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## The Australian ground beetle genus *Porocara* Sloane. Second revision

(Insecta, Coleoptera, Carabidae, Odacanthinae)

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Baehr, M. (1996): The Australian ground beetle genus *Porocara* Sloane. Second revision (Insecta, Coleoptera, Carabidae, Odacanthinae). – *Spixiana* 19/3: 253–265

The Australian odacanthine genus *Porocara* is revised again based on newly collected and detected material from the northern parts of the Northern Territory and Western Australia. *P. ulrichi*, spec. nov. is described and the closely related species *P. occidentalis* Baehr, *P. nigricollis* Baehr and *P. punctata* Sloane are newly defined. For the population of *P. punctata* that inhabits far Northern Territory a new subspecies *P. punctata arnhemensis*, subsp. nov. is described. In the tropical parts of the Northern Territory and of Western Australia the genus forms an assemblage of extremely closely related, commonly syntopic taxa that are very similar in external morphology and habits, though are mainly defined by differences in their genitalic characters. The coexistence of up to three species in northern and northwestern Australia is the result of repeated colonizations of the northern and western refugia by *Porocara* stocks during late ice-age, and of subsequent isolation and speciation of these populations.

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### Introduction

The odacanthine genus *Porocara* was erected by Sloane (1917) for the unique species *P. punctata* Sloane that was then known only from the lower Cape York Peninsula in North Queensland. Despite of the large type series collected by Sloane, this species has been rarely recollected since description. My revision of the genus (Baehr 1986) was mainly based on material collected by me in the far Northern Territory and in northwestern Australia and on the moderately rich material of the ANIC, Canberra. Therein I described three new species from far Northern Territory and from different parts of northwestern Australia, and an additional new subspecies of *P. punctata* from the Kimberleys. During a recent collecting trip to the same areas I collected again many specimens of *Porocara* in different localities and found another new species in the northwestern part of the Northern Territory that occurs syntopic with populations of *P. punctata kimberleyana* Baehr and in some localities was found even in the same Barber traps. Although the new species is externally extremely similar to *P. punctata*, the aedeagus is quite different.

Based on material from the western escarpment of Arnhem Land, loaned from the Northern Territory Museum (MNTD), a new subspecies of *P. punctata* is described that coexists with *P. nigricollis* Baehr, which means that *P. punctata* extends from north Queensland through far Northern Territory to the Kimberleys in far northern Western Australia. In this vast area, *P. punctata* is syntopic with three different species in different parts of its range as tabulated below (see tab. 2). This common syntopic occurrence of two, in one locality even of three species is rather surprising in species with extremely similar external morphology that most probably have a very similar way of life.

Main differentiating characters of the taxa are in the male genitalia, but even the externally most similar taxa show faint though rather constant differences in shape of pronotum, shape and relative length of elytra, density of puncturation of pronotum, and degree of microreticulation of elytra. As a consequence, all species can be distinguished without regarding of genitalic characters, when comparison with related species is possible.

Unlike typical odacanthine beetles, species of *Porocara* live in pure wet sand of rivers and larger creeks near water, where during daytime they are buried in the sand or under stones and boulders. At night they come out of their holes to forage around the pools. I never found them in dry river or creek beds far away from water. The yellow or light reddish colouration matches very well the colour of the sand, and the elytral pattern is in all species rather inconspicuous, except for fully coloured specimens of *P. nigricollis*, and it serves as a purpose to obscure the body shape. Only in *P. nigricollis* of far Northern Territory that is a species of the full wet tropical zone the colour pattern is more accentuate and may be regarded an example of Gloger's rule.

### Material

This second revision is based on altogether 90 additional specimens representing 5 taxa (excluding *P. p. punctata* and *P. glabrata*) from my own recent collections in far northern and northwestern Australia, my collections in the Hamersley area in 1987, the Museum and Art Gallery of the Northern Territory, Darwin, and a small collection from northwestern Australia kindly received from Miss S. Hogenhout, Leiden.

### Revised key to the species of *Porocara* Sloane

This key refers partly to the key in my previous revision (Baehr 1986). Figures from that revision are labelled **B86**.

1. Surface of pronotum and posterior part of head impunctate or nearly so. Postmedian vitta of elytra narrow, conspicuously serrate and sinuate (**B86**, fig. 4). Apex of aedeagus virtually not thickened (**B86**, fig. 9). Southeastern margin of Kimberley Division, northwestern Australia ... *glabrata* Baehr
- Surface of pronotum and posterior part of head coarsely punctate. Postmedian vitta of elytra wide, less serrate and sinuate (**B86**, figs 1-3). Apex of aedeagus more or less thickened (Figs 1-3, 11, 13). Northern tropical parts of Australia from Queensland to Western Australia ..... 2.
2. Aedeagus smaller and shorter, length <1.8 mm, apex less upturned and barely curved to right side (Figs 1-3, 10). Elytra shorter, laterally less regularly rounded (Figs 14-17). Basal part of lateral borders of pronotum more abruptly sinuate (Figs 4-7) ..... 3.
- Aedeagus larger and longer, length >2.2 mm, apex markedly upturned and curved (Figs 11, 13). Elytra longer, laterally more regularly rounded (Figs 18, 19). Basal part of lateral borders of pronotum not abruptly sinuate (Figs 8, 9) ..... 6.
3. In fully coloured specimens prothorax, vertex, and most of lower surface black; in teneral specimens at least part of proepipleurae and base of head darker than remaining parts. Elytra markedly square, with accentuate shoulders, lateral margins almost parallel (Fig. 17). Microsculpture of elytra very conspicuous, at 10x magnification seemingly isodiametric. Lower surface of aedeagus gently curved, apex rather elongate, not turned down (Fig. 10). Far Northern Territory . *nigricollis* Baehr
- Even in fully coloured specimens prothorax, vertex, and most of lower surface not darker than remainder. Elytra not square, with less accentuate shoulders, lateral margins perceptibly convex (Figs 14-16). Microsculpture of elytra less conspicuous, at 10x magnification distinctly transverse. Lower surface of aedeagus gently or markedly curved, apex short or elongate, but when elongate, then apex turned down or aedeagus markedly curved (Figs 1-3) ..... 4.

4. Pronotum more densely and regularly punctate, basal part of lateral borders less abruptly sinuate (Figs 4, 6). Aedeagus more compact, apical part at orificum (as seen from below) distinctly widened, lower surface gently or markedly concave, but when gently concave, then apex short (Figs 1, 3). North Queensland, far Northern Territory ..... 5.
- Pronotum less densely and regularly punctate, basal part of lateral borders abruptly sinuate (Fig. 5). Aedeagus more delicate, apical part at orificum (as seen from below) barely widened, lower surface gently concave, apex elongate (Fig. 2). Northwestern part of Northern Territory to northwestern Australia north of Great Sandy Desert ..... *punctata kimberleyana* Baehr
5. Elytra shorter, more square, ratio  $l/w < 1.58$  (Fig. 14). Lower surface of aedeagus gently concave, apex short, less club-shaped, almost straight (Fig. 1). Northern Queensland .... *punctata punctata* Sloane
- Elytra longer, more egg-shaped, ratio  $l/w > 1.62$  (Fig. 16). Lower surface of aedeagus markedly concave, apex longer, distinctly club-shaped, pointed down (Fig. 3). Arnhem Land, far Northern Territory ..... *punctata arnhemensis*, subspec. nov.
6. Pronotum rather densely punctate. Basal lobe of aedeagus less curved, apex more upturned though less asymmetric, lower surface of aedeagus barely striate (Fig. 11). Northwestern part of Northern Territory, adjacent northern Western Australia ..... *ulrichi*, spec. nov.
- Pronotum rather sparsely punctate. Basal lobe of aedeagus more curved, apex less upturned though more asymmetric, lower surface of aedeagus conspicuously striate (Fig. 13). Northwestern Australia south of Great Sandy Desert ..... *occidentalis* Baehr

### *Porocara punctata* Sloane

Sloane, 1917, p. 416; Csiki 1932, p. 1537; Baehr 1986, p. 719.

Diagnosis. Distinguished by slightly rounded, moderately to rather elongate elytra, absence of black colour on head and pronotum, and small aedeagus with moderately elongate, slightly thickened apex.

Distribution. The whole of tropical northern Australia from Queensland to the Kimberleys.

### *Porocara punctata punctata* Sloane

Figs 1, 4, 14, 20

Sloane, 1917, p. 416; Csiki 1932, p. 1537; Baehr 1986, p. 719.

Diagnosis. Distinguished from the other subspecies of *P. punctata* by rather short and wide elytra (Fig. 14), rather dense puncturation of pronotum, less markedly divergent basal angles of pronotum (Fig. 4), and aedeagus with rather straight lower surface and short apex (Fig. 1).

Additional distinguishing character states

Ratio length / width of elytra: 1.55-1.58.

♂ genitalia (Fig. 1). Genital ring comparatively wide, laterally convex. Aedeagus small, <1.8 mm long, gently curved, lower surface almost straight, apex short, thickened, gently turned to right side, orificium with a fold at apex. Right paramere fairly elongate.

Distribution (Fig. 20). Eastern subspecies distributed through North Queensland from the middle of the Cape York Peninsula west to Normanton and south to about Mackay.

Habits. Lives in wet sand near rivers and creeks like other species of this genus.

New records: No new material recorded.

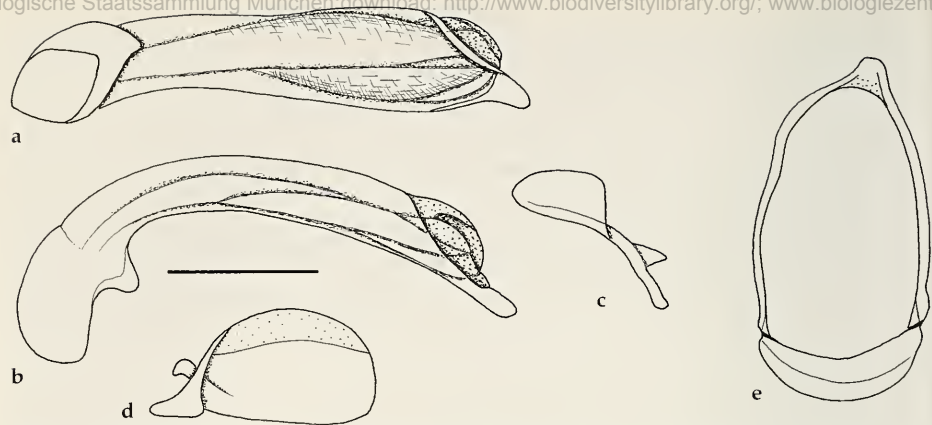


Fig. 1. *Porocara punctata punctata* Sloane. ♂ genitalia. a. Aedeagus, left side. b. Aedeagus, lower surface. c. right paramere. d. left paramere. e. Genital ring (not to scale). Scale: 0.5 mm.

*Porocara punctata kimberleyana* Baehr

Figs 2, 5, 15, 20

Baehr, 1976, p. 721.

Diagnosis. Distinguished from the other subspecies of *P. punctata* by moderately elongate elytra (Fig. 15), markedly divergent basal angles of pronotum (Fig. 5), and aedeagus with rather straight lower surface and elongate apex (Fig. 2).

Additional distinguishing character states

Ratio length / width of elytra: 1.62-1.64.

♂ genitalia (Fig. 2). Genital ring comparatively wide, laterally convex. Aedeagus small, <1.8 mm long, gently curved, lower surface slightly concave, apex fairly elongate, thickened, gently turned down and to right side, orificium with a fold at apex. Right paramere fairly elongate.

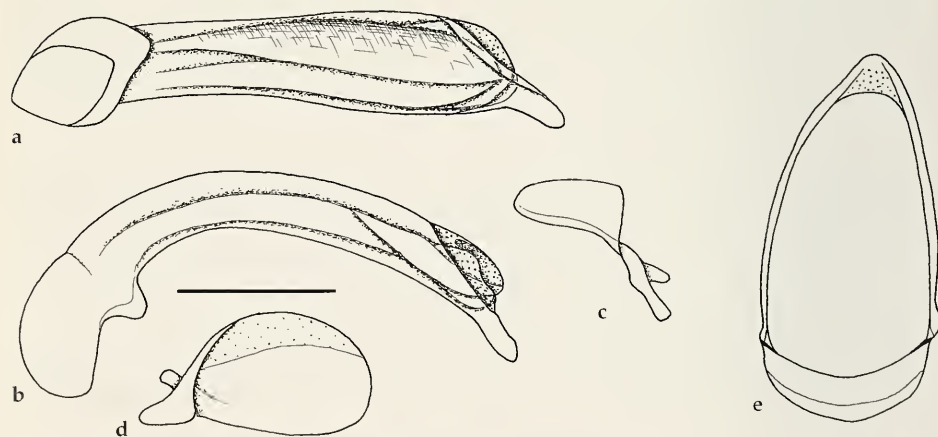


Fig. 2. *Porocara punctata kimberleyana* Baehr. ♂ genitalia. For legend see Fig. 1.



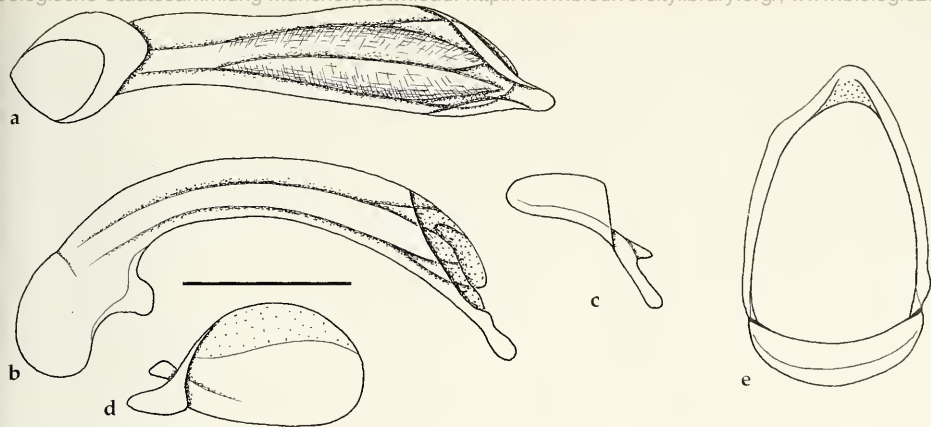


Fig. 3. *Porocara punctata arnhemensis*, subspec. nov. ♂ genitalia. For legend see Fig. 1.

Distribution (Fig. 20). Western subspecies known thus far from the eastern and southern border of Kimberley Division, northern Western Australia and adjacent northwestern Northern Territory.

Habits. Lives in wet sand near rivers and creeks like other species of this genus. Commonly collected at light and in Barber traps exposed in wet sand close to pools in large river beds.

New records: 6♂♂, 8♀♀, WA95/24, Durack R., 87 km w. Pentecost R., 11.-12.8.1995, M. Baehr (CBM, ZSM, MNTD); 6♂♂, 2♀♀, NT95/42, West Baines River, 23.-24.8.1995, M. Baehr (CBM); 2♂♂, NT95/44, Victoria River, 5 km w. Victoria R. Cr., 24.-25.8.1995, M. Baehr (CBM); 4♂♂, 5♀♀, W.A. Upper Panton River, 30 April 1994, S. A. Hogenhout, River bank, at light (CBM, Coll. Hogenhout).

***Porocara punctata arnhemensis*, subspec. nov.**

Figs 3, 6, 16, 20

Types. Holotype: ♂, 12.52S 132.47E Nourlangie Creek, 8 km E of Mt. Cahill, N. T. 7.X.1975 A. Allwood & T. Angeles, 12673 (MNTD).

Diagnosis. Distinguished from the other subspecies of *P. punctata* by moderately elongate elytra (Fig. 16), not divergent basal angles of pronotum (Fig. 6), and aedeagus with markedly concave lower surface and moderately elongate apex (Fig. 3).

**Description**

Measurements. Length: 8.15 mm, width: 3.1 mm. Ratio length/width of elytra: 1.64.

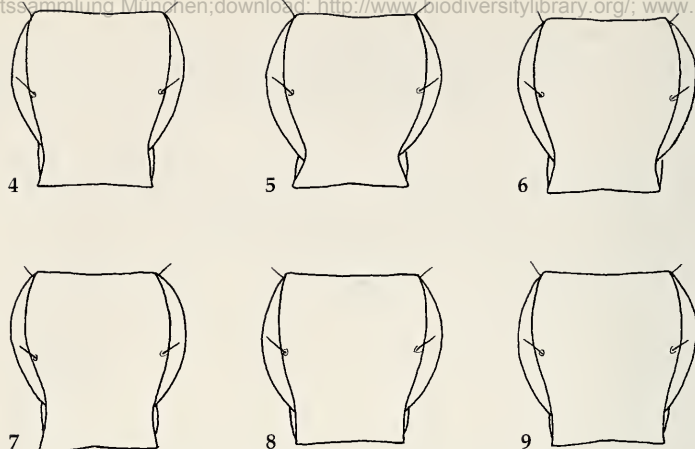
Colour. Light reddish, elytral pattern blackish, rather indistinct, forehead, mouth parts, legs, and basal antennomeres yellowish. Lower surface yellowish to red, only prosternum and mesosternum blackish.

Head. Of average size, puncturation of basal part moderately dense, otherwise similar to other subspecies.

Prothorax (Fig. 6). Rather convex, about as long as wide, puncturation fairly dense, rather regular, punctures mostly smaller than distance between them. Lateral margins near basal angles concave, though basal angles not markedly divergent.

Elytra (Fig. 16). Rather elongate, lateral border slightly convex. Microreticulation conspicuous, consisting of transverse meshes. Elytral pattern little contrasting, basal spot large, attaining base, postmedian vitta large, barely serrate. Otherwise similar to other subspecies.

♂ genitalia (Fig. 3). Genital ring comparatively wide, laterally convex, slightly asymmetric. Aedeagus small, <1.8 mm long, markedly curved, lower surface regularly concave, apex moderately elongate, considerably thickened, barely turned to right side, orificium with a fold at apex. Right paramere rather elongate.



Figs 4-9. Outline of prothorax. 4. *Porocara punctata punctata* Sloane. 5. *P. punctata kimberleyana* Baehr. 6. *P. punctata arnhemensis*, subspec. nov. 7. *P. nigricollis* Baehr. 8. *P. ulrichi*, spec. nov. 9. *P. occidentalis* Baehr.

♀ genitalia. Unknown.

Variation. Unknown.

Distribution (Fig. 20). Western escarpment of Arnhem Land, far Northern Territory. Known only from type locality.

Habits. Lives probably in wet sand near rivers and creeks like other species of this genus. Sympatric and at the type locality probably even syntopic with *P. nigricollis* Baehr.

Etymology. The name refers to the range of the subspecies.

### *Porocara nigricollis* Baehr

Figs 7, 10, 17, 21

Baehr 1986, p. 722.

Diagnosis. Distinguished by black colour of pronotum, basal part of head, and proepisternum, short and remarkably parallel elytra (Fig. 17), and small, rather straight aedeagus with fairly elongate apex (Fig. 10).

Additional distinguishing character states

Ratio length / width of elytra: 1.56-1.62.

♂ genitalia (Fig. 10). Genital ring comparatively wide, laterally convex, symmetric. Aedeagus small, <1.8 mm long, gently curved, lower surface almost straight, apex fairly elongate, slightly thickened and hooked, gently turned to right side, orificium with a fold at apex. Right paramere rather elongate.

Distribution (Fig. 21). Far Northern Territory south to about Katherine.

Habits. Lives probably in wet sand near rivers and creeks like other species of this genus. Most specimens collected at light. Sympatric and probably even syntopic with *P. punctata arnhemensis*, subspec. nov.

New records: 2♂♂, 3♀♀, 12.52S 132.47E Nourlangie Creek, 8 km E of Mt. Cahill, N. T. 7.X.1975 A. Allwood & T. Angeles, 12673 (CBM, MNTD); 1♂, 12.52S 132.46E Nourlangie Creek 6 km E. of Mt. Cahill, N. T. 12.X.1972 T. Weir (MNTD); 1♂, 12.17S 133.20E Cooper Creek 11 km S by W of Nimbuhwah Rock, N. T. 1.XI.1972 T. Weir & T. Angeles (MNTD); 1♂, 1♀, NT Kakadu N. P. Magela Creek OSS Site/009 Mv 12°42'S 132°57'E 8 July 1991 Wells & Webber (MNTD).

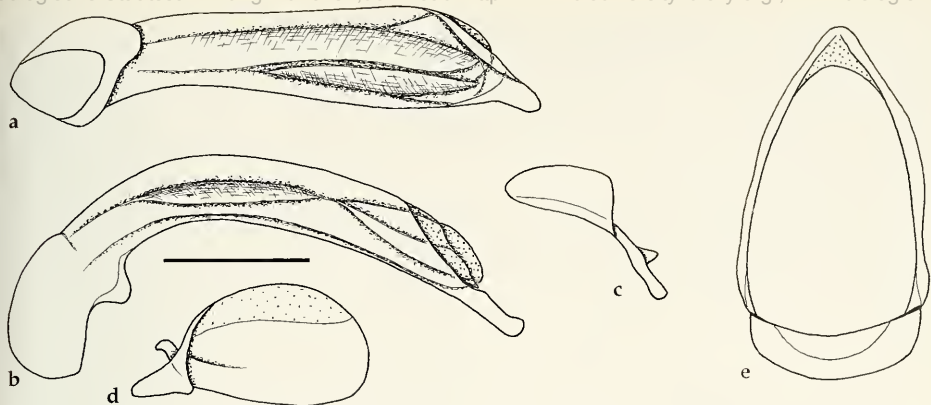


Fig. 10. *Porocara nigricollis* Baehr. ♂ genitalia. For legend see Fig. 1.

*Porocara ulrichi*, spec. nov.

Figs 8, 11, 12, 18, 21

Types. Holotype: ♂, NT95/42, West Baines River, 23.-24.8.1995, M. Baehr (MNTD). - Paratypes: 15♂♂, 15♀♀, same data, (ANIC, CBM, ZSM); 1♀, West Baines River, 9.-10.8.1995, M. Baehr (CBM); 1♀, NT95/44, Victoria River, 5 km w. Victoria R. Cr., 24.-25.8.1995, M. Baehr (CBM); 1♂, WA95/30, Fitzroy Crossing, 18.-19.8.1995, M. Baehr (CBM).

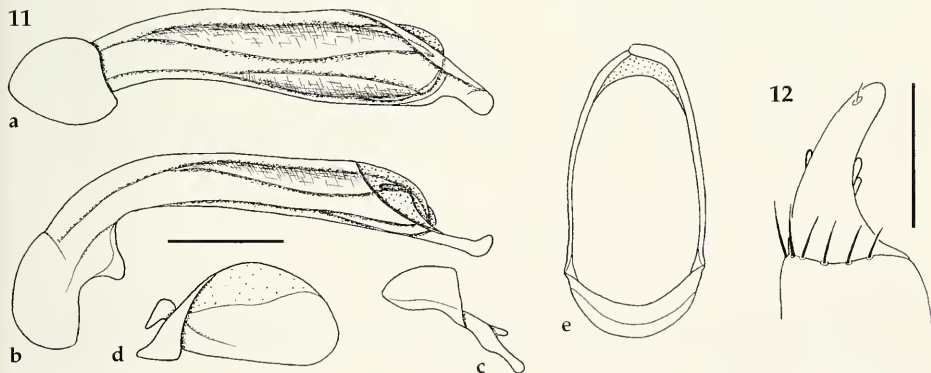
Diagnosis. Distinguished by elongate, laterally evenly convex elytra (Fig. 18), rather regular puncturation of head and pronotum, and large, at apex markedly upturned aedeagus that is barely striolate at lower surface (Fig. 11).

Description

Measurements. Length: 8.4-9.4 mm; width: 3.2-3.45 mm. Ratio length/width of elytra: 1.64-1.68

Colour. Light reddish, elytral pattern black, fairly distinct, forehead, mouth parts, legs, and basal antennomeres yellowish. Lower surface yellowish to red, only base of abdomen blackish.

Head. Of average size, puncturation of basal part moderately dense, otherwise similar to other species.



Figs 11-12. *Porocara ulrichi*, spec. nov. 11. ♂ genitalia. For legend see Fig. 1. 12. ♀ stylomere 2 and base of stylomere 1. Scale: 0.2 mm.

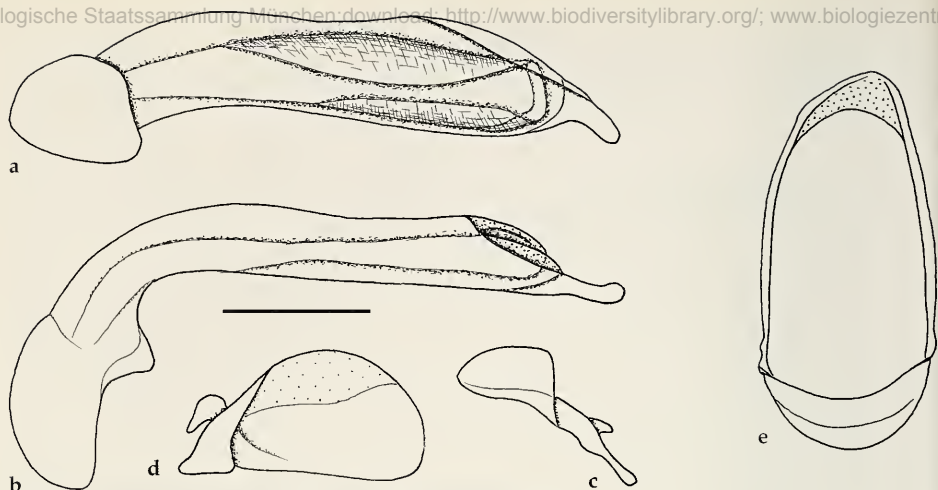


Fig. 13. *Porocara occidentalis* Baehr. ♂ genitalia. For legend see Fig. 1.

Prothorax (Fig. 8). Rather convex, slightly longer than wide, lateral border moderately convex, near basal angles concave, though basal angles not markedly divergent. Puncturation fairly dense, rather regular, punctures mostly smaller than distance between them.

Elytra (Fig. 18). Elongate, lateral border evenly convex. Microreticulation conspicuous, consisting of transverse meshes. Elytral pattern rather contrasting, basal spot large, not attaining base, postmedian vitta large, barely serrate. Otherwise similar to other species.

♂ genitalia (Fig. 11). Genital ring comparatively narrow, laterally barely convex, almost symmetric. Aedeagus large, >2.2 mm long, curved only in basal part, lower surface straight, barely striolate, apex elongate, markedly upturned at tip, rather abruptly turned to right side, orificium with a fold at apex. Right paramere rather short.

♀ genitalia (Fig. 12). Stylomere 1 large, at apex with 5-6 elongate setae. Stylomere 2 elongate, little curved, obtuse, with 2 short ventral ensiform setae, one short dorsal ensiform seta, both arising in middle, and one short nematiform seta situated near apex and originating from a pit.

Variation. Little variation noted, only variation of size rather important.

Distribution (Fig. 21). Northwestern part of far Northern Territory, adjacent northern Western Australia, from Victoria River west to Fitzroy River.

Habits. Lives in wet sand near rivers and creeks like other species of this genus. Mainly collected at light and in Barber traps exposed in wet sand close to pools in larger river beds, also found under pebbles imbedded in sand. When disturbed or at light, they are extremely agile, fast running beetles. In the eastern part of the range of *P. punctata kimberleyana* Baehr sympatric and even syntopic with this subspecies.

Etymology. Named in honour of my little son who enthusiastically helped collecting these fast running beetles.

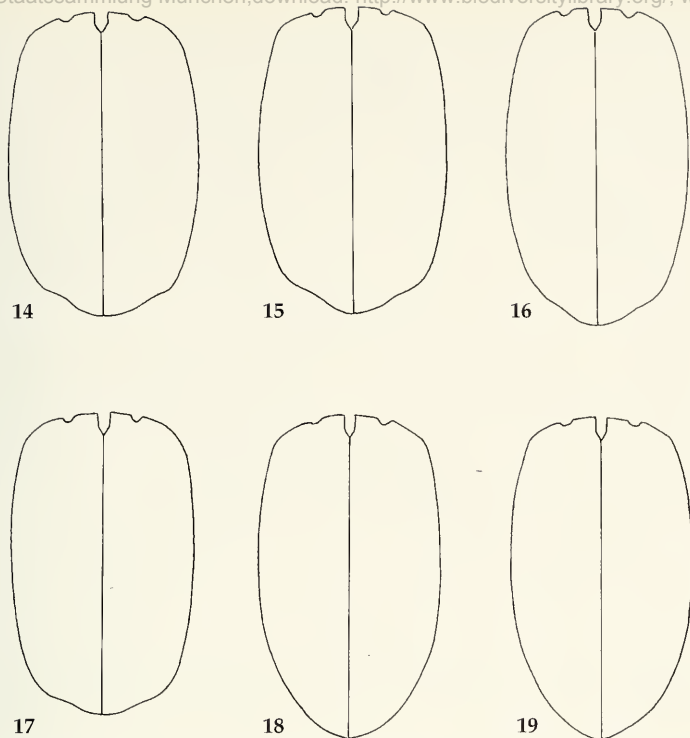
### *Porocara occidentalis* Baehr

Figs 9, 13, 19, 21

Baehr 1986, p. 723.

Diagnosis. Distinguished by elongate, laterally evenly convex elytra (Fig. 19), rather sparse, irregular puncturation of head and pronotum, and large, at apex markedly upturned aedeagus that is conspicuously striolate at lower surface (Fig. 13).





Figs 14-19. Outline of elytra. 14. *Porocara punctata punctata* Sloane. 15. *P. punctata kimberleyana* Baehr. 16. *P. punctata arnhemensis*, subsp. nov. 17. *P. nigricollis* Baehr. 18. *P. ulrichi*, spec. nov. 19. *P. occidentalis* Baehr.

#### Additional distinguishing character states

Ratio length/width of elytra: 1.62-1.67.

♂ genitalia (Fig. 13). Genital ring comparatively narrow, laterally barely convex, slightly asymmetric. Aedeagus large, >2.2 mm long, markedly curved in basal part, lower surface straight, conspicuously striolate, apex elongate, rather upturned at tip, abruptly turned to right side, orificium with a fold at apex. Right paramere rather short.

Distribution (Fig. 21). Northwestern Australia south of Great Sandy desert to Carnarvon in the south.

Habits. Lives in wet sand near rivers and creeks like other species of this genus. Mainly collected in Barber traps exposed in wet sand close to pools in large river beds.

New records: 10♂♂, 6♀♀, WA 18, Ashburton River b. Nanutarra, 3.-4.11.1987, M. Baehr (CBM).

#### *Porocara glabrata* Baehr

Baehr 1986, p. 724.

Diagnosis. Easily distinguished by absence of puncturation on head and pronotum, weak microreticulation on elytra, narrow, markedly serrate postmedian elytral vitta, and simple apex of aedeagus.



Fig. 20. Distribution of *Porocara punctata punctata* Sloane: ●, *P. punctata arnhemensis*, subsp. nov.: ◆, and *P. punctata kimberleyana* Baehr: ■.

Additional distinguishing character states

Ratio length / width of elytra: 1.56-1.60.

Aedeagus. Rather short and compact, lower surface almost straight. Apex short, not at all thickened or upturned.

Distribution. Southeastern margin of Kimberley Division, northwestern Australia.

Habits. Lives in wet sand near rivers and creeks like other species of this genus. Commonly collected at light.

New records: No new material recorded.

Tab. 1. Comparison of size and of length/width ratio of elytra in the taxa of *Porocara*.

	length(mm)	l/w ratio
<i>P. p. punctata</i> Sloane	8.6-9.4	1.55-1.58
<i>P. p. arnhemensis</i> , subsp. nov.	8.15	1.64
<i>P. p. kimberleyana</i> Baehr	8.1-9.3	1.62-1.64
<i>P. nigricollis</i> Baehr	8.1-8.7	1.56-1.62
<i>P. ulrichi</i> , spec. nov.	8.5-9.5	1.64-1.68
<i>P. occidentalis</i> Baehr	9.4-9.8	1.62-1.67
<i>P. glabrata</i> Baehr	8.8-9.6	1.56-1.60



Fig. 21. Distribution of *Porocara nigricollis* Baehr: ●; *P. ulrichi*, spec. nov.: ■, and *P. occidentalis* Baehr: ◆.

## Discussion

### Origin of the genus *Porocara*

As explained in my previous revision (Baehr 1986), *Porocara* is perhaps an old Australian faunal element, and altogether, it is perhaps the most primitive odacanthine genus at all that exhibits few of the special "odacanthine" morphological features. The primitive status of *Porocara*, both in morphology and way of life, but also the possible origin of the genus in Australia, has been recently supported by examination of *Grundmannius dispar* (Péringuey), an "aberrant" South African beetle belonging to the subfamily Chlaeniinae. *Grundmannius*, though characterized as a chlaeniine by some of its technical characters, has exactly the same bulky and convex body shape, relatively short and wide, though convex elytra, elongate mandibles, very elongate legs, and light reddish colour with blackish basal and postmedian transverse fasciae on the elytra, as *Porocara*. The single examined specimen has been likewise obtained in sand of a river bed, and hence, it probably has the same way of life as *Porocara*. Although *Grundmannius* is slightly larger than *Porocara* and occurs in subtropical southern Africa (northern Natal), it exhibits exactly the same life style type. Like *Porocara*, *Grundmannius* does not show the usual body shape, colour, and way of life of its subfamily. Therefore, I think that occurrence in pure wet sand of river beds, nocturnal habits, light reddish colour, convex body shape, very elongate legs, and large eyes represent the original state in both, primitive Odacanthinae and Chlaeniinae. If this hypothesis is true, then both subfamilies would still have their most plesiotypic members in the southern continents, and this would support the idea of the Gondwanan origin of Odacanthinae (as well as of Chlaeniinae).

This idea is further supported by the occurrence of several other rather primitive odacanthine genera in Australia and New Guinea, some of which, at least, occur in sandy river beds. Generally, however, they are found under stones and between low vegetation, rather than in pure sand.

This scenario would also confirm Erwin's (1985) hypothesis of "taxon pulse's" in many carabid groups.

Erwin's idea was that the original stocks of most carabid groups lived in wetlands or near water in tropical lowlands, from where they spread to other biotas and to the highlands. In Odacanthinae, for example, this would mean an ecological shift to life on the forest floor of tropical rain forest (e.g. in certain New Guinean and north Australian species) and another shift to life on vegetation (in many of the "higher" odacanthine genera throughout the world).

To conclude, there is some reason to believe that *Porocara* belongs to the so-called "Old Gondwanan faunal element" (Mackerras 1970, Howden 1981, Baehr 1991) in Australia that is part of a very old fauna, remnants of which still exist in subtropical-tropical parts of Africa and South America, and in Australia.

Hence, probably *Porocara* is an old indigenous faunal element of Australia that was primarily adapted to warm temperate to subtropical conditions, but was subsequently adapted to tropical climatic conditions when the Australian plate during Tertiary drifted in northerly direction.

### Distribution and zoogeography of the species

Although all species of *Porocara* are extremely similar in body shape, colour pattern, and structure of surface (the last except for *P. glabrata* Baehr), they clearly divide in three groups according to size and structure of aedeagus. The most outstanding group, represented by *P. glabrata* only, has a small, straight aedeagus with simple apex. This group is further characterized by the loss of the punctuation on the upper surface of head and pronotum. The second group (*P. punctata* and its subspecies, and *P. nigricollis*) has small, more or less curved aedeagi with thickened but less upturned apex. The third group (*P. ulrichi*, *P. occidentalis*) has large, straight aedeagi with distinctly upturned apex. Therefore, three separate stocks of *Porocara* exist in Australia that all broadly coexist in vast parts of tropical northern Australia, moreover, that are syntopic in several localities, and have been found even in the same barber trap (see tab. 2).

In all species body shape and pattern, length of mandibles, length of legs, size of eyes, and the habits of hiding in wet sand during daytime and foraging at night around pools, are extremely similar. That means that the life style type ("Lebensformtyp" sensu Koeppcke) of all taxa is also similar. This would raise the question, how it is possible that two or even three closely related taxa with exactly the same way of life can coexist in the same place.

Some ideas about the phylogenetic relations within the genus were presented in the previous revision (Baehr 1986) and are not repeated here, but are used for the subsequent discussion.

With regard to distribution, occurrence of two species in far Northern Territory and of four species in northwestern Australia is most essential, especially, as three of the latter have almost exactly the same ranges and even coexist in some places. In north Queensland, on the other hand, only a single species exists.

This distribution pattern is another conspicuous evidence of the importance of refugia in northern and northwestern Australia. Although humid Queensland should offer better and more diverse conditions for ripicolous beetles than the partly semiarid Kimberley and Hamersley areas, obviously these suitable conditions have not been favoured the evolution of additional species in North Queensland, whereas under the less suitable climatic conditions in northern and northwestern Australia such evolution occurred. This can be only explained by repeated colonizations of Arnhem Land and the Kimberleys by different stocks of *Porocara*, that were subsequently isolated, and thus evolved to separate species in the refugias, whereas in Queensland comparable isolations of populations did not occur.

The first stock to invade the Kimberleys and to become isolated there was that from which present *P. glabrata* is derived, the species that is now phylogenetically most isolated.

The second stock has split in the present *P. ulrichi* and *P. occidentalis* that at present are distributed in the Kimberleys and in the Hamersley area, i.e. to the north and to the south of the Great Sandy Desert,

Tab. 2. Records of syntopic occurrence of different species of *Porocara*.

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<i>P. punctata arnhemensis</i> , subsp. nov. - <i>P. nigricollis</i> Baehr: Nourlangie Creek, Arnhem Land, Northern Territory.
<i>P. punctata kimberleyana</i> Baehr - <i>P. ulrichi</i> , spec. nov.: Victoria River, 5 km w. of Victoria River Crossing; West Baines River at highway crossing; both localities in northwestern Northern Territory.
<i>P. punctata kimberleyana</i> Baehr - <i>P. ulrichi</i> , spec. nov. - <i>P. glabrata</i> Baehr: Fitzroy Crossing, northern Western Australia.

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respectively. In northwestern Australia the Great Sandy Desert extends as a several hundred kilometers wide corridor right to the coast and at present acts as a major barrier for the fauna. This applies in particular for ripicolous beetles, because between Fitzroy River at the southern margin of the Kimberleys, and De Grey River north of the Hamersley area no rivers or creeks exist.

Diversification of the third stock occurred more recently, but presumably in two events: first the stock of present *P. nigricollis* invaded into or was isolated in far northern Territory, later the present species *P. punctata* either extended over whole northern tropical Australia and afterwards evolved into separate subspecies; or, in the case this species originally ranged over the whole area it inhabits at present, three populations were isolated and evolved into the present subspecies.

Because phylogenetic evidence shows that in both, the *punctata*- and *ulrichi*-stocks the western taxa are most apotypic in certain character states, it can be argued that range spreading generally proceeded in an easterly to westerly direction, and /or that in the western populations evolution was enforced. So, altogether four speciation events occurred at different times, resulting in a threefold colonization of the Kimberley area, and a double colonization of Arnhem Land.

Due to the close relationships of most taxa (apart from *P. glabrata*) dating of the speciation events is difficult. It is possible that the most recent speciation, namely evolution of the subspecies of *P. punctata*, was even a postglacial event, because slow drying out of the faunal barriers south of the Gulf of Carpentaria and in northwestern Northern Territory would have supported isolation. Certainly, this event did not occur before last interglacial, but most probably during one of the more recent interstadials of the last glaciation period. Presumably *P. nigricollis* did not evolve much earlier according to the still close relationship with *P. punctata*. Separation of the *ulrichi*-stock and subsequent separation into present *P. ulrichi* and *P. occidentalis* probably occurred not later than during last interglacial, whereas the origin of the *glabrata*-stock probably was an event prior to last interglacial.

As a conclusion it can be stated that in *Porocara*, although the genus represents an old Australian faunal element, speciation occurred but recently and perhaps exclusively during (late) ice-age. *Porocara* shares this pattern of biogeographical history with several other carabid (and non-carabid) groups occurring throughout northern tropical Australia.

The recent discovery of two new taxa is evidence that still additional new taxa may be detected in future. Then, some aspects of relationships and biogeographical history of the genus may change again.

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