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Aenigmatistes (Diptera: Phoridae), Aschiza with a ptilinum!

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Abstract. A revised key to *Aenigmatistes* Shelford 1908, is provided. The unknown males of *A. africanus* Shelford 1908, and *A. latifrons* Schmitz 1924, are described along with the unknown female of *A. herero* (Enderlein 1912): and *A. londti* sp. n. is described from a male from Malawi. The anterior face of the peculiar frons of *Aenigmatistes* is interpreted as a permanently exposed ptilinum, which has elvolved independently of the ptilinum of Schizophora (which is invaginated after adult emergence is complete) or of the ptilinum of some Syrphidae (which is lost by contraction after adult emergence).

Key words. Diptera, Aschiza, Phoridae, key, new species, ptilinum, phylogeny.

Introduction

Shelford (1908) described the genus *Aenigmatistes* on the basis of a single female. He rightly emphasised the curious frons, whose anterior part, facing forwards, is almost at right angles to the posterior part, facing upwards (cf. Figs 18—19). This feature subsequently proved to be characteristic of the males also (e. g. Figs 1—2). Otherwise our knowledge of *Aenigmatistes* has largely increased by the addition of new species; culminating in Beyer's (1959) key to the males of seventeen species, but omitting the two species then only known in the female sex. The latter, however, are included in Schmitz's (1933) key to the known females.

While Beyer's key has been useful for the specialist, it has proved frustrating for others. The key has a number of couplets based on unsatisfactory distinctions. Furthermore it includes a number of significant errors. It perpetuates Schmitz's (1929) error that characterised *A. foveolatus* Schmitz as lacking scutellar bristles. The type lacks bristles, but their sockets are present. The bristles are only absent from the specimen through damage. Beyer adds errors of his own. For example he attributes ocelli to *A. ocelliscaptus* Schmitz, when Schmitz (1955) unequivocally states "Ozellen fehlen gänzlich". Likewise Beyer states that *A. ovalifacies* Schmitz has a hair palisade on the fore tibia when Schmitz (1941) clearly states "Vorderschienen ohne Börstchen und ohne Palisade".

Having experienced difficulties with Beyer's key, I drafted an alternative. This in turn led to recognition of an undescribed species and of the undescribed males of the two species omitted from Beyer's key. In addition the undescribed female of *A. herero* (Enderlein) has been recognised. In the course of examining a range of specimens I have been led to a re-assessment of the peculiar frons in this genus. This paper presents my revised key, describes the new species and undescribed sexes of known species, and discusses the peculiar frons.

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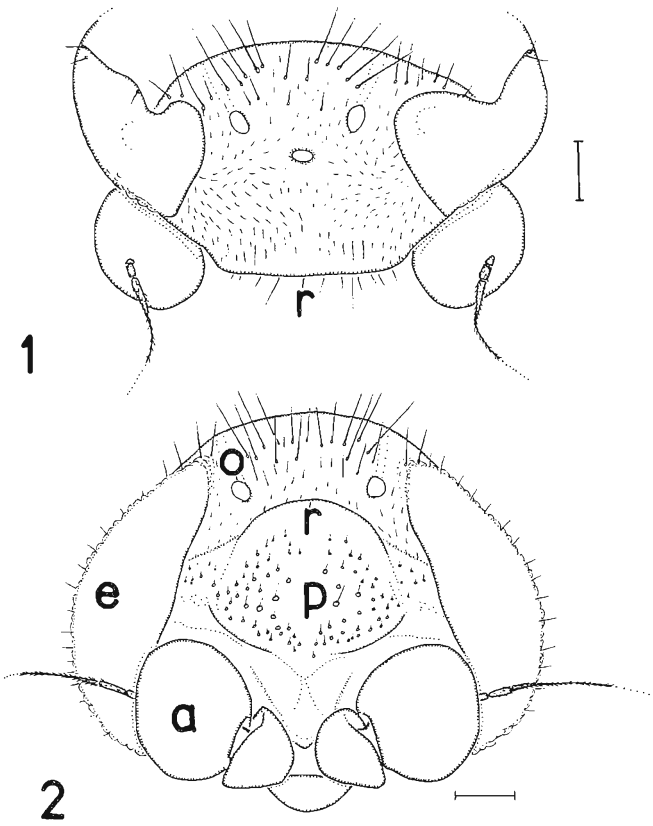


Figs 1—2: *Aenigmatistes foveolatus* male frons. 1, from above; 2, from front. a = antenna (segment 3), e = eye, o = a posterior ocellus, p = ptilinum, r = post-ptilinal ridge (or arch). (Scale bars = 0.1 mm).

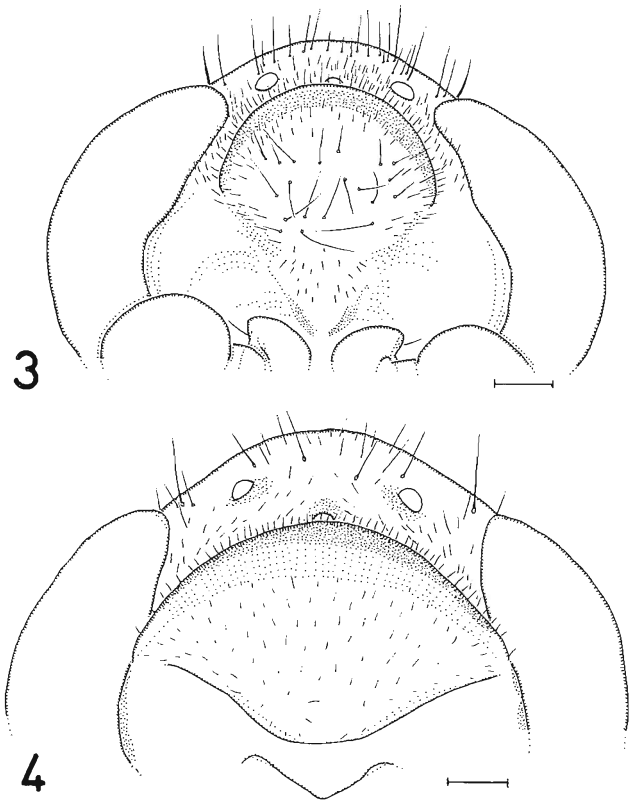
Key to species of *Aenigmatistes*

(The females of most species are unknown, so the key to females needs to be used with caution).

1 Wings fully developed. Males 2
— Wings vestigial (Figs 13—14). Females 22

Males:

2 Ocelli absent 3
— At least the posterior pair of ocelli present 8
Note: doubtful cases are keyed both ways.



Figs 3—4: *Aenigmatistes* males, frons from front. 3, *A. africanus*; 4, *A. herero*. (Scale bars = 0.1 mm).

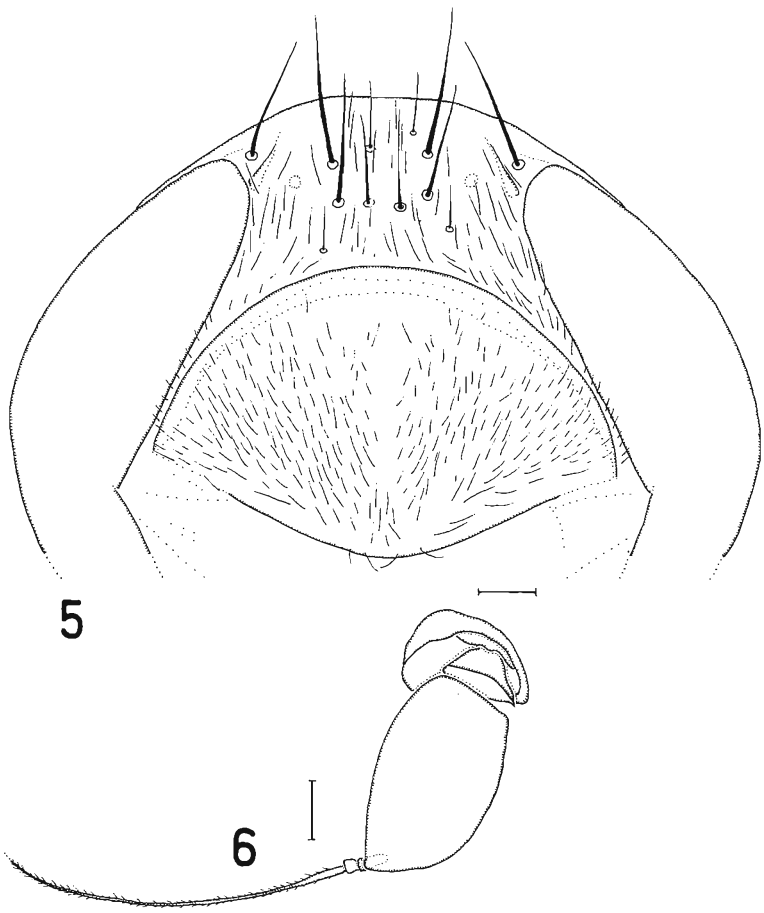
3 A pair of bristles present in middle of upper face of frons ("pre-ocellar" bristles) . 4
— No "pre-ocellar" bristles present 6
4 With six bristles on scutellum. Wing length less than 5 mm 5
— With 12—14 bristles on scutellum. Wing length more than 7 mm .....
..... *ocelliscaptus* Schmitz, 1955
5 With two, widely separated, "pre-ocellar" bristles. With only three bristles on notopleuron ..... *pictus* Schmitz, 1955
— With four "pre-ocellar" bristles in a transverse row (Fig. 5). With six bristles on notopleuron 11
6 Scutellum without hairs or bristles. (Also the scutum lacks bristles, and the hairs of the tegula are stronger than any on scutum or mesopleuron) ... *nudus* Schmitz, 1924
— Scutellum with bristles 7
7 Wing length >3.0 mm ..... *ovalifacies* Schmitz, 1941
— With length <2.5 mm ..... *ocelliprivus* Schmitz, 1941
8 A pair of pre-ocellar bristles present, adjacent to, or just in front of, anterior ocellus 9
— No pre-ocellar bristles 11

9 The transition from the upper face of the frons to the anterior face marked by a sharply demarcated arch-shaped, angled in profile, ridge (e. g. Figs 2—5) 10
— This transition gradual and there is no arch-shaped ridge ..... *priscus* Beyer, 1959
10 Inner margin of eye very close to posterior ocellus. An antero-lateral pair of bristles on upper face of frons ..... *reichenspergeri* Schmitz, 1953
— Inner margin of eye well separated from a posterior ocellus. No antero-lateral bristles on upper face of frons ..... *angolanus* Schmitz, 1955
11 At most with only the two posterior ocelli present, and these are reduced (Fig. 5) or even absent. Third antennal segment clearly longer than broad (Fig. 6) ..... *elongatus* Beyer, 1959
Note: If scutum and scutellum lack bristles return to couplet 6.
— With three ocelli. Third antennal segment never as elongated as in Fig. 6 12
12 Hairs on frons more or less uniform in size ..... *scutellatus* (Becker, 1909)
— Some hairs on vertex of frons are clearly longer and more robust (e. g. Figs 1—4). 13
13 Hind tibia with at least two postero-dorsal bristles in basal half. Mesopleuron bare ..... *transvaalensis* Schmitz, 1940
— Hind tibia with at most a single postero-dorsal bristle in basal half. Mesopleuron with hairs, at least in upper half 14
14 Front tibia with 1—3 short, spine-like, bristles in basal half (Figs 7—8) ..... *herero* (Enderlein, 1912)
— Front tibia without bristles in basal half 15
15 Antero-dorsals of hind tibia hair-like. Legs yellowish grey. (Anterior ocellus at most only half diameter of a posterior ocellus) ..... *suppar* Schmitz, 1955
— Antero-dorsals of hind tibia usually more spine-like; when reduced (e. g. Fig. 12) then the legs are brown 16
16 A longitudinal hair palisade on posterior face of front tibia (Fig. 9) 17
— Front tibia without a longitudinal hair palisade 18
17 Vein h brown and it slopes backwards (Fig. 21). Scutellum with 8—12 bristles. Haltere dark greyish brown (Frons as Fig. 20) ..... *latifrons* Schmitz, 1924
— Vein h pale and almost straight (Fig. 22). Scutellum with 6—8 bristles. Haltere pale brown. (Frons as Fig. 3) ..... *africanus* Shelford, 1908
18 Hind tibia with only antero-dorsal bristles in basal three quarters, and even these may be weak and few in number (Fig. 12) 19
— Hind tibia with both antero-dorsals and anterior bristles in basal three quarters .. 20
19 Hind tibia with a single, longitudinal, dorsal hair palisade (Fig. 12). (Frons as Figs 1—2) ..... *foveolatus* Schmitz, 1929
— Hind tibia with two longitudinal hair palisades, one dorsal and a weaker postero-dorsal, and with a row of robust hairs between them (Fig. 24) (Frons as Fig. 23; hypopygium as Figs 25—26) ..... *londti* sp. n.
20 Costal section 1 <2.5x section 2 ..... *armiger* (Brues, 1910)
— Costal section 1 >2.5x section 2 21
21 Haltere knob dark brown ..... *blattiformis* (Schmitz, 1933)
— Haltere knob pale brown, and in part devoid of pigment ..... *cilipes* Schmitz, 1927

Females:

Note: The females of most species are unknown. Certain identification will depend, therefore, on association with males.

22 Thorax and abdominal tergites with some long hairs, as well as general clothing of short hairs 23
— Thorax and abdominal tergites with clothing of short hairs only 25
23 The long hairs on thorax and abdomen are largely restricted to hind margins of the sclerites 24
— The long hairs in these positions are clearly not restricted to hind margins of sclerites ..... *reichenspergeri* Schmitz
24 Abdomen generally brown ..... *angolanus* Schmitz
— Abdomen very dark brown ..... *pictus* Schmitz



Figs 5—6: *Aenigmatistes elongatus* male. 5, frons from front; 6, right antenna, inner face. (Scale bars = 0.1 mm).

25 Upper frons relatively short but very broad (e. g. Fig. 15) 26
— Upper frons relatively long and not so broad (e. g. Fig. 19) 28
26 Wing rudiment only about half length of side of abdominal tergite 2 *armiger* (Brues)
— Wing rudiment about as long as side of abdominal tergite 2 (Fig. 13) 27
27 Hairs on wing rudiment in two rows along the leading edge only *blattiformis* Schmitz
— Hairs on wing rudiment in several rows, not restricted to leading edge (Fig. 13) ... . *herero* (Enderlein)
28 Palp with strongly differentiated apical bristle (Fig. 18). Eyes relatively large (Fig. 19) ..... *latifrons* Schmitz
— Palp without such a differentiated bristle. Eyes relatively small .... *africanus* Shelford

Aenigmatistes Shelford, 1908

Aenigmatistes Shelford, 1908: 150
Type-species: *A. africanus* Shelford, by monotypy.

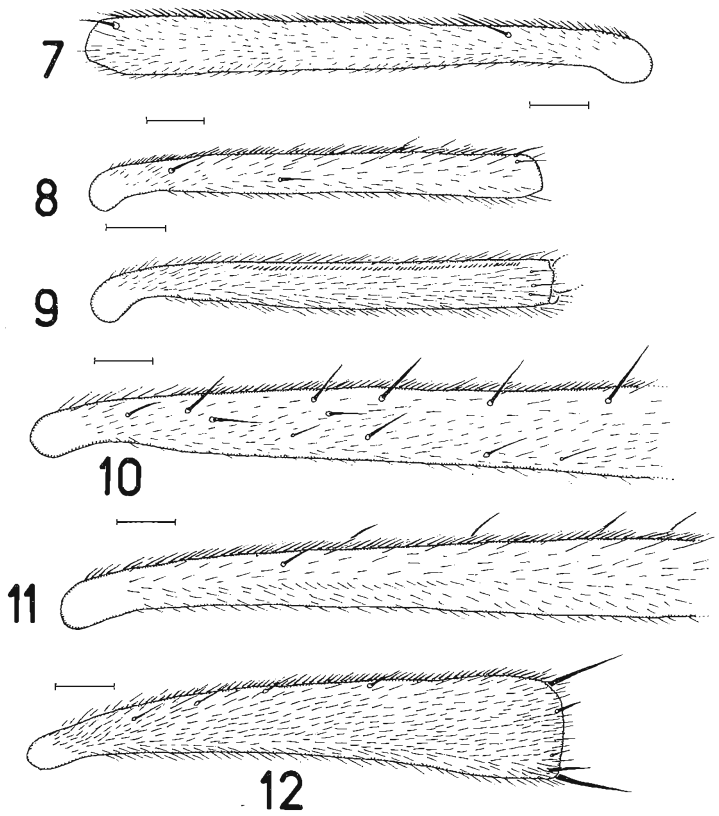
Diagnosis: Male: Frons with upper face almost at right angles to lower face, typically with the angulation forming a sharply-ridged arch. The lower face of frons below this arch essentially unsclerotised, and bears scattered hairs. Supra-antennal bristles lacking. Upper face of frons without a median furrow and with chaetotaxy tending to be reduced from the front rearwards. Arista pre-apical in position. Thorax a little flattened dorso-ventrally. Anterior spiracles somewhat high on pleural region. Mesopleuron undivided and usually hairy. Hind tibia with one or more longitudinal hair palisades. Mid tibia usually with at least one hair palisade. Tibiae generally with scattered, short bristles. Wing with vein 3 unforked and costal cilia short.
Female: Dorso-ventrally flattened. Abdominal tergites occupy entire dorsal side. Thorax with tergites fused into a single structure, embracing the dorsally-situated anterior spiracles. Wings reduced to rudiments. Halteres absent. Frons modified as in male. Upper frons broader than long. Ocelli absent. Chaetotaxy greatly reduced or absent. Arista as in male. Legs as male, but with femora and tibiae much shortened.

Aenigmatistes africanus Shelford, 1908

Aenigmatistes africanus Shelford, 1908: 151. Holotype ♀, KENYA, Kisumu, Victoria Nyanza (Paris Museum) [Not examined, as it has been lost. A neotype is designated below].

Male (Figs 3, 9, 22): Lower frons as Fig. 3. Upper frons with three well-developed ocelli and differentiated bristles restricted to vertex. Palps and third antennal segments brownish orange. A differentiated bristle at apex of palp. Scutellum with 6—8 bristles. Mesopleuron with numerous hairs. Legs pale brown. Hind tibia with an irregular row of 3—7 anterior and 3—4 antero-dorsal short, spine-like, bristles and a single, dorsal, hair palisade. Mid tibia with a dorsal to antero-dorsal palisade in basal half and a posterior to postero-dorsal palisade in apical half, but dorsally with spaced hairs, which are more spine-like in lower half. With 2—4 short, antero-dorsal spines in upper half and 2—3 anterior spines near middle. Front tibia with a longitudinal, postero-dorsal, hair palisade, starting just before mid point (Fig. 9). Haltere knob mainly brown, but with paler patches. Wing length 3.45—3.58 mm. Costal index 0.63—0.65. Costal ratios 1.57—1.63 : 1. Costal cilia 0.06 mm long. With 3—6 hairs at base of vein 3. With 2—3 hairs on axillary ridge. Vein Sc fading away long before reaching R1. Thick veins pale greyish yellow. Thin veins pale grey. Membrane only lightly tinged grey. Vein h pale and angle with costa of at least 75° (Fig. 22).

Material examined: 2 ♂, MALAWI, Zomba, 1100 m altitude, at light, 24—27. IX. 1980 (J. G. H. Londt & B. R. Stuckenberg). In view of the loss of the holotype of *A. africanus*, one of these specimens has been designated the Neotype. It is deposited in the Natal Museum, South Africa. The other specimen is deposited in the University Museum of Zoology, Cambridge.



Figs 7—12: *Aenigmatistes* males. 7—9, front tibiae. 7—8, *A. herero* anterior face of a larger and a smaller specimen; 9, *A. africanus* posterior face. 10—12, hind tibiae. 10, *A. herero* anterior face; 11, *A. herero* posterior face; 12, *A. foveolatus* anterior face. (Scale bars = 0.1 mm).

Aenigmatistes elongatus Beyer, 1959

Aenigmatistes elongatus Beyer, 1959: 56. Holotype ♂, ANGOLA, Benguela District, Marco de Canavezes (Musée Royal de l'Afrique Centrale, Tervuren, Belgium) [not examined].

Male (Figs 5—6): It is evident that the posterior pair of ocelli may be so reduced that they are seemingly absent. Such specimens would run to couplet 3, rather than 4, in Beyer's (1959) key.

Material examined: 1 ♂, ZAMBIA, Lusaka, I. 1980 (R. A. Beaver).

Aenigmatistes foveolatus Schmitz, 1929

Aenigmatistes foveolatus Schmitz, 1929: 200. Holotype ♂, SUDAN, Gell River Post, 70 miles from Bahr-el- Gebel. (British Museum — Natural History) [examined].

Male (Figs 1—2, 12): as pointed out above, Schmitz (1929) mistakenly reported that

this species had no scutellar bristles. In Beyer's (1959) key this species should have run out at couplet 13 or 15, not at 10.

Material examined: Holotype ♂. 13 ♂, SENEGAL, Forêt de Fathala, Forêt de Bandia, and Ferlo Fété Olé 16—17. VIII, 20. IX. and 13. XII. 1976 respectively (G. Couturier).

Aenigmatistes herero (Enderlein, 1912)

Metopotropis herero Enderlein, 1912: 52. Holotype ♂, NAMIBIA, Aubes. (Stettiner Zoologisches Museum) [not examined].
Conoprosopa herero Brues, 1915: 105.

Male (Figs 4, 7—8, 11): The males of this species do not key out satisfactorily in Beyer's (1959) key.

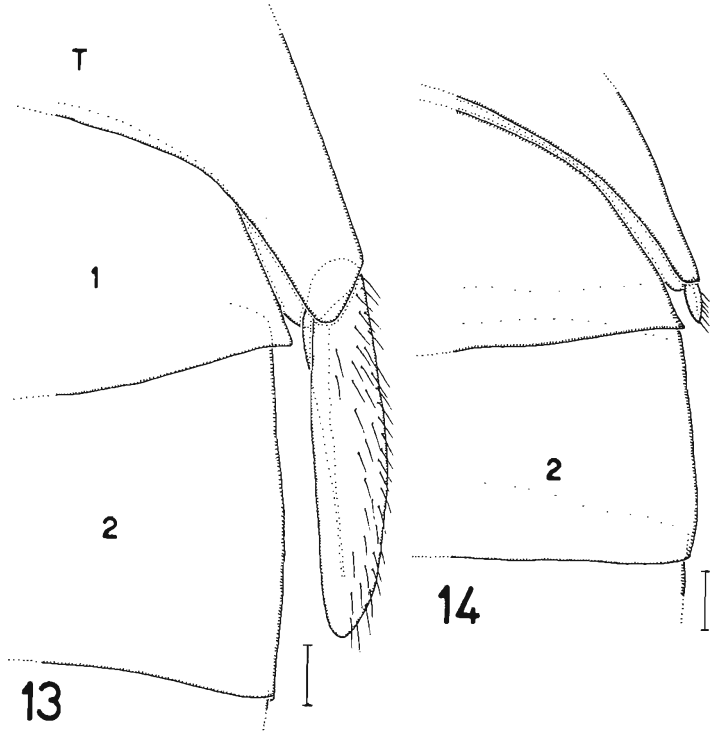
Female (Figs 13, 15—17): Generally brown, but head and thorax tending to be paler. Frons, thorax and abdomen devoid of bristles. The clothing hairs weakest on frons and strongest on abdominal tergites. Frons as Figs 15—16. The pale brown antennae and palps as Fig. 17. The only differentiated bristle at apex of palp is very short. The thorax is longer than the first abdominal tergite. Wing rudiment as Fig. 13. Abdominal venter with a few hairs along midline of segments 4—5 and many in a broad band across the whole of 6. The pale cerci are short, but broad, with pale hairs. Legs pale dirty yellow. Fore femur broad. Fore tibia with a short dorsal and antero-dorsal spine at apex. Fore tarsus with segment 5 almost as long as metatarsus. Segments 2—4 short. Segments 1—4 with a short, blunt, postero-dorsal, apical spinule. Mid femur somewhat broad. Basal half of mid tibia with 1—4 (usually 3) strong antero-dorsal spines and sometimes a weaker postero-dorsal one as well. The apical spurs and spines all strong. Mid tarsus with 5—6 spines on metatarsus, 3—5 on segment 2, and two on both segments 3 and 4. Hind femur sharply broadening in first quarter, so that dorsal edge forms a bulge. Hind tibia with 3—5 (usually 3) antero-dorsal spines in basal third and 2—4 dorsal (or near-dorsal) spines below these.

Material examined: 1 ♂, 5 ♀, BOTSWANA, Farmer's Brigade, IX. 1986 and IV. 1987 (P. Forchhammer); 1 ♀ Serowe, IX. 1986 (P. Forchhammer). 1 ♂ SOUTH AFRICA, Pietermaritzburg, Merrivale. 20. X. 1979 (B. R. Stuckenberg). 1 ♂ ZIMBABWE, Binga District, 17° 20' S, 28° 04' E, 9. VI. 1988 (C. Tingle). 2 ♂, ZAMBIA, near Namibian border, Sesheke, c. 950 m altitude, X. 1989—III. 1990 (W. Slobbe).

Aenigmatistes latifrons Schmitz, 1924

Aenigmatistes latifrons Schmitz, 1924: 298. Syntype ♀, KENYA, Tana River (Paris Museum). [examined, a syntype ♀ was also found in the Museum Alexander Koenig, Bonn. This specimen has been designated the lectotype and retained in Paris. The Paris specimen then becomes the paralectotype. It has been deposited in Bonn].

Female (Figs 14, 18—19).
Male (Figs 20—21): upper frons brown, but almost black just behind front edge and around ocelli, and as Fig. 20. Palps and third antennal segments pale brownish orange. A differentiated bristle at apex of palp. Scutellum with 8—12 bristles. Mesopleuron with numerous hairs. Legs pale brown. Hind tibia with 8—11 anterior and 1—4 antero-dorsal, short, spine-like bristles and a single dorsal hair palisade.



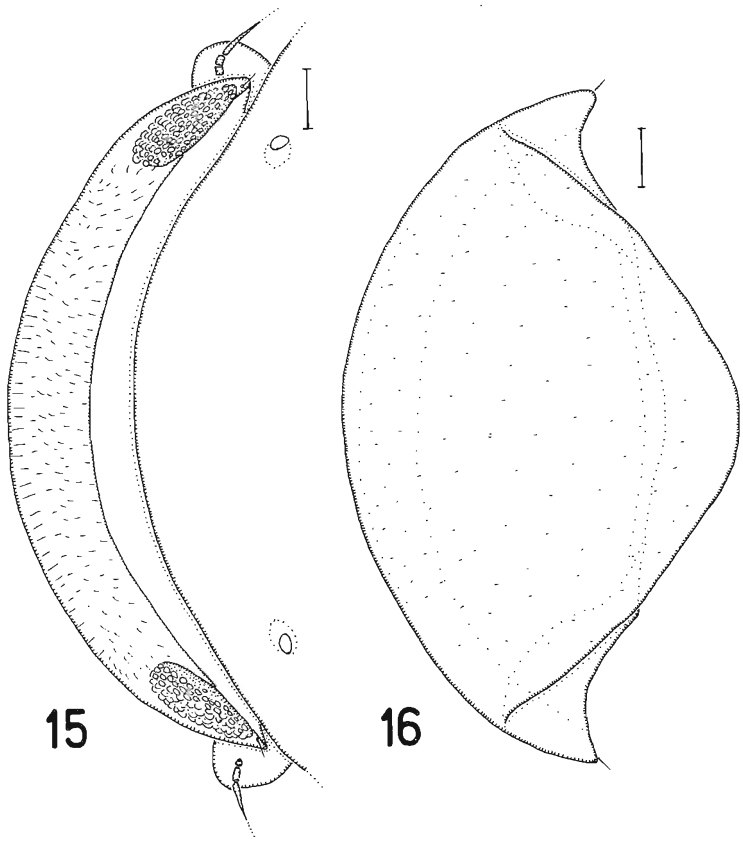
Figs 13—14: *Aenigmatistes* females, wing rudiments from above (T = thorax, 1 and 2 = 1st and 2nd abdominal tergites). 13, *A. herero*; 14, *A. latifrons*. (Scale bars = 0.1 mm).

Mid tibia similar to *A. africanus*, there being an irregular scatter of 4—8 spines on anterior face. Postero-dorsal palisade of front tibia starts well before middle. Haltere with dark greyish brown knob and paler stem. Wing length 3.0—3.4 mm. Costal index 0.61—0.63. Costal ratios 1.22—1.52 : 1. Costal cilia 0.05—0.07 mm long. With 2—7 hairs at base of vein 3. With 3—8 hairs on axillary ridge. Vein Sc distinct at base only. Vein h distinctly brown and angle with costa at most 70°, so that distal end is clearly nearer wing base than basal end (Fig. 21). Veins and membrane generally darker than in *A. africanus*.

Material examined: Lectotype and paralectotype (see above). 3 ♂, 3 ♀, ZAMBIA, Lusaka, XI & XII. 1979, I. 1980 (R. A. Beaver).

Aenigmatistes londti sp. n.

Male (Figs 23—26): upper frons mainly brown but extensively almost black between and around the three ocelli, and paler, more orange to yellow, postero-laterally. Only the hairs on vertex are more bristle-like (Fig. 23). Lower frons and appendages as Fig. 23. The dorsal, pre-apical, arista is so finely haired that it appears naked at less than x100 magnification.

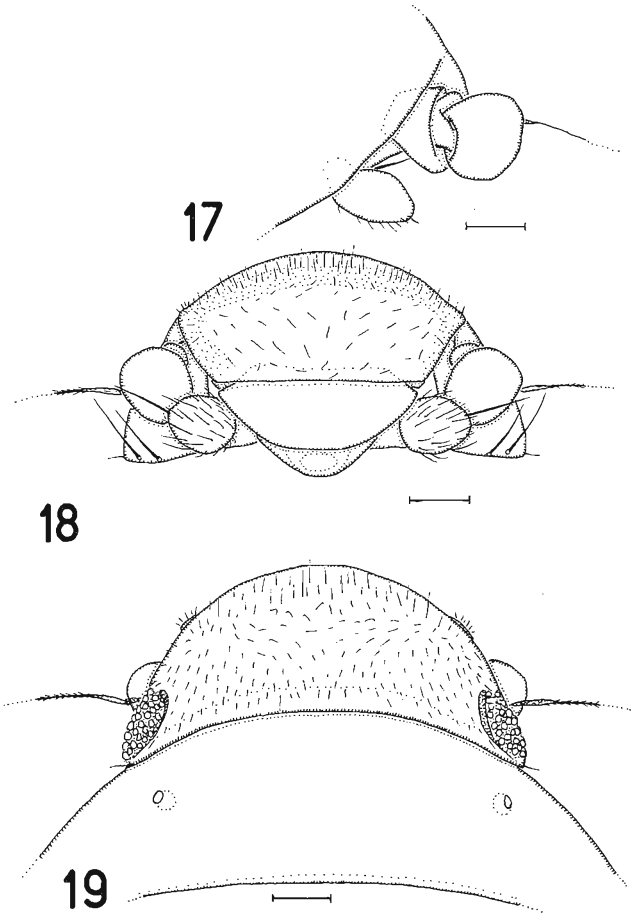


Figs 15—16: *Aenigmatistes herero* female frons (facing left). 15, from above; 16, from below. (Scale bars = 0.1 mm).

Thorax mainly brown but scutum almost black anteriorly and laterally; and with a more orange region towards rear on top. Scutellum with 10 robust bristles. Mesopleuron with hairs.

Abdominal tergites brown, being darker laterally and especially on portions extending around flanks onto ventral face. All tergites with a general clothing of medium-sized hairs. Dorsally the integument between the tergites is densely shagreened. Venter pale dusky yellow. Hypopygium brown, with a pale dirty yellow anal tube, and as Figs 25—26.

Legs brown. Hind tibia with 6—8 short antero-dorsal spines and two longitudinal hair palisades, one dorsal and one weaker postero-dorsal (Fig. 24). Hairs below basal half of the somewhat slender hind femur not differentiated. Mid tibia likewise with two hair palisades, one dorsal and one postero-dorsal. The row of hairs between these palisades are more spine-like, especially in last quarter; otherwise without differentiated pre-apical spine-like hairs. Front tibia without a longitudinal hair



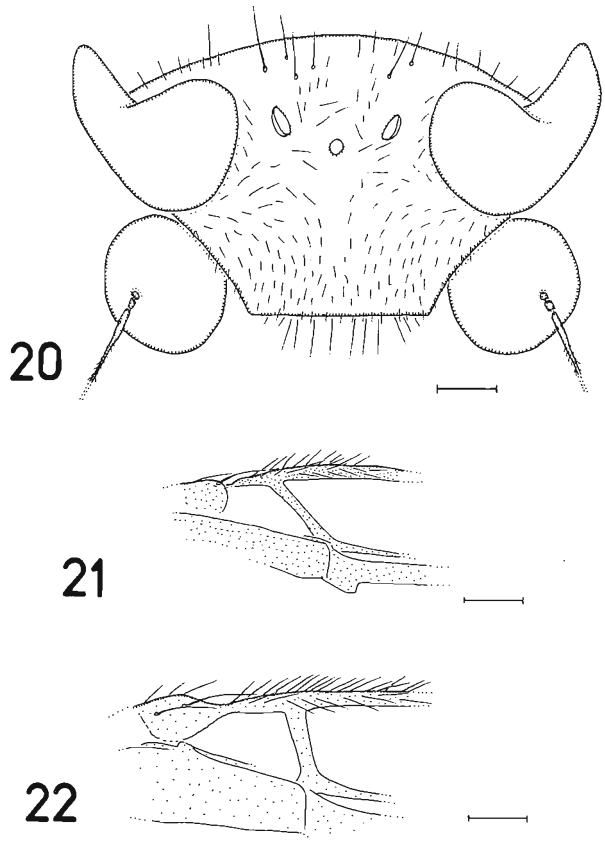
Figs 17—19: *Aenigmatistes* females. 17, *A. herero* right antenna and palp from below; 18—19, *A. latifrons* head. 18, from below; 19, from above. (Scale bars = 0.1 mm).

palisade or spines. Front tarsus with a postero-dorsal palisade and a small posterior apical spine on segments 1—4.

Wings 3.13 mm long. Costal index 0.55. Costal ratios 1.68 : 1. Costal cilia 0.07 mm long. Axillary ridge with three bristles. Basal third of vein 3 with 6—10 hairs in an irregular row. Vein Sc obscure, but evident basally. Thick veins yellow basally but yellowish brown distally. Thin veins pale grey. Membrane scarcely tinged grey. Haltere with knob partly brown and partly pale, and stem pale.

Holotype ♂, MALAWI: Mulanje Mnt., Likabula River Valley, 1000 m altitude, in *Brachystega* woodland, 28—30. XI. 1980 (J. G. H. Londt & B. R. Stuckenberg) (Natal Museum).

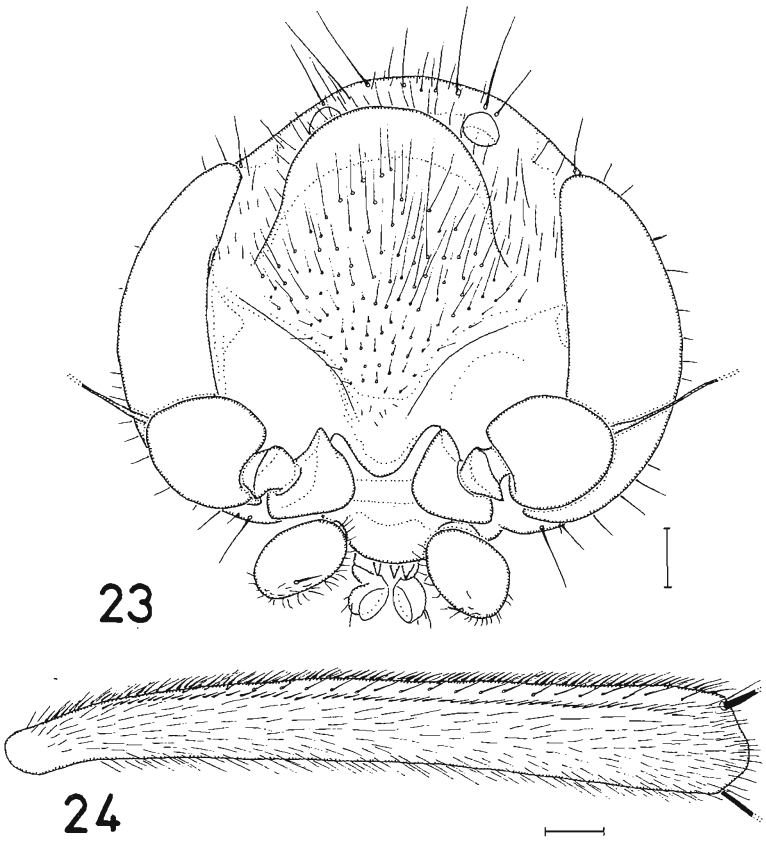
Etymology: The species is named after one of the collectors, Dr J. G. H. Londt.



Figs 20—22: *Aenigmatistes* males. 20, *A. latifrons* upper frons; 21, *A. latifrons* vein h (humeral cross vein); 22, *A. africanus* vein h. (Scale bars = 0.1 mm).

A new interpretation of the frons

Ever since Shelford (1908) described the genus *Aenigmatistes*, the peculiar frons has been regarded as its principal diagnostic feature. He described it thus "the morphologically anterior part lies in a plane almost at right angles to the plane of the posterior part and the middle region of the frons is produced and sharply ridged, making the angulation more pronounced". All species described to date possess this angulated frons. All except *A. priscus* have the transition from the upper face to the anterior face marked by a sharp, heavily-sclerotised, transverse ridge, which forms a dorsally-convex arch (Figs 1—5, 15—16, 18—21, 23). Above this arch the frons is well sclerotised. Below the arch the anterior face is essentially unsclerotised until the mid-ventral region, just above the antennae, and the ventro-lateral zones of increasing sclerotisation as it merges with the walls of the cavities embracing the antennae. This membranous region, covered with fine hairs, remains deformable.



Figs 23—24: *Aenigmatistes londti* male. 23, head from front; 24, posterior face of hind tibia. (Scale bars = 0.1 mm).

The other Phoridae with a frons somewhat resembling *Aenigmatistes* belong to the highly aberrant genus *Misotermes* Schmitz. However, in this case the form seems to result primarily from an extreme shortening of the frons (Schmitz 1938, Borgmeier 1967).

Many Phoridae possess a median furrow running from just in front of the anterior ocellus to just above the base of the antennae. It is now thought to be a plesiomorphic feature, homologous with the anterior part of the epicranial suture still present in some Nematocera (Disney 1981). When it is reduced and then lost it disappears from the posterior end forwards, and in many species it is only represented by the anterior (lower) part just above the bases of the antennae. Frequently this anterior part is isolated from the upper part by an incipient transverse ridge, indicated by a sudden change of slope. Furthermore it has been suggested that in the Schizophora this ridge becomes sharply demarcated to form the posterior margin of the ptilinal

suture. The opened-out remnant of the median furrow behind (above) this post-ptilinal ridge becomes the frontal vitta, and the remaining, invaginated, part of the furrow below the ridge is transversely widened to form the ptilinum (Disney 1988).

In the context of the above hypothesis the anomalous frons of *Aenigmatistes* not only finds a simple interpretation, but would appear to represent an independent evolution of a ptilinum with respect to the Schizophora. This hypothesis is considered below.

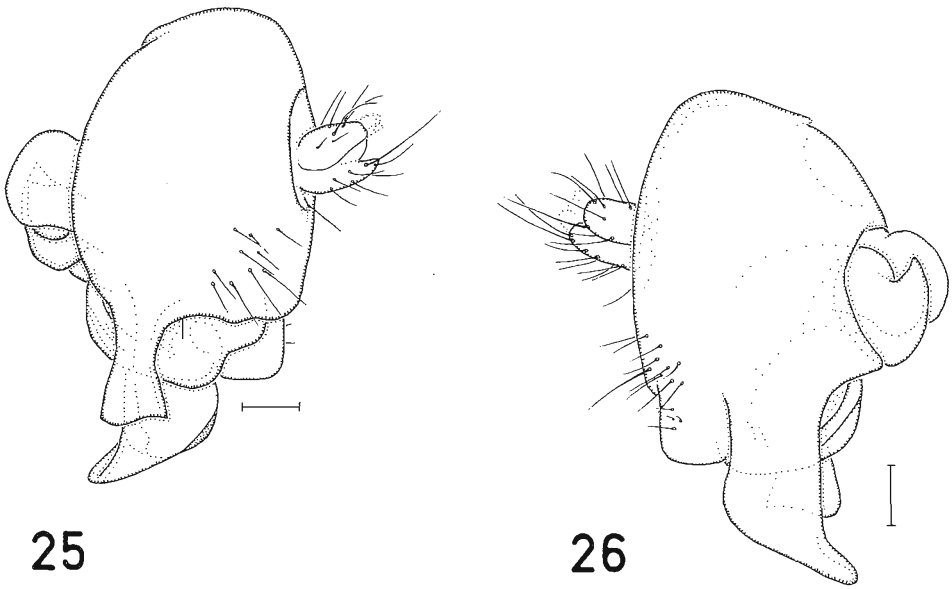
I suggest that the evolution of the *Aenigmatistes* frons started with the loss of the median furrow from the anterior ocellus forwards. However this process was halted by the formation of an incipient transverse ridge, below which the median furrow remained intact. The transverse ridge became more marked as the frons opened out sideways. The opened-out median furrow on the anterior face, below the increasingly arched and angulated ridge, became a ptilinum. The transverse arch became more heavily sclerotised as it became the posterior margin of the ptilinum. This interpretation is illustrated in Figs 1—2.

It is suggested that the evolution of a ptilinum in *Aenigmatistes* is an example of parallel evolution with respect to the Schizophora. In the latter, however, the ptilinum is greatly expanded. At the time of eclosion from the puparium it extensively bulges forwards (inflated by haemolymph), to be subsequently invaginated below the post-ptilinal ridge (or arch) (the posterior boundary of the ptilinal suture). By contrast the ptilinum of *Aenigmatistes* remains exposed after eclosion; and the arch is more prominent (Figs 1—2), except in *A. priscus*. Associated with these changes the anterior frontal bristles are lost, apart from weak antero-laterals in some species. Whether *A. priscus* represents a plesiomorphic stage in the development of the post-ptilinal arch is not known. Beyer's (1959) description does not allow detailed morphological analysis. However, it is one of the species with double hair palisades on both the middle and hind legs. This feature is thought to be plesiomorphic (Disney 1988, 1990).

Hinton (1946) discussed the presence of a simple ptilinum in some Syrphidae. In these cases following eclosion the ptilinum is neither retracted (as in Schizophora) nor left exposed (as is suggested for *Aenigmatistes* above). On the contrary, it contracts and disappears when the adult fly dries out after emergence. The former position of the ptilinum is indicated by a slight, but persistent, groove.

Hinton (1946) also discussed the function of the ptilinum at the time of adult eclosion from the puparium. The essential point is that the thorax and abdomen of the fly are too broad to pass through the narrow exit hole in the puparium. This problem is overcome by contracting the diameter of the body, a bit at a time, by alternately passing haemolymph forward into the ptilinum and back again. The pre-adult stages of *Aenigmatistes* are still unknown. One is only able to speculate that the function of the ptilinum in this genus is as in other Diptera possessing this feature.

Anyone who has reared Cyclorrhapha knows that a point of high mortality is when the fly is partly emerged from the puparium. The intensity of the selection pressure favouring successful escape from the puparium would seem sufficient to account for the independent evolution of a ptilinum in *Aenigmatistes*, some Syrphidae and the Schizophora; given the presence of a suitable precursor. The hypothesis that the lower (anterior) end of the median furrow (epicranial suture)



Figs 25—26: *Aenigmatistes londti* male hypopygium. 25, left face; 26, right face. (Scale bars = 0.1 mm).

represents precisely the necessary precursor required follows from the evidence that a median furrow is part of the ground plan of the Phoridae, and of the Aschiza in general.

Whether other "Aschiza" have evolved a ptilinum independently is not known. It is also possible that the ptilinum evolved independently in the Acalyptratae and the Calyptratae. The principal character postulated as the synapomorphy allowing characterisation of the Schizophora is the ptilinum (e. g. McAlpine 1989). If this hypothesis were to prove unsound then a rather different picture of Cyclorrhaphan phylogeny would be likely to emerge from a fresh evaluation of the available data. Our present schemes tend to minimize the possibilities of the parallel evolution of critical features. While parsimony is a sensible methodological strategy for generating hypotheses, it must not be forgotten that these hypotheses still require testing. Parallel evolution has clearly been much commoner than has often been supposed. Indeed the occurrence of a ptilinum in both *Aenigmatistes* and in Schizophora would appear to represent a striking example. This in turn suggests that a puparium confers a considerable advantage. It is more than probable, therefore, that the puparium has evolved, independently, several times. A field inviting research is the relation between the degree of develoment of the ptilinum and the form and relative size of the exit hole from the puparium.

Zusammenfassung

Ein revidierter Bestimmungsschlüssel der Buckelfliegen der Gattung *Aenigmatistes* Shelford, 1908 (Diptera: Phoridae) wird vorgelegt. Die bisher unbekannten Männchen von *A. africanus* Shelford und *A. latifrons* Schmitz, das unbekannte Weibchen von *A. herero* (Enderlein), sowie *A. londti* sp. n. (1 Männchen aus Malawi) werden beschrieben. Die Vorderkante des merkwürdigen Stirnbuckels von *Aenigmatistes* wird als dauerhafte Kopfblase (Ptilinum) interpretiert, welches sich unabhängig von der Kopfblase der Schizophora (bei denen sie nach dem Abschluß des Schlupfvorganges eingestülpt wird) oder der einiger Syrphidae (bei denen sie nach dem Schlupfvorgang durch Kontraktion abgestoßen wird) entwickelt hat.

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