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ZOOGEOGRAPHY OF THE LAOPHONTID GENUS *AFROLAOPHONTE* (COPEPODA, HARPACTICOIDA), WITH DESCRIPTION OF *A. STOCKI* N. SP. FROM GUADELOUPE

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ABSTRACT

Afrolaophonte stocki n. sp. from Guadeloupe is described and *A. aequatorialis* is reported from the southern coast of Papua New Guinea. The pantropical genus *Afrolaophonte* comprises twelve different species. Based on the chaetotaxy and the segmentation of the P_3 and P_4, three species groups are defined within the genus. Each group shows a distribution area limited to a certain oceanic basin.

RÉSUMÉ

Afrolaophonte stocki n. sp. provenant de Guadeloupe est décrite et *A. aequatorialis* est signalée sur la côte sud de la Papouasie Nouvelle Guinée. Ce genre pan-tropical comprend douze espèces. D'après la chaetotaxie et la segmentation de P_3 et P_4, trois groupes d'espèces sont définis à l'intérieur du genre. Chaque groupe a une aire de distribution limitée à un bassin océanique particulier.

INTRODUCTION

The laophontid genus *Afrolaophonte* (Chappuis, 1960) is one of those remarkable interstitially living genera characterized by their cylindrical body and highly reduced appendages. *Afrolaophonte* shares these peculiar adaptations with other genera such as *Laophontina*, *Galapalaophonte*, etc., but is easily recognized by its morphology of the P_4 in both sexes (see Lang, 1965 for discussion).

The species of this genus occur exclusively in the interstitial realm of the intertidal zone of sandy beaches. They often penetrate the sediment rather deep and may be found, although less abundant, near the groundwater table.

Eleven species have been assigned to the genus *Afrolaophonte*. In the present paper, a new species. *A. stocki* n. sp., is described from a sandy beach in Guadeloupe. This new species and *A. renaudi*, known from the Bahamas, are the sole representatives of the genus in the western central Atlantic.

Each species of the genus shows a rather limited distribution. Most of them (8 out of 12) are known from their type-locality (-region) only and have never been reported since. However, the genus shows a typical pantropical distribution with representatives in the Pacific (2 species), Indian Ocean (5 species), Atlantic Ocean (4 species) and the Mediterranean Sea (1 species).

Based on the chaetotaxy and segmentation of the exopodal rami of P3 and P4, the genus can be divided into three species groups, with each group represented by a monophyletic assemblage within the genus. Moreover, each group shows a limited distribution area, restricted to one oceanic basin.

MATERIALS

Of the species of *Afrolaophonte* reported in the present paper, *A. stocki* n. sp. was found in a sample from Guadeloupe while *A. aequatorialis* was collected along the southern coast of Papua New Guinea.

The samples were fixed with a 4-5% buffered formaldehyde solution. The copepods were picked from the residues after the samples were washed above a sieve (0.039 mm) and stored in 75% buffered ethylalcohol. The localities are: *A. stocki* n. sp. (type-locality): Guadeloupe, Grand Terre, Anse des Châteaux (16°15′N-61°14,4′W); Karaman-Chappuis (40 cm deep) of poorly sorted coral sand situated above the low tide mark; 14 April 1979. Granulometric data in Renaud-Mornant & Gourbault (1981), referred as Station 7, sample #: 44.
A. aequatorialis Cottarelli & Mura, 1981: Papua New Guinea, Capital District, Motupore Island (near Port Moresby, ± 9°30′S-147°7′E); Karaman-Chappuis at the northeastern edge of the island; intertidal, 2 m from the low tide mark and 30 cm deep; fine sand with large coral fragments between; 23 November 1986, Leg. F. Fiers (field # 86-88, I.G. 27.213).
Dissected specimens are mounted in lactophenol. The preserved male specimen of *A. stocki* n. sp. and the specimens of *A. aequatorialis* (COP 2027: 3 ♀♀, 2 ♂♂, 1 cop IV, 1 cop III) are stored in 75% buffered ethylalcohol. The specimens are deposited in the collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels.

SYSTEMATICS

Afrolaophonte stocki n. sp.

Type-material. — Holotype: one female dissected and mounted on a slide, COP 1988: allotype: one male dissected and mounted on a slide, COP 1989; one male paratype preserved in alcohol, COP 1990.

Type-locality. — Guadeloupe, Grande-Terre: Anse des Château.

Etymology. — The specific name is chosen in honour of Prof. Dr. J. H. Stock (Amsterdam).

Figures. — Holotype: Fig. 2a, b, d, e, f, h, i; allotype: Fig. 2c, g, j, k and l; paratype (male): Fig. 1a, b.

Description. — Female (holotype): length 430 μm; habitus cylindrical; lateral margins of the cephalothorax slightly tapering towards the anterior edge; anal segment with a constriction in the anterior half of the lateral margins; anal operculum convex, furnished with two parallel rows of minute spinules.

Integumental structures: integument of the cephalothorax, thoracic and abdominal segments covered with minute spinules; pleural regio of the thoracic segments and lateral margins of the genital and abdominal segments furnished with hairs (structures not shown in Fig. 1).

Furcal rami (Fig. 2a and b) twice as long as wide; dorsal surface with transversal rows of strong spinules and with two blunt upward directed thorns in front of the implantation of the dorsal seta; lateral setae implanted in the distal half of the lateral margin; outer apical seta strongly developed and feathered; inner apical seta smooth.

Antennule five-segmented; first segment with an inner lateral and an inner distal row of spinules; second segment with an outer thorn; aesthetasc implanted on the third segment.

Antenna typical, bearing a one-segmented exopodite with four setae.

P1 (Fig. 2e): coxa with a row of spinules implanted parallel with the outer margin; exopodite one-segmented, bearing two lateral and two apical setae; endopodite slender, having some spinules on the apical edge of the second segment and an unarmed claw.

P2 (Fig. 2h): intercoxal plate, coxa, basis and exopodal segment fused; two exopodal setae.
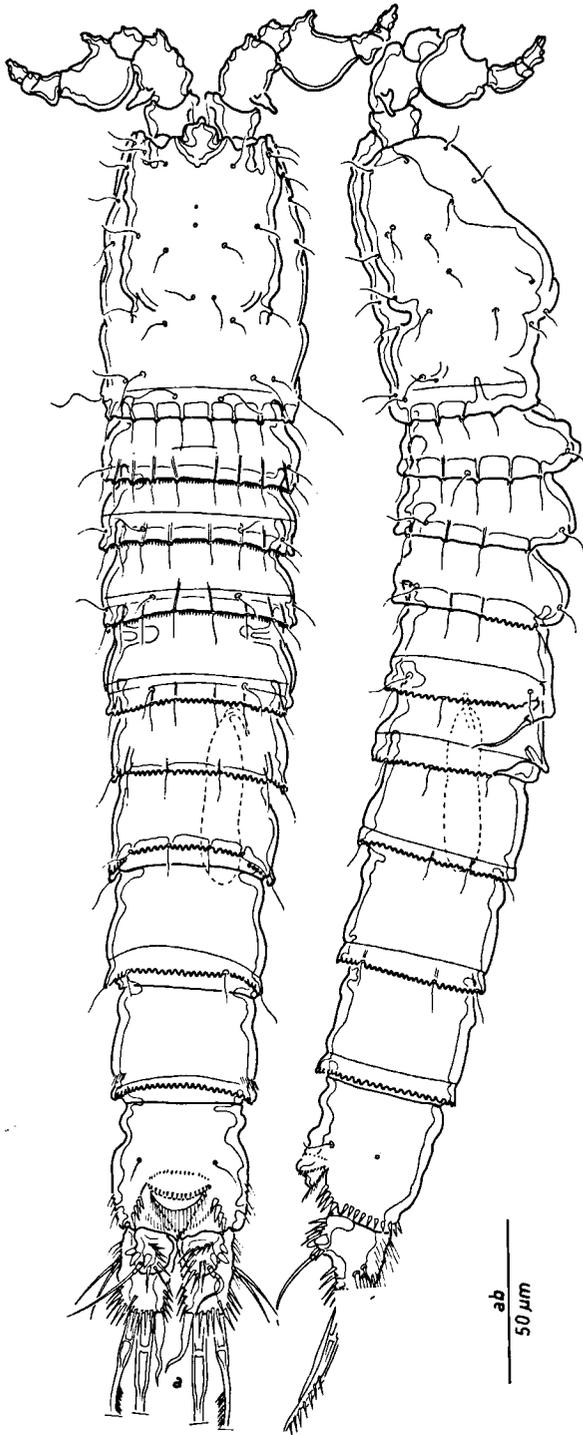
Fig. 1. *Afrolaophonte stocki* n. sp. (paratype, male): a, habitus in dorsal view; b, habitus in lateral view.

P$_3$ (Fig. 2i): coxa, basis and endopodite fused; the latter prominent and bearing one outer long and one inner dwarfed seta; exopodite two-segmented, having four spines on the second segment.

P$_4$ (Fig. 2f): coxa distinct; endopodite typical and fused with the basis; exopodite three-segmented bearing three spines on the ultimate segment.

P$_5$ (Fig. 2d): baseoendopodite with a prominent endopodal process and bearing four setae; both proximal setae more or less spiniform; exopodite slightly longer than wide and having four setae.

Male (allotype):

Habitus (Fig. 1a, b) and length as in the female except for the free genital segments.

Antennule (Fig. 2c): first and second segment as in the female; third to seventh segments forming the sub-chirocer apparatus.

P$_3$ (Fig. 2j): coxa distinct and furnished with spinules; exopodite three-segmented; endopodite two-segmented; second endopodal segment prolonged into a long curved apophysis bearing one smooth seta.

P$_4$ (Fig. 2g): coxa with a transversal row of spinules; basis with an inner seta, representing the vestigial endopodite; exopodite three-segmented, having a very strong spine on the first segment.

P$_5$ (Fig. 2k): baseoendopodite fused with the supporting segment; exopodite small and bearing three setae; margin of the baseoendopodite furnished with long hairs.

P$_6$ (Fig. 2l): right leg somewhat larger than left one; both legs represented by two setae and an inner row of spinules.

Discussion. — From table I, it clearly appears that *A. stocki* n. sp. is most closely related to *A. monodi* Chappuis, 1960. As will be discussed below, both species belong to the atlantic species-group and are characterized within this group by their two-segmented P$_3$ exopodite.

A. stocki n. sp. differs from its sisterspecies in the shape of the female P$_5$ and in the chaetotaxy of the P$_3$ and P$_4$. The exopodite of the P$_5$ in *A. monodi* is nearly 2.5 times as long as wide. In *A. stocki* n. sp. this ramus has a much

rounded appearance and is only slightly longer than wide.

More important is the chaetotaxy of the endopodites of P_3 and P_4. In *A. stocki* n. sp., the female endopodite P_3 bears, besides a long smooth seta, a small fragile seta implanted on the innermost edge of the segment. The male P_4 bears also a distinct seta representing the endopodite. It is possible that Chappuis (1960)

overlooked the dwarf seta in the P_3 of *A. monodi*, but the absence of an endopodal seta in the male P_4 of this species clearly discriminates it from *A. stocki* n. sp.

Including *A. stocki* n. sp., the genus *Afrolaophonte* comprises twelve species (see Table I). The most recent key (Cottarelli & Mura, 1981) mentions only seven species out of twelve, so an updated key is added here. Since
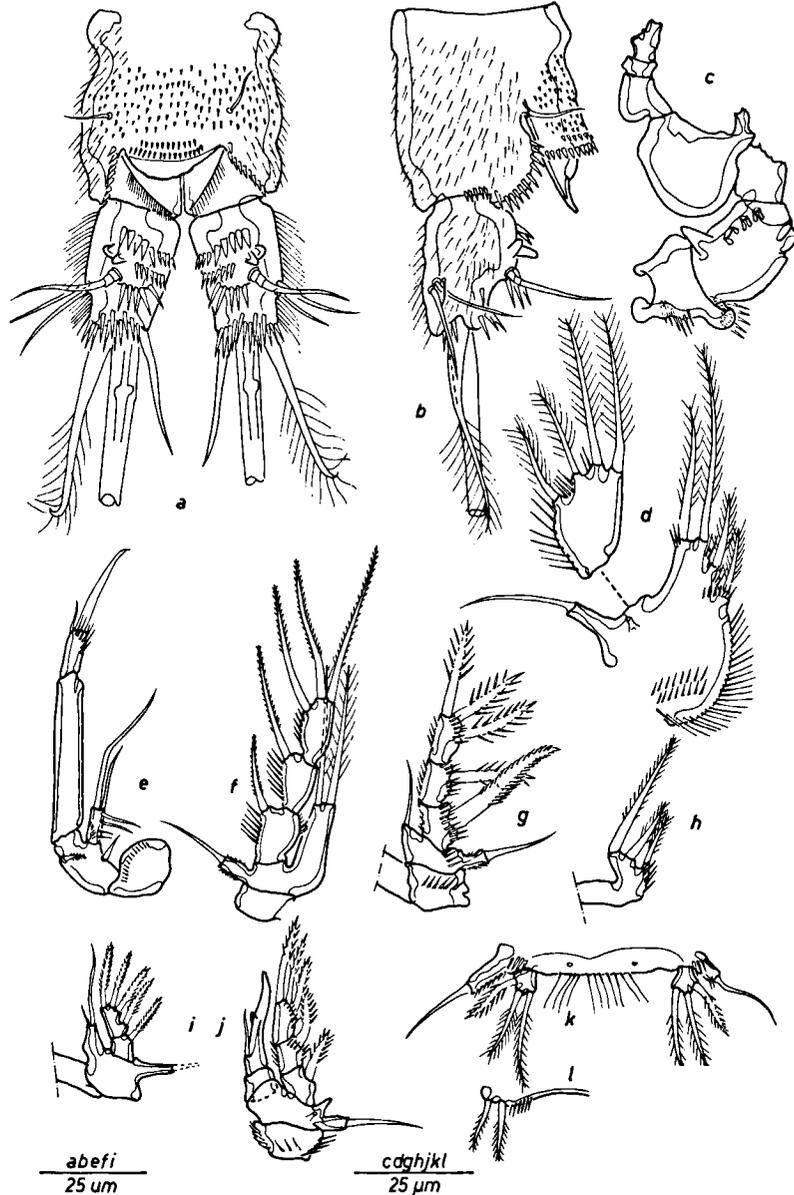

Fig. 2. *Afrolaophonte stocki* n. sp.: a, anal segment and furcal rami, dorsal view; b, idem, lateral view; c, antennule; d, P_5; e, P_1; f, P_4; g, P_4; h, P_2; i, P_3; j, P_3; k, P_5; l, P_6 (a, b, d-f, h-i of the female; c, g, j, k, l of the male).

the males of this genus do not differ greatly from each other, the following key deals exclusively with females.

1. Exopodite of P3 and P4 three-segmented, their terminal segments with four setae and spines 2
— These characters do not combine 3
2. Exopodite of P5 with four setae; P3 endopodite articulating with the basis ...... *A. schmidti* Mielke
— Exopodite P5 with five setae; P3 endopodite fused with the basis .... *A. chilensis* Mielke
3. Exopodite of P3 and P4 three-segmented; their terminal segments with three setae/spines 4
— These characters do not combine 5
4. Endopodite of P3 two-segmented ... *A. pori* Masry
— Endopodite of P3 at most one-segmented ....
.... *A. leonis* Cottarelli
5. Exopodite of P4 three-segmented, of P3 two-segmented 6
— These characters do not combine 7
6. Endopodite of P3 with a long and a dwarf seta; P5 exopodite at most 1.5 times as long as wide ....
.... *A. stocki* n. sp.
— Endopodite of P3 with one large seta; exopodite of P5 more than two times as long as wide ....
.... *A. monodi* Chappuis
7. Exopodite of P4 three-segmented, of P3 one-segmented
.... *A. renaudi* Chappuis & Delamare Deboutteville
— These characters do not combine 8
8. Exopodites of P4 and P3 two-segmented 9
— These characters do not combine 10
9. P2 exopodite fused with the basis, bearing three setae and spines; furcal rami as long as wide ....
.... *A. michae* Cottarelli
— P2 exopodite articulate with the basis and bearing two setae/spines; furcal rami 1.5 times as long as wide
.... *A. brevipes* Chappuis
10. Exopodite of P4 two-segmented, of P3 one-segmented 11
— Exopodites of P4 and P3 one-segmented ....
.... *A. renaudi* Chappuis
11. Terminal segment of P4 exopodite with three spines and setae; baseoendopodite of P5 with three setae
.... *A. michaelae* Cottarelli & Mura
— Terminal segment of P4 exopodite with four setae and spines; baseoendopodite of P5 with four setae ....
.... *A. brignolii* Cottarelli

PHYLOGENETIC CONSIDERATIONS

The genus *Afrolaophonte* is known for its remarkable interspecific homogeneity of most characteristics. Indeed, the cylindrical body shape, the morphology of the P1, the one-segmented endopodite P4 and the robust furcal rami are identical in all the species. More than females,

males of the known species resemble each other in nearly all respects; in so far, that species discrimination upon male characteristics is extremely difficult and even impossible. They exhibit however, such typical dimorphic features in the P3 and P4 that generic designation is obvious.

As shown in the key, species specific characteristics are exhibited in the setal ornamentation and in the segmentation of the exopodites of P3 and P4. To a lesser extent, species are distinguished upon the chaetotaxy of P2 (2, 3 or 4 setae) and the P5 (baseoendopodite, L/W-ratio of the exopodite). Other discriminating characteristics such as the number of segments in the antennule and the articulation of a segment with the basis of a leg have to be used with caution. The number of segments beyond the aesthetasc bearing segment of the antennule is found to be very variable in other laophontid genera. Moreover, the first segment beyond the third antennular segment is rather small, hidden behind the aesthetasc socle in dorsal view, and probably often overlooked. The same problems apply for the articulation of a segment with the basis of a leg. For most species, information on the variability is wanting and regarding the small dimensions of the rami, presence or absence of an articulation may be misinterpreted.

Table I summarizes the chaetotaxy of the legs of all known species of the genus. Apparently, reduction of the chaetotaxy and segmentation of the rami occurred at random within the genus, forming a weird assemblance of primitive and advanced character states for each species. Unfortunately, since the other characteristics are far too constant to be of any use, a phylogenetic analysis can only be based on these character states mentioned in table I.

The setal formulae presented in the form used in table I, hide several important features. Reduction of segments does not imply that the original morphology of the rami is lost. Considering each leg in detail, the original setal formula can be reconstructed, providing interesting clues for a sound phylogenetic hypothesis.

Table I. Chaetotaxy of the species of *Afrolaophonte*.

	P2	P3		P4		P5		P5
	exo	exo	end	exo	end	exo	exo	exo
A. chilensis	111	0-0-112	1	0-0-112	020	5	4	4
A. schmidti	111	0-0-112	010	0-0-112	020	4	4	3
A. aequatorialis	112	114	010	114	020	5	4	3
A. pori	011	0-0-012	0-020	0-0-012	020	4	4	3
A. monodi	011	0-013	1	0-0-012	020	4	4	3
A. leonis	011	0-0-012	1	0-0-012	020	4	4	?
A. renaudi	011	014	010	0-0-012	020	4	4	?
A. stocki	011	0-013	020	0-0-012	020	4	4	3
A. brevipes	011	0-012	1	0-013	020	4	4	3
A. michaelae	111	013	1	0-012	020	4	3	3
A. michae	111	0-012	1	0-013	020	4	4	?
A. brignolii	011	013	1	0-013	020	4	4	3

Note: the rami of the legs are sometimes fused with the basis.

As generally accepted, a three-segmented ramus, bearing the highest number of setae/-spines represents the most plesiomorphic state (Boxshall et al., 1984). In *Afrolaophonte*, A. *schmidti* and A. *chilensis* show the most primitive legs. The first and second segment of the exopodal rami in P3 and P4 are furnished each with an outer spine while the ultimate segment has four appendages.

In the genus two different reduction patterns are recognizable, causing the decrease of the number of segments and the setal ornamentation.

Reduction of the articulation between the segments may results in a one-segmented ramus which, most important, still shows the original chaetotaxy. For the most plesiomorphic chaetotaxy, the formula for such reduced type should be 114 but is basically the same as 0-0-112.

The second pattern affects the number of setae on the rami. Some species still have a three-segmented exopodite but bear only three spines on the ultimate segment. It is clear that one of the setae on the third segment is lost. In other species, having two-segmented exopodites, the setal ornamentation of the distal segment resembles the arrangement of the setae of the most primitive ones. These species lack one of the outer spines. Personal observations of the development of the chaetotaxy and segmentation of the legs in other laophontid genera, showed that such type resembles the legs of the fourth copepodids in all aspects. In other words, this type of reduction in *Afrolaophonte* results from a heterochronic shift in the development of the rami, resulting in a reduced setal ornamentation in the adult.

Based on the above discussed reduction patterns, three different species groups are distinguishable. They represent three monophyletic groups within the genus. After each group branched off from their common ancestral stock, the groups evolved separately causing the scattered patterns of apomorphic and plesiomorphic traits.

The most primitive group, the *chilensis*-group comprises A. *chilensis*, A. *schmidti* and A. *aequatorialis*. The group is characterized by the (originally) three-segmented exopodal rami in P3 and P4, bearing four setae/spines on the ultimate segment. A. *aequatorialis*, at first sight should not be assigned to this group because of the one-segmented exopodal rami in P3 and P4. Regarding however, the total number of setae/spines on the rami, it appears that the rami of A. *aequatorialis* have lost their segmentation but retained the typical (plesiomorphic) setal arrangement. Another indication sustaining the assignment of this species to the *chilensis*-group is the presence of five setae on the baseoendopodite of the female P5, a feature it shares with A. *chilensis*.

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Furthermore, *A. aequatorialis* is unique within the genus because of the distinct one-segmented P_2, bearing four setae. This may indicate that *A. aequatorialis* evolved from an early branch within the *chilensis*-group.

The three species of this group have nearly the same body length. The lengths range from 420 µm to 450 µm in the females and from 360 µm to 470 µm for the males.

The second group, herein named the *brevipes*-group, unifies four species, namely: *A. brevipes*, *A. michaelae*, *A. brignolii* and *A. michae*. This group is characterized by the originally two-segmented exopodites in P_3 and P_4, bearing respectively three and four setae on the last segments. Comparing these character states with these of the *chilensis*-group, it appears that the P_4 has lost the outer spine of the original median segment while the P_3 lost the same median spine and a spine on the ultimate segment.

Two species, *A. michaelae* and *A. brignolii* have a one-segmented exopodite in the P_3. However, the number of setae on this segment is the same as in the two-segmented rami of the two other members of the group. *A. michaelae* differs also in the chaetotaxy of the ultimate segment of the P_4 and the chaetotaxy of the baseoendopodite of the female P_5, bearing three setae instead of four. All other features of this species, especially the number of setae on the P_3, resemble its congeners.

The four species of the *brevipes*-group are considerably smaller than these of the *chilensis*-group. Lengths range from 223 µm (*A. michaelae*, male) to 380 µm (*A. brignolii*, female). The species of this group probably occupy sediments with smaller interstitial cavities than the species of the *chilensis*-group.

The *monodi*-group, comprises the remaining five species: *A. monodi*, *A. leonis*, *A. pori*, *A. renaudi* and the here described *A. stocki*. All these species have a three-segmented exopodite in the P_4, bearing three spines on the ultimate segment. Two species, *A. pori* and *A. leonis* still have an, original, three-segmented P_3 exopodite which bear three spines on the last segment. *A. monodi* and *A. stocki* bear a two-segmented exopodite while *A. renaudi* is characterized by a uni-segmented P_3. Nothwithstanding the reduction of the segments, the total number of setae/spines on the P_3 exopodite is identical in the five species of this group. The three-segmented rami resemble the rami of the *chilensis*-group but they differ from the latter because of the absence of a fourth spine on the ultimate segment.

Regarding the dimensions, the *monodi*-group shows two size ranges. *A. monodi* and *A. stocki* have a mean body length of 455 µm (430-480 µm. The other are minimum 250 µm (*A. pori*, male) and maximum 340 µm (*A. leonis*, female) long.

Within this species group, *A pori* represents the most primitive branch. The two-segmented endopodite in the P_2 differentiates this species from all other ones. *A. leonis* takes an intermediary position between *A. pori* and the two species with a two-segmented exopodite in the P_3. The most advanced species in this group clearly is *A. renaudi*, bearing a one-segmented P_3 exopodite.

It is clear that the *chilensis*-group is the most primitive subgroup in the genus. The *brevipes* group, having four appendages on the ultimate segment of the P_4 exopodite but only two-segmented rami, seems to be directly related to the *chilensis* group.

The two primitive species of the *monodi* group (*A. pori*, *A. leonis*) with their three-segmented exopodites in P_3 and P_4, indicate that the *monodi* group branched off from the common ancestor with the *chilensis*-group. Because of the primitive segmentation of the rami, the origin of the *monodi* group must be situated before the *brevipes* group deviated from its sister taxon.

The presented analysis of the genus *Afrolaophonte* does not explicitly indicate an outgroup. Simply, because we cannot define a suitable genus or genus group. However, it is generally accepted that interstitially living taxa exhibit a distinct trend to reduce the appendages. Anyway, the reduction of setae and rami of the legs is a common phenomenon within the family Laophontidae, and in harpacticoids in general. Reduction of the segmentation and/or

chaetotaxy is considered as a derived condition. Therefore, the herein defined species groups, are considered as monophyletic groups within the taxon *Afrolaophonte*.

ZOOGEOGRAPHY

The genus *Afrolaophonte* shows a typical pan-tropical distribution with representatives in each oceanic basin and the Mediterranean Sea. So far, all the known species were reported from interstitial localities in the intertidal zone, which are characterized by a fairly well sorted sediment. The small size, the cylindrical body shape and the highly reduced (specialized) appendages are undoubtedly adaptations for these animals, spending their entire life cycle in their preferred sediment.

In a detailed study of the local distribution of *A. schmidti* in a Galapagos beach. Mielke (1981) demonstrated the preference of the species to the central parts of the intertidal zone. *A. schmidti* occurs most abundantly in the deeper parts of the sediment. Although the description of the localities of the other species is far less documented, it appears that their habitats resemble closely those of *A. schmidti*.

Five species out of twelve are known only from their type-locality. The other species were mentioned from several localities either in the same paper or in successive contributions. The distribution of the twelve *Afrolaophonte* species, as it is actually known, is shown in Fig. 3.

Within the Pacific Ocean, the genus is represented by *A. chilensis* and *A. schmidti*. The former has been reported from some localities along the chilean coast (Mielke, 1985), the latter from the Galapagos (Mielke, 1981) and the pacific coast of Panama (Mielke, 1982). *A. aequatorialis*, the third member of the *chilensis* species group, has been described from the Maldives (Cottarelli & Mura, 1981) and is reported here from the southern coast of Papua New Guinea. Regarding the two widely separated localities, we probably may expect this species on many more beaches of the Indonesian island arc.

The *chilensis* group, indicated with the code 3-4 in Fig. 3, penetrates the Indian Ocean via the numerous islands of the Indonesian Archipelago. To what extent this species group ranges eastwards is unknown since data from islands in the western Pacific Ocean are not yet available.

The *brevipes* group, in Fig. 3 indicated as 2-4, occurs exclusively in the Indian Ocean. *A. brevipes*, described from Madagascar (Chappuis, 1954), has been reported from Inhaca by Wells (1967). *A. michaelae*, *A. brignolii* and *A. michae* are known from the type-locality, respectively the Maldives (Cottarelli & Mura, 1981), the Sunda Isles (Cottarelli, 1985) and Sulawesi (Cottarelli, 1985). Thus, the eastern part of the range of the *brevipes* group overlaps completely the range of the western extension of the distribution area of the *chilensis* group. However, the body size of the species of the *brevipes* group is markedly smaller than that of the *chilensis* species group. Apparently, both groups prefer a different type of sediment.

The *monodi* group (3-3 in Fig. 3) is represented in the Mediterranean Sea by *A. pori*. This species has been found along the Israelean coast (Masry, 1970) but has never been reported from elsewhere, although many contributions on the interstitial fauna of this sea and adjacent basis were published.

Two species of the *monodi* group occur along the West African coast. *A. monodi* has been reported from Senegal (Chappuis, 1960) and from Ghana (Chappuis & Rouch, 1961), while Cottarelli & Mura (1981) described *A. leonis* from Sierra Leone. The eastern central Atlantic lodges the herein described *A. stocki* (Guadeloupe) and the highly advanced *A. renaudi* which has been described from the Bahamas (Chappuis & Delamare Deboutteville, 1956; Renaud-Debyzer, 1963).

In Fig. 3 all the known localities of the species are plotted. The range of each group is tracked and indicated with a code referring to the original segmentation (first numeral) and the original chaetotaxy of the last segment (second numeral) of the P_4.
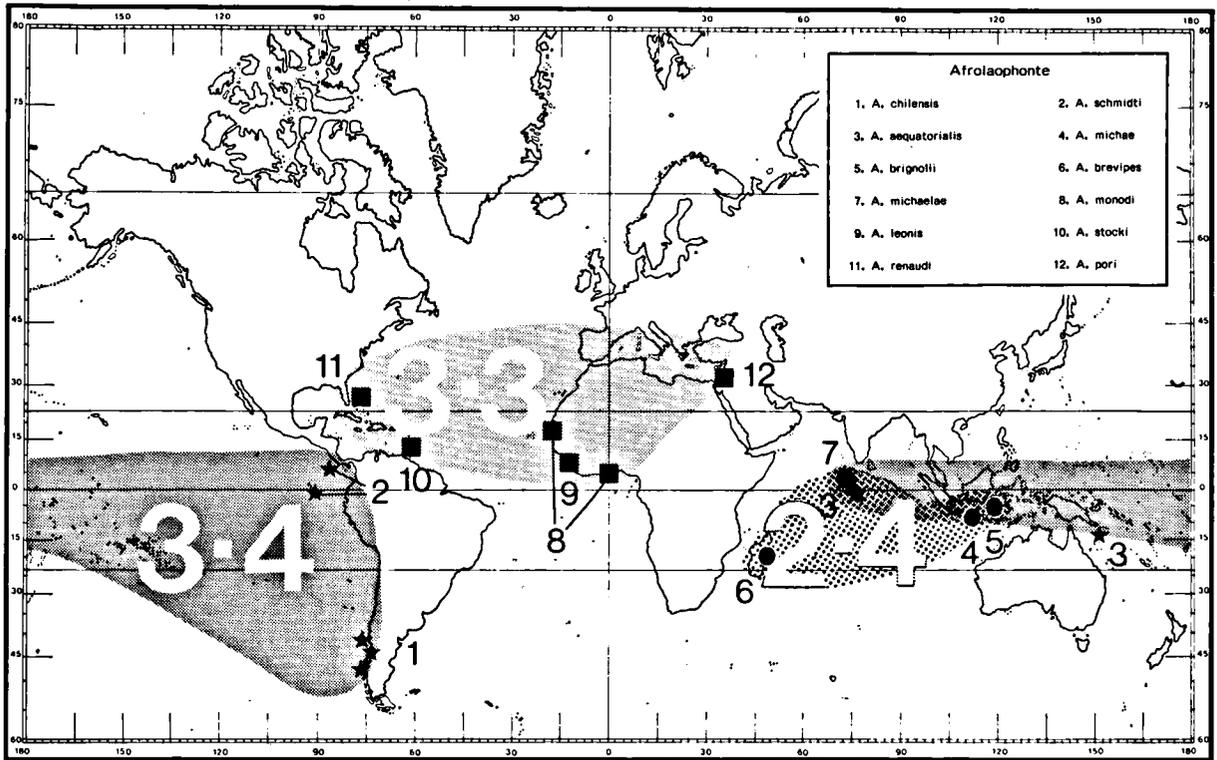
Fig. 3. Distribution of the genus *Afrolaophonte*. Numerals indicate respectively *chilensis*-group (3-4), *brevipes*-group (2-4) and *monodi*-group (3-3).

CONCLUSIONS

Summarizing the data on marine benthic harpacticoids gathered during almost two centuries of research, Wells (1986) could only demonstrate: "the depth of our ignorance" and underline: "the obvious conclusion that a rational theory of the biogeography of the marine benthic harpacticoid copepods is not yet possible" (p. 133-134). The reasons are clear. Detailed research on systematic relationships at any level is rare in harpacticoid systematics and large areas in all oceanic basins have never been part of a study of the copepod fauna.

Rejecting traditional views of trans-oceanic dispersal, Wells (1986) concluded that only alongshore migration and continental drift explains the far-flung distributions. In a recent paper, Ho (1988) illustrated such in detail for the canuellid genus *Sunaristes* and showed thus, that modern systematic and biogeographic

methods are conceivable in harpacticoid research.

In contrast with the canuellid genus *Sunaristes* which lives in association with hermit crabs, the species of *Afrolaophonte* are exclusively inhabitatns of the interstitial realm. In other words, they are sediment bound and probably spend their entire life cycle in the interstitial cavities of that sediment. The same geological events used to support the hypothesis of the historical biogeography of *Sunaristes* in Ho (1988), form the basis of the explanation of the present day distribution of the genus *Afrolaophonte*.

It is supposed that the ancestral stock of the genus *Afrolaophonte* lived along the shores of the circumglobal aequatorial Tethys Sea. Eventually, when that part of the Tethys which constitutes the present day mediterranean, was cut off from the Indo-Pacific area, the ancestral stock became subdivided in two groups.

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Separated from the original stock, the mediterranean population developed into the *monodi* group which dispersed in westward direction. That the *monodi* group did not originate in the Caribbean, as a branch from the eastern Pacific fauna, is based on the observation that the most primitive species of this group are known from the Mediterranean Sea and the West African coast. The representatives of the genus in the Caribbean seem to be part of the Eastern Atlantic (West African)-Caribbean track (Rosen, 1976).

The Indo-Pacific population, which probably had many features in common with the actually known *chilensis* group, split up. The *brevipes* group originated and became dispersed into the Indian Ocean. As illustrated in Fig. 3, the range of the *brevipes* group shows an important overlap with the track of the *chilensis* group in the Indonesian Archipelago. A possible explanation for this peculiar pattern may be the several eustatic sea level changes and their consequent effects on the beaches of those islands. As illustrated by Potts (1984) such drastic changes remodel the archipelago in an almost continuous landmass. The influence of such events on the sediments of the beaches, especially on the sorting of sediments and the creation of landlocked basins, are obvious. The *brevipes* group, with its remarkably smaller members, branched off from the ancestral Indo-Pacific group, because of their preference for a different type of sediment. The several successive changes of sea level probably explain also the diversity and the high degree of endemism among the several islands.

The biogeography of the genus *Afrolaophonte* can be described in terms of panbiogeography. However, explaining the widespread distributions of some of these interstitially living animals based on the alongshore dispersal and continental drift remain problematical. For example, we saw that *A. schmidti* inhabits the beaches of the Galapagos. Apparently, some kind of dispersion mechanism made it possible for this species or an ancestor to invade these beaches since the Galapagos are typical oceanic islands. The same question arises for the papuan locality of *A. aequatorialis*. Even with the eustatic sea level changes, the papuan-australian land mass has been always separated from the Indonesian island arc by a deep sea way (Potts, 1984). Dispersion of phytal harpacticoid copepods is fairly well documented (Yeatman, 1962) but for interstitial faunal elements we still lack information which explains the widespread distribution of some of its members.

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