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RELATIONSHIPS IN THE TRIBE ADESMIINI (COLEOPTERA: TENEBRIONIDAE) AND A REVISION OF THE GENUS STENODESIA REITTER

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A cladistic analysis is made of the relationships between the genera of the tribe Adesmiini (Coleoptera: Tenebrionidae). As a result of the analysis, two genera, *Physosterna* Solier and *Cauricara* Penrith, are reduced to subgenera of *Adesmia* Fischer and *Stenocara* Solier respectively. The North African monotypical genus *Megagenius* Solier is removed from the tribe Adesmiini and placed in the tribe Tentyriini. The genus *Stenodesia* Reitter is revised and two new species, *Stenodesia montiscedrae* and *S. oosthuizeni*, and a new subspecies, *S. globulum kaokoensis*, are described. As a result of the discovery of the latter, *S. verruculifera* (Haag) and its subspecies *marshalli* Koch are reduced to subspecies of *S. globulum* (Haag). Keys to the genera and subgenera of Adesmiini and to the species and subspecies of *Stenodesia* are given. The biogeography and centre of origin of the tribe are discussed.

INTRODUCTION

The southern African Adesmiini were revised by Penrith (1979). No cladistic analysis was attempted then, although the genera were defined as far as possible according to cladistic principles, i.e., where character evaluation was possible, they were based on apomorphies.

An examination and evaluation of the tribe Adesmiini, including a wide variety of tropical and Palaearctic species not examined in the previous revision, has enabled me to make a cladistic analysis of the relationships in the tribe. While the results of this analysis indicate no changes in the composition of the groupings proposed in the previous revision, the status of some of those groupings, used at generic level, has to be changed according to strict cladistic practice. Accordingly, the genera *Physosterna* Solier and *Cauricara* Penrith are reduced to subgenera of *Adesmia* Fischer and *Stenocara* Solier respectively. The present paper also includes the transfer of a genus formerly included in Adesmiini to the tribe Tentyriini, a key to the genera and subgenera of Adesmiini, descriptions of new taxa in the genus *Stenodesia* Reitter, a

checklist of the genera and subgenera of Adesmiini, and a revised checklist of the genus Stenodesia.

SYSTEMATIC POSITION OF MEGAGENIUS FRIOLI SOLIER

The monotypical North African genus *Megagenius* Solier was placed in the Adesmiini at the time of its description by Solier (1835). When Casey (1907) and Gebien (1910) separated Epiphysini as a tribe from Adesmiini, *Megagenius* was placed with *Epiphysa* in Epiphysini. Koch (1955) disagreed with the separation, and reunited Epiphysini with Adesmiini, which he defined as having the following characters: 'epimeron of mesosternum elongate, subparallel anteriorly and running parallel with elytral margin from base to metasternal episternum; intercoxal process of abdomen very broad, distinctly, and often much, broader than either submentum or anal sternite; antennae with eleven segments; postgenal margin with maxillary tooth; body not tomentose, with strongly raised and laterally declivous elytra'.

The most important of these characters is the shape of the epimeron of mesosternum. Only the first two characters listed are definitive of the Adesmiini, the remaining characters being rather widely distributed in the tentyrine Tenebrionidae. The broad intercoxal process of the abdomen is associated with the characteristically broad shape, and occurs in members of other tribes that exhibit this shape, e.g. Eurychorini, Molurini, and Cryptochilini. *Megagenius* is relatively broad and convex, although it would be the least inflated of the Adesmiini, and the intercoxal process of the abdomen is rather broad. However, the epimeron of mesosternum of *Megagenius* is typical for Tentyriini and unlike that in Adesmiini (Fig. 1a, b). The head, which strongly resembles that of *Epiphysa*, with expanded genae and the dorsal mandibular process developed, is of a type widespread in the Tentyriini. On the character display of the two tribes, I regard the Tentyriini as being the sister-group to the Adesmiini; this is discussed in more detail below. The remaining listed characteristics of Adesmiini are shared with the Tentyriini.

Megagenius is therefore removed from Adesmiini and placed in the tribe Tenty-



Fig. 1. Mesepimeron of a. *Megagenius frioli*, b. *Epiphysa ciliata, in situ.* 1 = mesepisternum, 2 = mesepimeron, 3 = metacoxa.

riini. The ancestral stock of Adesmiini may have resembled *Megagenius*, in that they would have been broad and probably rather large Tentyriini-like beetles, but, as indicated below, their area of distribution was probably in southwestern Africa.

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Fig. 2. Distribution of apomorphic character states in the tribe Adesmiini. Apomorphic character states 1–19 are as follows: 1: Mandible with deep concavity at base. 2: Prosternal apophysis extremely wide. 3: Outer surface of mandible concave. 4: Labrum strongly convex and posteriorly impressed. 5: Genal canthus lost. 6: Sides of clypeus parallel. 7: Labrum distinctly transverse, often convex. 8: Labrum strongly transverse, convex. 9: Clypeus strongly produced. 10: Lower part of eye (i.e., part below genal canthus) hypertrophied. 11: Upper part of eye (i.e., part above genal canthus) hypertrophied. 12: Tibial spurs and tarsal claws elongate. 13: First metatarsal segment shortened. 14: Tibial calcaria hypertrophied. 15: Upper mandibular process lost. 16: Gular sulcus filled with setae. 17: Setose brushes developed dorsally on meso- and metafemora. 18: Genae strongly expanded. 19: Mesepimeron elongate and parallel.

RELATIONSHIPS IN THE TRIBE ADESMIINI

A cladistic analysis of the relationships within the Adesmiini has been made. As with most rather homogeneous and strongly radiated groups, difficulty was experienced in finding suitable characters on which to base such an analysis, i.e., characters whose polarity could be established by comparison with the Tentyriini as an out-group, and which did not show convergence, as is very usual in adaptive characters in groups of Tenebrionidae (Koch, 1963, Penrith, 1980, 1984a). The main lineages are considered to be well established by the analysis, but, although some of the relationships within lineages could be indicated, complete analysis of relationships within lineages, as made for the genus Onymacris (Penrith, 1984b) are not included. The characters used and their distribution in the tribe are shown in Fig. 2. A much greater variety of characters was originally examined, but most of these were rejected because their polarity could not be determined and their appearance in the tribe seemed to be random and not associated with any of the clear transformation series that were found. These characters, to mention a few, included the callosity of the anterior part of the mesosternum, the position of the humeri in relation to the posterior pronotal angles, the elytral and pronotal sculpture, the deflection of the prosternal apophysis, the antennal length and thickness, the development or absence of grooves on the femora and tarsal segments, and the shape of the male genitalia. For ethical reasons the female reproductive system was not examined, as it forms the subject of a doctoral thesis that was in preparation at the time of this study. The larvae of several Adesmiini have been studied and described by Schulze (1962, 1964), but I was unable to assess the polarity of the larval characters without a much wider knowledge of the larvae of all related Tenebrionidae.

Nomenclatural changes have been made only where they seem essential on the basis of the cladistic analysis. Where a change of status seems to be indicated in the cladogram (Fig. 3) but has not been made, the point is discussed in some detail.

The Adesmiini are considered to have as their sister-group the Tentyriini, with which they share an enlarged mentum. The remaining tentyriine tribes with this character are Erodiini, Asidini, Eurychorini, and Zophosini, all of which are excluded from the possible ancestry of Adesmiini by specialized characters. The ancestral adesmiine is assumed to have been a large nocturnal or crepuscular tentyriinelike beetle, possibly similar to *Megagenius frioli*, in which the mesosternal epimeron became narrow and subparallel posteriorly. The mandible had a dorsal process such as occurs in a wide variety of Tentyriini, of which representatives of 108 genera were examined. The dorsal mandibular process has not been observed in any of the other tribes.

The genus *Epiphysa* is considered to represent the oldest surviving lineage of Adesmiini. Its species are predominantly crepuscular to nocturnal, and the mandibular process is retained. Several apomorphic features such as the exceedingly short and broad thoracic sternites, the setose gular sulcus, and the setose head patch, as well as the general body form, exclude *Epiphysa* from the ancestry of any of the remaining lineages. Its nine species are distributed from southern Angola to the southwestern Cape (Penrith, 1979).

The mandibular process is retained in another lineage, the genus *Alogenius*. In the remaining lineages of Adesmiini this process has been lost, and I have assumed for reasons of parsimony that this took place in a single common ancestor to those lineages. The members of *Alogenius* show a transition from the nocturnal to the diurnal habit of the remaining Adesmiini. The two species of *Alogenius s. str.* are active in the



Fig. 3. Cladogram showing relationships in the tribe Adesmiini. The numbers of apomorphies (see Fig. 2) are indicated on the branches; unique apomorphies are enclosed in circles, synapomorphies in squares. Solid circles indicate character states that are not strong or unique apomorphies, but are considered to exclude the genera involved from the ancestry of the succeeding branches: the globosity of *Physadesmia*, the longer legs of Stenocara, and the more strongly convex mentum of *Metriopus*.

late afternoon, while the single species of the subgenus *Aequigula* appears to be diurnal, at least under some circumstances. The development of setose brushes on the dorsal surface of the meso- and metafemora excludes *Alogenius* from the ancestry of the remaining lineages.

Among the lineages without a mandibular process, the genus Renatiella appears to be the most plesiomorphic. Both *Renatiella* and the lineage formed by the genera Physadesmia, Onymacris and Eustolopus have the labrum of the plesiomorphic type in the Adesmiini, flat and not or only weakly transverse; in the remaining lineages it is transverse and often convex. A flat and at most weakly transverse labrum is the norm in the Tentyriini and all the related tribes; the apomorphic development in Adesmiini is apparently unique. In the cladogram, *Physadesmia* and the two related genera are shown as diverging before *Renatiella*, but this sequence is not proven. The unique apomorphy of the *Physadesmia* lineage is that the eye is strongly enlarged above the genal canthus, the part below being somewhat reduced. In Epiphysa and Alogenius the cye is considered to represent the plesiomorphic state in Adesmiini, being reniform with the genal canthus situated more or less in the middle of the anterior margin, a state observed in various Tentyriini, including Megagenius, and from which the remaining states of the eye in Adesmiini are most easily derived. In Renatiella and Adesmia, also with a reniform eye, the lower part of the eye is elongate, and the genal canthus is situated in the upper half. It is not possible to tell from the eve of the Physadesmia lineage whether its ancestor shared the displacement of the canthus shown in *Renatiella* and *Adesmia*, or whether it diverged before this took place. However, since the main development of the eye in the *Physadesmia* lineage has taken place above the canthus, without strong evidence of a dorsal displacement (e.g., eyes situated high up on the head, and prominent), I have assumed that the lineage diverged before hypertrophy of the lower part of the eye occurred.

The lineage consisting of the three genera *Physadesmia*, *Eustolopus* and *Onymacris* is distributed throughout the arid western parts of southern Africa. All are relatively long-legged fast-moving diurnal beetles. *Physadesmia* consists of three species, *Eustolopus* of two, and *Onymacris* of 14 (Penrith, 1984b). In *Eustolopus* and *Onymacris* the tibial spurs and tarsal claws are elongate, the spurs being strongly hypertrophied and foliaceous in *Eustolopus*. In *Onymacris* the first metatarsal segment is very short in comparison with the other segments, the plesiomorphic state being that the first is about equal in length to the following two together. *Physadesmia* has no unique apomorphy in relation to all other Adesmiini, but its species are all strongly inflated and globose, and are thus excluded from possible ancestry to *Onymacris* and *Eustolopus*.

The three species of *Renatiella* are, as mentioned above, strongly plesiomorphic, and are close to the ancestral line of *Adesmia*, and possibly of *Physadesmia* as well. The clypeus in all three species is very long, produced forwards from the eye without a notch at the clypeal sulcus, and this would probably exclude them from direct ancestry to any other lineage and justify the generic rank accorded to the lineage by Koch (1947).

The remaining lineages all share a transverse and often convex labrum. The more plesiomorphic lineage, consisting of the genus Adesmia, is characterized by a transverse rather strongly convex labrum (Koch, 1944, 1948). A labrum of this type is developed in all species of the southern African genus Physostema except P. cribripes, in which the labrum is strongly transverse but flat. Comparison of the northern African/Asian (adesmioid) groups of Adesmia, as well as the macropodioid groups, indicated that there are no cladistic grounds for separating Physostema from Adesmia at generic level, as they lack any unique apomorphies in relation to one another, and Physostema is here reduced to a subgenus of Adesmia. P. cribripes is retained in the subgenus Physostema, because its affinities are certainly with the species of that group. The labrum of certain of the adesmioid Adesmia species is scarcely more convex than that of P. cribripes, and the strongly transverse shape may be more important than the actual convexity.

The most apomorphic lineage of Adesmiini, which includes the genera Stenocara, Metriopus, Orientacara and Stenodesia, probably evolved from an Adesmia-like ancestor with a transverse and weakly convex labrum, an enlarged oval eye, no genal canthus, and the clypeus parallel-sided from the sulcus forwards. The labrum shows a transition from scarcely convex in the species of Stenocara, to strongly convex and posteriorly impressed in Stenodesia and Orientacara, culminating in the condition observed in Metriopus, in which the division between the strongly swollen anterior part of the labrum and the impressed posterior part is sharply linear.

Cauricara was separated as a genus by Penrith (1979) because of the short, emarginate epistome and the position of the eye. I now believe the dorsalward shift of the eye to be secondary, and not related to the eye development in *Eustolopus*, *Physadesmia* and *Onymacris*, and consider the loss of the genal canthus and the parallel-sided epistome to be more important characters. The last two characters relate *Cauricara* unquestionably to *Stenocara*. While only the species of *Cauricara* combine the short and emarginate epistome with the short maxillary processes of the postgenal mar-

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gin, Stenocara magnophthalma Koch displays the former character and S. batesi Haag displays the latter. It seems likely that the species of Cauricara simply represent a derived lineage of Stenocara, and as such should not be separated at more than subgeneric level. The subgenus Cauricara is therefore used for the species velox, phalangium, eburnea, and albomarginata. Although S. brunnipes Haag and S. desertica Koch form part of the Cauricara lineage, the subgenus Arenacara Penrith is retained for them, in view of their specialized labrum, which has the anterior margin thickened and perpendicular. It is likely that the Cauricara/Arenacara line diverged early from ancestors like Stenocara batesi. Stenocara lacks a unique apomorphy, but all the members of Stenocara have longer legs than at least the more plesiomorphic members of Stenocara would be excluded from their ancestry. It is likely, however, that the common ancestor of Stenocara and the Metriopus-Stenodesia-Orientacara line would have resembled Stenocara batesi, but would have had shorter legs and long maxillary processes of the postgenal margin.

In Orientacara and Stenodesia the outer surface of the mandible is concave, with a very deep cavity near the base in Stenodesia only. I have treated this character as a unique apomorphy of Stenodesia, but something like it is in found in the members of the subgenus Spongesmia Koch of Adesmia. In Orientacara the prosternal apophysis is extremely wide. In the previous revision (Penrith, 1979), Orientacara was treated as a subgenus of Metriopus, but the conformation of the labrum in it and in Stenodesia suggests that these two lineages diverged before the state of the labrum found in the three subgenera of Metriopus was reached. The concave mandibular surface of both Orientacara and Stenodesia excludes them from the ancestry of Metriopus. Orientacara and Stenodesia are excluded from each others' ancestry by the broad prosternal apophysis of Orientacara and the mandibular cavity of Stenodesia, and they are therefore treated as genera.

BIOGRAPHY AND CENTRE OF ORIGIN

The geographic distribution of the lineages of Adesmiini is shown in Fig. 4, and that of the genera in Figs 5-14. All the genera except the monotypical Orientacara are represented in southwestern Africa between 20° S and 30° S and between 10° E and 20° E. North of 20° S, only four genera, Renatiella, Adesmia, Metriopus, and Stenocara, extend east of 20° E. In Fig. 15 the highest number of species and genera occurring in each block of four degree squares, south of 15° 00' S and east of 11° 00' E, are shown. Actual records per degree square were condensed on account of patchincss of collecting and possible brief intervention of unfavourable ecotypes. It is evident that the highest number of genera and species occurs in the western region of southern Africa from southern Angola to Namaqualand, the numbers dropping abruptly eastwards. All the lineages and all the genera except Orientacara occur here. This suggests to me that the tribe has had a long history in the area and may have originated here, in the area indicated in Fig. 16. The tribe is likely to be of post-Gondwana origin, since it is not represented on the other southern continents. Southwestern Africa has a relatively long history of aridity (Brain, 1981). The implication is not that the area remained unchanged climatically throughout the evolutionary history of the tribe, for then we would hardly expect the observed diversity. I suggest that the different lineages represent the results of environmental changes (for example the Physadesmia-Eustolopus-Onymacris lineage having developed with the increase in sandiness of the substratum), but that the availability of refugia led to the

continued representation of several lineages in the area. The lineages could have dispersed from the centre of origin as environmental conditions permitted. It is not impossible that Adesmiini originated elsewhere, in an area from which they have all but disappeared, and are merely favoured by conditions in southwestern Africa at present, but if this is so, their representation by a single, fairly apomorphic lineage in apparently equally favourable areas such as northeastern Africa is surprising.

The earliest development of the tribe probably took place in the northern part of the area of origin. Both the earliest lineages, *Epiphysa* and *Alogenius*, occur in this part of the area (Figs 5, 6), as do representatives of all the present-day lineages. From this restricted area the ancestors of the more derived lineages dispersed southnorth-, and eastwards. Alogenius remained more or less confined to the original area of origin and has diversified relatively little, with three species, two of which are polytypic. These two species, which are slow-moving and mainly petrophilous, are particularly liable to isolation, and unlikely to disperse over a wide area. Epiphysa has spread far southwards into the Karroo. Its most plesiomorphic species are found in the northernmost part of the distribution range of the genus, while the more apomorphic species are found in the south. The species of Epiphysa are also slow-moving, and several are petrophilous, but two species in particular, E. arenicola Penrith and E. flavicollis (Fabr.), have invaded the plains, where they use plants and animal burrows as well as rocky outcrops for shelter during the day. Both are very widespread (see Penrith, 1979, for detailed distribution), and through such species the dispersal of *Epiphysa* far to the south must have been effected. The genera *Epiphysa* and Alogenius, which are considered to be derived from a very early stock, might at present be regarded as 'refugees', since their preferred habitats and mainly crepuscular habit protect them from exposure to extremes of aridity.

The next lineages to diverge, Renatiella, Adesmia and Physadesmia-Eustolopus-Onymacris, are presumed to have originated in the area of origin of the tribe, but their main radiation took place elsewhere after initial dispersal of the ancestral stock. Renatiella and Adesmia are the only genera that have dispersed far north of the southern African region, Adesmia being the only genus of Adesmiini to reach the Palaearctic Region including India. Renatiella consists of three species only, two of which are widely distributed (Fig. 7). The westernmost species, Renatiella fettingi (Gebien), with an antennal sulcus like that found in *Epiphysa* and *Alogenius*, and the shortest legs in the genus, appears to be the most plesiomorphic species, and the easternmost, R. reticulata (Gerstaecker), a widespread polytypic species with rather long legs, the most apomorphic. This suggests that the genus evolved in the western part of the area of origin when savanna prevailed there. Later it dispersed eastwards and eventually almost disappeared from the western part as it dried up and savanna became semi-desert. The western species Renatiella fettingi and R. scrobipennis (Haag) have adapted to less favourable conditions, the former by living mainly in rocky outcrops and sheltered habitats, and the latter perhaps by having a very wide habitat preference. The adults of both are seasonal, emerging after rain and avoiding the most unfavourable periods. Adesmia probably followed a similar course, since the subgenus Spongesmia Koch at present found in the centre-of-origin area, may be relatively plesiomorphic. Both Renatiella and Adesmia must have spread through a savanna corridor, which is considered to have existed more than once, to East Africa (see Endrödy-Younga, 1978). Adesmia reached not only North Africa, but western Asia, which suggests that its dispersal occurred before the separation of India and Africa, whereas Renatiella reached only East Africa. Their dispersal

through a central African corridor therefore could have occurred at different times. Ancestral Adesmia stock also moved southwards, the lineage which became Physosterna reaching the southern tip of the continent. In the genus Adesmia, the tropical species, especially those of the subgenera Spongesmia and Macropoda, appear to be the most plesiomorphic, as Koch (1944, 1948) suggested. The northern (adesmioid) subgenera are all relatively derived. The members of Physosterna are also more derived than the macropodioid Adesmia, with the southernmost members being the most derived (A. (P.) porcata Solier, A. (P.) goryi Solier).

The ancestral stock of *Physadesmia/Eustolopus/Onymacris* dispersed southwards from the centre of origin (Figs 9-11). *Eustolopus* consists of two species, both highly apomorphic, so that it is difficult to say which is the more plesiomorphic. There are three species of *Physadesmia*, of which the middle one in the distribution range (Fig. 9) is the most plesiomorphic. *Onymacris* is much more diversified, with 14 species. Their distribution in the light of their phylogeny suggests that the accumulation of sand in the lower Orange River region as a result of aridification provided the impulse for their evolution (Penrith, 1984b).

The Metriopus-Stenocara-Stenodesia-Orientacara lineage also seems likely to have originated in the centre of origin of the tribe. Stenocara is a western component that spread far southwards and, in the case of one widespread species, to eastern Zimbabwe, but the majority of its species occur from Namaqualand to southern Angola (Fig. 12). The three subgenera occur together in an area that corresponds with the western part of the suggested centre of origin of the tribe. Metriopus probably followed a similar course of evolution and dispersal to Renatiella, not extending quite as far northeastwards. Alternatively, it may have originated somewhat east of the centre of origin of the tribe, in the northwestern Kalahari, and from there radiating northeast-, south-, and westwards. The highest number of plesiomorphic features are found in the western subgenus, Metriopus s. str. The eastern subgenus, Coeladesmia, also has plesiomorphic features. The most derived subgenus, Ceradesmia, occupies the central part of the distribution area shown in Fig. 13. It is a strongly psammophilous subgenus, and presumably arose during a period of extensive exposure and accumulation of loose sand, possibly in the region of the Zambezi River. The southernmost and most derived species, M. (C.) albicollis (Haag), has a very wide distribution, presumably the result of very arid periods when dry loose sand was widely available over the Kalahari area.

At a fairly early stage the ancestor or ancestors of *Stenodesia* and *Orientacara* diverged from the *Metriopus* line. I believe them to have arisen from a common stock, part of which spread southwards and from which *Stenodesia* evolved, and part of which spread southeastwards. The latter lineage to a large extent may have become extinct during an arid period of extensive sand exposure, *Orientacara* being a relic of this line. The species of *Stenodesia* prefer hard substrata, and it is likely that this preference applied to the ancestral stock as well, psammophily being exceptional in the tribe. *Stenodesia* shows a radiation centre in the Karroo. The northern species *S. globulum* (Haag) and *S. thomseni* (Gebien), although possessing apomorphic features, are in general morphology plesiomorphic compared to the Cape *Stenodesia* that Koch (1952) placed in a subgenus *Karroocara*. They are considered to have radiated in the Karoo after reaching the area from the north via Namaqualand.

To summarize, present-day biogeography of the Adesmiini suggests the following course of development of the tribe. This is illustrated in Fig. 16. After the South American and Australian land-masses had separated from Africa, the ancestral adesmiine stock arose from a large tentyriine ancestor in the southwestern region of the African continent, in or close to what is now southern Angola and northern South West Africa/ Namibia. The event preceding this was the onset of aridification of the southern part of the African continent. The earliest lineages remained crepuscular to nocturnal, as were their tentyriine ancestors, but others became fastrunning diurnal bectles whose behaviour and structure allowed them to become successful in arid open-country conditions and also increased their potential for dispersal. Arid conditions spread over most of southern Africa (present-day Namib and pro-Namib Deserts, Kalahari, Namagualand, and Karroo) (see Brain, 1981), and with them the tribe Adesmiini dispersed widely throughout these regions. The sand dunes of the western Cape coastal belt were occupied by Adesmiini that were already adapted for arid conditions during the southward dispersal of their ancestors. During one or morc periods when uniform savanna conditions extended from southwestern to East Africa (Endrödy-Younga, 1978) certain adesmiine lineages spread northwards, reaching East Africa. One of these extended its distribution further northwards from East Africa through the Sahel to the Sahara and also to Asia Minor, the latter dispersal probably (although not necessarily) having occurred before the present-day separation of Africa from India was accomplished. This Palaearctic line subsequently speciated in a number of centres. Its members bear a close superficial resemblance to those of the southernmost branch of the same lineage, the subgenus *Physostema*, presumably because both have evolved in more open and arid conditions than the savannas in which their ancestors evolved, and in which their more plesiomorphic relatives (macropodioid subgenera of Adesmia) are found today. In southern Africa, while all the lineages have their suggested centre of origin within or close to the suggested centre of origin of the tribe, subsequent speciation centres are evident in various lineages. For example, both Onymacris in the west and the subgenus Ceradesmia of Metriopus in the Kalahari are believed to have evolved in response to the exposure and accumulation of large quantities of loose sand in the ancestral area, a process that is one of the end products of aridification. In the Kalahari, an ancient sand repository, such a process may have taken place several times with pluvial periods in between resulting in modification and shrinking of the sand deposits by increased vegetation cover (Lancaster, 1979, 1980, 1981), and consequent isolation and disjunct distribution of psammophilous populations (as observed in Ceradesmia). In the Namib, it is likely that the process was more recent, and the evolution of Onymacris correspondingly so, including its invasion of only the southwestern corner of the Kalahari. Its dispersal pattern in general follows that suggested by Endrödy-Younga (1982) for Namib psammophilous Tenebrionidae, but it has dispersed south and eastwards as well because the components involved are not restricted to the barren sands of wind-blown dunes. On the other hand, sand accumulation in the Kalahari is considered to have possibly interrupted the continuity of the Stenodesia-Orientacara lineage, before the characteristics of either genus had been fully achieved, and resulted in the isolation of the latter genus.



Fig. 4. Distribution areas of the four lineages of Adesmiini. The shaded areas lack Adesmiini.

Fig. 5. Alogenius.

Figs. 5–14. Distribution areas of the genera of Adesmiini. For the sake of clarity, national boundaries have been omitted. The figures indicate the maximum number of species found in the enclosed area. Therefore at any given point in the area indicated as having one species, only one species will be found, although it may not be the same species throughout the area in which only one species occurs.

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FIg. 8. Adesmia. a. Distribution areas of the different lineages within the genus Adesmia: A = adesmioid Adesmia, M = macropodioid Adesmia, P = subgenus Physosterna. b. Distribution of the genus Adesmia in southern Africa.

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Fig. 12. Stenocara.





Fig. 15. Number of genera (roman figures) and species of Adesmiini recorded from each four degree block in southern Africa, starting at 15° south and 11° east.

Fig. 16. Proposed centre of origin of the tribe Adesmiini, showing the direction of dispersion of two lineages, Adesmia-Renatiella (vertical lines), and Stenocara-Metriopus-Stenodesia (stippled). The supposed centre of origin is indicated by horizontal line shading.

KEY TO THE GENERA AND SUBGENERA OF ADESMINI

- 1(6) Upper edge of mandible with a process; genae strongly expanded, projecting far beyond temporal outlines of head.
- 2(5) Upper surface of meso- and metafemora with setose brushes; apex of clypeus slightly to strongly downbent; genae continuous with clypeal sides; gular sulcus shallow to deep, but never filled with setae Alogenius Gebien
- 3(4) Gular sulcus very deep, head strongly hypognathous; anterior part of clypeus strongly downbentsubgenus Alogenius Gebien
- 4(3) Gular sulcus shallow to evanescent, head not strongly hypognathous; anterior part of clypeus slightly downbentsubgenus Aequigula Penrith
- 6(1) Upper edge of mandible inermous; genae not strongly expanded, not projecting far beyond temporal outlines of head.
- 7(30) Eye narrowly to broadly reniform, with genal canthus at upper third; upper part may be somewhat expanded (though always shorter than part below canthus), in which case labrum convex.

- 10(13) Metatibiae strongly compressed, broad.
- 11(12) Labrum flat, broadly emarginate apically; compressed tibiae knife-edgedsubgenus Oteroscelis Solier
- 12(11) Labrum convex, with apical notch; metatibiae strongly compressed but

- 15(14) Labrum evenly convex or flat.
- 16(25) Pronotum with sides subparallel or rounded, broadest at middle or between base and anterior fourth, sides not distinctly converging anteriorly from broad base.
- 17(22) Labrum with anterior margin subtruncate to broadly and evenly emarginate, without distinct notch at middle.
- 18(19) Pronotum with fine smooth sculpture; eye rather broadly reniform; antennae compressed, the inner edge with rather dense golden setae (North Africa) subgenus Adesmia Fischer
- 19(18) Pronotum with coarse tuberculate to reticulate sculpture; eye narrowly reniform; antennae subcylindrical, with scattered setae (central and eastern Africa).
- 20(21) Pronotum of male without a large smooth and raised tubercle on either side, similar in both sexes, a little broader in females subgenus Macropoda Solier
- 21(20) Pronotum of male with a large smooth and raised tubercle on either side
- 22(17) Labrum with distinct notch in middle of anterior margin.
- 23(24) Posterior angles of pronotum situated well below level of humeri

......subgenus *Macradesmia* Solier

- 24(23) Posterior angles of pronotum level with humeri subgenus Macropodesmia Koch
- 25(16) Pronotum broadest at base, sides strongly convergent anteriorly.
- 26(29) Mentum plane, or with longitudinal median impression, without transverse impression in thickened anterior part.

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27(28)	Elytral sculpture reticulate, formed by a raised network enclosing small to large impressed areas; pronotum without lateral margins, continuous with proepisterna subgenus Spongesmia Koch
28(27)	Elytral sculpture not as above; costate, tuberculate, or with impressed foveate punctures; pronotum with distinct lateral margins
29(26)	Mentum anteriorly thickened, with a transverse impression (Somalia) subgenus Somaladesmia Koch
30(7)	Eye not as described: either with the part above canthus greatly enlarged and the part below reduced, shorter than upper part, or broadly oval, anterior part without a canthus.
31(36)	Eye with anterior margin indented at genal canthus, the part above canthus enlarged; labrum flat.
32(35)	Metatibial calcaria longer, to much longer, than first metatarsal segment; body ovate to round, but not inflated and globose.
33(34)	First metatarsal segment shorter than following two together; tibial calca- ria long but not spatulate or foliaceous
34(33)	First metatarsal segment as long as following two together; tibial calcaria very long, expanded or foliaceous <i>Eustolopus</i> Gebien
35(32)	Metatibial calcaria about as long as first metatarsal segment; body inflated, globose
36(31)	Eye ovate, with anterior margin entire; labrum usually somewhat convex.
37(48)	Outer surface of mandible plane, not concave.
38(43)	Labrum almost flat to distinctly but evenly convex
39(42)	Epistome short, anterior margin strongly emarginate; maxillary processes of postgenal margin very short; either the labrum with anterior margin thickened and vertical, or eyes with a distinctly raised supraorbital ridge.
40(41)	Anterior margin of labrum thickened and vertical; elytra ovate, with three low more or less smooth costae or without costae; legs moderately long; elytra without white patterns; head without distinct supraorbital ridge subgenus Arenacara Penrith
41(40)	Labrum sometimes swollen and convex but anterior margin normal, not thickened or vertical; elytra rounded, globose, with three denticulate costae; legs very long and slender; elytra either white or with a white margin (if this is absent, there is a distinct impression on either side of suture at top of apical declivity); head with raised supraorbital ridge from eve to gena
42(39)	Épistome short to rather long, anterior margin usually subtruncate; maxil- lary processes of postgenal margin long (one exception, <i>Stenocara batesi</i>); labrum never with anterior margin thickened; no distinct supra- orbital ridge developedsubgenus <i>Stenocara</i> Solier
43(38)	Labrum with anterior part strongly convex, sharply separated from poste- rior, impressed part
44(45)	Middle of posterior margin of pronotum thickened, anterior margin raised; sides of epistome separated from supra-antennal portions by a rounded sinussubgenus <i>Ceradesmia</i> Gebien
45(44)	Middle of posterior margin of pronotum not thickened nor anterior margin raised; no sinus at junction of epistome and supra-antennal portions, which are not raised.
46(47)	Elytra with only the second costa prominent; sides of pronotum rounded subgenus <i>Coeladesmia</i> Reitter
47(46)	Elytra with three costae, or without costae; sides of pronotum subparallel, or divergent posteriorly
48(37)	Outer surface of mandible concave, sometimes with deep cavity; labrum anteriorly strongly swollen.

- 49(50) Prosternal apophysis very broad, much broader than procoxa at level of middle of procoxa; outer surface of mandible evenly concave Orientacara Koch

NEW TAXA OF STENODESIA

Examination of new material from the northern Kaokoveld has indicated that *Stenodesia globulum* (Haag) and *S. verruculifera* (Haag) represent a single polytypic species with four subspecies, one of which is described as new below. Two further new species are described from the western Cape and the Karroo. A revised key to the species and subspecies of *Stenodesia* is given.

KEY TO THE SPECIES AND SUBSPECIES OF STENODESIA

1(8)	Two transverse patches of setae between pronotum and elytra; prosternal apophysis projecting horizontally between coxae; proepisterna with a deep antennal sulcus; mesosternum with two sharp tubercles anteriorly
2(3)	Anterior mesosternal tubercles situated opposite apical lobes of pro- sternal apophysis, so that a pair of parallel lines drawn backwards from outer margins of prosternal apophysis would enclose the mesosternal tubercles; intercostae with tubercles only; integument strongly metallic <i>S. globulum globulum</i> (Haag)
3(2)	Anterior mesosternal tubercles situated partly or entirely lateral to apical lobes of prosternal apophysis, so that a pair of parallel lines drawn backwards from outer margins of prosternal apophysis would pass through or between the mesosternal tubercles.
4(7)	Reflected part of elytra usually without an unevenly reticulate appearance, with fine punctures only, or with scattered tubercles as well, but punctures always a conspicuous element of sculpture; inner dorsal costa more con- spicuous element of sculpture; inner dorsal costa more or less straight, situated further from suture, not meeting or coalescing with it; outer dorsal interval not or scarcely concave (seen in caudal view).
5(6)	Reflected part of elytra punctate only, without granules or tubercles; inter- costae of elytra with transverse rugosities, the areas in between punctate (Angola)
6(5)	Reflected part of elytra often with granules or tubercles as well as punc- tures, if punctate only then intercostae of elytra with few transverse rugosities, mainly with scattered tubercles; intercostae of elytra either as described or extensively transversely rugose, but then areas between rugosities with small granules (Kaokoveld south of the Kunene River)
7(4)	Reflected part of elytra usually with unevenly reticulate appearance, mainly with tubercles, without conspicuous punctures; inner dorsal costa curved, approaching suture closely posteriorly, usually meeting it near top of apical declivity; outer dorsal interval distinctly concave (seen in caudal view) (Angola)
8(1)	Pronotum and elytra without setose areas between them; prosternal apo- physis apically deflected behind coxae; no antennal sulcus on proepisterna; mesosternum without sharp tubercles.
9(10)	Epistome separated from frons by a deep transverse groove; sides of pro- notum diverging posteriorly; basal metatarsal segment shorter than ungual segment
10(9)	Epistome not separated from frons as above; sides of pronotum subparal- lel to converging posteriorly; basal metatarsal segment longer than ungual segment.

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11(16)	Reflected part of elytra with a sharply raised costa or costate row of gran- ules.
12(13)	Head between antennae with a very deep V-shaped excavation, which has steep sides
13(12)	Head without such an excavation.
14(15)	At least outer dorsal costa strongly serrate; pronotum with coarse reticu- late punctures
15(14)	All costae minutely serrulate; pronotum smooth, with large shallow scat- tered punctures
16(11)	Reflected part of elytra without a costa or costate row of granules.
17(20)	Pronotum strongly narrowed posteriorly, with a broad transverse impres- sion in front of posterior margin.
18(19)	Lateral elytral costa single to top of apical declivity, where it divides into two
19(18)	Lateral elytral costa double over whole length, the two rows diverging at top of apical declivity
20(17)	Pronotum not strongly narrowed or impressed posteriorly.
21(22)	Lateral elytral costa double; lateral margin of pronotum briefly carinate at anterior angles
22(21)	Lateral elytral costa single; lateral margin of pronotum without any trace of a carina

Stenodesia globulum (Haag)

Stenocara globulum Haag, 1875: 38; Allard 1885: 203; Gebien 1920: 52, 1937: 159. *Stenodesia globulum*: Koch 1952: 175; Penrith 1979: 73.

At the time of the previous revision (Penrith, 1979), the two closely related species Stenodesia globulum and S. verruculifera appeared to be well separated geographically as well as morphologically. Series of beetles of this group collected recently in northern Kaokoland just south of the Kunene River are intermediate in the morphological characters used to separate the two species. Stenodesia globulum was separated from S. vertuculifera by the position of the mesosternal tubercles, as well as the intercostal sculpture of the elytra. The northern Kaokoveld series, from Baynes and Ehomba mountains and from Ehomba settlement, are intermediate between the two species. The mesosternal tubercles are situated lateral to the prosternal apophysis, as in S. verruculifera. In the Baynes and Ehomba mountains specimens from higher altitudes, the elytral intercostal sculpture consists mainly of tubercles, only a few being joined, although intercostal rugosities are more common in the Ehomba mountain than in the Baynes mountains specimens. The specimens from Ehomba settlement have the elytral intercostae joined by irregular rugosities, as in S. verruculifera, but the intervals between rugosities are granular (punctate in S. verruculifera). In both S. globulum and S. verruculifera f.t. the reflected part of the elytra has fine punctures only. In S. verruculifera marshalli the reflected part of the elytra is uneven, with small to large tubercles, any punctures being inconspicuous. In the northern Kaokoveld series, the majority of specimens have mainly punctures on the reflected part of the elytra. These punctures may be intermixed with a few tubercles, but some from the Baynes mountains have punctures only, while some from the Ehomba settlement have the reflected part of elytra somewhat uneven, as in S. v.marshalli, although the punctures remain a conspicuous sculptural element. S. v. marshalli has the inner elytral costa posteriorly approaching and often meeting the suture, while in S. verruculifera f.t. and the northern Kaokoveld specimens they are

further from the suture posteriorly, and end abruptly without reaching the suture.

The northern Kaokoveld specimens are described as a new subspecies of *Stenodesia* globulum, and *S. veruculifera* is reduced to a subspecies of *S. globulum*, its subspecies marshalli also becoming a subspecies of *S. globulum*.

A diagnosis of the species is given below, followed by diagnoses of the subspecies.

Stenodesia globulum (Haag)

DIAGNOSIS. Two transverse setose patches enclosed between pronotum and elytral base. Prosternal apophysis horizontal, produced behind coxae, apex bilobate. Proepisterna with a deep antennal sulcus immediately below lateral pronotal margin. Mesosternum with two sharply raised tubercles anteriorly.

DISTRIBUTION (Fig. 17). Southern Angola to central escarpment region of South West Africa/Namibia.

Stenodesia globulum globulum (Haag)

DIAGNOSIS. Mesosternal tubercles situated opposite apices of prosternal apophysis, the distance between them less than greatest width of prosternal apophysis. Elytral intercostae with scattered tubercles. Reflected part of elytra with fine, scattered punctures. Inner elytral costa not meeting or closely approaching suture posteriorly, straight.

DISTRIBUTION (Fig. 17). Southern Kaokoveld to central escarpment region of South West Africa/Namibia.

Stenodesia globulum verruculifera (Haag) stat. nov.

Stenocara verruculifera Haag, 1879: 296; Gebien 1937: 158. Stenodesia verruculifera: Koch 1952: 175, 179; Penrith 1979: 73.

DIAGNOSIS. Mesosternal tubercles situated lateral to apices of prosternal apophysis, the distance between them greater than greatest width of prosternal apophysis. Elytral intercostae with irregular transverse rugosities joining costae; areas between rugosities punctate. Reflected parts of elytra with fine, scattered punctures. Inner elytral costae straight, not meeting or closely approaching suture posteriorly.

DISTRIBUTION (Fig. 17). Southwestern Angola.

Stenodesia globulum marshalli Koch stat. nov.

Stenodesia marshalli Koch, 1952: 176. Stenodesia verruculifera marshalli: Penrith 1979: 73.

DIAGNOSIS. Mesosternal tubercles situated lateral to apices of prosternal apophysis, the distance between them greater than greatest width of prosternal apophysis. Elytral intercostae with irregular transverse rugosities joining costae, areas between rugosities punctate. Reflected part of elytra uneven, with tubercles joined by raised

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areas, punctures inconspicuous or absent. Inner costae incurved posteriorly, closely approaching or meeting suture.

DISTRIBUTION (Fig. 17). Southwestern Angola, south and east of distribution area of *S. g. vertuculifera*.

Stenodesia globulum kaokoensis subspec. nov.

DIAGNOSIS. Mesosternal tubercles situated opposite outer edge of lobes of prosternal apophysis, or lateral to them, distance between them always greater than greatest width of prosternal apophysis. Elytral intercostae with at least a few transverse rugosities as well as scattered tubercles, sometimes entirely with rugosities (Ehomba settlement), area between rugosities granular. Reflected part of elytra with punctures, usually with a few scattered small to large tubercles, sometimes uneven, but punctures always conspicuous. Inner elytral costae not meeting or closely approaching suture posteriorly, straight.

DISTRIBUTION (Fig. 17). Northern Kaokoveld of South West Africa/Namibia.

MATERIAL. Holotype: 3, 7,3 mm elytral length (Transvaal Museum), Baynesberge - 2000 m, SE1713Ac, 11-14.xii.1982, E. Holm & C. H. Scholtz, singled and light (these specimens were singled, day).

Allotype: 9, 8,5 mm elytral length (Transvaal Museum), data as holotype.

Paratypes: 46 ex.: 16 (Transvaal Museum and University of Pretoria), data as holotype; 16 (Transvaal Museum and University of Pretoria), Ehomba Mt-1 870 m, SE1713Db, 11-14.xii.1982, E. Holm & C. H. Scholtz, meatbaited pit trap; 14 (Transvaal Museum), Ehomba Mt, 17.30 S. - 13.49 E., 7.2.1975, E-Y:1634, singled, leg. Endrödy-Younga.

Stenodesia oosthuizeni spec. nov.

DIAGNOSIS. Elytral length 5,2-8,0 mm. Integument including appendages black, dorsum with a brownish pulverulent layer, often rubbed off in preserved specimens. Supra-antennal region strongly raised. Head shallowly concave between supraantennal eminences, reticulate and setose (as in S. gibbipennis, see Penrith, 1979). Anterior margin of pronotum strongly raised and produced forwards, not as strongly as in S. gibbipennis. Sides of pronotum finely marginate at least in anterior half. Pronotum narrowing posteriorly, with deep transverse impression just in front of posterior margin, about as long as distance between primary costae of elytra. Sculpture of coarse reticulate punctures, anterior margin of pronotum with scattered granules. Elytra rounded, strongly convex, with three denticulate costae, the lateral one forming edge of elytral disc double. Inner (dorsal) costa meeting middle (primary) costa at top of apical declivity; lateral costa, whose two elements diverge at about this level, meeting other, united costae as follows: upper branch meeting them in middle of apical declivity, lower branch meeting others close to apex. Intercostae with irregular transverse rugosities (more numerous than in S. gibbipennis) and with scattered granules, situated mainly but not exclusively on raised rugosities. Reflected part of elytra punctate; areas between punctures sometimes slightly raised, especially just below lateral costa. Prosternal apophysis as wide as procoxa, strongly deflected behind coxae, concave, apex truncate. Mesosternal apophysis about twice width of prosternal apophysis, concave medially. Legs long, slender,

basal mesotarsal segment about equal to ungual segment or a little longer (as S. gibbipennis).

MATERIAL. Holotype: J, 5,5 mm elytral length (Transvaal Museum), S. Afr., Cape – Karroo, Zwartzkraal farm, 33.10 S. - 22.32 E., 8.11.1980, E-Y:1738, groundtraps, 42 days, leg. R. Oosthuizen, groundtraps with meat bait.

Allotype: 9, 8,0 mm elytral length (Transvaal Museum, locality as holotype, 23.7.1979, E-Y:1636, groundtraps, 44 days, leg. R. Oosthuizen, groundtrap with banana bait.

Paratypes: 43 ex.: 39 from type locality (Transvaal Museum): (3) data as allotype, but also from meat and faeces bait; (2) data as holotype, but faeces bait; (3) 5.9.1979, E-Y:1640, groundtraps, 50 days, leg. R. Oosthuizen, groundtraps with faeces bait; the following all leg. R. Oosthuizen, groundtraps: (2) 25.10.1979, E-Y:1673, 50 days, faeces & banana bait; (1) 6.5.1980, E-Y:1708, 41 days, meat bait; (1) 18.3.1980, E-Y:1703, 49 days, meat bait; (4) 26.6.1980, E-Y:1711, 41 days, meat bait; (1), 1.2.1980, E-Y:1700, 48 days, faeces bait; (2), 1.2.1979, E-Y:1546, 30 days, banana bait & unbaited; (2), 2.3.1979, E-Y:1553, 30 days, faeces bait; (1), 15.12.1979, E-Y:1694, 45 days, meat bait; (1), 5.9.1979, E-Y:1638b, 50 days, meat bait; (1), 15.12.1979, E-Y:1692b, 45 days, meat bait; (1), 5.9.1979, E-Y:1638b, 50 days, meat bait; the following from groundtraps: (6), 8.11.1978, E-Y:1540a, 38 days, leg. Endrödy-Younga, unbaited/meat/ferm. banana bait; (3) 22.9.1980, E-Y:1718, 47 days, leg. Endrödy-Younga/R. Oosthuizen, banana/meat/faeces bait; (4), 5.9.1979, E-Y:1634, singled, leg. Endrödy-Younga; 4 in South African Museum: (2) Bosluis Pass, C.P., Mus. Expd., Oct. 1952; (2) Gamka's Poort, C.P., Mus. Expd., Oct. 1952.

REMARKS. The new species, with its posteriorly narrowing and transversely impressed pronotum, is closely related to *Stenodesia gibbipennis*. It differs from that species in having the lateral costa of elytra double, as well as in the reduced lateral pronotal carination, less produced anterior margin of pronotum, details of elytral sculpture, and larger average size. Two of the characters that separate this species from *S. gibbipennis*, viz. lateral elytral costa and lateral pronotal margination, are the same as those used to separate another closely related pair of species, *S. mesembryanthemi* and *S. zinni*. These two species are separated from *S. gibbipennis* and *S. oosthuizeni* by the pronotal shape. All four species are very similar and undoubtedly share a common ancestor.

The new species is named in honour of Mr R. Oosthuizen, of the farm Zwartzkraal, who kindly maintained groundtraps on his farm over a long period and thereby contributed much valuable material to the Transvaal Museum, including most of the type series of this species.

Stenodesia montiscedrae spec. nov.

DIAGNOSIS (holotype): Elytral length 6,4 mm. Integument of body black, appendages dark red. Supra-antennal portions slightly raised, head between them flat. Anterior margin of pronotum simple. Sides of pronotum carinate, rounded. Pronotum with large, shallow, mainly reticulate punctures; two smooth and impunctate areas in posterior half. Elytra convex, with four serrate costae, third forming lateral edge of elytral disc, fourth running just above middle of reflected part of elytra. Innermost costa terminating above apical declivity, close to suture, the rest uniting successively on apical declivity. Intercostae somewhat uneven, with scattered granules; reflected part of elytra below costa uneven, with scattered granules; a band of microgranules in third intercosta close to lateral costa. Prosternal apophysis a little narrower than procoxa, deflected, with apex produced as in *S. serrata*; mesosternum, and legs except for rcd colour as in *S. serrata*.

MATERIAL. Holotype: 3, 6,4 mm elytral length (Transvaal Museum), S. Afr., W. Cape, Cedarberg, Oukraal, 32.25 S. - 19.25 E., 2.9.1979, E-Y:1630, sandblown mt., leg. Endrödy-Younga.

REMARKS. The single specimen differs so markedly from the related *Stenodesia serrata* that its recognition as a different species seems justified. The extremely wide range of variation in *S. serrata* was described by Penrith (1979), and the present specimen falls even far outside that range. In the inermous anterior margin of pronotum and rounded pronotal sides it differs from all the other Cape species of *Stenodesia*; in these features it is more plesiomorphic than all of them.

It is named after the Ccdarberg mountains, in which it was collected.



Fig. 17. Distribution of revised and new taxa of *Stenodesia*: Stenodesia globulum: *S. g. globulum* (solid circles), *S. g. veruculifera* (open triangles), *S. g. marshalli* (solid triangles), *S. g. kaokoensis* subspec. nov. (open circles); *Stenodesia montiscedrae* spec. nov. (open square); *Stenodesia oosthuizeni* spec. nov. (solid square).

CHECKLIST

A checklist of the southwestern African Adesmiini, with their known distribution ranges, was given by

Penrith (1979). The present checklist is restricted to a list of the genera and subgenera of Adesmiini, except where name changes occur or new taxa have been described.

Epiphysa Blanchard Alogenius Gebien subgenus Alogenius Gebien subgenus Aequigula Penrith Physadesmia Penrith Onymacris Allard Eustolopus Gebien Renatiella Koch Adesmia Fischer subgenus Adesmia Fischer subgenus Oteroscelis Solier subgenus Adesmina Reitter subgenus Macradesmia Solier subgenus Oteroscelopsis Koch subgenus Somaladesmia Koch subgenus Macropodesmia Koch subgenus Macropoda Solier (sensu Koch) subgenus Zambesmia Koch subgenus Spongesmia Koch subgenus Physosterna Solier stat. nov. Adesmia (Physosterna) torulosa (Pallas) Adesmia (Physosterna) armatipes (Koch) comb. nov. Adesmia (Physosterna) cribripes Haag Adesmia (Physosterna) foveipennis Haag Adesmia (Physosterna) goryi Solier Adesmia (Physosterna) porcata Solier Stenocara Solier subgenus Stenocara Solier subgenus Cauricara Penrith stat. nov. Stenocara (Cauricara) velox Péringuev Stenocara (Cauricara) albomarginata (Penrith) comb. nov. Stenocara (Cauricara) eburnea (Pascoe) Stenocara (Cauricara) phalangium Gebien subgenus Arenacara Penrith stat. nov. Stenocara (Arenacara) brunnipes Haag Stenocara (Arenacara) desertica Koch Metriopus Solier subgenus Metriopus Solier subgenus Coeladesmia Reitter subgenus Ceradesmia Gebien Orientacara Koch Stenodesia Reitter Stenodesia globulum (Haag) Stenodesia globulum globulum (Haag) Stenodesia globulum kaokoensis subspec. nov. Stenodesia globulum marshalli Koch stat. nov. Stenodesia globulum verruculifera (Haag) stat. nov. Stenodesia cavifrons (Solier) Stenodesia gibbipennis (Haag) Stenodesia mesembryanthemi Koch Stenodesia montiscedrae spec. nov. Stenodesia oosthuizeni spec. nov. Stenodesia serrata (Fabr.) Stenodesia thomseni (Gebien) Stenodesia zinni Koch

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REFERENCES

- ALLARD, E., 1885. Classification des Adesmiides et des mégagénides. Annales de la Société entomologique de France (6)5: 154-208.
- BRAIN, C. K., 1981. The evolution of man in Africa: was it a consequence of Cainozoic cooling? Alex L. du Toit Memorial Lecture Series, No. 17, The Geological Society of South Africa, 84, annexure: 1-19.
- CASEY, T. L., 1907. A revision of the American components of the tenebrionid subfamily Tentyriinae. Proceedings of the Washington Academy of Sciences 9: 275-522.
- ENDRÖDY-YOUNGA, S., 1978. Coleoptera. In WERGER, M. J., ed., Biogeography and ecology of southern Africa. W. Junk, The Hague.
- ENDRÖDY-YOUNGA, S., 1982. Dispersion and translocation of dune specialist tenebrionids in the Namib area. Cimbebasia 5: 257-271.
- GEBIEN, H., 1910. Coleopterorum catalogus, pars 15. (Tenebrionidae). 1. W. Junk, Berlin.
- GEBIEN, H., 1920. Käfer aus der Familie der Tenebrioniden gesammelt auf der "Hamburger deutschsüdwestafrikanischen Studienreise 1911". Abhandlungen aus dem Gebiet der Auslandskunde 2: i-viii, 1-168.
- GEBIEN, H., 1937. Katalog der Tenebrioniden. Teil I. Pubblicazioni del Museo entomologico "Pietro Rossi" Duino: 1-381.
- HAAG-RUTENBERG, G., 1875. Beiträge zur näheren Kenntnis einiger Gruppen der Familie der Tenebrioniden. I. Adesmiides. Deutsche entomologische Zeitschrift 19(7): 1-44.
- HAAG-RUTENBERG, G., 1879. Fernere Nachträge zu den Heteromeren-Monographien der Moluriden, Eurychoriden und Adesmiiden. Deutsche entomologische Zeitschrift 23: 289-296.
- KOCH, C., 1944. Die Adesmiini der tropischen und subtropischen Savannen Afrikas. Revue de zoologie et de botanique africaines 38: 139-191.
- KOCH, C., 1948. Die Adesmiini der tropischen und subtropischen Savannen Afrikas. (Schluss). Revue de zoologie et de botanique africaines. 41: 133-201.
- KOCH, C., 1952. The Tenebrionidae of southern Africa. XII. Supplementary notes to preliminary articles nos I, III, V, and VII. Annals of the Transvaal Museum 22: 79-196.
- KOCH, C., 1955. Monograph of the Tenebrionidae of southern Africa. I. (Tentyriinae, Molurini Trachynotina: Somaticus Hope). Transvaal Museum Memoir No. 7: 1-242.
- KOCH, C., 1963. The Tenebrionidae of southern Africa. XXIX. Luebbertia plana gen. et spec. nov., with a dichotomic analysis of Stizopina (Opatrini). Scientific Papers of the Namib Desert Research Station No. 18: 1-87.
- LANCASTER, I. N., 1979. Evidence for a widespread late Pleistocene humid period in the Kalahari. Nature 279: 145-146.
- LANCASTER, I. N., 1980. Dune systems and palaeoenvironments in southern Africa. *Palaeontologica africana* 23: 185-189.
- LANCASTER, I. N., 1981. Palaeoenvironmental implications of fixed dune systems in southern Africa. Palaeogeography, Palaeoelimatology, and Palaeoecology 33: 327-346.
- PENRITH, M.-L., 1979. Revision of the western southern African Adesmiini (Coleoptera: Tenebrionidae). Cimbebasia (A)5: 1-94.
- PENRITH, M.-L., 1980. Revision of the Zophosini (Coleoptera: Tenebrionidae). Part 1. Introduction. Cimbebasia (A)6: 1-16.
- PENRITH, M.-L., 1984a. Two new species of Stizopina (Coleoptera: Tenebrionidae: Opatrini) from Namaqualand, southern Africa, and the relationships between the psammophilous genera. Annals of the Transvaal Museum 33: 353-363.
- PENRITH, M.-L., 1984b. New taxa of Onymacris Allard, and relationships within the genus (Coleoptera: Tenebrionidae). Annals of the Transvaal Museum 33(31): 511-533.
- SCHULZE, L., 1962. The Tenebrionidae of southern Africa. XXXIII. Descriptive notes on the early stages of Onymacris rugatipennis Haag and Lepidochora discoidalis Gebien and keys to genera and species of Adesmiini and Eurychorini. Annals of the Transvaal Museum 24: 161-180.
- SCHULZE, L., 1964. The Tenebrionidae of southern Africa XXXIX. A revised key to the larvae of Onymacris Allard (Coleoptera: Adesmiini). Scientific Papers of the Namib Desert Research Station No. 23: 1-7.

SOLIER, A., 1935. Essai sur les Collaptèrides (suite), 3e Tribu. Macropodites. Annales de la Société entomologique de France 4: 509-572.

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