DESCRIPTION OF AN INDIVIDUAL POSSIBLE HYBRID TENEBRIONID BEETLE AND THE HABITAT PREFERENCE OF THE PARENTAL SPECIES

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Abstract

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The structure and behavior of a sterile male intergeneric hybrid tenebrionid beetle from the Namib Desert are described. Compared with the courtship performance of males of the parental types the hybrid male was intermediate in choice of females. The parental species occur together in the field and there is a broad habitat overlap in utilized parts of the environment. Intergeneric courtship was regularly observed, but only one instance of hybridization was noted.

Introduction

The sand dunes on the banks of the Kuiseb River at Gobabeb, South West Africa, are the habitat of two diurnal adesmiine tenebrionid beetles, *Onymacris rugatipennis* (Haag) and *Physosterna globosa* (Haag). The flood plain is a mixture of diverse habitats, each used to some degree by these two species. This paper describes a male adult hybrid individual between these two species. Also described is the courtship behavior of this hybrid and observations of the habitat preference of the two species, together with their daily activity cycle at Gobabeb.

Some aspects of the distribution and diversity of some of the unique Namib Desert tenebrionids have been reviewed by Koch (1962) and Penrith (1975). Descriptions of existing specimens of the numerous Namib species to date have involved clearly assignable material. Elsewhere Penrith (1975) described a hybrid swarm between *Onymacris marginipennis* and *O. candidipennis* in Angola.

Materials and Methods

Despite an extensive search we found only a single hybrid specimen. While there are inherent dangers in an analysis based upon a single specimen, the data presented, i.e. structure of adult specimens, courtship behavior, and the habitat preferences of the parental species, provide evidence which may not soon become available again.

We collected the hybrid near the Desert Ecological Research Station at Gobabeb, South West Africa. The specimen was referred to the adesmiine species complex. While the shape of the elytral sculpture is suggestive of facies of *Physosterna* species the legs are too long for species in that genus. The probability that the specimen is a hybrid is thus considered.

Behavior of the hybrid. The hybrid specimen was captured alive at Gobabeb. It was placed in a container with other *O. rugatipennis* and *P. globosa* and immediately began courting activities. A series of experiments were performed to determine species preference for females. In these experiments three plastic garbage cans with an upper diameter of 31 cm were filled with sand to within 4 cm of the rim. Each of these containers was supplied with one adult female *O. rugatipennis* and one female *P. globosa*. The hybrid was introduced into one of these containers and an adult male of the parental species was introduced into the other two containers. At the end of 1 min, courtship (following) activity of the three males was noted. Then each test male was removed and placed in a different container. As soon as each male had been introduced to each female, a new group of females was introduced and the experiment was continued. When each male had made 10 choices (following movements active at the end of test minutes) the experiment was terminated. If 10 following responses did not result during 15 introductions for all three males, that experiment was aborted. Twelve complete experiments of this sort were completed.

Four species of *Onymacris* and two species of *Physosterna* occur in the vicinity of Gobabeb. These are *O. rugatipennis* (Haag), *O. unguicularis* (Haag), *O. plana* Peringuey, *O. laeviceps* Gebien, *P. globosa* (Haag), and *P. cribripes* (Haag). In addition, *O. subelongata* Gebien has been recorded rarely from the area, although not in the habitat where the hybrid and the parental species occur.

On morphological grounds the most likely parent species are *P. globosa* and *O. rugatipennis*. The putative hybrid specimen resembles *P. globosa* in body shape, particularly in the rounded elytra and the steep apical declivity and strongly caudate

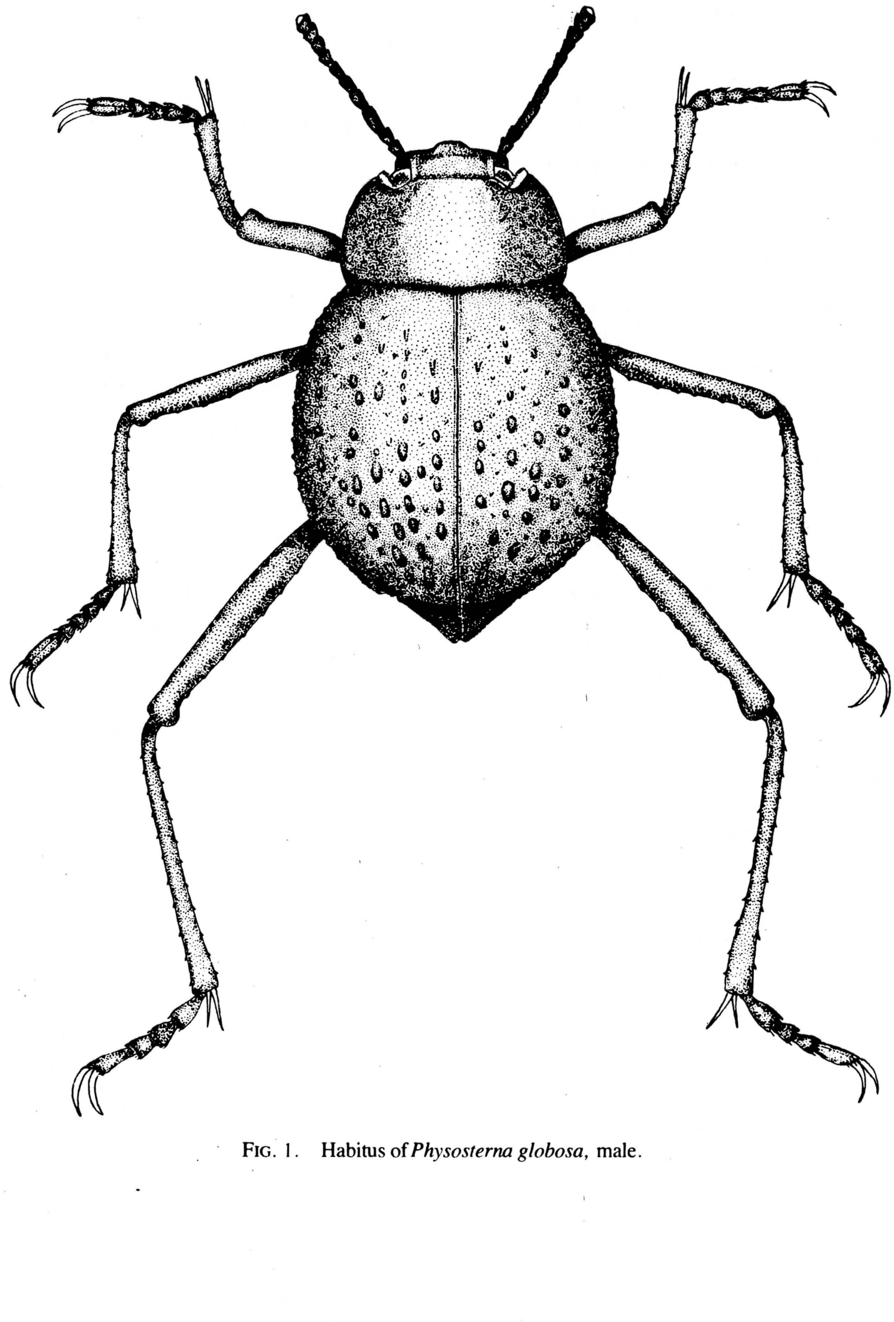

FIG. 1. Habitus of *Physosterna globosa*, male.

apex of elytra. Of the above mentioned *Onymacris* species, only specimens of *O. rugatipennis* possess the rather large round punctures found on the head and pronotum of the putative hybrid. Specimens of *O. subelongata, O. unguicularis,* and *O. laeviceps,* like *P. globosa,* have the pronotum and head smooth and virtually or entirely impunctate, while specimens of *O. plana* have prominent rugose sculpture on the head and pronotum. The intermediacy of the hybrid specimen between *P. globosa* and *O. rugatipennis* in several other characters is discussed below.

P. globosa, the putative hybrid, and *O. rugatipennis* are illustrated in Figs. 1–3. Detailed descriptions of the parental types are provided in Penrith (1975).

DESCRIPTION OF *P. globosa* × *O. rugatipennis* (Fig. 2). Material: 1 male, 11.7 mm elytral length, from Gobabeb (23°34′ S., 15°13′ E.) deposited in the State Museum, Windhoek, South West Africa.

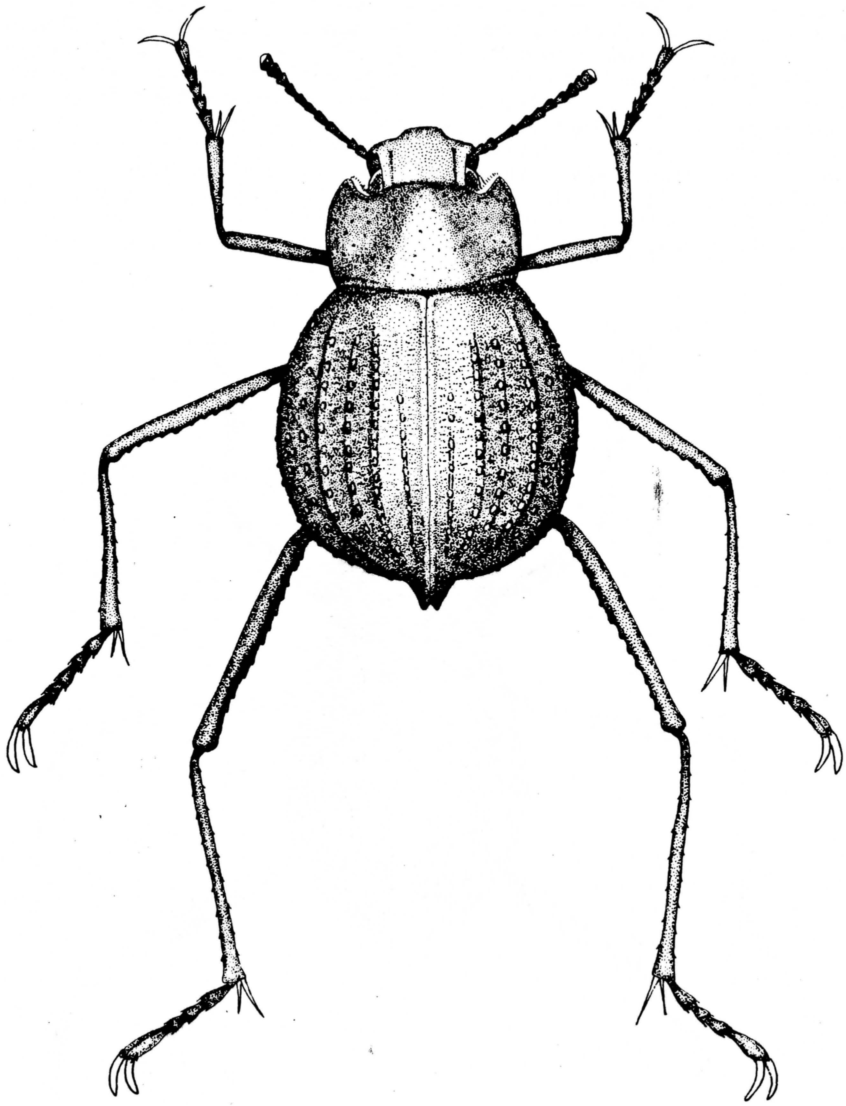

FIG. 2. Habitus of a hybrid *Physosterna globosa* × *Onymacris rugatipennis,* male.

Color: Integument: including the appendages and the entire underside, black. **Structure:** Epistome damaged, apparently truncate, dull, with scattered granules; sides converging posteriorly. Clypeal sutures extremely faint. Genal angles obtuse, not prominent. Frons flat, separated from epistome by a shallow depression, dull with small round scattered punctures. Supraorbital ridges straight, parallel, moderately raised. Eyes subreniform, narrowed ventrally. Labrum as in *P. globosa*. Mandibles with dense granules on outer surface. Maxillary palpi missing. Mentum more or less as in *P. globosa* but median depression only on anterior half and anterior edges not as strongly reflected. Submental parts as in *P. globosa*. Pronotum convex, smooth, dull, with moderate round scattered punctures, becoming larger at sides. Length 35.0% elytral length, width 64.1% elytral length. Anterior angles produced forwards to in front of front margin of eye, narrowly rounded. Anterior margin broadly carinate, carina obsolete on middle of disc, with fringe of pale setae. Lateral margins slightly rounded, sharply carinate. Two very faint subbasal depressions. Proepipleura with fine scattered punctures. Epipleural sutures very fine and faintly marked. Prosternum with anterior margin strongly carinate, with fringe of pale setae. Rugose on disc, smoothed with scattered punctures

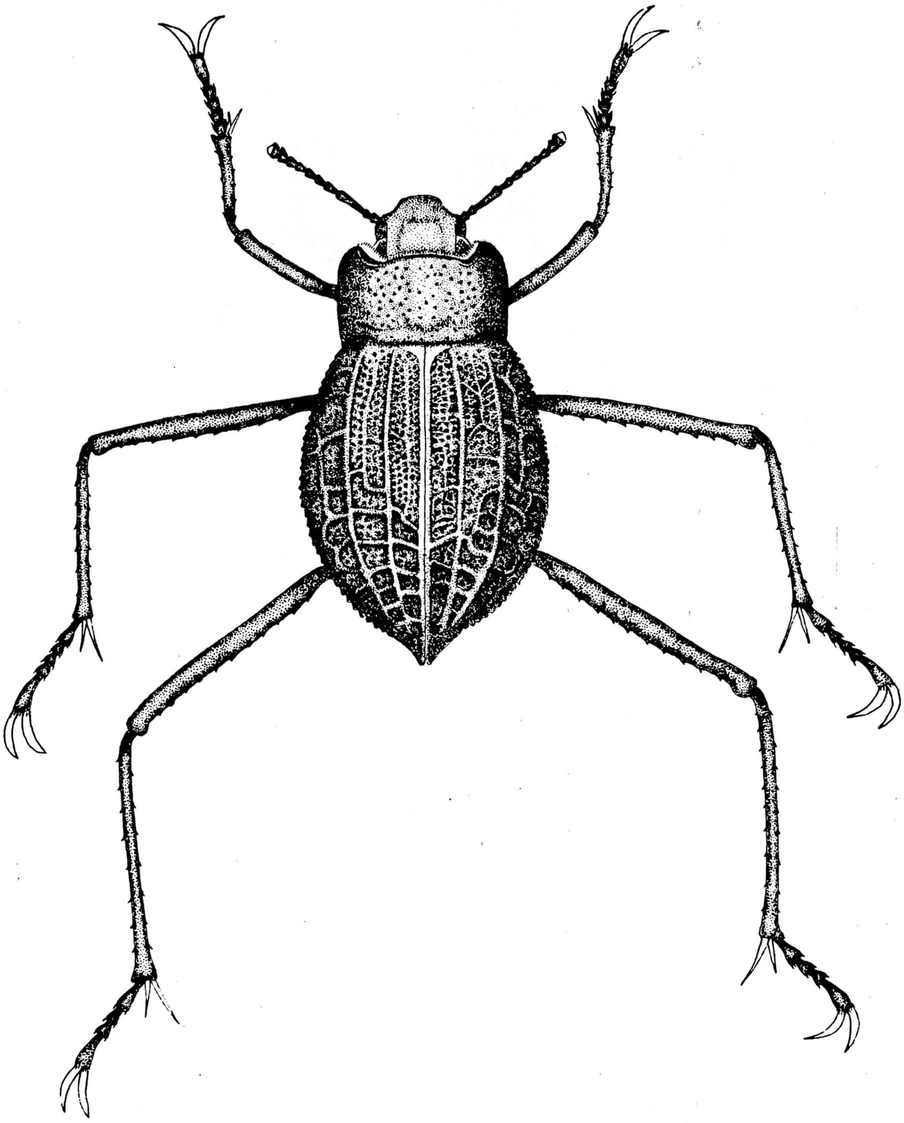

FIG. 3. Habitus of *Onymacris rugatipennis*, male.

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Table I.

Physosterna glob

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Apex strongly c
Suture flat
Sculpture of mo
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laterally. Prosternal apophysis intercoxally a little more than half-width of procoxa at narrowest point, about two-thirds at widest, sides converging distally, apex narrowly rounded, horizontally projecting between coxae, level with but not quite meeting raised anterior part of mesosternum. Sculpture rugose intercoxally, smoothed with scattered punctures distally. Mesosternum, episterna, and epipleura as in *P. globosa*. Metasternum about half-length of mesosternum, anterior margin straight, posterior margin concave, intercoxally less than twice width of coxa; with median longitudinal depression; sculpture of broad shallow rugosities between meso- and metacoxae, smoothed on disc, and with scattered granules at sides. **Elytra:** convex, inflated sides rounded, posterior declivity steep, with strongly produced caudate apex. Width 95.7% elytral length, height at middle 46.1% elytral length. Suture slightly raised. Lateral edge consisting of a row of flattened dentiform granules. Surface dull, microgranulate. Two fine costae on either side of suture bearing a row of flattened dentiform granules, with a flatter row of large granules between the suture and the first costa and between the two costae. Interval between second costa and lateral edge with scattered large and small granules, those nearest the second costa arranged more or less in a row. Apical declivity smoothed. Reflected part of elytra with scattered flat dentiform granules. Pseudo-pleura narrow, smooth. Abdomen is with first segment as in *P. globosa*, the second to fourth are regularly decreasing in length, granular, the second with faint impressed longitudinal lines. The abdominal segment V is as in specimens of *P. globosa* but the granules are larger and denser. **Legs:** long, moderately stout. Coxae rounded. Trochanters small, oblique. Femora cylindrical, ventrally sulcate, more or less straight. Tibiae straight, cylindrical, distally slightly expanded, with an apical coronula of short spines; sculpture of femora and tibiae as in other species. Calcaria absent from specimen. Tarsi moderately stout (anterior tarsi missing), segments as in other species; ventral ungual flap narrowly produced apically but not spiniform. Claws equal in length, subfoliaceous, as long as ungual article. **Antennae:** 47.0% elytral length, broken from specimen, but would reach to beyond pronotal base, moderately stout, with the third article about twice the length of the second. **Aedeagus:** The specimen is a male and the genital apparatus is small and weakly sclerotized; it is similar in shape to that of *P. globosa* but was too delicate and incomplete for successful extraction and could not be illustrated.

A comparison of these characteristics with the salient features of the parental types is included in Table I.

Environmental Relationships of Parental Species

In addition to the structural characters suggesting *P. globosa* and *O. rugatipennis* as parents these species occur together in large numbers along the Kuiseb River bed. *P. cribripes* is also ecologically sympatric with them; *O. plana*, *O. unguicularis*, and *O. laeviceps* are confined to the main sand dunes mass. *O. subelongata* is rare at Gobabeb, and natural history of this species is as yet poorly known.

The Kuiseb River bottom at Gobabeb is used by a diversity of diurnal tenebrionid beetles. An analysis of the habitat preference and temporal rhythm of activity of these two species and another adesmiine tenebrionid, *Stenocara gracilipes*, demonstrate the extent of the opportunity for interaction by the parental species. The third species, *S. gracilipes*, is included in this analysis to show how another species living sympatric-

Table I. Comparison of the structure of *Onymacris rugatipennis*, *Physosterna globosa*, and a hybrid between them

Physosterna globosa	Hybrid specimen	*Onymacris rugatipennis*
	Elytra	
Strongly convex	Moderately convex	Moderately convex
Apical declivity vertical	Apical declivity vertical	Apical declivity oblique
Apex strongly caudate	Apex strongly caudate	Apex minutely caudate
Suture flat	Suture slightly raised	Suture raised
Sculpture of more or less 5 rows of granules with scattered granules in between	Costate and granulate but non-rugose sculpture	Costate and granulate sculpture with strongly raised rugosities in posterior half
	Metasternum	
Intercoxally twice width of coxa	Intercoxally less than twice width of coxa	Intercoxally less than twice width of coxa

ally with *P. globosa* and *O. rugatipennis* may have a much more restricted choice of habitats. The data for this species also provide additional bases for interpreting the results of the correlation coefficient analyses of the use of time and space by the supposed parental species of the hybrid.

A transect of some of the well-defined environments shows the degree of overlap of the parental species. The habitats identified in this analysis include:

1. Clumps of *Eragrostis spinosa* which collect wind-driven sand and form small dunes rising as much as a meter above the surrounding substrate.
2. *Nicotiana glauca* plants and fallen leaves which are concentrated in the dry pale sand wash of the riverbottom. This vegetation is on the average well apart from other woody vegetation in the area.
3. *Acacia giraffae* and *A. albida* woodland. The canopy formed by trees may be closed, especially in the case of *A. albida*. In some other places there are broad gaps between adjacent trees.
4. *Acanthasicyos horridus* mounds. The naras bush is concentrated on the dunes side of the riverbottom. This leafless spiny shrub is penetrated by filtered sunlight and collects large quantities of wind-driven sand. Individual naras bushes are separated from other riparian vegetation and at other locations away from Gobabeb extend far into the interdune valleys. At such locations the naras beetle, *Onymacris plana,* replaces *O. rugatipennis* as a dominant species.
5. *Salvadora persica* clumps. The *Salvadora* bushes form dense thickets about the trunks of acacia trees. In most places the censuses described below did not include visual inspection of the interior of these clumps.
6. Dead logs and branches. These rubble piles form from the natural collapse of woody vegetation where they accumulate about the parental trees, acacias in particular, and hence are lightly to completely shaded throughout the day.
7. Open river sands. Vegetationless coarse sand of the riverbottom.
8. River bar debris. River flooding transports logs and branches which collect on bars and against trees as the river recedes.

The habitat preference of the three adesmiine tenebrionids considered was determined by laying out a transect through the eight habitats. This transect was walked in the same way and at the same pace 13 times during a day in January. All tenebrionid beetles within 3 m of this transect line were noted and assigned to one of the eight habitat types. If an individual was on the edge between two habitats it was scored as half for each of the bordering types (Table II).

Samples of the three species were paired and tested for significant differences with respect to activity and occurrence by habitat (Table III).

These data for habitat preference and courtship activities are concentrated into 1 day. The daily activity cycle of the diurnal Namib Desert Tenebrionidae is adjusted to the variable daily thermal cycle (Hamilton 1971, 1973, 1975; Hamilton *et al.* 1976; Holm and Edney 1973). Pooled data for 2 or more days show greater apparent activity spans than those that really exist and would show less synchrony of interspecific and intraspecific actions.

These data illustrate several features of the natural history of these species relative to one another: (1) There is a high degree of overlap in use of time and space by these species. (2) Certain habitats are used more extensively by one species than the others. (3) There is a bimodal activity cycle for all three species.

The general features of courtship by both *P. globosa* and *O. rugatipennis* are described in detail elsewhere (Hamilton *et al.* 1976). Females are passive. All individuals initiate each daily activity cycle from a buried position. In the course of surface activities they are followed by males. This following action is here termed courtship. Relatively few of these courtships end in copulation.

Table II. Habitat pref
River bed and of (C) S
Times are solar time,
habitat during 13 cens
expressed as a percent
eleventh column sums
number o

Time	1	2
0633	2	
0726	2	
0821	8	
0946	14	
1118	4	
1301	2	
1411	12	
1511	14	
1631	13	
1736	13	
1846	8	
1914	2	
2010	0	
T (n)	94	
0633	0	
0726	0	
0821	1	
0946	0	
1118	0	
1301	0	
1411	0	
1511	0	
1631	3	
1736	13	
1846	0	
1914	0	
2010	0	
T (n)	17	
0633	0	
0726	0	
0821	0	
0946	0	
1118	0	
1301	0	
1411	0	
1511	0	
1631	0	
1736	0	
1846	0	
1914	0	
2010	0	
T (n)	0	

Table II. Habitat preference of (A) *Onymacris rugatipennis* and (B) *Physosterna globosa* from the Kuiseb River bed and of (C) *Stenocara gracilipes* living in the Kuiseb River bottom at Gobabeb, South West Africa. Times are solar time, not standard time. The first eight columns represent number of individuals active per habitat during 13 censuses. The ninth column sums these counts and the figures in the tenth column are expressed as a percentage of maximum activity (that time with the greatest number of individuals active). The eleventh column sums the number of males found courting, and the twelfth expresses this sum in relation to the number of males active (in column 9, half of those active are males and half females).

	Habitat type										Courting	
Time	1	2	3	4	5	6	7	8	T	%T	T	%
					(A) *Onymacris rugatipennis*							
0633	2	1	1	5	1	0	0	0	10	10.6	0	0
0726	2	0	1	11	9	0	1	1	25	26.6	0	0
0821	8	16	0	8	8	1	3	5	49	52.1	4	16.3
0946	14	43	3	10	22	0	2	0	94	100.0	11	23.4
1118	4	35	12	2	4	0	0	0	57	60.6	18	63.2
1301	2	15	5	0	3	0	0	0	25	26.6	4	32.0
1411	12	12	2	1	3	0	0	0	30	31.9	0	0
1511	14	24	11	0	2	3	0	0	54	57.4	2	7.4
1631	13	31	16.5	1	21	0.5	0	0	83	88.3	8	19.3
1736	13	34	5	7	5	0	4	0	68	72.3	0	0
1846	8	11	0	6	3	0	0	0	28	29.8	0	0
1914	2	0	0	0	0	0	0	0	2	2.0	0	0
2010	0	0	0	0	0	0	0	0	0	0.0	–	–
T (n)	94	222	56.5	51	81	4.5	10	6	525	–	47	–
					(B) *Physosterna globosa*							
0633	0	0	0	0	0	0	0	0	0	0	0	0.0
0726	0	1	1	0	3	0	0	0	5	4.2	0	0.0
0821	1	0	1	1	15	0	2	0	20	16.9	3	30.0
0946	0	6	5.5	4	35.5	10.5	2.5	0	64	54.2	13	40.6
1118	0	0	42.5	0	5.5	0	0	0	48	40.7	11	45.8
1301	0	0	34	11	2	0	0	0	47	39.8	13	55.3
1411	0	0	6	0	1	0	0	0	7	5.9	1	28.6
1511	0	0	5	0	6	12	0	0	23	19.5	4	34.8
1631	3	1	60	20	0	2	0	0	86	72.9	25	58.1
1736	13	2	41	5	41	7	9	0	118	100.0	25	42.4
1846	0	2	32	1	5	0	2	0	42	35.6	4	19.0
1914	0	0	0	0	0	0	0	0	0	0.0	0	0.0
2010	0	0	0	0	0	0	0	0	0	0.0	0	0.0
T (n)	17	12	228	42	114	31.5	15.5	0	459.5	–	99	–
					(C) *Stenocara gracilipes*							
0633	0	0	0	0	0	0	0	0	0	0.0	0	0
0726	0	0	0	0	0	0	0	0	0	0.0	0	0
0821	0	0	0	0	3	1	0	0	4	50.0	0	0
0946	0	0	0.5	0	5	2.5	0	0	8	100.0	0	0
1118	0	0.5	0.5	0	4	0	0	0	5	62.5	0	0
1301	0	0	0	0	2	0	0	0	2	25.0	0	0
1411	0	0	1	0	1	0	0	0	2	0.0	0	0
1511	0	0.5	0	0	3	2.5	0	0	6	75.0	0	0
1631	0	0	0	0	4	3	0	0	7	87.5	0	0
1736	0	0	0	0	2	2	0	0	4	50.0	0	0
1846	0	0	0	0	0	0	0	0	0	0.0	0	0
1914	0	0	0	0	0	0	0	0	0	0.0	0	0
2010	0	0	0	0	0	0	0	0	0	0.0	0	0
T (n)	0	1.0	2	0	24	11	0	0	38	–	0	–

Table III. Results of the statistical comparisons described in the text

	Kruskal-Wallis	Chi-square	Kruskal-Wallis	Chi-square
	Species vs. time		Species vs. habitat	
O. r. vs. *P. g.*	>.05	<.01	>.05	<.01
O. r. vs. *S. g.*	<.01	<.05	<.01	<.01
P. g. vs. *S. g.*	<.01	<.05	<.01	<.01

The courtship activity cycle of both species overlaps strongly. Male *P. globosa* court more persistently than do *O. rugatipennis* males. For *P. globosa* 42.5% of all males were involved in courtship activities during census observations. This value for males represents an approximate time budget for time allocated to courtship activities. The comparable figure for *O. rugatipennis* is 17.9%.

Physosterna males follow females closely and persistently and in the course of their courtship activities they change partners less frequently than do males of *O. rugatipennis*. *Physosterna* is a more robust and slower moving animal than *Onymacris*, and their close following, often with forelegs held to the hind part of the female's elytra, fits the morphology of the species.

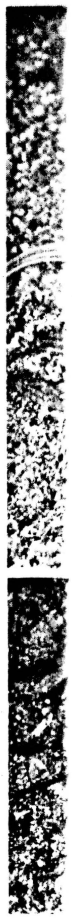
We regularly observed males of these two species courting females of the other species in the field, but no quantification of such actions was made. Usually these interspecific following activities are less durable than is conspecific courtship. Two examples of interspecific courtship are shown in Figs. 4 and 5.

The results of the courtship choice experiments when analyzed with a Chi-square test show that the parental type males are highly oriented to conspecifics ($p < .001$ for both species). *P. globosa* are more highly oriented than *O. rugatipennis* ($p < .0005$), in agreement with our observations of the pattern of following in the field.

The hybrid male was less committed to either parental type female when he was put into the container with the same females ($p < .0001$). He showed a significant preference for the *P. globosa* females offered to him. This apparent preference is not necessarily due to a real behavior preference for *P. globosa*. It may instead reflect the intermediate structure of the hybrid between the parental types, making it slower in high speed locomotion than *O. rugatipennis*. *O. rugatipennis* has longer legs than *P. globosa*, runs more rapidly, and penetrates more open environments well away from the sites where it spends the night buried in the sand. During active locomotion, which included escape movements by the experimental females, the hybrid could not always approach the female *O. rugatipennis*.

Discussion

These observations support the idea that the specimen described above is a hybrid of the parent species *P. globosa* and *O. rugatipennis*. The specific integrity of *P. globosa* and *O. rugatipennis* seems well established. The structural differences between these species are numerous and constant over large samples and from diverse geographic areas. The hybrid specimen is not an extreme structural variant of either species, as it cannot by any single character be assigned to either species. It is intermediate between *P. globosa* and *O. rugatipennis* in the sides of the metasternum, the shape of the prosternal apophysis, the stoutness of the antennae and tarsi, the degree of vaulting of the elytra, the shape of the tarsal claws, and the degree of development of the supraorbital ridges. In the remaining characters which show measurable differences between the parent species, namely body shape and length of legs, particularly the intermediate and posterior femora, the specimen is interesting in that its body proportions tend to fall with those of *P. globosa*, while the leg measurements agree with



FIGS. 4–5. 4, a fem cular tag on his thorax *P. globosa*. This is the

Table

Sample size:

Anterior
Intermediate
Posterior

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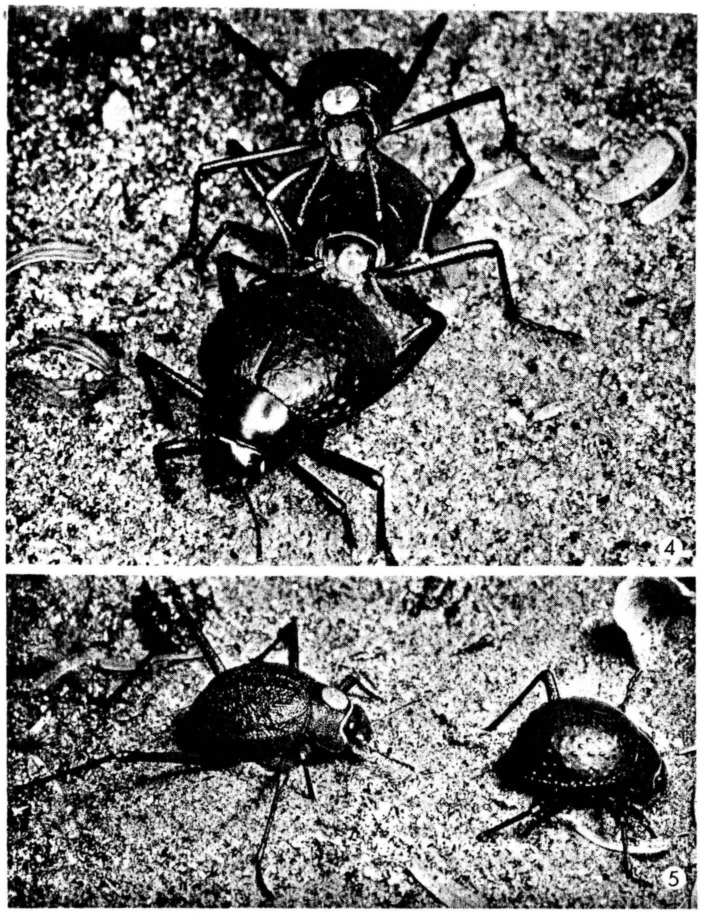

FIGS. 4–5. 4, a female *P. globosa* courted by a male *P. globosa*. A male *O. rugatipennis* with the circular tag on his thorax (#28) climbs on the courting male. 5, a male *O. rugatipennis* (#30) courts a female *P. globosa*. This is the usual distance at which male *O. rugatipennis* follow females.

Table IV. Leg proportions as per cent of elytral length. Mean in parentheses

	Physosterna globosa	*Hybrid*	*Onymacris rugatipennis*
Sample size:	40	1	65
Femur			
Anterior	35.9–58.2 (45.2)	64.4	37.7–60.0 (48.1)
Intermediate	53.7–79.3 (64.3)	90.6	65.2–95.5 (82.3)
Posterior	66.7–93.0 (78.8)	107.0	81.1–111.7 (94.7)
Tibia			
Anterior	24.3–40.1 (31.3)	36.7	25.0–38.3 (31.6)
Intermediate	24.4–55.0 (43.1)	59.0	35.7–62.2 (50.2)
Posterior	55.5–85.3 (68.5)	89.7	61.0–91.0 (74.9)
Tarsus			
Anterior	20.4–33.0 (26.8)	–	17.8–30.9 (24.1)
Intermediate	23.9–40.4 (31.7)	40.2	23.6–38.7 (31.6)
Posterior	24.7–38.5 (31.5)	37.6	27.1–35.7 (30.4)

those of *O. rugatipennis*. In all cases except elytral height the hybrid is at the extreme of the range (Table IV). Thus its intermediacy lies not in each individual character, but rather in that it resembles one putative parent in half the characters and the other in the other half.

The species that are included in the genera *Onymacris* and *Physosterna* are closely related. In a study of adesmiine larvae, Schulze (1962) found that the larvae of *P. globosa* more closely resembled a group of *Onymacris* larvae than any other Adesmiini. Other evidence relevant to interpretation of the apparent hybrid includes the ambivalence of its courtship activities and the overlap of the activity cycle, habitat preference, and courtship times of the parental types as well as the regular occurrence of interspecific courtship.

The abnormalities of the reproductive structures of the hybrid suggest sterility of this specimen.

Taxonomists traditionally have emphasized the risk of hybridization and gamete wastage as the central problem in interspecific interactions. Another possibly more serious problem is the loss of time by the participants in inaccurate social interactions. Recently ecologists have emphasized the role of time in the acquisition of food resources and mates (e.g. Hamilton and Watt 1970). Thus, while the rate of hybridization is low, interspecific encounters and interference are commonplace. Hence the significance of these species to one another is probably greater than the rare occurrence of a hybrid specimen suggests.

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