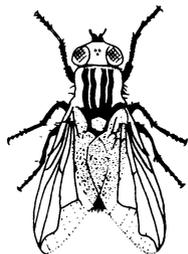


Revision of the bird-parasitic blowfly genus *Trypocalliphora* Peus, 1960 (Diptera: Calliphoridae)

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European material of the bird-parasitic blowfly genus *Trypocalliphora* Peus, 1960, including type material of *Avihospita braueri* Hendel, 1901 and *Trypocalliphora lindneri* Peus, 1960, has been examined. The genus is redefined on the basis of the male phallosome structure and its systematic position and status discussed. The genus contains a single Holarctic species, *Trypocalliphora braueri* (Hendel, 1901); *Protocalliphora hirudo* Shannon & Dobrosky, 1924, *T. lindneri* Peus, 1960 and *T. compacta* Grunin, 1966 are new synonyms. Knowledge of the biology is summarised and a host list for the Palaearctic Region is given.

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The genus *Trypocalliphora* Peus, 1960 was erected for blowflies of Phormiinae (Phormiini sensu Zumpt 1956) with larvae living obligatorily as subcutaneous parasites on birds (nestlings and juveniles). Peus removed these flies from the genus *Protocalliphora* Hough, 1899 where they had been placed previously (e.g. by Zumpt 1956). Larvae of *Protocalliphora* are external blood-sucking parasites in birds' nests that feed intermittently on the nestlings (Sabrosky & Bennett 1958; Rausch 1971). 3 nominal species were originally included in *Trypocalliphora*: the Palaearctic *braueri* (Hendel, 1901) and *lindneri* Peus, 1960 and the Nearctic *hirudo* (Shannon & Dobrosky, 1924). Most European workers have accepted Peus' genus (except Zumpt 1965) but North American ones have not. The purpose of this paper is to redescribe *Trypocalliphora* with emphasis on the male phallosome (not considered by Peus), discuss its status and its position within the Phormiinae, establish some new specific synonymies and summarise existing knowledge on its biology and host range.

The study is based on European material (adults and puparia) in the following institutions: British Museum (Natural History), London (BMNH), Museum für Naturkunde der Humboldt-Universität, Berlin (MNHU), Naturhis-

torisches Museum, Vienna (NMW), Staatliches Museum für Naturkunde, Stuttgart (SMN), Zoologisk Museum, Bergen (ZMB) and Zoological Museum of the University, Helsinki (ZMUH). Adults and some puparia of *Protocalliphora azurea* (Fallén), *P. chryssorrhoea* (Meigen), *P. nuortevai* Grunin, *P. proxima* Grunin, *Boreellus atriceps* (Zetterstedt), *Protophormia terraenovae* (Robineau-Desvoidy), *Phormia regina* (Meigen) (Phormiinae) and *Chrysomya albiceps* (Wiedemann), *C. megacephala* (Fabricius) (Chrysomyinae) have been available for comparison in Norwegian museum collections (Bergen, Oslo, Tromsø) and in my own collection.

Genus *Trypocalliphora* Peus, 1960

Trypocalliphora Peus, 1960: 199. Type-species: *Avihospita braueri* Hendel, 1901, by original designation. (Sabrosky (1967) erroneously cited *Trypocalliphora lindneri* Peus, 1960 as type-species).

Diagnosis. Phormiine genus with male frons at narrowest point $0.05\times$ head width, parafrontals subcontiguous; female frons at vertex $0.20\times$ head width, parafrontal half as wide as interfrontal stripe and without a prevertical seta; female parafacial on upper part in certain views showing large, triangular dark spot; arista with long hairs above and below; basicosta, squamae, subcostal sclerite, anterior spiracle and palp yellow to light brownish yellow; subcostal sclerite with black setulae; haltere

yellow; posterior spiracle brown; squamae and postalar wall bare; body colour metallic greenish blue in male, brassy green with white pruinosity in female; male distiphallus (Fig. 1) with very wide apical opening nearly of same calibre as base of phallus; hypophallic lobes small, pointing laterally, not ventrally; ventral surface flat, evenly sclerotised, with spinules widely distributed but most concentrated in two subapical ventral fields; a complete ring-shaped sclerotisation around apex; a distinct dorsal sclerotisation extends towards base from ring structure; no midventral sclerotisation (mesohypophallus) developed; ventral surface with stripe of hyaline membrane along midline; male surstylus as in Figs. 9–20. Female with telescopic ovipositor with well developed sclerites; probably oviparous. Third stage larva without a crown of setae on pseudocephalon; anterior spiracle with 2–4 branches.

Systematic position

Zumpt (1956) and Schumann (1973a; 1973b; 1974) used the structure of the male distiphallus to split *Onesia* Robineau-Desvoidy, 1830 (s. lat.) into the genera *Onesia* (s. str.), *Melinda* Robineau-Desvoidy, 1830 and *Bellardia* Robineau-Desvoidy, 1863. Similarly, the structure of the distiphallus readily defines *Trypocalliphora* as a valid genus. Apparently, this taxon differs from all species of *Protocalliphora* by the absence of a mesohypophallus (a torpedo-shaped ventral sclerotisation on distiphallus). Further, in *Protocalliphora* the ventral surface of distiphallus forms a deep groove in which the mesohypophallus lies, the hypophallic lobes point ventrally, spinules are confined to two sub-lateral fields apically, no apical ring-shaped or dorsal longitudinal sclerotisations are developed, and the apical aperture is narrow (compare Figs. 1 and 2; see also Hall 1948 (as *Apaulina*); Gregor & Povolný 1959; Grunin 1966; 1970; 1971b; 1972; Kano & Shinonaga 1968). In the Phormiinae a mesohypophallus is also present in *Protophormia teraenovae* (Fig. 3) and *Boreellus atriceps* (personal observations) and in *Phormiata phormiata* Grunin (Grunin 1971a). The distiphallus in *Phormia regina* is very different, and without a midventral sclerotisation representing the mesohypophallus.

Peus (1960) divided the Phormiinae in two groups: (1) *Trypocalliphora* + *Phormia* Robineau-Desvoidy, 1830 and (2) *Boreellus* Aldrich & Shannon, 1923 + *Protophormia* Townsend, 1908 + *Protocalliphora*. The first group he defined by alleged absence of flattening of mesonotum, yellow colour of anterior spiracle, basicosta and wing veins, and contiguous para-

frontals in male; the second group by mesonotal flattening, dark colour of above mentioned structures and separated parafrontals in male. Zumpt (1965) did not accept Peus' genus and treated its nominal species in *Protocalliphora*. He admitted that the absence of the crown of setae on the pseudocephalon and other features of the third stage larva might justify *Trypocalliphora* as a separate genus but considered this premature in view of the overall insufficient knowledge of the larvae of bird-parasitic blowflies. Neither Peus nor Zumpt considered the structure of the phallosome. Sabrosky (1967), in a catalogue entry, recognised *Trypocalliphora* as a subgenus of *Protocalliphora* and thus, by implication, viewed *Trypocalliphora* and *Protocalliphora* (s.str.) as sister-groups. However, I have not been able to find synapomorphic characters of these two taxa (apart from the bird parasitic habit) to support this. Alternatively, *Trypocalliphora* could be the sister-group of *Protocalliphora* + *Boreellus* + *Protophormia* + *Phormiata* Grunin, 1971. *Trypocalliphora* has at least two good autapomorphic characters: (1) absence of a prevertical seta in female, (2) male distiphallus with dorsal longitudinal sclerotisation apically. The monophyly of the sister-group is suggested by two assumed autapomorphies: (1) a mesohypophallus of characteristic shape present in male distiphallus, (2) interfrontal stripe in male frons usually broader than one parafrontal. The group *Trypocalliphora* + (*Protocalliphora* + *Boreellus* + *Protophormia* + *Phormiata*) is probably monophyletic, its monophyly suggested by two assumed autapomorphies: (1) presence of 2 apical clusters of spinules on male distiphallus, (2) conspicuous flattening of mesonotum between suture and scutellum (variable in *Trypocalliphora*, indistinct in *Boreellus*, condition unknown in *Phormiata*). The group *Boreellus* + *Protophormia* is probably monophyletic, as evidenced by at least six good autapomorphies: (1) both squamae dark brown, (2) black hairs on disc of upper squama, (3) hind coxa with hairs laterally on posterior surface (an overlooked character, also present in Chryso-myinae, but occasional specimens may lack the hairs), (4) *prst acr* absent, (5) body dark metallic bluish-green, non-pollinose, (6) hypophallic lobes with spinules distally. Collin (1925) and Séguy (1928) even regarded the constituent species (*atriceps* Zetterstedt = *boganidae* Erichson and *teraenovae* Robineau-Desvoidy = *groenlandica*

Zetterstedt) as congeneric. *Phormia* has 3 apomorphic characters which elsewhere are present only within the Chrysomyinae (personal observations, see also Séguy 1928; Patton & Cushing 1934a; 1934b; Thomas 1951; Emden 1954): (1) inconspicuous white hairs laterally on disc of upper squama, (2) phallosome with dense cover of short hairs on ventral surface proximal to hypophallic lobes, (3) hypophallic lobes circular. It may therefore be more closely related to the Chrysomyinae than to the other phormiine genera.

According to the above analysis *Protocalliphora* is a member of a monophyletic group not including *Trypocalliphora*. This means that these two taxa entered the bird niche independently at different times which was also suggested by Peus (1960). This is perhaps reflected in the different larval habits of the two genera, and in the fact that *Protocalliphora* contains about 50 species (Grunin 1971a) (many still undescribed) which are generally either Nearctic or Palaearctic, whereas *Trypocalliphora* (like the remaining four phormiine genera) is monotypic. In view of these considerations it appears preferable to retain a generic status for *Trypocalliphora*.

Trypocalliphora braueri (Hendel, 1901)

Figs. 1, 4–23, Tables 1–5.

Avihospita braueri Hendel, 1901: 29. Lectotype ♂, Austria, ex nestling of *Passer domesticus*, date and further locality unknown, Brauer leg. et cult. (NMW), by designation of Hennig (1939: 361) [examined].

Protocalliphora hirudo Shannon & Dobrosky, 1924: 252. Holotype ♂, U.S.A.: Colorado, ex "nestling warbler", 10.vii.1911, Palmer leg. et cult. (U.S. National Museum, Washington, No. 26862) [examined on my behalf by C. W. Sabrosky]. **Syn. n.**

Trypocalliphora lindneri Peus, 1960: 227. Holotype ♂, West Germany: S. Baden, Kreis Kehl, Diersheim, ex *Alauda arvensis*, 1.viii.1951, Schlörner leg., Lindner cult. (SMN) [examined]. **Syn. n.**

Trypocalliphora compacta Grunin, 1966: 902 (as ssp. of *lindneri* Peus). Syntypes 5 ♂ 12 ♀, U.S.S.R.: Leningrad Prov., Luga district, ex *Phylloscopus trochilus*; Tatar A.S.S.R., Zelenodol'sk district, Raifa, ex *Sturnus vulgaris*; Okeanskaya railway station near Vladivostok, ex *Passer* sp. (Institute of Zoology, U.S.S.R. Academy of Sciences) [not examined]. **Syn. n.**

Notes on type material

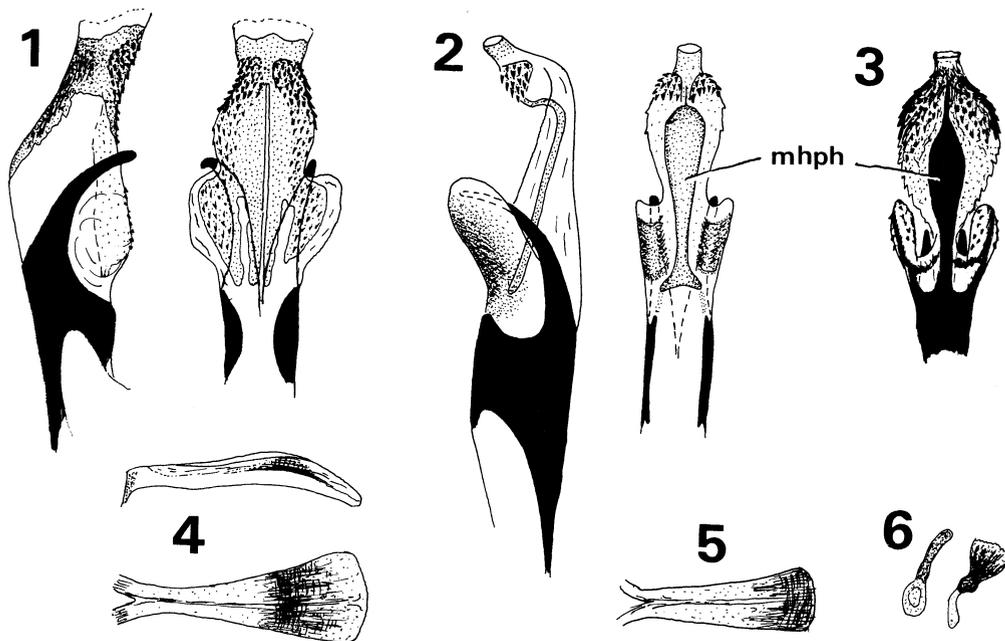
Avihospita braueri Hendel. In NMW 3♂ 3♀, all examined. All are more or less teneral. 2♂ 2♀ un-

equivocally belong to the syntypic series and have the following white labels in common: (1) "Brauer [print]; Austria [faded ink]" (2) "Braueri [faded ink]; det. B. B. [print]" (3) "Avihospita; braueri H. [ink]; det. Hendel [print]" (4) "Trypocalliphora ♂ [or ♀]; braueri (Hendel); F. Peus det. 1959 [ink]". The lectotype ♂ carries an additional red "Paratypus" label [print]. It is lacking the abdomen and I believe this to be the specimen dissected by Hennig, as removal of the whole abdomen was his way of making genital preparations (A. C. Pont in litt. from J. P. Dear 24.ii.1981). His reference to the "Typus von braueri Hend." whose hypopygium he examined (Hennig 1939: 361) I choose to interpret as the first valid lectotype designation. Hennig's preparation was illustrated by Peus (1960: 223, 224, fig. 18), but could not be traced in NMW, MNHU, DEI, or coll. Peus (Frankfurt, Geneva). The paralectotype ♂ carries an additional red "Type" label and a red label reading "braueri" [pencil]. This must be the "Holotypus" mentioned by Peus (1960: 226, note page number). The abdomen appears intact but is without terminalia (dissected?). A paralectotype ♀ with an additional red "Type" label is the "Allotypus" of Peus (1960: 226). A second paralectotype ♀ carries an additional red "Paratypus" label.

The additional two specimens (1♂ 1♀) in NMW have the following labels in common: (1) "Coll. Bgst. [print]" (2) "azurea [faded ink]; det. Bergent. [print]" (3) "Paratypus [print, red label]" (4) "Trypocalliphora ♂ [or ♀]; braueri (Hendel); F. Peus det. 1959 [ink]". The male carries the following additional labels: (5) "Calliphora azurea Fall. [ink, yellow label]" (6) "Calliphora azurea aus Sperling [pencil]". The pin also carries an empty puparium. As these two specimens are without Hendel's determination labels, Peus may be wrong in having labelled them as authentic syntypes. I assume, however, that they were bred from the same young sparrow as the syntypes (cf. Hendel 1901: 31). Brauer (1883: 74) did not state the number of specimens bred.

Note that after Hennig's valid indication of a lectotype Peus (1960) designated a lectotype for *braueri* twice. The first is on p. 224 fig. 18, where he figures the preparation made by Hennig (see above) and in the legend says it to be from the "Holotypus", which means that the specimen dissected by Hennig and illustrated by Peus by implication is designated as lectotype (ICZN, Art. 74 (b), Designation by means of a figure). The second designation is made on p. 226 where he identifies a specimen carrying certain labels as the "Holotypus". He is clearly referring to the ♂ carrying the "Type" label, dealt with above. These designations, which do not apply to the same specimen, are invalid and unnecessary because of Hennig's previous action.

Trypocalliphora lindneri Peus. In SMN 3♂ 3♀, including holotype, all examined; 2♂ 1♀, MNHU, 1♂ 1♀ examined, including genital preparations. Peus (1960) gives information on labels. For details on the types and further specimens bred from the same lark, see Heinz (1954), Zumpt (1956), Lindner (1957), Gregor & Povolný (1959), Peus (1960). Terminalia of the holotype dissected and kept in glycerol in micro-vial on separate pin labelled: (1) "Holotype ♂ Trypocalliphora lindneri Peus, 1960" (2) "Genitalprep. 23 Knut Rognes prep. 1980 ♂" (3) "Trypocalliphora braueri (Hendel) K. Rognes det. 1981".



Figs. 1–6. Male genitalia. – 1. *Trypocalliphora braueri*; distiphallus, left and ventral view. – 2. *Protocalliphora azurea*; distiphallus, right and ventral view. – 3. *Protophormia terraenovae*; distiphallus, ventral view. – 4–5. *T. braueri*; phallopodeme, profile and surface view. – 6. *T. braueri*; ejaculatory sclerite. – mhph: mesohypophallus.

Other *Trypocalliphora* material examined

FINLAND. Lapponia kemensis: Sodankylä, Seipäjoki, 1♂, with empty puparium, ex *Oenanthe oenanthe* (Grunin, Nuorteva & Rajala 1969), terminalia glued to piece of celluloid with the specimen; Regio kuusamoensis: Salla, Värriötunturi, 2♂, ex *Anthus pratensis* (Hakannen, Grunin & Nuorteva 1974), dissected; Karelia ladogensis: Parikkala, Siikalahti, 1♂, with empty puparium, ex *Luscinia luscinia*, 17.vi.1970, pupated 20.vi., emerged 29.vi., J...S...leg. (illegible); Ostrobottnia borealis: Pello 2♀, one with intact puparium, the other with empty puparium and semipupated larva, ex *Motacilla alba*, 24.vi.1973, J. Halonen leg. All ZMUH. – NORWAY. Buskerud, Ål: Ål, 2♂ 7♀, with 5 puparia of which 4 empty, ex *Ficedula hypoleuca* (nestlings in nest-box), 6.vii.1944, L. O. Odde leg., one male dissected; Sogn og Fjordane, Balestrand: Brekkestølen, Brekka 15♂ 3♀, with 3 empty puparia, ex *Oenanthe oenanthe*, 8., 9., 14.vii.1935, 2♂ 1♀ as larvae 23.vi from an approx. 7 days old nestling, pupated 24–25.vi, emerged 14.vii, O. Meidell leg. et cult., 4 males dissected. ZMB and coll. Rognes. – U.S.S.R. Karelian A.S.S.R.: near Kivach, 1♂, with empty puparium “s de-reven. lastochki” [ex *Hirundo rustica*], 15.vii.1974, 1♀, with empty puparium, ex “penochka-vesnich” [*Phylloscopus trochilus*], 10.vii.1974, both A. Pokrovskiy leg., male dissected. BMNH. – WEST GERMANY. No locality, 1♂, ex *Emberiza schoeniclus*, 28.vii.1961, Schlö-

rer leg.; Beckenwört, 1♂, ex *Emberiza schoeniclus*, 29.vi.1963, Isenmann leg., dissected. SMN.

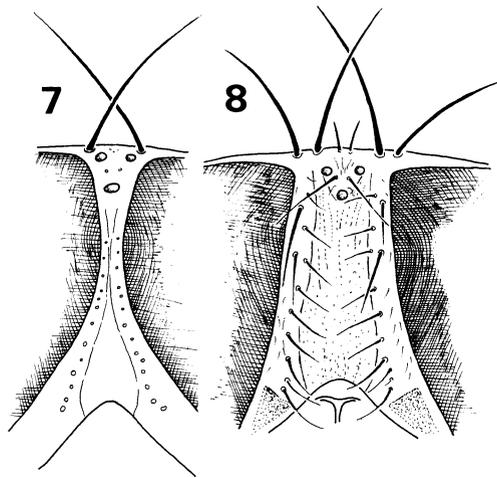
Diagnosis. See above diagnosis for the genus.

Description

Male. Length: 6.1–9.3 mm. *Head.* Black; frontal stripe blackish brown to reddish brown; lunula bare, brown to brownish black, shining; face and mouth-edge black; facial ridge yellowish below; genae reddish or brown; occipital dilation black; 1. ant.segm. black or reddish; 2. ant.segm. reddish in apical half; 3. ant.segm. reddish basally and along hind edge; arista black, yellow in middle; hairs of occiput whitish with slight yellowish sheen, 1–3 rows of black setulae behind postocular row of setae; frons at narrowest 0.034–0.064× head width (Fig. 7, Table 1); parafrontal with 12–14 inclinate frontal setae, foremost at lunula, hindmost separated from anterior ocellus by length of ocellar triangle; *iv* strong, no *ev*; parafrontals with black setulae in front half; parafacialia with parallel edges and numerous

setulae arranged in 2–3 irregular rows in upper 1/2 or 2/3; large vibrissa above mouth-edge by distance about 1/2–1/3 × width of 3. ant. segm.; facial ridges with 10–15 hairs in double or triple rows to slightly below middle, reaching level of lowermost parafacial hairs; 5–8 subfacials; mouth-edge just visible in profile; arista with longest hairs 1/2–2/5 × length of arista. *Thorax*. Sometimes flattened on dorsum between suture and scutellum; 3+3–4 *acr*, 3+3–4 *dc*; 5*h*; 1+3 *ia*; 2 strong + 1–3 weak *npl*; 5–8 weak *ptpl* distinguishable among hairs; postalar wall bare, rarely with a few short hairs visible at middle; propleuron, prosternum and basisternum setose; posterior spiracle brown to yellowish brown with a few minute setulae near ventral edge; subapical scutellars strong, 1.5–2 × length of scutellum; apical scutellars hair-like, well in front of apex; 2–3 lateral scutellars 1/2 × length of subapicals; basal scutellars slightly shorter than subapicals; lateral slopes of scutellum hairy, underside with small whitish hairs. *Legs*. Black with some reddish transparency affecting all *t* and *p* surface of *f*₃; claws slightly shorter than apical tarsal segment; *t*₁ with a single *pv* at apical 1/3; *t*₂ with strongest *ad* as strong as *v*, both at same level at apical 1/3; *f*₂ without *pv* ctenidium apically; *cx*₃ bare behind. *Wings*. Veins normally yellowish brown, more brownish apically, sometimes all yellow; 1–4 small hairs sometimes present at junction of *h* and *sc* on underside of wing; *r*₄₊₅ above with setulae halfway to *r-m*; node at base of *r*₄₊₅ hairy below; costal spine at exit of *sc* at most 2 × length of neighbouring spinules; *cs*₂ bare below; *cs*₄ with spinules in basal 1/2; bend of *m*₁ as distant from hind margin of wing as from *m-cu*; apical crossvein 2.5 × length of *m*₁ between bend and *m-cu*, slightly concave near bend. *Terminalia*. Surstylus variable (Figs. 9–20); phallosome (Fig. 1) normally straight, no angle between basal and apical parts of distiphallus in profile view; paraphallic processes projecting ventrally slightly below ventral surface; phallapodeme as in Figs. 4–5; ejaculatory sclerite as in Fig. 6.

Female. Length: 6.0–8.7 mm. *Head*. Frons at vertex 0.18–0.22 × head width (Fig. 8, Table 2); parafrontal with 9–11 inclinate frontal setae, hindmost at level with anterior ocellus, proclinate orbitals, without prevertical seta, *iv* and *ev* strong (Fig. 8); interfrontal stripe below anterior ocellus 1.63–2.28 × width of parafrontal (Table 3) and 1.0–1.5 × distance between outer rims of posterior



Figs. 7, 8. *Trypocalliphora braueri*; frons. – 7. Male. – 8. Female.

ocelli (Table 4); parafrontal with setulae for whole length; parafacialia becoming narrower downwards. *Wings*. Veins more yellow than in male. *Terminalia*. Described by Gregor & Povolný (1959) and Lobanov (1976). T8 with complete marginal row of setae, not interrupted in middle.

Eggs. Unknown.

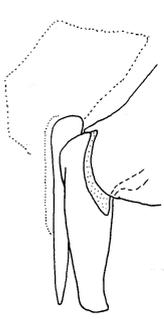
Larvae. 1st and 2nd stage larvae unknown. 3rd stage larva: Length 6–12 mm; width up to 6 mm. No crown of setae on pseudocephalon. Mouthparts as in Fig. 21 (Rodendorf 1957, as “Genus species”; Gregor & Povolný 1959; Cais 1965; Zumpt 1965; Hakanen, Grunin & Nuorteva 1974).

Puparium. Length 5.3–7.6 mm, maximum dorso-ventral depth 2.4–3.4 mm (n=10). Brown, truncate at both ends, maximum depth a little behind middle and with bands of rather small spinules. Anterior stigma usually with 3, rarely 2 or 4 branches (Fig. 22). Posterior stigmata as in Fig. 23.

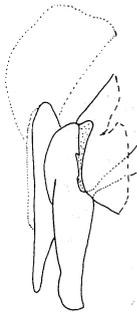
Variation and notes on synonymy

The status of Trypocalliphora lindneri Peus

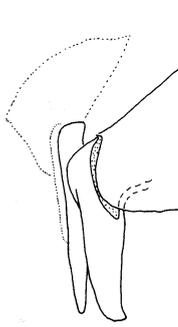
Peus (1960) described a number of supposed morphological differences between *Trypocalliphora lindneri* and *T. braueri*:



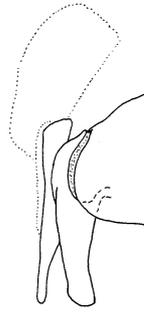
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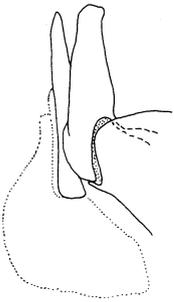
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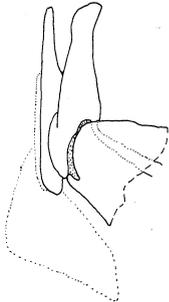
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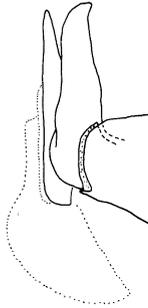
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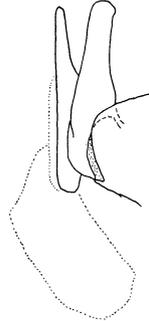
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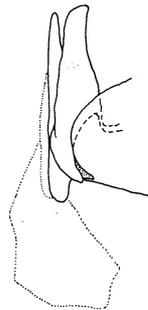
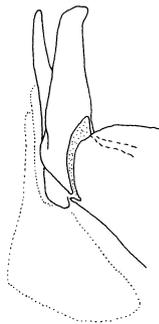
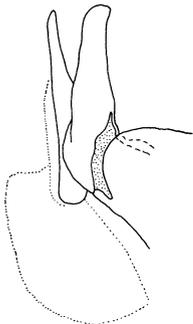
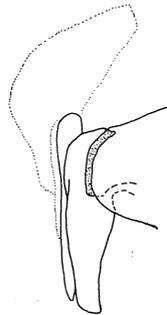
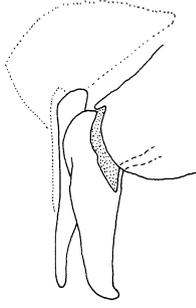
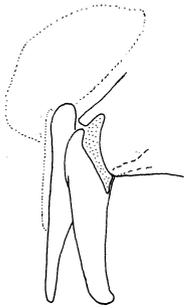
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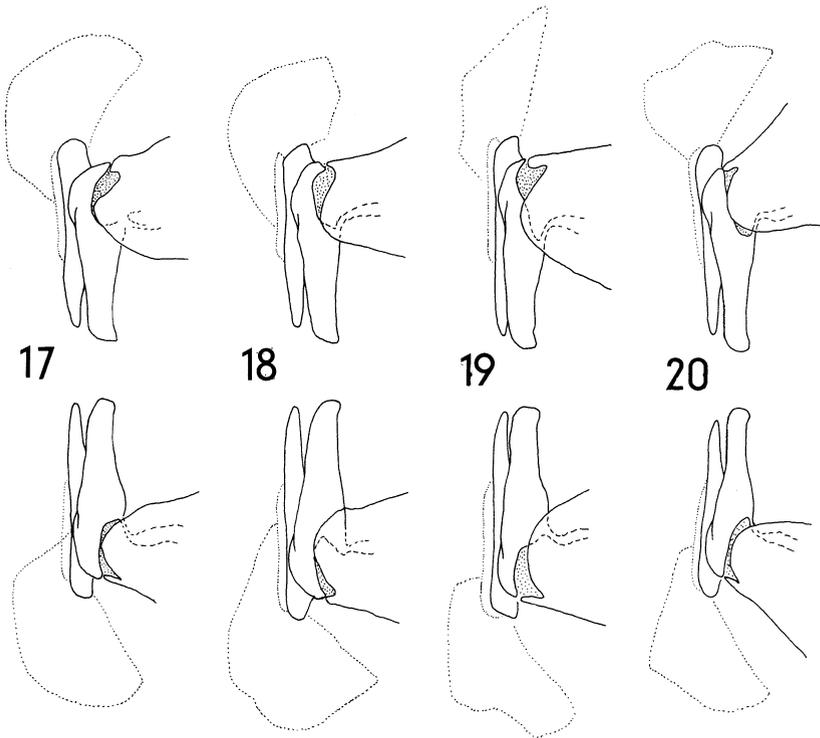


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Figs. 9–20. *Trypocalliphora braueri*; cerci and surstyli, right (upper) and left (lower) profile views. – 9. Holotype of *lindneri* (SMN). – 10. Paratype of *lindneri* (MNHU). – 11. West Germany. – 12. U.S.S.R. – 13, 14. Finland, Salla. – 15. Finland, Sodankylä. – 16. Norway, Ål. – 17–20. Norway, Balestrand.

Male surstylus. The type material of *lindneri* (Figs. 9–10) and other material from the same series (Heinz 1954; Gregor & Povolný 1959) show a variability of the same range as in Figs. 9–20. The ♂ paratype in MNHU, on which Peus based his description of the surstylus in *lindneri*, is unusual in having a distinct “präapikale Einschnürung”. Evidently the surstylus of the lectotype ♂ of *braueri*, figured by Peus (1960: 224, fig. 18), falls within the variational range of that structure in *lindneri*.

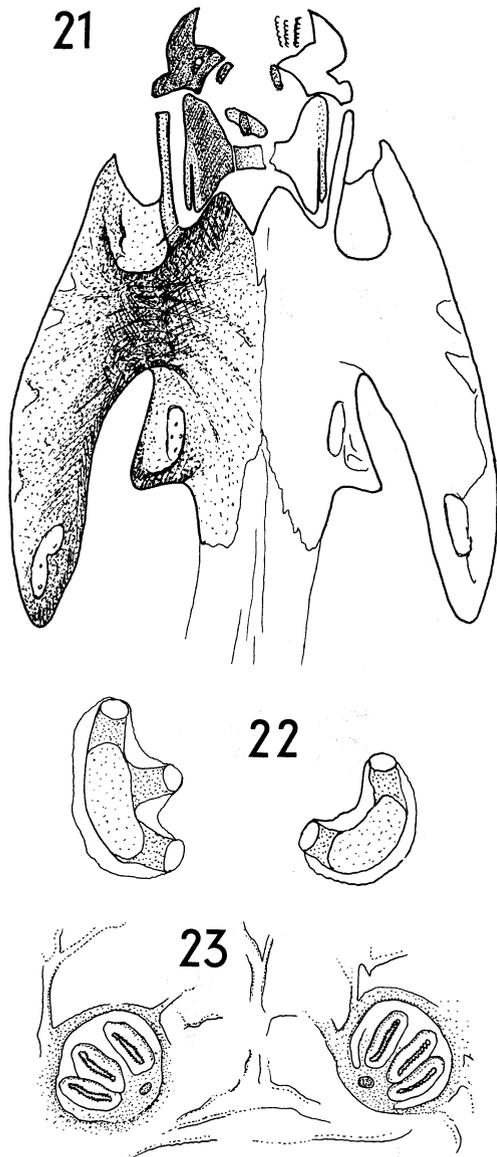
Male frons. The parafrontals were described as narrowly separated in *lindneri*, and contiguous in *braueri*. The holotype of *lindneri* agrees with Peus' description, but one of the ♂ paratypes in SMN has contiguous parafrontals. Most males have a frons as in Fig. 7. Frons/head ratios (Table 1) show the type material of *braueri* to lie in the lower part and that of *lindneri* in the upper part of the variability range. The Norwegian material shows intermediate values.

Female frons. The interfrontal stripe was described as scarcely broader than a parafrontal in *braueri*, and twice as broad in *lindneri*. The ratio (Table 3) actually shows a continuous range of variability. The interfrontal stripe was also described as exactly equal to the distance between the outer rims of the posterior ocelli in *braueri*, and distinctly broader in *lindneri*. This ratio (Table 4) also shows a continuous range of variability.

Colour of female abdomen. I do not agree with Peus (1960: 224–225) as to colour differences between the type material of *braueri* and *lindneri*.

Colour of posterior spiracle. Peus gives “hellbraun” for *braueri* and “braun” for *lindneri*. I agree with this with regard to the type material, but the difference is slight and Norwegian material shows intermediate colours.

Colour of wing veins. These were described as yel-



Figs. 21–23. *Trypocalliphora braueri*; puparium. – 21. Mouthparts of 3rd stage larva. – 22. Anterior spiracles. – 23. Posterior spiracles.

low or brownish yellow in *braueri* and as becoming darker towards the wing margin in *lindneri*. Most specimens examined agree with the description applying to *lindneri*, but a few Norwegian specimens are exactly like the type material of *braueri*.

Table 1. *Trypocalliphora braueri*; males. Ratio frons width (narrowest point)/head width. Specimens with a teneral frons have been omitted.

Origin of material	Ratio
Austria (type material of <i>braueri</i>)	0.034, 0.049, 0.050
W. Germany (type material of <i>lindneri</i>)	0.056, 0.060, 0.062, 0.064
Finland	0.038, 0.045, 0.046, 0.049
W. Germany	0.046, 0.050
Norway, Ål	0.050, 0.058
Norway, Balestrand	0.045, 0.047, 0.048, 0.049, 0.051, 0.051, 0.053, 0.054, 0.057, 0.060
U.S.S.R.	0.056
Range: 0.034–0.064	Mean: 0.051 N=26

Table 2. *Trypocalliphora braueri*; females. Ratio frons width (at vertex)/head width. Specimen from Finland with a teneral head has been omitted.

Origin of material	Ratio
Austria (type material of <i>braueri</i>)	0.19, 0.19, 0.19
W. Germany (type material of <i>lindneri</i>)	0.20, 0.21, 0.21, 0.21
Finland	0.22
Norway, Ål	0.19, 0.19, 0.19, 0.19, 0.19, 0.20, 0.20
Norway, Balestrand	0.18, 0.20, 0.21
U.S.S.R.	0.20
Range: 0.18–0.22	Mean: 0.20 N=19

The status of Trypocalliphora lindneri compacta Grunin

Grunin (1966) described a subspecies *compacta* which differed from the nominate form in having “less curved and thicker harpes not protruding on the ventral side of the phallosome” (cited from the Ent. Rev. Wash. translation). None of the 12 phallosomes I have seen has the paraphallic processes as slender and strongly curved as in Grunin’s fig. 25 which represents the nominate form. All have the paraphallic processes shaped as in his fig. 26 which represents *compacta*. In the latter figure, however, the acrophallus is distinctly bent relative to the base of the distiphallus, the unsclerotised membrane is less distended than in his

Table 3. *Trypocalliphora braueri*; females. Ratio interfrontal stripe width/parafrontal width (measured at tip of ocellar triangle). Parafrontal width defined as half the difference between frons width and interfrontal stripe width. Specimens with a teneral frons have been omitted.

Origin of material	Ratio
Austria (type material of <i>braueri</i>)	1.63, 1.92, 2.00
W. Germany (type material of <i>lindneri</i>)	1.81, 1.87, 1.87, 2.14
Finland	1.77
Norway, Ål	1.93, 2.00, 2.07, 2.14, 2.15
Norway, Balestrand	1.92, 2.00, 2.28
U.S.S.R.	2.00
Range: 1.63–2.28	Mean: 1.97 N=17

Table 4. *Trypocalliphora braueri*; females. Ratio interfrontal stripe width (at tip of ocellar triangle)/distance between posterior ocelli inclusive. Specimens with a teneral frons have been omitted.

Origin of material	Ratio
Austria (type material of <i>braueri</i>)	1.00, 1.09, 1.18
W. Germany (type material of <i>lindneri</i>)	1.22, 1.26, 1.27, 1.35
Finland	1.10
Norway, Ål	1.17, 1.18, 1.26, 1.26, 1.30
Norway, Balestrand	1.04, 1.26, 1.50
U.S.S.R.	1.41
Range: 1.0–1.50	Mean: 1.23 N=17

fig. 25, and the paraphallic processes do not protrude on the ventral side. In these respects *compacta* disagrees with all material I have examined and also with material from Poland (Cais 1965). However, I believe that these differences are merely artifacts.

The status of Protocalliphora hirudo Shannon & Dobrosky

Specimens of the type series of *lindneri* and other specimens bred from the same lark were originally identified by Heinz (1954) as *Protocalliphora hirudo* Shannon & Dobrosky, a species until then only known from North America. This identifica-

tion was verified by C. W. Sabrosky who had access to the type material of *hirudo* in the U. S. National Museum, Washington. Despite of this Peus (1960) concluded, after comparison with specimens of *hirudo* (1♂ 1♀, alcohol preserved, Sabrosky det.) from Wyoming, U.S.A., and Shannon & Dobrosky's (1924) description, that the Schlörer material from West Germany was sufficiently different to require status of a new species, *lindneri*. Apart from minor details concerning the male and female frons and the male surstylus which are of no taxonomic value (see above) the differences between *lindneri* and *hirudo* mentioned by Peus concern the colour of the wing base and squamae and (female only) the amount of pollinosity on the ocellar triangle. He found additional support in the fact that *hirudo* in North America apparently infests a wider range of birds of different ecology. Sabrosky (in litt. 2.iii.1981) informs me that the colour of the squamae of *hirudo* in the U.S. National Museum "varies somewhat with the condition of the specimens, and possibly with latitude. I would describe those of the holotype male as light brownish yellow, but I have seen males that would be called brown to dark brown. Females are brighter than males, and could often be called yellow, even females in the same reared series with dark brown males." I regard this information together with the present knowledge about morphology and host range of the Palaearctic species as sufficient evidence for regarding *hirudo* as identical with *braueri*.

Number of branches of the anterior stigma of 3rd stage larva and puparium

Rodendorf (1957) first described the anterior spiracle of the *T. braueri* 3rd stage larva as 3-branched. Sabrosky reports (in litt. 2.iii.1981) that the few puparia present in the U. S. National Museum also have a low number (2–4) of spiracular branches. Species of *Protocalliphora* and other Phormiinae have a higher number (5–15) as far as this is known (Engel 1920; Séguy 1941; Hall 1948; Rodendorf 1957; Zumpt 1965; Ishijima 1967).

Distribution

Europe: Austria, Czechoslovakia, East Germany, Finland, Hungary, Norway, Poland, U.S.S.R.,

West Germany. – Asia: U.S.S.R. (east to Vladivostok). – North America: Alaska to Quebec, south to New Mexico and Georgia. (Rodendorf 1957; Peus 1960; Cais 1965; Hall 1965; Grunin 1966; Draber-Mońko 1971; Rausch 1971; Bedard & McNeal 1979; Cepelak 1982, and present study.)

Biology and hosts

The information given below is compiled from labels on examined specimens, letters from A. Løken (10.x.1980) and L. O. Odden (7.xii.1980) concerning Norwegian material, and from Zumpt (1956, 1965), Rodendorf (1957), Gregor & Povolný (1959), Peus (1960), Cais (1965), Grunin (1966), Grunin, Nuorteva & Rajala (1969), Rausch (1971), Hakanen, Grunin & Nuorteva (1974), Itämies & Ojanen (1975) and Bedard & McNeal (1979).

Eggs. Probably laid in clusters directly upon nestlings of various ages, apparently also on newly hatched ones.

Larvae. These make permanent subcutaneous burrows (up to 12 mm deep and 4.1 mm broad) on various parts of the body (from nostrils to feet) but most frequently on the wings. Extensive tissue destruction may occur. The digestive tract of the larvae mostly contains blood. A single infested nestling usually supports 9–20 larvae but numbers vary from 1 to 57. Not all nestlings of an attacked brood may be affected although this is usually the case. Duration of the larval stage is 8–9 days. Mature larvae leave the host at death or at fledgling stage (thus outside nest). Pupation takes place in the ground or in the nest. Infestation weakens the host and is frequently lethal. Nestlings may recover if the larvae are removed artificially.

Pupal stage. Duration 7–19 days.

Adults. Rarely captured in the open. Myślicka (1968) and Cepelak (1982) reported captures from 8.viii and 3.ix. Bred material has emerged on 10.vi – 10.viii. Adults hibernate in unknown locations.

Host range. A wide range of passeriform birds with different nesting habits, even box-nesting ones, are attacked, but the fly may prefer ground breeders in open environments. Known hosts in the Palaearctic Region are listed in Table 5.

Hirundo rustica, *Luscinia luscinia* and *Ficedula hypoleuca* are recorded for the first time.

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References

- Bedard, J. & McNeal, J. N. 1979. *Protocalliphora hirudo* (Diptera: Calliphoridae) infesting Savanna Sparrow, *Passerculus sandwichensis* (Aves, Fringillidae), in Eastern Quebec. – *Can. Ent.* 111: 111–112.
- Brauer, F. 1883. Die Zweiflügler des kaiserlichen Museums zu Wien. III. Systematischen Studien auf Grundlage der Dipteren-Larven nebst einer Zusammenstellung von Beispielen aus der Literatur über dieselben und Beschreibung neuer Formen. – *Denschr. Akad. Wiss., Wien* 47: 1–100.
- Brauer, F. & Bergenstamm, J. E. von 1894. Die Zweiflügler des kaiserlichen Museums zu Wien. VII. Vorkommen zu einer Monographie der Muscaria Schizometopa (exclusive Anthomyidae). Pars IV. – *Ibidem* 61: 537–624.
- Cais, L. 1965. *Protocalliphora hirudo* Shannon & Dobrosky, 1924 (Diptera, Calliphoridae) w Polsce. – *Fragm. faun.* 12: 183–191.
- Cepelak, J. 1982. Some groups of higher flies of the Malé Karpaty (Diptera, Brachycera). II. – *Biologia Bratisl.* 37: 599–607. (In Czech, with English summary).
- Collin, J. E. 1925. Diptera (Cyclorrhapha) from Spitsbergen. Results of the Oxford University Expedition to Spitsbergen 1924. – *Ann. Mag. nat. Hist.* (9) 16: 332–337.
- Draber-Mońko, A. 1971. Niektóre Calyptrata (Diptera) Bieszczadów. – *Fragm. faun.* 17: 483–543. (In Polish, with Russian and German summaries).
- Emden, F. I. van 1954. Diptera Cyclorrhapha Calyptrata (I) Section (a) Tachinidae and Calliphoridae. – *Handbk Ident. Br. Insects* 10 (4) (a): 133 pp.
- Engel, E. O. 1920. Dipteren, die nicht Pupiparen sind, als Vogelparasiten. – *Z. Wiss. InsektBiol.* 15: 249–258.
- Gregor, F. & Povolný, D. 1959. Kritischer Beitrag zur Kenntnis der Tribus Phormiini (Diptera, Calliphoridae). – *Cas. čsl. Spol. ent.* 56: 26–51.
- Grunin, K. Ya. 1966. New and little known Calliphoridae (Diptera), mainly bloodsucking or subcutaneous parasites of birds. – *Ent. Obozr.* 45: 897–903. (In Russian, English translation in *Ent. Rev., Wash.* 45: 503–506).
- 1970. New species of Calliphoridae (Diptera: Calliphoridae). – *Ibidem* 49: 471–483. (In Russian, English translation in *Ent. Rev., Wash.* 49: 282–289).
- 1971a. *Phormiata* Grunin, gen. n. – A sixth genus of the tribe Phormiini (Diptera, Calliphoridae). – *Ent.*

Table 5. Host list for *Trypocalliphora braueri*; Palaearctic Region only. The classification and nomenclature of the birds follow Voous (as in Haftorn 1979), vernacular names Peterson, Mountfort & Hollom (1963). For sources, see text.

Host		Country
PASSERIFORMES		
Alaudidae		
<i>Alauda arvensis</i>	Sky Lark	Austria, Czechoslovakia, West Germany
Hirundinidae		
<i>Hirundo rustica</i>	Swallow	U.S.S.R.
Motacillidae		
<i>Anthus pratensis</i>	Meadow Pipit	Finland, U.S.S.R.
<i>Anthus trivialis</i>	Tree Pipit	Poland, U.S.S.R.
<i>Motacilla alba</i>	White Wagtail	Finland, Hungary
<i>Motacilla flava</i>	Yellow Wagtail	? (Zumpt 1965)
Turdidae		
<i>Luscinia luscinia</i>	Thrush Nightingale	Finland
<i>Oenanthe oenanthe</i>	Wheatear	Finland, Norway, U.S.S.R.
<i>Oenanthe</i> sp.		U.S.S.R.
Sylviidae		
<i>Sylvia communis</i>	Whitethroat	West Germany
<i>Phylloscopus bonelli</i>	Bonelli's Warbler	Austria
<i>Phylloscopus trochilus</i>	Willow Warbler	U.S.S.R.
Muscicapidae		
<i>Ficedula hypoleuca</i>	Pied Flycatcher	Norway
Paridae		
<i>Parus major</i>	Great Tit	Finland
Corvidae		
<i>Cyanopica cyanus</i>	Eastern Blue Magpie	U.S.S.R.
Sturnidae		
<i>Sturnus vulgaris</i>	Starling	U.S.S.R.
Passeridae		
<i>Passer domesticus</i>	House Sparrow	Austria, East Germany, Czechoslovakia
<i>Passer</i> sp.		U.S.S.R.
Fringillidae		
<i>Carduelis flammea</i>	Redpoll	Finland
Emberizidae		
<i>Emberiza schoeniclus</i>	Reed Bunting	West Germany
<i>Miliaria calandra</i>	Corn Bunting	Norway

Rev., Wash. 50: 253. (Russian original in Ént. Obozr. not seen).

— 1971b. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 277. Calliphoridae (Diptera) II. — Acta zool. hung. 17: 255–259.

— 1972. Beschreibung einer ornithoparasitischen Fliege, *Protocalliphora nuortevai* Grunin, sp. n. (Dipt., Calliphoridae) aus Nord-Finland. — Suom. hyönt. Aikak. 38: 156–158.

Grunin, K. Ya., Nuorteva, P. & Rajala, P. 1969. *Trypocalliphora lindneri* Peus (Dipt., Calliphoridae)

as a subcutaneous parasite of the Wheatear in northern Finland. — Ibidem 35: 56–57.

Haftorn, S. 1979. Våre fugler. En felthåndbok. — Oslo.
Hakanen, R., Grunin, K. Ya. & Nuorteva, P. 1974. Larvae of *Trypocalliphora lindneri* Peus (Dipt., Calliphoridae) as subcutaneous pathogens on nestlings of the Meadow Pipit and Common Redpoll in the subarctic. — Suom. hyönt. Aikak. 40: 15–18.

Hall, D. G. 1948. The blowflies of North America. — [6+] 477 pp., 51 pls., Lafayette, Ind.

— 1965. Family Calliphoridae. — Pp. 922–932, in: Stone, Sabrosky, Wirth, Foote & Coulson, A catalog of the

- Diptera of America north of Mexico. — Agric. Handb. 276: iv+1696 pp., Washington D. C.
- Heinz, H. J. 1954. Weitere Vogelblutfliegen (Gattung *Protocalliphora*, Dipt.) in Deutschland und Österreich. — Vogelwarte 17: 39–42.
- Hendel, F. 1901. Beitrag zur Kenntnis der Calliphorinen (Dipt.). — Wien. ent. Ztg 20: 28–33.
- Hennig, W. 1939. Über Namen und Artenzahl der deutschen "Vogelblutfliegen". — Arb. physiol. angew. Ent. Berl. 6: 359–364.
- Ishijima, H. 1967. Revision of the third stage larvae of synanthropic flies of Japan (Diptera: Anthomyiidae, Muscidae, Calliphoridae and Sarcophagidae). — Jap. J. sanit. Zool. 18: 47–100.
- Itämies, J. & Ojanen, M. 1975. *Trypocalliphora lindneri* Peus (Dipt. Calliphoridae) infesting a great tit nestling (*Parus major* L.). — Suom. hyönt. Aikak. 41: 42.
- Kano, R. & Shinonaga, S. 1968. Calliphoridae (Insecta: Diptera). — Fauna japon., 166 pp, 23 pls., Tokyo.
- Lindner, E. 1957. Vogelblutfliegen (*Protocalliphora*, Calliphorinae, Diptera). Ein Beitrag zur Kenntnis ihrer Systematik und Biologie. — Vogelwarte 19: 84–90.
- Lobanov, A. M. 1976. Opredelitel' samok sem. Calliphoridae (Diptera) fauný SSSR po yaitsekladam. — Opređ. Faune SSSR 109: 1–48.
- Myślicka, Z. 1968. Muchówki podrodziny Calliphorinae (Diptera) Gór Świętietokrzyskich. — Zesz. nauk. Uniw. Łódz. (2) 28: 125–136. (In Polish).
- Patton, W. S. & Cushing, E. C. 1934a. Studies on the higher Diptera of medical and veterinary importance. A revision of the genera of the subfamily Calliphorinae based on a comparative study of the male and female terminalia. The genus *Chrysomyia* Robineau-Desvoidy (sens. lat.). — Ann. trop. Med. Parasit. 28: 123–130.
- 1934b. Studies on the higher Diptera of medical and veterinary importance. A revision of the genera of the subfamily Calliphorinae based on a comparative study of the male and female terminalia. The genus *Phormia* Robineau-Desvoidy (sens. lat.). — Ibidem 28: 305–314.
- Peterson, R. T., Mountfort, G. & Hollom, P. A. D. 1963. A field guide to the birds of Britain and Europe. — 318 pp., London.
- Peus, F. 1960. Zur Kenntnis der ornithoparasitischen Phormiinen (Diptera, Calliphoridae). — Dt. ent. Z. (N. F.) 7: 193–235.
- Rausch, R. L. 1972. Cutaneous myiasis in a bird by the larval *Protocalliphora h. hirudo* Shannon and Dobrosky, 1924 (Diptera: Calliphoridae). — Aquilo (Zool.) 13: 1–4.
- Rodendorf, B. B. 1957. On the parasite flies, injurious to nestling singing birds. — Ént. Obozr. 36: 116–124. (In Russian with English summary. English translation in the British Library also seen).
- Sabrosky, C. W. 1967. Corrections to A catalog of the Diptera of America north of Mexico. — Bull. ent. Soc. Am. 13: 115–125.
- Sabrosky, C. W. & Bennett, G. F. 1958. The utilization of morphological, ecological, and life history evidence in the classification of *Protocalliphora* (Diptera: Calliphoridae). — Proc. 10. Int. Congr. Ent. (1956) 1: 163–164.
- Schumann, H. 1973a. Bemerkungen zum Status der Gattungen *Onesia*, *Melinda* und *Bellardia* (Diptera, Calliphoridae). — Mitt. zool. Mus. Berl. 49: 333–344.
- 1973b. Revision der palaearktischen *Melinda*-Arten (Diptera: Calliphoridae). — Dt. ent. Z. (N. F.) 20: 293–314.
- 1974. Revision der palaearktischen *Bellardia*-Arten (Diptera, Calliphoridae). — Ibidem 21: 231–299.
- Séguy, E. 1928. Études sur les mouches parasites. Tome I Conopides, Oestrides et Calliphorines de l'Europe occidentale. Recherches sur la morphologie et la distribution géographique des Diptères à larves parasites. — Encycl. ent. (A) 9: 1–251.
- 1941. Études sur les mouches parasites. Tome II Calliphorides. Calliphorines (suite), Sarcophagines et Rhinophorines de l'Europe occidentale et méridionale. Recherches sur la morphologie et la distribution géographique des Diptères à larves parasites. — Ibidem 21: 1–436.
- Shannon, R. C. & Dobrosky, I. D. 1924. The North American bird parasites of the genus *Protocalliphora* (Calliphoridae, Diptera). — J. Wash. Acad. Sci. 14: 247–253.
- Thomas, H. T. 1951. Some species of the blow-fly genera *Chrysomyia* R.-D., *Lucilia* R.-D., *Hemipyrellia* Tnsd. and *Calliphora* R.-D. from South-Eastern Szechuan, China. — Proc. zool. Soc. Lond. 121: 147–200.
- Zumpt, F. 1956. 64i. Calliphorinae. — In: Lindner, Fliegen palaearkt. Reg. 11: 1–140, Stuttgart.
- 1965. Myiasis in man and animals in the Old World. A textbook for physicians, veterinarians and zoologists. — xv+267 pp., London.

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