

Observations on the life cycle of *Neottialges (Pelecanectes) evansi* Fain, 1966 and *Phalacrodes whartoni* Fain, 1967 with descriptions of new taxa (Acari, Hypoderatidae)

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Summary

The family Hypoderatidae Murray (Acari, Astigmata) now comprises, including the new taxa described herein, 68 species or subspecies grouped in 30 genera or subgenera. In the present paper we describe the life cycle of a second species *Phalacrodes whartoni* Fain, 1967 and we add new data on the life cycle of *Neottialges (Pelecanectes) evansi* Fain, 1966. The following new taxa are described from adults, from a nest of a cattle egret, *Bubulcus ibis*, in Panama: *Phalacrodes panamensis* n. sp., *Neottialges (Heronidectes) mendezi* n. subg., n. sp. *Neottialges (Ardeidectes) ibis* n. subg., n. sp. and *Bubulcodectes brevitarsis* n. g., n. sp. An additional new species *Hypodectes (Hypodectoides) samsinaki* is described from the nest of a wild pigeon from Czechoslovakia. A key to the adult forms is given and the evolution of this group of mites is discussed.

Introduction

The family Hypoderatidae currently comprises, including the new taxa described herein, 68 species or subspecies and 30 genera or subgenera. Most of these species were described from their heteromorphic deutonymphs (hypopi) living in the subcutaneous tissues of birds. Only two species are known from rodents. The life cycle has been elucidated for only one species, *Hypodectes (Hypodectoides) propus* (Nitzsch, 1861). The hypopi parasitize pigeons and the adults live free in the nests of these hosts (Fain & Bafort, 1967). In two other species the life cycle is incompletely known. In *Neottialges (Pelecanectes) evansi* Fain, 1966 only three stages have been observed, the hypopus, parasitic in cormorants, and the male and the active tritonymph, both living free in the nest of these birds (Fain & Beaucournu, 1972). In *Frehelectes*

gaudi Fain & Beaucournu, 1972 the hypopi are also parasitic under the skin of cormorants. Some of these hypopi were found free in the nest and they contained an inert tritonymph with reduced legs and gnathosoma. Two species are represented only by the adult females, *Neotytoctes mexicanus* OConnor, 1981 from the nest of a Mexican owl (*Glaucidium* sp.) and *Gypsodectes verrucosus* Fain, 1984, described from the nest of a South African vulture (*Gyps coprotheres*).

In this paper we describe the life cycle of *Phalacrodes whartoni* Fain, 1967 and provide new data on the life cycle of *Neottialges (Pelecanectes) evansi* Fain, 1966. In addition, we describe the following new taxa: *Phalacrodes panamensis* n. sp., *Neottialges (Heronidectes) mendezi* n. subg., n. sp., *Neottialges (Ardeidectes) ibis* n. subg., n. sp., *Bubulcodectes brevitarsis* n. g., n. sp. and *Hypodectes (Hypodectoides) samsinaki* n. sp. All these

new species were found in a nest of the cattle egret, (*Bubulcus ibis*) in Panama except for *H. samsinaki*, which was found in a nest of a wild pigeon in Czechoslovakia.

Materials and methods

We have re-examined the material found in the nest of a cormorant from Cape Frehel, France and described previously (Fain & Beaucournu, 1972). This material contained two males tentatively identified as *Neottialges (Pelecanectes) evansi*. We can now bring new arguments confirming this identification.

Recently, we received from Dr. E. Mendez, Panama, numerous hypoderid mites found in the nest of a cattle egret (*Bubulcus ibis*) in Panama. This material had been collected by A. Herrera. It contains the following species:

(1) Hypopi of *Phalacrodes whartoni*. Several specimens are in the moulting stage and contain an inert tritonymph with vestigial legs and gnathosoma. One of these tritonymphs, still enclosed in the hypopial skin, contains a fully-developed female. Numerous free females identical with the latter, and males obviously of the same species, were also present in this nest.

(2) One free male of a new species, *Phalacrodes panamensis* n. sp.

(3) Numerous females and males of a new species that we include in a new subgenus *Heronidectes* of the genus *Neottialges*, *Neottialges (Heronidectes) mendezi* n. subg., n. sp.

(4) Two females assigned to a new species and subgenus of the genus *Neottialges*, *Neottialges (Ardeidectes) ibis* n. subg., n. sp.

(5) Several females and males of *Bubulcodectes brevitarsis* n. g., n. sp.

All the measurements in the description are in μm . The setal nomenclature of the idiosoma is that of Fain (1963).

The holotypes of the new species are deposited in the Institut royal des Sciences naturelles de Belgique, Rue Vautier, 31, Brussels. Paratypes of *N. mendezi* and *B. brevitarsis* and adults of *P. whartoni* are deposited in the British Museum

(Natural History), London, the Museum National d'Histoire naturelle, Paris, the U.S. National Museum, Washington and in the collections of the authors.

Hypoderid mites recorded from birds of the family Ardeidae

Hypoderid mites have not previously been found in the nests of *Bubulcus ibis*, or any other ardeid. However, the following hypopi had been recorded from these birds:

(1) *Hypodectes (Hypodectoides) propus bubulci* Fain, 1967. Recorded from the following ardeids: *Bubulcus ibis* (type host) from Rwanda (type locality) and the U.S.A.; *Ardea herodias* from the Galapagos Is. and the U.S.A.; *Florida caerulea* from the U.S.A. and Cuba; *Leucophoyx thula* from the U.S.A.; *Dichromanassa rufescens* from the U.S.A.; *Ardeola ibis* and *Casmerodius alba egretta* from Cuba; *Egretta garzetta* from Australia (see Fain, 1967; Cerny, 1969; Pence, 1972; Janssen Duijghuisen et al., 1979). This species has also been recorded from a stork *Tantalus ibis* (Ciconiidae) from India (Fain, 1967).

(2) *Hypodectes (Hypodectes) nycticoracis* Filippi, 1861. The type host is *Nycticorax nycticorax* from Italy. Fain found it in the same host in Belgium (1967). Other records: *Ixobrychus exilis* and *Florida caerulea* from the U.S.A. (Pence, 1972).

One can surmise that at least one of the five species found in the nest of *Bubulcus ibis* actually belongs to *H. (H.) propus bubulci* or to *H. (H.) nycticoracis*. It seems that we can exclude the four species which obviously belong to the genus *Neottialges* or *Phalacrodes*. The only genus and species whose taxonomic status is unclear is *Bubulcodectes brevitarsis*. This taxon may actually represent the adults of *H. (H.) propus bubulci*. If this proves to be the case then the name *brevitarsis* would become a synonym of *bubulci* and *Bubulcodectes* would become the generic name for this species.

Key to the genera and species of Hypoderatidae based on adults

1. Female physogastric, with gnathosoma either modified (palps of one free segment) or strongly reduced, the chelicerae either reduced or vestigial. Male heteromorphic with very strong chelicerae, modified gnathosoma and rounded abdomen 2.
Female not physogastric with chelicerae not reduced. Male homeomorphic with normal gnathosoma; abdomen lobed (the males are unknown in *Gypsodectes* and *Neotytoectes*) 4
2. Palps with one free article. Tibiae I-III with thin setae, tibia IV lacking a seta *Hypodectes* (*Hypodectoides*) Fain & Bafort, 1966 3.
Palps with two free articles. Tibiae I-II with 2 thick spines, tibiae III-IV with one thick spine. Anterior tarsi short *Bubulcodectes* n. g. One species: *B. brevitarsis* n. g., n. sp.
3. Male: setae *sc i* much shorter (75–100) than *sc e* (650); *fl* is 100 long. Idiosoma 690 to 810
. *H. (Hypodectoides) propus* (Nitzsch, 1861)
Male: setae *sc i* and *sc e* subequal (400–500); *fl* is 600 long. Idiosoma 580 long *Hypodectes* (*Hypodectoides*) *samsinaki* n. sp.
4. Setae *s* of tarsi I, II and IV piliform, that of tarsus III a spine. Tarsus IV with 7 setae in female and 5 setae and 2 suckers in male. Pharyngeal plate sclerotized with small, rounded or elongate pits. Chelicerae elongate *Phalacroductes* (*Phalacroductes*) Fain, 1966 5.
Setae *s* of tarsi I-IV are spines. Tarsus IV with 8 setae in female and 6 setae and 2 suckers in male. Pharyngeal plate with longitudinal anastomosed lines (character not known for *Neotytoectes*). Gnathosoma and palps not elongate 6.
5. Male with leg I not distinctly dilated, tarsi I-II only slightly narrower than corresponding tibiae. Tarsus IV in male with a narrow chitinous crest in its basal half dorsally. Tarsi I-IV in female longer: 60-60-90-90. Seta *s cx* short (5). Setae of tibia III in male is a spine (both sexes). Palps and chelicerae distinctly elongate
. *P. (P.) whartoni* Fain, 1967
Male with legs I distinctly dilated (except tarsi). Tarsi I-II much narrower than corresponding tibiae. Tarsus IV in male without a crest. Tarsi I-IV in female shorter: 40-42-55-57. Setae *s cx* 30 long. Seta of tibia III in male piliform. Palps and chelicerae slightly elongate
. *P. (P.) panamensis* n. sp.
6. Tibiae I-III with thin setae, tibia IV lacking a seta. All dorsal setae thin and short. Male unknown *Neotytoectes* OConnor, 1981. One species: *N. mexicanus* OConnor, 1981
Tibiae I-II with either thin setae or short spines, tibiae III-IV with either a spine or a thin seta 7.
7. Dorsal surface covered with numerous irregular, wart-like formations. Absence of a distinct propodonal shield. Tarsi III-IV with 8 setae (not 9 as described). Seta *w* of tarsus IV is a spine (Male unknown) *Gypsodectes* Fain, 1984. One species: *G. verrucosus* Fain, 1984
Dorsal surface not verrucose. Propodotum with 2 parallel, longitudinal, paramedian, punctate bands. Seta *w* of tarsus IV is either a spine or a thin seta *Neottialges* Fain, 1966 8.
8. Tibiae I-II with 2 thin setae 9.
Tibiae I-II with a thin seta and a spine. Seta *w* of tarsi III-IV are thin. (Male unknown)
Neottialges (*Ardeidectes*) n. subg. One species: *N. (A.) ibis* n. sp.
9. Male: setae *w* of tarsi III-IV and setae of tibiae III-IV are spines. Dorsum covered with small scales. Copulatory suckers of tarsus IV replaced by small rod-like setae *Neottialges* (*Pelecanectes*) Fain, 1966. Type species: *N. (P.) evansi* Fain, 1966
Male: setae *w* of tarsi III-IV are thin. Setae of tibiae III-IV are either thin or spinous. Dorsum without scales. Copulatory suckers of tarsi IV variable 10.
10. Male: setae of tibiae III-IV are spines. Copulatory organs of tarsi IV are suckers
. *Neottialges* (*Heronidectes*) n. subg. Type species: *N. (H.) mendezi* n. sp.
Male: setae of tibiae III-IV are thin. Copulatory organs of tarsus IV are small rod-like setae *Neottialges* (*Neottialges*) Fain, 1966. Studied species: *N. (N.) eurafer* Fain, 1966

Definition of the Hypoderatidae

OConnor (1981) gave a new definition of this family based on the taxa known at that time. The discoveries of several new taxa and of the life cycle of the genus *Phalacrodectes* give us the opportunity to redefine this interesting group of mites.

Adults: Body size from median to large (length of females 411–990 μm , of males 440–800 μm). Cuticle either soft or with dorsal punctate shields; some species bear on dorsum either scales or verrucosities. Posterior extremity of body in males either rounded or truncate with posterior border incised forming 2 wide lobes. Sejugal furrow either complete or poorly developed. Oil glands orifices either ventral or dorsal. In some species well-developed oil grooves originate from these orifices and run along dorsal surface. There are 4 pairs of lyrifissures. Genital orifice situated between coxae III or IV, or slightly behind latter. Genital suckers small, unisegmented. Vulva in an inverted 'V'. Epigynium small or absent. Bursa copulatrix lacking (or overlooked) in only one species (*Neotytoedectes mexicanus*). Male with one pair of paranal suckers; tarsus IV with two copulatory organs either suckers or small, rodlike setae. Legs with long ambulacral peduncles without apical claw. Idiosoma with one complete set of hairs except the *ve* is lacking, in the female there are only 4 pairs of anals, and setae *s cx* is lacking (or overlooked) in one genus (*Neotytoedectes* OConnor). Leg chaetotaxy: Tarsi 11-10-8-8(7), tibiae 2-2-1-1(0), genua 2-2-1-0, femora 1-1-0-1, trochanters 1-1-1-0. On all tarsi setae *p* and *q* are big spines, setae *s* are either spines or thin setae. Solenidia: $\omega 3$ is always apical, $\omega 2$ is long and situated in apical third of tarsus or subapical. Genu 1 with 2 unequal solenidia. *Tritonymph*: variably developed. In *Neottialges* it is active and morphologically similar to female. In *Phalacrodectes* it is inert and mouth parts, legs and chaetotaxy are very poorly developed or vestigial. In *Hypodectes* (*Hypodectoides*) *propus* it is reduced to a verrucose sac devoid of any appendages.

Hypopi: Palposoma absent; palposomal setae are present or absent; solenidium alpha absent. Sexual orifice flanked by 2 suckers. Anus vestigial. Legs I-II ending in a curved spine (not a claw); legs III

ending either in a spine or in a long barbed seta. Leg IV with a long barbed apical seta.

Protonymph: Normally developed in *Neottialges*. Reduced to a verrucose membrane in *H. propus*.

Larva: Normally developed in *Bubulcodectes*, but without Claparede organ. In *H. propus* it is reduced to a striated membranous sac bearing setae and vestigial legs (rounded stumps) and gnathosoma.

Prelarva: Reduced to ecdysing organ formed of 2 small sclerotized cones with pointed apex. Observed in *H. propus* (this paper) and in *Bubulcodectes brevitarsis*.

Remarks on some morphological characters in the Hypoderatidae

Morphologically the Hypoderatidae present close affinities with the most primitive groups of the Acaroidea. They differ, however, from these groups by the presence of both regressive and specialized characters.

Regression is observed in the chaetotaxy of the idiosoma (e.g. absence of setae *ve*, reduction in size of the *s cx* and, in the female, reduction in the number of anal setae to 4 pairs) and of the legs (tarsi I-IV with 11-10-8-8(7): the seta of tibia IV may be lacking). It is not quite certain that the setae *v* and *u* of tarsi are completely lacking. These setae could be fused with the ambulacra (see the description of *Bubulcodectes brevitarsis*). The genital suckers in both sexes are short and they lack their basal segment. Tarsal suckers in the male are very small or replaced by two very small rod-like setae. The anus is very short, almost vestigial in both sexes of *H. propus* and *B. brevitarsis*. Ambulacra are elongate but lacking a terminal claw. The gnathosoma and the chelicerae are strongly reduced in size in the female of some species and the chelicerae may even be vestigial.

Specialized characters are observed in all the species, but their importance varies according to the species or genus. In all species the solenidium $\omega 3$ has become apical, and the $\omega 2$ has also migrated towards the apex and is situated in the apical third of the tarsus or more apically. In some species $\omega 2$ is

distinctly ventral. The $\omega 1$ of tarsus I may be displaced to the middle of the tarsus. In both sexes of *H. propus* the three solenidia of tarsus I are situated in the apical half of the tarsus, while the famulus still remains in the basal half of the segment.

Other specialized characters observed in some species are the verrucose or scaly aspect of the cuticle (recalling the Glycyphagidae), the great development of the oil grooves (as in the Hyadesiidae), the modification of the gnathosoma (highly sclerotized in *H. propus* and in *B. brevitarsis*), the palps (fusion of the two segments) and the chelicerae (simply elongate in *Phalacrodes*, long and very strong in *Hypodectes* and *Bubulcodectes*).

In the genera *Gypsodectes* and *Neottialges* a horse-shoe shaped sclerite is visible in the depth of the tissues beneath the vulva. Its significance is unknown. In the genera *Hypodectes* and *Bubulcodectes* the females are physogastric and have reduced or vestigial chelicerae while the males are heteromorphic and bear enormous chelicerae. In both sexes the anus is vestigial. These characters suggest that these species do not feed and have a short life span. The exact role of these abnormal chelicerae of the male is unknown, but one can surmise that they are used by the male for tearing open the abdomen of the female and so contribute to the liberation of the eggs.

Evolution of some genera of the Hypoderatidae whose adults, tritonymphs and hypopi are known

The genus *Neottialges* is the most primitive and also the least specialised of the Hypoderatidae. In the adults of this genus the gnathosoma, the palps and the chelicerae are normal, the pharyngeal plate is well developed with strong sclerotized lines and the anus is long 80–105 μm in *N. evansi* (male) and *N. mendezi* (male and female). This suggests that these adults are normally feeding in the nests of the birds. The tarsi bear 11-10-8-8 setae in the female and 11-10-8-6 in the male. The setae *s* are spines and the tibiae IV bear one seta. The setae *s* *cx* are relatively long (20–30 μm). The tritonymph is normally developed and resembles the female. In the

hypopus the tarsus IV is long, in some species as long as tarsus III, and tibia IV bears a solenidion.

The genus *Phalacrodes* is more regressed (thus more evolved) and in some characters, more specialised than *Neottialges*. In the adults the gnathosoma, the palps and the chelicerae are elongate (narrower and relatively longer), the pharyngeal plate has no sclerotized lines and the anus is distinctly shorter (60 μm long in both sexes of *P. whartoni* and 40 μm in the male of *P. panamensis*). These adults probably feed occasionally in the nests and one can surmise that they have a shorter life span than *Neottialges*. In *Phalacrodes* the solenidion $\omega 2$ is more apical than in *Neottialges*. The tarsus IV bears only 7 setae in the female and 5 in the male, and its tibia IV has a seta as in *Neottialges*. The tritonymph is inert and strongly regressed, and the legs, the mouth-parts and the chaetotaxy are vestigial. In the *hypopus* the leg IV is more regressed than in *Neottialges* and in *Hypodectes* (*H. propus*). The tarsus IV is strongly reduced and the tibia IV lacks a solenidion. On tarsus I-II the apical spine is shorter than in *Neottialges*.

The genus *Hypodectes* (*Hypodectoides*) (represented by *H. propus*) is highly specialised and in some characters more regressed than the two previous genera. In the adults the gnathosoma is modified in shape and strongly sclerotized and the palps are elongate and unisegmented. The pharynx is as in *Phalacrodes*. In the female the chelicerae are vestigial, but in the male they are abnormally developed and sclerotized. The anus is vestigial in both sexes (12–15 μm long). These mites are obviously non-feeding. Tarsus IV is as in *Phalacrodes* (7 setae in female and 5 in male). Tibia IV lacks a seta. The tritonymph is reduced to a structureless, verrucose sac. In the *hypopus* the leg IV is slightly less regressed than in *Phalacrodes*, and the tarsus is short as in that genus, but the tibia has retained its solenidion. The tarsi I-II end in a long spine (not a claw). The elongation of this apical spine is probably an adaptation enabling these very large hypopi to cross the skin of the bird and to reach the nest. The size of these apical spines is probably related to the size of the hypopi, at least in very large hypopi. In this respect the hypopi of

Hypodectes nycticoracis, whose body length reaches 1800 μm , also have very long apical spines on their anterior tarsi. The *protonymph* is reduced to an inert verrucose structureless membrane. The *larva* is reduced to a striated membrane bearing long setae, vestigial gnathosoma and legs, the latter being reduced to very short, rounded stumps (see below). A prelarva is present in *H. propus*. It resembles that of *Bubulcodectes brevitarsis* and consists of a pair of small conical and pointed sclerites (= ecdysing organs).

Descriptions of the species

Genus *Neottialges* Fain, 1966

With the two new subgenera described herein, the genus *Neottialges* currently contains five subgenera:

1. *Neottialges* Fain, 1966: Type species *N. (N.) geopeliae* Fain, 1966.
2. *Caloenectes* Fain, 1966: Type species *N. (C.) giebeli* Fain, 1966.
3. *Pelecanectes* Fain, 1966: Type species *N. (P.) evansi* Fain, 1966.
4. *Ardeidectes* n. subg.: Type species *N. (A.) ibis* n. sp.
5. *Heronidectes* n. subg.: Type species *N. (H.) mendezi* n. sp.

In 1972 Fain & Beaucournu elevated *Pelecanectes* to generic rank, but later Fain & Laurence (1974) re-established the original status.

Subgenus *Neottialges* Fain, 1966

1. *Neottialges (Neottialges) eurafer* Fain, 1966

This species has been described from hypopi found in a pigeon, *Columba palumbus*, in Belgium. These hypopi were mixed with those of *Hypodectes (Hypodectoides) propus*. We now believe that the homeomorphic male that we described in our previous paper (Fain & Bafort, 1967), and named *Hypodectes (Hypodectoides) propus*, actually represents the male of *N. eurafer*. In fact this male is

morphologically very similar to the males of the two other species known in this genus, *N. evansi* and *N. mendezi*. The main similarities that we observe are the following: the same shape of propodotal shields (two longitudinal paramedian punctate bands), the normal aspect of gnathosoma and chelicerae and the same aspect of the leg chaetotaxy, especially the presence of 6 setae on tarsus IV and the spinous aspect of setae *s* of tarsi I-IV. Tarsus IV does not bear two small copulatory suckers, as in *N. mendezi*, but two small specialised rodlike setae, as in *N. evansi*. This male differs, however, from *N. evansi* and *N. mendezi* in the piliform aspect of the setae of tibiae III-IV (spines in these species). This difference may justify its separation as a distinct subgenus.

Subgenus *Pelecanectes* Fain, 1966

The hypopi of this subgenus differ from those of the nominate subgenus and of *Caloenectes* by the following characters: the cuticle is poorly sclerotized, the primary median genital sclerite is present but sometimes incomplete, and the setae *d 1* to *d 3* are long or very long except in three species, *P. elani* Fain and *P. apunctatus* Pence (with short *d 1* to *d 3*) and in *P. hawaiiensis* Fain & Amerson (with short *d 2* and *d 3*).

Pelecanectes (type species: *N. (P.) evansi* Fain, 1966) contains at present 15 species from various birds, especially Ciconiiformes (with 6 species, 5 in the Threskiornithidae and 1 in the Ciconiidae) and Pelecaniformes (6 species, 2 in the Phalacrocoracidae, 1 in the Fregatidae, 2 in the Pelicanidae and 1 in the Sulidae). One species is known from the Falconidae (Falconiformes), 1 from the Columbidae (Columbiformes) and 1 from the Grallinidae (Passeriformes).

2. *Neottialges (Pelecanectes) evansi* Fain, 1966 (Figs 14, 18, 19, 26-28)

Life cycle

Fain & Beaucournu (1972) discovered in a nest of a

cormorant at Cape Frehel, France, free hypopi of *N. (P.) evansi* in the moulting stage and containing well-developed, active tritonymphs (with legs and gnathosoma normally developed). This nest also contained two adult males which are assumed to belong to the same species owing to their similarities with these tritonymphs. In this nest we also found hypopi of *Phalacrodectes (Frehelectes) gaudi* n. subg., n. sp., some of them containing an inert tritonymph with vestigial legs and gnathosoma and very distinct from those of *P. evansi*.

In order to ascertain that the males actually correspond with *Pelecanectes* and not to another subgenus we have re-examined this material. This new study enabled us to find several characters that we had overlooked previously and so confirm that the males correspond to the males of *P. evansi*. One of these characters is the shape of the pharyngeal plate. In both tritonymphs and males this plate is formed of longitudinal anastomosed lines (Figs 18–19) while in the adults of *Phalacrodectes whartoni* (Fig 23; see below) this plate bears numerous rounded or elongate pits. Another character present in both tritonymphs and males is the nature of the leg setae. In both stages the setae *s* of tarsi I–IV and the setae *w* of tarsi III–IV are spines, and the seta of tibia IV is a spine. In the male of *Phalacrodectes whartoni* (and probably also in the male of *Frehelectes gaudi*) the setae *s* of tarsi I, II and IV are thin, that of tarsus III is a spine and the seta of tibia IV is piliform. We also found that the organ of Grandjean has the same shape in both the tritonymphs and the males (two rounded thorny processes) (Fig. 28). It should be noted that in our drawing of the tritonymph of *N. evansi* (Fain & Beaucournu, 1972) the ventral spines of tarsi and tibiae were depicted erroneously as thick setae. We, therefore, present corrected drawings of tarsi I and IV and of tibia IV of this tritonymph (Figs 26–27).

Hosts and localities

This species is only known from cormorants of the genus *Phalacrocorax* (Pelecaniformes, Phalacrocoracidae):

1. The type series, only represented by hypopi,

was found in two different species of cormorants: *Phalacrocorax aristotelis*, from Thetford, Norfolk and from the Marine Biological Station, Isle of Man, U.K., and *P. atriceps*, from Shagnasty, Orkneys, U.K. (Fain, 1967).

2. Free hypopi, some containing a tritonymph, free tritonymphs and 2 males were found in the nest of *P. aristotelis* from Cape Frehel, France (see Fain & Beaucournu, 1972).

3. From *Phalacrocorax auritus*, from Louisiana, U.S.A. (Pence, 1972) and Cuba (Cerny, 1969).

4. From *Phalacrocorax carbo*, from Kenya (Schwan & Sileo, 1978) and Tasmania, Australia (Fain & Domrow, 1979).

Subgenus *Heronidectes* n. subg.

Diagnostic characters of male. Dorsum without scales; copulatory suckers of tarsus IV normally formed; seta *w* of tarsi III–IV piliform (they are spines in *P. evansi*). Type species: *N. (H.) mendezi* n. sp.

3. *Neottialges (Heronidectes) mendezi* n. sp.

This species is named for Dr E. Mendez, Panama, who sent us the specimens.

Female (Figs 1, 4–6, 9, 15). Holotype 579 long (idiosoma) and 390 wide. Measurements in 3 paratypes: 630 × 375, 600 × 380 and 570 × 388. *Dorsum:* Sejugal furrow incomplete. Cuticle soft except in small median area in middle of opisthonotum bearing a few triangular scales. Propodnotum with 2 longitudinal paramedian, punctate bands 38 apart and extending posteriorly close to scapular setae. Oil gland orifices at about 30 from lateral margins. Two wide grooves originate from these orifices, one posterior reaching posterior margin of body and one anterior which immediately bifurcates into secondary branches, a lateral and an internal, latter ending close to seta *l*₁. There are 4 pairs of lyrifissures, 3 opisthogastric (2 ventral and one dorsal) and one dorsal metapodogastric. *Venter:* Posterior border with 2 small areas with scales.

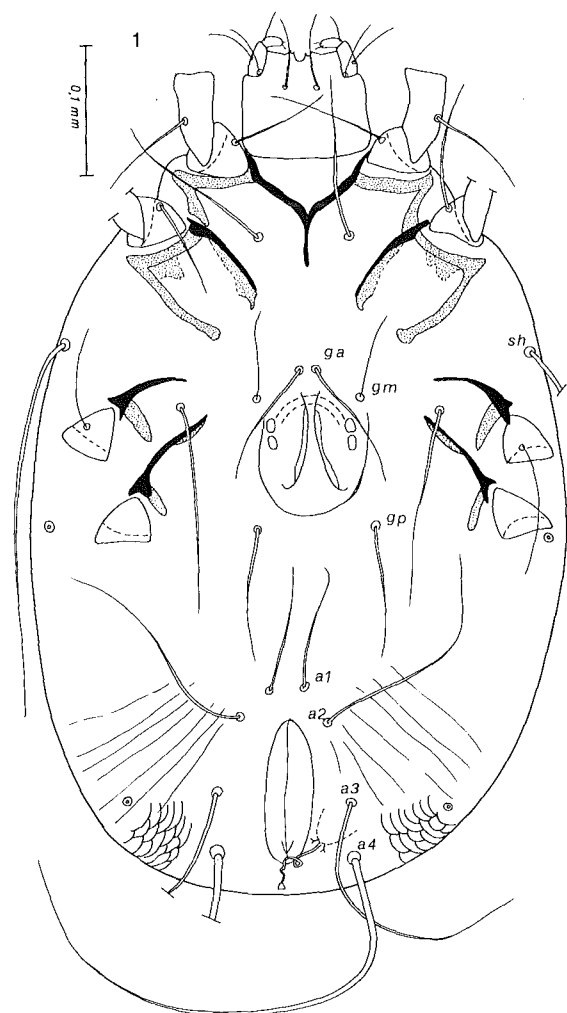


Fig. 1. *Neottialges (Heronidectes) mendezi* n. sp. Holotype female in ventral view.

Vulva between coxae III and IV. Thick sclerite present in depth of vulva which is concave posteriorly. Copulatory orifice situated immediately behind anus; bursa short describing 2 or 3 loops. Gnathosoma normal. Palps and chelicerae normal and short. Pharyngeal plate with numerous longitudinal, anastomosed lines. Legs long and narrow. Length of tarsi I-IV 98-98-135-154. *Chaetotaxy of idiosoma* (length of setae): *vi* 135; *sc i* 100; *sc e* 400; *d 1* to *d 4* 85 to 105 and spinous; *d 5* 600; *l 1* and *l 2* 90 (spinous); *l 3* 105 (spinous); *l 4* 75; *l 5* 570; *h* 470; *sh* 300. There are 4 pairs of anals; the *a 4* 475. Seta *s cx* very thin about 30 long.

Chaetotaxy of legs: Tarsi I-IV with 11-10-8-8 setae.

Setae *s*, *p* and *q* are spines. Tibiae I-II with 2 thin setae; tibiae III and IV with one long spine.

Solenidiotaxy: $\omega 2$ is situated at the base of the apical third of tarsus I; $\omega 1$ is situated in basal quarter of tarsus I; $\omega 3$ is apical.

Male (Figs 2, 3, 10, 20). Length and width in 2 paratypes (idiosoma) 510 × 295 and 504 × 320. Posterior extremity bilobed. *Dorsum* as in female but there are 2 punctate lateral shields on opisthonotum and no scales on hysteronotum. Sejugal furrow complete. *Venter*: genital organ between coxae IV. Penis small. Para-anal suckers surrounded by rather strongly sclerotized punctate areas forming 2 concentric zones. Gnathosoma and palps as in female. Chelicerae with digits slightly different from those of female, teeth being situated farther from apex. Legs as in female, except tarsus IV. *Chaetotaxy of idiosoma* as in female, but there are only 3 pairs of anals and setae are generally shorter. *Chaetotaxy of legs* as in female, but tarsus IV has only 6 setae, 2 other setae being replaced by 2 suckers.

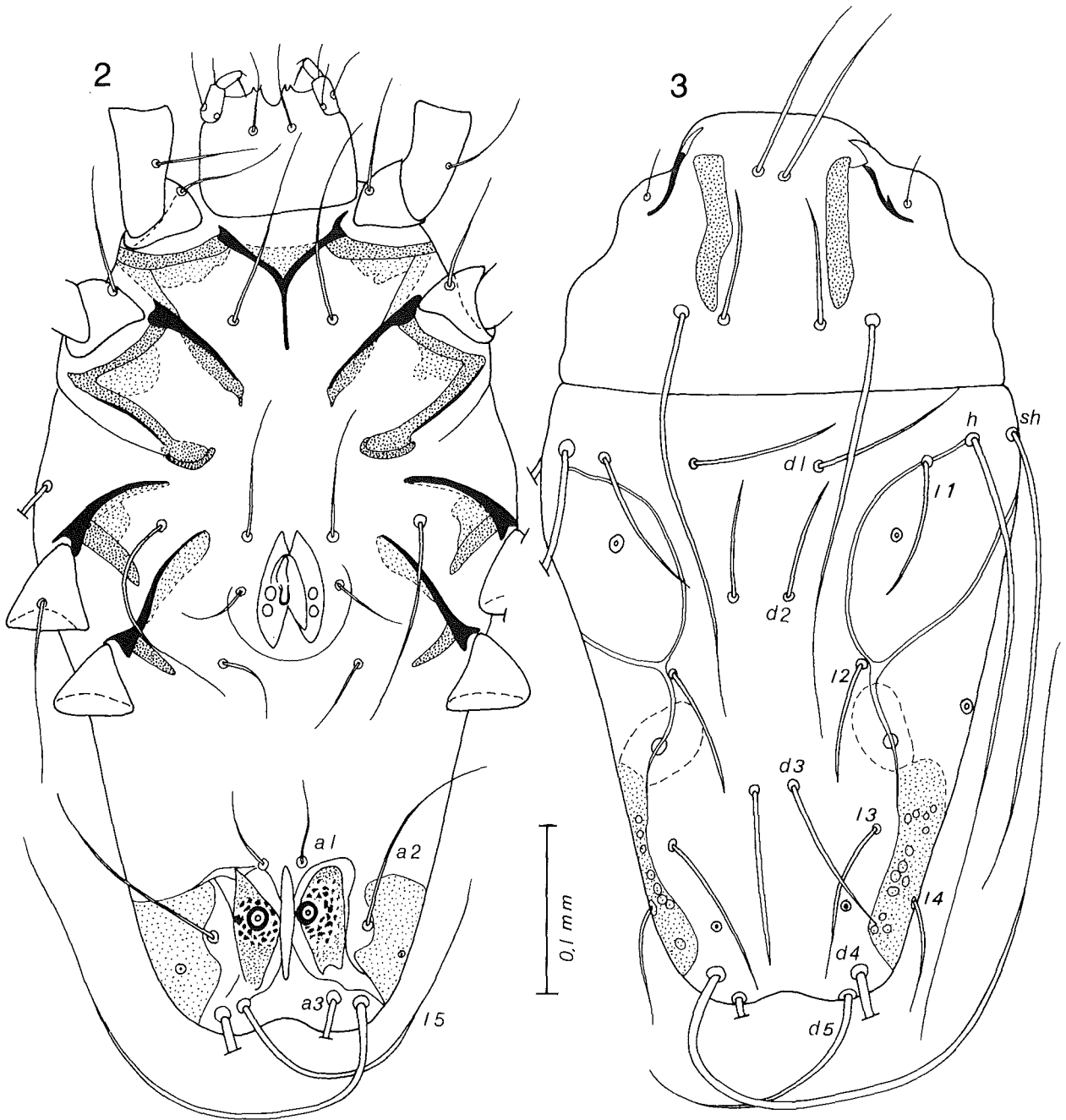
Protonymph. Length 234, width 158. *Dorsum* as in female, with 2 longitudinal punctate bands on propodonotum. *Venter*: vulva replaced by short slit flanked by one pair of suckers and one pair of setae. Gnathosoma, chelicerae and pharynx as in female. *Chaetotaxy* as in female, but setae are smaller and there are only 3 pairs of anals. *Chaetotaxy of tarsi I-II and tibia III* as in female. Tarsus III with at least 7 setae, *s* being a thin spine. Tarsus IV with 5 setae (of which 2 are apical spines). Tibia and femur IV and trochanters I-III without setae.

Remark

This species is included in the genus *Neottialges* owing to the similarities between the male and *N. (P.) evansi* (same propodonotal punctate bands, similar sclerotisation around the adanal suckers, same pharynx, similar tarsal and tibial chaetotaxy).

Habitat

Holotype and 8 female paratypes, 5 male paratypes

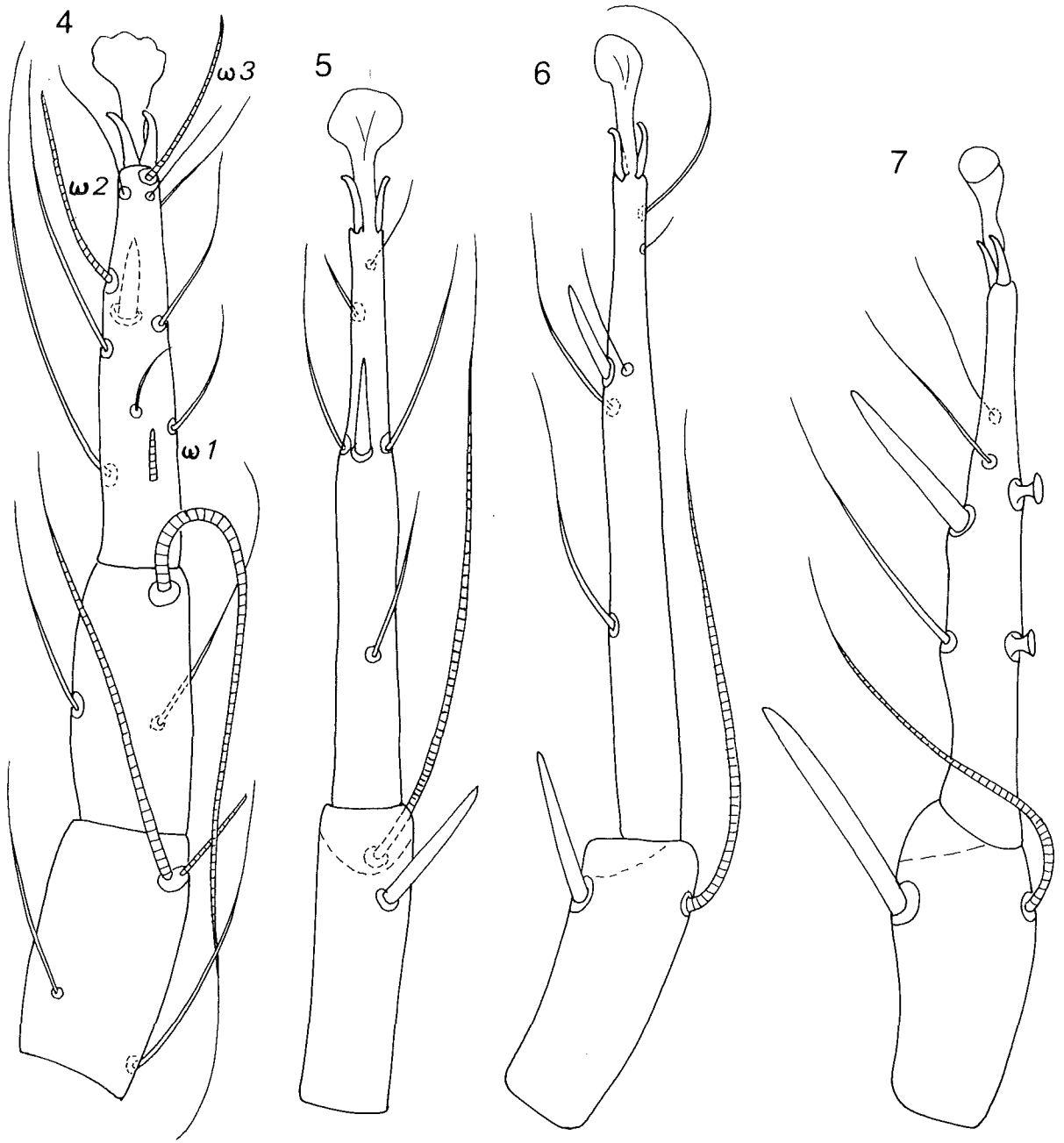


Figs 2-3. *Neottialges (Heronidectes) mendezi* n. sp. Male in ventral (2) and dorsal (3) view.

and 1 protonymph paratype from the nest of *Bubulcus ibis* from Panama (Coll. A. Herrera, 30.IX.1982).

Subgenus *Ardeidectes* n. subg.

Diagnostic characters. This genus is known only from adult females. It differs from the female of *N. (H.) mendezi* by the presence on tibiae I-II of a spine and a thin seta. Other characters resemble

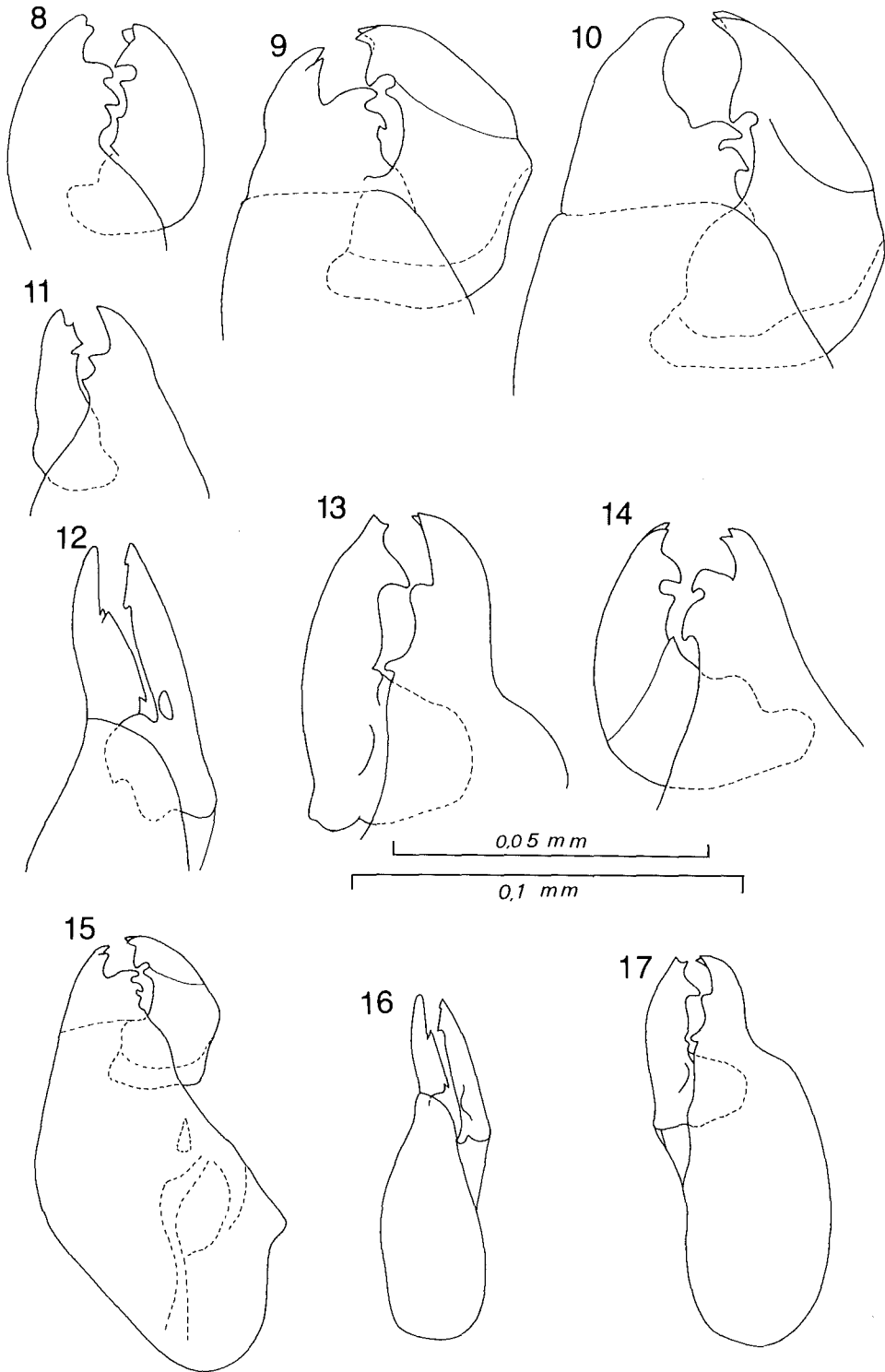


Figs 4-7. *Neottialges (Heronidectes) mendezi* n. sp. Female: apical segments of leg I (4), III (5) and IV (6). Male: leg IV (7).

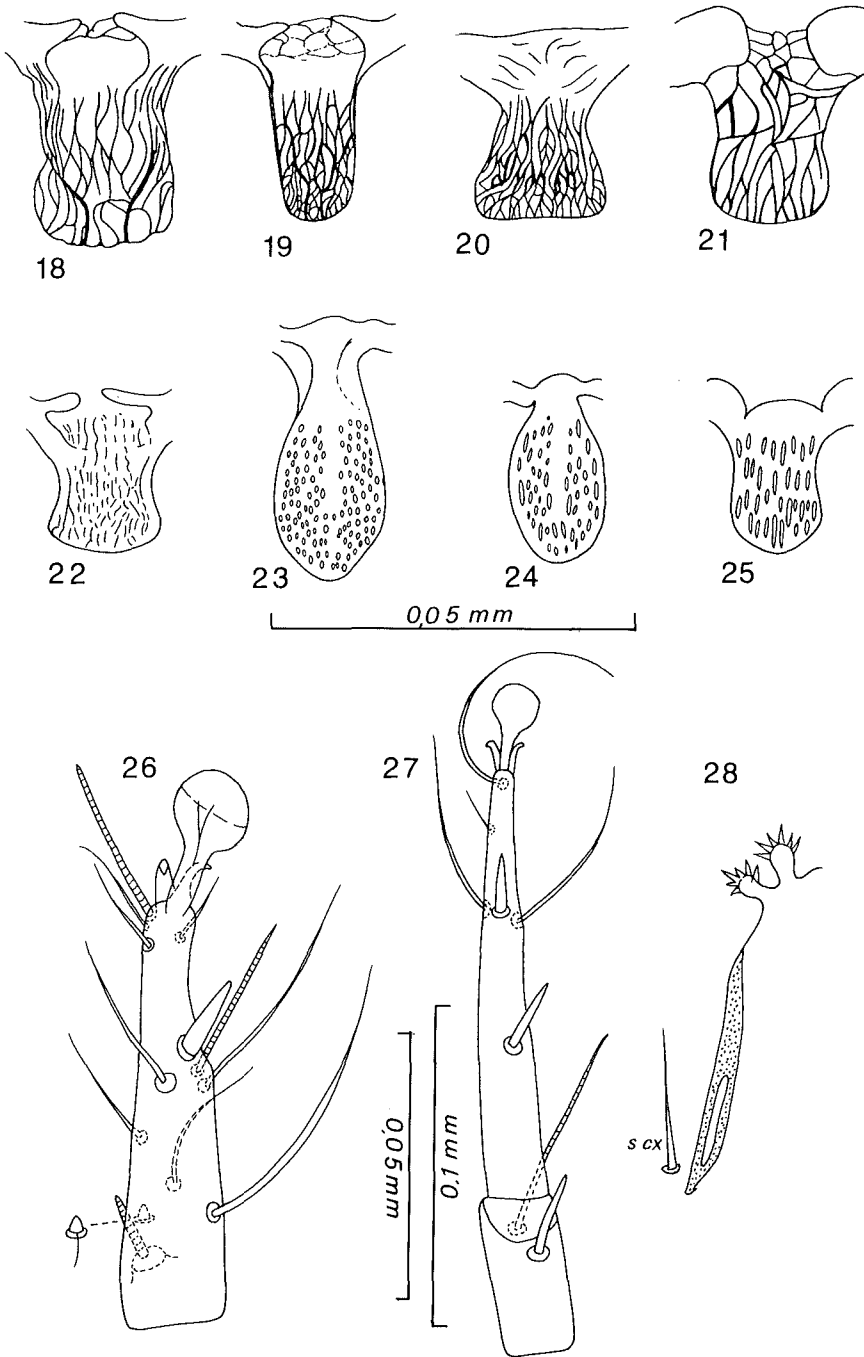
those of *N. mendezi*. Type species: *N. (A.) ibis* n. sp.

4. *Neottialges (Ardeidectes) ibis* n. sp.

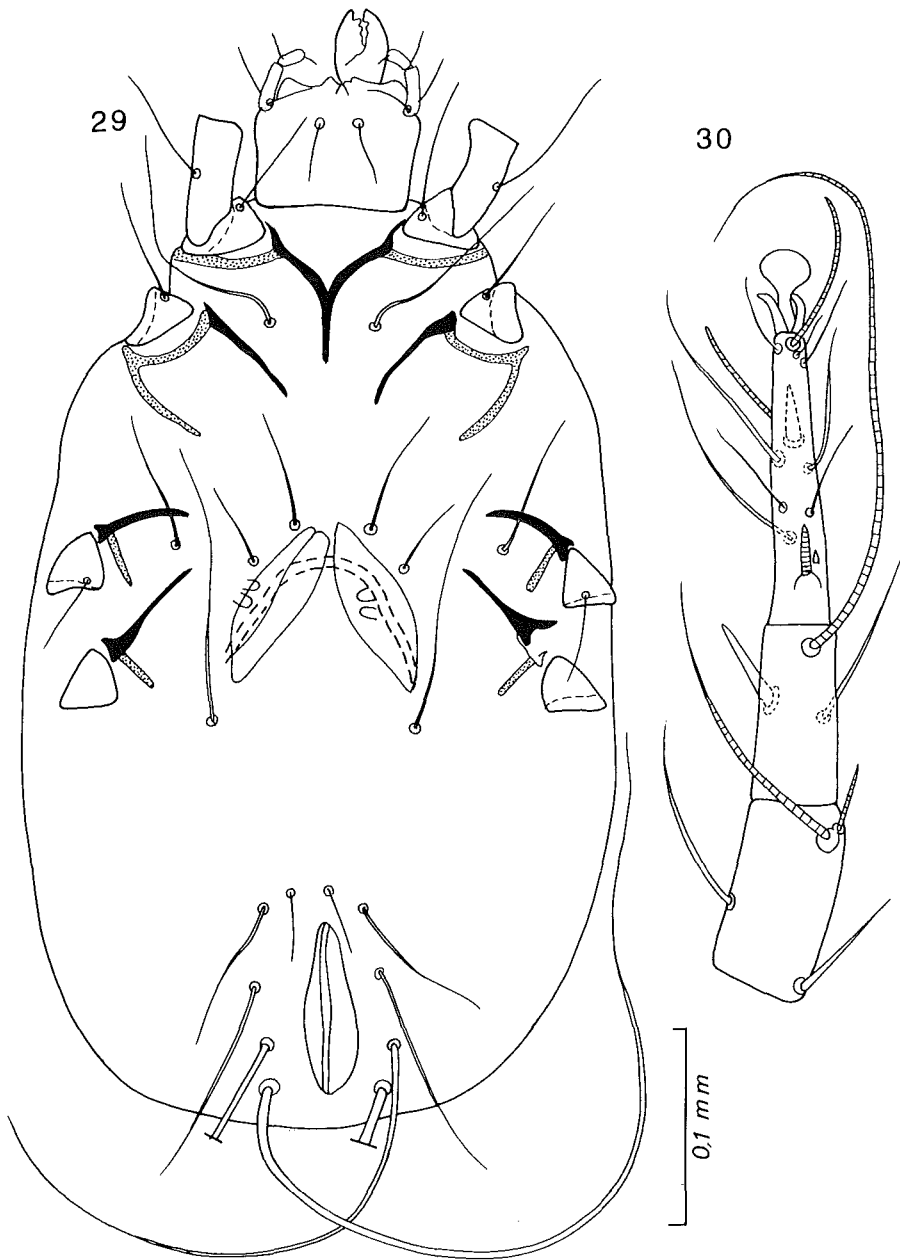
Female (Figs 8, 29-33). In holotype and paratype cuticle is partly torn and some dorsal setae are displaced or lost. Holotype approximately 480 long and 330 wide, paratype 450 × 250. *Dorsum*: sejugal



Figs 8–17. (8–14) Cheliceral digits: *Neottialges ibis* n. sp. female (8); *N. mendezi* n. sp. female (9) and male (10); *Bubulcodectes brevitarsis* n. sp., female (11); *Phalacrodes whartoni* Fain, female (12); *P. panamensis* n. sp., male (13); *Neottialges evansi* Fain, male (14). (15–17) Chelicerae: *N. mendezi* n. sp., female (15); *P. whartoni* Fain, female (16); *P. panamensis* n. sp. male (17).



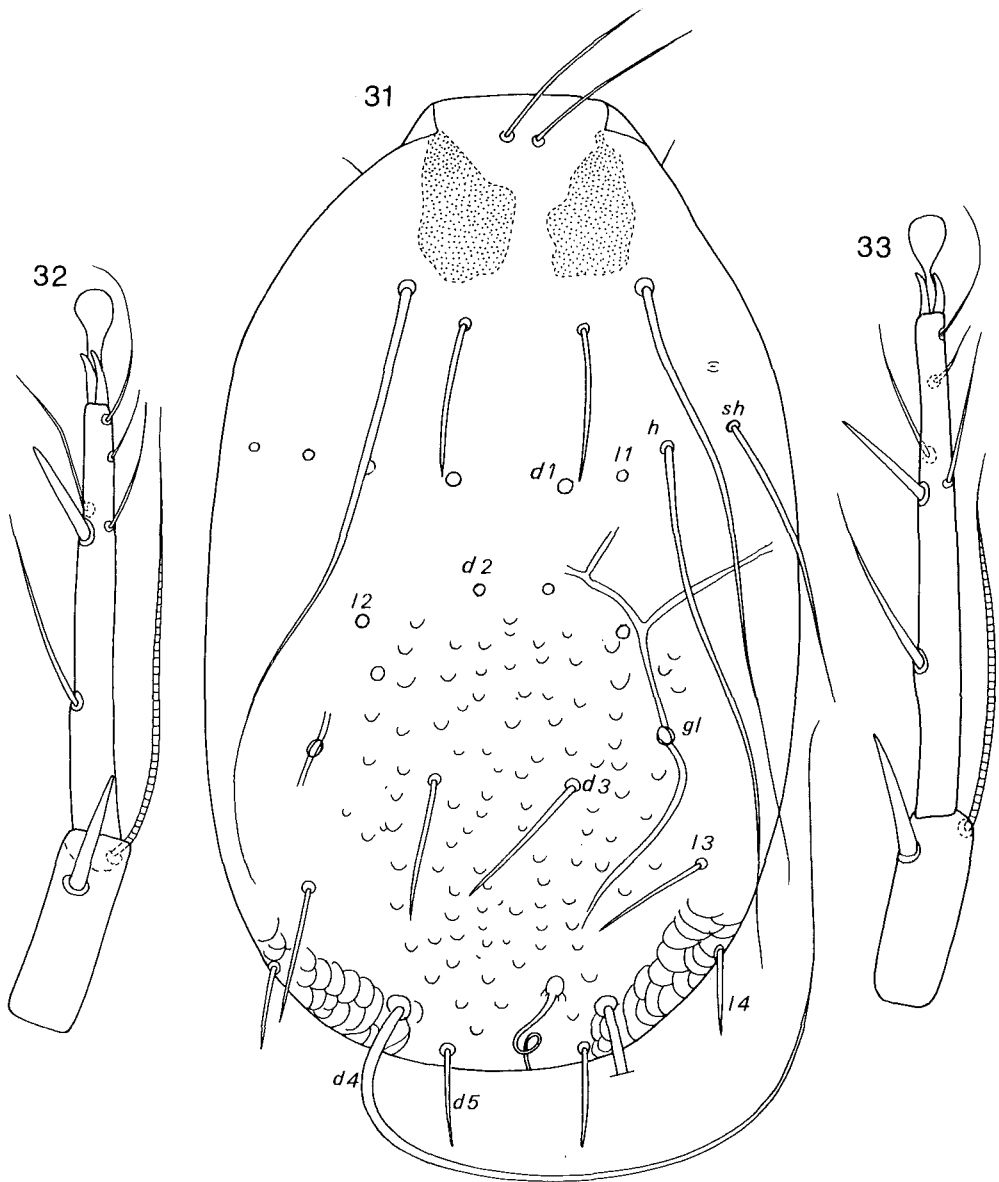
Figs 18-28. (18-25) Pharyngeal plate: *Neottialges evansi* Fain, male (18) and tritonymph (19); *N. mendezi* n. sp., male (20); *Bubulcodectes brevitarsis* n. sp., male (21); *Gypsodectes verrucosus* Fain, female (22); *Phalacrodes whartoni* Fain, male (23); *P. panamensis* n. sp., male (24); *Hypodectes propus* Nitzsch, male (25). (26-28) *Neottialges evansi* Fain, tritonymph: leg I (26) and IV (27); male: organ of Grandjean and seta *s cx* (28).



Figs 29-30. *Neottialges (Ardeidectes) ibis* n. sp. Holotype female in ventral view (29), leg I dorsally (30).

furrow not observed (probably because of the bad condition of cuticle). Propodonotum bearing 2 wide, triangular, para-median, longitudinal punctate bands. Hysteronotum with median field of small, rounded scales. Oil grooves visible only on one side. Posterior margin of body with scaly appearance as in *N. mendezi*. *Venter*: vulva with a

deeply-situated horse-shoe shaped sclerite, better developed than in *N. mendezi*. Bursa well formed but short; copulatory orifice at posterior border of body. Coxae without punctate areas. Legs long and thin. Length of tarsi I-IV: 77-79-120-135. Gnathosoma and chelicerae normal in shape and length. *Chaetotaxy of idiosoma* (length of setae in holotype



Figs 31–33. *Neottialges (Ardeidectes) ibis* n. sp. Holotype female in dorsal view (31), legs III (32) and IV (33).

and paratype): *vi* 90; *sc i* 75 (a spine); *sc e* 360; *d1* and *d2* are lacking; *d3* 75 (a spine); *d4* 450; *d5* 50 (a spine); *l1* to *l3* 80 (spines); *l4* 40 (a spine); *l5* 420; *a1* 30; *a2* 100; *a3* 170; *a4* 350; *s cx* 20.

Chaetotaxy of legs (number of setae): Tarsi I–IV: 11–10–8–8. Setae *s* are spines. Setae *w* of tarsi III–IV are piliform. Tibiae I–II with one spine and one simple seta. Tibiae III–IV with one long spine.

Habitat

Holotype and one paratype female from a nest of *Bubulcus ibis*, Panama.

Genus *Phalacrodes* Fain, 1966

The genus *Phalacrodes* has been divided into three subgenera:

1. *Phalacrodes* Fain, 1966. Type species: *P. (P.) schoutedeni* Fain, 1966. The complete life cycle is known for *P. (P.) whartoni* (see below).

2. *Peledectes* Cerny, 1969. Type species: *P. (Peledectes) punctatissimus* Cerny, 1969.

3. *Frehelectes* Fain & Beaucournu, 1972. Type species: *P. (F.) gaudi*. Fain & Beaucournu, 1972; known from the hypopus and the tritonymph.

Peledectes is probably a synonym of *Phalacrodes*. *Frehelectes* has been elevated to generic rank by Fain (1984). It differs from *Phalacrodes* in the hypopus by the absence of setae on tibia IV and the presence of three spines and a long apical hair on tarsus IV (in *Phalacrodes* tibia IV bears a spine and tarsus IV bears 2 spines and a long apical hair). Moreover, the tritonymph is completely devoid of setae while in the tritonymph of *Phalacrodes whartoni* the idiosoma bears numerous short setae.

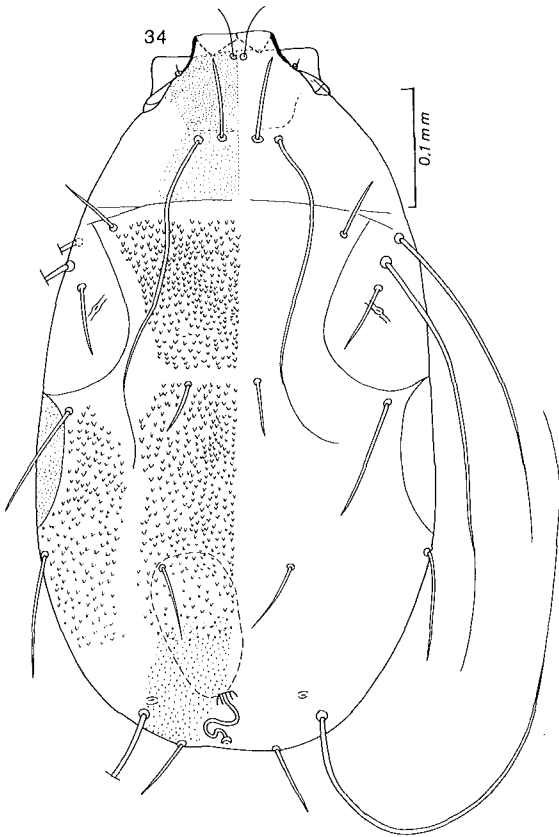


Fig. 34. *Phalacrodes whartoni* Fain. Female in dorsal view.

1. *Phalacrodes (Phalacrodes) whartoni* Fain, 1967

The adults of the genus *Phalacrodes* were previously unknown, but the life cycle of *P. whartoni* can now be described. The specimens were collected from a nest of *Bubulcus ibis* in Panama. The following stages have been observed: numerous free males, females and hypopi, some of the latter being in the moulting stage and containing an inert tritonymph with vestigial legs and gnathosoma. One hypopus contained a completely developed tritonymph which in its turn contained a fully developed female.

Female (Figs 12, 16, 34, 35, 39–41). Length and width of idiosoma in 4 specimens: 600 × 315; 595 × 320, 570 × 310, 565 × 312. There are 4 pairs of

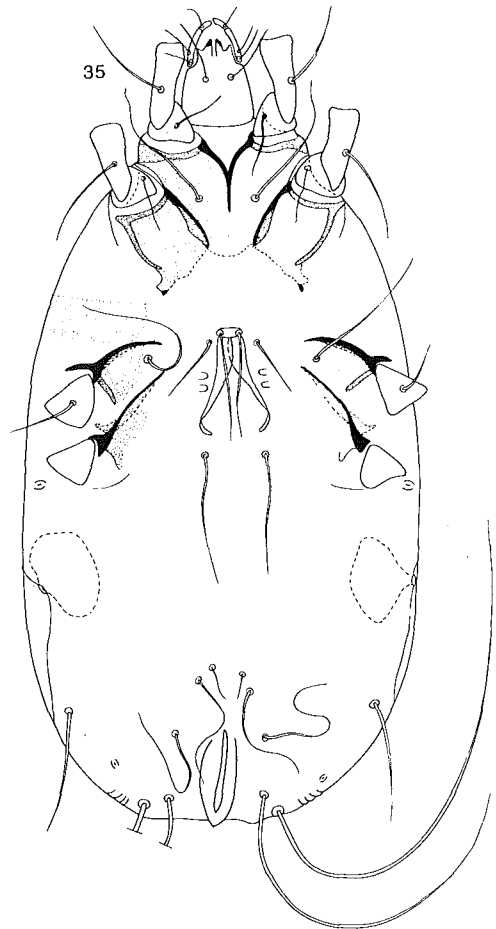
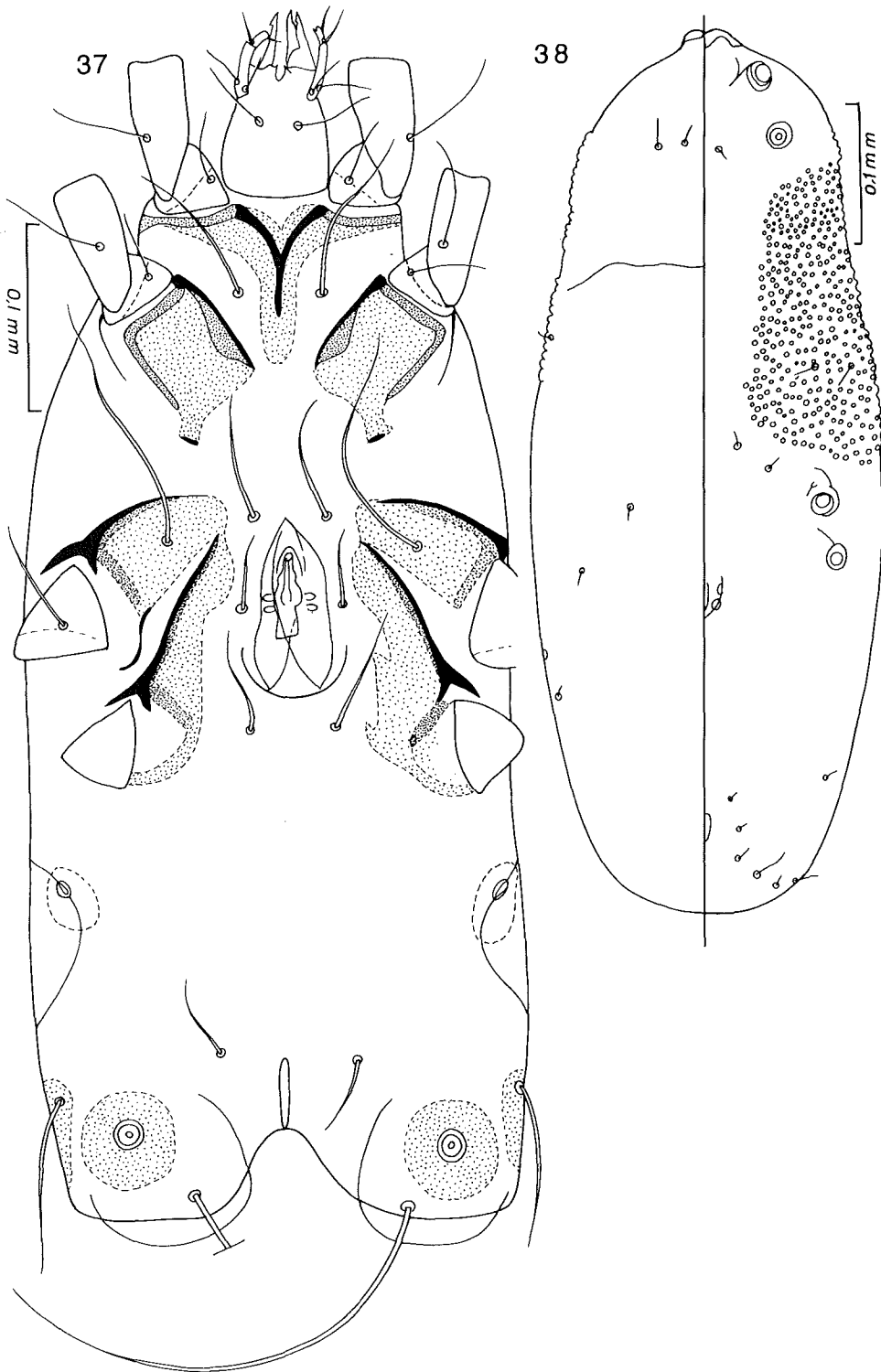
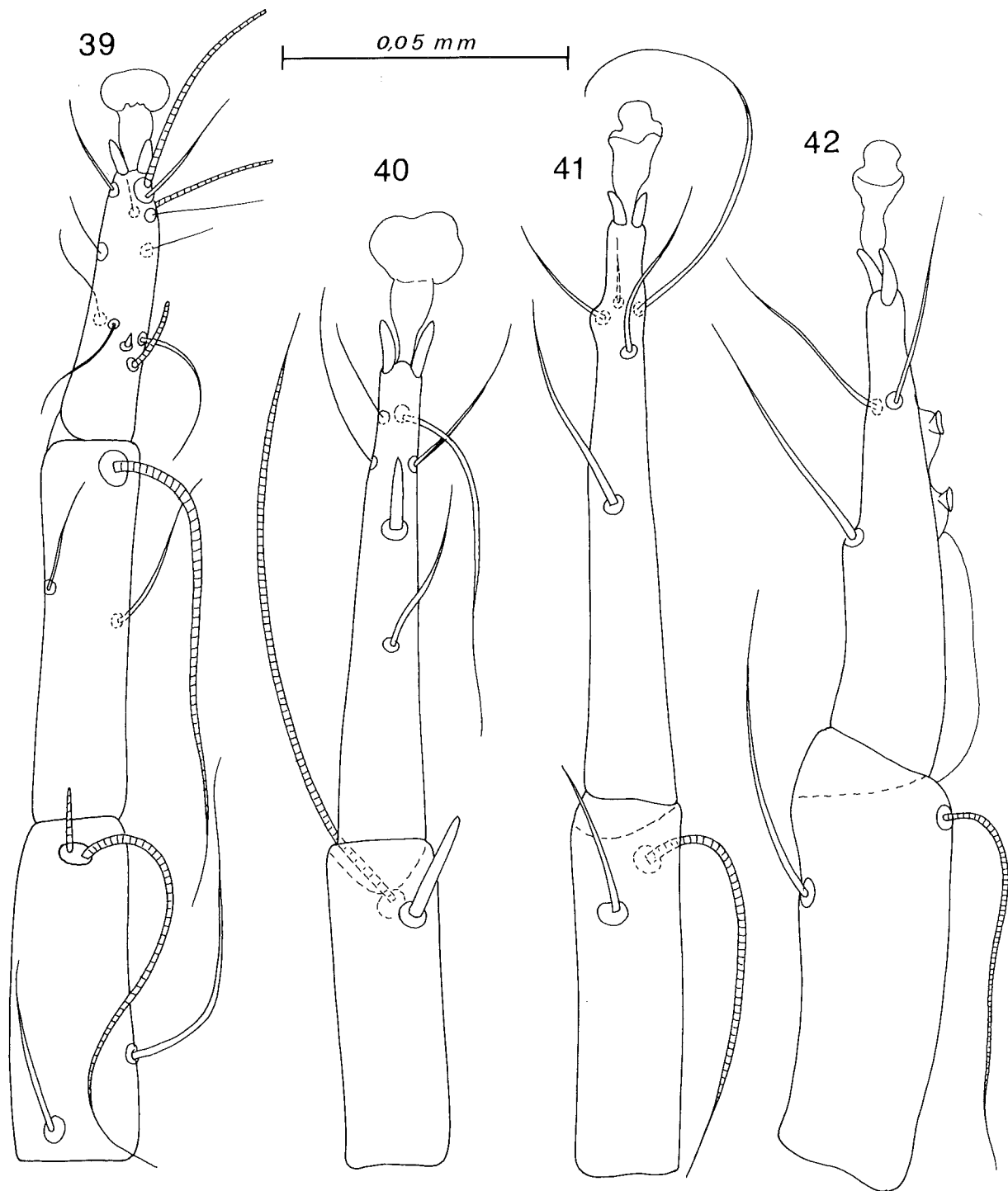


Fig. 35. *Phalacrodes whartoni* Fain. Female in ventral view.



Figs 37-38. *Phalacrodectes whartoni* Fain. Male in ventral view (37); tritonymph in dorsal view (left) and in ventral view (right) (38).



Figs 39-42. *Phalacroectes whartoni* Fain. Female, legs I (39), III (40), IV (41). Male, leg IV (42).

Length of tarsi I-IV 57-60-93-93. Chaetotaxy of legs as in female, but tarsus IV bears only 3 thin setae and 2 apical spines and dorsally 2 suckers.

Hypopus. It is not distinguishable from the type specimens.

Tritonymph (Fig 38). Four hypopi were in moulting stage and contained a tritonymph. One of these tritonymphs, still enclosed in hypopus, contained a completely developed female. We succeeded in dissecting and isolating these different stages. The tritonymph is described as follows: Length 630, width 240. Gnathosoma represented by a bilobed formation without structure. Chelicerae absent. Legs represented by short, conical structures without distinct segmentation or setae. Anus and genital orifice very small, latter flanked by one pair of very small suckers. Ventro-laterally and between legs II and IV there is, at both sides, a large verrucose area. *Chaetotaxy*. Length of setae: *sc i* 9; *sc e* 18; *d5* 30; *l5* 32; *sh* 15; *h* 18. Other setae: *cx I*, *d2* to *d4*, *l1* to *l4*, *ga* and *gm* are microsetae.

Hosts and localities

1. Type series consisted of hypopi and was found in a roseate spoonbill, *Ajaia ajaja* which died in Antwerp Zoo.

2. Hypopi recorded from the white ibis, *Eudocimus albus*, from the U.S.A. (Pence, 1971, 1972).

3. From the nest of *Bubulcus ibis*, from Panama: males, females, hypopi containing or not inert tritonymphs.

2. *Phalacrodectes (Phalacrodectes) panamensis* n. sp.

This species is represented by a single male specimen.

Male (Figs 13, 17, 24, 43-48). Holotype 440 long and 228 wide (idiosoma). Posterior margin slightly lobed. *Dorsum*: sejugal furrow complete. Propodonotum with broad, well-punctate shield 70 long and 66 wide. Hysteronotum with 2 posterolateral punctate areas. There are no scaly areas.

Oil-gland aperture very lateral. Oil grooves poorly developed. *Venter*: male organ slightly behind coxae IV. Coxae II completely and coxae I almost completely punctate. Gnathosomal base slightly wider than long, basal article of palps slightly elongate about 4.5 times as long (32) as wide. Chelicerae elongate; base much longer (75) than wide (40); digits elongate (moveable digit 42 long), with stronger teeth than in *P. whartoni*. Pharyngeal plate as in *P. whartoni*. Legs long; I distinctly thicker than legs II-IV, except tarsi which are narrow. Length of tarsi I-IV: 40-42-55-57.

Chaetotaxy of idiosoma (length of setae): *vi* 45; *sc i* 48; *sc e* 210; *d1*, *d2*, *d3* and *d5* 45 to 55; *d4* 250; *l1*, *l2* and *l3* 60 to 65; *l4* 40; *l5* 120; *h* 240; *sh* 160; *a1* 21; *a2* 210; *a3* 350; *s cx* 30. Setae *sc i*, *d1*, *l1* are spinous.

Chaetotaxy of legs (number of setae): tarsi I-IV as in male of *P. whartoni*. Tibiae III and IV with a piliform seta.

Solenidiotaxy: tarsus with $\omega 1$ in basal third of tarsus; $\omega 2$ is subapical; $\omega 3$ is apical.

Locality

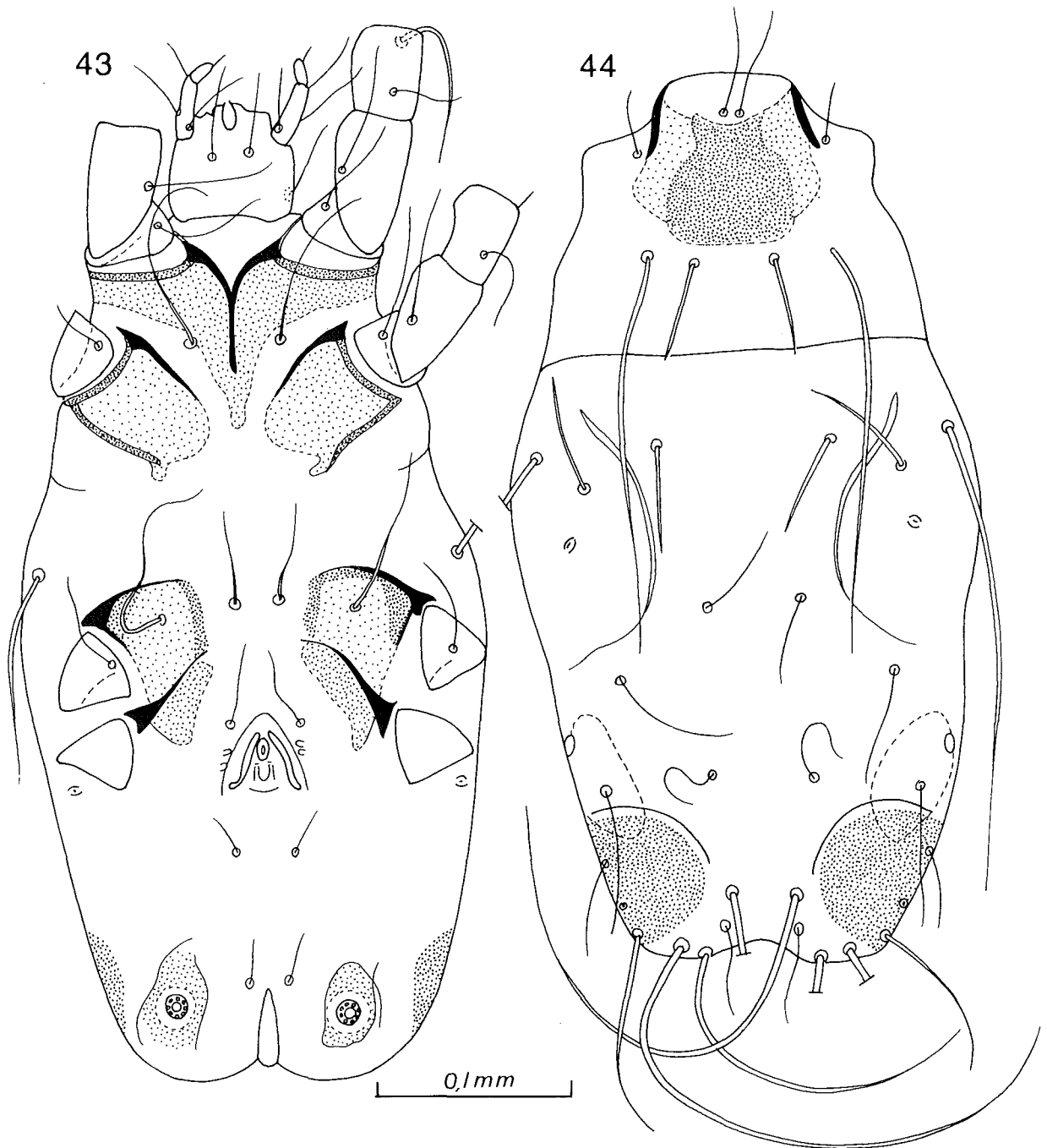
Holotype male found in a nest of *Bubulcus ibis* from Panama amongst specimens of *P. whartoni* and other species described herein.

Remarks

This species differs from the male of *P. whartoni* in the following characters: much smaller size of body, absence of a crest on tarsus IV, chelicerae less elongate and with larger teeth on digits, greater length of setae *s cx*, shape of tarsi I-II relatively narrow compared to tibiae, genital organ more posterior, and presence of thin seta on tibia III.

Genus *Bubulcodectes* n. g.

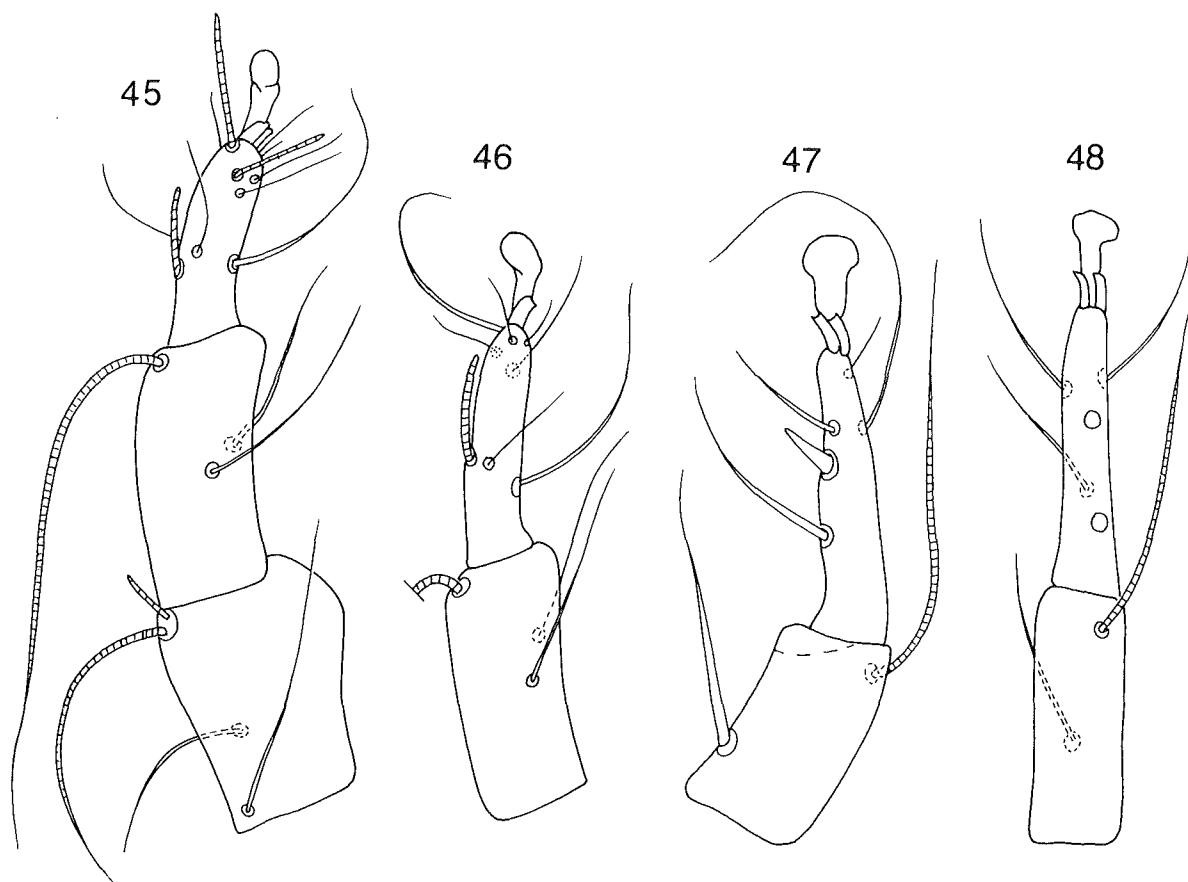
Diagnostic characters (of both sexes). Sejugal furrow well developed in male, variably developed in female. Anus very short. Anterior legs short and thick. Oil grooves well developed in males, indistinct in female. Setae *s* of tarsi I-IV are spines. All setae of tibiae I-IV are thick spines. Genua I with 2



Figs 43–44. *Phalacrodectes panamensis* n. sp. Holotype male, in ventral (43) and dorsal (44) view.

unequal solenidia. Solenidion $\omega 2$ of tarsus I situated ventrally in apical quarter of tarsus. There are 4 pairs of lyrifissures. Pharyngeal plate as in *Neotialges*. Female physogastric, containing about 10 eggs. Cuticle poorly sclerotized, without dorsal

shields. In some specimens eggs contain fully-developed larvae. The most mature eggs contain a prelarva formed of 2 small sclerotized pointed cones (ecdysing organs). Gnathosoma and chelicerae normal in shape but very small. Vulva be-



Figs 45–48. *Phalacrodectes panamensis* n. sp. Holotype male. Legs I (45), II (46), III (47) and IV (48).

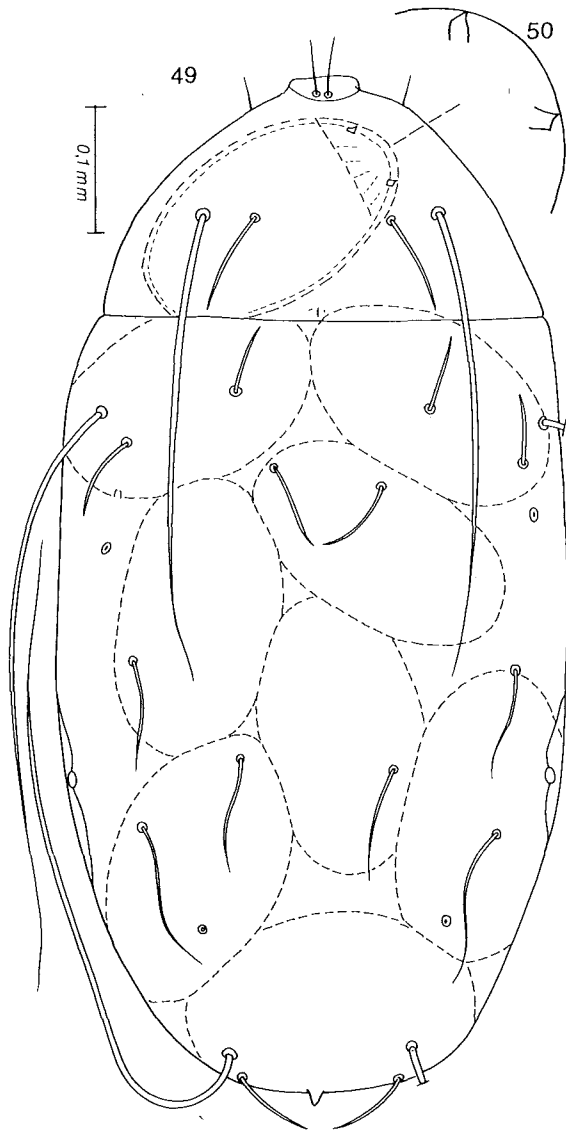
tween coxae III, without internal house-shaped sclerite. Setae *s cx* and bursa copulatrix present. Leg chaetotaxy: tarsi I–IV 11–10–8–8, male heteromorphic. Propodosoma very wide, propodonotum almost completely punctate. Opisthosoma very short. Posterior extremity rounded. Base of gnathosoma modified, heavily sclerotized and bearing laterally one pair of triangular processes. Palps strongly sclerotized and with basal article long and narrow and bearing one apico-lateral process; palpal tarsus short. Chelicerae very strongly developed but normal in shape. Genital organ situated slightly behind coxa IV. Adanal suckers surrounded by oval, incomplete, sclerotized ring which is open internally. Leg IV with 2 small suckers. Type species: *Bubulcodectes brevitarsis* n. sp.

1. *Bubulcodectes brevitarsis* n. sp.

Female (Figs 11, 49, 51, 55–58). Holotype 780 long and 360 wide (idiosoma). Measurements in 3 paratypes: 665 × 375; 680 × 400; 690 × 390. *Dorsum*: cuticle poorly sclerotized, without distinct shields or scales. Distinct copulatory conical papilla visible on posterior border of body. *Venter*: vulva small with sclerotized lips. Legs: length of tarsi I–IV 42–42–75–92.

Chaetotaxy of idiosoma (length of setae): *vi* 60; *sc i* 63; *sc e* 130; *d1* and *d2* 60 (spinous); *d3* 70; *d4* 540–600; *d5* 55 (spinous); *l1* 82 (spinous); *l2* 80; *l3* 120; *l4* 100–120; *l5* 400–450; *a1* 120; *a2* 150; *a3* 220–250; *a4* 300–330.

Solenidiotaxy: tarsus with *ω1* situated in basal third, *ω2* pre-apical and ventral, *ω3* apical.



Figs 49–50. *Bubulcodectes brevitarsis* n. sp. Holotype female in dorsal view (49). Detail of the prelarva (ecdysing cones) (50).

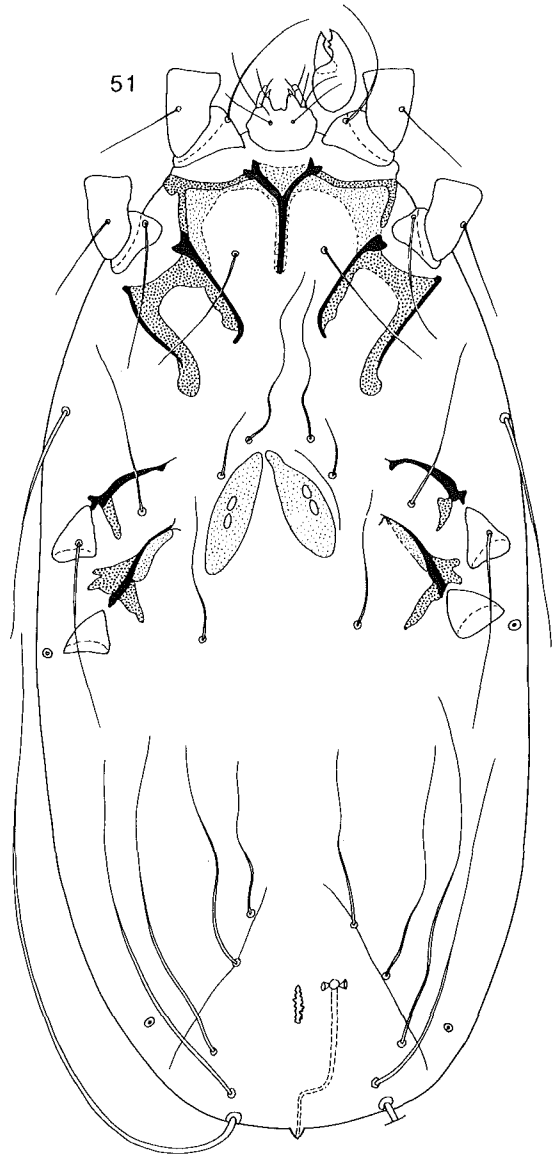


Fig. 51. *Bubulcodectes brevitarsis* n. sp. Holotype female in ventral view.

Male (Figs 21, 52–54, 59–62). Length and width (idiosoma) in 4 paratypes: 530 × 360; 468 × 309; 465 × 291; 440 × 300. All males are heteromorphic. Posterior border of body rounded with an indistinct median incision. **Dorsum**: propodonotum almost completely punctate, with 2 para-median longitudinal bands more sclerotized. Oil-gland orifices situated laterally. Oil grooves well developed. **Venter**: epimeres as in female. Length of chelicerae varies according to the specimen. In 5 paratypes

these lengths are 159, 170, 180, 210 and 270. Leg I much larger than other legs. Length of tarsi I–IV: 51–48–51–43.

Chaetotaxy of idiosoma (in a male of 465 long): *vi* 90; *sc i* 60–75; *sc e* 320; *d1* 30; *d2* and *d3* 60–75; *d4* 540; *d5* 80–110; *l1* 75–90; *l2* 60; *l3* 50–75; *l4* 60–75; *l5* 450.

Chaetotaxy of legs (number of setae): as in female but tarsus IV with 6 setae and 2 small suckers.

In some males we have distinctly observed on

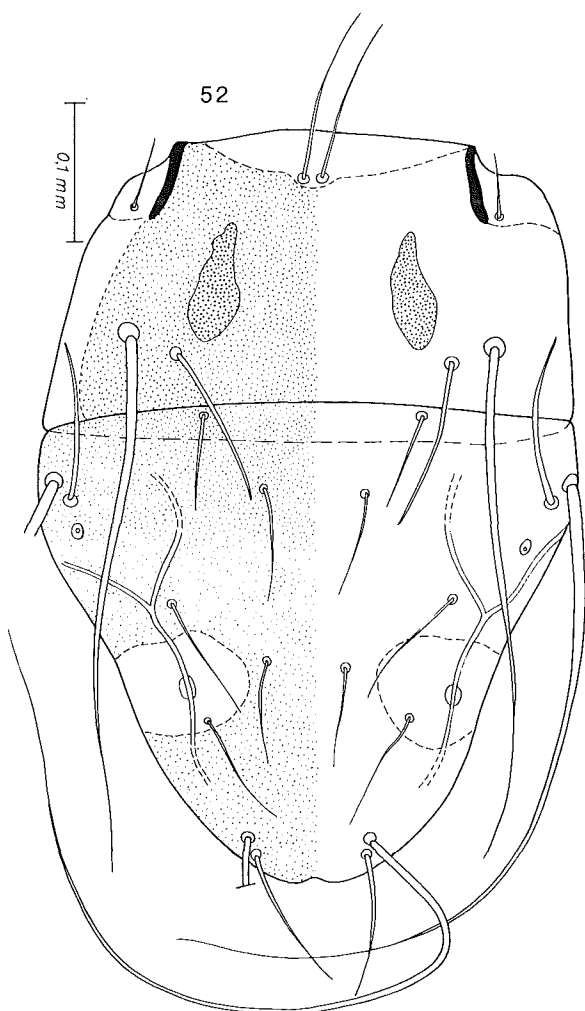
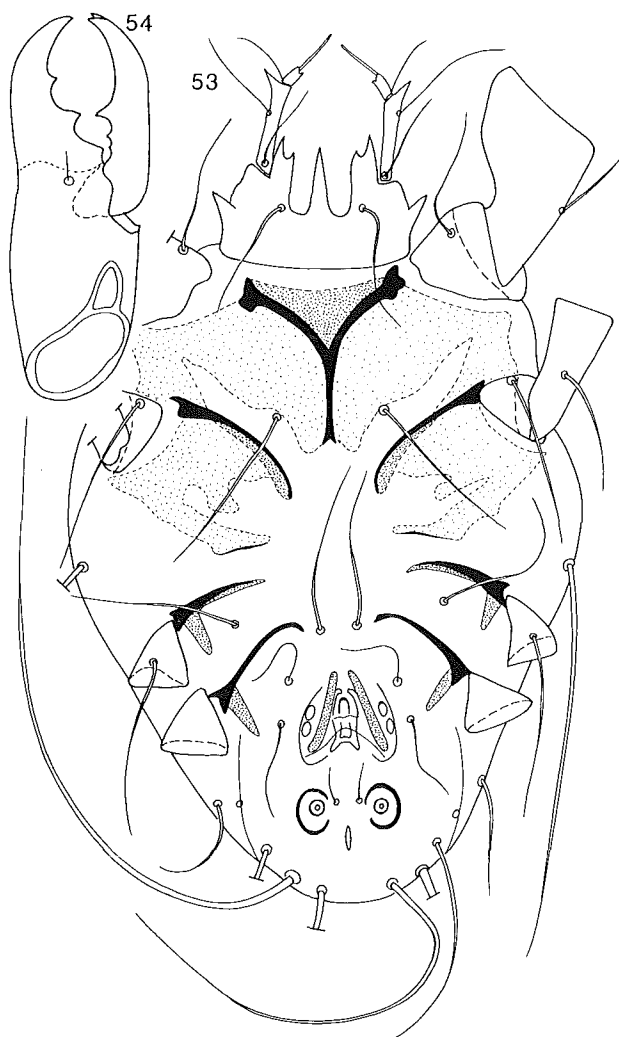


Fig. 52. *Bubulcodectes brevitaris* n. sp. Male in dorsal view.

different legs very thin and relatively long setae emerging from the tarsi between spines *p* and *q*. These very thin setae are sometimes slightly dilated at their apex (Fig 62). They may represent setae *v* and *u* which are present in the primitive Astigmata. We believe that in the Hypoderatidae these setae actually exist but are usually fused with the anterior surface of the ambulacrum. In some cases they are detached and visible.

Tritonymph and *protonymph*: unknown.

Larva: a specimen extracted from egg is 160 long and 120 wide. Cuticle finely striated. This specimen is poorly sclerotized and most of the organs are



Figs 53–54. *Bubulcodectes brevitaris* n. sp. Male in ventral view (53), chelicerae (54).

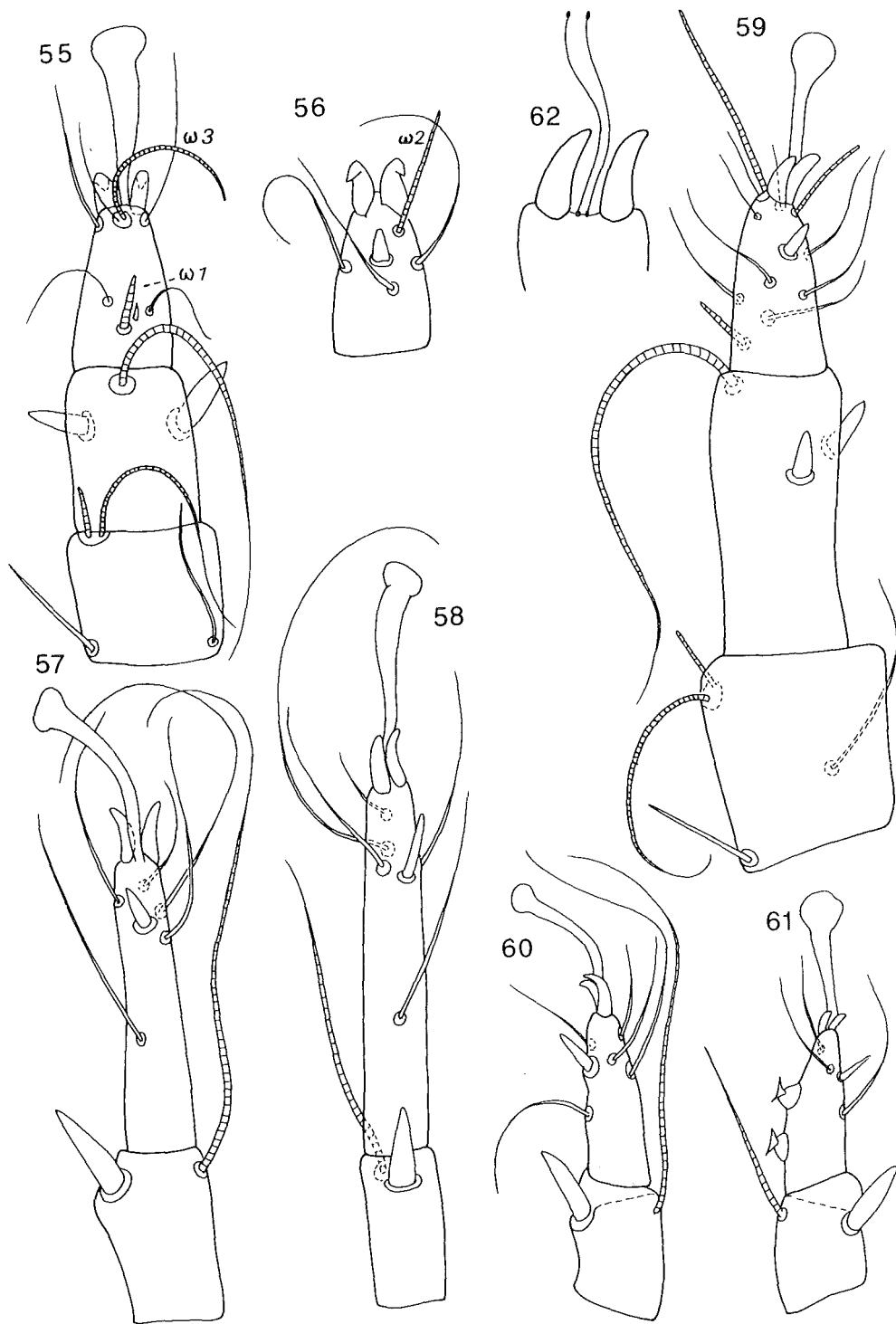
difficult to observe. Organ of Claparede not present.

Prelarva: mature eggs contain 2 conical and pointed sclerites which represent the prelarve reduced to an ecdysing organ (Fig 50).

Egg: average 195 in length and 120 in width.

Locality

Holotype and 15 paratype females, 5 paratype males from a nest of *Bubulcus ibis* in Panama.



Figs 55–62. *Bubulcodectes brevitarsis* n. sp. Female: leg I dorsally (55), tarsus I ventrally (56), leg III (57), IV (58). Male: legs I (59), III (60) and IV (61); apex occurring on some tarsi showing free setae u and v (62).

Genus *Gypsodectes* Fain, 1984***Gypsodectes verrucosus* Fain, 1984**

This species has been described from a female found in a nest of a vulture, *Gyps coprotheres*, from South Africa.

The original description mentions the presence of 9 setae on tarsi III and IV instead of 8-8 or 8-7 as in the other species of the Hypoderatidae. In this single female the posterior legs are badly oriented and the apical setae difficult to observe. This ninth seta on the posterior tarsi could be an artifact or it could also be one of the two setae *v* or *u* which are normally attached to the ambulacra but may occasionally be broken and free (see in description of *Bubulcodectes brevitaris* and Fig 62).

Genus *Hypodectes* Filippi, 1861**Subgenus *Hypodectoides* Fain and Bafort, 1966****1. *Hypodectes (Hypodectoides) samsinaki* n. sp.**

Syn. *Hypodectes (Hypodectoides) propus* (Nitzsch, 1861) of Samsinak (1982).

Samsinak (1982) recorded a new 'form' of male as *Hypodectes (Hypodectoides) propus* (Nitzsch, 1861), in addition to the heteromorphic male that we had described (Fain & Bafort, 1966, 1967). In this male the size of the body is shorter (length of idiosoma 580) than in our specimens (690 to 810) and all the dorsal setae are much longer.

We have re-examined our material, consisting of 19 heteromorphic males and 13 females. In all these males the length of the setae *sc i* varies from 75 to 90 (in one specimen 110), while the setae *sc e* reach about 650. The setae *d1* to *d3* are 60–70 long and the *l1* to *l4* 75 to 100. The *h* and *sh* are very long. In the specimen of Samsinak the *sc i* and *sc e* are subequal and about 400 to 500 long, the *d1* to *d3* measure about 150 to 200, the *l2* to *l4* 200 and the *l1* about 600. In our specimens the setae *s cx* are quite distinct and 27–30 long and the tarsi III bear 8 setae. In the male of Samsinak the setae *sc x* have

not been observed and tarsus III bears 9 setae. It is possible that the ninth seta is actually a seta *u* or *v* that has been detached from the pulvillum (see above).

The females of our collection have much longer setae on the dorsum, except the *sc i* which are only slightly longer (75–120) than in our males. The *d1* to *d3* and the *l1* to *l4* measure from 400 to 500 and are, therefore, longer than in the specimen of Samsinak, except for the *l1* which is longer (600) in the latter.

We believe, therefore, that the male described by Samsinak belongs to a new species close to *H. (H.) propus*. We have already removed from *H. (H.) propus* the single homeomorphic male that we had described as belonging to that species and have included it in the species *Neottialges eurafer* Fain, 1966 (see above). Samsinak in this paper believed that our males of *H. (H.) propus* should be called pleomorphic instead of heteromorphic. The term pleomorphic had been proposed by Türk & Türk (1957) for males with heteromorphic legs (or chelicerae) and whose body setae are distinctly longer than in the females. In all our specimens most of the body setae are *much shorter* than in the corresponding females and, therefore, do not correspond with the definition of pleomorphism as defined by Türk & Türk (1957).

The holotype female of *H. (H.) samsinaki* was found in the nest of a wild pigeon from the tower of the Kost Castle, NW Bohemia. It is in the collection of Dr. K. Samsinak.

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