.09 | 0.17 | 0.05 | 0.01 | 0.38 | 0.06 |
| | Minimum | 3.70 | 3.14 | 0.62 | 0.92 | 0.76 | 1.04 | 0.32 | 0.09 | 1.02 | 0.52 |
| | Maximum | 4.53 | 3.86 | 0.73 | 1.02 | 0.85 | 1.21 | 0.36 | 0.10 | 1.40 | 0.58 |
| Females N = 9 | Mean | 3.96 | 3.54 | 0.68 | 1.08 | 0.94 | 1.24 | 0.33 | 0.11 | 1.12 | 0.67 |
| | Standard Deviation | 0.49 | 0.36 | 0.06 | 0.06 | 0.03 | 0.09 | 0.02 | 0.01 | 0.07 | 0.05 |
| | Range | 1.53 | 1.15 | 0.16 | 0.19 | 0.03 | 0.30 | 0.06 | 0.01 | 0.21 | 0.15 |
| | Minimum | 3.00 | 2.80 | 0.58 | 0.97 | 0.90 | 1.06 | 0.30 | 0.10 | 1.01 | 0.58 |
| | Maximum | 4.53 | 3.95 | 0.74 | 1.16 | 0.96 | 1.36 | 0.36 | 0.11 | 1.22 | 0.73 |
| ***Hyoidea stehliki*** | | | | | | | | | | | |
| Males N = 5 | Mean | 5.30 | 4.39 | 0.88 | 1.09 | 0.93 | 1.45 | 0.47 | 0.12 | 1.66 | 0.58 |
| | Standard Deviation | 0.21 | 0.28 | 0.06 | 0.02 | 0.02 | 0.06 | 0.04 | 0.01 | 0.06 | 0.03 |
| | Range | 0.58 | 0.70 | 0.17 | 0.05 | 0.04 | 0.15 | 0.10 | 0.01 | 0.15 | 0.07 |
| | Minimum | 5.00 | 3.95 | 0.80 | 1.07 | 0.91 | 1.41 | 0.44 | 0.11 | 1.58 | 0.56 |
| | Maximum | 5.58 | 4.65 | 0.97 | 1.12 | 0.95 | 1.55 | 0.53 | 0.13 | 1.72 | 0.63 |
| Females N = 3 | Mean | 4.70 | 4.31 | 0.87 | 1.15 | 0.98 | 1.46 | 0.48 | 0.14 | 1.54 | 0.66 |
| | Minimum | 4.19 | 4.19 | 0.85 | 1.12 | 0.95 | 1.41 | 0.46 | 0.14 | 1.48 | 0.65 |
| | Maximum | 5.12 | 4.53 | 0.90 | 1.19 | 1.01 | 1.50 | 0.51 | 0.14 | 1.62 | 0.68 |

1.3–1.4 × as long as width of head and 1.0–1.1 × as long as width of pronotum; pronotum 1.7 × as wide as long and 1.2–1.3 × as wide as head; abdomen larger and usually partly extending beyond apex of membrane; membrane reaching at least base of segment IX.

**Differential diagnosis.** Distinguished by the following combination of characters: dark minute spots on pronotum and hemelytron absent; two black spots on vertex not confluent (Fig. 16–17); vestiture on dorsum composed of silvery scales and very short simple setae, uniformly dark everywhere except head; genital capsule with large tooth on left side of genital opening (Fig. 32); sensory lobe of left paramere flattened, apically widened and serrate, caudal process short, thick and serrate (Fig. 44); left spicule of aedeagus long and thin, slightly curved, with denticles on the top; one of the branches of right spicule long and thin with apical serration and basal tooth, another branch broad and curved, with serrate apical margin (Fig. 56). Clearly differs from all other species in combination of large body size and presence of small black setae on thorax and hemelytron in absence of dark minute spots; male specimens also clearly differs in peculiar shape of vesical spicules.

**Host associations.** Baena & Günther (2001) and Günther et al. (2007) record the host plant as *Ephedra fragilis* Desf.

**Distribution.** So far known exclusively from the type locality, Almeria Prov., Spain (Fig. 19) (Baena & Günther 2001, Günther et al. 2007).

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## Appendix.

USI numbers of figured specimens:

| Figure | Species | Sex | USI number |
|---|---|---|---|
| 1, 33, 40, 49 | *Hyoidea hannothiauxi* | male | 337189 |
| 2, 53 | *Hyoidea hermione* | male | 312777 |
| 42 | *Hyoidea hermione* | male | 337187 |
| 3 | *Hyoidea hermione* | female | 312778 |
| 57, 59, 61 | *Hyoidea hermione* | female | 312779 |
| 4, 43, 50 | *Hyoidea horvathi* | male | 340440 |
| 5 | *Hyoidea horvathi* | female | 340430 |
| 6 | *Hyoidea kerzhneri* | male | 312257 |
| 45 | *Hyoidea kerzhneri* | male | 312659 |
| 54 | *Hyoidea kerzhneri* | male | 311261 |
| 7 | *Hyoidea kerzhneri* | female | 311289 |
| 21–26 | *Hyoidea kerzhneri* | female | 311276 |
| 58, 60, 64–65 | *Hyoidea kerzhneri* | female | 311277 |
| 8, 30, 37, 46, 55 | *Hyoidea lindbergi* | male | 311349 |
| 28–29 | *Hyoidea lindbergi* | male | 311348 |
| 9 | *Hyoidea lindbergi* | female | 311354 |
| 66–67 | *Hyoidea lindbergi* | female | 311357 |
| 10, 41, 51 | *Hyoidea lopezcoloni* | male | 337184 |
| 11 | *Hyoidea lopezcoloni* | female | 337185 |
| 12 | *Hyoidea notaticeps* | male | 312732 |
| 14 | *Hyoidea notaticeps* | male | 337222 |
| 31, 34, 38, 47, 52 | *Hyoidea notaticeps* | male | 312729 |
| 35 | *Hyoidea notaticeps* | male | 312735 |
| 36, 48 | *Hyoidea notaticeps* | male | 337220 |
| 13 | *Hyoidea notaticeps* | female | 312722 |
| 15 | *Hyoidea notaticeps* | female | 337225 |
| 20, 27 | *Hyoidea notaticeps* | female | 312721 |
| 62–63 | *Hyoidea notaticeps* | female | 312723 |
| 16, 32, 39, 44, 56 | *Hyoidea stehliki* | male | 334229 |
| 17 | *Hyoidea stehliki* | female | 337442 |