Description of the new species *Sigambra nkossa* (Annelida, Pilargidae), with an analysis of the distribution patterns of polychaetes associated with artificially hydrocarbon-enriched bottoms

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The monitoring of the N'Kossa offshore oil and gas fields (Republic of Congo) allowed us to assess the ecological traits of two polychaete species belonging to *Sigambra* (Annelida, Pilargidae): *Sigambra parva*, occurring in very low densities in all bottoms except the most impacted, where it is totally absent, and an undescribed species that reached > 4,000 ind/m^2 in hydrocarbon-enriched sediments. Their distribution patterns are compared with those of other polychaetes showing a range of affinities for hydrocarbon-enriched sediments in the N'Kossa region. Our results suggest that *S. parva* would be a representative of the original local fauna, while the species associated with artificial hydrocarbon-enriched sediments, including the other *Sigambra*, six more polychaetes and a bivalve, could be natively associated with natural hydrocarbon-enriched sediments, using the former as alternative habitats and as dispersal stepping stones. This ecological segregation, together with a careful morphological and morphometric analyses led us to describe the latter as a new species, namely *Sigambra nkossa* sp. nov. Moreover, the morphometric analysis allowed us to discuss on the taxonomic robustness of the key morphological characters of *S. nkossa* sp. nov., as well as to emend the generic diagnosis of *Sigambra* to accommodate the new species.

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21 ## Abstract

22 The monitoring of the N'Kossa offshore oil and gas fields (Republic of Congo) allowed us to
23 assess the ecological traits of two polychaete species belonging to *Sigambra* (Annelida,
24 Pilargidae): *Sigambra parva*, occurring in very low densities in all bottoms except the most
25 impacted, where it is totally absent, and an undescribed species that reached $> 4,000$ ind/m^2 in
26 hydrocarbon-enriched sediments. Their distribution patterns are compared with those of other
27 polychaetes showing a range of affinities for hydrocarbon-enriched sediments in the N'Kossa
28 region. Our results suggest that *S. parva* would be a representative of the original local fauna,
29 while the species associated with artificial hydrocarbon-enriched sediments, including the other
30 *Sigambra*, six more polychaetes and a bivalve, could be natively associated with natural
31 hydrocarbon-enriched sediments, using the former as alternative habitats and as dispersal
32 stepping stones. This ecological segregation, together with a careful morphological and
33 morphometric analyses led us to describe the latter as a new species, namely *Sigambra nkossa*
34 sp. nov. Moreover, the morphometric analysis allowed us to discuss on the taxonomic robustness
35 of the key morphological characters of *S. nkossa* sp. nov., as well as to amend the generic
36 diagnosis of *Sigambra* to accommodate the new species.

37

38 ## Introduction

39   The structure of the meio- and macroinfaunal assemblages has been often used as a
40 bioindicator to assess the environmental impact of both crude oil spills (e.g., Gómez Gesteira &

41 Dauvin, 2005; Washburn, Rhodes & Montagna, 2016) and offshore hydrocarbon (HYD)
42 extraction activities (e.g., Montagna & Harper, 1996; Carroll et al., 2000). The drill mud disposal
43 in offshore oil and gas fields off the Congolese coasts of the Gulf of Guinea (Western Africa) is
44 not an exception (see Denoyelle et al., 2010, and references therein). HYDs are an important
45 component of drilling muds that often accumulate in the bottoms surrounding offshore oil and
46 gas platforms, leading to the presence of highly modified macroinfaunal assemblages.
47   Alterations caused by HYD accumulation may occur both at assemblage and individual
48 levels and may include decreasing abundances and diversities or reduced growth and
49 reproductive rates, respectively (e.g., Olsen et al., 2007; Washburn, Rhodes & Montagna, 2016
50 and references therein). The macroinfaunal patterns in the vicinity of drilling platforms acting as
51 local sources of HYD enriched sediments (HES) often do not differ from those related to other
52 sources of organic enrichment. It is thus possible to find the typical succession mirroring an
53 organic enrichment gradient, ranging from more diverse assemblages with low abundant,
54 sensitive species to low diverse assemblages with highly abundant, opportunistic species, while
55 the most enriched (i.e. polluted) areas are devoid of infauna in extreme cases (Pearson &
56 Rosenberg, 1978). The main difference in the succession patterns affects the indicator species
57 associated with the source of organic enrichment, which in this case, are obviously HYD tolerant
58 (Montagna & Harper, 1996; Dalmazzone et al., 2004; Denoyelle et al., 2010).
59   Private companies are responsible for many worldwide activities related with offshore
60 HYD routine exploration and extraction. Thus, access to these highly interesting macrofaunal
61 and environmental data is often only possible through environmental assessment or monitoring
62 projects. These projects are frequently a legal imperative to companies exploiting natural
63 resources in the sea and habitually include benthic monitoring. Thus, they regularly generate
64 large macrobenthic datasets, sometimes including reference invertebrate collections and
65 interesting information from often previously poorly known or non-studied areas. This can be
66 seen in a recent study carried out in the Falkland Islands, where only a 16% of the 191 species
67 found were known species described from the region, while 13% were uncertain (i.e., damaged,
68 presumed cosmopolitan or having poor original descriptions) and the remaining ones (almost
69 70%) were unknown, likely new (Neal et al., 2020). A similar situation occurs with the surveys
70 carried out in association to the oil and gas activities of TotalEnergies in the Atlantic coasts of
71 the Gulf of Guinea facing the Republic of Congo. The datasets of benthic macrofauna generated
72 have been partly managed through the long-term collaboration between the scientists of the
73 Centre d'Estudis Avançats de Blanes (CEAB-CSIC) and the French company CREOCEAN. The
74 in-deep analysis of these datasets proved to have a high scientific and management interest,
75 including studies on sediment toxicity and recolonization (Dalmazzone et al., 2004) or on the
76 contrasted role as indicators of foraminifers *vs*. macrofauna (Denoyelle et al., 2010).
77   Framed within the monitoring studies sponsored by TotalEnergies E&P Congo around the
78 N'Kossa field off the Republic of Congo, we are here analyzing the influence of the
79 environmental characteristics of the area on the distribution of several polychaete species
80 showing a range of affinities for HES, which were found during the monitoring surveys carried
81 out by CREOCEAN and the CEAB-CSIC. Based on previous results on the macrofauna of the
82 area (Dalmazzone et al., 2004; Denoyelle et al., 2010), the species selected to be studied in deep
83 include *Capitella* sp. (Capitellidae), *Raricirrus* sp. (Ctenodrilidae), *Paramphinome trionyx* Intes
84 & Le Loeuff, 1975 (Amphinomidae), *Oxydromus berrisfordi* (Day, 1967) (Hesionidae),
85 *Lindaspio sebastiena* Bellan, Dauvin & Laubier, 2003 (Spionidae), a unidentified species of
86 Ampharetidae (referred to as Ampharetidae sp.) and two species of *Sigambra* (Pilargidae),

87   *Sigambra parva* (Day, 1963) and an undescribed species (Day, 1963; Day, 1967; Intes & Le
88   Loeuff, 1975; Bellan, Dauvin & Laubier, 2003). The implications of the presence of HES-
89   associated species in artificially enriched, off-shore, shallow-water soft bottoms are discussed in
90   light of the currently available knowledge on the ecological relationships between polychaetes
91   and HYD.
92   We would also like to stress the importance of the studies focusing on taxonomy, which
93   constitute an excellent example of the potential contribution of monitoring surveys to increase
94   the current knowledge on marine biodiversity. Accordingly, several new species have been
95   described from areas of the Congolese Oil & Gas licenses exploited by TotalEnergies E&P
96   Congo. These include the vesicomyid bivalve *Isorropodon bigoti* Cosel & Salas, 2001 and two
97   polychaete annelids, *L. sebastiena* and *Anotochaetonoe michelbhaudi* Britayev & Martin, 2006
98   (Polynoidae) (Cosel, Salas & Høisæter, 2001; Bellan, Dauvin & Laubier, 2003; Britayev &
99   Martin, 2006). To date, the first two species are known only from their type localities, which are
100 the HES bottoms just below the extraction platforms of the N'Kossa field, while the third one
101 was also reported from muddy bottoms in the Gulf of Cádiz, in an area rich in mud volcanoes
102 and pockmarks (Ravara et al., 2017).
103   In the present paper, we are reporting a third new species of polychaete for the N'Kossa
104 field, which belongs to the genus *Sigambra* (Pilargidae). Together with its formal description, we
105 are comparing *S. nkossa* sp. nov. with all previously known species of *Sigambra*, we are
106 performing a morphometric analysis of the relationships between size and several taxonomically
107 relevant features, which allows us to discuss on its taxonomic robustness, and we are amending
108 the generic diagnosis of *Sigambra* to accommodate the new species.
109

Materials & Methods
Sample collection, treatment and statistical analyses
112   During regular environmental monitoring surveys approved by TotalEnergies E&P Congo,
113 samples for macrofaunal analyses were collected around the NKF I and NKF II platforms in the
114 N'Kossa oil and gas field (180 m depth, 60 km off the coast of the Republic of Congo, Gulf of
115 Guinea, Atlantic coasts of western Africa) (Fig. 1) as described in Britayev & Martin (2006) and
116 Denoyelle et al. (2010). Specifically, stations 2, 3, 4 and 6 were sampled in November 2000,
117 March 2002 and April 2003; stations 1, 5 and 7–10 only in 2000; stations 13 and 16 in 2002 and
118 2003; station 15 only in 2002; and stations 17–20 only in 2003. All specimens of the eight target
119 polychaete species were identified, counted and their densities expressed as number of
120 individuals per m^2 (ind/m^2, Supplementary table 1).
121   The stations were environmentally characterized by the distance from drilling point (DDP)
122 expressed in meters (m), as well as by a series of physical-chemical sediment descriptors
123 (Supplementary table 1), which were analyzed in the Laboratoire Municipal et Régional de la
124 Ville de Rouen (France) as described in Dalmazzone et al. (2004).
125   The possible existence of temporal and spatial differences in sediment descriptors, as well as
126 in the presence of the target species was assessed by Parametric MultiDimensional Analysis
127 (PMDA), based on the Mahalanobis distance and applying the Bonferroni correction to prevent
128 Type I errors (Bland & Altman, 1995). The influence of sediment descriptors on the studied
129 samples was analyzed by Principal Component Analysis (PCA). Both types of data, sediment
130 descriptors and polychaete densities, were plotted on the obtained axis to graphically visualize
131 their distributions. The relationships between species densities and sediment descriptors were
132 assessed by Pearson correlation. The significance of the differences between the sample groups

133 obtained in the PCA was assessed by Analysis of Similarity (ANOSIM) and confirmed by
134 PMDA (same procedure as above), both for sediment descriptors and target species. The
135 significance of the differences for each sediment descriptor and target species was then assessed
136 by independent one-way Analysis of Variance (one-way ANOVA), and the group(s) responsible
137 for the observed differences were assessed by a post hoc Tukey test. All analyses were based on
138 log-transformed data to meet with the assumptions of normality and homoscedasticity required
139 for parametric analyses (Zar, 1984) and were performed with the XLSTAT software, version
140 2016.02.27390 (copyright Addinsoft 1995–2016), except the PCA and ANOSIM, which were
141 performed with the respective routines of the Primer 6 software, version 6.1.11, and
142 PERMANOVA, version 1.0.1 (copyright Primer-e Ltd. 2008). Other abbreviations used in the
143 text are: Ba, Barium; CS, coarse sand; DDP, distance from drilling point; DW, dry weight; HES,
144 hydrocarbon enriched sediments; HYD, hydrocarbon; N, Nitrogen; OM, organic matter; P,
145 Phosphorous; PW, pore water; SEM, Scanning Electron Microscope; S&C, silt and clay.
146
147 **Taxonomy**
148 Light micrographs of preserved specimens were made with a Zeiss Axioplan (body) and a
149 Zeiss Stemi 2000–c (chaetae) stereomicroscopes equipped with a CMEX5 digital camera
150 (Euromex). For Scanning Electron Microscope (SEM) observations, the worms were prepared
151 using standard SEM procedures as described in Martin et al. (2003).
152 Type and non-type specimens of the new species are deposited in the Biological
153 Collections of the Centre d'Estudis Avançats de Blanes (CEAB, Blanes, Catalunya, Spain), the
154 Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain), Museu Nacional de História
155 Natural e da Ciência (MB, Lisboa, Portugal), National Museum Wales (NMW, Cardiff, Wales,
156 UK) and Senckenberg Research Institute and Natural History Museum (SMF, Frankfurt,
157 Germany). The specimens of *S. parva* are deposited in the CEAB and the MNCN.
158 The electronic version of this article in Portable Document Format (PDF) will represent a
159 published work according to the International Commission on Zoological Nomenclature
160 (International Commission on Zoological Nomenclature, 1999), and hence the new names
161 contained in the electronic version are effectively published under that Code from the electronic
162 edition alone. This published work and the nomenclatural acts it contains have been registered in
163 ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science
164 Identifiers) can be resolved and the associated information viewed through any standard web
165 browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication
166 is: urn:lsid:zoobank.org:pub:0FCB04BD-5ACA-4808-8091-67F7EF106021. The online version
167 of this work is archived and available from the following digital repositories: PeerJ, PubMed
168 Central SCIE, DigitalCSIC and CLOCKSS.
169
170 **Morphometry**
171 The number of chaetigers was used as surrogate of size. All relevant morphological features
172 susceptible to be size-dependent were identified and counted or measured in a selected subset of
173 21 entire individuals of the new species of *Sigambra* (Supplementary table 2). Dry weight was
174 estimated after drying (60°C) for 24 h. The relationships between size and morphological
175 features were assessed by Pearson correlation, using the same procedures and software as for the
176 ecological analyses.
177
178 **Results**

179
180 **Ecology**
181   Neither the most relevant environmental descriptors, DDP and HYD, nor the populations of
182 the targeted polychaetes show significant differences during the three surveys (Supplementary
183 tables 3A, 3B). Thus, for the purposes of this study, all surveys are considered together.
184   When analyzing the distributions of the target species with respect to the sediment
185 descriptors (Supplementary table 3C), the most common pattern is a significant increase with
186 rising levels of Ba, occurring for all species except *S. parva* and *P. trionyx*. The new species of
187 *Sigambra*, *L. sebastiena*, *Raricirrus* sp. and Ampharetidae sp. also show significant increasing
188 densities with rising levels of HYD. Among them, the first two show the same trend in relation
189 with OM, but the density of *L. sebastiena* decreases with the rise of PW. Finally, both the
190 densities of *Capitella* sp. and Ampharetidae sp. increase with rising levels of N and decrease
191 with increasing levels of CS and P, with those of *Capitella* sp. also increasing with S&C and
192 those of Ampharetidae sp. significantly decreasing with DDP.
193   The first axis of the PCA (Eigenvalue 15.5, 84.4% of the explained variation) is defined by
194 the opposite trend of Ba and, especially HYD, on the negative (left) sector and DDP on the
195 positive (right) sector (Fig. 2). Axis two (Eigenvalue 2.15, 11.7% of the explained variation) is
196 defined by the opposite trend of S&C on the negative (left) sector and, especially CS, on the
197 positive (right) sector (Fig. 2). The densities of the new species of *Sigambra* and *S. parva* plotted
198 on the PCA axis clearly show their disjunct distributions, highlighting the particularly high
199 densities of the former in the stations with HES (Fig. 2).
200   The sampling stations cluster in three significantly different groups (ANOSIM: Global R =
201 0.846, significance level = 0.1%) according to the PCA, which coincide with markedly different
202 HYD ranges (Fig. 2). The significance of the differences is confirmed by PMDA (Supplementary
203 table 4B). Group I includes the stations 5 and 6 (HYD > 20000 mg/kg DW), group II includes
204 the stations 4, 7, 13, and 18 (HYD: 20000–100 mg/kg DW) and group III includes the stations 1–
205 3, 8–11, and 15–16 (HYD < 100 mg/kg DW). The most significant differences occur always
206 when group III is involved (Supplementary table 4A). Group I is very homogeneous but, within
207 groups II and III, two subgroups can be respectively distinguished. Characteristically, the
208 smallest subgroups including stations 4, 13 and 18 (from 2003) and 13 (from 2002) in group II,
209 and 2, 13, and 19 (all from 2003) in group III, are mainly isolated from the other stations due to
210 the extremely low CS (< 2%). The differences between these two subgroups and the remaining
211 stations of each group prove to be also significant (ANOSIM: Global R = 0.944 / 0.630,
212 significance level = 2.9% / 1.5%, respectively).
213   When analyzed individually, DDP, HYD, and Ba show highly significant differences
214 between the PCA groups, but also S&C and P slightly differ (Supplementary table 4D, Fig. 3).
215 The pairwise analyses (Supplementary table 5) show that: in group III, DDP is always
216 significantly higher and HYD and Ba are always significantly lower; neither DDP, nor Ba differ
217 between groups I and II, while HYD is significantly much higher in the former; S&C is only
218 slightly lower in group I than in group II, while none of them differ from group III, and there is
219 no clear pattern for P (Fig. 3). Finally, CS, PW, OM and N do not show significant differences
220 between the PCA groups (Supplementary table 5, Fig. 3).
221   The density of the target benthic species also shows significant differences in the PCA
222 groups (Supplementary table 4C), with all species having also clearly different distribution
223 patterns (Supplementary table 5, Fig. 2). The new species of *Sigambra*, *Capitella* sp. and *O.*
224 *berrisfordi* have non-significantly different densities between groups I and II, which are

225 significantly higher than those in group III. In fact, the new species of *Sigambra* and *O.*
226 *berrisfordi* are completely absent from group III, as it is *L. sebastiena*. *Raricirrus* sp. shows
227 significantly higher densities in group I than in group III, while those in group II do not differ
228 from those in groups I and III. *Paramphinome trionyx* shows non-significant differences in
229 density between group I and groups II and III, while the density is significantly higher in group II
230 than in group III. Ampharetidae sp. shows significantly higher densities in group II than in
231 groups I and III, which, do not differ from each other. Finally, *Sigambra parva* is completely
232 absent form group I, and shows similar low densities in groups II and III.
233
234 **Taxonomic account**
235
236 Family Pilargidae Saint-Joseph, 1899
237
238 *Sigambra* Müller, 1858
239 *Sigambra.* Müller (1858): 214 (original description); Pettibone (1966): 179 (genus
240 reinstated with key to species); Licher & Westheide (1997): 2 (key to species and synoptic
241 table with characters of all species); Nishi et al. (2007): 65 (synoptic table with characters
242 of all species); Salazar-Vallejo et al. (2019): 24 (diagnosis), 44–46 (key to species).
243
244 *Type species. Sigambra grubii* Müller, 1858, by monotypy.
245
246 *Diagnosis.* Based on Glasby & Salazar-Vallejo (2022). Pilarginae with body depressed, usually
247 obconic. Prostomium with three antennae, longer than palps; palps biarticulate. Tentacular cirri
248 as long as half width of tentacular segment. Parapodia biramous. Dorsal and ventral cirri foliose
249 to tapered, dorsal ones usually longer than ventral ones. Notopodium with one strongly recurved
250 dorsal hook, or with one strongly recurved dorsal hook and one slightly bent spine along many
251 chaetigers, sometimes with capillary chaetae or with protruding tips of notoaciculae. Neuropodia
252 with shorter pectinate capillaries, medium-sized denticulate capillaries, and longer finely
253 denticulate capillaries, often twisted distally.
254
255 *Remarks.* Virtually all morphological features characterizing *Sigambra* have been well defined in
256 recent literature (Salazar-Vallejo et al., 2019; Glasby & Salazar-Vallejo, 2022). Our observations
257 on the species found in the N'Kossa field, complemented with the original descriptions and
258 figures of other species of the genus (Supplementary table 6), lead us to suggest that the generic
259 diagnosis probably requires to be amended in what concerns the so called "capillary chaetae"
260 associated with the notopodial hooks/spines. In our specimens, these supposed "capillary
261 chaetae" revealed to be the tips of the notoaciculae protruding from the acicular lobes.
262 Accordingly, the notopodial character "sometimes with accessory capillaries" probably has to be
263 replaced by "sometimes with protruding tips of notoaciculae". However, further examination of
264 other species having these "capillary chaetae" is required prior to confirm the necessity of
265 amending the generic diagnosis. While waiting for this review, we have included in the diagnosis
266 "sometimes with capillary chaetae or with protruding tips of notoaciculae", instead of just
267 "sometimes with capillary chaetae".
268
269 *Sigambra nkossa* sp. nov.
270 LISID: urn:lsid:zoobank.org:act:9015B0CC-4C6B-4DFF-A9AE-F403F512AE2B.

271 Figures 4–5

272

273 *Material examined:* Holotype: CEAB-A.P. 913A, entire specimen, N'Kossa oil and gas field, St.
274 13(2), Republic of Congo, Gulf of Guinea, Atlantic coasts of western Africa (approximately
275 05º16'S, 11º34'E), collected by DM in April 2003, on soft sediments at around 180 m depth,
276 fixed in a 4% formaldehyde/seawater solution, preserved in 70% ethanol. Paratypes: CEAB-A.P.
277 913B, 1 specimen in two fragments, anterior end dissected to reveal the pharynx, other data as in
278 holotype; CEAB-A.P. 913C, 1 entire specimen, prepared for SEM, collected in March 2002, St.
279 13.2, other data as in holotype; CEAB-A.P. 913D: 245 specimens, collected in March 2002, St.
280 6.2, other data as in holotype; CEAB-A.P. 913E: 173 specimens, collected in March 2002, St.
281 4.3, other data as in holotype; CEAB-A.P. 913F: 153 specimens, collected in March 2002, St.
282 6.3, other data as in holotype; CEAB-A.P. 913G: 431 specimens, collected in March 2002, St.
283 13.2, other data as in holotype; CEAB-A.P. 913H: 267 specimens, collected in April 2003, St.
284 4.3, other data as in holotype; CEAB-A.P. 913I: 749 specimens, collected in April 2003, St. 6.1,
285 other data as in holotype; CEAB-A.P. 913J: 479 specimens, data as in holotype; MNCN
286 16.01/19138: 10 specimens, data as in holotype; MB29-000359 – MB29-000368: 10 specimens,
287 data as in holotype; NMW.Z.2022.002.0001: 10 specimens, data as in holotype; SMF 31812 –
288 31821: 10 specimens, data as in holotype. Additional specimens are available from the authors.

289

290 *Diagnosis.* Prostomium bilobed, with biarticulate palps; median antenna ca. 1.7 times longer than
291 lateral ones; proboscis with fourteen pointed distal and numerous subdistal papillae; peristomium
292 with a transverse row of epidermal papillae; dorsal tentacular cirri ca. 1.8 times longer than
293 ventral ones, dorsal parapodial cirri 1.5 to 3 times longer than ventral cirri (which are absent in
294 chaetiger 2); pointed neurochaetae serrated and pectinated; notopodial hooks from chaetiger 5 to
295 body end, notopodial spines from chaetiger 9 to body end and tips of notoacicula protruding
296 from acicular lobe from mid-body parapodia to body end.

297

298 *Description.* Body measuring 2.8–26 mm long, 0.6–1.9 mm wide (with parapodia) for 23–134
299 chaetigers. Body dorsoventrally flattened, with faint blackish dorsal and ventral pigmentation on
300 prostomium, peristomium, antennae and tentacular cirri, almost disappearing in preserved
301 specimens (Fig. 4A–C). Eyes lacking (Fig. 4A, B). Prostomium bilobed; palps biarticulated, with
302 large palpophores and small palpostyles (Fig. 5A, C, D); interpalpal area distinct, anteriorly
303 depressed, widely expanded posteriorly (Fig. 4B, C). Three antennae slender, tapering distally,
304 on posterior half of prostomium; median antenna 1.5 to 2.0 (1.7 on average) times longer than
305 lateral ones; lateral antennae clearly surpassing palp tips, median antenna reaching chaetiger 2
306 when folded backwards (Fig. 4A, B); lateral antennal furrow distinct, slightly divergent (Fig.
307 5A).
308   Tentacular segment three times wider than longer, with two pairs of slender and subequal
309 tentacular cirri, ventral one as long as lateral antennae, dorsal cirri ca. 1.8 times longer than
310 ventral cirri; two small anteriorly projected lobes between lateral antennae and tentacular cirri
311 and a central anteriorly projected lobe ventrally (Figs. 4B, C and 5A, D). Small epidermal
312 papillae, 5–9 µm in diameter, near posterior prostomial margin, in a single row laterally, in
313 several rows medially, between bases of lateral antennae (Fig. 5A, B). Rows of similar epidermal
314 papillae on posterior margin of each parapodium, dorso-laterally near bases, 11–16 papillae on
315 each side.
316   Proboscis with fourteen distal conical papillae, with long pointed ends in two lateral groups

317   of four papillae, usually bigger than dorsal (three papillae) and ventral (three papillae) groups
318   (Figs. 4F and 5C, D); curved surface with two central longitudinal rows with numerous randomly
319   distributed small papillae on both sides dorsally (Fig. 4E), numerous randomly distributed small
320   papillae ventrally (Fig. 4F) and five bigger papillae on a transversal row and several randomly
321   distributed and progressively smaller papillae laterally (Fig. 4G, 5D); all papillae pointed, with
322   cusps directed backwards in totally everted proboscis.
323   Parapodia sesquiramous; dorsal and ventral cirri tapering distally; first dorsal cirri 1.7 times
324   longer than central antenna, 1.6 times longer than dorsal tentacular cirri, 2.5 times longer than
325   remaining dorsal cirri; following dorsal cirri 1.5 longer than ventral cirri in anterior chaetigers,
326   becoming progressively longer and slender in middle and posterior chaetigers, to up to three
327   times longer in posterior most chaetigers; second chaetiger with dorsal cirri shorter than
328   following ones, lacking ventral cirri (Figs. 4A–C, H, I, K). Notopodia with dorsal cirrus and one
329   or two pointed aciculae, one with curved end protruding from acicular lobe in posterior
330   chaetigers and one straight, non-protruding; one emergent hook from chaetiger 5 (5–6), one
331   emergent spine from chaetiger 9 (9–12), both present until posterior-most chaetigers, more
332   exposed posteriorly (Figs. 4I–L and 5G, H). Neuropodia well-developed; ventral cirri similarly
333   shaped but shorter than dorsal ones, extending far beyond neuropodial lobe tips, longer
334   posteriorly (Fig. 4A, B, D); acicula straight, pointed, sometimes slightly protruding outside
335   acicular lobe; parapodial lobe blunt, almost square; about 10 short pectinate supraacicular
336   chaetae with long spinulation and filiform tips; about same number of slightly longer, distally
337   pointed pectinate chaetae; numerous minutely serrated, distally pointed, capillary chaetae of
338   variable length but much longer than the other neurochaetae; spinulation always directed
339   upwards, thicker in shorter chaetae and in proximal part of longer chaetae (Fig. 5E, F).
340   Pygidium with two slender anal cirri, pointed, of about same length as first dorsal cirri (Fig.
341   4A).
342
343   *Remarks. Sigambra nkossa* sp. nov. perfectly fits all diagnostic characters of the genus, except
344   for the presence of spines in addition to hooks and protruding tips of notoacicula in most
345   notopodia along the body, a peculiar feature also described for *Sigambra robusta* (Ehlers, 1908),
346   *Sigambra bassi* (Hartman, 1947) and *Sigambra healyae* Gagaev, 2008 (Ehlers, 1908; Hartman,
347   1947; Licher & Westheide, 1997; Gagaev, 2008) that allows distinguishing them well from all
348   other species of the genus (Supplementary table 6). The presence or absence of stout emergent
349   notochaetae and, when present, whether they are hooked or straight, were considered to be
350   diagnostic characters at generic level within Pilargidae (Pettibone, 1966; Blake, 1997; Gil, 2011).
351   However, we agree with Glasby & Salazar-Vallejo (2022) in that the presence of stout emergent
352   notopodial chaetae must prevail over the fact that these may be represented by both hooks and
353   spines in at least part of the notopodia along the body in the generic diagnosis. The origin of
354   these spines and their relationships with the notopodial hooks and aciculae needs to be further
355   investigated, but their singularity seems to indicate an apomorphic character.
356   Other species of *Sigambra* were previously found in the same region. Among them, *S.
357   robusta* was collected by the German *Valdivia* Expedition (10–12 October 1898) in the muddy
358   sediments of the "*Große Fisch-Bucht*" (Baía dos Tigres or Tigres Bay, southern Angola) (Chun,
359   1903; Ehlers, 1908), an area geographically close to the offshore Congo location where we found
360   *S. nkossa* sp. nov. Tigres Bay was formerly delimited westwards by a long sandy peninsula
361   running parallel to the coast and connected to mainland in its southern region by an isthmus;
362   besides, it had muddy sediments that were organically enriched in some parts (Chun, 1903). The

363   isthmus was disrupted by the ocean in 1962 giving rise to Tigres Island, which is separated from
364   mainland by the Tigres Strait. This changed the prevailing ecological conditions of the type
365   locality of *S. robusta*, which were since then under the direct influence of the local coastal
366   currents.
367   *Sigambra robusta* was reported in *Valdivia* stations 76 and 77 (Ehlers, 1908), with the
368   station 76 being the type locality according to Licher & Westheide (1997). While the depth of
369   these stations was not referred in the original description, it was mentioned as being "ca. 14 m"
370   for station 76, in the collection data of *Nereis lucipeta* Ehlers, 1908. However, this last species
371   was based on epitokous males collected in mass on the surface of the water during the night,
372   attracted by lights, as mentioned by Ehlers (1908, pag. 71): "*Die beigelegte Etikette enthält die*
373   *Angabe: 'In Masse an der Oberfläche des Wassers, unter den Lampen*". Thus, the associated
374   station depth seems to be an estimate, as it was not mentioned elsewhere in the publication. Still,
375   both the official contemporary charts of the bay (Commissão de Cartographia, 1896;
376   Hydrographic Office, 1915) and the official expedition account (Chun, 1903) reported the overall
377   maximum depth in the collection area (i.e, the northern region of Tigres Bay), as being around
378   20 m depth. The species was posteriorly recorded from other regions of Angola (including the
379   exclave of Cabinda, just 70 km away from N'Kossa) and Namibia, between 20–150 m depth
380   (Kirkegaard, 1983; Licher & Westheide, 1997), and there is a possible report from Senegal at 23
381   m (Augener, 1918).
382   Indeed, although the lower bathymetric limit of *S. robusta* reaches the depth of the bottoms
383   around the N'Kossa platforms, its recorded habitat is overall around ten times shallower than that
384   of *S. nkossa* sp. nov. Moreover, the new species shows pigmentation in the anterior end (absent
385   in *S. robusta*), lacks the second ventral cirri (present in *S. robusta*) and has notopodial hooks
386   from chaetiger 5–6 (instead of 43–70 in *S. robusta*).
387   *Sigambra nkossa* sp. nov. differs from *S. healyae* from the Arctic Ocean in having faint
388   blackish dorsal and ventral pigmentation on prostomium, peristomium, antennae and tentacular
389   cirri (instead of red spots on prostomium in *S. healyae*), notopodial hooks starting from chaetiger
390   5–6 (instead of 4 as in *S. healyae*), notopodial spines from chaetiger 9–11 (instead of 12–15 in *S.*
391   *healyae*) and neuropodial capillaries present (absent in *S. healyae*), as well as in being reported
392   from different geographical locations and depths (off Congo, 180 m depth vs. Canadian Basin,
393   1,800 m depth).
394   *Sigambra bassi* was originally described from Florida (Gulf of Mexico) and reported
395   repeatedly since then as having notopodial hooks together with emergent spines (Pettibone,
396   1966; Wolf, 1984; Blake, 1997; Licher & Westheide, 1997; Moreira & Parapar, 2002). However,
397   in its original extended description, Hartman (1947) clearly distinguishes the acicula from the
398   notopodial spines, while discussing the presence of structures such as "*notoacicular spines*
399   [whose] *free end is strongly curved*", "*dorsal acicular spines*", "*recurved acicular spines*" or
400   "*projecting hooks*". Moreover, she illustrated a parapodium with an emerging straight spine that
401   seems to be the prolongation of the acicula, being thus difficult to ascertain if spines were really
402   present along with hooks, or if she was referring to the emerging tips of the acicula. This
403   question was clarified by Pettibone (1966), who revised type and non-type material from Florida
404   and stated "*stout notopodial hooked notoseta beginning about setiger 14 (11–15); occasionally*
405   *additional single emergent notoseta, straight or slightly curved (called an aciculum by*
406   *Hartman)*", while representing the notopodial hooks and spines as structures clearly independent
407   from the notoacicula, originating from a different and much more superficial region (Pettibone,
408   1966, Fig. 16), just as it occurrs in *S. nkossa* sp. nov.

409   With just a few exceptions (e.g., Pettibone, 1966; Wolf, 1984), most available descriptions
410 of *S. bassi*, including the original one, comprehended material from both Atlantic and Pacific
411 USA coasts (e.g., Hartman, 1947; Licher & Westheide, 1997) or just from the Pacific coasts
412 (Blake, 1997). This mixture of different populations, representing very likely different taxa,
413 explain certainly the wide range of registered character variation, such as the starting of
414 notopodial hooks between chaetigers 3–25 (Licher & Westheide, 1997). This drawback was
415 previously referred by other authors, and work is now under progress to solve it, likely implying
416 erecting new taxa (see Salazar-Vallejo et al., 2019 and references herein). This fact led us to
417 compare *S. nkossa* sp. nov. only with descriptions from the Gulf of Mexico, discarding both
418 those based on (or including) the Pacific specimens referred above and those based on American
419 Atlantic populations recorded outside the Gulf of Mexico (e.g., Gardiner, 1976). Accordingly, *N.*
420 *nkossa* sp. nov. can be distinguished by the presence of notopodial hooks from chaetigers 4–6,
421 instead of 10–15 in *S. bassi* and, also, by having a median antenna reaching only chaetiger 2
422 when bent backwards, instead of chaetiger 12 in *S. bassi* (but see comments on this last character
423 in Discussion).
424
425 *Etymology.* The specific epithet "*nkossa*" is considered as a substantive in apposition, referring
426 to the N'Kossa oil and gas field, off the Republic of Congo, the type locality of the species.
427
428 *Distribution.* Known only from the N'Kossa oil and gas field (approximately 05º16'S, 11º34'E),
429 western Atlantic Ocean, about 60 km off the coasts of the Republic of Congo (Gulf of Guinea);
430 associated with HES (Fig. 1).
431
432 *Sigambra parva* (Day, 1963)
433 Figures 6–7
434
435 *Material examined.* All specimens collected in the N'Kossa oil and gas field, Republic of Congo,
436 Gulf of Guinea, Atlantic coasts of western Africa (approximately 05º16'S, 11º34'E), by ED and
437 DM, on soft sediments at around 180 m depth, fixed in a 4% formaldehyde/seawater solution,
438 preserved in 70% ethanol. CEAB-A.P. 922A, 1 specimen, collected in November 2000, St. 1;
439 CEAB-A.P. 922B, 1 specimen, collected in March 2002, st. 2.6; CEAB-A.P. 922C, 2 specimens,
440 collected in March 2002, st. 3.1; CEAB-A.P. 922D, 3 specimens, collected in March 2002, st.
441 3.1; CEAB-A.P. 922E, 1 specimen, collected in March 2002, st. 2.1; CEAB-A.P. 922F, 2
442 specimens, collected in April 2003, st. 2.1; CEAB-A.P. 922G, 4 specimens, collected in March
443 2002, st. 4.3; CEAB-A.P. 922H, 4 specimens, collected in March 2002, st. 15.3; CEAB-A.P.
444 922I, 2 specimens, collected in March 2002, st. 16.1; CEAB-A.P. 922J, 3 specimens, collected in
445 March 2002, st. 16.2; CEAB-A.P. 922K, 4 specimens, collected in April 2003, st. 18.1; CEAB-
446 A.P. 922L, 7 specimens, collected in April 2003, st. 18.2; CEAB-A.P. 922M, 1 specimen,
447 collected in April 2003, st. 18.3; MNCN 16.01/19139, 4 specimens collected in April 2003, st.
448 18.2.
449
450 *Description of specimens from the study area.* Body dorsoventrally flattened, tapering toward
451 pygidium. Prostomium bilobed, with palps fused at basis, biarticulate, with large palpophores
452 and small palpostyles (Fig. 6A–C, E); with three slender antennae on posterior prostomium
453 region, tapering distally (Fig. 6A, C); median antenna about 1.5 times as long as lateral ones;
454 four subdermal eyes in trapezoidal arrangement, sometimes non-visible. Peristomium with two

455   pairs of slender tentacular cirri, subequal or with dorsal one slightly longer, and longer than
456   lateral antennae (Fig. 6A–B); two small anteriorly projected lobes between lateral antennae and
457   tentacular cirri (Fig. 6A, D). Small epidermal papillae dorsally on posterior prostomium margin
458   (Fig. 6A, D), and on posterior dorsolateral margin of each chaetiger and near parapodial bases.
459   Fourteen distal proboscideal papillae, conical with round tips (laterally, one pair on each side,
460   big; two groups of five small papillae each, one ventral and one dorsal) (Fig. 6A–B, E); curved
461   surface with two subdistal rows of oval, non-pointed papillae; three triangular, pointed papillae,
462   one median and two on each lateral behind subdistal rows, with cusps pointing backwards (Fig.
463   6E). Parapodia sesquiramous. Notopodia with 1–2 aciculae and pointed, slender dorsal cirrus.
464   First chaetiger with dorsal cirri longer than tentacular cirri and following dorsal cirri; second
465   chaetiger with much shorter dorsal cirri; hooks from chaetiger 4–5, more strongly recurved and
466   emergent posteriorly (Fig. 7A–B). Neuropodia well-developed, with conical acicular lobes, one
467   straight acicula and ventral cirri similar to dorsal ones but shorter, extending beyond tip of
468   acicular lobes and absent in chaetiger 2 (Fig. 6B); numerous pointed, minutely serrated simple
469   chaetae (Fig. 7C); 1–6 short pointed pectinate supracicular chaetae on posterior chaetigers (Fig.
470   7D). Anal cirri slender, as long as dorsal tentacular cirri (Fig. 6F).
471
472   *Remarks.* The morphology of the specimens of *S. parva* found in the N'Kossa field agrees
473   overall with that of the types redescribed by Moreira & Parapar (2002) from Cape Province
474   (South Africa), except in the number of supracicular pectinate neurochaetae, which may be up to
475   6 in the Congolese specimens and were reported as being 1–2 in the type specimens. Some
476   Congolese specimens showed four subdermal eyes, which were not visible in others, while the
477   apparent lack of eyes in the South African specimens may be attributed either to the fading effect
478   of their long storage in preservation fluid or to the hiding by a thicker epidermal layer.
479   There seem to be some slight differences (mainly concerning the distribution of the
480   proboscideal papillae) between the Congolese specimens and both the types of *S. parva* and the
481   specimens from the Iberian Peninsula (Columbretes, NW Mediterranean; Baiona, NE Atlantic),
482   identified as *S. parva* by Moreira & Parapar (2002). However, we have not been able to either
483   confirm or reject this statement in light of our own observations, which were inconclusive.
484   Considering the great distances separating the different populations, it is plausible to think that
485   further work based on larger sets of specimens and, ideally, combining additional morphological
486   observations with morphometric and molecular analyses, will help in assessing whether these
487   and other populations considered as belonging to *S. parva* from areas far from the type locality
488   may represent or not different taxa.
489
490   *Distribution.* Originally described from the south coast of Cape Province, South Africa (34°10'S,
491   23°32'E), where it occurred down to 100 m depth on muddy bottoms (Day, 1963), and later
492   reported from the Atlantic and Mediterranean coasts of the Iberian Peninsula between 2-122 m
493   depth in muds and shelly and fine sands with seagrass meadows (Moreira & Parapar, 2002), in
494   the Aegean Sea (Arvanitidis, 2000; Faulwetter et al., 2017), in the western coast of South Africa
495   (Kirkegaard, 1983) and in the N'Kossa field off the Republic of Congo (this paper).
496
497   **Morphometric analysis of *S. nkossa* sp. nov.**
498
499   Most morphological characters measured are size-dependent (Pearson correlation > 0.7),
500   particularly dry weight, width of chaetiger 15 (with parapodia), length of median antennae, and

501 length of the first dorsal and ventral cirri (Pearson correlation > 0.9) (Supplementary table 7, Fig.
502 8). Conversely, only a few characters do not vary with size, most of them being ratios between
503 different anterior appendages (antennae and tentacular dorsal and ventral cirri) and only three
504 (i.e., the starting chaetiger of notopodial hooks and spines, and the absence of ventral cirri on
505 chaetiger 2) refer to characters previously considered as species-specific (Supplementary table
506 6).
507
508 ## Discussion
509
510 ### Ecology
511 The first benthic samples here analyzed were collected one year after the impact on the
512 sediments caused by oily drill cuttings. Drilling muds were mostly deposited in the surrounding
513 bottoms just below the two N'Kossa platforms and their amount was clearly decreasing with the
514 increasing DDP, as previously reported by Denoyelle et al. (2010). This pattern was highly
515 consistent during all three surveys, to the extent that, with a few exceptions, the environmental
516 parameters analyzed did not differ with time, in a similar way as it happened with the density
517 distribution patterns of the population of the polychaete species targeted in this paper.
518   As a result, the stations located at a greater distance from the platforms (PCA group III)
519 were clearly isolated from the impacted ones (PCA groups I and II), as proven by the significant
520 presence in the latter of Ba. In all three surveys, the stations were grouped in one or another of
521 the two impacted groups independently, to some extent, from DDP. This was caused the local
522 dominant currents that generated different levels of accumulation whose distribution depended
523 not only on DDP, but also on the location around the platforms. In turn, our statistical analyses
524 showed very small differences in granulometry, except for the slight gradient observed in the
525 second PCA axis, which is likely a residual effect of the drilling deposits causing the presence of
526 slightly bigger particles in the most HYD enriched stations (Dalmazzone et al., 2004; Denoyelle
527 et al., 2010). This clearly supported that, before the impact, the analyzed stations had all the
528 same type of sedimentary bottoms. Nevertheless, the drilling disposal caused the HYD
529 concentration to be much higher in group I than in group II stations. Therefore, the main reason
530 explaining the differences in the distribution patterns observed for the polychaete species here
531 targeted was the presence of HYD, as it also occurred for the whole macrofaunal community
532 (Denoyelle et al., 2010).
533   Slope and shelf seeps represent organic-rich areas in the overall poor deep-sea bottoms
534 (Washburn, Demopoulos & Montagna, 2018), where they may function as local, ephemeral
535 disturbances supporting infaunal species pre-adapted to organic-rich, reducing environments
536 (Levin et al., 2000). Natural HYD seeps provide unique habitats to many different species,
537 although macrofaunal organisms often receive less attention than megafauna and
538 microorganisms (Levin, 2005). However, it has been suggested that, at higher taxonomic levels,
539 there was no specific infauna that may be considered as seepage indicators (Washburn,
540 Demopoulos & Montagna, 2018). Conversely, at the species level, there are numerous well-
541 known inhabitants of these particular environments, such as siboglinid tubeworms (Schulze &
542 Halanych, 2003; Bright & Lallier, 2010; Karaseva et al., 2020) and other polychaete species
543 belonging to Orbiniidae (Blake, 2000), Chrysopetalidae (Aguado, Nygren & Rouse, 2013),
544 Dorvilleidae (Ravara, Wiklund & Cunha, 2021) and Hesionidae (Desbruyères & Toulmond,
545 1998). Among hesionids, for instance, *Hesiocaeca methanicola* Desbruyères & Toulmond, 1998
546 was originally described from methane seeps (Desbruyères & Toulmond, 1998) and later found

547 also inhabiting fossil fuel reserves (Fisher et al., 2000).

548   *Sigambra nkossa* sp. nov. responded positively to the presence of Ba in the sediments,
549 indicating a connection with drilling cuttings, but the relationship was stronger with respect to
550 the effective presence of HES. Specimens of *Sigambra* were already present in a survey carried
551 out in 1994, just at the starting of the drilling activities. However, their identity cannot be
552 confirmed and there are no materials available to be revised (J.M. Amouroux & C. Labrune,
553 2022, pers. comm.). This *Sigambra* showed densities from 3 to 30 ind/m^2 and hardly tolerated
554 HES (CREOCEAN, unpublished data), which agrees with the 2000–2003 pattern of *S. parva* (up
555 to 50 ind/m^2), rather than with that of *S. nkossa* sp. nov. (from 1,000 ind/m^2 in 2000 to more than
556 4,000 ind/m^2 in 2003). We thus suggest that: (1) the specimens of 1994 could belong to *S. parva*,
557 whose presence followed the typical composition of the local benthic assemblages in non-
558 disturbed bottoms and, although it tolerated HYD to some extent, it did not proliferate in HES,
559 and (2) that *S. nkossa* sp. nov. appeared in the study area in connection with the presence of
560 HES, with its bloom (and thus its close relationship with HYD) being certainly unique among the
561 currently known species of Pilargidae.

562   Similar to *S. nkossa* sp. nov., all other polychaete species targeted in this paper were
563 present in HES and virtually absent (or showed very low densities) in non-impacted sediments.
564 The distribution patterns of the whole macrofaunal assemblage were suggested to be equivalent
565 to those traditionally associated with eutrophication phenomena in areas impacted by waste
566 disposals (Denoyelle et al., 2010). However, only *S. nkossa* sp. nov. and *L. sebastiena* responded
567 positively to an increase in OM, and only *Capitella* sp. showed increasing densities in correlation
568 with increasing S&C. In turn, all studied species responded positively to Ba (except *P. trionyx*
569 and, obviously, *S. parva*), while *S. nkossa* sp. nov., *Raricirrus* sp., *L. sebastiena*, and
570 Ampharetidae sp. also responded specifically to HYD.

571   Among the described species of *Raricirrus*, *R. maculatus* Hartman, 1961 was found as
572 living in highly organically enriched sediments off California, while *R. beryli* Petersen &
573 George, 1991 was locally abundant in sediments from northern North Sea oil fields (Hartman,
574 1961; Petersen & George, 1991). *Lindaspio sebastiena* is, at present, known only from the
575 N'Kossa field. Curiously enough, despite being relatively highly abundant in 2000 and 2002, it
576 almost disappeared in 2003, in parallel with the enormous increase in abundance of *S. nkossa* sp.
577 nov. exactly in the same bottoms. Therefore, as suggested by Dalmazzone et al. (2004), we
578 cannot discard a cause relationship between these two trends, with the competence with the
579 pilargiid (which was effectively able to reproduce in the area) explaining the rapid decrease in
580 abundance of the spionid (which reproduction in the area has not been observed).

581   The relationship with HES in the N'Kossa field was not restricted to polychaetes, as the
582 large vesicomyid bivalve *I. bigoti* was originally described there (Cosel & Salas, 2001) and later
583 found in cold seeps and methane hydrate areas off Gabon and in the Congo basin (Rodrigues et
584 al., 2012). This species was misidentified as either *Anodontia* cf. *edentula* or *Loripes* cf.
585 *contrarius* by Denoyelle et al. (2010). It was very abundant (> 500 ind/m^2) in the same HES
586 sediments inhabited by *S. nkossa* sp. nov. and the other HES associated polychaetes studied here,
587 and was completely absent from bottoms devoid of HYD. The depth in the N'Kossa region
588 (around 150 m depth) is unusually shallow for vesicomyids and its presence was initially
589 explained as a result of the high OM concentration caused by the Congo River discharges (Cosel,
590 Salas & Høisæter, 2001). The low salinities associated with the Congo River plume were
591 detectable on the water surface even at 200 km offshore (Vangriesheim et al., 2009), which
592 included the waters surrounding the N'Kossa platforms (i.e., about 60 km offshore). This was

01

593 also perceptible by the recurrent presence of small "floating islands" formed by living fragments
594 of riverine vegetation, sometimes with animals on them (D. Martin, 2003, pers. obs.). However,
595 the riverine influence was not specifically concentrated in the immediate vicinity of the
596 platforms. Moreover, according to our data, the unusually high OM concentrations underneath
597 the platforms were only related to drilling mud disposals and, thus, to the presence of HES.
598 Taking into account that Vesicomyidae include well-known inhabitants of chemosynthetic
599 environments like hydrocarbon seeps (Audzijonyte et al., 2012), we strongly suggest that the
600 occurrence of *I. bigoti* below the N'Kossa platforms, rather than being caused to the riverine
601 influence, was instead following the presence of HES, as reported for other vesicomyids in the
602 region (Cosel & Olu, 2009).
603   Deep-sea hydrocarbon seeps occur all around the world oceans (Sibuet & Olu, 1998;
604 Levin, 2005) and are particularly abundant in the West African oceanic region (e.g., Olu et al.,
605 2009; Warén & Bouchet, 2009; Jatiault et al., 2018). Therefore, we suggest that some of the
606 species here studied and, particularly, the polychaetes *S. nkossa* sp. nov., *L. sebastiena* and
607 *Raricirrus* sp., and the bivalve *I. bigoti*, may be native inhabitants of natural HES that colonized
608 alternatively the unusual shallow depths around the N'Kossa platforms thanks to the HYD
609 artificial source provided by drilling muds. Consequently, better than an opportunistic response
610 associated with an anthropogenic disturbance, its presence in the artificial HES around these
611 platforms could be an expression of its normal mode of life, with the human driven offshore
612 HYD routine exploration and extraction activities acting as stepping stones facilitating dispersal
613 and colonization of these somewhat atypical shallow bottoms to species natively associated with
614 deeper environments having natural HES.
615
616 **Morphometry**
617 In addition to the rise of modern molecular techniques, morphometric analyses have also shown
618 to be a valid and trustful method to assess morphological discrimination between cryptic
619 polychaete species (Koh & Bhaud, 2001; Koh & Bhaud, 2003; Ford & Hutchings, 2005; Glasby
620 & Glasby, 2006; Lattig, San Martín & Martin, 2007; Martin et al., 2017). Morphometry is
621 particularly useful when some of the relevant characters routinely used to define the species
622 within a genus are quantitative and may be, to some extent, size-related. In traditional
623 approaches, ranges are often provided, but this usually depends on the author, so that they are not
624 available for all affected species and relevant characters, as can be easily perceived for the
625 known species of *Sigambra* (Supplementary table 6).
626   Moreover, morphometric observations may be also used to determine whether a single
627 measurement from a single individual may or may not be taxonomically relevant by assessing
628 the variability at the population level. Based on a series of specimens representative of the whole
629 size range of the population of *S. nkossa* sp. nov., we demonstrate that most quantitative
630 characters commonly used to define species in the genus *Sigambra* are strongly size-dependent
631 and show a highly significant positive correlation with size. This correlation may explain more
632 than 70% of their variability, or even more than 90% in the case of dry weight, width of
633 chaetiger 15 (with parapodia), length of median antenna, and length of the first dorsal and ventral
634 cirri. Therefore, these characters should be avoided when diagnosing a species, unless their
635 variability at the population level can be reported and, if possible, statistically compared to those
636 of the closely related species.
637   Conversely, a robust taxonomic relevancy can be attributed to size-independent
638 characters. These include the length ratios for the main anterior appendages (i.e., the dorsal

639 tentacular cirri being much longer than the ventral ones, and the dorsal parapodial cirri being
640 much longer than the ventral ones), as well as the only three discrete or binary features referring
641 to specific morphologic characters (i.e., in the case of *S. nkossa* sp. nov., the starting of the
642 notopodial hooks at chaetiger 5–6, the starting of the notopodial spines at chaetiger 9–12, and the
643 absence of the ventral cirri at chaetiger 2), which are consistently constant all along the size
644 range of the studied population. Thus, these characters can be considered unambiguous at the
645 species level and species-specific at the individual level.
646   In the particular case of the presence of hooks, the starting chaetiger has been recently
647 reported as being either invariable (or vary for a very few chaetigers, more or less at random) or
648 as starting more posteriorly in larger specimens (Salazar-Vallejo et al., 2019). Therefore, care
649 should also be taken when attributing size-independence to a given character, as this may also
650 vary significantly according to the species and along its ontogeny.
651

Conclusions

653   Our results allowed us to suggest that native inhabitants of natural deep-sea HES may
654 alternatively colonize unusual shallow depths around oil and gas platforms thanks to the HYD
655 artificial sources provided by drilling mud deposits. Off the Republic of Congo, in the N'Kossa
656 oil and gas field, the polychaetes *L. sebastiena*, *Raricirrus* sp. and *S. nkossa* sp. nov., together
657 with the bivalve *I. bigoti*, may be examples of this circumstance. Therefore, their association
658 with artificial HES would be more an expression of their normal mode of life, rather than just an
659 anthropogenically triggered opportunistic response.
660   Accordingly, the offshore oil and gas routine exploration and extraction activities could act
661 as stepping stones for the dispersal of benthic inhabitants native from different natural deep-sea
662 environments with HES.
663   The current knowledge on the species of Pilargidae, and particularly on those belonging to
664 *Sigambra*, seems to be incorrect in what concerns to the presence of the "capillary chaetae"
665 accompanying the notopodial hooks and spines. According to our observations, at least in *S.
666 nkossa* sp. nov. these structures are, in fact, protruding tips of notoacicula. However, examining
667 other species having these "capillary chaetae" is required prior to decide whether the generic
668 diagnosis should be amended by replacing the notopodial character "sometimes with accessory
669 capillaries" by "sometimes with protruding tips of notoaciculae".
670   Moreover, generic diagnostic characters such as "presence/absence of stout emergent
671 notochaetae" or "stout notochaetae either as hooks or as spines" seem to be in conflict with the
672 definition of some of the current known genera of Pilargidae, as well as with most of the
673 identification keys available for the family (e.g., Pettibone, 1966; Blake, 1997; Gil, 2011). If
674 these identification keys are followed strictly, species having both types of stout notochaetae
675 (straight and hooked) on the same notopodial bundle (such as *S. robusta*, *S. bassi*, *S. healyae* and
676 *S. nkossa* sp. nov.) would be keyed as probably belonging to a new genus. Therefore, while
677 waiting for further studies (including molecular analyses) helping to clarify the taxonomic
678 weight of the presence and type of these notopodial spines, we consider the character "presence
679 of stout emergent notochaetae" as prevailing over "stout notochaetae either as hooks or as
680 spines". Also, we agree with Glasby & Salazar-Vallejo (2022) in that the diagnosis of *Sigambra*
681 must include the character "*notopodium with one strongly recurved dorsal hook or with one
682 strongly recurved dorsal hook and one slightly bent spine along many segments*". As so,
683 forthcoming identification keys of the family should state "*stout emergent notochaetae straight,
684 not hooked*" vs. "*stout emergent notochaetae also **including hooked chaetae***", instead of "*stout

685 *emergent notochaetae straight, not hooked*" vs. "*stout emergent notochaetae* **hooked**".
686   Finally, our morphometric analyses allowed us to demonstrate that most quantitative
687 characters commonly used to define the species of *Sigambra* are strongly size-dependent,
688 proving that they must be avoided for species definition, except when it is possible to define
689 statistically their interpopulation variability to be compared with those of the most closely related
690 species. Conversely, size-independent characters must be considered as taxonomically robust and
691 unambiguous at the species level, as well as species-specific at the individual level.
692

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707

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919

Figure 1

Geographical location of the study site and sampling stations.

(A) Map of Africa showing the location of the Republic of Congo. (B) Map of the Republic of Congo showing the location of the N'Kossa field. (C) Location of the drilling points at NKF 1 and NKF2 and sampling stations in the N'Kossa field.
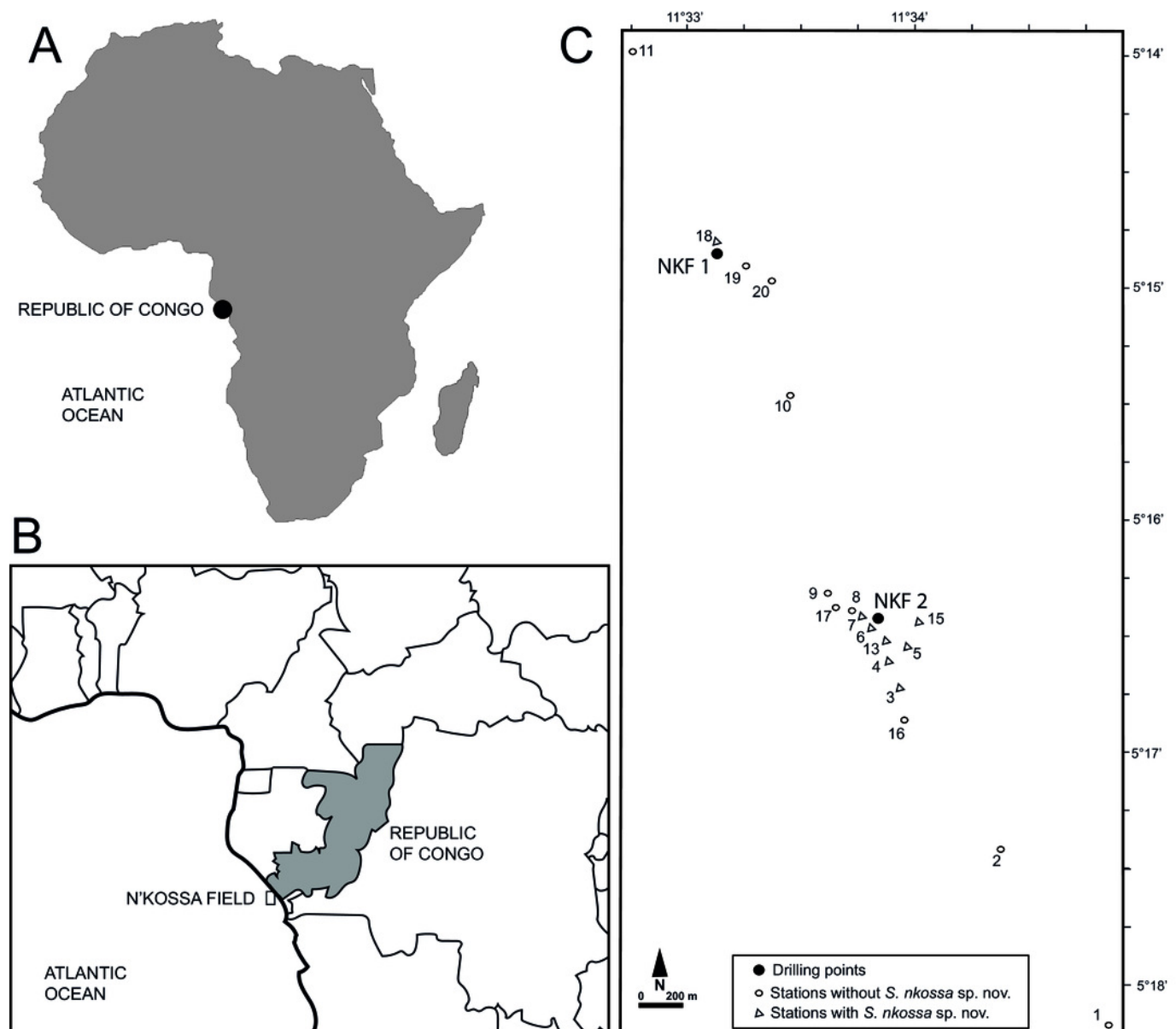
Figure 2

Results of the PCA based on environmental parameters.

Samples grouped according to groups I, II and III; species densities (ind/m^2) plotted as grey circles. DDP: distance from drilling point; HYD: total hydrocarbons; Ba: Barium; CS: coarse sand; S&C: silt and clay; OM: organic matter; PW: pore water; N: Nitrogen; P: Phosphorous; *Snk*: *Sigambra nkossa* sp. nov.; *Sp*: *S. parva*; *Csp*: *Capitella* sp.; *Pt*: *Paramphinome tryonix*; *Rsp*: *Raricirrus* sp.; *Ob*: *Oxydromus berrisfordi*; *Ls*: *Lindaspio sebastiena*; *Amp*: Ampharetidae sp.

Figure 3

Environmental descriptors in the N'Kossa field, plotted against the groups I, II and III obtained in the PCA.

DDP: Distance from drilling points (m); HYD: Total hydrocarbons (as kg/kg of sediment). Ba: Barium (mg/kg of sediment). CS: Coarse sand (%). S&C: Silt and clay (%). PW: Pore water (%). OM: Organic matter (%). N: Nitrogen (%). P: Phosphorous (%).
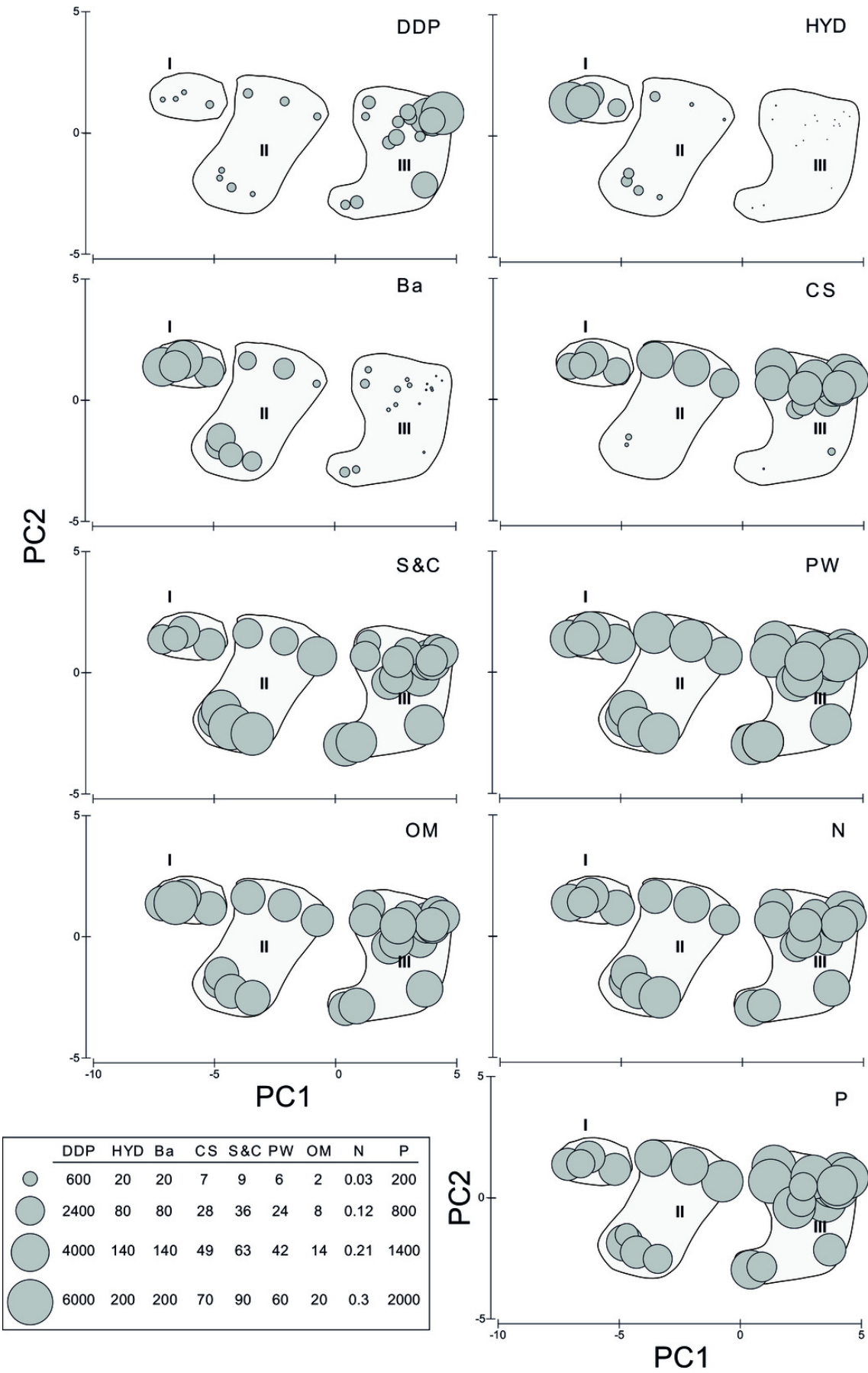
Figure 4

Sigambra nkossa sp. nov. light microscopy images.

(A) Whole body, dorsal view. (B) Anterior end, dorsal view. (C) Anterior end, ventral view. (D) Detail of chaetigers 2 (lacking ventral cirrus) and 3, ventral view. (E) Everted proboscis, dorsal view. (F) Everted proboscis, ventral view. (G) Everted proboscis, lateral view. (H) Parapodium 3. (I) Midbody parapodium. (J) Detail of hook (right) and spine (left) from I. (K) Posterior-most parapodium. (L) Detail of hook (right) and spine (left) from K.
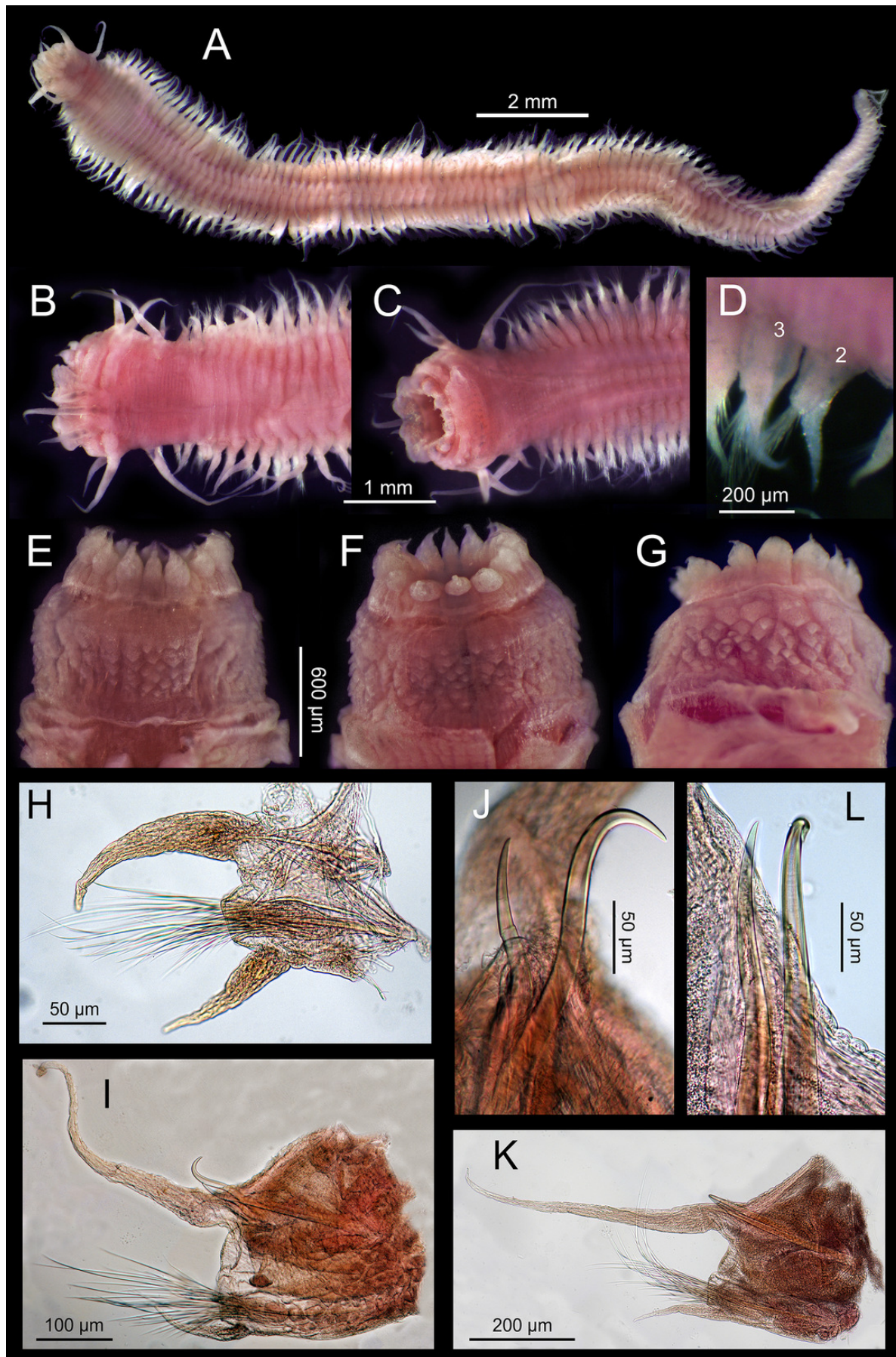
Figure 5

Sigambra nkossa sp. nov. SEM images.

(A) Anterior end, dorsal view. (B) Detail of the anterior end, dorsal view. (C) Anterior end with everted proboscis, frontal view. (D) Anterior end with everted proboscis, lateral view. (E, F) Neuropodial chaetae from mid-body. (G) First segments with notopodial hook and spine (white arrows pointing on the first two spines). (H) Notopodial hook and spine from mid-body (white arrow pointing on protruding tip of notoacicula).
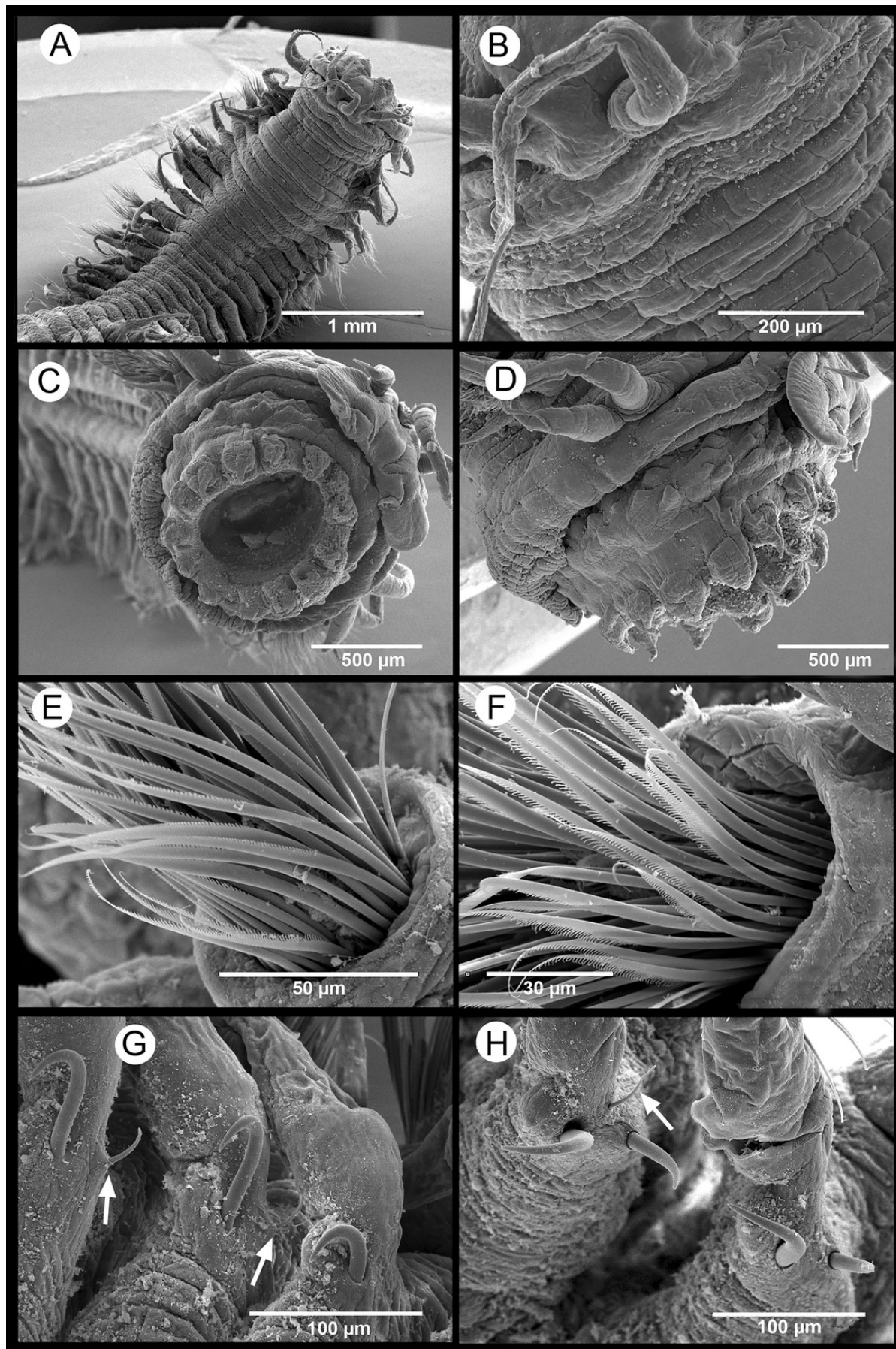
Figure 6

Sigambra parva. SEM images.

(A) Anterior end, lateral view. (B) Anterior end, ventral view. (C) Detail of anterior end, frontal view. (D) Detail of anterior end, dorsal view. (E) Anterior end with everted proboscis, lateral view. (F) Posterior end.
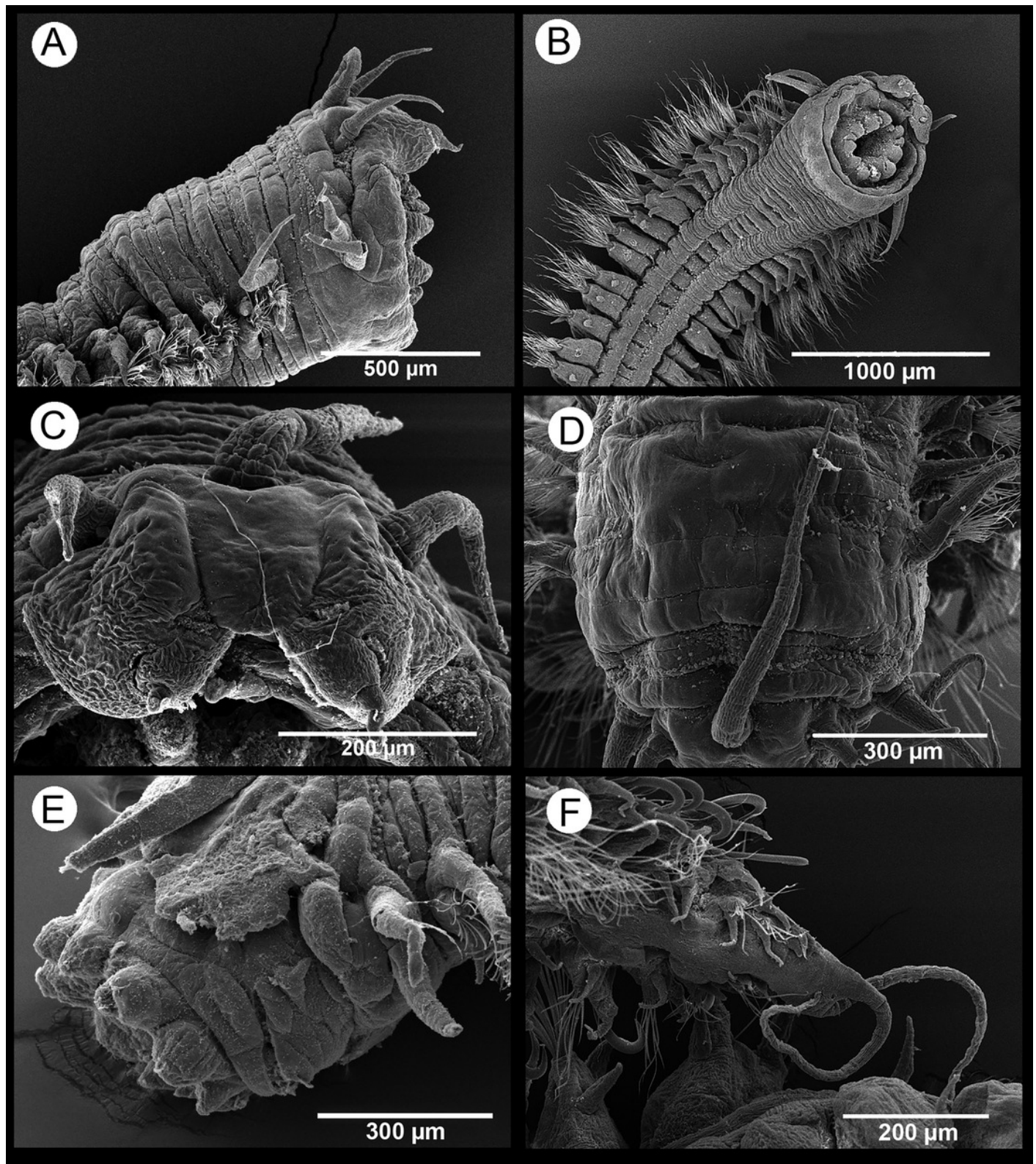
Figure 7

Sigambra parva. SEM images.

(A) Mid-body parapodia, dorsal view. (B) Detail of hooks from mid-body parapodia. (C, D)
Neuropodial chaetae from mid-body.
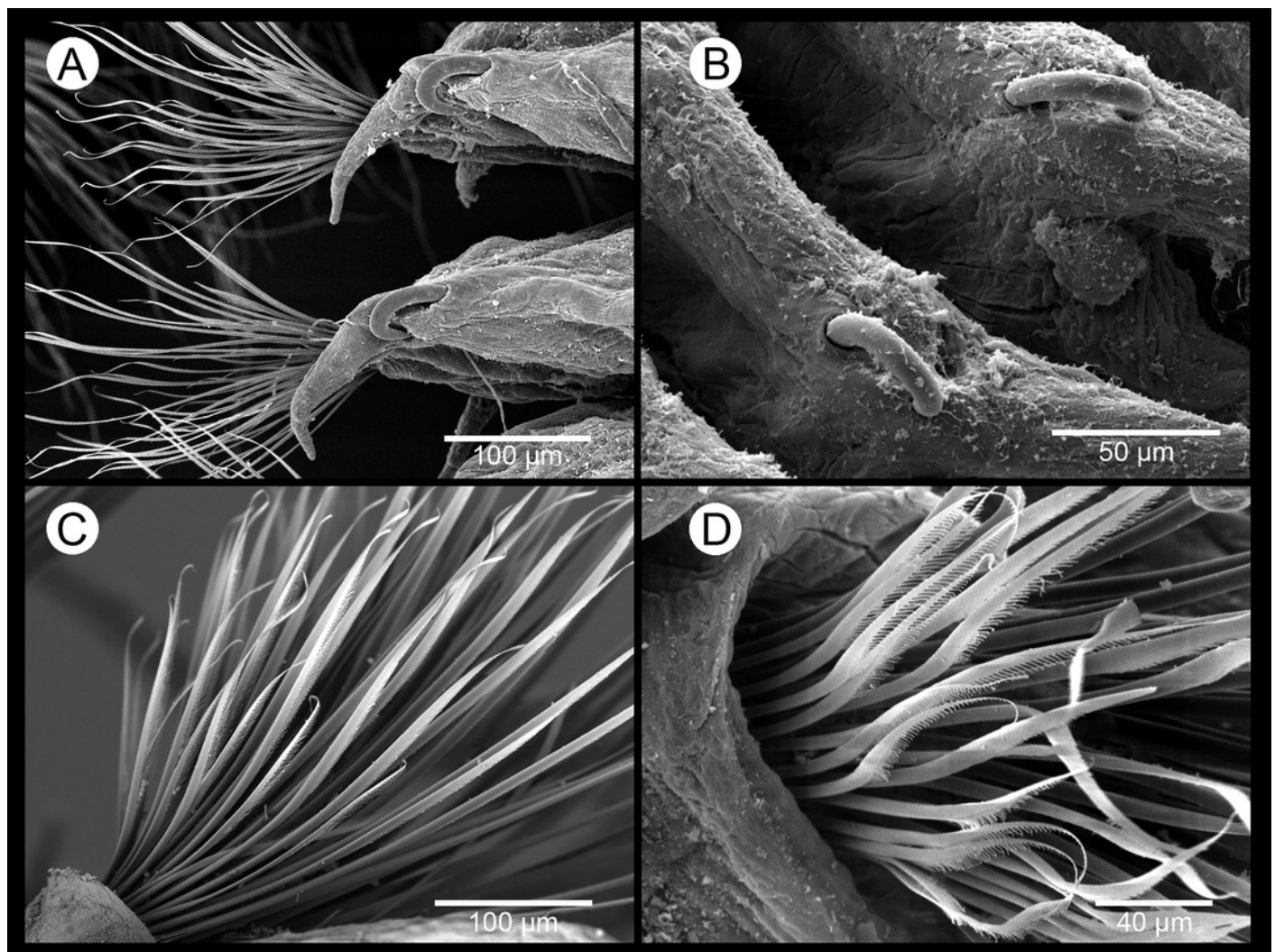
Figure 8

Sigambra nkossa sp. nov. *s*elected morphological features and their respective relationships with size, expressed as number of chaetigers.

(A) Total length (µm). (B) Dry weight (mg). (C) Width of chaetiger 15 (with parapodia, µm). (D) Length of median antennae (µm). (E) Length of first dorsal cirri (µm). (F) Starting segment for the dorsal capillary chaetae. (G) Length ratio for the antennae (middle / lateral). (H) Length ratio for the tentacular cirri (dorsal / ventral). (I) Starting segment for the notopodial hook. A–F: size-dependent characters; H–I: size-independent characters.