

Another Lesson From Beautiful Monsters: the Case of 'sex Reversals' in the Ammonoidea and Their Significance

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Research Article

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Abstract

Background: Expression of a sexual dimorphism is recognised in various fossil groups of molluscs such as the Ammonoidea, an extinct group of shelled cephalopods. During the Mesozoic, the best documented sexual dimorphic examples are seen in the Jurassic superfamily Perisphinctoidea. It is most usually expressed by distinct adult size and apertural modifications between the antidimorphs. Putative males (otherwise referred to as microconch) are small in size and develop lappets at the end of the shell while the females (macroconch) are larger and bear a simple peristome. Dubious cases are, however, known in that superfamily. They most often relate to taxonomic biases or lack of diagnostic characters, and some others expose ontogenetic anomalies illustrated by ‘sex reversals’ in the shell morphology and ornamentation.

Results: The discovery of two specimens of the Callovian Aspidoceratidae *Peltoceras athleta* (Phillips), having both **female** and **male** features, questions the significance and causes of ‘sex reversals’ in the Ammonoidea. The two specimens have started with the macroconch ontogeny of *Peltoceras athleta*, and show an apparent change toward maleness in the adult, as illustrated by their rounded whorl section, ribs retroversion, fading of the tubercles and lappets typical of the microconchs. Few other cases of female-to-male ‘sex reversal’, as well as male-to-female ones, are known in the fossil record, all belonging to the Jurassic Perisphinctoidea (families Perisphinctidae or Aspidoceratidae). Since all Jurassic Perisphinctoidea are strictly gonochoric, these ‘sex reversals’ are pathological in nature and are herein referred to as a new forma-type pathology: namely “forma hermaphrodita”.

Conclusions: In the absence of any clear evidence of injury or parasitism, we hypothesize that such “forma hermaphrodita” individuals illustrate pathologic cases of intersexuality. Little is known about the ammonoid soft parts, and it is not possible to determine which internal sexual organs occur in specimen having both male and female external shell features. Abnormal feminisation and/or masculinisation also occur in modern cephalopods; the latter also grouping only gonochoric species. This phenomenon is similarly illustrated by a change in the adult body size and a mixing of both female and male structures. In that case, intersexuality is either advantageous in the population or caused sterility. The causes of intersexuality are not clearly established but environmental pollutants are evoked in modern cephalopods because they act as endocrine disrupters. ‘Sex reversals’ and/or non-functional reproductive abnormalities have also been caused by endocrine disrupters in various gonochoric gastropods species, but infestation, genetic abnormalities, temperature fluctuations or viruses are multiple causes which can stimulate or inhibit neural-endocrinal activity by direct gonadal influence, and ultimately lead to feminisation or masculinisation in fishes, isopods, crustaceans, and gastropods as well. Regardless of whether “forma hermaphrodita” is due to an exogenic or endogenic cause, the high frequency of intersex Perisphinctoidea in the Jurassic can be explained by the readily recognition of dimorphic pair, and the easy collection of large and sufficiently preserved fossil palaeopopulations in which intersex specimens have statistically more chance to be found.

Background

Dimorphism of sexual nature have been reported in various fossil groups of molluscs by analogy with recent species. De Blainville (1840) first suggested that sexual dimorphism occurs in the Ammonoidea – an extinct group of shelled cephalopods – by comparison with the living nautiloid species *Nautilus pompilius* Linnæus, 1758. Nowadays, the presence of a sexual dimorphism in the ammonoids is widely accepted and its palaeobiological criteria are based on: (i) a change in shell morphology and aperture; (ii) similar early developmental stages; (iii & iv) same stratigraphic range and overlapping geographic occurrence; (v) common ancestors; (vi) similar numerical ratio between antidimorphs through time and throughout the evolution of the clade (Klug et al. 2015).

During the Mesozoic, the Jurassic Perisphinctoidea provide the best-known examples of sexual dimorphism (e.g. Makowski 1962; Callomon 1963; Tintant 1963; Westermann 1964a, b; Elmi 1967; Schweigert 1997; Schweigert et al. 2003, 2007; Parent et al. 2008a, b, 2009; Zatoń 2010; Frau et al. 2015, 2016). In this superfamily, the sexual dimorphism is most often expressed by distinct adult size and apertural modifications. Supposed males (otherwise referred to as microconch, [m]) are usually small in size, and develop lappets at the end of the growth while the females (macroconch, [M]) are distinctly larger and bear a simple peristome.

However, many sexual dimorphism cases remain dubious due to taxonomic biases and lack of diagnostic features in the adult (Davis et al. 1996). An increase of doubtful cases is observed in the Perisphinctoidea between the Callovian and the Kimmeridgian stages, as the ones listed by Brochwicz-Lewiński & Różak (1976). These authors have illustrated apparent ‘sex reversals’ in the adult shell of various perisphinctoid species known to be dimorphic. The authors thus concluded that these specimens “represent a new type of dimorphism not encountered in other groups of ammonites and that [...] the hypothesis of the sexual dimorphism is not so universal as it was considered to be”.

The discovery of two specimens of the Callovian Aspidoceratidae *Peltoceras athleta* (Phillips, 1829), having both **male** and **female** features, questions the significance of these ‘sex reversals’ in the Ammonoidea.

Materials And Methods

Origin of the material

The two specimens of *P. Athleta*, labelled mbe.9305 and mbe.1401 were collected by one of us (P.-Y.B.) in the industrial area of Méron, in the vicinity of Montreuil-Bellay, Maine-et-Loire, France (Fig. 1A–B). There, Bonnot et al. (2005) documented two condensed, oolitic limestone beds of late Callovian age. These beds yield abundant and well-preserved dimorphic-paired ammonite populations (see Bonnot et al., 2005, 2008, 2014). The studied material originates from the upper limestone bed dated to the *Peltoceras athleta* Horizon, which characterizes the upper *P. athleta* Zone (Fig. 1C).

Method

Shell parameters and ornamental features of the two specimens have been compared to the ontogeny and intraspecific variability of the dimorphic species *Pathleta* documented by Bonnot (1993, 1995). Two macroconch (e.g. *Athleta* Phillips and *Baylei* Prieser) and two microconch (e.g. *Annulosum* Quenstedt and *Pseudotorosum* Prieser) morphotypes of *P. athleta* are recognized by the same author. Typical representatives of the *Athleta*, *Annulosum* and *Pseudotorosum* morphotypes are herein illustrated for comparison (Fig. 2). Bonnot (1995, p. 267-272) provided a detailed biometric database of shell parameters of the four morphotypes based on juvenile and adult specimens from references localities of France and Switzerland. The database is based on standard measurements of the shell, given in millimetres and as percentages of total diameter. The following abbreviations indicate: D = maximum diameter; Uw = umbilical width; Wh = whorl height; Ww = whorl breadth and K = number of ribs per half a whorl. The ratios of morphological features (Uw/D, Wh/D, Wb/D and Wb/Wh) and rib density (K/D) to diameter are investigated and compared the dimensions of our specimens (Table 1).

According to Bonnot (1995, p. 272-273), six ornamental stages characterize the *P. athleta* macroconchs (Dmax ~ 240 mm): (i) smooth initial whorls with a sub-circular whorl section; (ii) approximated, prorsiradiate, bifurcate and single ribs that cross the venter; (iii) ribs become radial and spaced; (iv) appearance of two lateral tubercles; Whorl section become markedly depressed and trapezoidal; (v) disappearance of intercalate ribs on the venter and (vi) broad single ribs that cross the venter. The microconchs (Dmax ~ 110 mm) possess the three first ontogenetic stages of the macroconchs but develop a more circular whorl section. In the microconchs, the fourth stage differs by rectiradiate ribs forming a slight chevron on the venter while the fifth stage develops spaced, strong, rursiradiate, bifurcate ribs approaching a lappeted aperture. The sixth stage is lacking. These stages are herein illustrated in both macro-, and microconchs morphotypes (see Fig. 2).

Results

shell shape

The two studied specimens are illustrated on figures 3A and 3B, respectively. Shell shape of specimens mbe.9305 and mbe.1401 is both characterized by a moderate size (62.3 \square D \square 66.6 mm), together with an extremely discoidal (Ww/D ~ 0.33), weakly depressed (Ww/Wh ~ 1.11), very evolute (U/Wh ~ 1.7) subophiocone coiling (Uw/D ~ 0.49). Specimen mbe.9305 is the most complete individual with almost four preserved whorls. Regarding their adult diameter, the two specimens fall in the peak of the normal distribution of the macroconch diameters (Fig. 4A). They are much larger than the *P. athletaannulosum* microconchs but falls in the normal distribution of the *P. athletapseudotorosum* diameters (Fig. 4B).

Shell parameters of the specimens are compared to the bivariate analysis of the four morphotypes of *Pathleta* provided by Bonnot (2005). The dimensional parameters growth of the shell (Wh, Ww and Uw as function of D - Fig. 5A–F) show homogeneous scatters around the mean curve (with R² still very high \pm 0.9) in each case. The growth of those parameters is isometric and harmonic and corresponds to the relationship Y=bD. Regardless of the shell parameters, specimens mbe.9305 and mbe.1401 have greater

affinities with the antidimorphs *P. athletaathleta* and *P. athletapseudotorosum*. Only the whorl width index (Ww/D) of the two specimens deviates from that of the two microconch morphotypes, and better fits into the point cloud of the macroconchs (compare Figs. 5C and 5F).

Finally, the subophiocone coiling of specimens mbe.9305 and mbe.1401 compares well to that of the macroconchs, since the microconchs have dactilicone to ophiocone conch shapes, rarely subophiocone (Fig. 5G).

Ornamentation

The faces of specimen mbe.9305 have similar ornamentation and succession of ontogenetic stages (Fig. 6). This conclusion cannot be reached in specimen mbe.1401 due to poor state of preservation of the right side. No scar or pathological shell compensation is observed exception made of the worn inner whorls. Comparison with the ornamental sequence of both macro-, and microconchs of *P. athleta* is as follows:

- The stage (*i*) is lacking in both specimens. Their ornamentation starts directly with the stage (*ii*), which occupies one whorl and a half in specimen mbe.9305. This stage is more anarchic in specimen mbe.1401 as illustrated by simple, bifurcate, polygyrate primary ribs, and irregular intercalatories not typical of that stage.
- The stage (*iii*) is presents in the two specimens and occupies half of a whorl. Ribs are more robust and spaced in specimen mbe.1401. They start to develop slight thickenings at the future emplacement of the tubercles.
- The stages (*iv*) and (*v*) are typical of *P. athleta* macroconchs and illustrated by strong bituberculate primary ribs, and the progressive disappearance of intercalatories on the venter. It is much longer in specimen mbe.9305 than the other one since it covers one whorl and a half. First peri-umbilical and upper lateral tubercles of the fourth ontogenetic stage are reported at a diameter of 24.3 mm in the specimen mbe.9305, and 35.4 mm in the specimen mbe.1401. The boundary between the phragmocone and the body chamber is located at the upper part of the stage (*iv*) in both specimens. It is at $D \sim 43.2$ in specimen mbe.1401, and at $D \sim 49.4$ in specimen mbe.9305.
- The stage (*vi*) is modified in both specimens compared to typical macroconchs. It develops an approximated, strongly flexuous single or bifurcate ribs crossing the venter, and followed by a slightly projected lappeted aperture typical of the microconchs. The section is markedly sub-rounded at the aperture of mbe.1401 and compares well to that of the *P. athleta* microconchs.

According to the criteria of Bonnot (1995), such ornamental sequence conforms well to that of the *Peltoceras athleta baylei* macroconch morphotype by their long ribbed stage (*ii*), late appearance of stage (*iv*) with reduced peri-umbilical tubercles, and persistence of stage (*v*) in the adult. They, however, develop a sub-rounded whorl section, strong rib retroversion, and a lappet at the end of the shell which are typical features of the *P. athleta pseudotorosum* microconchs. Regarding the number of primary ribs during the

ontogenesis (Fig. 7A–B), our specimens fall in the variability of the two macroconch morphotypes. The low density of primary ribs on the body chamber excludes these specimens to the rib variability of the *P. athleta* microconchs.

Discussion

'Sex reversals' in ammonoid shells and definition of a new forma-type pathology

The species *P. athleta* is widely identified as a dimorphic Aspidoceratidae, including large-sized macroconchs with six ornamental stages and a simple aperture *versus* small-sized microconchs with lappets and modified/truncated ornamental sequence (Bonnot, 1995, and references therein). The individuals at our disposal start with a female ontogeny typical of the *P. athleta* macroconchs and show an apparent change toward maleness in the adult. The ornamental and dimensional parameters of their phragmocones conform well to those of the *P. athletabaylei* macroconch morphotype, but the adult ornamental modifications better compare to that of the *P. athletapseudotorosum* microconch morphotype (i.e. rounded whorl section, ribs retroversion and fading of the tubercles).

Similar 'sex reversals' have been reported by Brochwicz-Lewiński & Różak (1976) in the Kimmeridgian dimorphic Perisphinctidae *Subnebrodites* (pro *Idoceras*) *planula* (Hehl) (Fig. 8A). The figured specimen has the shell features of the macroconchs, but it bears a large lip-like peristome typical of the microconchs at the end of the shell. The phenomenon is also reported in the Oxfordian Perisphinctidae dimorphic pair *Microbiplices* [m] – *Ringsteadia* [M] by Brochwicz-Lewiński & Różak (1976), and by Parent et al. (2008a) based on the specimen of Sykes & Callomon (1979, pl. 121, fig. 9) (Fig. 8B). The figured specimen develops a macroconch sculpture through its growth but has a microconch peristome at the end of the shell. The significance of the apertural structures has been much debated in the literature, but it is now accepted that they correspond to the ultimate stage of sexual maturation of the males (Davis et al. 1996; Klug et al., 2021). A such, the abovementioned specimens illustrate female-to-male 'sex-reversals'.

It is worth noting that male-to-female 'sex reversals' are also reported in the fossil record. For example, Cope (1967, p. 16) reported four out of sixty specimens (6%) of the Kimmeridgian Perisphinctidae *Pectinatites* (*Virgatophinctoides*) *reisiformis* Cope which "appear to be normal macroconchs but have on their inner whorls structures resembling those of the horn of the microconch" (Fig. 9A). Also, fourth *Pectinatites* specimens are "intermediate in size between the two (micro- and macroconch) groups, [...] have the typical microconch horn developed, but show the beginnings of the macroconch type of ribbing". Another case of male-to-female 'sex reversal' is reported by Brochwicz-Lewiński & Różak (1976) based on a specimen of the Oxfordian Perisphinctidae *Subdiscosphinctes* *cracoviensis* (Siemiradzki) figured by Méléndez & Fontana (1993). This specimen displays the onset of macroconch ornamentation [i.e. assigned to the subgenus *S.(Aureimontanites)* or *Larcheria*], after a youthful peristome typical of the microconchs. The most recent documented case is to be found within the Kimmeridgian Aspidoceratidae dimorphic pair *Physodoceras* [M] – *Sutneria* [m] (Parent et al., 2008a)

(Fig. 9B). These authors illustrated a lappeted specimen of *Sutneria subeumela* showing a bituberculate sculpture stage in the sub-adult whorls typical for female. In summary, the Mesozoic ammonoids with apparent 'sex reversals, either male-to-female or female-to-male, belong to the superfamily Perisphinctoidea (families Perisphinctidae or Aspidoceratidae) and occur between the Callovian and the Kimmeridgian stages.

Many pathologies modifying the shell geometry and/or ornamentation of ammonoids is documented in the fossil record and classified into categories called forma-types (see review by Hengsbach, 1996). These forma-types usually result of exogenic cause (e.g. sublethal injury, parasitism) and their expression reflect the developmental response of the ammonoids to a perturbation. The study of such 'monsters' has greatly contributed to the understanding of ammonoid evolution and biology in the past decades (Jattiot et al., 2019 and references therein). To our knowledge, no one ever defined a forma-type for ammonoids showing apparent 'sex reversals' during the shell growth. We, therefore, erect a new forma-type pathology here named "forma hermaphrodita" (from Hermaphrodite, the Greek god who displayed both characteristics of male and female). We include the specimens of Brochwicz-Lewiński & Róża, 1976, Parent et al. (2008a) and the *P. athleta* individuals from Méron in the "forma hermaphrodita" pathology. None of these specimens presents any clear evidence for injury or parasitism although the early whorls are not preserved for further confirmation. Note that the specimen mbe.1401 of *P. athleta* has anarchic stage (ii) that could pinpoint some perturbations during the early growth.

Based on the published cases listed above, all the individuals referred to as "forma hermaphrodita" belong to perisphinctoid species in which a classic sexual dimorphism is encountered. The rarity of such "forma hermaphrodita" specimens in the fossil record thus pinpoints a pathological nature for explaining these apparent 'sex reversals'.

'Sex reversals' in the Ammonoidea and their significance

Little is known about the ammonite soft parts (Klug & Lehmann 2015), and it is not possible to determine which internal sexual organs occur in specimen which has both male and female external shell features. In gonochoric species, the anomalous case of individual possessing gonadal tissue of one sex but exhibits external phenotype of the opposite sex has been previously referred to as pseudohermaphroditism. According to Lee et al. (2006). pseudohermaphroditism is only a manifestation of anomalous sex development among a large mosaic of sex disorders observed in gonochoric species and the term intersexuality should be preferentially used. Considering that the Ammonoidea is a strictly gonochoristic group as the modern cephalopods (Klug et al. 2015), the new "forma hermaphrodita" pathology likely illustrates intersex specimens. This met previous suggestion made by Cope (1967).

The modern cephalopods also group strictly gonochoric species, but external sexual features are generally lacking. The sexual distinction is based on the presence of a hectocotylized arm in males, which transfers the spermatophores to the female. Cases of intersexuality have been reported by Ortiz & Ré (2006) and Hoving et al. (2006). The abnormal cephalopod specimen of *Enteroctopus megalocyathus* described by Ortiz & Ré (2006) is sexed as a female (i.e. absence of the hectocotylus) but shows

internally male structures with normal genital female characteristics and orientated as in normal octopuses. The authors noticed out that "*the presence of mixed female and male structures may not have caused sterility for the female function*" (Ortiz & Ré, 2006, p. 321). The intermediate-sized squid specimens *Ancistrocheirus lesueurii* described by Hoving et al. (2006), show female nidamental glands in the mantle cavity associated with normally developed male reproductive system. According to the authors, these intersex specimens are common in the population and these 'sex reversals' did "*not seem to affect male functionality and is apparently advantageous in that larger body size is accompanied by larger testis and spermatophores*".

In these cases, the causes of intersexuality are not clearly established but environmental pollutants arising from human activity are evoked. According to Hoving et al. (2006), environmental pollutants may have conducted to abnormal feminisation and/or masculinisation because they act as endocrine disrupters. 'Sex reversals' and/or non-functional reproductive abnormalities have also been documented in various gonochoric gastropods and linked to endocrine disrupters (Oberdorster & Cheek 2000). Sexual pathologies in gastropods can also result from the infestation by trematod larvae which stimulate or inhibit neural-endocrinal activity by direct gonadal influence (LeBreton, 1977). This infestation ultimately leads to feminisation or masculinisation. Besides, genetic abnormalities (Hough et al., 1992), temperature fluctuations (Devlin & Nagahama, 2002) or viruses (Rousset et al. 1992) are mentioned in intersex fishes, isopods and crustaceans as causes for intersexuality.

The Middle to Upper Jurassic transition is not recognised as a critical period for biosphere which had to face deep climatic disturbances, except maybe in the Boreal Realm (Wierzbowsky et al., 2018). This period records a low magnitude, short-term global climate cooling at the Upper Callovian–Middle Oxfordian boundary followed by a subsequent warming in the Upper Oxfordian–Lower Kimmeridgian (Dromart et al., 2003). At that time, the perisphinctoid ammonites became extremely diverse and have colonised a wide range of habitat in different bioprovinces of the world (Schweigert, 2015). Thus, it can hardly be argued that intersexuality in the Perisphinctoidea point to the occurrence of a new reproductive strategy illustrating a veritable hermaphroditism due to changing environmental conditions. Regardless of whether "forma hermaphrodita" is due to an exogenic (infestation, virus) or endogenic cause (genetic abnormalities), the high frequency of intersex Perisphinctoidea in the Jurassic deposits can be explained by the two observations: (1) the readily recognition of dimorphic pair, and (2) the easy collection of large and sufficiently preserved fossil palaeopopulations in which intersex specimens have statistically more chance to be found (see also discussion in Klug et al., 2015, §7.3.7.3).

Conclusions

We here document a new case of 'sex reversal' in the ammonoid shells, based on two specimens of the Callovian Aspidoceratidae *Peltoceras athleta*. Those specimens have started with a female ontogeny and show an apparent change toward maleness in the adult. Other cases of female-to-male 'sex reversal', as well as male-to-female 'sex reversal' are known in the ammonoid record, all belonging to the Jurassic superfamily Perisphinctoidea (families Perisphinctidae or Aspidoceratidae). These 'sex reversals' are

pathological in nature and are herein referred to the new forma-type pathology “forma hermaphrodita”. Regardless of whether “forma hermaphrodita” is due to an exogenic or endogenic cause, those specimens illustrate pathologic cases of intersexuality in the Ammonoidea.

Declarations

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Authors' contributions

CF conceived and designed the study. CF and P-YB interpreted the specimen and its significance, as well as contributed text, figures, and revisions. All authors read and approved the final version of manuscript.

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Availability of data and materials

The Méron specimens are deposited in the private collection of P-YB under collection number mbe.9305 and mbe.1404.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Tables

Due to technical limitations, table 1 is only available as a download in the Supplemental Files section.