

Egg shape and size in Phaneropterinae and other Tettigoniodea (Orthoptera, Ensifera): A global review with new data

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Abstract

Tettigonioids typically deposit their eggs within the substrate, whether in the soil or in plants. Consequently, these eggs often exhibit a rounded shape with a relatively smooth surface. Despite this, various studies have consistently demonstrated that egg shape is a stable characteristic within species, differing between distinct groups. However, to date, no comprehensive comparative analysis has been conducted, even though regional studies have suggested that the eggs of Phaneropterinae differ from all others. In this study, we present data on the length, width, and height of 352 species and subspecies, including measurements for 158 species that were newly assessed. Our findings substantiate the claim that the eggs of the Phaneropterinae subfamily can be distinguished by their flattened shape. Based on this important and diagnostic characteristic, we advocate for the re-transfer of the genus *Brinckiella* into Meconematinae. We propose a hypothesis suggesting that the evolution of the flattened egg shape in Phaneropterinae may have conferred advantages during the adhesive process of attaching eggs to plants—an assumed ancestral method of oviposition in this subfamily. Subsequently, these flat eggs found their way onto leaves or into the ground. While some other subfamilies exhibit eggs conforming to the basic tettigonioid shape, they showcase distinct features (e.g., Pseudophyllinae, Mecopodinae). We anticipate that future investigations into the lesser-explored Meconematinae, focusing on the small eggs and the oviposition behavior within this subfamily, will yield intriguing insights.

Keywords

oviposition, Phaneropteridae, tettigoniid subfamilies

Introduction

A significant proportion of animals engage in oviparity, or the laying of eggs. During the egg stage, individuals are typically most immobile and least capable of defending themselves. None of the species-specific adult morphological characteristics are discernible during this phase. Nevertheless, substantial variation exists

in the eggs of different species, as demonstrated convincingly by Church et al. (2019a), who also explored the reasons for this diversity. Perhaps not surprisingly, they argue that oviposition sites and styles play a crucial role in explaining egg diversity. While the variability in egg size spans ten magnitudes when comparing all insects, it gradually diminishes when examining selected groups. In Polyneoptera, for example, egg volume varies by more than six magnitudes (Church et al. 2019a, fig. S3), whereas in Orthoptera, the range is less than three magnitudes, from 0.1 mm³ to about 40 mm³. Similarly, in Tettigoniodea, the range is from 1.3 to 17 mm³ (Church et al. 2019b). The situation for egg shape appears to be analogous, with related taxa exhibiting relatively small differences. However, despite studying more than 6700 species, Church et al. (2019b) only provided data sets for 30 tettigonioid species from seven papers. In contrast, early comparative studies of tettigonioid eggs by Cappe de Baillon (1920) depicted diverse eggs from taxonomically different groups. Over 30 years later, Bei-Bienko (1954) proposed a distinctive flattened egg shape as a diagnostic characteristic of the subfamily Phaneropterinae (“The markedly flat form of the egg is highly typical of the subfamily Phaneropterinae, in contrast to other Palearctic Tettigoniidae” p. 18, Bei-Bienko 1954).

These interesting observations, however, were possibly overlooked, and eggs have not received much attention in either general biology or taxonomy, except for a few studies in selected tettigonioid species from European countries (Hartley 1964, Hartley and Warne 1972, Mazzini 1976). It was only in 1993, within the second volume of his *Monograph of the Tettigoniidae of Australia*, that Rentz initiated the comparative description and illustration of eggs from various species, continuing this project in subsequent papers (see Suppl. material 2). Later, Rentz et al. (2007) utilized the characteristic shape of eggs to place the newly described genus *Alinjarria* Rentz, Su & Ueshima, 2007 in Listroselidini, aligning with karyological data. For most areas outside Australia, such

discussions and decisions often lack comprehensive knowledge. In the description of Lipotactinae eggs, Ingrisch (1995) briefly touches on egg shape and color in some other subfamilies but without providing fundamental data on the studied genera and species. Mazzini (1987) and Ingrisch (1995) corroborate Bei-Bienko's (1954) observations regarding the peculiar egg shape of phaneropterines, yet data for all three spatial dimensions are nearly always absent for this subfamily.

This paper aims to document the morphology and size of approximately 150 previously unstudied species' eggs and to compare them with published data from a similar number of species. It is crucial to bear in mind that, despite their well-defined shape, eggs are evidently not as stable as other chitinous structures, such as the pronotum or hind femora. In 1909, Vosseler described and figured changes in egg shape and an increase in volume during embryonic development in a species of *Eurycorypha*. Similar changes were observed by Eluwa (1970), supported by quantitative data. Ingrisch (1988) noted a 50–150% increase in egg mass during development. This change is based on resorption of contact water, with the percentage differing between species (Ingrisch 1988). Of course, this increase changes the dimensions of an egg considerably, as evidenced by Vosseler's (1909; p. 163) figures and Únal and Beccaloni's (2017; fig. 119) photos showing newly laid and old eggs. The issues associated with increasing mass may be less significant when comparing only newly laid or ripe eggs taken from females. However, the effects of water uptake and loss can manifest in various ways, including the potential for eggs preserved dry to lose water and size without visible collapsing. Conversely, immersing eggs in distilled water for 24 hours before study, as done by Mazzini (1976), may artificially inflate them. Fortunately, in most cases, the basic shape of the egg seems unaffected, making the relationships of dimensions more reliable than one-dimensional measurements, although the numerous potential sources of inaccuracies should not be overlooked.

Materials and methods

For this study, 458 eggs from 158 species and subspecies were examined. The locality data of the females the eggs came from are given in Suppl. material 1. Species names are used as proposed in OSF (Cigliano et al. 2023). In addition, all literature data we could localize were included, increasing the number of species/subspecies to 352. A complete list of species including data and references is presented in Suppl. material 2.

The eggs were obtained in various ways. (1) Mated and unmated females, kept in captivity, laid eggs (relatively few species). (2) For the majority of species, ripe eggs were taken from females immediately after preparation (e.g. for chromosome studies). (3) In other cases, eggs were received from specimens preserved in ethanol. The eggs were preserved in 70% ethanol or as dried specimens.

The eggs were photographed (OLYMPUS SZ Binocular Stereo Zoom Microscope equipped with a digital camera SONY Cyber-shot DSC-P120), all at the same magnification, placing them horizontally and vertically using plasticine. In the photos, the eggs were measured, the largest dimension defined as length, the second largest as width, and the smallest as height (= thickness). Following Church et al. (2019a), the ratio of length to width is called aspect ratio. Relative thickness is defined as (length × width) / height. Egg volume is estimated as $\pi/6 \cdot \text{length} \cdot \text{width} \cdot \text{height}$ [volume of an ellipsoid $V=(4/3)\pi \cdot (\text{length}/2) \cdot (\text{width}/2) \cdot (\text{height}/2)$], with height being replaced by width in approximately cylindrical eggs.

Results

The majority of Tettigonioida exhibit ovoid-cylindrical eggs where the width is approximately equal to the height (Fig. 1A) and both ends are rounded. These eggs can be either straight or slightly curved, characterized as "generally rather sausage-shaped" by Preston-Mafham (1990). However, the subfamily Phaneropterinae deviates from this norm; their eggs consistently exhibit a flattened shape, varying in degree (Fig. 1), with only rare instances approaching a cylindrical form. Consequently, the aspect ratio (length/width) is notably low in all phaneropterines, rarely exceeding three and never reaching four (Fig. 1B; for *Brinckiella*, see below).

In terms of egg size, within our sample of 339 tettigonioid species, the length of eggs ranged from 1.6 mm (*Amyttosa insectivora* Naskrecki, 2008) to 12.6 mm (*Saga ephippigera* Fischer von Waldheim, 1846). The volume (n=291) ranged from 0.1 [*Indiamba malkini* (Jin, 1993) in Kevan and Jin 1993] to 46 mm³ (*Philoscirtus cordipennis* Karsch, 1896) (refer to Suppl. material 2 for detailed information).

Table 1 provides an overview of the subfamilies and tribes along with the number of species for which data on egg morphology are available (see Suppl. material 2 for details). Subsequent sections will address each of these groups separately.

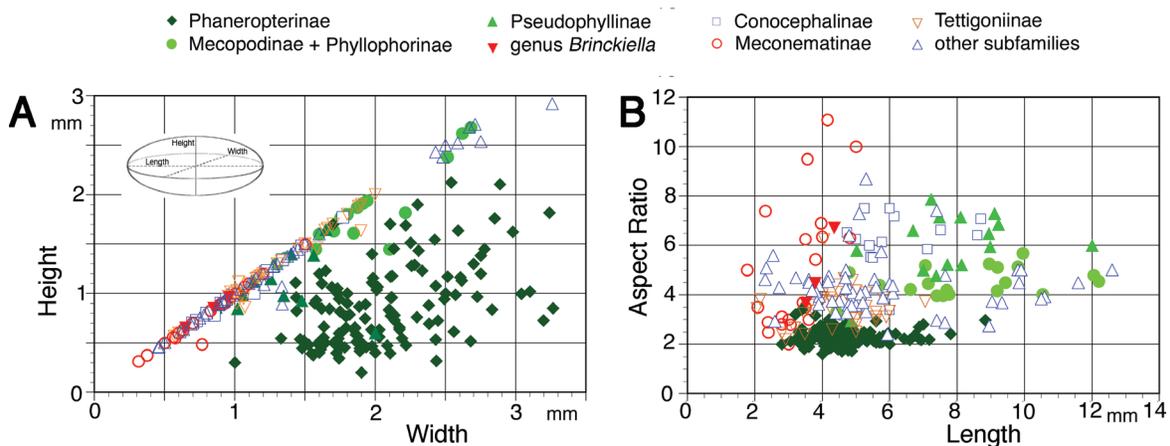


Fig. 1. Dimensions of eggs in different tettigonioid groups. A. Height versus width; B. Aspect ratio versus length.

Table 1. Number of species with detailed egg data in families, subfamilies, and tribes of Tettigonioidae (for full data, see Suppl. material 2).

Family	Subfamily	Tribe / species group	Number of species	
Phaneropteridae	Mecopodinae		16	
		Phaneropterinae	Acrometopini	5
	Amblycoryphini		18	
	Barbitistini		49	
	Ducetiini		3	
	Elimaeini		4	
	Ephippithyae		7	
	Holochlorini		14	
	Insarini		3	
	Letanini		2	
	Microcentrini		2	
	Odonturini		7	
	Phaneropterini		18	
	Steirodontini		3	
	ungrouped		9	
	groups with single representatives		9	
	Phyllophorinae		3	
	Pseudophyllinae		16	
	Tettigoniidae	Tettigoniinae	Arytropteridini	2
			Decticini	2
Nedubiini			6	
Platycleidini			44	
Tettigoniini			3	
groups with single representatives			2	
Bradyporinae			Bradyporini	1
			Ephippigerini	12
			Zichyini	1
Austrosaginae			6	
Hetrodinae / -ini		4		
Listroscolidinae		Requenini	8	
		Terpandrini	6	
ungrouped		4		
[Conocephalinae gr.]		Conocephalinae	Agraeciini	10
	Conocephalini		5	
	Copiphorini		6	
	Euconchophorini		2	
	Hexacentrini		3	
	Hexacentrinae	3		
	Lipotactinae	1		
	[Meconematinae gr.]	Meconematinae	Meconematini	5
			Phisidini	6
			Phlugidini	4
Meconematinae ?			3	
<i>Brinckiella</i>	3			
[unknown gr.]	Phasmodinae	1		
	Saginae	5		
	Tympanophorinae	3		
	Zapochilinae	5		

Phaneropteridae Phaneropterinae (153 species studied)

Fig. 2 illustrates examples of phaneropterine eggs. Based on the still-limited sample, the most prevalent shape is depicted by Fig. 2A [*Elimaea subcarinata* (Stål, 1861)], characterized by a very flat profile with a height of approximately 0.5 mm. This particular shape is observed in Phaneropterini, Amblycoryphini (mainly the genus *Eurycorypha*), and Elimaeini (Fig. 3). Notably, these eggs are not always elliptical and occasionally exhibit asymmetrical shapes (e.g.,

Paraplangia Heller et al., 2018). Among the larger Holochlorini, there is a tendency for slightly thicker eggs. In the case of Barbitistini, a flightless tribe with abundant species, most members have relatively thick eggs. A few even approach the cylindrical egg shape of other subfamilies (e.g., Fig. 2B; *Poecilimon pergamicus* Brunner von Wattenwyl, 1891), while others have larger eggs without a proportionate increase in absolute height (e.g., Fig. 2C; *Polysarcus denticauda* (Charpentier, 1825)). However, the eggs of the genus *Brinckiella* Chopard, 1955, previously transferred from Meconematinae to Phaneropterinae by Naskrecki (1996), significantly differ from all other known Phaneropterinae. The figured eggs (Naskrecki and Bazelet 2009) are elongated and cylindrical (Fig. 1, red triangles). We propose a provisional re-transfer of *Brinckiella* to Meconematinae due to the unique mix of characters in this genus (Naskrecki and Bazelet 2009).

In Phaneropterinae, egg length varies between 2.8 mm (*Caedicia flexuosa* Bolívar, 1902) and 8.8 mm (*Zeuneria biramosa* Sjöstedt, 1929). The size of these eggs, like tettigonioid eggs in general, correlates strongly with the body size of the respective species (compare, e.g., the eggs of the small *Poecilimon pergamicus* with those of the large *Zeuneria biramosa* Sjöstedt, 1929; Fig. 2B vs. 2D). However, quantifying this correlation is challenging due to the absence of mass data, and morphological characteristics, such as the length of the pronotum or hind legs, may be influenced by genus-specific differences. To address this issue, we used data from the genus *Poecilimon* sensu lato (Borissov et al. 2023), where male body mass data were available and utilized as a proxy for female body mass. Egg volume was then calculated from size measurements and compared with the mass data (Fig. 4). The regression line ($f(x) = 0.005371x + 1.375$; $r^2 = 0.80$) indicates that an increase in (male) body mass by one gram results in a slight increase of more than five mm³ per egg. These volume changes can be directly correlated with changes in egg mass, as evidenced by the close relationship between volume and mass in the two studied species.

Among the extensive collection of phaneropterid eggs (>150 species), some exhibit unique characteristics. Notably, the eggs of *Debrona cervina* Walker, 1870 (Fig. 2E) are particularly unusual, with the female laying “eggs individually on the upper surface of leaves, with each egg placed on a short vertical stalk” (Naskrecki and Guta 2019; fig. 37G; Hemp 2021, fig. Debr 8, p. 301). Three African species, still ungrouped systematically, share another distinctive feature. The very thin eggs of *Tropidonotacris grandis* Ragge, 1957 (Fig. 2F) and two species of *Ectomoptera* (Fig. 2G; *E. spec.*) possess a flat lateral extension on one side. A similar extension is found in three Asian Holochlorini. The eggs in these species [Fig. 2I–K; *Arnobia ocellata* (Ingrisch, 1994), *Arnobia spec.*, *Stictophaula armata* Ingrisch, 1994] are also very thin, but the extension runs around the egg, with varying widths between species. Ingrisch (1994) provides photos of living eggs of *Arnobia ocellata* just before nymphal eclosion. It is possible that *Leucopodoptera eumundii* Rentz & Webber, 2003, exhibits a similar modification (Webber et al. 2003, fig. 11). Another uncommon egg shape is found in *Phlaurocentrum mecopodoides* Karsch, 1892, where the egg is flattened but has a peak on the upper and lower sides (Fig. 2H; Massa 2013).

Mecopodinae (16 species studied) and Phyllophorinae (3 species studied)

Examples of eggs from both subfamilies are represented in Fig. 5A–E. Characteristic of most mecopodine eggs are an “elongate shape, the furrow [groove in Rentz et al. 2006], and the hook at one of the poles,” as concluded by Hemp (2021) based on observations

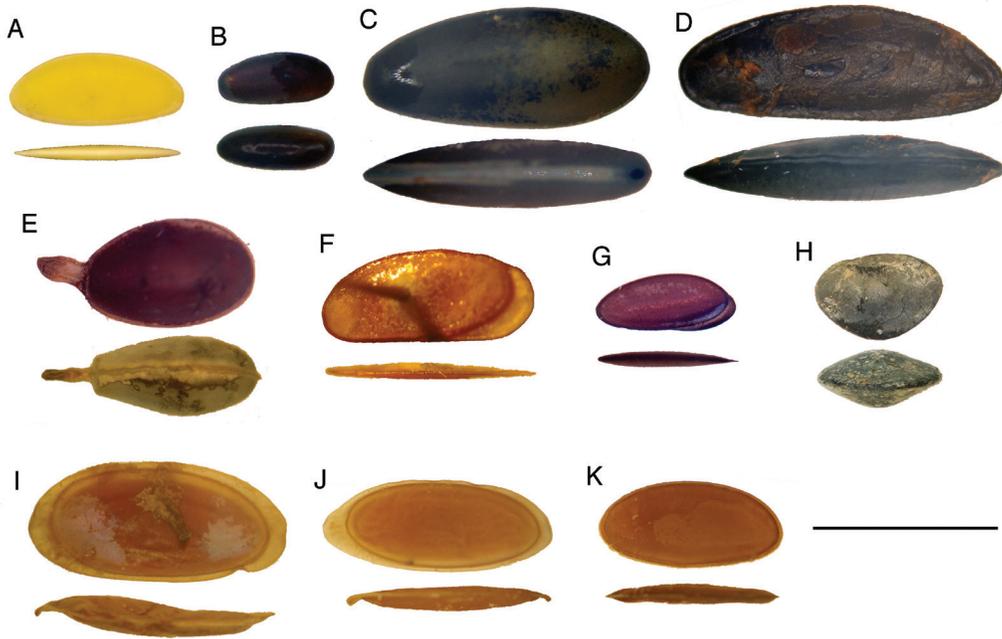


Fig. 2. Eggs of Phaneropterinae (above dorsal view, below lateral view). A–D. ‘Typical’ eggs: A. *Elimaea subcarinata*; B. *Poecilimon pergamicus*; C. *Polysarcus denticauda*; D. *Zeuneria biramosa*; E–H Peculiarly shaped eggs: E. *Debrona cervina*; F. *Tropidonotacris grandis*; G. *Ectomoptera* sp.; H. *Phlaurocentrum mecopodoides* [from Massa 2013; length 3.2 mm (Massa, per email)]; I. *Arnobia ocellata*; J. *Arnobia* sp.; K. *Stictophaula armata*. Scale bar: 5 mm.

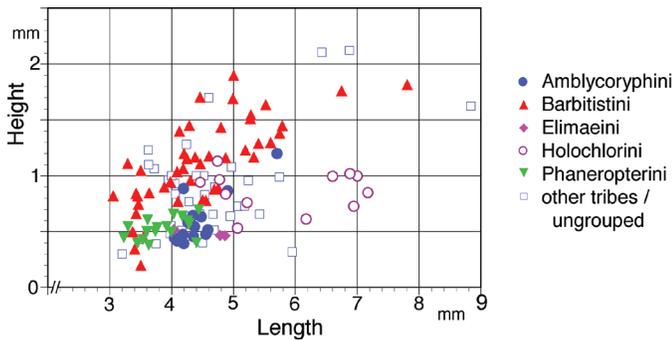


Fig. 3. Dimensions of eggs in different phaneropterine tribes.

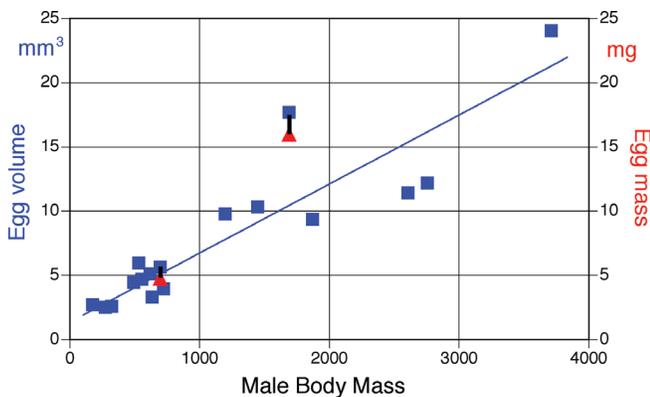


Fig. 4. Relationship of egg volume and egg mass to body size (proxy male body mass) in the genus *Poecilimon* s.l. (data of male body mass from Vahed and Gilbert 1996, Borissov et al. 2023; data of egg mass from Hartley and Warne 1972, Reinhold and Heller 1993).

of six East African species (fig. Mepo 41, p.179). In some species, either the longitudinal groove or the hook may be absent. However, the eggs of *Griffiniana duplessisae* Naskrecki & Bazelet, 2012 [and likely those of *Macroscirtus acutipennis* (Karsch, 1886) as per Eluwa 1970 and *Corycoides kraussi* Kirby, 1906 as per Eluwa 1971] lack both of these characteristics, described as rounded spindle-shaped (see Naskrecki and Bazelet 2012, fig. 2K). In certain species, such as those in the genus *Philoscirtus*, the choria (egg coverings) exhibit unusually strong sculpturing (see fig. Mepo 41 in Hemp 2021).

The egg shape in the few studied Phyllophorinae closely resembles that of Mecopodinae. In *Phyllophorella queenslandica* Rentz, Su & Ueshima, 2009, both a groove (referred to as sulcus by Rentz et al. 2009) and a hook are visible. In *Siliquofera grandis* (Blanchard, 1853), only the groove is recognizable, distinguished by a different chorion coloration (Korsunovskaya et al. 2020, fig. 2F). The eggs of *Phyllophorina kotoshoensis* Shiraki, 1930 exhibit a similar shape but lack both a groove and a hook (Fig. 5E).

Pseudophyllinae (16 species studied)

Examples of pseudophylline eggs are depicted in Fig. 5F–J. Historically, Pseudophyllinae eggs have been documented in six studies, with five dealing with a single species each (Cappe de Baillon 1920, Leroy 1969, Eluwa 1975, Vera 2010, Rentz et al. 2010), and one covering two species (Rentz et al. 2015). Most of these papers do not mention others, except for Rentz et al. (2015), which refers to Rentz et al. (2010), and Leroy (1969), which cites Cappe de Baillon (1920).

In contrast to other subfamilies, the eggs of nearly all pseudophylline species exhibit distinct structural differences between both poles and the surrounding regions (up to half of the egg’s length). Eluwa (1975) observed the oviposition (in wood), and his description may also be valid for most other species: “The anterior one-fifth of the egg is covered by a parchment-like spongy

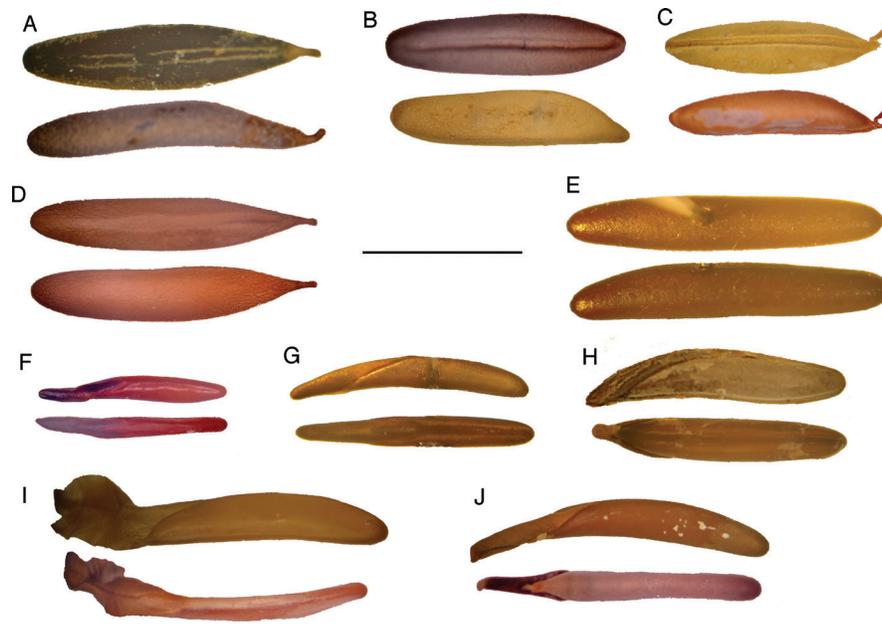


Fig. 5. Eggs of Mecopodinae (A–D), Phyllophorinae (E) and Pseudophyllinae (F–J) (above dorsal view, below lateral view). A. *Mecopoda elongata*; B. *Afronemopoda preussiana*; C. *Leprosirtus granulatus*; D. *Apteroscirtus densissimus*; E. *Phyllophorina kotoshoensis*; F. *Zabalius apicalis*; G. *Pseudotomias usambaricus*; H. *Gnathoclitia vorax*; I. *Onomarchus cretaceus*; J. *Onomarchus uninotatus*. Scale bar: 5 mm.

process which during oviposition is moulded into a flat strip of tissue along the plane corresponding to the broad sides of the egg." The eggs laid by a female of *Onomarchus cretaceus* (Serville, 1838) align well with this description (Fig. 6), although the strip is much longer than that illustrated by Eluwa (1975) for *Zabalius apicalis* (Bolívar, 1886). On the other hand, in *Acauloplacella hasenpuschae* Rentz, Su & Ueshima, 2010 (Rentz et al. 2010) and *Mastighaphoides tuberculatus* Rentz, Su & Ueshima, 2015 (Rentz et al. 2015), the strips are smaller and assume different shapes. Eggs of *Sathrophyllia rugosa* (Linnaeus, 1758) (Cappe de Baillon 1920) and *Aphractus acuminatus* Brunner von Wattenwyl, 1895 (Vera 2010) exhibit essentially similar shapes, although eggs taken from deceased females may not fully display their natural form. While the eggs of most species in this subfamily are cylindrical, they are exceptionally flat in *Cocconotus insularis* (Bruner, 1906) (as *Bliastes insularis* in Leroy 1969). Even in this species, "the egg has a well-marked polarity, with one end lined with a very characteristic fishnet extending over one of the keels of the egg in its anterior third" (Leroy 1969). Surprisingly, the eggs of *Chloracantha garradunga* Rentz, Su & Ueshima, 2015—originally described under Mecopodinae (Hebard 1922)—lack a strip or grooves and are flattened, similar to typical phaneropterine eggs (Rentz et al. 2015).

Tettigoniidae

Tettigoniinae (59 species studied),
Bradyporinae (14 species studied), Listrosclidinae
(18 species studied), Hetrodinae (4 species studied),
and Hexacentrinae (3 species studied)

Examples of eggs from these five subfamilies are represented in Fig. 7A–H. To the best of our knowledge, nearly all species within these subfamilies exhibit typical ovoid-cylindrical or sausage-shaped "tettigoniid" eggs, with only very few being slightly wider than high.

Conocephalinae (23 species studied)

Examples of conocephaline eggs are depicted in Fig. 7I–J. As highlighted by Ingrisch (1995), eggs in this subfamily are frequently characterized by a thin-elongate shape featuring a high aspect ratio (refer to Fig. 1B) and a semi-transparent appearance. It is worth noting that the aspect ratio values for both Euconchophorini species studied are the lowest within the subfamily.

Meconematinae (15 species studied)

Examples of meconematine eggs are presented in Fig. 7K–M. The eggs within this subfamily, while small as expected for the body size of the species, exhibit unusual diversity. This diversity may be partly attributed to the possibility that the tribe Phlugidini does not belong to Meconematinae; in the phylogenetic tree of Mugleston et al. (2018), it is positioned distant from the other Meconematinae. The eggs of this tribe differ from those of all other tettigoniid subfamilies and bear a slight resemblance to those of the phaneropterid Pseudophyllinae. In all four examined species (from Africa, Australia, and South America), one pole of the egg terminates in a 'cap' (Rentz 2001) or 'egg cover plate' (Eichler 1938). Following oviposition, this plate lies flat on the plant surface (see, e.g., Leroy 1969) and is opened by the hatching nymph (Eichler 1938).

However, even the eggs of the remaining and possibly closely related Meconematinae (Meconematini and Phisidini, according to Mugleston et al. 2018) display significant diversity. Notably, the eggs of *Amyttosa insectivora* (Fig. 7N; from Naskrecki 2008) stand out, differing from all other Tettigoniioidea and resembling those of many Phasmatodea. These insects drop their eggs to the ground, where ants find, bury, and securely store them underground (see Hughes and Westoby 1992; Naskrecki 2008). Favorable preconditions for the evolution of such behavior may have been eggs like in *Amytta* (Fig. 7K) with deep indentations in the shell, although the function of these indentations remains unknown.

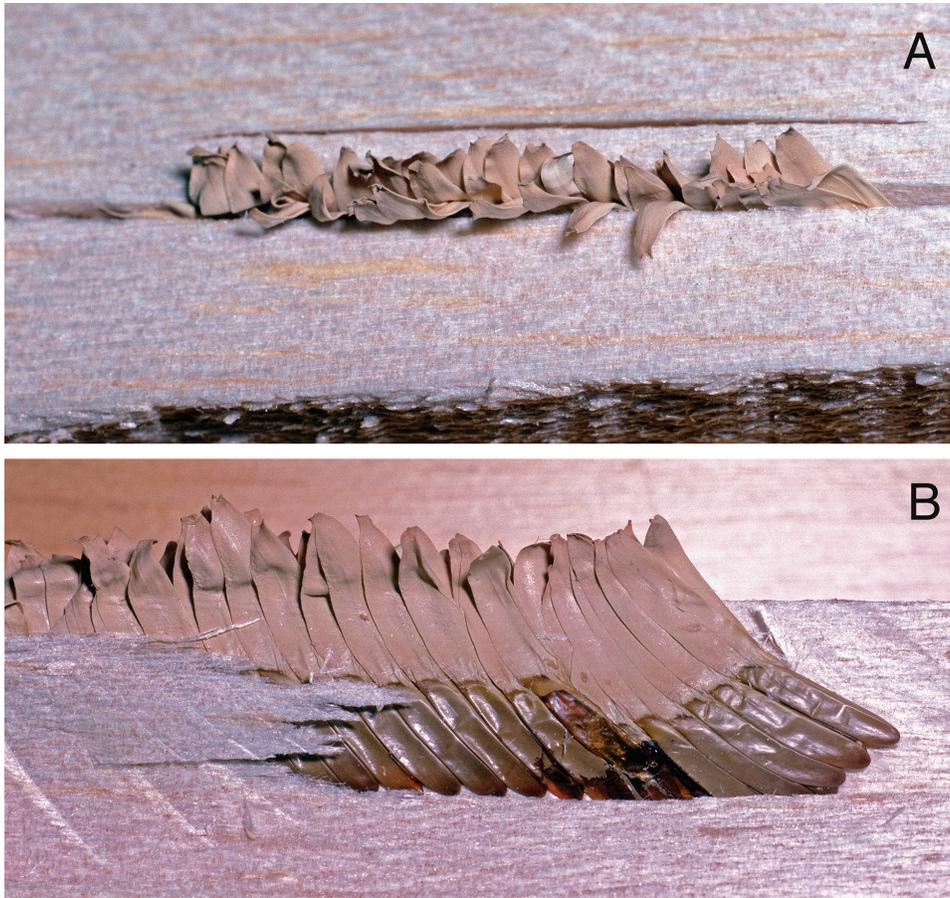


Fig. 6. Eggs of *Onomarchus cretaceus*. A. Oviposition site with only the strips of the eggs visible; B. Wood opened with eggs completely visible (eggs damaged - dried out).

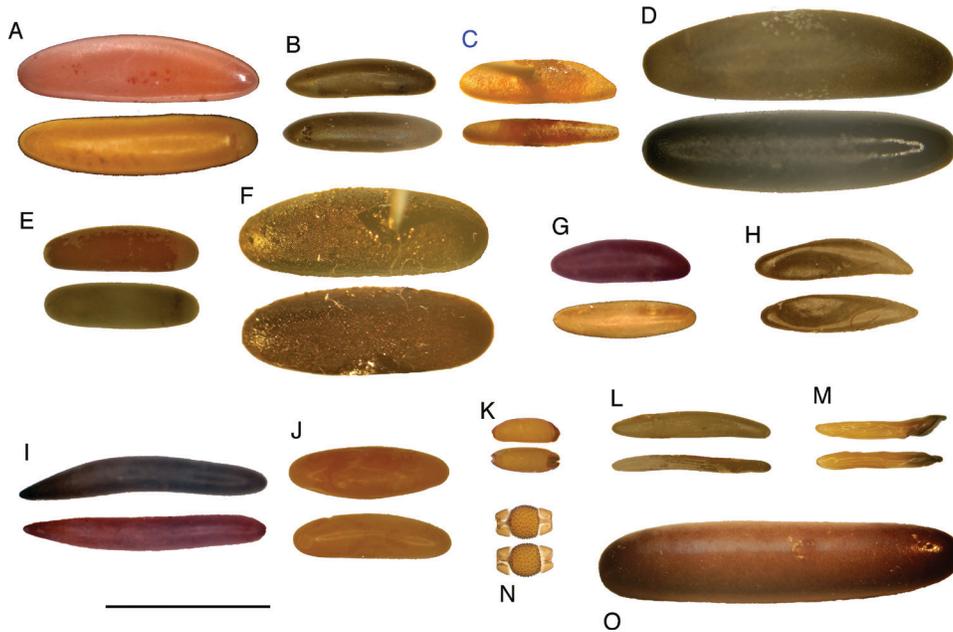


Fig. 7. Eggs of Tettigoniidae (above dorsal view, below lateral view). A. *Glyphonotus sinensis* (Tettigoniinae); B. *Parnassiana fusca* (Tettigoniinae); C. *Uromenus idomenaeus* (Bradyporinae); D. *Deracantha onos* (Bradyporinae); E. *Neobarretia imperfecta* (Listrosclidiinae); F. *Spalacomimus verruciferus* (Hetrodinae); G. *Hexacentrus unicolor* (Hexacentrinae); H. *Aerotegmina kilimanjarica* (Hexacentrinae; egg damaged - dried out); I. *Afroagraecia* sp. (Conocephalinae); J. *Amblylakis nigrolimbata* (Conocephalinae); K. *Amytta mramba* (Meconematinae); L. *Neophisis siamensis* (Meconematinae); M. *Phlugidia kisarawe* (Meconematinae); N. *Amyttosa insectivora* (Meconematinae; from Naskrecki 2008); O. *Saga natoliae* (Saginae; dorsal = lateral view). Scale bar: 5 mm.

In terms of general shape, the other Meconematini exhibit typical tettigoniid eggs, but in African species, their two poles are more distinct (Fig. 7K; Naskrecki 2008). Finally, eggs of Phisidini mostly feature high aspect ratio values, meaning they are long and slender (see Fig. 7L).

**Saginae (5 species studied) and other subfamilies
(Austrosaginae, Lipotactinae, Phasmodinae,
Tympanophorinae, Zaprochilinae; 16 species studied)**

An example of a saginae egg is shown in Fig. 7N. Saginae stands out among Tettigonioida species, featuring some of the largest eggs (refer to Suppl. material 2). In terms of shape, the eggs of Saginae, as well as those from other subfamilies with available data (though not illustrated here), exhibit the typical ovoid-cylindrical or sausage-shaped morphology characteristic of 'tettigoniid' eggs.

Discussion

The eggs of most Tettigonioida exhibit a relatively simple shape, lacking the diversity observed, for instance, in Phasmatoidea. This apparent uniformity may stem from the prevalent practice of depositing eggs within the substrate, whether in various types of plant material or in the ground (see Gwynne 2001). In such environments, ovoid-cylindrical eggs, resembling cylinders with rounded ends, appear to be the most advantageous. Only a few groups deviate from this general pattern, with the subfamily Phaneropterinae being the most notable exception.

As evident from the presented data and highlighted by various authors, the eggs of Phaneropterinae consistently exhibit a flattened shape, albeit to varying degrees. The thinnest eggs, as seen in *Phaneroptera*, *Eurycorypha*, and *Elimaea*, are typically inserted between the upper and lower epidermis of leaves (first described by Riley 1874; see figures, e.g., in Hemp 2021, fig. Eury 82, Naskrecki and Guta 2019, fig. 44). The females of this subfamily display remarkable skill in egg placement (see figures in Massa and Rizzo 1998), capable of depositing eggs even within sheets of paper (Grasse and de Vichet 1924, own observations of *Letana inflata* (Brunner von Wattenwyl 1878) laying into blotting paper). The short, sickle-shaped ovipositors of many Phaneropterinae species are well-suited for this behavior.

However, oviposition in phaneropterines exhibits considerable diversity (see e.g., Rentz 2010; Hemp 2021) and is not always confined to the substrate. Even species with thin and flat eggs can use places other than leaf edges. While most *Eurycorypha* species insert their eggs into leaves, some (e.g., *E. pseudomeruensis* Hemp, 2017) adhere the eggs to the surface of leaves or in crevices (Hemp, 2021), and others (e.g., *E. curviflava* Hemp, 2017) prefer foamy material (Hemp, 2021). The use of fluids to adhere eggs to plants appears to be crucial for phaneropterines. Many species directly attach eggs, uncovered, to leaves or twigs, as first described by Riley (1874; Fig. 8). Even species depositing their eggs in leaves often employ glue, as noted by Riley (1874) and Vosseler (1909). The use of fluids is also observed in ground-laying barbitistines (Reinhold 1999; also in *Poecilimon affinis* (Fridvaldszky, 1868), Fig. 8). Some species even attach additional material to the eggs, possibly to conceal them or prevent desiccation (*Polichne*: Rentz 1996; *Arantia*, *Terpnistria*: Naskrecki and Guta 2019). Little is known about the nature of these fluids or their origin, which could be from glands in the oral cavity (as the mouthparts are highly active during oviposition), the abdomen, or both. The adhesive function of these fluids may be central to understanding the evolution of egg shape; flattened eggs provide a larger surface area for adhesion, ensuring better stickiness and reduced risk of falling. This holds true even for eggs too thick to be inserted into

plants. Following this line of reasoning, thin eggs placed in leaves might have evolved as a secondary adaptation.

The flatness of eggs in Phaneropterinae exhibits a notable degree of flexibility but is almost never entirely lost, even when genera "return" to ground oviposition. The tribe Barbitistini is a flightless and speciose group in the western Palearctic, well supported by molecular data (Ullrich 2010, Grzywacz et al. 2018, Borissov et al. 2023). Some species within the genus *Leptophyes*, a member of this tribe, produce eggs ranging from flat to very flat (see Suppl. material 2). These eggs are often laid in bark or old galls, deviating from the typical leaf deposition (Deura and Hartley 1990; Cerasa and Massa 2016). Some other genera oviposit in bark and soil [species of *Barbitistes*, see Gottwald et al. 2002; *Metaplastes ornatus* (Ramme, 1931), own unpublished data] but have thicker eggs. The largest genera of the Barbitistini tribe, *Isophya* and *Poecilimon* s.l., predominantly lay eggs in the ground (Fig. 8G–H; see also Heller 2021). Despite their thickness, these eggs maintain a flattened shape (wider than high), with *Poecilimon pergamicus* (Fig. 2B) coming closest to a cylindrical form (see Suppl. material 2). Even in species with peculiar egg shapes (Fig. 2E–H), the flattened form persists. In some of these species, the eggs exhibit flat lateral extensions. Given the thinness of these eggs, one may hypothesize that these flat parts serve to stabilize the egg, particularly during oviposition. The distinct shapes of these extensions (see Fig. 2F–G, I–K) suggest a separate origin in at least two groups.

While gluing appears to be infrequent in other subfamilies, related traits are known. Ingrisch (1998) reported a secreted envelope around each egg in *Pseudosubria*, deemed "unique in tettigoniids." For *Acanthopus discoidalis* (Walker, 1869), Power (1958) described nests of egg packets, each consisting "of a hard roughly rectangular pellet of clay in which the eggs are firmly cemented." Although more instances may emerge with increased research, gluing and the distinct egg shape remain characteristic of Phaneropterinae.

Egg color does not appear strictly correlated with oviposition. Eggs laid in leaves may be bright, as seen in *Elimaea* (Fig. 2A) and *Eulioptera*, or dark brown, as in *Eurycorypha*.

Most species in the subfamilies Mecopodinae and Pseudophyllinae feature cylindrical eggs. These eggs are distinguished by variations in the structure of both egg poles. While many mecopodines have a stalk-like process on one pole (Fig. 5A, C, D), in Pseudophyllinae, nearly half of the egg is typically modified. Both structures were described by Cappe de Baillon (1920) and are thought to be crucial for air regulation, a conclusion based on egg anatomy. Rentz et al. (2015) suggested that one "end protrudes slightly above the substrate, presumably to capture moisture to prevent the egg from desiccating." However, water uptake for development is also necessary (Vosseler 1909, Ingrisch 1988). In *Onomarchus cretaceus*, one end even carries a large soft elongation (strip; Fig. 6), possibly serving the same function. Such modifications, potentially produced by glands, may be more widespread in the subfamily but not easy to detect in dead specimens.

Many other subfamilies exhibit simple ovoid-cylindrical eggs, including Conocephalinae with high aspect ratios (Fig. 1B). The diverse egg shapes within Meconematinae are described above, and it remains to be seen if other intriguing egg shapes, akin to that of *Amyttosa insectivora* (Naskrecki 2008), will be discovered. For example, what does the eggs of the minute *Phlugiolopsis* look like? The lack of information on egg characteristics for certain subfamilies and tribes, such as Microtettigoniinae and Pterochrozinae, underscores the importance of further research, particularly when considering egg size. In our dataset of approximately 350 tettigonioid species, egg volume ranged from 0.1 to 46 mm³, already exceeding the scale presented in Church et al. (2019b) by more than one order of magnitude. However, data for very small species are still absent.



Fig. 8. Phaneropterine eggs in situ and oviposition. A–F. Eggs on and in plants after oviposition. A, B. Eggs glued on leaves: A. *Catoptropteryx aurita*; B. *Gonatoxia maculata*; C–E. Eggs inserted into leaves: C. *Gonatoxia immaculata*; D. *Eurycorypha resonans*; E. *Plangia multi-maculata*; F. Eggs inserted into twigs: *Dioncomena tanneri*; G, H. Oviposition into the ground: *Poecilimon affinis*, G. Female ovipositing; H. Immediately after oviposition. Note the moist sand around the oviposition site.

Conclusions

It appears that the evolution of egg shape in Tettigoniidae, particularly in the subfamily Phaneropterinae, might have been influenced by oviposition behavior and method of attaching eggs to plants. The flattened shape of the eggs in Phaneropterinae is suggested to be advantageous for gluing them to surfaces. Flat eggs might provide better stability and adhesion, thereby reducing the risk of eggs falling down. The flattened shape is even maintained when some genera within the subfamily return to ovipositing in the ground.

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Supplementary material 1

Author: Klaus-Gerhard Heller, Claudia Hemp

Data type: xls

Explanation note: Collection data of studied specimens.

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Link: <https://doi.org/10.3897/jor.33.116173.suppl1>

Supplementary material 2

Author: Klaus-Gerhard Heller, Claudia Hemp

Data type: xls

Explanation note: Species list including measurements and references.

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Link: <https://doi.org/10.3897/jor.33.116173.suppl2>