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Two new genera of parathalassiine-like flies from South Africa (Diptera, Empidoidea)

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A b s t r a c t. Two new genera, *Plesiothalassius* and *Amphithalassius*, and four new species, *Plesiothalassius natalensis*, *P. flavus*, *Amphithalassius piricornis* (type species) and *A. latus*, are described from sandy biotopes of the South African sea coast. *Parathalassius capensis* Smith, 1972 is included in and designated type species of *Plesiothalassius*. A preliminary discussion of the phylogenetic relationships of the new genera leads to the conclusion that they can be ascribed to a monophyletic group including *Parathalassius* Mik, *Microphorella* Becker and the Dolichopodidae, but excluding *Microphor* Macquart (Microphorinae). A further subdivision of the group into monophyletic units of equivalent rank is still impossible, and if the new genera are included in the Parathalassiinae, the concept of this subfamily may become paraphyletic.

K e y w o r d s. Diptera, Empidoidea, Dolichopodidae, Microphoridae, Parathalassiinae, new genera, new species, southern Africa, phylogeny.

Introduction

The genera *Parathalassius* Mik and *Microphorella* Becker are of particular interest to dipteran phylogeny since both are considered to represent the sister group of the Dolichopodidae (Colless 1963, Hennig 1971, Chvála 1981—88). Both were traditionally included in the Empididae. Chvála (1981) united them in a tribe, Parathalassiini, or subfamily, Parathalassiinae (1986), and placed them provisionally in the Microphorinae, a taxon subsequently raised by him to family rank, Microphoridae (Chvála 1983).

Parathalassius is only known from sandy sea coasts of the northern temperate and Mediterranean zones. Under similar conditions, on coastal sand dunes, Stuckenberg discovered a species in South Africa, which was described as *Parathalassius capensis* by Smith, 1972 on the basis of the available, pinned material. A re-examination of a small series of similar flies sent to me by Dr. M.E. Irwin (Natal Museum, Pietermaritzburg, now University of Illinois, Urbana) and representing another species, led me to the preliminary conclusion that they do not fit either in *Parathalassius* or *Microphorella*. In order to collect more material for a detailed morphological study, I undertook a journey to South Africa and Namibia in October 1989.

On dry sand, mostly dunes with sparse vegetation, along the coast of the Indian Ocean, both species mentioned and a third one were collected in both sexes. In the present paper they are ascribed to a new genus, *Plesiothalassius*, and the new species described. Under the same conditions four species of another new genus, here called *Amphithalassius*, were collected, two represented by both sexes and two by a single female each; furthermore, two females from the Atlantic coast representing a fifth species were found among unidentified material in the collection of the Natal Museum. The two species with both sexes available are described in this paper,

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whereas the other three are only briefly referred to in the key to species. Although the scanty material available of the latter is deemed insufficient for species descriptions, it is appropriate at least to furnish some additional information about intrageneric variation and geographical distribution of the genus.

Little is known about the biology of the new genera. The flies were difficult to observe in their natural habitat, owing to their small size and white appearance contrasting little against the dry sand. They were most easily discovered when moving or when light was reflected from their wings. Flies were only seen landing on the sand, standing still for a few seconds at most, and taking off. They seemed to be very shy, taking flight at the slightest disturbance, and when an individual was discovered on the sand it could be taken only by quickly putting the net over it. The flies could also be collected by sweeping close to the ground and around the plants growing on the sand. Gentle sweeping movements, as demonstrated by Dr. B. R. Stuckenberg (Natal Museum, Pietermaritzburg) on a joint collecting trip, seemed to be essential for getting the flies into the net; in contrast, sweeping by quick net strokes was unsuccessful. When caught, all three *Plesiothalassius* species differed strikingly from *Amphithalassius* (and *Parathalassius*, as observed on other occasions) by running about quickly and continuously in the net or tube, whereas *Amphithalassius* exhibited a jerky manner of locomotion, stopping after a few steps and often changing position by a jump or short flight. In nature on sand, however, *Plesiothalassius* was never seen running; if it did so, it should be easier to discover.

All specimens collected were anaesthetized with ethyl acetate before they were transferred into preserving fluids. Those destined for taxonomic work were preserved in 75 % ethanol, those for more detailed morphological studies including histology were fixed in Schaffer's fluid (96 % ethanol, 2 parts, and 40 % formaldehyde, 1 part) mixed with glacial acetic acid in a ratio of 10 : 1 (FEA, formaldehyde-ethanol-acetic acid) (Burck 1973, p. 51) and stored in 70 % ethanol. A few specimens were later dried and pinned, applying the method proposed by Sabrosky 1966.

In the following descriptions most characters, including shape of parts, ground colours and wing measurements, are reported as observed on specimens in ethanol, whereas "pruinosity" could be better discerned on dried specimens where available. The figures, both photographs and drawings, were taken from flies in ethanol without further treatment, except those of female abdomens which had been macerated and stained with Delafield's haematoxylin. The wings were drawn from slide mounts with supplementary details from specimens in ethanol.

A detailed study of the thorax and male postabdomen in one species each of both genera is being prepared and will be published separately. In order not to anticipate the results, the structure of the male genitalia will not be considered in the present descriptions. As to the phylogenetic relationships of the new genera, only preliminary remarks will be given, pending further results.

Deposition of material: The holotypes and some of the paratypes of the new species will be deposited in the Natal Museum, Pietermaritzburg (NM), the other paratypes in the author's home institution, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). The specimens destined for detailed morphological work are not given type status although there is no doubt that they are conspecific with the types; all material remaining from that study will be stored in ZFMK.

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Acknowledgements: As stated above, Dr. M. E. Irwin set the initial stimulus to the present study by providing the first material. He sent it in 1974, when I was still unable to assess the generic status of the flies in the absence of true *Parathalassius* material for comparison. Dr. B. R. Stuckenberg kindly offered his co-operation since he knew about my interest in the group as early as 1972. The collecting success of my journey is largely due to his advice and generous assistance both in the preparatory stages and during the trip. As Director of the Natal Museum he kindly made available to me all the facilities for studying my material and the collections of the Museum. The chemicals for anaesthetizing, fixing and preserving the flies collected were kindly provided by the South African Museum, Cape Town (Dr. H. G. Robertson, Dr. V. B. Whitehead) and the State Museum, Windhoek (J. Irish). The journey was jointly sponsored, in equal part, by my home institution and the German Research Organization (Deutsche Forschungsgemeinschaft, project Ul 43/5-1). For other empidoid species, some of which are also new to science and will be studied later, the Director-General of the Department of Environment Affairs, Republic of South Africa granted a permission to collect insects on state forest land (permit K 219541). I am grateful to all these persons and institutions who by their help contributed to the practicability and success of the journey. Last but not least, I wish to thank Dr. Brian Stuckenberg again for productive discussions and a critical review of the manuscript, Dr. D. J. de Courcy Henshaw (London) for revising the English text, K. G. V. Smith (London) for reading the manuscript and his affirmative comments, A. Whittington (Natal Museum) for examining the holotype of *Plesiothalassius capensis*, Drs H. Schumann, R. Contreras-Lichtenberg, M. Fischer, P. C. Barnard, B. R. Pitkin and D. J. and D. de Courcy Henshaw for loan of material and for their hospitality and assistance when I visited the Zoological Museum of Humboldt University, Berlin, the Natural History Museum, Wien and the British Museum (Natural History), London to study type material, and Prof. Dr. T. Saigusa (Kyushu University, Fukuoka, Japan) who recommended Delafield's haematoxylin as a dye for distinguishing sclerites and membranes in pale, macerated preparations.

Descriptions

Plesiothalassius gen. n.

Type species: *Parathalassius capensis* Smith, 1972.

Diagnosis: Small flies inhabiting sandy coastal biotopes, shining white as if heavily pruinose, similar to *Parathalassius* Mik in most characters but differing as follows: Prothorax without precoxal bridge, one pair of scutellar bristles only; head more rounded in lateral view, face moderately wide in both sexes and more or less narrowing in middle (not upper) part, eyes shining golden, antennae with third segment globular or oval, broadly rounded at apex, palpi much dilated toward apex; male genitalia smaller and different in structure, fourth abdominal sternite unmodified, symmetrical and forming part of preabdomen; female abdomen with eighth tergite deeply cleft from behind, tenth hemitergites short, not projecting above cerci and bearing bristles, not spines. The known species are largely pale in ground colouration including the major part of the antennae, the legs up to their bases or nearly so, and varying parts of the trunk.

Differs from *Amphithalassius* gen. n. in its head being smaller and more rounded behind and the thorax more curved between anterior and dorsal surfaces, both characters contributing to a more humpbacked appearance; rounded shape of third antennal segment, golden shine of eyes, multiseriate postocular occipital bristles; entire lack of a prothoracic precoxal bridge, bristles longer and well developed even on anterior part of thorax, acrostichals paired and flanked by accessory bristles; dif-

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ferent structure of male genitalia; female postabdomen slender, eighth tergite deeply cleft; and a greater extension of pale ground colour as stated above.

Among the characters mentioned above, the following are apomorphous when compared with both *Parathalassius* and *Amphithalassius*: Pale ground colouration of entire legs and most of the antennae, rounded shape of third antennal segment, and golden shine of the eyes.

Generic characters: Small flies, the known species with ground colour partly black or brown, partly yellow or white, with a dense covering of microtrichia causing a whitish pruinose appearance, and with most of the bristles and hairs white or yellowish.

Head (Figs 2—3, 8—9, 17—18) medium-sized, appearing globular or broad oval in lateral view (Fig. 7), with occiput rounded and projecting far beyond hind margin of eye; upper median part of occiput, behind vertex, flattened and slightly concave. Eyes pubescent and with golden shine, green in life under daylight conditions. Dichoptic in both sexes, face moderately wide, narrowest in middle and widening both above and below, frons slightly or much wider, jowls (parts of head capsule below eyes) narrow. Bristles on head well developed, normally one pair each of converging fronto-orbitals and postverticals, two pairs of diverging ocellars the posterior of which are weak and may be missing; postocular occipital bristles multiseriate, evenly covering lateral occiput. Antennae inserted above middle of eyes, mainly pale, segments 1 and 2 short, 1 bare except covering of microtrichia, 2 with a circlet of short bristles, 3 globular or short oval, pubescent; arista inserted apically, without visible segmentation and with or without pubescence, sometimes with secondary sexual adornments. Proboscis short and pointing downward, labella partly membranous, palpi one-segmented, dilated toward apex and club-shaped or flattened.

Thorax: Mesoscutum with dorsal surface moderately arched yet appearing humpbacked by a marked and nearly angular bend of contour at transition into vertical anterior surface (side view, Figs 1, 7, 16), and with a flattened area on posterior slope in front of scutellum. Bristles well developed, scutellar (1), postalar (1), notopleurals (2), posthumeral (1), dorsocentrals (about 5—7) and hindmost supra-alar being the longest. Acrostichals short, biserial (paired), flanked by accessory bristles, ending in front of flattened posterior area and preceded by one pair, rarely two, of stronger bristles which are inserted on upper part of vertical anterior surface and touch occiput when head is raised (apparently proprioceptive in function). Accessory bristles, similar in size to acrostichals and more or less clearly arranged in rows, between acrostichals and dorsocentrals, nearly in line with dorsocentrals and laterad of both dorsocentrals and supra-alars; their number is variable and seems to depend both on species and individual size, larger individuals having more bristles than smaller ones. Flattened posterior area normally bare but sometimes bearing a few accessory bristles. Anterior supra-alars short and hard to distinguish from accessory bristles. Humeral callus with several short setae but no long humeral bristle. Proepisternum and lateral lobe of antepronotum below humeral callus with one or several short or medium-sized bristles; otherwise pleura bare. Prothoracic basisternum lying isolated in membrane, tapering craniad with anterolateral angles blunt or indistinct and therefore widely separated from episterna (Fig. 11).

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Wing shape and venation (Fig. 6) as in *Parathalassius*, with axillary lobe weakly developed, the known species with white fringe on hind margin and white microtrichia causing a milky appearance. Costa running around the wing to posterior base, Sc ending in costa, faint in its apical section, R_{4+5} simple. Basal cells short, discal cell long, incompletely separated from second basal cell by M_{3+4} interrupted at base, normally closed distally by M—M crossvein and emitting three medial branches to wing margin. Cubital cell short, closed by CuA_2 which is straight or slightly curved and roughly perpendicular to both CuA and A_1, CuA_2+A_1 short and ending far from wing margin. A row of about 3—5 bristles on basal section of costa, increasing in length distad, the most distal bristle much longer than the one preceding it. More distally up to wing tip costa bears short spine-like bristles in addition to the usual fine hairs. Hairs of hind marginal fringe long near wing base.

Legs moderately long, their bristles short except on coxae: those on fore coxa short, longer near apex; on mid coxa long, including a fan-like vertical row of 2—4 erect bristles on lateral surface; hind coxa laterally with a vertical row of 2—4 bristles of varying lengths. Prominent femoral bristles include posterodorsals on fore femur, an anteroventral row toward apex on mid and hind femora, a few posterior and posteroventral bristles near apex of fore and mid femora, and a few erect dorsal bristles near base of hind femur. The anteroventral bristles are the longest but not longer than femur is deep, even shorter in the female. Tibiae and tarsi appearing ciliated by their coat of even-sized bristles. Fore tibia with an anterior apical comb of closely set setulae, mid tibia with several spine-like bristles around apex, a ventral preapical one being the longest, hind tibia and metatarsus with a spine-like ventral apical bristle and a posterior apical comb. Short spine-like bristles on plantar surface of tarsal segments 1—4, most conspicuous on mid leg where stouter spines are located at apices of segments in groups of four and weaker ones distributed over length of metatarsus in a double row. Tarsal claws, pulvilli and setiform empodium developed on all legs, ventral side of pulvilli and empodium haired.

Abdomen with short bristles. Male segments 1—4 forming preabdomen, symmetrical with simple sternites; postabdomen spirally contorted, segment 5 asymmetrical with tergite bent to the left, and sternite short and indented at hind margin to form anterior border of a groove concealing tip of hypopygium, segments 6—8 confined to left half, sternite 8 lying at hind end and exposed posterolaterad, tergite 8 atrophied; hypopygium occupying right half, inverted and with caudal pole directed forward, smaller than in *Parathalassius*, asymmetrical. (A detailed description of the hypopygium will be given in a separate paper.) Female segments 1—5 forming preabdomen into which posterior segments are retracted; postabdomen slender (Fig. 13, compare with *Amphithalassius*, Fig. 39), tergite 8 deeply cleft from behind, ventral plate of segment 8 much produced in median line with apex cleft to form a pair of paramedian tips (Figs 14—15, v8); terminalia not acanthophorous, apparently not adapted for digging: hemitergites 10 small, not projecting and with bristles not forming spines, cerci at tip of abdomen, broad, rounded and moderately sclerotized.

Etymology: A name referring to *Parathalassius* was chosen to connote that the species included agree with that genus in two respects, namely, living in sandy

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seashore habitats and showing the same set of characters from which the groundplan of the Dolichopodidae is considered to have evolved. It is derived from the Greek words πλησίον, near, and θάλαττα, sea, or θαλάσσιος, belonging to or concerned with the sea, and means, "living near the seashore". Gender masculine.

Key to species

1. Thorax largely brown or black. Male arista spatulate 2
— Thorax pale except postscutellar area and, sometimes, brown spots or stripes on mesoscutum and scutellum. Male arista simple ..... *flavus* sp. n.
2. Postvertical bristle widened and flat, tapering toward base (Figs 2—3). Hind metatarsus distinctly longer than second tarsomere. Male: Dilated apical section of arista as deep as ⅔—¾ depth of third antennal segment (Fig. 4), abdominal sternites 6 and 7 pale or light brownish at most; hypandrium pale, dark area of right periandrial lamella narrowest at base and wider in middle (Fig. 5). Female: Abdominal tergite 6 dark at least in anterior half ..... *capensis* (Smith)
— Postvertical bristle not widened or slightly so at most, not tapering toward base (Figs 8—9). Hind metatarsus in general hardly longer than second tarsomere. Male: Dilated apical section of arista half as deep as third antennal segment (Fig. 10), abdominal sternites 6 and 7 dark brown; hypandrium mainly brown, dark area of right periandrial lamella wide at base and narrowest in middle (Fig. 12). Female: Abdominal tergite 6 pale, at most with a pair of small brown spots at anterior margin ..... *natalensis* sp. n.

Fig. 1: *Plesiothalassius capensis* (Smith) ♂. Scale bar 0.5 mm.

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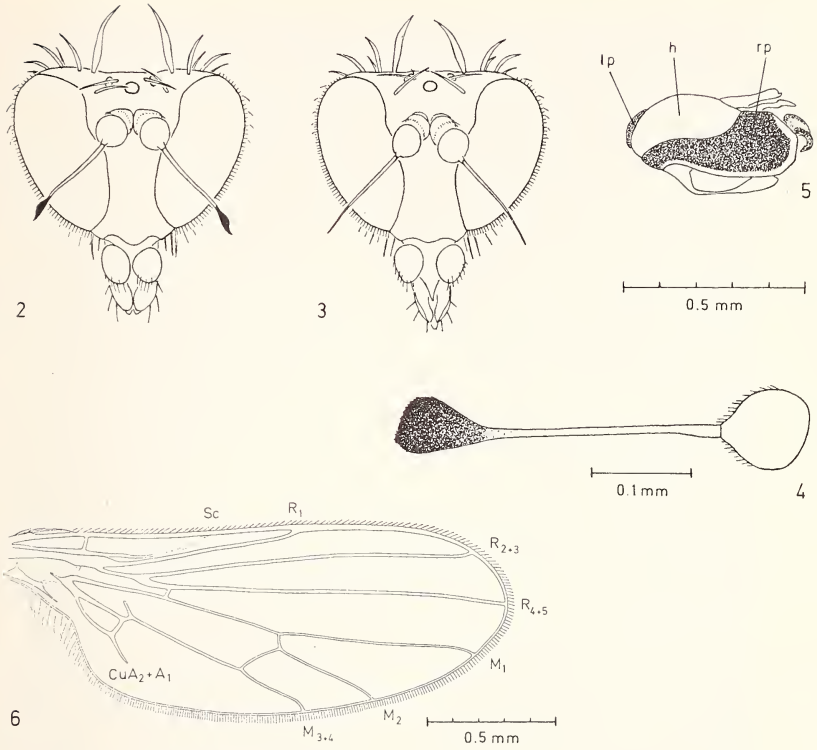

Figs 2—6: *Plesiothalassius capensis* (Smith). 2, ♂, and 3, ♀ head in anterior view. 4, third antennal segment and arista of ♂. 5, hypopygium, right lateral view; h hypandrium, lp left and rp right periandrial lamella. 6, wing of ♂. Longer scale bar 0.5 mm refers to Figs 2, 3 and 5.

Plesiothalassius capensis (Smith)

Parathalassius capensis Smith, 1972, Ann. Natal Mus. 21: 456—458, figs 1—5.

The original description is detailed enough to render this species easily recognizable, so a full redescription is considered unnecessary. Only an apparent error is corrected and those characters are described below in which *P. capensis* differs from the similar *P. natalensis* sp. n.

The eyes were described as touching on the face in the male, nearly touching in the female. These observations do not agree with mine and are obviously due to shrinkage of the specimens on which the description was based; in fact, the heads of all type specimens are so much shrunken that the shape of the face cannot be ascertained on them.

Male and female (Figs 1—6): Face entirely white, without yellowish tinge, wider than in *P. natalensis* and of nearly equal width in both sexes, 1.5 times to nearly twice depth of third antennal segment. Dilated apical section of male arista larger, as deep

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as ⅔—¾ depth of third segment of antenna. Postvertical and upper postocular occipital bristles distinctly widened and flat, postvertical widest at some distance from base and distinctly tapering to base (anterior view, Figs 2 and 3). Thorax: Dark areas more evenly shaded, dark brown or black, ventral half of metathoracic dorsal episternum dark; remainder of metathorax and posterior part at least of prothoracic basisternum white as in *P. natalensis*. Legs: Hind coxa narrowly darkened at lateral base, with a brownish spot at least. Hind metatarsus distinctly longer than second tarsomere, about 1.3—1.4 times its length.

Male abdomen: Tergites 1—7 dark brown or black, 2—6 with white hind margins, sternites 1—4 white or yellow, 4 sometimes brownish in its anterior half, sternites 5—7 pale brownish at most, sternite 8 entirely pale. Hypopygium: Hypandrium white or yellowish, periandrium dark brown or black with pale apices and right lamella with narrow pale lower margin which tapers off to base. Right periandrial lamella narrowest at base, widening to middle and more so toward apex, its dark area narrow and of even width in basal third, then widening toward middle and apex.

Female abdomen: Tergites 1—5 brown or black, 2—5 with pale hind margins, tergite 6 dark at least in anterior half and pale in posterior part, tergites 7 and 8 pale; sternites white, yellowish or pale brownish at most; ventral plate of eighth segment yellowish with a brown T mark, hemitergites 10 brown, cerci brown, paler in ventral part.

Wing length measurements: Male 1.85, 2.0 and 2.2 mm, female 2.25 and 2.4 mm.

Material examined: All from South Africa, south coast of Cape Province. 3♂ 2♀, Buffelsbaai, coastal sand dunes, 12. (1♂ 1♀), 13. (1♂ 1♀) and 14. X. 1989 (1♂), H. Ulrich, (in ethanol), in ZFMK. The paratypes deposited in the British Museum (Natural History) (4♂ 2♀) were checked for those characters mentioned which can be recognized in dried material. The males and one of the females agree with the above description, whereas the other female proved to belong to the following species. Mr. A. Whittington kindly examined the holotype in NM and confirmed that it shows the characters given in the key for the present species.

Plesiothalassius natalensis sp. n.

Male (Figs 7, 8, 10—12): Entire body appearing white pruinose, bristles and pubescence white unless otherwise stated.

Head: Upper frons, vertex and occiput black in ground colour, lower frons to a varying extent and face pale, white except lower face above clypeus yellow, line of anterior tentorial invagination marking the border between pale and black areas below the eyes. Face relatively narrow, slightly wider at narrowest point than third antennal segment is deep. Antennae: Segments 1—3 yellow, arista white in basal, black in apical section; third antennal segment globular; arista without pubescence, long, spatulate, its basal section stout, its apical section dilated dorsoventrad and compressed to form a vertical leaf-like structure which is about half as deep as third segment and irregularly serrated along its apical rim. Proboscis and palpi pale yellowish, palpi club-shaped, little flattened. Postvertical and upper postocular occipital bristles normally shaped or very slightly widened at most, not tapering toward base.

Thorax predominantly brown in ground colour, darkest on mesonotum, with a variable pattern of paler areas ranging from light brown to white, which generally

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Fig. 7: *Plesiothalassius natalensis* sp. n., holotype ♂. Scale bar 0.5 mm.

affect the following sclerotized parts: most of prothorax, with basisternum always white, mesothoracic pleural region between wing base and postnotum, anterior part of meron above mid coxa, ventral part of katepisternum, mesothoracic midventral region (sternum?), postalar callus with neighbouring areas, and entire metathorax, the last mentioned white with lower angle of dorsal episternum rarely brownish. A pair of more or less discernible longitudinal stripes laterad of the acrostichal bristles. Mesoscutum with numerous accessory bristles, more than 15 (generally 20—25) laterad of dorsocentrals on area in front of transverse suture and notopleural depression. Accessory bristles between acrostichals and dorsocentrals generally include a row midway between both and a more lateral row roughly in line with dorsocentrals;

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however, this arrangement may be so irregular that no fixed number of rows can be stated. Dorsocentrals 5—7, acrostichals 10—15 in each row; among supra-alars only posterior 1—3 identifiable by size or position, anterior ones not clearly distinguishable from accessory bristles.

Wing venation as in *P. capensis* (see Fig. 6), veins pale, bristles on base of costa white, costal spines black. Squamae white, with white fringe, halteres white.

Legs white, more or less yellowish distally, hind coxa not darkened at base. Fore and mid metatarsi as long as the following three segments together, hind metatarsus in general hardly longer than second segment (about 1.1 times its length; exceptionally longer, as in *P. capensis*). Longest anteroventral bristles on hind femur slightly shorter than greatest depth of femur. Bristles white to yellowish, tibial spines white to pale brownish, most of the spines on mid tarsus black. Tarsal claws varying from black to pale with darker tip, pulvilli and empodium pale.

Abdomen largely white in ground colour, particularly so on preabdomen, with a variable pattern of darker, brownish to yellow areas: Segments 1—4 entirely pale in general, rarely tergites 2—4 or 3—4 with a yellow or pale brown transverse band each, tergite and sternite 5 generally brown in part, tergites and sternites 6 and 7 dark brown, sternite 8 usually darkened at margins and pale in central part, sometimes entirely pale or uniformly pale brown. Hypopygium: Hypandrium and periandrium mainly brown, with pale apices and right periandrial lamella with pale upper and lower margins which are widest in middle section and taper off toward base. Right periandrial lamella broad at base, tapering to middle and widening again toward apex, therefore narrowest in middle section; this applies even more to its dark area. Periandrial appendages (possibly homologous to the musculated appendages, Ulrich 1988) partly brown.

Wing length 1.55—2.0 mm.

Female (Figs 9, 13—15): Similar to male but larger on average; face wider, about 1.5 times depth of third antennal segment and ⅕ width of head or slightly more, entirely white; apical section of arista generally darkened as in male but not dilated; anteroventral bristles on hind femur shorter. Abdominal tergites 2—5 largely pale, white or yellow, generally each with a brown transverse band which may be interrupted medially; tergite 6 pale, at most with a pair of small brown spots at anterior margin; seventh and eighth tergites and all sternites white; ventral plate of eighth segment pale or brownish, tenth hemitergites and cerci generally brown.

Wing length 1.65—2.3 mm.

Type material: All from South Africa, coast of Natal. Holotype ♂ (Fig. 7), paratypes 2♂ 1♀, Umdloti Beach (northeast of Durban), sandy beach, 25. X. 1989, B. R. Stuckenberg, (holotype and paratypes 1♂ 1♀ in ethanol, 1♂ pinned). Paratypes 2♂, Umdloti Beach, sandy beach, 26. X. 1989, H. Ulrich, (in ethanol). Paratype 1♀, Kingsburgh, coastal sand dunes, 20. X. 1989, H. Ulrich, (in ethanol). Paratypes 3♂ 5♀, Mtunzini, coastal sand dunes, 27. X. 1989, H. Ulrich, (2♂ 3♀ in ethanol, 1♂ 2♀ pinned). Paratypes 3♀, St. Lucia, coastal sand dunes and river estuary, 28. X. 1989, H. Ulrich, (in ethanol). — Holotype and 8 paratypes (3♂ 5♀, one of each sex pinned) in NM, type number 703; 9 paratypes (4♂ 5♀, one of each sex pinned) in ZFMK.

Additional specimens not given type status: All from South Africa. Material for detailed morphological studies, a series each from Umdloti Beach, Natal (28♂ 3♀) and Marina Beach, Natal (15 km northeast of Port Edward) (5♂ 6♀), B. R. Stuckenberg and H.

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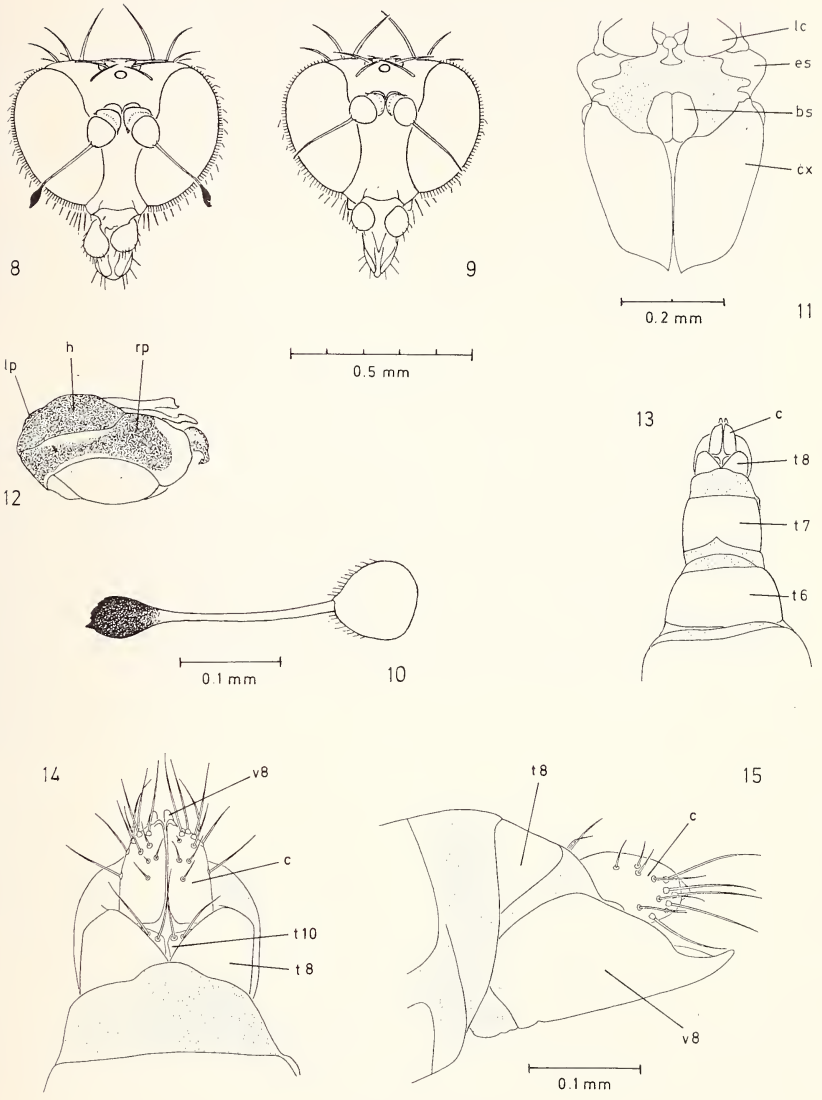

Figs 8—15: *Plesiothalassius natalensis* sp. n. 8, ♂ (holotype), and 9, ♀ head in anterior view. 10, third antennal segment and arista of ♂ (holotype). 11, prothoracic pleurosternal region of ♂ in anteroventral view; bs basisternum, cx coxa, es episternum, lc laterocervicale. 12, hypopygium, right lateral view; h hypandrium, lp left and rp right periandrial lamella. 13, ♀ postabdomen, dorsal view (macerated and stretched). 14 and 15, ♀ terminalia, dorsal and lateral views respectively (same preparation as in 13). c cercus, t6—t10 tergites 6—10, v8 ventral plate of 8th segment, perhaps laterotergite (Deuve 1988). Membranes dotted in Figs 11 and 13—15. Scale bar 0.5 mm refers to Figs 8, 9, 12 and 13, scale bar 0.1 mm below Fig. 15 applies to fig. 14 too.

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Ulrich, (in ethanol, fixed FEA), in ZFMK. 1♀ from the type series (paratype) of *Plesiothalassius capensis* (Smith), Zwartkops River near Port Elizabeth, Cape Province, B. & P. Stuckenberg, (pinned), in British Museum (Natural History). 7 specimens with darker areas pale orange instead of brown (faded post mortem?), from 50 km southeast of Bizana, Transkei (apparently near the border to Natal) (1♂ 2♀) and St. Lucia, Natal (3♂ 1♀), M. E. and B. J. Irwin, (in ethanol, 1♂ 1♀ from St. Lucia fixed Kahle's fluid), in NM.

Etymology: Latinized, *natalensis*, occurring in Natal, to compare with *P. capensis* which was described from Cape Province.

Remark: *Plesiothalassius natalensis* strongly resembles *P. capensis* and both are obviously closely related. As far as is known to date, *P. capensis* has a more western, *P. natalensis* a more eastern distribution. At the locality near Port Elizabeth both species occur sympatrically.

Plesiothalassius flavus sp. n.

Male (Figs 16—17): A small pale species with white "pruinosity" most conspicuous on head and thorax; bristles mainly white, yellow on thorax and partly darker on dorsal sides of tibiae and tarsi, pubescence white.

Head: Upper frons, vertex and occiput black in ground colour, lower frons and face white, pale colour of face extending more or less back below eyes beyond the line of anterior tentorial invagination and dorsad along the posterior eye margin. Face relatively wide, at its narrowest point nearly twice as wide as third antennal segment is deep. Antennae with segments 1—3 white or yellowish, third segment deeper than long, arista pubescent and without apical dilation, pale at base, progressively darkened distad and black in apical half at least. Proboscis yellowish, palpi white, relatively wider at apex and more flattened than in the other species. Postvertical and upper postocular occipital bristles simple, not widened.

Thorax pale in ground colour except postscutellar area: Mesothoracic scutum and scutellum yellow, scutum in holotype with traces of brown stripes which are more developed in females, median area of postnotum brown, sutures about the lateral angles of scutellum and trans-scutellar suture brown to a varying extent, lateral area of tergal region and pleura pale yellowish to cream-coloured, sternal area white. Accessory bristles few, their number apparently depending on body size and varying from 5 to 12 on presutural area laterad of dorsocentrals. Acrostichals 3—7 in each row, dorsocentrals 5; generally 1 identifiable supra-alar only, preceded by a group of 3—5 accessory bristles; on left side of holotype 2 anterior supra-alars can be identified, forming a straight line with the long posterior supra-alar and being slightly longer than the surrounding accessory bristles.

Wings with yellow veins and white marginal fringe, bristles on base of costa yellow, costal spines black. There is a tendency toward reduction of M—M crossvein and (observed in females) M_2 either in its basal or apical section. Squamae white, with white fringe, halteres white.

Legs entirely white. Fore and mid metatarsi about as long as the following three segments taken together, hind metatarsus distinctly longer than second segment but shorter than second and third segments together. Longest anteroventral bristles on hind femur shorter than femur is deep. Tibial and tarsal spines mainly pale, tarsal claws varying from pale to black, pulvilli and empodium pale.

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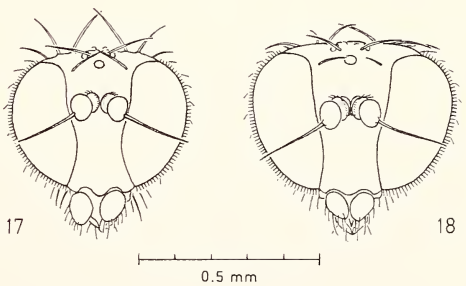
Fig. 16: *Plesiothalassius flavus* sp. n., holotype ♂. Scale bar 0.5 mm.



Figs 17—18: *Plesiothalassius flavus* sp. n. 17, ♂ (holotype), and 18, ♀ head in anterior view.

Abdomen mainly white in ground colour, tergites 2—4 with a pale yellowish transverse band, that on tergite 4 may be darkened anteriorly, tergites 5 and 6 contrasting by brown colour, tergite 7 light brown or with a brown spot; hypopygium white except brown tips of periandrial appendages.

Wing lengths measured 1.45 and 1.55 mm.

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Female (Fig. 18): Similar to male but larger and generally with a more developed brown pattern, face slightly wider, about twice as wide as third segment is deep, anteroventral bristles on hind femur shorter. Yellow ground colour of mesonotum deeper than in male, more or less distinctly interrupted by a pair of paler stripes which run along each dorsocentral row, widen in front toward humeral calli and thus leave a broad median and a pair of broad but shorter lateral yellow stripes. The yellow areas may be darkened brown centrally to a varying extent, the brown pattern when well developed consisting of a median stripe, narrow in front and widening behind to form a large median spot on flattened area and scutellum, and three pairs of lateral spots in front of transverse suture, above wing base behind notopleural depression, and between posterior dorsocentrals and long supra-alar respectively. 9—16 accessory bristles on presutural area laterad of dorsocentrals, 3—10 in front of long supra-alar, acrostichals 6—9 in each row, dorsocentrals 5. An increase in number of strong bristles was observed in a female bearing an additional bristle on each side anterolaterad of the foremost dorsocentral, 3 bristles on the left half and 2 on the right half of the scutellum. Abdominal tergites 2—5 with a brown anterior transverse band each, hemitergites 10 and cerci brown, ventral plate of eighth segment varying from white through yellow to pale brownish.

Wing length 1.6—2.2 mm.

Type material: South Africa, coast of Natal. Holotype ♂ (Fig. 16), paratypes 3♀, Umdloti Beach (northeast of Durban), sandy beach, 25. X. 1989, B. R. Stuckenberg, (in ethanol, 2♀ fixed FEA). Paratypes 1♂ 1♀, same locality, 26. X. 1989, H. Ulrich, (in ethanol). — Holotype and 2 paratypes ♀ in NM, type number 704; 3 paratypes (1♂ 2♀) in ZFMK.

Etymology: Latin, *flavus*, yellow, refers to the yellow colouration of the thorax.

Remark: Although some variation has been found regarding the pattern of ground colouration and the numbers and colours of bristles, it is impossible to assess its extent on the basis of the small type series.

Amphithalassius gen. n.

Type species: *Amphithalassius piricornis* sp. n.

Diagnosis: Small flies of sandy coastal biotopes, appearing heavily white pruinose, similar to *Parathalassius* Mik in general appearance and most characters but differing as follows: Prothoracic precoxal bridge incomplete, acrostichal bristles uniserial (unpaired) at least behind, sometimes reduced and never flanked by accessory bristles, one pair only of scutellars, bristles on anterior part of mesonotum short; face wide in both sexes, not narrower in upper part, postocular occipital bristles uni- to biseriate, palpi broad and flattened apically; male genitalia smaller, fourth sternite unmodified, symmetrical, forming part of preabdomen; female abdomen gradually tapering caudad with segments 6—8 wider than long, female terminalia with tenth hemitergites short, not projecting and bearing bristles instead of spines.

Differs from *Plesiothalassius* gen. n. in general appearance partly due to a larger head and the thorax more gently curved in profile, therefore appearing less hump-

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backed; by the third antennal segment conical or pear-shaped, tapering toward apex, eyes without golden shine; a partly developed prothoracic precoxal bridge; strikingly different structure of the male genitalia; broad female postabdomen, eighth tergite not cleft; furthermore by predominantly dark ground colouration and the characters of thoracic and head bristle inventory mentioned above except identical number of scutellars.

Among the characters listed above, the unpaired condition of the acrostichals and reduction in size of the anterior mesonotal bristles are apomorphous as compared with both *Parathalassius* and *Plesiothalassius*.

Generic characters: Small flies, the known species with ground colour mainly black, appearing whitish pruinose by reflection from a dense covering of microtrichia and with bristles and hairs predominantly white.

Head (Figs 21—23, 31—33) large, distinctly higher and wider than deep, occiput flattened and slightly concave in upper median part, more so in male. Eyes pubescent, without golden shine. Dichoptic in both sexes, frons and face wide, jowls narrow. Rostral membrane extending far onto face thus forming a membranous surface between broad rounded clypeus and narrow orbital stripe. Bristles on head short, including one pair each of converging fronto-orbitals and postverticals, and two pairs of diverging ocellars the posterior of which are smaller or even absent; postocular occipital bristles in one row or two above and in middle, irregularly arranged below. Antennae inserted near middle of eyes, segments 1 and 2 short, 1 bare except coat of microtrichia, 2 with a circlet of short bristles, segment 3 conical or pear-shaped, pubescent, arista inserted apically, pubescent and without visible segmentation. Proboscis short and pointing downward, labella partly membranous, palpi one-segmented, dilated and flattened toward apex.

Thorax: Mesoscutum moderately arched (Figs 19, 29), with a bare flattened area on posterior slope. Bristles short on anterior part, longer behind, the scutellar (1), posterior dorsocentrals, postalar (1) and notopleurals (2 or 3) being the longest. Acrostichals unpaired, most distinctly so behind, forming a more or less irregular row with some of the bristles a short distance outside median line, sometimes very small or even lacking; not flanked by accessory bristles. One pair, rarely two, of longer bristles the tips of which touch the occiput when head is raised (apparently proprioceptors), before acrostichals on anterior slope. Dorsocentrals originally about 6—10, becoming progressively longer behind, the anterior ones may be as short as acrostichals. A row of supra-alars, also longest behind, the foremost, or sutural, inserted on transverse suture. Humeral calli with a few tiny setae at most, posthumeral short and inserted far from humeral callus near upper angle of notopleural depression. Some additional small bristles may be present in front of transverse suture. Sometimes a weak bristle on lateral lobe of antepronotum below humeral callus and another on proepisternum; otherwise pleura bare. Prothoracic basisternum with anterolateral angles distinct and more or less extended toward episterna, thus indicating tendency to form a precoxal bridge (Figs 27 and 37, compare with Fig. 11); the width of membrane separating basi- and episternum is subject to both inter- and intraspecific variation and may even differ on both sides of the same individual.

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Wing shape and venation as in *Parathalassius*, with axillary lobe weakly to moderately developed, the known species with white marginal fringe and white microtrichia causing a milky appearance. Costa running around the wing to posterior base but strong only along anterior margin up to a short distance beyond apex of R_{4+5}, weak along hind margin. Sc reduced to a fold in its apical section, ending in costa. R_{4+5} simple. Basal cells short, discal cell variable in length, incompletely separated from second basal cell by M_{3+4} interrupted at base, closed distally and emitting three longitudinal veins to wing margin. Cubital cell short, closed by CuA_2 which is straight or slightly curved and roughly perpendicular to both CuA and A_1, CuA_2+A_1 reduced to form a short stump at most. A row of about 3—5 bristles on basal section of costa, their length increasing distad. More distally along anterior margin, costa bears short spine-like bristles in addition to the usual fine hairs. Hairs of hind marginal fringe long near wing base.

Legs moderately long, with short bristles. Fore and mid coxae with bristles on anterior and anterolateral surface, the longest near apex; hind coxa usually with two bristles on lateral surface, a basal (upper) and a distal (lower) one. Prominent bristles of femora include several irregular rows on posterodorsal and posterior surface of fore femur, an anteroventral row on mid and hind femora and several irregular dorsal rows on hind femur. The longest among these bristles are not longer than greatest depth of hind femur, shorter in female. Tibiae and tarsi appearing ciliated by their coat of even-sized bristles. Fore tibia with an anterior apical comb, mid tibia with a ventral preapical and a shorter anterior apical spine-like bristle, hind tibia and metatarsus with a posterior apical comb and with one and two ventral apical spines respectively. Short spine-like bristles on tarsal soles, paired and in groups of four, may contrast with the other bristles and hairs by black colouration, most conspicuous on mid tarsus. Tarsal claws, pulvilli and setiform empodium well developed on all legs, ventral side of pulvilli and empodium with a dense coat of hairs.

Abdomen with short bristles. Male segments 1—4 symmetrical with simple sternites, forming preabdomen; postabdomen spirally contorted, segment 5 asymmetrical with tergite bent to the left and hind margin of sternite indented, segments 6—8 confined to left half, sternite 8 exposed posterolaterad, tergite 8 atrophied; hypopygium lying on right side, inverted and with caudal pole directed forward, smaller than in *Parathalassius*, asymmetrical. (A detailed description of the hypopygium will be published separately.) Female abdomen gradually tapering toward tip with posterior segments broad, therefore ovipositor is not offset from the preabdomen (Fig. 39, for comparison see *Plesiothalassius*, Fig. 13), eighth tergite unpaired and not cleft from behind, at most with a shallow indentation at hind margin; terminalia not acanthophorous: hemitergites 10 short and broad, not projecting and with bristles not forming spines, cerci occupying tip of abdomen, broad, neither pointed nor heavily sclerotized.

Etymology: As for *Plesiothalassius* and for the same reasons a name suggestive of *Parathalassius* is proposed: Greek, ἀμφί, around or near, θάλαττα, sea, and θαλάσσιος, belonging to the sea. It means, "living along the seashore". The prefix ἀμφι- may even express the notion that this genus occurs on both sides of the South African subcontinent and may have a vast distribution along the coasts of the southern oceans. Gender masculine.

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Key to species

1. Legs except coxae entirely pale. Third antennal segment short, about 1½ times as long as deep, arista distinctly longer than half this segment. Discal cell of normal length, R—M crossvein well basad of its middle..two undescribed species (1 female each from Natal)
— At least femora largely black 2
2. Tibiae largely black. Third antennal segment short, arista of equal length or longer. Discal cell of normal length, R—M crossvein well basad of its middle .....
.....undescribed species (2 females from Atlantic coast)
— Tibiae entirely pale 3
3. Third antennal segment elongate pear-shaped, about twice as long as deep, arista at most half its length (Fig. 24). Palpi black. Discal cell of normal length, R—M crossvein well basad of its middle (Fig. 28). Prothoracic basisternum and episternum narrowly separated (Fig. 27), sometimes meeting each other. Thorax slender, more rounded anteriorly (dorsal view, Figs 25—26). Hind coxa with one well developed bristle and the other (lower) one much weaker .....*piricornis* sp. n.
— Third antennal segment short, about 1½ times as long as deep, arista at least ⅔ length of third segment (Fig. 34). Palpi pale in male, brown at base and along dorsal rim, brown in female, sometimes with pale apex and ventral rim. Discal cell short, R—M crossvein near its middle (Fig. 38). Prothoracic basisternum and episternum widely separated (Fig. 37). Thorax broad, nearly square anteriorly (Figs 35—36). Hind coxa with two bristles of equal size .....*latus* sp. n.

Amphithalassius piricornis sp. n.

Male (Figs 19—22, 24, 25, 27, 28): Entire body appearing covered with whitish pruinosity which is most conspicuous on dark ground; bristles and pubescence white unless otherwise stated.

Head black in ground colour except pale areas around antennal insertions and on sides of lower face (Figs 21—22, dotted lines), the upper pale area transverse and excised above in midline by a small black triangle, each of the lower lateral areas passing below into the equally pale membrane laterad of clypeus, the sclerite-membrane border being hard to locate; the pale areas are variable in extent and the upper transverse and lower lateral spots may either be separated from each other as figured, or confluent. Frons and face wide, both with nearly parallel sides, eyes with a shallow indentation level with anterior ocellus. Bristles on frons and vertex relatively short. Antennal segments 1—3 black, arista pale; third segment elongate pear-shaped, about twice as long as deep; arista short, at most half the length of third segment. Palpi black.

Thorax more slender than in the other known species, rounded anteriorly (dorsal view, Fig. 25), black in ground colour. Dorsocentrals 6—8, acrostichals 6—8, supra-alars in general 4 (including sutural), exceptionally 3, notopleurals 2. Prothoracic basisternum and episternum narrowly separated, exceptionally meeting each other.

Wings: Veins white to yellowish at base, brown more apically as follows: costa from apex of R_1 to wing tip, apical section of R_1 to a varying extent, R_{2+3} and R_{4+5} except their extreme bases, M_{1+2} and M_{3+4}, both in their basal sections only, and, subject to variation, R—M crossvein and cubital branches at distal ends of second basal and cubital cells; apical sections of medial branches, including apical limit of discal cell and M—M crossvein, faint. Discal cell of normal length, measured along its anterior margin (M_{1+2}), more than twice as long as second basal cell (stem of vein M), R—M crossvein distinctly basad of its middle, at between ⅓ and ⅖ its

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Figs 19—20: *Amphithalassius piricornis* sp. n., holotype ♂. Scale bar 0.5 mm. 20, head in anterior view to show ground colour pattern of face and frons; compare with Fig. 22. The white shine on vertex is due to reflection from microtrichia ("pruinosity").

length. CuA_2+A_1 rudimentary. Bristles on basal section of costa white, gradually becoming longer distad, the most distal bristle only slightly longer than the one preceding it; costal spines black. Squamae white with white fringe, halteres with white knob and yellowish shaft.

Legs black at base, including coxae, trochanters and more than basal half of each femur; yellow to white more distally on approximately apical third of fore, ⅖ of mid and ⅕—¼ of hind femora, and on all tibiae; tarsi entirely pale or apical segments and apices of basal segments darkened to a varying extent. Fore and mid metatarsi as long as the following three segments taken together, hind metatarsus slightly shorter than segments 2 and 3 together. Bristles on legs short, at most as long as hind femur is deep, white except some of the tarsal spines black. Lower bristle on hind coxa short and weak, about half length of upper one. Ciliation of tibiae is longest

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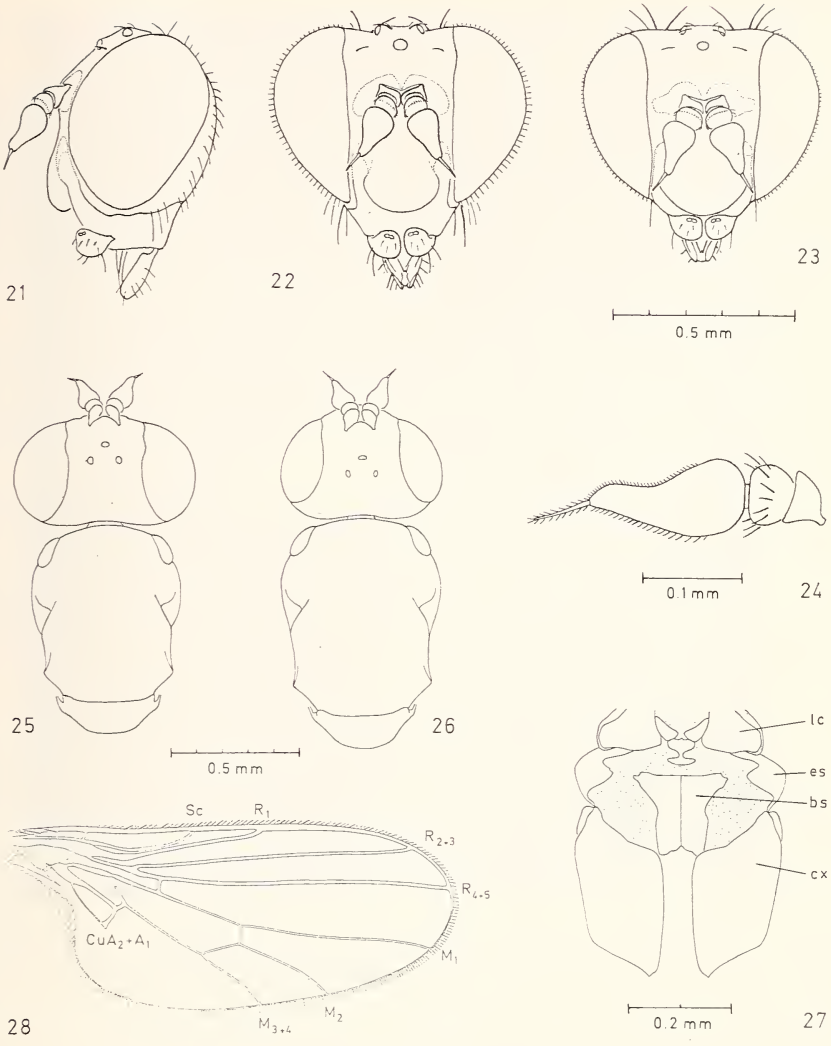

Figs 21—28: *Amphithalassius piricornis* sp. n. 21 and 22, ♂ head in lateral and anterior views respectively (holotype). 23, ♀ head, anterior view. 24, antenna of ♂. 25, ♂, and 26, ♀ head, pronotum and mesothoracic alinotum, dorsal view. 27, prothoracic pleurosternal region of ♂ in anteroventral view; membranes dotted, bs basisternum, cx coxa, es episternum, lc laterocervicale. 28, wing of ♂. Longer scale bar 0.5 mm refers to Figs 21—23, shorter to Figs 25, 26 and 28.

on hind leg but still hardly as long as tibia is deep. Tibial spines white or pale brownish, tarsal claws black, pulvilli and empodium pale.

Abdomen about as long as head and thorax together. First sternite not developed. All pregenital tergites and sternites 5—8 black or dark brown, sternites 2—4 paler

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brown; hypopygium black, appearing darker than rest of body by lighter pruinosity.

Wing length 1.7—1.9 mm.

Female (Figs 23, 26): Similar to male but larger, head narrower because of less bulging eyes, indentation of eyes on frons even more shallow or indistinct, thoracic bristles slightly more numerous with 7—9 dorsocentrals, 8—11 acrostichals and 4—5 supra-alars. Pale colour on legs slightly more extended, both on femora and on tarsi which are at most very slightly darkened toward apex; bristles on femora shorter. Abdominal tergites and sternites black or brown, ventral plate of eighth segment dark with hind margin narrowly pale, cerci yellow or pale brownish.

Wing length 1.95—2.1 mm.

Type material: All from South Africa, coast of Natal. Holotype ♂ (Fig. 19), paratypes 7♂ 4♀, Mtunzini, coastal sand dunes, 27. X. 1989, H. Ulrich, (holotype and paratypes 5♂ 3♀ in ethanol, paratypes 2♂ 1♀ pinned). Paratype 1♀, Umdloti Beach (northeast of Durban), sandy beach, 25. X. 1989, B. R. Stuckenberg & H. Ulrich, (in ethanol). — Holotype and 5 paratypes (3♂ 2♀, one of each sex pinned) in NM, type number 705; 7 paratypes (4♂ 3♀, one of the males pinned) in ZFMK.

Etymology: Latin, *pirum*, pear, and *cornu*, horn; the name alludes to the elongate pear-shape of the third antennal segment.

Remark: The above description was based on a small series only. Some of the characters, particularly the ground colour pattern, may prove more variable when additional material becomes available.

Amphithalassius latus sp. n.

Male (Figs 29—32, 34, 35, 37, 38): The entire fly appearing whitish pruinose, particularly where ground colour is dark, with bristles and pubescence white unless otherwise stated.

Head black in ground colour except pale areas around antennal insertions and on sides of face, forming a variable pattern similar to that of *A. piricornis*. Independently of the ground colours, the frons, vertex and occiput appear more grey, the face more white; between both, a short distance above antennae, a sharp transverse line of demarcation which may be accentuated by a dark band on each side of the antennae depending on light incidence (Fig. 30). This pattern, hardly visible in dried specimens, seems to be due to differences in length, density or structure of the microtrichia. Frons and face wide, their side margins distinctly diverging toward vertex and slightly so toward the lower end of face. Antennae with segments 1—3 black and arista white; third segment short conical to pear-shaped, about 1.5 times as long as deep; arista from ⅔ of, to slightly more than, length of third segment. Palpi pale, brownish at base and along dorsal rim. Anomalies with two fronto-orbital bristles on one side are frequent. No posterior ocellars.

Thorax broad and squarish, particularly in anterior part, mesoscutum nearly as broad as long; black in ground colour. Bristles short, only scutellar, postalar, notopleurals, posterior dorsocentrals and hindmost supra-alar fairly well developed; acrostichals and anterior dorsocentrals and supra-alars shorter than diameter of an ocellus. Reduction in size of bristles is combined with an increase and more variation in number and with irregularities in the linear arrangement both of dorsocentrals

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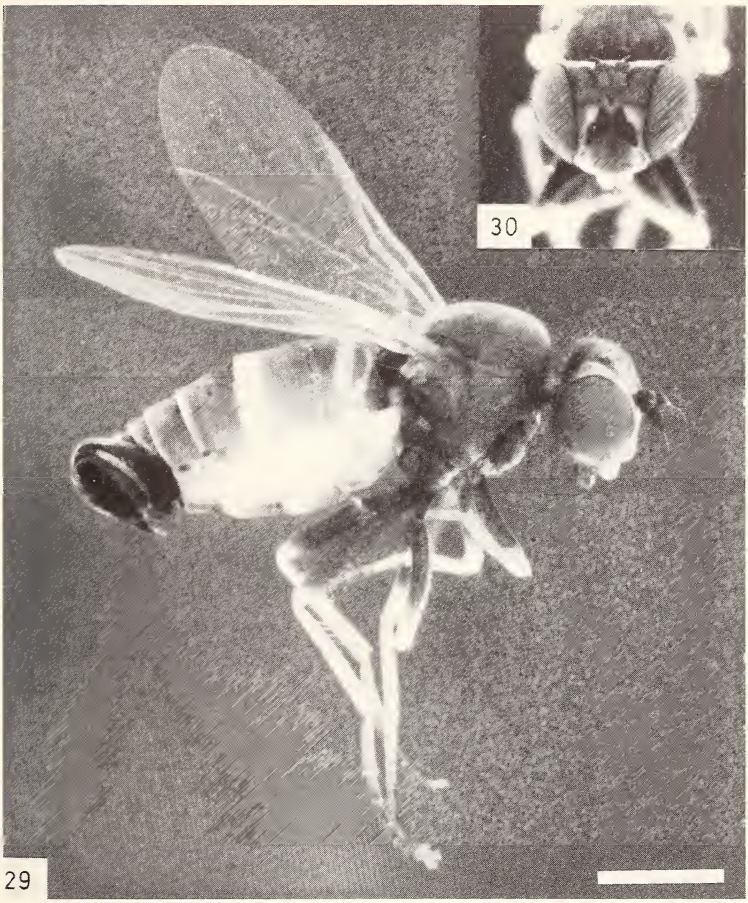

Fig. 29—30: *Amphithalassius latus* sp. n. Scale bar 0.5 mm. 29, holotype ♂. 30, ♂ head in anterior view to show pattern due to ground colours and "pruinosity".

and supra-alars. Counts reveal variation as follows: dorsocentrals 9—15, acrostichals 0—10, supra-alars 2—8, the foremost supra-alar usually well behind transverse suture. Notopleurals normally 2, exceptionally 3, 1 or missing on one side. Prothoracic basisternum and episternum widely separated, anterolateral tips of basisternum sometimes hardly developed.

Wings: Radial stem more or less brownish dorsally, otherwise veins white at base, brownish more apically, and apical sections of medial branches faint, thus forming a pattern similar to that of *A. piricornis*. The brown sections of medial branches may or may not include the apex of discal cell. Discal cell short, measured along its anterior margin (M_{1+2}), about 1½ length of second basal cell (stem of M), R—M crossvein near its middle. CuA_2+A_1 variably developed, either rudimentary as in *A. piricornis*, or forming a stump of varying length (maximum as figured). Bristles on basal section of costa white, the most distal one not much longer than the one

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preceding it, costal spines black. Squamae white with white fringe, halteres with white knob and more or less darkened shaft.

Legs black at base, including coxae, trochanters and basal parts of femora; yellow to white more distally on apical quarter to half of fore and mid femora, tenth to quarter of hind femur, all tibiae and bases of tarsi; tarsi distinctly darkened from second or apex of first segment to tip. Fore and mid metatarsi as long as the following three segments taken together, hind metatarsus as long as segments 2 and 3 together. Bristles on legs shorter than greatest depth of hind femur, white except some of the tarsal spines black. Both bristles on hind coxa of equal size. Tibial ciliation longest on ventral side in basal half of hind tibia, attaining length equal to greatest depth of tibia. Tibial spines varying from white to black, tarsal claws black, pulvilli and empodium pale.

Abdomen distinctly longer than head and thorax together (Fig. 29). First sternite developed. Posterior tergites and sternites 5—8 black or dark brown, anterior tergites and sternites paler brown; hypopygium black, less obscured by pruinosity.

Wing length 1.45—1.8 mm.

Female (Figs 33, 36, 39—41): Similar to male but generally larger, face and lower part of frons wider, side margins nearly parallel on face and less diverging on frons toward vertex; palpi brown, sometimes pale at apex and lower rim; bristles on legs shorter. Abdominal tergites dark brown to black, sternites paler brown, ventral plate of eighth segment dark brown in anterior and lateral parts, pale brownish at tip, cerci dark brown or pale.

Wing length 1.75—2.3 mm.

Type material: All from South Africa, south coast of Cape Province and coast of Natal. Holotype ♂ (Fig. 29), paratypes 4♂ 3♀, Buffelsbaai, Cape Province, coastal sand dunes, 14. X. 1989, H. Ulrich, (holotype and paratypes 2♂ 1♀ in ethanol, paratypes 2♂ 2♀ pinned). Paratypes 4♂ 4♀, Buffelsbaai, Cape Province, coastal sand dunes, 12. (4♂ 2♀) and 13. X. 1989 (2♀), H. Ulrich, (in ethanol). Paratypes 3♂, Suiderkruis near Groot Brakrivier mouth, Cape Province, coastal sand dunes, 16. X. 1989, H. Ulrich, (in ethanol). Paratypes 2♂ 1♀, Swartkops River Mouth (north of Port Elizabeth), Cape Province, coastal sand dunes, 18. X. 1989, H. Ulrich, (in ethanol). Paratypes 4♂ 3♀, Mtunzini, Natal, coastal sand dunes, 27. X. 1989, H. Ulrich, (in ethanol). — Holotype and 14 paratypes (8♂ 6♀, one of each sex pinned) in NM, type number 706; 14 paratypes (9♂ 5♀, one of each sex pinned) in ZFMK.

Additional specimens not given type status: South Africa, south coast of Cape Province. Material for detailed morphological studies, 30♂ from Buffelsbaai, H. Ulrich, (in ethanol, fixed FEA), in ZFMK.

Etymology: Latin, *latus*, broad, refers to the broad head and thorax.

Figs 31—41: *Amphithalassius latus* sp. n. 31 and 32, ♂ head, lateral and anterior views. 33, ♀ head in anterior view. 34, antenna of ♂. 35, ♂, and 36, ♀ head, pronotum and mesothoracic alinotum, dorsal view. 37, prothoracic pleurosternal region of ♂, anteroventral view; bs basisternum, cx coxa, es episternum, lc laterocervicale. 38, wing of ♂. 39, ♀ postabdomen, dorsal view (macerated and stretched). 40 and 41, ♀ terminalia in dorsal and lateral views respectively (same preparation as in 39). c cercus, t6—t10 tergites 6—10, v8 ventral plate of 8th segment, perhaps laterotergite (Deuve 1988), vp ventral plate of proctiger (10th sternite?). Membranes dotted in Figs 37 and 39—41. Longer scale bar 0.5 mm refers to Figs 31—33 and 39, shorter to Figs 35, 36 and 38.

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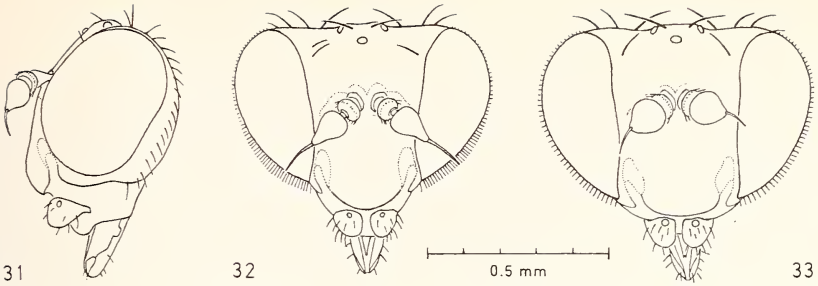

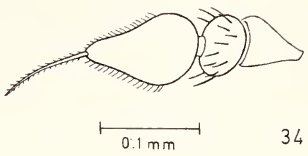

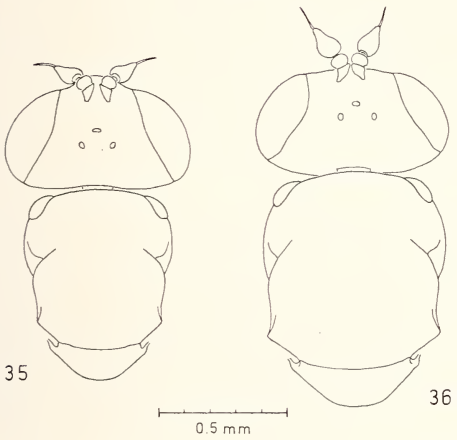

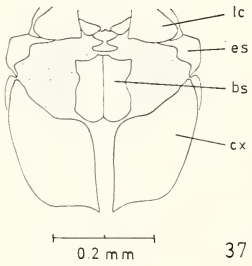

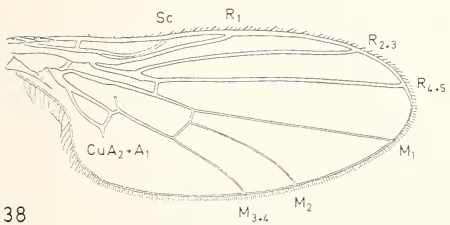

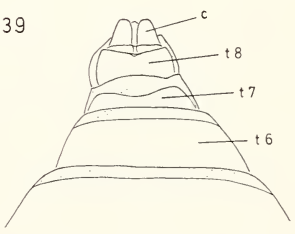

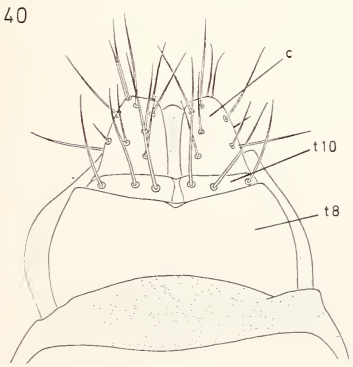

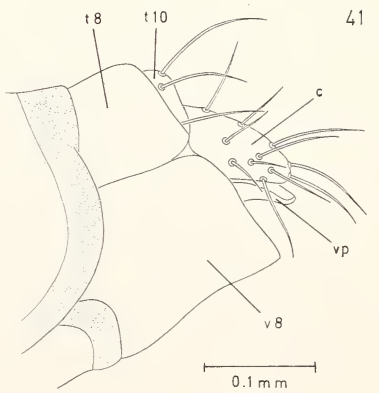

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Preliminary remarks on phylogeny

In the following paragraphs the significance of some characters for reconstruction of the phylogenetic position of the new genera is discussed. Thoracic and hypopygial morphology, which will be treated in detail in subsequent papers, are not considered here except one externally visible character included in the foregoing descriptions (character 10 below). The discussions are focused on the phylogenetic relationships of *Plesiothalassius* and *Amphithalassius* to *Parathalassius* and *Microphorella* (which will be referred to as "the conventional Parathalassiinae") and to the Dolichopodidae. As a representative of the closest outgroup, the Microphorinae, *Microphor* Macquart was included in the comparison. *Schistostoma* Becker, which has been assigned to the Microphorinae but has some additional apomorphous characters in common with the Dolichopodidae (see Chvála 1987), and *Thalassophorus* Saigusa, which may be closely related or even belong to the Parathalassiinae-Dolichopodidae group (see its original description, Saigusa 1986), are not considered as they have not been studied by me; both will be included in the comparative study when material becomes available.

As revealed in the foregoing descriptions and a preliminary study of macerated preparations of *Plesiothalassius natalensis* and *Amphithalassius latus*, both genera agree with *Parathalassius* and *Microphorella* in several characters discussed by Hennig (1971) and Chvála (1981 and 1983) as probable synapomorphies as opposed to the plesiomorphous condition in the Microphorinae, and either shared with the Dolichopodidae or not. These characters will be discussed first, starting with those shared by the Dolichopodidae (Nos 1—7). For each character the numbers given in brackets are those under which it was treated by Hennig and Chvála (1983).

1. Clypeus not separated from upper face and/or convex (Chvála 3), rigidly and immovably joined to praefrons and projecting nose-like (Hennig 2): The conditions found in *Parathalassius* and *Microphor* were described in detail and well figured by Hennig whose words were very descriptive and impressive, but Chvála was certainly right in defining the character more cautiously. The first statement regarding connection of the clypeus with the upper face, without a membrane between both or any other clear-cut border-line, is applicable in principle to the new genera too, despite modifications in shape of the parts concerned. However, I cannot agree with Hennig's view that the clypeus is immovable, since the cuticle is thin and the surface flat enough to permit elastic deformations. More important in the present context, outgroup comparison suggests that the condition in *Parathalassius* reflects the plesiomorphous, that in *Microphor*, with a membrane at the base of the clypeus, the apomorphous state. Thus this character may perhaps prove useful for establishing monophyly of the Microphorinae but not of the Parathalassiinae, the Dolichopodidae, or both. The second statement, concerning convexity of the clypeus, was correctly perceived by Chvála as facultative only. This character is subject to variation: a nose-like projection may be distinct in *Parathalassius* females and less so in males, but *Microphorella* looks quite different, and in *Amphithalassius* at least convexity may change with protrusion and retraction of the proboscis, as to be expected if one admits that the face can be deformed elastically. So there does not remain much of this character that could be used for phylogenetic considerations.

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2. Antenna placed above middle of head (Chvála 2), shifted dorsad (Hennig 5): The validity of this character is doubtful for *Amphithalassius* and for *Microphorella praecox* (Loew), the type species of its genus (type series studied at the Zoological Museum of Humboldt University, Berlin, dried specimens only with shrunken heads), and is still imperfectly understood. It is thus impossible at present to assess its value for reconstruction of phylogeny. Hennig explained it by an elongation of the lower face as a consequence of the alleged fusion of the clypeus with the upper face (see previous character), but these are speculations based on doubtful assumptions. In the present state of knowledge, a high position of the antennae may be useful to characterize individual genera or species groups, but not to draw conclusions on phylogenetic relations between genera.

3. Maxillary laciniae absent, reduced (Chvála 4, Hennig 3): This character apparently applies to the new genera too, but this has still to be confirmed by a more detailed study. As in other cases, when parts are absent by reduction, one must be cautious in drawing conclusions on phylogeny since there are no criteria except the statistical one by which synapomorphy could be deemed more probable than parallel evolution. In fact the laciniae have been reduced elsewhere in the Empidoidea too, as described in the Hybotidae and in *Wiedemannia* among the Clinocerinae (Empididae) (Laurence 1953, Krystoph 1961, Chvála 1981, 1983). This character has obviously much to do with functioning of the mouthparts and there may be a close causal connection with the following one.

4. Labial paraphyses attached to maxillary stipites (Chvála 5, Hennig 4): The same condition appears to be present in both of the new genera. This might be a good character whose distribution may be best explained by a synapomorphy common to all four genera and the Dolichopodidae, although here too, homoplasy cannot be ruled out at present. A similar evolution appears to have occurred in the Clinocerinae and Hybotidae (Laurence 1953, Krystoph 1961), and if there are differences between the groups concerned, these should be worked out and their significance for phylogenetic conclusions analyzed.

5. Basal section of vein M_{3+4} separating discal from second basal cell ("basal crossvein", t_b) incomplete, absent in Dolichopodidae (Chvála 6, Hennig 6): This character applies to the new genera in the same way as to the conventional Parathalassiinae, and it looks so similar in all four genera that synapomorphy is considered to be the easiest explanation, the more so as no case of parallel evolution is known within the Empidoidea. Apparently the parathalassiine condition marks a first step toward complete fusion of the neighbouring cells as found in the Dolichopodidae. Although it looks like a simple stage of reduction, the fine structures affected may be more complex and it may prove an important innovation when its functional aspect is better understood.

6. Males dichoptic (Chvála 7, Hennig 7): Although this character cannot be definitely appraised, outgroup comparison suggests that it is apomorphous. Dichopticism in the male has evolved several times independently within the Empidoidea, for instance in the Clinocerinae and Tachydromiinae (Chvála 1983), and in the former the front may be as wide as in the flies considered here. That the males of the new genera, the conventional Parathalassiinae, and in the groundplan of the Dolichopodidae, agree in their dichoptic head structure, may well be due to

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synapomorphy but homoplasy cannot be ruled out (for the value of holopticism or dichopticism as characters for study of phylogeny see Chvála 1983).

7. Eyes pubescent (Chvála 8, Hennig 8): This character, which is shared by the new genera too, is also to be found elsewhere within the Empidoidea, as in the Drapetini (Tachydromiinae) and most of the Clinocerinae (Chvála 1983). It is to be interpreted in the same way as the preceding one: synapomorphy within the Microphoridae-Dolichopodidae group is not improbable, but parallel evolution cannot be precluded.

Among the characters discussed above, the first two are deemed useless in the present context because they are either plesiomorphous (1) or doubtful as a character common to more than a single genus (2), whereas the other five were interpreted as apomorphies. Among the latter, synapomorphy was considered to be highly probable for one character only (5), whereas homoplasy could not be ruled out for the remaining four. But even if each of these four is not conclusive if taken alone, together they can support the assumption to be based on character 5, that the new genera, the conventional Parathalassiinae and the Dolichopodidae, are united in a monophyletic group. This is confirmed by a current study of thoracic morphology. The thoracic skeleton of both South African genera agree with that of *Parathalassius* and *Microphorella* in all apomorphous characters found to link the latter two with the Dolichopodidae, except lack of a complete prothoracic precoxal bridge as discussed below (see also Ulrich, in preparation). However, no characters were found that suggest a closer relationship to the Microphorinae. Monophyly of the whole group being fairly well established, the next question should be how this group can be further subdivided.

The following character described from the Parathalassiinae is lacking in the Dolichopodidae:

8. Antennal arista without visible segmentation (Chvála 1, Hennig 1): Lack of aristal segmentation was interpreted by both authors as a synapomorphy of *Parathalassius* and *Microphorella*. The same condition is found in both South African genera and since there is little doubt that it is apomorphous, it might be taken as evidence that all four genera form together a monophyletic group. One must, however, bear in mind that this is a simple character of reduction for which homoplasy cannot be ruled out, and that it has been studied externally only and cannot be assessed with certainty. In fact, loss of visible aristal segmentation seems to have occurred several times in the Empidoidea and even in the Microphoridae-Dolichopodidae group. According to Chvála (1983) a one-articulated arista occurs in representatives of the Hemerodromiinae, Clinocerinae (both Empididae) and Ocydromiinae (Hybotidae), and in the genera described by Negrobov (1978) from Upper Cretaceous amber, *Cretomicrophorus*, *Archichrysotus* and *Retinitus*, which are supposed to be more closely related to the Dolichopodidae than the Parathalassiinae. Examination of a pair of *Microphor* in Baltic amber, probably *M. rusticus* (Meunier), in the ZFMK collection, revealed an apparently unsegmented arista in the female at least, where the external structure of the base of the arista is clearly visible, contrary to Hennig's fig. 4.

The next two characters to be discussed are common to *Parathalassius*, *Microphorella* and the Dolichopodidae but missing in the new genera:

9. Tenth tergum of female abdomen cleft and spinose (Chvála 9): The tergal

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sclerites considered here were assigned to the ninth segment by Hennig and Chvála, and interpreted as derivatives of the fused ninth and tenth terga (hemitergites 9+10) by Irwin (1974) and Ulrich (1988). In the present paper they are assigned to the tenth segment in agreement with Lobanov's statement (1980) that the ninth tergite is reduced in the Empidoidea. The new genera agree with the conventional Parathalassiinae and the Dolichopodidae in having the tenth tergum divided into a pair of hemitergites. This may be due to synapomorphy, since according to Chvála the tergal plate is still undivided in the Microphorinae. However, *Microphor sycophantor* (Melander) and *M. holosericeus* (Meigen) show the paired condition (Hennig 1976, Ulrich 1988). If the tenth tergite is unpaired in the groundplan of the Microphorinae and *Microphor*, bisection must have occurred at least twice independently in the Microphoridae-Dolichopodidae group and then this character does not provide conclusive evidence for monophyly. The females of *Parathalassius* and *Microphorella* have an acanthophorous postabdomen with the bristles of the tenth hemitergites transformed to spines. The same condition is found in many Dolichopodidae and may form part of the groundplan of that family, but this is not certain. In both new genera the tenth hemitergites bear simple bristles as in *Microphor holosericeus* and thus apparently present the plesiomorphous condition. This might be taken as evidence that the conventional Parathalassiinae and the Dolichopodidae together form a monophyletic group opposed to the new genera. However, the acanthophorous condition has obviously evolved several times not only in the Asiloidea but also in the Empidoidea and even among the closer relatives of the group considered here: Chvála (1987) found it in *Schistostoma* and Hennig (1976) figured it in *Microphor sycophantor*. So in this case, too, homoplasy cannot be ruled out. Woodley (1989) even considers that the acanthophorous condition might be plesiomorphous within the Empidoidea and reduced where missing.

10. Prothoracic basisternum and episternum fused to form a precoxal bridge: *Parathalassius* and *Microphorella* agree in having a narrow but complete prothoracic precoxal bridge which looks so similar in both that there may be good reason to explain this agreement by synapomorphy. The Dolichopodidae also have a precoxal bridge, but it is broader and may have developed independently, esspecially as a similar structure has obviously evolved several times in the Empidoidea. In *Plesiothalassius* the isolated basisternum is probably a plesiomorphous structure and constitutes a symplesiomorphy with the Microphorinae (for *Microphor* see Ulrich 1984). The condition found in *Amphithalassius*, with an incomplete precoxal bridge, is less clearly understood: it may represent an intermediate stage either in formation or reduction of a complete bridge. Since no case of reduction of a precoxal bridge is known, at least in the Empidoidea, it seems reasonable to prefer the first alternative. This would mean that the condition in *Amphithalassius* is plesiomorphous when compared with the conventional Parathalassiinae and apomorphous when compared with *Plesiothalassius* and the Microphorinae. One could infer from this not only that *Parathalassius* and *Microphorella* form a monophyletic group, perhaps together with the Dolichopodidae, but also that *Amphithalassius* is more closely related to this group than *Plesiothalassius*. However, the latter hypothesis at least would rest on a weak argument since independent evolution toward a precoxal bridge cannot be precluded.

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The last character to be considered here seems to be common to the conventional Parathalassiinae only:

11. Male genitalia hypertrophied and postabdomen beginning with sternite 4 or even 3: The males of both *Parathalassius* and *Microphorella* have a strikingly large hypopygium and, related to this character, their fourth or even third abdominal sternite is modified by an indentation of its hind margin and by asymmetry. In the South African genera the hypopygium is smaller and the fifth sternite is the first to be modified. Comparing both conditions, that of *Parathalassius* and *Microphorella* is obviously apomorphous. It is apparently not shared by the groundplan of the Dolichopodidae and may constitute a synapomorphy confined to these two genera, a statement which, however, needs confirmation by a detailed study.

No character has been found to date which could be taken as indicating that the new genera are more closely related to the Dolichopodidae than the conventional Parathalassiinae.

As stated above, the Dolichopodidae, the conventional Parathalassiinae and the new genera probably form together a monophyletic group. The question of how this group has to be subdivided cannot yet be answered satisfactorily.

Two characters (10 and 11) may suggest a closer relationship between *Parathalassius* and *Microphorella*, but this hypothesis still rests on a weak foundation. If it holds, the South African species cannot be included in *Parathalassius* even if that genus is regarded as extremely varied, as long as *Microphorella* is retained as a separate genus. This was the final reason why new genera were proposed for them.

The phylogenetic affinities between the new genera, whether they form together a monophyletic group or not, are still open to question. That both genera have markedly widened maxillary palpi is too weak an argument for a close relationship. However, the incomplete precoxal bridge in the prothorax of *Amphithalassius* cannot be used as evidence for a closer relationship between that genus and those which have a complete bridge.

The problem about the sister group of the Dolichopodidae is also still unresolved. Among the possible hypotheses, two are more probable since they can be based on character agreements which may be due to synapomorphy: Distribution of the characters of the prothoracic pleurosternal region (10) and of the female postabdomen (9) might be taken as indicating a sister group relationship with the conventional Parathalassiinae; this would mean that the ancestors of the new genera split off earlier from the common stem. The structure of the arista (character 8), however, might be evidence that the conventional Parathalassiinae and the new genera form together a monophyletic group, which, if so, would be the sister group of the Dolichopodidae. Only the latter hypothesis would justify inclusion of the new genera in the subfamily, Parathalassiinae. As pointed out above, all three characters are not sufficiently conclusive for making a decision.

To sum up, phylogeny within the group established above is still entirely unknown, and any effort to make progress in this field requires additional characters which may be furnished by more detailed studies.

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Zusammenfassung

Von sandigen Küstenbiotopen Südafrikas werden zwei neue Dipterengattungen, *Plesiothalassius* und *Amphithalassius*, mit vier neuen Arten beschrieben: *Plesiothalassius natalensis*, *P. flavus*, *Amphithalassius piricornis* und *A. latus*. *Parathalassius capensis* Smith 1972 wird zu *Plesiothalassius* gestellt und zur Typusart dieser Gattung erklärt. Typusart von *Amphithalassius* ist *A. piricornis* n. sp.

In einer vorläufigen Diskussion zur Stellung der neuen Gattungen im phylogenetischen System der Empidoidea werden die gegenwärtig bekannten Merkmalsverteilungen einer kritischen Bewertung unterzogen. Danach kann angenommen werden, daß beide Gattungen mit *Parathalassius* Mik, *Microphorella* Becker und den Dolichopodiden näher verwandt sind als *Microphor* Macquart (Microphorinae) und mit ihnen eine monophyletische Gruppe bilden. Eine weitere Unterteilung dieser Gruppe in monophyletische Einheiten gleichen Ranges (Schwestergruppen) ist zur Zeit noch nicht möglich; zu diesem Zweck sind weitere Untersuchungen aufgenommen worden. Es wäre verfrüht, die neuen Gattungen zu den Parathalassiinae zu stellen, da dies zu einem paraphyletischen Gruppenkonzept führen könnte.

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