1   **Exceptional Late Devonian arthropods document the origin of decapod**

2   **crustaceans**

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30   **Abstract**

31   With over 15,000 extant species, Decapoda—or ten-legged crustaceans such as crabs, shrimp,

32   lobsters, and relatives— are among the most speciose and economically important group of

33   crustaceans. Despite of their diversity, anatomical disparity, and remarkable fossil record

34   extending back to the Late Paleozoic, the origins of Decapoda and their phylogenetic

35   relationships with eumalacostracans remains elusive and inconclusive. Molecular dating

36   suggests that decapods originated in the Late Ordovician (~450 Mya), but no reliable fossil

37   crown groups are found until the Late Devonian. Moreover, there is no consensus on which

38   lineages belong to stem groups, obscuring our understanding of the roots of the ten-legged

39   decapod body plans as a whole, and how they relate to other non-decapod crustaceans. We

40   present new, exceptional fossils from the Late Devonian of Czech Republic and Poland that

41   belong to †Angustidontida, an odd shrimp-looking crustacean with a combination of anatomical

42   features unlike those of any crown eumalacostracan known—extinct or extant. Our

43   phylogenetic analyses, including representatives of all major lineages of crown

44   eumalacostracans plus †Angustidontida, identify angustidontids as the only known stem-group

45   decapod, and give hints about the transformation series, polarity of change, and evolutionary

46   pathways leading to the modern decapod body plans seen today.

47

48   **Keywords**: Angustidontida, Konservat Lagerstätte, origins, Paleozoic, phylogeny, evolution

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51   **1. Introduction**

52   Among crustaceans, the representatives of the order Decapoda are easily recognizable due to

53   their distinctive body forms. They have a carapace that is fused to the underlying thoracic

54   segments, an abdomen (pleon) constituted by six segments or pleonites, and most lineages

55   other than crabs have a telson and uropods that often form a tailfan. Moreover, crown-group

56   decapods have eight pairs of thoracic appendages or thoracopods, from which the first three

57   pairs are modified into maxillipeds for feeding, while the remaining five pairs are developed

58   into true thoracic legs (pereopods), hence the name of the order (Decapoda = ten-footed

59   crustaceans) (e.g. [1]). Despite of such a distinctive body arrangement, the deep relationships

60   among decapods have long been conflicting and unresolved. Recent phylogenomic analyses

61   with assembled sequence data from 94 species (including 11 of the 12 major lineages)

62   recovered a robust extant decapod tree of life [2]. Unfortunately, the origin of Decapoda

63   remains obscure as i) there is no consensus on the sister group to crown-group Decapoda, and

64   ii) no stem-group decapod forms have been confirmed from reliable Paleozoic (Late Devonian-

65   Carboniferous) fossils [3], with the latter being too derived or insufficiently preserved to be

66   informative about the origins of the total-group Decapoda [1,3,4]. Furthermore, molecular

67   divergence times suggest that crown decapods diverged in the Late Ordovician, leaving a gap of

68   nearly 70 million years between their estimated split and their earliest confirmed fossils, and

69   implying a significant cryptic Paleozoic history [2].

70   Among the few known middle Paleozoic eumalacostracan crustaceans, the iconic

71   shrimp-looking †Angustidontida from Late Devonian and Early Carboniferous of North America

72   and Europe have been envisioned as closely related to decapods [1,2,4,5]. Unlike crown

73   decapods, †Angustidontida bears one or two pairs of elongated comb-like maxillipeds (figure

74   1*a*; one pair in †*Angustidontus* Cooper, 1936, two pairs in †*Schramidontus* Gueriau,

75   Charbonnier & Clément, 2014 [4]). Isolated remains of such comb-like maxilliped were

76   described as either actinopterygian fish jaws, eurypterid raptorial appendages, or crustacean

77   appendages [1, 5], until more complete and articulated material confirmed their crustacean

78   affinities. †Angustidontida is morphologically similar to Decapoda [4], but differs from it in the

79   number of maxillipeds and the size and connection of the pleonal segments (uniform in

80   angustidontids; variable in most decapods, with an expanded second pleonal pleuron and an

81   enlarged third pleonal somite). In particular, angustidontids exhibit remarkable similarity with

82   †*Palaeopalaemon newberryi* Whitfield, 1880, another fossil crustacean from the Late Devonian

83   recognized undoubtedly as a crown decapod [6,7], yet †*P. newberryi* is distinct from

84   angustidontids [7]. Gueriau et al. [4] postulated that angustidontids were early decapods that

85   filled the gap between krill or Euphausiacea (no maxillipeds) and Decapoda (three pairs of

86   maxillipeds), and that they were closer to Decapoda than to the extant *Amphionides reynaudii*

87   Milne Edwards, 1832 (a rare crustacean bearing a single pair of maxillipeds). This apomorphic

88   trait placed *Amphionides* as the sister taxon to Decapoda, and it was so unique that merited its

89   own order Amphionidacea [8]. The single pair of maxillipeds of *A. reynaudii* told a beautiful

90   story about the possible origins of Decapoda, and filled the gap between Euphausiacea and

91   Decapoda, but it took an unexpected turn when molecular phylogenetics identified

92   Amphionidacea as the larval form of a caridean decapod shrimp [9]. As a consequence,

93   †Angustidontida stood as the only remaining sister group candidate to Decapoda, or at least

94   the only extinct lineage recognizable between euphausiaceans and decapods [1]. However, the

95   angustidontid material described so far does not exhibit any character autapomorphic of

96   Decapoda [4], for which new material and a revision in a more explicit phylogenetic framework

97   is still lacking [2].

98   Here, we describe new anatomical features of †Angustidontida based on new,

99   exceptional fossils from the Late Devonian of Czech Republic and Poland, showing in

100   exceptional detail pleonal and caudal features that allow us to explore their phylogenetic

101   position within Malacostraca, and its systematic implications for understanding the origins of

102   crown decapod crustaceans.

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105   **2. Materials and methods**

106   **(a) Material**

107   The fossil specimens investigated herein come from the Hády quarry (lower Fammenian, Czech

108   Republic; see next section for geological settings) and the Kowala quarry (lower Fammenian,

109   Holy Cross Mountains, Poland; see [10] for geological settings), and are housed at the Czech

110   Geological Survey, Prague, and the Institute of Earth Sciences, University of Silesia, Sosnowiec,

111   respectively. Fossils from the Hády quarry presented herein (figure 1*b*–*e* and electronic

112   supplementary material, figure S1) have never been published or mentioned before; the

113   specimen from the Kowala quarry (figure 1*f*–*h*) have been mentioned, but not figured in [10].

114   They were studied under a binocular microscope, both dry and covered in water with a low

115   angle light to better reveal relief, and photographed with a SLR camera coupled with macro lens

116   equipped with polarizing filters. Interpretative line drawings were produced on the

117 photographs while observing the specimens with different light angles under the binocular

118 microscope. Drawings and figures were made using Adobe Illustrator.

119

120 **(b) Geological settings and stratigraphy of the Hády quarry, Czech Republic**

121 The new angustidontid material from Czech Republic comes from section H33 of the Hády

122 quarry (part Městký lom), northeastern outskirts of Brno, Czech Republic. The Hády quarry

123 exposes a southernmost outcrop of the Moravian Karst Paleozoic, belonging to the Variscan

124 Brunovistulian Unit. Devonian and Carboniferous sedimentary rocks of the Brunovistulian Unit

125 were deposited at a southern margin of Laurussia [11,12,13,14].

126 In the Hády quarry, Late Frasnian pure massive limestones of the Macocha Formation

127 are overlain by the latest Frasnian to late Famennian nodular to well bedded limestones of the

128 Líšeň Formation (electronic supplementary material, figure S1). A drowning of the Frasnian

129 outer ramp and transition to an Famennian hemipelagic slope environment with turbiditic

130 influence is recorded in the studied section [15,16,17]). Angustidontid-bearing bed is one of the

131 calcareous shale intercalations, which alternate with platy calcilutites and occasional banks of

132 medium-grained calcirudites (electronic supplementary material, figure S1). The calcareous

133 shales represent "background" hemipelagic facies deposited in relatively low-energy slope

134 environment, well below storm-wave base. The platy limestones were interpreted as

135 calciturbidites (e.g. [16,18,19]). Limestone sample just below the angustidontid-bearing shale

136 yielded 110 conodonts, which are typical for the lower Famennian *Palmatolepis minuta minuta*

137 to *Palmatolepis crepida* conodont zones interval (*sensu* [20]), involving *Pa. triangularis*, *Pa.*

138 *minuta minuta, Pa. delicatula delicatula* and *Icriodus alternatus*.

139

140 **(c) Phylogenetic analysis.**

141 We investigated the phylogenetic position of †Angustidontida using a modified morphological

142 dataset for malacostracan crustaceans after [8] (characters 1–93). Following [21], we added

143 four additional characters related to the morphology of the basipods and uropods (characters

144 94–97). The operational taxonomic unit (OTU) 'Amphionidacea', included in the analyses of [8],

145 was culled from our analysis as it has been demonstrated that amphionidaceans are the larvae

146   of a decapod shrimp rather than a distinct malacostracan order [1, 9]. The final data matrix,

147   containing 19 OTUs (3 in outgroup, 16 in ingroup) and 97 adult morphological characters, was

148   built in Mesquite 3.51 [22]. Undetermined or not preserved characters were scored as '?', and

149   inapplicable characters as '–'. Multiple character states present in a given OTU were scored as

150   polymorphisms.

151   We analyzed the dataset using Bayesian inference (BI) as implemented in MrBayes

152   v.3.2.5 [23]. The dataset was analyzed under the traditional Mk model [24] with an

153   ascertainment bias correction to account for scoring only variable morphological characters,

154   and gamma distributed rate variation. Each analysis was performed with two independent runs

155   of 3×10^7 generations each. We used the default settings of four chains per independent run.

156   The relative burn-in fraction was set to 25%, and the chains were sampled every 200

157   generations. We used Tracer v. 1.7.1 [25] to determine whether the runs reached stationary

158   phase and to ensure that the effective sample size for each parameter was greater than 200.

159   Results of the Bayesian runs were summarized as a majority-rule consensus tree of the post-

160   burnin sample (figure 2).

161   We also conducted maximum parsimony (MP) phylogenetic analyses in TNT v.1.5 [26].

162   The data was analyzed under implicit enumeration for equally weighted maximum parsimony

163   (EWMP) (figure S2*a*), and different implied weights (K=3, 6, 12) as additional tests of placement

164   of †Angustidontida (electronic supplementary material, figure S2*b–d*). Bootstrap and jackknife

165   values were calculated after 10,000 replications each using default settings. Bremer support

166   values for the EWMP implicit enumeration were calculated under tree bisection reconnection,

167   and retained trees suboptimal by 30 steps. All characters were unordered.

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169

170   **3. Results and discussion**

171   New material assigned to †*Angustidontus* aff. *moravicus* Chlupáč, 1978 [11] collected from

172   Czech Republic (figure 1*b–e* and electronic supplementary material, figure S1), and

173   †*Angustidontus* aff. *seriatus* Cooper, 1936 from Poland (figure 1*f–h*) reveals fine details of the

174   anatomy of their tailfan previously unknown, which in turn allow for a detailed taxonomic and

175 phylogenetic comparison with other malacostracans. The angustidontid tailfan consists of a

176 triangular telson flanked by two pairs of leaf-shaped uropods (figure 1*b–d,g,h*; see also [4,5]).

177 The uropodal exopod bears a carina, and prolongs latero-distally in a non-articulated, spiky

178 outgrowth (figure 1*d,h* arrowheads). The lateral, distal, and median margins of the endopod

179 and exopod (up to the spiky outgrowth for the latter) are surrounded by plumose setae of

180 different length, longest distally and shortest proximo-medially and latero-distally (figure 1*g,h*).

181 The basipod is sub-conical and possesses a latero-distal, tipped prolongation (figure 1*e,h*

182 arrows; see also [5]). According to Kutschera et al. [21]'s work on the phylogenetic signal

183 conveyed by malacostracan basipods and uropods morphology, such combination of characters

184 is unique to Decapoda. It is worth noting that, as described by Rolfe and Dzik [5], the uropodal

185 exopod is not divided into two portions by a medio-lateral suture or diaeresis, a feature also

186 absent in Euphausiacea and Dendrobranchiata (though some fossils assigned to the group do

187 possess one [27,28,29]) but found in Caridea [21]. The presence or absence of a longitudinal

188 median keel on the basipod, specific to Decapoda [21], is impossible to determine on our

189 flattened fossil material. Aside this, the anatomy of the angustidontid tailfan is virtually

190 identical to that of decapods (figure 1*i*), adding support to an alliance between these groups.

191 Bayesian inference and maximum parsimony phylogenetic analyses recover

192 †Angustidontida as the sister group to the crown-group Decapoda (figure 2, and electronic

193 supplementary material, figure S2). Besides filling the gap between Euphausiacea and

194 Decapoda, an affiliation of angustidontids as the closest known sister taxon to crown group

195 Decapoda, i.e. as part of total-group Decapoda, has important implications for reconciling

196 molecular divergence dates for decapods (Late Ordovician [2]) and their earliest known fossil

197 record (Late Devonian [1,3,4,6,7]). Our findings identify angustidontids as the only stem-group

198 decapod known to date, and suggest that their apparently cryptic Paleozoic history [2] might be

199 an artifact of the overlooked disparate stem-decapod body plans, compared to crown-group

200 forms. Our results indicate that the origin of decapod-like eucaridans lies within more than ten-

201 footed crustaceans, and gives hints about the transformation series, polarity of change, and

202 evolutionary pathways leading to the characteristic decapod body arrangement and

203 thoracopod configuration seen across the main crown groups as recognized today.
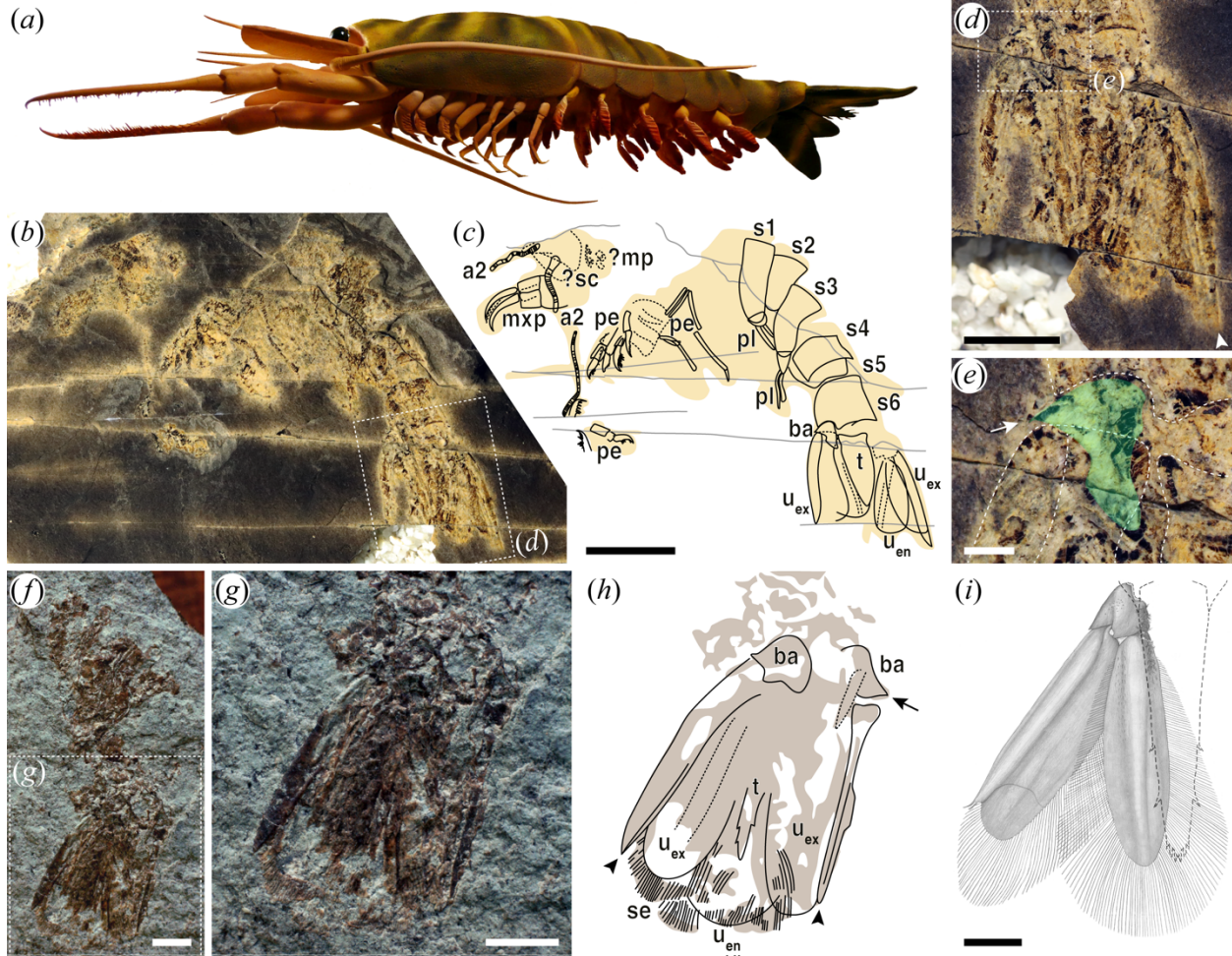
Figure 1. Angustidontid tailfan anatomy. (*a*) Reconstruction of †*Angustidontus* in ventro-lateral view; SHAPE-PLAST thermoplastic model by T.V. (*b*–*e*) †*Angustidontus* aff. *moravicus*, H33/1A, complete specimen (likely an exuvia) in dorso-lateral view from the Hády quarry (lower Fammenian, Czech Republic). (*b*) Photo of specimen covered in water. (*c*) Interpretative line drawing. (*d*) Close-up of the tailfan, from the box area in *b*. (*e*) Close-up of the basipod (highlighted in green), from the box area in *d*. (*f*–*h*) †*Angustidontus* aff. *seriatus*, GIUS 4-3622/kor112, articulated pleon in dorso-lateral view from the Kowala quarry (lower Fammenian, Holy Cross Mountains, Poland). (*f*) Photo dry. (*g*) Close-up of the tailfain, from the box area in *f*. (*h*) Interpretative line drawing. (*i*) Pencil drawing of the uropods of the extant shrimp *Crangon crangon* Linnaeus, 1758. Illustration by Dr. Verena Kutschera. Abbreviations: a2, antenna; ba, basipod; ?mp, ?mouth parts; mxp, maxillipeds; pe, pereopods; pl, pleopods; s1-s6; pleonal somites 1 to 6; se, setae; ?sc, ?scaphocerites; t, telson; u_{en}, uropodal endopod; u_{ex}, uropodal exopod. Arrowheads and arrows point out the latero-distal spiky outgrowth of u_{ex} carina, and the latero-distal tipped prolongation of the basipod, respectively. Scale bars, 1 cm in *b* and *c*, 5 mm in *d*, 2 mm in *f*–*h*, and 1 mm in *e* and *i*.
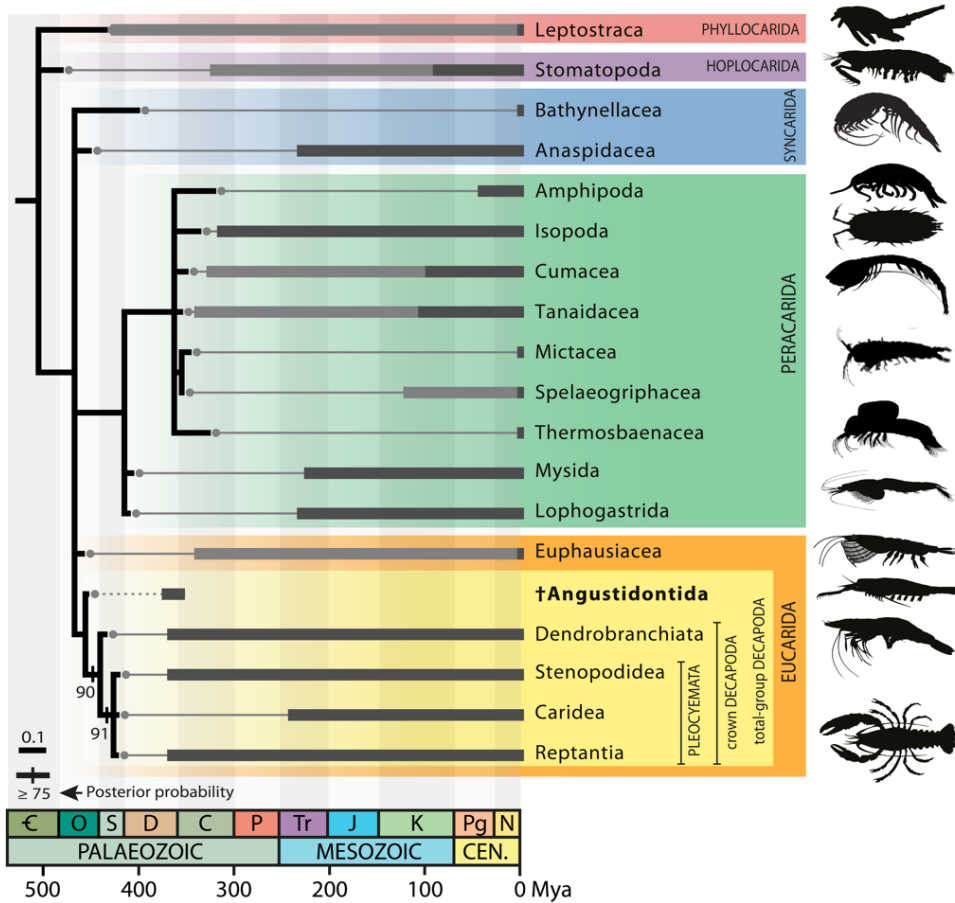
Figure 2. Phylogenetic position of angustidontids within malacostracan crustaceans. Bayesian majority-rule consensus topology of the post-burnin sample of trees, plotted on stratigraphy. The obtained tree (black line) was scaled to accommodate a Late Ordovician divergence date for Decapoda [2] and the stratigraphic ranges of terminal taxa (light and dark grey thick lines for stem- and crown-groups, respectively; see electronic supplementary material, table S1, for ages justification) here constrained by the first occurrence of stem Leptostraca. Posterior probability support values indicated above branches. Branches with posterior probability support < 75% are collapsed.

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Additional information