

THE TENEBRIONIDAE OF SOUTHERN AFRICA
 PART XLII: DESCRIPTION OF THE EARLY STAGES OF
CARCHARES MACER PASCOE AND *HERPISCIUS SOMMERI* SOLIER
 WITH A DISCUSSION OF SOME PHYLOGENETIC ASPECTS
 ARISING FROM THE INCONGRUITIES OF
 ADULT AND LARVAL SYSTEMATICS

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(With 19 figures)

INTRODUCTION

The Scaurini are represented in Southern Africa by two genera only. In the present paper a description is given of one larva of each genus.

The distribution of the genus *Carchares* Pascoe is confined to the western coastal regions of Southern Africa. *Carchares macer* Pascoe is endemic to the littoral plains of the Namib Desert. *Herpiscius sommeri* Solier inhabits the Cape Province and Orange Free State.

The larvae of these species have been reared in the insectarium of the Transvaal Museum and are described for the first time.

DESCRIPTIONS

Carchares macer Pascoe

The description is based on a larva 25 mm long, 1.9 mm broad (pronotum), head 1.6 mm wide. Cylindrical of subequal width, weakly sclerotized, ivory, cuticle glossy, bare, abdominal segments slightly longer than broad. Mandibles with five strong setae on well developed soft elevation. Legs with long, sharply pointed claws. Ninth abdominal notum elongate-pentagonal, apex prolonged into an upright bifid process.

Head (Text-figs. 1—5): About twice as broad as long and one sixth narrower than pronotum, weakly convex, sides slightly rounded; disc with two pointed setae at frontal margin, one seta on each side somewhat below antennal articulation, a transverse row of four distantly placed setae on basal third, a few small setae bordering lateral articulation of antenna and four to five setae along lateral margin; the outer border of ventral epicranium fairly densely set with pointed setae of varying length, some long setae along hypostomal margin. Ocelli wanting. Clypeus strongly transverse with two strong discal setae and one finer, longer seta latero-anteriorly. Labrum transverse with straight anterior and weakly rounded lateral margin, somewhat more than half the width of clypeus; two strong discal setae and eight pointed, marginal setae, the two median setae somewhat distant from anterior margin. First two antennal segments subequal in length, twice as long as broad at base, dilated anteriorly, apical sensorium of second segment horseshoe-shaped, apex with three small setae, two dorsally, one ventrally, third segment one seventh of second with one median apical seta and three surrounding apex. Mandibles large, strongly projecting beyond clypeus and labrum, upper half keeled, recessed in front of the dorsally strongly developed soft, membranous elevation, which bears

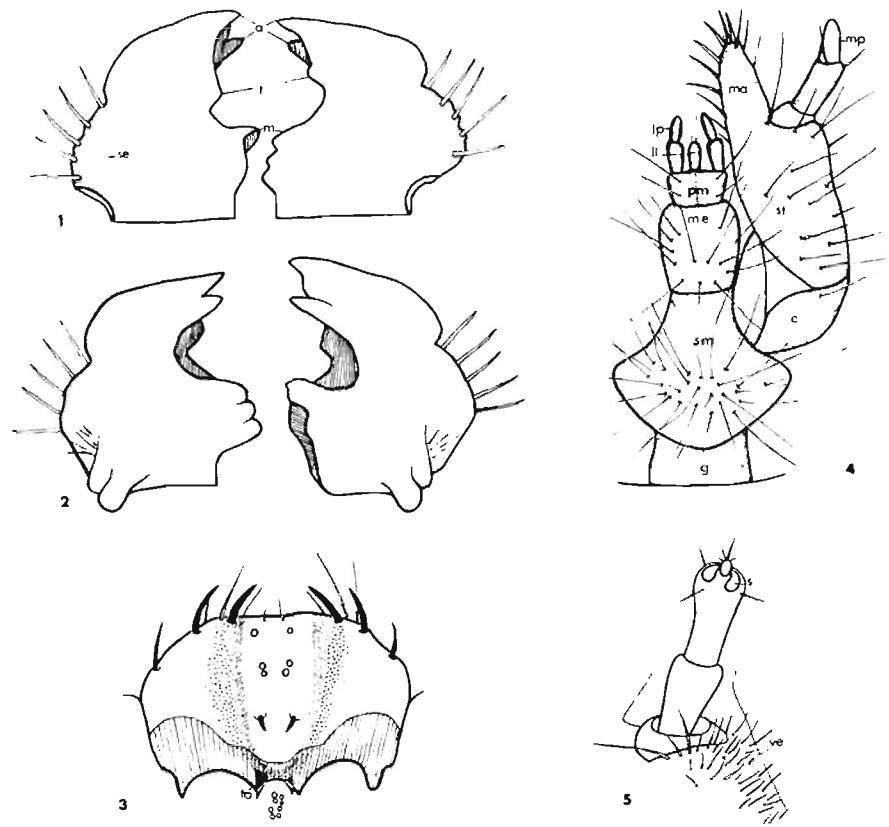
*Carchares macer* Pascoe

Fig. 1: Mandible, dorsally;
 Fig. 2: Id., ventrally;
 Fig. 3: Epipharynx;
 Fig. 4: Maxilla and labium;
 Fig. 5: Antenna, latero-dorsally.

a:	apical teeth;
c:	cardo maxillaris;
g:	gula;
li:	ligula;
lp:	palpus labialis;
m:	molar;
ma:	mala;
me:	mentum;
mp:	palpus maxillaris;
s:	sensorium;
se:	membranous, setose elevation;
sm:	submentum;
st:	stipes maxillaris;
t:	median teeth;
to:	triangular process of torma;
ve:	ventral epicranium.

four to five strong spines, the two apical teeth sharply pointed, the right upper one ventrally broadest; the left molar pointed, projecting, the right molar with three chewing plates; a few short, fine setae ventrally next to articulation. Epipharynx bare apart from microfilaments accompanying the median sensory area, which shows six sensory cups, four grouped in a square on upper half, two underneath anterior margin, medianly two spines, the basal sclerotized band (torma) medianly with two triangular processes, the left one usually somewhat larger, underneath two vertical rows of four sensory cups each; outer margin set on each side with three stout, flattened setae and two small setae medianly. Stipes of maxilla rather stout, surface medianly with some long, pointed setae, mala slender, bare with marginal spines only; first and third segment of maxillary palpus of subequal length, the first stout, the third conical and one third narrower, second segment one and a half times longer than third, apically with one ventral seta and one at outer margin. Submentum with numerous long, pointed setae, mentum barrel-shaped with fewer and somewhat shorter setae than on submentum, prementum subsquare about one half the length of mentum with one seta underneath palpal articulation and one more basally, often depressed medianly and lateral surface

somewhat sclerotized; ligula elongate-coniform, of same length as first segment of labial palpus; segments elongate, of subequal length, the second one-third narrower, both segments bare. Hypopharynx tricuspidate.

Thorax: Pronotum large, more than twice as long as head, about one-seventh wider than long, mesonotum one third, metanotum about one tenth shorter than pronotum; mesonotum with a sinuate, sclerotized ridge anteriorly; all nota bare apart from two widely spaced setae at basal margin, one seta in each basal corner. Epipleural margins with a few short setae; pre- and eusternum of prosternum bare, a few microsetae on pre-eusternum, lower half of postcoxal area with fine, pointed setae, their length increases basally; postcoxal areas and poststernella of meso- and meta-sternum with medium-long setae, eusterna with a few single setae. Mesothoracic spiracle large, transverse-ovate, about as long as middle claw, metathoracic spiracle obsolete.

Legs (Text-figs. 6, 7): Front legs large, mid and hind legs half their size and their segments much more elongated. Front coxa stout with one strong, pointed seta at inner, anterior corner, one similar seta more basally, between them a few smaller, finer ones, the outer margin bordered by strong, pointed setae; trochanter somewhat longer

than coxa with two strong setae at the base of a stronger sclerotized round projection in front of articulation, disc with one pointed median seta and one near outer margin; femur stout with somewhat wavy, sclerotized inner contour, along which five strong setae are inserted, a smaller one in front of them, one pointed seta at some distance from base and outer margin, a second one somewhat more anteriorly, next to outer margin; tibiotarsus elongate, as long as femur at outer margin, four strong, pointed, medium-sized setae at anterior two-thirds of inner margin, originating from projecting, sclerotized bases, ventral disc with one fine, long seta underneath base of claw, a second seta one third from base, lateral outer surface with two fine setae only; claw long, strongly pointed, over three times as long as broad at base, unsclerotized base well developed with one strong seta at inner and one at outer margin with an indication of a more strongly sclerotized joint basally. Mid and hind legs much more slender and delicate than front legs, hind legs somewhat smaller, all segments elongated and set with relatively large, strong spines, the setae on ventral disc of same size as along margins, claws long and narrow.

Abdomen (Text-figs. 8—11): First, second and eighth notum subsquare, the remainder somewhat longer than broad. The same arrangement of very fine and inconspicuous setae on these nota as on the thoracic ones, but lateral setae missing. Anterior margin of first sternum with short, fine setae, four fine setae in a basal row, the following six sterna with one fine seta in each corner, eighth sternum with four setae in an anterior row and

four setae in a posterior row, two median setae much shorter, space between posterior setae and base with some microsetae. Abdominal spiracles small, round. Ninth abdominal notum somewhat shorter than the preceding one, pentagonal, rounded sides tapering towards two small, pointed lateral projections and thence going in a slightly concave contour towards a reflected bifid apical process; in front of the lateral processes one small, dark spine, two similar spines at medium level underneath apical process¹⁾; sides not quite one and a half times longer than apical width (measured across lateral processes); apical process about one ninth of the total length; the basal third of notum strongly convex, remaining disc hollowed, somewhat below base of excavation a transverse row of four distantly placed setae, one marginal seta in front of each angular process; caudal surface with two setae at each basal corner of apical process and one seta underneath each lateral process, caudal declivity with three transverse rows of widely spaced long setae, some shorter setae, more densely set, along sternal border, extending up to eighth segment, basal lateral surface bare. Ninth abdominal sternum considerably shorter than notum, pygopodia very small, straight, tubiform, on their lateral surface two to three small, stronger setae, above these and caudally some finer setae; basal lateral surface of sternum with an aggregation of small pointed

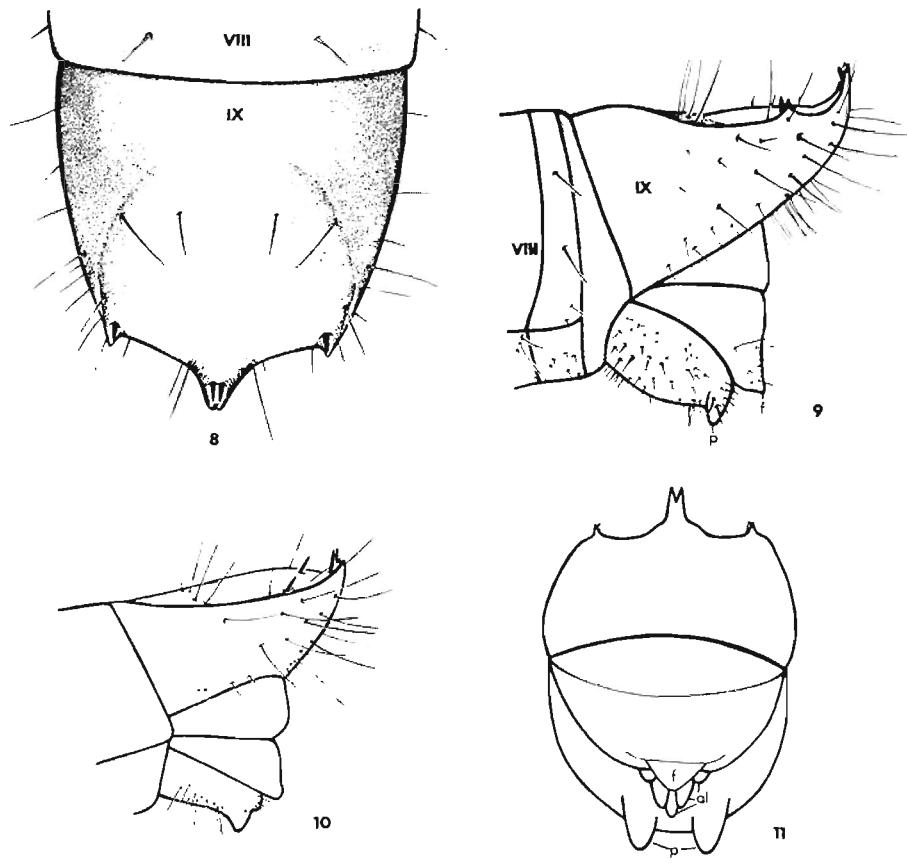
¹⁾ In one just moulted specimen of 25 mm length the apical inner half of the process is set with numerous small setae.

Carchares macer Pascoe

Fig. 6: Front leg;
Fig. 7: Middle leg.

c: coxa;
cl: claw;
f: femur;
m: muscle attachment;
sc: sclerotized joint;
ti: tibiotarsus;
tr: trochanter.





Carchares macer Pascoe

Fig. 8: Part of eighth and the ninth abdominal notum;

Fig. 9: Part of eighth and the ninth abdominal segment, lateral view;

Fig. 10: Second stage larva: ninth abdominal segment;

Fig. 11: Ninth segment, caudal view.

al: anal lobes;
f: flap;
p: pygopodium.

spines, next to pygopodia a vertical stripe of similar setae. Anus surrounded by small lobes and covered by a triangular flap. These anal structures and the anus itself often strongly projecting in lateral view.

The egg and second stage larva (Text-fig. 10): Egg elongate-oval about 1.7 mm long and half as wide, ivory. A first-stage larva was not obtained. The second stage is 4.7 mm long, head 0.5 mm broad, ivory, very delicate, only tips of mandibles and claws sclerotized. Setae on head and body same as in older stages, but as usual relatively much longer. Inner margin of tibiotarsus with two strong, pointed setae only. The angular pointed processes on ninth abdominal notum of older larvae not developed yet, the setae situated later in front of them, longer than in more mature larvae, but scarcely sclerotized, the apical process is not as long and pointed as in later stages, the apical setae are as long as the process itself; as they are inserted just below its apex, they overtop the same considerably. In the third stage larva these setae are still large and prominent, but now more strongly sclerotized; the angular small processes are not developed yet.

Material: 13 larvae: Largest larva 25 mm long, 2.1 mm broad (pronotum), head 1.8 mm wide.

Parents from Swakopmund, South West Africa. X. and XI. 1961, C. Koch. 12 larvae: Largest larva same measurements as above. Parents from Walvis Bay, South West Africa. IX. 1962, C. Koch.

Herpiscius sommeri Solier (Text-figs. 12, 13).

With regard to general features this species is very close to *Carchares macer*, but setose areas are furnished with less and mostly shorter setae. The main difference is evident in the formation of the ninth abdominal notum which is more primitive, bluntly triangular with four strong, short apical spines and four discal fine, pointed setae in a transverse row, the two lateral setae somewhat more basally; disc convex, somewhat sloping towards apex, not excavated, caudal surface with fewer setae than in *C. macer*. The same applies to the ninth sternum and the pygopodia.

Distribution of setae on body, head, clypeus and labrum the same as in *C. macer*. Along hypostomal margin, on ventral surface of mentum and stipes maxillaris four to six setae only. Distribution of setae on front legs identical to *C. macer*, but setae on inner margin of tibiotarsus shorter, those on trochanter and femur small and blunt; setae on mid and hind legs shorter, inner margin of femur with two strong and two finer setae only.

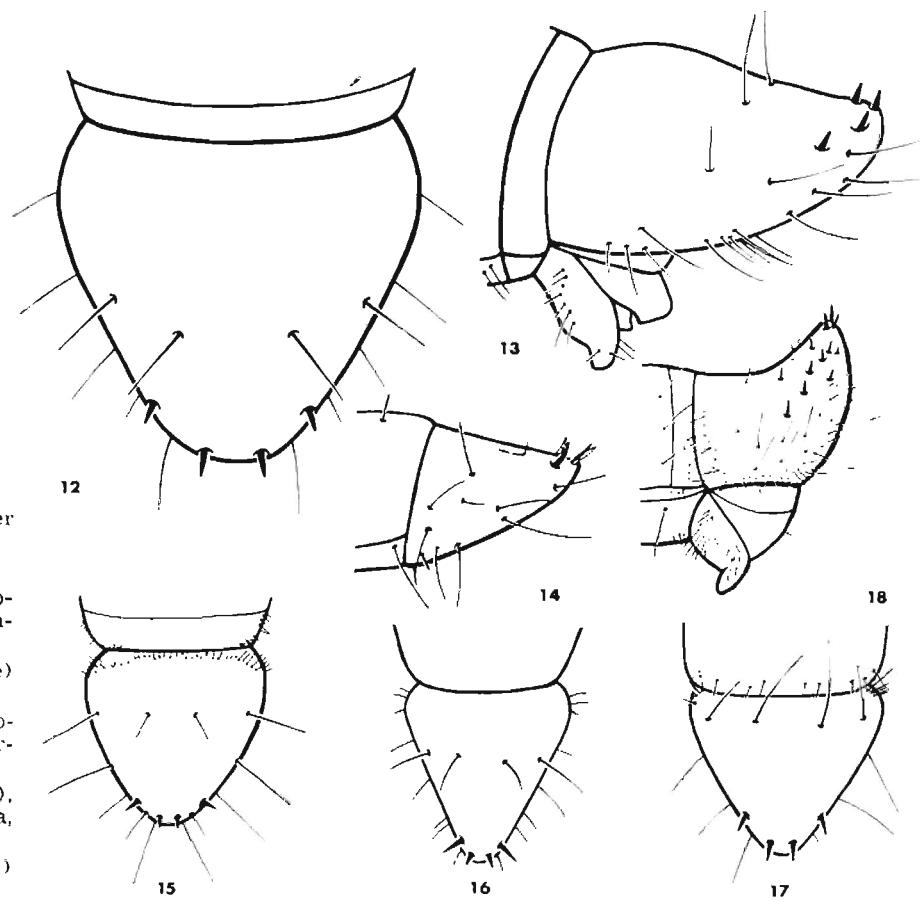
Material: 14 larvae, 1 pupa. Largest larva 20 mm long, 2 mm broad, head 1.6 mm wide. Parents from Allanridge, 9 miles NW of Odendaalsrus, Orange Free State. Found in mole heap. II. 1962. O. P. M. Prozesky.

DISCUSSION

The two described larvae, *Carchares macer* from the coastal plains of the Namib Desert and *Herpiscius sommeri* occurring in the Cape Province and Orange Free State, exhibit a strong similarity in general appearance, mouthparts and feet. The ninth abdominal notum of *H. sommeri* appears more primitive in its simple, rounded outline without excavation or apical process, its caudal surface is more strongly developed than in *C. macer*, as a result the sternum is greatly reduced. The well separated four apical spines are homologous to the four small spines in front of the angular and apical processes of *C. macer*. The fact that the desert form shows a modification of the basic tribal design in the structure of the ninth abdominal notum has been found formerly and this phenomenon will be discussed later.

To my knowledge the only description available of a Palaearctic Scaurini larva is that of *Scaurus atratus* F. by Schioedte, if one disregards Mulsant's description of *Scaurus tristis* Olivier, which Perris already mentions as very doubtful. Schioedte's detailed description and seemingly accurate drawings show a larva which has nothing in common with the South African species. Features of this larva which are especially puzzling are the formation of the front leg with a strongly reduced setose tibiotarsus, a large claw which is one and a half times longer than the tibiotarsus and numerous conical spines on inner margin of femur and trochanter, as well as the completely spinose ninth abdominal notum terminating into two spiny processes. Combined with the characteristics of the ninth abdominal sternum, the pygopodia and the head, this larva shows all features of an Asidin larva and most probably is not a Scaurini larva at all.

The two Southern African species show relationship to the North American larva of *Cerenopus concolor* L. (Marcuzzi and Rampazzo, 1960), a further strengthening of the assumption of Reitter (1914) and Koch (1958) from the evidence of adult features, that the American Scaurini belong to a



Ninth abdominal notum:

Fig. 12: *Herpiscius sommeri* Solier (Scaurini), Southern Africa.
 Fig. 13: Id., lateral view.
 Fig. 14: *Crypticus quisquilius* L. (Crypticini), Palaearctic (after Emden 1947).
 Fig. 15: *Quadrideres femineus* (Lesne) (Platynotini), East Africa.
 Fig. 16: *Crypticus quisquilius* L. (Crypticini), Palaearctic (after Korschefsky, 1943).
 Fig. 17: *Pedinus femoralis* L. (Pedinini), Palaearctic (after Keleinikova, 1961 b).
 Fig. 18: *Gonocephalum* sp. (Opatriini) South Africa.

separate tribe. Likewise there is no affinity to the Pimeliini larvae. The latter tribe, together with the Scaurini, Blaptini and Platyscelini formed Reitter's (1917) subfamily Blaptinae.

During the past fifty years efforts have been made, to give a broader base to the classification of insects in order to arrange the enormous variety of individual forms into a system which would, in the ideal case, be a representation of the phylogenetic affinities existing between lower and higher categories of the respective orders. Since Linné the principle applied in systematics had been almost entirely founded on the comparative anatomy and morphology of the adults. This classical approach yielded remarkable results, but, in some instances, it was felt that the grouping of units according to their structural similarities only would not reflect their natural relationship. Therefore in more recent times coleopterologists tried to incorporate chorology, ecology, ethology and not at last post-embryology as the main auxiliary methods. From several sides the urgency of the consideration of larval systematics was proclaimed. In 1919 Verhoeff draws attention to the importance of larval studies for the detection of phylogenetic trends in the Staphylinidae. Boeing and Craighead (1931) compiled a synopsis of the principal larval forms of Coleoptera and scientists like Emden (1929, 1947), Korschefsky (1943), Skopin (1958, 1960, 1962, 1964) and Keleinikova (1961, 1964) contributed greatly to our knowledge of tenebrionid larvae and the two latter tried to present a phylogenetic system of the larvae of the Tenebrionidae, based essentially on Palaearctic material. This system was in neither case completely congruent with the adult taxonomy. Watt (1967) has recently given a critical review of both attempts, which must be considered as very valuable contributions. That modifications will be necessary for a wider application of these systems is self-evident, if one considers the diversity of forms and the complexity of Tenebrionid systematics and our limited knowledge of the larval forms, especially of the Southern African ones, which is still very scanty and holds an abundance of surprising evidence for modifications undergone, not only by adults but by larvae as well in one of the main centres of tenebrionid development. These new discoveries very often will not fit into the concepts of Palaearctic larval systematics as is already evident in many cases. In the larval systematics of Tenebrionidae the structure of the ninth abdominal segment plays a decisive role and Keleinikova (1964) founded her system of six different larval types practically entirely on this feature, but it can not be applied indiscriminately to the tenebrionid larvae of Southern Africa as we encounter strong modifications of the ninth abdominal tergum in some tribes. It is an interesting fact, that up to now those species which show a caudal segment with features strongly

deviating from the norm in the respective tribe, are almost exclusively desertic, ultra-psammophilous species. *Carchares macer*, deserticolous occurring strictly in littoral sands, exhibits a transformation of the ninth abdominal notum, the structural features of which can still be traced as homologues of the more primitive form found in *Herpiscius sommeri*. As we have in *C. granulosa* a species which occurs on wind-blown sand and on the foot of marginal dunes, it would be interesting to obtain the larva of this species. In one ultra-psammophilous species of each, the Adesmiini (*Onymacris laeviceps* Gebien) and the Zophosini (*Cardiosis fairmairei* Péringuey) a convergent development of the ninth notum has taken place. In these species the notum is extremely prolonged, but still retains the basic features of the tribe, the pygopodia are reduced and the disc is covered with a dense setose "fur". Another characteristic, apparently connected with the ecology of desertic, psammophilous species, is the tendency to transform pointed setae to knob-like spherical ones as on the ninth notum, femur and trochanter of *Onymacris bicolor* ssp. *marshalli* Koch and *O. brincki* Koch. Furthermore spherical setae with pointed apices are encountered on the ninth abdominal notum of all known *Lepidochora* species. In addition the notum is semiglobular and the pygopodia are nearly obsolete, while nine other genera of Eurychorini in our collection have a triangular, apically reflected notum with pointed setae. According to Keleinikova's larval arrangement one would be tempted to put the *Lepidochora* species to the erodiodid type, the remaining Eurychorini into the opatroid group, thus transferring most of the Eurychorini from the Tentyriinae to the tenebrionid Tenebrioninae. This serves only to show that other criteria have to be found, if we want to incorporate Southern African tribes into a natural system. A similar development as in the Eurychorini we find in the Stizopina (Opatriini) larvae. Again the ultra-desertic species *Psammogaster malani* Koch and *Periloma alfkensi* Gebien exhibit a completely modified ninth notum, again both are semi-globular, in *Periloma* in addition with a centro-apical cavity, in *Psammogaster* with spherical setae, similar to those found in *Lepidochora* and in the *Onymacris bicolor* *marshalli* group. The remaining species of this subtribe have "opatroid" nota, which in this case reveals a true relationship. It is doubtful if somebody working on the Eurychorin and Stizopin larvae without knowledge of their adult relationship would place those modified forms in their respective tribes, as sometimes other features, mouthparts and legs as well do not clearly indicate their affinity with the "normal" forms.

It is interesting to notice that, as far as our limited knowledge goes, the larvae of Namib Desert species only show these radical transformations, but not the species from the Kalahari Desert. As the Namib Desert originated in and remained



Fig. 19: Larvae (from left to right) of:

Heryiscius sommeri Solier (Scaurini).
Quadrideres femineus (Lesne) (Platynotini).
Buntdemus lucidus Koch (Platynotini).
Carchares macer Pascoe (Scaurini).
Heteropsectroynus sp. (Oncotini).

undisturbed since Cretaceous times, while the Kalahari Desert was formed much later during the Miocene-Pliocene period, one may be tempted to ask if only those species which ventured early enough into the Namib dunes had time to develop special adaptations. The fact, that more decisive modifications occur in the caudal segment of desertic, dune-living Eurychorini and Stizopina than in the Adesmiini and Zophosini seems easy to explain, as the flat, sleek shape of the latter tribes appears to need little or no change for effective locomotion in loose sand, whereas the upcurved last segment of the Eurychorin and Stizopin larvae should offer a considerable resistance. Mutations with a more rounded hind body and reduced pygopodia will certainly derive advantage over the original form.

While checking the Scaurin larvae on their possible relationship with other tribes I met with a different problem. The more primitive larva of *Herpiscius sommeri* recalls the characteristics of larvae of other tribes to an astonishing extent (Fig. 19). Figures 14-17 demonstrate three examples of the ninth abdominal notum of *Crypticus quisqui-*

lius L., *Pedinus femoralis* L. and *Quadrideres femineus* (Lesne) (other related species could still be added) to be compared with that of *H. sommeri*. As can be readily seen the nota are almost identical in the main features, shape and chaetotaxy, but not only the ninth notum shows such near congruity, mouthparts as well as feet are of the same, similar pattern in all species, yet they belong to four different tribes, three different subfamilies according to Reitter (1917); spread from the Tropical African to the Southern African Region. They show more affinity to each other than each of them shows to members of its own genus. One distinct characteristic which separates *Herpiscius* from the three other species is the absence of ocelli, which is not a positive character, otherwise all species seem to follow the same pattern. In other words the morphology of the larvae does not correspond with that of the adults, for the latter can be readily distinguished generically.

The tribes concerned all belong to the tenebrionid Tenebrioninae (Koch, 1955), which are not as sharply separated and specialised as the Tentyriid tribes and would fall under Skopin's Blapimorpha

or Keleinikova's "opatroid" larvae, I should like to point out, that there is a definite difference between the structure of the ninth abdominal notum of the Opatrini-Blaptini group and that of the Scaurini, Platyscelini²⁾, Platynotina of Platynotini, Pedinini, Phaleriini and Crypticini, which was not distinguished by former authors. In the larvae of the Opatrini and Blaptini the ninth abdominal notum is wider than long, subcordiform, the strong apical reflection originates from the middle of dorsum, the caudal declivity is strongly convex and steep until it meets the sternum, thence it recedes abruptly angularly towards base. Seen from the side its appearance is extremely compact with a strong latero-discal convexity. The armature consists mostly of numerous short spines along apical margin, which may extend further unto disc (Fig. 18). In sharp contrast to these features the ninth abdominal notum of the above mentioned tribes is of oval shape, longer than wide; there may be a shallow concavity on disc, but the apical portion of notum is never reflected as a whole, but rather slanting towards apex (in *C. macer* a small apical process only is bent backwards). In lateral view the caudal contour is weakly convex and curves gradually towards base. There is not the cubical compactness of the Opatrini-Blaptini notum, but an elongated, dorsally somewhat flattened, shape instead with a weak latero-discal convexity. There are only four to (seldom) twelve apical spines and in most cases only single discal setae, spines never go beyond the apical margin. Probably the two groups present sister groups. If we turn back now to the problem of the discussed larvae and their relationship to each other, we find that recently in the adult systematics any affinity between Oriental-Southern African and Palaearctic tribes of the Opatrinae are rejected. Koch (1956) undertook the difficult task of a preliminary revision of the African Opatrinae. He conceived a completely new grouping and stated "The supposed connections between the Opatrinae of the Palaearctic Region and those of the Tropical and Southern African Regions are clearly refuted." The greater part of the Pedinini Gebien was included in the Platynotini. "From this change it follows that the supposed Pedinini from South of Sahara do not belong to a North-West African - Mediterranean - Palaearctic - Asiatic group, but represent an independent Tropical- and Southern-African, Madagascar, American and Indian tribe." And yet some larvae of just this Palaearctic tribe, as well as those from Palaearctic Crypticini, Phaleriini, Platyscelini are morphologically extremely close to East- and Southern African Platynotini (Platynotina) and Southern African Scaurini.³⁾ We admit that the possibilities for comparisons of this kind are quite inadequate at this time owing to the lack of larval material. With this respect it would be interesting to obtain larvae from the Oncotini (Koch)⁴⁾, which comprise former

South African Pedinini and Platyscelini, of the Litoborini (Antoine), in which Pedinini, Opatrini and Helopinini (sensu Gebien) are incorporated and of the Loensini (Koch), formerly part of the Pedinini.

Nevertheless the astonishing fact of morphological conformity of larvae of different tribes and remote distribution remains, and the question arising is: How is it possible that from larvae of extreme similarity structurally completely differentiated adults emerge? Is the uniformity of larval characteristics an indication of close affinity or only of a parallel development? In other words is this apparently primitive ninth notum a feature of a common ancestor, which is retained in a number of species of different tribes, whose adult stages have long ago developed along different lines or is it a case of homology, where in species of related groups similar characters are developed independently without descent from a common predecessor or is it a convergent development on parallel lines caused in adaption to similar external factors?

We can conclude from the criterion of the frequency of the occurrence of characteristics (Kriterium der Häufigkeit des Vorkommens der Merkmale, Hennig, 1950), that features which are primitive ("plesiomorph") and common to a large range of species indicate a more distant relationship than those, which are common to a smaller number only. And in our case this criterion certainly stands, the widespread occurrence of morphologically similar larvae does not constitute an evidence of closer relationship between any of the tribes. We have to conclude that the similarities observed rest on symplesiomorphy and the groups discussed are paraphyletic not monophyletic. As larvae and adults represent two completely different systems which can adapt themselves each in its own way to environmental factors which may vary tremendously, the rate and the quality of the transformations of the two stages may diverge considerably. It

²⁾ According to Emden's key (1947). I have no possibility to compare Kolobova's description of *Platyscelis gages* Fisch.

³⁾ I should like to mention a peculiar convergence in the Scaurini and Akidini. Koch (1958) compared the aedeagus of *Akis opaca* von Heyden with that of certain Scaurini, as the Akidini "superficially recall the Scaurini by a similar shape of head", though belonging to different sub-families. Amazingly enough the ninth abdominal notum of the larva of *Carchares macer* resembles the structure of the notum of *Sarathropus depressus* Zoubk. (Skopin, 1960), which is likewise pentagonal with two lateral and two apical spinose processes and a discal depression, otherwise there is no likeness between the larvae.

⁴⁾ Just before this paper went to press we obtained larvae of an Oncotini species, the characters of which conform with those of the above-mentioned tribes in all discussed respects. (Cf. Fig. 19)

is feasible, that in soil-living larvae, like most of the apterous Tenebrionidae, the ecological conditions for the early stages remain relatively constant even if a dispersal over wide geographical areas takes place accompanied eventually by a multiplication of the species. The adult stage is forced to undergo more or less radical changes to adjust to varying ecological conditions. But only where the larvae too meet with extreme conditions like for example those in the Namib Desert, the conservative pattern is broken and the species is compelled to adjust its early stages as well. Though we are here mainly concerned with the morphological evidence, physiological and ethological adaptations will play their role in a very complex reaction. Though the discussed larvae are phenotypically very close their genetic make-up responsible for the realisation of the adult characters must differ considerably. If *Drosophila* species are only to be distinguished by their chromosomes or if it is impossible to forecast which adult species will emerge from a certain Chironomid larva or pupa, we encounter a similar problem.

Shall we be able to satisfy the high hopes entertained by coleopterologists the world over for a phylogenetic hierarchical system supplied by the study of larval and pupal affinities? Would such a system solve all problems encountered in the attempt to build up a natural classification reflecting the results of a complex evolution? This hope takes for granted that the evolutionary stage of a species will be evident morphologically in adult and postembryonic stages to the same degree and will manifest itself accordingly.

The assumption is further, that we should be able to evaluate morphological characters correspondingly as evidently some features will indicate affinities more clearly than others. But where is the objective standard to be applied? In the ideal case the scientist should be able to alter his conception of the decisive characters of either larva or adult or both until a complete agreement is reached. The difficulty lies in the fact that evolution is based on genetic constellations which may not manifest themselves in morphological characters, the phenotype may obscure the genotype.

There will be and are many cases, perhaps even the majority, where a congruity between postembryonic and adult systematics can be obtained. On the other hand we will struggle with the "missing links", the many species which are lost on the evolutionary path and with those cases where the development diverged and one of the two stages led the way and manifested itself in a new form, while the other retained its original identity. In this case we have to apply criteria other than comparative morphology and anatomy. As the comparison of chromosome structures or biochemical and serological methods cannot practically be applied on a large scale, ecology, ethology and

above all chorology, the distribution of species and higher groups, are the most reliable sources for phylogenetic investigations. Larval and adult systematics have to be cross-checked and balanced against each other, in order to maintain the entity of the species. We have to consider incongruity in larva-adult relationship with similar criteria as sexual or seasonal dimorphism. We have to agree with the statement of Hennig (1965, 1966), that monophyletic groups may be recognized only in the larval or pupal stages and others only in the imaginal stage.

The eventual unification of adult and larval systematics should be our aim, though it may be unavoidable and even desirable in the process of clarification to emphasize differences where they occur. We should however be aware of the fact that in certain cases the morphological evidence may not be sufficient and be even misleading, if not interpreted in the right way.

SUMMARY

Two larvae of the South African Scaurini (Tenebrionidae) *Carchares macer* Pascoe and *Herpiscius sommeri* Solier are described. Though the ninth abdominal notum of the desert species, *C. macer*, shows a remarkable transformation, the two larvae are closely related.

No affinity was found with the North American larva of *Cerenopus concolor* L. This assists the assumption that the American Scaurini form another tribe.

The description and drawings by Schioedte of *Scaurus atratus* F. are regarded as being of an Asidin larva.

A short review of the attempts of coleopterologists to assist phylogenetic systematics through the study of larvae and the compilation of larval systems is given.

Reference is made to some difficulties in the application of the larval systems of Skopin and Keleinikova to the Southern African Tenebrionidae, because of marked transformations, particularly in desert species, which are especially pronounced in the structure of the ninth abdominal notum.

Examples of special desert adaptations are given, one of which is also evident in the described larva of *Carchares macer*. It is pointed out that Namib Desert species only show these modifications and not the Kalahari Desert species. This fact can probably be attributed to the longer adaptation period available in the Namib Desert.

Inferences drawn from the fact that the "primitive" ninth abdominal notum of *Herpiscius sommeri* recalls almost in every detail the last segment of representatives of different Palaearctic tribes as

well as of one member of the East African and of some South African Platynotina are discussed and the consequences of the incongruity of larval and adult systematics are referred to. It is assumed that in some cases the development of post-embryonic and adult characteristics of a species does not take place simultaneously. A possible explanation for this phenomenon is tentatively given. Furthermore the genetic factors of evolution are referred to pointing out that a phenotypical appearance may obscure the genotype. In some cases it may be possible to trace a close phylogenetic relationship by means of the characters of a single stage only.

Stress is laid on the cross-checking of post-embryonic and adult systematics and their eventual unification. The limitations of a merely morphological approach have to be avoided and should, where necessary, be supplemented by ecology, ethology and, most important, biogeography in the attempt to construct a sound phylogenetic system which reflects the contemporary state of evolution in the Tenebrionidae.

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