A model for exploring lactic acidosis: 1. Model description

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ABSTRACT. Incorporating our experimental data with information in the literature, a computer model was developed using the program STELLA II to study acid production and absorption, to predict the concentrations of volatile fatty acids (VFAs) and lactic acid as well as pH, and to control acid-base balance during rumen fermentation in sheep. The features of this model are based on authors’ experimental data and these data have been supplemented by and checked against a wide range of additional information described in the scientific literature. The rate of buffering capacity and the relative rates of absorption of VFAs and lactic acid from the rumen were used to control lactic acid build up that are novel of this model. This model is a first step in the building of a rumen model suitable for exploring lactic acidosis.

KEY WORDS: model, volatile fatty acids, lactic acid, acidosis, rumen, sheep.

INTRODUCTION

The importance of the rumen fermentation as a means of digestion is demonstrated by the high proportion (64 - 71 %) of digesta residing in the rumen relative to the whole digestive tract in cattle and sheep. It has been estimated that about 88% of VFAs produced in the rumen of sheep are directly absorbed from the rumen and only about 12% flow to the omasum (SUTHERLAND, 1963; DING, 1997).

Mechanistic model is increasingly being used as a research tool. Following the work of BALDWIN et al. (1970), some models of whole rumen function have been developed (DIJKSTRA et al., 1992; POPPI et al., 2001; KEUNEN et al., 2002; KNOTT & KERNER, 2003; KOHN, 2003). These models have endeavoured to represent the digestion and passage of ingested nutrients, microbial metabolism and the formation of end products of digestion. The use of model in optimization of rumen processes has been reviewed in different ideas (BANNINK et al., 1997; LOPEZ et al., 1999; ZIEMER et al., 2000). Although a number of issues related to rumen model require further research, the model of whole rumen function has advanced greatly over the last few decades. The whole rumen function models provide a framework to integrate knowledge on various features of rumen fermentation from which to supply the stock of nutrients to ruminants. However, so far the rumen models do not focus on the development and prevention of lactic acidosis.

Lactic acidosis arising from rapid fermentation of carbohydrate is widespread in ruminant production systems and is a condition with severe consequences for the animal (NIKOLOV, 1996, 1998; PATRA et al., 1996; DING & XU, 2003). There is a complex range of factors leading to the development of lactic acidosis (ROWE, 1997; DING et al., 1998; MULLER et al., 2002; BECKER et al., 2004). The control of the concentrations of lactic acid and volatile fatty acids (VFAs) as well as pH in the rumen during rumen fermentation is becoming the focus of more and more research in this area. As our understanding improves, a computer model of fermentation in the rumen of sheep fed grain as a dietary supplement has a potential role in predicting animal responses to different feeds, processing techniques and feeding patterns.

The objective of this study was to develop a computer model of rumen fermentation integrating knowledge on the development and control of lactic acidosis in the rumen so that we can investigate effective methods and their mechanisms for the prevention and treatment of lactic acidosis. The present paper defines the model and the data used in developing the model to explore lactic acidosis in the rumen of sheep.

THE MODEL

The model was developed using the software ‘STELLA II’ (High Performance Systems Inc. 45 Lyme Road, Suite 300, Hanover, NH) and was run on a Macintosh computer.

Overall structure and notation

The model is presented schematically in Fig. 1. The abbreviations used to denote entities in the model are given in Table 1. A rumen size of five liters was used as being representative of an adult sheep (DIJKSTRA et al., 1992; DIJKSTRA & FRANCE, 1996; DING, 1997). Many of the features of this model are based on experimental data described by DING et al. (1996, 1997, 1998), DING (1997),
and Ding & Xu (2003). These data have been supplemented by and checked against a wide range of additional information described in the scientific literature as indicated in the following sections.

Fig. 1. – **Diagrammatic representation of the model for the rumen fermentation of sheep.** The model includes three major sections: (i) nutritional input; (ii) acid conversion, absorption and outflow; and (iii) regulation. The rectangular boxes indicate pools or state variables. The circles indicate metabolites, absorption and outflow of acids, and regulating factors. Spirals indicate beginnings or ends. Arrows indicate fluxes. Locks and triangles indicate the states and directions of three major sections, respectively.
The following description of the model involves the three parts shown in Fig. 1: 1) nutrition input; 2) acid conversion, absorption and outflow; and 3) regulation.

**Nutrition input**

The ‘diet’ in the model can be set for any ingredients and the period over which the model runs can be set for any duration. However, basically, dietary nutrients entering the ‘rumen’ included grain and hay, and running time was normally 24 h (1440 min). The iteration interval was set at 1 min. Therefore, all flows of material are described in g/min or mmol/min. ‘Intake’ levels for the basic investigation of the model were set at 300 g/d grain and 700 g/d hay. The pattern of ‘intake’ of grain (G) and hay (H) can be defined in Equations 1a and 1b. LAG, VFAG, LAH, and VFAH will be defined in Equations 4a, 4b, 5a and 5b, respectively. LAG, VFAG, LAH, and VFAH are determined by the effects of pH on hay fermentability (HFpH % of PFH1) (Ding et al., 1997; Ding, 1997; Rowe, 1997).

The hay ration of 700 g/d entered the ‘rumen’ over the full 24 h period at a constant rate of 0.486 g/min.

The hay and grain in the rumen are ‘fermented’ and converted to metabolites, such as acids (VFAs, lactic acid etc.). These ‘precursors’ or ‘products’ are described as follows:

\[ FSG = G \times PFG \]  \hspace{1cm} (1a)

\[ FSH = H \times PFH2 \]  \hspace{1cm} (1b)

where FSG (mmol acids/min) and FSH (mmol acids/min) are the fermentable substrates from grain and hay capable of producing organic acids. Their values are the mass of grain (G) and hay (H) multiplied by potential fermentability of grain (PFG) and actual fermentability of hay (PFH2), respectively.

The actual fermentability of hay (PFH2, mmol acids produced/g) was calculated from the potential fermentability of hay (PFH1, mmol acids produced/g) multiplied by the effect of pH on hay fermentability (HFpH, % of PFH1) (Ding et al., 1997; Ding, 1997; Rowe, 1997). The potential fermentability of hay (PFH1) was modified in this way to take account of the negative effect of acidic conditions on fiber digestion.

\[ PFH2 = PFH1 \times HFpH \]  \hspace{1cm} (2)

The potential fermentabilities of grain (PFG) and hay (PFH1) were set at 8-mmol acids produced/g and 5.5-mmol acids produced/g, respectively (Leng & Leonard, 1965; Bergman et al., 1965; Wellner et al., 1967; Bergman, 1990; Murray et al., 1990).

One of the most important factors influencing the fermentable substrate derived from hay in the rumen is pH. The pH effect on hay fermentability (HFpH, % of PFH1) was included as a function by which the pH altered fermentation of hay, however, the effect of pH on fermentation rate of hay would not differ significantly between different diets of hay (Tilley et al., 1963; Rowe, 1983; Rowe et al., 1991). Therefore, for the effect of pH used in the model as the parameter of HFpH, the extent of fermentation at pH 6.5 was taken to be maximal (1, i.e. 100%) and was reduced to 0.685 (68.5%) of the maximum rate with decreasing pH to 5.5 (Ding, 1997; Rowe, 1997). In the model, lactic acid and VFAs are produced from the pools of fermentable substrates from grain (PFG) and hay (PFH1). The pools are the state variables calculated as follows (Ding, 1997; Rowe, 1997):

\[ PFSG(t) = PFSG(t - dt) + (FSG - LAG - VFAG) \times dt \]  \hspace{1cm} (3a)

\[ PFSH(t) = PFSH(t - dt) + (FSH - VFAH - LAH) \times dt \]  \hspace{1cm} (3b)

where t is time in min from the beginning of the simulation and dt is the time step (1 min). FSG and FSH have been defined in Equations 1a and 1b. LAG, VFAG, LAH and VFAH will be defined in Equations 4a, 4b, 5a and 5b, respectively.

**Acid conversion, absorption and outflow**

**Acid conversion**

Lactic acid and volatile fatty acids (VFAs) are produced by fermentation of both grain and hay. The percentages of lactic acid and VFAs production are determined from the pools of fermentable substrates from grain (PFG) and hay (PFH1). The pools are the state variables calculated as follows (Ding, 1997; Rowe, 1997):

\[ PFSG(t) = PFSG(t - dt) + (FSG - LAG - VFAG) \times dt \]  \hspace{1cm} (3a)

\[ PFSH(t) = PFSH(t - dt) + (FSH - VFAH - LAH) \times dt \]  \hspace{1cm} (3b)

where t is time in min from the beginning of the simulation and dt is the time step (1 min). FSG and FSH have been defined in Equations 1a and 1b. LAG, VFAG, LAH and VFAH will be defined in Equations 4a, 4b, 5a and 5b, respectively.
by rate of fermentation and pH (TILLEY et al., 1963; LENG & LEONARD, 1965; LENG & BRETT, 1966; WESTON & HOGAN, 1968). Lactic acid does not normally accumulate in the rumen of a sheep fed hay (GALL et al., 1953; JAYASURIYA & HUNGATE, 1959; NAKAMURA et al., 1971). However, in sheep fed grain-based diets, lactic acid can accumulate with rapid fermentation and reduced rumen pH (ROWE, 1997; ROWE et al., 1991). The relationship between lactic acid production and pH is an inverse one, where increases in lactic acid production lead to a reduction in pH (DUNLOP, 1972; ROWE, 1983, 1997; ROWE et al., 1991, 1993). The relationship between lactic acid production and pH used in the model can be seen in Fig. 2.

Equations 4a and 4b describe the production of lactic acid from grain and hay, respectively (TILLEY et al., 1963; WESTON & HOGAN, 1968; ROWE, 1983; ROWE et al., 1991; GODFREY et al., 1992).

\[
\text{LAG} = \text{PFSG} * \text{LAR} \quad \quad \quad \quad (4a)
\]

\[
\text{LAH} = \text{PFSH} * 0.01 \quad \quad \quad \quad (4b)
\]

where LAR is the proportion of the pool of fermentable substrate from grain (PFSG) converted to lactic acid and varies depending on pH. LAG (mmol/min) is the amount of lactic acid produced from the pool of fermentable substrate from grain (PFSG) and is mostly influenced by pH via LAR. LAG is calculated by multiplying PFSG by LAR. However, LAH (mmol/min) is the amount of lactic acid produced from the pool of fermentable substrate from hay (PFSH) and is not affected by pH. LAH produced from PFSH was negligible and constant at 0.01 (1%) (JAYASURIYA & HUNGATE, 1959; NAKAMURA et al., 1971). The remaining PFSG and PFSH are converted to VFAs using Equations 5a and 5b, respectively (WESTON & HOGAN, 1968; ROWE, 1983; ROWE et al., 1991; DING, 1997).

\[
\text{VFAG} = \text{PFSG} * (1 - \text{LAR}) \quad \quad \quad \quad (5a)
\]

\[
\text{VFAH} = \text{PFSH} * 0.99 \quad \quad \quad \quad (5b)
\]

where VFAG (mmol/min) is the amount of VFAs produced from the pool of fermentable substrate derived from grain (PFSG) and is most influenced by pH via LAR which depends on pH. VFAH (mmol/min) is the amount of VFAs from the pool of fermentable substrate produced from hay (PFSH). A further two state variables, namely LAP (LA pool, mmol) and VFAP (VFAs pool, mmol), are used in the model and their initial values were 0 and 500 mmol, respectively (ROWE, 1983; ROWE et al., 1991; DING, 1997). However, their values at any time (t) are expressed as:

\[
\text{LAP}(t) = \text{LAP}(t - dt) + \\
(\text{LAG} + \text{LAH} - \text{OLA} - \text{ALAC}) * dt \quad \quad \quad \quad (6a)
\]

\[
\text{VFAP}(t) = \text{VFAP}(t - dt) + \\
(\text{VFAH} + \text{VFAG} + \text{ALAC} - \text{AB} - \text{OVFA}) * dt. \quad \quad (6b)
\]

where t is time in min from the beginning of the simulation and dt is the time step (1 min). LAG and LAH have been defined in Equations 4a and 4b, respectively. OLA (mmol/min) and OVFA (mmol/min) are the amount of outflow of lactic acid and VFAs from the rumen in the fluid phase, respectively (WESTON & HOGAN, 1968; DING, 1997). ALAC (mmol/min) is the amount of lactic acid converted to VFAs and is calculated as follows:

\[
\text{ALAC} = \text{LAP} * \text{LAPR} \quad \quad \quad \quad \quad (7)
\]

where LAP has been defined above and LAPR (% of LAP) is the proportion of lactic acid pool converted to VFAs. Again the LAPR value depends on pH (JAYASURIYA & HUNGATE, 1959; PATRA et al., 1996; PITT & PELL, 1997; NIKOLOV, 1998) and is calculated according to the relationship shown in Fig. 3.
Acid absorption

VFAs are mainly absorbed from the rumen; however, lactic acid is apparently not absorbed from the rumen (DING et al., 1998; DING & XU, 2003). Lactic acid is either converted to VFAs or flows out of the rumen. Absorption (AB) (mmol/min) of VFAs is calculated using Equation 8 where VFAP (mmol) is the VFAs pool. AR (% of VFAP) is the absorption rate and is mainly influenced by pH and osmotic pressure (OP) (WESTON & HOGAN, 1968; GODFREY et al., 1992; ROWE, 1997; DING, 1997; DING & XU, 2003). The calculation of AR, pH and OP are described more fully in Equation 13 of the regulation section.

\[ AB = VFAP \times AR \]  \hspace{1cm} (8)

Acid outflow

In addition to fermentation and absorption in the rumen, some nutrients flow to the omasum, abomasum and the small intestine. The outflow of VFAs and lactic acid from the rumen depends on the VFAs pool (VFAP), the lactic acid pool (LAP) and outflow rate (OFR). According to the work of WESTON & HOGAN (1968), about 24% of VFAs produced in the rumen flowed out of the rumen in the fluid phase. Therefore, a value of 0.4% min for VFAs and lactic acid was taken as the outflow rate (OFR) in Equation 9 used in the model. Again this value was dependent on the pH and osmotic pressure (WESTON & HOGAN, 1968; GODFREY et al., 1992; ROWE, 1997; DING, 1997; DING & XU, 2003).

\[ OFR = \frac{(1 - AR)}{155.6} \]  \hspace{1cm} (9)

where OFR (% of VFAP and LAP/min) is outflow rate of VFAP and LAP from the rumen. OFR is mainly affected by pH and osmotic pressure (OP) via absorption rate (AR) which varies depending on pH and OP. The constant 155.6 is calculated on the basis of AR described in Equation 13.

\[ OVFA = VFAP \times OFR \]  \hspace{1cm} (10)

where OVFA (mmol/min) is outflow of VFAs from the rumen and its value equals the product of the VFAs pool (VFAP) and the outflow rate (OFR).

\[ OLA = LAP \times OFR \]  \hspace{1cm} (11)

where OLA (mmol/min) is the outflow lactic acid from the rumen determined as the product of lactic acid pool (LAP) and outflow rate (OFR). OLA and OVFA change with pH since the formation of lactic acid (LA) and VFAs from the pool of fermentable substrate from grain (PFSG) is affected by pH (Equations 4a and 5a)

Regulation

The regulating system in the model includes buffer, pH and osmotic pressure (OP). There are many other factors, like substrate, recycling of microbial matter within the rumen, effects on digesting bacteria, affecting the regulating system (RUSSELL, 1984; JOUANY et al., 1988; ZIEMER et al., 2002; GALBRAITH et al., 2004), however, so far these informations are not fine enough to be included.

Buffer system is often included in the prevention of lactic acidosis (COUNOTTE et al., 1979; ROGERS & DAVIS, 1982; KOVACIK et al., 1986; CUMBY et al., 2001). The inclusion of additional buffer (B) is a decision variable in the model which can be altered over time Sodium bicarbonate (NaHCO₃) was used as a standard buffer in a series of experiments and was therefore chosen for use in this model. The buffering capacity (BC) used in the model was 15 mmol VFAs per gram of NaHCO₃. This is 76% of the theoretical value determined by titration in the experiments (DING, 1997; DING et al., 1996, 1997) (24% of additional NaHCO₃ was assumed to flow out of the rumen with the fluid or solid phase). In the experiments of DING (1997) and DING et al. (1996, 1997), it was shown that 1 g NaHCO₃ can buffer 20 mmol acetic acid at pH 6.

The total amount of lactic acid and VFAs present in the rumen directly affects pH. The total acids (TA, mmol) in 5 liters of ‘the rumen’ were considered together with the amount of additional buffer (B) to calculate the total effective acid concentration (TAPL, mmol/L) as described in Equation 12.

\[ TAPL = \frac{(TA - B \times BC)}{5} \]  \hspace{1cm} (12)

where TA (mmol) is total acids, i.e. the sum of lactic acid pool (LAP) and VFAs pool (VFAP). If no additional buffer (B) is added, B * BC will be zero and TAPL will equal TA/5.

The relationships between TAPL (mmol/L), pH and OP are shown in Figs 4 and 5, respectively.
The pH and osmotic pressure (OP) were found to be very important factors affecting the absorption of VFAs both in the experiments of Ding et al. (1997) and the work of Williams & Mackenzie (1965). The effects of pH and osmotic pressure (OP) on the absorption of VFAs from the VFAP in the rumen are included in the model through absorption rate 1 (AR1) and absorption rate 2 (AR2), respectively. The absorption of VFAs depends on VFAP (VFAs pool) and VFAs absorption rate (AR). AR (% of VFAP/min) was calculated in the model using Equation 13.

\[
AR = AR1 \times AR2/31.25 \quad \text{. . . . . . . . . . . . . . . . . (13)}
\]

where AR1 (% of VFAP/min) is absorption rate 1 (pH effect on VFAs absorption rate), and AR2 (% of VFAP/min) is absorption rate 2 (Osmotic pressure effect on VFAs absorption rate). The constant 31.25 is calculated on the basis of outflow rate (OFR) described in Equation 9. Equation 13 represents base rate of absorption of approximately 76% h of VFAs production in the rumen of sheep, but it is mainly dependent on the pH, osmotic pressure and substrates (Weston & Hogan, 1968; Ding, 1997; Ding et al., 1997).

**SUMMARY OF THE MODEL**

All aspects of the model are represented in Equations (1) to (13) and Figs 1 to 5. Table 1 lists the abbreviations used in the Fig. 1. The differential equations can be solved numerically for a given set of initial conditions and parameter values.

This model is a first step in the building of a rumen model suitable for exploring lactic acidosis. There is another continuous paper of this model, entitled ‘a model for exploring lactic acidosis: 2. model valuation and validation’ in the same issue of this journal, to evaluate the present model to key parameters and validate it by performance against experimental results in sheep.

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A model for exploring lactic acidosis :
2. Model evaluation and validation

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ABSTRACT. For exploring lactic acidosis, a computer model based on incorporating our experimental data with information in the literature was evaluated its sensitivity to key parameters and validated by performing against experimental results in sheep. The model produced reasonable, interesting responses in the concentrations of lactic acid and volatile fatty acids (VFAs) as well as pH and the predicted data was relatively stable over the range of the values of the parameters tested. The results suggest that the rate of fermentation and the amount of substrate are important factors in terms of the development of fermentative acidosis. The model described here can be usefully employed in the design and interpretation of experiments to study lactic acid production and the prevention of acidosis in the rumen.

KEY WORDS : model, lactic acid, acidosis, volatile fatty acids, rumen, sheep.

INTRODUCTION

As our understanding improves, some models of whole rumen function have been developed (PITT & PELL, 1997; KYRIAZAKIS, 2001; KEUNEN et al., 2002; KNOTT & KERNER, 2003). Although a number of issues related to rumen model require further research, the whole rumen function models have endeavoured to represent the digestion and passage of ingested nutrients, microbial metabolism and the formation of end products of digestion (ZIERER et al., 2000; POPPI et al., 2001; KEUNEN et al., 2002; KOHN, 2003).

Lactic acidosis arising from rapid fermentation of carbohydrate is a condition with severe consequences for the animal and wide-spread in ruminant production systems (ROWE, 1997; DING et al., 1998; MULLER et al., 2002; DING & XU, 2003; BECKER et al., 2004). The control of the concentrations of lactic acid and volatile fatty acids (VFAs) as well as pH in the rumen during rumen fermentation is becoming the focus of more and more research in this area. Based on incorporating our experimental data with information in the literature, we have developed a computer model on the development and prevention of lactic acidosis in sheep and entitled ‘a model for exploring lactic acidosis : 1. model description’ in the same issue of this journal. However, the model was not validated and validated.

This paper is a continuance of the model to valuate it to key parameters and validate the model by performance against experimental results in sheep. The model was also used to determine the relative effectiveness of four different ways of controlling acidosis in the rumen.

MATERIALS AND METHODS

Experimental design

Eighteen (18) wether (Merino sheep), weighing 30 to 50 kg and aged approximately 2 years, were necked in the rumen and penned individually. The sheep were originally fed 900 g/day hay containing 1% urea for other experiments. They were fed the same diet for 4 weeks before this experiment and the feed was given hourly in equal amounts. Then the sheep were randomly divided into six groups for two experiments as follows :

(1) Experiment 1

Each rumen-nocked wether of Group 1 to 3 (N = 9) was fed a diet of 460 g hay in 24 h and 540 g wheat with 20 g NaHCO3 in 3 h. The feed was given hourly in equal amounts.

(2) Experiment 2

Every rumen-nocked wether of Group 4 to 6 (N = 9) was fed a diet of 320 g hay and 480 g wheat in 3 h. The feed was given hourly in equal amounts.

Collection and analysis of samples

During 0-8 h in the experiments, the rumen digestive liquid was hourly collected from the rumen-nock of experimental sheep and filtered/stained separately into tube in 38°C water bath with cheese cloth to remove raw dietary residue. The tubes with rumen digestive liquid in 38°C water bath were covered with films of plastic and rapidly moved into a 37°C room to determine pH, lactic acid, and VFAs.
The pH of samples was measured immediately after sampling, using a pH-meter with a glass electrode (0-14 pH ± 0.01 pH (Beckman, USA)).

Concentrations of VFAs were determined using a gas-liquid chromatography (GLC, Model 304, Pye Unicam Ltd, Cambridge, Cambs) based on the method of ERWIN et al. (1961).

Lactic acid concentrations were assayed using a Cobas Mira Auto-analyser (Roche Diagnostics Inc., Frenchs Forest, NSW) and enzyme kits (D-Lactic acid/L-Lactic acid kit, Cat. No. 1112821, Boehringer-Mannheim, Mannheim, Germany).

**Statistical methods**

Data were analyzed using an analysis of variance (ANOVA) and Student Newman-Keuls Multiple Comparison Methods.

**RESULTS AND VALIDATION OF THE MODEL**

The experiments were conducted for validating the model so that we can perform the model effectively to predict and treat lactic acidosis. Therefore, the experimental results are present here by comparing to the predictions of the model.

In experiment 1, every rumen-nocked sheep consumed a diet of 460 g hay in 24 h and 540 g wheat with 20 g NaHCO₃ in 3 h. The same in the model, 540 g wheat with 20 g NaHCO₃ entered the ‘rumen’ over a 3 h period at a constant rate of 3 g/min wheat with 0.111 g NaHCO₃. The 460 g hay entered the ‘rumen’ over the full 24 h period at a constant rate of 0.319 g/min. The results predicted by the model were similar to those of the experimental sheep fed the same diets (P >0.05). The greatest effect was on lactic acid and pH, however, the recorded parameters changed at their peaks that appeared in 2 h after sheep had NaHCO₃ (Fig. 1). The experimental lactic acid and pH changed a little narrower and lighter than those predicted by the model (P >0.05).

In experiment 2, each rumen-nocked sheep consumed another diet of 320 g hay and 480 g wheat in 3 h. The feed was given hourly in equal amounts. In the model, ‘feeding’ 320 g hay and 480 g wheat was over a 3 h period at constant rates of 1.778 g and 2.667 g, respectively. The results from sheep were compared to the predictions of the model using a potential fermentability for grain of 8 mmol acids produced/g and hay 5.5 mmol acids produced/g. The two supposed potential fermentabilities are mean quantitative values for fermentation of grain and hay, respectively, from the work of LENG & LEONARD (1965), BERGMAN et al. (1965), WELLER et al. (1967),
BERGMAN (1990) and MURRAY et al. (1990). The peaks for the model predictions and the experimental observations were ‘displaced’ with the peaks for rumen pH and VFAs concentration (Fig. 2) being approximately 2 h earlier in the model predictions. The prediction VFAs and pH varied a little wider and deeper than those of in vivo experimental observations ($P > 0.05$).

In two experiments, the lactic acid, pH, and VFAs changed a little narrower and lighter than those predicted by the model ($P > 0.05$). These may be due to a complicated living organism that is capable of preventing strong changes in certain ways in the cases.

**VALUATION OF THE MODEL**

The model was subjected to sensitivity and general behavioural tests and the tests were compared to the results from published studies. The model was also used to simulate experiments to create and control lactic acidosis in sheep.

**Sensitivity and behavioural tests**

The model was tested for its sensitivity to two key parameters, potential fermentability of grain (PFG) and potential fermentability of hay (PFH). All tests in the model were run for 24 h (1440 min). However, the X axis (time) in the figures has been truncated to 210 or 240 min or 24 h since each variable presented maintained a somewhat steady state after that time. The effect of altering the values of parameters in the model was tested with respect to pH, the pools of lactic acid and VFAs, and VFAs absorption. The results presented in Fig. 3 illustrate five levels (4, 6, 8, 10, 12 mmol acids produced/g grain consumed) of potential fermentability of grain (PFG) to VFAs. In the work of LENG & LEONARD (1965), BERGMAN et al. (1965), WELLER et al. (1967), BERGMAN (1990) and MURRAY et al. (1990), there is quite a wide range of values for VFA production per gram of substrate fermented and values for grain vary from 4 to 12 mmol VFAs/g. The values depend on the efficiency of cell production per unit of fermentable substrate. For this reason, the model was tested for sensitivity to the potential fermentability values before finalising the value. Rumen pH (a), VFAs pool (c) and VFAs absorption (d) varied significantly depending on potential fermentability of grain (PFG). The higher potential fermentability of grain (PFG), the greater VFAs pool and VFAs absorption, but the lower the pH. The lactic acid pool increased with increasing PFG, however, lactic acid accumulation only occurred when PFG was 12 mmol acids produced/g. The values of PFG below 12 mmol acids produced/g were not high enough for lactic acid accumulation on the basis of the diet consumed.

Fig. 4 presents the results which express three levels (4.5, 5.5, 6.5 mmol acids produced/g hay consumed) of
assumed potential fermentability of hay (PFH1) to VFAs since the values for VFAs production of hay are from 4.5 to 6.5 mmol VFAs/g in the literature (LENG & LEONARD, 1965; BERGMAN et al., 1965; WELLER et al., 1967; BERGMAN, 1990; MURRAY et al., 1990). The results in Fig. 4 are similar to those of Fig. 1: the higher potential fermentability of hay (PFH1), the greater the VFAs pool (c) and VFAs absorption (d), but the lower the pH (a). However, the changes were limited because hay is fermented more slowly than grain. Therefore, only traces of lactic acid (b) were observed even at the highest levels of PFH1. This is consistent with the natural life of sheep.

Fig. 3. – Effects of varying potential fermentability (mmol/g) of grain (PFG) on model behavior. The X axis (time) in the figure has been truncated to 240 min since each variable presented maintained a somewhat steady state after that time. Four lactic acid pools for different PFGs in the Y axis in b were overlaid except a lactic acid pool for PFG = 12 mmol acids produced/g. (a) pH, (b) lactic acid pool, (c) VFAs pool, and (d) VFAs absorption. PFG = 4 mmol acids produced/g (O), PFG = 6 mmol acids produced/g (●), PFG = 8 mmol acids produced/g (△), PFG = 10 mmol acids produced/g (▲) and PFG = 12 mmol acids produced/g (□).
Simulated experiments of lactic acid production and its control

A series of experiments was designed to simulate the production of lactic acid and its treatment in the model, including:

(i) control of pH using different levels of buffer;
(ii) blocking lactic acid production;
(iii) enhancing the conversion of lactic acid to VFAs; and
(iv) gradual ‘intake’ of grain.

Fig. 4. – Effects of varying potential fermentability of hay (PFH1) on model behaviour. The X axis (time) in the figure has been truncated to 240 min since each variable presented maintained a somewhat steady state after that time. Two lactic acid pools for different PFH1s in the Y axis in b were overlaid except a lactic acid pool for PFH1 = 6.5 mmol acids produced/g. (a) pH, (b) lactic acid pool, (c) VFAs pool, and (d) VFAs absorption. PFH1 = 4.5 mmol acids produced/g (O), PFH1 = 5.5 mmol acids produced/g (●) and PFH1 = 6.5 mmol acids produced/g (Δ).
In order to compare the effects of these treatments, the ration in all these experiments was standardized at 1000 g/d consisting of hay 460 g/d and grain 540 g/d in order to produce fermentation conditions for ‘mild’ fermentative acidosis in the ‘rumen’. The grain ration of 540 g/d entered the ‘rumen’ over a 3 h period at a constant rate of 3 g/min. The hay ration of 460 g/d entered the ‘rumen’ over the full 24 h period at a constant rate of 0.319 g/min. The results in sensitivity tests indicated a stable pattern of fermentation with diurnal fluctuations when the potential fermentability of grain (PFG) was set at 8 mmol acids produced/g and for the potential fermentability of hay (PFH1) 5.5 mmol acids produced/g. The model predictions with these potential fermentabilities were also similar to those observed in practice (Reid et al., 1957; Leng & Leonard, 1965; Wellner et al., 1967; Bergman, 1990; Murray et al., 1990). These values of parameters were therefore used for simulated experiments as well as for the basic model. The results of simulated experiments are described as follows.

Different levels of buffer and effect on pH

Buffer is often used to prevent lactic acidosis because of its buffering capacity and sodium bicarbonate (NaHCO₃) is a good buffer in practice (Rogers & Davis, 1982a; Kovacic et al., 1986; Ding et al., 1997; Cumby et al., 2001). There were two ways in which the buffer, NaHCO₃, could be ‘fed’ to the animal to control pH in the model experiments. One way was to add NaHCO₃ at a constant rate with the grain over a 3 h period. Another way was to add NaHCO₃ at a constant rate over the full 24 h period with the hay. NaHCO₃ played a greater buffering role when added with the grain and less of a role when ‘fed’ with the hay based on the same total amount of NaHCO₃ (Fig. 5). Although all recorded parameters, including pools of VFAs and lactic acid, VFAs absorption, and pH, changed at their peaks, the greatest effect was on lactic acid and then on pH. Lactic acid pool decreased 14% with the addition of 20 g NaHCO₃ in 3 h; 28% for addition of 50 g NaHCO₃ in 3 h; 2% for addition of 20 g NaHCO₃ in 24 h; and 5% for addition of 50 g NaHCO₃ in 24 h. The pH increased between 0.01 and 0.04 units in response to the buffer. The model did not include HCO³⁻ and HCO₃⁻/H⁺ + CO₃²⁻ in the saliva and the movement of bicarbonate and CO₂ across the gut wall in vivo that need to be studied.

Fig. 5. – Effects of buffer (NaHCO₃) on model behavior. The X axis (time) in the figure has been truncated to 24 h since each variable presented maintained a somewhat steady state after that time. The pHs in a and lactic acid pools in b for different amounts of NaHCO₃ in the Y axis were overlaid. (a) pH and (b) lactic acid pool. 0 g NaHCO₃ (○), 20 g NaHCO₃ in 3 h (●), 50 g NaHCO₃ in 3 h (▲), 20 g NaHCO₃ in 24 h (△), and 50 g NaHCO₃ in 24 h (‡).

Blocking lactic acid production

The effect of virginiamycin in reducing the risk of acidosis is thought to be due to its reduction of lactic acid production during rapid fermentation of carbohydrate (Rowe & Zorrilla-Rios, 1993; Rowe et al., 1995; Godfrey et al., 1995a, b; Nagaraja et al., 1995). When lactic acid produced from grain (LAG) and from hay (LAH) was constrained to zero in the model, all fermentable substrates were converted to VFAs. Under these conditions, the VFAs pool increased 11% and the pH increased 0.17 units at their peaks (Fig. 6). The effect of the control of
lactic acid production simulated in this situation produced a greater positive effect on pH than that which was achieved at high levels of additional buffer.

**Enhancing conversion of lactic acid to VFAs**

Another approach to controlling acidosis is to increase the rate of conversion of lactic acid to VFAs. This can be done, theoretically, by the addition of 'probiotics' in the form of Gram-positive lactic acid utilizers to the 'rumen'. The use of probiotics is based on the theory that bacterial pre-treatment can prevent acidosis by increasing lactate utilization in animals. In practice, the probiotic Yea Sacc 1026 (Alltech) was shown to reduce the accumulation of lactic acid in the rumen fermentation of starch (NEWBOLD, 1990; WILLIAMS & NEWBOLD, 1990; GIRARD et al., 1993; NEWBOLD et al., 1996). In this experiment, the proportion of lactic acid pool converted to VFAs (LAPR) in the model was changed to 1 (100%). The response to this change was that the lactic acid pool was reduced to one-tenth of the value for basic run at its peak. At the same time, VFAs pool increased 10% and pH increased 0.14 units (Fig. 6). The change of pH was of a similar level to that observed when 'blocking' lactic acid production.

This is to be expected since both methods of interaction have similar effects on reducing the lactic acid pool.

**Gradual 'intake' of grain**

Current practices to prevent acidosis in livestock depend largely on gradual adaptation to diets high in readily fermentable carbohydrates and careful management while feeding such diets (HUNTINGTON, 1988; GODFREY et al., 1992; WIRYAWAN & BROOKER, 1995). Adaptation is based on changes in microbial species and relative population densities in response to changes in substrate. The most common way of feeding grain to ruminants is through a gradual introduction followed by regular feeds. In the model gradual ‘intake’ of grain was simulated by feeding grain at a constant rate over the full 24 h period. The result in Fig. 6 showed that a gradual ‘intake’ of grain even as high as 1950 g/d over the full 24 h period at a constant rate of 1.354 g/min did not result in the accumulation of lactic acid and did not reduce pH (maintained at pH 6.5). At the same time, the VFAs pool (round 502 mmol) and VFAs absorption (7.7 mmol/min) were always maintained at higher levels.

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**Fig. 6. – Comparisons of the different ways of controlling lactic acidosis on model behavior.** The X axis (time) in the figure has been truncated to 24 h since each variable presented maintained a somewhat steady state after that time. Some of pHs in a, lactic acid pools in b and VFAs pools in c for different amounts of NaHCO₃ in the Y axis were overlaid. (a) pH, (b) lactic acid pool and (c) VFAs pool. Base run (O), no lactic acid (●), conversion of lactic acid to VFAs (Δ), 20 g NaHCO₃ in 3 h (▲) and grain 1950 g in 24 h (□)
To make comparisons among the different ways of preventing lactic acidosis, a rank of the effectiveness was as follows: gradual ‘intake’ of grain > blocking lactic acid production > conversion of lactic acid to VFAs > NaHCO₃. The best way of preventing acid accumulation in the rumen is to add grain gradually at a constant rate over the full 24 h period. However, this is not practical as animals tend to consume ‘meals’ at varying intervals throughout the day. It is only practical to feed grazing animals once or twice per week. Under these conditions, the use of virginiamycin to control acidosis may be important.

**DISCUSSION**

*Sensitivity and behavioural analyses*

Fermentation of grain results in rates of VFAs production within the rumen ranging from 4 to 12 mmol/g of feed, whereas fermentation of hay yields VFAs 4.5 to 6.5 mmol/g (Leng & Leon, 1965; Leng & Brett, 1966; Weller et al., 1967; Bergman, 1990; Murray et al., 1990). When the sensitivity and behaviour of the model were tested by altering the potential fermentability of grain (PFG) over ranges of 4 to 12 mmol acids produced/g, the model was relatively stable and produced acceptable response patterns: the higher the potential fermentability of grain, the greater the VFAs pool and VFAs absorption, but the lower the pH (Fig. 3). When the grain with higher potential fermentability was fermented in the ‘rumen system’, greater quantities of VFAs were produced. Increased VFAs promoted the absorption of VFAs and increased total acids resulted in a fall in the ‘rumen’ pH. When the sensitivity and behaviour of the model were tested by altering the potential fermentability of hay (PFH1) over ranges of 4.5 to 6.5 mmol acids produced/g, the model produced similar response patterns to those recorded in the case of grain. However, the model was more stable than when it underwent the sensitivity test of grain and the changes were limited, i.e. the model, like the rumen, was only partially sensitive to potential fermentability of hay (PFH1). This is because hay is fermented more slowly and has a lower PFH1 than grain. This, too, is consistent with the response feature of the ruminant rumen to feed in which the rumen is more sensitive to grain than hay. The model is sensitive to potential fermentabilities, i.e. fermentation rates, because the model, like the rumen, is able to accommodate a range of metabolic interactions.

Lactic acid production increased with increasing potential fermentability of grain (PFG), however, lactic acid accumulation only occurred when PFG was 12 mmol acids produced/g (Fig. 3b). This is because the values of PFG below 12-mmol acids produced/g were not high enough for lactic acid accumulation on the basis of the diet consumed. When the potential fermentability of grain (PFG) was 12 mmol acids produced/g, which is the highest potential fermentability of grain in the ranges tested, the highest level of lactic acid was produced and the level exceeded the capacity for conversion of lactic acid to VFAs to be absorbed and resulted in the accumulation of lactic acid (Fig. 3b). However, the accumulation of lactic acid did not appear to influence proportionally the pH level in Fig. 1a because the total acid level had not increased proportionally due to the conversion of lactic acid to VFAs and the absorption of VFAs. This result supports the theory that lactic acidosis is affected by total acids and all acids contribute to the acidosis by disturbing the acid-base status (Rowe, 1997; Ding et al., 1998; Ding & Xu, 2003).

The model ‘fermentation’ is similar in many ways to the fermentation in the ruminant rumen and the predictions are comparable with the observations in practice. If a potential fermentability 8 mmol acids produced/g for grain and 5.5 mmol acids produced/g for hay were used, the model predictions had similar patterns in rumen pH and VFAs concentration as the experimental sheep consumed the same diet of 320 g hay and 480 g wheat in 3 h (Fig. 2). The results from sheep consumed a diet of 460 g hay in 24 h and 540 g grain with 20 g NaHCO₃ in 3 h were also similar to the predictions of the model ‘fed’ the same diet (Fig. 1). The predictions of the model were comparable with experimental results of the ruminant rumen because the parameters employed in the model were derived from experimental observations. The observation results appeared approximately 2 h after sheep fed experimental diets and changed a little narrower and lighter. These are reasonable since the experimental diets need to be ingested, absorbed and reacted with complicated systems in vivo while they are immediately proceeded in the model; there are many control systems in vivo that lack in the model.

In summary, the sensitivity and behavioural analyses indicate that the values of parameters arising from in vitro kinetic experiments can be employed in the model of rumen fermentation and that the model described here can be usefully employed in the design and interpretation of experiments to study lactic acid production and the prevention of acidosis in the rumen.

**Features of the model**

There are a number of very useful predictions in this model with respect to the potential efficacy of various methods of managing lactic acidosis. These are:

1. (1) relative effects of acid production and absorption of acids and pH;
2. (2) benefits of neutralizing acids and buffering pH by addition of buffers;
3. (3) efficacy of blocking the production of lactic acid by addition of antibiotics; and
4. (4) efficacy of enhancing the conversion of lactic acid to VFAs using microbiological methods.

These features of the model are different from those of published models of rumen function and discussed in detail below.

**Predicting the relative effects of acid production and absorption on acids and pH.**

When the model ‘rumen’ ‘fermented’ 540 g/d of grain in 3 h (3 g/min) with production of 8 mmol acids/g and 460 g/d of hay over the full 24 h period (0.319 g/min) with production of 5.5 mmol acids/g, the predictions showed that the fermentation occurred rapidly with significant accumulation of lactic acid (156 mmol) and...
VFAs (Fig. 6b, c) and a lower pH (pH 4.83, Fig. 6a) at their peaks. This is because the production rate of acids exceeded the removal rate of the acids and lactic acid could not be converted to VFAs below pH 5 (DING, 1997; DING et al., 1997; ROWE, 1997). The removal of acids from the rumen includes the absorption of VFAs into blood and the passage of lactic acid and VFAs to the abomasum. However, if the ‘rumen’ was gradually ‘fed’ grain at a constant rate over a 24 h period, there was no accumulation of lactic acid nor a fall in ‘rumen’ pH even as high as 1950 g/d of grain (1.354 g/min) was ‘fermented’ (Fig. 6). This is due to the fact that the ‘rumen’ kept an equilibrium in terms of acid production and removal so that the total acid concentration was maintained at a constant level in the ‘rumen’ and the pH was unchanged from its initial value of pH 6.5 in the predictions. This is similar to gradual adaptation in the animal to a carbohydrate-rich diet followed by regular feeding of small amounts of grain. Under these conditions, the microbial population adapts with a rise of lactic acid-metabolizing bacteria and an ecological balance between production and utilization so that the animal can prevent acidosis from the diets high in readily fermentable carbohydrates. In practice, however, it is not always as easy to achieve a regular pattern of intake, as it is in the model.

Predicting the benefits of neutralizing acids and buffering pH by addition of buffers.

Lactic acid and VFAs accumulated to result in acidosis and a lower pH when the model ‘rumen’ ‘fermented’ 540 g/d of grain in 3 h at a rate of 3 g/min (Figs 5 and 6). However, the predictions showed that the addition of NaHCO₃ as supplement with grain could decrease the accumulation of lactic acid and VFAs as well as could increase the pH (Fig. 5). Compared to other methods of preventing lactic acidosis in the model, the effects of NaHCO₃ on lactic acid and pH were not very great (Fig. 6). Probably the additional buffer partially neutralized the acids and buffered the pH, but did not alter the rate of fermentation of starch and did not prevent the microbial changes in the gut which are responsible for rapid fermentation of readily fermentable carbohydrates and the accumulation of lactic acid. The ‘fermentation’ produced much more acid than could be buffered by the amount of NaHCO₃ added. The effects in vitro for the supplement of NaHCO₃ may be more greatly associated with other reactions (BIGHAM et al., 1973; COUNOTTE et al., 1979; CUMBY et al., 2001) and the buffering capacity of NaHCO₃ varies depending on the rumen pH. Experiments showed that 1 g NaHCO₃ can buffer 20 mmol acetic acid in vitro at pH 6 (DING, 1997; DING et al., 1996, 1997). When the rate of buffering capacity and the relative rates of absorption of VFAs and lactic acid from the rumen were used to control lactic acid build-up in the model, the predicted results agreed with the observations in the experiments in that the addition of NaHCO₃ resulted in an increase in pH and buffering capacity of rumen and caecal digesta (ROGERS & DAVIS, 1982a, b; KOVACK et al., 1986; DING et al., 1997; CUMBY, 2001).

Predicting the efficacy of blocking the production of lactic acid by addition of antibiotics.

When lactic acid produced from grain (LAG) and from hay (LAH) were constrained to zero in the model, the predictions showed that VFAs pool and pH were increased greatly by 11% and 0.17 pH units at their peaks, respectively, as shown in Fig. 6. This is mainly because fermentable substrates from grain and hay passed through VFAs and VFAs were absorbed from the ‘rumen’. This was to simulate the application of antibiotics and the predicted results are consistent with those of virginiamycin application (ROWE et al., 1989; GODFREY et al., 1992; THORNLEY et al., 1994; NAGARAJA et al., 1995) in that virginiamycin was found to be effective in preventing lactic acid accumulation and very low pH. Rowe et al (1989) found that virginiamycin prevented lactic acid production even at a concentration of 0.5 mg/ml using an in vitro fermentation of rumen fluid taken from sheep. ROWE & ZORRILLA-RIOS (1993) observed no signs of acidosis in cattle when virginiamycin was included at a concentration of 20 mg/kg in a complete diet containing 80% barley even without a gradual increase in grain content of the diet. Antibiotics have been found to inhibit the production of lactic acid by controlling the populations of the major lactate-producing bacteria, Streptococcus bovis and lactobacillus. The consistent results between observations and predictions implied that the application of antibiotics can be simulated in the model to predict their effects.

Predicting the efficacy of enhancing the conversion of lactic acid to VFAs using microbiological methods.

If the proportion of lactic acid pool converted to VFAs (LAPR) was maintained at 100% in the model, then lactic acid pool was reduced to one-tenth of the control value. This was associated with increased production and absorption of VFAs and higher pH (Fig. 6) because of the conversion of lactic acid to VFAs. This was to simulate the use of probiotics capable of using lactic acid. In this case, the ‘rumen’ converted all lactic acid to VFAs, however, a little lactic acid was still accumulated in the pool in the predictions. This means that although enhancing the conversion of lactic acid to VFAs using microbiological methods is a way to treat lactic acidosis, it is only a temporary strategy. The predicted results are consistent with those reported by NEWBOLD (1990), WILLIAMS & NEWBOLD (1990), GIRARD et al. (1993) and NEWBOLD et al. (1996) in that the probiotic Yeasacc (Altech) was shown to reduce the accumulation of lactic acid in the rumen fermentation of starch.

The area in need of development

For the model, the fermentation, absorption and outflow of the rumen are three of the key parameters which are highly complex and hard to quantify. The fermentation depends on substrate, animal, animal state, microorganisms and pH etc (WESTON & HOGAN, 1968; BIGHAM et al., 1973; JOUANY et al., 1988). Absorption and outflow rates depend on pH and osmotic pressure (WILLIAMS & MACKENZIE, 1965; DING et al., 1997, 1998), particle size, density, hydration rate of the gut content as well as feed (WELCH, 1986; DUKSTRA et al., 1992). The relationships
of these factors and the absorption and outflow rates need to be investigated further. Some factors are therefore difficult to be included in the model. VAN STRAALLEN & TAMMINGA (1989) pointed out that information is limited or highly variable on similar foodstuffs in different papers. These differences in sheep may be due to differences in

(i) substrate (like sort of carbohydrates and chain length of fatty acids) utilization (RUSSELL, 1984);
(ii) outflow rate from the rumen with the fluid or solid phase (CHENG & COSTERTON, 1980); and
(iii) recycling of microbial matter within the rumen (JOUANY et al., 1988);
(iv) effects on digesting bacteria (ZIEMER et al., 2002; GALBRATH et al., 2004).

These differences would affect accuracy of the model simulations and, hence, further efforts to standardize these techniques and determine are required.

The model has simplified many steps and it is likely that greater accuracy could be achieved by including more detail and more pools. The purpose of the present model was to focus on the key factors associated with acidosis in order to provide a better understanding of the relative importance of the major management options. In its present form, it appears to achieve this objective.

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Description of the structure of different silk threads produced by the water spider Argyroneta aquatica (Clerck, 1757) (Araneae : Cybaeidae)

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ABSTRACT. The ultrastructure of the different silk threads (walking threads, diving bell, cocoon-sac, egg-sac, anchor threads) produced by the water spider Argyroneta aquatica (Clerck, 1757) has been analysed by means of Scanning Electron Microscopy (SEM). Possibilities for future research linking the observed structure with the particular way of life (life under water) are discussed.

KEY WORDS : Argyroneta aquatica, spider silk, microscopy, SEM

INTRODUCTION

Spiders are distributed in all kinds of environments and hence they have to adapt to different environmental conditions. However, most species prefer a particular climatic zone and occupy a specific strategic niche in consonance with the availability of prey. Because of their trophic level (predators) and their special way of prey capture (by means of web building, sit-and-wait predators and visual hunters), spiders have colonized almost every known terrestrial ecosystem and play a major role in regulating insect abundances (e.g. MOULDER & REICHLE, 1972; RIECHERT & LOCKLEY, 1984). Spiders have exploited even non-terrestrial ecosystems : Argyroneta aquatica (Clerck, 1757) is the only spider known to live most of its life under water (SHUNMUGAVELU & PALANI-CHAMY, 1992; SELDEN, 2002). Although a wide range of animals produce silk (e.g. KOVOOR, 1987; CRAIG et al., 1999), former studies have put emphasis on silk produced by the caterpillar Bombyx mori (Linnaeus, 1758) and by spiders. Recently, the structure of spider silk threads has been intensively analysed because of its unusual chemical and physical characteristics (high strength and high elasticity) (review in VOLLRATH, 2000). Most of these studies are restricted to the threads used in webs and draglines, while almost no data on cocoon fibres and structure is found. The available research on cocoon structure includes a detailed study of the cocoon within one genus : Argoipe bruennichi (Scopoli, 1772) (BERGTHALER, 1995) and A. aurantia Lucas, 1833 (HIEBER, 1985 & 1992a,b), within one family : Uloboridae (OPELL, 1984) and within this family more specifically Polencica producta (Simon, 1873) (PETERS & KOVOOR, 1989) and between different spider genera and species : Digueta canities (McCook, 1889) (CAZIER & MORTENSON, 1968), Nephila clavipes (Linnaeus, 1767) (CHRISTENSON & WENZL, 1980) and Cyrtophora citricola (Forskål, 1775) (KULLMANN, 1961). The studies of BARGHOUT et al. (1999, 2001) only deal with the molecular (crystalline) structure of the cocoon thread (by means of Transmission Electron Microscopy) without describing the structure of the cocoon itself. A more formal structural description (in the framework of egg-cocoon parasites) has been done for three mimetid spiders (Mimetus notius Chamberlin, 1923, M. puritanus Chamberlin, 1923 and M. epeiroides Emerton, 1882) (GUARISCO & MOTT, 1990, GUARISCO, 2001a,b) and the linyphiid spider Pityohyphantes costatus (Hentz, 1850) (MANUEL, 1984). So until now, no study has been done on the structure of threads used by the water spider Argyroneta aquatica. With regard to the special way of life of this species, it is obvious that the structure of the different threads can yield interesting questions related to the adaptation to this specific environment. This work examines the types of threads produced by the water spider by means of Scanning Electron Microscopy. Furthermore, although substantial work is available on the biology of Argyroneta aquatica, no information on the morphology of silk threads of this species has been published.

Systematic position and distribution of the water spider Argyroneta aquatica (Clerck, 1757).

Argyroneta aquatica is a spider, which is hard to classify in spider taxonomy. Originally, it was placed in the family Agelenidae, afterwards it was classified in a separate monotypic family Argyronetidae (ROTH, 1967), which was approved and noted in the catalogue of BRIGNOLI (1983) mainly on the basis of the special way of life. Later, the species was returned to the Agelenidae (subfamily Cybaeinae) (GROTHENDIECK & KRAUS, 1994), but finally it was moved to the newly appointed family...
Cybaeidae (due to an elevation of the former subfamily Cybaeinae into a new family), which is the current systematic position according to Platnick (2006). A recent comparison with fossil material states, that Argyroneta aquatica indeed belongs to Cybaeidae and that differences from other cybaeids are due to specializations for aquatic life or derived with respect to other cybaeids (Selden, 2002). Nevertheless many authors question this positioning because several studies on the karyotype of the Argyroneta aquatica sex chromosomes revealed it to be different from that of most members of the Cybaeidae (haploid versus diploid) (Kral et al., pers. comm.). Despite all arguments, the systematic position of the species is still questionable.

Argyroneta aquatica is a palearctic species living even as far as in Siberia and in Central Asia (Platnick, 2006). In Europe, the occurrence of the species is restricted to Northern and Central Europe. The species is widespread in our country and especially in Flanders in the Campine and the coastal region (Ransy & Baert, 1987). In all countries, it was observed that the species is preferably found in places with a fluctuating water level. In Belgium, the species is not found in areas with upwelling water (although not all areas have been investigated), but it is more abundant in marshes, lakes, moors and canals where it lives between water plants. The species can be found the whole year through, but there are no records of captures in January.

**Biology of Argyroneta aquatica (Clerck, 1757).**

In order to be able to live under water, Argyroneta aquatica has a number of adaptations to this unusual environment for spiders and numerous authors have dealt with the aquatic mode of life and associated morpho-physiological adaptations (e.g.; Braun, 1931, Bristowe, 1958; Schmidt, 1959; Crome, 1951, 1952; Bromhall, 1987, 1988; Izumi 1991; Kayashima, 1991; Grothendieck & Kraus, 1994; Kotiaho, 1998; Masumoto et al., 1998; Toshiya et al., 1998a,b; Schütz & Taborsky, 2002).

**MATERIALS AND METHODS**

The spiders (adults and subadults, no juveniles) were caught in a small ditch in the nature reserve Bourgoyen-Ossemeersen near the city of Gent. Each spider was isolated in separate plastic bottles filled with aerated water (this to eliminate chlorine in the water which is often a limiting factor for lots of invertebrates). A polystyrene cube was pierced with plastic straws and/or wooden sticks and placed in the water so that spiders had an attachment for building diving bells and ‘walking’ threads (Fig. 1). Apart from the difference in material for
the sticks, all constructions were made as uniform as possible so that any difference between housing possibilities could be excluded. To avoid the spiders from escaping, the top of the bottle was cut off and placed in reverse on the rest of the bottle. Spiders were fed with 20 water isopods (Asellus aquaticus) each week found in ponds of Ghent University’s botanical garden. When available, the diet was enriched with water fleas (Daphnia spec.), mosquito larvae (Culex spec. and Chaoborus spec.) and fairy shrimps (Branchipus spec.). Samples were taken from each type of threads and investigated under a Scanning Electron Microscope (SEM, JEOL JSM 840). To this end the samples were fixed in 70% isopropyl solution, dried and covered with a tiny layer of gold.

To have an idea of the diameter of the different threads, twenty-five observations were made on the selected pictures (the average value and standard deviation are mentioned).

RESULTS AND DISCUSSION

Within a few days, the spiders had constructed a network of silk threads together with a diving bell attached to the straws or wooden sticks in the water bottles (Fig. 2). The difference in material for the sticks has no significant influence on the web building behaviour of the spider for both males and females.

Argyroneta aquatica makes four kinds of threads under water: a diving bell (functions as an air reservoir), anchor threads: firm threads used to attach the diving bell to the substrate (mostly water plants), so-called ‘walking’ threads used for movement when a prey is near and threads produced when making the egg-cocoon and the cocoon threads themselves. Differences are observed between the web construction of males and females. Males tend to build a large diving bell that is suspended in the four corners of the polystyrene cube with only a few threads while females build a smaller, more rounded diving bell that is attached by anchor threads to the nearby straws/sticks. Males make larger diving bells probably because they are larger than females and need more space to live in. As to anchor threads, males apparently produce less of them than females. This confirms the assertion of Crome (1952) that males are less careful in building their diving bell. It is not clear why this difference between sexes occurs since these threads (diving bell and anchor threads) are necessary for everyday life. Conversely, males make more walking threads than females (although this cannot be generalized). It hasn’t been investigated if this difference can be explained by the need for a higher mobility of males (in search for food and females), which is still doubtful.

Threads of the diving bell

The SEM images (Fig. 3) show that the diving bell threads consist of three different types in congruence with earlier findings (Schollmeyer, 1913). We observe thick threads (1.05-1.15 µm); loose, thin, single-stranded threads (0.34 ± 0.04 µm) and thin threads that are aggregated, but visible as separated threads. Furthermore, the threads have no clear spatial ordination: they are all woven very chaotically without any clear direction. It is noticed that a kind of film was present, draped over and woven between the strands. It is not certain whether this film is produced by the spider (serving probably as a water repellent layer) or deposited by other aquatic organisms. In Fig. 3, a diatom and some globular objects (possible bacteria) can be seen, which are known to produce some kind of biofilm (Bosselaers, pers. comm.). However, future research is required to check whether these organisms are responsible for producing this film (see further). The presence of the film is certainly connected with the physical-chemical properties of the diving bell. The diving bell, when pulled out of the water, became shiny, lost its suppleness and became fragile. When replaced into the water, its original suppleness and roughness was regained. The real structure and clarification of the film has not been investigated and could be a subject of future research.

Anchor threads

Anchor threads seem to consist of a crowded mass (possible anomaly occurring with preparation), which is held together with threads (Fig. 4). The most probable function of the threads is tightening the film of the diving bell to the substrate. When viewed more in detail, the anchor threads consist of several small threads (Fig. 5). It seems that anchor threads are tightly connected to each other through smaller threads and that interstitial space is filled up with dirt. The smaller threads are similar to a cable, consisting of several smaller fibres covered by some kind of casing (Fig. 5). Whether this casing consists of the same material than that of the diving bell film is not clear.
Walking threads

The walking threads were not analysed due to logistic reasons (difficulties when making a preparation due to the thinness and delicacy of the threads). However, we did observe that the walking threads are spun as one strand, but are branched off into several fibres as soon as the substrate is reached. These threads form a close network of fibres (comparable to the anchor threads, but smaller) along the substrate (downwards) and end somewhere where no further attachment is possible. A lot of ‘dirt’ is incorporated into the threads, probably because the spider itself actively incorporates parts onto the threads, as it also does in or around the diving bell (Kayashima, 1991).

The egg-cocoon

The egg-cocoon is formed within the diving bell. The spider builds a vast structure in the upper part of the diving bell (‘cocoon-sac’) that follows the shape of the diving bell and is sometimes even, for a certain part, incorporated into the diving bell. Partial incorporation of the cocoon-sac in the diving bell is often observed with large cocoons. It is a separate structure that can be removed from the diving bell without destroying the latter. In this structure, a second sac is woven (consisting of fine threads) that is attached with several threads to the interior of the cocoon-sac, called the ‘egg-sac’. The egg-sac does not make contact with the cocoon-sac. The two constructions are sealed off with a very thick and closely woven sheet. Our observations of the structure were somewhat different from those of Wagner (1894) and Hamburger (1910). In our case, an egg-sac was built and in that of Schollmeyer (1913) a third division was observed. According to our own observations, the shape of the egg-cocoon differed between individuals (intraspecific variability) although there were no environmental influences (all individuals received the same breeding regime in the lab). Since environmental influences were not discussed in other articles concerning the cocoon shape, no final conclusions of our observations with those of others can be made. It is not clear whether the observed differences depend on the specific microhabitat in which the species lives or on physiological limitations of the several individuals. Both structures (cocoon-sac and egg-sac) will be discussed separately.

The thread of the cocoon-sac consists of a single fibre type (there are no different types like those in the diving bell). Nevertheless, the fibres were observed to be different in thickness ($0.37 \pm 0.10 \mu m$) and to lie randomly orientated (Fig. 7). Bundles of fibres are observed in which the fibres are wrapped around each other (like some kind of coiling). On the outer side, a film was observed although not as thick as in the case of the diving bell (Fig. 8). Due to the presence of the film, at first sight no differences were observed between the threads (diameter: $0.41 \pm 0.04 \mu m$) when investigated through light microscopy. The structure of the film that closes the
whole ‘cocoon-sac’ comprises several layers of single thick and thin fibres put over each other combined with a film that does not cover the whole of the fibre-matrix (interstitial space is present in some parts of the sheet) (Fig. 10). Moreover, no differences were observed between fertilized and non-fertilized cocoons.

The threads of the ‘egg-sac’ consist of only one type (no big differences in thickness: 0.24 ± 0.06 µm). In comparison with the ‘cocoon-sac’, the ‘egg-sac’ threads are loosely woven (Fig. 9). This kind of pattern is also observed within a non-fertilized cocoon and a film was not present. Fig. 7 shows that the kind of thread is the same as the type used for building the ‘cocoon-sac’ (coiled threads).

**Conclusion and remarks on future research**

Although this work gives a first analysis of the different threads and structures made by *Argyroneta aquatica*, it is clear from our findings that a lot of questions remain unanswered. It is not clear how the threads and structures are produced in order to be adapted for life under water. Further investigation is necessary to look for the differences in physical-chemical properties between the different types of threads produced by this spider species in order to find in which way the spider alters the chemical-physical properties of its silk as an adaptation for life under water. Another possible experiment is to check whether diatoms and bacteria could be responsible for producing the film and/or if this film is made as an answer to this particular way of life. It would be possible by comparing spiders raised in sterilised containers (and initially sterile water) with spiders kept in ‘normal’ conditions after which threads could be plated in several agarmedia. It is obvious that the special structures found with this species raise a lot more questions and that further research on the chemical-physical composition (in relation to an adaptation to life under water) is necessary.

**ACKNOWLEDGEMENTS**

First of all, we would like to thank Mr. Martin Saille for all his help in the field and his enthusiasm on this subject. Furthermore, Mr. Bart De Muynck and Mrs. Mia Meirsschaut (Nature Reserve Bourgoyen-Ossemeersen) are acknowledged for giving
us access to the nature reserve so that we could study this spider. We thank Dr. Hendrik Segers for his assistance in making the SEM photographs. Finally, we thank Tom Geysens and Dr. Lynda Beladjal for their help in various ways.

REFERENCES


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Uropodine mite communities (Acari: Mesostigmata) in birds’ nests in Poland

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ABSTRACT. Knowledge of uropodine mite communities in birds’ nests in Poland and surrounding areas is very poor. We therefore conducted a survey of 338 nests belonging to 36 bird species, and found that they contained 28 species of Uropodina. The most frequent species were Trichouropoda orbicularis, Apionoseius infirmus, Urobovella pyriformis, Uropoda orbicularis, Nenteria pandionii, and T. ovalis. The dominant species were T. orbicularis, and U. pyriformis, which constituted up to 68% of the total specimens. The majority of species of these mites reproduce sexually. The species whose populations consist only of females, reproducing by thelytoky, are rather rare. There is distinct variation in the species composition and dominance structure of uropodine communities in the nests of particular bird species, which seems to be largely caused by differing types of nests. The most species-rich uropodine communities were found in large, perennial nests (white stork and raptors), the poorest ones (usually one or two species) occurred in the material collected from nest boxes.

KEY WORDS: mites, Uropodina, nesting biology, nest of birds, unstable microhabitats

INTRODUCTION

More than 70 years have passed since the first attempts to examine the relationship between birds and the invertebrate inhabitants of their nests, including mites (Nordberg, 1936). Much of the research on this subject has been essentially faunistic in character (e.g. Patan, 1969; Zukowski & Bitkowska, 1973; Kaczmarek, 1977, 1981a, 1981b, 1982a, 1982b, 1986; Philips, 1981; Chimelewski, 1982; Philips et al., 1983; Kaczmarek & Pajkert, 1987; Ambros et al., 1992; Fain et al., 1993; Maśan & Orszaghova, 1995; Fenda & Pinowski, 1997; Krumpal et al., 1997; Fenda et al., 1998; Madej & Stańska, 1999; Fenda & Schnierova, 2004), or has discussed parasitic groups of mites (Haitlinger, 1987; Philips, 2000). Few studies have involved mites of the suborder Uropodina occurring in birds’ nests.


Due to this rather superficial knowledge of the uropodine fauna of nests, we conducted a survey to examine this microhabitat in more detail. We evaluated museum-based nest collections to investigate the effects of a number of factors on the mite communities of these nests in particular, the bird species present, nest size and durability; the building material and location of the nest; and the biology of the host.

MATERIAL AND METHODS

Bird nests and material from nest boxes were collected over a period of more than 40 years from a variety of regions and habitats in Poland. Whole nests were collected from passerines and from birds using nest boxes, while samples of 0.5 - 0.8 litres of material were collected from the large perennial nests of birds of prey (raptors), and the white stork. A total of 338 samples were collected from the nests and nest boxes of 36 species of birds. In 15 nests (4%) it was impossible to determine the species of the host (Table 2).
TABLE 1
List of the uropodine mites reported in birds’ nests in Europe

<table>
<thead>
<tr>
<th>Mite species</th>
<th>Bird species</th>
<th>Reference</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trachytes aegrota</em> (C.L. Koch, 1841)</td>
<td>Stock dove (Columba oenas), Starling (Sturnus vulgaris), House martin (Delichon urbica), Great tit (Parus major), Fieldfare (Turdus pilaris), Bullfinch (Pyrrhula pyrrhula), Carrion crow (Corvus corax), Pied flycatcher (Ficedula hypoleuca)</td>
<td>Nordberg 1936</td>
<td>Scandinavia</td>
</tr>
<tr>
<td><em>Blackbird (Turdus merula)</em></td>
<td></td>
<td>Błoszyk &amp; Olszanowski 1985</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Dipper (Cinclus cinclus)</em></td>
<td></td>
<td>Fenda et al. 1997</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Greylag Goose (Anser anser)</em></td>
<td></td>
<td>Masan &amp; Kristofik 1993</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Great spotted eagle (Aquila clanga)</em></td>
<td>White-tailed Sea Eagle (Haliaeetus albicilla), Osprey (Pandion haliaetus)</td>
<td>Gwiazdowicz et. al. 1999, 2000</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Polyaspinus cylindricus</em> (Berlese, 1916)</td>
<td>Red-backed shrike (Lanius collurio), Yellow bunting (Emberiza citronella)</td>
<td>Tryjanowski et al. 2001</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Uroseius hunzikeri</em> (Schweizer, 1922)</td>
<td>Sand martin (Riparia riparia), Bee-eater (Merops apiaster)</td>
<td>Masan 2001</td>
<td></td>
</tr>
<tr>
<td><em>Nenteria breviangualculata</em> (Willmann, 1949)</td>
<td>Mallard (Anas platyrhynchos), Coloured Flycatcher (Ficedula albicilla), Great reed warbler (Acrocephalus arundinaceus)</td>
<td>Fenda et al. 1998</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Nenteria floralis</em> (Karg, 1986)</td>
<td>Great spotted eagle (Aquila clanga)</td>
<td>Gwiazdowicz et al. 1999, 2000</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Nenteria hirschmanni</em> (Wisniewski, 1979)</td>
<td>White-tailed Sea Eagle (Haliaeetus albicilla)</td>
<td>Gwiazdowicz et al. 2000</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Nenteria stylifera</em> (Berlese, 1904)</td>
<td>Great reed warbler (Acrocephalus arundinaceus)</td>
<td>Kristofik et al. 2001</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Trichouropoda longiovalis</em> (Hirschmann et Zimgiebl-Nicol, 1961)</td>
<td>Sand martin (Riparia riparia), Great tit (Parus major)</td>
<td>Masan &amp; Kristofik 1993</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Trichouropoda orbicularis</em> (C.L. Koch, 1839)</td>
<td>Blackbird (Turdus merula), Starling (Sturnus vulgaris), Tree sparrow (Passer montanus), Nuthatch (Sitta europaea), Pied flycatcher (Ficedula hypoleuca), Great tit (Parus major), Blue tit (Parus caeruleus), Redstart (Phoenicurus phoenicurus)</td>
<td>Błoszyk &amp; Olszanowski 1985, Błoszyk &amp; Olszanowski 1986</td>
<td>Poland</td>
</tr>
<tr>
<td>*Mallard (Anas platyrhynchos), Coloured Flycatcher (Ficedula albicilla), Great reed warbler (Acrocephalus arundinaceus)</td>
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</table>
# Table 1

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<th>Bird species</th>
<th>Reference</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trichouropoda ovalis</em> (C.L. Koch, 1839)</td>
<td>Pied flycatcher (<em>Ficedula hypoleuca</em>)</td>
<td>Nordberg 1936</td>
<td>Scandinavia</td>
</tr>
<tr>
<td></td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Bloszyk &amp; Olszanowski 1985</td>
<td>Poland</td>
</tr>
<tr>
<td></td>
<td>Penduline tit (<em>Remiz pendulinus</em>)</td>
<td>Masan &amp; Kristofik 1995</td>
<td>Slovakia</td>
</tr>
<tr>
<td></td>
<td>Great reed warbler (<em>Acrocephalus arundinaceus</em>)</td>
<td>Kristofik et al. 2001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sparrow (<em>Passer sp.</em>)</td>
<td>Fenda et al. 1998</td>
<td>Slovakia</td>
</tr>
<tr>
<td></td>
<td>Mallard (<em>Anas platyrhynchos</em>)</td>
<td>Fenda &amp; Pinowski 1997</td>
<td>Poland</td>
</tr>
<tr>
<td></td>
<td>Great spotted eagle (<em>Aquila clanga</em>), White-tailed Sea Eagle (<em>Haliaeetus albicilla</em>), Osprey (<em>Pandion haliaetus</em>)</td>
<td>Gwiazdowicz et al. 1999, 2000</td>
<td>Poland</td>
</tr>
<tr>
<td></td>
<td>Red-backed shrike (<em>Lanius collurio</em>)</td>
<td>Trijanowski et al. 2001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Bloszyk &amp; Olszanowski 1985</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Dinychus carinatus</em> (Berlese, 1903)</td>
<td>Penduline tit (<em>Remiz pendulinus</em>)</td>
<td>Kristofik et al. 1995</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Dinychus inermis</em> (C.L. Koch, 1841)</td>
<td>Mallard (<em>Anas platyrhynchos</em>), Great Reed Warbler (<em>Acrocephalus arundinaceus</em>)</td>
<td>Fenda et al. 1998</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Greater spotted eagle (<em>Aquila clanga</em>), White-tailed Sea Eagle (<em>Haliaeetus albicilla</em>)</td>
<td>Fenda &amp; Schnierova 2004</td>
<td></td>
</tr>
<tr>
<td><em>Dinychus perforatus</em> Kramer, 1882</td>
<td>Great tit (<em>Parus major</em>)</td>
<td>Fenda et al. 1998</td>
<td>Slovakia</td>
</tr>
<tr>
<td></td>
<td>Great spotted eagle (<em>Aquila clanga</em>)</td>
<td>Gwiazdowicz et al. 1999</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Uroobovella advena</em> (Trägardh, 1912)</td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Bloszyk &amp; Olszanowski 1985</td>
<td>Poland</td>
</tr>
<tr>
<td></td>
<td>Common gull (<em>Larus canus</em>), Water pipit (<em>Anthus spinolletius</em>), Carrion crow (<em>Corvus corax</em>), Goldcrest (<em>Regulus regulus</em>), Redstart (<em>Phoenicurus phoenicurus</em>)</td>
<td>Nordberg 1936</td>
<td>Scandinavia</td>
</tr>
<tr>
<td></td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Bloszyk &amp; Olszanowski 1985</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Uroobovella fimicola</em> (Berlese, 1876)</td>
<td>Penduline tit (<em>Remiz pendulinus</em>)</td>
<td>Masan &amp; Kristofik 1995</td>
<td>Slovakia</td>
</tr>
<tr>
<td><em>Uroobovella nova</em> (Oudemans, 1902)</td>
<td>Northern Lapwing (<em>Vanellus vanellus</em>)</td>
<td>Fenda et al. 1998</td>
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<tr>
<td><em>Uroobovella obovata</em> (Canestrini et Berlese, 1884)</td>
<td>Great spotted eagle (<em>Aquila clanga</em>)</td>
<td>Gwiazdowicz et al. 1999</td>
<td>Poland</td>
</tr>
<tr>
<td><em>Uroobovella pyriformis</em> (Berlese, 1920)</td>
<td>Blue tit (<em>Parus caeruleus</em>)</td>
<td>Bloszyk &amp; Olszanowski 1986</td>
<td></td>
</tr>
<tr>
<td><em>Discourcella modesta</em> (Leonardi, 1899)</td>
<td>Red-backed shrike (<em>Lanius collurio</em>)</td>
<td>Trijanowski et al. 2001</td>
<td></td>
</tr>
<tr>
<td><em>Carpodola hamulifera</em> Michael, 1894</td>
<td>Great spotted eagle (<em>Aquila clanga</em>)</td>
<td>Gwiazdowicz et al. 1999</td>
<td></td>
</tr>
<tr>
<td><em>Carpodola minima</em> (Kramer, 1884)</td>
<td>Blackbird (<em>Turdus merula</em>)</td>
<td>Bloszyk &amp; Olszanowski 1985</td>
<td></td>
</tr>
<tr>
<td><em>Carpodola orbicularis</em> (Müller, 1776)</td>
<td>Penduline tit (<em>Remiz pendulinus</em>)</td>
<td>Masan &amp; Kristofik 1995</td>
<td>Slovakia</td>
</tr>
<tr>
<td></td>
<td>Mallard (<em>Anas platyrhynchos</em>)</td>
<td>Fenda et al. 1998</td>
<td></td>
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<tr>
<td></td>
<td>White-tailed Sea Eagle (<em>Haliaeetus albicilla</em>)</td>
<td>Gwiazdowicz et al. 2000</td>
<td>Poland</td>
</tr>
<tr>
<td></td>
<td>Red-backed shrike (<em>Lanius collurio</em>)</td>
<td>Trijanowski et al. 2001</td>
<td></td>
</tr>
</tbody>
</table>
Mites were extracted from nests or nest material using Tullgren funnels and preserved in 75% ethanol. Temporary slide preparations were made in lactophenol in order to examine the specimens using a light microscope. When specimens were particularly valuable or difficult to identify, permanent preparations were made in polyvinyl alcohol. The specimens were deposited in the Invertebrate Databank Collection in the Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Poznañ and the Department of Forest and Environment Protection, August Cieszkowski Agricultural University, Poznañ. The classification of birds used in this paper is in accordance with ‘Checklist of Animals of Poland’ (WIŚNIEWSKI, 1997).

### Table 2

List of Uropodina mites found in the investigated nests of birds

<table>
<thead>
<tr>
<th>Mite species / Bird species</th>
<th>White stork (Ciconia ciconia)</th>
<th>Black kite (Milvus migrans)</th>
<th>Red kite (Milvus milvus)</th>
<th>White-tailed Sea Eagle (Haliaeetus albicilla)</th>
<th>Marsh harrier (Circus aeruginosus)</th>
<th>Greater Spotted Eagle (Aquila clanga)</th>
<th>Rock Dove (Columba livia)</th>
<th>Tawny Owl (Strix aluco)</th>
<th>White wagtail (Motacilla alba)</th>
<th>Wren (Troglodytes troglodytes)</th>
<th>Redstart (Phoenicurus ochruros)</th>
<th>Blackbird (Turdus merula)</th>
<th>Goldcrest (Regulus regulus)</th>
<th>Pied Flycatcher (Ficedula hypoleuca)</th>
<th>Blue Tit (Parus caeruleus)</th>
<th>Great Tit (Parus major)</th>
<th>Nuthatch (Sitta europaea)</th>
<th>Treecreeper (Certhia sp.)</th>
<th>Starling (Sturnus vulgaris)</th>
<th>Tree Sparrow (Passer montanus)</th>
<th>Unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type of nest (A-perennial nests; B – one-year nests, C – nest boxes)</td>
<td>AAAABAABBBBBBBCCBBCCBB</td>
<td>Trachytes aegrota (C.L. Koch, 1841) + + + + + + + + + 19 0.32 2.3 6</td>
<td>Polyaspis cylindricus (Berlese, 1916) + 1 0.02 0.3 1</td>
<td>Polyaspis patavinus Berlese, 1881 + 2 0.03 0.3 2</td>
<td>Apionoseius infirmus (Berlese, 1887) + + + + + + + + + 509 8.55 7.3 138</td>
<td>Nenteria pandioni Wiśniewski et Hirschmann, 1985 + + + + + 551 9.25 5.5 386</td>
<td>Nenteria floralis Karg, 1986 +</td>
<td>Trichouropoda elegans (Kramer, 1882) + 7 0.12 0.3 7</td>
<td>Trichouropoda karavaiwei (Berlese, 1904) + + + + 93 1.56 0.8 85</td>
<td>Trichouropoda obscurasimilis (Hirschmann et Zirngiebl-Nicol, 1961) + + + 29 0.49 0.3 29</td>
<td>Trichouropoda arboecularis (C.L. Koch, 1839) + + + + + + + + + + 2708 45.48 20.1 630</td>
<td>Trichouropoda ovalis (C.L. Koch, 1839) + + + + + + + + + + 92 1.55 5.2 26</td>
<td>Trichouropoda penicillata Grein, 1952 + + 9 0.15 0.3 9</td>
<td>Trichouropoda structura (Hirschmann et Zirngiebl-Nicol, 1961) +</td>
<td>Trichouropoda sp. +</td>
<td>Dinychus arcuatus (Trägardh, 1922) +</td>
<td>Dinychus perforatus (Kramer, 1882) + + 3 0.05 0.8 1</td>
<td>Urodiaspis pannonica (Willmann, 1952) + 1 0.02 0.3 1</td>
<td>Urodiaspis tecta (Kramer, 1876) + 4 0.07 0.5 3</td>
<td>Uroobovella flagelliger (Berlese, 1910) +</td>
<td></td>
</tr>
</tbody>
</table>
| Numbers of mite specimens | 148 Jerzy Blószyk, Daria Bajerlein, Dariusz J. Gwiazdowicz, Robert Bruce Halliday & Magdalena Dylewska
RESULTS

Species composition and community structure of Uropodina in birds’ nests

Among the 338 nests and boxes examined, 134 (39.6%) contained uropodine mites, belonging to 28 species (total 5954 specimens) (Table 2). No mites were found in the nests of the Buzzard (Buteo buteo), Lesser spotted eagle (Aquila pomarina), Kestrel (Falco tinnunculus), Barn owl (Tyto alba), Woodpecker (Dendrocopus sp.), House sparrow (Passer domesticus), Redstart (Phoenicurus ochruros), Great tit (Parus major), and Treecreeper (Certhia sp.). Single species of mites were found in the nests of the Marsh harrier (Circus aeruginosus), Rock dove (Columba livia), Greater spotted eagle (Aquila clanga), Rock dove (Columba livia), L. domesticus, Wren (Troglodytes troglodytes), Blackbird (Turdus merula), Wren (Troglodytes troglodytes), Redstart (Phoenicurus ochruros), Blackbird (Turdus merula), Pied flycatcher (Ficedula hypoleuca), Blackbird (Turdus merula), Nuthatch (Sitta europaea), Tree sparrow (Passer montanus), and Starling (Sturnus vulgaris). The remaining species of mites were recorded in the nests of one, or rarely two, bird species.

The most abundant species of mites were Trichouropoda orbicularis and Uroobovella pyriformis, which made up more than 68% of all specimens. Nenteria pandioni, Apionoseius infirmus, Uroobovella flagelliger, Uropoda orbicularis, Trichouropoda karawaiw and T. ovalis occupied the nests of the highest number of bird species, (nine). Trachytes aegrota and Apionoseius infirmus were found in the nests of eight species of birds, and Nenteria pandioni in six. Dinychus perforatus and Uropoda orbicularis were found in the nests of four bird species, while Trichouropoda karawaiw and Uroobovella pyriformis in nests of three bird species. The remaining species of mites were recorded in the nests of one, or rarely two, bird species.

The most abundant species of mites were Trichouropoda orbicularis and Uroobovella pyriformis, which made up more than 68% of all specimens. Nenteria pandioni, Apionoseius infirmus, Uroobovella flagelliger, Uropoda orbicularis, Trichouropoda karawaiw and T. ovalis were also quite numerous, while the remaining 20 species occurred only sparsely, and constituted 2% of the total mites. The most frequent species (i. e., the species that occurred in the highest proportion of nests), was T. orbicularis (Frequency F = 20.1%). Other frequently occurring species were U. pyriformis (F = 7.0%) and A. infirmus (F = 7.3%), U. orbicularis (F = 6.5%), N. pandioni (F = 5.5%), and T. ovalis (F = 5.2%).

**TABLE 2**

List of Uropodina mites found in the investigated nests of birds

| Mite species / Bird species | White stork (Ciconia ciconia) | Black kite (Milvus migrans) | Red kite (Milvus milvus) | Marsh harrier (Circus aeruginosus) | Greater spotted eagle (Aquila clanga) | Osprey (Pandion haliaetus) | Rock dove (Columba livia) | L. domesticus | Wren (Troglodytes troglodytes) | Blackbird (Turdus merula) | Pied flycatcher (Ficedula hypoleuca) | Blackbird (Turdus merula) | Goldcrest (Regulus regulus) | Green tit (Parus major) | Treecreeper (Certhia sp.) | Starling (Sturnus vulgaris) | Tree sparrow (Passer montanus) | Unknown | Numbers of mite specimens | Dominancy % | Frequency % | Maximum number of specimens in nest |
|----------------------------|-------------------------------|-------------------------------|--------------------------|-----------------------------------|--------------------------------------|--------------------------|--------------------------|--------------------------|-----------------------------------|--------------------------|--------------------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| Urobovella marginata       | C.L. Koch, 1839               | +                            | +                        | +                                 |                                      |                          |                          |                          | +                                 | +                        | +                                    |                          |                          |                          |                          | +                        |                                      |
| Urobovella obovata         | (Canestrini et Berlese, 1884) | +                            | +                        | +                                 |                                      | +                        | +                        | +                        | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Urobovella pyriformis      | (Berlese, 1920)               | +                            | +                        | +                                 | +                                    | +                        | +                        | +                        | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Urobovella sp.             |                               | +                            |                          | +                                 | +                                    |                          |                          |                          | +                                 | +                        | +                                    |                          |                          |                          |                          | +                        | +                        |
| Discourella cordieri       | (Berlesee, 1916)             | +                            |                          | +                                 |                                      |                          |                          |                          | +                                 | +                        | +                                    |                          |                          |                          |                          |                          | +                        |
| Uropoda hamulifera         | Michael, 1894                | +                            |                          | +                                 | +                                    |                          |                          |                          | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Uropoda minima             | (Kramer, 1882)               | +                            |                          | +                                 | +                                    | +                        |                          |                          | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Uropoda orbicularis        | (Müller, 1776)               | +                            |                          | +                                 |                                      | +                        | +                        | +                        | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Uropoda selnicki           | (Hirschmann et Zirngiebl-Nicol, 1969) | + |                          | +                                 | +                                    | +                        |                          |                          | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |
| Total                      |                               | +                            |                          | +                                 | +                                    | +                        | +                        | +                        | +                                 | +                        | +                                    | +                        | +                        | +                        | +                        | +                        | +                        |

Number of collected nests | 12               | 2                            | 2                          | 12                                 | 4                                    | 2                         | 14                       | 1                         | 2                                 | 3                         | 2                         | 43                       | 1                         | 79                       | 15                       | 78                       | 3                         | 1                         | 3                         | 36                        | 9                         | 15                       |

Numbers of mite species    | 12               | 2                            | 2                          | 4                                 | 1                                     | 8                         | 3                        | 1                         | 2                                 | 6                         | 6                         | 1                         | 9                         | 3                        | 4                         | 2                         | 1                         | 2                         | 1                         | 2                         | 2                        | 4                         |

Average numbers of mite specimens | 74                   | 4                            | 24                         | 16                                 | 3157                                  | 10                        | 1                         | 6                         | 50                                 | 1                         | 1                         | 6                        | 1                         | 7                        | 3                         | 31                       | 1                         | 33                       | 10                        | 1                         |
Variability of mite communities across nest types

The collected samples came from nest boxes, one year nests, and perennial nests. The majority of uropodine species (19) were found in one year nests, and a minority (6) in nest boxes. Perennial nests were occupied by 17 mite species.

The dominance structure of particular nest types was diverse. One-year nests were dominated by T. orbicularis, whose specimens made up more than 82% of the total number of Uropodina found there. The second most abundant species was T. karawaiewi, approaching almost 8%. The low frequency of occurrence of particular mite species in one-year nests (below 10%) is quite remarkable. The average number of mite specimens in these nests was 15.

The communities of mites in perennial nests were dominated by two species, U. pyriformis and T. orbicularis, which constituted 62% of all Uropodina found there. The frequency of occurrence of both species was also relatively high, more than 35%. The average number of specimens was much higher than in the other nest types, at more than 50 specimens per sample.

T. orbicularis was the most abundant species in the material collected from nest boxes, with more than 81% of the total number of specimens. However, the average number of specimens per sample was low (4.2), and it occurred in only 20% of the nests.

Variability of mite communities across bird species

Eight of the 31 bird species were represented by more than 10 nests (Table 2). Some examples of the relative abundance and frequency of occurrence of mites in the nests of these species are presented in Table 3.

<table>
<thead>
<tr>
<th>Mite species / Bird species</th>
<th>White stork (Ciconia ciconia)</th>
<th>White-tailed Sea Eagle (Haliaeetus albicilla)</th>
<th>Black bird (Turdus merula)</th>
<th>Starling (Sturnus vulgaris)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D%</td>
<td>F%</td>
<td>D%</td>
<td>F%</td>
</tr>
<tr>
<td>A. infirmus</td>
<td>0.92</td>
<td>26.32</td>
<td>45.69</td>
<td>50.00</td>
</tr>
<tr>
<td>T. orbicularis</td>
<td>31.97</td>
<td>73.68</td>
<td>13.51</td>
<td>23.33</td>
</tr>
<tr>
<td>U. ovalis</td>
<td>0.28</td>
<td>2.63</td>
<td>22.34</td>
<td>75.00</td>
</tr>
<tr>
<td>U. minima</td>
<td>0.04</td>
<td>2.63</td>
<td>2.70</td>
<td>2.33</td>
</tr>
<tr>
<td>N. pandioni</td>
<td>0.46</td>
<td>15.79</td>
<td>31.47</td>
<td>50.00</td>
</tr>
<tr>
<td>T. karawaiewi</td>
<td>0.04</td>
<td>2.63</td>
<td>18.92</td>
<td>9.30</td>
</tr>
<tr>
<td>U. marginita</td>
<td>0.28</td>
<td>13.16</td>
<td>0.51</td>
<td>8.33</td>
</tr>
<tr>
<td>U. pyriformis</td>
<td>48.73</td>
<td>65.79</td>
<td>8.11</td>
<td>26.32</td>
</tr>
<tr>
<td>Trichouropoda sp.</td>
<td>0.39</td>
<td>5.26</td>
<td>10.50</td>
<td>31.58</td>
</tr>
<tr>
<td>U. flagelliger</td>
<td>0.04</td>
<td>2.63</td>
<td>0.04</td>
<td>2.33</td>
</tr>
<tr>
<td>Uroobovella sp.</td>
<td>6.36</td>
<td>55.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. structura</td>
<td></td>
<td></td>
<td>2.70</td>
<td>2.33</td>
</tr>
<tr>
<td>U. tecta</td>
<td></td>
<td></td>
<td>8.11</td>
<td>2.33</td>
</tr>
<tr>
<td>U. pannonica</td>
<td></td>
<td></td>
<td>2.70</td>
<td>2.33</td>
</tr>
<tr>
<td>T. segrota</td>
<td></td>
<td></td>
<td>5.41</td>
<td>2.33</td>
</tr>
</tbody>
</table>

The richest community of mites was found in the nests of the White Stork (Ciconia ciconia). The frequency of mites in these samples was very high, 89.47%. The number of specimens recorded in individual nest varied from 1 to 522 (average 74 ± 234). The mite species found most frequently in nests of the white stork were T. orbicularis, U. pyriformis and U. orbicularis. Less frequent were U. flagelliger, A. infirmus and N. pandioni. The most abundant species in White Stork nests were U. pyriformis and T. orbicularis, whose population comprised 81% of the total Uropodina. The next two most numerous species, U. flagelliger and T. orbicularis, together constituted about 17% of the specimens. The remaining species were sparse or occurred only once, and it is possible that they were in the nests by accident.

The second most diverse mite community came from the nests of the Blackbird Turdus merula, which hosted nine species. However, the occurrence of mites was sporadic. The frequency of Uropodina reached only 16.3%, and the number of specimens per nest varied from 1 to 15 (average 0.9 specimen ± 2.88). T. ovalis was the most frequent species in the nests of the Blackbird but its frequency was very low, less than 10%. The occurrence of other species was accidental, and the mites in general were very sparse in this habitat. A. infirmus, T. ovalis, T. karawaiewi, and T. orbicularis were the most numerous species, with populations that totalled 78.4% of the overall number of specimens. The rest of species were infrequent or occurred only once.

Four species of Uropodina were found in 79 nest boxes of the Pied flycatcher Ficedula hypoleuca. The frequency of mites in these nests was very low, only 16.5%, and the number of specimens from the collected nests varied from 1 to 33 (average 0.9 specimen ± 4.02).

Trichouropoda orbicularis is the only species of Uropodina that occurred in the nests built in nest boxes by the Great tit Parus major. Its frequency was less than 10% and the number of specimens in particular nests varied from 1 to 215 (average 3.1 ± 24.36).
A similar situation was found in nests of the Blue tit P. caerulescens, where only T. orbicularis is found, except for the rare occurrence of U. pyriformis. The frequency of Uropodina in the nests of this bird species was higher, more than 33%, and the number of specimens varied from 1 to 103 per nest (average 7.3 ± 26.5).

The mite community in the nests of the European Starling Sturnus vulgaris included two species, T. orbicularis and A. infirmus. The frequency of mites in these nests was greater than 40%, and the number of specimens per nest varied from 1 to 630 (average 24.53 ± 105.52). T. orbicularis occurred in some starling nests in large numbers. A. infirmus was rather more sporadic, with a maximum of 4 specimens in one nest.

The perennial nests of the White-tailed Sea Eagle Haliaeetus albicilla were occupied by only four species of Uropodina, much poorer than those of the white stork, which are similar in construction and size. Nonetheless, the frequency and the number of mites in eagle nests were very high. The number of specimens per sample varied from 1 to 51 (average 16.33 ± 17.13).

T. ovalis, A. infirmus and N. pandioni are the most characteristic species for of this raptor’s nests. Specimens may be found in every second nest, or even more frequently. A. infirmus is the most numerous species in the White-tailed Sea Eagle nests, and it constitutes more than 45% of the total number of Uropodina. The maximum number of specimens of this species found in one sample was 40.

**DISCUSSION**

Thus far, 28 mite species of the suborder Uropodina have been recorded from birds’ nests in the European literature (Table 1). These results come from only Scandinavia, Poland, and Slovakia, indicating that the rest of Europe is under-researched in this particular area.

Our results show that different mite communities occur in one-year nests, perennial nests, and nest boxes. This is presumably the result of variability of life history strategies as well as the dispersal ability of the particular mite species that occur in these three microhabitats. Many soil species were found in one year nests, mainly those built by Turdus merula, which coats the bottom and sides of its nests with soil.

Twelve out of the 28 Uropodina species found in our material have never been seen in nests before. The low frequency of common soil species in the nest communities is noteworthy, for example, Trachytes aeegra, Uropoda minima, and Urodeapsis tecta. T. orbicularis and A. infirmus should be considered as typical nest-inhabiting (nidicolous) species. Uroseius hunzikeri, U. marginata and U. flagelliger are also nidicolous, previously recorded in the nests of birds and small mammals (Błoszyk, 1985; Karg, 1989; Mašan & Kristofík, 1993; Mašán 2001).

Uroobovella pyriformis, the most numerous uropodine species represented in the nests of the White Stork, was previously known in Poland as a species that is numerous and frequent in tree holes (Błoszyk, 1990). It is a phoretic species which disperses on flies (Diptera) (Błoszyk et al., 2003).

Another species that occurs in storks’ nests, U. orbicularis, is associated with other kinds of unstable microhabitats. It spreads phoretically, and its deutonymphs can be found in masses on coprophagous beetles (Błoszyk et al., 2002; Baierlein & Błoszyk, 2003, 2004).

Phoresy may be one of the primary means of dispersal for many uropodine species found in birds’ nests. In addition to U. pyriformis and U. orbicularis, N. pandioni, T. ovalis, U. marginata, and A. infirmus are also spread phoretically. Typical soil species, such as U. tecta, U. panonica, U. minima, and T. aeogra, get into nests accidentally, sometimes brought in with building material or nest lining, or sometimes directly on the bird’s feathers. Typically, soil species do not occur in perennial nests, but phoretic species are common there. Uropodine communities in nest boxes consist mainly of species which spread phoretically. This may suggest that it is possible for them to colonise nest boxes only with the help of insects.

Contrary to most soil-dwelling Uropodina, such as T. aeogra, Polyaspinus cylindricus, U. tecta, or U. panonica, which are entirely female, the Uropodina inhabiting birds’ nests consist mainly of bisexual species. All-female species found in the nests are accidental and do not play an important role in the structure of the communities. This is consistent with observations of other authors (Walter & Lindquist, 1995; Błoszyk et al., 2004) who suggested that apogamic species colonise unstable microhabitats rather unwillingly.

It is also possible that birds’ nests may have served as refuges for many Uropodina species, for which local populations survived glaciation and subsequently spread to occupy other habitats after the glacial recession in Poland, by means of phoresy on insects or birds.

Currently, due to fragmentation and isolation of forest habitats, birds’ nests might again be of crucial importance for the dispersal of Uropodina mites. Both phoresy and direct spread by birds, along with the nest building material or on feathers, may enable the migration of mites between isolated ‘forest islands’. This could allow for the maintenance of species diversity and gene flow within many species of Uropodina.

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Uropodine mite communities (Acari: Mesostigmata) in birds’ nests in Poland


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Surface architecture of the mouth cavity of a carnivorous fish *Rita rita* (Hamilton, 1822) (Siluriformes, Bagridae)

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ABSTRACT: The topological characteristics of the mouth cavity of the carnivorous fish *Rita rita* were explored by means of scanning electron microscopy. The mouth cavity lining of *R. rita* may be distinguished into the roof and the floor. Papilliform teeth present on the premaxillae and the anterior regions of the dentaries are associated with seizing, grasping and holding of prey. The molariform teeth on the palatine regions and the dentaries are used for crushing and grinding of food items. The taste buds in the mouth cavity are of three types (types I, II, and III). The different types of taste buds are elevated from the epithelium at different levels, which may be useful for ensuring full utilization of the gustatory ability of the fish, detection and analysing of taste substances, as well as for assessing the quality and palatability of food, during its retention in the mouth cavity. A firm consistency or rigidity of the free surface of the epithelial cells may be attributed to compactly arranged microridges. These structures protect against physical abrasions potentially caused during food manoeuvring and swallowing. Furthermore, protection of the epithelium from abrasion is enhanced with mucous cell secretions, which lubricate ingested food items. Observations of the surface architecture of the mouth cavity of *R. rita* are discussed within the context of feeding and habitat preferences as well as ecomorphological adaptation of the species.

KEY WORDS: *Rita rita*, mouth cavity, surface architecture, SEM.

INTRODUCTION

The mouth cavity is an important component of the alimentary canal. It may be involved in the seizure, the selection of food, rejection of undesirable items ingested by fish and pre-digestion preparation of food. Among species, the mouth cavity shows great plasticity and structural adaptability for the exploitation of different food items (Kapoor et al., 1975; Kapoor & Khanha, 1994; Horn, 1998).

Literature on the surface ultra-structure of the mouth cavity in fish is scanty. Surface organisation of the mouth cavity, using scanning electron microscope, was studied for the carnivorous fishes *Gadus morhua* Linnaeus, 1758 (Bishop & Odense, 1966); *Sparus aurata* Linnaeus, 1758 (Cataldi et al., 1987) and the surface plakton feeder, *Catla catla* Hamilton, 1822 (Sinha & Chakrabarti 1985). Meyer-Rochow (1998) described the distribution and surface morphology of taste buds on the tongue of a variety of fishes having different food habits and inhabiting a variety of habitats. Ezeasor (1982) described taste buds in the oropharyngeal cavity of an active predator *Salmo gairdneri* Richardson, 1836. Hansen et al. (2002) reported the development of taste buds at different locations including the oropharyngeal cavity of *Danio rerio* Hamilton, 1822. More recently, Fishelson & Delarea (2004) and Fishelson et al. (2004) described the form and distribution of taste buds and dentition in the oropharyngeal cavity of several benthic, gobbiid and cardinal fish species.


*Rita rita* Hamilton, 1822 (Bagridae, Siluriformes) is a sluggish, bottom dwelling, carnivorous catfish and the bulk of its food primarily consists of molluscs. In addition, it feeds on small fishes, crustaceans, insects, as well as on decaying organic matter.

The objective of this study was to examine the surface architecture of the mouth cavity of *R. rita* to better understand its role in relation to the species’ food and habitat preferences.
MATERIALS AND METHODS

Live specimens of *R. rita* (mean ± SD standard length, SL, 105 ± 6 mm; n = 10) were collected from the river Ganges at Varanasi, Uttar Pradesh. The fishes were maintained in a laboratory aquarium with a layer of sand at the bottom for 24 – 48 h at 25 ± 2°C and were fed with minced goat liver. The fishes were cold anaesthetised following MITTAL & WHITSEAR (1978), to excise the roof and the floor of the mouth cavity. The excised tissues were treated and prepared for scanning electron microscopy following PINKY et al. (2002). Critical point dried tissues were attached to stubs with the roof or floor facing upwards, were coated with gold and were then examined with a scanning electron microscope (Leo, 435 VP, England). The results were recorded on a Pentium IV computer (Vintron).

OBSERVATIONS

In *R. rita* the mouth cavity is spacious and opens anteriorly through a wide transverse mouth, which is bordered by the upper and the lower lips. The mouth cavity lining was, for convenience, divided into two regions – the dorsal roof and the ventral floor.

The roof of the mouth cavity comprised antero-posteriorly an upper jaw consisting of the premaxillae and the maxillae; the velum – a thin fold at the inner boundary of the upper jaw; the palatine regions bilaterally supported by the palatine bones; and the palate extending up to the pharynx (Fig. 1a). The upper jaw displayed two ovoid areas borne on the premaxillae that appeared fused in the middle of the jaw. The palatine regions, in general, were ovoid, separated from each other by a part of the palate; they converged or even merged anteriorly (Fig. 1a).

The floor of the mouth cavity comprised antero-posteriorly a lower jaw consisting of the dentaries and the angulars; the velum - a thin fold at the inner boundary of the lower jaw; and the tongue extending up to the pharynx (Fig. 1b). In the lower jaw, an elongated ridge-like structure occurred between the dentaries (Figs 1b, c, d). The ridge was narrow at the anterior side and gradually widened towards the posterior side of the jaw (Fig. 1c). The tongue consisted of an anterior region and the major posterior region extending up to the pharynx. The middle part of the posterior region was differentiated into an elongated ridge-like structure similar to that between the dentaries (Figs 1b, e).

The palatine regions, the dentaries and the oval areas on the premaxillae were characterized by the presence of teeth (Figs 1a, b). In contrast, the palate, the tongue, the velum, the maxillae and the angulars, were edentulous. In addition, the teeth were papilliform on the premaxillary regions (Figs 1a, f), molariform on the palatine regions (Fig. 1a) or both on the dentaries (Figs 1b, c).

The papilliform teeth were short, conical shaped, relatively widely spaced and irregularly distributed on the entire surface of the oval area of each premaxilla (Figs 1a, f). They were, however, restricted to the outer regions of the anterior areas of the dentaries (Fig. 1b). The papilliform teeth pierced through the epithelium, thus only the distal part of each tooth was exposed. The tooth tips appeared fragile and often showed wear and breakages. The proximal part of the tooth remained covered under the epithelium (Fig. 1g).

The molariform teeth in the palatine region and on the dentaries were arranged in several rows. They were round and small in diameter at the anterior and outer areas with their diameter gradually increasing towards the posterior and inner areas (Figs 1a, b). The rows of these teeth on the dentaries and palatine regions were generally oriented parallel to their outer margins. The small molariform teeth, probably in developing stage and on their way of eruption, remained covered by the epithelium, which at times was seen ruptured at one or several places (Figs 1h, i). In contrast, the large molariform teeth pushed their way through the epithelium and their free surfaces were thus exposed (Fig. 1i).

The epithelial surface of the mouth cavity appeared smooth. In the anterior region of the tongue, however, it was folded into extensive horizontal ridges separated by shallow grooves (Fig. 1j). Further, the surface of the epithelium covering the lateral sides of the molariform teeth was uneven or indented like a honeycomb as the epithelial cells showed characteristic depressions or invaginations (Fig. 1h).

The epithelium of the mouth cavity consisted of a mosaic pavement of irregular polygonal epithelial cells of varied dimensions (Figs 2a - d). The free surface of each epithelial cell was characterised by the presence of a series of microvridges. The microridges of the cells appeared smooth, uniform in width and sinuous. They were compactly arranged, extensive and often form maze-like patterns (Figs 2a, b) or extensively branched and interwoven to form web-like patterns (Figs 2c, d).

On the epithelium, rounded or somewhat triangular crypts were evident between 2-3 epithelial cells at irregular intervals. These crypts represented the mucous cell openings (Figs 2a, c, d) as well as the taste pores of the taste buds, which were either slightly sunken or at the level of the epithelium. The taste buds were characterised by the presence of several microvridges, each representing a taste hair, projected at the surface through the taste pore (Fig. 2d). The mucous cell openings and the taste buds, however, could not be observed in the epithelium covering the surface of the molariform teeth (Fig. 2b).

Furthermore, the epithelium was characterised by the presence of a large number of prominent, irregularly distributed conical or papillate epithelial protrusions (Figs 1a, b, c), which were either isolated or in small groups of 2-5 (Figs 1d, i, j; Figs 2e, f, g). The protrusions on the palate, the tongue, the velum and in between the papilliform teeth on the jaws were small in dimensions and low in height. In contrast, protrusions in the vicinity of the molariform teeth on the palatine region and dentaries, were often relatively large in dimensions (Fig. 1i; Fig. 2g), concentrated and projected well above the surface of the epithelium.

The characteristic ridge-like structures between the dentaries (Figs 1b, c, d), in the lower jaw, and on the posterior region of the tongue (Figs 1b, e) were formed by clusters of large, conspicuous, irregularly polyhedral, mound-like epithelial elevations, which were separated from each other by deep clefts. On the surface of each such elevation, several prominent papillate or conical epithelial protrusions were evident (Fig. 1e).
Fig. 1. – Scanning electron photomicrographs of the surface architecture of (a, f-i) the roof and (b-e, j) the floor of the mouth cavity of R. rita. In figures anterior is to the top except in (d) where anterior is to the left. (a) UJ: Upper Jaw; V: Velum; PR: Palatine Regions; and P: Palate. Upper lip: arrowhead; Papilliform teeth on UJ: arrows; Molariform teeth on PR: barred arrows; and dots like epithelial protrusions on P, V and in between the teeth. (Scale bar = 1mm). (b) LJ: Lower Jaw; V: velum and T: Tongue. Lower lip: asterisk; Papilliform (arrows), and molariform teeth (barred arrows) on dentaries, ridge-like structure (arrowhead) between the dentaries and on T (open arrow); and dots like epithelial protrusions on T, V and in between the teeth. (Scale bar = 1mm). (c) Ridge-like structure (arrowheads) between the dentaries. Papilliform (arrows) and molariform teeth (open arrows) on the dentaries. Epithelial protrusions (barred arrows) on V and in between the teeth. (Scale bar = 200µm). (d) V and ridge-like structure between dentaries: asterisk. Taste buds: arrows (Scale bar = 100 µm). (e) Ridge-like structure on T with clusters of mound-like epithelial elevations separated by deep clefts. Taste buds: arrows. (Scale bar = 100 µm). (f) UJ with papilliform teeth. (Scale bar = 100µm). (g) Papilliform tooth piercing through the epithelium. (Scale bar = 30µm). (h) PR with a part of small molariform tooth (asterisk), which in lower magnification (i) is indicated by arrowhead. Ruptures of epithelium: arrows. Epithelial cells at the lateral side of the tooth were invaginated. (Scale bar = 10µm). (i) PR with a small tooth (arrowhead) covered with epithelium and a large tooth (open arrow) with exposed surface. Conical epithelial protrusions: arrows. (Scale bar = 100µm). (j) Anterior region of T with ridges separated by shallow grooves. Conical or papillated epithelial protrusions: arrows. (Scale bar = 100µm)
The epithelial protrusions were covered with concentrically arranged epithelial cells (Figs 2f, g). The latter often showed shallow depressions or invaginations. At the peak of each protrusion, a taste bud was located, with closely packed microvilli serving as taste hairs, which protrude to the surface through a rounded taste pore (Figs 2f, g). The microvilli, as viewed from the top, could be divided into two types: (a) those small in diameter, short and papillate, in the centre of the taste pore (Fig. 2h); and (b) those relatively large in diameter, elongated in the peripheral region of the taste pore (Fig. 2h).

The taste buds, on the basis of the degree of elevation and external surface morphology, were grouped into three categories (i.e., Type I, Type II and Type III) following REUTTER et al. (1974) and EZEASOR (1982). The type I taste buds were prominently elevated being located on
epithelial protrusions (Fig. 2g), projected well above the surface, often in the vicinity of molariform teeth (Fig. 1i) and on the ridge like structures between the dentaries and on the tongue (Figs 1c, e). The type II taste buds were slightly elevated being located on small, low-height epithelial protrusions, on the palate, the tongue and the velum (Fig. 1d; Figs 2e, f). The taste pores of these taste buds appear in slight depressions at the apices of the epithelial protrusions. The type III taste buds were located either slightly sunken or at the level of the general epithelium throughout the mouth cavity (Fig. 2d). Furthermore, REUTTER et al. (1974) postulated that the taste bud Type I and II are mostly mechanoreceptors and Type III are essentially chemoreceptors.

DISCUSSION

Differences described for the dentition, the distribution of taste buds and mucous cells and the patterns of microridges on the epithelial cells at different regions of the roof and the floor of the mouth cavity of R. rita could be considered as adaptations to various food preferences and feeding behaviour of the fish.

The presence of papilliform teeth on the premaxillae and the outer regions of the dentaries may be associated with seizing, grasping, holding and preventing the escape of small prey, occurring in the diet of R. rita. Notwithstanding, ISLAM (1951) failed to mention the presence of teeth in the mouth cavity of several teleost fishes, including R. rita, whereas KHANNA (1962), using light microscopy, reported their presence on the premaxillae but not on the dentaries. Nonetheless, recent scanning electron microscope studies have shown the presence of similar elongated conical and spine-shaped teeth on the jaws of Denticeps clupeoides Clausen, 1959 (SIRE et al., 1998), Atherion elymus Jordan & Starks, 1901 (SIRE & ALLARD, 2001) and several cardinal fish species (FISSHELSON et al., 2004). These fishes feed also on small prey. Teeth on jaws, similar to the papilliform teeth of R. rita, have also been described light microscopically in several other catfishes [e.g. Mystus (= Sperata) aor Hamilton, 1822 and Silonia silindia Hamilton, 1822; KHANNA, 1962; Clarias batrachus Linnaeus, 1758; SAXEN, 1973; Mystus gulio Hamilton, 1822; PASHA, 1964; Heteropeutes fossilis Bloch, 1794; CHITRAY & SAXENA, 1962; ANDERSONIA leptura and Siluranodon auritus; GOLUBTSOV et al., 2004]. Most of these fishes are bottom-dwelling species and their food primarily consists of small fish and invertebrates. KHANNA (1962) reported pronounced, large, curved teeth on the jaws as well as on vomers and palatines of piscivores Muraenesox (=Congresox) talabon Cuvier, 1829, Harpadon nehereus Hamilton, 1822, Notopterus (=Chitala) chitala Hamilton, 1822, and Channa marulius Hamilton, 1822. He suggested that such teeth are intended to hold securely the prey in the mouth. BISHOP & ODENSE (1966) also reported simple, pointed curved teeth in the mouth cavity of the carnivorous Gadus morhua Linnaeus, 1758 and suggested that they help impale prey. In herbivorous fishes however (e.g. Labeo horie Heckel, 1846-49; GIGGIS, 1952; Cirrhinus mrigala Hamilton, 1822; KHANNA, 1962; SAXEN, 1973; Labeo (=Sinilabeo) dero Hamilton, 1822; SAXENA, 1980; HILSA (=Tenualosa) ilisha Hamilton, 1822 and Mugil (=Rhinomugil) corsula Hamilton, 1822; SAXEN, 1973), where holding or grasping of food is not required, the jaws are edentulous.

The presence of molariform teeth with rounded and blunt surfaces have also been reported for R. rita in the past (KHANNA, 1962). These structures may be associated with the crushing and grinding of hard bodied prey (e.g., molluscs, crustaceans). BOND, 1979 suggested that in Anarrhichthys ocellatus Ayres, 1855, which feed on shelled animals, molariform teeth on the jaws are used to crush the shells. Molar-like or plated teeth have also been reported in adult Sperata auritus Linnaeus, 1758, which feed mainly on molluscs, polychaetes, and crustaceans (Cataldi et al., 1987). Molariform teeth may also be used to compress food into a manageable lump, prevent its escape and ensure its progress towards the throat (WHITEHEAD, 1977).

Sense of taste is an important property in fish for distinguishing from a variety of food available to them in an aquatic environment (HARA, 1994). In R. rita, the presence of taste buds could be considered as an adaptation to its bottom dwelling and sluggish feeding behaviour compensating for the restricted visibility in the foul turbid water it inhabits. KHANNA (1968) studied the distribution of taste buds in the mouth cavity of a variety of fishes. He showed that taste buds were rare or absent from highly predaceous carnivores – Muraenesox (=Congresox) talabon Cuvier, 1829 and Harpadon nehereus Hamilton, 1822), which rely more on their eyesight for detecting prey. Channa striata Bloch, 1793, a carnivorous fish, which feed both by sight and taste, has a better gustatory sense; and Tor tor Hamilton, 1822, a hill stream carnivorous fish, which selects its food from among the mud, has the best developed gustatory faculty with numerous taste buds in the buccal cavity. Further, KHANNA (1968) reported that in the plankton feeder Ilisha filigera Valenciennes, 1847 taste buds are present but in much less number than in Tor tor. In addition, MEYER-ROCHOW (1981) also reported few taste buds on the tongue of Carapus mourlani Petit, 1934 and absence of taste buds on the tongue of Diretmus sp. Johnson, 1864. These two mesopelagic species possess poorly developed taste receptors, for they inhabit areas of low prey abundance and diversity (MEYER-ROCHOW, 1981).

In fish, food items seized, grasped, snapped, or nibbled with jaws, in general, are retained in the mouth cavity. During the retention period these are subjected to final sensory judgement. As a result, a food item can then be either rejected or swallowed (For review of the literature see KASUMYAN & DOVING, 2003). In R. rita, prominent taste buds may be useful in assessing the palatability of the food and decide whether to swallow or spit it out (e.g., KASUMYAN & DOVING, 2003). The decision is made when contact of food with taste buds results into a mechanical impulse perceived and transmitted from the sensory cells to the brain centres (ATEMA, 1971; REUTTER et al., 1974; REUTTER & BREIPOLH, 1975). Furthermore, the location of the taste buds (type I and type II) at the summit of the conspicuous epithelial protrusions may increase the probability of contact between the receptors and the food items when retained in the mouth cavity. The latter may
result in enhanced efficiency in perception and sorting of food types as well as in assessing the quality and palatability of food items. Meyer-Rochow (1981), who observed taste buds on distinct dome-like elevations on the surface of tongue of several fish species, suggested that elevated taste buds could have a superior perception of taste, in contrast with non-elevated ones or with receptors sunken below the level of the tongue. The same was also suggested for Salmo gairdneri (Ezeasor, 1982).

Structures similar to the type III taste buds in the mouth cavity of R. rita were also observed on the snout, lips and barbel epithelium of Gadus morhua Linnaeus, 1758 (Harvey & Batt, 1998), on the head, lips and gill rakers of Danio rerio Hamilton, 1822 (Hansen et al., 2002), on the lips and mouth of some blenniid and gobiid fishes (Fieshelson & Delarea, 2004), and in the oro-pharyngeal cavity in a number of cardinal fishes (Fieshelson et al., 2004). Further, Fieshelson et al. (2004) in addition to the taste buds belonging to the type III category reported yet another category the type IV.

The presence of ridge-like structures on the tongue and in between the dentaries of R. rita is important, for it results in the projection of taste buds above the level of the surface of the epithelium. In addition, the occurrence of taste buds on these structures may be associated with the high degree of competence of the fish in taste preference and selection of food. Furthermore, these ridges may be considered to guide the food particles in the mouth cavity towards the pharynx. Islam (1951) while describing the mouth cavity of R. rita made no reference of such structures. Khanna (1962) also did not report such a ridge in between the dentaries in R. rita. However, he reported the presence of a prominent longitudinal ridge on the tongue but made no reference of epithelial protrusions and taste buds on it. No additional information on similar structures was found in the literature for other fishes.

Presence of taste buds on the velum in R. Rita may serve to screen the quality of food before it is passed onto the mouth cavity. Fieshelson et al. (2004) also reported a large number of taste buds in the oral valves in cardinal fishes. The same, however, was not true for Salmo gairdneri (Ezeasor, 1982).

The free surface of the epithelial cells at different locations (e.g., skin, lips, mouth cavity, pharynx, gills) of different fishes, is characteristically differentiated into series of microridges, and referred to as cytoplasmic folds, microvilli, microfolds, microvillar ridges, ridges or microridges (For review of literature see Garg et al., 1995). The microridges are organized in different ways to form intricate patterns and are thought to be involved in various functions; e.g., absorptive or secretory activities, to aid in laminar flow, holding mucous secretions to the cell surface, to provide reserve surface area for stretching or distortion, to facilitate the spread of mucus away from the goblet cells, to provide mechanical protection, to enhance mechanical flexibility (For review of literature see Whitear, 1990; Olson, 1995).

The form of microridges corresponds to type and rate of secretion at the apex. Some variations in surface pattern may reflect the stage of maturation of a particular cell, or groups of cells that have recently reached the surface. Furthermore, the development of microridges are then a consequence of the arrival of new membranes, as vesicles carrying the secretion fuse with the apical plasmalemma and high ridges would indicate a rapid sequence of arrival of secretory vesicles at the surface (Whitear, 1990). In the mouth cavity of R. rita, presence of prominent microridges could thus be considered to reflect high secretory activity of epithelial cells.

Compactly arranged microridges, often interconnected with microbridges, may also be considered to provide rigidity to the free surfaces of the epithelium, in order to protect against physical abrasions, when manoeuvring of ingested prey (e.g., Mittal et al., 2004).

Invaginations and shallow depressions of the epithelium at the lateral sides of molariform teeth and the tongue of R. rita may also enhance plasticity and allow the stretching of the epithelial cells during the manipulation of food consumed by the fish. Mucus is elaborated by mucous cells distributed in the mouth cavity of R. rita. Secreted mucus is used to lubricate both the epithelium and ingested food items, in order to assist the smooth passage of food and thus protect the epithelium from possible mechanical injury (Ezeasor & Stokoe, 1980; Martin & Blaber, 1984; Sinha & Chakraborti, 1985, 1986; Anderson, 1986; Chakraborti & Sinha, 1987; Park & Kim, 2001; Podkowa & Goniakowska-Witalinska, 2003). Mucus has also been associated with various food-processing activities: e.g., particle entrainment (Friedland, 1985; Tibbetts, 1997; Eiras-Stofella & Chartvet-Almeida, 1998); pregastric digestion (Murray et al., 1994); absorption process (Grau et al., 1992; Ezeasor & Stokoe, 1980); and extraction of nutrients from plant material digested by fish (Tibbetts, 1997).

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First record of *Craspedacusta sowerbyi* Lankester, 1880 (Cnidaria: Limnomedusae: Olindiidae) in the Proserpina Reservoir (Extremadura, SW Spain) with notes on their feeding habits

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ABSTRACT. The first record of the invasive freshwater jellyfish *Craspedacusta sowerbyi* Lankester in the Proserpina Reservoir, a shallow reservoir in the Extremadura region of SW Spain is reported in this paper. *C. sowerbyi* was recorded in open water away from the immediate littoral zones. All individuals captured were females with bell diameters ranging from 7-21 mm. Tentacle numbers ranged from 218 to 398. The stomach contents included most of the taxa abundant in the zooplankton, with *Daphnia longispina* being the most abundant.

KEY WORDS : freshwater medusa, feeding habits, Iberian Peninsula

INTRODUCTION

The freshwater jellyfish *Craspedacusta sowerbyi* Lankester, 1880 is an invasive species native of China. Apart from China, *C. sowerbyi* has colonized most continents (Dumont, 1994) but only at the end of the 19th and into the 20th century. The first records from non natural open waters correspond to the end of 19th century. It has been recorded in Italy, France, Sweden, Central Europe, Portugal (Ferreira, 1985), U.S.A. (Devries, 1992), Canada (Mcalpine et al., 2002), Hawaii, South Australia (Thomas, 1950), New Zealand, Philippine Islands, China, Japan, Central Asia, South America (Acker, 1976) and Africa (Rayner, 1988), as well as in Spain (in Cordoba and Madrid provinces, M. Villena, pers. comm., Fig. 1).

The life cycle of *C. sowerbyi* includes both a polyp and a medusa stage. It belongs to the Order Hydroidea; Suborder Limnomedusae, which have only a tiny and solitary polyp. *Craspedacusta sowerbyi* produce free-swimming medusae, which bud off from the side of the polyp (Barnes, 1980; Pearse et al., 1987). The active medusa stage of cnidarians is the sexually reproducing stage. The polyp is rarely encountered, despite its ability to withstand long periods of food shortage and tolerate extreme variations in temperature and light conditions by encysting as resting bodies consisting of a ball of cells surrounded by a membrane (Acker, 1976; Acker & Muscat, 1976).

Although freshwater medusae have been known for more than 100 years (Lankester, 1880) (in China for centuries) and much literature is available, our knowledge (systematic, ecological) of these animals is unsatisfactory (Dumont, 1994). This paper presents the results of a study of the spatial distribution, population size structure, and diet of the medusae in the Proserpina Reservoir, in the south-western Iberian Peninsula.

MATERIAL AND METHODS

The Proserpina Reservoir is located in the centre of Extremadura (SW Spain, Fig. 1), and covers an area of 42.15 ha at an altitude of 290 m a.s.l. Its maximum length is 1177 m, maximum width 726 m, and maximum water depth about 8 m. However the reservoir is not thermally stratified. The aquatic vegetation includes *Chara* spp., *Ranunculus* spp., and *Potamogeton pectinatus*, with *Phragmites* spp. and *Typha angustifolia* along the shores. The site is surrounded by *Quercus rotundifolia* woodland, which has been cleared in the region of the dam wall, and some limited areas of non-irrigated agriculture have been developed. No data on water quality of the reservoir exist.
Collections of *C. sowerbyi* were performed during daylight hours on 7 October 2004. Climatic conditions during the summer in the Extremadura region are generally hot (mean September air temperature at the study site is 30.1°C), with a September mean rainfall of 23 mm (mean annual rainfall is 624 mm). No further temporal sampling was undertaken to measure population growth and development. Densities of *C. sowerbyi* in the waterbodies were estimated at 20 m intervals along two bisecting transect of the lake (Fig. 1). Counts were made within a 60 s period of the numbers of medusae visible in 1 m² of surface water (n = 76) on both sides of each transect. Samples for measurement and gut analysis were collected by lowering a 50 µm mesh net to the lake bottom and rowing approximately 5 m, hauling the net diagonally to the surface. Samples were preserved with 70% ethanol. Zooplankton samples were also collected. Temperature, pH, dissolved oxygen, conductivity, and Secchi depth were measured at 11:00 h from surface water (n = 1).

The umbrellar diameter, gonad length, and number of tentacles were determined from medusae randomly selected from the net samples (n = 172). Sex of *C. sowerbyi* was determined by examining the gonadal tissue under a microscope. Mature females have eggs clearly visible as relatively large round cells embedded in the gonad surface (visible already under intermediate magnification of the dissecting microscope), usually in clusters. Juvenile females still usually have small immature eggs, distinguishable as cells significantly larger than most of the tissue, whereas males have much more uniform sized gonadal cells which are all fairly small. Sperm cells are usually present in mature male gonads. However, they are very small, distinguishable only under high magnification in the microscope (A. Petrusék, pers. comm.). Measurements were made using a stereomicroscope fitted with a calibrated ocular micrometer one day after the captures.

A random sub-sample of 41 medusae was used to identify and count prey items within the gastrovascular cavity. Items were identified under a compound microscope, and the diet was expressed as the percent frequency of occurrence (%FO) and percentage of prey (%N) of each prey according to Hyslop (1980).

Prey selection of the more commonly eaten prey was examined by Pearse’s (1982) prey selection index (V):

\[ V = \frac{a_e b_d - a_d b_e}{a_d b_e} \]

The significance of V was tested with a \( \chi^2 \) evaluation (\( \chi^2 = \frac{(a_e b_d - a_d b_e)^2}{a_d b_e} \), where \( a_e \) and \( a_d \) are the numbers of a given prey taxon in the diet and in the environment, respectively; \( b_d \) and \( b_e \) are the numbers of all other prey taxa in the diet and environment respectively; and \( a_e + a_d, b_d + b_e, d = a_e + b_d, e = a_d + b_e, \) and \( n = a_e + a_d + b_d + b_e \). Values of V can range from -1 to +1, representing complete avoidance and high selection, respectively, whereas 0 implies no selection.

### RESULTS

A total of 374 individual medusae were counted in the two transects across the reservoir (density = 2.52 ind./m²). Patches of *C. sowerbyi* were recorded in open water away from the immediate littoral zones. The number of medusae did not differ between transects (chi-square test, \( \chi^2 = 20.81, P < 0.05 \)). However, there were significantly more prey in the north part of transects (chi-square test, \( \chi^2 = 20.81, P < 0.05 \)). Mean umbrellar diameter was 14.75 mm (S.D. = 3.47, n = 172), minimum 7 mm and maximum 21 mm. Mean tentacle number was 320 (S.D. = 3.47, n = 172), minimum 7 mm and maximum 398. All the medusae examined were females, and had a typical number of four gonads. The percentage of medusae containing prey was 63.4%. The number of prey items per
medusa varied from 1 to 4 (mean S.D. = 2.69 ± 0.23). Most of the animal taxa found in the gut contents were common components of the zooplankton community of the lake, with the most frequently (Table 1) occurring prey items being Daphnia longispina, Megacyclops viridis, and D. magna. The same prey also dominated in absolute number. Other zooplankton species found in Proserpina Reservoir but not found as prey were the copepods Eucyclops serrulatus and Diaptomus spp., the cladocerans Diaphanosoma spp., and Ceriodaphnia spp., and the rotifers Anuraeopsis fissa, Filinia spp., and Polvarthra spp. No nauplii were found in gut contents.

PEARRE’S (1982) prey selection indices are presented in Table 2. M. viridis and D. longispina corresponded to the highest positive prey selection indices.

**DISCUSSION**

This study represents the first attempt to characterize morphometric characteristics and feeding biology of *C. sowerbyi* in the Iberian Peninsula. The size ranges of the medusae found in the Proserpina Reservoir were within the ranges recorded elsewhere. PENNAK (1956) noted that the medusae are often not noticed until they are over 10 mm in diameter, although smaller size ranges have been recorded (BYERS, 1945; BECKETT & TURANCHIK, 1980; RAYNER, 1988). In a temporal study in Louisiana, ZISER & BURKE (1984) found that the size range of medusae during each month of summer (April–October) was highly variable (1–17 mm), although they observed a general trend toward an increasing mean medusa diameter over their study period. In New Zealand, the umbrella diameter of *C. sowerbyi* ranged between 3.2 and 16.8 mm (BOOTHROYD et al., 2002).

*C. sowerbyi* medusae were found only in open water in the Proserpina Reservoir. This is a common feature of *C. sowerbyi* medusae, which occur in surface and deeper waters as reported by BYERS (1945) and ZISER & BURKE (1984). KIMMEL et al. (1980) found *C. sowerbyi* mid-lake in Broken Bow Reservoir with no additional sightings near shore, while in the Ohio River medusae were recorded at the surface and as deep as 3 m both day and night (BECKETT & TURANCHIK, 1980). The abundance of *C. sowerbyi* medusae in the Proserpina Reservoir was lower than the range reported by ANGRADI (1998) and BOOTHROYD et al., (2002), but higher than reported by SPADINGER & MAIER (1999) or DAVIS (1955). However, the number of medusae per m² was probably underestimated in our study due to the water’s turbidity.

In Proserpina Reservoir, *C. sowerbyi* did not show any regular distribution, as has been reported in other studies as well. BOOTHROYD et al. (2002) found a patchy distribution of *C. sowerbyi* in a New Zealand lake. They suggest that the patchy distribution occurred as a result of feeding, reproductive, or defensive activities, or possibly a wind-driven current system in the lake. Likewise, ANGRADI (1998) found a highly localized distribution of medusae in a reservoir, and suggests that the distribution of medusae may result from the pattern of dispersion from a location determined by the habitat requirement of the polyp. We have not analysed the factors affecting the distribution of *C. sowerbyi* in the Proserpina Reservoir. However, we suspect that the wind direction (from the northwest) may have been the principal factor affecting that distribution.

*Craspedacusta sowerbyi* tentacles consist of three sets of variable length (PAYNE, 1924), with shorter tentacles for food capture, and longer tentacles acting as stabilizers during swimming and predatory behaviour (PENNAK, 1956). Tentacle numbers increase with age and maturity (BOOTHROYD et al., 2002), with a clearly greater number of tentacles in mature medusae (348, PAYNE, 1924; 350, FERREIRA, 1985; 200-400, JANKOWSKI, 2001; 497, BOOTHROYD et al., 2002).

*Craspedacusta sowerbyi* medusae reach sexual maturity after 5–6 weeks, and occur more frequently in late summer (ACKER & MUSCAT, 1976; ZISER & BURKE, 1984). Estimates of optimum growth temperatures vary in the literature (25º C, McCLOY, 1959; 19-23º C, ACKER, 1976), but are generally considered to be lower for polyps than for medusae. ACKER & MUSCAT (1976) found that the polyps disintegrated at temperatures of 30º C. Medusae of *C. sowerbyi* have been reported from waters >30º C (PENNAK, 1956; ZISER & BURKE, 1984). Medusae of *C. sowerbyi* have generally only been recorded during summer in most temperate countries. Most records of polyps have also been during summer (DEVRIES, 1992), indicating increased growth and reproductive activity during warm periods. The presence of medusae of *C. sowerbyi* in the Proserpina Reservoir in summer is consistent with the widely-reported observation of *C. sowerbyi* occurring at times of high water temperatures, although water level and food abundance (LYTLE, 1962) have also been suggested as regulating mechanisms.

A common feature of records of *C. sowerbyi* has been the lack of encounters of male and female medusae together. Outside China, a very few observations have been made of populations with medusae of both sexes (PAYNE, 1924; RICE, 1958; DEACON & HASKELL, 1967). Some studies report only female medusae (e.g., PENNAK, 1956; ZISER & BURKE, 1984), although in other areas populations composed exclusively of males have also been found (BYERS, 1945; FISH, 1971; BOOTHROYD et al., 2002; LUNDBERG et al., 2005).

The present observation of the diet of *C. sowerbyi* is similar to previous reports. It includes a variety of cladocerans, copepods, and rotifers (e.g., DODSON & COOPER, 1983; SPADINGER & MAIER, 1999; BOOTHROYD et al., 2002). Medusae are active predators, and when moderately abundant can be a key factor influencing the population dynamics of other zooplankton (MATSUKI & CONOVER, 1991; GOPAL SARMA & CHAKRABARTI, 2000). Thus, predation by *C. sowerbyi* causes significantly lower abundances of bosminids and cyclopoid copepods (JANKOWSKI & RATTLE, 2000; JANKOWSKI, 2004).

Similarly to other published data (BOOTHROYD et al., 2002), nauplii were not recorded in the gut content of *C. sowerbyi* in the Proserpina Reservoir. Whether this was because they were not preyed upon, or because they were more rapidly digested and thus were missed in the analysis, is uncertain. DODSON & COOPER (1983) found in laboratory experiments that nauplii were consumed at high rates by *C. sowerbyi*. In our study, *C. sowerbyi* fed on five rotifer taxa, whereas in New Zealand (BOOTHROYD et al., 2002) only Asplanchna was recorded in jellyfish stom-
achs. DODSON & COOPER (1983) also demonstrated that *C. sowerbyi* selected large and predaceous rotifers such as *Asplancha*, and avoided small rotifers.

As in other studies (DODSON & COOPER, 1983; BOOTHROYD et al., 2002), a positive selection by *C. sowerbyi* towards copepods and cladocerans was observed in Proserpina Reservoir. However the calculated selectivity values should be interpreted with caution since *C. sowerbyi* can follow particular day-night vertical migrations (SPADINGER & MAIER, 1999), and sampling in the present study was restricted to daytime only. Thus our results may underestimate predation if it occurs at other times of the 24-h period.

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Ravens, *Corvus corax* (L. 1758), nesting on high-voltage transmission line pylons in Croatia

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ABSTRACT. This paper presents the first data on the occurrence of nesting of ravens *Corvus corax* on transmission line pylons in south-eastern Europe, based on research in Croatia. Field-work was carried out in the period 1995-2001, in the area of eastern Croatia. By 2001, 93 breeding pairs of ravens were nesting on pylons over the 380 km length of transmission lines under observation, comprising 14 surveyed routes. The breeding population increased over the period of seven years to a population density of 2.45 pairs per 10 km of the line, which is the highest recorded in the world, for ravens breeding on electricity pylons. Ravens breeding in eastern Croatia often leave a particular pylon and/or change the nest position on the pylon in a subsequent year. Evidence suggested that some ravens may disintegrate their nests on the pylons, after their young have fledged.

KEY WORDS : Raven, nesting, Croatia, pylons.

INTRODUCTION

Over the past 50 years, electric power-lines have been a conspicuous part of the landscape of industrialized countries. These lines and supporting structures are known to cause wildlife mortality, especially in birds, and in recent decades this has been increasingly documented throughout the world (O’NEIL, 1988; FERRER et al., 1991; BEVANGER, 1994; BROWN & DREWEN, 1995; NEGRO & FERRER, 1995). However, data on the utilization by birds of these structures as nest supports are not as abundant (INFANTE & PERIS, 2003).

Raven breed almost throughout the west Palearctic, except in certain densely-settled and cultivated regions (CRAMP & PERRINS, 1994). The raven is typically a forest-habitat nesting species, but a new nesting mode on high-voltage pylons has appeared as a relatively recent phenomenon in Europe. The first such cases were reported in the early 1960s from the European part of Russia (BEDNORZ, 2000), in 1969 from Great Britain (RATCLIFFE, 1997), in 1970 from Germany (STEGEMANN, 1971), in 1979 from the Vojvodina province of Yugoslavia (ZAKINSZKI, 1982), and in 1981 from Poland (BEDNORZ, 2000). In Croatia the first record of a raven’s nest on a transmission-line pylon was in 1988, in eastern Slavonia (J. MIKUSKA, pers. comm.). Outside Europe this way of nesting has also been reported from North America (WHITE & TANNER-WHITE, 1988; STEENHOF et al., 1993).

The only extensive investigation of raven nesting on transmission lines in Europe was carried out in Poland, NE Europe (BEDNORZ, 2000). The purpose of the study reported in this paper, carried out in SE Europe, was to precisely determine ravens’ utilisation of power-line supports as nest-sites in agricultural and forested lowland of eastern Croatia, and to assess the type of poles used, breeding density and distribution patterns.

MATERIAL AND METHODS

Eastern Croatia is a lowland continental region, covering 11090 km², with a population density of 78.2 inhabitants per km². The climate is continental, with an average temperature of minus 1°C in January, the coldest month, and 22°C in the warmest month, July. The mean annual precipitation is 652-754 mm. The landscape of the region is predominantly agricultural, and forests cover about 30%.

The research was carried out between 1995 and 2001. Field-work started at the end of January and proceeded till the beginning of May each year with the exception of 1998. Observations were performed using 8x30 and 10x50 binoculars and a 16-48x zoom telescope, from a vehicle and on foot. A laser range-finder (Bushnell 400) was used for measuring the height of each nest above ground. Because of the specific nesting mode on the high-voltage pylons, the line transect method (BIBBY et al., 1993) was applied instead of the standard census method of counting. Transect routes followed the existing transmission lines in the study area. Based on a map of existing power-lines supplied by the utility company in the region, transects were made on 23 transmission lines in the major part of the region. However, because of damage to some of these lines incurred during the Homeland War, complete data were available from the utility company for only 14 of these lines. Thus, although additional data on nesting were obtained, only those results that pertain to those lines for which all necessary information was available, were used for statistical calculations. Pylons are made of reinforced concrete along one of the transmission lines, while the pylons of the remaining 22 power lines are a steel-latticed type. In the base of every pylon is an identification tag with the name of the transmission line and ordinal number of the pylon. Thus, every raven nest
was given its own ‘address and home number’, which was useful for the field-research.

Since calculated variables did not indicate normal distribution (Triola, 1989), the relationship between nesting pairs of ravens and transmission line pylon types was analysed using statistical data analyses according Kruskal-Wallis test (Heath, 1995).

RESULTS

In the first year of study (1995), 30 breeding pairs of ravens were found along 190 km of transmission lines. Total length of the regularly observed lines increased in the successive years, as did the number of ravens’ nests that I found. In 1996, 61 breeding pairs were noted over 320 km of line, in 1997, 73 pairs over 330 km of line, and in 1999, 74 pairs over 330 km of line. Raven nests were not counted in 1998. In the breeding season of 2000, only a third of the regularly observed transmission line routes were checked. Thus, the low number of nests recorded in 2000 (29) cannot be interpreted as a decrease in the breeding population. In the last year of study 93 breeding pairs were found on a total of 380 km of power lines in eastern Croatia (Table 1).

During the seven-year study period (observations made in six of those years), raven nests were found on pylons of 23 power lines in the study area. Ravens nesting on five different pylon types (Fig. 1). The majority of the nests (71.74%) were built on the type B, which is the commonest type in the area. They were followed by the type C (15.45% of the nests), type D (10.16%), type A (2.43%) and type E (0.22%). The pylons of A, B and C type have three consoles, while type E has two consoles in the upper part of the pylon. With regard to the console on which the raven pair built the nest, upper, middle and lower positions were distinguished. During the study period, ¼ of the nests were built on the upper position of the pylon, while ½ was built on other positions. Pylons of type D have no consoles, and the nests were built on one or the other side of the crosswise beam. Orientation of the nest was classified as ‘southern’ or ‘northern’ with regard to the cardinal point where the settled side of the beam was directed. The majority of the nests (69.57%) were built on the north side of crosswise beams.

Density of raven nesting on transmission lines in the study area ranged from 1.58 pairs per 10 km of power lines in the north side of crosswise beams. The majority of the nests (69.57%) were built on the type B, which is the commonest type in the area. They were followed by the type C (15.45% of the nests), type D (10.16%), type A (2.43%) and type E (0.22%). The pylons of A, B and C type have three consoles, while type E has two consoles in the upper part of the pylon. With regard to the console on which the raven pair built the nest, upper, middle and lower positions were distinguished. During the study period, ¼ of the nests were built on the upper position of the pylon, while ½ was built on other positions. Pylons of type D have no consoles, and the nests were built on one or the other side of the crosswise beam. Orientation of the nest was classified as ‘southern’ or ‘northern’ with regard to the cardinal point where the settled side of the beam was directed. The majority of the nests (69.57%) were built on the north side of crosswise beams.

Density of raven nesting on transmission lines in the study area ranged from 1.58 pairs per 10 km of line (1995) to 2.60 pairs (2000). Only lines that were surveyed completely (from the first to the last pylon) have been included in density calculations. The breeding density and population size increased from year to year (Table 1).

Only 14 years passed from the appearance of the first raven nest on a transmission line pylon (1988 year - J. Mikuska, pers. comm.) to the time when numerical stability was reached (93 pairs in 2001 year). The mean population density over the whole period is 2.16 pairs per 10 km of the line (Table 1), i.e. raven nests were, on average, situated on every 5 km of the line. Although the density of breeding pairs of ravens was higher on medium-voltage transmission lines than on high-voltage lines (Table 2, comparing only pylon type B), the difference was not statistically significant (Kruskal-Wallis test: $H = 4.551; p > 0.05$).

The height of occupied pylons ranged from 24.60 m to 36.55 m, mean of 28.71 m. The height of raven nests on pylons ranged from 18.57 m to 30.10 m, mean of 24.74 m. Ravens built their nests at from 69% to 91% of the pylon’s height, at 85.55% on average.

Ravens breeding in eastern Croatia often abandoned the pylon, and/or changed the nest position on the pylon in the next year. Ravens moved from one to the first nearby pylon in 66% of cases, two pylons further in about 25%, and three pylons further in 8% of cases (Fig. 2). Removal to the fourth pylon away was noticed only once. Among 212 pylons settled by ravens, during the study period 50% were occupied only in one year. Only 2.8% of raven nests nested on the same pylon each year over the whole six-year period. Thus, ravens nesting on electricity pylons in eastern Croatia are not faithful to one, chosen pylon.

An observation in May 2000 suggested that ravens may destroy their nests on the transmission line pylons. About a week after the young birds had left the nest, an adult raven was seen holding a twig in the beak beside the nest remains (J. Mikuska, pers. comm.). In 2001 I checked a few more transmission lines where raven nestings had been reliably confirmed in the previous year. I found no nests nor nest remains. A week later, while observing the same power lines, I found three current year nests, two of which were already completed. The Croatian Electricity Company affirmed that neither protection nor renovation work had been done on those pylons in the investigated period, so human intervention was not responsible for the nest destruction. Although the study area is open agricultural landscape, there are no strong autumnal or winter winds that might have caused the nest disappearance. Further investigations of this phenomenon are needed.

TABLE I

Distribution of raven nests on different types of transmission-line pylons in eastern Croatia during the period 1995-2001 (no data for 1998).

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of controlled lines</th>
<th>Length of controlled lines (km)</th>
<th>No. of breeding pairs</th>
<th>Total No. of pylons</th>
<th>Frequency of occupied pylons (%)</th>
<th>No. of breeding pairs /10 km of the line</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>6</td>
<td>189.98</td>
<td>30</td>
<td>578</td>
<td>5.19</td>
<td>1.58</td>
</tr>
<tr>
<td>1996</td>
<td>10</td>
<td>320.41</td>
<td>61</td>
<td>941</td>
<td>6.48</td>
<td>1.90</td>
</tr>
<tr>
<td>1997</td>
<td>11</td>
<td>330.89</td>
<td>73</td>
<td>972</td>
<td>7.51</td>
<td>2.21</td>
</tr>
<tr>
<td>1999</td>
<td>11</td>
<td>330.89</td>
<td>74</td>
<td>972</td>
<td>7.91</td>
<td>2.24</td>
</tr>
<tr>
<td>2000</td>
<td>3</td>
<td>111.49</td>
<td>29</td>
<td>327</td>
<td>8.88</td>
<td>2.60</td>
</tr>
<tr>
<td>2001</td>
<td>14</td>
<td>380.24</td>
<td>93</td>
<td>1,143</td>
<td>8.33</td>
<td>2.45</td>
</tr>
</tbody>
</table>

7.30 = Avg 2.16 = Avg
DISCUSSION

Infrastructural objects with linear direction, such as highways, power transmission lines or railway tracks, modify ecosystems, whether through simple habitat conversion or through the creation of habitat edge, resulting in either population declines or increases (Knight et al., 1995). Although these energy and transportation conveyance systems are commonplace in the world, their impacts on vertebrate populations are poorly understood (Knight & Kawashima, 1993; Steenhof et al., 1993; Bednorz, 2000). Ravens live commensally with humans, and are capable of population increases and distributional changes, responding to perturbations in the man-made landscape (Knight et al., 1995).

Ravens nesting on electricity pylons in Croatia were recorded only in the eastern region. There have been no reports of this way of nesting in other regions of the country (Kralj, 1997; Lukac, 1998). It has to be emphasized

### TABLE 2

Distribution of raven breeding population on electricity pylons in eastern Croatia during the 1995-2001 period (no data for 1998).

<table>
<thead>
<tr>
<th>Pylons type</th>
<th>Voltage (kV)</th>
<th>Avg No. of pairs</th>
<th>Total No. of pylons</th>
<th>Frequency of occupied pylons (%)</th>
<th>Length of line (km)</th>
<th>Avg No. of pairs /10 km of the line</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>110</td>
<td>2.2</td>
<td>102</td>
<td>2.16</td>
<td>31.46</td>
<td>0.7</td>
</tr>
<tr>
<td>B</td>
<td>220</td>
<td>6.50</td>
<td>65</td>
<td>10</td>
<td>26.35</td>
<td>2.47</td>
</tr>
<tr>
<td></td>
<td>110</td>
<td>6.73</td>
<td>687</td>
<td>7.82</td>
<td>232.21</td>
<td>2.77</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>2.87</td>
<td>158</td>
<td>7.58</td>
<td>43.14</td>
<td>2.53</td>
</tr>
<tr>
<td>C</td>
<td>2x110</td>
<td>11.5</td>
<td>131</td>
<td>8.78</td>
<td>47.08</td>
<td>2.54</td>
</tr>
</tbody>
</table>

Fig. 1. – Types of pylons with raven nests, and nest location sites on the pylons in eastern Croatia over the period 1995-2001.

Fig. 2. – Percentage of pylons occupied for a given number of years during the period 1995-2001 (no data for 1998).
that under similar ecological conditions in neighbouring Hungarian steppe, a total of only 100 breeding pairs of ravens has been noticed (Haraszthí, 1984), while my research has shown that in eastern Croatia more than 100 pairs of ravens were nesting just on transmission line pylons. Forests in this region of Croatia have their own breeding population of ravens, too.

Studies of distribution patterns of raven population nesting on rocks and trees showed that among 27 investigated European regions, high population density (17-21 pair/100 km²) has been recorded only in three regions (Nogales, 1994). A single North American study noted 72.6 pairs/100 km², which is the highest known density for the species (Nogales, 1994). The breeding density recorded on El Hierro (35 pairs/100 km²) is the highest in any island ecosystem and the second highest recorded anywhere in the species range (Nogales, 1994).

The only reported data in Europe are on the average number of breeding pairs nesting on pylons in Wielkopolska region in Poland, which is 0.6 pairs per 10 km of the line (Bednorz, 2000). In the States of Idaho and Oregon (USA) it was on average 1.3 pairs per 10 km of the line over a 596 km long section (Steenhof et al., 1993). The average number of raven breeding pairs on electricity pylons in eastern Croatia reached 2.45 pairs per 10 km of the line by 2001 (this study). This number is 3.6 times higher than in Poland and 1.7 times higher than in the USA, and is the highest recorded on any transmission lines within the world range of the species.

Nest distribution is significantly affected by food availability. At least 70% of the nests in Wielkopolska region were built near farms, slaughterhouses, communal waste dumps and nearby to heavy-traffic roads (Bednorz, 2000). Higher density of breeding ravens in eastern Croatia was also noticed near a hog-breeding farm, cattle-breeding farms and near a slaughterhouse.

Knight et al. (1995) suggested that land-use patterns influence raven numbers. They found that ravens are more abundant in urban and suburban areas in irrigated farmlands, because of the greater abundance and availability of food sources. While an animal component to the diet is essential from a bioenergetics’ point of view, herbaceous elements represent only complementary food sources for ravens (Nogales & Hernandez, 1994).

In contrast to literature data, ravens nesting on electricity pylons in Croatia often left the pylon in the following year and/or changed the nest position on the pylon, but the pair still remained in their breeding area. Results of observations in Wielkopolska region indicate that ravens are faithful to once-choosen pylons. Among 175 pylons occupied by the ravens in the years 1996-1998, seventy-seven (44%) were occupied for all three years, and in 66 cases the nest were built not only on the same pylon, but on exactly the same spot. In Poland the most common reason for birds leaving pylons unoccupied in a following year was disturbance caused by protection and renovation works on those pylons (Bednorz, 2000). The same author also mentioned five cases of occupation of the same pylon for 11 to 13 years in Poland.

Disappearance of raven nests from transmission line pylons in eastern Croatia, in conjunction with re-building in the following breeding season, is in contrast to the literature data. Bibby et al. (1993) suggested that raven nests on trees last for a few breeding seasons. Nests are frequently re-used, often over many years (Cramp & Perrins, 1994). In the Berlin area in Germany, 60% of 75 nests over 10 years were new, while 40% were refurbished old ones. New nests were usually built on top of the previous year’s nest (Sommer, 1991).

There are several possible reasons for the disappearance of nests from pylons: humans, wind or the ravens themselves. Humans and strong winds probably play only a small part in the destruction of nests on pylons. Knight & Kawashima (1993) found that the beams and lattice work of power-line pylons help to anchor the nest and secure it against extreme winds. Nest destruction by humans is less possible where nests are placed on pylons, than on forest trees. The most probable cause of disappearance of ravens’ nests in Croatia is destruction by ravens themselves after their young have left the nest. Bird nests are rich in ectoparasites (Wimberger, 1984; Heeb et al., 2000), therefore building a new nest every year may lower the possibility of ectoparasites attacking the nestlings.

ACKNOWLEDGMENTS

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LITERATURE


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Contribution to the knowledge of the Linyphiidae of the Maghreb. Part X. New data on Leptophyantes Menge (sensu lato) species (Araneae, Linyphiidae)

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ABSTRACT. The following new species are described : Megaleptophyantes auresensis sp. n., M. hellinckxorum sp. n., Palliduphantes tricuspis sp. n. and P. yakourensis sp. n. The unknown male of Leptophyantes aelleni and the unknown female of Palliduphantes cadizensis are described for the first time, and Leptophyantes afer is redescribed. The following new combinations are proposed : Canariphantes atlassahariensis (Bosmans) comb. n., transferred from Leptophyantes, Canariphantes zonatus (Simon) comb. n., transferred from Bolyphantes and Improphantes djazairi (Bosmans) comb. n., transferred from Leptophyantes. An overview of all Maghrebian species and new distribution data of several species are presented.

RÉSUMÉ. Les espèces nouvelles suivantes sont décrites : Megaleptophyantes auresensis sp. n., M. hellinckxorum sp. n., Palliduphantes tricuspis sp. n. et P. yakourensis sp. n. Le mâle inconnu de Leptophyantes aelleni et la femelle inconnue de Palliduphantes cadizensis sont décrits pour la première fois et Leptophyantes afer est redécrit Les combinaisons nouvelles suivantes sont proposées : Canariphantes atlassahariensis (Bosmans) comb. n., transféré de Leptophyantes, Canariphantes zonatus (Simon) comb. n., transféré de Bolyphantes et Improphantes djazairi (Bosmans) comb. n., transféré de Leptophyantes. Toutes les espèces Maghrébiennes sont revues et de nouvelles dates de distribution sont présentées.

KEY WORDS : Leptophyantes, Maghreb, new species and records

INTRODUCTION

BOSMANS (1985) revised the species of Leptophyantes sensu lato living in the Maghreb countries of Morocco, Algeria and Tunisia. Since then, after a stay of 6 years in Algeria and some additional collecting trips to Tunisia and Morocco, many additional data have been gathered. New species, unknown males or females and new distribution data of known species were collected. The results are given below.

Since 1985, Leptophyantes has been reclassified in several smaller genera. Because of these nomenclatural changes, the following genera are now represented in the Maghreb : Canariphantes Wunderlich, 1992, Improphantes Saaristo & Tanasevitch, 1996, Megaleptophyantes Wunderlich, 1994, Palliduphantes Saaristo & Tanasevitch, 2001 and Temuiphantes Saaristo & Tanasevitch, 1996. Since taxonomic changes to the Leptophyantes group of genera have progressed in a piecemeal fashion with contributions from many authors, the systematics of these species has become rather complicated. Some of the species occurring in the Maghreb have been transferred to alternative genera, but the others remained in Leptophyantes, despite the fact that they do not meet the definition of Leptophyantes sensu strico as proposed by SAARISTO & TANASEVITCH (1996). In the absence of new taxonomic work, they are left in the genus Leptophyantes. The present paper, catalogs all known Leptophyantes sensu lato living in the Maghreb and in the references below each species, only data concerning the Maghreb are presented.

The type material is deposited in the collection of the KBIN and the MNHN; the rest of the material is temporarily deposited in the author’s collection.

ABBREVIATIONS

CRB : Collection R. Bosmans;
KBIN : Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel;
MNHN : Muséum national d’Histoire naturel de Paris;
Fe, Pa, Ti, Mt, Ta : femur, patella, tibia, metatarsus, tarsus; FeI, FeII, Fe III, FeIV : femur of first, second, third, fourth leg; d, pl, rl, pv, rv : dorsal, prolateral, retro-lateral, proventral, retroventral.
G. : Gouvernorat (Tunisia); P. : Province (Morocco); W. : Wilaya (Algeria).
Measurements are in mm.

SYSTEMATICS

Genus Leptophyantes Menge sensu strico

SAARISTO & TANASEVITCH (1996, 1999, 2000, 2001) redefined the genus Leptophyantes and in their view, only a few species are placed in this genus. All other species
were or will have to be transferred to other genera, which leaves the genus *Lepthyphantes* in a mess. In the Maghreb, *Lepthyphantes minutus* is the only species that remains. Some species were transferred to the genera *Canariphantes*, *Impropolpantes*, *Megalephyphantes*, *Palphenyphantes* or *Tentipolpantes* (Saariesto & Tanasevitch, 1996, 2000, 2001). Seven Maghreb species belong in the *afer*-complex, as first defined by Brignoli (1971) and confirmed by Saariesto & Tanasevitch (1993). Finally, another seven species have, at the moment, an uncertain position.

*Lepthyphantes minutus* (Blackwall, 1833)

*Lepthyphantes minutus*; Bosmans 1985 : 142; Saariesto & Tanasevitch, 1996 : 177, 177, figs 2A, 4A-B, 10A.

Description and diagnosis

See Bosmans (1985).

New material examined

**ALGERIA**

W. Batna : Aures Massif, Ain Targa, 1600m, 2 males, pitfalls in *Cedrus atlantica* forest, 4 XI.1987.

W. Setif : Djebel Babor, 1950m, 2 females in pitfalls in *Cedrus atlantica* forest, 22 XI.1989.

W. Tizi Ouzou : Djurdjura Massif, Talal Guilef, 1550m, 1 male, pitfalls in *Cedrus atlantica* forest, 12 XI.1988.

Distribution

A common species in temperate Europe, in Algeria limited to forests at high altitude : the Djurdjura and Aures Massifs and the Djebel Babor. Probably also present in the Moroccan Atlas.

*Lepthyphantes* species belonging to the *afer* complex

*Lepthyphantes afer* Simon, 1913

(Figs 1-5)

*Troglophyphantes afer* Simon, 1913 : 374 (descr. male).

*Lepthyphantes afer*; Fage, 1919 : 72, fig. 30; Fage, 1931 : 189, 233, fig. 33 (descr. female); Bosmans, 1985 : 167.

Citations

**ALGERIA**

W. Tizi Ouzou : Djurdjura massif ; Ifri Bou Anou, Douar Iboutarene, type locality; Simon, 1913; Djebel Azzerou Tidjer, Ifri Maareb (Simon, 1913); Dra-el-Missan, Tesseretef Boorfrichen (Fage, 1919, 1931); Anou ‘t Azzerou, Ihou Bou N’Taya (Fage, 1931); Tesseretef el hadj ou-Kaci (Fage, 1931).

Remarks

Bosmans (1985) was unable to locate the material mentioned above and the species thus could not be re-described. Newly collected material allows us to do so now.

Diagnosis

Males are recognised by the basal spine on the paracymbium and by the shape of the lamella (Fig. 1), females by the shape of the protruding sigmoid scape (Figs 3-4). For this and related species, Brignoli (1971) created the *afer*-group, which Saariesto & Tanasevitch (1993) named the *afer*-complex.

Description

Measurements : Male : total length 2.8-3.4; prosoma 1.36-1.42 long, 1.04-1.12 wide. Female : total length 2.6-3.8; prosoma 1.31-1.42 long, 1.02-1.16 wide.

Colour : Cephalothorax, chelicerae, sternum and legs yellowish orange, abdomen pale grey, nearly white.

Legs long, Fe I 1.8 times as long as prosoma.

Spination : Fe I : 2 or 3 pl, Fe II-IV spineless; Ti I : 2d, pl, rl; Ti II : 2d, rl; Ti III : 2d; Mt I-III : d; MtIV spineless.

Palp (Figs 1-2) : Patellar and tibial spine 1.5 times as long as their diameter; tibia twice as long as wide; proximal part of paracymbium with 5 scattered spines, distal part slender and with mesal tooth, invisible in lateral view; suprategular apophysis pointed, with basal tooth; radix with strongly pointed basal tooth; lamella long and pointed; terminal apophysis U-shaped, distally rounded; embolus compact, distally with small tooth.

Epigyne (Figs 3-5) : With strongly protruding, sigmoid scape; anterior part of scape nearly circular, slightly longer than wide, distal part gradually narrowing into the stretcher; median plate strongly elongate, twice as long as wide.

New material examined

**ALGERIA**


*Lepthyphantes brevihamatus* Bosmans, 1985

*Lepthyphantes brevihamatus* Bosmans, 1985 : 157, figs 8a-g (descr. male, female).

Description and diagnosis

See Bosmans, 1985.

New material examined

None.

Distribution

Morocco, caves in the High Atlas.

*Lepthyphantes emarginatus* Fage, 1931

*Lepthyphantes emarginatus* Fage, 1931 : 190 fig. 35 (descr. male, female); Bosmans, 1985 : 168, figs 13a-f (redescr. male, female).

Description and diagnosis

See Bosmans, 1985.
**Lepthyphantes sensu lato** in the Maghreb

**New material examined**

**ALGERIA**

W. Bouira : Djurdjura massif : Tala Rana, 1310m, 2 males 3 females, pitfalls in open *Cedrus* forest, 6.X.1987-1.VI.1988; Tigounatine, 1460m, 1 female in pitfalls in *Cedrus* forest, 5.I.1988.


**Distribution**

Algeria, Djurdjura Massif. In the past the species was only collected in caves, and we recollected it there. As we collected it also outdoors in pitfall traps, the species appears not to be a true troglobiotic.

**Lepthyphantes longihamatus** Bosmans, 1985

*Lepthyphantes longihamatus* Bosmans, 1985 : 155, figs f. 6a-c, 7a-d, 8h, 11c (descr. male, female).

**Description and diagnosis**

See Bosmans, 1985.

**New material examined**

None.

**Distribution :**

Morocco, caves in the High Atlas.

**Lepthyphantes ritaee** Bosmans, 1985

*Lepthyphantes ritaee* Bosmans, 1985 : 159 figs 9a-c, 10a-c, 11b (descr. male, female); Bosmans 1993 : 133 (citation).

**Description and diagnosis**

See Bosmans (1985).

**New material examined**

**ALGERIA**

W. Aïn Defla : Col Kandek, 600m, 1 female in pitfall in *Pistacia* maquis, 18.II.1988.


W. Boumerdes: Reghaia, 20m, 1 female in pitfall in Olea maquis, 6.IV.1986.

W. Ech Chleff: Damous, 50m, 1 female in pitfall in Pinus halepensis forest, I.1989.

W. El Tarf: El Kala, Lake Tonga N., 10m, 7 males 1 female in Pinus halepensis litter, 28.III.1988; El Kala, Lake Ouibeira N., 2 males in Quercus suber litter, 30.III.1988.

W. Oran: M’sila forest, 400m, 1 female, litter in Quercus suber forest, 24.IV.1984.

TUNISIA


Distribution
Formerly known from one locality in Morocco and from the wilaya’s Alger and Annaba in Algeria (BOSMANS, 1985), later also cited from the south of Spain (BOSMANS, 1993). New localities are added here from the Algerian wilaya’s of Ain Defla, Blida, Boumerdes, Ech Chleff, Oran, Souk Ahras, Tipasa and Tlemcen and from one gouvernorat in Tunisia. The species thus occurs all over the north of the Maghreb.

Description and diagnosis

New material examined
None.

Distribution
Algeria, cave near Tlemcen.

‘Lepthyphantes’ species of uncertain position.

Lepthyphantes aelleni Denis, 1957
(Figs 6-11)

Lepthyphantes aelleni Denis, in Denis & Dresco, 1957: 50, figs 1-3 (descr. female); BOSMANS, 1985: 166 (citation).

Type material
Holotype female from Morocco, probably the province of Taza, from the abyss ‘Kaf el Bouk’; exact locality unknown (DENIS & DRESCO, 1957); not examined, unavailable.

Remarks
The type material mentioned above could not be traced in the MNHNP or in any other museum. Newly collected material which undoubtedly belongs to this species allows us to redescribe it.

Diagnosis
The species is easily recognised by the strongly elongated, triangular lamella in the male (Fig. 6) and the shape of the strongly protruding scape in the female (Figs 9, 10). It cannot be placed in any recently created genus of the Lepthyphantes group. The elongated, unfolded scape covered with hairs reminds of the scapes of L. ajoti BOSMANS, L. exvaginatus Deeleman and L. maurius Brignoli and these species merit to be united in the same, yet undefined species group.

Description
Measurements: Male: total length 2.4-3.0; prosoma 1.26-1.41 long, 1.08-1.14 wide. Female: total length 3.2-3.8; prosoma 1.48-1.84 long, 1.06-1.44 wide. Legs long, Fe I 1.5 times as long as prosoma.

Colour: Cephalothorax yellowish orange, margin greyish; sternum grey suffused with yellowish orange; legs yellowish orange; abdomen grey, posterior half with 4-5 whitish chevrons.

Spination: FeI: 1 pl, FeII-IV spineless; TiI-IV: 2d, 2pl, 2rl; Mt I-IV: d.

Palp (Figs 6-8): Patellar and tibial dorsal spines not strongly developed, 1.5 x the diameter of each segment; tibia twice as long as wide; proximal part of paracymbium with strong basal tooth and about 20 scattered spines, distal part gently curved, terminally rounded;
lamella bifid, lateral branch L-shaped, distally denticulate and gradually narrowing, mesal branch shorter and wider.

Epigyne (Figs 9-11) : With strongly elongated proscape, with narrower basal part, gradually widening and becoming rhomboid, posteriorly with concave margin and ventrally strongly excavated, with small stretcher.

**New material examined**

**MOROCCO**

P. Taza : Taza S., Friouato abyss, 1550m, 5 males 43 females in mosses, 8.V.1984 (CRB, KBIN, MNHN).

**Distribution**

Morocco, region of Taza in the northeast.

**Lepthyphantes ajoti** Bosmans, 1991


**Description and diagnosis**

See Bosmans, 1991.

New material examined

None.

Distribution

Algeria, Saharian Atlas.

Lepthyphantes exvaginatus Deeleman, 1984


Description and diagnosis


New material examined

None.

Distribution

Algeria, cave near Tlemcen.

Lepthyphantes lagunculus Denis, 1937

Lepthyphantes lagunculus Denis, 1937 : 1045, pl. 4, figs 13-17 (descr. male, female); Bosmans, 1985 : 172 (citation).

Description and diagnosis

See Denis, 1937. This is one of the few species that was not recollected by us in Algeria, although the area was well prospected. The type material was not available, so a redescription cannot be given.

New material examined

None.

Distribution

North Algeria, Zouagha forest.

Lepthyphantes linyphioides Denis, 1937

Lepthyphantes linyphioides Denis, 1937 : 1045, pl. 4, figs 9-10 (descr. male); Bosmans, 1985 : 173 (citation).

Description and diagnosis

See Denis, 1937. This species belongs in another genus Theonina as described in (Bosmans, 2005).

New material examined

None.

Distribution

North Algeria, Zouagha forest.

Lepthyphantes maurusius Brignoli, 1978


Description and diagnosis

See Brignoli, 1978. As the type material was not available a redescription cannot be given. As illustrated by Brignoli, the species has a very typical scape which allows an easy identification.

New material examined

None.

Distribution

Morocco, cave near Taza.

Lepthyphantes pietlaini Machado, 1940

Lepthyphantes pietlaini Machado, 1940 : 515, figs 1-6 (descr. male); Bosmans, 1985 : 167 (citation).

Description and diagnosis

See Machado, 1940. This is one of the few species that was not recollected by us in Morocco, and a redescription thus cannot be given. The type material was not available.

New material examined

None.

Distribution

Described from Spanish Morocco, El Ajmas, presently in Morocco in the region of Chechaouen.

Canariphantes (Wunderlich, 1992)

Remarks

The genus Canariphantes was established by Wunderlich (1992) for two species, one from the Canary Islands (C. alpicola Wunderlich), the other from Central Europe (C. nanus (Kulczyn’ski)). Following the diagnosis given Wunderlich (1992), Saaristo & Tanasevitch (2001) transferred Lepthyphantes homonymus and L. nali into the genus Canariphantes. Two more species obviously belong there and are here transferred to it: Canariphantes atlassahariensis from Palliduphantes and Canariphantes zonatus from Bolyphantes (contra Saaristo & Tanasevitch, 2000, 2001).

Diagnosis

Leg spinulation : Fe I pl, Fe II-IV spineless, Ti I 2d, pv, rv, Ti II 2d with or without pv, rv, Mt I-IV d. Male palp : Cymbium without hump; patella and tibia with one short dorsal spine; paracymbium with specific dentation, distal part often translucent; lamella simple, pointed or bifurcate; embolus with subterminal lobe. Epigyne : Small, with flat unfolded scape and small stretcher, flanked by large lateral lobes.

Canariphantes atlassahariensis

(Bosmans, 1991) Comb. n.

Lepthyphantes atlassahariensis Bosmans 1991 : 64, figs 1-2, 5-8 (descr. male, female).

Palliduphantes atlassahariensis; Saaristo & Tanasevitch, 2001 : 6 (transfer from Lepthyphantes).
Lepthyphantes sensu lato

in the Maghreb

Remarks

SAARISTO & TANASEVITCH (2001) transferred Lepthyphantes atlassahariensis to Palliduphantes. Two synapomorphies characteristic for this genus are however not present in the species: the lamella of the male palp is not long, narrow and sigmoid, but short and L-shaped; the scape of the epigyne is short and copulation ducts do not run throughout the scape, as in other species of this group. These characters are typical for the genus Canariphantes and L. atlassahariensis is therefore transferred to this genus.

Description and diagnosis


New material examined

ALGERIA

W. Laghouat : Oued M’zi, 750m, 6 males 13 females, pitfalls in Phragmites belt along the river, 21.V.1990.

Distribution

Only known from two localities in the Saharian Atlas in Algeria. The new material was collected at the type locality.

Canariphantes homonymus (Denis, 1934)

Lepthyphantes homonymus Denis, 1934 : 76, fig. 3 (descr. male); Denis, 1950 : 102, fig. 40; Bosmans & Bouragba, 1992 : 259, figs 28-34 (descr. male, female).

Canariphantes homonymus; Saaristo & Tanasevitch, 2000 : 264 (transfer from Lepthyphantes).

Description and diagnosis


New material examined

MOROCCO

P. Taroudannt : between Aoulouz and Taliouine, 600m, 1 female, stones in Arganier steppe, 4.II.1996.

Distribution

Formerly known from the extreme southeast of France, Portugal and the steppe region in Algeria (BOSMANS & BOURAGBA, 1992) and cited here for the first time from Morocco.

Canariphantes naili

(Bosmans & Bouragba, 1992)


Canariphantes naili; Saaristo & Tanasevitch, 2000 : 264 (transfer from Lepthyphantes).

Description and diagnosis


New material examined

None.

Distribution

Algeria, Ouled Nail Mountains, Aures and Djurdjura massifs.

Canariphantes zonatus

(Simon, 1881) Comb. n.

Figs 12-17

Lepthyphantes zonatus Simon 1881 : 322, fig. 91 (descr. male, female); Simon 1885 : 27; Denis 1936 : 1045 (citation); Bosmans 1985 : 148 (citation).

Bolyphantes zonatus; Saaristo & Tanasevitch, 2000 : 256 (transfer from Lepthyphantes).

Remarks

SAARISTO & TANASEVITCH (2000) transferred Lepthyphantes zonatus to Bolyphantes, but in the revision of this genus, VAN HELSDINGEN et al. (2001) correctly considered the species misplaced. An analysis of palpal organ and epigyne shows that the species has a short, L-shaped lamella and that the scape of the epigyne is very short with the copulation ducts not running throughout the scape. These characters are typical for the genus Canariphantes and L. zonatus is therefore transferred to it.

Description and diagnosis

See MACHADO (1949) and figures 12-17 in present paper.

New material examined

ALGERIA


W. Annaba : Chetaibi, 810m, 2 males 5 females, stones in grassland, 1.III.1990.

W. Bouira : Col de Dirah, 900m, 2 males 3 females in pitfalls in Juncus along Oued Djennane, 10.IV.1988; Ighrem, 490m, 1 female in pitfall in Tamarisk bushes along Oued Sahel, 20.IV.1989; Saharidj, 650m, 1 male in pitfall in Pistacia maquis, 5.I.1988.

Boumerdes : Bordj Menael, 30m, 4 females, stones in Eucalyptus plantation, 4.II.1988; Reghaia, 5m, 2 males 6 females, pitfalls in Quercus suber maquis, 12.IV.1985; Sidi Daoud, 35m, 1 female, stones along Oued Sebaou, 4.XII.1987; Thenia E., 150m, 1 female in litter in Eucalyptus plantation, 18.III.1988; Zemmouri, 10m, 17 males 7 females in pitfalls in Cistus maquis, 12.IV.1985.

W. El Tarf : El Kala, N. Lake Tonga, 10m, 7 males 2 females in pitfalls in Pinus halepensis forest, 28.III.1988; idem, 4 females in grassland along the lake, 28.III.1988; El Kala, E. Cap Rosa, 2 males in pitfalls in Quercus suber forest, 30.III.1988; El Kala, Lake Oubeira, 10m, 4 females in Quercus suber forest, 29.III.1988.

W. Mostagenem: Ben Abdel Malek Ramdane, 25m, 1 female in pitfall in young *Pinus* plantation, 25.V.1990.

W. Skikda: Ben Azouz, 200m, 1 male 1 female in *Eucalyptus* plantation, 2.III.1990; W. Collo, Tamanart, 25m, 1 male 1 female, stones in grassland, 6.VI.1987.


W. Tizi Ouzou: Aïn-el-Hammam, 1150m, 1 female, stones around hotel, 9.III.1990; Boukhalfa, 180m, 1 male 1 female in *Olea* maquis, 8.III.1990; El Tetla, 180m, 1 female in pitfalls in grassland, 16.III.1990; Oued Assi, 250m, 2 females, stones along Oued Assi, 15.IV.1982.

MOROCCO

P. Casablanca: Casablanca, 1 male, IV.1984, J. Mertens leg.

P. Rabat: Aïn-el-Aouda N., 1 female, 8.II.1996.

P. Taza: cascades de Ras-el-Oued, 1000m, 1 male in herbs, 22.IV.1984.


TUNISIA


G. Le Kef: Sakiet Sidi Youcef E., 850m, 1 female, stones in *Pinus* forest, 5.III.2005.


**Distribution**

BOSMANS (1985) cited the species from Algeria in the wilaya’s of Annaba, Bejaia and Tizi Ouzou, and from one locality in Tunisia. Several new localities from Algeria, Morocco and Tunisia are added here. *Canariphantes zonatus* appears to be a common species in the north of the Maghreb.

Lepthyphantes sensu lato in the Maghreb

Improphantes
(Saaristo & Tanasevitch, 1996)

The genus *Improphantes* was recently created by Saaristo & Tanasevitch (1996) for several species formerly included in *Lepthyphantes*. While males of the genus are diagnosed by the sickle-shaped embolus with open sulcus, no unambiguous characters common for the females are actually known. In Northern Africa, *Lepthyphantes decolor* Westring was placed in *Improphantes* and *Lepthyphantes djazairi* Bosmans is here transferred to it as well.

Improphantes decolor
(Westring, 1862)


*Improphantes decolor*; Saaristo & Tanasevitch, 1996 : 177 (transfer from *Lepthyphantes*).

Description and diagnosis
See Bosmans, 1985.

New material examined

**ALGERIA**

W. Batna: Belezma Mountains, Col Telmet, 1820m, 2 males in pitfalls in *Cedrus atlantica* forest, 28.II.1988.

W. Blida: Atlas Blidéen, Meurdja, 950m, 2 females in pitfalls in *Cedrus atlantica* plantation, 10.III.1988; Bougara, Djebel Bou Noua, 850m, 1 female, stones in mixed forest, 1.XII.1983; Djebel Mouzaia, 1400m, 1 male in *Quercus faginea* litter, 4.XI.1985, and 2 females, 22.V.1985.

W. Bouira: Djurdjura massif: Tala Rana, 1310m, 2 females in pitfalls in open *Cedrus atlantica* forest, 24.IX.1987-12.IV.1988; Tigounatine, 1460m, 7 males 3 females in pitfalls in *Cedrus atlantica* forest, 6.X.1987-1.VI.1988.

W. Chleff: Damous, 50m, 1 female in pitfall in *Pinus halepensis* forest, 11.IV.1979; Tacheta, 850m, 2 females in pitfalls in *Quercus faginea* forest, 4.II-25.IV.1988.

W. M’sila: Hodna Mountains, Djebel Maadid, 1600m, 4 females in pitfalls in grassland, 1.I.1990.

W. Tizi Ouzou: Azazga, 750m, 1 female in pitfall in *Quercus suber* forest, 25.XI.1989; Yakouren, 820m, 3 females in litter of *Quercus faginea* forest, 4.XII.1986, and 1 female, 24.II.1988. Djurdjura massif: Aït Ouabane, 1410m, 1 male 6 females, pitfalls in *Cedrus atlantica* forest, 6.X.1987-1.VI.1988; Tizi Boussouil, 1750m, 3 males 5 females, pitfalls in grassland, 1.XII.1991.

Distribution
South Scandinavia, Central and southwest Europe, Algeria.

*Improphantes djazairi*
(Bosmans, 1985) Comb. n.


Remarks

*Lepthyphantes djazairi* is transferred here to the genus *Improphantes*, because it corresponds to the diagnosis proposed by Saaristo & Tanasevitch (1996). It is closely related to *I. decolor*.

Description and diagnosis

New material examined
None. All additional records were already cited in Bosmans & Bouragba, 1992.

Distribution
A species with a large distribution at higher altitudes in the Algerian Atlas.

Genus Megalepthyphantes
(Wunderlich, 1994)

The genus was *Megalepthyphantes* created by Wunderlich (1994) for the larger *Lepthyphantes* species of the *nebulosus* group, first defined by Wiehle (1956). Saaristo & Tanasevitch (2000) transferred *L. bkheitae* Bosmans & Bouragba to the new genus, and two more new species are described here.

Megalepthyphantes bkheitae
(Bosmans & Bouragba, 1992)


*Megalepthyphantes bkheitae*; Saaristo & Tanasevitch, 2000 : 264 (transfer from *Lepthyphantes*).

Description and diagnosis

New material examined
None.

Distribution
Only known from Algeria in the region of Djelfa.

Megalepthyphantes auresensis
(sp. n. (Figs 18-24)


Type material

Holotype male from Algeria, W. Batna, Aures Massif, Belezma Mountains, Kef Islane, 1800m, pitfall in *Cedrus atlantica* forest, 26.II.1988. Paratypes: 3 males, same data; 2 females, in mosses, 8.IV.1982; deposited in KBIN and CRB.

Diagnosis
Closely related to *M. bkheitae*, males clearly differentiated by 3 unequal terminal teeth of the lamella (Fig. 18),
and females by the strong posterior incision of anterior part of the epigynal scape (Fig. 22).

**Etymology**

The name is derived from the type locality, the Aures Massif in the Algerian Tell Atlas.

**Remarks**

This species was cited in Bosmans (1985) as *Lepthyphantes cfr. collinus*.

**Description**

Measurements: Male: total length 3.3-3.8; prosoma 1.72-1.76 long, 1.36-1.44 wide. Female: total length 3.4-4.6; prosoma 1.30-1.68 long, 1.04-1.36 wide.

Cephalothorax yellowish brown with broad median and lateral grey stripes; legs yellowish brown, Fe and Ti with two dark grey annulations; abdomen pale grey, with darker chevrons.

Legs: Spination: FeI: pl; Ti: 2d, 2pv, 2 rv, 1 pv, 1 rv; Mt: d, pl, rl.

**Measurements:**

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<tr>
<th></th>
<th>Fe</th>
<th>Pa</th>
<th>Ti</th>
<th>Mt</th>
<th>Ta</th>
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<tr>
<td>I</td>
<td>3.16</td>
<td>0.53</td>
<td>2.84</td>
<td>3.08</td>
<td>1.74</td>
</tr>
<tr>
<td>IV</td>
<td>2.86</td>
<td>0.44</td>
<td>2.60</td>
<td>2.84</td>
<td>1.30</td>
</tr>
</tbody>
</table>

Palp (Figs 18-21): Tibia with two long, curved spines; distal part of tibia strongly chitinised, with blunt anterodorsal apophysis; proximal part of paracymbium with blunt median tooth; lamella curved, prolateral part with three unequal teeth, retrolateral part larger and curved, terminally pointed; embolus sigmoid.

Epigyne (Fig. 22): Scape folded, anterior part of scape wider than long, with strong lateral and posteromedian incisions, posterior part of scape visible in the incision.

Vulva (Figs 23, 24): Copulation ducts running throughout the scape.
Other material examined

ALGERIA

‘Alger’, 1 female (MNHNP 4259).

W. Batna : Aures Massif, S’gag forest, 1800m, 2 females in pitfalls in *Cedrus atlantica* forest, 18.IV.1982; between Tazoult Lambese and S’gag, 1650m, 1 subadult female among stones in grassland, 16.X.1987.

W. Setif : Djemilia, 950m, 1 female, stones in ruins, 6.II.1988.

W. Aïn Sefra : Mecheria, 5 females (MNHNP 6179).

Distribution

Only known from mountains in Tell and Sahara Atlas in Algeria.

Ecology

A species of forests of high altitudes in the inland of Algeria, with adults collected at the end of the winter and in the beginning of spring.

Megalepthyphantes hellinckxorum sp. n.

(Figs 25-31)

Type material

Holotype male from Algeria, W. Tissemsilt, Ouarsenis Massif, Theniet-el-Had, Djebel Meddad, 1400m, pitfall in open *Cedrus atlantica* – *Quercus ilex* forest, 23.III.1988; paratypes: 2 females, idem, 1500m, pitfall in dense *Cedrus atlantica* forest, 4.V.1989; deposited in KBIN (1 male, 1 female) and CRB (1 female).

Diagnosis

*M. hellinckxorum* is closely related to *M. bkheitae* and *M. auresensis*. Males are easily distinguished by the ribbon-like lamella with terminal denticules (Fig. 27), and females by the less incised anterior part of the scape (difference with *auresensis*), and by the quadrangular posterior part of the scape (Fig. 28; rectangular in *bkheitae*).

Etymology

The species is dedicated to the Hellinckx family, especially to Bram Hellinckx, in commemoration of the birth of his son Beau.

Description

Measurements: Male: total length 3.6; prosoma 1.94 long, 1.60 wide; chelicerae 0.72 long. Female: total length 4.0-4.3; prosoma 1.52-1.76 long, 1.26-1.30 wide.

Colour and spination as in *L. bkheitae*.

Legs: Measurements:

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<tr>
<th></th>
<th>Fe</th>
<th>Pa</th>
<th>Ti</th>
<th>Mt</th>
<th>Ta</th>
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</thead>
<tbody>
<tr>
<td>I</td>
<td>3.04</td>
<td>0.54</td>
<td>2.48</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>IV</td>
<td>2.68</td>
<td>0.48</td>
<td>2.44</td>
<td>2.76</td>
<td>1.46</td>
</tr>
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</table>

Palp (Figs 25-27): Differing from the preceding species in the following aspects: tibia dorsally with well developed, blunt apophysis and strongly elevated dorsal ridge, delimiting a deep depression; basal branch of paracymium with relatively small median tooth; prolateral part of lamella a straight sclerite with subterminal concavity, retrolateral part longer, ribbon-like, terminally denticulate.

Epigyne (Figs 28-29): Anterior part of scape rather elongated, only slightly wider than long. Posterior part of scape rectangular.

Vulva: Figs 30-31.

Other material examined

A female in the MNHNAP has an epigyne that is very similar to the epigyne of *M. hellinckxorum* and is here, in the absence of males, provisionally listed: W. El Bayadh: El Bayadh (as Géryville; MNHNAP 4279).

Distribution

Algeria, the Ouarsenis Massif and one probable record 200 km to the south.

**Genus Palliduphantes**

(Saaristo & Tanasevitch, 2001)

The genus *Palliduphantes* was recently created by Saaristo & Tanasevitch (2001) for species formerly included in the pallidus-, insignis- and spelaeorum group of *Lepthyphantes*. They included 48 species, but some seem to be misplaced, as for instance *P. atlassahariensis*, transferred here to *Canariphantes*. In Northern Africa, *Lepthyphantes cadiziensis* Wunderlich, *Lepthyphantes kalaensis* Bosmans and *Lepthyphantes labilis* Simon were included in *Palliduphantes*. Recently, Bosmans (2003) described *Palliduphantes chenini* and in the present paper, two more species are described.

**Palliduphantes cadiziensis**

(Wunderlich, 1980)

(Figs 32-39)

*Lepthyphantes cfr. bolivari*; Brignoli 1978 : 108, fig.1 (descr. male; misidentified).


**Palliduphantes cadiziensis**; Saaristo & Tanasevitch, 2001 : 6 (transfer from *Lepthyphantes*).

Type material

Holotype male from Spain, Cadiz, 12 km WNW Algeciras, Sierra del Niòo, 3.IV.1972 (Wunderlich 1980); not examined.

Diagnosis

Males of this species may easily be recognised by the long, bifurcate lamella (Fig. 32), females by the strongly folded scape with narrowing distal part (Figs 34, 35).

Remarks

In his original description, Wunderlich (1980) placed *L. cadiziensis* in the tenius group of *Lepthyphantes*. However, the shape of the embolic division and the folded epigyne indicate that it has to be placed in the pallidus group of *Lepthyphantes*, so Saaristo & Tanasevitch (2001) correctly integrated the species in the genus *Palliduphantes*.

Brignoli (1978) identified a male from Gibraltar as *L. cfr. bolivari* Fage, but according to his figure of the male palp, it is *P. cadiziensis* as well. *P. bolivari* has a much shorter lamella in the male palp and a wider distal part of the epigynal scape in the female.

Description

Measurements: Male: total length 1.6-1.9; prosoma 0.80-0.88 long, 0.64-0.68 wide. Female: total length 2.1-3.5; prosoma 0.88-0.98 long, 0.72-0.84 wide.

Colour: Prosoma and legs pale yellowish to yellowish orange, eyes surrounded with black; abdomen grey to dark grey, often with paler spots and bars.

Legs: Fe I: pl; Ti I: 2d, pl, rl; Ti II: 2d, rl; Ti III-IV: 2d; Mt I-IV: d.

Palp (Figs 32-33): Dorsal spines on patella and tibia of equal length, twice the diameter of the segment; cymbium without tubercle; proximal branch and median part of paracymium both with basal tooth; retrolateral part longer, ribbon-like, terminally denticulate.

Epigyne (Figs 34-37): Strongly protruding; anterior part of scape semi-circular, with two lobe-like internal appendages; posterior part of scape rhomboid; stretchd small, slightly wider than long.


Previous citations

**GIBRALTAR**

St. Michael’s Cave, 1 male, 19.V.1973 (Brignoli, 1978, sub *L. cfr. bolivari*).

**SPAIN**

Cadiz: 12 km WNW Algeciras, Sierra del Niòo (Wunderlich, 1980).

New material examined

**MOROCCO**

P. Tetouan: between Tetouan and Chechaouen, 520m, 2 males 3 females in herbs along a rivulet, 30.IV.1984; Tetoutan S., 10m, 1 female, dunes along Oued Hadjera, 20.IV.1984.

**Distribution**

Andalucia in the southwest of Spain and the northwest of Morocco.

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**Palliduphantes chenini**

*Bomsans, 2003*

*Palliduphantes chenini* Bosmans, 2003 : 104, figs 1-6 (descr. male, female).

**Description and diagnosis**

See BOSMANS (2003).

**New material examined**

None.

**Distribution**

The extreme south of Tunisia.

*Palliduphantes kalaensis*

(Bosmans, 1985)

*Leptyphantes kalaensis* Bosmans 1985 : 145, figs 3a-d, 4a-c, 11a (descr. male, female).

*Palliduphantes kalaensis*; Bosmans, 2003 : 104 (transfer from *Leptyphantes*).
Description and diagnosis

See BOSMANS (1985).

Further material examined

ALGERIA

W. El Tarf: Lake Tonga, 10m, 1 male 2 females, pitfalls in Alnus forest, 28.III.1988.

Distribution

Only known from the region of El Kala in the extreme northeast of Algeria.

Palliduphantes labilis (Simon, 1913)

Lepthyphantes labilis Simon 1913 : 370, fig.3 (descr. male, female); Bosmans 1985 : 142 figs 4d-f, 5a-d, 11d (descr. male, female).

Palliduphantes labilis; Saaristo & Tanasevitch, 2001 : 6 (transfer from Lepthyphantes).

Description and diagnosis

See BOSMANS (1985).

New material examined

ALGERIA


W. Annaba : Chetaibi, 810m, 1 female, stones in grassland, 27.II.1990.

W. Bejaia : between Aokas and Tizi Ghenif, 5m, 1 male, pitfalls in Pistacea maquis in dunes, 25.XI.1989; El Flaye, 800m, 1 female, pitfalls in Zizyphus bushes, 1.III.1989.

W. Blida : Chrea, 1000m, 2 males in pitfalls in Quercus faginea forest, 10.V.1982; La Chiffa, 250m, 3 males, pitfalls in orange garden, 21.II.1989.

W. Bordj Bou Arreridj : Sidi Embarek, 900m, 3 females, stones in cultivated land, 27.II.1990.

W. Bouira : Djurdjura massif, Tigounatine, 1460m, 1 female, pitfalls in Cedrus atlantica forest, 12.VII.1988.

W. Boumerdes : Ain Taya, 50m, 3 males 2 females, pitfalls in garden, 20.VI.1989; Lakhdaria, 115m, 1 male in Olea litter along Oued Olla, 1 male in herbs along Oued Bou-Hamoud, 20.IV.1990.

W. El Tarf : Lake Tonga, 10m, 1 male 2 females, pitfalls in Alnus forest, 28.III.1988; Sidi Embarek, 10m, 1 male 1 female in pitfalls in Olea maquis, 2.III.1990.

W. Guelma : Ain Regada, 600m, 2 females, herbs along Oued Zenati, 22.XI.1989; Boucheougouf, 600m, 3 females, herbs along Oued Seybousse, 22.XI.1989; Hammam Mezkoutine, 410m, 1 male in grass tuussocks, 28.II.1990.

W. Souk Ahras : Hadjar N.E., Barrage de la Cheffia, 250m, 2 males in pitfalls in Pistacea maquis, 28.II.1990.

W. Skikda : Bouchata, 400m, 1 male, stones in grassland, 12.II.1990.

W. Tissemsilt : Theniet-el-Had, Djebel Meddad, 1500m, 1 male, pitfalls in Cedrus atlantica forest, 4.V.1989.

W. Tizi Ouzou : Azeffoun S., Alma Guechtourm, 600m, 1 female, Olea maquis, 27.IV.1990; forêt de Mizrana, 300m, 4 males 1 female, stones in Quercus suber forest, 26.I.1990; Tzigirt E., 50m, 1 male 1 female, stones in grassland, 26.I.1990; Timizar Laghbar, 210m, 1 male 1 female, stones in Quercus faginea forest, 25.I.1990; Tizi Ouzou, 5km E., 180m, 1 male 6 females, wet grassland on slope, 25.I.1990 and 1 male 4 females, 11.III.1990; Djurdjura massif : Tala Guilef, 1420m, 1 male 1 female, pitfalls in Cedrus atlantica forest, 21.III.1989; idem, Col de Tizi ’n Kouillal, 1510m, 2 males 6 females, pitfalls in montane grassland, 1.XII.1991; idem, Tizi Boussouil, 1750m, 1 male 4 females, pitfalls in montane grassland, 1 XII.1991.

W. Tlemcen : Traras Mountains, between El Arba and El Araribienne, 300m, 1 male, pitfalls in Pistacea maquis, 24.V.1990.

TUNISIA

G. Beja : Beja 15 km N., 250m, 1 male, stones bordering fields, 27.II.2005.

G. Jendouba : Chemtou, 250m, 2 females, stones in roman ruins, 6.III.2005; Fernana N., 450m, 1 male 1 female, stones in maquis, 6.III.2005; Tabarka, at E. entrance of the city, 50m, 1 male, stones in wasteland, 28.II.2005; Tabarka S., plain of Oued Kebir, 1 female, stones in grassland, 7.III.2005; Tabarka, 1 female, around fortress, 7.III.2005.

G. Le Kef : Hammam Mellégue, 800m, 2 females, stones in small Pinus forest, 4.III.2005; Touiref SE., 650m, 1 male 1 female, stones in grassland, 5.II.2005.


G. Zaghouan : Saouaf E., 250m, 1 female, stones in maquis, 27.II.2005.

Distribution

The north of Algeria and Tunisia, where it is a common species.

Palliduphantes tricuspis sp. n.

(Figs 46-47)

Type material

Holotype male from Algeria, W. Skikda, between Djeeldel and Larbi Ben Mhid, 200m, litter of Quercus ilex, 2.3.II.1990; deposited in KBIN.

Diagnosis

This species is closely related to L. yakourensis sp. n., described further in this paper. Males differ by the disposition of the hairs on the paracymbium, by the trifid lamella (Fig. 46) and by the differently shaped terminal apophysis (Fig. 47). The female is unknown.
Etymology

The name is derived from the Latin 'tricuspis' (‘with three teeth’), referring to the trifid distal part of the lamella.

Description

Measurements: Male: total length 1.8; prosoma 0.78 long, 0.60 wide.

Colour: Prosoma olive brown, fovea, margin and striae suffused with grey; legs yellowish brown; abdomen dark grey, with a pair of elongated, pale grey antero-dorsal spots.

Posterior median eyes separated by 3/4 their diameter.

Chelicerae: with 14-15 indistinct stridulating ridges, and with 3 anterior and 5 small posterior teeth.

Legs: Fe I: pl; Ti I: 2d, pl, rl; Ti II: 2d, rl; Ti III-IV: 2d; Mt I-IV: d. Measurements:

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<th></th>
<th>Fe</th>
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<tr>
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<td>0.24</td>
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<td>IV</td>
<td>1.06</td>
<td>0.20</td>
<td>1.01</td>
<td>1.02</td>
<td>0.68</td>
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</table>

Palp (Figs 46-47): Dorsal spines on patella and tibia of equal length, twice the diameter of the segment; cymbium without tubercle; proximal branch and median part of paracymbium both with sharp basal tooth, distal part with blunt lateral tooth, terminally rounded; lamella elongated, terminally trifid; terminal apophysis composed of several teeth, all pointed, three directed anteriorly, one shorter and directed antero-laterally; embolus nearly straight.

Female: Unknown.

Other material examined

None.

Distribution

Only known from the type locality in the northeast of Algeria.

Palliduphantes yakourensis sp. n. (Figs 40-45)

Type material

Holotype male from Algeria, W. Tizi Ouzou, forest of Yakouren, 820m, litter in Alnus forest, 24.I.1990 (deposited in KBIN); paratypes: 2 males 7 females, same data (1 male 4 females deposited in KBIN, 1 male 3 females in MNHN).

Diagnosis

This species is closely related to L. kalaensis, occurring in the Northeast of Algeria. Males differ by the bifid tip of the lamella (Fig. 40), females by details in the shape of the scape: the longer anterior part of the scape and the longer lateral lobes, as visible in lateral view, and the less curved stretcher (Figs 42, 43).

Etymology

The species is named after the forest where it was first discovered, the Yakouren forest.

Description

Measurements: Male: total length 1.6-2.1; prosoma 0.74-0.90 long, 0.62-0.74 wide. Female: Total length 2.0-2.4; prosoma 0.70-0.92 long, 0.62-0.74 wide.

Colour: Prosoma yellowish brown, margin, striae and fovea region grey; legs yellowish brown, dark specimens
with faint grey annulations on femora and tibiae; abdomen grey, distal part darker and with 4-5 pale chevrons; some females with dark grey abdomen, with clearly marked pale chevrons; two females collected in an ancient mine are much paler.

Eye disposition, chelicerae and spination as in the preceding species.

Leg measurements:

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<th>Fe</th>
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<tr>
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<td>1.30</td>
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<tr>
<td>IV</td>
<td>1.23</td>
<td>0.22</td>
<td>1.34</td>
<td>1.18</td>
<td>0.82</td>
</tr>
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</table>

Palp (Figs 40-41): Dorsal spines on patella and tibia of equal length, twice the diameter of the segment; cymbium without tubercle; proximal branch and median part of paracymbium with sharp basal tooth, distal part with blunt lateral tooth, terminally rounded; lamella very long, terminally bifid; terminal apophysis trifid, with a short, laterally directed tooth, a long and pointed median tooth, and a somewhat shorter mesal one, strongly widened in the middle.

Epigyne (Figs 42-43): Lateral plates strongly developed; scape elongated, folded, anterior, visible part gently curved, median hidden part straight, distal part a small stretcher.

Vulva (Figs 44-45): Spermathecae oval; sperm ducts running throughout the scape, terminating just before the stretcher in poorly defined copulation pores.

Material examined

ALGERIA


W. Boumerdes: between Zougarra and Toulmout, 350m, 2 females in abandoned mine, 18.X.1989.

W. Ech Chleff: forêt de Tacheta, 850m, 1 male 1 female in litter Quercus faginea forest, 29.IV.1987.

W. Tizi Ouzou: forêt d’Akhadou, S. Col de Tagma, 910m, 1 female in litter of mixed Quercus faginea and Q. suber forest, 25.II.1988; forêt de Yakouren, 820m, 3 females in litter of forest of Quercus faginea, 24.II.1988; idem, 850 m, 1 male 5 females in litter of mixed Quercus faginea and Q. suber forest, 4.XII.1986.

Distribution

The extreme central north of Algeria, from Ech Chleff in the west to Tizi Ouzou in the east.
The genus *Tenuiphantes* was recently created by Saaristo & Tanasevitch (2001) for several species formerly included in the well-known tenuis group of *Lepthyphantes* (see Van Helsdingen et al., 1977). In the Maghreb, *Lepthyphantes herbicola* Simon and *Tenuiphantes tenuis* (Blackwall) have been included in it.

### *Tenuiphantes herbicola*


*Tenuiphantes herbicola*; Saaristo & Tanasevitch, 1996: 182 (transfer from *Lepthyphantes*).

### Description and diagnosis

See Van Helsdingen et al., 1977.

### New material examined

**ALGERIA**

W. Algar: Forêt de Bainem, 300m, 2 females, litter in *Pinus canariensis* forest, 30.IV.1984.

W. Blida: Atlas Blidéen, Chrea, 1000m, 2 males in pitfalls in *Quercus faginea* forest, 20.V.1985 and 1290m, 1 male in pitfalls in *Cedrus atlantica* forest, 16.VII.1988; Meftah, 450m, 4 females in litter of *Arbutus unedo*, 7.III.1984.

W. Boumerdes: Reghaia, 20m, 2 females in pitfalls in *Olea* maquis, 15.I.1984; Reghaia, 45m, 8 females in pitfalls in *Quercus suber* forest, 2.V.1984.

W. El Tarf: El Kala, Lake Tonga N., 10m, 6 males 5 females in pitfalls in *Pinus halepensis* forest, 28.III.1987; El Kala, Lake Oubeira, 10m, 2 males 1 female in pitfalls in *Quercus suber* forest, 30.III.1988 and 1 female, 15.I.1996, K. de Smet leg.; Haddada, 6 males 10 females, 5.IX.1996, K. de Smet leg.

W. Tipasa: Bouchoudi, 95m, 4 males 7 females in pitfalls in *Ulmus* forest, 27.I.1987; Sidi Fredj, 25m, 10 males 5 females in pitfalls in *Pinus halepensis* forest, 18.XII.1986-20.XII.1987; idem, 10m, 3 males 7 females in pitfalls in *Olea* maquis, 19.I.1987; Zeralda, Oued Mazafan, 5m, 2 males 3 females in litter of *Quercus faginea* forest, 24.II.1988.

W. Tizi Ouzou: Yakouren E., 820m, 4 females in litter in *Quercus faginea* forest, 4.XII.1986; idem, 4 females in pitfalls in *Alnus* forest, 27.IV.1990.

### Distribution

Occurring in the humid zone of Algeria, in Bosmans (1985) only cited from the wilaya’s of Alger and El Tarf, here also cited from the wilaya’s of Blida, Boumerdes, Tipasa and Tizi Ouzou.

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**Lepthyphantes sensu lato in the Maghreb**

### *Lepthyphantes tenuis* (Blackwall, 1852)


*Tenuiphantes tenuis*; Saaristo & Tanasevitch, 1996: 182 (transfer from *Lepthyphantes*).

### Description and diagnosis

See Van Helsdingen et al., 1977.

### New material examined

**ALGERIA**


W. Algar: Bainem, 100m, 1 male 1 female in *Pinus maritimus* forest, 12.V.1986; Beaulieu, 50m, 1 female in garden, 19.V.1988; Housssein Dey, 50m, 3 females in litter in park, 29.XIII.1987.

W. Bejaia: Aokas, 10m, 2 females in grassland in dunes, 22.X.1989; mouth of Oued Daas, 10m, 1 female, stones bordering maquis, 22.V.1988.

W. Blida: Ain-el-Hammam, 125m, 1 female, stones along Oued Bou Maan, 23.V.1989; Atlas Blidéen, Chrea: 850m, 2 males 2 females, pitfalls in *Quercus suber* forest, 23.III.1985, K. De Smet leg.; idem, 1045m, 7 males 5 females, pitfalls in *Quercus ilex* forest, 28.IV.1987; idem, 1200m, 1 male 1 female, stones near fountain in forest, 8.IV.1985, K. De Smet leg.; idem, les Glacières, 1290m, 12 males 2 females, pitfalls in *Cedrus atlantica* forest, 15.II.1987-9.V.1988; idem, Ghellai, 1350m, 16 males 10 females in pitfalls in planted *Cedrus atlantica* forest, 20.IV.1987-9.V.1988; idem, Pic Fertas, 1450m, 25 males 7 females, pitfalls in *Cedrus atlantica* forest, 12.IV.1987-9.V.1988; Djebel Mouzaia, 1200m, 1 female, stones around lake, 10.IV.1987, and 1350m, 1 male 1 female, stones in maquis, 6.X.1987, K. De Smet leg.; Meftah, Djebel Zerouela, 480m, 2 males 2 females in pitfalls in *Quercus suber* forest, 6.V.1987; Meurjda, 1000m, 6 males 6 females in pitfalls in planted *Cedrus atlantica* forest, 15.VI.1987-22.IX.1988.

W. Bouira: Djurdjura massif, Tigounatine, 24.IV.1988; Djebel Mouzaia, 1200m, 1 female, stones around lake, 10.IV.1987, and 1350m, 1 male 1 female, stones in maquis, 6.X.1987, K. De Smet leg.; Meftah, Djebel Zerouela, 480m, 2 males 2 females in pitfalls in *Cedrus suber* forest, 6.V.1987; Meurjda, 1000m, 6 males 6 females in pitfalls in planted *Cedrus atlantica* forest, 15.VI.1987-22.IX.1988.

W. Boumerdes: Reghaia, 20m, 2 females in pitfalls in *Olea* maquis, 15.I.1984; Reghaia, 45m, 8 females in pitfalls in *Quercus suber* forest, 2.V.1984.

W. El Tarf: El Kala, Lake Tonga N., 10m, 6 males 5 females in pitfalls in *Pinus halepensis* forest, 28.III.1987; El Kala, Lake Oubeira, 10m, 2 males 1 female in pitfalls in *Quercus suber* forest, 30.III.1988 and 1 female, 15.I.1996, K. de Smet leg.; Haddada, 6 males 10 females, 5.IX.1996, K. De Smet leg.

W. Tipasa: Bouchoudi, 95m, 4 males 7 females in pitfalls in *Ulmus* forest, 27.I.1987; Sidi Fredj, 25m, 10 males 5 females in pitfalls in *Pinus halepensis* forest, 18.XII.1986-20.XII.1987; idem, 10m, 3 males 7 females in pitfalls in *Olea* maquis, 19.I.1987; Zeralda, Oued Mazafan, 5m, 2 males 3 females in litter of *Quercus faginea* forest, 24.II.1988.

W. Tizi Ouzou: Yakouren E., 820m, 4 females in litter in *Quercus faginea* forest, 4.XII.1986; idem, 4 females in pitfalls in *Alnus* forest, 27.IV.1990.
Robert Bosmans

W. Laghouat: Oued M’zi, 750m, 1 male 1 female, Phragmites litter, 12.XII.1987.

W. Medea: Col des Deux Bassins, 920m, 1 male 1 female, Phragmites litter, 12.XII.1987.

W. Oran: Daiet el Bragat, 100m, 2 females, dry Salicornia tufts, 25.IV.1984.

W. Setif: Djemila, 950m, 1 male, stones in ruins, 6.II.1988; Djebel Babor, 1850m, 2 males 3 females, litter in Cedrus atlantica forest, 20.VI.1986 and 1550m, 4 males in pitfalls in Cedrus atlantica forest, 2.XII.1988.

W. Skikda: W. Collo, Tamanart, 15m, 1 female, beating Alnus branches, 6.VI.1987.

W. Souk Ahras: Bou Hadjar, 900m, 1 female, litter in degraded Quercus ilex forest, 9.II.1988.

W. Tissemsilt: Theniet-el-Had, 1540m, 1 male, pitfall in Cedrus atlantica forest, 18.V.1988.

W. Tizi Ouzou: Azeffoun S., Alma Guechtoum, 600m, 1 female, litter in maquis, 27.IV.1990; El Tetla, 180m, 1 male, litter along Oued Boghni, 10.V.1986; Hammam Melouane, 200m, 1 female, stones along Oued El Harrach, 15.III.1987; forêt de Mizrana, 300m, 1 female, stones bordering Quercus suber forest, 26.I.1990; Sebaou-el-Kedim, 50m, 2 females, stones in dry grassland, 10.V.1988; Tigzirt, 50m, 1 female, stones in grassland, 26.I.1990; Djurdjura massif: Aït Ouabane, 1410m, 8 males 7 females, pitfalls in Cedrus atlantica forest, 24.IX.1987-23.VII.1988; idem, Tizi Boussouil, 1750m, 8 males 5 females, I-XII.1989; idem, Col de Tizi ‘n Koulilal, 1480m, 7 males 3 females, pitfalls in alpine grassland, I-XII.1999; Tala Guilef, 1400m, 9 males 5 females, pitfalls in Cedrus atlantica forest, 18.IX.1989.

MOROCCO:

P. Chechaouen: Chechaouen E., 500m, 1 male 1 female, litter in Quercus suber forest, 15.V.1984; Bab Bered W., 1525m, 5 males 4 females, stones in Quercus faginea forest, 15.V.1984.

P. Ifrane: Dayet Ifrah, 1780m, 1 female, grasses around lake, 14.V.1984.

P. Khenifra: Aguelmane Azigza, 1550m, 3 females, stones bordering lake, 13.V.1984.


P. Taza: Cascades de Ras-el-oud, 1000m, 4 females, grasses near water, 22.IV.1984; Djebel Tazeka, 1850m, 1 male, pitfall in Cedrus atlantica forest, 8.V.1984.

P. Tetouan: Tetouan, Oued Hadjera, 10m, 1 female in abandoned garden, 20.IV.1984.

TUNISIA

G. Ain Draham: Djebel Rhorra, 1 male 1 female, 18.IX.1996, K. De Smet leg.

Distribution

Cosmopolitan. In the Maghreb, it is one of the most common linyphiid spiders.

REVIEW OF SPECIES OF THE MAGHREB

The following species of Lepthyphantes sensu lato occur in the Maghreb countries:

Genus Lepthyphantes sensu stricto
Lepthyphantes minutus Blackwall

The afer complex
Lepthyphantes afer (Simon)
Lepthyphantes brevihamatus Bosmans
Lepthyphantes emarginatus Fage
Lepthyphantes longihamatus Bosmans
Lepthyphantes rita Bosmans
Lepthyphantes strinatii Hubert
Lepthyphantes venereus Simon

Not placed in any complex by Saaristo & Tanasevitch (1996):

Lepthyphantes aelleni Denis
Lepthyphantes ajoti Bosmans
Lepthyphantes exvaginatus Deeleman
Lepthyphantes lagunculus Denis
Lepthyphantes linyphioides Denis
Lepthyphantes maurius Brignoli
Lepthyphantes pieltaini Machado

Genus Canariphantes
Canariphantes alassahariensis (Bosmans) Comb. n.
Canariphantes homonymus (Denis)

Genus Improphantes
Improphantes decolor (Westring)
Improphantes djazairi (Bosmans)

Genus Megalepthyphantes
Megalepthyphantes auresensis sp. n.
Megalepthyphantes bkheitae (Bosmans & Bouragba)

Genus Palliduphantes
Palliduphantes cadiziensis (Wunderlich)
Palliduphantes chenini Bosmans
Palliduphantes kalaensis (Bosmans)
Palliduphantes labilis (Simon)
Palliduphantes tricuspis sp. n.
Palliduphantes yakourensis sp. n.

Genus Tenaihantes
Tenuiphantes herbicola (Simon)
Tenuiphantes tenuis (Blackwall)

ACKNOWLEDGEMENTS

Christine Rollard (MNHN) is thanked for the loan of specimens.

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Studies on the biology of two species of catfish *Synodontis schall* and *Synodontis nigrita* (Ostariophysi : Mochokidae) from the Ouémé River, Bénin

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ABSTRACT. The abundance and distribution, length-weight, condition factor, diet and reproduction of *Synodontis schall* and *S. nigrita* from the Ouémé (Bénin) are described. *S. nigrita* is less abundant than *S. schall* in the river. Both species are euryphagous with their diet containing a wide variety of food items that include various types of plankton, invertebrates and plants. This high diversity of the food composition indicates a wide adaptability to the habitats in which they live. This is an important strategy for survival and an advantage over the fish species competing for a specific food item. Size at maturity differs between species for both males (15 cm TL for *S. schall* and 21 cm TL for *S. nigrita*) and females (16 cm and 22 cm, respectively). Fecundity range is higher for *S. schall* (1841 - 15076 oocytes) compared to that of *S. nigrita* (2647 - 9212). Peak values of GSI for males and females in both species occurred from mid- to late July, indicating one season of major spawning activity per year.

KEY WORDS : *Synodontis schall*, *Synodontis nigrita*, biology, Ouémé river, Bénin

INTRODUCTION

Catfishes support the thriving commercial fisheries in many West African countries (OFORI-DANSON, 1992; OFORI-DANSON et al., 2002). Catfishes of the genus *Synodontis*, are small to medium-sized fish belonging to the family Mochokidae. These are a highly valued food-fish in Benin (BARAS & LALÈYÈ, 2003) and contribute an unquantified but significant proportion to the fishery of the rivers. The genus contains approximately 110 species (POLL, 1971), and hence, have more species than any teleost genus in Africa other than *Barbus* and *Haplochromis* (WILLOUGHBY, 1979). In Bénin, about 11 species of *Synodontis* have been identified and 3 species, *S. schall*, *S. nigrita* and *S. sorex*, are known from the Ouémé River (LALÈYÈ et al., 2004). Previous work on the genus in West Africa has been carried out by DAGET (1954) in Lake Chad, BISHAI & GIDEIRI (1965a, 1965b, 1968) in the Nile River, WILLOUGHBY (1976, 1979) in Lake Kainji, HALIM & GUMA’ A (1989) in the White Nile, OFORI-DANSON (1992) in the Kpong Headpond (Ghana), OLOJO et al. (2003) in the Osun River (Nigeria). In Bénin, there is however, no information on many aspects of the genus. This paper investigates the abundance, growth condition, reproduction and diet of *S. schall* and *S. nigrita* in the Ouémé River basin, Bénin.

MATERIAL AND METHODS

Study area and sampling sites

The Ouémé River (Fig. 1) is the largest fluvial basin of Bénin, with a catchments’ area of 50000 km², extending to about 510 km in length originating in from the Tanéka mountains (north of the country) (COLOMBANI et al., 1972). Input waters originate from two main tributaries, Okpara (200 km length) and Zou (150 km length). Peak discharge is rapid and occurs in August-September. It crosses many agro-ecological zones draining to the downstream side of the Nokoué Lake and Porto-Novo lagoon complex connected to Atlantic Ocean. It has an average slope of 0.9 m/km, except along the upstream area of the basin where it measures 0.9 m/km. For the purpose of fish sampling, 4 stations were selected (Fig. 1). The first sampling station is situated on the Okpara tributary river at Kpassa village (09°17’N – 02°43’E). The second sampling station at Atchakpa (08°04’N – 02°22’E) on the Ouémé River is located along a coarse, rocky zone with swift water currents. Toué (07°12’N – 02°17’E) is the third sampling station on the Zou tributary. This station marks the transition between the zones of swift water and the delta. The forth station at Aogolín Lowé’s village (06°39’N – 02°28’) is situated in the Ouémé Delta.

The river is influenced by two distinct climates due to its geographic location. The northern basin (near the sources), a tropical tendency of dry and rainy seasons and...
high varying temperature (10-40°C) are observed throughout the year. From November to March, rains can be rare or turbulent. Furthermore, the harmattan wind, which blows from November to April, accentuates the thermic and hygrometric amplitudes. The rainy season extends from May to September. The southern basin is characterized by a sub-equatorial climate with two rainy and two dry seasons. The great rainy season occurs from April to July with the greatest amount in June. The second rainy season occurs in September. Temperature remains relatively constant varying from 18 to 35°C.

The degree of stomach fullness of the all samples was estimated by the same person by an arbitrary 0-4 points scale defined as follows: 4 points for full, 3 for ¾ full, 2 for ½ full, 1 for ¼ full and 0 for empty stomachs. The fullness index (FI) was considered as the percentage of estomachs completely filled, as well as those considered 75% filled. Stomach contents were sorted into groups and the sex of fish determined according to Lagler (1971), using macroscopic evaluation.

A total of 3646 specimens of both species were collected. These were dominated by S. schall (77%) and data collected were used to length-weight relationships based on the method of LE CREN (1951) and is expressed as follows: Log W = Log a + bLog TL, with W fish weight, TL fish total length and a and b the constants. Relative growth condition factor (Kn, coefficient of condition), which measures physiological well-being of the fish (WOOTTON, 1994) was estimated using the formula proposed by TESCH (1971):

\[ Kn = \frac{W}{aTL^b} \times 100 \]

Maturity stages gauged according to the macroscopic evaluation of gonads (LAGLER, 1971 and LALEYE et al., 1995) were recognized for Synodontis species as: I - immature (very small sexual organs close under the vertebral column; testes and ovaries colourless; eggs invisible to naked eye); II - developing (Testes and ovaries translucent; small eggs can be seen with aid of magnifying glass); III - mature (Ovaries orange-reddish; eggs clearly discernible to eye; ovaries occupy about two-thirds of central cavity; anterior testis whitish with short fingerlike processes and those in posterior appear slightly translucent; milt drops from whitish process under slight pressure); IV - ripe (ovaries freatling ventral cavity; eggs light green in colour, completely round and fall from ovary with little pressure; eggs oocytes diameter (measured from fresh material) varied from 0.5 mm to 1.0 mm (mean 0.8 mm ± 0.2) in S. schall and from 0.8 mm to 1.5 mm (mean 1.1 mm ± 0.3) in S. nigrita); V - spent (not yet fully empty; no opaque eggs left in ovaries; ovaries large but flabby; testes thread-like with no granules and are pink-white shrivelled bodies). Average size at first maturity (L50) was defined as the length at which 50% of the females are at an advanced stage of the first sexual cycle (at least in stage III of the maturity scale) as suggested by TWEDDLE & TURNER (1977). This is based on the previously determined reproductive season to avoid bias in classifying resting females as immature (PANFIL et al., 2004). The gonado-somatic index (GSI) was calculated based on the formula suggested by LAGLER (1971) which is expressed as:

\[ GSI = \frac{\text{Gonad weight (g)}}{\text{Total body weight (g)}} \times 100 \]

Fecundity was determined from 27 and 26 mature gonads of S. schall (13.5 cm - 21.7 cm TL, 30 g - 100 g TW) and S. nigrita (14.0 - 23.5 cm TL, 32g-125 g TW), respectively. Absolute fecundity, probably number of oocytes which will be released at the following spawning, was determined by taking two portions of the ovary (500 fresh eggs ± 50) which are then weighed and initially fixed in modified Gilson’s fluid (BAGENAL & BRAUM, 1971) for about 2 - 3 weeks until oocytes obtained a free and hard texture. The relationship between fecundity and some morphometric measurements were determined by relating total fecundity (F) data to total length (TL), total weight (TW) using the following formulae :

\[ F = a \times TL^b \quad F = a \times TW^b \]

The degree of stomach fullness of the all samples was estimated by the same person by an arbitrary 0-4 points scale defined as follows: 4 points for full, 3 for ¾ full, 2 for ½ full, 1 for ¼ full and 0 for empty stomachs. The fullness index (FI) was considered as the percentage of stomachs completely filled, as well as those considered 75% filled. Stomach contents were sorted into groups and
items identified accordingly. Occurrence percentage (F) (HYSLOP, 1980) was estimated using the formula:

\[ F = \frac{N_{ei}}{N_{t}} \times 100 \]

Where Nei = number of stomachs containing a type of prey i and Nt = total number of full stomachs examined. SCHONER’S (1970) index was used for establishing diet overlaps between the two species and is calculated as:

\[ S = 1 - 0.5 \sum_{i=1}^{n} \left( P_{ij} - P_{ik} \right) \]

where \( n \) = number of food categories, \( P_{ij} \) = proportion (% by weight) of food category i in diet of species j and \( P_{ik} \) = proportion (by weight) of food category i in diet of species k. This is considered as the most satisfactory method in the absence of any food estimate data. Diet overlaps were considered to be biologically important when \( S \) exceeds 0.60 (WALLACE, 1981).

RESULTS

Abundance and distribution

The total number, and weight of Synodontis caught during the 12-month sampling period is shown in Table 1. Synodontis abundance decreases from southern to northern basin. The numbers and weights of the two species in Agonlin Lowé were significantly higher than in other locations (P < 0.05). No S. nigrita have been caught in Kpassa by experimental fishing during the study. S. schall was observed to be more abundant at all the stations compared to S. nigrita. Seasonal variations in numbers and weights are shown in Fig. 2. For both species, peak catches occurred in May and December. In S. schall, peak catches also occurred in July and in January-February and in April (2000). Significant yields catches peak were also observed in August for S. nigrita. Significant reductions in catch were observed for S. schall in August (1999) and in September (2000) for both species.

Size range and population structure

Total lengths of S. schall ranged from 6.2 to 34.3 cm. The difference in fish length between males (range 6.6 cm - 31.5 cm TL, mean 15.1 cm ± 4.7 cm TL, N = 1314) and females (6.2 cm - 34.3 cm, mean 15.9 cm ± 5.03, N = 1199) is not significant (P > 0.05) (Fig. 3). In S. nigrita, the total length ranged from 6.0 cm to 33.5 cm. No significant (P > 0.05) length differences were observed between males (range 6.0 cm - 31.9 cm TL, mean 16.5 cm ± 4.1 cm TL, N = 436) and females (range 6.2 cm - 33.5 cm TL, mean 17.0 cm ± 5.3 cm TL, N = 399). Comparing the two species, the difference in fish length is not significant (P > 0.05).

<table>
<thead>
<tr>
<th>Sampling stations</th>
<th>Synodontis nigrita</th>
<th>Synodontis schall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>% Total no of fish</td>
</tr>
<tr>
<td>Kpasa</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Atchakpa</td>
<td>9</td>
<td>0,16</td>
</tr>
<tr>
<td>Toué</td>
<td>165</td>
<td>0,87</td>
</tr>
<tr>
<td>Agonlin Lowé</td>
<td>715</td>
<td>2,43</td>
</tr>
<tr>
<td>Total</td>
<td>889</td>
<td>–</td>
</tr>
</tbody>
</table>

Fig. 2. – Change in seasonal abundance of S. schall and S. nigrita in Ouémé river basin
Length-weight (L-W) relationship

This relationship was described for the two species based on the linear equations:

- S. schall: \( \log T_W = -4.212 + 2.832 \log T_L \) \( (r = 0.982) \)
- S. nigrita: \( \log T_W = -4.047 + 2.779 \log T_L \) \( (r = 0.973) \)

No significant difference in L-W relationship \( (P > 0.05) \) was obtained between these two catfish species. In both species, the constant \( b \), which describes the slope of the regression line, is smaller than 3 \( (p < 0.01) \):
- \( t(2511) = 5.78; \) S. schall
- \( t(831) = 3.459; \) S. nigrita. This implies that the tendency of the two species is to increase more in size than in mass.

**Condition factor (Kn)**

The mean monthly relative condition \( (Kn) \) value obtained was 1.513 ± 0.005 for S. schall while 1.741 ± 0.088 in S. nigrita (Fig. 4). Significant difference in average Kn values was observed between species \( (P < 0.01; F (1,22) = 60.55) \). Peak of condition factor occurred during the flooding season which falls in September for S. schall and in October for S. nigrita. In both species, a relative increase of condition factor has also been observed in July (1999) and from December to February (2000). Lowest value was observed in June and November for both species.

**Trophic biology**

Of the 2016 stomachs of S. schall (3.0 - 34.3 cm TL) examined, about 44% (886) were observed full, 20% (410) were partially filled and 36% (720) were empty. In the case of the 675 S. nigrita (3.4 - 33.5 cm TL) stomachs examined, 42% (283) were full, 24% (159) were partially filled and 35% (233) were empty. In general, stomachs of both species were more than half full (Fig. 5). During the year, the mean stomach fullness index estimated as 50.4 ± 9.6 in S. schall while 53 ± 16.7 in S. nigrita. This indicates a constant level of feeding activity by the two species. Highest index value was observed in June for both species. Lowest values were observed in July and November for S. schall and S. nigrita, respectively. Similar food items were consumed by both species (Table 2) though varying proportions among prey (Table 3) were observed. Macrophytes and algae were the most frequent food items observed in the stomachs of the two species. Animal prey types are larvae and adults of various insects, crustaceans, rotifers, as well as possible parasitic nematodes. Mud and some unidentified particles were also observed. For S. schall, however, molluscs seems to be a preferred prey following macrophytes and algae. The proportion of eggs and fish scales is more important in the stomach contents of S. schall (frequency of occurrence, 40.35%) compared to that of S. nigrita (1.56%). However, in both species, complete fishes were never found in their stomachs. Diet overlap is biologically important between the two species \( (S = 0.755) \).
TABLE 2
Plant and animal species identified in the stomachs of either *Synodontis schall* or *S. nigrita*

<table>
<thead>
<tr>
<th>Food category</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Machrophytes</td>
<td>Maize, Azolla sp., leaves.</td>
</tr>
<tr>
<td>Algae</td>
<td>Actinocyclus sp, Amphora commutata, Anabaena affinis, Ankistrodesmus fusiiformis, Anabaena sp, Calothrix hervés-sima, Anabaenopsis circularis, Centrarchus belonocephalus, Anomoeneonea sphaerophora, Closterium acciculare, Ceratophyllum natalensis, Closterium acutum, Ceratophyllum sp, Closterium ehrenbergii, Chrccocus limneticus, Closterium leiblini, Closteriopsis longissima, Closterium moniliferum, Closterium lanceolatum, Ferrisia eburneensii, Closterium parvulum, Closterium lineatum, Closterium pseudolunaria, Closterium tumidum, Closterium strictum, Closterium venus, Cocconeis placenta, Closteriopsis sp, Cosmarium brebisonii, Coelomoronois paullus, Cosmarium granatum, Cosmarium connatum, Cosmarium vexatum, Cosmarium contractum, Cyclotella meneghiniana, Cosmarium decoratum, Cymbella silicica, Cosmarium pulchellum, Diplomotes ovalis, Cosmarium pseudodecoratum, Elgloon glaziovii, Cosmarium pseudopyramidatum, Eluotia daphna, Cosmarium quadram, Elouotia monodon, Cosmarium retusi-forme, Eluotia soleirolii, Cymbella caespitosa, Frustula rhomboïde, Eluotropic germanicum, Gomphonema granula, Eluotropic pseudopunctatum, Hantzschia amphiioxys, Eluotropic sphyroides, Heterosaces elegans, Euglena proxima, Micrasteria sp, Fragilaria virescens, Microchloris orix melitensis, Gomphonema gracile, Microcystis sp, Gompho-phaeria naegiliana, Monoraphidium sp, Gonatozygus monotaenium, Navicula eypto, Lyngbya bourellyana, Navicula pygmaea, Lyngbya cebennensis, Navicula splendida, Lyngbya contorta, Nitzschia recta, Merisopedia punctata, Nitzschia scalaris, Micrasteria foliacea, Oedogonium globosum, Microcystis crux-meltensis, Oscillatoria ornata, Micrasteria radians, Pinnularia brauniana, Microcystis aeruginosa, Pinnularia glibba, Microcystis aquatilis, Pinnularia mesolepta, Microcystis delicatissima, Pinnularia nomajor, Microcystis elachistica, Scenedesmus microspina, Microcys-tis sp, Scenedesmus obliquus, Microcystis weenbergii, Spirogyra sp, Monoraphidium griffithii, Spondylosom planum, Mougeotia sp, Spondylosom seedens, Navicula cebennensis, Spondylosom tetragonum, Navicula cryptosphaella, Saur-rastrum forficulatum, Navicula cupulata, Saurastrum polymorphum, Navicula placenta, Stauroneis phoenicer-tion, Navicula pygmaea, Navicula sp, Nitzschia sigma, Nostoc setophyllum, Nostoc piscinale, Oscillatoria platenis, Oscillatoria pseudolahyrinthiformis, Oscillatoria sp, Pandorina sp, Pediasstrum diastrum, P. lucis-vida, Pinnularia acrophaeria, Pinnularia borealis, Pinnularia brebissonii, Pinnularia cardinallis, Pleurotaenium cylindricum, Pleurotaenium trapezida, Pseudanabaena catenata, Scenedesmus ecorzis, Senedesmus naegii, Senedes-mus quadrandca, Spirulina gigantea, Spirulina linearis, Stauroneis phoenicenteron, Synechococcus aestivale, Surirella splendida, Synechococcus aquaticus, Syndra ulna, Tetraedriella gigas, Tetraedron muticum, Ulothrix sp, Ulothrix zonata.</td>
</tr>
<tr>
<td>Rotifer</td>
<td>Asplanchna girodi, Brachionus plathus, Keratella cochlearis, Lapadella patella, Lecane leontina, Pompolyx sulcata, Prolales deaprens, Cepadella</td>
</tr>
<tr>
<td>Insect larvae</td>
<td>Ceratopogonidae larva, Chironomidae larva and pupa, Coleoptera larva, Other Coleoptera, Euparyphus larva, Ephemeroptera larva, Heteroptera larva, Hydropsychidae larva, Odonata larva, Culicidae larva and pupa, Lepidoptera larva, Trichoptera pupa, Neotrichia larva, Anisoptera pupa, Pterostichus borealis, Pterostichus mazaja, Pterostichus angulatus, Pterostichus cardinallis, Pleurotaenium cylindricum, Pleurotaenium trapezida, Pseudanabaena catenata, Scenedesmus ecorzis, Senedesmus naegii, Senedes-mus quadrandca, Spirulina gigantea, Spirulina linearis, Stauroneis phoenicenteron, Synechococcus aestivale, Surirella splendida, Synechococcus aquaticus, Syndra ulna, Tetraedriella gigas, Tetraedron muticum, Ulothrix sp, Ulothrix zonata.</td>
</tr>
<tr>
<td>Aquatic insects</td>
<td>Chaoboridae, Chironomidae, Elmidae, Grillo sp, Pleidae, Hymenoptera, Heteroptera, Mosquito, Orthoptera, Taban-idae,</td>
</tr>
<tr>
<td>Crustacea</td>
<td>Copepoda, Cladocera, Ostracoda, Macrobrachium,</td>
</tr>
<tr>
<td>Mollusca</td>
<td>Bellamyu unicolor, Bulinus sp, Bulinus jousseaumei, Bulinus senegalensis, Biomphalaria pfeifferi, Biomphalaria sudanica, Eupera parasitica, Caetera sp, Cleopatra bulimoides, Gabriella senaeriensis, Limnea natalensis.</td>
</tr>
<tr>
<td>Nematoda</td>
<td>Miscellaneous Pisces scales and eggs, Sand particles, Mud, decomposed matter</td>
</tr>
</tbody>
</table>

TABLE 3
Percentage frequency of occurrence of different category in stomachs of *Synodontis schall* and *Synodontis nigrita* caught from the Ouémé River, May 1999-April 2000

<table>
<thead>
<tr>
<th>Food category</th>
<th><em>S. schall</em> (%)</th>
<th><em>S. nigrita</em> (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrophytes</td>
<td>59.65</td>
<td>43.70</td>
</tr>
<tr>
<td>Algae</td>
<td>35.10</td>
<td>45.63</td>
</tr>
<tr>
<td>Insect larvae</td>
<td>17.54</td>
<td>8.40</td>
</tr>
<tr>
<td>Aquatic insects</td>
<td>7.02</td>
<td>4.80</td>
</tr>
<tr>
<td>Crustacea</td>
<td>5.26</td>
<td>2.94</td>
</tr>
<tr>
<td>Rotifer</td>
<td>5.45</td>
<td>0.02</td>
</tr>
<tr>
<td>Mollusca</td>
<td>19.30</td>
<td>2.10</td>
</tr>
<tr>
<td>Nematoda</td>
<td>12.28</td>
<td>2.52</td>
</tr>
<tr>
<td>Fish eggs and scales</td>
<td>40.35</td>
<td>1.56</td>
</tr>
<tr>
<td>Unidentified decomposed matter</td>
<td>26.32</td>
<td>2.94</td>
</tr>
<tr>
<td>Sand particles</td>
<td>3.51</td>
<td>0.00</td>
</tr>
<tr>
<td>Mud</td>
<td>7.02</td>
<td>12.18</td>
</tr>
</tbody>
</table>

Reproduction

Sex-ratio

Sampling of fish from the different stations in the river ensured a representative distribution of males and females species. In general, in both species, males were observed numerically dominant than females (P < 0.05). According to the months, the sex ratio is in favour of the males (Table 4, P 0.01, ÷² (1,11) = 29.06 for *S. schall* and 40.50 for *S. nigrita*) except in October for *S. schall* and in June, July, December, January and February for *S. nigrita* where the females were slightly dominant numerically. The same result was obtained in different sizes of the fish.
Size at maturity

For both females and males, the sizes at first maturity is higher for *S. nigrita* (21 - 22 cm) than *S. schall* (15-16 cm). This observation is the same when considering the smallest sizes at maturity for both species: *S. nigrita* at 10 cm (male) and 12.5 cm (female) while 7.8 cm (male) and 8.4 cm (female) for *S. schall*.

Gonado-somatic index (GSI) and spawning period

GSI values varied from 0.12% ± 0.1 to 1.854% ± 1.47 and 0.43% ± 0.25 to 9.874% ± 7.38 in *S. schall* males and females, respectively. For *S. nigrita*, values obtained range from 0.29% ± 0.05 to 0.808% ± 0.565 and 0.33% ± 0.01 to 9.88% ± 9.01 in males and females, respectively. GSI values for the two species were found to vary considerably with time, and this variation was at its maximum during July to October (Fig. 6). Peak values for males and females occurred from mid- to late July, indicating one season of major spawning activity per year for both species. Major spawning activity coincided with the high water period (August to October).

Fecundity

The fecundity ranged from 1841 to 15076 eggs in *S. schall* and from 2647 to 9212 eggs in *S. nigrita*. Between species, fish observed with the highest fecundity had a length of 20.8 cm TL and weighed 85 g in *S. schall*. For *S. nigrita*, fecundity is highest in species of 23.5 cm TL in length and 100 g in total weight (TW). The fish with the lowest number of eggs had 13.5 cm TL and 35 g TW in *S. schall* and 14.0 cm and 32 g TW in *S. nigrita*. The relationship between fecundity (F), fish length and weight was investigated and described by the following equations:

\[
F = 1.978 \times TL^{2.817} (r = 0.717) \text{ and } F = 18.53 \times TW^{1.425} (r = 0.8088) \text{ for } S. \text{schall}.
\]

\[
F = 5.951 \times TL^{2.3008} (r = 0.835) \text{ and } F = 190.068 \times TW^{0.7591} (r = 0.7605) \text{ for } S. \text{nigrita}.
\]

High positive exponential fecundity-length and fecundity-weight correlations (p < 0.001) were obtained in the two species. No difference were observed between the two species related to each relationship ((t, 45), P > 0.05).

DISCUSSION

Based on results obtained from experimental and artisanal fishing, *S. nigrita* is less abundant than *S. schall* in the Ouémé River (Table 1). This species was absent in the experimental fishing at Kpassa, but is present in the captures of the fishermen when traps are used.
In general, abundance and distribution of both Synodontis are similar to what was observed earlier on the ichthyofauna of the Ouémé River (LALÈYÉ et al., 2004). According to LALÈYÉ et al. (2004), the stations of Agonlin Lowé and Toué are, by far, the richest in species (Agonlin Lowé, 71 species, = 59.2% of the total ichthyofauna; Toué, 67 species, = 55.8% ichthyofauna). These stations are situated in a vast floodplain whose ecological characteristics favour the colonization by fish. Floodplains present a great variety of habitats of which distribution and dynamics vary according to hydrological seasons (WELCOMME & DE MEERNA, 1988).

OFORI-DANSON (1992) reported that S. schall contributed about 50% of the biomass of the 5 Synodontis spp found in Kpong Headpond (Ghana). ARAOYE (1999) indicated that S. schall was caught abundantly in As lake (Nigeria). S. schall seems to be an ubiquitous species, being found in all aquatic habitats including headwaters of tributaries, pools in dry sandy river beds, as well as in river and marshes. The high occurrence of S. schall within different ecological niches can be attributed to its diverse feeding habits.

The seasonal fluctuations in the numbers and weights of the Synodontis spp caught using gillnets suggest four interrelated factors: changes in the behaviour of the fish, fishing activities, rainy season and recruitment. High species yield in catches during April and May corresponds to the beginning of the rainy seasons when food availability is highest due to the flood-introduced nutrients and mixing of water body by rapid currents. Such ecological conditions are favourable to fishes and may allow them to leave their hiding places making them vulnerable for fishing. Increase in fish abundance due to the combination of physico-chemical properties and the presence of food items has already been reported by FAGADE & OLANIYAN (1974) for the Lagos lagoon (Nigeria). In May (1999), the abundance of vulnerable fishes reached its maximum. This situation can justify the importance of catches obtained in this month. The stock of fishes falls down in June due to the intensity of the fishing.

This numerical and ponderal increases of Synodontis are then followed by a decrease in June which will increase again during July and August for S. schall and S. nigrita, respectively. The lowest numerical abundances are registered in August – September for S. schall and in October - November for S. nigrita when water level is at its highest. The one-month gap noted between the two species could be due to behavioural differences aside from other factors. Decrease in fishing vulnerability may be due to the increased catchments area allowing these species to disperse and hide during spawning. Catch rates increase progressively starting from December when water level and catchments are decreasing. Catch rate for S. nigrita starts to decline in January. Decrease in catch of S. schall, however, starts only in March.

Decrease in abundance after flooding may be due to the decrease of river margins suitable for feeding and for spawning (HAKANSON & BOULION, 2002).

Increase in abundance is highly correlated with success recruitment. The viability of these species may be largely enhanced by the reproductive behaviour (guarders), enhancing survival due to decreased predation, of these species (OFORI-DANSON, 1992) complemented by their high reproductive rates.

About size structure of the populations studied, the maximum size for S. schall is superior to that indicated by ALBARET (1982) for Ivory Coast (22 cm) while lower to the value indicated by OFORI-DANSON (1992) for S. schall (26.7 cm SL, or about 33.5 cm TL) in Kpong Headpond (Ghana). This difference of sizes is even better illustrated by the condition factor for S. schall (1.49 ± 0.19), which is lower than that indicated by OFORI-DANSON (1992), 2.54 ± 0.002 for male and 2.91 ± 0.018 for females. Among factors which can explain the difference obtained in the average condition factor (see LE CREU, 1951) of a fish species in two or more habitats, the fact that the fish are in better condition of feeding in a habitat than in the second one can play an important role in this specific case.

Estimated growth factor indices (Kn) for both species, S. schall = 1.49 and S. nigrita = 1.73, are lower than the estimated range of mean values (2.65 - 3.32) indicated by BAUDOT et al. (1997) for some slow-growing important fishes in Africa.

The food items in the stomach of both Synodontis species suggest that they are omnivorous feeders as the diet covers a wide spectrum of food ranging from various types of plankton to invertebrates and plants. This is in agreement with the finding of LAUZANNE (1988) who considers the Synodontis genus as eclectic. OLOO et al. (2003) observed the same food habits in S. nigrita from the Osun River (Nigeria). This high diversity of the food composition of both Synodontis species indicates a wide adaptability to the habitats in which they live. Many catfishes, such as the Chrysichthys spp, are benthic omnivores with a strong tendency to predation (BARAS & LALÈYÉ, 2003). This is an important strategy for survival and an advantage over the fish species competing for a specific food item (P AUGY, 1994; LÉVÈQUE, 1997). A clear morphological explanation for its feeding versatility may be due to the ventral location of the mouth of both Synodontis species which encourages a detritivorous mode of feeding while the simple horny structures around the mouth enable it to adapt to filter feeding (OLOO et al., 2003). These structures also help Synodontis to gnaw at any hard plant tissue which form part of its rich diet. WINEIMILLER & KELSO-WINEIMILLER (1996) stated that Synodontis leopardinus, S. nigromaculatus, S. woosnamai, S. macrostigma, S. macrostoma of the Upper Zambezi River floodplain (Zambia) were omnivores, but interspecific differences were however noted. In Ouémé River, the most frequent food items in the stomachs of both species were macrophytes and algae. The diversity of algae consumed by both species is high (more than 100 species, Table 2). In Kpong Headpond (OFORI-DANSON, 1992), the frequent food item in S. schall were chironomids. The insects, fish eggs and scales clearly originated from both the bottom (with organic sediment and pieces of wood often present) and from periphyton of flooded trees, grasses and aquatics plants. These categories of food items were more frequent in S. schall stomachs compared to that of S. nigrita, suggesting that the habitats used by the two species for their food are not rigorously the same. The presence of sand grains and mud in the stomachs

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indicates that these species browse on benthic deposits in the river. The presence of nematodes in many stomachs almost in *S. schall* could explain some diseased and parasitized specimens observed during the study. Size-dependent (ontogenic) variation in occurrence of different categories of food in stomachs of the two species is not clear. The overall picture of the diet of *S. schall* and *S. nigrita* that emerges from this study is that of two species which are largely unspecialized in their feeding habits. Unspecialized dietary habits are an optimal strategy for survival in habitats where food sources are subject to fluctuation (WELCOMME, 1979; PAUGY, 1994; LÉVÊQUE, 1997).

There is an important difference in reproductive biology between the two species of *Synodontis*. Size at maturity was observed higher for *S. schall* compared to that of *S. nigrita*. In Lagoon Ebrie (Ivory Coast), ALBARET (1982) obtained 15.5 cm of size at maturity for *S. schall*, HALIM & GUMA’A (1989) observed different values (14.0 - 15.0 cm SL) for *S. schall* in White Nile (Sudan). In Lake Kainji (Nigeria), WILLOUGHBY (1979) reported smaller sizes at maturity for *S. schall*, 10.4 and 11.8 cm for male and female, respectively. The highest values (20.0 cm) were obtained by OFORI-DANSON (1992) for female of *S. schall* in the Kpong Headpond (Ghana). Maturation of fish may be affected by several physical and biological factors, and these may account for the discrepancies observed between the findings of different authors. The influence of varying environmental conditions on maturity and reproductive traits have been shown in studies by LÆ (1997), LÉVÊQUE (1997), DUPONCHELLE et al. (1998), DUPONCHELLE & LEGENDRE (2001) and PANFILI et al. (2004) in other West African aquatic systems.

It is clear from the drop in monthly G.S.I that spawning of *S. schall* and *S. nigrita* in the Ouémé River occurs from August to October which coincides with the flooding period of the river. This, however, is not in agreement with other observations on fish reproduction ecology in other floodplain environments. WELCOMME (1979) and BARAS & LALÈYÈ (2003) indicated that the majority of floodplain fish species initiate spawning after horizontal flooding has begun, i.e. well into the rainy season. In Lake Chad, the spawning activity for *S. schall* occurs from mid-July through September (BLACIE, 1964). The different environmental and climatic conditions in the habitats could explain the discrepancies observed. As conditions change during the year with the change in season, the suitability of the environment for the vulnerable early life-history stages will vary. A fish should reproduce at that time of year that will tend to maximize its lifetime production of offspring. The larval fish must hatch into a world that can provide appropriate food, protection from predators and benign abiotic conditions (WOOTTEN, 1994).

The two species have different fecundities. Though, *S. nigrita* produces more oocytes compared to *S. schall*, when comparing the smallest sizes at maturity, egg production by *S. schall* out-numbers that of *S. nigrita* after reaching the size of 20 cm TL. These values varied greatly from counts given for *S. schall* by OFORI-DANSON (1992) from Kpong-Headpond (14000-165000 eggs), NAWAR (1959) from the Nile River (7000-130000 eggs), HALIM & GUMA’A (1989) from the White Nile River (10000-90000 eggs), OLATUNDE (1989) from Zaria (Nigeria) (2014 - 13262). The great variations in the number of eggs produced by the individual of a certain species were demonstrated for a large number of other tropical fishes (NAWAR, 1959; AWACHIE & Eazenwaji, 1981; LALÈYÈ et al., 1995; BARAS & LALÈYÈ, 2003 and many others). Apart from the environmental factors, the differences observed may be, in part, attributed to the methods used for fecundity estimation.

Eggs diameters at ripe stage were greater (0.8 mm-1.5 mm) in *S. nigrita* than in *S. schall* (0.5 mm-1.00 mm). For *S. schall*, HALIM & GUMA’A (1989) reported a range of 0.6 mm to 0.9 mm from White Nile in Khartoum. The greatest estimation (1.15 mm to 1.20 mm) was given by ALBARET (1982) for *S. schall* from Ivory Coast. Such variations in the eggs diameters were similarly reported for other tropical fishes (i.e. AWACHIE & Eazenwaji, 1981).

**CONCLUSION**

The feeding versatility of *S. schall* and *S. nigrita* coupled with the high fecundity enables these species to overcome perturbations, natural or human induced, in the Ouémé River. Life-history of species is influenced by varying ecological conditions and highly tolerant species, such as the catfishes, are promising candidates for commercial exploitations.

**ACKNOWLEDGEMENTS**

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Description of Hypogeoppia belgicae, a new species of cave mite (Acari, Oribatida), and comments on some characters

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ABSTRACT. The Oppiidae (Acari, Oribatida) are one of the largest families of Circumdehiscentiae. Within this family, the genus Hypogeoppia comprises few species, all soil organisms. Here we describe a new species, \textit{H. belgicae}, from adult specimens collected in caves in South Belgium. Several characters showed a substantial variability in the two populations studied. In addition, \textit{H. belgicae} displays some uncommon or unique apomorphic features such as a notogasteral posteromedian notch, prodorsal and podosomatic tae nidia, elongated chelicerae, internal subcapitular septa, and tracheal vesicles III.

KEY WORDS : Oribatida, Oppiidae, Circumdehiscentiae, Hypogeoppia, taxonomy, description, cave, Belgium

INTRODUCTION

The present paper describes a new species of Oppiidae Grandjean, 1951 (see Grandjean, 1953, for a definition of the family) which, according to Subias (1981) and Subias & Balogh (1989), we assign to the genus \textit{Hypogeoppia} Subias, 1981. Beside the new species, the genus \textit{Hypogeoppia} consists of five species, one subspecies and two varieties. Most \textit{Hypogeoppia} have a limited distribution, and have been collected only in Europe (but see Subias, 1981, for an outstanding exception). They are soil dwelling organisms lato sensu. To date, no \textit{Hypogeoppia} was found in Belgium. The new species, \textit{H. belgicae}, has been collected exclusively in earth deposit from nine caves located in South Belgium (Ducarme et al., 2003).

New and uncommon characters were detected in this species. Additional information regarding some of these characters and in particular the possible role of some of them is provided in the discussion below.

MATERIAL AND METHODS

The terminology used follows that of F. Grandjean (see Van der Hammen, 1980, for definitions and references). Yet it should be noted that : (1) the terms ‘adaxial’ and ‘abaxial’ used for an element (a structure, a segment or a phanere) mean ‘drawn up to’ and ‘moved away from’ the plane of symmetry, respectively; (2) the prime (’) and double prime (’’) symbols are equivalent to the terms anterior and posterior, respectively; in the appendages, a ’ phanere is anteriad of the plane of pseudosymmetry, and a ’’ phanere is posterior; in addition, due to the destruction of the plesiomorphic, perpendicular parallelism of appendages (see Grandjean, 1961a, for a discussion), the ’ phaneres are adaxial in the pedipalpi and legs I and II, and abaxial in the legs III and IV, and the ’’ phaneres are abaxial in the legs I and II and adaxial in the legs III and IV; (3) the brackets are used to indicate the setae of a pair. The abbreviations not used in the text are defined in the keys of figures.

The length of the body, excluding the gnathosoma, was determined in dorsal projection. The length and height of chelicerae and rutella were measured in lateral projection (the largest sizes were taken into account for these measurements as well as for the data reported here). Some characters were studied by comparison with two closely related species, namely \textit{H. perezinigoi}, some specimens of which were generously sent by Dr. L.S. Subias, and \textit{Berniniella sigma conjuncta} (Strenzke, 1951), a soil dwelling oppid mite collected in some caves inhabited by \textit{H. belgicae} (Ducarme et al., 2003). Observations were conducted in light microscopy (LM), in scanning electron microscopy (SEM) and, in collaboration with Prof. G. Alberti, in transmission electron microscopy (TEM).

DESCRIPTION OF HYPOGEOPPIA BELGICAЕ

(FIGS 1-6)

\textbf{Diagnosis}

\textit{Hypogeoppia} with the rostral setae \textit{ro} inserted close to the plane of symmetry. A long and sinuous gutter \textit{tp} developed on both sides in the prodorsum, and regarded as a taenidium. Notogaster : with anteromedian region occupied to a large extent by a pair of dorsosseugal apophyses \textit{Dp} and their companion carinae \textit{ke} and \textit{ki}; with adaxial companion carinae \textit{ki} substantially elongated; and with posterior border provided with a median, U-shaped notch. Epimeric furrows \textit{4} transformed into gutters.
regarded as taenidia. Tracheae III with two branches, the lower one in the form of a vesicle. Penis apparently with only two pairs of egumental setae. Subcapitulum with a pair of strong internal septa separating on both sides the pharynx from the base of the pedipalpi. Mentum with a large, unpaired and U-shaped carina cc. Rutella with a pad-like free extremity. Chelicerae elongated.

**Size, color, cerotegument, setae**

Mean total length: 257 μm in males (n = 10; range 248-271 μm); 266 μm in females (n = 10; range 256-282 μm). Body colour yellowish brown, yet cheliferae and pedipalpi paler, dorsal region of the subcapitulum and rutella colourless and distal part of the leg tarsi apparently whitish when observed in reflected light.

Cuticle: (1) apparently smooth except in some places where a granular microsculpture exists (see below); (2) bright in reflected light, yet duller where a layer of cerotegument is developed. Parts of the body usually covered by the cerotegument according to observations in transparent light: (1) dorsally, the anterior and posterior, dorsosejugal apophyses Da and Dp, the prodorsum between the apophyses Da, the sejugal furrow ssj, and the parts of the notogaster abaxially with respect to apophyses Dp; (2) laterally, a large zone from the lateral gutter tp of the prodorsum to the border of the notogaster bng, except above the bothridia, and all the podosomatic region; (3) ventrally, the environs of the podocephalic fissures F; and a strip running abaxially on all the metapodosoma and widening out posteriorly. Note that observations by means of sections through freshly-collected individuals confirmed the existence of the cerotegument in the prodorsal gutters tp and in the epimeric gutters 4, and revealed that it spread out inside the bothridia (Alberti, pers. com.). Cerotegument composed of numerous, conical and pointed microprojections.

Setae: (1) usually in the form of thin phaneres tapering off substantially so that they end with a long point; (2) without a base tubercle discernible in LM, with a few exceptions (e.g. all the setae of the prodorsum).

**Prodorsum**

Rostral hood ending in a quite broad limbus (the breadth of the limbus near the plane of symmetry can be estimated in Fig. 1a insofar as its base corresponds to the extremity of the ducts originating from the alveoles of the rostral setae ro). The two rostral slits clearly V-shaped in apical view. Rostrum lanceolate between the slits.

Dorsovertex: (1) in the form of a robust bulge with well discernible, anterior and lateral borders, and depressed sagitally; (2) lateral borders forming steep carinae frequently obliterated anteriorly, and sometimes interrupted by a shallow groove not reaching the plane of symmetry, at the level with the interlamellar seta in. No true lamellae. Yet, anteriad of the dorsovertex, a pair of low and oblong convexities kd, parallel to the plane of symmetry, on which the lamellar setae la are inserted anteriorly. Prodorsal surface depressed between the convexities kd, and inclined up down to the sejugal furrow ssj, posterior of the dorsovertex, between the dorsosejugal apophyses Da; ordinarily with an elongate, more or less oblique concavity in the middle of the sloping zone. Apophyses Da prolonged adaxially, by a companion carina ordinarily bent towards the plane of symmetry, and abaxially, by the lateral border of the dorsovertex. Note that: (1) in some individuals, the apophyses Da were broader or narrower than in Fig. 1a; (2) in two individuals, the apophyses were divided into two on the left side.

Gutters tp. Higher extremity located just underneath the convexity kd (Figs 1a and 2); prolonged in front by an elongated hollow also situated below the convexity kd. Lower ending formed by an oblique carina kt in front of the legs I (Figs 1b and 2; note that, in Fig. 1b, the carina is merged into the lateral apparent outline of the podosoma). Between these two extremities, gutter tp made up of an upper part, directed upwards and backwardly curved, and a lower part, forwardly curved and encompassing dorsally and anteriorly the circumtrochanteral opening of the legs I, with an elbow-shaped junction (Fig. 2). Borders obvious everywhere except frequently above the carina kt for the anterior border, and less frequently above the elbow and in the elbow itself for the posterior border. Note that: (1) a broadening of the gutters was sometimes detected at the level with the elbow, whereas the lower part habitually widens out in front of the legs I; (2) in some cases, there was a narrowing before the gutter widens out. Dorsally, upper part of the gutters with a microsculpture made of roughly widthwise orientated ridges which usually block the gutter incompletely, and tend to demarcate small curved-walled chambers of variable number and outline. Moreover, often an oblique ridge, sometimes thick, at the level with the elbow (Fig. 2). Note that: (1) in consideration of their microsculpture, the prodorsal gutters comply unambiguously with the definition of taenidia sensu Grandjean (1944); (2) analogous lateral taenidia exist in Berninella sigma conjuncta, yet they are missing in H. perezinigoi.

Bothridia wide-open; borders: (1) provided with striae (not represented in Fig. 1a; as shown in Fig. 2, they are less numerous anteriorly); (2) higher, wider and longitudinally grooved posteriorly (the grooves are well marked and their walls are steep; they get narrower in their mid part so that the borders of bothridia seem to possess two small tubercles backwards). Sensilli bo with a relatively short stem, and with a fusiform club bearing small thorns at wide intervals. Region close to the trichobothria embossed and variable between individuals, yet with three elements usually found: (1) in front of the trichobothria, a short, transversal ridge sometimes changed into a small tubercle; (2) above the trichobothria, a longitudinal, curved convexity (note that the interlamellar seta in is inserted between the convexity and the lateral border of the dorsovertex); (3) posteriorly, an ordinarily rounded protuberance between the convexity and the apophysis Ba.

Setae. Lamellar setae le very short and slender. Other prodorsal setae long and thin. Setae le and apparently exobothridic setae ex smooth. Setae in and rostral setae ro bearing small barbs. Setae in longer than the others, similar to notogasteral setae; making their way upwards. Setae ex and ro oriented forwards. Base tubercle of the setae ex changed into a robust nodosity. Setae ro clearly bent to the plane of symmetry; their insertion slightly but invariably asymmetric.

Granular microsculpture constantly detected: (1) on a small surface before the upper part of the gutters tp as well as in the gutters tp; (2) behind this surface; (3) above the legs 1; (4) on the apophyses Da.
Anterior border clearly convex in its middle (Fig. 1a). Dorsosejugal apophyses Dp and companion carinae ki and ke robust (Figs 1a and 2). Free border of the apophyses Dp: (1) forming an oblique and convex forwards line in dorsal projection (Fig. 1a) (note that, in some individuals, the free border was more rectilinear than in Fig. 1a, on one side or on both sides); (2) making a contrasted angle with the abaxial carina ki, yet prolonged linearly by the abaxial carina ke; (3) in contact with the prodorsal dorsosejugal apophysis Da when the animal is contracted. Carinae ki usually a bit undulating horizontally (even sometimes distinctly sinuous), and extending longitudinally and a bit obliquely so that they meet posteriorly. Notogasteral surface depressed between the two carinae ki; ordinarily with one, rarely two short and weakly curved ridges in the depression. Oblique and more or less robust convexity developed on both sides between the carina ke and lyrifissure ia.

Articular cuticle present everywhere at the limit between the notogaster and the rest of the body: (1) anteriorly, narrow and tending cleanly in the dissections; (2) posteriorly, making up a sagittal fold due to the notch of the notogaster (the cuticle of dorsoventral connection is labelled tgs in Fig. 3a); when the animal is contracted, the fold is directed towards a fossa located on the ventral shield behind the anal opening.
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(postanal fossa), in the bottom of which it ends (Fig. 3b); beyond, directed upwards and backwards before attaching to the ventral shield (the line of attachment is labelled at in Fig. 3) so that, in lateral projection (Fig. 3b), conspicuously bent in the plane of symmetry. Note that according to observations in SEM, the borders of the notogasteral notch can draw even nearer to each another than represented in Fig. 3a. 

Dorsophragma and pleurophragma absent. Circumdorsal groove apparently deficient according to a careful examination in transparent light, even after heating in lactic acid (this contrasts with many other Circumdehiscentiae, yet see similar examples in the Autognetidae, a family closely related to the Oppiidae; GRANDJEAN, 1963). Lyrifissures ia, im and ip (slit sense organs) well distinguishable; lyrifissures ih and ips apparently missing.

With 20 setae. Note that: (1) the chaetotaxy corresponds to the Dometorina type (GRANDJEAN, 1950, 1956a) shown by many Circumdehiscentiae in which the centrodorsal setae and two setae of the row c are lost; (2) for labelling the notogasteral setae, we used the Dometorina notations modified by LIONS (1970). All the setae long and slightly barbed, except the setae ps2 and ps3, which seem smooth. Setae c2 inserted on the lower wall of the carinae kl (Fig. 2), and with a base tubercle distinguishable in LM. On both sides, seta cp inserted at the junction of two short ridges, which diverge posteriorly.

Lateroabdominal glands gla similar to small, oblong bags; usually opened near the setae h3.

**Ventral region of the podosoma**

Epimeric furrow 3 absent. Epimeric furrow 2 and epimeric sejugal furrow obstructed by several short ridges arranged crosswise (some ridges robust, with widened extremities). Epimeric gutters 4 (labelled tv in Figs 1b and 2): (1) ornamented with granules and ridges of variable size, and roughly widehwise orientated; note that this microsculpture, though more compact and more variegated than that of the prodorsal gutters tp, led us to class the epimeric gutters tv as taenidia (GRANDJEAN, 1944); (2) adaxially, narrowing and ending close to the circumgenital opening; (3) with an anterior border obvious everywhere, and with a posterior border less pronounced abaxially; (4) showing a V-shaped deviation at the level with the seta 4a, in some individuals, in one side or in both sides; (5) passing round the acetabular region IV abaxially, and making their way longitudinally and a bit obliquely on the pleural region towards the large carina kl (Fig. 2). Note that epimeric taenidia with an analogous course were found in H. perezinigoi and B. sigma conjuncta.

Sagittal region of the podosoma, in the epimeron 1, with a chitinous thickening anteriorly, joining the base of the mentotectum in front, and usually with a roughly triangular outline in ventral projection (note that, in some individuals, its surface was substantially reduced), and a sternal apodeme posteriorly (hatched in Fig. 1b). Sternal furrow absent.

Three conspicuous apodemes present, namely ap.1, ap.2 and ap.sj, each consisting of two half apodemes large and apparently not perforated. Half apodemes ap.1: (1) in their longitudinal part, connected with the lateral edges of the

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**Fig. 3. – Hypogeoppia belgicae n. sp., female. – Posterior parts of the notogaster and ventral shield in a contracted animal, partial, with the anal valves removed. – a, seen from the back. Lines (broken) of apparent outline in the median, posterior fold of the articulat cuticle tgs of dorsoventral connection are shown through the cuticle of the notogaster. The part of tgs which turns beyond the fold towards the line at of attachment to the ventral shield and emerges from the postanal fossa (its border is indicated by the dotted line fp), is not distinguishable in this orientation. mu.mv, marginoventral alignment of insertions of dorsoventral, opisthosomatic muscles – b, right lateral. The horizontal hatching represents an optical section of the tegument passing through the plane of symmetry. bs, border of the ventral shield.**
sagittal thickening and with the free border of the sternal apodeme (note that the half apodemes 1 are not represented Fig. 1b except their posterior limit indicated by a transversal, forwardly curved broken line behind the seta 1a; note also that, in apical projection, the longitudinal parts of the half apodemes 1 appear to be directed obliquely upwards; ALBERTI, in litt.); ordinarily, as shown in Fig. 1b, connexion not extending to the posterior end of the sternal apodeme; (2) in their transversal part, united as usual with the base of the mentotectum and with the cotyloid wall cot of the acetabulum I (GRANDJEAN, 1952, 1968). Half apodemes 2 apparently a bit higher than half apodemes ap.sj, yet with a base approximately of a size (Fig. 1b). Epimeric band borders bo3 indistinct. Band borders bo1, bo2 and bo.sj relatively narrow. Band borders bo2 and bo.sj apparently connected to each other in the sagittal region; connections usually broad (Fig. 1b), yet scarcely visible and even imperceptible in some individuals.

Setae. Formula of coxisternal setae : (3-1-3-3), i.e. the formula characterizing the Circumdehiscentiae without deficiency (GRANDJEAN, 1934). Setae 3b, 3c and 4c longer than the other setae. Setae 3c and 4c bearing some minute barbs; other setae apparently smooth. Setae 4c with a discernible base tubercle. Note that the labels 4a and 4b used for the posterior epimeric setae in Fig. 1b require a confirmation in so far as immatures are unknown.

Sculpture. On both sides : (1) anteriorly, a longitudinal carina kv extending from the mentotectum to the epimeric furrow 1; (2) in the propodosoma, a lateral and longitudinal carina km usually divided into two anteriorly, and to which three oblique carinae are joined posteriorly; (3) in the metapodosoma, a lateral and curved carina (not labelled) stretching between the sejugal furrow ssj and the discidium di. In addition, an unpaired, thin and apparently continuous ridge kz running parallel to the anterior border of the circumgenital opening and ending laterally close to the extremity of the gutters tv. Granular microsculpture only in the posteroabaxial areas of the ventral region of the podosoma.

**Tracheal system**

Tracheae I : (1) in contrast with many other Circumdehiscentiae (GRANDJEAN, 1968), common trunk orientated forwards, and posterior branch tr.1p usually not longer than the anterior one tr.1a; (2) posterior branch not entering into the opisthosoma.

Sejugal tracheae with the abaxial branch tr.sj.a going in the opisthosoma, and longer than the adaxial one tr.sj.p which ordinarily ends in the prosoma. Vestibulum short and narrow, located near the abaxial extremity of the half sejugal apodemes. Sejugal stigmata in the form of a small hole situated in the sejugal furrow ssj, at the level with the legs.

Tracheae III : (1) lower vesicle (labelled tr3i in Fig. 4a) a bit curved; (2) upper branch tr3s long, clearly twisted in the opisthosoma. Note that the position of the stigmata III could not be precisely determined, yet they definitely have an anterior location on the cotyloid wall of the acetabula III.

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Fig. 4. – *Hypogeoppia belgicae* n. sp. – a, male, right trachea III, partial, and acetabulum III seen through the cuticle in a dissected fragment of the podosoma. The hind leg is on the left. The horizontal hatching marks the circumtrochanteral opening of the leg III. The oblique hatching represents an optical section of the cotyloid wall III cot and the posterior tooth Δ” of the trochanter III-podosoma articulation. – b, female, genital region, partial, in ventral projection, with the right genital valve removed so as to have a direct sight at the genital papillae. A part of the median papillaVm is not represented in order to completely show the small papilla Va. The papillae are invaginated in their sheath. The sheath of papilla Va is pointed out by two lines of apparent outline whereas the sheath of papillae Vm and Vp are not discernible. The dots indicate the base of the two posterior genital setae. The granulation lateral and behind the circumgenital opening is partially shown. np, posterior, internal nervure of the genital valve. – c, male, preanal organ (hatched) in ventral projection after the removal of anal valves. The organ is almost horizontal. It has remained near the border of the circumanal opening. – d, same organ (vertically hatched) in lateral view. The gnathosoma is on the right. The oblique hatching represents an optical section of the cuticle passing through the plane of symmetry.
Lateral characters

Genal incisions, tutoria and pedotecta absent. Prominences P, thick, similar to low laminae (Figs 1 and 2), variable in form and size; not homologous with usual pedotecta, in consideration of their distance from the circumtrochanteral openings of the legs I (see discussion in GRANDJEAN, 1960a). Surface behind the circumtrochanteral opening of the legs I transformed into a crescentiform depression with a steep border (mean depth, measured just behind the trochanter, of around 4 µm; n = 4). Note that the border of the depressions coincides anteriorly with the free border of the acetabulal tectum I, and posteriorly with the prominence P on a short distance. Discidia di robust (Figs 1, 2 and 4a).

Sculpture: (1) discidual carinae cdi prolonging in front the discidium and becoming a tectum as it crosses the segjugal furrow sjs; crossing tecta bearing the epimeric setae 3c on their upper side, often on a short ridge, and usually joining in front the lateral carina km of the propodosoma; (2) two anterior carinae getting to the podocephalic fissure F on both sides; upper one elongated and originating from the prodorsum; lower one thin, short and parallel to the lateral border of the cameroosome bl.cam; (3) longitudinal carinae kl, long, robust, rugose and embossed (Figs 1a and 2); crossing the segjugal furrow sjs; habitually interrupted in one place at the level with the acetabular region II (more rarely with two cuts as exemplified in Fig. 2); upper side depressed at the level with the segjugal furrow sjs, reaching anteriorly the posterior border of the gutter tp of the prodorsum; made up posteriorly of two elements, namely a longitudinal, sometimes shortened carina, and a transversal, bulge-like element extending towards the circumtrochanteral opening of the legs III; (4) parietal, wavy carinae ks stretched out dorsally and anteriorly close to the circumtrochanteral opening of the legs II (2 in Fig. 1a); attaining posteriorly the circumtrochanteral opening after a bend; (5) several more or less elongated ridges associated with the carinae kl and ks; substantially variable in their aspect and characters (e.g., behind the prominences P, ridges tend to unite and form a reticulate microsculpture, including one to five depressed cells, different in size and shape); (6) posterior, oblique carinae kp extending above the discidium, between the carina kl and the circumtrochanteral opening of the legs IV; sometimes divided into two. Note that the carinae kl, kp, cdi and km, together with the posterior border of the gutter tp, form a sort of roughly trapezoidal structure enclosing completely the legs I, II and III.

Borders of the segjugal furrows sjs ordinarily ridge-shaped in places above the cariniae kl (Fig. 2), yet sometimes slightly or incompletely discernible; usually well visible below the cariniae kl. On both sides, two apophyses in opposition across the segjugal furrow sjs, referred to as postbothermal enantophysis Ba-Bp in GRANDJEAN's (1960a) nomenclature (see also BEHAN-PELLETIER & NORTON, 1985); posterior apophysis Bp in contact with an elongated and oblique convexity. Bright spots: (1) upper one located near the exobothridic seta ex; sometimes indiscernible; probably a small, alveolar vestige of the second exobothridic seta; (2) lower one (labelled z in Fig. 2) situated near the posterior curvature of the carina ks; without doubt, the opening of a supracoxal gland, which is frequently found in oribatids at this place. Granular microsculpture developed here and there on the pleural regions: frequently in the surroundings of the legs IV, and constantly on the carinae kl, the discidual apophyses di, the carinae kp and the adjacent surface, and the apophyses Ba.

Ventral region of the opisthosoma

Except regarding the postanal fossa (Figs 1b and 3) and the anterior minitectum mi.a in the genital valves (Fig. 1b), the ventral superficial characters of the opisthosoma have nothing unusual. Yet note that: (1) the anal setae ad3 are in front of the anal valves and far apart from the plane of symmetry; (2) the anal lyrifissures iad are large, close to the border of the circumanal opening bta, and parallel to this border (i.e. in ‘paraanal’ position according to SUBIAS & BALOGH, 1989).

Valves. Genital minitectum mi.a in the form of a narrow, abaxial shouldering at the anterior extremity of the hinge of the valves; note that similar Shouldering is observed in oribatid mites possessing teanidial epimeric furrows 4 ( GRANDJEAN, 1968). As often in the Circumdehiscentiae, genital and anal valves with anterior and posterior internal nervures, and with a lock coaptation system on their adaxial border, consisting here of tooth-like or laminar-like elements and cavities which fit together; elements of the lock coaptation system, as follows: (1) small teeth in the anal valves in both sexes; (2) in the genital valves, a tooth-like piece in both sexes, anteriorly, and two teeth in the males and one lamina in the females, posteriorly.

Anterior genital papillae Va cone-shaped and pointed; much smaller and more distant from the surface of the genital valves than the other papillae (Fig. 4 b), as in several other Oppiidae (BEHAN-PELLETIER, 1991). Genital organs not studied in detail. Yet we report here the following observations regarding the ovopositor: (1) long and enlarged, with elongated lobes; (2) as in some other Circumdehiscentiae (LIONS, 1982), coronal setae at the circular stricture absent; (3) as usual, six pairs of eggunital setae detected on the lobes; (4) in each lobe, two setae clearly more proximal than the other two. Penis: (1) with two large and unpaired internal processes, i.e. an anterior rod-like piece and a posterior lamina, egg-shaped in ventral projection, and fringed except in its proximal part; (2) the four eggunital setae long, and in an anterolateral position.

Preanal organ: simple, similar to a chitinous lamina with a roughly trapezoidal outline in ventral view (Fig. 4c); convex in lateral projection (Fig. 4d); fastening to the border of the circumanal opening by means of two small articular sockets; note that in some individuals one articular socket was minute or even scarcely visible.

Cuticle, frequently in males and rarely in females, cut behind the genital opening by a pair of internal and longitudinal furrows of variable breadth. Note that the anoprogenital muscles are likely to be situated in the furrows. Anal lyrifissures absent.

Setae: (1) 11 pairs of setae present, namely five pairs of genital setae, one pair of aggenital setae ag, three pairs of anal setae ad1-3, and two pairs of anal setae an1-2; (2) only anal setae barbed, the others smooth; (3) setae ad2 longer than the other setae of the region, and the three...
posterior genital setae the shortest; (4) the two anterior genital setae with a base tubercle.

Granular microsculpture found only in the genital region: (1) constantly in a zone situated behind the adaxial part of the gutter tv and laterad of the circumgenital opening; note that the granulation close to the circumgenital opening is usually thick and gives sometimes the impression that the cuticle is reticulated; (2) more rarely, behind the circumgenital opening.

**Genathosa, chelicerae and pedipalpi**

Subcapitulum diarthric, with atelebasic rutella (cf. Grandjean, 1957a), and elongated so that its anterior elements, i.e. the rutella and lips, appear to be imperfectly protected by the rostral tectum at rest.

Mentum: (1) with a pair of deep, lateral notches in which the propodosomatic condyles K are placed; note that the notches are likely to be hollowed in the procuticle and covered by the epicuticle; (2) large carina cc everywhere parallel to the border (Fig. 1b); its posterior, rounded part robust, yet its anterior, longitudinal parts lessening in front; carina kx escaping forwards on both sides from the carina cc, and curved towards the plane of symmetry. Labiogenal suture lg broader in the sagittal region than laterally where it becomes thin and poorly discernible as coming near the base of the pedipalpi. As in some other orbibid mites (Grandjean, 1964b; Alberti & Coons, 1999; Alberti et al., 2003), ventral cuticular ridge (or sclerite) vR associated with the pharynx floor, and connected with the tegument of the mentum over a short distance just behind the labiogenal suture lg (in Fig. 1b, the posterior limit of the attached part is marked by a transversal broken line). Note that: (1) the ridge appears to be developed a bit in front of the suture lg; (2) an analogous ridge exists in *H. perezinigoi* and *B. sigma conjuncta*.

Genae: (1) without lateral tectum for coaptation with the border of the camerostome; as a result, the pedipalpi are not completely hidden at rest as they keep discernible ventrally; (2) ventral side with a few scarcely discernible lines which appear to be external thin ridges attaining the adaxial border rather than grooves, yet a confirmation is required. Labrum and lateral lips not studied. Regarding the dorsal region of the subcapitulum, we report here only the following observations: (1) as in several other orbibid mites (Grandjean, 1957b), a pair of dorsal and elongated apodemes ne (note that, in Fig. 1b, they are seen though the cuticle of the mentum); (2) opening of subcapitular glands (Grandjean, 1957b) quite broad. Setae: (1) as usual, three pairs of subcapitular setae present, namely a, m and h (Grandjean, 1957a); (2) two pairs of adoral setae; indiscernible in LM; actually, laid on the ventral, concave side of lateral lips according to observations in TM; (3) supracoxal spines of pedipalpi similar to baculiform and straight phaneres with a rounded tip. Subcapitular septa: (1) originating dorsally from the bottom of the cheliceral groove, in front of the nerve tv (Alberti, in litt.); (2) attached ventrally to the lateral region of genae (note that, in Fig. 1b, the ventral insertions are indicated by a thick broken line, and not represented in front because they are concealed by the pedipalpal femora); (3) merging anteriorly into the lateral wall of genae. Note that: (1) further work examining the relationships between the subcapitular septa and genae is currently under way; (2) analogous septa seem to exist in *H. perezinigoi* and *B. sigma conjuncta* in so far as elements likewise shaped and similarly located are present.

Rutella: (1) plump shape demonstrated distally in dorsal or ventral projection (Fig. 1b) due to a lateral (abaxial) deviation of their free extremity; (2) showing a roughly trapezoidal outline in lateral projection (Fig. 5a); (3) actually, in the form of elongated laminae a bit widthwise curved, thicker dorsally than ventrally, and forming an imperfect gutter in so far as, despite the existence of small ventral lobes, their ventral borders are not joined axially (Fig. 1b); (4) devoid of distal teeth, yet with a dorsal denticle, and with a minute notch at the ventrodorsal angle; (5) adaxial side with a comb made up of five or six bars, and with two ridges: a longitudinal ridge ku which, according to observations in TEM, forms the boundary line between the dorsal and ventral parts of rutella (note that it was not possible to determine whether the ridge ku actually is longer than what is shown in Fig. 5a), and a transversal ridge developed at the base of the distal, inflected part (not shown in Fig. 5a). Manubrial zone large and punctuated (in Fig. 5a, the line af represents the abaxial part of the manubrial articulation; cf. Grandjean, 1957a).

Chelicerae (Fig. 5b) remarkable for: (1) their lengthening since they show a height/length ratio of around 0.28, i.e. according to Grandjean (1964a), a value significantly below the mean value in the Circumdehiscentiae (see illustrative data in Schuster, 1956); (2) the weakness of their dentition since the proximal teeth are blunt, some being even rounded in lateral projection (Fig. 5b). As usual, two setae on each chelicera, namely cha, proximal and barbed, and chh, distal and smooth. Ventral intumescentia, denticate crests and squama (Grandjean, 1959) absent, yet with the following elements: (1) a Trägårdh’s organ Trg, as in several other Circumdehiscentiae (Grandjean, 1959); (2) a pair of minute spines ep close to cha; (3) as usual (Norton, 1998), a striated fossa fc on the adaxial side (striations not shown in Fig. 5b); (4) two fossae, not striated, on the abaxial side; (5) a proximal, ventral extension e beyond the thickened base border. Cuticular punctuation indistinguishable except proximally on the abaxial side, behind the fossa fc. Tendons hard to see except the abaxial tendons ta of cheliceral retractor muscles.

Pedipalpi five-segmented (Fig. 1b). Tarsi slightly (but indubitably) curved downwards (Fig. 5c). Ventral ridges: (1) proximal and longitudinal in femora; (2) oblique in patellae (apparently replaced by a furrow in some patellae); (3) in tarsi, U-shaped and intersecting the plane of pseudosymmetry just behind the seta vt’ (the ridge clumps up further on the adaxial side than on the abaxial side). Solenidion w (probably an olfactory organ; cf. Alberti, 1998): baculiform, with a rounded tip, and hard to see in LM because it is laid dorsolaterally on the tarsal cuticle; note that, according to observations in TEM, its base is likely to be more proximal than what is represented in Fig. 5c. Setae: (1) formula normal: (0-2-1-3-9); (2) all the setae apparently smooth except the tarsal, posteroventral setae vt’ equipped with barbs; (3) lower femoral setae v clearly ventral and inserted far from the
other setae (an uncommon position; cf. GRANDJEAN, 1935); (4) in patellae seta \(d\) in a dorsal position (a primitive condition; cf. GRANDJEAN, 1935); (5) anteroculminal eupathidium \(acm\) in tarsi (probably a gustatory receptor; cf. ALBERTI, 1998) not associated with the solenidion \(\omega\) (i.e. no double horn); note that the internal canal in all the eupathidia of pedipalpal tarsi was undiscernible in LM even at high magnification and after heating in lactic acid; actually, observations in TEM were required to attest the existence of an internal canal; (6) shiftings: no basculation in the paired ultimal eupathidia \(ul\) (a primitive condition; GRANDJEAN, 1958); paired ventral setae \(vt\) nearly lined up longitudinally, demonstrating a clear (double prime) disjunction. Apparently only the femoral setae \(v'\) and tarsal setae \(lt''\) with a base tubercle perceptible in LM.

![Diagram](image)

Fig. 5. – Hypogeoppia belgicae n. sp., female. – a, right rutellum, seen laterally, with a part of the gena. The dots below the line \(ku\) depict the base of barbs of the comb on the adaxial side of the rutellum seen through the cuticle. The labrum and the lateral lips are not represented. \(c\), collar of the rutellum – b, right chelicera, separated and seen laterally. Only the proximal part of Trägårdh’s organ \(Trg\) is shown. The part of the chelicera behind the line of attachment \(en\) of the cheliceral sheath is inside the body. It is represented as if it is exposed. In this orientation, the dorsal adaxial spine is hidden by the abaxial spine \(ep\) which is the only spine to be shown through the dorsal cuticle. The weakly undulating line behind the movable digit marks a longitudinal carina on the abaxial side of the cheliceral body. The hatching directed to the left covers the posterior, more coloured part of the movable digit. The hatching directed to the right indicates partially the base border of the cheliceral body. – c, tarsus of the right pedipalp seen laterally. The solenidion \(\omega\) is vertically hatched. The oblique hatching marks an optical section of the tegument through the plane of pseudosymmetry of the segment. \(cm\), culminal seta. \(su\), subultimal eupathidium.

**Legs**

Noticeable traits in the leg setae: (1) a lot of tibial and tarsal setae contrasting by their bulk with the setae of proximal segments which are thin and similar to most setae borne by the body (Figs 1 and 6); note that some setae of proximal segments appear slightly more robust than the others (e.g. the anterolateral seta \(l'\) in the patellae I and II); (2) in the tarsi II, a clearly proximal location of the anterolateral seta \(a'\) (Fig. 6b); note that the double prime disjunction of the anterolateral pair resulting from the displacement of the seta \(a'\) towards the body is consistent with the rule enacted for other lateral setae (GRANDJEAN, 1960a).

Legs moniliform in dorsal projection, with clearly bulbous segments beyond the trochanters; note that this aspect is less apparent in lateral projection for the tarsi I, II and III because the peduncle is poorly discernible dorsally in these segments (Fig. 6). Legs IV longer than the other legs, and legs II the shortest.

Formulae of the phaneres: for setae, from trochanters to ambulacra: I (1-5-2-4-20-1), II (1-5-2-4-13-1), III (2-3-1-3-13-1), IV (1-2-2-3-10-1); for solenidia, from patellae to tarsi: I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0). Taking into consideration that (1) there is no dorsal companion seta \(d\) in patellae and tibiae, (2) the iteral pairs \(it\) are found only in I, II and III, (3) the fastigial seta \(ft'\) is lost in IV, (4) there are two accessory setae (i.e. \(v'\) and \(v''\)) in the tarsi I, and (5) the proral pairs \(p\) are suppressed in II, III and IV as in other Oppiidae (GRANDJEAN, 1953), the formulae for setae appear to be ordinary.
Hypogeoppia belgicae n. sp., females, legs seen laterally, partial. The femur in the legs I and II and trochanter in the leg IV are incompletely represented. No indication is shown for the dorsoproximal, tarsal lyrifissures \( \lambda \) except in II. A hatching marks the solenidia. The limit of punctuated areas developed on the segments is indicated by a dotted line (the punctuation is not depicted). – a, a distal segments of the right leg I. – b, idem, right leg II. The seta without label in the patella is the posterolateral seta \( \lambda _ I \). In the tibia, only the root (partially hidden by the seta \( \lambda _ l \)) and mid part of the seta \( \lambda _ I \) are drawn. In the tarsus, the broken line below the seta \( \lambda _ I \) marks the dorsal outline of the seta \( \lambda _ I \) seen through the cuticle. – c, left leg III, without the trochanter. As usual, no convexity is developed dorsoproximally on the femur. There are three thin ridges on the tarsus. – d, left leg IV. The proximal, adaxial ridge of the femoral bulb is partially seen through a punctuated area of the anterior (abaxial) side. The proximal convexity of the femur is poorly marked dorsally but discernible whereas in some other femora it was non-existent. Eight thin ridges are found on the tarsus.

Solenidia. Number usual for the Circumdehiscentiae, corresponding to the first hitch in the numerical regression which affects the solenidia in this group (Grandjean, 1964c). Tactile solenidia (sensu Grandjean, 1935), namely \( \sigma _ I, \varphi _ I, \sigma _ II \) and \( \varphi _{II} : \) (1) quite elongated, yet \( \sigma _{II} \) and \( \varphi _{II} \) less long than the others; (2) \( \sigma _ I \) and \( \varphi _ I \) taking a direction towards the body (Fig. 6a); \( \sigma _ I \) frequently twisted (Fig. 6a), with a distal part usually orientated towards the ambulacrum; (4) course shown by \( \sigma _{II} \) variable, yet frequently twisted with the distal curvature directed towards the ambulacrum as shown in Fig. 6b; (5) \( \varphi _{IV} \) usually directed towards the ambulacrum (Fig. 6d). Baculiform solenidia, namely \( \omega _ I, \varphi _{II} \) and \( \omega _{II} : \) (1) \( \omega _{II} \) thick and short, and \( \omega _ I \) and \( \varphi _{II} \) thin and longer; (2) \( \omega _ I \) curved upwards, and \( \varphi _{II} \) and \( \omega _{II} \) bent towards the ambulacrum, the former also being curved abaxially. Ceratifform solenidia, namely \( \omega _ I, \varphi _ I, \omega _{II} \) and \( \varphi _{II} : \) (1) relatively thick, yet \( \varphi _{II} \) more slender than the others; (2) \( \varphi _{III} \) rectilinear, and the others bent towards the ambulacrum, an additional curvature being detected in \( \omega _ I \) (adaxial curvature) and frequently in \( \omega _{II} \) (abaxial curvature).

Areae porosae apparently absent. Yet areas clearly punctuated but not really porous detected in all the segments except in the patellae and trochanters I and II, as follows: (1) in the trochanters III and IV where they are the largest, and extend over the dorsal and lateral sides (Figs 1 and 6); (2) in femora where they are the most numerous; (3) in tibiae where, in addition to a ventral area in I, III and IV, there are a dorsal area in III and IV, a quite large dorsoabaxial one in I and II, and an adaxial one in III; (4) in tarsi where they are located dorsally in I and II, and abaxially in all the legs.

Trochanters. Trochanters I and II similar ventrally to a protrusion on which their seta (labelled \( \nu R \) in Fig. 1b) is inserted. Trochanters III and IV apparently rounded in dorsal projection (see the left trochanter III in Figs 1a and b), and elongated and approximately oval in lateral view (see the left trochanter IV in Fig. 1b). Note that some trochanters III surveyed in this study appeared perceptibly more angular in dorsal projection as their dorsal side was depressed adaxially. Trochanters III with a distal rim indented adaxially so that the anterior condyle of the trochanterofemoral joint is substantially more proximal than the posterior condyle. Trochanters IV with two thin ridges on the adaxial side, the upper ridge being shorter than the lower one. Setae: (1) all the trochanteral setae bearing small barbs; (2) trochanteral setae in III and VI with a base tubercle.

Femora. Sculpture: (1) a pad-like convexity developed in the proximal part of the bulbs, as follows: on all the sides in the femora I in most females (note that as shown in Fig. 1 the convexity in the femora I is always more pronounced than in the other legs); on all the sides in some femora IV in both sexes (Fig. 6d); usually on the adaxial side, sometimes on the dorsal and ventral sides, and rarely on the abaxial side in the femora II and III; (2) a pair of short, transversal, roughly parallel but not adjoining ridges on the adaxial side of the femora IV (Fig. 6d).

Setae: (1) all the femoral setae equipped with small barbs; (2) lateral pair (l) in I and II showing both a double prime basculation and a prime disjunction.

Patellae. Approximately all of a size. Bulb II ordinarily with a thin ridge on the dorsal, abaxial and ventral sides. Solenidia \( \sigma \) without a base tubercle. Chaetotaxy normal, i.e. abiding by the rules of numerical predominance (Grandjean, 1942). Setae: (1) dorsal seta \( d \) in patellae IV apparently smooth; (2) usually no disjunction or a weak disjunction of the lateral pair \( l \) in I and II, yet some patellae I with a disjunction more marked than in Fig. 6a; note that, in agreement with the rule, the disjunction was double prime (cf. Grandjean, 1960d).

Tibiae. Peduncle IV longer than in the others, and bulb I the most voluminous. Sculpture: (1) a low, strip-like convexity in I, II and III; in I and II, developed proximally on the bulb (in I, in the dorsal and lateral sides, and more rarely in the ventral side; in II, only in the dorsal and adaxial sides); in III, making dorsally and abaxially the distal limit of the peduncle; note that the convexity extended on the ventral side in some tibiae, and was replaced by a ridge in some others; (2) two furrows \( s p \) and \( s a \) on the dorsal side of the bulb I; note that the proximal furrow \( s p \) was occasionally prolonged on the abaxial side, and that the distal furrow \( s a \) was sometimes scarcely perceptible; (3) a poorly prominent carina on the dorsal and lateral sides of the bulb II; (4) thin ridges in the peduncle III and IV; in III, one or two ridges on the dorsal and lateral sides; note that, in some tibiae, the distal ridge was adaxially indiscernible; in IV, two ridges on both the dorsal and abaxial sides, which unite ventrally in the abaxial side; sometimes a third ridge found a bit more distally on the dorsal side. Solenidia: (1) \( \varphi _ I \) not inserted at the anterodorsal extremity of the tibia, yet in an unusual, dorsal and a bit abaxial position; borne on a large and not very salient prominence; note that sometimes the prominence was less perceptible in lateral projection than in Fig. 6a; (2) \( \varphi _{II} \) inserted anteriad of \( \varphi _{II} \) on the prominence; (3) \( \varphi _{II} \) dorsal and slightly abaxial; (4) \( \varphi _{III} \) and \( \varphi _{IV} \) axiodorsal or nearly axiodorsal. Setae: (1) lateral seta \( \lambda _ I \) in I and II with a base tubercle; (2) lateral pairs (l) with a double prime basculation in most of tibiae I and II; note that sometimes the basculation was weak or null, and a slight, usually double prime disjunction was observed in...
I; (3) ventral setae \( v' \) and \( v'' \) in I and II, and seta \( v' \) in III and IV affected by a conspicuous downward displacement so that pairs \( (v) \) with a prime basculation in III and IV; (4) pairs \( (v) \) with a double prime disjunction in I, and a prime disjunction in III and IV; note that only the disjunctions in III and IV are consistent with the rule of prime disjunction applied to tibial ventral pairs (cf. Grandjean, 1960a).

Tarsi. Peduncles III and IV longer than the others, and bulb I the most voluminous. Sculpture: (1) in I, two furrows on the ventral side, proximally with regard to the antelateral pair \( (a) \), the distal furrow apparently forming the limit between the bulb and the slimmed part of the segment, and the proximal furrow ordinarily climbing up the adaxial side of the bulb; (2) in the other tarsi, thin ridges developed at least on the dorsal and lateral sides; only one ridge found in the slimmed part in II, yet two to four ridges in III and still more in IV; note that one or two ridges in III and the majority of the ridges in IV showed a circular course. Dorsoproximal lyrifissures \( b' \) : (1) lateral shifting in prime direction detected in I, III and IV, yet in double prime direction in II; consequently, the displacement of lyrifissures appears to be an evolution not consistent with the rule of ‘parallel homology’ (see a definition in Grandjean, 1939); (2) lyrifissure II longer than the others; as a result its shifting seems relatively less pronounced than it is in the other segments. Solenidia: (1) in I, solenidia \( o' \) and \( o'' \) in a dorsoabaxial position (Fig. 6a); (2) in II, proximal solenidion \( op \) axiodorsal or nearly axiodorsal, and distal solenidion \( ox \) dorsoaxial. Setae. Subunguinal setae \( s \) in I not eupathidic but ordinary setae just as exemplified by a few other oribatids in which the setae \( s \) are inserted in the vicinity of the antelateral pair \( (a) \) (see e.g. Grandjean, 1948); note that: (1) accordingly, the proral setae \( (p) \) in I are the only eupathidia found in the legs; (2) just as indicated above for the distal setae of pedipalpi, the internal canal in the setae \( (p) \) was unperceivable in LM. As usually observed in eupathidia, setae \( p \) in I smooth. Distal setae, i.e. ultimal setae \( u \) and ultimal setae \( it \), bearing short barbs, and more robust barbs detected in the other setae, with a few exceptions (e.g. the tectal setae \( tc \) in I and IV). A small base tubercle detected in: (1) the seta \( u' \) in all the legs; (2) the pair \( (it) \) in the legs I, II and III; (3) the seta \( a'' \) in the legs I, III and IV; (4) the seta \( u'' \) in the legs II, III and IV; (5) the setae \( tc' \), \( a' \) and \( s \) in the legs I and III; (6) the setae \( tc'' \) and \( pv'' \) in the legs I; (7) the seta \( ft'' \) in some tarsi IV. Disjunctions (see Grandjean, 1960a, for the rules of disjunction): (1) in I, the fastigial pair \( (ft) \) (prime disjunction, as in many other orbibatid mites), the tectal pair \( (tc) \) (prime disjunction, contrary to the rule; in some tarsi, the disjunction was more marked than in Fig. 6a), the primilaterial pair \( (pl) \) in several tarsi (prime disjunction, contrary to the rule), and the ventral pair \( (v) \) (double prime disjunction, contrary to the rule); (2) in II, besides the antelateral pair \( (a) \) (see above), the ultimal pair \( (u) \) (double prime disjunction, contrary to the rule applying to other ventral setae); (3) in III, the fastigial pair \( (ft) \) (double prime disjunction, according to the rule); (4) in IV, the antelateral pair \( (a) \) (prime disjunction, contrary to the rule applying to other lateral setae), and the primiventral pair \( (pv) \) (prime disjunction, according to the rule). Basculations: (1) in I, the primilaterial pair \( (pl) \) (double prime basculation; note that, in some tarsi, the basculation was less pronounced than in fig 6a), and the ventral pair \( (v) \) (double prime basculation; note that sometimes a slight basculation was observed, always on account of a descent of the seta \( v' \) rather than an ascent of the seta \( v'' \)); (2) in II, the primiventral pair \( (pv) \) (double prime basculation); (3) in III, the fastigial pair \( (ft) \) (prime basculation, as in many other orbibatid mites; cf. Grandjean, 1961b); (4) in IV, the antelateral pair \( (a) \) (prime basculation). Famuli \( e \) in the form of a thin, erected and relatively long phanere with a rounded tip. Lower tendons of the ambulacrum guided proximally owing to a canal bored through the ventral cuticle of the peduncle; as shown in Fig. 6, all the canals have a thick roof.

Apotene. Ungues simple, without tooth and without either ridges or barbs; in the legs I and II more curved and shorter than in the legs III and IV.

Type material

The material examined for this description consisted of some thirty males and females from two caves: a cave in Freyr near the city of Dinant, and a cave in Tilff near the city of Liège (Ducarme et al., 2003). Samples were collected from earth deposit, on locations that were not flooded at any time of the year. The mites were extracted using Berlese-Tullgren method or dibromoethane flotation (Ducarme et al., 1998). Immatures are unknown.

The types, namely one male holotype and three female paratypes, are deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels. In pursuance of Trave’s (1965) recommendations, the type specimens were not dissected but used only for a rough study.

DISCUSSION

Key to the species and subspecies of Hypogeoppia

The position of the rostral setae \( ro \) and the existence of unpectinate sensilli allow \( H. belgicae \) to be unambiguously distinguished from the other Hypogeoppia. On the other hand, as in \( H. dungeri \) Schwalbe, 1995, and \( H. exempta \) (Mihelčič, 1958), the anterior border of the notogaster in \( H. belgicae \) is equipped with a pair of dorsal apophyses between the bothridia and the plane of symmetry. In fact, in \( H. belgicae \), \( H. dungeri \) and maybe \( H. exempta \), the notogasteral apophyses and the apophyses located in front on the prodorsum appear to be analogous with the dorsosejugal enantiophyses \( Da-Dp \) found in other Circumdehiscentia as e.g. in the Damaeidae (Grandjean, 1960a; Behan-Pelletier & Norton, 1985), a circumdehiscent family not closely related to the Oppidiidae (note that enantiophyses are apophyses in opposition staking off a primitive furrow; Grandjean, 1954; Norton, 1978). By contrast, two pairs of notogasteral apophyses, a culminodorsal pair \( Cp \) and a laterodorsal pair \( Lp \) in Grandjean’s (1960a) nomenclature, are detected in \( H. perezinigoi \) Subias & Arillo, 1996, \( H. terricola terricola \) Subias, 1981 (note that according to Schwalbe, 1995, \( H. festonata \) Moraza & Moreno, 1988, is a synonym of \( H. terricola terricola \); see also Subias & Arillo, 1996, and Subias, 2004), and \( H. terricola sal-
Annotations on some unusual characters

1. To our knowledge, all the observations performed to date in the Oribatida indicated that the penis bears six to eight pairs of eugenital setae (e.g. GRANDJEAN, 1955, 1956b; LIONS & NORTON, 1998). Yet two remarks must be made, as follows: (1) to demonstrate that the partial denudation of the penis in H. belgicae is an uncommon trait, the examination of the penis in a greater number of oribatid species is imperiously required; (2) in consequence of the small size of the organ making its study difficult, minute, poorly discernible setae could have escaped our investigation.

2. Rather than areae porosae, the punctuated zones detected in the legs (Figs 1 and 6) could be muscular insertions. Yet observations by SHULTZ (1989) on the leg musculature in mites (see also YASTREBTSOV, 1987) provide strong evidence that the ventral areas in the tibiae I, III and IV (Fig. 6) are not muscular insertions. This is probably also the case for the area on the abaxial side in all the tarsi. As a result, further work is needed to determine the nature of punctuated zones shown by the legs.

3. The setae labelled v' in the femora I and II (Fig. 1a) are probably metahomologous (i.e. had primitively the same position on the femora I and II). The phaneres v could then be regarded as abaxial setae v" having shifted in lateral (adaxial) direction. Another possibility is that the seta v" in the femora I is actually an adaxial seta v' , yet this seta is less frequent in the Circumdehiscentiae (see e.g. GRANDJEAN, 1960b, 1965).

Considerations on the role of some uncommon characters

1. It appears that taenidia running laterally on the prodorsum in H. belgicae (Figs 1a and 2) and B. sigma conjuncta have no equivalent among Oribatida (TRAVE, 1986). By contrast, the ventral taenidia tV in H. belgicae, H. perzinigoi and B. sigma conjuncta are analogous with epimeric taenidial furrows found in some Circumdehiscentiae (GRANDJEAN, 1968). Yet there is one main difference: the taenidial cuticles are open in the oppiid species whereas they are covered with a minitectum in the other species. According to GRANDJEAN (1964a, 1968) and TRAVE (1986), the main role of taenidia would be both to hold out against moistening and to keep some air in reserve against the body during a period of immersion. Yet no air pellicle was detected in taenia of living H. belgicae plunged in water, in glycerine or in liquid paraffin. Therefore, a question remains to be answered concerning the function of taenidia in this species.

2. The action of dorsoventral opisthosomatic muscles generates not only a lowering of the notogaster towards the ventral region of the body but also a forward movement of the notogaster caused by the elements contained in the opisthosaoma, which oppose the compression. In fact, this latter movement is prevented by the anterior part of articular cuticle of the notogaster, which acts as a fixed (immobilizing) point. Since the extremity of notogasteral dorsosejugal apophyses Dp rests on the prodorsal dorsosejugal apophyses Da in contracted individuals (Fig. 2), it is possible that the apophyses Dp are also fixed points of the notogaster.

The lowering of the notogaster is the usual method of haemolymph pressure generation in the body. In oribatid mites, several motions and functions have been reported to rely on internal haemolymph pressure (see e.g. WOODRING & COOK, 1962; GRANDJEAN, 1969; AKIMOV & YASTREBTSOV, 1991; ALBERTI & COONS, 1999): (1) limb extension; (2) protraction and retraction of the mouthparts; (3) opening of genital and anal valves; (4) extrusion and turgidity of the penis and ovipositor; (5) circulation of haemolymph; (6) mix of the contents of tubular organs (e.g. digestive tract); (7) expulsion of genital products and fecal pellets; (8) discharge of products secreted by exocrine glands. In addition to the lowering of the notogaster, contraction of dorsoventral opisthosomatic muscles might also induce a lateral compression of the notogaster in H. belgicae. This view is supported by observations with SEM, which show that borders of the notogasteral notch (Fig. 3) are appreciably brought together in contracted individuals. If the two movements were independent, lateral compression would allow a
more acute control of haemolymph pressure to be achieved (e.g. to fill a specific leg). If the two movements were concomitant, lateral compression would counterbalance the drop in internal pressure due to haemolymph flow from the dorsal region of the notogaster towards its ventral, larger region, when the notogaster comes down. The latter hypothesis suggests that internal hydraulic pressure might be high under certain circumstances. In this case, it could be that the capability to reach high internal pressure and the enlarging of apophyses $Dp$ combined with the addition of robust companion carinae became linked in $H. belgicae$.

It should be noted that the existence of a postanal fossa (Figs 1b and 3) should also contribute to the generation of high hemolymph pressures at least if the postanal fossa is designed to allow an important lowering of the notogaster with regard to the ventral shield to occur.

3. The existence of two branches in tracheae III has been reported to date only in some Liacaridae (Grandjean, 1968), a circumdehiscent family not closely related to the Oribiidae. In contrast with $H. belgicae$, the lower branch in Liacaridae is shaped either like a more or less elongated simple duct or like a bud. Even though most of the surveyed populations inhabited parts of caves irregularly flooded or apparently never immersed (Ducarme et al., 2003), we cannot neglect the possibility that the vesicles III could improve the resistance to immersion in water. Indeed, the vesicles III appear to be air holders just as the external taenia usually are (see references above). Further information on the ability to survive a long period of dipping in water is necessary to assess this hypothesis (note that preliminary observations revealed no mortality in individuals immersed in water for more than 16 hours).

The acquisition of a respiratory vesicle, a very peculiar apomorphic character, agrees with the fact that evolution has given rise to a significant novelty occurring in the most lately derivative oribatid mites, i.e. the Circumdehiscentiae (Grandjean, 1966; Ducarme et al., 2004).

4. The large carina $cc$ of the mentum is probably used for the coaptation with both the camerostome and the mentotectum. Indeed, in contracted individuals studied with SEM, the carina is drawn close to the border $bl\ cam$ of the camerostome anteriorly, and to the border $bm$ of the mentotectum laterally and posteriorly. Thus, the carina $cc$ appears to be analogous with the hysterostomatic carina found in the Plasmatobatidae (Grandjean, 1961b), a circumdehiscent family not closely related to the Oribiidae.

5. The modifications undergone by both the chelicerae (i.e. lengthening of the cheliceral body and weakening of the teeth) and rutella (e.g. lengthening, loss of distal teeth, and deviation of the free extremity) abide by the rule of concomitant evolution of these two organs in the Oribatidae (e.g. Grandjean, 1957a, c). The lengthening of chelicerae and rutella in $H. belgicae$ is similar to that detected in the Suctobelbidae, a circumdehiscent family closely related to the Oribiidae. For instance, the height/length ratio for the chelicerae is a bit lower than 0.3 in $H. belgicae$ and in the suctobelbid Allosuctobelba grandis studied by Grandjean (1951) (see Woas, 1986, for other examples in the Suctobelbidae). In the same way, the ratio for the rutella is lower than 0.5 in the two species, i.e. clearly below the values yielded by rutella regarded as typical in the Circumdehiscentiae (between 0.75 and 1.10).

The gnathosoma of the Suctobelbidae has been affected by a suctorial evolution characterized by both a lengthening of chelicerae and a transformation of rutella into elongated and edentate laminae. Yet, in contrast with many suctorial oribatids (Grandjean, 1957a), the rutella in $H. belgicae$ are not typically foliaceous since, for instance, they are partially thinned down and incompletely edentate. In addition, $H. belgicae$ possesses two characters that a lot of non suctorial oribatids exhibit: (1) a labiogenal zone (labelled $lg$ in Fig. 1b) (Grandjean, 1957a); (2) long cheliceral setae $cha$ and $chh$, whereas a shortening or a complete loss of these setae is usually associated with suctorial evolution (Grandjean, 1964a). In fact, regardless of their evolutionary origin, cheliceral and rutellar modifications would denote a peculiar diet in $H. belgicae$.

Attempts to determine the diet using food choice experiments in the laboratory were unfortunately unsuccessful (Ducarme, 2003).

In other respects, it should be noted that elongated chelicerae have already been reported in the genus Chelopippia Hammer, 1971, classified by Subias & Balogh (1989) in the Oribiidae, yet a careful study of the chelicerae and rutella has not been done.

6. The function of subcapitular septa is unclear except that they induce an increased stiffness in the surrounding exoskeleton. Now, if this reinforcement affects the movements of genea and rutella (see Grandjean, 1957a, for a discussion), an increased expenditure of energy for feeding might be required, at least if the rutella still ensure their scraping function in $H. belgicae$.

ACKNOWLEDGEMENTS

We thank Gerd Alberti for the lot of inestimable information supplied; Nouzar Banaï for enlightening discussions; Johan Billen, Jean-Claude Lions, Sergey Mironov, L. S. Subias and Raymond Terefe for their help. Thanks are also due to Julien Cillis, Richard D. Kime, Marylise Leclercq and Harry Van Paesschen for their valuable assistance. This study is a part of the ‘Microarthropod Biodiversity in Walloon Caves’ project led by Ph. Lebrun (Université Catholique de Louvain) and supported by the Fonds national de la Recherche scientifique and by a grant of the Région wallonne.

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A comparative analysis of biodiversity and distribution of shallow-water marine isopods (Crustacea: Isopoda) from polar and temperate waters in the East Pacific

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ABSTRACT. Checklists of isopods currently reported for the polar and temperate waters of the East Pacific, in depths of 200 m or less, are presented, and compared with an updated list of species known to the eastern tropical Pacific (ETP). A total of 213 species are recorded for the northern subregion (Arctic, Aleutian, and Oregonian Provinces), 133 for the southern subregion (Peru-Chile, Temperate Transitional, and Magellan Provinces) and 134 for the ETP. In total, 420 species are known to occur in the East Pacific. Considering the entire East Pacific region, the isopods fauna is dominated by the Cymothoida (36.4% of total), followed by the Asellota (21.9%), the Valvifera (17.3%), the Sphaeromatidea (16.2%), the Oniscidea (6.2%), the Limnoriidea (1.4%) and the Microcerberidea (0.5%). The northern and southern polar-temperate faunae include a total of 340 species, with only seven species in common. The northern and southern subregions share only 34 out of 160 genera; of these, 103 occur in the northern subregion, 76 in the ETP and 65 in the southern subregion. The southern and northern subregions share 34 genera and 21 genera are shared by the three subregions, of which 12 belong to the Cymothoida. Forty-three families are registered in the East Pacific, 41 in the northern subregion and only 22 in the southern subregion, of which 18 are common to both. Comparatively, the ETP contains 25 families and 12 families are found in all three subregions. An analysis by provinces indicates that, according to our present knowledge, the highest number of species in the East Pacific is recorded in the Oregonian Province (140 species), followed by the Californian (128), Cortés (95), Magellan (75), Temperate-Transitional (61), Aleutian (61), Mexican (53), Panamic (52), Peru-Chile (43), and Arctic (15) provinces. Sixteen species are reported for the Galapagos, 10 each for the Juan Fernandez and Guadalupe Islands. A cluster analysis based on presence-absence of species revealed four major groups among the 10 previously recognized provinces, both when species and genera were used. The grouping of provinces into southern, ETP and northern subregions appears well defined and with comparable values of the similarity index, with the exception of the Arctic Province.

KEY WORDS: Isopoda, East Pacific, checklists, distribution

INTRODUCTION

Estuarine and marine isopods are among the most common crustaceans found worldwide. The order Isopoda contains approximately 10 000 species, of which about half are terrestrial. Most of the rest are found in brackish, marine and occasionally hypersaline waters (BRUSCA & BRUSCA, 2002; WILLIAMS, 1983). They are found in virtually all kind of habitats, either as free living organisms or partly or exclusively parasites (SCHULTZ, 1961; DEXTER, 1972; 1974; 1976; RIBI, 1981; DELANEY, 1984; KANG & YUN, 1988; ELLISON & FARNSWORTH, 1990; ARRONTES & ANADÓN, 1990; TAYLOR & MOORE, 1995; BRUSCA & BRUSCA, 2002).

The East Pacific is one of the large marine zoogeographic regions of the World. It covers approximately 127 degrees of latitude, from the Sea of Bering to the tip of Tierra de Fuego and has been traditionally divided into eight zoogeographic provinces (BRUSCA & WALLERSTEIN, 1979b; HENDRICKX, 1992), two of which (Arctic and Magellan provinces) also extend beyond the boundaries of the East Pacific. For the sake of clarity, the entire East Pacific will be considered herein as a zoogeographic region divided into three subregions (the northern temperate subregion; the eastern tropical Pacific subregion; and the southern temperate subregion), each of these subregions being divided in a number of zoogeographic provinces (Fig. 1). An analysis of the biodiversity and distribution of the isopods inhabiting the Mexican Pacific was presented by ESPINOSA-PÉREZ & HENDRICKX (2002) who partly based their analysis on a species checklist they established earlier (see ESPINOSA-PÉREZ & HENDRICKX, 2001a) for the entire eastern tropical Pacific (ETP).

An analysis of the distribution and zoogeographic affinities of the isopods occurring in the northern and southern temperate subregions of the east Pacific is not available, and the zoogeographic affinities of the isopod fauna in the ETP have not been addressed. Some considerations have been presented for restricted geographic areas (see MENZIES, 1962a; AUSTIN, 1985; BRUSCA & IVerson, 1985; MARKHAM, 1992; BRANDT, et al., 1999; THIEL, 2002; THIEL et al., 2003) or for some groups of
isopods (i.e., at generic, family or higher taxonomic level) (see Brusca & Wallerstein, 1979b; Brusca, 1981; Delaney, 1984; Brusca et al., 1995).

Checklists of species are important for the study of ecosystems in general and provide comparative data for biodiversity studies. Although some urgently need updating, lists of estuarine and marine isopods that concern one or several zoogeographic provinces are available for the NE Pacific (Austin, 1985), the Antarctic (Brandt, 1991), the West Atlantic (Kensley & Schotte, 1989), Europe (Costello et al., 2005), and Australia (Poore, 2005). Several smaller geographic areas also have checklists, e.g., Italian waters (Stoch, 2003), California (Brusca et al., 2006), and Costa Rica (Brusca & Iverson, 1985).

The objective of this paper is to present a distributional checklist of all species of marine and estuarine isopods known from the southern and northern temperate and cold water of the East Pacific and to compare biodiversity within the currently recognized zoogeographic provinces, including the provinces of the eastern tropical Pacific.

**MATERIAL AND METHODS**

The area covered during this study corresponds to the shallow-water (< 200 m) of the warm temperate (Californian), cold temperate (Oregonian and Aleutian), and polar (Arctic) provinces located in the northern hemisphere (the northern subregion), and the warm temperate (Peru-Chile), transitional (Temperate-Transitional), and cold temperate (Magellan) provinces in the southern hemisphere (the southern subregion), of the east coast of America; both subregions are part of the East Pacific region that extends from the Bering Sea to the Magellan Strait (see Fig. 1). In addition to this, the East Pacific possesses several oceanic Islands (as opposed to the close-to-continent islands) characterized by a certain degree of endemism; each island or group of islands has been considered as isolated zoogeographic entities (see Briggs, 1974; Brusca & Wallerstein, 1979b; Hendrickx, 1992). Although the Arctic and Magellan provinces extend beyond the geographic limits of the east Pacific, only records from the East Pacific were considered; thus, Punta Barrow, Bering Sea, and the southern tip of Chile were considered as our boundaries. The lists of isopods for these southern and northern subregions of the eastern Pacific.
Biodiversity and distribution of marine isopods in the East Pacific were established on the basis of published literature, list of species available in websites and some unpublished data from the authors’ files. It should be remember at all times, however, that the information compiled corresponds to our present knowledge of isopods and their distribution in the region. These lists are presented in two appendices and include the name of each species and its currently recognized geographic distribution within the East Pacific. Additionally, the presence of some species in other geographic regions is indicated using the following abbreviations: ATL, Atlantic Ocean; W-ATL, West Atlantic; E-ATL, East Atlantic; I-PAC, Indo-Pacific; I-WPAC, Indo-West Pacific; MED, Mediterranean Sea; ART, Arctic Ocean; ANT, Antarctic Ocean; HAW, Hawaii; COS, Cosmopolitan. The composition of the isopod fauna of the eastern tropical Pacific (ETP) (including the Cortés, Mexican and Panamic provinces, as defined by Hendrickx, 1992) extending between the northern and the southern temperate subregions was used as a comparative element in this analysis. The ETP data were taken from Espinosa-Pérez & Hendrickx (2001a, 2002) and updated on the basis of recently published information or distribution data that was not previously available. All bibliographic references used during this process are cited in the appendices. In addition, two major websites were used; one established by Kensley & Schotte (2006) and the other recently made available by Brusca et al. (2006).

The recent classification proposed by Martin & Davis (2001) for Isopoda was used in a former draft of this paper. It includes nine suborders, of which seven (Anthuridea Monod, 1922; Microcerberidea Lang, 1961; Flabellifera Sars, 1882; Asellota Latreille, 1802; Valvifera Sars, 1882; Epicaridea Latreille, 1831; and Oniscidea Latreille, 1802) had representatives in the East Pacific. Virtually all recent literature available for east Pacific isopods is based on a classification similar to the one proposed by Martin & Davis (2001). The Flabellifera, however, have long been considered a paraphyletic group and reviewed recently by Brandt & Poore (2003). On the basis of a thorough cladistic analysis, these authors proposed a reviewed classification of the flabelliferan and related Isopoda which was adopted here (see appendices).

Using the information contained in the two checklists presented herein, and the updated data for the ETP checklist, an analysis of the currently known biodiversity for each currently recognized polar or temperate marine biogeographic province in the East Pacific is proposed, together with a comparative analysis of species, genera and family in each subregion of the East Pacific. The analysis was made possible using a data base containing distributional data of all species known to occur in the East Pacific with at least one record in water no deeper than 200 m (defined herein as shallow water). A cluster analysis was used to classify currently recognized 10 marine biogeographic provinces according to the presence or absence of species. The phenogram was constructed with the Multivariate Statistical Package (version 3.13c) (copyright) 1985-2002 Kovach Computing Services, using clustering with the Unweighted Pair Group Method with Arithmetic Mean (UPGMA).

RESULTS

Biodiversity of isopods in the East Pacific

The updating of the list of species known to occur in the ETP (Table 1) and the two checklists of species recorded in the northern and southern subregions of the East Pacific (Appendices 1, 2) indicate that there are 420 species of isopods inhabiting estuarine and marine ecosystems, in depths <200 m. The Cymothoida are by far the dominating suborder (153 species; 36.4% of total), followed by the Asellota (92; 21.9%), the Valvifera (73; 17.4%), the Sphaeromatidea (68; 16.2%), the Oniscidea (26; 6.2%), the Limnoridea (6; 1.4%) and the Microcerberidea (only 2 species, or 0.5%) (Fig. 2).
Diversity by subregion

The number of species currently recorded for the northern polar and temperate zoogeographic provinces, or northern subregion of the East Pacific, is 213 (Appendix 1) vs. only 133 species for the southern temperate provinces (Appendix 2). Comparatively, 134 species are now registered for the ETP. This figure includes the 119 shallow water species reported by Espinosa-Pérez & Hendrickx (2001a) and an additional 15 species overlooked by these authors, described or registered since for the area, including two Anthuridae, four Cymothoidae, one Gnathiidae (the first recorded for the ETP), one Idoteidae, one Sphaeromatidae, four Bopyridae, one Porcellionidae and one Scyphasidae (see Table 1). When lists are compared, the northern and southern polar-temperate fauna include a total of 340 species, with only seven species in common: Eurylana arcuata (Hale, 1925), an introduced species; Excarrallana brasiliensis (Richardson, 1912); Natatolana californiensis (Schultz, 1966), Ceratothoa gaudichaudii (H. Milne-Edwards, 1840); Ianiropsis tridentis (Menzies, 1952); Munnogonium trillerae (Menzies & Barnard, 1959) and Idotea metallica (Bosch, 1802). Of a total of 43 families recorded in the East Pacific (for the purpose of this paper, incertae sedis species are accounted for as a distinct family), 41 occur in the northern subregion and only 22 in the southern subregion, of which 18 are common to both. Comparatively, the ETP contains 25 families (Table 2). Although the northern and southern subregions experience similar climatic conditions, they share only 34 (21.3%) out of 160 genera (Table 3). Comparatively, the ETP shares 12 families with the southern region (28%), while the ETP contains 25 families (Table 2). The Limnoriidea is better represented in the northern subregion, vs. 29 and 18 species in the other two. The Microcerberidea is the most diverse group in all three subregions and represents a major portion of the isopods fauna in the southern region (28.1%), in the northern subregion (31.5%), and in the ETP (60.7%) where it dominates. All seven suborders of isopods known to the East Pacific are present in the northern and the ETP subregions, while the Microcerberidea (only two species are known into the East Pacific) and Oniscidea are missing altogether in the southern subregion. The analysis of number of species by suborders indicates that the Cymothoida is the most diverse group in all three subregions and represents a major portion of the isopods fauna in the southern region (28.1%), in the northern subregion (31.5%), and in the ETP (60.7%) where it dominates. Assellota and Valvifera are both very diverse in the northern subregion (42 and 47 species, respectively) and Assellota is second in diversity in the southern subregion. Sphaeromatidea is represented by twenty-four species in the southern subregion, vs. 29 and 18 species in the other two. The Limnoriidea is better represented in the northern and ETP subregions (4 and 2 species, respectively) than in the south (1 species). From a general viewpoint, Cymothoida dominates in the ETP (82 spp.), and Cymothoida (37 spp) and Assellota (49 spp) in the southern region (28.1%), while the northern subregion is also dominated by Cymothoida (67 spp.), followed by Assellota (42 spp) and Valvifera (47 spp.), and posses a comparatively higher diversity for Oniscidea (23 species vs. 0 and 9) and Valvifera (47 species vs. 22 and 18) (Table 2).

TABLE 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Halothamnus curri</td>
<td>Paul &amp; Menzies, 1971</td>
<td>Kensley, 1980</td>
</tr>
<tr>
<td>Skaphomura ecuadoriensis</td>
<td>Kenseley, 1980</td>
<td>Kensley, 1980</td>
</tr>
<tr>
<td>Bopyrissa magellaniana</td>
<td>Nierstrasz &amp; Brender à Brandis, 1931</td>
<td>Nierstrasz &amp; Brender à Brandis, 1931</td>
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<tr>
<td>Orbimorphus constrictus</td>
<td>Richardson, 1910</td>
<td>Richardson, 1910</td>
</tr>
<tr>
<td>Pleurocryptella woffii</td>
<td>Bourdon, 1972</td>
<td>Kenseley &amp; Schotte, 2001</td>
</tr>
<tr>
<td>Segias angusta</td>
<td>Nierstrasz &amp; Brender à Brandis, 1931</td>
<td>Kenseley &amp; Schotte, 2001</td>
</tr>
<tr>
<td>Elthusa californica</td>
<td>Schiödte &amp; Meinert, 1884</td>
<td>Kenseley &amp; Schotte, 2001</td>
</tr>
<tr>
<td>Mithoeca rosea</td>
<td>Bruce, 1986</td>
<td>Bruce, 1986</td>
</tr>
<tr>
<td>Mithoeca arrosor</td>
<td>Bruce, 1986</td>
<td>Bruce, 1986</td>
</tr>
<tr>
<td>Paradella tiffany</td>
<td>Bruce &amp; Wetzer, 2004</td>
<td>Brusca et al., 2001</td>
</tr>
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<td>Gnathia margaritana</td>
<td>Monod, 1926</td>
<td>Kenseley &amp; Schotte, 2001</td>
</tr>
<tr>
<td>Idotea metallica</td>
<td>Bosch, 1802</td>
<td>Bruce, 1986</td>
</tr>
<tr>
<td>Porcellionides floriana</td>
<td>Bruce, 1986</td>
<td>Bruce, 1986</td>
</tr>
<tr>
<td>Alloniscus mirabilis</td>
<td>Garthwaite &amp; Sassaman, 1985</td>
<td>Brusca et al., 2001</td>
</tr>
<tr>
<td>(1) Exosphaeroma bruscai</td>
<td>Espinosa-Pérez &amp; Hendrickx, 2001</td>
<td>Espinosa-Pérez &amp; Hendrickx, 2001b</td>
</tr>
<tr>
<td>(2) Paracerceis spinulosus</td>
<td>Espinosa-Pérez &amp; Hendrickx, 2002</td>
<td>Espinosa-Pérez &amp; Hendrickx, 2002a</td>
</tr>
</tbody>
</table>
TABLE 2
Number of isopods (by family) in the three subregions of the East Pacific (N, Northern subregion; S, southern subregion; ETP, eastern tropical Pacific).

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>N</th>
<th>S</th>
<th>ETP</th>
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</thead>
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<tr>
<td><strong>CYMOTHOIDA</strong></td>
<td></td>
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<td>7</td>
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</tr>
<tr>
<td>Cirolanidae</td>
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<td>11</td>
<td>18</td>
</tr>
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</tr>
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<td>4</td>
<td>16</td>
</tr>
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<td>2</td>
<td>1</td>
</tr>
<tr>
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<td>2</td>
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<td>0</td>
</tr>
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<td>Bopyridae</td>
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</tr>
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<tr>
<td>Criptoniscoidea</td>
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<tr>
<td><strong>TOTAL</strong></td>
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<td>83</td>
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<tr>
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<td>Microcerberidae</td>
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<td>Serolidae</td>
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<tr>
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<tr>
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<td>16</td>
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<tr>
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</tr>
<tr>
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<td>0</td>
</tr>
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<td>Janiridae</td>
<td>20</td>
<td>16</td>
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Species diversity by province

The northern subregion

According to present records, the American continent section of the Arctic Province (East Pacific only) is by far the less diverse, with only 15 species recorded to date, followed by the Aleutian Province (61 species), the Californian Province (128 species) and the Oregonian Province (140 species) (Fig. 3). Anthuoidea (i.e., the superfamily) and Microcerberidea are absent from the two northernmost Provinces, and Microcerberidea is also absent from the Californian Province; another species of Microcerberidea has been recorded in the ETP, and there is no record for this suborder in the southern subregion. Cymothoidea and Valvifera represent 60% of the known isopods fauna in the Arctic Province, 63% in the Aleutian Province, 46% in the Oregonian Province (where Asellota accounts for 21% of the total of the species vs. 13%, 15%, and 10% from north to south in the other Provinces), and 59% in the Californian Province. Bopyroidea and Cryptoniscoidea (i.e., the two superfamilies) and Oniscidea are rare in the Arctic and their diversity increases towards the warmer water, with a maximum in the Oregonian Province (Fig. 3).

### TABLE 3

Number of genera of isopods registered in each subregion of the East Pacific and common to each pair of subregions and to the three subregions (N, northern subregion; S, southern subregion; ETP, eastern tropical Pacific).

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<th>N-S</th>
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The southern subregion

Off all three Provinces (Juan Fernandez being considered separately; see infra) included in the southern subregion of the East Pacific, the Peru–Chile Province appears to be the less diverse with 43 species known to date; the Temperate-Transitional and Magellan (East Pacific only) Provinces feature similar number of species (61 and 75, respectively). Four suborders are not represented in the Magellan Province, which is clearly dominated by Asellota (48% of the species) and Sphaeromatidea (21%). The third suborder in this Province, the Valvifera (20%), is actually poorly represented in the entire southern subregion (a total of 22 species) comparatively with the northern subregion (47 species) (Fig. 4). The Cymothoida again dominate the other two Provinces (Temperate-Transitional, 41%; Peru–Chile, 32%); the Asellota are numerous (34%) in the Temperate-Transitional Province, but not in the Peru-Chile Province (only 18%). Sphaeromatidea correspond to 30% of the species occurring in the Temperate-Transitional Province, and 23% in the Peru-Chile Province. Only one species of Anthuroidea, Paranthura porteri (Boone, 1920), is known from the southern subregion but do not seems to extend into the Magellan Province (Fig. 4; Appendix 2). No species of the superfamilies Bopyroidea and Cryptoniscoidea has been recorded from the East Pacific section of the Magellan Province, and only eight species are known from the other two Provinces, five of these occur in the Temperate–Transitional Province and three in the Peru-Chile Province (Fig. 4). The Oniscidea are absent altogether from the southern subregion.

The ETP subregion

The analysis of the distribution of the isopods throughout the different Mexican Provinces of the ETP was presented by Espinosa-Pérez & Hendrickx (2002) on the basis of records for 120 species. The addition of 15 species to the ETP isopods fauna does not modify substantially their conclusions, which were drawn at suborder level only, although it increases the number of known Mexican species from 120 to 128 (see Table 1 and Fig. 4). The updating checklist of isopods of the ETP resulting from the addition of these 15 species allows reporting a total of 134 known species (Table 2). All seven suborders considered herein are represented in the ETP. The Cymothoida is by far the dominant group (61% of the species); Valvifera (18 species) are as diverse as in the southern subregion (22 species) but far less so than in the northern subregion (47 species) (Table 2). With 18 species, Sphaeromatidea represents 13.3% of the species for the entire ETP and are less diverse than in the south (24 species) or in the north (29 species). Anthuroidea are more diverse in the ETP than in the two others subregions (12 vs. 8 and 1 species) (Table 2). The updated distribution of the ETP species by suborder in the three eastern tropical Provinces is presented here (Fig. 4) in order to complete the information available.
Oceanic islands

Of the 420 species of isopods recorded for the East Pacific, 40 have been cited for at least one oceanic island in the region. Most belong to the Cymothoidea (25 spp), and the rest belong to the Sphaeromatidea (1 sp), Valvifera (4 spp), Oniscidea (2 spp) or Asellota (1 sp). To our present knowledge, however, number of species known to occur in each oceanic island (or group of islands) is highly variable, from 16 in the Galapagos to only one in the Revillagigedo (Table 4) and ten in the Juan Fernandez Archipelago (Table 5). None of the Juan Fernandez species is reported in any other offshore islands of the East Pacific, thus reinforcing the idea that this group of islands is strongly isolated from the other oceanic islands in the region, a fact partly demonstrated by its endemic component (3 of 9 species, or 33%: Paranthura skottsbergii (Nordenstam, 1930), P. gracilipes (Nordenstam, 1930) and P. nana (Nordenstam, 1930)). Of the 31 species recorded in Table 4, none is found in the seven islands or group of islands; only one species (Eurydice caudata (Richardson, 1899)) is found in four islands and another (Rocinela signata (Schioedte & Meinert, 1879)) in three; six are found in two islands and the rest in one. The vast majority of these species (31) are found in one or two subregions of continental America (29) or in another zoogeographic region (Rocinela hawaiiensis (Richardson, 1904)) (see Appendices 1, 2 and ESPINOSA-PÉREZ & HENDRICKX, 2001a). The only endemic species recognized to date, Metacirolana calypso (Brusca, Wetzler & France, 1995), is only known from the Galapagos.

Zoogeographic affinities

Cluster analysis using the 10 previously recognized provinces (see Fig. 5), reveals a clear and somewhat similar pattern of similarity when both species and genera were used. The northern, ETP and southern provinces form well separated clusters, although the Arctic Province (I) remains more isolated in both cases, more strongly so when genera are used. The three southern provinces form a well defined second cluster (II) at a point corresponding...
to roughly 30% of similarity when species are used and 55% when genera are used. When only species are considered, this cluster is also strongly independent from the others (i.e., I, III, IV), thus reflecting the reduced number of species shared between the southern region and the rest of the East Pacific region. Cluster III corresponds to the northern provinces and shows a very similar pattern, well defined for both species (ca 40% similarity) and genera (ca 54% of similarity). In both species and genera clusters, the tropical provinces provided the better defined cluster (cluster IV) (pairs of provinces form clusters at ca 46 and ca 64% of similarity, respectively). When genera are used, the cluster analysis shows a better affinity between the ETP and the northern subregion fauna (clusters III and IV), but when species are used there is a weaker link and it also includes the Arctic Province (cluster I). Magellan fauna is also less similar than the Peru-Chile/Temperate-Transitional fauna (both when species and genera are compared); Aleutian fauna shows a similar pattern when compared to Californian/Oregonian fauna. One should be aware, however, that a strict comparison with the Arctic and Magellan isopods fauna should include all records for this group in these two provinces, not only the East Pacific, but this is beyond the scope of this study. We are not aware of any report on total number of Arctic isopods; there are 157 described species for the entire Magellan province (both East Pacific and West Atlantic) (BRANDT, 1991), thus indicating that the Chilean section of this province is probably somewhat under-documented (75 species in our records, including species with a distribution range including the Magellan province but with no sampling record there).

In the ETP the similarity among provinces is higher than in any other cluster, although the Cortés Province is slightly isolated from the two other, probably due to its subtropical character. Also noteworthy is the fact that in all three subregions (excluding the Arctic Province), three pairs of provinces (Temperate-Transitional, Panamanian-Mexican, and Californian-Oregonian) have the highest similarity both when species (ca 53-57%) and genera (ca 66-68%) are used.
DISCUSSION

A significant proportion (87 species, or 20.6%) of the 420 species recorded for the East Pacific is found in one or several other marine zoogeographic regions of the world; thus proportion of species endemic to the East Pacific is just below 80%. Of the 213 species of isopods recorded for the northern subregion, 40 (18.7%) are found in at least one other zoogeographic region; the rest (173 species; 81.3%) are endemic to the East Pacific. The majority of these 40 species occur in the Pacific Ocean (West Pacific, 1; Hawaii, 4) or in the Indo-Pacific (15). As many as 15 species are recorded in the Atlantic Ocean (West Atlantic, 6; North Atlantic, 1; throughout the Atlantic, 9). Finally, 5 species have been found in the Mediterranean Sea, 9 in the Arctic and 3 are considered cosmopolitan. The extended list of species available for the ETP (134 known species) indicates that 109 species (81.3%) are endemic to the East Pacific; the rest, 25 species (18.7%) have one or more records in another zoogeographic region. Of these, 10 are found throughout the Atlantic and 8 in the West Atlantic; the Indo-West-Pacific component is also important (Indo Pacific, 7; West Pacific, 2; throughout the Pacific, 2; Hawaii, 3) and two species have been recorded in the Mediterranean. Of the 133 species of isopods recorded for the southern subregion, 40 (29.6%) are found in at least one other zoogeographic region; the rest (90 species; 70.4%) are endemic to the East Pacific, of which as many as 87 are endemic to the southern subregion. Of these 40 species, the majority is found in the Atlantic (West Atlantic, 23; South
Atlantic, 2; throughout the Atlantic, 2) and in the Antarctic (8), and mostly correspond to species belonging to the Magellanic Province. Eight species occur in the Indo-Pacific, and the remaining species (2) are either cosmopolitan or Indo-West Pacific. These observations coincide with conclusions of Menzies (1962a), who established a clear affinity of the Chilean isopods fauna with the southern circumpolar fauna.

According to Briggs (1974), the Juan Fernandez Archipelago should be considered as a subprovince of the Peru–Chile Province, a suggestion that coincides with our present knowledge of level of endemism registered for isopods (33%) and with the fact that non-endemic species belong to the Peru–Chile Province. Although we can speculate on the lack of sampling effort in several other oceanic islands of the East Pacific, the presence of a single endemic (in the Galapagos) is rather surprising. The presence of two species of Ligia (both found in the ETP; one found in the Indo-Pacific and Hawaii) on Clipperton is probably due to accidental introduction. Considering all (non Juan Fernandez) oceanic islands of the region, and exception for the endemic Metacricotoma calypso, only one species (Anilocra meridionalis; Galapagos) is not found on continental East Pacific and originates from the Pacific.

To our knowledge and previous to this study, there was only one list of marine isopods available for any major zoogeographic region: the Antarctic region (Brandt, 1991), where 226 shallow-water (shelf) species are reported of a total of 346 species. The isopods of the other major regions (e.g., the tropical east Atlantic, west Atlantic, east Pacific, and Indo-Pacific; and the Arctic) have been compiled only for some sections (see Table 6). The one presented for the Caribbean area (West Atlantic) by Kensley & Schotte (1989) covers the entire Caribbean Sea, the Bahamas, the southern tip of Florida and the southern coastline of the Gulf of Mexico; as such, the area is typically tropical-subtropical. It included 298 species but is over 15 years old and needs some updating. Austin (1985) listed 155 species of isopods for the NE Pacific, roughly from Kodiak Island, Alaska, to Point Conception, California, USA, including the Oregonian Pacific and the southern part of the Aleutian Province (both cold temperate), while Brusca et al. (2006) listed 191 species for California, USA. In both cases there is a clear dominance of Cymothoida and Asellota. Information presented by Austin (1985) and Brusca et al. (2006) was considered in the present study, verified and eventually included in the corresponding checklist (see Appendix 1) and in Table 6. The European list roughly corresponds to cold and warm temperate provinces in the northeastern Atlantic and included 614 species (Costello et al., 2005). Another list is available for Italian waters and includes 203 species (Stoich, 2003), presumably covered by the European list. In their review of Costa Rican isopods, Brusca & Iverson (1985) included 33 species, all included in the checklist presented by Espinosa-Pérez & Hendrickx (2001a). According to Thiel et al. (2003), there are 133 species of marine isopods in Chile (including deep water species); these authors refer to a web site where the list of species can be consulted, but the site in question is not reachable and we cannot compare our data with theirs. All species of our southern subregion list (see Appendix 2; 135 species, excluding species found exclusively below 200 m) occur in Chilean water and we were able to consult all the sources used by Thiel et al. (2003). With 879 species, the Australian list provided by Poore (2005) corresponds to several cold–temperate, warm–temperate and tropical provinces of the western Pacific (see Briggs, 1974 for details) and, as such, is the most complete list available to-date for comparison purposes with the East Pacific, although it includes several records for deep-water species and our list does not. The Australian list is the only one using the classification proposed by Brandt & Poore (2003) for higher categories.

Because all checklists compiled for the geographic areas considered above, except the one for Australia, were built using a classification similar to the one proposed by Martin & Davis (2001), comparison of number of species by suborders is presented using both the classification proposed by Martin & Davis (2001) and by Brandt & Poore (2003) (Table 6). Numbers of species on record for the Microcerberoidae, Asellota, Valvifera and Oniscidea remain constant between the two classifications. In the new classification, however, Cymothoida is granted the category of suborder, and includes the superfamilies Cirolanoidea (Dana, 1852), Cymothoidae (Leach, 1814), Bopyridae (Rafinesque, 1815), Cryptoniscoidea (Kosmann, 1880), and Anthurioidea (Leach, 1914), thus making it the dominant suborder for all areas considered in our comparative analysis instead of Flabellicea (see Table 6).

### TABLE 6

Number of species of marine and brackish water isopods recorded for some selected geographic areas. Numbers are presented using both classifications proposed by Martin & Davis (2001) and Brandt & Poore (2003). Other sources as indicated.

<table>
<thead>
<tr>
<th>REGION</th>
<th>TOTAL</th>
<th>ANT</th>
<th>MIC</th>
<th>FLA</th>
<th>ASE</th>
<th>VAL</th>
<th>EPI</th>
<th>ONI</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Costa Rica</td>
<td>33</td>
<td>6</td>
<td>1</td>
<td>29+1</td>
<td>30</td>
<td>28</td>
<td>19</td>
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<tr>
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<td>11</td>
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<td>2</td>
<td>126+10</td>
<td>31</td>
<td>11</td>
<td>53</td>
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<td>34</td>
<td>16</td>
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<td>1</td>
<td>461+45</td>
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<tr>
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<td>169+26</td>
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<td>58</td>
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<td>Costello et al., 2005</td>
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<tr>
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<td>420</td>
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<td>157+10</td>
<td>92</td>
<td>73</td>
<td>43</td>
<td>26</td>
<td>This study</td>
</tr>
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</table>
Cymothoida is the dominant suborder of isopods in the East Pacific (36.4% of the 420 spp). This is not surprising as Cymothoida is one of the most diverse group of marine isopods worldwide (WETZER & BRUSCA, 1997), is commonly found in great numbers and generally features large size compared to other groups of minute isopods (SCHULTZ, 1969; BRUSCA & IVERSON, 1985). Cymothoida is by far the dominating group in Australian waters (458 spp, ca. 52.1%) and in the Caribbean with 200 species (67% of total) but not in cooler, European waters where it represents only 38.9%. The latter figure is closer to the proportion of Cymothoida occurring in the cold-temperate Oregonian Province (27.90%), warm-temperate Californian Province (39.1%), and Temperate-Transitional Province (32.2%). In the East Pacific, proportion of continental Cymothoida increases from the north (approx. 39, 58, 70 and 73% for the Californian, Cortés, Mexican and Panamic Provinces, respectively), and from the south (approx. 33 and 41% for the Temperate–Transitional and the Peru–Chile Provinces, respectively) towards the tropics. Asellota have been extremely successful in a wide variety of habitats (WILSON, 1980) but their fragility and small size required specific collecting strategies (WETZER & BRUSCA, 1997). With 1800 known species worldwide, Asellota is the second most abundant suborder of isopods for the East Pacific (22.8% of all species) and shows a different distributional trend, with proportion of 0 to ca. 5% in the three ETP provinces and a tendency to increase towards the highest latitude, particularly in the southern hemisphere (approx. 16, 34 and 49% for the Peru-Chile, the Temperate–Transitional and the Magellan Provinces, respectively). Asellota are also the dominant component of European isopods fauna (45.8%) but represent a small fraction of the Caribbean fauna (31 species, or 10.4%) and Australian fauna (74 spp, or 8.4%). With 17.5% of the total of species, the Valvifera (ca 570 species known worldwide) (KENSLEY & SCHOTTE, 2006) is the third sub-order best represented in the East Pacific, particularly in cold provinces. Preference of this suborder for cooler water was previously emphasized by BRUSCA & WALLERNSTEIN (1979b); in the East Pacific, the group is clearly more abundant in the northern (47 species) than in the southern (22) subregion, while it is represented by 18 species in the ETP. Comparatively, Valvifera account for 8.6% (58 species) of European isopods fauna, 8.4% (74 species) of Australian fauna, and a surprisingly low 3.9% (11 species) in the fully tropical Caribbean area (Table 6). The ETP (mostly tropical) hosts 18 species of Valvifera, or 13.4% of the total number of isopods species known to date for this subregion.

The Bopyroidea and Cryptoniscoidea, a group of obligate parasites, is represented in the East Pacific by 43 species (10.2%) and is better represented in the ETP; comparatively, these two superfamilies represent 17.8% of the isopod fauna in the Caribbean, 8.3% in Europe and only 4.4% in Australia. The Oniscidea, a suborder containing ca 5000 species of mostly terrestrial isopods (BRUSCA & BRUSCA, 2002), is represented in the East Pacific by 26 species (6.2%), with no species recorded for the southern subregion and almost all of them (23 out of 26) occurring in the northern subregion, despite the fact that environmental conditions (i.e., water temperature, substrate, currents) are very similar in both areas. There is only one species on record for Europe, 11 in the Caribbean (3.7%), and 37 in Australia (4.2%). With only 17 recorded species, Anthuroidea account for only 4.7% of the East Pacific isopods fauna. Comparatively, Anthuroidea represent 18.1% of the Caribbean fauna, 17.0% of the Australian fauna, and 7.3% of the European fauna, thus reflecting their stronger affinity for tropical and subtropical water. Nevertheless, there is a strong contrast between the two cold-temperate areas studied herein; there is only one record for Anthuroidea in the southern subregion of the East Pacific but seven in the northern subregion. Finally, the small suborder of Microcerberidea (45 known species) (KENSLEY & SCHOTTE, 2006) is represented by two species in the East Pacific, vs. none in Australia, two in the Caribbean and five in Europe.

Strong differences are noted when number of genera and species known for the three East Pacific subregions are compared. The highest genera and species diversity occurs in the northern subregion (213 spp vs. 134 in the ETP and 130 in the south; 103 genera vs. 76 in ETP and 65 in the south). This N to S gradient has also been observed for decapod crustaceans (WICKSTEN, 1989), amphipods (BOUSFIELD & HENDRICKS, 1995), some groups of brown algae (ESTES & STEINBERG, 1988) and some families of fishes (HERALD, 1961). The similarity of the northern and southern temperate faunae with the adjacent ETP also varies; as many as 50 genera are shared between the ETP and the northern subregion, but only 21 between the southern subregion and the ETP.

In all the oceanic islands of the East Pacific, including the Galapagos, efforts have mostly been orientated towards the study of terrestrial flora and fauna, and of large, more accessible marine species. Only a few species of isopods have so far been reported from these islands and this evidently reflects a lack of sampling effort, even though availability of habitats might somewhat be restricted in some of these islands. Excluding the peculiar case of Juan Fernandez, only one endemic isopod has been recognized for these islands (Metacirolana calypso, off the Galapagos). In the decapod crustacean, the next best known major group of Crustacea in the East Pacific, the insular component includes over 40 species endemic to one or several East Pacific islands (excluding Juan

<table>
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<th>REGION</th>
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<th>MIC</th>
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<th>SPH</th>
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<td>32</td>
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<td>879</td>
<td>458</td>
<td>-</td>
<td>28</td>
<td>74</td>
<td>74</td>
<td>208</td>
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<td>672</td>
<td>261</td>
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<td>4</td>
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<tr>
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<td>92</td>
<td>73</td>
<td>68</td>
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ACKNOWLEDGEMENTS

One of us (MCEP) was supported by a PhD grant from CONACyT, Mexico (159145). Part of this study was supported by CONABIO, Mexico (Project S 063). We thanks many colleagues who provided information and literature dealing with East Pacific isopods, particularly Margarita Hermoso, Regina Wetzer, Ramiro Roman, Marilyn Schottle, Niel Bruce, Daniel Roccatagliata, Gary Poore, Buz Wilson, Clara Ramirez, and Angelika Brandt. Germán Ramirez Reséndiz provided assistance with computer programmes and Mercedes Cordero with data edition.

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<table>
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<th>Author(s)</th>
<th>Title and Details</th>
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</table>

**APPENDIX 1.**

**List of species of isopods reported for the Californian, Oregonian, Aleutian, and Arctic zoogeographic provinces (213 species).**

Species reported only in oceanic islands not included. Sequence of orders and families is according to Brandt & Poore (2003)

**CYMOTHOIDA Wägele, 1989**

**Aegidae White, 1850**

1. **Aega lecontii** Dana, 1854
   - Monterey Bay, California, USA (RICHARDSON, 1905; KENSLEY & SCHOTTE, 2006).
2. **Aega microphthalma** Dana, 1854
   - Monterey Bay, California, USA (BRUSCA et al., 2006).
3. **Aega symmetrica** Richardson, 1905
   - Southern Alaska to California, USA (RICHARDSON 1905a; HATCH, 1947; BRUSCA et al., 2006). ART.
4. **Rocinela angustata** Richardson, 1904
   - From Bering Sea south to central western Baja California, Mexico (HATCH, 1947; BRUSCA & FRANCE, 1992; BRUSCA et al., 2006).
5. **Rocinela belliceps** Stimpson, 1864
   - Aleutian Islands, Alaska, to Channel Islands, California, USA. Gulf of California, Angel de la Guarda Island (29°19.9′N, 113°10.4′W) and Mazatlán, Sinaloa, Mexico. Clarion Island (BRUSCA & FRANCE, 1992; ESPINOSA-PEREZ & HENDRICKX, 2001a).
6. **Rocinela laticauda** Hansen, 1897
   - Piedras Blancas, California, USA, and from Guaymas, Sonora, to Acapulco, Guerrero, Mexico (RICHARDSON, 1905; BRUSCA & FRANCE, 1992; CALDERÓN & CAMPION, 1993).
7. **Rocinela propodialis** Richardson, 1905
   - From British Columbia, Canada to Washington, USA (RICHARDSON, 1905; HATCH, 1947).
8. **Rocinela signata** Schödte & Meinert, 1879
   - From Newport Bay, California, USA, to Gulf of Guayaquil, Ecuador, including the whole Gulf of California, Mexico. Galapagos Islands (BOWMAN, 1977; BRUSCA & FRANCE, 1992). W-ATL.
9. **Rocinela tridens** Hatch, 1947
   Known only from Canoe Island, Washington, USA (Hatch, 1947).

**Corallanidae Hansen, 1890**

10. **Excorallana tricornis occidentalis** Richardson, 1905
    From Santa Catalina Island, California, USA, south to Panama, including the whole Gulf of California, Mexico (Delaney, 1984; 1989; 1993; Guzman et al., 1988; Brusca, pers. comm., April 2000).

**Cymothoidea Leach, 1814**

11. **Anilocra occidentalis** Richardson, 1899
    Known only from Monterey Bay, California, USA (Richardson, 1899).

12. **Ceratobothia gaudichaudii** (H. Milne-Edwards, 1840)
    From southern California, USA, south to Cape Horn, Chile, including the whole Gulf of California, Mexico. Galapagos Islands (Brusca, 1981; Molina & Manrique, 1996; Espinosa-Pérez & Hendrickx, 2001a). I-PAC.

13. **Ceratobothia gilberti** (Richardson, 1904)
    From southern California, USA, to Punta Banda, west coast of Baja California; Tortugas Bay, Southern Baja California, and Mazatlan, Sinaloa, Gulf of California, Mexico (Brusca, 1981).

14. **Elthusa californica** (Schiodte & Meinert, 1884)
    From Boundary Bay, British Columbia, Canada to Peru (Hatch, 1947; Brusca, 1981; Brusca et al., 2006).

15. **Elthusa menziesii** (Brusca, 1981)
    Todos Santos and San Quintin Bays, west coast of Baja California, and Gulf of California, Mexico. Alijos Rocks. Guadalupe Island (Campos et al., 1986; Wetzler et al., 1991; Espinosa-Pérez & Hendrickx, 2001a).

16. **Elthusa vulgaris** (Stimpson, 1857)
    From Washington, USA, south to off Puerto Madero, Chiaapas, including the whole Gulf of California, Mexico. Near Malpelo Island (Brusca, 1981; Austin, 1985; Espinosa-Pérez & Hendrickx, 2001a).

17. **Enispa convexa** (Richardson, 1905)
    Channel Islands, California, USA, to Gulf of Guayaquil, Ecuador. A single record at Playa Novilleros, southern Gulf of California, Mexico (Brusca, 1977; 1981; Brusca & Iverson, 1985; Wetzler et al., 1991).

18. **Mothocya gilli** Bruce, 1986
    From Asuncion Bay to Almeja Bay, west coast of Baja California, and from Guaymas, Sonora, Gulf of California, to Manzanillo, Colima, Mexico (Bruce, 1986; Wetzler et al., 1991).

19. **Mothocya rosea** Bruce, 1986
    San Diego, California, USA to Nicaragua (Bruce, 1986).

20. **Nerocila acuminata** Schiodte & Meinert, 1881
    From Long Beach, California, USA, south to Peru, including the whole Gulf of California, Mexico. Galapagos Islands (Brusca, 1981). HAW. W-ATL.

21. **Renocila thresherorum** Williams & Williams, 1981
    From Newport, California, USA to southern Gulf of California, Mexico (Williams & Williams, 1981; Brusca, 1981).

**Gnathiidae Leach, 1814**

22. **Caecognathia crenulatifrons** (Monod, 1926)
    From Point Santa Cruz, Monterey Bay, California, USA to Point Banderas, Baja California, Mexico. Off Santa Cruz Island, Santa Cruz Canyon, California, USA (Iverson, 1974; Brusca et al., 2006).

23. **Caecognathia sanctaeccruis** (Schultz, 1972)
    Santa Maria Basin, Santa Cruz Canyon, Southern California, USA (Brusca et al., 2006).

24. **Gnathia hantinensis** Schultz, 1966
    Known only from San Clemente Canyon, California, USA (Schultz, 1966; Brusca et al., 2006).

25. **Gnathia productatridens** Menzies & Barnard, 1959
    Point Conception to Santa Barbara County, California, USA (Wetzler et al., 1991; Brusca et al., 2006).

26. **Gnathia steveni** Menzies, 1962
    From southern California, Los Angeles, USA to San Quintin Bay, northwestern Baja California, Mexico (Wetzler et al., 1991; Brusca et al., 2006).

27. **Gnathia tridens** Menzies & Barnard, 1959
    Point Conception and San Clemente Island, California, USA. A single record from Gulf of Alaska (Wetzler et al., 1991; Brusca et al., 2006).

28. **Gnathia trilobata** Schultz, 1966
    Off Point Loma, San Diego County, California, USA. La Jolla and San Diego Canyons (Wetzler et al., 1991; Brusca et al., 2006).

**Tridentellidae Bruce, 1984**

29. **Tridentella glutacantha** Delaney & Brusca, 1985
    Farallon Islands, near San Francisco, to Santa Catalina Island, southern California, USA (Hatch, 1947; Wetzler et al., 1991; Brusca et al., 2006). May include two species (Bruce, 2002).

30. **Tridentella quinicornis** Delaney & Brusca, 1985
    Southern California, Channel Islands, USA (Wetzler et al., 1991; Brusca et al., 2006).

**Bopyridae Rafinesque, 1815**

31. **Anathelges hyphalus** Markham, 1974
    From Carmel Cove, California, USA, to Baja California, Mexico (Wetzler et al., 1991; Brusca et al., 2006).

32. **Aporobopyrus mugensis** Shiino, 1964
    From Bodega Harbor, southern California, USA, to Ensenada, Baja California, Mexico (Campos & Campos, 1989; Brusca et al., 2006).

33. **Aporobopyrus oviformis** Shiino, 1934
    Point Mugu, Ventura, California, USA (Brusca et al., 2006). I-PAC.
34. **Argeia pugettensis** Dana, 1853
   From off Nanaimo, British Columbia, Canada south to South Humboldt Bay, California, USA (Hatch, 1947; Jay, 1989; Brusca et al., 2006). I-PAC.

35. **Asymmetrione ambodistorta** Markham, 1985
   Known only from Corona del Mar, New Port, California, USA (Markham, 1985).

36. **Bopyriscus calmani** (Richardson, 1905)
   Southern and central California, USA (Richardson, 1905; Brusca et al., 2006).

37. **Bopyroides hippolytes** (Kroyer, 1838)
   Unalaska Island, Aleutian Islands, Alaska to Heceta Bank, Oregon, USA (Hatch, 1947). I-PAC.

38. **Hemiarthrus abdominalis** (Kroyer, 1840)
   From Queen Charlotte Islands, British Columbia, Canada, south to Alki Point, Seattle, Washington, USA (Hatch, 1947). N-ATL. ART.

39. **Ione cornuta** Bate, 1864.
   Boundary Bay, British Columbia, Canada to San Francisco Bay, California, USA (Hatch, 1947; Brusca et al., 2006).

40. **Munidion parvum** Richardson, 1904
   From British Columbia, Departure Bay, Canada to Juan de Fuca Strait, Washington, USA (Richardson, 1904; Hatch, 1947).

41. **Munidion pleurocondis** Markham, 1975
   Central coast of California, USA, to west coast of Baja California, Mexico (Markham, 1975; Salazar-Vallejo & Leija-Tristán, 1989).

42. **Phyllodurus abdominalis** Stimpson, 1857
   From southern British Columbia, Canada south to northwest Baja California, Mexico (Champion, 1968; Salazar-Vallejo & Leija-Tristán, 1989).

43. **Progebiophilus bruscai** Salazar-Vallejo & Leija-Tristán, 1989
   West coast of Baja California, Tortugas and Todos Santos Bays, and on the west coast of the Gulf of California, from San Felipe, Baja California, to Las Paz, South Baja California, Mexico (Salazar-Vallejo & Leija-Tristán, 1989).

44. **Pseudione galacanthae** Hansen, 1897
   Coast of Canada and into the Gulf of California, Mexico (Brusca, 1980; Austin, 1985; Salazar-Vallejo & Leija-Tristán, 1989).

45. **Pseudione giardi** Calman, 1898
   Bering Sea to Puget Sound, Washington, USA (Calman, 1898; Markham, 1974).

46. **Schizobopyrina striata** (Nierstrasz & Brender à Bandis, 1929)
   Southern California, USA and Puertecitos, Baja California, Gulf of California, Mexico (Campos & Campos, 1990).

**Dajidae Giard & Bonnier, 1887**

47. **Holophryxus alaskensis** Richardson, 1905
   Behm and Lynn Cannal zone, Alaska, and Santa Barbara Channel, California, USA (Richardson, 1905; Brusca et al., 2006).

48. **Oculophryxus bicaulis** Shields & Gómez-Gutiérrez, 1996
   West coast of Baja California (20-29°N – 112-118°W), Mexico (Shields & Gómez-Gutiérrez, 1996). W-PAC. W-ATL.

**Entonisidae Kossmann, 1881**

49. **Portunion conformis** Muscatine, 1956
   Marin County to San Francisco Bay, California, USA (Brusca et al., 2006).

**Cabiropidae Giard & Bonnier, 1887**

50. **Cabirops montereyensis** Sassaman, 1985
   Known only from Monterey Bay, California, USA (Sassaman, 1985).

**Hemioniscidae Bonnier, 1900**

51. **Hemioniscus balani** Buchholz, 1866
   From Alaska, USA south to west coast of Baja California, Mexico (Cramp, 1968; Campos & Campos, 1989; Brusca et al., 2006).

**Fabidae Danforth, 1963**

52. **Faba setosa** Nierstrasz & Brender à Bandis, 1931
   Central California, USA (Brusca et al., 2006).

**Anthuridae Leach, 1814**

53. **Amakusanthura californiensis** (Schultz, 1964)
   Known only from SSW Santa Monica, California, USA (Schultz, 1964).

54. **Cyathura munda** Menzies, 1951
   Marine County, California, USA, to Mexican border. Gulf of California, Mexico (Menzies, 1951; Wetzer & Brusca, 1997).

55. **Haliophasma geminatum** Menzies & Barnard, 1959
   Puget Sound, Washington, USA south to San Quintin Bay, at the west coast of Baja California, Mexico, including Channel Islands, California, USA (Menzies & Barnard, 1959; Menzies, 1962b; Schultz, 1964; Austin, 1985).

**Antheluridae Poore & Lew Ton, 1988**

56. **Ananthura luna** (Schultz, 1966).
   Santa Monica Bay to San Diego, California, USA, including Santa Monica, La Jolla, Coronado and Tanner Canyons (Schultz, 1966; Brusca et al., 2006).

**Paranthuridae Menzies & Glynn, 1968**

57. **Califanthura squamosissima** (Menzies, 1951)
   Marine County, California, USA, to Tangola-Tangola Bay, Oaxaca, Mexico, including the east coast of the Gulf of California, probably to Puerto Peñasco, Sonora (Nunomura, 1978; Hendrickx & Van der Heiden, 1983; Poore, 1984a; Wetzer et al., 1991; Calderon & Campbell, 1993).

58. **Colanthura bruscai** Poore, 1984
   Off San Clemente (33°22.9’N, 117°35.8’W), California, USA, to Salinas Bay, Costa Rica, including
the east coast of the Gulf of California, Mexico (POORE, 1984; WETZER et al., 1991).

59. *Paranthura elegans* Menzies, 1951
Tomasles Point, Marine County, California, USA, to San Quintin Bay, Baja California, Mexico; including the east coast of the Gulf of California, north to Guaymas, Sonora, Mexico (MENZIES, 1951; WETZER & BRUSCA, 1997; ESPINOSA-PÉREZ & HENDRICKX, 2001a)

60. *Paranthura linearis* (Boone, 1923)
Only known for Laguna Beach, California, USA (BOONE, 1923; BRUSCA et al., 2006).

**Cirolanidae Dana, 1852**

61. *Cirolana harfordi* (Lockington, 1877)
Vancouver Island to Magdalena Bay, west coast of Baja California, Mexico. A single record at La Paz, southwestern tip of the Gulf of California (BRUSCA et al., 1995). I-PAC.

62. *Eurydice caudata* Richardson, 1899
From San Diego, California, USA, to La Libertad, Ecuador, including the Gulf of Mexico. Guadalupe, Revillagigedo, Coco and Galapagos Islands (BOWMAN, 1977; WALLERSTEIN, 1980; BRUSCA et al., 1995).

63. *Eurylana arcuata* (Hale, 1925)
From San Francisco Bay, California, USA and Antofagasta, Chile (BRUSCA et al., 2006; CARVALHO, 1977). I-PAC. W-ATL.

64. *Excirolana chilioni* (Richardson, 1905)
From British Columbia, Canada south to Los Angeles, California, USA (HATCH, 1947; GEORGE & STROMBERG, 1968; IVESON, 1974; BRUSCA et al., 2006). W-ATL.

65. *Excirolana linguifrons* (Richardson, 1899)
Monterey Bay to southern California, USA (RICHARDSON, 1905; BRUSCA et al., 2006).

66. *Natatolana californiensis* (Schultz, 1966)
From southern California, USA, to Cedros Island, west coast of Baja California, Mexico. In the Gulf of California, at Angel de la Guarda Island and off La Paz, South Baja California, Mexico (BRUSCA & NINOS, 1978; BRUSCA et al., 1995). A single record in Costa Rica (BRUSCA et al., 2006) and another in the Peru-Chile Trench (7°7.9’S, 80°37’W) (MENZIES & GEORGE, 1972).

From Cedros Island, west coast of Baja California, Mexico, to Secas Island, Panama, including the whole Gulf of California, Mexico (BRUSCA et al., 1995).

**LIMNORIDEA Brandt & Poore, 2002**

**Limnoridiidae White, 1850**

68. *Limnoria algarum* Menzies, 1957
Oregon south to San Diego, California, USA (MENZIES, 1957; BRUSCA et al., 2006).

69. *Limnoria lignorum* (Rathke, 1799)
From Kodiak Island, Alaska to Point Arena, California, USA (MENZIES, 1957; BRUSCA et al., 2006). ATL.

70. *Limnoria quadrupunctata* Holthuis, 1949
From Humbolt Bay to San Diego, California, USA (MENZIES, 1957; BRUSCA et al., 2006).

71. *Limnoria tripunctata* Menzies, 1951
From San Francisco Bay, California, USA south to Mazatlan, Sinaloa, including the whole Gulf of California, Mexico (MENZIES, 1951; BRUSCA & IVESON, 1985). W-ATL.

**SPHAEROMATIDEA Wägele, 1889**

**Sphaeromatidae Latreille, 1825**

72. *Bathycopea daltonae* (Menzies & Barnard, 1959)
From Monterey Bay to San Miguel Island, California, USA (WETZER et al., 1991; BRUSCA et al., 2006).

73. *Discerceis granulosa* (Richardson, 1899)
Southern California, USA to Cedros Island, western coast of Baja California, Mexico (RICHARDSON, 1905; BRUSCA et al., 2006).

74. *Dynamene tuberculosa* Richardson, 1899
From Aleutian Islands, Alaska to southern California, USA (BRUSCA et al., 2006).

75. *Dynamenella benedicti* (Richardson, 1899)
A single record from Monterey Bay, California (BRUSCA et al., 2006).

76. *Dynamenella conica* Boone, 1923
From San Francisco Bay to Monterey Bay, California, USA (BRUSCA et al., 2006).

77. *Dynamenella dilatata* (Richardson, 1899)
Monterey Bay, California, USA (HATCH, 1947; BRUSCA et al., 2006).

78. *Dynamenella glabra* (Richardson, 1899)
From Coos Bay, Oregon to Monterey Bay, California, USA (HATCH, 1947; BRUSCA et al., 2006).

79. *Dynamenella shearei* (Hatch, 1947)
From Coos Bay, Oregon south to southern California, USA (BRUSCA et al., 2006).

80. *Dynoides elegans* (Boone, 1923)
San Pedro to La Jolla, California, USA (BOONE, 1923; BRUSCA et al., 2006).

81. *Exosphaeroma aphrodita* (Stimpson, 1857)
From Kyska Harbor, Alaska south to Los Angeles, California, USA (RICHARDSON, 1905; HATCH, 1947; BRUSCA et al., 2006).

82. *Exosphaeroma amplexicauda* (Stimpson, 1857)
From Puget Sound, Washington south to San Diego, California, USA (IVESON, 1978; BRUSCA et al., 2006).

83. *Exosphaeroma inornata* Dow, 1958
From Point Arena, California, USA to La Libertad, California, USA (HATCH, 1947; BRUSCA et al., 2006).

84. *Exosphaeroma octoncum* (Richardson, 1899)
From Monterey Bay to Monterey Bay, California, USA (IVESON, 1978; BRUSCA et al., 2006).
85. *Exosphaeroma rhomburum* (Richardson, 1899) Monterey Bay, California, USA (Brusca et al., 2006).

86. *Gnorimosphaeroma insulare* (Van Name, 1940) From Popoff Island, Aleutian Islands, Alaska to San Nicolas Island, Channel Islands, California, USA (Wetzer et al., 1991; Brusca et al., 2006).


88. *Gnorimosphaeroma oregonensis* (Dana, 1853) Kyska Harbor, Alaska south to Monterey Bay, California, USA (Menzies, 1954; Brusca et al., 2006).


90. *Paracerceis cordata* (Richardson, 1899) Aleutian Islands, Alaska to southern California, USA (Richardson, 1905; Brusca et al., 2006).

91. *Paracerceis gilliana* (Richardson, 1899) From Mendocino County to Santa Catalina Island, California, USA (Richardson, 1905; Brusca et al., 2006).

92. *Paracerceis sculpta* (Holmes, 1904) From San Clemente Island, California, USA, south to San Juan de Alima, Michoacan, Mexico, including the whole Gulf of California, Mexico (Richardson, 1905; Brusca, 1980; Espinosa-Perez & Hendrickx, 2001a). Atl. Med.

93. *Paradella dianae* (Menzies, 1962) Los Angeles, California, USA, to San Juan de Alima, Michoacan, Mexico. Gulf of California, San Felipe, Baja California (northwest coast) and Mazatlán, Sinaloa (southeast coast) (Glynn & Glynn, 1974; Wallerstein, 1980; Van der Heiden & Hendrickx, 1982).

94. *Ancinidae Dana, 1852*  

99. *Ancinus granulatus* Holmes & Gay, 1909 Southern California, USA, to Cedros Island, west coast of Baja California, Mexico. Gulf of California, San Felipe, Baja California (northwest coast) and Mazatlan, Sinaloa (southeast coast) (Glynn & Glynn, 1974; Wallerstein, 1980; Van der Heiden & Hendrickx, 1982).

95. *Sphaeroma walkeri* Stebbing, 1905 Known only from Whidbey Island, Washington, USA (Hatch, 1947).

98. *Microcerberidae Lang, 1961*  

101. *Coxicerbus abbotti* (Lang, 1960) Central California, USA (Brusca et al., 2006).

102. *Caecidotea tomalensis* (Harford, 1877) Vancouver Island, British Columbia, Canada south to Klamath L., Oregon, USA (Hatch, 1947).

103. *Caeciasirops psammophila* Menzies & Pettit, 1956 Tamales Point, Marin County, to Asilomar, Monterey County, California, USA (Wetzer et al., 1991; Brusca et al., 2006).

104. *Caecijaera horvathi* Gurjanova, 1933 Known only from Whidbey Island, Washington, USA (Hatch, 1947).

105. *Iais californica* (Richardson, 1904) Humbolt Bay south to San Diego, California, USA (I-Pac. Atlantic, 1974; Brusca et al., 2006).

106. *Ianiropsis analoga* (Menzies, 1952) From San Juan Islands, Washington south to Marin County, California, USA (Menzies, 1952). Art.

107. *Ianiropsis derjugini* (Gurjanova, 1933) Monterey Bay, California, USA (Brusca et al., 2006). Art.

108. *Ianiropsis kincaidii* (Richardson, 1904) Aleutian Islands, Yakutat Island, Alaska, south to Monterey Bay, California, USA (Richardson, 1904; Brusca et al., 2006). Art.
110. *Ianiropsis magnocula* Menzies, 1952
From San Juan Islands, Washington to off Russian River, California, USA (MENZIES, 1952; BRUSCA et al., 2006).

111. *Ianiropsis minuta* Menzies, 1952
Munna, County, California, USA (MENZIES, 1952; BRUSCA et al., 2006).

112. *Ianiropsis montereyensis* Menzies, 1952
From Monterey County, California, USA (MENZIES, 1952; WETZER et al., 1991; BRUSCA et al., 2006).

113. *Ianiropsis tridens* Menzies, 1952
From San Juan Islands, Washington to off Monterey County, California, USA. A single record at Iquique, Chile (MENZIES, 1952; 1962a; WETZER et al., 1991; BRUSCA et al., 2006).

114. *Jaera wakishiana* Bate, 1865
Known only from Esquimalt Harbor, British Columbia, Canada (RICHARDSON, 1905).

115. *Janira maculosa* Leach, 1814
From Depature Bay, British Columbia, Canada to San Juan Islands, Washington, USA (HATCH, 1947).

116. *Janiralata erostrata* (Richardson, 1899)
Aleutian Islands, Attu Island (Chichagof Harbor), Alaska, USA (RICHARDSON, 1899).

117. *Janiralata davisi* Menzies, 1951
Known only from Carmel Cove, Monterey County, California, USA (MENZIES, 1951).

118. *Janiralata holmesi* (Richardson, 1905)
Alaska, USA (RICHARDSON, 1905).

119. *Janiralata occidentalis* (Walker, 1898)
From San Juan Islands, Turn Island, Washington to Oregon, USA (HATCH, 1947, BRUSCA, et al., 2006).

120. *Janiralata rajata* Menzies, 1951
Monterey Bay, California, USA (BRUSCA et al., 2006).

121. *Janiralata solasteri* (Hatch, 1947)
From Dall Island, Gulf of Alaska south to southern California, USA (HATCH, 1947).

122. *Janiralata triangulata* (Richardson, 1899)
Known only from Monterey Bay, California, USA (BRUSCA et al., 2006).

**Joeropsisidae Nordenstam, 1933**

123. *Joeropsis concava* (Schultz, 1966)
Southern California, Santa Cruz Island and San Diego, USA (WETZER, et al., 1991; BRUSCA et al., 2006).

124. *Joeropsis dubia dubia* (Menzies, 1951)
Newport Bay, Orange County, California, USA, to San Quintin Bay, west coast of Baja California, Mexico. Gulf of California, Percebu Lagoon and Conception Bay, Mexico (MENZIES, 1962b; CARVACHO, 1983; WETZER et al., 1991).

125. *Joeropsis dubia paucispinis* (Menzies, 1951)
Marin County, California to Santa Monica Canyon, California, USA (SCHULTZ, 1966; BRUSCA et al., 2006).

126. *Joeropsis lobata* (Richardson, 1899)
From Coos Bay, Oregon to Monterey Bay, California, USA (BRUSCA et al., 2006).

**Munnidae Sars, 1897**

Known only from San Juan Island, Washington, USA (GEORGE & STROMBERG, 1968).

128. *Munna chromatocephala* Menzies, 1952
From Puget Sound, Washington south to Marin County, California, USA (MENZIES, 1952; BRUSCA et al., 2006).

129. *Munna halei* Menzies, 1952
Coast of California, from San Luis Obispo to Marine County, California, USA (MENZIES, 1952; BRUSCA et al., 2006).

130. *Munna kroyeri* Goodsir, 1843
North Beach, Washington, USA (HATCH, 1947). ATL.

131. *Munna minuta* Hatch, 1947
Carkeek Park, Washington, USA (HATCH, 1947).

Point Conception to Point Loma, San Diego, California, USA. (MENZIES & BARNARD, 1959; BRUSCA et al., 2006).

133. *Munna stevenseni* Gurjanova, 1933
From Bering Sea to central California, USA (BRUSCA et al., 2006).

134. *Uromunna ubiquita* (Menzies, 1952)

**Munnopsidae Sars, 1869 (sensu lato Wilson, 1989)**

135. *Ilyarachna acarina* Menzies & Barnard, 1959
Point Conception to Point Loma, San Diego, California, including Santa Maria, San Pedro and Santa Catalina Basins, USA (MENZIES & BARNARD, 1959; BRUSCA et al., 2006).

**Paramunidae Vanhöffen, 1914**

136. *Munnochion erratum* (Schultz, 1964)
Off Gaviota Pier, Santa Barbara Channel, California, USA (SCHULTZ, 1964).

137. *Munnochion tillerae* (Menzies & Barnard, 1959)
From Satellite Channel, British Columbia, Canada. A single record for the Strait of Magellan, Chile (MENZIES & BARNARD, 1959; WETZER et al., 1991; WINKLER, 1994).

Southern Channel Islands and Tanner Bank, California, USA (IVERSON & WILSON, 1981; WETZER et al., 1991).

139. *Pleurogonium californiense* Menzies, 1951
From off Russian River, Sonoma County south to Point Loma, San Diego, California, USA (SCHULTZ, 1966; BRUSCA et al., 2006).
Santiidae Wilson, 1987

140. Santia hirsuta (Menzies, 1951)
Known only from Tomales Point, California, USA (MENZIES, 1951).

Incertae sedis

141. Tole alascensis (Benedict, 1905)
Known only from Alaska coast (71°2°N, 157°46'W), USA (BENEDICT, 1905).

142. Tole sarsi (Richardson, 1905)
Amchitka Island, Aleutian Islands, Alaska, USA (RICHARDSON, 1905).

143. Tole triangulata (Richardson, 1899)
Monterey Bay, California, USA (RICHARDSON, 1899).

VALVIFERA Sars, 1882

Arcturidae Dana, 1849

144. Arcturus brevispinis Richardson, 1909
Aleutian Islands, Alaska, USA (BENEDICT, 1898).

145. Arcturus glaber Benedict, 1898
Aleutian Islands, Alaska, USA (RICHARDSON, 1909).

146. Arcturus diversispinis Richardson, 1909
Aleutian Islands, Alaska, USA (RICHARDSON, 1909).

147. Arcturus magnispinis Richardson, 1909
Bering Sea (RICHARDSON, 1909).

148. Idaturus allelomorphus Menzies & Barnard, 1959
From Monterey Bay to Point Loma, California, USA, including Cortes and Tanner Banks (MENZIES & BARNARD, 1959; IVESON, 1974; BRUSCA et al., 2006).

149. Idaturus hedgpethi Menzies, 1951
Tomales Bay, California, USA (MENZIES, 1951; BRUSCA et al., 2006).

150. Neastacilla californica (Boone, 1918)
Southern California, USA, and Gulf of California, Mexico and from Montevideo to Beagle Channel, Chile (RICHARDSON, 1905; SCHULTZ, 1969; BRANDT et al., 1999; BRUSCA et al., 2006). COS.

151. Plesiopriprion murdocchi (Benedict, 1898)
Bering Sea, west of Point Franklin, Alaska, USA (BENEDICT, 1898).

Chaetiliidae Dana, 1849

152. Mesidotea entomon (Linnaeus, 1767)
From Aberdeen, Washington south to Monterey Bay, California, USA (HATCH, 1947; BRUSCA et al., 2006). ART.

Holognathidae Thomson, 1904

153. Cleetonioides occidentalis (Richardson, 1899)
From the southern coast of California, USA south to Ecuador, including the east coast of the Gulf of California, from Puerto Peñasco, Sonora, to Mazatlan, Sinaloa, Mexico. Galapagos Islands (KENSLEY & KAUFMAN, 1978; BRUSCA & IVESON, 1985; BRUSCA et al., 2006).

Idoteidae Sambouille, 1819

154. Colidotea findleyi Brusca & Wallerstein, 1977
From San Diego, California, USA to San Eugenio Point, west coast of Baja California, Mexico. Gulf of California, from San Felipe, Baja California and Puerto Peñasco to Lobos Point, Sonora. Guadalupe Island (WETZER et al., 1991; BRUSCA et al., 2006).

155. Colidotea rostrata (Benedict, 1898)
From San Pedro, California, USA to Point Sal-sipuedes, Baja California, Mexico (DELANEY, 1993; BRUSCA et al., 2006).

156. Colidotea wallersteini Brusca, 1983
Known only from Point Santa Clara, northwestern Baja California, Mexico. Guadalupe Island (BRUSCA, 1983; WETZER, et al., 1991).

157. Edotia sublitoralis Menzies & Barnard, 1959
Vancouver Island, Canada to Newport, California, USA. A single record from Gulf of Nicoya, Costa Rica (VARGAS et al., 1985; BRUSCA et al., 2006).

158. Eusymmerus antennatus Richardson, 1899
From San Eugenio Point, west coast of Baja California, south to Gulf of Nicoya, Costa Rica, including the east coast of the Gulf of California (BRUSCA & WALLERSTEIN, 1977; VARGAS et al., 1985; CALDERÓN & CAMPY, 1993).

159. Eusymmerus pseudoculata (Boone, 1923)
From Point Conception to San Diego, California, USA (SCHULTZ, 1969; BRUSCA et al., 2006).

160. Idotea aculeata ( Stafford, 1913)
British Columbia, Canada, to Cedros Island, west coast of Baja California, Mexico. Gulf of California, Mexico, Guaymas, Sonora and La Paz, South Baja California (MENZIES, 1950; BRUSCA & WALLERSTEIN, 1977; AUSTIN, 1985; CALDERÓN & CAMPY, 1993; BRUSCA et al., 2006).

161. Idotea fowkesi Richardson, 1905
Gulf of Alaska south to Monterey Bay, California, USA (HATCH, 1947; BRUSCA et al., 2006).

162. Idotea kirchanskii Miller & Lee, 1969
From Oregon to southern California, USA (SCHULTZ, 1969; BRUSCA et al., 2006).

163. Idotea metallica Bosc, 1802
Coast of California, USA, and Gulf of California, Mexico and from Montevideo to Beagle Channel, Chile (RICHARDSON, 1905; SCHULTZ, 1969; BRANDT et al., 1999; BRUSCA et al., 2006). COS.

164. Idotea montereyensis (Maloney, 1933)
From British Columbia Estuary, Canada to northwestern Baja California, Mexico (BRUSCA et al., 2006).

165. Idotea obscura Rafi, 1972
British Columbia, Canada (KENSLEY & SCHOTTE, 2006).
167. **Idotea ochotensis** Brandt, 1851
   From Vancouver Island, Canada south to San Francisco Bay, California, USA (Hatch, 1947; Brusca et al., 2006). ART.

168. **Idotea resecata** Stimpson, 1857
   From Karta Bay, Gulf of Alaska, USA, south to Tortola Bay, west coast of Baja California, Mexico; San Lucas Cape and La Paz, South Baja California, Gulf of California. Alijos Rocks (Brusca & Wallerstein, 1977; Austin, 1985; Brusca et al., 2006).

169. **Idotea rufescens** Brandt, 1851
   From Gabriola Pass, British Columbia, Canada to Coronados Island, central western Baja California, Mexico (Menzies, 1950; Wetzer & Brusca, 1997; Brusca et al., 2006).

170. **Idotea schmitti** Menzies, 1950
   Bering Sea to Banda Point, northwestern Baja California, Mexico (Richardson, 1909; Iverson, 1974; Brusca et al., 2006).

171. **Idotea stenops** Benedict, 1898
   From Alaska, USA, to San Eugenio Point, west coast of Baja California, Mexico, and from San Telmo Point to La Paz, South Baja California, Mexico (Brusca & Wallerstein, 1977; Austin, 1985; Brusca et al., 2006).

172. **Idotea urotoma** Stimpson, 1864
   From Alaska, USA, to the west coast of Baja California, Mexico. Guaymas, Sonora and La Paz, South Baja California, Gulf of California (Brusca & Wallerstein, 1977; Austin, 1985; Calderón & Campoy, 1993; Brusca et al., 2006).

173. **Idotea wosnesenskii** Brandt, 1851
   Aleutian Islands, Alaska, to southern California, USA. A single record at La Paz, South Baja California, Gulf of California, Mexico (Brusca & Wallerstein, 1977; Brusca, 1980; Austin, 1985). I-PAC.

174. **Synidotea angulata** Benedict, 1897
   From British Columbia Estuary, British Columbia, Canada south to Eureka, California, USA (Hatch, 1947; Brusca et al., 2006).

175. **Synidotea bicuspida** (Owen, 1839)
   Northern Aleutian Islands, Alaska, USA (Richardson, 1909).

176. **Synidotea berolzheimeri** Menzies & Miller, 1972
   Central California, from Sonoma County to San Luis Obispo, USA (Menzies & Miller, 1972; Brusca et al., 2006).

177. **Synidotea calcarea** Schultz, 1966
   Tanner and Santa Rosa Canyons, California, USA (Schultz, 1966; Brusca et al., 2006).

178. **Synidotea consolidata** (Stimpson, 1857)
   Southern Alaska to San Francisco Bay, California, USA (Brusca et al., 2006).

179. **Synidotea cornuta** Rafi & Laubitz, 1990
   British Columbia, Canada (Kensley & Schotte, 2006).

180. **Synidotea harfordi** Benedict, 1897
   Oregon County, USA, to Gulf of Nicoya, Costa Rica, including whole Gulf of California, Mexico (Brusca & Wallerstein, 1979a; Wallerstein, 1980; Vargas et al., 1985). I-PAC.

181. **Synidotea laevis** Benedict, 1897
   Northern Aleutian Islands, Alaska, USA (Benedict, 1897).

182. **Synidotea laticauda** Benedict, 1897
   From Willapa Bay, Washington to San Francisco Bay, California, USA (Benedict, 1897; Poore, 1996; Brusca et al., 2006).

183. **Synidotea magnifica** Menzies & Barnard, 1959
   San Luis Obispo, California, USA to northwestern Baja California, Mexico (Menzies & Barnard, 1959; Brusca et al., 2006).

184. **Synidotea media** Iverson, 1972
   Point Soberanes to Santa Maria Basin, California, USA (Iverson, 1972; Brusca et al., 2006).

185. **Synidotea minuta** Rafi & Laubitz, 1990
   British Columbia, Canada (Kensley & Schotte, 2006).

186. **Synidotea nebulosa** Benedict, 1897
   From Kyska Harbor, Alaska south to Whidbey Island, Washington, USA (Benedict, 1897; Hatch, 1947). I-PAC.

187. **Synidotea nodulosa** (Kroyer, 1846)
   From Bering Strait to Dixon Entrance, Washington, USA (Benedict, 1897; Hatch, 1947). ATL.

188. **Synidotea pettiboneae** Hatch, 1947
   British Columbia, Canada to Monterey Bay, California, USA (Hatch, 1947; Kensley & Schotte, 2006).

189. **Synidotea ritteri** Richardson, 1904
   From Vancouver Island, Canada to Shell Beach, California, USA (Menzies & Miller, 1972; Brusca et al., 2006).

190. **Synisoma wetzerae** Ormsby, 1991
   Santa Catalina Island, California, USA, and Guaymas, Sonora, Gulf of California, Mexico (Ormsby, 1991; Espinosa-Pérez & Hendrickx, 2001a).

**ONISCIDEA Latreille, 1802**

191. **Armadillidae Brandt, 1831**

192. **Cubaris affinis** (Dana, 1854)
   Coast of California, USA (Brusca et al., 2006).

193. **Cubaris californica** (Budde-Lund, 1885)
   San Francisco Bay to San Pedro, Los Angeles, California, USA (Richardson, 1905; Brusca et al., 2006).

194. **Ligia occidentalis** Dana, 1853
   From Oregon, USA, south to Chamel Bay, Jalisco, Mexico, including the whole Gulf of California,
195. *Ligia pallasii* Brandt, 1833  
From Kyska Harbor, Alaska south to Santa Cruz Island, California, USA (Richardson, 1905; Hatch, 1947; Brusca et al., 2006).

196. *Ligidium gracile* (Dana, 1856)  
Aleutian Islands, Alaska to Santa Clara, California, USA (Jackson, 1923; Hatch, 1947; Brusca et al., 2006).

197. *Ligidium hypnorum* (Cuvier, 1792)  
From Canada to coast of California, USA (Jackson, 1923).

198. *Ligidium latum* Jackson, 1923  
San Francisco Bay to Santa Barbara, California, USA (Brusca et al., 2006).

199. *Littorophiloscia richardsonae* (Holmes & Gay, 1909)  
Vancouver Island, Canada south to Cedros Island, western Baja California, Mexico (George & Ströemberg, 1968; Hatch, 1947; Brusca et al., 2006).

200. *Niambia capensis* (Dollfus, 1895)  
From Washington to southern California, USA (Brusca et al., 2006). I-PAC.

201. *Platyarthrus aiasensis* Legrand, 1953  
Dana Point, California, USA (Garthwaite & Taiti, 1989). ATL. MED.

202. *Porcellio dilatatus* Brandt, 1833  
Coast of California, USA (Brusca et al., 2006). MED.

203. *Porcellio laevis* Latreille, 1804  
Coast of California, USA (Brusca et al., 2006). COSMO

204. *Porcellio scaber* Latreille, 1804  
From Queen Charlotte Island, British Columbia, Canada south to San Mateo, California, USA (Hatch, 1947; Brusca et al., 2006). COSMO

205. *Porcellionides flora* Garthwaite & Sassaman, 1985  
Southern California, USA and Gulf of California, Mexico (Garthwaite & Sassaman, 1985; Brusca et al., 2006). ATL.

206. *Alloniscus mirabilis* (Stuxberg, 1875)  
From San Mateo, California, USA to Magdalena Bay, Mexico (Schultz, 1984; Brusca et al., 2006).

207. *Alloniscus perconvexus* Dana, 1856  
From Tofino, British Columbia, Canada south to Magdalena Bay, west coast of Baja California, Mexico (Mulaik, 1960; George & Ströemberg, 1968).

208. *Armadillonicus coronacapitalis* Menzies, 1950  
From Marin County to San Miguel and Anacapa Islands, California, USA (Brusca et al., 2006).

209. *Armadillonicus holmesi* Arcangeli, 1933  
From British Columbia, Canada, to Magdalena Bay, west coast of Baja California, Mexico (Mulaik, 1960; Bowman, 1977; Wallerstein, 1980; Austin, 1985).

210. *Armadillonicus lindahlii* (Richardson, 1905)  
From Tomales Bay, southern California, USA to Cedros Island, western Baja California, Mexico (Richardson, 1905; Brusca et al., 2006).

211. *Detonella papillicornis* (Richardson, 1904)  
Cook Inlet, Alaska to San Francisco Bay, California, USA (Hatch, 1957; Brusca et al., 2006). ART.

212. *Brackenridgia heroldi* (Arcangeli, 1932)  
Central and southern California, USA (Brusca et al., 2006).

213. *Tylos punctatus punctatus* Holmes & Gay, 1909  
San Diego, California, USA, to Ensenada, west coast of Baja California, Mexico. Gulf of California, Mexico, Puerto Peñasco, Sonora to Mazatlan, Sinaloa (east coast) and la Paz, South Baja California (west coast) (Schultz, 1970; Austin, 1985; Espinosa-Pérez & Hendrickx, 2001a).

APPENDIX 2.
List of species of isopods reported for the Peru-Chile and Magellan zoogeographic provinces (133 species). Species reported only in oceanic islands not included. Sequence of orders and families is according to Brandt & Poore (2003).

**CYMOTHOIDA Wägele, 1889**

**Aegidae White, 1850**

1. *Aega magnifica* (Dana, 1853)  
Gulf of Ancud, Strait of Magellan and Beagle Channel, Chile (Menzies, 1962a; Lorenti & Mariani, 1997; Brandt et al., 1999; Bruce, 2004). ATL.

2. *Aega semicarinata* Miers, 1875  
Gulf of Ancud and Juan Fernández Archipelago, Chile (Nordenstam, 1930; Menzies, 1962a).

3. *Aega webbi* (Guérin-Meneville, 1836). Known only from Juan Fernández Archipelago, Chile (Rozbacylo & Castilla, 1987; Kensley & Schotte, 2006). MED (?).

4. *Aega uschakovi* Kussakin, 1967  
Coast of Chile (Kensley & Schotte, 2006).

5. *Rocinella australis* Schödte & Meinert, 1879  
Strait of Magellan, Chile (Schödte & Meinert, 1879).
Corallanidae Hansen, 1890

   Chilean coasts north off Valparaiso, Chile (Carvacho, 1977; Lancellotti & Vasquez, 2002).

7. *Lanocira hirsuta* Nordenstam, 1930
   Known only from Juan Fernández Archipelago, Chile (Rozbcylo & Castilla, 1987).

Cymothoidae Leach, 1814

8. *Anilocra huacho* Rokicki, 1984
   From Huacho to Chancay, Peru (Rokicki, 1984).

   From southern California, USA, south to Cape Horn, Chile, including the whole Gulf of California, Mexico. Galapagos Islands (Brusca, 1981; Molina & Manrique, 1996; Espinosa-Pérez & Hendrickx, 2001a). I-PAC.

10. *Ceratothoa trigonocephala* (Leach, 1818)
    From Iquique to Talcahuano, Chile (Aldana, et al., 1995). I-PAC.

    Northern Gulf of Ancud, Chile (Menzies, 1962a). I-PAC.

Gnathiidae Leach, 1814

12. *Caecognathia antarctica* (Studer, 1884)
    Beagle Channel, Chile (Brandt et al., 1999). ANT.

    Gulf of Ancud, Chile (Menzies, 1962a).

Tridentellidae Bruce, 1984

    Northern and central Chile, from Mejillones Peninsula to Gulf of Ancud (Menzies, 1962a; Carvacho, 1977).

Bopyridae Rafinesque, 1815

15. *Anathelges thompsoni* Nierstrasz & Brender a Brandis, 1931.
    Valparaiso, Chile (Nierstrasz & Brender a Brandis, 1931; Boyko & Williams, 2003).

16. *Ione ovata* Shiino, 1964
    San Vicente and Coliumo Bays, Concepcion, Chile (Munoz, 1997; Astete-Espinoza & Caceres, 2000).

17. *Ionella agassizi* Bonnier, 1900
    San Vicente and Coliumo Bays, Concepcion, Chile (Munoz, 1997; Astete-Espinoza & Caceres, 2000).

    Coliumo Bay, Dichato, Chile (Stuardo, Vega & Cespedes, 1986; Munoz, 1997).


20. *Pseudione galacantae* Hansen, 1897
    Coast of Canada and into the Gulf of California, Mexico, and from Gulf of Penas to Strait of Magellan, Chile (Brusca, 1980; Austin, 1985; Stuardo et al., 1986; Salazar-Vallejo & Leija-Tristán, 1989). W-ATL

    Off the coast of Chile, from 26°58’S-56’S to 32°01’81’S (Prado et al., 1998).

22. *Pseudione tuberculata* Richardson, 1904
    Off Archipelado of Los Chonos south to Strait of Magellan, Chile (Boschman, 1962; Miranda-Vargas & Roccatagliata, 2004). W-ATL.

Paranthuridae Menzies & Glynn, 1968

23. *Paranthura porteri* (Boone, 1920)
    From Arica south to Archipelago of Chiloe, Chile (Lancellotti & Vasquez, 2002).

24. *Paranthura scottsbergi* Nordenstam, 1930
    Known only from Juan Fernández Archipelago, Chile (Rozbcylo & Castilla, 1987).

25. *Paranthura gracilipes* Nordenstam, 1930
    Known only from Juan Fernández Archipelago, Chile (Rozbcylo & Castilla, 1987).

26. *Paranthura nana* Nordenstam, 1930
    Known only from Juan Fernández Archipelago, Chile (Rozbcylo & Castilla, 1987).

Cirolanidae Dana, 1853

    From Antofagasta to Concepcion, Chile (Menzies, 1962a; Carvacho, 1977).

    From Antofagasta to Boca del Guapo, Chile (Menzies, 1962a; Carvacho, 1977).

29. *Eurylana arcuata* (Hale, 1925)
    From San Francisco Bay, California, USA and Antofagasta, Chile (Brusca et al., 2006; Carvacho, 1977). I-PAC. W-ATL.

30. *Excirolana braziliensis* Richardson, 1912
    From the northern Gulf of California, Mexico, to Concepcion, Chile (Espinosa-Pérez & Hendrickx, 2001a). ATL.

    From Coquimbo south to Gulf of Ancud, Chile (Menzies, 1962a; Carvacho, 1977; Jaramillo, 1982).

32. *Excirolana monodi* Carvacho, 1977
    From Aconcagua Province to Gulf of Ancud, Chile (Carvacho, 1977; Jaramillo, 1982).

33. *Natatolana albinota* (Vanhoffen, 1914)
    Northern Gulf of Ancud, Chile (Menzies, 1962a).

34. *Natatolana californiensis* (Schultz, 1966)
    From southern California, USA, and in the Gulf of California, Mexico, to Perú-Chile Trench (Espinosa-Pérez & Hendrickx, 2001a).

35. *Natatolana chilensis* (Menzies, 1962)
    Gulf of Ancud, Chile (Menzies, 1962a).

36. *Natatolana pastorei* (Giambiagi, 1924)
    Strait of Magellan to Punta Arenas, Chile; doubtful in Beagle Channel (Wägele & Bruce, 1989;
37. *Pseudolana concinna* (Hale, 1925)
Gulf of Ancud, Chile (MENZIES, 1962a). I-PAC.

**LIMNORIDEA** Brandt & Poore, 2002

Limnoriidae White, 1850

From Valparaiso south to Archipelago of Los Chonos, Chile (LANCELLOTTI & VASQUEZ, 2002). W-ATL.

39. *Amphoroidea typa* H. Milne-Edwards, 1840
Coast of Chile, from Coquimbo to Port Lagunas (MENZIES, 1962a).

40. *Cassidinopsis emarginata* (Guérin-Méneville, 1943)
Strait of Magellan to Cape Horn, Chile (LANCE-LLOTTI & VASQUEZ, 2002). W-ATL.

41. *Cassidinopsis typa* Menzies, 1962
Northern and central Chile, from Iquique to Archipelago of Los Chonos (MENZIES, 1962a).

42. *Dynamenella acuticauda* Menzies, 1962
Southern coast of Chile, from Point Corona to Port Arenas, Strait of Magellan, Chile (MENZIES, 1962a).

43. *Exosphaeroma gigas* (Leach, 1818)
From San Vicente Bay south to Strait of Magellan, Chile (MENZIES, 1962a; BRANDT et al., 1999; THIEL, 2002). I-PAC.

44. *Exosphaeroma lanceolata* (White, 1847)
From northern Iquique south to Cape Horn, Chile (MENZIES, 1962a; LANCELLOTTI & VASQUEZ, 2002). W-ATL.

45. *Exosphaeroma studeri* Vanhoefsen, 1914
Strait of Magellan, Chile (MENZIES, 1962a; LORENTE & MARIANI, 1997).

46. *Ischyromene eatoni* (Miers, 1875)
From Valparaiso south to Point Santa Maria, Strait of Magellan, Chile (MENZIES, 1962a).

47. *Ischyromene tuberculata* (Menzies, 1962)
Coquimbo to Point Corona, Chile (MENZIES, 1962a).

48. *Isocladus bahamondei* Carvacho, 1997
Coast of Chile, from Concepción Bay to off Lar River (CARVACHO, 1997).

49. *Isocladus calcarus* (Dana, 1853)
From Coquimbo south to Cape Horn, Chile (LANCE-LLOTTI & VASQUEZ, 2002). W-ATL.

50. *Isocladus integra* (Heller, 1868)
Coast of Chile (KENSLEY & SCHOTTE, 2006).

51. *Moruloidae darwini* (Cunningham, 1871)
Strait of Magellan and Beagle Channel, Chile (MENZIES, 1962a; LORENTE & MARIANI, 1997). W-ATL.

52. *Paradella bakeri* (Menzies, 1962)
Iquique to Point Corona, Chile (MENZIES, 1962a; LANCELLOTTI & VASQUEZ, 2002).

Known only from Chile, Coquimbo to Archipelago of Los Chonos (MENZIES, 1962a; CARVACHO, 1975).

54. *Sphaeroma guyi* Nicolet, 1849
Coast of Chile (KENSLEY & SCHOTTE, 2006).

55. *Sphaeroma propinquus* Nicolet, 1849
Coast of Chile (KENSLEY & SCHOTTE, 2006).

56. *Acanthoserolis schythei* (Lukten, 1858)
Gulf of Ancud south to Cape Horn, Chile (MENZIES, 1962a; LANCELLOTTI & VASQUEZ, 2002).

57. *Cristaserolis gaudichaudii* (Audouin & Milne-Edwards, 1841)
From Valparaiso south to Strait of Magellan, Chile (MENZIES, 1962a; LORENTE & MARIANI, 1997; LANCELLOTTI & VASQUEZ, 2002). W-ATL.

58. *Cristaserolis plana* (Dana, 1853)
Point Wether, Boca de Guano, south to Cape Horn, Chile (AUDOUIN & MILNE-EDWARDS, 1841; LANCELLOTTI & VASQUEZ, 2002).

59. *Neoserolis exigua* (Nordenstrom, 1823)
Beagle Channel, Chile (BRANDT et al., 1999). W-ATL.

60. *Septemserolis ovata* (Sheppard, 1957)
Beagle Channel, Chile (BRANDT et al., 1999). ANT.

61. *Seroserolis paradoxa* (Fabricius, 1775)
From Valparaiso south to Cape Horn, Chile (MENZIES, 1962a; LANCELLOTTI & VASQUEZ, 2002). W-ATL.

62. *Thysanoserolis elliptica* (Sheppard, 1933)
Strait of Magellan, Chile (LORENTE & MARIANI, 1997). W-ATL.

**ASELLOTA** Latreille, 1803

Acanthaspidae Menzies, 1962

63. *Ianthopsis bovalli* (Studer, 1884)
Strait of Magellan and Beagle Channel, Chile (LORENTE & MARIANI, 1997; BRANDT et al., 1999). W-ATL.

64. *Ianthopsis laevis* Menzies, 1962
Known only from Las Cruces, Province of Santiago, Chile (WINKLER, 1992).

**Janiridae** Sars, 1897

65. *Austrofilius furcatus* (Hodgson, 1910)
Beagle Channel, Chile (BRANDT et al., 1999).

66. *Iais chilense* (Winkler, 1992)
South coast of Chile, from Gulf of Ancud to Strait of Magellan (MENZIES, 1962a; WINKLER, 1992).
69. *Ianiropsis kussakini* Carvacho, 1982
   Province of Concepcion (36-37°S), Chile (Carvacho, 1982).

70. *Ianiropsis perplexus* Menzies, 1962
   Archipelago of Los Chonos, Chile (Menzies, 1962a).

71. *Ianiropsis tridens* Menzies, 1952
   From San Juan Islands, Washington south to Monterey County, California, USA. A single record at Iquique, Chile (Menzies, 1952; 1962a; Wetzler et al., 1991; Brusca et al., 2006).

72. *Ianiropsis varians* Winkler & Brandt, 1993
   Strait of Magellan, Chile (Brandt et al., 1999).

73. *Iathrippa hirsuta* (Carvacho, 1981)
   Known only from Dichato Beach, Concepcion, Chile (Carvacho, 1981).

74. *Iathrippa menziesi* Sivertsen & Holthuis, 1980
   From Gulf of Ancud to Strait of Magellan, Chile (Menzies, 1962a).

75. *Iathrippa multidens* Menzies, 1962
   Strait of Magellan (53°11'S, 70°55'W), Chile (Menzies, 1962a).

76. *Iathrippa longicauda* (Chilton, 1884)
   Coast of Chile; doubtful record from Beagle Channel, Chile (Menzies, 1962a; Brandt et al., 1999). WPAC. W-ATL.

   Known only from Dichato Beach, Concepcion, Chile (Carvacho, 1981).

78. *Neojaera antarctica* (Pfeffer, 1887)
   Strait of Magellan and Beagle Channel, Chile (Winkler, 1994; Brandt et al., 1999). ANT

79. *Neojaera elongata* Menzies, 1962
   From Iquique south to Valparaíso, Chile (Menzies, 1962a).

80. *Notasellus chilensis* (Menzies, 1962a)
   Gulf of Ancud to Strait of Magellan, Chile (Menzies, 1962a; Winkler & Brandt, 1993; Brandt et al., 1999). ANT

**Joeropsideidae Nordenstam, 1933**

   North coast of Chile, from Iquique south to Gulf of Ancud (Menzies, 1962a).

82. *Joeropsis curvicornis* (Nicolet, 1849)
   Strait of Magellan to Beagle Channel, Chile (Lorenti & Mariani, 1997; Brandt et al., 1999). W-ATL.

83. *Joeropsis intermedius* Nordenstam, 1933
   Beagle Channel to north of the gulf of Ancud, Chile (Menzies, 1962a; Lorenti & Mariani, 1997; Brandt et al., 1999). W-ATL.

**Munnidae Sars, 1897**

   Strait of Magellan and Beagle Channel, Chile (Menzies, 1962a; Brandt et al., 1999).

85. *Munna gallarroi* Winkler, 1992
   Strait of Magellan and Beagle Channel, Chile (Lorenti & Mariani, 1997; Brandt et al., 1999).

   Known only from Strait of Magellan (53°11'S, 70°55'W), Chile (Menzies, 1962a).

   Strait of Magellan and Beagle Channel (Lorenti & Mariani, 1997; Brandt et al., 1999). W-ATL.

88. *Uromunna nana* (Nordenstam, 1933)
   From Iquique, northern Chile, south to Strait of Magellan and Beagle Channel (Menzies, 1962a; Brandt et al., 1999).

89. *Uromunna schauinslandi* (G.O. Sars, 1905)
   Gulf of Ancud, Guar Island, Chile (Menzies, 1962a).

**Munnopsidae Sars, 1897**

90. *Ilyarachna antarctica* Vanhöffen, 1914
   Beagle Channel, Chile (Brandt et al., 1999). ANT

**Paramunniidae Vanhöffen, 1914**

91. *Allostrata ovalis* Winkler, 1994
   Strait of Magellan and Beagle Channel, Chile (Winkler, 1994; Brandt et al., 1999).

92. *Austrosignum dentatum* Winkler, 1994
   Strait of Magellan and Beagle Channel, Chile (Winkler, 1994; Brandt et al., 1999).

   Known only from Strait of Magellan, Chile (Menzies, 1962a).

94. *Austrosignum latifrons* Menzies, 1962
   Northern Gulf of Ancud, E Quellin Island, Chile (Menzies, 1962a).

95. *Magellanianira serrata* Winkler, 1994
   Known only from Strait of Magellan (Winkler, 1994).

96. *Munnogonium trillerae* (Menzies & Barnard, 1959)
   From Satellite Channel, British Columbia, Canada. A single record for the Strait of Magellan, Chile (Menzies & Barnard, 1959; Wetzler et al., 1991; Winkler, 1994).

97. *Paramunna integra* Nordenstam, 1933
   Strait of Magellan and Beagle Channel (Winkler, 1994; Brandt et al., 1999).

98. *Paramunna magellanensis* Winkler, 1994
   Strait of Magellan and Beagle Channel (Winkler, 1994; Brandt et al., 1999).

   Known only from Strait of Magellan (Winkler, 1994).

100. *Paramunna parasimplex* Winkler, 1994
    Strait of Magellan and Beagle Channel, Chile (Winkler, 1994; Brandt et al., 1999).

    Known only from Strait of Magellan (Winkler, 1994).
From Seno Reloncavi, northern Gulf of Ancud, south to Strait of Magellan, Chile (MENZIES, 1962a; WINKLER, 1994).

104. *Paramunna subtriangulata* (Richardson, 1908)
Strait of Magellan, Chile (MENZIES, 1962a; WINKLER, 1994).

Gulf of Ancud to Strait of Magellan, Chile (MENZIES, 1962a; BRANDT et al., 1999).

106. *Pleurosignum magnum* Vanhöffen, 1914
Northern Gulf of Ancud, Maillen Island, Chile (MENZIES, 1962a). ANT.

Santiidae Wilson, 1987

Strait of Magellan and Beagle Channel, Chile (WINKLER, 1994; BRANDT et al., 1999). S-ATL

108. *Santia dimorphis* (Menzies, 1962)
From Archipelago of Chiloe south to Cape Horn, Chile (LANCELLOTTI & VASQUEZ, 2002).

109. *Santia hispina* (Vanhöffen, 1914)
Strait of Magellan and Beagle Channel, Chile (WINKLER, 1994; BRANDT et al., 1999). S and W-ATL.

110. *Santia laevifrons* (Menzies, 1962)
Central coast of Chile, from Montamar south to Peñon Blanco, Chonos Archipelago (MENZIES, 1962a; LANCELLOTTI & VASQUEZ, 2002).

111. *Santia mawsoni* (Hale, 1937)
From Montamar, N of Valparaiso, to Cape Horn (LANCELLOTTI & VASQUEZ, 2002).

**VALVIFERA Sars, 1882**

Arcturidae Dana, 1849

112. *Astacilla diomedea* Benedict, 1898
Strait of Magellan, Chile (RICHARDSON, 1909).

113. *Litarciturus americanus* (Beddard, 1886)
Strait of Magellan, Chile (MENZIES, 1962a).

114. *Neastacilla magellanica* (Ohlin, 1901)
Strait of Magellan, Chile; doubtful record in the Beagle Channel (OHLIN, 1901; MENZIES, 1962a; BRANDT et al., 1999).

115. *Rectarcturus kophameli* (Ohlin, 1901)
Strait of Magellan, Chile (LORENTI & MARIANI, 1997). W-ATL

Strait of Magellan, Chile (LORENTI & MARIANI, 1997). W-ATL

117. *Xenarcturus spinulosus* Sheppard, 1957
Strait of Magellan, Chile (LORENTI & MARIANI, 1997). W-ATL

**Chaetiliidae Dana, 1849**

118. *Chaetilia paucidentis* Menzies, 1962
From Montamar, northern Valparaiso to Chiloe Island, Chile (MENZIES, 1962a; JARAMILLO, 1982).

119. *Macrochiridothea kruimeli* Nierstrasz, 1918
Strait of Magellan, Chile (MENZIES, 1962a). ANT.

120. *Macrochiridothea mehuinensis* Jaramillo, 1977
Southern Chile (JARAMILLO, 1982).

121. *Macrochiridothea michaelseni* Ohlin, 1901
Strait of Magellan, Chile (MENZIES, 1962a).

Southern Chile (MENZIES, 1962a; JARAMILLO, 1982).

123. *Macrochiridothea stebbingi* Ohlin, 1901
Gulf of Ancud from Strait of Magellan and Beagle Channel, Chile (MENZIES, 1962a; LORENTI & MARIANI, 1997; BRANDT et al, 1999). W-ATL

**Holognathidae Thomson, 1904**

Known only from Tocopilla, Chile (MENZIES, 1962a).

125. *Cleantis gayi* Miers, 1881
Coast of Chile (KENSLEY & SCHOTTE, 2006).

126. *Cleantis linearis* Dana, 1849
Central Chile (MENZIES, 1962a).

**Idoteidae Samouelle, 1819**

127. *Edotia chilensis* (Gay, 1849)
Coast of Chile (KENSLEY & SCHOTTE, 2006).

Northern Valparaiso south to Strait of Magellan, Chile (MENZIES, 1962a).

129. *Edotia doellojuradoi* Giambiagi, 1922
Coast of Chile (KENSLEY & SCHOTTE, 2006). W-ATL.

130. *Edotia magallanica* Cunningham, 1871
From Santiago Bay south to Strait of Magellan, Chile (MENZIES, 1962a; JARAMILLO, et al., 1981).

Gulf of Ancud, Chile (MENZIES, 1962a).

132. *Edotia tuberculata* Guérin-Méneville, 1843
Strait of Magellan, Chile (MENZIES, 1962a). W-ATL.

133. *Idotea metallica* Bosc, 1802
Coast of California, USA, and Gulf of California, Mexico and from Montevideo to Beagle Channel, Chile (RICHARDSON, 1905; SCHULTZ, 1969; BRANDT et al., 1999; BRUSCA et al., 2006). COS.

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Embryology of decapod crustaceans III: Embryonic development of *Eurypanopeus canalensis* Abele & Kim, 1989, and *Panopeus chilensis* H. Milne Edwards & Lucas, 1844 (Decapoda, Brachyura, Panopeidae)

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**ABSTRACT.** Embryonic development in two coastal lagoon crabs, *Eurypanopeus canalensis* and *Panopeus chilensis*, is described. Embryos were sampled and illustrated at intervals of 48 hours. The complete embryonic development at 26-28°C was similar (13 ± 1 day) for both species. Growth was synchronous and appendages were formed during the same periods for the two species. Differences were observed in eye size and cephalothorax-abdomen proportions. The egg-volume increased significantly, three differences statistically in volume were detected for *E. canalensis* and two for *P. chilensis*, especially at the two last stages of development.

**KEY WORDS:** Brachyura, Panopeidae, Embryology, Coastal Lagoons.

**INTRODUCTION**

Most knowledge associated with brachyuran crabs of the west coast of Mexico concerns geographic distribution and habitat. Few autecological studies are available and, although many species are easy to recognize in the field, there has been little study on their biology. A few species of brachyuran crabs (e.g., *Callinectes* spp.; *Cancer jonngarthi* Carvacho, 1989; *Maiopsis panamensis* Faxon, 1893) are important fishery resources in the area, but their biology is poorly documented (Hendrickx, 1984; 1995).

Topics related to the ontogeny of eastern tropical Pacific brachyuran species have received little attention (García-Guerrero & Hendrickx, 2004). Brachyurans show great diversity in reproductive strategies, especially in egg number and size (Anderson, 1982; Hines, 1982). Females incubate eggs attached to the abdomen, from spawning to hatching (Anderson, 1982). The incubation period depends on species (Nagao et al., 1999) and temperature (García-Guerrero et al., 2003a). Most studies of crab embryology are recent and deal with species of only a few families (see Nagao et al., 1999; Bas & Spivak, 2000; Yamaguchi, 2001; Pinheiro & Hattori, 2003).

Coastal lagoons associated with mangrove forests in the eastern tropical Pacific are highly suitable habitats for permanent populations of panopeid crab genera such as *Panopeus*, *Eurypanopeus* and *Hexapanteus*. Some of these crabs are associated with the red mangrove aerial roots, oyster and mussels banks, and any hard substrate (e.g., pier, ropes) introduced in these ecosystems. There is, however, no information available on the embryology of these crabs even though most species are well known, generally abundant and easy to collect (Hendrickx, 1984; Salgado-Barragán & Hendrickx, 2002). In the Western Atlantic, more attention has been allocated to larval development of panopeid and other crabs and, to some extent, to their embryonic development (Martin et al., 1985; Pinheiro & Hattori, 2003). Because it represents the first step in the life cycle and probably is one of the most sensitive to external factors, study which describes the embryonic development of species associated to critical ecosystems (i.e., ecosystems with strong ecological stress) is considered important to their biology.

Among the crabs associated with mangrove forests of the SE Gulf of California, *Eurypanopeus canalensis* Abele & Kim, 1989 and *Panopeus chilensis* H. Milne Edwards & Lucas, 1844 were studied in order to describe and compare their embryonic events.

**MATERIAL AND METHODS**

A group of adult males and females of *P. chilensis* and of *E. canalensis* was captured in August 2003 associated with *Rhizophora mangle* prop roots in the Estero de Urias, SE Gulf of California, Mexico. Specimens were transported to the laboratory and placed separately in plastic aquaria (LxWxH= 60x40x40). Aquaria were filled with filtered marine water, maintained with constant aeration and provided with bricks with holes as shelter. Photoperiod was kept 12 :12 h (light :dark). Water was maintained at room temperature (26 to 28°C) and at salinity of 35-36 ‰. Commercial shrimp pellets were offered every other day as food. During the first two weeks of captivity,
three ovigerous females of *P. chilensis* and five of *E. canalensis* lay eggs. Each female was immediately transferred to an individual three-liter glass jar with continuously aerated sea water. A sample of at least 10 eggs was removed from each female every 48 hours beginning on the day they were first detected as ovigerous. Eggs were placed into depression slides in seawater and examined *in vivo* to describe the morphology with an optical microscope (25x and 40x magnification). Embryo morphology, growth and yolk-tissues proportion were observed for each sample, in lateral and frontal views. The colouration pattern was also noted. Development was divided into periods 48 hours from ovoposition to hatching in agreement with GARCÍA-GUERRERO & Hendrickx (2004) who recommended the use of the term ‘periods’ instead of ‘stages’ or ‘steps’ in order to reflect the nature of the embryonic development, which is a continuum. Illustrations were made with the aid of a camera lucida, as a composite of observations made on every egg in each sample. Smallest and largest diameters of the eggs were measured to ± 0.01 mm with ocular micrometer. Egg volume was calculated as a perfect sphere. Diameter was considered as the average between the largest and the smallest width of all measured eggs within a particular period. Accumulated increase of egg volume was calculated by using average volumes observed at the end of each period. A one-way ANOVA test (*p*>0.05) was applied to egg volume to detect possible significant differences over the course of development.

**RESULTS**

Average diameter, volume and accumulated increase of egg volume are presented in Table 1. The complete embryonic development of both species lasted 13±1 days and included eight embryonic periods from egg extrusion to hatching. In *E. canalensis* major volume increase was observed during period 8, while in *P. chilensis* major volume increases were observed in periods 7 and 8; overall, accumulated increase at the end of the development was 101.4% for *E. canalensis* and 45.8% for *P. chilensis*, respectively (Table 1). Although in both species an increase in average egg volume from one period to another is evident, the one-way ANOVA followed by post hoc Tukey test, revealed that egg volume generally increased significantly only when several successive periods are clustered. Three statistically different size increases were detected in *E. canalensis* (i.e., total increase during periods 1-4, 5-7 and during period 8 were different, *F*=583.6, *p*=0.001) and two in *P. chilensis* (i.e., size increase during periods 1-6 and 7-8 were different, *F*=4021.1; *p*=0.002) (Table 1).

Descriptions and illustrations are presented for each 48-hour period of development (Figs 1-3).

<table>
<thead>
<tr>
<th>Period</th>
<th>Diameter (µm)</th>
<th>Volume [µm³ x 10⁶]</th>
<th>Accumulated growth [%]</th>
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<tr>
<td>1</td>
<td>300±11.1</td>
<td>14.1±4.5</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>298±21.7</td>
<td>14.0±7.0</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>309±14.4</td>
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<td>4</td>
<td>321±17.7</td>
<td>17.3±9.9</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>333±9.4</td>
<td>19.3±5.8</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>337±14.2</td>
<td>20.0±8.0</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>349±11.7</td>
<td>22.2±7.6</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>380±12.4</td>
<td>28.7±0.9</td>
<td>-</td>
</tr>
</tbody>
</table>

**Eurypanopeus canalensis**

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** TABLE 1 **

**Eurypanopeus canalensis** and **Panopeus chilensis** during periods of embryonic development. Periods were arbitrarily designated as 48-hours intervals over the time-course of development. From ANOVA, different letters = statistically significant differences (*p*<0.05).

**Eurypanopeus canalensis**

Period 1. Recently laid eggs (Fig. 1A). The eggs are macrocelith-centrolecithal and spherical, filled with a uniform purple yolk mass. No tissue evidences.

Period 2. Day 2 (Fig. 1B). The yolk is fragmented into small oily droplets. Yolk colour is lighter than in period 1. A cluster of presumptive primordial cells begins to form as a patch located in ventrolateral position.

Period 3. Day 4 (Fig. 2A). The cluster of primordial cells has differentiated into major embryonic structures, placed in ventral position (ocular, antennule-antenna, maxillule-maxilla, maxilliped and thoracic-abdominal).

Period 4. Day 6 (Fig. 2B). Abdominal and cephalothoracic primordia have increased in size and are now separated. Antennule-antenna, maxillule-maxilla and maxillipeds are now tiny buds rising below and back to the optical primordial structures. Tissues and yolk appear transparent.

Period 5. Day 8 (Fig. 2C). Antennule-antenna, maxillule-maxilla and maxilliped primordia have grown. Abdomen is incompletely divided into segments (metameres). Ocular processes are developing a slightly darker oval-shaped core (retina) in the fore portion of the embryo.

Period 6. Day 10 (Fig. 2D). Depletion of yolk is substantial. Cephalothorax is now formed, abdomen is enlarged and its segmentation is almost complete. Eyes are enlarged, differentiated in cornea and retina, and densely pigmented. All appendages are segmented, enlarged. The heart beats slowly. Contractions of thoracic and abdominal processes are observed.

Period 7. Day 12 (Fig. 2E). Embryo occupies all the space within the egg. Yolk droplets are still stored dorsal to cephalothorax, which is entirely visible. Abdomen is
fully segmented. Telson is formed and bears chromatophores, also present on the abdomen. The heart has grown and beats vigorously.

Period 8. Day 13±1 (Fig. 2F). A few small yolk droplets remain dorsally on the carapace. The abdomen shows a pair of chromatophores on each segment. Maxillipeds are complete with long setae. The embryo is about to hatch.

**Panopeus chilensis**

Period 1. Recently laid eggs (Fig. 1A). The eggs are macrolecithal-centrolecithal and spherical, filled with a uniform brown yolk mass. No tissue evidences.

Period 2. Day 2 (Fig. 1B). The yolk has fragmented into small oily droplets. Colour is lighter than in period 1. A cluster of presumptive primordial cells begins to form as a patch located in ventrolateral position.

Period 3. Day 4 (Fig. 3A). The cluster has differentiated into main transparent embryo structures in ventral position, separated by slits (ocular, antennule-antenna, maxillule-maxilla, maxilliped and thoracic-abdominal).

Period 4. Day 6 (Fig. 3B). Abdominal and cephalothoracic primordia have increased in size and are now separated. Antennule-antenna, maxillule-maxilla and maxillipeds are now tiny buds rising below and back to the optical primordial structures. Tissues and yolk appear transparent.

Period 5. Day 8 (Fig. 3C). Antennule-antenna, maxillule-maxilla and maxilliped primordia have grown. Abdomen is divided incompletely into segments (metameres). Ocular lobes are oval-shaped and have developed a dark core (retina).

Period 6. Day 10 (Fig. 3D). Consumption of yolk is noticeable, exposing the cephalothorax. Abdomen has grown and its segmentation is almost complete. Heartbeat and contractions of the embryo are registered. Eyes fully pigmented, differentiated in cornea and retina. Chromatophores present on abdominal somites.

Period 7. Day 12 (Fig. 3E). Embryo occupies all the space within the egg. Yolk droplets are still stored dorsal to cephalothorax, which is entirely visible. Abdomen is fully segmented. Chromatophores have appeared on abdomen and telson. Eyes have grown and are triangle-shaped. The heart is beating continuously. Cephalic appendages and telson bear setae.

Period 8. Day 13±1 (Fig. 3F). Few traces of yolk in some embryos. Maxillipeds are well developed. The embryo is about to hatch.
DISCUSSION

When the two species included in the present work are compared, developmental events were similar, particularly during the first and second periods. Embryos of both species form their appendages during equivalent periods, approximately halfway in the developmental process in terms of ontogenetic progression, and after major primordial structures have differentiated. Growth and complexity of abdominal and ocular processes are also equivalent.

In both species, eye formation clearly follows the pattern described by Cronin & Jinks (2001) for crustacean vision ontogeny. In both species, major differentiation events occur during the first week whilst growth of structures and segments prevail during the second week. Primordial cells are more evident in the eggs of E. canalensis. In terminal periods, the cephalothorax-abdomen proportion, the shape of the eyes and the pattern of chromatophores formation are slightly different between both species. Furthermore, non-brachyuran decapods follow very similar larval succession of events, as previously observed by Hel- 

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Furthermore, non-brachyuran decapods follow very similar larval succession of events, as previously observed by Hel- 

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SHORT NOTES

A new record of Placozoa from the Mediterranean Sea

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KEY WORDS. placozoans, Spanish Mediterranean coasts, biogeography, diet

Trichoplax adhaerens is the only recognized species from the phylum Placozoa described up to now. It was discovered in 1883 by Schulze in a seawater aquarium at the Graz Zoological Institute in Austria. The water in the aquarium came from the Adriatic Sea (Italy). The interest sparked by finding this organism and the possibility of clarifying the origin of Metazoa flagged shortly thereafter when a work published by Krumbach in 1907 considered it to be a modified planula larva of a hydromedusa, and thus, the discovery lost its relevance (Grell & López-Ochoterena, 1988) (1). Subsequently, it was rediscovered and meticulously studied by Grell, 1973 (2); 1982 (3) and Grell & Ruthmann, 1991 (4), among others, with material from Red Sea coral reef microfauna. Recently, Voigt et al., 2004 (5) showed that the phylum Placozoa is significantly more diverse than previously thought on the genetic level and that its species richness is still to be determined. Also, they report two divergent lineages of placozoans from the Mediterranean Sea. At this time, the phylum is considered essential to understand the origin of bilaterian Metazoa (Collins, 1998) (6).

Regarding the biogeography, placozoans have been cited in seawater puddles and aquariums with water from different parts of the world: the Bermudas (North Atlantic Coasts), the Mexican Caribbean Sea, Eastern Australia -the Great Barrier Reef-, Guam (Mariana Islands -Philippine Sea-), Japan, Hawaii and Western Samoa (Polynesia -Pacific Ocean-), Palau (Andaman Sea), Papua New Guinea, the Red Sea and Vietnam. On all occasions, the individuals were found in tropical and subtropical locations. Here we report the third finding of placozoans from Mediterranean Sea waters and the first citing from the Spanish Mediterranean waters of the Granada coast (Spain).

Our observation of placozoans on walls of the aquarium at the University of Granada’s Marine Zoology investigation area in September 2003 was fortuitous, as in most cases of reported findings. This 250 litre-capacity aquarium held water and sand from the Almuñecar coast (Granada) sampled in October 2002. It is used to maintain the different animals and algae included in the water and sand samples for teaching purposes and research. Thus, the water, sand and the organisms in the aquarium have never come from anywhere other than the coast of Granada and an introduction of the placozoans from other sources can be excluded. A film of diatom algae from the genera Cocconeis, Amphora and Achnanthes had formed a deposit on the aquarium walls, with the diatom Cocconeis populations especially abundant. Placozoans must feed on diatoms from the cited genera. Individuals probably feeding on protozoa associated with a lay of opistobranchs were also found in the same aquarium. It is known that placozoans can feed on protozoa and even bigger organisms (Nielsen, 1995 (7); Grell, 1983 (8)).

A visual count found several hundred individuals, which appeared as small off-white dots, mostly moving around very slowly. In some areas, the individuals were arranged in closer formations, while in others they were more dispersed. Microscopic preparations were made of different individuals extracted and prepared ‘in vivo’ for drawing with the help of a camera lucida combined with an optical microscope to obtain the measurements. It was possible to distinguish between bigger and smaller individuals. Both showed amoeba-like movements. When flattened out, the bigger individuals had a diameter between 1.5 and 2.5 mm and the smaller individuals between 300 and 800 mm. Photographs of different individuals of the placozoans appear in Fig. 1.

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Fig. 1. – (a-d). Photographs of four different individuals from placozoans: a,b,c: bigger individuals and d: smaller individual.

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Egg dimensions variation in relation to the laying order in Black Redstart (*Phoenicurus ochruros* Gmelin, 1774) in NW Croatia

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Egg size dimensions are generally held to be important indices of egg quality and correlate with chick survival in many bird species (e.g. Murton, 1974; Amat et al., 2001) (1) (2). Birds possess several mechanisms by which they can adjust the magnitude and pattern of their breeding effort to environmental conditions and their own breeding condition (Slagsvold et al., 1984) (3). In birds, egg size varies with laying date (e.g. Hill, 1984) (4), female age (e.g. Desrochers & McGrath, 1993) (5), year (e.g. Perrins, 1969) (6), seasonal variations (e.g. Coulson, 1963) (7), laying order (e.g. Murphy, 1994) (8), female condition (e.g. Hörak et al., 1995) (9) and other factors. Different patterns of egg size versus laying order have been recognized, with egg size decreasing (e.g. Heeb, 1994; Eriksstad et al., 1998) (10) (11), increasing with each sequence (Häftorn, 1986; Enêmar & Arheimer, 1999) (12) (13) or unrelated (e.g. Mitrus & Rogala, 2001; Hagitai et al., 2005) (14) (15). Slagsvold et al. (1984) (3) analysed intra-clutch variation in egg size in 67 bird species and identified two strategies : birds which lay relatively larger final eggs are adopting the ‘brood survival strategy’ (the last nestling is capable of rivalry with its older siblings), whereas birds which lay relatively small final eggs are adjusting to the ‘brood reduction strategy’ (the last nestling will be sacrificed in the event of food shortage).

This study has two tasks. First, to investigate the influence of laying order on egg dimensions and second, to calculate the deviation of the final egg from mean referred here as %D (according to Slagsvold et al., 1984) (3).

Research took place in Hrvatsko Zagorje region (45º58’ – 46º10’N, 15º50’ – 16º08’E) in NW Croatia, in 2002 and 2004. Nests were visited daily during laying period. Eggs were marked with pens. All eggs were measured to the nearest 0.01 mm (maximum length and maximum breadth). Egg volume was calculated from the formula \( V = 0.51 \times L \times B^2 \), where \( L \) is maximum length and \( B \) is maximum egg breadth (Hoyt, 1979) (16). Egg shape index (ES) was calculated using the formula \( ES = \frac{LENGTH}{BREADTH} \). The relative size of the final egg laid (%D) was calculated according to Slagsvold et al. (1984) (3) as the percentage deviation from the mean egg size of all the eggs in the clutch. Nests with abandoned clutches were excluded from analysis. As different internal and external factors can obscure a potential pattern of variation in egg size in relation to the laying sequence (Baňura & Ziešinski, 1995) (17), this analysis includes only first clutches with 5 eggs where first eggs were laid within three-days period (from 13 to 15 April 2002 and from 19 to 21 April 2004). These two periods were in the middle of breeding season and were chose because most birds started their breeding in this period. The five-egg clutch is the dominant clutch size of the first clutch in the study area (Dolenec, 1999) (18). Statistical analyses were performed using the SPSS 12.0 statistical package.

A total of 125 Black Redstart eggs from 25 clutches were used in the analysis. Basic egg characteristics are presented in Table 1. Both in 2002 (11 clutches) and 2004 (14 clutches) egg volume sequences were significantly concordant (Kendall’s coefficient of concordance : 2002, \( W = 0.326; \text{df} = 4; p = 0.006 \); 2004, \( W = 0.282; \text{df} = 4; p = 0.003 \)) and correlations between egg volume and laying order were statistically significant (Pearson : 2002, \( r = -0.039; p = 0.779 \); 2004, \( r = 0.338; p = 0.004 \)). By contrast, analyses for the egg shape index revealed statistically non-significant results (Kendall’s coefficient of concordance : 2002, \( W = 0.326; \text{df} = 4; p = 0.006 \); 2004, \( W = 0.737; \text{df} = 2.0; p = 0.025 \)). For clutches with 5 eggs values of %D in 2002 and 2004 was 5.63 and 6.12 resp. To my knowledge, no other intraclutch egg dimensions (laying order and/or values of %D) data of importance have been published for this bird species. Following the arguments of Slagsvold et al., this Black Redstarts population therefore would adopt a ‘brood survival strategy’ where females allocate greater resources in the final eggs of the clutch which have a high reproductive value. This is consistent with the view put forward by Howe (1976) (19) that larger egg size (weight or volume) represents parental effort to increase the survival chances of the late hatched young. A life-history framework adds an important dimension to the study of ‘brood strategy’, but also makes the task for field workers more complex (Mock & Forbes, 1994) (20).

REFERENCES


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**TABLE 1**

Egg dimensions of Black Redstart in 2002 and 2004. SD = standard deviation, n = number of clutches

<table>
<thead>
<tr>
<th>Year</th>
<th>Length, mm</th>
<th>Breadth, mm</th>
<th>Volume, mm³</th>
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<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
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<tr>
<td>2002</td>
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