

The burrow morphology of mole crickets (Orthoptera: Gryllotalpidae): terminology and comparisons

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Abstract

Since the publication of [1] three additional burrow casts, unknown to the author, were located in the Natural History Museum, London (NHM) collection by George Beccaloni. These casts were provisionally identified as *Gryllotalpa ?vineae*. In order to establish whether this identification was correct a literature survey of the casts of mole crickets (Orthoptera: Gryllotalpidae) was conducted. Through this process a standardised terminology for mole cricket burrows has been established.

The application of eccentricity measurements to burrow structures has identified measurements that can potentially be used to discriminate those species for which suitably detailed burrow descriptions have been made available. It is demonstrated that the eccentricity of the restrictions on either side of the bulb, as well as the eccentricity of the horn opening, are useful diagnostic characters.

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1 Introduction

In a previous work [1] digital scans of the burrow casts of mole crickets (Orthoptera: Gryllotalpidae) held by the Natural History Museum, London were presented, alongside sound recordings of Gryllotalpidae made available via the BioAcoustica platform [2]. A subsequent donation of burrow casts of mole crickets has since been added to the collection (accession BMNH(E):2016-33).

In order to make meaningful comparisons between the burrows of different species a standardised terminology and measurement system is here presented. This is based on terminology drawn from several prior works [11, 22] with modifications to create a more standardised system for measurement. The acoustic burrows of mole crickets receive particular attention due to the importance of standardised measurements in future theoretical acoustic studies.

2 Terminology of burrow structures

The burrow structures of mole crickets can be categorised into two types. The term 'living burrows' is here applied to the feeding and hiding burrows produced by both sexes. In some species the male additionally creates a specialised 'singing burrow' to accentuate the courtship song.

2.1 Living burrows

Living burrows can be subdivided into those that are horizontal, and those that are vertical. These burrows can be constructed independently, or as part of a system of interconnected burrows ([11]). Endo [11] defines the burrow angle (Figure 1) and considers horizontal burrows to have a burrow angle less than 20° . Measurements of length and depth are illustrated in Figure ??.

Recent research (REFs) indicate that horizontal and vertical tunnels are likely to have different purposes and the proportion of horizontal to vertical burrows may reflect dietary preference of the species concerned.

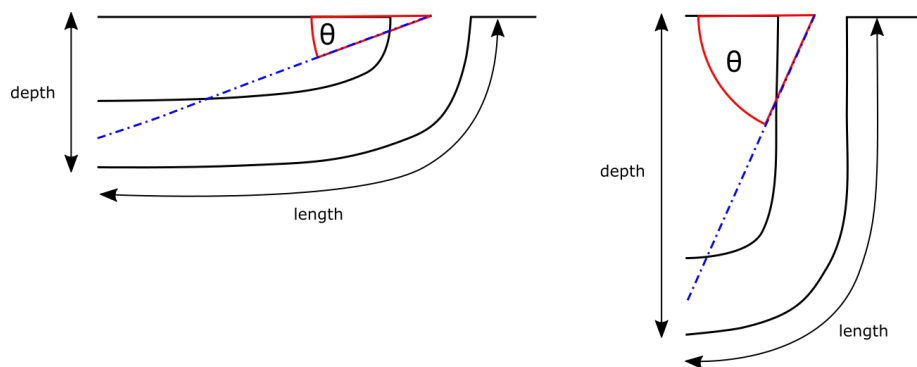


Figure 1: Burrow angle and measurements as defined by Endo [11].

2.1.1 Horizontal burrows

Horizontal burrows may be used for feeding on creeping plants with shallow root systems [11]. Endo [11] found that the horizontal burrows of *Gryllotalpa orientalis* had a number of openings (windows) that may act as traps for small arthropods. These arthropods enter the burrow system and may become prey for the mole cricket. Horizontal burrows may also provide shelter from predators and act as routes to access potential mates [11].

Branch Points and Intersections Branch points occur when a living burrow (either horizontal or vertical) forks. They are distinct from intersections which is where a horizontal and vertical tunnel meet.

Escape Efficiency Index An additional use of horizontal burrows is as an escape route from predators. Endo [10] proposes an escape efficiency index by dividing the total length of the horizontal burrows by the number of branching points in the horizontal tunnels (Equation 1).

$$EE = \frac{\sum \text{Length of horizontal branches}}{\text{Number of horizontal branch points}} \quad (1)$$

Fractal Dimension Fractal dimension analysis of horizontal burrows has been studied by Endo [10]. The degree to which horizontal branching (leading to a higher fractal dimension) occurs in a given species may be closely linked to their foraging strategy.

2.1.2 Vertical burrows

Vertical burrows may be used for feeding on plants (e.g. grasses and rushes) that have subterranean stems. It has been suggested that mole crickets may dig vertical burrows in pursuit of prey animals [6].

The depth of vertical burrows provides protection from predators and is used by mole crickets as a safe place for moulting and overwintering [11].

2.1.3 Entrances

Entrances to the burrow are often concealed, and an individual burrow may have multiple entrances depending on the species. In *Neoscapteriscus borelli* most burrows have a Y-shaped appearance due to the presence of two entrances [6].

Living burrow entrances should not be confused with the more elaborate openings of the acoustic burrows of the males, which are predominantly shaped to improve transmission of the male's courtship song.

2.1.4 Egg Chambers

Egg chambers are generally sealed to prevent predators from entering the chamber. They may be located besides a horizontal burrow [11].

2.2 Acoustic Burrows

The acoustic burrows of *Gryllotalpa* (Figure 2) consist of an acoustically tuned bulb and between one and four exponential horns (see species accounts). The openings of the horns of at least one species (*Gryllotalpa major*) vary in shape [14]. The bulb also has an exit tunnel leading away from the horns, which connects to the main burrow network. This provides protection to the male and his mate once she has located his burrow, or an escape route should his song inadvertently attract a predator.

2.2.1 Orientation

When describing the shape of the horn opening (see below) it is useful to arbitrarily define an orientation for the burrow system. The anterior end of the acoustic burrow is defined as the end with the horn opening. This terminology is currently only used to describe the arrangement of horns when they occur in more than one row.

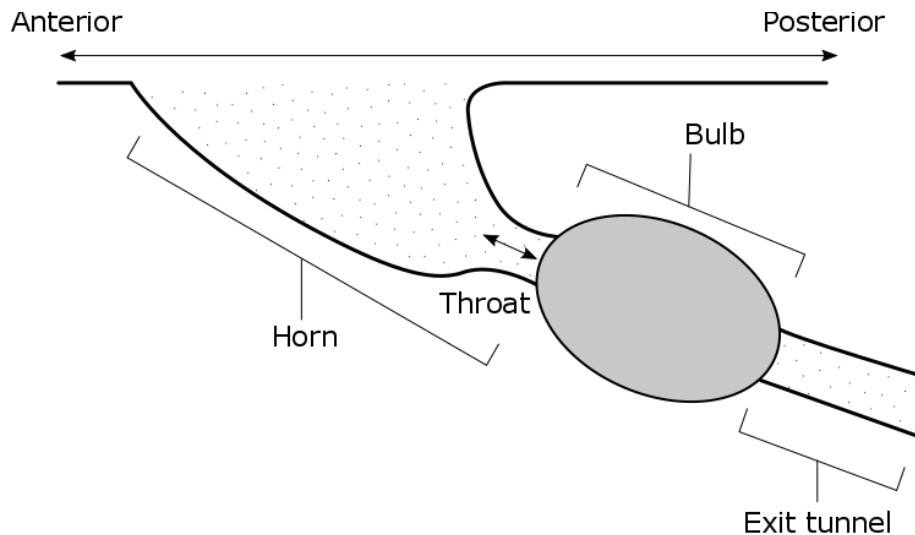


Figure 2: Overview of an acoustic burrow of *Gryllotalpa major* showing the exponential horn and bulb. Based on [22].

2.2.2 Offset horn

Hill et al [14] differentiate between 'slit' and 'L-shaped' burrows of *Gryllotalpa major* that has a single highly elliptical horn opening. The actual horn opening of these two burrow forms are however the same. The difference between these two burrow forms is actually an offsetting of the horn from the normal plane of the bulb, perhaps due to soil conditions.

The term offset is used here as a measure of the asymmetry of the burrow (Figure 3).

2.2.3 Horn number and arrangement

The horn number is defined simply as the number of horns present in the burrow. The naming of individual horns is defined simply by number in the case of the horns being approximately along a straight line (Figure 4).

In the case of *Gryllotalpa australis* where the burrow consists of four horns arranged in two rows the rows are identified as anterior and posterior using the orientation of the burrow, and then numbered individually.

The use of a numerical system, or when needed a numerical system with a named row is used rather a more vernacular system (left, right, centre) to allow for flexibility in describing as yet unknown burrows.

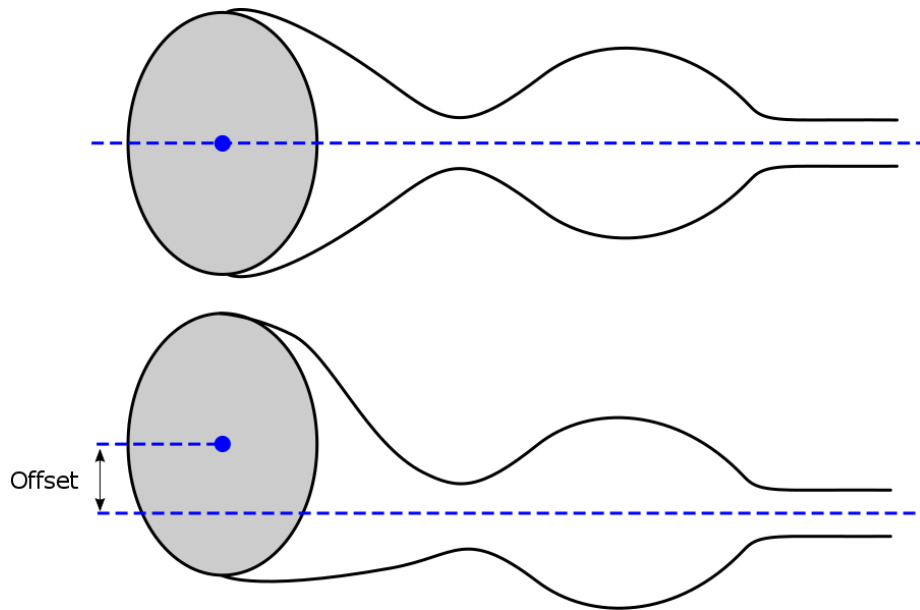


Figure 3:

2.2.4 Horn Opening

In their study of the burrows of *Gryllotalpa major* Walker & Figg [22] transpose the axes of width and length between the bulb and horn opening, a practise followed by [15]. I propose here to switch the opening length and opening width (sensu [22]) in order to provide a consistent system, with all length measurements along the same axis (Figure 5).

Horn length The horn length is taken by previous authors to be the distance of an imagined wire following the centre of the horn from the throat to the opening. It is not clear whether [15] followed this procedure. As measurement of this property is practically difficult it may be better to measure the smallest horn length (from the top of the throat to the rear of the opening) and largest horn length (from the bottom of the throat to the front of the horn).

Opening shape The opening shape terminology used by Hill et al [14] is adopted with modifications. 'Oval' is added to account for the oval horn openings of *Gryllotalpa vineae* (and others), and L-shaped is dropped as this is not a feature of the horn opening, and is covered above in Offset Bulbs. Opening shapes are shown in Figure 6.

Eccentricity of oval openings TODO: Orientation

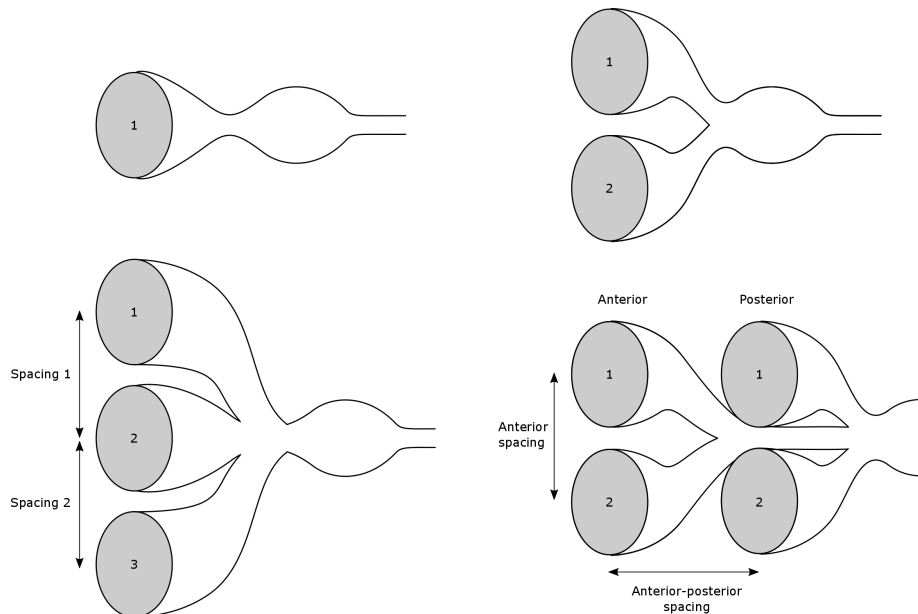


Figure 4: Arrangement and identification of horns and horn openings.

2.2.5 Horn spacing

Along with the dimensions of the horn openings, the spacing between openings may have an impact on the acoustic properties of the overall acoustic burrow system. For an acoustic burrow with two horns the horn spacing is the distance between the midpoints of the two horn openings. For acoustic burrows with three or more horn openings the horn spacings are a series of measurements between the midpoints of horn openings. In the case where there are two rows of horn openings measurements should be taken of the anterior spacing, the anterior-posterior spacing and the posterior spacing (Figure 4).

2.2.6 Bulb

All reports of acoustic burrows in the literature have a single bulb. A cast of *Gryllotalpa gryllotalpa* held in the NHM (NHMUK010211142) however could be considered to have two bulbs (FIG). For now the specimen is treated as having a single bulb.

2.2.7 Throat and exit

The acoustic burrow of mole crickets has two constrictions, one between the horn(s) and the bulb, and another between the bulb and the exit to the main tunnel system. I have followed the terminology used by [15], with the constriction between the horn and bulb being the 'throat' and the constriction between

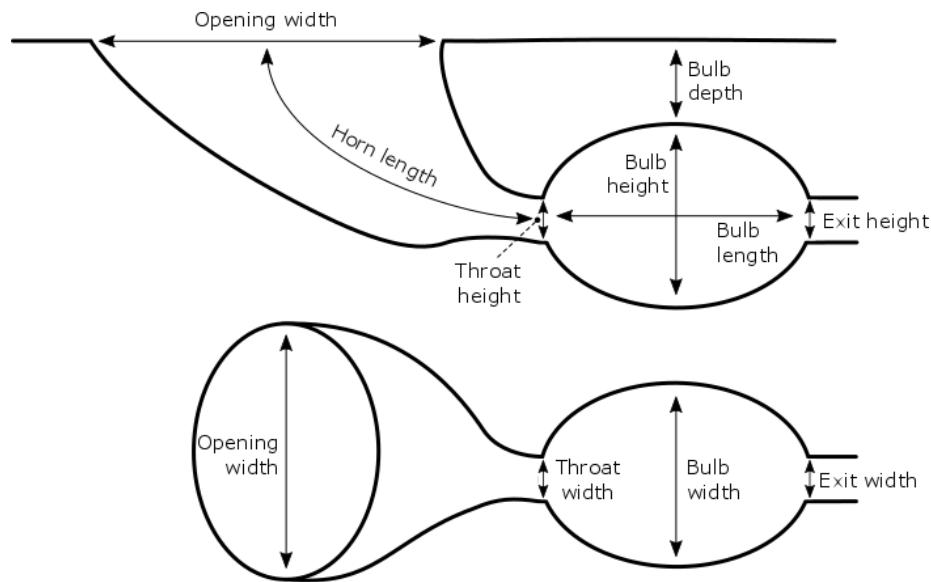


Figure 5:

the bulb and the exit tunnel(s) being the 'exit'.

While some authors have measured the height and width of the constrictions separately (citejafari2015) others have only specified a single diameter measurement ([16]).

2.2.8 Exit number and orientation

Previous publications on the morphology of acoustic burrows have shown the bulb to have two openings - one to the horn system and another, the exit tunnel, that links to the mole crickets living burrows. One burrow cast in the Natural History Museum (NHMUK010211180) however has two distinct exit tunnels (Figure 7). This is likely to be caused by the cricket constructing the acoustic burrow at a point along an existing horizontal burrow, rather than at its terminus. Exit tunnels are numbered in clockwise series from the horn opening. The exit angle is defined as the angle between the horn opening and the exit tunnel under consideration (Figure 8).

2.2.9 Turn around

Nickerson et al [18] show that the burrows of *Neoscapteriscus* have an additional chamber to the bulb that appears to allow the insect to turn around while within the acoustic burrow complex (presumably to allow it to turn around into singing position after entering the acoustic burrow from the living burrow system).

3 The burrows of *Gryllotalpa* Latreille, 1802

3.1 *Gryllotalpa africana* Palisot de Beauvois, 1805 [19]

The burrows of this species cause damage to turfgrass and crops [6]. Brandenburg et al [6] report the species from heavy clay soil in South Africa. Typical living burrows are Y-shaped (figured in [6]).

3.2 *Gryllotalpa australis* Erichson, 1842 [12]

The acoustic burrow of this species (figured in [16]) has four exponential horns, with the anterior horns being smaller and more closed placed than the posterior horns. The front horns are sometimes, particularly in shallower soil, fused with the rear horns. The exit tunnel may link to an extensive living burrow system [16].

3.3 *Gryllotalpa gryllotalpa* (Linnaeus, 1758) [17]

Gryllus gryllotalpa Linnaeus, 1758

The acoustic burrow of this species has between one and six horns arranged in a single line. Single horn acoustic burrow structures in Iran are discussed by [15]. Bennet-Clark [4] reports the burrow as generally being double horned with up to six openings. A burrow cast in the NHM collection (NHMUK010211142) appears to have three horns. A 3D scan of the three-horned acoustic burrow cast held by the Natural History Museum, London is described in [1]. Bennet-Clark [4] states, and the burrow cast he donated to the NHM agrees with this, that the burrow structure is somewhat irregular. The difference in regularity between Bennet-Clark's casts of *gryllotalpa* and *vineae* is striking (FIG).

3.4 *Gryllotalpa major* Saussure, 1874 [20]

Walker and Figg [22] describe the song and burrow. Variation in the burrow mouth morphology is discussed by [14].

3.5 *Gryllotalpa orientalis* Burmeister, 1838 [7]

Living burrows range from a single shallow horizontal burrow to of a network of branching horizontal burrows, with or without one or more vertical burrows [11, 10].

3.6 *Gryllotalpa vineae* Bennet-Clark, 1970 [3]

The usual form of the acoustic burrow has two horns, although on irregular terrain they may have three or more [4]. A 3D scan of an acoustic burrow cast held by the Natural History Museum, London is described in [1]. The burrow

5 BURROW CASTS HELD AT THE NATURAL HISTORY MUSEUM,
EWB5 LONDON

structure seems to be much more regular, and smoother, than the burrow of *gryllotalpa*.

4 The burrows of *Neoscapteriscus* Cadena-Castaeda, 2015

Unlike *Gryllotalpa* several species of *Neoscapteriscus* are known to plug their acoustic burrows with soil when not in use [22].

Taxonomic Note The genus *Neoscapteriscus* contains a number of species previously in the genus *Scapteriscus*. The nomenclature has been updated following the Orthoptera Species File [9].

4.1 *Neoscapteriscus borellii* (Giglio-Tos, 1894) [13]

Scapteriscus borellii Giglio-Tos, 1894
= *Scapteriscus acletus* Rehn & Hebard, 1916

The burrows of this species are known to damage turfgrass on sandy loam soil in the southeastern USA. The species is mainly herbivorous [6]. Typical living burrows are Y-shaped with two entrances (figured in [6]).

Acoustic burrows have a single horn and a turn-around.

4.2 *Neoscapteriscus vicinus* (Scudder, 1869) [21]

Neoscapteriscus vicinus Scudder, 1869

The burrows of this species are known to damage turfgrass on sandy loam soil in the southeastern USA. The species is mainly carnivorous [6]. Typical living burrows have a single entrance and are branched (figured in [6]).

Acoustic burrows have a single horn and a turn-around.

5 Burrow casts held at the Natural History Museum, London

The Natural History Museum has a small collection of five mole cricket burrow casts (Table 1). Measurements of these casts are also provided (Table 2).

5 BURROW CASTS HELD AT THE NATURAL HISTORY MUSEUM,
EWB5 LONDON

The first burrow casts presented to the museum were burrow casts of *Gryllotalpa gryllotalpa* and *Gryllotalpa vineae* by H. C. Bennet-Clark in YEAR. *Gryllotalpa vineae* was described in 1970 [3] by the collector. Although the cast of *vineae* is labelled as being a 'type burrow cast' it does not form part of the type series.

A later donation of three burrow casts was made by Professor David Pye, which show a striking similarity to the double horned burrow of *Gryllotalpa vineae*. As the burrows of mole crickets appear to be closely tuned to the song of the crickets themselves [5, 8] and there is variation in the dominant frequency of song between species, it seems probably that identification of species is possible from burrow casts.

Measurements of the burrows held by the NHM, and measurements collected from the scientific literature have been collated in an attempt to determine if species identification from burrows is possible (see below).

5.1 Response to obstructions

NHMUK010211181

5 BURROW CASTS HELD AT THE NATURAL HISTORY MUSEUM,
EWB5 LONDON

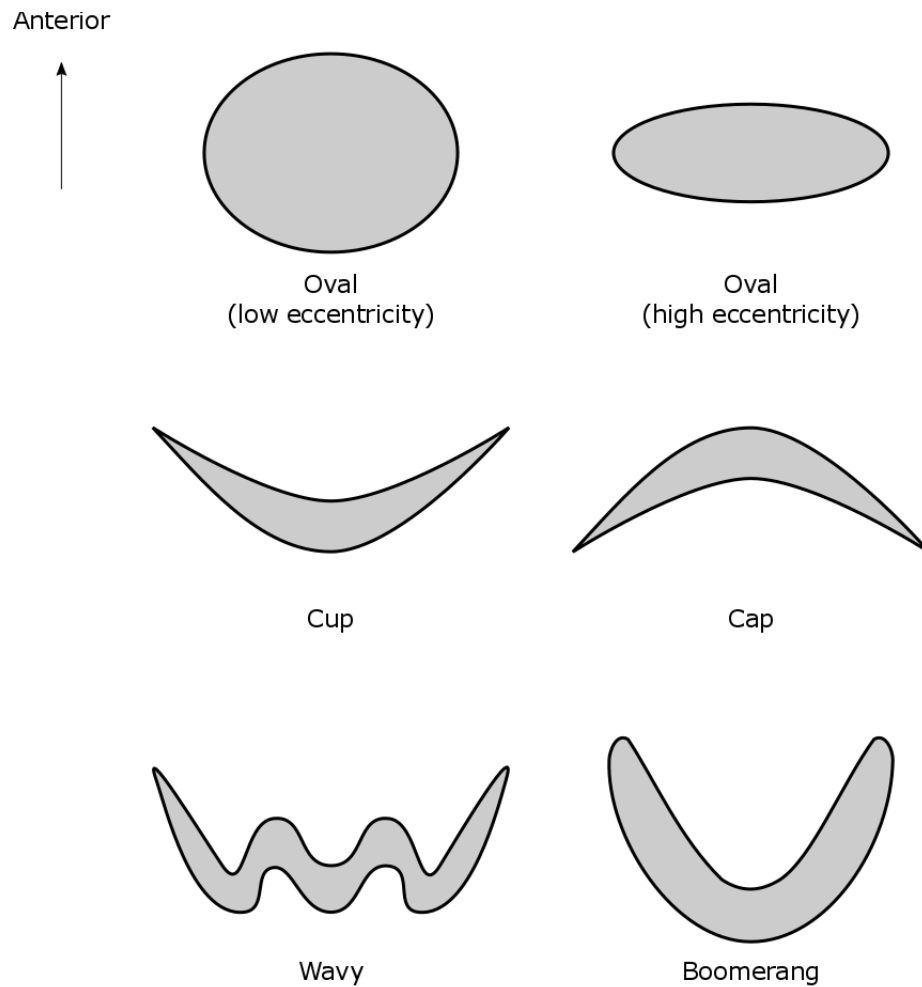


Figure 6:

5 BURROW CASTS HELD AT THE NATURAL HISTORY MUSEUM,
EWB5

LONDON



Figure 7:

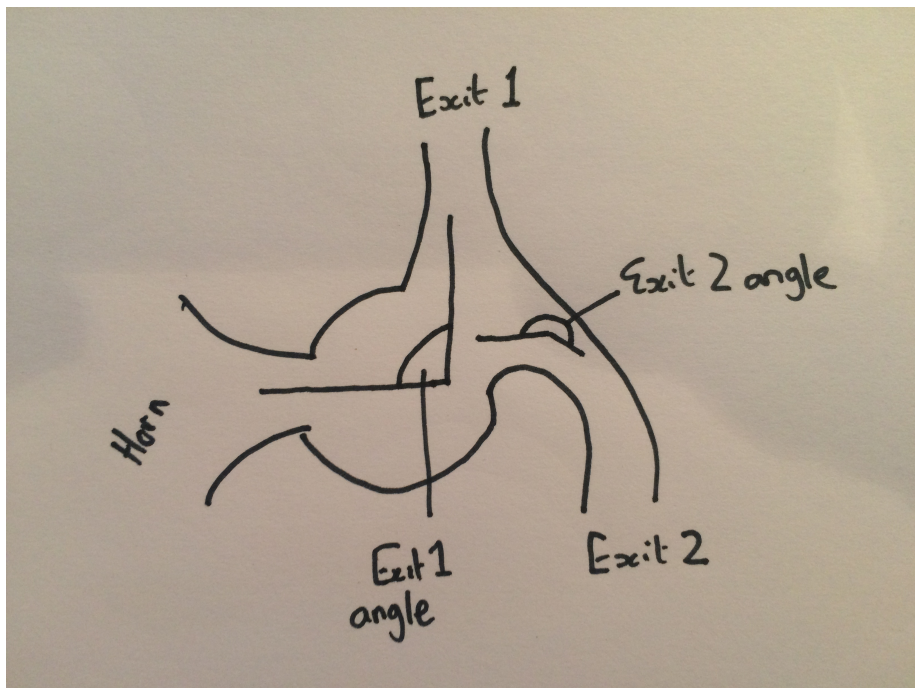


Figure 8:

5 BURROW CASTS HELD AT THE NATURAL HISTORY MUSEUM,
EWB5 LONDON

Specimen ID Accession Number	Verbatim ID	Material	Notes	3D Scan URL
NHMUK010211141 BMNH(E) 1969-431	<i>G. vineae</i>	Plaster	Col. H. C. Bennet-Clark	
NHMUK010211142 BMNH(E) 1969-431	<i>G. gryllotalpa</i>	Plaster	Col. H. C. Bennet-Clark	
NHMUK010211179 BMNH(E) 2016-33	<i>G. ?vineae</i>	Builders' Cement	Olive grove in Vale de Boa Hora, Algarve, Portugal 25.xii.1974 Presented by Prof. David Pye	
NHMUK010211180 BMNH(E) 2016-33	<i>G. ?vineae</i>	Builders' Cement	Olive grove in Vale de Boa Hora, Algarve, Portugal 25.xii.1974 Presented by Prof. David Pye	
NHMUK010211171 BMNH(E) 2016-33	<i>G. ?vineae</i>	Builders' Cement	Olive grove in Vale de Boa Hora, Algarve, Portugal 25.xii.1974 Presented by Prof. David Pye	

Table 1: Burrow cast specimens held by the Natural History Museum, London

Cast	Opening 1 Length	Opening 1 Width	Opening 2 Length	Opening 2 Width	Opening 3 Length	Opening 3 Width	Opening Spacing	Throat Height	Throat Width	Bulb Length	Bulb Height	Bulb Width	Exit 1 Height	Exit 1 Width	Exit 2 Height	Exit 2 Width
NHMUK010211141	42	25	36	25			29	19	16	29	27	29	16	15		
NHMUK010211142	30	23	20	31	44	26	40	18	34	33	30	17	13			
NHMUK010211179	35	21	35	23			30	24	17	37	34	30	14	15		
NHMUK010211180	31	28	40	27			28	29	18	32	35	36	17	19	20	21
NHMUK010211181	40	19	34	23			29	20	17	27	28	30	17	15		

Table 2: Burrow cast measurements of NHM material. All measurements are in mm, to the nearest mm. Measurements were made using Mitutoyo Absolute Digimatic digital calipers.

EWB56 COMPARISON OF ACOUSTIC BURROWS BETWEEN SPECIES

6 Comparison of acoustic burrows between species

Table 3 gives a comparison of measurements of mole cricket acoustic burrows taken from the literature and from specimens at the Natural History Museum, London (NHMUK).

Species	Number of Openings	Opening Length	Opening Width	Opening spacing	Horn Length	Throat Height	Throat Width	Bulb Length	Bulb Height	Bulb Width	Depth	Exit Height	Exit Width
<i>Gryllotalpa australis</i> from [16]	4					11.5 ± 1		24.3 ± 1.5	22.8 ± 3.4	20.6 ± 2.9		13.8 ± 1.4	
<i>Gryllotalpa gryllotalpa</i> from [15]	1	32.6 ± 1.86	42.8 ± 1.69		45.2 ± 2.13 but see text	21.2 ± 0.59	20 ± 0.83	28 ± 2.13	22.8 ± 2.01	25 ± 2.03		18 ± 0.07	20 ± 0.04
<i>Gryllotalpa major</i> from [22]	1	26 ± 1.2	86 ± 4.4		64 ± 2.0	19 ± 0.7	14 ± 0.6	39 ± 0.8	33 ± 1.2	37 ± 1.4	19 ± 5	14 ± 0.4	14 ± 0.5
<i>Neoscapierisus horvilli</i> from [18]	1					12 ± 1		19 ± 4	15 ± 1	14 ± 2		12 ± 1	
<i>Neoscapierisus vicinus</i> from [18]	1					13 ± 1		19 ± 1	16 ± 1	14 ± 1		12 ± 1	

Table 3: Comparison of measurements of acoustic burrows between different species, compiled from literature and the NHM collection.

EWB56 COMPARISON OF ACOUSTIC BURROWS BETWEEN SPECIES

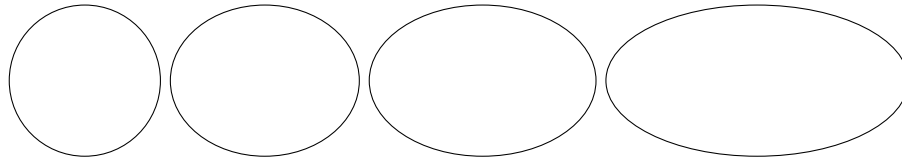


Figure 9: Ellipses with eccentricity of (left to right) 0, 0.6, 0.75 & 0.87

6.1 Eccentricity

The eccentricity of an ellipse is a quantitative measure of how much that ellipse deviates from a perfect circle. A circle has an eccentricity of 0, while an ellipse that has been so greatly deformed from a circle that is essentially a line has an eccentricity of 1.

Since the eccentricity of an ellipse is independent of its orientation, we must specify the orientation of the ellipse relative to the burrow. This is easiest achieved by specifying the direction of the major axis (length, width, height).

The eccentricity of a burrow is a measure of shape, rather than size, so accounts for size between the burrows of individuals of varying size within a single species.

6.2 Calculation of eccentricity

The calculation path here is used as measuring the length of the major axis (L) and minor axis (l) is straightforward for a burrow. The major axis is the longest measurement of opening length or opening width, with the other measurement becoming the minor axis (FIG). The calculation of the distance between the centre of the ellipse and one of the foci is calculated as follows.

$$\text{Major radius : } M = \frac{L}{2}$$

$$\text{Minor radius : } m = \frac{l}{2}$$

$$\text{Focal distance : } F = \sqrt{M^2 - m^2}$$

$$\text{Eccentricity : } e = \frac{F}{a} = \frac{F}{\sqrt{F^2 + m^2}} \quad (2)$$

Examples of varying eccentricity is given in Figure 9.

EWB56 *COMPARISON OF ACOUSTIC BURROWS BETWEEN SPECIES*

6.3 Constriction eccentricity

As previously noted, there has been variation in the published literature as to whether to estimate a single diameter for the two constrictions, or measure both height and width. The shape of the constriction will be influenced by the shape of either the horn or exit tunnel it attaches to the bulb.

6.3.1 Throat eccentricity

Table 4 shows throat eccentricities.

6.3.2 Exit eccentricity

Table 5 shows exit eccentricities.

TODO: Add note on height/width or diameter measurement previously.

Species	Plane of Eccentricity	Eccentricity
<i>Gryllotalpa gryllotalpa</i> from [15]	high	0.33
<i>Gryllotalpa major</i> from [22]	high	0.68
<i>Gryllotalpa vineae</i> NHM Bennett-Clark	high	0.54

Table 4: Throat eccentricities of mole cricket burrows.

Species	Plane of Eccentricity	Eccentricity
<i>Gryllotalpa gryllotalpa</i> from [15]	wide	0.44
<i>Gryllotalpa major</i> from [22]		0
<i>Gryllotalpa vineae</i> NHM Bennet-Clark	high	0.35

Table 5: Exit eccentricities of mole cricket burrows.

6.4 Horn opening eccentricity

The eccentricity of the horn openings for species with data available in Table 3 are given in Table 6.

Species	Plane of Eccentricity	Eccentricity
<i>Gryllotalpa gryllotalpa</i> from [15]	wide	0.65 ± 0.08
<i>Gryllotalpa major</i> from [22]	wide	0.95 ± 0.01
<i>Gryllotalpa vineae</i> NHM Bennett-Clark	long	0.76 ± 0.04
<i>Gryllotalpa gryllotalpa</i> NHM Bennett-Clark	either	variable (0.64-0.81)

Table 6: Acoustic horn eccentricities of mole cricket species.

EWB56 COMPARISON OF ACOUSTIC BURROWS BETWEEN SPECIES

6.5 The identity of NHMUK010211179-81

The horn eccentricity of these (assumed conspecific) casts were calculated as 0.72 ± 0.14 in the length direction. It can be seen from Table 6 that the only species that overlaps in horn opening shape is *Gryllotalpa vineae*. Further comparisons are given in Table 7.

It can be seen (Figure 10) there is close agreement between the three more recent specimens and the Bennett-Clark specimen of *vineae*. Given that only a single confirmed specimen of *vineae* for comparison, it is likely that the three newer casts fall within the normal bacoustic burrow range of that species. They appear distinct from other species of *Gryllotalpa* on factors including number of horns and horn opening eccentricity. As shown by Bennet-Clark the shape of the exit tunnel has little effect on the burrow acoustics, so there is less evolutionary pressure to maintain a uniform shape of this section between burrows. In addition the species varies from the NHM *G. gryllotalpa* cast by its regular and smooth structure.

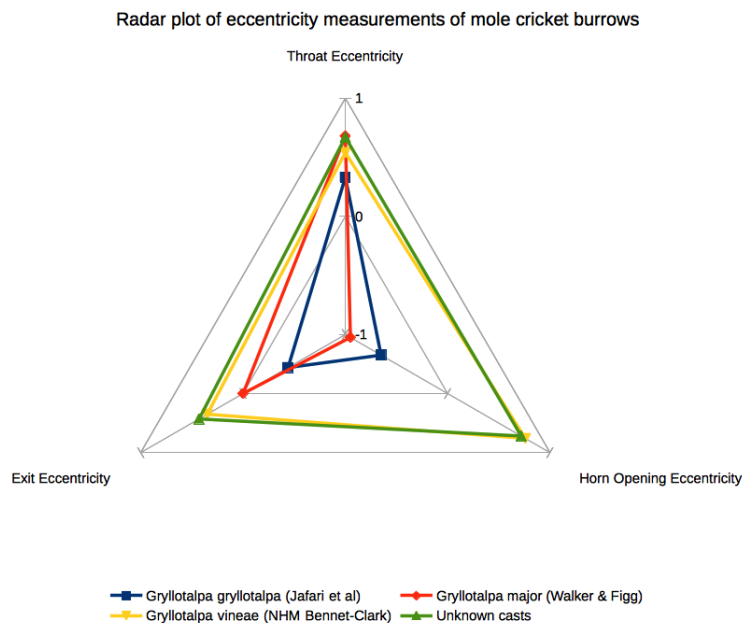


Figure 10: Radar plot of eccentricity measurements of mole cricket burrows. Eccentricities along the anterior-posterior axis are given positive values, those orthogonal to it are given negative values.

6.6 *Gryllotalpa gryllotalpa*: highly variable?

There is a striking difference between the cast of this species donated by Bennett-Clark to the NHM and the Iranian specimens examined by [15]. This species is known to have multiple races across Europe, and it is possible that acoustic burrow structure also varies considerably across this range.

Measurement	NHMUK010211179-81	<i>Gryllotalpa vineae</i> NHM Bennett-Clark
Horn opening eccentricity	length 0.72 ± 0.14	length 0.76 ± 0.04
Throat eccentricity	height 0.67 ± 0.10	height 0.54
Exit eccentricity	various 0.43	height 0.35

Table 7: Comparison of measurements of NHMUK010211179-81 with *Gryllotalpa vineae*.

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