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PHYLOGENY OF THE WORLD SPECIES OF *MUSTHA* AMYOT AND SERVILLE (HEMIPTERA: PENTATOMIDAE: PENTATOMINAE: HALYINI) BASED ON MORPHOLOGICAL CHARACTERS

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ABSTRACT

A phylogenetic analysis of all 10 species of the Palaearctic genus *Mustha* Amyot and Serville is presented here, together with a key. Thirty morphological characters were analyzed using parsimony, including characters of the internal and external male and female genitalia. Using the genus *Orthoschizops* as an outgroup, only a single most-parsimonious shortest tree resulted. Two species (*izmirensis* and *serratta*) were plesiomorphic in the tree. Although only with weak bootstrap support, three distinct clades were evident. A relatively plesiomorphic clade consisted of *baranovi, longispinis, gigantea* and *vicina*; the second contained two species, *incana* and *morgani*; and the third clade also contained two species, *spinosula* and *spinosus*.

Key words: Phylogeny *Mustha*, Halyini, Pentatomidae

INTRODUCTION

Mustha Amyot and Serville (1843) is one of the richest Palaearctic genera of the tribe Halyini, with ten species described: *baranovi* Kiritshenko 1952, *M. gigantea* Horvath 1906, *M. incana* Stål 1876, , *M. izmirensis* Memon and Ahmad 2009, , *M. longispinis* Reuter 1890, , *M. morgani* Horvath 1906, , *M. serrata* Fabricius 1974, , *M. spinosula* Lefebvre 1837, , *M. spinosus* Ahmad and Kamaluddin 1984 and, *M. vicina* Hoberlandt 1995. The genus is widely distributed throughout the world, in Pakistan, Afghanistan, India, Tajikistan, Iran, Egypt, Syria, Israel, Jordan, Turkey, Eastern Europe and South Africa. Of the ten species, six had been described by 1952: the three most recently described species are: *spinosus* (Abasi and Ahmad 1971) from Pakistan, *vicina* Hoberlandt 1995 from Iran and *izmirensis* Memon and Ahmad 2009 from Turkey. *M. spinosus* was initially misidentified and placed in the genus *Orthoschizops* Spinola (1850) by Abbasi and Ahmad (1971), based only on a female specimen. Ahmad and Kamaluddin (1984) transferred *O. spinosus* to the genus *Mustha* without mentioning that it was the first record from Pakistan of either genus. Hoberlandt (1995) synonymized *spinosus* with *gigantea* Horvath, but here we have maintained its independent status, following Ahmad and Kamaluddin (1984): they described this species on the basis of both male and female specimens, including describing and illustrating the male genitalia. *M. gigantea* is based only on female specimens. Many *Mustha* species resemble one another in external characters, and we do not consider this an adequate basis for synonymy without information on the genitalia. Abbasi and Ahmad (1971) did describe the external genital plate of the female, but this is almost identical in all *Mustha* species. Rider (2006) followed Hoberlandt (1995) by including only eight species in his catalogue, excluding *spinosus.*

Despite having such a wide distribution, most species of *Mustha* vary little in external characters (e.g. colouration, shape and length of antennal segments, length and width of head and pronotum), even though many species have been described only on the basis of external character, particularly by older authors (Lefebvre 1837, Fabricius 1874, Stål 1876, Reuter 1890, Horvath 1906, Kiritshenko 1952). Some contemporary workers did some work on the internal and external male genitalia in establishing their new species, but while revising the genus they ignored female external and internal genitalia: for example, Hoberlandt (1995) and Ahmad and Kamaluddin (1984), who gave descriptions of the male genitalia of *spinosula* and *spinosus*, but mentioned female specimens including the holotype and paratype in the material they examined. Memon and Ahmad (2008) were the first authors to describe and illustrate the internal female genitalia.

While revising the Halyini, Hoberlandt (1995) recorded six *Mustha* species (*serrata, gigantea, baranoui, spinosula, morgani* and *incana*) but described only his new species *Mustha vicina* from Faras (S. Iran) and redescribed *M. longispinis* along with a detailed synonymy. In the description he described the male genitalia, but nothing about those of the female. He keyed out seven species of *Mustha*, and suggested the

synonymy of *M. spinosus* with *gigantea*. In drawings he showed only the outer margins of the head, pronotum and abdomen of three species (*vicinia, serrata* and *longispinis*), while providing illustrations of the male pygophore and paramere only of his new species *vicina*. This was the first detailed work on the genus *Mustha*.

In the Halyini, *Mustha* is known for a set of unique characters, i.e. the presence of very distinct spines on the lateral margins of the entire body (head, pronotum, abdomen), and also on the posterior margin of the eighth paratergite of the female genitalia. Species of *Phricodus* and *Orthoschizops* also have dentition on the head and pronotum, but none has spines on the connexiva and the eighth paratergite, although *Phricodus* species have a single small spine in the middle of the eighth paratergite.

Taxonomic and systematic work on the genus by various workers in the last one hundred years has included and/or transferred many species, but these studies were mostly regional or country-based. Phylogenetic work is lacking. Furthermore, no-one has described the internal female genitalia except Memon and Ahmad (2008) in their new species *M. izmirensis*. They only described and illustrated the spermathecal bulb, while not describing the external terminalia because these were damaged in the paratype. Although Memon and Ahmad (2008) did estimate the phylogeny of nine species and gave a key to these nine species, the phylogeny was not numerically based, and they ignored *M. spinosus* in the key even though it was described from Pakistan.

The goal of the present study is to estimate the phylogenetic relationship of all ten known species of the genus *Mustha* using adult morphological characters, including the male and female genitalia. Characters were extracted from the literature and by observation of material, including the holotype and paratype of the species.

MATERIALS AND METHODS

All known species of the genus *Mustha* were included: *baranovi* Kiritshenko 1952, *gigantea* Horvath 1906, *incana* Stål 1876, *izmirensis* Memon and Ahmad 2009, *longispinis* Reuter 1890, *morgani* Horvath 1906, *serrata* Fabricius 1974, *spinosula* Lefebvre 1837 and *vicina* Hoberlandt 1995. We examined the phylogenetic relationships among these species using adult morphological characters, including male and female genitalia. The characters were extracted from the literature and by observation of material, including the holotype and paratype of all taxa. Literature data were essential in some cases: for example, *baranovi*, *longispinis* and *morgani* were described by old authors and then catalogued or keyed by current authors (e.g. Hoberlandt 1995, Rider 2006). We used both presence/absence coding and true multistate characters, the latter because of the structural diversity in some external morphological characters and particularly in male genitalia (usual in most halyine species). In total 30 characters were used (Table 1). As far as is known, most are constant among individuals within species. In the data matrix (Table 1), *baranovi*, *longispinis*, *serrata* and *morgani* have missing data for twelve male and female genital characters, *gigantea* for seven male genital and *spinosus* for three female genital characters.

The genus *Orthoschizops* was chosen as the outgroup: this genus has dentition on the anterior margin of the head, distinct dentition on the entire lateral margin of the pronotum (although few in comparison to *Mustha*), the humeral angles are broad and spinose (usually with two spines) and to some extent there is also a resemblance in the male pygophore. *Mustha* is closer to *Orthoschizops* than *Phricodus* in having five-segmented antennae, the 1st antennal segment is distinctly shorter than the head apex, the second is a little shorter or longer than the third, the labium reaches or exceeds the level of the hind coxae, and the female spermathecal bulb is with processes. In an analysis of many of the genera of Halyini (Memon et al., 2011), *Orthoschizops* was placed very close to *Mustha*.

The shortest tree was found with Paup version 4.0 (Swofford, 2003) under the parsimony criterion, using heuristic search with the default settings; all character states were treated as unordered. There was only one single most-parsimonious tree; we used the bootstrap command on this tree to assess confidence in each branch.

RESULTS

Cladogram: The single most parsimonious tree resulting from the data is shown in Fig 1. The only branch with appreciable bootstrap support is that leading to node 2 (see Fig 1), perhaps because only 12 characters were parsimony informative. The character-state changes of this tree are listed in Table 2.

With *Orthoschizops* as an outgroup, *izmirensis* is placed closest to it, and is clearly very different from the other species; *serrata* is also placed in a fairly isolated position. Other recognizable groups of species are the *gigantea* group (*baranovi*, *gigantea*, *vicina* and *longispinis*), the *incana* group (*incana* + *morgani*) and the *spinosula* group (*spinosula* + *spinosus*).

Characters: In total 30 characters were defined and scored (Table 1); 18 were parsimony-uninformative but are included because they are mostly male and female genital characters important as diagnostic characters for the species. Character state 0 in all cases is the state scored for *Orthoschizops*.

1. *Head and pronotum colour*: (0) ochraceous, punctures reddish brown in the form of light and dark stripes, clypeus pale; (1) unicoloured

black/blackish-brown, punctures black, thick, with a small ochraceous fascia on posterior margin; (2) brown, with dark-brown punctures.

The colour of the head is almost the same in all *Mustha* species (1) except *gigantea* which is a bit different in this trait (2).

2 *Colour of hemelytra*: (0) ochraceous, with reddish-brown punctures; (1) black or dark-brown, with very few indistinct ochraceous spots; (2) reddish-brown with many scattered ochraceous spots; (3) yellow; (4) yellowish-brown with light-brown punctures; (5) light-brown with orange-ish apical margin; (6) corium reddish-brown with whitish hair.

In *Mustha* species, the hemelytra is the only body part which has variation in the colour pattern: the group of four genera, *baranovi*, *izmirensis*, *vicina* and *serrata* have state (1); *spinosula* and *spinosus* with state (2); *longispinis* (3); *gigantea* (4); *incana* (5); *morgani* (6)

3 *Colour of scutellum*: (0) yellowish ochraceous, punctures reddish, light and dark stripes, apical lobe lighter, with a few scattered spots; (1) black or dark-brown, apical margin ochraceous; (2) light-brown with dark-brown punctures, with a very small central ochraceous fascia at the base.

Like the head and pronotum, the colour of the scutellum is dark and looks the same in almost all species (1), but *gigantea* has a different pattern, light-brown with dark-brown punctures, and a very small central ochraceous fascia at the base (2)

4 *Colour of connexiva:* (0) brownish; (1) dark-brown or black; (2) black with exterior margin along whole length yellow.

The connexiva is unicoloured and looks the same in all *Mustha* species (1) apart from *longispinis*, the only species in which the connexiva has a yellow exterior margin (2)

5 *Shape of head*. (Fig. 3): (0) three-quarters of head only very slightly narrowed, nearly parallel-sided; (1) parallel-sided on posterior part, anterior part gradually tapering upward; (2) gradually tapering upward along whole length; (3) sub-triangular, conspicuously narrowed along whole length; (4) head sharply narrowed towards apex, triangular in shape.

The shape of the head is almost rectangular in *vicina* and *serrata* (0) but in *serrata* the apex is sub-acute rather than broad as in *vicina* (see Fig. 3); most *Mustha* species are either state 1 or 2, with *Orthoschizops* having state 1 ; *gigantea* and *longispinis* (3); *incana* (4).

6 *Ratio of head length and width*: (0) slightly longer than broad; (1) distinctly longer than broad.

In almost all species of *Mustha*, the length of the head is slightly longer than wide (0) except *gigantea*, which has head distinctly longer than wide (1), sharing this trait with the outgroup *Orthoschizops* and many other halyine genera (1).

7 *Shape of lateral margins of head*: (Fig. 3) (0) straight; (1) moderately round; (2) laterally slightly elevated.

Most of the species have state (0); in group of three species, *baranovi*, *gigantea*, and *longispinis*, it is modified (1); and in *vicina* this state is more modified (2).

8 *Shape of dentition on lateral margin of head:* (Fig. 3) (0) distinct/ indistinct small dentine may or may not present only on anterior part of head; (1) large, triangular, distinct dentine present only on anterior part; (2) small dentine on entire margin; (3) entirely armed, usually with long or short spines.

This trait is diagnostic and constant in all *Mustha* species, but with variation in number and shape: it distinguishes *Mustha* from almost all other halyine genera and species. Among *Mustha* species, *vicina* is the only one with few denticles only on the anterior part (1); in *serrata* it is little more modified (2); but all remaining species have very well developed large and/or small spines on the entire lateral margin (3).

9 *Number of teeth on lateral margins of head:* (Fig. 3) (0) 3-4 distinct or indistinct teeth on anterior part of head; (1) long distinct denticles on anterior part; (2) entirely finely irregularly dentate; (3) entirely armed with 7-8 distinct upwardly directed spines; (4) entirely armed with 10 or more distinct upwardly directed spines.

The presence of denticles on the lateral margin of the head is a constant for all species, but their number is variable: *vicina* has only a few (1); in *serrata* they are small, but on the entire lateral margins (2); of the remaining eight species, *baranovi*, *longspinis*, *spinosula*, *izmirensis* and *spinosus* have seven to eight denticles (3); but *gigantea*, *longispinis* and *morgani* have greater numbers with more than ten spines (4).

10 *Width between paraclypeal lobes*: (fig. 3): (0) apical part widely separated from each other; (1) entirely enclosing clypeus.

This character divides *Mustha* species in two groups, *spinosula* and *izmirensis* with state (0); all remaining species with state (1).

11 *Ratio of length and width of pronotum*: (0) twice as broad as long; (1) transverse, not more than 2.3 times as broad as long; (2) very broad, always more than 2.9 times as broad as long. The pronotum length-width ratio is almost constant in all species (1) except *longispinis* (2).

12 *Shape of lateral margins of pronotum*: (Fig. 4 A-E) (0) entirely armed, but with few long and some small denticles; (1) usually armed with moderate-to-long spines.

The presence of spines on the lateral margin of the pronotum is constant and a distinguishing character of the genus *Mustha*, separating it from other genera of Halyini (1). Two other genera, the outgroup *Orthoschizops* and *Phricodus*, share this trait with *Mustha*, but in comparison to *Orthoschizops*, all *Mustha* species have very modified spines on the lateral margins.

13 *Shape and number of teeth of lateral margins of pronotum*: (Fig.4 A-E) (0) usually 4-6 long denticles irregularly arranged, with gaps, and a few small denticles in between; (1) with 10- 11 spines of medium size; (2) with 12 irregularly arranged spines; (3) with 13-14 irregularly arranged spines; (4) 15 long acute spines of almost equal size; (5) 15-16 broadly triangular spines of unequal size; (6) with 19 mostly long, acute spines; (7) 21-22 small and unequal spines.

The shape and number of pronotal spines is variable among species: *vicina* (1); *baranovi* (2); *gigantea* (3); *longispinis* (4); a group of four species (*morgani, spinosula, spinosus* and *serrata*) with state 5; *izimirensis* (6); and *incana* with the largest number of spines of unequal size (7).

14 *Shape of humeral angles*: (Fig.4 A-E) (0)) less thick and smooth, entirely spinose (1) broad, thick, a little elevated, entirely spinose; (2) distinctly produced laterally, more or less elevated upward, usually with two dentine, apical margin straight or concave.

This trait is constant in most species (0); but there is a group of three species (*gigantea*, *vicina* and *spinosus*) with state (1).

15 *Shape of lateral margins of corium*: (Fig. 4F-J) (0) sinuate; (1) with 3-6 short and long acute spines

This state is constant in all species with little variation in shape and size (1).

16 *Shape of lateral margins of abdomen*: (Fig. 4F-J) (0) sinuate; (1) armed with distinct dentine / spines

The presence of spines on the lateral margin of the abdomen is constant in all species, and is the most diagnostic character of *Mustha* within the Halyini.

17 *Shape, size and number of spines on each connexivum*: (Fig. 4F-J) (0) spines absent; (1) with backwardly directed flat teeth, five on each connexivum; (2) with five comb-like thin spines of equal length; (3) usually five spines of medium size on each connexivum; (4) with 5-6 long spines on each connexivum; (5) ten short upwardly directed teeth on each connexivum.

This state has modifications among the species of *Mustha*; *serrata* (1); *vicina* (2); half of the species of the genus (*baranovi, morgani, spinosula, izmirensis* and *spinosus*) with state (3); *gigantea* and *longispinis* (4); and *incana*, with a more modified trait with ten spines on each connexivum (5).

18 Length of body: (0) 13.5- 16.6; (1) 17.3-18.7 mm; (2) 19.23 - 19.9 mm; (3) 21 mm; (4) 22-25 mm; (5) 28-35 mm.

All *Mustha* species are larger in size than most halyine species, but variation occurs in the size among species: *longispinis* and *vicina* (1); *incana* and *izmirensis* (2); *serrata* (3); *baranovi, morgani, spinosula* and *spinosus* (4); *gigantea* is the largest of the species with a bodylength of 28-35 mm (5).

19 *Shape of dorso-posterior cavity of pygophore*: (Fig. 5A-C) (0) deep, rounded, with a broad, sclerotized, triblobate median projection; (1) shallow, without a median projection; (2) deep, with a small conical median projection; (3) relatively small but broad, distinctly depressed in the middle, the median projection with a sub-acute apex; (4) broad, long, distinctly bilobed median projection with lobes rounded at the apical margin; (5) broad, much longer and slightly depressed at apex.

Among species where the male is known, *izmirensis* is the only species in which dorsoposterior cavity is without a median projection (0); the remaining species have a very well-developed median projection, *vicina* (2); *spinosus* (3); *spinosula* (4); *incana* (5).

20 *Shape of ventro-posterior cavity of pygophore:* (Fig. 5A-C) (0) relatively shallow median excavation, with small rounded triangular projections on the sides; (1) usually distinctly V-shaped with smooth lateral margin, without a median excavation; (2) shallow, with distinct and narrow U-shaped median excavation, with triangular lobes on sides of excavation; (3) shallow cavity with broad, rounded median excavation and triangular lobes on sides, lateral margin sinuate; (4) shallow cavity with deep V-shaped median excavation.

This trait has some variation among species: *spinosula* (1); *izmirensis* (2); *spinosus* (3); *incana* (4).

21 *Shape of lateral lobes of pygophore*: (Fig. 5A-C) (0) a little produced, apex rounded; (1) slightly broad, not produced, apical margin straight; (2) slightly produced, apical margin rounded; (3) narrow, produced upward with apex rounded and slightly notiched in the middle; (4) produced like a separate lobe with distinct demarcation, tip concave with acute lateral apices.

Out of five species, *baranovi, gigantea, longispinis, morgani* and *serrata* have missing data in the literature while *gigantea* is a species based on only on females. Among remaining species this trait has a little modification, *incana* (1); *vicina* (2); *spinosula* and *spinosus* (3); but it is very distinct in *izmirensis* in which lateral lobes produced with distinct demarcation, apex concave with acute lateral apices. (4).

22 *Shape of paramere*: (Fig. 5D-H) (0) L-shaped, without inner process; (1) F-Shaped, with a well-developed inner process, with long golden hairs on the upper margin.

Izmirensis shares this trait with the outgroup *Orthoschizops* (0); all other species have a very well-developed inner process of stem (1).

23 *Shape of paramere stem*: (Fig. 5D-H) (0) long and broad, sometimes with a small triangular inner spine; (1) short, narrow, with very indistinct inner spine; (2) short, relatively broader, outer margin rounded, inner process present at base, long, finger-like, basal part semi-sclerotized, apical part sclerotized and conical; (3) long, broad, somewhat rectangular, outer margin straight, inner process broad, apical margin, tapering downward, semi-sclerotized; (4) long, thin, with outer margin roundish, inner process sharply triangular, occurring at the middle of the stem; (5) long, outer margin straight, inner process large, thumb-like, apex subacute.

Like other halyine species, this character plays a vital role in identifying *Mustha* species; in all *Mustha* species the stem has a very well-developed inner process with long golden brown hairs on upper side, except *izmirensis*, which has a thin small stem with an indistinct spine (1); *incana* (2); *spinosus* (3); *vicina* (4); *spinosula* (5).

24 *Shape of paramere blade*: (Fig. 5D-H): (0) elongated, apex little produced, ridge area very distinct, upper margin slightly rounded, lower tapering downwards; (1) blade as narrow as stem, apex slightly produced like small spine; (2) somewhat rectangular, upper margin and outer margin straight, apex broad with apical margin a little notched (3) narrow, curved and sharply tapering towards apex, a little rounded projection on the upper margin, resembling a bird's head; (4) narrow, elongated, ridge area distinct, apex broad with apical margin straight, tapering downwards; (5) short, somewhat square, upper margin roundish, apical margin concave.

The shape of the paramere blade is important in diagnosing individual halyine species and genera; this trait is very modified and variable in all *Mustha* species; *izmirensis* (1); *incana* (2); *spinosula* has unique blade, like a bird's beak (3); *spinosus* (4); and *vicina* with state (5).

25 *Shape of vesica*: (0) straight, tube-like or slightly zigzag; (1) distinctly curved.

This character is invariable and constant in all *Mustha* species (1).

26 Shape of posterior margin of first gonocoxae: (0) rounded; (1) distinctly lobed at inner angle; (2) oval.

Spinosula and *spinosus* share this trait with the outgroup *Orthoschizops* (0); *gigantea* and *spinosus* (1); *incana* and *vicina* (2).

27 Shape of posterior margin of second gonocoxae; (0) almost straight (1) slightly concave; (2) distinctly rounded.

The posterior margin of the second gonocoxae has very little modification among the species: *spinosula* and *spinosus* (1); *gigantea* and *incana* (2)

28 Posterior margin of female eighth paratergite; (0) smooth; (1) entire posterior margin armed with four spines; (2) entire posterior margin armed with six spines.

The presence of spines on the posterior margin of the eighth paratergite is a constant and unique character among all species of *Mustha* - usually there are eight spines (1); *gigantea* and *spinosus* have twelve spines (2).

29 *Length of ninth paratergite*: (0) equal to eighth; (1) distinctly shorter than eighth, almost equal to proctiger.

Like most halyine species, all *Mustha* species have state (1).

30 *Shape of spermathecal bulb processes*: (Fig. 6A-E) (0) two finger-like processes; (1) three finger-like processes of unequal size; (2) three processes, two finger-like and one thick, forked at apex; (3) three processes, one long, reaching to half the length of first flange, bent at apex, second shorter, and third very short, highly sclerotized; (4) three processes, one very long, reaching to three-quarters of first flange and bent at apex, 2nd shorter, finger-like, 3rd very short.

Like other halyine species, the spermathecal bulb processes is a variable trait in different species: *incana* (0); *izmirensis* (2); *vicina* (3); *gigantea* (4)

Key to the species of the genus Mustha Amyot and Serville

1. Head nearly parallel-sided, almost rectangular, apex broad anterior part of lateral margins of head with 4-6 irregular-shaped but distinct dentine; lateral margins of pronotum with eleven unequal long acute spines; margins of connexivum with comb-like thin spines of equal length; dorsoposterior cavity of male pygophore with small conical median projection, ventroposterior cavity shallow with broad roundish median excavation and triangular lobes on sides; spermathecal bulb with three processes, one short, highly sclerotized, a second a little longer, semi-sclerotized and a little bent at apex, and the third thick, very long, reaching middle of first flange *M. vicina* Hoberlandt

- Head distinctly narrow at anterior part, tapering upward along whole length, more or less triangular with sides slightly rounded or sharply triangular, entire lateral margins of head armed with very distinct dentine, lateral margin of pronotum with more spines; male pygophore not as above, spermathecal bulb with two or three processes with little variation in shape and size2

2. Paraclypeal lobes apically wider apart, leaving clypeus free3
- Paraclypeal lobes entirely enclosing clypeus4
3. Pronotum with sixteen regularly arranged spines; corium with sparse very small dentine; dorsoposterior cavity of male pygophore with broad bilobed median projection, ventroposterior cavity distinctly v-shaped, lateral lobes of pygophore produced with apex a little depressed, paramere stem broad, elongated with well-developed inner process, blade relatively thin bend, anterior part acutely tapered with small round projection on upper margin, spermethecal bulb with three finger-like processes *M. spinosula* (Lefebvre)
- Pronotum with nineteen long spines, some of them relatively short; corium with six short denticles of unequal size; dorsoposterior margin of pygophore without median projection, ventroposterior margin with U-shaped median excavation and triangular lobes on sides, lateral lobes prominent with distinct demarcation, apical margin depressed with acute apices, parameral stem very thin, without an inner process, blade as thin as stem, with apex a little produced like a thin spine; spermathecal bulb with three processes, two thin and finger-like, one thick, forked at apex *izmirensis* Memon and Ahmad
4. Head sub triangular, lateral margins moderately round, with seven to eight spines.5
- Head distinctly triangular, lateral margin almost straight with ten or more spines.8
5. Pronotum trapezoid, 2.9 times as broad as long, lateral margins, straight, flattened and distinctly raised with fifteen long, acute, upwardly projecting spines of unequal length; costal margin of hemelytra yellow, callus with three short stout yellowish teeth, connexiva black, with exterior margin along whole length yellow, moderately raised, armed with 5-6 teeth on each connexivum *M. longispinis* Reuter
- Pronotum transverse, no more than 2.3 times as broad as long; costal margin of hemelytra and connexiva entirely black or dark brown; teeth on connexiva not as above. 6
6. Head margins moderately round along the whole length; pronotum 2.3 times as broad as long; hemelytra and connexivum, unicoloured, entirely black or dark brown without any yellow spots, 7
- Lateral margins of head almost straight with seven upwardly directed spines, hemelytra reddish-brown with some scattered yellow patches; pronotum twice as broad as long, with twelve spines; dorsoposterior cavity of male pygophore with broad, medially depressed projection, ventroposterior cavity medially notched and with sinuate margins, lateral lobes broad with apical margin a little depressed in middle, paramere stem short relatively narrow with very prominent conical-shaped inner process, blade thin long with apex acute.*M. spinosus* Abbasi and Ahmad
7. Lateral margins of head irregularly dentate with small teeth along whole length; lateral margins of pronotum regularly arranged with 19 flat teeth; each connexivum with five backwardly directed flat teeth *M. serrata* (Fabricius)
- Lateral margins of head with eight distinct spines along whole length; lateral margins of pronotum with 12 irregularly arranged spines; each connexivum with five irregularly arranged spines *M. baranovi* Kiritshenko

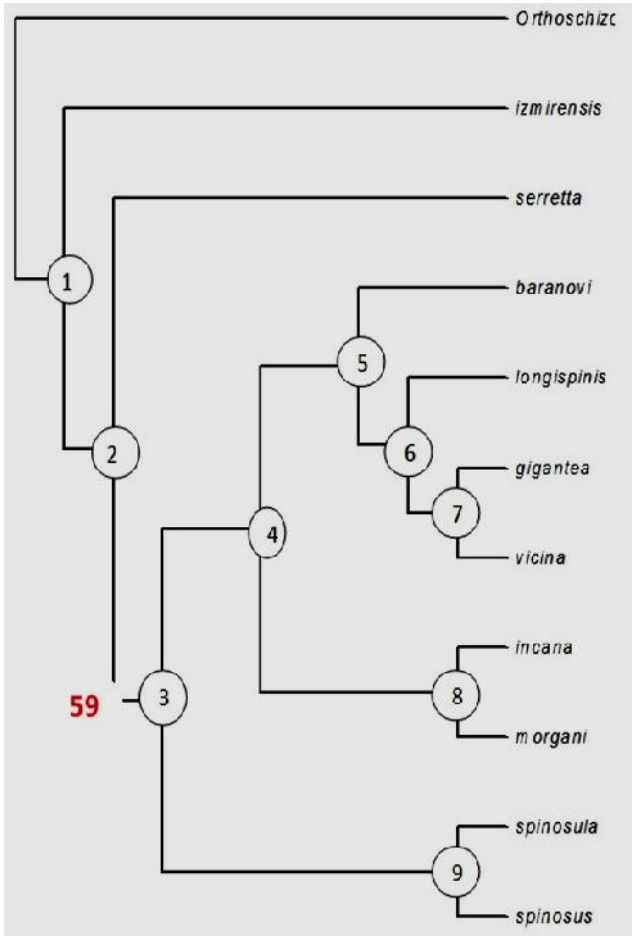


Figure 1.The single most parsimonious consensus tree generated from characters scored for the 11 species. Figures in circles are node numbers. Figures in red are bootstrap supports for branches with values above 50%

tree length = 93, Consistency index (CI) = 0.9247, Homoplasy index (HI) = 0.0753, CI excluding uninformative characters = 0.8511, HI excluding uninformative characters = 0.1489, Retention index (RI) = 0.6316, Rescaled consistency index (RC) = 0.5840, f value = 12, f-ratio = 0.0968

8. Lateral margins of head straight, spines stout, present along whole length; lateral margins of pronotum straight with 15-16 medially long acute spines; corium reddish-brown with short dense depressed whitish hair, *M. morgani* Horvath

- Lateral margins of head a little rounded; lateral margins of pronotum not as above, corium not reddish-brown and without short dense whitish hair 9

9. Head relatively broad at apical part, lateral margins with 11 spines, labium extends to the metacoxae; lateral margins of pronotum slightly elevated with 18-21 short upwardly directed spines of medium size; labium just extending in between meso thorax, each connexivum with nine short broad dentine, spermathecal bulb with two finger-like processes, one short and one relatively longer, *M. incana* Ståal

- Head sharply triangular, lateral margins with ten spines; labium extending to third abdominal sternum, lateral margins of pronotum with 13 acute spines of unequal size; each connexivum with five long acute spines; spermathecal bulb with three processes, one reaching to ¾ of first flange, bent at apex, second short and curved, third very short, finger-like and highly sclerotized *M. gigantea* Horvath.

Table 1 Character table for characters scored on taxa, and reconstructed on the cladogram of Figure 1.

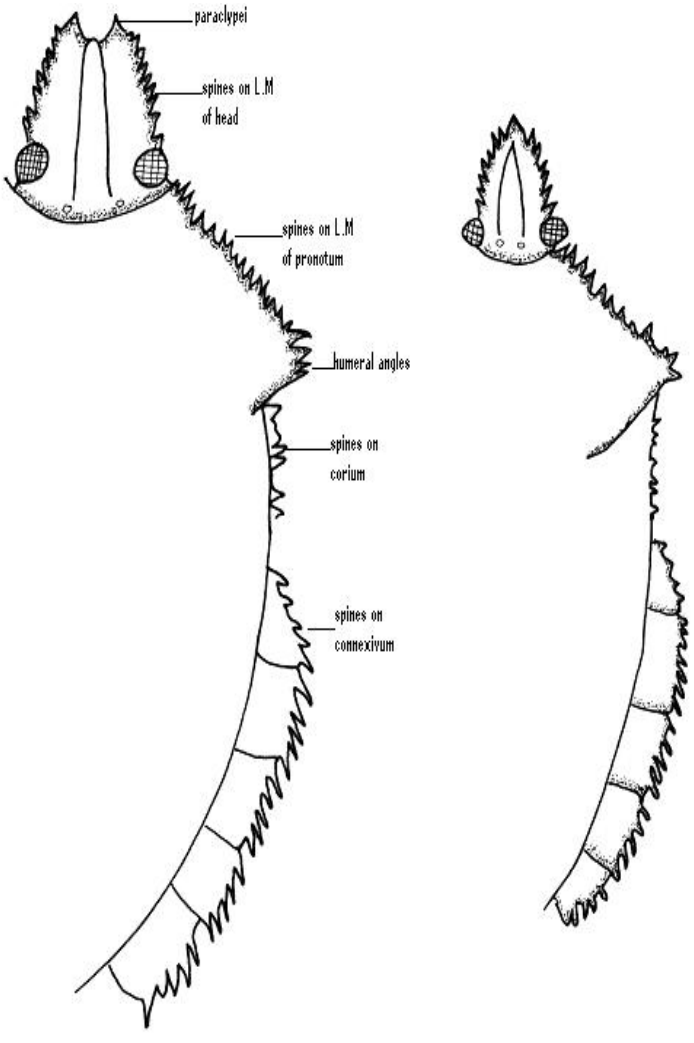
Character	1111111111	2222222222	
	1234567890	1234567890	1234567890
Orthoschizops	0000110001	0002000010	0000000001
baranovi	1111201330	11201134??	??????????
gigantea	2421311340	11311145??	?1??112114
longispinis	1312301330	21401141??	??????????
Incana	1511400340	1170115254	1122122110
morgani	1611200340	11501134??	??????????
spinosula	1211200331	1150113441	3153101111
izmirensis	1111200331	1160113202	40111??112
Vicina	1111002110	1111112125	2125122113
Serrata	1111100220	11501113??	??????????
spinosus	1211200330	1151113433	31341??21?
12	1111301310	1111114125	2125122113
13	1111301330	1110114125	2125122113
14	1111201330	1110113425	2125122113
15	1511200340	1150113454	1122122110
16	1111200330	1150113424	1122122110
17	1211200330	1150113431	3133101111
18	1111200330	1150113421	1122101111
19	1111200330	1160113321	1122101111
20	1111200331	1160113000	0000100111

Table 2: Apomorphy lists for the character changes along the tree of Figure 1.

Branch	Character	Steps	CI	Change
node_20 --> Orthoschizops	1	1	1.000	1 ==> 0
	2	1	1.000	1 ==> 0
	3	1	1.000	1 ==> 0
	4	1	1.000	1 ==> 0
	5	1	0.800	2 ==> 1
	6	1	0.500	0 ==> 1
	8	1	1.000	3 ==> 0
	9	1	0.800	3 ==> 0
	11	1	1.000	1 ==> 0
	12	1	1.000	1 ==> 0
	13	1	1.000	6 ==> 0
	14	1	0.667	0 ==> 2
	15	1	1.000	1 ==> 0
	16	1	1.000	1 ==> 0
	17	1	1.000	3 ==> 0
	19	1	1.000	0 ==> 1
	25	1	1.000	1 ==> 0
	28	1	1.000	1 ==> 0
	29	1	1.000	1 ==> 0
node_20 --> node_19	10	1	0.333	1 ==> 0
	18	1	0.833	0 ==> 3
	19	1	1.000	0 ==> 2
	20	1	1.000	0==> 1
	21	1	1.000	0 ==> 1
	22	1	1.000	0 ==> 1
	23	1	1.000	0==> 2
	24	1	1.000	0==> 2
	27	1	1.000	0 ==> 1
node_19 --> node_18	13	1	1.000	6 ==> 5
	18	1	0.833	3 ==> 4
node_18 --> node_16	20	1	1.000	1 ==> 4
	26	1	1.000	0 ==> 2
	27	1	1.000	1 ==> 2
	30	1	1.000	1 ==> 0
node_16 --> node_14	7	1	1.000	0 ==> 1
	13	1	1.000	5 ==> 1
	20	1	1.000	4 ==> 5
	21	1	1.000	1 ==> 2
	24	1	1.000	2 ==> 5
	30	1	1.000	0 ==> 3
node_14 --> baranovi	13	1	1.000	1 ==> 2
node_14 --> node_13	5	1	0.800	2 ==> 3
	17	1	1.000	3 ==> 4
	18	1	0.833	4 ==> 1
node_13 --> node_12	9	1	0.800	3 ==> 1
	14	1	0.667	0 ==> 1
node_12 --> gigantea	1	1	1.000	1 ==> 2
	2	1	1.000	1 ==> 4
	3	1	1.000	1 ==> 2
	6	1	0.500	0 ==> 1
	9	1	0.800	1 ==> 4
	13	1	1.000	1 ==> 3
	18	1	0.833	1 ==> 5
	26	1	1.000	2 ==> 1
	30	1	1.000	3 ==> 4
node_12 --> vicina	5	1	0.800	3 ==> 0
	7	1	1.000	1 ==> 2

	8	1	1.000	3 ==> 1
	10	1	0.333	0 ==> 1
	17	1	1.000	4 ==> 2
node_13 --> longispinis	2	1	1.000	1 ==> 3
	4	1	1.000	1 ==> 2
	11	1	1.000	1 ==> 2
	13	1	1.000	1 ==> 4
node_16 --> node_15	2	1	1.000	1 ==> 5
	9	1	0.800	3 ==> 4
	19	1	1.000	2 ==> 5
node_15 --> incana	5	1	0.800	2 ==> 4
	13	1	1.000	5 ==> 7
	17	1	1.000	3 ==> 5
	18	1	0.833	4 ==> 2
node_15 --> morgani	2	1	1.000	5 ==> 6
node_18 --> node_17	2	1	1.000	1 ==> 2
	19	1	1.000	2 ==> 3
	21	1	1.000	1 ==> 3
	23	1	1.000	2 ==> 3

	24	1	1.000	2 ==> 3
node_17 --> spinosula	10	1	0.333	0 ==> 1
	19	1	1.000	3 ==> 4
	23	1	1.000	3 ==>5
node_17 --> spinosus	14	1	0.667	0 ==> 1
	20	1	1.000	1 ==> 3
	24	1	1.000	3 ==> 4
node_19 --> serretta	5	1	0.800	2 ==> 0
	8	1	1.000	3 ==> 2
	9	1	0.800	3 ==> 2
	17	1	1.000	3 ==> 1
node_20 --> izmirensis	18	1	0.833	0 ==> 2
	20	1	1.000	0 ==> 2
	21	1	1.000	0 ==> 4
	23	1	1.000	0 ==> 1
	24	1	1.000	0 ==> 1
	30	1	1.000	1 ==> 2



A **B**

Fig.2. Dorsal view of two representative species of *Mustha* showing the features of the head (lateral margins, length of paraclypeal lobes and width between paraclypei), pronotum (shape and number of spines on lateral margins and

shape of humeral angles), abdomen (shape and number of spines on lateral margin), (A)*Mustha izmirensis,*; (B) *Mustha spinosus*,

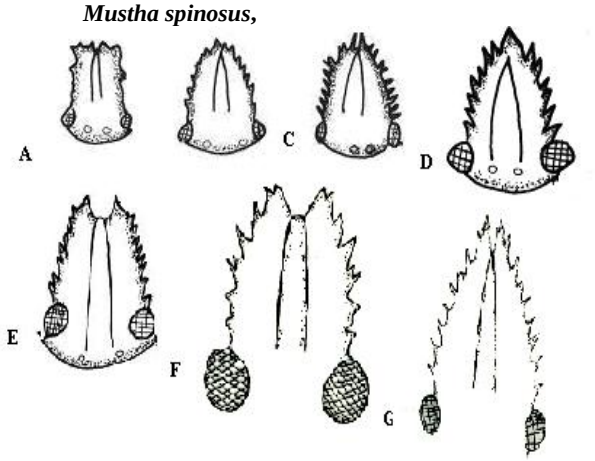
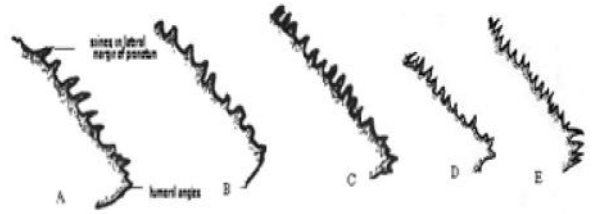


Fig.3. Head of some representative species of Mustha showing the features of the head (number and shape of spines on lateral margins, length of paraclypeal lobes, apex of paraclypei and width between paraclypei), (A) *Mustha vicina*, (B) *M. serrata*, (C) *M. longispinis*, (D), *M. spinosus* , (E), *M. izmirensis*, (F), *M. spinosula*, (G*), *M. gigantea*



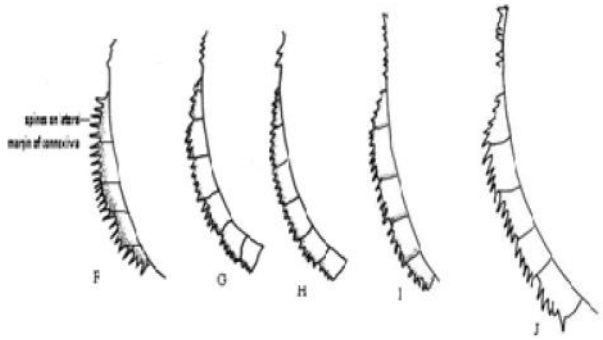


Fig.4. Pronotum of some representative species of Mustha showing the lateral margin (shape and number of spines, humeral angles); (A), *M. vicina*, (B), *M. serrata*, (C*), M .longispinis*, (D), *M. spinosus* , (E), *M. izmirensis*; abdomen, showing lateral margins (shape and number of spines on callus, shape and number of spines on connexiva); (F), *Mustha vicina*, (G), *M. serrata*, (H*), M. longispinis*, (I) *M. spinosus* (J), *M. izmirensis*

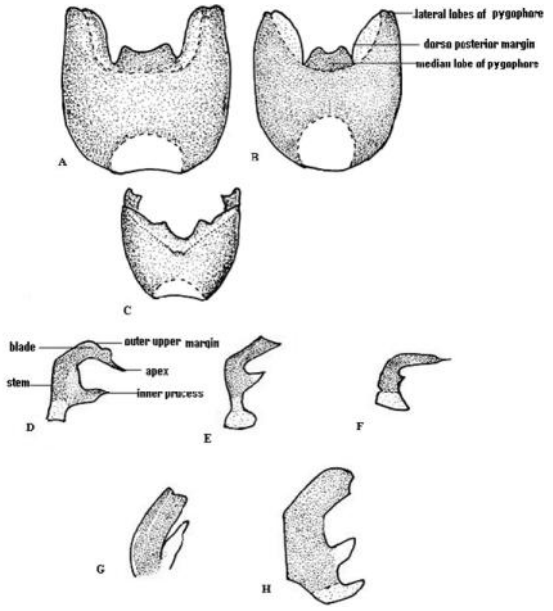
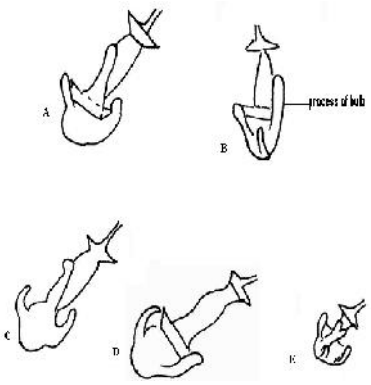
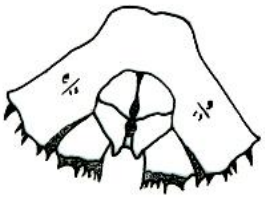


Fig.5. Male genitalia of some representative species of *Mustha*; pygophore dorsal view showing dorsoposterior cavity (inner margins, median excavation / lobe, shape of lateral lobes), (A), *Mustha. spinosula*, (B), *M. Spinosus*, (C*), M. izmirensis*; paramere, lateral view showing the shape of stem and blade (outer, upper and inner margins and the apex), (D), *Mustha spinosula*, (E), *M. spinosus*, (F*), M. izmirensis*, (G*), M. vicina* (H), *M. Incana*





F

Fig.6. Female Genitalia; spermathecal bulb of some representative species of *Mustha* showing the bulb processes (shape and number of bulb processes) (A), *Mustha. spinosula,* (B), *M. vicina,* (C), *M. gigantea,* (D), *M. incana,* (E), *M. izmirensis;* (F), *M. spinosus,* female terminalia, showing shape and number of spines,

DISCUSSION

The morphological characters and analysis of this study indicates that all species have characters which distinguish the genus from almost all other genera of Halyini: for example, the paraclypei are distinctly longer than clypeus; the presence of spines on the entire lateral margin of the head, pronotum and abdomen (the number and shape of spines is variable among species); the humeral angles entirely spinose; and the entire posterior margin of the eighth paratergite with distinct acute spines. Although *Mustha* shares the head and pronotum traits (although in slightly different form) with two other halyine genera *Orthoschizops* and *Phricodus*, neither has spines on the abdomen: *Phricodus* has just a single small tooth in the middle of the posterior margin of the eighth paratergite, while *Orthoschizops* has no teeth or spines.

In our analysis, several nodes of the single final tree of Fig. 1 are supported by multiple apomorphies. The separation of the outgroup *Orthoschizops* from all species of *Mustha* is supported by almost all character-state changes of the characters scored (Table 2).

Our tree indicates that the two most plesiomorphic species are *izmirensis* and *serrata*. *M. izmirensis* has many unique characters, particularly in the male genitalia. It is the only species of *Mustha* which has the dorso-posterior cavity without a median lobe (present in all other species, with variable shape and size); its ventro-posterior cavity has a distinct U-shaped excavation (character 20); it has a unique shape of the lateral lobes (21); it is the only species with a very narrow parameral stem and without an inner process (23); it has a distinctive shape of the parameral blade (24), and also the spermathecal bulb processes - like all other species it has three, but unlike them one is thick and forked at the apex.

M. serrata also has some strong apomorphies: the shape of the head is nearly parallel-sided (5) (rather like *Orthoschizops*, which also has parallel sides but only in the posterior three-quarters of the head); the anterior part is distinctly tapered upwards; the shape and number of denticles on the lateral margin of the head (8, 9); and the shape, size and number of spines on each connexivum (17).

Although not supported by many characters (as evidenced by the bootstrap results), there are some species-groups indicated by the tree. One clade is the *gigantea* group, which includes *baranovi*, *gigantea*, *vicina* and *longispinis*, defined by the synapomorphies of the shape of the lateral margins of head (7), and the shape and number of teeth on the lateral margins of the pronotum (13). There may be synapomorphies in genital characters too, but *baranovi* and *longispinis* lack any genitalic data, while *gigantea* lacks data for male genitalic characters: *vicina* is the only species of the clade with complete data. Although monophyly of *vicina* + *gigantea* is supported by the shape of the humeral angles (14), *vicina* is the only species of *Mustha* which has dentine only on the anterior part of the lateral margin of the head, a trait it shares with the outgroup *Orthoschizops* (but it has more distinct and modified denticles in comparison to *Orthoschizops*, which has only a few very small denticles).

The monophyly of *incana* + *morgani* is supported by three syapomorphies: the colour of the hemelytra (2), the number of teeth on the lateral margin of the head (9), and the shape of the dorso-posterior cavity of the pygophore (19).

The monophyly of *spinosula* + *spinosus* is supported by four characters: the colour of the hemelytra (2), the shape of the dorso-posterior cavity of the pygophore (19), the shape of the lateral lobes of the pygophore (21), and the shape of the parameral stem (23). In the whole tree this is the only clade where all species have more or less complete data. Like most halyine species, however, their parameral blades are very different from each other (24), and they also have many unique characters. The most important of these is the gap between the projected part of the paraclypeal lobes in *spinosula*, which it shares with *izmirensis* (in all other species the lobes entirely enclose the clypeus) and also the outgroup *Orthoschizops*

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Material Examined:

Musth gigantea Horvath:1 ♀; Kirt (Iran), with three tags, KY III a – JL a pyM 6 a, E a M II vp; 10 B II epcia 3 a py∂ H 6-10 v 01, B.M 1925-265, deposited at BNHM by P. Kment

Mustha hoberlandti (manuscript name): 1 paratype ♂; North Persia (Iran), 2006, expedition 1961, deposited at BNHM by P. Kment and Z. Jinda

Mustha incana Stal: 1♂; with two tags*; M. incana* (1976), M. *spinosula* identified by Dallas, deposited by P. kment 2006, 1♀; with three tags, first same, second Muscat Ruwi and third K. Ghichard, B. M 1976, deposited by P. kment 2006

*Mustha izmirensis;*1 ♂ holotype , 29 –VI- 1978, 1♀ paratype, 12-VII-1978, from Barnova, Izmir, Turkey, collected by Ahmad , deposited at Natural History Museum (NHMUK) , University of Karachi, Pakistan

Mustaha spinosula Lefebvre: 5 ♂; Parnass Gracia and 4♀; Constantinople, 2009, deposited at BNHM by P. Kment;

Mustha spinosus (Abbasi and Ahmad): 1♀, holotype; Quetta, Vam Valley, on willow, , collected by S.M. Khan 25-IV- 1964 deposited in Forest Research Institute, Peshawar, Pakistan, 1♂; Quetta,- Ziarat road near Ahmadoon on Malus pumila Mill. Collected by I. Ahmad 30-VII-1983, deposited at Natural History Museum (NHMUK) , University of Karachi, Pakistan

Mustha vicina Hoberlandt: 1♂; with four tags, Hoberlandt 1996, dposited by P. Kiment 2006, Turkey Adana 1973-74 on Piotochio No 6 22, M. *longispinis* Rent, deposited M.S. K Ghauri 1975, Pres by Conn bst Ent B.M 1975, 1♀; two tags, paratype (red tag) M. *vicina,* deposited by L. Hoberlandt 1988, S. Iran, Mian Jangal, 30-5, 5.6 1973

Orthoschizops lineaticeps Stall with tag (Distant collection 1911)

Orthoschizops latispinis with tags, South Africa 44-6, collected by D. Simth

Orthoschizops reticulata 1 ♂ with tags, South Africa, R.E. Tarner, BM, 192`-119, Cape province, 1♀, with tag Grese, Cape province Fab. Nov. 1921, deposited at BMNH