Sci. Rep. Kanazawa Univ.,
Vol. 12, No. 2, pp. 215—254
December 1967

Comparative Anatomy of the Internal Organs of the Calyptrate Muscoid Flies V. Consideration on the Phylogeny of the Calyptratae

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(Received 20 September 1967)

Introduction

The Calyptratae* are considered as a rather well-defined group which is fairly large and originated monophyletically from the common acalyptrate stock according to some recent Dipterists. Owing to the vastness of the number of closely resembling species, the classification of the Calyptratae has given rise to many disputes for several decades. Practically no two authors of the Diptera have agreed either on the subject of major groupings of the Calyptratae or the principle of the classification to be used. In most of these works, with the exception of Townsend's paper (1935-42) and few others, the taxonomic criteria for generic and supergeneric classification have mainly been the external morphological characters of the adult flies, and those for specific classification the characteristics of the genitalia of both sexes as well as the adult external morphology. The larval characters, with the exception of Townsend (1935-42), Hall (1948), Roback (1951), etc., have not been used to any great extent in the classification of the Calyptrate Diptera. Most of the systems proposed until now have been mainly founded upon the characters of the venation, the antennae, chaetotaxy, etc., together with the genitalia. In the past, therefore, it is not too much to say that the family limits within the Calyptratae as well as the subfamily or tribal limits within one family of the same have been subject to much shifting. It is, therefore, clear that the co-ordinate comparison of the external and internal morphological characters at all the stages is to be more reliable than the results obtained from a comparison only in the external morphology of the adult stage.

* The terms Schizometopa, Thecostomata, Muscomorpha, Calyptrata, Calypterata, Calypteratae, Calypterae, Calyptrates, Calypterates, etc., are also used by Dipterists.

Systematic works along this line have not yet been carried out in this field of study. The present author, therefore, undertook the comparative anatomy of the internal organs of the adult flies which had been ignored by many previous Dipterists (1960, 1961, 1962a, 1962b). The results obtained from these works, which are based on 83 Japanese species, were summarized here and the data of every trait were arranged in ascending or descending orders to clarify, if possible, the relationships amcng the different groups of the Calyptratae.

Some important external characters adopted by the former Dipterists such as the arista, the fourth longitudinal vein, the squamae, the notopleurals, the hypopleurals, the head width of the adult flies, though most of these were used for the separation of families, genera or species for the past 100 years or more, are here also shortly treated in discussing this problem co-ordinately from the evidences of external morphology as well. Since the materials in this series of papers are very limited, the resulting conclusions should be regarded only as purely tentative, and, therefore, a great deal of additional detailed works on many more materials, especially those belonging to the Scatophagidae, Anthomyiidae, Tachinidae (s. lat.) and several other small groups will certainly shed light on this interesting but difficult problem. Such detailed studies, however, are beyond the possibilities of my present work.

As far as the present author is aware, the scientific names of several of the species treated in this series of the author's work are recently revised by some Dipterists as follows:—

Orthellia latipalpis Zimin → *O. caerulea* Wiedemann
[see Hennig (1963): Die Fliegen...., pp. 928–9.]

Dasyphora cyanella (Meigen) → *D. cyanicolor* Zetterstedt
[see Hennig (1963): Die Fliegen...., p. 952.]

Morellia hortorum (Fallén) → *M. simplicissima* Zimin
[see Hennig (1963): Die Fliegen...., p. 976.]

Strongyloneura prasina Bigot → *Isomyia senomera* (Séguy)
[see Hori (1964): Kontyū, vol. 32, p. 511.]

Stomorhina discolor (Fabricius) → *St. obsoleta* (Wiedemann)
[see Kurahashi (1967): Sci. Rep. Kanazawa Univ., 12(2): p. 282]

Onesia sp. → *Melinda pusilla* Meigen
[see Hori (1961): Kontyū, vol. 29, p. 194.]

Calliphora vomitoria (Linné) → *C. lata* Coquillett
[see Hori and Kurahashi (1963): Kontyū, vol. 31, p. 284.]

Sarcophaga kinoshitai Hori → *Sarcophaga gravelyi* (Senior-White)
[see Kano et al., (1967): Fauna Japonica, Sarcophagidae (Insecta: Diptera), p. 91.]

Many mordern Dipterists have attempted to divide the Sarcophagidae into many genera mainly on the shape of the male genitalia. This divisicn, however, is not accepted here.

The author wishes to offer his sincere thanks to Prof. M. Katō of Tōhoku University for his kind advice and criticism. The author's cordial thanks are also due to Prof. T. Okada of Tokyo Metropolitan University and Dr. M. Tsukamoto of Nagasaki University for the loan of their own literature and also for their valuable suggestions.

Historicals

The history of the classification of the Calyptratae as well as that of other groups of insects begins with Linnaeus (1758), who described three genera, *Musca*, *Oestrus*, and *Conops*, in which many extant calyptrate flies were contained. The systematic characters of the Diptera adopted by him were mainly the morphological differences of the mouth-parts. The important systematic characters of the Calyptratae such as wing venation, mouth-parts, arista, the size of the squamae, habits, immature stages, oral vibrissae, ptilinum, head sclerites, transverse mesonotal suture, chaetotaxy, etc., were already recognized by older Dipterists such as Harris (1776), Duméril (1801, 1806), Meigen (1803, 1830, 1838), Latereille (1805), Fallén (1814-20), Rondani (1850), Robineau-Desvoidy (1830, 1863), Osten-Sacken (1881, 1884), Brauer and Bergenstamm (1889-94), and many others. The systematic values of these characters adopted by these pioneers in this field are of great importance and of general use even at the present time. The erection of the Calyptratae is accredited to Robineau-Desvoidy. He, according to Osten-Sacken (1896), divided the Myodaires into nine groups, which he called families (gentes), and the first of these, on the basis of the large size of their squamae, he called Calypteratae. This division, however, was not quite equivalent to the Calyptratae of later authors, because it did not include the Anthomyiidae.

The first major systematic work on the Calyptratae was done by Girschner (1893), who offered a new system of classification on the basis of many characters of the adult flies. In this system he first divided the Muscidae Calypterae into two families, Anthomyidae and Tachinidae, on the basis of the presence or absence of the hypopleural bristles. This Girschner's system is not so widely different from the recent ones.

Girschner's classification

I. Abteilung Muscidae Acalypterae
II. Abteilung Muscidae Calypterae
  I. Familie Anthomyidae
    1. Gruppe Coenosiinae
      Gattung *Cordylura*
      Gattung *Scatophaga*
      Gattung *Fucellia*
      Gattung *Lispe*
      Gattung *Coenosia*
      Gattung *Dialyta*
    2. Gruppe Muscinae
      Gattung *Hydrotaea*
      Gattung *Myospila*
      Gattung *Musca*
      Gattung *Stomoxys*
      Gattung *Haematobia*

Gattung *Graphomyia*
Gattung *Pyrellia*
Gattung *Mesembrina*
Gattung *Dasyphora*
II. Familie Tachinidae
1. Gruppe Oestridae
2. Gruppe Calliphorinae
3. Gruppe Verwandte von *Masicera*, *Gonia*, *Phorocera*, etc.
4. Gruppe *Sarcophaga*- und *Dexia*-artige Tachiniden, Phasiden, Gymnosominen, etc.

Modifying the systems of older workers, Coquillett, in 1901, proposed another system. He believed that this arrangement would indicate the natural relationships of the various families in a clearer manner than any of those that had been thus far proposed.

Coquillett's classification

Suborder Proboscidea
Section Orthorhapha
Section Cyclorhapha
Superfamily Muscoidea
Group Calypteratae
Family Oestridae
Family Tachinidae
Family Dexiidae
Family Sarcophagidae
Family Muscidae
Family Anthomyidae
Group Acalypterae
Family Scatophagidae
Suborder Eproboscidea
Family Hippoboscidae
Family Nycteribidae

Williston (1908) offered a system on the basis of examination of the North American specimens. In this system he divided the Calyptratae into six families. The Cordyluridae are included in the Acalyptratae. The genera *Hydrotaea*, *Ophyra*, *Limnophora*, *Mydaea*, *Hydrophoria*, *Anthomyia* and *Lispe* are included in the Anthomyidae. In the Muscidae most of the Calliphorid genera such as *Calliphora*, *Lucilia*, *Phormia* and *Mesembrina* are included in addition to the typical Muscids. The Miltogramminae are included in the Tachinidae.

Williston's classification

Acalypterae
Cordyluridae
Calypterae
Anthomyidae
Muscidae
Oestridae
Sarcophagidae
Dexiidae
Tachinidae

Townsend (1908) divided the Schizometopa, or Calyptratae, of Diptera into two superfamilies, Anthomyoidea and Muscoidea, by the presence or absence of the hypopleural bristles, pteropleural bristles, course pattern of fourth longitudinal vein, number and arrangement of sternopleural bristles, etc. The genera *Myiospila*, *Muscina*, etc., are included in the Anthomyioidea. In the superfamily Muscoidea, three families; Macronychiidae, Tachinidae, Muscidae, are recorded. The family Muscidae are divided into two subfamilies; Calliphorinae and Muscinae. In the subfamily Muscinae the genus *Mesembrina* is included together with typical Muscids such as *Musca*, *Stomoxys*, *Morellia*, etc.

Townsend's classification

Order Diptera
  Suborder Orthorrhapha
  Suborder Cyclorrhapha
    Series Aschiza
    Series Schizophora
Section Myodaria
  Subsection Schizometopa
    Superfamily Anthomyioidea
      Genus *Myiospila*
      Genus *Muscina*
    Superfamily Muscoidea
      Family Macronychiidae
      Family Tachinidae
      Family Muscidae
        Subfamily Calliphorinae
          Genus *Calliphora*
          Genus *Eucalliphora*
          Genus *Lucilia*
          Genus *Protophormia*
        Subfamily Muscinae
          Genus *Musca*
      Family Phasiidae
Section Pupipara

In 1911 Schnabl and Dziedzicki published their voluminous work, *Die Anthomyiden*, in which the Anthomyidae are divided into three groups. The genus *Lispe* is included in the Mydaeidae. The genera *Graphomyia*, *Muscina*, *Morellia*, *Musca*, *Stomoxys*, *Lyperosia*, etc., are placed in the Muscinae Ordo I, and in the Muscinae Ordo II the genera *Mesembrina*, *Dasyphora*, *Pyrellia*, etc., are included. The classification adopted by Schnabl and Dziedzicki in this work is based largely on the male genitalic characters.

Schnabl and Dziedzicki's classification

Anthomyidae
  1. Gruppe: Coenosinae
  2. Gruppe: Anthomyinae
    1. Formenreihe: Hylemyidae
    2. Formenreihe: Homalomyidae
    3. Formenreihe:
      A. Mydaeidae
      B. Muscinae Ordo I
    4. Formenreihe:
      A. Aricinae
      B. Muscinae Ordo II
  3. Gruppe: Gastrophilinae

Stein (1918) divided the Muscidae Calyptratae into two families; Anthomyidae and Tachinidae, on the bareness or plumosity of the hypopleuron.

Séguy (1923) divided the Anthomyidae into two subfamilies; Anthomyinae and Gasterophilinae. In his Anthomyinae, eight groups, that is, subfamilies, such as Fanninae, Stomoxydinae, Muscinae, etc., are recognized.

Séguy's classification

Anthomyidae
  Anthomyinae (s. l.)
    1er Groupe Coenosiinae
    2e Groupe (a). Hylemyinae
      (b). Pegomyinae
    3e Groupe Pegomyinae transitoriae
      Eginiinae
    4e Groupe Mydaeinae
    5e Groupe Fanniinae
    6e Groupe Ariciinae
  Muscinae (s. l.)
    Muscinae (1er groupe) ou Muscinae limnophoraeformes Schnabl
    7^{e} Groupe Stomoxydinae
    8^{e} Groupe Muscinae (s. s.)
    Muscinae (2^{e} groupe) ou Muscinae polietesformes Schnabl
  Gasterophilinae

Shannon (1923) endeavoured to maintain the Calliphorids as a distinct family.

Shannon's classification

Family Calliphoridae
  Subfamily Phorminae
    Tribe Chrysomyini
    Tribe Phormini
  Subfamily Calliphorinae
    Tribe Lucilini
    Tribe Calliphorini

Senior-White (1924) divided the Calyptrata into two large families; Muscidae and Tachinidae, and in the former three subfamilies are included, in the latter five subfamilies are listed.

Senior-White's classification

Acalyptrata
Calyptrata
  Family Muscidae
    Subfamily Anthomyiinae
    Subfamily Muscinae
    Subfamily Stomoxydinae
  Family Tachinidae
    Subfamily Calliphorinae
    Subfamily Rhiniinae
    Subfamily Sarcophaginae
    Subfamily Dexiinae
    Subfamily Tachininae

Imms (1925) divided the section Schizophora, or Muscoidea, of Diptera into the two undermentioned superfamilies. The Cordyluridae are included in the superfamily Acalypterae, and the superfamily Calypterae are subdivided into three families. Both the Muscids and Glossinids are included in his Anthomyidae. The Tachinidae are again subdivided into three subfamilies.

Imms's classification

Superfamily Acalypterae
  Family Cordyluridae
Superfamily Calypterae
  Family Anthomyidae
  Family Tachinidae
    Subfamily Sarcophaginae
    Subfamily Calliphorinae
    Subfamily Tachininae
  Family Oesteridae

Comstock (1924) divided the section Myodaria, or Schizophora, of Diptera into two subsections; Acalyptratae and Calyptratae. The family Cordyluridae were assigned to the Acalyptratae. In the Calyptratae two superfamilies, Anthomyioidea and Muscoidea, are recognized, The superfamily Muscoidea are subdivided into eight families. The Muscids, Calliphorids and Sarcophagids are each treated as a distinct family in the Muscoidea.

Comstock's classification

Section I. Myodaria
  Subsection I. Acalyptratae
    Family Cordyluridae
  Subsection II. Calyptratae
    Superfamily Anthomyioidea
      Family Anthomyiidae
    Superfamily Muscoidea
      Family Gastrophilidae
      Family Oestridae
      Family Phasiidae
      Family Megaprosopidae
      Family Calliphoridae
      Family Sarcophagidae
      Family Tachinidae
      Family Muscidae

Lundbeck (1927) divided the Schizometopa, or Calyptratae, into two large families; Anthomyidae and Tachinidae, and the latter are again subdivided into nine subfamilies.

Lundbeck's classification

Family Anthomyidae
Family Tachinidae
  Subfamily Gastrophilinae
  Subfamily Oesterinae
  Subfamily Hypoderminae
  Subfamily Phasiinae
  Subfamily Calliphorinae
  Subfamily Sarcophaginae
  Subfamily Rhinophorinae
  Subfamily Dexiinae
  Subfamily Tachininae

Karl (1928) divided the Muscidae into six subfamilies.

Karl's classification

Familie Muscidae
  Unterfamilie Muscinae
    Tribus Muscini
    Tribus Stomoxydini
  Unterfamilie Phaoniinae
    Tribus Phaoniini
    Tribus Hydrotaeini
    Tribus Fanniini
  Unterfamilie Eginiinae
    Tribus Azeliini
    Tribus Mydaeini
    Tribus Limnophorini
  Unterfamilie Mydaeinae
  Unterfamilie Anthomyinae
    Tribus Anthomyini
    Tribus Fucelliini
  Unterfamilie Coenosiinae
    Tribus Chelisiini
    Tribus Coenosiini

Hendel (1928) divided the Muscoidea, or Calyptratae, into the Haplostomata and Thecostmata, the former correspond to the Muscidae acalyptratae and the latter to the Muscidae calyptratae. The Thecostomata are divided into four families. The family Cordyluridae are included in the Thecostomata. The Calliphorids and Sarcophagids are recognized each as a subfamily in the Larvaevoridae.

Hendel's classification

Superfam. Muscoidea (Schizophora)
  Haplostomata (Muscidae acalyptratae, Myodaria inferiora)
  Thecostomata (Muscidae calyptratae, Myodaria superiora)
    Fam. Cordyluridae
    Fam. Oestridae
    Fam. Muscidae
    Fam. Larvaevoridae (Tachinidae)
      Unterfam. Calliphorinae
      Unterfam. Sarcophaginae
      Unterfam. Rhinophorinae
      Unterfam. Phasiinae
      Unterfam. Dexiinae
      Unterfam. Larvaevorinae (Tachininae)

Using the hypopleural character, viz, bareness or plumosity, Wainwright (1928) divided the Calyptratae into two large families: Anthomyidae and Tachinidae. The Calliphorids, Sarcophagids, Tachinids, etc., are recognized respectively as a subfamily of the Tachinidae.

Wainwright's classification

Calyptratae
  Family Anthomyidae
  Family Tachinidae
    Subfamily Tachininae
    Subfamily Sarcophaginae
    Subfamily Calliphorinae
    Subfamily Phasiinae

Séguy (1928) divided the Oestridae (auct., s. lat.) into two large families: Anthomyiidae and Tachinidae. In the Tachinidae three subfamilies are recognized. The subfamily Calliphorinae of this family are large and contain seven tribes.

Séguy's classification

Oestridae auct., s. l.
  Anthomyiidae
    Anthomyiinae
    Gasterophilinae
  Tachinidae
    Oestrinae
    Hypodermatinae
    Calliphorinae
      Oestrocalliphorini
      Rhynchoestrini
      Microcerellini
      Sarcocalliphorini
      Eucalliphorini
      Polleniini
      Rhiniini

Malloch (1934) divided the family Muscidae into seven subfamilies.

Malloch's classification

Family Muscidae
  Subfamily Anthomyiinae
  Subfamily Fanniinae
  Subfamily Coenosiinae
  Subfamily Lispinae
  Subfamily Phaoniinae
  Subfamily Stomoxydinae
  Subfamily Muscinae

Curran(1934) recognized six subfamilies in the Calyptratae. In his Muscidae, the Scatophagids, Anthomyiids and some members of Muscids which lack the hypopleural bristles are included. The family Metopidae are newly erected for the combination of the Sarcophagids, Calliphorids, some members of Muscids which have hypopleural bristles, and a few Tachinids.

Curran's classification

Family Muscidae
Family Gasterophilidae
Family Metopiidae
Family Tachinidae
Family Oestridae
Family Cuterebridae

Townsend (1935—42) made an extensive contribution to the study of the Calyptrate Diptera of the entire world. In his work the Rhiniidae are proposed for the combination of the Mesembrinellini, Bengaliini, Rhiniini and Polleniini. The Stephanostomatidae are also recognized as a distinct family for the combination of the Agrini, Miltogramini, Metopini and their allies. But his work, though excellent, is far from the current systems now used by students.

Enderlein (1936) divided the Schizophora into three "Untergruppe"; Protomuscaria,

Acalyptrata, and Calyptrata. The family Cordyluridae and Scatophagidae are assigned to the Protomuscaria. In this system he recognized three superfamilies in the Calyptrata; Muscoidea, Protachinoidea, and Tachinoidea. In the superfamily Muscoidea the Stmoxidae are entered as a separate family together with the Anthomyiidae, Muscidae. The Gastrophilidae are also included in this superfamily. *Fannai* and its allies are listed as a tribe Fanniini in the subfamily Phaoniinae. The members of *Lispe* are assigned to a separate subfamily in the Anthomyiidae. The superfamily Tachinoidea are divided into seven families; Phasiidae, Hypodermidae, Calliphoridae, Sarcophagidae, Rhinophoridae, Tachinidae and Dexiidae.

Enderlein's classification

- Untergruppe Protomuscaria
  - Familie Cordyluridae
- Untergruppe Acalyptrata
- Untergruppe Calyptrata
  - Superfamilie Muscoidea
    - Familie Anthomyiidae
      - Unterfamilie Phaoniinae
        - Tribus Phaoniini
        - Tribus Hydrotaeini
        - Tribus Fanniini
      - Unterfamilie Lispinae
      - Unterfamilie Mydaeinae
        - Tribus Azeliini
        - Tribus Mydaeini
      - Unterfamilie Fucelliinae
      - Unterfamilie Anthomyiinae
      - Unterfamilie Coenosiinae
    - Familie Muscidae
      - Unterfamilie Morelliinae
      - Unterfamilie Pyrelliinae
      - Unterfamilie Muscinae
    - Familie Stomoxidae
    - Familie Gastrophilidae
  - Superfamilie Protachinoidea
    - Familie Eginiidae
  - Superfamilie Tachinoidea
    - Familie Phasiidae
    - Familie Hypodermidae
    - Familie Calliphoridae
      - Unterfamilie Phorminae
        - Tribus Chrysomyiini
        - Tribus Phormiini
      - Unterfamilie Calliphorinae
        - Tribus Calliphorini
        - Tribus Luciliini
      - Unterfamilie Polleniinae
      - Unterfamilie Engyzopinae
      - Unterfamilie Rhynchomyiinae
        - Tribus Rhynchomyiini
      - Unterfamilie Rhiniinae
    - Familie Sarcophagidae
      - Unterfamilie Moriniinae
      - Unterfamilie Sarcophaginae
        - Tribus Sarcophagini
        - Tribus Bellieriini
      - Unterfamilie Miltogrammatinae
        - Tribus Metopiini
        - Tribus Miltogrammatini
      - Unterfamilie Agriinae
        - Tribus Agriini
        - Tribus Nyctiini
    - Familie Rhinophoridae
    - Familie Tachinidae
    - Familie Dexiidae

Rohdendorf (1937) divided the Sarcophagidae into six families.

Rohdendorf's classification

- Familie Sarcophagidae
  - Subfamilie Sarcophaginae
    - Tribus Sarcophagini
    - Tribus Raviniini
  - Subfamili Agriinae
  - Subfamilie Chrysogrammatinae
  - Subfamilie Metopiinae
  - Subfamilie Macronychiinae
  - Subfamilie Mimodexiinae

Senior-White, Aubertin and Smart (1940) divided the Calyptrata into four families; Muscidae, Oestridae, Calliphoridae, and Tachinidae. The Sarcophagids are retained as a subfamily in the Calliphoridae.

Senior-White, Aubertin and Smart's classification

Calyptrata
- Family Muscidae
- Family Oestridae
- Family Calliphoridae
  - Subfamily Calliphorinae
  - Subfamily Chrysomyiinae
  - Subfamily Rhiniinae
  - Subfamily Sarcophaginae
- Family Tachinidae

Hennig (1941) recognized twelve families in the superfamily Calyptratae. The Rhiniids, Melanophorids, Phasiids, Dexiids, Prosenids, Exoristids, etc., are treated as a distinct family respectively. In the Anthomyiidae eight subfamilies; Anthomyiinae, Fanniinae, Lispinae, Coenosiinae, Phaoniinae, Eginiinae. Muscinae, and Stomoxydinae, are listed. The genus *Ophyra* is included in the subfamily Phaoniinae.

Hennig's classification

Superfamilie Calyptratae
- Familie Cordyluridae
- Familie Rhiniidae
- Familie Calliphoridae
- Familie Sarcophagidae
- Familie Melanophoridae
- Familie Phasiidae
- Familie Dexiidae
- Familie Oestridae
- Familie Prosenidae
- Familie Tachinidae
- Familie Exoristidae
- Familie Anthomyiidae
  - Subfamilie Anthomyiinae
  - Subfamilie Fanniinae
  - Subfamilie Lispinae
  - Subfamilie Coenosiinae
  - Subfamilie Phaoniinae
  - Subfamilie Eginiinae
  - Subfamilie Muscinae
  - Subfamilie Stomoxydinae

Crampton (1942-4) divided the Calypteratae into two principal superfamilies, Muscoidea and Tachinoidea, on the basis of the study of the male genitalia. The superfamily Muscoidea contain four families; Scatophagidae, Glossinidae, Anthomyiidae and Muscidae. The superfamily Tachinoidea include the Phasiidae, Dexiidae, Tachinidae (or Larvaevoridae), Oestridae, Cuterebridae, Sarcophagidae (or Metopiidae), Calliphoridae, and Gastrophilidae. The genitalic characters of the families Cuterebridae and Gastrophilidae were generally considered sufficient to place them as a separate Oestroid superfamily. He thought that if the Cordyluridae were to be regarded as a true Calyptratae, it might be advisable to place them in a separate superfamily Cordyluroidea.

Crampton's classification

Calypteratae
- Superfamily Muscoidea (or Muscomorpha)
  - Family Scatophagidae
  - Family Anthomyiidae
  - Family Muscidae
  - Family Glossinidae

Superfamily Tachinoidea
- Family Phasiidae
- Family Dexiidae
- Family Tachinidae
- Family Oestridae
- Family Cuterebridae
- Family Sarcophagidae
- Family Calliphoridae
- Family Gastrophilidae

Tokunaga (1943) concurred with Williston's view (1908), and divided the Calyptratae into five families; Anthomyiidae, Muscidae, Sarcophagidae, Oestridae and Tachinidae. The Muscinae, Calliphorinae, Glossininae, Stomoxyidinae and Philaematomyiinae are retained respectively as a separate subfamily in the Muscidae.

In the system proposed by Mesnil (1944), three families, Muscidae, Calliphoridae and Larvaevoridae, are recognized in the Thecostomata, or Calyptratae. The Calliphorinae, Hypoderminae, Sarcophaginae and Rhinophorinae are all retained as a subfamily in the Calliphoridae.

Mesnil's classification

I. Haplostomata
II. Thecostomata
- A. Muscidae
- B. Calliphoridae
  - a. Calliphorinae
  - b. Hypoderminae
  - c. Sarcophaginae
  - d. Rhinophorinae
- C. Larvaevoridae
  - a. Phasiinae
  - b. Dexiinae
  - c. Larvaevorinae

The system adopted by Essig (1947) in his text-book followed in many points that of Enderlein.

Hall (1948) divided the Calypteratae into two groups, Anthomyiaria and Oestromuscaria, and the latter into three superfamilies; Oestroidea, Muscoidea and Sarcophagoidea. In the Sarcophagoidea, two families, Sarcophagidae and Calliphoridae, are adopted. The Calliphoridae are further divided into five subfamilies.

Hall's classification

Calypteratae
- Anthomyiaria
- Oestromuscaria
  - Oestroidea
  - Muscoidea
  - Sarcophagoidea
    - Family Sarcophagidae
    - Family Calliphoridae
      - Subfamily Mesembrinellinae
      - Subfamily Rhiniinae
      - Subfamily Chrysomyinae
      - Subfamily Calliphorinae
      - Subfamily Polleniinae

In the system adopted by Colyer and Hammond (1951) four families, Cordyluridae, Muscidae, Calliphoridae and Larvaevoridae, are recognized in the Calypterates. The family Calliphoridae are divided into three subfamilies; Calliphorinae, Sarcophaginae and Rhinophorinae. The family Muscidae are also subdivided into eight subfamilies.

Colyer and Hammond's classification

Cyclorrhapha
- Acalypterates
- Calypterates
  - Family Cordyluridae (Scatophagidae)
  - Family Larvaevoridae (Tachinidae)
  - Family Calliphoridae
    - Subfamily Rhinophorinae
    - Subfamily Sarcophaginae
    - Subfamily Calliphorinae
  - Family Muscidae (Anthomyiidae)
    - Subfamily Muscinae
    - Subfamily Gasterophilinae
    - Subfamily Phaoninae
    - Subfamily Lispinae
    - Subfamily Mydaeinae
    - Subfamily Fucellinae
    - Subfamily Anthomyiinae
    - Subfamily Coenosiinae

Zimin (1951) divided the subfamily Muscinae into two tribes, Muscini and Stomoxydini, and the genus *Graphomyia* is transferred to the tribe Stomoxydini.

Zimin's classification

Family Anthomyidae
Family Muscidae
- Subfamily Muscinae
  - Tribe Muscini
    - Genus *Orthellia*
    - Genus *Musca*
    - Genus *Pyrellia*
    - Genus *Rypellia*
    - Genus *Dasyphora*
    - Genus *Morellia*
    - Genus *Mesembrina*
  - Tribe Stomoxydini
    - Genus *Graphomyia*
    - Genus *Stomoxys*
    - Genus *Haematobia*
    - Genus *Lyperosia*

The Calyptratae are divided into three superfamilies, Muscoidea, Sarcophagoidea and Oestroidea by Roback (1951). The fannines are advanced to a family of the Muscoidea. The Scopeumatinae are included together with the Anthomyiinae in the family Anthomyiidae. The Stomoxyids are recognized as a separate subfamily Stomoxyinae in the Muscidae. In the Sarcophagoidea two families, Calliphoridae and Sarcophagidae, are listed.

Roback's classification

Calyptratae
- Superfamily Muscoidea
  - Family Anthomyiidae
    - Subfamily Anthomyiinae
    - Subfamily Scopeumatinae
  - Family Fanniidae
  - Family Muscidae
    - Subfamily Coenossiinae
    - Subfamily Lispinae
    - Subfamily Phaoniinae
    - Subfamily Muscinae
    - Subfamily Stomoxyinae
- Superfamily Sarcophagoidea
  - Family Calliphoridae
    - Subfamily Mesembrinellinae
    - Subfamily Rhiniinae
    - Subfamily Chrysomyinae
    - Subfamily Calliphorinae
    - Subfamily Polleninae
  - Family Sarcophagidae
    - Subfamily Miltograminae
    - Subfamily Sarcophaginae
- Superfamily Oestroidea

In the Muscidae (=Anthomyiidae) Ringdahl (1954—9) recognized nine subfamilies. The genera *Graphomyia* and *Muscina* are included in the Muscinae.

Ringdahl's classification

Holometopa
Schizometopa
  Fam. Cordyluridae
  Fam. Muscidae (Anthomyiidae)
    Underfam. Muscinae
    Underfam. Stomoxydinae
    Underfam. Phaoniinae
    Underfam. Fanninae
    Underfam. Mydaeinae
    Underfam. Lispinae
    Underfam. Coenosiinae
    Underfam. Fucellinae
    Underfam. Anthomyiinae

Van Emden (1954) divided the Calyptrata into four families; Cordyluridae, Muscidae, Calliphoridae and Tachinidae. The Calliphorinae and Sarcophaginae appear respectively as a separate subfamily in the Calliphoridae.

van Emden's classification

Calyptrata
  Family Cordyluridae
  Family Muscidae
  Family Tachinidae
    Subfamily Phasiinae
    Subfamily Dexiinae
    Subfamily Macquartiinae
    Subfamily Tachininae
    Subfamily Goniinae
  Family Calliphoridae
    Subfamily Rhinophorinae
    Subfamily Sarcophaginae
    Subfamily Polleniinae
    Subfamily Calliphorinae

In his text-book Shiraki (1954) adopted the system proposed by Enderlein (1936).

Hennig (1955—64) retained the fannines in the subfamily status, and included the genus *Graphomyia* together with *Myospila* in his Mydaeinae and the genera *Ophyra*, *Muscina*, etc., in his Phaoniinae. The genera *Stomoxys*, *Siphona*, etc. remain as a tribe in the Muscinae.

Hennig's classification

Familie Muscidae
  Unterfamilie Fanniinae
    Gattung *Fannia*
  Unterfamilie Mydaeinae
    Tribus Azeliini
    Tribus Mydaeini
      Gattung *Myospila*
      Gattung *Helina*
      Gattung *Graphomyia*
    Tribus Limnophorini
      Gattung *Limnophora*
    Tribus Lispini
      Gattung *Lispe*
    Tribus Coenosiini
      Gattung *Lispocephala*
  Unterfamilie Phaoniinae
    Tribus Achantipterini
    Tribus Hydrotaeini
      Gattung *Pegonomyia*
      Gattung *Ophyra*
      Gattung *Hydrotaea*
    Tribus Phaoniini
      Gattung *Muscina*
      Gattung *Phaonia*
    Tribus Dichaetomyiini
      Gattung *Dichaetomyia*
  Unterfamilie Muscinae
    Tribus Muscini
      Gattung *Mesembrina*
      Gattung *Orthellia*
      Gattung *Rypellia*
      Gattung *Pyrellia*
      Gattung *Dasyphora*
      Gattung *Morellia*
      Gattung *Musca*
    Tribus Stomoxyini
      Gattung *Stomoxys*
      Gattung *Stygeromyia*
      Gattung *Siphona*

In the Calyptratae Herting (1957) recognizes six families; Muscidae, Cordyluridae, Glossinidae, Calliphoridae, Tachinidae and Oestridae. The family Muscidae are divided into three subfamilies; Anthomyiinae, Fanniinae and Muscinae. The genera *Fucellia*, *Pegomyia* together with *Hylemyia*, *Anthomyia* are included in the subfamily Anthomyiinae, and the genera *Ophyra*, *Lispe*, *Muscina* and *Graphomyia* are all placed in the subfamily Muscinae. The Calliphorids and Sarcophagids remain respectively in a subfamily rank.

Herting's classification

Fam. Muscidae
- Subfam. Anthomyiinae
- Subfam. Fanninae
- Subfam. Muscinae

Fam. Cordyluridae
Fam. Glossinidae
Fam. Calliphoridae
- Subfam. Calliphorinae
- Subfam. Sarcophaginae
- Subfam. Rhinophorinae

Fam. Tachinidae
- Subfam. Echinomyiinae
- Subfam. Dexiinae
- Subfam. Phasiinae

Fam. Oestridae

Zumpt (1960) divided the Calliphoridae into two subfamilies, and continued to treat the Calliphorids and Sarcophagids respectively as a subfamily in the Calliphoridae.

A system adopted in *A Catalog of the Diptera of America North of Mexico* by American Dipterists (1965) is as follows:—

Section Calyptratae
- Superfamily Muscoidea
  - Family Anthomyiidae
    - Subfamily Scatophaginae
    - Subfamily Fucelliinae
    - Subfamily Anthomyiinae
  - Family Muscidae
    - Subfamily Coenosiinae
    - Subfamily Lispinae
    - Subfamily Limnophorinae
    - Subfamily Mydaeinae
    - Subfamily Fanniinae
    - Subfamily Phaoniinae
    - Subfamily Muscinae
    - Subfamily Stomoxyinae
- Superfamily Oesteroidea
  - Family Calliphoridae
    - Subfamily Rhiniinae
    - Subfamily Chrysomyinae
    - Subfamily Calliphorinae
    - Subfamily Polleniinae
  - Family Sarcophagidae
    - Subfamily Miltogramminae
    - Subfamily Sarcophaginae
  - Family Tachinidae (Larvaevoridae)
    - Subfamily Rhinophorinae (Melanophorinae)
    - Subfamily Phasiinae
    - Subfamily Proseninae
    - Subfamily Tachininae (Larvaevorinae)
    - Subfamily Dexiinae

Hennig (1965) recognized nine subfamilies in his Muscidae (s. str.), and maintained that the Fanniinae have a sister-group relation to his family Muscidae.

Hennig's classification

Familie Muscidae
- Unterfamilie Fanniinae
- Unterfamilie Achanthipterinae
- Unterfamilie Muscinae
- Unterfamilie Phaoniinae
- Unterfamilie Mydaeinae
- Unterfamilie Limnophorinae
- Unterfamilie Coenosiinae

Unterfamilie Cryptoneurinae
Unterfamilie Stomoxydinae
Familie Glossinidae
Familie Hippoboscidae
Familie Nycteribiidae
Familie Streblidae

In his monograph Fan (1965) recognized four superfamilies in the Calyptratae. The superfamily Muscoidea are divided into three families. The genera *Fannia* and *Lispe* are each treated as a subfamily in the family Muscidae. The genera *Ophyra*, *Muscina*, and *Graphomyia* are contained in the subfamily Phaoniinae of the Muscidae. The Calliphorids and Sarcophagids are treated respectively as a family in the superfamily Calliphoroidea.

Fan's classification

Calyptratae
- Superfam. Muscoidea
  - Fam. Anthomyiidae
    - Subfam. Fucelliinae
    - Subfam. Anthomyiinae
  - Fam. Muscidae
    - Subfam. Fanniinae
    - Subfam. Lispinae
    - Subfam. Coenosiinae
    - Subfam. Phaoniinae
    - Subfam. Muscinae
    - Subfam. Stomoxydinae
- Superfam. Calliphoroidea
  - Fam. Calliphoridae
    - Subfam. Polleniinae
    - Subfam. Calliphorinae
    - Subfam. Chrysomyiinae
    - Subfam. Phormiinae
    - Subfam. Rhiniinae
  - Fam. Sarcophagidae
    - Subfam. Sarcophaginae
    - Subfam. Agriinae
    - Subfam. Metopiinae

Relevance of Characters to the Relationships of the Calyptrate Taxa Studied

(a) The male accessory glands

The male accessory glands are wanting in the families Scatophagidae and Muscidae here examined, while they are fully developed in the Calliphoridae, Sarcophagidae, Phasiidae, Dexiidae and Tachinidae (s. str.) (Hori, 1960). In the Anthomyiidae they are wanting in the genera *Ophyra* and *Pegomyia*, but they are developed in the genera *Fannia* and *Anthomyia*. Thus, on the basis of presence or absence of the male accessory glands, the Calyptratae are separable into two main groups. The absence of the male accessory glands and the similarity of other internal male organs in addition to the known facts about the terminalia and other adult characters link the genus *Ophyra* with the Muscidae as assumed by some recent Dipterists as Crampton (1944), Hennig (1954—64), Huckett (1965).

The shape of the male accessory glands of the calyptrate muscoid Diptera also makes them roughly divisible into three groups; (a) spherical or ellipsoidal which occur in *Fannia*, *Anthomyia*, *Isomyia*, *Echinomyia*, *Chrysosoma*, *Succingulum* and *Ectophasia*, (b) banana-shaped which are observed in *Hydrophoria*, *Metopia*, *Prosena* and nine genera of the Calliphoridae, and (c) coiled which are peculiar to the Sarcophagidae (Hori, 1960).

(b) Shape of the testes

The testes of the adult Calyptrate Diptera greatly vary in shape with the advance of the age after the emergence. This intraspecific age variation is caused mainly by the discharge of the spermatozoa. Consequently the shape of the testes in a newly emerged fly has taxonomic significance. The shapes of the testes of the Calyptrate Diptera are, from this point of view, roughly divisible into three groups: (a) oval, (b) spongecucumber-shaped, (c) lamp-shaped (Hori, 1960). The morphological evidence of the testes indicates that the genus *Lispe* resembles those of Scatophagidae rather than those of the other Anthomyiidae or Muscidae, and *Ectophasia* also appears to be related to the Sarcophagidae rather than to the rest of the Tachinidae (s. lat.).

(c) Colour of the testes

The colours of the testes of the adult flies just emerged are divided into three groups: (a) reddish orange, (b) brown or fuscous, (c) pale greenish yellow (Hori, 1960). In the Tachinidae (s. str.) examined, the testes are pale greenish yellow in colour, while only in the genera *Ectophasia* and *Succingulum* they are reddish orange, resembling those of the Sarcophagidae, Calliphoridae, and many others.

(d) The fat-body

The fat-body which densely invests the adult testes of the Calyptrate Diptera is observed in all the members of the Calliphoridae and also in some Tachinids (Hori, 1960).

(e) The ejaculatory apodeme

The ejaculatory apodeme is a chitinous sclerite of the ejaculatory sac. In the three species of the genus *Fannia*, no trace of this is to be found, which indicates their probable primitive condition. This morphological evidence indicates that the genus *Fannia* has a very primitive nature considerably different from most of the Anthomyiidae examined. The shape of the apodeme was roughly classified into the following two types: (a) rod-shaped, and (b) fan-shaped, the latter being advanced (Hori, 1960).

(f) Length of the ejaculatory duct

There can be little doubt that a straight tube connecting the vas deferens with its aedeagus is the ejaculatory duct of the primitive insects, a longer one meaning a later development. To compare the length of the ejaculatory ducts of the Calyptratae, the ejaculatory duct indices of 83 species are measured (Hori, 1960). The Scatophagidae, Anthomyiidae, Calliphoridae and Tachinidae examined all belong to the first group in which the indices are below 50. In the Muscidae, the genera *Musca*, *Graphomyia*, *Pyrellia*, *Dasyphora*, *Orthellia*, *Myiospila* and *Muscina* of the subfamily Muscinae all belong to the second group in which the indices are generally

over 50. While the values of the genera *Stomoxys* and *Siphona* which belong to the subfamily Stomoxydinae remain below 50.

In the Sarcophagidae genera *Metopia*, *Leucomyia*, *Blaesoxipha* and several members of the genus *Sarcophaga* (s. lat.) which have three dorso-centrals all belong to the first group, and the others of this genus belong to the second group.

(g) Torsion of the ejaculatory duct

The modes of the torsion of the ejaculatory duct round the hind-gut are of two types; (a) counterclockwise torsion, and (b) clockwise torsion. Of 83 species examined, only *Lispe* belongs to the first type (Hori, 1960). This evidence as well as the known facts of other internal organs indicates that *Lispe* is considerably different from those of the typical Anthomyiid or Muscid Diptera. According to Milani and Rivosechi (1957) the direction of the torsion is, in *Musca domestica*, determined by a single gene. Therefore the taxonomic value of this character must await further study.

(h) The rectal papillae

The arrangement of the rectal papillae of the males was divided into three types: (a) bilateral type, (b) cruciate type A, and (c) cruciate type B. (Hori, 1962a).

(i) Position of the rectal valve

The rectal valve indices (I/L × 100; I-length of the distal intestine, L-length between the commencement of the hind-gut and the rectal pouch) of 82 adult flies are measured (Hori, 1962a). The values indicate the relative position of the rectal valve from the commencement of the hind-gut. Generally speaking the values among a single genus or allied groups are nearly constant. In most of the Anthomyiidae the values are 50 to 40, while in *Lispe* the value is over 90, differing clearly from the rest of the same family. It is, therefore, clear that *Lispe* is remotely related to other Anthomyiids examined.

(j) Coiling degree of the proximal intestine

The coiling degrees of the proximal intestine of the male adult flies are observed (Hori, 1962a). The degrees are smaller in the Scatophagidae, Anthomyiidae, Sarcophagidae and Tachinidae, and larger in the Muscidae and Calliphoridae. In the respective subfamilies of the Anthomyiidae, Muscidae, Calliphoridae and Sarcophagidae, the degrees increase proportionately from more primitive to more advanced (see Table I). The small values of the degrees of the Tachinidae are probably the result of the parasitic habit in their larval stages. It is noticeable that the values of the Sarcophaginae examined are subject to but little variation, in contrast to those of the others. This may indicate that the food habits of the Sarcophaginae are nearly the same.

(k) Length of the mid-gut

The double coils of the proximal intestine are in most cases more or less irregular. Consequently the measurement of the mid-gut indices, besides the coiling degree of that part, is necessary. The mid-gut indices, as has been expected, are inclined to increase in many cases parallel with the values of the coiling degree (Hori, 1962a).

(l) Arrangement of the Malpighian tubules

The arrangement taken by the anterior pair of the tubules was grouped into the following three main types: (a) Y-shaped, (b) M-shaped, and (c) fused (Hori, 1962 b). The arrangements of the tubules of the Phasiinae and Dexiinae appear transitional from the Tachinidae (s. str.) to the Calliphoridae, Sarcophagidae and other families. In the Tachinidae examined, the Malpighian tubules are generally short, but their diameters are usually very large. This is regarded as a compensatory growth of the tubules for the loss of the length of the tubules. These three kinds of arrangement, including the transitional one, may well have developed in the following direction:

Y-shaped → (transitional) → M-shaped → fused

The tubules of *Graphomyia* fused into a loop must definitely be regarded as one rare noticeable case of specialization. Judging from the morphological characters of the tubules as well as other external and internal features, *Graphomyia* appears to be considerably different from the rest of the Muscidae.

(m) Number and arrangement of the spermathecae

In the majority of the Calyptrate Diptera examined, the spermathecae are usually three in number, but in exceptional cases such as three species of the Stomoxydinae and the lesser house-fly, they are only two (Hori, 1961). At this time, however, it is difficult to arrive at any firm conclusion regarding their primitive number in the Calyptrate Diptera. Very tentatively, the number two appears to be the most probable primitive of these organs in the Calyptrate Diptera.

This fact as well as other external characters such as the mouth-parts suggests that the Stomoxydinae as well as Glossinidae occupy an interesting position in the Calyptratae genealogy. The spermathecae on the common oviduct are bilaterally arranged in three ways: 2:0 or 0:2; 2:1 or 1:2; 1:1:1 (Hori,1961).

(n) The female accessory glands

From the morphological evidences the female accessory glands are divided into three groups: (a) oval or elongate oval, (b) banana-shaped, and (c) clavate. Among these three types the first mentioned type is the most primitive, and the second is the most developed, while the last type occupies a position intermediate between these two types (Hori, 1961). Relations among these three types are considered

as follows:—

Oval or elongate oval → banana-shaped → clavate

Because of similarity in the shape of the female accessory glands together with the shape of the testes, the Scatophagidae and Sarcophagidae appear to have some affinity.

(o) The uterovaginal tube

From the morphological evidences the uterovaginal tube is divisible into three groups: (a) a straight, simple-shaped, (b) a straight tube with a large incubatory pouch, and (c) coiled when matured. Among these three groups the first group is, without doubt, the most primitive, and the second and third groups are derived independently from the first respectively (Hori, 1961).

(p) The arista

In the higher Diptera, the segments distal to the third antennal segment are greatly reduced and appear to be merely a slender appendage of the antenna. They are called arista. The differentiation of the arista from the fourth and its succeeding terminal antennal segments is first recognized in the Nematoceran Diptera by Robineau-Desvoidy (1830). In the Calyptrate Diptera, therefore, a bare or sparsely haired arista is, without doubt, in the primitive condition. The significance of the arista in the taxonomy of the Diptera was already recognized by Linnaeus (1758). In the Calyptratae it is said that the arista is well developed and affords taxonomically important specific characteristics.

In the Scatophagidae which are supposed to be the most primitive, the arista is bare, representing their least modified condition. In the Anthomyiidae it is bare in *Ophyra* and *Fannia*, short plumose in *Pegomyia* and *Lispe*, plumose in *Hydrophoria*. In the Muscidae it is plumose in *Muscina*, *Morellia*, *Orthellia*, *Dasyphora*, *Pyrellia*, *Musca* and *Graphomyia* all of which are here included in the subfamily Muscinae; while it is semiplumose in *Stomoxys* and *Siphona* which belong to the subfamily Stomoxydinae, indicating some resemblance to that of *Glossina*. In the Stomoxydinae, however, this condition of the arista is not a group character, for, even within these two genera, several exotic forms including *Stomoxys chinensis*, *Siphona stimulans* and some others have a more or less plumose arista.

In the Calliphoridae it is short plumose in *Stomorhina*, while all other members have a deeply plumose arista. In the Sarcophagidae it is bare in *Metopia*, pubescent in *Leucomyia*, while it is well plumose in all the members of the genera *Blaesoxipha* and *Sarcophaga* (s. lat.) examined. In the Phasiidae and Tachinidae examined it is bare, while the Dexiids examined bear short pubescence.

From the above mentioned, it is noteworthy that the arista of the Calyptratae

presents varying degrees of hairiness according to their systematic position, and the filiform type of arista doubtlessly indicates the basic or primitive type, haired ones being a later development. The hairiness of the arista must, generally speaking, have had, from the primitive to the advanced, the following two sequences:

bare → pubescent ↗ semiplumose → long plumose (Stomoxyids)
pubescent ↘ short plumose → plumose → long plumose (many Muscids)

(q) Distal bend of the fourth longitudinal vein

It is a well known fact that the venation of the wing veins of insects is so stable within a species, but between different species or groups it is considerably so variable that it is very useful for purposes of classification. In the Calyptratae the fourth longitudinal vein (m_{1+2}) is of considerable importance, since it is very long and stout and anchors the posterior half of the wing to its anterior part by a cross-vein (r-m) and also connects it with the tip end of costa.

Many Dipterists consider the fourth longitudinal vein to be a fusion of m_1 and m_2, while recently Lower (1951) believes that, in the Muscoidea calyptratae such as *Calliphora* (Calliphoridae) and *Cylindromyia* (Tachinidae), this is not m_1 as usually understood, but an union of r_5 and m_1, distally the former sharply bending upwards and the latter running straight beyond the turning point of the former as a stub vein.

In the Scatophagidae the fourth vein runs straight in parallel with the vein r_{4+5}. The almost similar course pattern of the fourth vein is also seen in all the members of the Anthomyiidae here examined. The subfamily Muscinae were formerly separated from the others of the Muscidae on the basis of the bend of this vein. In the Muscinae, however, the fouth vein is gently bent anteriorly towards the third vein before reaching the wing margin in the genera *Siphona*, *Stomoxys*, *Muscina* and *Myiospila*, while it is broadly curved in the genera *Morellia*, *Orthellia*, *Dasyphora*, *Pyrellia* and *Graphomyia*, and sharply bent upwards in the genus *Musca*.

In the Calliphoridae the fouth vein is gently curved in *Isomyia* and *Stomorhina*, sharply bent up in all the remaining members of this family.

In the Sarcophagidae and Tachinidae (s. str.) examined also the fourth vein is sharply bent up, showing its marked approximation to the third vein and corresponding narrowing of the cell R_5.

These facts may possibly be taken to indicate that the fourth vein of the primitive Calyptrate Diptera is a little diverted from the hypothetical primitive type which runs probably almost straight to the wing margin as shown in nearly all the extant Acalyptrate Diptera and that the curved ones of the fourth vein are found in the evolved flies.

This distal bend of the fourth vein, namely the directing forwards to the anterior costal margin, which is already used by Meigen (1803) to separate the Anthomyiids

from the other Muscid flies, frequently occured in the higher Calyptrate Diptera as above-mentioned. I propose to term this phenomenon here "***costalization***", which is probably effective in increasing the strength of the wing indispensable for the quick and strong vibration of the wing in the "higher, or larger, flies", with due result of the degeneration of the hind part of the wing and also with due change of the general form of it. From above it is clear that the distal bend of the fourth vein of the Calyptratae is an evolutionary trend and increases with the advance of their phylogenetic position as shown above. This view has, however, met opposition in van Emden (1956). According to him this bend of the fourth vein, however, has now been known in so many unrelated forms that its use as a group character should be abandoned. The investigation of this possibility must be a subject of future study.

(r) Size of the squamae

The squamae or calypters* are flap-like membranous region at the base of the wing, the upper being the alar or upper squama which is attached to the wing, and the lower is the thoracic or lower squama which is attached to the thorax. The upper squama is an apparently modified portion of the basal membrane of the wing, while the thoracic squama is open to considerable doubt as to its primitive status or origin, and is inconspicuous in most Diptera including the Acalyptratae, but in the higher Diptera it is usually well developed and often conceals the haltere. On the basis of this they are called the Calyptratae or Calypterae.

The Calypteratae, according to Osten-Sacken (1884), are erected by Robineau-Desvoidy as the first, from the large size of their squamae, of his nine groups of Myodaires in 1830. This division of Diptera, however, was not completely equivalent to the Calyptratae of later authors, because it did not include the Anthomyiidae. In other words the Calyptratae here in question are a group of "higher flies" characterized by the good development of the thoracic squama which used to be considered to be taxonomically of no importance by some Dipterirts.

In order to indicate the degree of the development of the thoracic squama into the alar squama, the mean value squamal index, which is the length of the thoracic sqama divided by that of the alar squama, was measured for each species as shown in Table I. The squamal indices are 0.2 in the Scatophagidae. In the Anthomyiidae the indices are 0.8 in *Pegomyia*, *Ophyra*, *Anthomyia*, *Hydrophoria*, 0.9 in *Fannia*, whereas in *Lispe* they are 1.5. In the Muscidae they are 1.2 in *Siphona*, 1.5 in *Stomoxys* (Stomoxydinae), whereas in the Muscinae they are 1.2 in *Muscina*, *Myospila*, 1.8 in *Musca*, 2.0 in *Morellia*, *Orthellia*, *Dasyphora*, *Pyrellia* and *Graphomyia*.

In the Calliphoridae they are 1.2 in *Isomyia* and *Stomorhina*, *Protophormia*,

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* The terms tegulae, alulae, etc., are also used by earlier Dipterists.

Phormia, 1.5 in *Chrysomya*, *Melinda*, *Triceratopyga* and *Calliphora*, 1.8 in *Lucilia*.

In the Sarcophagidae they are always 2.0 in *Metopia*, *Leucomyia*, *Blaesoxipha* and *Sarcophaga* (s. lat.) here examined.

In the Tachinidae (s. lat.) they are 2.0 in *Ectophasia*, *Prosena*, *Servillia*, *Echinomya*, *Chrysosoma*, 2.2 in *Succingulum* and *Sturmia*.

Although the function of the squamae of the Calyptratae is not studied yet and remains subjected to considerable doubt, it is quite possible that the thoracic squama is little- or weakly-developed in the primitive members even within the Calyptratae.

From the above mentioned it is likely that the squamal index increases gradually from the primitive to the advanced accoring to their systematic position.

(s) Number of the notopleural bristles

The bristles occuring on the notopleura are termed the notopleural bristles or simply notopleurals. They are typically two, as seen in the *Drosophila*, in the families Scatophagidae, Anthomyiidae, Muscidae, Calliphoridae and Tachinidae here examined. In the Sarcophagidae, however, there are two in *Metopia*, but in *Leucomyia* there are occasionally one or two small bristles in addition to the usual two strong ones, and there are constantly two small bristles besides the usual two strong ones in *Sarcophaga*. Thus the number of the notopleural bristles of the Sarcophagidae ranges, though within narrow limits, from the usual strong two to four, mostly in accordance with their systematic position seen from internal anatomy. This evolutional trend will be supported by the fact that some Acalyptrates such as the Drosophilids have only two notopleural bristles.

(t) Development of the hypopleural bristles

The bristles occuring on the hypopleura are termed the hypopleural bristles or simply hypopleurals. They are absent in the families Scatophagidae, Anthomyiidae (s. str.) here examined. In the Muscidae they are, as I expected, absent in *Siphona*, *Stomoxys*, *Muscina*, *Myiospila*, *Morellia*, *Orthellia*, *Pyrellia* and *Musca*, while some short hairs are present in the genera *Dasyphora* and *Graphomyia*. Similarly in the Calliphoridae the primitive groups such as *Isomyia* and *Stomorhina* have only several short bristles on their hypopleura, while the genera *Protophormia*, *Phormia*, *Chrysomya*, *Melinda*, *Triceratopyga*, *Calliphora* and *Lucilia* have a row of well developed bristles. In the Sarcophagidae there are several short hairs on the hypopleura of the genera *Metopia*, *Leucomyia* and *Blaesoxipha*, and the hypopleura of all the members of the genus *Sarcophaga* (s. lat.) here examined have a row of bristles. All the Tachinid flies here studied have a row of well developed hypopleural bristles.

On the basis of presence or absence of the hypopleural bristles, it was customary to divide the Calyptratae into two large families, Anthomyiidae, or Muscidae, and Tachinidae by older Dipterists since Osten-Sacken. According to Shannon (1924), the

presence or absence of the hypopleural bristles is mainly correlated with their larval food habits, and the groups lacking the hypopleural bristles are the most primitive. But the developmental status of the hypopleural bristles of the Calyptratae is not always clear cut among the different groups of the Calyptratae, and many intermediate conditions, as above mentioned, are frequent. These morphological evidences suggest that the hypopleuron of the ancestral calyptrate prototype must have been bare or poorly haired. From the above mentioned it is clear that the evolutionary trends of the hypopleurals are the change from a bare or weakly haired condition through a haired to a bristling with the advance of their phylogenetic position. Hence, their taxonomic values are of great importance not only on the family level but also on the genus level, or sometimes on the species level.

(u) Head widths of the adult flies

For the purpose of estimating the body size of the adult flies the head widths of the males of 83 species were, on an average, measured (Table I).

The head widths are 2.2-2.3mm in the Scatophagidae. In the Anthomyiidae they are 1.6-2.0mm in *Fannia*, 1.7mm in *Anthomyia*, 1.8mm in *Pegomyia*, 2.0mm in *Lispe*, 2.1mm in *Hydrophoria*, 2.1-2.4mm in *Ophyra*.

In the Muscidae they are 1.1mm in *Siphona*, 2.2mm in *Stomoxys* (Stomoxydinae), 1.6mm in *Pyrellia*. 1.8-3.3mm in *Musca*, 2.4mm in *Myiospila*, 2.7-3.4mm in *Muscina*, 2.8mm in *Morellia*, 2.9mm in *Orthellia*, 3.0mm in *Dasyphora*, 3.9mm in *Graphomyia*.

In the Calliphoridae they are 2.4mm in *Stomorhina*, 2.5mm in *Isomyia*, 2.2mm in *Melinda*, 3.3mm in *Triceratopyga*, 3.9-4.2mm in *Calliphora*, 2.9mm in *Hemipyrellia*, 2.4-3.6mm in *Lucilia*.

In the Sarcophagidae they are 2.5mm in *Metopia*, 2.6mm in *Leucomyia*, 2.3-2.6mm in *Blaesoxipha*, 2.0-4.3mm in *Sarcophaga* (s. lat.).

In the Tachinidae (s. lat.), they are 2.7-3.1mm in *Succingulum* and *Prosena* (Dexiidae), 3.2mm in *Ectophasia* (Phasiidae), 3,5-4.8mm in the Tachinidae (s. str.).

From the above it is noticeable that the head widths of *Scopeuma* here examined are much larger than those of most of the lower Calyptratae. But most of the Scatophagidae, especially those of the primitive of this group, according to Sack (1937), are small slender flies about 3-6mm in body length. The head width of these primitive Scatophagids, therefore, must be much smaller than those of *Scopeuma* here measured. From the above it may be said that the head widths increase in size in an ascending series, with some exceptions, from the primitive forms to the evolved, exhibiting a considerable variation of more than twice the width of the smallest.

This evolutionary trend in the Calyptratae is also backed up by evidence from the Acalyptratae, where a small or slender body is the most common condition.

Table 1. Characteristics of the adult flies of the Calyptratae

Species	Family & Subfamily (⟶Course of differentiation)	Male										
		Reproductive organs							Digestive organs			
		Accessory glands	Testes		Fat-body tissue	Ejaculatory duct			Arrangement of rectal papillae	Rectal valve index	Mid-gut	
			Shape	Colour		Torsion	E-index	Apodeme			Coiling degree	Mid-gut index
Graphomyia maculata	Muscidae Muscinae	un-developed	oval	brown	un-developed	cw	long	rod-shaped	cruciate A	39.0	3.0	2.1
Musca domestica vicina	↑	〃	〃	〃	〃	〃	〃	〃	bilateral	59.0	2.5	1.9
Musca sorbens		〃	〃	〃	〃	〃	〃	〃	〃	56.6	2.5	2.0
Musca hervei		〃	〃	〃	〃	〃	〃	〃	〃	58.0	2.5	2.4
Musca convexifrons		〃	〃	〃	〃	〃	〃	〃	〃	56.0	2.5	2.0
Pyrellia cadaverina		〃	〃	orange	〃	〃	〃	〃	cruciate A	46.6	4.0	2.1
Dasyphora cyanicolor		〃	〃	〃	〃	〃	〃	〃	〃	52.7	4.0	2.5
Orthellia caerulea		〃	〃	〃	〃	〃	〃	〃	〃	37.0	4.0	2.5
Morellia simplicissima		〃	〃	brown	〃	〃	〃	〃	〃	40.2	3.0	2.1
Myiospila meditabunda		〃	〃	〃	〃	〃	〃	〃	〃	55.0	3.0	2.3
Muscina stabulans		〃	〃	orange	〃	〃	〃	fan-shaped	〃	46.7	3.0	1.8
Muscina angustifrons		〃	〃	〃	〃	〃	〃	〃	〃	46.6	3.0	2.0
Muscina pabulorum		〃	〃	〃	〃	〃	〃	〃	〃	43.0	3.0	1.8
Stomoxys calcitrans	Stomoxydinae	〃	〃	〃	〃	〃	short	rod-shaped	〃	45.2	2.5	2.1
Siphona exigua	↑	〃	〃	brown	〃	〃	〃	〃	〃	18.3	2.5	2.0
Ophyra nigra	Anthomyiidae Phaoniinae	〃	〃	〃	〃	〃	〃	〃	〃	58.0	2.0	1.2
Ophyra leucostoma	↑	〃	〃	〃	〃	〃	〃	〃	〃	60.2	2.0	1.5
Ophyra chalcogaster		〃	〃	〃	〃	〃	〃	〃	〃	59.0	2.0	1.7
Pegomyia virginea	Anthomyiinae	〃	〃	orange	〃	〃	〃	〃	bilateral	57.7	2.5	1.9
Scopeuma stercorarium	Scatophagidae Scatophaginae	〃	oblong	〃	〃	〃	〃	〃	〃	41.2	2.0	1.2
Scopeuma mellipes	↓	〃	〃	〃	〃	〃	〃	〃	〃	44.0	2.0	1.6
Lispe orientalis	Anthomyiidae Lispinae	rod-shaped	〃	brown	〃	ccw	〃	〃	〃	98.0	2.5	1.8
Fannia scalaris	Phaoniinae	spherical	oval	orange	〃	cw	〃	un-developed	〃	59.0	1.5–2.0	1.3
Fannia sp.		〃	〃	〃	〃	〃	〃	〃	〃	60.7	1.5–2.0	1.2
Fannia canicularis	↓	〃	〃	〃	〃	〃	〃	〃	〃	60.4	1.5–2.0	1.9
Anthomyia illocata	Anthomyiinae	〃	〃	〃	〃	〃	〃	rod-shaped	〃	52.6	2.5	2.0
Hydrophoria ruralis	↓	banana-shaped	〃	〃	〃	〃	〃	〃	〃	50.3	2.5	1.9
Isomyia senomera	Calliphoridae Rhiniinae	ellipsoidal	〃	〃	developed	〃	〃	fan-shaped	〃	69.0	2.5	1.5
Stomorhina obsoleta	↓	banana-shaped	〃	〃	〃	〃	〃	〃	〃	67.7	2.5	1.9
Protophormia terraenovae	Chrysomyinae	〃	〃	〃	〃	〃	〃	〃	〃	62.9	2.5	1.6
Phormia regina		〃	〃	〃	〃	〃	〃	〃	〃	67.0	2.5	1.6
Chrysomya megacephala		〃	〃	〃	〃	〃	〃	〃	〃	65.0	4.0	2.4
Chrysomya pinguis	↓	〃	〃	〃	〃	〃	〃	〃	〃	70.7	4.0	2.3
Melinda pusilla	Calliphorinae	〃	〃	〃	〃	〃	〃	small-fan-shaped	〃	79.0	1.5	1.0
Triceratopyga calliphoroides		〃	〃	〃	〃	〃	〃	fan-shaped	〃	85.8	3.5	2.4
Calliphora lata		〃	〃	〃	〃	〃	〃	〃	〃	83.7	3.5	2.7
Calliphora grahami		〃	〃	〃	〃	〃	〃	〃	〃	87.7	3.5	2.0
Hemipyrellia liguriens		〃	〃	〃	〃	〃	〃	〃	〃	90.5	3.5	2.5
Lucilia bufonivora		〃	〃	〃	〃	〃	〃	〃	〃	—	—	—
Lucilia cuprina		〃	〃	〃	〃	〃	〃	〃	〃	92.0	2.5	1.9
Lucilia sericata		〃	〃	〃	〃	〃	〃	〃	〃	90.0	4.0	2.8
Lucilia illustris		〃	〃	〃	〃	〃	〃	〃	〃	86.3	4.0	2.8
Lucilia caesar		〃	〃	〃	〃	〃	〃	〃	〃	90.6	4.0	3.1
Lucilia ampullacea		〃	〃	〃	〃	〃	〃	〃	〃	93.0	4.0	2.8
Lucilia porphyrina		〃	〃	〃	〃	〃	〃	〃	〃	94.3	4.0	2.6
Lucilia papuensis	↓	〃	〃	〃	〃	〃	〃	〃	〃	87.0	4.0	2.6
Metopia leucocephala	Sarcophagidae Metopiinae	〃	oblong	brown		〃	〃	〃	〃	58.0	2.0	1.2
Leucomyia cinerea	Agriinae	coiled	〃	orange	〃	〃	〃	small-fan-shaped	〃	61.8	2.5	1.8
Blaesoxipha laticornis	Sarcophaginae	〃	〃	〃	〃	〃	〃	fan-shaped	〃	56.7	1.0	0.9
Blaesoxipha japonensis		〃	〃	〃	〃	〃	〃	〃	〃	55.0	1.0–1.5	1.2
Sarcophaga melanura		〃	〃	〃	〃	〃	〃	〃	〃	58.4	2.5	1.3
Sarcophaga sp.		〃	〃	〃	〃	〃	〃	〃	〃	56.4	2.5	1.3
Sarcophaga ugamskii		〃	〃	〃	〃	〃	〃	〃	〃	59.6	2.0	1.5

Internal characters										External characters					
						Female									
Malpighian tubules						Reproductive organs									
Arrangement		Colour		Anterior tubules		Spermathecae		Accessory glands	Utero-vaginal tube	Arista	Fourth longitudinal vein	Squamal index	Notopleural bristles	Hypopleural bristles	Head width
Anterior tubules	Posterior tubules	Anterior tubules	Posterior tubules	M-index	Fusing degree	Number	Arrangement								
fused	3	fuscous	fuscous	2.7	7.0	3	1:2	banana-shaped	simple	plumose	gently curved	2.0	2	short hairs	3.9
M-shaped	1	yellow	yellow	2.0	11.2	3	1:2	clavate	〃	〃	sharply curved	1.8	2	bare	2.4
〃	1	〃	〃	2.3	8.5	3	1:2	〃	〃	〃	〃	1.8	2	〃	1.8
〃	1	〃	〃	3.1	13.8	3	1:2	〃	〃	〃	〃	1.8	2	〃	2.6
〃	1	〃	〃	3.0	7.0	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.3
〃	2	〃	〃	2.8	6.8	3	1:2	〃	〃	〃	gently curved	2.0	2	〃	1.6
〃	2	〃	〃	3.0	5.2	3	1:2	〃	〃	〃	〃	2.0	2	short hairs	3.0
〃	2	〃	〃	3.5	6.9	3	1:2	〃	〃	〃	〃	2.0	2	bare	2.9
〃	1–2	〃	〃	3.0	10.2	3	1:2	〃	〃	〃	〃	2.0	2	〃	2.8
〃	1	〃	〃	1.8	5.4	—	—	—	—	〃	bowed	1.2	2	〃	2.4
〃	1–2	〃	〃	2.5	16.7	3	1:2	clavate	simple	〃	〃	1.2	2	〃	3.0
〃	1–2	〃	〃	2.8	15.9	3	1:2	〃	〃	〃	〃	1.2	2	〃	2.7
〃	1–2	〃	〃	3.9	12.2	—	—	—	—	〃	〃	1.2	2	〃	3.4
〃	3	〃	〃	2.0	11.1	2	0:2	clavate	simple	semi-plumose	〃	1.5	2	〃	2.2
〃	1	〃	〃	2.1	11.3	2	0:2	〃	〃	〃	〃	1.2	2	〃	1.1
〃	3	〃	〃	1.5	4.7	—	—	—	—	bare	straight	0.8	2	〃	2.3
〃	3	〃	〃	1.5	5.3	3	1:2	clavate	simple	〃	〃	0.8	2	〃	2.4
〃	3	〃	〃	1.4	5.9	3	1:2	〃	〃	〃	〃	0.8	2	〃	2.1
〃	2	〃	〃	1.6	4.3	—	—	—	—	short plumose	〃	0.8	2	〃	1.8
〃	1–2	〃	〃	1.5	3.2	3	1:2	oval	simple	bare	〃	0.2	2	〃	2.2
〃	2	〃	〃	1.6	3.6	3	1:2	〃	〃	〃	〃	0.2	2	〃	2.3
〃	1	〃	〃	2.4	4.8	3	1:2	〃	〃	short plumose	〃	1.5	2	〃	2.0
〃	1	white	〃	1.5	4.1	3	1:2	banana-shaped	〃	bare	〃	0.9	2	〃	1.9
〃	1	〃	〃	1.7	3.9	—	—	—	—	〃	〃	0.9	2	〃	1.6
〃	1	〃	〃	1.5	4.4	2	0:2	banana-shaped	simple	〃	〃	0.9	2	〃	2.0
〃	2	yellow	〃	1.7	5.6	3	1:2	〃	〃	short plumose	〃	0.8	2	〃	1.7
〃	2	〃	〃	1.8	6.0	—	—	—	—	plumose	〃	0.8	2	〃	2.1
〃	3	〃	〃	1.6	5.8	3	1:2	banana-shaped	simple	〃	gently curved	1.2	2	small bristles	2.5
〃	3	〃	〃	2.4	5.5	3	1:2	〃	〃	short plumose	〃	1.2	2	〃	2.4
〃	3	〃	〃	2.5	7.7	3	1:2	clavate	〃	plumose	sharply curved	1.2	2	well-developed	3.3
〃	3	〃	〃	2.6	8.5	3	1:2	〃	〃	〃	〃	1.2	2	〃	3.2
〃	3	〃	〃	3.2	9.8	3	1:2	〃	〃	〃	〃	1.5	2	〃	4.5
〃	3	〃	〃	3.4	8.5	3	1:2	〃	〃	〃	〃	1.5	2	〃	4.5
〃	1	〃	〃	1.0	7.7	—	—	—	—	〃	〃	1.5	2	〃	2.2
〃	3	〃	〃	3.1	8.3	3	1:2	clavate	simple	〃	〃	1.5	2	〃	3.3
〃	3	〃	〃	3.0	7.1	3	1:2	〃	〃	〃	〃	1.5	2	〃	4.2
〃	3	〃	〃	3.0	9.3	3	1:2	〃	〃	〃	〃	1.5	2	〃	3.9
〃	1	〃	〃	3.0	8.1	3	1:2	〃	〃	〃	〃	1.5	2	〃	2.9
—	—	—	—	—	—	—	—	—	—	〃	〃	1.8	2	〃	2.4
M-shaped	3	yellow	yellow	2.2	6.9	3	1:2	clavate	simple	〃	〃	1.8	2	〃	2.6
〃	3	〃	〃	2.8	6.8	3	1:2	〃	〃	〃	〃	1.8	2	〃	2.9
〃	3	〃	〃	2.8	9.6	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.2
〃	3	〃	〃	3.2	10.1	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.6
〃	3	〃	〃	3.6	9.0	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.3
〃	3	〃	〃	2.8	8.0	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.3
〃	3	〃	〃	3.5	9.1	3	1:2	〃	〃	〃	〃	1.8	2	〃	3.4
〃	1	〃	〃	1.0	6.5	—	—	—	—	bare	〃	2.0	2–4	small bristles	2.5
〃	3	〃	〃	1.8	7.9	3	1:1:1	oval	incubatory pouch	pubescent	〃	2.0	4	〃	2.6
〃	1	〃	〃	0.9	7.6	3	1:1:1	〃	〃	plumose	〃	2.0	4	〃	2.6
〃	1	〃	〃	0.9	10.4	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	2.3
〃	3	〃	〃	1.5	5.3	3	1:1:1	〃	〃	〃	〃	2.0	4	well-developed	3.4
〃	3	〃	〃	2.0	6.6	—	—	—	—	〃	〃	2.0	4	〃	2.3
〃	3	〃	〃	1.2	8.6	—	—	—	—	〃	〃	2.0	4	〃	2.5

Table 1 (Continued)

Species	Family & Subfamily (⟶Course of differentiation)	Male										
		Reproductive organs							Digestive organs			
		Accessory glands	Testes		Fat-body tissue	Ejaculatory duct			Arrangement of rectal papillae	Rectal valve index	Mid-gut	
			Shape	Colour		Torsion	E-index	Apodeme			Coiling degree	Mid-gut index
Sarcophaga caudagalli		〃	〃	〃	〃	〃	〃	〃	〃	55.2	2.0–2.5	1.2
Sarcophaga erecta		〃	〃	〃	〃	〃	〃	〃	〃	60.0	2.0	1.1
Sarcophaga josephi		〃	〃	〃	〃	〃	〃	〃	〃	53.2	2.5	1.4
Sarcophaga kagaensis		〃	〃	〃	〃	〃	〃	〃	〃	55.0	2.5	1.1
Sarcophaga jezensis		〃	〃	〃	〃	〃	〃	〃	〃	54.7	2.5	1.2
Sarcophaga basalis		〃	〃	〃	〃	〃	long	〃	〃	50.0	2.0	1.4
Sarcophaga peregrina		〃	〃	〃	〃	〃	short	〃	〃	55.3	2.0–2.5	1.6
Sarcophaga septentrionalis		〃	〃	〃	〃	〃	〃	〃	〃	52.0	2.5	1.5
Sarcophaga similis		〃	〃	〃	〃	〃	long	〃	〃	51.0	2.5	1.5
Sarcophaga kawayuensis		〃	〃	〃	〃	〃	short	〃	〃	62.0	2.0	1.2
Sarcophaga antilope		〃	〃	〃	〃	〃	〃	〃	〃	52.0	2.5	1.1
Sarcophaga albiceps		〃	〃	〃	〃	〃	long	〃	〃	56.3	2.5	1.3
Sarcophaga tsushimae		〃	〃	〃	〃	〃	〃	〃	〃	55.2	2.5	1.2
Sarcophaga brevicornis		〃	〃	〃	〃	〃	〃	〃	〃	60.6	2.5	1.5
Sarcophaga misera		〃	〃	〃	〃	〃	〃	〃	〃	55.3	2.5	1.4
Sarcophaga harpax		〃	〃	〃	〃	〃	〃	〃	〃	57.5	2.5	1.8
Sarcophaga kobayashii		〃	〃	〃	〃	〃	〃	〃	〃	53.6	2.5	1.3
Sarcophaga hokurikuensis		〃	〃	〃	〃	〃	〃	〃	〃	55.7	2.5	1.3
Sarcophaga crassipalpis		〃	〃	〃	〃	〃	〃	〃	〃	52.2	2.5	1.4
Sarcophaga schützei		〃	〃	〃	〃	〃	〃	〃	〃	52.0	2.5	1.3
Sarcophaga hozawai		〃	〃	〃	〃	〃	〃	〃	〃	51.0	2.5	1.5
Sarcophaga gravelyi		〃	〃	〃	〃	〃	〃	〃	〃	52.0	2.5	1.5
Sarcophaga hakusana		〃	〃	〃	〃	〃	〃	〃	〃	50.0	2.5	1.5
Ectophasia sinensis	Phasiidae	banana-shaped	〃	〃	〃	〃	short	rod-shaped	cruciate B	97.0	1.0–1.5	1.7
Succingulum transvittatum	Dexiidae	spherical	lamp-shaped	〃	〃	〃	〃	small fan-shaped	bilateral	96.0	1.0	1.2
Prosena siberita		banana-shaped	〃	yellow	developed	〃	〃	rod-shaped	〃	96.0	1.0	1.1
Servillia jakovlewii	Tachinidae	〃	〃	〃	un-developed	〃	〃	〃	〃	83.0	2.0	1.0
Echinomya micado		〃	〃	〃	〃	〃	〃	〃	〃	83.0	1.5–2.0	1.0
Chrysosoma aurata		〃	〃	〃	developed	〃	〃	〃	〃	77.0	2.0	1.7
Sturmia sericariae		papillary	〃	〃	un-developed	〃	〃	〃	〃	96.0	2.0	0.7

Synthetic Consideration of the Phylogeny of the Calyptratae

Some internal and external characters of the Calyptratae examined are arranged in descending or ascending successive orders of their morphological resemblance on the basis of the fact that the degree of morphological resemblance in the true sense which exists between different organisms indicates usually the closeness of their phylogenetic relation (Table I).

As it is clear from this Table, the Japanese Calyptrate Diptera here treated were, by the presence or absence of the accessory glands of the male reproductive system, divided into two groups; (a) that which has the organs, and (b) that which lacks them. The Scatophagidae and Muscidae are included in the group (a), and the Calliphoridae, Sarcophagidae and Tachinidae are all included in the group(b). The Anthomyiidae here studied are divided into two groups: (1) to which genera *Fannia*,

Internal characters										External characters					
						Female									
Malpighian tubules						Reproductive organs									
Arrangement		Colour		Anterior tubules		Spermathecae		Accessory glands	Utero-vaginal tube	Arista	Fourth longitudinal vein	Squamal index	Notopleural bristles	Hypopleural bristles	Head width
Anterior tubules	Posterior tubules	Anterior tubules	Posterior tubules	M-index	Fusing degree	Number	Arrangement								
〃	3	〃	〃	1.7	7.0	—	—	—	—	〃	〃	2.0	4	〃	2.0
〃	3	〃	〃	1.5	8.3	—	—	—	—	〃	〃	2.0	4	〃	2.1
〃	3	〃	〃	2.2	10.0	3	1:1:1	oval	incubatory pouch	〃	〃	2.0	4	〃	3.3
〃	3	〃	〃	2.1	7.0	—	—	—	—	〃	〃	2.0	4	〃	2.8
〃	3	〃	〃	1.3	5.6	3	1:1:1	oval	incubatory pouch	〃	〃	2.0	4	〃	2.3
〃	3	〃	〃	2.7	7.1	—	—	—	—	〃	〃	2.0	4	〃	3.2
〃	3	〃	〃	2.3	7.3	3	1:1:1	oval	incubatory pouch	〃	〃	2.0	4	〃	3.3
〃	3	〃	〃	2.8	10.4	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.5
〃	3	〃	〃	2.8	6.1	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.0
〃	3	〃	〃	2.0	7.3	—	—	—	—	〃	〃	2.0	4	〃	2.5
〃	3	〃	〃	2.0	5.5	3	1:1:1	oval	incubatory pouch	〃	〃	2.0	4	〃	2.8
〃	3	〃	〃	2.2	5.6	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.5
〃	3	〃	〃	2.1	9.8	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	2.9
〃	3	〃	〃	1.9	9.7	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.1
〃	3	〃	〃	2.2	6.5	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.1
〃	3	〃	〃	2.3	11.7	—	—	—	—	〃	〃	2.0	4	〃	3.1
〃	3	〃	〃	2.0	6.7	—	—	—	—	〃	〃	2.0	4	〃	4.3
〃	3	〃	〃	2.3	6.6	—	—	—	—	〃	〃	2.0	4	〃	2.7
〃	3	〃	〃	2.1	7.2	3	1:1:1	oval	incubatory pocuh	〃	〃	2.0	4	〃	4.2
〃	3	〃	〃	1.6	7.7	3	1:1:1	〃	〃	〃	〃	2.0	4	〃	3.1
〃	3	〃	〃	1.9	10.8	—	—	—	—	〃	〃	2.0	4	〃	3.0
〃	3	〃	〃	1.9	8.0	3	1:1:1	oval	incubatory pouch	〃	〃	2.0	4	〃	3.2
〃	3	〃	〃	2.4	9.0	—	—	—	—	〃	〃	2.0	4	〃	4.1
Inter-mediate	1	〃	〃	1.3	9.0	3	1:1:1	clavate	simple	bare	〃	2.0	2	〃	3.2
〃	1–2	〃	〃	0.8	13.3	—	—	—	—	plumose	〃	2.2	2	〃	2.7
〃	2	〃	〃	0.8	6.2	3	1:1:1	banana-shaped	coiled	pubescent	〃	2.0	2	〃	3.1
Y-shaped	2	〃	〃	1.3	8.0	3	1:1:1	〃	〃	bare	〃	2.0	2	〃	4.5
〃	2	〃	〃	1.0	11.5	3	1:1:1	〃	〃	〃	〃	2.0	2	〃	3.6
〃	1–2	〃	〃	1.3	11.1	—	—	—	—	〃	〃	2.0	2	〃	3.5
〃	1–2	〃	〃	0.5	8.1	3	1:1:1	banana-shaped	coiled	〃	〃	2.2	2	〃	4.8

Anthomyia and *Hydrophoria* belong, and (2) to which genera *Ophyra* and *Pegomyia* belong. Thus the lack of the male accessory glands is in the Calyptratae of great taxonomic value since it indicates that the Scatophagidae and Muscidae should be considered the more primitive of the Calyptratae. The Scatophagidae, or Cordyluridae, on the basis of their retention of so many of the features of the archetype, e.g. the well separated eyes in both sexes, the weak thoracic squamae, the retention of five, sometimes six evident abdominal segments, one sternopleural bristle, etc., are usually considered the most primitive of the Calyptratae, and in the past, therefore, they were sometimes included in the Acalyptratae as a distinct family or a subfamily rank by some older workers such as Schiner (1862-4), Coquillett (1901), Williston (1908), Comstock (1924), Imms (1925), etc. Enderlein (1936) raised the Scatophagidae, including the Cordylurids, to a new series Protomuscaria as a distinct rank co-ordinate with the Acalyptratae or the Calyptratae in the Schizophora of

Diptera. Essig (1947), Shiraki (1954), etc., adopted this system of Enderlein's.

On the other hand, it is a known fact that the Scatophagidae have Anthomyiid-like male genitalia together with some other primitive characters peculiar to the Calyptratae (Crampton, 1944). Therefore, recent specialists such as Hendel (1928), Crampton (1942, 1944), Hennig (1941), Colyer and Hammond (1951), Roback (1951), Oldroid (1954), van Emden (1954), Ringdahl (1954), Vockeroth (1965), etc., regarded the Scatophagidae as belonging to the Calyptratae and forming a link between the lower and higher Schizophora. Recently Roback (1951) takes the position that the Scopeumatinae and the Anthomyiinae have almost without change the generalized pattern of the ancestral Calyptrate muscoid postulated by himself. Van Emden (1941) thought the Scatophagidae, or Cordyluridae, should be regarded as a mere subfamily of the Muscidae. Judging only from the absence of the male accessory glands the Scatophagidae (s. str.) here examined are internally similar to the typical Muscidae, but the shape of the testes of this Scatophagid *Scopeuma* here examined do resemble not those of the Muscidae, but those of the Sarcophagidae (Hori, 1960). As many of the Scatophagids, especially primitive smaller ones are not internally examined, their affinities and systematic position can but be, at present, provisional.

It is a well known fact that the Anthomyiidae have been considered by many Dipterists to be the most primitive of the Calyptratae, and also to be closely related to the Scatophagidae on one hand, and to the Muscidae on the other hand. Coquillett (1901), Williston (1908), Comstock (1924), Enderlein (1936), Crampton (1942, 1944), Tokunaga (1943), Essig (1947), Zimin (1951), Roback (1951), Shiraki (1954), Fan (1965), Huckett (1965), etc., all regarded the Anthomyiids as a distinct family separable from the Muscidae. Some authors including Girschner (1893), Stein (1918), Séguy (1923), Imms (1925), Hennig (1941), etc., included the Muscids in their family Anthomyiidae. Senior-White (1924), Karl (1928), Hendel (1928), Malloch (1934), Curran (1934), Colyer and Hammond (1951), Herting (1957), etc., on the contrary, amalgamated the Anthomyiids into their family Muscidae. Roback (1951) believes that the Anthomyiidae have diverged very little from the generalized adult and larval patterns of the prototype of the Calyptrate Muscoids.

The genus *Fannia* and its allies were previously placed in the Anthomyiidae by many older Dipterists. Schnabl and Dziedzicki (1911) erected the "Formenreihe Muscinae fanniaeformes vel Homalomyidae", and placed under this taxon the Fanniinae, including five genera together with the Azelinae. Some Dipterists such as Malloch (1934), van Emden (1941, 1951), Ringdahl (1954), Hennig (1941, 1955), Herting (1957), Chillcott (1960), Huckett (1965), Fan (1965), etc., treated them as a subfamily or tribal rank in the family Muscidae. Crampton (1944) also noticed that the *Fannia* is closely related to both the Anthomyiids and the Muscids, and seems to be more in favour of regarding it as a true Anthomyiid than as a Muscid. Roback (1951), on the basis of the larval characters and the male genitalia, raised the

fannines to family rank and placed them between the Anthomyiidae and Muscidae. On the basis of their peculiar aedeagi which have no close resemblance to the other Muscoid flies, Chillcott (1960) suggests that the fanniines had a separate evolution instead of having any relationship with the rest. Hennig (1965) followed suit and treated them as a subfamily of the Muscidae and thought that the Fanniinae are monophyletic and have doubtlessly a sister-group relation to the Muscidae (s. lat.). It may be remarked here that the male internal sexual organs of two species of the *Fannia* here examined were distinctly Anthomyoid in their characteristics (Hori, 1960). If the evidence of the internal organs is reliable, the fannines bear close relationship to *Anthomyia illocata* which is considered the typical Anthomyiid, not to the Muscidae. The shape of the male accessory glands, the lack of the sperm pump sclerite, etc., are also characteristic to this genus *Fannia*. Another point of interest is that the larvae of the fanniines show much more clear cut differences from those of the typical Muscids, and may possibly be taken to indicate some resemblance to those of the Phoridae.

To clear the systematic status of the Anthomyiidae (s. str.,), including the fanniines, more accurate comparative studies on both the external and internal morphologies of many more materials are to be waited. Crampton (1944) considers the Anthomyiidae (s. str.) are the key group to solve the relationship among the different groups of the Calyptratae upon which many Calyptrate families converge. The present author too believes that this view of Crampton's is very reasonable.

The genus *Ophyra* together with *Pegomyia* is classed in the Anthomyiidae by many older workers. Karl (1928), Ringdahl (1954), Hennig (1941, 1962), Fan (1965), Huckett (1965), etc., placed the genus *Ophyra* in the subfamily Phaoniinae of the Muscidae. Herting (1957) placed the genus *Ophyra* in the Muscinae by its *Hydrotaea*-type of ovipositor. Van Emden (1943) thought that the genus *Ophyra* together with the genus *Hydrotaea* is closely related to his *Limnophora*-group of the subfamily Phaoniinae and these two genera seem to connect the latter group with the Fanniinae. But their female reproductive organs such as accessory glands and rectal papillae as well as the male reproductive organs, especially the absence of male accessory glands are remarkably similar to those of the Muscids rather than to the Anthomyiids (Hori, 1960, 1961, 1962a).

The genus *Lispe* was placed in the Anthomyiidae by some older Dipterists including Séguy (1923), Karl (1928), etc. However, some recent Dipterists such as Malloch (1934), Enderlein (1936), Roback (1951), Colyer and Hammond (1951), Ringdahl (1956), Fan (1965), etc., treated it as a separate subfamily Lispinae in the Muscidae. Herting (1957) thought the female ovipositor of this genus belongs to the *Limnophora*-type in the Muscinae. The shape of the testis of *Lispe*, however, is banana-shaped in contrast to the oval ones of the other Anthomyiids or Muscids, and the torsion of the ejaculatory duct is characteristic in being counterclockwise (Hori,

1960). The other internal morphology of *Lispe* such as the rectal valve also is anomalous and clearly too different from the typical Muscids to warrant it in the Muscidae, and the shape of proboscis, predatory habit, etc., are more suggestive of those of the Scatophagidae. The author believes that the differences, mainly with respect to the male internal sexual organs and the external characters are systematically so important that the genus *Lispe* should be excluded from the typical Anthomyiidae or the Muscidae (s. str.). The internal organs of *Lispe* and its relatives are, at present, poorly known and it is believed that more evidences in them would do much to clear their relationship among the Calyptratae. Thus, the systematic position of *Lispe* shown in the Fig. I can be at present only tentative.

From the above it is clear that most, if not all, Anthomyiids (s. lat.) examined here, even if they were so limited in number, show many morphological divergences in their internal organs. This fact suggests that the Anthomyiidae as we define them in this paper contain some heterogenous or distantly related groups.

Many Dipterists such as Senior-White (1924), Malloch (1934), van Emden (1939), Hennig (1941, 1965), Tokunaga (1943), Roback (1951), Ringdahl (1954), Fan (1965), Huckett (1965), etc., all recognized the Stomoxyids as a subfamily in the Muscidae. Some authors including Karl (1928), Townsend (1935), Zimin (1951), Hennig (1964), etc., retained them as a tribe in the family Muscidae. Enderlein (1936) raised the Stomoxyids to a separate family Stomoxidae. Shiraki (1954) followed this Enderlein's system and adopted his family name Stomoxidae. Essig (1947) named this family Stomoxyidae, while recently Drensky (1957)* adopted the family name Stomoxydidae. The only one but decisive diagnostic character of Stomoxyids adopted by these workers is the piercing mouth-parts. These piercing mouth-parts, however, are also more or less developed even in the different families, e.g. *Scatophaga* (Scatophagidae), *Lispe* and *Lispocephala* (Muscidae). It is clear, therefore, that these mouth-parts are undoubtedly adaptive and this alone does not allways constitute a great distinction on the family or subfamily level. The genera *Graphomyia*, *Musca*, *Pyrellia*, *Dasyphora*, *Orthellia*, *Morellia*, *Myiospila*, *Muscina*, *Stomoxys* and *Siphona* of the Muscidae are all distinct in lacking the male accessory glands (Hori, 1960). But on the basis of the arrangement of the rectal papillae, the number and arrangement of the spermathecae, the length of the ejaculatory duct, the Muscidae are divided into two groups, (a) the Muscinae in which *Musca*, *Orthellia*, *Muscina*, etc., are included, and (b) the Stomoxydinae in which *Stomoxys* and *Siphona* are included (Hori, 1960, 1961, 1962a). The length of the ejaculatory duct, the position of the rectal valve, the number of the spermathecae, the coiling degree of the proximal intestine, the hairiness of the arista, the distal bend of the fourth vein, the head width, etc., all indicate that the Stomoxyids are more primitive than the typical Muscids. These primitive characters of the internal morphology together with the piercing mouth-parts offer a

* Hennig (1964), p. 1033.

very valuable basis for separating the Stomoxyids from the typical Muscidae.

Many Dipterists including Séguy (1923), Karl (1928), Hennig (1941) Colyer and Hammond (1951), Ringdahl (1954), etc., placed *Graphomyia* in the Muscinae on the basis of the sharp distal bend of the fourth vein, plumose arista, holoptic eyes of males, etc. Enderlein (1936) shifted the genus *Graphomyia* to the Morellinae on the basis of the bend of the fourth vein, the absence of the posterior bristle on second tibia. Zimin (1951) transferred the *Graphomyia* from the Muscini to the Stomoxydini by the presence of the concaved posterior margin of the compound eyes, slender proboscis, a small labellum, narrow thoracic squamae, the absence of a posterior bristle of third tibia, etc. But this Zimin's transfer is not generally favoured yet. Van Emden (1956) believes that the Muscinae were formerly separated from the rest of the Muscidae by the bend in the vein *m*, and thus *Graphomyia* was included in this subfamily. This bend, according to him, was now known in so many unrelated forms that its use as a subfamily character had to be abandoned. The external pattern, head shape, the dense pollinosity of the adult and aquatic larval type, etc., of *Graphomyia*, according to van Emden (1956), are suggestive of those of the *Limnophora*-group. Hennig (1958) placed *Graphomyia* in the Mydaeinae on the basis of the absence of the postero-dorsal bristle on third tibia. So far as the evidences of these foregoing works are concerned, it is clear that the genus *Graphomyia* has some affinity to the *Limnophora* and also to the *Stomoxys* and its allies, and may be originated from the common ancestor of these flies. We can, on the basis of the above evidences and those of internal morphology, say that the *Graphomyia* has no such close kinship to the typical Muscinae as many older Dipterists claimed. The exact placement of the genus *Graphomyia*, however, may be a difficult problem.

Séguy (1923), Karl (1928), Colyer and Hammond (1951), Ringdahl (1954) and many other older authors placed the *Muscina* in the subfamily Muscinae. Enderlein (1936) transferred the genus *Muscina* to his subfamily Morellinae together with the genera *Graphomyia*, *Myiospila*, *Mesembrina*, *Morellia*, where the second tibia is without a poterior bristle. Recently Hennig (1962) included, because of the lack of proclinate orbitals, the genus *Muscina* in the tribe Phaoniini of the Muscidae. But three years after this he thought over again and decided that this character is only the result of convergence. He transferred it again to the tribe Hydrotaeini of the Muscinae. Fan (1965) and Zumpt (1966) placed the genus *Muscina* in the Phaoniinae.

The genus *Muscina* has primitive features such as the slightly curved fourth vein on one hand and the advanced characters such as the comparatively larger size of body, the well developed, fan-shaped sperm pump sclerite, etc., on the other. All these indicate that the genus *Muscina* seems to have no close kinship to the typical Muscinae. Neither do its lateral sacs in the uterovaginal tube show any clear relation to any other typical Muscinae. The posterior spiracular slits of the genus *Muscina* are also more suggestive of those of the genera *Myiospila*, *Mydaea*, etc., than they

are of the typical Muscids such as the genera *Mesembrina*, *Dasyphora*, *Morellia*, etc. (see Roback's plate IV).

Girschner (1893) recognized the Calliphorids as a subfamily rank, or a subfamily group, in the family Tachinidae, and included the genera *Pollenia*, *Onesia*, *Cynomyia*, *Acrophaga*, *Rhyncomyia*, *Calliphora* and *Lucilia* in this subfamily. Some older Dipterists, e.g. Williston considered that the Calliphorids are closely related to the Muscids and included most of the typical Calliphorid genera such as *Calliphora*, *Lucilia*, *Phormia*, *Mesembrina*, etc., in his Muscidae. Crampton (1942) considers that the evidences of the male terminalia indicate that the Calliphorids appear to be somewhat closer to the Anthomyiidae than they are to the Muscidae. This view of Crampton's may also be supported by the male internal sexual organs secured by the present writer (1960).

Senior-White (1924), Imms (1925), Lundbeck (1927), Hendel (1928), Wainwright (1928), etc., all recognized the Calliphorids as a subfamily of the Tachinidae. Shannon (1923), Comstock (1924), Enderlein (1936), Crampton (1942), Tokunaga (1943), Essig (1947), Roback (1951), Hall (1948), Fan (1965) etc., all treated the Calliphorids as a distinct family. Séguy (1928), Senior-White, Aubertin and Smart (1940), Mesnil (1944), Colyer and Hammond (1951), van Emden (1954), etc., united the Calliphorids and the Sarcophagids to form the Calliphoridae. Curran (1934) includes the Calliphorids and Sarcophagids together with some Muscids in his new family Metopiidae. It is, however, clear that the Calliphorids, on the basis of the presence of the male accessory glands, and of the fat-body envelopes of the testes, are clearly distinct, on one hand, from the Muscids and differ, on the other hand, from the Sarcophagids by the shape of the testes and male and female accessory glands, the arrangement of the spermathecae, the morphology of the utero-vaginal tube, etc. The typical genera of the Calliphoridae such as *Phormia*, *Protophormia*, *Chrysomya*, *Melinda*, *Calliphora*, *Triceratopyga* and *Lucilia* have many internal characters in common. The banana-shaped male accessory glands, oval-shaped testes, organge colour of the testes, the presence of the fat-body envelopes of the testes, the arrangement of the rectal papillae, etc., are all quite common in these genera.

The male and female accessory glands of the genera *Isomyia* and *Stomorhina* are, however, somewhat different from those of the rest of this family. On the basis of the distal bend of the fourth vein, the squamal index, poorly developed hypopleural bristles, smaller width of the head, the genera *Isomyia* and *Stomorhina* which belong to the subfamily Rhiniinae can be considered more primitive than the Chrysomyinae or Calliphorinae. The valve indices, the coiling degree of the proximal intestine, the fusing degree of the anterior Malpighian tubules, etc., also increase from the Rhininae through the Chrysomyinae to the Calliphorinae.

From the internal morphology (Hori, 1960, 162a, 1962b) it is clear that, in the Calliphorinae, the primitive characters such as the small size of the ejaculatory

apodeme, the coiling degree of the proximal intestine, the arrangement of the posterior Malpighian tubules, the index of the anterior Malpighian tubules, and the small size of the adult head, etc., were retained in the genus *Melinda*. On the other hand in the genus *Lucilia* (s. lat.) here examined, two species of the "*richardsi*-group" of Kurahashi (1967): *L. sericata* and *L. cuprina*, on the basis of the internal characters and the small size of the body, well separated dichoptic eyes in the male, are undoubtedly the most primitive of the tribe Lucilini. The differences between these primitive forms and the advanced *Lucilia* (s. lat.), however, do not seem to me so remarkable as to warrant their separation into different genera. In the Calliphoridae, of all the internal organs, the differentiation of the digestive organs and the Malpighian tubules were most noticeable (Hori, 1962a, 1962b).

Some older workers such as Senior-White (1924), Imms (1925), Lundbeck (1927), Hendel (1928), Wainwright (1928), etc., all placed the Sarcophagids together with Calliphorids in the family Tachinidae. Recently Senior-White, Aubertin and Smart (1940), Séguy (1941), Mesnil (1944), Colyer and Hammond (1951), van Emden (1954), Herting (1957), Zumpt (1960), etc., all amalgamated the Sarcophagids with the Calliphorids to form the family Calliphoridae. Curran (1934) included the Sarcophagidae together with the Calliphoridae and some others in his new family Metopiidae. Coquillett (1901), Williston (1908), Comstock (1924), Enderlein (1936), Rohdendorf (1937), Tokunaga (1943), Crampton (1942, 1944), Essig (1947), Roback (1951), Shiraki (1954), Downes (1965), etc., regarded the Sarcophagids as a distinct family rank. Crampton (1944) believes that the Sarcophagids have, on the basis of the terminalia, some, not much, affinity to the Calliphoridae on one hand, and to the Tachinidae on the other hand. But the evidences of the internal morphology such as the testes, male and female accessory glands, the arrangement of the spermathecae, the presence of the incubatory pouch, the presence of four notopleurals in the adults, etc., all indicate that the Sarcophagidae are considerably different from the Calliphoridae than the latter are from the Tachinidae. The shapes of the testes are more similar to that of the Scatophagidae than to that of the Calliphoridae.

The aedeagi of the primitive Sarcophagids such as *Camptops unicolor* are, according to Roback (1954), very close in form to those of some extant Scatophagids such as *Scopeuma stercorarium* and *Sapthiophora cincta*. This indicates that the Sarcophagidae probably arose from the ancestor of the more primitive of the Scatophagids.

In the Sarcophagidae it was noted by the author (1960) that the ejaculatory duct increases in length generally in accordance with the rise of their systematic position. Generally speaking, in the genus *Sarcophaga* (s. lat.) both the external appearance and the internal organs were seen to have remained remarkably unaltered in contrast to their male and female terminalia in which considerable variation had occured.

Of the three subfamilies of the Sarcophagidae here treated which have been

classified, on the basis of the coiling degree of the proximal intestine, the characters of the Malpighian tubules as well as the adult characters such as the bare arista, weakly developed hypopleurals, small size of adult head, etc., the subfamily Metopiinae can be considered the most primitive and the Sarcophaginae are, on the basis of the well developed male genitalia, probably the most specialized and have become the largest group in the Sarcophagidae.

Some Dipterists including Allen (1926), Roback (1954), etc., thought that the general characteristics of the Metopiinae are essentially sarcophagoid and have probably arisen from the same ancestor as the Sarcophaginae. The banana-shaped male accessory glands of *Metopia* seem, however, expressive that this is also a connectant leading to the Calliphoridae.

The genus *Leucomyia* is closely related to the Sarcophagids. The short ejaculatory duct, small ejaculatory apodeme, pubescent arista, three to five hypopleurals, etc., of *Leucomyia* are also primitive features.

In the Sarcophaginae the genus *Blaesoxipha* is, without doubt, primitive on the basis of the coiling degree of the proximal intestine, short ejaculatory duct, the arrangement of the Malpighian tubules, three to five hypopleurals, etc.

The general external morphology including chaetotaxy of the Sarcophaginae together with their internal morphology shows a few characters that are of value in determining the course of evolution of these flies, but the aedeagi with their wealth of diverse structures as noticed by many Dipterists have been found to offer valuable systematic evidences upon which relationships and phylogenetic conclusions within the Sarcophaginae can be based.

Accordingly, the sequential arrangement of each species of the *Sarcophaga*-group in Fig. I can but be, at present, quite provisional, and their definitive arrangement will have to wait for further increase in our knowledge.

In the past the close relationship between the Sarcophagidae and Calliphoridae has been overrated by some Dipterists (Curran, 1934; Senior-White et al., 1940; Séguy, 1941; Mesnil, 1944; Colyer and Hammond, 1951; van Emden, 1954; Zumpt, 1956). The evidences of the internal organs of the Sarcophagidae together with their peculiar external morphological characteristics will distinctly separate them from the Calliphoridae or Tachinidae.

Some authors such as Stein (1918), Senior-White (1924), Imms (1925), Séguy (1928), Ringdahl (1954—9), etc., adopted a classification of the Calyptratae which divided them into two families: Anthomyiidae, or Muscidae, and Tachinidae. In this Tachinidae both the Calliphorids and Sarcophagids together with typical Tachinids are included. Comstock (1924), Crampton (1942), Colyer and Hammond (1951), van Emden (1954), Oldroid (1954), etc., excluded them from the Tachinidae.

Some authors such as Hennig (1941), Crampton (1942), Essig (1947), etc., recognized the Phasiids and Dexiids as a distinct family respectively. But Crampton

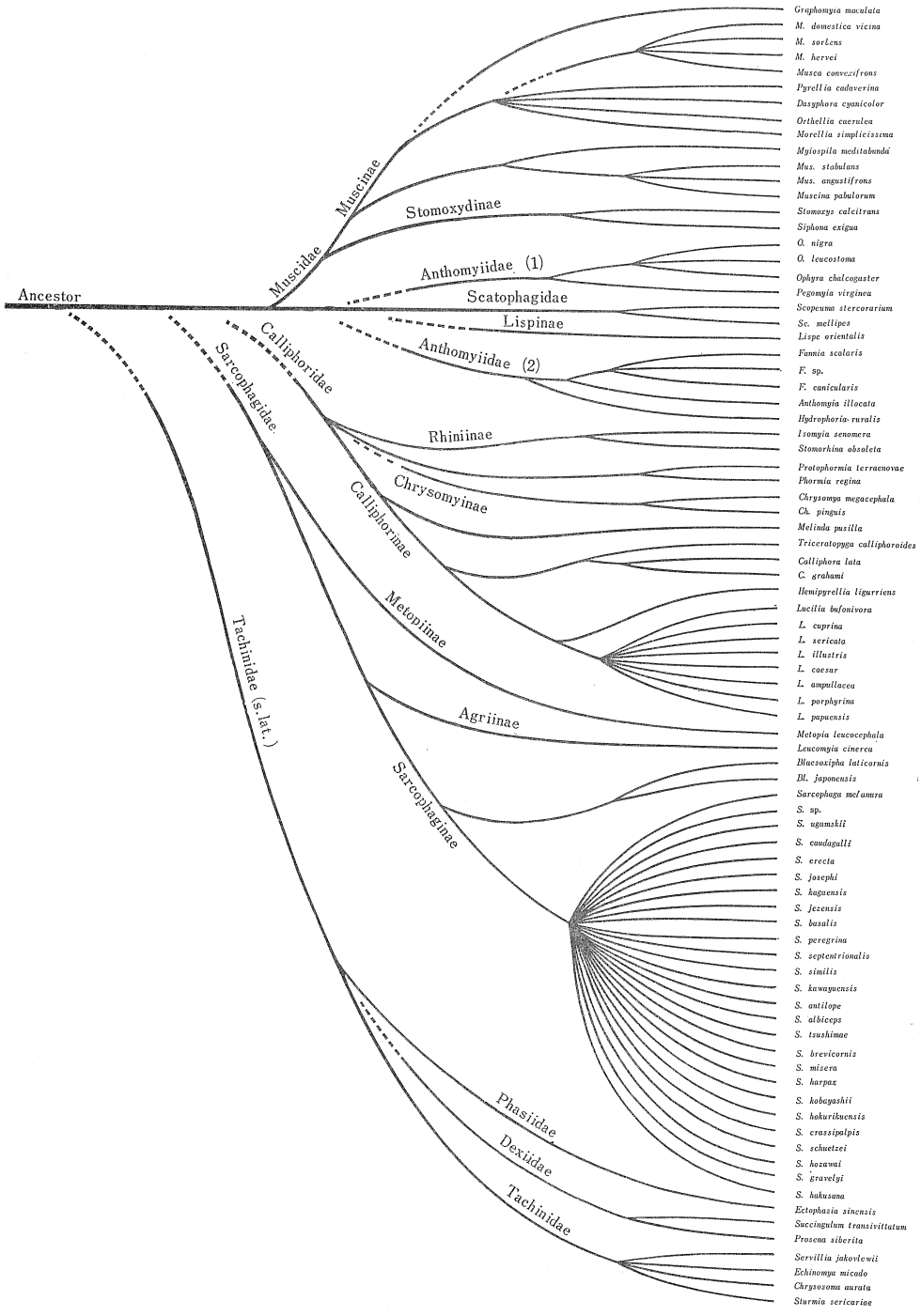

Fig. 1. A probable phylogeny of the Calyptratae.

(1944) thought that the Phasiidae, on the basis of the evidence of the male terminalia, apparently descended more or less directly from the Tachinid ancestor. The Phasiids and Dexiids are sometimes treated as subfamilies of the Tachinidae, but they are here regarded as a separate family respectively. The Phasiids are, in either case, considered to be the more primitive of the Tachinidae by many Dipterists. As a matter of fact the testes of a Phasiid *Ectophasia* are remarkably similar to those of the Sarcophagids, and their male accessory glands recall those of the Calliphorids (Hori, 1960). The lamp-shaped testes which were observed in the typical Tachinids examined seem to be a characteristic to the Tachinidae (Hori, 1960).

The number of species here treated is, however, too small to discuss the relationship of the Tachinidae in any finer details. From Table I it is seen that the internal organs of the Tachinidae such as the alimentary canal and the Malpighian tubules indicate at least their primitive or reduced condition.

Considering their morphological distinctness above mentioned together with their larval parasitism, it appears likely that the ancestral Tachinids represent a phylogenetic line which diverted early from the main stem of the Calyptratae, and the Phasiids show several features which connect them to both the Calliphoridae and Sarcophagidae.

From the foregoing discussion, it is clear that the major characters which were sufficient to regroup the families of the Calyptratae into some superfamilies were here not found, thus it may be advisable to place them in a separate family respectively. The probable phylogenetic relationships of all the forms discussed here are tentatively shown in Fig. I.

Summary

In the past various systems have been proposed for the classification of the Calyptratae mainly on the basis of the external characters of the adult flies, the male genitalia, the larval characters, etc. No two authors, however, have fully agreed on the supergeneric, generic or specific divisions to be used.

In the present account a co-ordinate consideration of both the adult internal organs and some external characters of 83 recognized species of the Calyptratae from Japan was made. The presence or absence, and the shape of the male accessory glands, the shape and colour of the testis, the length of the ejaculatory duct, the position of the rectal valve, the coiling degree of the proximal intestine, the arrangement of the Malpighian tubules, etc., as well as some external adult characters such as the hairiness of the arista, the distal bend of the fourth longitudinal vein, the size of the squamae, the hypopleural bristles, the head width, etc., have proved to be of major systematic importance in elucidating the relationship in the Calyptratae. It was made clear from the present study of these that the male accessory glands have great

taxonomic value above the generic level. Thus the Calyptratae are, on the basis of presence or absence of the male accessory glands, separable into two main groups. Several genera such as *Anthomyia, Fannia, Ophyra, Pegomyia, Lispe,* etc., which are sometimes included in the Anthomyiidae (s. lat.) by some older Dipterists, are likewise divided into two groups. This indicates that these small Anthomyiid flies are the key-group to solve the relationships among the Calyptratae as suggested by Crampton (1944). This study emphasizes also a need for examination of far more materials of this group than is now available in order to establish the relationships among the Calyptratae.

The differentiation of the internal organs has not always the same trend in the higher divisions such as the Muscidae, Calliphoridae, Sarcophagidae, etc. This could indicate that they were established very early from the common ancestor as a quite different respective systematic group. These probable relations of all the groups are tentatively figured. It is also noticeable that the differentiation of the internal organs are closely correlated to the external characters such as the body size of the adult flies.

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