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Heterochrony in the Late Devonian arthrodiran fishes *Compagopiscis* and *Incisoscutum*

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Abstract – The ontogenetic trajectories of dermal plates of the arthrodiran placoderms *Compagopiscis croucheri* and *Incisoscutum ritchiei* from the Late Devonian Gogo Formation, Canning Basin, Western Australia were compared to assess the impact of heterochrony. Most characters showed peramorphosis. Allometric predisplacement occurred in: the biting division of the inferognathal; the anterior ventrolateral; and the median dorsal plate's breadth. Allometric hypermorphosis was seen in the increases of the prepineal length of the skull roof and the median dorsal plate length. Peramorphic traits contributed to a trend of skull elongation. Fewer paedomorphic features were found. Allometric postdisplacement that resulted in paedomorphosis occurred in the postmesial breadth and the orbital diameter of the skull roof. It is suggested that lengthwise growth occurs earlier in ontogeny than breadthways growth, and that dissociated heterochrony was an important mechanism in the evolution of these arthrodires.

INTRODUCTION

The Late Devonian (Frasnian) fish fauna from the Gogo Formation in the Canning Basin, Western Australia ranks as, arguably, the most significant of its kind of Palaeozoic age. Despite more than 40 species of these exquisitely, three-dimensionally preserved fishes having been described (see Long 1988a and Long *et al.* 1997, for a review), to date few ontogenetic studies have been carried out. While the "Gogo fishes" are of immense phylogenetic importance in terms of the early evolution of fishes, understanding both evolutionary relationships and assessing the mechanisms that cause them are difficult without ontogenetic data. To this end we present here the first detailed ontogenetic analysis of any of the Gogo fishes, and utilize the information in a study of the role that heterochrony might have played in their evolution. Given that the head shield and trunk shield are composed of interlocking plates (Figure 1), and that each plate is likely to have had its own ontogenetic history discrete from its neighbour, unravelling the relative differences in ontogenetic development of the skull and trunk plates between species has the potential to contribute greatly to our understanding of evolution within these fishes.

Heterochrony, that is change to the timing and rate of development, plays a pivotal role in evolution (McKinney and McNamara 1991; McNamara 1997). A major focus of many heterochronic studies has been how allometry is affected by heterochrony, insomuch as heterochrony involves the interrelationships between size, shape and time (Alberch *et al.* 1979), while allometry is the relationship between size and shape during growth (Gould 1966; Blackstone 1987a, 1987b; Strauss 1987; German and Meyers 1989; Klingenberg 1998). Heterochronic changes to descendant ontogenies encompass either changes to the onset or offset of growth, or to the rate of growth. The obvious outcome of these changes will be changes to allometries, or to the duration of allometric growth. If the duration of the growth period is extended, then ancestral allometries will be extended resulting in relative changes in shape and size. Likewise if the duration of growth is reduced, so the extent of shape change will correspondingly be changed. Relative changes in growth rates, not only of different structures within an organism, but even of different growth vectors within the same structure, will result in changing allometries. The challenge when trying to undertake heterochronic analyses of fossil material, when age data is lacking, is to attempt to unravel the processes that have produced the allometric changes, for these will always be an outcome of heterochrony.

The extent to which changes in shape and size relate to time have been the subject of much debate. Blackstone (1987a, 1987b) has viewed chronologic

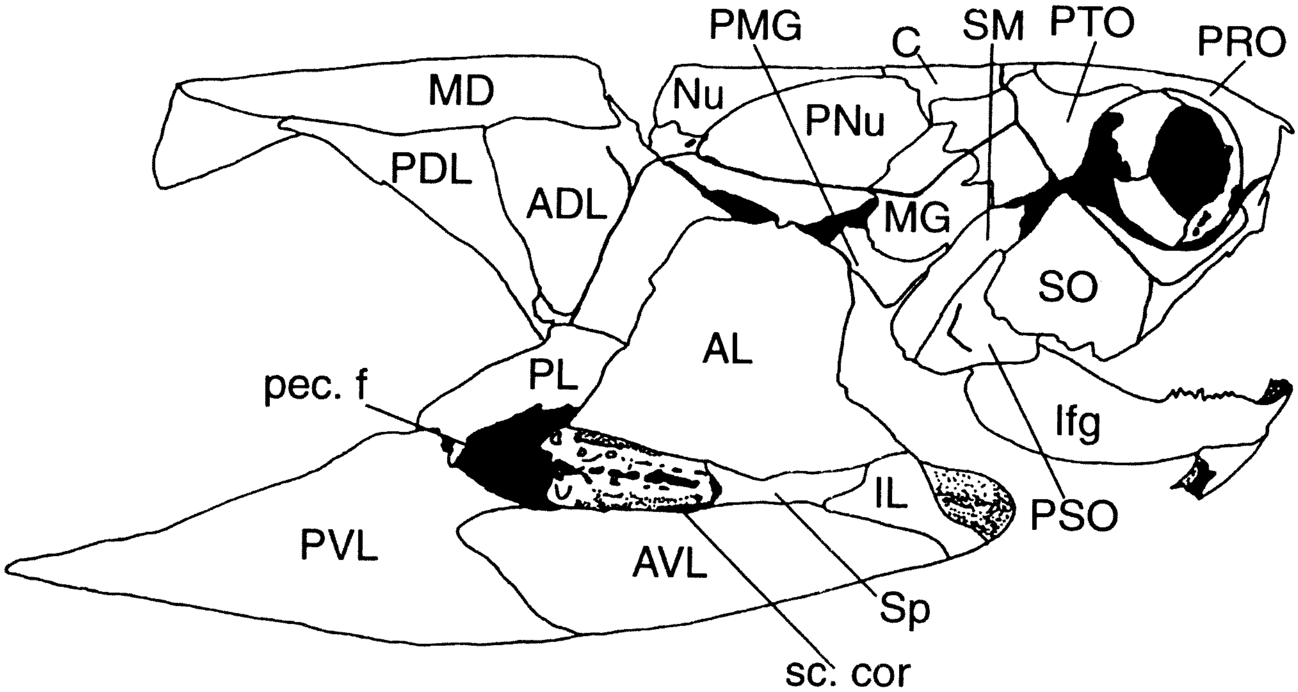

Figure 1 Lateral view of *Compagopiscis croucheri* (WAM 90.12.139), indicating plates of the head and thoracic armour. Abbreviations: ADL, anterior dorsolateral; AL, anterior lateral; AVL, anterior ventrolateral; C, central; Ifg, inferognathal; IL, interolateral; MD, median dorsal; MG, marginal; NU, nuchal; PDL, posterior dorsolateral; pec.f, pectoral fenestra; PL, posterolateral; PMG, postmarginal plate; PNu, paranuchal; PRO, preorbital; PSO, postsuborbital; PTO, postorbital; PVL, posterior ventrolateral; sc.cor, scapulocoracoid, SM, submarginal; SO, suborbital; Sp, spinal.

age as the independent variable in studies of allometry. However Lande (1985) and Strauss (1987) have argued that bivariate allometric relationships arise from growth curves as a function of time. Consequently, any allometric analysis will incorporate the concept of time. As a number of authors have pointed out, the analysis of changing form leads naturally on to a quantitative extrapolation of heterochronic evolutionary change (Bookstein *et al.* 1985; Creighton and Strauss 1986; Klingenberg 1998).

In dealing with fossil material, many workers have used size as a proxy for time. While there is no doubt that size can, as Blackstone (1987b) has pointed out, "act as an environmentally adjusted measure of the chronological time an organism has been growing", a one-to-one correlation between size and time can only be made if two criteria are met: relationships between growth of parts must remain constant, despite the effect of environmental change altering overall growth rate; and growth rates must be constant among organisms under comparison (Blackstone 1987b). While on a bacteria-to-whale scale there is a correlation between size and age, and even at much lower taxonomic levels, environmental factors, such as temperature and nutrient levels can break down this correlation.

The problem of understanding the inter-relationships between allometry and heterochronic processes has been discussed in detail by McKinney and McNamara (1991). They concluded that while ontogenetic age is needed in order to confidently assign particular processes of heterochrony, allometric plots are important because size change is a metric of an organism's "internal" age. Often this is more significant that its "external" age. This is because many ontogenetic events are size-specific, rather than age-specific. McKinney (1988) suggested the application of heterochronic terms to allometric plots, with the understanding that they may or may not be the same as "true" heterochronies. He termed this "allometric heterochrony". Thus the x variable is size rather than time.

One group in which few studies have been carried out on allometric growth patterns and heterochrony is placoderm fishes. The only significant work has been that of Werdelin and Long (1986) and Long and Werdelin (1986) who looked at allometry and heterochrony in the antiarch *Bothriolepis*. In this paper we seek to determine to what extent heterochrony played a role in the evolution of other placoderms by examining allometry in the arthrodire *Compagopiscis croucheri* Gardiner and Miles, 1994 and allometric heterochrony in this species and in the pachyosteomorph arthrodire *Incisoscutum ritchiei* (Dennis and Miles, 1981). Both species are from the Gogo Formation.

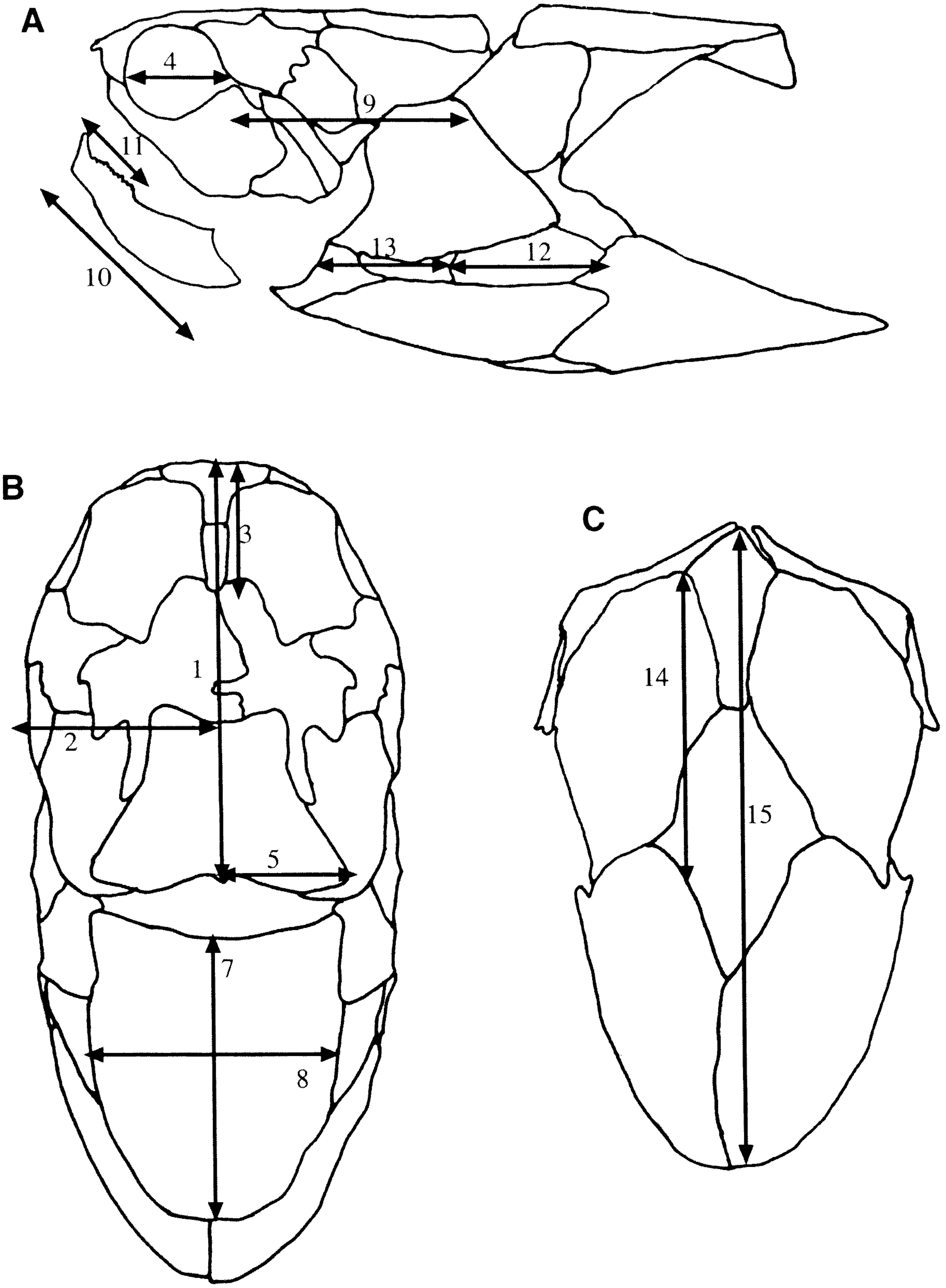

Figure 2 Measurements (1–15) made on head and trunk shield of *Compagopiscis croucheri* and *Incisoscutum ritchiei*. A, lateral, B, dorsal, C, ventral views. Details are given in Materials and Methods section in text.

MATERIALS AND METHODS

The specimens used in this study are held in the collections of the Western Australian Museum, Perth (WAM) and the Australian Museum, Sydney (AM). Published measurements (Miles and Dennis 1979; Dennis and Miles 1981; Gardiner and Miles 1994) were used for specimens located in the Natural History Museum, London (BMNH), with additional measurements being provided by Dr K. Dennis-Bryan. All specimens were collected from the Gogo Formation in the northern Canning Basin, Western Australia.

Measurements of traits (Table 1) were taken from the skull and trunk of all WAM and AM specimens using digital callipers to the nearest 0.01 mm. In total 50 specimens were measured. Those giving too little information were eliminated prior to the analysis. However, although growth is being examined, it must be noted that the specimens examined here represent a static sample and not a growth series.

Plots of bivariate traits were constructed using log transformed data, on those specimens from which a midline skull measure could be obtained (Figure 2). Skull length was chosen as the independent variable because this measure was present for most specimens. Variables were chosen on the basis of the completeness of the data, and prior to performing the regression analysis samples were tested for normality using the statistical tests command in the software package Statworks (Cricket Software Inc. 1985) on a Macintosh computer. Since data being analysed were from the same individual, true independence of characters could not be assured, as all traits represent the same growth system (McKinney and McNamara 1991).

The following list of measurements represents the 15 traits used in the calculation of allometry and allometric heterochrony (Figure 2):

(1) Length of head shield — midline length of head shield excluding obtected nuchal area.
(2) Width of head shield — distance from the postmesial corner x 2. This system minimises preservation distortion and allows the inclusion of specimens with only half the head shield preserved.
(3) Length of the prepineal — midline length from the posterior pineal to the anterior midline point of the rostral.
(4) Orbital width — lateral measure at widest portion of the orbit from inside the skull.
(5) Nuchal length — measured from nuchal/central/paranuchal point to posterior of nuchal.
(6) Nuchal breadth — measured from posterior contact point to the midline x 2.
(7) Median dorsal length — midline length of the plate.
(8) Median dorsal width — midline width of the plate.
(9) Cheek length — length of the postorbital division of the cheek.
(10) Length of the inferognathal — distance from the anterior to the posterior point along the midline of the plate.
(11) Biting division of the inferognathal — distance from the anterior denticle or plate to the posterior denticle or plate along the anterior portion of the inferognathal.
(12) Pectoral fenestra — midline from the spinal plate to the postpectoral process.
(13) Spinal plate — distance from the anterior to posterior points.
(14) Length of the anterior ventrolateral — midline length.
(15) Trunk length — midline length of ventral portion of the trunk shield.

Calculations of Allometric Heterochrony

Bivariate plots were constructed for the traits which showed allometric changes in *Compagopiscis croucheri* (Figure 3). When these traits were compared with the same traits in a more derived arthrodire, *Incisoscutum ritchiei*, it was possible to relate the allometric changes to the heterochronic processes that initiated the change. Linear regression lines were fitted for each species using Cricket graph (Cricket Software Inc. 1985). The slope (k), which according to Alberch *et al.* (1979) is an estimation of shape change relative to size, and the intercept (y) which indicates onset and offset signals, of each species were tested against each

Table 1 Results for the allometric regression for growth in dermal plates of *Compagopiscis croucheri*. Abbreviations: RMA = Reduced major axis; r = Regression coefficient; Sa = Standard error of the linear regression; Ts = Hotteling's test of the regression coefficients; df = degrees of freedom; NS = not statistically significant.

Skull Variable	Slope (k)	RMA	r	Sa	Ts	df	sig level
Nuchal length	1.35	1.42	0.9	0.32	0.40	18.0	***
Nuchal breadth	1.70	2.39	0.5	1.07	0.16	24.0	NS
Prepineal length	1.08	1.20	0.8	0.37	1.20	18.0	**
Cheek length	0.17	0.23	0.5	0.78	0.22	16.0	NS
Inferognathal length	1.65	1.72	0.9	0.39	0.42	18.0	***
Inferognathal biting division	1.22	2.41	0.9	0.52	4.29	17.0	***
Median dorsal length	0.62	0.70	0.8	0.56	0.11	18.0	NS
Median dorsal breadth	1.07	0.95	0.5	0.95	0.73	18.0	**
Orbital diameter	0.88	1.06	0.7	0.31	2.81	16.0	**
Post mesial breadth	1.31	1.4	0.9	0.44	2.96	18.0	**
Pectoral fenestra length	0.6	0.81	0.5	1.05	0.57	11.0	NS
Spinal length	1.39	1.91	0.5	0.88	1.57	19.0	NS
Anterior ventrolateral length	0.77	0.55	0.7	0.55	1.40	15.0	NS

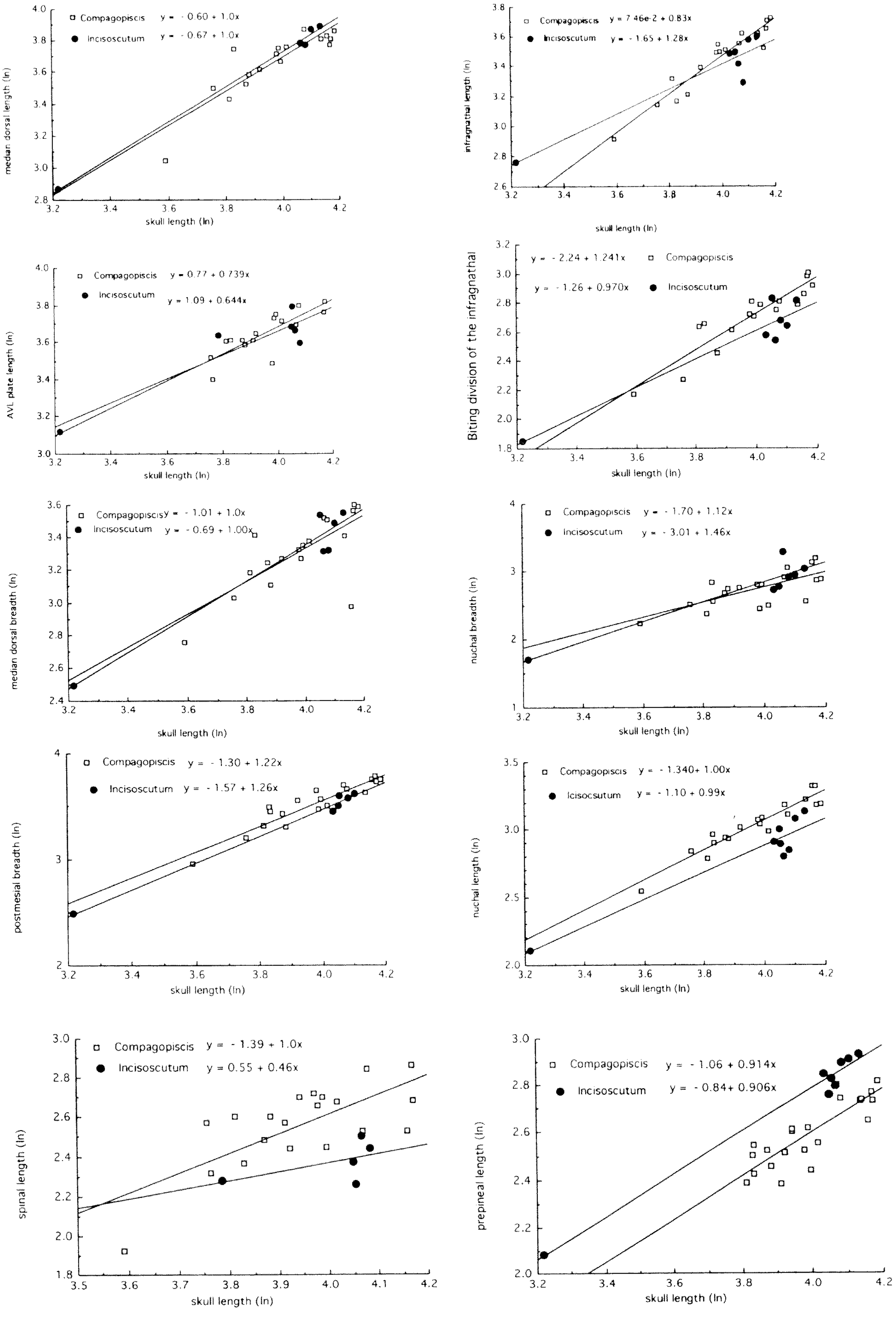

Figure 3 Log/log plots of plate parameters against skull length for *Compagopiscis croucheri* and *Incisoscutum ritchiei*.

Table 2 Results for testing the difference of the *y* intercept from origin in the allometric regression for growth in eight dermal plates of *Compagopiscis croucheri*.

Skull/variable	*y* intercept	Sa	Ta	Sig level
Pectoral fenestra length	0.910	0.264	3.450	**
Spinal plate length	1.000	0.224	4.470	***
Anterior ventrolateral	0.912	0.173	5.270	***
Trunk shield length	0.906	0.108	8.380	***
Median dorsal length	1.080	0.140	7.680	***
Median dorsal breadth	1.000	0.238	4.220	***
Nuchal breadth	1.120	0.268	4.160	***
Cheek length	0.810	0.190	4.150	**

other for differences by analysis of covariance (Berenson *et al.* 1983). As no real age data were available for the specimens examined, only allometric heterochrony (McKinney and McNamara 1991) is discussed.

Results

Normality Test

Samples of *Incisoscutum* and *Compagopiscis* were found to be normally distributed making the assumption that there is a direct relationship between the specimen's age and size. As the sample size was small (26 *Compagopiscis* and 9 *Incisoscutum*) the results should be considered with some caution.

Allometric Regression

The results of the regression analysis (Table 1) indicate that from 13 variables for which regression coefficients were calculated, eight appeared to show isometric growth (*k* not significantly different from unity) and the remaining five showed some degree of allometry. However, as linear regressions with a *y* intercept significantly different from zero indicate allometry (Gould 1966), the *y* intercept was tested for significance against zero (Table 2).

From the additional information provided in Table 3, it can be seen that all variables tested showed allometry. The nuchal, length of the inferognathal, postmesial breadth of the skull roof, prepineal length of the skull roof and biting division of the inferognathal represent positive allometry and the orbital diameter shows negative allometry. As the results in Table 2 refer only to the *y* intercept, and as the slope and *y* intercept are interdependent, i.e., points of intersection can be varied by changing the unit of measure, the type of allometry (positive or negative) cannot be determined for the variables in Table 2. While the results obtained are not representative, as the variables used do not represent a random sample, these tests do indicate that many of the plates in *C. croucheri* showed a great deal of variation throughout ontogeny.

ALLOMETRY, HETEROCHRONY AND THEIR EVOLUTIONARY SIGNIFICANCE

Through comparison of the slopes and *y* intercepts of the variables (Table 3) it can be shown that allometric hypermorphosis occurred in two variables, allometric postdisplacement also occurred in two variables and allometric predisplacement occurred in four variables. While allometric heterochrony could be described for the variables in Table 3, there were insufficient data available for *I. ritchiei* to determine any relationship between heterochrony and allometry, or the mechanisms involved in allometric heterochrony for the cheek plates. The analysis for the spinal plates, inferognathals, nuchal breadth and trunk shield (Table 3) showed significant differences in slopes and *y* intercepts, so no inferences about allometric heterochrony could be made.

In *C. croucheri* all of the features that showed significant allometry (Table 1) represented traits that have been used in the phylogenetic analysis of arthrodires and have previously been indicated as varying throughout the evolution of the arthrodires (Gardiner and Miles 1975, 1990; Denison 1984; Leliévre 1991; Carr 1991). Werdelin and Long (1986) proposed that the strongest allometry should occur in anatomical regions of phylogenetic importance. It is here suggested that this has occurred in the evolution of the eubrachythoracid arthrodires.

Table 3 Bivarate growth trajectories for *Incisoscutum ritchiei* (descendant) relative to *Compagopiscis croucheri* (ancestor).

Trait	Slope	*y* intercept	Allometric heterochronic change
Prepineal length	equal	equal	allometric hypermorphosis
Orbital diameter	equal	less	allometric postdisplacement
Median dorsal length	equal	equal	allometric hypermorphosis
Nuchal length	equal	higher	allometric predisplacement
Infragnathal biting division	equal	higher	allometric predisplacement
Post mesial breadth	equal	less	allometric postdisplacement
Anterior ventrolateral length	equal	higher	allometric predisplacement
Median dorsal breadth	equal	higher	allometric predisplacement

Prepineal length

The extensive development of the prepineal region of the skull roof in the more derived species, *I. ritchiei*, when compared with the presumed ancestral condition present in *C. croucheri*, appears to result from a combination of allometric predisplacement and hypermorphosis. Predisplacement is characterized by earlier onset of growth, and hypermorphosis by a late cessation of developmental events. Both processes result in a peramorphic structure in the adult descendant (McKinney and McNamara 1991). It is here suggested that these processes were significant factors in the elongation of the prepineal region that occurred in the evolution of coccosteomorph arthrodires (Figure 5).

Denison (1984) first noted the close relationship of *Incisoscutum* to the Camuropiscidae and considered that the camuropiscids were derived from coccosteid stock. Denison (1984) and Long (1988b) have suggested that *Incisoscutum* served to bridge the gap between the coccosteids and the camuropiscids and it is here suggested that *Compagopiscis* provides an earlier link between these taxa. The rostral plate of *Compagopiscis* appears to show a large amount of developmental plasticity and it has been noted by Dennis and Miles (1981) that the rostral plate of *I. ritchiei* also demonstrates this same developmental plasticity. The pineal plates of both juvenile and adult *Compagopiscis* are proportionally the same length, however the rostral plate in the juveniles is much shorter than the rostral of the adult. It is proposed that the extension of the prepineal area occurred primarily due to allometric predisplacement and hypermorphosis of the rostral plate, since in the Camuropiscidae, the rostral and the pineal plates became separated by the preorbital, growth in the pineal would not necessarily have resulted in elongation of the rostral. Long (1990) has suggested that the long snouts of the camuropiscids *Tubonasus* and *Fallacosteus* evolved independently from the similar condition exhibited in *Rolfosteus* and *Camuropiscis*. However, it is likely that the same allometric mechanisms were involved in both elongation events.

Orbits

The larger orbits of *I. ritchiei* are paedomorphic in comparison with *C. croucheri*, as orbit diameter shows negative allometry. Interpretation of the allometric regression lines, showing *I. ritchiei* with a *y* intercept less than that of *C. croucheri*, indicated that the mechanism that resulted in the paedomorphosis is postdisplacement. This occurs when there is a late initiation of developmental events in the descendant relative to the ancestor (McKinney and McNamara 1991). As the eyes are very important throughout development it seems surprising that they would evolve by this mechanism rather than by progenesis or neoteny. It is possible that onset of negative allometry in the orbit would have been delayed. The material studied indicates that *Incisoscutum* had a larger body size than *Compagopiscis*, making it unlikely that progenesis occurred.

Neoteny is another possible mechanism which would result in the formation of larger orbits, as this is the result of a slower rate of development in the descendant rather than a late onset of development. As neoteny involves changes in both time and shape this process is difficult to interpret from the fossil record when there is absence of age data (McNamara 1988). Long (1994) has observed that large orbits are a distinguishing feature of the incisoscutids and the camuropiscids and are possibly related to a more active, predatory life. The orbits of *C. croucheri* are larger than in either *Coccosteus* or *Harrytoombsia* and there is also an increase in the orbit size within the lineage Brachydeiroidea – Rhachiosteidae (Denison 1984). Thus within arthrodires a paedomorphoclade in orbit size exists from *Coccosteus* and *Harrytoombsia* to *Compagopiscis* and then to *Incicoscutum* (Figure 5). Accompanying the increase in orbit size is an increase in the length of the preorbital plates (Denison 1984). A comparable paedomorphoclade has been observed by Long (1990a) in the Devonian lungfishes *Dipnorhynchus – Chirodipterus – Dipterus*. Such parallel evolution suggests strong selection pressure for larger orbit size.

Preorbitals

Both the increase in the prepineal length and the increase in the orbit size are associated with changes in the preorbital plate. There is a large amount of ontogenetic change in the preorbital plate as well as significant phylogenetic change. In *Compagopiscis* the preorbitals are always separated by the pineal plate, however in *Incisoscutum* the preorbital plates are polymorphic, some individuals having a contact region anterior to the pineal plate which results in the rostral and pineal plates being separated. This character is further developed in the camuropiscids where the preorbitals always have a large contact area anteriorly to the pineal. As the postnasal plates in the camuropiscids are very well developed compared with other coccosteomorphs and these plates are supported by the preorbitals, this change in the preobital plate may be associated with support for the increased rostrum.

Postmesial breadth

Log/log plots of postmesial breadth against skull length indicate that the reduced postmesial breadth in *Incisoscutum* when compared with *Compagopiscis* arose from postdisplacement. Delaying the time when cells are committed to a particular skeletal element means that there are fewer cells available to form the structure (Hall 1983). This results in the development of an organ of a different (reduced) size and/or shape. The decrease in postmesial breadth appears to be a consequence of changes in both nuchal breadth and changes in the proportions of the paranuchals. The log/log plot does not demonstrate allometric postdisplacement for the nuchal breadth as both the *y* intercept and slopes are significantly different. The narrow head is more pronounced in the juvenile specimen.

Coupled with the decrease in breadth, is a relative increase in length of the head shield, and this results, in part, from allometric predisplacement of the nuchal length (Table 3), producing peramorphic traits in the adult of the descendant species. The nuchal in *Compagopiscis* shows highly significant positive allometric growth throughout ontogeny (Table 1) and morphologically it appears almost square in the juveniles, becoming trapezoidal in the adults. The skull proportions have been important in characterizing taxa amongst arthrodires, with a definite trend towards longer and narrower skulls through phylogeny, and it appears that *Compagopiscis* is the first genus of the lineage to display this narrowing and lengthening of the head shield. This arose from decoupling of the breadthways and lengthwise growth, reflecting a developmental trade-off of breadth for length. Thus, the nuchal length appears to change as a result of predisplacement and the nuchal width by postdisplacement. This results in quite different length to breadth ratios in juveniles and adults.

Inferognathals

Although the inferognathal showed significant allometric change in *Compagopiscis* (Figure 4), no relationship between allometry and heterochrony could be determined from the allometric plot as differences in both the *y* intercept and the slope were evident. However, a relationship between allometry and heterochrony was found for the biting region of the inferognathal, and the developmental change indicated by the log/log plots was allometric predisplacement. The biting division of the inferognathal changes from a denticle-covered division that exerted a shearing effect in *Compagopiscis* to a durophagous, crushing plate in the incisoscutids and camuropiscids. This modification of the jaw which requires a firm contact between the cheek and the skull, and a reduction in the size of the postsuborbital plate allowed more pressure to be exerted in the bite (Long 1990b). The postsuborbital is small in *Compagopiscis* in comparison with *Harrytoombsia.* However it is larger than the postsuborbital found in *Incisoscutum* and the camuropiscids. This suggests that there has been a reduction in the size of this plate within the coccosteomorphs. Long (1988b) has noted that the inferognathal of *Incisoscutum* is similar to that of the juvenile of the more derived *Camuropiscis*, indicating peramorphic trends in the evolution of this feature.

Cheek Unit

The cheek unit of *Compagopiscis* grew allometrically (Table 2). The cheek has been

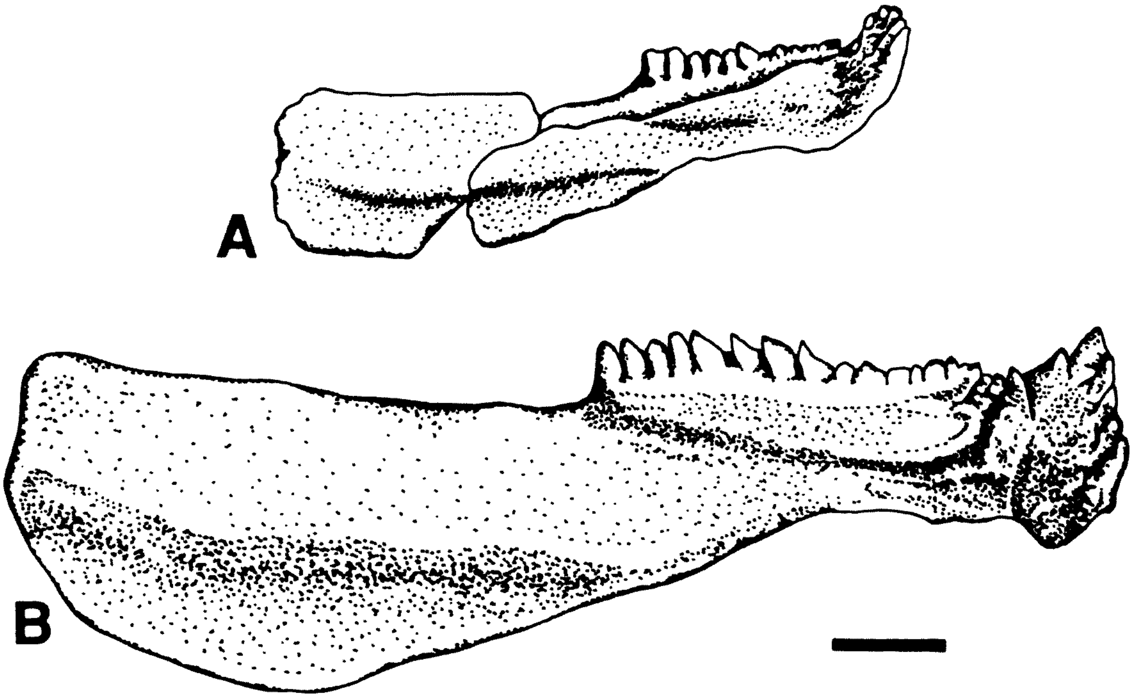

Figure 4 Ontogenetic change in inferognathals of *Compagopiscis croucheri*. A, WAM 94.5.1; B, WAM 86.9.675. Scale bar = 10 mm.

considered a morphological unit of great evolutionary significance in the higher arthrodires (Dennis and Miles 1981; Long 1994), that is believed to have evolved in response to selection for a durophagous diet (Long 1990b). It is possible that different ontogenetic trajectories were followed by different plates of the cheek, analogous to what occurred in the head. To determine if this is the case with *Compagopiscis*, the individual plates that make up the cheek were examined in isolation. Allometric heterochrony could not be determined for the cheek plates from *Compagopiscis* compared with *Incisoscutum* because both the slope and the intercept differed (Table 3). This result is probably due to the disproportionate number of specimens of *C. croucheri* compared with *I. ritchiei*, as the cheek unit was only preserved in five specimens of *I. ritchiei*. Preparation of further specimens may enable the calculation of allometric heterochrony in the cheek unit.

Median Dorsal

The trend of narrowing and lengthening, evident in the head shields of the more derived taxa, is repeated, not surpisingly, in the trunk shield. Again different allometric heterochronic mechanisms affect different trunk shield plates. Furthermore, there appears to have been a dissociation between growth lengthwise and breadthways. The increased length of the median dorsal in *Incisoscutum* relative to *Compagopiscis* is due to allometric hypermorphosis, whereas the decrease in the breadth of the median dorsal appears to indicate allometric postdisplacement as the mechanism of change. The coefficient of determination for the median dorsal breadth in *Incisoscutum* was only 0.5, suggesting that there were either insufficient data for the test, or that there is great intraspecific variation in the breadth of the median dorsal. If the latter statement is correct then the increased growth breadthways must have occured at a slower rate than the increased growth lengthwise, as there is a definite morphological trend towards narrower median dorsals within the higher arthrodires. Breadth to length ratios of the median dorsal plate supports the second hypothesis with the juvenile *Compagopiscis* (WAM 91.4.3) having a breadth/length ratio of 75, the adult *Compagopiscis* (WAM 86.9.704) having a ratio of 73 and the adult *I. ritchiei* having a ratio of 66.8 (WAM 95.9.1).

Anterior laterals

Log/log plots of anterior lateral length/skull length indicate that allometric predisplacement was the mechanism involved in the elongation of the anterior ventrolaterals in *Incisoscutum*, which are longer than those of *Compagopiscis* and the plourdosteids. Denison (1984) has noted that three taxa, the Camuropiscidae, Leptosteidae and Brachydeiroidea, have evolved long, narrow bodies. The incisoscutids are phylogenetically close to the camuropiscids (Long 1988a, 1988b). Whether this peramorphic trait arising from allometric predisplacement was the principal developmental mechanism involved in the elongation of the anterior ventrolaterals in the coccosteomorphs awaits more research.

Spinal plate

In association with the lengthening of the anterior ventrolateral, there have also been changes in the dimensions of the spinal plate. The structure of the spinal appears very variable in *Compagopiscis*. Moreover, it changed markedly throughout the evolution of the arthrodires. In less derived arthrodires, such as *Harrytoombsia*, the plate is a true spinal and extends markedly from the trunk armour (Denison 1978). *Compagopiscis* is the least derived genus to be described, exhibiting what Dennis and Miles (1980) defined as the "pseudospinal". Unlike the plourdosteids, this plate is anteriorly narrowed and posteriorly widened and does not possess a spinal pit. However, the spinal plate in *Compagopiscis* does maintain extensive contact with the interolaterals. Within the Incisoscutoidea, *Gogosteus* has retained a long spinal plate; however there is reduced contact between the spinal plate and the interolaterals, while in *I. ritchiei* the spinal plate is reduced.

In the Camuropiscidae there is a further reduction in the length of the spinal plate which results in contact between the anterior lateral and anterior dorsal lateral. The reduction in the spinal is completed in the more derived aspinothoracids, (e.g. *Dinichthys*), where it is completely lost. The mechanism which results in the reduction and final loss of the spinal plate could not be determined (Table 3). The low correlation coefficient (0.3) for the regression line plotted for *Incisoscutum* is probably indicative of an insufficient sample size. The most probable mechanism resulting in the reduction of the spinal plate is allometric postdisplacement, as this results from a delayed onset time in relation to developmental events (McKinney and McNamara 1991), and produces paedomorphosis when expressed in the more derived adult phenotype. The allometric change described was in the *y* axis which Gould (1969) defines as the axis depicting changes in offset and onset time. Further evidence to support this hypothesis is provided by the similarities between the breadth/length ratios of the spinal plate of juvenile *Compagopiscis* and the spinal plate of adult *Incisoscutum*, these being 19 and 19.4, respectively. These values are lower than those for the specimens of the adult *Compagopiscis* which range between 23 and 27. It then appears that juveniles present a more derived condition than the adults.

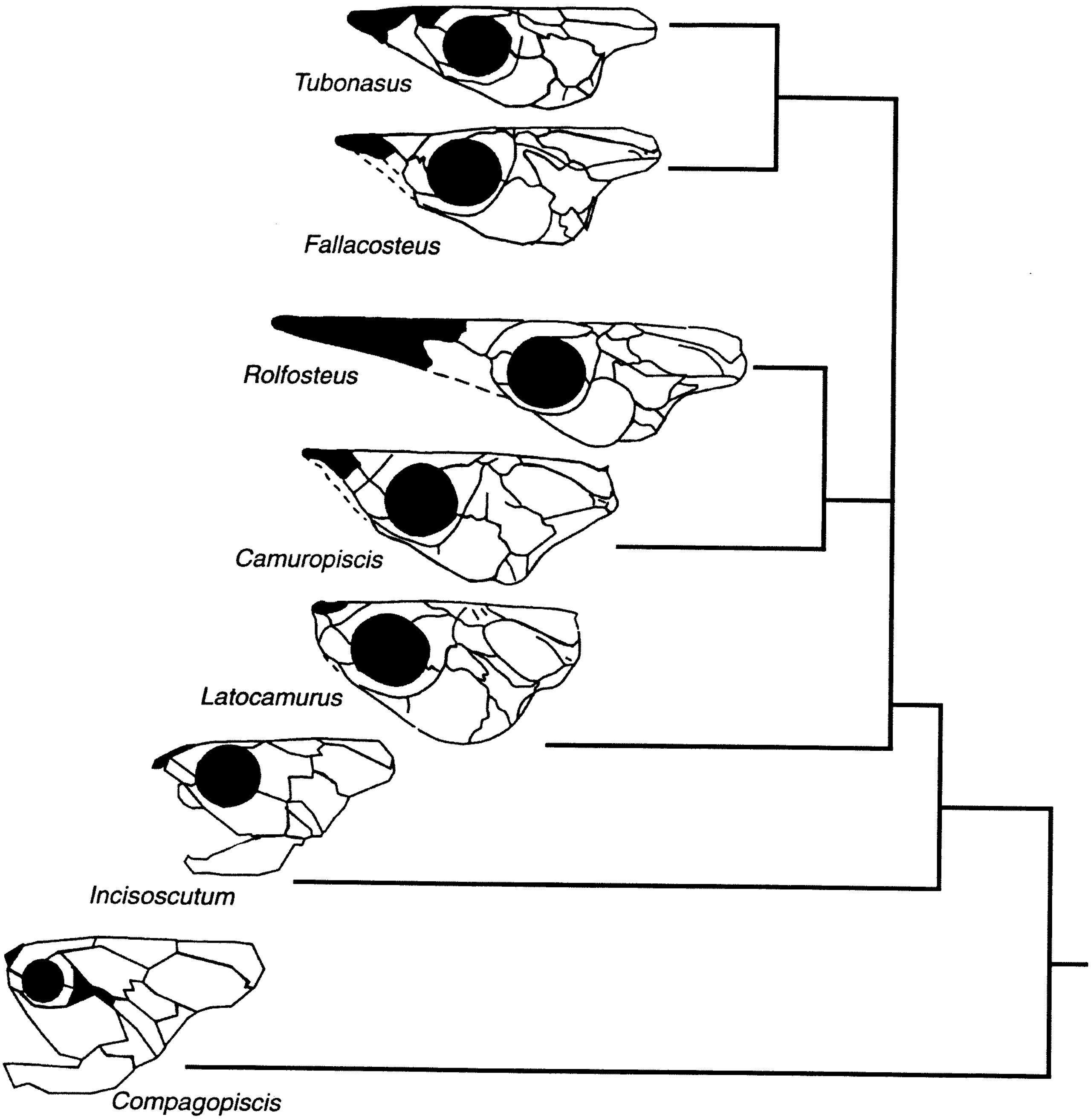

Figure 5 Allometric hypermorphosis of the prepineal region in the higher arthrodires (not drawn to scale).

Qualitative Allometry

There are several morphological characteristics within *Compagopiscis* that changed as the species increased in size but which we are unable to quantify by the methods currently available, due to the complexity of shape in many of the characters. As many of these complex structures are very small, accurate measurement is currently impossible.

Morphometric studies undertaken on placoderm parasphenoids from Morocco, North Africa and Gogo, Western Australia (Dennis-Bryan 1995) suggest that the primitive parasphenoid was flat, lacking notches and grooves, with an expansive tubercle-covered ventral surface. The transverse lateral groove did not traverse the whole plate and there were no hypophysial openings. As arthrodires evolved, the parasphenoid increased in thickness and the distribution of the tubercles on the ventral surface became restricted or was lost, the transverse lateral groove extended across the whole plate and the opening for the hypophysial became present (Dennis-Bryan 1995). This present study confirms that such a sequence occurs during the ontogeny of *Compagopiscis*, suggesting that the changes in arthrodire parasphenoids as a whole are peramorphic. The smallest specimen has a relatively simple parasphenoid that is thin and low, with tubercles scattered across the anterior portion. As the species matured the parasphenoid increased in thickness and the posterior region widened, changing from a thin point to a rounded margin and the distribution of tubercles became restricted to the transverse lateral groove.

The parasphenoid of adult specimens of *Compagopiscis* resembles those described for *I. ritchiei* (Dennis and Miles 1981) and *Gogosteus sarahae* (Long 1994). It has a more elongated, although deep, parasphenoid, resembling that described in the camuropiscids (Long 1988b). Long (1988b) postulated that this narrow, deep type of parasphenoid was a specialized feature of the Camuropiscidae and from the static ontogenetic series presented here, it would appear that the camuropiscid parasphenoid developed as a result of paedomorphosis.

Another character that changes markedly is the breadth of the posterior region of the anterior median ventral. This plate is unfortunately not preserved in the smallest specimen of *Compagopiscis croucheri*. However, in other juvenile specimens the plate is preserved and medially there is a very narrow ridge that terminates approximately half way along the plate. In slightly larger specimens this narrow ridge extends posteriorly to produce an elongated kite shape, and as the specimens increased in size the posterior portion widened until it eventually came to resemble a narrow rectangle (Figure 6). As the narrow kite-shaped anterior median ventral is still found in relatively large specimens, up to 53 mm, it would seem that the individuals first increase in length and then, when almost mature, increase in breadth. A similar growth pattern is observed in *Incisoscutum*, the smallest specimens having a very narrow anterior median ventral with a pointed posterior region and the larger specimens having a wider anterior median ventral with a rectangular posterior region. However, the posterior region never achieved the

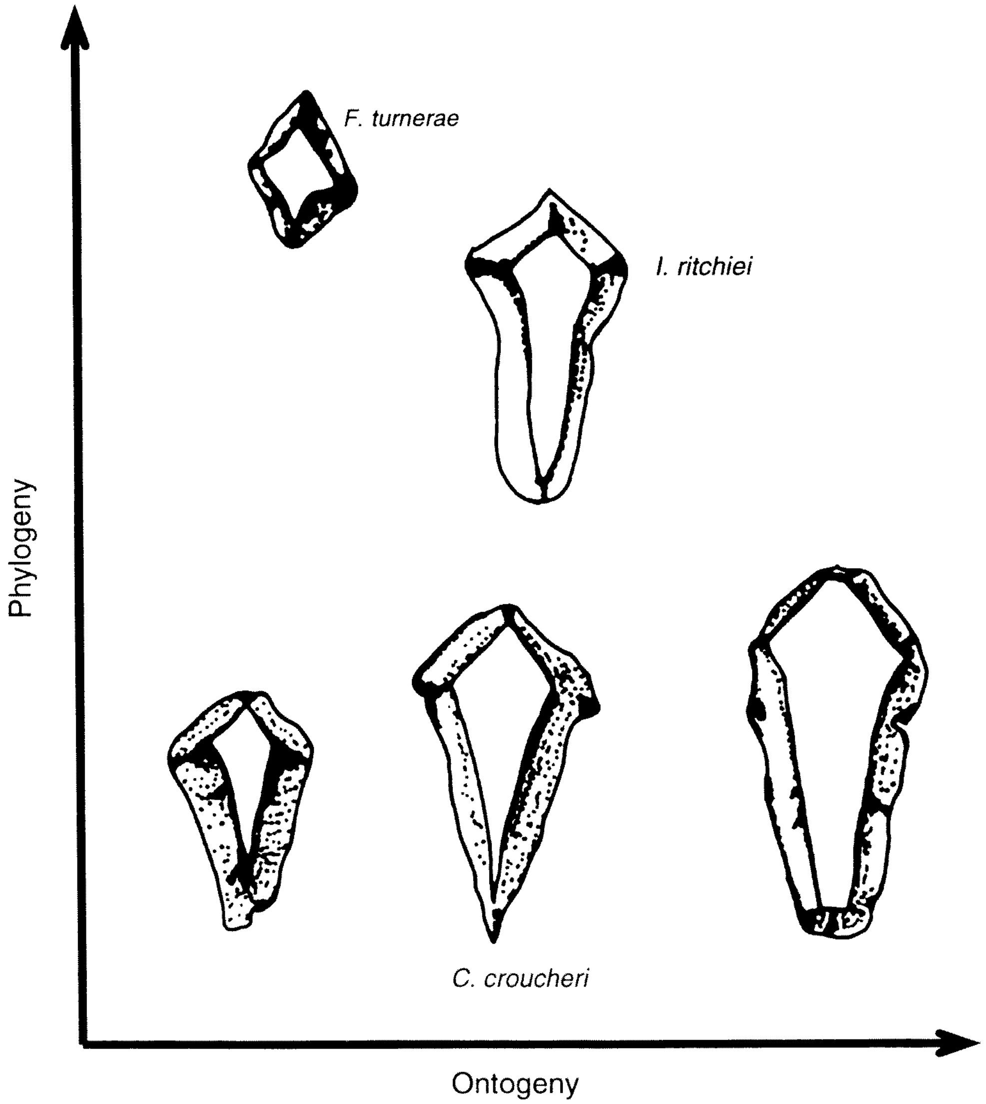

Figure 6 Paedomorphic evolution of the anterior median ventral plate in three species of arthrodires from the Gogo Formation, *Compagopiscis croucheri*, *Incisoscutum ritchiei* and *Fallacosteus turnerae*.

relative width found in *Compagopiscis*. The anterior median ventral in the Camuropiscidae, such as in *Fallocosteus turnerae* is very short and narrow and resembles that found in juvenile specimens of *Incisoscutum* and *Compagopiscis*. It would seem that the anterior median ventral has evolved through paedomorphosis, but the exact mechanism cannot be determined without quantitative data.

The ornamentation of the head and trunk armour is another feature that changed both ontogenetically and phylogenetically. In the juvenile *Compagopiscis* the plate ornamentation is extensive and the tubercles well defined. This extensive ornamentation also occurs in *Incisoscutum*, a more derived taxon than *Compagopiscis*. However, in *Incisoscutum*, the ornamentation is further developed, having a stellate form rather than simple domed tubercles, whereas in the adult *Compagopiscis* ornamentation is sparse and usually only present around the margins of the plates and on the spinals and interolaterals.

CONCLUSIONS

Dissociated heterochrony has been an important mechanism in the evolution of the arthrodires. Classic dissociated heterochrony involves paedomorphic and peramorphic changes affecting different structures in the same organism (McKinney and McNamara 1991; McNamara 1997). Dissociated heterochrony can also occur in a single structure, involving peramorphic increase in length and paedomorphic decrease in width, for instance. Such developmental trade-offs are commonplace in another group of organisms that, like arthrodires, have an outer covering of independently growing plates, namely echinoids (McNamara 1987). In *Compagopiscis* and *Incisoscutum* dissociated heterochrony is seen in both the head and trunk shield plates. Different heterochronic processes have also operated. Thus when *Incisoscutum* is compared with *Compagopiscis*, for example, the nuchal length can be seen to have increased through allometric predisplacement, while the prepineal length increased through allometric hypermorphosis. This implies relative differences in the timing of onset and offset of growth of particular plates.

The predominant type of heterochrony indicated by the quantitative data in *Incisoscutum* and *Compagopiscis* was peramorphosis. Peramorphic structures include the prepineal plate, median dorsal length, nuchal length, inferognathal biting region, anterior ventral laterals and parasphenoids. Many of these changes relate to an overall increase in relative length of the head and body armour, a trend occurring in many different lineages of arthrodires. The streamlining of the body, characteristic of the higher arthrodires, coevolved with the elongation of the head and trunk shields. Modifications to streamline the body armour helped to decrease drag when actively swimming, either for predator avoidance or for the pursuit of prey (Long 1990b). The fact that significant allometry was found in the jaws could also be related to the lengthening and narrowing of the head and trunk shields, supporting Long's (1990b) view that the major modifications in these higher eubrachythoracid arthrodires were a response to a durophagous diet.

Interestingly, one of the few paedomorphic features revealed by the morphometric study is in the orbit, indicating selection for a larger eye, as orbit size ontogentically shows negative allometry. What this really means in terms of the circumorbital plates is that they are undergoing positive allometry during ontogeny, producing the ontogenetic increase in orbit size. Thus the paedomorphic retention of the larger orbit can be construed as an outcome of relative paedomorphosis in the circumorbital plates. Selection pressure favouring a larger orbit can be correlated with the development of a more streamlined body shape and development of a more active, predatory mode of life.

In conclusion, if, as seems likely, these patterns of ontogenetic change in *Incisoscutum* and *Compagopiscis* mirror what was happening in other arthrodires, then it is likely that the wide range of cranial shapes and architectures found in this group is a function of dissociated heterochrony. With each plate essentially following its own ontogenetic trajectory, beginning and ending growth at varying times relative to other plates, and each with their own particular rate of growth that can be speeded up or slowed down relative to others, then the potential range of body architectures that could be formed, and upon which natural selection could act, was potentially enormous.

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APPENDIX

Museum Number	Species	Skull ln	nuchal ln	prepineal ln	cheek ln	infragnathal ln	median dorsal ln	median dorsal bth	nuchal bth	orbit dimametre	infragnathal bite	post mesial bth
70.4.264	*C croucheri*	63.93	27.60	14.16	37.40	33.74	46.03	19.58	22.98	16.47	17.50	42.40
86.9.702	*C croucheri*	58.48	24.13	16.44	34.74	34.89	43.54	33.70	18.36	16.43	15.62	40.52
94.5.1	*C croucheri*	50.50	20.47	12.34	30.15	29.64	37.00	26.40	15.70	16.47	13.61	34.91
spec 5	*C croucheri*	48.00	19.00	12.50	26.00	24.76	33.78	25.70	14.67	15.50	11.63	30.98
86.9.675	*C croucheri*	46.00	19.35	12.21	30.29	23.68	42.40	30.41	16.91	12.90	14.28	32.80
94.8.1.	*C croucheri*	42.80	17.17	10.90	24.01	23.20	33.08	20.61	12.32	12.76	9.72	24.51
91.4.3	*C croucheri*	36.25	12.77	9.32	18.66	18.33	21.00	15.67	9.33	12.83	8.76	19.19
P50940	*C croucheri*	53.90	21.00	13.70	37.40	34.70	42.60	26.30	11.50	16.20	16.60	34.30
86.9.674	*C croucheri*	53.47	21.58	12.49	25.11	32.75	41.00	27.80	16.59	15.53	15.16	38.23
70.4.263	*C croucheri*	59.11	22.50	15.55	30.48	37.24	47.83	33.25	21.14	16.11	16.62	38.80
P50948	*C croucheri*	65.80	24.30	16.70	24.90	41.50	47.21	36.20	17.92	18.20	18.50	42.40
p50942	*C croucheri*	64.80	24.00	15.40	36.94	40.80	45.00	36.50	17.65	16.40	20.20	41.90
90.12.139	*C croucheri*	64.59	27.62	15.97	37.11	38.40	43.37	35.15	24.17	16.43	19.68	43.75
86.9.673	*C croucheri*	62.72	24.99	15.43	37.26	37.31	45.07	30.16	12.96	16.32	16.24	37.68
spec 6	*C croucheri*	54.36	21.98	11.50	33.00	32.97	39.00	28.57	16.45	16.42	14.98	35.24
P50941	*C croucheri*	55.50	19.90	12.90	38.00	33.30	42.80	29.30	12.00	16.40	16.20	33.30
P50904	*C croucheri*	45.30	16.20	10.90	28.50	27.60	30.80	24.20	10.60	14.10	13.90	27.40
91.4.1	*I ritchiei*	57.40	20.08	15.79					17.29		33.11	16.12
86.9.683	*I ritchiei*	56.26	18.36	17.28	31.82	32.46			16.44	13.07	31.50	15.33
94.7.1	*I ritchiei*	22.38	8.25	8.00	29.67	15.80	17.60	12.18	10.49	6.36	12.06	5.47
spec 8	*I ritchiei*	60.34	21.75	18.36		35.87	47.94	32.79	17.12	14.01	36.97	19.10
spec 9	*I ritchiei*	62.17	22.87	18.72	31.50	36.60	48.91	34.80	16.95	16.78		20.70
P509929	*I ritchiei*	57.40	18.17	16.96	34.47	33.12		34.47	9.87	16.95	36.60	
94.6.8	*I ritchiei*						41.68	24.05	15.96			
86.9.668	*I ritchiei*	59.15	17.12	18.17		26.84	43.38	27.66	17.12	14.59	35.87	18.36
AMS95644	*I ritchiei*	58.56	16.45	16.44	35.16	31.27	43.82	27.39	17.81	12.68		26.84

Species	Skull length	nuchal length	prepineal length	cheek length	infragnal length	median dorsal lengt	Median dorsal breadt	nuchal breadth	orbit diametre	Infragnathal bite	Post mesial breadth
C croucheri		3.32E+00	2.65E+00	3.62E+00	3.52E+00	3.83E+00	2.98E+00	3.14E+00	2.80E+00	2.86E+00	3.75E+00
C croucheri	4.07E+00	3.18E+00	2.80E+00	3.55E+00	3.55E+00	3.77E+00	3.52E+00	2.91E+00	2.80E+00	2.75E+00	3.70E+00
C croucheri	3.92E+00	3.02E+00	2.51E+00	3.41E+00	3.39E+00	3.61E+00	3.27E+00	2.75E+00	2.80E+00	2.61E+00	3.55E+00
C croucheri	3.87E+00	2.94E+00	2.53E+00	3.26E+00	3.21E+00	3.52E+00	3.25E+00	2.69E+00	2.74E+00	2.45E+00	3.43E+00
C croucheri	3.83E+00	2.96E+00	2.50E+00	3.41E+00	3.17E+00	3.75E+00	3.42E+00	2.83E+00	2.76E+00	2.66E+00	3.49E+00
C croucheri	3.76E+00	2.84E+00	2.39E+00	3.18E+00	3.14E+00	3.50E+00	3.03E+00	2.51E+00	2.55E+00	2.27E+00	3.20E+00
C croucheri	3.59E+00	2.55E+00	2.23E+00	2.93E+00	2.91E+00	3.05E+00	2.75E+00	2.23E+00	2.55E+00	2.17E+00	2.95E+00
C croucheri	3.99E+00	3.04E+00	2.62E+00	3.62E+00	3.55E+00	3.75E+00	3.27E+00	2.44E+00	2.79E+00	2.81E+00	3.48E+00
C croucheri	3.98E+00	3.07E+00	2.53E+00	3.22E+00	3.49E+00	3.71E+00	3.33E+00	2.81E+00	2.74E+00	2.72E+00	3.64E+00
C croucheri	4.08E+00	3.11E+00	2.74E+00	3.42E+00	3.62E+00	3.87E+00	3.50E+00	3.05E+00	2.78E+00	2.81E+00	3.66E+00
C croucheri	4.19E+00	3.19E+00	2.82E+00	3.22E+00	3.73E+00	3.86E+00	3.59E+00	2.89E+00	2.90E+00	2.92E+00	3.75E+00
C croucheri	4.17E+00	3.18E+00	2.73E+00	3.61E+00	3.71E+00	3.81E+00	3.60E+00	2.87E+00	2.80E+00	3.01E+00	3.74E+00
C croucheri	4.17E+00	3.32E+00	2.77E+00	3.61E+00	3.65E+00	3.77E+00	3.56E+00	3.19E+00	2.80E+00	2.98E+00	3.78E+00
C croucheri	4.14E+00	3.22E+00	2.74E+00	3.62E+00	3.62E+00	3.81E+00	3.41E+00	2.56E+00	2.79E+00	2.79E+00	3.63E+00
C croucheri	4.00E+00	3.09E+00	2.44E+00	3.50E+00	3.50E+00	3.66E+00	3.35E+00	2.80E+00	2.80E+00	2.71E+00	3.56E+00
C croucheri	4.02E+00	2.99E+00	2.56E+00	3.50E+00	3.51E+00	3.76E+00	3.38E+00	2.49E+00	2.80E+00	2.79E+00	3.51E+00
C croucheri	3.81E+00	2.79E+00	2.39E+00	3.35E+00	3.32E+00	3.43E+00	3.19E+00	2.36E+00	2.65E+00	2.63E+00	3.31E+00
C croucheri	3.88E+00	2.93E+00	2.46E+00	3.47E+00		3.59E+00	3.11E+00	2.73E+00	2.79E+00		3.31E+00
C croucheri	3.83E+00	2.90E+00	2.55E+00	3.33E+00				2.56E+00	2.60E+00		3.45E+00
C croucheri	3.91E+00		2.38E+00								
C croucheri	3.83E+00		2.43E+00								
C croucheri	3.94E+00		2.60E+00								
C croucheri	3.94E+00		2.61E+00								
C croucheri	4.14E+00		2.73E+00								
C croucheri	3.76E+00		2.34E+00								
I ritchiei	4.05E+00	3.00E+00	2.76E+00					2.85E+00		3.50E+00	2.78E+00
I ritchiei	4.03E+00	2.91E+00	2.85E+00	3.46E+00	3.48E+00			2.80E+00	2.57E+00	3.45E+00	2.73E+00
I ritchiei	3.22E+00	2.11E+00	2.08E+00	3.39E+00	2.76E+00	2.87E+00	2.50E+00	2.35E+00	1.85E+00	2.49E+00	1.70E+00
I ritchiei	4.10E+00	3.08E+00	2.91E+00		3.58E+00	3.87E+00	3.49E+00	2.84E+00	2.64E+00	3.61E+00	2.95E+00
I ritchiei	4.13E+00	3.13E+00	2.93E+00	3.45E+00	3.60E+00	3.89E+00	3.55E+00	2.83E+00	2.82E+00		3.03E+00
I ritchiei	4.05E+00	2.90E+00	2.83E+00	3.54E+00	3.50E+00		3.54E+00	2.29E+00	2.83E+00	3.60E+00	
I ritchiei						3.73E+00	3.18E+00	2.77E+00			
I ritchiei	4.08E+00	2.84E+00	2.90E+00		3.29E+00	3.77E+00	3.32E+00	2.84E+00	2.68E+00	3.58E+00	2.91E+00
I ritchiei	4.07E+00	2.80E+00	2.80E+00	3.56E+00	3.41E+00	3.78E+00	3.31E+00	2.88E+00	2.54E+00		3.29E+00