# Ceratothoa steindachneri (Isopoda: Cymothoidae) new to British waters with a key to north-east Atlantic and Mediterranean Ceratothoa

# T. Horton

The University of Reading, Whiteknights, PO Box 228, Reading, RG6 6AJ. E-mail: t.horton@reading.ac.uk

This paper presents the first record of *Ceratothoa steindachneri* from Cornwall, making it the first resident species of the fish-parasitic isopod family Cymothoidae in Britain. The host is *Echiichthys vipera* (Trachinidae) the lesser weever fish, the isopod attaching to the host tongue. A complete redescription and reillustration for *C. steindachneri* is given, and a neotype is selected for the species *Ceratothoa parallela*. A key to the north-east Atlantic and Mediterranean species of *Ceratothoa* is included, with a brief illustrated account for each species.

#### INTRODUCTION

Cymothoid isopods are ectoparasites of marine, fresh, and brackish water teleost fish. The records of cymothoids from elasmobranchs probably represent trawl transfers (Brusca, 1981). Cymothoids parasitize numerous families and species of fish, including many of commercial importance. Cymothoids attach externally, occur as more intimate ectoparasites in the buccal-cavity/gill-chamber, or burrow inside the fish to develop in a pouch. Species of the family Cymothoidae are rarely found in the cool and cold temperate latitudes (Brusca, 1981). Thus the recent discovery of cymothoids attached in the buccal cavity of lesser weever fish (Echiichthys vipera (Cuvier), Trachinidae) in Whitsand Bay, Cornwall, is unusual. This discovery reveals the first established population of any cymothoid in Britain and represents a new host and range extension of Ceratothoa steindachneri Koelbel,

Identifying known species of cymothoids is highly problematic and, as a result, the taxonomy of the group is far from clear. Original illustrations of species of cymothoids are frequently inadequate and superficial, often consisting of a single dorsal view of a single adult female. Original descriptions are also often insufficient, describing characters known to be highly variable or polymorphic, whilst the more important taxonomic characters, such as mouthparts and pleopods, are omitted. Thus, although descriptions and illustrations of most of the seven Mediterranean and north-east Atlantic species exist, they are in need of revision. Furthermore, an identification key to the *Ceratothoa* in these regions is lacking.

This paper contains a thorough redescription of the female, male and pullus secundus of *C. steindachneri*, and includes a key to the *Ceratothoa* in the north-east Atlantic and Mediterranean. A full synonymy and information on the geographical range and host specificity for each of the species featured in the key is also provided.

## MATERIALS AND METHODS

The majority of specimens of *Ceratothoa steindachneri* were obtained in 1996 by B. Okamura from lesser weever fish (*Echiichthys vipera*) in Whitsand Bay, Cornwall (NHM reg. nos. 2000.1823–1828). Comparisons were made with specimens identified by J.P. Trilles at the MNHN, Paris (reg. nos MNHN-Is28-33), and specimens taken from *E. vipera* in the collections of the Paris Museum (reg. nos MNHN-Is5696 & MNHN-Is5697) and Natural History Museum (reg. nos NHM 1999.1295-1301). Holotypes were examined of all species in the following key.

Segments of the pereon (pereonites), coxae (coxal plates) and pereopods are numbered with Roman numerals. Segments of the pleon (pleonites) and pleopods are numbered with Arabic numerals. The anterior (or ventral) lamella of the pleopods is taken to be the exopod, the posterior (or dorsal) lamella, the endopod. Sex and life stage of the specimen is given. Sizes are indicated both by the scale bars on the illustrations and in the text where necessary. Complete synonymy, and information on geographic range and host preferences are provided.

# GEOGRAPHIC RANGE

The geographic range covered by this work extends from as far south as Senegal in north-west Africa, around the coast of the Mediterranean, and as far north as Britain.

# Genus Ceratothoa Dana, 1852

Ceratothoa Dana, 1852: 303; Schiædte & Meinert, 1883: 332; Bowman, 1978: 217; Brusca, 1981: 177; Bruce & Bowman, 1989: 2.

Codonophilus Haswell, 1881: 471.

Rhexana Schicedte & Meinert, 1883: 289.

Cteatessa Schiædte & Meinert, 1883: 296.

Meinertia Stebbing, 1893: 354.

Rhexanella Stebbing, 1911: 179.

Not Ceratothoa; Dana, 1853: 747; Richardson, 1905: 236; Schultz, 1969: 155; Kussakin, 1979: 287. (=Glossobius Schiœdte & Meinert, 1883.)

#### Remarks

Two species were originally assigned to *Ceratothoa* by Dana in 1852; *Cymothoa gaudichaudii* Milne-Edwards, 1840 and *Cymothoa parallela* Otto, 1828. The type species for this genus must therefore be one of these two. The lectotype of *C. gaudichaudii* in the MNHN, Paris, is badly damaged (Trilles, 1972b). A male specimen at the MNHN also has a type label, but from its size it cannot be the specimen described by Milne-Edwards (1840). It is likely that this was found with the now damaged female lectotype. The type material of *C. parallela* was cited by Schicedte & Meinert (1883) to be deposited at the Museum of Göttingen '(Otto, Mus. Vratisl.—Specim. Typ.; Mus. Goting.)' but is no longer extant. For a provisional diagnosis of the genus see Bruce & Bowman (1989).

Three species of the genus *Ceratothoa* parasitizing the Exocoetidae and Hemiramphidae were dealt with in detail in Bruce & Bowman (1989). Two monotypic genera were synonymized with *Ceratothoa*, namely *Cteatessa retusa*, and *Rhexana verrucosa* (placed in *Rhexanella* by Stebbing (1911) and also synonymized in Bruce & Bowman, (1989)).

Ceratothoa poutassouiensis (Brian, 1939) has been mentioned in two papers, Brian (1939) and Penso (1939). Both authors state that it is found in Gadus potassou, however it is described inadequately, and, although it appears in two figures in Penso (1939), these are insufficient to describe the species. There is no mention of the location of type material in either paper. Brian (1939) states that 'this species of Meinertia deserves to be described as it seems to be a new species, I hope to be able to publish the description of this species which I call Meinertia poutassouiensis'. Due to the lack of holotype, adequate description or illustration, this is deemed to be a nomen nudum.

# Ceratothoa steindachneri Koelbel, 1878 Figures 1–4

Ceratothoa steindachneri Koelbel, 1878: 403; Schiœdte & Meinert, 1883: 364; Carus, 1885: 443; Rokicki, 1984: 1–220; 1985: 95; Trilles et al., 1989: 294; 1999: 6; Trilles, 1979: 257; 1994: 127; Bruce & Bowman, 1989: 2.

Meinertia steindachneri Montalenti, 1948: 36; Trilles, 1968: 131; 1972a: 1215; 1972b: 1237; Trilles & Raibaut, 1971: 76; Dollfus & Trilles, 1976: 822; Capapé & Pantoustier, 1976: 202.

*Ceratothoa gobii* Schiœdte & Meinert, 1883: 356; Carus, 1885: 443; Trilles, 1994: 119.

Meinertia gobii Montalenti, 1948: 36.

#### Material

Atlantic Ocean. (NHM reg. nos 2000.1823–1828) United Kingdom, Whitsand Bay, Cornwall ( $50^{\circ}20'N$  04°14′W). Otter trawl over sandy bottom at depths of 4–14 m. Found in buccal cavity of *Echiichthys vipera* (Trachinidae). MNHN Collection: Is 29, 30, 31—Agay, Var, France ( $43^{\circ}26'N$  06°51′E), from *Serranus hepatus*. Holotype material, see below.

#### Type material

Holotype female (length 23 mm, width 9 mm) is in the Naturhistorisches Museum, Vienna (reg. no. NHMW 6230), from Lissabon.

## Description of female—(Figures 1A–K & 2A–G)

Length 15–23 mm, width 7.8–9.0 mm, body index (length/width) 1.88–2.24 (mean 2.03) (holotype 2.42). Width greatest at pereonite IV/V. Body oval to rounded, very stocky. Colour in alcohol tan/ivory, with occasional chromatophores around coxal plates (Figure 1A,B).

Cephalon: cephalon width 1.88–2.66 times length (mean 2.24). Rounded anteriorly following line of anterolateral margins of pereonite I to form blunt pointed rostrum which

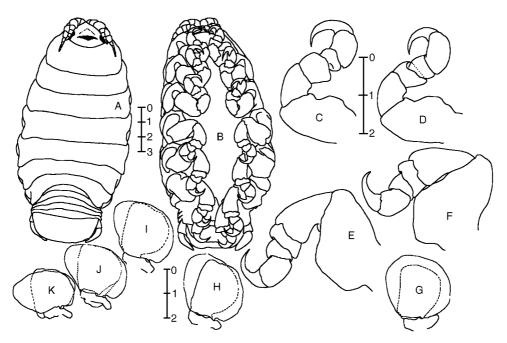


Figure 1. Ceratothoa steindachneri (ovigerous female): (A) dorsal view; (B) ventral view; (C-F) pereopods I, II, VI & VII; (G-K) pleopods 1–5. Scale bars in mm.

Figure 2. Ceratothoa steindachneri (ovigerous female): (A) antenna; (B) antennule; (C) maxillule; (D) maxilla; (E) mandible; (F) maxilliped; (G) pleotelson and uropods. Scale bars in mm.

does not protrude between antennae. Distinct dorsal curve towards rostrum at the level of the eyes. Eyes small, hidden by antennae, but distinct outlines (Figure 1A,B).

Antennule extending to middle of eye, composed of seven articles; first three articles in some specimens expanded and dorsoventrally flattened; group of sensory setae on ventral side on the anterior margin of the last four articles (Figure 2B). Antennae extending to posterior margin of cephalon sometimes to the middle of pereonite I; comprising 10–12 articles (Figure 2A).

Maxillule simple with three terminal, recurved spines, two long and one short (Figure 2C); medial lobe of maxilla with five recurved spines, partly fused to lateral lobe, with eight spines; both lobes covered with setae (Figure 2D). Last article of mandible palp with setae on anterolateral margin (Figure 2E). Maxilliped of ovigerous female composed of three articles, and weakly segmented basal article (Figure 2F); article one with lamellar oostegital lobe; a second, smaller oostegital lobe arising from the basal article; oostegital lobes bordered by numerous plumose setae. Palp article three with five spines (three recurved, larger spines, and two slender smaller ones which are not shown in Figure 2F). Labrum simple, crescent shaped.

Pereon: pereonite I with anterolateral angles extended to anterior margins of eyes; Pereonite I longest, pereonites II-V shorter and equal in length but increasing in width to a maximum at pereonite V. Pereonites VI and VII decreasing in width and length, becoming progressively more rounded and concave to incorporate the pleon (Figure 1A). Coxae rounded, compact, never produced, not reaching the posterior margins of their respective segments, (Figure 1A).

Pereopods I–III increasing gradually in size; bases without carinae. Pereopod IV-VII, with square carinae on bases, progressively more expanded posteriorly (Figure 1C-F).

Pleon: pleonites 2-4 equal in length and width. Pleonite 5 longer than preceding pleonites, with slight trisinuate border with pleotelson. Pleotelson wider than long (average 2.3 times as wide as long) (Figure 2G), widest at base. Pleopods simple without accessory folds or lamellae, decreasing in size posteriorly (Figure 1G–K).

Uropods extending to, or slightly beyond posterior margin of the pleotelson if stretched out. Exopod ramus shorter and wider than endopod ramus; both rami with convex lateral margins, that of exopod more exaggerated (Figure 2G).

Description of male (Figure 3A-M)

Body = 4.75 - 5.3 mm(mean=5.02 mm);10-12 mm(mean=11.0 mm) long. Body index=2.1-2.4 (mean=2.13).Similar to female except for the following: body less rotund and stocky, more rectangular. Anterolateral margins of pereonite I less produced. Antennae less robust, sometimes reaching the posterior margin of pereonite I, comprised of up to 13 articles (Figure 3C). Pleopod 2 with an appendix masculinum (Figure 3F); penes present between pereopods VII.

Description of pullus secundus (Figure 4A-S)

Body length=1.5 mm, width=0.75 mm. Mouthparts similar to those of the male, except mandibular palp is composed of three elongate articles with two long terminal setae on article three (Figure 4D–G). Pereopods I-VI simple and elongated, without carinae, spines increasing from I-VI (Figure 4H-M). Antennule comprised of seven articles and adorned with a number of long setae on articles one, two, five, six and seven (Figure 4C); antenna is comprised of 15-18 articles (Figure 4B). Pleopods 1-3 have long setae on both exopod and endopod with four short bristles on the basis (Figure 4N-P); pleopods 4-5 similar but without setae on the endopods (Figure 4Q-R). Both rami of the uropods have long setae along margins, and short spines on margin of the pleotelson (Figure 4S).

# Remarks

According to Bruce & Bowman (1989), species of Ceratothoa can be grouped according to their pereopod morphology. A typical feature of the genus is a prominent expansion of the basis of the posterior pereopods. Bruce & Bowman (1989) state that 'Most Ceratothoa species... have this character, but... it is only weakly developed in C. steindachneri Koelbel 1878 (see Trilles, 1972)'. The latter is not supported by the present study. This comment that the expansion in C. steindachneri was only weakly developed was probably taken from the illustrations given by Trilles (1972), which fail to adequately emphasize this character.

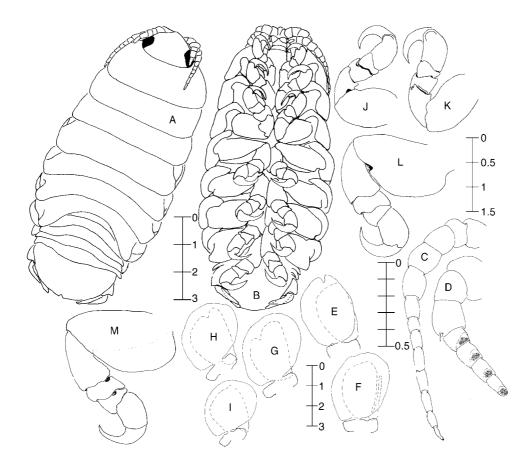
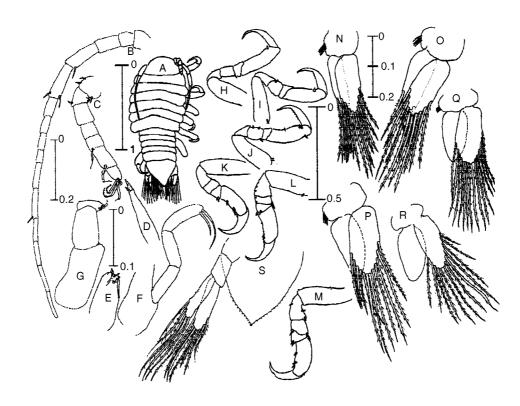


Figure 3. Ceratothoa steindachneri (male): (A) dorsal view; (B) ventral view; (C) antenna; (D) antennule; (E–I) pereopods I, II, VI & VII; (J–M) pleopods 1–5. Scale bars in mm.



 $\label{eq:Figure 4. Ceratothoa steindachneri} \begin{tabular}{l} Figure 4. Ceratothoa steindachneri (pullus secundus): (A) dorsal view; (B) antenna; (C) antennule; (D) maxillule; (E) maxilla; (F) mandible; (G) maxilliped; (H-M) pereopods I-VI; (N-R) pleopods 1-5; (S) pleotelson and uropods. Scale bars in mm. \\ \end{tabular}$ 

There are some slight variations between the specimens collected in Britain, and those found on a different host (Serranus hepatus) from the coast of France. For instance, the anterolateral margins of pereonite I are produced anteriorly by varying amounts and can possess dorsal ridges on the shoulders. Variation is also observed in the number of articles of the antenna and in the degree of expansion and dorsoventral flattening of the first three articles. One specimen was examined with eight and nine articles of the antennae. It is not uncommon for the number of articles to be unequal, but these are unusually low numbers. For figures of the pullus primus stage see Trilles (1972a).

Ceratothoa gobii, Schicedte & Meinert, 1883, in the Museum of Comparative Zoology, Harvard (MCZ), has only been recorded once, from Messina, Italy, on Gobius niger, and Pomatoschistus minutus (Gobiidae). One of the specimens re-examined was taken from the intestine of the fish and has been identified as a male C. parallela (MCZ 3708). The other specimen, is the holotype (MCZ 3707). The only description of C. gobii is that of Schiædte & Meinert (1883). It seems likely from examination of the holotype and the description that the species could be synonymized with C. steindachneri. However, until further material is collected from the family Gobiidae, this species is retained.

#### Distribution

The species was first collected by Steindachner (described by Koelbel in 1878) in the Atlantic ('Mare Atlanticum, Ulysipponem'). Schiædte & Meinert (1883), later described it from the Mediterranean and Atlantic, ('ad Ulisipponem...ad Nizzam...ad Villafrancam'). The geographical range has not been fully elucidated, but records exist from Tunisia (Trilles & Raibaut, 1971), Tabarka, on the northern coast of Tunisia (Capapé & Pantoustier, 1976), Bay of Kotor, Yugoslavia (Radjukovic et al., 1985), Montenegro, Adriatic (Trilles et al., 1989), Casablanca, Morocco (Trilles, 1979; Dollfus & Trilles, 1976), La Rochelle, Agay (Var) (Trilles, 1972b), and the Mediterranean (Trilles, 1968). The species is reported here for the first time in British waters.

#### Hosts

Koelbel (1878) first noted C. steindachneri on Pagri vulgaris (Sparidae). It has also been reported from Serranus cabrilla, S. hepatus, S. scriba, (Serranidae), Diplodus annularis, D. vulgaris (Sparidae), Raja asterias, R. polystigma, R. albas (Rajidae) although the records from Rajidae may be a result of trawl transfers and have yet to be verified.

The new host Echiichthys vipera (Trachinidae) has never before been reported as being parasitized by C. steindachneri, and the geographical range of C. steindachneri was not previously reported as extending into British waters. Increases in sea temperatures off the south-west coast of Britain may explain the recent discovery.

## Key to the north-east Atlantic species of Ceratothoa

- Prominent expansions of the merus of some or all of the pereopods (Figures 5B & 6B) ......3
- 2. Expansions of the basis of pereopods VI and VII on both upper and lower edges (Figure 6G); body distinctly parallel sided not round or oval (Figure 6D)
- Expansions on the pereopods VI and VII on the lower edge only. Body distinctly elliptical, not parallel sided,

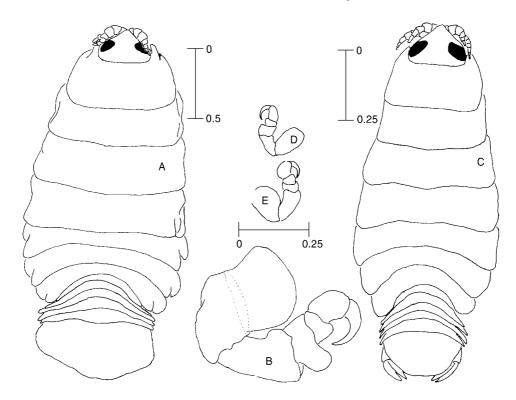


Figure 5. (A) Ceratothoa oxyrrhynchaena, (Holotype, reg. nos NHMW 6216); (B) pereopod VII; (C) Ceratothoa capri (reg. nos NHM 1961:8:25:4); (D) pereopod I; (E) pereopod VII. Scale bars in mm.

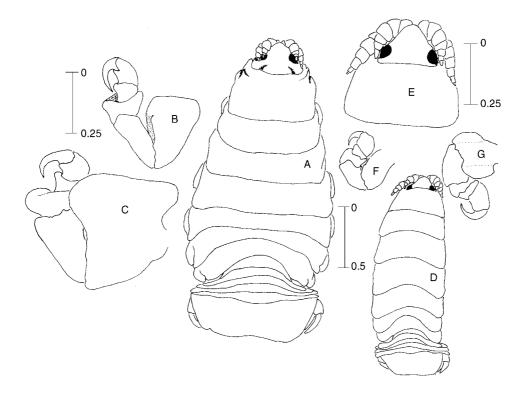


Figure 6. (A) Ceratothoa collaris, (reg. nos NHM 1963:3:10:2-5); (B) pereopod I; (C) pereopod VII; (D) Ceratothoa parallela (reg. nos NHM 1911:11:87790); (E) cephalon; (F) pereopod I; (G) pereopod VII. Scale bars in mm.

- 3. Posterior margin of pleonite 5 strongly trisinuate (Figure 7C) ...... 4
- Posterior margin of pleonite 5 not trisinuate, either smooth or weakly bisinuate ...... 5
- 4. Pleotelson much wider than long and as wide or wider than pereonite VII. Prominent merus expansions on pereopods I-III, less prominent on pereopods V-VII.
- Pleotelson wider than long but not as wide as pereonite VII. Very prominent expansions of the merus on pereopods I-III, not significant on pereopods IV-VII. Body oval, widest as pereonite V ...... C. oestroides
- 5. Cephalon deeply curved towards rostrum at the level of the eyes (Figure 1A). Pereopods without prominent expansions on the merus. Expansion of pereopod VII basis not reaching level of propodus
- Cephalon not curved towards rostrum. Prominent merus expansion on all pereopods, most noted on pereopod VII. Very prominent expansions of the basis on pereopod VII reaching the level of the propodus ..... 6
- 6. Pleotelson not wider than pereonite VII, body rectangular in shape. Cephalon deeply immersed, shoulders of pereonite I level with anterior margin
- Pleotelson wider than pereonite VII, body almost triangular in shape. Cephalon not completely immersed, (shoulders of pereonite I reaching level of

General remarks. Figures of Ceratothoa capri, C. italica, C. oestroides, C. oxyrrhynchaena, C. steindachneri and C. parallela can be found in Trilles' paper covering the species of the coasts of France (1972a). Figures of C. italica, C. oestroides and C. oxyrrhynchaena can also be found in Montalenti (1948).

# Ceratothoa capri (Trilles, 1964) (Figure 5C-E)

Meinertia capri Trilles, 1964: 188, figures 1-41; 1968: 129, plates 32-34; 1972a: 1218, figures 219-263, plates II & III; Trilles & Raibaut, 1973: 277; Brusca, 1981: 178.

Ceratothoa capri; Trilles, 1994: 116.

### Distribution

Mediterranean (Nouvelle, France), Tunisia (La Galite, Tabarka).

# Hosts

Capros aper (Zeiformes) in buccal cavity.

# Holotype

Muséum National d'Histoire Naturelle, Paris (MNHN-Is 81). Female (length=19.5 mm, width=8.5 mm) La Nouvelle, France (43°01'N 03°03'E).

A description and figures of this species can be found in the original paper by Trilles (1964).

# Ceratothoa collaris Schicedte & Meinert, 1883 (Figure 6A-C)

Ceratothoa collaris Schicedte & Meinert, 1883: 366, table XVI (Cym. XXIII) figures 8-9; Carus, 1885: 433; Rokicki, 1984: 1-220, figures 1-68; 1985: 95; Trilles, 1994: 117.

Meinertia collaris; Monod, 1924a: 31; 1924b: 430; 1925: 103; Trilles 1972b: 1240, plate I; 1977: 10; 1979: 521; Capapé & Pantoustier, 1976: 203; Avdeev, 1979: 54.

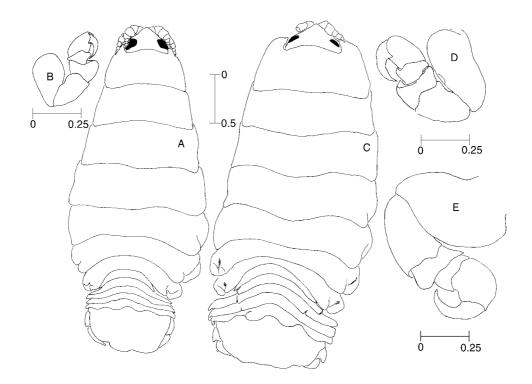


Figure 7. (A) Ceratothoa oestroides, (Holotype, reg. nos MNHN 1895:5:28:12); (B) percopod I; (C) Ceratothoa italica (Holotype, reg. nos ZMUC-CRU-6914); (D) pereopod I; (E) pereopod VII. Scale bars in mm.

#### Distribution

Algeria (Gulf of Oran, Alger) Morocco (Safi) and coast of Mauritanian Sahara, Tunisia (Tabarka), coasts of north-west Africa (Port Etienne, Senegal).

# Hosts

Dentex filosus, Pagellus erythrinus, P. acarne, Pagellus sp. (Sparidae) Corvina cameronensis.

#### Holotype

Muséum National d'Histoire Naturelle, Paris (MNHN-Is 40), Female (length=38 mm) Algeria.

# Remarks

Originally divided into three 'forms' by Monod (1924a,b) forma typica, forma globuligera, and forma africana, according to the morphological variations of the head and antennae. Similar variations are also seen in C. steindachneri.

# Ceratothoa italica Schicedte & Meinert, 1883 (Figure 7C-E)

Ceratothoa italica Schicedte & Meinert, 1883: 347, table XV (Cym. XXII) figures 1-4; Carus, 1885: 442; Trilles, 1979: 521; 1994: 121; Brusca, 1981: 178; Rokicki, 1984: 1-220, figures 1-68; 1985: 95; Trilles et al., 1989: 279, figure 8.

Meinertia italica; Monod, 1924a: 34; Montalenti, 1948: 42, figures 11–13; Trilles, 1964: 106; 1968: 122, plates 25–27; 1972a: 1212, figures 156–187, plate II; 1972b: 1238.

# Distribution

Mediterranean (Fiume, Cap Blanc, Yugoslavia (Montenegro), Gulf of Naples, Tunisia, Morocco (Port Etienne), north-west Africa, (Mauritania).

Pagellus mormyrus, P. erythrinus, Oblada melanura, Canthurus lineatus, Sargus sp. (Sparidae).

#### Holotype

Zoologiske Museum, University of Copenhagen (ZMUC-CRU-6914). Female (length=33.5 mm, width= 15.5 mm), Fiume, Adriatic  $(45^{\circ}56' \text{N} \, 12^{\circ}44' \text{E})$ .

# Ceratothoa oestroides (Risso, 1826) (Figure 7A,B)

Canolira oestroides Risso, 1826: 123.

Cymothoa oestroides; Milne-Edwards, 1840: 272; White, 1847: 110; Lucas, 1849: 78, plate 8, figure 4; Hope, 1851: 33; Heller, 1866: 737; Barcelo y Combis, 1875: 68; Bullar, 1876: 118; 1878: 505, plates 45-47; Stalio, 1877: 236; Mayer, 1879: 176; Stossich, 1880: 45; Bonnier, 1887: 133; Odon de Buen, 1887: 418; 1916: 363; Monticelli, 1890: 420; Gilbert i Olivé, 1919–1920: 88; Sanada, 1941: 209.

Cymothoa (Meinertia) oestroides; Taschenberg, 1879: 245; Dollfus, 1922: 287.

Ceratothoa oestroides; Schicedte & Meinert, 1883: 350, table XV (Cym. XXII) (figures 5-11); Carus 1885: 442; Barrois, 1887: 12; 1888: 63; Gourret, 1891: 14, plate IV (figures 10 & 11); Bolivar, 1892: 133; Koelbel, 1892: 107; Gerstaecker, 1901: 255; Zimmer, 1926-1927: 746; Dudich, 1931: 18; Trilles, 1979: 515; 1994: 122; Renaud et al., 1980: 467; Radujkovic et al., 1984: 161; Rokicki, 1984: 1-220, figures 1-68; 1985: 95; Trilles et al., 1989: 279, figure 9.

Ceratothoa sargorum Gourret, 1891: 16, plate I, figure 17 and plate IV, figures 1–4.

Meinertia oestroides; Nierstrasz, 1915: 89; Monod, 1923a: 82; 1923b: 18; 1924a: 432; 1924b: 34; Montalenti, 1948: 47;

Amar, 1951: 530; Houdemer, 1951: 39; Balcells, 1953: 548; Euzet & Trilles, 1961: 190; Trilles, 1962: 118; 1964: 107; 1968: 53, plates XIII—XVIII, photographs 9–12; 1972: 1201, figures 90–136, plates I, III; 1972: 1233; 1977: 8; Vu—Tân—Tûe, 1963: 225; Quintard—Dorques, 1966: 10; Berner, 1969: 93; Roman, 1979: 501; Trilles & Raibaut, 1971: 73; Thampy & John, 1974: 575; Romestand, 1974: 571; 1979: 423, plates I—IV; Romestand & Trilles, 1976: 87, figure 1; 1977: 47, figures 1–11; 1977: 91, figures 1 & 2; 1979: 195; Romestand et al., 1976: 981; Chaigneau, 1977: 403; Romestand et al., 1977: 171, plate III (10–14); Thuet & Romestand, 1980: 240; 1981: 15; Quignard & Zaouali, 1980: 357; Brusca, 1981: 125; Radujkovic, 1982: 155; Brusca & Gilligan, 1983: 813, figures 1 & 2; Segal, 1987: 351; Wägele, 1987.

Ceratothoa (Meinertia) oestroides; Brusca, 1981: 123.

#### Distribution

Mediterranean (Algeria, French coast, Spanish coast, Balearic Islands, Turkey, Iberian Peninsula, Yugoslavia and Tunisia) and north-east Atlantic coasts (Azores, Canary Islands, north-west Africa, Spanish and French coasts).

#### Hosts

This species is found on many different host species, the Centracanthidae and Sparidae are the most frequently parasitized groups but members of the Clupeidae, Mullidae and Carangidae have also been recorded. Trilles (1994) lists the known hosts and locations for this species.

# Syntypes

Muséum National d'Histoire Naturelle, Paris (MNHN-Is431 (6)). Two Females (lengths=20 mm, 22 mm), Nice, France (43°42′N 07°16′E).

# Ceratothoa oxyrrhynchaena Koelbel, 1878 (Figure 5A,B)

Ceratothoa oxyrrhynchaena Koelbel, 1878: 401, plate I; Gerstaecker, 1901: 261; Trilles, 1979: 521; 1994: 124; Bruce, 1980: 320, figures 3–4; Avdeev, 1982: 65; 1982: 69; Rokicki, 1984: 1–220, figures 1–68: 1985: 95; Trilles et al., 1989: 279, figure 10; 1999: 6.

Ceratothoa oxyrrhynchoena; Schicedte & Meinert, 1883, 368, table XVI (Cym. XXIII) figures 10–14.

Meinertia oxyrrhynchaena; Nierstrasz, 1915: 89; Gurjanova, 1936: 84; Montalenti, 1948: 51; Euzet & Trilles, 1961: 190; Quintard-Dorques, 1966: 10; Trilles, 1968: 125, plates 28–31; 1972a: 1208, figures 137–155, plates I–III; 1972b: 1250; 1977: 10; 1979: 421; Trilles & Raibaut, 1971: 74, plate 4; Capapé & Pantoustier, 1976: 201; Avdeev, 1978: 30; Bruce, 1980: 320.

Codonophilus oxyrrhynchaenus; Nierstrasz, 1931: 132.

#### Distribution

Japan and China, Mediterranean (France, Italy, Tunisia, Algeria, Montenegro, Yugoslavia) north-east Atlantic coasts (Mauritania).

#### Hosts

Boops boops, Spicara maena, (Centracanthidae). Has also been noted on, Zeus faber (Zeiformes), Scyliorhinus stellaris, Torpedo marmorata (Rajidae), and on Scolopsis sp. (Nemipteridae).

#### Holotype

Naturhistorisches Museum, Vienna (NMHW 6216). Female (length=26 mm, width=11.5mm), Japan, Drasdie, 1877.

# Ceratothoa parallela (Otto, 1828) (Figure 6D-G)

Cymothoa parallela Otto, 1828: 351, table XXII (figure III); Milne-Edwards, 1840: 273; Lucas, 1849: 78, plate 8 (figure 24); Hope, 1851: 33; Dana, 1852: 303; Heller, 1866: 738; Stalio, 1877: 236; Bullar, 1878: 505; Stossich, 1880: 45; Gerstaecker, 1901: 255; Gilbert i Olivé, 1919: 88; Belloc, 1929: 250; Bowman, 1978: 217–218.

Ceratothoa parallela; Schiœdte & Meinert, 1883: 329, table XIII (Cym. XX) (figures 3–10); Carus, 1885: 442; Gourret, 1891: 15, plate IV (figures 12–15); Koelbel, 1892: 107; Bolivar, 1892: 133; Szidat, 1955: 16; 1956: 254; Bowman, 1978: 217; Trilles, 1981: 585; 1994: 125; Brusca, 1981; 127; Radujkovic et al., 1984: 161; Rokicki, 1984: 1–220, figures 1–68; 1985: 95; Trilles et al., 1989: 279, figure 11.

Meinertia parallela; Montalenti, 1948: 36; Amar, 1951: 530; Euzet & Trilles, 1961: 190; Trilles, 1964: 106; 1968: 38, plates VII—XII, photographs 6–8; 1972: 1271, figure 2; 1972: 1196, figures 46–89, plate I (4 & 5), III (19); 1972: 1236; 1977: 9; Berner, 1969: 93; Geldiay & Kocatas, 1972: 24; Thampy & John, 1974; 580; Capapé & Pantoustier, 1976: 202; Bowman, 1978: 217; Romestand & Trilles, 1979: 195; Brusca, 1981: 119.

Ceratothoa triglae Gourret, 1891: 19, plate XI, figures 14–19. Ceratothoa deplanata Bovallius, 1885: 20, plate IV, figures 41–46; Menzies & Frankenberg, 1966: 9; Schultz, 1969: 157, figure 235; Trilles, 1981: 585, plates 1 & 2; Brusca, 1981: 178.

Meinertia deplanata; Richardson, 1905: 240, figure 246. Codonophilus deplanatus; Nierstrasz, 1931: 132.

# Distribution

Mediterranean and Atlantic. This species has been collected in many places in these areas (Trilles, 1994).

#### Hosts

Ceratothoa parallela has been found parasitizing diverse fish species, particularly the Centracanthidae, and especially the common bogue, Boops boops.

# Neotype

Muséum National d'Histoire Naturelle, Paris (MNHN-Is415 (24)). Female (length=24 mm).

#### Remarks

The Crustacea collection of the Museum of Göttingen, where Otto's type material is cited as being found (Schiœdte & Meinert, 1883), was transferred to the Senckenberg Research Institute, Frankfurt, in 1985 and the collection has since undergone a major revision. The holotype of *C. parallela* is no longer extant (Dr M. Tuerkay, personal communication). However, in Schiædte & Meinert (1883) there is a reference to a 'specim. typ.' from 'Oran (Bravais, Mus. Paris)'. This specimen has been examined and is designated as the neotype.

Ceratothoa directa (Otto, 1821) was originally described with a short paragraph in Latin, without figures and without reference to the location of a type specimen. In 1828, Otto described C. parallela using a similar Latin description, with only a few omissions, in addition to a German description and a figure. There is little doubt that they are the same species, but since C. directa has not been used since 1821 and C. parallela has been widely used, the latter name is valid in accordance with Article 23.9.1 of the International Code of Zoological Nomenclature. Ceratothoa parallela becomes a nomen protectum, whilst the invalid Ceratothoa directa, becomes a nomen oblitum.

Ceratothoa deplanata Bovallius, 1885, was described only once and has since been mentioned in the literature five times by different authors using the same figures. In the original description the author states that "the animal comes nearest to Ceratothoa parallela Otto, but is to be distinguished by the broadly rounded front, the rhomboidal eyes, the form of the hinder corners of the pereonal segments, the free, narrow, first pleonal segment and the form of the urus". Since the holotype is unknown and these features are insufficient to distinguish the two species, C. deplanata is placed in synonymy with C. parallela.

# **SUMMARY**

This manuscript has provided a complete redescription and re-illustration of Ceratothoa steindachneri with a key to the north-east Atlantic and Mediterranean species of Ceratothoa. A specimen of C. parallela held at the Paris Museum is designated as the neotype of the species.

Seven of the 27 species of Ceratothoa noted by Trilles (1994) are found in Mediterranean and north-east Atlantic waters. In addition, C. deplanata, C. directa, and C. poutassouiensis are here synonymized, designated as nomen nudum, or nomen oblitum for reasons outlined above. In order to clarify the status of C. gobii it is necessary to obtain more specimens from the family Gobiidae. This leaves a remaining 16 species. Of these, almost half are of questionable validity. Two species, Ceratothoa venusta, and Ceratothoa hemiramphi were synonymized by Bruce & Bowman (1989) with C. retusa and C. guttata respectively. Others are described on the basis of juveniles, have only been collected once, or have no holotype. Although the problems with the species of Ceratothoa from the north-east Atlantic and Mediterranean region have been dealt with, there is clearly more work to be done with the remaining members of the genus.

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# REFERENCES

- Avdeev, V.V., 1982a. Peculiarities of the geographic distribution and the history of the marine isopod fauna formation (the family Cymothoidae s. str.). Parasitologia, 16, 69-77.
- Avdeev, V.V., 1982b. Some ecological and geographical peculiarities of isopods of the genus Glossobius, parasites of fishes of the world ocean's epipelagic zone. Biologiya Morya, Vladivostok, 3, 65–67. [In Russian.]
- Avdeev, V.V., 1979. Parasitic isopods of the genus Meinertia from Australian, New Zealand region. Biologiya Morya, Vladivostok, **2**, 48–54.
- Avdeev, V.V., 1978. Parasitic isopods of the family Cymothoidae (Crustacea, Flabellifera) from the Red Sea. Biologiya Morya, Vladivostok, 4, 30–35. [In Russian.]
- Amar, R., 1951. Isopodes marins de Banyuls. Vie et Milieu, 2, 529-530.
- Balcells, R., 1953. Sur des isopodes parasites de poissons. Vie et Milieu, 4, 547-552.
- Barcelo y Combis, F., 1875. Apuntes para la fauna Balear. Catalogo de los Crustaceos marinos observados en las costas de las Islas Baleares. Memorias de la Real Sociedad Española Historia Natural, 4, 53-68.
- Barrois, T., 1887. Note préliminaire sur la faune Carcinologique des Açores. Lille: Bigot Frères.
- Barrois, T., 1888. Catalogue des Crustacés marins recueillis aux Açores, durant les mois d'Août et Septembre 1887. Lille: Bigot Frères.
- Belloc, C., 1929. Etude monographique du Merlu (Merlucius merluccius L.) (deuxième partie). Revue des Travaux de l'Office Scientifique et Technique des Pêches Maritimes. Paris, 2, 231-288.
- Berner, L., 1969. Les principaux Cymothoides (Crustacés Isopodes) du Golfe de Marseille. Bulletin du Muséum National d'Histoire Naturelle de Marseille, 29, 93-95.
- Bolivar, J., 1892. Liste de la colección de Crustacos de España y Portugal del Museo de Historia Natural de Madrid. Anales de la Sociedad Española de Historia Natural, serie II, 21, 124–141.
- Bonnier, J., 1887. Catalogue des Crustacés Malacostracés recueillis dans la Baie de Concarneau. Paris: Octave Doin.
- Bovallius, C., 1885. New or imperfectly known Isopoda. Part I. Kungliga Svenska Vetenskapsakademiens Handlingar, 10, 1–32.
- Bowman, T.E., 1978. Nomenclatural problems in the Cymothoid Isopod genera, Ceratothoa, Codonophilus, and Meinertia—their solution by applying the law of priority. Crustaceana, 34,
- Brian, A., 1939. I parassiti del nasello nel mare Ligure (Clavella stellata) (Kröyer) nuova del Mediterraneo. Corriere della Pesca, **32**. 20–24.
- Bruce, N.L., 1980. On a small collection of marine Isopoda (Crustacea) from Hong Kong. In Proceedings of the First International Marine Biological Workshop, Hong Kong. The Marine Fauna of Hong Kong and China, pp. 315-324. Hong Kong: Hong Kong University Press.
- Bruce, N.L. & Bowman, T.E., 1989. Species of the parasitic isopod genera Ceratothoa and Glossobius (Crustacea: Cymothoidae) from the mouths of flying fishes and halfbeaks (Beloniformes). Smithsonian Contributions to Zoology, 489, 1–28.
- Brusca, R.C., 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society, 73, 117-199.
- Brusca, R.C. & Gilligan, M.R., 1983. Tongue replacement in a marine fish (Lutjanus guttatus) by a parasitic isopod (Crustacea; Isopoda). Copeia, 3, 813-816.
- Buen, O. de, 1887. Catalogo de Crustaceos Españoles. Anales de la Sociedad Española de Historia Natural, 16, 407-434.

- Buen, O. de, 1916. Los Crustaceos de Baleares. Boletin de la Real Sociedad Española de Historia Natural, 16, 355-367.
- Bullar, J.F., 1876. The generative organs of the parasitic Isopoda. Journal of Anatomy and Physiology, 11, 118-123.
- Bullar, J.F., 1878. On the development of the parasitic Isopoda. Philosophical Transactions of the Royal Society, 169, 505-521.
- Capapé, C. & Pantoustier, G., 1976. Liste commentée des Isopodes parasites de Sélaciens des côtes Tunisiennes. I. Côtes septentrionales, de Tabarka à Bizerte. Archives Institut Pasteur de Tunis, 3, 197-210.
- Carus, J.Y., 1885. Prodromus faunae mediterraneae sive Descriptio Animalium maris Mediterranei incolarum quam comparata silva rarum quatenus innotuit adiectis locis et nominibus vulgaribus eorumque auctoribus in commodum zoologorum. I. 525 pp. Stuttgart: Schweizerbart.
- Chaigneau, J., 1977. L'organe de Bellonci des Crustacés. Mise au point sur l'ultrastructure et sur l'homologie des types avec et sans corps en oignon. Annales de Sciences Naturelles, Zoologie et Biologie Animale. Extrait, 12ème série, 19, 401–438.
- Dana, J.D., 1852. On the classification of the Crustacea Choristopoda or Tetradecapoda. American Journal of Science, 14,
- Dana, J.D., 1853. Crustacea, part II. United States Exploring Expeditions, 14, 689-1618.
- Dollfus, R.P., 1922. Cyclobothrium charcuti, n. sp. Trematode ectoparasite sur Meinertia oestroides (Risso). Parasites recueillis pendant la croisière océanographique du 'Pourquoi-pas?' sous le commandement du Dr. J.B. Charcot, en 1914. lère note. Bulletin de la Société Zoologique de France, 47, 287-296.
- Dollfus, R.P. & Trilles, J.P., 1976. A propos de la collection R.P. Dollfus, mise au point sur les Cymothoadiens jusqu'à présent récoltés sur des Téléostéens du Maroc et de l'Algérie. Bulletin du Muséum National d'Histoire Naturelle, Paris. 3ème série, **390**, 821–830.
- Dudich, E., 1931. Systematische und biologische Untersuchungen über die Kalkeinlager rungendes Crustaceenpanzers in polariserstem Lichte. *Zoologica*, **30**, 1–154.
- Euzet, L. & Trilles, J.P., 1961. Sur l'anatomie et la biologie de Cyclocotyle bellones (Otto, 1821) (Monogenea-Polyopistocotylea). Revue Suisse de Zoologie, 68, 182-193.
- Geldiay, R. & Kocatus, A., 1972. Isopods collected in Izmir Bay, Aegean Sea. Crustaceana, 3, supplement, 19-30. [Studies on Peracarida.]
- Gerstaecker, A., 1901. Isopoda. In Die Klassen und Ordnungen der Arthropoden wissenschaftlich dargestelt in Wort und Bild., Fünther Band. II Abtheilung. Crustacea. (Zweite Hälfte: Malacostraca) (ed. H.G. Bronn), pp. 8–278. C.F. Winter'sche Verlagshandlung.
- Gilbert i Olivé, A.M., 1919-1920. Crustacis de Catalunya. Treballs de la Institució Catalana d'Histoire Natural, 1919-1920,
- Gourret, P., 1891. Les Lémipodes et les Isopodes du Golfe de Marseille. Annales du Musée d'Histoire Naturelle de Marseille, 4, 1-44.
- Gurjanova, E.F., 1936. Isopodes des Mers Orientales (Crustacés). Faune de l'U.R.R.S. Edition de l'Académie des Sciences de l'U.R.R.S. Nouvelle Série 6, 7, 1-278.
- Haswell, W.A., 1881. On some new Australian marine Isopoda. Part I. Proceedings of the Linnean Society of New South Wales, 5, 470-481.
- Heller, C., 1866. Carcinologische Beiträge zur Fauna des adriatischen Meeres. Verhandlungen der Zoologische-botanischen Gesellschaft in Wien, 16, 723-760.
- Hope, F.G., 1851. Catalogue dei Crostacei italiani e di molti altri del Mediterraneo. Stabilemento Tipografico di Fr. Azzilono,
- Houdemer, E., 1951. Liste commentée des poissons de mer observés à Ajaccio et leurs parasites. Bulletin de la Societé de Recherches et d'Études Historiques Corses, Ajaccio, 39-40.

- Koelbel, C., 1878. Uber eininge neue Cymothoiden. Sitzungsberichte der Akademie der Wissenschaften in Wien, 78, 401-416.
- Koelbel, C., 1892. Beiträge zur Kenntnis der Crustaceen de Canarischen Insein. Annalen des Naturhistorischen Museums in Wien, 7, 105-116.
- Kussakin, O.G., 1979. Marine and brackish water isopod Crustacea, suborder Flabellifera. Leningrad, USSR: Academy of Sciences.
- Lucas, H., 1849. Histoire naturelle des animaux articulés. In Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Paris: Imprimerie nationale.
- Mayer, P., 1879. Carcinologische Mittheilungen. VI. Ueber den Hermaphroditismus bei einigen Isopoden. Mittheilungen Zoologische Station zu Neapel, 1, 165–179.
- Menzies, R.J. & Frankenberg, D., 1966. Handbook on the common marine isopod Crustacea of Georgia. Athens: University of Georgia
- Milne-Edwards, H., 1840. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Librairie Encyclopédique de Roret, Paris, 3,
- Monod, T., 1923a. Prodrome d'une Faune des Tanaidacea et des Isopoda (Excl. Epicaridae) des côtes de France (excl. Mediterranée). Annales de la Société des Sciences Naturelles de la Charente Inférieure. La Rochelle, 37, 19-124.
- Monod, T., 1923b. Notes carcinologiques (parasites et commensaux). Bulletin de l'Institut Océanographique de Monaco, 427, 1-23.
- Monod, T., 1924a. Parasitologia Mauritanica. Materiaux pour la faune parasitologique en Mauritanie (II Isopoda). Bulletin du Comité d'études Historiques et Scientifiques de l'Afrique Occidentale Française, 9, 67-84.
- Monod, T., 1924b. Note sur la morphologie et la distribution géographique de Meinertia collaris Schiædte et Meinert. Bulletin de la Société Zoologique de France, 49, 31-34.
- Monod, T., 1925. Parasitologia Mauritanica. Matériaux pour la faune parasitologique en Mauritanie. Bulletin du Comité d'études Historiques et Scientifiques de l'Afrique Occidentale Française. Pêches et Productions Coloniales d'origine Animale, Jan-Mars, 93-104.
- Montalenti, G., 1948. Note sulla sistematica e la biologia di alcuni Cimotoidi del golfo di Napoli. (Gen. Emetha, Meinertia, Mothocya, Anilocra, Nerocila). Archivio di Oceanografia e Limnologia, Venezia, 5, 25-81.
- Monticelli, F.S., 1890. Elenco degli Eminti studiati a Wimeraux nella primavera del 1899. Bulletin Scientifique de la France et la Belgique, 22, 417-444.
- Nierstrasz, H.F., 1910. Die Isopoden—Sammlung Naturhistorischen Reichs—Museum zu Leiden. Cymothoidae. Zoölogische Mededeelingen, Leiden, 1, 71–108.
- Nierstrasz, H.F., 1931. Die Isopoden der Siboga—Expedition III. Isopoda guenuina. II. Flabellifera. Siboga Expeditie Monograph, 32a, 123-232.
- Otto, B.C., 1821. Conspectus animalium quorundam maritimorum nondum editorum. Pars prior . . . Adolphus Guilelmus Otto. Vratislaviae Typis Universitatis, 1-20.
- Otto, A.W., 1828. Bechreibung einiger nueun, in den Jahren 1818 und 1819 im Mittellandischen meere gefundener Crustaceen. Nova Acta Academiae Caesareae Leopoldino Carolinae Germanicae *Naturae Curiosorum*, **14**, 331–354.
- Penso, G., 1939. Nuovo parassita e nuova parassitosi del "Gadus potassou". Corriere della Pesca, 12, 1.
- Quignard, J.P. & Zaouali, J., 1980. Les lagunes périméditerranées. Bibliographie icthyologie annotée. Première partie. Les étangs français de Canet à Thau. Bulletin de l'Office National des Pêches de Tunisie, 4, 293-360.
- Quintard-Dorques, B., 1966. Contribution à l'étude des poissons de la famille des Centracanthidae, Genre Spicara de la région de Sète. Annales de l'Université et de l'Association Régionale pour l'étude et la Recherche Scientifiques, 4, 79-88.

- Radujkovic, B.M., 1982. Isopoda—parasites of the south Adriatic economically important fish species. Acta Adriatica,
- Radujkovic, B.M., Romestand, B. & Trilles, J.P., 1984. Les Isopodes parasites de la faune Yougoslave. I. Cymothoidae parasites de poissons marins de la région de l'Adriatique méridionale. Acta Adriatica, 25, 161–181.
- Renaud, F., Romestand, B. & Trilles, J.P., 1980. Faunistique et écologie des métazoaires parasites de Boops boops Linnaeus (1758) (Téléostéen, Sparidae) dans le golfe du Lion. Annales de Parasitologie, Paris, 55, 467-476.
- Richardson, H., 1905. A monograph on the Isopods of North America. Bulletin. United States National Museum, 54, 17–27.
- Risso, A., 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes. Chez F.G. Levrault, Librairie, Paris, 5, 120-126.
- Rokicki, J., 1984. Parasitic isopods of the N.W. African shelf in connection with their occurrence in fish. Zedzyty Naukowe. Rozpawy i Monografie, **50**, 1–222. [In Polish.]
- Rokicki, J., 1985. Biology of adult Isopoda (Crustacea) parasitising fishes of the north west Africa shelf. Acta Icthyologica et *Piscatoria*, **15**, 95–120.
- Roman, M.L., 1970. Contribution à l'étude de la biologie des Cymothoidae (Crustacés, Isopodes) de la Baie de la Ciotat. Théthys, 2, 501-504.
- Romestand, B., 1974. Variations des protéines de l'hémolymphe de deux Cymothoadiens (Isopoda, Flabellifera; parasites de poissons): Meinertia oestroides (Risso, 1826) et Anilocra physodes (L. 1767). Extrait du Bulletin de la Société Zoologique de France, 99, 571 - 591
- Romestand B. & Trilles, J.P., 1976. Au sujet d'une substance à activité antithrombinique, mise en évidence dans les glandes latéro-sophagiennes de Meinertia oestroides (Risso, 1826) (Isopoda, Flabellifera, Cymothoidae: parasite de poissons). Zeitschrift fur Parasitenkunde, 50, 87–92.
- Romestand, B. & Trilles, J.P., 1977. Dégénérescence de la langue des Bogues (Boops boops L., 1758) (Téléostéens, Sparidae) parasités par Meinertia oestroides (Risso, 1826) et Anilocra physodes (L., 1758) (Isopoda, Flabellifera, Cymothoidae). Zeitschrift fur *Parasitenkunde*, **54**, 47–53.
- Romestand, B. & Trilles, J.P., 1979. Influence des Cymothoadiens Meinertia parallela et Anilocra physodes (Crustacés, Isopodes; parasites de poissons) sur la croissance des poissons hôtes Boops boops et Pagellus erythrinus (Sparidés). Zeitschrift fur Parasitenkunde, 59, 195-202.
- Romestand, B., Voss-Foucart, M.F., Jeuniaux, C. & Trilles, J.P., 1976. Les acides aminés libres du sérum des Cymothoidae (Crustacés, Isopodes, parasites de poissons) et de quleques Téléostéens. Archives Internationales de Physiologie et de Biochimie, **84**, 981-988.
- Sanada, M., 1941. On sexuality in Cymothoidae, Isopoda. I. Rhexana verrucosa Schicedte, J.C. and Meinert, parasitic in the buccal cavity of the porgy Pagrosomus major (Temminck & Schlegel). Journal of Science of the Hiroshima University, Série B Div I, 9, 209–217.
- Schiædte, J.C. & Meinert, F.R., 1883. Symbolæ ad Monographiam Cymothoarum Crustaceorum Isopodum familiæ. III: Saophridæ, IV: Ceratothoinæ. Naturhistorisk Tidsskrift, series 3, 13, 281–378.
- Schultz, G.A., 1969. The marine Isopod Crustaceans: the Pictured Key Nature Series. Dubuque. Iowa Brown Company Publishers.
- Segal, E., 1987. Behavior of juvenile Nerocila acuminata (Isopoda, Cymothoidae) during attack, attachment and feeding on fish prey. Bulletin of Marine Science, 41, 351–360.
- Stalio, L., 1877. Catalogo metodico e descrittiodei Crostacei podottalmi ed Edriotalmi dell'Adriatico. Atti dell'Istituto Veneto di Scienze Lettere ed Arti Venezia, 3, 12-74.

- Stebbing, T.R.R., 1911. Indian isopods. Records of the Indian Museum, 6, 179-191.
- Stebbing, T.R.R., 1893. A history of Crustacea. Recent Malacostraca. New York: D. Appleton & Co.
- Stossich, M., 1880. Prospetto della Fauna del mare Adriatico. Parte III. Bollettino della Società Adriatica di Scienze Naturali in
- Szidat, L., 1955. La fauna de parasitos de Merluccius Hubbsi como caracter auxiliar para la solucion de problemas sistematicos y zoogeograficos del genero Merluccius L. Comunicaciones del Instituto Nacional de Investigation Ciencas *Naturales*, **3**, 1–54.
- Szidat, L., 1956. Geschichte, Anwendung und einige Folderungen aus den Parasito genetischen regeln. Zeitschrift fur Parasitenkunde, **17**, 237–268.
- Thampy, D.M. & John, P.A., 1974. Sex reversal and the androgenic gland in the fish parasite Irona far (Cymothoidae: Isopoda: Crustacea). International Parasitology, 4, 575–583.
- Thuet, P. & Romestand, B., 1980. Flux de diffusion de l'eau, localisation et estimation des surfaces d'échanges chez Meinertia oestroides (Risso, 1826) et Anilocra physodes (L., 1758) (parasites de poissons marins). Archives Internationales de Physiologie et de Biochimie, **89**, 15–33.
- Thuet, P. & Romestand, B., 1981. Les transferts d'eau en fonction de la salinité du milieu chez deux Isopodes Cymothoidae: Meinertia oestroides (Risso, 1826) et Anilocra physodes (L., 1758) (Parasites de poissons marins). Archives Internationales de Physiologie de Biochimie et de Biophysique, **89**, 15–33.
- Trilles, J.P., 1962. Remarques morphologiques et biologiques sur les 'Isopodes Cymothoidae' parasites de poissons de l'étang de Thau. Naturalia Monspeliensis, série Zoologie, 3, 101 - 124.
- Trilles, J.P., 1964. Un nouveau Cymothoidien, Meinertia capri n. sp. (Isopoda), Parasite de Capros aper Lacépède, 1803 (Téléostéens, Caproidae) en Méditerranée. Crustaceana, 7,
- Trilles, J.P., 1964. Spécificité parasitaire chez les Isopodes Cymothoidae Méditerranéens. Note préliminaire. Vie et Milieu, 15, 105-116.
- Trilles, J.P., 1968. Recherches sur les Isopodes Cymothoidae des côtes françaises. Volume I: Bionomie et parasitisme; volume II: Biologie générale et sexualité. I. Systématique et faunistique. PhD thesis, Montpellier, France.
- Trilles, J.P., 1972a. Les Cymothoidae (Isopoda, Flabellifera) des côtes françaises (systématique, faunistique, écologie et répartition géographique. I. Les Ceratothoinae Schiœdte et Meinert, 1883. Bulletin du Muséum National d'Histoire Naturelle de Paris, 3ème série, **91**, 1191–1230.
- Trilles, J.P., 1972b. Les Cymothoidae (Isopoda, Flabellifera) du Muséum National d'Histoire Naturelle de Paris. Étude critique accompagnée de précisions en particulier sur la répartition géographique et l'écologie des différentes espèces représentées. I. Les Ceratothoinae Schiædte et Meinert, 1883. Bulletin du Muséum National d'Histoire Naturelle de Paris, 3ème série, 91, 1231-1266.
- Trilles, J.P., 1972c. Sur la structure des pléopodes et des oostégites chez les Cymothoidae (Isopoda, Flabellifera) et ses rapports avec les caractéristiques écologiques des espèces. Bulletin du Muséum National d'Histoire Naturelle de Paris, 3ème série, **91**, 1269–1278.
- Trilles, J.P., 1977. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Historie de Leiden. Méditerranée et Atlantic Nord-Oriental. Zoologishe Mededeelingen de Leiden, **52**, 7–17.
- Trilles, J.P., 1979. Eléments pour la faune parasitaire du Sénégal. Sur quelques Cymothoidae (Isopoda, Flabellifera: parasites de poissons) en collection à l'IFAN. Bulletin de l'Institut Fondamental d'Afrique Noire, série A, 41, 513-530.

- Trilles, J.P., 1979. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) Du Rijksmuseum van Natuurlijke Histoire de Leiden II. Afrique, Amerique et régions Indo-ouest-Pacifiques. Zoologishe Mededeelingen de Leiden, 54, 245–275.
- Trilles, J.P., 1981. Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) des Antilles. *Bulletin du Muséum National d'Histoire Naturelle de Paris, 4ème Série,* **3a**, 583–602.
- Trilles, J.P., 1994. Les Cymothoidae (Crustacea, Isopoda) du monde (Prodrome pour une faune). *Studia Marina*, **21/22**, 1–288.
- Trilles, J.P. & Raibaut, A., 1971. Aegidae et Cymothoidae parasites de poissons de mer Tunisiens: premiers résultats. Bulletin de l'Institut Océanographique. Péche, Salammbô, 2, 71–86.
- Trilles, J.P. & Raibaut, A., 1973. Sur les Cymothoidae (Isopoda, Flabellifera) parasites de poissons marins de Tunisie (2è note). Bulletin du Muséum National d'Histoire Naturelle de Paris, 3ème série, 114, 273–281.
- Trilles, J.P., Radujkovic, B.M. & Romestand, B., 1989. Parasite des poissons marins du Montenégro: Isopodes. Acta Adriatica, 30, 279–306.

- Trilles, J.P., Colorni, A. & Golani, D., 1999. Two new species and a new record of Cymothoid Isopods from the Red Sea. *Cahiers de Biologie Marine*, **40**, 1–14.
- Vu-Tân-Tûe, K., 1963. Sur la présence de dents vomériennes et pterygoïdiennes chez Boops boops (L.) (Pisces: Sparidae), en rapport avec L'Isopode phorétique intrabuccal Meinertia. Vie et Milieu, 14, 225–232.
- Wägele, J.W., 1987. Evolution und Phylogenetisches system der Isopoda. Habilitations schrift zur Erlangung der venia legendi des Fachbereichs Biologie der Universität Oldenburg.
- White, A., 1847. List of the specimens of Crustacea in the collection of the British Museum, London, 1–8, 1–143.
- Zimmer, C., 1926–1927. Ordnung der 'Reihe Peracarida' der Crustacea Malacostraca. 11. Ordnung der Crustacea; Isopoda = Asseln. In *Handbuch der Zoology, Dr. Kükenthal, Dritter Band-Erst Hälfte*, pp. 697–766.

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