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Revision of the genera of the tribe Julodini (Coleoptera: Buprestidae)

by

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The validity of the six genera in the tribe is confirmed and one new subgenus, *Protojulodis*, is described. Generic characters are reviewed, and the relevant external morphology is illustrated. Distribution maps of the genera and a phylogram and key are provided. The zoogeography of the tribe is described and interpreted and a possible phylogeny is suggested.

INTRODUCTION

The problem of the relative age of the tribe Julodini and its genera is a traditional one for buprestologists, as the tribe has some primitive but also some highly specialized features as compared with other tribes in the family. The generic units are ill-defined and often include remnant species with hardly any variation near to highly variable species that are obviously in a state of flux. Probably on account of the contrast in biology between this tribe and the rest of the family, adult synapomorphic characters of the tribe are distinct, though they changed little along its lineages. In the Julodini neither adults nor larvae occur in wood: all known larvae are free-living root-feeders, while adults are apparently short-lived leaf- and flower-feeders.

In this paper I have assembled existing information on the morphology and distribution of the tribe and tried to find more characters that help to clarify the phylogeny (*sensu* Mayr) and aid in interpreting the distribution of the group. Of the characters previously overlooked, the most useful proved to be the ovipositor, hind wing venation and metacoxal sculpture.

The limited discussion of zoogeography is largely based on recent summaries by Tarling & Tarling (1975), Axelrod & Raven (1972) and Endrödy-Younga (1978).

The terminology of Matsuda (1976) is used for male genitalia, the system of Cobos (1958) for general external morphology, and the wing venation is annotated according to Crowson (1967), and not as von Gebhardt (1932).

Tribe JULODINI Lacordaire

Chrysochroites Castelnau & Gory, 1835: 1 (*pars*)
Julodides Lacordaire, 1857: 10; Marseul 1865: 27
Julodini Le Conte & Horn, 1883: 195; Kerremans 1893: 37; Kerremans 1904: 97; Heyne-Taschenberg 1907: 123; Obenberger 1924: 7; Obenberger 1926: 6; Théry 1928: 12; Lotte 1946: 126; Théry 1946: 23; Cobos 1953: 12; Cobos 1955; 22 (*pars*); Ferreira & Ferreira 1958: 11

Juloditae Péringuey 1886: 1; Cobos 1955: 22
Julodines Kerremans 1904: 97 (*pars*)
Sternocerini Reitter 1911: 178; Yakobson 1912: 773;
Amblysternini Cobos 1955: 22 (*pars*)

Type genus (by absolute tautonymy): *Julodis* Eschscholtz, 1829.

Subdivisions

Cobos (1955) recognized a separate tribe, the Amblysternini, on the strength of the meso-metasternal suture being interrupted by the sternal cavity. This is the only subdivision that has been suggested, and it is unwarranted (see discussion of genera below).

Morphology

The morphological features that are most characteristic of the tribe are the following:

Antennal pores and pubescence diffuse over both sides of widened 5th to 11th segments.
Body shape cylindrical-elyptical, size from medium (10 mm long) to very large (60 mm).
Lateral ridge on pronotum absent.
Prosternum short, length less than diameter of procoxae anterior to them.
Head nearly obscured by pronotum from above.
Larvae free-living root-feeders with a specialized first instar.
Metacoxa hardly dilated proximally.
Base of pronotum bisinuate, retracted in the middle between elytra.
Wing venation as in figs 51–53.

The following characters attributed to the Julodini in the literature either apply only to some genera, occur also in other tribes of the Buprestidae, or are variable:

Antennae next to anterior margin of epistome (Lacordaire 1857).
Genae shorter than diameter of eyes (Reitter 1911).
Scutellum absent (Lacordaire 1857; Kerremans 1893, 1904; Heyne-Taschenberg 1907; Reitter 1911; Cobos 1953).
Body pilose dorsally (Reitter 1911).
Sternal cavity formed by mesosternum only, or by meso- and metasternum (Lacordaire 1857; Le Conte & Horn 1883; Kerremans 1893, 1904; Heyne-Taschenberg 1907; Théry 1928; Cobos 1955).
Tarsal segments large, flat, square (Kerremans 1893, 1904; Heyne-Taschenberg 1907; Cobos 1955).
Lateral portions of metathorax narrow (Kerremans 1893).
Frons not retracted around antennae (Le Conte & Horn 1883).
Sexual dimorphism absent (Kerremans 1904).

Evolutionary age

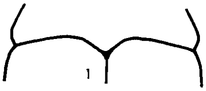
As reflected by its leading position in most of the older systematic studies and catalogues, the phylogenetic position of this tribe within the family Buprestidae was held to be primitive. Both Kerremans (1904) and Obenberger (1924) held this opinion—the former on the grounds of the 'absence' of the scutellum, diffuse antennal pores, and 'undivided' mesosternum, the latter without clearly stating reasons.

Kerremans was led to believe that the absence of the scutellum was primitive because it is present in such 'recent' tribes as the Agrilini and Sphenopterini. It seems, however, that the scutellum is of little phylogenetic significance in the family and is either present or absent within the Julodini and at least one other tribe, the Polycestini. The diffuse antennal pores could indeed be considered primitive, but the accompanying pubescence is specialized. The form of the mesosternum, which is highly variable within the tribe, and the general body shape, prosternum, head and metacoxa are all adaptations to a free-living life style as opposed to the wood-boring or mining habits of the other tribes in the family. As to the life style of the primordial Buprestidae, a free-living mode could be argued for by claiming that the Julodini are the most primitive, and therefore near the ancestral group. Specialization of a primordial wood-borer to a free-living life style is, however, equally possible and supported, for example, by the overwhelming majority of living buprestids being wood-borers (see below).

Opposed to the views of Kerremans and Obenberger are those of Théry and Cobos. Théry (1924) regarded the Julodini as 'advanced' on account of their unique biology and larval forms, their large body size, and the lack of fossils. He argued that the lack of a scutellum is not archaic and that the high degree of variability of species indicated a young group. Cobos (1953) subscribed to Théry's views, and added to Théry's (1924) characters a loss of setation on the aedeagus, and also argued that the loss of the scutellum and limitation of the antennal pores to some segments only are advanced characters.

In the above-mentioned (and other) discussions of phylogeny, much confusion arises through misunderstandings about terminology. Many taxonomists seem to regard 'old', 'primitive' and 'primordial', and 'recent', 'specialized' and 'advanced' as two sets of synonyms. In the present discussion I use these terms as three pairs of antonyms, as follows: old-recent: denoting absolute time of origin; primitive-specialized: implying relative degrees of apomorphism (or rates of evolution); primordial-advanced: indicating relative positions (in time), where one taxon derives from another. Of two forms of equal phylogenetic age, therefore, one may be primitive and the other may be specialized. Either of the two forms may give rise to more advanced forms, and become primordial relative to those advanced forms.

Returning to the arguments of Théry and Cobos, I should therefore argue, first, that body size is not connected with evolutionary age as such, or with primordial or advanced status. Rather, it seems to be one (possibly very common) result of specialization (as in Cope's rule for mammals). Secondly, the relatively limited distribution and poor differentiation in adult morphology as compared with other Buprestid tribes may indicate a recent radiation or a very slow rate of evolutionary change or a recent origin. The fact that some species show little variation and are geographically restricted while others are highly variable and widespread suggests a combination of a slow rate of change and a recent radiation rather than a recent origin. Thirdly, the specialized larval forms and aedeagi in all Julodini are part and parcel of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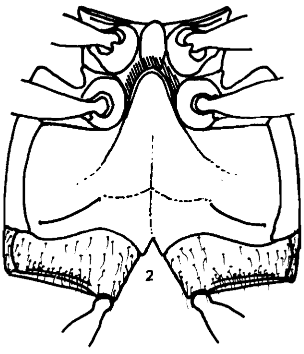
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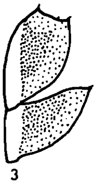
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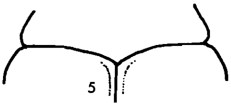
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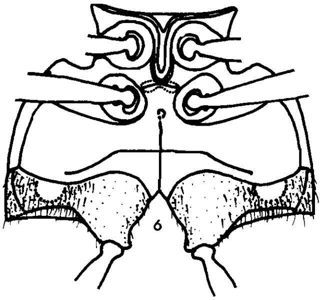
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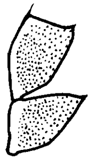
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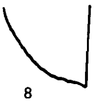
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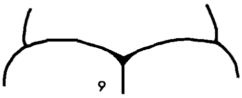
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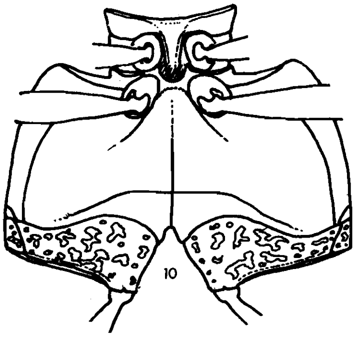
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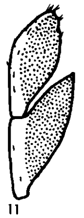
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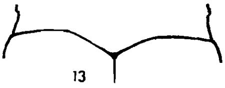
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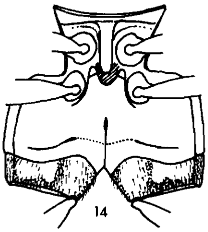
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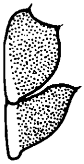
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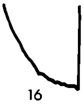
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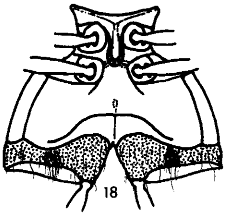
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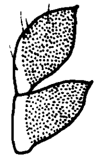
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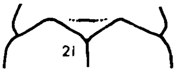
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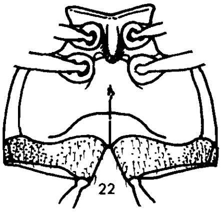
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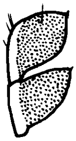
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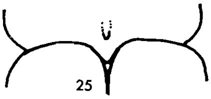
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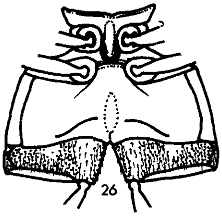
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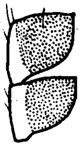
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their original derivation (synapomorphism) and have no direct bearing on evolutionary age. Finally, the only character that seems to support a recent origin is the absence of fossils. This could, however, have come about through an early origin and recent success and radiation and is not good evidence because fossils of many other old groups are lacking.

I conclude from the foregoing that the Julodini are highly specialized on a line strongly divergent from the typical buprestid line. The morphology of the tribe cannot be derived from any other existing buprestid tribe, and an advanced position relative to other tribes is ruled out. Also, no tribes in the family can be derived from the specialized Julodini, which therefore excludes the possibility of a primordial position for this tribe in the Buprestidae. In this connexion the monotypic Australian genus *Julodimorpha* Thomson provides interesting evidence. It has several features that are common to members of the Julodini, such as general body shape, loss of apical spinae on elytra, shortened prosternum and large size. The whole morphology is, however, based on the Chalcorphorini pattern, as indicated by wing venation, lateral ridges on pronotum, shape of mesosternum, pores on antenna and shape of metacoxa. This genus very probably split off from the main body of the Chalcophorini at an early stage and occupied a macroniche similar to that of the Julodini, and then evolved convergent to the latter. The fact that *Julodimorpha* is in the tribe closest to the Julodini, yet evolved analogous rather than homologous structures, makes a recent derivation of the Julodini most unlikely. As regards their age, an early separation, with a low rate of subsequent diversification followed by a relative recent success period and radiation, seems to fit the present state of knowledge best.

Geographical origin

A phylogram of the tribe is shown in fig. 55, based chiefly on synapomorphy, distribution patterns and lack of apomorphs. In it, the oldest surviving genera are *Aaata* and *Julodella*. In both *Julodella* and *Julodis*, the more primitive and at the same time more variable and actively radiating species occur in the north. Both these genera, as well as *Aaata*, are found in the Near East, which may therefore reasonably be supposed to be the area of origin of the tribe. It is interesting to note that in variable and widespread species, the geographically terminal elements seem to have a reduced variation and are more specialized than those in the core area. This applies within the Ethiopian Acmaeoderini (Holm 1978) and Julodini (Holm, unpublished). The above argument for the origin of the Julodini is based on the assumption that the same rule applies to genera.

Figs 1–28. External morphology of the genera of Jolodini. 1–4. *Sternocera orissa* Buquet. 1 base of elytra; 2 thorax, ventral; 3 last two antennal segments; 4 apex of left elytron. 5–8. *Julodis caffra* Castelnau. 5 base of elytra; 6 thorax, ventral; 7 last two antennal segments; 8 apex of left elytron. 9–12. *Aaata finchi* (Waterhouse). 9 base of elytra; 10 thorax, ventral; 11 last two antennal segments; 12 apex of left elytron. 13–16. *Amblysterna natalensis* (Fahraeus). 13 base of elytra; 14 thorax, ventral; 15 last two antennal segments; 16 apex of left elytron. 17–20. *Neojulodis (Neojulodis) hirta* (L.). 17 base of elytra; 18 thorax, ventral; 19 last two antennal segments; 20 apex of left elytron. 21–24. *Neojulodis (Protojulodis) vittipennis* (Fahraeus). 21 base of elytra; 22 thorax, ventral; 23 last two antennal segments; 24 apex of left elytron. 25–28 *Julodella globithorax* Semenow. 25 base of elytra; 26 thorax, ventral; 27 last two antennal segments; 28 apex of left elytron.

The distribution maps of genera (fig. 54) show the highest number of genera and species to be in the eastern Ethiopian region; there is one very recent invasion of the Mediterranean area in *Julodis* only according to Cobos (1953), while all genera except *Aaata* occur elsewhere in the Ethiopian region. *Sternocera* is distributed throughout the Oriental region as well. Théry (1949) suggested a Jurassic origin of the tribe in the present Palearctic after the separation of Madagascar, on which no Julodini occur. With glaciation, the primordial Julodini would have been displaced southward. This suggestion still seems plausible and is not, as Théry felt, contradicted by the presence of *Amblysterna* in Africa, because he was wrong in believing this to be the most primitive genus in the tribe. Cobos (1953) placed the origin in the same period, but in Africa, and also stated *Amblysterna* to be a relatively advanced genus. The date of origin, however, seems likely to have been earlier.

The distribution and origin of individual genera are discussed below.

Primitive characters

On the assumption (Théry 1927) that the signs of evolutionary development are an increase in the size, complexity, diversity, etc of organs and a decrease in the overall complexity of organisms, the most primitive forms of the morphological characters that are useful for distinguishing genera in the Julodini are as follows (fig. nos. refer to best extant example.)

1 Last antennal segment undifferentiated (fig. 19)
2 Anterior rim of prosternum with a continuous ridge (fig. 22)
3 Procoxae far removed from anterior rim of prosternum (fig. 14)
4 Meso-metasternal suture at posterior end of sternal cavity (fig. 26)
5 Metasternal sulci well developed (fig. 10)
6 Metacoxal sculpture evenly spread, undifferentiated (fig. 2)
7 Pronotum globose, rounded off to elytral base dorsally and laterally (fig. 25)
8 Elytral base open, scutellum visible (fig. 25)
9 Apical spinae on elytra present (fig. 12)
10 Ovipositor membranous on the sides (fig. 50)
11 Tegmen of male genitalia undifferentiated (fig. 48)
12 Meta-wing with A_1 branch present (fig. 53)
13 Meta-wing with distal cell complete and elongate (r cross-vein present) (fig. 51)
14 Hair on body short

The characters most doubtfully interpreted as plesiomorphic in this list are numbers 4, 6 and 14, since the indications within the tribe, and in the other buprestid tribes, as to what these structures would have looked like in the ancestral form are inconclusive. The arguments in this paper do not much depend on these characters, and would be little changed if they were regarded as apomorphic.

The numbers preceding these characters in the above list correspond with those in the lists below under genera, where A = apomorphism, P = plesiomorphism and brackets indicate that apomorphism is poorly expressed or dubious.

Key to the genera of Julodini

1(6) Last antennal segment concave (figs 3, 15) or irregular (fig. 11) terminally; ovipositor completely sclerotized (figs 29, 33, 43) 2

2(5) Last antennal segment concave terminally (figs 3, 15); suture of meso- and metasternum interrupted by sternal cavity (fig. 14) or along a hornlike protrusion (fig. 10); A_1 branch-vein on hind wing absent (fig. 51); length between 20 and 50 mm 3

3(4) Suture of meso- and metasternum interrupted by sternal cavity (fig. 14); procoxa far removed from front rim of pronotum (fig. 14), which has a rim along its front edge; ovipositor with segmentation invisible on sides and bristles apically (fig. 34); aedeagus with parameres strongly overlapping dorsally (fig. 36) and without membranous lobes ventrally (fig. 35) .... **Amblysterna**

4(3) Suture of meso- and metasternum along a horn-like protrusion (fig. 10); procoxa separated from head only by a thin rim of prosternum, which rim is not continued in the middle (fig. 2); ovipositor with lateral segmentation clearly visible, naked (fig. 30); aedeagus with parallel parameres (fig. 32) and characteristic membranous lobes, which may vary in shape and size ventrally (fig. 31) .... **Sternocera**

5(2) Last antennal segment irregular terminally (fig. 11); suture of meso- and metasternum curved and well behind sternal cavity (fig. 10); A_1 branch-vein on hind wing present (fig. 53); length more than 55 mm .... **Aaata**

6(1) Last antennal segment truncate terminally (fig. 7) or normal (figs 19, 23, 27); ovipositor membranous on sides (figs 38, 39, 46, 48).

7(8) Last antennal segment truncate terminally (fig. 7); apical spines on elytra absent (fig. 8); ovipositor completely sclerotized at apical end, which is raised to a blade or horn (figs 37–40); anterior rim of prosternum declivous and without rim in the middle (fig. 6); metacoxa with a prominent shiny median spot; size usually more than 25 mm long; body usually hairy .... **Julodis**

8(7) Last antennal segment normal (figs 19, 23, 27); apical spines on elytra discernible (figs 20, 24, 28); ovipositor without sclerotization or raised apical end (figs 46, 48); prosternum with a rim along the whole of anterior edge 9

9(10) Distal cell on hind wing complete, r cross-vein present (fig. 51); elytral base open, with scutellum visible (fig. 25) .... **Julodella**

10(9) Distal cell on hind wing incomplete, with r cross-vein absent (fig. 52); elytral base closed (figs 17, 21) 11

11(12) Metacoxa with a dense median hair-tuft; distribution limited to SW Cape Province .... **Neojulodis (Neojulodis) subgen. nov.**

12(11) Metacoxa smooth and with sparse hair in middle; distribution African, excluding Karoo and SW Cape Province .... **Neojulodis (Protojulodis) subgen. nov.**

AAATA Semenow

Aaata Semenow, 1906: 152; Yakobson 1912: 774; Obenberger 1926: 18; Théry 192: 178

Type species (by monotypy): *Julodis finchi* Waterhouse, 1884.

MATERIAL EXAMINED. *A. finchi* (Waterhouse) (3)

Morphology

This genus is easily recognized by its exceptional size and lack of the apomorphic characters of the other large Julodini, *Sternocera* and *Julodis*. The single and very stable species, as Théry (1927) pointed out, represents an evolutionary dead end and probably changed little over millions of years apart from increasing in size. The morphology is described by Waterhouse (1884), and the thirteen characters studied are as follows:

1 (A) Last antennal segment with distal end irregular (fig. 11)
2 (A) Anterior rim of prosternum with ridge ill-defined (fig. 10)
3 P Procoxa far removed from anterior rim of prosternum (fig. 10)
4 (A) Meso-metasternal suture situated behind and detached from sternal cavity (fig. 10)
5 P Metasternal sulci well developed (fig. 10)
6 P Metacoxal sculpture undifferentiated (fig. 10)
7 P Pronotum globose (fig. 9)
8 (A) Elytral base slightly open, but scutellum not discernible (fig. 9)
9 P Apical spinae on elytra well developed (fig. 12)
10 A Ovipositor sclerotized, segmentation visible on sides (figs 43, 44)
12 P Meta-wing with A_1 branch present (fig. 53)
13 P Meta-wing with distal cell complete and elongate (r cross-vein present) (fig. 53)
14 P Hair on body short, zoned.

Aaata is obviously a remnant of old origin. Derived characters are few and ill-defined, and all seem to lead to *Sternocera* and to exclude the derivation of other genera (see below). The backward position of the meta-mesosternal suture (fig. 10) is difficult to place in the sequence of development of the Julodini, and is provisionally regarded as a synapomorph of *Sternocera* and *Aaata*. The elongate distal cell on the meta-wing (fig. 53) and evenly distributed metacoxal sculpture of both are equally difficult to place, and are tentatively interpreted as symplesiomorphic. The most likely synapomorphic character in *Sternocera* and *Aaata* is the identical sclerotization of the ovipositor (figs 30, 44).

Aaata is the most primitive genus in the Julodini in having a branched A_1 vein (fig. 53), best developed apical spinae on the elytra (fig. 12) and lowest number of derived characters in general.

Semenow (1906) distinguished the genus from *Julodis* by its large size, convex metasternum, grooved prosternal process, horizontal clypeus and body sculpture. All these characters recur in *Sternocera*, or vary in the tribe at the species level. The sexual dimorphism mentioned by Semenow (bispinose elytral apex in the male) could not be investigated, since I could not procure a male specimen.

Biology

The biology is unknown, but from the general body shape, size and ovipositor may be assumed to be similar to *Sternocera.*

Phylogeny and distribution

The geographical origin of *Aaata* is difficult to decide, since the only species occurs on the junction of the ancient African and Eurasian continents. Apart from the genus *Sternocera,* which was derived from the same stock and has an Afro-Indian distribution, *Aaata* has no direct relatives in the Julodini.

A possible hypotheses that fits the present theories of continental drift

(Tarling & Tarling 1975), would be that *Aaata* was either already a remnant at an early stage (perhaps over 200 million years ago), and represented an extension of the primordial Gondwanaland stock into the Palearctic. With progressive separation of the two continents, *Sternocera* replaced the original stock in the African continent, while *Aaata* could survive free from julodine competitors on the separate Eurasian continent for the duration of its separation, which lasted about 150 million years (Tarling & Tarling 1975).

Alternatively, *Aaata* could have crossed to the Palearctic during a geocratic period, or even have remained on the extreme north-east of the primordial African continent, while *Sternocera* evolved further south. In the latter case it would have been displaced or restricted to its present distribution recently, probably by competitive pressure of the expanding northern *Julodis*.

Théry (1927) wrongly assumed *Aaata* to be closest to *Amblysterna* and (Théry 1931) assumed it to be ancestral to both *Sternocera* and *Julodis*. As argued below (under *Sternocera*) *Aaata* is ancestral only to *Sternocera*.

STERNOCERA Eschscholtz

Sternocera Eschscholtz, 1829: 18; Solier 1833: 273; Castelnau & Gory 1835: 1; Lacordaire 1857: 11; Marseul 1865: 27; Kerremans 1888: 56; 1893: 114; 1903: 7; 1904: 98; Heyne-Taschenberg 1907: 123; Yakobson 1912: 773; Théry 1924: 72; Obenberger 1926: 6; Théry 1927: 178; 1949: 157; Ferreira & Ferreira 1958: 137.

Type species (new designation on partial tautonomy): *Buprestis sternicornis* L.

MATERIAL EXAMINED. Oriental region: *S. laevigata* (Oliver) (1); *S. aequisignata* Saunders (1); *S. dasypleura* Kollar (2); *S. chrysis* (F.) (4); *S. sternicornis* (L.) (2). Ethiopian region: *S. wahlbergi* Boheman (3); *S. hunteri* Waterhouse (3); *S. interrupta* (Olivier) (2); *S. cariosicollis* Fairmaire (2); *S. castanea* (Olivier) (5); *S. hildebrandti* Harold (5); *S. syrica* Saunders (1); *S. variabilis* Kerremans (2); *S. orissa* Buquet (65).

Morphology

The genus is recognized by all authors by the presence of a sternal process behind the sternal cavity (fig. 2). The degree of development of this process is, however, variable (Théry 1931). Few other characters are given in the various keys and descriptions. Lacordaire (1857) and Théry (1949) mention absence of sexual dimorphism. The male of *S. chrysis* (F.), however, has a completely modified and cornute first abdominal segment not present in the female, of which the function remains a mystery.

The fourteen characters studied are as follows:

1 A Last antennal segment with a concave terminal edge (fig. 3)
2 A Anterior rim of prosternum with the ridge interrupted (fig. 2) by a bulging mid-section
3 A Procoxa very near anterior rim of prosternum (fig. 2)
4 A Meso-metasternal suture situated on a horn-like protrusion (fig. 2)
5 A Metasternal sulci indistinct in middle (fig. 2)
6 P Metacoxal sculpture evenly spread, undifferentiated (fig. 2)
7 A Pronotum steeply declivous and attenuated anteriad (fig. 1)
8 A Elytral base completely closed, scutellum invisible (fig. 1)
9 P Apical spinae on elytra present (fig. 4)

10 A Ovipositor sclerotized, segmentation visible on sides (figs 29, 30)
11 A Aedeagus with strongly protracted membranous lobes on inside of parameres below, parameres often with grooved sculpture (figs 31, 32)
12 A Meta-wing with A_1 branch absent (fig. 51)
13 P Meta-wing with distal cell complete and very elongate (r cross-vein present)
14 (A) Hair on body either short, in sharply defined zones, or absent

A number of characters of dubious diagnostic value are mentioned in the literature, e.g., tarsal pads flat and square to triangular (Eschscholtz 1829; Solier 1833; Lacordaire 1857; Marseul 1865; Kerremans 1888); shape of palpi, trilobate epistome, mandibles and eyes (Solier 1833; Castelnau & Gory 1835; Lacordaire 1857; Marseul 1865). Both the wing and the aedeagus (which happens to portray an ovipositor of a *Julodis*) illustrated in von Gebhardt (1932) are inaccurate, and his system of labelling of veins is completely different from that of modern authors.

Sternocera seems to derive from an ancestor close to *Aaata* (Théry 1931). Ovipositors are virtually identical in the two genera and not highly complex as in *Julodis*, as Théry (1927) stated (see figs 29–50). In addition, the last antennal segments and the position of the meso-metasternal suture in *Sternocera* may be derived from the condition in *Aaata*, while the elongate distal cell is a symplesiomorph exclusive to these two genera. *Sternocera* is undoubtedly further evolved than *Aaata*, as can be seen by comparing the number of derived characters of each.

Sternocera is adapted to a moist savanna habitat, and a number of its characters, not surprisingly, recur in *Amblysterna* and *Neojulodis* (*Protojulodis*), both of which probably invaded the moist savanna independently. These similarities are partly true convergence and partly 'delayed' homologies or parallelism (*sensu* Mayr 1974) as explained below under *Amblysterna*.

The most extremely specialized species of *Sternocera*, without hair on body and with long sternal process, are found in India and the Far East. These species are also supposed to be distinct in having a groove on the frons (Kerremans 1888; Heyne-Taschenberg 1907). This character is, however, either present or absent both in the species of Africa and the East.

Biology

The adults of *Sternocera* in the savanna parts of Africa are found semi-gregariously on flowering trees, mostly *Acacia* species, but also other such as *Dichrostachys cinerea*. They are clumsy and reluctant fliers, and use their sternal process as a lever to present plant tissue to the mouth-parts while feeding. Their enormous eggs are occasionally simply dropped to the soil, but it can be assumed that the sclerotized ovipositor is normally used to deposit eggs in the soil, where the larvae are free-living root-feeders.

Phylogeny and distribution

Théry (1949) argues a recent origin for *Sternocera* on the grounds of its high degree of variation. The untenability of such a conclusion has already been discussed above. Hennig (1965) clearly defines the difference between age of origin and age of division of a monophyletic group. Théry (1949) postulates that the oldest elements in the genus are Ethiopian. He disagrees with Kerremans (1904), who regards *S. chrysis* *chrysiodoides* as the most archaic form in the East, and singles out *S. sternicornis* and *S. multipunctata* for this position. It is fairly certain that the origin is on the Ethiopian side of Gondwanaland, where the least specialized elements survive today. Plesiomorphy, species diversity and variability are highest in East Africa (fig. 54), while the fauna in the Oriental region is generally less variable and more specialized, suggesting a terminal and derived fauna.

The clear separation and lack of common species, and therefore the apparently long period of separate evolution of the western and eastern elements, would suggest a radiation of the genus before the break between India and East Africa but after the southern separation of Madagascar 70 to 100 million years ago (Axelrod & Raven 1972; Tarling & Tarling 1975). At that time the genus must already have contained a fairly large number of species, of which the more variable and less specialized core remained on the African continent. This would place the origin of *Sternocera* at an early date, probably well before *Julodis*, as suggested by Cobos (1955).

The variable species on the northern and southern limits of distribution in Africa represent secondary radiation into relatively arid savanna regions. In the east some secondary radiation into China accounts for most of the variable species (e.g. *S. aequisignata* Saunders).

The present distribution (fig. 54), which covers wet and arid savanna, as well as tropical forest in the west and semi-desert in the horn of Africa, must be interpreted with caution. Both the latter biomes are possibly invaded along savanna intrusions only, since distribution records for *Sternocera* are very patchy in both. It is noteworthy that both the general distribution (Kerremans 1904), and centres of high diversity (fig. 54) are roughly mutually exclusive between *Sternocera* and *Julodis* (the two largest genera in the tribe). In Africa *Sternocera* may well be responsible for a competitive barrier between the northern and southern *Julodis*, while the north-African *Julodis* may similarly separate the eastern and western *Sternocera*. A similar mutually exclusive distribution occurs between the two genera with small body-size, *Julodella* and *Neojulodis*.

JULODELLA Semenow

Julodis (Julodella) Semenow, 1893: 311; Kerremans 1904: 323; Théry 1927: 178; 1928: 12
Julodis (Julodella) Kerremans 1903: 13; Heyne-Taschenberg 1907; 125
Julodiella Yakobson 1912: 775: Obenberger 1926: 31

Type species (by indication): *Julodis globithorax* Steven.

MATERIAL EXAMINED. *J. abeillei* Théry (6); *J. schochi* Théry (4); *J. brevilata* Semenow (1); *J. globithorax* (Steven) (13); *J. kaufmanni* Ball (1); *J. cicatricosa* (Germar) (151 + types); *J. bicolor* (Obst) (14 + types); *J. abyssinica* (Théry) (2 types).

Morphology

The genus is clearly defined by the primitive character of the exposed scutellum. It shows very little apomorphism, and is on the whole defined by plesiomorphic characters, as follows:

1 P Last antennal segment undifferentiated (fig. 27)
2 P Anterior rim of prosternum with ridge (fig. 26)
3 P Procoxa far removed from anterior rim of prosternum (fig. 26)
4 P Meso-metasternal suture at posterior end of sternal cavity (fig. 26)

5 (A) Metasternal sulci indistinct in middle, longitudinal sulcus often indiscernible (fig. 26)
6 (A) Metacoxal sculpture reduced in middle (fig. 26)
7 (A) Pronotum globose, rarely attenuated, and uneven on sides (fig. 25)
8 P Elytral base open, scutellum visible (fig. 25)
9 P Apical spinae on elytra present (fig. 28)
10 P Ovipositor membranous on sides (fig. 50)
11 P Aedeagus undifferentiated
12 A Meta-wing with branch on A_1 absent (fig. 51)
13 (A) Meta-wing with distal cell complete but shortened (r cross-vein present) (fig. 51)
14 P Hair on body short

It is obvious that the morphology of *Julodella* is unspecialized, primitive, and that the genus is different from but more or less on a par with *Aaata*. The five important apomorphic characters separating these two genera (ovipositor sclerotization, closed scutellum, position of meso-metasternal suture, loss of A_1 branch and reduction of metasternal sulci) draw a dividing line through the remaining genera. These characters make it possible to trace all other genera to either an *Aaata*-like or a *Julodella*-like ancestor. While *Aaata* is more primitive in wing venation, *Julodella* has the more primitive visible scutellum.

Kerremans (1904) and Heyne-Taschenberg (1907) use the open elytral suture at apex as diagnostic, but this character is unreliable.

Biology

The biology is unknown, but the functional morphology indicates at least some agreement with the general biology of the tribe. The habitat niche seems to be arid to arid savanna.

Phylogeny and distribution

The greatest species diversity, plesiomorphism and variation in this genus are at present found in north-east Africa and the Near East. The southern range contains only two species, which are both morphologically and distributionally terminal and

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Figs 29–53. External genitalia and hind wing venation of the genera of Julodini. Median lobe of aedeagus and sclerotized parts of ovipositor shaded. 29–32. *Sternocera* Eschscholtz. 29–30. *S. orissa* Buquet. 29 ovipositor, ventral; 30 ovipositor, lateral. 31–32. *S. wahlbergi* Boheman. 31 aedeagus, ventral; 32 aedeagus, dorsal. 33–36. *Amblysterna natalensis* (Fahraeus). 33 ovipositor, ventral; 34 ovipositor, lateral; 35 aedeagus, ventral; 36 aedeagus, dorsal. 37–42. *Julodis* Eschscholtz. 37–38. *J. caffra* Castelnau. 37 ovipositor, ventral; 38 ovipositor, lateral. 39–40. *J. onopordi* (Fabricius). 39 ovipositor, ventral; 40 ovipositor, lateral. 41–42. *J. caffra*. 41 aedeagus, ventral; 42 aedeagus, dorsal. 43–44. *Aaata finchi* (Waterhouse). 43 ovipositor, ventral; 44 ovipositor, lateral. 45–48. *Neojulodis (Neojulodis) hirta* (L.). 45 ovipositor, ventral; 46 ovipositor, lateral; 47 aedeagus, ventral; 48 aedeagus, dorsal. 49–50. *Julodella globithorax* Steven. 49 ovipositor, ventral; 50 ovipositor, lateral. 51–53. Wing venation of hind wing. 51 *Julodis, Sternocera, Amblysterna, Julodella* (generalized); 52 *Neojulodis* (arrow: absent r cross-vein); 53 *Aaata* (arrow: forked A_1 vein).


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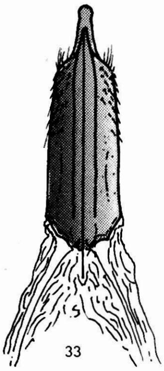
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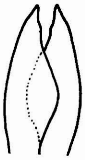
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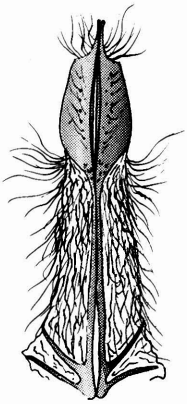
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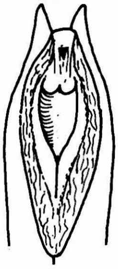
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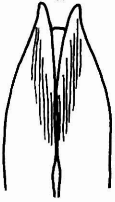
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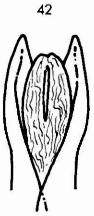
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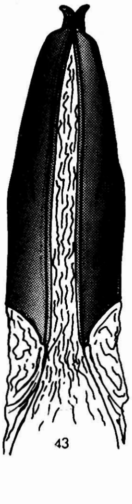
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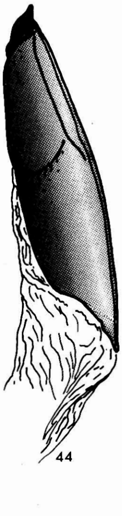
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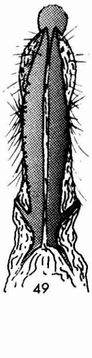
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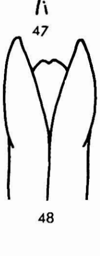
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stable. The genus probably had a Pan-African distribution about 150 million years ago and gave rise to the next-related, but savanna-adapted, *Neojulodis* (*Protojulodis*) in East Africa. This must have displaced *Julodella* in Africa except in the arid south-west and north-east, possibly on the pattern of the 'fold catastrophe' (Dodson & Hallam 1977).

Secondary radiation is limited to the northern elements and was probably initiated at the time of the collision of the African and Eurasian continents and closure of the Tethys sea, when competition-free semi-arid areas became available in the Near East. The majority of the *Julodella*, and all of its variable species, occur in this northern region. In the south, all radiation must have been forestalled by the emergence of *Neojulodis* (*Neojulodis*) in the new semi-arid regions (see below).

The separation of the southern and northern elements must be of long standing, and the relative lack of differentiation may be attributed to a slow intrinsic rate of change or to a lack of environmental change in the areas. The southern species do, however, show certain more specialized characters, such as brown elytral colour, extremely reduced scutellum and attenuated rather than globose pronotal shape. This apomorphism leads over to *Julodis* and *Protojulodis*, which supports the supposition that these two genera are derived from primitive African *Julodella* and that the northern *Julodella* evolved independently.

JULODIS Eschscholtz

Jalodis (*sic*) Eschscholtz, 1829: 9
Julodis Solier 1833: 270; Castelnau & Gory 1835: 1; Lacordaire 1857: 12; Marseul 1865: 29; Kerremans 1893: 114; 1903: 9; 1904: 192; Théry 1927: 125; Heyne-Taschenberg 1907: 125; Yakobson 1912: 77; Obenberger 1924: 6; 1926: 18; Théry 1927: 178; 1928: 12; 1946: 26; Cobos 1953: 4; Ferreira & Ferreira 1958: 12
Saccosoma Motschulsky, 1859: 294

Type species (new designation): *Buprestis onopordi* F.

Material examined. Palearctic and North-Ethiopian group: *J. onopordi* (F.) (17); *J. aristidis* Lucas (3); *J. aequinoctalis* Olivier (3); *J. variolaris* Pallas (1); *J. manipularis* (F.) (14); *J. vylderi* Kerremans (62 + types); *J. caillaudi* Latreile (8); 5 spp. indet. (18). South-Ethiopian group: *J. echo* Gory (20); *J. gariepina* Péringuey (9); *J. caffra* Castelnau (16); *J. amoena* Péringuey (6); *J. chevrolati* Castelnau & Gory (16); *J. chirrhosa* Schoenherr (7); *J. fascicularis* (L.) (10); *J. hirta* Herbst (4); *J. albomaculata* (Voet) (44); *J. hirtiventris* Castelnau (22); *J. sulcicollis* Castelnau & Gory (20); *J. thunbergi* Chevrolat (2); *J. humeralis* Gory (36); *J. kochi* Ferreira & Ferreira (1); *J. viridipes* Castelnau (22); *J. brevicollis* Théry (5); 4 spp. indet. (13).

Morphology

The genus *Julodis* is the largest and best-known of the tribe. Obenberger (1926) listed 42 Palearctic and 38 Ethiopian species. The latter were reduced to 19 by Théry (1928), while Ferreira & Ferreira (1958) recognized 26. A thorough revision would undoubtedly also reduce the East African and Palearctic species. The estimate of 25 southern and 36 northern species (fig. 54), is based on some published synonymies and on inferences from material at my disposal.

The genus is most often identified by elimination, not having a cornute or forked metasternum. The meso-metasternal suture is more or less straight, at the period of folding of the Alps. He also correctly observed that, apart from the actively radiating northern *J. onopordi*, the southern species are the more variable. Obenberger (1924) regarded *Julodis* as an old genus, while Cobos (1953) argued for a more recent origin than *Sternocera* on grounds of the greater variation in the genus *Julodis*. Both authors, as well as Kerremans (1904), commented on the very obvious separation of the genus into a northern group (roughly north of the tropic of cancer) and a southern group (roughly south of the tropic of capricorn). No satisfactory explanation for this division has been offered in the literature.

It seems to me that the origin of *Julodis* from an early *Julodella*-like ancestor would have occurred in the north-east Ethiopian region, where most archaic elements of *Julodis* occur today (Cobos 1953). The distribution must have been limited to a temperate-to-arid biome and probably never extended to the tropical areas of Central or East Africa, where *Sternocera* had gained a foothold, since *Julodis* never reached present India. At the same time, the niche occupied by *Julodis* must have been greatly different from that of *Julodella* (then more or less sympatric). The striking difference in size and body hair is greatest where these two genera are at present sympatric.

The southern group of species is more specialized and obviously derived from the northern group. The similarity in form of the ovipositor within the two groups indicates that the split was at an early stage and that the diversification into further species occurred after separation. The southern species are centred on the western Cape mountains, while species at present seem to radiate into the Karoo. I would expect this Cape fauna to have crossed Africa in temperate conditions, probably along the old temperate montane belt (Tinley 1975). One dwarfed southern species (*J. vylderi*), which has all the features characteristic of the northern group (including the form of the ovipositor), is an exception to the pattern of distribution just described. This species might be a remnant of an earlier Pan-African distribution of the northern *Julodis*, but that would imply an origin and diversification of *Julodis* antedating that of *Sternocera* and seems cladistically unlikely. The more likely explanation is that this species migrated or extended south through Africa along the 'arid tendency' belt (Tinley 1975) during a relatively recent interpluvial (fig. 54). It is most closely related to the highly evolved and specialized species-group of *J. aristidis* Lucas, found in Somalia and Egypt, and this, together with its small size, suggests that it is a recent intrusion rather than a remnant of an early distribution.

The invasions of north-western Africa and southern Europe are recent, post-dating the closure of the Tethys sea and folding of the Alps (Cobos 1953). The high variation in some northern species, notably *J. onopordi* (F.), described by Obenberger (1924) and Cobos (1953) is due to this secondary radiation into competition-free temperate regions.

AMBLYSTERNA Thomson

Amblysterna Thomson, 1878: 8; Kerremans 1903: 15; Semenow 1906; Heyne-Taschenberg 1907: 126; Obenberger 1926: 32; Théry 1927: 179; 1946: 27; Cobos 1955: 22; Ferreira & Ferreira 1958: 76

Julodis (*Amblysterna*) Kerremans 1904: 362

Type species (by subsequent designation: Kerremans 1903): *Julodis natalensis* Fahraeus 1851.

MATERIAL EXAMINED. *A. natalensis* (Fahraeus) (231 + types); *A. johnstoni* Waterhouse (58 + types).

Morphology

The genus is recognized by the forked metasternum or interrupted meso-metasternal suture. This striking derived character is shared with *Neojulodis* and led Théry (1927) to synonymize the latter genus with *Amblysterna*. Both species are large and have the smooth torpedo-shape of a *Sternocera*. Several other characters link *Sternocera* and *Amblysterna*, but the extreme differences in apomorphism of the meso-metasternal suture separate the two genera conclusively (see below).

The fourteen characters studied are as follows:

1 A Last antennal segment with a concave terminal margin (fig. 15)
2 P Anterior rim of prosternum with a continuous ridge (fig. 14)
3 P Procoxa far removed from anterior rim of prosternum (fig. 14)
4 A Meso-metasternal suture interrupted by sternal cavity (fig. 14)
5 A Metasternal sulci indistinct in middle (fig. 14)
6 (A) Metacoxa with sculpture sparse in middle (fig. 14)
7 A Pronotum not globose, irregular on sides (fig. 13)
8 A Elytral base closed, scutellum invisible (fig. 13)
9 P Apical spinae on elytra present (fig. 16)
10 A Ovipositor simple and without clear segmentation, fully sclerotized (figs 33, 34)
11 (A) Aedeagus with parameres broadly overlapping dorsally (figs 35, 36)
12 A Meta-wing with A_1 branch absent (fig. 51)
13 (A) Meta-wing with distal cell complete, shortened (r cross-vein present) (fig. 51)
14 P Hair on body zoned, short

Kerremans (1904) and Heyne-Taschenberg (1907) mention unlobed tarsal pads and sexual dimorphism (carinate last abdominal sternite in the male). Both characters are poorly defined in all Julodini.

The morphological analogies between *Sternocera* and *Amblysterna* are most probably due to the similar habitat (fig. 54) and niche occupied by the two genera. The meta-wing, prosternum and metacoxa fit best on the *Julodella*-line. The large size may be an expression of specialization, since *Amblysterna* is obviously a terminally specialized remnant (see characters 1, 10, 11), from which none of the other genera can be derived.

Biology

Unknown, but presumably similar to *Sternocera*. Trees on which adults were collected are mainly *Acacia* spp.

Phylogeny and distribution

Théry (1949) regarded *Amblysterna* (including *Neojulodis*) as the most primitive genus of the tribe, and singled out *J. vylderi* and *J. aristidis* as its closest relatives in *Julodis*. Cobos (1953) pointed out the impossibility of an apomorphic character like the forked metasternum reverting to the primitive state and also that *Julodis* and *Amblysterna* are only related via *Julodella* (fig. 54). Therefore, both statements of Théry are unrealistic. The other characters that Théry (1927) puts forward in favour of a 'primitive' position for *Amblysterna* are the simple ovipositor (which, in reality, is highly specialized), and the small size and range of variation (both of which apply to *Neojulodis* only and are indicative of lack of specialization and recent radiation rather than of evolutionary age).

The morphology indicates a *Julodella*-like ancestor, and the present distribution must have resulted from an invasion of this ancestor into the East African tropical area, as in the case of *Sternocera*. The parallel evolution of *Amblysterna* and the tropical *Neojulodis (Protojulodis)* poses a problem, since they are at present sympatric. Subsequent invasions are unlikely to be the explanation because of the obvious holophyletic origin and absence of both outside East Africa. The striking differences in size and ovipositor structure suggest an early specialization of *Amblysterna* to a different niche, but an allopatric pattern for the division between *Amblysterna* and *N. (Protojulodis)* is not clear.

Species diversity was probably never very great in *Amblysterna*. The one northern and one southern species both have a wide distribution and show hardly any variation.

The presence of the *Neojulodis-Amblysterna* complex in East Africa probably prevents the intrusion of *Julodella* and separates its northern and southern species, just as *Sternocera* separates the two *Julodis* groups.

The *Julodella*-derived, but completely opposite, apomorphisms of *Amblysterna* and *Julodis* correspond with the opposite extremes of habitat-niche. These divergent characters are particularly obvious in the body hair, prosternum, ovipositor and aedeagus. The similarities between the genera *Sternocera* and *Amblysterna*, which are separated by four cladistic divisions, merit further discussion. The similar body outlines and sclerotized ovipositors are classical cases of convergence, and both are analogous rather than homologous. (In *Amblysterna* the ovipositor is unsegmented and differently derived, while the body outline is only superficially similar, *Amblysterna* having the largest and *Sternocera* the smallest head in the tribe Julodini.) The similarity in shape of the last antennal segment and sharply zoned short hair on the body are, however, more than accidental. These characters are directly based on the same plesiomorphs, carried to both lines ('concealed genotype' of Mayr (1974)), and are therefore 'parallelisms' in the sense of Mayr.

NEOJULODIS Kerremans

Julodis (Neojulodis) Kerremans, 1903: 13; 1904: 333; Heyne-Taschenberg 1907: 125
Neojulodis Obenberger 1926: 32; Ferreira & Ferreira 1958: 79
Amblysterna Semenow 1906: 152 (*pars*); Théry 1927: 179 (*pars*)

Type species (new designation): *Buprestis hirta* L., 1758.

Morphology

Neojulodis shares the derived character of a forked metasternum (or divided meso-metasternal suture) with *Amblysterna*. It is, however, easily distinguished by its primitive ovipositor and unmodified last antennal segment (both inherited from the ancestor near *Julodella*), as well as the apomorphic open distal cell on hind-wing (or lost r vein). All these characters, as well as the apical spines on the elytra and backward position of the procoxa, rule out a derivation from *Julodis*. Five characters in the list of fourteen differ between the two subgenera, and the remainder are as follows:

1 P Last antennal segment undifferentiated (figs 19, 23)
3 P Procoxa far removed from anterior rim of prosternum (figs 18, 22)

4 A Meso-metasternal suture interrupted by sternal cavity (figs 18, 22)
8 A Elytral base closed, scutellum invisible (figs 17, 21)
9 P Apical spinae on elytra present (figs 20, 24)
10 P Ovipositor membranous, typically with sensory bristles on tip (figs 45, 46)
11 P Aedeagus undifferentiated (figs 47, 48)
12 A Meta-wing with A_1 branch absent (fig. 52)
13 A Meta-wing with distal cell open (r cross-vein lost) (fig. 52)

The apomorphism of *Neojulodis* is not strongly divergent from *Julodella*, as is the case with *Amblysterna* and *Julodis*. It consists mainly of reductions, the common phenomenon in 'vertical' evolution. Its line of evolution, therefore, superficially appears to be intermediate between *Amblysterna* and *Julodis* (Kerremans 1904). Kerremans (1904) distinguished the two species-groups '*N. hirta* (L.)' and '*N. vittipennis* (Fahraeus)'. (These same two species have here been designated the type species of *Neojulodis s. str.* and *N. (Protojulodis)* respectively.

Kerremans (1904) also mentioned the unlobed tarsal segments, a character which may be disregarded (Semenow 1906). Ferreira & Ferreira (1958) correctly observed that the metasternum may be salient, although this structure only occurs in the tropical species of *Protojulodis*, and is less developed than, and probably not homologous with, this structure in *Sternocera*.

Semenow (1906) synonymizes *Neojulodis* with *Amblysterna*, and Théry (1946) discusses the genus as *Amblysterna*.

Biology

This is dealt with below under the two subgenera.

Phylogeny and distribution

Neojulodis probably originated from a *Julodella*-like stock in the north-east Ethiopian region, and radiated southwards into more tropical areas. Of the two subgenera, *Protojulodis* is the more primitive, and the most primitive species occur in the present tropical Central Africa. The evolution and distribution are discussed further under the subgenera below.

NEOJULODIS (PROTOJULODIS) subgen. nov.

Type species: *Julodis vittipennis* Fahraeus, 1851

MATERIAL EXAMINED. *N.* (*P.*) *rufolimbata* Fairmaire (34 + type); *N.* (*P.*) *myrmido* Fairmaire (131 + type); *N.* (*P.*) *bequaerti* Kerremans (10 + type); *N.* (*P.*) *clermonti* Théry (4 + type); *N.* (*P.*) *vittipennis* (Fahraeus) (819 + types); *N.* (*P.*) *laticollis* Gahan (6 + types)

Morphology

The morphological characters studied (other than those listed under the genus above) are as follows:

2 P Anterior rim of prosternum with a complete ridge (fig. 22)
5 P Metasternal sulci complete (fig. 22)

6 P Metacoxal sculpture and hair sparse in middle (fig. 22)
7 P–A Pronotal shape variable from globose to declivous (fig. 21)
14 P Hair on body short

From this list it is apparent that *Protojulodis* is the least specialized of all the lineages with the forked metasternum. It is the most heterogeneous group of all the Julodini, containing some of the most primitive, relatively large, species with limited variation (*laticollis, clermonti, bequarti*), which must be very close to the ancestral *Julodella* forms. These species all have very limited distributions in the tropical Central Africa. The two species *myrmido* and *vittipennis* are savanna forms, corresponding in distribution with the two *Amblysterna* species, but, unlike them, are highly variable. The combination of interrupted meso-metasternal suture, lost r cross-vein on hind-wing and short hair clearly separate the subgenus from all other groups in the tribe.

Biology

Unlike the species of *Neojulodis s. str.*, those of (*N*). *Protojulodis* are distributed in tropical forest and savanna. The biology of the forest species is completely unknown, while only some of the plants on which adults were collected have been recorded for the savanna species.

Phylogeny and distribution

The present distribution of *Protojulodis* seems to represent a radiation of the genus *Neojulodis* from the ancestral *Julodella* habitat in the North-West to Central and East Africa. This radiation (as in *Amblysterna*) probably post-dated the separation of India from Africa, since no *Protojulodis* species are found in India, while *Sternocera* is well represented there. This would put the origin of *Protojulodis* at about 70 million years ago or later.

The recent radiation of two species into savanna could have been the result of the recession of forest from East Africa and subsequent adaptation of the resident *Protojulodis* to savanna conditions. (That East Africa was forested before the split between Africa and India is strongly suggested by the presence of *Sternocera* in tropical forests on both continents.)

As in the southern *Julodis* and *Neojulodis s. str.* and the northern *Julodis* and *Julodella*, the genera *Amblysterna* and *Protojulodis* are an example of two julodine groups occupying the same biotope but differing considerably in size.

Neojulodis (Neojulodis)

Type species: (See nominate genus above)

MATERIAL EXAMINED. *N.* (*N.*)*subcostata* (Castelnau) (98 + types); *N.* (*N.*) *picta* (Thunberg) (266); *N.* (*N.*) *hirta* (L.) (173); *N.* (*N.*) *integrovittata* Théry (183 + types); *N.* (*N.*) *tomentosa* (Olivier) (353).

Morphology

The morphological characters studied (other than those listed under the genus above) are as follows:

2 (A) Anterior rim of prosternum with a continuous ridge, but from this ridge triangularly declivous anteriad from the middle (fig. 18)
5 (A) Metasternal sulci often indistinct in the middle (fig. 18)

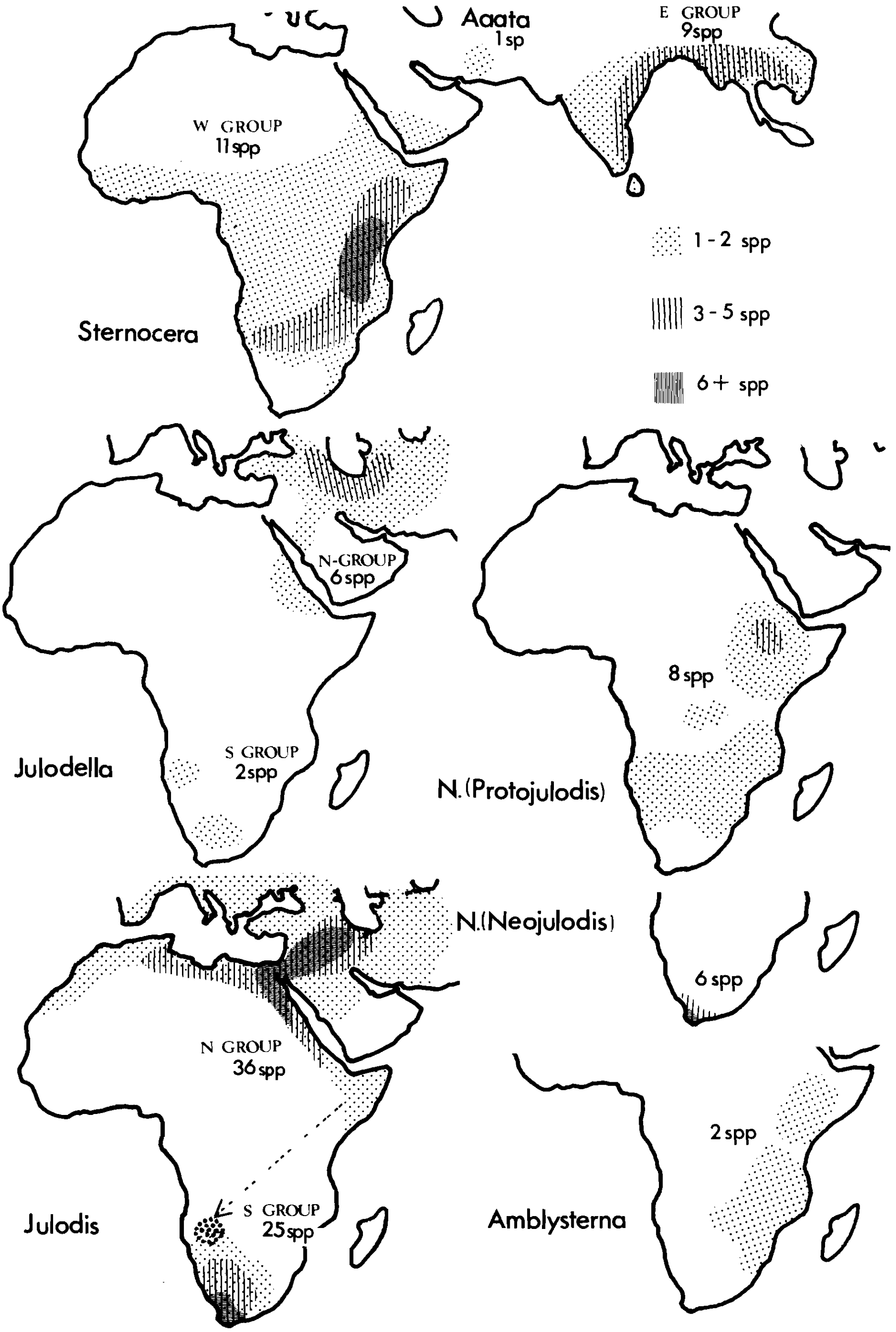

Fig. 54. World distribution of species of the genera *Julodis* (northern (N) group after Obenberger (1926), Théry (1928), Lotte (1943) and Cobos (1953); southern (S) group after Obenberger (1926) and Ferreira & Ferreira (1958)), *Julodella* (northern group after Obenberger (1926)), *Sternocera* (eastern (E) group after Théry (1949), western (W) group after Théry (1924), *Aaata, Neojulodis* (with subgenus *Protojulodis*) and *Amblysterna.*

6 A Metacoxa with dense sculpture and a hair-tuft in the middle (fig. 18)
7 (A) Pronotal shape between globose and attenuated (fig. 17)
14 A Hair on body long, at least on some parts.

The highly apomorphic morphology can, without doubt, be traced to the more plesiomorphic *Protojulodis*, while the latter has no apomorph characters that are not present in *Neojulodis s. str.* The subgenus is easily recognized among all Julodini by the median hair-tuft on the metacoxa.

Biology

The subgenus *Neojulodis* is primarily montane; adults are found on shrubs in the temperate biome of the Western Cape, and the larvae probably feed on the roots of the shrubs. Adults of *N. hirta* were observed in one instance on snow-covered shrubs (A. J. Hesse, pers. com.) indicating an adaptation to a high-altitude climate in Africa.

Phylogeny and distribution

The derivation of *Neojulodis s. str.* from a *(N.) Protojulodis*-like ancestor can most easily be explained by a southward migration along a temperate belt along the montane biome (Tinley 1975) on the eastern side of Africa. Erosion of these mountains, and changes to a more tropical climate, left only the southern remnants of this radiation. With the increase in aridity of the western Cape and Karoo and the spread of temperate flora down the mountains, a new radiation of *Neojulodis s. str.* set in, repeating the pattern of the southern *Julodis* (see above). This radiation is, however, much less advanced in *Neojulodis s. str.*, and species in the lower-lying areas of the western Cape are so variable and ill-defined that it is difficult to separate species, subspecies and local populations from one another. The invasion of the Karoo-Namaqualand regions is not as extensive in *Neojulodis s. str.* as in *Julodis* (fig. 54). *Neojulodis s. str.* could thus have derived at any time after the origin of *Neojulodis s. lat.*, since the radiation of the Cape *Neojulodis s. str.* seems very recent and contemporaneous with or even later than the radiation of *Julodis* into the Palearctic in the Montian period (Cobos 1955).

The long body hair, anterior rim of prosternum and pronotal shape are all similar to *Julodis*. These similarities must be attributed to convergence resulting from specialization to a similar climatic niche, as a direct relationship is ruled out by the shape of metasternum and ovipositor and the wing venation. As in *Sternocera* and *Amblysterna*, both parallelism and convergence may be involved here, and the relationship of *Julodis* and *Neojulodis s. str.* in the temperate biome is in many ways analogous to that between *Sternocera* and *Amblysterna* in the tropical savanna.

DISCUSSION

The system of classification of the Julodini proposed here is consistent with a cladistic system in that polyphyletic groups are avoided through the use of synapomorphic characters for basic grouping. A number of paraphyletic groups are, however, recognized. These are based on the absence of certain apomorphs as well as on distributional evidence. A full account of the reasons for adopting this procedure is in preparation.

Because (*N.*) *Neojulodis* and *N. (Protojulodis)* share the cladistically important characters of wing venation and ovipositor-type to the exclusion of all other genera, and share significantly more derived and primitive characters than any two genera, I chose to regard them as one genus. On the other hand, they constitute two clearly different lineages, and I therefore separated them on a subgeneric level.

A few trends in the Julodini are worth mentioning. As these observations are based on this very limited group only, they are inadequately proved but might be of interest when compared with findings in other groups.

1. Recent invasions (northern *Julodis* in the Palearctic; *Neojulodis* in the Karoo; *Protojulodis* in southern African savanna; *Sternocera* in China) include highly variable species, while geographically persistent groups do not. Species diversity is, however, not higher in recent invasions.
2. Geographically terminal and isolated populations of species and species of genera that are stable and not radiating tend to be individually less variable than the parental groups.
3. Body size increases with time on non-radiating lines. (*Sternocera, Aaata, Julodis* large, *Amblysterna* intermediate; others small.)
4. Species diversity and variability are generally higher in the evolutionarily more recent branches as compared with the next older branches (in fig. 55, compare, e.g., D and B; H and B; C and A).

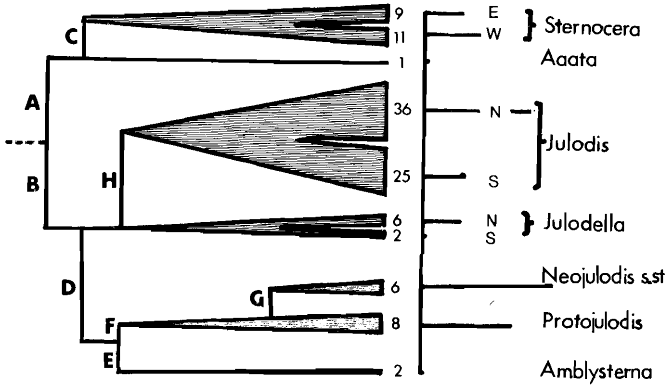

Fig. 55. Phylogram of the Julodini: width of branches indicates species diversity, each branch or geographically isolated part of branch is followed by the estimated number of species (based on references in legend to fig. 54). The lengths of lines opposite the branches indicate estimated relative morphological variation of the most variable species of each group. Apomorphic characters on branches A-H as follows: A. ovipositor sclerotized; scutellum invisible; meso-metasternal suture well behind sternal cavity. B. metacoxa with sculpture reduced medially; fork in A_1 vein lost. C. last antennal segment modified; procoxa near anterior rim of prosternum; meso-metasternal suture on a horn-like protrusion; fork in A_1 vein lost; aedeagus with membranous lobes ventrally; metasternal sulci reduced in middle. D. meso-metasternal suture interrupted by sternal cavity; scutellum invisible. E. ovipositor completely sclerotized; aedeagus with widely overlapping parameres; last antennal segment modified; metasternal sutures vague in middle. F. loss of r cross-vein; ovipositor with sensory bristles. G. metacoxa with hair-tuft in middle; long pilosity at least on pronotum. H. scutellum invisible; metacoxa with very marked median shiny spot; last antennal segment truncate; procoxa near anterior rim of prosternum; apical spinae on elytra absent; ovipositor modified.

5 The greater the distance between a derived and a parental genus (as expressed in number of derived characters: fig. 55), the greater the immediate crop of congeneric species in the derived genus, but the fewer the consecutive cladic divisions on the line.

Paleogeographic and paleoclimatic information, such as recent modern insights into continental drift (Tarling & Tarling 1975; Axelrod & Raven 1972) are valuable for reconstructing phylogenies. Unfortunately the geological history of the regions in the Near East that are crucial in the evolution of the Julodini are still not accurately reconstructed. The scarcity of dated paleoclimatic information on the African continent is a further difficulty in making evolutionary interpretations. In Africa, the present distribution and probable phylogeny of julodine genera corroborates some present and past zoogeographic sub-zones and ecological biomes suggested by Endrödy-Younga (1978) and Tinley (1975). These are as follows:

1 The montane-temperate belt that at one time probably virtually encircled the continent is at present best preserved from north-east to south-west. This biome was fractured by erosion and climatic changes. Two groups in the Julodini, the southern group *Julodis* and *Neojulodis s. str.*, clearly have their recent epicentres of speciation in the extreme south-west montane temperate region. The former was probably connected to the Mediterranean along the montane biome (Endrödy-Younga 1978: 807–808). It seems that the most variable and therefore probably the youngest members of both groups are at present radiating northwards into the semi-arid and arid regions of Endrödy-Younga's 'south-western zone'. This radiation route has been recorded for several beetle groups by that author and is also known to me from studies on the *Acmaeoderini* and *Nothomorphini* (Buprestidae) (Holm 1976; 1978) and on the Trogidae (C. H. Scholtz, pers. com.). The repeated occurrence of this northward radiation suggests a recent climatic change on the south-western side of the continent that favours the hardy Cape montane relict fauna, probably through an increase in the aridity of these areas.

2 The tropical region, which was continuous from the central-west to the south-east of the continent during pluvials, but which was probably repeatedly interrupted by the arid belt (see below) during interpluvials, is not extensively inhabited by the Julodini. Apart from the invasion of *Sternocera*, only two isolated remnant species of *Protojulodis* occur in the true tropical biome.

3 The savanna biome connected south-west and north-east Africa in interpluvials in the form of a dry belt which intersected the tropical biome. This is the most important pattern where the Julodini are concerned. The ancestors of the single northern *Julodis* and two southern *Julodella* species that occur in south-western Africa undoubtedly originally linked with those of their northern counterparts along this route. Most of the species of *Sternocera, Protojulodis* and *Amblysterna* are distributed along the same route, the two former across to South West Africa along the 'Trans Botswana transitional belt' (Endrödy-Younga 1978). These three genera obviously adapted to the moister savanna conditions that prevailed in this biome during pluvials.

4 True desert biomes are not extensively invaded by the Julodini. The hardiest desert forms occur in the genera *Julodis* and *Julodella*, and these show extensions into desert areas, both in the north and in the south. All can probably be traced to montane ancestral forms (see 1 above), while migration of northern and southern desert-adapted forms took place along the savanna belt (see 3 above).

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