I—Introduction

The Clavicornia pose some of the most difficult problems in family classification in the order Coleoptera, in particularly the characterisations and constitutions of the families Cryptophagidae and Languriidae have hitherto been very unsatisfactory and controversial. The previous tendency has been to place all the small brown and pubescent species in the Cryptophagidae. Most of the nineteenth century and later taxonomists have based their classifications on very few characters. To obtain a phylogenetic classification, as many morphological and biological characters as possible need to be studied and characters of the larvae should be accorded equal importance with those of the adults. The aims of our investigation have been first, to improve the definition of the family Languriidae, second, to review its internal hierarchy down as far as the generic level and third, to clarify the relationships of the family to other groups of Clavicornia. Our third objective seems particularly important, as Languriidae with apparent affinities to Cryptophagidae, Erotylidae, Endomychidae and perhaps Biphyllidae seem to link several major divisions of the Cucujoidae; to achieve a true understanding of the relationships of the family will be to have taken a major step towards a correct appreciation of the phylogentic history of this large and complex superfamily.

II—History of the Family Languriidae

The first established genus of the family was *Languria* Latreille (1802) including two species described under *Trogosita* by Fabricius (1798); *Languria* was more fully described by Latreille in 1807. Crotch (1873) placed this genus under Erotylidae; Lacordaire (1842) omitted the genus *Languria* from Erotylidae but Chapuis (1876), who finished the great work of Lacordaire, treated *Languria* and the related genus *Macromelea* Hope (1840) as a subfamily (tribe) Languriides of Erotylidae. Harold (1879) published a valuable work on Oriental and Australian species of Languriides; Leconte and Horn (1883) characterised the genera of North American Languriini. Lewis (1884) studied Japanese Languriides and was the first author to consider this group as an independent family. Gorham (1891) studying the Languriidae of Indo-China, and Kraatz (1899) on Languriidae of Sumatra followed Lewis.

Fowler (1908), studying the genera of the entire world, treated Languriinae as a subfamily of Erotylidae. Arrow (1925) restored the independent family Languriidae and first distinguished subfamilies Languriinae and Cladoxeninae; in 1929 he revised the African Languriidae.

Subsequently Zia (1934) studied Indo-Chinese Languriidae; Blackwelder (1945) made a checklist of Central American, South American and West Indian species ; Vaurie (1948) monographed those of North America; Villiers (1961) revised the African Languriidae, and more recently Martins (1965) has revised the Neotropical species; all these writers accepted the family as characterised by Arrow (1925).

One of us, Crowson (1955), added another two subfamilies Pharaxonothinae and Setariolinae, to it, and suggested a transference of *Loberus* Leconte and its allies from Cryptophagidae to Languriidae-Cladoxeninae. Bruce (1951) tentatively suggested in Cryptophagidae a subfamily Loberinae for such genera as *Hapalips* Reitter, *Loberus* Leconte, *Toramus* Grouvelle and *Leucohimatium* Rosenhauer; this subfamily was transferred to Languriidae by one of us, Sen Gupta (1968). An additional subfamily Toraminae has already been characterised by one of us, Sen Gupta (1967), and yet another, Cryptophilinae, is described in this work.

A REVIEW OF CLASSIFICATION OF THE FAMILY LANGURIIDAE (COLEOPTERA : CLAVICORNIA) AND THE PLACE OF LANGURIIDAE IN THE NATURAL SYSTEM OF CLAVICORNIA

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(With 14 Text-figures)

CONTENTS

III—Key to separate adults of the families Cryptophagidae, Languriidae, Erotylidae and Propalticidae

1. First ventrite markedly longer than the rest (Text-fig. 8A). Front coxal cavities always widely open behind externally; trochanters with few exceptions narrow-elongated. Elytra confusedly punctured, usually hairy, epipleura distinct only in basal half. Fronto-clypeal suture usually absent; anterior part of gular region often with a pair of longitudinal grooves (Text-fig. 8B) but never with a transverse groove. Stridulatory files on head absent (except in a few species of *Atomaria*). Tarsi often 5-5-4 in male; antennal club never with more than three joints. Aedeagus without paired median struts, not turned on one side, with or without articulated parameres. Wing often with five anal veins and never with subcubital fleck .. .. Cryptophagidae.

All ventrites more or less equal in length (Text-fig. 4B). Front coxal cavities often partially or completely closed behind externally (Text-fig. 4B); trochanters usually broadly elongated, sometimes short and broad (Text-fig. 4A), rarely narrow-elongated. Elytra usually with punctures in regular rows, often with scutellary striole, glabrous or hairy, epipleura well developed up to the apex. Fronto-clypeal suture often present (Text-fig. 1H); usually with a transverse groove (Text-fig. 7G) or cavity on anterior part of gular region, but longitudinal grooves absent. Stridulatory files on head often present. Antennal club sometimes with more than three joints. Tarsal formula 5-5-5 in both sexes. Retraced aedeagus turned on one side, with articulated parameres and long double median struts (Text-fig. 2E), except in *Propalticus*. Wing always with subcubital fleck (Text-fig. 3F), except in *Propalticus*, and never with five anal veins. 2

2. Form broad and flat; eyes on the top of the head; prothorax markedly large, with a longitudinal groove on middle line of pronotum. All the coxae widely separated; sternal fitting between the mesocoxae in straight line; front coxae strongly transverse. Wing without subcubital fleck; elytra irregularly punctured. Aedeagus without long median struts. Front tibiae with a large spur. Lacinia glabrous. .. .. Propalticidae.

Form not as above; eyes on lateral sides of the head; prothorax not as above. Coxae usually closely situated; eternal fitting between mesocoxae usually with single or double knobs; front coxae more or less rounded. Wing always with subcubital fleck; elytra usually punctured in regular rows. Aedeagus with a pair of long median struts. Front tibiae not as above. Lacinia almost always with setae. 3

3. Front coxal cavities usually open behind (Text-fig. 1G), if closed (*Xenoscelis* Wollaston, Text-fig. 2B, and Cryptophilinae, Text-fig. 3B) species narrow-elongated and sternal fitting between mesocoxae with single knob (*Xenoscelis*) or very small, with front coxal cavities internally closed behind (Cyrptophilinae, Text-fig. 7A). Sternal fitting between mesocoxae usually with single knob (Text-fig. 1B), if double (Text-fig. 6G) front coxal cavities internally closed behind (Text-fig. 7A) and wing without anal cell (Text-fig. 6A). Mesoepisternal pockets usually well developed (Text-fig. 3B). Species often with recumbent pubescence, narrower and usually more elongate, with front and middle coxae rather narrowly separated. .. .. Languriidae.

Front coxal cavities always externally closed and internally open behind. Sternal fitting between mesocoxae with two well separated knobs (Text-fig. 8F). Wing, when fully developed, with an anal cell. Mesoepisternal pockets absent. Species usually glabrous, very rarely with recumbent pubescence dorsally and of relatively broad form with front and middle coxae more widely separated .. .. Erotylidae

IV—Key to separate larvae of the families Cryptophagidae, Languriidae, Erotylidae and Propalticidae

1. Labial palpi single-jointed and spiracles bicameral or labial palpi two-jointed and spiracles annular. Mandible with two apical teeth, one of them dentate on inner margin; prostheca narrow and pointed at apex, which is often bifid, its caudal margin often serrated; mola always distinct. Maxillary mala falciform. Urogomphi often absent. Ocelli never more than four on each side of head, and upper surface of body never granulated. Metopic suture and endocarina absent. Species usually small .. .. Cryptophagidae

Labial palpi always two-jointed (Text-fig. 9C); spiracles bicameral, or if annular, species large and mandible without mola. Mandible usually with three apical teeth, inner margin rarely serrated; prostheca not as above apex never bifid or caudal margin serrated. Maxillary mala falciform or obtuse. Urogomphi always present. Ocelli often five or six on each side of head. Metopic suture or endocarina often present. 2

2. Maxillary mala falciform (Text-fig. 9C). Mandible with normal ridged mola (Text-fig. 9D); maxillary mala with an inner dorsal row of setae (Text-fig. 9C); if not larvae white and internal feeding with not more than two ocelli on each side of head. Spiracles always bicameral and ligula absent. Larvae not feeding on fruit bodies of higher fungi. 3

Maxillary mala obtuse. Mandible usually without ridged mola; maxillary mala often without dorsal row of setae. Ocelli five to six on each side of head. Spiracles sometimes annular and ligula often distinct. Larvae feeding on fruit bodies of higher fungi. .. .. Erotylidae.

3. Mandible with large membranous prostheca, tarsungulus with single seta; five ocelli on each side of head; mola with lines of asperities extending far on to ventral surface. .. .. Propalticidae

If tarsungulus with single seta, mandible without distinct prostheca; ocelli usually six or less than five ocelli on each side of head; mola with asperities not extending on to vsntral surface .. .. Languriidae

V— DEFINITION OF THE ADULT LANGURIIDAE

With general characters of Polyphaga-Cucujoidea and of Clavicornia.

Head : Usually transverse, rarely with distinct tempora; occipital region often with a pair of stridulatory files (Text-fig. 2A) or occasionally a single file in the centre (Text-fig.3E). A transverse line on vertex posterior to the eyes often present (Text-fig. 2A), sometimes hiddened under the front margin of pronotum. Fronto-clypeal suture often present mainly in Languriinae and Toraminae, if so, antennal insertions usually somewhat exposed (Text-fig. 1H.) Anterior part of gular region usually with a transverse groove (Text-fig. 7G), sometimes replaced by a large cavity. Longitudinal grooves extending backwards from articulation of maxillae as in Cryptophagidae (Text-fig. 8B) absent. Eyes usually of moderate size, hemispherical in shape, facets variable. Gular sutures well separated; tentorium more or less similar throughout the family, with a narrow corpotentorium, broad plate-like laminatentorium and short supratentorium (Text-fig. 1H). Antenna eleven jointed, scape relatively smaller than in Cucujidae or Atomariinae (Cryptophagidae), club variable, rarely two jointed (*Setariola* Jacobson).

Mouthparts : Mandible usually with two apical teeth, mola well developed (Text-fig. 5F) or poorly developed (Text-fig. 1A), sometimes a minute tubular opening present on ventral side, near the middle (*Setariola sericea* Muls. and Rey, Text-fig. 5F, and *Anadastus filifosmis* Fabr., Text-fig. 1A). Maxilla with well developed lacinia, galea and palpi. Lacinia usually with three apical spines (Text-fig. 1B), rarely with two or without spines. Galea rather narrow, elongated with few hairs at apex (Text-fig. 7B) or short, broad with densely hairy apical half (Text-fig. 1B). Palpi four-jointed apical segment never securiform, unlike Erotylidae segment 2 longer than segment 3 (Text-fig. 1B). Labium with mentum usually moderately transverse (Text-fig. 1D), rarely elongate (*Thallisella* Crotch), markedly transverse (*Xenoscelinus* Grouvelle, Text-fig. 7C). Sometimes on ventral surface of mentum with a paired (*Leucohimatium* Rosenh., Text-fig. 3D) or single (*Eicolyctus* Sahlb.) cavity, which opens ventrally or laterally. Labial palpi three jointed, apical segment largest and somewhat truncate at apex rarely narrow and rather pointed at apex; ligula either poorly developed or well developed and bilobed (Text-fig. 1D).

Prothorax : Shape variable, usually with a pair of prebasal impressions on pronotum. Front coxal cavities usually open behind externally, sometimes very narrowly so or completely closed behind (Text-figs. 2B, 7A) & internally open (Text-fig. 3A) or closed (Text-fig. 7) behind. Front coxae usually more narrowly separated than in Erotylidae.

Elytra and wing : Unlike those of Cryptophagidae the elytra usually bear regular rows of punctures ; a scutellary striole often present ; pubescence present or absent. Epipleura sharply defined to the apex. On the inner face of the elytron, just above the epipleura at posterior one-third there is always a small asperated area which probably rubs with subcubital fleck of wing (Arrow, 1925). Wing never with five anal veins, usually with four (Text-fig. 3F), sometimes less than four anal veins. When wing with four anal veins, often with an anal cell. Anal cell always absent if wing has less than four anal veins. Subcubital fleck always present but radial cell and r-m cross vein often absent in those wings which have less than four anal veins. In *Xenoscelinus* Grouvelle, the first anal vein running into the subcubital fleck (Text-fig. 6B) as in Biphyllidae, in *Loberoschema aeneum* Germain anel veins somewhat peculiar, one of the anal veins running into the subcubital fleck. A spur on r-m cross vein rarely present, e.g. in *Eicolyctus* Salhb. and *Crotchia* Fowler.

Meso and Metathorax : Unlike Erotylidae, mesocoxae only narrowly separated ; their cavities always closed outwardly by sterna (Text-fig. 1J). Mesoepisterna usually with pockets near inner angles, opening outwardly (Text-fig. 3C) ; mesosternum sometimes with a pair of such pockets, opening outwardly. In some species of *Toramus* Leconte, with three pairs of pockets on anterior margin of met sternum, opening postero-ventrally. The sternal fitting between the mesocoxae is variable, usually mesosternal process betwee the

mesocoxae receives a single knob-like projection from metasternum in its internal pocket (Text-fig. 1A). In Toraminae, metasternal process bears two distinctly separated knobs as in Erotylidae, in Cryptophilini Casey, metasternal process has two weakly separated or one bifid knob (Text-fig. 6G). Some genera, *Xenoscelinus* Grouvelle and *Pseudhenoticus* Sharp have the Cucujidae type of fitting, in a straight line (Text-fig. 5E). Metasternum except in wingless forms, well developed ; mesocoxal lines sometimes present. Metendosternite variable, usually anterior tendons moderately separated (Text-fig. 3B), never as close as in Cryptophagidae.

Legs : Usually moderately long, sometimes very long and slender. Trochanters usually broadly elongate, sometimes short and broad (Text-fig. 4J) or narrow and elongate, never heteromeroid. Tibiae often widened or truncated at apex, usually with two normal spurs. Tarsal formula always 5 : 5 : 5 in both sexes, usually pseudotetramerous (Text-fig. 1B), sometimes simple with segment 4 little shorter than segment 3 (Text-fig. 2C). Tarsal segment 1 always slightly longer than or equal to the length of segment 2 ; claws simple.

Abdomen : Completely hidden by elytra. All ventrites freely articulated, and unlike Cryptophagidae all more or less equal in length (Text-fig. 4B) ; ventrite 1 usually with a pair of femoral lines. In resting condition tergite 8 hidden under tergite 7 in both sexes ; seven pairs of abdominal spiracles, the first six on membrane outside edges of tergites. Aedeagus similar throughout the family, Cucujoid-type, with articulated parameres and long slender, thread-like double median struts, in resting condition aedeagus turned on one side (Text-fig. 2E). Ovipositor occasionally much reduced, usually more or less elongated, and often with coxites apically pointed and bearing the styli laterally (Text-fig. 1F.)

VI—Larvae of Languriidae

Not much is known about the larvae of Languriidae. No larvae are yet descsibed of Cladoxenini, Thallisellini, Toraminae and Setariolinae. Our larval characterisation of the family is based on Languriidae larvae described by Rymer Roberts (1939), and Böving & Craighead (1931), and also on larvae of *Hapalips prolixus* Sharp, *Eicolyctus brunneus* Gylenhall and two supposed Cryptophilinae larvae.

Chief larval characters

General body form usually only slightly narrowed in front and behind, urogomphi always present, usually short and upturned. Upper surface granulated, except in the specialised endophytic larvae of Languriini ; vestiture often including blunt or frayed setae.

Head usually with distinct frontal sutures of typical Cucujoid shape, sometimes with endocarina or metopic suture. Ocelli typically five to six, sometimes reduced to 0-2. Antenna rather short with segment 2 longest (except in Cryptophilini), sometimes apical segment markedly shorter than segment 2, segment 1 as long as or shorter than apical segment ; sensory appendage lying ventrally, usually minute.

Mandible with two or three teeth, inner margin rarely dentate (*Caenolanguria nilgirensis* Gorham). Mola well developed, often projecting and with transverse ridges ; rarely a fleshy lobe present at the base of mola (*Languria bicolor* Fab., *Eicolyctus brunneus* Gullen.). Prostheca never narrow and elongated as in Cryptophagidae, usually triangular, fleshy translucent and pointed at apex, absent in *Teretilanguria metallica* Gorh. and Cryptophilinae (Text-fig. 9D). Ventral crushing tubercle (Text-fig. 9D) often well developed. Maxillary mala falciform (except in *T. metallica*, where its apex is slightly obtuse) usually with three apical spines. A row of dorsal setae present on inner margin of mala, except in *T. metallica*. Groups of denticles often present dorsally on basal part of mala and palpiger ; a rounded process sometimes present on inner and/or outer margins of stipes. Cardo and maxillary articulating area well developed, the former usually indistinctly divided in middle, the latter more or less oval in shape. Labium free as far as base of mentum, palpi two

jointed. Hypopharynx usually with well developed anterior horns ; ligula not distinguishable ; super lingue usually well developed and spinous; hypopharyngeal bracon well developed.

Prothorax usually slightly longer and less transverse than meso-and metathorax, First five to six abdominal segments are as broad as metathorax, sometimes slightly shorter than latter. Urogomphi usually short, upturned and hooked (except in *Hapalips prolixus*). Pregomphal process or a pair of setiferous tubercles often present on disc of abdominal tergite 9, anterior to urogomphi. Pygopod usually projecting backwards and slightly downwards.

Spiracles bicameral, usually lying on body surface.

Legs with moderately widely separated coxae, claws simple with two tarsungular setae (except in Cryptophilinae) lying side by side.

VII—KEY TO THE SUBFAMILIES, TRIBES AND GENERA OF ADULT LANGURIIDAE

1. Front coxal cavities externally open behind, if closed (*Xenoscelis*) then internally open behind and elytra with scutellary striole. Stridulatory files on head if present usually double except in *Leucohimatium*. First anal vein of wing not running into subcubital fleck except in *Loberoschema aeneus* Germain 2

Front coxal cavities externally as well as internally closed behind (Text-fig. 7A). Elytra without scutellary striole. Stridulatory file on head if present single and median. Wing sometimes with first anal vein running into subcubital fleck (Text-fig. 6B) Cryptophilinae subfam. nov.....5

2. Trochanters narrow and markedly elongated ; sternal fitting between the mesocoxae with two distinc separate knobs. Scutellary striole on elytra, and stridulatory files on head absent. Wing with less than four anal veins, radial cell usually open and anal cell always absent. Front coxal cavities internally closed behind, metendosternite without lateral plates and anterior tendons widely separated . Toraminae Sen Gupta . 7

Trochanters not as above ; sternal fitting between the mesocoxae with single knob (Text-fig. 1J), rar y in a straight line. Scutellary striole on elytra and stridulatory files on head often present. Wing usually with four anal veins, and closed radial cell, sometimes with anal cell. Front coxal cavities internally open (Text-fig. 3A) or closed (Text-fig. 1G) behind. Metendosternite not as above except in apterous forms, *Setariola* and *Platoberus* 3

3. Antennal club two jointed ; wing with two anal veins (Text-fig. 5D); front coxal cavities internally closed behind. Trochanters short and broad ; femoral lines on first ventrite absent. Metendosternite of Toraminae-type. Species of Cisid-like appearance. subfamily Setariolinae Crowson *Setariola* Jacobson.

Antennal club with more than two joints ; wing not as above. Front coxal cavities internally open or closed behind. Trochanters short and broad or broadly elongated ; femoral lines on first ventrite present or absent. Metendosternite not as above. Species not of Cisid-like form 4

4. Ovipositor with coxites more or less pointed apically and bearing styli laterally, at some distance from apex (Text-fig. 1F). Front coxal cavities internally closed behind (Text-fig. 1G). Antennal club often more than three-jointed. Galea often short and broad (Text-fig. 1B) and mandible with poorly developed mola (Text-fig. 1A). Antennal insertions usually dorso-lateral and head with fronto-clypeal suture. Metendosternite often with broad plate-like lateral plates and anterior tendons separated by slightly more than width of basal stalk (Text-fig. 1E). Species usually larger. subfamily Languriinae 10

Ovipositor with coxites blunt apically and bearing styli at apex (Text-fig. 2D). Front coxal cavities internally open behind (Text-fig. 3A). Antennal club three-jointed. Galea narrow and elongate ; mandible with well developed projecting mola. Antennal insertions lateral ; fronto-clypeal suture on head never present (Text-fig. 2A). Metendosternite with narrow lateral plates and anterior tendons separated by slightly less than width of basal stalk (Text-fig. 3B). Species often small and Cryptophagid-like subfamily Loberinae Bruce 17

5. Tarsi lobed below with minute segment 4 ; wing with anal vein 1 not running into subcubital fleck (Text-fig. 6A). Trochanters broadly elongated. Head with single stridulatery file (Text-fig. 7G) ; sternal fitting between the mesocoxae with closely situated double knobs (Text-fig. 6G) ; metendosternite as figured (Text-fig. 6C) Cryptophilini Casey 6

Tarsi simple with segment 4 little shorter than segment 3 ; wing with anal vein 1 running into subcubital fleck (Text-fig. 6B). Trochanters broad and short. Head without stridulatory file ; sternal fitting between the mesocoxae in a straight line (Text-fig. 6D). Metendosternite not as above (Text-fig. 6D) . Xenoscelinini trib. nov. *Xenoscelinus* Grouvelle

6. Prothorax weakly transverse and slightly widened to front margin. Tarsal segments 2 and 3 strongly lobed below ; elytral punctures minute and in more or less regular rows. . *Coelocryptus* Sharp

Prothorax strongly transverse and front margin slightly narrower (Text-fig. 7A). Tarsi with only segment 3 strongly lobed below ; elytral punctures irregular and larger. *Cryptophilus* Reitte

7. Prothorax unusually large, slightly longer in middle line than width at its front angles ; apex of prosterna process emarginate in middle *Atomarops* Reitter

Prothorax not as above, more or less transverse ; prosternal process not emarginate 8

8. Prothorax slightly narrowed in front, its side margins undulate. Wing with three anal veins, antenna segments 1-6 not alternately long and short *Empocryptus* Sharp

Prothorax with side margins not as above and not narrowed in front. Wing rarely with three anal veins, antennal segments 1-6 often alternately long and short . 9

9. Prothorax not parallel sided ; tarsal segment 3 strongly lobed below and segment 1 about double the length of segment 2. Antenna often with some darker segments and head often with fronto-clypeal suture and transverse line on vertex behind the eyes . . *Toramus* Grouvelle

Prothorax parallel sided ; tarsal segment 3 rather weakly lobed below and segment 1 slightly longer than segment 2. Antennal segments unicoloured ; fronto-clypeal suture and transverse line on vertex absent *Loberoschema* Reitter

10. Antennal club usually three-jointed (except in *Thallisella*), subsymmetrical and usually not flattened ; galea elongate with few setae at apex ; mandibular mola usually well developed, except in *Crotchia* and ligula poorly developed, not or weakly lobed. Species comperatively small, not markedly linear in shape 11

Antennal club often with more than three joints, flattened and more or less asymmetrical ; galea (Text-fig. 1B) short, broad with very brushy apical part ; mandibular mola (Text-fig. 1A) poorly developed ; ligula (Text-fig. 1D) well developed and strongly lobed. Species larger, usually narrow and linear in shape . . Languriini (=Languriinae Arrow)

11. Tarsi with first three segments strongly lobed below ; lacinia with two spines at apex, galea pointed at apex ; mentum rather long ; antennal club sometimes four-jointed ; tibiae without spurs at apex. Form rather short and broad *Thallisellini* Sen Gupta 12

Only tarsal segment one strongly lobed below ; lacinia with three spines at apex, galea blunt at apex ; mentum transverse ; antennal club three-jointed ; tibiae with two spurs at apex. Form more narrow and elongate . . Cladoxenini (=Cladoxeninae Arrow) 13

12. Upper surface glabrous ; antennal club four-jointed and rather flattened. Trochanters rather broad . . *Thallisella* Crotch

Upper surface pubescent ; antennal club three-jointed, not flattened. Trochanters narrow and elongated *Platoberus* Sharp

13. Prothorax subquadrate, almost parallel sided ; antennal club rather flattened ; wing with a spur on r-m cross vein . . . . *Crotchia* Fowler

Prothorax rather elongate, not parallel sided ; antennal club not flattened ; wing without spur on r-m cross vein . . 14

14. Eyes coarsely facetted ; head without stridulatory files . . . . . *Microlanguria* Lewis

Eyes finely facetted, or wing absent or reduced, metasternum strongly transverse, and femoral lines absent on first ventrite. Head with a pair of stridulatory files . . . 15

15. Eyes coarsely facetted ; wing absent or reduced ; metasternum strongly transverse. Intercoxal process of first ventrite broad and rounded at apex. . . . . *Paracladoxena* Fowler

Eyes finely facetted ; wing well developed ; metasternum not transverse. Intercoxal process of first ventrite rather narrow and pointed 16

16. Tarsal segment 1 longer than 2 ; anterior one-third of elytra not parallel sided ; metasternum more elongate and scutellum rather large . . . *Cladoxena* Motschulsky

Tarsal segment 1 and 2 equal in length ; anterior one-third of elytra parallel sided ; metasternum less elongate and scutelum smaller . . *Penolanguria* Kolbe

17. Trochanters short and broad (Text-fig. 4J); tarsi usually not (Text-fig. 2C), rarely very slightly lobed below (*Xenoscelis*), with segment 4 little shorter than segment 3. Femoral lines on first ventrite absent (Text-fig. 4B) ; anterior part of gular region without transverse groove (Text-fig. 2A), except in *Othniocryptus*. Front coxal cavities usually narrowly open behind, rarely completely closed behind (*Xenoscelis* Text- fig. 2B) . Pharaxonothini Sen Gupta and Crowson 18

Trochanters broadly elongate ; tarsi distinctly lobed below with minute segment 4. Femoral lines on first entrite present ; anterior part of gular region with a transverse groove (cf. Text-fig. 7G). Front coxal cavities

usually widely and rarely narrowly open behind.
Loberini Sen Gupta 2

18. Front coxal cavities completely closed behind (Text-fig. 2B) *Xenoscelis* Wollaston
Front coxal cavities never completely closed behind 19

19. Elytra densely pubescent, their puncturation irregular. 20
Elytra glabrous or sparsely pubescent (except *Henoticonus*), with puncturation in regular rows 21

20. Prothorax slightly narrowed behind; tibiae widened at apex and with two distinct normal spurs. Elytral pubescence recumbent, dense and short; elytra unicolorous *Macrophagus* Motschulsky=*Haplolophus* Fabricius
Prothorax narrowed behind; tibiae narrow and not broadened at apex, apical spurs apparently absent Elytral pubescence rather sparse, longer and slightly raised. Elytra with patches of colour in characteristic pattern, as in *Othnius* *Othniocryptus* Sharp

21. Tibiae short, strongly broadened to the truncate apex, with spines on external apical angles 22
Tibiae much less broadened apically, without spines on outer apical angles. 23

22. Antenna with loosely articulated club. Prebasal impressions minute on basal margin of pronotum stridulatory files on head, and transverse line on vertex present. *Xenocryptus* Arrow
Antennal club compact and strongly flattened with large apical segment. Prebasal impressions more distinct and situated unusually distant from basal marign of pronotum; stridulatory files on head, and transverse line on vertex absent *Rhopalocryptus* Arrow

23. Antenna markedly long and slender with a weak club (Text-fig. 4K). Pronotum more elongate, shape as figured (Text-fig. 4L). Elytra narrowed in front and broadest across the posterior one-third *Hoplepiscapha* Lea

24. Antenna shorter and club more strongly developed. Pronotum more transverse, shape not as above. Elytra not narrowed in front and broadest across the middle 25

25. Front angles of prothorax with callosities (Text-fig. 3A). Scutellary striole on elytra absent. Mentum with a pair of cavities (Text-fig. 3D). *Leucohimatium* Rosenhauer
Front angles of prothorax without callosities. Scutellary striole present. Mentum with or without single cavity 26

26. Gular region and mentum with large cavities *Eicolyctus* Sahlberg
Gular region and mentum without cavities 27

27. Antennal segments 3 much longer than pedicel; intercoxal process of first ventrite rounded at apex *Loberogosmus* Reitter
Antennal segment 3 almost equal to pedicel; intercoxal process of first ventrite pointed at apex. 28

28. Elytra glabrous with five rows of punctures between suture and humeral angle. Prosternal process widened in middle and straight at apex. Eyes very weakly projecting beyond the outlines of head *Pharaxonotha* Reitter
Elytra pubescent with ten rows of punctures between suture and humeral angle. Prosternal process not widened at middle and apical margin obtusely angled in middle. Eyes much projecting beyond the outlines of head *Henoticonus* Reitter

29. Mesocoxae more widely separated and sternal fitting between them in a stright line. Prothorax with anterior part of side margins undulated. Intercoxal process of first ventrite broad with more or less rounded apical margin *Pseudhenoticus* Sharp
Mesocoxae more closely situated and sternal fitting between them with a single knob. Prothorax not as above. Intercoxal process of first ventrite narrow and pointed, except in *Bolerus* 30

30. Prothorax as figured (Text-fig. 8D) with prosternal process broad at apex. Elytra glabrous; mesocoxal lines on metasternum present. Intercoxal process of first ventrite broad, as figured (Text-fig. 8C) *Bolerus* Grouvelle=*Thallisellodes* Arrow=*Platycladoxena* Kraatz
Prothorax with prosternal process not as above. Elytra usually hairy; mesocoxal lines on metasternum usually absent Intercoxal process of first ventrite narrow and pointed 31

31. Species larger, narrow and elongated, less Cryptophagid-like in form. Elytra usually with scutellary striole wing often with anal cell. Tibiae broad and truncated at apex; tarsal lobes broad. Metasternum less transverse 32

Species smaller, less narrow and elongated, of Cryptophagid-like form. Elytra without scutellary striole; wing without anal cell. Tibiae slender, not broadened at apex; tarsal lobes narrow. Metasternum more transverse. 34

32. Prothorax with side margin dentate or undulate, front angles projecting forward. Tarsal segment 2 and 3 lobed below. Anterior part of dorsal side of head with transverse ridge.
Pseudhapalips Champion

Prothorax not as above, side margins not dentate or undulate, front angles not projecting forwards. Only tarsal segment 3 lobed below. Head not as above 33

33. Head with a pair of humps on antero-dorsal side of eyes. Prebasal impressions on pronotum obscured. Elytra pubescent *Truquiella* Champion

Head without such humps. Prebasal impressions on pronotum usually visible. Elytra glabrous or pubescent. *Hapalips* Reitter

34. Prothorax narrowed in front. Antenna with segment 9 considerably smaller than segment 10, which is very broad
Telmatoscius Sharp

Prothorax not narrowed in front. Antennal segment 9 very little shorter than segment 10, which is less transverse. *Loberus* Leconte

VIII—Key to the known Larvae of the Subfamilies and Tribes of Languriidae.

1. Dorsal surface usually non-granulated; ocelli 0-2 on each side of the head. Mandibular prostheca small and tooth-like (absent in *Teretilanguria*). Claw with two setae. Species endophytic Languriinae

Dorsal surface granulated; ocelli usually 5-6, rarely absent on each side of the head. Mandibular prostheca larger and translucent (except in *Hapalips* sp. described by Rymer Roberts 1939), if absent, claw with single seta. Species not endophytic. 2

2. Mandible with prostheca. Claw with two setea
Loberinae 3

Mandible without prostheca. Claw with single seta.
Cryptophilinae

3. Granules of tergites confusedly punctured. Frontale with an endocarina. *Pharaxonothini*

Granules of tergites arranged in regular rows. Frontale without an endocarina. *Loberini*

IX—Discussion of Relationship within the Family Languriidae

Of all groups of Languriidae, the subfamily Languriinae seems to be among the most advanced form as shown by the adult mouth-parts and ovipositor modified for piercing, also reduced sclerotization and ocelli of the larva. This subfamily is probably related to Loberinae through Thallisellini. The latter tribe are clearly related to Cladoxenini, in which group the genus *Crotchia* Fowler shows maximum resemblance to Languriini, and probably links the two tribes.

In Loberinae the tribe Pharaxonothini shows several similarities both in adult and larval characters with Erotylidae, mainly Dacninae. The tribe Loberini is probably linked with Pharaxonothini through *Hapalips*.

The subfamily Toraminae might be an off-shoot of Loberini, perhaps derived from *Loberus*-like forms. On the other hand, species of Toraminae have some similarities with Cryptophilinae, e.g., front coxal cavities internally closed behind. sternal fitting between the mesocoxae with two knobs, absence of anal cell and radial cell in wing, and also some Cryptophilines have the metendosternite somewhat as in Toraminae.

In the subfamily Cryptophilinae there are several similarities with Endomychidae or other members of the Cerylonid groups in both adult and larval stages (discussed latter). This subfamily seems to be the most aberrant in Languriidae, but may be related to Loberini through Toraminae.

Lastly Setariolinae, including single small cisid-like species, very different in appearance from other Languriidae, may be an off-shoot of Pharaxonothini, as suggested by its more or less simple tarsi, ventrite 1 without femoral lines and short trochanters ; on the other hand, the internally closed front coxal cavities and perhaps the habits suggest a possible connection with Languriinae.

X—Systematic Account

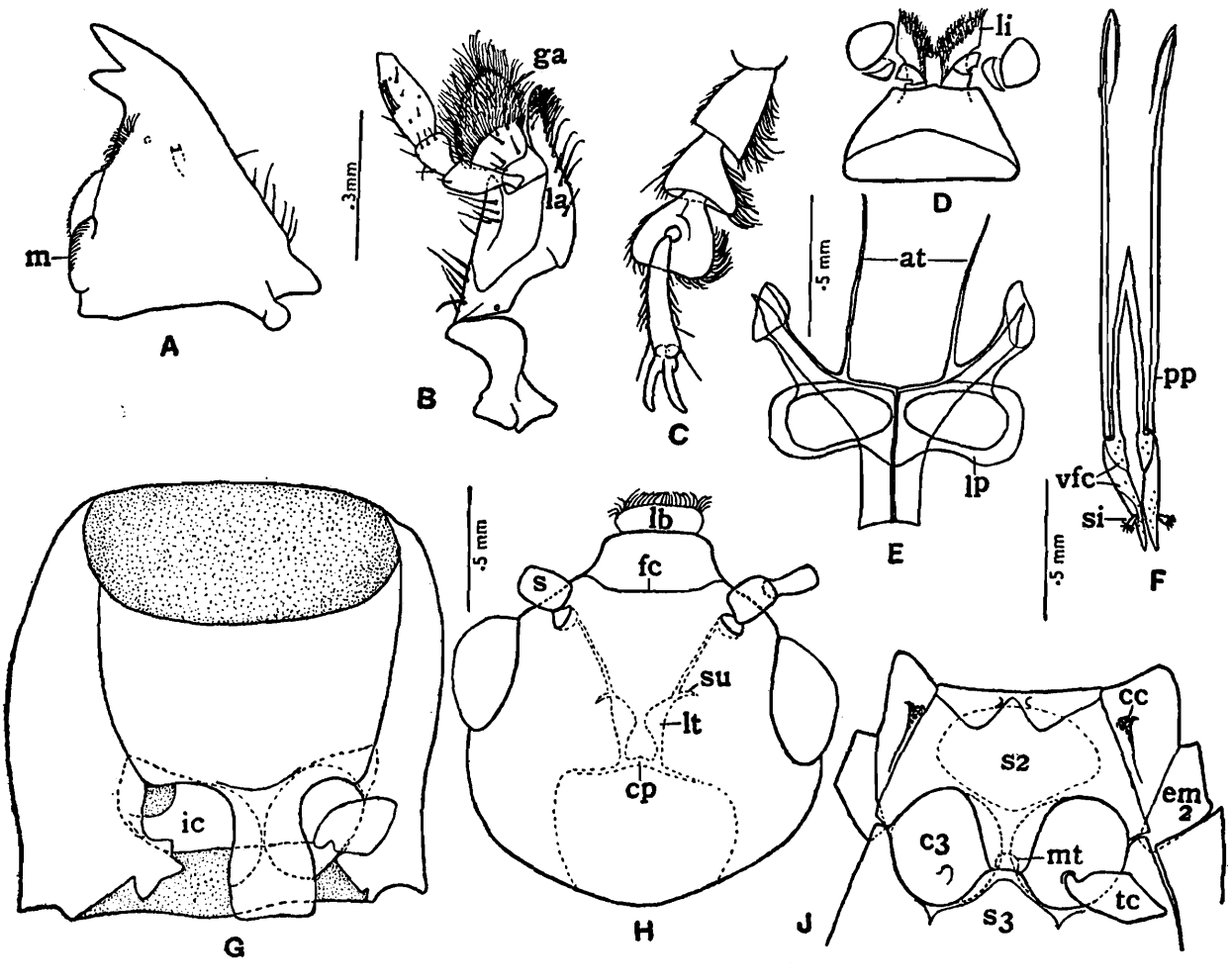
Subfamily (a) Languriinae Crotch

The history of this subfamily is that of the family Languriidae, already discussed previously. One of us Crowson (1955) suggested that typical Cladoxeninae Arrow are not satisfactorily distinguished from Languriinae. We have studied most of the genera of Cladoxeninae in detail and reached the same view as Crowson (*loc. cit.*). In the present work subfamilies of Arrow are considered as tribes, Languriini and Cladoxenini ; another tribe Thallisellini has already been characterised by one of us (Sen Gupta, 1968) for the genera *Thallisella* Crotch and *Platoberus* Sharp.

Habitat.—The adults usually occur on flowers and foliage, and known larvae have been found to be stem borers in herbaceous plants.

Geographical distribution.—Mainly tropical and subtropical climatic zones.

The subfamily Languriinae can be characterised by the following characters :



Text-fig. 1. A. Left mandible, ventral view of *Anadastus filiformis ;* B. Left maxilla, dorsal view of *Anadastus filiformis ;* C. Front tarsi of *Promecolanguria* sp. ; D. Labium, ventral view of *Anadastus filiformis ;* E. Metendosternite of *Promecolanguria* sp ; F. Ovipositor of Promecolanguria sp. ; G. Prothorax, ventral view *Anadastus filiformis ;* H. Head, dorsal view of *Anadastus filiformis ;* J. Mesosternum and anterior part of metasternum, ventral view of *Anadastus filiformis.*

With general characters of Languriidae.

1. Head usually with fronto-clypeal suture (Text-fig. 1H), antennal insertions facing dorso-laterally (Text-fig. 1H). Transverse line on vertex absent; stridulatory files on occipital region often present: transverse groove on anterior part of gular region often with a crenulated hind margin. Antennal club often asymmetrical, usually rather flattened and often with more than three joints. Mandible often with very poorly developed mola (Text-fig.1A), except in Cladoxenini and Thallisellini where the mola is rather more developed. Maxillary lacinia with three apical teeth (Text-fig. 1B), galea either short and broad with apical half densely hairy (Text-fig. 1B) or narrow and elongated with few hairs at apex. Ligula often well developed and setose : bilobed (Text-fig. 1D).

2. Prothorax usually elongate and more or less constricted towards the posterior margin. Front coxal cavities moderately widely open externally and closed behind internally (Text-fig. 1G).

Elytra usually glabrous, often with a scutellary striole. Wing with four anal veins, anal cell, radial cell and r-m cross vein distinct.

Sternal fitting between the mesocoxae with a single knob-like projection (Text-fig. 1J). Metendosternite usually with anterior tendons separated by slightly more than the width of basal stalk, lateral plates well developed, broad and plate-like (Text-fig. 1E).

Legs usually long, with broadly elongated trochanters, tarsi pseudotetramerous (Text-fig. 1C).

3. Abdomen narrow and markedly elongated, often with a pair of femoral lines. Aedeagus of Erotylidae-Languriidae type. Ovipositor with styli attached at a distance from the more or less pointed apex of coxities (Text-fig. 1F).

4. Larvae as far as known, with mandibular prostheca small and tooth-like (absent in *Teretilanguria*); ocelli 0-2 on each side of the head. Dorsal surface usually not granulated; tarsungular setae two. Species endophytic.

Tribe LANGURIINI (=LANGURIINAE Arrow)

This tribe includes typical Languriids, which have been extensively studied by different authors, Harold (1875), Gorham (1891), Fowler (1908), Arrow (1925, 1929), Zia (1934), recently Villiers (1961) and Martins and Peravia (1965). Distinguishing features of the tribe are included in the key.

Tribe CLADOXENINI (=CLADOXENINAE Arrow)

Distinguishing features of the tribe are included in the key. The genera of this tribe have already been revised by one of us ((Sen Gupta, 1968).

Tribe THALLISELLINI Sen Gupta. 1968.

Distinguishing features of the tribe are included in the key.

Subfamily (b) LOBERINAE Bruce

Distinguishing features of the subfamily are included in the key. This subfamily includes two tribes Loberini and Pharaxonothini. The tribe Loberini has already been described in detail by one of us (Sen Gupta, 1968).

Habitat.—The habitats of Loberinae are much more diverse than those of Languriinae, species having been recorded from stored grains, under leaf-bases of palm trees, tree-fern, corn stalks, seed pods, male cone of cycads, dead *Euphorbia* stem, forest litter, under stones, in bees' and wasps' nest, and as ectoparasites of mammals.

Geographical distribution.—The distribution is wider than in Languriinae and extends into Europe. The distribution of Pharaxonothini is noteworthy (see map, Fig. A) and quite different from other groups of this family. The genera are relatively numerous, but all small and mostly monotypic ; at least *Pharaxonotha* is represented in both the New and the Old Worlds. The Australian representation of the group is by two well-marked endemic genera, which is suggestive of greater antiquity for this group than for most of the comparable ones considered here. An unusual feature, in a presumably old group, is the apparent absence of endemic representatives in South America. The genus *Loberopsyllus* Martínez and Barrera is represented on the distribution map, as from the characters given in the description it probably belongs to Pharaxonothini.

Tribe PHARAXONOTHINI Sen Gupta and Crowson

Arrow (1925) transferred the genus *Pharaxonotha* Reitter to Languriidae-Cladoxeninae from Cryptophagidae. One of us (Crowson 1955) defined a new subfamily Pharaxonothinae of Languriidae, Sen Gupta and Crowson (1967) considered this group as a tribe of Loberinae, including nine genera, *Xenoscelis* Wollaston, *Xenocryptus* Arrow, *Rhopalocryptus* Arrow, *Pharaxonotha* Reitter, *Henoticonus* Reitter, *Loberogosmus* Reitter, *Eicolyctus* Sahlberg, *Leucohimatium* Rosenhauer and *Macrophagus* Motschulsky. Further study has revealed that another three genera belong to this group, *Hoplepiscapha* Lea from Western Australia, *Othniocryptus* Sharp from Panama and *Loberopsyllus* Martinez and Barrera from Mexico. Most of the above mentioned genera (except *Xenoscelis* and *Hoplepiscapha*) were placed under Cryptophagidae because of their open front coxal cavities and Cryptophagidae-like appearance. The genus *Xenoscelis* was placed under Erotylinae by Ganglbauer (1899) and subsequent authors on account of visibly closed front coxal cavities. Detailed study of adult *Xenoscelis* revealed that all the characters except for the front coxal cavities are similar to those of Pharaxonothini, moreover, in some genera of this group the front coxal cavities are almost closed behind. Unlike Erotylidae *Xenoscelis* have closely situated middle coxal cavities, and the sternal fitting between them has a single knob-like projection as in Pharaxonothini, whereas in Erotylidae the coxae are fairly widely separated and the sternal fitting between them has two distinct well separated knobs. A distinct anal cell, a regular feature of wing of Erotylidae except for brachypterous forms, is absent in *Xenoscelis* as in other Pharaxonothini. The second genus, *Hoplepiscapha*, was described under Erotylidae by Lea (1922), its front cavities being nearly closed behind ; it has all the essential characters of Pharaxonothini. Most of the genera of this tribe have been studied in slide preparations, except for *Henoticonus*, *Hoplepiscapha* and *Othniocryptus*, of which we have been able to study only external features. Characters for *Loberogosmus* and *Macrophagus* taken from Ganglbauer's description, and that of *Loberopsyllus* from Martínez and Barrera's description. The genus *Eicolyctus* has been redescribed by us (1967).

Definition of Pharaxonothini modified from that given by Sen Gupta and Crowson (1967).

With general characters of Languriidae and of Loberinae.

1. Head often with a transverse line (Text-fig. 2A) on vertex behind the eyes, stridulatory files (Text-fig. 2A) often present. Gular region without a transverse groove, except in *Othniocryptus* but sometimes with a cavity. Mentum sometimes with single or paired cavities (Text-fig. 3D).

2. Front coxal cavities rather narrowly open behind, fully closed in *Xenoscelis* (Text-fig. 2B). Elytra usually glabrous and with regular rows of punctures, often with scutellary striole. Wing rarely with closed anal cell. Tarsi not lobed below (Text-fig. 2C), rarely

N.B. The genus *Micrambina* Reitter from Columbia, may belong to Loberini. The type species of this genus *Amitta* Reitter was based on a single specimen subsequently lost, which had rows of elytral punctures like Languriidae, and Reitter himself noted that it was related to *Loberus* Leconte.

very slightly so in *Xenoscelis* ; tarsal segment 4 little shorter than segment 3 ; trochanters short and broad (Text-fig. 4J) and tibiae usually with two spurs at the apex.

3. First ventrite without femoral lines (Text-fig. 4B). Ovipositor (Text-fig. 2D) of Loberinae-type, styli attached at the apex of coxites, except in *Leucohimatium*, where styli attached slightly on the lateral side of coxities (Text-fig. 3E).

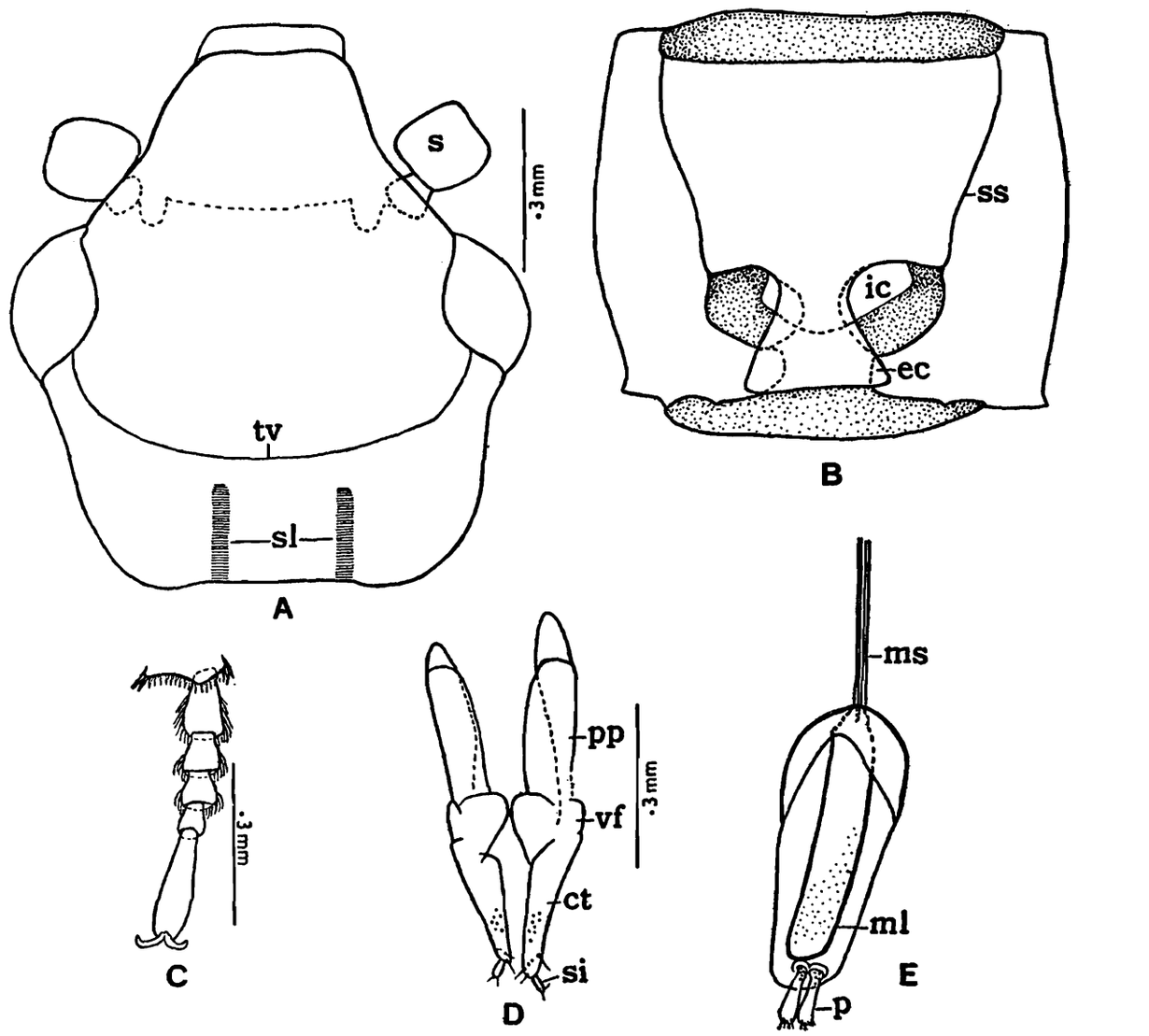
4. Larvae as far as known with granules of tergites confusedly arranged, not in regular rows as in Loberini ; frons with a short endocarina, and mandible with a hairy appendage at the base of mola.

1. Genus **Xenoscelis** Wollaston (nom. nov. for **Pristoscelis** Wollaston 1862 nom. preoccup.).

Type.—*X. deplanatus* Woll.

The genus *Xenoscelis* was described by Wollaston (1864) under Cucujidae-Silvaninae; Reitter (1879) followed Wollaston, Ganglbauer (1899) transferred it to Erotylidae-Erotylinae-Xenoscelini, and his view has been followed by subsequent authors.

With general characters of Languriidae and of Loberinae-Pharaxonothini.



TEXT-FIG. 2. A. Head, dorsal view of *Pharaxonotha kirschi;* B. Prothorax, ventral view of *Xenoscelis deplanatus ;* C. Hind tarsi of *Xenocryptus tenebrioides ;* D. Ovipositor of *Xenoscelis deplanatus ;* E. Aedeagus of *Pharaxonotha kirschi.*

Head without transverse line on vertex behind the eyes ; a pair of moderately separated stridulatory files weakly diverging towards front, number of ridges in a file about 12 in ·03 mm, measured in *X. deplanatus* female. Eyes not very large, coarsely facetted ; front margin of clypeus weakly angularly emarginate. Antenna with scape and pedicel equal in length, latter shorter than segment 3, segments 4-8 equal in length, segments 9-11 slightly elongate, forming a weak club, apical segment slightly narrower than segment 10. Prothorax (Text-fig. 2B) more or less parallel sided, very slightly wider in middle, length almost equal to breadth. Prebasal impressions obscured ; front coxal cavities externally closed behind (Text-fig. 2B) and coxae not very closely situated ; prosternal process rather broad with straight apical margin. Elytra with strial punctures small and in regular rows with a distinct scutellary row. Wing as figured (Text-fig. 4C) without anal cell. Mesocoxae closely situated ; mesoepisternal pockets very poorly developed ; metasternum elongated ; median impressed line extending slightly more than $\frac{1}{2}$ of its length. Metendosternite as in *Leucohimatium* (Text-fig. 3B). Tarsal segment 1 very slightly longer than segment 2, segment 3 equal to segment 2 and weakly lobed below, segment 4 smallest, segment 5 more or less equal to 1st 2 segments together ; tibiae long, weakly broadened at apex with two spurs. Intercoxal process of 1st ventrite narrow and pointed. Ovipositor as figured (Text-fig. 2D).

Habitat :—*X. deplanatus* adults occur in dead *Euphrbia* stems, and *X. costipennis* under stones. Larva undescribed.

Geographical distribution :—Tenerife (Canary Islands) and Mediterranean region.

2. Genus **Leucohimatium** Rosenhauer (1856)

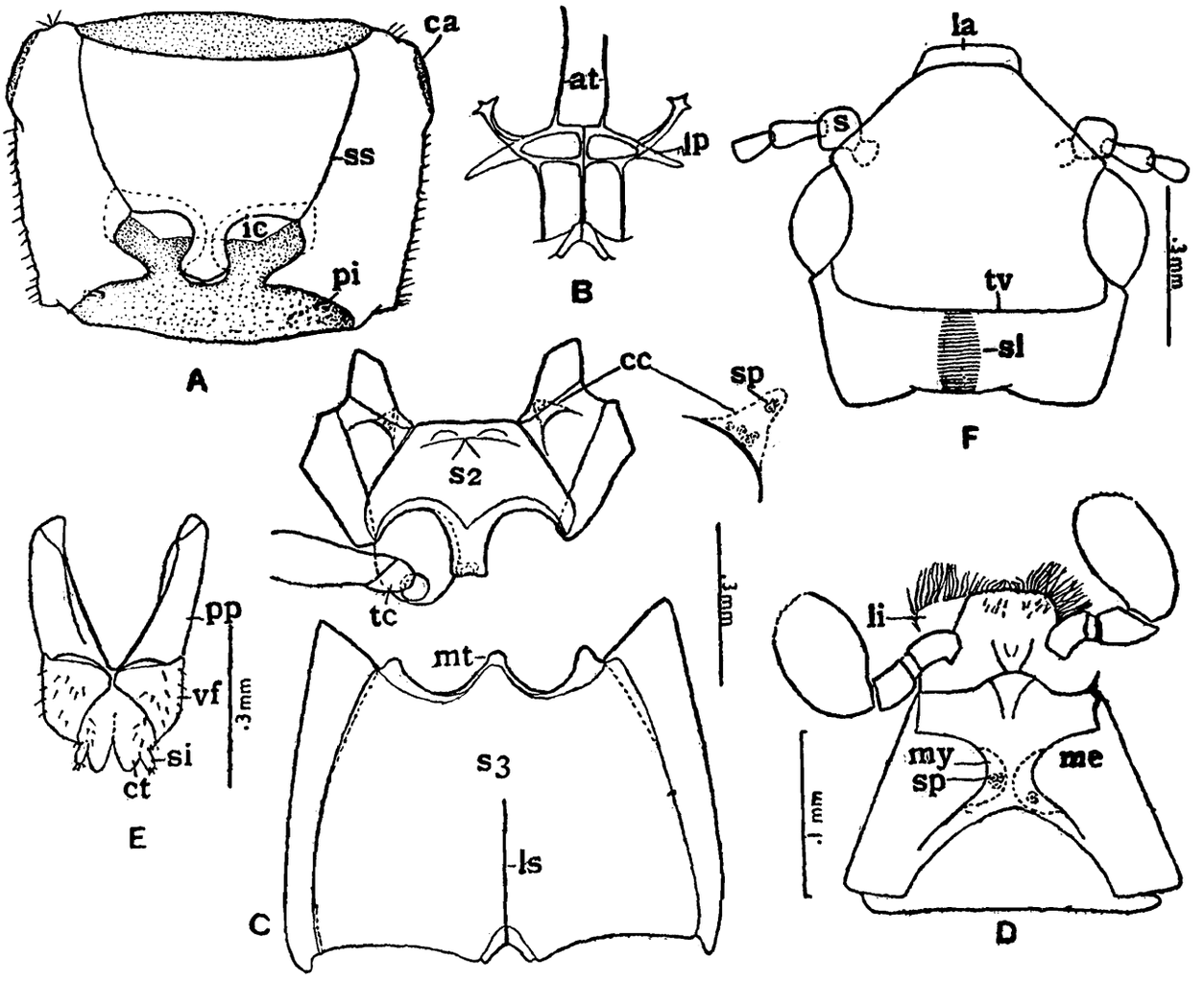
Type :—*L. arundinaceum* Forskäl=*L. elongatum* Erichson=*L. angustum* Rosenhauer.

The first described species of this genus was *Tenebrio arundinaceum* Forskäl ; Rosenhauer (1856), established within Cryptophagidae the genus *Leucohimatium* for the species *L. angustum*, later synonymised by Reitter (1875) with *Paramecosoma elongatum* Erichson (1846) and by Bedel (1916) with *T. arundinaceum* Forsk. Bruce (1951) seems to have been the first author to question the attribution to Cryptophagidae, he showed with figure of male genitalia of *Leucohimatium* that it differs in this character from Cryptophagidae and resembles *Hapalips*, *Loberus* and *Toramus*. The genus *Leucohimatium* is easily recognised by the callosities of the front angles of its prothorax, and seems to be related to *Pharaxonotha* and *Eicolyctus*.

With general characters of Languriidae and of Loberinae-Pharaxonothini.

Species narrow, elongated, rather parallel sided and of some what *Xenoscelis*-like facies. Head (Text-fig. 3F) with single rather broad stridulatory file, number of ridges 12 in ·03 mm. in *L. arundinaceum* female. As in *Pharaxonotha* and *Xenocryptus*, on the vertex of head there is a transverse line present (Text-fig. 3F) ; clypeus broad at base, weakly convex at apical margin. Antenna with scape slightly shorter than pedicel, which is equal to segment 3, segment 4-7 equal in length, segment 8 slightly longer than segment 7, club rather weak, segments 9, 10 and 11 more or less equal in size and apical segment somewhat rounded. Maxillary lacinia without apical spines ; mentum with a pair of cavities on ventral surface, opening outwardly (Text-fig. 3D). Prothorax (Text-fig. 3A) weakly transverse, slightly narrowed posteriorly, side margins finely crenulated provided with short setae, front angles with large callosities, hind angles weakly acute. Front coxal cavities moderately open behind ; prosternal process narrow with somewhat rounded apex ; prebasal impressions on pronotum well marked. Elytra with strial punctures in regular rows, puncturation of interstices absent, scutellary striole absent ; pubescence fine and recumbent. Wing as in *Xenoscelis* (Text-fig. 4C). Mesocoxae closely situated,

mesoepisternal pockets well developed (Text-fig. 3C); metasternal length and breadth almost equal, median impressed line extending 1/2 of its length. Metendosternite as figured (Text-fig. 3B). Legs long and slender; tarsal segment 1 slightly longer than 2, which is equal to segment 3, segment 4 smallest and about 1/2 the length of segment 1, segment 5 equal to 1st



TEXT-FIG. 3. *Leucohimatium arundinaceum*. A. Prothorax, ventral view; B. Metendosternite; C. Mese- and metasternum, ventral view; D. Labium, ventral view; E. Ovipositor; F. Head, dorsal view.

two segment together; tibiae slender, not broadened at apex, with 2 spurs. Ovipositor as figured (Text-fig. 3E), unlike other members of Pharaxonothini *Leucohimatium* has a Languriinae-type ovipositor, withthe styli attached before the apex of coxites.

Habitat:—Unknown, larva undescribed.

Geographical distribution:—S. Europe, N. Africa, Crimea, Caucasus, Japan and S. Africa.

3. Genus **Xenocryptus** Arrow (1929)

Type by monotypy:—*X. tenebrioides* Arrow (1929)

Arrow (1929) established this genus as an aberrant Cryptophagid related to *Pharaxonotha*. One of us Crowson (1955) included this genus in Pharaxonothinae under family Languriidae. The present study confirms Crowson's view; the genus seems to be related to both *Pharaxonotha* and *Rhopalocryptus* Arrow. Relationship with *Pharaxonotha*, according to Arrow, is indicated by the presence of stridulatory files and a transverse line on the vertex but we are anable to find any stridulatory files on the head of female *Xenocryptus*. Like *Rhopalocryptus*, it has a broad apically rounded clypeus and completely covered antennal

insertions, elytra with short scutellary striole and tibiae broad and truncated at apex and bearing spines.

With general characters of Languriidae and of Loberinae—Pharaxonothini.

General appearance resembles *Tribolium* and related genera of Tenebrionidae. Head with a distinct transverse line on vertex behind the eyes ; clypeus broadly rounded at apex ; eyes rather small and coarsely facetted. Antenna rather short, scape longer than pedicel, which is shorter than segment 3, segments 4-8 equal in length and shorter than segment 3, segments 9 and 10 equal in size and semicircular, apical one nearly circular, slightly tapered to apex. Ligula projecting, moderately well developed and bilobed ; apical segment of labial palpi elongate. Prothorax transverse, narrowed in front, front angles rounded, hind angles rather acute. Front coxae very closely situated, cavities narrowly open behind ; prebasal impressions on pronotum minute ; prosternal process rather narrow at base, apex projecting posteriorly and rounded. Elytra sparsely pubescent with fine recumbent setae, strial punctures minute in regular rows, scutellary striole short, punctures on interstices in regular rows. Wing (Text-fig. 4A) with a closed anal cell. Mesocoxae nearly contiguous ; mesoepisternal pockets obscured ; metasternum strongly transverse ; median impressed line extending 2/3 of its length ; metendosternite of Loberinae-type. Legs short and stout ; tibiae short and markedly widened to apex, which is spinous ; tarsal segment 1 slightly longer than segment 2, segments 2-4 more or less equal in length but progressively narrower, segment 5 about as long as 1st 3 segments together ; front legs slightly shorter than rest. Intercoxal process of 1st ventrite narrow and pointed. Ovipositor of Loberinae-type, styli attached laterally, slightly before the apex of coxites.

Habitat : on cycad (Macrozamia)—P. J. Darlington coll. larva undescribed.

Geographical distribution : West Australia.

4. Genus **Rhopalocryptus** Arrow (1929)

Type by monotypy : *R. pulcher* Arrow (1929)

This genus was established by Arrow (1929) under Cryptophagidae, and placed close to *Pharaxonotha.* With general characters of Languriidae and of Loberinae—Pharaxonothini.

Head without stridulatory files ; eyes moderately large and finely facetted ; transverse line on vertex behind the eyes apparently absent. Antenna with scape longer than pedicel which is slightly shorter than segment 3, segments 4-7 equal in length and shorter than segment 3, segment 8 slightly wider than segment 7, club compact, short and rather flattened with segments 9 and 10 very broad, segment 10 wider than segment 9, and segment 11 slightly longer than its breadth, about equal to the length of segments 9 and 10 together. Prothorax transverse, side margins curved and smooth, front angles slightly projecting forward, hind angles rather rounded, front and hind margins equal in breadth. Prebasal impressions present and unusually distant from basal margin of pronotum ; front coxal cavities very narrowly open behind ; prosternal process narrow, its apical margin obtusely angulate. Elytra glabrous, strial punctures large, in regular rows, with a scutellary striole. Mesocoxae closely situated ; metasternum strongly transverse and median impressed line obscured. Tarsi short but rather narrow, tarsal segment 1 longer than segment 2, which is equal to segment 3, segment 4 little shorter than segment 3, segments 1-4 progressively narrower, segment 5 equal in length to 1st 3 segments together ; apex of tibiae broad and spinous as in *Xenocryptus.* Intercoxal process of 1st ventrite narrow, apex rounded and somewhat expanded.

Habitat : Decaying inflorescence of *Colocasia indica ;* larva undescribed.

Geographical distribution : Fort de Kock (Sumatra).

5. Genus **Pharaxonotha** Reitter (1875)

Type by monotypy : *P. kirschi* Reitter (1875)

The genus *Pharaxonotha* was attributed by Reitter (1875) to the family Cryptophagidae. Ganglbauer (1899) placed it in Erotylidae-Cryptophaginae ; Sharp (1900), Champion (1913) and Grouvelle (1919) followed the view of Reitter. Arrow (1925) was the first to transfer the genus to Languriidae-Cladoxeninae but in 1929 he again retransferred it back to Cryptophagidae on account of the simple tarsal segments. Böving and Craighead (1930-1931) and Rymer Roberts (1939), studying the larvae of *Pharaxonotha*, placed the genus under Languriidae ; the latter author, who described *P. zamiae* Blake larvae, noted their resemblence to *Bolerus* grouvelle=*Platycladoxena* Kraatz and *Hapalips* Reitter and placed all 3 genera in Cladoxeninae. Hinton (1945) and one of us (Crowson 1955) followed the view of Rymer Roberts.

With general characters of Languriidae and of Loberinae-Pharaxonothini.

Head (Text-fig. 2A) elongate, with a pair of moderately separated stridulatory files in *P. kirschi* male each file with about 18 ridges in .05 mm.; transverse line on vertex behind the eyes present (Text-fig. 2A) ; clypeus narrower than in *Xenocryptus*, front margin slightly sinuate. Eyes of moderate size, coarsely facetted, distinct short tempora present. Antenna rather short with scape and segment 3 slightly longer than pedicel, segments 3-8 equal in length, club rather weakly developed, segments 9 and 10 semicircular, apical segment more or less of same size as segment 10 and slightly asymmetrically rounded at apex. Unlike *Xenocryptus*, ligula poorly developed. Prothorax weakly transverse, narrowed in front, side margins smooth, front angles obtuse, hind angles more acute. Prebasal impressions on pronotum minute, front coxal cavities narrowly open behind, prosternal process rather narrow, slightly widened at the middle, its apical margin straight. Elytra glabrous, or finely pubescent strial punctures small and in regular rows, scutellary striole well developed, punctures on interstices obscured. Wing without anal cell, as in *Xenoscelis* (Text-fig. 4C). Mesocoxae very closely situated ; mesoepisternal pockets well developed ; metasternum weakly transverse ; median impressed line extending 2/3 of its length ; metendosternite of Loberinae-type. Tarsi narrow and elongate, segment 1 longer than segment 2, which is equal to segment 3, segment 4 about 1/2 of the segment 2, segment 5 equal to two basal segments together ; tibiae elongate, weakly broadened at apex, without spines. Intercoxal process of abdomen narrow and pointed. Aedeagus as figured (Text-fig. 2E).

Habitat : Very diverse, *P. kirschi* recorded in cotton boll, corn meal and edible tubers, store maize, wheat and beans, and *P. zamiae* in male cones of the Cycad *Zamia*. Chittenden (1911) studied the life-history of *P. kirschi* and Zacher (1926) stated that adults and larvae of this species can be bred in flour. An undescribed South African species on Encephalastos (Cycadaceae).

Geographical distribution : Indo-malayan region, C. America and southern part of N. America ; *P. kirschi* recorded indoor from Europe and N. America. We have seen related undescribed forms from S. Africa.

6. Genus **Henoticonus** Reitter (1878)

Type by monotypy : *H. triphylloides* Reitter

With general characters of Languriidae and of Loberinae-Pharaxonothini.

Reitter (1878) attributed this genus to Cryptophagidae, since when the only reference we have seen to it is by Grouvelle (1919), who added another species *H. bouchardi* which he stated was somewhat intermediate in its characters between *Pharaxonotha* and *H. triphylloides*. We have found another difference, in that Reitter's species is densely pubescent,

N. B. Henticonus bouchardi Grouv., which we have not been able to study, might prove to be better placed under the genus *Pharaxonotha*.

whereas Grouvelle's *bouchardi* is described as glabrous. The species *H. triphylloides* has been studied, but we have been unable make a slide preparation for detailed study. The dense, semirecumbent pubescence of the elytra separates this species not only from *H. bouchardi* but also from *Pharaxonotha*, *Rhopalocryptus*, etc. The prebasal impressions of pronotum are obscured in *H. triphylloides*. We were not able to established whether or not stridulatory files or a transverse line on vertex are present in this species, as the basal part of the head of the specimen seen was hidden under the pronotum. Clypeus moderately broad with rounded apical margin as in *Rhopalocryptus* but antennal insertions less fully covered by frons. Eyes large, rather projecting and coarsely facetted. Antenna with scape longer than pedicel, which is more or less equal to segment 3, segments 4-8 equal in length and shorter than first 3 segments, segments 9 and 10 equal sized and weakly transverse, terminal one rather elongate with rounded apex. Prothorax very weakly transverse, narrowed in front, front angles rounded, hind angles obtuse and side margins smooth. Front coxal cavities narrowly open behind ; prosternal process narrow, its apical margin obtusely angled in middle. Elytral puncturation in regular rows with rather distinct scutellary striole. Mesocoxae closely situated ; metasternum transverse, median impressed line obscured. Tarsal segment 1 longer than segment 2, which is equal to segment 3, segment 4 shorter than segment 3 and first 4 segments progressively narrower, segment 5 equal to the length of first 2 together. Intercoxal process of first ventrite narrow and pointed.

Habitat : Not known and larva undescribed.

Geographical distribution : Sumatra, Java and Japan.

7. Genus **Hoplepiscapha** Lea (1922)

Type by monotypy : *H. longicornis* Lea (1922).

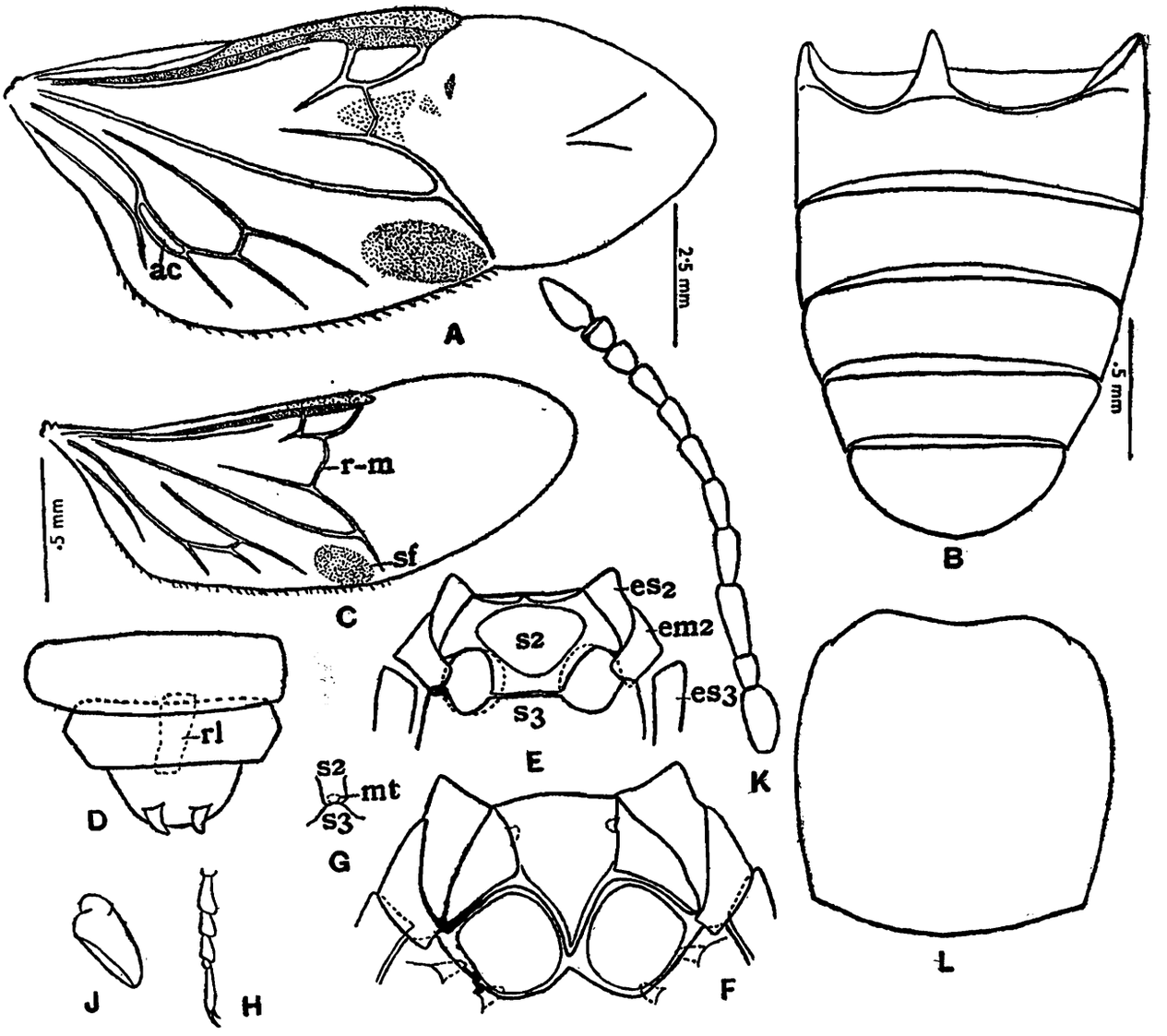
The genus was attributed by Lea (1922) to the family Erotylidae near *Episcaphula* Crotch. More detailed study reveals that it has front coxal cavities narrowly open behind ; although the mesocoxae are fairly widely separated, the fitting of the sterna between them is by a single broad knob, rather than a pair as in Erotylidae, and in several other characters it resembles Pharaxonothini.

With general characters of Languriidae and of Loberinae-Pharaxonothini.

The genus is easily distinguished from other genera of this group by its narrow, elongated body form and markedly long and slender antenna with very weakly developed club (Text-fig. 4K). Head rather elongate, the eyes small, not projecting and moderately facetted ; transverse line on vertex behind the eyes absent ; stridulatory files apparently absent ; clypeus narrowed in front, antennal insertions somewhat exposed. Antenna as figured (Text-fig. 4K), with a long scape, pedicel about 1/2 of the length of scape and of segment 3, segments 4-6 equal in length, shorter than segment 3 and slightly longer than segments 7 and 8, which are equal in length, segments 9 and 10 are very weakly transverse, each about 1/2 of the length of segment 11, which is narrow and pointed at apex. Prothorax elongate as figured (Text-fig. 4L), pronotum without prebasal impressions, front coxal cavities narrowly open behind, prosternal process weakly broadened at apex with straight margin. Elytra glabrous, strial punctures in regular rows with a distinct scutellary striole, elytra narrowed in front and widened across the posterior 1/3. Metasternum strongly transverse, width about double its length. Tarsal segment 1 longer than segment 2, segments 2-4 more or less equal in length and progressively narrower, segment 5 almost equal to the length of first 4 together ; tibiae slender, weakly broadened at apex. Intercoxal process of first ventrite rather broad with rounded apex.

Habitat : Not known and larva undescribed.

Geographical distribution : West Australia.



TEXT-FIG. 4. A. Wing of *Xenocryptus tenebrioides;* B. Ventrites, ventral view of *Pharaxonotha kirschi;* C. Wing of *Xenoscelis deplanatus;* D. Posterior segments, dorsal view of the larva of *Dacne;* E. Meso- and metasterna, ventral view of *Pediacus* sp.; F. Meso-and metasterna, ventral view of *Dapsa denticolls;* G. Sternal fitting between mesocoxae of *Othniocryptus variegatus;* H. Hind tarsi of *Othniocryptus variegatus;* J. Hind trochanter of *Pharaxonotha kirschi;* K. Antenna of *Hoplepiscapha longicornis;* L. Pronotum of *Hoplepiscpha longicornis.*

8. Genus **Othniocryptus** Sharp (1900)

Type by monotypy : *O. variegatus* Sharp (1900).

With general characters of Languriidae and of Loberinae-Pharaxonothini.

Sharp (1900) placed this genus under Cryptophagidae after *Pharaxonotha ;* it is unusual in its pubescent elytra with irregular puncturation. In general appearance it resembles *Othniidae* (Elacatidae : Heteromera), and is unlike other members of this group. Head with a pair of fairly widely separated stridulatory files ; eyes large, somewhat projecting and moderately facetted ; transverse line on vertex absent ; a weak transverse groove present in gular region as in Loberini ; clypeus not very broad, frons scarcely extended over the antennal insertions. Antenna moderately long, segments 1-6 alternately weakly longer and shorter, segments 6-8 equal in length and slightly shorter than segment 5, segments 9 and 10 more or less ogival in outline and slightly elongate, apical segment longer than its width and more or less rounded at apex. Prothorax weakly transverse, front angles rather obtuse and hind angles more acute, prebasal impressions on pronotum well marked. Front

coxal cavities fairly widely open behind ; prosternal process parallel sided and of moderate breadth, its apical margin almost straight. Elytra with long, semirecumbent pubescence. Tarsi (Text-fig. 4H) with first 4 segments progressively shorter and narrower, first 3 segments slightly lobed below, segment 5 equal to the length of first 2 together ; tibiae slender, not broadened at apex, without evident apical spurs. Ventrite 1 with intercoxal process narrow and pointed.

Habitat : Not known and larva undescribed.

Geographical distribution : Panama.

Subfamily (c) Setariolinae Crowson (Setariini Casey parfim)

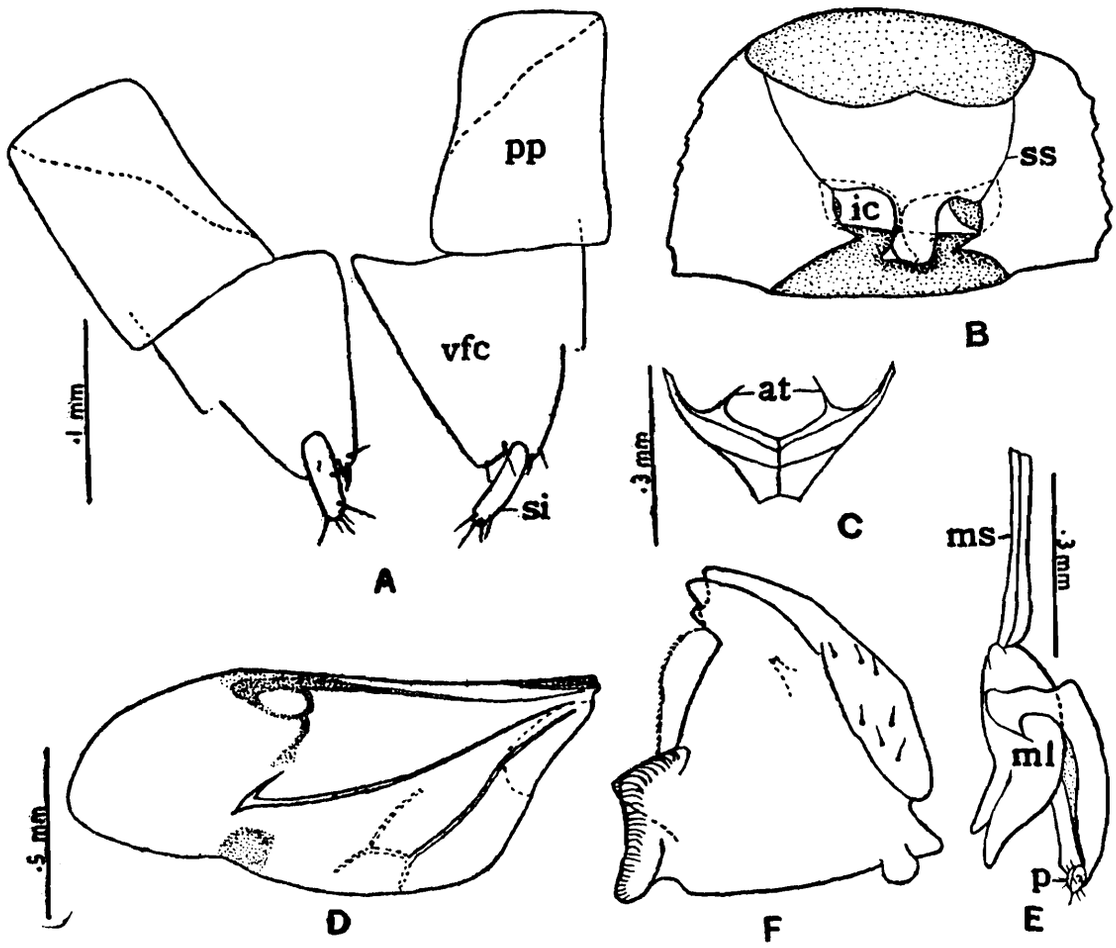
One of us, Crowson (1955), established this subfamily in Languriidae for the genus *Setariola* Jacobson, hitherto placed in Cryptophagidae. This subfamily includes only one genus, whose single species in general appearance very much resembles species of Cisidae. The differences from other subfamilies are given in the key to adult Languriidae.

1. Genus **Setariola** Jacobson (1915)=**Setaria** Mulsant and Rey (1863)

Type by monotypy : *S. sericea* Muls. and Rey (1863).

With general characters of Languriidae.

This genus includes only one small species, unlike any other Languriidae in appearance. Head without transverse line on vertex but occipital region clearly differentiated into a posterior unpunctured and anterior punctured region. Stridulatory files paired, narrowly separated, ridges very fine, about 30 striae in .03 mm. Transverse groove on anterior part of



Text-fig. 5. *Setariola sericea.* A. Ovipositor ; B. Prothorax, ventral view ; C. Metendosternite ; D. Wing; E. Aedeagus ; F. Left mandible, ventral view.

gular region present. Antennal insertions hidden under sides of frons. Antenna with scape equal in length to pedicel, which is slightly shorter than segment 3, segments 4-8 equal in length and shorter than segments 3 and 9, latter markedly shorter than segment 10, which is larger than apical segment. Mandible (Text-fig. 5F) with well developed mola and two apical teeth, on ventral surface a small tubular opening present, similar to that of *Anadastus filiformis* Fabricius (Text-fig. 1A). Maxillary lacinia with two apical spines, galea short and narrow ; labium with apical segment of palpi narrowed at apex ; ligula poorly developed.

Prothorax (Text-fig. 5B) narrowed in front, side margins with few weak serrations, prebasal impressions on pronotum obscured. Front coxal cavities internally closed and externally open behind (Text-fig. 5B). Pro- and mesocoxae narrowly separated. Elytra irregularly punctured, with fairly dense pubescence. Wing (Text-fig. 5D) with two anal veins, anal cell absent, radial cell and r-m cross vein rather indistinct. Sternal fitting between the mesocoxae with a single knob ; mesoepisternal pockets well developed. Metasternum twice as wide as long ; median impressed line very short ; metendosternite as figured (Text-fig. 5C). Tarsi with segment 3 very slightly lobed below, segment 1 distinctly longer than segment 2, segment 4 minute, segment 5 about equal to segment 1 ; tibiae broadened at apex ; trochanters short and broad.

Ventrite 1 without femoral lines, intercoxal process broad at base but pointed at apex. Aedeagus as figured (Text-fig. 5E). Ovipositor (Text-fig. 5A) reduced, styli attached at the apex of coxites.

Habitat : On Tamarix bushes ; larva undescribed.

Geographical distribution : Mediterranean shores of Europe.

Subfamily (d) Toraminae Sen Gupta 1967

Distinguishing features of the subfamily are included in the key.

Habitat : Unknown, larvae undescribed.

Geographical distribution : Restricted to warmer climates, a few species extend into the warm temperate zone, unrepresented in Europe and not yet recorded from Australia.

Subfamily (e) Cryptophilinae Casey 1900

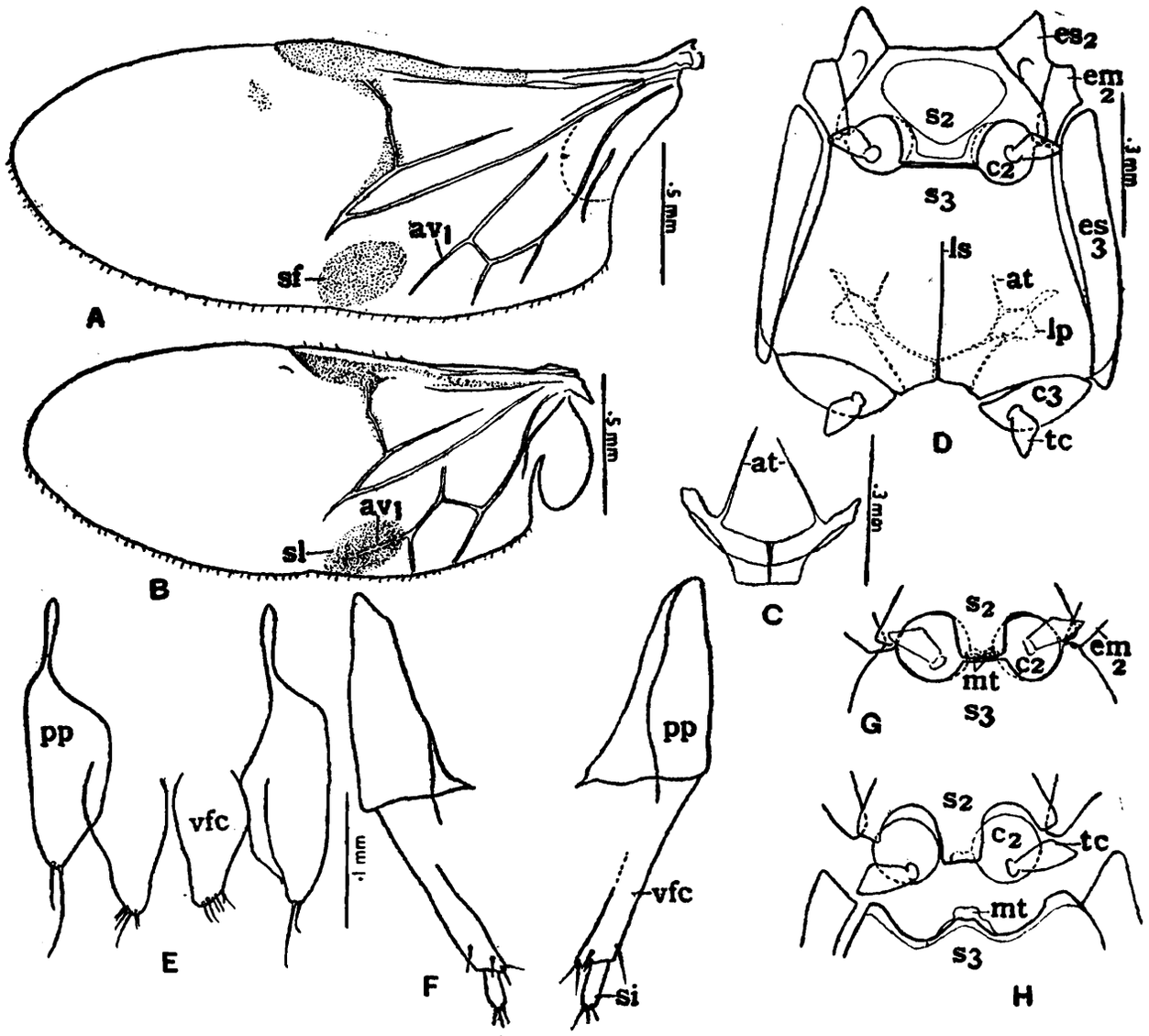
According to present knowledge this subfamily includes two tribes Cryptophilini Casey (1900) and Xenoscelinini trib. nov., the former including two genera, *Cryptophilus* Reitter and *Coelocryptus* Sharp, and the latter with only one *Xenoscelinus* Grouv. (described below). Beginning with *Cryptophilus*, the earliest described species was *Cryptophagus integer* Heer (1838) ; for it and 3 additional species the genus *Cryptophilus* was established by Reitter (1874), and placed under Cryptophagidae. The placing of the genus by subsequent authors has varied, Ganglbauer (1899) placed it under Diphyllini (Erotylidae) on account of the closed front coxal cavities and presence of femoral lines on 1st ventrite, in this he was followed by Kuhnt (1909) and in Junk's Catalogue (1911). Casey (1900) established a new tribe Cryptophilini in Cryptophagidae. Grouvelle (1919) included both Biphyllidae and *Cryptophilus* in Cryptophagidae. Leng (1920) in his Catalogue of North America and Mexico, included a tribe Cryptophilini in Cryptophagidae. Arrow (1929) described *Cryptophilus* as an aberrant Biphyllidae linking the family with Cryptophagidae ; in Junk's Catalogue Schenkling (1934) followed Arrow's view. Hinton (1945) and one of us (Crowson, 1955) suggested that Erotylidae are related to Biphyllidae through *Cryptophilus ;* more recently Bruce (1963) referred *Cryptophilus* to Cryptophagidae—Telmatophilinae. We have seen no published reference to *Coelocryptus* other than Sharp's original description of it under Cryptophagidae. After detailed study of adult characters, it appears that Cryptophilinae are more nearly related to Languriidae than to Cryptophagidae, Erotylidae and Biphyllidae ; the group is here tentatively considered as a new subfamily of Languriidae.

The main characters separating the Cryptophilinae from Cryptophagidae are as follows :—

1. Wing with subcubital fleck (Text-fig. 6A).
2. Elytra with sharply defined epipleura.
3. Aedeagus (Text-fig. 7D) of Erotylidae—Languriidae type.
4. All the ventrites equal in length.
5. Front coxal cavities closed behind externally (Text-fig. 7A).

Despite slight similarities to Biphyllidae in wing venation, Cryptophilinae can readily be distinguished from that group by the following characters :—

1. Normal trochanters (Text-fig. 6H).
2. Concealed trochantins of front coxae (Text-fig. 7A).
3. Mesocoxal cavities closed outwardly by sterna (Text-fig. 6G).
4. Aedeagus (Text-fig. 7D) of Erotylidae-Languriidae type.
5. Stridulatory files on head often present (Text-fig. 7G).
6. Tarsal lobes (Text-fig. 7E) different.
7. Wing (Text-figs. 6A, 6B) without anal cell and radial cell.



TEXT-FIG. 6. A. Wing of *Cryptophilus obliteratus* ; B. Wing of *Xenoscelinus maculosum* ; C. Metendosternite of *Coelocryptus mexicanus* ; D. Meso-and metasternum, ventral view of *Xenoscelinus maculosum* ; E. Ovipositor of *Xenoscelinus maculosum* ; F. Ovipositor of *Cryptophilus obliteratus* ; G. Meso-and metasternal junction of *Cryptophilus integer* ; H. Meso- and metasternal junction of *Coelocryptus mexicanus*.

The distinction of the group from Erotylidae is less clear, but there are several respects in which Cryptophilinae differ from Erotylidae and resemble various Languriidae. The principal ones are as follows :—

1. Front coxal cavity internally as well as externally closed behind (Text-fig. 7A), a condition unknown in Erotylidae. Front coxae rather more closely situated dorsal to prosternal process, whereas in Erotylidae coxae relatively widely separated.

2. Meso- and metasternal fitting between the mesocoxae either by two closely situated knobs (Text-fig. 6G) or in a straight line (Text-fig. 6D), whereas in Erotylidae the two knobs are well separated.

3. Wing without anal cell and radial cell unlike fully-winged Erotylidae.

4. Metendosternite (Text-figs. 6C, 6D) unlike those of Erotylidae, rather similar to that of Languriid subfamily Toraminae.

5. General appearance very similar to small hairy Toraminae, and unlike any true Erotylidae.

The visibly closed front coxal cavity has previously been the main character used to relate this group to Erotylidae but a complete gradation from open to closed front coxal cavities is found in one tribe Pharaxonothini of Languriidae, while in being internally (as well as externally) closed behind, the front coxal cavities of Cryptophilinae differ from those of any Erotylidae and resemble those of the Languriid subfamilies Languriinae, Toraminae and Setariolinae.

Subfamily Cryptophilinae can be distinguished by following characters :—

1. Cephalic stridulatory file, if present single and median (Text-fig. 7G).

2. Fronto-clypeal suture and transverse line on vertex behind the eyes absent ; transverse groove on gular region usually present (Text-fig. 7G).

3. Mandible with well developed mola ; maxillary galea narrow and elongate (Text-fig. 7B) ; ligula poorly developed.

4. Front coxal cavity (Text-fig. 7A) with visible external closure and also an internal closure as in Biphyllidae, Byturidae, Helotidae and many Nitidulidae.

5. Wing with 4 anal veins, sometimes 1st anal vein running into the subcubital fleck (Text-fig. 6B), anal cell and radial cell absent but r-m cross vein present.

6. Elytra, if with regular rows of punctures without scutellary striole.

7. Mesocoxae moderately to widely separated, meso-and matesternal fitting between the mesocoxae either by two closely situated knobs (Text-fig. 6G) or in a straight line (Text-fig. 6D). Mesoepisternal pockets and other meso- and metasternal pits or pockets absent.

8. Metendosternite as figured (Text-fig. 6C, 6D).

9. Tarsi (Text-figs. 7E, 7F) with segments 2-3 with or without ventral lobes. Trochanters either short and broad or elongate and rather narrow.

10. Ventrite 1 with a pair of femoral lines.

11. Aedeagus (Text-fig. 7D) of Erotylidae-Languriidae type.

12. Ovipositor (Text-figs. 6E, 6F) rather reduced, of Loberinae-type, with paraprocts valvifers fused with coxites, the styli apical, the latter sometimes obsolete.

13. Species small and pubescent.

Larvae of this group not properly described, Rey (1894) described a supposed *Cryptophilus integer* larva very briefly and without figures, according to his description the larva seems to be rather similar to those of Cryptophagidae, whereas Peyerimhoff (1919) remarked on the great dissimilarity between reared *Cryptophilus* larvae and the Cryptophagid type Later in this paper we described two larvae which may belong to the genus *Xenoscelinus* and *Cryptophilus*. both are indeed very unlike a Cryptophagid larva.

Tribe CRYPTOPHILINI Casey

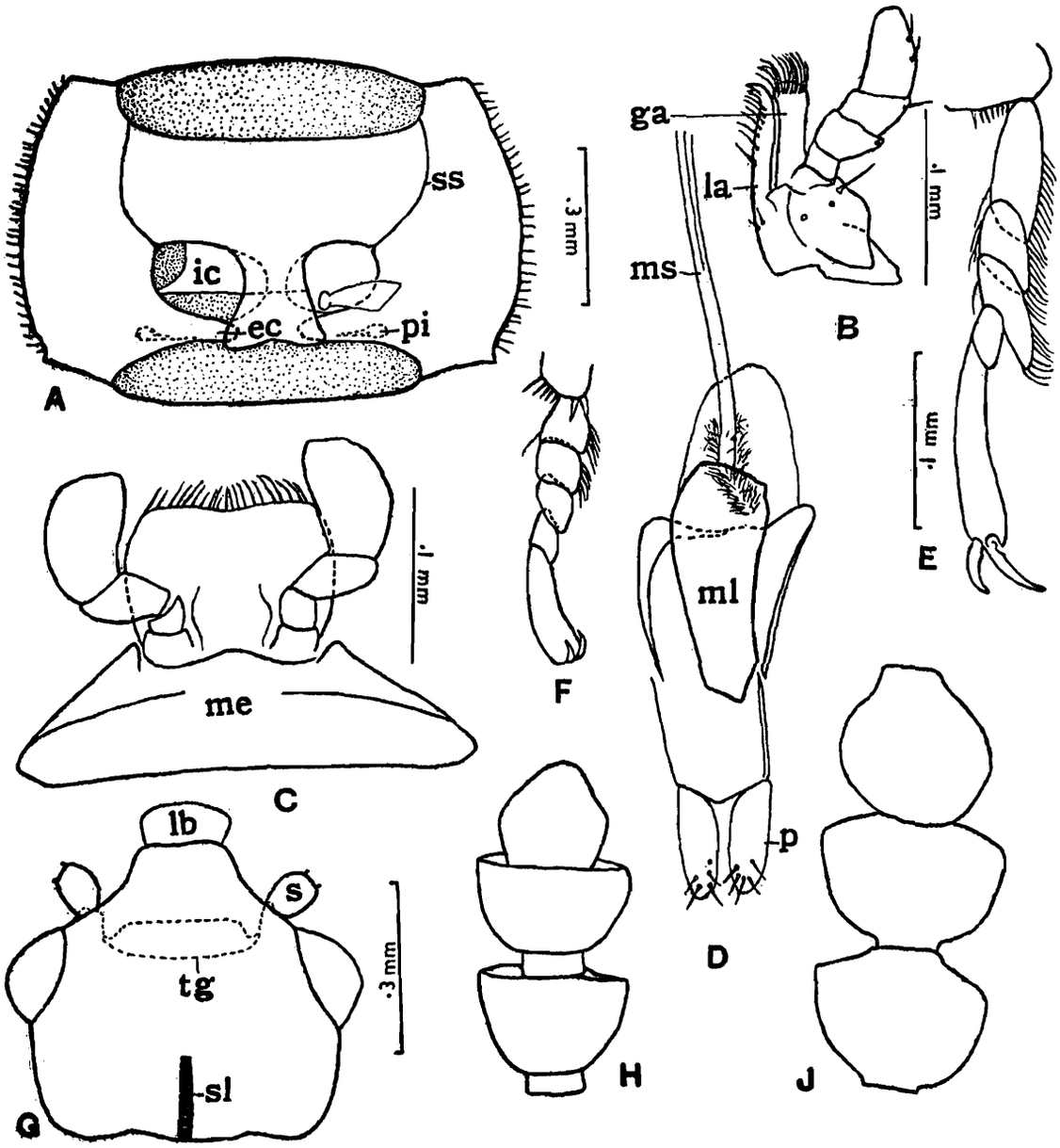
This group consist of two genera, *Cryptophilus* and *Coelocryptus*. Distinguishing features for the tribe are given in the key.

1. Genus **Cryptophilus** Reitter (1874)

Type : *C. integer* Reitter.

With general characters of Languriidae and of Cryptophilinae-Cryptophilini.

This problematic genus includes a rather uncertain number of species, recorded from most of the parts of world, mainly from warmer temperate and subtropical climates. Grouvelle (1919) excluded *C. alluaudi* Grouv. on account of its open front coxal cavities and established a new genus *Cryptophagops* for it ; he synonymised *C. ceylonicus* Motsch., *C. frater* Grouv., and *C. propinquus* Reitt. with *C. integer*, also *C. brahminus* Motsch. with *C.*



TEXT-FIG. 7. A. Prothorax, ventral view of *Cryptophilus obliteratus ;* B. Right maxilla. dorsal view of *Xenoscelinus maculosum ;* C. Labium, ventral view of *Xenoscelinus australiensis ;* D. Aedeagus of *Coelocryptus mexicanus ;* E. Hind tarsi of *Cryptophilus obliteratus ;* F. Hind tarsi of *Xenoscelinus maculosum ;* G. Head, dorsal view of *Cryptophilus obliteratus ;* H. Antennal club of *Xenoscelinus australiensis ;* J. Antennal club of *Xenoscelinus muaculosm.*

obliteratus Reitt. More recently Bruce (1953, 1957, 1959, 1961 and 1963) described 8 species from Africa, later he transferred 3 of the species, *C. leonensis*, *C. mnionomoides* and *C. allotrius*, to the genus *Cryptophagops* Grouv.; considering the previous facts there appear to be 13 species of this genus at present valid.

General appearance similar to Cryptophaginae. Head as figured (Text-fig. 7G), occipital region pale and impunctate, the boundary between it and the punctured vertex forming an almost straight transverse line behind the eyes ; stridulatory file single and narrow (in *C. integer* female and *C. obliteratus* female with about 20 ridges in ·03 mm.). Antennal insertions hidden by frons, segments 1-8 alternately weakly longer and shorter, segments 9 and 10 weakly transverse, terminal one more or less rounded and slightly less transverse than preceding two segments. Mandible with two apical teeth, one of them bifid ; maxilla as figured (Text-fig. 7B), lacinia with two apical spines : labium with mentum transverse, apical segment of palpi more or less securiform, ligula poorly developed. Prothorax (Text-fig. 7A) strongly transverse, hind angles acute, prosternal process with apical margin angularly emarginate ; prebasal impressions on pronotum present. Elytra with puncturation irregular, pubescence rather dense and semi-recumbent. Wing as figured (Text-fig. 6A). Mesocoxae moderately separated, meso-and matasternal fitting between the mesocoxae with two closely situated knobs (Text-fig. 6G). Metasternum weakly transverse, median impressed line extending about 2/3 of its length ; metendosternite with basal stalk very broad and short, anterior tendons widely separated, lateral plates absent. Legs narrow and long, tarsi (Text-fig. 7E) with segment 1 distinctly longer than segment 2, which is not lobed, segment 3 strongly lobed below, segment 5 as long as 1st 3 segments together ; trochanters elongate and rather narrow. Intercoxal process of 1st ventrite broad, its apex rounded. Ovipositor short as figured (Text-fig. 6F).

The only species for which there is any available information about habits and habitat is *C. integer*. Hinton (1945) cites a number of records of this species from stored food products. According to Peyerimhoff (1919) it is essentially mycophagous, he records it from decaying vegetation in Algeria, and also reared adults of this species from larvae found in association with those of *Ceroplatus* fungus-gnats on the under side of the bracket-fungus *Polyporus* (? *Fomes*) *fomentarius*. Rey (1894) had previously reported adult *C. integer* with supposed larvae (according to Peyerimhoff (*l.c.*) wrongly identified) under dead leaves in France in October. We have seen adults of *C. integer* or a very similar form collected under a heap of dead grass near Brisbane Australia, by R. A. Crowson.

2. Genus **Coelocryptus** Sharp (1900)

Type : *C. mexicanus* Sharp

With general characters of Languriidae and of Cryptophilinae-Cryptophilini.

This genus includes 4 species described by Sharp (1900), all from the New World. *C. mexicanus* male has been studied in details by slide preparation. General appearance resembling species of *Toramus*. Head very similar to *Cryptophilus*, except that weak tempora are present behind the eyes ; stridulatory file with about 18 ridges in ·03 mm. ; unlike *Cryptophilus* dorsal side of head without sharp demarcation between smooth occipital region and punctured vertex. Antenna more slender and longer, segments 1-8 more markedly alternately longer and shorter, club rather loose, shaped as in *Cryptophilus*, mouth parts similar to those of *Cryptophilus*. Prothorax much narrower than elytra, very weakly transverse, narrowed posteriorly, side margins smooth, front angles rounded, posterior angles not acute. Front coxal cavities and prosternal process as in *Cryptophilus ;* prebasal impression on pronotum well marked. Elytra with punctures in more or less regular rows, pubescence dense and recumbent. Wing as in *Cryptophilus* (Text-fig. 6A). Meso-and metasternal fitting between the mesocoxae and metendosternite as in *Cryptophilus* ; metasternum more transverse than in latter. Legs longer, and femora narrower than in *Cryptophilus*, tarsi with 1st 3 segments lobed below, progressively shorter

in length, segment 4 minute, segment 5 slightly shorter than 1st 3 together, trochanters as in *Cryptophilus*. Intercoxal process of 1st ventrite broad and truncate at apex. Aedeagus as figured (Text-fig. 7D).

Habitat: Unknown, larva undescribed.

XENOSCELININI trib. nov.

According to the present knowledge this group includes only one genus, which consists of five species, one of which described as new, all from the Old World. The species *maculosum* was attributed by Broun (1881) to *Paramecosoma* (Cryptophagidae). Bruce (1943) stated that *Paramecosoma maculosum* Broun is very similar to *Xenoscelinus malaicus* Grouvelle, except in body colour. More careful study reveals that *P. maculosum* has tarsal formula 5-5-5 in both sexes, whereas Grouvelle (1910) described *Xenoscelinus malaicus* as having 5-5-4 tarsi in the male. The combination of heteromerous tarsi in the male with both front and middle coxal cavities closed is not known in other Clavicornia. We have studied *Xenoscelinus bicolor* and found tarsal formula 5-5-5 in both sexes as in other species of the genus *Xenoscelinus*. We consider that Grouvelle may have been mistaken about the tarsi of male *malaicus*.

1. Genus **Xenoscelinus** Grouvelle (1910)

Type : *X. malaicus* Grouvelle (1910)

With general characters of Languriidae and of Cryptophilinae-Xenoscelinini.

General appearance more or less as in *Cryptophilus*, except that the elytra have regular rows of punctures. Head more or less as in *Cryptophilus* except that the stridulatory file is absent ; transverse groove on gular region sometimes present. Antenna with scape moderately large, pedicel shorter than scape and segment 3, segments 4-8 equal or alternately slightly longer and shorter, club 3-jointed, shape as figured (Text-figs. 7H, 7J). Mouthparts more or less similar to those of *Cryptophilus*, except mentum more transverse and apical segment of labial palpi more elongate and less truncate at apex (Text-fig. 7C). Prothorax transverse, side margins slightly undulate, front angles rather obtuse and hind angles acute, prosternal process broad with apical margin straight. Prebasal impressions on pronotum present. Elytra with strial punctures in regular rows, with fine and recumbent pubescence or glabrous. Wing with first anal vein running into subcubital fleck (Text-fig. 6B). Mesocoxae widely separated ; meso-and metasternal fitting between the mesocoxae in as traight line (Text-fig. 6D) ; median impressed line of metasternum extending two-thirds of its length or more. Metendosternite as figured (Text-fig. 6D). Legs of moderate length, tarsal segments not lobed below, first three segments more or less equal in length, segment 4 slightly shorter than segment 3, segment 5 about equal to first four together ; tibiae moderately long, slightly broadened at apex with two normal spurs ; trochanters broad and short (Text-fig. 6D) or slightly elongate. Intercoxal process of ventrite 1 broad with rounded apical margin. Aedeagus similar to that of *Coelocryptus* (Text-fig. 7D). Ovipositor reduced as figured (Text-fig. 6E).

Geographical distribution: India, Sumatra, Australia and New Zealand.

X. australiensis sp. n.

With general characters of Cryptophilinae and of Xenoscelinini-*Xenoscelinus*.

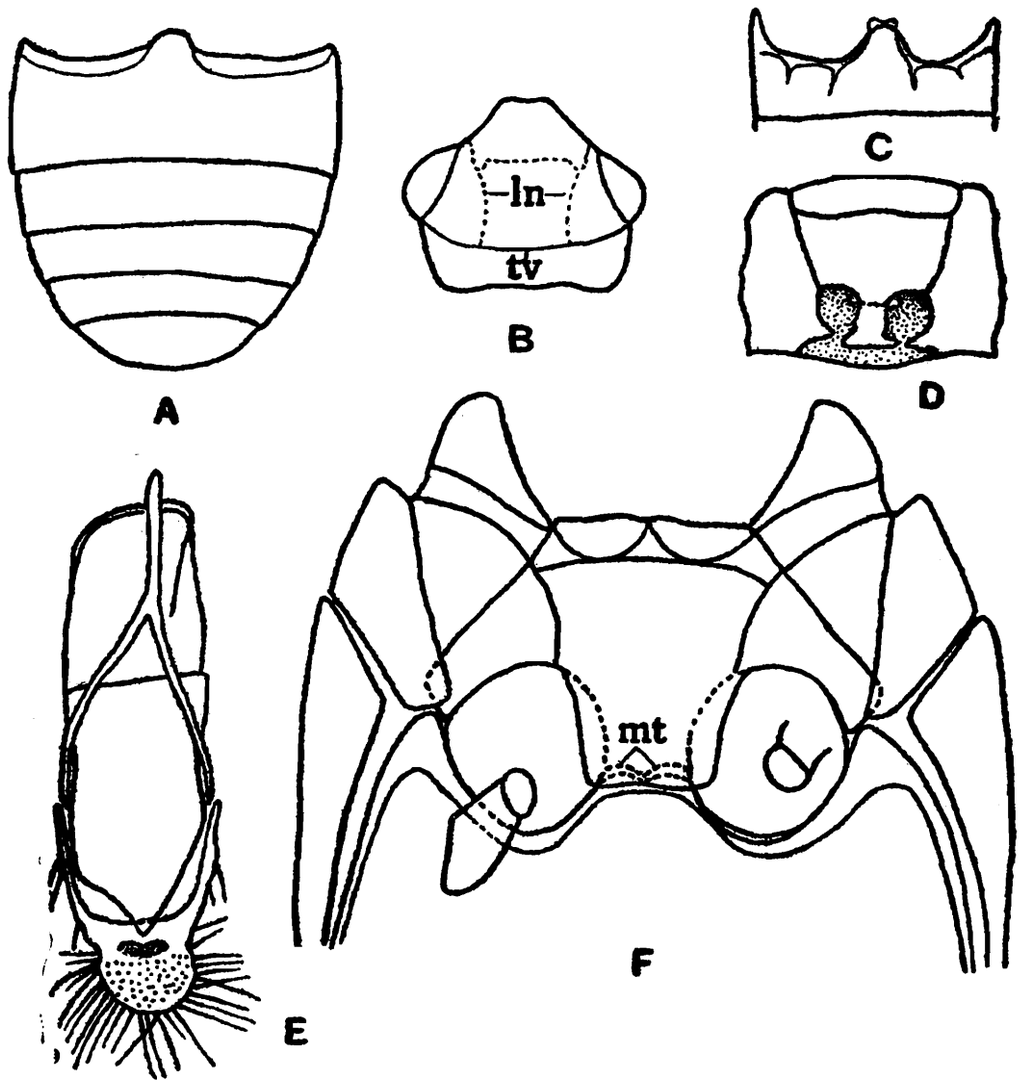
Over-all length 2·00 mm. to 2·60 mm. width of head across the eyes ·66 mm. ; length of antenna ·58 mm.; width of prothorax across the front margin ·88 mm. and across the posterior margin ·66 mm.; length of elytra 1·36 mm. and maximum width across the middle 1·00 mm.

Species of narrow elongated Cryptophagid-like appearance, with blackish head and pronotum, elytra ochreous brown. Head weakly transverse, dorsal surface very finely punctured and glabrous ; front margin of clypeus rather straight ; eyes not very big and finely facetted. Antennal insertions hidden under frons, antenna rather short with scape about twice as long and wide as pedicel, which is slightly shorter than segment 3, segments 4-8 equal in length, shape of the club as figured (Text-fig. 7H). Prothorax transverse, narrowed posteriorly ; pronotal punctures as in vertex of head, pubescence fine, directed towards centre. Scutellum minute, transverse and glabrous. Elytra with strial punctures in regular rows, somewhat confused towards the apex and side margins, punctures of interstices irregular near the base and apex, pubescence short and recumbent. On the ventral side punctures on thoracic sternites are more distinct than those of on ventrites. Femoral lines on first ventrite well developed extending to the apex.

Habitat : Under the fungusy bark of logs, in Lamington National Park, Queensland (Australia), collected by R. A. Crowson. Holotype and five paratypes in British Museum collection.

Key to the available species of *Xenoscelinus.*

1. Elytra with three dark spots, one on the centre of each elytron, third one shared at the apex. Trochanters more elongate, and antennal club as figured (Text-fig. 7J). Prothorax slightly narrowed in front. *X. maculosum* Broun.



TEXT-FIG. 8. A. Ventrites, ventral view of *Henoticus serratus* ; B. Head, dorsal view of *Cryptophagus* sp. ; C. First ventrite of *Bolerus minutus* ; D. Prothorax, ventral view of *Platycladoxena minutus* ; E. Aedeagus of *Atomaria fimetarii* ; F. Mesosternum and anterior part of metasternum, ventral view of *Thallis compta.*

Elytra unicolorous. Trochanters short and broad, and antennal club different, as figured (Text-fig. 7H). Pro-thorax narrowed behind. .. .2.

2. Species broader; eyes larger with comparatively large facets. Elytra glabrous and punctures on intertices absent. ....*X. bicolor* Grouvelle

Species narrower and more elongated; eyes smaller with finer facets. Elytra pubescent, punctures on interstices present. .*X. australiensis* sp. n.

The adult of *X. maculosum* has been recorded by one of us, R. A. Crowson, under the bark of dead Tawa trees (*Beilschmiedia*) from Te Aroha (New Zealand).

Larvae of Cryptophilinae :—

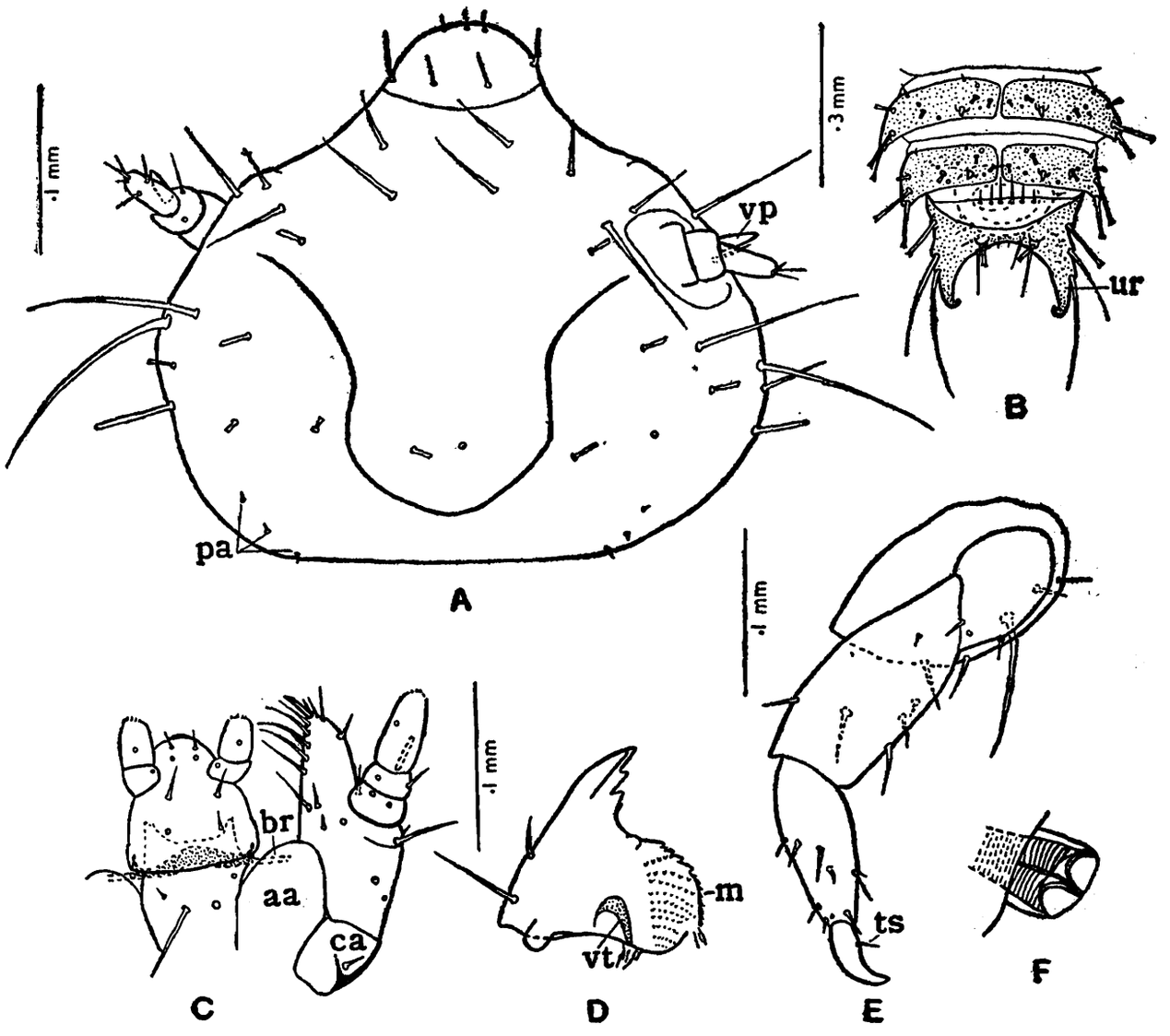
Two larvae were collected by one of us (R. A. Crowson), one (*Xenoscelinus australiensis ?*) from Lamington National Park, Queensland, Australia, September 2, 1966, in fungusy bark of logs; adults of *X. australiensis* were collected from a similar habitat in the same area. The other larva (*Cryptophilus integer* ?) was collected from marshy *Eucalyptus-Casuarina* forest, Strathpine, Brisbane, Queensland, Australia, August 26, 1966, under fungusy bark of a log, adults of *Cryptophilus* had been found previously under a pile of dead grass in a nearby area of South Queensland. It is to be noted that Peyerimhoff (1919) reported *Cryptophilus integer* adults from dead grass etc. in North Africa and reared adults from the larvae found in a fungus on a tree in a marshy area. The larva of *X. australiensis* is described below in full and distinguishing features of *Cryptophilus* larva also indicated.

Description of a supposed *Xenoscelinus australiensis* larva.

Overall length 1·90 mm.; width of head across the midle about 0·6 mm.; width of third abdominal segment 0·44 mm.; width of ninth abdominal segment across the midde 0·24 mm.

General body form moderately elongate, somewhat depressed and dorsally flattened, slightly narrowed in front and behind. Dorsal surface of each segment with a transverse brownish granulated area divided in the middle line, on either side of this line is a setiferous tubercle. Each abdominal segment with the posterior angles projecting posteriorly and bearing two fairly long frayed setae (Text-fig. 9B). Head transverse, side margins evenly rounded, shape of frontal suture and arrangement of setae on dorsal surface as figured (Text-fig. 9A). Endocarina and metopic suture absent. Setae on posterior half of head short and blunt, on anteror half and towards sides, setae more elongated and pointed; at the base, on either side of occipital foramen with three microscopic peg-like setae (Text-fig. 9A). Five distinct ocelli present, three in a vertical row behind the antenna, other two form a second row behind it, sixth one is obscured. Antenna (Text-fig. 9A) rather short, length of the segments 1 : 1 : 2, sensory appendage lying ventrally, about two-thirds of the length of segment 3. Mandible (Text-fig. 9D) with two unequal apical teeth, the larger one dentate on its inner margin. Mola well developed with nine rows of asperites, inner margin finely serrated, its basal part hairy. Prostheca between mola and apical teeth absent; ventral crushing tubercle well developed. Maxillary mala (Text-fig. 9C) moderatey sharply pointed at a pex, with a strong spine at tip; at base of apical spine on outer margin with two setae, another seta present on outer margin behind these two setae. A row of about seven setae present along the dorsal side of inner margin. Cardo well developed, indistinctly divided in the middle. Maxillary articulating area (Text-fig. 9C) well defined and oval. Labium (Text-fig. 9C) free as far as base of mentum; palpi two-jointed. Hypopharynx moderately well developed, with two short anterior horns; hypopharyngeal bracon present. Prothorax about as broad as head, narrower and longer than meso- and metathorax, which are as broad as first five abdominal segments but longer. Abdominal segments 6-9 progressively narrower.

N.B. Grouvelle (1919) described *X. bicolor* and *X. concolor*, but he did not compare them with *X. malaicus*. We have seen only one species of Grouvelle (*X. bicolor*) and have not been able to include in our key the other two species, which may be near to *X. australiensis*.



TEXT-FIG. 9. Larva of *Xenoscelinus australiensis* A. Head, dorsal view; B. Posterior segments, dorsal view; C. Right maxilla and labium, ventral view: D. Right mandible, ventral view; E. Front leg; F. Mesothoracic spiracle.

Pronotum with three transverse rows of short frayed setae, each row with six setae, each side margin with four long setae. Arrangement of setae of meso- and metathorax as in abdominal segments (Text-fig. 9B). Urogomphi (Text-fig. 9B) well developed, directed rather posteriorly, apical half curved dorsally to form a hook, their inner margins forming a continuous curve and with a pair of long pointed setae, outer margins bearing three long setae, posterior two are pointed at apex. At the base of urogomphi on either side of middle line, with a tubercle bearing frayed setae. On front part of ninth tergite with six internal tapering tubes projecting anteriorly (Text-fig. 9B). Pygopod small and projecting.

Spiracles (Text-fig. 9F) bicameral borne on short tubes, projecting postero-laterally from posterior half of each segment.

Legs moderatey widely separated, rather short, claws with single tarsungular seta (Text-fig. 9E).

Single specimen in Glasgow University Zoological Department.

Difference between supposed *X. australiensis* and *Cryptophilus integer* larvae.

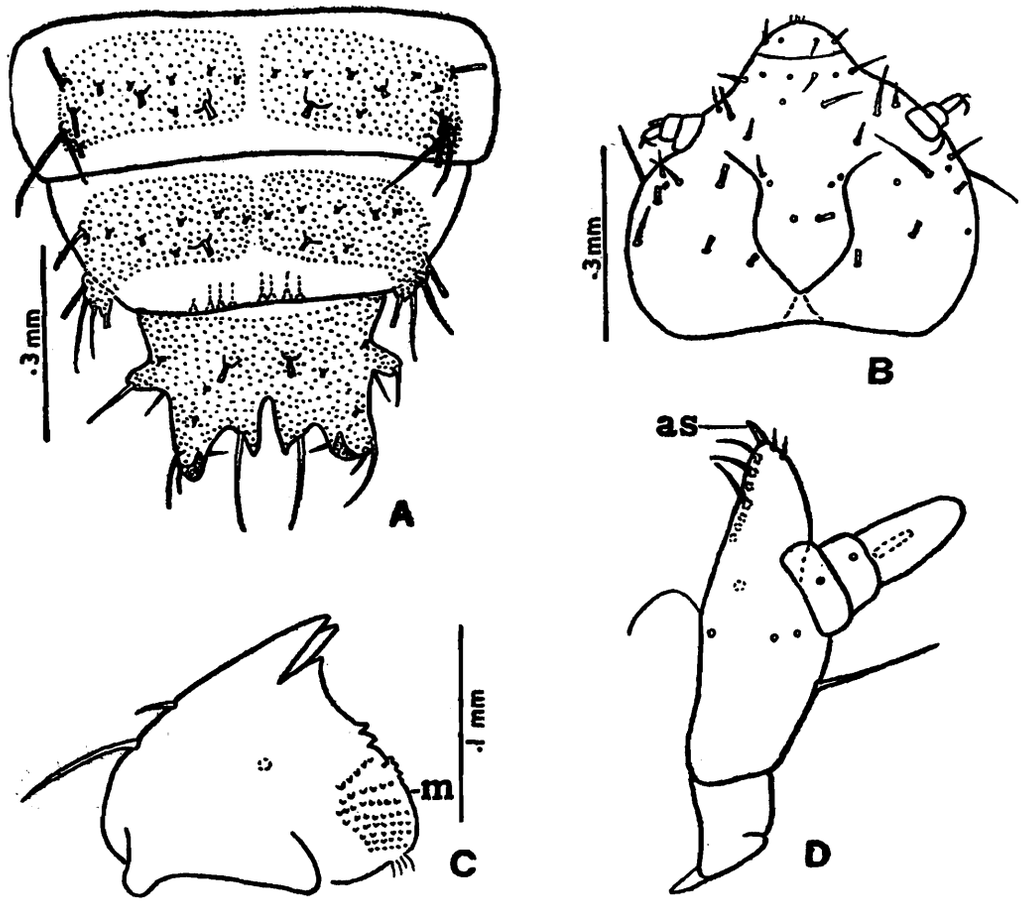
Shape of segment 9 with urogomphi as figured (Text-fig. 9B). Arrangement of setae and shape of frontal a sutures on dorsal side of head as figured (Text-fig. 9A). Ocelli 5 on each side behind the base of antenna (larva smaller, 1·90 mm. in length).

Xenoscelinus australiensis sp. n.

Shape of segment 9 with urogomphi are different, a' figured (Text-fig. 10). Arrangement of setae and shape of frontal sutures on dorsal side of head are different, as figured (Text-fig. 10B). Ocelli six on each side behind the base of head are different, 4·16 mm. in length).....*Cryptophilus integer* Reitter

XI —TABULATION OF TAXONOMIC CHARACTERS IN LANGURIIDAE AND RELATED FAMILIES

In order to elucidate the natural (phylogenetic) affinities of the families, we need first to distinguish the characters which are primitive from those which are derived. Supposedly primitive characters are represented by white squares, derived characters by black squares when modifications take two different forms, the derived characters are represented by two different half-black squares ; cross-hatched squares indicate both primitive and derived conditions within the same group. We are less sure about the primitive condition of characters which are marked with an asterisk. In some cases the derived condition seems to be subject to secondary loss, possible instances of this will be discussed in connection with the charts concerned. Again in some cases a character may be primitive in one family whereas in another it may be developed secondarily. For this reason, this type of matrix analysis, which underlies the procedures of 'numerical taxonomy', can sometimes lead to false conclusions.

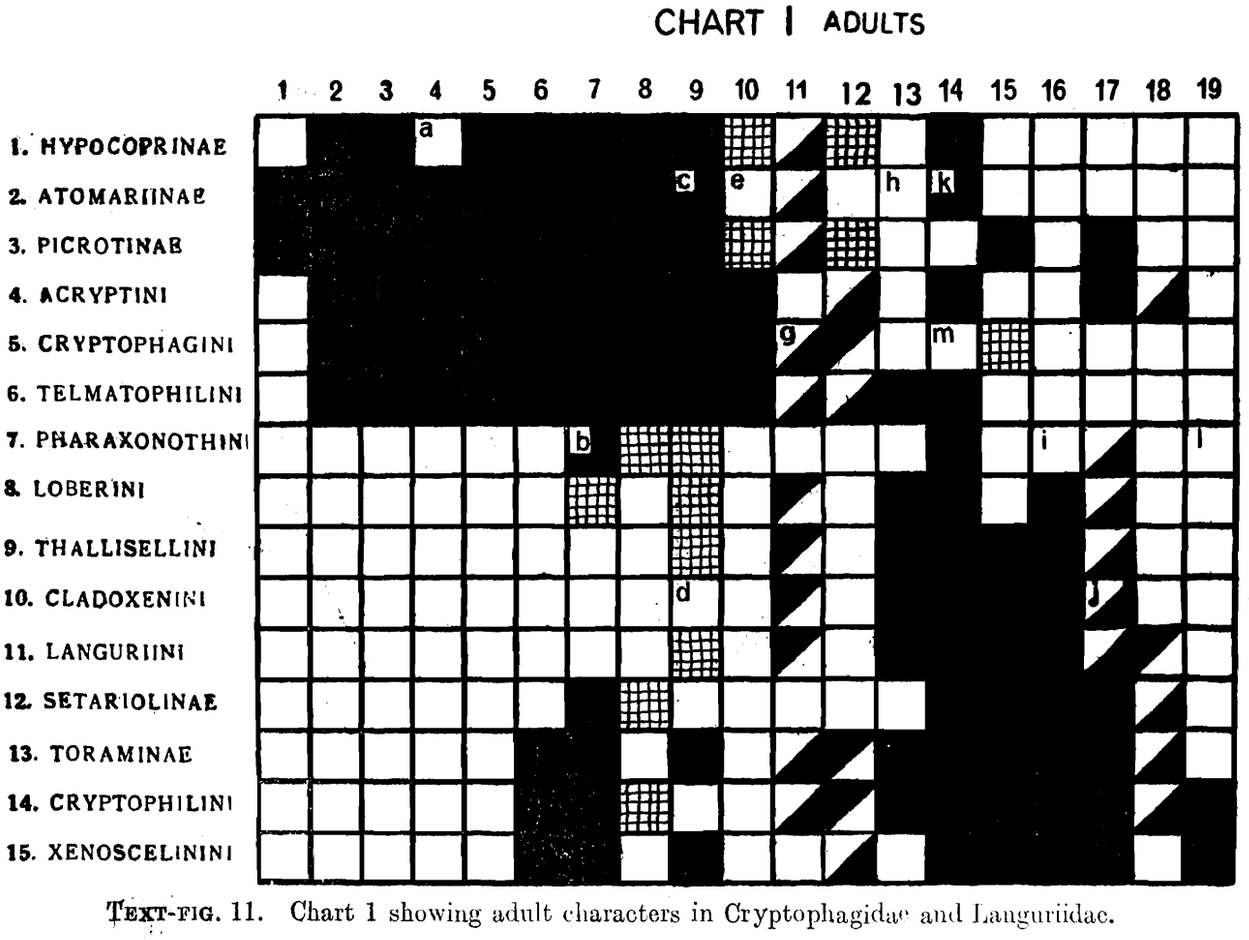


TEXT-FIG. 10. Larva of *Cryptophilus integer*(?) A. Posterior segments, dorsal view ; B. Head, dorsal view ; C. Right mandible, ventral view ; D. Left maxilla, dorsal view.

The adult characters have been tabulated in chart 1 and 2, and those of larvae in chart 3. We have not had time to study the families of the Cerylonid group in detail, but the family Endomychidae, the genus *Sphaerosoma*, and the Cerylonidae-Euxestinae between them probably show as much similarity to Languridae as there is to be found in the group as a whole, hence we have tabulated the characters of these group in our charts 2 and 3. (Text-figs. 12, 13).

CHART 1 (Text-fig. 11)

Nineteen selected characters are represented by numbered columns, while fifteen tribes and subfamilies of Cryptophagidae and Languriidae correspond to the rows. We are less sure about which condition is primitive in columns 3, 4, 9, 10, 11, 13, 15 and 16, than the others. In Cryptophagidae the ancestral forms probably did not have the subcubital fleck in their wing (column 3), or cephalic stridulatory files (column 9), which are indicated by black squares (derived characters), stridulatory files may have developed independently in *Atomaria*. The transverse groove (column 16) on anterior part of gular region is absent in all Cryptophagidae and present in most of the Languriidae, probably the ancestors of Cryptophagidae never possessed this character, whereas its absence in some Languriidae might be a result of secondary loss, though this absence is indicated by the same white square in Languriidae as in Cryptophagidae. A comparable example is longitudinal grooves on the anterior part of the gular region (column 10), whose presence in Cryptophagidae is indicated by black squares and their absence by white in Languriidae, the absence of these grooves in some Cryptophagidae is probably a secondary condition. The modification of sternal fitting between mesocoxae (column 12) takes two different forms (double knobs or a straight line). The trochanters (column 11) may be narrow and long, broadly elongate or short and broad, making a difficult character to show in the chart. In the former character, both the derivative conditions may occur in the same subfamily, e.g. rows 14 and 15, and rows 4, 5 and 6. The short trochanters found in Cryptophagidae *Antherophagus* (row 5, column 11) is probably a derived character, whereas in Languriidae the short and broad



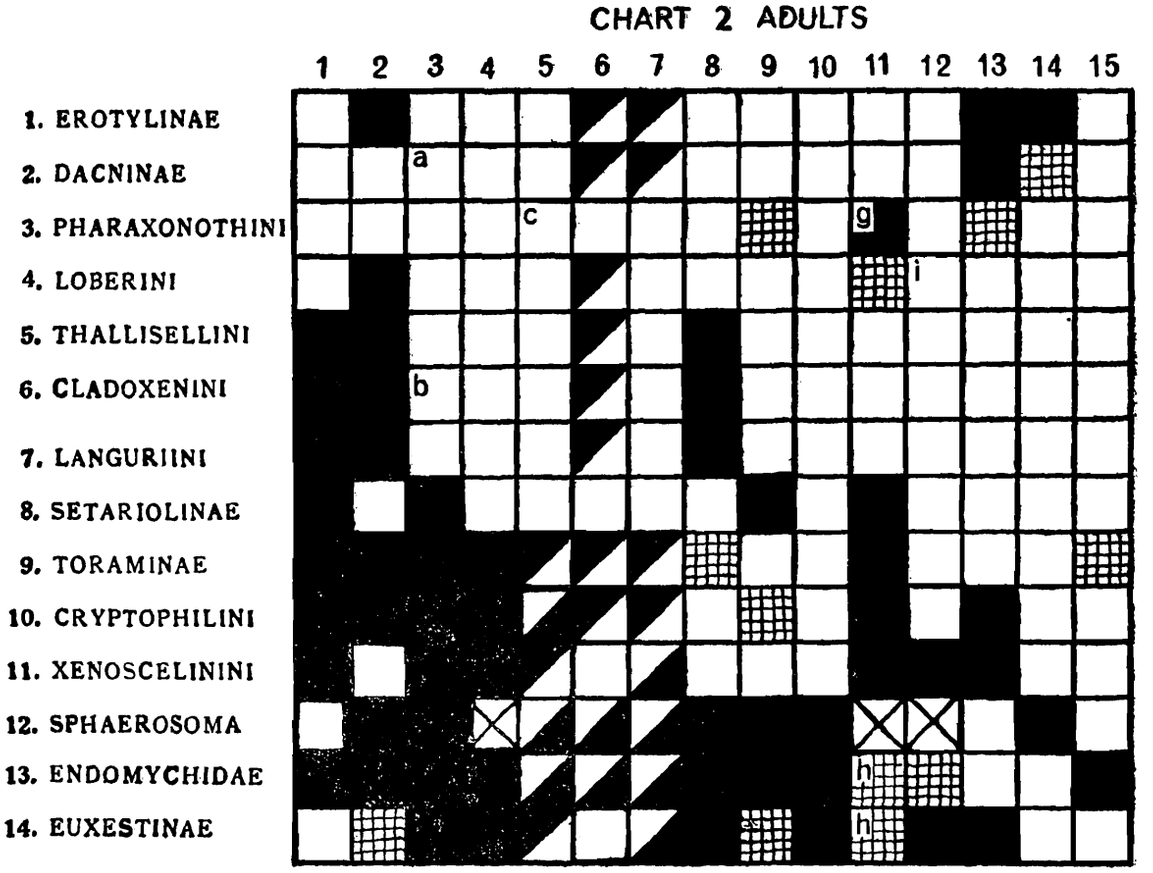
TEXT-FIG. 11. Chart 1 showing adult characters in Cryptophagidae and Languriidae.

trochanters of Pharaxonothini (row 7 and column 11) may be primitive. However, in spite of such difficulties, it is evident from this chart that Cryptophagidae and Languriidae are very distinct groups, as shown by the strong demarcation line between rows 6 and 7. According to this chart Pharaxonothini (row 7) is the most primitive group of those tabulated.

The geographical distribution of Pharaxonothini also suggests considerable antiquity of the group (*see* Text-fig. 14, Fig. A).

CHART 2 (Text-fig. 12)

Eleven subfamilies and tribes of Erotylidae and Languriidae, together with the genus *Sphaerosoma*, the family Endomychidae and the subfamily Euxestinae (Cerylonidae) are represented by the fourteen rows, while fifteen selected characters are represented by numbered columns. The primitive condition of the characters in columns 1, 2, 6, 8, 12 and 13, is more doubtful. The separations between the families appear much less sharp than that between Cryptophagidae and Languriidae shown in chart 1. According to this chart Pharaxonothini (row 3) and Loberini (row 4) could be included within Erotylidae, as the separation between rows 4 and 5 is at least as sharp as between rows 2 and 3. The rows 9, 10 and 11, Toraminae, Cryptophilini and Xenoscelinini form a group with clear similarities to rows 12 and 13, *Sphaerosoma* and Endomychidae, but the separation between rows 11 and 12 seems to be slightly sharper than that between rows 7 and 9 (row 8 represents a rather aberrant group). This chart seems to justify a family division between rows 11 and 12 but hardly suggests a higher level division at this point. Among the Languriidae the sufamily Setariolinae (row 8) shows several dissimilarities from other groups of Languriidae and it is probably justified to treat it as a separate family. The anal cell of wing (column



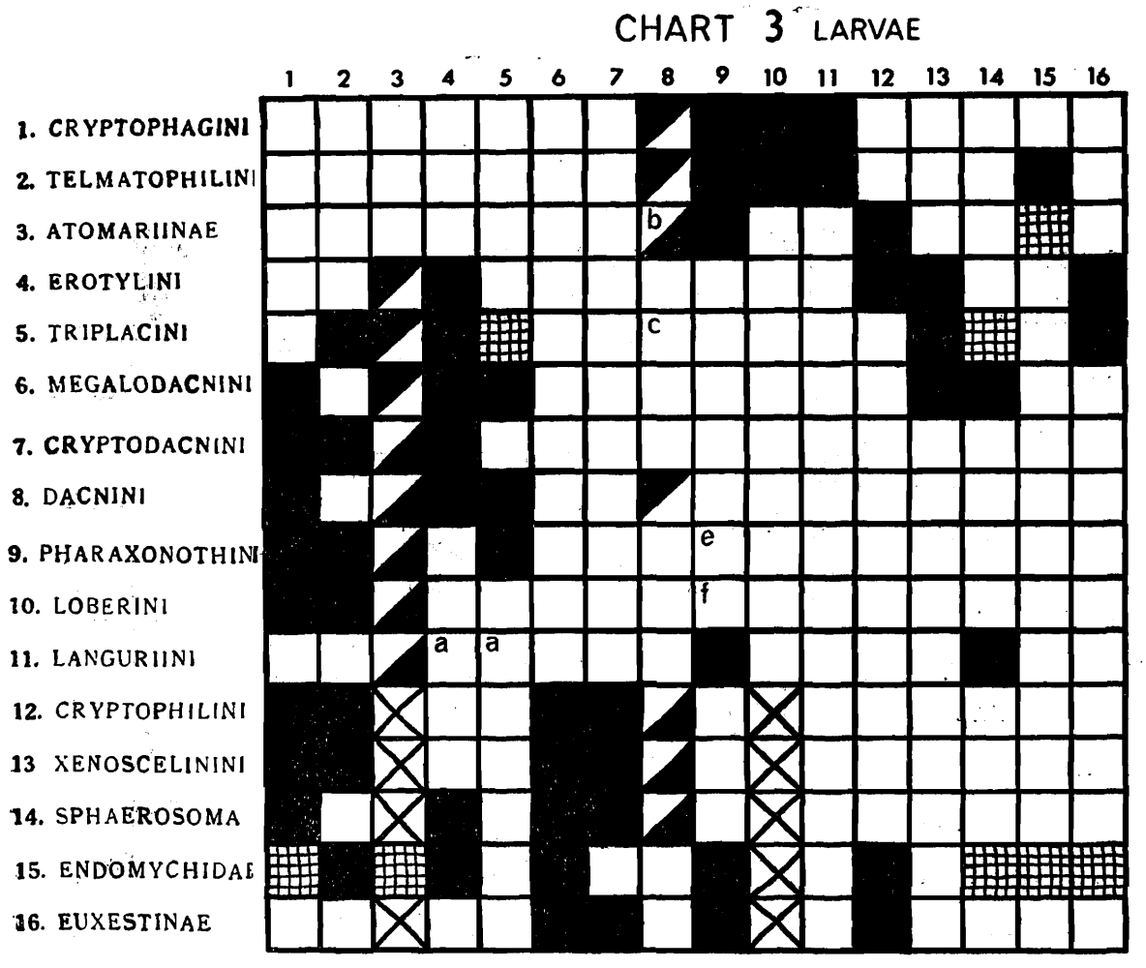
TEXT-FIG. 12. Chart 2 showing adult characters in Erotylidae, Languriidae, Sphaerosoma, Endomychidae and Euxestinae (Cerylonidae).

11) found in some Endomychidae and Euxestinae may not be homologous with that found in Erotylidae-Languriidae. The separation between Erotylidae, rows 1 and 2, and Languriidae, rows 3—11, is evidently far less sharp than the Cryptophagidae-Languriidae one in chart 1 (Text-fig. 11).

CHART 3 (Text-fig. 13)

The known larvae of the tribes and subfamilies of Cryptophagidae, Erotylidae, Languriidae, together with larvae of *Sphaerosoma globosa*, Endomychidae and a supposed larva of

Euxestus are represented by sixteen rows, and sixteen selected characters by columns. Like chart 1, the larval chart shows that Cryptophagidae (rows 1—3) are clearly different from the rest. The tribes Pharaxonothini of Languriidae (row 9) and Dacnini of Erotylidae (row 8) are very closely related. On the other hand, the supposed larvae of Cryptophilini and Xenoscelinini (rows 12 and 13) show several similarities to *Sphaerosoma globosa* and Endomychidae (row 14). We are less sure which are derived and which are primitive conditions in column, 1, 2, 3, 8, and 10. The absence of granulated upper surface in Languriinae (row 11, column 1), represented by a white square, is not likely to be a primitive condition, but it is probable that the absence of granulation on the upper surface of larva is a primitive condition in Cryptophagidae. From the characters tabulated in this chart, it is by no means evident that the most natural dividing lines (other than that between Cryptophagidae and Languriidae) should be drawn between rows 8 and 9, or 13 and 14– a line between rows 11 and 12, and perhaps one between 10 and 11, would seems to be the most obvious divisions. The apparent gap between taxa 10 (Loberini) and 11 (Languriini) might well be bridged by the as yet unknown larvae of Cladoxenini and Thallisellini, and it is possible that the



TEXT-FIG. 13. Chart 3 showing larval characters in Languriidae and related families.

equally unknown larvae of Toraminae may do something to bridge the gap between taxa 10 Loberini) and 12 (Cryptophilini).

CHART 1 (Text-fig. 11)

Antennal insertions
on top of head—■
on sides of head—□

2. *Elytral epipleura*
incomplete—■
complete—□

*3. *Subcubital fleck (wing)*
present—□
absent—■

*4. *Aedeagus*
Cryptophagidae-type—■
Languriidae-type—□

CHART 1 (Text-fig. 11)

5. *Ventrites*
   1 longer than 2—■
   1 equal to 2—□

6. *Radial cell (wing)*
   absent—■
   present—□

7. *Anal cell (wing)*
   absent—■
   present—□
   present/absent—▦

8. *Elytral puncturation*
   irregular—■
   regular—□
   irregular/regular—▦

*9. *Stridulatory files on head*
   absent—■
   present—□
   absent/present—▦

*10. *Longitudinal grooves on gular region*
   present—■
   absent—□
   present/absent—▦

*11. *Trochanters*
   narrow and long—◪
   broadly elongate—◪
   short and broad—□

12. *Sternal fitting between mesocoxae*
   double knobs—◪
   straight line—◪
   single knob—□
   doule knobs/straight l ne—▦

*13. *Tarsi*
   lobed—■
   simple—□

14. *Tarsal formula*
   5-5-5 in both sexes—■
   5-5-4 in male—□

*15. *Front coxal cavities internally*
   closed—■
   open—□
   closed/open—▦

*16. *Transverse groove on gular region*
   present—■
   absent—□

17. *Anterior tendons of metendosternite*
   widely separated—■
   narrowly separated—◪
   contiguous—□

18. *Lateral plates of metendosternite*
   absent—◪
   very broad p'ate-like—◪
   narrow—□

*19. *Front coxal cavities externally*
   closed—■
   open—□

Exceptions

a. In *Hypocoprus*, where aedeagus turned on one side but somewhat different from Erotylidae-Languriidae b. *Xenocryptus*, c. few species of *Atomaria*, d. *Microlanguria*, e. *Paratomaria*, a undescribed genus from New Zealand, g. *Antherophagus*, h. *Para- tomaria*, i. *Othniocryptus*, j. *Paracladoxena*, where anterior tendons very widely separated, k. *Caeno- scelis*, l. *Xenoscelis*, m. few species of *Cryptophagus* and *Micrambe*.

CHART 2 (Text-fig. 12)

*1. *Front coxal cavities internally*
   closed—■
   open—□

*2. *Tarsi*
   lobed—■
   simple—□
   lobed/simple—▦

3. *Anterior tendons of metendosternite*
   widely separated—■
   narrowly separated—□

4. *Radial cell (wing)*
   absent—■
   present—□

5. *Stridulatory files on head*
   if present single—◪
   always absent—◪
   if present double—□

*6. *Trochanters*
   broadly or narrowly elongated —◪
   short and heteromeroid—◪
   short and simple—□

7. *Sternal fitting between mesocoxae*
   double knobs—◪
   straight line—◪
   single knob—□

*8. *Fronto-clypeal suture* (head)
   present—■
   absent—□
   present/absent—▦

9. *Elytral puncturation*
   irregular—■
   regular—□
   regular/irregular—▦

10. *Tarsal formula*
   4-4-4—■
   5-5-5—□

11. *Anal cell (wing)*
   absent—■
   present—□
   present/absent—▦

CHART 2 (Text-fig. 12)

12. *Anal vein running into subcubital fleck*
yes—■
not—□

*13. *Front coxal cavities internally*
closed—■
open—□
closed/open—▦

14. *Apical segment of maxillary palpi*
securiform—■
not securiform—□
securiform/not—▦

15. *Metasternal pockets*
present—■
absent—□
present/absent—▦

Exceptions

a. *Cryptodacne*, b. *Paracladoxena*, c. *Leucohimatium*, g. *Xenocryptus*, i. *Loberoschema*, h. anal cell rather different than in Languriidae-Erotylidae, X. wingless form, character not applicable.

CHART 3 (Text-fig. 13)

*1. *Dorsal surface*
granulated—■
not granulated—□
granulated/not—▦

*2. *Type of setae on dorsal surface*
various—■
all pointed—□

*3. *Shape of prostheca*
triangular—◪
rounded/irregular—◪
narrow and pointed at apex—□

4. *Maxillary mala*
obtuse—■
falciform—□

5. *Endocarina*
present—■
absent—□
present/absent—▦

6. *Tarsungular setae on claw*
one—■
two—□

7. *Prostheca*
absent—■
present—□

*8. *Antenna*
segment 3 longer than 2—◪
segment 3 equal to 2—◪
segment 3 smaller than 2—□

9. *Ocellioon each side of head*
less than 5—■
5 to 6—□
5-6/less—▦

*10. *Position of tarsungular setae*
one above other—■
side by side—□

11. *Labial palpi*
single jointed—■
two jointed—□

12. *Spiracle*
annular—■
bicameral—□

13. *Mandibular mola*
absent—■
present—□

14. *Metopic suture*
present—■
absent—□
present/absent—▦

15. *Urogomphi*
absent—■
present—□
present/absent—▦

16. *Dorsal row of setae on inner side of maxillary mola*
absent—■
present—□
present/absent—▦

Exceptions

a. *Teretilanguria* b. *Paratomaria*, an undescribed genus from New Zealand, where segments 2 and 3 of antenna are equal in length, c. *Triplax*, where segments 2 and 3 of antenna equal in length, e. *Eicolyctus*, f. *Hapalips prolixus*, X. as prostheca absent and claw with single tarsungular seta, characters not applicable.

XII.—The Place of Languriidae in the Natural System of Clavicornia

A close relationship between Languriidae and Erotylidae, assumed by almost all previous systematists who have considered the group, is fully supported by the results of the present study. The two families seem to be linked particularly by way of the

Pharaxonothini, in which group a whole series of Erotylid-like characters may be seen—in the adult, short trochanters, lack of femoral lines, tendency to loss of mesepisternal pockets, externally (but not internally) closed front coxal cavities in *Xenoscelis*, compact body form and glabrous upper surface (*e.g.* in *Pharaxonotha*), and in the larva a distinct endocarina. It seems perfectly possible that the Erotylidae arose from an ancestor which, if we were able to study it, we should place in Pharaxonothini. If this is so, then the separation of Languriidae (including Pharaxonothini) from Erotylidae as at present accepted would not be phylogenetically justified ; we should either include Erotylidae in Languriidae or transfer Pharaxonothini to Erotylidae. The genus *Cryptophilus*, which we have transferred to Languriidae, has been placed in Erotylidae by certain authors, *e.g.* Hinton (1945) and Crowson (1955); more detailed studies of adults of *Cryptophilus* and related forms and of supposed larvae of Cryptophilinae, have not supported any direct relationship between the group and Erotylidae. The special features of Erotylidae may well be directly or indirectly related to the basic larval habit of living on or in the fruit bodies of the higher fungi, a habit not yet reported for any larvae of Languriidae. This may account for particular similarities between Erotylid larvae and those *e.g.* of the heteromerous *Tetratoma*, which led van Emden to transfer the latter genus to Erotylidae.

Our subfamily Languriinae, it will be noted, includes the former subfamily Cladoxeninae, here reduced to tribal status. It is noteworthy that the genera of Languriinae, unlike *Loberus*, *Hapalips*, *Toramus* etc., are all restricted to the Old World or the New World, not a single one being common to the two. The probable explanation of this is that the genera of Languriinae represent decidedly younger taxa than do most of those in other groups of Languriidae. This in turn may not be unconnected with the fact that the species of Languriinae, are as a rule larger and more strikingly coloured insects than other Languriidae, which makes them more attractive to collectors and predisposes systematists to adopt a decidedly "splitting" attitude in dealing with them, very much as has happened in other "attractive" groups like butterflies, birds, and orchids.

A large part of our Languriidae, including the entire subfamilies Loberinae and Toraminae, has been placed by nearly all previous systematists in Cryptophagidae; this might be taken as *prima facie* evidence that the two families are nearly related. Our studies have revealed, however that the distinction between the two families is perfectly sharp, and that there are remarkably few common "positive" characters which might indicate a particular affinity between them. In adult structure, one might perhaps cite the closure of the middle coxal cavities by the sterna, and perhaps the presence of mesepisternal pockets, as features common to many or all Cryptophagidae and Languriidae but not usually found in primitive Clavicornia, though we are unable to indicate even a single larval character of comparable import. Each of the two families possesses basic derivative features which would seem to preclude it from including the ancestors of the other. In the wings, for example, the Cryptophagid type, lacking a closed Radial cell, could hardly be ancestral to the Languriidae type where this cell is normally complete, and the Languriid type with never more than 4 anal veins could hardly be ancestral to the Cryptophagid wing with its basic number of 5 Anal veins. The front coxal cavities of many Cryptophagidae preserve a primitive condition, unknown in Languriidae, in having a narrow lateral extension exposing a small part of the trochantin, whereas the elytra of typical Languriidae, in possessing complete epipleura and punctured striae, preserve what are probably primitive characters which had been lost in the ancestors of Cryptophagidae.

There can be little doubt that, on the whole, the Cryptophagidae are closer to the "lower" Clavicornia, such as Boganiidae, Cucujidae, Protocucujidae, Rhizophagidae etc., than are Languriidae ; in a serial ordering of the families of Cucujoidae, it would be natural to place Cryptophagidae before Languriidae. The precise relationships of Cryptophagidae, however, seem at the moment more enigmatic than those of Languriidae and call for further, intensive investigation.

Our investigations have provided new, and somewhat unexpected evidences for an affinity of Languriidae to Endomychidae and other families of what one of us (Crowson 1955) has previously called the Cerylonid group. Previous advocates of a relationship between Languriidae and Endomychidae have included Verhoeff (1895) and Arrow (1925), basing their conclusions entirely on the structure of the adults; such an affinity does not seem to have been noticed by previous systematists dealing with the larvae, *e.g.* Böving and Craighead, Rymer Roberts or van Emden.

In general, the best evidence for a natural relationship between two taxa comes from the existence of forms intermediate between them. In the case of Languriidae and Endomychidae, some degrees of intermediacy are manifest in the subfamilies Toraminae and Cryptophilinae, in the family Propalticidae (*see* Crowson & Sen Gupta 1969), in Cerylonidae-Euxestinae and in the genus *Sphaerosoma* (Sphaerosomatidae or Endomychidae). Some of the significant characters of these forms are analysed in our charts numbers 2 and 3. As far as we are aware, there is only one character occurring in Endomychidae or others of the Cerylonid group which might be taken as primitive and which is not found in the Languriidae—that is, the middle coxal cavities not closed outwardly by the sterna. Within the Cerylonid group this character seems to be confined to the Coccinellidae, Endomychidae and the genus *Sphaerosoma*, closed middle coxal cavities being the rule in Cerylonidae, Corylophidae, Merophysiidae, Lathridiidae and Discolomidae. If the Cerylonid group has come from Languriid ancestors, the condition of the middle coxal cavities in Endomychidae etc. must be a secondary one.

In Coleoptera generally, it seems that the development of outwardly closed middle coxal cavities is an evolutionary step which is rarely reversed. In the entire superfamily Curculionoidea we know of no instance where the original closure of these cavities has been lost, and in the Carabidae-Harpalinae the genus *Mormolyce*, supposedly derived from Thyreopterini (*see* Bell 1967) or something close to them, constitutes the only known case where such a change is likely to have taken place. In the Bostrychoidea, closed middle coxal cavities seem to be a fundamental feature, which appears to have been lost only in the Malacoderm-like *Psoa*—in the Anobiidae it is preserved even in the Dascillid-like *Cerocosmus*. In the Heteromera, phylogenetic relations are as yet too uncertain for us to be able to say with any certainity whether closed middle coxal cavities have been lost in any families of that group.

A possibly significant fact is that the middle coxal cavities of *Sphaerosoma*, Endomychidae and Coccinellidae show a small but apparently constant difference from the primitively open ones of such forms as Cucujidae, Sphindidae, Nitidulidae etc.; in these latter groups, the outer anterior angles of the metasternum always overlap (as seen from the ventral side) the apical part of the mes-epimeron (Text-fig. 4E), whereas in Endomychidae etc. the broad apex of the mesepimeron always overlaps the tips of the metasternum (Text-fig. 4F). This difference might perhaps serve to distinguish secondarily from primarily open middle coxal cavities in Clavicornia, and enable us to reconcile the phenomena with Dollo's Law.

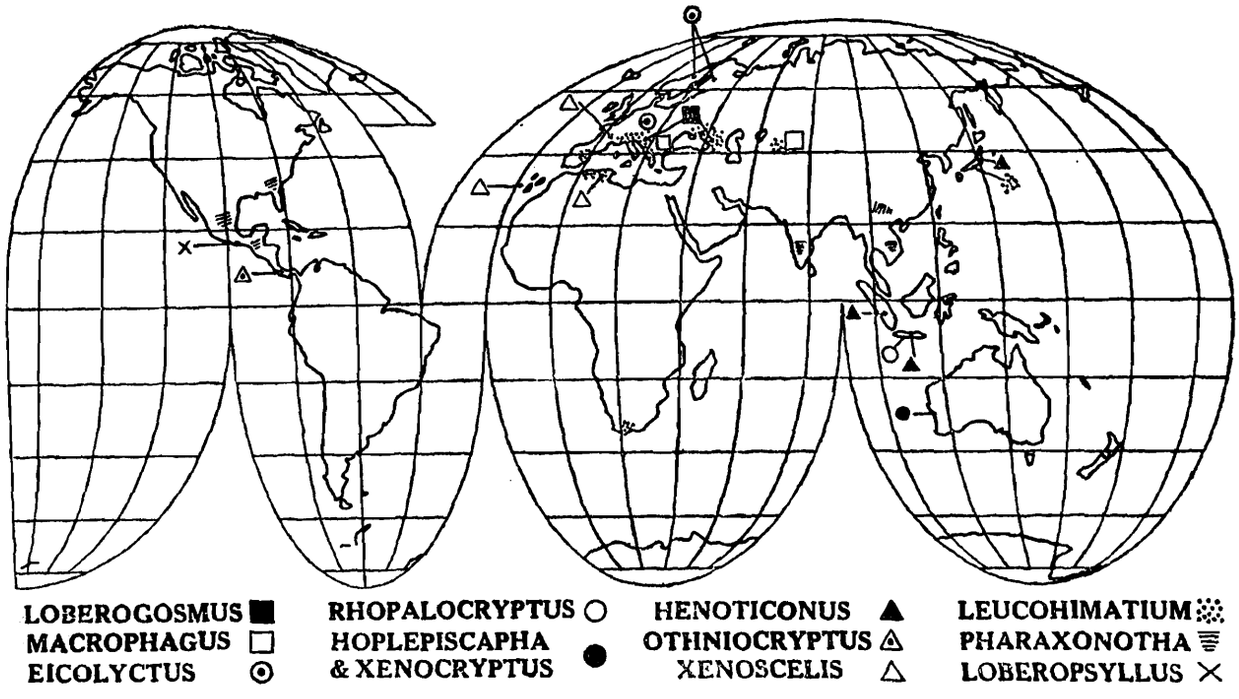
Once it is conceded that the open middle coxal cavities of Endomychidae, etc. might have been derived from closed ones, it becomes possible to derive the entire Cerylonid group from Euxestinae-like ancestors, and these in turn form something akin to Toraminae, Cryptophilinae and Propalticidae (Crowson & Sen Gupta: 1969). An interesting pointer in this direction is the universal absence of a scutellary striole in those members of the Cerylonid group with regular rows of elytral punctures; this character also serves to distinguish the Toraminae and Cryptophilinae from most other sections of our Languriidae. It seems that a scutellary striole, once lost, is rarely regained. Such a derivation is perfectly consistent with the characters of the larvae as far as known, and is strongly supported by those of the larvae we have attributed to the genera *Cryptophilus*, *Xenoscelinus* and *Propalticus* (Crowson & Sen Gupta, 1969) our identifications of these larvae, and our hypothesis about the ancestry of the Cerylonid group, are mutually supporting in the sense

that any evidence in favour of one will help to strengthen the other—and any evidence against one also tells against the other.

A family whose characters were not included in our comparative charts but which may be truly related to the ancestors of Languriidae etc. is Biphyllidae. Adult Biphyllidae differ from Languriidae and Cryptophagidae notably in having the middle coxal cavities not closed outwardly by the sterna ; Biphyllid larvae, as far as known, differ from those of most Languriidae in lacking pre-gomphal processes on the 9th abdominal tergite and in the non-tuberculate dorsal surface. In these characters, Biphyllidae may well preserve primitive features which have been lost in Languriidae, but this does not rule out the possibility that the Biphyllids are the nearest surviving relatives of the ancestors of the Erotylid-Languriid-Cerylonid group. If they are, then presumably closed middle coxal cavities have developed independently in the Cryptophagid line and the Languriid line.

The hypothesis that the Languriidae and their close allies come from a common ancestry with Biphyllidae however raises other difficulties. The relationships of Biphyllidae seem to be particularly towards *Byturus*, as was pointed out long ago by Falcoz, and the Byturidae in turn shown so many points of similarity to various Heteromera that a true relationship to that group seems highly probable. In both Biphyllidae and Byturidae, the larval tarsungulus is unisetose, whereas most Heteromera like typical Languriidae and Erotylidae have it bisetose. Byturid larvae have rather specialised claws, and it may be that the reduction of the tarsungular setae to 1 is connected with this rather than inherited from a common ancestor with Biphyllidae. However, the most Biphyllid-like of Languriidae, *i.e.* the Cryptophilinae, have a unisetose larval tarsungulus ; if this is not a coincidence, then either the two tarsungular setae of typical Languriidae have arisen from an ancestral one, in defiance of Dollc's Law, or the Languriidae are an unnatural grouping. In the latter case, we should probably have to postulate a diphyletic origin of the closed middle coxal cavities within our Languriidae.

Among the Languriidae and their allies (including the Cerylonid group), phylogenetic problems also arise in connection with the various forms of the front coxal cavities. These



Text-fig. 14. Geographical distributions of Pharaxonothini in the World.

may be externally and/or internally closed behind or entirely open ; the presence of both internal and external closures corresponds more or less to the condition in Carabidae (*see* Bell, 1967) which Sloan designated as "biperforate" The evidence of the Tenebrionidae (*e.g. Zolodinus*) indicates that an external closure of the front coxal cavities may be secondarily lost in some cases, and a recent study of Melandryidae by one of us (Crowson, 1966) suggests that an internal closure too is liable to at least occasional loss. It may well be that an internal closure usually originates by the occlusion of a preceding external closure. Although an internal closure of the cavities seems to be universal in Toraminae and Cryptophilinae, as also in *Propalticus*, it is lacking in many of the Cerylonid group though present in Endomychidae and Coccinellidae, it is lacking in *Sphaerosoma*. Internal closure seems to be the rule in Corylophidae. The Biphyllidae, which in some respects resemble the Cryptophilinae, have internally and externally closed front coxal cavities.

At least in the present state of our knowledge, it seems advisable to be very cautious in drawing phylogenetic conclusions from the various forms of the front coxal cavities, even though these provide good classificatory characters for many groups. The number of tarsal segments, on the other hand, not only provides good classificatory characters but also seems to be strictly subject to Dollo's Law—4 segmented tarsi, as in the Cerylonid group, can be derived from 5-segmented ones, and 3 segmented ones from 4 segmented, by evolutionary changes which are effectively irreversible. The development of lobing on the basal tarsal segments, also a useful classificatory character, is however clearly reversible, as is shown by Curculionoid forms like *Platypus*, Cerambycid forms like *Hypocephalus*, and Chrysomelid forms like Donaciinae. This character, like the form of the front coxal cavities, is one to be used with caution in drawing phylogenetic conclusions.

Wing-venation offers useful, if not infallible, phylogenetic indications ; such changes as the loss of the Radial cell and reductions in the number of Anal veins seem rarely if ever to be reversed. Thus a closed Radial cell seems never to occur in the Cerylonid group, and only in the Cerylonidae of the families of that group do we ever find as many as 4 anal veins. The number of ocelli in the larvae has a rather comparable value ; the basic Languriid number is undoubtedly 6, whereas in the Cerylonid group we never find more than 5 (*e.g.* in *Sphaerosoma*), while 4 is the basic number for Endomychidae and 3 for Coccinellidae. In the larval spiracles, the change from the doubtless primitive bicameral form to annular seems rarely if ever to be reversed ; annuliform spiracles seem to characterise the entire Cerylonid group except for the genus *Sphaerosoma*. Probably the same holds for reductions of the tarsungular setae from 2 to 1, though both these changes may be polyphyletic within the Clavicornia as a whole.

A larval character hitherto unrecorded in these forms but which may prove to be ol considerable systematic and phylogenetic importance is the presence of sclerotised ring or loops in the wall of the rectum. Similar structures have been described in the recta wall of various adult Curculionidae by Kuschel (1964), and had been previously noted by Cawthra (1958). Kuschel distinguished between an approximately circular or hexagonal "rectal ring" and a more or less elongate "rectal loop", pointing out that while a rectal ring was widespread in Curculionoidea, the rectal loop occurred in only a few groups and seemed to have considerable classificatory importance. A rectal loop as defined by Kuschel has been observed by us in larvae of *Eicolyctus* and *Hapalips*, in an undetermined Loberini larva from Chile and in Erotylidae-Dacninae (Text-fig. 4D), but we have not found it in the presumed larvae of *Cryptophilus*, *Xenoscelinus*, *Propalticus*, the Cerylonid group or in Cryptophagidae or Biphyllidae. The character provides additional evidence for a special relationship of Loberinae to Erotylidae, and might be taken to support the idea that Cryptophilinae (and probably Toraminae) should be separated from Languriidae, either to be incorporated in an enlarged and redefined Propalticidae or to form a family of their own.

XIII—SUMMARY

The history and constitution of the family Languriidae are reviewed, and the adults and larval characters are redefined. Separate keys to the adults and larvae of the families Cryptophagidae, Languriidae, Erotylidae and Propalticidae, and a key to the subfamilies, tribes and genera of adults of Languriidae are provided. The family Languriidae is reclassified, and divided into 5 subfamilies—Languriinae, Loberinae, Setariolinae, Toraminae and Cryptophilinae. The subfamilies Languriinae, Setariolinae and Cryptophilinae are characterised, and also the genera of Pharaxonothini, Setariolinae and Cryptophilinae are redefined. Systematic relationships within the family Languriidae, and its relationship with other families are discussed.

XIV—ACKNOWLEDGEMENTS

We are deeply indebted to Professor D. R. Newth for provision of all requisite facilities in the Department of Zoology, University of Glasgow for our studies. Likewise, the staff of Entomology Department of British Museum (Natural History) and particularly Mr. R. D. Pope for so kindly allowing us to study their collections. We wish to thank Dr. A. Villiers for the loan of adult *Xencelinus bicolor*. This study has been partly supported by a research grant of Science Research Council.

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XVI—Explanation of letterings in Text-figure

aa—maxillary articulating area
as—apical spine
at—anterior tendon
avl—first anal vein
br—hypopharyngeal bracon
c2—mesocoxa
c3—metacoxa
ca—cardo
cc—mesoepisternal pocket
co—callosity
cp—Corpotentorium
ct—coxite
ec—external closure
em2—mesoepimera
es2—mesoepisternum
es3—metaepisternum
fc—fronto-clypeal suture
ga—galea
ic—internal closure
la—lacinia
lb—labrum
li—ligula
ln—longitudinal groove on anterior part of gular region
lp—lateral plate
sl—longitudinal line of metasternum
.t—laminatentorium
m—mola
me—mentum
ml—median lobe
ms—median strut
mt—metasternal knob or projection
my—mycangium or pocket
p—paramere
pa—peg-like seta
pi—prebasal impression
Pp—paraproct
r-m—radio-median cross vein
r.—rectal loop
s—scape
s2—mesosternum
s3—metasternum
sf—subcubital fleck
si—styli
sl—stridulatory file
sp—spore
ss—sternopeural suture
su—supratentorium
tc—trochanter
tg—transverse groove on anterior part of gular region
ts—tarsungular seta
tv—transverse line on vertex
vf—valvifer
vfc—valvifer fused with coxite
vp—sensory appendage
ur—urogomphi
vt—ventral crushing tubercle

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