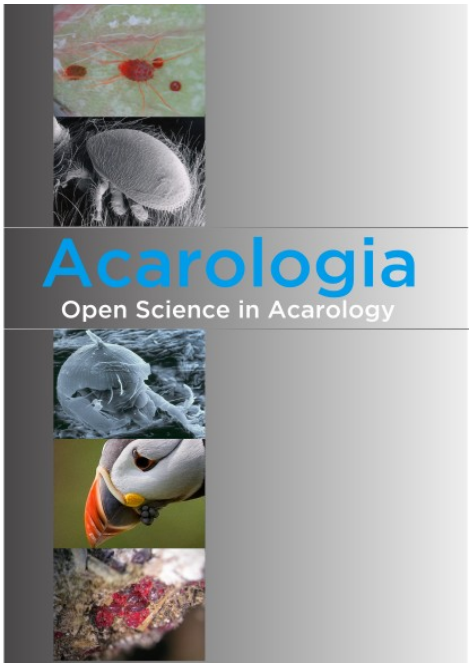

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Arhodeoporus, *Camactognathus*, *Plegadognathus*, and *Winlundia* (Acari: Halacaridae), re-evaluation and geographical distribution

Ilse BARTSCH

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Forschungsinstitut Senckenberg, c/o DESY, Notkestr. 85, 22607 Hamburg, Germany. ibartsch@senckenberg.de

ABSTRACT — *Arhodeoporus*, *Camactognathus, Plegadognathus*, and *Winlundia* are very similar in their general shape, they share numerous characters but differ in the position of the solenidion on tarsus II, and also in the number of gland pores and the chaetotaxy of the legs. Comparison with other halacarid genera proved, the position of the solenidion is stable within a species and genus, no variants are known, whereas in respect to the other characters, various states within a genus are documented. Because of differences in the position of the solenidia, the genus *Arhodeoporus* Newell has to be splitted. Species of *Arhodeoporus* s.str. have the solenidion on tarsus II dorsolateral in position; the genus includes the two species once described by Newell (1947), namely *A. arenarius* and *A. submarinus*. The other species have this solenidion on the dorsomedial flank of claw fossa. The species once referred to as the *bonairensis* group are moved to the re-established genus *Plegadognathus*, the other species are included in the new genus *Maracarus*. *Camactognathus* shares with *Arhodeoporus* s.str. the position of the solenidion on tarsus II but differs in other characters; the genus is solidly diagnosed. The differences between *Winlundia* and *Plegadognathus* are small, with an increase of knowledge of the species, *Winlundia* may turn out to be a synonym of *Plegadognathus*. The five genera have records from tropical and temperate coastlines but not from polar waters. *Maracarus* and *Plegadognathus* are spread all around the globe whereas *Arhodeoporus* s.str. and *Winlundia* are restricted to the north-eastern Atlantic and south-eastern Pacific, respectively.

KEYWORDS — Halacaroidea; *Arhodeoporus* s.l. and s.str; new diagnoses; *Maracarus* n. gen.; biogeography

INTRODUCTION

The genus *Arhodeoporus* was introduced by Newell (1947), first in the rank of a subgenus, later raised to that of a genus (Newell 1971). Species by Newell (1947) placed in this new subgenus/genus were *Copidognathus* (*Arhodeoporus*) *arenarius* Newell, 1947, *C.* (*A.*) *submarinus* Newell, 1947, *C. gracilipes gracilipes* (Trouessart, 1889), *C. gracilipes quadricostatus* (Trouessart, 1894), *C. gracilipes largiforatus* (Trouessart, 1899). *Arhodeoporus arenarius* and *A. submarinus* were taken on the Atlantic coast of North America, the others from the opposite side of the North Atlantic, from European coastlines.

The definition presented by Newell (1947: 173ff) said, the subgenus *Arhodeoporus* includes *Copidognathus* s.l. species in which (1) tibia I has two pairs of ventral setae (instead of three unpaired setae); (2) rostrum is wide at base and scarcely extends beyond middle of P-2 [second palpal segment]; (3) rosette pores are absent, and (4) OC [ocular plates] are drawn out into a long, posterior, caudiform projection (in the species known at present). Characters they share with *Copidognathus* are (Newell 1947: 129): 'Palpi attached to capitulum laterally;

bases of palpi separated by a distance considerably greater than width of P-1 [first palpal segment], and clearly visible in ventral view. Palpi distinctly 4-segmented. P-4 [fourth palpal segment] usually longer than P-2, slender, tapering; attenuate distal portion longer than basal portion. P-2 with a single, usually long dorsal seta. P-3 [third palpal segment] without setae; P-4 with 3 setae on thick basal portion. Palpi distinctly geniculate. Genital suckers internal'. Three of the four above mentioned discriminating characters of *Arhodeoporus* are expected to include a wide range of states, depending on mode of life, feeding, substratum, actually Newell (1947: 34) already had stated 'the form of the ocular plates may be a useful key character, but its use as a subgeneric character is more of an impediment than an aid in the taxonomy of the groups'. Accordingly, the only difference that could be used to distinguish between *Arhodeoporus* and *Copidognathus* was the number of ventral setae of tibia I, four (two pairs) in *Arhodeoporus* but three in *Copidognathus*. Later Newell (1984: 202) added, *Arhodeoporus* female with two pairs of subgenital setae, male with either four or five pairs.

In the same paper, Newell (1984) described the new genera *Camactognathus* and *Winlundia*, both very similar to *Arhodeoporus*. Characterization of *Camactognathus* was (Newell 1984: 201, 202): dorsal gland pores not enlarged; adanal setae in margin of posterodorsal plate; female of type species with one pair of subgenital setae; palps inserted laterally; third palpal segment without seta; fourth segment with three basal setae; genu II shorter than telofemur or tibia; tibiae I and II with four ventral setae; solenidion posterior in position on both tarsi I and II.

The diagnosis of *Winlundia* reads (Newell 1984: 197, 198): Palpi four-segmented, attached laterally to gnathosoma, P-2 with one seta; no seta on P-3; P-4 with three setae; genu of leg II much shorter than telofemur and tibia II; tibia I with three dorsal and four ventral setae; ambulacra I and II similar in form, solenidia I and II both on posterior aspect of tarsi (but on page 201, position of solenidia on tarsi I and II posterior and anterior in position, respectively, and in the tabular key on page 12, solenidia on tarsi I and II equal a posterior:anterior combination); tarsus I with two ventral setae; adanal setae on anal papilla; female with two pairs of subgenital setae, male with five pairs (in type species *W. filistoma*, but three pairs in *W. forcipata*).

Plegadognathus, another genus most similar to *Copidognathus* and *Arhodeoporus*, was introduced and described by Morselli (1981). Its characters (page 266) are: dorsum with postocular plates; palps four-segmented, laterally attached; P-4 with two basal setae; tarsi and tibiae I with two and four ventral setae, respectively.

In the beginning of the 1970s three new species were added to *Arhodeoporus*, *A. mammillifer* Newell, 1971, taken in the south-eastern Pacific, and *A. brevocularis* Bartsch, 1973 and *A. lineatus* Bartsch, 1973, both from the north-eastern Atlantic (Newell 1971; Bartsch 1973b). The two last-mentioned species nicely agreed with the generic characters outlined for *Arhodeoporus arenarius* and *A. submarinus*. The only serious difference was, the solenidion on tarsus II of *A. brevocularis* and *A. lineatus* was on the dorsomedial fossa membrane, in contrast to the dorsolateral position of the north-western Atlantic and Pacific species mentioned by Newell (1947, 1971). *Halacarus gracilipes* Trouessart, 1889, by Newell (1947) included in the genus *Arhodeoporus*, agreed with *A. brevocularis* and *A. lineatus* in that the solenidion was on the dorsomedial fossa membrane (Bartsch 1973b, 1977a). This difference raises the questions, is the position of the solenidion on tarsus II of generic importance? Can the solenidion move from one side to the other? What is the correct position in present-day known *Arhodeoporus*, *Camactognathus* and *Winlundia* species, and do they belong to just one genus?

MATERIALS AND METHODS

Arhodeoporus s.l. means the genus is used in the present-day definition, independent of the changes proposed in this paper, *Arhodeoporus* s.str. is used according to the new definition presented. Table 1 includes *Arhodeoporus* s.l., with its presently accepted 32 species, *Camactognathus*, *Winlundia*, and *Copidognathus*, with three, two and more than 340

TABLE 1: Characters of *Arhodeoporus* s.l., *Camactognathus*, *Winlundia*, and *Copidognathus*.
abs, absent; B, gnathosomal base; dl, dorsolateral; dm, dorsomedial; pre, present; Ro, rostrum; sgs, subgenital setae; 1(f), one faintly pectinate seta);?, no data available or character state in need of verification; ( ), rare character state.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Arhodeoporus s.l.																																
arenarius	pre	4	1	2	4	B	0	3	2	5	5	3	3	4	4	8(-9)	7	5	4(-5)	3	1(f)	2	1	1	dl	4	3	3	1	0	2	2
bonairensis	pre	3	1	2	5	B	0	2	2	4	3	2	2	3	3	7	6(-5)	5	4	(2-)3	0	(1-)2	1	0	dm	3	3	2	0	0	2	2
brevocularis	pre	4	1	?	5	B	0	2	2	5	3	3	3	4	4	8	7	5	4	3	0	2	1	1	dm	4	3	?	1	0	2	?
bucculentus	pre	3	1	2	5	B	0	2	2	3	3	2	2	4	4	7	6	5	4	3	2	2	1	1	dm	3	3	3	0	0	2	2
caudatus	pre	4	1	2	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	0	1	1	1	dm	4	3	3	0	0	2	?
clypeatus	pre	4	1	2	3?5?	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	1	2	1	1	dm	4	3	3	0	0	2	?
corallicolus	pre	4	1	3	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	1	2	1	1	dm	4	3	3	0	0	2	2
disparilis	pre	3?	1	?	5	B	0	2	2	4	3	2	2	3	3	7	6	5	4	3	0	2	1	0	dm	3	3	2	0	0	2	?
eclogarius	?	4	1	?	?	B	?	?	?	5?	?	?	?	5?	?	8	?	5	4	3	0	2	1	0	dm	3	3	3	1	1	?	?
gracilipes	pre	4	2	2	5	B	0	2	2	5	5	3	(2-)3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	0	2	2
kunzi	pre	4	1	2	?	B	0	2	2	5	3	3	3	4	4	8	7	5	4	3	0	2	1	1	dm	4	4	3	1	0	2	?
labronicus	pre	3	1	2	4	B	0	2	2	3	3	2	2	3	3	7	6	5	4	3	2	2	1	1	dm	3	3	2	0	0	2	?
leptopus	pre	4	1	2	?	B	0	2	2	5	6	3	3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	1	1	?
lineatus	pre	4	1	1	5	B	0	2	2	4	4	3	3	3	3	8	8	5	4	4	0	2	1	1	dm	4	3	3	0	0	2	2
lizardensis	pre	4	1	?	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	0	2	1	1	dm	4	3	3	0	0	2	?
longicrus	pre	4	1	0	?	B	0	2	2	6	5	3	3	4	4	8	8	5	4	4	0	2	1	0	?	4	3	3	1	1	1	?
longirostris	pre	4	1	2	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	0	1	1	1	dm	4	3	3	0	0	2	2
mactanus	pre	4	1	2	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	0	2	1	1	dm	4	3	3	0	0	2	2
mammilifer	pre	4	?	2	5	B	0	2	2	5	5	3	3	4	4	8	7	5	4	4	?	?	?	?	dl?	4	3	3	1	1	1	?
minor	pre	4	2	2	5(-6)	B	0	2	2	5	5	3	3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	0	2	2
minusculus	pre	4	1	0	3	B	0	2	2	3	3	2	2	2	2	8(-9)	8	5	4(-5)	4	2	2	1	0	dm	3	3	3	1	1	0	2
mirabilis	pre	4	1	2	?	B	0	2	2	6	5	3	3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	1	1	?
mooreus	pre	4	1	2	?	B	0	2	2	6	6	3	3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	1	1	?
nanus	pre	4	1	0	?	B	0	2	1	3	3	2	2	2	2	7	6	5	4	3	0	2	1	0	dm	3	3	3	0	1	1	2
perlucidus	pre	4	2	2	5	B	0	2	2	4	5	3	3	4	4	8	8	5	4	4	0	2	1	0	dm	4	3	3	1	0	2	2
psammophilus	pre	4	1	2(-3)	5	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	1	2	1	1	dm	4	3	3	0	0	2	2
robustus	pre	3?	1	?	5	B	0	2	2	4	3	2	2	3	3	7	6	5	4	3	0	2	1	0	dm	3	3	3	0	0	2	?
submarinus	pre	4	1	(1-)2	5	B	0(-1)	3	2	5	5	3	3	4	4	8	7	5	4	3	1(f)	2	1	1	dl	3	3	3	1	0	2	2
subtilis	pre	4	2	2	?	B	0	2	2	5	5	3	3	4	4	8	8	5	4	4	0	2	1	0	?	4	3	3	1	0	2	?
tanzanicus	pre	4	1(-0)	2	?	B	0	2	2	3	3	2	2	4	4	8	7	5	4	3	0	2	1	1	?	4	3	3	0	0	2	?
thyreophorus	?	?	1?	?	?	?	?	?	?	1?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	?	?	?	?
wadjemupis	pre	3	1	1-2	5	B	0	2	2	3	3	2	2	4	4	7	6	5	4	3	2	2	1	1	dm	3	3	3	0	0	2	?
Camactognathus																																
borealis	abs	?	1	1	?	Ro	1	2	2	4	3	2	2	4	4	8	6	5	4	2	2	1	1	1	dl	4	3	1	1	0	2	2
grossipes	abs	?	1	1	2	Ro	1	?	?	5	?	?	?	4	?	10	?	6	4	?	1	?	?	0	dl	4	3	1	1	?	?	?
tesselatus	abs	3	1	1	3	Ro	1	2	1	4	3	2	2	4	4	8	5	5	4	2	2	1	1	1	dl	4	3	1	1	0	2	2
Winlundia																																
filistoma	pre	3	1	2	5	B	0	2	2	4	3	2	2	3	3	7	6	5	?	?	1	2	1	0	dm	3	3	2	0	0	2	2
forcipata	pre	3	1	?	3	B	0	2	2	5	5	2	3	3	3	7	6	5	4	3	0	2	1	0	dm	3	3	2	0	0	2	?
Copidognathus	pre	(2?-)4	1	1	(2-)4	B	0	2	(1-)2	(3-6)5	(3-)5	2-3	2-3	4(-2)	4(-2)	(5-)7	(5-)7	5	(2-)3	(2-)3	(1-)2	(1-)2	(0-)1	0-1	dl	(3-)4	3(-4)	3	0	0(-1)	(1-)2	0

Characters: 1, epimeral pores, present (pre) or absent (abs); 2, number of gland pores; 3, number of dorsal setae on PE; 4, female, number of pairs of sgs; 5, male, number of pairs of sgs; 6, position of basal pair of maxillary setae, on gnathosomal base (B) or on rostrum (Ro); 7, trochanter IV, number of setae; 8, basifemur II, number of setae; 9, basifemora III and IV, number of setae; 10, telofemur I, number of setae; 11, telofemur II, number of setae; 12, telofemur III, number of setae; 13, telofemur IV, number of setae; 14, genu I, number of setae; 15, genu II, number of setae; 16, tibia I, number of setae; 17, tibia II, number of setae; 18, tibiae III and IV, number of setae; 19, tibia I, number of ventral setae; 20, tibia II, number of ventral setae; 21, tibia I, number of pectinate setae (0, no setae pectinate, 1, one seta coarsely pectinate, 1(f), one seta faintly pectinate); 22, tibia II, number of pectinate setae; 23, tibia III, number of pectinate setae; 24, tibia IV, number of pectinate setae; 25, tarsus II, position of solenidion, dorsolateral (dl) or dorsomedial (dm); 26, tarsus III, number of dorsal setae; 27, tarsus IV, number of dorsal setae; 28, tarsus I, number of ventral setae; 29, tarsus II, number of ventral setae; 30, tarsi III and IV, number of ventral setae; 31, tarsi III and IV, number of parambulacral setae; 32, last nymphal stage, number of pairs of perigenital setae.

species, respectively (Chatterjee *et al.* 2008; Bartsch 2009a, b, 2013, 2015a; Chatterjee and Pešić 2014). The table is prepared mainly on the basis of published data, partly on re-examined specimens. Rare character states are in parentheses. A question mark is added in case a character state is not known or in need of verification because of discrepancies in the descriptions or between text and figures. Character data of Table 1 are used in the parsimony analysis, *Copidognathus* represents the out-group. Rare variants are excluded from the analysis. In case of discrepancies between text and figures or supposed lapsus, a character state is treated as unknown. The description of *A. thyreophorus* (André, 1959) and

A. eclogarius (André, 1959) are fragmentary, hence the species are excluded from the parsimony analysis. The analysis was run with PHYLIP version 3.6. (Phylogeny Inference Package) (Felsenstein 2005)

The abbreviations used in the text are: AD, anterior dorsal plate; AE, anterior epimeral plate; ds, dorsal idiosomatic seta(e), ds-1 to ds-6, first to sixth pair numbered from anterior to posterior; GA, genitoanal plate; GO, genital opening; OC, ocular plate(s); P-2 to P-4, second to fourth palpal segment; pas, parambulacral seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate(s); pgs, perigenital setae, numbered from anterior to posterior; sgs, subgenital setae.

RESULTS

The parsimony analysis is prepared on the basis of 30 *Arhodeoporus* s.l. species, three *Camactognathus* and two *Winlundia* species, the genus *Copidognathus* is used as outgroup. Discrepancies within a description or differences between description and examined species are:

A. bonairensis (Viets, 1936): In contrast to the figures in Viets (1936: fig. 44) and Sarma and Chatterjee (1993: figs 7 and 8), telofemora I and II bear four and three setae, respectively, tibia I seven setae, tibia II three and tarsus I two ventral setae. Though not mentioned in the description (Viets 1936; Newell 1947; Sarma and Chatterjee 1993; Otto 2000a; Bartsch 2009b), a pair of gland pores is present in the posterior part of the PD, immediately adjacent to the medial costae. The pores are similar to the cup-like alveoli of the costae, hence difficult to recognize. These pores have also been found in *A. bucculentus* Bartsch, 1977 and *A. wadjemupis* Bartsch, 1997. As illustrated in Bartsch (2009b: fig. 12) (though not in Sarma and Chatterjee 1993, figs 2 and 3), the AE bears a pair of epimeral pores. Re-examination of *P. bonairensis* (from Western Australia and Singapore) proved that females and deutonymphs have two pairs of internal genital acetabula, instead of a single pair as mentioned by Bartsch (2015b).

A. clypeatus Otto, 2000: The characters given for the male are size and number of pgs, else it is said (page 5) 'other characters as for *A. caudatus*'. Males of the latter species have five pairs of sgs but according to Otto (2000a: fig. 3e), there are three pairs of sgs on the male genital sclerites of *A. clypeatus*.

A. mammillifer Newell, 1971: The solenidion on tarsus II is said to be posterodorsal in position (dorsolateral) (Newell 1971: 27) but the species is so very similar to a group of others (*eclogarius* group), that the statement by Newell (1971) is expected to be a lapsus.

A. submarinus Newell, 1947: Newell (1947: 180) mentioned one seta on trochanter IV, in material studied (from Rhode Island, US) no seta was found.

Winlundia Newell, 1984: The description of the position of the solenidion on tarsus II is contradicting (cf. Newell 1984: 12, Key Group 2000; 198, 199, 200, 201). Examination of slides with *W. forcipata* Newell 1984 and *W. filistoma* proved, the solenidion is dorsomedial in position (Figure 1A), and both species have a pair of epimeral pores (Figure 1D and G).

The tree (Figure 2) reveals several clusters of species. *Camactognathus* species, which had been included in the analysis, turn up as a basal clade. One of the following clusters holds the species *bonairensis*, *bucculentus*, *disparilis*, *labronicus*, *robustus*, *wadjemupis* but also the two *Winlundia* species, another cluster includes a species group with *caudatus*, *clypeatus*, *corallicolus*, *lizardensis*, *longirostris*, *mactanus*, *psammophilus*, *tanzanicus* as well as with *gracilipes*, *minor*, *perlucidus*, *subtilis* and *leptopus*, *longicrus*, *mammillifer*, *mirabilis*, *mooreus*. The latter cluster should also include *eclogarius*, as proven by re-examination of the holotype (Table 1). The two *Arhodeoporus* species *A. arenarius* and *A. submarinus* share a branch with the two last-mentioned clusters though have a separate position.

The tree largely supports the natural groups within the genus *Arhodeoporus* s.l. proposed by Bartsch (1983a), namely the *bonairensis*, *eclogarius*, *gracilipes*, and *longirostris* group. The species of the *bonairensis* group share external characters, e.g. number of gland pores reduced, porose areolae of dorsal and ventral plates not evenly punctate but with cup-like alveoli or foveae, tibiae I with no more than seven setae, tibia II with six setae. On the basis

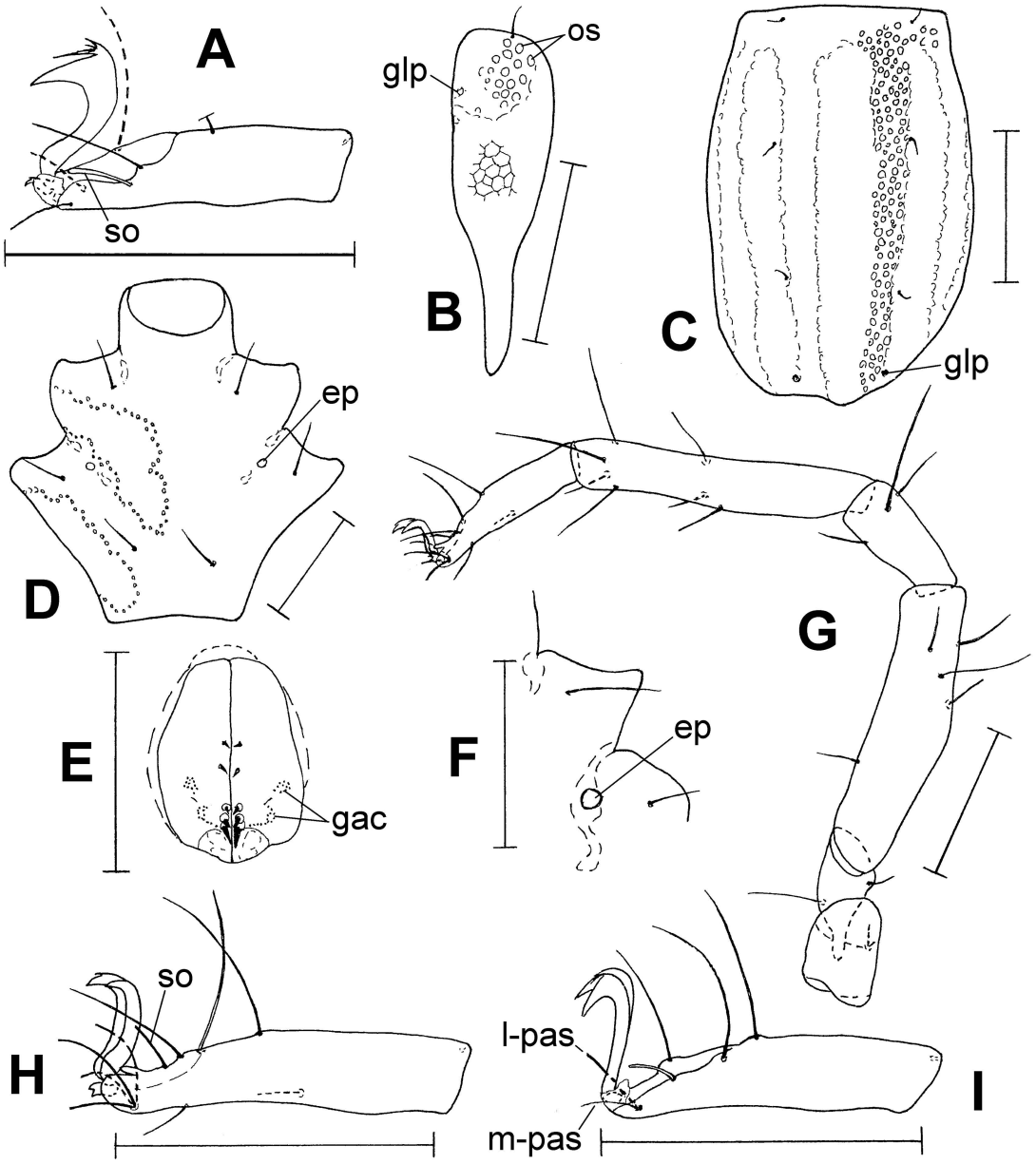

FIGURE 1: A-E: *Winlundia filistoma* Newell, 1984, male: A – tarsus II, medial (lateral setae in broken line, lateral claw omitted); B – OC; C – PD (of a slightly compressed male); D – AE (areolae with ostia illustrated on one side only); E – GO. F-I: *Winlundia forcipata* Newell, 1984, male: F – part of left AE with epimeral pore; G – leg I, lateral; H – tarsus I, lateral; I – tarsus II, medial. (ep, epimeral pore; gac, genital acetabula; glp, gland pore; l-pas, lateral parambulacral seta; m-pas, medial parambulacral seta; os, ostia of rosette pores; so, solenidion) Scale = 50 μm A-E, Chile, Arica, 20 June 1966, stones and worm tubes, intertidal; F-I, Peru, Lima, La Herradura, 16 June 1966, coarse sand pockets between boulders.

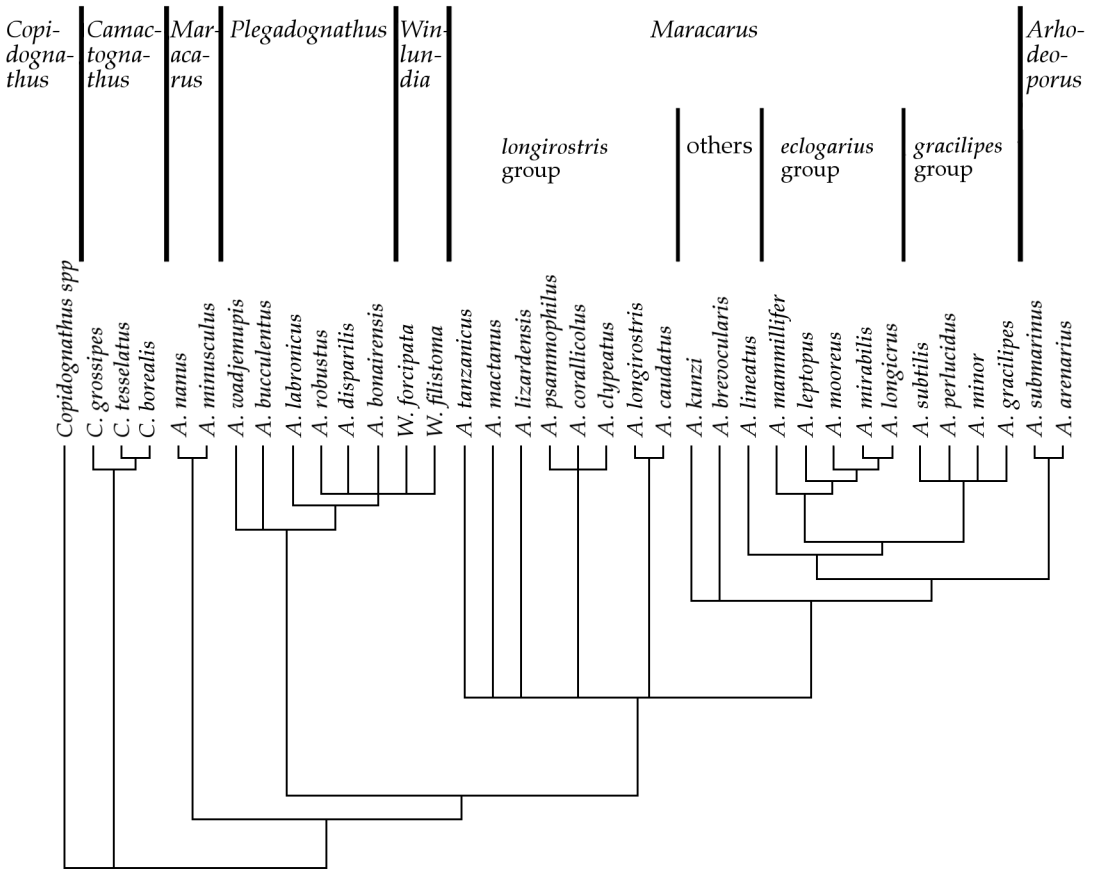

FIGURE 2: Phylogenetic tree of *Arhodeoporus* s.l., *Camactognathus* and *Winlundia* and a new classification, prepared on the basis of characters mentioned in Table 1, with *Copidognathus* as outgroup. (*A. eclogarius* and *A. thyreophorus* omitted)

of these characters, species of the *bonairensis* group can be separated from the other species of *Arhodeoporus* s.l. The group also includes *A. thyreophorus* which had been excluded from the data matrix.

Arhodeoporus s.l. *eclogarius* is characterized by its coarsely reticulated dorsal plates, the four pairs of gland pores opening subapically on conspicuously raised, pointed cones, the legs being long and slender, tibiae I and II bearing eight setae, and each of tarsi III and IV a large ventral seta but a single pas, the medial one. These characters are found in all species of the *eclogarius* group.

Characters of the *gracilipes* group are, dorsal plates with reticulate ornamentation, AD with pair of circular porose areolae and PD with porose costae, PE with two dorsal setae, tibiae I and II with eight setae, tibiae I to IV with 0, 2, 1, 0 pectinate setae, and tarsi I to IV with 3, 1, 0, 0 ventral setae.

The presently known species of the *longirostris* group have punctate but else rather smooth dorsal and ventral plates, costae are lacking, major parts of the plates are almost evenly punctate, tibiae I and II bear eight setae, on both tibia III and IV one of the two ventral setae is bipectinate, and tarsi I to IV have 3, 0, 0, 0 ventral setae.

The two species *A. minusculus* and *A. nanus* are on a basal branch, characters they share are, ornamentation of plates rather weak, genua I and II with no more than two setae, tibia IV with two slender ventral setae, and both tarsus III and IV with a small ventral seta.

Arhodeoporus arenarius and *A. submarinus* are close to species of the *gracilipes* and *eclogarius* groups but distinctly differ from these in the posi-

tion of the solenidion on tarsus II. The two species have, same as *Camactognathus* and *Copidognathus* species, the solenidion of tarsus II in a dorsolateral position, in the other above mentioned species the solenidion is in a dorsomedial one.

Discussion and Conclusion

Classifications of Halacaridae (Halacaroidea) have been prepared mainly on the basis of external morphological characters of adults, rarely juvenile stages or internal characters have been included, e.g. number of genital acetabula and number and shape of female genital spines (Viets 1927; Newell 1947, 1984; Bartsch 1983b, 2015b; Abé 1998). The spermatopositor has as yet been excluded but its shape, though species specific, demonstrates intrageneric similarities. An example of similarity is its shape in species of the *Agauopsis brevipalpus* group (Bartsch 2015a, c). Sufficient information on spermiogenesis and genetic data are lacking. Many of the external characters are correlated with the environment and mode of living and feeding, this means both, similar features may be found in different genera, evolved independently, and one can expect a range of characters states within a given genus. In parsimony analyses important phylogenetic characters may be masked by a large number of irrelevant ones. An example of morphological similarity is demonstrated by species of the *Arhodeoporus* s.l. *eclogarius* and *Copidognathus tricorneatus* group (cf. Bartsch 1997c). Tarsi III and IV of *Copidognathus* and *Arhodeoporus* species in general have a pair of parambulacral setae, on tarsus III one seta is flattened, the other eupathid, on tarsus IV either both are flattened or one flattened, the other slender (Figure 3C and E), but in a few species of the *C. tricorneatus* group the lateral pas is moved to a ventral position (cf. Bartsch 1973a: fig. 12, 1973b: fig. 14), just as in *A.* s.l. *eclogarius* (Figure 3A) and the other species of this group. Species of both groups (*eclogarius* and *tricorneatus*) have slender legs, striking similar reticulate ornamentation on the dorsal plates, a PD with a pair of narrow medial costae, demarcated porose areolae on the ventral plates, and a divided posterior cornea on the OC. The same arrangement of setae on tarsi III and IV, namely a single parambulacral but one ventral seta, is also found in *Simognathus* species, three examples, *Simognathus abnormalus* Otto, 2000, *S. gibberosus* Bartsch, 1994, and *S. gracilis* Bartsch, 1994) (Otto 2000b, Bartsch 1994).

Newell (1947) listed four characters which could be used to discriminate between the new subgenus *Arhodeoporus* and *Copidognathus* s.str., one was the absence of rosette pores. Raised areolae with typical rosette pores, namely an alveolus, in deeper layers of the procuticula surrounded by canaliculi (pore channels), opening to the exterior via an ostium (Newell 1947; Crowe and Camara 1973), are present only in species which live in a marine environment (at least 28 ‰), here amongst surface substrata, e.g. amongst coralline algae, colonial organisms or upper sediment layer. Species generally inhabiting low saline environments have less cuticularized plates, less pronounced costae, canaliculi seem to open directly to the exterior, rosette pores, if present, have often the shape of porose foveae or polygons. The plates of interstitially living species are rather uniformly ornamented, reticulated or foveate, with or without small pores.

Also a reduction of the size and number of setae is expected to be the result of chemical, physical and biological parameters. *Copidognathus* species with reduced numbers of setae on the genua and tibiae are generally from sandy deposits, examples are *C. cribellus* Bartsch, 1993, *C. psammobius* Bartsch, 2008 and *C. viridulus* Bartsch, 2009 (Bartsch 1993a, 2008, 2009b). *Isobactrus* species which live between and feed on delicate algal covers exposed to long-term desiccation have a lower number of setae than congeners from almost permanently wet habitats. One can expect that during periods of desiccation, when the mites become dehydrated, food intake and digestion are interrupted. Though speculative, as data of inorganic and organic components in interstitial water of sandy deposits as well as feeding rates during unfavourable periods are not known, the reduction of number of setae on the legs as well as thickness and ornamentation of the integument is expected to be correlated with life at permanently reduced diets. Will say, due to reduction in the exoskeleton, number of setae included, the species could compensate a restricted supply of or-

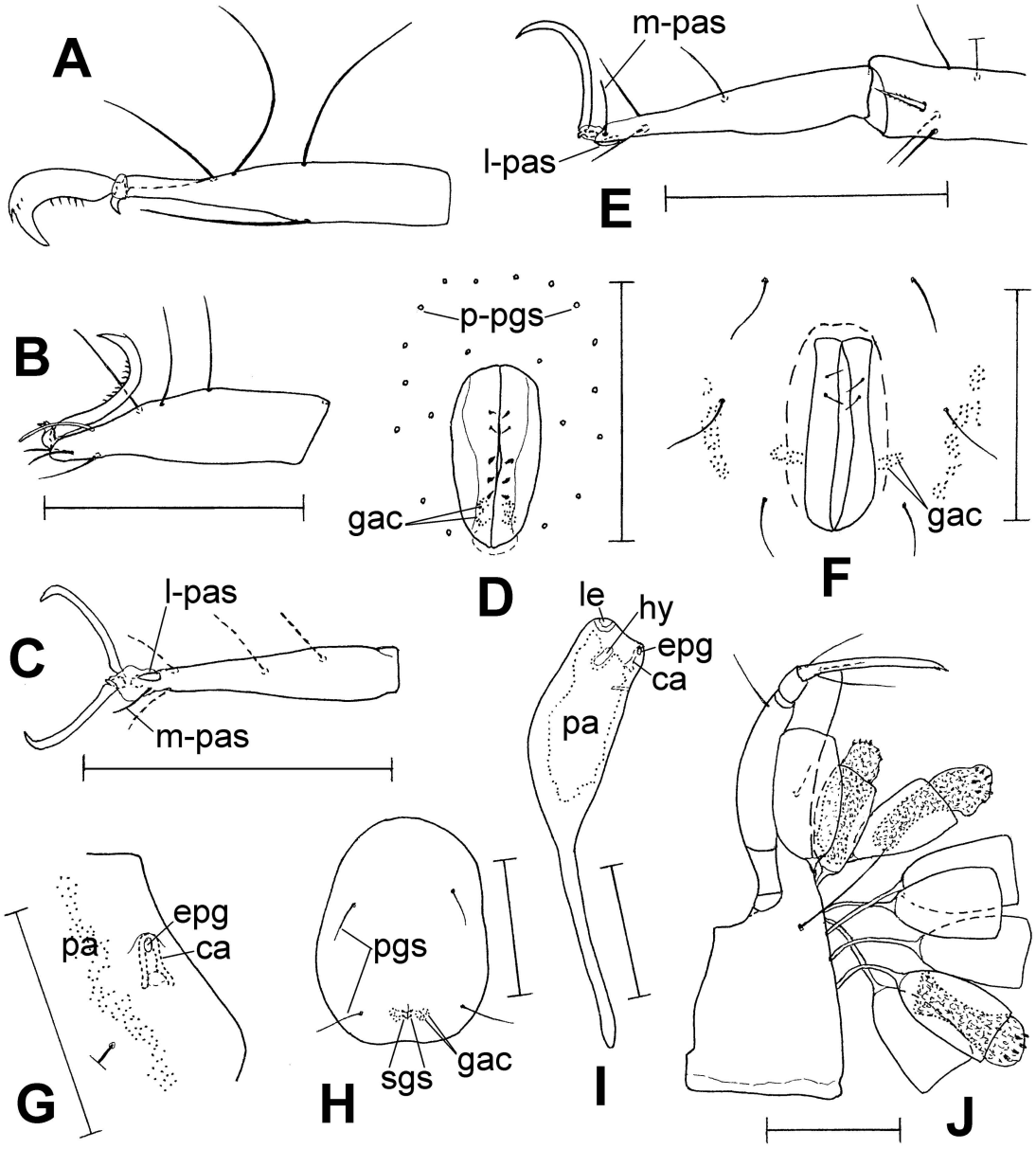

FIGURE 3: A – *Maracarus eclogarius* (André, 1959), female: tarsus IV, lateral (medial pas obscured, medial claw omitted); B – *Maracarus kunzi* (Bartsch, 1987), female: tarsus II, medial. C-E: *Maracarus brevocularis* (Bartsch, 1973), male: C – tarsus III, ventral (dorsal setae in broken line); D – GO and perigenital setae; E – tibia and tarsus IV, ventromedial. F – *Plegadognathus bonairensis* (Viets, 1936), female: GO and perigenital setae. G-J: *Maracarus corallicolus* (Otto, 2000): G – right part of AD with gland pore, male; H – genital plate with two pairs of pgs, sgs and internal acetabula, deutonymph; I – right OC, male; J – gnathosoma with suctoria, lateral aspect, male. (ca, canal of gland pore; epg, external porus of gland; gac, genital acetabula; hy, hyaline area; le, lens; l-pas, lateral parambulacral seta; m-pas, medial parambulacral seta; pa, porose areola; p-pgs, pori from perigenital setae; pgs, perigenital setae; sgs, subgenital setae) Scale = 50 μm. A, Gulf of Suez, 30 Dec. 1928, on sponges; B, South Africa, East London, broken shells; C-E, North Atlantic, Josephine Bank, 1 July 1967, 206 m, sediment; F, Indian Ocean, Australia, Dampier, Watering Cove, 8 Aug. 2000, algal turf on pneumatophores; G-J. Southwestern Pacific, Australia, Great Barrier Reef, Lizard Island, 13 Oct. 1998.

ganic and inorganic matter. Such compensation has certainly evolved independently in different genera. The faint ornamentation and reduced number of setae of the two psammobiont *Arhodeoporus* s.l. *minusculus* and *A. nanus* may be due to the environment and the separate basal position on a phylogenetic tree just be an artificial one.

Newell (1947, 1953, 1984) drew attention to setae of the tarsi and said 'The chaetotaxy of the tarsi is especially important at the generic level, in particular with regard to the placement of the solenidion (bacillum) on tarsus I and II' (Newell 1984: 7). The shape and position of these setae seem to be very conservative. They are present in all instars, from larva to adult. There is no reliable evidence of a major change in position and shape of the solenidia from larva to adult, and no report of any anomaly on the right or left leg. The few reported differences are obviously due to lapsus when interpreting or recording what had been seen on the microscopical slide. In all halacarids studied, the solenidion on tarsus I is dorsolateral in position, it may be clavate, as in all *Isobactrus* species (Bartsch 2003a: fig. 4A-E), or setiform, as in the majority of halacarids, it is shorter than the fossary setae (Figure 1H). Adjacent to the solenidion is a famulus, in shape and length similar to the solenidion, e.g. in *Metarhombognathus* and *Rhombognathides* (Newell 1953: fig. 2B and C) or reduced, even to a small, cap-like structure, but recognizable due to the afferent canal within the often enlarged fossa membrane. Almost all halacarid species have a solenidion on tarsus II, but here either dorsolateral, dorsal or dorsomedial in position. The solenidion may be similar to the one on tarsus I, e.g. in *Isobactrus* (Newell 1953: fig. 2A; Bartsch 2003a: fig. 4F-J), but often it is setiform (Figures 1A, I, 3B). Position and shape is the same in all instars. Many species have a fourth dorsal seta on tarsus III (commonly present in *Copidognathus*, *Halacarus*, *Isobactrus*, *Rhombognathus* species), the length of this seta is often somewhat less than that of the three fossary setae and in contrast to these never tapering, always ending bluntly and including a distinct internal lumen. In species with this sensory seta, by Newell (1984) called proximodorsal seta, it is present in all stages from larva to adult. In a few species a fourth (or more) tapering dorsal seta is present which is no sensory seta but an additional dorsal seta. In *Isobactrus levis* (Viets, 1927), the dorsal fossary seta is duplicated on all tarsi. *Thalassarachna* larvae have no more than three dorsal setae on the tarsi (Bartsch 2015d: fig. 2H), only the following instars may have an increased number of setae, all of them are tapering.

When regarding phylogeny, the position of the solenidion is a significant character, certainly more important than the ornamentation of plates or number of setae as these may be correlated with the environment and similarities are expected to have evolved independently in different genera and lineages. Because of the different position of the solenidion on tarsus II, the former genus *Arhodeoporus* s.l. has to be splitted. *Arhodeoporus* s.str. includes *A. arenarius* and *A. submarinus*, both with the solenidion on tarsus II dorsolateral in position. The other species, which have the tarsus II-solenidion dorsomedial in position, are transferred to the reestablished *Plegadognathus* Morselli, 1981 and to *Maracarus* n. gen. *Camactognathus* is considered a separate, valid genus.

Plegadognathus includes the species of the *bonairensis* group, namely *bonairensis*, *bucculentus*, *disparilis*, *labronicus*, *robustus*, *wadjemupis*, and *thyreophorus*. The dorsal and ventral plates (André 1959: fig. 13 D and V) of the last-mentioned species show an ornamentation typically found in *P. bonairensis*, hence *P. thyreophorus* may be a junior synonym of *P. bonairensis*. Compared to the other species once united in the genus *Arhodeoporus* s.l., the gland pores of *Plegadognathus* are small, not on cone-like projections, there are three (or less?) pairs of glands present, not four pairs, the dorsal plates are neither uniformly reticulated nor have punctate areolae, instead there are cup-like pores or subsurface alveoli with a few canaliculi opening to the exterior, and tibia I bears seven instead of eight setae.

For the remaining species, when the two *Arhodeoporus* s.str. and the seven *Plegadognathus* species are removed, a new genus has to be erected, namely *Maracarus* n. gen., with the type species *Maracarus gracilipes* (Trouessart, 1889). *Maracarus* has the solenidion on tarsus II dorsomedial in po-

sition (Figure 3B) (in contrast to *Arhodeoporus* s.str.) and there are four pairs of gland pores (in contrast to *Plegadognathus*), these open to the exterior via a very distinct, sclerotized canal which is at least twice as long as wide (Figure 3G) (versus gland pores not on cones, canal rather inconspicuous, not longer than wide).

Winlundia shares a cluster with species of the *bonairensis* group. Newell (1984: 198) already noted that there are several points of similarity between the type species of *Winlundia* and the species now called *P. bonairensis*, amongst others the arrangement of the porose areolae on the ventral plates of *W. filistoma*. The most striking difference between species of the two genera is the length of the gnathosoma. In *Winlundia filistoma* and *W. forcipata* it is very slender, in the type species the gnathosoma is 3.3 – 3.8 times longer than wide. In *Plegadognathus* species the length:width ratios lie between 1.2 – 1.7:1, in the type species of *Plegadognathus* the gnathosoma is 1.2 times longer than wide, in *P. bonairensis* 1.6 – 1.7 times. The length of the gnathosoma is no reliable generic character. Intrageneric different length:width ratios are documented. Most *Agaue* species have a long, slender gnathosoma, in *A. circellaris* Bartsch, 1999 the gnathosoma is four times longer than wide, in *A. scita* Bartsch, 1999 only two times, the rostrum is 3.8 times longer than the gnathosomal base (*A. circellaris*) versus both similar in length (*A. scita*) (Bartsch 1999a, b). The gnathosoma of *Copidognathus guttatus* Bartsch, 1977 is 4.3 times longer than wide, in *C. lutarius* Bartsch, 2003 only slightly longer, the rostrum of *C. guttatus* is 1.4 times longer than the gnathosomal base, that of *C. lutarius* only half that length (Bartsch 1977b, 2003b). Many *Lohmannella* species have a slender gnathosoma, in *L. fukushimai* Imamura, 1968 it is longer than the idiosoma, its rostrum almost twice as long as the gnathosomal base, whereas in *L. kervillei* Trouessart, 1894 the length of the gnathosoma is less than half that of the idiosoma and the length of rostrum less than that of the base (Imamura 1968; Bartsch 1977c). Moreover, halacarids demonstrate an allometric growth, legs and gnathosoma of adults are longer and more slender than those of larvae (Bartsch 2007a). Another discriminating character mentioned by Newell (1984) is the number of ventral setae on tarsus I, two setae in the two *Winlundia* species (Figure 1A and G), two to three in *Plegadognathus* species, both the type species *P. labronicus* as also *P. bonairensis* and *P. disparilis* have two setae (Morselli 1981: fig. 2Z1; Bartsch 1997: 270, 2009b: fig. 16). Intrageneric differences in the number of ventral setae are known. *Werthella* species bear either three (*W. crinata* Bartsch, 2005), two (*W. terella* Bartsch, 1993) or just one ventral seta (*W. atlantica* Bartsch, 1986) on tarsus I (Bartsch 1986, 1993b, 2005). A reduction of the assumedly plesiomorphic state with three ventral setae is no unique phenomenon. Characters *Winlundia* and *Plegadognathus* species share are a reduced number of gland pores, generally one pair on AD, OC and PD (Figures 1B and C), seven and six setae on tibiae I (Figure 1G) and II, respectively, and often no more than three setae on genua I and II. Adults of both genera are expected to have two pairs of internal genital acetabula, in *W. filistoma* one pair is wide, one slender (Figure 1E), in *P. bonairensis* both are delicate (Figure 3F). Noteworthy is that in *Winlundia forcipata* the medial pas on tarsus II is more slender than the eupathid lateral one (Figure 1I). In *W. filistoma* the pas only slightly differ in width (Figure 1A). In *P. bonairensis* the lateral pas is distinct, eupathid, the medial pas slender; in most of the *Maracarus* species the pas of either side are equal-sized. At present, *Winlundia* is retained as a valid genus, though studies on more material may prove it to be a junior synonym of *Plegadognathus.*

As to *Camactognathus*, the result of the character compilation and parsimony analysis supports the position as a genus. Discriminating character states of *Camactognathus*, in contrast to *Arhodeoporus*, *Plegadognathus* and *Maracarus* n. gen. are, epimeral pores lacking (versus present in the other genera); both pairs of maxillary setae on the rostrum (versus rostrum with a single pair); solenidion on tarsus II in dorsolateral position (shared with *Arhodeoporus* s.str.); tarsus I with a single ventral seta (versus two or three setae in the other genera).

DIAGNOSES

Arhodeoporus

Type species — *Arhodeoporus arenarius* Newell, 1947

Idiosoma — Dorsal plates AD, OC and PD with faint, uniform ornamentation. Dorsum with four pairs of gland pores and six pairs of setae, gland pores not on raised cones. AE with pair of epimeral pores and three pairs of setae, pair of PE each with one dorsal and three ventral setae. Female GA with three pairs of pgs, each genital sclerite with (one to) two sgs. Male GA with numerous pgs scatteredly arranged around GO, genital sclerites with four to five pairs of sgs.

Gnathosoma — Somewhat longer than wide. Rostrum triangular. Basal pair of maxillary setae on gnathosomal base, following pair on rostrum. Palps four-segmented, laterally attached. P-2 with one dorsal seta, P-4 with three setae in basal whorl; no seta on P-3.

Legs — Slender. Genua distinctly shorter than adjacent segments. Basifemora I to IV with 2, 3, 2, 2 setae, telofemora with 5, 5, 3, 3. Tibia I to IV with 8, 7, 5, 5 setae, included 4, 3, 2, 2 ventral setae. Solenidia on tarsi I and II dorsolateral in position. Tarsus I to IV with 3, 1, 0, 0 ventral setae. Tip of tarsi with pairs of parambulacral setae. Tarsi end with paired claws and a distinctly smaller median claw.

Deutonymph — With two pairs of pgs and two pairs of internal acetabula.

Camactognathus Newell, 1984

Type species — *Camactognathus grossipes* Newell, 1984

Idiosoma — Dorsum with (two? to) three pairs of gland pores and (five? to) six pairs of setae. Gland pores small, not on raised cones. Epimeral pores lacking; AE with three pairs of setae, pair of PE each with one dorsal and three ventral setae. Female GA with three to four pairs of pgs, each genital sclerite with one pair of sgs. In male, each genital sclerite with two to three sgs.

Gnathosoma — Rostrum slender. Both pairs of maxillary setae on rostrum. Palps four-segmented, attached laterally. P-2 with one dorsal seta, P-4 with three setae in basal whorl; no seta on P-3.

Legs — Genua much shorter than telofemora and tibiae. Basifemora I to IV with 2, 2, 1-2, 1-2 setae, telofemora with 4-5, 3, 2, 2, tibiae with 8-10, 5-6, 5, 5 setae, of these 4, 2, 2, 2 ventral in position. Solenidia on tarsi I and II dorsolateral in position. Tarsus I with single ventral seta, tarsi II to IV with 1, 0, 0 ventral setae. Tarsi with paired claws and a distinctly smaller median claw.

Deutonymph — Genital plate with two pairs of pgs and two pairs of internal acetabula.

Maracarus n. gen.

Type species — *Halacarus gracilipes* Trouessart, 1889

Etymology — Derived from mare (Latin), the sea, and acarus (Latin), a mite. Gender. Masculine.

Idiosoma — Dorsal plates AD, OC and PD often with punctate areolae but major parts uniformly ornamented, often reticulated. AD and OC each with one pair, PD with two pairs of gland pores, pores generally opening to exterior via conspicuous internal canal, this being two or more times longer than wide (Figure 3G and I), aperture often situated apically or subapically on domes or cones. Dorsum with six pairs of idiosomatic setae. AE with pair of epimeral pores and three pairs of setae, pair of PE each with one or two dorsal and three ventral setae. Female GA with three (rarely four) pgs on either side of GO, genital sclerites with two, rarely three pairs of sgs. Male GA with numerous pgs scatteredly arranged around GO, genital sclerites generally with five pairs of sgs, rarely with three, four or six setae on either sclerite. Adults with two pairs of internal acetabula (Figure 3D).

Gnathosoma — Longer than wide. Rostrum generally slender, triangular. Basal pair of maxillary setae on gnathosomal base, following pair on rostrum. Palps four-segmented, laterally attached. P-2 with one dorsal seta, P-4 with three setae in basal whorl; no seta on P-3.

Legs — Genua distinctly shorter than telofemora and tibiae. Basifemora I to IV with 2, 2, 2, 1-2 setae, telofemora with 3-6, 3-6, 2-3, 2-3. Tibia I to IV with

7-8, 6-8, 5, 5 setae. Solenidion on tarsus I dorsolateral in position, on tarsus II dorsomedial. Tarsus I to IV with 3, 0-1, 0-1, 0-1 ventral setae. Tarsi I and II each with pair of pas, tarsi III and IV with single-sided pas (species with one ventral seta) or pair of pas (species without ventral seta), in the latter case on tarsus III generally a slender and a flattened seta; on tarsus IV pas the same as on tarsus III or both flattened. Tarsi end with paired claws and a distinctly smaller median claw.

Deutonymph — Genital plate with two pairs of internal acetabula and two pairs of pgs (Figure 3H).

Plegadognathus Morselli, 1981

Type species — *Plegadognathus labronicus* Morselli, 1981

Idiosoma — AD, OC and PD with raised areolae which include cup-like foveae or alveoli, remainder of plates coarsely pitted, foveate or reticulate. AD and OC with pair of gland pores, PD with (zero? or) one pair of gland pores near posterior margin; pores not on cones. Dorsum with pairs of ds-1 to ds-6. AE with epimeral pores and three pairs of setae, pair of PE each with one dorsal and three ventral setae. GA of female with three (rarely four) pairs of pgs, genital sclerites with two pairs of sgs, rarely a single pair, GO with two pairs of internal acetabula (Figure 3F). Male GA with numerous pgs, genital sclerites with five, rarely four pairs of sgs.

Gnathosoma — Slightly longer than wide. Rostrum triangular. Basal pair of maxillary setae on gnathosomal base, following pair on rostrum. Palps four-segmented, laterally attached. P-2 with one dorsal seta, P-4 with two (?) or three setae in basal whorl; no seta on P-3.

Legs — Slender. Genua distinctly shorter than adjacent segments. Basifemora I to IV with 2, 2, 2, 2 setae, telofemora with 3-4, 3, 2, 2 and genua with 3(-4), 3(-4), 3, 3 setae. Tibia I to IV with 7, 6, 5, 5 setae, of these 4, 3, 2, 2 ventral in position. Solenidion on tarsus I dorsolateral, on tarsus II dorsomedial in position. Tarsus I to IV with 2-3, 0, 0, 0 ventral setae. Tarsi end with paired parambulacral setae, paired claws and a distinctly smaller median claw.

Deutonymph — Genital plate with two pairs of pgs and two pairs of internal acetabula.

Winlundia Newell, 1984

Type species — *Winlundia filistoma* Newell, 1984

Idiosoma — Dorsum with three pairs of gland pores, one on AD, OC and PD, and (five? to) six pairs of dorsal setae. Gland pores not on cones. AE with epimeral pores and three pairs of ventral setae, pair of PE each with one dorsal and three ventral setae. Female GA with three pairs of pgs and each genital sclerite with two sgs. Male genital sclerites with three to five pairs of sgs; GO with two pairs of internal acetabula (Figure 1E).

Gnathosoma — Slender, with long, narrow rostrum. Basal pair of maxillary setae on gnathosomal base. Palps four-segmented, laterally attached. P-2 with one dorsal seta, P-4 with three setae in basal whorl; no seta on P-3.

Legs — Genua shorter than telofemora and tibiae. Basifemora I to IV with 2, 2, 2, 2 setae, telofemora with 4-5, 3-5, 2, 2-3 (in *W. filistoma* 4, 3, 2, 2, in *W. furcata* 5, 5, 2, 3) and genua with 3, 3, 3, 3 setae. Tibiae I to IV with 7, 6, 5, 5 setae, of these 4, 3, 2, 2 in ventral position. Tarsi I and II with dorsolateral and dorsomedial solenidion, respectively. Tarsus I with two ventral setae, a basal slender one ventromedial in position and an apical eupathid one ventrolateral in position; tarsi II to IV lack ventral setae.

Deutonymph — Genital plate of *W. filistoma* with two pairs of pgs and two pairs of internal acetabula.

Distribution and Biology

Records of *Arhodeoporus*, *Camactognathus*, *Maracarus*, *Plegadognathus*, and *Winlundia* (Table 2) are plotted on a map (Figure 4). The genera are wide-spread in tropical and warm-temperate, but rare in cold-temperate and lacking in polar waters. The absence or low numbers of records may partly be due to the restricted collecting activities in these regions, e.g. in the southern Atlantic, but at least along the northern cold-temperate Atlantic and Pacific coast, the halacarid fauna has been studied intensely. About 50 species are recorded from the north-western Pacific, from Hokkaido and northern part of the Sea of Japan to the Bering Strait (Sokolov 1952; Makarova 1972a, b, 1974, 1977, 1978; Abé

TABLE 2: *Arhodeoporus*, *Camactognathus*, *Maracarus*, *Plegadognathus*, and *Winlundia* species, with notes on distribution and habitat.

SPECIES	DISTRIBUTION	HABITATS AND COMMENTS	REFERENCES
Arhodeoporus arenarius Newell, 1947	**Northwestern Atlantic**: United States (Massachusetts, Rhode Island, Connecticut, Maryland, North Carolina, South Carolina)	Lower tidal to subtidal; various substrata, sediment, broken shell, hydrozoa, sponges, algae	Newell 1947; Bartsch 1982a
Arhodeoporus submarinus Newell, 1947	**Northwestern Atlantic**: United States (Rhode Island)	Tidal and subtidal (0–34 m) sediment and small algae	Newell 1947; Bartsch 1982a
Camactognathus borealis Bartsch, 1991	**Northeastern Atlantic**, North Sea, Skagerrak: off Sweden	Subtidal sediment	Bartsch 1991a
Camactognathus grossipes Newell, 1984	**Southeastern Pacific**: Chile (Punta Arenas, Punta Caldera)	Tidal and subtidal; coarse sand, kelp holdfasts	Newell 1984
Camactognathus tesselatus (Morselli and Mari, 1982)	**Mediterranean** and **Black Sea**: Italy (Leghorn coast) and Turkey (off Sinop)	Shallow water sediment	Morselli and Mari 1982; Bartsch 2013
Maracarus brevocularis (Bartsch, 1973)	**Northeastern Atlantic**: Josephine Seamount	Surface sediment in 206 m depth	Bartsch 1973b
Maracarus caudatus (Otto, 2000)	**Western Pacific**: northeastern Australia, Queensland (Great Barrier Reef)	Lower tidal and subtidal sediment, 0–10 m	Otto 2000a
Maracarus clypeatus (Otto, 2000)	**Western Pacific**: northeastern Australia, Queensland (Great Barrier Reef)	Coarse subtidal sediment, 3–7 m	Otto 2000a
Maracarus corallicolus (Otto, 2000)	**Western Pacific**: northeastern Australia, Queensland (Great Barrier Reef). Indian Ocean, northwestern Australia (Dampier)	Coarse subtidal sediment (2–13 m)	Otto 2000a
Maracarus eclogarius (André, 1959)	**Red Sea:** Gulf of Suez	Amongst sponges	André 1959
Maracarus gracilipes (Trouessart, 1889)	**Northeastern Atlantic Ocean**, English Channel, North Sea, Skagerrak, Öresund, Norwegian Basin: Açores (unpublished record, coll H. Kunz), Senegal (Dakar), Spain, France, Eire, United Kingdom, Germany, Denmark, Sweden, Norway (Bergen, Tromsö); **Mediterranean** and **Black Sea**: France, Italy, Croatia, Bulgaria, Crimea, Russia	Amongst sediment and various algal substrata, from low water edge to at least 42 m depth.The records from 318 m (Açores) and 1410 m (Golfe de Gascogne) (Trouessart 1896; André 1946) are in need of verification, the records may refer to one of the subspecies which proved to be representatives of the genus *Copidognathus*	Viets 1956; Bartsch 1985, 2004, 2009a; Riesgo *et al.* 2010)
Maracarus kunzi (Bartsch, 1987)	**Western Indian Ocean**: South Africa (East London)	Amongst shell fragments	Bartsch 1987
Maracarus leptopus (Bartsch, 1997)	**Eastern Indian Ocean**: southwestern Australia (Rottnest Island off Perth)	Algae, sponges and corals. Subtidal (30 m)	Bartsch 1997b
Maracarus lineatus (Bartsch, 1973)	**Northeastern Atlantic**: Great Meteor Seamount	Upper sediment layers, 295–488 m depth	Bartsch 1973b
Maracarus lizardensis (Otto, 2000)	**Southwestern Pacific**: northeastern Australia, Queensland (Great Barrier Reef)	Tidal sand	Otto 2000a
Maracarus longicrus (Otto, 2000)	**Southwestern Pacific**: northeastern Australia, Queensland (Great Barrier Reef)	Fine to medium subtidal sand from 51 m depth	Otto 2000a
Maracarus longirostris (Bartsch, 1981)	**Western Indian Ocean**: Mozambique Channel	Littoral and bathyal, 26–440 m	Bartsch 1981, 1982b
Maracarus mactanus (Bartsch, 1991)	**South China Sea**: Philippines (Mactan Island)	Inter- and subtidal sediment (0–15 m) with epiflora and fauna	Bartsch 1991c
Maracarus mammilifer (Newell, 1971)	**Southeastern Pacific Ocean**: off Chile, ca 26°S, 80°W	From 160–170 m	Newell 1971
Maracarus minor (Bartsch, 1977)	**Northeastern Atlantic Ocean**, English Channel, Irish Sea, North Sea: France, Eire, United Kingdom;**Mediterranean**: France (off Marseille, new record, coll. C. Poizat), Spain (off Alicante, new record, coll. T. Wittling)	Tidal to subtidal (0–56 m). Various sandy shallow water substrata	Bartsch 1977a; Green and MacQuitty 1987
Maracarus minusculus (Bartsch, 1991)	**South China Sea**: southern China (Hong Kong)	Sandy beach, from coarse sediment and hapteres	Bartsch 1991d
Maracarus mirabilis (Bartsch, 1983)	**Caribbean Sea**: Gulf of Honduras, Belize	Subtidal (15 m)	Bartsch 1983a
Maracarus mooreus (Bartsch, 1992)	**Pacific**: Society Islands (Moorea)	Coral rubble in shallow subtidal zone	Bartsch 1992
Maracarus nanus (Bartsch, 2009)	**South China Sea**: Singapore	Amongst unsorted sediment, low water edge	Bartsch 2009b
Maracarus perlucidus (Bartsch, 1983)	**Northwestern Atlantic** and **Caribbean Sea**: Bermuda Islands and off Panama	Shallow subtidal, 1–2 m	Bartsch 1983a
Maracarus psammophilus (Bartsch, 1993)	**Eastern Indian Ocean**: western Australia (Rottnest Island off Perth, Esperance)	Tidal and shallow subtidal (0–8 m), coarse sedimen	Bartsch 1993a, 2007b
Maracarus subtilis (Otto, 2000)	**Southwestern Pacific**: northeastern Australia, Queensland (Great Barrier Reef)	Subtidal, 3–15 m, sand and rubble	Otto 2000a
Maracarus tanzanicus (Chatterjee, Pešić and De Troch, 2008)	**Western Indian Ocean**: east coast of Zanzibar	Amongst coral rubble; subtidal, 0.5 m	Chatterjee *et al.* 2008
Plegadognathus bonairensis (Viets, 1936)	**Caribbean area and western Atlantic** Bonaire and Florida;**Pacific**: Hawaian Islands (Oahu, Kauai), Galapagos Islands (Santa Cruz), Australia, Queensland (Great Barrier Reef and off Brisbane);**South China Sea**: Hong Kong, Philippines (Mactan Island), Singapore; **Indian Ocean**: northwestern Australia (Dampier);**Bay of Bengal**: Andaman and Nicobar Islands;**Arabian Sea**: Kerala coast, Goa	Low water edge and subtidal; sandy deposits, coral rubble, amongst corallines and hapteres	Viets 1936; Newell 1947; Bartsch 1977b, 2009b; Sarma and Chatterjee 1993; Otto 2000a
Plegadognathus bucculentus (Bartsch, 1977)	**Eastern Pacific**: Galapagos Islands (Santa Cruz)	Tidal and subtidal sediment	Bartsch 1977b
Plegadognathus disparilis (Bartsch, 1997)	**Eastern Indian Ocean**: southwestern Australia (Rottnest Island off Perth)	Lower tidal algae (corallines)	Bartsch 1997b
Plegadognathus labronicus Morselli, 1981	**Mediterranean**: Italy (Tuscany Coast)	Coarse sand, 8–10 m	Morselli 1981
Plegadognathus robustus (Bartsch, 2007)	**Eastern Indian Ocean**: southwestern Australia (Esperance)	Tufts of algae at low tide mark	Bartsch 2007b
Plegadognathus thyreophorus (André, 1959)	**Red Sea**: Gulf of Suez	Subtidal	André 1959
Plegadognathus wadjemupis (Bartsch, 1997)	**Eastern Indian Ocean**: southwestern Australia (Rottnest Island off Perth)	Coarse subtidal sediment	Bartsch 1997b
Winlundia filistoma Newell, 1984	**Southeastern Pacific**: Chile (Arica, Punta Caldera, Valparaiso, Punta Arenas)	Tidal; coarse sand, shell debris, worm tubes, kelp holdfasts	Newell 1984
Winlundia forcipata Newell, 1984	**Southeastern Pacific**: Peru (Lima)	Tidal; coarse sand	Newell 1984

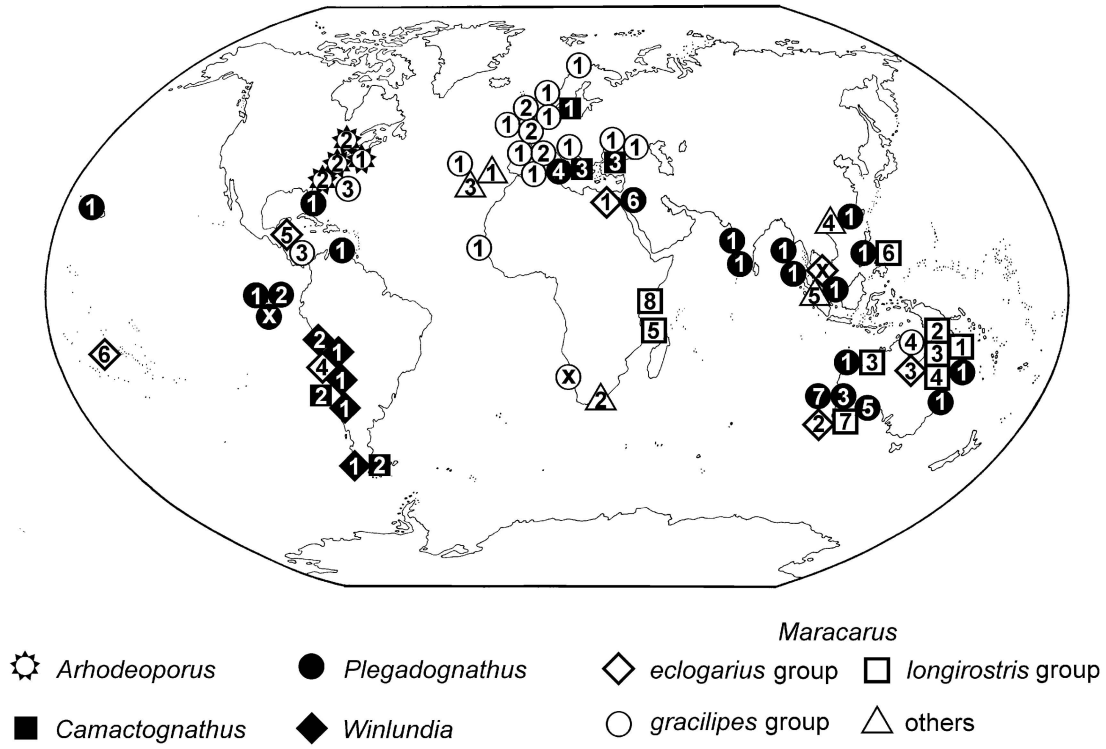

FIGURE 4: Geographical distribution of the genera *Arhodeoporus* s.str., *Camactognathus*, *Plegadognathus*, *Winlundia*, and *Maracarus* n. gen., the latter with the natural groups *eclogarius* (diamond), *gracilipes* (circle), *longirostris* (quadrat) and five species not belonging to any of these groups (triangle); *Arhodeoporus*: 1, *arenarius*; 2, *submarinus*. *Camactognathus*: 1, *borealis*; 2, *grossipes*; 3, *tesselatus*. *Plegadognathus*: 1, *bonairensis*; 2, *bucculentus*; 3, *disparilis*; 4, *labronicus*; 5, *robustus*; 6, *thyreophorus*; 7, *wadjemupis*, x, spec. *Maracarus eclogarius* group (diamond): 1, *eclogarius*; 2, *leptopus*; 3, *longicrus*; 4, *mammillifer*; 5, *mirabilis*; 6, *mooreus*; x - spec. *M. gracilipes* group (circle): 1, *gracilipes*; 2, *minor*; 3, *perlucidus*; 4, *subtilis*; x, spec. *M. longirostris* group (quadrat): 1, *caudatus*; 2, *clypeatus*; 3, *corallicolus*; 4, *lizardensis*; 5, *longirostris*; 6, *mactanus*; 7, *psammophilus*; 8, *tanzanicus*. *Maracarus*, others (triangle): 1, *brevocularis*; 2, *kunzi*; 3, *lineatus*; 4, *minusculus*; 5, *nanus*.

1990a, b, 1991, 1996, 1997, 1998; Tuzovski 2010), almost the same number is mentioned from the eastern part, along the coast of North America to Oregon (Newell 1949, 1950, 1951a, b, c; Viets 1951; Krantz 1973, 1976; Chatterjee *et al.* 2011), but there is not a single record of one of the above diagnosed genera. The cold-temperate European Atlantic, from the English Channel, along the southern coast of Iceland to the White Sea, holds about 80 shallow water halacarid species (Viets 1927, 1928; Motas 1961; Green and MacQuitty 1987; Bartsch 1979, 1991a), just two of them belong to *Maracarus* and one to *Camactognathus*. The most northerly record of *Maracarus gracilipes* is from northern Norway, from Tromsö (Bartsch and Schmidt 1979) which is under the influence of the warm water Gulf Stream. The knowledge of the fauna along the American Atlantic coast is more meagre. A list of species from Massachusetts (Cap Cod) to the eastern edge of New Foundland includes 21 halacarid species but just one *Arhodeoporus* (Newell 1947; Bartsch 1982a, 1997a). From Massachusetts to South Carolina two *Arhodeoporus* species are listed. A record of *Maracarus gracilipes* from Nova Scotia (Anderson 1933) is excluded, it is in need of verification.

Arhodeoporus, with just two species, is according to present records restricted to north-eastern North America. *Plegadognathus* has records from tropical and warm-temperate waters, there are no from cold-temperate coastlines. Seven species are described but *P. thyreophorus* is expected to be a junior synonym of *P. bonairensis*. The latter species is

spread in tropical waters, in the the Caribbean Sea, the Pacific and Indian Ocean. The wide geographical distribution raises the question: is it just one or several cryptic species? More studies are necessary. An unnamed species, found on the Galapagos Island, Santa Cruz, Bahia Academy, rockpool, is the male by Bartsch (1977b: 60-61, figs 234, 235, 237, 241) erroneously identified as '*Arhodeoporus bonairensis*'. In the meantime, males of *P. bonairensis* have been found and described (Sarma and Chatterjee 1993; Bartsch 2009b) and it is proven, there is no sexual dimorphism in the ornamentation of the dorsal and ventral plates. *Camactognathus* is known from both the south-eastern Pacific and the north-eastern Atlantic and the adjacent Mediterranean and Black Sea. The genus *Maracarus* is most rich in species; 18 of the 23 presently described taxa can be attributed to one of the species groups *eclogarius*, *gracilipes* or *longirostris*. Records of the six species of the *eclogarius* group are at present restricted to the tropical and warm-temperate Pacific and Indian Ocean (Gulf of Suez). Included in Figure 4 is an undescribed record from the South China Sea, Peninsula Malaysia (off Mersing, coral rubble, 1 – 3 m; 12-17 April 1991, coll. H.G. Müller). Most wide-spread is the *gracilipes* group. Of the four species described, three have records from the North Atlantic, one from the West Pacific. A larva of *Copidognathus* sensu Viets, mentioned from southern Africa, Lüderitz Bay (Bartsch 1972), is a *Maracarus* species. Characters of that larva are: AD with pair of circular, raised areolae, PD with pair of porose costae, remainder of plates coarsely reticulated; dorsum with four pairs of glands which open via narrow canals on small domes. Tarsi I to III with 4/3, 4/1, 4/0 dorsal/ventral setae (solenidia included); solenidion on tarsus II dorsomedial in position; claws with pectines. The larva is most similar to the *gracilipes* group. The *M. longirostris* group includes eight species, they are concentrated within the Indo-West Pacific region. At present there are no records from other parts of the world. Most descriptions of the species are based on rather few individuals, characters may vary (e.g. the punctation of the plates, from coarse to delicate with intermediate stages) or be differently interpreted (e.g. the hyaline, ovate spot posterior to the distinct sperical lens (Figure 3I), can it be called a cornea or not?, or the slightly thickened basal seta on tibia I, is it pectinate or not?). The one or other species may turn out to be an ecovariant.

Most of the species mentioned above have been taken in shallow water, from near the low water edge to a depth of almost 500 m. The abyssal record listed by Trouessart (1896), namely *Halacarus gracilipes quadricostatus*, is no variety or subspecies but belongs to *Copidognathus* (cf. Bartsch 1991b). Still there is no reason to expect that the four above mentioned genera are restricted to the continental shelf and upper bathyal. A species of *Arhodeoporus* s.l. recorded from the Mozambique Channel, from 700 m (Bartsch 1982b), can be ignored, it was a decaying protonymph which most likely had been washed into this depth.

According to present records, the majority of *Arhodeoporus*, *Camactognathus* and *Maracarus* species live within sandy deposits, in surface and sub-surface layers, an exception, species of the *eclogarius* group are expected to be epibenthic. *Plegadognathus* is found amongst surface deposits, sand and pebbles on the ground or an epifauna (sponges, hydrozoans, bryozoans) and -flora (corallines).

Psammophilous halacarids are known to bear suctorians, examples of infested genera are *Actacarus*, *Halacarellus*, *Copidognathus* (Abé 1997; Bartsch 1998, 2003c) and consequently, it is not surprising that suctorians have been found on *Maracarus*. Figure 3J shows the gnathosoma of *M. corallicolus* Otto, 2000 with eight suctorians (*Praethecacineta* sp.) attached to it, another three suctorians were found on each of the two telofemora I. The thecae of the suctorians are 40 – 48 μm long, 21 – 26 μm wide, their stalks 27 μm long. The mite is from medium coarse, shallow water sediment.

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