# DANISH REVIEW GAME BIOLOGY

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Vol. I, Part 3

#### **HOLGER MADSEN:**

Studies on Species of Heterakis (Nematodes) in Birds

F. JENSENIUS MADSEN & R. SPÄRCK:

On the Feeding Habits of the Southern Cormorant (Phalacrocorax carbo sinensis Shaw) in Denmark

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### Studies

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by

Holġer Madsen

Copenhagen 1950

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#### INTRODUCTION

During my investigations on the parasites of the Danish game birds a number of systematic and nomenclatoral problems turned up. This was, to a very great extent, the case with species of Capillaria (Holger Madsen 1945), and with the genus Heterakis (worms found in the ceca) some points of interest appeared during a closer investigation. In my material from the Game Investigations I have found members of this genus in pheasants, partridges and black grouse only, but not at all in the material of 516 ducks (river and pond ducks, diving and fish-ducks). The distribution of the host material can be found in my above mentioned paper of 1945. Although the many thousands of worm specimens were submitted to a minute investigation, only one species has been found, namely Heterakis gallinae (Gmelin 1790) auctt. nov. On revision of the literature the name has proved not to be correct. The right name is Heterakis gallinarum (Schrank 1788). The closer line of demonstration is given below.

Through the late Mr. Hørring, M. Sc., Zool. Mus., I received the ceca (with nodules) of a Crossoptilon auritum, from a flight cage in South Jylland (March 18th, 1939). It contained a large number of Heterakis isolonche v. Linstow 1906. Through professor M. Thomsen (Veterinary School) I got the species of Heterakis in the collections of the late Danish parasitologist H. Krabbe. Here specimens of Heterakis papillosa from the type host were found. Further I succeeded in finding Heterakis dispar in some domestic geese. Since in these latter species I have also observed some points of interest, especially concerning the spicules, a more detailed comment has been made, with the most important synonymy. Further, I have added a revised list of species of Heterakis known in birds, and also a host list.

#### REMARKS ON THE SPECIES OF HETERAKIS

Most previous investigators emphasise the number and distribution of the caudal papillae of the male as systematically important. (As underlined by Maplestone (1932), it is in most cases impossible to distinguish the females). But the work of English investigators in particular (Lane, Baylis, Chandler, Maplestone) has clearly shown the relative insignificance of these structures in the case of many species. This fully agrees with my experience, since I have not been able to find any differences in this respect between H. gallinarum and H. isolonche on one side and H. dispar and H. papillosa on the other, species I have investigated myself. Much the same can bee said about the frequently used diameter of the preanal sucker, since this in some degree increases with the size of the worm. It must be said, however, that in some species characteristic differences may be found.

As pointed out e. g. by Lane and by Maplestone, the spicules present the most important systematic features which has also proved to be the case in the species of *Capillaria*. Especially the distal part of the left spicule in many cases constitutes a safe mark of distinction. This in connection with the length of the spicule, and with their mutual length makes it possible with certainty to distinguish species, of course mostly in connection with other characters. Unfortunately in a number of cases the spicular features are insufficiently known and therefore in the following alphabetic list I will mark off these species with the indication "species inquirendae". In the future a description of the lips should also be given (see Baylis 1944).

In the domesticated birds of Europe three types of species of Heterakis are now rather well known: Heterakis gallinarum, with a long, and a short spicule, Heterakis isolonche, with long spicules of the same length, common in confined pheasants and Heterakis dispar, in ducks and geese, with short equal spicules. Besides these, a number of other species are known, especially in the Indian and East Asian region. The species of Heterakis can be grouped on lines similar to those given by RAILLIET & HENRY (1914). These authors mentioned the vesicularistype and the dispartype. The following groups are more readily distinguished: The H.gallinarum group, the H. is olonche group and the H. dispargroup. The H. gallinarum group has very unequal spicules. Generally the right spicule is the longer and is then mostly I mm or more. In two species the left spicule is the longer but then it is only about 0,5 mm, The H. isolonche group has rather long equal or subequal spicules, mostly measuring about 1 mm or more. The H. dispar group has short equal or subequal spicules, as a rule not exceeding 0,7 mm (whereas the the length of spicules in the H. isolonche group is only very exceptionally less than 0,8 mm). The species H. fariai is doubtfully placed in the latter group because of obscurities in the original description (see table 8, p. 24). From fowls in non-European regions the species H. beramporia and H. brevispiculum (both of the dispar group) are recorded several times, in some cases with uncertain descriptions. Probably a closer investigation will show that a number of species have not yet been discovered.

Finally I want to point out that the list of species can only be preliminary

because the final clearing up of questions concerning many species must be based on investigations on large new collections and a reinvestigation of the old material available.

#### Heterakis gallinarum (Schrank 1788) sensu nov.

Synonyms and main references: Ascarides teretes, Mittelrundwurm der Hennen, Goeze 1787, p. 76, 86, Pl. 1, Fig. 4. Ascaris gallinarum Schrank 1788, p. 9. Ascaris phasiani Gmelin 1790 (?). Ascaris galli, Ascaris gallinae Gmelin 1790, p. 30, 34, part. Ascaris vesicularis Froelich 1791, p. 85, Pl. 3, Figs. 12—14. Fusaria reflexa Zeder 1800, p. 33—36, Pl. 4, Fig. 7. Ascaris gallinarum Froelich 1802, p. 49. Fusaria reflexa Zeder 1803, p. 102—103. Ascaris vesicularis Rudolphi 1808, I, p. 129, part. 1819, p. 38, 268, part. Creplin 1825 p 20-21. Heterakis vesicularis Dujardin 1845, p. 223-225. Ascaris vesicularis Diesing 1851, II, p. 148-149, part. Ascaris undulosa-striata Baird 1853 (see Baylis 1916, p. 418). Heterakis vesicularis Eberth 1860, p. 41-66, Pl. 2-4, Figs. 1-33. Heterakis longecaudata v. Linstow 1879, p. 174, Pl. 11, Figs. 22-22 a. H. papillosa Railliet 1885 (nec Ascaris papillosa Bloch 1782 = H. papillosa (Bloch 1782), nec Ascaris papillosa Molin 1860 = Subulura papillosa (Molin 1860)). H. papillosa Cobb 1897, p. 752—753, Fig. 8. H. parisi Blanc 1913, p. 1272; 1914, p. 78, Figs. 1—2. Non H. vesicularis Travassos 1913, p. 279—280, Pl. 27, Fig. 1 (= Heterakis brevispiculum Gendre 1911 (?)). H. vesicularis Skrjabin 19162, p. 488—491. H. papillosa Baylis & Daubney 1922, p. 289. H. longecaudata Baylis & Daubney 1922, p. 290—291. H. papillosa Smit 1922, p. 526-527, Fig. 10. H. gallinae Freeborn 1923, p. 692. H. vesicularis Yorke & Maplestone 1926, p. 216, Fig. 146. H. gallinae Cram 1927, p. 52-54, Figs. 65-67. H. longecaudata Cram 1927, p. 66—67, Figs. 89. H. parisi Cram 1927, p. 69, Figs. 93. H. gallinae Tubangui 1927, p. 23—25 Figs. 10. Non H. gallinae Canavan 1929 = H. isolonche v. Linst. 1906. Non \*H. gallinae Hsü 1932¹) = H. pavonis Maplestone 1932. H. gallinae Maplestone 1932, p. 404, Pl. 12, Figs. 1, Sprehn 1932 p. 550-551, Figs. 264-269. H. parisi Li 1933, p. 1316-1317, Pl. 2, Figs. 15-16. H. gallinae Clapham 1933, p. 67—82, 16 Figs., Baker 1935, p. 189—215, 1936, p. 51—86, 16 Pl., Baylis 1936, p. 112—115, Figs. 52—53, Neveu-Lemaire 1936, p. 734—737, Figs. 405. H. parisi Neveu-Lemaire 1936, p. 741. H. longecaudata Wu & Liu 1940, p. 401—402, Fig. 2. H. gallinae Holger Madsen 1941, p. 32. Non \*H. gallinae Wu & Kung 1944 = H. pavonis Maplestone 1932. H. gallinarum Holger Madsen 1949.

1) The names with an asterisk are here recorded as synonyms for the first time.

Since CRAM (1927) the identification of the current species Heterakis vesicularis (Froelich 1791) in fowl etc. by Freeborn (1923) has been generally accepted. This was given in a brief report with the main stress laid upon other than systematical studies. He considered the Ascaris gallinae of GMELIN (1790, p. 3034) as the first name referring to the said species. GMELIN diagnoses it as Ascaris gallinae with reference to Goeze (1787, p. 86): "Habitat in gallinae intestino coeco". It is not probable that the worms briefly mentioned by Goeze really belong to our species. But in Pl. I, Fig. 4 Goeze illustrates a species, which undoubtedly is the one in question (see Fig. 1). This is mentioned by GMELIN under the name Ascaris galli. This name also comprises specimens by Goeze, which are, however, Ascaridia galli (Schrank 1788) (see Baylis 1932). Referring to Goeze (1787, p. 76, Pl. 1, Fig. 4) Schrank names the species Ascaris gallinarum. Therefore it is without doubt that the correct name of the common species of Heterakis with the short spicule curved at the tip in a cha-

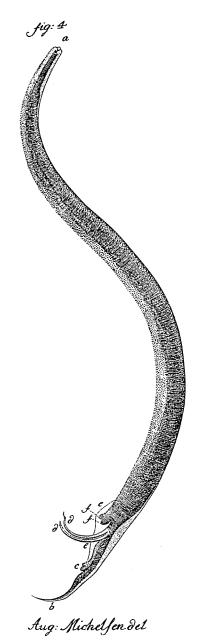


Fig. 1. Heterakis gallinarum. (After Goeze 1787, Pl. 1, Fig. 4). Goeze's ''Mittelrund wurm'' aus dem Hahn (p. 76).

racteristic manner occurring in the ceca of fowl etc, especially in Europe, is Heterakis Gallinarum (Schrank 1788).

The name *H. papillosa* has also been used very much for this species since *Railliet*'s erroneous determination (1885) (see below p. 00). But both his and many other authors' descriptions and illustrations clearly show that their *H. papillosa* is the same as the well established *H. vesicularis* which again is *H. gallinarum*. Walton (1924, p. 194 ff.) describes the gametogenesis of a species which he calls *H. papillosa*. But after his indications it must be *H. gallinarum*. Due to differences in the gametogenesis from that of *H. vesicularis*, described by Gulick (1911, p. 344 ff.) (18 chromosomes found in the spermatogonia by him, 9 by Gulick, but both 4 + x in the meiosis of the males) he concludes that the species are only partly synonymous. According to the above mentioned it seems reasonable to assume that it is here a question of a diploid and a tetraploid form which cannot be distinguished morphologically, like in certain plants (see e.g. Sweschnikowa 1928). However, the case demands further investigations.

Heterakis gallinarum is the only species of the genus which has been examined anatomically (EBERTH 1860, CLAPHAM 1933, BAKER 1935—36). EBERTH and BAKER agree in all essentials, and especially the latter describes the anatomy very much in detail. CLAPHAMS results differ somewhat (although all three investigators evidently had the same species before them), but her description and illustrations are rather sketchy.

Heterakis gallinarum has previously been found in Denmark, in fowl, turkey, guinea fowl, and pheasant (Bonnesen 1911). Besides this Skrjabin 1916, p. 488) mentions Ascaris urogalli as a synonym of H. vesicularis, quoted from Viborg (1795, p. 236). This author really, in an enumeration of the collection of helminths in the Veterinary School in Copenhagen, mentions (as No. 30) Ascaris urogalli. Besides this species he enumerates also as No.'s 38, 40 and 41 Ascaris vermicularis gallinarum, A. v. phasiani colchici and A. v. gallopavonis respectively. It seems reasonable to assume that the three latter forms are H. gallinarum. The indication ,, vermicularis" shows that it is a small species whereas Ascaris urogalli is Ascaridia compar (Schrank 1790) (compare Müller 1806). Further H. gallinarum is in the collections of the late Danish parasitologist H. Krabbe (the Veterinary School), not only from fowls but also from Meleagris gallopavo and Otis tarda, in the latter host together with H. papillosa. Finally, together with H. dispar I have found some few specimens in domestic goose. In Sweden Koffmann (1939) met with this parasite in domestic fowl and in capercailzie.

In Table 1 and Fig. 2 some characteristic features of the species are given. For the sake of comparison, the measurements reported by previous authors are given in Table 2. It is very characteristic for *Heterakis gallinarum* that

Table 1. Measurements of Heterakis gallinarum♂♂

Ak       54, I       4,18       0,14       73         2       5,58       0,14       73         3       5,58       0,19       61       1         4       6,96       0,23       67       1         A*) 119, I       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         5       —       —       49         A       120, 3       3,26       0,12       38         A       120, 3       3,26       0,12       38         A       120,       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk       28,5       —       —       57         Fk       33,3       8,14       0,23       81         8       8,14       0,23       86         Fk       67,1       7,90       0,28       78         2       8,83       0,42 <th></th>	
Ak       54, I       4,18       0,14       73         2       5,58       0,19       61       1         4       6,96       0,23       67       1         A*) 119, I       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         4       6,04       —       52         5       —       49       49         A 120, 3       3,26       0,12       38         A 120, 3       3,26       0,12       38         A 120, 3       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28,5       —       —       57         Fk 33,3       8,14       0,23       86         Fk 67,1       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       84       1         F 28, 2       —       —	Length of left spicule, in mm Length of right spicule, in mm representations of right spicule, in mm representations of right spicule divided by left spicule
Ak       54, I       4,18       0,14       73         2       5,58       0,19       61       1         4       6,96       0,23       67       1         A*) 119, I       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         4       6,04       —       52         5       —       49       49         A 120, 3       3,26       0,12       38         A 120, 3       3,26       0,12       38         A 120, 3       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28,5       —       —       57         Fk 33,3       8,14       0,23       86         Fk 67,1       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       84       1         F 28, 2       —       —	7.80
2 5,58	52 0,73 1,83 2,5
3       5,58       0,19       61       1         4       6,96       0,23       67       1         A*) 119, 1       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         5       —       49         A 120, 3       3,26       0,12       38         A 120       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28, 5       —       —       57         Fk 33, 3       8,14       0,23       86         Fk 67, 1       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       89       2         F 28, 1       —       —       81       1         2       —       84       1         F 31, 1       8,14       0,23       73       1         F 31, 2       7,80       0,26 <td>92 0,46 1,22 2,7</td>	92 0,46 1,22 2,7
4       6,96       0,23       67       I         A*) II9, I       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         5       —       —       49         A 120, 3       3,26       0,12       38         A 120       6,96       0,28       110       I         2       6,50       0,27       91       I         3       5,58       0,23       85       I         Fk 28, 5       —       —       57         Fk 33, 3       8,14       0,23       86         Fk 67, I       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       89       2         F 28, I       —       81       I         2       —       84       I         F 31, I       8,14       0,23       73       I         F 31, I       7,80       0,26       73       I         F 32, I       Io,00	92 0,73 1,53 2,7
A*) 119, 1       4,88       —       49         2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         5       —       —       49         A 120, 3       3,26       0,12       38         A 120,       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28, 5       —       —       57         Fk 33, 3       8,14       0,23       81         8       8,14       0,23       86         Fk 67, 1       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       —       89       2         F 28, 1       —       —       81       1         2       —       —       84       1         F 31, 1       8,14       0,23       73       1         F 31, 2       7,80       0,26       73       1         F 32, 1 </td <td>04 0,61 1,13 1,9</td>	04 0,61 1,13 1,9
2       5,12       —       54         3       6,04       —       52         4       6,04       —       52         5       —       49       49         A       3,26       0,12       38         A       8,37       0,28       81         Fk*) 20, 1       6,96       0,28       110         2       6,50       0,27       91       11         3       5,58       0,23       85       1         Fk       28,5       —       57       57         Fk       33,3       8,14       0,23       86         Fk       67,1       7,90       0,28       78         2       8,83       0,42       84         F**)       2       —       89       22         F       28,1       —       81       11         2       —       84       11         F       28,2       —       84       12         F       31,1       8,14       0,23       73       13         F       31,2       7,80       0,26       73       12 </td <td>10 0,67 1,74 2,6</td>	10 0,67 1,74 2,6
3       6,04       —       52         4       6,04       —       52         5       —       —       49         A 120,3       3,26       0,12       38         A 120       8,37       0,28       81         Fk*) 20,1       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28,5       —       —       57         Fk 33,3       8,14       0,23       81         8       8,14       0,23       86         Fk 67,1       7,90       0,28       78         2       8,83       0,42       84         F**) 2       —       —       89       2         F 28,1       —       —       81       1         2       —       —       84       1         F 31,1       8,14       0,23       73       1         F 31,2       7,80       0,26       73       1         F 32,1       10,00       0,31       85       1	- 0,49 I,40 2,9
4       6,04       —       52         5       —       49         A. 120,3       3,26       0,12       38         A. 120,       8,37       0,28       81         Fk*) 20,1       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk       28,5       —       —       57         Fk       33,3       8,14       0,23       81         8       8,14       0,23       86         Fk       67,1       7,90       0,28       78         2       8,83       0,42       84         F**)       2       —       89       2         F       28,1       —       —       81       1         2       —       —       84       1         F       28,2       —       —       84       1         F       31,1       8,14       0,23       73       1         F       31,2       7,80       0,26       73       1         F <td>- 0,52 I,40 2,7</td>	- 0,52 I,40 2,7
5       —       —       49         A 120, 3       3,26       0,12       38         A 120       8,37       0,28       81         Fk*) 20, 1       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk 28, 5       —       —       57         Fk 33, 3       8,14       0,23       81         8       8,14       0,23       86         Fk 67, 1       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       89       2         F 28, 1       —       81       1         2       —       84       1         F 31, 1       8,14       0,23       73       1         F 31, 2       7,80       0,26       73       1         9       7,44       0,25       —         F 32, 1       10,00       0,31       85       1	— o,61 1,34 2,3
A       120, 3       3,26       0,12       38         A       120       8,37       0,28       81         Fk*) 20, I       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk       28,5       —       —       57         Fk       33,3       8,14       0,23       81         8       8,14       0,23       86         Fk       67, I       7,90       0,28       78         2       8,83       0,42       84         F*)       2       —       89       2         F       28, I       —       81       1         2       —       84       1         F       28, 2       —       84       1         F       31, I       8,14       0,23       73       1         F       31, 2       7,80       0,26       73       1         F       32, I       10,00       0,31       85       1	- 0,55 I,34 2,2
A       120       8,37       0,28       81         Fk*)       20,1       6,96       0,28       110       1         2       6,50       0,27       91       1         3       5,58       0,23       85       1         Fk       28,5       —       —       57         Fk       33,3       8,14       0,23       81         8       8.14       0,23       86         Fk       67,1       7,90       0,28       78         2       8,83       0,42       84         F*)       2       —       89       2         F       28,1       —       —       81       1         2       —       84       1       1         F       28,2       —       —       84       1         F       31,1       8,14       0,23       73       1         F       31,2       7,80       0,26       73       1         F       32,1       10,00       0,31       85       1	- 0,61 1,40 2,5
Fk*) 20, I       6,96       0,28       IIO       IIO         2       6,50       0,27       9I       II         3       5,58       0,23       85       II         Fk 28, 5       —       —       57         Fk 33, 3       8,14       0,23       8I         8       8,14       0,23       86         Fk 67, I       7,90       0,28       78         2       8,83       0,42       84         F*) 2       —       —       89       2         F 28, I       —       —       84       II         F 31, I       8,14       0,23       73       II         F 31, 2       7,80       0,26       73       II         F 32, I       I0,00       0,31       85       II	- 0,37 0,85 2,3
2     6,50     0,27     91     1       3     5,58     0,23     85     1       Fk 28,5     —     —     57       Fk 33,3     8,14     0,23     81       8     8,14     0,23     86       Fk 67,1     7,90     0,28     78       2     8,83     0,42     84       F*) 2     —     —     89     2       F 28,1     —     —     84     1       F 31,1     8,14     0,23     73     1       F 31,2     7,80     0,26     73     1       9     7,44     0,25     —       F 32,1     10,00     0,31     85     1	— I,40 2,02 I,3
3     5,58     0,23     85     I       Fk 28,5     —     —     57       Fk 33,3     8,14     0,23     81       8     8,14     0,23     86       Fk 67, I     7,90     0,28     78       2     8,83     0,42     84       F*) 2     —     —     81     I       2     —     —     84     I       F 28, 2     —     —     84     I       F 31, I     8,14     0,23     73     I       F 31, 2     7,80     0,26     73     I       9     7,44     0,25     —       F 32, I     10,00     0,31     85     I	65 0,86 1,77 2,1
Fk     28, 5     —     —     57       Fk     33, 3     8,14     0,23     81       8     8,14     0,23     86       Fk     67, 1     7,90     0,28     78       2     8,83     0,42     84       F*)     2     —     —     89     2       F     28, 1     —     —     84     II       F     28, 2     —     —     84     II       F     31, 1     8,14     0,23     73     II       F     31, 2     7,80     0,26     73     II       F     32, 1     10,00     0,31     85     II	147 0,67 1,68 2,5
Fk       33, 3       8,14       0,23       81         8       8,14       0,23       86         Fk       67, 1       7,90       0,28       78         2       8,83       0,42       84         F**)       2       —       —       89       2         F       28, 1       —       —       84       II         F       28, 2       —       —       84       II         F       31, 1       8,14       0,23       73       II         F       31, 2       7,80       0,26       73       II         F       32, 1       10,00       0,31       85       II	2,4 0,61 1,46 2,4
8     8,14     0,23     86       Fk     67,1     7,90     0,28     78       2     8,83     0,42     84       F*)     2     —     89     2       F     28,1     —     —     81     I       2     —     —     84     I       F     28,2     —     —     84     I       F     31,1     8,14     0,23     73     I       F     31,2     7,80     0,26     73     I       9     7,44     0,25     —       F     32,1     10,00     0,31     85     I	- 0,46 0,92 2,0
Fk       67, I       7,90       0,28       78         2       8,83       0,42       84         F*)       2       —       —       89       2         F       28, I       —       —       81       II         2       —       —       84       II         F       28, 2       —       —       84       II         F       31, I       8,14       0,23       73       II         F       31, 2       7,80       0,26       73       II         9       7,44       0,25       —         F       32, I       I0,00       0,31       85       II	— 0,67 I,7I 2,5
2       8,83       0,42       84         F*)       2       —       89       2         F       28, 1       —       —       81       I         2       —       —       84       I         F       28, 2       —       —       84       I         F       31, 1       8,14       0,23       73       I         F       31, 2       7,80       0,26       73       I         9       7,44       0,25       —         F       32, 1       10,00       0,31       85       I	- 0,73 I,83 2,5
F*)     2     —     —     89     2       F     28, 1     —     —     81     I       2     —     —     84     I       F     28, 2     —     —     84     I       F     31, 1     8,14     0,23     73     I       F     31, 2     7,80     0,26     73     I       9     7,44     0,25     —       F     32, 1     10,00     0,31     85     I	- 0,73 I,83 2,5
F 28, I — — 81 II 2 — — 84 II F 28, 2 — — 84 II F 31, I 8,14 0,23 73 II F 31, 2 7,80 0,26 73 II 9 7,44 0,25 — F 32, I 10,00 0,31 85 II	- 0,85 2,14 2,4
2     —     —     84     I       F 28, 2     —     —     84     I       F 31, 1     8,14     0,23     73     I       F 31, 2     7,80     0,26     73     I       9     7,44     0,25     —       F 32, 1     10,00     0,31     85     I	216 0,85 2,44 2,9
F 28, 2 — — 84 II F 31, 1 8,14 0,23 73 II F 31, 2 7,80 0,26 73 II 9 7,44 0,25 — F 32, 1 10,00 0,31 85 II	2,20 2,8
F 31, 1 8,14 0,23 73 1 F 31, 2 7,80 0,26 73 1 9 7,44 0,25 — F 32, 1 10,00 0,31 85 1	184 0,79 2,44 3,1
F 31, 2 7,80 0,26 73 1 9 7,44 0,25 — F 32, 1 10,00 0,31 85 1	157 0,79 2,35 3,0
9 7,44 0,25 — F 32, 1 10,00 0,31 85 I	140 0,73 2,30 3,I
F 32, 1 10,00 0,31 85 1	140 0,73 2,10 2,9
-,5=	— 0,73 2,08 2,8
- I I	159 0,79 2,20 2,8
7 10,04 0,37 —	— 0,79 2,22 2,8
	183 0,83 2,22 2,7
	192 0,86 2,80 3,3
	220 0,92 2,44 2,7
F 117, 1 11,60 0,47	- o,85 2,38 2,8
F 137 13,50 — 84	- o,85 2,74 3,2
U*) 36, 1 6,96 0,23 92 1	147 0,76 2,14 2,8
2 6,96 0,19 85 I	771 0,76 2,14 2,8
3 8,37 0,32 85	140 0,79 2,38 3,0
	126 0,78 2,32 2,7
	171 0,78 2,14 2,5
	165 0,82 2,50 3,0

<sup>\*)</sup> Ak = partridge chick, A = partridge, Fk = pheasant chick, F = pheasant, U = black grouse.

Table 2. Important features of Heterakis gallinarum dd.

	1 0	-			
	Length of male in $\mu$	Diameter of preanal sucker, in $\mu$	Distance of posterior border of sucker from cloaca in $\mu$	Lengths of spicules in mm	Hosts
Heterakis vesicularis Dujardin (1845)	8,59,5	90	250	1,6—2,0 0,55—0,66	Gallus gallus dom. Chry- solophus pictus, Mele- gris gallopavo dom., Per- dix perdix.
Heterakis longecaudata. v. Linstow (1879)	8,2			2,3 0,72	Macrocephalon maleo.
Heterakis parisi	79	100	125	2,2 0,64	Rhea americana, zool. garden.
Heterakis vesicularis Lane (1917)		6573	127	1,78—2,0 0,70	Fowl.
Heterakis longecaudata. Baylis & Daubney (1922)	7,9—9,1	80—90	100—150	2,38 0,75	Lophophorus impeianus, Tragopan satyra, Fran- colinus gularis, Galloper- dix spadicea, zool. gar- den.
Heterakis papillosa Smith (1922)	5—8			1,6 0,6	Fowls.
Heterakis papillosa Uribe (1922)	7—8	60	90110	2,0 0,42—0,65	Fowls.
Heterakis gallinae Tubangui (1927)	7—8	60	_	2,0 0,65	Fowls.
Heterakis gallinae Cram (1927)	7—13	60—75		2,0—2,17 0,70—1,10	Colinus virginianus, fowl.
Heterakis gallinae Maplestone (1932)	5,7—9,8	68—104	140—200	1,6—2,6 0,6—1,3	Gallus gallus dom., Chlamy dotis undulata macque eni, Alectoris graeca chu car, Gennæus nyctheme rus, Gennæus leucomela nos, Phasianus colchicutorquatus, Chrysolophupictus, Acryllium vultutinum, Lophura rufa.

	Length of male in μ	Diameter of preanal sucker, in μ	Distance of posterior border of sucker from cloaca in $\mu$	Lengths of spicules in mm	Hosts	
Heterakis parisi Li (1933)	7,9— 9,8	70—80		2,05—2,45 0,74—0,76	Phasianus colchicus.	
Heterakis gallinae Yamaguti (1935)	—10,7	—114		2,2 1,0	Gallus gallus dom., Phasia- nus colchicus versicolor, Graphophasianus söm- meringii.	
Heterakis gallinae Boughton (1937)	7—13	60—75		2,0—2,7 0,7—1,1	Bonasa umbellus Pedioe- cetes phasianellus cam- pestris.	
Heterakis gallinarum Own measurements	4,2—13,5	38—110	92—220	0,85—2,80 0,37—0,92	Phasianus colchicus, Perdix perdix, Lyrurus tetrix.	

the left spicule is much shorter than the right. The latter is normally more than twice, sometimes more than three times as long. Also in very many cases in which the spicules have not been actually measured, the proportions are practically the same. Only in one case I noticed the left spicule to be extraordinarily long, namely 1,40 mm, whereas the normal length is about 0,7—0,8 mm. In this case the other spicule was also long, but the proportion between the left and right spicule was still only 1,3. The tip of the left spicule with its characteristic curve, shows, however, that the specimen belongs to the same species as the other. It will be seen that the length of the spicules can vary to some degree independently of each other, but as a whole the left spicule gets longer in much the same proportion as the right spicule. This is also the case of the relative proportions between the length of the body and the length of the spicule.

On account of the confusion in the synonymy of H. gallinarum the current host lists are not all correct. In the following list I have tried to give the entirely certain hosts. Although this species most commonly occurs in gallinaceous birds, especially in the freely living wild ones, it has also been found in other hosts, for instance such remotely related species as Rhea americana, Sarcorhamphus papa and Chenopis atrata, all of which, however, came from zoological gardens. Under such circumstances H. gallinarum surely will be found in many other hosts in the future. The host list is elaborated from the hitherto cited literature, from Cobbold (1879, p. 447), Shipley (19092—1).

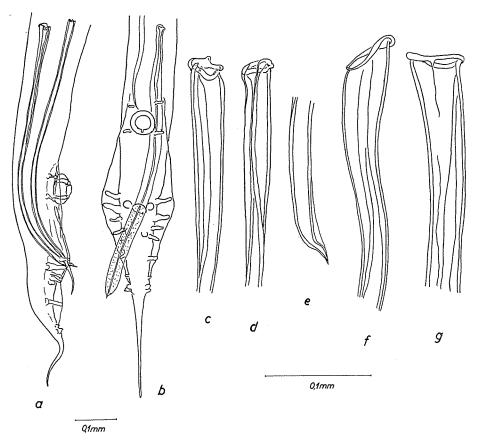


Fig. 2. Heterakis gallinarum.

a, Lateral view of the male tail. b, Ventral view of another specimen. c, Proximal end of the left spicule. d, The same of the right spicule. e, Distal end of the left spicule, (c—e from the specimen in a). f—g, Proximal end of the left and right spicule respectively of a third specimen. — All from pheasants.

Galli-Valerio (1931), Clapham (1935, p. 147, 1938, p. 48), Boughton (1937, p. 16), Simon (1940), Johnston & Mawson (1941, p. 251), Morgan & Hamerstrom (1941, p. 194) and Beer (1944, p. 91).

Occurrence: Rhea americana, Chenopis atrata, Anser anser dom., Tadorna tadorna (?), Sarcorhamphus papa, Alectura lathami, Macrocephalon maleo, Tetrao urogallus, Lyrurus tetrix (BAYLIS 1939; own find), Dendrogapus obscurus, Lagopus lagopus scoticus, Lagopus mutus, Tetrastes bonasia, Tympanuchus cupido, Bonasa umbellus, Pedioecetes phasianellus, Centrocercus urophasianus, Colinus virginianus, Alectoris graeca, Alectoris rufa, Francolinus gularis, Francolinus chinensis, Perdix perdix, Arborophila torqueola, Coturnix coturnix,

Galloperdix spadicea, Tragopan satyra, Lophophorus impeianus, Crossoptilon mantschuricum, Gennæus leucomelanos, Gennæus nycthemerus, Gallus gallus dom., Catreus wallichii, Phasianus colchicus f. div., Syrmaticus sømmeringi, Syrmaticus reevesi, Chrysolophus pictus, Chrysolophus amherstiae, Pavo cristatus, Acryllium vulturinum, Meleagris gallopavo, Chlamydotis undulata macqueeni, Otis tarda (new host), Kakatoe leadbeateri. — Most of the non-European species are from zoological gardens.

#### Heterakis isolonche v. Linstow 1906.

Synonyms and main references: H. isolonche v. Linstow 1906, p. 252, Fig. 7, Lucet & Henry 1911, p. 320—333, 15 Figs. H. putaustralis Lane 1914, p. 658, Figs. 4—7, nec H. putaustralis Maplestone 1932 = H. beramporia Lane 1914. H. neoplastica Wassink 1917. H. hastata Chandler 1926, p. 619, Pl. 31, Fig. 3. H. lanei Chandler 1926, p. 618, Pl. 31, Figs. 1—2. H. variabilis Chandler 1926, p. 619—620, Pl. 31, Fig. 4. \*H. bonasae Cram 1927, p. 75, Figs. 104—105 (?). H. gallinae Canavan 1929, p. 78. H. isolonche Canavan 1929, p. 78. \*H. bonasae Cram 1931, p. 275—276, Fig. 13 (?). H. isolonche Maplestone 1932, p. 406—407, Pl. 12, Figs. 2—3 d—e. H. variabilis Maplestone 1932, p. 407—409, Pl. 12, Figs. 3 a—c.H. isolonche Sprehn 1932, p. 553—554, Fig. 273. H. putaustralis Sprehn¹) 1932, p. 554. H. isolonche Baylis 1936, p. 119—121, Fig. 55, Neveu-Lemaire 1936, p. 738—740. H. putaustralis Neveu-Lemaire 1936, p. 742¹). \*H. tragopanis Lal 1942, p. 388—389, Fig. 1—2.

1) Neveu-Lemaire and Sprelin here only quote Lane (1914), with the measurements given by him. Baylis (1936, p. 119, footnote) has shown that Lane's measurements were erroneous, his specimens being H. isolonche.

As seen in the list of synonyms, this species has not been recognized in several cases. In the first description of *Heterakis bonasae*, CRAM (1927), the main distinguishing character seemed to be the presence of an extra pair of papillae (the spicules apparently being identical with *H. isolonche*, as described by i. a. MAPLESTONE (1932) and BAYLIS (1936)). Later (CRAM 1931) this character appeared not to be constant. It seems to be the only instance of this species in a wild living bird, together with the worm found by CANAVAN (1929), in *Colinus virginianus texanus* (see the synonyms). The bird had only lived in a zoological garden for 48 days and therefore probably acquired the parasite before confinement. Besides this he (as the first) mentions *H. isolonche* from *Crossoptilon auritum*. Since the spicules, according to the description cannot be distinguished from those of *H. isolonche*, I have preferred to list this species here.

Heterakis isolonche can be distinguished by its spicules, which are long, mostly about 1,5 mm, according to my measurements (Table 3) but lengths from 0,99—2,20 have also been found (Table 4). The left spicule is most often the longer, but in a few cases they are of the same length or the right a little longer. Both spicules are alate but the left is the broader; at the tip the curve which is so characteristic for Heterakis gallinarum is missing (Fig. 3 c). The most important features given by previous authors are summarized in Table 4.

Table 3.

Measurements of Heterakis isolonche  $\mathcal{F}\mathcal{F}$ .

	Length, in mm	Diameter of precloacal sucker, in µ	Distance be- tween sucker and cloaca, in µ	Length of left spicule, in mm	Length of right spicule in mm	Index right spicule divi- ded by left spicule
₹1 ₹2	7,7	128	146	1,83	1,55	0,85
d 2	10,1	140	128	1,80	1,49	0,83
♂3⋯⋯	8,7	134	134	1,62	1,46	0,90
₹4	8,0	134	122	1,95	1,34	0,69
₹5	10,6	122	140	1,86	1,71	0,92
₹7	8,8	116	171	1,58	1,46	0,92
♂8	9,7	122	165	1,77	1,61	0,91
g 9	9,0	139	128	1,68	1,55	0,93
♂11	9,8	122	158	1,68	1,74	1,04
♂12	7,7	120	106	1,65	1,49	0,91
d 14	9,7	146	120	1,77	1,65	0,93
♂15	10,0	140	171	1,67	1,67	1,00
♂ 17····	8,7	146	116	1,95	1,40	0,72
♂18	8,0	134	134	1,89	1,89	1,00
♂ 19	9,3	146	134	1,74	1,65	0,95
₹20	9,3	128	116	1,62	1,52	o,94

Occurrence: Bonasa umbellus (H. bonasae), Colinus virginianus (H. bonasae), Ithaginis cruentus, Tragopan satyra, Lophophorus impeianus, Crossoptilon manchuricum, Crossoptilon auritum, Gennæus leucomelanus, Gennæus nycthemerus, Lophura rufa, Phasianus colchicus f. div., Chrysolophus pictus, Chrysolophus amherstiae, Polyplectron bicalcaratum. Almost all except the species with the worm called H. bonasae from zoological gardens. — Anas platyrhynchos dom. (?) (Johnston & Mawson 1941, p. 115).

Table 4. Important features of Heterakis isolonche of of.

, , ,	J				
	Length of male, in mm	Diameter of preanal sucker, in µ	Distance of posterior border of sucker from cloaca, in $\mu$	Length of spicule in mm	Hosts
Heterakis isolonche v. Linstow 1906	7,8			1,41	Chrysolophus amher- stiae.
Heterakis isolonche Lucet et Henry 1911	7,5-9	<del></del>		1,40 1,75	Chrysolophus pictus.
Heterakis neoplastica Wassink 1917	15	140	310	both 1,8	Phasianus c. colchicus, Phasianus c. satche- vensis, Chrysolophus pictus, C. p. var. obscurus.
Heterakis hastata Chandler 1926	10,511,5	145	150	1,65 1,75	Lophura rufa.
Heterakis lanei Chandler 1926	9—9,6	140	175	2,0	Lophura rufa.
Heterakis variabilis Chandler 1926	9—10	85	180	0,72-0,88	Polyplectron bicalcaratum.
Heterakis bonasae Cram 1927	7	100—120	116	1,1—1,3 1,4—1,6	Bonasa umbellus.
Heterakis gallinae Canavan 1929	II,I	130—150		1,72—1,92 1,78—1,93	Colinus virginianus tex- anus, Chrysolophus pictus.
Heterakis isolonche Maplestone 1932	7,0—9,6	92—121	140—170	0,99—1,37 1,48—2,1	Gennæus nycthemerus, Gennæus leucomela- nos, Tragopan satyra, Lophophorus impeia- nus.
Heterakis variabilis Maplestone 1932	5,9—9,1	130140	420—530	0,69—1,94 1,11—2,33	Tragopan satyra, Polyplectron bicalcaratum.
Heterakis isolonche Li 1933	11,5—12,3	140—150		1,4—1,61 1,56—1,70	Chrysolophus pictus.
Heterakis tragopanis Lal 1942	8,0	70 × 40	160	1,6(r) 1,5(l)	Tragopan satyra.
Heterakis isolonche Own measurements	7,7—10,6	116—146	106—171	1,34-1,89(r) 1,58-1,95(l)	Crossoptilon auritum.

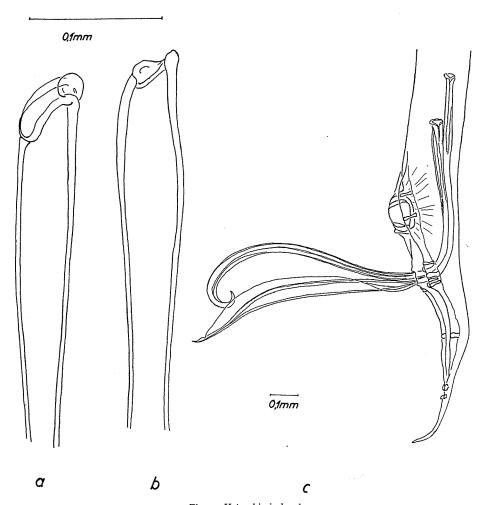


Fig. 3. Heterakis isolonche.

a—b, Dorsal view of proximal end of left and right spicule respectively. c. Lateral view of male tail of another specimen. The long, broad alate spicule is the left one.

#### Holger Madsen

#### Heterakis dispar (Schrank 1790).

Synonyms and main references: Ascaris dispar Schrank 1790, p. 120; 1793, p. 94-98, Fig. 3—4. Fusaria dispar Zeder 1800, p. 52—53, 1803, p. 109. Ascaris dispar Rudolphi 1808, p. 157; 1819, p. 45, Creplin 1823, p. 17—20. Heterakis dispar Dujardin 1845, p. 225—226. Ascaris dispar Diesing 1851, II, p. 149. Heterakis dispar? Cobbold 1859, p. 365, Pl. 63, Fig. 26. \*Strongylus acuticaudata Cobbold 1861, p. 123, Pl. 20, Fig. 5-6. (?). Non \*Heteracis dispar Molin 1861 = Heterakis sp.? H. dispar Schneider 1866, p. 75, 1 Fig., Railliet 1895, p. 408, Fig. 268. \*H. caudata v. Linstow 1906<sub>2</sub>, p. 250—251, Fig. 4.\*H. circumvallata v. Linstow 19062, p. 251, Fig. 5. \*H. chenonettae Johnston 1912, p. 71—72, Pl. 4, Fig. 31—33 (?). *H. dispar* Skrjabin 1916<sub>2</sub>, p. 492—493, Fiebiger 1923, p. 309, Fig. 265, Petroff 1926, 2 Figs. (Reproduced by Skrjabin, Schulz etc. 1934, p. 217, Figs. 219—220). \*H. caudata Cram 1927, p. 59-60, Fig. 79. \*H. circumvallata Cram 1927, p. 61-62, Fig. 81. H. dispar Cram 1927, p. 62, Fig. 82, Rezsö & Kotlan 1931, p. 304—305, Fig. 152. \*H. hyperborea Swinyard 1931, p. 266—269, Figs. 1—4. \*H. papillosa Maplestone 1932, p. 412—413, Pl. 13, Fig. 11. \*H. caudata Maplestone 1932, p. 413—414, Pl. 13, Figs. 12—14. H. dispar Sprehn 1932, p. 552, Figs. 270 —272. \*H. papillosa Baylis 1936, p. 121—122 part. H. dispar Neveu-Lemaire 1936, p. 737, Fig. 406. \*H circumvallata Neveu--Lemaire 1936, p. 738. \*H. chenonettae Johnston & Mawson 1941, p. 115, Fig. 13 (?).

As is the case with the two species treated previously this species has not been recognized in several cases, owing to the lack of adequate figures. Not until more than 130 years after the first description of the species does the first really adequate figure appeare (Petroff 1926), but it is difficult for most investigators to obtain. The same can be said about the rather good figure of Rezsø & Kotlán (1931). The rather recent figure of Sprehn is useful, but does not illustrate the spicules quite correctly. Because of these difficulties I examined about 25 domestic geese, and eventually succeeded in finding several

Table 5. Measurements of Heterakis dispar, &.

	Length, in mm Diameter precloace sucker, in		Distance be- tween sucker and cloaca, in $\mu$	Length of left spicule, in mm	Length of right spicule, in mm
σ¹ 1 σ¹ 2	12,1	183	384	0,61	0,61
	12,4	204	397	0,63	0,63
o 3 · · · · · · · · · · · · · · · · · ·	13,7	250	482	0,70	0,64
of 4 ·····	14,1	256	39 <b>0</b>	0,67	0,73
of 5 ······	13,7	208	415	0,70	0,70
of 6	14,8	189	453	0,67	0,67
of 7 ·····	13,5	202	518	0,67	0,67
oੁੱ 8 ·····	13,2	183	403	0,61	0,61
of 9 ······		229	427	0,61	0,67
Q_10		238	415	0,67	0,67
♂ · · · · · · · · · · · · · · · · · · ·	_	238	396	0,67	0,67
on 12		208	274	0,55	0,64

specimens, associated with a few specimens of H. gallinarum. As a contribution to the knowledge of the species I give measurements in the tables 5 and 6, and illustrations (Figs. 4 a-c, 5 a -c), and for comparison also previous figures (Figs. 6 a-i, 7 a-h).

The females normally have papillae in various shapes and number around

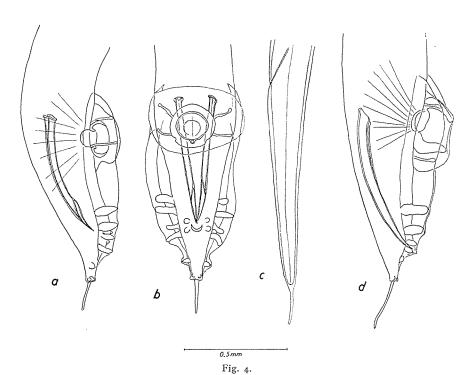
Table 6. Important features of Heterakis dispar, ♂♂.

	Length of male, in mm.	Diameter of preanal sucker, in $\mu$	Distance of posterior border of sucker from cloaca, in $\mu$	Length of specule in mm	Hosts
Heterakis caudata v. Linstow 1906	7,8	180		both 0,44	Aix sponsa, zool. gar- den.
Het. circumvallata v. Linstow 1906	13,1	190	, and the second se	both 0,48	Cygnus atratus, zool. garden.
Heterakis dispar Cram 1927	11—18			both 0,400,50	Anser anser dom., Anas plathyrhynchus dom. and several other anatine birds.
Heterakis hyperborea Swinyard 1931	13,6	195	338	both 0,53	Chen h. hyperborea
Heterakis caudata Maplestone 1932	7,3-9,6	109—158	180—240	both 0,39—0,51	Cereopsis novae-hollan- diae.
Heterakis papillosa Maplestone 1932	8,411,8	216—220	210—300	both 0,50-0,54	Gennaeus nycthemerus.
Heterakis dispar Sprehn 1932		185	400	both 0,47	Domestic goose.
Heterakis chenonettae Johnston & Mawson 1941	6,8	800(?!) probably 180	200	both 0,40—0,42	Chenonetta jubata, zool garden.
Heterakis dispar Own measurements	12,1—14,8	183—256	293—518	left 0,55—0,70 right 0,61—0,73	Domestic goose.

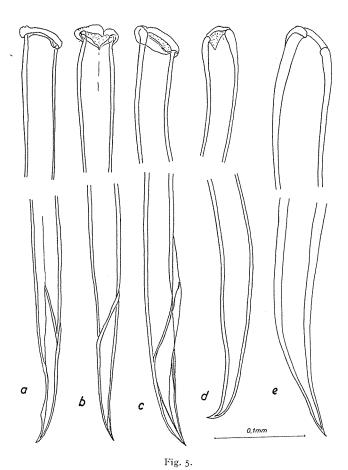
the vulva, and which have been demonstrated by several authors to originate from the sucker of the male. These papillae are very seldom seen in H. gallinarum, with its small sucker, but more often in H. isolonche, and especially in H. dispar and H. papillosa with their larger suckers. The tail tip of the female differs in shape from that of the females of H. gallinarum and H. isolonche, which tapers gradually (Fig. 4 c).

Occurrence: Chenopis atrata, Anser anser dom., Anser fabalis, Chen hyperborea, Nesochen sandvicensis (?), Chloephaga poliocephala (?), Cereopsis novaehollandiae, Chenonetta jubata (?) (H. chenonettae), Cairina moschata dom., Tadorna tadorna, Anas platyrhynchos dom., Aix sponsa, Gennaeus nycthemerus.

— Most hosts domesticated or in zoological gardens. Only some geese wild living: Anser fabalis, Chen hyperborea. Babić (1936) without description, mentions this species from Alectoris graeca. But it is doubtful to which species his specimens belong. H. dispar has also been found in domestic goose in U.S.A. (Hall 1924).

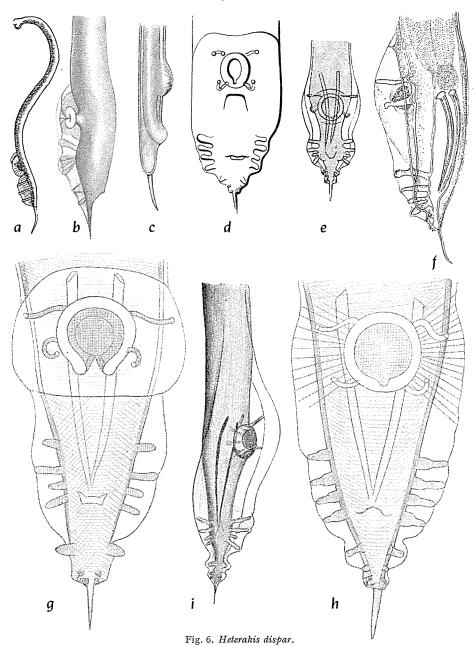


a—c, Heterakis dispar. a—b, Male tail, seen laterally and ventrally. c, Female tail. d, Heterakis papillosa, Male tail seen laterally,



a—c. Heterakis dispar. a, Left spicule, b, Right spicule, both from same specimen, seen from the right side. d—e, Heterakis papillosa. d, Left spicule, seen obliquely from the ventral side. e, Right spicule from another specimen, seen from the right

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a, Ascaris dispar, after Schrank (1793). b, Strongylus acuti caudatus, after Cobbold (1861). c, Heterakis dispar? after Cobbold (1859). d, H. dispar, after Schneider (1866). e, after Railliet (1895). f, after Sprehn (1932). g, H. circumvallata and h, H. caudata, after v. Linstow (1906). i, H. dispar, after Fiebiger (1923).

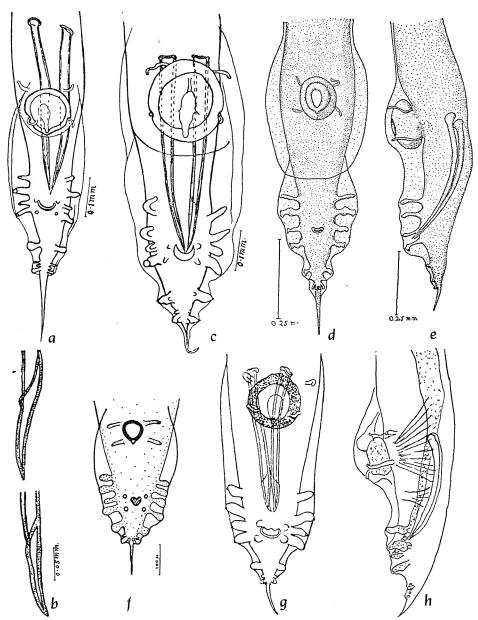
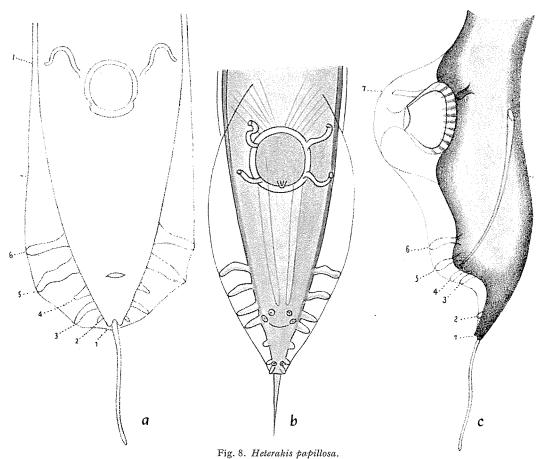


Fig. 7. Heterakis dispar.

a—b, H. caudata = H. papillosa, after Maplestone (1932). b, Tip of left spicule, two specimens. c, H. papillosa, after Maplestone (1932). d—e, H. hyperborea, after Swinyard (1931). f, H. chenonettae, after Johnston & Mawson (1941). g, H. dispar, after Petroff 1926. h, H. dispar, redrawn after Rezsö & Kotlán (1931).



a, c, H. monticelliana, after Stossich (1892). b, H. stylosa, after v. Linstow (1907).

#### Heterakis papillosa (Bloch 1782).

Synonyms and main references: Ascaris papillosus Bloch 1782, p. 32, Pl. 9, Figs. 1—6, Schrank 1788, p. 12, Gmelin 1790, p. 3034. Ascaris vesicularis Rudolphi 1808, p. 129, part; 1819, p. 38, 268, part., Diesing 1851, II, p. 148—149, part. Non A. papillosa Molin 1860 = Subulura papillosa (Molin 1860). Non Heterakis papillosa Railliet 1885 = H. gallinae auctt. nov. = H. gallinarum sensu nov. H. monticelliana Stossich 1892, p. 72, Pl. 2, Figs. 7—9. H. stylosa v. Linstow 1907, p. 253, Pl. 6, Fig. 6. H. monticelliana Skrjabin 19162, p. 493, Baylis 1923, p. 10—11. H. papillosa Cram 1927, p. 67—68, Figs. 91—92. H. monticelliana Sprehn 1932, p. 554. Non \*H. papillosa Mapleston 1932 = H. dispar (Sckrank 1790). Non \*H. papillosa Li 1933 = H. silindae Sandground 1933 (?). \*H. papillosa Baylis 1936, p. 121—122, part.

My specimens (origine, see p. 1) occurred in *Otis tarda*, the type host, from a zoological garden, associated with *H. gallinarum*. They are evidently

identical with those of Stossich and of Baylis, named H. monticelliana. This name was given by Stossich in order to avoid the confusion with H. gallinarum, which has often been called H. papillosa (see the synonymy list of H. gallinarum, p. 00). But this is not allowable according to rules of nomenclature. Cram (1927, p. 67) accordingly revived the name H. papillosa. The description of Bloch (1782) is somewhat confusing, but the presence of papillae on the side of the females in his illustration (Pl. 9, Fig. 2) (these papillae are very conspicuous in the present species, as in H. dispar), and the host makes it probable that he had the present species before him.

No measurements have been available before, and only the incomplete figures of Stossich and of von Linstow. Therefore the measurements in table 7, and the illustrations (Fig. 4, d; 5, d—e; 8, a—c) are given. Owing to the difficulties mentioned, Maplestone (1935) used the name for specimens which are, evidently *H. dispar*. The *H. papillosa* of Li (1933) is not the present species either. Possibly it is identical with *H. silindae* Sandground 1933.

Occurrence: Otis tarda, Tetrax tetrax.

Table 7. Measurements of Heterakis papillosa, od.

	Length, in mm	Diameter of precloacal sucker, in $\mu$	Distance be- tween sucker and cloaca, in $\mu$	Length of spicules in mm
7	THE PROPERTY OF THE PROPERTY O		100	0,73
Q,1	12,3	250	433	
d2	12,1	280	469	0,79
♂3	12,1	274	415	0,70
Z4	7,5	171	238	0,55
♂5 ······	7,5	220	274	0,58

#### LIST OF SPECIES OF HETERAKIS FOUND IN BIRDS

(The species marked with an asterisk are suggested as synonyms for the first time).

#### \*Heterakis sp. (?)

Synonyms: *Heteracis dispar* of Molin 1858, p. 150; 1861, p. 291—292; (nec *H. dispar*(Schrank 1790)).

Molin's description comprises, among other things: "Vagina penis" (by this he means the left spicule as his figure of *Heteracis vesicularis* = *Heterakis gallinarum* (Schrank 1788) shows) "monopetala, linearis, brevis, utrinque

Heteraki <b>s</b> gallinarı	ım group	Heterakis isoloncl	ne group	Heterakis dispar group		
Unequal spic	ules	Long equal sp	icules	Short equal sp	icules	
Left spicule short	Length of spicules		Length of spicules	1 West and	Length of spicules	
H. gallinarum	0,85—2,80 0,37—0,92	H. isolonche	0,69—2,0 1,04—1,18	H. dispar	0,390,73	
H. bosia	1,48—1,85 0,87—1,03	H. altaica	0,73	H. aləta	o, <b>6</b> 3—0,65	
H. indica	0,99—1,19 0,29—0,40	H. arquata	2,6	H. beramporia	0,32—0,51 0,30—0,36	
H. pavonis	1,20—1,90 0,59—0,98	H. bancrofti	0,86—1,23	H. brasiliana	0,26—0,39	
H. valvata	2,6 1,0	H. crypturi	1,13—1,7 1,08—1,70	H. brevispiculum .	0,27—0,40	
Right spicule short.		H. fariai	0,9	H. chenonettae	0,4	
H. pusilla	0,53 0,15	H. interlabiata	1,25	H. hamulus	0,32 0,37	
H. vulvolabiata	0,54—0,60 0,29—0,32	H. nattereri	ca. I	H. macroura	0,13 0,11	
		H. skrjabini	0,85	H. multidentata	0,38—0,48	
######################################		H. tenuicauda	0,89—0,96	H. papillosa	0,55-0,79	
	The state of the s		To the second se	H. parva	0,28	
		•		H. psophiae	0,63	
		-		H. silindae	0,44-0,46	

alata, alis latiusculis; penis'' (here he means the right spicule) "longissimus'' (whereas the same in *Heterakis gallinarum* is only "longus'') "filiformis, spiraliter tortus''. Further: "In intestino tenui'' (other species of *Heterakis* 

#### Studies on Species of Heterakis

are found in the ceca). "Esso differiva dall' H. vesicularis specialmente per la forma della guaina del pene la quale era molto piu larga". For these reasons Molin's species cannot be identical with H. dispar, which has two short, equal spicules, but is seemingly a Heterakis. It seems impossible to refer it to any of the other nematodes known from owls.

Occurrence: Glaucidium passerinum; Athene noctua (?) (Cram 1927, p. 388 and p. 417, error).

\*Heterakis acuticaudata (Cobbold 1861) sp. inqu. (= H. dispar (Schrank 1790) (?)).

Synonyms: Strongylus acuticaudata Cobbold 1861, p. 123, Pl. 20, Figs. 5—6. H. acuticaudata Cram 1927, p. 77, Figs. 106—107.

As already shown by CRAM (1927), this species is quite uncertain. The facts known about it do not prevent it belonging to H. dispar, which has been found in several anatine birds.

Occurrence: Chloëphaga poliocephala, Zool. garden, London.

Heterakis alata Schneider 1866 sp. inq.

Synonyms: *H. alata* Schneider 1866, p. 76, r Fig., Travassos 1913, p. 280—281, Pl. 27, Fig. 2, Cram 1927, p. 55, Fig. 68.

Occurrence: Crypturellus sp. and Tinamus sp.

Heterakis altaica Spaul 1929, sp. inq.

Synonyms: H. altaica Spaul 1929, p. 455-457, Fig. 4-8.

Occurrence: Tetraogallus tibetanus.

Heterakis arquata Schneider 1866, sp. inq.

Synonyms: H. arquata Schneider 1866, p. 77, I Fig., Travassos 1913, p. 281—282, Pl. 27, Fig. 3. Ascaridia arquata Railliet & Henry 1914, p. 677. Non H. arquata Skrjabin 1916 = H. skrjabini Cram 1927. H. arquata Cram 1927, p. 55, Figs. 69—70.

Occurrence: "Crypturus cupreus"1) and Psophia viridis.

1) A tinamid with this name does not exist. Dr. NIELS GYLDENSTOLPE, Naturhistoriska Riksmuseet, Stockholm, kindly informs me (in letter of March 1946): "It does not seem impossible that the label of the host specimen has been marked "Crypturus" cupreus, the latter "name" only indicating the colour of the bird. — According to a paper by O. NEUMANN (Verh. Ornith. Ges Bayern 20, I, p. 180, 1933) some old specimens of Crypturellus o. obsoletus (Temm.), collected by SELLO and VON OLFERS in the neighbourhood of Rio de Janeiro, can or could be found in the Museum of Berlin. Further I have found a notice indicating that the same gentlemen also collected C. undulatus vermiculatus (Temm..) In Sao Paulo /Mus. Berlin No. 11929. The host is possibly one of these specimens". SCHNEIDER (1866, p. 77) indicates Olfers and Sello as collectors of his material of H. arquata.

#### Holger Madsen

#### Heterakis bancrofti Johnston 1912, sp. inq.

Synonyms: *H. bancrofti* Johnston 1912, p. 72—74, Pl. 4, Figs. 28—30, Cram 1927, p. 56, Fig. 71, Johnston & Mawson 1941<sub>2</sub>, p. 251, Fig. 5.

Occurrence: Alectura lathami, Leucosarcia melanoleuca, Australia.

#### Heterakis beramporia Lane 1914.

Synonyms: *H. beramporia* Lane 1914, p. 658—660, Figs. 1—3, Schwartz 1925<sub>1</sub>, p. 2—4, Figs. 1—7, 1925<sub>2</sub>, p. 2, Cram 1927, p. 56—57, Fig. 72. Tubangui 1927, p. 25—26, Fig. 11. *H. putaustralis* Maplestone 1932, p. 411—412, Pl. 13, Figs. 9—10. *H. beramporia* Sprehn 1932, p. 551, Li 1933, p. 1315, Pl. 3, Figs. 18—19, Baylis 1936, p. 122—123, Neveu-Lemaire 1936, p. 741—742, Wu 1937, p. 4, Bhalerao & Rao 1944, p. 36—37, Wu & Kung 1944, p. 120.

Occurrence: Gennæus nycthemerus, Gallus sonneratii (Zool. garden, India) Gallus gallus dom., India, Philippines, Indo-China, China. Anas platyrhynchos dom., China (?).

Heterakis bonasae Cram 1927 = Heterakis isolonche v. Linst. 1906 (?).

#### Heterakis bosia Lane 1914.

Synonyms: *H. bosia* Lane 1914, p. 657—658, Figs. 8—10, Cram 1927, p. 57—58, Fig. 73, Maplestone 1932, p. 409, Pl. 12, Fig. 4, Baylis 1936, p. 116—117, Fig. 54, Chakravarty 1944, p. 72.

Occurrence: Tragopan satyra, India (Zool. garden).

#### Heterakis brasiliana v. Linstow 1899.

Synonyms: *H. brasiliana* v. Linstow 1899, p. 11—12, Pl. 2, Fig. 21. *Ascaridia brasiliana* Travassos 1913, p. 295—296, Pl. 28, Fig. 17. *H. brasiliana* Travassos 1918, p. 96—97, Fig. 1, Cram 1927, p. 58, Fig. 74.

Occurrence: "Perdix sp." (possibly a tinamou), Rhynchotus rufescens.

#### Heterakis brevispiculum Gendre 1911.

Synonyms: H. brevispiculum Gendre 1911, p. 72—73, Figs. 1—4. H. vesicularis Travassos 1913, p. 279—280, Pl. 27, Fig. 1. H. brevispiculum Cram 1927, p. 59, Figs. 75—78, Baylis 1930, p. 118. \*H. travassosi Khalil 1932, p. 448—450, Fig. 13—14. H. brevispiculum Sprehn 1932, p. 552, Neveu-Lemaire 1936, p. 740—741, Pinto 1938, p. 238, Fig. 855. \*H. putaustralis Wu & Kung 1944, p. 119—120 (?).

I have seen Baylis' specimens myself, and must, after discussion with him agree in the above synonymy.

Occurrence: Gallus gallus dom. (Brazil, Africa, China [?]), Gallus bankiva (Dutch India) (Kraneveld & Douwes (1940)), Polyplectron bicalcaratum, Numida meleagris (Africa).

Mentioned without description by Lewis (1927) from Wales, in the latter host.

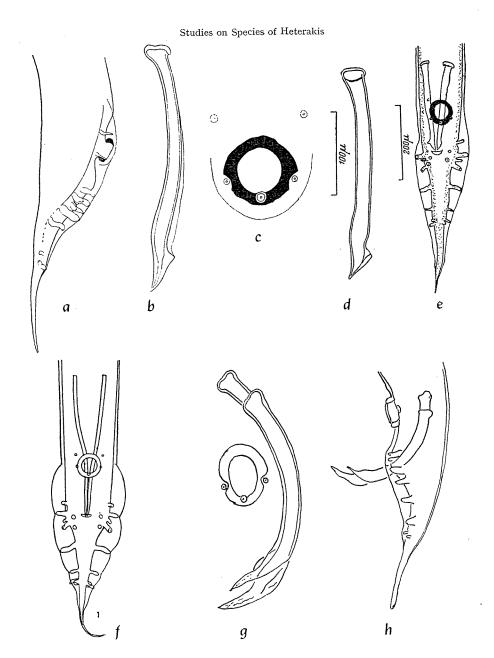


Fig. 9. Heterakis brevispiculum.

a—c, H. brevispiculum, after Gendre (1911). c, Precloacal sucker, with a notch in the edge, from the papillae. b, Spicule (if right or left is not indicated). f, H. vesicularis, after Travassos (1913). d—e, H. travassosi, after Khalil (1932). e, Spicule (right?). g—h, H. brevispiculum, redrawn after Pinto (1938). g, both spicules and ventral view of sucker.

#### Holger Madsen

\*Heterakis caudata v. Linstow 1906 = Heterakis dispar (Schrank 1790).

Heterakis chenonettae Johnston 1912, sp. inq.

Synonyms: *H. chenonettae* Johnston 1912, p. 71—72, Pl. 4, Figs. 31—33, Cram 1927, p. 60—61, Fig. 80, Johnston & Mawson 1941, p. 115, Fig. 13.

Description improved by Johnston & Mawson 1941, but still insufficient. The species is probably  $H.\ dispar.$ 

Occurrence: Chenonetta jubata, Australia (Zool. garden).

\*Heterakis circumvallata v. Linstow 1906 = Heterakis dispar (Schrank 1790).

Heterakis crypturi Baylis 1944.

Synonyms: H. crypturi Baylıs 1944, p. 621—626, Figs. 1—5.

Occurrence: Crypturellus variegatus, British Guiana.

Heterakis curvata v. Linstow 1883 = Subulura curvata (v. Linstow 1883).

The reason why this species is listed here is that Stossich (1888, p. 287) records it as a species of *Heterakis* in a modern sense, and also on Pl. 6, Fig. 23 illustrates a species with the preanal sucker of the *Heterakis* or *Ascaridia* type. His figure, in comparing it with those of Schneider (1866) turns out to be the doubtful species *Heterakis retusa* (Rud. 1819), from *Dasypus novemcinctus*. (See Travassos 1913, p. 286). This figure should be Fig. 22, whereas this latter presumably is a very diagrammatic and incomplete redrawing of v. Linstow's *H. curvata* (p. 292, Pl. 7, Fig. 23). All the illustrations in Stossich's above mentioned paper are redrawn, often very badly and with important particulars omitted. But since the paper pretends to be a monograph of the genus discussed here it seems necessary to take it in consideration. But owing to the incorrectness of the paper, and since it is quite uncritical, being exclusively compilatory, I have deemed it superfluous to cite it in detail in the synonymy lists.

Heterakis dispar (Schrank 1790).

For synonymy etc. see above p. 16.

Heterakis fariai Travassos 1913, sp. inq.

Synonyms: H. fariai Travassos 1913, p. 284, Pl. 28, Fig. 10, Cram 1927, p. 63, Fig. 83.

Description somewhat confusing, possibly identical with H. isolonche.

Occurrence: Odonthophorus capueira, Brazil.

#### Studies on Species of Heterakis

Heterakis gallinae (Gmelin 1790) auctt. nov. = Heterakis gallinarum (Schrank 1788) sensu mea.

For particulars, see above p. 5. Non *H. gallinae* (Gmelin 1790) Canavan 1929 = *H. isolonche* v. Linstow 1906. Non \**H. gallinae* (Gmelin 1790) Hsü 1932; Wu & Kung 1944 = *H. pavonis* Maplestone 1932.

Heterakis hamulus v. Linstow 1906, sp. inq.

Synonyms: *H. hamulus* v. Linstow, 1906<sub>2</sub>, p. 251—252, Fig. 6, Cram 1927, p. 63—64, Fig. 8<sub>4</sub>, Sprehn 1932, p. 552, Baylis 1936, p. 123, Neveu-Lemaire 1936, p. 740.

Occurrence: Pavo muticus, Königsberg (Zool. garden?), Pavo cristatus (?).

Heterakis hastata Chandler 1926 = Heterakis isolonche v. Linstow 1906.

\*Heterakis hyperborea Swinyard 1931 = Heterakis dispar (Schrank 1790).

Heterakis indica Maplestone 1932.

Synonyms: H. indica Maplestone 1932, p. 410, Pl. 12, Figs. 7—8. \*H. lingnanensis L1 1933, p. 1310—1311, Pl. 2, Figs. 10, 13 & 14. H. indica Baylis 1936, p. 115. \*H. lingnanensis Neveu-Lemaire 1936, p. 742—743.

Occurrence: Gallus gallus dom., India and China.

Heterakis interlabiata Ortlepp 1923.

Synonyms: H. interlabiata Ortlepp 1923, p. 63—64, 2 Figs., Cram 1927, p. 64, Figs. 85—86.

Occurrence: Rhizothera longirostris, London (Zool. garden).

Heterakis isolonche v. Linstow 1906.

For details see above p. 12.

Heterakis lanei Chandler 1926 = Heterakis isolonche v. Linstow 1906.

\*Heterakis lingnanensis Li 1933 = Heterakis indica Maplestone 1932.

Heterakis longecaudata v. Linstow 1879 = Heterakis gallinarum (Schrank 1788).

Heterakis longespiculum Maplestone 1931 = Pseudaspidodera voluptuosus minor Chandler 1926. (See Maplestone 1932, p. 415).

#### Holger Madsen

Heterakis macroura v. Linstow 1883.

Synonyms: H. macroura v. Linstow 1883, p. 293, Fig. 28, Cram 1927, p. 67, Fig. 90.

Occurrence: Tetraogallus himalayensis, Turkestan.

Heterakis monticelliana Stossich 1892 = Heterakis papillosa (Bloch 1782).

Heterakis multidentata Baylis 1944.

Synonyms: H. multidentata Baylis 1944, p. 626-630, Figs. 6-7.

Occurrence: Crypturellus variegatus, British Guiana.

Heterakis nattereri Travassos 1923, sp. inq.

Synonyms: H. nattereri Travassos 1923, p. 38-39, Cram 1927, p. 75-76.

The description is without illustrations and is therefore of little value.

Occurrence: Crax blumenbachi, Brazil.

Heterakis neoplastica Wassink 1917 = Heterakis isolonche v. Linstow 1906.

Heterakis numidae (Leiper 1908) = Ascaridia numidae (Leiper 1908).

This species is mentioned here because Seurat (1918, p. 53) and Yorke & Maplestone (1926 p. 216) assume it to be identical with  $H.\ tenuicanda$ .

Heterakis papillosa (Bloch 1782).

Non H. papillosa (Bloch 1782) Railliet 1885 et auctt. = H. gallinarum (Schrank 1788). Non \*H. papillosa (Bloch 1782) Maplestone 1932 = H. dispar (Schrank 1790). Non \*H. papillosa (Bloch 1782) Li 1933 = H. silindae Sandground 1933 (?).

For particulars see above p. 22.

Heterakis parisi Blanc 1913 = Heterakis gallinarum (Schrank 1788).

Heterakis parva Maplestone 1931.

Synonyms: H. parva Maplestone 1931, p. 128—129, Figs. 85—87, Baylis 1936, p. 118—119.

Occurrence: Gennæus nycthemerus, India (Zool. garden).

#### Studies on Species of Heterakis

#### Heterakis pavonis Maplestone 1932.

Synonyms: *H. pavonis* Maplestone 1932, p. 410, Pl. 12, Figs. 5—6. \**H. gallinae* Hsü 1932, p. 100—101, Pl. 1, Figs. 1—2. *H. pavonis* Baylis 1936, p. 115—116. \**H. yamadori* Yamaguti 1941, p. 447—449, Figs. 8—10 (?). \**H. gallinae* Wu & Kung 1944, p. 119.

Closely related to *H. gallinarum*. It is possibly only a variety of this species. It has, however, never occured in my abundant material of *Heterakis gallinarum*.

Occurrence: Gennæus nycthemerus, India (Zool. garden), Indo-China. Gallus gallus dom., China. Syrmaticus soemmeringi, Phasianus coldicus versicolor, Nycticorax nycticorax, Japan (?).

Heterakis psophiae Travassos 1913, sp. inq.

Synonyms: *H. psophiae* Travassos 1913, p. 285, Pl. 28, Figs. 11—12, Cram 1927, p. 69—70, Figs. 94—95.

Occurrence: Psophia viridis, Brazil.

Heterakis pusilla v. Linstow 1906, sp. inq.

Synonyms: *H. pusilla* v. Linstow 1906<sub>1</sub>, p. 167, Pl. 1, Fig. 9, Cram 1927, p. 70, Fig. 96, Baylis 1936, p. 116, Neveu-Lemaire 1936, p. 738.

Occurrence: Gallus lafayeti, Ceylon.

#### Heterakis putaustralis Lane 1914 =

Heterakis isolonche v. Linstow 1906. Non H. putaustralis, Maplestone 1932 = H. beramporia Lane 1914. Non \*H. putaustralis, Wu & Kung 1944 = H. brevispiculum Gendre 1911 (?).

#### Heterakis silindae Sandground 1933.

Synonyms: H. silindae Sandground 1933, p. 272—273, Fig. 3. \*H. papillosa Li 1933, p. 1314, Pl. 3, Fig. 17 (?).

Occurrence: Pternistis afer swynnertoni, Rhodesia. Tetrastes bonasia, China (?). (See fig. 10).

Heterakis skrjabini Cram 1927, sp. inq.

Synonyms: H. arquata Skrjabin 1916<sub>1</sub>, p. 742—744, Pl. 24, Fig. 11, nec H. arquata Schneider 1866. H. skrjabini Cram 1927, p. 71—72, Fig. 99.

Occurrence: Tinamus sp., Paraguay.

Heterakis spiculata (Cobbold 1861), sp. inq.

Synonyms: Strongylus spiculatus Cobbold 1861, p. 123, Pl. 20, Figs. 7—8. Ascaris strongylina Cobbold 1879, p. 447. H. spiculatus Travassos 1923, p. 38, Subulura strongylina Cram 1927, p. 128, partim (see also p. 77). H. spiculatus Travassos, Freitas & Lent 1939, p. 227.

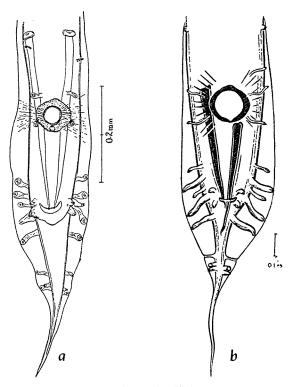


Fig. 10. Heterakis silindae. a, H. silindae, after Sandground (1934). b, H. papillos, after Li (1933). See the text.

According to Cobbold's later identification (1879) Cram (1927, p. 77 and 128) considers this species as belonging to *Subulura*. But his illustration (1861) undoubtedly shows a species of *Heterakis*. It can not be identified with certainty. The species has been mentioned, without description, by Travassos (1923) and by Travassos, Freitas & Lent (1939).

Occurrence: Tinamus sp. (Zool. garden, London), Crypturellus noctivagus and Crypturellus tataupa.

Heterakis stylosa v. Linstow 1907 = Heterakis papillosa (Bloch 1782).

Heterakis tenuicauda v. Linstow 1883.

Synonyms: *H. tenuicauda* v. Linstow 1883, p. 293, Figs. 26—27, Seurat 1918, p. 53—54, Fig. 1, Baylis 1923, p. 11, Cram 1927, p. 73—74, Figs. 100—101.

Occurrence: Alectoris graeca, Ammoperdix griseogularis, Turkestan, Alectoris barbara, Algeria.

#### Studies on Species of Heterakis

\*Heterakis tragopanis Lal 1942 = Heterakis isolonche v. Linstow 1906.

\*Heterakis travassosi Khalil 1932 = Heterakis brevispiculum Gendre 1911.

Heterakis (?) valdemucronata (Molin 1860), sp. inq.

Synonyms: Ascaris valdemucronata Molin 1860, p. 339. H. (?) valdemucronata Cram 1927, p. 74--75.

This species is inadequately described, without illustrations and can not be identified, until new material from the same host is available. Very uncertain whether it is a *Heterakis* in the modern sense.

Occurrence: Proventriculus of Ardea maguari, Brazil.

Heterakis valvata Schneider 1866.

Synonyms: H. valvata Schneider 1866, p. 76, 1 Fig., Travassos 1913, p. 282—283, Pl. 27, Fig. 5, Cram 1927, p. 74, Figs. 102—103.

Occurrence: "Crypturus cupreus") and Crypturellus noctivagus, Brazil.

1) See footnote p. 25.

Heterakis variabilis Chandler 1926 = Heterakis isolonche v. Linstow 1906.

Heterakis vesicularis (Froelich 1791) et auctt. sen. =
Heterakis gallinarum (Schrank 1788). Non H. vesicularis Travassos 1915 =
H. brevispiculum Gendre 1911.

Heterakis vulvolabiata Chandler 1926.

Synonyms: H. vulvolabita, H. vulvolabiata Chandler 1926, p. 620—621, Pl. 32, Figs. 5—8. H. vulvolabita Cram 1927, p. 387, Maplestone 1932, p. 414—415, Pl. 13, Figs. 15—16. H. vulvolabiata Baylis 1936, p. 118.

Occurrence: Arborophila torqueola, India (Zool. garden).

\*Heterakis yamadori Yamaguti 1941 = Heterakis pavonis Maplestone 1932 (?).

Occurrence: Syrmaticus soemmeringi, Phasianus colchicus versicolor, Nycticorax nycticorax, Japan.

## LIST OF BIRDS, IN WHICH SPECIES OF HETERAKIS HAVE BEEN FOUND

(Systematic order and nomenclature mainly after Peters (1931-1937)).

## RHEIFORMES

Rhea americana (L.) H. gallinarum.

#### TINAMIFORMES

Tinamus sp. H. alata, H. skrjabini, H. spiculata.

Crypturellus sp. H. alata.

Crypturellus noctivagus (Wied.) H. valvata, H. spiculata.

Crypturellus variegatus (Gmelin) H. crypturi, H. multidentata.

"Crypturus cupreus" H. arquata, H. valvata.

Crypturellus tataupa (Temm.) H. spiculata.

Rhynchotus rufescens (Temm.) H. brasiliana.

## CICONIIFORMES

Ardea maguari Gmelin H. (?) valdemucronata.

Nycticorax nycticorax (L.) H. pavonis (H. yamadori).

## ANSERIFORMES

Chenopis atrata (Latham) H. gallinarum, H. dispar.

Anser anser (L.) dom. H. dispar, H. gallinarum.

Anser fabalis (Latham) H. dispar.

Chen hyperborea (Pall.) H. dispar.

Nesochen sandvicensis (Vigers) H. dispar (?).

Chloëphaga poliocephala Sclater H. acuticaudata.

Cereopsis novae-hollandiae Latham H. dispar.

Chenonetta jubata (Latham) H. dispar (?) (H. chenonettae).

Cairina moschata (L.) dom. H. dispar.

Tadorna tadorna (L.) H. dispar, H. gallinarum (?).

Anas platyrhynchos (L.) dom. H. beramporia (?), H. dispar, H. isolonche.

Aix sponsa (L.) H. dispar.

## FALCONIFORMES

Sarcorhamphus papa (L.) H. gallinarum.

1) See footnote p. 25.

#### GALLIFORMES

MEGAPODIDAE; Alectura lathami Gray H. bancrofti, H. gallinarum. Macrocephalon maleo S. Müller H. gallinarum.

CRACIDAE; Crax blumenbachi Spix H. nattereri.

TETRAONIDAE; Tetrao urogallus L. H. gallinarum.

Lyrurus tetrix (L.) H. gallinarum.

Dendrogapus obscurus (Say.) H. gallinarum.

Lagopus lagopus scoticus (Latham) H. gallinarum.

Lagopus mutus (Moutin): H. gallinarum.

Tetrastes bonasia (L.) H. gallinarum, H. silindae (?).

Bonasa umbellus (L.) H. gallinarum, H. isolonche (?) (H. bonasae).

Pedioecetes phasianellus (L.): H. gallinarum.

Tympanuchus cupido (L.) H. gallinarum.

Centrocercus urophasianus (Bonaparte) H. gallinarum.

# PHASIANIDAE; Colinus virginianus (L.) H. gallinarum, H. isolonche (?) (H. bonasae).

Odonthophorus capueira (Spix) H. fariai.

Ammoperdix griseogularis (J. F. v. Brandt) H. tenuicauda.

Tetraogallus himalayensis (Gray) H. macroura.

Tetraogallus tibetanus Gould H. altaica.

Alectoris barbara (Bonnaterra) H. tenuicauda.

Alectoris graeca (Meissner) H. gallinarum, H. tenuicauda, H. dispar (?).

Alectoris rufa L. H. gallinarum.

Francolinus gularis (Temm.) H. gallinarum.

Francolinus chinensis Osbeck H. gallinarum.

Pternistis afer (P. L. S. Müller) H. silindae.

Perdix sp. (probably a tinamou) H. brasiliana.

Perdix perdix (L.) H. gallinarum.

Rhizothera longirostris (Temm.) H. interlabiata.

Coturnix coturnix (L.) H. gallinarum.

Arborophila torqueola (Valenc.) H. gallinarum.

Galloperdix spadicea (Gmel.) H. gallinarum.

Ithaginis cruentus (Hardwicke) H. isolonche.

Tragopan satyra (L.) H. bosia, H. isolonche, H. gallinarum.

Crossoptilon manchuricum Swinhoe H. gallinarum, H. isolonche.

Crossoptilon auritum (Pall.) H. isolonche.

Gennæus leucomelanos (Latham) H. gallinarum, H. isolonche.

Gennæus nycthemerus (L.) H. beramporia, H. dispar, H. gallinarum, H. isolonche, H. parva, H. pavonis.

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Lophura rufa (Raffl.) H. isolonche.

Gallus gallus (L.) dom. H. beramporia, H. brevispiculum, H. gallinarum, H. indica, H. pavonis.

Gallus g. bankiva. Temm. H. brevispiculum.

Gallus lafayeti Lesson H. pusilla.

Gallus sonnerati Temm. H. beramporia.

Catreus wallichi (Hardwicke) H. gallinarum.

Phasianus colchicus L. f. div. H. gallinarum, H. isolonche.

Ph. c. chrysomelas Severtz H. isolonche.

Ph. c. satchevensis Pleske H. isolonche.

Ph. c. versicolor (Vieill.) H. gallinarum, H. pavonis (?) (H. yamadori).

Syrmaticus sömmeringi (Temm.) H. gallinarum, H. pavonis (?) (H. yamadori).

Syrmaticus reevesi (I. E. Gray) H. gallinarum.

Chrysolophus pictus (L.) H. gallinarum, H. isolonche.

Chrysolophus amherstiae (Leadb.) H. gallinarum, H. isolonche.

Polyplectron bicalcaratum (L.) H. brevispiculum, H. isolonche.

Pavo cristatus L. H. gallinarum, H. hamulus (?).

Pavo muticus L. H. hamulus.

NUMIDIDAE; Numida meleagris (L.) dom. H. brevispiculum. Acryllium vulturinum (Hardw.) H. gallinarum.

### GRUIFORMES

PSOPHIIDAE; Psophia viridis Spix H. arquata, H. psophiae.

OTIDAE; Tetrax tetrax (L.) H. papillosa.

Otis tarda L. H. gallinarum, H. papillosa.

Chlamydotis undulata (Jacquin) H. gallinarum.

## STRIGIFORMES

Glaucidium passerinum (L.) H. sp.

#### COLUMBIFORMES

Leucosarcia melanoleuca (Lath.) H. bancrofti.

## **PSITTACIFORMES**

Kakatoe leadbeateri Vig. H. gallinarum.

## SUMMARY

I) The species Heterakis gallinarum (Schrank 1788), Heterakis isolonche v. Linstow 1906, Heterakis dispar (Schrank 1790) and Heterakis papillosa (Bloch 1782) have been redescribed, with particular reference to the spicules, which possess the most important distinguishing characters. The name Heterakis gallinarum has been shown to be the correct one for Heterakis gallinae (Gmelin 1790) of authors since CRAM (1927). Otis tarda is recorded as a new host for this species.

2) In fowls and other domestic birds in Europe notably three species of Heterakis have been found: Heterakis gallinarum, with a short and a long spicule, Heterakis isolonche with two long spicules of equal length; and Heterakis dispar with two short equal spicules. A number of species of Heterakis have been listed as synonyms for the first time (in the alphabetical list marked with an asterisk). The species can bee arranged in three groups on the basis

of the relative lengths of the spicules (see Table 8).

3) A critically revised list of species of *Heterakis* in birds, and a host list has been presented. It has been stressed that for a final arrangement of the species new investigations and re-examinations of old material are necessary.

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#### ADDENDUM

In a paper recently received, C.R.LOPEZ-NEYRA (Helmintos de los vertebrados Ibéricos, Tome I—III, pp. I—I2II, 174 pls., Granada, 1947) also deals with species of *Heterakis*. He undertakes the attempt of subdividing the genus in two genera, *Heterakis* s.str. and *Ganguleterakis* Lane, 1914, using as differential character if the spicules are unequal or equal, respectively. It may appear from the present paper that such a subdivision is rather arbitrary, especially so, since the inequality of the spicules is not to the same side in all species, and more or less apparent inequalities are present in every species of *Heterakis*. Characters being used as basis for a separate genus must give an expression of some natural relation. I can not, therefore, accept this subdivision in genera, but prefer, like CRAM (1927), to regard all of the species as belonging to the genus *Heterakis* Dujardin, 1845.

Lopez-Neyra still accepts several of the species which have been shown above to be only synonyms. The following species are treated with more in detail: Heterakis gallinarum (called H. gallinae, with original illustrations, which, however, do not show the most characteristic feature of the spicules), H. tenuicaudata (called Ganguleterakis tenuicaudata var. hispanica, with instructive pictures), found in the new host Alectoris rufa, and Heterakis dispar (Ganguleterakis dispar), with the bad illustration by Fibiger). He is not aware that H. monticelliana is not a synonym of H. gallinarum, but of H. papillosa. The differences which he uses for differentiating his new varieties of H. tenuicauda: hispanica, turquestanica and africana seem to be ascribable to differences in size. I find such a differentiation premature.

# ON THE FEEDING HABITS OF THE SOUTHERN CORMORANT (Phalacrocorax carbo sinensis Shaw)

## IN DENMARK

By F. JENSENIUS MADSEN & R. SPÄRCK

The Cormorant (*Phalacrocorax carbo* L.) is a cosmopolitan species, occurring in a number of races throughout the world: Greenland, Northeast America, Iceland, Europe, Africa, China, Japan, Australia, and New Zealand.

The Cormorant in Denmark. In the first half of the nineteenth century large colonies of the Southern Cormorant (P. c. sinensis Shaw) bred in various localities in Denmark: Bornholm, Zealand, Lolland, Langeland, Funen, and Jutland; in the latter part of the country e. g. on the isle of Vorsø in Horsens' Fjord, and at the lakes near Skanderborg in the middle of Jutland. The Cormorants, however, were condemmed as fish-enemies, as also on account of the damage done to the trees in which they nested. A vigorous persecution of them was therefore commenced. Tens of thousands of birds were killed, and eventually, in 1864-70, the last ones of the large colonies were exterminated. In the last part of the ninetieth century then only a few nesting pairs of Cormorants were found in Northern Jutland and North Zealand, and moreover these may have belonged to the northern race, the Common Cormorant (P. c. carbo L.). Thereupon the only Cormorants met with in this country for many years were occasional visitors, at the Baltic coasts mostly the Southern Cormorant, coming from Germany and the Netherlands, and in the Kattegat mainly the Common Cormorant, otherwise occurring north and west of Denmark.

In 1938, however, the Southern Cormorant again appeared in Denmark as a nesting bird, probably immigrating from the colonies on the Baltic coast of Germany. The first colony, with the number of breeding pairs amounting to a few hundreds, settled at the border of a little lake near Tranekær in the island of Langeland in the Great Belt. In the course of a few years this colony without interference by man migrated to a non-protected wood in the neighbourhood; they were here persecuted in the period before the

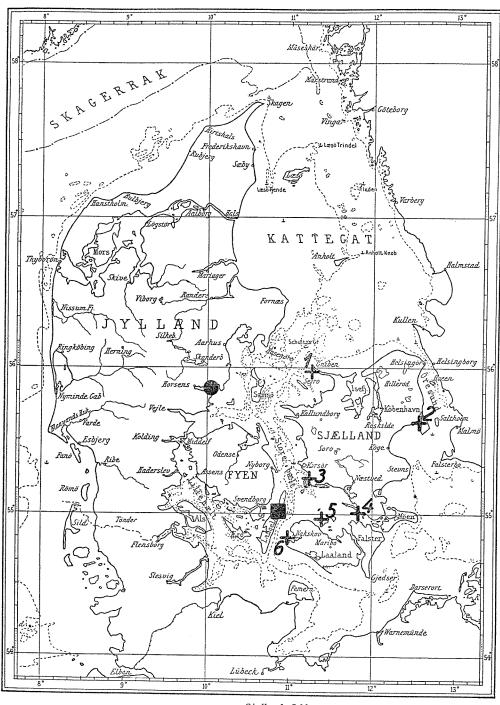
breeding season and the colony disappeared in 1946. Another colony was founded in 1944 on the island of Vorsø in Horsens fjord on the east coast of Jutland, also a bird sanctuary. In this colony the number of breeding pairs culminated in 1947. From this year, in which the number of breeding pairs exceeded 500, the colony again declined and in 1949 only a few breeding pairs were left. The cause of this decline was partly the shooting of birds for the present investigation, partly the Crows, which on a large scale fed on the Cormorant's eggs. In 1948 a colony of a little more than 100 breeding pairs appeared in the small isle of Ormsø, near Skelskør on the west coast of Zealand. In the following year the Cormorants were persecuted in the spring and in 1949 the colony consisted of only a few breeding pairs. In 1949 two new colonies appeared, one in Hønsehals wood near Holbæk on Zealand, one at Ålholm near Nysted on Lolland. The colony at Hønsehals, which at the beginning of the breeding season counted about 75 nests, disappeared again by the end of May; only 4-5 breeding pairs hatched their eggs. There was no shooting in this colony and the disappearance may be due to the many visitors who came to look at the Cormorants, partly also due to the Crows. The colony at Alholm on Lolland in which the breeding pairs arose to upwards of 300 was the only large colony left in Denmark in 1949. It was partly established by Cormorants from Vorsø, as it appeared from some ringed specimens born on Vorsø in 1947. Besides the about 300 breeding pairs of Cormorants in the Ålholm colony there were only a few scattered nests on Ormsø, Vorsø and Hønsehals and perhaps in some other places in 1949.

Banding experiments of the Vorsø colony have shown that the Danish Cormorants wander far about, banded birds from there having been shot in Southern Norway, Great Britain, Germany, Netherlands, France, Spain, Italy Yugoslavia, and North Africa. There exists also a record of a Cormorant banded in the Netherlands and two years later shot in Minnesota in America (Tåning 1944).

The Cormorants in Denmark are, at present, protected in their breeding season, from May the 1st to July the 31st. The fishermen, however, insist on having them persecuted, accusing them of doing considerable damage to the fisheries. Also the foresters want the numbers of Cormorants decimated, since the birds, at their nesting places, ruin the trees by their fæces and especially by their habit of breaking off all twigs of the branches that these may be more comfortable to sit on.

The present paper is an attempt at elucidating the influence of the Cormorants on the Danish stock of fish, and also forms part of the general investigation of the feeding habits of the Danish birds.

Map showing the localities whence the Cormorants examined were taken.



- The Vorsø Colony.
- The Tranekær Colony.
- 1. Sjællands Odde.
- ${\it 2.\ Kalve bodstrand.}$
- 3. Skelskør.
- 4. Vordingborg.
- 5. Fejø.
- 6. Langø.

365 Cormorants have been examined for their food contents. The present investigation is based on an analysis of the stomachs and gullets of altogether 365 birds, killed in the years 1942—48. A considerable number of the birds examined, however, did not contain any food remains. Some of them may have gulped up the contents of their stomachs when they were disturbed by the hunter, others may have been taken in the early morning before they yet had commenced feeding. The Cormorants also do not feed continually. They have a rapid digestion, and—the indigestible remains of fish bones eventually being gulped up more or less completely—their stomachs are empty or very nearly so only a few hours after foraging.

In the statistical analysis below no respect has been paid to birds with empty stomachs, nor to birds in which the contents of the stomachs consisted only of accidental items as e.g. pebbles, bits of twigs or other vegetable remains, or chitinous remains of Crustaceans and Polychaetes, these latter items deriving from the stomachs of eaten, but now entirely digested fishes. Some birds also have been omitted although they contained traces of food fishes, because these have been in a state or quantity insufficient for identification, as e.g. lenses of eyes or particles of vertebrae.

258 birds with recognizable food-remains in their stomachs then remained for the statistical analysis of the composition of the food. The majority of this collection, 189 birds, originated from the colony in Vorsø, shot here in 1945—48 at different times in the period—April to October—in which the colony is inhabited. Of the rest, 45 were shot in the colony at Tranekær in April and May in 1946—47; and the remaining 24 were killed as stragglers in different localities, cf. the map, from the middle of August to the middle of December, in the years 1942—48. Of these latter birds those taken at Skelskør and Vorsø in September seem to have belonged to the Tranekær colony. Those taken from October to December, however, may have been only visitors to Denmark; and one bird shot together with those from Langø also belonged to the other race, the Common Cormorant, and the same may have applied to the single bird from Sjællands Odde.

The material consisted of 191 adult birds and 67 juveniles, large nestlings or fledglings. These have all been treated together in the statistical analysis, since no difference in the food found in the adults and juveniles respectively can be expected, the latter ones being fed with fishes brought them by their parents in their gullets from where the young ones themselves take out the food.

The birds were sent by the hunters intact to the Institute of Game Biology. The decomposition—by the digestive fluids—of the food content thus has continued some time after the death of the birds, so that also fishes which

may have been in the gullets have been so much dissolved that they could not be identified alone on their general appearance, with the exception of eels, but had to be skeletonized. This has often been a very time-consuming procedure. The exactness of the identifications of the fishes, however, has not been influenced by the continued digestion, since all the species of fish found during the present investigation were recognizable on their skeletal parts alone—even on very fragmentary remains. In a similar investigation, made by Steven, 1933, on the food of the Cormorant and Shag in Cornwall, the stomachs were opened and their contents examined immediately after the birds have been killed. A comparison which STEVEN made with a previous investigation on the food af the Shag in the same area, but based on birds, which, like the present ones, had been dead some time before the food content could be recorded, showed, however, that the results obtained in this way were perfectly reliable, as was also to be expected. The continued digestion mostly concerns the soft parts of the food, and not the skeleton, and thus does not influence the number of eaten fishes which can be recorded.

The fishes found in each Cormorant have been counted and measured. Any specimen of fish of which even the slightest trace could be ascertained in the stomachs has been recorded as one eaten. The number of food fishes listed in the tables thus does not show whether an intact fish or only a single identifiable fragment of e.g. a jaw has been present. Remnants of the dental bones of Cod sometimes were the only remains of fish found in the stomachs, and Cod therefore would seem to be recorded too often in comparison with some of the other species of food fishes. On the other hand, a single vertebra or a fragment of such is sufficient for identifying e.g. an Eel or a Mackerel; and, altogether, any heterogeneousness in the frequency of records of food fishes due to varying resistance to the treatment in the stomachs may reasonably be disregarded as insignificant.

In the numerical representation of the results it is impossible to give any statement of the size of the fishes eaten, and small species therefore become too dominant in relation to their actual value in the diet of the Cormorant. The size of every eaten fish, of which traces could be found, has, however, been ascertained as exactly as possible, and the information hereby gained has been used in the representation below of the composition of the food expressed in percentages of weight of the different species of fish consumed.

The results of the investigation are summarized in the tables on pp. 56 and 60. Before the discussion of the results, however, some general remarks on the feeding biology of the Cormorant will be given, and also some references to the records in the literature on the food consumed by the Cormorant in Northern Europe.

The diving and fishing of the Cormorant. The Cormorant fetches its food in the water; and it may therefore seem strange that the bird, apparently, is badly fitted for such a mode of living, its plumage getting wet through in the water, while the plumage of most other swimming and diving birds repels water. But just this feature appears to be advantageous if considered more closely (cf. O. & M. Heinroth 1928 p. 120). Since the Cormorant is a large bird a considerable amount of air would adhere to its body beneath the feathers in the case the plumage was water-repelling and thus would give the bird an inconvenient buoyancy during the chase of the prey beneath the surface. This inconvenience is mainly avoided when the plumage gets wet through. On the other hand, the inconvenience of getting wet causes the Cormorant to stay in the water generally only as long as it is fishing. The bird usually would seem to leave the water as soon as it is satisfied, whereupon it selects a sitting place on a stone, a pole, or the like above the water, and after having shaken off as much water as possible it may sit here for a long time, even for hours, in the wellknown position with extended wings.

The hunting Cormorant while swimming on the surface often, before diving, at short intervals, will dip its head below the water to up over the eyes, and then, in this position, will swim forward looking for prey. When diving the Cormorant may leap right out of the water before gliding headwards, and noiselessly, down, but may also slip head forwards directly under the water, which the bird especially does when it has already been fishing for some time and has become gorged.

The Cormorant keeps its wings close to the body during the dive and swims forward by simultaneous strokes with its webbed feet, whereas, when swimming on the surface, it uses its feet alternately.

The Cormorant would seem to dive usually at depths between I and 3 metres with an average stay under the water for  $\frac{1}{2} - \frac{3}{4}$  of a minute. The longest stay below the water recorded with certainty (Dewar 1924, p. 133) is 71 seconds, and the greatest depth where dived  $9\frac{1}{2}$  m; this, moreover, is the record among the 6000 dives Dewar observed. Blasius, in Naumann 1905 XI p. 60, records that a Cormorant has been observed bringing up a flatfish, thus a bottom fish, in a place where the depth was more than 42 m, and during the dive having been below the surface for a couple of minutes only. The bird in a minute or two could easily have covered the distance of the 40 metres to the bottom and back again and also have had some time for searching the bottom for prey, but, if compared with Dewar's statements, the observation, nevertheless, would seem to be erroneous, at any rate very exceptional. Perhaps, in this particular case, the Cormorant has found the flatfish high over the bottom.

The silvery covering formed by the air bubbles adhering to the feathers of the Cormorant, when swimming below the surface, sometimes has been assumed to make the bird invisible to the fish, but has also, on the contrary, by other authors been assumed to attract the fish, it being said to resemble the flashes of the bellies of the individual fishes in a school.

WARD, who especially studied animals under water, describes (1919 p. 30 ff.) how the Cormorant under water flashes from the black, glossy lustre of its plumage when it twists and turns during the search for fish. WARD suggests that this 'flash' attracts the fish, and describes also how the flash from the head of the Cormorant, when it swims forward in the above mentioned way with the head submerged and looking for prey, may lure a codling or the like up from the bottom. WARD expresses it as follows: 'I do not suggest that the Cormorant puts its head under in order to flash; he does it so as to see below the surface. Incidentally the flash attracts the prey to the bird.' And WARD is of the opinion that this way of fishing is much more efficient for the Cormorant than just diving under and then starting the search for prey.

It may be that WARD is right in his view that fishes may sometimes be attracted by the flashing Cormorant; but, as he himself has shown through his studies of the Cormorant in aquaria, it is the swiftness of the bird under the water which enables it to catch the prey. Its long, flexible neck must also be a great help. That the Cormorant is an able fish-hunter is illustrated from the fact that it may be seen to fetch e.g. Eel upon Eel up in a place where the fishermen believe they are fairly rare. WARD continues thus: 'I watched a Cormorant in Port Erin harbour behave in the manner I have described. Pollack were in the bay. I had fished for an hour, but never touched a fin; the bird came up five times with a nice fish'. But, of course, fish may be numerous in a place even though they do not bite.

The smaller prey is swallowed immediately below the water, while larger fishes are brought to the surface where the Cormorant then turns and twists them in the beak, throws them up into the air and catches them again, all in order to stun them that they will not sprawl too much in the gullet.

The gullet of the Cormorant may be dilated quite incredibly and the same applies to the stomach which is only slightly provided with muscles.

The feeding habits of the Cormorant as known from the literature. Already the old and still used trivial name of the Cormorant in Denmark, Aalekrage (i.e. Eel-crow), imparts an observation on its feeding habit. And so does also its Dutch name, Aalscholver. As will appear from the results of this investigation Eels do form a considerable part of the fishes consumed by the Cormorant in Denmark, but, on the other hand, Eels are just the fish which

most often are seen to be caught, since if they are not quite small, they cannot be swallowed easily under the water, but must be brought to the surface and before swallowing stunned or killed in the manner described above. In other areas the same applies to flatfish. Steven (1933) in his report on 'The food consumed by Shags and Cormorants around the shores of Cornwall (England)' thus states that 40% of the food of the Cormorant in the river-estuaries consist of flatfish; but, nevertheless, he thinks the fishermen in the area may have got an exaggerated impression of the depredation of the Cormorant, writing (p. 289 footnote): 'Because of their shape, flats are difficult fishes to swallow. A bird's efforts to dispose of a large individual, therefore, often attracts the attention of onlookers, whereas ordinary round fishes are swallowed too quickly and easily to be seen and recognized except on very rare occasions'.

In general works on birds it is usually stated that the main food of the Cormorant is fish, but that also some Crustaceans, Crabs and Prawns, are included in its diet. A long, varied list of food fishes can be compiled from the literature. Collett (1921 p. 291) states how in Norway he saw a Cormorant (the Common C.) which was stuffed with several Codlings up to 20 cm in length besides some Rock Wrasses (Ctenolabrus rupestris) Of three Cormorants shot inland he found the one filled with Perchs (Perca fluviatilis), and the other two with 2 and 3 Trouts (Salmo trutta) respectively. Collett further reports a case of a Cormorant which at Aasvær on August 9th 1899 was seen trying to swallow a fish larger than itself, and, when it ultimately succeeded, soon afterwards was seen to waver and to be unable to fly up; eventually the bird fell dead, and when it was opened the swallowed fish proved to be a Wolf-fish (Anarrichas lupus).

KOLTHOFF (cited from EKMAN-BREHM: Djurens Liv 1943) once, at Bohuslen in Sweden, saw a Cormorant with a quite deformed, enlarged neck, and with something protruding from the beak which in vain it tried to swallow. The bird was shot and the prey proved to be a Pollack (Gadus pollacius) almost ½ m long.

In Naumann, Op. cit. p. 60, it is stated that it is unknown whether the Cormorant eats other things than fish, and that the bird prefers bottom forms, but otherwise eats all kind of fish apart from armoured or spiny species ('Panzer-, Kugel- und Stachelfishe'). Of marine fishes taken by the Cormorant (the Southern C.) the following are recorded in Naumann: Eel (Anguilla vulgaris), Father-lasher (Cottus scorpio), Sprat (Clupea sprattus), Flounder (Pleuronectes flesus) and Halibut (Pl. hippoglossus). Of freshwater species besides Eel: Pike (Esox lucius), Perch (Perca fluviatilis), Carp (Cyprinus carpio), Chub (Leuciscus cephalus), and other Cyprinidae ('Weissfische').

WITHERBY (1924 p. 400) states the food of the Cormorant in Great Britain (the Common C.) to comprise: Trout, Eel, Pike, Flounder, Plaice, Sand-launce (Ammodytes), 15-spined Stickleback (Spinachia spinachia), Haddock (Gadus aeglefinus), young Coalfish (G. poutassou), Mullet (Mugil), and Conger, besides occasionally Crustaceans, Crabs and Prawns.

JOURDAIN (1940 p. 5), on the basis of records from British sources, states the food fo the Common Cormorant in Britain to include 'Codling, young Coal-fish, Haddock, Whiting, Wrasse (to 13½ ins.), Mullet, Conger-eel (to 2½ ft.), also flat-fish such as Plaice, Flounder, etc., Sand-eel (Ammodytes), 15-spined Stickleback and other small species', and of freshwater species 'chiefly Trout, Eel (to 15½ ins.), Pike (to 13½ ins.), etc.'. And p. 9 JOURDAIN gives the food of the other race, the Southern Cormorant, as 'Almost entirely fish, both fresh- and salt-water species. Marine forms include nearly all kinds not too large, especially Sprats (Clupea sprattus) and flat-fish, such as Flounder, Plaice, etc., also Cottus scorpio, Halibut, etc. Fresh-water species include Eels, Carp, Pike, Dace, Perch, and Bleak, but Eels are favourite prey'.

SALOMONSEN (1935 p. 59) says that the food of the Common Cormorant in the Faroes consists mainly of one year-old *Gadus* spp, and *Cottus*.

FABER (1822 p. 53) states that the Common Cormorant in Iceland 'ist der ärgste Feind des Cottus scorpius'.

Collinge (1924—27 pp. 216—218) in his work 'The food of some British birds' on the basis of an examination of the stomach contents of 43 birds from all seasons and from four different localities: Aberdeen coast, West coast, Cumberland coast, and Cornwall coast, came to the result that the food consumed by these Cormorants consisted of 98.86% (volumen percentage) of animal matter, of which 95.80% were food fishes, mostly Cod, but also Haddock and Whiting, and 0.75% remains of Crustaceans, about which Collinge, however, says that they were 'probably obtained from the stomachs of the fishes eaten', whereas 2.31% of the animal matter could not be identified. The remaining 1.14% of the stomach contents consisted of remains of algae.

Steven (1933) as mentioned above investigated the food consumed by the Common Cormorant of Cornwall, England. He had at his disposal 27 birds with recognizable food remains in their stomachs, killed, mostly in the riverestuaries, in the months January to February, and July to December. In all the stomachs he found the following fishes: 9 Herring (Clupea harengus), I Sprat (C. sprattus), 2 Eels (Anguilla vulgaris), I Conger (Conger vulgaris), I Grey Mullet (Mugil chelo), 5 Father-lashers (Cottus sp.), 4 Dragon-fish (Callionymus sp.), 31 Gobies (Gobius spp.), 17 Flounders (Pleuronectes flesus), 11 Plaices (P. platessa), 7 Dabs (P. limanda), 12 unidentifiable flatfishes, I Gurnard (Trigla sp.), 9 Pogges

(Agonus cataphractus), 6 Ballan Wrasses (Labrus berggylta), I Corkwing Wrasse (Crenilabrus melops), and 2 Gold-spiny Wrasses (Ctenolabrus rupestris).

HARTLEY (1948 p. 375) records the food found in 9 Common Cormorants shot inland, in December, at the lake Windermere in Westmorland, North England, to be: 3 Perchs (*Perca fluviatilis*), 2 Trouts (*Salmo trutta*), 4 Chars (*S. willoughbyi*), 2 Pikes (*Esox lucius*), and I Eel (*Anguilla vulgaris*). WARD (Op. cit. p. 29) tells about a Common Cormorant 'which contained respectively a Conger 2 ft. 6 in. in length, a Grilse weighing 3 lb. 2 oz., and six Trout weighing 2 lb. 4 oz.'.

Outside Europe investigations on the food of the Cormorant have been made in S.W.-Australia, by Serventy (1938), and in freshwater in New Zealand, by Falla & Stokell (1945). As the fishes eaten in these areas are quite other species than those occurring in Europe it should only be mentioned that in the freshwaters of New Zealand species of Eels are the most important food items, and that in S.W.-Australia 20—60% of the food consumed by the Cormorant is considered to comprise fishes of commercial value.

The literature also contains a few records of birds as food items for the Cormorant. Collett (1894 p. 323) thus reports a Norwegian newspaper communication according to which a Cormorant killed on March 15th 1891 at the mouth of Oslo Fjord should have contained the remnants of a bird in its stomach. Collett puts a query to this formation, but it may be true; in fact, if considering some other information in the literature there is no reason at all to doubt it. Portielje (1927) thus states that the Cormorant in Balkan sometimes catches flying Swallows. In Zoological Gardens Cormorants may also be seen snatching after Swallows flying low over them,—but Cormorants in Zoos, as will be known, are also used to being fed with fish thrown to them. Kortland (1940 p. 402) reports that the Cormorant in the Zuider Sea is often seen eating ducklings. This may happen if a duckling accidentally is carried beneath the water by the diving Cormorant (cf. Portielje Op. cit. p. 109), and a Cormorant in this way may perhaps be led to take ducklings also on the surface (?).

Mammals may also occasionally be eaten by the Cormorant. KORTLANDT (Op. cit.) thus reports that he has reliable information of a Cormorant who caught and swallowed a Water-vole (*Arvicola amphibia*). This, of course, is not surprising. JOURDAIN (Op. cit.), however, after enumerating the various species of fishes found in the Common Cormorant in Great Britain, adds: 'Kitten, II ins. long, once found in stomach'. And how this happened is more difficult to imagine.

The food of the Cormorant in Denmark, as will appear from the table p. 60, is composed of only a small number of species of fish, smaller, e.g., than that found by Steven (Op. cit.) for the Cormorant of Cornwall, in spite of the

much larger material of birds which has been examined from Denmark. This of course is dependent on the richer fish fauna at the Atlantic coast of England in comparison with the inner Danish waters where the Danish Cormorants forage. It is also evident that a considerable number of species of fish other than those actually found during the present investigation are normally included in the diet of the Cormorant in Denmark. Of marine species e.g.: Plaice, Sprat, Gold-spiny Wrasse, Gobies, and Whiting; and of non-marine species probably all, at any rate when they have reached a certain size. These species, however, are eaten only in so small a percentage that it is quite accidental whether they are listed or not in a material of the size as the present one. Just as it is due to mere accident that a species as e.g. the 15spined Stickleback has been recorded as a food item. Further material of Cormorants from the same areas may displace the results achieved from the present material; but, due to the large number of birds examined, there can not be any doubt that such a displacement of the percentage figures stated should be only insignificant. This especially applies to the results found on the material of Cormorants from the Vorsø colony, when treated separately, the number of birds examined from this colony being large, and, since they were taken at the nests, containing food fishes from all the hunting areas visited.

In the summary p. 56 of the results of the investigation the material is grouped according to locality and time of capture. Statements are given of the number of birds in which each species of food fish has been found, and besides of the number of individuals of each species of fish present in all the birds. The table p. 60 gives in the first place a representation of the material treated as a whole, and, secondly, a representation of the material from Vorsø treated separately.

Pronounced freshwater species (Rudd and Roach), as will appear from the summary, are found in only 7 of the examined birds. All these birds were from the Vorsø colony and they probably got the fishes from the lakes in Jutland situated at a distance of 25—30 kilometres from the colony. Three of the birds were large nestlings, and one of these was also fed with a small Eel besides the four Roaches found in its stomach. It cannot be excluded that some of the Eels recorded were taken in freshwater. The material shows, however, that this may apply only to a smaller number, since the Eel sare often present in the stomachs together with marine species or remains of their food in form of fragments of Prawns or the like.

It is thus evident that the Cormorant in Denmark takes most of its food in the sea, as was also to be expected, or, expressed in percentages, that only about 2% of the food of the entire stock of Cormorants in Denmark originate from inland waters.

Table 1. Summary of the Results of the investigation on the Food
In total 365 birds were examined, only 258 of which, however, contained identifiable food items in their stomachs.

was found, the ciphers in italics the total

	1							7743 1			phers			ne tota
	The whole material	Vorsø												
Date:	37		15-18/ <sub>4</sub> 1948			10/ <sub>6</sub>	13/ <sub>6</sub>	17/ <sub>5</sub>	<sup>9</sup> / <sub>7</sub> 1948	1	15-20/ <sub>8</sub>	1		
Number of birds:	258	13	31	17	17	4	26	8	16	II	21	7	18	189
Name of food fish:														
Eel Anguilla anguilla L.	98,127	<b>5</b> <sub>5</sub>	<b>5</b> <sub>6</sub>	8,10	89	44	11,19	<b>5</b> <sub>5</sub>	13,14	<b>6</b> <sub>6</sub>	8,16	2,	<b>3</b> <sub>5</sub>	78,,,,
Viviparous Blenny Zoarces viviparus L.	64,129	511	<b>5</b> <sub>7</sub>	34	12		11 <sub>23.</sub>	I	<b>3</b> <sub>5</sub>	<b>4</b> <sub>5</sub>	920	<b>2</b> <sub>2</sub>	921	53,01
Herring Clupea harengus (L.)	<b>64</b> <sub>253</sub>	12	1229	424	5,16		I		1,	<b>3</b> <sub>6</sub>		ĭ	<b>5</b> <sub>33</sub>	<b>33</b> <sub>123</sub>
Cod Gadus morrhua L.	<b>46</b> <sub>57</sub>	<b>3</b> <sub>3</sub>	13 <sub>15</sub>	<b>2</b> <sub>2</sub>	<b>3</b> <sub>3</sub>		4 <sub>4</sub>	<b>2</b> <sub>2</sub>		I		I,	6,10	35 <sub>41</sub>
Father-lasher  Myoxocephalus scorpius (L.)	16,19	<b>5</b> <sub>7</sub>		<b>3</b> <sub>3</sub>			<b>2</b> <sub>2</sub>	1,			ĭ			12
Flounder Platessa flesus (L.)	12,43	I		I,			<b>2</b> <sub>4</sub>	<b>2</b>	ĭ	I	424			12 <sub>43</sub>
Mackerel Scomber scombrus L.	10,15	A STATE OF THE STA	A		24		$\mathbf{I}_{I}$				<b>1</b> <sub>3</sub>	I,	<b>2</b> <sub>2</sub>	7,,,
3-spined Stickleback Gasterosteus aculeatus L.	1227		514					I,						<b>6</b> 5
15-spined Stickleback Spinachia spinachia (Sauv.)	<b>3</b> <sub>3</sub>													
Butterfish Pholis gunellus (L.)	I	The state of the s	NAME OF THE PROPERTY OF THE PR											
Perch Perca fluviatilis L.	<b>3</b> <sub>3</sub>													
Rudd Scardinius erythropthalmus (L.)	<b>4</b> <sub>7</sub>			I	I <sub>I</sub>		<b>2</b> <sub>5</sub>			the state of the s				<b>4</b> <sub>7</sub>
Roach Rutilus rutilus (L.)	33		I		I					OT A COURT A COURT AND A COURT	ı			<b>3</b> <sub>3</sub>

## On the Feeding Habits of the Southern Cormorant

## of the Southern cormorant (Phalacrocorax carbo sinensis Shaw) in Denmark

In the summary regard is paid only to these latter. The fat ciphers indicate the number of birds in which the food fish number of fish found in all the birds.

fish number of fish found in all the birds.											
	Tra	neka	er	In total from Tranekær	Kalvebod- strand	Skælskør	Vordingborg	Langø	Lolland	Fejø	Sjællands Odde
Date:	<sup>23-26</sup> / <sub>4</sub> 1947	<sup>28</sup> / <sub>4</sub>	<sup>5</sup> / <sub>5</sub> 1946		<sup>12</sup> / <sub>8</sub> 1943	10/ <sub>9</sub> 1943	16-28/ <sub>9</sub>	<sup>25</sup> / <sub>10</sub> 1948	<sup>10</sup> / <sub>11</sub> 1942	<sup>15</sup> / <sub>11</sub> 1945	<sup>18</sup> / <sub>12</sub> 1944
Number of birds:	30	8	7	45	I	4	12	3	I	2	1
Name of food fish:	Manager and the second		-								
Eel Anguilla anguilla L.	4,	22	<b>6</b> <sub>8</sub>	12 <sub>14</sub>		<b>1</b> <sub>3</sub>	<b>5</b> <sub>6</sub>	12	ı		
Viviparous Blenny Zoarches viviparous L.	I,	<b>2</b> <sub>6</sub>		<b>3</b> <sub>7</sub>		<b>4</b> <sub>15</sub>	46	Commission of the commission o			
Herring Clupea harengus (L.)	<b>24</b> <sub>107</sub>	3,2	<b>1</b> <sub>5</sub>	<b>28</b> <sub>124</sub>			<b>3</b> <sub>6</sub>				
Cod Gadus morrhua L.	<b>2</b> <sub>4</sub>	<b>2</b> <sub>3</sub>		<b>4</b> <sub>7</sub>			<b>3</b> <sub>3</sub>	ı		<b>2</b> <sub>3</sub>	<b>1</b> <sub>2</sub>
Father-lasher Myoxocephalus scorpius (L.)							<b>3</b> <sub>3</sub>	T,	and the second s		
Flounder Platessa flesus (L.)							An a a a a a a a a a a a a a a a a a a a		TO THE PERSON AND AND AND AND AND AND AND AND AND AN		
Mackerel Scomber scombrus L.							3,4				
3-spined Stickleback Gasterosteus aculeatus L.	THE CONTRACTOR OF THE CONTRACT				<b>1</b> 6		<b>4</b> <sub>5</sub>		ı		
15-spined Stickleback Spinachia spinachia (Sauv.)		I		I,			I,				
Butterfish Pholis gunellus (L.)							I,				
Perch Perca fluviatilis L.								<b>3</b> <sub>3</sub>			
Rudd Scardinius erythropthalmus (L.)	Market and the second										
Roach Rutilus rutilus (L.)						ALALA ALA DO CALADO DE CONTROLA ALARA			Account a distribution of the commodutors		

The species of fish which is present as food item in the largest number of Cormorants is the freshwater Eel, which occurs in no less than 38% of all the examined birds with recognizable food remains in their stomachs, and in 41%, if the material from Vorsø is considered separately. The next-commonmost species are the Viviparous Blenny, occurring in 25% of all the birds and in 28% of the Vorsø birds alone, and the Herring, which occurs in 25% of all the birds, but only in  $17\frac{1}{2}\%$  of the birds from Vorsø, the considerable difference in the figures in this case being due to the fact that the 30 Cormorants from Tranekær 1947, almost half of the whole material of Cormorants from other places than Vorsø, had fed almost exclusively on Herrings. The fourth commonmost food fish is the Cod, present in about 18% of the stomachs, and then there is a distinct break to the fifth commonmost species, the Fatherlasher, which is found only in about 6% of the birds. Then follow Flounder in 5-6%, Mackerel and 3-spined Stickleback each in 3-4%, and then the other recorded food fishes, all in a percentage occurrence below about 2. (See the second and seventh columns in the summary p. 60).

Eels, as also Viviparous Blennies and Cods, would appear to be more staple food items than Herrings, dependent on the fact that the latter species is included in the diet of the Cormorants mostly when these have access to spawning schools, in which case, on the other hand, Herrings, for the time being, are almost solely fished. While 24 of the 30 adult Cormorants taken in the Tranekær colony in April 1947 have fed on altogether 107 Herrings, only one of these birds, besides a Herring, has also caught a Viviparous Blenny. In the representation of the percentage occurrence of Herrings this material from Tranekær consequently may give a wrong impression of the importance of Herrings as food for the Cormorant throughout the season in comparison with the other food species. The best representation of the relative importance of the different food fishes recorded for the Cormorant as a whole in Denmark—as already mentioned—is obtained by considering the Vorsø material separately.\*)

<sup>\*)</sup> In 1943 a preliminary report on the food of the Cormorant in Denmark was placed before the Department of Fisheries. This report, which forms the basis of the information of the feeding habit of the Cormorant given in the handbook 'Danmarks Fiskerier', was based on an examination of the 24 birds available at that time, of which, however, only 17 contained any food remains. In all 50 food fishes were counted in the 17 stomachs, viz. 21 Viviparous Blennies, 8 Eels, 6 Herrings, 3 Cods, 3 Father-lashers, 7 Three-spined Sticklebacks, and 1 Butterfish. The picture of the feeding habits of the Danish Cormorants obtained through this material thus is not quite in agreement with that found through the study of the larger material now available. Viviparous Blennies, and also Sticklebacks were considered much more important as food items than was actually the case.

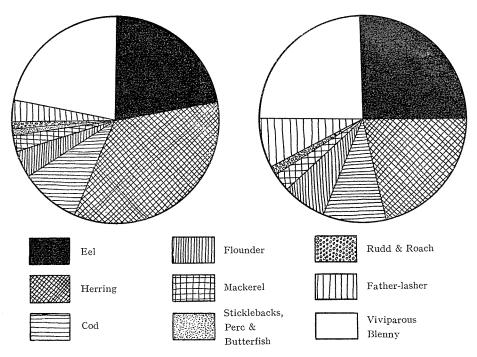
If the total number of specimens eaten of each food fish is considered, instead of the frequency of occurrence in the stomachs, it will be seen that Herrings are eaten in the largest number, Herrings in the whole material amounting to 37% of all the fishes eaten, and in the Vorsø material alone to 27%. Then follow Eels and Viviparous Blennies, amounting to 18-19% in the whole material and 22% in the Vorsø material respectively. Cods amount to 18-19%, and Father-lashers to about 3%, whereas the number of Flounders eaten amounts to 5% of the fishes in the whole material and  $9\frac{1}{2}\%$  of the fishes eaten by the Vorsø material alone.

The above numerical representations of the results obtained may be of interest if compared with other food investigations represented in a similar way. The relative importance in the diet of the Cormorant of the different food fish, however, can only with difficulty be estimated on the numerical representation alone, since several of the species are of very different size. But, as already mentioned, the size of each fish recorded in the stomachs has been estimated as exactly as possible even if only fragmentary remains were present. It hereby appeared that the lengths of the Eels eaten varied from about 10 cm to 60 cm, generally from 15 cm to 30 cm, while the average length seems to have been 20-25 cm. The average length of the Viviparous Blennies eaten is 20 cm or a little more, and the same applies to the Cods, Fatherlashers, and Mackerels. The average weights of all these food fishes have been estimated at about 125 g. The three only Perchs recorded were somewhat larger, but have also been treated as if they weighed 125 g on average. The Herrings eaten are on average smaller than the previously mentioned food fishes; their average weight may have been 90 g. Most of the Flounders eaten were fairly small and, together with the Butterfishes, Rudds, and Roachs, they have been estimated at 75 g on average. The 3-, and 15-spined Sticklebacks, finally, were estimated at 10 g on average.

Herrings, Eels, Viviparous Blennies, and Cods are the staple food of the Cormorant in Denmark. On the basis of the above estimates of the average weights of the fishes eaten, the percentage value in weight of each of the species of fish recorded as food for the Cormorant in Denmark has been calculated. If considering the whole material the composition of the food is as follows: 34% Herring, 22% Eel, 22% Viviparous Blenny, and 10% Cod; Father-lasher and Flounder each 4%, Mackerel 2½%, and each of the other species less than 1%. If the Vorsø material is considered separately the composition of the food is: Eel and Viviparous Blenny 25% each, Herring 22%, Cod 10%, Father-lasher 8%, Flounder 6%, Mackerel 3%, and the other species less than 1% each. (See the fifth and tenth columns in table 2 p. 60, and the diagrammatic representation p. 61).

	ii.	-		the results material: 25		Tabular representation of the results on the material from Vorsø alone: 189 birds								
Food fish:	Number of birds in which found	Percentage of birds in which found*	The total number of fish found	Numerical percentage of the fish eaten	Estimated weight percentage of the fish eaten	Number of birds in which found	Percentage of birds in which found	The total number of fish found	Numerical percentage of fish found	Estimated weight percentage of fish eaten				
Eel Anguilla anguilla L.	98	38%	127	18,5%	21,5%	78	41,3%	101	22,1%	24,9%				
Viviparous Blenny Zoarces viviparus L.	64	24,8%	129	18,9%	22%	53	28%	ioi	22,1%	24,9%				
Herring Clupea harengus (L.)	64	24,8%	253	36,8%	34,5%	33	17,5%	123	26,9%	21,8%				
Cod Gadus morrhua L.	46	17,8%	57	8,3%	9,7%	35	18,5%	41	9%	10,2%				
Father-lasher Myoxocephalus scorpius (L.)	16	6,2%	19	2,8%	3,3%	12	6,4%	15	3,3%	7,7%				
Flounder Platessa flesus (L.)	12	4,7%	43	6,3%	4,4%	12	6,4%	43	9,4%	6,4%				
Mackerel Scomber scombrus L.	10	3,8%	15	2,2%	2,5%	7	3,7%	11	2,4%	2,7%				
3-spined Stickleback Gasterosteus aculeatus L.	12	4,7%	27	3,9%	0,4%	6	3,2%	15	3,3%	0,3%				
15-spined Stickleback Spinachia spinachia (Sauv.)	3	1,2%	3	0,4%	0,04%									
Butterfish Pholis gunellus (L.)	I	0,4%	ı	0,1%	0,07%									
Perch Perca fluviatilis L.	. 3	1,2%	3	0,4%	0,5%									
Rudd Scardinius erythropthalmus (L.)	4	1,6%	7	1,0%	0,7%	4	2,1%	7	0,9%	0,6%				
Roach Rutilus rutilus (L.)	3	1,2%	3	0,4%	0,3%	3	1,6%	3	0,7%	0,5%				

<sup>\*</sup> It should be noted that these ciphers of percentage refer only to the 258 birds with recognizable food remains in their stomachs; if the percentage were represented in relation to the whole material including the 107 'empty' birds the ciphers would be only about half as large.



Diagrammatic representation of the food of the Cormorant in Denmark, to the left when the whole material is considered, to the right when the Vorsø material is considered alone.

The fishes eaten by the Cormorant are mostly bottom forms, or such which usually go near the bottom. Herring and Mackerel are decidedly pelagic forms, but they often occur in dense schools near the surface and in the spawning time go near the coast, and thus become an easy prey to the Cormorant.

A seasonal change in the food. During the year there is some change in the composition of the food of the Cormorant. In the summary p. 60, however, no regard has been paid to this fact, which is considered justified since the change is only slight, and the material not large enough to allow a separate treatment of each month and thus a numerical representation of the change. The change also sets in in winter time when by far the greater part of the Cormorants have left. Eels, Viviparous Blennies, and Cods, as already mentioned, are constant elements of the food throughout the year, and the same applies to Father-lashers. Herrings, as also pointed out above, are included among the fishes caught by the Cormorant when spawning schools go near the coast, and thus are mostly taken in the months of spring and autumn. Mackerels are absent from the food of the Cormorant during the winter as

this fish at that time has left the Danish waters. Flounders also have not been found in the stomachs of Cormorants taken in the winter, corresponding with that at this time they will remain in deeper waters than during spring and autumn. As to the freshwater species they also are not persecuted in the winter when the Cormorants are fewer in number and mostly visitors staying by the sea.

The Cormorant is a voracious bird and sometimes, when considering its own size, may swallow very large prey. Instances of this have already been given in the above, and in one of the recorded cases its voracity even cost the bird its life. Concerning the size of the Eels taken the Common Cormorant is known to take Conger-Eels as long as 75 cm (WITHERBY a. o.), and in the present material of the somewhat smaller Southern Cormorant some few of the birds contained Freshwater Eels measuring 60 cm in length. Such catches consequently seem to be fairly common. Viviparous Blennies and Mackerels often measured 30 cm, of the Cods one measured about 40 cm; and in the above a case of a Common Cormorant taking a Pollack almost 50 cm long is recorded. The flatfishes found to have been eaten during this investigation were all small; Lumsden & Haddow (1945), however, tell about a Cormorant (presumably the Common C.) which swallowed a Plaice I feet (30 cm) long.

The number of fish found in a single bird sometimes was fairly great. The stomach and gullet of one of the adult birds examined were thus enormously dilated through the more or less intact remains of about 20 Herrings, all about 15 cm long. In another adult bird remains were found of 11 Viviparous Blennies of which 4 may have been about 30 cm long and some of the others nearly of the same size. Usually only single specimens of Eels were present in the stomachs, though in one of the adult birds from Vorsø there were in the gullet 2 whole Eels about 25 cm long and in the stomach the remains of no less than 7 more measuring from 15 cm to 20 cm.

The Cormorants, like many other birds, may often specialize on a special kind of food. It goes without saying that an investigation of the feeding habit like the present one cannot show whether such an individual feeding specialization is a common phenomenon or not. In about one fifth of the birds, both adults and juveniles, more than one kind of food fish were, however, recorded. An adult bird shot at Vordingborg in September thus contained the remains of five different species, viz. I Eel about 25 cm long, 2 Viviparous Blennies of about 10—15 cm, I Father-lasher measuring 15 cm, I Butterfish, and I Three-spined Stickleback.

The food-requirements of the Cormorant. Feeding experiments with Cormorants in captivity have proved that the bird in a single meal may dispose

of an incredible number of fish, which has contributed to the exaggerated concept often met with as to its food requirements. WARD (1919 p. 29) says about the Common Cormorant that 'though a bird only weighs six to eight pounds, it consumes at least fifteen pounds weight of fish a day', and WARD further adds that 'some authorities place the total considerably higher'. Collinge (Op. cit.) says about some of the specimens of the Common Cormorant examined by him that they 'averaged 8 lb. 4 oz. in weight' (i.e. 3¾ kg), and were full all of fish and that 'the average weight of such was 4 lbs. 10½ oz.' (slightly more than 2 kg). Collinge further says: 'About three and a half hour is necessary for the digestion of this bulk of food, and presuming that it is repeated three times a day, the total bulk of fish taken would weigh slightly under 14 lbs., and this, we believe, to be a fairly accurate figure. If we take the average of Robinson's and Ward's figures, we get 16 lbs., or from all three a mean of just over 15 lbs. 4 oz.'

That the Cormorant would require a daily food ration twice its own weight sounds incredible. No doubt the above records are based on exceptionally large meals. In the course of the present investigation some of the large meals actually found in the stomachs and gullets have been weighed; and when the stomach and gullet of the Southern Cormorant are filled to their capacity their content would seem to weigh not more than 3/4 kg. Predatory animals. like the Cormorant, fill themselves to the utmost when occasion arises, but at other times they may have to fast for a long period of time. A more correct estimation of the daily food requirement of the Cormorant than that given by the above authors must be gained through an examination of the amount of fish required to keep captive birds in good health. Specimens of the Southern Cormorant in the Copenhagen Zoo get a daily fish ration of 5 Herrings, corresponding to somewhat less than half a kilo of fish, or to about one fifth of the body weight of the bird; and this is considered a large food ration for a bird of that size. The Heinroths (1928 p. 123) report how they once brought up some large nestlings of the Southern Cormorant. They fed them 3-4 times a day with as many fish as they would take, and under this condition they ate about I kg fish on average per day. The Heinroths also state that Cormorants in Zoos have been known to breed on a daily food ration of 3/4 kg fish.

Serventy (1938 p. 298), on the basis of information obtained from Wetmore concerning Cormorants kept in an aviary and fed with as many fish as they would take, calculated that under these conditions the Cormorants ate a daily amount of fish corresponding to 17% of their own body weight. This corresponds with the food ration given the Cormorants in the Copenhagen Zoo. Since young birds when growing may be supposed to require more food than the adult ones, this figure also corresponds to the amount which Hein-roth found eaten by the large nestlings. Serventy, however, with a reference to Nice (1938), states that this amount of fish, 17% of the body weight of the bird, is a much larger daily consumption than that of other fisheating birds of a corresponding size. Therefore, he is of the opinion that it may be doubted that Cormorants at liberty would eat as much, since they would then themselves have to procure the food, and consequently would not eat more than just the amount required for being satisfied.

It is difficult to say whether or not this is really the case. Serventy's view seems well founded when considering the great voracity of captive Cormorants in comparison with other birds of similar size. On the other hand, it might be supposed that the food requirements of the Cormorant at liberty would be greater than in captivity, due to the waste of energy in hunting and catching the food fishes, especially in the breeding season in which each adult bird also has to procure food for a couple of nestlings.

If the daily food requirement of the Southern Cormorant is estimated at half a kilo of fish, which would be rather near the truth, then a stock of 100 Cormorants in Denmark would consume 50 kilo fishes daily, viz. 10½—12½ kg Eels, 11—12½ kg Viviparous Blennies, 10—17 kg Herrings, 5 kg Cods, 1½—4 kg Father-lasher, 2—3 kg Flounder, 1½ kg Mackerel, and about 1 kg of other fish.

Assessment of the influence of the Cormorant on the fisheries in Denmark. Concerning the influence of the Cormorant on the sea fisheries the following information can be given: the Herring is one of the more, if not the most important of the food fishes, constituting  $^1/_5$  to  $^1/_3$  of the food of the Cormorant. Herrings, however, are so abundant in Danish waters that thousands of Cormorants might feed on them without the slightest effect on the fishery of man. The same applies to the Mackerel. The question of damage to the fisheries, however, becomes more intricate if the consumption of Eel is considered. The total number of Cormorants in Denmark at present seems to be about 300 breeding pairs, these stays in Denmark for 6-7 months on average, and each pair generally produce 3 young ones. The annual taxation of such a population of Cormorants on the Danish fish stock would amount to about 100 tons of fish, or maybe somewhat more (100 - < 150 t). Of this quantity Eels would constitute about twentyfive tons or somewhat more. This may seem a formidable figure, but, on the other hand, it is less than 1% of the annual catch of Eels by man in the Danish waters inside the Skaw, with which quantity the amount eaten by the Cormorants may reasonably be compared, since the birds hunt over wide areas.

Whether the presence of the Cormorant colony in Vorsø has had any appreciable influence on the stock of Eels in Horsens Fjord cannot be ascertained, since the annual catch of this fish by man in the Fjord has risen after the Cormorant settled on the isle. But considering this fact the decimation of the stock of Eels, if any, can only have been negligible.

As to the other food fishes of the Cormorant in Denmark it can be noted that the Viviparous Blenny is not regarded fit as food for man and is only used as bait. The about 25—40 tons of Viviparous Blennies which a Cormorant stock of the above mentioned size would consume annually thus are of no economic importance; and, since the Viviparous Blenny in its diet competes with the Eel, its decimation might be considered beneficial to the fishery of man.

The Father-lasher is a predatory species of no economic importance, and is by man considered injurious to his fisheries. The about 5—10 tons of Father-lashers which the said stock of Cormorants consumes annually thus may be placed at its credit.

Of Cods 10-15 tons would be consumed and of Flounders about 5-10 tons. Large amounts, indeed, but insignificant compared with the quantity which man himself fishes in the same areas.

The fishermen often complain that the Cormorants choose for sitting places the poles of their seines, and from there go fishing among the captured fishes, and, besides eating part of these, hunt the others around so that they may escape from the seine or be damaged in the nets. To prevent this the fishermen drive nails into the poles so that the Cormorants cannot gain a foothold on them. That the Cormorant may steal fish also from lines is illustrated by the fact that two of the Cormorants examined here had fishing hooks in their stomachs. The Cormorant may also, while fishing, injure or destroy a number of fishes which escapes it; and WARD (Op. cit.) even considers this number to be larger than the number actually devoured.

The Southern Cormorant preys mostly on fish 15 cm or more in length. Steven (Op. cit.), besides investigating the feeding habit of the Common Cormorant, also investigated the feeding habit of the Shag (P. aristotelis L.), within the same area, and found that the latter species, as distinct from the former, predominantly fed on Sand-eels (Ammodytes). Lumsden & Haddow's investigation on the Shag in the Clyde Sea area confirmed that the most important food item of this species in the sea were Sand-eels. That Sand-eels are not generally included in the diet of the Cormorant is borne out by the present investigation, in which Sand-eels have never been found in the stomachs. On the other hand, skeletal remains of Sand-eels, owing to their delicacy,

would be more rarely recorded in the stomachs than the skeletal remains of the other food fish, even if Sand-eels were regularly eaten. The list which Witherby (Op. cit.), gives of the diet of the Cormorant also includes Sand-eels. It can, however, only be exceptional that this fish is taken by the Cormorant. Sand-eels may be too swift for the Cormorant to catch, and further the fish is probably too small to be accepted by the Cormorant as prey. Their small size also explains why Gobies have never been recorded as food in the present material of Cormorants, though this fish otherwise is most vigorously persecuted by the other fish-eating diving birds in Denmark. Steven (Op. cit.), records Gobies from three of the 27 Cormorants which he examined, in one of them a number of no less than 26; but Gobies can not be a normal element in the diet of the Cormorant.

It can be concluded from the present investigation that the Southern Cormorant usually does not take fish below a length of about 15 cm, though it may happen. In 3-5% of the examined Cormorants remains were found of Three-spined Sticklebacks which measure only about 6-7 cm. The stomach content of a Cormorant taken in Kalvebodstrand in August e.g. consisted solely of 6 Three-spined Sticklebacks, and it thus could be ascertained that the bird had actually caught and eaten the Sticklebacks. In most of the other cases, however, the possibility cannot be excluded that the Sticklebacks may have been present in the stomachs only as a secondary element, derived from the stomachs of predatory species eaten, like Cod or Father-lashers. That this, at any rate, applies to some of the Sticklebacks found in the stomachs seem quite certain, and it may apply to most of the records of this species. HARTLEY (1948) as said above recorded the stomach contents of 9 Cormorants shot at an inland lake in England, and, in addition, he examined the contents of 5 Shags from the same locality. The staple food of the Shags proved to be Three-spined Sticklebacks, whereas such were not found at all in the Cormorants. That the above mentioned Cormorant from Kalvebodstrand had taken to Sticklebacks may be due to the fact that in this locality other species of fish are not easily accessible, whereas the Sticklebacks are very abundant.

The Cormorant does not usually eat Crustaceans. In the literature it is often stated that part of the food of the Cormorant, though only a smaller part, normally consists of Crustaceans such as Crabs and Prawns. Steven (Op. cit. p. 288 footnote) e. g. states that several of the stomachs of Cormorants examined by him contained Shrimps, Prawns, etc., adding that they 'could not possibly have been derived from the stomachs of the fishes eaten'. It may be, of course, that a Cormorant, very exceptionally, might take such food, but otherwise the supposition that Crustaceans form part of the food of

the Cormorant is unfounded. It is true that remains of Crustaceans are fairly common in the stomachs, which may give the impression that the Cormorant itself will hunt and eat such prey. But, whenever a more substantial amount of Crustacean remains have been present in this material there have also been remains of larger fishes, as e.g. Cods and Father-lashers, which do feed partly on Crabs and Prawns. A stomach, e. g. which contained the remains of a Shore-crab (Carcinus maenas) with a shield about 35 mm broad also included the remains of a Father-lasher; and in other birds fairly large Crabs and Prawns have been found in the stomachs of only partly digested fishes. In some stomachs chitinous fragments of Crustaceans have been present alone, not together with any recognizable remains of fish; but this is due to the greater resistance of the chitin to the digestive fluids. The chitin of the Crustaceans will be quite soft when the lime is dissolved, and thus the remains of Crabs etc. do not cause the bird to vomit. The size of the Crustaceans also is decidedly against the supposition that the Cormorants themselves would have fed on them.

The strong, chitinous jaws of the large Polychaeta (*Nereis* spp.) which likewise are an important fish food are even more common in the stomachs of the Cormorant than the remains of Crustaceans. In one stomach as many as 50 large Nereis jaws were present.

In about 15% of the stomachs examined,—and in nearly every bird taken in Vorsø in the months September—October—remains of the strongly chitinized forepart of the Cod parasite, Lernaea branchialis, were also present; in one stomach e. g. remains of no less than 12 specimens. Only in some stomachs there were, besides these chitinous remains, also remnants of Cod, or other fishes, from which the parasites might originate, which shows how much longer chitin may remain in the stomachs than the skeletal remnants of the food fishes. In a juvenile bird from Vorsø chitinous remnants were present of: the Cod parasite Lernaea, Crabs, and a Hydroid colony, besides jaws of Nereis, and lids of the large snail the Common Welk, and the only remains of fishes were a few eye lenses.

Pebbles and objects other than fish found in the Juvenile Cormorants are probably derived from mock-hunting. In the above it was stated that no difference as to the contents of food fishes in the stomachs of adult and juvenile birds respectively could be expected. Nevertheless, it could generally be decided from the stomach contents alone whether the bird in question had been adult or juvenile (nestling or fledgling), the juvenile Cormorants practically always containing a number of pebbles. (Compare table 3 p. 68-69 showing the various items found in the Cormorants from Vorsø 13/6 1946, 14 of which

		Adult birds:														
	Serial number of bird:		78	79	80	81	82	84	88	89	90	91	94	96	98	
	Contents of birds stomachs:															
	Eel Anguilla anguilla L.	ı	NA COLUMN TO THE PROPERTY OF T	THE SAME PURIOR AND	I			ı		The same of the sa		**************************************	3	5	3	
	Viviparous Blenny Zoarces viviparus L.					3	The state of the s	I	I	ı	3	4			r	
	Herring Clupea harengus (L.)								W A A STATE OF THE REAL PROPERTY AND A STATE OF THE PROPERTY AND A STATE OF THE PROPERTY AND A STATE OF THE PROPERTY AND A STATE OF		10					
	Cod Gadus morrhua L.		r				I									
	Father-lasher  Myoxocephalus scorpius (L.)													Office and the state of the sta		
	Flounder Platessa flesus (L.)			-				-								
	Mackerel Scomber scombrus L.		William Annual American	THE POLICE CONTRACTOR AND ADDRESS OF THE POLICE									7			
	Rudd Scardinius erythropthalmus (L.)			r	And a street of the street of						And the second s					
	Annelida															
n fish achs	Crustacea			×		×			×	×						
	Mollusca														~	
	The cod parasite  Lernaea branchialis L.	-	-	The second secon					ı		and the same of th					
	Vegetable matter: Sea Grass (Zostera), Wrack (Fucus), etc.		The second secon	PRIOR DE LA CONTRACTION DE LA	And de la company of the property of the party of the par	THE STATE AND ADDRESS OF THE PERSON.	A Addison to Provide the State of the State	×	×		A STATE OF THE PERSON NAMED IN COLUMN 1					
	Bits of twigs															
	Pebbles															

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## the birds from Vorsø $^{13}/_{6}$ 1946.

	Large nestlings:																
Serial number of bird:	83	85	86	87	92	93	95	97	99	100	101	102	103	104	105		
Contents of birds stomachs								,					- Address - Addr				
Eel Anguilla anguilla L.	4	And the second s		I		I		I	I			r					
Viviparous Blenny Zoarces viviparus L.								3		I					I		
Herring Clupea harengus (L.)																	
Cod Gadus morrhua L.			and the second s							I	I						
Father-lasher Myoxocephalus scorpius (L.)		And the state of t					I								ı		
Flounder Platessa flesus (L.)	3													I			
Mackerel Scomber scombrus L.		ALL THE PROPERTY OF THE PROPER											1				
Rudd Scardinius erythropthalmus (L.)									4		A 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1						
(Annelida				×	×	×	×					×	×	×	×		
Crustacea		×						×		×	×				×		
Mollusca	×						×										
The cod parasite  Lernaea branchialis L.				I		The second secon		THE OWNER WAS ASSESSED.	A STATE OF THE STA		I		ı				
Vegetable matter: Sea Grass (Zostera), Wrack (Fucus), etc.				×	The state of the s			And the state of t		And the second s		×		×			
Bits of twigs		×				×	×	×	×			×		×	×		
Pebbles	2	2		30	60	20	100		20	10		80	50	10	20		

From fish stomachs

were adults and 15 juveniles). In a single juvenile stomach as many as 120 pebbles measuring up to 16 mm in diameter may sometimes be present; and one stomach also contained a small stone,  $29 \times 26 \times 8$  mm. Besides the pebbles the juvenile birds usually also contained some more or less macerated remains of twigs; in three stomachs e. g. twigs measuring 7.5, 11, and 13 cm respectively were found.

In the adult Cormorants, on the contrary, pebbles or remains of twigs were present only rarely; never more than 5 pebbles in a single bird, and that amount only in one case. The pebbles found in the young birds, at any rate for the greater part, thus cannot have been obtained from the parents. From the tables which Falla & Stokell (1945 p. 325) give of the contents of the stomachs of Cormorants from New Zealand it appears that also in this material the juveniles, in contrast to the adults, contained pebbles and plant remains.

The supposition that the pebbles should have any significance to the preparing of the food in the stomach, as e.g. in gallinaceous birds, can be dismissed at once, owing to the fact that the stomach walls of the Cormorant are far too poorly provided with muscles. Steven (Op. cit.) in the stomachs of the Shag sometimes found large numbers of otoliths accumulated; he ventured to set forth the supposition that they were possibly used for breaking up the food, but, as stated for the pebbles, they cannot have such a function. Otoliths have never been found accumulated in the stomachs of the present Cormorants; only in single cases fragments of one or a few otoliths of Cod were found without other vestiges of the fish.

The explanation of the presence of the pebbles and the twigs in the juvenile birds is no doubt that they have been swallowed accidentally during the bird's 'play' with them. The nestlings already when very young begin to make tentative catching movements and later on to 'mock-hunt' such objects as they can get hold on in the nests, like twigs, and small stones carried to the nests among the sea-weed which partly constitutes the nesting material. When the young are fledged and leave the nests they rely for another couple of weeks on food brought them by their parents; and during this time they themselves 'mock-hunt' various objects on the ground or the bottom of the sea in the vicinity of the colony before they start real fishing, and thereupon, at an age of two months or slightly more, leave the colony. In some of the juvenile birds remains of hazel shells were found, and these as well as the larger number of pebbles no doubt have been found in such fledglings which have 'mock-hunted' on the ground. The fact that the juvenile Cormorants leave the colonies definitely when they themselves start fishing makes it rather certain that the young examined during this investigation, which were all taken at the nests, have been of an age at which they did not fish themselves. (For more detailed information on the behaviour of the Cormorant see KORT-LANDT (Op. cit.).

The few pebbles found in the adult Cormorants may have been derived from the stomachs of fishes eaten, or may have been eaten accidentally during the catching of a bottom fish. The twigs found in the adults may have been swallowed accidentally when breaking off the twigs of the branches on which they sit.

FALLA & STOKELL (Op. cit.) in the stomachs examined of juvenile Cormorants from freshwater in New Zealand found quite a large number of larvae of Trichoptera, whereas only small numbers of such larvae were found in the stomachs of the adults. Falla & Stokell were of the opinion that the presence of these insect larvae in the young could not be explained alone as derived from the stomachs of the fishes eaten and therefore suggested a difference in the feeding habit of the juvenile and the adult Cormorants respectively. The explanation may, however, be that these larvae, which build for themselves a case of sand and grit or vegetable matter, were swallowed accidentally during the 'play' of the juvenile birds with them, like the pebbles found in the young Cormorants examined here. Chitin, as shown above, may remain in the stomachs for a long time, and thus the accumulation of the numerous insect larvae might find a reasonable explanation, many of them probably also deriving from fish stomachs. Although the young Cormorants in this way get a lot of insects in their diet they cannot be said actually to have fed on insects.

How the parents feed and water their young. The nestlings in the first time after hatching are fed by their parents with a regurgitated fluid of an already much digested stomach content, the parents carefully taking the head of the young in their lower beak and then pouring the fluid into them. In this investigation the stomach of a single, small, naked nestling, which weighed only 86 g, was also opened for examination. The stomach and whole gullet, which parts of the intestinal system occupy nearly the whole body cavity of the small nestlings, were found to be full of a fine porridge-like substance, in which, however, also a few chitinous fragments of an Isopod and of a Prawn were found, as also a few vertebrae of an Eel, besides a macerated bit of a twig, about 25 mm long.

Somewhat larger nestlings themselves take out their food of the gullet of their parents. That the parents will sometimes gulp up the fishes on the edge of the nest, and the nestlings then take them there, according to Portielje and Kortlandt (Op. cit.) never occurs. Kortlandt also—during his

2300 hours of observations in a Cormorant colony, saw that fish, or fish remains, which were gulped up and accidentally fell on the edge of the nests were always removed by the birds with obvious disgust.

The Cormorants sometimes water their nestlings. KORTLANDT (Op. cit.) says, however, that it is only some few Cormorants which do so; and nor do all the young ones know how to receive the water. The adults fill their gullet and mouth cavity with water and squirt it in a fine jet over the nestlings, and when these open their beaks the water is squirted directly down into their gullet.

H. Madsen (1946) described how in Vorsø for some days he took care of some young Cormorants from a nest which was blown down, and how, since the weather was extremely hot, he tried to give them water to drink. The Cormorants, however, would not take the water, but in spite of this, Madsen says, drops of water were seen hanging from the point of their beaks the whole day. When the drop grew so large that it was almost falling the bird would shake its head with a vigorous cast and fling off the water. Madsen wondered from where all the water came and says that, though making inquiries, he was not able to get any satisfactory explanation. The explanation, however, is simple: In the hot weather the young Cormorants had gaped so that the evaporation from their respiratory tract might keep down their body temperature (cf. Portielje 1927 p. 109), and the evaporated humidity then condensed on their upper beak as a 'drop of perspiration'.

Parasites etc. Attention may finally be drawn to the fact that a very considerable part of the Cormorants examined were found to be infested with parasitic *Nematoda* in their stomachs and gullets, in birds with only a small quantity of stomach content especially in the proventriculus. In the adult birds the infestation was almost 100%, and sometimes the parasites (presumably *Contracoecum spiculigerum*) were present in very large numbers, in one bird thus between 100 and 150, in another no less than 200.

A periodical shedding of the cuticle of the ventriculus is known to take place in many species of birds. In seven of the stomachs examined here a more or less advanced shedding of the cuticle of the ventriculus was observed. In all these cases the stomachs were entirely or almost empty.

Each of the Cormorants examined was weighed, and the maximum weight recorded for an adult Southern Cormorant without stomach content was 3300 g for a very fat, not one year old male shot in the middle of October 1945.

Summary of the assessment of the feeding of the Southern Cormorant in Denmark in relation to the fisheries. If summarizing the influence of the

Cormorants on the fisheries in Denmark it cannot be disputed that these birds eat quantities of fish — although not so many as often believed. It must be admitted that no small part of these fishes are species of a certain economic importance to man. The damage which may be done to the sea fisheries is, however, not so important as often supposed. For species as Cod, Herring, Viviparous Blennies and freshwater fish the amount found in the stomachs of the Cormorant is so inconsiderable as compared to the stock of these fishes that the damage cannot be considered significant. As regards the Eel the quantities devoured by the present stock of nesting Cormorants constitute about one per cent of the yield of the Eel fishery in Danish waters inside the Skaw. It must, however, be realized that the actual damage is smaller than this figure seems to indicate. For many of the Eels eaten by the Cormorants would never have been caught by the fishermen anyway, but would either have escaped their gear or been devoured by other enemies. Consequently the damage caused by the Cormorants can be estimated to represent much less than one per cent of the fishermens catch. Hence the damage is not so great as to justify an extermination of the Cormorants, although it would be reasonable to keep the size of the population controlled. One or two colonies ought to be allowed to exist, particularly the one on the isle of Vorsø, in accordance with the will of the founder of this sanctuary.

The Cormorant colonies in Denmark have hitherto foraged mainly on the sea; hence the damage done to the freshwater fisheries have not been of any importance here. Otherwise such damage might be considerable. It may be supposed that it is mainly the same individuals which, having specialized on freshwater fishing, will visit lakes again and again. Consequently, by shooting such individuals it will be possible to prevent damage done to freshwater fisheries without exterminating a colony of Cormorants otherwise feeding on sea fishes to which the damage, if any, is of minor importance.

## POSTSCRIPTUM

After this paper went to press the stomach contents of half a hundred Cormorants from the colony at Ålholm have been examined. The fishes found to be eaten were of the same species as more commonly occurring in the above presented material and were present in about the same percentages. No new species of fish was added to those already recorded as food for the Cormorant in Denmark,

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