Who's who in *Magelona:* Phylogenetic hypotheses under Magelonidae Cunningham & Ramage, 1888 (Annelida: Polychaeta)

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Known as shovel head worms, members of Magelonidae comprise a group of polychaetes readily recognised by the uniquely shaped, dorso-ventrally flattened prostomium and paired ventro-laterally inserted papillated palps. The present study is the first published account of inferences of phylogenetic hypotheses within Magelonidae. Members of 72 species of *Magelona* and two species of *Octomagelona* were included, with outgroups including members of one species of Chaetopteridae and four of Spionidae. The phylogenetic inferences were performed to causally account for 176 characters distributed among 79 subjects, and produced 2,417,600 cladograms, each with 404 steps. A formal definition of Magelonidae is provided, represented by a composite phylogenetic hypothesis explaining seven synapomorphies: shovel-shaped prostomium, prostomial ridges, absence of nuchal organs, ventral insertion of palps and their papillation, presence of a burrowing organ, and unique body regionation. *Octomagelona* is synonymised with *Magelona* due to the latter being paraphyletic relative to the former. The consequence is that Magelonidae is monotypic, such that *Magelona* cannot be formally defined as associated with any phylogenetic hypotheses. As such, the latter name is an empirically empty placeholder, but because of the binomial name requirement mandated by the International Code of Zoological Nomenclature, the definition is identical to that of Magelonidae. Several key features for future descriptions are suggested: prostomial dimensions, presence/absence of prostomial horns, morphology of anterior lamellae, presence/absence of specialised chaetae, and lateral abdominal pouches. Additionally, great care must be taken to fully describe and illustrate all thoracic chaetigers in descriptions.

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ABSTRACT

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recognised by the uniquely shaped, dorso-ventrally flattened prostomium and paired ventro-

laterally inserted papillated palps. The present study is the first published account of inferences

of phylogenetic hypotheses within Magelonidae. Members of 72 species of *Magelona* and two

species of *Octomagelona* were included, with outgroups including members of one species of

Chaetopteridae and four of Spionidae. The phylogenetic inferences were performed to causally

account for 176 characters distributed among 79 subjects, and produced 2,417,600 cladograms,

each with 404 steps. A formal definition of Magelonidae is provided, represented by a composite

phylogenetic hypothesis explaining seven synapomorphies: shovel-shaped prostomium,

prostomial ridges, absence of nuchal organs, ventral insertion of palps and their papillation,

presence of a burrowing organ, and unique body regionation. *Octomagelona* is synonymised

with *Magelona* due to the latter being paraphyletic relative to the former. The consequence is

that Magelonidae is monotypic, such that *Magelona* cannot be formally defined as associated

with any phylogenetic hypotheses. As such, the latter name is an empirically empty placeholder,

but because of the binomial name requirement mandated by the International Code of Zoological

Nomenclature, the definition is identical to that of Magelonidae. Several key features for future

descriptions are suggested: prostomial dimensions, presence/absence of prostomial horns,

morphology of anterior lamellae, presence/absence of specialised chaetae, and lateral abdominal

pouches. Additionally, great care must be taken to fully describe and illustrate all thoracic

chaetigers in descriptions.

44 INTRODUCTION

45 *Felix qui potuit rerum cognoscere causas* – Virgil, *Georgics, Vol. 1, Books I–II*

46 The Magelonidae, known commonly as the shovel head worms, gain their name from their

47 uniquely flattened, spade-shaped prostomia used in burrowing through soft sediments. They

48 comprise a relatively small family of marine annelids, with members distributed among 77

49 species, although many more individuals to which new species hypotheses will refer are likely.

50 Magelonids are generally found at depths of less than 100 m, although members of deeper water

51 species at depths of 1000–4000 m have been recorded (Hartman, 1971; Aguirrezabalaga, Ceberio

52 & Fiege, 2001). They predominately burrow through sands and muds, although members of

53 several tubicolous species are known (Mills & Mortimer, 2019; Mortimer, 2019). Individuals

54 feed using two slender palps (Mortimer & Mackie, 2014), which are unique amongst polychaetes

55 in being papillated and ventrally inserted.

56 The unusual morphology of magelonids has often led to difficulties in relating them to

57 other annelid groups. Johnston (1865), puzzled by their peculiar external form, placed them at

58 the end of his catalogue, under the family Maeadae, based on the new genus and species *Maea*

59 *mirabilis*. Later, McIntosh (1877) included magelonids within the Spionidae, after synonymising

60 *Maea* Johnston, 1865 with *Magelona* Müller, 1858. Whilst Cunningham & Ramage (1888)

61 erected the family Magelonidae stating "We have formed a special family for it, as it cannot be

62 admitted into the Spionidae, with which it is most nearly allied, or into any other family."

63 McIntosh, who published extensively on magelonid morphology (McIntosh, 1877, 1878, 1879,

64 1911), suggested similarities with spioniforms such as members of *Prionospio* Malmgren, 1867,

65 and *Heterospio* Ehlers, 1874, but also with the chaetopterid *Spiochaetopterus* Sars, 1853. He

66 additionally noted that the way the "proboscis" (cf. **Character descriptions** below regarding

67   terminology) operated and the structure of the "snout and circulatory organs" are features *sui*

68   *generis*. However, the placement of magelonids with spioniform polychaetes has continued until

69   semi-recently. The latest studies have proposed placement alongside the Chaetopteridae,

70   Sipuncula, and Oweniidae (Struck et al., 2015; Weigert et al., 2014; Helm et al., 2018), or as

71   sister taxon of all other annelids along with the Oweniidae (Palaeoannelida) (Weigert et al.,

72   2016). These phylogenetic considerations will be discussed more fully later in this paper.

73   Whilst the systematic position of the family may have received some attention,

74   phylogenetic relationships within have received far less. Perhaps the relatively uniform bodies of

75   magelonids have been a contributing factor. Currently the family contains two genera: the type

76   genus *Magelona* F. Müller, 1858, and the monotypic *Octomagelona* Aguirrezabalaga, Ceberio &

77   Fiege, 2001, differentiated by the number of thoracic chaetigers. All previously introduced

78   generic names for the group have been synonymised (*Maea* Johnston, 1865, *Rhynophylla*

79   Carrington, 1865, *Meredithia* Hernández-Alcántara & Solís-Weiss, 2000). Brasil (2003) inferred

80   phylogenetic hypotheses among members of the family based on external morphological

81   characters, confirming the monophyletic status of the group. Her analysis concluded that both

82   *Octomagelona* and *Meredithia* were paraphyletic, but no further conclusions could be made. The

83   present study aims to expand the unpublished analysis performed by Brasil (2003) to include

84   additional taxa and characters.

MATERIAL AND METHODS

Methodological considerations

88   What is and is not contained in the present study is based on several interrelated principles that

89   initially might not appear consistent with some of today's thinking regarding biological

90   systematics. These principles are not of our making, but rather are firmly established

91   perspectives within philosophy of science, and familiar to many fields of science beyond

92   systematics. The last several decades have witnessed systematics engaging in a growing

93   tendency toward developing insular views that are at odds with basic tenets of logic, reasoning,

94   and scientific inquiry. For these reasons, we regard it as imperative to present justifications for

95   what is and is not included in this study from a methodological perspective. The disinterested

96   reader can ignore this section without damage, but the information provided does offer a useful

97   summary for those more inclined toward a much-needed critical thinking in systematics.

98   *The goal of scientific inquiry*

99   As systematics is a field of science and subfield of evolutionary biology, it should cohere with

100   the acknowledged goal of scientific inquiry. That goal is to not only describe phenomena but also

101   pursue causal understanding of what is encountered (Hanson, 1958; Hempel, 1965; Rescher,

102   1970; Popper, 1983, 1992; Salmon, 1984b; Van Fraassen, 1990; Strahler, 1992; Mahner &

103   Bunge, 1997; Hausman, 1998; Thagard, 2004; Nola & Sankey, 2007; de Regt, Leonelli & Eiger,

104   2009; Hoyningen-Huene, 2013; Potochnik, 2017, 2020; Anjum & Mumford, 2018; Currie,

105   2018). In the context of systematics that pursuit includes describing the characteristics of

106   organisms, in the form of differentially shared characters, as well as exploring possible past

107   causal events that account for those characters, either as matters of proximate and/or ultimate

108   causes *sensu* Mayr (1961, 1993; Fitzhugh, 2012, 2016a). As aptly expressed by Uller & Laland

109   (2019: 1), "Scientific inference typically relies on establishing causation. This is also the case in

110   evolutionary biology, a discipline charged with providing historical accounts of the properties of

111   living things, as well as an understanding of the processes that explain the origin of those

112   properties."

113   Whilst it is fashionable to speak of "*the* phylogeny" of a group of organisms, this is

114   something of a misnomer. Inferring phylogenetic hypotheses from a set of observed character

115   data only achieves the objective of explaining those data, with implicit acknowledgement that no

116   phylogenetic inference can exhaustively account for all potentially observable characters of

117   organisms. Phrases of the form "*the* phylogeny of *X*" incorrectly connote that a final solution is

118   being offered, when in fact such would be impossible. Emphasising the term phylogeny has the

119   undesirable consequence of suggesting that this is the objective of systematics, thus

120   overshadowing the pursuit of causes, which is the real aim of scientific inquiry. The same

121   critique applies to the commonly used phrase "molecular phylogeny." There can be no

122   "phylogeny" of molecules, just as there can be no separate phylogenies for any arbitrary

123   subdivisions of classes of characters that are in need of being explained.

124   The causal objective in systematics is the arena within which taxa are considered. Taxa are best

125   regarded not as either class constructs, mere groupings, things, entities, or ontological

126   individuals, but rather as the variety of explanatory hypotheses routinely and purposely inferred.

127   These hypotheses include species and phylogenetic hypotheses, albeit there are other classes of

128   explanatory hypotheses that in their own right deserve to be called taxa (Fig. 1; cf. Hennig, 1966:

129   fig. 6) given that they as well are inferred causal accounts (Fitzhugh, 2012, 2016a; see also

130   Fitzhugh, 2005b, 2006a, 2008a, 2009, 2013, 2015). Consider for instance the phylogenetic and

131   specific "relations" shown in Fig. 1. Each clearly illustrates that individuals along the top of the

132   diagram are what exist in the present, and lines connecting to lower individuals indicate past

133   tokogenetic events. This diagram also implies past, albeit quite vague, causes such as novel

134   character origin and fixation events among individuals in populations, as well as population

135   splitting events. To say Fig. 1 shows several "lineages" is just an imprecise way of referring to

136   the totality of past causal events that account for what are observed of the organisms in the

137   present. A further consequence is that taxa are neither described, discovered, nor delimited; they

138   are inferred as reactions to what we observe of the properties of organisms. What *are* described

139   are individuals at specific moments in their life history (Fitzhugh, 2012, 2016a, see also

140   Fitzhugh, 2008a, 2009, 2013, 2015; operational examples include Fitzhugh, 2010b; Nogueira,

141   Fitzhugh & Rossi, 2010; Nogueira, Fitzhugh & Hutchings, 2013; Nogueira et al., 2017, 2018;

142   Fitzhugh et al., 2015); what Hennig (1966) termed semaphoronts (Fig. 1; cf. Hennig, 1966: fig.

143   6). The interplay between the descriptive and the explanatory will become apparent later (cf.

144   ***Phylogenetic inference = abduction***).

145   The present study seeks to infer taxa in the form of phylogenetic hypotheses, which are

146   subsumed under the more inclusive (composite) phylogenetic hypothesis formally called

147   Magelonidae. We acknowledge that species hypotheses have been previously and separately

148   inferred and are not the focus of this paper. Whilst this distinction between phylogenetic and

149   specific hypotheses has been the typical and inferentially appropriate approach in systematics,

150   exceptions can be found among some publications (e.g., Nygren et al., 2018; Shimabukuro et al.,

151   2019; Radashevsky et al., 2020), in which species hypotheses are simultaneously inferred with

152   phylogenetic hypotheses that only causally account for sequence data, after which morphological

153   characters are incorrectly introduced in a post hoc manner. Notwithstanding the fact that the

154   requirement of total evidence (RTE; Fitzhugh, 2006b; see ***Sequence data and explanatory***

155   ***hypotheses***, below) is violated, such inferences have questionable merits for the fact that

156   explaining shared nucleotides or amino acids requires, at a minimum, discriminating between

157   causes such as genetic drift, and selection via downward causation (see ***Sequence data and***

158   ***explanatory hypotheses***, below). The nature of phylogenetics algorithms is such that they are

159   agnostic as to detailed causal parameters, requiring that one must give specific consideration to

160   drift or selection, which can determine whether or not sequence data can be directly explained

161   via phylogenetic inferences. This is an issue that has been largely ignored in discussions of

162   phylogenetic inference (Fitzhugh, 2016b). Once again, the objective of inferring these different

163   classes of hypotheses is to pursue causal understanding of the properties of organisms.

164   ***Characters and observation statements***

165   Scientific inquiry is in reaction to the objects and events we perceive in the universe.

166   Conceptualising and then communicating our perceptions require accurate conveyance of

167   observation statements. Systematics has had a long tradition of speaking of organismal

168   observations in terms of characters and states (Sokal & Sneath, 1963; Sneath & Sokal, 1973).

169   Fitzhugh (2006c) remarked on the fact that the character/state distinction as well as other, similar

170   perspectives in systematics are not accurate representations of observation statements, especially

171   compared to the established views in epistemology, where observation statements are presented

172   as relations between subjects and predicates (Strawson, 1971; Alston, 1993; Audi, 1998).

173   Consider for instance, the statement, "These chaetae are bidentate." The terms chaetae and

174   bidentate do not refer to character and state, respectively. That one can observe objects they call

175   chaetae is because of the properties or characters of those objects. Instead of character and state,

176   the observation statement refers to the *subject* chaetae, and the *predicate* bidentate is applied to

177   that subject, reflecting a particular property or character perceived of the object as subject

178   (Hanson, 1958; Mahner & Bunge, 1997; Strawson, 1971; Gracia, 1988; Armstrong, 1997).

179   Whilst observation statements of organisms are often of intrinsic properties, there also are

180   relational or extrinsic characters (Findlay, 1936; Sider, 1996; Armstrong, 1997; Francescotti,

181   2014; Allen, 2016). A common example in systematics involves sequence data, e.g., "Individuals

182   to which species hypothesis *X-us x-us* refer have [subject] nucleotide G at [predicate] position

183   546." Being in a particular position is relative to other objects. The character/state distinction

184   ignores this relational aspect, leading to nonsensical characterisations, such as, "…if nucleotide

185   A is observed to occur at position 139 in a sequence, 'position 139' is the character [sic] and 'A'

186   is the state assigned to that character" (Swofford et al., 1996: 412). Obviously, a position cannot

187   be a character of an object since the position is dependent upon other objects.

188   The traditional emphasis on "character coding" leading to compilations of observations in

189   the form of the data matrix has treated columns as "characters" and each cell as a "state."

190   Fitzhugh (2006c: fig. 1) pointed out, however, that if observations are to be accurately implied

191   by entries in a matrix then each cell represents a complete observation statement of subject-

192   predicate relations, such that each column denotes each subject (Fig. 2A). This also

193   accommodates relational characters (Fitzhugh, 2016b). But with the emphasis on causal inquiry

194   in systematics, a data matrix is not only a codified representation of observation statements. The

195   matrix must also imply the why-questions that inquiry seeks to answer in the form of explanatory

196   hypotheses known as taxa. This necessitates knowing the formal structure of those questions and

197   how they, like observation statements, are implied by the matrix. This will be addressed next.

198   ***Basis for phylogenetic inference: why-questions***

199   The inferences of explanatory hypotheses vis-à-vis taxa do not appear *ex nihilo*. As a significant

200   role of scientific inquiry is the pursuit of causal understanding, there is a vital conceptual link

201   between our observations and explanatory hypotheses. That link exists through the implicit or

202   explicit why-questions that are prompted by observations, such that the hypotheses we infer are

203   intended as answers to those questions. The formal structure of why-questions has relevance to

204   systematics for the fact that those questions are implicitly present in a character data matrix

205   provided to a computer algorithm that infers phylogenetic hypotheses (Fitzhugh, 2006c, 2016b).

206   Whilst we tend to think of why-questions as having the form, "Why (is) *q* (the case)?,"

207   such a structure is an incomplete representation. The form of why-questions is instead what is

208   often referred to as contrastive, "Why (is) *q* (the case) in contrast to *p*?" (Salmon, 1984b; Sober,

209   1984, 1986, 1994; Salmon, 1989; Van Fraassen, 1990; Lipton, 2004; Fitzhugh, 2006a, 2006b,

210   2006c; 2016b; Lavelle, Botterill & Lock, 2013). A contrastive why-question contains

211   observation statement *q*, the *fact* to be explained, and *p*, the *foil*, which is usually a condition

212   ordinarily expected or previously explained. Asking a why-question often occurs because we are

213   faced with a situation that is unexpected or surprising (the *fact*), and it is that element of surprise,

214   against what is expected (the *foil*), that leads to the desire for an explanation. The fact/foil

215   distinction associated with implied why-questions can be found in the data matrices used to infer

216   phylogenetic hypotheses, when "outgroup" (= *foil*) and "ingroup" (= *fact*) taxa are designated

217   (Fitzhugh, 2006c, 2016b) (Fig. 2B).

218   It is often acknowledged (Bromberger, 1966; Sober, 1986, 1988; Barnes, 1994; Marwick,

219   1999; Sintonen, 2004; Schurz, 2005) that why-questions include the presupposition that fact and

220   foil statements must be true, otherwise there is no basis for asking such questions. This also

221   follows from the common-sense notion that we assume the truth of our observation statements;

222   otherwise, scientific inquiry would not be feasible. This assumption has special implications for

223   explaining sequence data when rates of substitution are involved, which will be addressed later

224   (see ***Sequence data and explanatory hypotheses***). Explaining a fact entails also explaining the

225   foil, and while those explanations are due to separate causal events, they should be due to the

226   same type of cause (Sober, 1986; Barnes, 1994; see also Cleland, 2001, 2002, 2009, 2011, 2013;

227 Tucker, 2004, 2011; Turner, 2007; Jeffares, 2008). Designations of outgroup and ingroup

228 accommodate this requirement (Fitzhugh, 2006c).

229 ***Forms of reasoning***

230 In speaking of inferring phylogenetic hypotheses, or any other class of taxon for that matter, it is

231 necessary to acknowledge the type of reasoning used to produce those hypotheses as well as the

232 reasoning available for empirically testing them. This provides a clear basis for establishing

233 which, if any, of the currently available phylogenetic inference procedures are logically and

234 scientifically sound.

235   Three forms of reasoning are often recognised: abduction, deduction, and induction.

236 Among formal treatments of logic, abduction, if acknowledged at all, is typically subsumed

237 under induction (e.g., Kneale & Kneale, 1964; Salmon, 1967, 1984a; Copi & Cohen, 1998),

238 since the purview of logic is to identify and discriminate logically valid (deductive: true premises

239 give a true conclusion) from invalid or fallacious (inductive: true premises do not guarantee true

240 conclusions) arguments. For purposes of explicating the processes of scientific inquiry, however,

241 it is appropriate to regard abduction as distinct from induction. Operationally each form of

242 reasoning plays a respective role in different stages of inquiry, where those stages include at a

243 minimum the inferences of theories and hypotheses, and the subsequent empirical testing of

244 those propositions. The stage of inquiry most associated with systematics is abduction (Peirce,

245 1878, 1931, 1932, 1933a, 1933b, 1934, 1935, 1958a, 1958b; Hanson, 1958; Achinstein, 1970;

246 Fann, 1970; Reilly, 1970; Curd, 1980; Nickles, 1980; Thagard, 1988; Josephson & Josephson,

247 1994; Baker, 1996; Hacking, 2001; Magnani, 2001, 2009, 2017; Psillos, 2002, 2007, 2011;

248 Godfrey-Smith, 2003; Norton, 2003; Walton, 2004; Gabbay & Woods, 2005; Aliseda, 2006;

249 Schurz, 2008; Park, 2017), i.e., the inferences of hypotheses as the means of causally accounting

250 for the various differentially shared characters observed among organisms (Fitzhugh, 2005a,

251 2005b, 2006a, 2006b, 2008a, 2008b, 2008c, 2009, 2010a, 2013, 2014, 2015, 2016a, 2016b,

252 2016c, 2016d, 2021). Subsequent empirical assessments of explanatory hypotheses rely on

253 deducing predictions of expected consequences – potential test evidence – if the causal claims in

254 hypotheses are true. The act of testing, which involves determining manifestations of test

255 evidence, is inductive. The operational relations between ab-, de-, and induction received

256 extensive attention in the 19th and early 20th centuries by the polymath, Charles Sanders Peirce

257 (1835–1914) (Peirce, 1931, 1932, 1933a, 1933b, 1934, 1935, 1958a, 1958b), but full

258 appreciation of Peirce's ideas did not become realised until the second half of the 20th century

259 (Hanson, 1958; Fann, 1970; Reilly, 1970; Thagard, 1988; Josephson & Josephson, 1994;

260 Magnani, 2001, 2009, 2017; Psillos, 2002, 2011; Walton, 2004; Gabbay & Woods, 2005;

261 Aliseda, 2006; Schurz, 2008; Park, 2017). As noted by Peirce (1932: 2.106),

262   Abduction[…]is merely preparatory. It is the first step of scientific reasoning, as

263   induction is the concluding step[…] Abduction makes its start from the facts,

264   without, at the outset, having any particular [hypothesis] in view, though it is

265   motivated by the feeling that a [hypothesis] is needed to explain the surprising

266   facts. Induction makes its start from a hypothesis which seems to recommend

267   itself, without at the outset having any particular facts in view, though it feels the

268   need of facts to support the [hypothesis]. Abduction seeks a [hypothesis].

269   Induction seeks for facts.

270 The "facts" Peirce refers to in relation to abduction are the various characteristics of organisms

271 in need of explanation, whereas the "facts" associated with induction are test evidence.

272   Discussions of relations between these stages of inquiry in systematics can be found in Fitzhugh

273   (2005a, 2006a, 2006b, 2008b, 2010a, 2012, 2013, 2016a, 2016c, 2016d).

274   Whilst systematics in recent decades, especially beginning with the school of thought

275   called cladistics, has laid great emphasis on the testing of hypotheses, usually at the expense of

276   conflating testing with hypothesis inference (reviewed by Fitzhugh, 2016c, 2016d). Actual

277   testing by way of induction of the variety of hypotheses implied by cladograms is rarely

278   performed. Instead, the tendency is to merely replace results of previous abductions with new

279   abductions as new observed effects become available, which is neither an act of testing nor a

280   basis for claiming that previous hypotheses have been "defeated" or overturned. Associated with

281   confusing hypothesis inference with testing has been the misconception that character data used

282   to infer hypotheses also provide evidential support for those hypotheses, leading to false claims

283   that phylogenetic hypotheses are "robust" or "strongly supported" by the characters used to infer

284   those hypotheses. We will address this misunderstanding later (see ***Explanatory hypotheses and***

285   ***the myth of evidential support***).

286   In the context of phylogenetic hypotheses, examples of each of the stages of inquiry can

287   be represented by the following abbreviated forms, where the premises lie above the double

288   (non-deductive) or single (deductive) line, and the conclusion(s) allowed by those premises

289   below the line(s):

290   **(1)   Abduction – inferring hypotheses as answers to why-questions:**

291   • background knowledge, *b*

292   • theory(ies) *t*, such as "common ancestry"

293   • observed effects, as differentially shared characters, *e*

294   • explanatory hypotheses, e.g., cladograms, *h*

295 **(2)** **Deduction – predictions of consequences given the truth of hypotheses:**

296 • background knowledge, b

297 • theory(ies) t relevant to the observed effects

298 • specific causal conditions presented in explanatory hypothesis via **(1)**

299 • proposed conditions needed to perform test

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300 • observed effects e, originally prompting h [cf. **(1)**]

301 • *predicted test evidence, i.e., effects related as closely as possible with the*

302 *specific causal conditions of the hypothesis*

303 **(3)** **Induction – hypothesis testing:**

304 • background knowledge, b

305 • theory(ies) relevant to observed effects, t

306 • test conditions performed

307 • confirming/disconfirming evidence, e_2 [observations of predicted

308   test evidence in **(2)**, or alternative observations]

===

309 • h is confirmed/disconfirmed.

310   A useful way to think of these inferences is as reactions to particular questions. The form

311 of each question determines what type of inference is used to produce a conclusion that serves as

312 an answer. Respective questions and inferences are shown in Table 1.

313   Several points of logic need to be highlighted regarding the three types of reasoning, as

314 they are relevant to inferences of phylogenetic hypotheses (in fact all taxa, for that matter). For

315 any inference to be deemed *factually correct*, premises must be assumed to be true. A deduction

316 is *valid* only if true premises guarantee a true conclusion, which is established by particular rules

317   of logic that can be found in standard logic textbooks. Because of those rules, the content of a

318   deductive conclusion is already present in the premises, such that information in the conclusion

319   cannot go beyond what is already stated in the premises (Salmon, 1984a). Such reasoning is said

320   to be non-ampliative. By its very nature, deduction cannot introduce new ideas. All non-

321   deductive reasoning is ampliative, thus does not satisfy the criterion of logical validity. This

322   makes abduction a fundamentally important mode of reasoning in everyday life as well as all of

323   science. Abduction is the only type of reasoning from which new ideas are conceived. With true

324   premises, abductive and inductive reasoning do not guarantee true conclusions. The content of

325   those conclusions will extend beyond what is provided in the premises. Abductive conclusions

326   can be regarded as merely plausible: "By plausibility, I mean the degree to which a theory [or

327   hypothesis] ought to recommend itself to our belief independently of any kind of [test] evidence

328   other than our instinct urging us to regard it favorably" (Peirce, 1958b: 8.223). Inductive

329   conclusions, on the other hand, are probable given that they are determined by available test

330   evidence.

331   *Phylogenetic inference = abduction*

332   Representing phylogenetic inference in a more complete form compared to what is shown in **(1)**,

333   the following example of abduction is somewhat closer to the actual abductive structure leading

334   to phylogenetic hypotheses. The basis for this abduction would be to answer the why-question,

335   "Why do semaphoronts to which specific hypotheses *x-us* and *y-us* refer have ventrolateral

336   margins with appendages in contrast to smooth as seen among individuals to which other species

337   hypotheses (*a-us*, *b-us*, etc.) refer?" (Fitzhugh, 2006c, 2012, 2013, 2015, 2016a, 2016b):

338   **(4)**   • *Background knowledge, b*

339   • *Phylogenetic theory*: If character $x(0)$ exists among individuals of a reproductively

340   isolated, gonochoristic or cross-fertilising hermaphroditic population and character $x(1)$

341   originates by mechanisms a, b, $c \ldots n$, and becomes fixed within the population by

342   mechanisms d, e, $f \ldots n$ (= ancestral species hypothesis), followed by event(s) g, h, $i \ldots n$,

343   wherein the population is divided into two or more reproductively isolated populations,

344   then individuals to which descendant species hypotheses refer would exhibit $x(1)$.

345   • *Observations (effects)*: Individuals to which specific hypotheses *x-us* and *y-us* refer

346   have ventrolateral margins with appendages in contrast to smooth as seen among

347   individuals to which other species hypotheses (*a-us*, *b-us*, etc.) refer.

348

349   • *Causal conditions (phylogenetic hypothesis X-us)*: Ventrolateral margin appendages

350   originated by some unspecified mechanism(s) within a reproductively isolated population

351   with smooth ventrolateral margins, and the appendage condition became fixed in the

352   population by some unspecified mechanism(s) (= ancestral species hypothesis), followed

353   by an unspecified event(s) that resulted in two or more reproductively isolated

354   populations.

355   *Background knowledge b*, as auxiliary theories and hypotheses, is generally not listed as a

356   premise, but instead is established knowledge accepted as true that is needed for the other

357   premises in an inference. Background knowledge is specified here for reference later when

358   considering abduction in relation to sequence data. The major premise, *Phylogenetic theory*, is

359   intentionally vague regarding causal specifics. This reflects the near-complete absence of causal

360   information that goes into the development of phylogenetic algorithms as well as the lack of

361   explanatory content in phylogenetic hypotheses implied by cladograms (Fitzhugh, 2012, 2013,

362 2016b). The theory as presented here is intentionally limited to gonochoristic or cross-fertilising

363 hermaphroditic organisms (Fitzhugh, 2013) since population-splitting events ("speciation") are

364 not relevant to asexually reproducing, obligate parthenogenetic, or self-fertilising hermaphroditic

365 organisms. The theory states a common cause, which is consistent with the necessary

366 presupposition that observation statements are true, mentioned earlier; if we assume the truth of

367 our observations, then we should pursue explanations of those observations in a manner that

368 maximises the truth element as much as possible in those explanatory accounts. The minor

369 premise in this example, *Observations (effects)*, presents only one set of observation statements,

370 as subject-predicate relations, i.e., ventrolateral body margins. This premise can be expanded to

371 include other relevant characters to be explained, as is typical of the standard character data

372 matrix. A data matrix implies both why-questions as well as the totality of observation

373 statements comprising this second premise (Fitzhugh, 2006c, 2016b). The conclusion, *Causal*

374 *conditions*, is the result of applying the *Phylogenetic theory* to *Observations* of effects. Such

375 conclusions, often represented by cladograms, serve as answers to the why-questions. The

376 limited causal details provided in the conclusion is a consequence of what little is offered in the

377 theory in terms of causal particulars. For this reason, cladograms are largely devoid of

378 explanatory information. As part of the ampliative nature of abduction, the premises can lead to a

379 single conclusion or multiple, mutually exclusive conclusions. Any valid deduction, on the other

380 hand, being non-ampliative, will only produce a single conclusion.

381   Whilst we often refer to a cladogram as a phylogenetic "hypothesis," they are in fact

382 composite constructs, implying a minimum of three classes of hypotheses: previously inferred

383 species hypotheses, hypotheses of character origin/fixation among members of ancestral

384 populations, and population splitting events ("speciation") (Fig. 3). A fourth, ad hoc class of

385 hypothesis is typically invoked, called homoplasy (Lankester, 1870).

386   To manifest abductive inferences in a phylogenetics computer algorithm that emulate

387 what is presented in **(4)**, the inferential form would be akin to the following (cf. Josephson &

388 Josephson, 1994),

389 **(5)**   • d is a collection of (presumed true) observation statements of differentially-

390   shared characters

391   • hypotheses, implied by cladograms $X_1, X_2 \ldots X_n$, are possible composite

392   explanations of d

393   • select subset of cladograms with score S_n (minimal "tree length" = minimise

394   ad hoc hypotheses of homoplasy)

395   ————————————————————————————————————

396   • cladograms with score S_n are most plausible, mutually exclusive explanations of

397   d.

398 The algorithm functions in a manner that produces conclusions *as if* the common cause

399 *Phylogenetic theory* in **(4)** were operative. Notice as well that the first premise in **(5)** contains the

400 assumption that observation statements regarding shared characters are true; the necessary

401 presupposition of truth associated with implied why-questions in data matrices, if one accepts

402 that the intent of these inferences is to explain observations. The phrase in the conclusion,

403 "cladograms with score S_n are most plausible," is intentional. Plausibility indicates hypotheses

404 are worthy of further consideration:

405   By Plausible, I mean a theory [or hypothesis] that has not yet been subjected to

406   any test, although more or less surprising phenomena have occurred which it

407   would explain if it were true, is in itself of such a character as to recommend it for

408   further examination or, if it be *highly* plausible, justify us in seriously inclining

409   toward belief in it, as long as the phenomena be inexplicable otherwise (Peirce,

410   1932: 2.662, emphasis original; Kapitan, 1997: 481).

411 Epistemically, a plausible hypothesis is far weaker than a hypothesis that has been successfully

412 tested with the introduction of test evidence, i.e., **(2)**, **(3)**; a distinction that is too often ignored in

413 the systematics literature because of the general misunderstanding of the meaning of evidential

414 support (see ***Phylogenetic hypotheses and the myth of evidential support***).

415   At first sight, the algorithmic representation of abduction in **(5)** might appear to be what

416 has often been called "parsimony analysis." The difficulty with this perspective is that parsimony

417 is not a form of reasoning that produces explanatory hypotheses. That responsibility resides with

418 abduction. Parsimony is a comparative measure, where for instance of two hypotheses that

419 predict the same results, the hypothesis that requires fewer assumptions is the simpler of the two.

420 The third premise in **(5)** invokes this principle. That intended action of selection, based on

421 minimising ad hoc hypotheses of homoplasy, is implemented for the sole purpose of serving as a

422 surrogate for the application of the *Phylogenetic theory* in **(4)**. This is not tantamount to a

423 parsimony analysis or method. It is an instance of abductive reasoning.

424   It was noted earlier that abduction is the only type of reasoning that produces explanatory

425 hypotheses; it is the only form of reasoning that introduces new ideas. The depiction of

426 abduction in **(4)**, or its algorithmic form in **(5)**, is not only at odds with "parsimony" being an

427 inference procedure but also contrary to claims in systematics that so-called "likelihood" or

428 "Bayesian" methods can infer explanatory hypotheses. With his introduction of the likelihood

429 principle, Fisher (1934; see also Hacking, 1965, 2001, Edwards, 1972) was clear that it is only

430   relevant to considerations of test evidence *subsequent* to inferring hypotheses. Evidence *e* in

431   representations of likelihood, e.g., $p(h \mid e) = l(h \mid e)$, refer to *test evidence* [cf. **(2)**, **(3)**].

432   Probability *p* quantifies anticipation of an outcome of testing, whereas likelihood *l* quantifies

433   trust in the hypothesis as a consequence of testing. Characters used to abductively infer

434   phylogenetic hypotheses [cf. **(1)**, **(4)**, **(5)**] do not constitute test evidence, and likelihood does not

435   provide the means to infer explanatory hypotheses (*contra* e.g., Felsenstein, 1981, 2004;

436   Swofford et al., 1996; Huelsenbeck & Crandall, 1997; Haber, 2011).

437   The intent of Bayes Theorem is to quantify changes in belief in hypotheses following the

438   introduction of test evidence (Salmon, 1967; Howson & Urbach, 1993; Hacking, 2001; *contra*

439   e.g., Huelsenbeck & Ronquist, 2001; Huelsenbeck et al., 2001; Archibald, Mort & Crawford,

440   2003; Felsenstein, 2004; Ronquist, van der Mark & Huelsenbeck, 2009). Bayesianism is

441   inductive *sensu* **[3]**; it has no relevance to abduction. The attempt to force Bayes' Theorem into

442   phylogenetic inference (e.g., Huelsenbeck et al., 2001: fig. 1) is represented as,

443    $$p(tree \mid characters) = \frac{p(characters \mid tree) \bullet p(tree)}{p(characters).}$$

444

445   This is not a meaningful implementation of the Theorem (Fitzhugh, 2010a, 2012, 2016a, 2016c,

446   2016d). The supposed prior probability, *p(tree)*, refers to all possible "tree topologies" for taxa

447   considered. Such topologies are nothing but branching diagrams devoid of the empirical content

448   typical of cladograms that imply the several classes of causal events discussed earlier (Fig. 2).

449   Tree diagrams disconnected from characters explained by those diagrams cannot be assigned

450   prior probabilities. More problematic is the use of differentially shared characters as "evidence"

451   to determine posterior probabilities. Character data cannot serve as test evidence for the

452   hypotheses intended to explain those data (see ***Phylogenetic hypotheses and the myth of***

453   *evidential support*). As with "parsimony" and "likelihood" methods, the "Bayesian" approach in

454   systematics fails to live up to its name.

455   In sum, neither "parsimony," "likelihood," nor "Bayesianism" are valid forms of

456   reasoning or methods for inferring explanatory hypotheses. Unfortunately, wider recognition of

457   the fundamental importance of abductive reasoning did not take hold among scientists until

458   Hanson (1958) pointed out its significance in his *Patterns of Discovery*, and later

459   acknowledgment of its importance in artificial intelligence (Thagard, 1988) and science in

460   general were embraced (Fann, 1970; Reilly, 1970; Thagard, 1988; Josephson & Josephson, 1994;

461   Magnani, 2001, 2009, 2017; Psillos, 2002, 2011; Walton, 2004; Gabbay & Woods, 2005;

462   Klienhans, Buskes & de Regt, 2005; Aliseda, 2006; Schurz, 2008; Klienhans, Buskes & de Regt,

463   2010; Park, 2017; Anjum & Mumford, 2018). In the absence of awareness about abduction,

464   systematics since the 1960's was left with an inferential void that was filled with incorrect

465   applications under the false dichotomy of parsimony versus induction vis-à-vis statistics, where

466   the latter led to incorrectly applying likelihood and Bayesianism. What is actually being

467   performed in phylogenetic inference under these labels is abductive reasoning, albeit in a most

468   peculiar and not entirely philosophically or scientifically acceptable manner.

469   Regarding abductive inferences of phylogenetic hypotheses to explain sequence data,

470   there are two significant issues to consider. One issue will be discussed here, while the other will

471   be addressed later (see *Sequence data and explanatory hypotheses*). The treatment of sequence

472   data has often been seen as requiring the assumption of rates of substitution as part of the

473   inferences of phylogenetic hypotheses, along with "branch lengths" (i.e., number of substitutions

474   or character changes that have occurred "along" the branches of phylogenetic trees) (Swofford et

475   al., 1996; Felsenstein, 2004; Schmidt & von Haeseler, 2009). Once we acknowledge that trees

476   are only graphic devices for implying the various classes of explanatory hypotheses accounting

477   for observed characters (Fig. 2), it becomes apparent that those trees cannot have properties like

478   lengths of branches. The need to consider substitution rates has warranted the development of so-

479   called "model-based" approaches (Jukes & Cantor, 1969; Felsenstein, 1978, 2004; Farris, 1983;

480   Swofford et al., 1996; Sullivan & Joyce, 2005; Rindal & Brower, 2011; Kapli, Yang & Telford,

481   2020), under the guises of "likelihood" and "Bayesian," versus the "model-free" method of

482   "parsimony analysis." It should be apparent by now that this distinction, just like the methods, is

483   without merit. If we accept that phylogenetic inferences are abductive, then the inclusion of

484   substitution rates within abduction would have the following form (Fitzhugh, 2021):

485   **(6)**   *Background knowledge* (partim): Observation statements assumed true, per alignments of

486   sequence data

487   *Theories*: (a) Rates of sequence substitution, applied to sequence data;

488   (b) Common cause *Phylogenetic theory* of common ancestry, cf. **(4)**, per

489   *Background knowledge*

490   *Observation statements*: Represented in data matrix as why-questions

491   ==

492   *Phylogenetic hypotheses*: Diagrammatically implied by graphic devices called

493   cladograms.

494   Notice that this inference relies on theories that are contradictory. The theory of rates of

495   sequence substitution is at odds with the *Background knowledge* of true observation statements

496   of aligned sequences, and by extension also at odds with the implied why-questions one would

497   ask for which the abduction seeks answers using a common-cause theory. Correcting for this

498   contradiction would necessitate removing the theory of substitution rates as a premise in the

499 abduction and placing it within the *Background knowledge*, such that originally aligned sequence

500 data would be modified to take substitution rates into consideration. By doing this, revised

501 observation statements could be presented, which re-establish assumptions that observation

502 statements are true. The *Background knowledge* in **(6)** would then have the following revised

503 form (Fitzhugh, 2021),

504 **(7)**   *Background knowledge, revised*:

505   (a) observation statements of differentially shared characters, are initially assumed

506   true, per alignments of sequence data;

507   (b) rates of sequence substitution taken into consideration;

508   (c) per (b), the assumption of truth of observation statements in (a) is not

509   necessarily correct;

510   (d) per (b) and (c), observation statements are revised such that apparent

511   shared nucleotides are renamed as *different* observation statements where

512   applicable to re-establish true statements.

513 With the revised *Background knowledge* in **(7)**, the ensuing abductive inference would then have

514 the form shown in **(4)**, which again provides answers to why-questions by way of common

515 cause; there is no need to consider substitution rates within the inference. The inherent difficulty

516 of accomplishing step **(7)**(d), however, will likely preclude even proceeding forward with

517 causally accounting for those sequence data given that there are no empirical criteria for

518 discerning identical nucleotides or amino acids as not being identical. This is a matter that has

519 been overlooked in systematics. The alternative solution is to simply accept the truth of shared

520 characters obtained through alignment, in which case abduction would again be as shown in **(4)**

521 and neither substitution rates nor branch lengths would be considered.

522   We have emphasised that cladograms or phylogenetic trees satisfy the goal of scientific

523   inquiry if they are interpreted as composite explanatory hypotheses (Fig. 3). Whilst the

524   explanatory nature of cladograms is sometimes explicitly acknowledged (e.g., Farris, 1983;

525   Swofford et al., 1996; Schmidt & von Haeseler, 2009; Kapli, Yang & Telford, 2020), often the

526   greater focus of phylogenetic studies is on just obtaining "trees," with little to no causal

527   considerations given (e.g., Felsenstein, 1981, 2004; Sullivan & Joyce, 2005; Kapli, Yang &

528   Telford, 2020). Consequences of this emphasis on trees as opposed to explanations includes an

529   erroneous method called character mapping (Fitzhugh, 2014). Mapping most often involves

530   obtaining phylogenetic trees using sequence data, then "optimising" other characters, usually

531   morphological, onto these diagrams, from which are determined vague evolutionary conclusions

532   regarding the mapped characters. This approach has become popular among polychaete

533   phylogenetic studies (e.g., Struck et al., 2011; Borda et al., 2012; Glasby, Schroeder & Aguado,

534   2012; Goto et al., 2013; Weigert et al., 2014; Aguado et al., 2015; Andrade et al., 2015; Struck et

535   al., 2015; Goto, 2016; Weigert & Bleidorn, 2016; Kobayashi et al., 2018; Nygren et al., 2018;

536   Langeneck et al., 2019; Shimabukuro et al., 2019; Radashevsky et al., 2020; San Martín et al.,

537   2020; Tilic et al., 2020; Gonzalez et al., 2021). Much credence has been given to mapping, albeit

538   without foundation. For instance, Kapli, Yang & Telford. (2020) state that,

539   Mapping heritable character states (phenotypic or genotypic) onto a tree is the

540   basis of different evolutionary analyses: it allows us, for example, to make

541   inferences [sic] about character homology and also to gain insights into

542   character loss and convergent evolution[….] Whereas trees were initially based

543   to a great extent on morphological characters, biological molecules – nucleic

544   acids and proteins – provide a far more powerful [sic] and plentiful source of

545   information for reconstructing trees.

546 Mapping is flawed for a simple reason. That phylogenetic inference is abductive means inferring

547 hypotheses, implied by a cladogram, for one set of characters produces conclusions relevant only

548 to those characters. Any subsequent "mapping" of additional characters on that cladogram is not

549 a legitimate form of inference, abductive or otherwise. The premises of a "mapping inference"

550 make this apparent:

551 **(8)**   • tree topology, (a-us (b-us (c-us (d-us, e-us))))

552   • observed effects, as differentially shared characters, e

553   • ???

554 As a premise, a tree topology is an empirically empty statement since it would have been

555 previously inferred to account for characters other than those in the second premise. Attempting

556 to apply that first premise to the second is pointless since this cannot lead to any interpretable

557 conclusion – certainly not explanatory hypotheses. As such it is impossible to speak of

558 explanations of mapped characters. Like the past and present uncritical advocacy of phylogenetic

559 methods called "parsimony," "likelihood," and "Bayesian," the popularity of character mapping

560 is a further testament to the lack of consideration of formal reasoning in systematics.

561 ***Phylogenetic hypotheses and the myth of evidential support***

562 The present study does not assess the veracity of either the Magelonidae or less inclusive

563 phylogenetic hypotheses in terms of evidential "support," nor are there attempts to use popular

564 methods such as the bootstrap or Bremer analysis to assert that hypotheses are either "strongly

565 supported" or "robust." Such perspectives have become all too common in systematics research,

566   including those on annelids (e.g., Struck et al., 2011; Borda et al., 2012; Weigert et al., 2014;

567   Aguado et al., 2015; Andrade et al., 2015; Struck et al., 2015; Weigert et al., 2016; Gonzalez et

568   al., 2018; Nygren et al., 2018; Shimabukuro et al., 2019; San Martín et al., 2020; Stiller et al.,

569   2020; Tilic et al., 2020; Gonzalez et al., 2021). Reasons for not speaking of support in the present

570   study follow from the basics of reasoning described above. More detailed treatments of

571   misconceptions regarding evidence of, and support for phylogenetic hypotheses can be found in

572   Fitzhugh (2012, 2016b, 2016c).

573   First, to correctly speak of *evidence* means to refer to the premises that allow for a certain

574   conclusion (Longino, 1979; Salmon, 1984a; Achinstein, 2001). Whilst that evidence is said to

575   "support" a given conclusion, it is only inductive, i.e., test evidence or support (cf. **[3]**) that

576   matters in the pursuit of empirical evaluation, whether in matters of everyday life or during

577   scientific inquiry. An emphasis on test evidence certainly permeates all of evolutionary biology

578   and by extension it is understandable that it would be of concern in systematics. But this requires

579   being clear about (1) what is meant by the test evidence, (2) if that evidence is being used in the

580   proper context, and (3) whether or not bootstrap and Bremer "support" values are meaningfully

581   interpretable in relation to phylogenetic hypotheses.

582   Recall that the examples of ab-, de-, and induction in **(1)**–**(3)** draw clear distinctions

583   between premises and conclusions derived from those premises. Those premises constitute the

584   *evidence for* the respective conclusions [see also **(4)**–**(6)**]. Beyond basic matters of logic, we

585   need to be cognisant of the way evidence is interpreted in the separate stages of inquiry.

586   Evidence in relation to abduction is unremarkable in the sense that conclusions must be as they

587   are because of the premises [cf. **(1)**, **(4)**, **(5)**] (Fitzhugh, 2010a, 2012, 2016a, 2016c, 2016d). As

588   well, abductive conclusions cannot be changed or "defeated" with the introduction of additional

589   effects to be explained. Adding those effects as premises only results in the inference of a new

590   set of hypotheses that have no relevance to previously inferred hypotheses.

591   A related misconception is that statistical consistency applies to phylogenetic inference

592   (e.g., Felsenstein, 1978, 2004; Swofford et al., 1996; Heath, Hedtke & Hillis, 2008; Assis, 2014;

593   Brower, 2018). When correctly interpreted, consistency is the view that as more and more *test*

594   *evidence* is introduced in support of a hypothesis, the closer one is supposedly getting to a true

595   proposition. The mistaken interpretation of consistency in systematics has led to the popular yet

596   erroneous view that sequence data are beneficial for discerning "phylogenies" because of the

597   vast increase in characters that are available (e.g., Goto, 2016; Tilic et al., 2020). For example, in

598   relation to phylogenetic inference, Felsenstein (2004: 107, 121, respectively) states,

599   "An estimator is consistent if, as the amount of data gets larger and larger

600   (approaching infinity), the estimator converges to the true value of the

601   parameter with probability 1…"

602   "The inconsistency of parsimony [sic] has been the strongest challenge to its

603   use. It becomes difficult to argue that parsimony methods have logical and

604   philosophical priority, if one accepts that consistency is a highly desirable

605   property."

606   Contrary to claims that consistency is relevant to phylogenetic inference, it has been

607   acknowledged since the early 20th century that continued additions of effects to abductive

608   inferences provides no indication that a true, as opposed to plausible, set of explanatory

609   hypotheses has been attained (Peirce, 1902, 1932: 2.774−777; Rescher, 1978; Fitzhugh, 2012,

610   2016b). As new effects in need of explanation are sequentially added to abductive premises, each

611   subsequent conclusion will only offer a new set of hypotheses that have no relevance to

612   previously inferred hypotheses. The emphasis on consistency in systematics is yet another

613   consequence of abduction not being recognised in lieu of a misplaced statistical (inductive)

614   mindset.

615   Deduction serves to conclude predictions of potential test evidence [cf. **(2)**] that might be

616   later sought during the process of testing. Much like premises-as-evidence in abduction, the

617   premises in deduction do not warrant any special attention in terms of "support." Where

618   evidence is of importance is during the act of testing, i.e., induction [cf. **(3)**]. For instance, a

619   conclusion that test evidence supports or confirms a hypothesis can be subsequently revised if

620   additional support through further testing is obtained, or additional test evidence might

621   eventually lead to a conclusion of disconfirmation. As noted by Lipton (2005), the process of

622   testing puts hypotheses at risk of being disconfirmed since there is no guarantee predicted test

623   evidence, via **(2)** and **(3)**, will be found. Obtaining contrary evidence is always a possibility. It is

624   test evidence that matters when speaking of support. Abductive "support" lacks that

625   qualification, and character data are not test evidence.

626   Because an emphasis on causality has been largely wanting in recent decades in relation

627   to inferences of taxa-as-explanatory-hypotheses, references to support for phylogenetic

628   hypotheses has centered on support [sic] for "groups" or "clades" within cladograms (Fitzhugh,

629   2012). Such claims of support are misleading for two reasons. First, as mentioned above,

630   "support" for any abductive conclusion is trivial since the conclusion could not be otherwise

631   given the premises. In other words, unlike test evidence associated with induction, observations

632   of characters do not present any risk to the hypotheses explaining those characters. To assert, for

633   example, that characters "support" some phylogenetic hypothesis verges on circularity: the

634   conclusion(s) is/are determined by the premises and the premises support the conclusion(s).

635   Second, our concern is not for groups, but rather various explanatory hypotheses. As all

636   phylogenetic hypotheses are composite (Fig. 3), an emphasis on groups is both artificial and

637   denies consideration of the variety of explanatory accounts implied by cladograms. Support in

638   relation to groups is epistemically meaningless.

639   There is a third difficulty, faced by the two popular "support" measures for phylogenetic

640   hypotheses [sic] (Efron, 1979; Efron & Gong, 1983; Felsenstein, 1985, 2004; Bremer, 1988,

641   1994; Efron & Tibshirani, 1993; Davis, 1995; Efron, Halloran & Holmes, 1996; Holmes, 2003;

642   Soltis & Soltis, 2003; Fitzhugh, 2006a, 2012, 2016c; Lemoine et al., 2018). Neither method

643   provides epistemically meaningful values regarding evidential support, contrary to the popularity

644   of their use, or claims that they provide a basis to say phylogenetic hypotheses are "robust." The

645   bootstrap was originally developed to test statistical hypotheses through a process of random

646   resampling from an original set of random samples taken from a population. The intent is to test

647   the hypothesis that a statistical parameter, inferred from the original samples, has the

648   hypothesised value, without having to perform additional sampling from the population. It is

649   important to note that the bootstrap approach is designed to test statistical, *not* explanatory

650   hypotheses. Phylogenetic hypotheses are not statistical constructs, as clearly shown in **(4)** and

651   **(5)**. Like explanatory hypotheses, however, hypotheses of statistical estimates are inferred by

652   way of abduction. Such estimates are generalisations that account for observed instances as

653   representative of the population from which the sample was drawn. For example,

654   **(8)**   • Some balls in this bag are red

655   • 25% of balls in this random sample are red
                            ═══════════════════════════════════════

656   • *Hypothesis*: 25% of all balls in this bag are red.

657   Testing the hypothesis would proceed by predicting what should be observed if additional

658   random samples are taken. Such an inference could not be deductive, but rather what Peirce

659   (1932: 2.268) called a "statistical deduction,"

660   **(9)**   • *Hypothesis to be tested*: 25% of all balls in this bag are red

661   • A random sample of balls will be taken from the bag

662   • *Predicted test evidence*: 25% of balls in the sample will be red.

663   Notice that the prediction of test evidence in **(9)** is different from what is shown for the

664   explanatory hypothesis in **(2)**. Statistical hypotheses are tested by seeking the same class of data

665   used to originally infer the hypotheses, whereas testing explanatory hypotheses requires test

666   evidence that is different from the effects originally used to infer the hypotheses (Fitzhugh,

667   2016c, 2016d).

668   As suggested by Felsenstein (1985, 2004), the bootstrap method applied to phylogenetic

669   hypotheses involves randomly sampling characters from an original character data matrix to

670   create contrived data sets of the same size from which new cladograms are produced. Keep in

671   mind that these cladograms, as "bootstrap replicates," are *not* explanatory hypotheses; they are

672   merely branching diagrams derived from artificial data sets. Yet, it is claimed that the more often

673   "clades" (actually only branching patterns) are obtained among these "replicates" that match the

674   original groupings indicates higher "support" for those clades. This claim is, however, entirely

675   incorrect. The "bootstrap replicates" have no epistemic relation to the original phylogenetic

676   hypothesis(es) under consideration, such that any measure of "support" would be impossible to

677   ascertain. Along with the statistical, i.e., inductive, mindset that was introduced into phylogenetic

678   inference in the 1970's, the bootstrap method applied to phylogenetic hypotheses was largely an

679   exercise in filling a perceived methodological void. Had the abductive nature of systematics been

680   recognised early on, and character data not confused with test evidence, the state of the field

681   might have avoided so many scientifically questionable schemes. The only support relevant to

682   cladograms is valid test evidence produced in the process of testing the various classes of

683   hypotheses within a (composite) phylogenetic hypothesis [Fig. 3; cf. **(2)**, **(3)**]. But as noted

684   earlier, such testing virtually never occurs, making the need for talk of support both gratuitous

685   and positively deceptive.

686   Just as the bootstrap provides results that cannot be interpreted as support for

687   phylogenetic hypotheses, the Bremer Index produces values that are equally impossible to

688   defend. Like the bootstrap, Bremer Index is claimed to determine support for groups, as opposed

689   to any particular hypotheses implied by cladograms. This support is based on the extent to which

690   groups or "clades" are present in cladograms of ever-increasing "length" beyond the original

691   minimum-length tree. The greater the tree length with a particular group still present is supposed

692   to represent greater "support" for or resiliency by that group. The problem is that trees of greater

693   length can only be interpreted as sets of explanatory hypotheses that have no epistemic relation

694   to the originally inferred hypotheses. The consequence is that values provided by the Bremer

695   Index offer no indication of support. Once again, in the absence of actually testing hypotheses, as

696   indicated in **(2)**–**(3)**, no evidential test support is possible for hypotheses.

697   Finally, an oblique yet equally specious approach to garnering support comes from

698   comparisons of cladograms inferred from different sets of characters, sometimes referred to as

699   taxonomic congruence (Fitzhugh, 2014, 2016c). The idea is that if tree topologies are identical,

700   or nearly so, this justifies a sense of greater confidence or belief in those topologies (not the

701   implied explanatory hypotheses). Just as was noted earlier with regard to the error of character

702   mapping, comparisons of cladograms are an inferentially indefensible approach. Cladograms

703 inferred to explain separate sets of characters are distinct compilations of explanatory constructs

704 that have no epistemic relevance to each other. A popular, somewhat related approach is to speak

705 of comparisons of past and present cladogram topologies inferred from updated compilations of

706 observations, remarking on the degree of similarities between groups in those topologies. The

707 same basic criticism against taxonomic congruence applies here. For example, previous

708 abductive inferences using data set D_1 give composite phylogenetic hypothesis H_1. With

709 subsequent characters added, D_{1+2}, a new composite phylogenetic hypothesis, H_2, is inferred. It

710 might seem reasonable to speak of topological similarities and differences between H_1 and H_2 but

711 this is a mistake. Again, H_1 and H_2 are distinct sets of explanatory hypotheses from different sets

712 of abductive premises. Just as there are no meaningful comparisons to be made between the

713 actual explanatory hypotheses implied by the different cladograms (cf. Fig. 2), there are no

714 relevant conclusions to be made regarding topological similarity or difference. In the absence of

715 recognising the nature of abduction or associated intent of those inferences, focusing on

716 phylogenetic tree comparisons offers no scientifically meaningful evaluation.

717 ***Sequence data and explanatory hypotheses***

718 The pursuit of sequence data was not given consideration in this study. The reasoning behind this

719 decision will be outlined in this subsection. A more complete account is presented in Fitzhugh

720 (2016b; see also Nogueira et al., 2017: 683–684, Lovell & Fitzhugh, 2020: 270, and Fitzhugh,

721 2021). Contrary to a claim made by a reviewer of an earlier draft of this paper, what is presented

722 in this section should not be interpreted as the assertion that we "do not believe in sequence

723 data." Rather, our intent is to point out inherent and significant difficulties that generally

724 preclude causally accounting for differentially shared nucleotides or amino acids via inferences

725 of phylogenetic hypotheses.

726   The line of argument developed in this more inclusive section – establishing the basis for

727   systematics – follows from the fact that the goal of scientific inquiry is to continually acquire

728   causal understanding of phenomena, in the form of differentially shared characters of organisms,

729   that we encounter as well as describe. The pursuit of that understanding begins with reactions to

730   those effects, in the form of implicit or explicit why-questions, and subsequently inferring

731   answers to those questions by way of abductive reasoning. As discussed earlier, abduction

732   produces hypotheses that posit possible past causal events/conditions that account for observed

733   effects, as shown in **(1)**, **(4)**, and **(5)**. And, almost all actions in systematics are centered around

734   abduction as opposed to testing hypotheses via induction (Fitzhugh, 2005a, 2006a, 2006b, 2008a,

735   2009, 2010a, 2012, 2013, 2014, 2015, 2016a, 2016b, 2016c, 2016d).

736   We pointed out earlier that composite phylogenetic hypotheses provide almost no causal

737   specifics among the four classes of hypotheses implied by cladograms (Fig. 3). This is a

738   consequence of the fact that phylogenetics computer algorithms emulate a vague form of

739   abduction [e.g., **(4)**, **(5)**]. Consider again what the *Phylogenetic theory* in **(4)** offers regarding

740   character origin/fixation:

741   character $x(1)$ originates by [unstated] mechanisms a, b, c… n, and becomes

742   fixed within the population by [unstated] mechanisms d, e, f… n (= ancestral

743   species hypothesis), followed by [unstated] event(s) g, h, i… n, wherein the

744   population is divided into two or more reproductively isolated populations.

745   The cause of character fixation in an ancestral population could at a minimum be assumed to be

746   natural selection or genetic drift. In the absence of explicit causal specifics being presented in the

747   *Phylogenetic theory*, it would have to be assumed that either selection or drift are reasonable

748   causal alternatives. This equivalence is plausible for explaining phenotypic characters but cannot

749 be applied to sequence data. For selection to operate, whether purifying or directional, variation

750 among heritable traits within a population must be identified that directly result in differential

751 fitness among individuals. Nucleotides and amino acids lack emergent properties that could

752 *directly* manifest fitness differences (for important nuances, cf. Linquist et al., 2020). Whilst

753 there are tests that can indicate whether selection has occurred in relation to sequence data, such

754 as the McDonald–Kreitman test (McDonald & Kreitman, 1991; Sawyer, 1994; Hey, 1999; Hurst,

755 2002; Biswas & Akey, 2006; Zhang & Yu, 2006; Koonin, 2012; Petrov, 2014), these tests cannot

756 discriminate at what organisational level selection might have been directed. It is at higher

757 organisational levels that phenotypic characters can result in fitness variation. If selection is a

758 causal factor, it comes into play due to phenotypic effects at these higher levels. Alternatively,

759 since there is no *direct* selection for sequence data, phenotypic characters have the potential to

760 lead to differential fitness and intergenerational selection that can influence the occurrences of

761 those sequence data that produce the selected characters. The result is a form of *indirect*

762 selection, termed downward causation by Campbell (1974: 180),

763   "Where natural selection operates through life and death at a higher level of

764   organisation, the laws of the higher-level selective system determine in part the

765   distribution of lower-level events and substances."

766 Since the 1970's the importance of downward causation has become increasingly recognised

767 (e.g., Vrba & Eldredge, 1984; Salthe, 1985; Lloyd, 1988; Auletta, Ellis & Jaeger, 2008; Ellis,

768 2008, 2012, 2013; Ellis, Noble & O'Connor, 2011; Jaeger & Calkins, 2011; Laland et al., 2011;

769 Martínez & Moya, 2011; Davies, 2012; Okasha, 2012; Walker, Cisneros & Davies, 2012;

770 Griffiths & Stotz, 2013; Martínez & Esposito, 2014; Walker, 2014; Mundy, 2016; Callier, 2018;

771   Pouyet et al., 2018; Salas, 2019; Yu et al., 2020), but its relevance to how sequence data are

772   explained via phylogenetic hypotheses has only recently been considered (Fitzhugh, 2016b).

773   If there can be no direct selection for sequence data, the issue then becomes one of

774   deciding to explain individual nucleotides or amino acids either directly via drift or indirectly

775   through downward causation. If the latter, it is first necessary to associate those sequence data

776   with the higher-level phenotypic characters to which selection is the hypothesised causal

777   condition. Those associated sequence data would then be excluded from phylogenetic inferences

778   since they would already be explained in conjunction with higher-level characters (Fitzhugh,

779   2016b). On the other hand, it might be argued that one could avoid the issue altogether by

780   assuming all sequence data should be explained by drift. This would be unrealistic as it

781   necessitates that selection at higher organisational levels never occurs. In the absence of being

782   able to discriminate between drift versus selection by downward causation, the only sensible

783   option is to forgo altogether attempts to causally account for shared nucleotides or amino acids

784   by way of phylogenetic inference. Otherwise, to explain shared nucleotides or amino acids with

785   phylogenetic hypotheses inferred under an entirely agnostic perspective [i.e., the *Phylogenetic*

786   *theory* in **(4)**] would be epistemically and scientifically unwarranted.

787   The inherent limitations for inferring explanatory hypotheses for sequence data have

788   associated relevant consequences for mapping morphological characters on cladograms only

789   inferred for sequence data. As discussed earlier (***Phylogenetic inference = abduction***; see also

790   (Fitzhugh, 2014), mapping is an epistemically unfounded approach to explaining characters. This

791   problem is compounded by the fact that not discriminating between genetic drift and natural

792   selection as possible causal factors when explaining sequence data yet again precludes rational

793   acceptance of phylogenetic hypotheses accounting for mapped characters.

794   Finally, it might appear at first sight that the exclusion of sequence data on either the

795   basis of downward causation or inability to distinguish drift from selection is at odds with the

796   requirement of total evidence (RTE; cf. Fitzhugh, 2006b, for a discussion of the RTE in relation

797   to systematics). Such is not the case. The RTE is a recognised maxim for all non-deductive

798   reasoning (the requirement is automatically satisfied in deduction), wherein rational acceptance

799   of a conclusion is based on considering all relevant evidence that can affect support (either

800   negative or positive) for that conclusion (Carnap, 1950; Barker, 1957; Hempel, 1962, 1965,

801   1966, 2001; Salmon, 1967, 1984a, 1984b, 1989, 1998; Sober, 1975; Fetzer, 1993; Fetzer &

802   Almeder, 1993): "All that the requirement of total evidence says is that one's confidence in a

803   hypothesis must be proportional to the support that that hypothesis receives from one's

804   evidence..." (Neta, 2008: 91). Nearly all of the philosophical literature on the RTE has focused

805   on test evidence in relation to induction [cf. **(3)**], which is understandable given that, for

806   instance, to exclude known test evidence that could enhance or compromise acceptance of a

807   theory or hypothesis would be less than rational.

808   Whilst abductive reasoning has almost never figured into discussions of the RTE, the

809   non-deductive nature of abduction necessitates its attention (Fitzhugh, 2006b). Consider the

810   following example. For members of three species, *a-us*, *b-us*, and *c-us*, there are characters

811   distributed among subjects 1–3 (cf. Fitzhugh, 2006c):

812

Subjects:	1	2	3
Outgroup	0	0	0
a-us	0	1	1
b-us	1	0	1
c-us	1	1	0.

817   If the characters among members of *a-us*, *b-us*, and *c-us* are explained separately, there would be

818   three sets of explanatory hypotheses (outgroup is excluded), represented here in parenthetical

819   form:

820   Subject 1:   (*a-us* (*b-us*, *c-us*))

821   Subject 2:   (*b-us* (*a-us*, *c-us*))

822   Subject 3:   (*c-us* (*a-us*, *b-us*)).

823   The three sets of hypotheses are contradictory, and while each is supported by abductive

824   evidence [cf. **(1)**], choosing among them based on the information provided would be

825   problematic. This is the sort of situation the RTE is intended to address, as well as those

826   instances that involve other degrees of data partitioning in relation to inferring phylogenetic

827   hypotheses and character mapping. The nature of the abductive inferences involves explaining

828   features of semaphoronts, such that the observed characters are part of the integrated network

829   that makes up those individuals. The various phylogenetic theories applied to those characters

830   [cf. **(1)**] assume that past causes operated on individuals, not distinct characters. Thus, explaining

831   the characters under each subject would be relevant to explaining the other characters. The

832   plausibility for any of the phylogenetic hypotheses would be based on an abductive inference

833   where all the characters are treated as part of the premises.

834   Related to the topic highlighted in this subsection, it would not be a violation of the RTE

835   to exclude from phylogenetic inferences those sequence data for which no empirical basis is

836   available for discriminating drift from selection-via-downward-causation for sequence data. The

837   difficulty faced is not a matter that falls under the purview of the RTE, but rather an inability to

838   engage in abductive reasoning for a particular class of characters.

839   ***Sequence data are not more objective than other classes of observations***

840   Consider the following statements,

841   "Molecular data are more objective and subject to considerably more rigor than

842   morphological data. DNA sequence contains four easily identified and mutually

843   exclusive character states[….] Morphological and embryological character

844   definitions and scoring of character states are far more subjective, and most

845   characters have been repeatedly used without critical evaluation, calling into

846   question the utility of morphological cladistic studies that span Metazoa[….]"

847   (Halanych, 2004: 230).

848   "As we move forward with the deep-animal tree [sic], we should not employ

849   morphology and developmental data to reconstruct the tree. There is too much

850   historical baggage and subjectivity with these data. We should reconstruct the tree

851   with molecular data and then use that tree to independently interpret the

852   morphology and development in light of that tree[….]" (Halanych, 2016: 325).

853   "We present the view that rigorous and critical anatomical studies of fewer

854   morphological characters, in the context of molecular phylogenies, is a more

855   fruitful approach to integrating the strengths of morphological data with those of

856   sequence data[....] We argue[...] that a main constraint of morphology-based

857   phylogenetic inference concerns the limited number of unambiguous characters

858   available for analysis in a transformational framework" (Scotland, Olmstead &

859   Bennett, 2003: 539).

860   Taken at face value, each statement appears damning of all or most observations of features of

861   organisms other than sequence data in relation to inferring phylogenetic hypotheses. We have

862   seen throughout this section, however, that the disconnect between principles of scientific

863   inquiry and recent views on phylogenetic inference have led to perspectives that cannot be

864   defended. This outcome extends to the notion that sequence data are somehow "more objective,"

865   "more fruitful," or more reliable than other observations. Asserting that one class of observations

866   is more effective than other classes presumes that the objective of phylogenetic inference is to

867   obtain "phylogenies" or "trees," which is at odds with pursuing explanations of all relevant

868   observations. If the objective of systematics is causal explanation, thus consistent with all of

869   scientific inquiry, then the pursuit of "phylogenies" or "trees" is not only contrary to that

870   objective but has led to erroneous inclinations in addition to the largely contrived

871   objective/subjective dichotomy. These erroneous pursuits include, but are not limited to (1)

872   inferring phylogenetic hypotheses for separate classes of characters, especially sequence data

873   versus morphology, and drawing comparisons between tree "topologies" (cf. ***Phylogenetic***

874   ***hypotheses and the myth of evidential support***), and (2) inferring phylogenetic hypotheses for

875   sequence data, then "mapping" morphological characters on the "tree" and making evolutionary

876   claims regarding the latter characters (cf. ***Phylogenetic inference = abduction***). To address the

877   claim that sequence data are more objective or less ambiguous requires that we first consider

878   what is meant by scientific objectivity. Then there are several additional issues in the above

879   quotes that need to be addressed.

880   As might be expected, objectivity has multiple meanings. Useful overviews can be found

881   in Daston & Galison (2007), Gaukroger (2012), Reiss & Sprenger (2017), and Wilson (2017).

882   Common interpretations of objectivity range from the view that judgements should be (a) free of

883   prejudice or bias, (b) free of assumptions, and/or (c) an accurate representation of, or

884   "faithfulness" to facts (Gaukroger, 2012). Each meaning can be applied to everyday life as well

885   as within fields of science. Regarding freedom from prejudice or bias, this is to speak of limiting

886   levels of distortion beyond what is perceived. Freedom from assumptions would be impossible to

887   accomplish given the theory-laden nature of observation statements and other types of

888   propositions: "Every instance of scientific inquiry, every study, rests on a vast submerged set of

889   political, moral, and ultimately metaphysical assumptions" (Wilson, 2017). Scientific objectivity

890   has often been interpreted along the lines of "faithfulness to facts" (Daston & Galison, 2007;

891   Reiss & Sprenger, 2017), where we attempt to minimise arbitrary judgements; we want to

892   answer questions on the basis of the most appropriate evidence we have available. Objectivity

893   occurs in degrees – there is no absolute objectivity, which is why objectivity cannot be equated

894   with truth, which is absolute. Ultimately, "While we can strive for objectivity, inquiry is

895   inherently subjective" (Spencer, 2020).

896   Reiss & Sprenger (2017) distinguish "product" and "process" objectivity. Product

897   objectivity regards the products of scientific inferences, such as theories, laws, and observation

898   statements, as accurate representations of the external world. Process objectivity refers to

899   processes and methods that are not dependent on social or ethical values, or the individual biases

900   of the scientist. It is product objectivity that is of concern when it comes to assessing the quotes

901   given above, claiming sequence data are in some way more objective or less ambiguous than

902   other classes of observations.

903   There is nothing in the conception of product objectivity that would support the claim

904   that observation statements of morphological features are less objective than sequence data,

905   much less that such a contrived distinction warrants the exclusion of an entire class of

906   observations from the goal of systematics. Indeed, that biologists hold different interpretations of

907   what they perceive of the properties of organisms is not tantamount to proffering less objective

908   observation statements. Those statements are themselves products of abductive reasoning

909   (Peirce, 1935; Hoffman, 1995; Burton, 2000; Magnani, 2009; Anjum & Mumford, 2018),

910   constrained by one's background knowledge, and like all hypotheses, are open to empirical

911   evaluation. If anything, it can be argued that sequence data are less than objective relative to

912   other classes of characters given the fact that attempted phylogenetic inferences explaining

913   differentially shared nucleotides or amino acids typically operate under the assumption that rates

914   of substitution must be imposed within abductive inferences (cf. ***Phylogenetic inference** =*

915   ***abduction***). That assumption carries with it the implication that observation statements of shared

916   characters must be treated as potentially false, hence the need to interject substitution rates

917   within inferences, as indicated by the all-too-common emphasis on branch lengths. Considering

918   the rule for valid reasoning – that we should assume the truth of premises, discussed earlier – the

919   treatment of sequence data with "likelihood" and "Bayesian" methods pales against any criterion

920   of objectivity.

921   Rather than focusing on the false argument from objectivity as a basis to eliminate

922   observations of morphological characters in need of explanation, systematists should embrace as

923   much as possible all relevant observations per the goal of scientific inquiry discussed earlier and

924   the requirement of total evidence (Fitzhugh, 2006b). Two notable exceptions to considering

925   explaining differentially shared characters by way of phylogenetic hypotheses come from

926   conditions discussed earlier: (1) why-questions addressing some characters might not be

927   amenable to being answered by phylogenetic hypotheses, but instead one of the other classes of

928   explanatory hypotheses applied in systematics (Fig. 1); (2) epistemic limitations to explaining

929   sequence data because of an inability to discern explanations due to genetic drift versus selection

930   by way of downward causation (cf. ***Sequence data and explanatory hypotheses***). Pursuing

931   causality is the intent – not producing "trees" or "phylogenies," which are typically devoid of

932   causal considerations in relation to sequence data.

Outgroup and ingroup taxa

934   Outgroup and ingroup taxa considered in thus study include the following:

935   outgroups – Chaetopteridae: *Phyllochaetopterus limicolus* Hartman, 1960

936   Spionidae: *Spio filicornis* (Müller, 1776)

937   *Prionospio ehlersi* Fauvel, 1928

938   *P. lighti* Maciolek, 1985

939   *Laonice cirrata* (Sars, 1851)

940   ingroup –   *Magelona* (72 species)

941   *Octomagelona* (2 species)

942   Descriptive details regarding members of the outgroups were obtained from the following

943   literature sources:

944   *P. limicolus* – Blake (1996a)

945   *S. filicornis* – Meißner, Bick & Bastrop (2011)

946   *P. ehlersi* – Blake (1996b)

947   *P. lighti* – Blake (1996b)

948   *Laonice cirrata* – Blake (1996b)

949   The choice of outgroups ideally would follow from more inclusive phylogenetic studies from

950   which the immediate sister groups to Magelonidae have been ascertained. In this regard, the

951   merits of recent phylogenetic hypotheses are questionable. In her review of the Magelonidae,

952   Mortimer (2019) summarised past studies of phylogenetic relationships of magelonids to other

953   groups within Polychaeta. As would be expected for a group as moderately disparate as

954   magelonids, earlier conclusions were that they exhibit close relations with other spioniforms.

955   Recent phylogenetic studies based exclusively on morphological (Capa, Parapar & Hutchings,

956   2012; Chen et al., 2020) or sequence characters (Weigert et al., 2014; Helm et al., 2018) have,

957   however, allied Magelonidae with Oweniidae, while Weigert et al.'s (2016) use of mitochondrial

958   sequences had Magelonidae and Chaetopteridae as sister taxa. Each approach has aspects that

959   call into question the respective conclusions. For instance, Capa, Parapar & Hutchings (2012; see

960   also Capa, Parapar & Hutchings, 2019) cautiously suggested a Magelonidae-Oweniidae clade

961   based on the absence of nuchal organs, fusion of pro- and peristomium, presence of a ventral

962   buccal organ, and monociliated cells. The absence of nuchal organs is not exclusive to

963   magelonids and oweniids (Purschke, 1997, 2005). Mortimer & Mackie (2014) and Mortimer

964   (2019) have shown that pro- and peristomium are not entirely fused, and the magelonid

965   "burrowing organ" is not homologous to the oweniid buccal organ [Mortimer, 2019; see also

966   **Character descriptions**, *Burrowing organ* (subject 14), below]. Monociliated cells have only

967   been recorded from among members of *Magelona mirabilis* (Johnston, 1865) (Bartolomaeus,

968   1995, N.B. fig. 1A in this publication is not *M. mirabilis*; Patrick, Helm & Bartolomaeus, 2019).

969   As part of their description of a fossil magelonid, Chen et al. (2020: fig. 8a; see also Parry et al.,

970   2016) presented phylogenetic hypotheses also suggesting Oweniidae and Magelonidae are

971   exclusive sister taxa, but their inferences are based on an overly broad taxon coverage and the

972   compilation of characters is inadequate to address phylogenetic relationships of magelonids to

973   other polychaetes. As discussed in the previous section (**Methodological considerations** –

974   ***Sequence data and explanatory hypotheses***), the inherent problems associated with attempting

975   to explain shared nucleotides or amino acids undermine the plausibility of phylogenetic

976   hypotheses inferred from those premises. With the emphasis on an extensive treatment of

977   magelonid morphological characters in this study, the greatest number of characters is shared

978   with members of Spionidae, making them an appropriate outgroup. Members of several genera

979   and species were included to accommodate variation within Spionidae. An additional spioniform

980   representative from the Chaetopteridae, *Phyllochaetopterus limicolus*, was also included.

981   Ideally, all currently recognised magelonid taxa would be included in inferences of the

982   phylogenetic hypotheses. This, however, relies on several factors. Initially, taxa were chosen

983   based on access to specimens, preferably type material, some of which had been observed

984   previously during descriptions and re-descriptions by the present authors. Specimens were

985   borrowed from the following institutions:

986   **BMNH** – Natural History Museum, London

987   **MB** – Museu Nacional de História Natural, Lisboa

988   **MNCN** – Museo Nacional de Ciencias Naturales, Madrid

989   **MNHM** – Muséum National d'Histoire Naturelle, Paris

990   **NHMG** – Gothenburg Museum of Natural History

991   **NHMLAC** – Natural History Museum of Los Angeles County

992   **NMW** – Amgueddfa Cymru – National Museum Wales

993   **PMBC** – Phuket Marine Biological Center

994   **SMF** – Senckenberg Research Institute and Natural History Museum, Frankfurt

995   **USNM** – Smithsonian National Museum of Natural History

996   **ZMBN** – University Museum of Bergen

997   **ZMHB** – Museum für Naturkunde der Humboldt-Universität zu Berlin

998   **ZMUC** – Zoological Museum, University of Copenhagen

999   **ZUEC** – Museu de Zoologia, Universidade de Campinas

1000   Where specimens were not available for observation, the remaining taxa were chosen

1001 based on the level of information and detail in the original descriptions. It is only comparatively

1002 recently that the importance of illustrating and fully describing all thoracic chaetigers has been

1003 realised for the treatment of taxa for example, and further characters defined. Thus, many of the

1004 earliest descriptions lack much of the detail required for the current analysis. All ingroup taxa

1005 included in the analyses are listed in Table 2, including which specimens were observed and the

1006 institution from which they were borrowed. Table 2 also indicates whether observations were

1007 based solely on published material. Species not included within the analysis: *Magelona agoensis*

1008 Kitamori, 1967, *M. americana* Hartman, 1965, *M. capax* Hartman, 1965, *M. capensis* Day, 1961,

1009 *M. japonica* Okuda, 1937, *M. kamala* Nateewathana & Hylleberg, 1991, *M. koreana* Okuda,

1010 1937, *M. longicornis* Johnston, 1901, *M. methae* Nateewathana & Hylleberg, 1991, *M.*

1011 *mickiminni* Nateewathana & Hylleberg, 1991, *M. noppi* Nateewathana & Hylleberg, 1991, *M.*

1012 *pectinata* Nateewathana & Hylleberg, 1991, *M. petersenae* Nateewathana & Hylleberg, 1991, *M.*

1013 *pettiboneae lanceolata* Jones, 1963, *M. rosea* Moore, 1907 and *M. sachalinenis* Buzhinskaja,

1014 1985.

1015 Character descriptions

1016 A total of 176 characters distributed among 79 subjects (Table 3; Table S1) were used to infer

1017 phylogenetic hypotheses. Descriptions of characters are presented here.

1018 ***Characters of the anterior end: prostomium (subjects 1–9)***

1019 The form of the magelonid prostomium **(subject 1)** is considered a synapomorphy of the group,

1020 the name "shovel head worms" having been coined due to its peculiar shape. The dorso-ventrally

1021 flattened, shovel-shaped prostomium [character 1(1), Figs. 4 and 5] is a feature not observed

1022   among members of the outgroups or any other polychaete group. Nuchal organs **(subject 2)** have

1023   not been recorded among adult members of any magelonid species [character 2(0)] but are

1024   present among all members of the outgroups [character 2(1)].

1025   The distal margin of the magelonid prostomium **(subject 3)** can vary from smooth

1026   [character 3(0), Figs. 4A and 4F], crenulate [character 3(1), Figs. 4B and 4C] or medially

1027   indented [character 3(2), Fig. 4D]. Uebelacker & Jones (1984) stated that the presence of a

1028   crenulated prostomial margin is an excellent character for separation of species, although the

1029   degree of crenulation present shows great intraspecific variability. The crenulations may differ in

1030   number and form, for example, the distinct, triangular crenulations of *Magelona* sp. L of

1031   Uebelacker & Jones (1984) or *M. crenulifrons* (Fig. 4B), in comparison to the numerous minute

1032   crenulations observed for *M. longicornis* or *M. wilsoni* (Fig. 4C). The crenulations among

1033   members of some species are difficult to discern and this is perhaps the reason they have been

1034   previously overlooked in some descriptions and erroneously reported as absent in others. The

1035   prostomial distal margin **(subject 4)** may additionally vary in shape, from triangular [character

1036   4(0), Fig. 4E], to rounded [character 4(1), Figs. 4A and 4F] or straight [character 4(2), Figs. 4G,

1037   4H, 5C and 5E]. As subjects 3 and 4 relate directly to the shovel-shaped prostomium,

1038   characteristic of magelonids, it does not apply to any members of the outgroups.

1039   Horns are the distal projections of the prostomium **(subject 5)** that occur among members

1040   of some species of magelonids [character 5(1)], such as *Magelona pacifica* (Fig. 5A), or *M.*

1041   *montera* (Fig. 5B). Uebelacker & Jones (1984) drew attention to this character for the initial

1042   separation of magelonid species. When present, horns can vary in size/shape **(subject 6)**, from

1043   rudimentary [character 6(0), Figs. 4G, 4H, 5C and 5E], such as those observed among members

1044   of *M. variolamellata* and *M. alleni* (often described as a squared anterior margin), or

1045   conspicuous structures as seen among members of species such as *M. posterelongata* [character

1046   6(1), Fig. 5D]. In the latter case, these are often very distinct from the distal prostomial margin.

1047   Prostomial horns do not occur in the outgroups, thus subjects 5 and 6 are not applicable.

1048   Several authors have identified dimensions of the prostomium **(subject 7)** as an important

1049   feature in the separation of magelonid species (Hartman, 1944; Wilson, 1958, 1959; Jones, 1963,

1050   1971, 1978; Uebelacker & Jones, 1984; Bolívar & Lana, 1986; Blake, 1996c; Mortimer, 2019).

1051   According to Uebelacker & Jones (1984), the general shape and relative dimensions are fairly

1052   constant within each species, something which the current authors are in agreement.

1053   Consequently, the ratio of width to length was used to recognise three prostomial characters:

1054   prostomium longer than wide [character 7(0), Figs. 4A, 4F, 5B and 5D], as wide as long

1055   [character 7(1), Figs. 4B, 4D and 4G], and wider than long [character 7(2), Figs. 4C, 4H and 5E].

1056   Members of three species within the outgroups (*Spio filicornis, Prionospio lighti* and *P. ehlersi*)

1057   are considered to possess prostomia which are longer than wide [character 7(0)], whilst members

1058   of *Phyllochaetopterus limicolus* and *Laonice cirrata* have prostomia which are wider than long

1059   [character 7(2)].

1060   Magelonid prostomia carry paired "muscular", dorsal longitudinal ridges **(subject 8)**,

1061   which extend from the base of the prostomium towards the distal tip [character 8(1)]. Jones

1062   (1968) stated that their "inner surfaces, particularly dorsally and ventrally, are provided with

1063   longitudinal muscles," describing them as hollow, cylindroid structures, which he presumed were

1064   fluid filled. The number of prostomial ridges **(subject 9)** varies from one pair [character 9(0),

1065   Fig. 4H], such as members of *Magelona equilamellae* or two pairs [character 9(1), Figs. 4A–C,

1066   4E and 5B], as observed among members of *M. pacifica* (Fig. 5A). The ridges may vary in size

1067   and distinctiveness, the outer pair among members of some species being more difficult to

1068   discern, e.g., *M. alleni* (Fig. 4G), to the distinct and transversely ridged structures seen in, for

1069   example, members of *M. wilsoni* (Fig. 4C). Prostomial ridges are not present among members of

1070   the outgroups [character 8(0)] and thus subject 9 is not applicable.

1071   ***Characters of the palps (subjects 10–13)***

1072   Magelonids possess two long palps, considered to be peristomial, arising from the larval

1073   prototroch (Wilson, 1982). There has been much discussion about palp origin **(subject 10)**, since

1074   they are ventrally inserted [character 10(1), Figs. 4F and 5G], rather than dorsally [character

1075   10(0)], the latter of which is seen among members of all other polychaete groups with palps,

1076   including the outgroups. In addition, the palps do not have the characteristic feeding groove seen

1077   among members of other taxa such as spionids and *Myriowenia*. However, an inconspicuous

1078   ventral line devoid of papillae is generally present. According to Orrhage (1966), palps among

1079   members of the Spionidae and Magelonidae are homologous because they are innervated by

1080   nerves from the same part of the brain. More recently Beckers, Helm & Bartolomaeus (2019)

1081   stated that two nerves innervate the palps of members of the Magelonidae, Spionidae,

1082   Chaetopteridae and Oweniidae, indicating the purported plesiomorphic condition in Annelida.

1083   Magelonid palp surfaces **(subject 11)** are uniquely papillated, with ampulliform to

1084   digitiform papillae arranged in rows along the longitudinal axis [character 11(1), Figs. 4H, 5B

1085   and 5F–H]. Members of the outgroups, along with all other polychaetes possess non-papillated

1086   palps [character 11(0)]. Although the number of rows of papillae varies among members of

1087   magelonid species, it is relatively stable among members of any particular species. As papillae

1088   are involved in obtaining food (Jones, 1968; Fauchald & Jumars, 1979; Mortimer & Mackie,

1089   2014), variations in number of papillae may reflect different feeding strategies. In general, the

1090   number of rows of papillae are fewer distally in comparison to proximally (Jones, 1963, 1971,

1091   1978). The number of rows of papillae in the proximal region of the palp **(subject 12)** were

1092   coded as three characters: two rows of papillae [character 12(0)], 4–8 rows [character 12(1)], and

1093   10–14 rows [character 12(2)]. The number of rows of papillae at the distal end **(subject 13)** were

1094   coded for 2 [character 13(0)], 4 [character 13(1)], or more than 4 rows [character 13(2)]. Where a

1095   range was observed among members of a species, the maximum number of rows was the value

1096   used. As with palps in other polychaete groups, those of magelonids are easily lost upon

1097   collection. Many descriptions do not include information about them, whilst others do not detail

1098   differences in number of papillae along the palp length. Many authors have undervalued the

1099   importance of palp characteristics in the descriptions of members of species. These two factors

1100   present the largest problem in coding these subjects. It should be noted that the number of rows

1101   of papillae may vary in animals with regenerating palps, particularly at the distal tips, thus

1102   affecting the ranges observed. Subjects 12 and 13 are not applicable to members of the outgroups

1103   since papillated palps are unique to magelonids.

1104   ***Burrowing organ (subject 14)***

1105   Magelonids have long been described to possess a ventral eversible proboscis. A heart-

1106   shaped sac (when fully everted; oval when only partially everted), carrying longitudinal ridges

1107   (Mortimer, 2019: fig. 4.2.4). However, recent studies show that this structure plays no part in

1108   feeding (and is not connected to the buccal region) but functions in burrowing only (Mortimer,

1109   2019). The term "burrowing organ" should be applied to this structure. The burrowing organ is

1110   present in members of all known magelonid species [character 14(1)] but not present in any

1111   members of the outgroups [character 14(0)].

1112   ***Characters of body regionation (subjects 15–16)***

1113   The body of magelonids **(subject 15)** is divided into an anterior region comprising the

1114   head and "thorax" (the latter of which is characterised by the presence of capillary chaetae), and

1115   an "abdomen" comprising many segments with hooded hooks [character 15(1)] (Figs. 6A and

1116   11A). As an aside, the terms thorax and abdomen are ill-defined when applied to polychaetes

1117   overall, other than to vaguely indicate anterior-posterior distinctions along the body.

1118   Unfortunately, the characters associated with these regions are not uniformly applied across all

1119   polychaetes.

1120   The body of members of the outgroups do not have this regionation [character 15(0)].

1121   Behind the head region **(subject 16)**, the thorax carries an achaetous first segment, followed by

1122   either eight [character 16(0), *Octomagelona*; Fig. 6] or nine [character 16(1), *Magelona*]

1123   chaetigers. Subject 16 does not apply to members of the outgroups.

1124   ***Characters of thoracic parapodia (subjects 17–30)***

1125   Unique terminology introduced and later modified by Jones (1963, 1971, 1978) has been applied

1126   to the family, particularly related to parapodial structures (Fig. 7). Brasil (2003: fig. 4) provided

1127   a comprehensive review of this terminology and problems related to inconsistencies in applying

1128   terms. Consequently, several authors have suggested its abandonment (Rouse, 2001; Mortimer &

1129   Mackie, 2003). Magelonid chaetigers possess biramous parapodia with lamellae in both the noto-

1130   and the neuropodia. Lamellae are generally postchaetal, flattened structures that range from

1131   filiform to foliaceous in shape. They encircle the chaetal bundle, attaching to a low, triangular or

1132   rounded prechaetal lamella, almost cuff-like (Fig. 8A). However, among members of some

1133   species, the lamellae are somewhat subchaetal in position, underneath the chaetal bundle and

1134   appearing somewhat U-shaped when viewed laterally (Figs. 8B, 8D). All members of all species

1135   in the ingroup and outgroups have postchaetal noto- and neuropodial lamellae in

1136 thoracic/anterior chaetigers **(subjects 17** and **19**, respectively**)** except for *Phyllochaetopterus*

1137 *limicolus*, in which they are absent [characters 17(0) and 19(0)].

1138   The development of notopodial **(subject 18)** and neuropodial lamellae **(subject 20)** along

1139 the anterior chaetigers may be similar in all chaetigers [characters 18(0) and 20(0), respectively],

1140 such as among members of *Magelona papillicornis*, and *M. minuta* (Fig. 7A), or vary along the

1141 thorax [characters 18(1) and 20(1), respectively]. Subjects 18 and 20 are considered inapplicable

1142 to members of all species in the outgroups. The variation in degree of development can be easily

1143 observed among members of *M. obockensis* (Fig. 7C), and *M. conversa* (Fig. 7D), in both the

1144 noto- and neuropodia, whilst among members of *Octomagelona bizkaiensis* it is evident only in

1145 the neuropodia (Fig. 6E). The lamellae of chaetigers eight and nine often vary in comparison to

1146 those of the first seven chaetigers, e.g., *M. crenulifrons*, and *M. johnstoni* (Fig. 9I). Thus,

1147 characters of the lamellae of the first seven chaetigers were coded separately **(subjects 21–30)** to

1148 those for chaetiger eight **(subjects 34–40)**, and chaetiger nine **(subjects 41–49)**.

1149   The notopodial lamellae in chaetigers 1–7 **(subject 21)** may be postchaetal [character

1150 21(0); noted also for members of the outgroups, except *Phyllochaetopterus limicolus*, for which

1151 the subject is not applicable] or subchaetal [character 21(1)], whilst neuropodial lamellae

1152 **(subject 26)** may be postchaetal [character 26(0); observed for members of the outgroups, except

1153 *P. limicolus*, for which the subject is not applicable], subchaetal [character 26(1)] or prechaetal

1154 [character 26(2)]. Prechaetal neuropodial lamellae, such as are observed among members of

1155 *Magelona conversa* and *M. mirabilis* (Figs. 7D and 8C), are less frequent than both post- (Fig.

1156 7A) or subchaetal (Fig. 9E). The position of the thoracic neuropodial lamellae **(subject 27)** may

1157 be consistent throughout the thorax [character 27(0)], or may vary [character 27(1)], e.g., being

1158 prechaetal on chaetiger 1, occurring in a ventral position in the mid-thorax, and distinctly

1159   postchaetal in the posterior thorax (Figs. 8F and 8G). This subject was not considered applicable

1160   to members of the outgroups.

1161   Thoracic notopodial lamellar shape **(subject 22)** may be filiform, having a long, tapering

1162   structure [character 22(0), Figs. 9A, 9B and 9G] or more foliaceous [character 22(1), Figs. 9C–

1163   F]. The margins of the latter **(subject 23)** may be smooth [character 23(0)], crenulate [character

1164   23(1), e.g., *M. montera*, Figs. 9D and 9E] or bilobed [character 23(2), e.g., *M. obockensis*, Fig.

1165   9F]. All members of the outgroups are considered to have foliaceous [character 22(1)], smooth-

1166   edged [character 23(0)] anterior notopodia, except for members of *Phyllochaetopterus limicolus*

1167   for which subjects 22 and 23 are not applicable. Above the notopodial lamellae and in a slightly

1168   prechaetal position, superior dorsal lobes **(subjects 24, 25, 37, 45)** (dorsal medial lobes sensu

1169   Jones) may be present (Figs. 7C, 7D, 8D, 8E and 9C–F) or absent [characters 24(0), 37(0),

1170   45(0)]. These structures are generally smaller than the notopodial lamellae and somewhat

1171   cirriform to digitiform in shape. However, among members of some species they may be larger

1172   and distinctly foliaceous. When present, superior dorsal lobes may be present on all thoracic

1173   chaetigers [characters 25(1), 37(1), 45(1)], on chaetigers 1–8 only [characters 25(1), 37(1),

1174   45(0)], or only occurring on a small number of thoracic chaetigers [often starting in the mid-

1175   thoracic region, e.g., *M. johnstoni* or *M. conversa*, character 25(0), Fig. 7D]. Superior dorsal

1176   lobes are absent among all members of the outgroups on chaetigers 1–9 (thus subject 25 is not

1177   applicable), and subjects 24, 25, 37 and 45 are considered inapplicable for *Phyllochaetopterus*

1178   *limicolus*.

1179   The shape of thoracic neuropodial lamellae **(subject 28)** may be filiform [character 28(0),

1180   Figs. 7C, 8F and 8G] or foliaceous [character 28(1), Fig. 9C, also seen in members of the

1181   outgroups, excluding *Phyllochaetopterus limicolus*, for which the subject is not applicable]. The

1182   distal ends **(subject 29)** of which may be pointed [character 29(0)], as among members of *M.*

1183   *equilamellae* (Figs. 8F and 8G), or distally expanded and scoop-shaped [character 29(1)] as

1184   observed among members of *M. cincta* (Figs 9H). The latter subject is not applicable to members

1185   of the outgroups. The lengths of noto- and neuropodial lamellae **(subject 30)** may be equivalent

1186   [character 30(0), Fig. 9G], the notopodial lamellae may be longer [character 30(1), Figs. 9D–F],

1187   or the neuropodial lamellae may be longer [character 30(2), Fig. 7D], e.g., chaetiger 8 of *M.*

1188   *conversa*. The thoracic notopodial lamellae among members of the outgroups, *Prionospio lighti*

1189   and *P. ehlersi* are longer than neuropodial lamellae [character 30(1)], whilst for members of *Spio*

1190   *filicornis* and *Laonice cirrata* they are equivalent [character 30(0)]. Subject 30 is not applicable

1191   to *P. limicolus.*

1192   ***Characters of the chaetae from chaetigers 1–8 (subjects 31–33)***

1193   Capillary chaetae **(subject 31)** occur only in the thorax of magelonids (Figs. 6, 8, 9, 10 and 11),

1194   but many authors have undervalued the differences between them, describing them simply as

1195   limbate capillary chaetae (Hartman, 1944, 1961, 1965; Nateewathana & Hylleberg, 1991). Jones

1196   (1977) was one of the few authors who referred to the presence of unilimbate [character 31(0),

1197   Fig. 10C] and bilimbate capillary chaetae [character 31(1)] in descriptions of members of

1198   species. For some individuals, both unilimbate and bilimbate chaetae have been recorded,

1199   however, the predominate form in each case was coded in the current analysis. Bolívar & Lana

1200   (1986) and Blake (1996c) additionally noted some members of species possess bilimbate chaetae

1201   **(subject 32)** with an irregular blade [character 32(1)], such as *Magelona variolamellata* (Fig.

1202   10E), and Brasil (2003) additionally noted it to occur among members of species such as *M.*

1203   *riojai* (Fig. 10D), *M. pacifica* and *M. pitelkai*. Members of the outgroups possess unilimbate

1204   capillary chaetae [character 31(0)], whilst subject 32 is not applicable. Additional to the

1205 limbations of capillary chaetae, the relative lengths of noto- and neurochaetae may vary **(subject**

1206 **33)**. Either being equivalent in length [character 33(0)] e.g., *M. nonatoi*, longer in the notopodia

1207 [character 33(1)], e.g., *M. sacculata*, or longer in the neuropodia [character 33(2)], e.g., *M.*

1208 *variolamellata*. For members of *Phyllochaetopterus limicolus, Spio filicornis* and *Prionospio*

1209 *lighti*, chaetae are longer in the notopodia [character 33(1)], whilst for members of *Laonice*

1210 *cirrata* and *P. ehlersi* they are equivalent in length [character 33(0)]. In some members of

1211 magelonid species chaetae of all thoracic chaetigers are similar, however, in others the chaetae of

1212 the ninth chaetiger are modified. For this reason, the chaetae were coded collectively for the first

1213 eight chaetigers, and separately for chaetiger nine (see below).

1214 ***Characters of parapodia of chaetiger 8 (subjects 34–40)***

1215 As described above, development of lamellae in the magelonid thorax may be similar on all

1216 chaetigers or vary between them. For members of species in which they vary, the parapodia of

1217 chaetigers 8 and 9 in particular may show larger differences in comparison to preceding

1218 chaetigers. However, the same characters that were coded for the first seven chaetigers can be

1219 applied to the posterior-most thoracic chaetigers. The notopodial lamellae (**subjects 34–36**) of

1220 chaetiger 8 may be postchaetal [character 34(0)] or subchaetal [character 34(1)] in position

1221 relative to the chaetal bundle, filiform [character 35(0)] or foliaceous [character 35(1)] in shape,

1222 with smooth [character 36(0)], crenulate [character 36(1)] or bilobed [character 36(2)] margins.

1223 Subjects 34–36 are considered not applicable to members of *Phyllochaetopterus limicolus*.

1224 However, remaining members of the outgroups possess postchaetal [character 34(0)], foliaceous

1225 [character 35(1)] parapodia with smooth margins [character 36(0)]. Superior dorsal lobes

1226 **(subject 37)** may be absent [character 37(0)] or present [character 37(1)]. The neuropodial

1227 lamellae (**subjects 38–40**) of chaetiger 8 may be postchaetal [character 38(0)], subchaetal

1228   [character 38(1)] or prechaetal [character 38(2)] in position relative to the chaetal bundle, and

1229   may be filiform [character 40(0)] or foliaceous [character 40(1)] in shape. However, an

1230   additional postchaetal expansion (**subject 39**), often triangular in shape, as is seen among

1231   members of *Magelona montera* (Fig. 9D) is sometimes observed in the neuropodia of chaetiger 8

1232   (and 9, see below) [character 39(1)]. Subjects 38–40 are considered not applicable to members of

1233   *Phyllochaetopterus limicolus*. Members of *Spio filicornis, Prionospio lighti, P. ehlersi* and

1234   *Laonice cirrata* have postchaetal [character 38(0)], foliaceous [character 40(1)] neuropodia in

1235   chaetiger 8, without an additional postchaetal expansion [character 39(0)].

1236   ***Characters of the parapodia of chaetiger 9 (subjects 41–49)***

1237   For chaetiger 9, observed characters were coded in the same way as for chaetiger 8. The

1238   notopodial lamellae (**subjects 41, 43–44**) of chaetiger 9 may be postchaetal [character 41(0)], or

1239   subchaetal [character 41(1)] in position in comparison to the notochaetae, and may be filiform

1240   [character 43(0)] or foliaceous [character 43(1)] in shape, with smooth [character 44(0)],

1241   crenulate [character 44(1)] or bilobed [character 44(2)] margins. Members of the outgroups

1242   possess postchaetal [character 41(0)] notopodia chaetiger 9 which are foliaceous [character

1243   43(1)], with smooth margins [character 44(0)]. However, subjects 41, 43 and 44 are not

1244   applicable to *Phyllochaetopterus limicolus*. Superior dorsal lobes (**subject 45**) may be present

1245   [character 45(1)] or absent [character 45(0)].

1246   The neuropodial lamellae (**subjects 46, 48**) of chaetiger 9 may be postchaetal [character

1247   46(0)], subchaetal [character 46(1)] or prechaetal [character 46(2)] in position in comparison to

1248   the chaetal bundle, and filiform [character 48(0)] or foliaceous [character 48(1)] in shape. As

1249   with chaetiger 8, an additional postchaetal expansion (**subject 49**) may be absent [character

1250   49(0)] or present [character 49(1)]. Members of the outgroups possess foliaceous [character

1251   48(1)], postchaetal [character 46(0)] lamellae without an additional postchaetal expansion

1252   [character 49(0)], except for *P. limicolus* for which these subjects are not applicable.

1253   The parapodia in chaetiger 9 among members of some magelonid species may be

1254   markedly different in comparison to preceding chaetigers. For example, the lamellae in chaetiger

1255   9 among members of *Magelona johnstoni* (Fig. 9I) are much broader and lower [characters 42(0)

1256   and 47(0)] in comparison to the elongate lamellae of chaetigers 1–8 in both the noto- and

1257   neuropodia, and the elongate lamellae of chaetiger 9 amongst members of other species, e.g., *M.*

1258   *equilamellae* [characters 42(1) and 47(1), Fig. 7B]. For this reason, additional subjects were

1259   added to accommodate the height of lamellae in both rami of chaetiger 9 (**subjects 42 and 47**).

1260   As members of *Octomagelona* species only possess eight thoracic chaetigers these subjects were

1261   coded as inapplicable for these taxa and additionally for members of *Phyllochaetopterus*

1262   *limicolus*. Members of *Spio filicornis* possess broad and low parapodia in chaetiger 9 [characters

1263   42(0) and 47(0)], whilst for members of *Prionospio lighti, P. ehlersi* and *Laonice cirrata* they are

1264   more elongate [characters 42(1) and 47(1)].

1265   ***Characters of the chaetae of chaetiger 9 (subjects 50–51)***

1266   The chaetae of chaetiger 9 in magelonids may be similar to or vary from those of chaetigers 1–8

1267   **(subjects 50 and 51)**. They may be the same length [character 50(0), as in the outgroups],

1268   shorter than [character 50 (1)], or longer than those of chaetigers 1–8 [character 50(2)]. The

1269   distal ends of chaetiger 9 chaetae may be gently tapered as is seen in the preceding chaetigers

1270   [character 51(0), Figs. 8F and 8G] (observed also for members of the outgroups), or have

1271   distinctly mammiform, expanded, mucronate tips [character 51(1), Figs. 7C, 7D, 9I and 10F–H]

1272   such as among members of *Magelona johnstoni* and *M. mirabilis*. In members of other species,

1273   the distal ends are pennoned [character 51(2), Fig. 10I], such as *M. pitelkai*, *M. hobsonae*, and *M.*

1274   *hartmanae*.

1275   ***Characters of the thoracic region (subjects 52–53)***

1276   Whilst many authors have noted the often-marked difference between thoracic and abdominal

1277   regions in magelonids (Fig. 8B), other characteristics of the thoracic region have been largely

1278   overlooked. Mortimer (2019) noted that among members of certain magelonid species, the

1279   thoracic interparapodial margins **(subject 52)** may be characteristically bulbous and rounded

1280   [character 52 (1), Fig. 11A], as seen among members of *Magelona alleni*, whilst among

1281   members of others, such as *M. johnstoni*, they are straight [character 52(0), Fig. 11B]. Members

1282   of the outgroups possess straight thoracic interparapodial margins [character 52(0)].

1283   Uebelacker & Jones (1984) first coined the phrase "oblique lateral slits" **(subject 53)** in

1284   relation to members of their undescribed species *Magelona* sp. I from the Gulf of Mexico. Later,

1285   Bolívar and Lana (1986) described "sulcos latero-dorsais" (dorso-lateral slits) and "sulcos

1286   transversais" (transverse slits) for members of *M. variolamellata* (Fig. 11C). Brasil (2003) used

1287   the term dorsal furrows/grooves, highlighting them to be present also among members of *M.*

1288   *polydentata* [character 53(1)], whilst herein, the term dorso-lateral grooves is utilised. Brasil

1289   (2003) stated that they vary in number, position, and location, and they were noted to be absent

1290   in the majority of members of magelonid species [character 53(0)] and are additionally absent

1291   among members of the outgroups.

1292   ***Dimensions of post-chaetiger 9 segments (subject 54)***

1293   Uebelacker & Jones (1984) described posterior segments that are much longer than wide

1294   [character 54(1), Fig. 12A] among members of an undescribed species, *Magelona* sp. H, from

1295   the Gulf of Mexico. Later, *M. posterelongata* was the first species with individuals formally

1296   described with this feature. Many authors have ignored this characteristic, a problem

1297   compounded by the difficulty in collecting entire specimens. A further problem in coding this

1298   character is that abdominal chaetigers may vary in proportion along the length of the posterior

1299   region. It is believed, however, that the majority of magelonid species possess abdominal

1300   chaetigers equal in length and width, or only marginally longer than their width; a characteristic

1301   shared with members of the outgroups [character 54(0)].

1302   ***Characters of the parapodia of post-chaetiger nine segments (subjects 55–59)***

1303   The abdominal region of magelonids consists of many chaetigers carrying biramous parapodia.

1304   In contrast to the thorax, the abdominal lamellae of the notopodia and neuropodia are generally

1305   symmetrical and of similar size and shape in both rami. The abdominal region starts at chaetiger

1306   9 for members of *Octomagelona* (Fig. 6) and chaetiger 10 for members of *Magelona* (Fig. 11A)

1307   and is marked by a change in chaetal type, from capillary chaetae to hooded hooks. Abdominal

1308   lamellar shape **(subject 55)** varies among members of species, from triangular to rounded. They

1309   may be basally constricted [those with rounded lamellae, character 55(1), Figs. 12C, 12H], or

1310   without a basal constriction, being broad based [character 55(0), Fig. 12B]. The latter situation

1311   being generally observed among members of species possessing more triangular lamellae,

1312   tapering to pointed tips (Fig. 12D). Subject 55 is not applicable to members of

1313   *Phyllochaetopterus limicolus*, however all other members of the outgroups have lamellae without

1314   a basal constriction [character 55(0)].

1315   At the inner margins of chaetal rows, triangular to digitiform processes **(subject 56)** may

1316   be present [character 56(1), Figs. 12C, 12F, 12H, 12I]. Jones termed these structures dorsal

1317   medial lobes (DML) for notopodia and ventral medial lobes (VML) for neuropodia. Uebelacker

1318   & Jones (1984) believed that they may occur universally throughout the family, but this is a

1319   viewpoint not shared by the current authors. They are absent [character 56(0)] in members of the

1320   outgroups, however, this subject is considered not applicable to *Phyllochaetopterus limicolus*. In

1321   members of magelonid species, the size of the medial lobes in the abdomen varies widely, from

1322   minute and difficult to discern, to long and conspicuous structures, e.g., among members of

1323   *Magelona montera*. For comparison, the medial lobes were coded depending on their height

1324   relative to abdominal hooded hooks **(subject 57)**: character 57(0) for members of species in

1325   which they are smaller than the hooks and character 57(1) when they are larger than the hooks.

1326   The latter subject is not applicable to the outgroups.

1327   The abdominal lamellae may extend behind chaetal rows **(subject 58)**. This postchaetal

1328   expansion (previously termed the interlamella) is often more conspicuous in the anterior

1329   abdomen and when present [character 58(1), Figs. 12C, 12E and 12H] it may be rounded to

1330   triangular. Among members of species in which it is absent [character 58(0), Figs. 12B, 13D and

1331   14B], the abdominal hooded hooks arise from a distinct ridge (Figs. 12B and 13E). Postchaetal

1332   expansions are absent among members of the outgroups, whilst in members of

1333   *Phyllochaetopterus limicolus* the subject is considered inapplicable.

1334   As stated above, abdominal lamellae **(subject 59)** in magelonids are generally

1335   symmetrical in size and shape [character 59(0), Figs. 12D and 12H] as in members of the

1336   outgroups. However, in some magelonids, such as members of *Magelona alleni*, the lamellae are

1337   sub-equal between the two rami [character 59(1), Fig. 12G]. This subject is inapplicable to

1338   members of *Phyllochaetopterus limicolus*.

1339   ***Characters of lateral abdominal pouches (subjects 60–65)***

1340   Lateral pouches **(subject 60)** are present among members of some species of magelonids, located

1341   laterally between the parapodia of certain abdominal chaetigers [character 60(1)]. Their presence

1342   [character 60(1)] or absence [character 60(0)] is often a key diagnostic feature, although their

1343   function is currently unknown (Jones, 1968; Mortimer & Mackie, 2014). Pouches vary in

1344   morphology, direction of opening, number, and location. However, descriptions of these

1345   structures have generally been limited, often only indicated as being present or absent. Fiege et

1346   al. (2000) described two types of lateral pouch: Σ-shaped occurring in the anterior abdomen,

1347   generally paired, and opening anteriorly, whilst C-shaped pouches were noted to occur on

1348   median and posterior abdominal chaetigers, opening posteriorly and occurring in pairs or singly.

1349   Mortimer (2010) suggested these terms should be abandoned to enable variations to be better

1350   understood, and subsequently, Mortimer & Mackie (2014) and Mortimer (2019) detailed further

1351   pouch morphologies. Following the latter authors, lateral pouches when present, were coded

1352   based on six subjects: arrangement of pouches **(subject 61)**, direction of pouch openings

1353   **(subject 62)**, posteriorly open lateral pouch arrangement **(subject 63)**, lateral pouch distribution

1354   **(subject 64)**, and margins of posteriorly open pouches **(subject 65)**. Firstly, pouches are either

1355   all paired [character 61(0), Fig. 13C] or unpaired [character 61(1), Fig. 13B], or both types are

1356   present [character 61(2), Fig. 13A]. Secondly, both anteriorly and posteriorly opening pouches

1357   are present [character 62(1), Figs. 13A, 13E and 13G], e.g., members of *Magelona johnstoni*, or

1358   only posteriorly open pouches are present [character 62(0), Figs. 13B and 13C]. Posteriorly open

1359   pouches may occur on alternate segments [character 63(1), Fig. 13B], or on consecutive

1360   segments [character 63(0), Fig. 13C], or alternatively, they may be present on both consecutive

1361   and alternating chaetigers at varying points along the abdomen [character 63(2)], e.g., members

1362   of *M. pulchella*. Fiege et al. (2000) described the first occurrence of lateral pouches on the body

1363   as an important distinguishing character between members of species and is relatively easy to

1364   observe. In members of some species, lateral pouches are present throughout most of the

1365   abdomen [character 64(0)], whilst in others they are present only on median and posterior

1366   chaetigers [character 64(1)], and in others restricted to the posterior abdomen only [character

1367   64(2)] (Mortimer & Mackie, 2014). Whilst the margins of most posteriorly open pouches are

1368   smooth [character 65(0)], in members of some species, such as *M. pacifica*, they are medially

1369   split [character 65(1), Fig. 13H]. One of the biggest problems in coding these characters is the

1370   lack of information known about the posterior regions of many magelonids, whilst some pouches

1371   are present throughout most of the abdomen and are therefore likely to be recorded even in

1372   posteriorly incomplete specimens. For members of species in which pouches only occur in the

1373   extreme posterior region, pouches are likely to be recorded as absent if individuals are described

1374   from anterior fragments only. Lateral pouches are present [character 60(1)] in members of

1375   outgroups, *Laonice cirrata* and *Prionospio ehlersi*. These are paired [character 61(0)],

1376   posteriorly open [character 62(0)] and with smooth margins [character 65(0)]. They occur on

1377   consecutive segments [character 63(0)] on median and posterior chaetigers [character 64(1)].

1378   Lateral pouches are absent [character 60(0)] in the remaining members of the outgroups.

1379   ***Characters of post-chaetiger 9 chaetae (subjects 66–74)***

1380   Magelonids possess hooded hooks in the abdominal region **(subject 66)**, located between the

1381   lamellae and medial lobes (when present). They are present [character 66(1)] in members of all

1382   magelonid taxa and members of the outgroup except *Phyllochaetopterus limicolus* [character

1383   66(0)]. In magelonids, hooded hooks generally occur in one row per ramus, but recent studies

1384   suggest that they can occur in two rows, at least in the medial part of the rami (Mortimer et al.,

1385   2020) (Fig. 14B for members of *M. equilamellae*). Although, this may prove to be an important

1386   characteristic in future studies, due to lack of information for the majority of species this was not

1387   considered in this study.

1388   The dentition of abdominal hooks **(subject 67)** may be bidentate [character 67(0), e.g.,

1389   members of *Magelona minuta* and *M. papillicornis*, Figs. 14C and 14D] with one secondary

1390   tooth above the man fang, tridentate [character 67(1), Fig. 14E], with two secondary teeth above,

1391   or polydentate [character 67(2)], having three or more secondary teeth above the main fang.

1392   Quadridentate, pentadentate, and hexodont hooks (Figs. 14F–H) have been recorded among

1393   Magelonidae, with some polydentate individuals carrying more than one type of hook. Where

1394   members of species have been recorded with more than one, the dentition which predominates

1395   was coded. For example, members of *M. minuta* are recorded to possess the odd sporadic

1396   tridentate hook (Mills & Mortimer, 2018), but carry predominately bidentate hooks. Members of

1397   the outgroup *Spio filicornis* possess bidentate [character 67(0)] hooded hooks, whilst members of

1398   *Prionospio lighti, P. ehlersi* and *Laonice cirrata* possess polydentate hooded hooks [character

1399   67(2)]. This subject is not applicable to members of *Phyllochaetopterus limicolus*, which have

1400   uncini.

1401   Jones (1971) was the first author to draw attention to the fact that in members of some

1402   species the hook at the base of the lamellae **(subject 68)** may be smaller than the others

1403   [character 68(1), Figs. 12E and 14I]. Later it has been suggested that not only their size but also

1404   their appearance may indicate groups of closely related species (*Magelona pitelkai, M.*

1405   *hobsonae, M. hartmanae, M. dakini, M. filiformis, M. capensis*). However, Brasil (2003), upon

1406   re-examination of the holotypes of the first four species, observed no differences in shape, only

1407   differences in size. Among members of other magelonid species, the hook at the base of the

1408   lamellae is of equivalent size to the rest [character 68(0), Fig. 13D]. The subject is not applicable

1409   to members of the outgroups.

1410   Uebelacker & Jones (1984) first reported the presence of enlarged chaetae **(subject 69)** in

1411   the abdominal region of members of four undescribed species from the Gulf of Mexico;

1412   *Magelona* sp. C, possessing an enlarged recurved hook with a minute apical tooth in each ramus;

1413   *Magelona* sp. D, with enlarged hooded apical spines (Fig. 12F); *Magelona* sp. E, possessing

1414   large bidentate hooks akin to "ordinary" hooks; and lastly *Magelona* sp. H, with large unidentate

1415   recurved spines. Hernández-Alcántara & Solís-Weiss (2000) formally described members of two

1416   of these species (*Magelona* spp. D and H) as *Meredithia spinifera* and *M. uebelackerae*,

1417   respectively, erecting the new genus based on this distinctive feature. The authors stated that

1418   "although this character is the only one that differentiates this group from the other species

1419   described in this monogeneric group, it is sufficiently distinctive to make it a valid generic level

1420   character." However, Mortimer & Mackie (2003) felt that stronger evidence for recognising

1421   other genera within the family was needed, preferring to follow Uebelacker & Jones (1984) by

1422   including species with enlarged abdominal chaetae in *Magelona*, and synonymising *Meredithia*

1423   with *Magelona*. Two additional species with enlarged abdominal chaetae have since been

1424   described: *Magelona magnahamata* and *Magelona falcifera*. For the current analysis, the

1425   presence [character 69(1)] and absence [character 69(0)] of enlarged chaetae in the abdomen was

1426   noted as well as the morphology of the distal ends **(subject 70)**, i.e., recurved [character 70(0),

1427   Fig. 14K], spine-like [character 70(1)], or an enlarged normal hook [character 70(2)]. Enlarged

1428   hooks are not present in members of the outgroups [character 69(0)], therefore subject 70 is not

1429   applicable (together with subject 69 for *Phyllochaetopterus limicolus*).

1430   The number of hooded hooks per ramus in abdominal chaetigers **(subject 71)** is variable

1431   and characters distinguished as eight or more hooks per ramus [character 71(0), e.g., members of

1432   *Magelona equilamellae*, Fig. 14B, and members of outgroups *Prionospio lighti, P. ehlersi* and

1433   *Laonice cirrata*], and less than eight [character 71(1), Fig. 14J], such as among members of *M.*

1434   *papillicornis* and members of outgroup *Spio filicornis*. This separation in number was based on

1435   the examinations of specimens from a number of different species and assessing several

1436   chaetigers of the same specimen. As variations in the number of hooks have been observed along

1437   the length of the abdomen (e.g., members of *M. papillicornis* have a higher number of hooks in

1438   the mid-abdominal region), the number of hooks was counted in the anterior abdomen. Subject

1439   71 is not applicable for members of *Phyllochaetopterus limicolus.* Hooks may be arranged in two

1440   formations **(subject 72)**: occurring in two groups per ramus with main fangs arranged face-to

1441   face (vis-à-vis) [character 72(0), Figs. 12C, 12G, 12H, 14B and 14J], or in unidirectional rows

1442   (vis-à-dos) with main fangs pointing in one direction [character 72(1), Fig. 13D]. Vis-à-vis

1443   orientation is more common among members of the Magelonidae, whilst vis-à-dos is present for

1444   all members of the outgroups (subject 72 is not applicable to *P. limicolus*).

1445   Neuropodia with sabre chaetae **(subject 73)** are present [character 73(1)] among

1446   members of the spionid outgroups. Such chaetae are absent [character 73(0)] among members of

1447   *Phyllochaetopterus limicolus* and all ingroup species.

1448   Internal support chaetae, or aciculae **(subject 74)**, have been reported among members of

1449   several magelonid species. These curved and slender chaetae support the bases of the lamellae,

1450   and it is possible that they are more prevalent among members of species with larger abdominal

1451   lamellae. The proximal ends of the aciculae may overlap in the junction between the noto- and

1452   neuropodia (Figs. 12C and 12H). Notes on their presence [character 74(1)] or absence [character

1453   74(0)], as well as their description, are poorly reported in the literature. Jones (1978) stated that

1454   all magelonid abdominal chaetigers are supported by these structures, although this is not an

1455   observation supported by the current authors. Aciculae are generally more conspicuous in larger

1456   specimens, whilst slide preparations of parapodia may be necessary for smaller individuals. The

1457   relative obscurity of aciculae may be a factor in the limited inclusion in descriptions of

1458   specimens. Aciculae are absent in all members of the outgroups [character 74(0)].

1459   ***Characters of body pigmentation (subjects 75–76)***

1460   Among members of some species pigmentation in the posterior thorax **(subject 75)** is evident

1461   even in fixed material [character 75(1)], often deep reddish to brown in colour. Very little is

1462   known about this character beyond presence or absence [character 75(0)]. When pigment is

1463   present, there are two patterns of distribution **(subject 76)**. Among members of some species,

1464   such as *Magelona alleni* and *M. equilamellae*, the pigment forms a distinct band [character

1465   76(0), Figs. 15A and 15C], often from chaetigers 4/5 to 8; among members of other species only

1466   light, dispersed pigmentation in posterior chaetigers is noted [character 76(1)], e.g., members of

1467   *M. symmetrica*. Moreover, members of *Magelona fasciata* Mortimer, Kongsrud & Willassen

1468   (2021) from West Africa are noted to have distinct stripy pigmentation over much of the body

1469   (Fig. 15B). Pigmentation on the palps of members of some species, such as *M. mirabilis*, has

1470   been noted (see Mills & Mortimer, 2019: fig. 4.2.6). However, insufficient information is

1471   currently available to enable coding of this character. Relevant pigmentation is absent in

1472   members of the outgroups [character 75(0)].

1473   ***Characters of granular bodies (subjects 77–78)***

1474   The surfaces of segments can have granular bodies **(subject 77)** appearing as spots, distributed in

1475   a variety of patterns on both the thorax and abdomen, and remain upon fixation and preservation

1476   of material [character 77(1), Figs. 6A, 9H and 15C]. Jones (1971) felt that this characteristic had

1477   no systematic significance. However, patterns appear to be species specific, particularly those of

1478   the thoracic region. The latter may appear as transverse stripes (Fig. 16A) or distinct smaller

1479   circular regions adjacent to the parapodia (Fig. 16B). Abdominal interparapodial areas

1480   commonly have granular bodies occurring in patches **(subject 78)** [character 78(1), Figs. 16C

1481   and 16D] among members of Magelonidae and may cover a large part of the lateral region

1482   between parapodia of adjacent chaetigers. Both thoracic and abdominal bodies may stain with

1483   dyes such as Rose Bengal, or be highlighted by methyl green, in which the granules appear white

1484   against the contrasting stain (Figs. 16B and 16C). Whilst staining patterns can be extremely

1485   useful in separating members of species (Figs. 11D, 11E and 16A), it was not included in the

1486   current study. However, it may prove useful in the future, as more methyl green patterns are

1487   described. Granular bodies and abdominal interparapodial areas are absent in members of the

1488   outgroups [character 77(0), character 78(0)].

1489   ***Tube construction (subject 79)***

1490   In general, magelonids are relatively motile, burrowing more or less continually through

1491   sediments (Jumars, Kelly & Lindsay, 2015), without constructing tubes [character 79(0)].

1492   However, members of several species are known to build distinct multi-layered tubes covered in

1493   sand [character 79(1), Fig. 16E]. Mills & Mortimer (2019) investigated the permanency of these

1494   tube-lined burrows among members of the European species, *Magelona alleni*. Members of

1495   some species, such as *M. filiformis*, have been described living in fragile tubes of a secretion to

1496   which sand grains adhere. These are not considered as tubes *per se* but are believed to be the

1497   worm's response to removal from its habitat. Members of the outgroups, *Spio filicornis* and

1498   *Phyllochaetopterus limicolus*, are known to build distinct tubes [character 79(1)], whilst the

1499   situation is unknown for members of *Prionospio lighti, P. ehlersi* and *Laonice cirrata*.

1500

1501   # Characters not included, but of possible future consideration

1502 ***Prostomial features***

1503 Magelonid prostomia may carry distinct markings on either side of the dorsal muscular ridges

1504 (Figs. 4A, 4C–E, 5A, 5B and 5E), the pattern of which is generally species specific, whilst

1505 members of other species show no obvious markings (Figs. 4G and 4H). Although this can be an

1506 important diagnostic feature, this was not included in the current analysis due to difficulties in

1507 adequately describing this character.

1508 ***Thoracic chaetae***

1509 Mills & Mortimer (2018) highlighted differences in the number of thoracic chaetae among

1510 members of different species, and additionally observed variations in number of chaetae on

1511 different chaetigers of the same animal for members of several magelonid species. They noted

1512 that members of some species, such as *Magelona cincta*, have distinctly splayed chaetae in the

1513 posterior thorax when compared to members of other species. Whilst these three characteristics

1514 may prove to be useful, limited information is currently available, prohibiting their use in the

1515 current study.

1516 ***Features of the thoracic region***

1517 More recently, several additional characteristics of the thoracic region have been noted.

1518 Mortimer & Mackie (2009) and Mortimer (2019) described distinct V- and X-shaped ventral

1519 markings in the mid-thoracic region of members of species such as *Magelona crenulifrons* and

1520 *M. pulchella* (Figs. 11D and 11E). Among members of other magelonid species, thoracic ventral

1521 pads/swellings have been recorded, such as those observed among members of *M. mirabilis*

1522 (Mortimer & Mackie, 2014) or *M. obockensis* (Mortimer, 2010). These swellings may be oval to

1523 reniform in shape (Figs. 11F and 11G). However, occurrence of these two features in members

1524 of the majority of species is unknown.

1525   Although, the constriction at the thorax/abdomen junction can be marked and may vary

1526   between species, the extent to which it is constricted can be greatly influenced by preservation

1527   and fixation and was not considered herein. Despite this, however, it is a character worthy of

1528   further study, and should be detailed more fully in future descriptions. Brasil (2003) indicated

1529   that members of *Octomagelona* present a constriction despite lacking a 9th "thoracic" chaetiger,

1530   suggesting that the character may not simply indicate a transition between the thorax and the

1531   abdomen.

1532   Whilst average length and the average number of chaetigers appear to be species specific,

1533   the lack of information for members of many species prohibits this as a character in the analysis

1534   at the present time. Many individuals of magelonid species are described from anterior fragments

1535   only. The breadth of individuals, however, may prove an important character. Members of

1536   species like *Magelona minuta,* true to their name, rarely attain widths greater than 0.5 mm, being

1537   somewhat long and slender. Members of species such as *M. alleni* are distinctly broad and stout,

1538   often measuring over 1 mm in width (Mortimer, Kongsrud & Willassen, 2021). Additionally,

1539   Mills & Mortimer (2019) indicate that stouter magelonid species generally are shorter in

1540   comparison to width and have a fewer number of chaetigers. This is something which warrants

1541   further investigation.

1542   ***Abdominal hooded hooks***

1543   Mills & Mortimer (2018) highlighted differences in the angle between the main fang and

1544   secondary teeth in abdominal hooded hooks of members of several magelonid species and

1545   further suggested characteristics such as the width and roundedness of the main fang, and the

1546   angle between it and the axis of the hook shaft, as noted for example by Jones (1963, 1977), may

1547   prove useful in future studies.

1548   *Pygidium*

1549   Magelonids possess a pair of digitiform pygidial cirri on either side of the pygidium (Figs. 16F

1550   and 16G). Uebelacker & Jones (1984) noted the presence of three pygidial cirri on individuals of

1551   an undescribed species, *Magelona* sp. B, from the Gulf of Mexico, however, it is believed that

1552   the third cirrus may actually represent the elongated, rounded tip of the pygidium itself. As this is

1553   the only magelonid that has been described with this feature, the number of pygidial cirri was not

1554   included in this study. Mills & Mortimer (2019) noted that pygidial cirri of members of *M. alleni*

1555   were more truncate and triangular (Fig. 16H) in comparison to other magelonids, however, this is

1556   something that warrants further investigation.

1557   Whilst Rouse (2001) stated that the magelonid anus is terminal, early illustrations from

1558   McIntosh (1878) of members of *Magelona mirabilis* (possibly *M. johnstoni*; see Fiege, Licher &

1559   Mackie, 2000) clearly show the anus in a distinctly ventral position. Unfortunately, for members

1560   of many species the pygidium is unknown, or the amount of information provided by authors has

1561   been relatively limited. When included in descriptions, the pygidium is often drawn from a

1562   dorsal perspective, thus conclusions about the position of the anus are often difficult to make.

1563   Mills & Mortimer (2019) investigated the situation among members of five European species,

1564   concluding that the anus was ventral in members of four species, whilst in the latter, *M. alleni*, it

1565   was distinctly terminal in position (Fig. 16H). Subsequently, Mortimer, Kongsrud & Willassen

1566   (2021) have noted that members of *Magelona fasciata* from West Africa also have a terminal

1567   anus. Whilst this may prove to be a valuable character in subsequent studies, the lack of

1568   information among individuals of many species precludes inclusion in the current study.

1569   **Inferring phylogenetic hypotheses**

1570   Phylogenetic inferences were performed using PAUP* 4.0b10 (Swofford, 2001), with all

1571   observations weighted equally and multiple subject–predicate relations ("multistate characters")

1572   treated as non-additive (Table S1). The following command string was executed (Larkin, Neff &

1573   Simpson, 2006; Fitzhugh, 2010b; Fitzhugh et al., 2015; Nogueira et al., 2010; Nogueira,

1574   Fitzhugh & Hutchings, 2013): hsearch enforce = no start = stepwise addseq = random nreps =

1575   100000 nchuck = 5 chuckscore = 1; hsearch enforce = no start = current chuckscore = no. As

1576   noted earlier in **Methodological considerations**, the commands used are not tantamount to what

1577   has been incorrectly called "parsimony analysis." Rather, implementation of these commands is

1578   consistent with abductive reasoning for the purpose of causally accounting for differentially

1579   shared characters by way of common causes as fully as possible. Character transformation series

1580   were examined using Mesquite 3.61 (Maddison & Maddison, 2011).

RESULTS
1581

1582   The phylogenetic inference using data in Table S1 produced 2,417,600 cladograms of 404 steps

1583   each. The consistency index for each is 0.243 and retention index is 0.744. The strict consensus

1584   tree for all cladograms is shown in Fig. 17. What is notable is the mix of clades and grades

1585   within the monophyletic Magelonidae. A consequence of the overall arrangements of these

1586   phylogenetic hypotheses is that there can be no generic-level phylogenetic hypotheses that can

1587   be formally named without also incurring paraphyletic taxa. The result, as will be pointed out in

1588   the **DISCUSSION**, is that the only (composite) phylogenetic hypothesis that can be formally

1589   recognised is Magelonidae. The Magelonidae clade involves seven phylogenetic hypotheses

1590   referring to the following respective characters:

1591   1. Shovel-shaped prostomium: absent (0) → *present* (1)

1592   2. Nuchal organs: present (1) → *absent* (0)

1593   8. Prostomial ridges: absent (0) → *present* (1)

1594   10. Palp origin: dorsal (0) → *ventral* (1)

1595   11. Palp surface: non-papillate (0) → *papillate* (1)

1596   14. Burrowing organ: absent (0) → *present* (1)

1597   15. Body regionation: non-magelonid (0) → *magelonid-like* (1).

1598   The present results indicate that *Octomagelona* cannot be maintained, given that the clade

1599   is nested within *Magelona*. And while the arrangements of the phylogenetic hypotheses among

1600   all the cladograms impose severe limits that only allow for formally recognising Magelonidae,

1601   there are no phylogenetic hypotheses to which the type genus *Magelona* refer. The implications

1602   of these results will be addressed in the **DISCUSSION**.

1603   In addition to the Magelonidae, there are 20 additional clades, indicated by letters **a**

1604   through **t** in Fig. 17, from which phylogenetic hypotheses deserve mention. None of these clades

1605   can be formally named, given the various grade groups also present among the cladograms.

1606   Whilst serving as synapomorphies for these clades, those characters that are homoplasious

1607   (including reversals and convergence) are denoted by an asterisk (*):

1608   **Clade a** – 22. Chaetigers 1–7 notopodial lamellae shape: foliaceous (1) →

1609   *filiform* (0)*

1610   26. Chaetigers 1–7 neuropodial lamellae position relative to neurochaetae:

1611   postchaetal (0) → *subchaetal* (1)*

1612   28. Chaetigers 1–7 neuropodial lamellae shape: foliaceous (1) →

1613   *filiform* (0)*

1614   **Clade b** – 5. Prostomial horns: present (1) → *absent* (0)*

1615   20. Development of neuropodia along thorax: different in some chaetigers,

1616   (1) → *all similar* (0)*

1617   26. Chaetigers 1–7 neuropodial lamellae position relative to neurochaetae:

1618   subchaetal (1) → *postchaetal* (0)*

1619   30. Chaetigers 1–7 lengths of noto- and neuropodial lamellae: notopodial

1620   longer (1) → *equivalent* (0)*

1621   **Clade c** – 4. Prostomium distal shape: straight (2) → *triangular* (0)*

1622   6. Shape of prostomial horns: rudimentary (1) → *distinct* (0)*

1623   46. Chaetiger 9 neuropodial lamellae position: postchaetal (0) →

1624   *subchaetal* (1)*

1625   **Clade d** – 67. Post-chaetiger 9 noto- and neuropodial hooded hooks dentition:

1626   bidentate (0) → *tridentate* (1)*

1627   **Clade e** – 16. Number of anterior body region chaetigers: nine (1) → *eight* (0)

1628   18. Development of notopodia along thorax: all similar (0) → *different in*

1629   *some chaetigers* (1)*

1630   **Clade f** – 29. Chaetigers 1–7 neuropodial filiform lamellae shape distal ends:

1631   pointed (0) → *distally expanded/scoop shaped* (1)

1632   60. Post-chaetiger 9 lateral pouches: absent (0) → *present* (1)*

1633   **Clade g** – 22. Chaetigers 1-7 notopodial lamellae shape: filiform (0) → *foliaceous* (1)*

1634   35. Chaetiger 8 notopodial lamellae shape: filiform (0) → *foliaceous* 35(1)*

1635   55. Post-chaetiger 9 lamellae shape: without basal constriction (0) → *with*

1636   *basal constriction* (1)*

1637   **Clade h** – 12. Number of rows of proximal palp papillae: 10–14 (2) → *4–8* (1)*

1638   43. Chaetiger 9 notopodial lamellae shape: filiform (0) → *foliaceous* (1)*

1639   75. Pigmentation in posterior thorax: present (1) → *absent* (0)*

1640   **Clade i** –   18. Development of notopodia along thorax: different in some chaetigers (1)

1641   → *all similar* (0)*

1642   45. Chaetiger 9 dorsal superior lobes: absent (0) → *present* (1)*

1643   **Clade j** –   38. Chaetiger 8 neuropodial lamellae position: subchaetal (1) → *prechaetal*

1644   (2)*

1645   60. Post-chaetiger 9 lateral pouches: absent (0) → *present* (1)*

1646   **Clade k** –   22. Chaetigers 1-7 notopodial lamellae shape: foliaceous (1) → *filiform* (0)*

1647   57. Post-chaetiger 9 dorsal medial lobes length: smaller than hooks (0) →

1648   longer than hooks (1)*

1649   68. Post-chaetiger 9 hooded hooks adjacent to notopodial subchaetal

1650   or neuropodial suprachaetal lamellae: same size (0) → *smaller than rest*

1651   (1)*

1652   **Clade l** –   46. Chaetiger 9 neuropodial lamellae position: subchaetal (1) → *prechaetal*

1653   (2)*

1654   **Clade m** –   4. Prostomium distal shape: straight (2) → *rounded* (1)

1655   5. Prostomial horns: present (1) → *absent* (0)*

1656   42. Chaetiger 9 notopodial lamellae height: elongate (1) → *low* (0)*

1657   50. Lengths of chaetiger 9 fascicles relative to chaetigers 1–8 fascicles:

1658   same length as chaetae in chaetigers 1–8 (0) → *shorter than chaetae in*

1659   *chaetigers 1–8* (1)

1660   51. Distal ends of chaetae in chaetiger 9: gently tapered, similar to

1661   chaetigers 1–8 (0) → *mucronate* (1)

1662   55. Post-chaetiger 9 lamellae shape: with basal constriction (1) →

1663   *without basal constriction* (0)*

1664   61. Post-chaetiger 9 lateral pouch arrangement: unpaired (1) → *both*

1665   *paired and unpaired* (2)*

1666   62. Direction of lateral pouch openings: posteriorly (0) → *posteriorly*

1667   *and anteriorly* (1)*

1668   **Clade n –**   13. Number of rows of distal palp papillae: four (1) → *two* (0)*

1669   **Clade o –**   36. Chaetiger 8 margins of foliaceous notopodial lamellae: smooth (0) →

1670   *bilobed* (2)

1671   44. Chaetiger 9 notopodial foliaceous lamellae margins: smooth (0) →

1672   *crenulate* (1)*

1673   **Clade p –**   72. Post-chaetiger 9 arrangement of hooded hooks: vis-à-vis (0) → *vis-à-dos*

1674   (1)*

1675   **Clade q –**   52. Shape of thoracic interparapodial margins: straight (0) → *rounded,*

1676   *bulbous* (1)*

1677   60. Post-chaetiger 9 lateral pouches: present (1) → *absent* (0)*

1678   **Clade r –**   26. Chaetigers 1–7 neuropodial subchaetal lamellae position relative to

1679   neurochaetae: varying in position along thorax (1) → *same position*

1680   *along thorax* (0)*

1681   41. Chaetiger 9 notopodial lamellae positions: postchaetal (0) → *subchaetal*

1682   (1)*

1683   **Clade s –**   57. Post-chaetiger 9 dorsal medial lobes length: smaller than hooks (0) →

1684   *longer than hooks* (1)*

1685   **Clade t –**   7. Prostomium dimensions: longer than wide (0) → *wider than long* (2)*

1686   33. Chaetigers 1-8 lengths of noto- and neuropodial capillary chaetae:

1687   equivalent (0) → *neuropodial longer* (2)*

1688

DISCUSSION

1690   A point mentioned in the **RESULTS** is that only one composite phylogenetic hypothesis can be

1691   formally recognised, i.e., Magelonidae. There can be no phylogenetic hypothesis(es) to which

1692   the name *Magelona* refers that is not redundant with Magelonidae. From a nomenclatural, as

1693   opposed to strictly scientific perspective, this assertion is contrary to what is required by the

1694   International Code of Zoological Nomenclature (ICZN; 1999): at least one formal name at the

1695   rank of genus must be established relative to the ranks of family and species. The present results

1696   offer another good example (see also Fitzhugh, 2008a, 2010b; Nogueira, Fitzhugh & Rossi,

1697   2010; Nogueira et al., 2017) of the conflict that can occur between the science of biological

1698   systematics and a mandated international nomenclature system that is not entirely aligned with

1699   the goal of that science. Compromise between these two positions currently favours the

1700   nomenclatural system, but by properly acknowledging that formal taxon names should be

1701   defined in terms of being explanatory hypotheses (cf. **Methodological considerations**), the

1702   conflict between naming and scientific practice can be somewhat mitigated. Emendations of the

1703   formal names Magelonidae, *Magelona*, and *Octomagelona* in relation to the phylogenetic

1704   hypotheses inferred in this study are presented below.

Morphological characters in future specimen descriptions

1706   Various authors have discussed the "crucial morphological characters" in differentiating

1707   members of magelonid species. Jones (1963), in his review of magelonids of the Gulf of Mexico

1708   listed six: (1) the fine structure of the hooded hooks of the posterior region (subject 67); (2) the

1709   presence or absence of prostomial horns (subject 5); (3) the presence or absence of medial

1710   lamellae in the posterior region (subject 56); (4) the presence or absence of specialised chaetae of

1711   various types on chaetiger 9 (subject 51); (5) the morphology of the anterior lateral lamellae

1712   (subjects 18–30, 34–49); and (6) the relative dimensions of the prostomium (subject 7). Blake

1713   (1996c) listed seven "principal diagnostic characters important in differentiating species," adding

1714   to Jones' list the following: (7) presence or absence of dorsal median lobes on thoracic notopodia

1715   (subjects 24, 37, 45, superior dorsal lobes); (8) presence and location of lateral pouches between

1716   abdominal segments (subjects 60, 64); and (9) the presence/absence and form of interlamellae on

1717   abdominal parapodia (herein termed the postchaetal expansion behind chaetal rows, subject 58).

1718   Brasil (2003: fig. 23) concluded that the position and form of noto- and neuropodial lamellae,

1719   and the division of the thorax into three different blocks of segments (i.e., A – all anterior

1720   chaetigers with identical morphology; B – first eight chaetigers being identical but possessing a

1721   ninth chaetiger having a distinct morphology; and C – in which the first seven identical

1722   chaetigers differ from chaetigers eight and nine) reflected the relationships found within clades

1723   and sub-clades within the family.

1724   Of the characters previously mentioned, the current results suggest those of particular

1725   importance to be included in future descriptions of members of species are: (1) the

1726   presence/absence of prostomial horns (in addition to their form, i.e., distinct or rudimentary); (2)

1727   the relative dimensions of the prostomium; (3) the morphology of the anterior lamellae,

1728   including presence/absence of superior dorsal lobes; (4) the presence/absence of specialised

1729 chaetae on chaetiger 9; and (5) the presence of lateral abdominal pouches. As highlighted by

1730 Brasil (2003), the thoracic lamellae are extremely diagnostic. Great care must be taken to fully

1731 describe and illustrate all thoracic chaetigers in descriptions, taking into account the size, shape

1732 and position of thoracic lamellae and whether/how they vary along the thorax. Often variations

1733 in position of the lamellae may be subtle between thoracic parapodia, particularly that of filiform

1734 subchaetal neuropodial lamellae. It is particularly important to examine the parapodia of

1735 chaetigers 8 and 9.

1736   In addition to the characters already highlighted, the prostomial distal shape (subject 3),

1737 the number of prostomial ridges (subject 9), the shape of thoracic interparapodial margins

1738 (subject 52), the arrangement of abdominal lateral pouches (subject 63) and the arrangement of

1739 abdominal hooded hooks (subject 72) warrant further investigation and inclusion in descriptions.

1740

Systematics

Magelonidae Cunningham & Ramage, 1888 (1865), emended

1743 Type genus. *Magelona* F. Müller, 1858, by monotypy.

1744 **Definition.** A composite phylogenetic hypothesis (Fig. 17), causally accounting for (a) presence

1745 of a shovel-shaped prostomium, (b) absence of nuchal organs, (c) presence of prostomial ridges,

1746 (d) ventral palps with (e) papillate surfaces, (f) presence of a burrowing organ, and (g)

1747 magelonid-like body regionation.

1748   Within a reproductively isolated population of individuals in the past, the following

1749 causal events occurred: (a′) the presence of a shovel-shaped prostomium [character 1(1)]

1750 originated by unspecified mechanism(s) among individuals with a rounded prostomium

1751   [character 1(0)], subsequent to which the novel character became fixed in the population by an

1752   unspecified mechanism(s); (b′) the loss of nuchal organs [character 2(1)] originated by

1753   unspecified mechanism(s) among individuals with nuchal organs [character 2(0)], subsequent to

1754   which the novel character became fixed in the population by an unspecified mechanism(s); (c′)

1755   the presence of prostomial ridges [character 8(1)] originated by unspecified mechanism(s)

1756   among individuals with no ridges [character 8(0)], subsequent to which the novel character

1757   became fixed in the population by an unspecified mechanism(s); (d′) the presence of ventrally

1758   inserted palps [character 10(1)] originated by unspecified mechanism(s) among individuals with

1759   dorsal palps [character 10(0)], subsequent to which the novel character became fixed in the

1760   population by an unspecified mechanism(s); (e′) the presence of palps with papillae [character

1761   11(1)] originated by unspecified mechanism(s) among individuals with smooth palps [character

1762   11(0)], subsequent to which the novel character became fixed in the population by an unspecified

1763   mechanism(s); (f′) the presence of a burrowing organ [character 14(1)] originated by unspecified

1764   mechanism(s) among individuals without such an organ [character 14(0)], subsequent to which

1765   the novel character became fixed in the population by an unspecified mechanism(s); (g′) the

1766   magelonid-like body [character 15(1)] originated by unspecified mechanism(s) among

1767   individuals without such body regionation [character 15(0)], subsequent to which the novel

1768   character became fixed in the population by an unspecified mechanism(s). Following character

1769   origin/fixation events (a′)–(g′) was a population splitting event by unspecified mechanism(s)

1770   leading to individuals to which subsequent phylogenetic and specific hypotheses refer.

1771   **Remarks.** Results of the phylogenetic inferences by Brasil (2003: figs. 45 and 46; Fig. 18)

1772   acknowledged the monophyly of Magelonidae based on three of the synapomorphies also

1773   referred to in this study (cf. **RESULTS**): presence of a spade-shaped prostomium [character

1774   1(1); phylogenetic hypothesis a′ in the above **Definition**] and ventral insertion of papillated palps

1775   [characters 10(1), 11(1); phylogenetic hypotheses d′ and e′, respectively, in the above

1776   **Definition**]. Fauchald & Rouse (1997: 103) stated evidence for monophyly of the Magelonidae

1777   as "Palps with rounded cross-section and a subdistal expanded area covered with papillae.

1778   Prostomium shovel-shaped." They additionally added that "chaetiger 9 often modified with

1779   unusual postchaetal lobes or different chaetae from those segments in front or behind it or both."

1780   This does not, however, follow for all members of species within the Magelonidae.

1781   The most basal group in the phylogenetic study by Brasil (2003) (Fig. 18: **clade I**) was

1782   that containing members of five species: *Magelona californica, M. minuta, M. pettiboneae, M.*

1783   *papillicornis* and *Magelona* sp. C of Uebelacker & Jones (1984). Members of these species

1784   possess postchaetal lamellae [characters 21(0), 26(0), 34(0), 38(0), 41(0), 46(0)] of equivalent

1785   size [character 30(0)] in both rami of thoracic chaetigers. **Clade b** in the current study (Fig. 17)

1786   contains the same five species, along with members of five additional species: *M. falcifera, M.*

1787   *fauchaldi, M. magnahamata, M. phyllisae* and *M. pygmaea*. As well as the characters highlighted

1788   by Brasil (2003), individuals in this clade possess smooth [characters 23(0), 36(0), 44(0)],

1789   filiform [characters 22(0), 28(0), 35(0), 40(0), 43(0), 48(0)] lamellae without superior dorsal

1790   lobes [characters 24(0), 37(0), 45(0)]. They also have prostomia the widths approximately

1791   equivalent to their lengths [character 7(1)], with straight [character 4(2)] and smooth [character

1792   3(0)] prostomial anterior margins, but only one pair of prostomial ridges [character 9(0)]. As the

1793   names of two species within the clade highlight, i.e., *M. minuta* and *M. pygmaea*, members of

1794   these species rarely attain the sizes seen in members of other magelonid species and are slender

1795   and thread-like. No lateral abdominal pouches have been recorded among members of these

1796   species [character 66(0)], although as noted above (cf. **Character descriptions**) this should be

1797   accepted with caution since lateral abdominal pouches are likely underreported within the

1798   family. As noted by Mills & Mortimer (2018) for members of *M. minuta*, granular bodies

1799   [subject 77(1)] appear as distinct transverse stripes in the thoracic region, and spots or stripes of

1800   this kind are certainly reported in over half of these species. This is a character worthy of further

1801   investigation.

1802   The analysis by Brasil (2003: fig. 47; Fig. 18) highlighted a **clade VIII.2** containing

1803   members of eight species: *Magelona mirabilis, M. johnstoni, M. riojai, M. crenulata, Magelona*

1804   sp. B of Uebelacker & Jones (1984), *M. obockensis, M. jonesi* and *M. sacculata*. The

1805   synapomorphies of the clade include the presence of mucronate chaetae [character 51(1)] and

1806   abdominal hooded hooks in a vis-à-dos orientation [character 72(1)], the latter of which is

1807   uncommon amongst members of Magelonidae. **Clade m** (Fig. 17) in the present study includes

1808   all the above species (except *M. jonesi* which will be discussed below) and additionally members

1809   of *M. conversa, M. debeerei, M. parochilis, Magelona* sp. A of Uebelacker & Jones (1984) and

1810   *M. tinae.* Members of these species possess longer than wide prostomia [character 7(0)], with

1811   rounded [character 4(1)], smooth anterior margins [character 3(0)], carrying two pairs of

1812   prostomial ridges [character 9(1)] but lacking prostomial horns [character 5(0)]. The

1813   development of lamellae along the thorax is different [characters 18(1), 20(1)], particularly the

1814   lamellae of chaetiger 9 which are low and broad [characters 42(0), 47(0)] in comparison to the

1815   elongate lamellae of preceding chaetigers. In addition to the chaetae of chaetiger 9 being

1816   mucronate, they are shorter than those occurring on chaetigers 1–8 [character 50(1)]. Lateral

1817   abdominal pouches are always present [character 60(1)] and whilst members of several species

1818   within the clade possess both anteriorly and posteriorly open pouches [characters 62(1)], only the

1819   latter is present in members of other species [character 62(0)]. **Clade m** is further divided into

1820   clades **o** and **p** (Fig. 17), separating the species based on arrangement of abdominal hooks (**clade**

1821   **o** with vis-à-vis and **clade p** with vis-à-dos). **Clade m** contains members of the species referred

1822   as a "*Magelona mirabilis*" group noted by several previous authors (Mortimer & Mackie, 2003;

1823   Clarke et al., 2010; Zhou & Mortimer, 2013). Clarke et al. (2010) additionally suggesting the

1824   arrangement of abdominal hooks separated members of species within the group.

1825   As noted above, *Magelona jonesi* in the present study is plesiomorphic to all magelonid

1826   species in **clade a** (Fig. 17). However, despite possessing tapering chaetae in chaetiger 9

1827   [character 51(0)], similar to preceding chaetigers, in the analysis of Brasil (2003) members of *M.*

1828   *jonesi* occurred in **clade VIII.4**, the synapomorphies of which were the presence of mucronate

1829   chaetae [character 51(1)] and abdominal hooded hooks in vis-à-dos orientation. Members of this

1830   species are in need of redescription and this may help to resolve the situation in a future study. It

1831   is perhaps the orientation of the abdominal hooded hooks which is in most need of examination.

1832   Whilst Hartmann-Schröder (1980) illustrated the abdominal hooks in a vis-à-dos orientation, she

1833   made no mention of that orientation in her description. Looking at her neuropodial figures

1834   (Hartmann-Schröder, 1980: figs. 116 and 117), several hooks are drawn facing anteriorly. It has

1835   been recently highlighted by Mortimer et al. (2020) that *M. filiformis*, a species also originally

1836   recorded as possessing vis-à-dos hooks and occurring in **clade VIII.3** of Brasil (2003: fig. 47;

1837   Fig. 18) along with *M. pacifica*, has in fact a vis-à-vis orientation. This misinterpretation of

1838   orientation can happen in members of species in which the hooks are not split equally between

1839   the two groups of a ramus, particularly if the quality of the material is poor. This warrants further

1840   clarification for *M. jonesi* and also *M. pacifica.* Unfortunately for the latter species, the

1841   abdominal hooks in the type material are mostly all broken (Mortimer et al., 2012) making it

1842   extremely difficult to discern. This may explain why these three species, *M. jonesi*, *M. filiformis*

1843   and *M. pacifica* were part of **clade VIII.2** with members of species possessing mucronate

1844   chaetae in Brasil's (2003) study.

1845   **Clade k** in the current results (Fig. 17) contains members of five species: *Magelona*

1846   *dakini, M. filiformis, M. hartmanae, M. hobsonae* and *M. pitelkai.* They share similarities in

1847   possessing prostomia which are longer than wide [character 7(0)], with straight [character 4(2)],

1848   smooth anterior margins [character 3(0)] formed into rudimentary horns [character 6(0)], and

1849   which carry two pairs of prostomial ridges [character 9(1)]. Individuals have similar

1850   development of lamellae along the thorax in the notopodia [character 18(0)] but varying

1851   development in the neuropodia [character 20(1)]. They possess smooth edged [characters 23(0),

1852   36(0), 44(0)], filiform thoracic lamellae [characters 22(0), 28(0), 35(0), 40(0), 43(0), 48(0)]

1853   which are larger in the notopodia [character 31(1)], and basally constricted abdominal lamellae

1854   [character 55(1)]. Posteriorly open lateral abdominal pouches are reported [character 60(1)] in all

1855   but one species, *M. hobsonae*, however members of this species are only known from short

1856   anterior fragments, so this character needs verification. Members of three species, *M. hartmanae,*

1857   *M. hobsonae* and *M. pitelkai*, within this clade also possess pennoned chaetae of chaetiger 9

1858   [character 51(2)].

1859   Perhaps worth of noting is **clade n** (Fig. 17), which includes members of species

1860   possessing prostomia with distinct horns [character 6(1)], triangular anterior margins [character

1861   4(0)] and two pairs of prostomial ridges [character 9(1)]. Specimens also possess foliaceous

1862   notopodial thoracic lamellae [characters 22(1), 35(1), 43(1)] which are larger than the

1863   neuropodial lamellae [character 30(1)]. Superior dorsal lobes are present on chaetigers 1–8

1864   [characters 24(1), 37(1)]. The thoracic neuropodial lamellae are filiform [characters 28(0),

1865   40(0),48(0)] with additional postchaetal expansions on chaetigers 8 and 9 [characters 39(1),

1866   49(1)] (N.B. the latter needs verifying in *Magelona anuheone*). Abdominal lamellae are rounded

1867   with basal constrictions [character 55(1)]. Whilst nothing more can be concluded from **clade r**

1868   (Fig. 17), which contains numerous polytomies, characters such as prostomial width may prove

1869   to be important characters in other clades. **Clade t** contains members of four species (Fig. 17),

1870   *M. berkeleyi, M. lenticulata, M. wilsoni* and *Magelona* sp. J of Uebelacker & Jones (1984),

1871   which all have wide prostomia [character 7(2)], rounded bulbous thoracic interparapodial

1872   margins [character 52(1)], and lack abdominal lateral pouches [character 60(0)].

1873

1874   *Magelona* F. Müller, 1858, emended

1875   *Maea* Johnston, 1865 (see below)

1876   *Rhynophylla* Carrington, 1865

1877   *Meredithia* Hernández-Alcántara & Solís-Weiss, 2000

1878   *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001

1879   **Definition.** Pursuant to ICZN (International Commission on Zoological Nomenclature, 1999)

1880   Article 12.1, the definition of *Magelona* is identical to that provided for the emended family-rank

1881   name Magelonidae, provided above (Fig. 17).

1882   **Remarks.** The monotypic name *Magelona* can only be defined as referring to the same

1883   phylogenetic hypotheses that define the name Magelonidae, in accordance with ICZN

1884   (International Commission on Zoological Nomenclature, 1999) Article 12.1's requirement that

1885   all names published before 1931 "must be accompanied by a description or a definition of the

1886   taxon that it denotes." This means that from a scientific perspective the name *Magelona* is an

1887   empirically empty placeholder that is only recognised to satisfy the requirement that species-rank

1888   names, as epithets, be binomial.

1889   Hernández-Alcántara & Solís-Weiss (2000) introduced the genus *Meredithia* for

1890   members of species possessing large hooded recurved spines on abdominal chaetigers [Table 3:

1891   character 69(1)], adding the two species *M. spinifera* and *M. uebelackerae*. However, the nature

1892   of the enlarged chaetae differ among members of the two species; members of *M. spinifera*

1893   possess enlarged spines [Table 3: character 70(1)], whilst members of *M. uebelackerae* possess

1894   unidentate, enlarged re-curved hooks [Table 3: character 70(0)]. The descriptions of specimens

1895   with enlarged abdominal chaetae, but which differ greatly in other aspects (e.g., lacking

1896   prostomial horns and in the nature of the thoracic lamellae), called the validity of the genus into

1897   question (Mortimer & Mackie, 2003). Subsequently in the phylogenetic analysis performed by

1898   Brasil (2003) it was concluded that *Meredithia* is paraphyletic, which is in agreement with the

1899   current results. Herein, members of species possessing enlarged chaetae appear in three separate

1900   clades (Fig. 17: **clades b**, **c** and **r**), and the two species originally assigned to *Meredithia* are split

1901   between **clades c** and **r**. *Magelona falcifera*, *M. magnahamata* and *Magelona* sp. C of

1902   Uebelacker & Jones (1984) (**clade b**) are all species with members lacking prostomial horns,

1903   having similar thoracic development with postchaetal, filiform lamellae in both the noto- and

1904   neuropodia but in lacking both thoracic superior dorsal lobes and abdominal lateral pouches,

1905   whilst *M. uebelackerae, Magelona* sp. E of Uebelacker & Jones (1984) (**clade c**) and *M.*

1906   *spinifera* (**clade r**) all possess distinct prostomial horns, have different thoracic development,

1907   with variations between the noto- and neuropodia in the thoracic region, but which possess

1908   subchaetal neuropodial lamellae. The present results therefore further support the

1909   synonymisation of *Meredithia* with *Magelona*.

1910   Results of the phylogenetic inferences by Brasil (2003: fig. 45) additionally shed doubt

1911   on the validity of *Octomagelona*, with *O. bizkaiensis* and an undescribed species from Mexico

1912 (not considered in this study) as a paraphyletic group nested within *Magelona* and closely related

1913 to species such as *M. variolamellata*, *M. equilamellae*, *Magelona* sp. I of Uebelacker & Jones

1914 (1984) and *M. polydentata*. This finding is in agreement with the current analysis, indicating that

1915 *Octomagelona* cannot be maintained (Fig. 17). Whilst members of *Octomagelona* may differ

1916 from other members of *Magelona* in possessing only eight thoracic chaetigers, they share

1917 similarities with members of some species in terms of possessing a prostomium which is wider

1918 than long [character 7(2)], with rudimentary horns [character 6(0)], but with only one pair of

1919 prostomial ridges [character 9(0)], filiform subchaetal thoracic lamellae in the noto- and

1920 neuropodia [characters 21(1), 22(0), 26(1), 28(0)], without superior dorsal lobes [characters

1921 24(0), 37(0), 45(0)] and abdominal lamellae without basal constrictions [character 55(0)].

1922 As discussed above Johnston (1865) erected the genus *Maea* for the species *M. mirabilis*

1923 Johnston, 1865, later referred to *Magelona.* Whilst only one composite phylogenetic hypothesis

1924 can be formally recognised from the current results, the type species of the genus, *Maea*

1925 *mirabilis*, appears in both consensus trees (that of the current results and Brasil, 2003) in a clade

1926 clearly different from the one including the type species of *Magelona*, *M. papillicornis* F. Müller

1927 1858. If, in future studies, **clade m** (a '*Magelona mirabilis*' group) is formally recognised, then

1928 this may see the re-establishment of *Maea*.

1929

1930

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1937

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Forms of questions leading to ab-, de-, and inductive inferences, and respective answers provided by those inferences.

1   **Table 1. Forms of questions leading to ab-, de-, and inductive inferences, and respective**

2   **answers provided by those inferences.**

Question	Inferential Reaction	Conclusion (= answer)
'Why is Y the case in contrast to X?'	Abduction, cf. **(1)**	Explanatory hypothesis
'What consequence(s) are expected if hypothesis h is true?'	Deduction, cf. **(2)**	Potential test evidence
'Should hypothesis h be accepted as true?'	Induction, cf. **(3)**	Hypothesis confirmation / disconfirmation

Sources from which character data were obtained for this study. Museum abbreviations are explained in the text.

1 **Table 2. Sources from which character data were obtained for this study. Museum**

2 **abbreviations are explained in the text.**

Species	Material
M. alexandrae Magalhães, Bailey-Brock & Watling, 2018	Original description plus photos provided by the authors
M. alleni Wilson, 1958	Holotype: BMNH 1958.5.2.1 Paratypes: BMNH 1958.5.2.2-10
M. annulata Hartmann-Schröder, 1962	Original description
M. anuheone Magalhães, Bailey-Brock & Watling, 2018	Original description plus photos provided by the authors
M. berkeleyi Jones, 1971	Original description
M. californica Hartman, 1944	Original description
M. cepiceps Mortimer & Mackie, 2006	Holotype: NMW.Z.2000.020.0209 Paratype: NMW.Z.2000.020.0208
M. cerae Hartman & Reish, 1950	Original description
M. cincta Ehlers, 1908	Holotype (ZMHB 4531)
M. cinthyae Magalhães, Bailey-Brock & Watling, 2018	Original description plus photos provided by the authors
M. conversa Mortimer & Mackie, 2003	Holotype: NMW.Z.2000.020.0001 Paratypes: NMW.Z.2000.020.0002-0007
M. cornuta Wesenberg-Lund, 1949	Holotype: (ZMUC–POL–969; two abdominal slide preparations ZMUC–POL–963)
M. crenulata Bolívar & Lana, 1986	Original description

M. crenulifrons Gallardo, 1968	Paratypes: (ZMUC–POL–1416- 1421)
M. dakini Jones, 1978	Original description
M. debeerei Clarke, Paterson, Florence & Gibbons, 2010	Original description
M. equilamellae Harmelin, 1964	Syntypes: SMF 4675
M. falcifera Mortimer & Mackie, 2003	Holotype: NMW.Z.2000.020.0009 Paratypes: NMW.Z.2000.020.0008, NMW.Z.2000.020.0010-0017
Magelona fasciata Mortimer et al. (2021)	Holotype: ZMBN132144 Paratypes: ZMBN; AC-NMW
M. fauchaldi Shakouri, Mortimer & Dehani, 2017	Holotype: NMW.Z.2015.012.0002a Paratypes: NMW.Z.2015.012.0001-0002; NMW.Z.2010.037.0002-0006
M. filiformis Wilson, 1959	Holotype: BMNH 1959.4.2.1 Paratypes: BMNH 1959.4.2.2-10
M. gemmata Mortimer & Mackie, 2003	Holotype: NMW.Z.2000.020.0019 Paratypes: NMW.Z.2000.020.0018 ; NMW.Z.2000.020.0020
Magelona guineaensis Mortimer et al. (2021)	Holotype: ZMBN132137 Paratypes: ZMBN; AC-NMW
M. hartmanae Jones, 1978	Original description
M. hobsonae Jones, 1978	Original description
M. johnstoni Fiege, Licher & Mackie,	Cited material from original description from

2000	NMW collections
M. jonesi Hartmann-Schröder, 1980	Original description
M. lenticulata Gallardo, 1968	Original description
M. lusitanica Mortimer, Gil & Fiege, 2011	Holotype: SMF 9246/1 Paratypes: MB29-000176-000181; NMW.Z.2010.010.0001-0006; SMF 9245/1
Magelona mackiei Mortimer et al. (2021)	Holotype: ZMBN107309 Paratypes: ZMBN; AC-NMW
M. magnahamata Aguado & San Martín, 2004	Original description
M. mahensis Mortimer & Mackie, 2006	Holotype: NMW.Z.2000.020.0188 Paratypes: NMW.Z.2000.020.0176-0187; NMW.Z.2000.020.0189-0193
M. marianae Hernández-Alcántara & Solís-Weiss, 2000	Original description
M. minuta Eliason, 1962	Holotype: NHMG Polych. 11491 Additional material: USNM 52510
M. mirabilis (Johnston, 1865)	Cited material from original description from NMW collections
M. montera Mortimer, Cassà, Martin & Gil, 2012	Holotype: MNHN A895
Magelona nanseni Mortimer et al. (2021)	Holotype: ZMBN132141 Paratypes: ZMBN; AC-NMW

M. nonatoi Bolívar & Lana, 1986	Original description
M. obockensis Gravier, 1905	Syntypes, MNHN Type 1357
M. pacifica Monro, 1933	Syntypes: BMNH Type 1933.7.10.65/70
M. papillicornis F. Müller, 1858	Redescription (Jones, 1977)
M. parochilis Zhou & Mortimer, 2013	Holotype: ECSFRI100532 Paratypes: ECSFRI100533-535; NMW.Z.2012.033.0001
M. paulolanai Magalhães, Bailey-Brock & Watling, 2018	Original description plus photos provided by the authors
M. pettiboneae Jones, 1963	Original description
M. phyllisae Jones, 1963	Original description
Magelona picta Mortimer et al. (2021)	Holotype: ZMBN107338 Paratype: ZMBN115737
M. pitelkai Hartman, 1944	Original description, Jones (1978)
M. polydentata Jones, 1963	Original description
M. posterelongata Bolívar & Lana, 1986	Original description
M. pulchella Mohammad, 1970	Holotype: BMNH 1969.391
M. pygmaea Nateewathana & Hylleberg, 1991	Paratype: PMBC 4220 Additional material: PMBC 4234; PMBC 4227; PMBC 4241
M. riojai Jones, 1963	Original description

M. sacculata Hartman, 1961	Holotype: NHMLA: LACM-AHF POLY 596
M. sinbadi Mortimer, Cassà, Martin & Gil, 2012	Holotype: NMW.Z.2010.037.0001
M. spinifera (Hernández-Alcántara & Solís-Weiss, 2000)	Original description
M. symmetrica Mortimer & Mackie, 2006	Holotype: NMW.Z.2000.020.0175
M. tehuanensis Hernández-Alcántara & Solís-Weiss, 2000	Original description
M. tinae Nateewathana & Hylleberg, 1991	Paratypes: PMBC 3180; PMBC 4251; PMBC 4253; PMBC 4254
M. uebelackerae (Hernández-Alcántara & Solís-Weiss, 2000)	Original description
M. variolamellata Bolívar & Lana, 1986	Original description
M. wilsoni Glémarec, 1967	Paratypes: MNHN Poly Type 1415
Magelona sp. A	Uebelacker & Jones, 1984
Magelona sp. B	Uebelacker & Jones, 1984
Magelona sp. C	Uebelacker & Jones, 1984
Magelona sp. D	Uebelacker & Jones, 1984
Magelona sp. E	Uebelacker & Jones, 1984
Magelona sp. F	Uebelacker & Jones, 1984
Magelona sp. G	Uebelacker & Jones, 1984

Magelona sp. H	Uebelacker & Jones, 1984
Magelona sp. I	Uebelacker & Jones, 1984
Magelona sp. J	Uebelacker & Jones, 1984
Magelona sp. K	Uebelacker & Jones, 1984
Magelona sp. L	Uebelacker & Jones, 1984
O. bizkaiensis Aguirrezabalaga, Ceberio & Fiege, 2001	Holotype: MNCN 16.01/6887 Paratype: SMF 10025
Octomagelona sp. (West Africa)	AC-NMW

Characters, as observation statements represented by subject-predicate relations, not 'characters' and 'states' (Fitzhugh, 2006c, 2008c), used in this study.

1   **Table 3. Characters, as observation statements represented by subject-predicate relations,**

2   **not 'characters' and 'states' (Fitzhugh, 2006c, 2008c), used in this study.**

3   1.   Shovel-shape prostomium: (0) absent; (1) present.

4   2.   Nuchal organs: (0) absent; (1) present.

5   3.   Prostomium distal margin: (0) smooth; (1) crenulate; (2) medially indented.

6   4.   Prostomium distal shape: (0) triangular; (1) rounded; (2) straight.

7   5.   Prostomial horns (including rudimentary): (0) absent; (1) present.

8   6.   Shape of prostomial horns [cf. character 5(1)]: (0) rudimentary; (1) distinct.

9   7.   Prostomium dimensions: (0) longer than wide; (1) as wide as long; (2) wider than long.

10   8.   Prostomial ridges: (0) absent; (1) present.

11   9.   Number of prostomial ridges [cf. character 8(1)]: (0) a pair; (1) two pairs.

12   10. Palp origin: (0) dorsal; (1) ventral.

13   11. Palp surface: (0) non-papillate; (1) papillate.

14   12. Number of rows of proximal palp papillae [cf. character 11(1)]: (0) 2; (1) 4–8; (2) 10–14.

15   13. Number of rows of distal palp papillae [cf. character 11(1)]: (0) 2; (1) 4; (2) more.

16   14. Burrowing organ: (0) absent; (1) present.

17   15. Body regionation: (0) non-magelonid; (1) magelonid-like.

18   16. Number of anterior body region chaetigers [cf. character 15(1)]: (0) 8; (1) 9.

19   17. Notopodial postchaetal lamellae: (0) absent; (1) present.

20   18. Development of notopodia along thorax: (0) all similar; (1) different in some chaetigers.

21   19. Neuropodial postchaetal lamellae: (0) absent; (1) present.

22   20. Development of neuropodia along thorax: (0) all similar; (1) different in some chaetigers.

23   21. Chaetigers 1–7 position of notopodial lamellae relative to notochaetae: (0) postchaetal; (1)

24   subchaetal.

25   22. Chaetigers 1–7 notopodial lamellae shape: (0) filiform; (1) foliaceous.

26   23. Chaetigers 1–7 margins of foliaceous notopodial lamellae [cf. character 22(1)]: (0) smooth;

27   (1) crenulate; (2) bilobed.

28   24. Chaetigers 1–7 dorsal superior lobes: (0) absent; (1) present.

29   25. Superior dorsal lobes [cf. character 24(1)]: (0) absent on some chaetigers between 1–7; (1)

30   present on chaetigers 1–7.

31   26. Chaetigers 1–7 neuropodial lamellae position relative to neurochaetae: (0) postchaetal;

32   (1) subchaetal; (2) prechaetal.

33   27. Chaetigers 1–7 neuropodial subchaetal lamellae position relative to neurochaetae [cf.

34   character 26(1)]: (0) same position along thorax; (1) varying in position along thorax.

35   28. Chaetigers 1–7 neuropodial lamellae shape: (0) filiform; (1) foliaceous.

36   29. Chaetigers 1–7 neuropodial filiform lamellae shape distal ends [cf. character 28(0)]: (0)

37   pointed; (1) distally expanded/scoop shaped.

38   30. Chaetigers 1–7 lengths of noto- and neuropodial lamellae: (0) equivalent; (1) notopodial

39   longer; (2) neuropodial longer.

40   31. Chaetigers 1–8 limbations of capillary chaetae: (0) unilimbate; (1) bilimbate.

41   32. Chaetigers 1–8 margins of bilimbate capillary chaetae [cf. character 31(1)]: (0) smooth;

42   (1) irregular blade.

43   33. Chaetigers 1–8 lengths of noto- and neuropodial capillary chaetae: (0) equivalent; (1)

44   notopodial longer; (2) neuropodial longer.

45   34. Chaetiger 8 notopodial lamellae position relative to notochaetae: (0) postchaetal;

46   (1) subchaetal.

47   35. Chaetiger 8 notopodial lamellae shape: (0) filiform; (1) foliaceous.

48   36. Chaetiger 8 margins of foliaceous notopodial lamellae [cf. character 35(1)]: (0) smooth; (1)

49   crenulate; (2) bilobed.

50   37. Chaetiger 8 superior dorsal lobes: (0) absent; (1) present.

51   38. Chaetiger 8 neuropodial lamellae position: (0) postchaetal; (1) subchaetal; (2) prechaetal.

52   39. Chaetiger 8 neuropodia: (0) without additional postchaetal expansion; (1) with an additional

53   postchaetal expansion.

54   40. Chaetiger 8 neuropodial lamellae shape: (0) filiform; (1) foliaceous.

55   41. Chaetiger 9 notopodial lamellae positions: (0) postchaetal; (1) subchaetal.

56   42. Chaetiger 9 notopodial lamellae height [cf. character 41(0)]: (0) low; (1) elongate.

57   43. Chaetiger 9 notopodial lamellae shape: (0) filiform; (1) foliaceous.

58   44. Chaetiger 9 notopodial foliaceous lamellae margins [cf. 43(1)]: (0) smooth; (1) crenulate; (2)

59   bilobed.

60   45. Chaetiger 9 superior dorsal lobes: (0) absent; (1) present.

61   46. Chaetiger 9 neuropodial lamellae position: (0) postchaetal; (1) subchaetal; (2) prechaetal.

62   47. Chaetiger 9 neuropodial lamellae height [cf. character 46(0)]: (0) low; (1) elongate.

63   48. Chaetiger 9 neuropodial lamellae shape: (0) filiform; (1) foliaceous.

64   49. Chaetiger 9 neuropodia: (0) without additional postchaetal expansion; (1) with additional

65   postchaetal expansion.

66   50. Lengths of chaetiger 9 fascicles relative to chaetigers 1–8 fascicles: (0) same length as

67   chaetae in chaetigers 1–8; (1) shorter than chaetae in chaetigers 1–8; (2) longer than

68   chaetae in chaetigers 1–8.

69   51. Distal ends of chaetae in chaetiger 9: (0) gently tapered, similar to chaetigers 1–8; (1)

70   mucronate; (2) pennoned.

71   52. Shape of thoracic interparapodial margins: (0) straight; (1) rounded, bulbous.

72   53. Dorso-lateral grooves, anterior chaetigers: (0) absent; (1) present.

73   54. Dimensions of post-chaetiger 9 segments: (0) as long as wide; (1) longer than wide.

74   55. Post-chaetiger 9 lamellae shape: (0) without basal constriction; (1) with basal constriction.

75   56. Post-chaetiger 9 dorsal and ventral medial lobes: (0) absent; (1) present.

76   57. Post-chaetiger 9 dorsal and ventral medial lobes sizes [cf. character 56(1) partim]: (0) smaller

77   than hooks; (1) longer than hooks.

78   58. Post-chaetiger 9 postchaetal expansion behind chaetal rows: (0) absent; (1) present.

79   59. Relative sizes of post-chaetiger 9 noto- and neuropodial postchaetal lamellae: (0) same size;

80   (1) different size.

81   60. Post-chaetiger 9 lateral pouches: (0) absent; (1) present.

82   61. Post-chaetiger 9 lateral pouch arrangement [cf. character 60(1)]: (0) paired; (1) unpaired; (2)

83   both paired and unpaired.

84   62. Direction of lateral pouch openings [cf. character 60(1)]: (0) posteriorly; (1) posteriorly and

85   anteriorly.

86   63. Post-chaetiger 9 posteriorly open lateral pouch arrangement [cf. character 62(0)]: (0) on

87   consecutive segments; (1) on alternating segments; (2) on both consecutive and

88   alternating segments.

89   64. Post-chaetiger 9 lateral pouches distribution [cf. character 60(1)]: (0) throughout most

90   abdominal chaetigers; (1) median and posterior abdominal chaetigers only; (2) posterior

91   abdomen only.

92   65. Margins of posteriorly-open pouches [cf. character 62(0)]: (0) smooth; (1) medially split.

93   66. Post-chaetiger 9 noto- and neuropodial hooded hooks: (0) absent; (1) present.

94   67. Post-chaetiger 9 noto- and neuropodial hooded hooks dentition [cf. character 66(1)]: (0)

95   bidentate; (1) tridentate; (2) polydentate.

96   68. Post-chaetiger 9 hooded hooks adjacent to notopodial subchaetal or neuropodial suprachaetal

97   lamellae [cf. character 66(1)]: (0) same size; (1) smaller than rest.

98   69. Post-chaetiger 9 enlarged hooded hooks: (0) absent; (1) present.

99   70. Post-chaetiger 9 enlarged hooded hooks distal ends [cf. character 69(1)]: (0)

100   recurved; (1) spine-like; (2) enlarged normal hook.

101   71. Post-chaetiger 9 number of hooded hooks per ramus [cf. character 66(1)]: (0) 8 or more; (1)

102   less than 8.

103   72. Post-chaetiger 9 arrangement of hooded hooks [cf. character 66(1)]: (0) vis-à-vis; (1) vis-à-

104   dos.

105   73. Neuropodial sabre chaetae: (0) absent; (1) present.

106   74. Post-chaetiger 9 noto- and neuropodial internal 'aciculae': (0) absent; (1) present.

107   75. Pigmentation in posterior thorax: (0) absent; (1) present.

108   76. Pigmentation pattern in posterior thorax [cf. character 75(1): (0) discreet band; (1) dispersed,

109   not forming band.

110   77. Granular bodies on surfaces of segments: (0) absent; (1) present.

111   78. Granular bodies within segments as abdominal interparapodial patches: (0) absent; (1)

112   present.

113   79. Tube construction: (0) absent; (1) present.

Figure 1

Classes of hypotheses in systematics. Relations between the eight classes (A–H) of explanatory hypotheses commonly inferred in biological systematics (adapted from Fitzhugh, 2013: fig. 1, 2016b: fig. 1; based on Hennig, 1966: fig. 6).
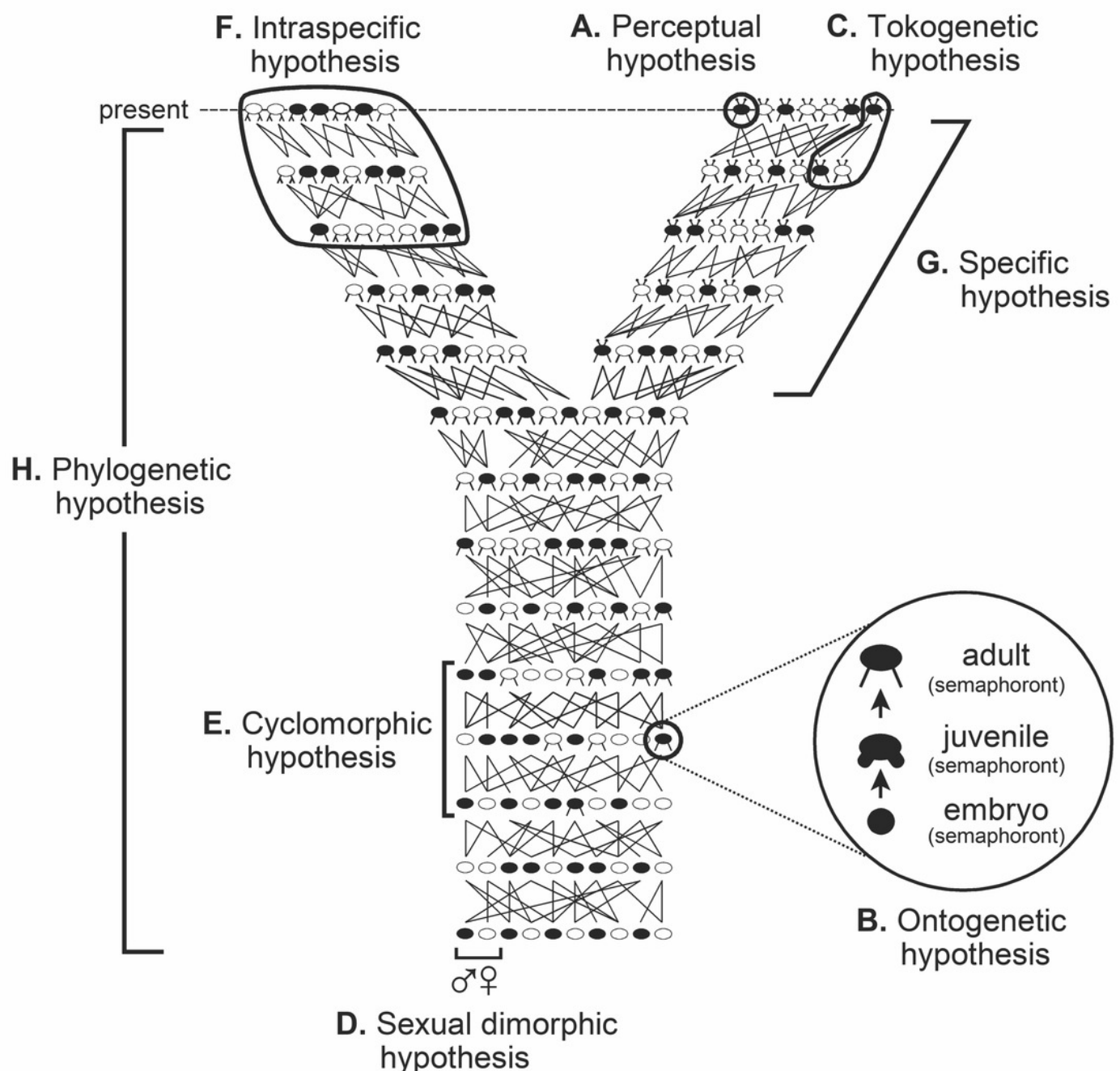
Figure 2

Observation statements, why-questions, and data matrix.

A data matrix used to infer phylogenetic hypotheses implies the why-questions to which inferences lead to answers as phylogenetic hypotheses, implied by cladograms (Fig. 1). (A) Observation statements, as subject-predicate relations, and contrastive why-questions implied by a data matrix. (B) The contrastive form of why-questions is maintained in a data matrix through the inclusion of outgroups, distinguishing foil and fact. Modified from Fitzhugh (2016b: fig. 3).

A.

subjects

		1	2	3	4	5
'outgroup'	a-us	0	0	0	0	0
	b-us	1	1	0	0	1
	c-us	1	1	1	1	2
	d-us	1	1	1	1	2

Why-question:

"Why do individuals to which species hypotheses c-us and d-us refer have character 4(1), *in contrast to 4(0) as observed among members of other species*?"

2(1): Subject-predicate relations among individuals to which species hypothesis *d-us* applies

B.

		1	2	3	4	5
foil:	'outgroup' a-us	0	0	0	0	0
	b-us	1	1	0	0	1
facts:	c-us	1	1	1	1	2
	d-us	1	1	1	1	2

Figure 3

Explanatory hypotheses implied by cladograms.

Cladograms imply two general classes of explanatory hypotheses (see also Fig. 1) – specific and phylogenetic – causally accounting for differentially shared characters. Inferences of specific hypotheses are distinct from phylogenetic inferences (cf. Fitzhugh, 2005b, 2009, 2013, 2015), but both typically offer vague explanations with largely unspecified causes. Modified from Fitzhugh (2016b: fig. 2).
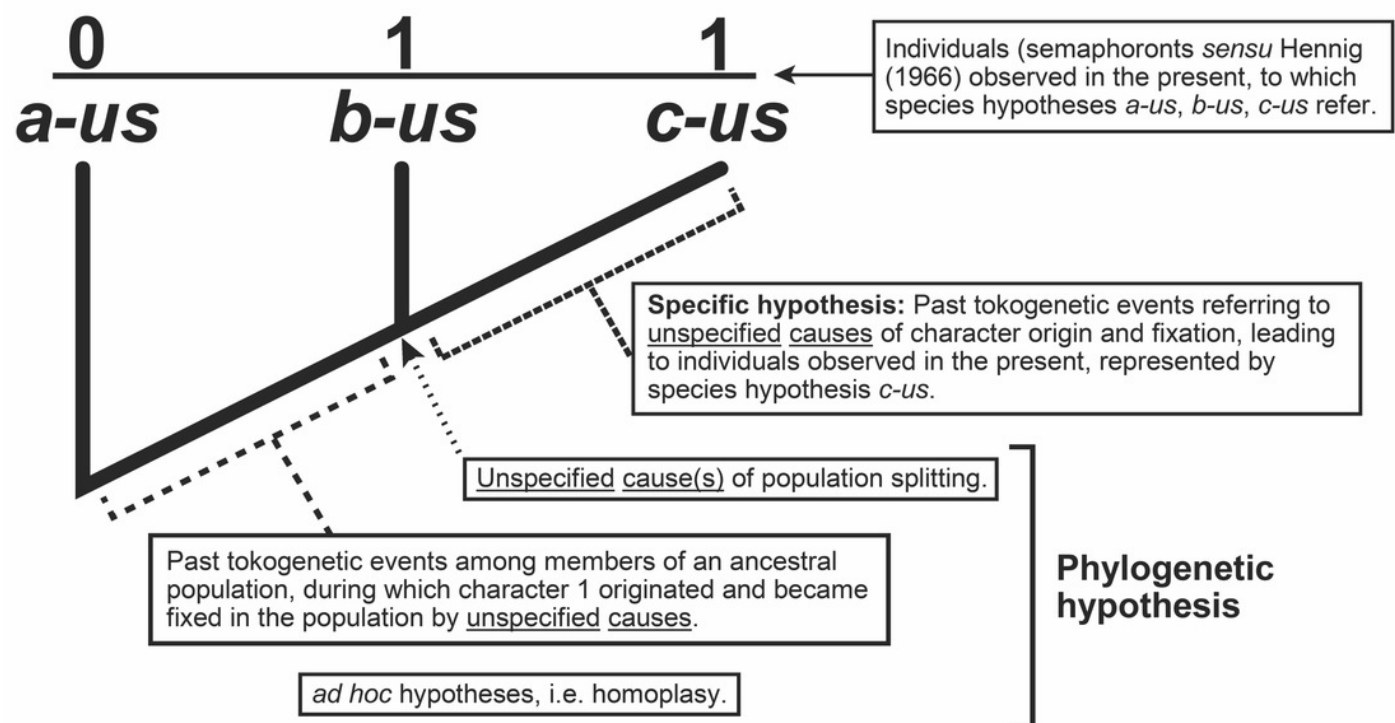
Figure 4

Magelonid prostomial characters.

A) smooth distal margin of *Magelona obockensis* (Kuwait, BMNH:ZB.1971.54; photo by J.
Turner); (B) distinctly crenulate distal margin of *M. crenulifrons* from Hong Kong
(NMW.Z.2007.033.0001); (C) minutely crenulate margin of *M. wilsoni* from the Gulf of Lions
(NMW.Z.2010.010.0008); (D) medially indented distal margin of *M. symmetrica* from the
Seychelles, holotype, from Mortimer & Mackie, 2006); (E) triangular distal margin of *M.
sinbadi* from Iran (holotype, NMW.Z.2010.037.0001); (F) rounded distal margin of *M.
johnstoni* from Berwick-upon-Tweed (NMW.Z.2013.037.0008); (G–H) straight distal margins
(often termed 'rudimentary horns') of *M. alleni* from Morocco (NMW.Z.2021.001.0001) and *M.
equilamellae* from Ebro Delta, Catalonia. A–E, G, H, dorsal views; F, ventral view; A, E, G,
stained with methyl green; H, stained with Rose Bengal. BO = burrowing organ, IM =
indented margin, IR = inner ridges, OR = outer ridges, PB = palp base, PH = prostomial
horns, Pp = palp, Pr = prostomium, RH = rudimentary horns.
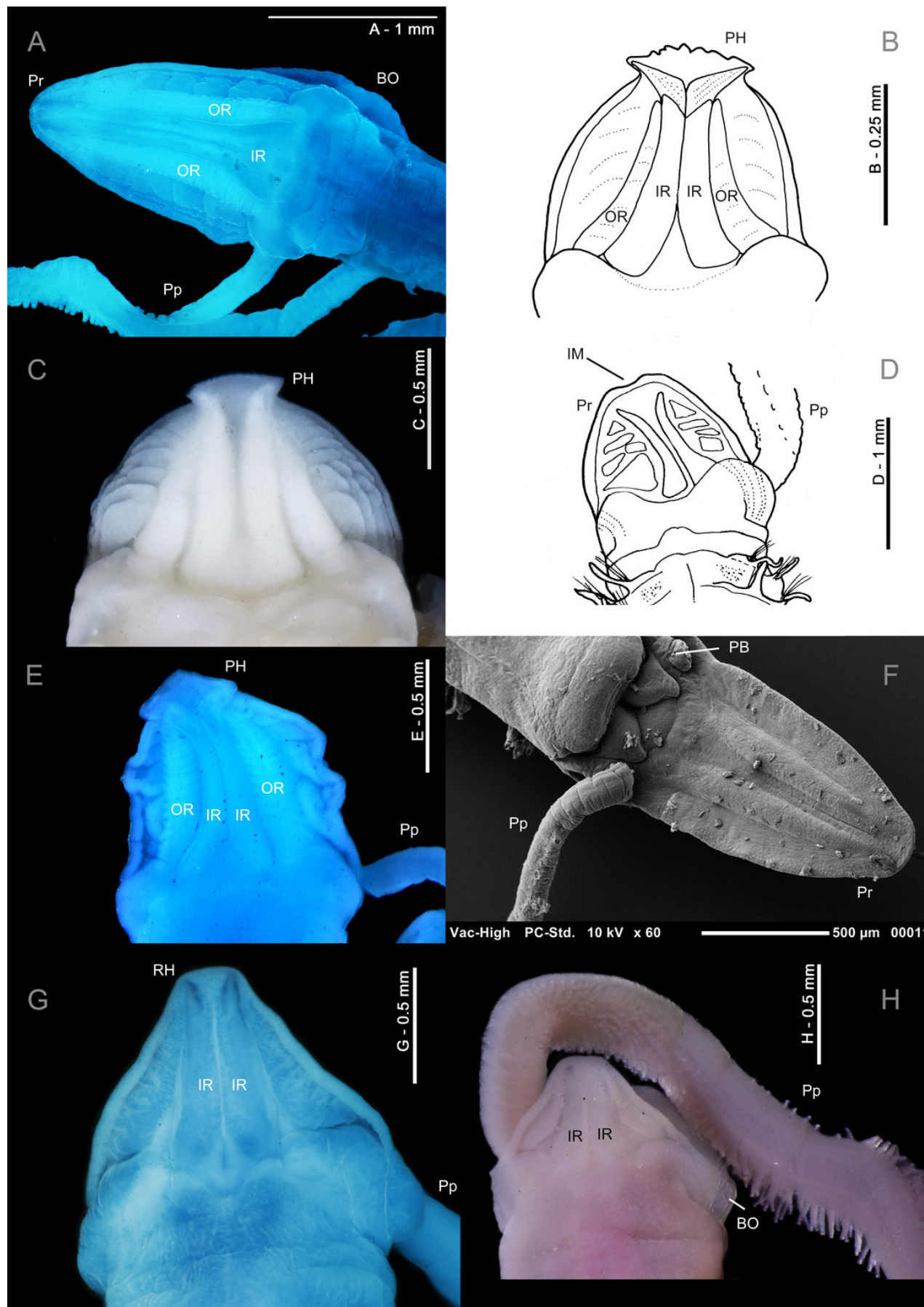
Figure 5

Magelonid anterior end and palp characters.

(A) prostomium and first chaetiger of *Magelona pacifica* from Panamá (syntype, BMNH Type 1933.7.10.65/70, dorsal view); (B) prostomium and first three chaetigers of *M. montera* from Gulf of Aqaba (holotype MNHN TYPE 1548, dorso-lateral view, stained with methyl green, photo by J. Turner); (C) prostomium and first three chaetigers of *M. filiformis* from Salcombe, England (paratype, BMNH 1959.4.2.6–10, dorso-lateral view); (D) prostomium of *M. posterelongata* from Paranaguá Bay, Brazil (dorsal view); (E) prostomium and first chaetiger of *Magelona nanseni* from Nigeria (Holotype, ZMBN132141, dorsal view); (F) mid-palp region of *M. johnstoni* from Berwick-upon-Tweed (NMW.Z.2013.037.0008c); (G) prostomium and anterior thorax of *M. johnstoni* from Berwick-upon-Tweed, showing ventrally inserted papillate palps, and partially everted burrowing organ (NMW.Z.2013.037.0008b); (H) distal palp end of *M. alleni* from Swansea (NMW.Z.2012.022.0001, SEM by K. Mills). Ach = achaetous first segment, BO = burrowing organ, IR = inner ridges, OR = outer ridges, PH = prostomial horns, Pp = palp, Pr = prostomium, RH = rudimentary horns. Numbers indicate chaetiger number.
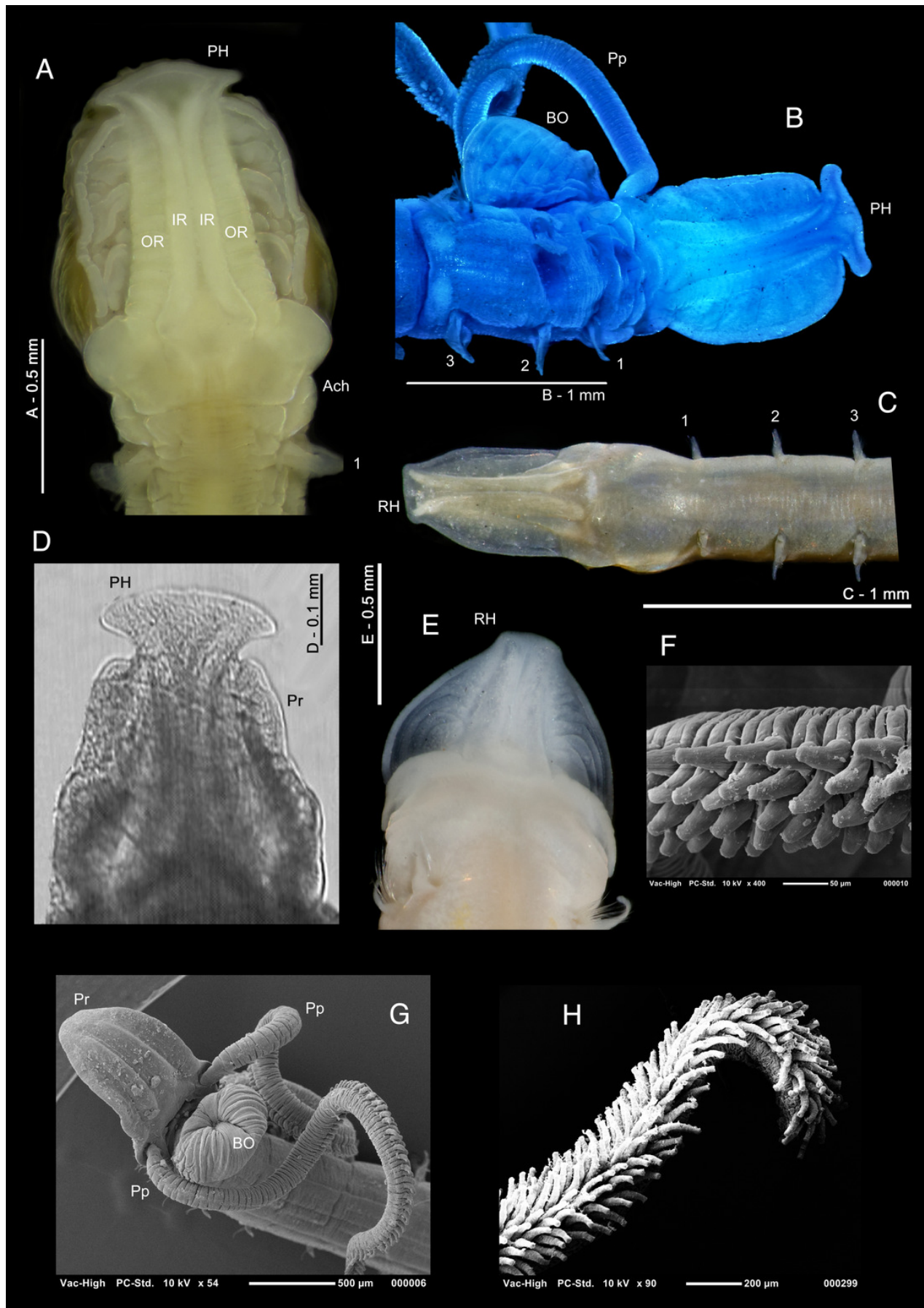
Figure 6

Octomagelona.

Octomagelona: (A, C–F) anterior of an undescribed species from West Africa (dorsal, ventral, antero-dorsal, postero-dorsal and lateral views respectively); (B) *Octomagelona bizkaiensis* from Capbreton Canyon (holotype, MNCN 16.01/6887, dorsal view). Ab = abdomen, Ach = achaetous first segment, Pr = prostomium, Th = thorax.
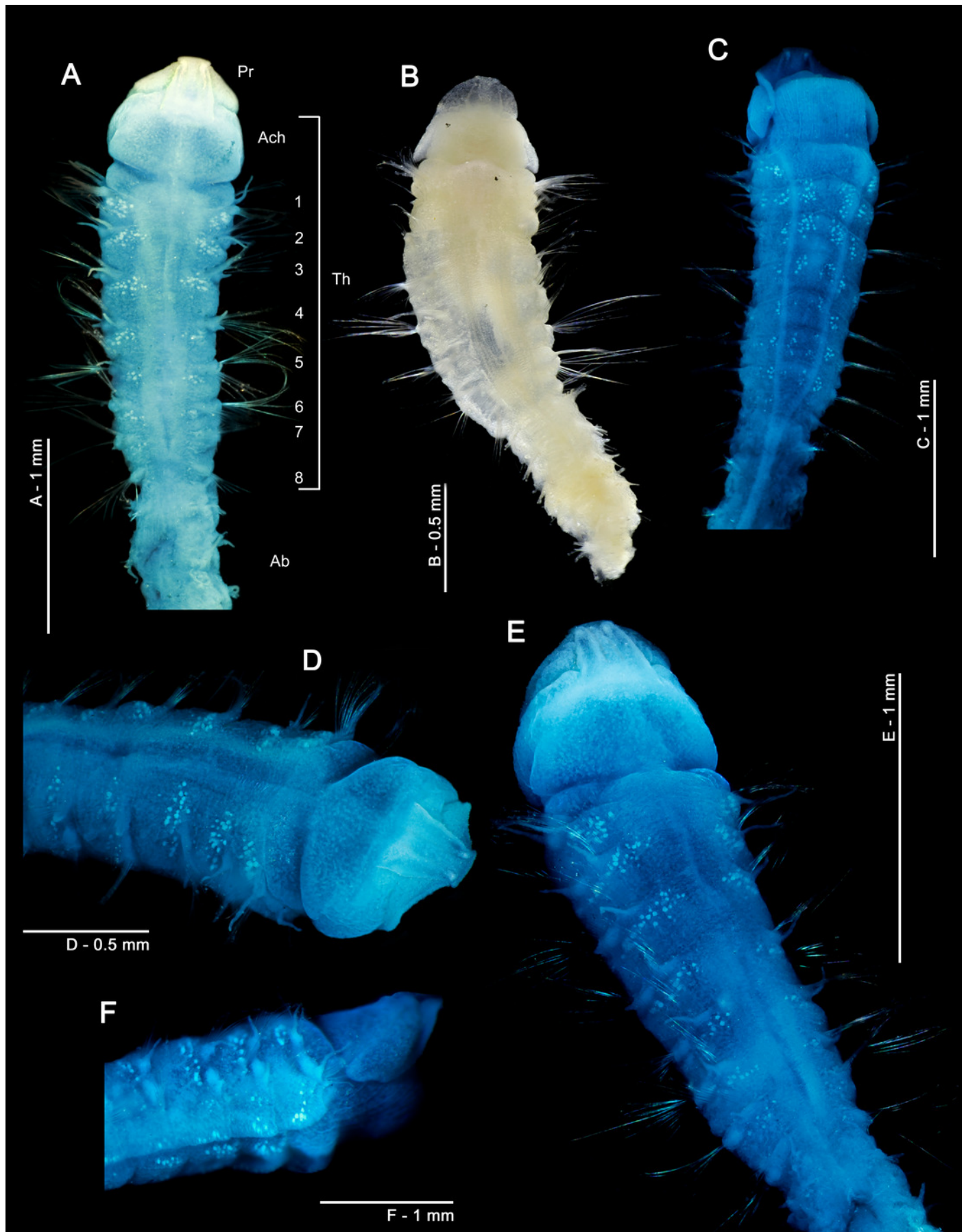
Figure 7

Development of magelonid thoracic parapodia.

(A) left-hand parapodia of chaetigers 1, 5, 8 and 9 of *Magelona minuta* from Öresund, Sweden (USNM 52510, anterior views); (B) parapodia of chaetigers 1, 6, 8 and 9 of *M. equilamellae* from France (syntype, SMF 4675, anterior views); (C) parapodia of chaetigers 2, 3, 4 and 9 of *M. obockensis* from Obock, Red Sea (syntype, MNHN Type 1357, anterior views); (D) left-hand parapodia of chaetigers 1, 5, 8 and 9 of *M. conversa* from Iran, NMW.Z.2010.037.0007, anterior views).
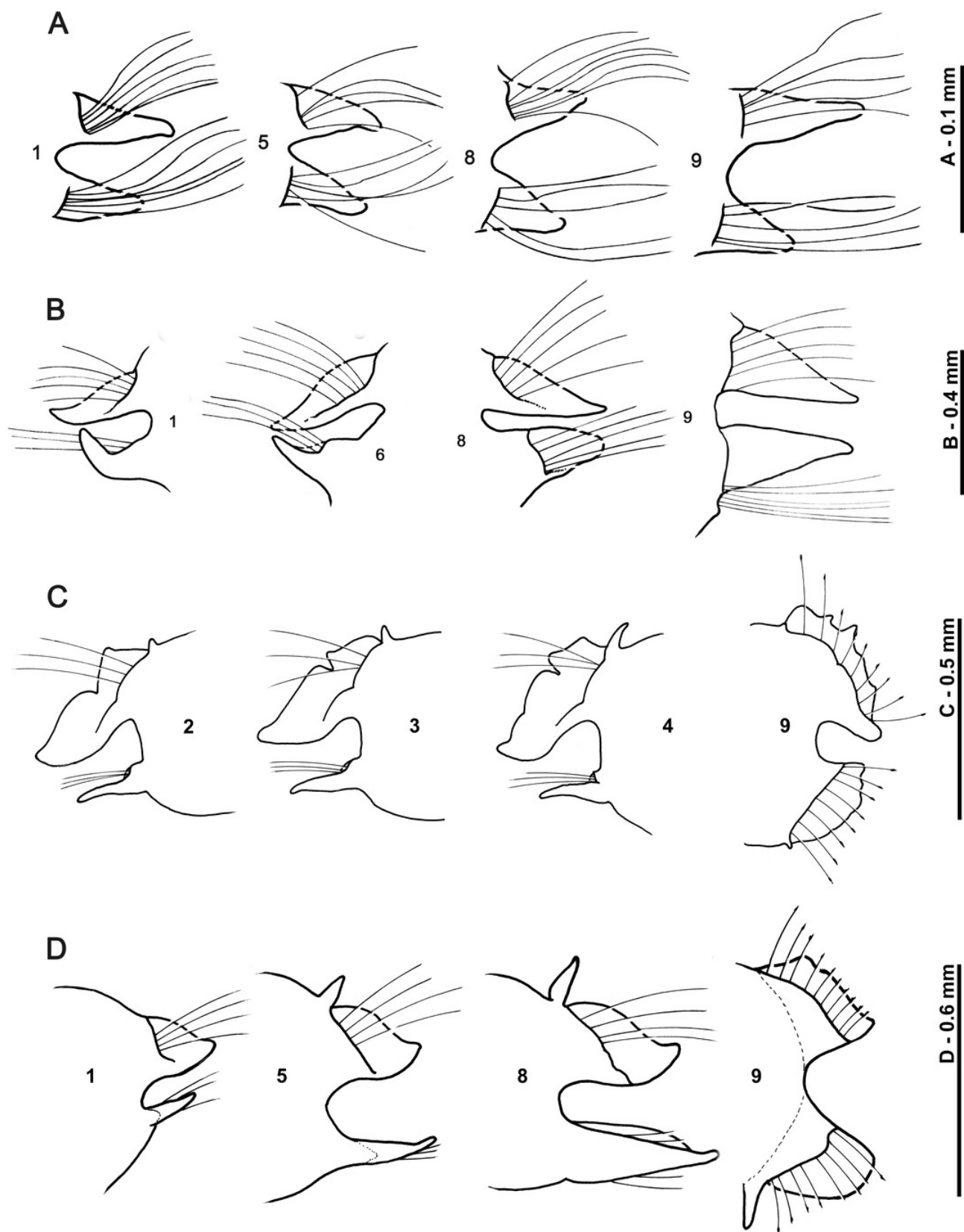
Figure 8

Magelonid thoracic parapodia.

(A) thoracic postchaetal notopodial lamellae of *Magelona mirabilis* from Berwick-upon-Tweed (anterior view, SEM by K. Mills); (B) chaetigers 7–10 of *M. alleni* from Morocco (NMW.Z.2021.001.0001, lateral view, stained with methyl green); (C) thoracic prechaetal neuropodial lamellae of *M. mirabilis* from Berwick-upon-Tweed (posterior view, SEM by K. Mills); (D) subchaetal notopodial lamellae of *M. riojai* from Corora Grande, Rio de Janeiro, Brazil; (E) left-hand parapodia of chaetiger 8 of *M. conversa* from Iran, (NMW.Z.2010.037.0007, anterior view); (F) right-hand parapodia of chaetigers 2–4 of *M. equilamellae* from Ebro Delta, Catalonia (NMW.Z.2019.100.0012–14, lateral view, SEM by K. Mills); (G) left-hand parapodia of chaetigers 7–9 of same specimen (SEM by K. Mills). Noto = notopodial, Neuro = neuropodia, Pre = prechaetal, Post = postchaetal, SDL = superior dorsal lobe. Numbers indicate chaetiger number.
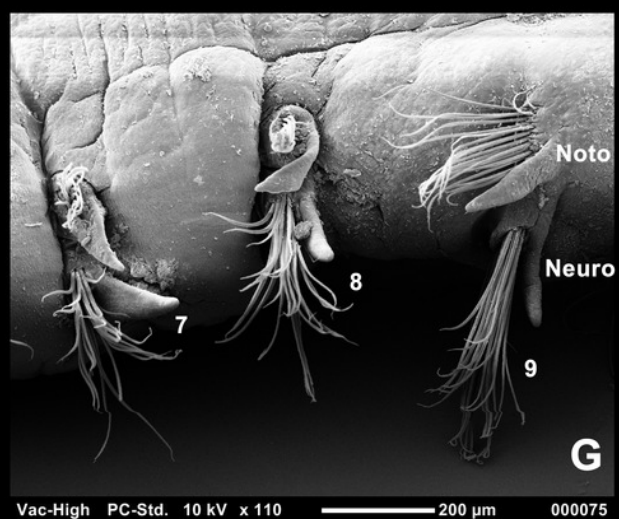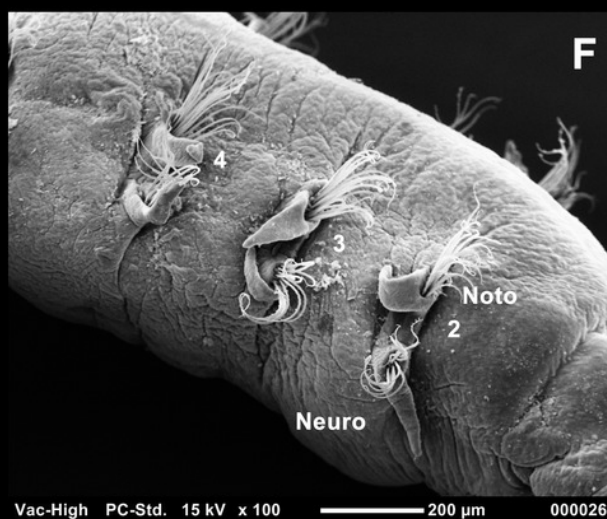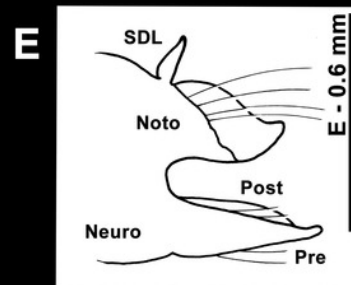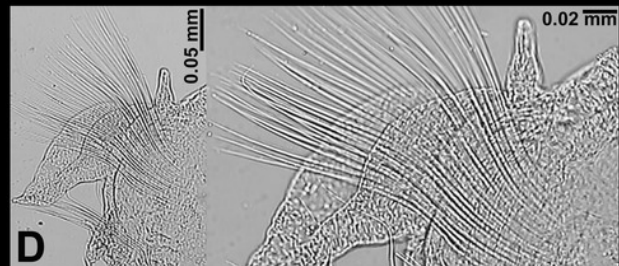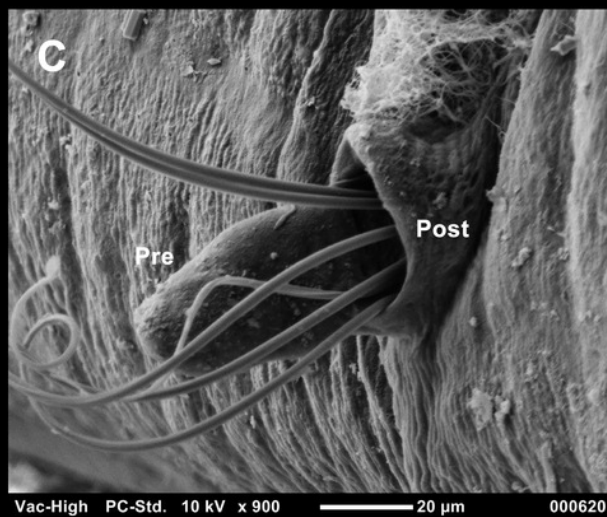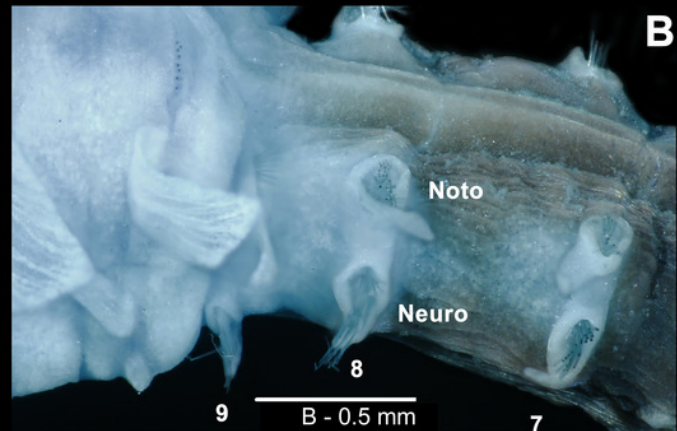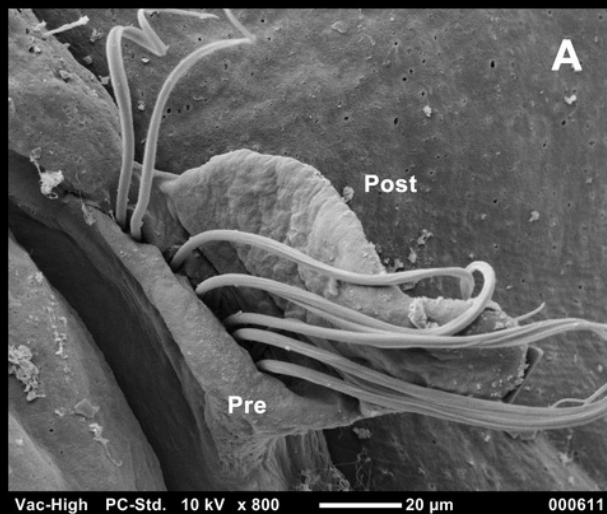
Figure 9

Magelonid thoracic parapodia.

(A) right-hand parapodia of chaetiger 4 of *Magelona fauchaldi* from Iran (paratype,
NMW.Z.2015.012.0002b, antero-lateral view); (B) right-hand notopodia of *M. equilamellae*
from Ebro Delta, Catalonia (NMW.Z.2019.100.0012–14,anterior view, SEM by K. Mills); (C)
foliaceous thoracic lamellae of *M.* sp. 2 from the Brazilian coast (from Brasil, 2003,anterior
view); (D–E) parapodia of chaetigers 8 and 4 of *M. montera* respectively from Gulf of Aqaba
(holotype, MNHN TYPE 1548, anterior views); (F) right-hand parapodia of chaetiger 2 of *M.
obockensis* from Obock, Red Sea (syntype, MNHN Type 1357, anterior view); (G) right-hand
parapodia of chaetiger 8 of *M. symmetrica* from the Seychelles(holotype,
NMW.Z.2000.020.0175, anterior view); (H) distally expanded and scoop-shaped neuropodial
lamellae of chaetigers 1–3 of *Magelona* sp. cf. *M. cincta* from Iran, NMW.Z.2015.012.0004,
posterolateral view, stained with methyl green); (I) notopodia of chaetigers 9 and 10 of *M.
johnstoni* from Berwick-upon-Tweed (anterior view). Noto = notopodia, Neuro = neuropodia,
Pre = prechaetal, Post = postchaetal, SDL = superior dorsal lobe.
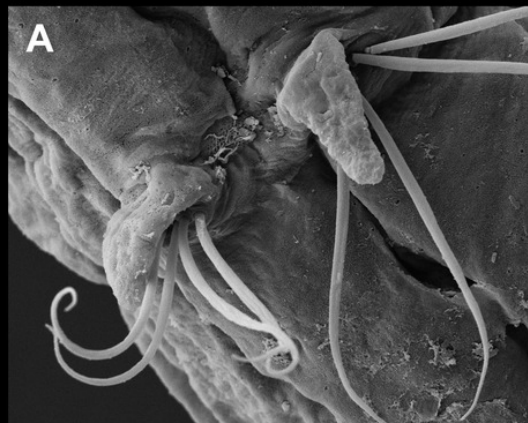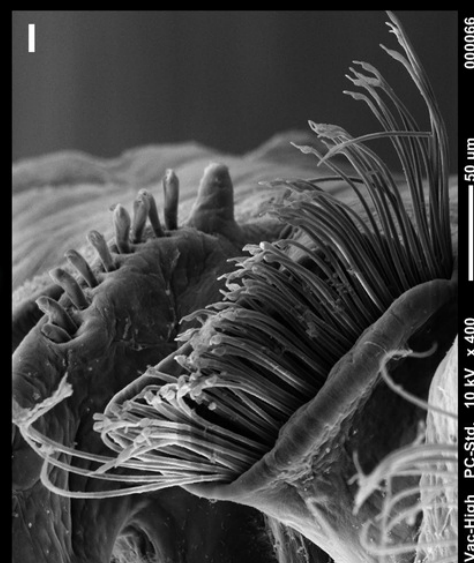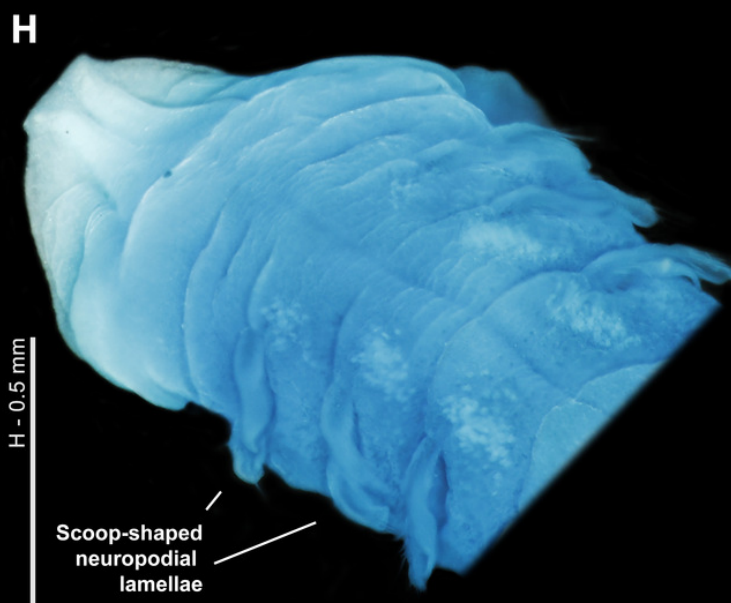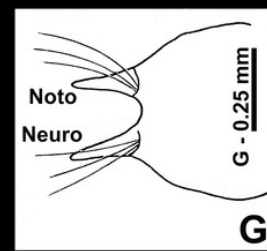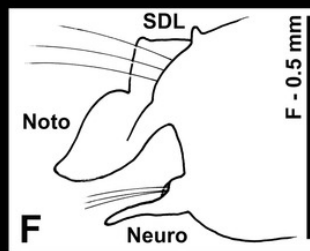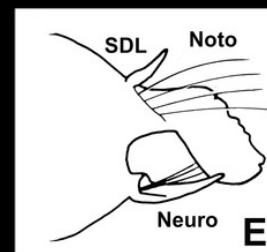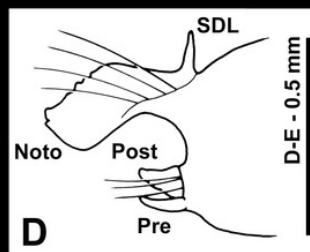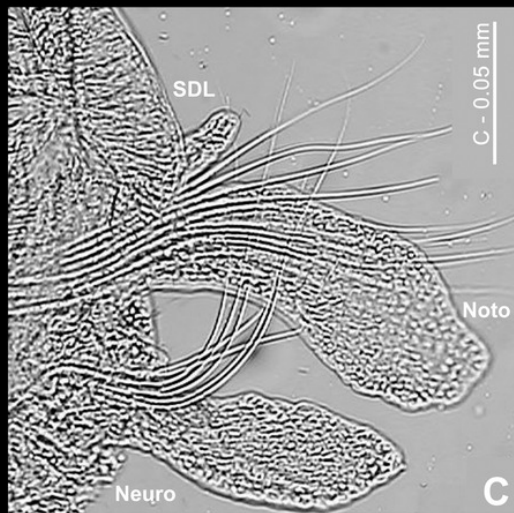
Figure 10

Magelonid thoracic chaetae.

(A) first five chaetigers, showing thoracic capillary chaetae in noto- and neuropodia, of *Magelona equilamellae* from Ebro Delta, Catalonia; dorsal view. SEM by K. Mills; (B) right-hand notopodia of chaetiger 5 (anterior view) of *M. equilamellae* from Ebro Delta, Catalonia, SEM by K. Mills; (C) unilimbate capillary chaetae of *M. minuta* from Öresund, Sweden (USNM 52510); (D) bilimbate capillary chaetae with irregular blades from chaetiger 4 of *M. riojai* from Coroa Grande, Rio de Janeiro, Brazil; (E) bilimbate capillary chaeta with irregular blade from chaetiger 2 of *M. variolamellata* from Paranaguá Bay, Brazil; (F–G) mucronate chaetae from chaetiger 9 of *M. riojai* from Coroa Grande, Rio de Janeiro, Brazil; (H) the same from *M. johnstoni* from Berwick-upon-Tweed (NMW.Z.2013.037.0011b); (I) pennoned chaetae from chaetiger 9 of *M. pitelkai, M. hobsonae, M. hartmanae* (respectively), modified from Jones (1978).
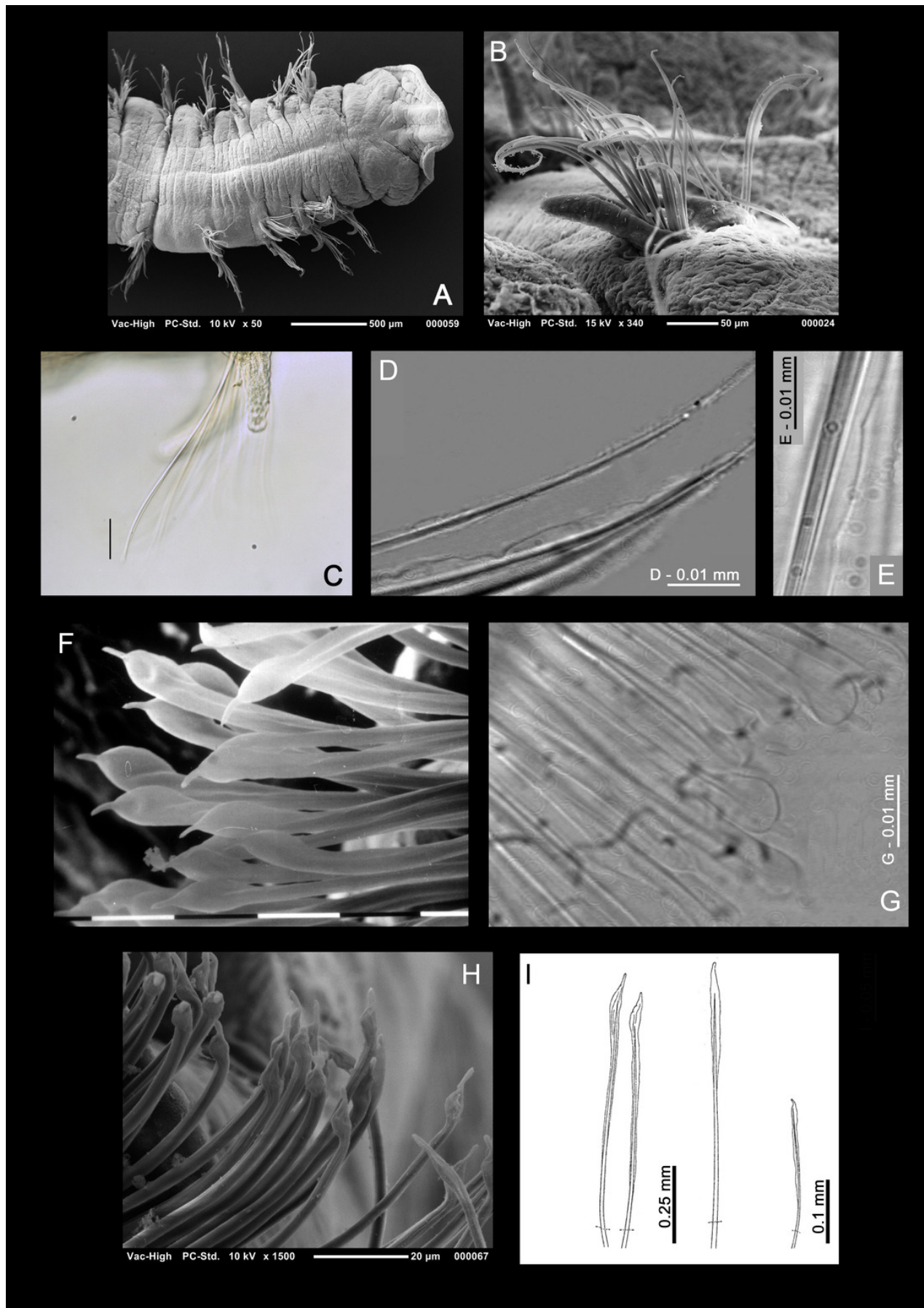
Figure 11

Magelonid thoracic region.

(A) characteristically bulbous and rounded thoracic chaetigers of *Magelona alleni* from Rame Head, England (holotype, BMNH 1958.5.2.1, dorsal view); (B) anterior end of *M. johnstoni* from Berwick-upon-Tweed (NMW.Z. 2013.037.0001, dorsal view, photo by A.S.Y. Mackie) showing straight thoracic interparapodial margins; (C) anterior end of *M. variolamellata* from Paranaguá Bay, Brazil (dorsal view) showing oblique lateral slits; (D) anterior end of *M. crenulifrons*from Hong Kong (ventral view, from Mortimer & Mackie, 2009) showing V-shaped ventral marking in the mid-thoracic region and methyl green staining pattern; (E) anterior end of *M. pulchella* from Kuwait (holotype, BMNH 1969.391, ventral view) showing X-shaped ventral marking in the mid-thoracic region, stained with methyl green; (F) thoracic ventral pads/swellings of *M. mirabilis* from Berwick-upon-Tweed in the mid to posterior thorax (NMW.Z.2013.037.0020, ventral view, photo by A.S.Y. Mackie); (G) posterior thorax of *M. obockensis* from Obock, Red Sea (syntype, MNHN Type 1357, ventral view) showing ventral swellings/pads. Ach = achaetous first segment, BO = burrowing organ, DS = dorsal slits, Pp = palp, Pr = prostomium, Th = thorax, V = ventral V-shaped marking, VS = ventral swellings, X = ventral X-shaped marking.
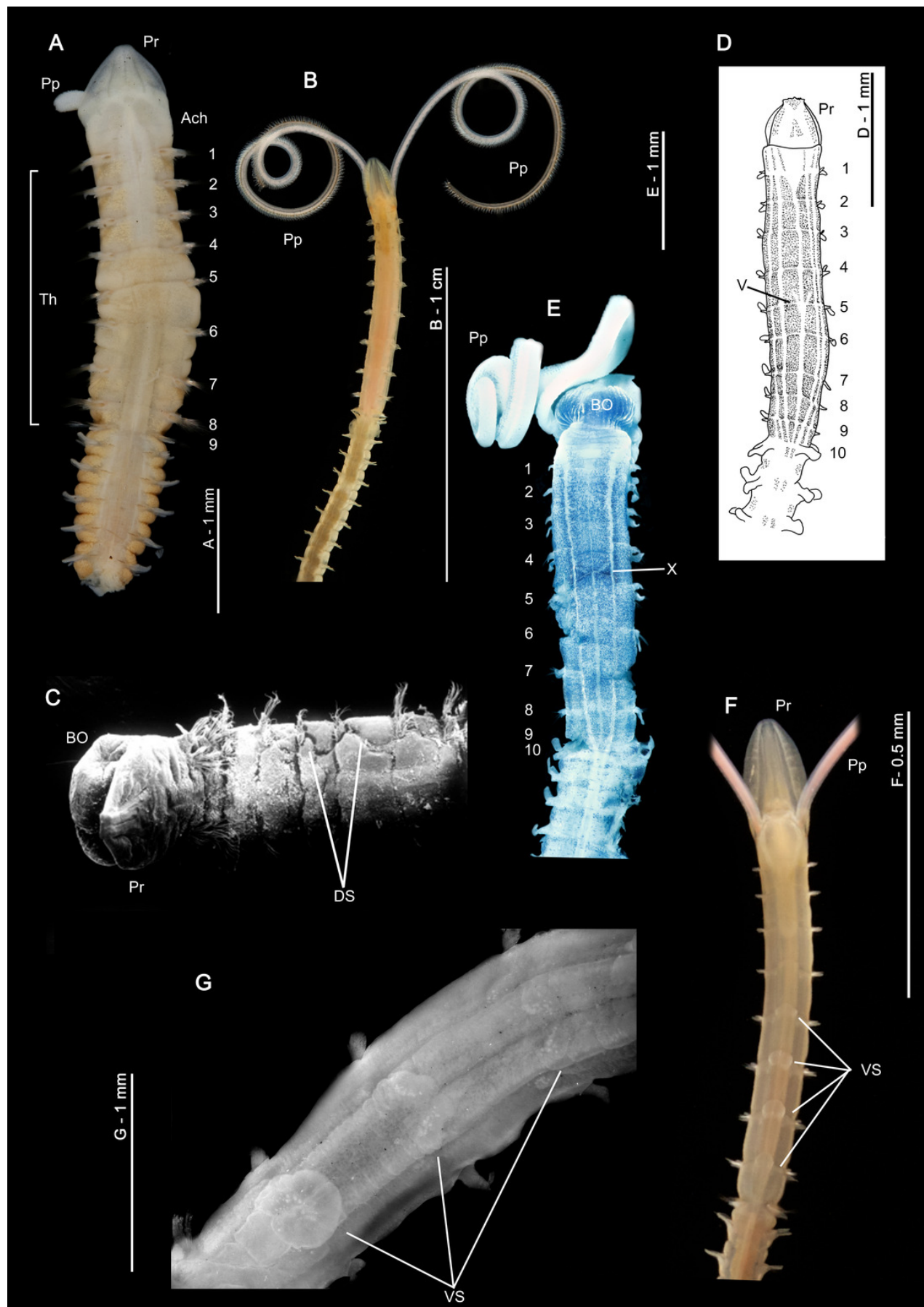
Figure 12

Magelonid abdominal chaetigers.

(A) wider than long abdominal chaetigers of *Magelona posterelongata* from Paranaguá Bay, Brazil (lateral view, scale 1 mm); (B) right-hand parapodia of chaetigers 10 and 11 of *M. johnstoni* from Berwick-upon-Tweed (NMW.Z.2013.037.0011b, anterior view), showing anteriorly open pouch; (C) left-hand parapodia of chaetiger 10 of *M. crenulifrons* from Iran (NMW.Z.2010.037.0034b, anterior view); (D) right-hand parapodia of chaetigers 9–11 of *M. equilamellae* from Ebro Delta, Catalonia, lateral view, SEM by K. Mills; (E) abdominal parapodium of *M.* sp. 2 from the Brazilian coast (from Brasil, 2003) anterior view; (F) right-hand parapodia of abdominal chaetiger of *M.* sp. D from the Gulf of Mexico of Uebelacker & Jones (1984) (modified from that publication); (G) left-hand parapodia of chaetiger 11 of *M. alleni* from Morocco (NMW.Z.2021.001.0001) showing sub-equal lateral lamellae; (H) right-hand parapodia of an abdominal chaetiger of *M.* sp. 2 from the Brazilian coast (from Brasil, 2003, anterior view); (I) thoracic-abdominal junction of *M. filiformis* from Salcombe, England (paratype, BMNH 1959.4.2.6–10, ventro-lateral view). AC = acicular chaetae, AH = abdominal hooks, DF = dorsal flap, DML = dorsal medial lobe, LO = lateral organ, Neuro = neuropodia, Noto = notopodia, PE = postchaetal extension of the lamellae, PM, pouch membrane, SAH = small abdominal hook, US = unidentate spine, VF = ventral flap, VML = ventral medial lobe. Numbers indicate chaetiger number.
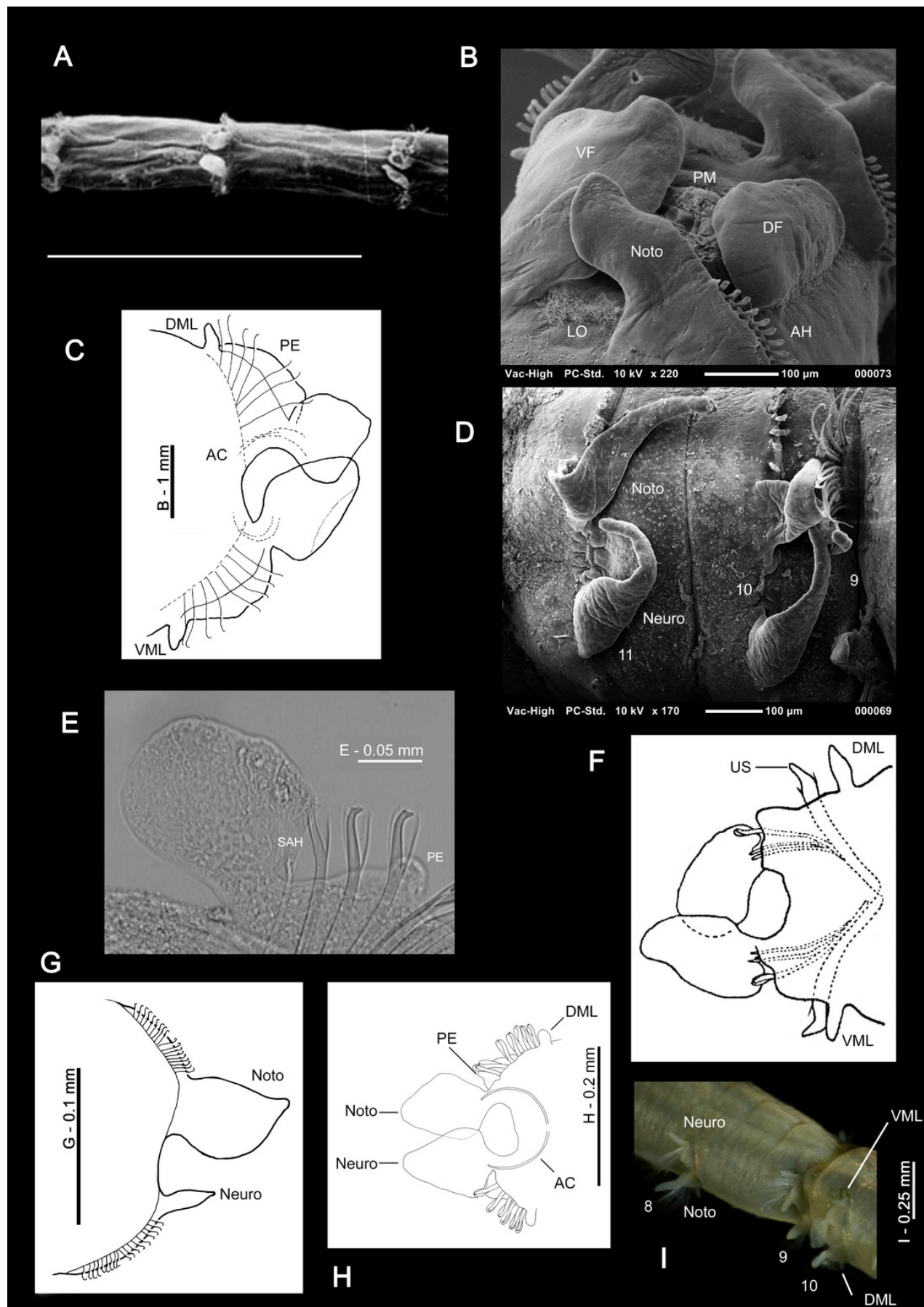
Figure 13

Magelonid lateral abdominal pouches.

(A) schematic diagram showing a 'magelonid' with paired anteriorly open pouches in the anterior abdomen, followed by unpaired posteriorly open pouches in the mid and posterior abdomen, on alternate chaetigers; (B) schematic diagram of a magelonid with unpaired posteriorly open pouches, on alternate chaetigers; (C) schematic diagram of a magelonid with paired posteriorly open pouches, on consecutive chaetigers; (D) transverse section through the body and an anteriorly opening pouch situated between chaetigers 10 and 11 of *Magelona johnstoni* from Berwick-upon-Tweed (posterior half of pouch and parapodia of chaetiger 11 visible) (NMW.Z.2013.037.0010c, anterior view); (E) left-hand anteriorly opening pouch between chaetigers 10 and 11 of *M. johnstoni* from Berwick-upon-Tweed (NMW.Z.2013.037.0011b, lateral view); (F) the same from another specimen collected from the same locality, ventrolateral view (NMW.Z.2013.037.0008c); (G) posteriorly open pouch of the same specimen (ventrolateral view); (H) posteriorly open pouches on consecutive segments of *M. pacifica* from Panamá (syntype, BMNH Type 1933.7.10.65/70, lateral view), pouches showing distinct medial splits. DF = dorsal flap, DML = dorsal medial lobe, LO = lateral organ, Neuro = neuropodia, Noto = notopodia, PM = pouch membrane, PO pouch = posteriorly opening pouch, VF = ventral flap. Numbers indicate chaetiger number.
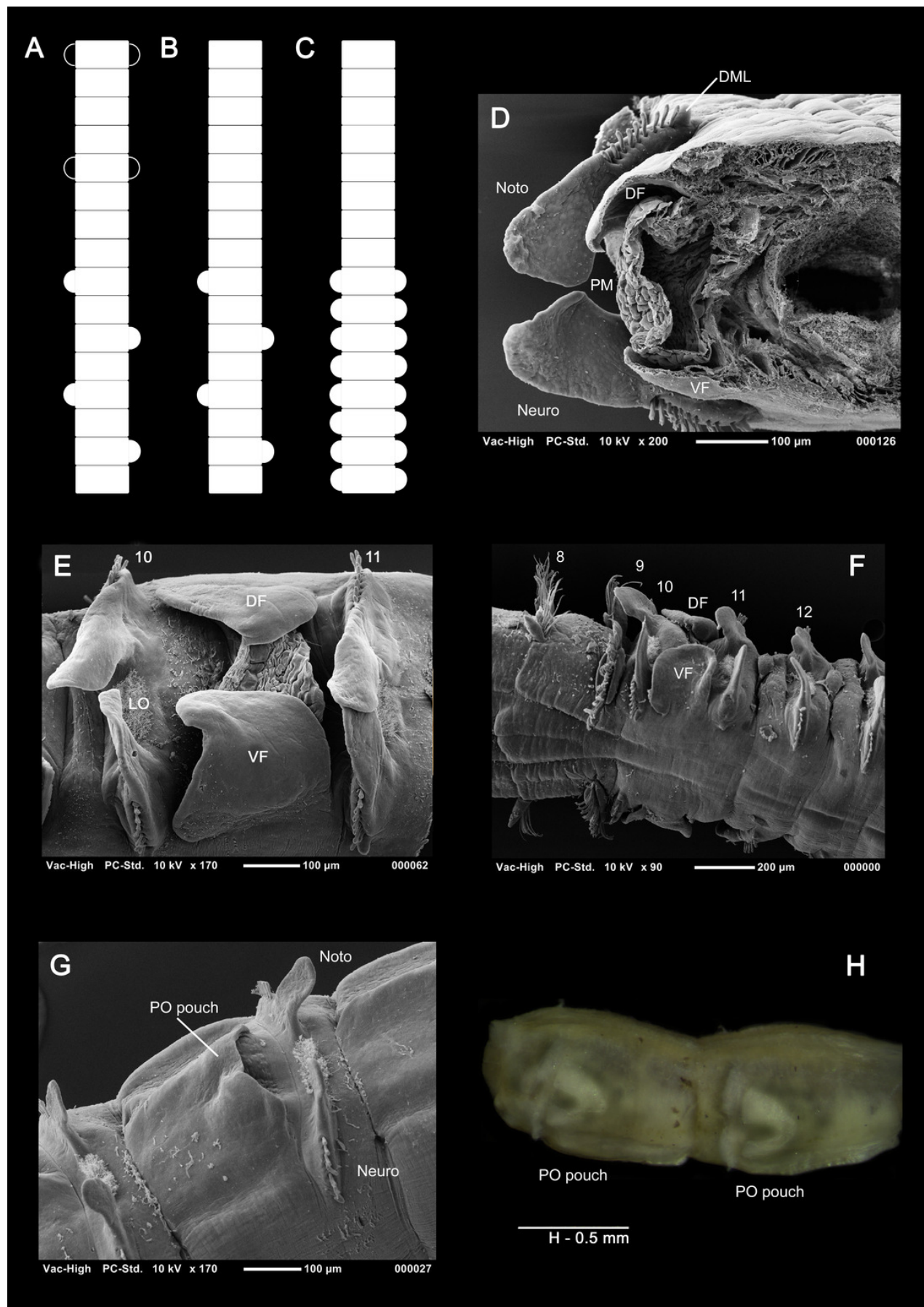
Figure 14

Magelonid abdominal hooded hooks.

(A) transverse section of the body of *Magelona johnstoni* from Berwick-upon-Tweed, between chaetigers 10 and 11 (posterior half of pouch and parapodia of chaetiger 11 visible) (NMW.Z.2013.037.0010c, anterior view); (B) row of hooded hooks arranged vis-à-vis of *M. equilamellae* from Ebro Delta, Catalonia; (C) bidentate hooded hooks from chaetiger 29 of *M. minuta* from the Irish Sea (NMW.Z.1991.075.1584a, lateral view); (D) bidentate hooded hook from *M. papillicornis* from Brazilian coast (lateral view, scale = 0.01 mm); (E) tridentate hooded hook from *M. alleni*; (F–H) quadridentate, pentadentate and hexodont hooded hooks from *M. fauchaldi* from Iran (paratypes, NMW.Z.2015.012.0002d–e); (I) small hooded hook adjacent to the lateral lamellae of *M.* sp. 3 from the Brazilian coast (from Brasil, 2003, anterior view); (J) bidentate hooded hooks of *M. papillicornis* from Brazilian coast, arranged vis-à-vis; (K) unidentate enlarged hook of *M.* sp. 3 from the Brazilian coast (from Brasil, 2003). C, E–H, hoods broken. Photos B, C, E by K. Mills. Neuro = neuropodia, Noto = notopodia, SAH = small abdominal hook.
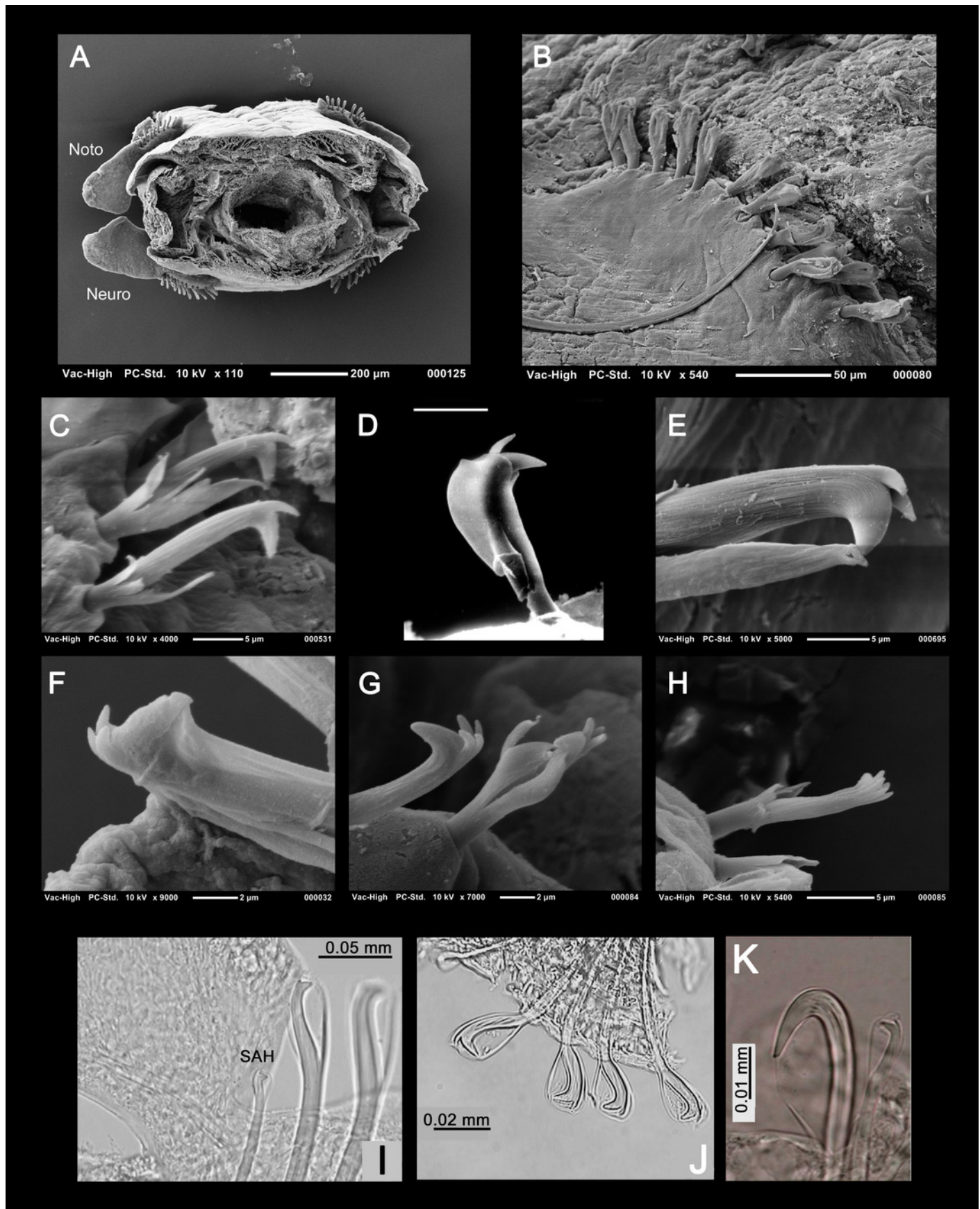
Figure 15

Magelonid pigmentation.

(A) anterior end of a live *Magelona alleni* (dorsal view) from Plymouth, showing thoracic pigment band on posterior thorax (photo by A.S.Y. Mackie); (B) anterior end (dorsal view) of *M. fasciata* from Senegal, West Africa (NMW.Z.2021.001.0009), showing distinct stripy pigmentation characteristic of the species; (C) pigment band of posterior thorax of *M. equilamellae* from Ebro Delta, Catalonia (MNCN 16.01/18576, photo by K. Mills). Pp = palp, Pr = prostomium.
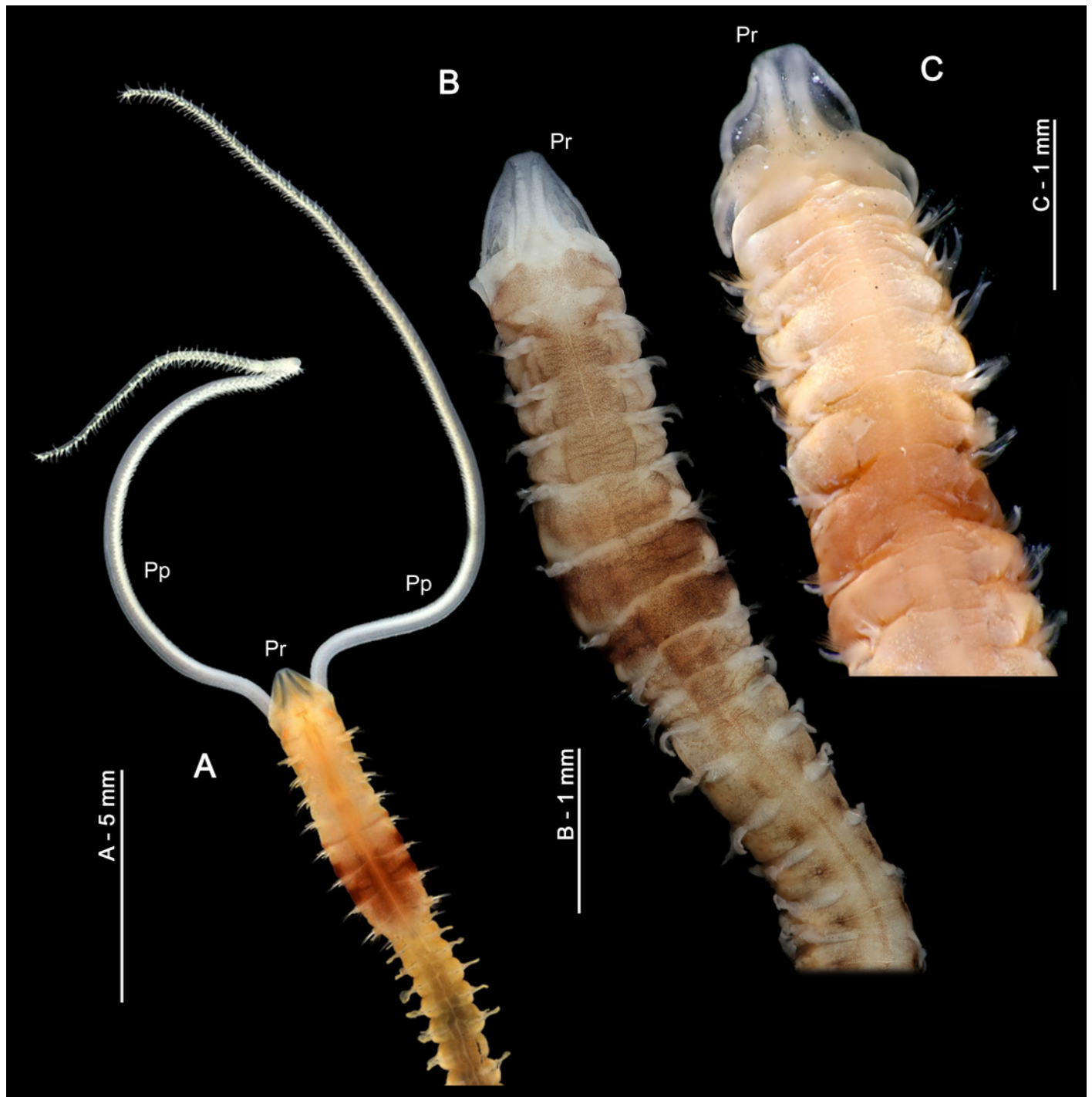
Figure 16

Magelonid pigmentation, granular bodies, tube, pygidial cirri.

(A) anterior region of *Magelona minuta* from the Celtic Sea (NMW.Z.2005.014.0111, dorsal view; photo by K. Mills) showing distinct transverse thoracic stripes; (B) anterior region of *Magelona* sp. cf. *M. cincta* from Iran (NMW.Z.2015.012.0004, dorsal view) showing distinct circular regions of granular bodies adjacent to the parapodia; (C) same specimen showing abdominal interparapodial patches and granular bodies along the mid-ventral line of the abdomen (ventral view); (D) granular bodies of the dorsal surface of the thoracic region of *M. papillicornis* from Brazilian coast;(E) distinct multi-layered tube covered in sand of *M. alleni* from the Irish Sea (NMW.Z.1969.104.1094; photo by K. Mills); (F) digitiform pygidial cirri either side of the pygidium (dorsal view) from Brasil (2003); (G) posterior region of *M. minuta* from the Outer Bristol Channel (NMW.Z.2003.047.5939, ventral view; photo by K. Mills); (H) posterior region of *M. alleni* from Plymouth, England (paratype, BMNH 1958.5.2.1, ventro-lateral view). A–C, G, H, stained with methyl green; E, stained with Rose Bengal. A = anus, Ab = abdomen, BO = burrowing organ, GB = granular bodies, PC = pygidial cirri, Pp = palp, Pr = prostomium, Th = thorax.
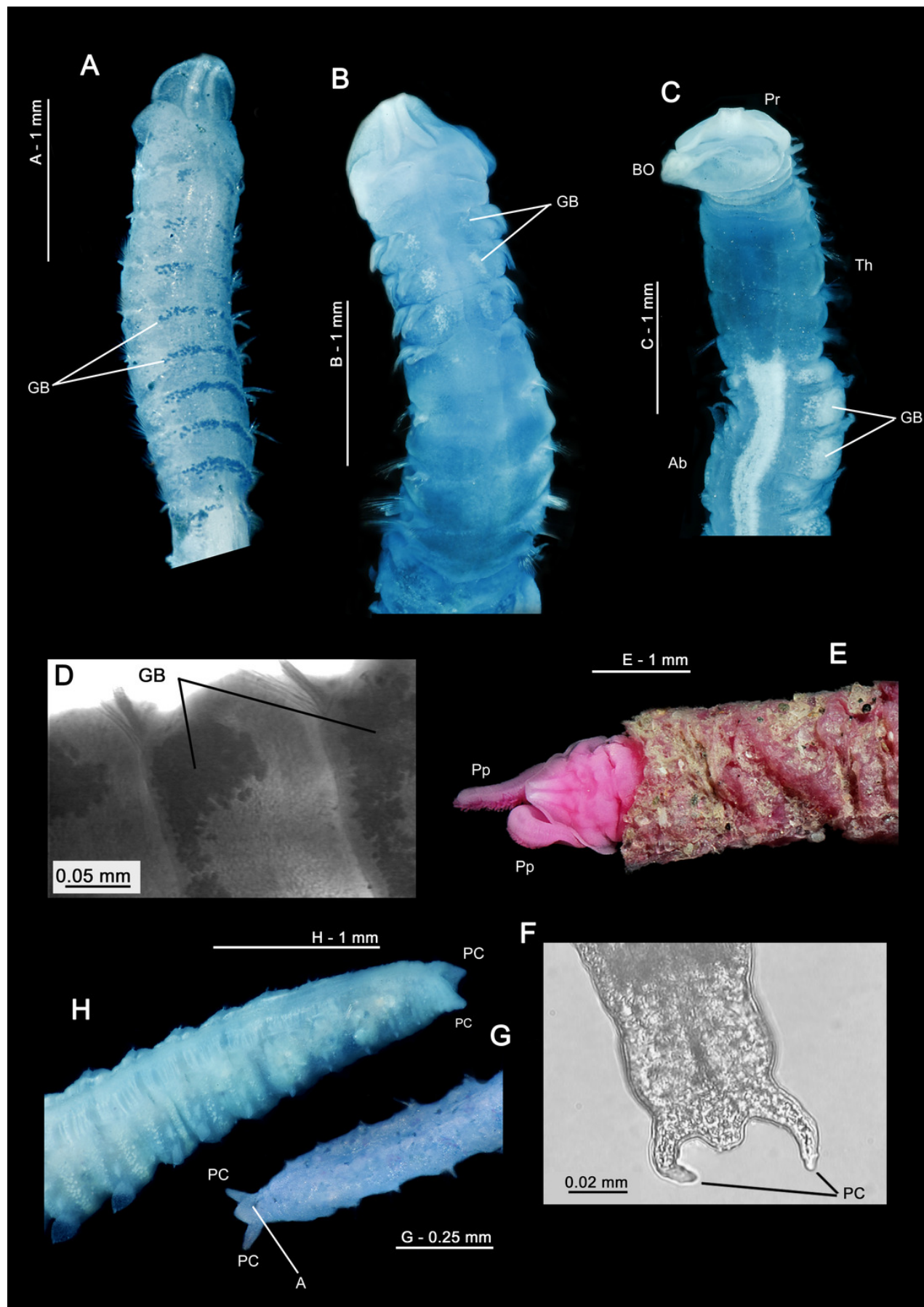
Figure 17

Phylogenetic results. Strict consensus tree for 2,417,600 cladograms produced from data matrix in Table S1.

Note that *Magelona* is paraphyletic relative to *Octomagelona*. Letters **a**–**u** indicate clades for which some character transformation series are presented in the **Results**.
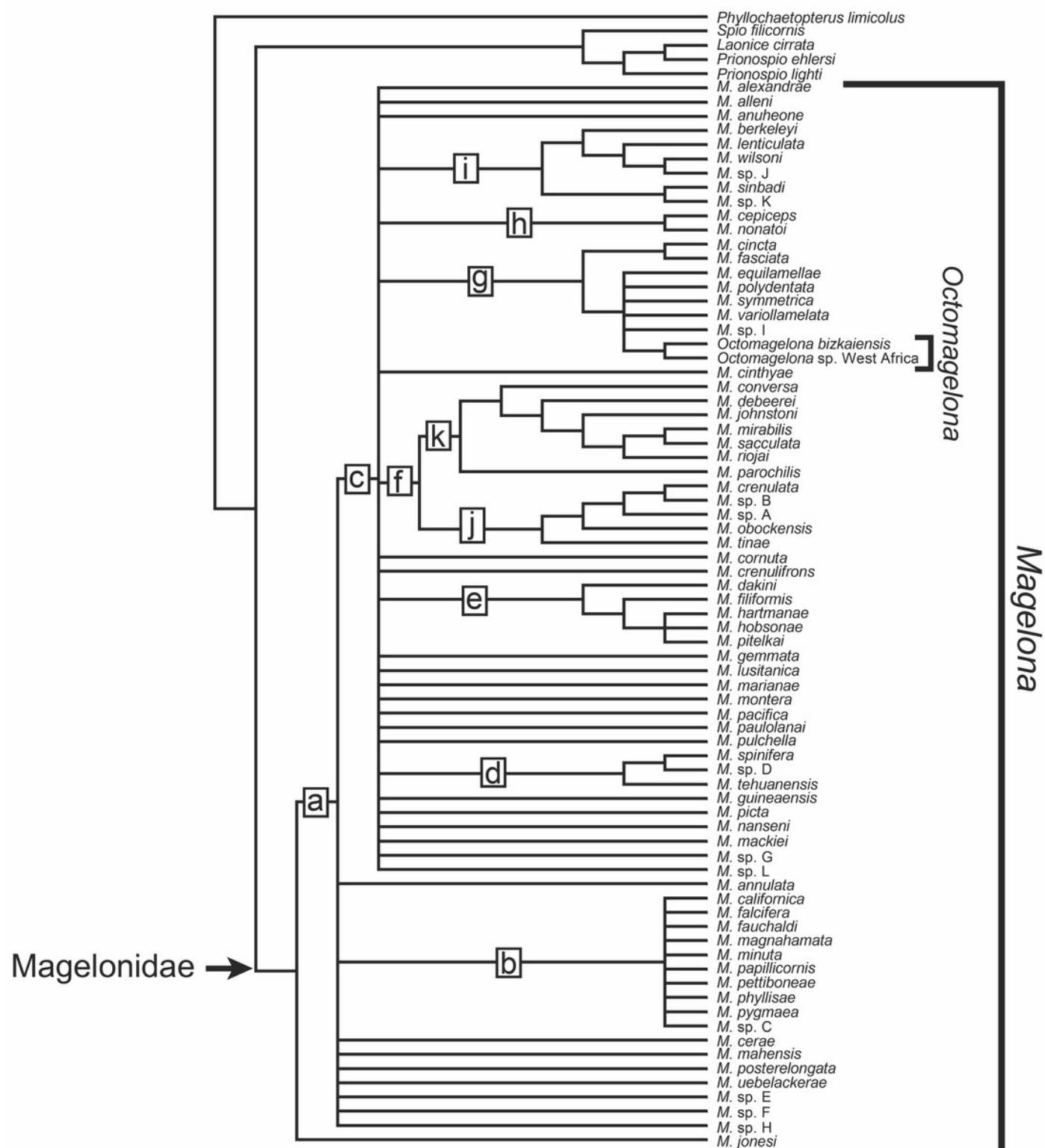
Figure 18

Phylogenetic results.

Fig 46 of the strict consensus tree for nine cladograms presented by Brasil (2003) of

Magelonidae phylogenetic hypotheses. Clades referred to in that study are indicated by the

Roman numerals. Reproduced as shown in Brasil (2003).