

FIG. 2B.—Aedeagus of a tentyrioid Tenebrionid (*Somaticus* [*Trichotrachys*] *metropolis* sp.n.).—a=dorsal surface of aedeagus; b=inner surface of penis; c=lateral aspect of penis, with the inner surface at right; d=outer surface of penis; e=ventral surface of aedeagus, with the penis extracted; f=lateral aspect of aedeagus, with the penis extracted. (ap=apicale; ba=basale; d=ductus ejaculatorius; g=ventral groove; ig=inner groove of penis.)

TENTYRIINAE

The subfamily Tentyriinae is sharply separated from all the other Tenebrionidae by the above-mentioned and very constant characters. Leconte and Horn divided the American Tenebrionidae into the three subfamilies Tentyriinae, Asidinae and Tenebrioninae. Gebien, 1937b, in his systematic catalogue of Tenebrionidae of the world, accepted the same three subfamilies, but in a different conception. While Leconte and Horn separate the Asidinae from the Tentyriinae, by the presence of a distinct trochantin of mesocoxae, Gebien uses as a criterion the size of mentum and places in the Asidinae all those tentyrioid tribes, the mentum of which leaves exposed the cardo and stipes of maxillae, whether or not exhibiting a trochantin of mesocoxae. However, he confesses that this division is weak, as the large tribe of Asidini ought to be placed in the Tentyriinae on account of the large mentum, concealing cardo and stipes of maxillae. I do not see the necessity of subdividing the tentyrioid tribes into subfamilies, as their separation from the many tenebrionid tribes is extremely sharp and constant on the basis of the absence of intersegmental membranes of distal sternites of abdomen.

Moreover, Leconte and Horn's criterion of the presence of a distinct trochantin of mesocoxae in the American Asidini, does not hold for the Southern African Asidini, in which the trochantin is lacking or punctiform. Gebien's Asidinae are an artificially mixed group of tribes and set up as a last resource as the author himself correctly confesses.

Consequently I shall not follow the modern interpretation of subfamilies, but unite under the subfamily of Tentyriinae all those Tenebrionidae in which the intersegmental membranes of abdomen are absent (tentyrioid Tenebrionidae).

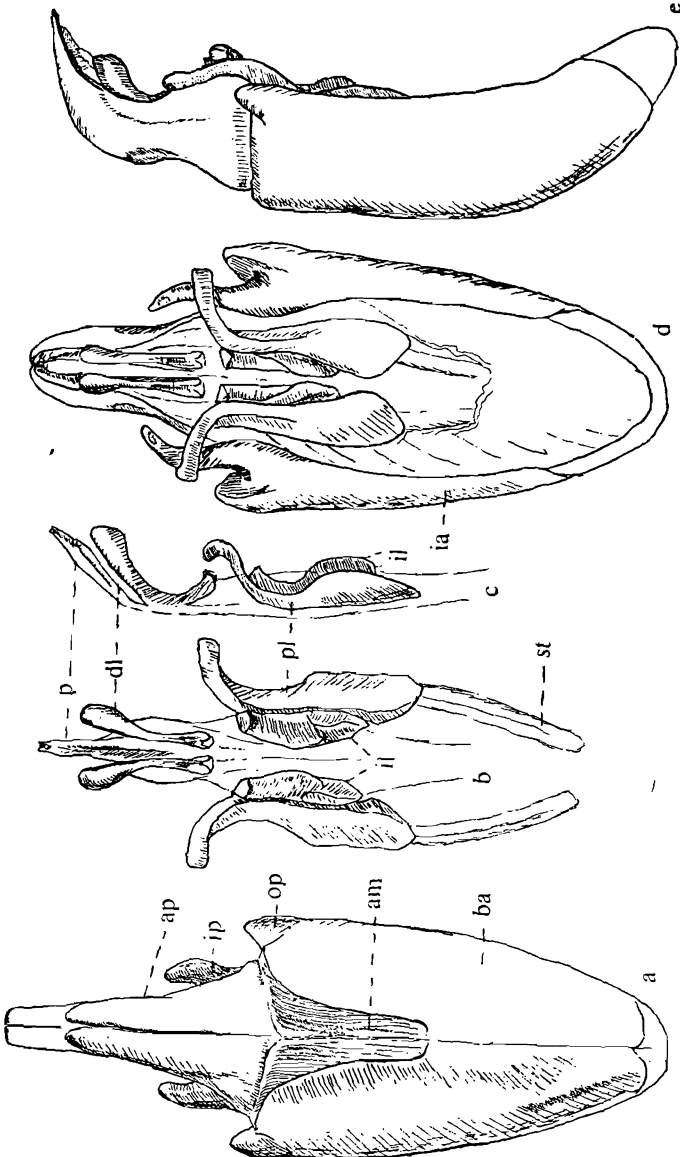


FIG. 2C.—Aedeagus of a tentyrioid Tenebrionid (*Anomalipus mastodon* Fähræus).—a = dorsal surface of aedeagus; b = outer surface of the penis with the triplicate pairs of lacinia; c = lateral aspect of penis with lacinia; d = ventral surface of aedeagus; e = ventral aspect of aedeagus, with the ventral surface at right. (am = articulation membrane; ap = apicale; ba = basale; dl = distal lacinia; ia = inflexed alae; il = inner lacinia; ip = inner process of basale; op = outer process of basale; p = penis; pl = proximal lacinia; st = struts of penis.)

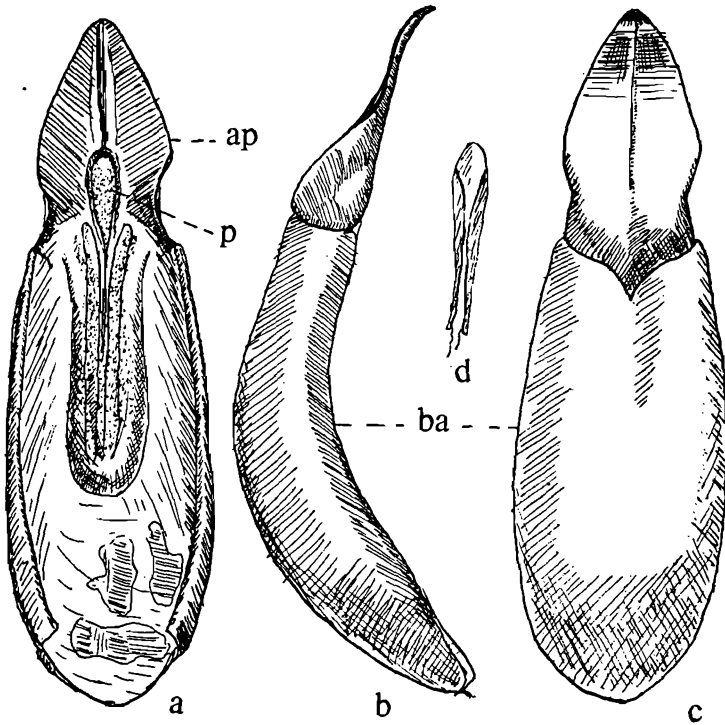


FIG. 2D.—Aedeagus of a tenebrioid Tenebrionid (*Anomalipus meles* Fähræus).—a=ventral surface of aedeagus; b=lateral aspect of aedeagus, with the ventral surface at right; c=dorsal surface of aedeagus; d=penis. (ap=apicale; ba=basale; p=penis.)

The tribes of Tentyriinae are all extremely specialized and sharply separated from one another. There are no more intermediate forms left and their morphology differs to such an extent that there are few characters which disclose or indicate their intertribal phylogenetic connection.

Their distribution covers the temperate zones of the world, but they are scattered in Australia, confined to the Southern and in particular Mediterranean countries in Europe, and have not developed endemic tribes on these two continents, nor in Asia. Their centre of evolution is undoubtedly Southern Africa, where twelve sharply defined tribes occur (text-fig. 3), composed of the most spectacular and specialized Tenebrionidae of the world. Of these tribes four (Dactylocalcarini, Cryptochilini, Calognathini and Vansonini) are endemic, two (Molurini and Eurychorini) are autochthonous to Africa, two (Zophosini and Adesmiini) are African-Asiatic, one (Asidini) is African-European-American, another one (Tentyriini) African-Asiatic-American, and two (Zopherini and Stenosini) are distributed discontinuously over all five continents. Casey assumes for America sixteen tribes, but these, with the exception of the world Zopherini, represent small, much less specialized and differentiated forms, the inter-tribal connections of which are not sharply interrupted as is the case in the Southern African tribes. Moreover, some of his tribes have not been recognized by later systema-

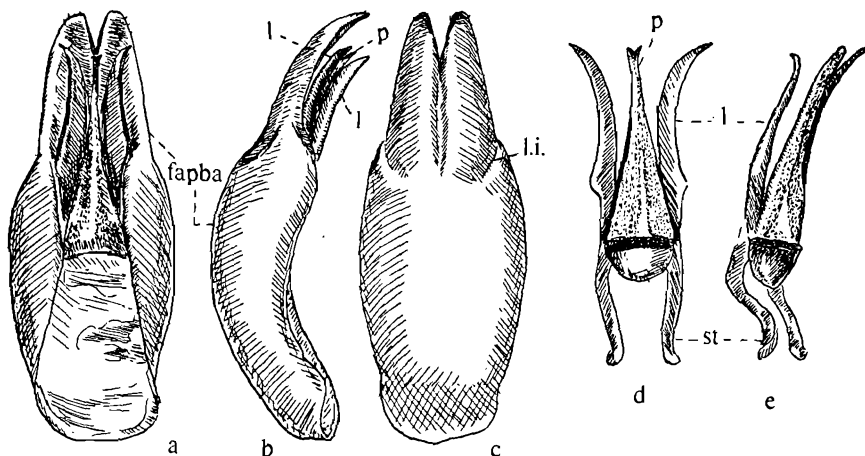


FIG. 2E.—Aedeagus of a tenebrioid Tenebrionid (*Zadenos [Serridenos] solenopistoma* Koch).—*a*=ventral surface of aedeagus; *b*=lateral aspect of aedeagus, with the ventral surface at right; *c*=dorsal surface of aedeagus; *d*=outer surface of penis with single pair of lacinia; *e*=latero-diagonal aspect of penis with lacinia. (*fapba*=the fused apicale and basale; *l*=lacinia; *li*=lateral impressions on dorsal surface of aedeagus; *p*=penis; *st*=basal struts of penis.)

tists, and I suspect that several of them may in actual fact belong to the Tentyriini. Unfortunately no inter-continental studies have been carried out.'

A single African-Asiatic tribe, the Erodijini, does not reach Southern Africa.

Phylogenetically the Tentyriinae may represent the most ancient group of Tenebrionidae, having derived from some extinct and alate group. They are all apterous and ground-living beetles, with the exception of most of the Epitragina of Tentyriini. The wings of the latter, however, as well as their arboreal habits, appear to be due to a recessive development, as they do not show any other relation with the many tenebrioid Tenebrionidae, which are alate and arboreal; on the other hand typically transitional forms occur in Southern Africa between alate Epitragina and apterous Tentyriina, which forbid the separation of both tribes.

All Tentyriinae are eremophilous, exhibiting in their extreme desertic forms the highest degree of adaptation in overcoming the difficulties of existence in the wastes of the barren desert. The most specialized of these forms are to be found in the South African Namib desert. They are relicts of an ancient African-Turanian primary fauna, which can be reconstructed by the recent distribution of Adesmiini and many Tentyriini (e.g. *Cyphostethe* [*]). The Sahara, although much greater in extent than the Namib, offers only a few, rather indifferent and homogeneous, poorly specialized forms of primary Tentyriinae, but is densely populated by a strongly specialized, secondary fauna of tenebrioid Tenebrionidae. The latter, to which belong also the Pimeliini and

(*) cf. Gridelli's important discussion on the African-Asiatic relations in the Tenebrionidae, published in his modern "Comprehensive Catalogue of Arabian Tenebrionidae," 1953.

Platyopini, have developed forms which closely resemble the desertic Tentyriinae. Phylogenetically, however, they are desertic tenebrioid Tenebrionidae of a younger and secondary fauna, overlapping the still existing primary representatives of Tentyriinae. As an example of such genetically convergent but non-related forms, I may quote here only the great similarity in habitus, vestiture and habitat in the Pro-Namibian (*) genus *Vansonium* Koch and the Saharan genus *Pseudostorthocnemis* Gridelli, as well as the similar habitus of certain Molurina and *Pimelia*, which has been taken by Solier and Lacordaire to express a phylogenetic relationship.

As observed in life the greater part of the South African Tentyriinae behave rather like small Vertebrata than insects. Most of them are slow-moving, nocturnal creatures, many umbral or crepuscular, but many also diurnal to highly heliotactic. Among the latter there are the fastest runners among the Coleoptera (e.g. *Cardiosis*, *Ophthalmosis*, *Onymacris*, *Stenocara*, etc.), some with extremely elongated legs, bearing the body high above the level of the soil (e.g. *Stenocara phalangium* Gebien, *Histrionotus lightfooti* [Péringuey]). Among the psammophilous groups there are heliotactic "sand-swimmers" and "sand-jumpers" (many Zophosini), nocturnal "sand-sinkers" (*Lepidochora* of Eurychorini) and an anophthalmous "sand-digger" (*Dactylocalcar*). Others are strictly petrophilous. Strongly pronounced myrmecophilous tendencies can be observed in many Zophosini, in nearly all the Adelostomina of Eurychorini and in the Stenosini. The only truly cavernicolous Tentyriin so far known is the stridulating *Symphochora simoni* (Fairmaire) from the Makapan caves in the Northern Transvaal.

Sound is produced in many ways. Apart from the unique knocking of "Tok-Tokkies" (Molurini), being the effect of rhythmic movements of the whole of hind-body, generally only in the ♂ (†), there exist occipital-prothoracic stridulatory organs in the Cryptochilini and Vansonini, abdominal ones in the Epitragina and pseudopleural-femoral ones in the Tentyriina of Tentyriini and in a few Molurini. The size of body varies to a very large extent, viz. from a little more than 2 mm. to almost 80 mm. in length, with the Kalaharian *Stridulomus sulcicollis* (Péringuey) representing the largest Tenebrionid in the world.

SYNOPSIS OF THE SOUTH AFRICAN TRIBES OF TENTYRIINAE.

1. Mentum moderately large to small, leaving exposed cardo and stipes of maxillae and prelabium (text-fig. 62). Anterior margin of postgenae with a maxillary ridge or emargination (*me* in fig. 62). (Either scutellum large and about as broad as inter-humeral space of elytral base [Pl. IV, fig. 5], or head elongate and with dorsally exposed basal peduncle [text-fig. 4], or the retracted portion of occiput with stridulatory organ [text-fig. 9], or mandibles strongly dimorphic, stag beetle-like and enlarged in the ♂ [text-fig. 5].)

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(*) cf. Koch, 1952c, on the extension and division of the Namib Province.

(†) Only the ♂ was believed to "knock" but Mrs. S. R. Zenzinger, who carried out observations on the specifically differing rhythm, watched also ♀♀ of *Phanerozoma quadricostatum* (Fähræus), producing knocking sounds with abdomen.

- Mentum very large, concealing at least cardo and stipes of maxillae and often also prelabium (text-fig. 11)*. Anterior margin of postgenae with a more or less produced and enlarged maxillary lobe, running close to lateral margin of mentum or submentum (*mp* in text-fig. 12). (Never exhibiting particulars of opposing paragrah.)
2. Mesocoxae with trochantin (text-fig. 46); the latter rarely reduced or practically absent (text-fig. 45), but in this case the anterior margin of pronotum with prominent lobiform structures (Pl. V, figs. 15—17). Scutellum very large, extending

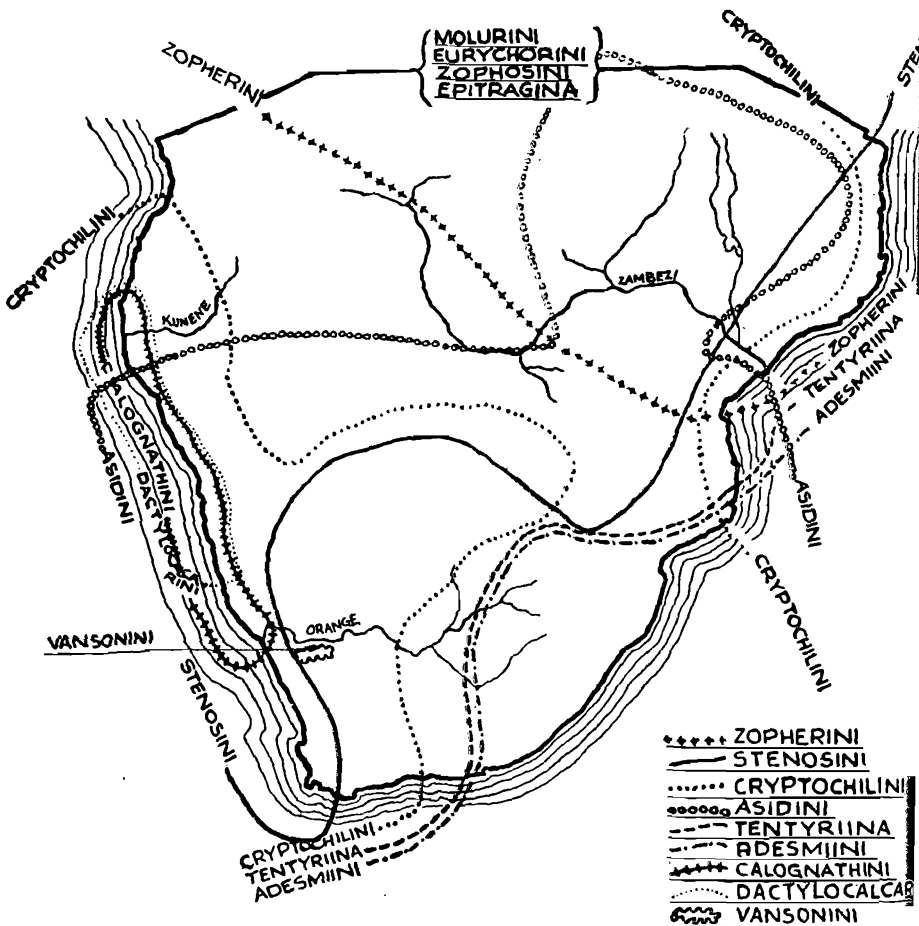


FIG. 3.—Distribution of the tribes of Tentyriinae in Southern Africa.—The Molurini, Eurychorini, Zophosini and Epitragina of Tentyriini occur over the entire territory.

(*) In the tenebrioid Tenebrionidae this particular is exhibited but in the Anomalipina of Platynotini (Opatrinae, cf. Koch, 1954b).

across entire width of mesothoracic peduncle; elytral base without vertical articulation face, the pronotum consequently freely movable on scutellum. Antennae with eleven segments (text-fig. 64). Head not pedunculate (text-fig. 63).

I. MOLURINI

(Pls. III—XXIV, with the exception of fig. 1 on Pl. III) (sensu Solier et Lacordaire [+ Sepidiini sensu Gebien, 1937b].)

Wingless ground-living beetles, about 1,000 species and many genera occurring all over the African continent (text-fig. 39), Arabia, Mesopotamia and the Circum-Mediterranean Province. The bulk of species and genera are Ethiopian and in particular Southern African, whereas only two genera of Sepidiina (*Sepidium* and *Vieta*) are represented in the Palaearctic and Saharan Regions.

Key to subtribes, see p. 33.

- Mesocoxae without trochantin (text-fig. 15) (*). Anterior margin of pronotum truncate or emarginate, without prominent and lobiform structures. Scutellum small or absent, in the former case occupying a small portion of the middle of elytral base; the latter with vertical articulation surface, opposing a similar articulation surface of pronotal base of prothorax, the pronotum thus prevented from moving on or overlapping scutellum and elytral base (text-fig. 4). In most cases, however, this structure is not visible, as both pronotal and elytral bases are solidly and closely attached to each other (which is never the case in the Molurini) (text-fig. 8). Antennae with ten or exceptionally nine segments, but in one tribe with eleven segments, when the head is strikingly elongate, with freely visible and demarcated cervical peduncle (text-fig. 4).
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- 3. Body linear and small, not more than 5 mm. in length. Antennae with eleven segments. Head free, prognathous, elongate, with exposed, sharply demarcated and sclerotized cervical peduncle; tempora and postgenae several times longer respectively than eyes and oral-frontal portion of underside (text-fig. 4). Prothorax elongate, sharply separated dorsally from elytra by the exposed mesothoracic peduncle; pronotum much longer than broad (text-fig. 4), prosternum several times longer than procoxal cavities. Metasternum long, not shorter than basal sternite of abdomen and about three times as long as metacoxal cavities; episternum linear, several times longer than broad. Elytra loosely attached to pronotum.

(*) Español, 1954, in his key to the tribes of Tenebrionidae, confounds trochanter with trochantin. He attributes to the Stenosini and Elenophorini "mesocoxas sin trocánteres", to the Akidini "mesocoxas con trocánteres". However, the trochanter is a divided or connate sclerite of the femur, not pertaining to the coxa itself, while the trochantin, in Coleoptera, is referred to a sclerite often present on the outer side of mesocoxa. He figures the mesocoxa of *Elenophorus* and *Akis* (figs. 6 and 7, loc. cit.), omitting to indicate the trochanter on fig. 6 of *Elenophorus* and the trochantin on fig. 7 of *Akis*. *Elenophorus*, in actual fact, exhibits a very reduced and small trochanter on intermediate femur and posterior one, whereas *Akis* possesses a large trochantin on mesocoxae, as well as a conspicuous trochanter on intermediate and posterior femora.