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I. Bartsch. The Agauopsis brevipalpus group (Acari: Halacaridae), descriptions of tropical Indo-West Pacific species, a key to all species, their geographical distribution and reflections on dispersal routes. Acarologia, 2015, 55 (2), pp.147-169. 10.1051/acarologia/20152158. hal-01548360

## HAL Id: hal-01548360 https://hal.science/hal-01548360

Submitted on 27 Jun 2017  $\,$ 

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The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d'avenir » programme (Labex Agro: ANR-10-LABX-0001-01)



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### The Agauopsis brevipalpus group (Acari: Halacaridae), descriptions of tropical Indo-West Pacific species, a key to all species, their geographical distribution and reflections on dispersal routes

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(Received 21 October 2014; accepted 03 February 2015; published online 30 June 2015)

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ABSTRACT — Amongst the genus *Agauopsis*, the *brevipalpus* group is the one most rich in species. The group can roughly be subdivided on the basis of the number of spines on telofemur I. The tropical and warm-temperate Indo-West Pacific region is dominated by species with four spines. A new species from this region, *Agauopsis dissimilis* **n.sp.**, is described, the characters of another seven species are outlined and a summary of the knowledge of the *Agauopsis* fauna of Singapore added. The *brevipalpus* group now includes 25 described species. A key and the geographical distribution are given. Species with three spines are spread in the temperate zones of the Pacific, in areas which formerly were part of the shoreline of Panthalassa. Species with four spines are most abundant in the tropical and warm-temperate Indo-West Pacific region and the North Atlantic; present-day records of this species group are primarily from areas once bordering the Tethys.

KEYWORDS — Halacaroidea; Agauopsis brevipalpus group; key; distribution; new species; Tethys; Panthalassa; Singapore

#### INTRODUCTION

The family Halacaridae includes more than 1120 species (Bartsch 2009, 2014). *Copidognathus* is the genus most abundant, holding 32% of all species, followed by *Rhombognathus* (9%) and *Agauopsis* (8%). Characters of the genus *Agauopsis* are: id-iosoma usually flattened and heavily armoured, its anterior and posterior dorsal plates often with slightly raised longitudinal costae, dorsum with small gland pores and three to six pairs of idiosomatic setae; female genitoanal plate with (two to) three pairs of perigenital setae, genital sclerites with 20-100 perigenital setae, often one pair of setae out-

lying, each genital sclerite with three to five subgenital setae; gnathosoma longer than wide; its base subquadrangular; rostrum almost parallel-sided; first (basal) pair of maxillary setae on gnathosomal base, near rostrum; second pair in distal third of rostrum, palps cylindrical, four-segmented, attached laterally, second segment with a dorsal seta in apical part, short third segment with medial bristle- or spiniform seta and fourth segment with one to three setae in basal whorl. Genua of all legs shorter than adjoining segments, leg I wider and longer than following legs and armoured with conspicuous ventral spines, viz. one to five on telofemur, two small ones (may be bristle-like) on genu, three to five on tibia, and one on tarsus, spines generally blunt and

delicately dentate, tibiae II to IV with two to three ventral spines or bristles, solenidion on tarsus I in dorsolateral, that on tarsus II in dorsomedial position; paired claws of tarsus I shorter than those of following tarsi, median claw small.

*Agauopsis* species run through one larval and two nymphal stages until the adults mould. The species are predatory, capturing and holding the prey between the femoral, genual and tibial crook and the spines of the first leg (Krantz 1970; Mac-Quitty 1984). In laboratory studies copepods, ostracods and halacarids have been accepted as prey (Krantz 1970; MacQuitty 1984). The genus is spread world-wide.

The majority of the *Agauopsis* species can be attributed to natural groups (Bartsch 1986a). Most rich in species is the *brevipalpus* group (Bartsch 2003). Representatives of the group live in tropical and warm temperate but not in polar waters. The number of dentate spines on telofemur I is a character easily recognized and used for further division of the *brevipalpus* group. Most abundant is the presence of four spines.

The paper presents a description of a new species with four spines on leg I and a short outline of another seven species known from the tropical Indo-West Pacific region, between about 28° north and south, moreover a key to all named species of the *brevipalpus* group and a map of their geographical distribution. The distribution of the sub-groups of the *brevipalpus* group is discussed.

#### MATERIALS AND METHODS

The short descriptions of the species are prepared on the basis of published data, examination of microscopical slides and new material collected on the shores of Singapore. To each of the species the publication with the original description is mentioned, as well as papers which add morphological data. Material from Singapore described in this paper was collected by the author. The illustrations were done with a drawing tube. In the descriptions, the position of a seta is given in a decimal system, with reference to the length of a given structure from its anterior to posterior or basal to apical margin. The position of the gland pore on the ocular plate refers to the length along the lateral margin. The length of a leg segment is that along the dorsal margin. Rarely occurring variants are in parentheses. The legs, their segments and claws are numbered I to IV, from anterior to posterior. The leg segments are trochanter, basifemur, telofemur, genu, tibia, and tarsus.

Abbreviations of depositories: ZMH, Zoologisches Museum, Universität Hamburg; ZRC.ARA., Arachnid Collection of the Zoological Reference Collection in The Lee Kong Chian Natural History Museum (The Raffles Museum of Biodiversiy Research); IB, the author's halacarid collection. The holotype and voucher specimens of species collected in Singapore are deposited in the ZRC.ARA., additional specimens in IB.

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

#### TROPICAL INDO-WEST PACIFIC Agauopsis SPECIES WITH FOUR SPINES ON TELOFEMUR I

With the new species described in this paper included, 89 named species belong to the genus *Agauopsis* (Chatterjee *et al.* 2009; Bartsch 2009a, b, 2015, this paper). Most of the species can be attributed to natural groups (Bartsch 1986a). The *brevipalpus* group is the one most rich in species (Bartsch 2003). The species of this group are characterized by a combination of: (1) plates AD and PD and pair of OC with coarse porosity, AD often with H-shaped, PD with one or two pairs of longitudinal costae; (2) ventral plates almost uniformly porose; (3) third palpal segment with blunt, denticulate medial spine; (4) fourth palpal segment with two setae in a basal whorl, rarely one seta; (5) telofemur I with one to three ventral and zero to two ventromedial bluntly ending dentate spines; (6) tibia I ventrally with three wide, dentate spines and one slender seta; (7) tarsus I with dentate ventromedial spine and pair of slender apical eupathidia; following tarsi without ventral setae; (8) tibia II with one wide bipectinate seta in ventromedial position and two, rarely one, spiniform, dentate setae in ventral position; tibiae III and IV with two, rarely three, either spiniform and dentate or slender and tapering setae; (9) tarsi III and IV with three dorsal setae each; (10) tip of tarsus II medially with spurlike pas, laterally with one or two setae; (11) tip of tarsus III and IV with spur-like lateral but no medial pas. In general, the integument of idiosoma, gnathosoma and legs is slightly brown in colour; on the dorsum there are three dark-brown eye spots. Twenty-five named species are known (the species described below included).

The number of dentate spines on telofemur I is a character easily recognized and is used for further division of the *brevipalpus* group. The number of spines lies between one and five. Anomalies, with differing numbers, are found but are rare (Bartsch 2003, 2015) and in general restricted to one side. Most abundant is the presence of four spines.

Eight species of this brevipalpus sub-group are at present known from the tropical Indo-West Pacific region, from between about 28° north and south. Morphological characters used for discrimination are the shape and size relationship of the dorsal and ventral plates, details in the ornamentation of these plates and position of setae and gland pores, the length of gnathosoma, rostrum and palps, the length:height ratio of palps (or length:width, the segments are almost cylindrical and the data similar), the number and arrangement of setae on P-4, the ornamentation of the leg segments, the shape of telofemora III and IV, and the pectines of the claws. Females and males differ in the genital area, its size and setation, ovipositor and spermatopositor but often also in the shape of the PD, which in turn will influence the length ratio and decimal notation of setae. Also the mounting of a threedimensional mite will have an influence on the results of length:width ratios and decimal notations, recently hatched individuals, with a still soft integument, are more easily compressed and distorted than old ones, females often have a more dilated striated integument than males.

The morphological differences between the eight tropical Indo-West Pacific species are often small and the range of variability of character states not known, neither the impact of external physical, chemical or biological parameters on the external morphology. A possible hybridization between related species and the effect on the morphology has never been studied. Consequently, the differences described below may prove to be inappropriate for separation of species. Data from forthcoming techniques may change the status of the one or other species.

#### Agauopsis arabia Bartsch and Chatterjee, 2001 Figure 1A-E

*Agauopsis arabia* Bartsch and Chatterjee 2001: 322-326, fig. 1-12.

Additional material examined — Two females, Bay of Bengal, Andaman Islands (by T. Chatterjee forwarded to the author for identification; cf. Chatterjee *et al.*, 2004).

Short description — Length of female 450 – 490 μm, of male 416 μm (according to Chatterjee et al., 2004, female 450 – 500 μm, male 410 – 450 μm). Dorsal plates with costae. Surface of costae not reticulated but canaliculi arranged in groups. Integument between costae with epicuticular droplets forming a reticulum; canaliculi within reticulum (polygons) more delicate than within costae. AD slightly more than 1.2 times longer than wide. Transverse costa on AD at about 0.5 and more narrow than longitudinal costae, middle part slightly curved posteriad (Figure 1A). Pair of ds-1 level with gland pores. OC 1.4 times longer than wide; glp on OC removed from posterior cornea, situated about halfway between that cornea and pc (Figure 1B) or at 0.4 along lateral margin of OC. PD of female and male almost equal-shaped, 1.2-1.3 times longer than wide. Medial costae on PD rather narrow, width in middle part of plate equalling three groups with canaliculi, else costae two groups wide. Pair of ds-4 level with



FIGURE 1: Agauopsis arabia Bartsch and Chatterjee, 2001: A – idiosoma, dorsal, female; B – lateral margin of OC, male; C – gnathosomal base, dorsal, female; D – gnathosoma, lateral, female; E – tip of tarsus IV, ventral, female. (glp, gland pore; pa, porose areola; pc, pore canaliculus; T, tectum) Scale line = 50 μm.

or immediately posterior to edge of OC; pair of ds-5 in anterior half of PD, outside costae, pair of ds-6 on PD.

Ventral plates faintly reticulated, with rather evenly spread canaliculi within each polygon, mostly with (6-)11-17(-18) canaliculi per polygon. Anterior margin of female GA truncate, that of male slightly convex. Male with 36-39 pgs around GO and pair of outlying setae. That pair of setae about halfway between ring of pgs and lateral margin of GA. Interval between anterior margin of each GA and GO equalling about length of GO. Spermatopositor large, 0.7 of length of GA and extending to anterior margin of that plate.

Length of gnathosoma 2.1-2.2 times its width. Rostrum somewhat longer (1.1-1.2 times) than gnathosomal base. P-2 2.7-2.9 times longer than high (Figure 1D). P-4 twice as long as P-3, its two basal setae almost equal in length. Tectum with scaliform lamella (Figure 1C).

Tibia II ventrally with one bipectinate and two dentate, spiniform setae. Tibiae III and IV with two dentate, spiniform setae. Telofemora III and IV 2.0-2.2 times longer than high. Ventral seta on telofemora III and IV in apical half. Tarsi III and IV with short lateral fossa membranes. Claws II to IV each with minute accessory process and pectines with delicate tines (Figure 1E).

Remarks — The rostrum of *Agauopsis arabia* is slightly longer than the gnathosomal base whereas in most of the species mentioned from the tropical Indo-West Pacific the rostrum is shorter than the base, exceptions are *A. longirostris* Bartsch, 2015 and *A. moorea* Bartsch, 1992. The rostrum of *A. longirostris* is distinctly longer (1.7-1.8 times) than the basis, that of *A. moorea* 1.0-1.1 times longer. Differences between *A. arabia* and *A. moorea* are in the position of the gland pore on the OC, in the anterior (*A. arabia*) and posterior half (*A. moorea*); furthermore, males of *A. moorea* have a small spermatopositor which does not extend to the anterior margin of the GA.

Distribution and Biology — Arabian Sea (Goa, Kerala), Bay of Bengal (Andrah Pradesh, Andaman Islands) (Bartsch and Chatterjee 2001; Chatterjee *et al.* 2004; Chatterjee and Guru 2011). Most records are from tidal algae.

#### Agauopsis arborea Bartsch, 2003

*Agauopsis arborea* Bartsch 2003: 242-247, figs 1A-K, 2A-K.

*Agauopsis arborea,* Bartsch 2005: fig. 8B; 2015: fig. 6A-P.

Short description — Length of female 415 - 434  $\mu m$ , of male 392 – 395  $\mu m$ . Integument of both costae and areas outside costae panelled. Polygons within medial costae of PD mostly with about 10-12 canaliculi, polygons between costae with five to eight canaliculi. Medial costae on PD approximately three porose panels wide. AD about as long as wide (1.0-1.1 times). Posterior margin of AD slightly concave. Transverse bar of H-shaped costa at 0.5-0.6; pair of ds-1 slightly posterior to the level of glp-1. OC elongate, 1.5 times longer than wide, and extending posteriad to or beyond the level of ds-4. Distance between glp and posterior cornea almost the same as that between glp and pc; glp at 0.4-0.5. In female PD 1.2 times longer than wide, anterior margin somewhat protruding (six females examined) and slightly extending anteriad beyond level of ds-4. In male PD longer, 1.4 times longer than wide, its anterior margin ovate. Pair of ds-5 in lateral margin of medial costae, at about 0.5 relative to length of PD, in both female and male.

Ventral plates evenly reticulated, each polygon with about 8-16 canaliculi; canaliculi mainly arranged along periphery of polygons. Female GA about as long as wide and as long as AE; anterior margin of GA wide and truncate. Length of GO 0.6 times that of GA. Male GA longer than AE and about as long as wide, anterior margin slightly arched; 43-49 pgs arranged around GO, 14-18 setae in an inner ring, 29-31 setae in an outer ring and two setae outlying. That pair removed from margins of plate. Distance from anterior margin of GO to that of GA somewhat less than length of GO. Spermatopositor extending to anterior margin of GA, its length 0.6 times that of GA.

Gnathosoma 1.7 times longer than wide. Tectum with short truncate lamella. Rostrum shorter (0.8 times) than gnathosomal base. P-2 cylindrical, 2.7 times longer than high. P-4 short, its length (without apical spurs) 0.4 times that of P-2; with one long and one short seta in basal third.

Telofemur, genu, tibia, and tarsus I ventrally with 4, 2, 3, 1 dentate, bluntly ending spines, respectively. Ventromedial spine on genu I longer than ventral one. Tibia II with wide bipectinate ventromedial seta and one to two ventral setae. Tibiae III and IV with pair of smooth tapering setae, length of setae same as height of tibiae. Telofemora III and IV 2.2-2.3 times longer than high. Tarsi III and IV without fossa membranes. Claws on tarsus II with line of minute tines along outer lateral and inner medial flank of claw arc. Claws III and IV with accessory process and a few very small tines (< 1µm).

Variants — In general telofemur I bears four ventral spines but specimens have been found which have five or three spines on one of the legs (Bartsch 2015). Tibia I of species of the *brevipalpus* group bears three spiniform ventral setae, amongst the material from the type locality one female had four spines (Bartsch 2003). Amongst 16 adults studied, 10 had three ventral setae on both tibiae II, three a combination of three and two setae and another three only two setae on both tibiae (Bartsch 2003, 2015).

Remarks — The most marked character of *Agauopsis arborea* is the pair of tapering ventral setae on tibiae III and IV, a character shared with *A. dissimilis* **n.sp.** (description below), but in contrast to the latter species, the rostrum of *A. arborea* is shorter and the P-4 bear two setae instead of a single seta.

Distribution and Biology — Dampier, Western Australia, and Singapore. All present records are from algal turf of red, brown and green algae (*Bostrychia*, *Caloglossa*, *Chaetomorpha*) growing in mangroves on trunks and pneumatophores (Bartsch 2003, 2015).

#### *Agauopsis dissimilis* n.sp. Figures 2A-J, 3A-I

Material examined — Holotype female (ZRC.ARA.1381), Singapore, Pulau Ubin, Chek Jawa, 1°24'N, 103°59'E, green algae (Cladophorales) on trunk of *Rhizophora* sp., 16 Oct. 2012. One male (ZRC.ARA.1382), one female (IB), Singapore, East Coast Park, 1°18'N, 103°55'E, green algae on stone packing, 06 Oct. 2004.



FIGURE 2: Agauopsis dissimilis n.sp.: A – median part of PD level with ds-5, female; B – idiosoma, dorsal, female; C – idiosoma, ventral, female; D – gnathosoma, ventral, female; E – lateral margin of OC, female; F – gnathosomal base, dorsal, female; G – palp, lateral, female; H – AD, OC and PD, dorsal, male; I – idiosoma, ventral, male; J – genitoanal plate, male. (ds-5, fifth dorsal seta; glp, gland pore; L-Ba, length of gnathosomal base; L-Ro, length of rostrum; pa, porose areola; pc, pore canaliculus) Scale line = 50 µm

Diagnosis — Length of female 414 and 445  $\mu$ m, of male 420 µm. AD with H-like costae; PD with two pairs of costae. Costae reticulated. Female PD almost as long as wide, male PD slightly longer than wide. Female and male PD about 1.3 times longer than AD. Anterior margin of female and male GA truncate. Male GA with 63 pgs; spermatopositor extending to anterior margin of GA. Length of gnathosoma about twice its width and 0.4 times the length of idiosoma. Length of rostrum almost same as that of gnathosomal base. Tectum with scaliform lamella. P-2 3.2-3.3 times longer than high. P-4 short, with single seta. Telofemur to tarsus I with 4, 2, 3, 1 blunt, denticulate spines. Tibia II with flattened, bipectinate ventromedial and spiniform, dentate ventral setae; tibiae III and IV with pair of slender, tapering setae. Claws II to IV with numerous delicate tines along medial flank.

Etymology — In its general shape this species is similar to other species of the *brevipalpus* group but differs in the character combination, hence the name derived from the Latin *dissimilis*, unlike, different.

Description — Females. Length 414 and 445 µm; holotype 414 µm long, 300 µm wide. Dorsal plates with costae, H-shaped on AD, oblique on OC and longitudinal on PD (Figure 2B). Costae with deep canaliculi, 6-10 arranged in polygons. Remainder of plates panelled, each polygon with about four to six delicate canaliculi (Figure 2A). AD slightly wider than long, length 148  $\mu\mathrm{m}$  , width 151  $\mu\mathrm{m}$  ; transverse bar of H-shaped costa closer to anterior than to posterior margin of AD. Pair of gland pores level with anterior end of costae. OC 95 µm long, 78 µm wide, length 0.6 times that of AD. OC with two corneae, glp and pc; glp at 0.4; distance between posterior cornea, glp and pc almost the same (Figure 2E). PD 198 µm long, 196 µm wide, with widely arched anterior margin. PD with two pairs of costae; medial costae about three polygons wide, lateral costae two to three polygons. Pair of ds-1 on AD medial to gland pores (left seta vestigial in holotype), ds-2 to ds-4 on minute sclerites within striated integument, ds-5 on PD, within lateral margin of medial porose costae and at 0.4 relative to length of PD. Pair of ds-6 in posterior margin of PD.

Ventral plates reticulated, with 9-11 peripherically arranged canaliculi within each polygon. AE 162  $\mu$ m long, 285  $\mu$ m wide, with three pairs of setae and pair of epimeral pores. Bases of trochanters I and II flanked by lamelliform epimeral processes. PE 162  $\mu$ m long, not markedly extending beyond aperture of leg IV, with one dorsal seta and three ventral setae. GA 140  $\mu$ m long, 147  $\mu$ m wide, shorter than AE; anterior margin almost truncate. GO 85  $\mu$ m long, 55  $\mu$ m wide. Three pairs of pgs as illustrated (Figure 2C).

Length of gnathosoma 166  $\mu$ m, width 82  $\mu$ m, i.e. 2.0 times longer than wide. Rostrum and gnathosomal base almost equal in length (Figure 2D). Major parts of dorsal, lateral and ventral flank of gnathosomal base with porose areolae, i.e. integument pierced by canaliculi. Canaliculi minute or absent within pharyngeal field and pair of circular areolae on either side of pharyngeal field. One pair of maxillary setae on gnathosomal base, one pair in posterior fourth of rostrum. Tip of rostrum with two pairs of short, slender rostral setae. Tectum scaliform (Figure 2F). P-2 3.2 times longer than high (Figure 2G). P-3 slightly longer than high, its delicately dentate spine longer than this segment. P-4 1.5 times longer than P-3; with a single long seta.

Lateral flank of telofemur I reticulate. Integument of this and other segments and legs almost evenly pierced by numerous canaliculi; canaliculi also present on lateral flanks of trochanters III and IV. Medial flanks with few, less conspicuous canali-Telofemora III and IV 2.4-2.6 times longer culi. than high. Leg chaetotaxy (solenidia, famulus and parambulacral setae excluded; on leg I setae in Arabic, spines in Roman numerals; leg IV on one side deformed, this leg not included in chaetotaxy formula): leg I, 1, 2, 4+IV, 3+II, 6+III, 5+I; leg II, 1, 2, 6, 5, 6, 3; leg III, 1, 2, 3, 3, 5, 3; leg IV, 0, 2, 3, 3-4, 5, 3. Ventral seta on telofemur III and IV near apical third of segment (Figure 3B and C). On genu I ventral spine shorter than ventromedial one (Figure 3A). Tibia II with two ventral spiniform setae, ventromedial one flattened, bipectinate, ventral seta dentate (cf. Figure 3E). Tibiae III and IV each with a pair of smooth, tapering setae; setae longer than height of tibia. Tarsus I with pair of doubled pas,



FIGURE 3: Agauopsis dissimilis n.sp.: A – leg I, medial, female; B – leg III, medial, female; C – leg IV, medial, female; D – malformed leg IV, medial, female; E – basifemur to tarsus II, medial, male; F – tip of tarsus I, lateral, female (medial setae and claw omitted); G – apical tibia and tarsus II, medial, male; H – tip of tarsus II, lateral, male (medial fossary seta and claw omitted); I – tip of tarsus II, medial, male (lateral fossary seta and claw omitted). (fa, membrane with famulus; so, solenidion) Scale line = 50 μm

a solenidion, 2  $\mu$ m long, and a famulus, the latter represented by an afferent canal within membrane of lateral fossa membrane (Figure 3F). Tarsus II medially with spiniform pas, laterally with one long and adjacent one short setiform pas (cf. Figures 3G and H); small medial fossa membrane with 3- $\mu$ m long solenidion on inner flank (cf. Figure 3I). Medial fossary seta slightly more slender than lateral seta. Tarsi III and IV each with spiniform lateral pas; medial pas lacking. No fossa membranes on these tarsi. Claws I shorter than following claws, median claw bidentate. Claws II to IV with accessory process and pectines. Tines of pectines almost 2  $\mu$ m long. Median claw of tarsi II to IV without dent-like process.

Male. Length 420  $\mu$ m. Dorsal aspect similar to that of female but PD more slender, its anterior margin somewhat ovate (Figure 2H) and ds-1 slightly anterior to the level of gland pores. GA 1.1 times longer than AE; its anterior margin widely arched (Figure 2I). Distance between anterior margin of GO and that of GA almost equalling length of GO. Perigenital setae slender, 61 arranged in two rings around GO, a pair of setae outlying. Each genital sclerite with four to five short, spur-like sgs (Figure 2J). Spermatopositor 112  $\mu$ m long, with three pairs of almost similar-sized lateral projections. Spermatopositor extending to anterior margin of GA.

Anomaly — Leg IV of the holotype is abnormal (Figure 3D), three tarsi arise from the tibia and the number and shape of setae differ from that generally found on this leg.

Remarks — The character slender, tapering ventral setae on tibiae III and IV is shared with *A. arborea*, a short P-4 with a single seta with *A. obtusa* Bartsch, 2005. In contrast to *A. arborea* and *A. obtusa*, the rostrum of *A. dissimilis* is about as long as the gnathosomal base, that of *A. arborea* and *A. obtusa* is shorter, 0.8 times and 0.9 times, respectively. *Agauopsis arborea* bears two setae on P-4 and *A. obtusa* has spiniform and dentate setae on tibiae III and IV.

Distribution and Biology — Singapore. The three individuals have been extracted from green algae growing in the upper and middle tidal area on a trunk and on stone packing.

#### Agauopsis longirostris Bartsch, 2015

#### Agauopsis longirostris Bartsch 2015: figs 7A-M, 8A-J.

Short description — Length of female 510  $\mu$ m, of male 450 - 460 µm. Dorsal plates with costae. Costae with groups of three to six canaliculi, these porose groups hardly delimited and costae without reticulate ornamentation. Remainder of plate reticulated, each polygon including about five to eight delicate canaliculi. AD 1.2 times longer than wide. Pair of ds-1 level with gland pores; transverse bar of H-shaped costa on AD at 0.5. Each OC with oblique costa; gland pore immediately posterior to cornea, at 0.4. PD with pairs of longitudinal medial and marginal costae. Medial costae in anterior half three to four porose groups wide. Female and male PD 1.1 and 1.3 times longer than AD, respectively. Female PD 1.1 times longer than wide, male PD prolonged, 1.2 times longer than wide. PD with pair of ds-5 in lateral margin of medial porose costae, at 0.4 relative to length of PD.

Polygons of ventral plates with 9-15 canaliculi; canaliculi in centre as well as along periphery of each polygon. Anterior margin of female and male GA truncate. Male GA with 36-38 perigenital setae arranged in two rings around GO and a pair of outlying setae distinctly separated from outer ring of pgs.

Gnathosoma elongate, 2.1-2.3 times longer than wide. Rostrum 1.7-1.8 times longer than gnathosomal base. Tectum with scaliform lamella. Palps elongate. P-2 4.1-4.2 times longer than high. Length of P-4 more than twice that of P-3. Two setae in about middle of P-4 almost equal-sized.

Telofemora III and IV 2.1-2.2 times longer than high. Tibiae II to IV with 3, 2, 2 spiniform setae, either pectinate or dentate. Claws II to IV with numerous delicate tines along medial flank.

Remarks — *Agauopsis longirostris* is characterized by its slender rostrum and palps, the P-2 are 4.1-4.2 times longer than high, in the other species known from the Indo-West Pacific the length of the P-2 is less than 3.5 times the height (width).

Distribution and biology — Singapore. The present records are from algal turf from sheltered

areas (mangroves) as well as moderately exposed sites (Bartsch 2015).

#### Agauopsis moorea Bartsch, 1992 Figure 4A-G

*Agauopsis moorea* Bartsch 1992a: 472-474, figs 25-32. *Agauopsis moorea*, Bartsch 2005: 353-355, fig. 6A-F.

Additional material examined — One female (IB), Singapore, St John's Island, from dead coral block, 01 Oct. 2004. One female, one male (ZRC.ARA.1383), Pulau Ubin, OBS, 1°25'N, 103°56'E, midtidal filamentous algae on rock, 28 Oct. 2012. One female (IB), same collection data.

Short description — Length of female 404 – 465  $\mu$ m, of male 364 – 405  $\mu$ m. Intensely armoured, colour of integument markedly brown. Dorsal plates with costae; integument within costae with almost evenly spread canaliculi, without reticulate pattern. Remainder of plates reticulate, polygons with slightly raised walls and each polygon with four to six delicate canaliculi. AD and OC 1.1-1.2 and 1.4-1.5 times longer than wide, respectively; ds-1 about level with gland pores. Gland pore on OC in posterior half of plate, at 0.6, immediately followed by pc (Figure 4C). Distance between posterior cornea and gland pore at least diameter of cornea, often more. Pair of ds-4 immediately posterior to corner of OC (Figure 4A). In female PD slightly, in male distinctly longer than wide. Anterior margin of female PD rounded, that of male PD ovate. Pair of ds-5 on female PD slightly anterior to midline, on male PD slightly posterior.

Reticulation of ventral plates indistinct but present; six to eight canaliculi evenly spread within each polygon. Anterior margin of both female and male GA truncate (Figure 4B). GO of male surrounded by almost 30 pgs; two setae outlying. These latter setae halfway between ring of pgs and margin of GA. Spermatopositor short, less than half the length of GA; anteriad hardly extending beyond level of outlying pgs and not reaching to anterior margin of GA (Figure 4D).

Gnathosoma 1.8-1.9 times longer than wide (Figure 4F). Rostrum approximately as long as gnathosomal base (1.0-1.1 times). Tectum with scaliform lamella (Figure 4E). P-2 3.0-3.3 times longer than high. P-3 about as long as high. P-4 slightly longer than P-3 but one-third or less than length of P-2. Two setae on P-4 almost equal in length.

Telofemur I with four spines, basalmost ventromedial spines shorter than the other spines. Ventral seta of telofemora III and IV situated in basal half. Tibia II with three short ventral setae, one bipectinate and two spiniform and dentate. Tibiae III and IV with two dentate, spiniform ventral setae and one bipectinate seta. Tarsus II laterally with a long and adjacent short pas, medially with a spiniform pas (Figure 4G). Tarsi III and IV laterally with narrow fossa membrane; medial membrane vestigial. Claws on tarsi II to IV with pectines arranged along outer and inner arc (Figure 4G), tines delicate but recognizable at 400x magnification.

Variants — One female (from Singapore, St John's Island) bears on telofemur I unilaterally five instead of four spines.

Remarks — The species can be identified on the basis of the uniformly arranged canaliculi on the costae (not in groups), the gland pore situated in the posterior half of the OC, distinctly removed from the cornea but close to the pc, and the ds-4 immediately posterior to the corner of the OC. The spermatopositor of males is smaller than in most of the other species, it extends to about the level of the pair of outlying setae and not to the anterior margin of the GA.

Distribution and Biology — Southern Pacific, Society Islands; eastern Indian Ocean, tropical Western Australia, Dampier (Bartsch 1992a, 2005), Southwestern Pacific, Australia, Queensland, North Stradbroke Island, Amity Point (new record, amongst epibios on trunk washed ashore, 12 Feb. 2005, and sponge with algae from 8-10 m depth, 15 Feb. 2005); South China Sea, Singapore. The species inhabits sand, coral rubble and algal turf from lower tidal areas to about 10 m depth, it is also, though rarely, found amongst epiflora on *Avicennia* pneumatophores.

#### Agauopsis obtusa Bartsch, 2005

*Agauopsis obtusa* Bartsch 2005: 355-358, figs 7A-J, 8A and B.



FIGURE 4: Agauopsis moorea Bartsch, 1992: A – idiosoma, dorsal, male; B – idiosoma, ventral, male; C – lateral margin of OC, female; D – genitoanal plate, male; E – gnathosomal base, dorsal, female; F – gnathosoma, ventral, female; G – tip of tarsus II, ventromedial, male (lateral fossary seta and claw omitted). (spp, spermatopositor) Scale line = 50 µm.

Short description — Length of female 450  $\mu$ m, of males 419 - 422 µm. Integument within and outside porose areolae reticulated. AD 1.1 times longer than wide, plate slender compared to PD, width of PD 1.4-1.5 times that of AD. Transverse bar of Hshaped costae in anterior half of AD; ds-1 level with gland pores. OC 1.3-1.4 times longer than wide. Posterior cornea, glp and pc almost equal distanced, glp slightly anterior to middle of lateral margin. PD in both female and male slightly longer than wide (length:width 1.0-1.1 times). Medial costae distinctly diverging, anteriorly with about 12 polygons between costae. Pair of ds-4 level with posterior corner of OC. Pair of ds-5 in lateral margin of medial costae of PD. Reticulum of ventral plates visible when focused on deeper integumental layers. Female GA slightly longer than wide, male GA somewhat wider than long. Longitudinal margins of female GA converging, anterior margin slightly arched. Anterior margin of male GA wide, almost truncate. Male with 51 pgs close around GO and a pair of outlying setae.

Gnathosoma — 1.8 times longer than wide, rostrum shorter than gnathosomal base. Length of P-2 2.7 times the height. P-4 short, about twice length of P-3, with single basal seta.

Both lateral and medial flank of telofemora pierced by canaliculi. Telofemora III and IV 2.5-2.6 times longer than high. Ventral seta in middle of these telofemora. Basal spines on telofemur I almost equal-sized. Tibia II with two ventral setae, ventromedial one bipectinate, ventral seta spiniform and dentate. Tibiae III and IV with pair of ventral spiniform and dentate setae. Tip of tarsus II with doubled medial pas, one of these setae long, one short. Claws on tarsi II to IV with accessory process and tines on both lateral and medial flank.

Remarks — *Agauopsis obtusa* has a wide PD but slender AD (width PD:AD 1.4-1.5:1), the transverse costae on the AD is in the anterior half of the plate, the ds-5 insert within the margins of the costae, the rostrum is shorter than the gnathosomal base, P-4 bears a single seta which is longer than this segment, the telofemora III and IV are slender, tibiae II to IV have two spiniform ventral setae each. The reduced number of setae on P-4 and tibia II is shared with *A. dissimilis*, but in that species the two setae on tibiae III and IV are slender, smooth, tapering. Only three individuals of each of these two species have been studied and the variability of characters is not known.

Distribution and biology — Eastern Indian Ocean, tropical Western Australia, Dampier. From turf on *Avicennia pneumatophores* (Bartsch 2005).

#### Agauopsis ripa Otto, 1999 Figure 5A-G

*Agauopsis ripa* Otto 1999: 809-811, figs 12A-D, 13A-D.

Material examined — Paratype male, ZMH A19/00, Great Barrier Reef, Tokolakea Beach, algae and tube-worm colonies on boulders, low tide level, 15 Jun. 1997.

Short description — Length of females 369 - 440 µm, of males 349 - 460 µm. AD 1.2 times longer than wide, ds-1 level with gland pores. OC slender, 1.5 times longer than wide (1.2 in compressed paratype). Gland pore at 0.4, removed from cornea by the latter's diameter. Distance from glp to cornea hardly longer than that to pc (Figure 5A). Pair of ds-4 in males level with posterior corner of OC. Male PD almost as long as or slightly longer than wide. Medial costae with groups of five to six canaliculi. Plate outside costae reticulated and with fine canaliculi.

Arrangement of canaliculi on ventral plates rather uniform, reticulation faint. GA in both female and male slightly longer than wide. Anterior margin of female GA truncate, that of male GA ovate (Otto 1999: fig. 12D), arched (Figure 5B) or rather truncate (Otto 1999: p. 810). Spermatopositor large, in compressed male extending beyond anterior margin of GA (Figure 5B). Male with 47-50 pgs and pair of outlying setae. That pair closer to lateral margin than to outer ring of pgs.

Gnathosoma about 1.8 times longer than wide (of slightly compressed paratype). Rostrum shorter than gnathosomal base (0.8:1) (Figure 5C). P-2 2.9-3.0 times longer than wide. P-4 short, about 1.5 times longer than P-3, two basal setae different in length (paratype) (Figure 5D). Tectum slightly arched.

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FIGURE 5: Agauopsis ripa Otto, 1999, male: A – lateral margin of OC; B – genitoanal plate; C – gnathosoma, ventral; D – P-3 and P-4; E – tip of tarsus I, ventromedial; F – tip of tarsus II, ventromedial (one of lateral parambulacral setae obscured, the other in broken line); G – tip of tarsus III, ventral. (T, tectum) Scale line = 50 μm.

Integument of lateral flank of legs pierced by canaliculi; medial flanks with few delicate pores. Lateral spine on genu I slightly smaller than medial one. Telofemur III 2.3 times longer than high. Ventral seta on telofemora III and IV in basal half, at about 0.4. Tibia II with three (rarely four) ventral setae. Tibiae III and IV with two spiniform, dentate ventral setae. Tip of tarsus II medially with spurlike pas, laterally with doubled pas, one of pas long, the other short. Fossa membranes on tarsi III and IV short and small. Claws on tarsus I (Figure 5E) shorter than following claws. Claws on tarsi II to IV with accessory process; pectines extending to about middle of claw shaft (Figure 5F and G).

Remarks — *Agauopsis ripa* is very similar to *A. sordida* Bartsch, 1992 (outlined below). According to Otto (1999), the two species differ in the length of the rostrum. According to the paratype studied there is no marked difference. Examination of more material from the type localities may prove *A. ripa* to be a synonym of *A. sordida*.

Amongst the material studied by Otto, one of the males had a GA with ovate anterior margin GA (Otto 1999: fig. 12D). In general males of tropical Indo-West Pacific *Agauopsis* species have a GA with a truncate to slightly arched anterior margin.

Distribution and biology — South-western Pacific, Australia, Queensland, Great Barrier Reef (Otto 1999). All records are from intertidal and lower tidal zones where it lived amongst algae, tube worm colonies, and sediment between mangrove roots.

#### Agauopsis sordida Bartsch, 1992 Figure 6 A-G

*Agauopsis sordida* Bartsch 1992b: 247-249, figs 3A-L, 4A-C.

Additional material examined — One female, 1 male (ZRC.ARA.1384), Singapore, Pulau Ubin, Chek Jawa, 1°24'N, 103°59'E, shells of *Saccostrea* (Bivalvia) on boulder, 16 Oct. 2012. Two females, 1 male, 2 deutonymphs (IB), Singapore, Labrador Park, 1°16'N, 103°48'E, *Catenella* sp. (Rhodophyta) on concrete piling, mid-tidal zone, 28 Sept. 2004. One male (IB), Singapore, south-west coast, 1°18'N, 103°46′E, red and green algae in concrete pipe (rain water run off), upper tidal zone, 26 Sept. 2004. Two males (IB), Singapore, West Coast Park, 1°18′N, 103°46′E, tufts of algae on sediment of sheltered bay, mid-tidal zone, 05 Oct. 2004. One female (IB), Singapore, East Coast Park, 1°18′N, 103°55′E, green algae on stone packing, 06 Oct. 2004. One male (IB), Singapore, Lazarus Island, coarse sediment from above low water edge, 03 Oct. 2004. One male, 1 deutonymph, 1 protonymph (IB), Singapore, Pulau Ubin, Chek Jawa, 1°24′N, 103°59′E, shells of *Saccostrea* (Bivalvia) on boulder, 16 Oct. 2012. Three females, 1 male, 1 deutonymph (IB), Singapore, Island Sekudu, 1°24′N, 103°59′E, small turf of algae on boulders, upper tidal fringe, 19 Oct. 2012.

Short description — Length of female 432 – 498  $\mu$ m, of male 322 – 425  $\mu$ m. Dorsal plates with costae. Costae with groups of four to six canaliculi (holotype), in specimens from Singapore six to eight canaliculi. Groups slightly delimited and costae faintly reticulated. Remainder of plate reticulated, each polygon including about 6-11 delicate canaliculi. AD 1.1-1.2 times longer than wide; transverse bar of H-shaped costa at 0.5. OC slender, 1.5 times longer than wide; glp in anterior half at about 0.4; distance between margin of posterior cornea, glp and pc almost the same (Figure 6C). PD about 1.1 times longer than wide. Anterior margin of male PD slightly more ovate than that of female (Figure 6A and E). In both female and male pair of ds-4 in striated integument between OC and PD. Pair of ds-5 in anterior half of PD, in lateral margin of medial costae.

AE reticulated, with 10-15 canaliculi in each polygon. Anterior margin of GA arched to truncate in both females and males (Figure 6B and F). In males distance between anterior margin of GA and that of GO almost equalling length of GO. Spermatopositor large, its length 0.6 times that of GA and extending to anterior margin of GA (Figure 6D). Male with 35-47 pgs arranged in two rings around GO and one pair of outlying setae, the latter separated from outer ring of setae.

Gnathosoma 1.8-1.9 times longer than wide. Length of rostrum 0.8 times that of gnathosomal base (Figure 6G). Tectum with short truncate or



FIGURE 6: Agauopsis sordida Bartsch, 1992: A – idiosoma, dorsal, female; B – idiosoma, ventral, female; C – lateral margin of OC, female; D – genitoanal plate, male; E – idiosoma, dorsal, male; F – idiosoma, ventral, male; G – gnathosoma, ventral, female. (pa, porose areola; spp, spermatopositor) Scale line = 50 µm.

slightly arched lamella. P-2 2.8-3.1 times longer than high (length:width ratio similar). P-4 short, only slightly longer than P-3 and with one long and one distinctly shorter seta. One of 16 adults studied unilaterally with a single seta on P-4.

Telofemora III and IV 1.9-2.2 times longer than high. One of 15 adults studied unilaterally with five spines on telofemur I and one adult unilaterally with two instead of three ventral setae on tibia II. Fossa membranes on tarsi III and IV reduced.

Remarks — Chatterjee *et al.* (2012) report on females and males from Brunei Darussalam with an idiosomal length of 390 - 402 and  $368 \mu m$ , respectively, accordingly the females are slightly smaller than in the present material.

Agauopsis sordida is most similar to A. arborea, both rostrum and palps are short and the number of setae on tibia II varies. The two species can be discriminated on the basis of the ventral setae on tibiae III and IV, slender, smooth and tapering in A. arborea but short and bluntly ending in A. sordida. These setae of A. sordida are not just broken, they are wider than in A. arborea and dentate.

Distribution and biology — South China Sea, Hong Kong (Bartsch 1992b), Brunei Darussalam (Chatterjee *et al.* 2012), Singapore (new record); Indian Ocean, tropical Western Australia, Dampier (new record, one female amongst coarse sediment from a small wooded area, 7 Aug. 2000, coll. I. Bartsch). From midtidal sediment, barnacles, bivalves (*Saccostrea*), green and brown algae.

#### THE Agauopsis FAUNA OF SINGAPORE

During two stays in Singapore, eight *Agauopsis* species have been collected in the tidal and shallow subtidal. The *Agauopsis* fauna in lenitic shallow water areas is dominated by representatives of the *A. brevipalpus* group, these are *A. arborea, A. dissimilis, A. longirostris, A. moorea,* and *A. sordida*. The other three species are *A. narinosa* Otto, 1999, *Agauopsis* sp. (cf. Bartsch 2009c), and an unpublished record of a representative of the *Agauopsis ornata* group. More *Agauopsis* species will be found in subtidal habitats but certainly also in shallow water around Singapore.

Agauopsis narinosa was extracted from algal turf growing at the low water edge on St John's Island (Bartsch 2009c). Agauopsis sp. was described but not named (Bartsch 2009c), it is psammobiont, lives near the groundwater table and is most similar to A. arenaria Bartsch, 1992 and A. hamata Newell, 1984. The first mentioned species is known from Hong Kong, the second from Chile (Newell 1984; Bartsch 1992c). The representative of the Agauopsis ornata group, a female, was extracted from small algal tufts growing on a boulder just below the low water edge of the Island Sekudu (19 Oct. 2012), a site moderately exposed to swell. Species of the ornata group are characterized by areolae with porose polygons, garland-like on the AE. The characters of that single female are: length of idiosoma 340 µm, width 239  $\mu$ m, anterior margin of AD with lamellar, almost rectangular projection, 22 µm wide; AD with pair of porose costae and anteriorly with median ovate porose areola; OC with two porose areolae, one immediately medial to two corneae, one halfway between corneae and medial corner of plate; porose longitudinal costae of PD separated from transverse posterior costa; AE with pair of garland-like areolae and a median areola, circular in outline and adjacent to posterior margin of plate; GA with two pairs of porose areolae, anterior one crescentic, posterior pair ovate; rostrum slightly shorter than gnathosomal base; ventral margin of telofemur I with two apically dentate spines and short rounded lamella. The species is most similar to Agauopsis calidictyota Bartsch, 2007, A. decorata Otto, 1999 and A. inflata Newell, 1984, the first mentioned species is known from the southern coast of Western Australia, the second from Queensland, eastern Australia and the third from Chile (Newell 1984; Otto 1999; Bartsch 2007). The AD of Agauopsis inflata bears a similar almost rectangular lamellar projection, but in contrast to the specimen from Singapore, the costae on the PD extend to the posterior transverse porose areola, there is no median porose areola adjacent to the posterior margin of the AE, and the rostrum is longer than the gnathosomal base. In A. calidictyota and A. decorata the anterior projection of the AD is triangular, moreover the AE of A. calidictyota has no median porose areola, and the telofemur I of A. decorata two ventral lamellae (a single one in the specimen from

Singapore). If the shape of the anterior projection of the AD and the lamellae on telofemur I turns out to be variable, then the Singaporean specimen may be conspecific with *A. decorata*, at least the arrangement of the porose areolae on the PD, AE and GA and the shape of the rostrum are the same in *A. decorata* and the specimen from Singapore.

#### KEY TO ADULT *Agauopsis* SPECIES OF THE *Brevipalpus* GROUP

Characters, especially the number and shape of setae and spines, are known to vary, hence microscopical examination of several individuals is recommended. Females and males share most of the characters but, in addition to the differences in the genital plate, males often have a somewhat longer and wider PD. The key cannot be used for identification of juveniles as the number of spines and setae and the outline of plates and segments change during development.

1. Telofemur I with one or two spines. AD a	and dor-
sal part of AE not fused	2
— Telofemur I with more than two spines.	AD and
dorsal part of AE fused	3

4(3). Telofemur I	with three spines.	5
— Telofemur I w	ith four spines	

7(6). Rostrum less than 0.6 times length of gnath	0-
somal base	. 8
— Rostrum and gnathosomal base equal	in
length	.9

8(7). Tibia II ventrally with one bipectinate seta and one dentate spine. (Southwestern Pacific: Australia, Queensland; tidal) ..... A. glabra Bartsch, 2009 — Tibia II ventrally with one bipectinate seta and two dentate spines. (Southwestern Pacific: New Zealand; tidal) ..... A. novaezelandiae Bartsch, 1986

9(7). AD with M-shaped costae. (Northeaste	rn Pa-
cific: Oregon, California; tidal)	
A. newelli Krantz	, 1973
— AD with H-shaped costae	10

12(11). P-2 3.7-4.1 times longer than high. ..... 13 — Length of P-2 less than 3.4 times the height. .. 15

 ventral setae......18

20(18). P-4 with single seta. Transverse bar of Hshaped costae near anterior third of AD. (Eastern Indian Ocean: tropical Western Australia, Dampier; tidal) ...... *A. obtusa* Bartsch, 2005 — P-4 with two setae. Transverse bar of H-shaped costae in middle or in basal half of AD......21



FIGURE 7: Geographical distribution of named and unnamed species of the *Agauopsis brevipalpus* group. Different symbols are used depending on number of spines on telofemur I. Species with one or two spines are marked by a diamond: (1, *collaris*; 2, *rosea*; X, *Agauopsis* sp.); with three spines by a circle: (1, *filirostris*; 2, *glabra*; 3, *ivanomorselii*; 4, *luxtoni*; 5, *newelli*; 6, *novaezelandiae*; 7, *reticulata*); with four spines by a quadrat (1, *arabia*; 2, *arborea*; 3, *atacamae*; 4, *borealis*; 5, *brevipalpus*; 6, *dissimilis*; 7, *ibssi*; 8, *legionium*; 9, *littoralis*;10, *longirostris*; 11, *moorea*; 12, *obtusa*; 13, *ripa*; 14, *sordida*; 15, *youngilensis*; X, *Agauopsis* sp.); with five or more spines by a triangle (1, *tricuspis*; X, *Agauopsis* sp.).

Australia, Queensland, Moreton Bay; Indian Ocean: tropical Western Australia, Dampier; South China Sea: Singapore) ...... *A. moorea* Bartsch, 1992

24(21). P-2 2.9-3.0 times longer than wide. Male with 47-50 perigenital setae. (Southwestern Pacific: Australia, Queensland, Great Barrier Reef; intertidal and lower tidal).....*A. ripa* Otto, 1999 — P-2 2.8-3.1 times longer than high. Male with 37-49 perigenital setae. (South China Sea: Hong Kong, Brunei Darussalam, Singapore; Indian Ocean, tropical Western Australia, Dampier; midtidal).....*A. sordida* Bartsch, 1992

# THE SPECIES AND THEIR GEOGRAPHICAL DISTRIBUTION

The records of species of the *brevipalpus* group are plotted on a map (Figure 7). Also included are three undescribed species, namely one record of

a species from Mauritius, from the intertidal, collected in March 2006 by Dr H-G. Müller, one from St. Croix Island, Algoa Bay, South Africa, collected in 1982(?) by Dr L. E. Beckly, and one from Rio Deseado, Provincia de Santa Cruz, southern Argentina, collected in 1975 by Dr C. Pastor de Ward. Not included in the map is an unpublished record of two specimens collected by the author on the coast of Brittany (France), in the upper tidal zone, specimens with a short rostrum (length 0.6 times that of the gnathosomal base), four spines on telofemur I and rather slender ventral spines on tibiae III and IV. The status of the specimens is not clear, at present they are expected to be anomalous variants of *Agauopsis tricuspis*.

The genus *Agauopsis* is known to inhabit all zones, from polar to tropical and from tidal to deepsea areas (Bartsch 2004, 2009a), but the *brevipalpus* group is obiously restricted to temperate and tropical zones and to tidal and subtidal habitats, there are no records from polar waters and no from the



FIGURE 8: Present day records of species of the *Agauopsis brevipalpus* group with three (circle) and four spines (quadrat) on telofemur I plotted on a map with Lower Jurassic land masses (solid line), ca 180 my ago (present-day plates in dotted line). A record from the Society Islands is omitted. (Lower Jurassic map modified from Howarth 1981; Vaughan & Livermore 2005; Stevens 2012).

deep sea. In periodically low salinity (<30 psu) areas, the *Agauopsis* fauna seems to be dominated by species of the *brevipalpus* group.

On the map (Figure 7) different symbols have been used for species with one or two, three, four or more than four spines on telofemur I. The species with four spines on telofemur I are most numerous, 14 species have been described, spread in the tropical and temperate warm-water zone; most records are from the western Pacific, Indian Ocean and North Atlantic. The seven species with three spines have been collected in warm- and cold-temperate regions of the eastern and western Pacific but not in the tropics; there are at present no records from the Atlantic and Indian Ocean. The two species with less than three spines, as well as a third undescribed one, have been taken in the southern hemisphere, in Australia and South America. Only two species have five spines on telofemur I, these are A. tricuspis, spread along the eastern North Atlantic and Mediterranean, and an undescribed species from the southern edge of South Africa.

The present-day records of species of the two

most abundant Agauopsis brevipalpus sub-groups are plotted on a map with the outline of the continental plates during the Lower Jurassic, about 180 million years ago (Figure 8). It is striking that species with four spines are primarily found in areas once bordering the Tethys whereas species with three spines live in regions which once belonged to the shoreline of Panthalassa. Arachnids have an evolutionary history extending back to the Cambrian, and mites have occurred at least since the Silurian (Arldt 1907; Vitzthum 1943). Because of the wide geographical distribution though low fecundity and restricted dispersal capacity, numerous halacarid genera and species are expected to have existed since 50-200 million years (Bartsch 1989, 1996a). It is tempting to propose that species of the Agauopsis brevipalpus group colonized the coastline of the Mesozoic land masses and species with four spines on telofemur I spread along the Tethys and the evolving Atlantic whereas species with three spines were transported along the coast of the Panthalassa. But one should keep in mind that the faunistic data are sparse and the phylogenetic relevance of the number of spines

on telofemur I not proven, though the number can be used to identify species. More faunistic and molecular data may be able to support or reject the idea of phylogenetic lineages and different routes of spreading.

#### Addendum

After having submitted the manuscript I became aware of the poster 'Koç, K., Türksel, M., (2014, June) — Ege Denizi'nden (?zmir) Türkiye Faunas? ?cin Yeni Bir Deniz Akar? (Acari: Halacaridae) Türü. — 22. Ulusal Biyoloji Kongresi, Eski?ehir'. The species recorded from the Aegean Sea (Koç and Türksel 2014) is no *A. arborea*, the gnathosoma of *A*. arborea is shorter than that illustrated by Koç and Türksel and the ventral bristles of tibiae III and IV are slender, not short and spiniform as illustrated (Koç and Türksel, 2014: fig. 1E and F). Having sent me figures, K. Koç was informed (e-mail, March, 4th, 2014) that the given mite belongs to the genus Agauopsis and, in case it is from the Mediterranean or Black Sea area, I expect it to be Agauopsis brevipalpus.

#### ACKNOWLEDGEMENTS

The collecting of the halacarid mites in Singapore in 2004 was financed by a grant of the National University of Singapore. The International Workshop 'Comprehensive Marine Biodiversity Survey of Singapore: Johor Strait Workshop (15 Oct-2 Nov 2012) and the author's participation in this workshop was supported by Shell Eastern Petroleum, Hong Kong and Shanghai Banking Cooperation Care-for-Nature Trust Fund, and Asia-Pacific Breweries (Singapore). Thanks are due to the staff of the Raffles Museum of Biodiversity Research (2004), organizers of the International Workshop Tan Koh Siang, Peter Ng, Tan Heok Hui, and Joelle Lai, National University of Singapore, Wong Tuan Wah, Lena Chan and Linda Goh, National Parks Board, and the sponsors.

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