ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN CULTUUR, RECREATIE EN MAATSCHAPPELIJK WERK)

Deel 42 no. 15 22 november 1967

NICOTHOE AUDOUIN & H. MILNE-EDWARDS, 1826 (CRUSTACEA, COPEPODA), A GENUS PARASITIC ON NEPHROPS LEACH, 1816 (CRUSTACEA, DECAPODA)

by

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With six text-figures

INTRODUCTION

The genus *Nicothoe* has been known until recently only from its type species, *N. astaci* Audouin & H. Milne-Edwards, 1826. This species is parasitic on the European lobster, *Homarus gammarus* (L., 1758), and has received a good deal of attention, in view of the economic importance of its host. Very recently, however, another species, *N. analata* Kabata, 1966, was described from a decapod host of another genus, *Nephrops*. Attached to the gills of *N. sinensis* Bruce, 1966, this parasite was discovered in the South China Sea. The two species differed only in the shape of the trunk, their appendages being identical in all respects.

Since the discovery of *N. analata*, its discoverer, Dr. A. J. Bruce, has been engaged in the study of various species of *Nephrops* from different parts of the world. His studies brought to light abundant *Nicothoe* material. The author has been given the opportunity to examine this material and has found that it contained two more new species of *Nicothoe*. The examination afforded also an opportunity of a closer study of the appendages of this genus. Such an opportunity was very welcome, since the description of *N. analata* had to be based on the study of a single specimen.

The present paper presents the results of this work. It contains comments on the previous description of the appendages (Kabata, 1966) and describes

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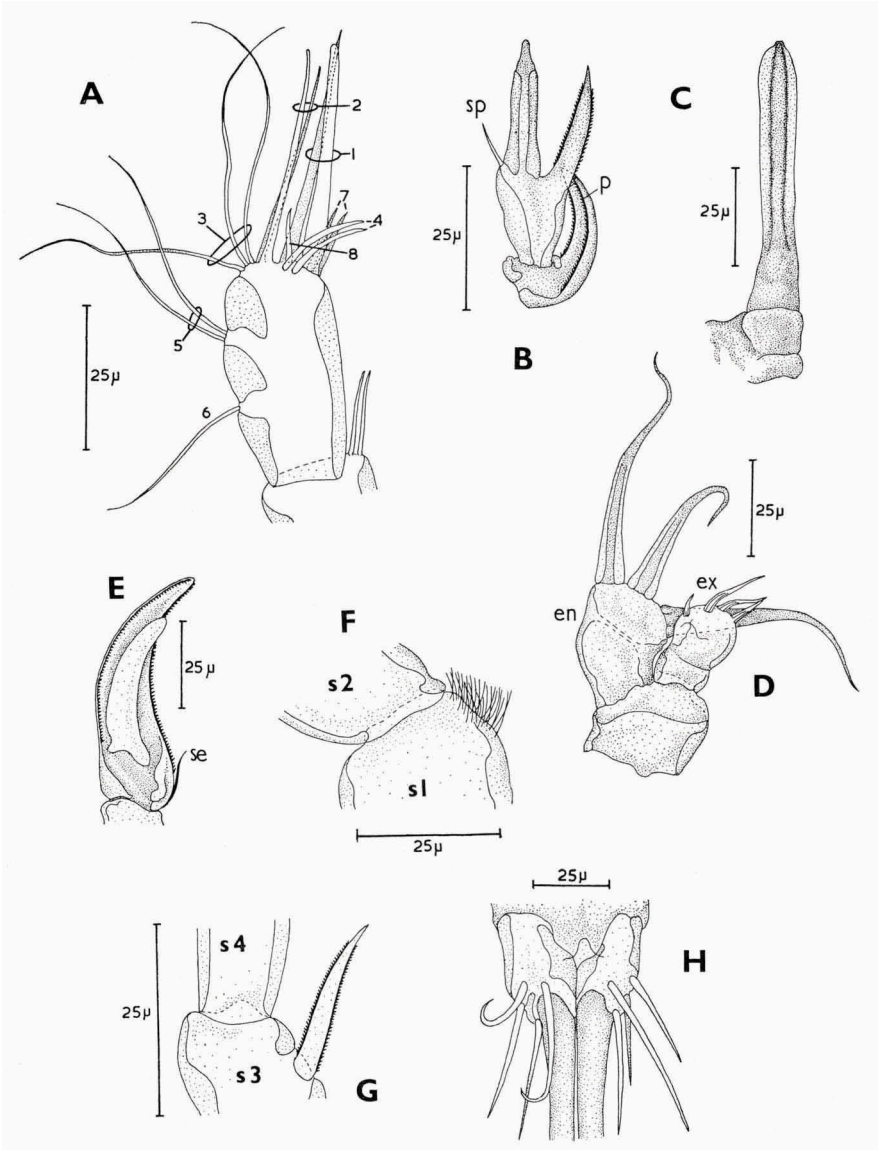

Fig. 1. *Nicothoe* spp. A, first antenna, terminal segment, ventral; B, second antenna, terminal part, ventral; C, mandible, entire, lateral; D, maxilla, entire, lateral; E, first maxilliped, terminal part, ventro-medial; F, second maxilliped, joint between the first and the second segment; G, second maxilliped, joint between the third and the fourth segment, showing serrated spine of the distal part of the third segment; H, caudal furca, ventral. en, endopod; ex, exopod; p, palp; s1-s4, segments 1 to 4; se, seta; sp, spine.

two new species: *N. brucei* and *N. simplex*. The methods employed in this study were similar to those used in the previous paper.

Comments on the appendages

As mentioned above, the appendages of *Nicothoe analata* have been found to be identical with those of *N. astaci*. The same proved true for the new species, described in this paper. The description of the appendages of *N. analata* applies in the same measure to all the other known species of the genus. Careful re-examination of the structural minutiae of the appendages has shown, however, that the previous descriptions require several amendments. These amendments are given below.

The first antenna (fig. 1A). Some details have been missed out of the apical armament of the somewhat disarrayed first antenna of the specimen described in the previous paper. The author has now found that the armament contains more elements than were seen on the previous occasion. The most conspicuous members of the apical armament are those labelled 1 and 2 in fig. 1A. The two setae marked 1 are quite dissimilar. One of them, slightly shorter, is by far the most robust in the entire set and appears to have a blunt, rounded tip. The other member of the pair ends sharply and is more slender and rather longer than the first. When examined under phase contrast illumination, this seta was observed to differ from all the others. It seemed fused of two longitudinal halves, appearing pale in the centre, with dark, well delimited margins. On no occasion, however, was it possible to show any division between the two halves, the sharp tip always remaining perfectly fused. The two slender, long setae, marked 2, are very close to each other and it is possible that their bases show some degree of fusion, though the author has not been able to demonstrate it quite conclusively. There are two other groups of long, flagellate setae, marked 3 and 5 in the drawing. The group 3 consists of three members, close together and of about the same length, while group 5 is composed of two similar members. The remaining setae are much shorter and more robust than those in the two groups just mentioned. They are distributed in three groups: (a) group 4, occupying the ventral aspect of the tip, projecting in an antero-ventral direction and consisting of two setae, closely resembling each other; (b) group 7, similar to the preceding one, and consisting of two setae disposed on the dorsal aspect of the powerful seta 1; (c) this consists of a single seta 8, close to the base of the pair 1, on its ventral aspect and near group 4. Seta 6 does not belong to the apical armament, being situated half way along the posterior margin of the limb, a position similar to that found in the first antenna of the caligid copepods. In

all, therefore, the apical armature of the first antenna of *Nicothoe* comprises 14 setae.

The second antenna (fig. 1B) was illustrated in the previous paper in fig. 2G. While the general description of the limb was accurate, some details must be corrected. The terminal segment was shown to have two small tuberosities on its margin. They were not seen in any specimens examined subsequently and must be regarded as artifacts. On the other hand, in addition to the powerful palp (p, fig. 1B), arising at the base of the penultimate segment, there exists also another structure, a fine spinule (sp, fig. 1B) at the base of the distal segment. This spinule was not observed previously. The outgrowth of the penultimate segment, almost matching in size that of the distal segment is now known to have serrated margins, just like those of the palp.

The mandible (fig. 1C) is a simple blade, with 'cutting edges' along both margins, but without any traces of denticulations. Its general shape resembles the mandibles of most of the copepods included in the Pectinata.

The maxilla (fig. 1D) is very difficult to observe in detail because of its small size and the difficulty of dissecting it without causing damage to its delicate structure. Careful re-investigation shows that it consists of a sympod, indistinctly divided into two segments, and of two rami, clearly delimited from the sympod. The endopod, situated dorso-medially to the exopod, appears to have two segments, though its division is rather indistinct. The distal margin of the ramus carries three very long setae, with robust bases and slender, flexible tips. The exopod is of about the same length, but is narrower. Its two component segments are much more easily distinguishable from each other than those of the endopod. The basal segment is smaller than the terminal one, which is rather bulbous. The tip of the ramus bears four setae, much smaller than those of the endopod. Three setae are grouped more closely together and are longer than a single fourth seta, situated farther dorsally.

The first maxilliped (fig. 1E) was also correctly described in the previous paper, but for a small seta (se, fig. 1E), which was not observed. This seta is near the base of the terminal structures, which form a chelate arrangement. While the larger half of the chela appears to be rigidly fixed to the preceding segment, the base of the smaller half is provided with musculature, obviously capable of changing its position relative to the larger half.

The second maxilliped (figs. 1F, G) was also accurately described, but the description omitted some structural details. The smaller, terminal spine, illustrated previously in fig. 2H (Kabata, 1966), has serrated margins. Similar, fine serrations are also present on the margins of the spine carried

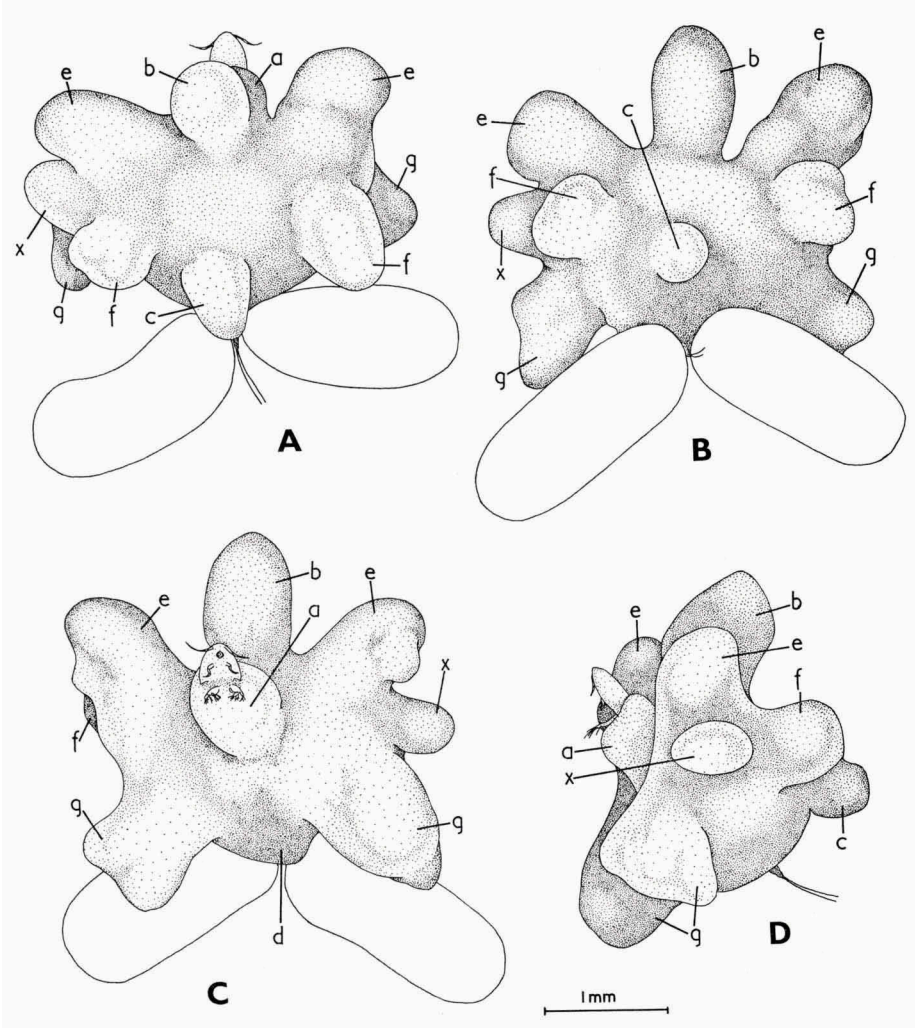

Fig. 2. *Nicothoe brucei* f. *brucei* nov., adult female, all drawings of the same specimen. A, dorsal view, in the plane of the long axis of the body; B, dorsal view, in the plane of the long axis of the trunk; C, ventral view; D, lateral view. Lettering in text.

by the third segment (s3, fig. 1G). Yet another newly discovered detail is a tuft of hairs, near the distal end of the first segment (s1, fig. 1F), directly at its junction with the second segment. The tuft is not readily observable in strictly lateral view of the limb, which has to be rotated round its longitudinal axis to expose the tuft to the observer.

The caudal furca (fig. 1H) consists of two blades, each armed with a stylus and with four shorter setae, not three, as described in the previous paper.

The structure and the armament of the swimming legs of all known species of *Nicothoe* is quite similar and had been adequately described. It should be noted, however, that the fringe of hairs, present on the outer margins of the endopod segments of legs I to IV might be difficult to find, since it seems to break off easily on handling. It is possible that the fringe, very clear in the copepodid stage, wears away with age and is partially lost in the adult.

Description of species

Nicothoe brucei sp. nov. (figs. 2A-D, 3A-J, 4A-E)

(i) Many ovigerous females were taken in 1961 in Tosa Bay, Japan. One of these specimens becomes the holotype of the species, B.M. (N.H.) Reg. No. 1966.12.8.3; the remainder become the paratypes, Reg. No. B.M. (N.H.) 1966.12.8.4.

(ii) Eleven adult females were taken, presumably at the same locality, undated. B.M. (N.H.) 1966.12.8.5.

(iii) Four females were collected 15 miles SE off Durban Bluff, South Africa, at the depth of 225 to 230 m, on 21 October 1965: B.M. (N.H.) 1966.12.8.6.

(iv) Numerous females were collected at the same locality, undated. Retained in the author's collection.

The host in: (i) and (ii) was *Nephrops sagamiensis* Parisi, 1917, in (iii) and (iv) *N. andamanicus* Wood-Mason, 1892. On the gills of host (i) some *N. analata* were found together with the present species.

Description of the adult female. — As mentioned above, the distinctive characteristics of each species of *Nicothoe* are provided by the trunk, consisting of the powerfully developed three thoracic segments (segments 3 to 5 of the thorax). The trunk of *N. brucei* varies greatly in shape, which at first sight makes it difficult to find common features in different individuals of the species. Fig. 2, showing different views of a single, fairly typical specimen, illustrates the main common features. The trunk of *N. brucei* has a number of outgrowths, arising from a central, more or less globular sac. The outgrowths can be divided into medial and lateral ones. The lateral ones consist of bilaterally symmetrical pairs. The medial outgrowths comprise: (a) an anterior swelling, more or less well developed and providing the base for the cephalothorax, as well as for the three pairs of swimming legs; (b) another, much better developed swelling, posterior to (a) and either simple or subdivided, straight or curving, usually towering above the cephalothorax, as can be seen in fig. 2C; (c) farther back, a swelling, usually situated in the centre of the dorsal surface of the trunk and mainly smaller than the previous one; (d) antero-ventral to the abdomen, a small swelling, less well defined than the other medial swellings. The lateral structures comprise three pairs: (e) aliform antero-ventral swellings; (f) similar antero-dorsal pair; these two pairs are usually well separated from each other, though in some specimens they may be quite extensively fused; (g) postero-ventral pair, near the end of the trunk and frequently of complicated, subdivided structure.

The longitudinal axis of the body runs between the cephalothorax and the abdomen. It is at an angle of about 40° to the longitudinal axis of the trunk, which runs from the tip of (e) to that of (g), as can be seen in fig. 2D. The parasite is shown in the plane of the long axis of the body in fig. 2A,

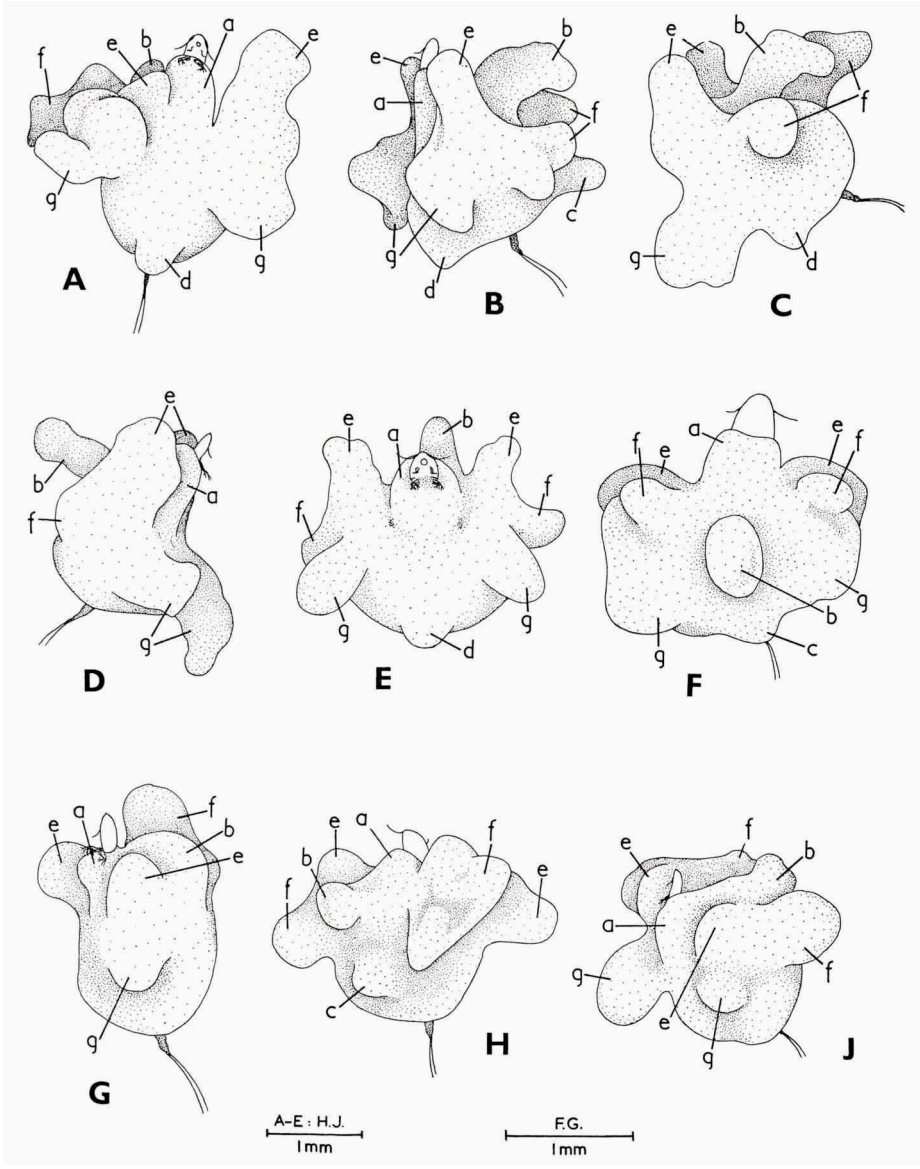

Fig. 3. *Nicothoe brucei* f. *brucei* nov., adult females. A, E, ventral; B-D, G, J, lateral; F, dorsal; H, dorso-lateral. H and J show the same specimen. Lettering in text.

while fig. 2B shows it in the plane of the long axis of the trunk. The specimen illustrated in fig. 2, in addition to the full set of outgrowths characteristic of the species, has also a 'spurious' outgrowth (x), which is not found in other specimens (x, fig. 2A, B, C, D). Such additional outgrowths occur in *N. brucei* in other parts of the trunk (x, fig. 4C). The essential similarity of the structure of the trunk, however, is not greatly obscured by the numerous possible modifications caused by the specific conditions of the place of attachment of each individual.

The complicated shape of the parasite makes it difficult to make any comparable measurements. To give a general idea of the size of the species, the following measurements were taken: (i) the length of the cephalothorax, from the mid-anterior point to the centre of the transverse line drawn between the posterior tips; (ii) the greatest width of the cephalothorax (near the posterior end of the carapace); (iii) the length of the trunk along the longitudinal axis of the body; (iv) the width of the trunk measured between the tips of the lateral outgrowths (e). The figures below (in mm) are based on 10 measurements for each of the two morphological forms (see Comments).

	N. brucei f. *brucei* nov.	f. *andamanica* nov. [1])
Cephalothorax length	0.42	0.36
Cephalothorax width	0.36-0.42	0.30-0.36
Trunk length	1.32-2.28	1.32-2.28
Trunk width	1.50-3.36	1.80-3.42
Egg-sac length	1.38-1.80	
Egg-sac width	0.72-1.02	

Comments. — The wide range of shapes assumed by the trunk of *N. brucei* is illustrated in fig. 3. Among some departures from the fairly typical shape shown in fig. 2 are: (i) the reduction or loss of (c) (fig. 3C, D, G); (ii) the reduction or loss of (d) (fig. 3B, G, J); (iii) the distortion of the lateral structures on one side (fig. 3A); (iv) the reduction or loss of one or both lateral structures (g) (fig. 3F, G, H, J); (v) the reduction and partial fusion of (a) and (b) (fig. 3G); (vi) the appearance of the additional structures mentioned above.

It is possible that the shape of the trunk does not remain the same throughout the life of the animal. Although all the specimens shown in fig. 3 were ovigerous, they were not all of the same size. It has been found that the smaller, and presumably younger, specimens had less well developed trunk outgrowths than the larger ones and resembled those shown in fig.

1) The spiral coiling of the egg-sac of this form makes the measurement of the sac impossible.

3G, H. In particular, the postero-ventral outgrowths (g) were poorly developed or absent.

N. brucei has two morphological forms, each associated with a distinct host. The author proposes to designate them *N. brucei* f. *brucei* and *N. brucei* f. *andamanica,* parasitic on *Nephrops sagamiensis* and *N. andamanicus*

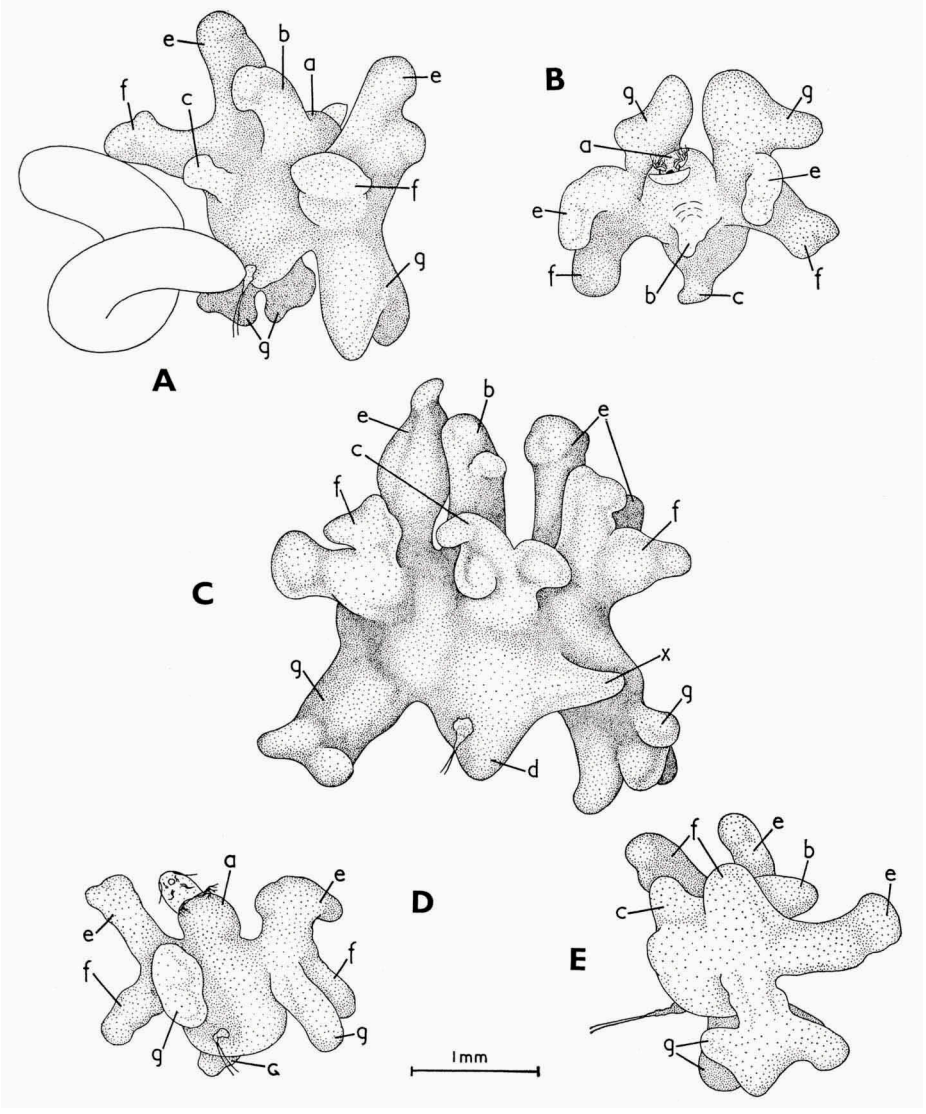

Fig. 4. *Nicothoe brucei* f. *andamanica* nov., adult females. A, dorso-lateral; B, anterior; C, dorsal; D, ventral; E, lateral. Lettering in text.

respectively. The first of these has been described above. The second can be readily distinguished (fig. 4) by the smaller central sac of the trunk and by relatively longer and more complicated outgrowths. The structures most subject to those changes are the outgrowths (g) and (e), but all can be affected. Even the medial outgrowths (b) and (c), which are almost always simple in the parasite of *N. sagamiensis,* can become bifid, or trifid, in that of *N. andamanicus,* as can be seen in Fig. 4C. In the specimen depicted in the figure, the right (g) is divided at the tip into four lobes.

Another difference between these forms is that of the shape of the egg-sac. The typical egg-sac of the *brucei* form is in the shape of a short, robust cylinder, often slightly bent to give it a sausage-like appearance (fig. 2A). The egg-sac of the *andamanica* form is more slender, longer and spirally twisted. Sometimes, as in fig. 4A, there is only one coil, but sacs with more coils occur quite frequently.

Nicothoe simplex sp. nov. (fig. 5A-F)

(i) Eight adult females were found in the collection of the British Museum, taken in Japan, undated. One of these females becomes the holotype of the species, Reg. No. B.M. (N.H.) 1966.12.8.1; the remaining ones are made paratypes, Reg. No. B.M. (N.H.) 1966.12.8.2.

(ii) A single ovigerous female was taken at Albatross Station No. 3738, off Honshu, Japan. It is stored in the Rijksmuseum van Natuurlijke Historie, Leiden, Reg. No. F. 779.

(iii) Six adult females are kept in the collection of the Museum National d'Histoire Naturelle, Paris, date and locality not specified.

The host in all cases is *Nephrops japonicus* Tapparone-Canefri, 1873.

Description of the adult female. — In contrast with the preceding species, *N. simplex* is distinguished by complete absence of any outgrowth of the trunk. The trunk has the shape of a simple sac, ovoid or pyriform, sometimes almost globular. It is interesting to note that in some specimens, the regular shape of the trunk is accompanied by pronounced asymmetry (fig. 5D). The longitudinal axis of the body becomes curved, the genital and abdominal segments being disposed antero-laterally to the apparent posterior extremity of the trunk. Fig. 5 illustrates the differences in the trunk shape of this species.

Some dimensions of *N. simplex,* based on 15 specimens are given below (in mm).

Cephalothorax length	0.42-0.48
Cephalothorax width	0.42
Trunk length	1.14-3.12
Trunk width	0.72-1.86
Egg-sac length	1.20-1.74
Egg-sac width	0.54-0.84

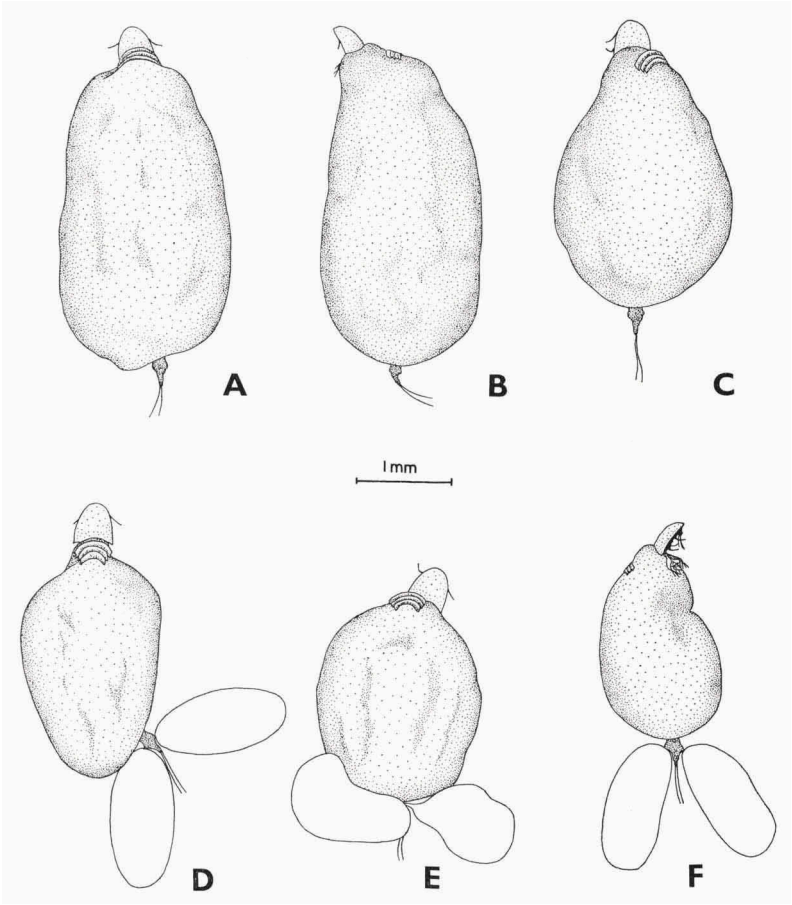

Fig. 5. *Nicothoe simplex* nov. spec., adult females. A, C-E, dorsal; B, lateral; F, cephalothorax and trunk lateral, genital region and abdomen ventral. A and B show the same specimen.

Comments. — The most characteristic feature of the trunk of this species is the fact that, in spite of fairly variable shape, it appears to be devoid of any outgrowths. The species, that is closest to *N. simplex* in the shape of the trunk, is *N. analata* Kabata, 1966. That species invariably retains at least vestiges of its outgrowths. The author saw no such vestiges in the specimens of *N. simplex* examined.

Nicothoe analata Kabata, 1966 (fig. 6A-G)

(i) Six females were collected by the 'Endeavour' Expedition in 1909-1914 in the Great Australian Bight, SE of Eucla, at the depth of 200-250 m. They are stored in the Rijksmuseum, Leiden, Reg. No. F. 777.

(ii) Numerous adult females and copepodid stages were taken by the same expedition near the previous locality, SW of Eucla, and are kept in Leiden, Reg. No. F. 778.

(iii) Four females were taken in Tosa Bay, Japan, undated. They are kept in the British Museum, London, Reg. No. B.M. (N.H.) 1966.12.8.7.

(iv) Numerous females, mainly ovigerous, were taken at the Siboga Expedition Station No. 254 (5° 40′ S 132° 26′ E, Banda Sea, near Kei Is., at depth of 310 m) on 10 October 1899. Kept in the collection of the Zoologisch Museum, Amsterdam.

(v) A single adult female was taken at Siboga Station 12 (7° 15′ S 115° 15′ E, in Bali Sea, at depth of 289 m), on 14 March 1899. In the collection of the Zoologisch Museum, Amsterdam.

The host in (i) *is Nephrops boschmai* Holthuis, 1964; in (ii) and (v) *N. andamanicus* Wood-Mason, 1892; in (iii) *N. sagamiensis* Parisi, 1917; in (iv) *N. sibogae* de Man, 1916.

Previous record. — The species has been originally described from *N. sinensis* Bruce, 1966, from the South China Sea (Kabata, 1966).

Description. — There is no need to add much to the original description of *N. analata.* As regards the structure of the trunk, the additional material has shown that it is quite variable. The trunk, however, always has a pair of outgrowths in the position in which *N. brucei* carries its lateral outgrowths (e). These processes might be fairly well developed (fig. 6E), or considerably reduced (fig. 6D), but at least one of them is present in every specimen.

Specimens parasitic on *N. andamanicus* and *N. sibogae* can be distinguished from those parasitic on other *Nephrops* species by being more globular in shape (fig. 6G) and by having, more often than those from the other species, yet another outgrowth, coincident in position with (b) of *N. brucei.* The outgrowth, however, is normally quite small and never reaches the size common in *N. brucei.*

In spite of these differences, the range of variability in the shape of the trunk of parasites from different host species is such as to make it impossible to make a clear differentiation between any morphological types.

Some dimensions (in mm) of *N. analata,* based on measurements of 20 specimens, are given below:

Cephalothorax length	0.48-0.60
Cephalothorax width	0.48-0.54
Trunk length	1.68-3.72
Trunk width	1.20-3.78
Egg-sac length	1.20-4.32
Egg-sac width	0.60-1.02

The material from the gills of *N. andamanicus,* collected in the Great Australian Bight, contained, in addition to the adult females, also copepodid stages. These have not been described before for any species except *N. astaci.*

A copepodid of *N. analata* is shown in fig 6A. The author could not find any features which would distinguish this stage from the corresponding one of *N. astaci*. The structure of its appendages cannot be distinguished from that of the adult of the species. With the exception of characteristically distended

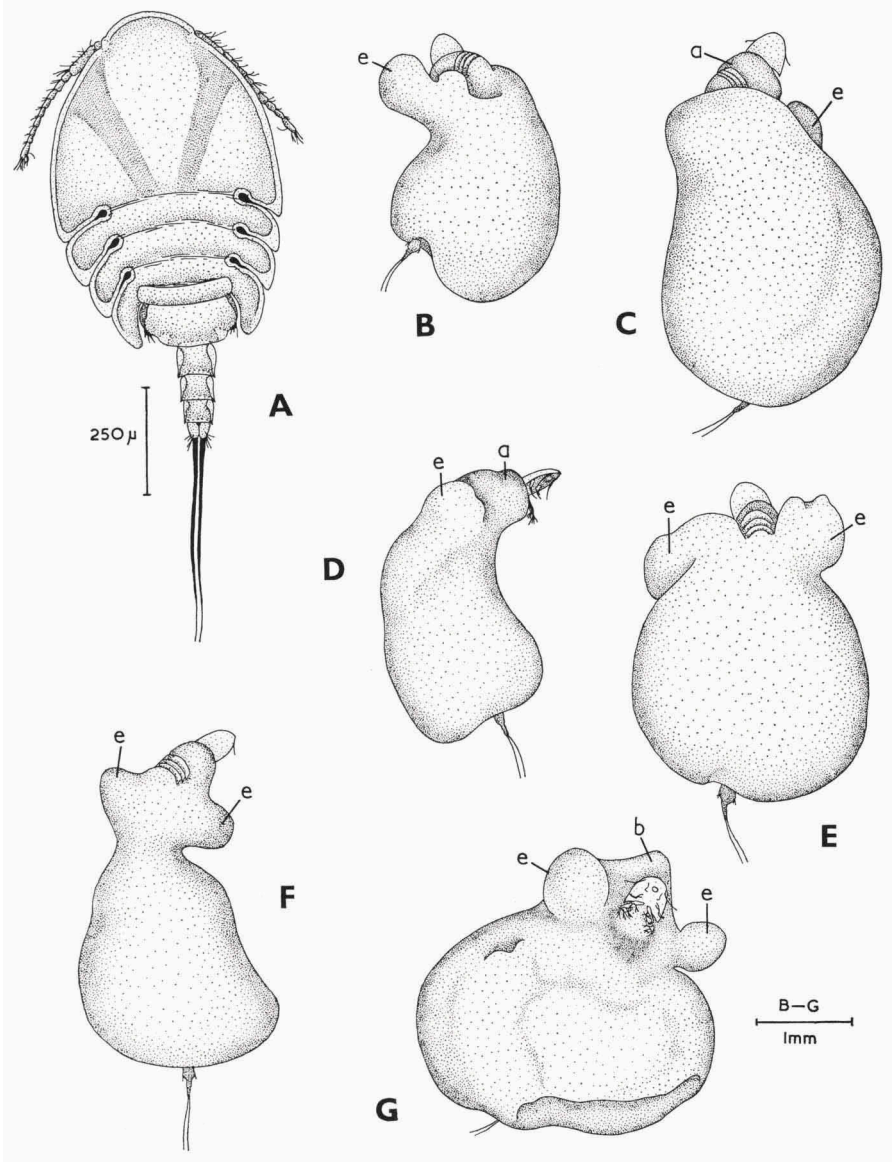

Fig. 6. *Nicothoe analata* Kabata, juvenile and adult females. A, copepodid stage; B-G, adults. A, C, E, F, dorsal; B, dorso-lateral; D, lateral; G, ventral. Lettering in text.

trunk, which disrupts the structural unity of the adult, the copepodid resembles the adult in all respects. Its cephalothorax is posteriorly articulated with the free thoracic segments, which, in turn, link directly with the posterior part of the body.

The dimensions of the copepodids (in mm), based on 10 measurements, are given below:

Total length (without caudal stylus)	0.91-1.00
Cephalothorax length	0.47-0.56
Cephalothorax width	0.49-0.54
Caudal stylus length	0.54-0.70

Comparing the dimensions of the cephalothorax of the copepodid with those of the adult female, one can see that the size of that part of the body is not materially affected during the post-copepodid period of development. Apart from the expansion of the trunk, the parasite has reached its definitive structure, when it had attained the copepodid stage.

Discussion

The re-examination of the structure of the appendages affords a good opportunity for consideration of the systematic position of the genus *Nicothoe*. Quite recently, Lemercier (1966), having carefully re-examined the buccal area of *N. astaci,* concurred with the earlier views of Gurney (1929), that *Nicothoe* is closely allied to Choniostomatidae, representing a primitive condition of that family. The views of both of these authors are opposed to the earlier opinion of Leigh-Sharpe (1926), who, while assigning *Nicothoe* to Ascomyzontidae, refers to some points of resemblance between it and the caligoid copepods.

The author agrees with Gurney and Lemercier, as regards the relationship between *Nicothoe* and Choniostomatidae. The interest, stimulated by the study of this genus, centres round possible position of Choniostomatidae in the system of the parasitic copepods. As far as the author is aware, no definite views have been expressed on this subject, Hansen (1897) suggesting only that some similarities exist between Choniostomatidae and Lernaeopodidae, although these two families differ in many essential details.

It appears that both *Nicothoe* and Choniostomatidae in general bear many resemblances to the rather loose group of copepods, referred to by Heegaard (1947) as Pectinata. The hallmark of the group is the structure of the mandible and that of *Nicothoe* fits closely with it. The other very important character of the group is the type of development, involving the chalimus or pupal stage and the use of the frontal filament as the means of attachment during those stages. Choniostomatidae share this feature with all the families

of Pectinata. *Nicothoe* itself is not known to have either pupal stages or a frontal filament, but this is due to the fact that its life history is not fully known and this part of it has never been discovered.

As regards the specific differences within the genus *Nicothoe,* it has been mentioned above that they consist solely of the shape of the trunk, each species being recognisable at the adult stage by its trunk. Since this part of the parasite is subject to extensive variation within each species, its diagnostic value may be open to doubt. However, the influences of the host species and of the site of attachment appear to be insufficient to obliterate all features which might be used as clues to the specific identity. This is, for example, evident from the fact that the gills of *Nephrops sagamiensis,* taken in Tosa Bay, Japan, carried two species, *Nicothoe brucei* f. *brucei* and *N. analata,* side by side. The trunks of the two species could be distinguished at a glance.

Some differences in shape, attributable to the host influence, are, however, present and are exemplified by the existence of the two forms of *N. brucei.* This type of morphological difference has been found previously in the members of the family Lernaeoceridae (cf. Delamare Deboutteville & Nunes, 1951) and in Lernaeopodidae (cf. Kabata, 1963).

Acknowledgments

The author wishes to express his thanks to Dr. A. J. Bruce, who was mainly instrumental in gathering together the material examined in this paper and who sent it to the author. He is also grateful to Dr. J. H. Stock, Amsterdam, who collected and sent to him *Nicothoe* from *Nephrops* and to Dr. P. F. Berry, Durban, who obliged him in the same way.

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